

# **Early Marine Distribution of Out-Migrating Juvenile Sockeye Salmon (*Oncorhynchus nerka*)**

**by  
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B.Sc., Simon Fraser University, 2005

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of the Requirements for the Degree of  
Master of Science

in the  
Department of Biological Sciences  
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## Abstract

The early marine phase is a critical period for out-migrating juvenile sockeye salmon (*Oncorhynchus nerka*). They undergo physiological changes while entering into a new environment, and this is thought to be a period of high mortality. This study examined factors affecting swimming depth as juveniles migrated through Rivers Inlet, and compared swimming depth at the point of ocean entry and life history strategies in sockeye salmon from Rivers Inlet and nearby populations on the Central Coast of British Columbia. Most juvenile sockeye salmon swam within two meters of the ocean's surface during their out-migration through Rivers Inlet, and were slightly deeper later in the out-migration. In addition, in a mesocosm experiment, Rivers Inlet juvenile sockeye salmon did not alter their swimming depth in response to increasing salinity at their preferred swimming depth, despite experiencing negative physiological effects when swimming in highly saline waters. Similar data on other nearby sockeye salmon populations were collected. Juvenile sockeye salmon from populations that out-migrate through brackish waters tended to be smaller than individuals from populations that leave fresh water and enter directly into highly saline marine environments, and they too tended swim within the top two to four meters of the surface. This shows that conditions in the top 4 m of the water's surface represent actual conditions experienced by out-migrating juvenile sockeye salmon in the early marine environment and is a critically important observation in terms of understanding such issues as prey availability, the potential role of brackish surface layers in coastal fjords, lagoons and estuaries, and susceptibility to predators. These findings will inform future sampling efforts on these populations, and also suggest that these populations maintain varying life history characteristics which enable them to survive early marine conditions within the top 4 m of the ocean.

**Keywords:** sockeye salmon; early marine environment, vertical distribution; *Oncorhynchus nerka*; Rivers Inlet; juvenile salmon

## **Dedication**

To Mom and Dad. Thank you.

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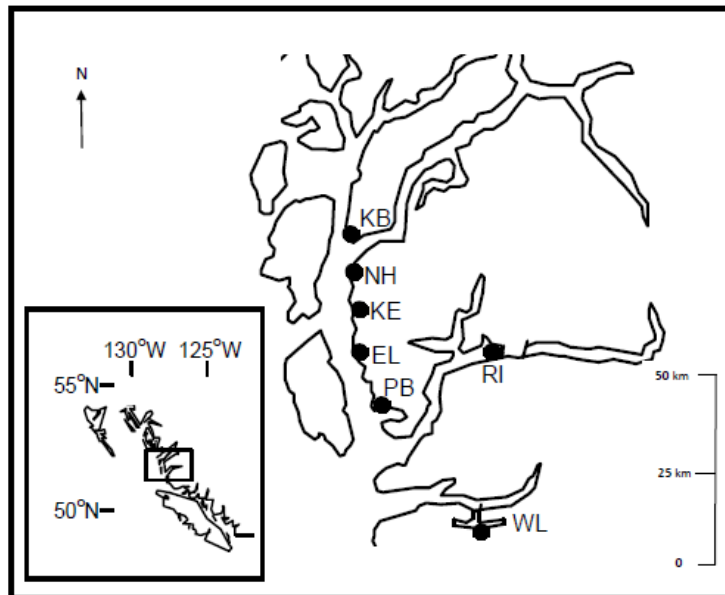
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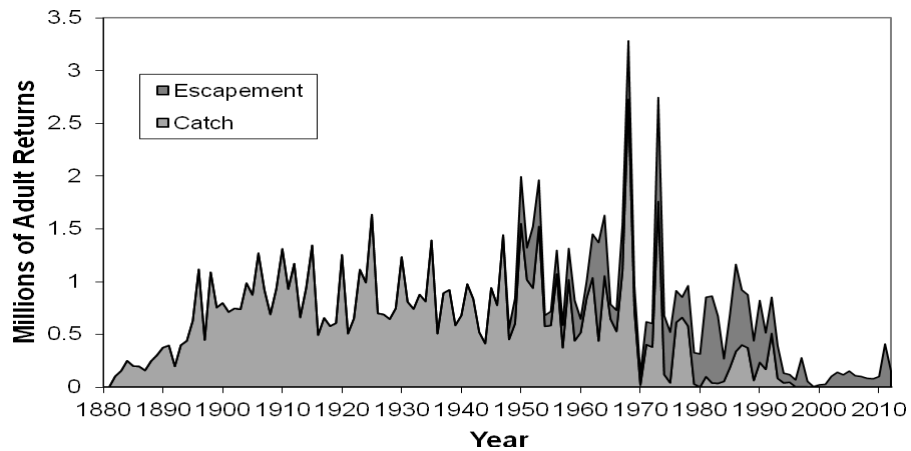
# 1. Introduction

When juvenile Pacific salmon migrate from fresh water to salt water they encounter new predators, diseases, parasites, and prey, while undergoing physiological changes to adapt to hypertonic waters. The conditions juvenile salmon encounter when entering the ocean vary between species and between populations, and a variety of life history strategies and behaviours exist to enable juveniles to adjust to the marine environment (Pearcy 1992). Some juvenile salmon may spend days or months migrating through estuaries or fjords before moving to more saline coastal waters, while others may enter highly saline waters directly from fresh water. In general, Pacific salmon may experience relatively high rates of mortality when they leave freshwater as juveniles and enter the marine phase of their lifecycle (Pearcy 1992, Beamish et al. 2010). This study examines the early marine vertical distribution and compares life history characteristics of out-migrating juvenile sockeye salmon from Rivers Inlet and several other sockeye salmon populations on the Central Coast of British Columbia (BC) (Figure 1).

Rivers Inlet sockeye salmon historically supported the third largest sockeye salmon fishery in Canada. The average annual commercial catch was approximately 750,000 fish per year, and in some years the total number of fish caught in Rivers Inlet was greater than the Skeena catch, placing Rivers Inlet second largest behind the Fraser River sockeye salmon fishery (McKinnell et al. 1998). The population began to show signs of instability by the early 1970's, as larger fluctuations in the annual numbers of returning adults became increasingly evident (Figure 2). In the 1990's, adult returns collapsed to less than 1% than their historical average. Despite closure of the commercial fishery since 1996, the population numbers have remained low. The leading explanation for the population decline is a high rate of mortality in the marine environment (McKinnell et al. 2001, Levy 2006).



**Figure 1** The study area, with the seven sampling sites labeled as follows (from south to north): Wyclees Lagoon (WL), Pierce Bay (PB), Rivers Inlet (RI), Elizabeth Lagoon (EL), Koeye Estuary (KE), Namu Estuary (NH), and Kisameet Bay (KB).



**Figure 2** Estimates of numbers of adult sockeye salmon returning to Rivers Inlet since the onset of the commercial fishery with estimates of numbers of adults that “escaped” the fishery to reach the spawning grounds added on after the estimation program began in 1948.

In addition to these larger coastal sockeye salmon populations, many small lakes on the Central and North Coasts of BC support sockeye salmon populations. These continue to be essential subsistence fisheries for Central and North Coast communities (Pauley et al. 1989). These small coastal lake populations are thought to exhibit a variety of ecotypes, molecular genetics, life history strategies and behavioural traits (Wood et al. 1994, Wood 1995). Seventy-four lake-type sockeye salmon populations on the BC Central Coast are designated as Conservation Units under the Canadian government's Wild Salmon Policy (Holtby and Ciruna 2007, DFO 2009). Some of these sockeye salmon populations are in decline and approximately half of the populations are sparsely monitored or have never been monitored, and therefore their population status is unknown (Riddell 2004). Juvenile sockeye salmon in these smaller populations experience a variety of conditions at their point of marine entry. Some juveniles leave fresh water and enter the ocean through open areas with highly saline surface waters, while others pass through tidal lagoons with brackish surface layers held in place by restrictions in their seaward passages.

The overall objective of this thesis is to determine the swimming depth of out-migrating juvenile sockeye salmon at the point of ocean entry and determine factors that influence swimming depth in the early marine environment. First, I examined the swimming depth of Rivers Inlet juvenile sockeye salmon as they swam from the point of ocean entry through the 40 km inlet. Next, I discussed factors that could have influenced their preferred swimming depth in the context of Gilliam's hypothesis regarding habitat selection (Werner and Gilliam 1984). Gilliam suggests that an individual will choose a habitat that minimizes the ratio of mortality risk to energy gain (Werner and Gilliam 1984, Gilliam and Fraser 1987).

The inlet contains a brackish surface layer typical of coastal inlets at the time of juvenile sockeye salmon out-migration, and I was particularly interested in whether juveniles were restricted to this surface layer. I expected that individuals with smaller fork lengths would be physiologically constrained to the brackish surface layer, whereas individuals with longer fork lengths would be able to swim in more saline, deeper waters where they could access a higher abundance and better quality of prey while reducing their mortality risk due to predation. Through a mesocosm experiment, I also addressed the question, "If the depth of the surface layer is changed, will the juvenile sockeye



salmon alter their swimming depth?” Exposure to highly saline water requires an increase in energy output in order to remove excess salts from a juvenile’s body. I expected that artificially increasing the salinity at the preferred swimming depth of Rivers Inlet juvenile sockeye salmon would cause juveniles to change their swimming depth, in order to reduce energy expenditure. I also anticipated that juvenile sockeye salmon would move deeper each day of the year as the stage of smoltification advanced and the fish grew. As smoltification progresses there is an increase in enzyme activity resulting in less energy needed to maintain homeostasis. This could then allow an individual to move into more saline, deeper water at a reduced energy cost (McCormick et al. 1987, McCormick et al. 1989). In addition, I expected juveniles to grow larger with each day of the year, and I expected larger individuals to swim in deeper, more saline waters. Then, I compared swimming depth at point of ocean entry in four populations to determine if population differences were present. Two study populations transitioned from fresh water through brackish waters and two study populations transitioned directly from fresh water into highly saline water. Finally, I compared juvenile size and age in seven populations to determine if juveniles that leave fresh water and enter highly saline estuaries are longer and older than juveniles that enter brackish estuaries. I hypothesized that juveniles entering into highly saline marine environments would need to be larger in order to survive the sudden transition into a highly saline environment, and that some individuals from these populations would remain in fresh water for a second year to grow larger before moving to the marine environment.

## **2. Marine Distribution of Out-Migrating Central Coast Sockeye Salmon**

### **2.1. Introduction**

Juvenile sockeye salmon may experience relatively high rates of mortality when they leave freshwater and enter the marine environment. Many populations begin their seaward migration through fjords, lagoons, and estuaries with brackish surface layers, which provide an opportunity for juvenile sockeye salmon to adjust more slowly to new predators, diseases, parasites, and prey while undergoing smoltification. This chapter reports evidence on the extent to which out-migrating juvenile sockeye salmon are restricted to near-surface waters in the early marine environment and discusses the potentially important role of a brackish surface layer to the survival of out-migrating juveniles in some populations of sockeye salmon.

The primary study site was Rivers Inlet, a 40 km long and 3 km wide fjord approximately 500 km northwest of Vancouver, BC (Figure 1). Each fall, sockeye salmon spawn in the numerous rivers surrounding Oweekeno Lake, and in spring the fry move into the lake where they rear for one year (McKinnell et al. 2001). The lake (Figure 1) is roughly as long and narrow as the inlet (56 km long and 3 km wide) and drains a 4100 km<sup>2</sup> watershed including two major ice fields. Large head-water glaciers generate silt that is transported to the lake, rendering it relatively unproductive (McKinnell et al. 2001). The following spring, the juveniles travel 5 km down the Wannock River and enter Rivers Inlet. The inlet is characterized by a deep bottom and steep sides. At the time of the juvenile sockeye salmon out-migration, the spring freshet creates a 2 – 4 m brackish surface layer which overlies more saline water. Juvenile sockeye salmon are thought to move through Rivers Inlet in 2 – 3 weeks (Buchanan 2006) before exiting the inlet to begin their migration north.

Studies of juvenile Pacific salmon in the early marine environment have often considered horizontal distribution; however, few studies address vertical distribution and movement patterns of juvenile salmon (reviewed by Beamish et al. 2003 and Brodeur et al. 2003). Both abiotic factors such as salinity, temperature, or contaminants, and biotic factors such as prey and predators can differ substantially on small vertical scales in estuaries. Therefore determining distribution on a vertical scale and determining how the aforementioned abiotic and biotic factors play a role in determining distribution may provide a better understanding of conditions faced by juvenile salmon during their early marine migration.

Optimization models are useful in studying animal habitat selection. Animals should select habitats that minimize the ratio of mortality risk to energy gain; striking a balance between predation risks, foraging success, and energy loss due to metabolic costs in a particular habitat (Werner and Gilliam 1984, Gilliam and Fraser 1987). As such, many Pacific salmon transition from fresh water to the marine environment where there is an abundance of high quality prey available. This transition is thought to occur when the fish has reached a large enough size that the risk of predation is less than the potential energy gained from prey species available in the marine environment (Gross 1987). By the same theory, sockeye salmon should select a habitat within the marine environment which minimizes the ratio of mortality risk to energy gain.

Mortality risk will arise from predators both above and below out-migrating juvenile sockeye (Hartt 1980, Olesiuk et al. 1990, Groot and Margolis 2001, Beamish and Neville 2001, Duffy and Beauchamp 2008). Avian predators will cause juveniles to swim deep enough below the surface of the water to avoid detection from above, whereas predatory fish and mammals will influence juveniles to move toward the surface. Optimal energy gain will result from a balance between consuming a large amount of high quality prey and energy loss due to metabolic costs (Werner and Gilliam 1984, Gilliam and Fraser 1987). Surrounding salinity and temperature, stage of smoltification (Otto and McInerney 1970, Morgan and Iwama 1991, 1998), and body size (Macdonald and Levings 1998, Levings et al. 1989) all impact net energy gain, and therefore should influence swimming depth of out-migrating juvenile sockeye salmon.

**Table 1**      *The seven sampled sockeye salmon populations.*

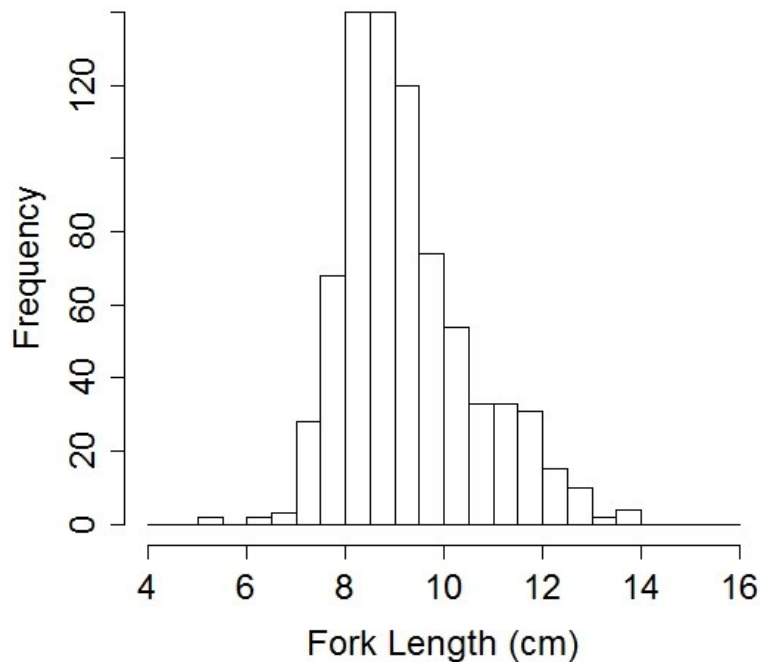
<b>Rearing Lake</b>	<b>Marine Entry Point</b>	<b>Type of Marine Entry</b>
Long Lake	Wyclees Lagoon	Inlet with reversing tidal rapids at its mouth
Elsie and Hoy Lakes	Pierce Bay	Small Bay near open Pacific Ocean
Oweekeno Lake	Rivers Inlet	Large inlet fed by glacial runoff
Elizabeth Lake	Elizabeth Lagoon	Tidal lagoon with reversing tidal rapids at its mouth
Koeye Lake	Koeye Estuary	Long estuary through tidal marshes
Namu Lake	Namu Estuary	Short estuary near mouth of a major inlet
Kisameet Lake	Kisameet Bay	Open bay near mouth of a major inlet

Marine studies that address depth of juvenile Pacific salmon often examine depths at 15 - 30 m increments, and very few studies consider, in detail, depths within 10 m of the surface (Emmet et al. 2004, Beamish et al. 2007). Large-scale trawl or seine nets are often used to sample for fish (reviewed in Beamish et al. 2003 and Brodeur et al. 2003). The nets reached depths of approximately 10 – 15 m or 30 m respectively and could not provide precise estimates of the actual swimming depths of the fish they caught. These studies compared the abundance of salmon caught in trawls at the surface to subsurface trawls in order to determine the vertical distribution of juvenile salmon. However, the opening of the trawl net could not be closed, and hence the net fished near surface waters effectively for a 5 – 10 min period during retrieval from subsurface trawls (Beamish et al. 2000, Emmet 2004). Therefore, these studies have potentially overestimated the number of fish at depth since the catch at depth was possibly augmented by the near-surface catch during net retrieval. Hydroacoustic techniques have been used to complement surface trawling in marine studies of juvenile sockeye salmon (Groot and Cooke 1987, Moulton 1997); however, small target sizes,

near-surface orientation of fish, lack of large, well-defined schools, and a noisy environment make this method difficult to implement (Moulton 1997).

Tagging studies are becoming increasingly popular for marine salmon studies in general (reviewed by Drenner et al. 2012). Recent developments in hydroacoustic telemetry technology are enabling more detailed information to be collected on the state and behaviour of a tagged fish. This method could have been useful in our study; however, the technology currently exists only to successfully tag individuals measuring at least 11 cm in length (Chittenden 2009), and the average length of juvenile sockeye salmon in this study was too small (Figure 3). Also, fish increase their air bladder volume in order to compensate for a tag, which will in turn alter the fish's buoyancy (Perry et al. 2001) and potentially a juvenile's marine swimming depth.

Here I present the first quantitative study of swimming depth as juvenile sockeye salmon enter the marine environment and migrate through Rivers Inlet. I relate their swimming depth to the specific abiotic and biotic conditions encountered to test for factors that determine swimming depth. Considering the small size of out-migrating juvenile sockeye in Rivers Inlet and the potential inability of these small juveniles to survive in saline water, I expected fish size and depth of the halocline to affect swimming depth, with larger fish swimming deeper than smaller fish and swimming depth to increase as halocline depth increases. Out-migrating juveniles from some sockeye salmon populations leave fresh water into brackish water whereas others leave fresh water and enter directly into highly saline water. Several other Central Coast sockeye salmon populations (as listed in Table 1 and displayed in Figure 1) were compared in order to determine if there are trends in early-marine swimming depth and life history characteristics associated with the presence or absence of brackish water upon ocean entry.



**Figure 3** *Fork length (cm) distribution of all 759 juvenile sockeye salmon measured in this study. The average fork length was 9.3 cm, the median was 9.0 cm, the minimum was 5.2 cm while the maximum was 14.0 cm.*

## 2.2. Methods

### 2.2.1. Methods Overview

Early marine vertical distribution of out-migrating juvenile sockeye salmon was examined using complementary methods and four sockeye salmon populations. First, an observational pen study (2010 and 2011), visual observations (2010 and 2011), and a mesocosm experiment (2011) were used to determine the distribution of out-migrating juvenile sockeye salmon in Rivers Inlet and provide insight into factors that determine swimming depth as the juveniles migrated through the 40 km inlet. Second, a population comparison of several Central Coast sockeye salmon populations was conducted (2011). Swimming depth at the time of ocean entry was assessed by an observational pen study and visual observations of Rivers Inlet, Pierce Bay, Namu Estuary and

Kisameet Bay sockeye salmon populations. Size at the time of ocean entry was examined for the aforementioned populations, and juveniles from Wyclees lagoon, Koeeye estuary, and Elizabeth lagoon were also included in the comparison. Preliminary results comparing age at the time of ocean entry were also obtained.

### **2.2.2. Sampling Methods**

Fish were collected by large purse seine, small purse seine, and trawl in the spring of 2010 and 2011. The larger purse seine was deployed from the M.V. Western Bounty, a 16 m seine vessel operated by the Wuikinuxv First Nation. The net measured 364 m long by 29 m deep with an effective fishing depth estimated to be 25-27 m. Mesh panels were 3.7 cm to 2.5 cm and 0.6 cm at the bunt end. In 2011, a small purse seine net, 60 m long by 6 m deep, was deployed from two, 4.3 – 4.8 m vessels. Mesh panels were 1.5 cm to 0.9 cm and 0.3 cm at the bunt. The net was extended between two 4.3 – 4.8 m vessels, then towed by the two vessels that travelled parallel directions approximately 30 m apart for 10 minutes. The net was then closed off and retrieved by hand until fish were trapped in the bunt. The trawl net was deployed from the M.V. Pacific Coast, an 11 m ex-commercial gillnet vessel. The net measured 18 m long and had a 5 m wide by 4.6 m deep opening. The net was fitted with a rigid holding box at the cod end for live capture (as described in Gottesfeld et al. 2007).

### **2.2.3. Observational Pen Study – Field Work**

Juvenile sockeye salmon were collected from sampling sites throughout Rivers Inlet from early May to early July of 2010 and from early May through to the end of June in 2011. Fish were collected by one of the three methods previously described, identified to species, and enumerated. Juvenile sockeye salmon to be used in the study were placed in a covered container and transported immediately to the experimental station, about halfway up Rivers Inlet. All other fish not needed for research were released at the capture site.

Over the two years of this study, 28 samples of juvenile sockeye salmon were collected for the observational pen study. Fish that were collected in each sample remained grouped together, and hence the number of fish used in each experimental

trial depended on the number of fish caught in the sample. The number of fish in a trial ranged from 5 to 128, with a mean of 37.9 and a median of 20.

Juvenile sockeye salmon were placed in a vertical pen for the observational study (Figure 4). The 3 mm mesh pen permitted relatively free passage of water and plankton, but blocked the passage of experimental and other similarly sized or larger fish. Metal rings held the shape at approximately a 1 m diameter and the pen extended 6.5 m below the surface. A wooden float supported the opening above the surface so that fish could not escape the pen and the pen could rise and fall with the tide. Floating lines were run from the float to the shore to prevent the pen from drifting. The pen was fitted with two choke mechanisms, one at each of 2 m and 4 m. At each of these depths, a cord was secured around the exterior of the pen and extended up to the surface so that the choke could be closed. The experimental fish were placed into the pen to acclimate for 120 min before closing the chokes. That time frame was chosen because fish were observed not to change depth after 120 min during preliminary trials. At 120 min, the chokes were simultaneously closed so that the net was sectioned off into three categories: 0 – 2 m, 2 – 4 m, and 4 – 6.5 m. The fish from the 0 – 2 m section were removed, counted, weighed (2011 only), and measured for fork length. With the 4 m choke still closed, the net was pulled towards the surface, and the process was repeated for the 2 – 4 m section. The entire process was then repeated for the 4 – 6.5 m section. Salinity profiles were taken at 0, 60, and 120 min for all trials in order to determine the depth of the halocline. During the juvenile sockeye salmon out-migration, the salinity in Rivers Inlet consistently rises from less than 10 ppt to over 20 ppt within 0.5m. Therefore, for data analysis, the depth of the halocline was arbitrarily defined as the depth at which the salinity measured 15 ppt.

#### **2.2.4. Observational Pen Study – Statistical Analysis**

The number of fish present in each of the three depth categories was counted, and the proportion of fish present in each category was used for data analysis. Proportional data cannot be less than 0 or greater than 1. Therefore, in keeping with common practice, a logistic curve, with asymptotes at 0 and 1, was used to model the data (Agresti 2013). Inferences were generated using generalized estimation equation methodology as described by Halekoh et al. (2006). This methodology required the

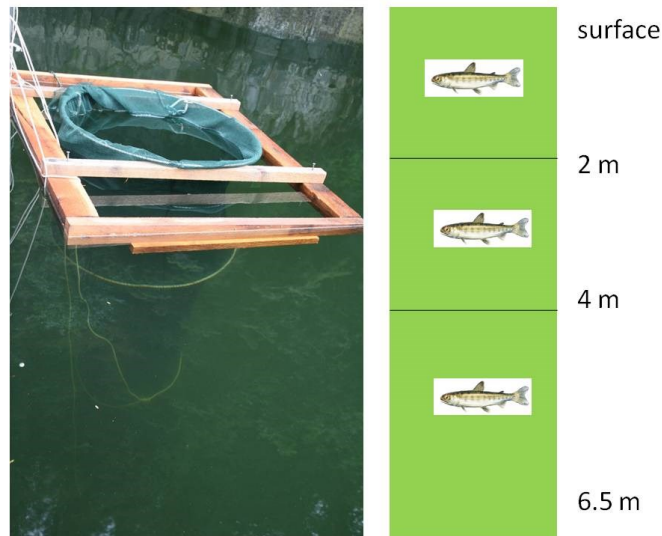


development of two models, one to model the proportion of fish found in 0 – 2 m versus 2 – 6.5 m, and a second to model the proportion of fish found in 0 – 4 m versus 4 – 6.5 m.

Factors included in the full models as potential sources of variation in swimming depth were (i) year, (ii) day (from the beginning of the year) that the fish were sampled, (iii) distance of the collection site from the head of the inlet, (iv) fork length, (v) depth of the halocline in the holding pen at the beginning of the trial, and (vi) number of fish in the trial. Some of the trials had a large number of fish. Year was included to permit the assessment for potential inter-annual differences in swimming depth. Day, distance from the inlet head, and fork length were included to account for possible changes as the fish grew and advanced through the smoltification process. Halocline depth was included since it seemed highly plausible that the fish would avoid more saline water, at least earlier on, given their small size. Number of fish in the trial was included as this variable could not be kept strictly controlled and might have had some influence if, for example, the fish might have spread out into less preferred depths to avoid overcrowding.

Therefore, in order to reduce stress, fork length was measured on a subset of the fish in such trials and the estimated mean fork length over the trial was used. Because each trial contained fish that were collected in the same sample and placed together in the experimental pen, the behaviour of individual fish may have been dependent, and individual fish cannot be treated as independent replicates. To account for potential dependent behaviour within a trial, an explicit random effect for trial was introduced.

A minimally adequate model was selected using a backwards elimination process as described by Agresti (2013). Beginning with the full model (all factors included), the parameter estimates and  $p$ -values were examined and the variable with the largest  $p$ -value was removed from the model. The model was refit and an analysis of variance was used to test for a significant difference between the model with and without the factor. If the test indicated that the two models were not significantly different, the factor was left out of the model. The factor with the next largest  $p$ -value was then considered for removal, and the process was repeated until all factors remaining in the model were significant.



**Figure 4** *The net used for observational pen studies and visual observations. Juvenile sockeye salmon were placed in the pen which was cinched off into three depth categories 0 – 2m, 2 – 4m, and 4 – 6.5m.*

### **2.2.5. Visual Observations – Field Work**

A video camera (FishTV) was used to determine precise swimming depth during fifteen trials of the observational pen study. The experimental pen was scanned from top to bottom by video camera at 60 and 120 min. The swimming depth of each fish was recorded in real time. If a large group of fish were schooled together, the fish were counted and the range of depth of the school was noted. This procedure was used instead of obtaining individual depths in order to maintain speed of data collection and to avoid recounting fish that moved lower or higher.

### **2.2.6. Visual Observations – Statistical Analysis**

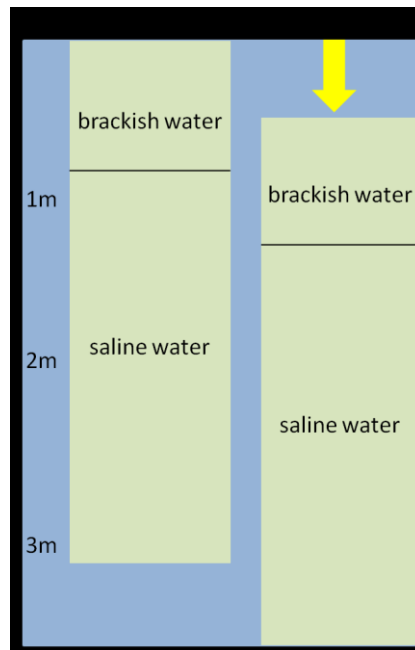
Visual observations of swimming depth for each fish in the trial were analyzed with a linear mixed-effect model. A model was constructed to determine factors that influence the average depth of the schools of fish in a trial. In line with the observational pen model, the following fixed factors were included in the full model (i) day (from the beginning of the year) that the fish were sampled, (ii) distance of collection site from the head of the inlet, (iii) depth of the halocline in the holding pen at the time of observation and (iv) number of fish in the trial. Fork length was not included because individual fish could not be measured or identified for later measurement during the visual

observations. Logistically observations were made consistently later in the year in 2010 and earlier in the year in 2011; therefore data from the two years was analyzed separately. Depth was recorded at 60 min and 120 min for each trial. These two observations were viewed as repeated measures and analyzed accordingly (v). The 60 min and 120 min observations were initially analyzed separately to detect possible interactions between the time of observation and the distance from the head of the inlet and the halocline depth. One interaction was detected in the 2010 analysis and included as a fixed effect in the full model: (vi) observation and halocline depth. Again, a random term was introduced into the model to account for dependence among fish in each trial. The best model was selected using a similar process as described for the observational pen study.

### **2.2.7. *Mesocosm Experiment – Field Work***

An experimental tank was used for two reasons: (i) to reduce the confounding effect in the observational study between the influence of the halocline and depth below the surface, and (ii) to observe changes in fish behaviour in response to imposed changes in depth (Figure 5). Twenty-four trials were conducted throughout June 2011, with samples collected throughout Rivers Inlet. A transparent, plexiglass tank measuring 0.61 m wide x 0.61 m across x 3 m long was constructed to run the experiments. The tank was set up on a pulley system and its depth was manipulated so that it was filled with seawater of a desired salinity from the surrounding environment. Again, fish that were collected in each sample remained grouped together, and hence the number of fish used in each experimental trial depended on the number of fish caught in the sample. The number of fish in a trial ranged from 3 to 20; the mean was 9, and the median was 10. The experimental design called for at least 10 fish in each trial; however, 2011 was a particularly difficult year to obtain juvenile sockeye salmon in Rivers Inlet. Therefore some trials had to be run with fewer fish. The trial fish were placed in the tank and at 60 min and 120 min, a video camera was lowered along the side of the tank in order to determine the depth of the fish as described earlier. Due to the small number of fish in the tank, individual depths were obtained for each fish in the trial. Following the visual observation at 120 min, the tank was sealed and lowered by 0.5 m. Visual observations of depth in relation to the surface were then taken at 180 min and 240 min from the beginning of the trial; i.e. after a further 60 min and 120 min. During the experiment, a

small leak was detected in the bottom of the tank. In order to minimize change to the internal environment of the tank, and to ensure constant experimental conditions, the tank was always at the surface for the first two observations (60 min and 120 min) and lowered by 0.5 m for the second two observations (180 min and 240 min). Therefore the observation number was confounded with the depth of the tank.



**Figure 5** *Diagram of mesocosm experimental set-up. Juvenile sockeye salmon were placed into the tank which maintained an artificial halocline. With the tank at the surface, observations were made at 60 min and 120 min. The tank was lowered by 0.5 m and visual observations were made at 180 min and 240 min.*

### **2.2.8. Mesocosm Experiment – Statistical Analysis**

Visual observations of swimming depth were analyzed in two stages with linear mixed-effect modeling. First, the 60 min and 120 min observations were modeled together in order to assess what factors might have affect the swimming depth of out-migrating juvenile sockeye salmon. In theory, this assessment was similar to the vertical distribution study. Hence we would expect to find comparable final models. As with the visual observation model, the following factors were included in the full model (i) day (from the beginning of the year) that the fish were sampled, (ii) distance of collection site from the head of the inlet, (iii) depth of the halocline in the holding tank at the time of observation, (iv) number of fish in the trial, and (v) observation number. Fork length was

not included because individual fish could not be identified during the experiment. In addition, this experiment was only run in 2011, and therefore, year was not included as a factor in this model. Again the model included a random term for trial.

A second analysis was performed in order to assess the extent to which lowering the tank by 0.5 m might have affected swimming depth in relation to the surface of the water. Four observations of swimming depth were included in the model; two when the tank was at the surface of the water (60 min and 120 min) and two after the tank was lowered to 0.5 m below the surface of the water (180 min and 240 min). To assess the effect of lowering the tank on fish swimming depth, the full model included all of the same fixed effects as the model generated when the tank was at the surface ( $i - v$ ), plus a further fixed effect for (vi) tank depth. The full model also included random factors for trial and the interaction between trial and observation number. If each fish could have been identified and tracked throughout the experiment, fish would have been included as a random factor, however, it was not possible to identify and track individual fish within a given trial. Had this been possible, we could likely have generated increased power through knowledge of individual fish movements.

### **2.2.9. *Population comparison field work***

Sampling took place in 2011 from April to June using the small seine net within several hundred meters of the river mouth in each system. All fish caught were identified to species and the fish not needed for research were released immediately. Twenty juvenile sockeye salmon were haphazardly selected to be used in the depth study and if fewer than twenty sockeye salmon were caught, all fish were included in the experiment. Other sockeye salmon were released after they were enumerated, weighed, and measured for fork length. Salinity profiles were obtained at the collection site for each population.

The same vertical pen and experimental procedure that was used for the depth study of Rivers Inlet juveniles was used for this study. The number of fish in a trial ranged from 10 to 21, with a mean 17 and a median of 18.

In addition, fish lengths were provided by Rick Ferguson at the Pacific Biological Station (DFO) for fish that he had sampled during the same time period from Wyclees

Lagoon. Scales were extracted from a subsample of juveniles, then aged by the Sclerochronology Laboratory at the Pacific Biological Station (DFO).

#### **2.2.10. *Population comparison observational depth study – Statistical Analysis***

The analysis used was similar to the methodology used in analyzing the observational pen study. The number of fish present in each of the three depth categories was counted, and the proportion of fish present in each category was used for data analysis. Inferences were made using generalized estimation equation methodology, which required the development of two models, one to model the proportion of fish found in 0 – 2 m versus 2 – 6.5 m, and a second to model the proportion of fish found in 0 – 4 m versus 4 – 6.5 m. Factors included in the full models as potential sources of variation in swimming depth were (i) day (from the beginning of the year) that the fish were sampled, (ii) fork length, and (iii) population of origin. Reasons for including these variables were as above, but with the following exceptions. Depth of the halocline was omitted for the following reasons: (i) it was consistently much deeper in Rivers Inlet than in the other systems, and hence was confounded with population, (ii) the surface salinities were hypertonic in these other systems, and hence the halocline was likely not as potentially important a demarcation for them, (iii) the halocline turned out not to be statistically significant in the Rivers Inlet observational studies and mesocosm experiment, and (iv) with so few trials (6), we did not have sufficient data to include many factors. Also, distance of collection site from the head of the inlet and year were no longer relevant since each had only one level in the systems other than Rivers Inlet.

#### **2.2.11. *Population comparison of juvenile size - Statistical Analysis***

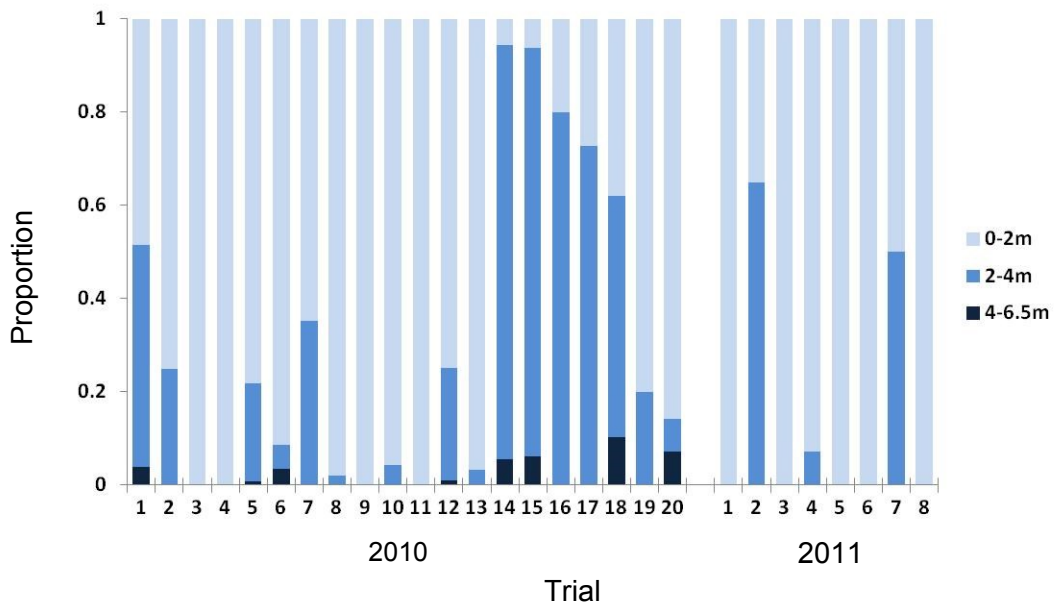
A linear mixed-effects model was used to detect differences in fish size associated with the surface salinity at the point of ocean entry. The full model included fixed effects for (i) surface salinity, which was used as an index of the availability of fresh water upon ocean entry, and (ii) day (from the beginning of the year) that the fish were sampled. Because fish were caught in seine sets, we included a random factor for seine set (nested within population) to account for possible dependencies between fish caught

in the same set. We also singled out Elizabeth Lagoon for special consideration since the freshwater component to the system appears to contain severely limited spawning habitat (Manzon and Marshall 1980). Severely limited spawning habitat could have allowed a restricted population of fry in the rearing lake to attain a larger body size. We therefore analyzed the size data twice - with Elizabeth Lagoon included and then excluded.

## **2.3. Results**

### **2.3.1. *Observational Pen Study***

In 2010, 69% of the fish were observed between 0 – 2 m, 29% were between 2 – 4 m, and only 2% were between 4 – 6.5 m (Figure 6). Overall 98% of the fish in the 2010 vertical trials were between 0 – 4 m. In 2011, 85% of the fish were between 0 – 2 m, 15% were between 2 – 4 m, and no fish were below 4 m (Figure 6). Over both 2010 and 2011, 74% of the fish were found in 0 – 2 m, 25% found in 2 – 4 m, and the remaining 1% were found below 4 m. Day (from the beginning of the year) and fork length were correlated ( $r=0.7$ ) and no other factors were correlated (Table 2). Day (from the beginning of the year) was a significant factor in both the 0-2 m versus 2-6.5 m model and the 0-4 m versus 4-6.5 m model, whereas no other factors were included in the final model (Table 3, Table 4). Figure 7 shows the following: (i) that the model-estimated probability that a fish will prefer to be in the top 4 m is consistently near 1 over June, the primary migration month, and (ii) that the model-estimated probability that a fish will prefer to be in the top 2 m decreases over this month from 85% to 50%.



**Figure 6** *Proportion of juvenile sockeye observed in 0-2m, 2-4m, and 4-6.5m depth ranges in 2010 and 2011.*

**Table 2** *Correlation coefficients of the variables included in the generalized estimation equation model of the proportion of fish in each depth category of an observational pen.*

Variable	day of the year	distance	fork length	year	number of fish	halocline depth
day of the year	1.00	0.33	0.71	-0.32	-0.37	0.22
distance		1.00	0.25	-0.37	0.05	-0.05
fork length			1.00	-0.15	-0.36	0.04
year				1.00	-0.47	0.21
number of fish					1.00	-0.48
halocline depth						1.00



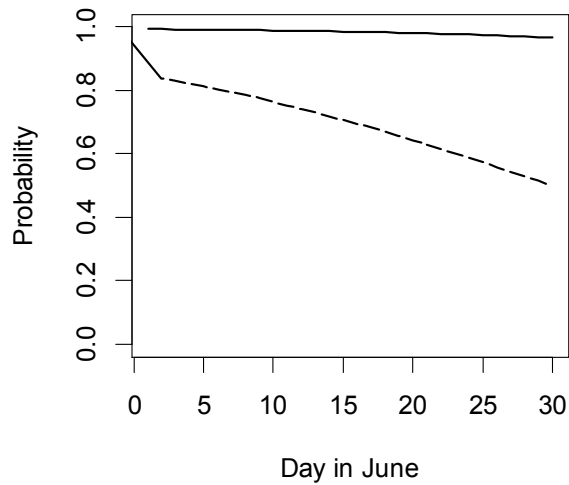
**Table 3** *Generalized estimation equation model results. Day of the year was a significant predictor of swimming depth of juvenile sockeye salmon out-migrating through Rivers Inlet. Variables are listed in the order they were removed from the model. P-values listed were obtained from model testing in the backwards elimination process.*

Model	Variable	p-value
0-2 m versus 2-6.5m	halocline depth	0.82
	year	0.77
	number of fish	0.74
	fork length	0.40
	distance	0.41
	day of the year	0.0054*
0-4 m versus 4-6.5m	year	1.00
	number of fish	0.29
	distance	0.23
	halocline depth	0.07
	fork length	0.06
	day of the year	0.02*

\* Denotes a significant predictor that remains in the final model.

**Table 4** *Summary coefficients in two final models of juvenile sockeye salmon swimming depth.*

Model	Parameter	Estimate	Standard error	p-value
0-2 m versus 2-6.5m	Intercept	-10.6402	3.4961	0.0023
	day of the year	0.0588	0.0211	0.0054
0-4 m versus 4-6.5m	Intercept	-13.4810	4.1008	0.001
	day of the year	0.0559	0.024	0.02



**Figure 7** *Model-estimated probabilities that a fish will prefer to be in the top 2 (---) or top 4 (—) m over June, the month during which most of the juvenile migration takes place. Virtually all the fish were in the top 4 m throughout the month, and the estimated preference for the top 2 m declined from 85% to 50% over this period.*

### 2.3.2. Visual Observations

Mean school swimming depth was 2.65 m in 2010 (SD 1.31 m) and 1.52 m in 2011 (SD 0.80 m). Distance from the head of the inlet and day of the year were significant predictors of swimming depth in 2010, ( $p = 0.03$ , Table 6, Table 7), whereas there was no predictor of swimming depth found in 2011 ( $p = 0.63$ , Table 6, Table 7). No other variables were found to be significant predictors of depth (Table 6).

**Table 5** *Correlation coefficients of the variables included in the linear mixed-effect model of visual observations of juvenile swimming depth.*

Year	Variable	day of the year	distance	halocline depth	number of fish	observation number
2010	day of the year	1.00	-0.68	-0.32	0.04	-0.08
	distance		1.00	0.20	-0.57	0.19
	halocline depth			1.00	-0.04	-0.19
	number of fish				1.00	-0.26
	observation number					1.00
2011	day of the year	1.00	0.36	-0.38	-0.75	-0.17
	distance		1.00	-0.67	-0.18	-0.27
	halocline depth			1.00	0.57	0.08
	number of fish				1.00	-0.40
	observation number					1.00

**Table 6** *Linear mixed-effect model results. Day of the year and distance from the head of the inlet were significant predictors of swimming depth of juvenile sockeye salmon out-migrating through Rivers Inlet in 2010. There were no predictors of swimming depth in 2011. Variables are listed in the order they were removed from the model. P-values listed were obtained from model testing in the backwards elimination process.*

Model	Variable	p-value
2010	halocline depth, halocline depth x observation number	0.4648
	observation number	0.544
	number of fish	1
	day of the year	0.0308*
	distance	0.0138 *
2011	observation number	0.7813
	distance	1
	day of the year	1
	halocline depth, halocline depth x observation number	1
	number of fish	0.6249

\* Denotes a significant predictor that remains in the final model.

**Table 7** *Parameter estimates from a linear mixed-effect model of the observed swimming depth of juvenile sockeye salmon. Day of the year and distance were significant predictors of swimming depth in 2010.*

Model	Parameter	Estimate	Standard error	p-value
2010	Intercept	37.743043	5.101131	
	distance	-0.055836	0.006734	0.0138
	day of the year	-0.18368	0.027044	0.0308
2011	Intercept	1.39937	0.07056	

### 2.3.3. Mesocosm Experiment

None of the variables included in the model were significantly correlated (Table 8). Analysis of the first two observations (60 min and 120 min) indicates that only (i) day (from the beginning of the year) affected depth of the fish ( $p = 0.027$ ), whereas (ii) distance of collection site from the head of the inlet, (iii) depth of the halocline in the holding tank at the time of observation, (iv) number of fish in the trial, or (v) observation number were not significant predictors of fish depth ( $p > 0.05$ , Table 9). On average, fish moved 0.0424 m (SE=0.0188 m) deeper with each day of the year (Table 10). Analysis of the second two observations (180 min and 240 min), when the tank was lowered by 0.5 m, indicates that none of (i) day (from the beginning of the year) that the fish were sampled, (ii) distance of collection site from the head of the inlet, (iii) depth of the halocline in the holding tank at the time of observation, (iv) number of fish in the trial, (v) observation number, or most notably (vi) tank depth were significant predictors of fish depth ( $p > 0.05$ , Table 9). Mean swimming depth below the surface of the water remained the same regardless of changes to any of these factors. In other words, when the tank was lowered by 0.5 m fish swam towards to the surface to return to their previous mean depth.

**Table 8** *Correlation coefficients of covariates included in linear mixed-effect model of swimming depth in a mesocosm.*

Variable	day of the year	distance	halocline depth	number of fish	observation number
day of the year	1.00	-0.23	-0.48	-0.29	0.24
distance		1.00	0.07	-0.11	-0.03
halocline depth			1.00	0.07	0.04
number of fish				1.00	-0.20
observation number					1.00

**Table 9** *Linear mixed-model results from mesocosm experiment. Day of the year was a significant predictor of swimming depth with the tank at the surface, there were no predictors when the tank was lowered. Variables are listed in the order they were removed from the model. P-values listed were obtained from model testing in the backwards elimination process.*

Model	Variable	p-value
at surface		
	distance	1
	observation number	0.4936
	number of fish	0.1983
	halocline depth	0.1667
	day of the year	0.0272*
at surface, then lowered		
	number of fish	1
	distance	1
	tank depth	0.6174
	halocline depth	0.4198
	day of the year	0.2218
	observation number	0.1472

\* Denotes a significant predictor that remains in the final model.

**Table 10** *Parameter estimates from linear mixed-effect modeling of a mesocosm experiment. Day of the year was a significant predictor of swimming depth of juvenile out-migrating through Rivers Inlet.*

Model	Parameter	Estimate	Standard Error	p-value
at surface				
	Intercept	-4.99325	3.08595	
	day of the year	0.04244	0.01876	0.0272
at surface, then lowered				
	Intercept	2.0011	0.1061	

### 2.3.4. Population comparison observational depth study

At least 60% of the juvenile sockeye salmon preferred the top 2 m in every population that we tested (Figure 8). Also, in the two less saline of the four systems that we tested, virtually all of the fish were in the top 2 m, whereas in the other two, substantial proportions of juveniles were found below 2 m. Nonetheless none of (i) day (from the beginning of the year) that the fish were sampled, (ii) fork length, or (iii) population of origin was significant ( $p > 0.05$ ). This may have been a result of the small number of trials. Hence the preeminent observation was the fact that the majority of the fish showed a preference for the top 2 m, across all populations tested.

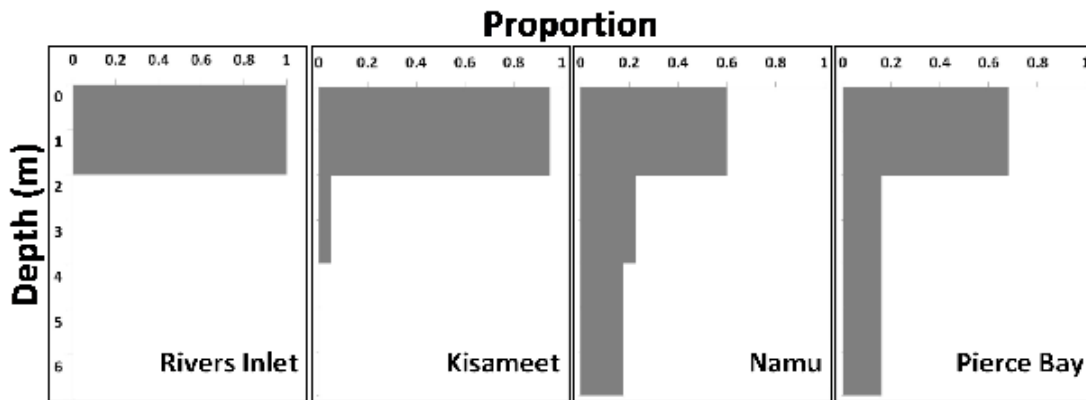
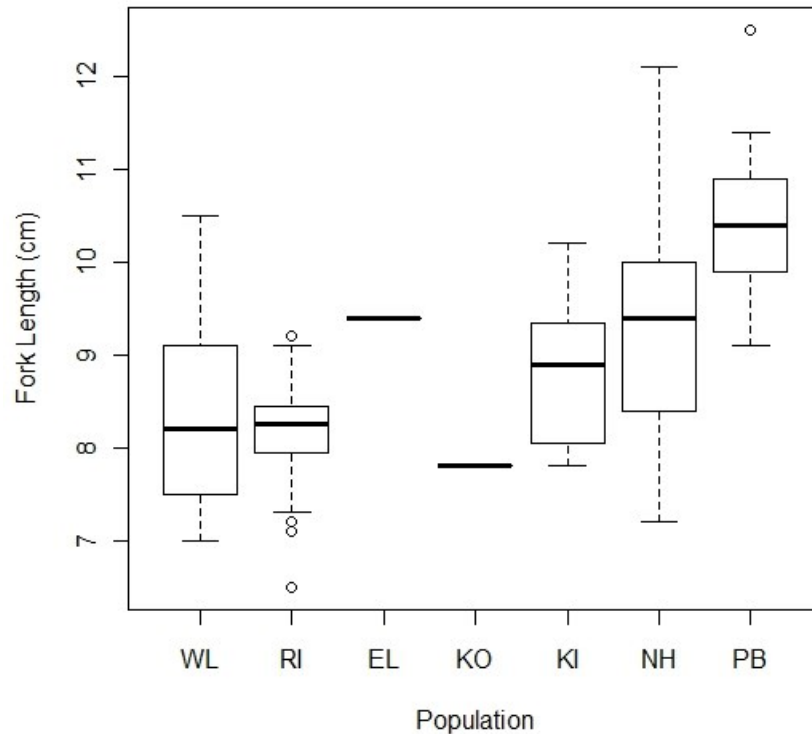


Figure 8 Depth distribution of juvenile sockeye salmon during vertical trials.

### 2.3.5. Population comparison of juvenile size

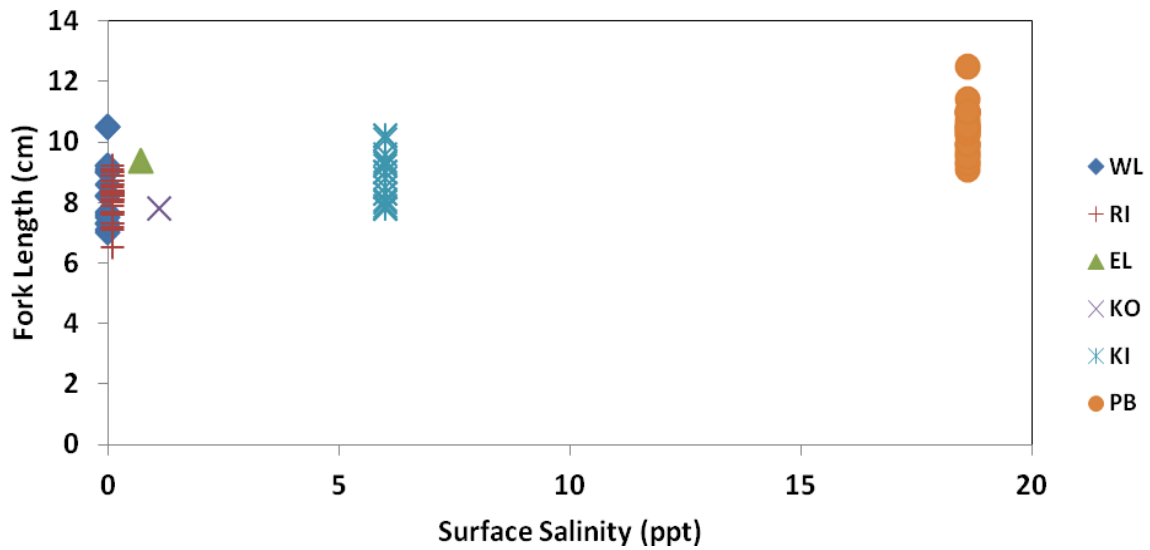
The juvenile sockeye salmon with the smallest fork length was collected in Rivers Inlet and measured 6.5 cm long, whereas the longest fork length measured was 13.1 cm from Pierce Bay (Figure 9 and Figure 10). None of the variables included in the model were significantly correlated (Table 11). Surface salinity and day of the year were significant factors in the models for the analysis with and without the Elizabeth Lagoon sample ( $p = 0.006$  for analysis with and without Elizabeth Lagoon, Table 12 and Table 13). Juvenile sockeye salmon from populations that encountered fresher water as they entered the marine environment were smaller on average than juvenile sockeye salmon from populations that transitioned from fresh water directly to more highly saline water

(Figure 9 and Figure 10). Some of the fish in the smaller populations had also spent a second year in fresh water (Table 14).



**Figure 9** Juvenile fork lengths (cm) by population (Wyclees Lagoon (WL), Rivers Inlet (RI), Elizabeth Lagoon (EL), Koeeye Estuary (KO), Kisameet Bay (KI), Namu Estuary (NH), and Pierce Bay (PB)). The thicker horizontal lines show the median fork length (cm), and the bottom and top of the box show the first and third quartiles respectively. Minimum and maximum values are depicted by whiskers. In the presence of outlying points (RI and PB), whiskers show 1.5 times the interquartile range and are plotted individually. Populations are listed in order of increasing surface salinity. Juvenile sockeye salmon from populations that emerged from fresh water into estuaries with higher surface salinities tended to be larger.





**Figure 10** Fork length measurements (cm) of juvenile sockeye salmon from seven Central Coast populations entering into estuaries of varying surface salinities. Juveniles were collected from Wyclees Lagoon (WL), Rivers Inlet (RI), Elizabeth Lagoon (EL), Koeeye Estuary (KO), Kisameet Bay (KI), Namu Estuary (NH), Pierce Bay (PB). Juvenile sockeye salmon that enter estuaries with lower surface salinities have a smaller fork length than juvenile sockeye salmon that enter estuaries with higher surface salinities.

**Table 11** Correlation coefficients of covariates included in linear mixed-effect model comparing juvenile fork length by population.

Variable	surface salinity	day of the year	population
surface salinity	1	-0.2349642	-0.51556
day of the year		1	-0.0844
population			1

**Table 12** *Linear mixed-model results from population fork length comparison. Surface salinity and day of the year were significant predictors of fork length. Variables are listed in the order they were removed from the model. P-values listed were obtained from model testing in the backwards elimination process.*

Model	Variable	p-value
Elizabeth Lagoon included	salinity	0.006546*
	day of the year	0.005747*
Elizabeth Lagoon excluded	salinity	0.00585*
	day of the year	0.006306*

\* Denotes a significant predictor that remains in the final model.

**Table 13** *Parameter estimates from linear mixed-effects models of fish size in relation to surface salinity at the point of ocean entry.*

Model	Parameter	Estimate	Standard Error	p-value
Elizabeth Lagoon included	Intercept	13.23204	1.248992	
	salinity	0.071251	0.025127	0.006546
	day of the year	-0.03357	0.009041	0.005747
Elizabeth Lagoon excluded	Intercept	13.20743	1.255083	
	salinity	0.073386	0.025515	0.00585
	day of the year	-0.03377	0.009083	0.006306

**Table 14**      *Juvenile age at point of ocean entry*

Population	Number of juveniles aged	Number of 2 year old juveniles
Pierce Bay	14	1
Namu Estuary	22	4
Kisameet Bay	12	0
Elizabeth Lagoon	1	0
Koeye Estuary	1	0

## **2.4. Discussion**

This study provides fine-scale estimates of vertical distribution of out-migrating juvenile sockeye salmon upon entry to the marine environment. In Rivers Inlet, most of the juvenile sockeye salmon preferred to be within 2 m of the surface, with almost all within 4 m. In addition, when the swimming depth of Rivers Inlet sockeye salmon was experimentally altered, juveniles generally returned to their initial swimming depth within two hours, suggesting that they returned to a preferred swimming depth relative to the distance below the water's surface which did not depend on the halocline depth. Furthermore, in all of the auxiliary study populations, most of the juvenile were in the upper 2 m upon ocean entry, though increasing proportions of juveniles swam deeper in populations that entered marine environments with a weak to non-existent fresh water surface layer. Hence, juvenile sockeye salmon appear to swim in shallow water upon marine entry.

According to Gilliam's hypothesis, swimming between the surface and four meters should provide an optimal trade-off between mortality risk and energy gain for juvenile sockeye salmon entering the marine environment (Werner and Gilliam 1984, Gilliam and Fraser 1987). A juvenile sockeye salmon's net energy gain is determined by energy gain due to foraging success and energy loss from metabolic costs. Both external factors, such as salinity, temperature and predation, and the physiological state of the juvenile, such as stage of smoltification (Otto and McInerney 1970, Morgan and Iwama 1991, 1998) and body size (Macdonald and Levings 1988, Levings et al. 1989) will affect net energy gain. In order to minimize energy needed to maintain homeostasis, a juvenile sockeye salmon should swim at a depth where the surrounding water is

isotonic to its internal body (Morgan and Iwama 1991, 1998). However, both the observational pen study and mesocosm experiment showed that swimming depth of juvenile sockeye salmon in Rivers Inlet was not significantly affected by the depth of the halocline. This was demonstrated particularly clearly in the second phase of the mesocosm experiment. Lowering the experimental tank to change the depth of the halocline in relation to the surface of the water had no effect on the swimming depth of fish in relation to the surface. The fish tended to remain at the same depth in relation to the surface of the water. Hence they moved towards the surface when the tank was lowered, rather than staying in the same position relative the halocline inside the tank. When the halocline in the tank was set shallower than the preferred swimming depth, the fish remained at their preferred swimming depth and did not move into shallower, less saline waters. It is possible that juveniles would not move into shallower waters due to an imbalance of the ratio between mortality risk and energy gain. Perhaps the perceived increase in risk from overhead predators at the shallower depth did not outweigh the increase in energy cost associated with the highly saline water, or the risk of mortality from an inability to survive at higher salinity levels. In addition, the halocline depth in Rivers Inlet during the juvenile migration period has uniformly been below 2 m in ten years of observations (R. Routledge, pers. comm.). Hence, the population may not have experienced evolutionary pressure to respond to the artificially shallow halocline level imposed in the mesocosm experiment. A juvenile salmon's stage of smoltification at the time of ocean entry will also affect metabolic costs. Smoltification involves changes to gill and kidney enzyme activity, changes to body colour and lipid loss to prepare a juvenile for survival in saline waters (McCormick 2001, Marshall 2002).

Day of the year was found to be a significant predictor in the observational study and mesocosm experiment. Smoltification begins in fresh water and can take several months to complete (Hoar 1988). Rivers Inlet sockeye salmon moved on average four centimetres deeper each day of their migration through the inlet. A time-dependent change, such as smoltification and growth may be associated with this shift in swimming depth. Fish size was not found to be a predictor of swimming depth in the Rivers Inlet study, though it plays an important role for early marine survival in some populations. One potential explanation for this somewhat counterintuitive finding is that perhaps stage

of smoltification exerts a stronger influence on swimming depth for Rivers Inlet juvenile sockeye salmon.

As smoltification progresses, the enzyme  $\text{Na}^+/\text{K}^+$ -ATPase becomes more active in removing salts from the gills. Therefore, a juvenile that is in a later stage of smoltification will have more active  $\text{Na}^+/\text{K}^+$ -ATPase and require less energy and be better able to maintain homeostasis than individuals at an earlier stage of smoltification (McCormick et al. 1987, McCormick et al. 1989). Therefore juveniles that are at a later stage of smoltification may have lower metabolic costs in deeper, more saline water whereas juveniles at an earlier stage of smoltification may have lower metabolic costs in shallower, brackish water. Furthermore, some juveniles in the mesocosm experiment that remained at their preferred depth in highly saline water, rather than moving to shallower brackish water became moribund when doing so. This suggests that smoltification may not be sufficiently advanced for them to be able to survive in deeper, more saline water. Thus, although there is evidence that the energy demands of gill  $\text{Na}^+/\text{K}^+$  pumps may constitute a relatively small component of the overall metabolism in juvenile salmon (Morgan and Iwama 1987), this mechanism may account for the gradual increase in preferred depth as the migration season in the inlet progressed.

Smoltification also causes lipid loss, which may cause an individual to become less buoyant and to move deeper in the water column (Hoar 1976, Sherridan et al. 1985). However, fish can effectively alter their buoyancy by controlling the volume of air in their swim bladder. Juvenile salmon can change their buoyancy within several minutes (Perry et al. 2001), and can effectively alter their buoyancy while transitioning from fresh to salt water (Weitkamp 2008). Rivers Inlet sockeye salmon are unusually small and could possibly encounter a unique difficulty in this regard (Rutherford and Wood 2000). It is conceivable that they are swimming at a depth at which they are neutrally buoyant, are not able to expel air from their swim bladders to move deeper in the water column, and must rely on losing lipids as smoltification progresses in order to move deeper in the water column once in the marine environment. The ability of out-migrating Rivers Inlet juveniles to regulate buoyancy could be examined to determine its role in determining swimming depth.

Although body size was not a predictor of swimming depth for Rivers Inlet juvenile sockeye salmon, it plays a key role in survival of juveniles in estuaries. Body size of juvenile sockeye salmon will affect metabolic costs, the risk of mortality due to predation, and the risk of mortality due to sudden changes in salinity in estuaries for some populations. Franklin et al. (1992) found that most 9 month-old sockeye salmon (23.1+ 3.4 g) that were transferred directly from fresh water to saline water (34% salinity) died within 24 – 48 hours and experienced 100% mortality within five days, with smaller fish dying before larger fish. However, when 15 month-old sockeye salmon (95.0 g +/- 13.0 SE) were transferred directly into highly saline water there was no mortality (Franklin et al. 1992). Furthermore, Heifetz et al. (1989) found that an Alaskan population of sea-type sockeye salmon had to reach a size of only 5 cm to obtain 100% survival in sea-water. Therefore it is clear that metabolic costs and the risk of mortality upon entry to saline water are population specific. In the mesocosm experiment, some juveniles became moribund when surrounded by highly saline water. Rivers Inlet sockeye salmon are known to be relatively small at the time of ocean-entry compared to other one-year old sockeye salmon populations (Rutherford and Wood 2000). Juveniles collected throughout Rivers Inlet in the present study, had an average fork length of 9.4 cm and weight of 5.7 g. Future studies could include measurements of whole body and plasma ion levels in order to assess how well Rivers Inlet juveniles are managing the transition to saline water and explore why Rivers Inlet juveniles did not move toward the surface of the water, where the risk from overhead predation increases, away from highly saline water at their preferred swimming depth, despite the risk of mortality due to intolerable salinity levels. The 2010 visual observations of swimming depth found evidence that fish depth increased slightly toward the mouth of the inlet. This may have been in response to increased mortality risk from predatory fish. Predatory fish were more commonly seen toward the inlet mouth (R. Routledge, pers. comm.).

Juvenile sockeye salmon vary in the number of years spent rearing in fresh water before migrating to the ocean. Generally, juvenile sockeye salmon will spend zero, one, or two years in fresh water (Burgner 1991). In some populations, the time spent in fresh water is consistent for all juveniles. For example, it is well established that Rivers Inlet juveniles are one-year old at the time of out-migration (Rutherford and Wood 2000, McKinnell et al. 2001). All juveniles that were aged from Kisameet Bay, Elizabeth

Lagoon, and Koeve Estuary were also determined to be one-year olds, whereas populations from Namu Estuary and Pierce Bay had out-migrating individuals that had spent one year in fresh water and individuals that had spent two years in fresh water (Table 2). Juveniles leaving fresh water and entering into Namu Estuary or Pierce Bay enter into relatively saline waters. These individuals may have been too small after one year in fresh water to survive the abrupt change in salinity when entering the marine environment.

The population comparison depth study showed a notable proportion of individuals in the Namu Estuary and Pierce Bay depth trials in the 2 – 4 m and 4 – 6.5 m depth categories, whereas most of the fish in Kisameet Bay were between 0 and 2 m. This difference, though not statistically significant, emerged from a very small number of trials and merits further investigation. Also, it may be possible that juveniles that migrate at age two swim deeper than juveniles that migrate as one-year olds, and further studies could test this hypothesis. In addition, fish size and growth rate are thought to affect out-migration timing (Barnaby 1944), and more intensive observations on the migration timing for these populations might reveal valuable insight on this hypothesis.

Prey distribution in estuaries should have an effect on the swimming depth of out-migrating juvenile sockeye salmon. Prey availability will directly affect energy gain and will also indirectly affect the costs and benefits associated with salinity and temperature (Webster and Dill 2006). The present study did not examine the vertical distribution of prey in the fjord; however, most out-migrating juvenile sockeye salmon were found within the top four meters of the water column, indicating that zooplankton communities in the top four meters of the water column will inform estimates of prey availability. Juvenile sockeye salmon are visual predators, and visibility is likely a factor in determining their swimming depth. Glacially silted fresh water often creates turbid conditions in estuaries. It is possible that juvenile sockeye salmon swim at shallow depths where there is enough light to detect prey.

An assessment of mortality risk faced by an out-migrating juvenile sockeye salmon must include the number and type of predators present, the ability of the predator to detect the juvenile sockeye salmon and the ability of the juvenile to avoid its predator. Juvenile sockeye salmon leaving fresh water and entering the marine

environment are faced with an abundance of novel predators. For example, observations of potential predators that were collected in the seine net during juvenile sockeye salmon sampling in Rivers Inlet include hake (*Merluccius productus*), mackerel (*Trachurus symmetricus*) flounder (Pleuronectidae), and adult chinook salmon (*Oncorhynchus tshawytscha*). Seals and birds were often observed in abundance at the head of Rivers Inlet (personal observation). Community assemblages will vary depending on both abiotic and biotic factors. Therefore Rivers Inlet, Kisameet Bay, Pierce Bay, and Namu Estuary populations may encounter different predators when they enter the marine environment. River lamprey, shore birds, chinook salmon, dogfish, seabirds, gulls, coho salmon, lingcod, seals, cutthroat trout, sea lions, and daggertooth are considered main predators of juvenile sockeye salmon (Hartt 1980, Olesiuk et al. 1990, Beamish and Neville 2001, Duffy and Beauchamp 2008). These are all visual predators and an assessment of the threat they pose to juvenile sockeye salmon needs to include measures of turbidity and predator effectiveness at that turbidity. Gregory and Levings (1998) found that Pacific salmon were detected and preyed upon by fish less often in turbid water than in clear water.



### 3. Conclusion

This study shows that most juvenile sockeye salmon swam within the top 2 m of the ocean during their out-migration through Rivers Inlet and fish tended to prefer slightly deeper water as the spring migration season in the inlet progressed. Interestingly, halocline depth had no apparent effect on swimming depth. Although Rivers Inlet juveniles could not tolerate highly saline waters, they would not swim to shallower, less saline water despite manipulations creating intolerable salinity levels at their preferred swimming depth.

This observation is critically important for assessing the role of potential changes to the inlet ecosystem in the demise of the Rivers Inlet sockeye salmon population. In particular, it focuses attention on potential prey species such as *Evadne nordmanni* that are found in brackish water (Poggensee and Lenz 1981) and, at least in some years, form a substantial component of the juvenile sockeye salmon diet (Buchanan 2006, Ajmani 2011).

Furthermore, for each of the other three juvenile sockeye salmon populations that were also tested, the preferred swimming depth at the point of ocean entry was consistently near the surface. Over 60% of the fish in each system preferred to be within 2 m of the surface, regardless of the salinity profile. It appears that the optimal swimming depth for juvenile sockeye salmon upon entry to the marine environment is driven by other factors than their inability to tolerate higher salinity levels at greater depths in some of these systems.

In addition, juveniles from populations that did not have access to an extensive fresh-to-brackish surface layer upon entry into the marine environment tended to be larger. Furthermore, at least some individuals from populations with no access to a brackish or freshwater surface layer once they leave the freshwater environment opt to spend an extra year in the rearing lake. By contrast, no such observations exist for Rivers and Smith Inlet sockeye salmon which have access to extensive brackish surface

layers. It appears likely that smaller individuals in populations that must adjust to hypertonic marine salinities immediately upon emergence from freshwater may choose to spend an additional year in freshwater in order to reduce the risk of mortality associated with the more abrupt transition to hypertonic marine salinity levels that they must eventually encounter.

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