ISBN 1-897176-79-1
ISSN 1198-273X

PICES SCIENTIFIC REPORT
No. 41, 2012

PICES Advisory Report on the Decline of Fraser River Sockeye Salmon *Oncorhynchus nerka* (Steller, 1743) in Relation to Marine Ecology

NORTH PACIFIC MARINE SCIENCE ORGANIZATION

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This report was developed under the guidance of the PICES Science Board. The views expressed in this report are those of participating scientists under their responsibilities.

This document should be cited as follows:

McKinnell, S.M., Curchitser, E., Groot, C., Kaeriyama, M. and Myers, K.W. 2012. PICES Advisory Report on the Decline of Fraser River Sockeye Salmon *Oncorhynchus nerka* (Steller, 1743) in Relation to Marine Ecology. PICES Sci. Rep. No. 41, 149 pp.

PICES Scientific Report No. 41
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PICES Advisory Report on the Decline of Fraser River Sockeye Salmon *Oncorhynchus nerka* (Steller, 1743) in Relation to Marine Ecology

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August 2012
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Preface

In the fall of 2009, the Government of Canada established a *Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River*. It was headed by Justice Bruce Cohen, with a staff of legal advisors, a fisheries scientist (Dr. David Levy), and technical, financial, and administrative support staff. The Commission's job was to consult widely on the cause(s) of the decline and to convene formal hearings where experts with relevant knowledge would be called to testify under oath before the Commissioner. Organizations with vested interests such as the Government of Canada, the Government of the Province of British Columbia, the Pacific Salmon Commission, First Nations coalitions, environmental coalitions, fisheries coalitions, *etc*. were each represented at the proceedings by separate legal counsel whose major role was to cross-examine the experts following a period of questioning by the Commission's legal counsel. Collectively, these groups were known as the "participants" in the inquiry.

As part of the inquiry, the Commission sought independent advice in the form of reports on various scientific, technical, and administrative matters related to the issues and written by experts with knowledge of the fishery but with no formal association with any of the participants. This group of authors generally included scientists in academia or private consulting firms. By chance, I happened to make a presentation in Vancouver on March 31, 2010, on what is known about sockeye salmon on the high seas at a meeting that was organized by Simon Fraser University. At the conclusion of the meeting, Dr. Levy invited me to write a report for the Commission on what was known about Fraser River sockeye salmon at sea and to consider in the report what might be responsible for their decline, and the extremely low returns in 2009. My response was that it would be of considerable benefit to the Commission to involve not only my expertise but that of PICES as well. As the PICES Science Board was planning to meet in Sendai, Japan, in late April 2010, the timing was ideal for the Commission to send an invitation to the Organization.

The request for advice from the Commission was tabled for discussion in Sendai. The North Pacific Ecosystem Status Report had just been completed with information on Pacific salmon and the state of their marine habitats. There was consensus at Science Board that this request would provide PICES with an opportunity to offer its expertise and further enhance its profile among stakeholders. Science Board supported the concept and invited me to develop an outline of the report with Dr. Levy, to recommend co-authors, and to communicate with Dr. Levy about the requirements and the approach to developing the report.

The report dealt initially with an encyclopedic review of what was known of the biology of Fraser River sockeye salmon at sea, and responses to two key questions: (1) Can the decline in Fraser River sockeye in 2009 be explained by the conditions the fish experienced in the marine environment? (2) Is there evidence for declines in marine productivity or changes in Fraser River sockeye distribution that can be associated with the 15-year gradual decrease in Fraser River sockeye productivity? While we were attempting to answer these in the summer of 2010, the largest return of sockeye salmon in 97 years appeared at the Fraser River. So a third question about their sudden abundance was added in August.

The initial team of co-authors was Michael Lapointe (Pacific Salmon Commission), Howard Freeland (Institute of Ocean Sciences), Kees Groot (scientist emeritus, Pacific Biological Station), Katherine Myers (University of Washington), Masahide Kaeriyama (Hokkaido University), and Enrique Curchitser (Rutgers University) but when the "no participants as authors" rule was established by the Commission, the team was reduced to five. Analysis and writing began in mid-June to meet a September deadline for completion of the first draft. The brief time allotted was a result of working backward from the date when the Governing Council might approve release of the report (late October), allowing time for a review organized by the Advisory Panel on *Status, Outlooks, Forecasts and Engagement* (SOFE) of PICES' scientific program, Forecasting and Understanding Trends, Uncertainty and Responses of North Pacific Marine Ecosytems (FUTURE), and revisions by the authors. The first draft was about 150 pages long and was made available to reviewers on September 10, 2010. The main problem with the first draft was that it lacked an answer to question (1).

The *eureka* arrived while working on the report in a hotel room in London in early October 2010, when it became clear that the only place in the ocean with extremely (not previously observed) high surface temperatures anywhere in the Northeast Pacific in 2007 occurred in Queen Charlotte Strait/Sound where the sockeye salmon returns of 2009 were migrating as juveniles. The cause of the high temperatures was eventually traced back to extreme snowpack in the central Coast Mountains of British Columbia in 2007 and equivalently anomalous wind patterns in Queen Charlotte Strait/Sound in the summer of 2007. It was a new idea that challenged the emerging dogma that the Strait of Georgia was the cause of their death.

It was not possible to re-write the report before the PICES Annual Meeting in Portland, USA, but the story was sufficiently compelling that Science Board and Governing Council agreed to release the draft report to the Cohen Commission by November 15, 2010 (the date in the contract). No written comments were received from the Commission so, after final revisions, the report was sent to the Commission on December 15, 2010. This publication is the December 15 version.

In early 2011, the Cohen Commission sent the final PICES report to external reviewers of their own choosing. I agreed to respond to their comments. These reviews and my responses to their comments were appended to the PICES report and published electronically as the Cohen Commission's Technical Report No. 4. It can be downloaded from their website (www.cohencommission.ca). They are not included in the present PICES Scientific Report because they were not a part of the advice provided by PICES to the Commission.

The contents of this report have been reformatted to match that of our Scientific Report Series. Only minor technical edits for spelling, grammar, or consistency have been applied to the text; otherwise, it is what was sent to the Cohen Commission by PICES.

Skip McKinnell
Deputy Executive Secretary, PICES
August 2012

Executive Summary

In the spring of 2010, the Government of Canada invited PICES to participate in a *Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River* by considering how marine ecology may have affected their abundance. A major objective that was achieved in this report was to assemble, within an eight week period, as comprehensive a summary as was possible of what is known about Fraser River sockeye salmon (*Oncorhynchus nerka*) in the ocean. While much of this effort involved summarizing information published in data/technical reports and the primary literature, where necessary, original data have been re-examined and new analyses conducted to fulfill the terms of the Statement of Work. The compilation provides a background of knowledge against which to judge what can be known regarding the two major questions posed by the Cohen Commission to PICES:

> *Can the decline in Fraser River sockeye in 2009 be explained by the conditions the fish experienced in the marine environment?*
>
> *Is there any evidence for declines in marine productivity or changes in Fraser River sockeye distribution that can be associated with the 15-year gradual decrease in Fraser River sockeye productivity?*

Most of the Fraser River sockeye salmon that did not survive to produce a fishery in 2009 entered salt water in 2007. The major challenge in answering the first question is a recognition that the ocean is shared by sockeye salmon from many areas of the Northeast Pacific, some which returned in 2009 in above average abundance. As a result, any hypothesis for the cause of low returns of Fraser River sockeye salmon from an oceanic cause must consider a mixture of contrasting observations:

- Double the average returns of Columbia River sockeye salmon in 2009 (2007 ocean entry year);
- Better than expected returns of Barkley Sound (west coast of Vancouver Island) sockeye salmon in 2009 (2007 ocean entry year);
- Very low returns of age-1.x ecotypes in most populations from the Fraser River that entered the Strait of Georgia in 2007;
- Record high returns to the Harrison River (lower Fraser River watershed) in 2010 from underyearlings that reared in the Strait of Georgia in 2007. This unique ecotype spends an extra year at sea, so its abundance was not known until 2010;
- Typical survival of acoustically-tagged hatchery-reared sockeye salmon from Cultus Lake northward through the Strait of Georgia in 2007.

Assessing the longer period of decline has its own challenges because impressions of the nature of the decline of Fraser River sockeye salmon are somewhat sensitive to how the production data are summarized. Our approach was to capitalize on the diversity and abundance of many reproductively isolated sockeye salmon populations, the existence of different ecotypes within each population (different ocean entry years by individuals of the same generation), and the lengthy time series of production data for many of these, to provide informative comparisons among populations and informative summary statistics across populations and ecotypes.

Long-term decline

1. What was described in the key question as a 15-year gradual decline in productivity actually bears a stronger resemblance to a shift to lower productivity in 12 of 16 stocks, rather than a gradual decline. In some stocks (*e.g.*, Raft River), the data cannot distinguish between these two alternatives. The "best" division of a time series of median total survival of age-1.x ecotypes, into periods of high then low productivity is the 1992 ocean entry year (1990 brood year for age-1.x).
2. The 1992 ocean entry year coincides with an abrupt decline in marine survival of Rivers Inlet sockeye salmon. Markedly diminished returns to Long Lake (Smith Inlet) probably[i] began with the 1992 smolt year. These stocks share a common migration route through Queen Charlotte Strait/Sound.
3. Returns of maturing sockeye salmon to Barkley Sound declined in 1994 (1992 smolt year) and remained relatively low until the 1998/99 la Niña. A similar period of decline was observed in sockeye salmon returns to the Columbia River in the same year. West coast sockeye salmon production remained low from the 1992 ocean entry year through the 1997/98 el Niño, but then experienced an increase in survival that was not reflected in the Fraser River stocks. The difference could be related to variable spatial scales of the oceanic forces that are associated with variable survival among stocks.
4. The winter of 1991/92 was the onset of what has been called a persistent el Niño. The same year was accompanied by relatively dramatic changes in many characteristics of the west coast ocean ecosystem that included the return of sardines to the west coast of British Columbia after more than a 45-year absence. The reappearance of sardines is not considered as having a direct effect on Fraser River sockeye salmon survival, but is reported here as a potential proxy for a persistent oceanographic change that is not fully understood. British Columbia lies in the transition zone between the Alaska Current to the north and the California Current to the south, whose locations and intensities are variable.
5. Apart from the el Niño of that year, 1992 is not recognized especially as a year of significant large-scale climatic change in the North Pacific; that occurred in 1989. How or if the two phenomena are connected is not known at this time.
6. Productivity of the age-2.x ecotypes from the Fraser River did not change in 1992. This may be because larger postsmolts have greater energy reserves for the migration northward to better feeding and growth in Alaska.
7. Not all sockeye salmon that migrate from the Strait of Georgia exhibited a decline in 1992. The endangered Sakinaw Lake population from the mainland side of the Strait of Georgia (northwest of Vancouver) declined in 1987 rather than 1992; perhaps for other reasons. It may be related to their migratory behaviour, which seems to differ from most Fraser River sockeye salmon by their using Juan de Fuca Strait to a greater extent to leave the Strait of Georgia.
8. Three years of very low returns of sockeye salmon to the Fraser River and curtailed fisheries from 2007 to 2009 can be explained by a sequence of independent events, two of them related to climate:
    a. 2007 returns: Low marine survival of the 2005 ocean entry year of sockeye salmon and coho salmon was expected (and was reflected in experimental forecasts). Canadian and U.S. oceanic and ecological indicators were consistent in recognizing 2005 as a warm and unproductive year which would likely be detrimental to salmon survival;
    b. 2008 returns: Median recruits per spawner across stocks were typical of the post-1992 era. The low return was most likely a consequence of one of the lowest numbers of spawners (in 2004) in recent years. Spawner abundance is the primary determinant of future returns in most Fraser River sockeye salmon populations.
    c. 2009 returns: The 2006/07 el Niño and a very anomalous spring/summer climate in 2007 conspired to generate a very atypical coastal ocean in 2007, one that could have been detrimental to Fraser River sockeye salmon growth and survival. The details are described more fully in the following section.

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[i] Annual returns to the Docee Fence include two brood years so the estimate of the decline is ±1 year.

2009 returns

Biologists rarely, if ever, observe a death by natural causes of juvenile Fraser River sockeye salmon at sea. As a consequence, the cause and location of mortality must be inferred from general ecological/physiological principles that have been accepted by the scientific community. An example of one of these principles is that faster growth leads to better survival. It appears to hold across the salmonids and other families of fishes. No one saw the deaths of large numbers of juvenile Fraser River sockeye salmon in 2007, or on the high seas from 2008–2009, so the best that can be done to understand the extremely low returns in 2009 is to identify the times and locations where there were extreme conditions that could potentially have caused the extremely low survival of one component of the Fraser River stocks. The general hypothesis of this study is that there were no extremes [scientific hypotheses are disproved rather than proved] in ocean physics, chemistry, or biology that could have been responsible for extreme mortality of Fraser River sockeye salmon, but not elsewhere (Columbia River or Barkley Sound). At least one scenario suggests that this hypothesis can be rejected.

1. The low return of sockeye salmon to the Fraser River in 2009 was due mostly to high mortality of age-1.x ecotypes of the cohort that was spawned in 2005 and migrated to sea in 2007. When all returns of the 2005 brood year are eventually counted in 2010 and 2011, the lowest median total survival of Fraser River sockeye salmon in contemporary records is the 2003 brood year, not the 2005 brood year. While returns of the 2005 brood year in 2009 were very low, they are noteworthy mostly for their remarkable departure from the official equi-probable[ii] forecast, with one exception: Chilko Lake.
2. Since the 1960s, infrequent years of very high numbers of smolts emigrating from Chilko Lake, such as occurred in 2007 and again in 2008, have routinely failed to reach even average postsmolt survival, suggesting that some fraction of the incremental mortality of this stock in the ocean is related to their own abundance. At 77 million, the emigration in 2007 was twice the previously observed maximum. The 2009 return year will be the lowest recorded age-1.x postsmolt survival for this stock.
3. Oceanic conditions with the strong potential to cause incremental sockeye salmon mortality began to develop from the effects of the el Niño of winter of 2006/07. The typical response of North Pacific climate to an el Niño is an intensification of cyclones combined with an eastward shift in the storm tracks. This creates enhanced atmospheric flow from the southwest that brings warmer, wetter air toward British Columbia where it is deposited as snow in the mountain ranges. At the end of the winter season in 2007, the northern and central coast mountains of British Columbia had some of the highest snowpacks observed since records began in 1953.
4. The cool spring of 2007 delayed the snow melt. It was followed by rapid warming in late May which was followed by an intense spring storm in early June that brought heavy rain on top of the deep snow. As a consequence of these coincidences, the summer of 2007 featured extreme discharge by central and north coast rivers. The northern part of the Fraser River drainage was exposed to this phenomenon but it led to high rather than extreme discharge in 2007. The highest weekly discharge in the Fraser River in 2007 ranked 23rd in the record of weekly discharges from records dating back to 1913. Discharges from the Wannock River into Rivers Inlet (eastern Queen Charlotte Sound) and the Klinaklini River (eastern Queen Charlotte Strait), for example, were the highest values ever recorded for the month of July.
5. Fisheries and Ocean Canada (DFO) surveys in late June/July 2007 (and other years) across southern Queen Charlotte Sound, east of Triangle Island, recorded the lowest average surface salinity (five stations) since sampling began in 1998. Closer to the freshwater sources, the Egg Island lighthouse in eastern Queen Charlotte Sound recorded the lowest July/August average salinity on record (since 1970). The extreme freshwater discharge from coastal watersheds created an ocean surface layer in Queen Charlotte Sound that was much fresher than normal and would have created a very stable water column (resistent to vertical mixing). Enhanced water column stability restricted the volume of water exposed to the overlying atmosphere in summer, and caused the surface ocean to warm more than it would have otherwise. Based on the NOAA (U.S. Government) global database from 1982 to 2010[iii], the only appearance of extreme sea

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[ii] Equal chance of getting more or less than this number.
[iii] The satellite remote sensing era.

surface temperatures in 2007 anywhere in the Gulf of Alaska in any month occurred at three grid points[iv] in Queen Charlotte Sound in August.

6. The relatively fresh ocean surface layer was retained within Queen Charlotte Sound by the most extreme southeasterly wind pattern in summer since 1948. Southeasterlies are normally considered as the winter wind regime. From April through July, May was the only month without much stronger than normal southeasterlies.
7. Fraser River sockeye salmon that were obligated to migrate through the Queen Charlotte Strait/Sound region met extreme temperatures[v], and even more extreme salinity/density and wind anomalies.
8. Since 1998, when SeaWiFS satellite ocean colour monitoring began, marine survival of Chilko Lake sockeye salmon has been highly correlated with the date of onset of biological production in Queen Charlotte Strait/Sound. The spring bloom in 2007 was the latest in the in record. No doubt the southeasterly wind regime in April contributed to the very late spring bloom in the Sound in 2007. The coastal migration of postsmolts from southern spawning habitats to northern feeding habitats (Southeast Alaska) requires sufficient energy for the migration. Energy for migration is a function of energy density leaving the Fraser River plus feeding success along the migration route. While the age-1.x postsmolts had poor survival in 2007, the larger age-2.x postsmolts, with their greater initial energy reserves, did not experience unusually low survival that year. The delayed spring in Queen Charlotte Strait/Sound, when combined with the incremental metabolic cost of migrating through a warm surface layer, with potentially lower prey densities in the fresher water, could be combined to reduce growth and survival. Sockeye salmon postsmolts caught in DFO summer surveys of Queen Charlotte Sound in 2007 had the smallest mean size since sampling began in the late 1990s. Where the growth reduction occurred along the migration route is unknown.
9. While the Gulf of Alaska was generally cool in 2007, the sockeye salmon migration route northward along the continental shelf region to Yakutat, Alaska had mean sea surface temperatures in August 2007 that were the second warmest since 1982, and feature the highest increase above spring sea surface temperatures since 1982, perhaps because the effect of the discharge anomalies was not restricted to Queen Charlotte Strait/Sound.
10. The extreme hydrographic and wind events that occurred in Queen Charlotte Strait/Sound during the summer of 2007 did not have equivalent extremes in the Strait of Georgia, or on the west coast of Vancouver Island or the U.S. mainland. So, if the extreme mortality of age-1.x Fraser River sockeye salmon from the 2007 ocean entry year was caused by an equivalent oceanic extreme, the more likely location is Queen Charlotte Strait/Sound region where extremes in physics and biology were evident in 2007.
11. Fraser River sockeye salmon underyearlings (age-0.x) were found in high abundance in DFO surveys of the Strait of Georgia in September 2007. These ecotypes returned in 2009/10 in unprecedented numbers to the Harrison River. If the Strait of Georgia was the site of enhanced mortality in 2007, the unknown force(s) must have:
    1. killed most age-1.x ecotypes in May and June,
    2. allowed age-2.x ecotypes to have average marine survival,
    3. allowed age-0.x ecotypes to survive in record numbers, and
    4. allowed acoustically tagged hatchery-reared smolts from Cultus Lake to survive through the Strait of Georgia in 2007, as in other years,

    …without observing extreme physical, chemical, or biological anomalies in the Strait of Georgia in 2007 that can be linked to sockeye salmon survival. Herring recruitment was observed to be low in the Strait of Georgia in 2007, but the lack of a long-term association between herring and Fraser River sockeye salmon mortality suggests a coincidence. The harmful algae, *Heterosigma akashiwo*, bloomed in the southern Strait of Georgia for most of the spring and summer of 2007. It has been implicated as the causative agent for high mortality of the age-1.x ecotype (Rensel *et al.*, 2010) but it did not appear to affect the smaller age-0.x ecotype as the latter returned in record high abundance.

[iv] Average monthly values are computed on a 1° × 1° lat./long. grid.

[v] Greater than any sea surface temperature measurements recorded in that month from 1982–2010.

2010 returns

1. Age-1.x Fraser River sockeye salmon postsmolts migrated through a relatively warm surface layer of the Strait of Georgia in 2008 (not significantly different from temperatures in 2007) into a coastal ocean that was significantly colder and more Subarctic in character than had been seen on the coast of British Columbia in decades. Average summer temperatures in 2008 along the coastal migration route from Johnstone Strait northward were up to 3.5°C cooler in 2008 than in 2007. Annual average sea surface temperature in the Gulf of Alaska in 2008 was the coldest observed since the early 1970s.
2. The Mackas ecosystem productivity index for the coastal ocean off the southwest coast of Vancouver Island reached its highest value on the "cool and productive" scale in 2008.
3. The numbers of effective female spawners in 2006 was the sixth highest since 1948, laying the foundation for a good return in 2010. Spawner abundance is the principal determinant of return abundance in Fraser River sockeye salmon.
4. Early signs of the bonanza that became the 2010 sockeye salmon return to the Fraser River were evident one year earlier in the returns of jack sockeye salmon in 2009 but there were few opportunities to notice their atypically high abundance. The appearance of relatively large numbers of jacks in 2009 in the seine test fisheries suggests that the abundance of the dominant cohort that returned in 2010 was determined before July of 2009.

Fraser River Sockeye

1 Introduction

1.1 Motivation

Fisheries for Fraser River sockeye salmon were severely curtailed or eliminated for an unprecedented period of three years from 2007 to 2009. The low returns in 2009 attracted special attention because the pre-season forecast used by managers implied a harvestable surplus that never materialized. In Chilko Lake (see Figure 3), for example, smolt-to-adult survival of the smolts that went to sea in 2007 and will return from 2008 to 2011 may turn out to be, when all of the returns are counted, the lowest in the history of records that extend back to the 1950s. Most Fraser River sockeye salmon spend more than half of their lives in the sea (Gilbert, 1914) so any consideration of the cause of low abundance must take into account that the factors which are responsible for the decline may be found in salt water. A preliminary review of evidence implicated a marine cause for the poor returns[1].

A related issue arose from an observation that the productivity of Fraser River sockeye salmon, measured as a ratio of aggregate adult returns to total spawners in all populations (Fig. 1), has declined since the mid-1980s and may have reached its lowest level since the late 1940s in the 2007 ocean entry year. However, ascertaining whether or not this observation was solely marine in origin can be a challenge because returns per spawner are determined by factors affecting survival in both fresh and salt water. This issue can be examined using data from Chilko Lake where spawner-to-smolt, smolt-to-adult, and total survival (returns per spawner) have been estimated for many years.

While this report was being written in the summer of 2010, the largest return of Fraser River sockeye salmon since 1913 reached the British Columbia coast. Comments were requested by the Cohen Commission (hereinafter, the Commission) on the contrast with 2009 and previous years but an extensive analysis was not possible in the time allowed.

Fig. 1 Ratio of aggregate (all stocks) sockeye salmon returns to the Fraser River to aggregate female spawners. Source: Pacific Salmon Commission.

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[1] http://www.sfu.ca/cs/science/resources/adaptingtochange/FraserSockeyeThinkTankStatement.pdf

1.2 Authorship – North Pacific Marine Science Organization

The North Pacific Marine Science Organization (PICES) is an international, intergovernmental marine science organization that was established by international convention in 1992 (Appendix 1). The current membership of the Organization includes Canada, Japan, People's Republic of China, Republic of Korea, Russian Federation, and the United States of America. They constitute all of the salmon-producing nations of the North Pacific except for North Korea.

The scientific committees of the Organization provide oversight of ocean/climate, fisheries science, biological oceanography, and marine environmental quality. The chairs of these committees and their relevant expert groups form the Science Board that is responsible for the science conducted by the Organization. The PICES Science Board is responsible for the scientific products of the Organization, including general oversight of the development of this report.

1.3 Organization of the Report

A primary objective of this report was to provide the Commission with a review of what is known about the ecology of Fraser River sockeye salmon in the sea. An historical approach was used so that an appreciation of what was learned, and when it was learned, can be ascertained. The basic material was organized around three life-history stages that correspond roughly to the age of sockeye salmon at sea. Each stage is considered separately in Sections 2 to 4. Section 2 reviews the coastal migration of Fraser River sockeye salmon postsmolts[2] and underyearlings through the Strait of Georgia and along the continental shelf. *Smolts* are juvenile sockeye salmon which have undergone the physiological changes to live in the ocean and have left the nursery lake where they have spent one or more years feeding and growing. This is to distinguish them from *underyearlings* which hatch and do not spend a winter in freshwater before entering the sea (Gilbert, 1914), however they may delay in sloughs and lagoons in the Fraser River delta (Birtwell *et al.*, 1987). The *postsmolt* stage is defined, arbitrarily, to begin with entry into salt water and end with the calendar year when ocean entry occurred. The coastal migration of postsmolts begins in April and continues throughout the summer and fall as the cohort migrates seaward from the Fraser River.

Section 3 is concerned with the offshore feeding migration beyond the continental shelf of *immature* sockeye salmon. This stage is defined, again arbitrarily, to cover the period from January 1 of the calendar year after the postsmolt year to the December 31 of the year before they return to spawn. The final phase, in Section 4, deals with sexual maturation and homeward migration to a natal stream. These individuals will be designated in this report as *maturing* sockeye salmon, again arbitrarily defined from January 1 in the year when maturation occurs. The durations of each of the final two phases varies somewhat among individuals but, overall, a total ocean phase of about 25 months is the most common among sockeye salmon in the Fraser River. Jacks (and jills) which mature after the postsmolt year do not have an immature phase according to this definition.

While it was not possible to describe in detail every study that has been conducted, it was possible to touch on those expeditions that have resulted in significant improvements in the understanding of Fraser River sockeye salmon. This perspective will provide a good background with which to compare any contemporary observations and provide the context for interpreting the questions of primary concern to the Commission. For the most part, the scientific history of Fraser River sockeye salmon can be determined by reviewing the results of publications that arose from each research project. However, some research programs produced data on Fraser River sockeye salmon for years but failed to produce data reports and/or failed to publish interpretations of the data. On those occasions when only the data were published, our approach was to analyze the data and report the results of those analyses. Likewise, if alternative interpretations of published results were possible, they were explored.

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[2] The definitions of terms used in this report can be found in Appendix 2.

Because of the general lack of stage-specific estimates of mortality for the life-history stages described above, the overview of marine survival of all life-history stages was placed in Section 5. The physical, chemical, biological oceanography and climate that were relevant to the periods of interest to the Commission were grouped in Section 6. Finally, Section 7 contains the discussion of the major questions posed to the researchers by the Commission.

This report deals with what is known about Fraser River sockeye salmon at sea, *i.e.*, not all sockeye salmon. Where comparisons with other stocks help to provide a better perspective on the former, they have been made. In large part, this was necessary because the science of determining the origin of sockeye salmon caught at sea, with reasonable accuracy, has only recently been developed. The report excludes a consideration of the effects of toxins, parasitism, disease, and predation, as these topics were considered in other reports to the Commission.

Readers must keep in mind that there is no observation system for Fraser River sockeye salmon on the high seas (beyond the continental shelf). Research and monitoring in the Strait of Georgia since 1997 has focused on coho salmon and chinook salmon in July and September after many sockeye salmon postsmolts have left the area, and the Fisheries and Oceans Canada (DFO) high seas salmon program has focused on postsmolt surveys on the continental shelf since the late 1990s and is contributing to new understanding of this region (Grimes *et al.*, 2007). Therefore, during the period of years of interest to the Commission, there are virtually no observations of Fraser River sockeye salmon during about 75% of their life at sea, and the value of coincidental samples taken during their emigration from the Strait of Georgia is debatable.

This discussion of the Commission’s two key questions is restricted in scope to an examination of the interconnections between climate, the ocean, and the fish at each oceanic life-history stage, *i.e.*, to what extent are “bottom-up” effects responsible for the status and trends of Fraser River sockeye salmon abundance. In simple terms, bottom-up forces are a result of the interplay of the physics, chemistry, and biology that provide for the growth and survival of sockeye salmon and other species at sea. For species that are resident on the west coast of British Columbia (not migratory), bottom-up forcing from year-to-year variations in phytoplankton at the base of the food web, through zooplankton production to fish production, has been reported (Ware and Thomson, 2005).

1.4 Research Directed at Salmon in the Ocean

> *The scientists I have known upon the river, men as great as they are obscure, came almost to worship the salmon and hid their worship under scientific jargon. Watching the inscrutable quest of the salmon, recognizing a principle beyond their power to explain, these men (though they would be the first to deny it) turn into religionists of a queer, incommunicable congregation. The greatest of them, a man who had spent his life and genius on the study of these fishes, once said to me, as we watched them surge up the river: “We really don’t know anything about them. I don’t think we ever will.”*
>
> Bruce Hutchison, The Fraser, 1950[3]

Indeed, what the greatest of them (whoever s/he may have been) could not have anticipated was that one of the great unknowns, the whereabouts of Fraser River sockeye salmon at sea, would remain a mystery only until the mid-1950s when the newly formed scientific committees of the International North Pacific Fisheries Commission (INPFC) began their work. This tripartite Commission of Canada, Japan, and the United States was established in 1953 as a result of a clause in the San Francisco Peace Treaty that required it. In the 1930s, Japanese fishing fleets had been moving into the eastern Bering Sea to fish for salmon and the American and

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[3] Bruce Hutchison (1901–1992) was Editor of the *Victoria Times* from 1950–1963 and the Editorial Director of the *Vancouver Sun* from 1963–1980; both are major newspapers in these cities.

Canadian governments did not want fish stocks that they had been conserving to be exposed to unregulated fishing by Japanese fishermen. When the INPFC was established, financial resources were made available by the Government of Canada to its Fisheries Research Board to resolve the many uncertainties about the life of salmon at sea. Much of what is known today about salmon at sea was a consequence of the Board's contribution to the international research program. Ocean-going studies of salmon at sea by Canadians were significantly reduced after the late 1960s.

High seas studies directed at salmon resumed in 1986 to investigate their potential exposure to the large-scale squid driftnet fishery (Bernard 1986; LeBrasseur *et al.*, 1987, 1988). The northern range of the target species, flying squid (*Ommastrephes bartrami*), was thought to overlap the southern end of the range of Pacific salmon. As a result, these surveys were directed at the southern fringe of the salmon distribution. The United Nations General Assembly declared a moratorium on large-scale driftnet fishing in the early 1990s; Canadian research cruises related to this study ended in 1990.

Surveys to test a thermal limit hypothesis to describe the oceanic range of salmon in the Gulf of Alaska began in 1995 (Welch *et al.*, 2002). After a few years of not catching salmon in the Gulf of Alaska beyond the continental shelf, it transformed into a successful coastal research program that, for the most part, focused on postsmolts and underyearlings in waters <200 m. As similar studies of juvenile salmon were being conducted in the United States, the coast-wide perspective, from California to Alaska, on postsmolt biology resulted in significant improvements in knowledge of this life history stage for all salmon species (Grimes *et al.*, 2007; Tucker *et al.*, 2009; Trudel *et al.*, 2009).

The first and most comprehensive review of the biology of sockeye salmon at sea was undertaken by the INPFC based on the results of its high seas research programme (Hanamura, 1966; Ricker 1966; French *et al.*, 1976). The first monograph on the sockeye salmon (in English) was published by the Fisheries Research Board of Canada (Foerster, 1968) and reviews and compilations appeared intermittently thereafter (Smith *et al.*, 1987; Burgner, 1991; Quinn, 2005). Reviews directed at Fraser River sockeye salmon first appeared in the early 20th century as scientific interest developed around variations in the fishery and recovery from the Hell's Gate rock slide in the river (Fig. 3; Babcock, 1918). The most comprehensive overview of Fraser River sockeye salmon was undertaken by Roos (1991) following the termination of the International Pacific Salmon Fisheries Commission, but it had a greater focus on the freshwater phases of sockeye salmon biology.

1.5 General Biology

There are seven species of Pacific salmon in British Columbia waters, namely sockeye salmon, pink salmon, chum salmon, coho salmon, chinook salmon, steelhead trout, and cutthroat trout, and all have anadromous ecotypes. They reproduce and incubate eggs in freshwater, move to salt water for a number of years to feed and grow, and then return to freshwater for spawning. Use of both the freshwater and oceanic environments implies important biological adaptations to each.

Fraser River sockeye salmon exhibit a diverse assemblage of life histories (Gilbert, 1914). Individuals can vary from a few months to a few years in age before migrating to sea. Once there, they can spend one to several years at sea before maturing and migrating back to their natal stream. On average, the duration of the oceanic phase is shorter for males than for mature females because of the former's tendency for some faster growing individuals to mature at an earlier age. As a consequence of this variability, the members of a single cohort can be exposed to very different freshwater and oceanic environments, depending on the year when they make the transition between these environments. This variability creates a bookkeeping challenge when comparing growth or survival or other aspects of biology to environmental variation. In general, the life history of sockeye salmon is relatively plastic so the durations of these phases are not fixed within a population. In the Fraser River, the dominant ecotype matures following the second winter at sea (see Appendix 3 for ecotypes by population).

1.5.1 Life cycle of sockeye salmon

The life cycle of Pacific salmon consists of a number of discrete life history phases, including spawning, incubation, rearing, migration to sea of the juveniles, feeding and growth in the ocean, return migration to the home stream, upstream migration of mature adults, and spawning. After spawning all Pacific salmon die.

In North America, sockeye salmon are economically the most important Pacific salmon, with the most complicated life cycle. They lay their eggs in nests dug in gravel beds in freshwater streams and rivers. The juveniles then migrate to the ocean, feed actively, and grow rapidly. Upon reaching maturity, after one, two, or more years in the ocean, depending on the population, they return to their freshwater home streams to spawn.

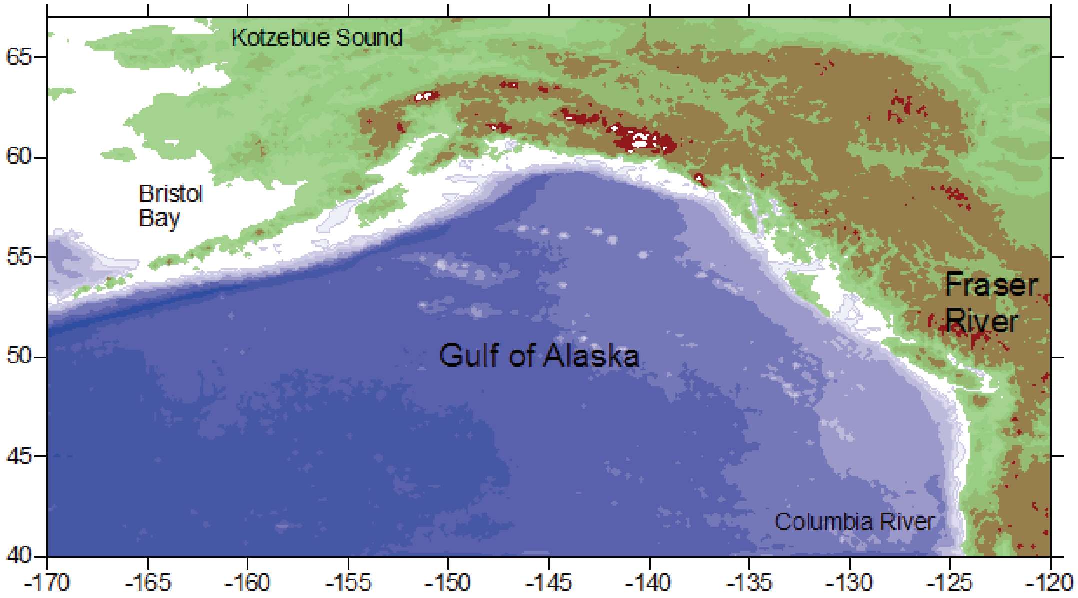

Fig. 2 Range of sockeye salmon in North America from the Columbia River to Kotzebue Sound, with colour shading representing bathymetry/topography. The continental shelf appears in white.

The geographic distribution of sockeye salmon covers vast areas of the North Pacific Ocean and adjacent landmasses during their life cycle. The North American spawning distribution ranges from the Columbia River northward to Kotzebue Sound in Alaska (Fig. 2), although during the last decade, they have been reported in the Arctic Ocean (Babaluk *et al.*, 2000). On the Asian side, sockeye populations are found from Cape Chaplina in the north, southward along eastern Kamchatka, the Kuril Islands to the north coast of Hokkaido, and then northward along west Kamchatka to the north coast of the Sea of Okhotsk. Some streams on the Komandorskiy Islands have small populations of sockeye salmon.

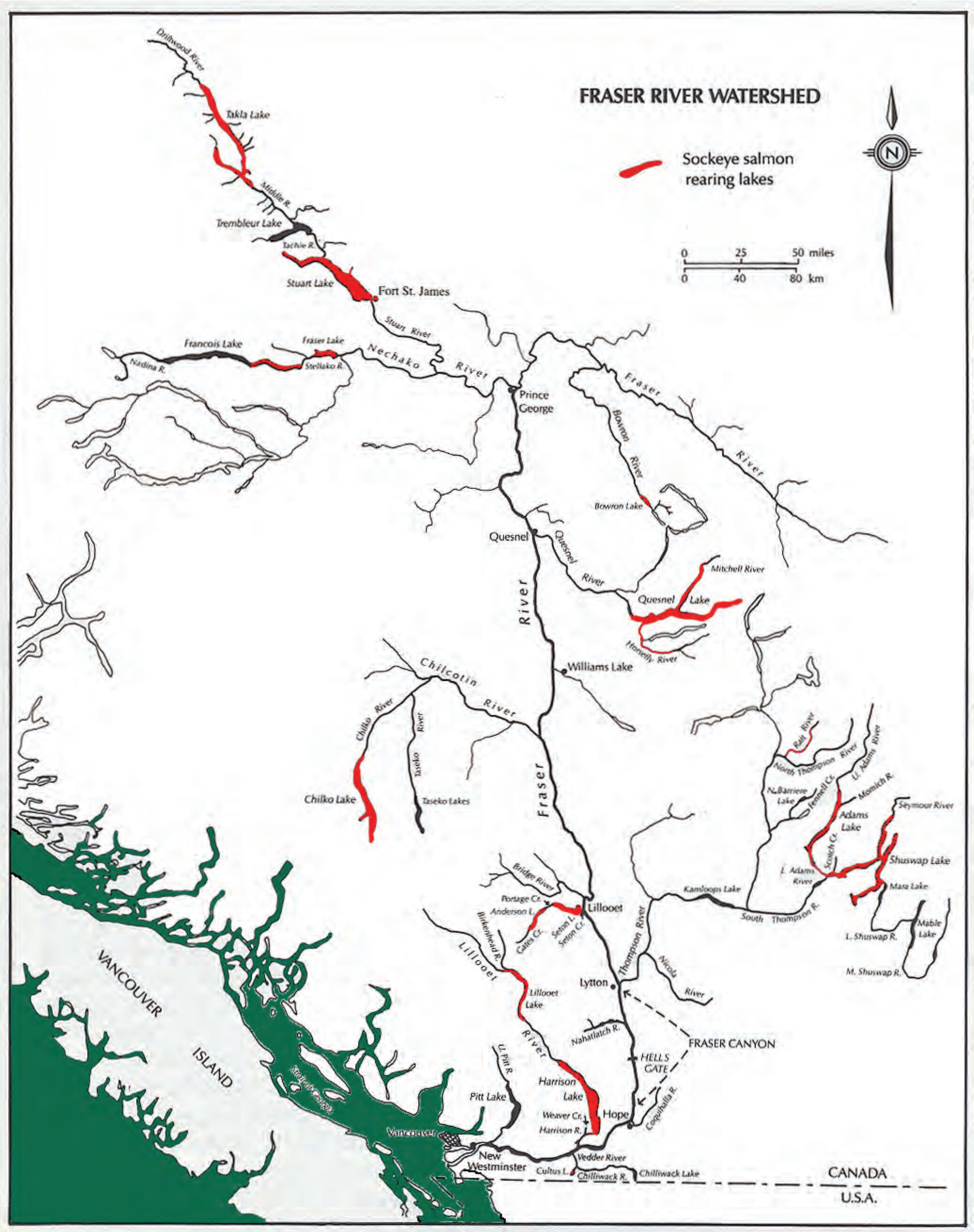

Fig. 3 Sockeye salmon nursery lakes in the Fraser River watershed.

In British Columbia, the Fraser, Skeena, Nass, and Somass river systems are significant sockeye salmon watersheds. About 40 unique populations of sockeye salmon spawn in 22 lakes in the Fraser River watershed (Fig. 3). Hereafter, one or more populations spawning in a specific lake will be referred to as a stock. The Adams River stock is generally considered the most abundant although on average, the Chilko Lake stock has greater production because its abundance does not exhibit the large interannual swings in abundance found in the Adams River stock. Large sockeye salmon runs used to appear in Rivers and Smith inlets, where they spawn in tributaries of Owikeno and Long lakes, respectively. Despite their relatively small size, these two lakes had the highest production per unit area in the world. Great Central, Sprout, and Kennedy lakes are significant sockeye salmon nursery lakes along the west coast of Vancouver Island. In addition, there are many smaller lake systems supporting small sockeye populations.

1.5.2 Spawning behaviour

Spawning behaviour of sockeye salmon consists of a combination of nest building activities by the female and courtship displays by the male, leading to deposition of fertilized eggs in a nest. The female is the dominant partner in this process and interacts with both the gravel environment and the courting male in a specific sequence of activities. The activities include nest site selection, nest construction, courtship display, oviposition, fertilization, and closing of the nest. The female digs four to five separate nests in the gravel, one nest per day. Each nest contains several hundred eggs. After all the eggs have been deposited, the female covers all nests under a large gravel mount called a redd and defends the area against intruders. A few days after she has completed spawning, she dies and her body floats away with the current. This creates room on the spawning grounds for the next wave of ripe females to occupy nesting territories. The whole spawning process from moving onto the spawning grounds to death lasts about 10 days.

Unless indicated otherwise, throughout this report quantitative references to spawner abundance are *effective female spawners* rather than a total of males and females. The estimated numbers of female spawners has been reduced in consideration of the effects of pre-spawning mortality, female fecundity, and percentage of eggs laid.

Salmon eggs develop in the gravel during the winter where they are protected from floods, ice conditions, and predators. The rate of egg development during incubation is dependent on water temperature and genetic characteristics related to environmental conditions of the specific population. Embryonic development is faster as temperature increases. For example, a 1°C difference in average incubation temperature can change emergence timing by four weeks.

A true larval stage does not exist in salmonids. When 10–20% of the yolk has been utilized, the alevin, a larva with a yolk-sac attached to its belly, hatches from the egg for further development in the protective gravel environment. When the yolk-sac has been absorbed, the young salmon, now called fry, emerge from the gravel in spring during the early hours of darkness within a narrow seasonal time window. Incubation, emergence, migration, and spawning are coupled and related to stream temperature and timed so that emergence of fry across stocks coincides with the development of plankton blooms in rivers, lakes, and the ocean. Differences in incubation temperatures between river systems are compensated for by changes in timing of spawning and differences in embryonic development rates. Fish that breed in relatively warm streams generally spawn later in the season, whereas those that breed in relatively cold streams, spawn earlier. The emergence time of fry is the major evolutionary influence that establishes spawning time. Fry from inlet streams will proceed downstream to a nursery lake whereas fry from lake outlets move towards the shorelines of the river and require a period of growth before migrating upstream to the nursery lake.

1.5.3 Migrations and habitat changes

In the nursery lake most of the surviving juveniles rear for one year before making the physiological transformation that prepares them for the ocean. Their water type preference changes accordingly from freshwater to salt water and their colour changes from a yellowish brown fish with parr marks to one with silver sides and a greenish back. They are now called smolts and are ready to migrate downriver to the ocean.

Upon entering the Strait of Georgia most sockeye salmon smolts turn northward and migrate primarily along the mainland shoreline. They exit the Strait of Georgia through channels among the islands and continue their migration through Johnstone and Queen Charlotte straits towards the North Pacific Ocean where they enter south of Haida Gwaii (Queen Charlotte Islands). Upon entering the North Pacific Ocean the postsmolts migrate north and westward in band within 35 km off the coasts of British Columbia and Central Alaska until they reach the overwintering grounds south of Alaska during late autumn and early December.

During their ocean residence sockeye salmon move relative to the annual temperature cycle in the Subarctic North Pacific Ocean. They are in waters colder than 7°C in winter, 10.5°C in spring, and 15°C in summer.

Thus, they move south in spring and summer and north in autumn and winter. This migratory pattern is the reverse of birds which move north during spring and south in autumn during the changing seasons.

When sockeye salmon mature, they first migrate north from the ocean feeding grounds in late summer, then journey to the outlets of their home streams and rivers and continue to migrate upstream to their ancestral spawning grounds. The migration north and then towards the Fraser River is apparent from the changes in distribution of sockeye salmon captured and tagged in the North Pacific Ocean in April through August and recovered in fisheries that operate in the approach routes to the Fraser River around Vancouver Island.

Sockeye salmon enter the Strait of Georgia on their way to the Fraser River estuary by taking either the southern route via Juan de Fuca Strait or the northern route via Johnstone Strait. Up to 1977 about 80% of the sockeye salmon, on average, used the southern route. Thereafter, an increasing number (average 50%) of the Fraser River sockeye salmon entered the Strait of Georgia via the northern route. Although the cause of the change is not yet known, years of warmer sea surface temperature on the West coast of Vancouver Island resulted in more sockeye salmon using the northern route.

Upon reaching the Fraser River estuary, many sockeye salmon stocks continue their upstream journey to the spawning grounds (Fig. 3). Some, like the Adams River population, may hold for up to three weeks off the Fraser River mouth before commencing migration upstream. The life cycle is completed by spawning and deposition of the eggs in gravel beds, and then death.

Thus, during their life cycle Pacific sockeye occupy a variety (12) of habitats (Fig. 4). Each is like a bead in a chain linked together by migrations. Therefore, it is important that each habitat is in prime condition and that migration routes between them are not hindered or blocked or made unsuitable. Any weak or broken link will significantly affect production and survival of the salmon.

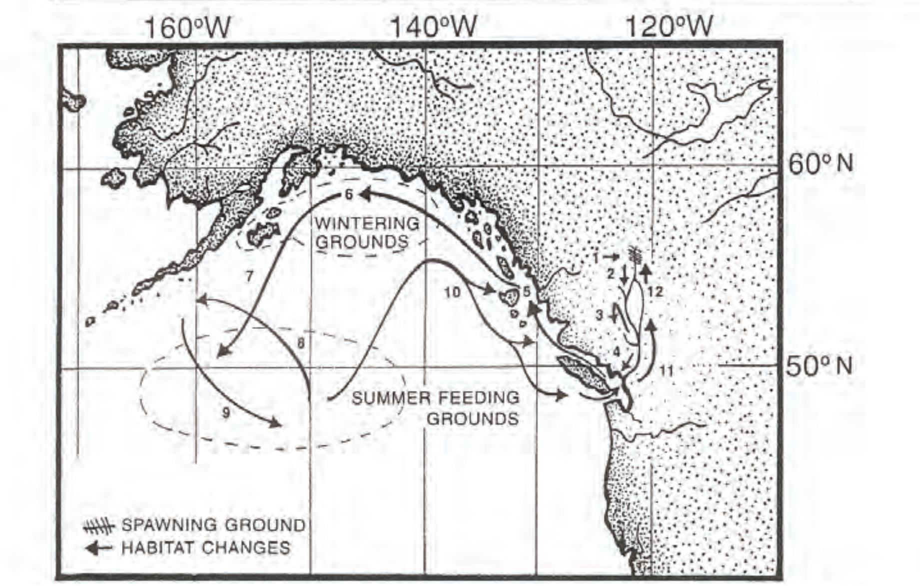

Fig. 4 Habitats occupied by a typical Fraser River sockeye salmon.

The long distance migrations of sockeye salmon from habitat to habitat provide some of the most enduring puzzles in salmon ecology. The migrations are well timed and well directed and can vary from a few hundred metres to thousands of kilometres. To perform these feats, sockeye salmon possess a remarkable set of direction-finding mechanisms that include sun compass and magnetic compass orientation. They are also able to distinguish water masses, such as between their natal tributary and nearby tributaries, and differences between stocks on the basis of odour.

Sockeye salmon are also able to migrate to a goal, such as the estuary of their natal stream, from any area in the North Pacific Ocean. This goal-finding ability is evident in the high rate of homing (>95%) to their ancestral spawning grounds. To quote Ferris Neave, a fisheries biologist who worked at the Pacific Biological Station in Nanaimo, British Columbia, for many years, "*It is difficult to avoid the conclusion that throughout the period of ocean life some awareness of position in relation to the place of origin is maintained*". The mechanisms underlying this capability are not well known, except that learning of the characteristics of the goal is involved.

Despite an understanding of the migratory patterns of sockeye salmon and some of the mechanisms involved in direction and position finding and water recognition, we are unable to predict accurately certain key events that are critical to the management of harvests. The least well known of these are properties associated with their life at sea.

1.5.4 Ecotypes

The strong tendency of sockeye salmon to return to their place of birth for spawning resulted in geographic and reproductive isolation that led to the development of many ecological forms during evolution. Differences can occur in many aspects of their biology, such as incubation period, age of seaward migration of juveniles, size of juveniles at a given age, ocean distribution, route and timing of migration shoreward, direction-finding abilities during migration, timing of stream entry, timing of spawning, fecundity, egg size and morphometric characteristics. These variations, which can vary both among, as well as within, stocks from region to region, are closely related to the ecosystems inhabited. There is sufficient evidence to conclude that many of the populations of sockeye salmon maintain such close associations with birthplace that they differ genetically from each other.

Many variations have developed in sockeye salmon upon the general pattern of movements between freshwater for rearing and reproduction and salt water habitats for feeding, by varying the duration of the juveniles in freshwater and of the immature in salt water from a few months to one or more years and by differences in timing of migratory patterns. Fry may move directly to salt water after emerging from the gravel; juveniles can spend two to three years in lake nursery areas before migrating to sea as smolts; maturing adults may return to their home river after one, two, or more years in the ocean; spawning can occur in inlet or outlet streams, along lake shores, or rivers. Also, the whole life cycle can be completed in freshwater, as in the case of kokanee. In total, sockeye salmon have about 18 different ecotypes.

Throughout this report, different ecotypes are identified by their age (x.y) where x = the number of complete winters (from fall through spring) spent rearing in freshwater after hatching, and y = number of winters spent at sea. The most common type in the Fraser River is age-1.2. Where age-1.x appears, for example, it refers to all fish that emigrated as one-year-old smolts, regardless how many years they spent at sea. Likewise age-2.x refers to all two-year-old smolts, without regard for their return year.

1.5.5 Production cycles

The majority of sockeye salmon in the Fraser River drainage system mature in their fourth year. A fixed age at maturity provides little opportunity for significant genetic exchange among cohorts. This has resulted in distinct reproductive lines between years in many stocks. The rigid four-year life cycle of Fraser River sockeye salmon has resulted in four reproductive lines. One of the lines often greatly exceeds the other three in abundance and is called the "dominant line". This phenomenon results in an imbalance in sockeye salmon population size in the Fraser River, producing a four-year cycle of abundance and catch. The dominant cycle often exceeds the others 100 to 1,000 fold.

In cases where strong cycles occur, elimination of a progeny line, by whatever cause, removes that line from the reproductive process and results in the loss of the genetic material of that particular year-class of a stock. Because of the inherited adaptations to the ecosystem, it may not be possible to easily restore lost populations of sockeye salmon in the event of natural or human-induced population failure. Many sockeye salmon stocks that disappeared from the Columbia and Fraser and other rivers never returned despite intensive restoration efforts.

2 Postsmolt Year

> *The author of* <u>*Our Heritage of the Seas*</u> *says "British Columbia salmon go to the Siberian shores and remain there until overcome with home-sickness, when they start back for the river of their birth. Others say that they only go out along the outer shores of our islands and there grow to maturity."*
>
> British Colonist, August 29, 1909

Population-specific studies of young Fraser River sockeye salmon during their first year at sea are rare because of the (historical) problem of identifying the origin of individual fish. While it is certainly possible that, of all sockeye salmon postsmolts sampled in the Strait of Georgia, some were from other stocks in the Salish Sea (*e.g.*, Sakinaw Lake, Lake Washington), we consider this probability to be relatively low because of the dominance of production from the Fraser River, and do not consider it further.

2.1 Postsmolt Migration Route

> *"After leaving the rivers, no young sockeyes are on record from salt water along the BC coast. The young of all other salmon species can be caught in traps in Juan de Fuca strait; the sockeye must pursue a different course."*
>
> C.H. Gilbert, 1914

The first reference to postsmolt migration routes from the Strait of Georgia was made by Charles Henry Gilbert (Gilbert, 1914). The coastal trap was a common method of fishing for salmon in British Columbia in the early 20th century. Operators of these traps in Juan de Fuca Strait reported that they did not find sockeye salmon postsmolts in their traps, although other salmon species were found. A similar result was reported following a summer of sampling in the San Juan Islands (see Figure 6). W.A. Clemens (University of British Columbia) was teaching at the University of Washington's Friday Harbor laboratory on San Juan Island (between Washington State and Vancouver Island) during the summer of 1950. Using a beach seine, he caught no sockeye salmon postsmolts that summer. As he concluded that he must have missed their outmigration by sampling in July and August, it appears that he expected to find them emigrating via Juan de Fuca Strait.

The first significant study of Fraser River postsmolt biology in the Strait of Georgia was conducted by the Fisheries Research Board of Canada from 1966–1969 using a surface trawl net that was towed between two boats (Barraclough 1967a–c; Barraclough and Fulton, 1967; Robinson *et al.*, 1968a,b; Robinson 1969a,b). Previous experimental fishing at different depths had shown that the greatest concentration of fry and postsmolts was found in the upper 3 m of the water column in this region (Barraclough and Phillips, 1978). Sampling that occurred in 1973 and 1975 was either brief (1973) or in different locations from the main investigation (1975) (Phillips and Barraclough, 1978). This investigation had a multi-trophic-level ecological perspective that was novel for the era (Parsons *et al.*, 1969a,b; Lebrasseur *et al.*, 1969). The focus of the study was the Fraser River plume (Fig. 5). Fieldwork included sampling juvenile salmonids and other fishes, their diets, and the prey field during spring and summer. The intensity of sampling was approximately monthly but varied from year to year with 1968 providing the most comprehensive sampling frequency because of additional sampling in Saanich Inlet, southern Vancouver Island.

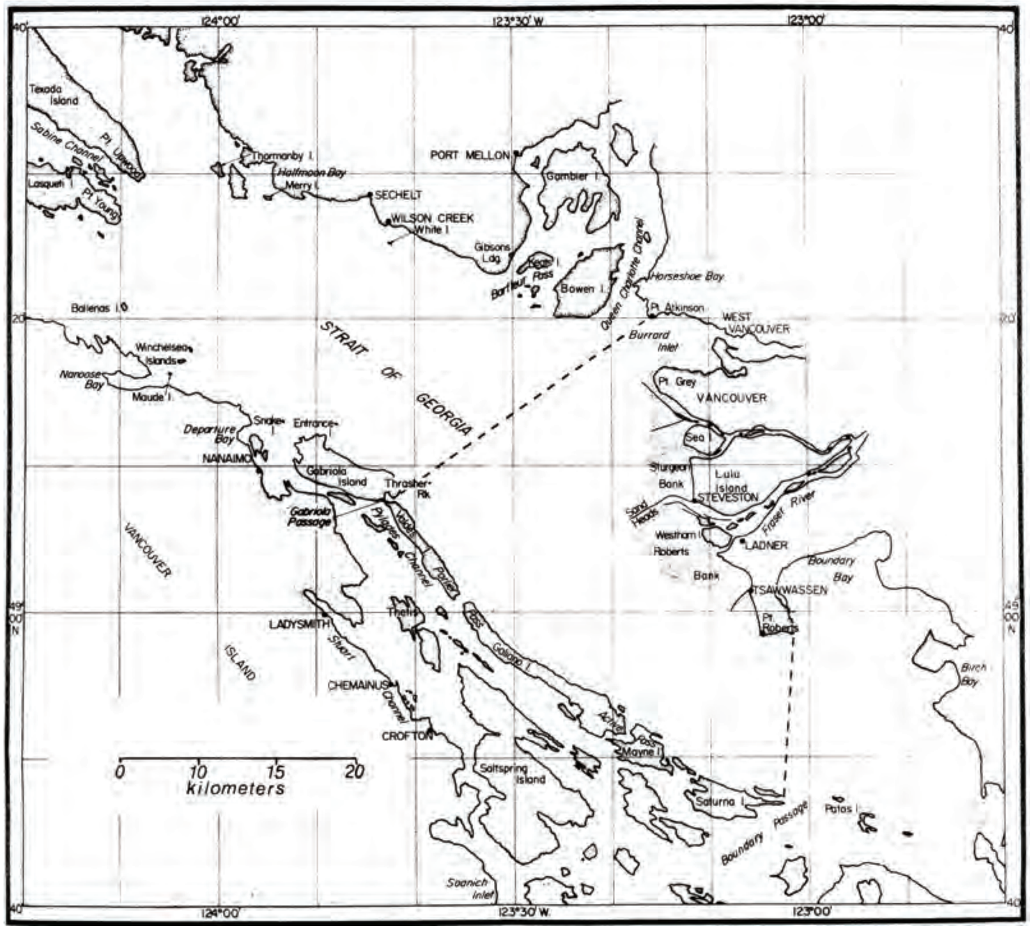

Fig. 5 Map of the Strait of Georgia showing the survey area between the dashed lines. Copied from Barraclough and Phillips (1978).

While the study was not designed to identify migration routes, a conclusion drawn from this investigation was that salmon from the Fraser River migrated in a southwesterly direction toward the Gulf Islands (see Figure 6).

> *"Young migrating salmon, in part directed by these currents, move across the Strait of Georgia, and through Active and Porlier passes and along the shores of Vancouver Island and the Gulf Islands where they may occupy nearshore areas temporarily before continuing through the Strait of Juan de Fuca[sic] to the open Pacific by late summer."*
>
> Barraclough and Phillips, 1978

In the summer of 1968, U.S. sampling under the auspices of the INPFC, of a three-station transect across Juan de Fuca Strait using a seine net took a total of only 54 sockeye salmon postsmolts in 37 seine samples collected from June 23 to July 17 and 13 sets collected from August 11 to 23 (Hartt and Dell, 1986). Of the five species caught, sockeye salmon was the least abundant. Of the few that were caught, most were taken in the July sampling on the Vancouver Island side of the strait, but because so few were caught, the authors felt that the June–July sampling in Juan de Fuca Strait had missed the sockeye salmon postsmolt outmigration. If this was true, the sockeye salmon postsmolt migration would have reached the west coast of Vancouver Island before June 23. This bit of logic does not agree with their general observation for the period April–June, described in a different part of the report, that "*juvenile sockeye salmon were just beginning to enter the open ocean in late June*."

In the mid-1970s, research on juvenile salmon ecology in the Strait of Georgia was continued by Dr. Michael Healey, then of the Department of Fisheries and the Environment. A review of this and previous studies in the Strait of Georgia led Healey to think that most juvenile sockeye salmon left the Strait of Georgia via the Gulf Islands and Juan de Fuca Strait (Healey, 1980). He also made note of underyearling sockeye salmon (age 0.x) accompanying the smolt migration downstream in the Fraser River (Healey, 1980). A study of Deas Slough, located 10 km upstream from the mouth of the Fraser River, in 1976 and 1977 found age 0.x migrants in abundance in 1976 and 1977 (Birtwell *et al.*, 1987). They were the most abundant salmonid and the fifth most abundant fish species caught in beach seine nets. The mean length of the underyearlings was ~30 mm when sampling began in April and May. By summer, the underyearlings had grown to a mean size of 60–80 mm in the slough and were approximately the same size as age 1.x sockeye smolts (Birtwell *et al.*, 1987). After emigrating to sea, age 0.x sockeye salmon remained in the Strait of Georgia in August and September to allow them to reach a larger size before emigrating to the west coast (Healey, 1980).

The next study in the Strait of Georgia, and one that focused on understanding Fraser River sockeye salmon postsmolt migration, was conducted by Dr. Kees Groot (Pacific Biological Station) from 1982–1984. As late as 1980, at least some scientists at the Pacific Biological Station thought that Fraser River sockeye salmon postsmolts left for the open sea via Juan de Fuca Strait (Barraclough and Phillips, 1978; Healey, 1980). In 1978, when the proportion of adult Fraser River sockeye salmon taking the northern route via Johnstone Strait increased substantially (Groot and Quinn, 1987; McKinnell *et al.*, 1999), it inspired an hypothesis that maturing Fraser River sockeye salmon were returning to the Strait of Georgia via the route that they had used as postsmolts to emigrate seaward (Groot and Cooke, 1987). Several years of sampling in the region confirmed an idea, first inferred in 1913, that sockeye salmon postsmolts tend to leave the Strait of Georgia via Johnstone Strait (Gilbert, 1914). Groot and Cooke (1987) found that Fraser River sockeye salmon postsmolts used two main routes during their migration through the Strait of Georgia (Fig. 6). One tracked along the eastern shore and one followed through the Gulf Islands and the western shore before migrating across the strait to the eastern shore.

A contemporary multi-year acoustic tagging study of hatchery-reared Cultus Lake sockeye salmon migration in the 2000s has shown that Johnstone Strait is not used exclusively as the route of emigration by this population (Welch *et al.*, 2009). Four percent of detections from 2004–2007 occurred at southern locations. Most (> 90%) of the acoustically tagged postsmolts from Cultus Lake, with their surgically implanted tags, headed up the strait and most of these left relatively quickly via that route (Welch *et al.*, 2009).

Since the mid-1990s, trawl surveys for juvenile salmon have been conducted routinely by various agencies along the North American coast (Fisher *et al.*, 2007). For the most part, these surveys confirmed the Hartt and Dell (1986) idea of a counterclockwise migration of postsmolts along the continental shelf. Migration was inferred from seasonally changing patterns of abundance in the trawls, with sockeye salmon showing the strongest north–westward shifts in relative abundance throughout the postsmolt migration season (Fisher *et al.*, 2007). There are always exceptions. A mid-water trawl survey in Hecate Strait, between Haida Gwaii (Queen Charlotte Islands) and the British Columbia mainland, in November 1963 (LeBrasseur and Barner, 1964) found a small number of sockeye salmon postsmolts at depth. They ranged in fork length from 168–198 mm and in weight from 50–90 g (LeBrasseur, 1965; LeBrasseur and Doidge, 1966a–d).

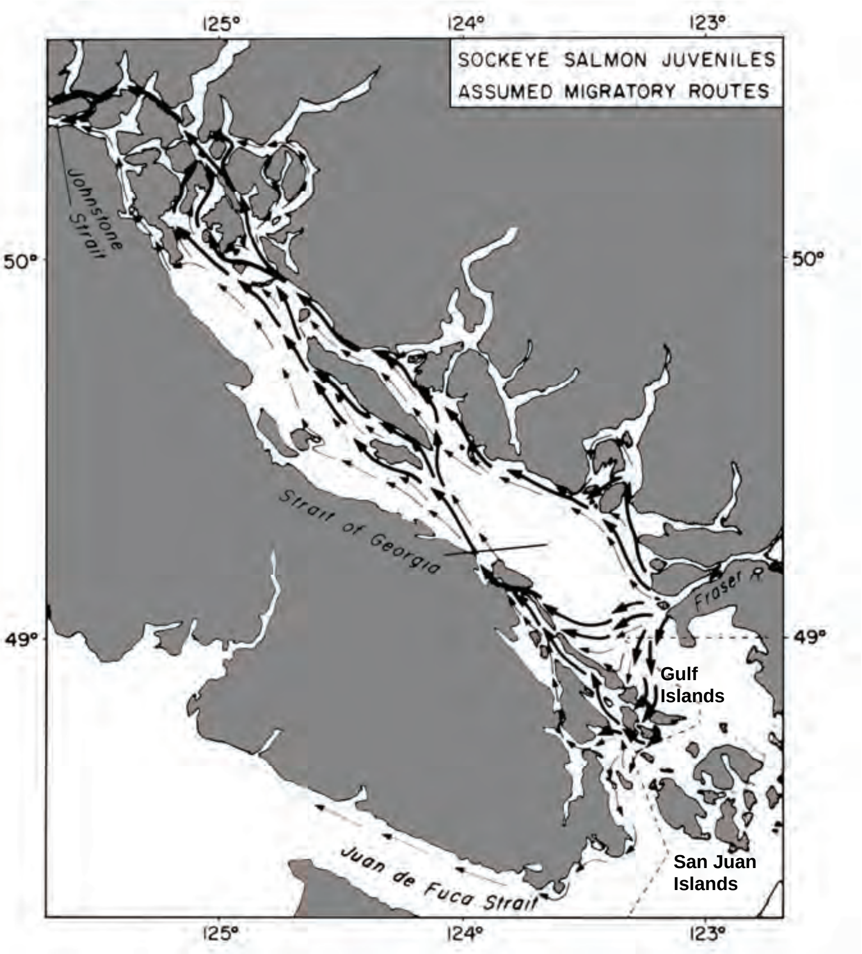

Fig. 6 Assumed migration routes of Fraser River sockeye salmon postsmolts based on surveys conducted from 1982–1984. Adapted from Groot and Cooke (1987).

The most recent review of Fraser River sockeye salmon postsmolt migration behaviour was developed from observations made during coastal trawl sampling from 1996 to 2007 (Tucker *et al.*, 2009). In total, across all years, the proportion of Fraser River sockeye salmon caught among the 4,062 sockeye salmon individuals taken from May to February was 0.42. From the spatial and temporal patterns of the composite catch (all years combined), the study found that after leaving the Strait of Georgia most of the postsmolts, identified by DNA as Fraser River sockeye salmon, were located north of Vancouver Island in May and June rather than on the west coast of Vancouver Island. Tucker *et al.* interpreted this finding as evidence of a Johnstone Strait migration route to the open sea.

From Queen Charlotte Sound, most migrated rapidly into northern British Columbia and Southeast Alaska (Fig. 7) via Hecate Strait (Tucker *et al.*, 2009). This migration route was inferred from fewer catches of Fraser River sockeye salmon postsmolts on the west coast of Haida Gwaii. Catches of Fraser River sockeye salmon postsmolts in summer (July–August) were highest in central British Columbia (Queen Charlotte Sound and southern Hecate Strait). Tucker *et al.* (2009) noted that sockeye salmon postsmolts from the Stuart Lake and Stellako River populations were not found in catches in central British Columbia by the fall whereas other populations were found there. From this, they inferred a different migration pattern with offshore migration occurring earlier than the other northward migrants. Winter sampling along the west coast produced much lower catches. A noteworthy feature of winter surveys was the appearance of Harrison River sockeye salmon along the west coast of Vancouver Island. From this observation, they inferred that Harrison River sockeye salmon migrated from the Strait of Georgia via Juan de Fuca Strait. Furthermore, winter was the only season when Harrison River sockeye salmon were caught. It is noteworthy, however, that some Fraser River sockeye salmon (other than Harrison River fish) were present in July samples, suggesting that some proportions of other stocks migrate via Juan de Fuca Strait in some years.

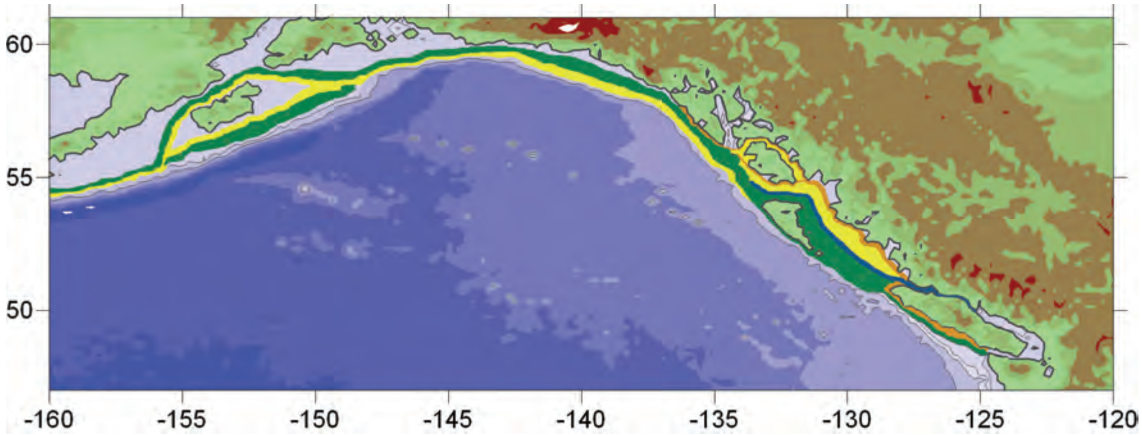

Fig. 7 Seasonal migration of Fraser River sockeye salmon postsmolts after leaving the Strait of Georgia (blue: May–June, green: July–August, yellow: October–November, orange: February–March, based on Tucker *et al.* 2009 (their Figure 5c). N.B. Relative amounts of colour are intended to reflect relative seasonal abundances at various locations along the coast rather than specific migration pathways (*i.e.*, Fraser River sockeye salmon do not migrate solely in the centre of Queen Charlotte Sound/Hecate Strait but are found in this region in lower abundance than in July–August and October–November).

Coastal trawling for juvenile sockeye salmon from 1996–2007 (Tucker *et al.*, 2009) confirmed previous conclusions that sockeye salmon postsmolts followed a northward and westward migration along the continental shelf (Hartt and Dell, 1986). The novel contributions of the recent surveys were made possible by the development and application of DNA stock identification to provide new information on stock-specific migration patterns. Unfortunately, annual differences and similarities in migration routes were not possible to identify because the numbers of sockeye salmon obtained from the trawl surveys were too few (Tucker *et al.*, 2009).

Summary – The first reference to any knowledge of the route taken by sockeye salmon postsmolts from the Strait of Georgia concerned their appearance, or more appropriately, their lack of appearance in fish traps in Juan de Fuca Strait (Gilbert, 1914). The juveniles of all other species of Pacific salmon were found there, but not sockeye salmon. This observation (all species but sockeye salmon) was repeated in July 1950 during beach seining in the San Juan Islands (Clemens, 1951). Scientific investigations in the 1960s and 1970s reported that sockeye salmon postsmolts left the Strait of Georgia via the Gulf Islands and Juan de Fuca Strait (Barraclough and Phillips, 1978; Healey, 1980) although sampling at the western entrance to the Juan de Fuca Strait in 1968 failed to find any abundance of them in June, July or August (Hartt and Dell, 1986). Intensive sampling (both spatially and temporally) for several years in the Strait of Georgia in the early 1980s found that most Fraser River sockeye salmon postsmolts were migrating from the Strait of Georgia via Johnstone Strait, including at least some of those found among the Gulf Islands. In the 2000s, acoustic tagging and stationary detection lines confirmed what Groot and Cooke had described (Welch *et al.*, 2009). While it is possible that the major migration route from the Strait of Georgia to the coastal ocean changed from Juan de Fuca Strait before the 1980s to Johnstone Strait from the 1980–2000s, the low abundance of sockeye salmon postsmolts found in the Juan de Fuca Strait in May through July in all sampling efforts suggests that they may have always used Johnstone Strait as the main pathway.

2.2 Postsmolt Migration Timing

Since 1997, the date of 50% emigration of Chilko Lake smolts from the lake has a range of 13 days (Fig. 8). The earliest peak date observed since 1997 was April 26 (2005) and the latest peak date was May 9 (2003) and there is no trend apparent. In 2007, the largest recorded smolt run had an intermediate emigration date of May 2, one day earlier than the average for this period. As flows in the Fraser River were higher than average during 2007, it is not unreasonable to assume that Chilko Lake smolts may have arrived at the Fraser River estuary no later than the average date of their arrival.

Acoustic tagging of age-2.x smolts as they left Chilko Lake in 2010 confirmed earlier thoughts about the duration of the migration from Chilko Lake to the Strait of Georgia. In 2010, preliminary results of the migration of tagged fish indicated that the average migration time in the river to the Strait of Georgia was eight days, with the earliest tagged fish arriving in four days and the latest fish arriving after 18 days (T. Clark and S. Hinch, UBC, pers. comm.). If applied to the 2007 emigration from Chilko Lake, the peak would be entering the Strait of Georgia on May 10. As flows were higher in 2007 than in 2010, arrival times in the Strait of Georgia may have been earlier. Applying the best estimates of migration time through the Strait of Georgia to these dates would easily place the Chilko Lake postsmolt migration in Johnstone Strait by the middle to end of June.

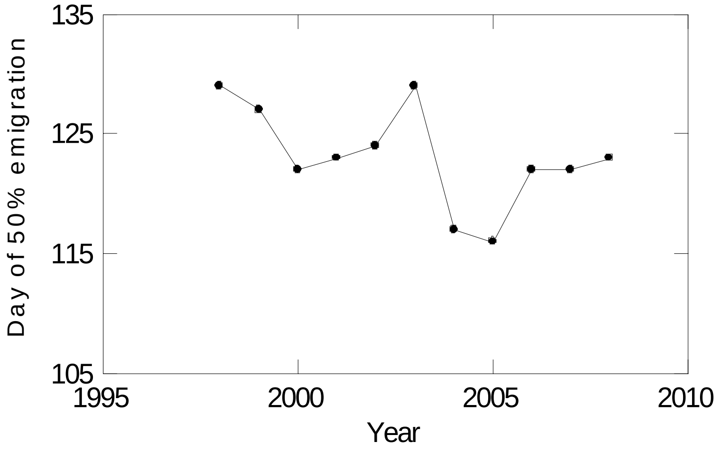

Fig. 8 Day of year, 1998 to 2008, when 50% of the smolt run passed the Chilko Lake smolt fence.

From 1966 to 1969, sockeye salmon postsmolts from the Fraser River did not appear in the samples in the southeastern Strait of Georgia until late April when their abundance increased abruptly (Barraclough and Phillips, 1978). The sockeye salmon were described as spending the least amount of time in the open waters of the southern Strait of Georgia. High abundance, compared to other species of salmon, in the clear saline waters of Porlier Pass and Active Pass was interpreted as an ability for rapid adaptation to the marine environment (Barraclough and Phillips, 1978). Their general abundance in the samples was described as less than pink and chum salmon, uniform through May and slightly higher in June and July, with considerable year to year variation (Barraclough and Phillips, 1978).

While the survey in the 1960s was not intended to determine sockeye salmon migration timing or routes, some patterns can be inferred from the changing relative abundances. A total of 785 sockeye salmon postsmolts were caught in the Strait of Georgia during these four years of sampling, with 85% taken by the end of June. The percentage of all sockeye salmon postsmolts that was collected in July varied annually from 4.9% to a high of 43% in 1967 (annual average, 14%). Those taken in July of 1967 had the smallest mean length

(65 mm) of any monthly averages during the study (Fig. 9). As salmon are not known to shrink in length, an observation of smaller mean size suggests a different population composition of the samples as the season progressed. These individuals have the approximate mean size of age 0.x sockeye salmon that Birtwell *et al.* (1987) reported from Deas Slough. The only source population with high proportions of small underyearlings is the Harrison River.

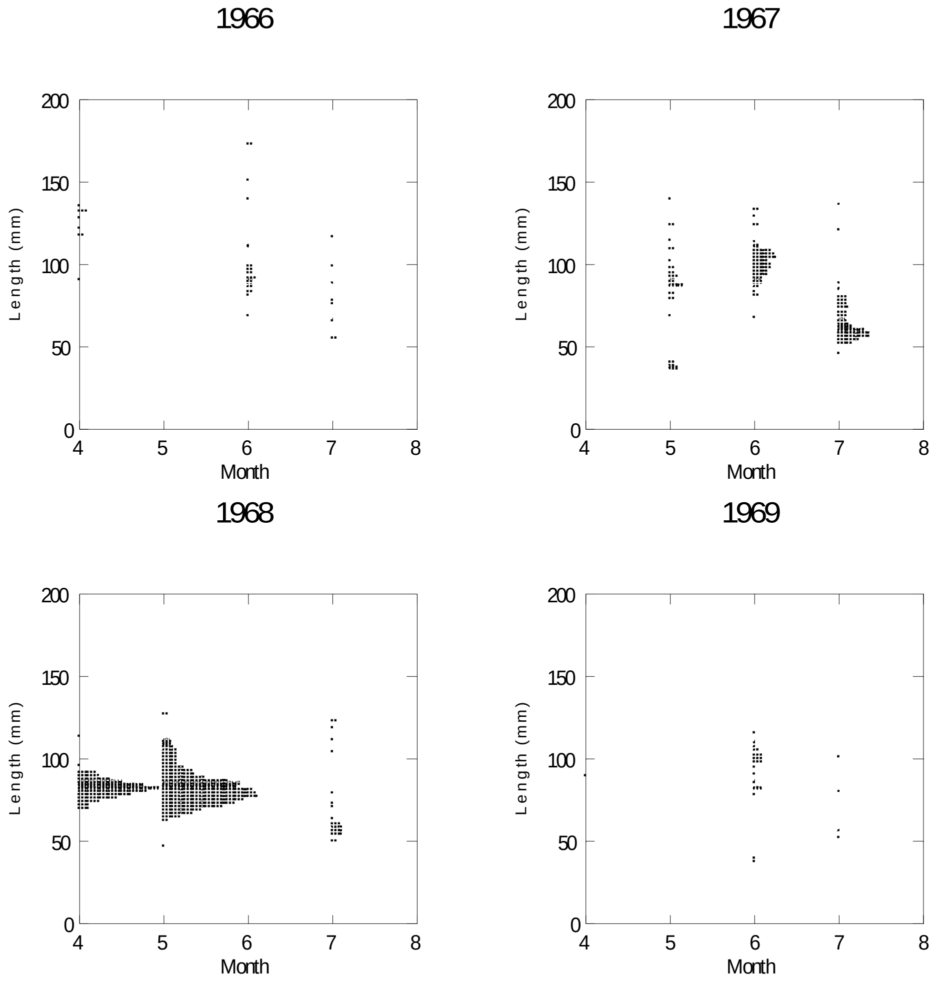

Fig. 9 Length frequency distributions of sockeye salmon taken in two boat surface trawls in the Strait of Georgia from 1966 to 1969. The overall declining trend in mean length in each year is a result of the seasonally changing composition of the samples, not negative growth. Each year includes three length frequency modes – underyearlings, age-1.x postsmolts, and age-2.x postsmolts. April 1966 is mostly age-2.x postsmolts while April 1968 is mostly age-1.x postsmolts. May 1967 included some underyearlings.

Sampling with a purse seine in the Gulf Islands from May to October of 1976 found the highest juvenile sockeye salmon catches in May and June (Healey, 1980). By July, the average catch per set was only 20% of what was caught in May and June (Fig. 10) and the maximum number caught in a set had declined from 102 to 15 in May and 53 in June. Fishing locations during this study were predetermined rather than adjusted according to what had been caught in previous sets. Based on the patterns of catch in the Fraser River plume and the Gulf Islands, Healey (1980) estimated that sockeye salmon postsmolts took 20–30 days to pass from the Strait of Georgia, but this estimate was developed with a Juan de Fuca Strait migration route in mind.

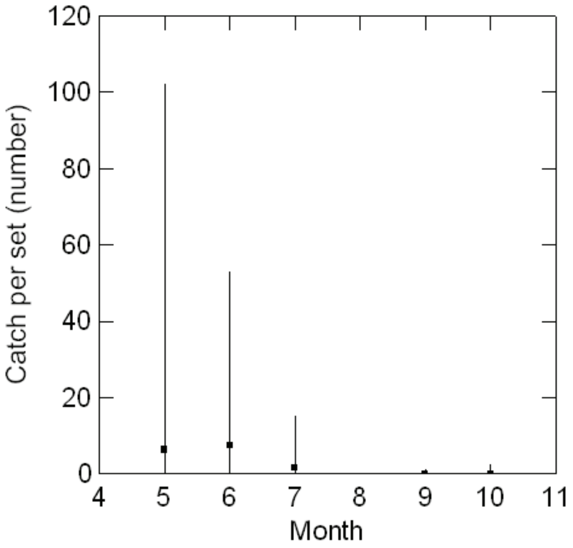

Fig. 10 Average numbers of juvenile sockeye salmon caught per set (solid squares) and range of numbers caught per set (vertical lines) around the Gulf Islands, May to October 1976. At least 40 sets occurred in each month except July (n = 26).

Extensive fine-mesh seine sampling from Washington State (Cape Flattery) northward to the Aleutian Island chain, under the auspices of the INPFC, led to the conclusion that...

> *"by the month of July, juvenile sockeye salmon were present in substantial numbers in coastal waters adjacent to most major production areas, showing that their oceanic embarkation was well underway." (Hartt and Dell, 1986)*

This conclusion was reached after examining 3,073 purse seine sets taken from throughout the Northeast Pacific Ocean, Bering Sea and Aleutian archipelago from 1956 to 1970, although specific efforts directed at juvenile salmon occurred from 1964 to 1968. Prior to July, sockeye salmon postsmolts were found only off the west coast of Vancouver Island and on the continental shelf near Sitka, Alaska (French *et al.*, 1976). By August, the overall range of locations where sockeye salmon postsmolts was found was similar to July but the relative abundance was diminished in the south off Juan de Fuca Strait and the west coast of Vancouver Island and increased in the northern Gulf of Alaska. By September and October, the range remained similar to that found in August but catches were significantly diminished in the eastern and southern Gulf of Alaska. Despite extensive offshore fishing with a fine-mesh purse seine from 1956 to 1970, sockeye salmon postsmolts were not found in the deeper waters of the Gulf of Alaska (French *et al.*, 1976).

Trawl surveys in July and September in the Strait of Georgia from 1997 to 2002 caught a total of 117,571 juvenile pink, chum, coho, and chinook salmon (Beamish *et al.*, 2004a). It was not possible to include sockeye salmon in the analysis because comparisons among years were complicated by spending less time in the Strait of Georgia compared to other species (Beamish *et al.*, 2004a).

2.3 Postsmolt Migration Speed

Rates of migration of individual sockeye salmon from the Fraser River are reported infrequently. Generally, estimates of migration rates are inferred from the changing spatial patterns of sockeye salmon distribution in surveys. Using this approach, Groot and Cooke (1987) reported that after three years of field studies, it appeared that Fraser River sockeye salmon postsmolts moved through the Strait of Georgia in about one month. Acoustically-tagged hatchery-reared sockeye salmon smolts from Cultus Lake had average residence times in the Strait of Georgia from 25.6 to 34.1 days, computed from four years of tagging studies from 2004 to 2007 (Welch *et al.*, 2009). These results may not reflect migration speed of the general population, however, as the average size of the tagged sockeye salmon smolts from Cultus Lake (159–189 mm) was nearly double the average size of a wild sockeye salmon smolt (~88 mm) (Foerster, 1954). The acoustic tags confirmed that most of these postsmolts used the eastern route of Groot and Cooke (1987). A diffusion model of the downstream migration of Chilko Lake sockeye salmon smolts (Crittenden, 1994) forced by 1984 environmental conditions placed all Chilko Lake postsmolts in the Strait of Georgia by the end of May (Peterman *et al.*, 1994).

Millions of coded wire tags have been applied to juvenile Pacific salmon but rarely were they used to study wild sockeye salmon. In rare recoveries of three coded wire tagged sockeye salmon postsmolts from the endangered Redfish Lake, Idaho (elev. 1996 m) sockeye salmon population, Tucker *et al.* (2009) reported that their average migration speed from the lake to the recovery location along the British Columbia coast varied from a low of 40 to 48 km d^{-1} during the 45 to 55 days at large. If these migration speeds are applied to the route travelled by most Fraser River sockeye salmon postsmolts, assuming a directed migration toward Johnstone Strait, they would travel from the mouth of the Fraser River to Desolation Sound at the northern end of the Strait of Georgia in about four days. This migration speed would take the peak of the smolt migration from Chilko Lake (May 3, average from 1998 to 2008) at 1285 m elevation to Queen Charlotte Sound (642 km downstream + 215 km by a great circle distance from Sandheads lightstation at the mouth of the Fraser River) in 19 days (May 22). Clearly this is too fast as limited contemporary sampling between mid-May and mid-June did not find Fraser River sockeye salmon postsmolts north of Queen Charlotte Sound (M. Trudel, DFO, pers. comm.), which also agrees with historical sampling (Hartt and Dell, 1986) that sockeye salmon postsmolts are not reaching Queen Charlotte Sound until at least the end of June. It suggests a migration speed of about half that of the Redfish Lake sockeye salmon.

Updated estimates of Redfish Lake sockeye salmon migration speeds are 14 to 35 km d^{-1} and new information on migration speeds of coded-wire tagged Cultus Lake sockeye salmon that were recovered in 2008 and 2009 indicated an estimated migration speed of 14 to 19 km d^{-1} (Trudel *et al.*, 2010). At this speed, travelling in a straight line, the fish would travel from Sandheads to Redonda Island at the northern end of the Strait of Georgia in about 15 days. In Barkley Sound, on the west coast of Vancouver Island, however, the estimated average migration speed in tidal waters was only 1.6 km d^{-1} from May to July (Wood *et al.*, 1993). The reason(s) for such highly variable migration speeds among populations entering the ocean at different locations is unknown, but those with the farthest to travel to better sockeye salmon feeding areas (Alaska Current) may have evolved this strategy.

2.4 Factors Affecting Postsmolt Migration Behaviour

A numerical hydrodynamic model (Crean *et al.*, 1988) forced by winds, Fraser River discharge, and tides indicated that surface currents in the Strait of Georgia, forced mainly by local winds, can affect the migration route used by Fraser River sockeye salmon postsmolts within the Strait of Georgia. Use of the western route by modelled sockeye salmon postsmolts increased only when a strong, persistent northwesterly wind pattern became established in the Strait of Georgia. Model results with migration routes of north, northwest, and west at 4 cm s^{-1} produced residence times in the Strait of Georgia at 21 to 38 days. The best fit between the model and observations for 1984 (24 days in the Strait of Georgia) was obtained using a 4 cm s^{-1} swimming speed and a northwest orientation (Peterman *et al.* 1994). Furthermore, the tides and discharge in 1984 had no discernable effect on the migratory route followed by sockeye salmon postsmolts in the model.

2.5 Postsmolt Feeding

Following LeBrasseur (1966), *stomach content* is used rather than *diet* because some unknown portion of the stomach contents may have been the prey of animals that the sockeye salmon ingested. Trophodynamic studies of fishes in the Strait of Georgia in the 1960s provided the first comprehensive data on sockeye salmon postsmolt diets. The earliest migrants into the Strait of Georgia had the least diverse diets (Table 1). Copepods were the dominant prey item in April. In all years, the percentage of copepods in diets diminished by month.

Copepods are an important trophic link between primary producers (phytoplankton) and higher trophic level carnivores in the Strait of Georgia (Evanson, 2000). The dominant copepod in the Strait of Georgia has been *Neocalanus plumchrus* but marked changes in species composition occurred in the 1970s with increases in *Calanus marshallae* and *C. pacificus* (Gardiner, 1976). *N. plumchrus* has a peak abundance in spring until the late-stage copepodites descend to enter diapause until the following spring. In preparation for diapause, this copepod stores lipids to utilize from summer to winter and this characteristic makes it an energetically rich prey but its seasonal timing makes it available to sockeye salmon for only a relatively short period. El-Sabaawi (2008) described an 87% decline in its abundance between 2001 and 2006. Because sockeye salmon tend to feed opportunistically, the full consequences of declining *N. plumchrus* abundance in the Strait of Georgia to sockeye salmon postsmolt growth and survival are unknown. As the field phase of this doctoral project ended in 2006, there were no equivalent zooplankton samples in 2007. During the years of *N. plumchrus* decline, the composition of the phytoplankton spring bloom varied annually among diatoms, diatoms and flagellates, and diatoms and dinoflagellates. The declines in *Neocalanus* were accompanied by longer term declines in copepod zooplankton biomass in the Strait of Georgia (D. Mackas, IOS, pers. comm.).

Table 1 Percentages of prey items in sockeye salmon postsmolt stomachs in the Strait of Georgia, by month, from 1966 to 1968.

Taxon	**4**	**5**	**6**	**7**	**Total**
Amphipod	6.8	10.5	0.8	8.7	2.5
Barnacle	0.0	0.2	0.4	0.2	0.3
Cladocera	0.0	0.1	4.2	0.0	3.2
Copepod	90.9	45.0	8.0	6.8	20.7
Decapod	0.2	0.3	0.2	14.3	0.4
Eggs	0.0	3.1	63.7	1.4	49.7
Euphausiid	0.1	0.6	12.4	0.8	9.7
Fish	1.6	2.2	0.7	3.7	1.0
Insect	0.1	0.5	1.3	39.6	1.6
Larvacean	0.0	35.5	7.9	0.2	9.9
Mollusk	0.0	0.0	0.0	9.3	0.1
Ostracod	0.0	1.1	0.4	3.9	0.5
Polychaete	0.0	0.0	0.0	10.1	0.2
Sagitta	0.2	0.6	0.0	0.7	0.1
Worms	0.0	0.0	0.0	0.4	0.0

Trawling in the Strait of Georgia in July and September between 1997 and 2002 provided 24,206 salmon stomachs (Beamish *et al.*, 2004a). Interannual differences in major taxa in the diets of pink, chum, coho, and chinook salmon were low, but the contents of sockeye salmon stomachs were not reported. Average stomach volumes and sample sizes were reported for non-sockeye salmon, but as the standard deviations were not reported, it was not possible to understand if there were statistically significant differences in mean stomach volumes between years. A later study of coho salmon stomach content composition in July and September in the Strait of Georgia from 1997 to 2007 (Sweeting and Beamish, 2009) suggests that the dominant factor determining the composition of stomach contents of coho salmon was related to seasonal changes in relative prey abundance or prey selection. Cluster analysis, which groups years based on their stomach content similarities, showed that coho stomach contents had more similarity within month across years than within year across months (Fig. 11). All of the July samples are in one large cluster and all of the September samples, except 2003, are in another. September 2003 had a substantially higher proportion of amphipods compared with all other years/months of sampling. Considering the coho salmon that entered the Strait of Georgia in 2007, the placements of 2007 within each cluster suggest that there was nothing unusual about the diet composition, although there were more empty stomachs in coho salmon in 2007 than in other years (Sweeting and Beamish, 2009). Extended periods with an empty stomach is a common feature of many families of piscivorous fishes (Arrington *et al.*, 2002) so it is not possible to attribute physiological status to these animals from these data.

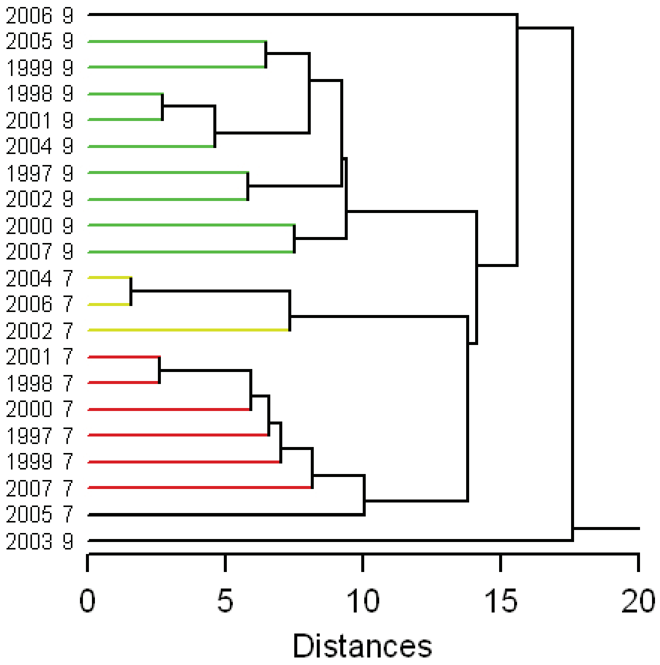

Fig. 11 Hierarchical cluster analysis of relative composition of coho salmon stomach contents by year and month from 1997 to 2009. Identifiers indicate the year and month of sampling. Colours indicate cluster memberships. Data from Sweeting and Beamish (2009).

Of the six sockeye salmon postsmolt stomachs examined from the mid-water trawl survey in Hecate Strait in November of 1963, three stomachs contained prey (*Limacina*, copepod, amphipod). These items were classified as undigested in two of the fishes. Whether these were Fraser River sockeye salmon is unknown but they are reported here because of the rarity of reports of autumnal samples in the coastal zone.

2.6 Postsmolt Growth

2.6.1 Strait of Georgia

The number of postsmolts, their average fork length, and the ranges of fork lengths of Fraser River sockeye salmon were summarized by year and month for the years 1966 to 1969 (Phillips and Barraclough, 1978). Growth rates of Fraser River sockeye salmon postsmolts in the Strait of Georgia could not be determined from these data because the population of origin was unknown (Phillips and Barraclough, 1978). The pooled data from the Strait of Georgia only (excluding Saanich Inlet) reveal the dominance of postsmolts (age-1.x and age-2.x) until June, until underyearlings form the larger component in July in most years.

In the summer of 1968, repeated samples taken in Saanich Inlet indicated that the abundance of sockeye salmon postsmolts increased rapidly from the end of May to a peak on June 7 after which their abundance declined rapidly (Fig. 12). If the same population had been sampled repeatedly, the growth rate would be estimated to be 0.8 mm d^{-1}, or 4.25% of body weight, but the authors had no way of knowing if they were sampling the same population each time.

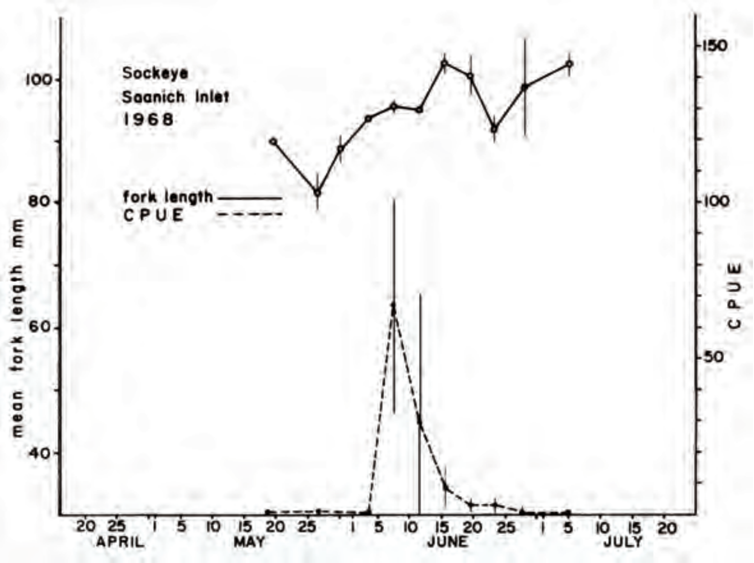

Fig. 12 Size and abundance of sockeye salmon in repeated samples in Saanich Inlet, southern Vancouver Island, in 1968. Vertical lines indicate ±2 standard errors. Reproduced from Phillips and Barraclough (1978).

In reviewing the studies conducted through the 1970s, Healey (1980) found that the average size of sockeye salmon postsmolts caught in the Fraser River plume and in the Gulf Islands did not increase with time through the months April, May, and June. He surmised that the sockeye salmon postsmolts spent too little time in the Strait of Georgia to allow them to increase significantly in size. A major problem with determining growth rates of sockeye salmon postsmolts from repeated sampling in the Strait of Georgia is the high probability of a variable composition of the catch. Without knowing which populations were measured, a change in mean size over time could be a simple consequence of measuring a sample that contains a different population or mixture of populations at each sampling rather than from an effect of the growth of individuals. Increasing numbers of sockeye salmon fry migrating into the Strait of Georgia in summer will cause the mean size of sockeye salmon taken in samples to decrease because the fry are smaller (and younger).

Trawl surveys were conducted in the Strait of Georgia from 1997 to 2002 (Beamish *et al.*, 2004a). Although the target sampling dates were July and September, problems associated with vessel scheduling did not permit the same locations to be sampled on the same dates each year. Nevertheless, it was possible to restrict the analysis of samples to two periods (July 1–15, and September 12–26) to provide more comparable results among years. Although not reported in the paper, it was possible to compute 95% confidence intervals on the mean lengths from the data reported (Table 3 in Beamish *et al.* 2004a). For samples collected in mid-September, at the end of the growing season, there were no significant differences among years in mean lengths of coho, pink, or chum salmon (Fig. 13). There were significant differences among years for chinook salmon with smaller mean lengths in 1997 and 2002.

Mean lengths were more variable among years in samples collected between July 1 and 15 (Fig. 14). The mean lengths of coho salmon sampled in July 2000, for example, were demonstrably larger than in other years, although its confidence interval overlaps that of the 1997 samples because of a small sample size in 1997. For chinook salmon, mean length was significantly different (smaller) from the other years only in 1998, otherwise there was no significant difference in mean length of chinook salmon among years. There was no significant difference in mean length of pink salmon in July among the three even years that were sampled. Mean lengths of chum salmon were significantly different among years in July, with 1997 and 2001 having the largest mean lengths.

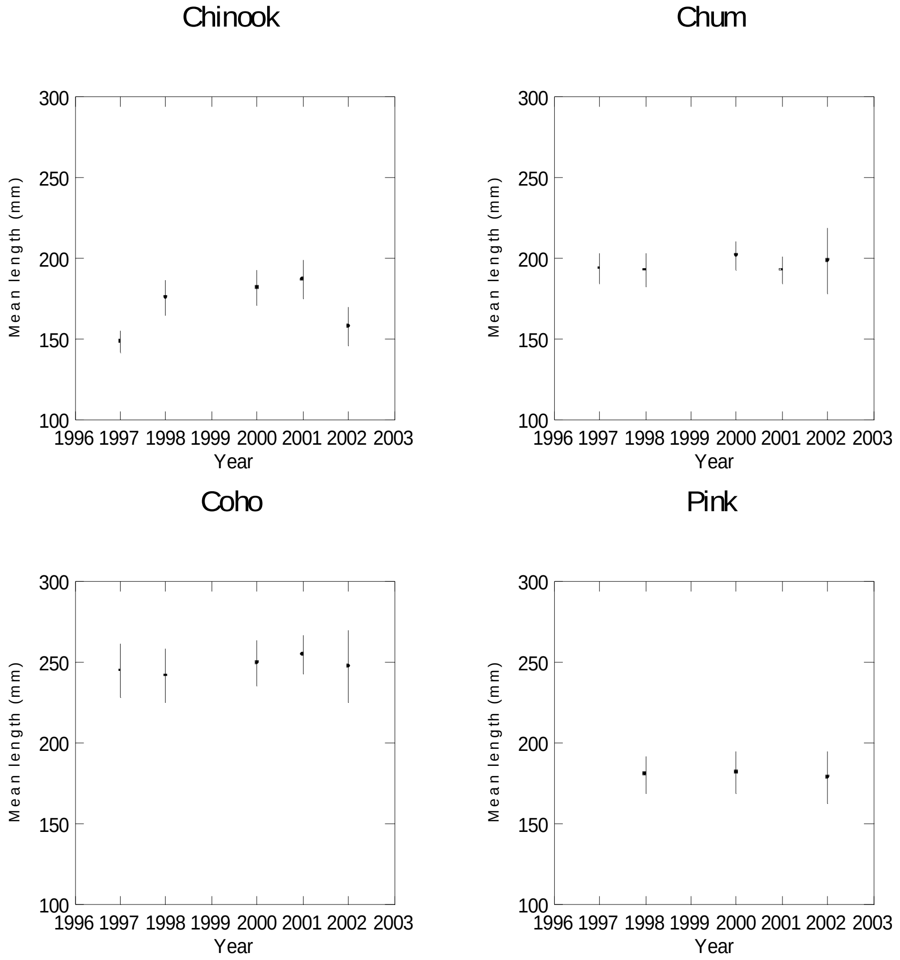

Fig. 13 Mean lengths and 95% confidence intervals by year and species for Pacific salmon juveniles sampled in trawl nets between September 12–26, 1997–2002. Results computed from Table 3 of Beamish *et al.* (2004a). Samples in 1999 were not taken within these dates and were omitted.

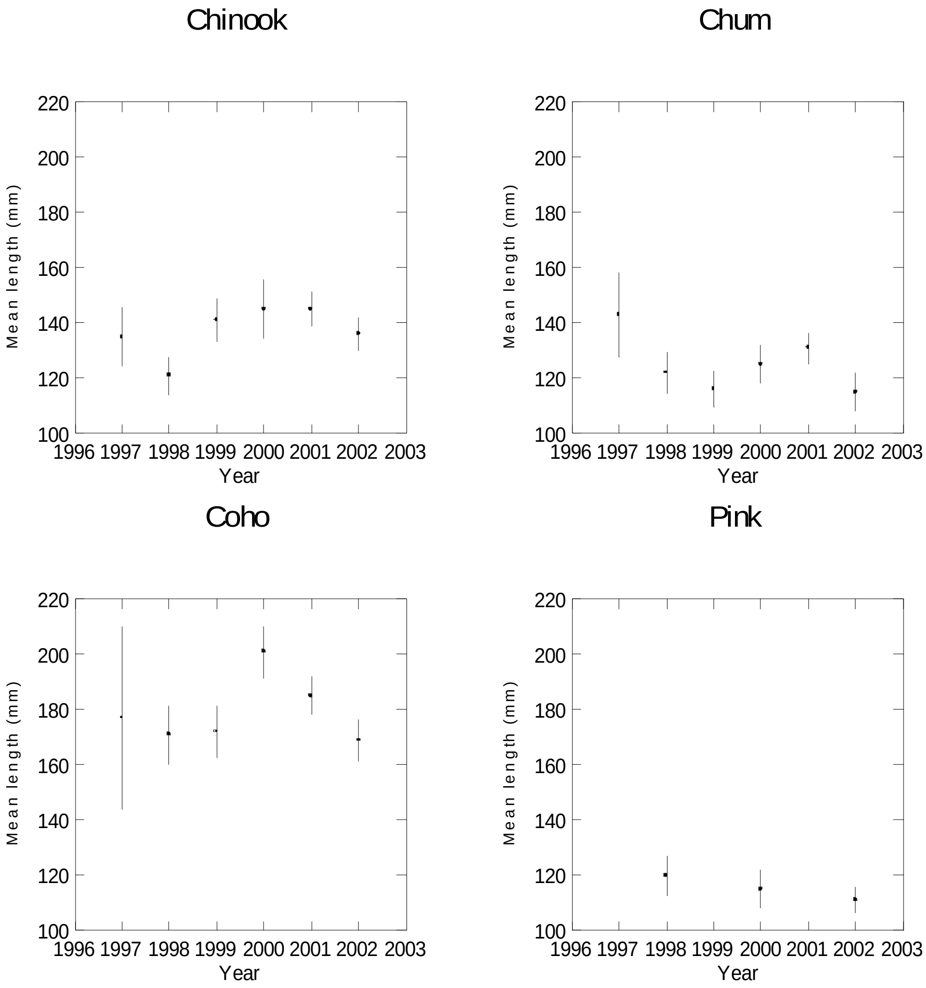

Fig. 14 Mean lengths and 95% confidence intervals by year and species for Pacific salmon juveniles sampled in trawl nets between July 1–15, 1997–2002. Results computed from Table 3 of Beamish *et al.* (2004a).

This comparison of mean lengths of non-sockeye salmon[4] in the Strait of Georgia provides an indication of year-to-year variability in mean size of the juvenile salmon that were available to the trawl. These results were interpreted as evidence for improved juvenile Pacific salmon production in the Strait of Georgia after 1998 which was thought to be caused by changes in the speed of rotation in the Earth (Beamish *et al.*, 2004a).

2.6.2 Continental shelf

Recoveries of maturing fish in southern British Columbia fisheries that were tagged and released as postsmolts from 1965 to 1968 indicated that they had been larger postsmolts (18–22 cm, N = 12 tags) than similar recoveries in northern B.C. fisheries (14–19 cm, n = 14 tags) (Hartt and Dell, 1986). The larger size of southern B.C. sockeye salmon postsmolts was thought to be related to their earlier entry into salt water and longer period of marine growth on the date of tagging. They also reported that the mean lengths of tagged postsmolts that survived two years to reach the fishery (0.8% of those tagged), tended to be larger than the

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[4] DFO reported to the Cohen Commission that it was unable to retrieve comparable data for sockeye salmon. (D.A. Levy, Cohen Commission, Sept. 10, 2010). As a result, an analysis of these data was not possible.

overall mean length of all tagged postsmolts. They inferred that tagging mortality might be a cause of fewer smaller postsmolts surviving.

Contemporary surface trawl sampling provides a composite view of regional and seasonal growth and net energy accumulation by sockeye salmon postsmolts (Tucker *et al.*, 2009). It was found that postsmolts sampled in northern locations had a larger mean size than those sampled in the south, and that energy density became progressively larger in northern than in southern samples from spring through fall. In general, larger postsmolts have greater energy density in each season (Fig. 15). The noteworthy outlier appeared in Southeast Alaska in spring where the median body size was largest and median energy density was lowest. As seasons were selected from calendar dates in this analysis, what was classified as spring in most locations (May–June 20) may have been ecological winter or early spring in Southeast Alaska. In all other seasons, higher median energy densities were found in samples with larger postsmolts. In each season except spring, the larger postsmolts with higher energy densities were found along the Alaskan coast rather than along the British Columbia coast. Note that energy was measured in joules g^{-1} to adjust for the effect of increasing mass on increasing energy, so the appearance of increasing energy density associated with increasing size suggests that larger size allows postsmolts to accumulate energy at a faster rate than for smaller postsmolts (Tucker *et al.*, 2009).

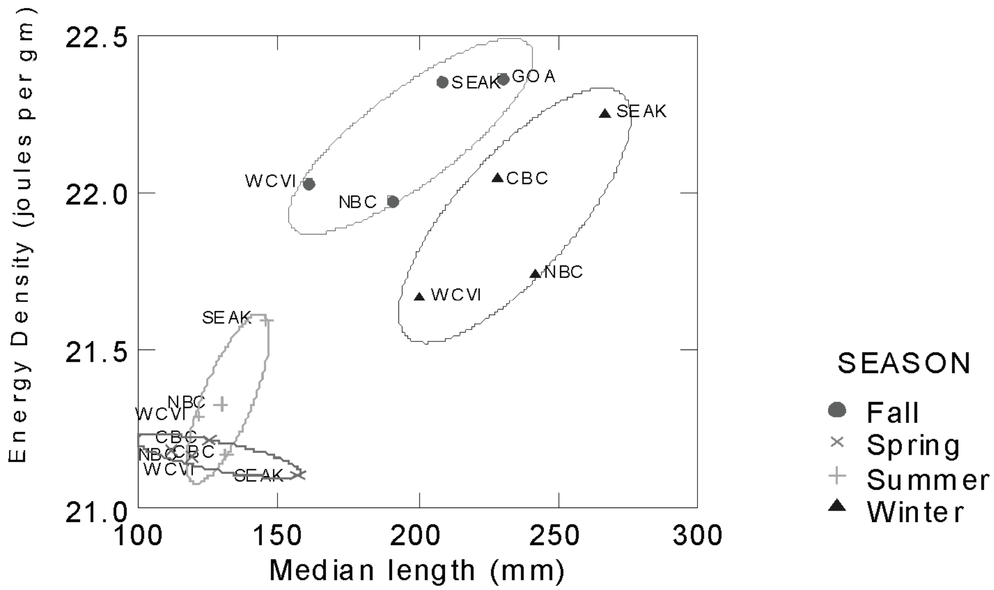

Fig. 15 The median energy density (joules g^{-1}) of sockeye salmon postsmolts, by region and season. Ellipses indicate the 75% probabilities where the bivariate mean values in each season may be found. Data reproduced from Figures 8 and 9 in Tucker *et al.* (2009). GOA = Gulf of Alaska, SEAK = Southeast Alaska, CBC = Central British Columbia, NBC = Northern British Columbia, WCVI = West coast of Vancouver Island.

The pattern of ellipses in Figure 15 reflects seasonal patterns in median length and energy content. The winter ellipse is somewhat lower and to the right of the fall ellipse, but the cause of the difference can only be a matter of speculation. The median length of a sample of postsmolts can be larger in winter than in the previous fall because the fish continue to increase in length, or because the median length becomes larger because the smaller individuals are dying faster rate than the larger ones. Although both processes may be at play in these data, it takes a rather substantial amount of mortality to change a mean/median length of a population by this process alone. Therefore, the different positions of the ellipses in Figure 15 likely reflect a winter feeding environment where less food is available. Some growth continues through the winter, but some energy reserves are used in metabolism.

Summary – Sockeye salmon emigrating from rivers in the southern part of their range have lower growth rates and lower average marine survival than their counterparts in Southeast Alaska (Trudel *et al.*, 2007; Tucker *et al.*, 2009). Therefore, it is not unreasonable to consider the initial period of their postsmolt migration as a “race” northward to find better feeding conditions in coastal Alaska. The idea of a race was motivated by the observation that the fastest observed migration speeds, measured from tagged individuals of known origin, were found in the southernmost populations. Others, like the age-0.x ecotypes from the Harrison River, have evolved a very different strategy of delaying migration to the continental shelf until autumn.

3 Beyond the Continental Margin

> *"The discovery is reported to have been taken as a result of the investigations of Professor David Starr Jordan and his assistants that the refuge of the salmon between the time of spawning in the Fraser and the return to the river fully matured is ten miles off the Vancouver Island."*
>
> British Colonist, August 18, 1909

Professor Jordan was President of Stanford University and a leading ichthyologist of his generation. His ideas about salmon migration and distribution at sea (Jordan, 1888), however, reflect how imagination (or bias) can entertain such fanciful stories when adequate data are not available to challenge them.

This section focuses on what is known about Fraser River sockeye salmon biology during the period after their postsmolt year and before the calendar year when they mature. For most Fraser River sockeye salmon, this is a 12-month period of finding food, growing, and avoiding predation and disease in the Northeast Pacific. For some life history types, typically those with slower growth rates, this can be a two-, or rarely, a three-year period.

3.1 Distribution and Migration

The distribution and movement of immature Fraser River sockeye salmon at sea is the least understood of all life history phases. Sockeye salmon that were tagged at sea were rarely recovered in fisheries the following calendar year, despite a significant effort directed at catching and releasing tagged salmon (Fig. 16). In 1962, for example, four Canadian chartered salmon fishing vessels were deployed from April to July, each making about seven trips of 10 to 15 days each during spring and summer throughout the Gulf of Alaska north of 45°N and west to 160°W (Anon., 1963). Each vessel was a ~24 m purse seiner that had been re-configured to catch salmon alive with baited floating longlines. Because it was not possible to determine, at the time of tagging, whether a fish was immature or maturing, it was not possible to know if the longline catches were representative of immature sockeye salmon populations. Only when the tag was recovered did the developmental state of the fish become known. The vast majority were maturing sockeye salmon.

Fishing gears tended to be selective for maturing sockeye salmon but the winter period, when the Gulf of Alaska is almost dominated by immature individuals, is poorly sampled. The first trans-Pacific winter survey for Pacific salmon was conducted by the Fisheries Agency of Japan only as recently as 1996 (Myers *et al.*, 1996). The *Kaiyo maru,* a large research stern trawler caught only 51 sockeye salmon from 22 stations in 1996 and half of these were taken in one set in the central Gulf of Alaska. Similar results with no catch were obtained from DFO surface trawl sampling the Gulf of Alaska in four years of sampling in the 1990s (Welch *et al.*, 2002b,c).

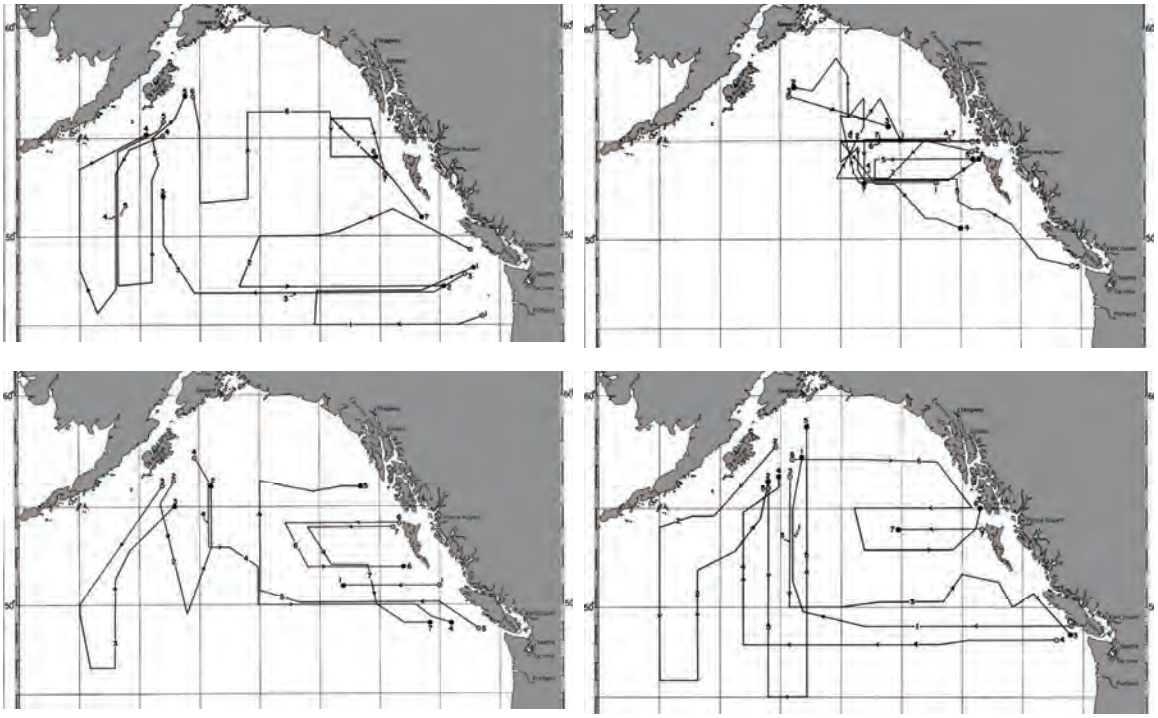

Fig. 16 Cruise tracks of four vessels conducting Fisheries Research Board of Canada salmon research with floating longline gear in the Gulf of Alaska in the spring and summer of 1962.

The distribution of immature Fraser River sockeye salmon on the high seas, determined from very few tags, differs somewhat from that of maturing fish (Fig. 17). Immature Fraser River sockeye salmon generally have a more southerly distribution (French *et al.*, 1976) than maturing fish and two immature Fraser River sockeye salmon were tagged considerably farther west than any maturing fish. Some of the difference between the two groups is a result of bias introduced by tagging maturing sockeye salmon during their homeward migration when they are expected to be closer to the Fraser River compared to fish that are not on a spawning migration.

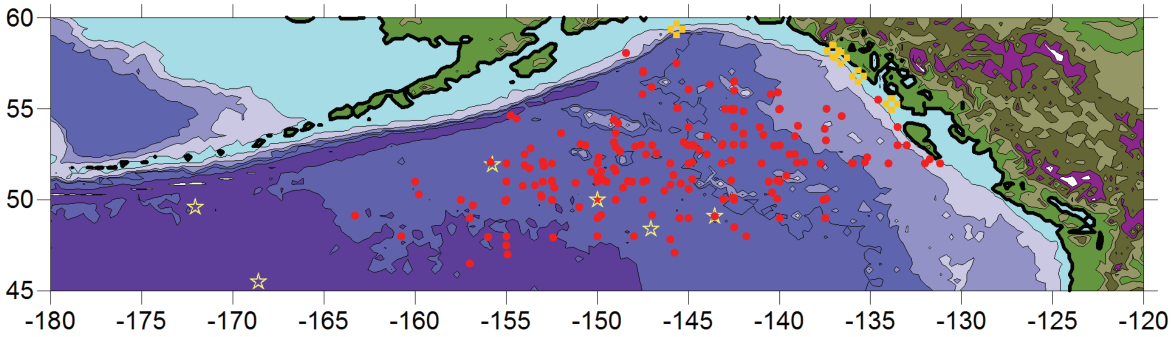

Fig. 17 Locations of sockeye salmon caught on floating longline gear, tagged and released on the high seas and subsequently recovered in Fraser River salmon fisheries. Life history stages are indicated by different symbols; red dots = maturing fish, beige stars = immature, mustard crosses = postsmolts. Database currently maintained by North Pacific Anadromous Fish Commission, Vancouver, B.C.

The feeding migrations of immature sockeye salmon are not well known because there are few direct observations (Royce *et al.*, 1968). Winter observations are rare so the period between postsmolt and immature is one of the least well known. Models of migration that involve loops around the Gulf of Alaska are among the more common because they follow the geostrophic currents (Fig. 18, Brett, 1983; Hinch *et al.*, 1995), but other models such as simple undirected swimming during the immature phase also gave satisfactory results when compared to the available data (Walter *et al.*, 1997).

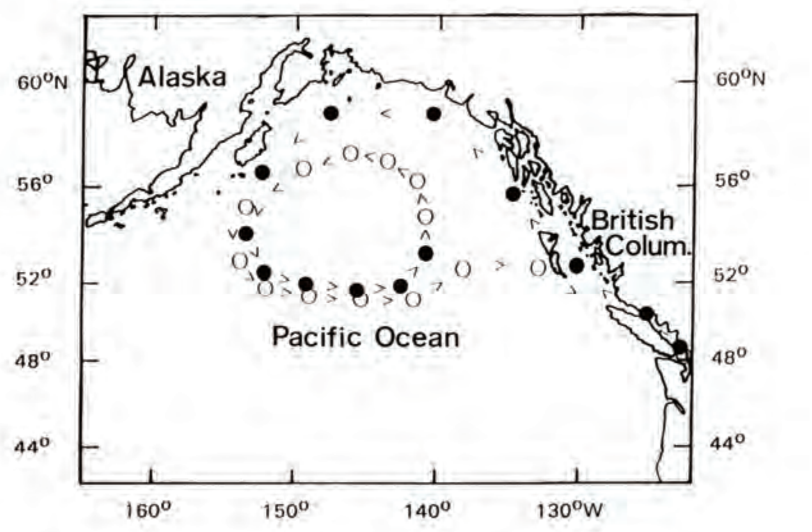

Fig. 18 Hypothetical migration of early Stuart sockeye. Closed and open circles represent the first and second year of ocean residency, respectively. From Brett (1983) in Hinch *et al.* (1995).

The general migratory routes of immature sockeye salmon at sea were not determined from tagging data alone (French *et al.*, 1976). Catches were taken by other gears for other purposes and these contributed significantly to the general understanding of the routes. However, they suffered from a lack of stock specificity. Sex and maturity were determined by visual inspection of the gonads. It is clear, however, from an examination of the length frequency data that immature sockeye salmon are under-represented in high seas catches, even when non-selective fishing gears (multi-mesh gillnets or seines) were used (Fig. 19). On average, immature fish must be more abundant than maturing fish because the latter have experienced at least an additional year of mortality that the former have not, yet the younger/smaller fish are rarely found as the most abundant size-class in the catch. Even in 1957, when the immature phase of a very large return of Late-run sockeye salmon to the Fraser River (in 1958) was at sea, the length frequency distribution resembled that of Figure 19. Either the gear favoured maturing salmon, or the immature salmon were elsewhere. As a consequence, it appears that some aspects of this life history stage are not as well known as for maturing fish.

French *et al.* (1976) described how immature sockeye salmon were found in winter (February) in parts of the ocean with sea surface temperatures (SSTs) in the range 5.6–6.7°C, whereas maturing sockeye salmon were found where SSTs in February were 2.2–4.4°C. In more contemporary sampling by Japanese research vessels to 2002, Nagasawa and Azumaya (2009) found that most age-x.1 sockeye caught in the North Pacific in June were immature and were found where the long-term average SSTs were in the range 5–8°C. The Gulf of Alaska was not sampled well during these surveys in June and long-term average temperatures there were higher. In July, immature sockeye salmon were found mainly along the Aleutian archipelago (probably Alaskan sockeye) and in the Gulf of Alaska (mixture of origins) at SSTs <12°C. The Gulf of Alaska was not sampled in August in Japanese research vessel surveys from 1972. The extent to which these temperature and abundance patterns applies to Fraser River sockeye salmon cannot be determined from these data.

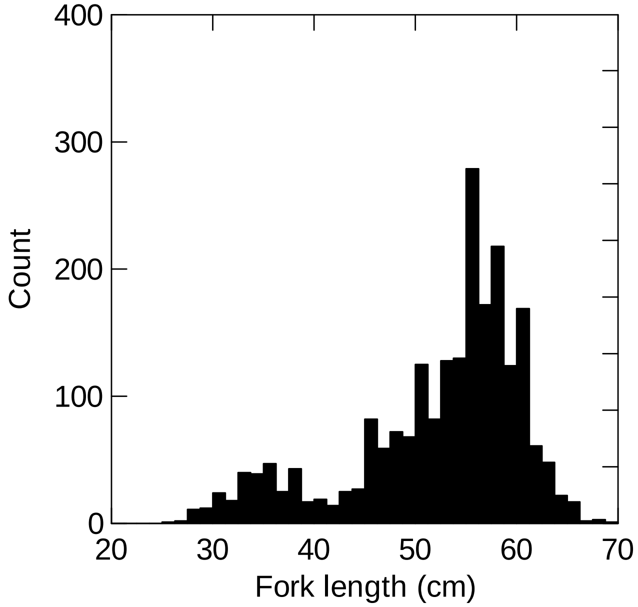

Fig. 19 Fork length distribution obtained from sockeye salmon caught multi-mesh gillnet sets in the Gulf of Alaska from 1956 to 1958. Data from Neave and Manzer (1957) and Manzer and Neave (1958, 1959).

While the general model of the distribution of sockeye salmon places them mostly offshore in their first year as immatures (Fig. 20), one cruise in late April to early May of 1998 (Fig. 21) found small (20–30 cm) immature sockeye salmon aggregated within 6 nmi of shore in the southeastern Bering Sea (Carlson *et al.*, 1998). This was the first such observation for the southeastern Bering Sea. The origins of these fish are unknown.

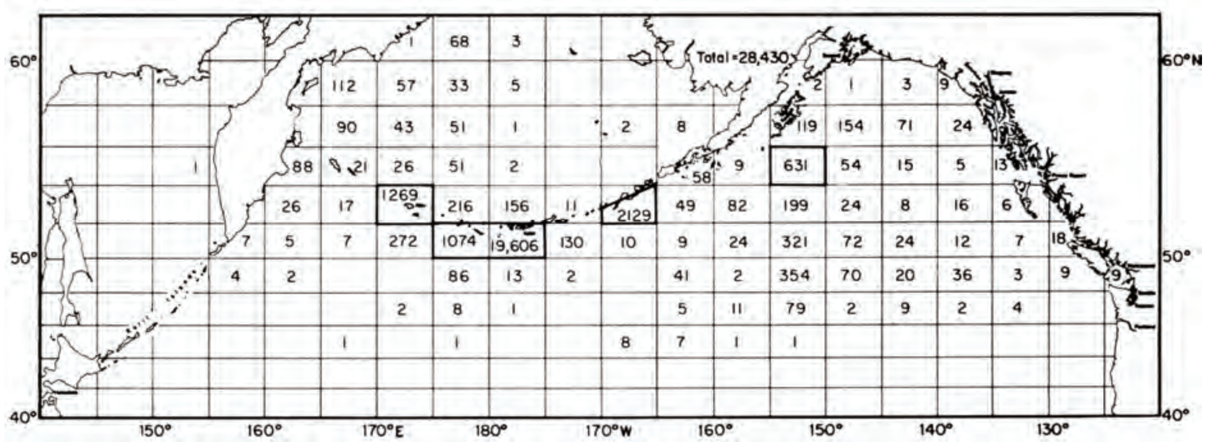

Fig. 20 Distribution of tagged age-x.1 sockeye salmon (nearly all immature) from 1956 to 1970. Areas with >500 fish tagged are outlined in bold. Reproduced from French *et al.* (1976).

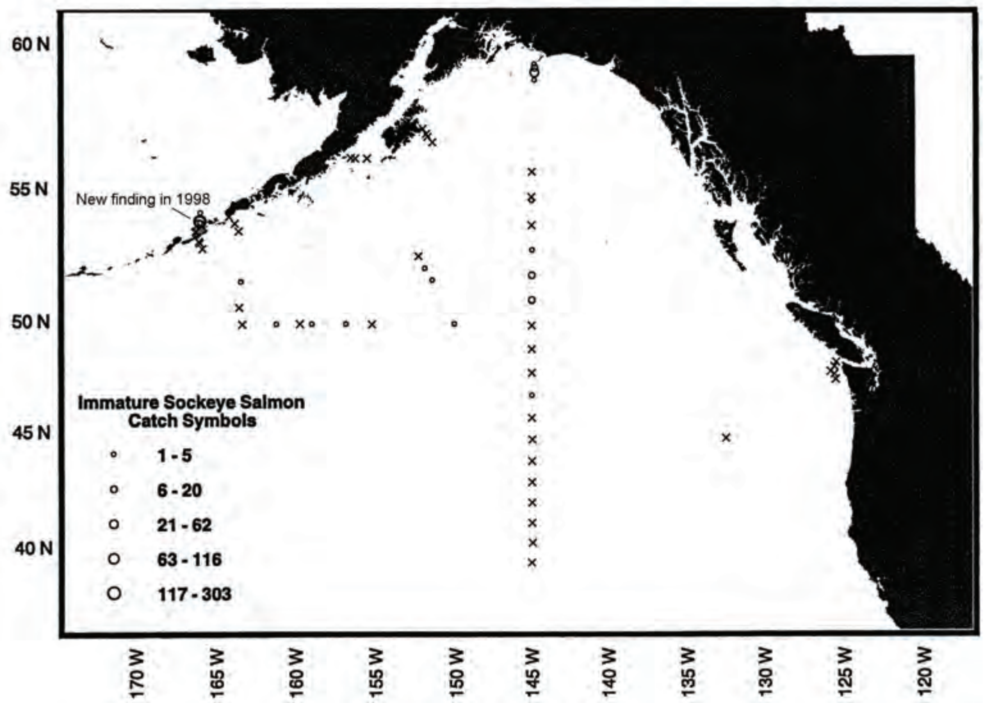

Fig. 21 Distribution of fishing stations (x) and catches of immature sockeye salmon in the Gulf of Alaska in spring 1998. Figure from Carlson *et al.* (1998).

Summary – From 1956 to 1970, 28,430 tags were applied to age-x.1 sockeye salmon and a Pacific-wide total of 150 of these tags was recovered (0.5%). The distribution of immature Fraser River sockeye salmon at sea is poorly known because so few tags have been recovered from these fish. A combination of factors is probably responsible for poor recoveries of immature sockeye: tagging mortality, high seas fisheries during that era, and natural mortality before maturing. Certainly, some postsmolts are known to follow the continental shelf. If all of them have this behaviour, it would place greater numbers of immature salmon in the western Gulf of Alaska by the end of the postsmolt migration. Indeed, the greatest number of tags applied to immature sockeye salmon of all origins in the Gulf of Alaska occurred south of Kodiak. As Alaskan sockeye salmon are known from this region, a significant fraction may have that origin. The fraction of westward migrating Fraser River sockeye salmon that leaves the shelf before reaching the western Gulf of Alaska is unknown. Neither gillnets nor longlines capture immature sockeye salmon in relation to their abundance. On average, it must be greater than the abundance of maturing fish because of the mortality that occurs in the year(s) between immaturity and maturity. However, most length frequency plots of sockeye salmon taken on the high seas feature a greater abundance of older fish (Fig. 19), so it is not unreasonable to assume that certain aspects of the distribution of this life history stage in the sea are known rather poorly.

3.2 Behaviour

Knowledge of the behaviour of immature sockeye salmon on the high seas has, for the most part, been obtained by catching salmon and inferring behaviour from the observed patterns in the catches. A potential explanation for the under-sampling of immature sockeye salmon in high seas catches (Fig. 19) is that they behave differently from maturing individuals, and as a result, are not equally vulnerable to the fishing gear.

Gillnet and floating longline are passive devices that require fish movement past the gear (directed in the case of gillnet) or feeding behaviour. The floating longline may also be selective for certain sizes of fish because of hook and/or bait size (Ralston, 1990). The purse seine, on the other hand, could potentially capture all size-classes if the immature and maturing fish occupy the same space.

Direct comparisons of the fishing characteristics of each gear at the same time and location in offshore waters are few. On May 26, 1964, a comparison of only longline and purse seine was conducted in INPFC area W5048 (between 48–50°N and 150–145°W). Immature sockeye salmon (~33 cm average) were fewer than larger individuals in both gears and the largest mode was represented in the longline but not the purse seine (Fig. 22). Potentially, immature fish are routinely under-represented in the seine gear in this region but this cannot be determined from one day of fishing. That the purse seine did not catch fish in the largest mode was attributed to their having set the net in only three of four compass directions during the experiment (Hartt, 1975). The inference is that they would have caught the larger mode if the 4th compass direction was sampled.

> *"a difference in behavior of a particular component of the stock that affected its availability to the gear could cause a serious bias in the composition of the catch."*
>
> Hartt, 1975

The same logic, turned around, may indicate that bias in the catch composition suggests that different components of the stock behave differently. How differently has yet to be fully examined.

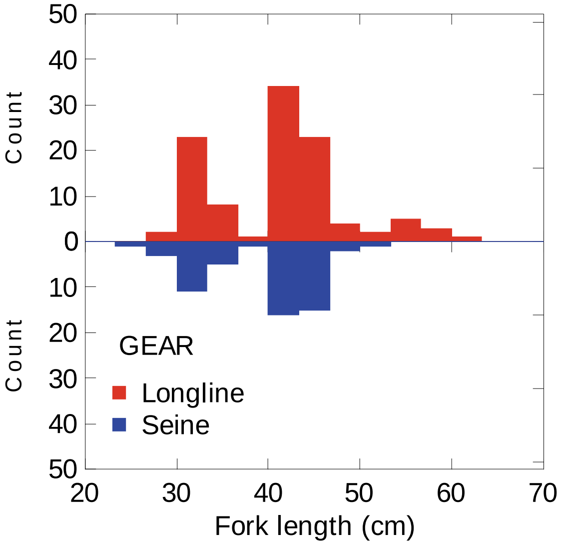

Fig. 22 Fork lengths of 167 sockeye salmon caught offshore in the Gulf of Alaska on May 26, 1964 during an experiment to compare the characteristics of seine (three sets combined) and longline gear (one morning set of 20 skates). Data from Hartt (1975).

Summary – The best evidence that immature sockeye salmon behave differently from maturing sockeye salmon it that they are not caught in adequate abundance in the gears typically deployed to catch them (purse seine, gillnet, longline). Multi-sized mesh gillnet and purse seine were thought to be non-selective. Immature salmon may lack the property of rapid and directed migrations that maturing salmon appear to exhibit. They have lower growth rates (Ishida *et al.*, 1998) than maturing fish and therefore, less energetic requirements. Immature sockeye salmon potentially have no need to maintain a near-surface distribution for orientation during migration so they may not be exposed equally to the floating longline bait. The nature of the behaviour difference is mostly a matter of speculation.

3.3 Feeding

> *"Nothing is known of their feeding-grounds in salt water as they [sockeye] are never found in the bays and inlets which distinguish the coast and where the spring and coho are so common. It is thought that their feeding-ground must be in the open sea."*
>
> Anonymous, 1911

Salmon on the high seas forage opportunistically with stomach contents often related to oceanic domains and availability of certain prey types (Pearcy *et al.*, 1988; Kaeriyama *et al.*, 2004). The first samples of sockeye salmon stomach contents from the Gulf of Alaska were collected by the Fisheries Research Board of Canada during a gillnet survey in the summer of 1958 (LeBrasseur, 1966). Immature fish were identified by visual inspection of the gonads. The most noteworthy characteristic of the stomach contents of immature sockeye salmon was the small amount of material found in the stomachs. Amphipods, euphausiids and squid contributed the most. LeBrasseur (1966) commented that there was a much greater difference in stomach contents among oceanographic domains than among species. Stomachs collected from salmon in the Alaskan Stream were dominated by fishes while those taken in the Subarctic Gyre were mostly squid.

A more complete analysis of the stomach content data that were collected from 1956 to 1964 (Table 2) considered the effects of SST, body weight, latitude, longitude, year, day of year, and time but they were able to describe only small amounts of variation in feeding probability (13%) and stomach fullness (16%) (Rand, 2002). The lengths and weights of these fishes reflect the multiple age-classes and their seasonal changes in the samples (Figs. 23 and 24). In this analysis, all individuals >500 g were pooled as "sub-adults" regardless of whether they would or would not mature in the upcoming summer, and there was no accounting for differences that might exist among stocks. LeBrasseur's comments, above, suggest that immature and maturing sockeye salmon have different feeding behaviours. Despite these shortcomings in the analysis, in the pooled results Rand (2002) found that the feeding and growth indices he developed were variable in space and time in the Gulf of Alaska. There was a negative association between increasing SST and feeding probability (determined from presence/absence of contents in stomachs) but stomach fullness increased in warmer SST. Feeding probabilities of larger sockeye salmon were higher in winter and spring and lower in summer. The lower feeding probability in larger sockeye salmon was interpreted as evidence of anorexia prior to the spawning migration (Rand, 2002) but the timing of the onset of anorexia is not well documented. He determined that there was a tendency for larger sockeye salmon to be caught farther north than smaller sockeye salmon in the winters of 1963 and 1964 (combined). There was a tendency for larger sockeye salmon to be caught further north in the spring of 1962. He also found that in both the springs of 1962 and 1963 there was a sharp reduction in his growth index along the southern Gulf of Alaska.

Table 2 Total numbers of immature sockeye salmon stomachs examined by the Fisheries Research Board of Canada from 1956 to 1964 by year and month.

Month	1956	1957	1958	1959	1960	1962	1963	1964	Total
1	0	0	0	0	0	0	37	35	72
2	0	0	0	0	0	0	1	11	12
4	0	0	0	0	0	11	69	0	80
5	9	3	70	29	0	14	93	0	218
6	1	132	39	177	2	78	0	0	429
7	49	113	0	19	7	18	0	0	206
8	0	17	4	0	0	0	0	0	21
11	0	0	0	0	0	0	3	0	3
Total	59	265	113	225	9	121	203	46	1041

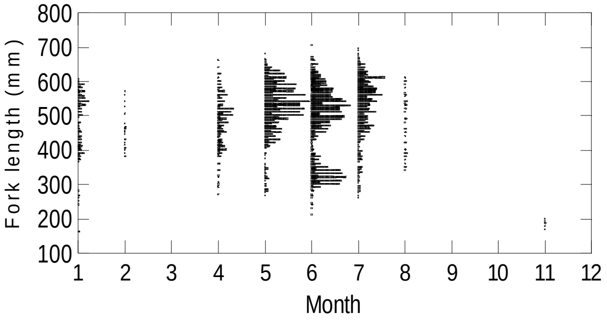

Fig. 23 Fork lengths (mm) of sockeye salmon taken by multi-mesh gillnets and floating longline gear in the Gulf of Alaska from 1956 to1964 that were examined for stomach contents. Samples in November were collected by mid-water trawl net in Hecate Strait.

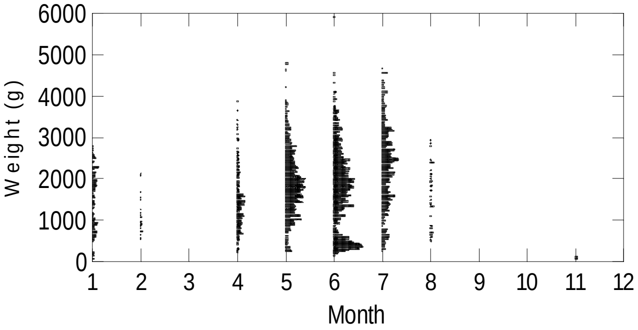

Fig. 24 Body weight (g) of sockeye salmon taken by multi-mesh gillnets and floating longline gear in the Gulf of Alaska from 1956 to 1964 that were examined for stomach contents. Samples in November were collected by mid-water trawl net in Hecate Strait.

In 1981, a joint Hokkaido University–Oregon State University study of diel feeding patterns was conducted during a 24-h period from July 13–14 on board the T/V *Oshoro maru* in the Subarctic Gyre between latitudes 54° 51.5′ and 54° 57.9′N, and longitudes 144° 55.1′ and 145° 11.3′W (Pearcy *et al.*, 1984). Two gillnets, each 800 m long and 6 m deep, with 300 m of 115-mm, 250 m of 121-mm, and 250 m of 130-mm (stretch) mesh, were alternately fished throughout the period. The total catch of sockeye salmon was the largest in night sets, as was the fraction of the catch taken in the uppermost part of the net. Prey composition for sockeye salmon had a diel pattern with euphausiids (predominantly *Euphausia pacifica* and *Thysanoessa longipes*) dominating at night (Pearcy *et al.*, 1984). Other common prey of sockeye salmon during this study were amphipods and fishes. Squids were more common in the afternoon/evening. Copepods formed <1% of the diet.

Kaeriyama *et al.* (2004) conducted an evaluation of salmon diets from 1994 to 2000 but did not distinguish between immature and maturing individuals. The stomach contents of sockeye, pink and chum salmon tended to be zooplankton during this period while the other species of salmon fed on squid and fishes.

Summary – Samples of stomach contents of sockeye salmon in the Gulf of Alaska were collected from 1956 to 1964. The results of a single year of sampling (1958) were published in 1966 (LeBrasseur, 1966). As there was a large return of Adams River fish in that year, it might be reasonable to assume that some of these fish were of Fraser River origin. Data from samples collected in the Gulf of Alaska in 1962 and 1963 were reported in 2002 (Rand, 2002) but this study did not distinguish between immature and maturing salmon although it did consider the effect of size (fork length) which can be a correlate of maturity at some sizes. Lebrasseur (1966) drew attention to how little material was found in the stomachs of immature sockeye salmon compared to maturing fish.

3.4 Growth

Stage-specific growth of individual immature Fraser River sockeye salmon can be measured from the amount of growth that occurred between the first and second marine annulus on fish scales (Fukuwaka and Kaeriyama, 1997), but this measurement was not made routinely, except during a brief period in the 1960s by the Stock Assessment Authority of the Fisheries Research Board of Canada. The growth of immature sockeye salmon can be measured on individual fish that were tagged as postsmolts and recovered at sea the following year (or more for fish older than age-1.2). Generally, fork length measurements will have been made on the latter, but they are so few that a representative estimate of the growth of immature sockeye salmon will not be possible. Furthermore, the stock of origin of these tagged fish will not be known.

3.4.1 Density-dependent growth (intra-specific)

Intra-specific density-dependent growth of Fraser River sockeye salmon during their immature year in the Gulf of Alaska has not been studied. However, it is known from other British Columbia sockeye populations that the largest correlations in mean fork length among different stocks are found in fish maturing in the same year. The mean size of returning adults in a cohort of sockeye salmon with a common ocean-entry year, but different return years, is uncorrelated (Godfrey, 1958; McKinnell, 1995). Examining immature Fraser River sockeye salmon for the property of density-dependent growth, in relation to salmon abundance (various species), will require annual measurements of mean growth from scales but this is not done routinely. One study examined annual growth variation in the Early Stuart stock (Fig. 25) and found that variations in the amount of growth in any year by a given fish is uncorrelated with the amount of growth observed at other ages for the same fish (Welch, 1997). The implication is that there is no persistence of faster or slower growth within individuals of a given stock. It was also found that the factors affecting growth in different years were correlated, suggesting that the oceanic factors affecting growth are stochastic rather than autocorrelated on an annual basis (Welch, 1997).

Long-term trends in growth of the Early Stuart stock were largely confined to postsmolts or maturing sockeye salmon (Welch, 1997). This was interpreted to mean that the coastal zone is food limited, *i.e.*, the increased salmon abundance that was observed at the time may have resulted in increased trophic competition in coastal waters. Long-term trends in growth were largely absent among immature stages in offshore regions for M2 in age-1.2 and -2.2. individuals, and M2 and M3 growth for age 1.3 individuals (see Figure 25 for definitions of M1 to M4).

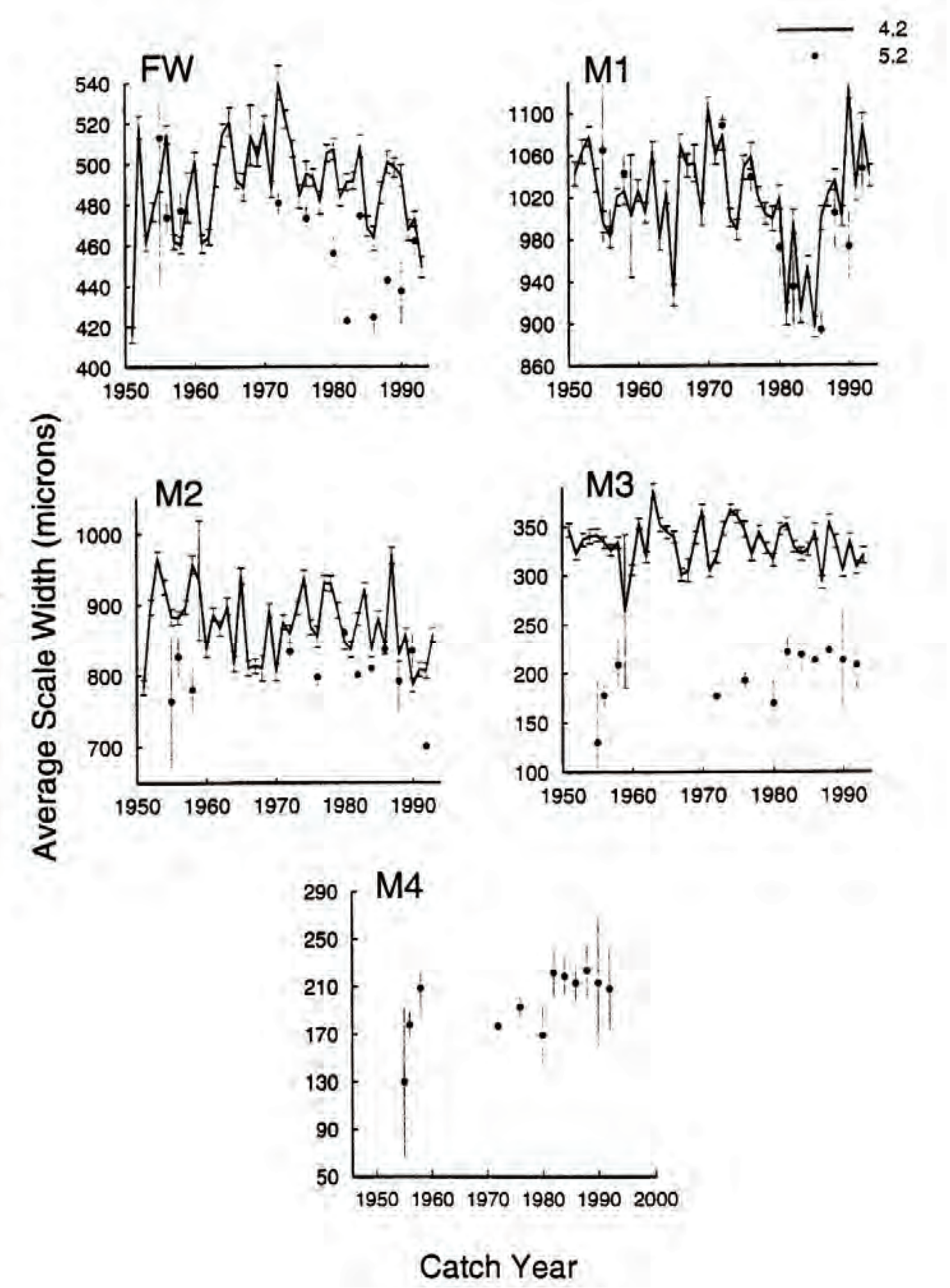

Fig. 25 Stage-specific variation in marine growth by year for the Early Stuart stock of Fraser River sockeye salmon. M1 to M4 indicates the years at sea. FW = freshwater, M1 = postsmolt, M2 = immature (mature for jacks), M3 = maturing year (age-1.2) or immature year (age-1.3) and M4 = maturing year (age-1.4). The pattern of variation at different ages is uncorrelated. Solid circles indicate fish that matured as age-1.3 and solid lines indicate fish that matured at age-1.2. Figure from Welch (1997).

Summary – Generally, the increase in fork length or mass of immature sockeye salmon is less than that of maturing sockeye salmon (Ishida *et al.*, 1998) because the immature fish do not have the joint energetic demands of a spawning migration and maturation. Maturing fish of the same length as immature fish tend to weigh more. Some measurements of annual growth of Fraser River sockeye salmon, determined from scale growth, exist but they are relatively rare.

3.5 *Thermal Limits to Oceanic Distribution*

In the 1990s, when the spectre of global warming began to feature more prominently in scientific discussion, a *thermal limit* hypothesis for Pacific salmon distribution attracted some attention (Welch *et al.*, 1995). The hypothesis followed from a report that the southern limit of Pacific salmon in the North Pacific Ocean is determined by the temperature of the surface waters. It argued that there are abrupt thermal limits to their horizontal distribution. The thermal limits in spring in the northeastern North Pacific were 8.9°C for sockeye salmon, 9.4°C for coho salmon, and 10.4°C for pink and chum salmon, although "spring" was not defined. This conclusion was followed by a more speculative paper (Welch *et al.*, 1998) showing how increasing concentrations of greenhouse gases in the atmosphere would lead to global warming which would raise near-surface ocean temperatures in the North Pacific, restricting the spatial distribution of Pacific salmon in July to a region of the northern Bering Sea, about 1300 km more northerly than latitudes they currently occupy (Fig. 26). The following material examines the thermal limit hypothesis using Intergovernmental Panel on Climate Change 4th Assessment Report (IPCC AR4; 2007) projections of SST in the North Pacific and salmon distribution data that were not available when the hypothesis was developed.

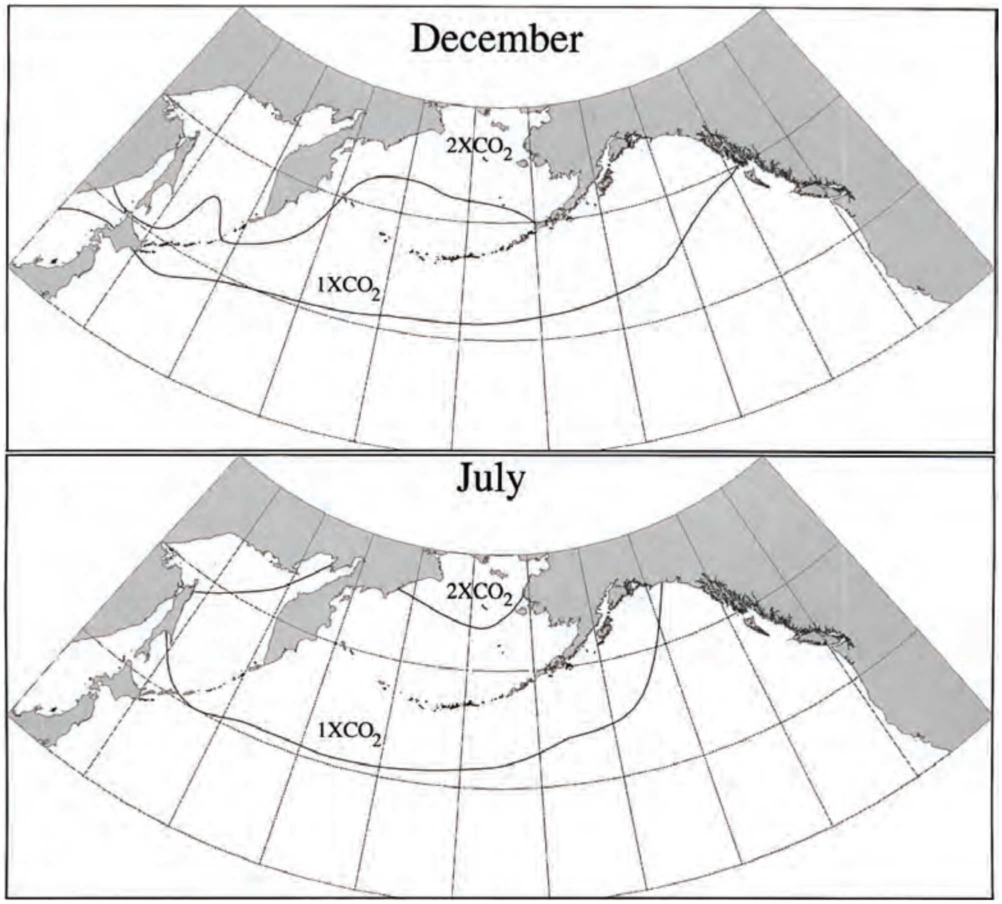

Fig. 26 Comparison of the predicted winter (7°C) and summer (12°C) positions of the sockeye salmon distribution under current and future climates. With a doubling of atmospheric CO_2, the area of acceptable thermal habitat in the North Pacific is predicted to decrease to zero in summer and decline sharply in winter. Figure from Welch *et al.* (1998).

3.5.1 Sockeye salmon in waters exceeding thermal limits

A survey to test the thermal limit hypothesis was conducted in March–April of 1995 (Welch *et al.*, 2002a). The 10.2°C isotherm was the hypothetical upper limit to salmon distribution. During the survey, 22 sockeye salmon were caught in two of a total of 44 tows that were distributed around the eastern Gulf of Alaska. No salmon of any species were caught at 75% of the stations. The survey was repeated in October–November of 1995 with essentially the same result: no salmon were caught in the Gulf of Alaska beyond 250 km from shore (Welch *et al.*, 2002b) although many (3,582) were caught on the shelf and 97% of these at bottom depths <200 m. After four years of catching no salmon in the deeper waters of the Gulf of Alaska, these offshore surveys were discontinued around 1998 (Welch *et al.*, 2002c). A number of explanations, some more plausible than others, come to mind for the lack of salmon: (1) the surveys were not conducted at locations where Pacific salmon occur, (2) the salmon were at depth beyond the reach of the surface trawl, or (3) the abundance of salmon was too low to be taken in the sampling conducted.

Welch *et al.* (1998) established the 12°C isotherm in July as a thermal limit to Pacific salmon distribution. The movement of this isotherm northward with global warming was hypothesized to restrict their distribution northward, eventually into the northern Bering Sea (Fig. 26). The ten warmest years (area-weighted average of gridded data within the bounds <160°W, >50°N) in July in the Gulf of Alaska were, in descending order: 1997, 2005, 2004, 1888, 1936, 1958, 1957, 1941, 1885, 1993). In some of these years, the T/V *Oshoro maru* made regular cruises to the Northeast Pacific. Until 2002, scientific activities in the region included the deployment of surface gillnets of varying mesh sizes during the night. The warmest years when the *Oshoro maru* was operating in the Gulf of Alaska were 1997, 1993, and 1983 but the ship cruise tracks in the Gulf of Alaska differed significantly among years. The only cruise with a north–south transect that spanned the hypothetical limit of 12°C was in 1997 (the warmest year). Sockeye salmon catches in July 1997 were more abundant at temperatures greater than the thermal limit (Fig. 27).

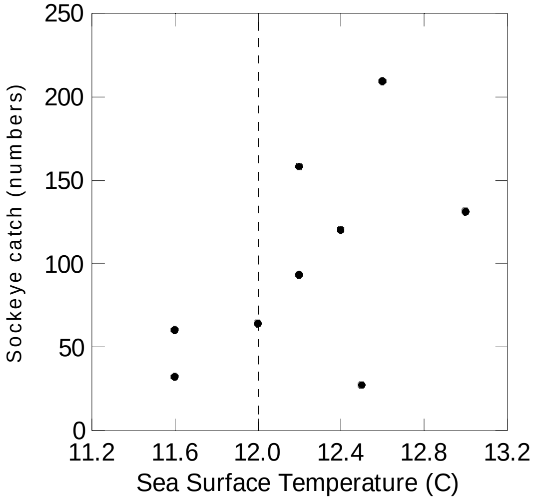

Fig. 27 Numbers of sockeye salmon caught in nightly gillnet sets by the T/V *Oshoro maru* at different stations along 145°W from July 3 to 12, 1997 *versus* SST measured at the stations. Vertical dashed line indicates the temperature of the Welch *et al.* (1998) thermal limit in July beyond which sockeye salmon should not be found.

During the latter half of the 1950s and in the 1960s, the Fisheries Research Board of Canada's North Pacific Survey conducted high seas fishing with gillnets and longlines throughout the Gulf of Alaska. Primary fishing stations were 50°N 155°W, 55°N 155°W, 50°N 145°W, 55°N 145°W, 58°N 145°W, 50°N 135°W, and 55°N 135°W. In 1957, for example, a total 997 sockeye salmon of unknown origin were caught in 71 nights of fishing. As the period of fishing extended from May until August of that year, it is possible to examine the relationship between the hypothesized thermal limit and sockeye salmon catches in the Gulf of Alaska. A two-sample Kolmogorov-Smirnoff test can be used to identify differences between catches above and below the hypothesized thermal limit. It indicated that there was no significant difference (P > 0.97) in the frequencies of sockeye salmon catches above and below the hypothesized thermal limit (Fig. 28).

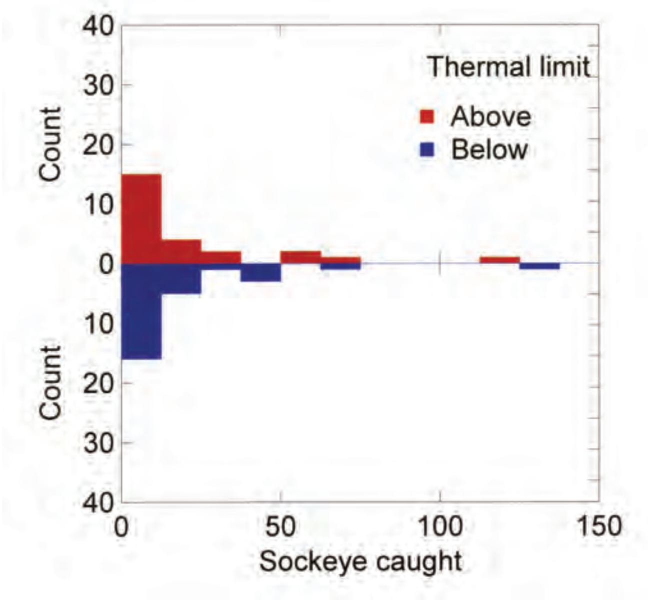

Fig. 28 Sockeye salmon caught above and below 12°C during exploratory fishing for salmon throughout the Gulf of Alaska, May to August 1957.

If the 12°C SST isotherm represents a physiological barrier to sockeye salmon distribution, they could not have reached the eastern Gulf of Alaska and its major southern sockeye salmon rivers (Skeena, Fraser, Columbia) in most years. From 1982 to 2009, surface waters >12°C in July occupy much, and in some years, all of the eastern Gulf of Alaska. In warmer years like 1997, 2004, and 2005, the northward (and westward) intrusion of the 12°C isotherm along the coast can extend past Kodiak Island (Fig. 29). In cold years, the 12°C isotherm extends in July only as far north as Haida Gwaii. Why 12°C should form a southern limit but not an eastern or northern limit is not explained by the hypothesis.

An alternative thermal response behaviour, where salmon might restrict their vertical migration to a few metres lower in the water column where water temperatures cool rapidly, was considered by the authors to be a novel behaviour that would not likely be adopted, even though this behaviour is used routinely by sockeye salmon fry in lakes (Levy, 1987; Clark and Levy, 1988; Schuerell and Schindler, 2003). Rand (2002) argued that the reduced abundance of sockeye salmon along the southern periphery of the Gulf of Alaska was equally likely to be explained by a sharp reduction in growth potential rather than a behavioural response to SST proposed by Welch *et al.* (1995). He described a sharp decline in both feeding and growth of sockeye salmon in 1962 and 1963 in a region south of 52°N. The part of the Gulf of Alaska from 55°N to 58°N was most favourable for sockeye salmon growth in these years. The growth potential dropped by one order of magnitude with a change in SST from 6 to 7°C.

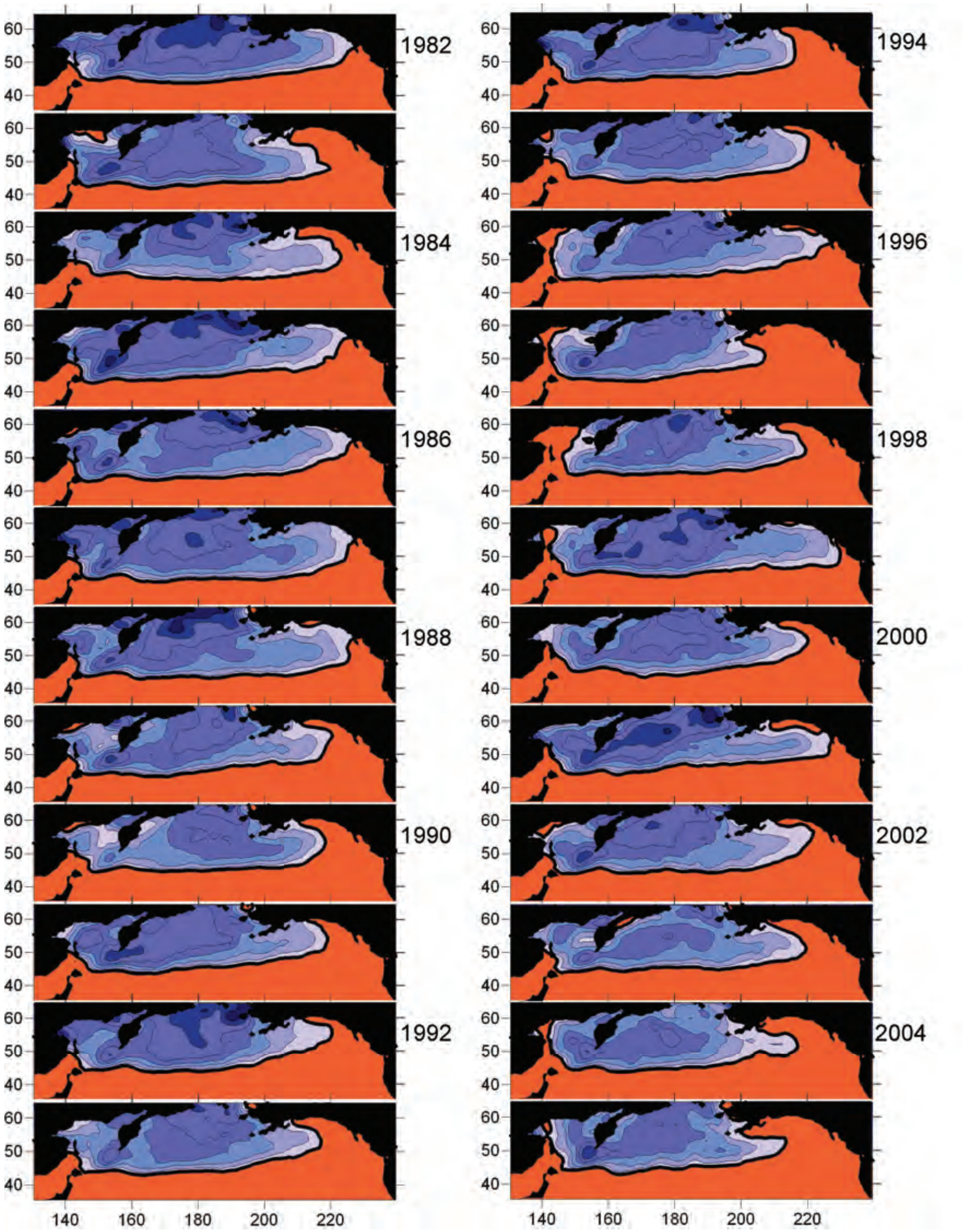

Fig. 29 Sea surface temperature contours for the month of July from 1982 to 2004 in the Gulf of Alaska. The thick contour indicates the 12°C isotherm and all regions warmer than that are coloured in red. Data are from the U.S. NOAA OIv2SST monthly gridded data.

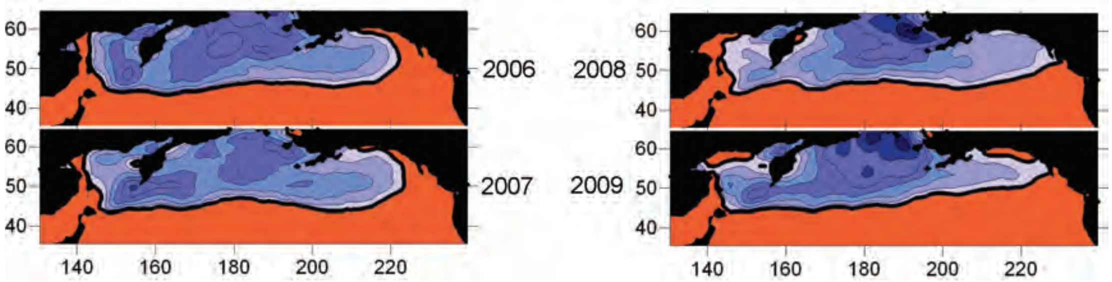

Fig. 29 Continued, 2006 to 2009.

3.5.2 Global climate model projections

IPCC AR4 (2007) model expectations for the future state of average July SST in the North Pacific are different from what was published over a decade ago, and was used to consider the future state of sockeye salmon distribution (Fig. 26). The IPCC A2 scenario (Fig. 30) anticipated a doubling of atmospheric CO_2, from late 20th century concentrations, by the mid-2080s. Four models (hadcm3, cccmat47, gfdl2.1, and mirocM) were selected for examination because they have a better representation of North Pacific SST variability (Wang *et al.*, 2010). For each model, the 10-year average July SST in the 2080s was computed from the average of 10 years of SSTs during the 2080s. Smoothing of the average SSTs was done by the kriging algorithm using the contouring package SURFER™.

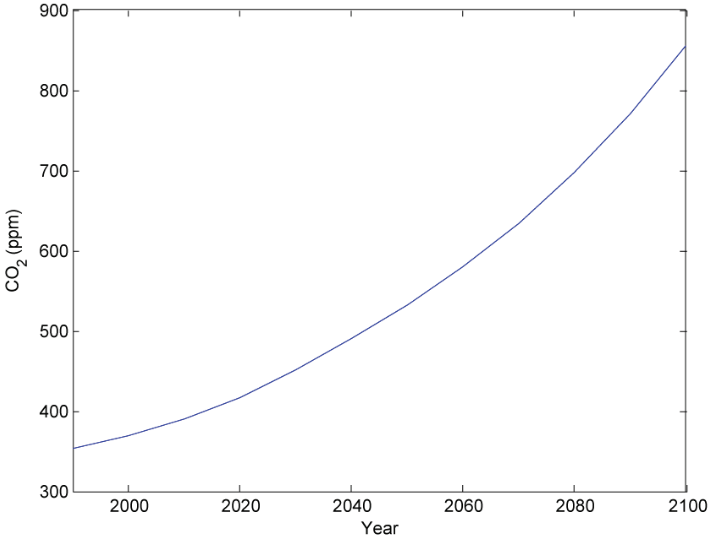

Fig. 30 Projections of atmospheric CO_2 concentrations under the A2 scenario (business as usual scenario).

With the exception of mirocM, these models suggest that, on average, SSTs <12°C will not be a significant part of the Gulf of Alaska at twice the late 20th century CO_2 concentrations (Fig. 31). However, none of these models yields a northward shift of the 12°C SST isotherm as extreme as was reported by Welch *et al.* (1998; see Figure 26). Each of these IPCC models has a region of the North Pacific, south of the Aleutian archipelago, with waters <12°C. It is worth remembering that these models are computed on a relatively coarse grid compared to the small- to meso-scale physical processes that can affect SSTs, especially on the continental shelves where these models are not expected to perform well.

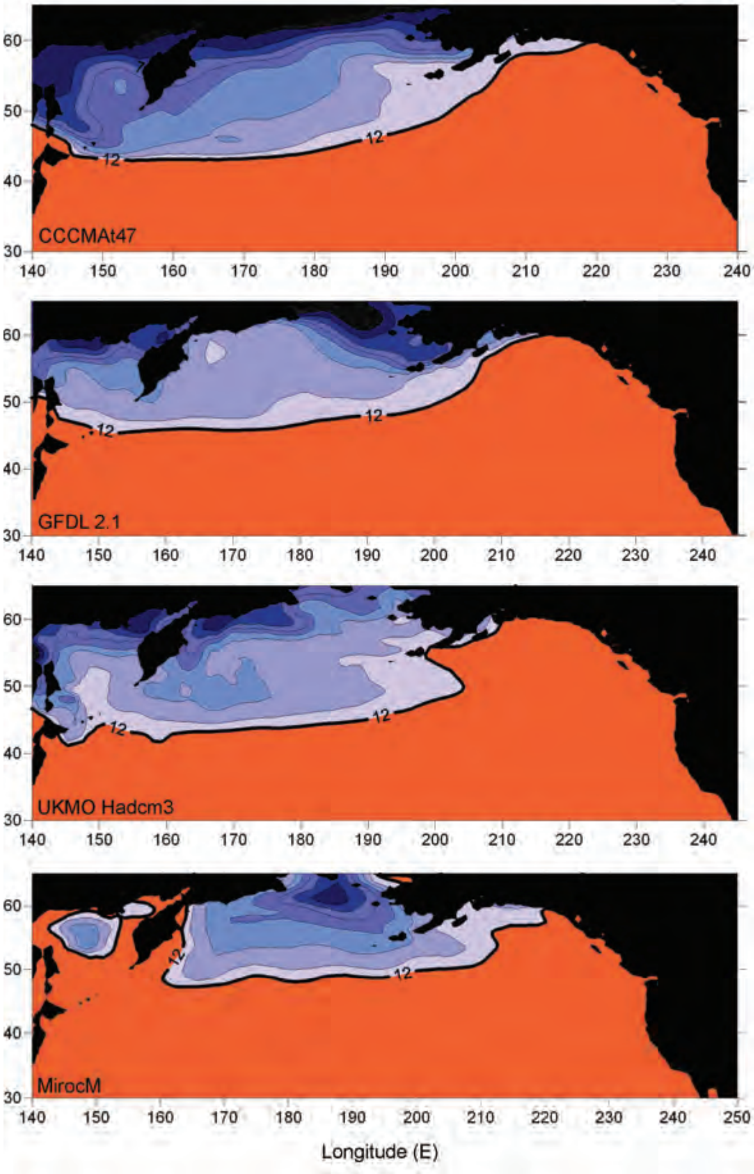

Fig. 31 Average location of the 12°C surface isotherm in the North Pacific Ocean in the 2080s based on output from four IPCC models (named in lower left of each panel). Red coloured regions exceed 12°C and contour intervals less than 12°C are spaced at 1°C.

What are currently considered July SST extremes at the beginning of the 21st century will become approximately the average state of nature with a doubling of CO_2 concentrations, according to these four models. The Julys of 1997 and 2005 (Fig. 29) were relatively extreme years of widespread strong, positive SST anomalies and they bear a qualitative resemblance to the projected average SSTs in the late 21st century, under scenario A2. Both of these years coincided with relatively strong biological anomalies in Fraser River sockeye salmon. The most noteworthy were later-than-average run timing in both years (Mcdonald, 2000; PSC, 2010), although much more extreme in 2005, and high in-river mortality in 1997 (Mcdonald, 2000). The total return of 7.1 million sockeye salmon to the Fraser River in 2005 was slightly higher than forecast but that total was a result of much lower than expected abundance of the Summer run and a much higher than expected abundance of the Late run (PSC, 2010). Peak run timing to Area 20 (western end of Juan de Fuca Strait) in 2005 exceeded previous extremes by six days (Early Stuart), seven days (Summer). The average timing for

Early Summers was exceeded by 29 days. The greater issue for the Fraser River sockeye salmon return in 1997 was the high in-river mortality and migratory anomalies (McDonald, 2000). However, both of these years of extreme SST had significantly greater returns than have occurred generally in the early 21st century.

The IPCC AR4 included an analysis of many numerical dynamical models to understand the future of Earth's climate in the 21st century (IPCC, 2007). Several of the models that are known to have a better representation of the North Pacific Ocean revealed that the location of the 12°C isotherm in July under a doubling of CO_2 (by the 2180s under the A2 scenario) is significantly farther south than was anticipated in the climate model used by Welch *et al.* (1998). The modelled future state of the surface ocean in the 2180s bears a qualitative resemblance to contemporary years that were considered relatively extreme (*e.g.*, 1957, 1983, 1997, 2005). In some of these years, salmon research was ongoing in July in the Gulf of Alaska so it is possible to examine their distribution relative to the thermal limit. For the years when comparisons are possible, salmon were equally abundant above and below the proposed thermal limit. Nevertheless, very warm years tend to affect some aspects of Fraser River sockeye salmon biology, such as the extremely late return timing in 2005 (Blackbourn, 1987; PSC, 2009).

Summary – The thermal limit hypothesis (Welch *et al.*, 1995) anticipates that SST, rather than other oceanographic properties, regulates the range of Pacific salmon in the North Pacific Ocean. It proposes that global warming will move the 12°C isotherm in July to the northern part of the Bering Sea and this will restrict the geographic range of sockeye salmon in the North Pacific Ocean to a region around Bering Strait by the year when atmospheric CO_2 concentration reaches double that observed in the late 20th century (Welch *et al.*, 1998). The hypothesis is controversial because it considers that horizontal movement in space is the only option available to the salmon to avoid warmer surface temperatures. Achieving a cooler temperature by vertical movement requires only a few metres of movement whereas achieving the same degree of temperature change requires a horizontal shift of hundreds of kilometres. Sockeye salmon are known to make vertical movements in the ocean (Pearcy *et al.*, 1984) and in lakes as juveniles to avoid warm surface temperatures.

4 Maturation and Migration

4.1 Distribution of Maturing Fraser River Sockeye Salmon

A detailed analysis of the age composition of approximately 32,000 maturing sockeye salmon caught by the Japanese mothership gillnet fishery in 1961 and 1962 in the northwestern Pacific Ocean and Bering Sea led to the conclusion that homogeneous populations of sockeye salmon (based on age composition) were found within 1° × 1–1.5° lat./long. blocks (Fukuhara, 1975). At a larger scale (2° × 5° lat./long.) age composition of the catches became heterogenous. This assessment was based on samples of catches that represented 35 and 38% of the total North Pacific sockeye salmon catch in these two years. An important result of this study, with regard to what can be inferred from typical research vessel catches that deploy a small amount of fishing gear at predetermined stations in the ocean, is that they are not likely to be representative of the population of maturing sockeye salmon in the region where they were taken (Fukuhara, 1975). This potentially limits what can be inferred from high seas research sampling.

Nevertheless, most of what is known about stock-specific distributions of maturing sockeye salmon has been obtained from high seas tagging data (Myers *et al.*, 1996), although other methods involving the identification of parasites with known distributions in freshwater (Margolis 1963; Bailey *et al.*, 1988), or the characteristics of scale patterns developed in freshwater (Bilton and Messinger, 1975) have also been used with varying degrees of success. Tagging was preferred, as the stock identification tended to be less ambiguous than the other methods. The distribution of stocks in the North Pacific was a particularly important area of investigation for the INPFC, as distribution affected vulnerability to high seas salmon fishing. Less attention was given during these studies to population-specific patterns of distribution, as the members of the Commission paid greater attention to the “continent of origin” or “national” distribution of stocks on the high seas.

From 1956 to the mid-1990s, the total number of sockeye salmon tagged at sea and recovered in British Columbia and reported to the INPFC or the NPAFC (North Pacific Anadromous Fish Commission) was 1,241 (Myers *et al.*, 1996)[5]. Only four additional tags have been recovered in British Columbia since that report was written so Myers *et al.* (1996) reflect what is known at present. Tags recovered in general areas that are associated with Fraser River sockeye salmon fisheries were a result of two approaches: (1) seine sampling on the continental shelf of the Gulf of Alaska (404 recoveries), especially along the west coast of Vancouver Island, and (2) floating longline sampling throughout the Gulf of Alaska basin (426 recoveries), mainly from 1962 to 1967.

Seining along the west coast of Vancouver Island in summer will tend to direct the tagging efforts toward maturing fish making their homeward migration. Considering only those recoveries of tagged fish that were taken in Fraser River recovery areas but were tagged offshore, where both maturing and immature sockeye salmon are expected to occur, there is a noteworthy imbalance in the ratio of mature:immature tags recovered (781 ÷ 10 = 78.1). Ten tags is the total number of recoveries of immature fish that were tagged the year before maturing and 781 is the number of recoveries of fish that matured in the same year as they were tagged. On average, this ratio must be <1.0 because cohorts are always more abundant when they are younger (immature) than when they are older (mature) owing to an additional year of mortality. If Ricker’s 1976 estimate of monthly natural mortality during the last year at sea ($0.015\ m^{-1}$) is used to approximate the abundance of a maturing cohort one year before maturity, it will be about 20% larger. In nature, therefore, the ratio of mature:immature should be about 0.83 if Ricker’s estimates are reasonable. Applying these estimates to the number of mature fish recovered (781) suggests that ~940 immature sockeye salmon from British Columbia should be in the records. Where are these *missing* fish?

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[5] The results of regional tagging studies associated with the activities of the Pacific Salmon Commission (*e.g.*, North Coast tagging in the 1980s) tend not to be reported to the INPFC/NPAFC.

Perhaps it is possible to understand something of sockeye salmon biology and/or sampling at sea by considering why the ratio is >>1.0 when it should be <1.0. One explanation is the possibility that there is differential tagging mortality; *i.e.*, catching an immature sockeye salmon on the high seas (~35 cm fork length) and tagging it induces a ~100-fold increase in mortality compared with catching and placing a tag on a maturing individual (~55 cm fork length). The next idea is that mature and immature fish have different spatial distributions (including depth). Floating longlines are baited hooks that dangle 1 m below the surface of the ocean. If maturing fish are migrating nearer to the surface at twilight (when the gear is deployed) than the immature fish, the gear would tend to encounter more mature fish. Another possibility is that the hooks and bait sizes are selective (Ralston 1990; M. Fukuwaka, pers. comm.). The limited recoveries of tagged immature fish suggest a more southerly and westerly distribution of Fraser River sockeye salmon in the Gulf of Alaska but with considerable overlap with maturing fish. Another possibility for the prevalence of maturing fish in the recoveries is the behaviour of maturing fish toward the gear. The caloric requirements of growth, maturation, and migration must be significantly greater than those of growth alone. The bait (salted anchovy/herring) provides a near-surface food for the migrants that is, perhaps, of less interest to the immature fish. Recall that immature sockeye salmon caught by gillnets in the Gulf of Alaska in 1958 had relatively little in their stomachs compared to that found in the maturing fish (LeBrasseur, 1966).

4.2 Diet and Feeding of Maturing Fraser River Sockeye Salmon

The first assessment of the stomach contents of maturing sockeye salmon was conducted in the summer of 1958 (LeBrasseur, 1966). The stock of origin of these fish is unknown, but as the 1958 return of sockeye salmon to the Fraser River was one of the largest of the 20th century, it is not unexpected that some of the fish sampled will have Fraser River origins. Sockeye salmon were identified as either immature or maturing based on a visual inspection of the gonads. Sockeye salmon was the only species of five examined (others included chum, coho, pink, and steelhead) to show a significant difference in stomach contents based on the state of maturity. Maturing fish had a greater incidence of squid in the stomach than immature fish. The stomach contents of maturing sockeye salmon were predominantly euphausiids, squid, and fish (LeBrasseur, 1966).

In the Subarctic Current region of the Gulf of Alaska (47–51°N, 145–165°W) stomach contents analysis (% weight or volume) found that the major taxa were: euphausiids, copepods, amphipods, crustaceans, squids, pteropods, fishes, polychaetes, chaetognaths, gelatinous zooplankton, miscellanious other animals, and unidentified material. A stomach content index (SCI) was calculated as SCW/BW × 100 (SCW: stomach content weight, BW: body weight). Fork length data were obtained from the Hokkaido University HUFODAT database. Stomach contents data were taken from LeBrasseur (1966), Pearcy *et al.* (1988), Kaeriyama *et al.* (2004), and previously unpublished data from M. Kaeriyama for 2003–2006.

Over many years, the gonatid squid (*Berryteuthis anonychus*) was generally the dominant prey of sockeye salmon collected at the Subarctic Current area in the Gulf of Alaska (Fig. 32). This is consistent with the generally southern locations of these samples in the Gulf of Alaska. LeBrasseur (1966) reported that the proportion of squid decreased and the proportion of fish in the diet increased at the Alaskan Stream to the north. The fraction of squid in sockeye salmon stomachs was positively correlated with the SCI (Fig. 33). Although the proportion of squid in the stomachs of sockeye salmon did not have temporal trend, it was less than 50% in 1982, 1983, 2000, and 2004 (Fig. 34), suggesting that feeding conditions were suboptimal in these years.

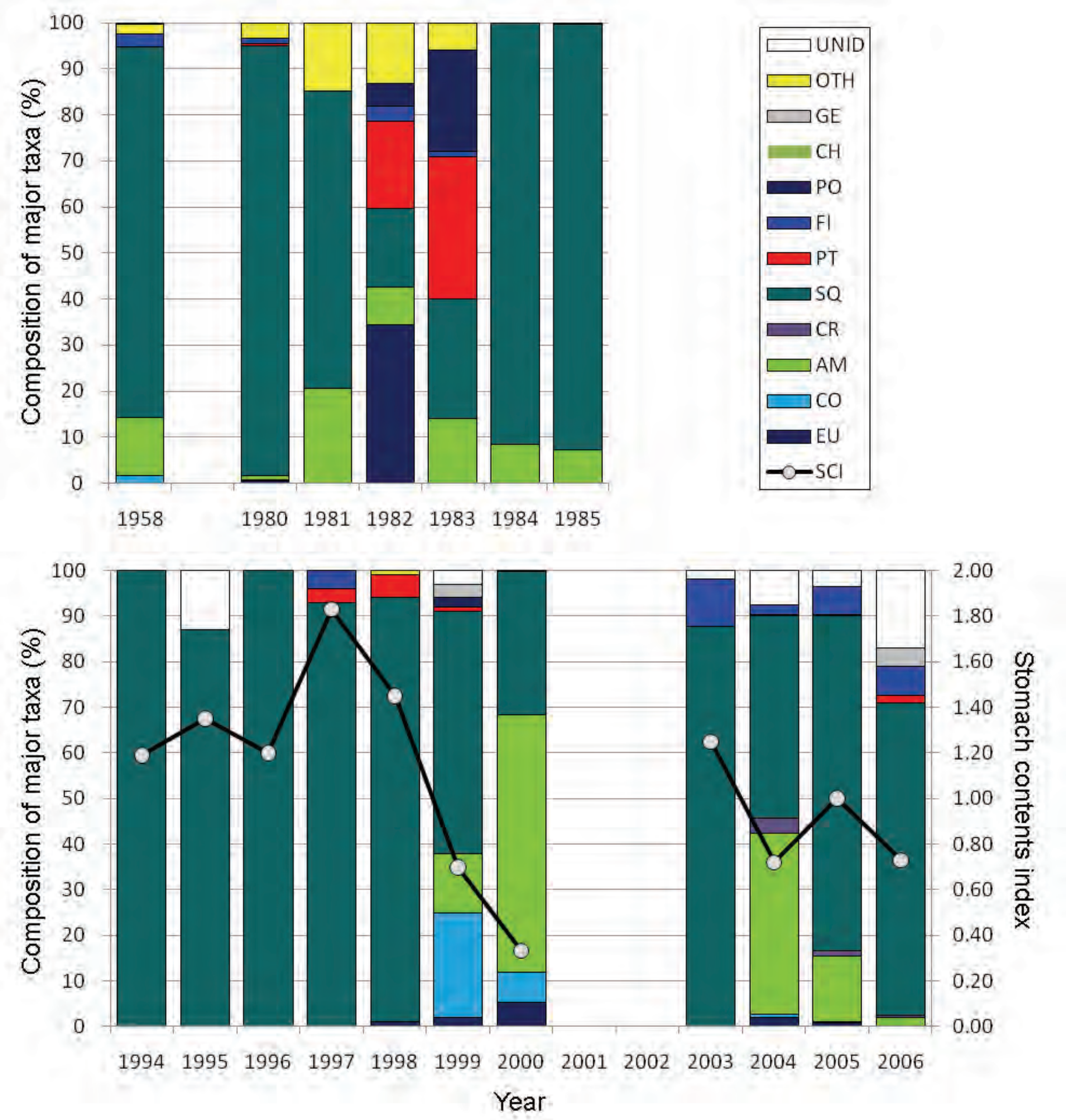

Fig. 32 Composition of stomach contents of sockeye salmon caught in the Gulf of Alaska (Subarctic Current) and the trend in the stomach contents index (see text for definition).

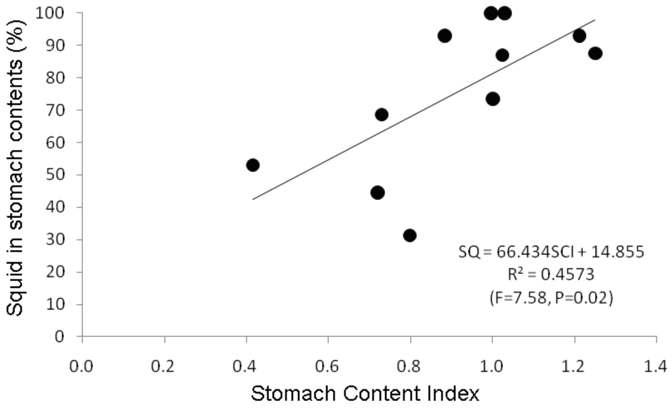

Fig. 33 Percentage of squid (by weight or volume) in the stomachs of sockeye salmon caught in the Gulf of Alaska in summer, 1980 to 2006 and 1958 *versus* the stomach content index (see text for description).

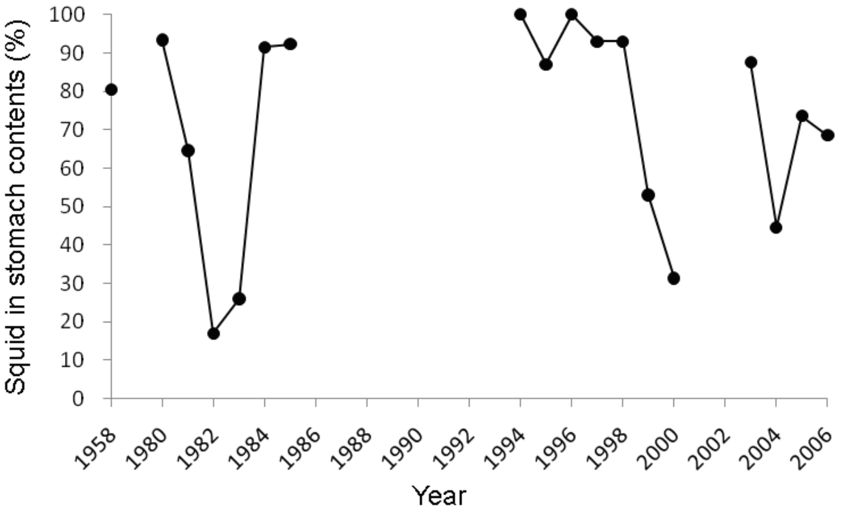

Fig. 34 Percentage of squid (by weight or volume) in the stomach contents of sockeye salmon caught in the Gulf of Alaska by year.

4.3 Growth of Maturing Fraser River Sockeye Salmon

> *"Yet it is only by tracing fluctuations in the growth of the individual from season to season that we can hope to ascertain whether such fluctuations can be correlated with each other, or with any external factors, and can also ascertain what, if any, regulatory mechanisms are involved."*
>
> Charles Henry Gilbert, 1914

4.3.1 Average size at age

At the beginning of the 20th century, it was understood that fish growth is the increase in mass (weight) of an individual fish with the passage of time, and that external factors might influence that process. It is rarely observed in nature. Occasionally, fish are tagged or marked as juveniles with marks that can be distinguished at recapture. If the mass at tagging and mass at recapture were recorded by the researchers, a measure of growth can be obtained for the interval of time that the fish was at large. In general, these data are never measured with sufficient frequency during a fish's life to understand the details of an individual salmon's growth, but there have been times in the past when the average mass of maturing salmon was measured routinely within some rivers.

The weights of individual maturing salmon were measured routinely (as was fork length) at canneries in the major sockeye salmon fisheries of British Columbia (Fraser, Rivers Inlet, Skeena, and Nass) by agents of the Province of British Columbia from 1913 to 1924 and the Biological (Fisheries) Board of Canada from about 1925. When the IPSFC was established in 1937, responsibility for biological measurements for the Fraser River was transferred to the new Commission. Routine measurement of sockeye salmon body weight and fork length were continued in the other major rivers (Smith Inlet replaced Fraser River) by the Board until the early 1970s when these responsibilities were transferred to biologists employed by the federal government department responsible for fisheries. Routine measurements of body weight of individual salmon diminished in the 1970s, and as a consequence, most contemporary studies of fish growth have considered only fish length (more easily measured) rather than mass. It is possible to obtain a reliable detailed measure of an individual fish's growth from the ring-like increments recorded in an otolith or fish scale (Fukuwaka and Kaeriyama, 1997), but this is (currently) a labour-intensive process that few agencies undertake as routine practice. Therefore, growth of sockeye salmon is assessed currently by examining the mean lengths of a population or a group of populations.

The mean fork length of Fraser River sockeye salmon caught in the fisheries has been reported routinely since the early 1900s (Gilbert, 1914). However, stock-specific measurements of fish escaping the fishery to the spawning grounds have been measured relatively consistently only since the 1950s. The fork lengths, computed as anomalies from the long-term age- and stock-specific average of stocks with the lengthier time series are shown in Figure 35. The grand means (average of mean values) of age-1.x smolts are: age-1.1 (39.8 cm), age-1.2 (54.2 cm), and age-1.3 (59.2 cm). Prior to the 1950s, the grand mean of age-1.2 sockeye salmon caught from 1914 to 1956 was 60.1 cm. The difference of –5.9 cm between the two periods (1914–1956) *versus* (1950–2009) may be the greater influence of gillnet selectivity, in addition to factors associated with abundance.

In what must have been one of the first biological samples of sockeye salmon size taken on the Fraser River, Charles H. Gilbert measured the sex and length of a sample of 500 fish collected from August 2 to 4, 1911 (Gilbert, 1912). He had just established a reliable method of determining fish age from the rings on their scales, and this was an essential prerequisite to measuring growth. Older sockeye salmon tend to be larger, but it is not diagnostic; there is considerable overlap in the size frequencies of each age-class (Gilbert, 1912). Therefore, it was necessary to understand whether a change in mean size from year to year was a consequence of interannual variations in growth, or simply a change in the age composition. A sample of sockeye salmon with more age-1.3 fish, for example, will tend to have an average mean size that is greater than a sample with a greater fraction of age-1.2 fish. The mean lengths of males in 1911 were: age-1.2 (65.0 cm, +10.2 cm), age-1.3 (67.1 cm, +7.9 cm) and of females were: age-1.2 (62.7 cm, +8.5 cm) and age-1.3 (65.9 cm, +6.7 cm). The signed values in parentheses indicate how much larger the mean values were in the 1911 sample. Some of the difference can be attributed to Gilbert's method of measuring fork length using a tape placed along the body of the salmon so the curvature of the body gives a slightly longer measure of length than that obtained by contemporary measuring boards, but this will be a relatively small adjustment.

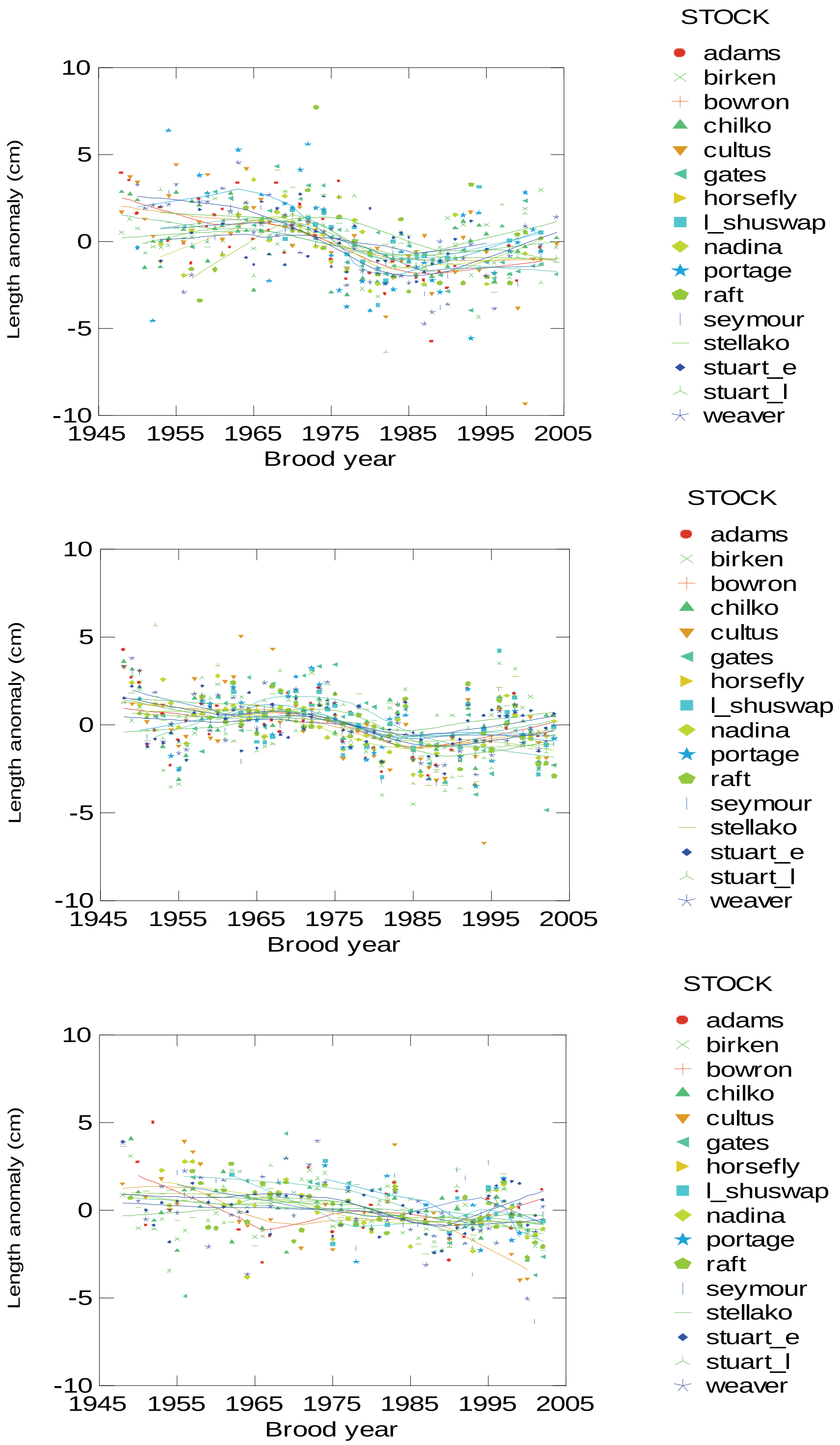

Fig. 35 Mean fork length anomalies (cm) for 16 populations with longer time series measurements for age-1.1 (top), 1.2 (middle) and 1.3 (bottom) panels. Each anomaly was computed by subtracting the long-term average, for each age and population, computed over the entire time series. The male and female fork lengths were averaged.

4.3.2 Trends

From 1952 to 1993, there was a significant linear trend (decrease) in mean size at maturity of 10 Fraser River stocks and the trend, it was felt, was due to increasing surface temperatures affecting sockeye salmon metabolism on the return migration (Cox and Hinch, 1997). Mathisen *et al.* (2007) used a subset of return years (1973–2000) and found that there was no significant linear trend in mean size of Cultus Lake, Adams River, and Chilko Lake populations, but significant declines in mean length were observed in the Nadina and Stuart stocks. However, when a more comprehensive view of the time series is considered (1952–2009 return years), it becomes evident that there is significant low-frequency variability in mean size (fork length) (Fig. 35) that is not a simple linear trend.

The grand mean fork length (across stocks) of age-1.1 jacks was above average up to the 1976 brood year (1979 return year). It dropped abruptly in the 1977 brood year, returned to average for the 1978 brood year and then remained below the long-term average until the present, except for the 1984 brood year when it was slightly above average. The 1977 brood year went to sea in the spring of 1979 and returned in the summer of 1980, so this was the first anomalous year for marine growth. Since the 1977 brood year, the overall trend in the grand mean has been positive.

The grand mean fork length of the more abundant age-1.2 sockeye salmon was near the long-term average in the early 1950s and increased through the mid-1970s to the largest mean fork length in the time series. The first appearance of an abrupt decline in mean fork length occurred in the 1976 brood year which entered the ocean in 1978 and returned to spawn in the summer of 1980. These years coincide with the return year of the first appearance of smaller-than-average age-1.1 jacks. A reasonable hypothesis for the coincident appearance of strongly smaller-than-average Fraser River sockeye salmon in two different brood years is that they were both affected by the 1979/80 ocean environment. The reduction was greater in age-1.1 than in age-1.2 sockeye salmon; the latter returned to nearer the long-term average for the late 1970s to mid-1980s when the mean fork length declined further.

From the mid-1980s, the grand mean fork length of age-1.2 sockeye salmon increased but was highly variable. In some years (1992, 1996) the grand mean was as large as the highest values seen in the mid-1970s. The general tendency from 1952 to 1993 was for Fraser River sockeye salmon to return at smaller mean size in years when the Gulf of Alaska surface waters were warmer (Cox and Hinch, 1997). A similar correlation sign was evident in subsequent data (Fig. 36) but the month of June has the strongest correlation during the recent period. The reason for the highest correlation appearing in the area of the California Current upwelling zone is unknown but it may be a result of the relatively short duration of the time series.

The grand mean fork length of age-1.3 sockeye salmon is more variable with a generally declining trend. The first noteworthy decline in mean size from previous years appeared in the 1975 brood year that went to sea in 1977 and returned to spawn in 1980. The observation of much lower mean fork length is shared among these three cohorts which have a common year of maturity. The grand mean fork length of age-1.3 sockeye salmon has tended to be below average since the mid-1970s brood year. The lowest values in the time series occurred in the 2000 and 2001 brood years.

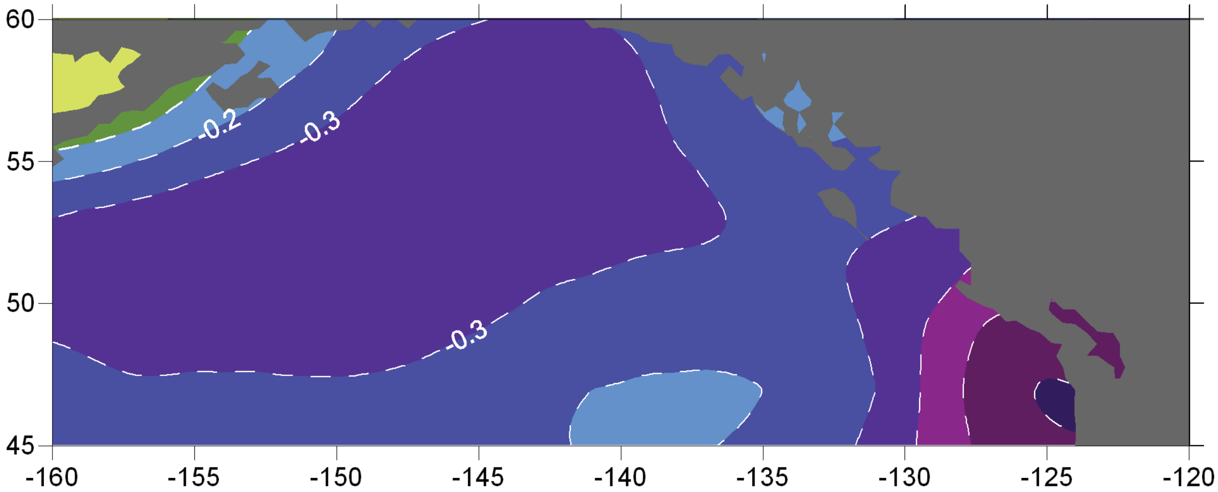

Fig. 36 Contours of correlations between a grid of June SSTs in the Gulf of Alaska with the annual grand mean length of Fraser River sockeye (pooled across 16 stocks and sex) from 1993 to 2007. Contour intervals are 0.1 and negative values are indicated by a dashed line. SST data are NOAAs Extended Reconstructed SSTs on a 2° × 2° lat./long. grid. June exhibited a significantly stronger correlation of SST with length than the previous 5 months.

4.3.3 Density-dependent growth (intra-specific)

> *"If competition in the sea with members of their own race exercises any influence on stature, this should become evident where the annual runs oscillate so extensively as they do on the Fraser. There is widespread impression that the fish of the big runs average smaller than those of other years, and canners generally assert that the fish run more to the case in the big years than at other times."*
>
> Charles Henry Gilbert, 1914

Gilbert's thoughts about variation in the average size of maturing Fraser River sockeye salmon in relation to their own abundance continues to attract the interest of scientists working nearly a century later. The fascination must, at least in part, be related to the conclusion that follows from this observation: that the sea provides only limited amounts of food for growing sockeye salmon. Bristol Bay sockeye salmon were also found to have a smaller mean size when they were more abundant (Rogers 1980). Fraser River sockeye salmon were found to be smaller when the total abundance of sockeye salmon in the Gulf of Alaska was greater (Peterman, 1984), but it was not a universal truth. In central and northern British Columbia, a density-dependent effect on mean size appeared only in age-1.3 sockeye salmon but not in age-1.2 (McKinnell, 1995). The difference was attributed to differences in the temporal/spatial patterns of the two age-classes in the Gulf of Alaska.

Considering how gross measures of sockeye salmon abundance in the Gulf of Alaska might affect average fork length of certain stocks may be appropriate if all stocks are broadly distributed in the Gulf of Alaska, but there are some interesting within-stock patterns in mean length and abundance. The Adams River population, for example, shows no significant relationship between the annual returns of age-1.2 fish and their mean fork length, in spite of annual returns that can vary over three orders of magnitude up to 20 million. Chilko Lake, on the other hand, has significantly smaller mean fork length in age-1.2 fish in years with its highest returns and these do not exceed five million. Furthermore, marine survival is reduced at what is considered a high return abundance for this stock. One is left with an impression that the Adams River population has an oceanic behaviour which allows all of its members to reach a fork length that is not affected by the population's own abundance, while the Chilko Lake stock has an oceanic behaviour that does not produce a similar result. When considered across all 16 stocks described in Section 4.3.2, an analysis of covariance indicated that, while mean fork length differed significantly among stocks ($P < 0.001$), there was no statistically significant general influence of within-stock abundance. Apart from Chilko Lake, the Gates and Late Stuart stocks were the only other two showing a significant abundance-related effect on mean length in age-1.2 returns.

