AN ABSTRACT OF THE THESIS OF

Londi M. Tomaro for the degree of Master of Science in Fisheries Science presented on October 1, 2010.

Title: Year-class Regulation of Mid-upper Columbia River Spring Chinook Salmon *Oncorhynchus tshawytscha*: The Role of Juvenile Size, Growth, and Migratory Behavior

Abstract approved:

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Early ocean residence is assumed to be a critical period for juvenile Pacific salmon *Oncorhynchus* spp. However, the specific mechanisms influencing growth and survival in the ocean have not been identified for most populations. Therefore, three hypotheses regarding the relationship between early marine residence and subsequent survival of mid-upper Columbia River spring Chinook salmon were evaluated: the 'bigger is better', 'stage duration', and 'match-mistmatch' hypotheses. Six metrics describing juvenile migration history and condition were developed, including 1) size at freshwater exit; 2) size at ocean capture; 3) initial ocean growth rates; 4) timing of ocean entrance; 5) duration of ocean residence; and 6) marine migration rates.

Retrospective estimates of size and growth using otolith analyses rely on the assumption that otolith and somatic size are related. Therefore, I verified this assumption for mid-upper Columbia River Chinook salmon and determined that a body-proportional back-calculation method was the best approach for this population. Fish length and otolith width were positively correlated ($r > 0.92$) and growth rates estimated from back-calculated sizes were positively correlated with observed growth rates ($r = 0.96$).

I also evaluated the utility of using the otolith Sr:Ca pattern as a marker of hatchery-origin and investigated potential mechanisms for the observed Sr:Ca pattern. Visual and

quantitative criteria were developed using otoliths of hatchery fish and were used to correctly classify 85% and 78%, respectively, of a sample of known hatchery-origin fish (n = 114) that were collected in coastal waters. Although Sr:Ca in water and hatchery food did not fully account for the observed pattern in otolith Sr:Ca, the pattern can be used to identify mid-upper Columbia River spring Chinook salmon of hatchery-origin with relatively high accuracy (>75%).

The six juvenile metrics were used to evaluate mechanisms potentially regulating establishment of year-class abundance. The only metrics found to be significantly related to future adult abundance were size at freshwater exit ($r^2 = 0.56$) and capture ($r^2 = 0.60$). These data support the 'bigger is better' hypothesis and indicate that factors influencing size and growth during freshwater residence should be investigated further. Juveniles resided in the brackish/ocean for one to two months prior to capture in May and June; therefore, ocean conditions after this period may be related to the 40% of variation in adult abundance unexplained by interannual variation in body size.

Year-class Regulation of Mid-upper Columbia River Spring Chinook Salmon *Oncorhynchus tshawytscha*: The Role of Juvenile Size, Growth, and Migratory Behavior

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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CHAPTER 1: GENERAL INTRODUCTION

Population abundance is determined by the number of individuals born into a population and the rate of mortality experienced. Different mortality rates are experienced during various life stages. Cohort (year class) size is influenced by early life stages that have disproportionate amounts of mortality and whose final abundances may be correlated with adult abundance (for review see, Houde 2008). Periods of high mortality that regulate recruitment of fish populations are termed 'critical periods' (Hjort 1914, Lasker 1975) and can occur at first feeding or various early life stages (Vladimirov 1975) as is likely for salmonids.

Chinook salmon *Oncorhynchus tshawytscha* are distributed along the Pacific Rim and, in North America, spawn from central California to western Alaska (Beacham et al. 2006). Juveniles spend a few weeks, months or more than a year in freshwater before migrating to the ocean (Taylor 1990), where most individuals spend two or more years before returning to spawn as adults (Quinn & Myers 2004). The Columbia River supports populations of four salmon species, including a variety of Chinook salmon populations with diverse life-history and ecological characteristics (Waples et al. 2008). The current annual return of spring run Chinook salmon in the mid-upper Columbia River (6,708 to 51,133 in the past 10 years, Columbia River Data Access in Real Time: http://www.cbr.washington.edu) is >90% lower than historical levels (Scheuerell & Williams 2005) and upper Columbia River spring Chinook are

listed as endangered under the Endangered Species Act (ESA) (NMFS 2009). Mid-upper Columbia River spring Chinook salmon generally spend an entire year in the freshwater (Rich 1920, Fryer 2009) and migrate downriver, through the estuary and into the ocean as yearlings (Healey 1982).

The early ocean period is assumed to be a critical period for juvenile salmon because of positive correlations between survival and environmental or biological factors during the first summer of marine residence (e.g. Beamish & Mahnken 2001, Beamish et al. 2004) and concurrence in population cycles at the ocean basin scale (Hare et al. 1999). For example, juvenile survival rates of some stocks were related to environmental factors in the ocean during the spring of the year the juveniles emigrate to the ocean (Scheuerell & Williams 2005, Petrosky & Schaller 2010) or during early ocean residence (for review see Pearcy & McKinnell 2007). Survival rates of salmon are often correlated regionally (Peterman et al. 1998, Hare et al. 1999, Pyper et al. 2005), implying that cohort size is established before the fish disperse and intermingle with fish from other regions. Additionally, adult returns of some stocks are positively related to the abundance of ocean juveniles at the beginning of the first ocean winter, after presumably high mortality during initial ocean residence (Pearcy 1992). Although there is evidence supporting the assumption that the period of early marine residence influences survival and abundance of adults, the specific causes of mortality have not been identified and may vary among years, species, or life histories.

Yearling Chinook salmon emigrants use freshwater, coastal and, to a lesser extent, estuarine habitats during their early life history and, therefore, factors present

in the freshwater or coastal environments likely act to regulate cohort size. To better understand regulation of the mid-upper Columbia River spring Chinook salmon population, I tested three mechanistic hypotheses: the 'bigger is better' hypothesis (Miller et al. 1988); the 'stage duration' hypothesis (Houde 1987); and the 'match-mismatch' hypothesis (Cushing 1974). These hypotheses posit that cohort abundance is positively related to body size, early growth rates, and spatiotemporal overlap with the prey field, respectively. Specifically, I investigated relationships between adult returns and 1) juvenile size at emigration into brackish waters, hereafter termed 'freshwater exit', and at capture in the nearshore ocean; 2) growth rate during early marine residence; and 3) the date of freshwater exit relative to indicators of marine productivity.

The techniques used to estimate somatic size and growth rate are dependent on a proportional relationship between otolith width and fish length. Otolith deposition can be influenced by factors other than somatic growth, such as temperature (Fey 2005), metabolic rate (Wright et al. 2001), and ontogeny (Wright et al. 1990). Otolith and somatic growth were positively correlated over a period of months in sub-yearling Chinook salmon; however, otolith growth was less variable than somatic growth (Bradford & Geen 1987). Less is known about whether somatic and otolith growth are coupled during the yearling stage. Therefore, in Chapter 2, I evaluated two approaches for using otolith measurements to estimate somatic growth: increment widths and change in otolith width. I evaluated the assumption that fish length and growth rate are

correlated with otolith width and growth rate and assessed the accuracy of back-calculations by using eight individually tagged fish.

I used data from field and laboratory analyses to evaluate factors influencing interannual variability in cohort abundance of the mid-upper Columbia River spring Chinook salmon population. In Chapter 3, I calculated juvenile size at freshwater exit and capture, marine growth rate, date of emigration and migration rate using fish and otolith measurements. Otoliths are useful for this type of study because they grow throughout the lifetime of the fish (Campana & Thorrold 2001), deposit material incrementally (daily in Chinook salmon (Neilson & Geen 1982, 1985)), and incorporate several chemical elements in proportion to their abundance in the environment (Bath et al. 2000, Kraus & Secor 2004, Elsdon & Gillanders 2005). I used the strontium (Sr) to calcium (Ca) ratio to identify the migration into brackish waters because the Sr:Ca is generally lower in freshwater than in the ocean and can be used to examine migratory history and maternal origin in a variety of diadromous fishes (Bacon et al. 2004, Kraus & Secor 2004, Donohoe et al. 2008, Miller & Kent 2009, Zimmerman et al. 2009).

Another important consideration is the potential influence of hatchery-reared salmon in the system. Hatchery-reared fish may be differentially affected by environmental conditions or respond dissimilarly to predator or prey populations. Previous studies have found that hatchery salmon exhibited higher mortality (Saloniemi et al. 2004), had lower reproductive fitness (Araki et al. 2007), and were less physiologically fit (Chittenden et al. 2008) and more susceptible to predation

(Fritts et al. 2007) than naturally-spawned conspecifics. Many hatchery fish are marked by adipose-fin clip; however, some hatchery-reared individuals are released into the wild without any fin-clips or other distinguishing marks to identify them. The ability to differentiate between all hatchery-reared and naturally-spawned individuals would enable more robust comparisons of the size, growth rates, and migration timing between the groups. My study describes an otolith chemical signature to distinguish between the two groups.

The rearing environments of hatchery-reared and river-origin fish differ and environmental variation can lead to differences in physical characters between the groups of fish. For example, otolith microstructure was successfully used to classify hatchery and naturally-reared individuals (Zhang et al. 1995, Barnett-Johnson et al. 2007). Chemistry of scales (Adey et al. 2009) and otoliths (Coghlan et al. 2007, Gibson-Reinemer et al. 2009) were used successfully to differentiate between rearing type using multi-elemental discriminant analysis. In Chapter 4, I evaluated the utility of using the pattern of otolith Sr:Ca to differentiate between hatchery-reared and naturally-spawned individuals from the mid-upper Columbia River spring Chinook salmon stock. Hatchery feed is comprised of predominantly marine-derived fish meal and reflects the higher Sr:Ca of the marine environment, and thus may cause elevated otolith Sr:Ca levels.

Mid-upper Columbia River spring Chinook salmon spend a year in freshwater as juveniles and thus the population's survival and recruitment may be more influenced by factors acting during freshwater residence as well as the early ocean

period than other life histories. The work presented here investigated whether juvenile size at freshwater exit and capture, growth rates during early marine residence, and timing of ocean entrance are related to the adult population abundance of this stock. The results of this study increase our understanding of the mechanisms acting during the juvenile life stage. Mean fish size at freshwater emigration was the best predictor of adult returns ($r^2 = 0.56$, $p = 0.03$); therefore, factors regulating growth during freshwater residence should be investigated more thoroughly.

CHAPTER 2: RELATIONSHIP BETWEEN OTOLITH AND SOMATIC GROWTH

INTRODUCTION

Size and growth are important metrics in studies of the early life stages of fishes. Size is often assumed to be positively related to survival, but the evidence is equivocal (for review, see Anderson 1988, Litvak & Leggett 1992, Sogard 1997). Mortality during a specific life-stage is related to the stage-specific mortality rate and the amount of time spent in that life stage (Takasuka et al. 2004, Houde 2008). The duration of a life-stage is determined by the growth rate (Chambers & Leggett 1987), which is often used as a proxy for stage duration (Takasuka et al. 2004). Therefore, accurate measurements of size and growth are important for investigating the impact of early life stages on interannual variability in year class abundance.

Otolith size can be used to back-calculate fish size and growth rates if otolith and somatic size and growth rates are coupled (Campana & Jones 1992). Proportional coupling between otolith and somatic size occurs in a wide variety of species. For example, otolith and somatic size are related in juvenile bluefin tuna *Thunnus thynnus* (Megalofonou 2006), juvenile bluefish *Pomatomis saltatrix* (Roemer & Oliveira 2007), larval Japanese anchovy *Engraulis japonicus* and sardine *Sardinops melanostictus* (Takasuka et al. 2008), and juvenile herring *Clupea harengus* and smelt *Osmerus eperlanus* (Fey 2006). Otolith size was also positively related to fish length in juvenile Chinook salmon during freshwater, estuarine, and early ocean residence (Neilson & Geen 1986, Bradford & Geen 1987, Titus et al. 2004, Miller et al. 2010b).

Chinook salmon *Oncorhynchus tshawytscha* from the interior Columbia River basin spend a few months to a year in freshwater as juveniles before migrating downriver through the estuary and into the ocean (Rich 1920). Size and growth during their migration and early marine residence may influence the survival of this stock. Because of the near impossibility of capturing the same fish as they move downriver toward the ocean, mean sizes at different points in time are compared to determine population growth and growth rates. However, individual measurements provide more detailed growth information and, if available, can be used to distinguish between growth and size-selective mortality. Repeated measurements of the same individuals through time are necessary to collect these data; however, they are often not possible in field studies. Otoliths provide the potential to collect data through time from individual fish because they grow incrementally throughout life and are not subject to resorption (Geen et al. 1985, Campana 1999, Campana & Thorrold 2001). In Chinook salmon, otolith increments are generally formed at daily intervals (Neilson & Geen 1982, Campana & Neilson 1985), and thus can provide a relative measure of fish size and growth through time.

