Factors affecting overwinter mortality and early marine growth in the first ocean year of juvenile Chinook salmon in Quatsino Sound, British Columbia

by

Katherine Rose Middleton
B.Sc., Queen's University, 2007

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of the Requirements for the Degree of

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Supervisory Committee

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Abstract

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Evidence suggests that the variability in recruitment of adult Pacific salmon is related to smolt survival during the first ocean year. Specifically, the first few weeks and first marine winter may be two critical periods of high mortality during early marine life. Mortality during early marine residency has been attributed to predation and size-dependent factors while high mortality during the first winter may be due to energy deficits and failure to reach a certain size by the end of the growing season. My study assessed factors influencing overwinter mortality and early marine growth in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from Marble River, Quatsino Sound, British Columbia. Juvenile salmon were collected during November 2005 and 2006 (fall) and March 2006 and 2007(winter). Mortality rates over the first winter derived from catch per unit effort across seasons ranged between 80-90% in all years. These are the first estimations of overwinter mortality in juvenile Pacific salmon. Fish size distributions showed no evidence of size-selective overwinter mortality between fall and winter fish in either 2005-2006 or 2006-2007. Otolith microstructure analyses showed no significant difference in circulus increment widths during the first four weeks after marine entry. Similarities in increment width indicated that early marine growth did not differ between fall and winter fish during early marine residency in 2006. These observations show that the high overwinter mortality rates of juvenile Chinook salmon in Quatsino Sound are not size-dependent. Total plankton biomass was significantly lower in the winter season but size distribution, gut fullness and energy density data did not show evidence of starvation. No correlation was found between early marine growth, size, energy accumulation and high mortality in Marble River juvenile Chinook salmon during their first ocean winter in Quatsino Sound. Possible factors influencing these high mortality rates may include non size-selective predation, disease, local environmental influences or an as yet unknown source. Future work should continue to focus on understanding the relationship between early marine survival and adult recruitment. The expansion of growth comparisons geographically and chronologically while determining the effects of predatory mortality on juvenile Chinook salmon along the north Pacific continental shelf and beyond are imperative to fully understanding this complex marine life stage.

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Thank you all very much.

Dedication

For Abby and Ollie and to the future of their oceans

"*For the children of today, for tomorrow's child, as never again, now is the time*"

Dr. Sylvia Earle

Chapter 1: General Introduction

1.1 Importance of Salmon to the British Columbia Coastal Ecosystem

Pacific salmon (*Oncorhynchus* spp.) have been culturally valued by communities along the west coast of Canada for thousands of years (Brodeur *et al.* 2000b, Lichatowich 2001). Historically, salmon were important for food, trade and cultural purposes by many First Nations people throughout the Pacific Northwest (McHutchinson and Roche 1998). In British Columbia salmon are essential for recreational, economic and cultural purposes and are highly valued by Canadian and global commercial and recreational fishing industries. Pacific salmon have been commercially harvested since the late 1800's (Brodeur *et al.* 2000b, Beamish *et al.* 2003) which has significantly contributed to the reduction of wild salmon populations over the last century (Schindler *et al.* 2003).

These fish are a keystone species and are ecologically important in aquatic ecosystems along the west coast of North America. As an anadromous fish, they spawn and die in natal streams becoming a major source of nutrients and energy for freshwater and terrestrial ecosystems (Schindler *et al.* 2003). Salmon affect the productivity and biodiversity of forests, rivers and estuaries and all organisms connected through this complex biological network (Groot and Margolis 1991). Although river and estuarial ecologies of Pacific salmon have a significant impact on the coastal environment, most of their life is spent in the open ocean, and a better understanding of this portion of their life cycle is crucial. If we can develop a significant knowledge base on the marine life of Pacific salmon, we will have better insight into one of the most important ecological foundations of the northwest coast.

1.2 Declines in Pacific Salmon

Returns of adult Pacific salmon are highly variable and difficult to predict. In some regions adult returns have been so low that fisheries have been closed for more than a decade to encourage recovery of the population (McKinnell *et al.* 2001, Irvine *et al.* 2005). Over the past 30 years there has been an overall decline in catches of some species of Pacific salmon (McFarlane *et al.* 2000, Noakes *et al.* 2000, Brodeur *et al.* 2004). Many stocks have gone extinct, such as populations in the Upper Columbia and Snake River (Gustafson *et al.* 2007), while others have been under serious threat (Nehlsen *et al.* 1991, Irvine *et al.* 2005). Although population numbers have been found to fluctuate naturally and have recently shown much resilience, the last century has shown significant loss from anthropogenic influences (Finney *et al.* 2000) including mining, agriculture, industrial development, and large-scale commercial fishing (Lichatowich 2001). With the decline of many Pacific salmon stocks, fishing restrictions, hatcheries and aquaculture facilities have been instigated to compensate for these losses (Nehlsen *et al.* 1991, Young 1999).

Canadian stocks of Pacific salmon began declining around 1990, hitting an all time low in 1998 due to a significant shift in climate that year (Noakes *et al.* 2000, Beamish *et al.* 2004). Climate-ocean changes and regime shifts have been found to limit salmon abundance and survival (Beamish and Bouillion 1993, Beamish *et al.* 1999, Moss *et al.* 2005, McFarlane *et al.* 2000, Mortensen *et al*. 2000, Farley and Trudel 2009), but how climate change causes these fluctuations is still not well understood (Beamish and Mahnken 2001). The cumulative effects of several factors may be responsible for the high inter-annual variability in the survival of Pacific salmon populations. The overall decline in survival of Pacific salmonids has also been linked to variability in prey quantity and quality, disease, habitat degradation and the influence of hatchery released fish on wild populations (Groot and Margolis 1991, Beamish *et al.* 1999, Noakes *et al.* 2000, Brodeur *et al.* 2003, Quinn 2005, Holt 2010). Recently, researchers have been investigating the effects of growth during early marine life to better understand this life stage as it could lead to better predictability of adult salmon returns (Hartt 1980, Beamish and Mahnken 2001).

1.3 Critical Size and Period Hypothesis

High mortality has been found to occur in juvenile salmon during their first year at sea (Parker 1968). Mortality during the juvenile stage is highly variable and can affect the recruitment dynamics and run size of Pacific salmon (Moulton 1997, Beamish and Mahnken 2001, Beamish *et al.* 2007, Beamish *et al.* 2010). Critical periods in survival are thought to occur within a few weeks following ocean entry and during the first winter at sea. These periods of high variability in survival have been directly linked to growth (Hartt 1980, Beamish and Mahnken 2001, Beamish *et al.* 2004, Moss *et al.* 2005, Duffy and Beauchamp 2011) but neither have been tested or proven. As juvenile salmon grow, their morality rates are expected to decrease suggesting faster growth may result in lower size selective mortality (Pearcy 1992, Farley and Trudel 2009). During the first few years, larger salmon show better future survival at sea as they tend to sustain lower predation and competition and are less likely to be affected by size-selective mortality (Beamish and Mahnken 2001, Beamish *et al.* 2004). My thesis focuses on the growth and mortality during these two critical periods.

1.3.1 Early Marine Growth

After hatching in the spring, Pacific salmon migrate into new environments (Groot and Margolis 1991). Some species immediately migrate into the marine environment, while others spend significant time in freshwater but regardless of the time of entry, these juvenile fish enter the ocean at small sizes (Quinn 2005). This early marine stage is a vital part of every juvenile Pacific salmon's life, and mortality during this time is thought to be high (Healey 1980, Quinn 2005, Welch *et al.* 2011). As a result, total marine survival has been related to environmental conditions experienced by juvenile salmon at this time, or by their specific characteristics (Welch *et al.* 2011).

Survival during this time is thought to be highly dependent on growth and the evasion of predators (Mortensen *et al.* 2000, Cooney *et al.* 2001, Beamish and Mahnken 2001, Beamish *et al.* 2004, Farley *et al.* 2007, Daly 2010). Studies have found various species which feed upon juvenile salmon including the spiny dogfish (*Squalus acanthias*), Pacific herring (*Clupea pallasii*) and the lamprey (*Lampetra* spp.) (Beamish *et al.*1995, Beamish *et al.* 2003). Rapid initial growth with an enhanced ability to evade these predators could be essential for the survival of juvenile Pacific salmon during the first few months at sea (Parker 1971).

There has been a growing amount of publications on the early marine growth of Pacific salmon since the 1950s (Beamish *et al.* 2003). Recent investigations on the early marine life stage of salmonids have focused primarily on the critical stages that occur in the first marine year in hopes of finding a better way of managing North Pacific salmon stocks. For example, research done in Alaska on juvenile pink (*O. gorbuscha*) salmon determined that juveniles grew significantly more in summer than in early spring. Higher summer temperatures were positively correlated to this growth (Mortensen *et al.* 2000). Similar results were found in Prince William Sound and Gulf of Alaska from 2001-2004 (Moss *et al.* 2005, Cross *et al.* 2009). By comparing adult and juvenile scale circulus widths, adult survivors were shown to have had higher growth in early marine life than the juveniles. Growth of the survivors increased from summer into the fall showing adult survivors may have been the fastest initial growers (Moss *et al.* 2005, Cross *et al.* 2009). Most studies have found significantly greater early marine growth in adult survivors including sockeye salmon (*O. nerka*) in Alaska (Farley *et al.* 2007, Ruggerone *et al.* 2007), where larger juvenile sockeye may have a survival advantage after the summer and into the first fall at sea. Most recently, hatchery Chinook salmon (*O. tshawytscha*) in Puget Sound showed a positive relationship between size and survival during early marine residency in 1997-2002 (Duffy and Beauchamp 2011). This study showed that growth and ocean conditions during the first marine spring and summer are linked to overall marine survival (Duffy and Beauchamp 2011).

In summary, these studies have shown that high growth may be essential during the first spring, summer and potentially fall of a juvenile salmon's first marine year and that significant size-selective mortality could be occurring in late summer and into the fall and winter.

1.3.2 Overwinter Mortality

A second wave of size-selective mortality is thought to occur during the first winter Pacific salmon endure at sea. Juveniles that survive the first spring and summer at sea by evading predation and size-dependent mortality as a result of rapid growth, are more likely to survive the winter (Beamish and Neville 2001, Beamish *et al.* 2004).

According to Beamish and Mahnken 2001, growth based mortalities may occur throughout the summer, but significant mortality occurs after the summer and into the fall and winter of the first marine year.

Metabolic allometry during winter seasons is significant in some fish populations where smaller fish have lower energy storage with a high metabolic rate while larger fish have higher energy storage and lower metabolism (Oliver *et al.* 1979, Post and Parkenson 2001, Trudel *et al.* 2007a, Kooka *et al.* 2007, Hurst 2007). Mortalities through starvation are expected to occur in fish when energy stores are completely used up. Fish may be much more vulnerable to energy loss during the long winter season due to low food productivity (Post and Evans 1989, Nagasawa 2000, Garvey *et al.* 2004, Beamish *et al.* 2004, Byström *et al.* 2006, Hurst 2007). Significant growth of juvenile Pacific salmon during the spring and summer may be critical for survival during the winter since these fish may have to depend on energy storage from the growing season to fuel their metabolic rate during that time (Beamish and Mahnken 2001, Beamish *et al.* 2004).

Previous studies have shown that high growth and large size are linked to over winter survival in fish. High mortality in small individuals occurred in age-0 largemouth bass (*Micropterus salmoides*) and was correlated with whole-body lipid content during the winter months in Bay Springs Reservoir (Miranda and Hubbard 1994). Individual fish had similar lipid levels in fall and decreased significantly over winter, indicating small fish did not have enough lipid reserves to survive (Miranda and Hubbard 1994). Hudson River striped bass (*Morone saxatillis*) were also greatly affected by winter mortality with an increase in mean length indicating size-selective mortality of smaller individuals

(Hurst and Conover 1998). In Prince William Sound, Alaska, Pacific herring were shown to endure significant loss in energy storage in their first winter at sea, where smaller fish were more affected by these overwinter energy losses than larger individuals (Foy and Paul 1999). Juvenile salmon have also been linked to size selective mortality during winter months due to energy depletion and starvation. Coho salmon (*O. kisutch*) smolt size was found to be related to marine survival in years of low survival during a 17 year study on the southwest end of Vancouver Island, British Columbia (Holtby *et al.* 1990). Ocean conditions and early marine growth were correlated to overall marine survival by comparing circuli spacing of scales in returning adults and environmental conditions between years (Holtby *et al.* 1990). In the Strait of Georgia, Coho salmon that had survived the winter also exhibited larger circuli widths than those that did not (Beamish *et al.* 2004). In the previously mentioned study by Cross *et al.* (2009), pink salmon showed significantly greater growth and body size in adult survivors than juveniles of the same year class during early marine life. Additionally, adult survivors showed higher growth than the average juvenile through the fall indicating size-selective mortality may have occurred after summer (Cross *et al.* 2009). These studies indicate that size-related mortality during the first fall and winter is a potential indicator of brood year strength for Pacific salmon stocks.

A combination of growing large enough to evade predators, feeding successfully during the spring and summer months and continuing a rapid growth pathway to survive the first winter at sea are all factors that may determine survival to adulthood

1.4 Otolith Microstructure and Growth

Otolith microstructure has been used to determine size and growth relationships as well as specific growth profiles of fish (Campana and Thorrold 2001, Sweeting *et al.* 2004). As seen with fish scales, otolith size is often proportional to fish length and the width of circulus increment spacing can reflect daily growth (Campana and Neilson 1985, Campana and Jones 1992, Zhang *et al.* 1995, Harvey *et al.* 2000, Zhang and Beamish 2000, Campana and Thorrold 2001). Otolith microstructure can provide a recorded history of somatic growth from the formation of these daily increments to date of capture is a useful tool for contrasting stage-specific growth performance and survival in fish (Volk *et al.* 1984, Campana and Thorrold 2001).

Freshwater and marine growth of juvenile salmon can be determined separately using daily increment widths by the identification of a freshwater to marine transition zone in the otolith (Neilson and Geen 1985). Application of this approach revealed no significant differences infreshwater and marine growth among species of Pacific salmon off the Washington coast in 1991 and 1992 (Miller *et al.* 1997). Beamish and Zhang (2000) used differences in daily otolith increment patterns to identify ocean-type, stream-type and hatchery-reared Chinook salmon in the Strait of Georgia, depending on time of marine entry and width of circuli increments. Although work has shown that the daily deposition of otolith increments in fish correlates with fish size this is one of the first studies to use otolith microstructure to reconstruct the early marine growth of juvenile Chinook salmon on the Pacific coast during the first year at sea.

1.5 Objectives

The main objective of this thesis was to evaluate factors influencing the overwinter mortality and early marine growth of juvenile salmon during their first year at sea. To evaluate these factors, I established four specific objectives:

1) Evaluate the magnitude of overwinter mortality in juvenile salmon.
2) Determine whether or not overwinter mortality is dependent on size.
3) Determine whether or not energy depletion was larger in smaller fish.
4) Determine whether or not overwinter mortality is dependent on early marine growth.

Chapter 2: Materials and Methods

2.1 Study Site

Juvenile Chinook salmon were caught at sea using a surface trawl in November 2005 and 2006 (fall) and in March 2006 and 2007 (winter) by Fisheries and Oceans Canada (Trudel *et al.* 2007a). Specifically, samples were obtained from the Marble River stock within Quatsino Sound located on the northwest corner of Vancouver Island (50°31.57N, 127°29.97W) (Figure 2.1).

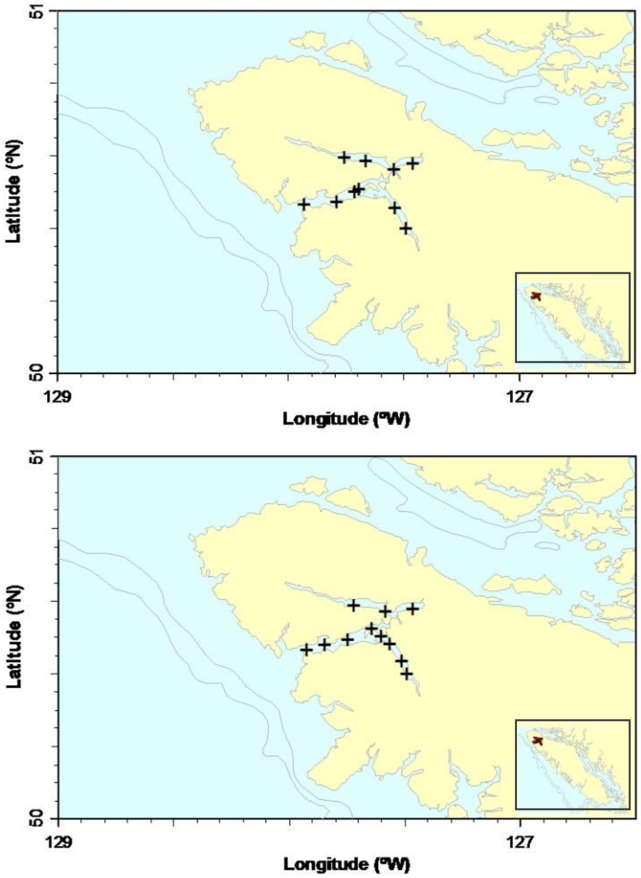

Figure 2.1: Fall (top) and winter (bottom) distributions of juvenile Marble River Chinook salmon collected from Quatsino Sound, British Columbia.

I focused on the Marble River Chinook salmon stock from west coast Vancouver Island (WCVI) as my sample species due to a large collection of data available from Fisheries and Oceans Canada. In addition, Pacific Chinook salmon stocks have had low marine survival and a decline in abundance since the early 1990s (Noakes *et al.* 2000). Chinook salmon are the largest species of Pacific salmon and are found in most of the major river systems along the Pacific coast (Groot and Margolis 1991). Quatsino Sound was chosen as a sample site since the Marble River stock are known to stay within the Sound during their first year at sea (S. Tucker, Fisheries and Oceans Canada, Nanaimo, personal communication). This made it possible to sample the same cohort over time and restrict the geographic range of environmental conditions experienced by these fish.

2.2 Sampling

Fish were collected on November 1-3 in 2005, March 7, 8 and 24 in 2006, November 15-17 in 2006 and March 5-6 in 2007 by a trawl net which was towed at the surface (0-15m) for 30 minutes at approximately five knots (~9.3km/h). Salmon were sorted by species, fork length and weighed on board. A skin sample was removed and preserved in 95% ethanol for subsequent DNA analysis. DNA analysis was used to determine the natal origin of the juvenile salmon caught at sea (Beacham *et al.* 2006, S. Tucker, Fisheries and Oceans Canada, Nanaimo, personal communication). Only juvenile Chinook salmon originating from the Marble River were retained for this study. Sagittal otoliths were removed and placed in organized trays. The remainder of the carcass was frozen for later analysis of stomach contents, stable isotopes and cesium content. A CTD (Conductivity-Temperature-Depth System) was deployed at each station from the surface to 5 metres from the bottom or to 250 metres when bottom depth was greater than 250 metres. Readings from the downcast and up cast were averaged into 1 metre bins.

2.3 Otoliths

2.3.1 Otolith Microstructure

Fish otoliths are an important tool for reconstructing the growth history of juvenile salmon during their freshwater and marine life stages (Zhang *et al.* 2000/1995?, Sweeting *et al.* 2004). Age determination and growth-rate estimation are possible by analyzing otolith growth ring increments and patterns (Fukuwaka 1998). Layers of calcium carbonate ($CaCO_3$) build upon one another daily as the fish grows forming dark and light lines within the otolith, proportional to the daily growth of the fish (Panella 1971, Brothers *et al.* 1974, Campana and Neilson 1985, Campana and Thorrold 2001, Saito *et al.* 2007). Visual marks can be seen when physiological changes occur such as the transition from freshwater to marine environments in anadromous fish. Significant marks include time of hatching, first feeding, marine entry and starvation periods (Panella 1971, Campana 1983). A distinct dark mark with wider daily increments and more uniform width is found to occur on anadromous fish otoliths upon entering saline water (Volk *et al.* 1984, Neilson *et al.* 1985b, Volk *et al.* 2000). Visually, a marine entry point can be seen on otoliths that have been properly prepared for microstructural analysis (Figure 2.2). A wide and much darker increment is found at similar distances from the primordial axis of the otolith (Zhang and Beamish 2000).

Visual estimates of marine entry point were measured to determine when juvenile Chinook salmon transitioned from the freshwater to marine environment. A distinctive mark was found on most otoliths and used for estimates of in otolith size at marine entry, back-calculations of fish length at marine entry, and early marine growth during the first month at sea.