As has been found commonly in other British Columbia sockeye salmon stocks (Godfrey, 1958; McKinnell, 1995), the mean length of the age-1.3 ecotype was highly positively correlated with that of the age-1.2 ecotype returning in the same year (Fig. 37), but not correlated with the mean length of its sibling age-1.2 ecotype that matured one year earlier. This provides strong evidence that mean length at maturity is determined in the final year at sea. Stock-specific differences in mean length and co-maturing age-1.2 mean length explain 75% of the variation in mean length of the age-1.3 ecotype. As was found in the age-1.2 ecotype in Chilko Lake, the mean length of the age-1.3 ecotype there was also significantly smaller ($P < 0.05$) when returns that accompanied it were high. As was observed in the previous paragraph for the age-1.2 ecotype in the Adams River, the mean length of the age-1.3 ecotype was also independent of the Adams River return abundance.

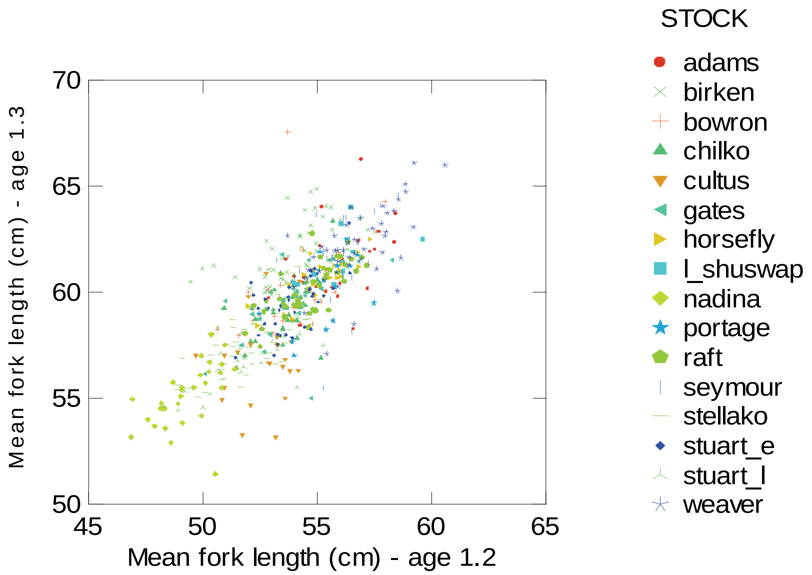

Fig. 37 Mean fork length (cm) of age-1.3 ecotype of sockeye salmon in year x *versus* mean fork length (cm) of age-1.2 ecotype of the cohort in year x + 1. These ecotypes mature and return to spawn in the same year.

Until the mid-2000s, the T/V *Oshoro maru* conducted annual cruises in summer to the Gulf of Alaska. Cruise tracks were typically, but not always, north–south transects along 145°W longitude. Each night while on station, a multi-mesh gillnet was set to obtain biological samples of salmonids. Fork lengths of the sockeye salmon caught in these surveys were recorded by sex and age. From 1980 to 2000, fork length did not have a temporally varying cycle or trend by sex and age (Fig. 38). This may reflect the composite multi-stock nature of these samples. As the data include only the period after 1980, it may not reflect the long-term pattern that is evident in samples taken of Fraser River sockeye salmon (Fig. 35).

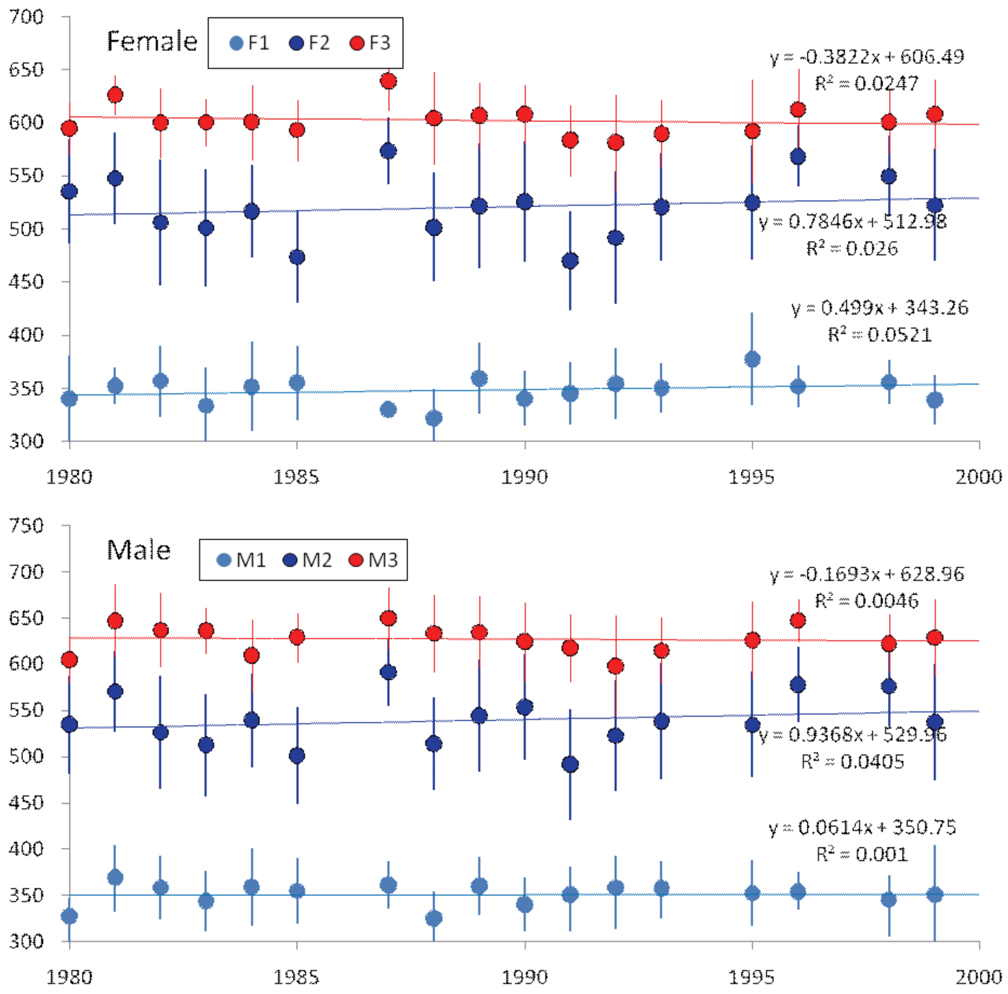

Fig. 38 Mean and standard deviation of sockeye salmon fork length, by sex and ocean age (M1 = age-x.1, M2 = age-x.2, and M3 = age-x.3), of sockeye salmon caught by gillnet in the Gulf of Alaska along 165°W and 145°W. Linear trend fits are indicated for each. None were statistically significant.

4.3.4 Density-dependent growth (inter-specific)[6]

When the ANCOVA described in Section 4.3.3 is repeated to include potential differences in mean fork length in odd/even years, it was found that the mean fork length of age-1.1 Fraser River sockeye salmon jacks was significantly smaller ($P < 0.05$), by 4 mm, in brood years that matured in odd years. Likewise, the average fork length of age-1.2 sockeye salmon maturing in odd years was significantly smaller ($P < 0.001$), by 8 mm, than age-1.2 sockeye salmon maturing in even years. Finally, the average fork length of age-1.3 sockeye salmon maturing in odd years was significantly smaller ($P < 0.05$), by 3.5 mm, than age-1.3 sockeye salmon maturing in even years. As the odd/even cycle of abundance of pink salmon (*O. gorbuscha*) to the Fraser River is potentially a source of competition for Fraser River sockeye returning the same year, it is normal to consider that a reduction in mean size in odd years is a consequence of competition for food with pink salmon during the period of overlap in the Gulf of Alaska. Presumably, the competition arises from the interactions of maturing sockeye salmon and maturing pink salmon, as the two groups do not likely share a common habitat until the pink salmon move off the continental shelf into the Gulf of Alaska.

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[6] See McKinnell and Reichardt (2012) for a discussion of the effect on first year marine growth.

If the biannual effect on maturing Fraser River sockeye salmon growth is due to maturing Fraser River pink salmon, the tagging data suggest that it must occur late in life because the high seas distribution of maturing sockeye salmon bound for the Fraser River is very different in time/space from that of Fraser River pink salmon (Fig. 39 top). It would seem, therefore, that the greater potential for the mean length of Fraser River sockeye salmon to be lower in odd years is due to competition with a greater overall abundance of pink salmon in Alaska and its biennial cycle (Fig. 40).

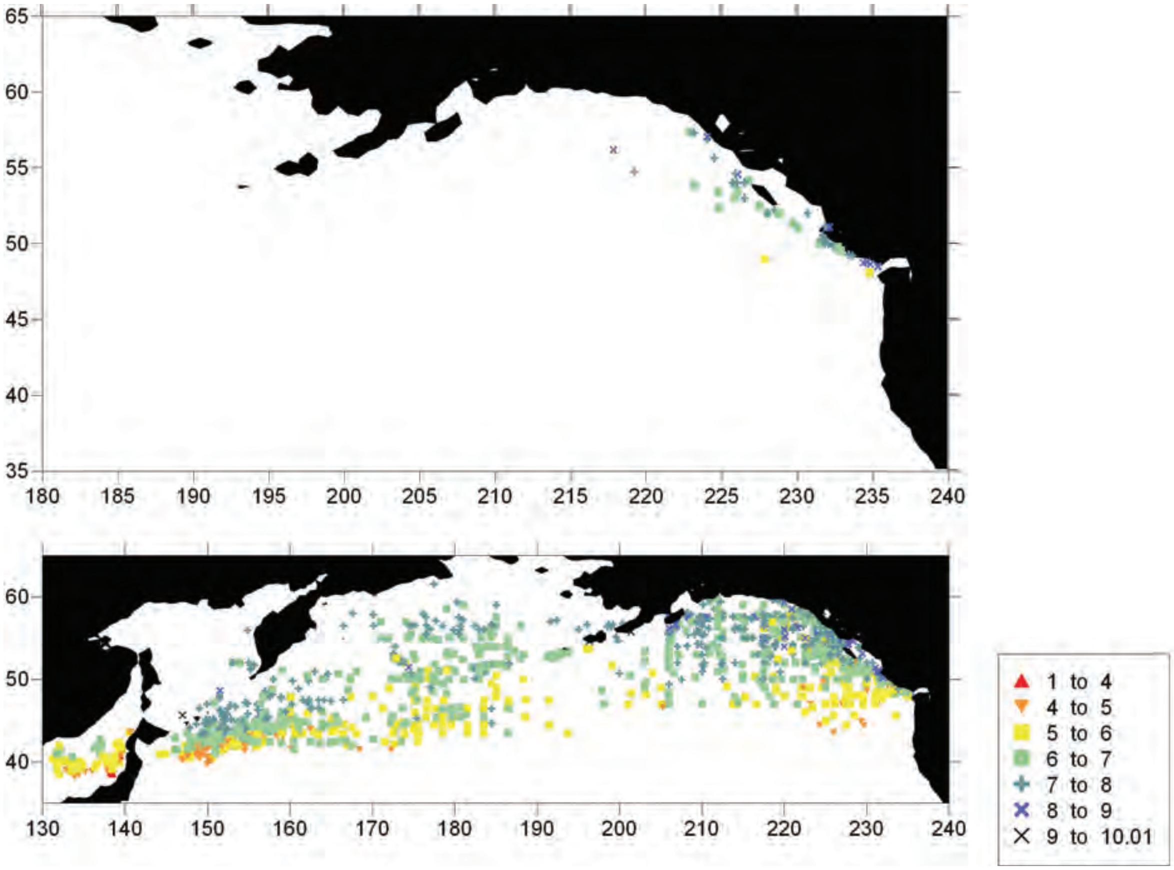

Fig. 39 (Top panel) Release locations of pink salmon that were tagged on the high seas and recovered in odd years in Fraser River salmon fisheries (same general recovery areas selected for sockeye salmon in Figure 17) compared to (bottom panel) the distribution of tagging locations of pink salmon (Myers *et al.*, 1996). Plot symbols indicate month of tagging.

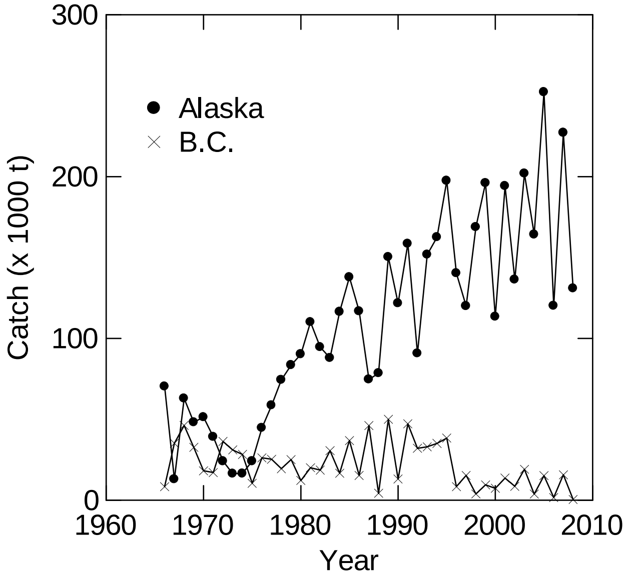

Fig. 40 Catch of pink salmon in Alaska (Southeast and Central) and British Columbia (including Washington State). Data from Irvine *et al.* (2009)

Ruggerone *et al.* (2003) found a similar interaction between Bristol Bay, Alaska, sockeye salmon growth and Russian pink salmon abundance. The competitive effect of pink salmon abundance is not always expressed at this life history stage, as it has appeared at different life history stages (Ruggerone *et al.*, 2007) and with varying degrees of influence. In Puget Sound, Washington, for example, pink salmon abundance appears to influence survival. The survival of hatchery releases of chinook salmon into Puget Sound was 59% lower for cohorts that were released in even years from 1984 to 1997 (Ruggerone and Goetz, 2004). Juvenile pink salmon, especially from the Fraser River, are orders of magnitude more abundant in even years in the Salish Sea (Strait of Georgia + Puget Sound) than in odd years.

An analysis of covariance of mean annual fork length (males and females averaged) of maturing age-1.2 Fraser River sockeye salmon stocks, from Figure 35, was used to examine correlations between mean fork length and coarse indicators of maturing Gulf of Alaska salmon abundance. Covariates were total Gulf of Alaska pink salmon catch, total Gulf of Alaska sockeye salmon catch, and total western Alaska sockeye catch. It was found that all three catch totals were statistically significant ($P < 0.001$) but the coefficients (relative influence on mean fork length) were largest for total Gulf of Alaska sockeye and least for Gulf of Alaska pink salmon catch. These covariates "explained" 70% of the interannual variation in Fraser River sockeye salmon mean length. The difficulty attributing catch (related to abundance) as the cause of the variation is that all catch time series and the mean length time series have a strong component of low frequency that may have arisen spuriously, and the catch time series are correlated with each other (Fig. 41). The low frequency component of variation in mean fork length seems, rather generally, to follow as an inverse of the commercial catch of sockeye salmon in the Gulf of Alaska. Larger Fraser River sockeye salmon and smaller catches are found in the early part of the time series, followed by smaller sockeye salmon and larger catches in the mid-period, by increased mean length and lower catches of sockeye salmon in the Gulf of Alaska in the latter part of the series. For unknown reasons, the mean length of age-1.2 Birkenhead sockeye salmon was uncorrelated with these catches but 13 other stocks had negative slopes.

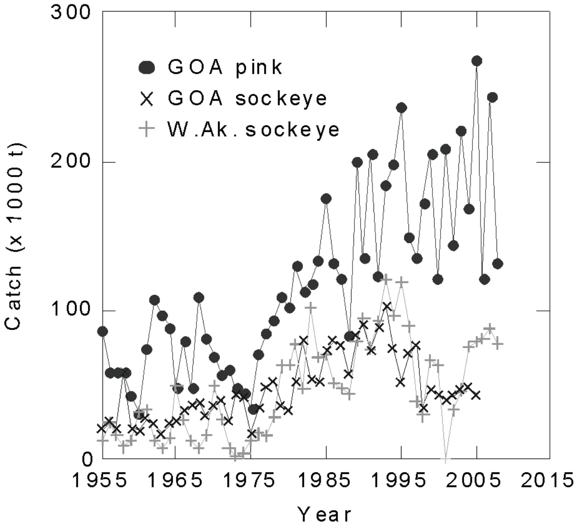

Fig. 41 Total commercial catch pink salmon and sockeye salmon (tonnes × 1000) in the Gulf of Alaska and total catch of sockeye salmon in western Alaska from 1955 to 2008. Data from Irvine *et al.* (2009).

Without considering population-specific differences in growth rates, Ishida *et al.* (1998) in their review of the growth of Pacific salmon, found that growth rates of maturing sockeye salmon, pink salmon, and coho salmon were higher than those of immature fish of the same age. They considered that life history stages with higher growth rates and higher food requirements would provide conditions that would allow for density-dependent growth.

Summary – For more than a century it has been recognized that the average size of sockeye salmon returning to the Fraser River varies from year to year. Overall, the mean fork length at maturity of age-1.1, 1.2, and 1.3 Fraser River sockeye salmon is independent of the abundance of the Fraser River cohort that survives to maturity. An exception appears to be Chilko Lake where the mean fork length of age-1.2 returns is negatively correlated with its abundance.

4.4 *Migration Behaviour and Timing*

> *"There is no evidence that fish can navigate in the open waters."*
>
> Wilbert A. Clemens, 1951

4.4.1 Depth of migration

The first applications of data storage tags to maturing sockeye salmon in the Gulf of Alaska were conducted by the Fisheries Research Institute of the University of Washington. These tags recorded ambient temperatures and pressures (depths) experienced by the fish at frequent intervals. There are no recoveries of Fraser River sockeye salmon with these tags, but the behaviour of a maturing fish that was recovered at the mouth of the Taku River (Southeast Alaska) confirmed some previous ideas about their migration depth. The median daily depth was routinely <10 m (Fig. 42). Only on the day of tagging was the median value >10 m. Excursions by the fish to deeper, colder waters were infrequent. This result has some similarities and some differences to what was observed with ultrasonically tagged Fraser River sockeye salmon in 1985. Quinn and terHart (1987) also observed a strong near-surface migration depth after the day of tagging in Queen Charlotte Strait, but the depth of migration deepened as the fish moved from that observed in the well mixed regions of Johnstone Strait/Discovery Passage into the stratified warmer and fresher waters of the Strait of Georgia.

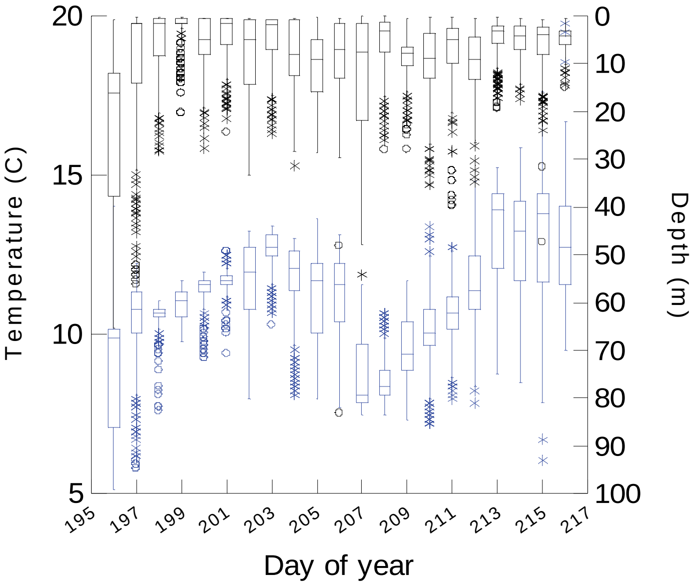

Fig. 42 Box and whisker plots of daily variation in depth (m), and temperature (°C, blue) of a sockeye salmon tagged with a data storage tag, from its release in the Gulf of Alaska (55° 10′ N 145° 04′ W) in July 1999 until its recapture three weeks later in a fishery in the Taku River (Southeast Alaska). The horizontal line within each vertical box indicates the median value over a 24-h period, and the extremes of each box indicate quartiles. Outliers (x) and strong outliers (○) within each day appear at deeper/colder locations. Data courtesy of the Fisheries Research Institute, University of Washington, Walker *et al.* (1999).

4.4.2 Migration timing

The common practice is to estimate, from available sources of run timing information, the date of the peak of the run in DFO Statistical Area 20 (western end of Juan de Fuca Strait). The temporal pattern of sockeye salmon abundance during the return migration is a key uncertainty at the beginning of each fishing season. The uncertainty arises in-season because, in different years, abundance in the test fishery does not necessarily reflect the abundance of the run until after the peak of the run has passed and its timing that year becomes understood. In different years, the same abundance can be an indicator of a weak, average, or a strong run.

Blackbourn (1987) reported a tendency for the return timing of seven Fraser River sockeye salmon stocks or stock groups and one sockeye salmon stock in Washington State (Quinault Lake) to be later during years in the Gulf of Alaska when SSTs were warmer. In contrast, he found that the return timing of many northern British Columbia sockeye salmon populations (Skeena, Copper River, Upper Cook Inlet, Chignik River) was early in warm years. This led him to develop a “displacement” hypothesis where warmer SSTs in the Gulf of Alaska restricted the distribution northward and cooler temperatures allowed a more southerly distribution that put Fraser River sockeye salmon closer to the Fraser River at the onset of migration. The ocean temperatures providing the greatest explanatory power were found to be those of the winter and/or spring immediately preceding their return to the Fraser River.

With the passage of more than 20 years, it is possible to test this hypothesis with additional data for at least some of the stocks. For Early Stuart, for example, the correlation of peak date with monthly SST in the NOAA Extended Reconstructed SST database (2° × 2° lat./long. grid) for the period 1985 to 2010 was r = +0.76, but the maximum correlation occurred in spring (April/May) rather than the previous December reported by Blackbourn (1987). Changes of a few months in these correlations are not entirely unexpected because of the autocorrelation in seasonal SST. The peak correlation was found near Ocean Station Papa (45°N 145°W), approximately the same location reported by Blackbourn (1987).

Estimates of the peak date of return through Area 20 from the 1950s to the present for Chilko Lake sockeye salmon are more variable (Fig. 43). Some of this variation may be due to co-migration with other Summer-run stocks and the need to use stock identification techniques to determine the proportion of Chilko Lake fish in the catch. The Early Stuart run is sufficiently early so that it does not have this additional source of observation error. Low frequency variability in Chilko Lake run timing is evident in Figure 43, largely due to later-than-average return dates in the early 1990s. The trend has been earlier for the most recent decade, with a noteworthy outlier in 2005 that most runs to the Fraser River experienced.

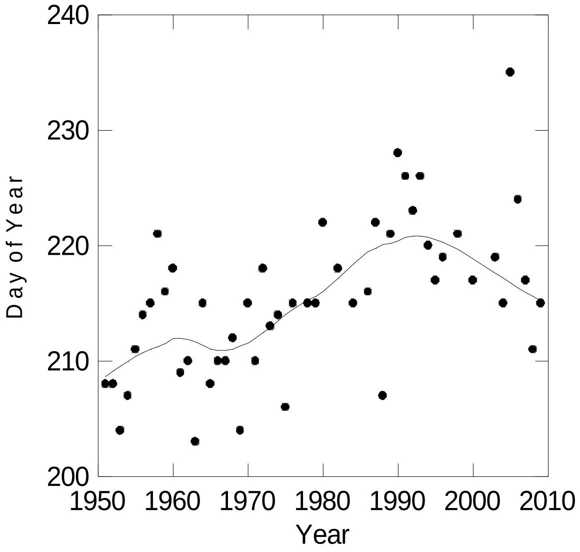

Fig. 43 Date of 50% return of maturing Chilko Lake sockeye salmon through DFO Statistical Area 20 (western Juan de Fuca Strait) from 1950 to present. Data since 1980 are based on run reconstructions by the Pacific Salmon Commission.

Using a more conservative test of hypothesis than Blackbourn (1987), Hodgson (2000) confirmed that the run timing of Fraser River populations, except Pitt and Adams, tended to be earlier after cold spring–summer periods and later following warm periods. Likewise, populations from the Cook Inlet, Kodiak Island (except Ayakulik), Alaskan Peninsula and Bristol Bay tended to be later following cold April–July periods and early migrations tended to follow warm periods. In populations from Washington State, central and northern British Columbia, Southeast Alaska and Prince William Sound, there were no consistent relationships with SST within regions.

Daily counts of sockeye salmon migrating past the Docee Fence (Long Lake) provide an opportunity to compare Fraser River sockeye salmon run timing with a central coast sockeye salmon population. Peak dates for the Long Lake sockeye salmon returns were calculated (Table 3) from 1990 to 2009 using a salmon fishery run timing model (Schnute and Sibert, 1983). During these years, selected only to provide a sample for comparison, the Long Lake sockeye salmon run arrived three weeks earlier, on average, than the Chilko Lake run and 10 days later than the Early Stuart run. Year-to-year variation in timing was positively correlated among these runs, more so with Chilko Lake timing ($r = 0.68$, $P < 0.01$) than with Early Stuart timing ($r = 0.45$, $P < 0.05$). There is no autocorrelation in the Long Lake time series but there is in both Fraser River time series, so the Early Stuart correlation is not statistically significant.

Table 3 Estimates of peak date sockeye salmon migration past the Docee Fence (Statistical Area 20, Long Lake) from 1990 to 2009 based on the method of Schnute and Sibert (1983). All dates are in July; subtract 181 from day of year to find the July date (182 for leap years). Sockeye salmon counts from http://www.pac.dfo-mpo.gc.ca/ northcoast/counts/ docee/default.htm.

Year	Day of Year
1990	209 (July 28)
1991	203
1992	195
1993	202
1994	202
1995	198
1996	197
1997	202
1998	194
1999	204
2000	196
2001	197
2002	196
2003	196
2004	198
2005	206
2006	204
2007	197
2008	197
2009	200

A recent study found that upon reaching the coast, sockeye salmon from Late-run populations (Adams River and Weaver Creek) had an average migration rate of approximately 20 km d^{-1} through the marine area and held at the river mouth and adjacent areas for approximately eight days before entering the river and Summer-run populations (Birkenhead, Chilko, Horsefly and Stellako) had a migration rate approximately 33 km d^{-1} but they held near the river mouth for only approximately 2 days (Crossin *et al.*, 2007). Males migrated at higher speed than females through the Strait of Georgia. Successful migrants had the property of delaying briefly before entering the Fraser River, combined with low plasma testosterone and high somatic energy.

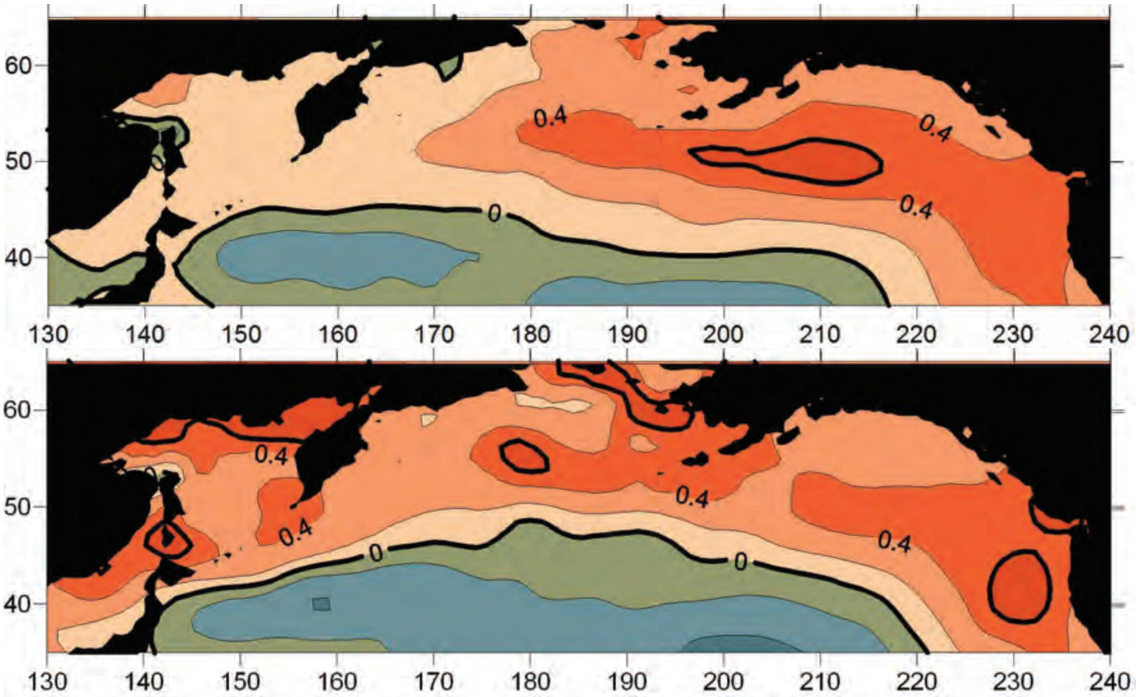

Fig. 44 Contours of correlation between date of peak abundance of Early Stuart (top panel) and Chilko Lake (bottom panel) sockeye salmon in DFO Statistical Area 20 *versus* mean April SSTs at each 2° × 2° lat./long. grid point in the northern North Pacific. Warmer colours are positive correlations (later arrival when warmer) and cooler colours are negative correlations (earlier arrival when cooler). Contour interval is 0.2 and contours equal to 0.0 and +0.5 are highlighted with thicker lines. Sources: SST data from the NOAA Extended Reconstructed SST database. Chilko Lake dates (1951–2009) from the Pacific Salmon Commission.

Summary – The geographic pattern of correlations between Fraser River sockeye salmon run timing and SST (Fig. 44) were developed from >50 years of run timing data. Blackbourn (1987) found that a warmer (colder) Gulf of Alaska before the return migration was associated with later (earlier) return timing. This observation has survived the addition of 25 years of additional data. For Early Stuart sockeye salmon, the largest positive correlation between temperature and run timing (r = 0.63) appeared near Ocean Station Papa (50°N 145°W), DFO's longstanding ocean/climate research and monitoring site in the Gulf of Alaska. The largest negative correlation (r = –0.51) was located northwest of the Hawaiian archipelago in March. The broad-scale patterns correlation patterns suggest that return timing is associated with the large-scale climate patterns of the North Pacific Ocean. During the period of record, one of the warmest years in the Gulf of Alaska, 2005, accompanied remarkably late run timing.

4.5 Landfall

The route used by Fraser River sockeye salmon to get from the central part of the Gulf of Alaska to the coast is known only in generality. It has been inferred from the seasonal development of catches along the British Columbia coast and from the patterns of catches in high seas studies of the 1960s and 1970s. Healey *et al.* (2000) described two general hypotheses for interannual variation in coastal migration routes. The first has the sockeye salmon following isotherms or other watermass properties that affect the distribution of their prey. The second is that large-scale ocean currents have sufficient influence that they deflect the migration northward in years of stronger circulation in the Alaskan Gyre.

A few modelling studies have addressed issues associated with landfall (Thomson *et al.*, 1992; Kolody and Healey, 1998; Healey *et al.*, 2000). Thomson *et al.* (1992) considered the hypothesis that the interannual variability of the Northeast Pacific Ocean circulation affected the latitude of landfall and the migration speed of maturing sockeye salmon returning to the Fraser River. By comparing the years 1982 and 1983 they concluded that large-scale ocean circulation had the potential to affect the migration of Fraser River sockeye salmon. Landfall is a loosely defined term, based on the idea that Fraser River sockeye salmon follow a compass orientation toward the coast until they make landfall at some average latitude which varies from year to year, then follow other cues presented along the coast as they migrate toward the Fraser River.

Coastal test fisheries were established to assess the in-season development of the annual migration. They provide one of the few opportunities to examine year-to-year differences in migration using standardized methods. The Round Island (Johnstone/Queen Charlotte Strait) and San Juan (Juan de Fuca Strait) gillnet test fisheries operate at the entrances to the approach routes to the Strait of Georgia. They provide daily indices of abundance (CPUE – catch per unit effort) as the run passes each location. Differences between these sites may provide an indication of where the returning sockeye salmon encounter the coast. If, for example, a group of fish made landfall at the latitude of Queen Charlotte Sound, some took the western route around Vancouver Island and some took the eastern route, and migrated at the same speed, they would appear first at the Round Island fishery. This would appear as a lag correlation in CPUE between the two fisheries. If the group of fish first appeared at San Juan, it would suggest a more southerly landfall. If the first part of the run appeared at San Juan and the latter part of the run took the eastern route down Queen Charlotte Strait, the ratio of San Juan:Round Island CPUE would decrease through the season.

To study these trends, a three-day running average of sockeye salmon CPUE was computed for each of the two gillnet test fisheries using data from 2000 to 2009. A cross-correlation was then computed between the two series in each year at various daily lags to understand whether the timing that was evident in the abundance index at San Juan led or lagged the timing of the abundance index at Round Island. In each year from 2000 to 2009, the maximum correlation between these two smoothed time series occurred when there was no lag between them, suggesting that the timing of the run occurs simultaneously at both test fisheries (Fig. 45). This analysis says nothing about the relative fractions of the run following one route or the other, but it reveals that the timing is the same. Except for the year 2000, there was no significant linear trend in the ratio of CPUE at the two fisheries (not shown), suggesting that the fractions migrating via either route does not change substantially through the season in most years. As these are not population-specific trends, a negative trend in this ratio for one stock might be offset by a positive trend in another but this pattern is not one that is thought to occur in nature.

The contemporaneous CPUE in the test fisheries across all 10 years of fishing examined in this study, suggests that there is no substantial alongshore migration of Fraser River sockeye salmon on the west coast of Vancouver Island (or it is equally northbound and southbound) so that the correlation between the two indices is maximum at zero lag. If landfall was north of Vancouver Island, there should be a several day lag for those migrants to reach the San Juan test fishery compared to those arriving at Round Island.

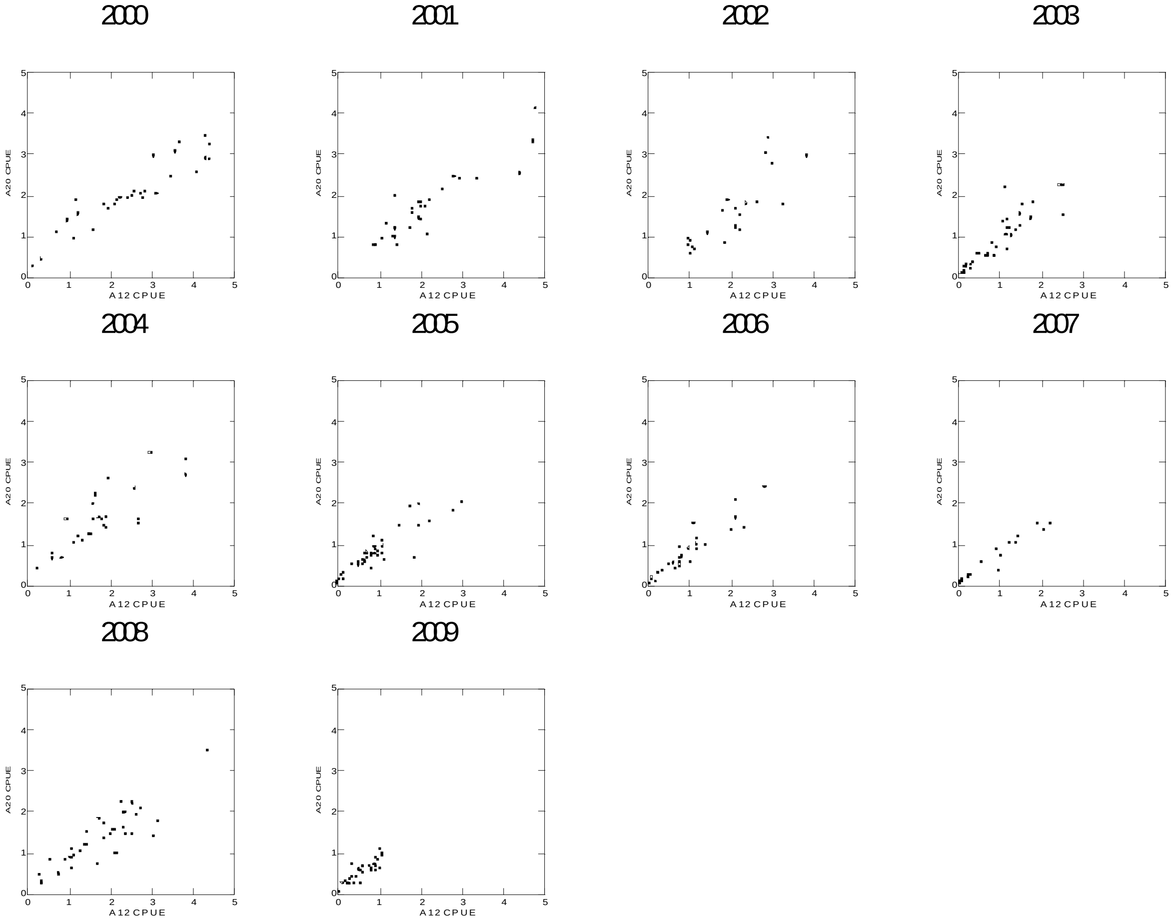

Fig. 45 Daily values of the three-day running mean of sockeye salmon catch per unit effort (CPUE) in the San Juan test fishery in DFO Statistical Area 20 (ordinate) *versus* the same at Round Island (abscissa) test fishery in DFO Statistical Area 12.

4.6 Northern Diversion

> *"The small catch [in 1936] in the Strait of Juan de Fuca and in Washington Sound and the large catch in the Johnstone Strait area presented a rather puzzling situation."*
>
> Wilbert A. Clemens, 1937

On their homeward migration, sockeye salmon take one of two routes around Vancouver Island to the Fraser River (Fig. 46). The average proportion entering the Strait of Georgia via Juan de Fuca Strait was relatively low until 1978 when a rather fundamental change occurred to increase the average proportion of migrants returning via Johnstone Strait (Hamilton, 1985; Groot and Quinn, 1987; McKinnell *et al.*, 1999). Prior to 1978, only the warmer El Niño years of 1936 (Tully, 1937) and 1958 (Royal and Tully, 1961) elevated the northern diversion significantly above 0.5, although case pack statistics from the canneries in 1937 indicated that modest (21%) northern diversions also occurred (Clemens, 1938). Because the norm was considered to be Juan de Fuca Strait, the fraction returning via Johnstone Strait was called the *northern diversion rate*.

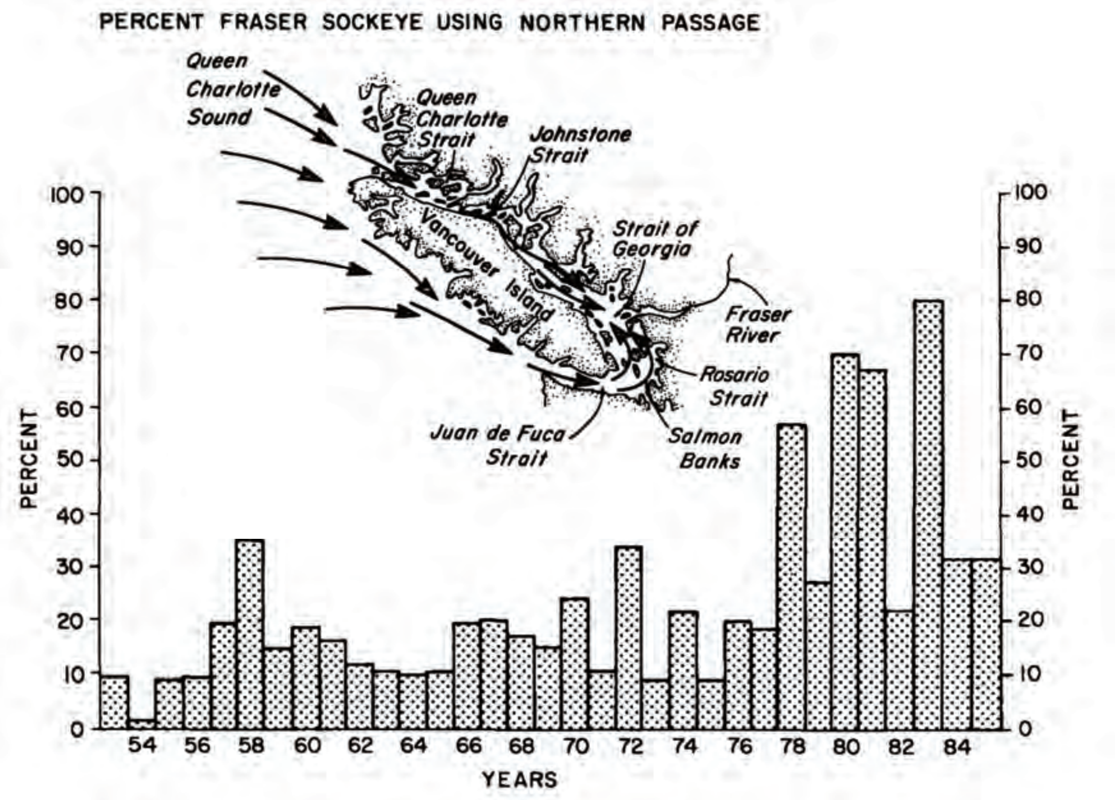

Fig. 46 Percentage of Fraser River sockeye salmon taking the northern diversion from 1953 to 1985. Figure from Groot and Quinn (1987).

The reason for migrating via one route *versus* the other is currently unknown, but higher northern diversion rates are generally associated with a warmer coastal ocean (Hamilton, 1985; Mysak, 1986; Groot and Quinn, 1987). The relationship between northern diversion and coastal SST was not a very useful predictor of the northern diversion rate before 1978, except perhaps in those few years of greatest positive temperature anomalies (McKinnell *et al.*, 1999).

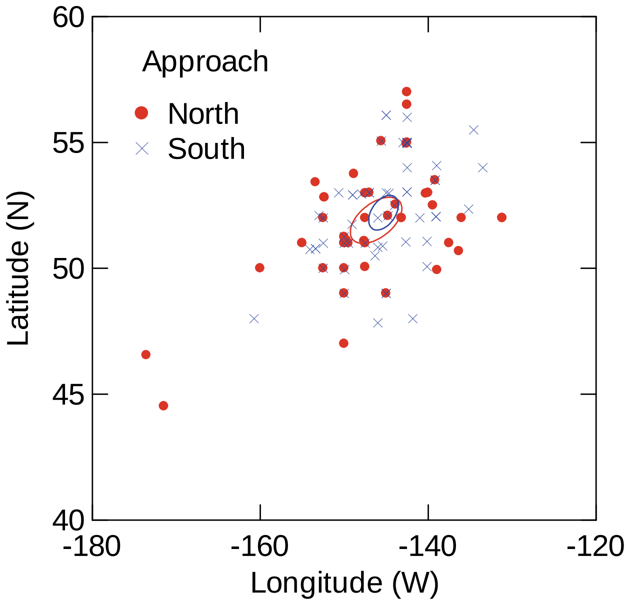

Fig. 47 Release locations of age-1.2 Fraser River sockeye salmon tagged on the high seas (west of 130°W) and caught the same year in the approach routes to the Strait of Georgia, by route, composite of all recoveries.

Likewise, the location where Fraser River sockeye salmon make their "decision" to migrate around Vancouver Island is not known. From high seas tagging studies, those individuals that were tagged in the Gulf of Alaska in spring west of 130°W longitude (to exclude fish that were tagged along the west coast of Vancouver Island) and recovered in the same year in fisheries in one of the two approach routes to the Strait of Georgia (Johnstone Strait and Juan de Fuca Strait) had no significant difference in the mean tagging location in the Gulf of Alaska (Fig. 47). The "centre of gravity" of the fish taking the Johnstone Strait route, for example, was no farther north and/or west than the fish taking the Juan de Fuca Strait route. Although this result was obtained from a composite of all release years, it suggests that the route taken around Vancouver Island by these sockeye salmon in the 1960s and 1970s was determined closer to the coast. There were insufficient recoveries in the approach routes to know whether this pattern holds within each year, or whether it still holds today.

5 Survival

5.1 *Productivity and Survival*

The theoretical maximum abundance that a cohort of sockeye salmon can have is determined by the number of fertilized eggs produced by its parents. The abundance of the cohort begins to decline immediately as eggs are eaten or damaged or die from any number of causes (Fig. 48). The expected schedule for the eventual disappearance of a cohort is called a life table. It documents the average probability of dying during various intervals between birth and the maximum age that the species can achieve. Births and deaths of human populations, for example, are so well documented that the probabilities of dying at any particular age are relatively well known.

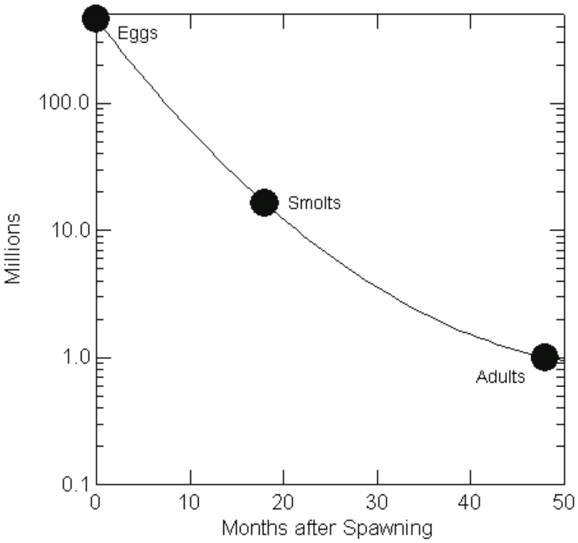

Fig. 48 Abundance of an idealized sockeye salmon cohort, approximated from Chilko Lake statistics of average numbers of female spawners, fecundity, freshwater survival, and smolt-to-adult survival. Minor ecotypes (*e.g.*, age-2.x smolts, jacks, 5- and 6-year old adults) are not shown. Note that abundance is plotted on a logarithmic scale.

> *"...it is evident that if we had some accurate method of determining from year to year the number of fish on the spawning grounds, this would afford data for prophecy"*
>
> Charles H. Gilbert, 1923

When Gilbert made the comment above, he was under contract to the Province of British Columbia to report on the returns of sockeye salmon to the major rivers of British Columbia. He was the professor of zoology at Stanford University from its inception. He was arguably the most influential Pacific salmon biologist during the first quarter of the 20th century, and perhaps not coincidentally, a colleague and friend of J. Pease Babcock, Deputy Commissioner of Fisheries for British Columbia. One can imagine that Gilbert's wishes for spawning ground censuses reflected the aspirations of salmon population biologists of the time. The key to building a life table is the census of population abundance. As late as the 1940s, salmon escapement was referred to as "seeding" and records of abundance were ordinal (Brett, 1950) but by the 1950s, the estimates became more quantitative.

5.2 Difficulties Estimating Salmon Abundance

The abundance of a salmon cohort is rarely taken by census. More often, it is the sum of an *estimate* of spawner abundance in a stream or lake plus an *estimate* of the catches of that population in the fisheries it encounters on its return migration. The reliability of the estimate of spawner abundance is determined by many factors but the counting fence has traditionally been considered to be the most reliable because an attempt is made to account for every individual migrating past a fixed point in the spawning migration. In the majority of cases, population abundance is estimated by stream walks, tagging and recapturing spawners, or some other method that relies on assumptions and inferences of varying reliability to produce an estimate of abundance.

The difficulties are relatively well known. One of the best documented examples of underestimating sockeye salmon abundance comes from the Babine River, part of the Skeena River drainage in northern British Columbia. The installation of a counting fence on the Babine River by the Fisheries Research Board of Canada in 1946 demonstrated that the estimate of abundance of sockeye salmon spawners, determined by walking streams and counting fish, was less than 50% of the total number reported migrating past the Babine River fence in the years 1946 and 1947, despite a conscientious effort of stream surveys.

> "*That stream counts will be minimal is apparent by their very nature, but the discrepancy [at Babine Lake] is beyond such expectations*"
>
> J. Roly Brett, 1952

Even an accurate census of spawner abundance each year allows only one element of a life table to be approximated: *total survival.* This is the proportion of a cohort surviving from hatching to maturity and spawning. But even this calculation requires an assumption about the average number of eggs that was fertilized by the spawning adults. That number varies from year to year and stock to stock, and from the age composition of the spawners (older females are usually larger and have more eggs). As a consequence, analysts typically avoid computing the initial size of a cohort from the number of fertilized eggs, but use instead the number of spawners (or number of female spawners) and assume that it will be a good index of the number of progeny. Compared to other sources of measurement error, this is likely a relatively small contributor.

5.3 Smolt-to-Adult Survival

One consequence of determining only *total survival* is that when the average survival changes, it is very difficult to determine where the change occurred. As Fraser River sockeye salmon spend their lives divided almost equally between freshwater and saltwater habitats, scientists who are interested in distinguishing how salmon survive in these environments must take a census of the population as it leaves freshwater. Ideally this would occur immediately upstream of an estuary but the mixing of many populations from many nursery lakes within the watershed, and an inability (historically) to identify them to population of origin in a mixture, has made it easier to census sockeye salmon populations as they leave the nursery lake. Mortality of sockeye salmon between the nursery lake and the estuary is normally included in marine mortality although it is understood that some mortality occurs in the river (Ricker, 1966).

Ricker (1962) described how marine survival of sockeye salmon generally increased from 4% to 30% as the mean size of the smolts increased from 70 to 140 mm, but then he pointed out that the mean size of Chilko Lake sockeye salmon smolts varies little from year to year and with no apparent relation to average size (Ricker, 1966), a situation that continues to the present. The first comprehensive study of smolt-to-adult survival patterns in sockeye salmon was conducted using data that had been produced by a long history of study at Cultus Lake (Foerster, 1954). From the 1927 to 1944 ocean entry years, smolt-to-adult survival varied from a low of 0.31% (1941) to a high of 5.78% (1936). Here, there was a significant positive relation between smolt size (both weight and length were measured) and survival, and Foerster (1954) described how 56% of the variation in adult returns was explained by the number of smolts emigrating and their average weight. Ricker's (1976) review of growth and survival in salt water has not been surpassed by any other work on the topic. The average of several methods of estimating natural mortality of Pacific salmon at sea, that were thought by Ricker (1976) to be without bias and had small or moderate sampling errors, in the last year at sea was 0.015 m^{-1} or 18% y^{-1}.

One pattern that the smolt-to-adult survival time series in Cultus Lake shares with its mid-Fraser neighbour, Chilko Lake, since the 1950s is that the worst survival occurred at the highest smolt abundance. Both lakes feature an underlying pattern of increasing returns from increasing numbers of smolts until a dramatic decline occurs. In Chilko Lake, all of the major deviations from this pattern are strongly negative at the highest smolt abundances. However, with only one year to make this point (Fig. 49), it is not possible to know whether or not this is a general characteristic of the Cultus Lake population. In both cases, density-dependent survival is suggested. It is a general pattern, observed in nature, where the capacity of nature to support an abundance of animals is limited by some or several resource limitations.

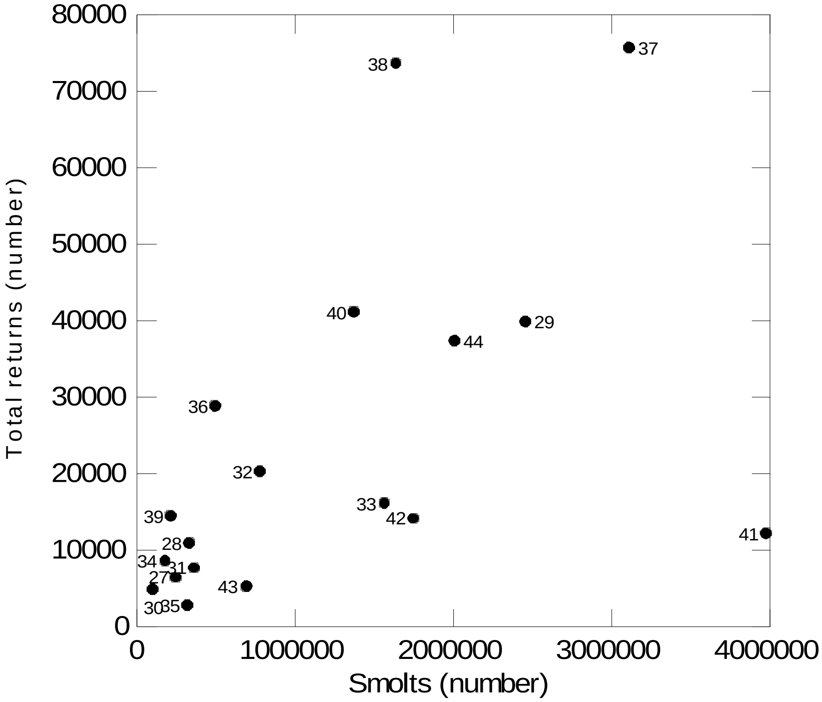

Fig. 49 Adult returns of sockeye salmon (ordinate) from the abundance of smolts of the same cohort (abscissa) at Cultus Lake, 1927 to 1944 ocean entry years.

The 1941 (ocean entry year) outlier was also the year of smallest mean size of smolts emigrating from Cultus Lake. It has been shown that smaller sockeye salmon smolts from Chilko Lake have greater mortality than larger individuals when a single cohort is examined (Henderson and Cass, 1991) but the principle does not apply to differences in mean smolt size among years in Chilko Lake. In Cultus Lake, however, there was a significant relationship between mean smolt size and smolt-to-adult survival during the years from 1927 to 1944. Years with smaller average smolt size have poorer smolt-to-adult survival. The 1941 anomaly in smolt-to-adult survival did not appear so unusual when considered within this framework. Why Chilko Lake and Cultus Lake should differ so clearly on this point is not known, other than to note that Chilko Lake is the most productive sockeye salmon population, on average, and Cultus Lake is the least productive of the Fraser River populations (McKinnell, 2008). Perhaps there are significant differences between the two populations in the energy density of smolts of equivalent size.

On average, 96% of the smolts leaving Chilko Lake are age-1.x and the remainder are age-2.x. Therefore, postsmolts of a single cohort can experience very different environmental conditions upon entering the sea. As a consequence, the marine survival of age-1.x smolts leaving Chilko Lake in any year is more similar to the marine survival of age-2.x smolts of the previous cohort than to the survival experienced by their siblings which leave one year later (Fig. 50). The correlation of the former is 0.45 ($P < 0.01$), whereas there is no correlation of the latter ($P > 0.05$). However, despite sharing a common ocean entry year and location, the amount of interannual variation in marine survival shared by the two groups entering the sea in the same spring is weak ($R^2 = 20\%$), and this drops to 16% if the calculation is made using only 44 years of data that exclude the two anomalous survivals in 1952 and 1954 at the earliest part of the time series. Without the two early outliers, the mean survival of age-2.x smolts across all other years was 12% and the mean survival of age-1.x smolts was 9% for calculations up to, and including, the 2004 brood year. Some of the poor correlation between groups that enter the sea in the same year may be due to inadequate biological sampling of age-2.x groups in the catch or on the spawning grounds. Because they are relatively rare, an inadequate sample of the adult returns can affect the survival estimates.

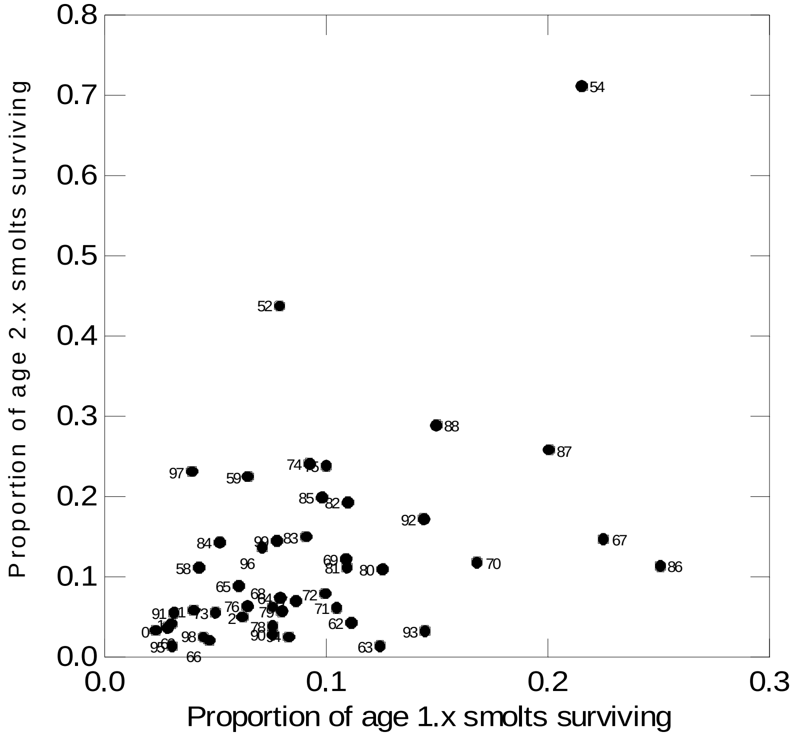

Fig. 50 Smolt-to-adult survival (√ transformed) of Chilko Lake sockeye salmon of different brood years but the same ocean entry year.

5.4 Variability at Different Temporal Frequencies

The statistics of Fraser River sockeye salmon population biology are, for the most part, summarized as annual values. The degree to which finer scale within-year statistics can be computed depends on the frequency of observation. Repeated measurements of the same features using the same, or very similar, methods lead to the establishment of time series of the annual characteristics of salmon biology. Statistics that appear to vary randomly from year to year are described as having interannual variation. Should a time series of seasonal observations have a trend or cycle, or some other longer-term pattern, variations of these kinds are often referred to as decadal-scale or even multi-decadal frequencies. A common approach in trying to understand the cause of variation in salmon biology is to see what other physical, chemical, or biological time series share the same pattern of variation. The physical effects of some cycles, such as the annual cycle of warming and cooling at higher latitudes, are well known so their effects on a time series is often removed to reveal the variation that is not related to the seasonal cycle of the Sun.

The scale of an effect can be an important clue to its origin. The cause of variation in a time series that has no apparent relation to environmental variation of other nearby measurements might arise from a local effect, whereas a pattern of variation in a time series that is shared regionally may have a regional origin. A technique used to study variation in time series is to understand the spatial scale of variation as a clue to its source. Time series that are a result of multiple influences present even greater challenges, particularly when the observations themselves are imprecise or biased by the methods used to make the original observations. The latter, if an important characteristic of a time series, means that weak sources of variation will be difficult to detect.

5.4.1 Interannual

The coefficient of variation (magnitude of variability in a time series in relation to its mean value) in the number of smolts produced per effective female spawner in Chilko Lake is 47%. The coefficient of variation of age-1.x adult returns per age-1.x smolt is 60%. The coefficient of variation of total returns per effective spawner in Chilko Lake is 96%. The latter is larger because it includes variation from both sources. The important result of this comparison is that returns per spawner, the normal measure of Fraser River sockeye salmon productivity, includes significant year-to-year variability from both freshwater and ocean sources. Because it has not been measured routinely at other lakes, the relative influence of each habitat on total survival cannot be determined. Returns per spawner is the measurement of choice (or default) for most Fraser River sockeye salmon populations because only adults are censused in every population.

For comparison, smolt-to-adult survival of age-1.x sockeye salmon from Babine Lake (Skeena River) had a coefficient of variation of 70% for brood years 1961 to 1977 (McDonald and Hume, 1984). This study evaluated four major assumptions surrounding the construction of spawning channels to increase adult sockeye salmon production. Assumptions about freshwater production were largely met, *i.e.*, more spawning habitat created by the channels provided for more eggs to survive, and this translated into more fry in the lake and more smolts emigrating to sea. Only during odd years did greater numbers of adults return from the increased numbers of smolts. There was no average increase in adult returns during even brood years (McDonald and Hume, 1984). The difference between odd/even brood year marine survival in Babine Lake is not apparent in more recent data (brood years 1970–2000). There is no significant difference between odd and even brood year smolt-to-adult survival in Chilko Lake sockeye salmon (1-way ANOVA, $P > 0.9$) over the period of record, but a more thorough analysis of this topic is warranted in the future because of its appearance in other species using the Strait of Georgia (Ruggerone and Goetz, 2004).

5.4.2 Decadal

Significant changes occurred in the North Pacific ocean−climate system around 1977 (Mantua *et al*., 1997) and around 1989 (Hare and Mantua, 2000), so these years are often used to delimit climate and productivity regimes. The local expressions of these phenomena vary around the North Pacific. Spring and summer SSTs at Kains Island on the northwest coast of Vancouver Island, for example, were significantly warmer (by 0.8°C) in August after 1989. In studies of Fraser River sockeye salmon productivity and climate, Beamish *et al.* (1997, 2004a) found a statistically significant change (increase) in Fraser River sockeye salmon productivity following the 1976/77 climate regime shift in a subset of the time series. However, using the entire period of record and a different analytical approach, no statistically significant change in total survival was found up to the 1999 brood year McKinnell (2008). In Chilko Lake, where freshwater and postsmolt survival can be distinguished, he found that average freshwater survival had declined after 1989 (up to the 1999 brood year) but he found no statistical evidence of a significant decline in average postsmolt survival during the same period. This result was likely due to having few complete years of data after the decline in survival, and by not recognizing 1992 as the year when the change occurred. However, by extending the time series to the 2004 brood year, using 1992 as the ocean entry year of change in mean survival ($\sqrt{}$ transformed), a significant decrease ($P < 0.05$) was found for both smolt ages. The difference in average freshwater survival seems to have disappeared because of recent, unexplained high freshwater survival of the 2005 and 2006 brood years in Chilko Lake.

5.4.3 Evolutionary-scale

Selective pressures in the environment affect the evolution of heritable characteristics of sockeye salmon populations. Populations that are found in the Fraser River have evolved to their contemporary diversity over millennia, since the start of the retreat of the Laurentide ice sheet from the coastal region of British Columbia approximately 10,000 years ago. Hodgson (2000) concluded that variation in migratory timing among sockeye salmon populations was related to spawning time, migration distance, river temperature and flow regimes. She found that long delays between migration and spawning occurred in coastal areas, some of which had warm freshwater temperatures during the migration. She suggested that long delays provided the means to avoid higher temperatures which occur after migration in freshwater. For some populations, it was unclear why they should return early, with a long delay before spawning, rather than return on a date that would provide a shorter delay before spawning, after freshwater temperatures had declined from their peak.

An alternative (and at this point, speculative) idea that has not been considered previously, entertains the possibility that migration timing in sockeye salmon at the southern end of the species range has evolved to the present state by selective forces operating in the ocean, enroute to freshwater. It has the following logic:

1. Some populations of sockeye salmon, especially near their southern ocean entry locations, migrate from salt water to freshwater far sooner than is expected from time of spawning.
2. Populations that exhibit the most extreme form of this type of behaviour have a shared geography in the northern California Current region.
3. The northern California Current region is subject to large interannual variations in physics, chemistry, and biology because of its proximity to the North Pacific Transition Zone between the Subarctic and the Subtropic.
4. The migration timing anomalies occur with diminishing frequency northward.
5. Fraser River sockeye salmon do not exhibit this behaviour because the Johnstone Strait approach route provides relief from the evolutionary forces that affect west coast populations.
6. High northern diversion rates in warm years are the interannual response to oceanic selective pressure.
7. Migration timing is a highly heritable characteristic and early arrival occurs in affected populations because evolution has extinguished later arrivals, suggesting that the ocean is unsuitable for sockeye salmon migration when they might otherwise (based on spawn timing) appear in freshwater.
8. A seasonal northward expansion of the Subtropical/Transition Zone region is the cause for reasons that keep sockeye salmon from this region on the high seas.
9. A less drastic result of this pressure is the role of the ocean in determining a high northern diversion.
10. Any expansion of the inhospitable region will provide greater selective pressures to avoid it.

5.5 Tag Recapture Rates as a Proxy for Survival

It is not uncommon to attempt to estimate marine survival of salmon using the percentage of tags recaptured. Where the fishing effort is high and the probability of detection is high, the result can be a good approximation, if not an absolute estimate, of marine survival. Coded wire tags have been used routinely to understand the migration and survival of coho salmon and chinook salmon (Weitkamp and Neely, 2002; Daly *et al.*, 2009; Teo *et al.*, 2009). From 1964 to 1968, sockeye salmon postsmolts, potentially of any population, were tagged and released throughout coastal North Pacific Ocean, including the Bering Sea (Hartt and Dell, 1986). A total of 40, or 0.4% of the 9,883 tagged in these years was subsequently recovered after two or three years at sea.

Of the 40 recoveries of tagged age-x.0 sockeye salmon that have ever been recovered, six (14.6%) were taken in one seine set on the coast of Southeast Alaska on July 24, 1968. Hartt and Dell (1986) did not report the numbers caught on that specific day, but they made only four sets during a 10-day period, with a total of 59 sockeye salmon caught in the four sets. If all 59 sockeye were taken in only one of these four sets, the minimum survival rate from that one set would have been approximately 10%. If each of the four sets caught ¼ of the 59 fish, the survival rate from the set with the tagged fish would be approximately 68%. Each of these six tagged sockeye salmon was recovered in fisheries along the British Columbia coast in 1970.

In general, however, the tag recapture rates measured in the seine operations from 1964 to 1968 were remarkably low, considering that the average smolt-to-adult survival for Chilko Lake sockeye salmon during brood years that correspond to these tagging years (~1961–1966) was approximately 8.5%. Why should the probability of survival of sockeye salmon tagged at sea at a later stage of life be more than an order of magnitude lower than the probability of survival of fish just leaving Chilko Lake? On average, it cannot be lower, so the results suggest either heavy mortality from tagging or a remarkably low probability of tag detection, or a combination of both. It suggests that reliable measures of survival will not be found in the existing high seas tagging data.

5.6 Leading Indicators of Survival

> *In generating the 2009 forecast, long-term average productivities had been assumed, which seemed reasonable given that marine indicators suggested that conditions for salmon going to sea in 2007 would be relatively good.*
>
> Crawford and Irvine, 2010

5.6.1 Comparisons with coho salmon survival

Most Fraser River sockeye salmon and most coho salmon rear in freshwater for one year before migrating to sea (Sandercock, 1991). The value of observing variations in the survival of coho salmon, for a study of sockeye salmon, is their habit of returning to spawn one year earlier than sockeye salmon of the same brood year. A large fraction of the year-to-year variation in marine survival of coho salmon is shared commonly with other coho stocks along the North American continent suggesting that a large-scale factor (or factors) is affecting all (Teo *et al.*, 2009). While the two species have different behaviours upon reaching the ocean, there is a potential for oceanic anomalies to affect both species, where they share a common environment. Indeed, this was the case for the 2003 brood year when both species entered a coastal ocean in 2005, which was not very hospitable for some salmonids (Mackas *et al.*, 2006, 2007).

Some experimental forecasts are beginning to consider how variation in the coastal oceanic environment affects salmon survival. Trudel *et al.* (2009), for example, described how low coho postsmolt growth is associated with poor coho marine survival. For the 2005 brood year (2007 ocean entry year), marine survival varied markedly among populations (Fig. 51). For the the Strait of Georgia populations, marine survival of the

2005 brood year was low but not the worst ever observed; that accolade belongs to the 2003 brood year. Marine survival of the 2005 brood year of Carnation Creek coho salmon near Barkley Sound was remarkably high, but this is (currently) a small run of coho salmon with few spawners where small changes in numbers can generate large changes in survival percentage. Marine survival of the larger Robertson Creek coho salmon population for the 2005 brood year was near the long-term average.

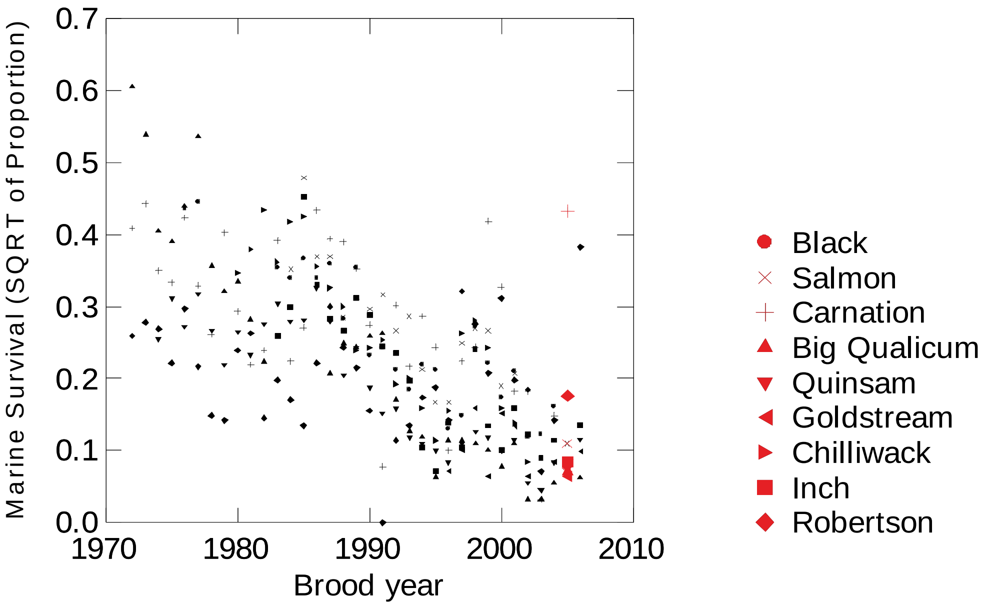

Fig. 51 Marine survival (√ transformed to emphasize variation at low survival) *versus* brood year for seven hatcheries in the Strait of Georgia and two (Robertson and Carnation) on the west coast of Vancouver Island. Marine survivals for the 2005 brood year (2007 ocean entry year) are highlighted in red.

Forecasts of survival and returns of Fraser River sockeye salmon have been made on the basis of the Strait of Georgia surveys by DFO but forecast performance has been highly variable during the short period it has been attempted. As the focus of sampling in the Strait of Georgia is coho and chinook salmon survival, its summer and fall sampling schedule captures only a fraction (probably variable from year to year) of the April–July migration of Fraser River sockeye salmon postsmolts from the Strait of Georgia. Nevertheless, these data were used to predict the returns of Fraser River sockeye salmon beginning in 2007 (DFO, 2008). The first forecast in 2007 was for above average marine survival and above average returns, based largely on the observation that the sockeye salmon postsmolts caught that year in the Strait of Georgia were larger than in previous years. Returns in 2007 were among the lowest observed, with the lowest marine survival ever recorded to that point in history. Likewise, sockeye salmon returns to the Fraser River in 2008, based on the Strait of Georgia sampling in 2006, were expected to provide above average returns. Returns in 2008 were below average, with no fishery permitted. The forecasts of Fraser River sockeye salmon returns in 2009, based on sampling in 2007, were expected to be extremely poor, and this was what occurred.

5.6.2 Preliminary signs of 2010 abundance[7]

Gillnet test fisheries in the approach routes to the Fraser River are augmented each year by purse seine test fisheries as the abundance of the annual return builds. They provide data on the abundance of maturing age-1.1 sockeye salmon (jacks) that the gillnet test fisheries miss. Jacks sockeye salmon spend only one year at sea before maturing and therefore are too small to be caught by the mesh size of commercial gillnets. Although they represent only a small fraction of the population each year, the value of jack abundance information, if a representative sample can be obtained, is a one-year look ahead at the magnitude of the cohort that will return the following year (assuming relatively constant age at maturity).

From 2000 to 2009, Fraser River sockeye salmon jacks in the Blinkhorn Island test fishery (upper Queen Charlotte Strait) are about twice as abundant as in the San Juan purse seine test fishery. Nevertheless, there is a highly significant positive correlation ($r = 0.97$, $P < 0.001$) between the aggregate annual CPUE of sockeye salmon jacks caught in the Blinkhorn Island purse seine test fishery and the same in the San Juan purse seine test fishery (Fig. 52). Although the magnitude of the correlation is heavily influenced by the high catches of jacks of the 2006 brood year, *i.e.*, jacks that returned in 2009, it suggests that over the range of observations the two independent purse seine test fisheries are detecting the same jack abundance signal. The correlation for older maturing sockeye salmon is 0.64.

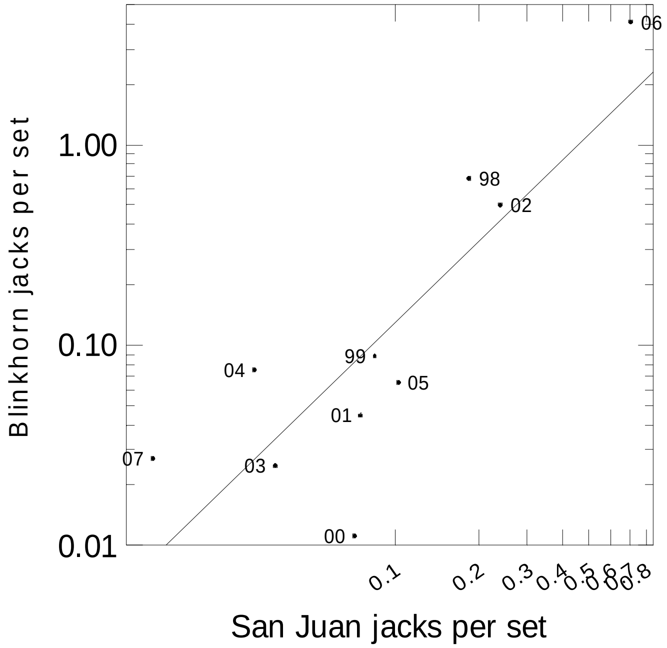

Fig. 52 Comparison of Blinkhorn Island sockeye salmon jacks per set *versus* the same at San Juan, on a log scale.

The relationship between the average CPUE of sockeye salmon jacks in the test fisheries and the following year's CPUE of adult sockeye salmon (Fig. 53) or total brood year returns (Fig. 54) indicates that this measure may be useful for detecting some of the large-scale changes in abundance that have been observed from 2000 to 2010. The 2006 brood year outlier was evident in 2009, but because it was more than five-fold greater than the next highest value (1997 brood year), it was difficult to know how large the return would be. As there was no fishery in 2009, the purse seine test fisheries were one of the few sources of this information.

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[7] Summary of a presentation to the DFO Fisheries Oceanography Working Group, February 16–17, 2010.

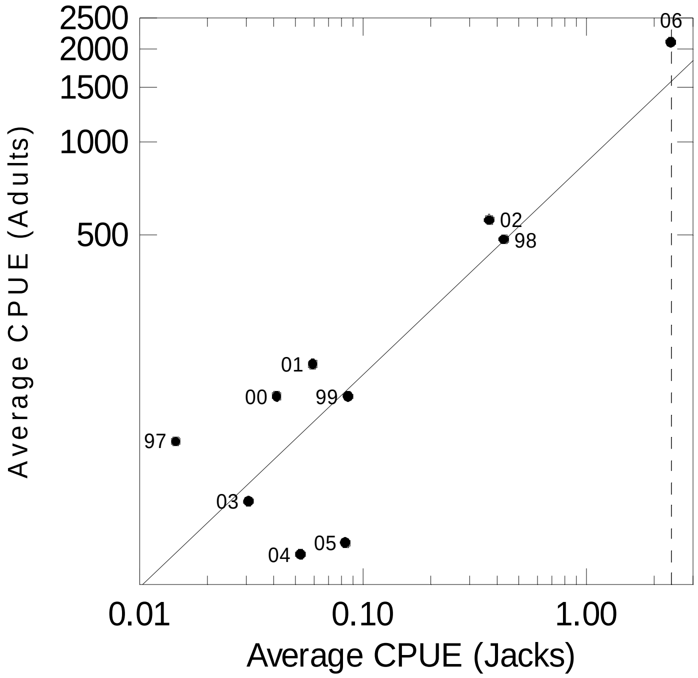

Fig. 53 Average CPUE of adult sockeye salmon in the Blinkhorn Island and San Juan purse seine test fisheries *versus* the same measure for sockeye salmon jacks, by brood year. Vertical dashed line indicates the jack CPUE measured in 2009 for the 2010 adult return. Data are presented on a logarithmic scale to emphasize variation at low CPUE.

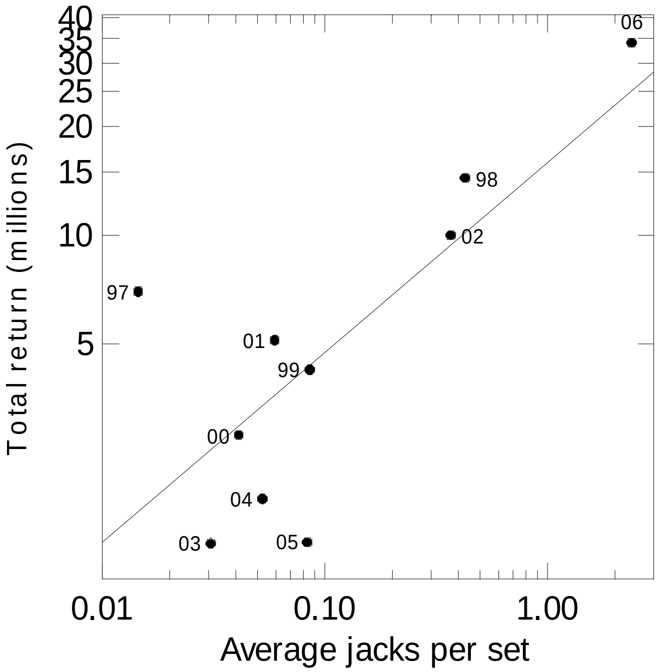

Fig. 54 Total returns of Fraser River sockeye salmon *versus* the average numbers of jacks caught in Blinkhorn Island and San Juan purse seine test fisheries, by brood year. The 2006 brood year total return is the in-season abundance estimate from August 31, 2010 provided by the Pacific Salmon Commission.

Sockeye salmon jack CPUE in the purse seine test fisheries does not appear to be very reliable when jack CPUE is <0.1 per set. The total return the following year can vary from 1.5 to 7 million. Most of the signal in this relationship is related to the abundance of Late-run sockeye salmon (as indicated by the four-year interval between years of high CPUE and high total returns). The relatively good return of the 1997 brood year was not detected by the jack CPUE index because the dominant populations that made up the return in 2001 do not have populations with significant numbers of jacks.

Summary – The existence of a relationship between the abundance of age-1.1 sockeye salmon in one year and the abundance of returns of age-1.2 sockeye salmon the following year is an indication that the magnitude of the sockeye salmon return to the Fraser River was largely determined prior to the time when the age-1.1 returned. If the major cause of variation in survival occurred after the age-1.1 sockeye salmon returned, there would be little reason for them to correspond. However, because most of the signal in that relationship comes from the Late-run sockeye salmon, it is not possible to know if it applies only to this component or to the others as well. Clearly, it cannot apply to stocks that lack detectable numbers of jacks.

6 Oceanography and Climate

In the eastern North Pacific Ocean, Pacific salmon are generally found in the Subarctic region of the Gulf of Alaska, although their range in North America extends from the Arctic Ocean to southern California (Groot and Margolis, 1991). While southern California is not normally considered Subarctic, it has a cool and productive coastal oceanic habitat because of summer upwelling winds. They create an oceanic habitat that makes it possible for the range of Pacific salmon to extend southward to latitudes they might not otherwise reach. The active upwelling zone is a relatively narrow band of water 10–25 km wide along the North American coast (Huyer, 1983), implying that unsuitable oceanic water is nearby and kept at bay by suitable winds. Their failure can have rather devastating effects. The widespread mortality of juvenile Pacific salmon in 2005 was attributed to the extremely delayed seasonal upwelling winds that year. For many populations of salmon that went to sea in 2005, from Vancouver Island southward, it was the worst survival on record. The low returns of maturing Fraser River sockeye salmon in 2007 were a result of the lowest recorded survival for this river. The remainder of this section considers sequentially, the oceanic environment along the migration route from the Strait of Georgia to the open Gulf of Alaska, with special attention given to the state of the environment while the 2007 ocean entry year of Fraser River sockeye salmon was at sea.

6.1 Strait of Georgia

6.1.1 Wind

Hourly meridional (V) and zonal (U) winds (m s^{-1}) from 1967 to the present (mid-2010) at the Environment Canada station at Sandheads (49°06′21.225″ N, 123°18′12.123″ W) were rotated by 125° to provide the along-strait and cross-strait components of wind speed in the Strait of Georgia instead of N–S/W–E components that are typically reported by Environment Canada. The rotated U component is the wind speed toward 35° compass direction and the V component is the wind speed toward 305°. Relatively rare gaps in the time series were filled by developing regression equations with Entrance Island (near Gabriola Island) winds. Weekly averages of the rotated winds were calculated from the hourly values using all years of data and from these, weekly anomalies were calculated.

Apart from the first week of 2007, average weekly cross-strait winds did not deviate much from average for most of 2007 (Fig. 55). Weekly average along-strait winds were more variable, with a tendency for stronger than average up-strait winds (southeasterlies) through most of the spring. Up-strait winds are the norm at Sandheads most of the year.

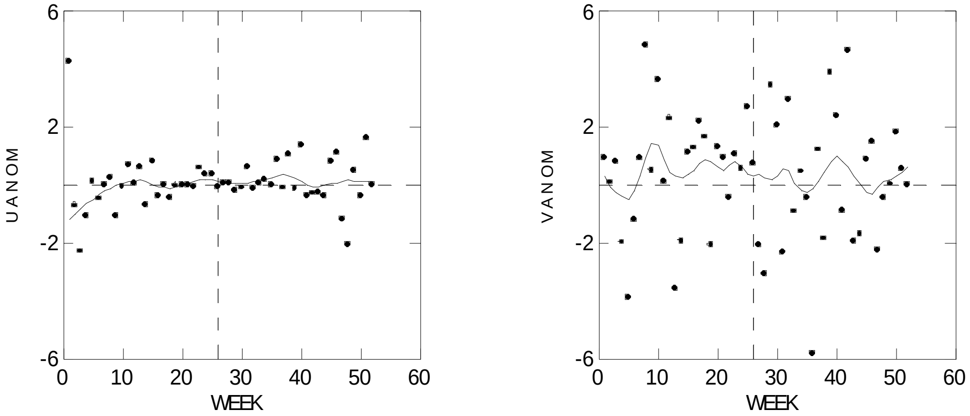

Fig. 55 Weekly cross-strait (left) and along-strait (right) wind speed anomalies by week in 2007. Vertical dashed line indicates the end of June. Horizontal dashed line is the average value from 1967 to 2010. A loess smoother was used to create the trend lines. Rotated data courtesy of Susan Allen and Jeremy Sklad (UBC).

6.1.2 Fraser River discharge

The Fraser River is the single largest source of freshwater in the Strait of Georgia (Waldichuk, 1957). Most of its annual discharge comes from melting snow and this is reflected in the sharp increase in volume in spring and summer. It creates a large plume of fresh and brackish water that spreads thinly across the Strait of Georgia and is mixed with the salty water below by tides, winds, and currents (Fig. 56). Estuarine flow carries most of the Fraser River discharge out Juan de Fuca Strait where it feeds the buoyancy-driven Vancouver Island Coastal Current (Freeland *et al.*, 1984). Within the Strait of Georgia, the fresh/brackish surface layer is buoyant because it is less dense than the colder, saltier water that lies beneath it. The surface layer is warmed by radiant energy from the Sun more than the deeper layers, which reinforces the density gradient. The Fraser River also provides the surface layer of the Strait of Georgia, with nutrients of anthropogenic (agricultural runoff, sewage) and natural origins. The daily volumes of freshwater entering the Strait of Georgia from the Fraser River were often in the upper quartile in the spring of 2007 (Fig. 57a) but at no time were they at extreme levels in the nearly 100-year historical record.

Fig. 56 Satellite image of lower Vancouver Island and surrounding waters. Note the muddy plume of the Fraser River discharging into the Strait of Georgia.

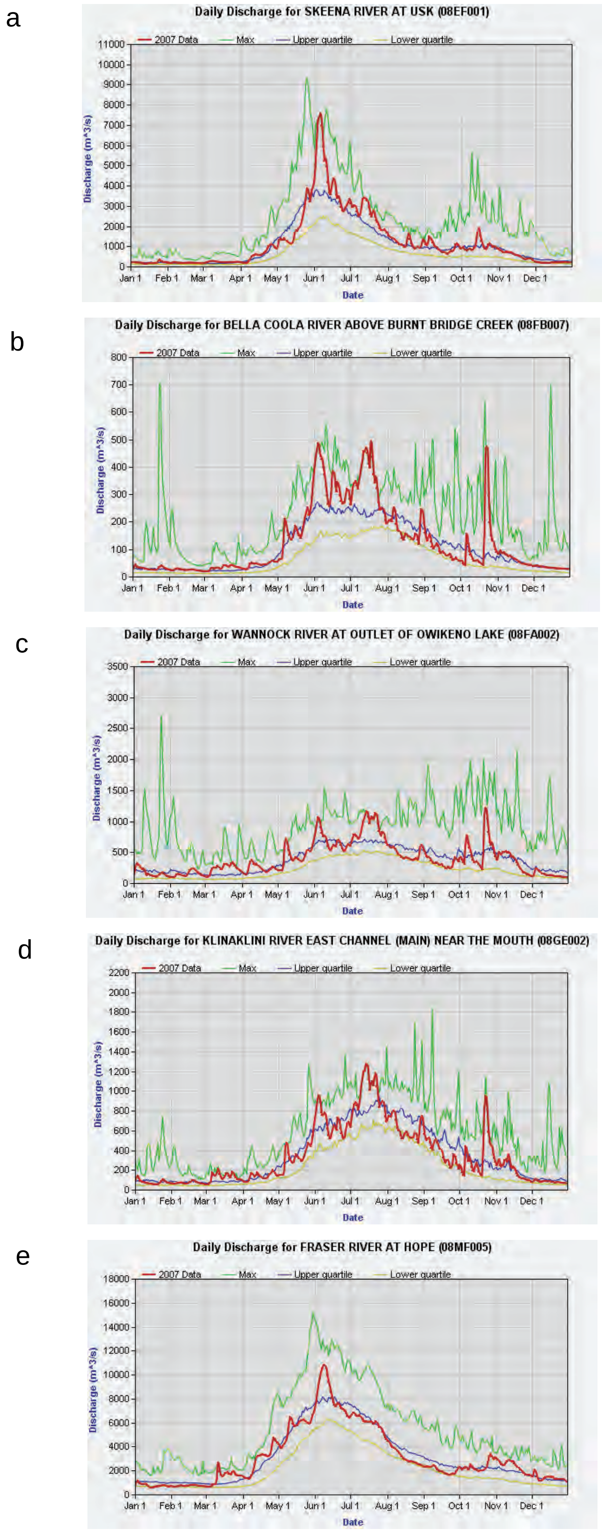

Fig. 57 From North (top panel) to South, daily river discharge plots of the Fraser (a), Klinaklini (b), Wannock (c), Bella Coola (d), and Skeena (e) rivers in 2007 (red) *versus* maximum (green), upper quartile (blue), lower quartile (yellow).

6.1.3 Surface water properties at lighthouses

Detailed surveys of temperature and salinity at depth in the Strait of Georgia have been conducted rather infrequently. As a consequence, it is difficult to follow the history of seawater in the Strait of Georgia in any detail from scientific cruise results without interpolating/imagining the kinds of variation that may have occurred between cruises. This may change in the future with the recent development of an undersea cabled network in the Strait of Georgia[8]. Sampling by the navy and DFO near Nanoose Bay is the only exception (see Section 6.1.4) but it is a single station that likely does not reflect the state of the Strait of Georgia as a whole. Therefore, the history of hydrographic properties in the Strait of Georgia often relies on frequently measured surface properties.

In 1934, John Tully, an oceanographer with the Fisheries Research Board of Canada, encouraged keepers at some coastal lighthouses to adopt standard practices for measuring temperature and salinity (Fig. 58). Other lighthouses, including some in the Strait of Georgia, joined the monitoring program in later years: Entrance Island (1936), Chrome Island (1961), and Sisters Islets (1968). The unique value of these records is that, for the most part, the methods or instrumentation have not been changed. Having more than one measuring site provides an opportunity to understand differences and similarities around the Strait of Georgia. Furthermore, sampling at the lighthouses will likely reflect the part of the ocean that sockeye salmon experience because properties there are measured at the surface where the fish are known to migrate (Groot and Cooke, 1987). The record of daily observations of temperature and salinity can be downloaded from the DFO website[9]. Density was computed from these observations using a 1985 algorithm developed by UNESCO/IOC and provided by DFO.

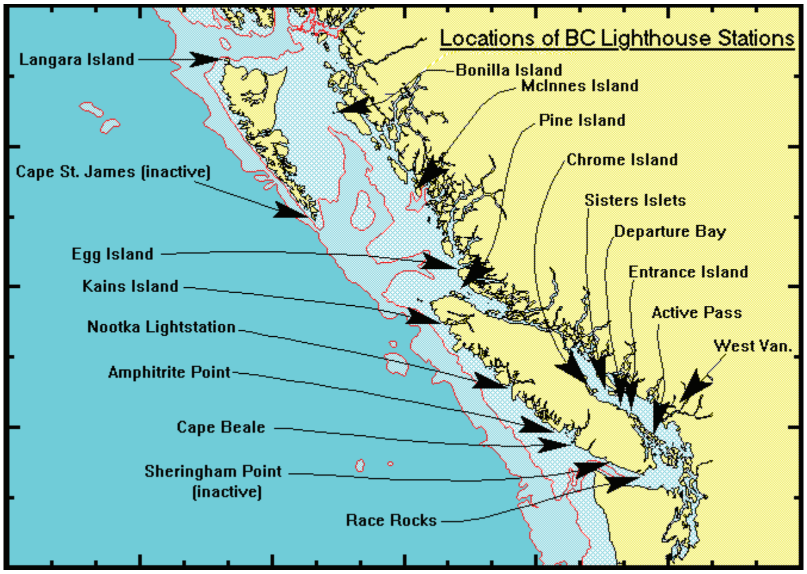

Fig. 58 Ocean–climate monitoring stations along the coast of British Columbia. Image from Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca).

Annually averaged temperature, salinity, and density at stations in the Strait of Georgia share a common pattern of interannual variation since 1968. Based on principal component analyses, the shared components are: SST = 92%, SSS = 86%, and density = 85%, based on measurements since 1968 (when Sisters Islets began recording data). So, it appears that if one station is warmer and fresher in any given year, so are the others. It also appears that if one station has highly variable temperature or salinity in one year, so have the

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[8] http://www.venus.uvic.ca

[9] http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm

others. This tendency to share averages or variances among stations is a result of physical forces (*e.g.*, winds, tides) which tend to affect all stations similarly. The station with the densest surface seawater is Chrome Island in the northwestern Strait of Georgia and the station with the least dense surface seawater is Entrance Island, across the strait from the Fraser River. A second property of these stations is the shared relationship between the annual mean value and the annual variance. At each station there is a significant negative correlation between the mean and variance indicating that years with higher average seawater density are years with lower variability in that property.

Daily observations not only reveal the nature of the seasonal fluctuations in surface water properties at various locations throughout the Strait of Georgia, but also show the ranges of these water properties (Figs. 59, 60, and 61). To make them more comparable, the data in these figures were restricted to the period from 1968 when the Sisters Islets record began. Against this historical background of daily observations it is possible to evaluate how the spring of 2007 (highlighted in red) compares with history. The comparison indicates that 2007 was not extreme in the historical record at any of the four the Strait of Georgia stations. Salinity and density at Departure Bay were lower than average for most of the year. Measurements at the Sisters Islets station were automated following a decision to de-staff the lighthouse in 1996/97. It did not have a full year of observations in 2007, and the salinity and density values are suspicious anomalies that look more like instrumentation errors that may have arisen from automating these measurements (Figs. 60 and 61). Salinities are never so high in the Strait of Georgia.

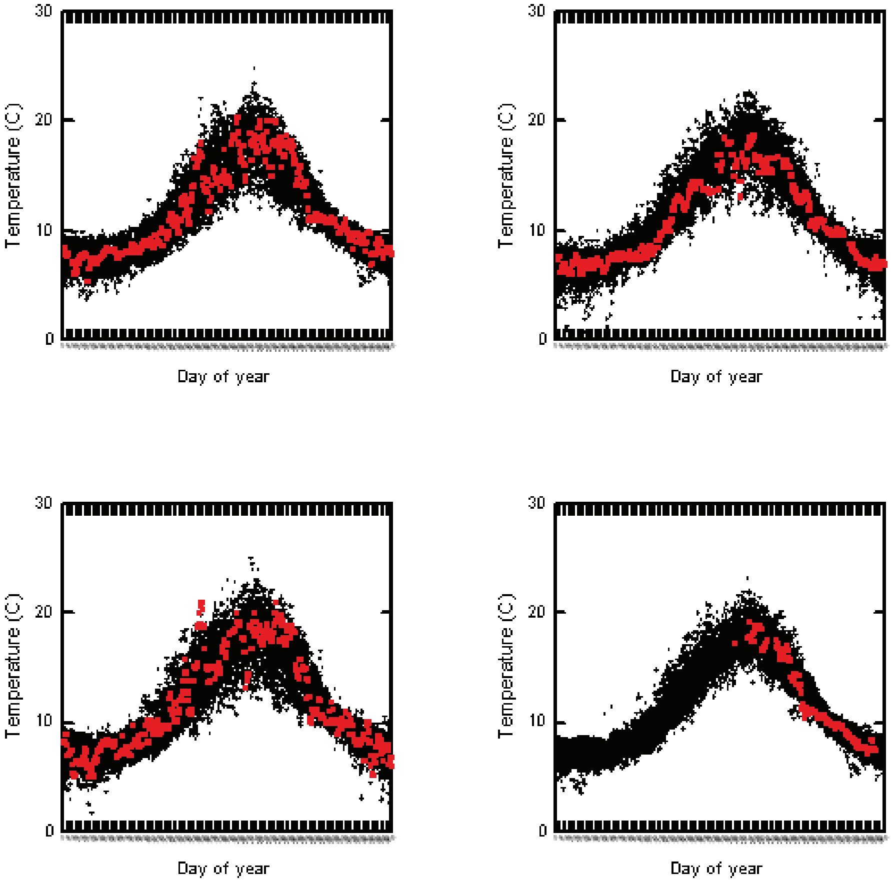

Fig. 59 Daily sea surface temperatures (°C) at four stations in the Strait of Georgia (clockwise from top left: Chrome Island, Departure Bay, Sisters Islets, Entrance Island). The year 2007 is highlighted in red against all other measurements observed at that station from 1968 to 2010. Data source: Fisheries and Oceans Canada.

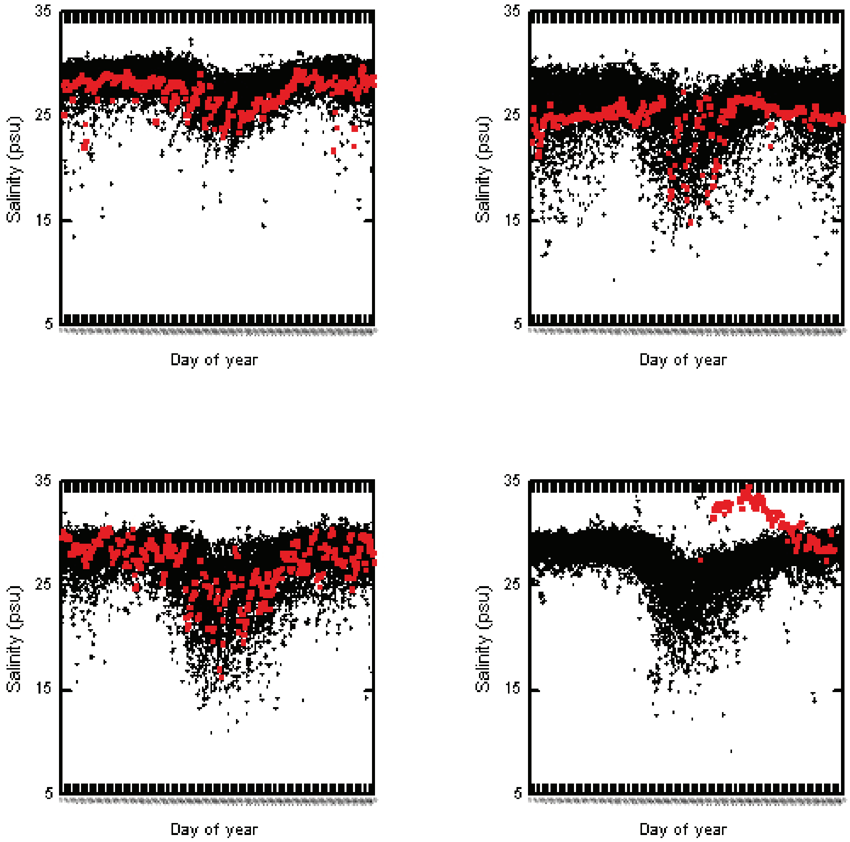

Fig. 60 Daily sea surface salinities (psu) at four stations in the Strait of Georgia (clockwise from top left: Chrome Island, Departure Bay, Sisters Islets, Entrance Island). The year 2007 is highlighted in red against all other measurements from 1968 to 2010. Data source: Fisheries and Oceans Canada.

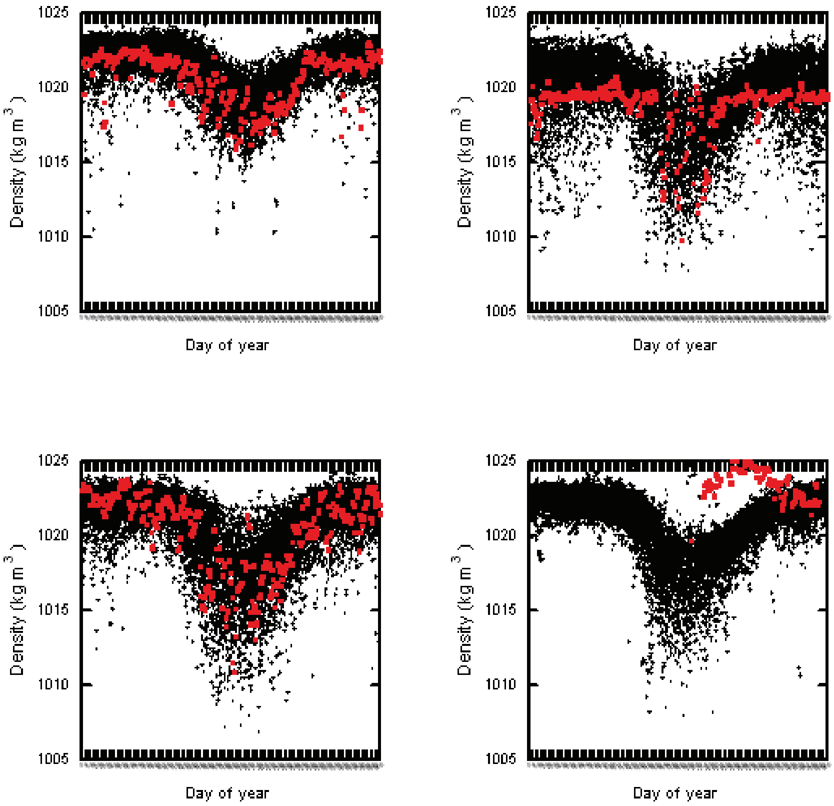

Fig. 61 Daily sea surface densities (kg m^{-3}) at four stations in the Strait of Georgia (clockwise from top left: Chrome Island, Departure Bay, Sisters Islets, Entrance Island). The year 2007 is highlighted in red against all other measurements from 1968 to 2010.

6.1.4 Hydrography at Nanoose station

The Nanoose station record of temperature, salinity, and depth extends from the late 1970s to the present (Fig. 62). This station is located (49° 18.7′ N, 124° 2.7′ W) on the opposite side of the Strait of Georgia from the main migration route of Fraser River sockeye salmon and the extent to which it reflects the general hydrography of the entire strait is unknown. Cold water intrusions into the deeper waters of the Strait of Georgia occurred in the spring and early summer of 2007 following four years of relatively warmer water at depth. This inflow of deeper water from the Pacific Ocean via Juan de Fuca Strait is a normal feature of water circulation in the Strait of Georgia (Masson, 2002). The 2007 intrusion returned the water column to the long-term average temperature measured over the period from 1999 to 2007 (Masson, 2008). The coldest intrusions in recent years occurred in 2001 and 2002 (Fig. 63).

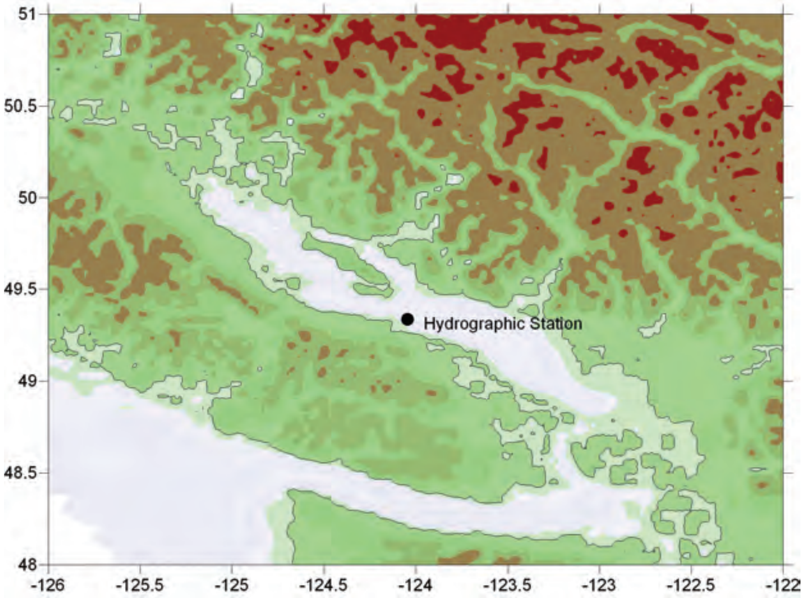

Fig. 62 Location of the Nanoose Bay hydrographic station in the Strait of Georgia.

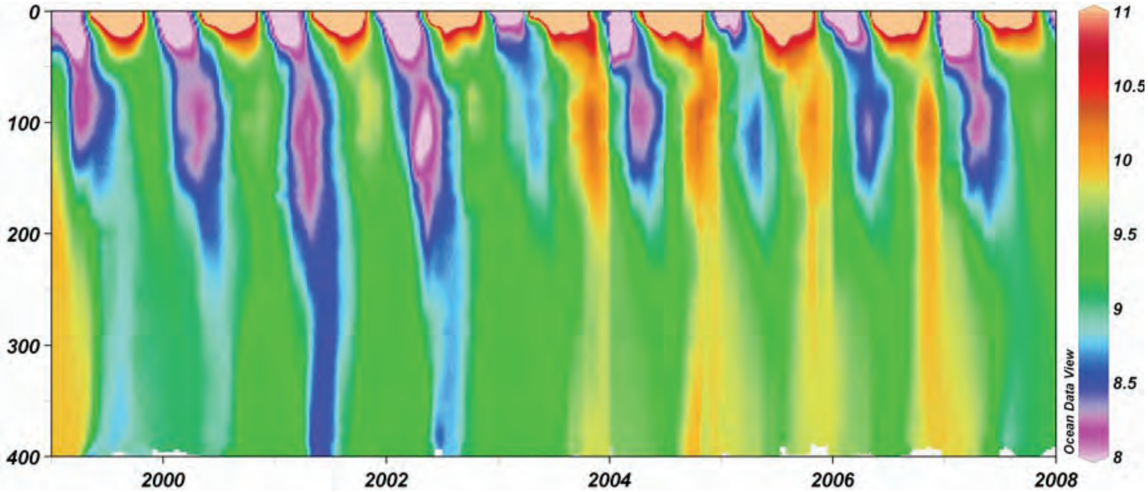

Fig. 63 Smoothed temperature (°C) by depth and year measured at the Nanoose Bay station (depth in metres) in the Strait of Georgia, starting from 1999. Figure from Masson (2008).

The Nanoose Bay station data have been collected regularly but less often than daily, so weekly average water density was computed at each depth from all casts to create a seasonal climatology at depth. For example, during the 13-week period from March 1 to May 31, 2007, 17 casts were taken. Departures from average were computed to generate a time series to indicate whether density was greater or less than average at each depth. An analysis of variance of the weekly density anomalies was used to determine if there were statistically significant differences among years during the period when most sockeye salmon are migrating through the Strait of Georgia (weeks in May–June pooled). The analysis indicated that there are significant differences in water density among years in the upper water column (Fig. 64). While the spring of 2007 was a strong negative anomaly (fresh) at Nanoose Bay, three other years (1994, 1996, 1997) were more extreme. A similar result was obtained if the analysis was done using only the upper 5 m instead of 10 m. What does appear in the analysis is that densities in the upper 10 m tended to be above average before 1993, and most are below average from 1993. However, considerable year-to-year variability precludes making a definitive statement about the nature of this low-frequency variability in the time series.

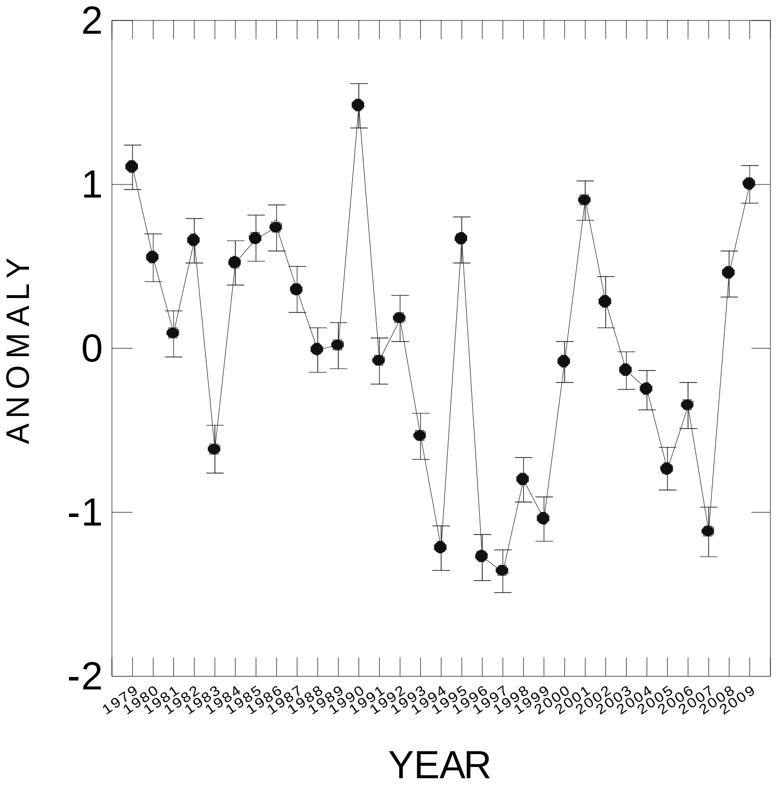

Fig. 64 Average water density anomalies near Nanoose Bay in the upper 10 m of the water column from 1979 during May and June. Vertical bars indicate ±2 standard error.

While the density of the surface layer of the water column is of general interest, the greater interest is whether the gradient with depth has increased, decreased or stayed the same. If the gradient has increased over time, or in any particular year, nutrient re-supply from depth would require more work to mix them to the surface. In regions like the Subtropical North Pacific, for example, the upper layer is permanently stratified leaving the upper water column with reduced phytoplankton production (Polovina *et al.*, 2001). A simple method of examining water column stability, based on Gargett (1997), is to look at the average density difference between an upper and lower layer to determine if it has changed. Average densities at Nanoose Bay station were computed by week. In consideration of the relatively shallow mixed layer in the Strait of Georgia, the difference of the average densities in the upper 5 m and the average densities in the 5–10 m layer was used as the index. As before, interannual variation in the stability index was examined by pooling the weekly results over the May/June period when most sockeye salmon are in the Strait of Georgia. This analysis indicated that seven years in the period from 1988 to 1999 tended to have higher water column stability in the upper 10 m than the period before or after (Fig. 65) but the median of weekly values for the spring of 2007 is not remarkably different from the rest of the decade.

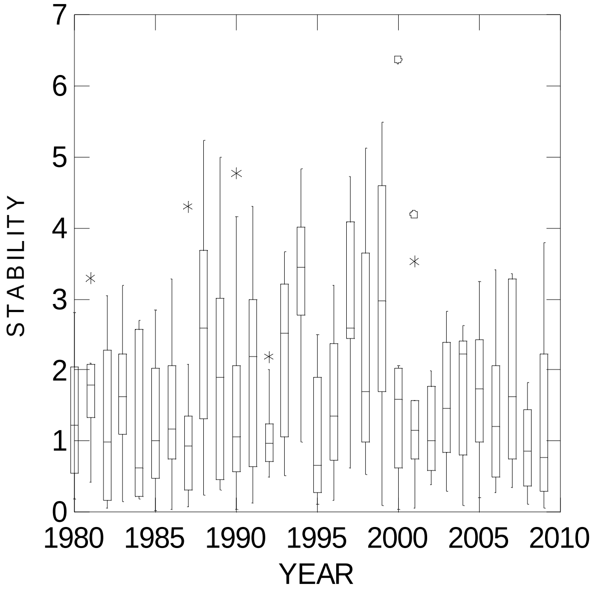

Fig. 65 Box and whisker plots indicating variation in a weekly water column stability index during May and June computed at the Nanoose Bay station by year for the months May and June, pooled. Units are σ_θ. The horizontal line at the center of each box is the median of weekly values. The limits of the box represent the 25 and 75% quartiles.

In March, April, and May 2007, a total of 17 hydrographic casts was conducted at the Nanoose Bay station. The depth at which the shallowest measurement was taken at each cast varied from 1–3.2 m from the surface and varied among casts. Six casts had shallowest observations at 1 m, ten casts at 2 m, and one cast had its shallowest measurement at 3.2 m depth. The average minimum observation was at 1.72 m depth. One estimate of the average depth of the mixed layer during these months in 2007, based on salinity measurements from these 14 casts was ~1.75 m which is shallower than most of the shallowest observations during this period (Beamish *et al.*, 2010). The very shallow average mixed layer depth for the period may have arisen because the mixed layer depth was set arbitrarily to zero if the algorithm failed to generate an estimate. If these zeros were included in the computation of the average, a shallow value would have been produced.

6.1.5 Nanoose Bay as an index of water properties in the Strait of Georgia

Comparing monthly averaged surface seawater density computed from lighthouse data with that measured at the Nanoose Bay hydrographic station since 1978 reveals a seasonal pattern of shared interannual variation between the three locations (Fig. 66). Monthly-averaged near-surface (<3 m) seawater density at Nanoose Bay is most similar to monthly-averaged surface seawater density at the Chrome Island lighthouse in February. The correlation diminishes through the late winter and spring to a low in June. Monthly-averaged near-surface (<3 m) seawater density at Nanoose Bay is most similar to monthly-averaged surface seawater density at the Entrance Island lighthouse in February. As with Chrome Island, the correlation diminishes to a minimum in June. It suggests that the density of the near-surface seawater at the Nanoose Bay station becomes least like that at the two lighthouses at other locations in the Strait of Georgia in June. Whether this reflects an increased spatial heterogeneity in surface seawater density at this time of year is unknown. Correlations between Chrome Island and Entrance Island lighthouses were highest in July. This may reflect a greater tidal influence at the lighthouses, where more intense tidal mixing over the rough bathymetry of the shoreline may tend to reduce differences that develop in less turbulent waters.

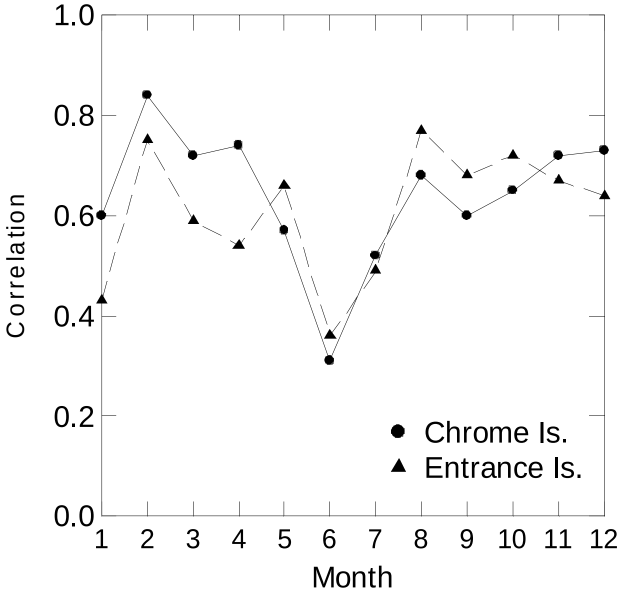

Fig. 66 Month-to-month correlation between surface seawater density at the Nanoose Bay hydrographic station and surface seawater density measured at two lighthouses in the Strait of Georgia. All are on the western side of the strait.

6.1.6 Nutrients and chlorophyll

A mid-channel transect of 20 stations through the Strait of Georgia and Juan de Fuca Strait has been sampled by DFO for *in situ* chlorophyll and nutrients since 2002. Phytoplankton and nitrate concentrations during the winter and spring of 2007 were found to be similar to what had been observed from 2002 to 2006 (Peña, 2008). During the summer of 2007, however, phytoplankton concentrations were higher at most of the stations. Phytoplankton species composition was determined in most of these years but 2007 was not among them. By autumn, phytoplankton concentrations were lower, and nitrate concentrations higher, than in previous years.

6.1.7 Zooplankton

Samples of zooplankton have been collected annually during the Strait of Georgia/Juan de Fuca Strait spring transect since 2002, however, no zooplankton data were collected in the survey of 2007.

6.1.8 Ichthyoplankton

An ichthyoplankton community is made up of fish eggs and larval fishes which have recently hatched. Fish eggs hatch into fish larvae in time to meet the seasonal abundance of prey that appears in spring. Hence, the greatest abundance of ichthyoplankton occurs in spring. DFO had an ichthyoplankton research program in the Strait of Georgia and on the west coast of Vancouver Island in the late 1970s and early 1980s. When the program ended, an extensive series of data reports was published (*e.g.*, Mason *et al.*, 1981a–c; Mason *et al.*, 1981a–d).

The University of Victoria resumed research on the larval fish (ichthyoplankton) community in the Strait of Georgia beginning in 2007. Annual surveys were designed to provide a representative overview of the ichthyoplankton community in spring. At each station, a Tucker trawl net was towed at 2 knots for 15 minutes. The samples were preserved for examination in the laboratory. From 2007 to 2010, the last week of April was sampled every year. Preliminary results indicate that the concentrations of ichthyoplankton sampled during the last week of April did not differ among years (J. Dower and L. Guan, UVic, pers. comm.).

6.1.9 Temperatures in the Strait of Georgia in 2008

Deep waters of the Strait of Georgia began cooling in mid-2007 and this continued and intensified into 2008. Surface temperatures in the strait, however, remained warmer than average or average (at Chrome Island) through the sockeye salmon outmigration (Masson, 2009). SSTs at Chrome Island were not significantly different (ANOVA: P = 0.52) in May–June of 2007 compared to May–June of 2008.

Summary – The stability of an ocean water column (resistance to vertical mixing) is determined by the characteristics of its density profile. As both temperature and salinity (and pressure) affect density, water column stability is determined by their joint influences. In the absence of other influences, higher salinity water is denser than lower salinity water, and colder water is denser than warmer water if there is no difference in salinity. A typical density profile in the Subarctic Pacific has a surface layer of uniform density overlying a transitional layer with rapidly changing density: higher density than the surface but less dense than the deep water. If the depth of the uniform surface layer is approximately equal to the depth of the euphotic zone (depth with enough light for plankton to grow), the surface mixed layer becomes nutrient depleted by the growing plankton, and because there is no recirculation by vertical mixing from below, biological production is limited. In the Strait of Georgia, however, the surface mixed layer is relatively shallow, on the order of a few metres, and much shallower than the euphotic zone so some nutrients remain available for plankton growth beneath the mixed layer during the summer when stratification is greatest. Year-to-year variations in these physical and chemical processes are responsible for establishing the biological characteristics that sockeye salmon postmolts experience upon entering the Strait of Georgia.

Sockeye salmon smolts begin to leave the Fraser River estuary during the last two weeks of April (Groot and Cooke, 1987) so their interaction with the Strait of Georgia waters occurs primarily in May and June, except for underyearling sockeye salmon, which tend to delay ocean entry until July (Birtwell *et al.*, 1987; Healey, 1980). Seawater density in the upper layer (<10 m) at Nanoose Bay was clearly lower than average in the spring of 2007, when the 2009 return year was just going to sea, but several other years in the 1990s had even lower values. There are more negative density anomalies in the latter half of the time series and more positive density anomalies in the earlier half, but there is also considerable interannual variation. The years 2008 and 2009 were strongly positive density anomalies. Water column stability in the top 10 m in May and June of 2007 at Nanoose Bay was within the range of variability observed there since 1979. Year-to-year variation in water properties in the near-surface layer at the Nanoose Bay station resembled that found at lighthouses distributed around the Strait of Georgia, but the resemblance varies seasonally. Near-surface water properties at the Nanoose Bay station are least correlated with these other locations in the Strait of Georgia (Chrome Island and Entrance Island) in the month of June. The mid-channel transects of water properties (since 1999), nutrients, and chlorophyll (since 2002) from the northern end of the Strait of Georgia to the mouth of Juan de Fuca Strait revealed that 2007 was not unusual except for higher than average nutrients and chlorophyll in summer. The abundance of icthyoplankton in the Strait of Georgia in the last week of April of 2007 was no different from that found during the same week from 2008 to 2010 (J. Dower and L. Guan, UVic, pers. comm.). May and June average SSTs at Chrome Island were not significantly different between 2007 and 2008.

6.2 *Coastal Gulf of Alaska*

6.2.1 General description[10]

The Gulf of Alaska coastal area has a nearshore, poleward, buoyancy-driven coastal current called the Vancouver Island Coastal Current in the south and the Alaska Coastal Current in Alaska. During the summer months, the Alaska Coastal Current has local reversals and small eddies which can concentrate plankton and small fishes in convergence zones for foraging fish, birds, and marine mammals (Kline, 2006).

The broad and sluggish Alaska Current (3–6 m min^{-1}) originates in the bifurcation of the North Pacific Current as it reaches the North American continent from Asia (Dodimead *et al.*, 1963). It carries variable portions of the warm North Pacific Current northward along the coasts of northern British Columbia and Southeast Alaska into the northern Gulf of Alaska (Freeland, 2006). The Alaska Current turns westward in the northern Gulf of Alaska, where it is separated from the low nutrient Alaska Coastal Current by a highly variable mid-shelf region. The mid-shelf region is characterized by pronounced changes in water properties, chemistry, and species compositions of phytoplankton, zooplankton, and fish along cross-shelf gradients. Superimposed on these cross-shelf gradients is considerable mesoscale variability resulting from eddies and meanders in the boundary currents (Weingartner *et al.*, 2002; Stabeno *et al.*, 2004; Crawford *et al.*, 2006; Ladd *et al.*, 2007). Forced to the south by the Alaska Peninsula, the Alaska Current continues as the much swifter (18–60 m min^{-1}) Alaskan Stream as it follows a southwestward course along the Alaska Peninsula and the Aleutian archipelago (Weingartner *et al.*, 2009). A portion of the Alaskan Stream turns south and recirculates as part of the North Pacific Current, closing the loop to form the Alaska Gyre. The position of the North Pacific Current and the volume of water transported vary on interannual and decadal time scales, with associated variations in the Alaska Current (Parrish *et al.*, 2000; Weingartner *et al.*, 2002).

Starting from south to north, lighthouses at Egg Island, McInnes Island, and Bonilla Island (see Figure 58), are situated along what could be considered as an "inside" migratory path of Fraser River sockeye salmon postsmolts, while Amphitrite Point, Kains Island, and Langara Island are located on the "outside" migratory route that is landward of the shelf break on the west coasts of Vancouver Island and Haida Gwaii. The oldest of the salinity and temperature time series from these lighthouses begins in 1935.

By 2007, most of the Gulf of Alaska was significantly cooler than the peaks reached in 2005 and this was reflected in below average to average daily SSTs at many coastal lighthouses. However, in about mid-June, there was an abrupt shift to warmer water at five of six lighthouses. Only the McInnes Island lighthouse in Hecate Strait did not indicate a summer anomaly but there are indications of it at other lighthouses beyond the Strait of Georgia. The number of days that SST anomalies exceeded +2°C between mid-June to mid-September 2007 were: Amphitrite Point (10 days), Kains Island (14 days), Egg Island (12 days), Langara Island (1 day), and Pine Island (4 days) (Fig. 67). Stations in the Strait of Georgia did not exhibit this anomaly pattern (Fig. 59).

Daily salinity anomalies in 2007 tended to be fresh at most of these lighthouses, and very fresh at Egg Island in eastern Queen Charlotte Sound (Fig. 68). The abrupt positive anomalies in SST that appeared at some lighthouses were not accompanied by a similarly timed pattern of salinity anomalies except at Egg Island where salinity decreased to record lows in summer and SST increased.

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[10] Abstracted from Mundy *et al.* (2010).

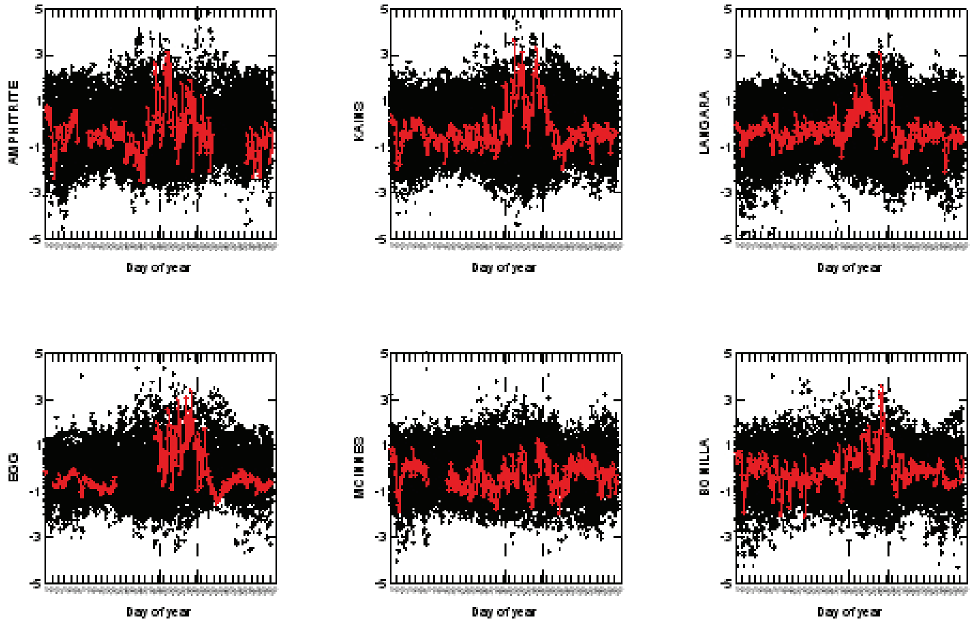

Fig. 67 Daily sea surface temperature anomalies (°C) at six ocean-climate monitoring stations beyond the Strait of Georgia (Amphitrite Point, Kains Island, Langara Island, Egg Island, McInnes Island, and Bonilla Island). The year 2007 is highlighted in red against all other anomalies observed at that station. Anomalies are observed values minus average values for each day of year. Average values are computed from the range of years, 1977 to present. Vertical dashed lines indicate July 1 and August 31 when most of the Fraser River sockeye salmon postsmolts would normally have left the Strait of Georgia.

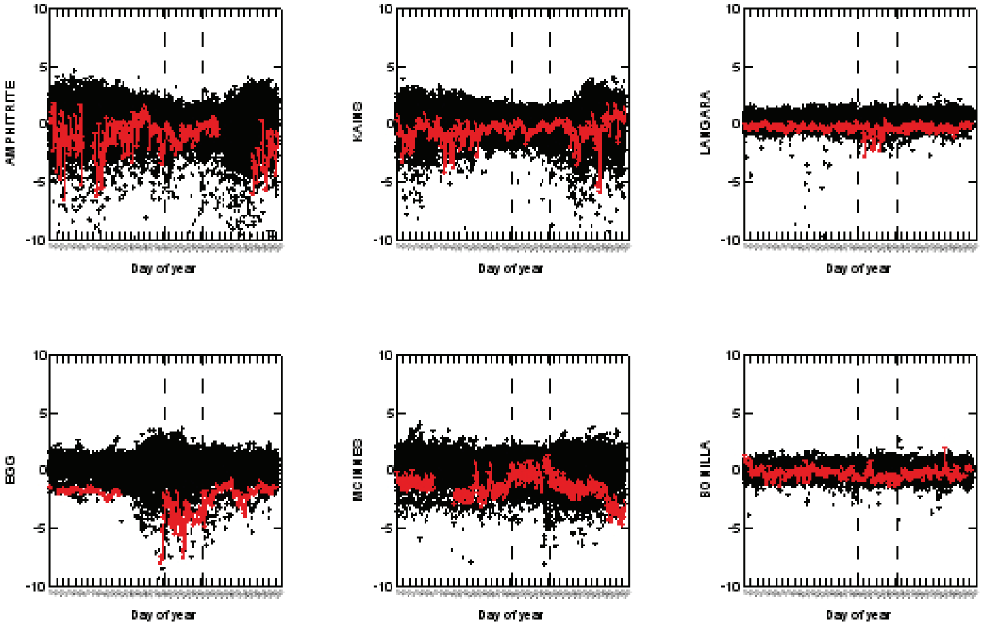

Fig. 68 Daily sea surface salinity anomalies (psu) at six ocean-climate monitoring stations beyond the Strait of Georgia (Amphitrite Point, Kains Island, Langara Island, Egg Island, McInnes Island, and Bonilla Island). The year 2007 is highlighted in red against all other anomalies observed at that station. Anomalies are observed values minus average values for each day of year. Average values are computed from the range of years, 1977–2008. Vertical lines indicate July 1 and August 31 when most of the Fraser River sockeye salmon postsmolts would normally have left the Strait of Georgia.

6.2.2 Queen Charlotte Sound

During the summer of 2007, the surface layer of eastern Queen Charlotte Sound in the vicinity of Egg Island had the lowest average salinity on record (since 1970; Fig. 69). Summer salinities at Egg Island had generally been lower on average since 2004, but 2007 was an extreme among the recent low salinities. Summer surface waters at Pine Island in Queen Charlotte Strait had the fourth lowest July and August average salinity since 1937. The extreme low salinity anomaly in 2007 was relatively widespread in the region. Repeated measurements from DFO ship surveys of average surface salinity along a transect from Triangle Island eastward in June and July from 1998 to 2009 found that 2007 was the most extreme fresh anomaly (Fig. 70).

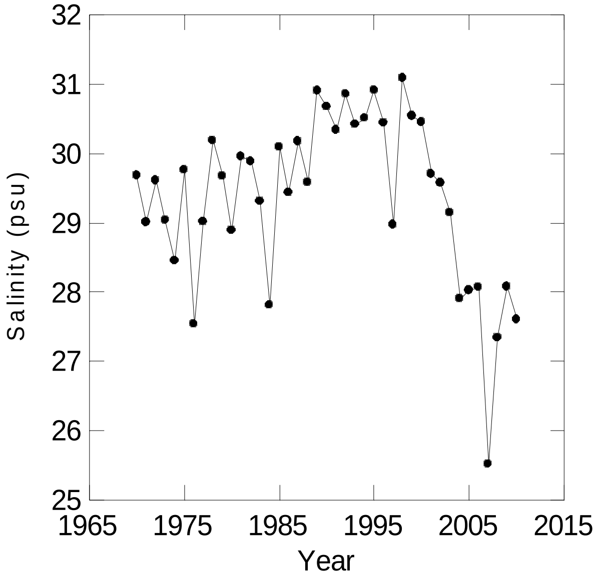

Fig. 69 Average of daily salinity measurements at Egg Island (eastern Queen Charlotte Sound) in July and August from 1970 to present. Data maintained by DFO.

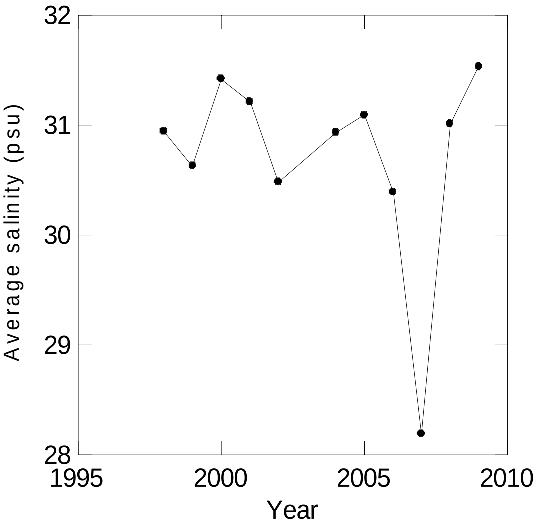

Fig. 70 Average surface salinity along a transect from Triangle Island eastward in Queen Charlotte Sound from 1998 to 2009 (no cruise in 2003). Data courtesy of Marc Trudel (DFO).

The unusual layer of low salinity water that appeared in Queen Charlotte Strait/Sound in the summer of 2007 was caused by extremely high river discharge volumes from snow melt combined with high precipitation in early June of 2007. The accumulation of snow in the coastal mountains during the winter of 2006/07 was exceptional and major flooding was anticipated[11]. Furthermore, the water content in the snow was much higher than normal. Cool weather during April of 2007 delayed or diminished the melt such that when the seasonal warming accelerated, the volume of meltwater was extreme. A significant storm in early June added considerable amounts of rain on the melting snow, but its effect was largely restricted to northern British Columbia rivers (Skeena, Bulkley) and the northern part of the Fraser River watershed. Fraser River discharge, while higher than normal in 2007, did not increase to record levels, as was expected in 2007. Discharge from the Wannock River (Rivers Inlet), a major freshwater source in eastern Queen Charlotte Sound, and the Klinaklini River (eastern Queen Charlotte Strait) were the highest on record in July 2007 (Fig. 71). The consequences of large volumes of freshwater on the surface of Queen Charlotte Strait/Sound are considered further in Section 6.4.

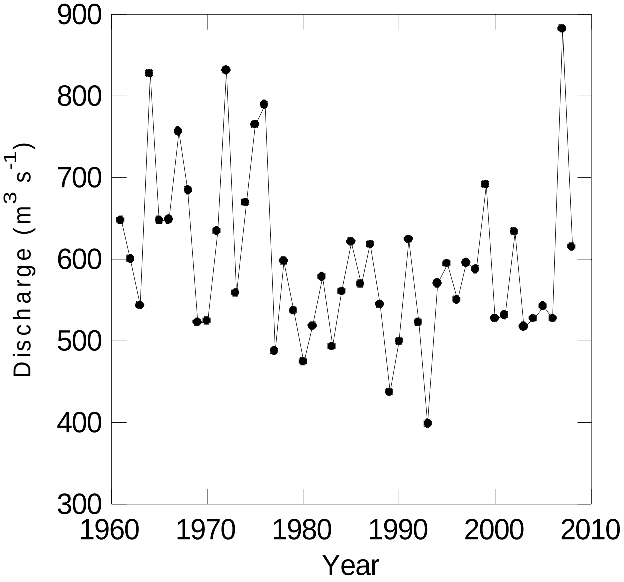

Fig. 71 Discharge from the Wannock River (Rivers Inlet) in July. The highest peak occurred in 2007. Data from Environment Canada.

Wind speed and direction in the Queen Charlotte Sound region can be approximated from the monthly average wind speeds at 52.5°N 130°W from the NOAA/NCAR NCEP re-analysis, a database that includes estimates of global monthly average wind speeds from 1948 to present on a 2.5° × 2.5° lat./long. grid. It is evident from these data that extreme wind anomalies can be added to the list of oceanic extremes that occurred in Queen Charlotte Sound in the summer of 2007. July 2007 had the highest average southeasterly flow in the 63-year time series. A strong southeasterly flow is the typical winter wind pattern along the coast of British Columbia. These winds cause ocean surface waters to be pushed into Queen Charlotte Sound, raising coastal sea levels, and generally enhancing poleward flow of surface water along the British Columbia coast. This wind regime caused the warm, low density surface layer in Queen Charlotte Sound to be retained within the Sound. The southeasterly wind anomaly in June 2007 was nearly as strong such that when the average is computed for both months, it is arguably the largest southeasterly wind anomaly in the record (Fig. 72).

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[11] http://www.ec.gc.ca/meteo-weather/default.asp?lang=En&n=C6C96BEE-1

The appearance of higher than average sea levels in Prince Rupert, central coast of British Columbia, during the summer of 2007 confirms the response of the ocean to southeasterly winds (Fig. 73). It may also explain why the coast of Southeast Alaska was so warm during the summer of 2007. Southeasterlies cause/enhance poleward surface flow along the coast, thereby advecting the generally warmer southern coastal waters poleward.

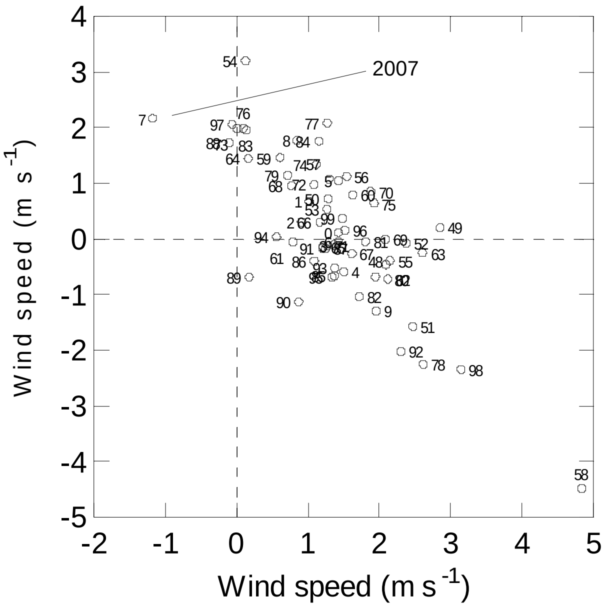


Fig. 72 Average June/July wind speed and direction over Queen Charlotte Sound starting from 1948. Negative values of the ordinate (left of the vertical dashed line) are easterlies. Positive values of the abscissa (above the horizontal dashed line) are southerlies. Plot point labels indicate year. June/July 2007 was either the strongest southeasterly regime in 63 years, or the second strongest depending on how 1954, with its stronger southerly than easterly component, is ranked. Southeasterly winds tend to retain water within Queen Charlotte Sound so the extreme freshwater discharge was held there.

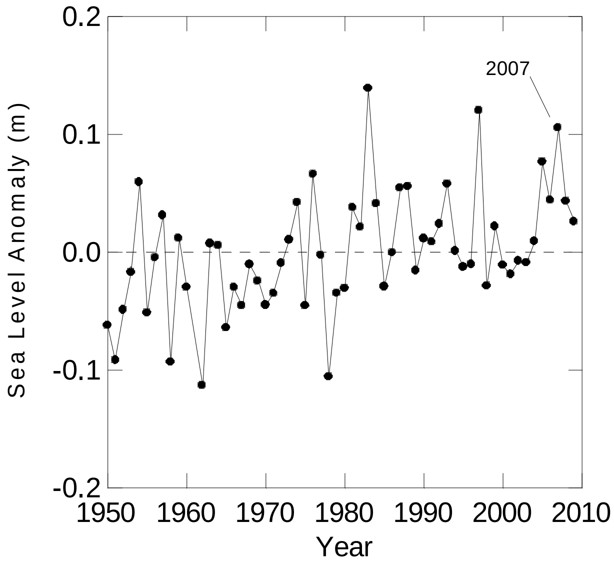


Fig. 73 July sea level anomalies from the 1950 to present average values, based on tide gauge data. Source: DFO/MEDS online tide gauge archive.

Along the North American coast, the summers of 2007 and 2008 were very different in character. July 2007 began with neutral to positive SST anomalies along the entire coast (Fig. 74). These strengthened in August and persisted at slightly lower levels through September. The warmest anomalies occurred on the northwestern side of Vancouver Island, also the location of the Kains Island lighthouse. Daily data collected at the lighthouses reflected the large-scale pattern of warm SST that existed along the coast. Warmer than average coastal temperatures are normally a sign of lower than average survival of Fraser River sockeye salmon (Mueter *et al.*, 2002, 2005).

The summer of 2008 was the opposite of 2007 (Fig. 74). SSTs along the North American coast were cool following what was the coldest year in the Gulf of Alaska since 1972 (Batten *et al.*, 2010), and these cool anomalies persisted along the coast through September. Unlike the Strait of Georgia, migrating sockeye salmon in 2008 would have had a very different thermal experience during their migration in 2008 compared to 2007 once they left the coastal straits. The temperature of surface seawater along the coast is often an indicator of major ecological changes that accompany the warmer/colder ocean (Mackas *et al.*, 2007).

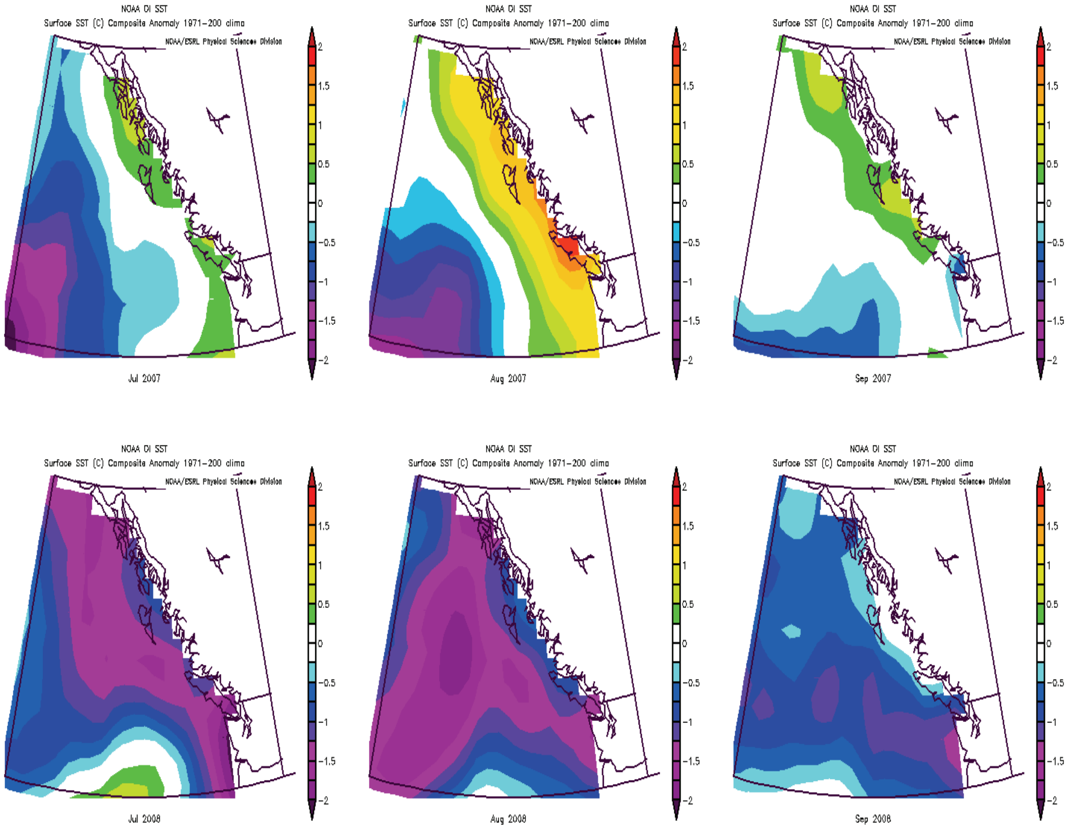


Fig. 74 Eastern Gulf of Alaska monthly SST anomalies (from 1971 to 2000 average) or (left to right) July to September in 2007 (top row) and 2008 (bottom row). Data are NOAA OIv2SST monthly averages.

The migration route of Fraser River sockeye salmon follows the continental shelf northward from Vancouver Island to Alaska. SST anomalies along the migration route in 2007 were warmer than average along most of the route (Fig. 74), especially in August. But many summers have warmer than average temperatures in summer, so what was unique about 2007? The data that were used to produce Figure 74 are the average coastal SST, determined from 1°× 1° lat./long. grid points. By selecting the grid points that abut the coast, it is possible to compute average temperatures along the expected migration route from northern Vancouver Island through Southeast Alaska. However, the average temperature in August is highly correlated with the average temperature in July each year, and the average temperature in July is highly correlated with the average temperature in the previous June. This autocorrelation effect was removed by analysis of covariance of July and August temperatures combined, using May as a covariate, along with latitude. The result of this analysis indicated that July and August 2007 was the most atypical year since 1982 (Fig. 75). The summer temperatures in 2007 were the largest outlier from what May SSTs might have predicted. The second most unusual summer occurred in 1997 but it is known that this was associated with the intense el Niño that year.

Considering the individual 1° × 1° lat./long. regions along the migration route, three coastal grid points in Queen Charlotte Sound had the warmest (unadjusted) observed monthly SST (since 1981) in August 2007. While other grid points were much warmer than average in August 2007, Queen Charlotte Sound was the only area that had the most extreme absolute SST in this database. The abrupt shift from negative to strong positive anomalies in the daily lighthouse data on the west coast (Fig. 67), but not in the Strait of Georgia, is suggestive of a different watermass but not sufficient to reject alternative explanations associated with heat fluxes. Salinity anomalies on the west coast of Vancouver Island were positive rather than negative.

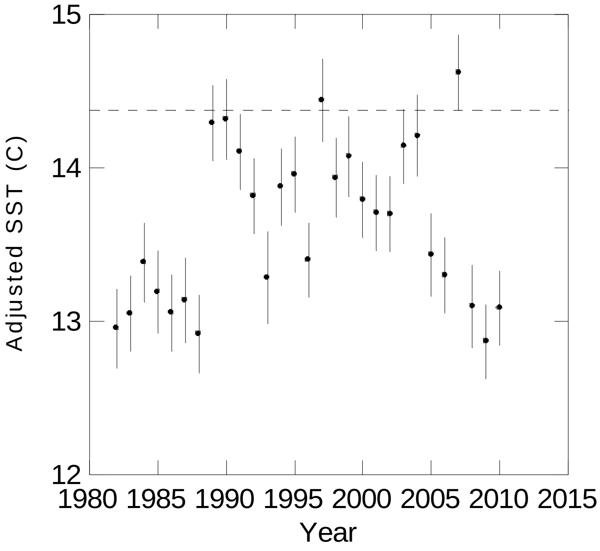
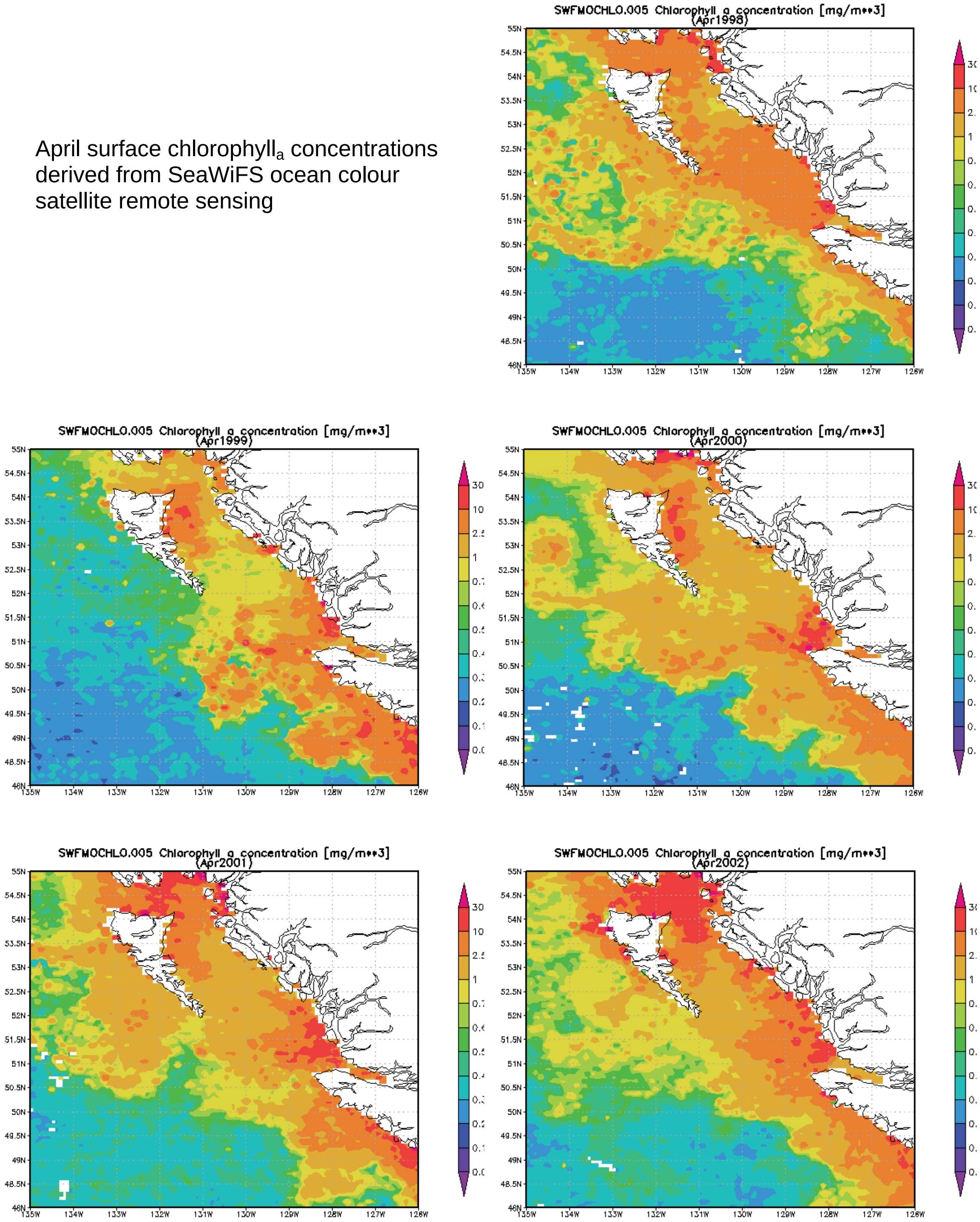


Fig. 75 Solid circles represent average adjusted July and August SST in the 1° × 1° lat./long. grid points along the North American coast from Vancouver Island through Southeast Alaska (after removing autocorrelation by including May sea surface temperature as a covariate in an analysis of covariance). The bars represent the 95% confidence intervals. Dashed horizontal line is the lower bound on the estimate of the mean value for 2007 and where it crosses other vertical lines of other years, there is no statistically significant difference between these years.

6.2.3 Coastal biological oceanography beyond the Strait of Georgia

The arrival of spring varies from year to year in the Gulf of Alaska (Mackas *et al.*, 2001; Batten *et al.*, 2010), and in the Queen Charlotte Strait/Sound region (Bertram *et al.*, 2001). Unless migratory predators like the sockeye salmon adjust their migration to match inseason production, emergence, or seasonal migrations of prey species into the region, they will face different prey fields from year to year. The spring chlorophyll bloom occurs first in coastal waters where nearby sources of freshwater facilitate the early development of water column stability. The dominant feature in SeaWiFS ocean colour satellite images of the region is the contrast between coastal and offshore waters (Fig. 76). The subdominant feature is the spatial variability among years. Year to year variability in the mean is evident, but it is difficult at this scale to see why 2005 and 2007 would produce the worst returns on record.



April surface chlorophyll$_a$ concentrations derived from SeaWiFS ocean colour satellite remote sensing

Fig. 76 Average surface chlorophyll concentrations from Queen Charlotte Strait to Dixon Entrance in April from 2001 to 2008. White regions over water indicate where cloud cover precluded generating an average value. Analyses and visualizations used in this figure were produced with the Giovanni online data system developed and maintained by the NASA GES DISC.

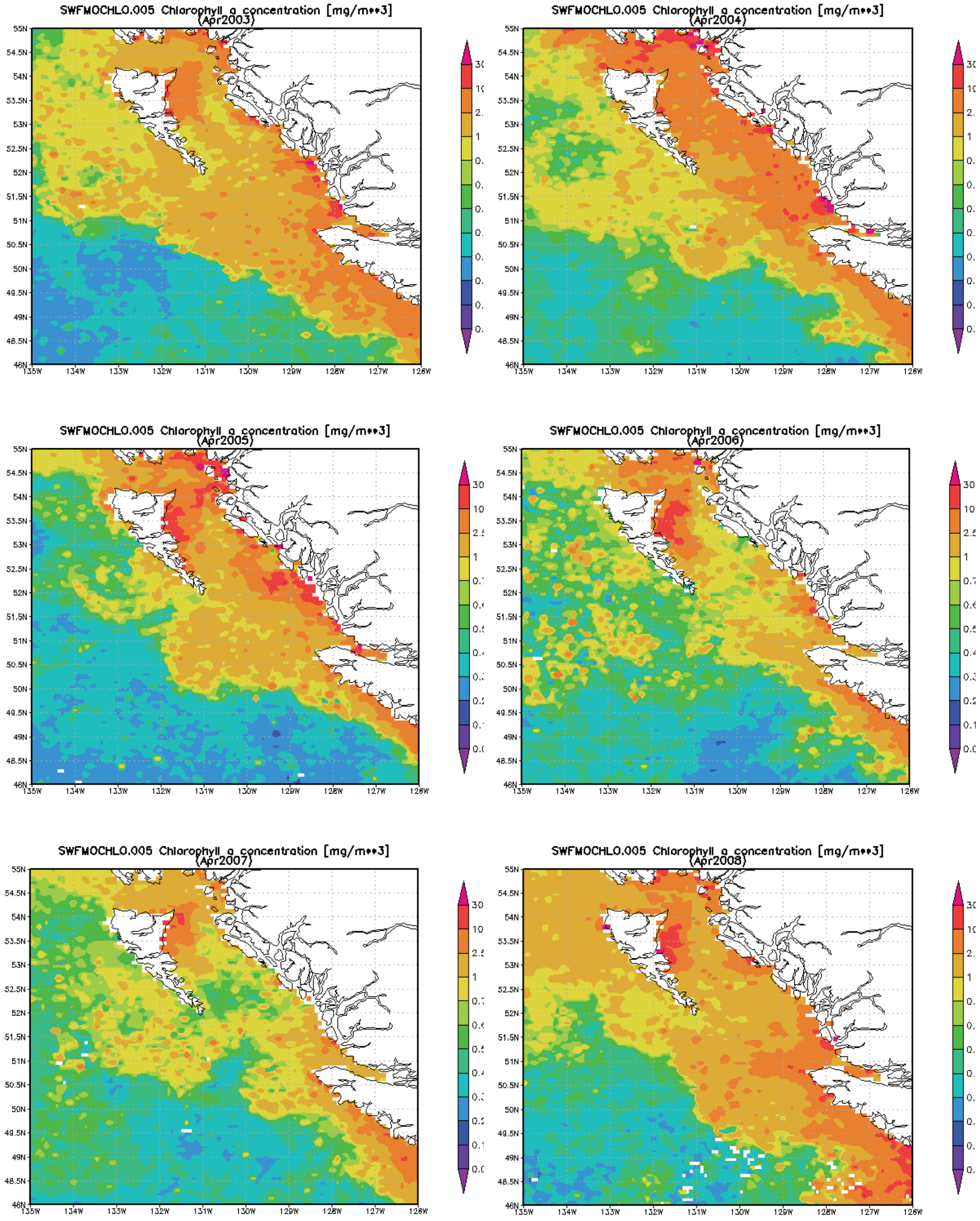


Fig. 76 Continued.

A high correlation was reported between average chlorophyll concentrations (which reflect phytoplankton densities) in Queen Charlotte Sound (Fig. 77) during the first three weeks of April and Chilko Lake sockeye salmon marine survival from 1998 to 2007 (Irvine *et al.*, 2010, Fig. 78). The remarkable contrast in average chlorophyll concentration between years in this month reflects the state of development of the spring bloom. In years when the spring bloom is delayed, marine survival of Chilko Lake sockeye salmon is low. The bloom in 2007 was the latest in the record since 1998. While there is likely no Fraser River sockeye salmon in Queen Charlotte Sound during April, the lag until their arrival in June and July allows time for their prey base (*e.g.*, euphausiids) to develop.

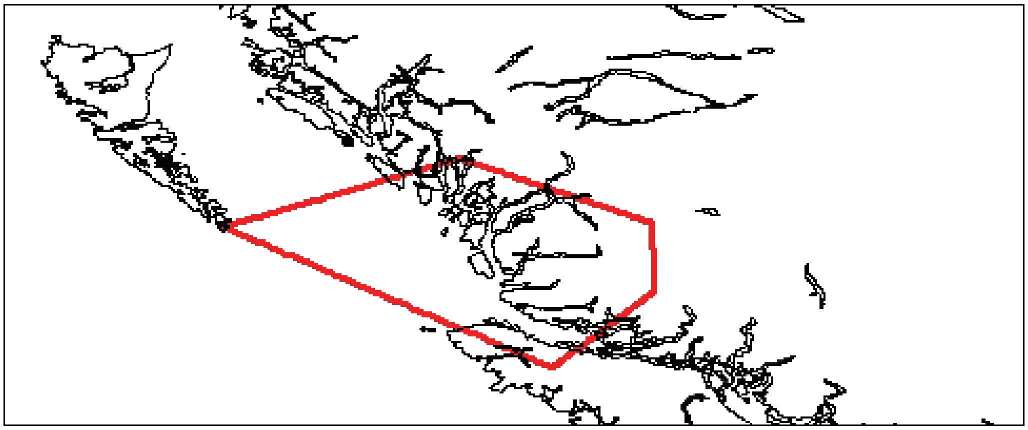


Fig. 77 Spatial domain used to generate a high correlation ($r^2 = 0.87$) between Chilko Lake sockeye salmon survival and SeaWiFS chlorophyll *a* concentration in the first three weeks of April from 1998 to 2007 (Irvine *et al.*, 2010). Triangle Island is located just outside the polygon at the northwestern tip of Vancouver Island.

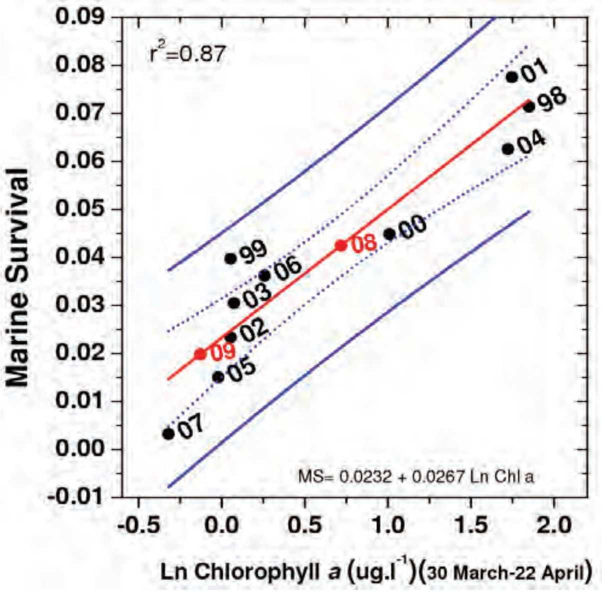


Fig. 78 Annual marine survival of Chilko Lake sockeye salmon *versus* chlorophyll *a* concentrations in Queen Charlotte Sound (log transformed) during the first three weeks of April. Reproduced from Irvine *et al.* (2010). Plot point labels indicate ocean entry years.

Another predator in Queen Charlotte Sound that feeds at a similar trophic level to sockeye salmon postsmolts is Cassin's auklet (*Ptychoramphus aleuticus*). It has a breeding colony on Triangle Island (50°52′ N 129°05′ W) in the Scott Islands chain off the northern tip of Vancouver Island at the entrance to Queen Charlotte Sound. Its diet is planktivorous, feeding primarily on copepods and euphausiids (Bertam *et al.*, 2001). The timing of the zooplanton biomass peak is more important than year-to-year variation in biomass in determining the availability of a preferred prey, *Neocalanus cristatus* (Hipfner 2008a). Cassin's auklet fledgling production in 2007 was not atypical (Hipfner 2008b, 2010). The western position of Triangle Island in Queen Charlotte Sound may have placed it beyond the range of greatest influence of high runoff, such that its feeding opportunities were more similar to those experienced by Barkley Sound and Columbia River sockeye salmon than by Fraser River sockeye. Two piscivorous species of seabirds which also breed on Triangle Island, had their lowest recorded breeding success in 2007 (Hipfner, 2008b).

6.3 Gulf of Alaska

6.3.1 Large-scale climate processes

A characteristic feature of the surface of the North Pacific Ocean is its tendency to persist in warm or cold phases, sometimes for decades (Mantua *et al.*, 1997). The phenomenon is known as the Pacific Decadal Oscillation (PDO). It has been observed that a warm phase in the Gulf of Alaska is accompanied by a cold phase in the central and western North Pacific, so the system is recognized as a large-scale climate phenomenon. In recent years, the alternation between positive and negative phases has occurred more frequently (Batten *et al.*, 2010). The negative phase of the PDO is associated with cooler SSTs along the North American continent (Mantua *et al.*, 1997). From 2003 to 2008, abrupt changes in short-term climate precluded establishing a clear climate regime in the Gulf of Alaska (Mundy *et al.*, 2010). The generally warm years of 2003 to 2005 were followed by generally cold years from about 2007. The winter of 2008 was one of the coldest in the Gulf of Alaska in 35 years (Batten *et al.* 2010). The negative phase of the PDO re-emerged in October 2007 and persisted until the 2010 El Niño. Summer temperatures from 2003 to 2005 in the Gulf of Alaska were among the warmest on record and their appearance coincided with a shift in factors that affect North Pacific climate.

The cold seasons (November–March) of 2003 to 2005 had relatively high sea level pressure (SLP) over western North America from British Columbia to California. The consequence for the Gulf of Alaska was anomalous low-level winds from the south, accompanied by relatively warm and wet weather. The cold seasons of 2006 to 2008 had anomalously high SLP extending from the Bering Sea to the U.S. mainland, with a small but prominent area of low SLP in the northwestern Gulf of Alaska. This configuration produced a cold flow of air from the northwest in the western Gulf of Alaska and a relatively stormy environment in the central and eastern parts. The warm seasons (April–October) of 2003 to 2005 had relatively weak SLP anomalies with a tendency for higher (lower) than normal SLP in the western (eastern) half of the Gulf of Alaska, indicating generally weak wind anomalies from the north. On the other hand, the warm seasons of 2006 to 2008 featured generally high SLP in the northwestern U.S. mainland, with low SLP over the Gulf of Alaska. This pattern generates modest storminess and upwelling in the central part of the Gulf (Mundy *et al.*, 2010).

The NINO3.4 index is a measure of SST along the Equator in the central Pacific Ocean (Fig. 79). It is generally accepted as the basis for evaluating the state of the el Niño–Southern Oscillation climate phenomenon. The index was positive during the el Niño in the winter of 2002/03, generally positive through to the el Niño in the winter of 2006/07, and mostly negative during the La Niña in the winter of 2007/08. The PDO index reflects the dominant spatial pattern of SST in the North Pacific. Positive (negative) values of the PDO index are associated with warmer (cooler) SST anomalies along the North American coast. The PDO index (Fig. 80) tracked the NINO3.4 index quite closely but with a slightly more prominent decreasing trend. The decline in the PDO index was accompanied by a concomitant decline in the SST along the west coast of North America from the Bering Sea to Baja California. The North Pacific Gyre Oscillation (NPGO)

(Di Lorenzo *et al.*, 2008) is the subdominant ocean–climate pattern in the North Pacific (not shown). A positive phase of the NPGO tends to be associated with anomalously strong equatorward flow in the California Current and relatively strong cyclonic flow along the periphery of the Gulf of Alaska. It was positive in 2003 and negative by about 2005. The North Pacific Index is an atmospheric index that reflects average SLP over the North Pacific (not shown). It was negative in 2003 in association with an anomalously deep Aleutian Low, and then varied with season, with a tendency for positive values from 2006 to 2008. The eastern North Pacific Ocean experienced the full range of atmospheric and oceanic variability from 2003 to 2008.

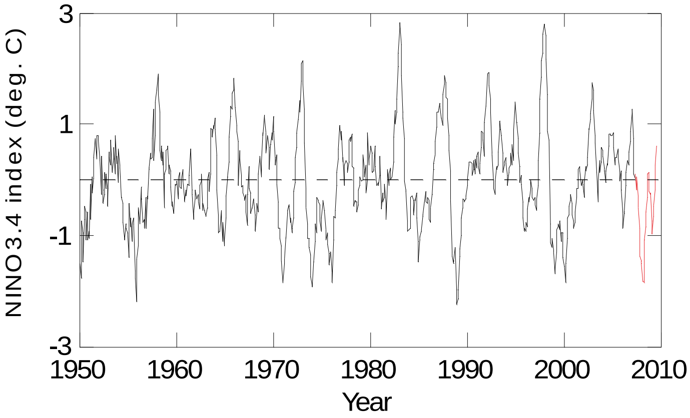


Fig. 79 NINO3.4 index from 1950 to 2009 (June). Red line indicates the period when the 2005 brood year was at sea. Large negative values indicate la Niña and large positive values indicate el Niño.

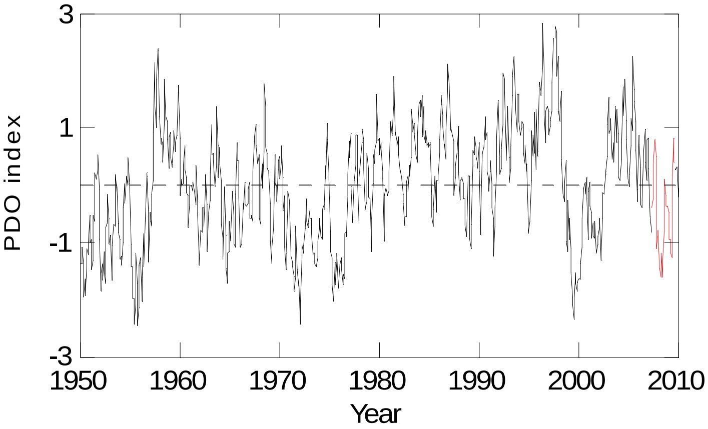


Fig. 80 Pacific Decadal Oscillation (PDO) index computed from sea surface temperature data for the period 1950 to 2009, inclusive. Red line indicates the period when age-1.2 sockeye salmon from the 2005 brood year were at sea.

6.3.2 Sea level pressure

SLP anomalies in the Northeast Pacific Ocean in 2007 were negative especially in July 2007 (Fig. 81). Given the position of the centre of these anomalies, between two climatological features, it reflects both a weakened Subtropical High and an enhanced Aleutian Low for this month. Negative anomalies persisted through the summer of 2007, whereas SLP anomalies in June 2008 were generally above average, lower in July although neutral over Vancouver Island and the U.S. west coast, and negative in August. Broad-scale low pressure anomalies over the Gulf of Alaska in August 2008 may have played a role in the anomalous chlorophyll blooms that occurred that summer (Hamme *et al.*, 2010).

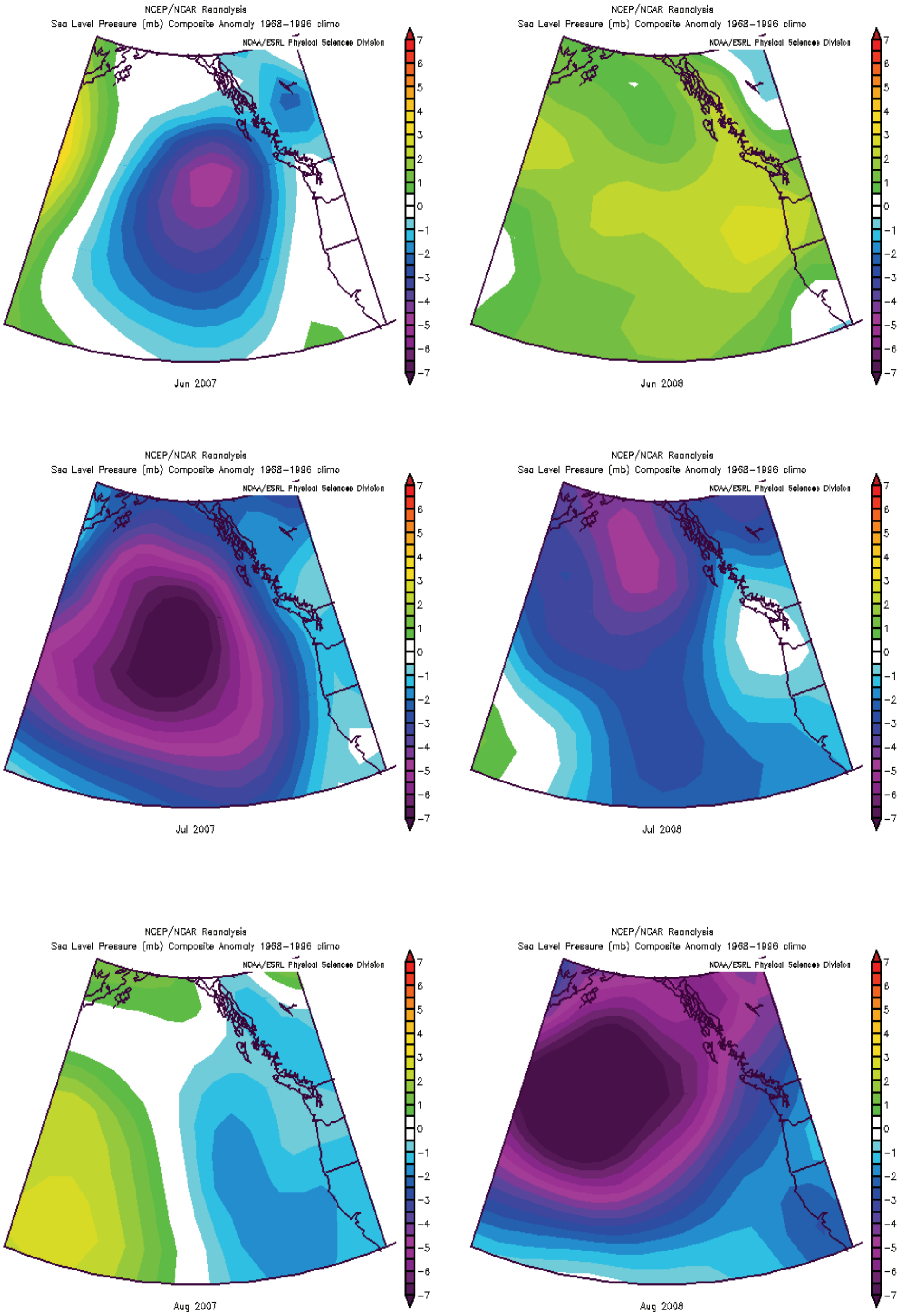


Fig. 81 Monthly averaged sea level air pressure anomalies for June to August 2007 (left) and 2008 (right).

6.3.3 Ocean circulation

The North Pacific Current is a large-scale feature of ocean circulation in the North Pacific Ocean. It follows an eastward path in the mid-latitudes from the Asian coast, crossing the Pacific before bifurcating into the poleward Alaska Current, and the equatorward California Current (Dodimead *et al.*, 1963). On average, the location of this British Columbia Bifurcation is Vancouver Island, however, from month to month the strengths of these currents vary (Fig. 81). An index of the strength of the North Pacific Current (Freeland, 2006) indicates that at the end of 2006, the North Pacific Current was enhanced and mean values stayed higher, on average, than were found in the earlier part of the time series that began in 2002. The maximum value occurred in June 2008. More of this enhanced circulation found its way into the California Current which is reflected in the low value of the Alaska Current:California Current strengths (Fig. 82, red line) and in the greater similarity of the California Current index to the North Pacific Current index during this period.

The strength of the Alaska Current varies according to variation in atmospheric circulation, especially during the stormier cool/cold seasons (Freeland and Cummins, 2005). A recent review of atmospheric patterns in the North Pacific from 2003 to 2008 found that average winter SLP was higher in 2007 and 2008 (McKinnell *et al.*, 2010) which reflects fewer or less intense storms. In the Gulf of Alaska, high SLP is associated generally with colder winters because enhancement of the winter atmospheric circulation during stormier winters tends to bring more warmer air from the south to the Gulf of Alaska.

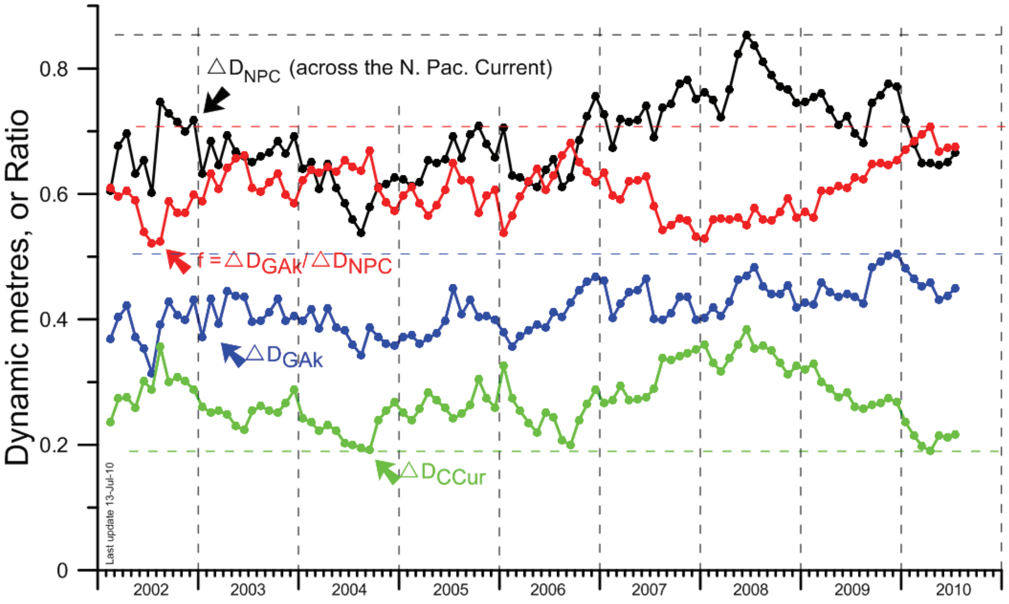


Fig. 82 Monthly indices of the strength of the North Pacific Current (black), Alaska Current (blue), and California Current (green) and the ratio of Alaska Current:California Current (red). Source: http://www.pac.dfo-mpo.gc.ca/science/oceans/Argo/Argo-currents-courants-eng.htm.

6.3.4 Hydrography

Physical forces (sun, wind, tides, gravity) and the properties of seawater (temperature, salinity) affect the extent of vertical mixing in the uppermost part of the ocean. In winter, when turbulent forces are greatest, the entire water column is mixed down to 100 m or more (Fig. 83, panels 1–4). Vertical mixing is an important component of ocean ecology because it is the major source of the nutrients (*e.g.*, nitrate, phosphate, silicate, iron) which are required for phytoplankton growth in the spring. With the advent of Project Argo, it is now possible to examine the characteristics of vertical mixing in the World Ocean at much finer resolutions of time and space than at any time in history.

In the Gulf of Alaska from 2003 to 2010, the average depth where the maximum change in seawater density occurred was deepest in April (Fig. 83, panel 4). As the surface of the ocean warms in spring, it becomes less dense at the surface. As the winds abate, the depth of mixing becomes significantly shallower. Indeed, it occurs so rapidly that a frequency distribution of mixed layer depths is strongly bimodal. Through the month June, for example, 62% of the Argo profiles in the Gulf of Alaska during these years showed surface mixing only to shallower summer mixed layer depths while 38% remained mixed to winter depths (mean = 107 m). Some profiles indicated the remnants of winter mixing into July (Fig. 83, panel 7). Surface cooling in autumn causes seawater to become denser and with the onset of autumn storms in September, the process of deepening the mixed layer is initiated.

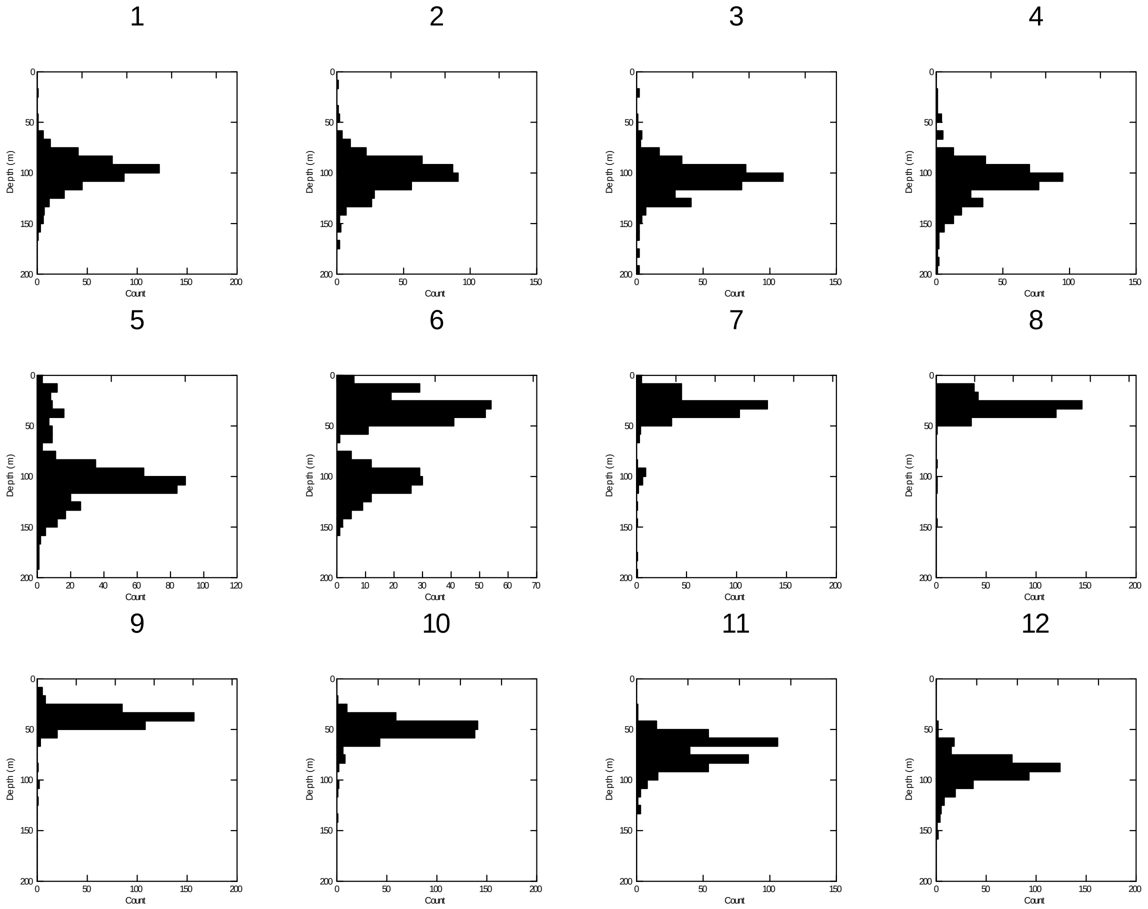


Fig. 83 Frequency distributions of depth, by month, at which the maximum rate of change in water density occurred in Argo profiles in the Northeast Pacific (>50°N, <160°W) from 2003 (January) to 2010 (May).

Much of what has been reported historically about the oceanography of the Gulf of Alaska has been a result of sampling along Line P, from Juan de Fuca Strait to Ocean Station Papa (Peña *et al.*, 2007). It has been considered that vertical mixing reaches its deepest extent in the Gulf of Alaska in March (Freeland *et al.*, 1997), rather than in April as was indicated by the Argo profiles from 2003 to 2010. The difference is likely due to the broader coverage provided by the Argo floats and their more northerly locations compared with Station Papa (50°N 145°W) where most of the historical oceanographic work has been conducted.

Figure 83 is based on all Argo profiles from 2003 to 2010 taken east of 160°W and north of 50°N. Pooling the data over such a large area fails to account for regional variation in mixing dynamics within the Gulf of Alaska, and the statistics fail to account for the variable distribution of floats in the Gulf of Alaska each year. These difficulties take on greater significance when considering observations for an individual year. Maximum mixed layer depth on the continental shelf on the Seward Line (Alaska), for example, occurs in January (Sarkar *et al.*, 2005).

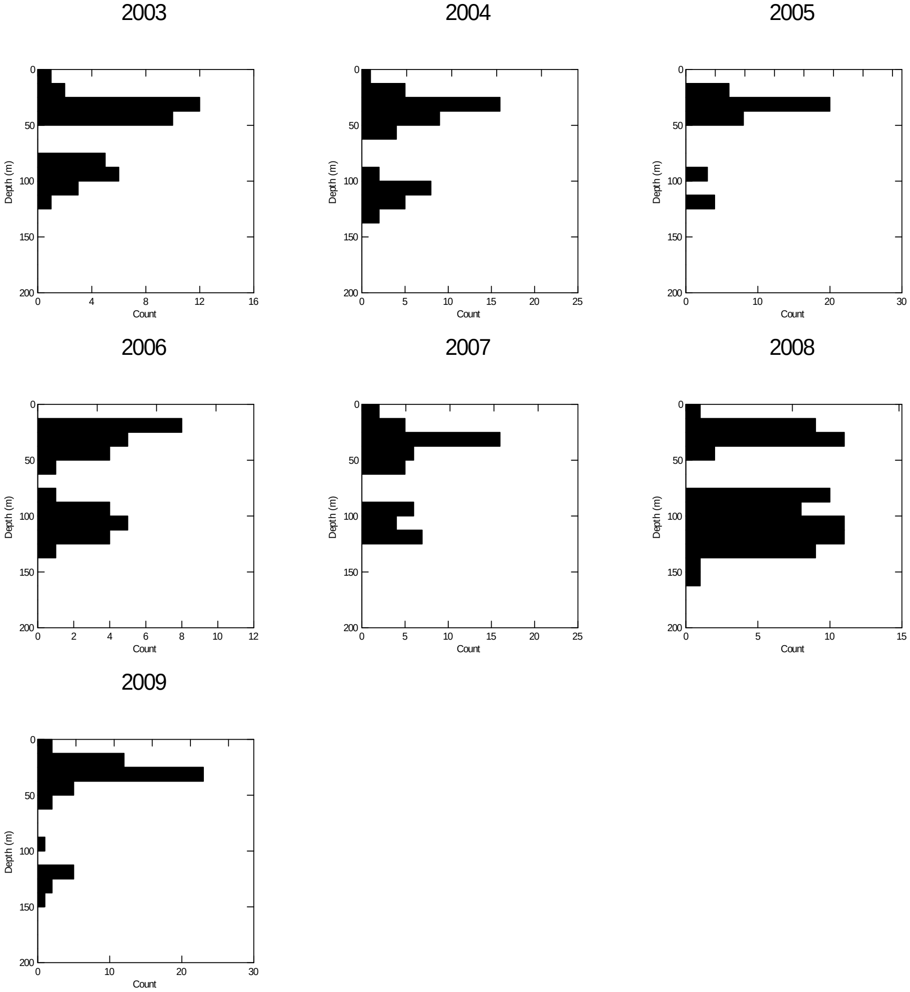


Fig. 84 As in Figure 83, but for the month of June only, by year.

Because the frequency distribution of the depths of maximum vertical density gradient is bimodal in spring, it suggests a relatively abrupt onset of shallow mixing depths. The greatest degree of bimodality occurs in the month of June (Fig. 83). From 2003 to 2009 the proportion of Argo profiles, indicating that deep winter mixing was occurring in June *versus* the number indicating shallower summer mixing, varied from year to year (Fig. 84). June of 2005 and 2009 had the smallest proportion (both 17%), indicating deep mixing while June 2006 had the largest proportion (45%) of profiles, indicating deep winter mixing in June.

At the depth where the maximum rate of change in density occurs, the magnitude of the change in density at that point is an index of the degree of water column stability. In July and August, the warm summer of 2005 had the most stable summertime water column whereas the summer of 2006 had the least stable water column. Only the summer of 2005 stands out as an unusual year among this collection of summers (Fig. 85).

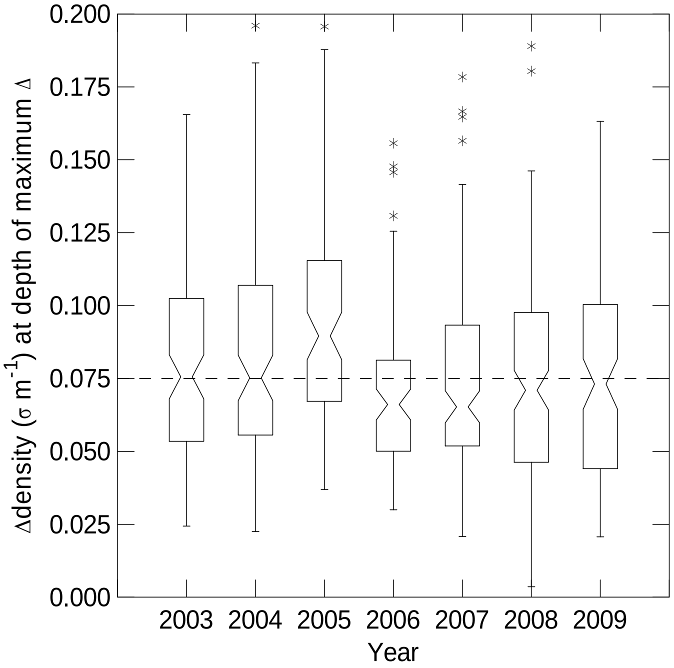


Fig. 85 Box and whisker plots of the magnitude of change in seawater density at the point of maximum change in each profile, July and August combined. The narrowest point of the box is the median value. If the indented portions of the notch (narrowed parts of the box) do not overlap between years, the median value is considered to be statistically different between years. For example, the bottom of the notch in 2005 is greater than the top of the notch in 2006 so the median values of the two years are statistically different. A dashed horizontal line appears at 0.075 to aid the eye in distinguishing differences in the locations of the statistical features across years. The symbol ✳ indicates outliers, in this case much stronger rates of change in density than were found in other profiles.

6.3.5 Physical spring in offshore Gulf of Alaska

Gargett (1997) developed a simple index of water column stability that considers the density difference between the 0–20 m depth layer and the 60–80 m depth layer within a single hydrographic profile. Using Project Argo data from January 2003 to June 2010, the average Gargett Stability Index (GSI) was computed within each 5° latitude × 10° longitude block north of 45°N and east of 160°W, by week, based upon whatever profiles were found within each year/week/block. A loess smoother of GSI *versus* week was applied each year to these averages. The dominant spatial pattern has water column stability lowest in the blocks adjacent to the North American coast and deepest in the block of longitude farthest from the coast. By arbitrarily choosing a value of the GSI that is approximately midway through the developing seasonal stability (GSI = 0.1), it is possible to compare the phenology of the process each year (Fig. 86). From 2003 to 2010, the achievement of this level of stability ranges over a period of between five to six weeks, between 160–150°W. The block between 150–140°W has about the same range of weeks and seasonal development. The range is about 7.5 weeks from 140–130°W, largely because of the late seasonal development in 2008 (Fig. 87). The range of weeks between the earliest year and the latest year was greatest (9.5 weeks) to the east of 130°W, again because of the 2008 outlier.

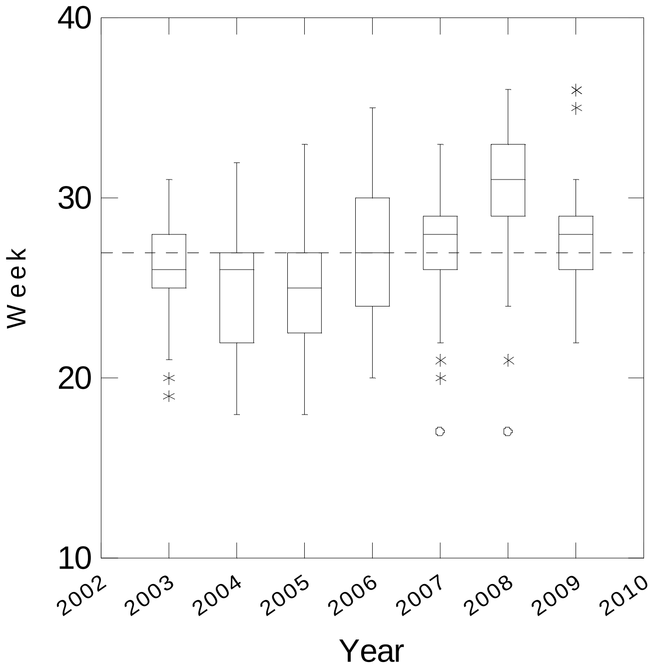


Fig. 86 Box and whisker plot indicating interannual variability in the establishment of water column stability. The values summarized in this figure are the weeks, within 5° latitude × 10° longitude blocks, when a Gargett Stability Index exceeds 0.1 for all such blocks east of 160°W, north of 45°N. The earliest year was 2005 (week 25) and the latest year was 2008 (week 31). The symbol ✳ indicates outliers and the symbol ○ indicates strong outliers. Original data are from Project Argo.

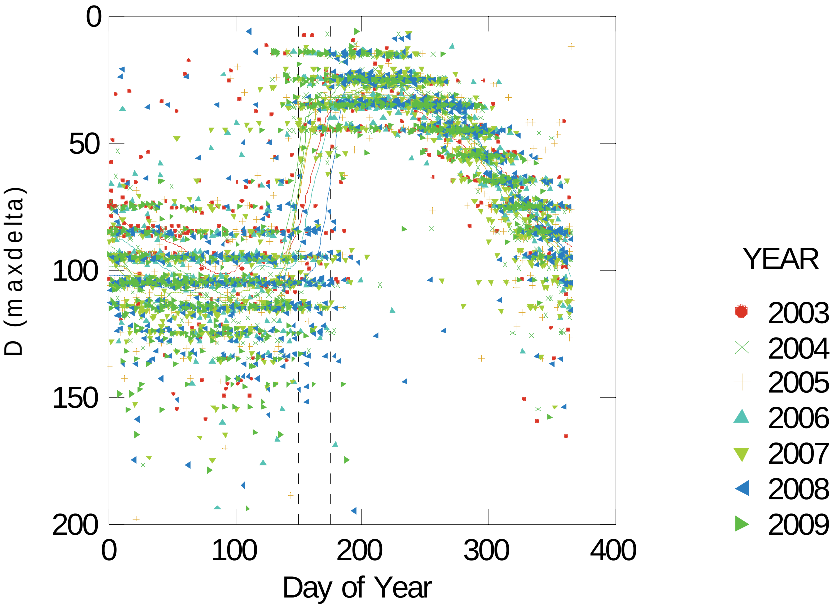


Fig. 87 Depth of the maximum rate of change in seawater density in Argo profiles by day of year from 2003 to 2009. Dashed vertical lines indicate approximately the earliest and latest (2008) years in the loess trend lines, a difference of 26 days.

6.3.6 Nutrients

The depth of vertical mixing in the Gulf of Alaska in winter is important because it provides the dominant source of nutrients for primary production in spring. As nutrient concentrations tend to increase with increasing depth, the depth of the winter mixed layer will affect the concentrations of nutrients such as phosphate, nitrate, silicate, and iron. The availability of iron regulates primary production in the open waters of the Gulf of Alaska (Martin and Fitzwater, 1988; Boyd *et al.*, 2004).

Following a two-year (1995–1997) period of monitoring surface nutrient concentrations in the North Pacific from a vessel of opportunity that began in 1987, Wong *et al.* (2002) reported little interannual variability in the seasonal nutrient cycle. While there was a period during the 1990s when nutrient re-supply to the surface layers was reduced at Station Papa (Whitney and Freeland, 1999), near the southern limit of sockeye salmon distribution, nutrient concentrations there have tended to be at or above average from 2003–2008 (Batten *et al.*, 2010).

A major biological "event" occurred in the Gulf of Alaska during the summer following the emigration of the 2008 smolt year (Fig. 88). Its cause has been attributed to the widespread deposition of volcanic ash in the Northeast Pacific following the eruption of Kasatochi (52.2°N 175.5°W) in the Aleutian Islands chain on August 7–8, 2008 (Hamme *et al.*, 2010). The oceanic response to adding iron of volcanic origin was enhanced primary production (Fig. 88) where iron is the limiting nutrient in the Northeast Pacific. Both the 2007 and 2008 smolt years of Fraser River sockeye salmon were in the Gulf of Alaska at this time. Assuming that the immature sockeye salmon distributions in the Gulf of Alaska in 2008 were what they were in the 1960s, immature fish would be feeding in the deep water regions of the Gulf of Alaska that summer. The enhanced productivity of chlorophyll in mid to late August likely provided little immediate benefit to immature sockeye salmon, as they do not eat diatoms. The dominant copepods, with an ability to sequester the enhanced production as stored lipids, would have entered diapause at depth by mid-August.

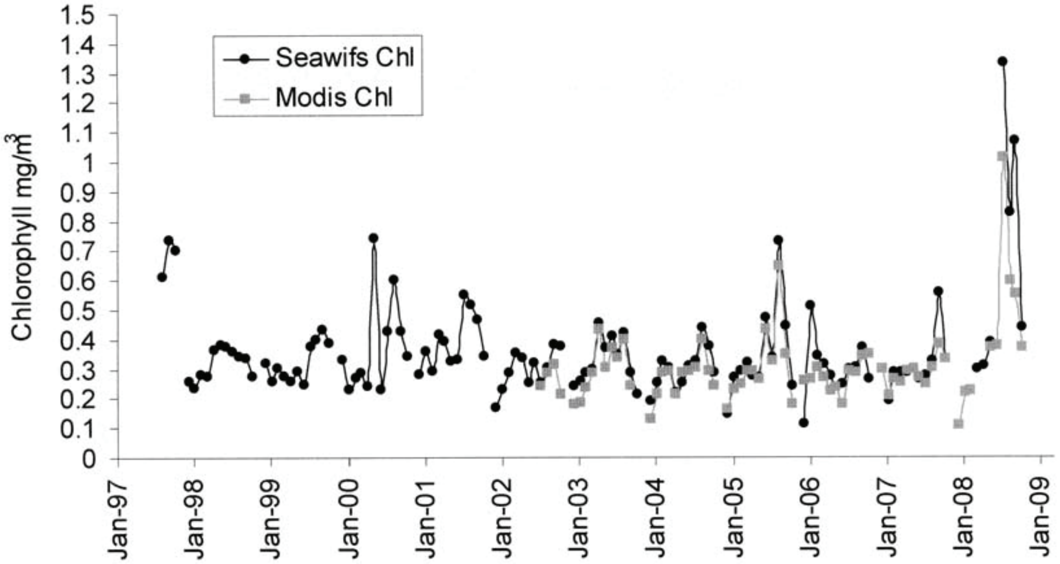


Fig. 88 Satellite-derived chlorophyll concentrations for a region of the Northeast Pacific centred on Ocean Station Papa (50°N 145°W) from the MODIS and SeaWiFS satellites. Produced with the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences (GES) Data and Information Services Center (DISC). Reproduced from Batten *et al.* (2010).

Based on current knowledge, the abundant 2008 sockeye salmon smolt year would have been migrating along the continental shelf. In this region, iron is not normally the limiting nutrient (Banse and English, 1999) so its addition would not have produced much benefit to this cohort in 2008. To have a direct benefit on the 2008 smolt year, the enhanced biological production would need to be entrained in the pelagic food web and stored through, or made available to the smolts over the winter. Data from the Continuous Plankton Recorder (CPR) program indicated that zooplankton biomass in 2009 was near the average (S. Batten, pers. comm.).

6.3.7 Biological spring

Broad-scale spatial patterns of chlorophyll concentration in the Gulf of Alaska (Fig. 89) are similar from year to year with chlorophyll concentrations in the deeper waters at much lower levels than the coastal region, although the influence of the coastal zone extends beyond the limits of the shelf.

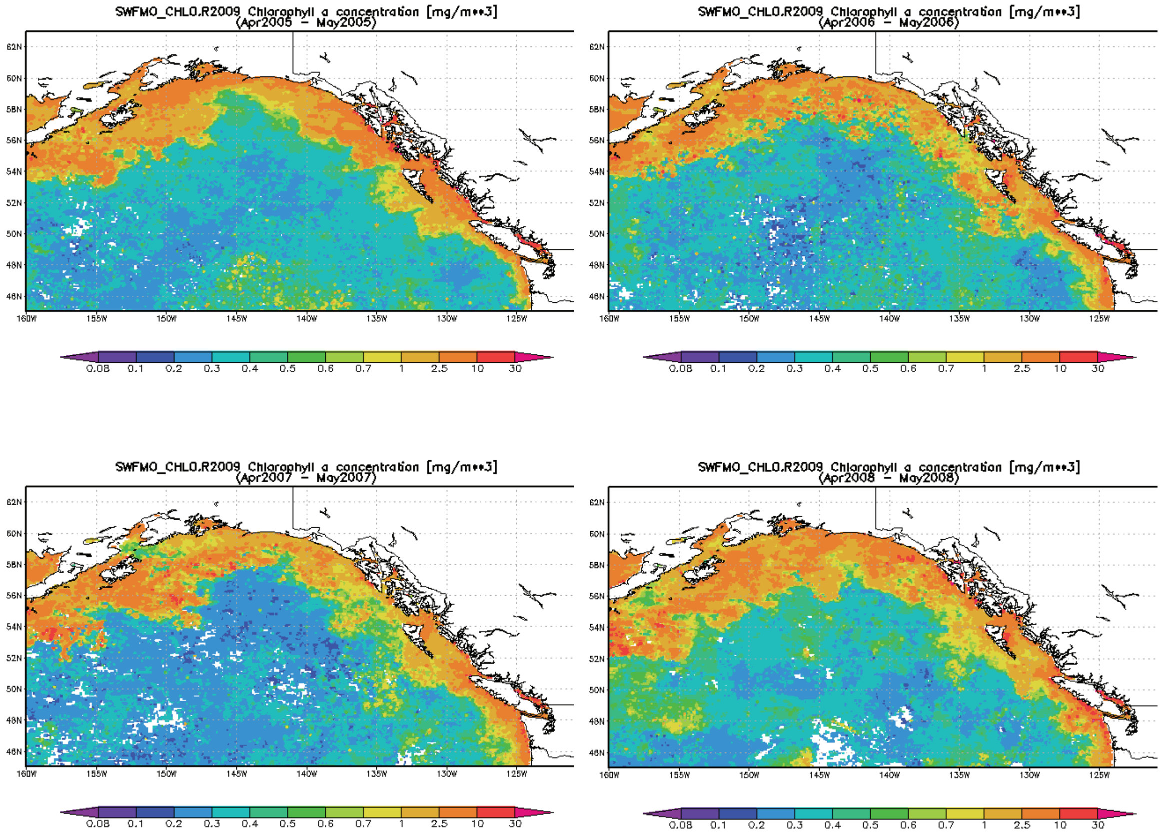


Fig. 89 Average surface chlorophyll concentrations in the Gulf of Alaska in April–May (2005–2008). The two ocean entry years (2005 and 2007) of worst survival are contrasted in the left column. White regions over water indicate where cloud cover precluded generating an average value. Analyses and visualizations used in this figure were produced with the Giovanni online data system, developed and maintained by the NASA (http://disc.sci.gsfc.nasa.gov/).

Year-to-year variation in the onset and development of physical spring in the Gulf of Alaska affects a biological/ecological response (Mackas *et al.*, 2001). The most abundant meso-zooplankter in the Subarctic North Pacific, for example, is the copepod, *Neocalanus plumchrus.* It is a small planktonic crustacean (<1 cm) with a one year life cycle, and grows by moulting through a series of stages from egg to nauplius to copepodite to adult. Prior to the adult stage, the final copepodite stage migrates to depth where it moults to the adult stage to reproduce after a summer of feeding and growing near the surface (Mackas *et al.*, 2001). The eggs are laid at depth where they hatch and the nauplii migrate to the surface in spring to repeat the cycle. The annual migration in spring of immense numbers of these animals from depth to the surface provides food for their predators. Their annual arrival at the surface is correlated with sea surface temperature (Batten and Mackas. 2009), but this empirical association between warmth and migration may be just a proxy for water column stability (Mackas *et al.*, 2001). Winter-like temperatures can persist in the Gulf of Alaska because of deep vertical mixing. When the water column stabilizes by radiant heating, it reduces the volume of water circulating near the warmer surface air temperatures, providing a positive feedback that reinforces the density gradient.

From 2003 to 2008, the timing of peak zooplankton biomass in the Gulf of Alaska was reflected in the variability of the physical ocean (Batten *et al.*, 2010). The annual biomass peak was early in the warmer years of 2003 to 2005, and the period spent at the surface during these summers was less. The peak biomass in colder years was later, with a more extended period at the surface, especially in 2008 (Fig. 90). The species abundance of Subarctic copepods and cool-water chaetognaths increased with upper-ocean cooling and with increases in the strength of the North Pacific Current.

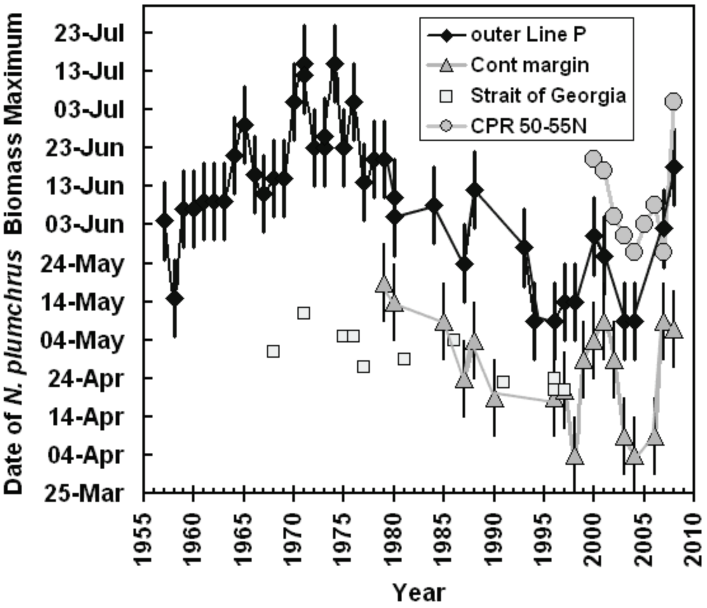


Fig. 90 Phenology time series for *Neocalanus plumchrus* populations in four subregions of the Northeast Pacific. Figure reproduced from Batten *et al.* (2010).

Summary – The seasonal peak in zooplankton biomass in 2008 had not developed as late since the 1970s when they occurred commonly. It was confirmed in two independent zooplankton observation programs located in different parts of the Gulf of Alaska (Line P and the CPR program) so the phenomenon was relatively widespread. Therefore, it is not unreasonable to propose that the delayed timing would have affected many of the sockeye salmon populations in the region in a similar manner. The stomachs of immature sockeye salmon on the high seas do not normally contain large fractions of copepods (See Section 4.2) because they generally feed at a higher trophic level.

6.4 Extreme Sea Surface Temperatures

NOAA data servers provide access to a 1° × 1° lat./long. grid of global monthly averaged SSTs from late 1981 to the present. These data were used to determine where or if there were any extreme monthly SSTs (high or low) while the 2007 smolt year was at sea. At each grid point, the historical record was searched to understand, for each calendar month, what year had the highest and what year had the lowest average SSTs in the record. A simple outcome of this exercise is an understanding of how many grid points had extreme values in each year (Fig. 91).

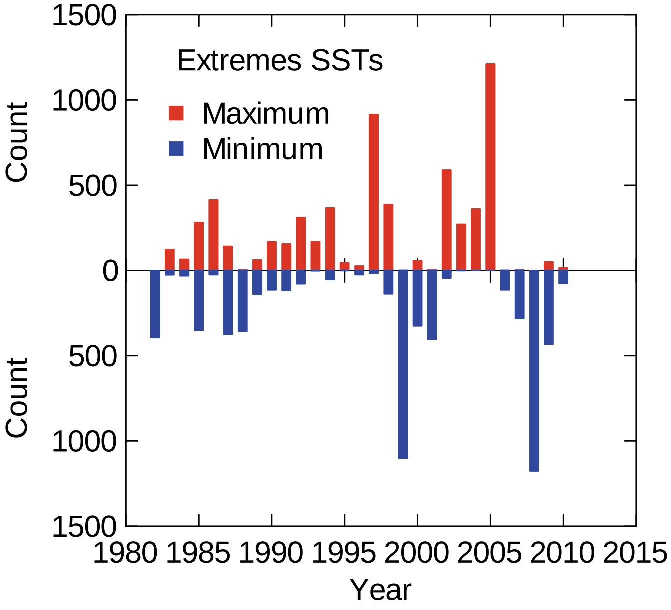


Fig. 91 Annual number of grid points with extreme SSTs in the Gulf of Alaska (>45°N, <160°W) from 1982.

From these data, it is possible to understand that SSTs have tended to exhibit more extreme monthly averages in the latter half of the record (beginning with the 1997/98 el Niño). The two years showing the most positive extremes were 1997 and 2005. These years were associated with later than average return timing of Fraser River sockeye salmon, especially in 2005, but not reduced survival. The two years with the most negative SST extremes were 1999 and 2008. There was also a tendency for the Gulf of Alaska to persist in either positive or negative phases. So the period when the 2007 smolt year was at sea was a period dominated by cold extremes, with the greatest number occurring in 2008. Within 2008, most of the extremes occurred in winter/spring, especially May. The only location in the entire Northeast Pacific with maximum historical (since 1981) temperatures in 2007 occurred in August in the area of Queen Charlotte Sound (Fig. 92).

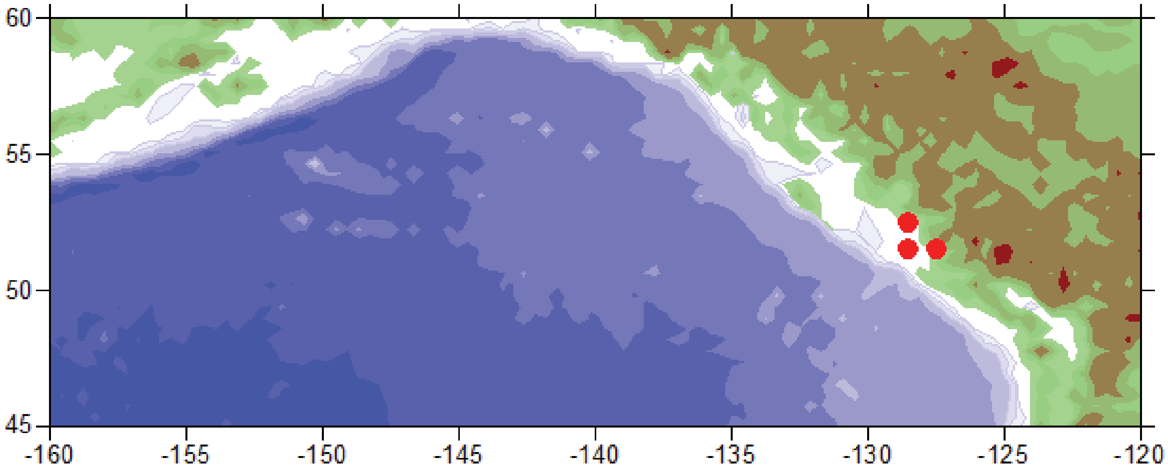


Fig. 92 Locations of the most extreme positive SSTs in the Gulf of Alaska during the period 1982 to 2010 that occurred in 2007. All maxima (red dots) observed in 2007 occurred only in Queen Charlotte Strait/Sound during the month of August.

6.5 *Future of the Gulf of Alaska*

Coupled ocean–atmosphere climate models are used both to evaluate both the present behaviour (dynamics) of the climate system and to predict its possible future states. Currently, the best known example of the use of these kinds of tools is the climate projections made by the IPCC concerning the future of Earth's climate. A shortcoming of the global models for use in studying coastal ecosystems is their relatively low resolution of these models. However, the global climate models can be used to downscale high-resolution regional models for the region of interest. One such set up is based on the Regional Ocean Modeling System (ROMS) which is used to downscale global climate models to the Northeast Pacific Ocean (NEP). ROMS is a free-surface, hydrostatic, terrain-following primitive equation ocean circulation model whose core was developed at Rutgers University and UCLA, with significant contributions from a large community of users. It has several advanced features including efficient parallelization for sustained performance on multi-processor computers, and numerous data assimilation capabilities.

6.5.1 NEP ROMS model description

The NEP model domain extends from approximately 20°N to 71°N and about 2250 km seaward of the North America west coast at a horizontal resolution of 10 km with 60 terrain-following vertical levels stretched towards the surface boundary. The terrain-following coordinate system has distinct advantages for modeling shelf regions. The full vertical coordinate system is compressed over the shelf resulting in high vertical resolution in a region of interest (shelf regions) and as a consequence, no computations are wasted in the deeper ocean. The grid is a rectangle, in a Lambert Conical projection, to reduce the amount of computation of wet cells over land.

To provide an historical analysis of performance, the model was run for the period from 1958 through 2004. The surface forcing for the NEP model is derived from the datasets for Common Ocean-ice Reference Experiments version 2 (CORE v2), which produces 6-hourly winds, air temperatures, sea level pressure and specific humidity, daily and short-wave and downwelling long-wave radiation, and monthly precipitation. Riverine inputs are implemented as surface freshwater which guarantees global conservation over long time scales. Boundary and initial conditions for this domain were derived from the Simple Ocean Data Assimilation (SODA 2.0.2) which is an ocean reanalysis product for the 1958 to 2006 period. The nominal spatial resolution of SODA is 0.5° and five-day averages were used for the boundary conditions. The northern boundary of the domain has a sink term which is set to enforce a 0.8 Sv northward transport through the Bering Strait.

Tidal forcing is implemented through the boundaries using the eight dominant diurnal and semi-diurnal components derived from Oregon State Tidal Prediction Software (Egbert and Erofeeva, 2002). Good simulations of tides require a good representation of the bathymetry, so a new Alaska region bathymetry was used. It was constructed solely from observational soundings blended with a conventional ETOPO dataset for the regions south of 45°N. To generate outlooks of future climate of the Gulf of Alaska, the A2 scenario (IPCC, 2007) from the Geophysical Fluid Dynamics Laboratory model was used.

6.5.2 Model sea surface temperature

Monthly climatologies of SST under the A2 CO_2 emissions scenario were computed by calendar month from the NEP5 climate ocean/climate simulation results for two periods, 2000–2010 and 2040–2050. These climatologies were differenced, month by month, to see how average SSTs might change between the present and 2050 (Fig. 93). The run of this model suggests that much of the Subtropical and Transition Zone regions of the northeastern North Pacific will be warmer by 2040–2050 and they appear to have expanded into the Gulf of Alaska (*sensu* Polovina *et al.*, 2008). Nevertheless, there is considerable spatial and seasonal variability in the response of the Gulf of Alaska to enhanced CO_2 emissions.

An interesting result of this NEP model is that average SST became cooler than at present along a broad expanse of ocean adjacent to the North American coast during the cold season, and in late summer by 2040–2050 (Fig. 93). The reduction of average SST during the cold season is due to a reduction in the cyclonic winds (Aleutian Low) that are responsible for the poleward advection of warmer surface water from the south. From May through July, however, average SSTs are generally warmer by 2040–2050 along the British Columbia and Southeast Alaskan coasts, suggesting poorer marine survival of Fraser River sockeye salmon. July is the month when they emerge onto the continental shelf and the consequence of warmer SST is usually poorer survival. By August, however, SSTs cooler than at present prevail along the coast because of enhanced winds producing upwelling throughout the Gulf of Alaska coastal areas. This may favour the survival of summer emigration from the coastal straits. Future research will consider the effects of tidal mixing (cooling) in coastal regions that are predicted to be warmer.

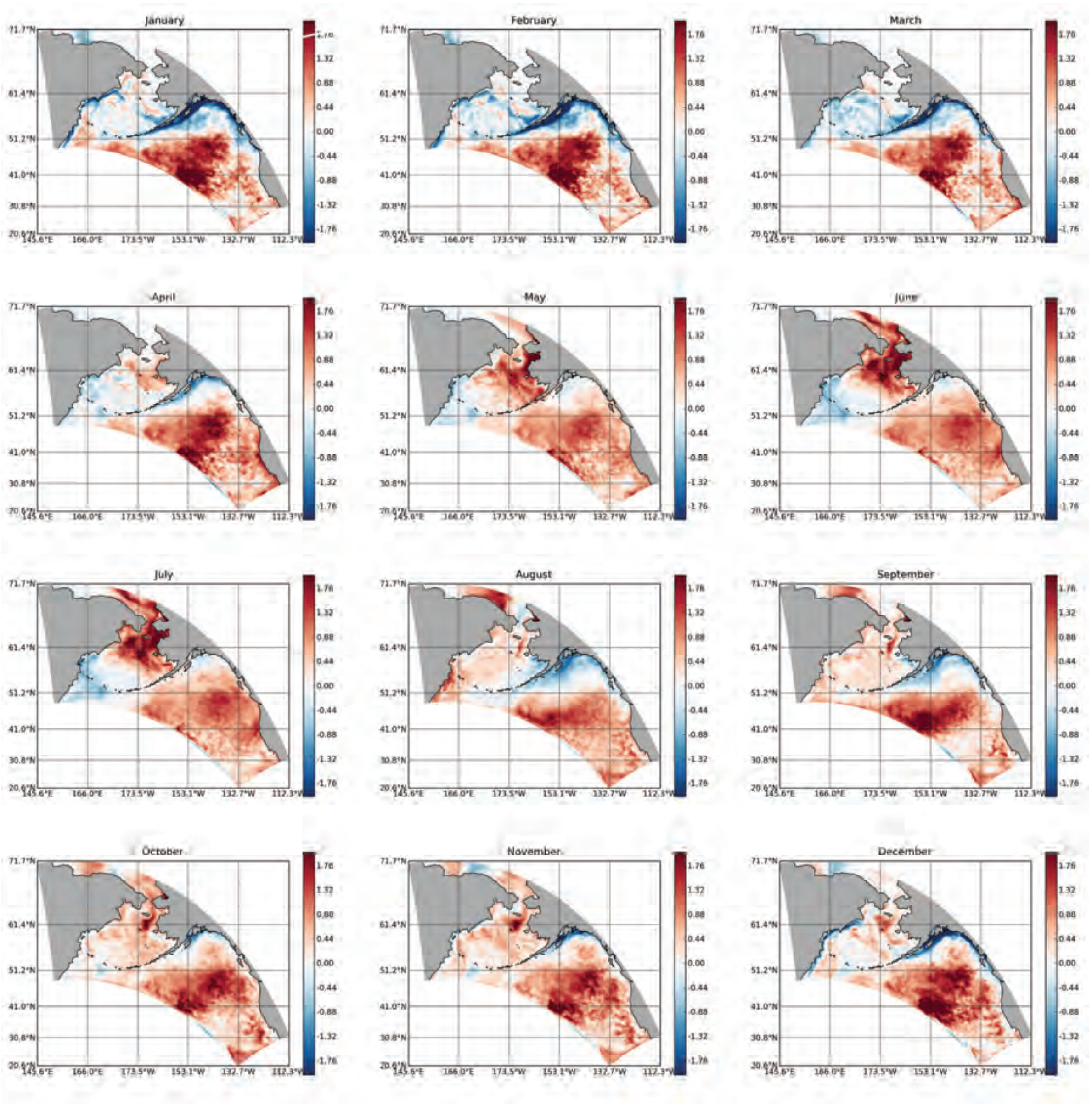


Fig. 93 NEP5 model projections of sea surface temperature change, by month, from the 2000–2010 average to the 2040–2050 average based on a single run of the NEP5 model. Red shades indicate regions of warming and blue indicates regions of cooling.

Summary – The NEP5 model suggests that within 40 years, the selective pressures on the survival and evolution of Fraser River sockeye salmon populations may favour those individuals that emigrate very early, perhaps in April and May, or those that emigrate later in summer and early fall. The current behaviour of mass emergence onto the continental shelf in July will be less than optimal if the correspondence between warmer than average SST and poor marine survival persists. However, this is only one potential outcome produced by one climate model, so more ensemble runs with more models will be needed to confirm the expected future of SSTs in the Gulf of Alaska.

7 Discussion

7.1 *Cause of Low Returns in 2009*

Key Question 1:
Can the decline in Fraser sockeye in 2009 be explained by the conditions the fish experienced in the marine environment?

Is it explained by the marine environment? – no; *can* it be explained by the marine environment? – yes. Current understanding of Fraser River sockeye salmon migratory behaviour and that of other less well studied populations is that all postsmolts of all southern populations eventually migrate northward toward the northern British Columbia/Alaskan coast (Tucker *et al.*, 2009). What each will encounter on their way to enhanced feeding and growth in Alaskan waters will differ depending on the location of ocean entry and the choice of migratory route. Oceanic conditions that are known to be associated with lower survival of Fraser River sockeye salmon occurred along much of the Fraser River sockeye salmon postsmolt migration route in 2007 where an extremely poor environment developed in Queen Charlotte Strait/Sound during the migration.

7.1.1 Data shortages

Very little is known about what the sockeye salmon actually experience in the ocean. Observations are not made routinely at the time and space scales of the fish (Peterman *et al.*, 1998). Impressions of the marine environment are often a result of observations made across broad regional scales at coarse resolution (relative to a sockeye salmon) when measured from satellites. From these data, ideas about what the sockeye salmon might have experienced are based on time–space averages of the environment which ignore finescale variability. The ocean can be, and is, often observed from a single location from which the state of the broader environment is often inferred. Whether a fish experiences what happens at a station depends on the de-correlation scale of the oceanic phenomenon of interest. A large de-correlation scale indicates that observations made at a station are indicative of a broader region than what was measured at the station, whereas small a de-correlation scale indicates that a station reflects only local variability. The scale is typically assumed to be large. Only data storage tags (Fig. 42) make it possible to record simple environmental characteristics, such as temperature, pressure (depth), and sometimes location, but these tags tend to be expensive and must be recovered before the results are known. Tag recovery rates from sockeye salmon are often low.

7.1.2 Warm and cool in 2007

> *"Juvenile salmon along the outer Vancouver Island coast generally survived very well in the cool years of 2007 and 2008"*
>
> DFO, 2010

Whether it was cool in 2007 depends on where one looks. Most of the Fraser River sockeye salmon that failed to return in 2009 went to sea as juvenile salmon in May or June of 2007. Salmon in the California Current system tend to have lower survival when they go to sea in warmer years (Mueter *et al.*, 2002; Mackas *et al.*, 2007). The DFO report, cited above, considered 2007 and 2008 to be cool years. The Gulf of Alaska began to cool in 2006, following an extremely warm year in 2005. By 2008, it had become extremely cold compared to recent norms (Batten *et al.*, 2010). However, on the time and space scales that are likely to affect Fraser River sockeye salmon, and perhaps others using the same migration route, the summer of 2007 was extremely warm in some important places (Fig. 92). There was a strong, abrupt, and generally persistent shift to warm sea surface temperature anomalies along the continental shelf in late June of 2007 (Fig. 67). Its magnitude exceeded the typical summer warming that occurs each year along the west coast and it appeared in both coastal lighthouse and satellite SST data. The surface waters of Queen Charlotte Strait/Sound were warmer in August of 2007 than in any other August from 1982 to 2010 and this was the only location in the Gulf of Alaska with SST extremes in 2007. Sockeye salmon that migrated along the outer coast (including those from the Columbia River) could have avoided the consequences of the phenomenon. The southeasterly wind regime that became established along the west coast in June and July 2007 could have retained the surface layer of warmer, fresher water within Queen Charlotte Sound.

7.1.3 Location of mortality

The emigration of about 77 million smolts from Chilko Lake in 2007 and their failure to return in large numbers in 2009 provides the best evidence, from the largest (multi-year average) sockeye salmon producer in the watershed, that the mortality occurred in the sea. It is based on an assumption, however, because the number of smolts that survived the 640 km journey downstream to the Strait of Georgia is unknown. Finding solid evidence for a solely marine source of mortality in populations other than Chilko Lake is even more challenging because of a lack of smolt/postsmolt abundance data. Some lakes have in-lake surveys of fry abundance before their last winter in freshwater, but the fraction of total mortality that occurs over the last winter in the lake is not measured (Irvine and Crawford, 2008). Therefore, all estimates of marine survival and/or productivity of sockeye salmon in the Fraser River include some component of freshwater mortality. In most stocks where only returns per spawner data are available, rates of marine and freshwater mortality are confounded (see Section 7.2.1).

Aggregate returns per spawner for sockeye salmon in the Fraser River watershed were very low for the 2007 smolt year. Most of these fish returned in 2009. Whether it will turn out to be the lowest on record depends to a certain degree on how the calculation is made and after learning the magnitude of the returns of this group in 2010 and to a much lesser degree in 2011. The approach used in the preparation of this report was to use the median annual value of returns per effective female spawner (as natural logarithms), calculated separately for each population. The logic of this approach is that each population is a genetically distinct entity that has evolved its own characteristics for survival such that each can be considered as an independent experimental trial (to the extent that methods of data collection/processing allow it). The returns observed up to 2009 were augmented by an estimate of the (small) numbers of older fish that are expected to return in 2010 and 2011. When the median values are considered, the 2007 ocean entry year will likely turn out to be the penultimate year of poor survival for the majority of stocks. However, in the specific case of Chilko Lake, postsmolt survival will likely be the lowest on record. Preliminary results from the 2010 returns indicate that the age-at-maturity of the 2005 brood year was not unusually delayed (M. Lapointe, Pacific Salmon Commission, pers. comm.), even though the average age-at-maturity of the returns has been getting older in this and some other stocks (Fig. 94).

The greatest impediment to demonstrating conclusively whether or not the mortality experienced by the many Fraser River sockeye salmon that went to sea in 2007 (mostly the 2005 brood year) occurred at sea is a lack of adequate observations. Most of the 2005 cohort would have entered the Strait of Georgia in May of 2007. A tiny fraction of non-Harrison River fish may have been collected during coho and chinook salmon surveys in the Strait of Georgia in July 2007, and another tiny fraction was collected farther north in the inside straits and on the continental shelf. Acoustic tags that were placed on large hatchery-reared sockeye salmon that were released from Cultus Lake from 2004 to 2007 had similar detection rates as they migrated northwestward through the Strait of Georgia in 2007 as in other years (Welch *et al.*, 2009). But for the most part, the survivors were not seen again for 24 months. Only the low returns of jacks (mostly age-1.1) in 2008 after 12 months at sea provided an early glimpse of the fate of these fish. The lack of observations of salmon at sea, at relevant time and space scales, severely limits the ability to draw firm conclusions about their fate (Peterman *et al.*, 1998; Trudel *et al.*, 2009). As the low return in 2009 was a rather extreme event, our approach was to look for potentially relevant extremes in the oceanic environment while these fish were at sea.

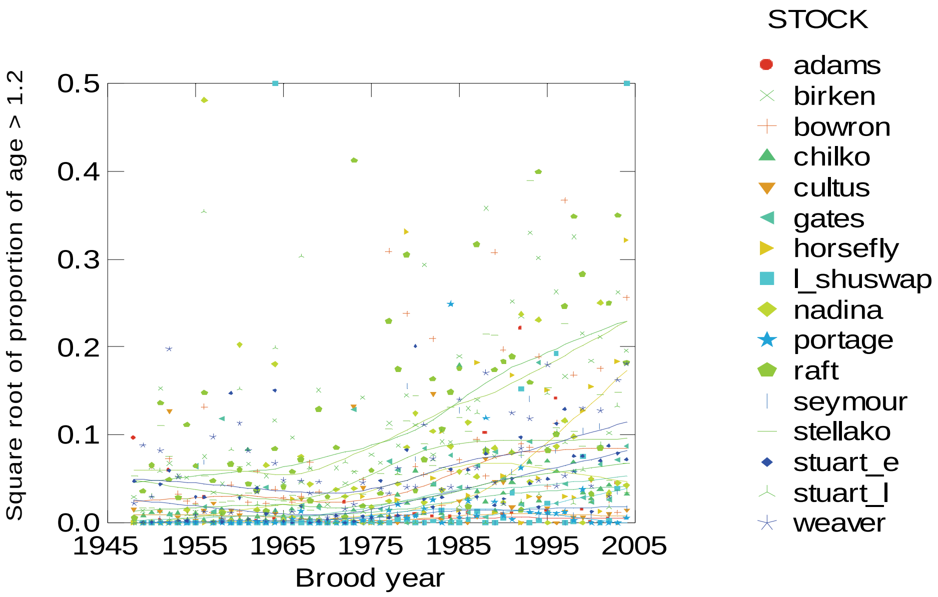


Fig. 94 Proportion of brood year returns at age-1.3 and 1.4.

Were Fraser River sockeye salmon the only populations affected? A comparison with survivals of other species/stocks with similar life histories is one approach to answering this question. There is a significant but weak positive correlation between the annual estimates of postsmolt survival of age-1.x Chilko Lake sockeye salmon and the average marine survival of wild and hatchery age-1.x coho salmon released into the Strait of Georgia in the same smolt year (McKinnell, 2009). This information may be of some value because the marine survival of these coho salmon postsmolts is known one year earlier than the equivalent group of Fraser River sockeye salmon. The Strait of Georgia coho salmon marine survival has persisted at low levels for decades. For the 2007 ocean entry year, the pattern of low survival continued, but it was not an extremum[12].

Some progress has been made to understand the kinds of ocean states that are associated with poor or good survival in the sea across multiple trophic levels (Mackas *et al.*, 2007). Composite indices of ocean state have been developed from physical and biological oceanographic data, and these are showing promise in contributing to improved forecasts of salmon returns. For example, the "Mackas ecosystem productivity index" or MEPI **(**Fig. 95) indicated that the state of the coastal ocean off Vancouver Island was near average or tending slightly toward cool and productive in the spring of 2007 (Mackas *et al.*, 2009), but the locations and seasonal timing of the variables used to develop this index would have reflected the cooler coastal ocean that likely facilitated average/good survival by some outer coast sockeye salmon stocks.

Official forecasts of Fraser River sockeye salmon return abundance do not include measurements of the state of the oceanic environment (DFO, 2010). Beginning in 2007, an informal annual salmon forecasting forum was established to record and review forecasts as part of the annual coastal salmon ocean ecology meeting. Forecasts of salmon returns generally ranged from poor to good for 2009 but only sockeye salmon expectations were singled out as not expecting good returns (McKinnell *et al.*, 2009). Whether this was simply a coincidence or a skillful forecast will require more years of trials.

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[12] Coho survival data spreadsheet by S. Baillie, DFO, pers. comm.

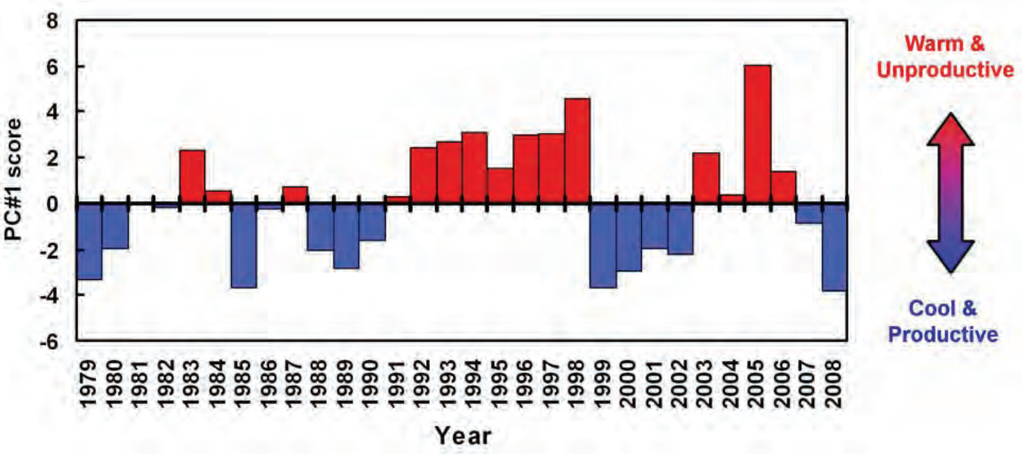

Fig. 95 Mackas ecosystem productivity index in coastal waters off Vancouver Island.

7.1.4 The Harrison River anomaly

> *"Harrison Sockeye from the 2006 brood year that returned as three year old fish in 2009, exhibited below average productivity (preliminary estimate). Harrsion [sic] Sockeye from the 2005 brood year that returned in 2009 as four year old fish and in 2008 as three year old fish, exhibited the lowest productivity on record for this stock.*
>
> DFO, 2010

Most sockeye salmon from the Harrison River migrate into the Strait of Georgia as underyearlings, which distinguishes them from most other populations in the watershed. The preliminary estimate of returns to the Harrison River for underyearlings that entered the Strait of Georgia in 2007 is approximately 1.5 million fish[13] which is approximately four times the previous maximum. The majority of these fish would have spent the summer of 2007 in the Strait of Georgia, where they were found in September sampling in 2007 to be rather abundant (Sweeting *et al.*, 2008). This suggests that the Strait of Georgia was the not the location of mortality of the 2009 returns of age-1.2 sockeye salmon. It would require conjuring a mechanism that keeps one ecotype alive and abundant while killing the rest. Harrison River sockeye salmon likely avoided the fate of the other ecotypes in 2007 by their normal habit of delaying migration from the Strait of Georgia and/or by emigrating via Juan de Fuca Strait to the west coast where they are typically the only Fraser River sockeye salmon found in fall samples (Tucker *et al.*, 2009).

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[13] http://www.psc.org/NewsRel/2010/NewsRelease11.pdf

7.2 Decline in Marine Productivity or Change in Distribution?

Key Question 2:
Is there any evidence for declines in marine productivity or changes in Fraser sockeye distribution that can be associated with the 15-year gradual decrease in Fraser sockeye productivity?

- **Gradual decline –** The gradual 15-year decline from average productivity before 1992 is a better model[14] than a "shift" to lower productivity in only three of 16 stocks (Adams, Bowron, Stellako). In 12 stocks, a shift to lower productivity is a better model. In one population (Raft), they are equally likely models. This may also be the case in other stocks where the pattern is not so clear. An accurate characterization of the nature of the decline is an important first step in searching for a cause.
- **Marine productivity –** There has been no trend in average nutrient concentrations in the southern Gulf of Alaska (Ocean Station Papa) since the 1950s, no trend in average chlorophyll *a* since 1998, and no trend in average zooplankton biomass.
- **Distribution –** Progress has been made to improve the knowledge of the coastal distribution of juvenile Fraser River sockeye salmon, but sampling to date has not been sufficient to make year-to-year comparisons in regional stock composition. The oceanic distributions of populations of Fraser River sockeye salmon are not known with sufficient accuracy to understand if they have varied from year to year or decade to decade. Surveys conducted during the 1950 and 1960s by the Fisheries Research Board of Canada were never repeated after the Board was disbanded.

7.2.1 Interpreting returns per spawner

The lengthy histories of returns per spawner provided by the Pacific Salmon Commission demonstrate a striking pattern of variation and co-variation in productivity in Fraser River sockeye salmon over the past six decades (Fig. 96). Some authors have argued that variation in Fraser River sockeye salmon productivity is a reflection of winter climate variation in the Northeast Pacific affecting sockeye salmon survival in the ocean (Beamish *et al.*, 1997; Beamish *et al.*, 2004b) while others have demonstrated very little, if any, of this effect on Fraser River stocks (Adkison *et al.*, 1996; Peterman *et al.*, 1998), and one author found that declining productivity in Chilko Lake through the early 2000s was a result of lower freshwater survival (McKinnell, 2008). Increasing the average number of spawners in Chilko Lake in the 1990s did not translate into an equivalent increase in the numbers of smolts leaving there. So the fundamental question concerning productivity is whether patterns of variation have arisen in freshwater, salt water, or both. Returns per spawner time series do not necessarily reflect where a change has occurred.

The one place where this evaluation can be attempted, without making strong assumptions, is in Chilko Lake. In this case, it is clear that attributing all of the variation in total survival to shared variation in the sea would be a mistake (McKinnell, 2008). In fact, over the history of observations of the Chilko Lake population, variation in returns per spawner appears to be almost equally shared by freshwater and marine (postsmolt) effects (Fig. 97). Bootstrapping each of these comparisons separately indicated that the correlations in the two panels of Figure 97 are not significantly different (Fig. 98).

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[14] Lower sum of squared deviations.

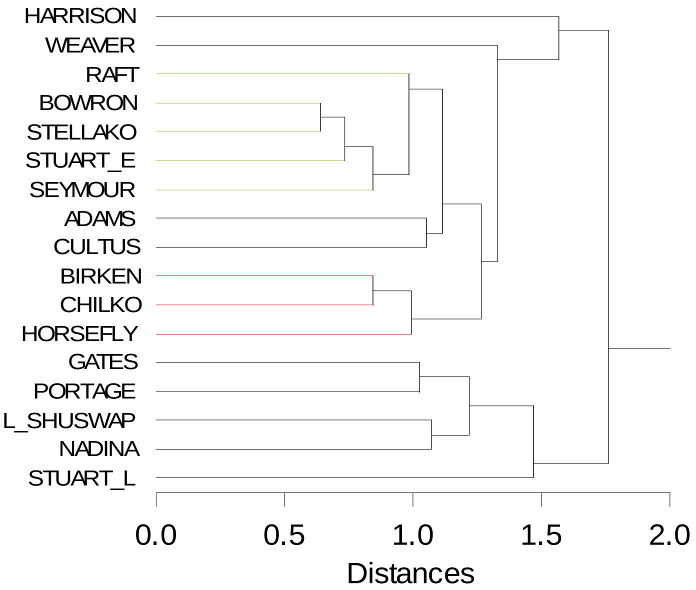

Fig. 96 Hierarchical cluster analysis of log(recruits per spawner) of 17 stocks with lengthy production data. Stocks clustered together have more similar histories than stocks not in a cluster. Note that the last stock to be included (Harrison) has the most dissimilar life history. BIRKEN = Birkenhead River population.

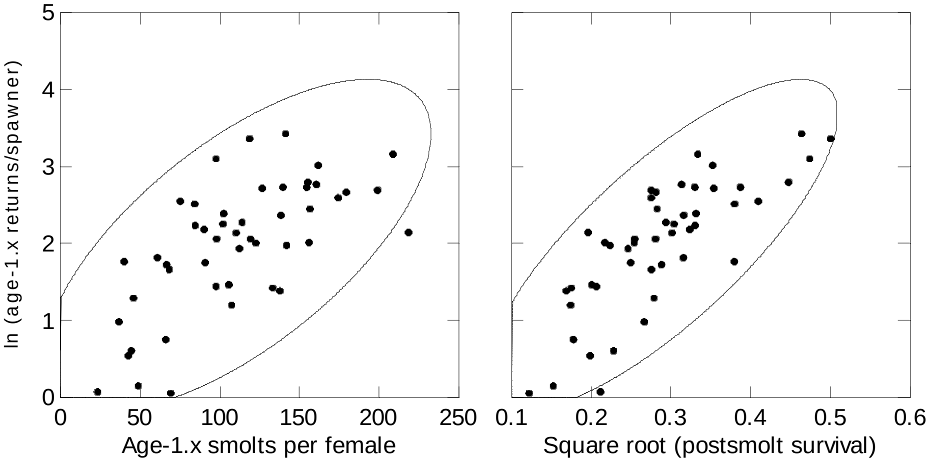

Fig. 97 (Left) Logarithm of returns of age-1.x sockeye salmon per effective female spawner *versus* freshwater survival (ratio of numbers of age-1.x smolts per effective female spawner), and (right) ordinate as in (left) *versus* smolt-to-adult survival (√ transformed) of age-1.x sockeye salmon from Chilko Lake. From the ordinate alone, as is the case in many Fraser River sockeye salmon populations, the source of variation in total survival (fresh or salt water) cannot be determined.

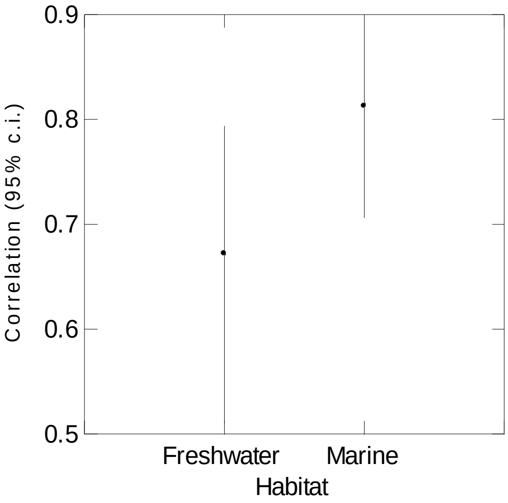

Fig. 98 Solid circles indicate the average of bootstrapped correlations and the whiskers indicate their 95% confidence intervals of total survival and freshwater survival, and total survival and marine survival, of Chilko Lake age-1.x sockeye salmon.

For the remaining populations where smolt abundance is not observed, the relative contributions of freshwater and marine effects on survival can only be assumed. Fry-to-adult survival tends to favour a marine origin for the decline (Peterman *et al.*, 2010). But the inclination is to presume that recent changes in productivity are largely of marine origin because these populations share a common ocean but not a common lake. These populations also share a common means of egress to the sea but this life history stage is rarely examined in detail because it is such a short period of their lives. Although they may rear in freshwater in different locations, some are exposed to similar effects of climate, particularly in winter (McKinnell and Crawford, 2007). These points have been raised, not to argue that a freshwater cause for the decline should be sought, but to highlight what can be known with certainty.

7.2.2 Gradual *versus* abrupt decline

The Key Question posed above by the Cohen Commission describes the decline in productivity as a 15-year gradual decline. This point deserves closer scrutiny because trend lines are designed to smooth discontinuous patterns of variation. Applying trend lines to total survival data such as is shown in Figure 99 leaves an impression of gradual downward change in total survival, accelerated recently by low values for the 2003 and the (incomplete) 2005 brood years. As the purpose of the trend line is to smooth over year to year variation and reveal longer term change, rapid and persistent changes in total survival from year-to-year are blurred by the smoother, and also because smolts of different ocean entry years from the same cohort are pooled when total survival is considered as the variable of interest.

An abrupt decline in productivity appeared beginning with the 1992 ocean entry year of the age-1.x ecotype (Fig. 99). No other year in the previous three decades was as low as this. It was the onset of a relatively persistent period of lower average survival of Fraser River sockeye salmon that continued through the 2007 ocean entry year. The 2005 and 2007 ocean entry years, and perhaps 1993 as well, are anomalous in the entire record. Keep in mind that the 2007 ocean entry year is incomplete and total survival of all ecotypes to date is only estimated.

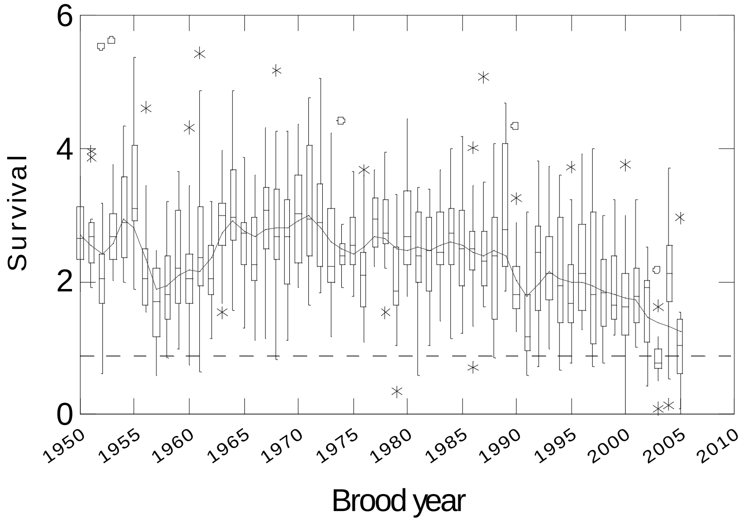

Fig. 99 Box and whisker plot indicating brood year by brood year variation in total survival among 16 major Fraser River sockeye salmon stocks (Harrison River excluded). The short horizontal lines in each box are median values. The black line is a loess smoother indicating a long-term trend. Data for the 2005 brood year were augmented with anticipated returns of older fish in 2010 (calculated from mean values observed from the 1983–2004 brood year). Survival of the 2005 brood year based on returns observed to 2009 is indicated by the dashed horizontal line.

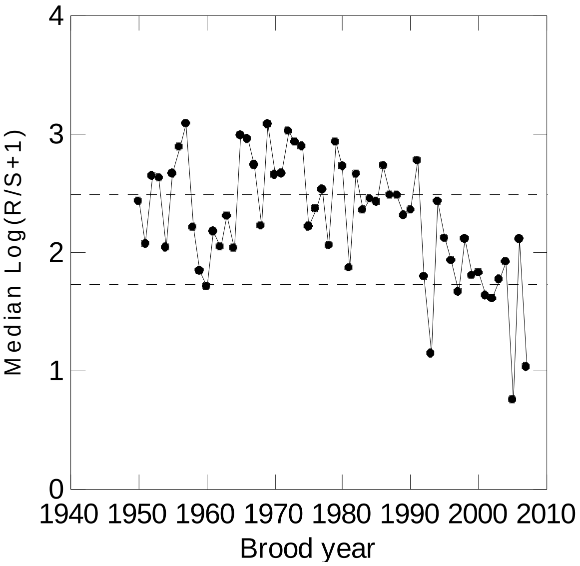

Fig. 100 Median total survival of the age-1.x ecotypes of sockeye salmon from 16 major stocks in the Fraser River (Harrison River excluded). The 2005 brood year was augmented with an estimate of the expected numbers of age-1.3 fish in 2010 (based on average proportions of these ecotypes). Horizontal lines indicate average values before and after 1992.

Using the data in Figure 100, each year was considered sequentially to determine if it was the year when average productivity declined (Equation 1). The year that provided the best fit (smallest residual sum of squared deviations from a "two mean state" model) was the 1990 brood year (1992 ocean entry year) for age-1.x smolts (Fig. 101). Furthermore, there was no statistically significant linear trend in the median from the 1992 ocean entry year to the present, and none from 1975–1991 ocean entry years, suggesting that the declining median value was a shift to lower productivity rather than a trend. The data prior to the 1975 ocean entry year also suggest persistent periods of higher and lower productivity in the earlier part of the record (Fig. 100). There was no equivalently timed change in median productivity of age-2.x smolts. The best division of this time series into periods of higher and lower productivity is the 1985 ocean entry year, although beginning with the 1981 ocean entry year, there was a marked improvement in fit. There was no known corresponding change in oceanic productivity in either of these years.

Equation 1 Formula for goodness of fit; rs_j is the median of ln(R/S + 1) from ocean entry year j across 16 major stocks, rs_1 is the average of rs_j in period 1 (from 1951 to year i – 1) and rs_2 is the average of rs_j in period 2 (from ocean entry year i to 2007). The largest change in mean survival occurs at the ocean entry year with the minimum RSS.

$$RSS_i = \sum_{j=1950}^{j-1} \left(rs_j - r\overline{s}_1 \right) + \sum_{j=1}^{2007} \left(rs_j - r\overline{s}_2 \right), \; i = 1951, 2007$$

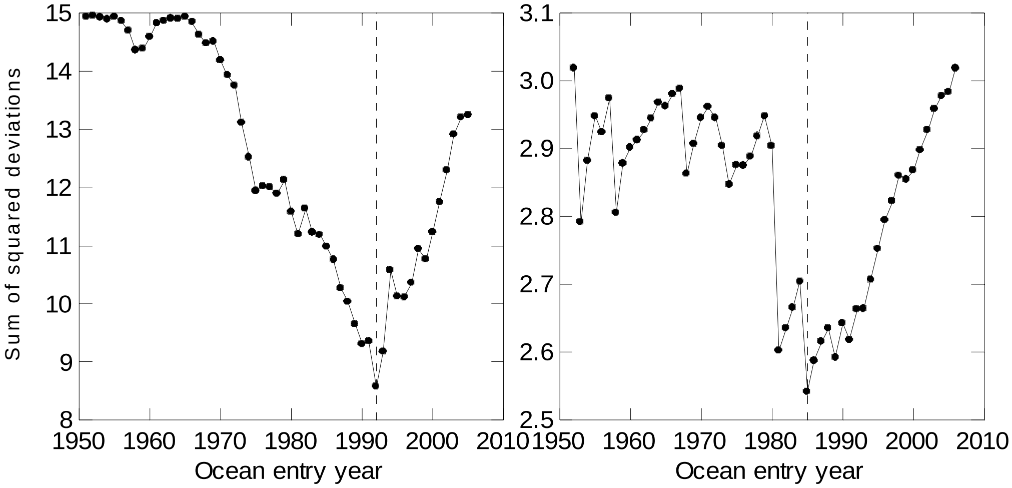

Fig. 101 Goodness of fit to a two state productivity model (left panel: age-1.x ecotypes and right panel: age-2.x ecotypes). The minimum value indicates the year of best fit for single step change in productivity. The vertical line indicates that the 1992 ocean entry year is the best year to divide the age-1.x series into two parts and the 1985 ocean entry for the age-2.x series.

Considering the alternative model of a gradual decline in productivity, log (returns per spawner) for each major stock (except Harrison River) was considered independently against two hypothetical models. The first model was the "two mean state" with a shift in 1992, described above. The second model was a linear decline from the pre-1992 mean state until 2006. The lower residual sum of squared deviations from these two models (with the same number of parameters) was used to judge which model was a better fit to the data. No attempt was made, given the available time, to determine whether the two models could be distinguished based on the observations.

The temporal pattern of log(returns per spawner) of the age-1.x ecotypes in 12 of the 16 stocks with the longest time series suggests that the decline in productivity that is described above as a “15-year gradual decrease” was a shift in the average (beginning with the 1992 ocean entry year) rather than a trend (Table 4). Of the four remaining stocks, one (Raft) has no significant change in the mean state and had no trend after 1992. The remaining three (Adams, Bowron, Stellako) indicated that a declining trend from 1992 to 2006 provides a better fit to the data. The change in the average productivity coincides with the overall decline in average sockeye salmon productivity, which occurred in 1992, that is most evident in populations producing small smolts that border Queen Charlotte Strait/Sound (McKinnell *et al.*, 2001). The cause of the downturn is not known but it appears, to varying degree, in most stocks that use Queen Charlotte Strait/Sound as a postsmolt migration route. The recent finding of a good correlation between chlorophyll concentrations at the northern end of Vancouver Island and Chilko Lake postsmolt survival may serve as a basis for future research. This is a region where seabird productivity, for example, is known to vary from year to year from changes in phenology and the state of the ocean (Bertram *et al.*, 2001).

Table 4 Comparison of goodness of fits (residual sum of squared deviations) to two simple two-parameter models of productivity (shift in average in 1992 from high to low, *versus* a linear downward trend after 1992 from the average value for years before 1992). The P(shift) column is the probability of no difference in mean values between the two periods. Values > 0.05 are generally considered to be differences in the mean that arose by chance.

Stock	Shift SS	P(shift)	Trend SS	Better Fit (T = trend, S = Shift)
Adams	48.12	0.09	47.06	T
Birkenhead	23.88	0.00	33.50	S
Bowron	26.63	0.02	24.58	T
Chilko	24.56	0.00	26.77	S
Cultus	36.62	0.10	37.49	S
Gates	42.93	0.00	44.52	S
Horsefly	30.21	0.00	30.34	S
Lower Shuswap	72.87	0.00	74.18	S
Nadina	40.66	0.00	41.37	S
Portage	83.14	0.01	84.08	S
Raft	28.58	0.80	28.58	–
Seymour	30.45	0.00	34.69	S
Stellako	17.68	0.00	14.49	T
Early Stuart	16.67	0.00	20.51	S
Late Stuart	63.93	0.00	67.76	S
Weaver	47.93	0.18	50.07	S

The abrupt decline in sockeye salmon productivity, which began in 1992, was most apparent in Owikeno Lake and in Long Lake (McKinnell *et al.*, 2001) in central British Columbia (Fig. 102). Evidence of this decline also appears in the Columbia River where adult returns in 1994 (the 1992 ocean entry year), measured at the Bonneville Dam, declined and remained low until the 1998/99 la Niña (J.G. Williams, NOAA/NWFSC, Seattle, pers. comm.), and in recent returns to Quinault Lake on the west coast of Washington State. Catches of Barkley Sound sockeye salmon declined from significantly above average to below average beginning in 1994 (1992 ocean entry year of the dominant age-1.2 ecotype) although they, too, recovered with the 1998/99 la Niña. The concomitant declines in sockeye salmon productivity from the Columbia River to Queen Charlotte Sound suggest that the factors which were responsible for initiating a period of lower survival affected a significant fraction of the west coast including Queen Charlotte Sound. A concomitant decline does not appear in Babine Lake sockeye production, but this is not unexpected, as the Skeena River delivers its smolts into a different biogeographic zone (Orsi *et al.*, 2007).

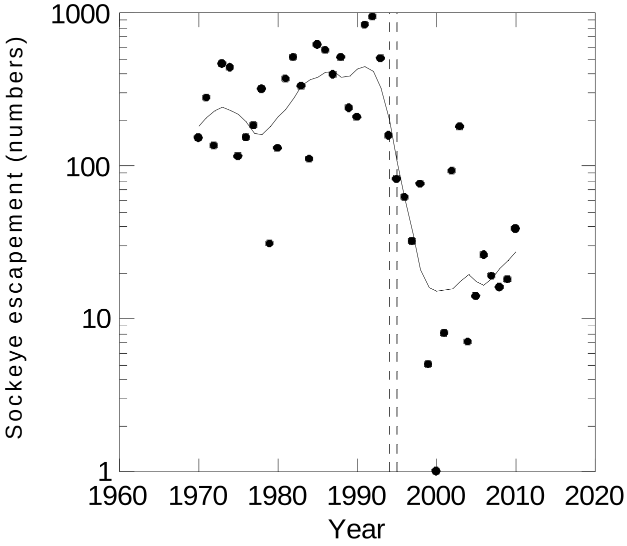

Fig. 102 Annual numbers of sockeye salmon migrating upstream at the Docee River fence. Vertical dashed lines indicate the return years of cohorts whose members went to sea in 1992. The trend line is a loess smoother. DFO data source: http://www.pac.dfo-mpo.gc.ca/northcoast/counts/docee/default.htm.

Some of these patterns of variability are expressed in ecosystem indicators for the west coast. The Mackas ecosystem productivity index (MEPI, Mackas *et al.*, 2007) integrates ecological observations (physical, chemical, and biological) related to the productivity of the ocean on the southwest coast of Vancouver Island. According to the MEPI, a warm and unproductive period in the coastal ocean began in 1992 (Fig. 95). Extreme values of the MEPI can reflect wholesale changes in the coastal ocean, not simply a change in temperature of the coastal ocean. The replacement of Subarctic copepods, for example, with species of more southerly origin, alters the makeup of the food web in ways that are just beginning to be explored. Shifts in species abundance occurred at various trophic levels in 1992 and it coincided with the return, after more than a 40 year absence, of the sardine (*Sardinops sagax*) to the west coast of Vancouver Island (Hargreaves *et al.*, 1994).

The MEPI returned briefly (1999–2002) to cool and productive but this was not reflected in a marked improvement in marine survival of Fraser River sockeye salmon. Either this reflects a transient connectivity between the MEPI and Fraser River sockeye salmon survival, or it reflects a coincidental association of extremes beginning in 1992. The latter seems less likely because the most positive year of the MEPI (2005) corresponds to the lowest median survival of a cohort (2003) of Fraser River sockeye salmon (Fig. 100) and served as a basis for reasonably accurate coast-wide predictions of returns of many salmonid species and stocks with that particular ocean entry year. The transient mismatches could be a result of variable spatial scales of the dominant forces affecting the MEPI, or of a mismatch between the dates of sampling of the variables that constitute the MEPI and the timing of the seasonal expression of the factor(s) that affect Fraser River sockeye salmon survival.

For the 20th century, the oceanic and atmospheric climates of the North Pacific have been described in terms of regimes; periods of persistence anomalies that shift abruptly among phases (Schwing *et al.*, 2010). The year 1989 was identified as a time of one of these climate shifts (Hare and Mantua , 2000; McFarlane *et al.*, 2000) but the common year of decline of Fraser River, Long Lake and Owikeno Lake, and to a lesser degree Columbia River, Quinault Lake, and Barkley Sound sockeye salmon was the 1992 ocean entry year. The extent to which the 1989 climate change and the 1992 sockeye salmon productivity change are interrelated is unknown, but it has been suggested (McFarlane 2001). The coincidence of a shared change in sockeye salmon productivity in 1992 suggests that these stocks were affected by a relatively large-scale coastal influence that had a more persistent effect on stocks using Queen Charlotte Sound and Strait.

Acknowledgments

Thanks are due to many people who have helped to make this report what it became. Dr. Muyin Wang, Joint Institute for the Study of Atmosphere and Ocean (JISAO), University of Washington, Seattle, U.S.A. made the IPCC model output for the North Pacific Ocean available to allow us to calculate average SSTs predicted for the 2080s. John Dower (University of Victoria) and his Ph.D. student, Lu Guan, allowed us to report some preliminary results of their ichthyoplankton surveys in the Strait of Georgia. Susan Allen (University of British Columbia) and her student, Jeremy Sklad, kindly provided their reconstructed Sandheads wind speed data for the Strait of Georgia. Jim Gower, Institute of Ocean Sciences, provided Nanoose Bay station hydrographic data for the Strait of Georgia. Michael Lapointe, Pacific Salmon Commission, provided Fraser River sockeye salmon production data and associated biological data and was always helpful with their interpretation. Hokkaido University recently opened their HUFODAT salmon catch and biological database to the public and for that we are very grateful. Much of what is learned about sockeye salmon at sea, particularly on the high seas, would not have been possible without the research initiatives of the (former) Fisheries Research Board of Canada, the Fisheries Research Institute of the University of Washington, and the Fisheries Agency of Japan. The work was improved greatly by comments from Michael Dagg (Louisiana State University), Michael Foreman (Institute of Ocean Sciences), Masa-aki Fukuwaka (Fisheries Research Agency of Japan), Phillip Mundy (U.S. National Oceanic and Atmospheric Administration), and Greg Ruggerone (Natural Resources Consultants, Inc.). In total, about 200 suggestions for revision/clarification were offered and we have endeavoured to consider and address each of them. Finally, the oceanographers of the Institute of Ocean Sciences were generous with their time and understanding when called upon to clarify aspects of ocean ecology, as were the many salmon biologists in the region who were generous with their data and advice.

References

Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M. and Korman, J. 1996. Alternative models of climate effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. *Fish. Oceanogr*. **5**: 137–152.

Anonymous. 1963. Data record of bathythermograms observed in the Northeast Pacific Ocean during the Gulf of Alaska Salmon Tagging Program April to July, 1962. Manuscr. Rpt. Series (Oceanographic and Limnological) 143, 74 p.

Arrington, D.A., Winemiller, K.O., Loftus, W.A. and Senol, A. 2002. How often do fishes "run on empty"? *Ecology* **83**: 2145–2151.

Babaluk, J.A., Reist, J.D., Johnson, J.D. and Johnson, L. 2000. First records of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) from Banks Island and other records of Pacific salmon in Northwest Territories, Canada. *Arctic* **53**: 161–164.

Babcock, J.P. 1918. Salmon fishery of the Fraser River District, pp. 140–153, *in* Ninth Annual Report of the Commission of Conservation, Ottawa, ON, Canada.

Bailey, R.E., Margolis, L. and Groot, C. 1988. Estimating stock composition of migrating juvenile Fraser River (British Columbia) sockeye salmon, *Oncorhynchus nerka*, using parasites as natural tags. *Can. J. Fish. Aquat. Sci.* **45**: 586–591.

Banse, K. and English, D.C. 1999. Comparing phytoplankton seasonality in the eastern and western subarctic Pacific and the western Bering Sea. *Prog. Oceanogr.* **43**: 235–288.

Barraclough, W.E. 1967a. Data record: number, size and food of larval and juvenile fish caught with a two boat surface trawl in the Strait of Georgia April 25–29, 1966. Manuscr. Rep. (FRBC) 922, 54 p.

Barraclough, W.E. 1967b. Data record: number, size and food of larval and juvenile fish caught with an Isaacs-Kidd trawl in the surface waters of the Strait of Georgia April 25–29, 1966. Manuscr. Rep. (FRBC) 926, 79 p.

Barraclough, W.E. 1967c. Data record: number, size composition and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 6–8, 1966. Manuscr. Rep. (FRBC) 928, 58 p.

Barraclough, W.E. and Fulton, J.D. 1967. Data record: number, size composition and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–8, 1966.

Barraclough, W.E. and Phillips, A.C. 1978. Distribution of juvenile salmon in the southern Strait of Georgia during the period April to July 1966–1969. Fish. Mar. Serv. Tech. Rep. 826, 47 p.

Batten, S. SAHFOS, pers. comm.

Batten S.D. and Mackas, D.L. 2009. Shortened duration of the annual *Neocalanus plumchrus* biomass peak in the Northeast Pacific. *Mar. Ecol. Prog. Ser.* **393**: 189–198.

Batten, S., Chen, X., Flint, E.N., Freeland, H.J., Holmes, J., Howell, E., Ichii, T., Kaeriyama, M., Landry, M., Lunsford, C., Mackas, D.L., Mate, B., Matsuda, K., McKinnell, S.M., Miller, L., Morgan, K., Peña, A., Polovina, J.J., Robert, M., Seki, M.P., Sydeman, W.J., Thompson, S.A., Whitney, F.A., Woodworth, P. and Yamaguchi, A. 2010. Status and trends of the North Pacific oceanic region, 2003–2008, pp. 56–105, *in* Marine Ecosystems of the North Pacific Ocean, 2003–2008, *edited by* S.M. McKinnell and M.J. Dagg, PICES Special Publication 4: 393 p.

Beamish, R.J., Neville, C.E. and Cass, A.J. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Can. J. Fish. Aquat. Sci.* **54**: 543–554.

Beamish, R.J., Sweeting, R.M. and Neville, C.M. 2004a. Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. *Trans. Am. Fish. Soc.* **113**: 1163–1175.

Beamish, R.J., Schnute, J.T., Cass, A.J., Neville, C.M. and Sweeting, R.M. 2004b. The influence of climate on the stock and recruitment of pink and sockeye salmon from the Fraser River, British Columbia, Canada. *Trans. Am. Fish. Soc.* **113**: 1396–1412.

Beamish, R.J., Riddell, B.E., Lange, K.L., Farley Jr., E., Kang, S., Nagasawa, T., Radchenko, V., Temnykh, O., Urawa, S., Azumaya, T., Brodeur, R., Emmett, R., Imai, H., Ishida, Y., Kaeriyama, M., Kim, S., Klyashtorin, L., Koval, M., Kristianson, G., Lee, C.S., Low, L.-L., Melnikov, I., Moss, J., Mundy, P., Myers, K., Naydenko, S., Nazarov, V., Ruggerone, G., Seeb, J., Seki, J., Seong, K.B., Smith, G., Sviridov, V., Templin, B., Trudel, M., Volobuev, V. and Young, S. 2009. A long-term research and monitoring plan (LRMP) for Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. NPAFC Special Publication 1.

Beamish, R., Sweeting, R., Lange, K., Neville, C., Preikshot, D., Thomson, R. and Beacham, T. 2010. An explanation for the poor return of sockeye salmon to the Fraser River in 2009. Presentation to the PSC Workshop

Bernard, F.R. 1986. Data record: flying squid drift-net and oceanographic cruise by W.E. Ricker, August–September 1986. Document submitted to the Annual Meeting of the INPFC. Anchorage, Alaska, November 1986.

Bertram, D.F., Mackas, D.L. and McKinnell, S. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. *Prog. Oceanogr.* **49**: 283–308.

Bilton, H.T. and Messinger, H.B. 1975. Identification of major British Columbia and Alaska runs of age 1.2 and 1.2 sockeye from their scale characters. *Intl. N. Pac. Fish Comm. Bull.* **32**: 109–129.

Birtwell, I.K., Nassichuk, M.D. and Beune, H. 1987. Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River, pp. 25–35, *in* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, *edited by* H.D. Smith, L. Margolis, and C.C. Wood, *Can. Spec. Publ. Fish. Aquat. Sci.* **96**.

Blackbourn, D.J. 1987. Sea surface temperature and pre-season prediction of return timing in Fraser River sockeye salmon (*Oncorhynchus nerka*), pp. 296–306, *in* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, *edited by* H.D. Smith, L. Margolis, and C.C. Wood, *Can. Spec. Publ. Fish. Aquat. Sci.* **96**.

Boyd, P.W., Law, C.S., Wong, C.S., Nojiri, Y., Tsuda, A., Levasseur, M., Takeda, S., Rivkin, R., Harrison, P.J., Strzepek, R., Gower, J., McKay, R.M., Abraham, E., Arychuk, M., Barwell-Clarke, J., Crawford, W., Crawford, D., Hale, M., Harada, K., Johnson, K., Kiyosawa, H., Kudo, I., Marchetti, A., Miller, W., Needoba, J., Nishioka, J., Ogawa, H., Page, J., Robert, M., Saito, H., Sastri, A., Sherry, N., Soutar, T., Sutherland, N., Taira, Y., Whitney, F., Wong, S.K.E. and Yoshimura, T. 2004. The decline and fate of an iron-induced subarctic phytoplankton bloom. *Nature* **428**: 549–553.

Brett, J.R. 1950. A study of the Skeena River climatological conditions with particular reference to their significance in sockeye production. *J. Fish. Res. Bd. Can.* **8**: 178–187.

Brett, J.R. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*, pp. 29–63, *in* Behavioral Energetics: The Cost of Survival in Vertebrates, *edited by* W.P. Aspey and S.I. Lustick, Ohio State University Press, Columbus.

Burgner, R.L. 1991. The life history of sockeye salmon (*Oncorhynchus nerka*), pp. 1–117 *in* Pacific Salmon Life Histories, *edited by* C. Groot and L. Margolis, UBC Press, Vancouver, Canada, 564 p.

Carlson, H.R., Farley, E.V., Myers, K.W., Martinson, E.C., Pohl, J.E. and Weemes, N.M. 1998. Survey of salmon in the southeastern Bering Sea, Gulf of Alaska and northeastern Pacific Ocean, April–May 1998. (NPAFC Doc. 344) Auke Bay Laboratory, National Marine Fisheries Service, Auke Bay, AK.

Clark, T. and Hinch, S. University of British Columbia, pers. comm.

Clark, C.W. and Levy, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* **131**: 271–290.

Clemens, W.A. 1938. Contributions to the life history of sockeye salmon. Report to the Provincial Fisheries Depeartment, Vol. 23.

Clemens, W.A. 1951. The migration of Pacific salmon (*Oncorhynchus*). *Trans. Roy. Soc. Canada, Sec. V, Ser. 3*, **45**: 9–17.

Cox, S.P. and Hinch, S.G. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature. *Can. J. Fish. Aquat. Sci.* **54**: 1159–1165.

Crawford, W.R., Onishi, H., Ueno, H. and Whitney, F. 2006. Influence of eddies and mesoscale variability in the Gulf of Alaska time series in the northeast Pacific and coastal Gulf of Alaska. A Symposium to Mark the 50th Anniversary of Line-P, Fisheries and Oceans Canada. PICES Symposium July 5–8, 2006, Victoria, B.C., Canada.

Crean, P.B., Murty, T.S. and Stronach, J.A. 1988. Mathematical Modelling of Tides and Estuarine Circulation. Lecture Notes on Coastal and Estuarine Studies, Vol. 30, Springer-Verlag, Berlin, 471 p.

Crittenden, R.N. 1994. A diffusion model for the downstream migration of sockeye salmon smolts. *Ecol. Modell.* **71**: 69–84.

Crossin, G.T., Hinch S.G., Cooke, S.J., Welch, D.W., Batten, S.D., Patterson, D.A., Van Der Kraak, G., Shrimpton, J.M. and Farrell, A.P. 2007. Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. *Mar. Biol.* **152**: 905–918.

Daly, E.A., Brodeur, R.D. and Weitkamp, L.A. 2009. Ontogenetic shifts in diets of juvenile and subadult coho and chinook salmon in coastal marine waters: important for marine survival? *Trans. Am. Fish. Soc.* **138**: 1420–1438.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Chhak, K., Franks, P.J.S., Miller, A.J., McWilliams, J.C., Bograd S.J., Arango, H., Curchister, E., Powell, T.M. and Rivere, P. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.* **35**: L08607, doi:10.1029/2007GL032838.

DFO (Fisheries and Oceans Canada). 2008. Stock Assessment Report on Strait of Georgia Pacific Herring. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/014.

DFO (Fisheries and Oceans Canada). 2010. State of the Pacific Ocean 2009. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/034.

Dodimead, A.J., Favorite, F. and Hirano, T. 1963. Review of oceanography of the subarctic Pacific region. *Int. N. Pac. Fish. Comm. Bull.* **13**: 1–195.

Dower, J. and Guan, L. University of Victoria, British Columbia, Canada, pers. comm.

Egbert, G.D. and Erofeeva, S.Y. 2002. Efficient inverse modeling of barotropic ocean tides. *J. Atmos. Oceanic Technol.* **19**: 183–204.

El-Sabaawi, R. 2008. Trophic dynamics of copepods in the Strait of Georgia. Ph.D. Dissertation, University of Victoria, British Columbia, Canada.

Evanson, M., Bornhold, E.A., Goldblatt, R.H., Harrison, P.J. and Lewis, A.G. 2000. Temporal variation in body composition and lipid storage of the overwintering, subarctic copepod *Neocalanus plumchrus* in the Strait of Georgia, British Columbia (Canada). *Mar. Ecol. Prog. Ser.* **192**: 239–247.

Farley Jr., E., Azumaya, T., Beamish, R., Koval, M., Myers, K., Seong, K.B. and Urawa, S. 2009. Climate change, production trends, and carrying capacity of Pacific salmon in the Bering Sea and adjacent waters. *N. Pac. Anadr. Fish. Comm. Bull.* **5**: 1–359 p.

Fisher, J., Trudel, M., Ammann, A., Orsi, J.A., Piccolo, J., Bucher, C., Casillas, E., Harding, J.A., MacFarlane, R.B., Brodeur, R.D., Morris, J.F.T. and Welch, D.W. 2007. Comparisons of the coastal distributions and abundances of juvenile Pacific salmon from Central California to the northern Gulf of Alaska, pp. 31–80, *in* The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons, *edited by* C.B. Grimes, R.D. Brodeur, L.J. Haldorson and S.M. McKinnell, Am. Fish. Soc. Symp. Ser. 57, 247 p.

Foerster, R.E. 1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. *J. Fish. Res. Bd. Canada* **11**: 339–350.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Bd. Can. 162, 422 p.

Freeland, H.J. 2006. What proportion of the North Pacific Current finds its way into the Gulf of Alaska? *Atmos.-Ocean* **44**: 321–330.

Freeland, H.J. and Cummins, P.F. 2005. Argo: A new tool for environmental monitoring and assessment of the world’s oceans, an example from the N.E. Pacific. *Prog. Oceanogr.* **64**: 31–44.

Freeland, H.J., Denman, K., Wong, C.S., Whitney, F. and Jacques, R. 1997. Evidence of change in the winter mixed layer in the Northeast North Pacific Ocean. *Deep-Sea Res.* **44**: 2117–2129.

Freeland, H.J., Crawford, W.R. and Thomson, R.E. 1984. Currents off the Pacific Coast of Canada. *Atmos.-Ocean* **22**: 151–172.

French, R., Bilton, H., Osako, M. and Hartt, A. 1976. Distributions and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. *Intl. N. Pac. Fish. Comm. Bull.* **34**: 1–113.

Fukuhara, F.M. 1975. An evaluation of the methods for estimating age composition and abundance of sockeye salmon on the high seas. *Intl. N. Pac. Fish. Comm. Bull.* **32**: 232–277.

Fukuwaka, M. Fisheries Research Agency of Japan, pers. comm.

Fukuwaka, M. and Kaeriyama, M. 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* **54**: 631–636.

Gardiner, G. 1976. The analysis of zooplankton population fluctuations in the Strait of Georgia, with emphasis on the relationships between *Calanus plumchrus* Marukawa and *Calanus marshallae* Frost. Ph.D. dissertation, University of British Columbia, Canada.

Gargett, A.E., 1997. The optimal stability ‘‘window”: a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.* **6**: 109–117.

Gilbert, C.H. 1912. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus. Fish. Bull.* **32**: 1–22.

Gilbert, C.H. 1914. Contributions to the life-history of sockeye salmon, No. 1. Report of the British Columbia Commissioner of Fisheries.

Godfrey, H. 1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. *J. Fish. Res. Bd. Can.* **15**: 331–354.

Grimes, C.B., Brodeur, R.D., Haldorson, L.J. and McKinnell, S.M. 2007. The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. Am. Fish. Soc. Symp. Ser. 57, 247 p.

Groot, C. and Cooke, K., 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? pp. 53–60, *in* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, *edited by* H.D. Smith, L. Margolis, and C.C. Wood, *Can. Spec. Pub. Fish. Aquat. Sci.* **96**.

Groot, C. and Margolis, L. 1991. Pacific Salmon Life Histories. UBC Press: Vancouver, Canada, 564 p.

Groot, C. and Quinn, T.P. 1987. Homing migration of sockeye salmon, *Oncorhynchus nerka*, to the Fraser River. *Fish. Bull.* **85**: 455–469.

Hamilton, K. 1985. A study of the return migration route of Fraser River sockeye salmon (*Oncorhyncus nerka*). *Can. J. Zool.* **63**: 1930–1943.

Hamme, R.C., Webley, P.W., Crawford, W.R., Whitney, F.A., DeGrandpre, M.D., Emerson, S.R., Eriksen, C.C., Giesbrecht, K.E., Gower, J.F.R., Kavanaugh, M.T., Peña, A., Sabine, C.L., Batten, S.D., Coogan, L.A., Grundle, D.S., Lockwood, D. 2010. Volcanic ash fuels anomalous plankton bloom in subarctic northeast Pacific. *Geophys. Res. Lett.* **37**: L19604, doi:10.1029/2010GL044629.

Hanamura, N. 1966. Sockeye salmon in the Far East. *Intl. N. Pac. Fish. Comm. Bull.* **18**: 1–28.

Hare, S.R. and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* **47**: 103–146.

Hargreaves, N.B., Ware, D.M. and McFarlane, G.A. 1994. Return of Pacific Sardine (*Sardinops sagax*) to the British Columbia Coast in 1992. *Can. J. Fish. Aquat. Sci.* **51**: 460–463.

Hartt, A.C. 1975. Problems sampling Pacific salmon at sea. *Intl. N. Pac. Fish. Comm. Bull.* **32**: 165–231.

Hartt, A.C. and Dell, M.B. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. *Intl. N. Pac. Fish. Comm. Bull.* **46**: 1–105.

Healey, M.C. 1980. The ecology of juvenile salmon in the Strait of Georgia, British Columbia, pp. 203–229, *in* Salmonid Ecosystems of the North Pacific *edited by* W.J. McNeil and D.C. Himsworth, Oregon State University Press, Corvallis, OR.

Healey, M.C., Thomson, K.A., Leblond, P.H., Huato, L., Hinch, S.G. and Walters, C.J. 2000. Computer simulations of the effects of the Sitka eddy on the migration of sockeye salmon returning to British Columbia. *Fish. Oceanogr.* **9**: 271–281.

Henderson, M.A. and Cass, A.J. 1991. Effect of smolt size on smolt-to-adult survival of Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Can J. Fish. Aquat. Sci.* **48**: 988–994.

Hinch, S.G., Healey, M.C., Diewart, R.E. and Henderson M.A. 1995. Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*), pp. 439–445, *in* Climate change and northern fish populations, *edited by* R.J. Beamish, *Can. Spec. Publ. Fish. Aquat. Sci.* **121**.

Hipfner, J.M. 2008a. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar. Ecol. Prog. Ser.* **368**: 295–304.

Hipfner, J.M. 2008b. Seabird reproductive performance on Triangle Island in 2007: A late and unsuccessful breeding season, pp. 62–63, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* J.R. Irvine and W.R. Crawford, DFO Can. Sci. Advis. Sec. Res. Doc. 2008/013.

Hipfner, J.M. 2010. Seabird breeding on Triangle Island in 2009: early and successful, pp. 72–73, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2009, *edited by* W.R. Crawford and J.R. Irvine, DFO Can. Sci. Advis. Sec. Res. Doc. 2010/053.

Hodgson, S. 2000. Marine and freshwater climatic influences on the migratory timing of adult sockeye salmon. Master's Thesis, University of Washington, WA, USA.

Huyer, A. 1983. Coastal upwelling in the California current system. *Prog. Oceanogr.* **12**: 259–284, doi:10.1016/0079-6611(83)90010-1.

IPCC (Intergovernamental Panel on Climate Change). 2007. Climate Change 2007. Cambridge University Press, Cambridge, UK.

Irvine, J.R. and Crawford, W.R. (eds.) 2008. State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems. DFO Can. Sci. Advis. Sec. Res. Doc. 2008/013.

Irvine, J.R., Fukuwaka, M., Kaga, T., Park, J.H., Seong, K.B., Kang, S., Karpenko, V., Klovach, N., Bartlett, H. and Volk, E. 2009. Pacific salmon status and abundance trends. NPAFC Doc. 1199, Rev. 1., 153 p.

Irvine, J.R., Godbout, L., Brown, L., Borstad, G., Mackas, D. and Thomson, R. 2010. Do marine conditions in Queen Charlotte Sound limit the marine survival of Chilko sockeye salmon?, p. 132, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2009, *edited by* W.R. Crawford and J.R. Irvine, DFO Can. Sci. Advis. Sec. Res. Doc. 20108/053.

Ishida, Y., Ito, S., Ueno, Y. and Sakai, J. 1998. Seasonal growth patterns of Pacific salmon (*Oncorhynchis* spp.) in offshore water of the North Pacific Ocean. *N. Pac. Anadr. Fish. Comm. Bull.* **1**: 66–80.

Jordan, D.S. 1888. The story of a salmon, pp. 9–19, *in* Science Sketches, *edited by* D.S. Jordan, A.C. McClurg & Co., Chicago.

Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V. and Myers. K.W. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* **13**: 197–207.

Kline, T.C. 2006. Carbon subsides derived from cross-shelf exchange: a 'missing link' in ecological models? *Eos Trans. Am. Geophys. Union* **87** (36 Supplement).

Kolody, D. and Healey, M.C. 1998. Numerical simulations of Fraser River sockeye salmon homing migration routes in a dynamic marine environment. *N. Pac. Anadr. Fish. Comm. Bull.* **1**: 118–128.

Ladd, C., Mordy, C.W., Kachel, N.B. and Stabeno, P.J. 2007. Northern Gulf of Alaska eddies and associated anomalies. *Deep-Sea Res. I* **54**: 487–509.

Lapointe, M. Pacific Salmon Commission, pers. comm.

LeBrasseur, R.J. 1965. Stomach contents of salmonids caught in the northeastern Pacific Ocean, 1958. Circular. Statistical series, Fish. Res. Bd. Can., Biological Station, Nanaimo, B.C., 15, Vol. 1.

LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the Northeastern Pacific Ocean. *J. Fish. Res. Bd. Can.* **23**: 85–100.

LeBrasseur, R.J. and Barner, L.W. 1964. Salmon catches in northern Hecate Strait, November, 1963. Fish. Res. Bd. Can. MS Rep. Ser. (O.&L.) 176, 13 p.

LeBrasseur, R.J. and Doidge, D.A. 1966a. Stomach contents of salmonids caught in the northeastern Pacific Ocean, 1962. Circular. Statistical series, Fish. Res. Bd. Can., Biological Station, Nanaimo, B.C., 20, Vol. 2.

LeBrasseur, R.J. and Doidge, D.A. 1966b. Stomach contents of salmonids caught in the northeastern Pacific Ocean, 1956 and 1957. Circular. Statistical series, Fish. Res. Bd. Can., Biological Station, Nanaimo, B.C., 20, Vol. 3.

LeBrasseur, R.J. and Doidge, D.A. 1966c. Stomach contents of salmonids caught in the northeastern Pacific Ocean, 1959 and 1960. Circular. Statistical series, Fish. Res. Bd. Can., Biological Station, Nanaimo, B.C., 21, Vol. 4.

LeBrasseur, R.J. and Doidge, D.A. 1966d. Stomach contents of salmonids caught in the northeastern Pacific Ocean, 1963 and 1964. Circular. Statistical series, Fish. Res. Bd. Can., Biological Station, Nanaimo, B.C., 23, Vol. 5.

LeBrasseur, R.J., Barraclough, W.E., Kennedy, O.D. and Parsons, T.R. 1969. Production studies in the Strait of Georgia. Part III. Observations on the food of larval and juvenile fish in the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 51–61.

LeBrasseur, F., Riddell, B.E. and Gjernes, T. 1987. Ocean salmon studies in the Pacific Subarctic boundary area. 16 p. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, Vancouver, B.C. Canada, October 1987. Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada.

LeBrasseur, F. J., Hargreaves, N.B. and Gjernes, T. 1988. Canadian mid-ocean salmon studies. W.E. Ricker, 1 June–12 July, 1988. 19 p. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, Tokyo, Japan, October, 1988. Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada.

Levy, D.A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (*Oncorhynchus nerka*), pp. 44–52, *in* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, *edited by* H.D. Smith, L. Margolis, and C.C. Wood, *Can. Spec. Publ. Fish. Aquat. Sci.* **96**.

Mackas, D., DFO, Institute of Ocean Sciences, pers. comm.

Mackas, D.L., Thomson, R.E. and Galbraith, M. 2001. Changes in the zooplankton community of the British Columbia continental margin, and covariation with oceanographic conditions, 1985-1998. *Can. J. Fish. Aquat. Sci.* **58**: 685–702.

Mackas, D.L., Peterson, W.T., Ohman, M.D. and Lavaniegos, B.E. 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. *Geophys. Res. Lett.* **33**: L22S07, doi:10.1029/2006GL027930.

Mackas, D.L., Batten, S. and Trudel, M. 2007. Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Prog. Oceanogr.* **75**: 223–252.

Mackas, D.L., Galbraith, M. and Faust, D. 2009. Zooplankton community returns to 'cool-ocean' pattern off Vancouver Island, pp. 62–67, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* W.R. Crawford and J.R. Irvine, DFO Can. Sci. Advis. Sec. Res. Doc. 2009/022. vi + 121 p.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. 1997: A Pacific decadal climate oscillation with impacts on salmon. *Bull. Am. Met. Soc.* **78**: 1069–1079.

Manzer, J.I. and Neave, F. 1958. Data record of Canadian exploratory fishing for salmon in the Northeast Pacific in 1957. INPFC Doc. 192.

Manzer, J.I. and Neave, F. 1959. Data record of Canadian exploratory fishing for salmon in the Northeast Pacific in 1958. INPFC Doc. 244.

Margolis, L. 1963. Parasites as indicators of the geographical origin of sockeye salmon, *Oncorhynchus nerka* (Walbaum) occurring in the North Pacific Ocean and adjacent seas. *Intl. N. Pac. Fish. Comm. Bull.* **11**: 101–156.

Martin, J.H. and Fitzwater, S.E. 1988. Iron deficiency limits primary production in the northeast Pacific subarctic. *Nature* **331**: 341–343.

Mason, J.C., Kennedy, O.D. and Mullin, T.H. 1981a. Canadian Pacific coast ichthyoplankton survey. 1980. Hydrography. Part one. Horizontal contours of temperature, salinity, and sigma-t, at selected depths, by monthly cruise. Can. Data Rep. Fish. Aquat. Sci. 279.

Mason, J.C., Kennedy, O.D. and Mullin, T.H. 1981b. Canadian Pacific coast ichthyoplankton survey, 1980. Hydrography. Part two, Vertical contours of temperature, salinity, and sigma-t on transect lines, by monthly cruise. Can. Data Rep. Fish. Aquat. Sci. 280.

Mason, J.C., Kennedy, O.D. and Mullin, T.H. 1981c. Canadian Pacific coast ichthyoplankton survey. 1980. Hydrography. Part three. Vertical profiles of temperature, salinity, and sigma-t by station. Can. Data Rep. Fish. Aquat. Sci. 281.

Mason, J.C., Kennedy, O.D. and Phillips, A.C. 1981a. Canadian Pacific coast ichthyoplankton survey. 1980. Ichthyoplankton. Cruise one (January 15–22). Can. Data Rep. Fish. Aquat. Sci. 275.

Mason, J.C., Kennedy, O.D. and Phillips, A.C. 1981b. Canadian Pacific coast ichthyoplankton survey. 1980. Ichthyoplankton. Cruise two (February 13–20). Can. Data Rep. Fish. Aquat. Sci. 276.

Mason, J.C., Kennedy, O.D. and Phillips, A.C. 1981c. Canadian Pacific coast ichthyoplankton survey. 1980. Ichthyoplankton. Cruise three (March 12–20). Can. Data Rep. Fish. Aquat. Sci. 277.

Mason, J.C., Kennedy, O.D. and Phillips, A.C. 1981d. Canadian Pacific coast ichthyoplankton survey. 1980. Ichthyoplankton. Cruise four (April 15–23). Can. Data Rep. Fish. Aquat. Sci. 278.

Masson, D. 2002. Deep water renewal in the Strait of Georgia. *Estuar. Coast. Shelf Sci.* **54**: 115–126.

Masson, D. 2008. Cooling in the Strait of Georgia, p. 93, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* J.E. Irvine and W.R. Crawford, DFO Can. Sci. Advis. Sec. Res. Doc. 2008/013.

Masson, D. 2009. Cooling in sub-surface Strait of Georgia waters, p. 107, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* J.E. Irvine and W.R. Crawford, DFO Can. Sci. Advis. Sec. Res. Doc. 2009/022.

Mathieson, O.A., Fair, L., Beamish, R.J. and Bugaev, V.F. 2007. Density-dependent growth of sockeye salmon in the North Pacific Ocean. *N. Pac. Anadr. Fish. Comm. Bull.* **4**: 299–310.

McDonald, J.S. (ed.) 2000. Mortality during the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*): a study of the effect of ocean and river environmental conditions in 1997. Can. Tech. Rep. Fish. Aquat. Sci. 2315, 120 p.

McDonald, J. and Hume, J.M. 1984. Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement program; testing some major assumptions. *Can. J. Fish. Aquat. Sci.* **41**: 70–92.

McFarlane, G.A. and Beamish, R.J. 2001. The re-occurrence of sardines off British Columbia characterises the dynamic nature of regimes. *Prog. Oceanogr.* **49**: 151–165.

McFarlane, G.A., King, J.R. and Beamish, R.J. 2000. Have there been recent changes in climate? Ask the fish. *Prog. Oceanogr.* **47**: 147–169.

McKinnell, S.M. 1995. Age-specific effects of sockeye abundance on the adult body size of major British Columbia sockeye stocks. *Can. J. Fish. Aquat. Sci.* **52**: 1050–1063.

McKinnell, S.M. 2008. Fraser River sockeye salmon and climate; a re-analysis that avoids an undesirable property of Ricker's curve. *Prog. Oceanogr.* **77**: 146–154.

McKinnell, S.M. 2009. Chilko Lake sockeye returns: A second look for 2009, pp. 120–121, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* W.R. Crawford and J.E. Irvine, DFO Can. Sci. Advis. Sec. Res. Doc. 2009/022.

McKinnell, S.M. and Crawford, W.R. 2007. The 18.61 lunar nodal cycle and surface temperature variation in the northeast Pacific Ocean. *J. Geophys. Res.* **112**: C02002, doi:10.1029/2006JC003671.

McKinnell, S.M. and Reichardt, M.R. 2012. Early marine growth of juvenile Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to juvenile pink (*Oncorhynchus gorbuscha*) and sockeye salmon abundance. *Can. J. Fish. Aquat. Sci.* **69**: doi:10.1139/F2012-078.

McKinnell, S.M., Freeland, H.J. and Groulx, S. 1999. Assessing the northern diversion of sockeye salmon returning to the Fraser River. *Fish. Oceanogr.* **8**: 104–114.

McKinnell, S.M., Wood, C.C., Rutherford, D.T., Hyatt, K.D. and Welch, D.W. 2001. The demise of Owikeno Lake sockeye salmon. *N. Am. J. Fish. Mgmt.* **21**: 774–791.

McKinnell, S.M., Emmett, R. and Orsi, J. 2009. 2009 salmon forecasting forum. PICES Press 17(2): 32–33.

McKinnell, S.M., Batten, S., Bograd, S., Boldt, J.L., Bond, N., Chiba, S., Dagg, M.J., Foreman, M.G.G., Hunt Jr., G.L., Irvine, J.R., Katugin, O., Mackas, D.L., Lobanov, V., Mundy, P., Radchenko, V., Ro, Y.J., Sugisaki, H., Whitney, F.A., Yatsu, A. and Yoo, S. 2010 Status and trends of the North Pacific Ocean, 2003–2008, pp. 1–55, *in* Marine Ecosystems of the North Pacific Ocean, 2003–2008, edited by S.M. McKinnell and M. Dagg, PICES Special Publication 4, 393 p.

Miller, K.M., Schulzea, A.D., Ginther, N., Lia, S., Patterson, D.A., Farrell, A.P. and Hinch, S.G. 2009. Salmon spawning migration: Metabolic shifts and environmental triggers. *Comp. Bioch. Phys. Part D: Genomics and Proteomics* **4**: 75–89.

Mueter, F.J., Peterman, R.M. and Pyper, B.J. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* **59**: 456–463.

Mueter, F.J., Pyper, B.J. and Peterman, R.M. 2005. Relationships between coastal ocean conditions and survival rates of Northeast Pacific salmon at multiple lags. *Trans. Am. Fish. Soc.* **134**: 105–119.

Mundy, P.R., Allen, D.M., Boldt, J.L., Bond, N.A., Dressel, S., Farley Jr., E.V., Hanselman, D.H., Heifetz, J., Hopcroft, R.R., Janout, M.A., Ladd, C., Lam, R.C., Livingston, P.A., Lunsford, C.R., Mathis, J.T., Mueter, F.J., Rooper, C.N., Sarkar, N., Shotwell, S.A.K., Sturdevant, M.V., Thomas, A.C., Weingartner, T.J. and Woodby, D. 2010. Status and trends of the Alaska Current Region, 2003–2008, pp. 142–195, *in* Marine Ecosystems of the North Pacific Ocean, 2003–2008, *edited by* S.M. McKinnell and M.J. Dagg, PICES Special Publication 4, 393 p.

Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S. and Dahlberg, M.L. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. NPAFC Doc. 192.

Mysak, L.A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **43**: 464–497.

Nagasawa, T. and Azumaya, T. 2009. Distribution and CPUE trends in Pacific salmon, especially sockeye salmon in the Bering Sea and adjacent waters from 1972 to the mid 2000s. *N. Pac. Anadr. Fish. Comm. Bull.* **5**: 1–13.

Neave, F. and Manzer, J.I. 1957. Data record of Canadian exploratory fishing for salmon in the Northeast Pacific in 1956. INPFC Doc. 114.

Orsi, J.A., Harding, J.A., Pool, S.S., Brodeur, R.D., Haldorson, L.J., Murphy, J.M., Moss, J.H., Farley, Jr., E.V., Sweeting, R.M., Morris, J.F.T., Trudel, M., Beamish, R.J., Emmett, R.L. and Fergusson, E.A. 2007. Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California Current and the Alaska Current, pp. 105–156, *in* The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons, *edited by* C.B. Grimes, R.D.Brodeur, L.J. Haldorson and S.M. McKinnell, Am. Fish. Soc. Symp. Ser. 57.

Parrish, R.H., Schwing, F.B. and Mendelssohn, R. 2000. Mid-latitude wind stress: the energy source for climatic shifts in the North Pacific Ocean. *Fish. Oceanogr.* **9**: 224–238.

Parsons, T.R., Stephens, K. and LeBrasseur, R.J. 1969a. Production studies in the Strait of Georgia. Part I. Primary production under the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 27–38.

Parsons, T.R., LeBrasseur, R.J., Fulton, J.D. and Kennedy, O.D. 1969b. Production studies in the Strait of Georgia. Part II. Secondary production under the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 39–50.

Pearcy, W.G., Nishiyama, T., Fujii, T. and Masuda, K. 1984. Diet variations in the feeding habits of Pacific salmon caught in gill nets during a 24-hour period in the Gulf of Alaska. *Fish. Bull.* **82**: 391–399.

Pearcy, W.G., Brodeur, R.D., Shenker, J.M., Smoker, W.W. and Endo Y. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches and oceanographic condition in the Gulf of Alaska, 1980–1985. *Bull. Ocean Res. Inst.* **26**: 29–78.

Peña, A. 2008. Phytoplankton in the Strait of Georgia, pp. 94–95, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* J.E. Irvine and W.R. Crawford, DFO Can. Sci. Advis. Sec. Res. Doc. 2008/013.

Peña, A., Bograd, S.J. and Bychkov, A. 2007. Time series of the Northeast Pacific. *Prog. Oceanogr.* **75**: 115–342.

Peterman, R.M. 1984. Effects of Gulf of Alaska sockeye salmon (*Oncorhynchus nerka*) abundance on survival, body size, growth rate, mean age at maturity of British Columbia and Bristol Bay, Alaska sockeye populations. Can. Tech. Rep. Fish. Aquat. Sci. 1302, 87 p.

Peterman, R.M., Marinone, S.G., Jardine, I.D., Crittenden, R.N., LeBlond, P.H. and Walters, C.J. 1994. Simulation of juvenile sockeye salmon (*Oncoryhnchus nerka*) migrations in the Strait of Georgia, British Columbia. *Fish. Oceanogr.* **3**: 221–235.

Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D. and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbia and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **55**: 2503–2517.

Peterman R.M., Marmorek, D., Beckman, B., Bradford, M., Mantua, N., Riddell, B.E., Scheuerell, M., Staley, M., Wieckowski, K., Winton, J.R. and Wood, C.C. 2010. Synthesis of evidence from a workshop on the decline of Fraser River sockeye. June 15–17, 2010. A Report to the Pacific Salmon Commission, Vancouver, B.C.

Phillips, A.C. and Barraclough, W.E. 1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Fish. Mar. Serv. Tech. Rep. 830, 19 p.

Polovina, J.J., Howell, E., Kobayashi, D.R. and Seki, M.P. 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Prog. Oceanogr.* **49**: 469–483.

Polovina, J.J., Howell, E.A. and Abecassis, M. 2008. Ocean's least productive waters are expanding. *Geophys. Res. Lett.* **35**: L03618, doi:10.1029/2007GL031745.

PSC (Pacific Salmon Commission). 2009. Report of the Fraser River Panel to the Pacific Salmon Commission on the 2005 Fraser River sockeye and pink salmon fishing season. Pacific Salmon Commission, Vancouver, 75 p.

PSC (Pacific Salmon Commission). 2010. Pacific Salmon Commission Production database, 1952–2009. Vancouver, BC.

Quinn, T. 2005. The Behaviour and Ecology of Pacific Salmon and Trout. University of Washington Press, WA.

Quinn, T.P. and terHart, B.A. 1987. Movements of adult sockeye salmon (*Oncorhynchus nerka*) in British Columbia Coastal Waters in relation to temperature and salinity stratification: ultrasonic telemetry results, pp. 61–77, *in* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, *edited by* H.D. Smith, L. Margolis and C.C. Wood, *Can. Spec. Publ. Fish. Aquat. Sci.* **95**.

Ralston, S. 1990. Size selection of snappers (Lutjanidae) by hook and line gear. Can. J. Fish. Aquat. Sci. 47: 696–700.

Rand, P. 2002. Modeling feeding and growth in Gulf of Alaska sockeye salmon: implications for high-seas distribution and migration. *Mar. Ecol. Prog. Ser.* **234**: 265–280.

Rensel, J.E., Nicola, H. and Tynan, T.M. 2010. Fraser river sockeye salmon marine survival decline and harmful blooms of *Heterosigma akashiwo*. *Harmful Algae* **10**: 98–115.

Ricker, W.E. 1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. *J. Fish. Res. Bd. Can.* **19**: 531–560.

Ricker, W.E. 1966. Sockeye salmon in British Columbia. *Intl. N. Pac. Fish. Comm. Bull.* **18**: 59–70.

Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *J. Fish. Res. Bd. Can.* **33**: 1483–1524.

Robinson, D.G. 1969a. Data record: number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia April 24–25, l968. Manuscr. Rep. (FRBC) 1067, 63 p.

Robinson, D.G. 1969b. Data record: number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–6, 1967. Manuscr. Rep. (FRBC) 1012, 71 p.

Robinson, D.G., Barraclough, W.E. and Fulton, J.D. 1968a. Data record: number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia May 1–4, 1967. Manuscr. Rep. (FRBC) 964, 105 p.

Robinson, D.G., Barraclough, W.E. and Fulton, J.D. 1968b. Data record: number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 5-9, 1967. Manuscr. Rep. (FRBC) 972, 109 p.

Roos, J.F. 1991. The History of the International Pacific Salmon Fisheries Commission, 1937–1985. Pacific Salmon Commission, Vancouver, Canada.

Royal, L.A. and Tully, J.P. 1961. Relationship of variable oceanographic factors to migrations and survival of Fraser River salmon. *Calif. Coop. Fish. Invest. Rep.* **8**: 65–68.

Royce, W.F., Smith, L.S. and Hartt, A.C. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. *Fish. Bull.* **66**: 441–462.

Ruggerone, G.T. and Goetz, F.A. 2004. Survival of Puget Sound chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **61**: 1756–1770.

Ruggerone, G.T., Zimmerman, M., Myers, K.W., Nielsen, J.L. and Rogers, D.E. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*Oncorhynchus nerka*) in the North Pacific Ocean. *Fish. Oceanogr.* **12**: 209–219.

Ruggerone, G.T., Nielsen, J.L. and Bumgarner, J. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1966–2002. *Deep-Sea Res. II* **54**: 2776–2793.

Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*), pp. 395–445, *in* Pacific Salmon Life Histories, *edited by* C. Groot and L. Margolis, UBC Press: Vancouver, Canada, 564 p.

Sarkar, N., Royer, T.C. and Grolsch, C.E. 2005. Hydrographic and mixed layer depth variability on the shelf in the northern Gulf of Alaska, 1974–1998. *Cont. Shelf Res.* **25**: 2147–2162.

Schnute, J. and Sibert, J. 1983. The salmon terminal fishery: a practical, comprehensive model. *Can. J. Fish. Aquat. Sci.* **40**: 835–853.

Schuerell, M.D. and Schindler, D.E. 2003. Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology* **84**: 1713–1720.

Schwing, F.B., Mendelssohn, R., Bograd, S.J., Overland, J.E., Wang, M. and Ito, S.-I. 2010. Climate change, teleconnection patterns, and regional processes forcing marine populations in the Pacific. *J. Mar. Sys.* **79**: 245–257.

Smith, H.D., Margolis, L and Wood, C.C. (eds.) 1987. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Can. Spec. Publ. Fish. Aquat. Sci.* **96**.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds.)] 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, N.B., Mordy, C.W. and Overland, J.E. 2004. Meteorology and oceanography of the northern Gulf of Alaska. *Cont. Shelf Res.* **24**: 859–897.

Sweeting, R.M. and Beamish, R.J. 2009. A comparison of the diets of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia from 1997-2007. *N. Pac. Anadr. Fish. Comm. Bull.* **5**: 255–264.

Sweeting, R.M., Beamish, R.J., Neville, C.M., Gordon, E. and Lange, K. 2008. Strait of Georgia juvenile salmon: The same in 2007, only different, pp. 102–105, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems, *edited by* J.R. Irvine and W.R. Crawford, DFO Can. Sci. Advis. Sec. Res. Doc. 2008/13.

Teo, S.L.H., Botsford, L.W. and Hastings, A. 2009. Spatio-temporal covariability in coho salmon (*Oncorhynchus kisutch*) survival, from California to southeast Alaska. *Deep-Sea Res. II* **56**: 2570–2578.

Thomson, K.A., Ingraham, W.J. Healey, M.C., Leblond, P.H., Groot, C. and Healey, C.G. 1992. The influence of ocean currents on latitude of landfall and migration speed of sockeye salmon returning to the Fraser River. *Fish. Oceanogr.* **1**: 163–179.

Trudel, M. DFO, Pacific Biological Station, pers. comm.

Trudel, M., Thiess, M.E., Bucher, C., Farley Jr., E.V., MacFarlane, R.B., Casillas, E., Fisher, J., Morris, J.F.T. and Murphy, J.M. 2007. Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the West Coast of North America, pp. 205–232, *in* The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons, edited by C.B. Grimes, R.D. Brodeur, L.J. Haldorson, and S.M. McKinnell, Am. Fish. Soc. Symp. Ser. 57.

Trudel, M., Fisher, J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., Hinton, S., Fergusson, E.A. and Welch, D.W. 2009. Distribution and migration of juvenile chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. *Trans. Am. Fish. Soc.* **138**: 1369–1391.

Trudel, M., Tucker, S. and Candy, J. 2010. Ocean distribution of two depressed sockeye salmon stocks, pp. 97–98, *in* State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2009, *edited by* W.R. Crawford, and J.E. Irvine, DFO Can. Sci. Advis. Sec. Res. Doc. 2010/053

Tucker, S., Trudel, M., Welch, D.W., Candy, J.R. Morris, J.F.T., Thiess, M.E., Wallace, C. Teel, D.J., Crawford, W., Farley Jr., E.V. and Beacham, T.D. 2009. Seasonal stock-specific migrations of juvenile sockeye salmon along the west coast of North America: implications for growth. Trans. *Am. Fish. Soc.* **138**: 1458–1480, doi: 10.1577/T08-211.1.

Tully, J.P. 1937. A warmer summer. *Biol. Bd. Can. Prog. Rep. Pac. Biol. Sta.* **31**: 16–18.

Waldichuk, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. *J. Fish. Res. Bd. Can.* **14**: 321–486.

Walker, R.V., Myers, K.W., Davis, N.D., Carlson, H.R. and Friedland, K.D. 1999. U.S. releases and recoveries of salmonid data storage tags and disk tags in the North Pacific Ocean and Bering Sea. NPAFC Doc. 412, Rev. 1, FR-UW-9910. Fisheries Research Institute, University of Washington.

Walter, E.E. and Scandol, J.P. and Healey, M.C. 1997. A reappraisal of the ocean migration patterns of Fraser River sockeye salmon (*Oncorhynchus nerka*) by individual-based modelling. *Can. J. Fish. Aquat. Sci.* **54**: 847–858.

Wang, M., Overland, J.E. and Bond, N.A. 2010. Climate projections for selected large marine ecosystems. *J. Mar. Sys.* **79**: 258–266.

Ware, D.W. and Thomson, R.E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Nature* **308**: 1280–1284.

Weingartner, T.J., Coyle, K., Finney, B., Hopcroft, R., Whitledge, T., Brodeur, R., Dagg, M., Farley, E, Haidvogel, D., Haldorson, L., Hermann, A., Hinckley, S., Napp, J., Stabeno, P., Kline, T., Lee, C., Lessard, E., Royer, T. and Strom, S. 2002. The Northeast Pacific GLOBEC program: coastal Gulf of Alaska. *Oceanogr.* **15**: 48–63.

Weingartner, T., Eisner, L., Eckert, G.L. and Danielson, S. 2009. Southeast Alaska: oceanographic habitats and linkages. *J. Biogr.* **36**: 387–400.

Weitkamp, L. and Neely, K. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. *Can. J. Fish. Aquat. Sci.* **59**: 1100–1115, doi:10.1139/f02-075.

Welch, D.W. 1997. Growth and energetics of salmon at sea, *in* Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop, *edited by* R.L. Emmett and M.H. Schiewe, U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-219.

Welch, D.W., Chigirinsky, A.I. and Ishida, Y. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. *Can. J. Fish. Aquat. Sci.* **52**: 489-503.

Welch, D.W., Ishida, Y. and Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* **55**: 937–948.

Welch, D.W., Morris, J.F.T., Demers, E. and Carlson, H.R. 2002a. *F.V. Anita J.* Gulf of Alaska salmon survey, March 25–April 29, 1995. Can. Data Rep. Fish. Aquat. Sci. 1097, 19 p.

Welch, D.W., Morris, J.F.T., Demers, E. and Wing, B.L. 2002b. *F.V. Columbia* Gulf of Alaska salmon survey, October 7–November 10, 1995. Can. Data Rep. Fish. Aquat. Sci. 1099, 112 p.

Welch, D.W., Morris, J.F.T., Demers, E. and Evenson, J.P. 2002c. *CCGS W.E. Ricker* Gulf of Alaska salmon survey, 1998. Can. Data Rep. Fish. Aquat. Sci. 1103, 188 p.

Welch, D.W., Melnychuk, M.C., Rechisky, E.R., Porter, A.D., Jacobs, M.C., Ladouceur, A., McKinley, R.S. and Jackson, G.D. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. *Can. J. Fish. Aquat. Sci.* **66**: 736–750.

Whitney, F.A. and Freeland, H.J. 1999. Variability in upper ocean water properties in the NE Pacific Ocean. *Deep-Sea Res. II* **46**: 2351–2370.

Williams, J.G. NOAA/NWFSC, Seattle, pers. comm.

Wong, C.S., Waser, N.A.D., Nojiri, Y., Whitney, F.A., Page, J.S. and Zeng, J. 2002. Seasonal cycles of nutrients and dissolved inorganic carbon at high and mid latitudes in the North Pacific Ocean during the SKAUGRAN cruises: determination of new production and nutrient uptake rates. *Deep-Sea Res. II* **49**: 5317–5338.

Wood, C.C., Hargreaves, N.B., Rutherford, D.T and Emmet, B.T. 1993. Downstream and early marine migratory behaviour of sockeye (*Oncorhynchus nerka*) smolts entering Barkley Sound, Vancouver Island. *Can. J. Fish. Aquat. Sci.* **50**: 1329–1337.

Appendix 1

North Pacific Marine Science Organization (PICES)

PICES is an international, intergovernmental organization that was created by Convention in 1992. The purpose of the Organization is:

- to promote and coordinate marine scientific research in order to advance scientific knowledge of the area concerned and of its living resources, including but not necessarily limited to research with respect to the ocean environment and its interactions with land and atmosphere, its role in and response to global weather and climate change, its flora, fauna and ecosystems, its uses and resources, and impacts upon it from human activities; and
- to promote the collection and exchange of information and data related to marine scientific research in the area concerned.

Scientific leadership in the Organization is the responsibility of its Science Board. Its authority is described in the Rules of Procedure of the Organization as follows:

i. The Science Board shall consist of the Chairmen of the Scientific Committees, Technical Committees, and Advisory Panels of Scientific Programs, together with a Chairman elected by the Science Board from among the nominees for a term of three years. The Chairman shall not concurrently be a Chairman of another group nor be eligible for re-election for successive terms. When the Science Board chairmanship becomes vacant for any reason, the Science Board shall elect a new Chairman at its earliest convenience;
ii. The Vice-Chairman of the Science Board shall be elected from amongst the members of the Science Board for a term of one year and shall be eligible for re-election for a successive term. The Vice-Chairman will normally reside on the opposite side of the Pacific to the Science Board Chairman. The Vice-Chairman shall act as Chairman whenever the Chairman is unable to act;
iii. Should a Contracting Party have no representation on the Science Board via committee or program chairmanship, it may appoint a suitably qualified member;
iv. The Science Board shall:
    a. have general oversight over
        i. the scientific interests of the Council and its scientific work;
        ii. the programs of research approved by the Council;
        iii. the arrangements for carrying out the Council's scientific work and the programs of research recommended or coordinated by it;
        iv. the organization of special scientific meetings.
    b. be responsible for advising the Council on all matters mentioned in sub-paragraph (a);
    c. provide guidance, as it may deem necessary, to groups under their jurisdiction, as to the performance of their functions;
    d. review and make recommendations to the Council concerning the provision of scientific advice to Contracting Parties or other international organizations requesting such advice;
    e. consider, at each Annual Meeting of the Science Board, reports from all groups under their jurisdiction and report thereon to the Council with special reference to any expenditures involved;
    f. advise the Council of its publication requirements.
v. Scientific Programs shall have a single vote in decisions of the Science Board.

In 1993, the Organization established a procedure to respond to requests for scientific advice made by Member Nations and other organizations. Requests are received by the Executive Secretary and directed to the PICES Chairman. After reviewing the request, the Chairman may bring the request to the Organization's Science

Board for consideration. After discussing the request, Science Board may agree to respond to the request. Their response is, generally, to form an *ad hoc* group to draft the Organization's response.

On April 23, 2010, the PICES Science Board discussed the request from the Cohen Commission at its meeting in Sendai, Japan and agreed to take on the project. Dr. Stewart (Skip) McKinnell, Deputy Executive Secretary of PICES, was asked by Science Board to lead the development of the response and to take responsibility for forming the *ad hoc* group and to develop, jointly with the Cohen Commission, the Table of Contents for the PICES response. Internal review of the report was conducted by the PICES Advisory Panel on Status, Outlooks, Forecasts and Engagement prior to approval by the Science Board and the Governing Council of PICES.

Further information is available at http://www.pices.int/about

Appendix 2

Terminology

Term	**Usage**
age-class	The *x.y* convention defines x = number of winters in freshwater after hatching, and y = number of winters in salt water. Each unique combination is an ecotype.
brood year	Year when salmon eggs are laid.
brood year return	See total returns.
ecotype	Distinguishes individuals that spend varying numbers of years in freshwater and salt water.
effective female	A reduction of the estimated numbers of female spawners due to pre-spawning mortality or incomplete egg deposition.
emergence	Developmental stage when juvenile salmon emerge from their gravel nest.
immature	Older than a postsmolt but will not mature in the current calendar year.
jack	A male anadromous sockeye salmon that matures after one year at sea.
jill	A female anadromous sockeye salmon that matures after one year at sea.
landfall	Latitude where sockeye salmon returning to the Fraser River from the central Gulf of Alaska reach the coast.
life history type	See ecotype.
life table	Table of stage-specific survivals of a population.
maturing	A salmon that will migrate to its natal river during a calendar year.
northern diversion rate	Proportion of the total return of Fraser River salmon that enter the Strait of Georgia via Johnstone Strait.
postsmolt	A juvenile salmon that has undergone the physiological changes necessary to live at sea, emigrated from freshwater, in its first calendar year at sea.
productivity	Numbers of returns per effective female spawner, by brood year.
returns	Catch plus escapement, by ecotype. See also total return.
smolt	A juvenile salmon that has undergone the physiological changes necessary to migrate to sea but has yet to reach the sea.
spawner	Males and females that reach the spawning grounds.
total return	A quantity calculated as the sum of the estimated numbers of adult salmon of a population taken in the catch plus the estimate of the number of spawners in that population, computed across all life-history types; sometimes called brood year returns.
total survival	The sum of the numbers of fish from one cohort (brood year) taken in fisheries and the numbers in the escapement, regardless of year of maturation, divided by the number of effective female spawners that gave rise to the cohort.
underyearling	A fish that enters the ocean in its first spring/summer after hatching.

Appendix 3

Average age composition based on brood year returns to 2004

	Ecotype								
Stock	0.1	0.2	0.3	1.1	1.2	1.3	2.1	2.2	2.3
adams	0.0000	0.0003	0.0026	0.0274	0.9210	0.0474	0.0000	0.0015	0.0000
birken	0.0000	0.0000	0.0000	0.0672	0.6381	0.2405	0.0091	0.0407	0.0044
bowron	0.0000	0.0001	0.0001	0.0011	0.8572	0.1405	0.0000	0.0010	0.0000
chilko	0.0000	0.0000	0.0000	0.0102	0.8792	0.0518	0.0020	0.0553	0.0014
cultus	0.0000	0.0007	0.0000	0.0257	0.6404	0.0244	0.0002	0.0037	0.0000
gates	0.0000	0.0000	0.0000	0.1044	0.8220	0.0633	0.0006	0.0098	0.0000
harrison	0.0016	0.4413	0.5541	0.0011	0.0017	0.0002	0.0000	0.0000	0.0000
horsefly	0.0000	0.0000	0.0004	0.0037	0.9156	0.0787	0.0000	0.0015	0.0000
l_shuswap	0.0000	0.0104	0.0012	0.0247	0.7681	0.0562	0.0003	0.1033	0.0000
nadina	0.0000	0.0000	0.0000	0.0018	0.8766	0.1205	0.0000	0.0010	0.0000
portage	0.0000	0.0000	0.0000	0.0413	0.9217	0.0263	0.0002	0.0105	0.0001
raft	0.0000	0.0005	0.0007	0.0024	0.7456	0.2381	0.0000	0.0098	0.0028
seymour	0.0000	0.0000	0.0000	0.0050	0.9241	0.0466	0.0005	0.0239	0.0000
stellako	0.0000	0.0000	0.0001	0.0008	0.8501	0.1489	0.0000	0.0001	0.0000
stuart_e	0.0000	0.0000	0.0000	0.0019	0.9130	0.0821	0.0000	0.0029	0.0001
stuart_l	0.0000	0.0000	0.0000	0.0037	0.8978	0.0982	0.0000	0.0002	0.0000
weaver	0.0000	0.0012	0.0007	0.0081	0.8631	0.1232	0.0001	0.0036	0.0000

Appendix 4

Comments on Pacific Salmon Commission workshop report

The Pacific Salmon Commission (PSC) held a workshop from June 15–17, 2010 to evaluate the cause of declining abundance of Fraser River sockeye salmon. An international panel of 11 scientists considered various hypotheses and brought data to bear on them. The results were consolidated in a report to the PSC that was later made available for information to PICES (Peterman *et al.*, 2010). Of the 11 hypotheses considered by the panel, #3 - *Oceanographic conditions (physical and biological) inside and/or outside the Strait of Georgia* is most closely aligned with the subject of this report. The key problem for this panel was an observation that 16 of 18 major Fraser River sockeye salmon populations have shown a decrease in productivity over the period of record (since ~1950). They reported that most, but not all, populations have a declining trend in total (generation to generation) survival.

The Cohen Commission requested comments.

►Main Conclusion: The Panel's judgments, summarized in their Table E-1, is that physical and biological conditions inside the Strait of Georgia during the juvenile life stage are very likely the major cause of poor survival of the cohort that returned in 2009.

- First, we note that *very likely* is codified language to describe the likelihood of an outcome. This codified language was used extensively in developing the widely read Intergovernmental Panel on Climate Change's (IPCC) 4th assessment report. The definition of *very likely* in that report is >90% chance of occurrence. Without a close reading of the PSC report, those more familiar with the more widely distributed IPCC report may inadvertently assume greater likelihoods than were intended by the authors.
- We noted that in their Table E-2(3), under "Plausibility and Realism of Proposed Mechanism", concerning the overall decline, "*a lack of detailed knowledge about spatial/temporal patterns of marine migration of juvenile sockeye, phytoplankton, and zooplankton abundance, and salmon mortality make it hard to distinguish between early mortality in Strait of Georgia and later mortality further North.*" This uncertainty is not reflected in their main conclusion, so perhaps its strength arose from hypotheses other than those related to the ocean. Examination of the physical, chemical, and biological data in the Strait of Georgia and, more importantly, extreme climatic events in Queen Charlotte Strait and Sound diminishes the likelihood of such strong attributions of cause to the Strait of Georgia.
- The smallest, and presumably most vulnerable juvenile sockeye salmon that the Fraser River produces (Harrison River) spent the summer of 2007 in the Strait of Georgia and returned in record numbers in 2009 and 2010 (combined). If the Strait of Georgia was the sight of incremental mortality, it must have changed from an extremely unfavourable environment to an extremely favourable environment between June and July, but only after allowing "normal" survival of large, acoustically-tagged smolts from Cultus Lake before the change.

►There is a positive correlation between the abundance of juvenile sockeye (catch per unit effort) in the Strait of Georgia and log(total Fraser SK production) two years later over 1998–2007 ($R^2 = 0.35$ with all of the data). Table E-2(3)

- Juvenile sockeye salmon have been caught incidentally (except 2003) in Fisheries and Oceans Canada (DFO) chinook and coho trawl surveys of the Strait of Georgia since 1997. Incidental catches of sockeye salmon have not been reported because they were considered to be too difficult to interpret

(Sweeting *et al.*, 2008). As of September 2010, DFO reported that the detailed sockeye salmon data were irretrievable so an analysis was not possible for this report[15].

- The Strait of Georgia sockeye salmon CPUE data have been used previously to forecast returns of Fraser River sockeye salmon beginning with the 2007 return year. These were reported annually in the DFO State of the Ocean report. Forecast skill level has been low. In 2007 and 2008, above average returns were predicted but below average returns occurred. In 2009, below average returns were anticipated and this indeed transpired. High sockeye salmon CPUE in the Strait of Georgia in September was considered previously as a harbinger of low survival (Sweeting *et al.*, 2008), yet the very high CPUE in September 2007 was matched by very high returns to the Harrison River in 2010 (most spend three years at sea).
- The overall coefficient of determination (percentage of variability explained) of total returns of Fraser River sockeye salmon to all stocks, based on the Strait of Georgia juvenile CPUE is reported as 35% (PSC, 2010). This would explain the relatively poor performance of previous forecasts and suggests that the source of the other 65% of the variability in total returns may lie beyond the Strait of Georgia. At issue is how much of the abundance of juvenile Fraser River sockeye salmon remains in the Strait of Georgia into July to be taken by the survey and whether it varies from year to year. A simple plot of annual sockeye salmon CPUE *versus* annual summer survey start date from 1997 may clarify this point. The hypothesis is that later starting dates will result in lower CPUE of age-1.x and age-2.x ecotypes.

►<u>This [Heydon Lake] favourable survival suggests that the unfavourable conditions affecting seaward migration of Fraser sockeye smolts in 2007 existed south of Johnstone Strait.</u>

- Heydon Lake is located north of Sayward, B.C. on the mainland side of Johnstone Strait. If Heydon Lake sockeye salmon entered the ocean in the same month as other southern populations, and travelled at similar speeds, their northward migration through Queen Charlotte Strait/Sound toward the Alaska would have preceded the period of extreme river discharge. With less distance to Alaska, they may be less reliant on productivity timing in Queen Charlotte Sound.

►<u>Eight stocks with additional data on juvenile abundance (fry or smolts), have shown no reductions in freshwater productivity.</u>

- Declining productivity in Chilko Lake, up to the 1999 brood year (2004 return year), was due largely to reduced average freshwater survival. Brood years of the mid-2000s had a period (unexplained, as yet) of remarkably good freshwater survival in Chilko Lake with record smolt abundances emigrating from the lake. The Chilko Lake freshwater time series cannot be characterized as "no reductions in freshwater productivity." For the other populations, it can only be assumed because no smolt counts are undertaken.

►<u>The shared downward trends in total and post-juvenile productivity indicate that the mortality causing declines occurred in habitats shared by the stocks. Table E-2(3)</u>

- While the shared trend suggests a shared habitat for those stocks exhibiting the trend, the appearance of a common trend is insufficient grounds for attributing the cause to the ocean. The scale of the forces that are responsible for the mortality must be taken into account. If it is large, the sockeye salmon inhabiting different locations can be affected by a common cause. The Chilko Lake stock shares the common trend but a large portion of its trend is due to factors operating in freshwater.

►<u>The total productivity (R/EFS) for most Fraser SK is much more highly correlated with post-juvenile (R/juvenile) than with juvenile productivity (juveniles/female).</u>

- In the one system where total freshwater productivity can be distinguished from postsmolt productivity (Chilko), this is a true statement if one considers only the maximum likelihood estimate of the parameter. The correlation with productivity is higher for marine survival but whether or no a strong inference can be made from this measure is less clear.
- A bootstrap program was written to measure the interval estimates of these correlations based on 48 years of data from Chilko Lake. To reduce the complications that arise from pooling smolts of different

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[15] D. Levy, Cohen Commission, personal communication.

age, the correlations were computed between log(returns/age-1 smolt) and freshwater survival of age-1 smolts (numbers of age-1 smolts/effective female), and the same *versus* marine survival of age-1 smolts (age-1.x returns/age-1.x smolts). The marine survival was square root transformed to de-emphasize the influence of very few years of very high survival. Based on 1,000 bootstrap iterations, the average correlation between total survival and freshwater survival was 0.62, and the average correlation between total survival and marine survival was 0.79. However, the 95% confidence intervals on these correlations, computed by bootstrapping, were not significantly different.

►There is a very strong correlation ($r^2 = 0.87$) between algal biomass (Mar. 30–Apr. 22 avg. chlorophyll *a*) in QCS and Chilko SK marine survival (1998–2007). However, the mechanisms are not understood.

- The observation of a correlation between chlorophyll concentration and sockeye salmon survival is consistent with Ware and Thomson's (2005) study that followed correlations of chlorophyll concentration through zooplankton biomass to resident (non-migratory) fish production. While the exact details of the mechanism may not be fully understood, a trophic/metabolic mechanism for reduced survival is at least plausible, and one that should not be rejected out of hand given the environmental extremes that occurred in Queen Charlotte Strait/Sound. What is yet to be resolved are the relative contributions of *in situ* production (interannual variation in primary production), phenology (interannual variation in timing of biological production), and advection (interannual variation in the locations of major currents/water masses) in creating the correlation. Each of these has the potential to make Queen Charlotte Sound unsuitable for sockeye salmon in spring. Cassin's auklets breed on Triangle Island, feed at a similar trophic level on similar prey as sockeye salmon, and their reproductive success is affected more by spring timing (Hipfner, 2008b).

►Two notable exceptions to the trends of decreasing productivity [...] are Harrison and Late Shuswap (the famed Adams River sockeye run).

- Harrison River sockeye salmon productivity has, indeed, increased in recent years, but the survival of the 2005 brood year (2006 ocean entry year) from the Harrison River was the lowest on record. Adams River productivity, described as trendless, appears to have the same general productivity pattern as many of the other Fraser River sockeye salmon populations. For the Adams River, the lowest returns per spawner occurred in the 2003 and 2004 brood years. The 2005 brood year was very similar to other values observed since 1992. Based on preliminary data for 2010, the returns to date are typical for a dominant cycle year at average productivity observed before the 1990 brood year. Some of the difference of opinion on the Adams River population trend may have arisen from pooling the data with other populations as an aggregate Late Shuswap stock.

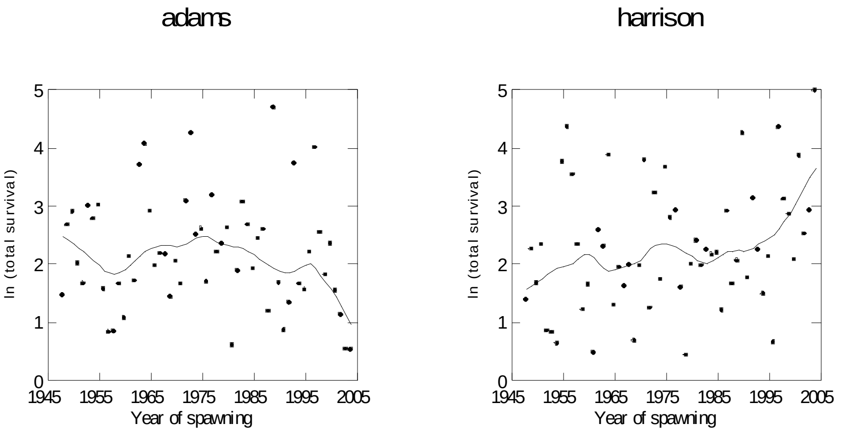

Fig. 103 Productivity of Adams River sockeye salmon (left) and Harrison River sockeye salmon (right).

Appendix 5

State of the Science

If you ask a physical oceanographer to describe the current temperature of the Gulf of Alaska, s/he may offer you the perspective from one of several temperature-recording earth-orbiting satellites, or a view of temperatures in the ocean depths from autonomous drifting ocean profilers that relay their daily measurements via satellite, or download the results of the latest cruise, or even take a historical view from century-old lighthouse time series, or a blend of all of the above. If you ask a salmon biologist about the current abundance of sockeye salmon in the Gulf of Alaska, you may not be able to get a reply.

In his book on the ecology of Pacific salmon in the ocean, William G. Pearcy (1992) expressed his view of the state of science and the major unknowns as they were in 1991:

- *We need to know more about the critical time and space scales in the ocean life of salmonids in order to hypothesize mechanisms that determine variations in growth, survival, and migratory behavior;*
- *How do the specific migratory routes of specific stocks of salmonids vary among years?*
- *Are the fish from a given stock found closer together in the ocean than fish from separate or distant stocks, resulting in keener intrastock than interstock competition?*
- *How are the distributions, growth, and survival affected by ocean circulation, both on the large-scale (100-1,000 km), such as the anomalous changes in circulation in the Subarctic Gyre that occurred in the early 1980s, and on the mesoscale (10–100 km), such as the persistent eddy found off Sitka, coastal frontal zones, or offshore banks?*
- *These features and variations in their intensity and location may have important influences on the concentration of salmonid food and predators, on the salmonid migratory routes, and, therefore, on salmonid survival in the coastal and oceanic regions of the North Pacific. Determining what those influences are is a challenging problem for the future.*

W.G. Pearcy, 1992

Some aspects of salmon biology have advanced by orders of magnitude (genetics) but examples of their application to the major questions raised by Pearcy (1992) are, as yet, few. It is no longer necessary to place a tag in a sockeye salmon in the Gulf of Alaska and await its recovery to understand where it may have originated. It is even possible to understand something of the physiological state of the fish through the genes that are being expressed (Miller, 2009). Nevertheless, the offshore habitat of Pacific salmon in the Gulf of Alaska has largely been abandoned by researchers, but not for lack of interesting questions that remain to be answered.

And Peterman's (1998) plea after their analysis of sockeye salmon survival:

- *We plea for collection of more extensive data on abundance of early life stages of Pacific salmon. One major reason why it is so difficult to understand the causes of spatial and temporal trends in survival rates, and to deal effectively with their management implications, is the lack of long-term data across numerous stocks on survival rates in different life stages.*

Peterman *et al.*, 1998

The observing system for Fraser River sockeye salmon can detect overall productivity changes in many individual populations and on multiple time scales. Many aspects of this observing system provide the basic information to influence decisions that are made in-season to regulate fisheries and implement conservation measures. Fishing is restricted or permitted as abundance in the observing system allows. However, when a change is detected, the observing system will be challenged to find a cause because it does not have this function as part of its design. Observations of juvenile salmon in the ocean are made by individual researchers who have an interest in a particular time and region. The DFO Strait of Georgia salmon trawl survey, for example, was established to determine the factors affecting chinook and coho salmon survival. As a consequence, the relevance of these surveys to the general biology of Fraser River sockeye salmon is a subject of debate.

The coincidental emergence of juvenile salmon research programs on the continental shelf by various U.S. and Canadian agencies has led to a better understanding of the biology of juvenile salmon at sea (Grimes *et al.*, 2007; Trudel *et al.*, 2009). The most promising result of these investigations, however, came from the integration of physical, chemical and biological oceanographic measurements that characterize the marine habitat of juvenile salmon.

There is an interesting dichotomy between the primary interests of scientists who study the cycle of salmon life and the primary observations they make. Most will never have observed the death, by natural causes, of a sockeye salmon in the ocean. Yet for many, the processes that affect the life and death of these animals and their effect on fisheries production is their primary focus. As a consequence, when salmon survive or die at greater than average rates, the scientific community is at a loss to understand why it occurred. The observation system is simply not designed to answer this question.

Some of Canada's international, intergovernmental research on Pacific salmon is coordinated by the North Pacific Anadromous Fish Commission (NPAFC). Its members include Canada, Japan, Republic of Korea, Russian Federation and the United States of America. Since 2002, its member nations have directed their efforts at clarifying the mechanisms of biological response by salmon to the conditions caused by climate change in the Bering Sea (Farley *et al.*, 2009). Canadian salmon of Yukon River origin rear in the Bering Sea but Fraser River sockeye salmon are not (yet) known to frequent the Bering Sea in large numbers and Canada has very limited salmon research activities in that region.

The over-arching questions for long-term research and monitoring for the NPAFC will address:

1. What are the current status and trends in marine production of anadromous stocks, and how are these trends related to population structure (spatial and temporal) and diversity of anadromous stocks in marine ecosystems of the North Pacific?
2. How will climate and climate change affect anadromous stocks, ecologically related species, and their North Pacific marine ecosystems?

Canada's contribution to research on Pacific salmon on the high seas (the continental shelf) was described recently (Beamish *et al.*, 2009) in the following:

Research topic	**Season**
Continue collection of biological information on Pacific salmon	All year
Describe ambient oceanographic conditions	All year
Quantify the biomass of zooplankton and describe the zooplankton species community composition	All year
Examination of trends in diet of all five species of Pacific salmon diet	Summer and fall
Examine growth and condition of juvenile Pacific salmon in relation to climate indices	Summer and fall
Determine causes for early marine mortality of juvenile coho and chinook salmon	Spring, summer and fall
Stock identification using DNA analysis and acoustic tag studies	Spring, summer and fall

Last word

"When it comes to sockeye salmon, don't move too quickly to generalize!"

K. Groot, 2010

Continued from inside back cover

Jamieson, G. and Zhang, C.-I. (Eds.) 2005. Report of the Study Group on Ecosystem-Based Management Science and its Application to the North Pacific. **PICES Sci. Rep. No. 29**, 77 pp.

Brodeur, R. and Yamamura, O. (Eds.) 2005. Micronekton of the North Pacific. **PICES Sci. Rep. No. 30**, 115 pp.

Takeda, S. and Wong, C.S. (Eds.) 2006. Report of the 2004 Workshop on *In Situ* Iron Enrichment Experiments in the Eastern and Western Subarctic Pacific. **PICES Sci. Rep. No. 31**, 187 pp.

Miller, C.B. and Ikeda, T. (Eds.) 2006. Report of the 2005 Workshop on Ocean Ecodynamics Comparison in the Subarctic Pacific. **PICES Sci. Rep. No. 32**, 103 pp.

Kruse, G.H., Livingston, P., Overland, J.E., Jamieson, G.S., McKinnell, S. and Perry, R.I. (Eds.) 2006. Report of the PICES/NPRB Workshop on Integration of Ecological Indicators of the North Pacific with Emphasis on the Bering Sea. **PICES Sci. Rep. No. 33**, 109 pp.

Hollowed, A.B., Beamish, R.J., Okey, T.A. and Schirripa, M.J. (Eds.) 2008. Forecasting Climate Impacts on Future Production of Commercially Exploited Fish and Shellfish. **PICES Sci. Rep. No. 34**, 101 pp.

Beamish, R.J. (Ed.) 2008. Impacts of Climate and Climate Change on the Key Species in the Fisheries in the North Pacific. **PICES Sci. Rep. No. 35**, 217 pp.

Kashiwai, M. and Kantakov, G.A. (Eds.) 2009. Proceedings of the Fourth Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 36**, 305 pp.

Jamieson, G., Livingston, P. and Zhang, C.-I. (Eds.) 2010. Report of Working Group 19 on Ecosystem-based Management Science and its Application to the North Pacific. **PICES Sci. Rep. No. 37**, 166 pp.

Pakhomov, E. and Yamamura, O. (Eds.) 2010. Report of the Advisory Panel on Micronekton Sampling Inter-calibration Experiment. **PICES Sci. Rep. No. 38**, 108 pp.

Makino, M. and Fluharty, D.L. (Eds.) 2011. Report of the Study Group on Human Dimensions. **PICES Sci. Rep. No. 39**, 40 pp.

Foreman, M.G. and Yamanaka, Y. (Eds.) 2011. Report of Working Group 20 on Evaluations of Climate Change Projections. PICES Sci. Rep. **No. 40**, 165 pp.

McKinnell, S.M., Curchitser, E., Groot, C., Kaeriyama, M. and Myers, K.W. 2012. PICES Advisory Report on the Decline of Fraser River Sockeye Salmon *Oncorhynchus nerka* (Steller, 1743) in Relation to Marine Ecology. PICES Sci. Rep. **No. 41**, 149 pp.

PICES Scientific Reports

Hargreaves, N.B., Hunter, J.R., Sugimoto, T. and Wada, T. (Eds.) 1993. Coastal Pelagic Fishes (Report of Working Group 3); Subarctic Gyre (Report of Working Group 6). **PICES Sci. Rep. No. 1**, 130 pp.

Talley, L.D. and Nagata, Y. (Eds.) 1995. The Okhotsk Sea and Oyashio Region (Report of Working Group 1). **PICES Sci. Rep. No. 2**, 227 pp.

Anonymous. 1995. Report of the PICES-STA Workshop on Monitoring Subarctic North Pacific Variability. **PICES Sci. Rep. No. 3**, 94 pp.

Hargreaves, N.B. (Ed.) 1996. Science Plan, Implementation Plan (Report of the PICES-GLOBEC International Program on Climate Change and Carrying Capacity). **PICES Sci. Rep. No. 4**, 64 pp.

LeBlond, P.H. and Endoh, M. (Eds.) 1996. Modelling of the Subarctic North Pacific Circulation (Report of Working Group 7). **PICES Sci. Rep. No. 5**, 91 pp.

Anonymous. 1996. Proceedings of the Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 6**, 426 pp.

Beamish, R.J., Hollowed, A.B., Perry, R.I., Radchenko, V.I., Yoo, S. and Terazaki, M. (Eds.) 1997. Summary of the Workshop on Conceptual/Theoretical Studies and Model Development and the 1996 MODEL, BASS and REX Task Team Reports. **PICES Sci. Rep. No. 7**, 93 pp.

Nagata, Y. and Lobanov, V.B. (Eds.) 1998. Multilingual Nomenclature of Place and Oceanographic Names in the Region of the Okhotsk Sea. **PICES Sci. Rep. No. 8**, 57 pp. (Reprint from MIRC Science Report, No. 1, 1998)

Hollowed, A.B., Ikeda, T., Radchenko, V.I. and Wada, T. (Organizers) 1998. PICES Climate Change and Carrying Capacity Workshop on the Development of Cooperative Research in Coastal Regions of the North Pacific. **PICES Sci. Rep. No. 9**, 59 pp.

Freeland, H.J., Peterson, W.T. and Tyler, A. (Eds.) 1999. Proceedings of the 1998 Science Board Symposium on The Impacts of the 1997/98 El Niño Event on the North Pacific Ocean and Its Marginal Seas. **PICES Sci. Rep. No. 10**, 110 pp.

Dugdale, R.C., Hay, D.E., McFarlane, G.A., Taft, B.A. and Yoo, S. (Eds.) 1999. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Summary of the 1998 MODEL, MONITOR and REX Workshops, and Task Team Reports. **PICES Sci. Rep. No. 11**, 88 pp.

Lobanov, V.B., Nagata, Y. and Riser, S.C. (Eds.) 1999. Proceedings of the Second PICES Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 12**, 203 pp.

Danchenkov, M.A., Aubrey, D.G. and Hong, G.H. 2000. Bibliography of the Oceanography of the Japan/East Sea. **PICES Sci. Rep. No. 13**, 99 pp.

Hunt, G.L. Jr., Kato, H. and McKinnell, S.M. (Eds.) 2000. Predation by Marine Birds and Mammals in the Subarctic North Pacific Ocean. **PICES Sci. Rep. No. 14**, 168 pp.

Megrey, B.A., Taft, B.A. and Peterson, W.T. (Eds.) 2000. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 1999 MONITOR and REX Workshops, and the 2000 MODEL Workshop on Lower Trophic Level Modelling. **PICES Sci. Rep. No. 15**, 148 pp.

Stehr, C.M. and Horiguchi, T. (Eds.) 2001. Environmental Assessment of Vancouver Harbour Data Report for the PICES MEQ Practical Workshop. **PICES Sci. Rep. No. 16**, 213 pp.

Megrey, B.A., Taft, B.A. and Peterson, W.T. (Eds.) 2001. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 2000 BASS, MODEL, MONITOR and REX Workshops, and the 2001 BASS/MODEL Workshop. **PICES Sci. Rep. No. 17**, 125 pp.

Alexander, V., Bychkov, A.S., Livingston, P. and McKinnell, S.M. (Eds.) 2001. Proceedings of the PICES/CoML/IPRC Workshop on "Impact of Climate Variability on Observation and Prediction of Ecosystem and Biodiversity Changes in the North Pacific". **PICES Sci. Rep. No. 18**, 210 pp.

Otto, R.S. and Jamieson, G.S. (Eds.) 2001. Commercially Important Crabs, Shrimps and Lobsters of the North Pacific Ocean. **PICES Sci. Rep. No. 19**, 79 pp.

Batchelder, H.P., McFarlane, G.A., Megrey, B.A., Mackas, D.L. and Peterson, W.T. (Eds.) 2002. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 2001 BASS/MODEL, MONITOR and REX Workshops, and the 2002 MODEL/REX Workshop. **PICES Sci. Rep. No. 20**, 176 pp.

Miller, C.B. (Ed.) 2002. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the PICES 2002 Volunteer Observing Ship Workshop. **PICES Sci. Rep. No. 21**, 38 pp.

Perry, R.I., Livingston, P. and Bychkov, A.S. (Eds.) 2002. PICES Science: The First Ten Years and a Look to the Future. **PICES Sci. Rep. No. 22**, 102 pp.

Taylor, F.J.R. and Trainer, V.L. (Eds.) 2002. Harmful Algal Blooms in the PICES Region of the North Pacific. **PICES Sci. Rep. No. 23**, 152 pp.

Feely, R.A. (Ed.) 2003. CO_2 in the North Pacific Ocean (Working Group 13 Final Report). **PICES Sci. Rep. No. 24**, 49 pp.

Aydin, K.Y., McFarlane, G.A., King, J.R. and Megrey, B.A. (Eds.) 2003. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: The BASS/MODEL Report on Trophic Models of the Subarctic Pacific Basin Ecosystems. **PICES Sci. Rep. No. 25**, 93 pp.

McKinnell, S.M. (Ed.) 2004. Proceedings of the Third Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 26**, 275 pp.

Kishi, M.J. (Ed.) 2004. Report of the MODEL Task Team Second Workshop to Develop a Marine Ecosystem Model of the North Pacific Ocean including Pelagic Fishes. **PICES Sci. Rep. No. 27**, 49 pp.

King, J.R. (Ed.) 2005. Report of the Study Group on the Fisheries and Ecosystem Responses to Recent Regime Shifts. **PICES Sci. Rep. No. 28**, 162 pp.

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Front cover figure

Mature sockeye salmon (*Oncorhynchus nerka* Steller, 1743) in the Adams River, British Columbia, in 2010. Photo credit, S.M. McKinnell.