In some species or under some conditions, external factors, such as temperature, can lead to uncoupling of the relationship between otolith and fish growth. For example in herring from Vistula Lagoon, Baltic Sea, somatic growth increased with temperature only for fish < 30 d old while otolith growth increased with temperature for all ages (Fey 2005). Additionally, juvenile fish growth rates increased ~20% with temperature while increment widths increased approximately

100% among temperature categories (Fey 2005). Temperature can influence otolith growth through metabolic rate separately from somatic growth rate; juvenile Atlantic salmon *Salmo salar* otolith growth rate and metabolic rate increased with temperature in the absence of somatic growth (Wright et al. 2001). Additionally, the relationship between somatic and otolith growth may change with ontogeny. For instance, otolith and somatic growth diverged in two subsets of a population of Atlantic salmon. Somatic growth rates slowed in fish that would become two-year-old smolts while otolith growth remained relatively constant (Wright et al. 1990). However, somatic and otolith growth rate remained constant in the fish that would smolt as yearlings (Wright et al. 1990). In contrast, previous studies have found that otolith growth and growth rates were more conservative (less variable) than somatic growth and growth rates in juvenile Chinook salmon (Bradford & Geen 1987). Therefore, it is important to perform species-specific validation studies to determine whether otolith and somatic growth are coupled.

In this study I used eight individually tagged Chinook salmon to evaluate two metrics for estimating somatic growth using otoliths in juvenile Columbia River Chinook salmon: 1) mean otolith increment width; and 2) mean daily otolith deposition rate during a defined period. Using the change in otolith size I also estimated mean daily somatic growth rate. I examined the relationship between otolith and fish size, assessed the accuracy of back-calculated estimates of fish length based on otolith width, and compared direct and proportional back-calculation approaches. Validation of back-calculation of fish size from otolith size is rarely done on an

individual level (Francis 1990). I also determined whether a direct or proportional back-calculation method was more appropriate to use in a study evaluating mechanisms influencing establishment of year class abundance of spring Chinook salmon.

METHODS

Fish Collection

Eight juvenile Chinook salmon with passive integrated transponder (PIT) tags were captured in purse seine collections in the Columbia River estuary during May and June 2008 (L. Weitkamp, National Oceanic and Atmospheric Administration Fisheries (NOAA), unpub. data). Field fork length measurements were confirmed in the laboratory so no size correction was necessary (L. Weitkamp, NOAA, pers. comm.). PIT tags are unique identifiers inserted into the body cavity that can be interrogated by detection arrays at dams and in bypass areas (Prentice et al. 1990a, Prentice et al. 1990b, Muir et al. 2001, Hockersmith et al. 2003). In addition to passage data, length at tagging was collected from the Pacific States Marine Fish Commission's online database, PTAGIS (accessible at http://www.psmfc.org/PIT_Tag_Information_System_PTAGIS).

Otolith Preparation and Image Capture

Sagittal otoliths were removed, cleaned of adhering tissue, and stored dry. Left and right otoliths do not differ significantly in size (Gauldie 1996), but for consistency I used the left otolith if available. Each otolith was mounted onto a glass slide using thermoplastic resin with the sulcus facing upwards, ground to expose the primordia,

flipped, and polished to expose the dorsal-ventral axis using sandpaper (240-2500 grit) and lapping film (1-30 μm grit). I captured digital images using a Leica DC300 camera coupled with a Leica MZ95 stereoscope (20x) and a Leica DM1000 compound microscope (40x, 100x, 200x, and 400x) and Leica IM50 Image Manager ®. I completed image analysis with ImagePro ® Plus (Media Cybernetics) software.

Size Estimates

I compared direct and proportional back-calculation approaches for estimating fish length (mm) from otolith width (μm) based on a regression incorporating 123 individuals from seven populations across six years (Equation 1) (Miller et al. 2010b):

$$S_{TE} = 6.91 + 0.06 \cdot O_T \ (r^2 = 0.93, p < 0.001) \quad (1)$$

where S_{TE} = estimated fish length at tagging and O_T = otolith width at tagging. Francis (1990) advocated the use of proportional adjustments to regression equations representing the relationship between otolith and fish size. Therefore, direct (Equation 1) and body-proportional (Equation 2) back-calculations were compared for estimating size at tagging.

$$S_{TE} = [(6.91 + 0.06 \cdot O_T) / (6.91 + 0.06 \cdot O_C)] \cdot S_C \quad (2)$$

where S_{TE} = estimated fish length at tagging, S_C = fish length at capture, O_T = otolith width at tagging, and O_C = otolith width at capture. I used correlation to determine whether the direct and proportional size estimates were linearly related to actual sizes.

Somatic size at tagging was back-calculated from otolith width, the distance across the dorsal-ventral axis at the widest point (Figure 2.1); (Titus et al. 2004, Miller

et al. 2010b). In order to measure otolith size at tagging, I counted the number of marginal increments corresponding to the number of days at liberty, i.e., the number of days between tagging and capture, which included some hatchery residence as well as in-river migration, and measured the otolith width along the dorsal-ventral axis of the increment associated with tagging (Figure 2.1). To meet parametric assumptions for correlation analysis, both variables were natural log - transformed.

Growth Rate Estimates

Otolith growth rates were estimated in two ways and both approaches were based on the time at liberty. Daily otolith increment formation has been demonstrated (Neilson & Geen 1982, 1985); therefore, I assumed that the increment count during the time at liberty was equal to the number of days at liberty. The first growth rate metric was the mean increment width deposited while at liberty (μm) (Equation 3).

$$\text{Mean I} = (\sum I_L) / D_L \quad (3)$$

where I_L = mean dorsal increment width while at liberty between 45° and 135° from the dorsal-ventral axis, and D_L = days at liberty. The second metric of growth rate was the otolith deposition rate ($\mu m \cdot d^{-1}$), defined as the mean daily increase in otolith width during liberty (Equation 4).

$$O_D = (O_C - O_T) / D_L \quad (4)$$

where O_D = otolith deposition rate, O_C = otolith width at capture, O_T = otolith width at tagging, and D_L = days at liberty. Additionally, somatic growth rate was estimated from the difference between back-calculated fish size at tagging and size at capture (Equation 5).

$$G_E = (S_C - S_{TE}) / D_L \quad (5)$$

where G_E = estimated somatic growth rate, S_C = fish length at capture, S_{TE} = estimated fish length at tagging, and D_L = days at liberty. I determined the relationship between otolith and fish size for the eight fish in the study population using simple correlation of somatic length and otolith width at tagging and capture to determine whether the relationship changed during the elapsed time, which would indicate uncoupling and potential back-calculation error.

Somatic growth rate ($mm \cdot d^{-1}$) was defined as the mean daily increase in size while at liberty (Equation 6).

$$G = (S_C - S_T) / D_L \quad (6)$$

where G = somatic growth rate, S_C = fish length at capture, S_T = fish length at tagging, and D_L = days at liberty. I used correlation analysis to assess whether mean otolith increment width, mean otolith deposition rate, and estimated somatic growth rate were related to actual mean somatic growth rate. Prior to analysis, I assessed the datasets for linearity, normality and homogeneity of variance and transformed the data if necessary.

RESULTS

Fish Collection

The eight Chinook salmon juveniles originated from seven release locations (Table 2.1). The fish were 70-146 mm FL at tagging and 115-165 mm FL at capture. Three of the fish were fall run Chinook salmon, three were spring run, and two were collected for tagging in-river and had unknown run-timing (Table 2.1).

Size Estimates

Otolith width was positively, linearly related to the somatic size at tagging ($r = 0.98$, $n = 8$, $p < 0.001$) and at capture ($r = 0.93$, $n = 8$, $p < 0.001$) (Figure 2.2). The direct and proportional regressions both under- and over-estimated actual sizes, the differences presented are absolute values. The direct estimates of fish size differed from observed length at capture by 1.3 – 13.8 % (Table 2.2, mean = 8.2%, CV = 0.5) and from observed length at tagging by 0.2 – 9.7% (Table 2.2, mean = 4.0%, CV = 0.9). Proportional estimates differed from reported length at tagging by 0.05 to 15.7% (Table 2.2, mean = 8.0%, CV = 0.7). Direct back-calculations over-estimated fish size at capture by ≤7% and under-estimated size at capture by 7 to 14% (Table 2.2). Direct back-calculations of size at tagging over-estimated observed size by 0.2 to 1.2% and under-estimated size at tagging by 4 to 10%; estimate error did not appear to be related to fish size. However, proportional estimates of size at tagging over-estimated sizes of small fish (< 95 mm FL) by 9 to 11%, and under-estimated sizes of medium and large fish (114 – 146 mm FL) by 0 to 16% (Table 2.2).

Growth Rate Estimates

Mean increment width during the time at liberty ranged from 1.4 to 2.9 μm; however, seven of the eight fish had mean increment width ≥2.3 μm (Figure 2.3). Mean increment width (Equation 3) was weakly correlated to somatic growth rate ($r = 0.71$, $n = 8$, $p = 0.05$). The mean otolith deposition rate (Equation 4), i.e., the daily change in otolith width, during liberty ranged from 4 to 8 $\mu m \cdot d^{-1}$ (Figure 2.4a). Mean

somatic growth rate was positively and linearly related to mean otolith deposition rate (Figure 2.4a, $r = 0.84$, $n = 8$, $p < 0.01$). Estimated somatic growth rates during liberty ranged from 0.14 to 0.84 $mm \cdot d^{-1}$ (Equation 5) and actual somatic growth rates (Equation 6) ranged from 0.10 to 0.89 $mm \cdot d^{-1}$. Estimated growth rates were positively linearly correlated with the observed growth rates (Figure 2.4b; $r = 0.96$, $n = 8$, $p < 0.001$).

Faster growing fish had smaller otoliths for their size than slower-growing fish. The change in otolith size per unit of fish growth was negatively related to the somatic growth rate (Figure 2.5; $r = -0.96$, $n = 8$, $p < 0.001$). Although fish with faster somatic growth rates had faster daily otolith deposition rates, they deposited less otolith material per unit of fish growth than slower growing fish.

DISCUSSION

Growth Rate Estimates

The primary purpose of this study was to evaluate two approaches for estimating somatic growth rates: mean increment width; and daily otolith deposition. Additionally, I evaluated estimating growth rate from back-calculated sizes. Mean increment width was weakly correlated with mean somatic growth rate. Otolith deposition rate, the rate of change in otolith width, was related to observed somatic growth rate. Mean growth rates based on back-calculated sizes were proportional to, and the most strongly correlated with, actual mean somatic growth rates. The method that provided the best growth rate estimates was based on the difference between size at capture and back-calculated size at tagging. This approach can be used on field-

collected specimens if the number of increments between otolith width measurements is determined. However, validation required individuals of known size at two points in time.

Otolith and fish size were related in juvenile Chinook salmon within the size range examined in this study (70-165 mm). The results of this study demonstrated that back-calculation using the regression equation described by Miller et al. (2010b) can be used to retrospectively estimate sizes of juvenile Columbia River Chinook salmon within this size range. The data also indicated that direct estimates were closer than proportional estimates to observed sizes. However, proportional estimates resulted in fewer instances of negative growth and were used for subsequent analyses.

The correlation between fish and otolith size was stronger at tagging ($r = 0.98$) than at capture ($r = 0.93$). Changes in the relationship between otolith width and fish length were likely driven by uncoupling of otolith and somatic growth and variation in riverine somatic growth rates. Juvenile Chinook salmon size and growth rates vary during freshwater migration (Muir et al. 2006, Achord et al. 2007). The data indicate that faster-growing fish deposit less otolith material per mm increase in fish length than their slower-growing counterparts, as previously noted (Templeman & Squires 1956, Krivobok & Shatunovskiy 1976, Fey 2006, Takasuka et al. 2008). If this variation in the fish – otolith size relationship was relatively recent, it may explain why variation in otolith size explained less of the variation in fish size at capture than at tagging.

The uncoupling of otolith and somatic growth between tagging and capture indicates that the increment widths do not reflect recent somatic growth in juvenile Chinook salmon. If otolith and somatic growth are coupled during early life (as demonstrated by Bradford & Geen 1987), then otolith widths should yield good size estimates for a period after uncoupling occurs because otolith width includes all of the previously deposited otolith material. However, mean increment widths in this study incorporate growth at the otolith margin, which was deposited after the uncoupling occurred, and does not reflect somatic growth. Similarly, Neilson and Geen (1982) demonstrated that the number and width of juvenile Chinook salmon otolith increments were affected by temperature and duration of light-dark cycles, while the otolith and somatic size relationship remained stable across treatments. To properly test the relationship between marginal increment width and recent somatic growth in juvenile Chinook salmon I would compare daily growth with individual increment widths over a short (~2 wk) period for individuals over broad size and age ranges.

Although there is an apparent growth rate bias in otolith deposition, other factors, such as ontogeny or stock-specific differences, may have also influenced the relationship between otolith and fish size. For example, the otolith-somatic size relationship differed among ontogenetic stages in larval and juvenile bluefish *Pomatomus saltatrix* (Hare & Cowen 1995). Some of the juvenile salmon may have experienced an ontogenetic shift during migration, such as smoltification, which affected the proportional coupling of otolith and fish size.

Collection of individual data on fish size at distinct points in time is possible with the technique presented here. Therefore, temporally and spatially distinct collections can be used to compare growth rates of different segments of a population and possibly differentiate between growth and size-selective mortality (Gleason & Bengston 1996, Takasuka et al. 2003, 2004, Plaza & Ishida 2008).

These results are limited to the size range examined and are based on a small, sample (n = 8), although there was no apparent difference in the error associated with yearling and subyearling fish. Additionally, there was evidence that the relationship between fish and otolith size changed at the upper end of the size range and underestimated length of larger fish. It may be possible to describe the fish length-otolith width relationship for all ages and sizes of fish in the population. Size- or growth rate- based changes in the fish – otolith size relationship may be accounted for by including data over the entire length and age range of a fish species. For example, Katakura et al. (2007) developed an allometric smoothing function with three inflection points to describe the relationship between otolith and fish size over the life time of walleye Pollock. Further research should examine specific stock groups and broader size and age ranges to address the weaknesses associated with limited samples, size range, and mixed stock groups.

Approaches similar to this study can be used to determine the appropriate model for retrospective size estimates and are useful in studies sampling a cohort through time or comparing annual cohorts. The results of this study also provide support for using the methodologies described above to collect data from individual

fish over time such as size at emigration and growth rates during specific stages to evaluate ecological hypotheses. For example, otolith width can be used to calculate fish length at freshwater exit and growth rates during early ocean residence across several years to determine how size and growth rates influence interannual variability in adult abundance, a proxy for survival. Additionally, variation in estimated fish metrics can be used to evaluate the ‘bigger is better’ (size) and ‘stage duration’ (growth rates) hypotheses and to elucidate the mechanisms affecting the establishment of year class size.

TABLES

Table 2.1. Tagging location, fish size (FL, mm) at tagging and capture and run type of the eight interior Columbia River Chinook salmon juveniles collected in 2008 and used in this study. NFH = National Fish Hatchery.

Tag Location	Run Type	Tag Length (mm)	Capture Length (mm)	Time at Liberty (d)	Growth Rate ($mm \cdot d^{-1}$)
Lower Granite Dam, WA	Unknown	141	145	20	0.20
Tucannon Hatchery, WA	Spring	146	158	124	0.10
Lower Granite Dam, WA	Unknown	114	139	28	0.89
Rapid River Hatchery, ID	Spring	126	150	116	0.21
Spring Creek NFH, WA	Fall	70	130	106	0.57
Little White Salmon, WA	Spring	131	165	77	0.44
Lyons Ferry Hatchery, WA	Fall	92	124	65	0.49
Umatilla Hatchery, OR	Fall	81	115	69	0.49

Table 2.2. Back-calculations of fish size (FL) at capture and at tagging. Estimates were made with direct (Equation 1) and proportional (Equation 2) regressions. Actual sizes at capture and tagging are listed in the shaded columns, followed by percent error of the estimates of size at capture and tagging.

Capture FL, mm	% Error Direct	Tagging FL, mm	% Error Direct	% Error Proportional
145	1.3	141	0.8	-0.5
158	7.1	146	-9.7	-15.7
139	-6.9	114	1.3	8.8
150	5.3	126	-2.6	-7.5
130	-13.7	70	--4.2	11.0
165	-7.6	131	-7.6	-0.1
124	-13.8	92	-5.7	9.4
115	-10.0	81	0.2	11.4

FIGURE LEGENDS

Figure 2.1. Otolith schematic showing representative increments. Otolith width at capture was defined as the distance across the otolith from the dorsal to the ventral edge at the widest point. Otolith width at tagging was defined as the distance across the otolith between the dorsal and ventral edges of the increment associated with tagging at the widest point.

Figure 2.2. Fish length versus otolith width. Fork length (FL, mm) plotted against otolith width (μm) at tagging (gray squares) and capture (black diamonds). Trend lines represent the positive linear relationships between otolith size and fish size at tagging ($r = 0.98$, d.f. = 6, $p < 0.001$) and capture ($r = 0.93$, d.f. = 6, $p < 0.001$).

Figure 2.3. Actual growth rate versus otolith increment width. Mean somatic growth rate during the time at liberty plotted against the mean (± SE) at liberty increment width. Mean somatic growth rate was not related to the mean otolith increment width ($r = 0.71$, $p = 0.05$).

Figure 2.4. Actual growth rate versus otolith deposition and estimated growth rate. Mean observed somatic growth rate during the time at liberty plotted against a) mean daily otolith deposition ($r = 0.84$, d.f. = 6, $p < 0.01$), and b) mean estimated somatic growth rate ($r = 0.96$, d.f. = 6, $p < 0.001$). The estimated growth rate was calculated from the difference between back-calculated size at tagging and observed size at capture for each fish.

Figure 2.5. The rate of otolith deposition relative to fish growth rate. Log-transformed change in otolith width (ΔOW) per mm somatic growth was negatively linearly related to fish growth rate ($r = -0.96$, d.f. = 6, $p < 0.001$).

FIGURES

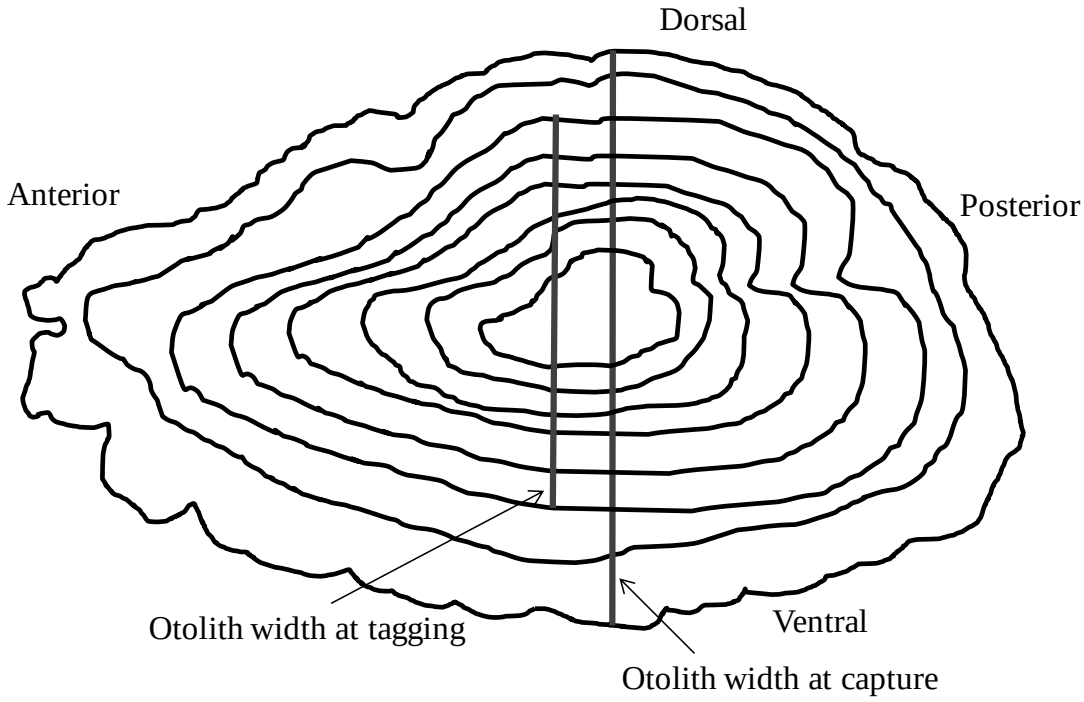


Figure 2.1

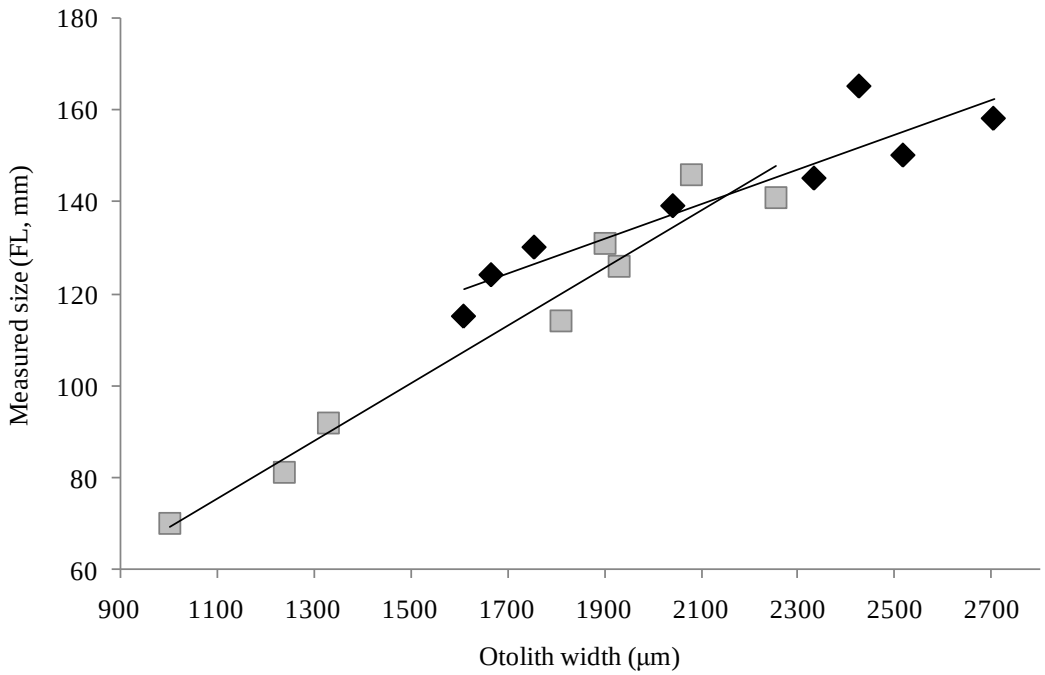

180
160
140
120
100
80
60
Measured size (FL, mm)
900
1100
1300
1500
1700
1900
2100
2300
2500
2700
Otolith width (μm)

Figure 2.2

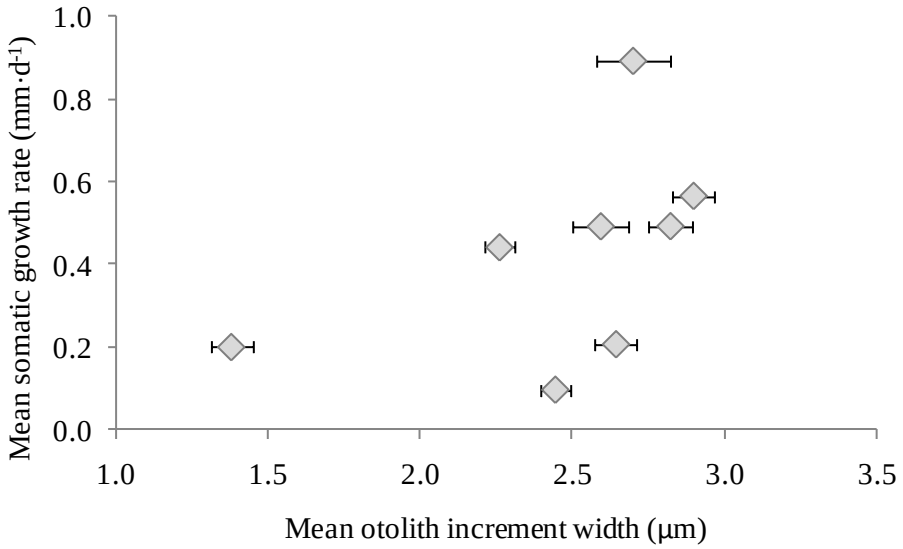
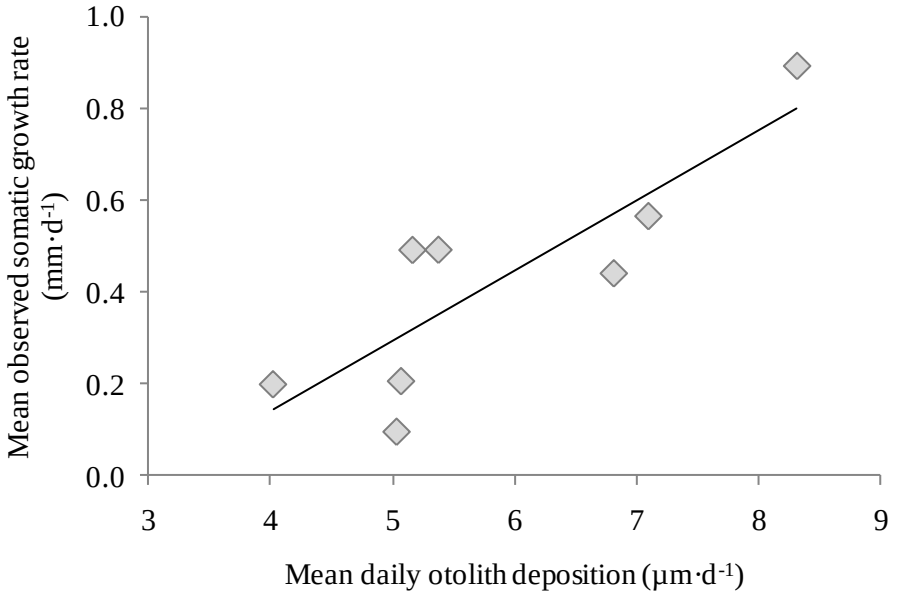

1.0
0.8
0.6
0.4
0.2
0.0
Mean somatic growth rate (mm·d-1)
1.0
1.5
2.0
2.5
3.0
3.5
Mean otolith increment width (µm)

Figure 2.3

a


Mean observed somatic growth rate (mm·d-1)
1.0
0.8
0.6
0.4
0.2
0.0
3
4
5
6
7
8
9
Mean daily otolith deposition (µm·d-1)

b

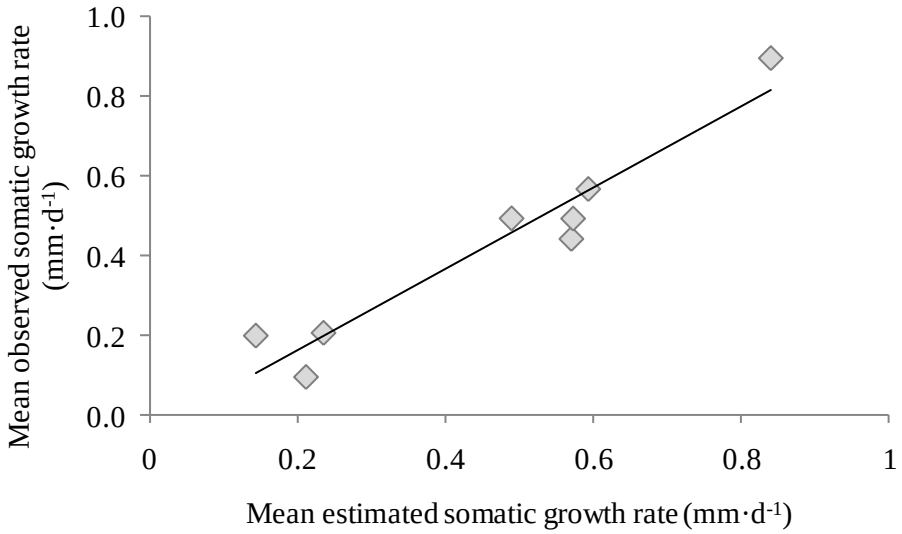

Mean observed somatic growth rate (mm·d-1)
1.0
0.8
0.6
0.4
0.2
0.0
0
0.2
0.4
0.6
0.8
1
Mean estimated somatic growth rate (mm·d-1)

Figure 2.4

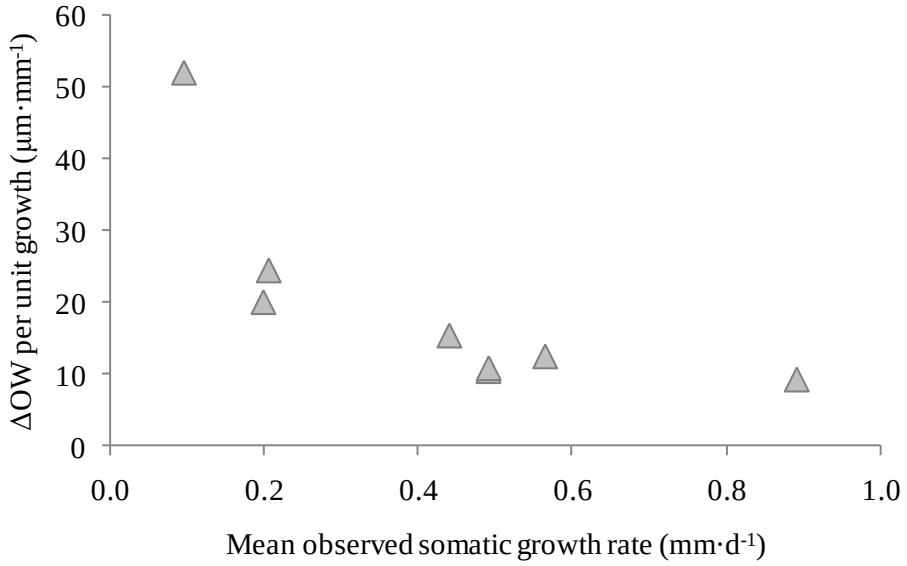

60
50
40
30
20
10
0
ΔOW per unit growth (μm·mm-1)
0.0
0.2
0.4
0.6
0.8
1.0
Mean observed somatic growth rate (mm·d-1)

Figure 2.5

CHAPTER 3: RELATING JUVENILE SIZE, GROWTH RATE, AND MIGRATION TIMING TO ADULT RETURNS OF MID-UPPER COLUMBIA RIVER SPRING CHINOOK SALMON *ONCORHYNCHUS TSHAWYTSCHA*

INTRODUCTION

The mechanisms that influence population regulation and recruitment act on various life-stages of fish. Often the stage at which year-class strength is established is known, but the mechanisms are not understood or identified. The critical period hypothesis states that population regulation occurs during a life-stage with disproportionate mortality and has been expanded from the original focus on first feeding to include other periods (Hjort 1914, and for review, Beamish & Mahnken 2001, Houde 2008). Hence, year class size after a critical period should be related to future abundance (Houde 2008).

Early ocean residence, i.e., the first few months at sea, is often considered a critical period for Pacific salmon (Pearcy 1992). Evidence is growing that survival rates of juvenile salmon are dependent on conditions during early marine life (Hobday & Boehlert 2001, for review, Pearcy & McKinnell 2007). One line of evidence supporting this hypothesis is that survival is related to environmental conditions during early ocean residence. For example, conditions during their first summer and fall in the ocean were related to survival of Snake River Chinook salmon *Oncorhynchus tshawytscha* stocks (Scheuerell & Williams 2005, Zabel et al. 2006). Additionally, interannual survival variability was more strongly related to marine conditions at regional, rather than ocean basin, scale factors. For example, egg-to-adult

survival rates of pink *O. gorbuscha*, chum *O. keta*, and sockeye *O. nerka* salmon covaried within ~500 km but not at greater distances (Pyper et al. 2005). Likewise, sockeye salmon survival covaried within regions (~500 km) but not between the two regions (1000s of km), indicating that survival variability was strongly influenced during early life prior to widespread dispersal of individuals (Peterman et al. 1998). A second line of evidence is that, in some stocks, the abundance of returning adults is correlated with the abundance of juveniles after the early ocean period. For example, adult abundance of Columbia River coho salmon *O. kisutch* was correlated with juvenile marine densities in September of the first ocean year (Van Doornik et al. 2007). Additionally, the abundance of precociously spawning Chinook salmon ('jacks') that return after one ocean year is correlated with June juvenile density while the abundance of adults returning to spawn after two years in the ocean is not (data from NOAA's Northwest Fishery Science Center, available at http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/ed-jun-sep-ycs-coho.cfm). Therefore, adult abundance is likely influenced by environmental conditions experienced during the first few months at sea. However, the mechanisms regulating survival during the early ocean period are not known and the influence of early ocean conditions may differ among species or life history strategies.

The Columbia River supports Chinook salmon runs with a variety of life histories and historically had the largest runs in the world (Scheuerell & Williams 2005). However, several stocks have experienced severe declines and are listed under the Endangered Species Act (ESA) (NMFS 2009), including upper Columbia River

spring Chinook salmon which are listed as endangered (NMFS 2009). As a consequence, management efforts are focused on increasing the survival of this particular stock.

Spring Chinook salmon display a high degree of life-history variation. Juveniles can rear in the freshwater for a few weeks, months, or a year or more (Taylor 1990) and adults spend two or more years at sea before returning to spawn (Quinn and Myers 2004). The majority of mid-upper Columbia River spring Chinook salmon rear in freshwater for a year before migrating to the ocean (Rich 1920). Therefore, I focused on yearling migrants, which are generally understood to move quickly downriver through the estuary and into the ocean (Healey 1982) to investigate juvenile characteristics that may be related to adult abundance. Identification of factors influencing cohort size will help elucidate mechanisms responsible for interannual survival variability.

Three mechanistic hypotheses for interannual recruitment variability are 'bigger is better' (Miller et al. 1988), 'stage duration' (Houde 1987), and 'match-mismatch' (Cushing 1974). The 'bigger is better' hypothesis states that larger fish have higher survival because they better avoid predators (Blaxter 1986, Butler & Pickett 1988, Miller et al. 1988) and more successfully capture prey (Bailey & Batty 1983, Blaxter 1986). The 'stage duration' hypothesis posits that faster-growing fish remain susceptible to predation for a shorter period (Takasuka et al. 2004, Houde 2008). Growth rate is a measure of how quickly fish move through a life-stage (Chambers & Leggett 1987) and is often used as a proxy for stage duration (Takasuka

et al. 2004). The ‘match-mismatch’ hypothesis states that young fish starve if they do not overlap temporally and spatially with their food source (Cushing 1974, Cushing 1990).

‘Bigger is Better’

The idea that larger fish have higher survival makes sense intuitively and is often assumed to be true. However, evidence for this hypothesis is equivocal. For example, in a mixture of prey sizes larger capelin larvae *Mallotus villosus* experienced higher mortality by visual and non-visual predators (Litvak & Leggett 1992). Whether larger individuals experience higher survival rates is dependent on a variety of factors such as prey availability, the predator pool, the presence of other potential prey species, and environmental conditions (Anderson 1988, Litvak & Leggett 1992, Sogard 1997). In salmonids, large size is generally associated with higher survival. For example, juvenile pink salmon in the Gulf of Alaska were larger during high survival years (Cross et al. 2008), and larger coho salmon emigrating from Auke Creek, Alaska experienced higher survival (Lum 2003). However, larger size is not always related to survival. Release length was not related to smolt-to-adult survival of spring Chinook salmon from three Deschutes River, Oregon hatchery facilities (Beckman et al. 1999). Additionally, the relationship between size and survival may vary. In a laboratory study, larger steelhead *O. mykiss* smolts had the highest percent lipids at 3°C and the lowest percent lipids at 9°C, suggesting that smaller fish would fare better during warm winters with low prey availability (Connolly & Petersen 2003). Therefore,

juvenile size may be related to interannual variability in adult abundance of mid-upper Columbia River spring Chinook salmon.

'Stage Duration'

Growth rate is the mechanism that directly affects the stage duration; the faster an individual grows, the less time it spends in a particular stage and shorter stage duration reduces stage-specific mortality. Therefore, researchers often focus on growth rates because size and growth are easier to measure than mortality and higher within-stage growth rates may indicate higher future survival. For example, spring growth rates of Deschutes River spring Chinook salmon yearlings were positively correlated with smolt-to-adult returns (Beckman et al. 1999). Spawning populations of pink salmon from Prince William Sound, AK and coho from the Strait of Georgia, BC exhibited disproportionately higher losses of slower-growing fish over the first ocean winter, based on scale analyses (Beamish et al. 2004, Moss et al. 2005). In contrast, early ocean growth rates of Oregon coastal coho salmon juveniles were not related to survival; growth rates were similar in years of low and high survival (Fisher & Pearcy 1988). Therefore, interannual abundance of mid-upper Columbia River spring Chinook salmon adults may be related to yearling growth rates during early ocean residence.

'Match-Mismatch'

At the most basic level, survival depends on whether juvenile fish find sufficient food to avoid starvation. If the time of prey abundance does not match the period that young fish are present in the ocean, the cohort (year class) will have low

survival (Cushing 1990). Juvenile pink salmon released during peak zooplankton abundance survived better than juveniles released during less optimal foraging conditions (Cross et al. 2008). Seasonal productivity in the coastal ocean off Washington and Oregon is highly influenced by the switch from winter (downwelling) to summer (upwelling) conditions, which is termed the spring transition (for review see, Checkley & Barth 2009). The quality and species composition of primary and secondary production can influence the fatty acid composition, a component of nutritional quality, of forage fishes (Litz et al. 2010), which are a significant prey source of juvenile Chinook salmon in the coastal ocean (Schabetsberger et al. 2003, Daly et al. 2009). The proportion of diatoms in the phytoplankton is positively related to upwelling and total primary productivity (Litz et al. 2010) and zooplankton community structure is influenced by basin scale climate factors (Hooff & Peterson 2006). Therefore, the timing of downriver migration and entrance into the marine environment relative to ocean conditions may influence survival of mid-upper Columbia River spring Chinook salmon.

Yearling Chinook salmon emigrants use freshwater, coastal and, to a lesser extent, estuarine environments during their early life history and, therefore, factors present in the freshwater or coastal environments likely act to regulate cohort size. I examined ocean-caught juvenile Chinook salmon collected in eight years to evaluate potential mechanisms influencing interannual variation in mid-upper Columbia River spring Chinook salmon population abundance. Smolt-to-adult returns (SARs) were positively correlated with adult returns for hatchery populations ($r^2 > 0.60$) and a wild

population (r^2 >0.2) in the mid-upper Columbia River (SARs provided by R. Zabel, National Oceanic and Atmospheric Administration (NOAA), unpub. data). Therefore, adult returns were used as a proxy for survival. I focused on three hypotheses for cohort abundance regulation: the 'bigger is better' hypothesis, the 'stage duration' hypothesis, and the 'match-mismatch' hypothesis. Specifically, I predicted that interannual variation in adult abundance was positively related to annual means of 1) size at juvenile migration into the ocean, and 2) growth rate during initial marine residence. Additionally, I investigated the relationship between adult abundance and timing of migration into the ocean relative to spring transition.

METHODS

I developed six metrics using ocean collections of juvenile salmon over eight years (details below) to test the hypotheses described above. Here, I define the metrics and, below, I explain how each was calculated. For the 'bigger is better' hypothesis, I used fish length (FL, mm) at ocean capture and at freshwater exit, i.e., the point at which a fish first enters brackish or saline waters. For the 'stage duration' hypothesis, I used growth rate during early ocean residence. For the 'match-mismatch' hypothesis, I used migration timing (date of freshwater exit) relative to physical and biological indicators of spring transition, duration of ocean residence, and ocean migration speed.

Most (75%) of the Columbia River spring Chinook salmon emigrate from freshwater as yearlings and return to spawn two years later (i.e., as three year olds) (Fryer 2009). Smolt-to-adult survival rates can provide a useful indicator of overall survival. However, survival rates were not available for the entire genetic stock, and

smolt-to-adult return estimates for three populations of mid-upper Columbia River spring Chinook salmon varied 11 to 500% within a year (R. Zabel, NOAA, unpubl. data). Therefore, I used the abundance of adult returns to Priest Rapids Dam, which is the lowermost Columbia River dam above the confluence with the Snake River, lagged two years from the migration year (hereafter referred to as adult returns) as a measure of survival for this stock. I used adult abundance at Priest Rapids Dam because it did not include any Snake River spring Chinook salmon. The juveniles in this study were yearling migrants and most (98.9%) of the adults returning to Priest Rapids Dam had emigrated as yearlings. Therefore, I did not adjust the adult returns based on juvenile migration year. Additionally, I compared the Priest Rapids dam counts with estimates of total escapement plus harvest (PFMC 2010) to determine whether adult returns were correlated with other metrics of abundance; adult returns were lower but were positively correlated with and followed the same general pattern as the combined escapement and harvest ($r^2 = 0.88$, $p = 0.002$). Therefore, the number of adults returning to Priest Rapids Dam is an appropriate index of spawner abundance for mid-upper Columbia River spring Chinook salmon.

Fish Collection

Juvenile salmon were collected during NOAA cruises off the coasts of Washington and Oregon during May and June from 1998-2008. Researchers trawled parallel to shore at stations along established transects perpendicular to the shoreline (Figure 3.2; study area described in) (Daly et al. 2009). Fish were collected using a 30 m wide by 20 m deep surface rope trawl (NET 264) towed for 30 min at ~ 6 $km \cdot hr^{-1}$,

and frozen immediately upon capture (Daly et al. 2009). In the laboratory, each juvenile was measured and weighed, checked for a coded-wire tag (CWT), and tissue samples, for genetic and other analyses, and otoliths were removed. The samples included in this study were collected in 1999, 2000, 2002-2004, and 2006-2008. Two years (2001 and 2005) were excluded due to low sample sizes (<20). All individuals included in this study were identified as mid-upper Columbia River spring Chinook salmon using a coast-wide microsatellite DNA baseline for Chinook salmon (D.Teel, NOAA NMFS, unpubl. data), which can be used to identify mid-upper Columbia River spring Chinook salmon with accuracy ≥94.5% (Seeb et al. 2007).

Otolith Chemical and Structural Analysis

Otoliths are useful for studying diadromous movements of fishes because the combination of chemical and structural analyses can be used to differentiate between freshwater and brackish/ocean habitats (Secor 1992, Limburg 1995). Otoliths grow continuously, are not subject to resorption, and lay down increments at regular intervals (Campana & Thorrold 2001), which are daily in Chinook salmon (Neilson & Geen 1982, 1985). Further, otoliths incorporate some elements, such as strontium (Sr), into the calcium (Ca) carbonate structural matrix in proportion to their abundance in the environment (Bath et al. 2000, Kraus & Secor 2004, Elsdon & Gillanders 2005). Mean Sr:Ca is ~2.4 $mmol \cdot mol^{-1}$ in the mid-upper Columbia River (National Quality Accounting Network (NASQAN); J. Miller, Oregon State University, unpubl. data) and ~8.5 $mmol \cdot mol^{-1}$ in the ocean (Zimmerman 2005, Miller et al. 2010b). Variation in Sr:Ca is limited above salinities of 8-10 because the mixing curve plateaus (Kraus

& Secor 2004, Zimmerman 2005, Miller et al. 2010b). Therefore, otolith Sr:Ca can be used to identify transitions from fresh to oceanic waters but cannot fully discriminate between estuarine and marine water signals.

Otolith Preparation and Analysis

Otoliths were measured (0.1 mm), and the left sagittal otolith was ground using sandpaper (240-2500 grit) and lapping film (1- 30 μm grit) to expose the dorsal-ventral growth axis. Otoliths were otherwise prepared with standard procedures for elemental analysis (as described in Miller 2009).

To determine the Sr:Ca composition of the otoliths, I used laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS) in the W.M. Keck Collaboratory for Plasma Spectrometry at Oregon State University. Data were collected along a transect that included 1) the entire growth axis or 2) the otolith radius from core to dorsal edge. Fifty percent of the otoliths were sampled along the otolith radius of the dorsal-ventral axis (Figure 3.1). To aid in chemical interpretation, the remaining 50% were scanned along the otolith diameter (Figure 3.1). The laser was set at a pulse rate of 8 Hz and translated across the sample at 5 $\mu m \cdot s^{-1}$ with a spot size of 30 or 50 μm, depending on instrument sensitivity. Normalized ion ratios were converted to elemental ratios using a glass reference standard from the National Institute of Standards and Technology (NIST 612) (Miller 2007) and then converted to molar ratios (Miller et al. 2010b). Instrument precision (the mean percent relative standard deviation) of NIST 612 was 3.2% for Ca and 3.7% for Sr across all samples

and days (n = 53). I used a carbonate standard developed by the US Geological Survey (MACS-1) to assess accuracy (Sr:Ca = 2%, n= 18).

Otolith width is positively and linearly related to fish fork length in juvenile Chinook salmon (< 170 mm) (Chapter 2). Therefore, I combined otolith Sr:Ca and structural analysis to identify freshwater exit and determine fish size at freshwater exit. I defined freshwater exit as the otolith increment corresponding to the inflection point where the Sr:Ca began to increase to marine values (as in Miller et al. (2010b).

Image analysis was used to measure otolith size and count increments. I captured digital images using a Leica DC300 camera coupled with a Leica MZ95 stereoscope (20x) or a Leica DM1000 compound microscope (40x, 100x, 200x, and 400x) and Leica IM50 Image Manager ® image capture software and performed image analysis with ImagePro ® Plus (Media Cybernetics). Otolith width was defined as the distance across the dorsal-ventral axis at the widest point. I measured otolith width at freshwater exit and capture (Figure 3.1).

Based on eight fish with known migration histories (Chapter 2), I determined that proportional back-calculation resulted in fewer over-estimates of fish length. Therefore, I used proportional regression (Francis 1990) to estimate fish size at freshwater exit for each individual based on the relationship in Miller el al. (2010b) (Equation 1).

$$S_{FE} = [(6.91 + 0.06 \cdot O_{FE}) / (6.91 + 0.06 \cdot O_C)] \cdot S_C \quad (1)$$

where O_{FE} = otolith width at freshwater exit, O_C = otolith width at capture, S_{FE} = fish length at freshwater exit, and S_C = fish length at capture.

I combined fish size at freshwater emigration and capture with otolith-derived estimates of growth and migration for the period of brackish/ocean residence, defined as the time between freshwater exit and subsequent capture. I estimated three additional metrics, including 1) brackish/ocean growth rate; 2) duration of marine residence; and 3) mean daily migration rate. I determined duration of marine residence (d) by counting the otolith increments from the point of freshwater exit to the outer edge. I calculated total growth in brackish/ocean waters (mm) for each fish and divided by duration of brackish/ocean residence (d) to determine growth rate ($mm \cdot d^{-1}$). Date of freshwater exit was determined by subtracting the residence duration from the capture date. Duration of residence and capture station were used to determine a conservative migration distance, calculated as the linear distance between the mouth of the Columbia River (N 46.253, W -124.059) and the capture station using global positioning system coordinates (http://www.movable-type.co.uk/scripts/latlong.html) plus an additional 32.1 km to account for the distance travelled through the estuary (Chawla et al. 2008). I divided the migration distance (km) by the brackish/ocean residence time (d) to calculate the mean daily migration rate ($km \cdot d^{-1}$) for each fish.

I analyzed a total of 238 otoliths; however, different numbers of fish were collected each year and some otoliths could be used in only a subset of the analyses due to otolith quality, image quality, or lack of external data. Therefore, sample sizes (fish/year) varied among metrics and years. I generated estimates of juvenile size at freshwater exit (n = 21-31) and capture (n = 21-34), duration of brackish/ocean residence (n = 21-31), growth rate (n = 20-30), freshwater exit date (n = 21-31), and

migration rate (n = 21-31) for each fish and calculated annual mean metrics for each cohort. The metrics were combined with adult returns and oceanographic data to address the three mechanistic hypotheses outlined above: the 'bigger is better' hypothesis; the 'stage duration' hypothesis; and the 'match-mismatch' hypothesis.

'Bigger is Better'

I determined whether interannual variability in adult returns was related to interannual variability in fish size at freshwater exit and capture. The relationships between adult returns and mean length at freshwater exit and capture were examined using linear regression.

'Stage Duration'

Slower-growing fish spend longer in each life stage or size category than faster growing fish. Therefore, I used the mean brackish/ocean growth rate as a proxy for stage duration. I determined whether variation in growth rate was related to interannual variability in adult returns using regression analysis.

'Match-Mismatch'

To evaluate the match-mismatch hypothesis, I determined whether migration timing relative to the spring transition was related to interannual variability in adult returns. I used the date of freshwater exit relative to the physical (T_P, based on oceanography) and biological (T_B, based on zooplankton community) spring transitions as metrics of migration timing. The physical spring transition was defined as the first day within each year that the ten-day average of upwelling was positive and of sea level height was negative (Logerwell et al. 2003). The biological spring

transition was defined as the first day within each year that the plankton community five miles offshore of Newport, OR was classified as the 'northern community' (Peterson & Schwing 2003, Hooff & Peterson 2006). The mean number of days between freshwater exit and each of the spring transitions was determined for each year class, i.e., FE - T_P and FE - T_B for the physical and biological transitions, respectively. The relationships between the timing of migration relative to these transitions and adult returns were evaluated using linear regression.

There are multiple ways to evaluate whether juvenile migrants 'matched' with their environment. One approach is to examine the amount of time spent in brackish/ocean habitat prior to capture. Therefore, I examined the frequency distribution of residence duration by collection transect and capture month. A second approach is to determine how quickly individuals move away from their ocean entry point, their migration rate. The relationships between migration rate and adult returns and migration timing (i.e., the date of freshwater exit) were evaluated using regression analysis.

Statistics

All data were examined for normality and homogeneity of variance and transformed when necessary. To examine interannual variation, I performed a multivariate analysis of variance (MANOVA) with the five juvenile metrics (i.e., the size at freshwater exit, size at capture, brackish/ocean growth rate, date of freshwater exit, and brackish/ocean migration rate) as dependent variables and year as the independent variable. Tukey's Honestly Significant Difference (HSD) test, which

accounts for multiple comparisons, was performed for pairwise comparisons when the MANOVA indicated a significant year effect (Zar 2010).

RESULTS

Fish collection

Collections of mid-upper Columbia River juvenile spring Chinook salmon were distributed unevenly amongst the transects and sample dates. The majority (74%) of the spring Chinook salmon used in this study were collected on the Columbia River, Grays Harbor, and La Push transects (Figure 3.2). None were collected south of the Columbia River. Fish were collected between 21 May and 29 June in each year. In 2000, 2002, 2007, and 2008 fish were collected in May, in 1999 and 2003 fish were collected in June, and in 2004 and 2006 fish were collected in both May and June.

The number of otolith increments during brackish/ocean residence were determined two times >2 d apart, and the error between reads was 4 ± 3 % (mean ± SD, n = 242). Brackish/ocean residence estimates were also compared to time at liberty based on CWT data (n = 63); two fish were excluded because of apparent reporting discrepancies associated with CWT information. For this analysis, under-estimates of brackish/ocean residence (81.0%) were considered acceptable because the duration of individual downriver migration was unknown. However, over-estimates would mean that fish reached brackish/ocean waters prior to hatchery release. Over-estimates of <10 days occurred in 11.1% and over-estimates of >10d occurred in 7.9% of the CWT fish. Therefore, residence durations were likely over-estimated for 8% of the fish.

'Bigger is Better'

There was interannual variation in fish length at freshwater exit (Figure 3.3; $F = 3.1$, d.f. = 7, $p = 0.004$) and at capture (Figure 3.3, Table 3.1; $F = 3.2$, d.f. = 7, $p = 0.003$). Mean size-at-freshwater exit ranged from 132.6 ± 2.8 mm (mean ± SE) in 2004 to 158 ± 4.3 mm in 1999 (Table 3.1). Mean size at capture ranged from 144 ± 16 mm in 2004 to 180 ± 26 mm in 1999 (Table 3.1). Fish size at freshwater exit and capture explained about the same amount of variation in adult returns. The mean size-at-freshwater exit was positively related to adult returns (Figure 3.4a; $r^2 = 0.56$, d.f. = 6, $p = 0.03$) as was the mean size at capture (Figure 3.4b; $r^2 = 0.60$, d.f. = 6, $p = 0.02$). The rank order of mean size at freshwater exit and capture were similar among years except for 2003 and 2006. However, mean sizes for these two cohorts were statistically indistinguishable ($p = 0.99$).

'Stage duration'

Annual mean brackish/ocean growth rates varied among years (Figure 3.3; $F = 2.6$, d.f. = 7, $p = 0.01$). The mean growth rate varied from 0.36 ± 0.02 $mm \cdot d^{-1}$ (mean ± SE) in 2004 to 0.51 ± 0.04 $mm \cdot d^{-1}$ in 2008 (Table 3.1). However, mean growth rate during early brackish/ocean residence was not related to adult returns ($r^2 = 0.05$, $p = 0.58$). The only significant pairwise difference was that the 2004 cohort had a significantly lower growth rate than the 2008 cohort ($p = 0.003$). In fact, the 2004 year class had the slowest growth rate, the smallest mean size at freshwater exit, and the smallest mean size at capture ($p < 0.01$).

'Match-Mismatch'

Migration Timing

Mean date of freshwater exit varied among years (Figure 3.3; $F = 10.2$, d.f. = 7, $p < 0.001$). Mean freshwater exit occurred between April 20 and May 2 in all years, with the exception of 2003 (later) and 2008 (earlier) (Table 3.1). Timing of freshwater exit relative to physical and biological spring transitions determines whether a cohort has a 'match' with its environment. The mean date of freshwater exit occurred after the date of physical spring transition in every year and after the biological spring transition in four of the eight years (Figure 3.5a). Mean freshwater exit for most year classes occurred >18 d after the physical transition (Figure 3.5b) and after or <20 d before the biological transition (Figure 3.5c). I compared the number of days between freshwater exit and the spring transition (negative = before, positive = after) to adult returns; there were weak positive relationships with mean freshwater exit relative to physical ($r^2 = 0.21$, $p = 0.25$) and biological ($r^2 = 0.12$, $p = 0.41$) spring transition.

Duration of Brackish/Ocean Residence

I calculated brackish/ocean residence duration for 223 fish captured along seven transects across eight years. Thirty-six percent (n = 80) had spent <30 d in marine waters before capture and 57% (n = 128) had spent between 30 and 60 d. Only 7% (n = 15) had brackish/ocean residence >60 d.

The Columbia River transect had the highest proportion of fish that had been in marine waters for ≤ two weeks (Figure 3.2). Transects north of the Columbia River had higher proportions of fish residing in the brackish/ocean >30 d, except for the Father and Son transect, along which only eight mid-upper Columbia River spring

Chinook juveniles were collected. The fish collected in May were captured primarily south of the Queets River while most of the fish collected in June were captured north of Grays Harbor. The majority of the fish with brackish/ocean residence > 60 d were collected in June and along the LaPush transect (Figure 3.2).

Migration Rate

Migration rate varied among years (Figure 3.3; $F = 7.13$, d.f. = 7, $p < 0.001$). The 2002 year-class had the slowest mean migration rate (2.36 ± 0.27 km·d^{-1}, mean ± SE) and the 2006 year-class had the fastest (Table 3.1; 5.02 ± 0.53 km·d^{-1}). Fish migrating quickly early in the season may have migrated out of the sampling area before samples were collected. Therefore, because interannual variation in capture date may bias comparisons of migration rate, I considered fish collected in May and June separately. Mean date of freshwater exit was not related to mean migration rate (May: $r^2 = 0.2$, d.f. = 4, $p = 0.37$, June: $r^2 = 0.2$, d.f. = 2, $p = 0.56$). However, for May and June samples, individual fish that entered brackish waters later in the year had faster migration rates (Figure 3.6; May: $r^2 = 0.46$, d.f. = 149, $p < 0.001$, June: $r^2 = 0.26$, d.f. = 70, $p < 0.001$).

DISCUSSION

I reconstructed aspects of the juvenile migratory history to test three hypotheses regarding the importance of early ocean residence to salmon survival. The combined genetic and otolith approach used in this study allowed me to collect data from juvenile emigrants as they transitioned from the freshwater to marine habitats. A key aspect of this approach was the ability to estimate individual size at freshwater

exit regardless of rearing history or mark status because most previous studies have used CWT fish, which are primarily hatchery-reared and may not be representative of the entire stock. Other important contributions were reconstruction of freshwater exit dates, and brackish/ocean residence times, distribution patterns, and migration rates of non-CWT fish.

The positive relationships observed between size at freshwater exit and capture and adult returns provide support for the bigger is better hypothesis. As demonstrated in other species and regions, year classes that entered marine waters at larger mean sizes appeared to survive better. For example, surviving steelhead in the Keogh River, B.C. (Ward et al. 1989) and coho salmon off of Oregon and Washington (Fisher & Pearcy 1988) had larger back-calculated size at ocean entrance than the original population. Therefore, it is possible that mid-upper Columbia River year classes with larger mean size experienced lower mortality rates. Survival may be higher for larger individuals because they are less likely to be consumed by predators. Larger spring Chinook salmon yearlings are expected to have lower predation pressure from northern pikeminnow *Pytchocheilus oregonensis* in the Columbia River and Pacific hake *Merluccius productus* in the coastal ocean (Muir et al. 2006). Additionally, fish prey of Pacific hake and jack mackerel *Trachurus symmetricus* off the Columbia River were generally <150 mm, therefore, Chinook salmon year classes with larger mean size likely have lower susceptibility to these predator species (Emmett & Krutzikowsky 2008). Finally, smaller subyearling Chinook salmon smolts were more susceptible to predation by cutthroat trout *O. clarkii clarkii* in Puget Sound than their

larger conspecifics. In contrast, avian predators may selectively prey on larger individuals; for example, Caspian terns *Sterna caspia* and double-crested cormorants *Phalacrocorax auritus* in the Columbia River estuary ate a larger proportion of the available steelhead than yearling Chinook salmon (Collis et al. 2001). Additionally, radio-tagged Chinook salmon juveniles, which are large individuals, had avian predation rates similar to those reported for steelhead (Schreck et al. 2006). Juvenile Chinook salmon have several potential predators during their freshwater migration and early ocean residence and, with the exception of avian predators, larger size decreases vulnerability to predation.

The relationship between fish size and adult returns was nearly the same between freshwater exit and capture. Growth during the first month at sea did not substantially alter the rank order of size among years and may have less impact on survival than in-river growth rate. Alternately, overall summer growth may be important but could not be addressed with the samples collected because sample collection occurred in May and June.

Low growth rates can negatively impact survival by limiting size or increasing the period of vulnerability. There may be a threshold growth rate below which survival is poor for mid-upper Columbia River spring Chinook salmon. The mean growth rate of the 2004 cohort was 0.36 $mm \cdot d^{-1}$, while all other cohorts grew at least 0.44 $mm \cdot d^{-1}$. Within a year class, slower growing coho salmon and Japanese anchovy *Engraulis japonicus* had lower survival (Beamish & Mahnken 2001, Takasuka et al. 2003). Slow growth during the early ocean period may influence mortality during

another life stage. For example, early ocean growth of juvenile coho and Chinook salmon in the Strait of Georgia and pink salmon in Prince William Sound influenced susceptibility to mortality during the following winter (Beamish & Mahnken 2001, Moss et al. 2005). Additionally, there may be a size threshold for good survival and low growth rates may result in smaller sizes. Therefore, the slow early marine growth rates of the 2004 cohort may have contributed to the cohort's low adult returns in a variety of ways.

Timing of freshwater emigration was similar among cohorts and occurred within an approximately two-week period in six of the eight years. Given the low interannual variability in freshwater exit date, migration timing did not display significant relationships with the variable physical parameters, such as spring transition. In general, years with early physical spring transitions (on or before Mar 31) were the years with high and medium adult returns, while years with later physical spring transitions (on or after Apr 19) had lower adult returns. The 2003 cohort is an exception to this observation; the physical spring transition was late (Apr 22) but adult returns two years later were mid-range. However, the two cohorts with the lowest adult returns had mean freshwater exit dates closer to (within a week) the physical transition and longer before (one to two months) the biological transition than other year classes.

There is no consistent pattern between freshwater exit relative to spring transition and adult returns. A large proportion (>80%) of the spring Chinook salmon juveniles in the Columbia River basin are hatchery-reared (Williams et al. 1999).

Therefore, the date of hatchery release may influence migration timing. Mean release timing from mid-upper Columbia River spring Chinook salmon hatcheries varied ~ 2.5 weeks among study years. With the exception of 2003, the similarity in date of freshwater exit may be related to the small degree of interannual variation in date of hatchery release.

A behavioral response to ocean conditions that are not conducive to feeding and growth is migration to new areas. The 2003 and 2006 cohorts, which were collected in June, had the fastest migration rates, which may indicate 'mismatches' with local ocean conditions. Alternately, migration rate may be a seasonally-modified behavior regulated by circadian rhythm, which is cued by day length (Gibson et al. 1978, Godin 1981, Meseguer et al. 2008, Lopez-Olmeda & Sanchez-Vazquez 2009). The samples available could not be used to differentiate between the two possibilities because in some years fish were collected only in May or June. However, individual fish caught in either May or June that exited freshwater later in the year had higher mean migration rates, which provides evidence that migration rate may be a behavioral modification. Juvenile salmon collected in the northern transects had higher levels of the growth hormone insulin-like growth factor (B. Beckman, NOAA, NWFSC, pers. comm.), indicating that fish from the northern end of the sampling area grew faster. Therefore, for late migrating fish, faster migration may be advantageous because the pre-winter growth period is short.

The mean migration rates of fish included in this study (2-5 $km \cdot d^{-1}$) are lower than migration rates estimated by two other studies. Migration rates based on CWT

fish ranged from 8.8-11 km·d^{-1} (J. Fisher et al. unpub. data) and 10-20 km·d^{-1} (Trudel et al. 2009). However, duration of brackish/ocean residence for 89% of the fish in my sample captured along the Washington coast were within the range calculated by Fisher et al. (unpub. data). CWT fish may not be representative of the general population because they are almost exclusively hatchery origin and often larger than the general hatchery population and naturally-spawned migrants. The approach presented here included fish of all size classes as well as hatchery-reared and naturally-produced fish; however, fish were collected across a smaller spatial area. Thus, the migration rates and durations of marine residence determined in this study are likely representative of all of the yearling spring Chinook salmon origin types from the mid-upper Columbia River but may be biased due to geographic limitations, i.e., fast migrators moved quickly out of the sampling area and were underrepresented.

The data presented here indicate several opportunities for further exploration. For example, future work should explore the relationship between freshwater conditions and size to elucidate the factors influencing size at freshwater exit. Previous studies have determined that water temperature and juvenile density (Crozier et al. 2010), and migration duration (Muir et al. 2006, Achord et al. 2007) influenced migrant size of Snake River spring Chinook salmon. Hatchery rearing practices are also likely important because, as noted above, the majority of Columbia River spring Chinook salmon are hatchery-origin. The mean size at hatchery release ranged from 126 to 149 mm among study years and explained 38% of the observed variation in size at freshwater exit. Therefore, factors influencing in-river growth after hatchery release

influence size at emigration. Additionally, further work needs to determine whether brackish/ocean growth rates are related to survival during a later stage, perhaps overwinter mortality, potentially accounting for some of the unexplained variation in adult abundance. Finally, the data presented here provided no clear evidence that timing relative to spring transition was important. However, ocean conditions may be important and studies investigating the influence of marine environmental factors on year class regulation should be pursued.

Summary and Conclusions

Size at freshwater exit and after initial ocean residence was correlated with adult returns in mid-upper Columbia River spring Chinook salmon. Size at freshwater exit was influenced by factors acting during freshwater residence and these factors should be investigated further.

Timing relative to spring transition may be more important for cohorts that enter the ocean at a smaller size or have experienced poor freshwater conditions. However, timing of migration may not be important if behavioral modifications can be used to mitigate a poor situation such as by migrating out of the ocean entry area.

Muir et al. (2006) argued that differences in fish size and timing of migration were the most influential factors related to mortality below Bonneville Dam for upriver yearling Chinook salmon. The data presented here support the hypothesis that size at emigration is related to future adult abundances.

TABLES

Table 3.1. Mean size at freshwater exit, size at capture, duration of brackish/ocean residence, brackish/ocean growth rate, date of freshwater exit and brackish/ocean migration rate for juvenile spring Chinook salmon. Number of adults returning to Priest Rapids dam (-2yr) are also presented. FE = Freshwater exit, standard error is shown in parentheses. Sample sizes ranged among years and metrics (minimum: n= 20, maximum: n=34).

Year	Size at FE (mm)	Size at capture (mm)	Brackish/ocean residence (d)	Brackish/ocean growth rate ($mm \cdot d^{-1}$)	Date of FE (ordinal day)	Migration rate ($km \cdot d^{-1}$)	Priest Rapids adult returns
1999	158 (4)	180 (4)	45 (2)	0.44 (0.02)	122 (2)	4.7 (0.4)	51,133
2000	152 (5)	168 (5)	31 (2)	0.50 (0.02)	113 (2)	3.6 (0.5)	34,066
2002	154 (5)	173 (7)	32 (3)	0.48 (0.04)	111 (3)	2.4 (0.3)	13,521
2003	135 (4)	154 (4)	39 (3)	0.49 (0.03)	137 (3)	5.1 (0.5)	14,148
2004	133 (3)	144 (3)	36 (3)	0.37 (0.03)	113 (3)	3.0 (0.3)	8,535
2006	138 (4)	153 (4)	36 (2)	0.48 (0.05)	120 (3)	5.2 (0.5)	12,178
2007	147 (5)	163 (6)	36 (3)	0.44 (0.03)	110 (3)	3.9 (0.4)	13,469
2008	148 (5)	164 (5)	38 (3)	0.51 (0.04)	108 (3)	3.0 (0.4)	30,539

FIGURE LEGENDS

Figure 3.1. Otolith schematic and representative Sr:Ca profile. The core, daily increments, point of freshwater exit, and laser path are depicted on the Sr:Ca scan.

Figure 3.2. Sampling area and collection stations. Percent frequency distributions for brackish/ocean residence of fish collected along each capture transect. Samples were pooled across years. Approximate locations of sampling stations are shown in relation to the coast line and shelf break.

Figure 3.3. Annual mean (± SE) for juvenile metrics. Values of a) size at freshwater exit; b) size at capture; c) date of freshwater exit; d) brackish/ocean growth rate; and e) brackish/ocean migration rate among years.

Figure 3.4. Adult returns versus juvenile size at freshwater exit. Relationship between adult returns to Priest Rapids dam (-2 yr) and juvenile size (mean ± SE) at a) freshwater exit ($r^2 = 0.56$, d.f. = 6, $p = 0.03$) and b) capture ($r^2 = 0.60$, d.f. = 6, $p = 0.02$). Points are labeled with the smolt migration year.

Figure 3.5.Freshwater exit and spring transition. a) Dates of freshwater exit with with physical (star) and biological (cross) spring transitions and dates of freshwater exit relative to b) physical and c) biological spring transition. Cohorts are ranked from highest (1) to lowest (8) adult returns and labeled by juvenile migration year. Boxes represent the middle 50% of the range of freshwater exit dates in each year.

Figure 3.6. Brackish/ocean migration rate. Migration rate ($km \cdot d^{-1}$) of mid-upper Columbia River spring Chinook salmon during early brackish/ocean residence plotted against date of freshwater exit for fish collected in a) May ($r^2 = 0.46$, d.f. = 149, $p < 0.001$), and b) June ($r^2 = 0.26$, d.f. = 70, $p < 0.001$) Cohort means are labeled with the smolt migration year.

FIGURES

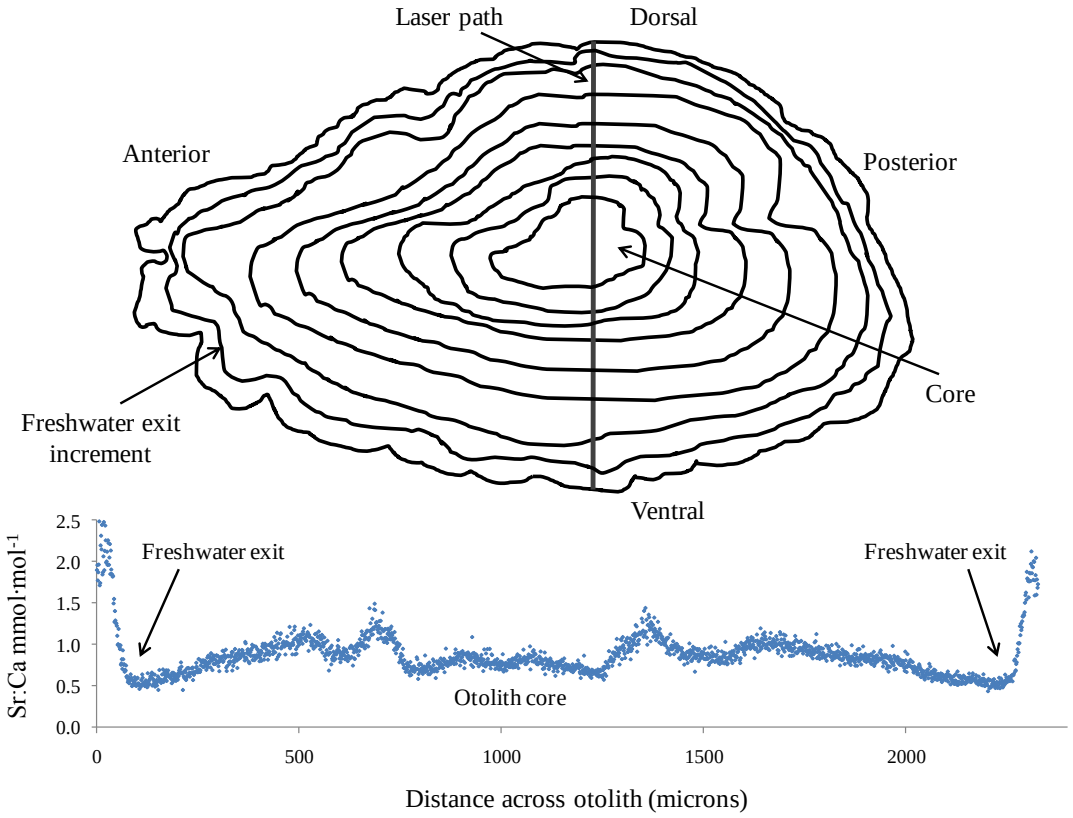
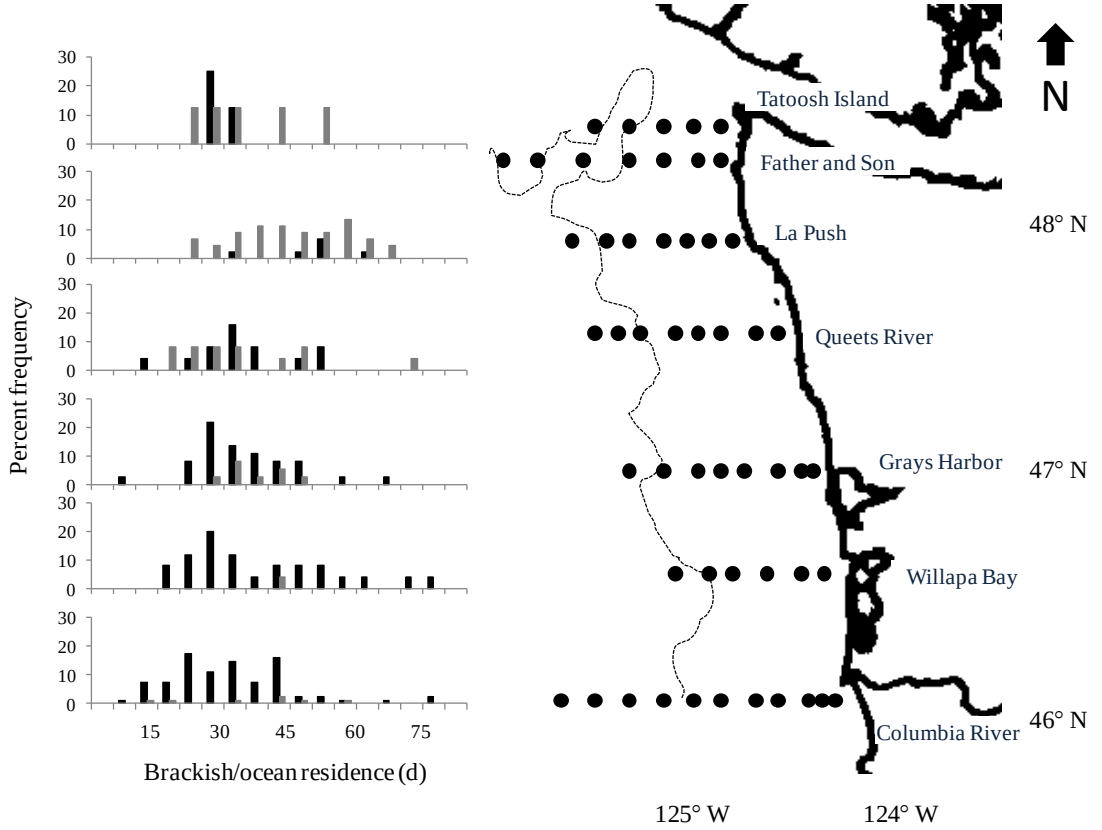


Figure 3.1


Percent frequency
30
20
10
0
15
30
45
60
75
Brackish/ocean residence (d)
Tatoosh Island
Father and Son
La Push
Queets River
Grays Harbor
Willapa Bay
Columbia River
N
48° N
47° N
46° N
125° W
124° W


Canada
Washington
Oregon
California

Figure 3.2

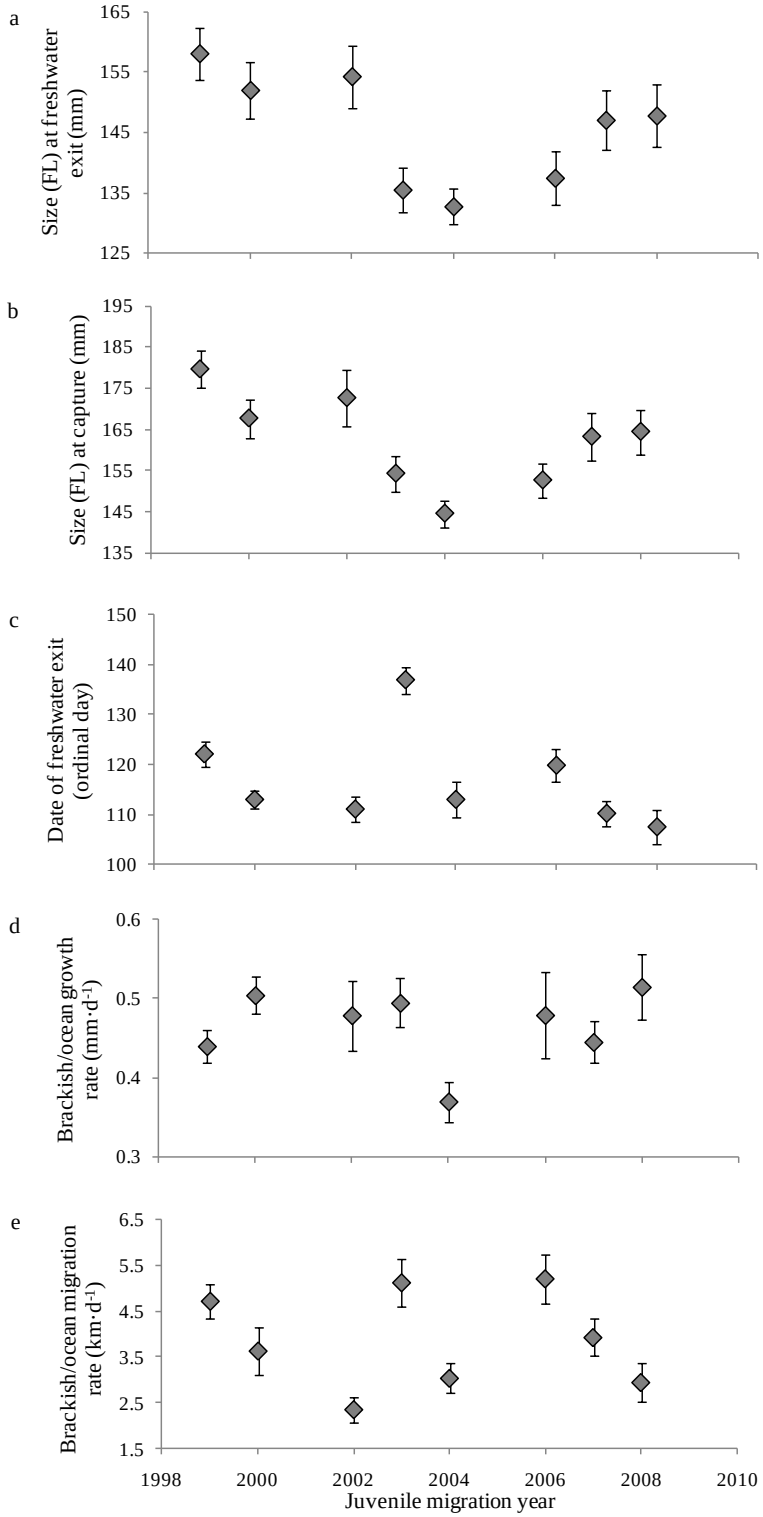

a
Size (FL) at freshwater exit (mm)
165
155
145
135
125
b
Size (FL) at capture (mm)
195
185
175
165
155
145
135
c
Date of freshwater exit (ordinal day)
150
140
130
120
110
100
d
Brackish/ocean growth rate (mm·d-1)
0.6
0.5
0.4
0.3
e
Brackish/ocean migration rate (km·d-1)
6.5
5.5
4.5
3.5
2.5
1.5
1998
2000
2002
2004
2006
2008
2010
Juvenile migration year

Figure 3.3

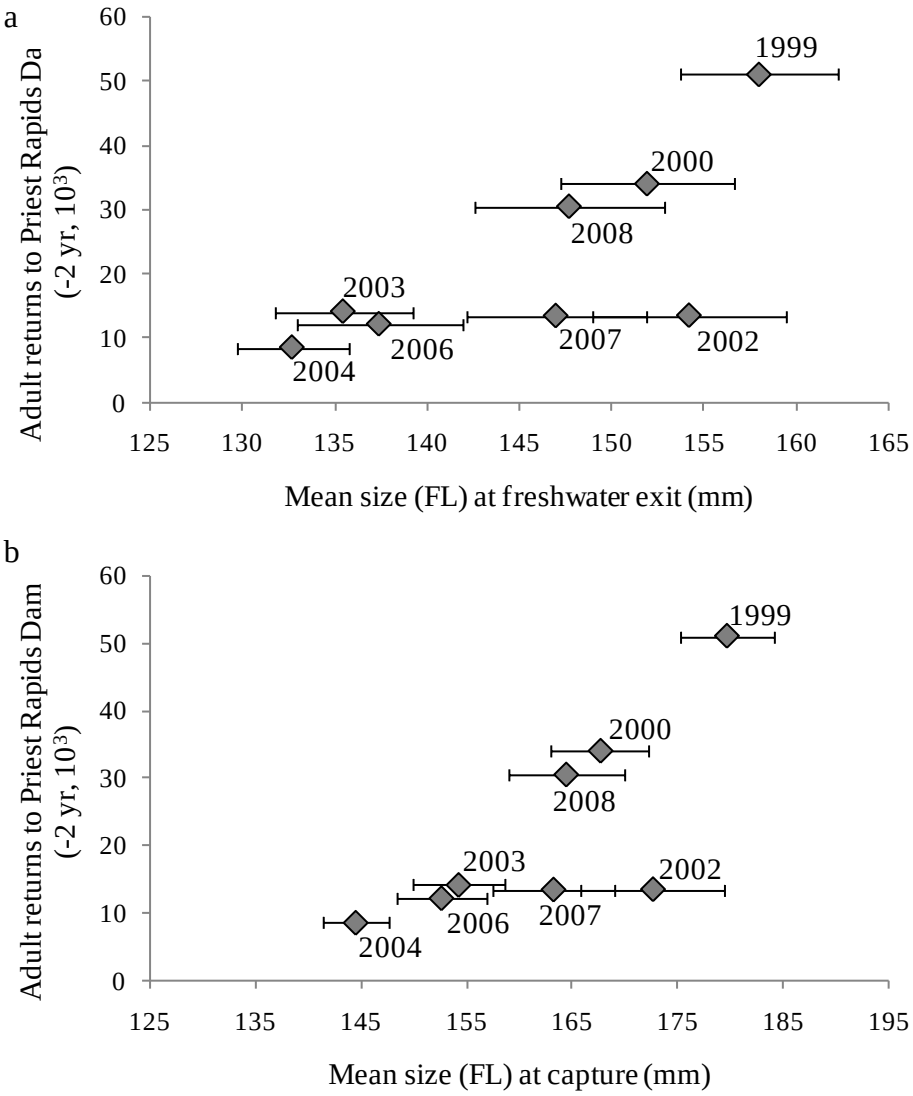

a
Adult returns to Priest Rapids Da
(-2 yr, 10³)
60
50
40
30
20
10
0
125
130
135
140
145
150
155
160
165
1999
2000
2008
2003
2006
2007
2002
2004
Mean size (FL) at freshwater exit (mm)
b
Adult returns to Priest Rapids Dam
(-2 yr, 10³)
60
50
40
30
20
10
0
125
135
145
155
165
175
185
195
1999
2000
2008
2003
2002
2006
2007
2004
Mean size (FL) at capture (mm)

Figure 3.4

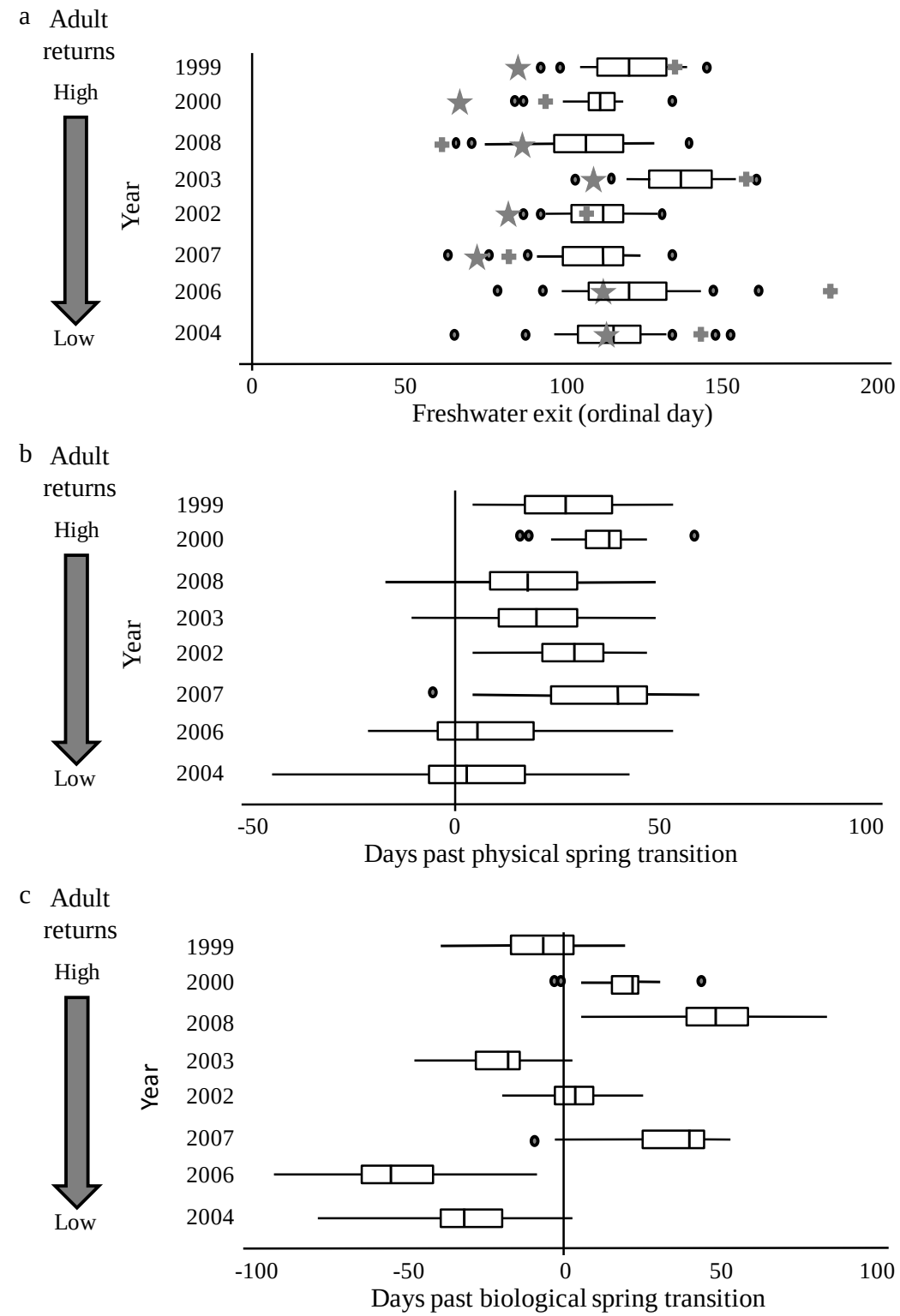

a Adult returns
High
Low
Year
1999
2000
2008
2003
2002
2007
2006
2004
0
50
100
150
200
Freshwater exit (ordinal day)
b Adult returns
High
Low
Year
1999
2000
2008
2003
2002
2007
2006
2004
-50
0
50
100
Days past physical spring transition
c Adult returns
High
Low
Year
1999
2000
2008
2003
2002
2007
2006
2004
-100
-50
0
50
100
Days past biological spring transition

Figure 3.5

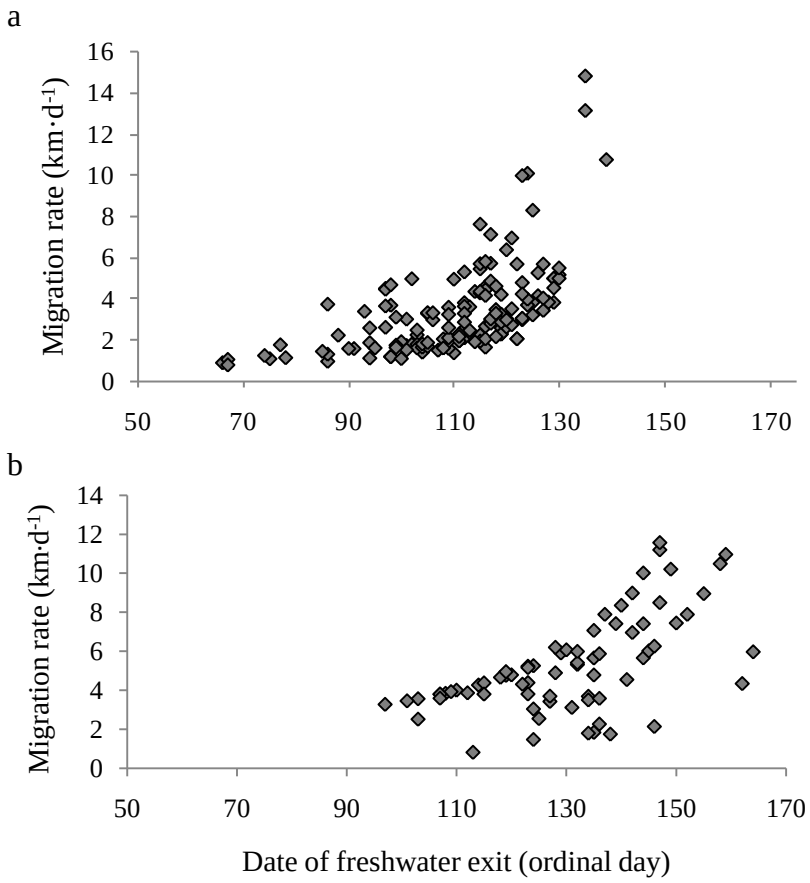

a
Migration rate (km·d-1)
16
14
12
10
8
6
4
2
0
50
70
90
110
130
150
170
b
Migration rate (km·d-1)
14
12
10
8
6
4
2
0
50
70
90
110
130
150
170
Date of freshwater exit (ordinal day)

Figure 3.6

CHAPTER 4: OTOLITH STRONTIUM TO CALCIUM PATTERN AS A HATCHERY MARK

INTRODUCTION

Efforts to elucidate behavioral and survival differences between wild and hatchery migrants will benefit from a technique to distinguish between the two groups. Hatchery-reared salmon are often released into the natural environment with no external marking designating hatchery origin. For example, in the Columbia River between 1998 and 2006, 65% of hatchery-reared spring Chinook salmon *Oncorhynchus tshawytscha* juveniles were marked before release, on average (http://www.rmpc.org/). Differences in otolith chemistry of salmonids from the same river may indicate rearing or migration differences (Kennedy et al. 2000, Bacon et al. 2004, Zimmerman et al. 2009). Additionally, otolith Sr:Ca incorporation can be influenced by food (Gibson-Reinemer et al. 2009, Miller et al. 2010a), temperature (Radtke 1989, Bath et al. 2000), and ontogeny (Kalish 1989, