FACTORS INFLUENCING THE EARLY MARINE ECOLOGY OF JUVENILE SOCKEYE SALMON (*O. nerka)* IN RIVERS INLET, BRITISH COLUMBIA

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ABSTRACT

The Rivers Inlet sockeye salmon (*Oncorhynchus nerka*) population was historically the third most numerous in British Columbia, with returns routinely exceeding one million adults. In recent years, the population has drastically declined, culminating in an utter failure of the adult spawning population in 1999, when returns were estimated at 3600 fish. Poor marine survival has been proposed as the primary cause of the decline. Existing evidence, including concurrent declines in sockeye salmon populations from nearby watersheds indicate the problem may lie in the early marine phase. We provide evidence suggesting that a crucial, population-limiting window may exist in the early marine phase, as the newly smolted juvenile sockeye salmon emerge into Rivers Inlet and nearby waters. Unless appropriate abiotic conditions exist in the lead-up to the juvenile migration, the brood year may suffer significant mortality. This, I propose, is a key contributor to reduced returns of Rivers Inlet sockeye salmon.

DEDICATION

To my mom, who always told me that I could be anything I wanted, who believed in me, and supported me in so many ways during my education. It was you who taught me the love of knowledge, to read and learn, and to explore my world and I thank you from the bottom of my heart.

ACKNOWLEDGEMENTS

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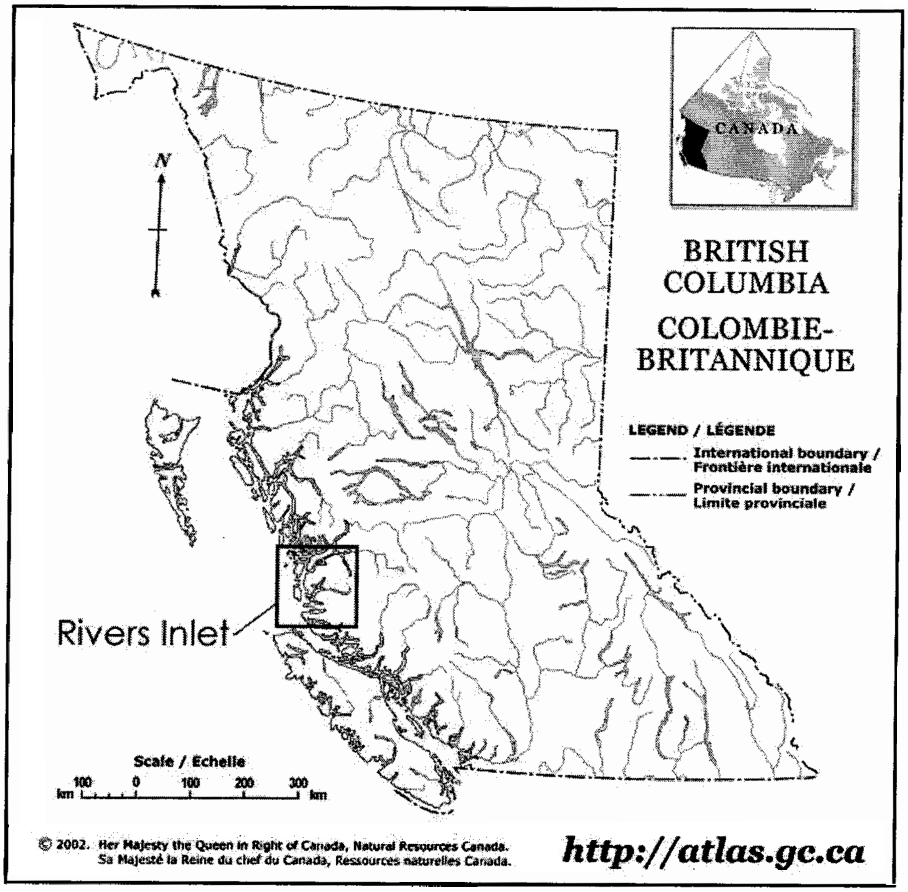
1 INTRODUCTION

1.1 Description of Study Area

Rivers Inlet is a large mainland inlet located on the remote central coast of British Columbia, Canada. It is one of a series of large fjords along the British Columbia coast that were scoured during numerous periods of glaciation (Thomson, R. E., 1981, page 8). The geologic history resulted in the formation of an extensive watershed at the head of the inlet that provides ideal spawning and rearing habitat for sockeye salmon (*Oncorhynchus nerka*), while the outer mouth opens into the pelagic conditions of Queen Charlotte Sound.

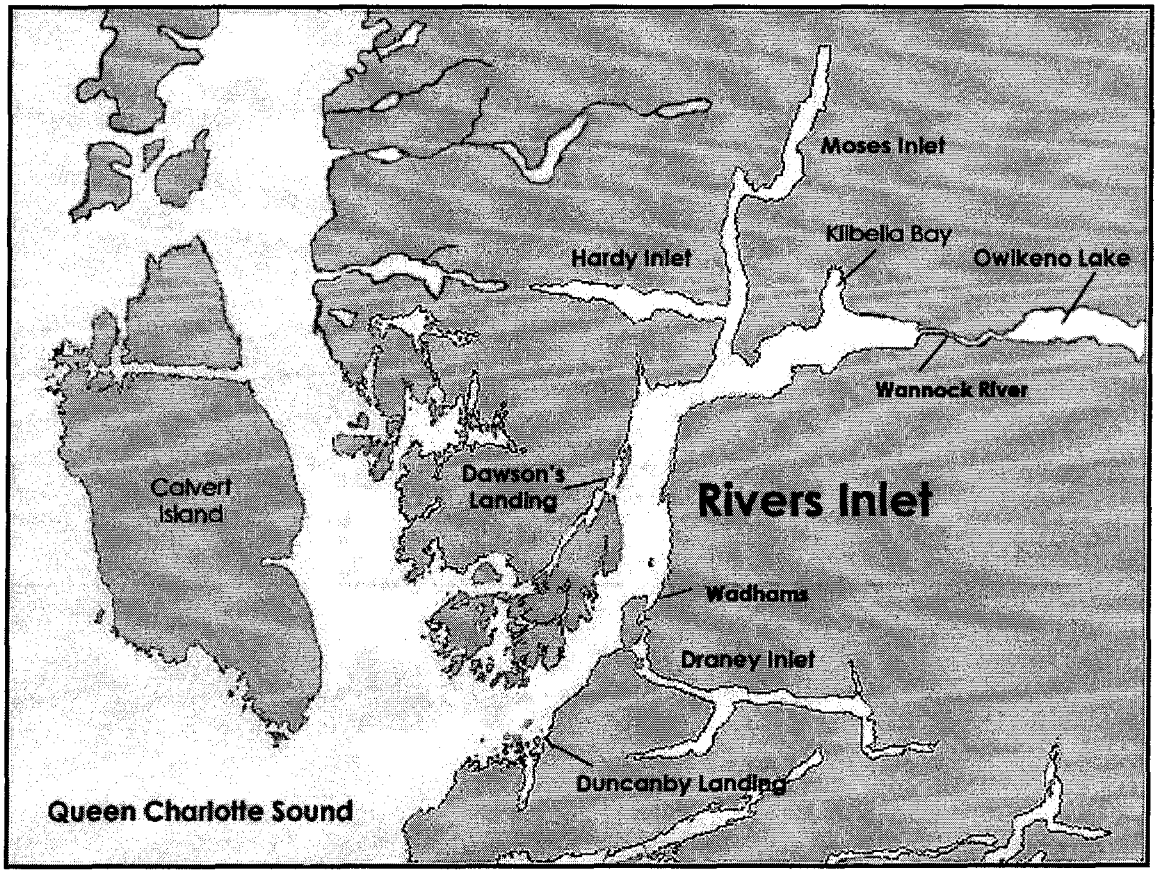
Queen Charlotte Sound is the only large section of the British Columbia mainland that is not protected by islands. The full fetch conditions make marine travel across the sound difficult even in good weather because the waters are continually subjected to large open-ocean swells. No outside road access exists and the closest supply point is Port Hardy, a six-hour trip across the sound in the research vessel. This feature made sampling challenging and expensive.

Figure 1-1 A map of British Columbia showing the location of Rivers Inlet on the central coast.



Rivers Inlet is extensive, approximately 40 km long and 3 km wide. In addition to the inlet proper, there are two side inlets; Moses near the upper end, and Draney Inlet towards the outside. Both side inlets are also branched. There is considerable turbulance at all inlet junctions most notably at Draney Narrows at the mouth of Draney Inlet. Major inflow rivers are the Wannock that drains the Owikeno Lake basin, the Kilbella and Chuckwalla rivers that empty into Kilbella Bay near the inlet head, and the Clyak River at the head of Moses Inlet.

Figure 1-2 Rivers Inlet, B.C. with important landmarks.



The major identified spawning area for sockeye salmon is the Owikeno Lake Watershed that drains into the inlet via the Wannock River at the inlet head. The sockeye salmon migrate between the Wannock River and the inlet mouth through either the main body of Rivers Inlet, or an alternate, narrower route on the northwest shore known as Darby Channel. The channel begins at a settlement known as Dawson's Landing and runs between the mainland and a series of islands, finally leading to the waters inside of Calvert Island known as Fitz Hugh Sound.

The only other local sockeye salmon rearing areas are (i) Elsie and Hoy lakes, below the mouth of Darby Channel and (ii) Elizabeth Lake west of the upper inlet. Both of these populations are small. Therefore, the juvenile sockeye salmon encountered during the study were primarily if not exclusively from a single source: Owikeno Lake.

The Kilbella, Chuckwalla, and Wannock rivers are the major Chinook spawning locations. There are also important chum salmon spawning areas in these rivers and in the Clyak River as well. Major spawning areas for pink salmon are present in Johnstone Creek, near the historic cannery site known as Wadhams, and the Kilbella, Chuckwalla, and Clyak rivers. Coho spawning is scattered throughout much of the area.

Owikeno Lake was aptly characterized by Foskett (1958) when he stated, "Owikeno Lake can be described as a fjord whose sill happened to be a little too high to maintain connection with salt water." The lake has an elevation of only 15 m and it is probable that at least the first basin was at one time marine. The lake is over 350 m (1200 ft) deep at it deepest point and is nearly the same size as the inlet; it is approximately 56 km (35 miles) long (all basins included), and total lake area is approximately 78 to 88 km^2 (Foskett 1958). Owikeno Lake has "low basic productivity" (Ruggles 1965) due to a shallow photic zone caused by turbidity from glacial silt. The lake has a deep, cold epilimnion and a poor zooplankton standing crop (Ruggles 1965).

The Owikeno Lake Watershed is also extensive, covering a drainage area of 4100 km^2 (Ruggles 1965). The lake consists of four distinct basins that are connected by narrow, shallow waters, an effect that means each basin provides a unique habitat. The features of the lake basins were extensively described by Ruggles (1965) and then Foskett (1958) and will be summarized here. The more seaward basins (1 and 2) are deep, 366 m and 146 m respectively, cold, and typically oligotrophic. The input of glacial silt is particularly strong in these basins, a feature that further limits primary productivity.

These two basins are large, comprising 90% of the total lake surface area, and are exposed to strong winds. In contrast, the upper basins (3 and 4) are relatively shallower, 78 m and 76 m respectively, more sheltered, and less turbid.

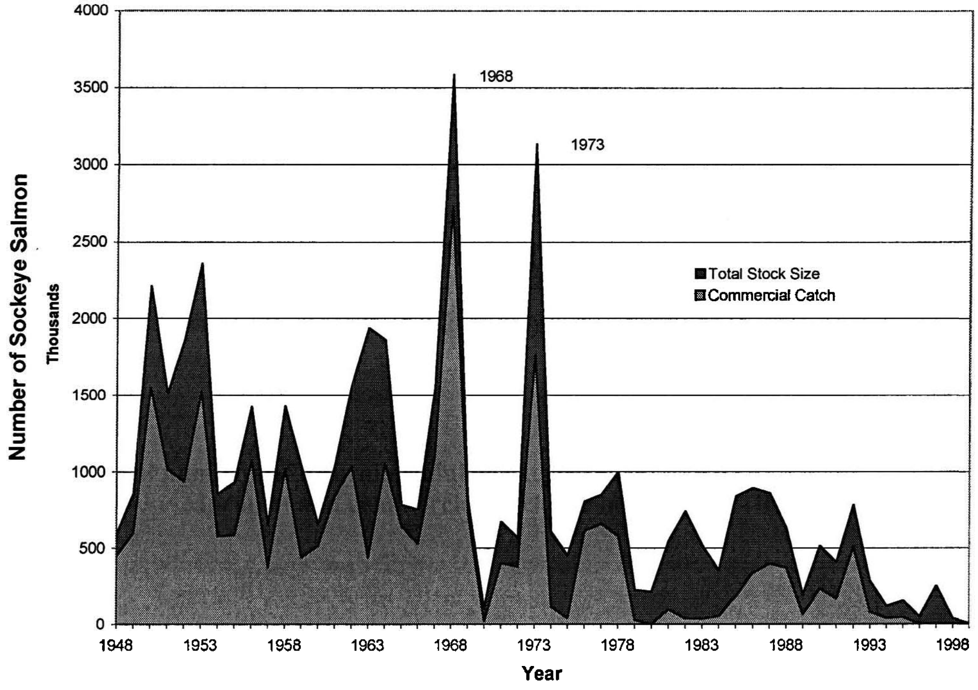
Sockeye salmon spawning occurs in various tributaries and along the lakeshore itself. The Machmell and Neechanz Rivers are the primary spawning streams in Basin 1, the Genesee and Shumahalt Rivers dominate Basin 2, and Basin 4 contains the Washwash, Inziana, and Tzeo Rivers. The Machmell and Shumahalt rivers are the two largest inflow sources and, because they both also originate from extensive ice fields at higher elevations, are responsible for the majority of the glacial silt deposition into the lake. There is also a component of the run that spawns in a section of the Wannock River.

Glacial melting and high rainfall can cause large changes in river volume and "spectacular changes in lake level." (Ruggles 1965). Forestry is the only industry present in the Owikeno Watershed. In recent years, the watershed has been logged extensively but these activities began much later than other parts of the BC coast, owing to the remoteness of the inlet. As recently as 1958, Foskett described the watershed as pristine…"conditions for spawning and incubation in the region are still practically in their natural state." Logging impacts have been cited as possible contributors to the decline of the sockeye salmon population. However, in an extensive review paper, McKinnell et al. (2001) refuted claims that freshwater conditions were to blame, and instead concluded that the source of the decline of the River Inlet sockeye salmon population was in the marine environment.

1.2 History of Decline

The Rivers Inlet sockeye salmon population provided historically one of the most productive salmon runs in British Columbia (Foskett 1958; Ruggles 1965; McKinnell et al. 2001). Returns routinely exceeded one million adults (Rutherford and Wood 2000), and at times even exceeded returns to the Fraser and Skeena systems. The robust population supplied a booming commercial fishery that lasted over half a century.

Figure 1-3 Historical numbers of returning adult sockeye salmon to Rivers Inlet, B.C. Total estimated escapement and commercial catch are both shown. (Rutherford and Wood, 2000)



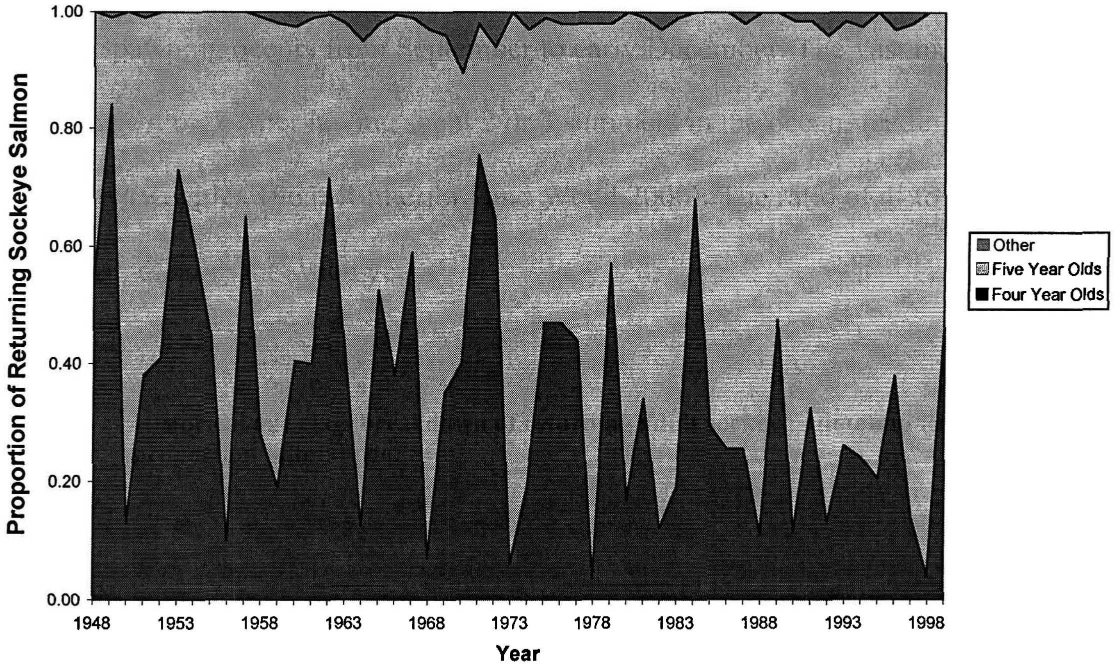
Beginning in the late 1960's, the Rivers Inlet sockeye salmon population experienced a period of instability. There were extremely large returns in 1968 and 1973, with a population crash in between in 1970. Subsequently, returns never rebuilt to the pre-crash levels. Commercial harvest rates were reduced from 1979 to 1984 in an early attempt at adaptive management (Walters et al. 1993). Returns did not increase. Then, following concerns over further decreases in returns from 1993 onwards, the commercial harvest was severely curtailed again, and finally closed altogether after the 1995 fishing season. It was hoped that the population would rebound with a complete relief from harvest pressure. That has not been the case. Instead, the period of instability and low returns culminated with an utter failure of the adult sockeye salmon spawning population; in 1999 the number of spawning sockeye salmon was estimated at 3600 fish (Rutherford and Wood, 2000). This event was one of the largest ecological disasters in recent history associated with Pacific salmon. For those involved in the business of salmon, it was an economic disaster as well. It was the northern equivalent of the collapse of the upper Fraser River salmon populations following the blockage of the river by the Hells Gate slide of 1914. However, unlike the Hells Gate disaster, the cause of this collapse was unclear. No enormous landslide or toxic chemical spill could explain the population collapse.

A number of theories emerged as interested parties attempted to explain what had happened. McKinnell et al. (2001) provided a review of possible causes for the decline. They concluded that poor marine survival was the primary culprit, and predicted that the population would likely rebuild when marine conditions improved.

1.3 Biology of Rivers Inlet Sockeye Salmon

Adult sockeye salmon begin to show up in the inlet in late July and the run continues until late August. The fish have typically held in the inlet before ascending the Wannock River and holding in the lake for a period of time before heading to their natal streams. Spawning occurs from September to early December. The vast majority of fish return at age 4 or 5, after having spent 2 or 3 summers in the ocean, feeding and growing to maturity (Ruggles 1965; Rutherford and Wood 2000). The ratio of 4- to 5-year-olds varies unpredictably between years.

Figure 1-4 **Historical age class breakdown of returning adult sockeye salmon to Rivers Inlet, by proportion of total run.**



After incubation in the spawning gravel, fry emerge and migrate to the lake in April and May. The fry then spend one year in the lake before heading seaward as smolts (Rutherford and Wood, (2000). For example, fry that were laid as eggs in the fall/early winter of 2000, entered the lake in the spring of 2001 and remained there until the spring of 2002 when the fish began their seaward migration. Thus, the fish pass two winters in freshwater. The surviving 2000 brood year fish will not return until 2004 or 2005 as spawning adults. These fish are referred to as four-year-olds and five-year-olds respectively.

Alterations to this life history strategy exist, but are uncommon, making up less than 2% of the population on average (Rutherford and Wood, 2000). For example, small components of the population can remain in the lake for an extra year (Gilbert 1920). In addition, a small number of males, referred to as "jacks", return to spawn after only one year at sea. These fish are easily distinguished from other age groups by their small size, "approximately 17 inches in length…" (Foskett 1958). There is also a component of the population of juvenile sockeye salmon that heads to the sea without spending a year in fresh water (Gilbert 1920)

The "juvenile' sockeye salmon or "smolts" that this study is concerned with are fish that appear to have recently undergone smoltification and are new to the marine environment. Rivers Inlet sockeye salmon smolts are historically some of the smallest on record in British Columbia, with an average weight of 2.0 grams (Gilbert 1915, 1916, 1918; Foskett 1958) "Smolts are unusually small in size, averaging about 2 grams… these are really tiny smolts – among the smallest known… the usual average size for British Columbia sockeye salmon smolts is 4 to 8 g…" (Foskett 1958). Thus, Rivers Inlet sockeye salmon smolts are extremely small when they enter the marine environment, and this has evidently been the case for many years before the stock declined; it is a natural state.

There are 12 identified spawning areas in the Rivers Inlet watershed. Currently available genetic evidence points to considerable straying within the watershed. For this reason, and for management tractability, Rivers Inlet sockeye salmon are managed as a single stock. No commercial fishing has been permitted on this stock since 1995.

1.3.1 Hatchery Fish

Hatchery-raised juvenile salmonids were present in Rivers Inlet at various times during the study. Sockeye salmon from the Snootli Creek hatchery were not adipose-fin clipped, but had otolith marks. Thus, it was not possible to distinguish between wild and cultured sockeye salmon visually. Therefore, otoliths from the sockeye salmon caught in 2002 and 2003 were extracted, mounted on slides, and examined for hatchery marks by a trained government employee. Analysis indicated that fewer than 5 hatchery sockeye salmon were identified within the fish examined. It was thus determined that sockeye salmon of hatchery origin did not form a significant component of the study population. Further to this, it was noted that despite large quantities of marked, hatchery-produced juvenile Chinook being released directly into the upper inlet during every sampling season, fewer than 10 of these juveniles were caught in total throughout the duration of the study.

1.4 The Early Marine Stage

Rutherford and Wood (2000) and later McKinnell et al. (2001) concluded that the population decline was due to reduced survival in the marine phase of life. We explored the most easily accessible and potentially most critical phase of this marine phase, namely the migration down the inlet.

The early marine phase is of particular interest for a number of reasons. First, the unusually small smolt size of these sockeye salmon makes them particularly vulnerable to mortality (Foskett 1958; Ward et al. 1989; Henderson and Cass 1991; Skilbrei et al. 1994; McKinnell et al. 2001). Second, the small size of the smolts coupled with the generally low abundance of zooplankton in the lower lake basins (Foskett 1958) suggests that the juvenile sockeye salmon have historically been food limited prior to entering the marine environment. Thus, the availability of prey for the smolts within the inlet should have an important impact on the survival and size of the smolts when they exit into Queen Charlotte and Fitz Hugh sounds. In these outer regions they must compete with juvenile salmon from other stocks and a plethora of other creatures for food, all while avoiding predators. Third, due to the expansive length of Rivers Inlet, it serves as an important intermediary habitat that the smolts must pass through and utilize. Fourth, a concurrent decline in sockeye salmon returns in nearby Smith Inlet suggests that both populations experienced similar difficulties in some shared habitat, with the prime suspect being the near-shore marine waters.

Further to this, recent investigations into potential predictors of adult salmon returns have provided new evidence of the importance of the marine environment. Recent analyses of spatial correlation patterns in salmon returns point to a critical role for the early part of the marine phase of their life cycle (Pyper et al. 2001, 2002). For these reasons, this study focused on the early marine life phase of juvenile sockeye salmon as they migrate out through Rivers Inlet.

This thesis provides evidence suggesting that a crucial, population-limiting, window may exist in the early marine phase, as the newly smolted juvenile sockeye salmon emerge into Rivers Inlet and nearby waters. Unless appropriate abiotic conditions exist in the lead-up to the juvenile migration, the brood year may well suffer significant mortality. This, I propose, is a key factor contributing to reduced returns of Rivers Inlet sockeye salmon.

2 METHODOLOGY

2.1 Overview

The juvenile seine-fishing program began with a preliminary sampling trip on April 30, 2002 to Rivers Inlet, B.C. The trip allowed the crew to become familiar with the specialized net, the fishing sites, and the sampling strategy before data collection began. During the trip it became apparent that the 1.3cm mesh size on the bunt end of the net was too large because juvenile salmon were observed to escape. To capture the extremely small juvenile sockeye salmon in Rivers Inlet the bunt was replaced with one composed of 0.6cm knotless marquisette web. The new net configuration was used in all subsequent sampling trips for the remainder of the project.

In Rivers Inlet, salmon and zooplankton samples were collected from April to July in the four years, 2002 to 2005. In addition, similar collections were made in Smith Inlet in 2002 and 2004.

All biological and oceanographic sampling was performed from the MV *Western Bounty*. This vessel is a 16 m aluminium commercial seine boat owned and operated by the Wuikinuxv First Nation of Rivers Inlet. The skipper and crew had previous experience with commercial seine fishing.

Juvenile salmon were sampled by fishing with a specially designed small-mesh seine net at designated stations within the marine waters of Rivers and Smith inlets. At each station, the net was set and retrieved until the bunt end was alongside the boat. The bunt was not dried up; instead enough web was left in the water to allow the fish to swim. The catch was sub-sampled via dip net, transferred to a live tank, and sorted by species. A few of each species of salmon, up to a maximum of 20 individuals, were kept for laboratory analysis. This included (i) confirmation of species identity, (ii) measurement of fork length and body weight, (iii) otolith and stomach content removal, (iv) weighing of stomach and stomach contents, and (v) identification of stomach contents. The sampling strategy was designed to limit the handling of the fish so that any potential physical damage or mortality was minimized. To this end, most of the fish caught in the seine were released directly from the net without being handled or removed from the water.

Plankton was sampled by a vertical plankton haul with a set of bongo nets at designated stations. There were fewer sampling stations for plankton than for the juvenile salmon work but the same geographic area was covered.

2.2 Selection of Sampling Sites

Before the 2002 field season, potential sites for juvenile salmon and zooplankton sampling were chosen based on the following criteria. First, it was necessary that the inlet be surveyed along all of its length; from the head to the mouth and outside. With this in mind, tentative sites were spread geographically along the length of the inlet. Second, special attention was paid to possible salmon migration routes along the north or south side of the inlets. Third, to investigate the importance of the proximity to shore some sites were paired; “shore” vs. “open” (offshore). In Rivers Inlet, the sites selected for juvenile sockeye sampling are shown in (Figure 2-1). Zooplankton sampling sites are shown in (Figure 2-2)

Figure 2-1 **The location of the standard sampling sites (*) for juvenile sockeye salmon in Rivers Inlet, B.C. The inlet zones used during statistical analyses are also shown.**

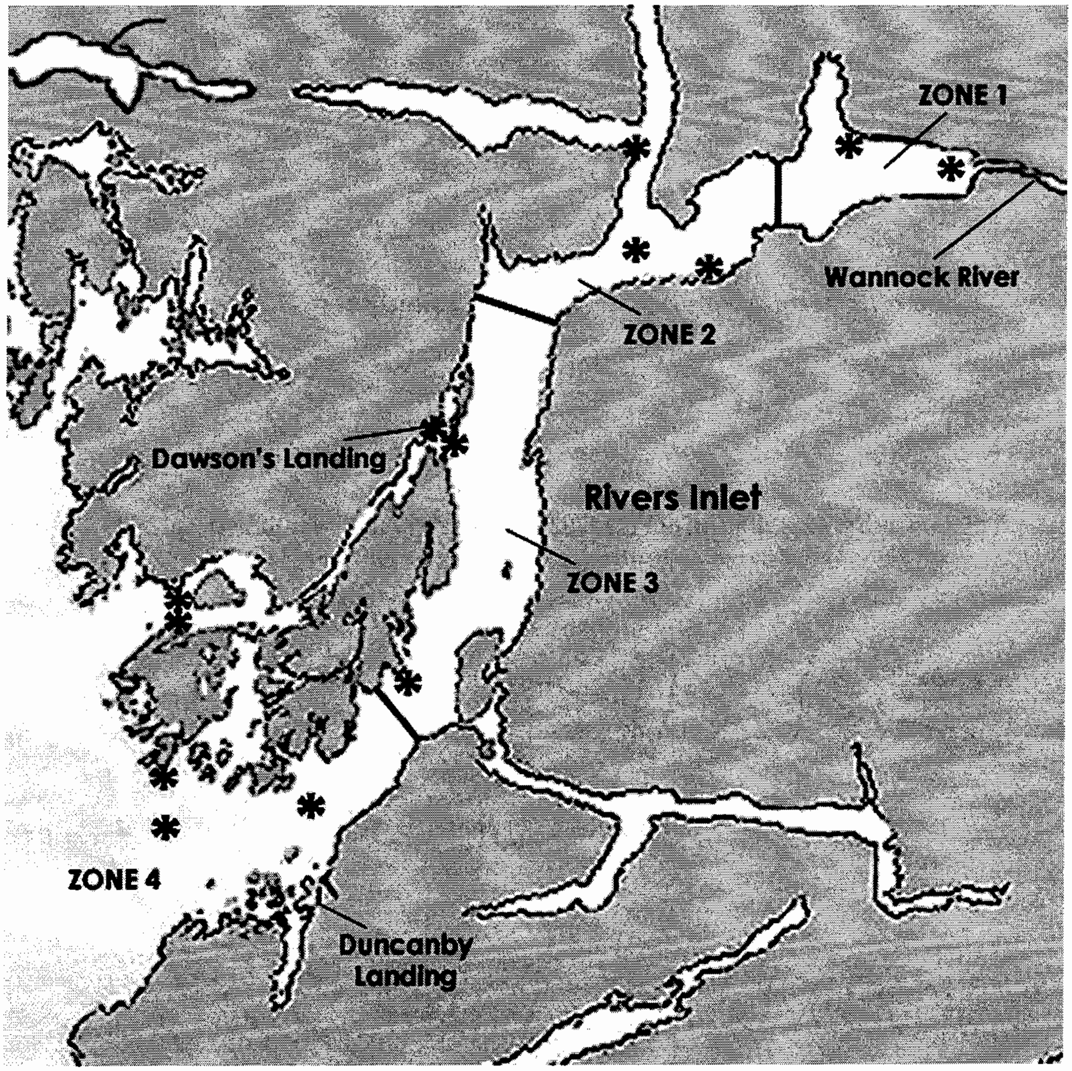
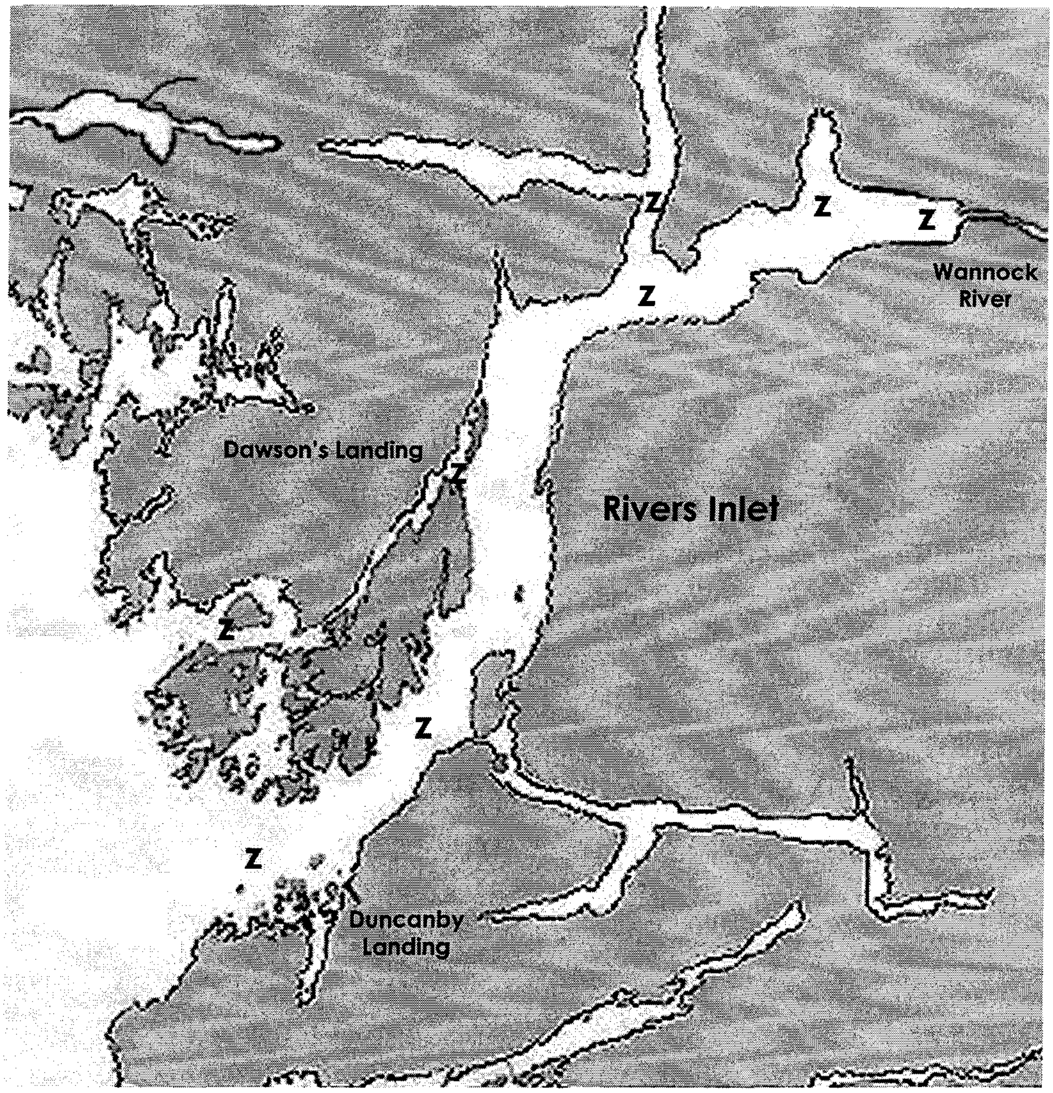


Figure 2-2 The location of the standard sampling sites (z) for zooplankton in Rivers Inlet, B.C.



2.3 Sampling Interval

Rivers Inlet was sampled in all four years, 2002 to 2005, inclusive. (Smith Inlet was also included in the study but for only two years; 2002 and 2004, due to budget constraints. Results for Smith Inlet will not be discussed in this thesis.) Juvenile salmon sampling was conducted roughly every two weeks, beginning in May and continuing into July. During the first sampling season in 2002, it became clear that during spring tide events, strong surface currents present in the inlets made seine fishing difficult. The problem was particularly acute in Smith Inlet. Therefore we decided to conduct juvenile salmon work in Smith Inlet only during neap tides when the surface currents would be reduced. Surface currents were not as strong in Rivers Inlet but the reduced turbulence during neap tide events was beneficial there as well. Thus, the juvenile salmon work was scheduled as near to the first quarter and third quarter moon phases as possible. In order to investigate the possible effect of bias in the salmon catch due to tidal cycle, a spring tide sampling trip was undertaken in Rivers Inlet during 2003. In the end, there was some variability in the timing of the sampling trips according to the lunar cycle, but the intent was to sample as close to neap tide as possible. In addition, water and oceanographic data was recorded on every trip.

Sampling for zooplankton was conducted roughly once a month. The lower frequency of plankton sampling compared to the fish sampling was due to budget constraints. More frequent plankton sampling would have increased the number of boat days per sampling trip beyond the capacity of the funding. However, in 2003 one trip was made to sample zooplankton and oceanographic measures. The goal was to sample the inlet conditions before the juvenile sockeye migration began to extend the temporal scope of the information on inlet productivity.

Table 2-1 The number of sampling trips to Rivers Inlet.

	2002	2003	2004	2005
Fish Only	4	3	2	1
Fish and Plankton	3	3	3	4
Plankton Only	0	1	0	0
Total	7	7	5	5

Total number of sets in each location per year, for fish, plankton-Table 2-2

Table 2-2 **Sites sampled for juvenile salmon in Rivers Inlet during each year. Clear cells represent exploratory sites that were only used in 2002. Hashed cells represent sites that were not sampled. Shaded cells represent the core sampling sites from which the catch data was analyzed.**

Site	**Type**	**2002**	2003	2004	2005
Head/R.I.C.	Open	■	■	■	■
Kilbella Point	Shore	■	■	■	■
Kilbella Bay	Open		╱	╱	╱
Rutherford Point	Shore		╱	╱	╱
McPhee Bay	Shore	╱	■	■	■
Scandanavia Bay	Open	■	■	■	■
Ralph Pt	Shore	╱	■	■	■
Dawson's Landing	Open	■	■	■	■
Dawson's Shore	Shore	■	■	■	■
Bickle Pass	Shore		╱	╱	╱
Whaddams	Mid		╱	╱	╱
Geetla Pt	Shore	■	■	■	■
Mouth	Open	■	■	■	■
Dimsey Open	Open	■	■	■	■
Dimsey Point	Shore	■	■	■	■
Darby Channel	Shore		╱	╱	╱
Bosquet Open	Open	■	■	■	■
Bosquet Point	Shore	■	■	■	■
Total Sites		16	13	13	13

2.4 Field Work

2.4.1 Net Configuration

A seine net originally designed for juvenile herring sampling was used with the permission of researchers with Fisheries and Oceans Canada at the Pacific Biological Station in Nanaimo, B.C. The net was 364 meters long and 29 meters deep; the effective fishing depth was estimated at 25 to 27 meters. The web was in panels and the colour varied from light and dark green to black. The mesh size varied from 2.5 to 3.75 cm (measured diagonally from knot to knot as is the standard for commercial nets). The web was hung in directly on the cork line to reduce the possibility of fish escapes at the surface.

The bunt was constructed of panels such that the finished size was 12.6 m long and 29 m deep. In 2002, the bunt was hung in to the net at a 1:1 ratio; and the effective length was 12.6 m. This was changed in 2003 when the bunt was hung in more loosely making the effective length approximately 9 m long.

In early 2002, a skiff was used to hold the free end of the net while setting out the net, but after it was determined that a sea anchor worked just as well, this was used in its place. This was a more efficient use of the small number of crew.

2.4.2 Set Protocol

Juvenile salmon sampling was always performed during daylight. The date, sampling station, time (set start, rings secured, set finish), weather, Beaufort wind scale estimate, tide, and how the net was set according to tide and wind were recorded. The number of fish caught of each species was documented as either an actual count or estimate according to the protocol used. Although the study was focused on juvenile sockeye salmon, catches of other, non-target species were recorded.

2.4.3 Sampling Protocol

There were two different sampling protocols, depending on the size of the catch, as follows:

Count Protocol

If the catch was small enough to be sampled completely by dip net, the whole catch was brought onboard and placed in a live tank. In this case, the exact count of fish by species was recorded, including non-target species. The sampling fraction was "100%". This usually meant that all juvenile salmon were retained. However, given the critical status of the stock an effort was made to keep no more than 12 individuals of each species (an average of 8) per set. Thus, some of the fish were identified to species in the live tank and then released over the side.

Estimate protocol

If the catch was larger than would fit in a dip net, a sub-sample was taken. Several dip net samples were taken at random out of the catch and transported to the live tank. Juvenile salmon were collected randomly from the live tank with a small dip net until the desired number of each species was retained. The rest of the fish in the live tank were identified to species, counted, and released. Thus, a count of fish by species was obtained for the sub-sample.

The total number of fish of each species caught was calculated from the sub-sample as follows. First, the size of the catch was estimated as the total number of dip net samples required to empty the net of fish. Then a sampling fraction was produced by dividing the "number of dip nets sampled' from the "total number of dips". For example, if 2 dip net samples were taken and approximately 8 were left in the net, the sampling fraction is 2 of 10, or 20%. The number of fish of each species in the sub-sample was then corrected to 100% to estimate the total catch as sampled catch divided by sampling fraction.

2.4.4 Collections

The specimens were anaesthetized in a mixture of clove oil and seawater as required by our animal care permit, and preserved in 95% ethanol. An incision was made into the body cavity with a scalpel to allow the ethanol to reach the gut more effectively.

2.4.5 Zooplankton Collection

Vertical hauls of varying depths were performed at night, at specified stations using bongo nets. The nets and bongo frames were black. The nets were 50 cm in diameter at the top, and 3 m long, with a 250 µm mesh. The assembly was weighted with a length of heavy chain or cannonball. Hauls were done as close to the bottom as safely possible, to within 20m of the bottom. The protocol was as follows:

1. Nets were lowered to within 20m of the bottom on a steel cable at a speed of approximately 2 m/s
2. When at desired depth, nets were raised at a rate of 1 m/s. When they reached the surface, the nets were rinsed with a hose to drain all the plankton into the cod-ends.
3. When the water had drained from the cod-ends, they were removed and the sample from a single cod-end was collected in a sample jar. The cod-end was rinsed repeatedly with seawater and emptied into the jar to ensure the entire sample was obtained.
4. The sample was then preserved with enough formaldehyde to make a 10% solution of seawater-based formalin in the sample jar.

5. The reading from the flow meter was recorded. The nets and cod-ends were then thoroughly rinsed and re-assembled, ready for the next station.

2.5 Lab Work

2.5.1 Fish Size

To restore pliability to the tissues before examination the preserved fish were removed from the ethanol and soaked in seawater for approximately 30 minutes. If species identification could not be confirmed by visual inspection, the first gill arch was removed and the gill rakers analyzed under microscope.

After species identification was confirmed, each fish was weighed, measured and numbered. Fork length was measured with callipers (+/- 0.1mm), and wet weight measured to the nearest mg. A slip of waterproof paper with a unique identification number was then inserted into the mouth and secured through the operculum of the fish. At this stage the fish was ready for stomach and otolith dissection.

2.5.2 Otoliths

A scalpel incision was made into the dorsal surface of the head at a position even with the insertion of the operculum and a shallow cut was made in an anterior direction to expose the brain cavity. The brain and surrounding tissues were removed until the location of the otoliths was visible. The otoliths were extracted and gently cleaned by rubbing them between the fingers with water. They were mounted in glue on a glass tissue slide, sulcus side up. The mounted otoliths were ground and examined for thermal marks at Robertson Creek hatchery on Vancouver Island by employees of the Department of Fisheries and Oceans Canada.

2.5.3 Stomach content dissection

The gut cavity was exposed via an incision from the anus to the pectoral girdle. After the oesophagus was severed, the stomach was dissected from the body cavity and placed in a Petri dish filled with seawater. Any other digestive tissue was removed from the outside of the stomach and the intact stomach was weighed (total wet weight).

The cardiac (descending) portion of the stomach was opened and the contents removed and placed in 5% formalin in a glass scintillation vial for later analysis. The half-full stomach was weighed and the difference noted. The pyloric (ascending) portion of the stomach was then opened and contents removed but discarded as the digestive process makes identification of this material problematic. Lastly, the empty stomach was weighed as above.

The three-step process allowed for the total weight of the stomach contents to be determined, as well as the weight of the portion of the contents that would be further analysed for diet information. The intention was to allow for the calculation of biomass of particular prey species in future analyses.

2.5.4 Stomach contents analysis

Al Hirst of JenSyd Biotech in Nanaimo, B.C, analyzed prey species composition for the cardiac stomach contents. A brief overview of the methods is as follows.

The vials containing the contents from the cardiac portion of the stomach were shipped to JenSyd Biotech. When the volume of contents was small, the entire sample was analysed. For larger samples, the volume of contents was repeatedly halved using a Folsom™ plankton splitter until an amount that could be accurately analysed was obtained. Thus, the accuracy of species counts and size measurements was maintained at a high level for all samples, regardless of initial volume.

The sample was analysed microscopically. A Ward™ counting wheel was employed for enumeration of contents. Analysis of stomach contents for species composition and measurement of prey items followed the protocol used for samples of zooplankton (see Tanasichuk 1998: Tanasichuk and Cooper 2002). All contents that could be identified were counted. The body size of a subset of individuals of each kind was measured with callipers according to standard practices and specific information on the larval stage of the individuals was recoded along with the measurements.

2.5.5 Plankton Biomass

To obtain an index of productivity in the various zones of Rivers Inlet over the course of the juvenile sockeye migration, the biomass and species composition of the zooplankton samples was investigated. The biomass of each plankton sample was measured as follows. The plankton sample was poured into a series of different-sized sieves. The first sieve had mesh of 1000μ diameter and whatever material was small enough to fit through this was passed through a 250μ sieve below. Each sieve was rinsed to lower the formaldehyde vapours, then weighed. In this way, the total wet weight (TWW) of each of two size classes of plankton was produced. In addition, microscopic analyses of zooplankton species were conducted as described for diet analysis above by Al Hirst.

2.6 Data Analysis

Data were summarized and graphed using Microsoft Excel 11.1.1 for the Macintosh computer. Statistical tests were performed with JMP 5.1 for the Macintosh.

Data analyses for this exploratory project were conducted iteratively. First, graphical summaries were generated, often in light of insight obtained informally in the field and laboratory work. This was then followed up, where feasible, with formal statistical modelling and hypothesis testing. Formal analyses were conducted on the following: catch numbers, fish fork length and weight, stomach fullness, and plankton abundance (total wet weight).

2.6.1 Catch Data

The distribution of the catch data was skewed, due to a high frequency of zero catches and a few sets containing many fish. In an effort to reduce the magnitude of the skewness, and the resultant heteroscadasicity of the residuals, a log transformation was applied. Both $\ln(catch+0.5)$ and $\ln(catch+1)$ were calculated and analyzed with the model. It was determined by visual inspection that the $\ln(catch+0.5)$ transformation performed best at in controlling the heteroscadasticity and thus was chosen as the transformation method. The transformed catch data were analysed with a general linear model. Factors included in the model were; *year, date* (converted to a lunar calendar for reasons explained later), distance down the inlet (*zone*), and interactions where relevant and feasible.

Zone

For the formal analysis, the sampling sites were grouped into four categories, as follows:

> *Zone 1*: Inlet Head, consisting of two sites; one from the head of the inlet and one at Kilbella Point.
>
> *Zone 2*: Upper Inlet, consisting of three sites at Rutherford Point/McPhee Bay, Scandinavia Bay, and Ralph Point.
>
> *Zone 3*: Middle Inlet, consisting of three sites at Dawson's Shore, Dawson's Open, and Geetla Point.
>
> *Zone 4*: Lower Inlet, consisting of five sites; one at the Mouth, Bosquet Shore, Bosquet Open, Dimsey Shore, and Dimsey Open.
>
> A map of the zones and sampling sites can be found in Figure 2-1.

Influence of Lunar Cycle

While examining graphs of the catch by date it was noted that the catch followed an approximately bell-shaped curve and the highest catch consistently fell within a two week interval in late May to early June. This peak also coincided with the spring tide at the first new moon in June. The occurrence of this key tidal state varied by up to ten calendar days, from year to year. A lunar date was therefore calculated in reference to the day of the key new moon in each particular year. The new moon was set at day zero and the calendar date was changed into a lunar date by subtracting the date of the new moon.

To facilitate some of the statistical modelling, lunar weeks were sometimes used. These were similarly calculated with the new moon placed in the middle of week zero.

2.6.2 General Linear Model

After the data were formatted as described, formal statistical analyses were performed via a general linear model. Two different model structures were employed.

Model A

The goal of *Model A* was to explore the catch data for possible differences amongst all sampling years: 2002 to 2005 inclusive. Model structure was as follows:

$$\ln(catch + 0.5) = year + zone + lunarweek + year * zone + \varepsilon$$

where:
$year$ is the sampling year
$zone$ is the inlet zone 1 - 4
$lunarweek$ is a measure of time relative to the new moon
$year * zone$ is an interaction term
ε is the residual error

Model B

Results from 2002 were anomalous, and by excluding this year, we found that we could reduce the unexplained variation and then obtain more precise parameter estimates and more powerful tests of significance. We therefore decided to perform further model-based analysis of the catch data from the years 2003 to 2005, excluding data from 2002. Model selection was performed as follows. The AIC value was calculated for different combinations of these factors that did not suffer from singularities, and the combination that produced the lowest AIC value was chosen. Due to the exploratory nature of the study, the catch data were somewhat imbalanced and it was not feasible to explore all combinations of interactions. Final model structure was as follows:

$$\ln(catch + 0.5) = year + zone + lunarweek + lunarweek * zone + \varepsilon$$

where:
year is the sampling year
zone is the inlet zone 1 - 4
lunarweek is a measure of time relative to the new moon
lunarweek * *zone* is an interaction term
ε is the residual error

2.6.3 Quadratic Regression

This analysis assumed a bell-shaped nature of the total catch over time in each year. We used this simplifying assumption to generate a more focused comparison of the timing of the peak catch. In particular, we could then assess how close the peak was to the new moon, and whether or not this timing was consistent from year to year. We also compared models based on calendar day versus lunar day to see which gave a simpler description of the timing. The model structure was as follows:

$$\ln(catch + 0.5) = \beta_0 + \beta_{1,year} + \left(\beta_2 + \beta_{3,year}\right)x + \beta_4 x^2 + \varepsilon$$

where:
x is the lunar or calendar day,
$\beta_{0,1,\ldots}$ are unknown coefficients, and
ε is the residual error

This model allowed for the following:

1) Through the year effects ($\beta_{1,year}$), differences in total abundances between years,

2) Through the linear coefficient, (β_2), a peak away from day 0 (new moon in the lunar day model), and

3) Through the ($\beta_{3,\,year}$) interaction coefficients, a different timing of the peak in different years, but

4) Through the exclusion of an interaction term for the coefficient of x^2, only a constant quadratic curvature term.

Finally, to estimate the date of the peak catch, the derivative of the regression equation could be set to zero and solved for the date. The value of *x* at this point corresponds to the timing of the estimated highest total catch of juvenile sockeye salmon.

2.6.4 Site Type

In addition, to test the hypothesis regarding possible effects of proximity to shore, analysis of Site Type was performed on a sub-set of the observations.

A subset of the locations sampled for fish were designed to function as paired sites in order to investigate whether a higher number of juvenile sockeye were encountered close to the shoreline or farther away in deeper water. The paired sites were distributed in all zones of the inlet with one shore site and one open site per pair (Table 2-3). Data from all four years and every sampling trip were included in the data set. This subset of catch data was analyzed separately because when analysis of site type was included in the initial model, it became too complex and broke down.

The smaller data set was analyzed with a general linear model similar to that employed in the investigation described above. The difference of $\ln(\text{catch} + 0.5)_{\text{shore}}$ - $\ln(\text{catch} + 0.5)_{\text{open}}$ was calculated for each site pair. Factors included in the analysis were year, zone, lunar day, and a day-zone interaction. Note that the descriptor of time used was lunar days and it was classified as a continuous variable.

Some of the catch data from the paired sites were excluded. A description of the criteria for exclusion follows. In the event that both sites in a pair had zero catch at the same time the data were excluded because it would make the data appear artificially similar. In this case, the zero difference was often an artefact caused by the timing of the migration; it was either too early for the fish to be there or too late. Thus, the zero difference between the two site types was not a reflection on the effect of site type, and it would have been misleading to leave the data in.

Table 2-3 A list of the site pairs used in the analysis of site type

Pair Number	Zone	Shore Site	Open Site
1	1	Kilbella Bay	Head
2	2	Rutherford Point	Scandinavia Bay
3	3	Dawson's Shore	Dawson's Open
4	4	Bosquet Pt. Shore	Bosquet Pt. Open
5	4	Dimsey Pt. Shore	Dimsey Pt. Open

2.6.5 Body Size

Body Size Correction Factor

Ethanol causes tissues to lose water. This causes bodies to "shrink" in both length and weight. To measure the degree of shrinkage from storage in ethanol, a small number (n=59) of juvenile sockeye salmon were frozen after collection (rather than placed in ethanol directly) and later thawed and wet weight (g) and fork length (mm) measurements were performed. With the initial weight and length measurements established, the fish were stored in ethanol and measurements of wet weight and fork length were repeated daily. After an initial reduction in body size over the first two days, the measurements stabilized and were virtually constant from three to six days post ethanol exposure. Shrinkage in length was considerably less than the loss of weight.

Post-ethanol weight was plotted against initial weight for each individual fish and a linear regression was fitted to find the mean change. The same was done for the fork length data. To assess whether a linear function adequately described the relationship, the residuals were plotted against initial length. The balanced distribution of the residuals indicated that a more complex regression analysis was not required. The linear regression equations were then applied as correction factors to the entire juvenile sockeye salmon body size dataset.

The weights and fork lengths were corrected for shrinkage using the functions:

$$\text{estimated initial weight (g)} = (\text{weight (g) after ethanol} \times 1.5203) + 0.1254$$

and

$$\text{estimated initial fork length (mm)} = (\text{fork length (mm) after ethanol} \times 1.022) + 0.5556$$

Mean fish weight and fork length for each particular set was calculated. The mean values were used in data summaries and analysis.

Statistical Analysis

A general linear model was used to test for significant effects of factors such as sampling year. Model structure was as follows:

Mean fork length (mm) = *year* + *zone* + *lunarweek* + *error*

Multiple comparison procedures (Tukey's MCP) were used to investigate the source of any significant effects found.

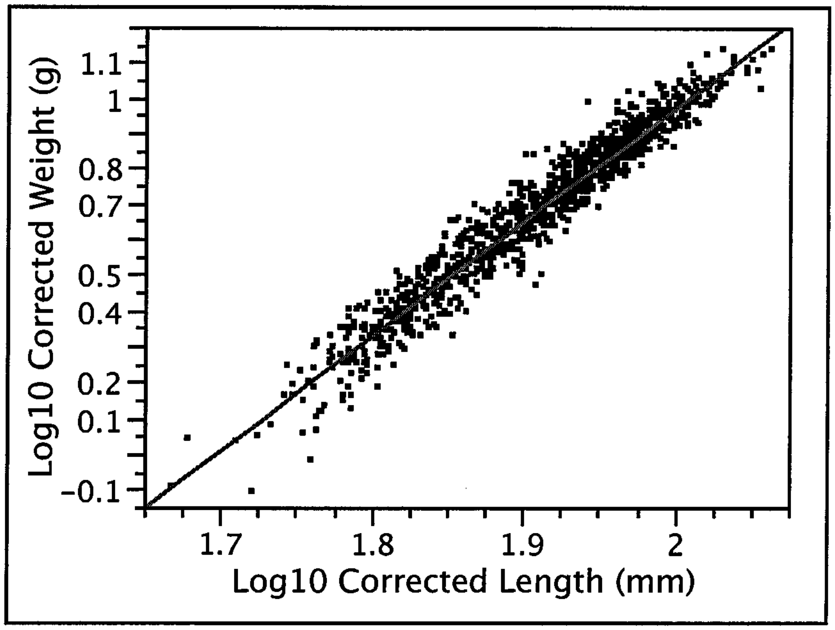
In addition, in order to obtain a robust analysis of the small dataset, the model was run again with fewer time categories. The model was simplified by converting the many categories of *lunar week* into 3 categories: 1: Early, 2: Middle, 3: Late. The categories were defined as follows:

Lunar Weeks ≤ -2 : "Early"
Lunar Weeks $-1 \leq x \leq 3$: "Middle"
Lunar Weeks ≥ 4 : "Late"

2.6.6 Body Size Condition Analysis-Robustness

Log transformed fork lengths and weights (n=1138, corrected for shrinkage) of the individual fish were plotted against one another and a linear regression was applied (Figure 2-3). The residuals were obtained and analysed with a general linear model as previously described. A fish with a positive residual value was considered to be relatively heavy (more robust) for its length, while a fish with a negative residual value was considered to be relatively slender for its length.

Figure 2-3 **A graph of the relationship between log transformed corrected fork length and log transformed corrected body weight with the regression line ($r^2 = 0.945$).**



2.6.7 Plankton Data Analysis

Zooplankton sampling sites were organised into the same four inlet zones as described for the juvenile salmon catch data. The mean total wet weight of zooplankton by zone was then calculated.

3 RESULTS

3.1 Sockeye Catch Data

3.1.1 Summary

The abundance of juvenile sockeye salmon varied over time (year-to-year and over the time course of the migration) and space (by distance down the inlet). The total catch and its distribution down the inlet varied considerably between years. By contrast, the timing was less variable. The first juvenile sockeye were caught in Rivers Inlet at the first new moon in May. Juvenile sockeye abundance increased afterwards and was highest between the last full moon in May and the next full moon toward the end of June, having appeared to peak at the new moon in between. The fish appear to have moved out of the inlet by the next new moon in July. Hence, despite annual variation in catch magnitude, the timing was consistent over years.

Note that data files and summaries, along with copies of this thesis, are available in electronic format at http://www.stat.sfu.ca/people/alumni.

3.1.2 Total Annual Catch

The total number of juvenile sockeye salmon encountered varied annually (Table 3-1). The fewest sockeye encounters occurred in 2002, with only 1583 caught during the entire season. The highest total catch occurred in 2003, followed by the 2004 and 2005 seasons.

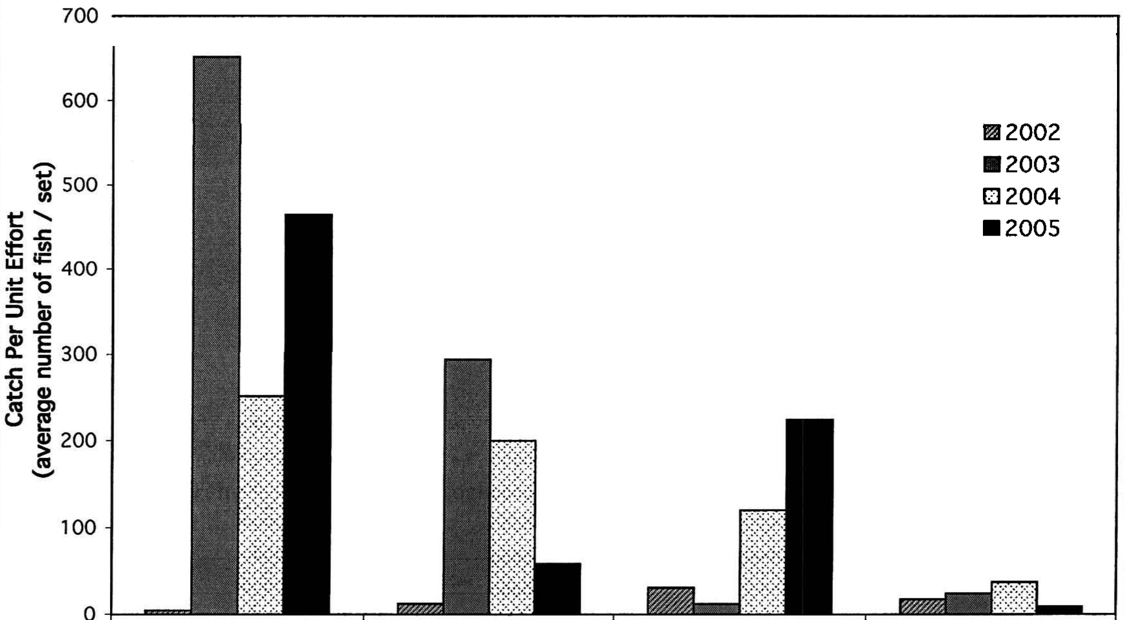
Table 3-1 Total number of juvenile sockeye salmon caught in Rivers Inlet by sampling year

Sampling Year	Total Catch of Juvenile Sockeye	Total Number of Sets Peformed	Overall Catch Per Unit Effort
2002	1583	90	18
2003	13015	72	181
2004	7990	64	125
2005	9109	65	140

3.1.3 Catch by Zone

The overall trend is that the catch of juvenile sockeye salmon was highest near the head of the inlet (*Zones 1 and 2*) and the catch generally decreased with distance down the inlet (Figure 3-1).

Figure 3-1 Differences in the juvenile sockeye salmon catch in Rivers Inlet by zone. Catch per unit effort in each zone, by year.

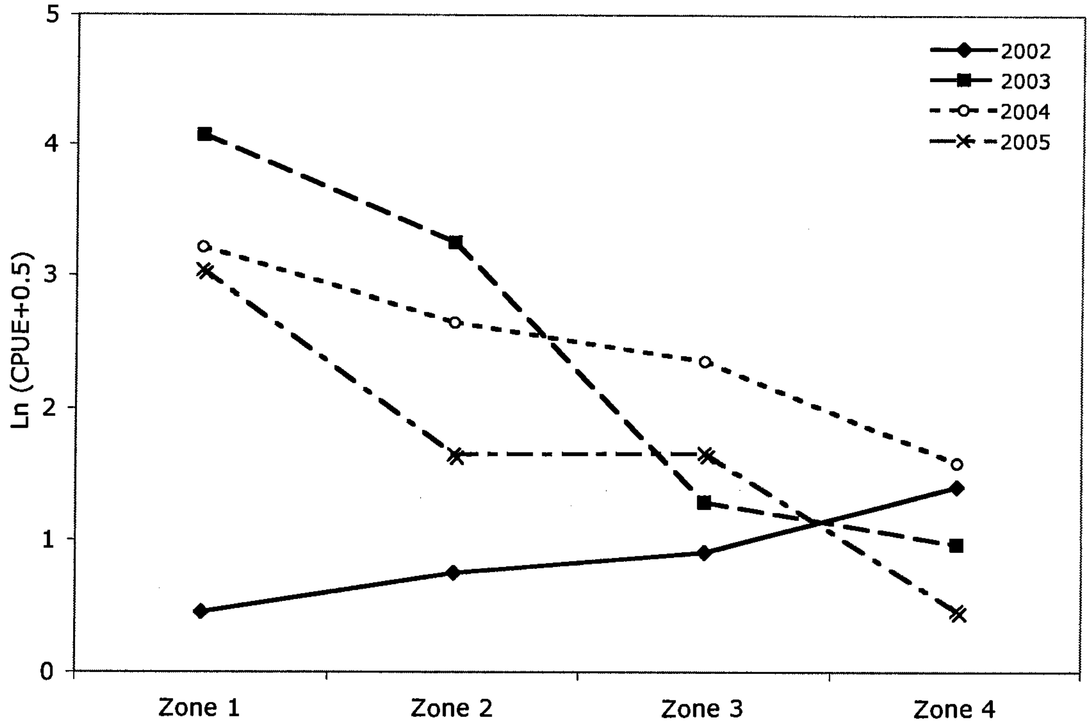


	Zone 1	Zone 2	Zone 3	Zone 4
▨2002	4	12	30	17
■2003	652	294	12	24
⊡2004	252	200	120	37
■2005	465	58	224	9

3.1.4 Year-Zone Interaction Pattern

In contrast to other years, the 2002 data show that juvenile sockeye catch was highest in zones further down the inlet (*Zones 3 and 4*). This pattern of abundance was unique to this year, while other sampling years showed the opposite trend. The number of juvenile sockeye salmon caught in each zone, year-to-year, on a log scale, is portrayed in Figure 3-2.

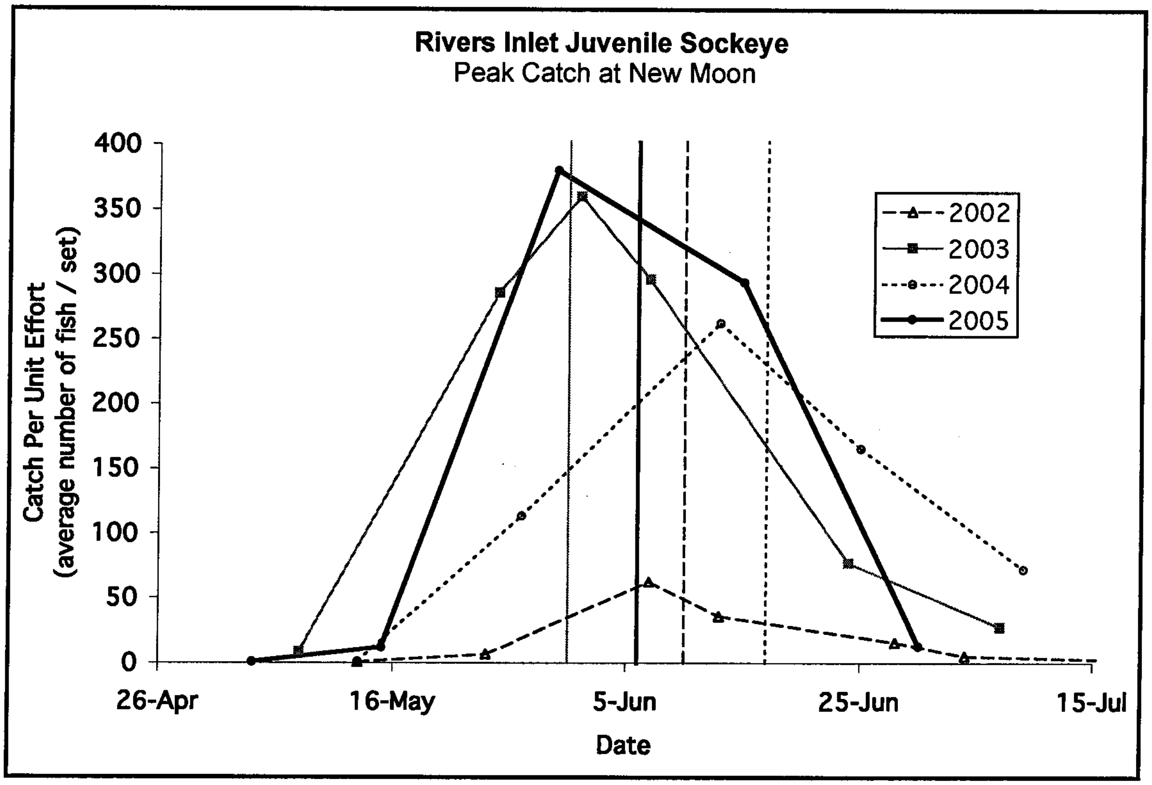
Figure 3-2 **Catch per unit effort of juvenile sockeye salmon per zone, by year, in Rivers Inlet. Values are log-transformed.**



3.1.5 Total Catch Over Time

The catch data for juvenile sockeye salmon show that the fish were not present in significant numbers before mid-May. There was a general trend of increasing catch numbers until approximately the first week in June, after which the catch dropped off. The fish were not present in significant numbers after the end of June. Some variability in this general pattern was present, as expected. Figure 3-3 illustrates the annual variation that existed in the overall timing of the migration by calendar date. It was earlier in 2003, later in 2004, while the 2002 and 2005 seasons appear to have been intermediate. There appears to be evidence of a link between the timing of the migration and the lunar cycle; the annual variation in the timing of the new moon matched that of the variation in the migration timing (Figure 3-3).

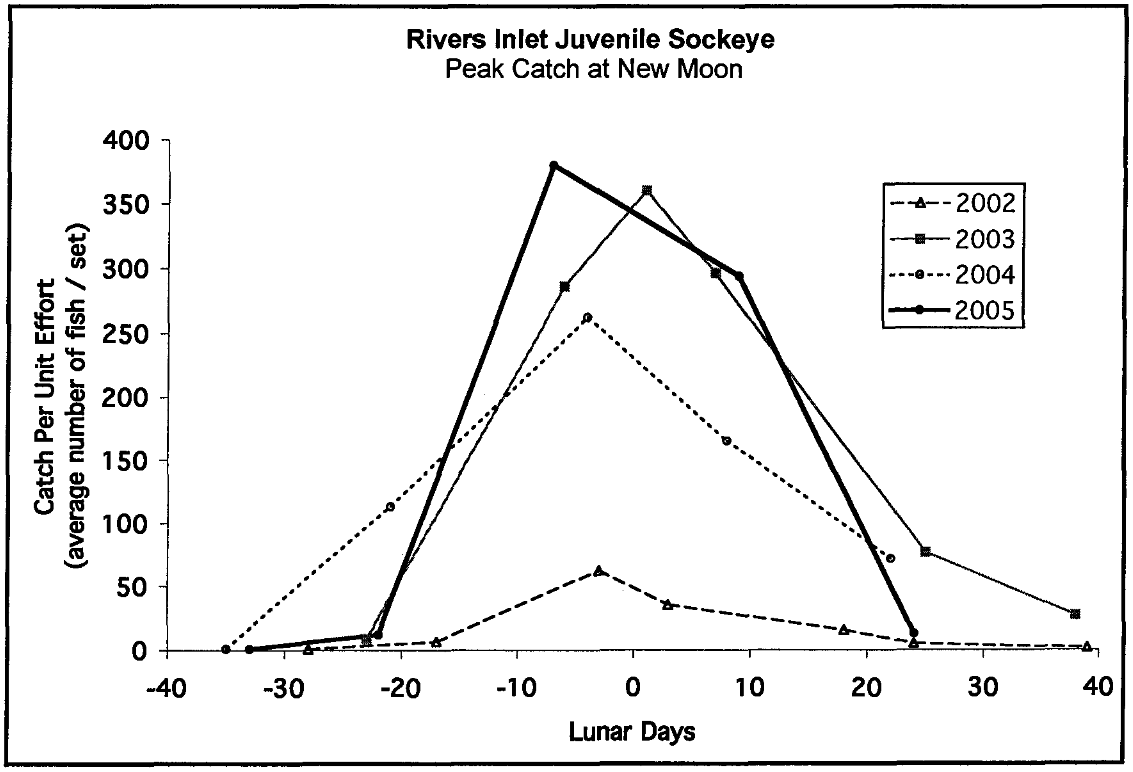
Figure 3-3 Catch per unit effort of juvenile sockeye salmon, by sampling date. The timing and total number of juvenile sockeye salmon encountered in Rivers Inlet in all sampling years. Vertical lines represent the date of the new moon in a particular sampling year



3.1.6 Influence of the Lunar Cycle

To further illustrate the connection between the timing of the sockeye salmon migration and the lunar state, the total catch of juvenile sockeye is plotted against lunar day, instead of calendar date (Figure 3-4). With this approach, the apparent year-to-year variability in migration timing disappears. The migration began at the time of the last full moon in May. Then the catch of juvenile sockeye salmon increased to a maximum near the new moon in mid June, and the migration was virtually complete by the next full moon in late June-early July. Thus, there is evidence of an important connection between the lunar calendar and the seaward migration of Rivers Inlet juvenile sockeye salmon.

Figure 3-4 **Catch per unit effort of juvenile sockeye salmon, by lunar day. The catch data for juvenile sockeye plotted in days relative to the key new moon (day zero) at the end of May-beginning of June in each year. When time is standardized in this way, the close relationship between the moon cycle and the juvenile sockeye migration is clear. The run takes a whole moon cycle to complete; it begins and ends with a full moon and the peak of migration occurs near the new moon.**



3.2 Statistical Analyses

3.2.1 Model A (2002-2005 Inclusive)

The selected model included factors for *year, lunar week, zone,* and a *year*zone* interaction. All four factors had a statistically significant effect on the number of juvenile sockeye salmon caught in Rivers Inlet (Table 3-2).

Table 3-2 Effects tests from model A (2002-2005 inclusive).

Source	Degrees of Freedom	Sum of Squares	*F*-Ratio	*p*-value
Year	3	62.34	5.18	0.0018
Zone	3	77.16	6.41	0.0003
Lunar Week	10	311.24	7.75	<.0001
Year*Zone	9	88.60	2.45	0.0109

Multiple comparison procedures (Tukey's) were employed to locate and describe the pattern of significance. The results are as follows:

Year Effect

Multiple comparison procedures indicated that the catch of juvenile sockeye salmon was significantly smaller in 2002 than in all other years, while there was no significant difference in the catch between the latter three years (Table 3-3).

Table 3-3 **Least Squares Means (LSM's) estimates by year from model A, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different (*p*≤0.05).**

Year	Least Squares Mean	Standard Error	Mean	Tukey's MCP
2002	-2.05	0.80	0.80	A
2003	0.63	0.76	1.98	B
2004	1.05	0.78	2.25	B
2005	1.10	0.73	1.41	B

Zone Effect

Multiple comparison procedures confirm that the catch did decrease with distance down the inlet (Table 3-4). The catch in *Zone 4* was significantly lower than that of *Zone 1* and *Zone 2*, while *Zone 3* did not differ from any other zone.

Table 3-4 **Least Squares Means (LSM's) estimates by zone from model A, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different (*p*≤0.05).**

Zone	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	0.18	0.52	2.42	A
2	-0.27	0.49	2.18	A
3	-0.78	0.48	1.48	AB
4	-1.29	0.46	1.02	B

Effect of Lunar Week

The multiple comparison procedures did not provide a clear picture of the effect of lunar week on the catch of juvenile sockeye salmon. A weak curvilinear relationship appears to exist in the Least Squares Means estimates from the general linear model with the highest catch predicted between *week 0* (new moon) and *week 4/5*. In contrast, the multiple comparison procedures only provided evidence of increased catch after *week –5* (Table 3-5). Closer examination reveals that the standard errors associated with the least squares means estimates are large relative to the means themselves. This is an indication that a large amount of variability exists within the catch data that is limiting the statistical investigations.

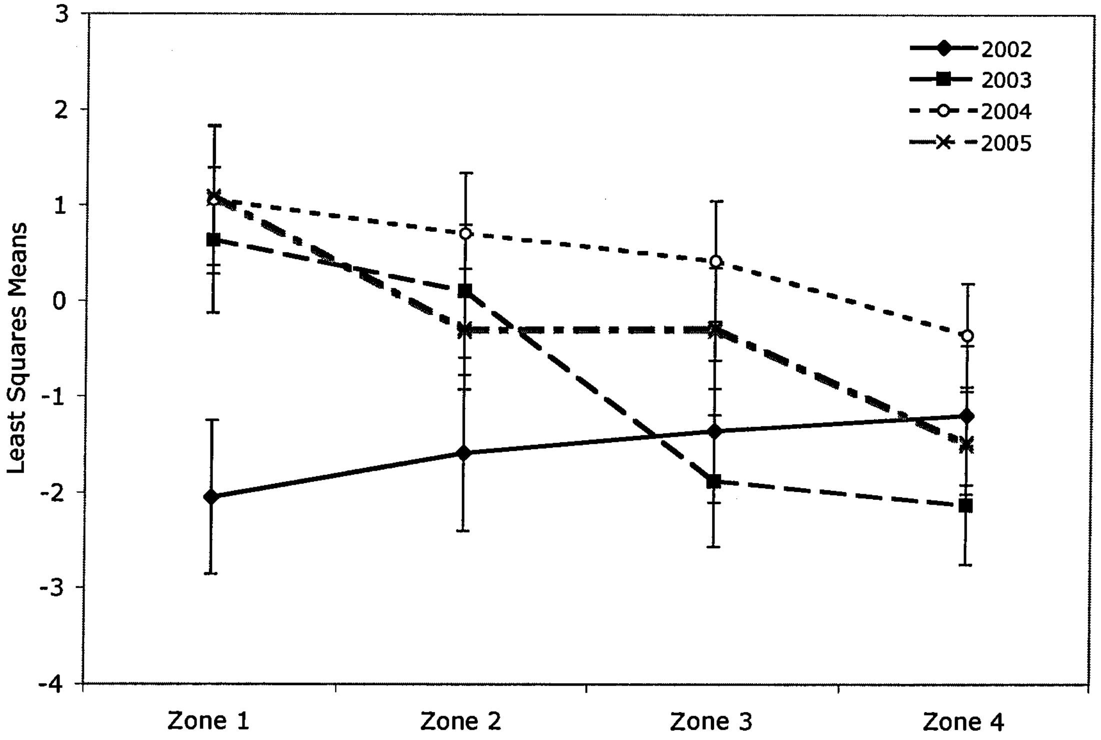
Table 3-5 **Least Squares Means (LSM's) estimates by lunar week from model A, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).**

Lunar Week	Least Squares Mean	Standard Error	Mean	Tukey's MCP
-5	0.18	0.52	-0.17	C
-4	1.22	1.00	-0.47	ABC
-3	1.37	0.45	0.75	BC
-2	1.98	0.92	0.20	ABC
-1	2.85	0.44	2.20	AB
0	3.52	0.49	2.01	A
1	3.81	0.44	3.17	A
3	2.43	0.42	1.50	AB
4	4.71	0.68	3.40	A
5	3.08	0.70	1.83	AB
6	1.61	0.75	-0.03	ABC

Year*Zone Interaction

The Least Squares Means estimates suggested that the zone-to-zone pattern of catch in the 2002 catch data was different from that of other years (Figure 3-5). Yet, in contrast, Tukey's multiple comparison procedures showed no significant difference between the catch by zone in 2002 vs. the catch by zone in any other year. Sporadic significance differences were found between zone and year combinations but were without a discernable pattern. Since the zooplankton surveys showed substantially lower abundance in the upper inlet in 2002 vs. the other years, we performed a preplanned test of the hypothesis that the only interactions were between 2002 and the other years, with no interactions amongst the years, 2003-5. We performed this test by fitting a restricted model in JMP and performing an *F*-test for significance of the increase in the error sum of squares. We found no significant interactions within the years, 2003-5 ($p = 0.37$).

Figure 3-5 Least Squares Means Estimates by year and zone from Model A. Error bars are +/- 1 standard error.



3.2.2 Model B (2003-2005)

Similar to the results from *Model A*, the model detected a significant effect of the *year, zone,* and *lunar week* on the catch of juvenile sockeye salmon, (Table 3-6). In contrast, *Model B* found no evidence of a *year*zone* interaction. In addition, a new significant interaction was detected between the lunar week (*weeks of the new moon)* and the *Zone*.

Table 3-6 Effects tests from Model B (2003-2005).

Source	Degrees of Freedom	Sum of Squares	*F*-Ratio	*p*-value
Lunar Week	7	83.43	3.03	0.0050
Zone	3	112.46	9.54	<.0001
Year	2	41.17	5.24	0.0062
Lunar Week*Zone	21	160.23	1.94	0.0112

Multiple comparison procedures (Tukey's) were employed to locate and describe the pattern of significance. The results are as follows:

Year Effect

Model B revealed a previously undetected significant difference in the total catch between the years 2003 and 2004, with the magnitude of the catch higher in 2004 than 2003, while 2005 did not differ substantially from either year (Table 3-7).

Table 3-7 **Least Squares Means (LSM's) estimates by year from model B, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).**

Year	Least Squares Mean	Standard Error	Mean	Tukey's MCP
2004	1.74	0.58	2.25	B
2005	0.92	0.58	1.41	AB
2003	0.45	0.69	1.98	A

Zone Effect

The results of *Model B* are in agreement with *Model A*, but with lower error in the Least Squares Means estimates and a more finely scaled pattern of significant differences between the zones (Table 3-8). The catch in Zone 4 is significantly lower than that of Zone 1 and Zone 2, while Zone 3 is significantly lower than Zone 1.

Table 3-8 **Least Squares Means (LSM's) estimates by zone from model B, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).**

Zone	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	3.46	0.40	3.34	A
2	2.77	0.33	2.55	AB
3	1.80	0.34	1.71	BC
4	1.22	0.26	1.01	C

Effect of Lunar Week

Similar to the results from *Model A*, the multiple comparison procedures did not provide a clear picture of the effect of lunar week on the catch of juvenile sockeye salmon. A curvilinear relationship appears to exist in the Least Squares Means estimates from the model with the highest catch predicted at *week 0* (new moon) (Table 3-9). Yet, just as in *Model A*, the multiple comparison procedures do not provide support for this pattern. There is statistical evidence only of an increase in the catch of juvenile sockeye salmon between *week –5* and *week 0/week -1*.

Table 3-9 Least Squares Means (LSM's) estimates by lunar week from model B, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

Lunar Week	Least Squares Mean	Standard Error	Mean	Tukey's MCP
-5	-0.06	1.15	-0.17	B
-3	2.87	0.81	0.75	AB
-1	4.80	0.81	2.20	A
0	6.97	1.43	2.01	A
1	3.68	0.81	3.17	AB
3	2.31	1.00	2.25	AB
4	4.87	1.43	3.40	AB
5	2.23	1.43	1.83	AB

Lunar Week*Zone Interaction

Sporadic significance between lunar week and zone combinations were found but were without a discernable pattern. For example, the catch of juvenile sockeye salmon was significantly lower in *week -5, zone 4* than in *week 3, zone 4, week 0, zone 3, week -1, zone 1*, or *week 4, zone 4*, amongst others. This is not surprising since the migration of juvenile sockeye salmon had barely begun at *week –5*, so the probability of finding juvenile sockeye all the way at the mouth of Rivers Inlet (*Zone 4*) at this time is small.

3.2.3 Moon Phase Quadratic Regression

Lunar Day

There was a significant effect of *year, lunar day,* and *lunar day*^{2} on the mean total catch of juvenile sockeye salmon, while the *year*lunar day* interaction was not significant (Table 3-10). The significant quadratic term confirms that the abundance rises to a peak and drops off. The slope coefficient is significantly different from zero, while the interaction is not. Therefore, we could estimate a constant timing of the peak relative to the new moon in every year at 5.11 days after the new moon.

Table 3-10 Effects tests from the quadratic regression with lunar day as the measure of time.

Source	Degrees of Freedom	Sum of Squares	*F*-Ratio	*p*-value
Year	3	20.09	11.52	0.0004
Lunar Day	1	11.17	19.22	0.0006
Lunar Day^2	1	40.94	70.40	<.0001
Year* Lunar Day	3	3.22	1.85	0.1850

Calendar Day

There was a significant effect of *year, calendar day, calendar day*^{2}, and *year*calendar day* on the mean total catch of juvenile sockeye salmon (Table 3-11). The finding of a significant interaction term with calendar day but not lunar day confirms the visual impression in Figures 3-3 and 3-4 that the timing of the juvenile sockeye salmon migration is driven by the lunar day rather than the calendar day.

Table 3-11 Effects tests from the quadratic regression with calendar day as the measure of time.

Source	Degrees of Freedom	Sum of Squares	F Ratio	p value
Year	3	22.75	13.04	0.0002
Calendar Day	1	42.92	73.82	<.0001
Calendar Day^2	1	40.94	70.40	<.0001
Year*Calendar Day	3	8.69	4.98	0.0148

3.2.4 Site Type

The results of the statistical model indicated that later in the year, juvenile sockeye are caught more offshore. A slope of -0.1 and overall difference of 4, both on a log scale, was found from day -35 to day 40 of the new moon. A significant "days of the new moon-zone" interaction was also found with a similar trend, although with some inter-annual variation in the strength of this relationship.

3.3 Sockeye Body Size

3.3.1 Overview

The juvenile sockeye encountered in Rivers Inlet were relatively small. Fork lengths ranged from 47 to 115 mm and weights ranged from 0.8 to 16 grams. The length-weight relationship is displayed in Figure 3-6. The relationship is most strongly defined for fish between 60 and 100 mm in length because of the small number of observations of fish outside this range. The variation in weight at a particular fork length increases with size.

Figure 3-6 **The size distribution of the juvenile sockeye encountered in Rivers Inlet, all years combined. Each point represents a single fish.**

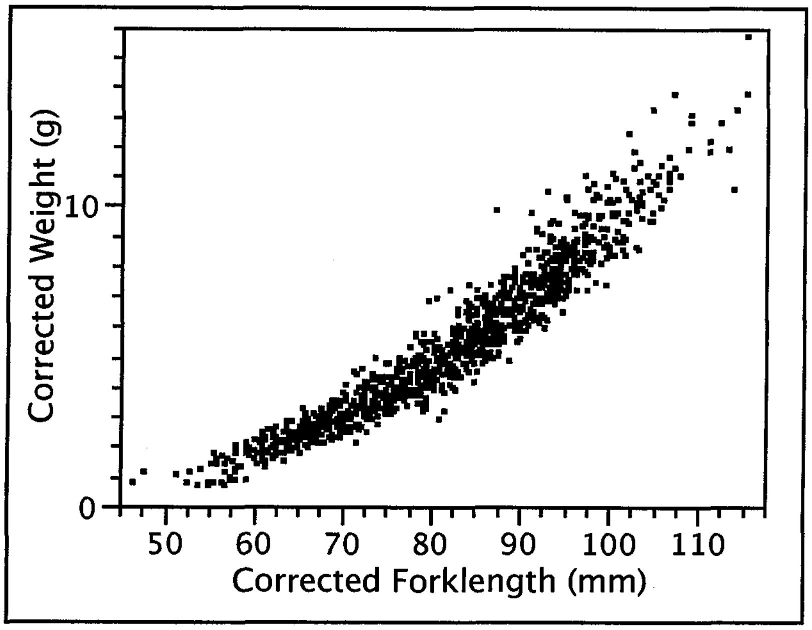


Table 3-12 **The size ranges of juvenile sockeye salmon encountered in Rivers Inlet, by year**

Year	2002	2003	2004	2005
Fork Length (mm)	46.6-109	53.7-115.4	55.3-113.8	47.6-100.9
Weight (g)	0.8-12.8	0.7-15.7	1.5-13.2	0.8-8.8

3.3.2 Raw Data

Year Effect

The mean weight of juvenile sockeye salmon encountered was higher than the historically reported weight of 2 grams at ocean entry (Foskett, 1958) in all years (Figure 3-7). Weights were similar in 2002, 2003, and 2004, but much lower in 2005. The fork length data showed a similar trend (Figure 3-8).

Figure 3-7 Wet weight (g) of the juvenile sockeye salmon in Rivers Inlet, by year. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.

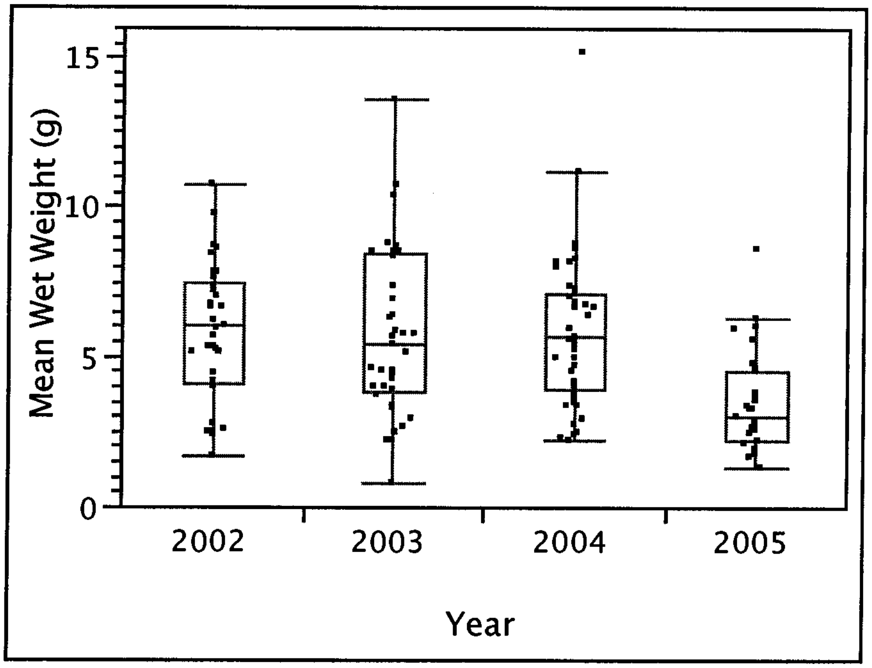
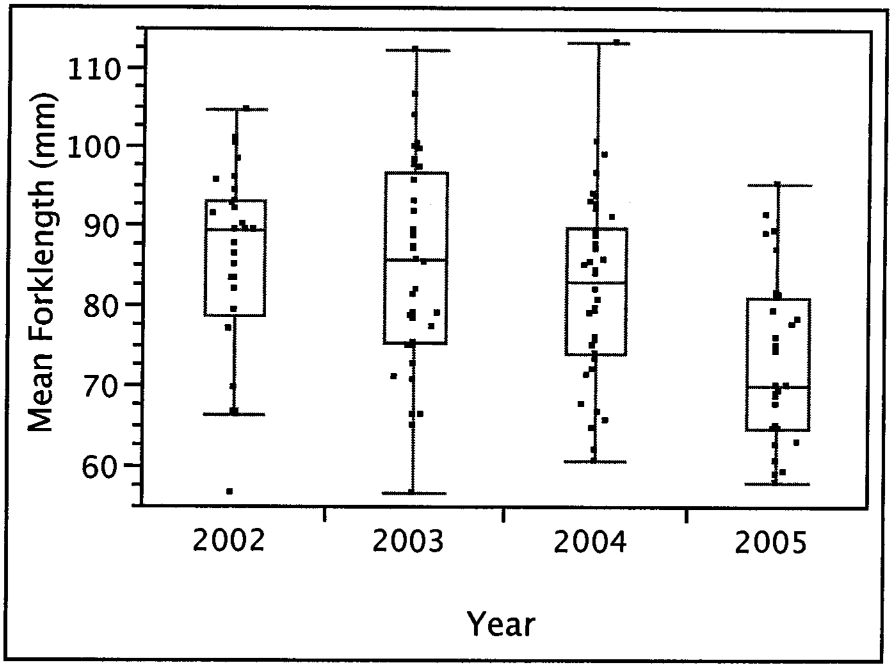


Figure 3-8 Fork length of the juvenile sockeye salmon in Rivers Inlet, by year. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.



Zone Effect

In every year sampled, the mean weight of sockeye caught increased with distance down the inlet, with an approximate doubling in the mean weight over the course of the migration down the length of the inlet (Figure 3-9). Fork lengths showed a similar pattern, with an approximate increase of 25 mm from between *Zone 1* and *Zone 4* (Figure 3-10).

Figure 3-9 Wet weight (g) of the juvenile sockeye salmon in Rivers Inlet, by zone. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.

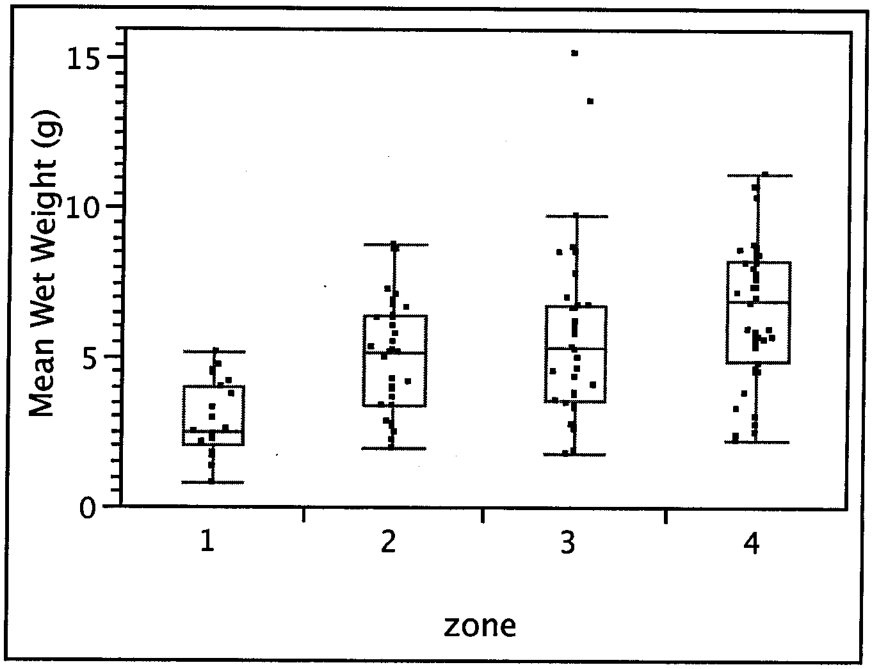
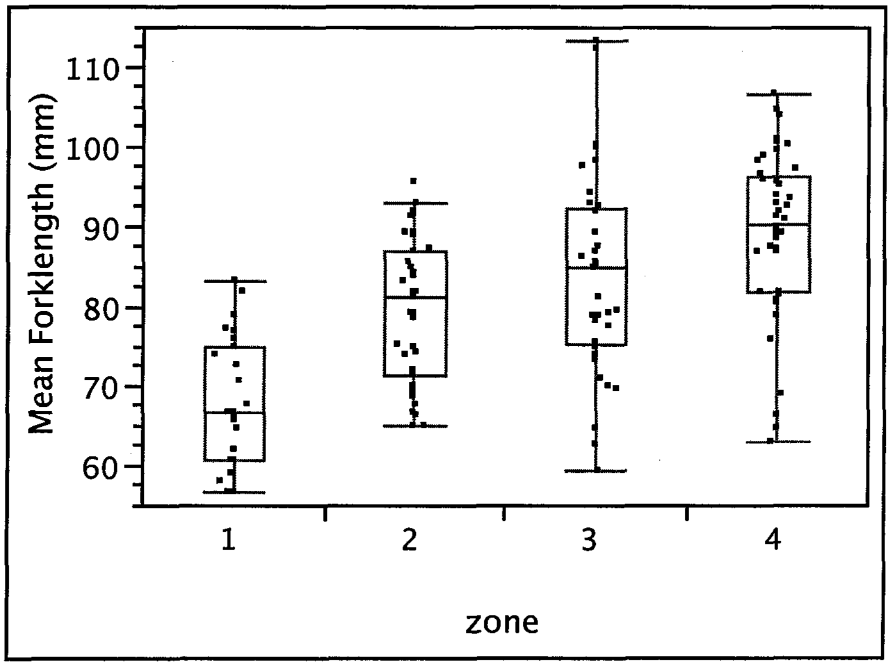


Figure 3-10 **Fork length of the juvenile sockeye salmon in Rivers Inlet, by zone. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.**



Effect of Lunar Week

The mean size of the juvenile sockeye salmon appears to be highest in the middle portion of the migration, with the smallest fish caught at the beginning and end of the run (Figure 3-11) and (Figure 3-12).

Figure 3-11 Wet weight (g) of the juvenile sockeye salmon in Rivers Inlet, by *Lunar Week*. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.

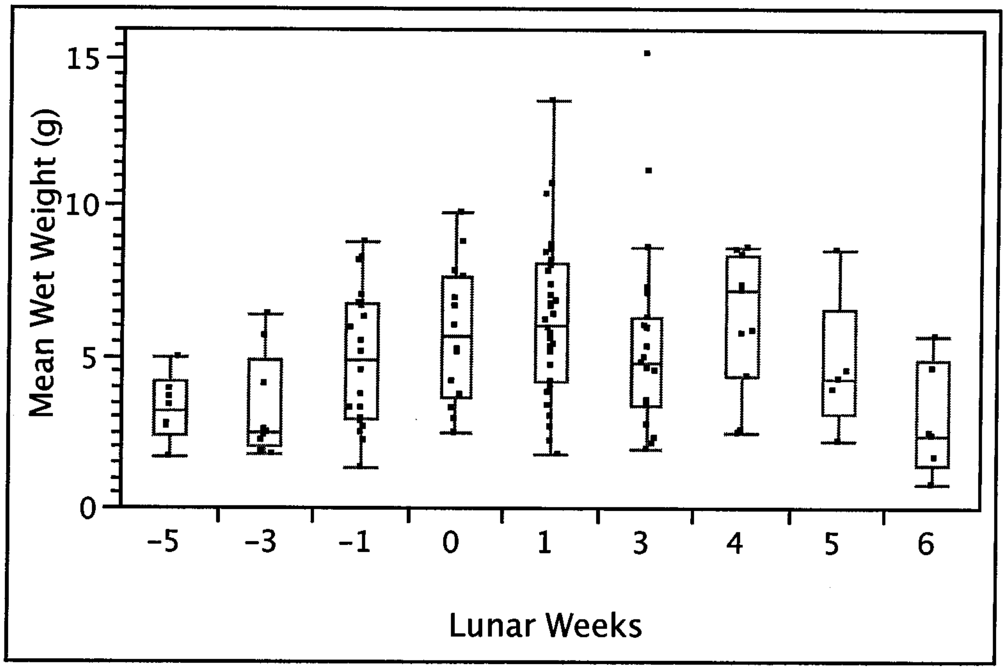
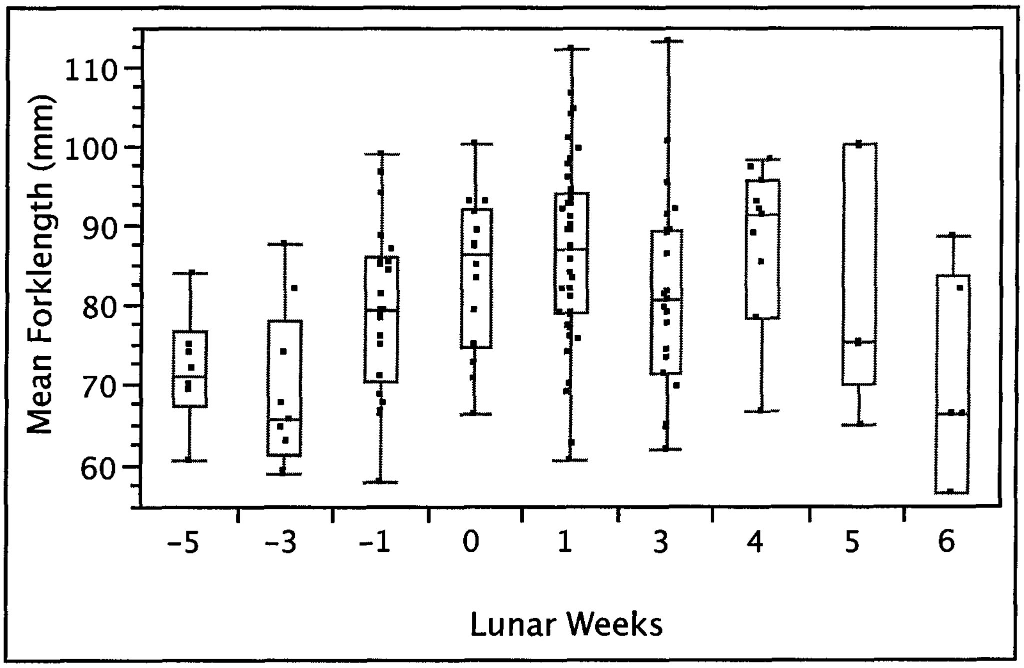


Figure 3-12 **Fork length of the juvenile sockeye salmon in Rivers Inlet, by *Lunar Week*. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.**



3.3.3 Statistical Analysis

The model included factors for *year, zone,* and *lunar week.* All three factors had a statistically significant effect on the mean weight and mean fork length of juvenile sockeye salmon caught in Rivers Inlet (Table 3-13) and (Table 3-14).

Table 3-13 **Effects tests from the general linear model analysis of mean wet weight.**

Source	Degrees of Freedom	Sum of Squares	F-Ratio	p-value
Year	3	94.33	7.87	<.0001
Zone	3	170.10	14.19	<.0001
Lunar Week	8	95.50	2.99	0.0043

Table 3-14 Effects tests from the general linear model analysis of mean fork length.

Source	Degrees of Freedom	Sum of Squares	*F*-Ratio	*p*-value
Year	3	1923.35	8.28	<.0001
Zone	3	5508.88	23.70	<.0001
Lunar Week	8	2607.30	4.21	0.0002

Multiple comparison procedures (Tukey's) were employed to locate and describe the source of significance. The results for the wet weight and fork length were nearly identical, the only exception being that the lower variability in the fork length data meant that a clearer pattern emerged. For simplicity, the results from the analysis of fork length will be shown. The results are as follows:

Year Effect

The fork length of the juvenile sockeye salmon was significantly lower in 2005 than all other years, with no difference between the other years (Table 3-15).

Table 3-15 Least Squares Means (LSM's) estimates by year from the general linear model analysis of fork length, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

Year	Least Squares Mean	Standard Error	Mean	Tukey's MCP
2002	70.99	4.70	85.45	A
2003	72.22	4.65	85.02	A
2004	66.93	4.00	82.06	A
2005	59.07	4.08	73.40	B

Zone Effect

The juvenile sockeye salmon were significantly larger in *Zone 4* than any other zone, and larger in Zones 2 and 3 than in Zone 1 (Table 3-16).

Table 3-16 Least Squares Means (LSM's) estimates by zone from the general linear model analysis of fork length, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

Zone	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	67.30	4.07	67.99	A
2	76.76	3.55	79.44	B
3	80.42	3.89	83.65	B
4	87.08	4.05	88.89	C

Effect of Lunar Week

The size of juvenile sockeye salmon was smaller at the end of the migration, compared to during the peak. The fork length was significantly lower in *Week 6* than *Weeks –1, 0, 1, 3, and 4.* No other differences in fork lengths between other week categories were found.

Coarser Time Category Analysis

The results with respect to effect of *year* and *zone* were identical to the original model. In addition, a different effect of time was found. The fork lengths of the juvenile sockeye salmon were significantly larger in time category 2 (close to the new moon) than in the categories before or afterwards (Table 3-17). However, this effect was not seen in the fish weight data, where evidence of a decline in the last category was the only significant effect of time.

Table 3-17 Least Squares Means (LSM's) estimates by week category from the general linear model analysis of fork length, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

Week Category	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	63.80	2.92	70.51	B
2	70.32	2.01	83.68	A
3	61.36	2.90	81.19	B

3.4 Condition of Fish; Robustness

There was a significant effect of *year, week category*, and *zone* on the robustness of the fish caught. In addition, significant interaction terms were found for *year*zone* and *week category*zone* (Table 3-18).

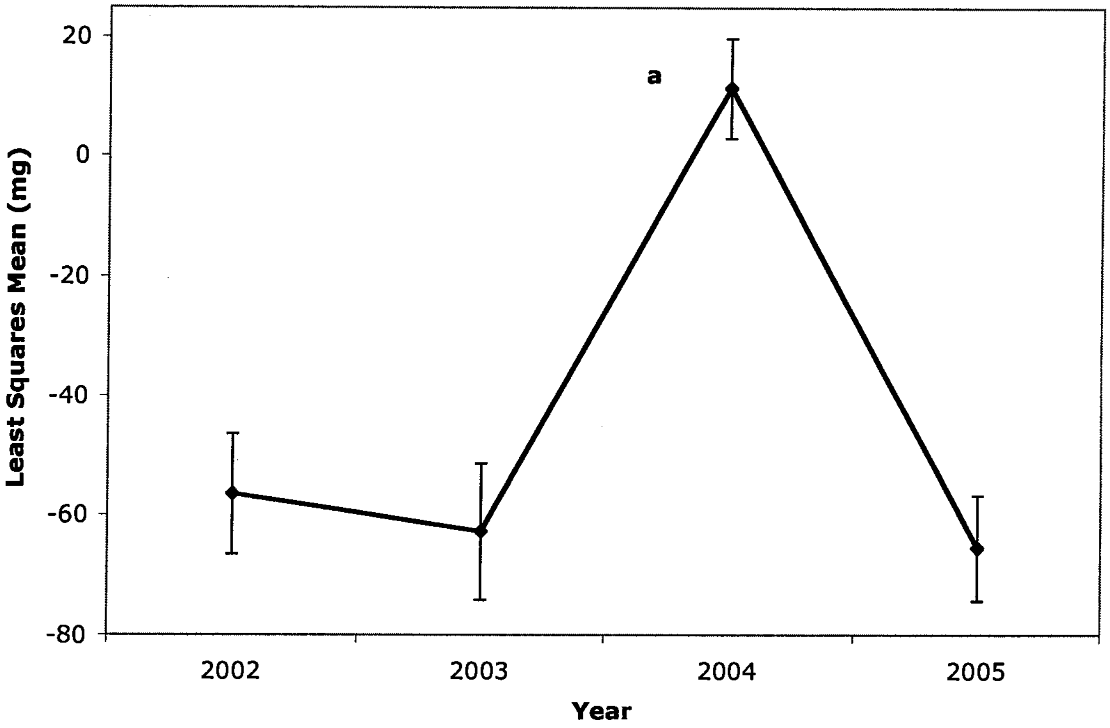
Table 3-18 Effects tests from the general linear model analysis of robustness.

Source	Degrees of Freedom	Sum of Squares	*F*-Ratio	*p*-value
Year	3	0.27	48.11	<.0001
Week category	2	0.06	14.58	<.0001
Zone	3	0.04	6.70	0.0002
Year*Zone	9	0.06	3.49	0.0003
Week category*Zone	6	0.07	5.89	<.0001

Year Effect

The juvenile sockeye salmon were significantly more robust in 2004 than in other years, while no difference was found between 2002, 2003, and 2005 (Figure 3-13).

Figure 3-13 **Least Squares Means (LSM's) estimates by year from the general linear model analysis of robustness. The LSM have been converted into mg from the log scale. The results of multiple comparison procedures (Tukey's MCP) are indicated by the letter "a"; robustness was significantly higher in 2004 ($p \leq 0.05$).**



Zone Effect

The juvenile sockeye salmon caught in zone 3 were significantly more robust than those caught in *Zone 2*, or *Zone 1*, and fish caught in *Zone 2* were significantly more robust than those in *Zone 1* (Table 3-19). Fish from *Zone 4* were not significantly different from those from any of the other zones.

Table 3-19 Least Squares Means (LSM's) estimates by zone from the general linear model analysis of robustness, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

Zone	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	-0.045	0.008	0.004	C
2	-0.017	0.008	0.011	B
3	0.027	0.015	-0.006	A
4	-0.025	0.031	-0.009	ABC

Effect of Lunar Week Category

The juvenile sockeye salmon were significantly more robust in the weeks before the new moon (*category 1*) than later on in the migration (Table 3-20).

Table 3-20 Least Squares Means (LSM's) estimates by week category from the general linear model analysis of robustness, with standard error. The actual mean is reported for comparison. The last column shows the results of multiple comparison procedures (Tukey's MCP); levels not connected by the same letter are significantly different ($p \leq 0.05$).

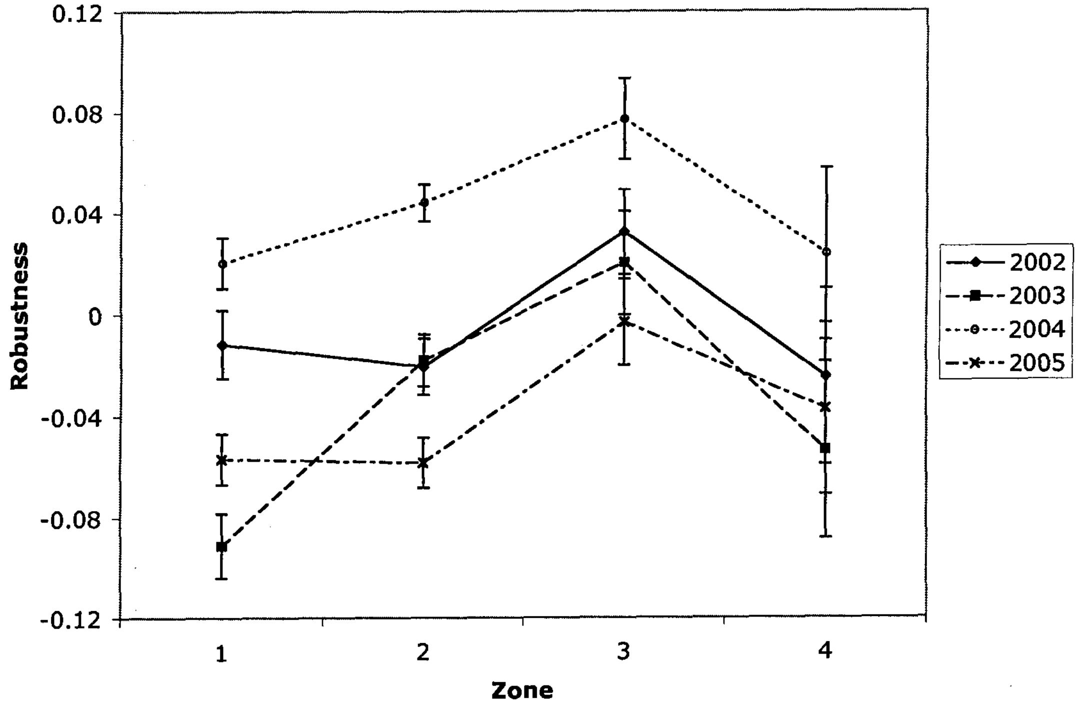
Week Category	Least Squares Mean	Standard Error	Mean	Tukey's MCP
1	-0.045	0.008	0.002	A
2	-0.001	0.004	0.003	B
3	0.007	0.0128	-0.018	B

Year*Zone Interaction

Zone 2: The significant interaction term is due mainly to year-to year differences in the fatness of juvenile sockeye caught in this zone. Results of the multiple comparison procedures indicate that for this zone of the inlet, fish caught in 2004 were significantly more robust than in all other years, and fish caught in 2005 were significantly slimmer than any other years, while fish from 2002 and 2003 were not significantly different, and intermediate to the other two years.

2004: Fish caught in this year were significantly more robust than in any other year. This trend was true for every individual zone.

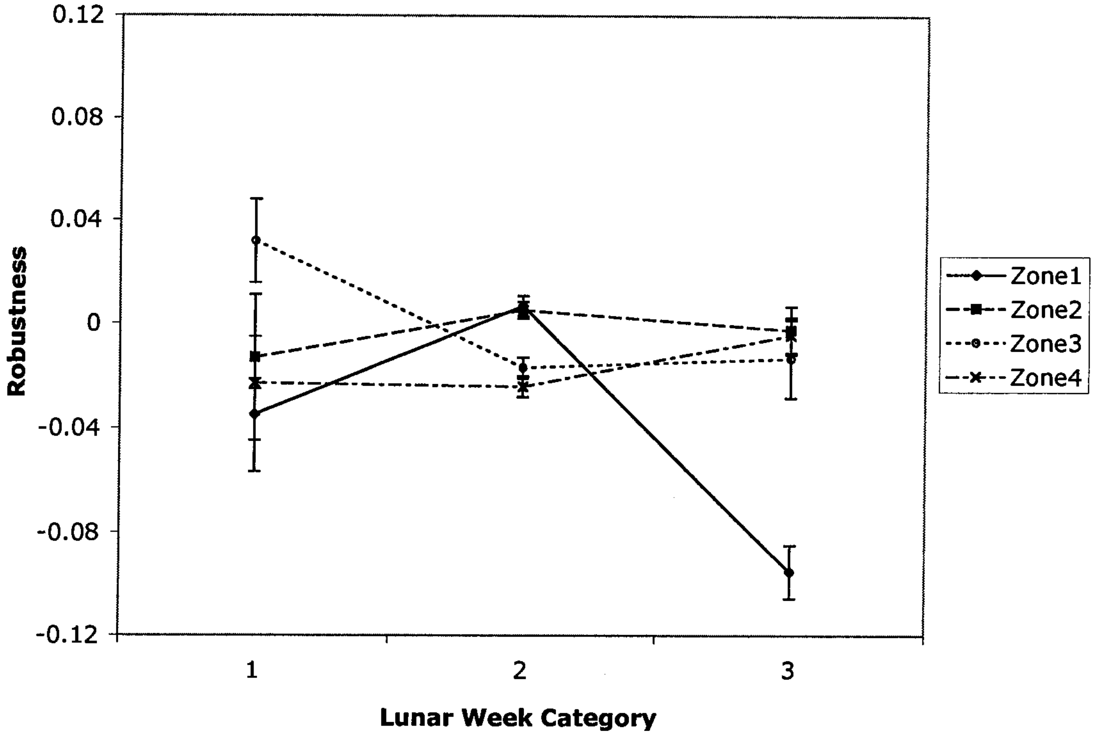
Figure 3-14 Least Squares Means (LSM's) estimates by year and zone from the general linear model analysis of robustness.



Zone*Week Category Interaction

Figure 3-18 shows only minor interaction effects that do not appear to carry much importance.

Figure 3-15 Least Squares Means (LSM's) estimates by week category and zone from the general linear model analysis of robustness.

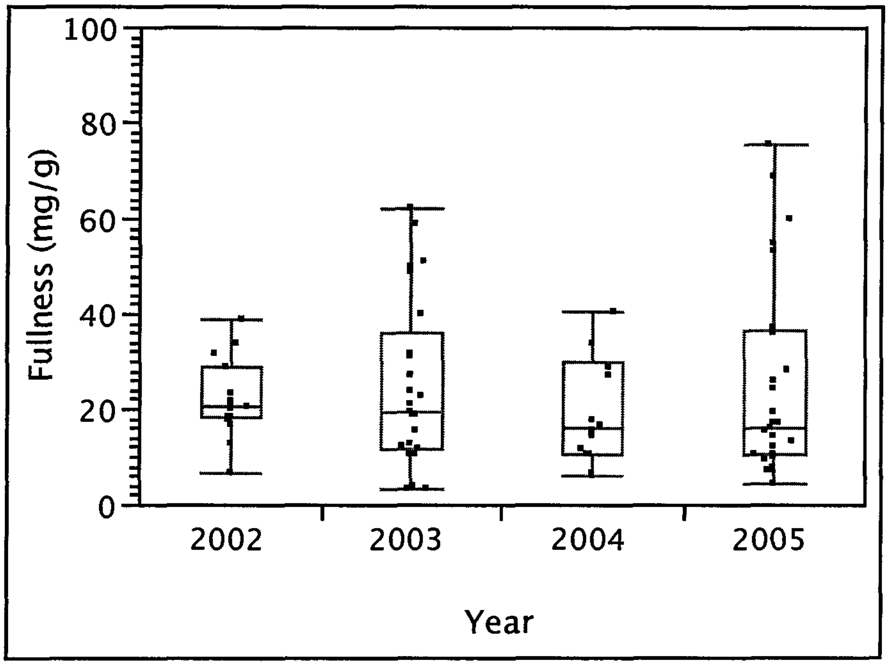


3.5 Sockeye Feeding biology/diet

3.5.1 Stomach Fullness

The distribution of stomach fullness varied considerably. This fact combined with the small data set meant it was not feasible to do any complex analysis. The mean fullness did not appear change from year to year.

Figure 3-16 Mean fullness (mg/g) of the juvenile sockeye salmon in Rivers Inlet, by year. Data points are mean value per set. Boxes encompass the 25th –75th percentiles, whiskers show 10th and 90th percentiles.



3.5.2 Prey Species Composition

The most numerous prey found in the stomachs of juvenile sockeye salmon from Rivers Inlet throughout the entire study period were pelecypods (bivalves), making up nearly half of all prey items (Table 3-21). The majority of prey species were small (Table 3-22).

Table 3-21 **Most numerous prey species of Rivers Inlet juvenile sockeye. Pooled estimate of all fish examined, all years.**

Prey Item	Mean Count	% Total Diet by number	mean size (μ)
1. Pelecypods	56.3	42.2	295
2. Oikopleura	14.4	10.7	411
3. Cypris of barnacle	12.1	9.1	637
4. Evadne	8.4	6.3	531
5. Calanoid copepod (spp.)	7.5	5.7	1121
Total		75%	

Table 3-22 **Rivers Inlet juvenile sockeye. Size distribution of most common prey items.**

Size Range (μ)	mean count	% total diet by number
<300	56.3	42.2
$300 < x \leq 500$	14.1	10.7
$500 < x \leq 1000$	20.5	15.4
> 1000	14.9	10.7

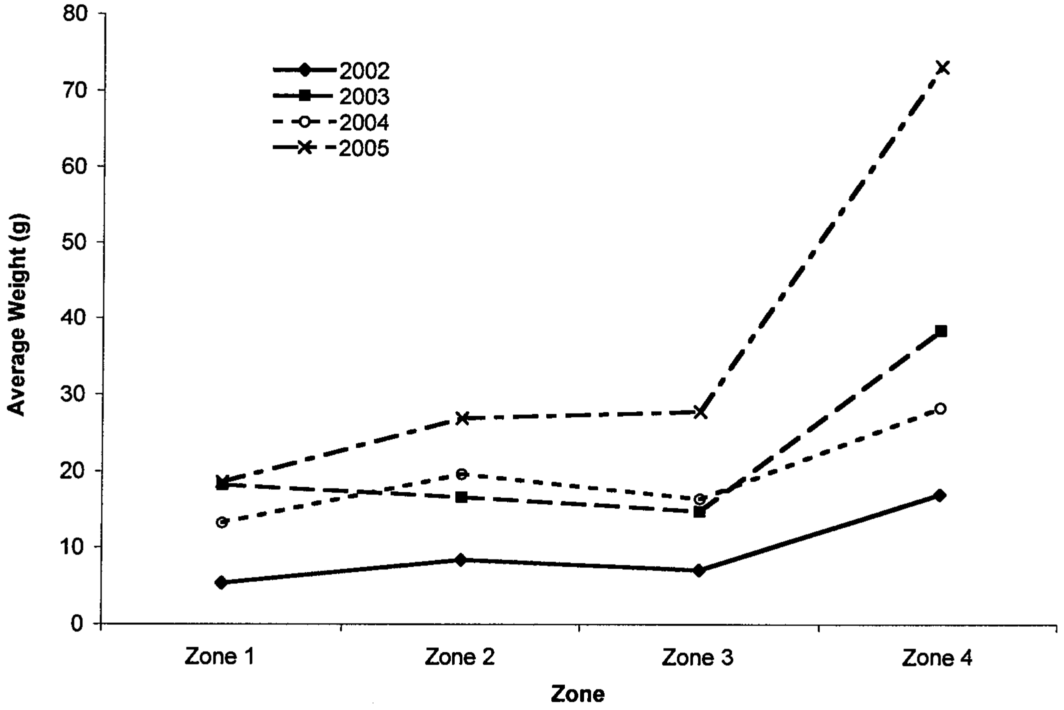
3.6 Zooplankton

3.6.1 Total Wet Weight

Zone Effect

The mean total wet weight of zooplankton is lower in the upper inlet (Zones 1 and 2) than in the outer inlet (Zone 4) (Figure 3-17). The general pattern is one of increasing zooplankton abundance with distance down the inlet. This pattern is consistent from year to year.

Figure 3-17 Mean total wet weight (g) of zooplankton samples from Rivers Inlet, by year and zone.



Annual Differences

The abundance of zooplankton was anomalously low in 2002 in all zones (Figure 3-20).

Of special concern, is plankton abundance in the upper inlet during the time leading up to and at the new moon, as the juvenile sockeye salmon are emerging into this first part of the marine environment at that time. Mean abundances over time for each year are portrayed for zones 1 and 2 in Figures 3-21 and 3-22, respectively. In 2002, plankton was relatively scarce in both zones in this critical phase. In contrast, 2003 had a three-fold higher amount of zooplankton in that period. In 2004, the plankton appeared to peak very early at a high level, whereas the 2005 season shows a rapid increasing trend in zooplankton abundance over this part of the season. The late timing of this increase in zooplankton abundance in 2005 suggests that the more abundant zooplankton levels may have developed too late to be encountered by the migrating juvenile sockeye salmon. This might in turn explain the lack of robustness of this cohort.

Figure 3-18 Mean total wet weight (g) of zooplankton samples from Rivers Inlet in Zone 1, by year.

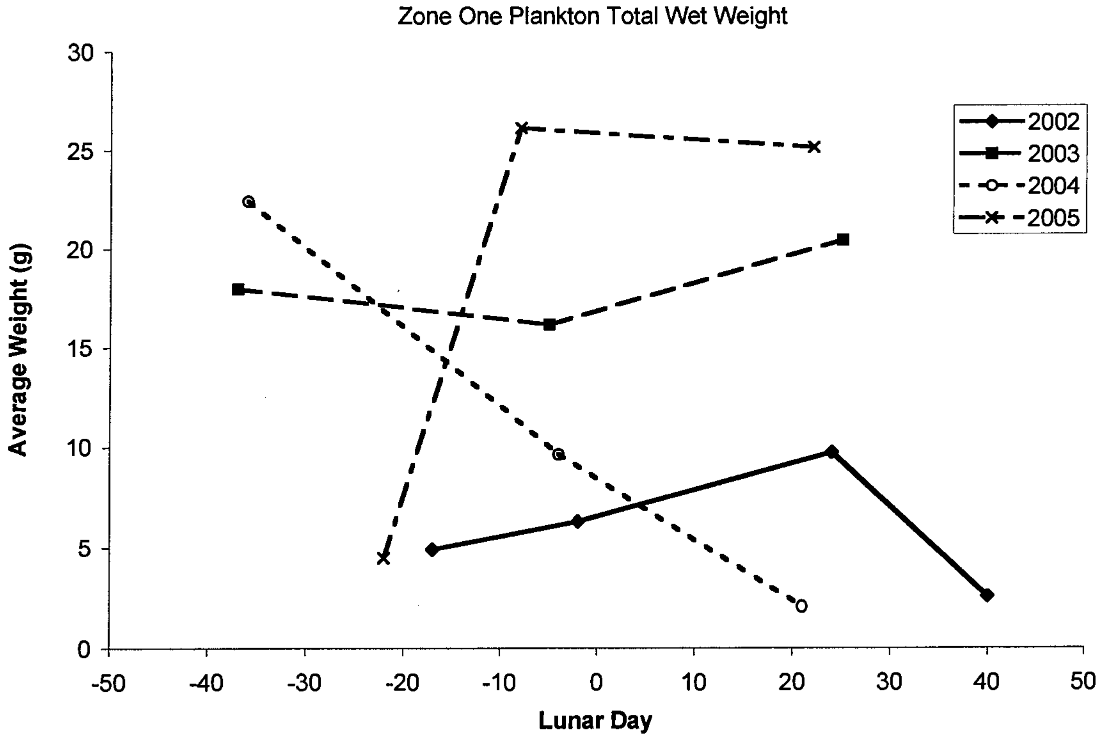
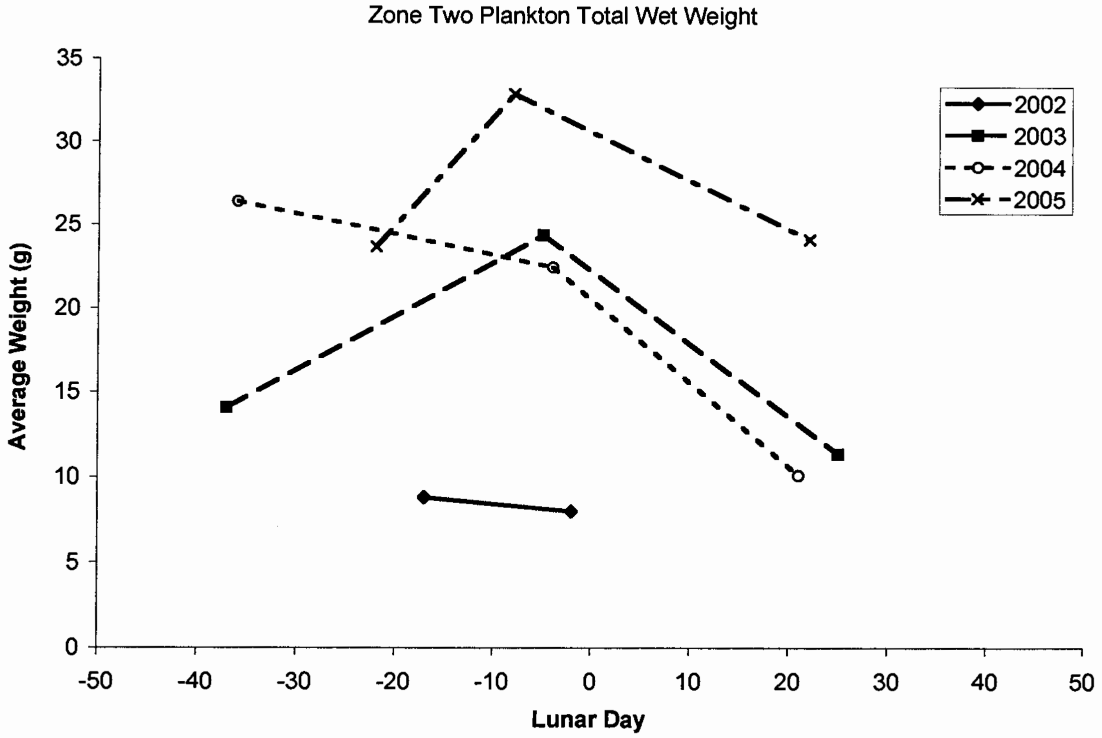


Figure 3-19 Mean total wet weight (g) of zooplankton samples from Rivers Inlet in Zone 2, by year.



3.6.2 Zooplankton Species Composition

In Rivers Inlet, the main prey species that make up the diet of juvenile sockeye are extremely rare in the zooplankton samples. Zooplankton samples contained very few organisms less than 500u in size.

3.7 Encounters of Non-Target Fish

3.7.1 Total Catch of Juvenile Salmon

There was considerable annual variation in the total number of juvenile sockeye encountered (Table 3-23). The 2002 sampling season had the fewest sockeye encounters with only 1583 caught during the entire year. In contrast, the 2003 sampling season showed a nearly ten-fold increase in sockeye encounters. The 2004-2005 seasons had sockeye catches intermediate between these two. With the exception of 2002, sockeye were the most numerous species of juvenile salmon encountered in Rivers Inlet.

Table 3-23 Total number of juvenile salmon encountered in Rivers Inlet; all sites.

Year	sockeye	chum	pink	coho	chinook	steelhead
2002	1583	226	4182	92	114	2
2003	13015	367	556	520	92	0
2004	7990	435	2313	196	53	0
2005	9109	192	66	250	27	0

3.7.2 Total Number of Juvenile Salmon Collected

It is important to note that very few juvenile salmon were retained; most were not handled nor removed from the water. Table 3-24 summarizes the number of fish of each species retained. Retained fish were preserved to facilitate later analysis of fork-length and weight, otolith extraction, and stomach content dissection. It also allowed the researchers to confirm the species identification performed in the field during the early phase of the project while the researchers familiarized themselves with the local fish appearance. The primary species retained was sockeye.

Table 3-24 Total number of juvenile salmon kept for lab analysis in Rivers Inlet; all sites.

Species	sockeye	chum	pink	coho	chinook	steelhead
2002	330	56	250	67	75	0
2003	535	71	189	122	65	0
2004	457	87	196	35	20	0
2005	234	68	31	67	20	0

3.7.3 Adult Salmon and Other Species

A small number of sub-adult and adult salmon were encountered during the study. All were released alive with the exception of one adult pink that died after being entangled in the web. The number of migrating adult salmon caught was highest in 2002. This may have been due to the more extensive length of the sampling season. In subsequent years, sampling ceased at an earlier date because the presence of adult fish made it difficult to estimate the number of juvenile salmon in the net, to avoid injuries to the juveniles, and to avoid encounters of returning River Inlet sockeye because of potential adverse effects of capture on the low population.

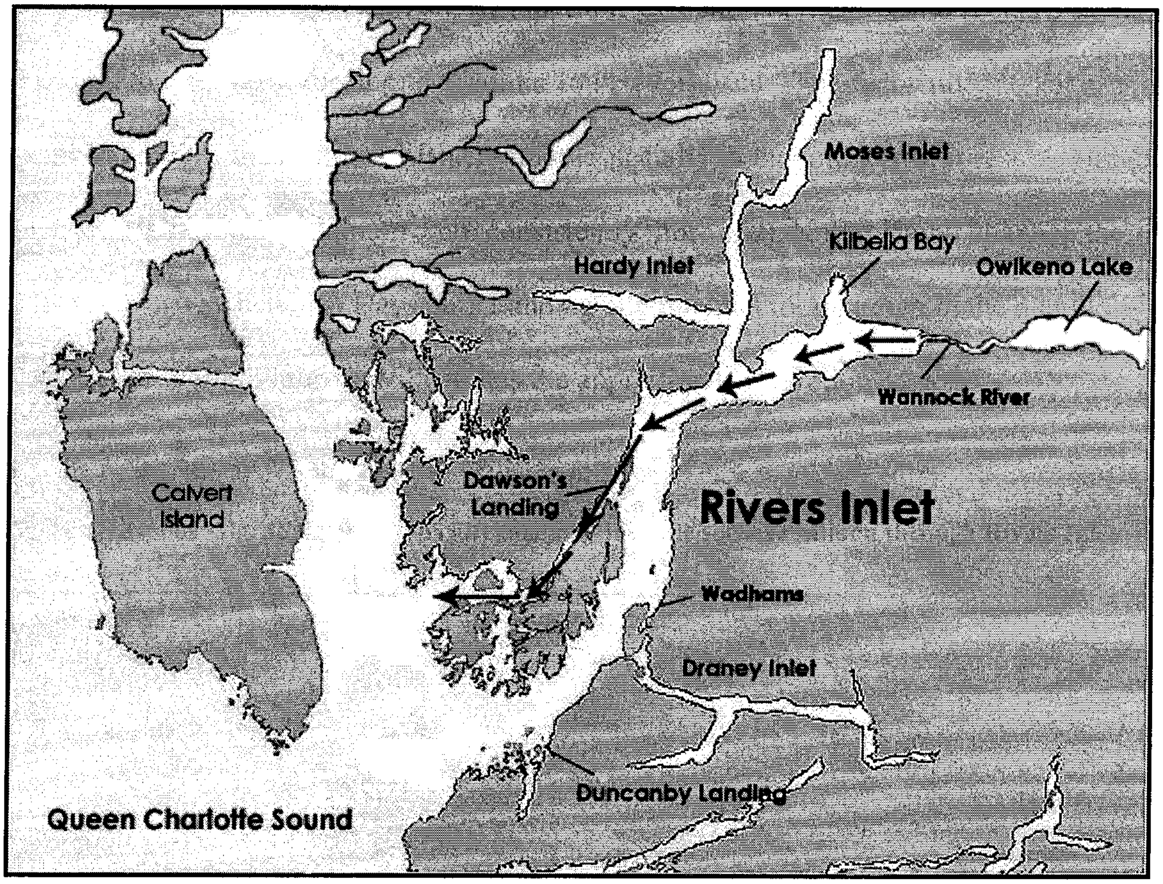
In addition, encounters of large numbers (thousands in some cases) of juvenile herring were at times problematic, as it made it difficult to estimate the number of juvenile salmon in the net. Further, the herring were approximately 15-20 cm in forklength and exactly the right size to become stuck in the mesh squares of the seine net. This was usually a lethal situation for the herring due to damage to the operculum and loss of scales. Juvenile herring encounters increased later in the sampling season and at locations farther down the inlet, from Dawson's Landing to the inlet mouth. The presence of large numbers of herring was a factor in excluding sampling sites during exploratory sampling in 2002. In particular, the outer part of Rivers Inlet that contains numerous bays and islands seemed to contain a lot of juvenile herring. In particular, Klaquaek Channel to the northwest of the inlet mouth was excluded from sampling for this reason.

Other fish species encountered during sampling include the three-spine stickleback *(Gasterosteus aculeatus)*, larval and juvenile herring *(Clupea harengus* *pallasi)*, starry flounder *(Platichthys stellatus)*, pilchard *(Sardinops sagax)*, rockfish *(Sebastes sp.)*, juvenile ocean whitefish *(Caulolatilus princeps)*, juvenile wolf eel *(Anarrhichthys ocellatus)*, juvenile Pollock *(Theragra chalcogramma)*, surf smelt *(Hypomesus pretiosus pretiosus)*, juvenile spiny dogfish *(Squalus acanthias)*, dolly varden *(Salvelinus malma)*, and juvenile sculpin *(Cottidae)*. With the exception of a few individuals sampled for confirmation of identification, none were retained. In addition, no birds or mammals were caught.

4 DISCUSSION AND CONCLUSIONS

Throughout the years of study, it became evident that the juvenile sockeye salmon appeared to migrate according to a similar route every year. The fish tended to keep to the northwestern-most shore of Rivers Inlet, especially in the mid to lower reaches of the inlet. Juvenile sockeye salmon were consistently more abundant in Darby channel, the narrow waterway between Dawson's Landing and the inlet mouth, than in the main inlet basin to the south. Figure 4-1 illustrates the approximate migration route.

Figure 4-1 The migration route typically taken by juvenile sockeye salmon through Rivers Inlet, B.C.



This study provides evidence that the juvenile sockeye salmon migrating seaward from Owikeno Lake are using the inlet for more than merely a route out to the sea. Indeed, Rivers Inlet serves as important habitat for the young fish. The juvenile sockeye make active use of the inlet to seek out available food and gain weight in the less saline waters of the inlet before migrating further out onto the Continental Shelf. In 2002, with scarce food in the upper inlet, they appear to have migrated rapidly through the upper inlet. In other years, they were frequently found in abundance at Ralph Point, located at the junction of Moses Inlet and Hardy Inlet. This represents a 2-kilometer diversion from the seaward migration route.

Furthermore, the catch data provide indirect evidence that the mean weight of the sockeye salmon approximately doubled as the fish migrated down the inlet. This is not to say that each individual fish doubled its body weight; indeed, there is certainly an expectation of variation. Nevertheless, if the approximate doubling in mean weight were attributable to growth over a 2 to 3 week migration period, this would correspond to an approximate 3-5% increase in body weight per day, on average. This corresponds to maximum growth rates of 4.7% per day (LeBrasseur 1968) and 4% per day (Koeller and Parsons 1977) obtained in studies on captive juvenile chum salmon (*O.keta*) fed a supplemental diet. However, the ability to estimate the amount of growth in the juvenile sockeye salmon from the present study is confounded by the fact that only the fish that survived could be measured. It is possible that the mean may have increased, in part, due to death of the small fish.

However, the juvenile sockeye salmon were indeed growing. If they were not, one would expect the variation in fish size to decrease between the head and outer inlet. The opposite is the case. In addition, while the median weight of the fish in *Zone 4* was 8.6 grams and the maximum was over 12 grams, no juvenile sockeye salmon over 6 grams was ever caught in *Zone 1.*

The importance of increased body size must not be overlooked, as it is a key factor related to survival for juvenile salmon. McKinnell et al. (2001) provide evidence from Owikeno Lake that large sockeye salmon fry are more likely to survive to adulthood. Conditions within Rivers Inlet that allow for maximum growth will contribute to better marine survival for the brood year of juvenile sockeye salmon.

In addition, the migrating fish spend a significant amount of time in Rivers Inlet. Juvenile sockeye salmon are abundant in the inlet for about four weeks. Informal attempts to follow peak abundances down the inlet suggested an average migration time of on the order of two or three weeks. This equates to an estimated speed of migration through the inlet of 1.9 to 2.9 km/d, slightly higher than reported elsewhere (1.3 to 1.9 km/d Wood et al. (1993)). Unfortunately, the modelling approach used in this thesis was not well suited to addressing this issue. A more specialized model incorporating basic features of the migration might be more effective, but this was beyond the scope of this thesis project.

The diet of juvenile sockeye in Rivers Inlet was composed mainly of small, neustonic species. These are creatures typically found near the surface of the water. The most numerous prey species, pelecypods (bivalves) are probably *Mytilus spp.*, blue mussels. In addition, the barnacle cyprids are a larval form of barnacle. Both these prey items are young forms of sedentary species that settle in the intertidal zone, in shallow water. It is important to note that the most numerous prey species are not necessarily the most energetically important prey items in the diet of the juvenile sockeye salmon. For example, amphipods and euphausiids comprise only 2.2 and 2.6% of the diet by number, but their larger size makes them a more important food source than a single pelecypod. Unfortunately, size meaurements of the larger prey species found in the stomach contents were not consistently obtained. Thus it is not possible to accurately compare the relative biomass or volume of different prey items. Based on five euphausiids measured from the stomach contents, the average size was 2150 μ. This is 7.3 times the size and approximately 389 times the volume of a pelecypod.

Total zooplankton abundance is a measure of general productivity and an indirect estimate of food availability for juvenile sockeye salmon. Unfortunately, a more detailed analysis of the zooplankton samples with respect to the prey items found in the stomachs of the juvenile sockeye salmon is not possible, as a different, specialized collection technique for zooplankton is required. Landingham et al. (1998) provide clear evidence that juvenile salmonids feed on a portion of the total zooplankton community, found near the surface of the water, known as neuston. Further, the researchers show little connection between the stomach contents of juvenile salmon and abundance of species in samples of zooplankton collected in traditional vertical hauls. In contrast, a horizontal tow designed to collect neustonic species is a more accurate measure of prey availability. This could explain the fact that juvenile sockeye prey items were virtually non-existent in the zooplankton samples. Nonetheless, the total wet weight of the zooplankton collected during this study provides important information regarding the overall abundance of the total zooplankton community. It is highly likely that the broad scale comparisons discussed here are a useful surrogate for more detailed information on abundance patterns of individual prey species.

Zooplankton was generally sparse in the upper inlet. The abundance of zooplankton is 2-7 times higher at the mouth of the inlet compared to the inlet head where the juvenile sockeye first enter the marine environment. A similar pattern of increase was found in the data on juvenile sockeye salmon robustness. Fish were more robust in zone 3 than in the upper inlet (zones 1 and 2). This is further indirect evidence of a link between the total wet weight of zooplankton and abundance of prey for juvenile sockeye salmon within Rivers Inlet.

Although the number of juvenile sockeye salmon caught was highly variable, this study revealed several consistent features. First, the timing: the seaward migration of juvenile sockeye salmon in Rivers Inlet began each year in mid-May and lasted until July. Of particular interest is the apparent connection to the lunar cycle, with fish abundance in the inlet consistently peaking in each of the four years at the first new moon in June. A similar connection to lunar activity is apparently evident in data presented by Wood et al. (1993), though no direct analysis was undertaken. Such links to lunar cycles in return adult migrations are common knowledge in all sectors of the salmon fishery. It makes sense to anticipate similar links in the juvenile phase. One plausible explanation here is that the juvenile fish can make use of the dark nights and strong, spring tidal currents at the new moon to move about the inlet more rapidly and safely. Further, the data show that there is very little flexibility to this pattern. The timing is consistent from year to year and is unchanged by the variable inlet conditions. The juvenile sockeye did not migrate early when there was food in the upper inlet due to an early bloom, as in 2004, nor delayed to wait for the zooplankton to build when it was late (2005) or nonexistent as in 2002. Such a consistent, tight timing mechanism leaves the fish vulnerable to vagaries in the timing of plankton blooms in the inlet.

Conditions in the upper inlet leading up to the juvenile sockeye migration appear to be very important. The juvenile sockeye salmon emerge small in size from the low food environment of Owikeno Lake with two needs; to grow as large as possible as fast as possible, and to migrate seaward. The data reveal a potentially crucial phase in the abundance of zooplankton in the upper inlet in the weeks before the peak of the juvenile sockeye migration. In particular, the higher robustness of the fish in 2004 when the zooplankton abundance peaked in *Zone 1* and *2* before *Lunar Day –14* suggests that early-season plankton abundance is important. I hypothesize that this is a key window in time and space that has an impact on the success of the population of migrating juvenile sockeye salmon in Rivers Inlet.

Comparisons of other years provide partial additional support. The total wet weight of zooplankton during this window has implications for fish condition, and large annual variation exists. In years when zooplankton is more abundant, the juvenile sockeye salmon are more robust. The year 2004 is a particularly good example of favourable conditions. Zooplankton abundance was high in both *Zone 1* and *2* throughout the window, and the juvenile sockeye salmon are more robust than in any other year. The least favourable year appeared to be 2002 because zooplankton was very scarce in the entire upper inlet. It is as if the spring plankton bloom simply did not occur. The data on fish condition show that the juvenile sockeye salmon were less robust this year than in 2004, but not significantly less robust than in the years 2003 and 2005. However, the number of sockeye encountered during the entire 2002 sampling season was 5 to 8 times smaller than in subsequent years. In addition, these fish were the progeny of a substantially smaller parent generation than were the later cohorts. It seems likely that there were indeed fewer out-migrating juvenile salmon in that year. Perhaps, the small population of juvenile sockeye in 2002 led to less competition and the amount of food available to each fish was not substantially different than the amounts in 2003 or 2005. Alternately, it is possible that there was high mortality amongst fish of lower condition and our study effectively only measured the more robust survivors.

In 2003, zooplankton abundance before *Lunar Day –14* was low in *Zone 1*, but relatively high in *Zone 2*, while the opposite was true in 2005. The corresponding fish condition data show the juvenile sockeye salmon were equally robust. It appears that as long as zooplankton are abundant in at least one of these zones, the juvenile sockeye can achieve an average degree of robustness.

This study has therefore generated insight into a potentially critical importance of inlet plankton dynamics in the lead-up to the juvenile migration. If the plankton bloom is diminished, or just timed incorrectly, marine survival of the out-migrating juveniles may well be severely reduced. However, evidence on the validity of the hypothesized connection between inlet conditions and marine survival is just now emerging. Adult sockeye returns for the 2000 brood year (juveniles sampled in 2002) were estimated at 156,595, remarkably favorable compared to the preceeding years. The high marine survival of the 2002 brood year was perhaps due in part to the large body size of the juveniles. It may be that inlet conditions are less important in years when the juveniles emerge from fresh water at a large size.

It is important that factors influencing the timing and magnitude of the spring plankton bloom be studied further. Of particular concern are climate change and its potential impacts on river discharge and ocean circulation patterns. Such insight is important for a number of reasons, and is critically important to the Wuikinuxv people, whose livelihood and culture are so closely tied to Rivers Inlet sockeye salmon and the ecosystem of which they are an integral part.

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