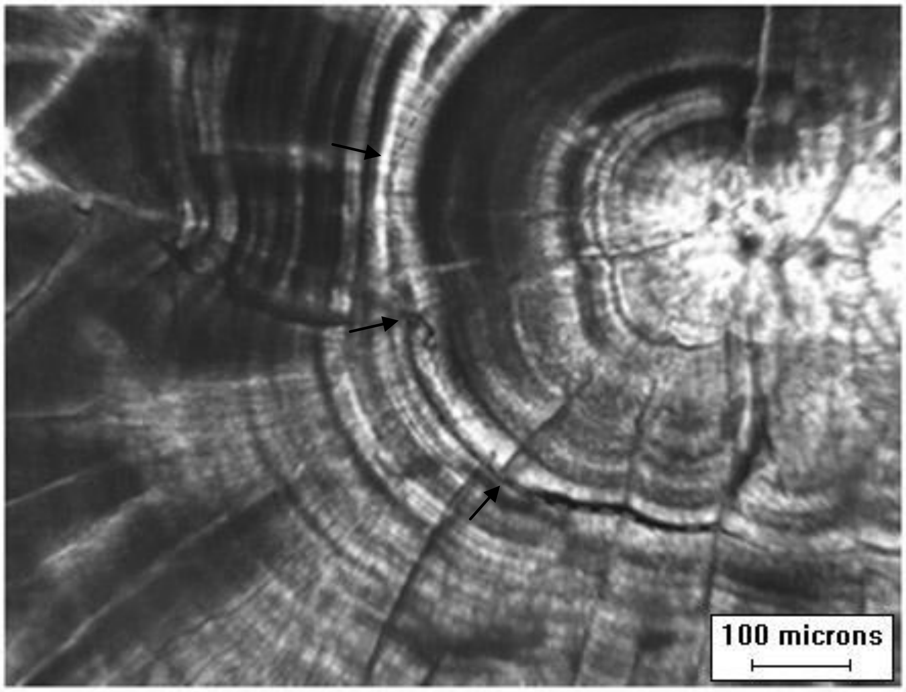

Figure 2.2: Marine entry point (arrows) showing transition between the freshwater and marine environment on the juvenile Chinook salmon sagittal otolith (100X magnification).

2.3.2 Otolith Chemistry

As Pacific salmon move from freshwater to marine environments the surrounding aquatic environment changes, including water chemistry (Quinn 2005). Otoliths do not reabsorb as do scales in many fish when they encounter stress but grow continuously (Campana and Thorrold 2001, Wells *et al.* 2003). Investigations on the use of the chemical analysis of otoliths have increased significantly over the years and more information has been available to researchers due to technological improvements (Campana and Thorrold 2001, Godbout *et al.* 2010). These ear bones have the ability to show chronological changes in temperature, marine and freshwater inhabitance, migration routes, age and natural thermal tagging (Campana 1999, Campana and Thorrold 2001, Macdonald and Crook 2010).

In this study, the trace element ratios of strontium and barium in juvenile Chinook salmon otoliths were analyzed to determine the freshwater to marine transition area on the otolith itself. This was necessary to determine whether or not the visual estimates of ocean entry lined up with the large changes in water chemistry. The ratios of both elements change with ambient salinity and have been readily used in determining marine entry and estuary residence of anadromous fishes (Bath *et al.* 2000, Campana and Thorrold 2001, Miller *et al.* 2010, Macdonald and Crook 2010). Physiological changes that occur when juvenile Pacific salmon enter the marine environment include a change of chemistry within the otoliths themselves. Otoliths grow continuously during the life of fish and elements such as Sr and Ba are permanently incorporated into the otolith on a daily basis from the ambient aquatic environment. Since otoliths are calcified material, chemical signatures of Sr and Ba remain stable as the fish migrate from freshwater to saline water allowing an accurate estimation of surrounding chemical composition when analyzing the otoliths (Campana 1999, Campana and Thorrold 2001, Bath *et al.* 2000, Wells *et al.* 2003). The ratio of Sr to Ca (Sr:Ca) often occurs in low concentrations in freshwater relative to Ca and the ratio is relatively stable in marine waters while on the contrary, the ratio of Ba to Ca (Ba:Ca) is lesser in marine waters and greater in freshwater (Bath *et al.* 2000, MacDonald and Crook 2010).

2.4 Otolith Growth Methods

Juvenile Chinook salmon otoliths were removed from fish collected during the 2006-2007 fall and winter seasons. Fish were selected to cover the observed range of size and were sorted by length from the smallest to largest. In total 83 Marble River otoliths were used for early growth analysis.

2.4.1 Measurements

Sagittal otoliths were removed, cleared of their outer sac, and placed in organized trays to dry. Left otoliths were used unless unavailable or broken during analysis in which case the right otolith was used. A replacement pair was obtained by using the otoliths removed from a fish that was not initially retained in the analysis. Each otolith was affixed, sulcus (medial) side up, to a glass slide with thermoplastic resin/crystal bond. Lapping film of various grit (60, 30, 0.3 µm) was used with water to grind the otoliths down to the primordial layer. The resin was then melted on a hotplate and otoliths were flipped over carefully (sulcus side down) and were ground down again to the primordial plane. Polishing continued with finer grit lapping film until daily increments were apparent on the dorsal side. Photos and measurements were made throughout the grinding process to ensure over grinding did not occur. Slides were allowed to dry, individually labelled and placed in slide trays for storage (Secor *et al.* 1992).

A compound microscope with a digital camera attached was used at various magnifications (25X – 400X) to take photos of otoliths at various stages. These stages include before grinding, when partially ground and the marine entry point was visible, and when daily increments were visible. Photos were taken using Spot® at the Advanced Imaging Laboratory at the University of Victoria. Photos were then imported into Adobe Photoshop® and converted to greyscale before measurement in ImagePro Plus 6.3®. Once imported, the images were calibrated to various magnifications. Measurements were made using a macro program specifically used for otolith and scale analysis.

Three main measurements were made per otolith:

1) Otolith radius at capture: from primordial plane to dorsal edge (Figure 2.3A)

2) Otolith radius at marine entry: from primordial plane to marine entry point on dorsal edge (visually estimated) (Figure 2.3B).

3) Early marine growth: measurements were made every 7th daily otolith increment (one week of growth) from the marine entry point (Figure 2.4).

Measurements were made 3 times per otolith per measurement type and an average was taken. The dorsal edge of the otolith was chosen as it showed the most consistent and clear daily increments and tended to crack less frequently than other areas of the otolith. Measurements were made for the first four weeks of marine entry (28 increment widths – or approximately one month at sea) as autocorrelation in increment widths is minimized in groups of 7-10 (Campana and Neilson 1985, Pepin *et al.*2001). In addition, measurement error was expected to be smaller on weekly versus daily growth estimates due to autocorrelation that occurs between 7-10 otolith increments (Pepin *et al.*2001).

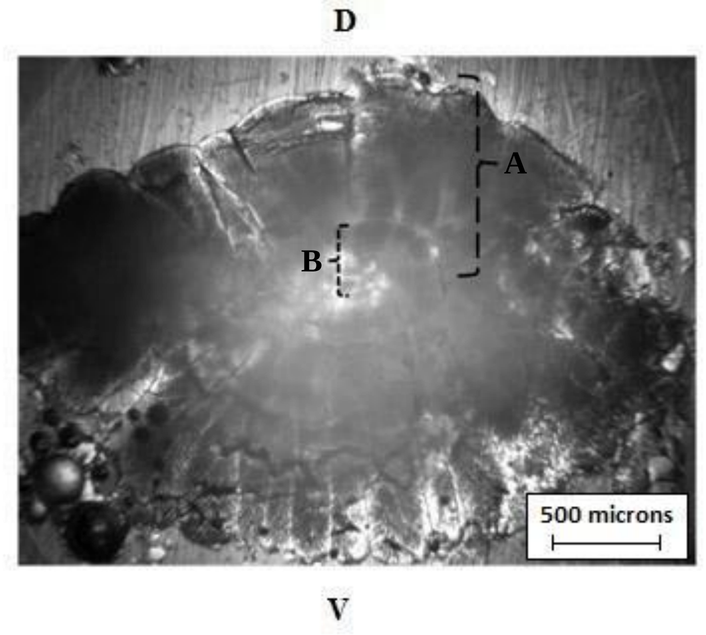

Figure 2.3: Photo showing measurements made after grinding otolith to primordia: **A)** Otolith radius from primordial axis to dorsal edge (D). **B)** Visually estimated otolith radius at marine entry from primordial axis to marine entry check (25X magnification). V represents the ventral side of the otolith.

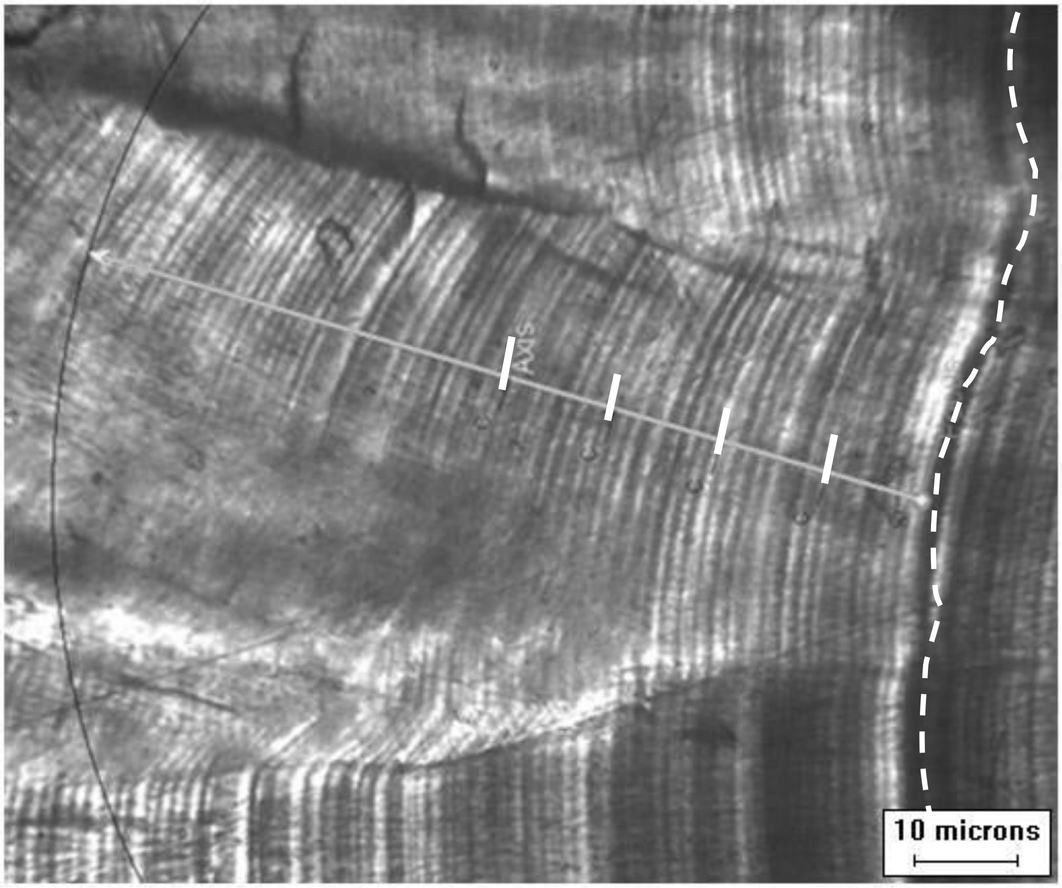

Figure 2.4: Early marine growth measurements of weekly increment widths (white dashes off of grey arrow) every 7 increments from marine entry point (dashed line) (400X magnification).

2.4.2 Error Analysis

A pilot study revealed that operator error was generally less than 5% regardless of otolith size or magnification at which the otolith was viewed (250X, 400X). Repeated measurements of otolith radius at capture and marine entry as well as weekly growth profiles were used to calculate error using a coefficient of variation (Appendix D). Additionally, right and left otoliths were assumed interchangeable and not significantly different (Secor *et al.* 1992, Harvey *et al.* 2000) but left otoliths were randomly chosen as the preferable type.

2.4.3 Chemical and Visual Validation of Marine Entry

In order to estimate early marine growth in the juvenile Chinook salmon sampled, a marine entry point on each otolith had to be determined. Visual and chemical estimate methodologies were used to establish otolith width at marine entry.

The marine entry point on 74 juvenile salmon otoliths was visually estimated in this study and 12 of these samples were then chemically analyzed to validate visual accuracy. Otolith chemistry analysis estimated otolith width at marine entry and not otolith radius at marine entry as previously measured. To determine otolith width at marine entry, six otoliths were re-measured for otolith width values. Four otoliths did not show marine entry check on the vental side and could not be re-measured therefore otolith radius values were doubled. Dorsal and ventral sides are not always symmetrical and I have taken these inaccuracies into account as potential error in my analysis.

Sagittae were prepared as described in Miller (2007) and were sent to Oregon State University, where otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were measured using a VG PQ ExCell inductively coupled plasma mass spectrometer (ICPMS) with a New Wave

DUV193 excimer laser. Data were collected along the ventral-dorsal axis on a transect that intersected the core region of the otolith (Figure 2.5). A laser pulse rate of 10 Hz with a 40 µm diameter spot size was set and travelled at 5 µm/s. Limits of detection (ppm) were calculated as 3 standard deviations of background measurements: Ca = 0.02, Sr = 0.03, and Ba = 0.008. Elemental ratios were converted from normalized ion ratios as described in Miller (2007), converted to molar ratios based on the molar mass of Ca, Sr, and Ba, and presented as mmol/mol for Sr:Ca and µmol/mol for Ba:Ca. The mean percent relative standard deviations (%RSD) for NIST 612 glass during data collection were ^{43}Ca = 2.9, ^{86}Sr = 6.7, and ^{138}Ba = 4.41%. A calcium carbonate standard of known composition developed by the US Geological Survey (USGS MACS-2) provided an estimate of accuracy: measured values of these elements were within 2% of known values for Sr:Ca and Ba:Ca and 11% low for Ba:Ca. Otolith Ba:Ca values were corrected for this difference. Otolith Sr:Ca and Ba:Ca data and structural analysis were then combined. For each otolith, the width at the time of marine entry was determined by the initial and abrupt increase in otolith Sr:Ca, which indicates exit from freshwater, prior to stabilizing at brackish/ocean values. This transition was verified by the occurrence of low or declining otolith Ba:Ca at the same time as the abrupt increase in otolith Sr:Ca (Miller *et al.* 2010) (Figure 2.6). These otoliths were analyzed by Dr. Jessica A. Miller at the Coastal Oregon Marine Experiment Station at Oregon State University.

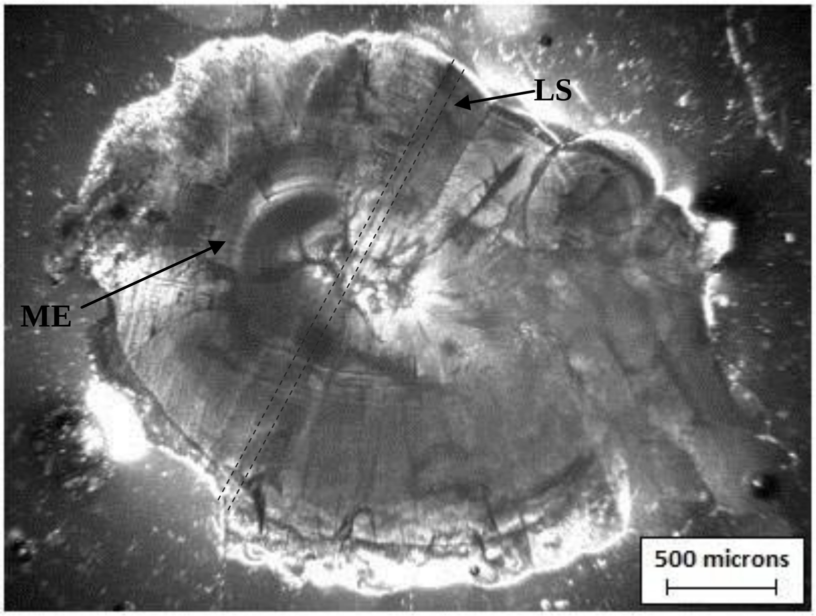

Figure 2.5: Juvenile Chinook salmon otolith showing the laser scar (LS) and marine entry point (ME) (25X magnification).

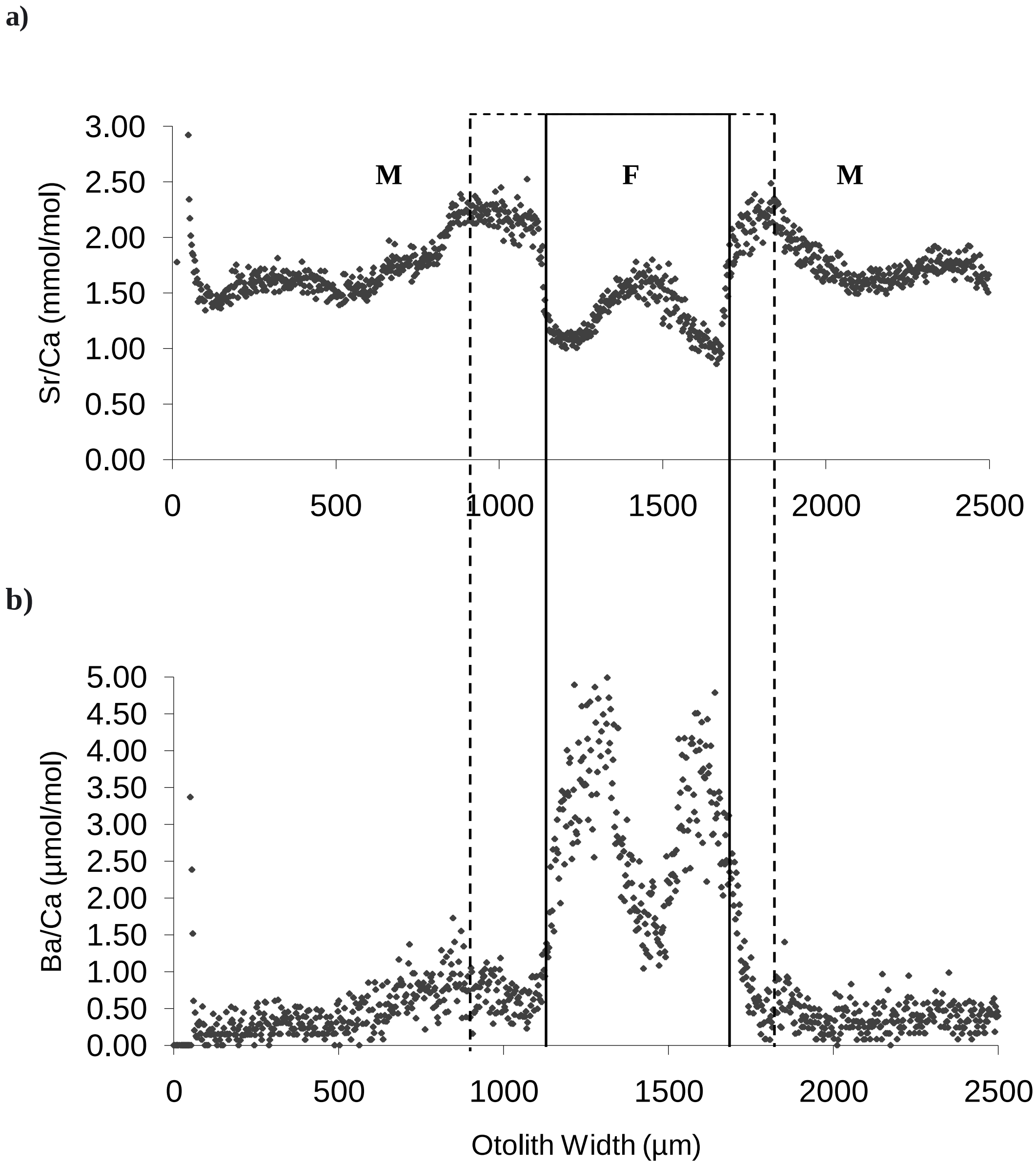

Figure 2.6: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at marine entry. Boxed area indicates freshwater residency (F), marine residency (M), and marine entry point (black lines). Dashed lines indicate a possible transition zone between freshwater and marine environments. Insignificant pre-ablation values are seen from 0-20µm.

2.5 Energy Density and Gut Fullness

Under starvation, smaller fish are expected to use up energy reserves faster than their larger counter parts due to higher weight-specific metabolic rates (Post and Evans 1989). In this study, I used total energy density derived from the percent dry weight of the fish as a surrogate for energy reserves. Energy density was calculated from percent dry weight using the following power function equation obtained from Trudel *et al.* (2007a):

$$ED = 0.031 * PDRYw^{1.62} \qquad (1)$$

Where ED represents energy density and $PDRY_w$ represents the percent dry wet weight. Dry weight was determined by drying the carcass at 60°C in a drying oven until no changes in mass was observed (ca. 3-4 days).

Stomach fullness has the potential to relate fish feeding success during fall and winter to energy storage, size-selective overwinter mortality and adult recruitment (Brodeur *et al.* 2000a). An index of gut fullness was used from Trudel and Boisclair (1993) was calculated by using the stomach contents and weight of the juvenile salmon as:

$$GF = \frac{SC}{W} * 100 \qquad (2)$$

Where GF represents gut fullness, SC represents stomach contents in gram wet weight and W represents weight in grams.

2.6 Data Analyses

2.6.1 Catch-per-unit-effort

Catch-per-unit-effort (CPUE) was estimated by dividing the total number of juvenile Marble River Chinook salmon caught in a tow by the product of the distance towed and width of the net. The CPUE data were log transformed after adding 1 to all data to avoid negative transformation ($\log_{10}$CPUE+1). Catch data were compared between seasons in all years using a two-way analysis of variance. Bartlett's test was used to determine if variances between seasons were equal for all years.

2.6.2 Overwinter Mortality

Overwinter mortality was determined by dividing the mean winter CPUE by the mean fall CPUE for each year as follows:

$$OWM = \left[1 - \left(\frac{\text{Mean Winter CPUE}}{\text{Mean Fall CPUE}}\right)\right] * 100 \tag{3}$$

Where OWM is the overwinter mortality (in percent). Overwinter mortality was calculated separately for 2005-2006 and 2006-2007.

2.6.3 Ocean Entry Size

Mean fall and winter otolith radius at capture were compared using one-way analysis of variance and Bartlett's test for variance. Otolith radius at marine entry required non-parametric analysis of medians (Mann-Whitney U-test) and variance (Levene's Test) since these data were not normal.

The back-calculated fork lengths at ocean entry of 70 juvenile Chinook salmon were determined using otolith measurement data. Back-calculations of ocean entry size of Marble River juvenile Chinook salmon in 2006-2007 were estimated using the Dahl Lea method as follows (Lea 1910, Carlander, 1977, Francis 1990):

$$\mathrm{Ln} = \frac{\mathrm{On}}{\mathrm{Oc}} * \mathrm{Lc} \tag{4}$$

Where *Ln,* is the fork length of fish at marine entry (mm),

On, is the otolith radius at marine entry (µm),

Oc, is the otolith radius capture (µm), and

Lc, is the fork length of fish at capture (mm),

The Dahl-Lea method was preferred over other methods, as it predicted ocean entry size closer to the expected size of ocean-type Chinook salmon smolts (Healey 1991, Groot and Margolis 1991, Quinn 2005). Back-calculated ocean entry size data were compared between seasons using non-parametric Mann-Whitney U-test for statistical analysis of means and Levene's test for variance.

2.6.4 Early Marine Growth

Early marine growth was estimated using otolith microstructure for 23 and 21 juvenile Chinook salmon in November 2006 and March 2007, respectively (Section 2.4). The distance on the otolith from marine entry point was measured for the first four weeks after marine entry. Mean weekly otolith growth measurements for each of the first four weeks and mean monthly measurements after marine entry were compared between fish collected in the fall and winter using a two-way analysis of variance, as these data were normally distributed. Bartlett’s test was used to compare variances between these groups. The slopes of these measurements were compared between fall and winter fish to determine growth differences using a one-way analysis of variance and Bartlett’s test for equal variance.

Monthly and weekly mean otolith widths were plotted against fork length at capture and marine entry to see if otolith growth during early marine residency was related to fish size at capture. A linear regression model was used to test the relationship between otolith growth and fish size.

2.6.5 Energy Density and Gut Fullness

Normal distribution assumptions were not met for data on energy density or gut fullness, therefore the Mann-Whitney U-test was used to compare differences between fall and winter seasons. Comparisons of variance in these groups were done using Levene’s test for homogeneity of variances.

Energy density was plotted against fork length in fall and winter seasons. A non-parametric ANCOVA was used to test for equality of the relationship between fall and winter energy density and size for 2005-2006 and 2006-2007. Lines were derived using a loess smoothing curve. As discussed in section 2.5, smaller individuals are expected to show significant depletion of energy reserves over winter, therefore the relationship between energy density and size is expected to decrease from fall to winter (Figure 2.7).

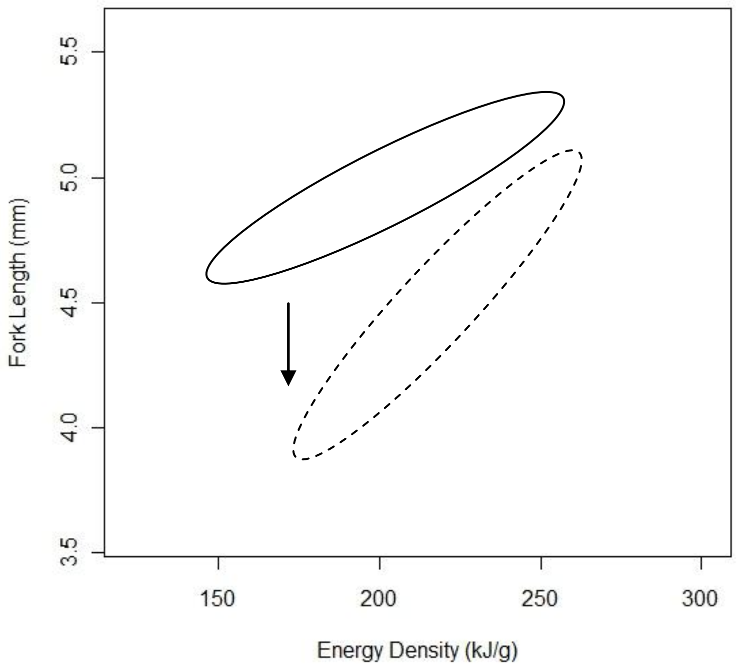

Figure 2.7: Expected relationship between energy density and size from fall (solid) and winter (dashed) fish. Arrow indicates downward shift in energy storage of smaller individuals.

2.6.6 Plankton Biomass

Total plankton biomass was compared between seasons for 2005-2006 and 2006-2007. Total plankton dry weight was normally distributed in 2006-2007 therefore a one-way ANOVA was used to compare biomass between seasons and Bartlett's test to compare variance. Similar data were not normal in 2005-2006 and a Mann-Whitney U-test was used to compare biomass between seasons and Levene's test to test for equal variance.

2.6.7 Size-selective Mortality

To determine whether size-selective mortality occurred between fall and winter, the mean size of fish caught in the fall was compared to those fish caught in the winter as well as the variance in size of those fish. If size-selective mortality has occurred, the fish collected in the winter should be larger with lower variance compared to the fall. Mean fork lengths were compared between seasons with the non-parametric Mann-Whitney U-test. Variance in fish size was analyzed using Levene's test for homogeneity since fork length data were not normal.

Additionally, empirical quantile-quantile plots were used to further determine evidence of size-selective overwinter mortality. An empirical quantile-quantile plot is a method for comparing two probability distributions by plotting paired-percentiles from two distributions (Post and Evans 1989). In this study, quantile-quantile plots were used to describe the shape of the distribution by plotting 10, 25, 50, 75, 90, 95 and 99th percentile of the winter size as a function of the same percentile for the fall size for years 2005-2006 and 2006-2007 (Appendix C). If the slope of the quantile line is significantly smaller than the 1:1 line it would indicate that size-selective mortality against smaller fish has occurred (Post and Evans 1989). A slope equal to the 1:1 line indicates that there was no significant size-selective mortality between the two periods (Post and Evans 1989). A t-test of slope and standard error was used to determine differences between the quantile and 1:1 lines.

Chapter 3: Results

3.1 Temperature and Salinity in Quatsino Sound

Juvenile Chinook salmon were collected in the fall (November) and winter (March) seasons during 2005-2006 and 2006-2007 in Quatsino Sound. Sea surface temperature (SST) and sea surface salinity (SSS) was recorded for fall and winter seasons in 2005-2006 and 2006-2007 (Table 3.1). Sea surface temperature was significantly different between seasons (W=590, p<0.01) and years (W=546.5, p<0.01), where 2005-2006 was significantly higher than 2006-2007. Sea surface salinity was significantly different between seasons (W=79.5, p<0.01) but not between years (W=368, p=0.4).

Table 3.1: Mean sea surface temperature (SST) and salinity (SSS) in the fall and winter seasons of 2005, 2006 and 2007 in Quatsino Sound, British Columbia.

Year	Dates	N	Mean SST (°C)	SD	Mean SSS (‰)	SD
2005	Nov. 1-3	15	10.1	0.39	24.2	4.13
2006	Mar. 7,8,24	16	8.6	0.37	29.4	1.16
2006	Nov. 15-17	10	8.6	0.54	25.8	3.67
2007	Mar. 5-6	11	7.9	0.21	27.6	1.66

3.2 Catch per Unit Effort and Overwinter Mortality

The number of juvenile Marble River Chinook salmon caught per km^2 decreased by 92% from fall to winter in 2005-2006 and 89% from fall to winter 2006-2007. A two-way analysis of variance showed that catch per unit effort ($\log_{10}$CPUE+1) of juvenile Marble River Chinook salmon showed that the number of fish caught per tow was significantly different between seasons (F=24.4, d.f=1,48, p<0.01) and years (F=9.8, d.f.=1,48, p<0.01) (Figure 3.2). Variance in $\log_{10}$CPUE+1 between seasons in 2005-2006 was significantly different (K^2=5.6, d.f.=1, p<0.05) but was not in 2006-2007 (K^2=1.2, d.f.=1, p=0.3).

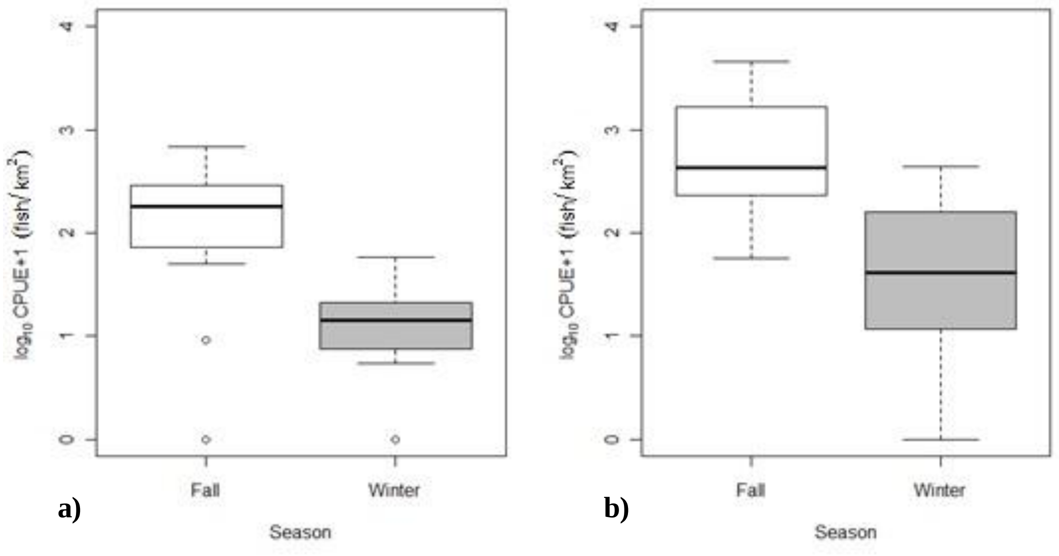

Figure 3.1: Catch per unit effort ($\log_{10}$CPUE+1) during fall and winter **a)** 2005-2006 and **b)** 2006-2007.

3.3 Fish Size

Fall juveniles averaged with a fork length of 163.0mm and winter fish at 211.7mm in 2005 and 2006 respectively. Corresponding values for the following cohort sizes were 166.4mm in the fall of 2006 and 204.2mm in the winter of 2007. Mean fork length at capture was significantly lower in fall samples than winter samples in 2005-2006 (W = 35, p< 0.01) (Figure 3.2a) and 2006-2007 (W=2022.5, p<0.01) (Figure 3.2b). There was no difference in variance of fish fork lengths between seasons in 2005-2006 (F=0.5, d.f.=1,181 p=0.48) or 2006-2007 (F=0.3, d.f.=1, 324, p=0.6).

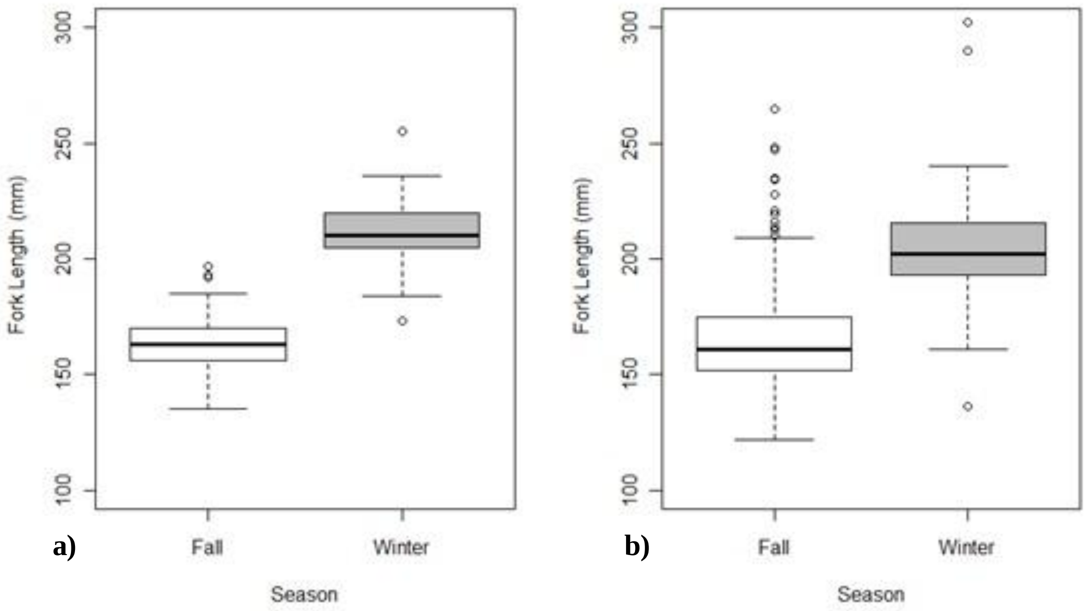

Figure 3.2: Mean fish fork lengths of fish captured in **a)** fall 2005 (N=151) and winter 2006 (N=32), and **b)** fall 2006 (N=254) and winter 2007 (N=72).

3.4 Marine Entry

3.4.1 Validation of Marine Entry Point

Visually estimated marine entry points on otoliths were successfully validated through chemical analyses. The relative differences in the visually estimated diameter of the otolith at marine entry and the diameter estimated though chemical analysis were generally within 10% (Table 3.2). The chemical estimation of otolith width at marine entry was lower for two fish (10, 11) compared to visual estimates (Table 3.2). Two otoliths (7, 8) were crystallized and did not show any chemical pattern for marine entry estimation thus were not used in the analysis. Various otoliths showed higher than typical levels of Sr and Ba upon ocean entry (Appendix B).

Table 3.2: Estimates of otolith size at marine entry for visual and chemical analysis of 12 fall and winter otoliths (Corresponding figures in Appendix B).

Otolith	Season	Fork Length at Marine Entry (mm)	Visual Estimation (mm)	Chemical Estimation (mm)	Relative Difference
1	Fall	72.9	0.81	0.86	0.07
2	Winter	52.5	0.61	0.58	-0.05
3	Winter	79.7	0.65	0.65	-0.01
4	Fall	61.3	0.67	0.68	0.01
5	Winter	55.6	0.61	0.61	0.01
6	Winter	70.9	0.75	0.71	-0.05
7	Winter	52.9	0.63	N/A	N/A
8	Fall	59.3	N/A	N/A	N/A
9	Fall	65.9	0.68	0.62	-0.09
10	Fall	53.4	0.63	0.54	-0.18
11	Fall	54.8	0.65	0.30	-1.15
12	Winter	60.9	0.69	0.61	-0.13

3.4.2 Otolith and Fish Size

Otolith size was positively correlated with fork length at capture (r^2=0.73, F=208.7, d.f.=74, p<0.01), (Figure 3.3a) indicating that otolith growth is correlated with somatic growth. Otolith radius at marine entry was not correlated to fork length at capture (r^2=0.05, F=3.8, d.f.=72, p=0.06), (Figure 3.3b). Two fish had a much larger size at ocean entry for their lengths which correspond to hatchery fish that were released at an abnormally large size (~25g) by the Marble River hatchery in 2006 (Figure 3.3b).

Mean otolith radius at capture was 0.97mm and 1.09mm in the fall and winter seasons, respectively. Mean otolith radius at marine entry was 0.32mm in the fall season and 0.33mm in the winter season. There were significant differences between mean otolith radius at capture of fall and winter juveniles (F=39.9, d.f.=1, 74, p<0.01) with no difference in variance (K^2=2.0, d.f.= 1, p=0.2) (Figure 3.4a) while mean otolith radius at marine entry was not different between fall and winter juveniles (W=703, p=0.8) with no difference in variance (F=0.9, d.f.=1,72, p=0.3) (Figure 3.4b).

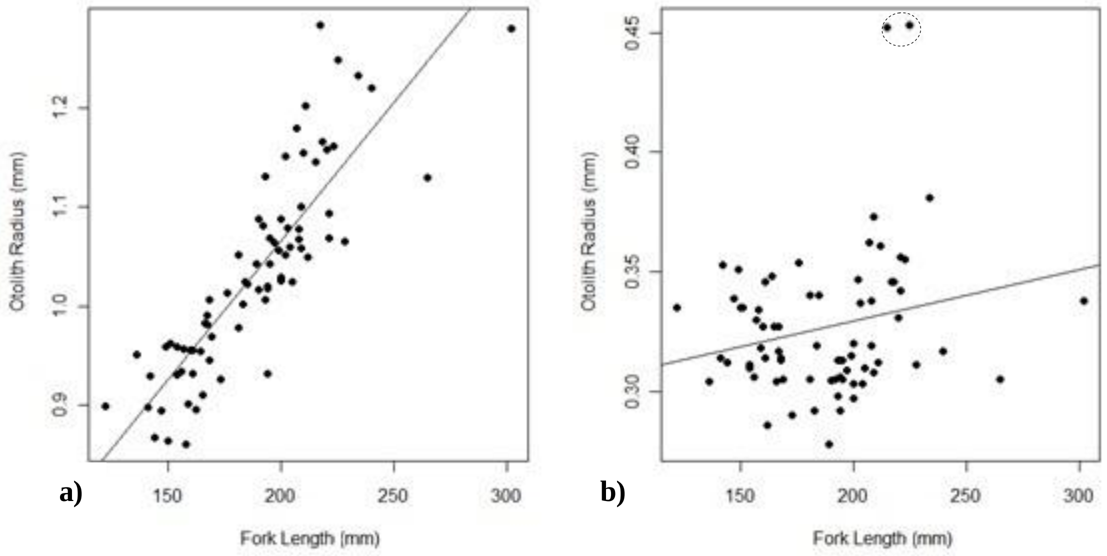

Figure 3.3: Relationship between otolith radius and fork length **a)** at capture (r^2 =0.73, N=77) and **b)** at marine entry (r^2=0.05, N=74) where the dashed circle represents two tagged fish.

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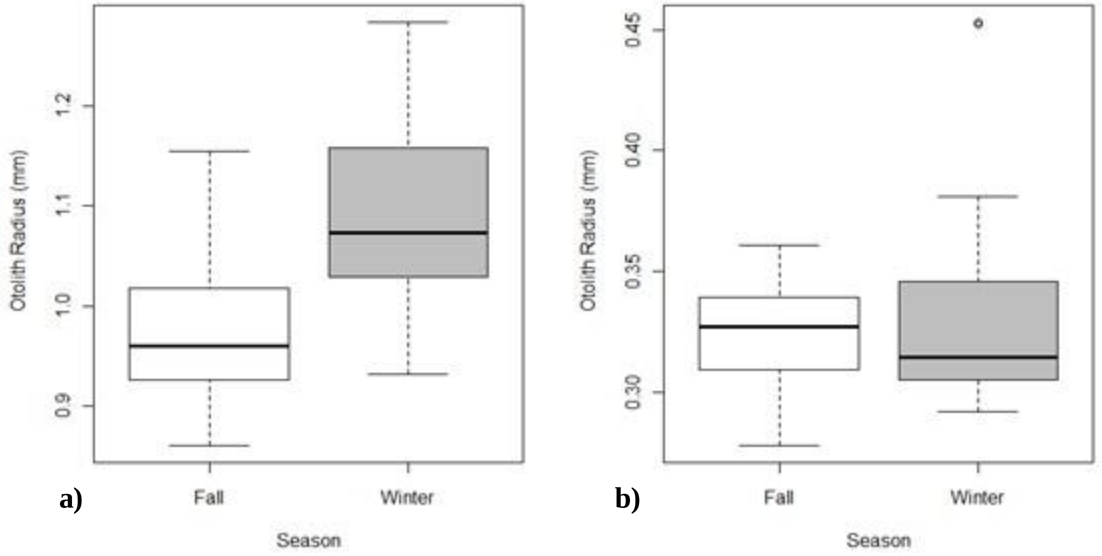


Figure 3.4: Otolith radius at **a)** capture (N=77) and **b)** marine entry (N=74) for fall and winter seasons of 2006-2007.

3.4.3 Ocean Entry Size

Ocean entry sizes of juvenile Chinook salmon in Quatsino Sound in 2006 were estimated using the Dahl-Lea back-calculation method as described in section 2.6.2. Mean fork lengths at marine entry were 56.59mm and 61.63mm for fall and winter fish, respectively. Average fork length at marine entry was significantly higher in winter fish than fall fish (W = 355, $p<0.01$) (Figure 3.5). No difference in variance was found between ocean entry size of fish caught in the fall and winter (F= 1.1, d.f.=1, 68, p= 0.3).

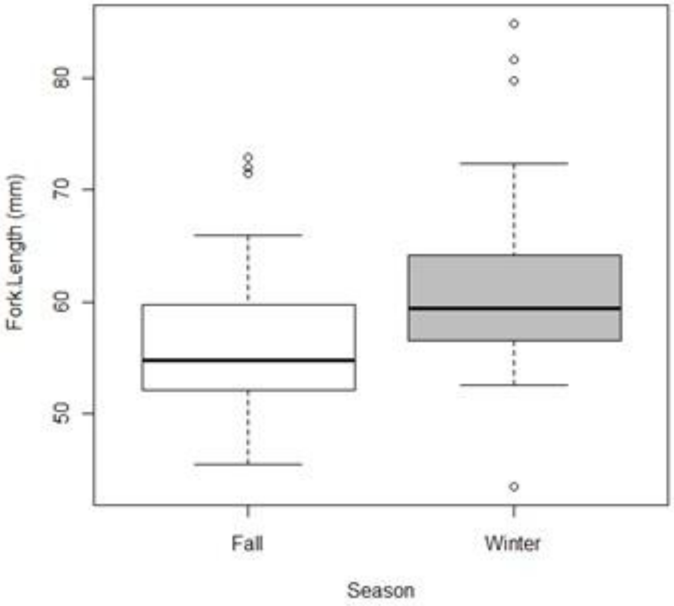


Figure 3.5: Mean fish fork lengths at ocean entry of juvenile Chinook salmon collected in the fall and winter 2006-2007 (N=70).

3.5 Early Marine Growth

There was no relationship in weekly growth increment width (for all four weeks) and fish fork length at marine entry (r^2= 0.03, F=0.3, d.f.=4,38, p=0.9) (Figure 3.6). Early marine growth profiles for fall and winter fish during the first month at sea (Figure 3.7 and 3.8) showed no significant difference in slope (F=0.3, d.f.=1,42, p=0.6) and no difference in variance (K^2=0.2, d.f.=1, p=0.7) (Figure 3.9).

Similarly, the weekly mean increment widths were not significantly different between fall and winter samples for all four weeks (F=0.9, d.f.=1,3, p=0.3) but were significantly different between weeks (F=6.65, d.f.=1,3, p<0.01) (Figure 3.10). Variance in growth did not change between all four weeks (K^2=7.4, d.f.=3, p=0.06) or between seasons (K^2= 1.6, d.f.=1, p=0.2). Average weekly otolith growth increased from 38.4µm to 48.9µm during the first and fourth week following ocean entry for juvenile Chinook salmon caught in the fall (Figure 3.10a). A similar pattern was observed with 37.5µm to 46.4µm for juvenile Chinook caught in the winter (Figure 3.10b).

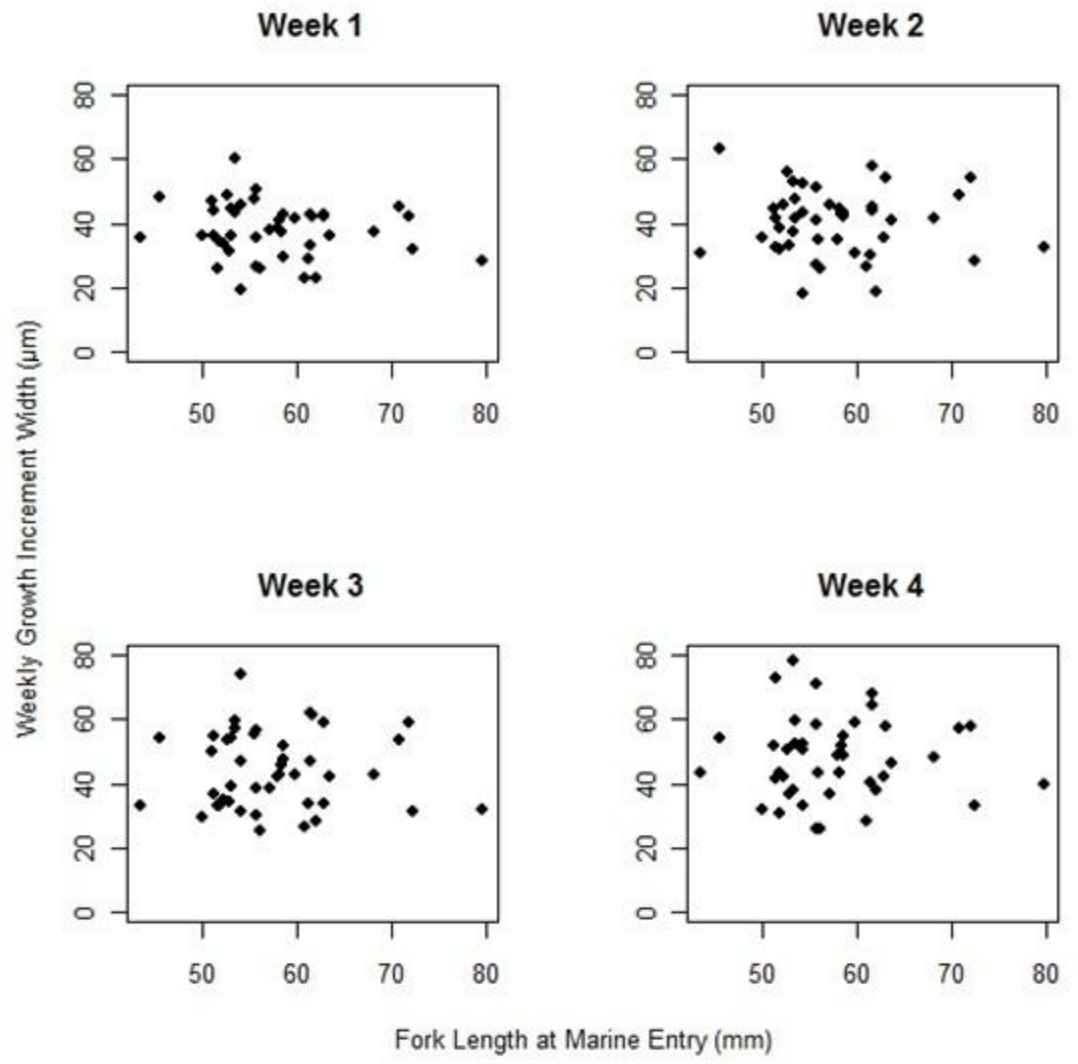


Figure 3.6: Weekly growth increment widths versus fork length at marine entry for the first four weeks of juvenile Chinook salmon ocean entry in 2006-2007 (N=44).

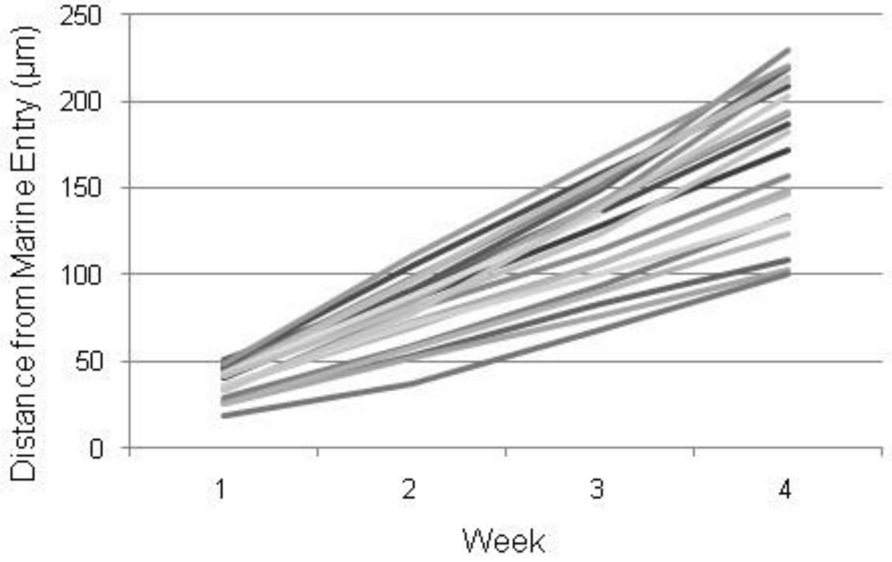


Figure 3.7: Distance from marine entry point to dorsal edge over the first four weeks of ocean residency from juvenile Chinook salmon otoliths collected in the fall of 2006 (N=23).

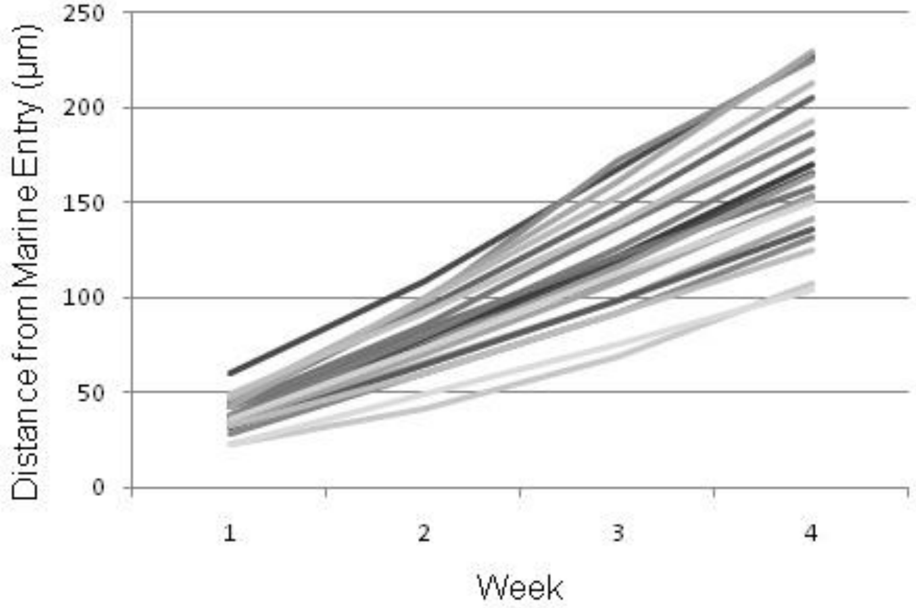


Figure 3.8: Distance from marine entry point to dorsal edge over the first four weeks of ocean residency from juvenile Chinook salmon otoliths collected in the winter of 2007 (N=21).

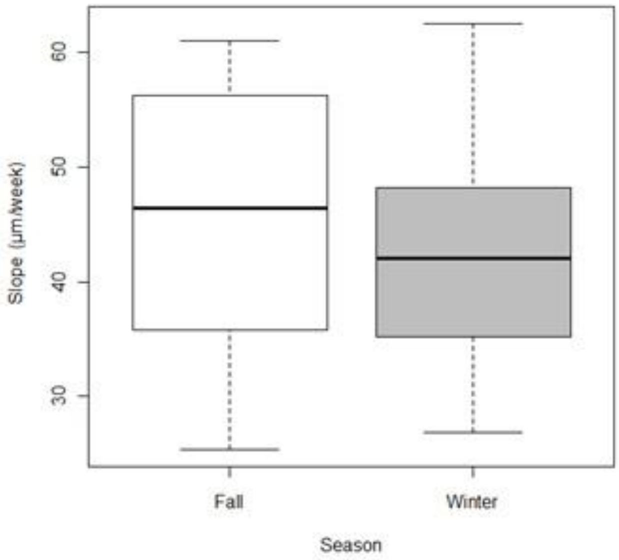


Figure 3.9: Slope of early marine growth profiles in fall 2006 and winter 2007 juvenile Chinook salmon (N=44).

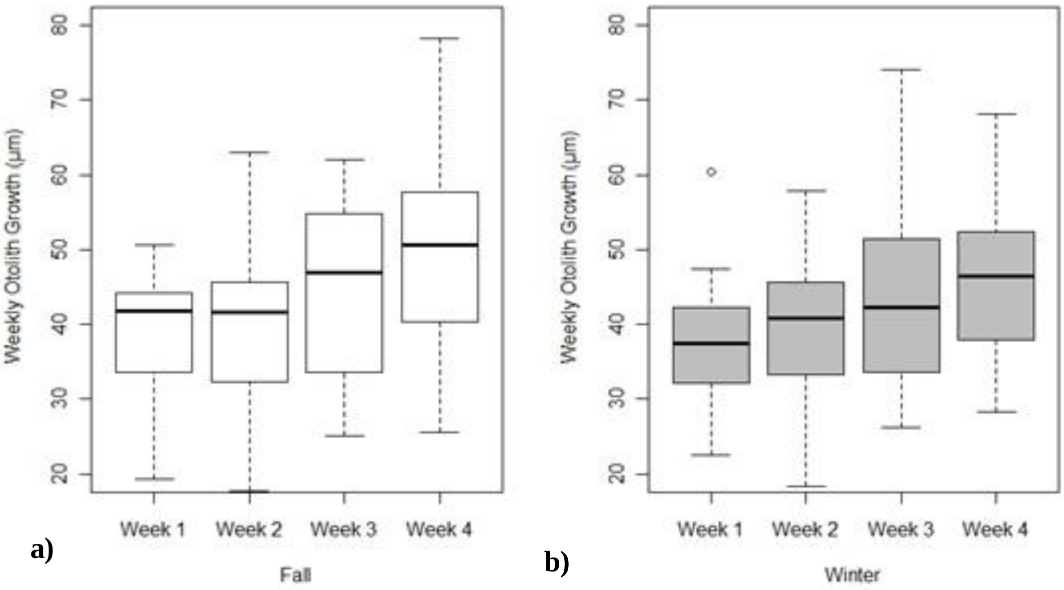


Figure 3.10: Comparison of weekly otolith growth during the first four weeks of marine residency in **a)** fall (N=23) and **b)** winter (N=21) juvenile Chinook salmon in 2006-2007.

3.6 Energy Density and Gut Fullness

Energy density of juvenile Chinook salmon averaged at 4.2kJ/g and 4.4kJ/g in the fall of 2005 and 2006, respectively. Corresponding values for the following cohort were 4.4kJ/g and 4.3 kJ/g (Figure 3.11). A significant difference in energy density was found between seasons in 2005-2006 (W=776, $p<0.01$) (Figure 3.11a) as well as variance (F=12.7, d.f.=1,129, $p<0.01$). Mean energy density and variance were higher in winter than fall during 2005-2006. There was a significant difference in energy density seasons in 2006-2007 (W=12546.5, p=0.05) (Figure 3.11b) but variance was equal (F=0.2, d.f.=1,296, p= 0.7).

Larger fish generally had higher energy densities than smaller fish, though energy density did not decrease faster over winter in smaller fish than in larger fish. Neither year showed any indication of loss in energy reserves in smaller fish between fall and winter seasons (Figure 2.7). The non-parametric regressions of energy density and fish size for fall and winter seasons in 2005-2006 were not equal (Non-parametric ANCOVA: h=4.9, p=0.06) (Figure 3.12a) while in 2006-2007 they were equal (Non-parametric ANCOVA: h=13.3, $p<0.01$) (3.12b).

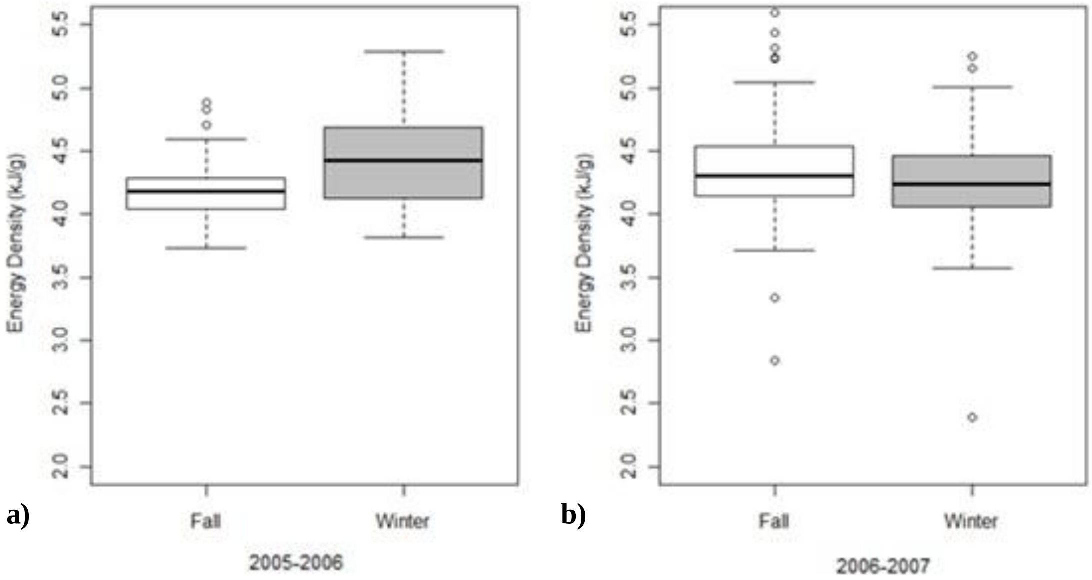


Figure 3.11: Energy density between fall and winter seasons **a)** in 2005-2006 (N=107, 24) and **b)** in 2006-2007(N=155, 141) juvenile Chinook salmon.

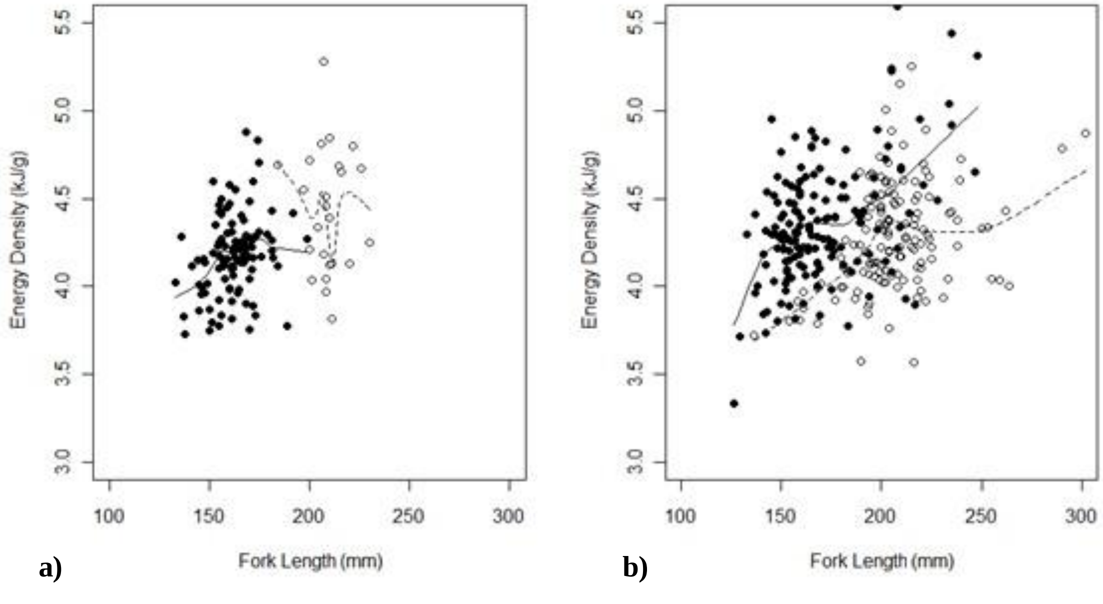


Figure 3.12: Energy density versus fork length at capture for **a)** 2005-2006 (N=107, 24) and **b)** 2006-2007 (N=155, 141). Solid lines and points are fall seasons and dashed lines and open points are winter seasons.

3.6.1 Plankton Biomass

Mean total plankton biomass was 42.1g/1000m^3 and 14.9g/1000m^3 in the fall and winter of 2005-2006, respectively. In 2006-2007, mean total plankton biomass was 42.0g/1000m^3 in the fall and 21.0g/1000m^3 in the winter. Total plankton biomass was significantly lower in winter than fall in 2005-2006 (W = 179, $p < 0.01$) with equal variance (F= 1.7, d.f.=1,27, p=0.2) (Figure 3.13a). Plankton biomass was also significantly lower in winter in 2006-2007 versus the fall (F=7.7, d.f.1,19, $p<0.05$) also with equal variance (K^2 = 1.3, d.f.= 1, p=0.3) (Figure 3.13b).

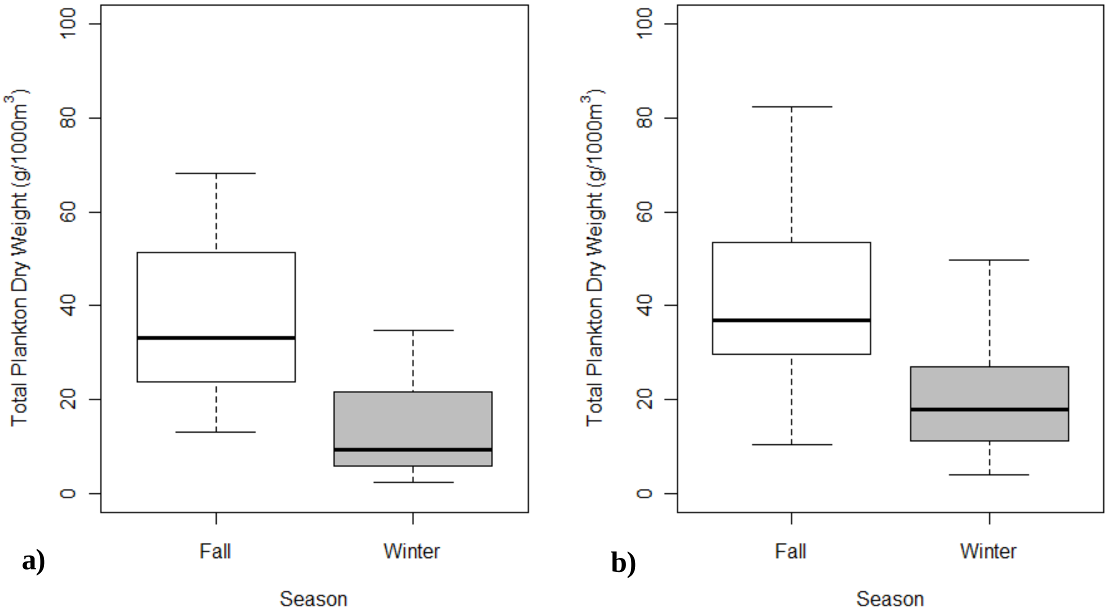


Figure 3.13: Comparison of total dry weight of plankton per 1000m^3 in Quatsino Sound in fall and winter seasons of **a)** 2005-2006 (N=29) and **b)** 2006-2007 (N=21).

3.6.2 Gut Fullness

On average, gut fullness was 1.6g wet/100g wet in the fall and 1.2g wet/100g wet winter of 2005 and 2006, respectively. Gut fullness was significantly different between seasons in 2005-2006 (W=6592, $p<0.01$) with equal variance (F= 0.5, d.f.=1,309, p=0.5)(Figure 3.17a). Mean gut fullness was 1.0g wet/100g wet in the fall of 2006 and 1.0g wet/100g wet in the winter of 2007. No significant difference was found between seasons in 2006- 2007 seasons (W=19878, p=0.4) and equal variance (F= 0.03, d.f.=1,405, p=0.9) (Figure 3.17b).

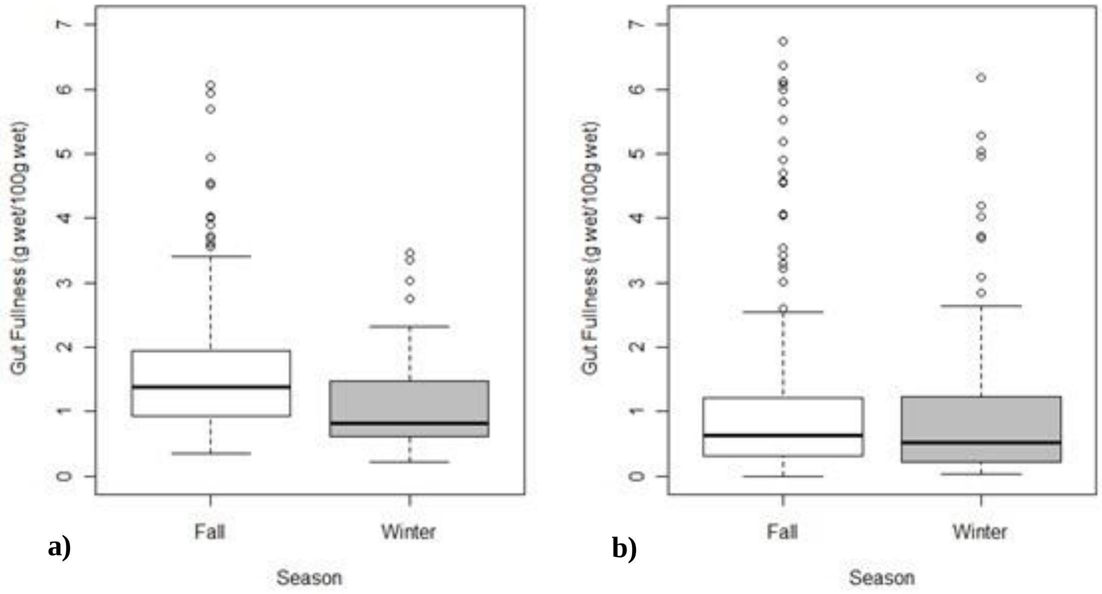
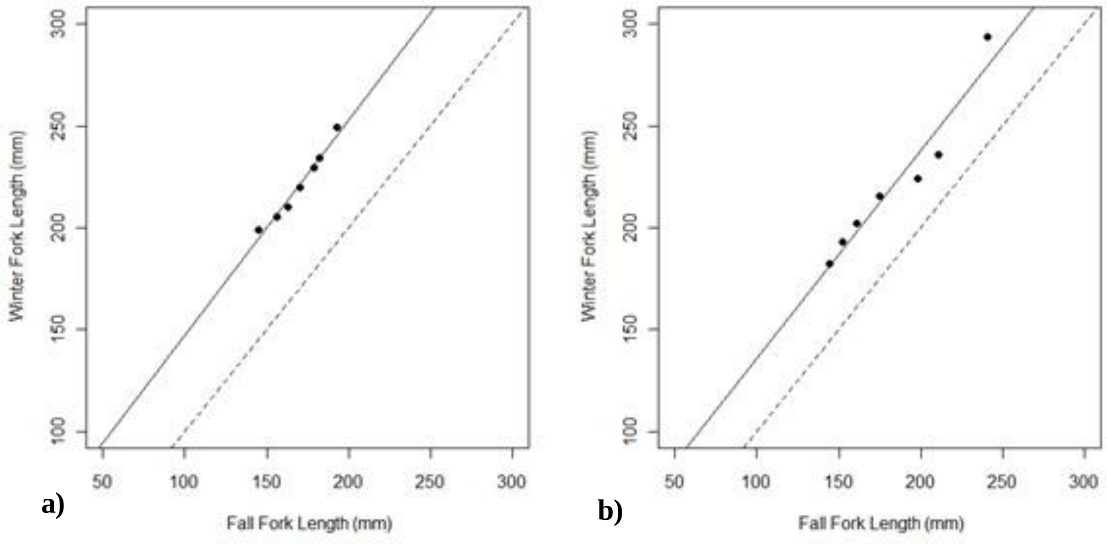


Figure 3.14: Gut fullness between fall and winter juvenile Chinook salmon in Quatsino Sound during **a)** 2005-2006 (N=311) and **b)** 2006-2007 (N=407).

3.7 Size-selective Overwinter Mortality

Quantile-quantile plots of winter and fall fork lengths during 2005-2006 show a slope of 1.06 with 95% confidence intervals 0.86 -1.26 (r^2=0.99, F=185.3, d.f.=5, p<0.01) (Figure 3.15a). The quantile-quantile line in 2005-2006 was not significantly different from the 1:1 line (t=0.34, d.f.=5, p=0.75). Quantile-quantile plots of winter and fall fork lengths during 2006-2007 had a slope of 1.02 with 95% confidence intervals of 0.7-1.34 (r^2=97, F=69.1, d.f.=5, p<0.01) (Figure 3.15b). The quantile-quantile line in 2006-2007 was not significantly different from the 1:1 line (t=0.1, d.f.=5, p=0.38).



a) b)

Figure 3.15: The empirical quantile-quantile plots derived from **a)** winter 2006 and fall 2005 fork length distributions (N=183) and from **b)** winter 2007 and fall 2006 fork length distribution (N=326). Solid lines represent the quantile-quantile while dashed lines represent the 1:1 line.

3.8 Unused otoliths

Of all the otoliths sampled, only 44 of the 76 otoliths sampled were usable for determining early marine growth. Problems encountered included breakage, the inability to see increments and marine entry points and the occurrence of vateritic otoliths. In total 42% of otoliths sampled for measurements were not usable due to these issues (Table 3.3). 8% of these otoliths were from hatchery fish, all of which were crystallized and therefore unusable for microstructural analyses.

Table 3.3: Summary of type, season and total number of unusable otoliths from 2006-2007.

Type	**Season**	**# per season**	**Hatchery**	**Total**	**Percentage (%)**
Broken	Fall	1	0	6	7.9
	Winter	5			
No Rings	Fall	9	7	20	26.3
	Winter	11			
Vaterite/ Crystallized	Fall	6	6	6	7.9
	Winter	0			
All	Fall	16	13	32	42.1
	Winter	17			

Chapter 4: Discussion

This study used catch and size data as well as otolith microstructure to determine if growth during early marine residency and energy accumulation overwinter was associated with survival through the first winter at sea for juvenile Chinook salmon on the northwest coast of Vancouver Island. It was determined that no size-selective mortality occurred over winter between fish captured in the fall and winter seasons of either 2005-2006 or 2006-2007. In addition, there was no evidence that smaller fish depleted their energy reserves faster than larger fish. The early marine growth of Marble River juvenile Chinook salmon was the same for both fall and winter juveniles during the 2006-2007 season in the first month at sea. Although no evidence of size-dependence was found during early marine life or over the first winter at sea, these juveniles exhibited a mortality rate of 80-90% over their first winter in both years. It is imperative to begin to understand the causes for high overwinter mortality in these juvenile Chinook salmon.

4.1 Overwinter Mortality

To date, there have been no estimates of juvenile overwinter mortality in Pacific salmon during their first year at sea. This study suggests that 80-90% mortality occurred in juvenile Marble River Chinook salmon in Quatsino Sound between fish captured in the fall and winter seasons in both 2005-2006 and 2006-2007. Since high mortality rates of juvenile Pacific salmon have been correlated with growth and predation during their first year at sea (Beamish and Mahnken 2001) I estimated the possible occurrence of size-selective mortality in smaller individuals over winter and during early marine residency.

In this study, fish collected in the winter were assumed to be overwinter survivors since Marble River juvenile Chinook salmon are known to stay within Quatsino Sound during their first year at sea (S. Tucker, Fisheries and Oceans Canada, Nanaimo, personal communication). The mean size of Marble River juvenile Chinook salmon in winter was significantly larger for both 2005-2006 and 2006-2007 indicating growth over time, as expected. Interestingly, variance in size did not differ significantly between fall and winter seasons for all years. Variance is expected to decrease when size-selective mortality occurs against smaller fish but no change in variance suggests that size-selective mortality was not occurring over winter during these years (Trudel *et al.* 2007a,b). Furthermore, evidence from empirical quantile-quantile plots of fork length distributions between seasons and years indicated that size-selective mortality did not occur in Quatsino Sound between the fall and winter seasons of 2005-2006 and 2006-2007. The slope of both the fall 2005 and winter 2006 and fall 2006 and winter 2007 comparison plots were parallel to the 1:1 line. An upward shift indicated an overall increase in fish size in winter compared to fall but the shift was the same for all sizes of fish.

Overwinter size-selective mortality occurs in fish species where larger and more robust individuals are the most likely to survive (Post and Evans 1989, Beamish *et al.* 2004, Trudel *et al.* 2007a,b). Evidence for overwinter size-selective mortality in Pacific salmon has been predominantly found in more northern latitudes in species of pink salmon (Moss *et al.* 2005, Cross *et al.* 2009) and sockeye (Farley *et al.* 2007) in central and northern Alaska. This may be due to greater capacity for growth and energy accumulation (Trudel *et al.* 2007a,b). It is possible that size-selective mortality and growth may not be as significant for salmon in southern latitudes in comparison to northern latitudes (Trudel *et al.* 2007a,b), but more research on central and southern populations is needed to determine this relationship.

To determine what factors may have caused this high overwinter mortality, I examined energy density, gut fullness and plankton data to see if starvation could have occurred over winter. I also compared early marine growth between fall and winter fish to see if overwinter survivors were initially the fastest growers upon marine entry.

4.2 Energy Accumulation

During ocean winters, some populations of juvenile fish may starve, forcing a reliance on food stores from the summer to survive (Post and Evans 1989, Conover 1990). If overwinter starvation were occurring in Quatsino Sound, smaller fish would be expected to show larger energy depletion at the end of winter relative to fall since smaller individuals have higher weight-specific metabolic rates (Shuter and Post 1990, Gillooly *et al.* 2001) and lower energy reserves compared to larger individuals (Post and Evans 1989, Johnson and Evans 1991, Post and Parkenson 2001). Post and Evans (1989) used empirical quantile-quantile plots to show size-selective over winter mortality occurring in young-of-the-year yellow perch (*Perca flavescens*) populations from fall to spring. This study estimated size-selective mortality in laboratory experiments as well as in the wild. Smaller fish lost more weight than larger fish in simulated overwinter environments showing energy loss may be higher in smaller individuals under starvation (Post and Evans 1989). Similar results were also found in white perch (*Morone Americana*) and yellow perch (Johnson and Evans 1991), Eurasian perch (*Perca fluviatilis*) and smallmouth bass (*Micropterus dolomieu*) (Shuter and Post 1990), age-0 largemouth bass

(*Micropterus salmoides*) (Fullerton *et al.* 2000), and age-0 rainbow trout (*Oncorhynchus mykiss*) (Post and Parkenson 2001, Biro *et al.* 2004).

The occurrence of size-selective mortality in smaller individuals has been shown to occur when food availability is low and fish are starving however many of these studies have made assumptions about how fish interact in the natural environment through small scale environmental studies (Byström *et al.* 2006). Some contradictory results exist and indicate the opposite relationship, where the metabolic rate of fish decreases with lower temperatures in winter, allowing smaller fish to sustain themselves over winter with less available resources (Nagasawa 2000, Connolly and Peterson 2003, Byström and Andersson 2005, Byström *et al.* 2006). Examples are seen in fish such as young-of-year steelhead trout (Connolly and Peterson 2003), age-0 walleyes (*Sander vitreus*) (Copeland and Carline 1998, Pratt and Fox 2002) and Arctic char (*Salvelinus alpines*) (Byström and Andersson 2005). This is also known as Critical Resource Density (CRD) (Byström and Andersson 2005), where small fish have lower CRD than larger ones and therefore are less likely to starve (Copeland and Carline 1998, Pratt and Fox 2002, Byström *et al.* 2006). This phenomenon occurs when individuals are capable of feeding over winter but once starvation occurs, fish are shown to exhibit evidence of energy storage loss in smaller individuals (Byström *et al.* 2006).

My results showed an overall drop in energy density between fall and winter seasons of 2005-2006 but no significant change in 2006-2007. Energy storage in smaller individuals did not drop from fall to winter seasons in all years. Furthermore, the quantile-quantile plots for Marble River juvenile Chinook salmon length distributions indicated no size-selective mortality over the first winter at sea. Therefore, size-selective starvation may not be a cause for the aforementioned evidence of high overwinter mortality. Critical resource density may cause size-selective overwinter mortality in small or large fish in a population or exhibit no size-dependent mortality at all, depending on the interactions between foraging, metabolism and energy storage (Pratt and Fox 2002, Byström *et al.* 2006). Therefore, since juvenile Chinook salmon did not show evidence of size-selective overwinter mortality and if juveniles were feeding over winter, this population may have exhibited evidence more closely related the CRD concept.

Despite that zooplankton biomass declined over winter, juvenile Chinook salmon appeared to feed during winter, although further sampling throughout the entire season is needed. Juvenile sub-yearling and yearling Chinook salmon have a highly variable diet compared to most Pacific salmon species, as they feed on fish, decapods, insects, hyperiids and euphausiids during early and late summer (Brodeur *et al.* 2007, Weitkamp and Studervant 2008). During winter on north WCVI, pteropods are more abundant, indicating a potential food source for these juveniles (Mackas *et al.* 2004). This may indicate that WCVI juvenile Chinook salmon in Quatsino Sound are potentially capable of feeding on more variable types of prey (Brodeur *et al.* 2007), which would allow them to feed over winter even if zooplankton abundance was low. The amount of food in their stomach was reasonably similar between fall and winter seasons showing similar gut fullness indices to summer values (Weitkamp and Sturdevant 2008).

Another factor that could affect size-dependent overwinter mortality is the severity of winter seasons and the ability for juvenile salmon to grow rapidly and accumulate lipids (Schultz and Conover 1997, Trudel *et al.* 2007a,b,). It is possible that this population of Chinook salmon has conserved energy reserves through feeding across all size classes during a potentially less severe winter. Evidence of non-size dependent overwinter mortality in this stock of juvenile WCVI Chinook salmon indicates that there are complex local environmental interactions between prey availability and quality, foraging ability, metabolic rate, energy storage and the length and severity of winter (Metcalfe and Thorpe 1992, Finstad *et al.* 1998, Mazumder and Edmunson 2002, Byström *et al.* 2006, Trudel *et al.* 2007a).

4.3 Early Marine Mortality

4.3.1 Somatic and Otolith Size

My results showed that otolith size (radius at capture) increased significantly ($r^2=0.73$, $p<0.01$) with fish fork length at capture for juvenile Chinook salmon in the 2006-2007 fall and winter seasons. With this correlation, I assumed that there was a linear relationship between daily increment width and daily somatic growth (Panella 1971, Fisher and Pearcy 1988, Fukuwaka and Kaeriyama 1997, Campana and Thorrold 2001). As expected, fall fish had significantly smaller otoliths than winter fish which further supports correlation between somatic and otolith growth. There was no significant difference in marine entry radius between fall and winter samples, which may indicate that these juveniles were approximately the same size upon entering the marine environment. This may indicate that the overwinter survivors were not the ones that were large at ocean entry or had fast freshwater growth.

4.3.2 Otolith Chemistry Analysis

Early marine growth and back-calculated lengths were determined using otolith microstructure by visually estimating the marine entry point. Although visual estimations of otolith width at marine entry have been used before (Marshall and Parker 1982, Campana and Neilson 1985, Volk *et al.* 1990, Zhang *et al.* 1995, Fukuwaka 1998), validation of the visual technique was needed to ensure accuracy of my measurements. Chemical analysis of 8/10 usable otoliths showed that my visual estimations of marine entry point were within 10% of the chemical estimations. Two of the ten usable otoliths did not line up with my visual estimates and it is possible that these were due to error in visual or chemical analysis.

A few of the chemically analyzed otoliths had surprisingly high levels of strontium after marine entry where 5 otoliths had an initial increase in Sr before levelling out to 1.5-2.5mmol/mol. Typically, high salinity is related to high Sr:Ca in otoliths (Zimmerman 2005), but salinity may not always correlate positively with water or otolith strontium concentrations having some freshwater salinity exceed those typically in marine environments (Kraus and Secor 2004). In some of the sampled otoliths, Ba is also slightly higher when Sr is high. These unexpected peaks may have been due to possible variable levels of salinity in Quatsino Sound but salinity levels at marine entry are unknown. It is believed that these fish likely entered some unknown region of water with higher Sr:Ca or experience an as of yet un-described physiological transition from freshwater to saltwater.

The Marble River and many surrounding rivers flow into Quatsino Sound but also exit into Rupert Inlet. Juvenile Chinook salmon in this area remain within Quatsino Sound and perhaps even Rupert Inlet for up to a year after emerging into the marine environment (S. Tucker, Fisheries and Oceans Canada, Nanaimo, personal communication). A copper mine was established in Rupert Inlet adjacent to Marble River in 1970 and was fully operational until 1995 (Poling *et al.* 2002). Island Copper Mine (ICM) released massive amounts of mine tailings through an outfall at 50m depth into Rupert Inlet a submerged pipe (Poling *et al.*2002). Although the ICM has been closed for 15 years there may still be trace elements in the area. Additionally, strontium and barium are known geochemical tools for finding copper ore sites (Warren *et al.* 1974). Salmon in the area at the time of mining were not required to be analyzed for trace elements from the ICM since researchers then assumed that these juveniles migrated past Rupert Inlet in a matter of days (Poling *et al.* 2002). Although there was no indication that water column trace elements were raised in ways in which the fish could directly absorb them (Poling *et al.* 2002), it could be possible that remaining trace elements from mine tailings and the surrounding high Sr and Ba geology may have been taken up by the juvenile salmon otoliths explaining these unexpectedly high strontium and barium levels at marine entry.

4.3.3 Size at Ocean Entry

For the back-calculation of fish fork lengths at marine entry, I used the Dahl Lea back-calculation method (Lea 1910, Francis 1990). Determining the fork length of these juveniles when they entered the ocean is important for the analysis of growth and size comparisons at that time. The Dahl Lea method assumes that otolith and somatic growth are linearly proportional (Carlander 1977). It assumes that when the sagittal otoliths formed, body length was at zero and that the biological intercept is at the origin (Lea 1910, Francis 1990).

Body lengths of fish have been documented lower than observed lengths when using the Dahl Lea method in comparison to the Fraser Lee method (Hudson and Bulow 1984) but biased size-at-age estimates are produced from the regression-based Fraser-

Lee method and similarly regression-based equations such as the linear Body Proportion Hypothesis (BPH) and Scale Proportion Hypothesis (SPH) (Vigliola and Meekan 2009). Fraser Lee, BPH and SPH models involve a positive intercept and the otolith radius to fork length relationship found in this study gave a negative intercept, therefore these methods could not be used.

The fork lengths at marine entry were within the range of body size of ocean-type Chinook salmon smolts when entering the marine environment (40-80mm) (Healey 1991, Groot and Margolis 1991, Quinn 2005). Additionally, otolith chemistry estimates of marine entry otolith size corresponded to visual estimates, showing that the marine entry otolith radius measurements were relatively accurate. Winter juveniles were back-calculated to be larger than fall fish at marine entry even though otolith radius measurements at marine entry were not significantly different. This was likely due to non-linearity in otolith to fish size calculations since the Dahl-Lea method is based off of the otolith size at capture measurements.

4.3.4 Early Marine Growth

This study correlated fish size to otolith size and showed that the marine entry point on juvenile Chinook salmon otoliths can be visually and chemically estimated. This information allowed me to determine juvenile Chinook salmon growth rates during the first month at sea. Weekly otolith growth was measured during the first month at sea for 44 juveniles captured in Quatsino Sound in November and March of 2006-2007. Although significant differences were found in fish size between fall and winter seasons at marine entry, these juveniles did not exhibit differences in growth during their first month at sea. Chinook salmon were growing at a similar rate regardless of being an overwinter survivor therefore no connection could be made between early marine growth and overwinter mortality for 2006-2007. These results show no evidence of size-selective mortality over the first month at sea in 2006 and further support results showing non size-dependent relationships during the first ocean winter. These results indicate that the first month of growth and size at ocean entry were not critical for winter survival.

I have only looked at the first month of early marine residency therefore it is possible that growth-based mortality had already occurred by the time of capture. Early marine growth rates increased significantly over the first 3-4 weeks with no difference in variance. An increase in overall increment width over the first few weeks is expected since higher growth has been shown to occur during marine residency compared to freshwater residency (Zhang and Beamish 2000, Daly *et al.* 2010). Increased growth has occurred in juvenile Pacific salmon over the first summer at sea (Cross *et al.* 2009, Duffy and Beauchamp 2011) therefore it is possible that growth dependent mortality occurred after the first month of marine residency prior to the fall. Other possible influencing factors include local environmental conditions such as climate, food availability and predation but more research on the early marine growth, extending past the first month at sea and between different regions is needed to examine this possibility.

4.3.5 Otolith Measurement Error

In this study I made the assumption that each daily increment represented the daily somatic growth of juvenile fish. Recently, Soliman *et al.* (2009) correlated daily increments with the growth of larval and juvenile golden spotted rabbitfish (*Siganus guttatus*). The comparison of otolith and somatic growth has also been used in many species of salmon (Volk *et al.* 1984, Campana 1984, Neilson and Geen 1985, Zhang *et al.*

1995, Miller and Simenstad 1997, Zhang and Beamish 2000, Barnett-Johnson *et al.* 2007) indicating that otolith microstructure can be a reliable tool in measuring growth in Pacific salmon. Some studies have found uncoupling between somatic and otolith size to occur when fish are under stress or starvation (Bradford and Geen 1987, Bradford and Geen 1992, Secor and Dean 1992, Francis *et al.* 1993). Slower-growing fish have been shown to have larger otoliths in comparison to fast-growing fish of the same size in some cases (Secor and Dean 1989, Campana 1990). The presence of sub-daily increments may also cause significant error in measurements of daily growth (Campana and Neilson 1985, Neilson 1993).

In order to reduce error during analyses of early marine growth, I measured weekly otolith growth since a strong temporal autocorrelation has been found to occur in otoliths between 7-10 increments where increments may not show changes in growth for at least 3 days (Molony and Choat 1990, Pepin *et al.* 2001). All measurements were made from the primordial plane to dorsal edge of each otolith and no sub-daily increments were found on these juvenile Chinook salmon otoliths.

4.4 Potential Factors Influencing Overwinter Mortality

This study did not find evidence of size-selective over winter mortality in Marble River juvenile Chinook salmon in Quatsino Sound in 2005-2006 or 2006-2007, but a mortality rate of 80-90% still occurred over that time period. It is possible that these juvenile salmon were impacted by other unknown factors which may have included commercial fisheries, non size-selective predation, vertical distribution or disease. I have outlined these possible explanations, but there is still a need for more research on juvenile

Chinook salmon in Quatsino Sound to determine why this mortality occurred over the first ocean winter during these years.

4.4.1 Commercial Fisheries

Commercial fisheries in Quatsino Sound include species such as Pacific herring (*Clupea pallasii*), rockfish (*Sebastes* spp.), lingcod (*Ophiodon elongates*), halibut (*Hippoglossus stenolepsis*) and many invertebrates (Quatsino Sound Coastal Plan 2004). Salmon and invertebrate aquaculture facilities are in the area but it is unknown if these commercial fisheries affected overwinter mortality in 2005-2006 and 2006-2007.

4.4.2 Predation

The extent of marine predation on juvenile salmon is not fully understood, but it is known that they may be consumed by a variety of fish, bird and marine mammal species in the marine environment (Fresh 1997). Early marine mortality has been thought to be due partially to predator-prey interactions when juveniles first transition from freshwater to marine ecosystems (Parker 1968, Fisher and Pearcy 1988, Beamish and Mahnken 2001). Predation could be one of the most significant potential sources of high mortality of Marble River juvenile Chinook salmon during their first winter at sea. Known predators of salmon in the marine environment include fish species such as the river lamprey (*Lampetra ayresi*) (Beamish *et al.* 1995), spiny dogfish (Beamish *et al.* 1992), Pacific herring (Ito and Parker 1971), Pacific hake (*Merluccius productus*) (Hargreaves *et al.* 1990) sablefish (*Anoplopoma fimbria*) and adult Coho salmon (Orsi *et al.* 2000). Bird and marine mammal species are also considered significant predators on marine salmonids, including common mergansers (*Mergus merganser*), terns (*Sterna* spp.) and murres (*Uria* spp.), (Simstead *et al.* 1979, Roby *et al.* 2003), local pinnipeds (Simstead *et al.* 1979, Fiscus 1980, Zamon 2001, Laake *et al.* 2002) and certain species of cetaceans (Meachum and Clark 1979, Fiscus 1980).

An important consideration about predation on juvenile Marble River Chinook salmon is that these fish have not exhibited any evidence of size-selective mortality. Predation is often size-dependent (Fresh 1997, Pratt and Fox 2002); therefore many of these predatory species may not be impacting this specific stock of juvenile Pacific salmon. Larger predators such as pinnipeds and small cetaceans are less likely to be size-dependent consumers of juvenile Chinook salmon since they primarily feed on prey within and beyond the range of this size (Fiscus 1980, Morton 2000). Pinniped and cetacean populations in Quatsino Sound include humpback whales (*Megaptera novaeangliae*), harbour porpoises (*Phocoena phocoena*), Dall's porpoises (*Phocoenoides dalli*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), harbour seals (*Phoca vitulina*) and Stellar sea lions (*Eumetopias jubatus*) which all feed on small fish, some including salmon (Fiscus 1980, Heise 1997, Brodeur *et al.* 2003, Quatsino Sound Coastal Plan 2004). It is possible that such a high decline in catch of juvenile salmon between fall and winter seasons in Quatsino Sound in 2005-2006 and 2006-2007 may have been due to non size-dependent predation, but more research in this area is required.

4.4.3 Depth Distribution

Pacific salmon have variable vertical distribution in the ocean depending on age, species, time of day and season (Beamish *et al.* 2000, Emmett *et al.* 2004). Specifically, Chinook salmon are known to dive deeper with increasing age and size (Orsi and Wertheimer 1995). The Marble River stock that was sampled in 2005-2006 and 2006-

2007 were caught within the top 15 metres in Quatsino Sound by surface trawl. The range of size of juveniles caught in this study in the winter seasons of all years was between 130-300mm and age-0 juvenile Chinook salmon of this size have been shown to remain within the range of 0-22 metres in the fall, but may move into deeper waters by February (Orsi and Wertheimer 1995). Emmett *et al.* (2004) showed the highest proportion of age-0 Chinook salmon caught within a surface trawl from 0-12m depth. It is possible that juvenile Chinook salmon moved outside of the range of the surface trawls (0-15m) but a significant portion of these fish are below the range of size or age that Chinook salmon dive to greater depths (Orsi and Wertheimer 1995). Another possibility is that these juvenile salmon were inshore, away from the sampling stations when trawling occurred. Near shore environments may be important for juvenile Chinook salmon through the spring and summer, but juveniles are absent by September, which may be due to migration to open ocean (Duffy *et al.* 2005). It is possible that Marble River juvenile salmon may be occupying near shore environments in Quatsino Sound during the winter but this information is as of yet unknown.

4.4.4 Disease

The impact of disease on salmon has been of widespread concern, especially with the current potential impact of climate change (Noakes *et al.* 2000). Some factors that increase disease outbreak include temperature, stress, genetics, population density and competition (Vethaak and ap Rheinallt 1992). It is possible that Marble River juvenile Chinook salmon are encountering potential disease issues that we are unaware of. With such a high rate of over winter mortality, it is possible that an outbreak of disease has affected this juvenile population. I cannot draw direct conclusions but there has been a significant amount of work on diseases such as bacterial gill disease, furunculosis, bacterial kidney disease and diseases caused by parasites (Rucker *et al.* 1954, Fryer and Lannan 1993). A large variety of diseases in Pacific salmon are of freshwater origin, but their impacts may transfer into early marine residency causing a reduction in overall health and may increase mortality from predation (Arkoosh *et al.* 1998). Much scientific work has been done on the potential spread of disease from farmed salmon to wild Pacific salmon stocks (Noakes *et al.* 2000). Salmon farming in Quatsino Sound is currently under management by the Kitasoo/Xai'xais and Quatsino First Nations and Marine Harvest Canada (MHC 2008, Young and Liston 2010). The impact of these aquaculture facilities are not thought to affect local marine populations including salmon and shellfish (Northern Aquaculture 2004) but no research has been done in this area so far. In general, pathogens found in fish farms are also found in wild populations (Kent *et al.* 1998) and farmed salmon health has recently improved with increased awareness and the instigation of vaccines (Noakes *et al.* 2000). The possibility of disease affecting Marble River juvenile Chinook salmon during their first winter at sea is possible but more work on this area is needed to draw any serious conclusions.

4.5 Unusable Otoliths

A significant portion of the otoliths analyzed were unusable due to crystallization, breakage, or a lack of daily rings. Aragonite is the typical crystalline form of calcium carbonate ($CaCO_3$) in teleost otoliths (Gauldie 1991, Secor *et al.* 1992, Gauldie 1996, Campana and Thorrold 2001). Vaterite is another crystalline form of $CaCO_3$ that is readily found in lamprey (*Lampetra tridenta*), hagfish (*Eptatretus* spp.) and sturgeon (*Acipenser* spp.) otoliths although it is typically rare in most teleost fish (Gauldie 1991, Sweeting *et al.* 2004). Crystallization, or vaterite, occurs in Pacific salmon otoliths but the cause is still not fully understood. Crystallized otoliths break up the progression of daily growth increments, or do not exhibit them at all, but they still grow proportionally with fish size and therefore can still be used for otolith size to somatic size analyses (Sweeting *et al.* 2004).

I believe that a significant portion of these unusable otoliths were lost to vaterite in this study. Although I visually identified a total of 6 otoliths as crystallized, I believe that the other significant portion of unused otoliths were partially vateritic. Two of the chemically analyzed otoliths did not show any Sr:Ca or Ba:Ca signals, which may be due to the potential substitution of strontium by magnesium in vateritic otoliths (Gauldie 1996).

Additionally, a large proportion of these unusable otoliths were from hatchery fish and crystallization has been found to occur more readily in hatchery than wild salmon (Sweeting *et al.* 2004). Some otoliths did not have evidence of daily ring patterns or just cracked and shattered easily which may have resulted from over grinding or the presence of accessory primordia (Neilson 1993). It is possible that the sampling process may have been biased due to the loss of these vateritic otoliths, but until the process is fully understood I am unsure how to reduce this type of sampling error.

Chapter 5: Conclusion

My research investigated factors influencing the overwinter mortality and early marine growth of Marble River juvenile Chinook salmon during their first year at sea in Quatsino Sound, British Columbia. This study is the first to have estimated overwinter mortality rates in juvenile Pacific salmon. Rates were found to range between 80-90% between the fall and winter seasons of 2005-2006 and 2006-2007 for Marble River juvenile Chinook salmon in Quatsino Sound, British Columbia. This research is unprecedented therefore a comparison of mortality rates in juvenile salmon is not yet possible. I have shown that these juvenile Chinook salmon did not experience size-dependent mortality during these years since there was no shift in size distribution between fall and winter seasons. Additionally, overwinter energy reserves of these juveniles did not support size-selective mortality in smaller individuals. Plankton biomass decreased from fall to winter seasons, but it is possible that these salmon were still feeding during winter as their stomach fullness was comparable to values reported for juvenile Chinook salmon in summer and fall. Therefore, it is unlikely that starvation occurred during these winter seasons.

Early marine growth was not correlated with overwinter mortality since no differences in growth rate occurred between fall and winter fish during their first month at sea. The first marine month may still be critical for these fish during their first summer but not for winter. Although researchers have theorized two critical periods of growth during the Pacific salmon early life stage, it may be that growth-based mortality during early marine life is more continuous for Marble River juvenile Chinook salmon. Early marine growth and overwinter mortality may vary between years and regions due to differences in environmental conditions that in turn may affect growth rates and predator abundance.

Further research on the relationship between early marine growth and marine survival is imperative to fully understand the variability in populations of Pacific salmon. My research was on a small regional and stock specific scale but future research must expand to a larger geographic area. Looking at one specific stock may not be enough to show growth differences in the first month and winter at sea therefore I suggest expanding growth comparisons geographically as well as chronologically while determining the effects of predatory mortality on juvenile Chinook salmon along the Pacific coastline.

The fact that this study only looks at the first month that these juveniles enter the ocean may be why I did not see any changes in growth. By expanding the area of research to the first summer up into the fall could result in a significant difference in growth patterns between seasons, years, and regions. Comparing the northern and southern ends of Vancouver Island may show a more significant difference in early marine growth as they are two distinctive ecosystems split by the California Current at Brooks Peninsula where significant upwelling and down welling occurs (Perry *et al.* 1996, Mackas *et al.* 2004). There is higher zooplankton biomass on the north coast compared to the south which may be indicating a limit in food availability in the south end of the island (Perry *et al.* 1996, Mackas *et al.* 2004). Additionally, Chinook salmon growth hormones (IGF-I) have been found to be significantly higher in the northern ecosystem compared to the south (Beckman and Orsi 2009). A comparison between larger regions such as British Columbian, Californian and Alaskan coasts as well as the

Bering Sea may also result in more significant differences in juvenile salmon growth and size-selective overwinter mortality. A comparison of juvenile Chinook salmon growth performance for early marine, summer, fall and winter seasons for these areas would be useful in determining the differences between northern and southern communities.

This research is a step forward in the understanding of growth and survival in juvenile Pacific salmon. Reasons for these mortality rates during winter are unknown, but may be due to non-size selective predator abundance, disease or local environmental influences. It is important to continue understanding the processes related to early ocean mortality in Pacific salmon and how these may be affecting variability in adult recruitment and overall marine survival.

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Appendix

Appendix A – Data Summary

Table A1: Summary of Fish Size Data

Year	Season	N	Mean FL(mm)	SD
2005-2006	Fall	151	163.0	12.43
	Winter	32	211.7	15.23
2006-2007	Fall	254	166.4	22.67
	Winter	72	204.2	23.46

Table A2: Summary of $\log_{10}$CPUE+1 data

Year	Season	Mean $\log_{10}$CPUE+1	SD
2005-2006	Fall	2.21	0.46
	Winter	1.18	0.31
2006-2007	Fall	2.71	0.56
	Winter	1.58	0.82

Table A3: Summary of Otolith Measurements

Season	N	FL (mm)	FL@ME (mm)	Wk1 (µm)	Wk 2 (µm)	Wk 3 (µm)	Wk 4 (µm)	Month (µm)	Slope (µm /week)
Fall	23	163.09	55.53	5.48	5.90	6.38	7.0	6.18	44.91
Winter	21	207.90	60.06	5.49	5.62	6.2	6.62	5.98	43.06

Table A4: Summary of Energy Density Data

Year	Season	N	Mean FL(mm)	SD	Mean Energy Density(kJ/g)	SD
2005-2006	Fall	107	162.1	11.62	4.18	0.23
	Winter	24	209.1	9.68	4.43	0.35
2006-2007	Fall	155	169.6	24.52	4.36	0.34
	Winter	141	206.2	23.58	4.28	0.30

Table A5: Summary of Plankton Data

Year	Season	N	Mean Total Plankton (g/1000m^3 dry)	Mean 0.25mm sieve	Mean 1.0mm sieve	Mean 1.7mm Sieve	Mean 8mm sieve
2005-	Fall	16	42.1	14.0	3.0	25.0	0.2
2006	Winter	13	14.9	5.7	0.1	8.2	0
2006-	Fall	10	42.0	8.0	2.3	31.8	0
2007	Winter	11	21.0	5.0	3.5	12.1	0.3

Table A6: Summary of Gut Fullness Data

Year	Season	N	Mean Gut Fullness (g wet/100g wet)	SD
2005-2006	Fall	276	1.61	0.96
	Winter	35	1.17	0.89
2006-2007	Fall	265	1.02	1.24
	Winter	143	0.98	1.18

Appendix B – Otolith Chemistry Data

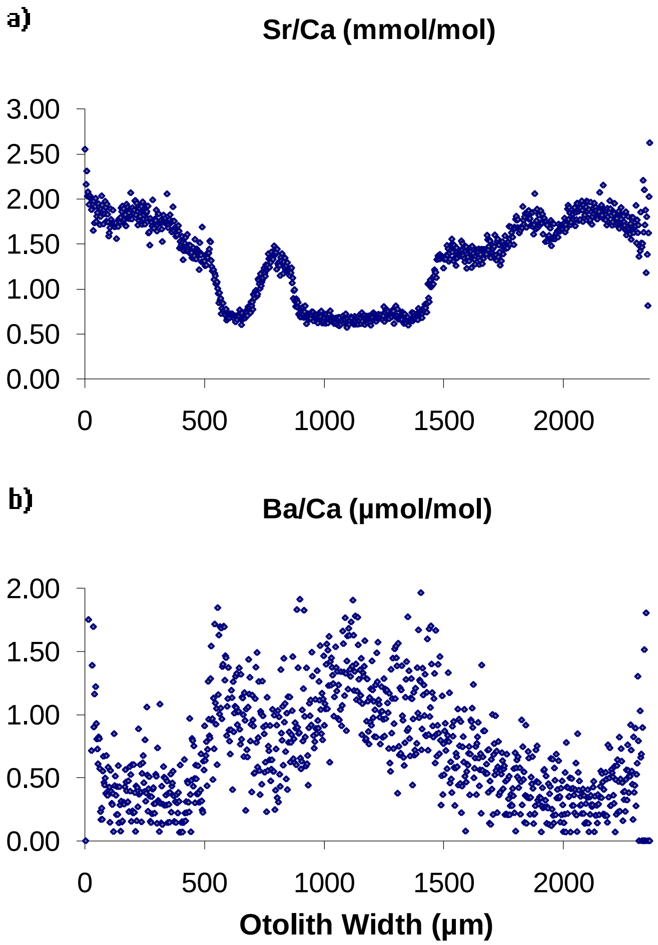

Figure B1: Chemical analysis of a fall 2006 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition

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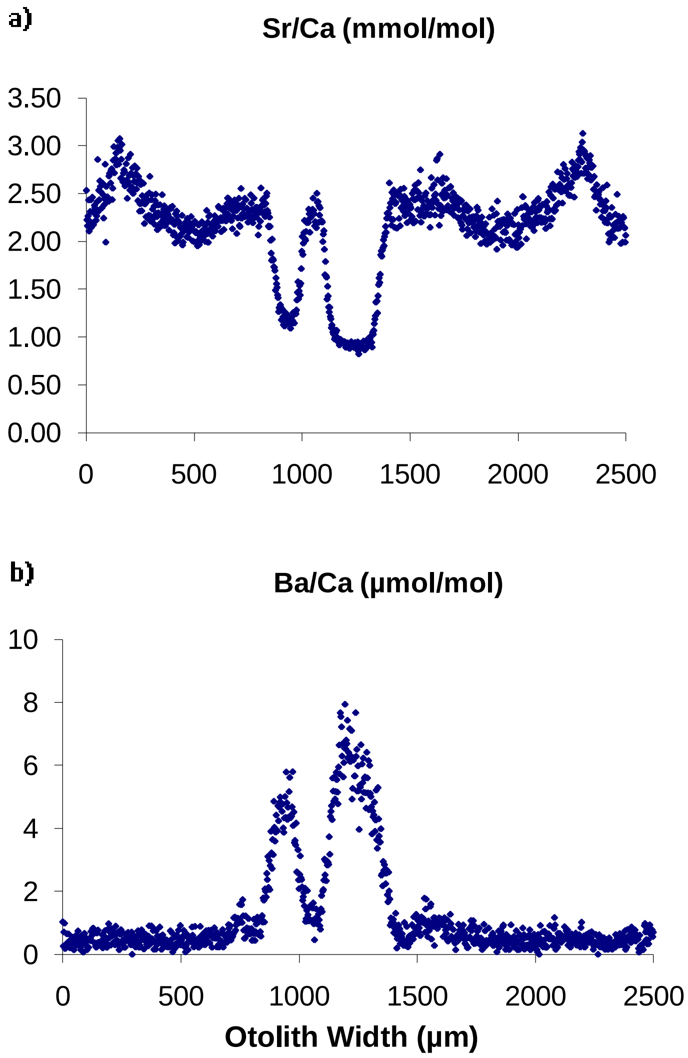

Figure B2: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition.

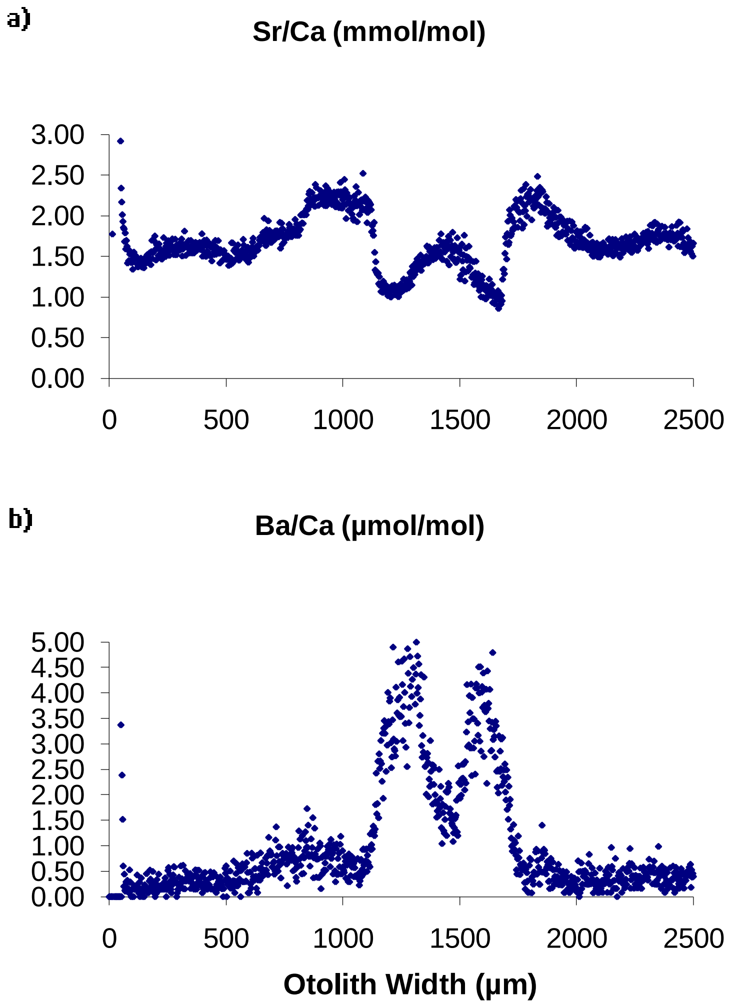

Figure B3: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition.

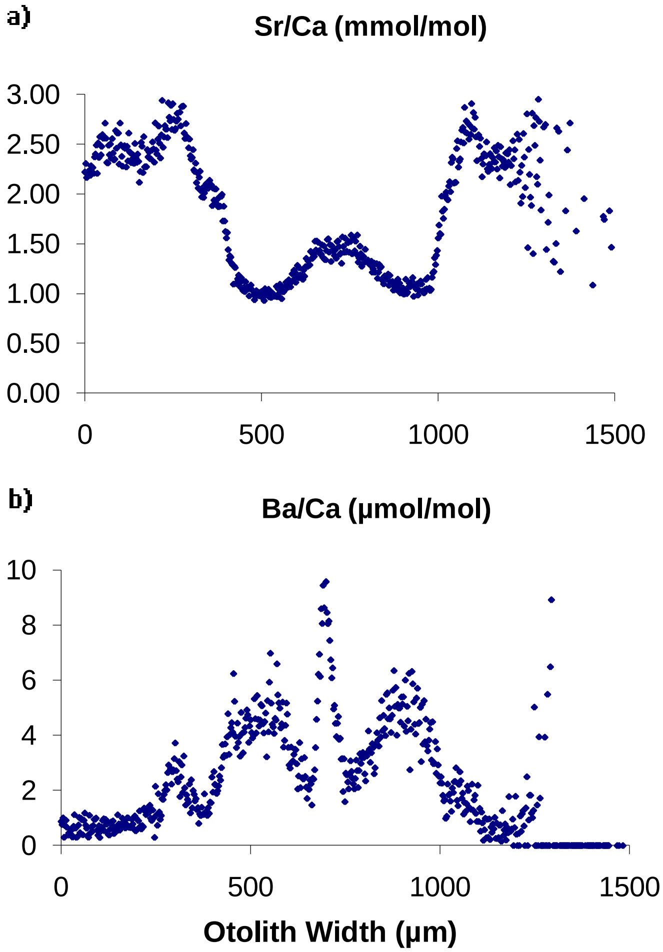

Figure B4: Chemical analysis of a fall 2006 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition.

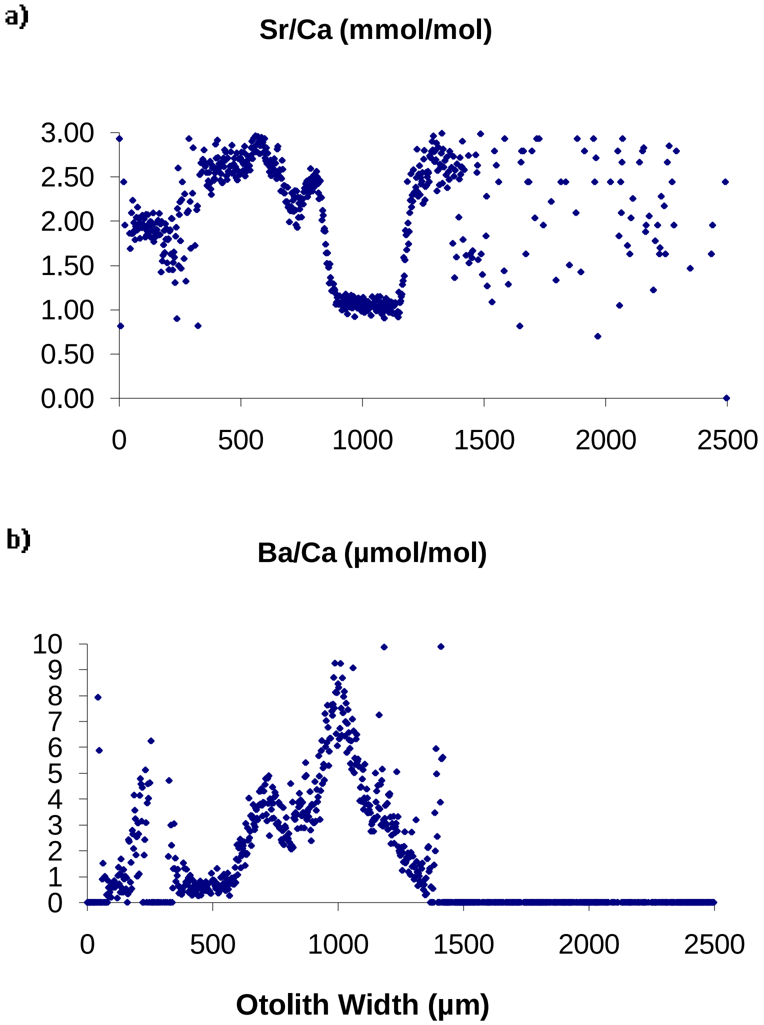

Figure B5: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition. Part of this otolith showed no change in chemistry due to vaterite.

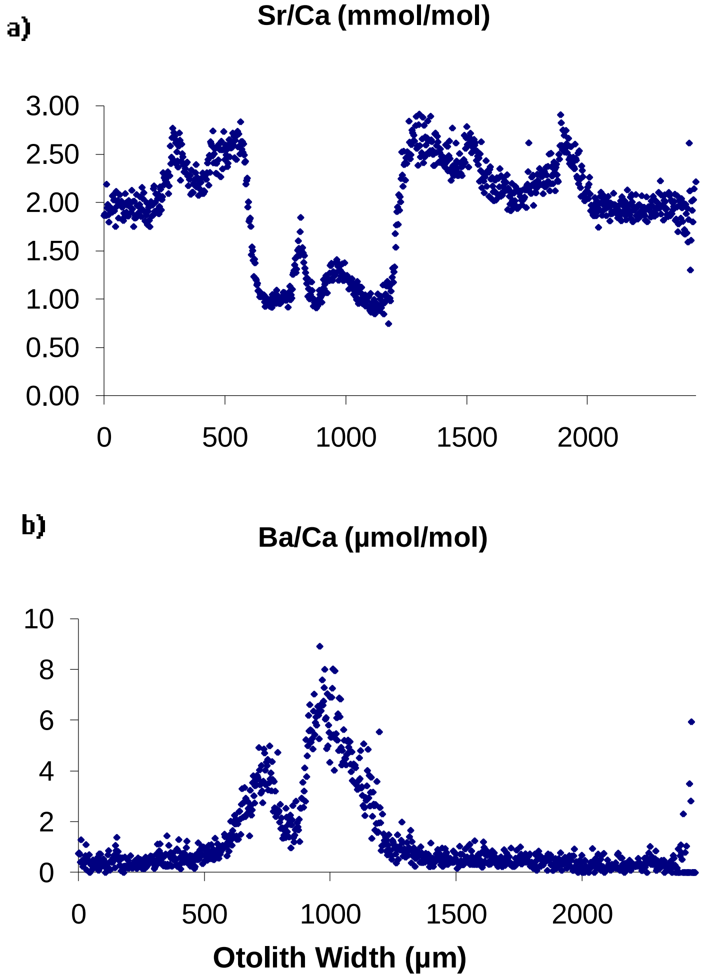

Figure B6: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition.

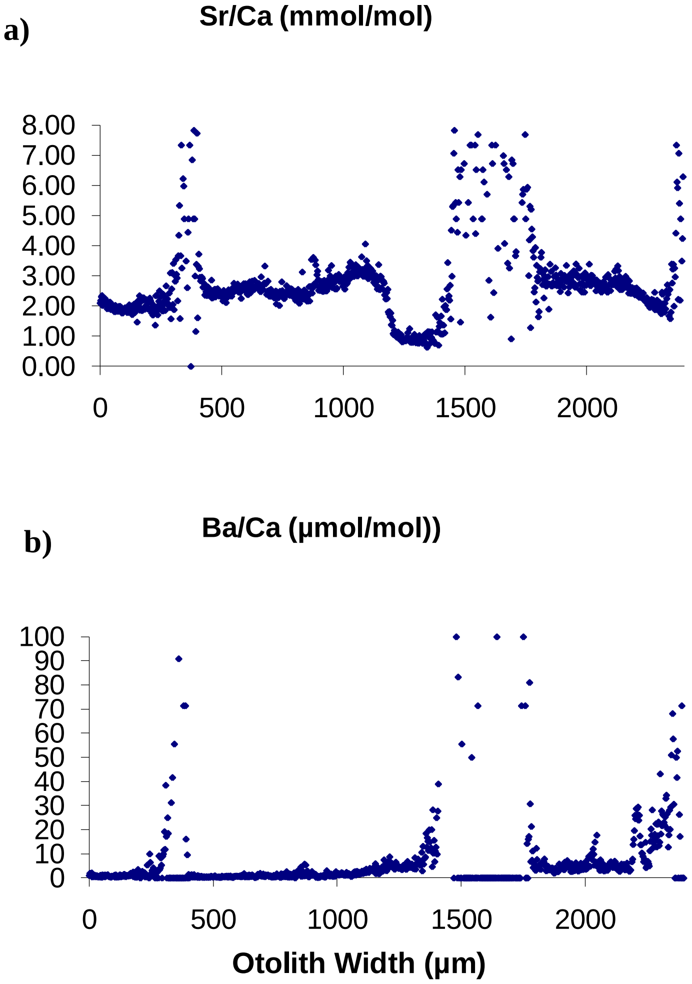

Figure B7: Chemical analysis of an unusable winter 2007 otolith showing no change in **a)** Sr:Ca (mmol/mol) or **b)** Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm).

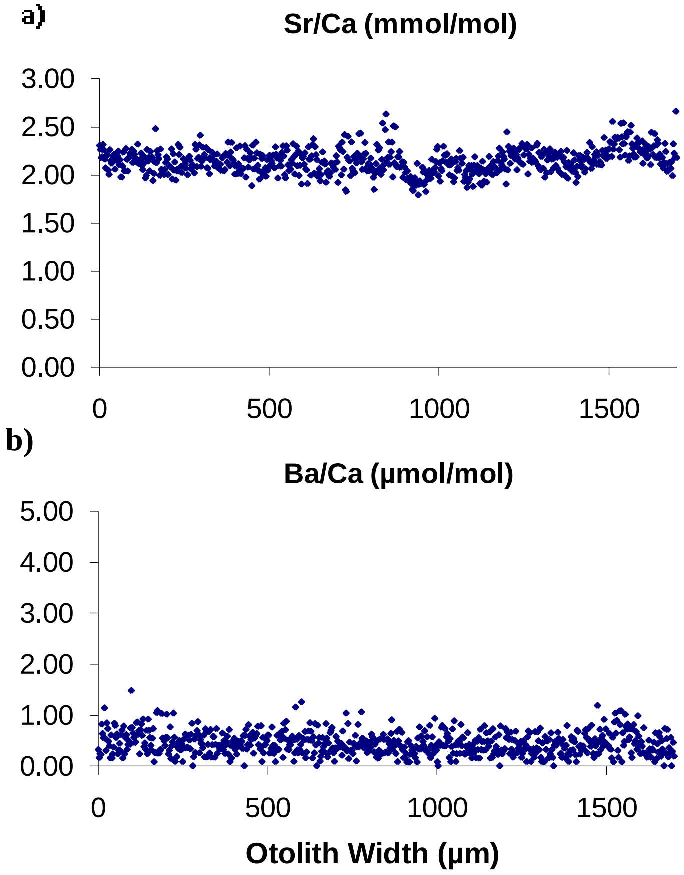

Figure B8: Chemical analysis of an unusable fall 2006 otolith showing no change in **a)** Sr:Ca (mmol/mol) or **b)** Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm).

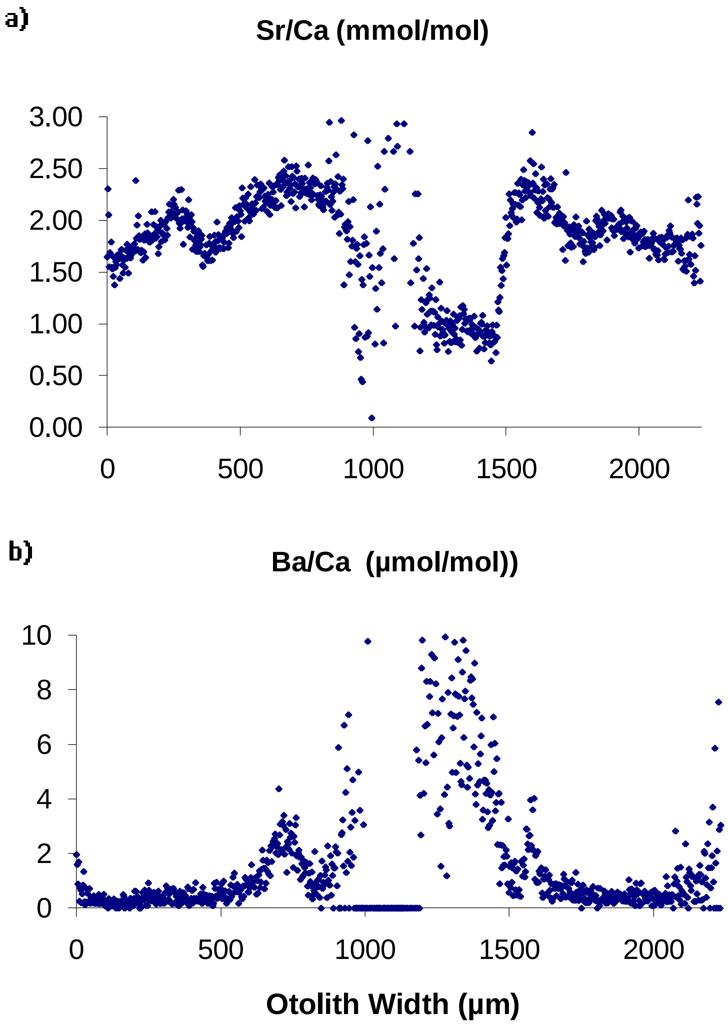

Figure B9: Chemical analysis of a fall 2006 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition. Part of this otolith showed no change in chemistry due to vaterite.

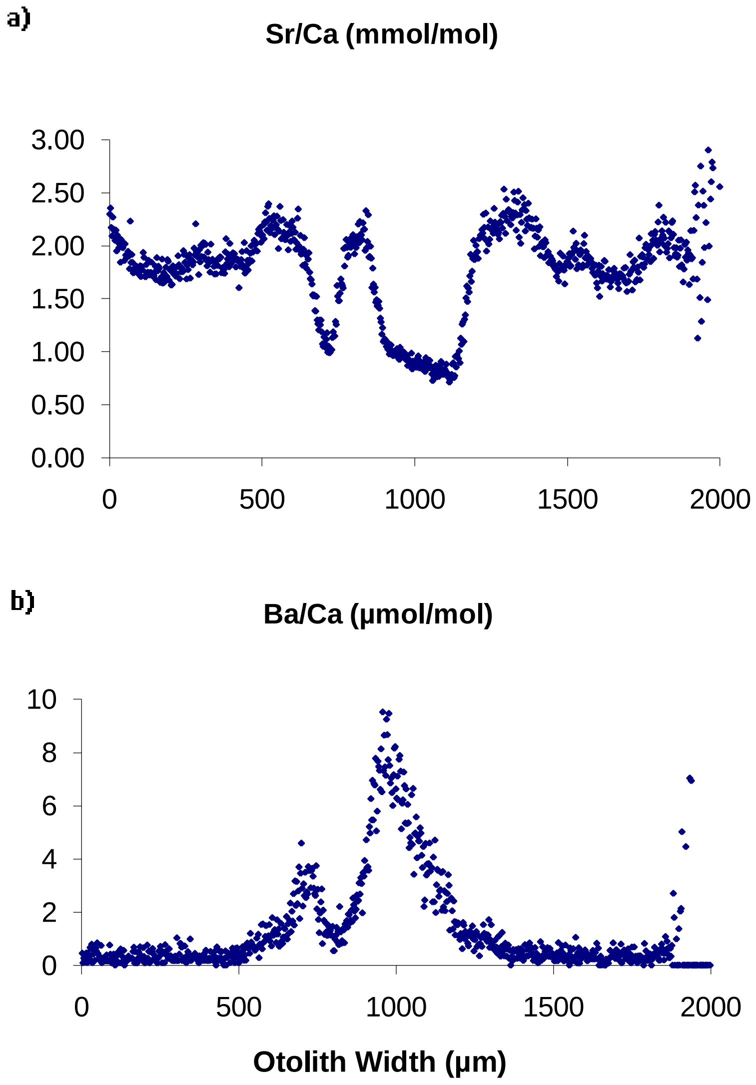

Figure B10: Chemical analysis of a fall 2006 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition.

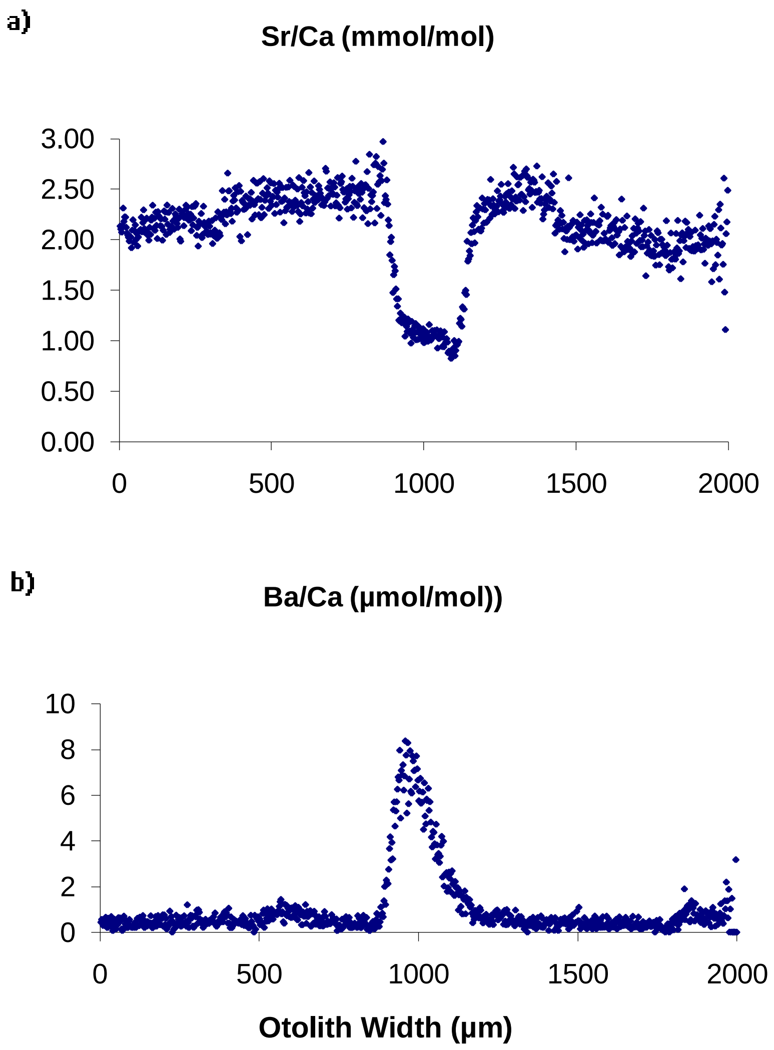

Figure B11: Chemical analysis of a fall 2006 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (µmol/mol) along the otolith width laser ablation pathway (µm) at freshwater to marine transition

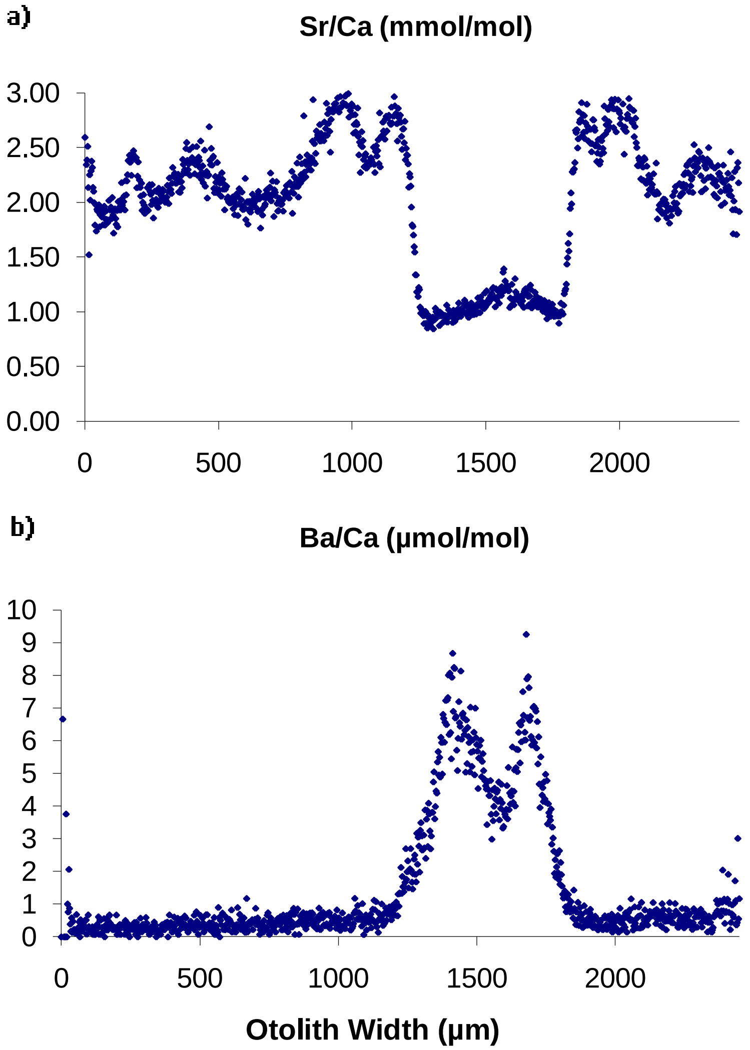

Figure B12: Chemical analysis of a winter 2007 otolith showing the **a)** increase in Sr:Ca (mmol/mol) and **b)** decrease in Ba:Ca (μmol/mol) along the otolith width laser ablation pathway (μm) at freshwater to marine transition.

Appendix C – Size Distribution Data

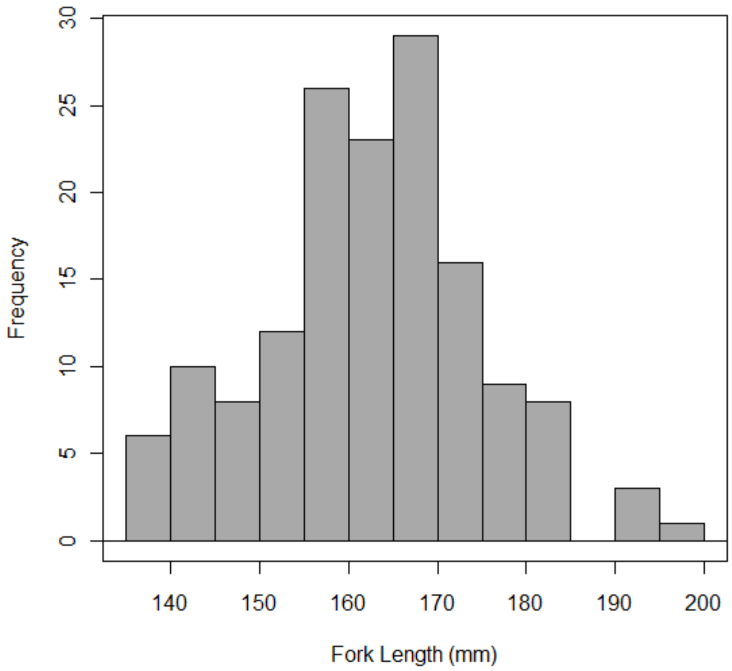

Figure C1: Fall 2005 Fork Length Fish Distribution (N=151)

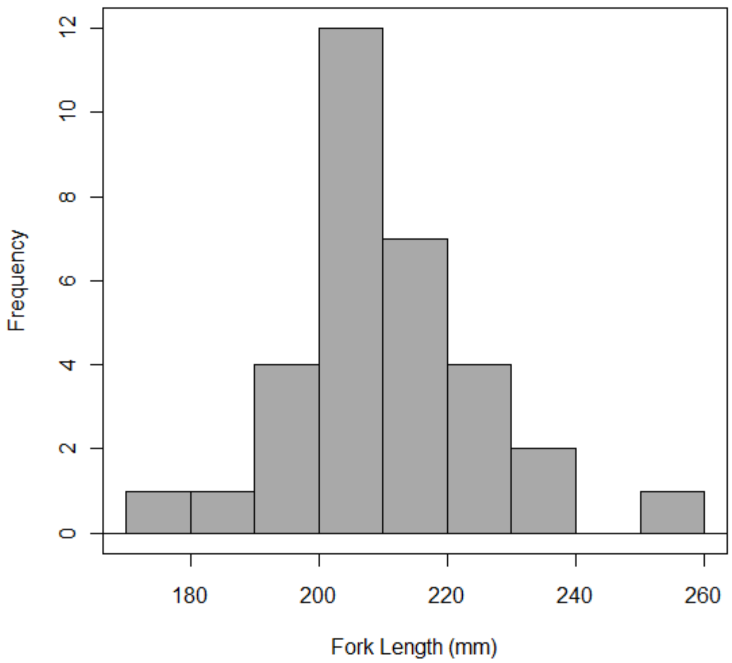

Figure C2: Winter 2006 Fork Length Fish Distribution (N=32)

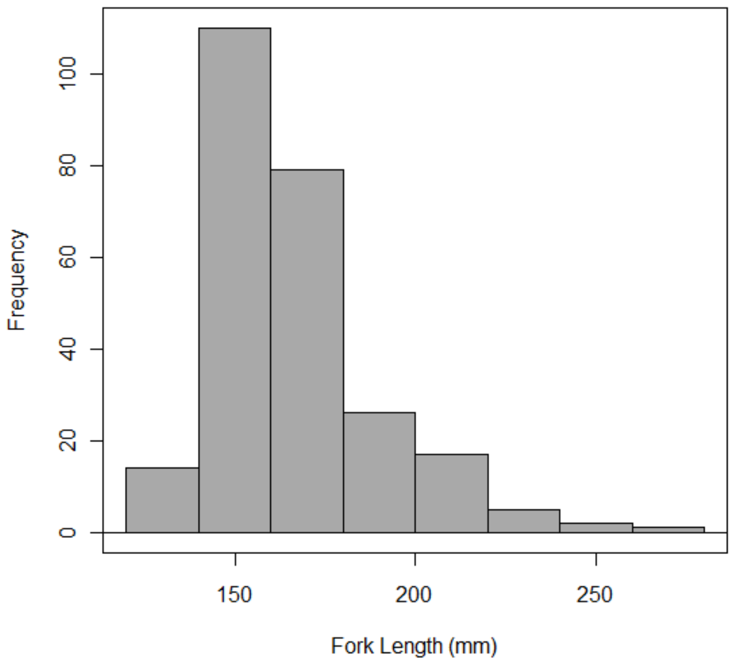

Figure C3: Fall 2006 Fork Length Fish Distribution (N=254)

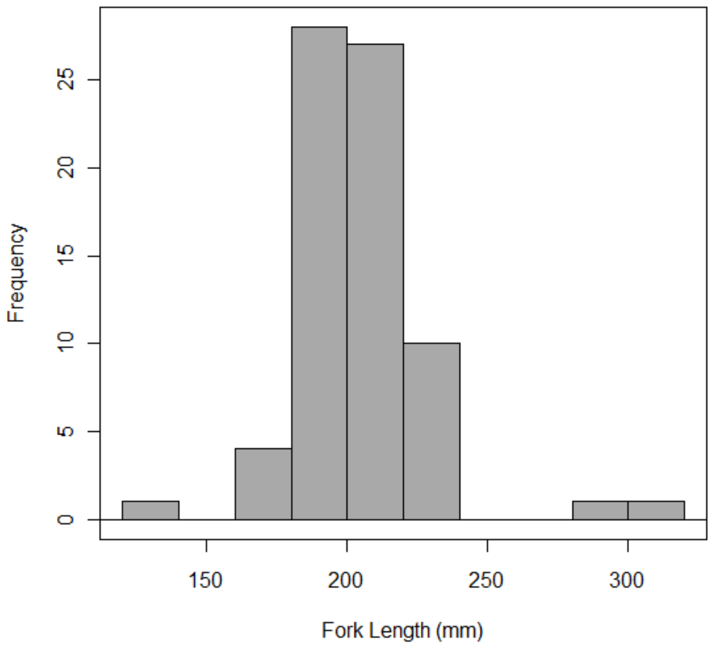

Figure C4: Winter 2007 Fork Length Fish Distribution (N=72)

Appendix D – Otolith Measurement Error Data

Table D1: Summary of data from pilot study on otolith measurement error. Mean measurements were from 20 repetitions per measurement type.

Size	Measurement	Mean	SD	CoefVar
Small	Radius at capture (mm)	0.88	0.01	1.08
	Radius at marine entry (mm)	0.30	0.01	2.09
	Week 1(µm)	46.62	2.18	4.68
	Week 2(µm)	113.43	5.61	4.95
	Week 3(µm)	166.59	2.84	1.70
	Week 4(µm)	217.78	3.13	1.44
Large	Radius at capture (mm)	1.29	0.01	0.66
	Radius at marine entry (mm)	0.33	0.01	1.87
	Week 1(µm)	33.72	0.83	2.47
	Week 2(µm)	61.99	2.22	3.58
	Week 3(µm)	91.60	1.74	1.90
	Week 4(µm)	125.93	1.04	0.83

Appendix E – Otolith Measurement Data

Season	R/L	Type	Mag.	FL (mm)	FL @ ME (mm)	Wk 1 (µm)	Wk 2 (µm)	Wk 3 (µm)	Wk 4 (µm)	Week Avg(µm)	Month Avg (µm)	Slope (µm/wk)
Fall	Left	No tag	400	122	45.46	6.894	8.996	7.781	7.740	7.853	54.18	56.931
Winter	Left	No tag	400	136	43.47	5.034	4.360	4.690	6.174	5.064	43.218	35.252
Fall	Right	No tag	400	144	51.82	4.910	5.541	4.746	6.149	5.336	43.043	37.836
Fall	Left	No tag	250	147	55.74	7.229	5.849	8.109	10.136	7.831	70.952	56.272
Fall	Left	No tag	400	150	58.16	5.862	6.355	6.141	6.166	6.131	43.162	43.490
Fall	Left	No tag	400	151	52.58	6.930	8.037	7.656	7.200	7.456	50.400	53.434
Fall	Left	No tag	400	154	49.94	5.141	5.050	4.205	4.525	4.730	31.675	31.881
Fall	Left	No tag	250	154	51.28	6.256	5.939	7.856	10.374	7.606	72.618	56.253
Fall	Right	No tag	400	156	51.11	6.668	6.356	7.111	7.374	6.877	51.618	48.743
Fall	Left	No tag	400	157	54.14	6.575	6.214	6.714	7.249	6.688	50.743	47.072
Fall	Left	No tag	250	158	61.29	4.143	4.315	4.851	5.770	4.770	40.390	34.761
Fall	Right	No tag	400	159	56.12	3.705	3.664	3.573	3.672	3.654	25.704	25.411
Winter	Left	No tag	400	161	52.88	4.497	4.760	4.875	5.236	4.842	36.652	34.642
Fall	Left	No tag	400	162	51.71	3.735	4.563	4.621	4.711	4.407	32.977	32.415
Fall	Left	No tag	250	164	59.82	5.961	5.546	6.083	8.465	6.514	59.255	46.455
Fall	Right	No tag	400	166	51.34	5.189	4.664	5.254	5.895	5.251	41.265	36.886
Fall	Left	Hatchery	250	167	53.42	3.761	3.848	4.311	3.652	3.893	25.564	27.820
Fall	Left	No tag	250	167	55.67	6.154	5.947	8.169	7.442	6.928	52.094	50.988
Fall	Right	No tag	400	168	52.27	4.835	6.550	4.958	5.992	5.584	41.944	40.221
Winter	Left	No tag	250	168	55.82	5.031	4.995	5.520	6.204	5.438	43.428	38.975
Fall	Left	No tag	400	169	53.19	6.369	7.591	7.714	11.188	8.215	78.316	61.036
Fall	Right	No tag	400	173	54.18	2.750	2.537	4.449	4.688	3.606	32.816	27.630
Fall	Right	No tag	250	176	61.50	6.120	6.487	6.707	-	6.438	-	46.177

Season	R/L	Type	Mag.	FL (mm)	FL @ ME (mm)	Wk 1 (µm)	Wk 2 (µm)	Wk 3 (µm)	Wk 4 (µm)	Week Avg(µm)	Month Avg(µm)	Slope (µm/wk)
Fall	Left	Hatchery	400	185	61.55	4.753	6.244	8.854	9.186	7.259	64.302	57.190
Winter	Right	No tag	250	192	54.17	6.559	7.449	10.588	7.486	8.020	52.402	61.010
Winter	Right	No tag	250	193	53.45	8.627	6.831	8.480	8.504	8.110	59.528	39.934
Winter	Left	No tag	250	193	57.17	5.427	6.527	5.463	5.206	5.655	36.442	55.947
Winter	Left	No tag	250	195	55.64	6.085	6.182	7.355	6.989	6.653	48.923	48.255
Winter	Left	No tag	250	195	58.52	6.763	7.305	7.937	8.355	7.590	58.485	55.110
Winter	Left	No tag	400	202	60.90	3.275	3.768	3.742	4.038	3.706	28.266	26.871
Winter	Left	No tag	250	204	58.37	5.363	6.120	6.548	7.379	6.353	51.653	46.683
Winter	Left	No tag	250	205	62.06	3.222	2.630	4.056	5.412	3.830	37.884	28.245
Winter	Left	No tag	250	207	63.56	5.118	5.826	6.058	6.632	5.908	46.424	43.124
Winter	Left	No tag	250	208	61.61	5.999	8.272	8.810	9.738	8.205	68.166	62.489
Winter	Left	No tag	250	217	58.52	7.075	6.008	6.754	7.822	6.915	54.754	47.955
Winter	Left	No tag	400	220	62.88	6.050	5.032	4.810	6.059	5.488	42.413	36.759
Fall	Right	No tag	250	221	71.98	5.997	7.730	8.390	8.231	7.587	57.617	57.011
Winter	Left	No tag	250	221	70.77	6.447	6.985	7.644	8.193	7.317	57.351	53.278
Winter	Left	No tag	250	223	68.19	5.340	5.914	6.146	6.891	6.073	48.237	44.101
Winter	Right	Hatchery	400	234	72.37	4.598	4.039	4.510	4.725	4.468	33.075	31.033
Winter	Right	No tag	400	290	53.18	5.164	5.312	5.616	5.394	5.372	37.758	38.208
Winter	Left	No tag	400	302	79.75	4.056	4.607	4.548	5.658	4.717	39.606	34.290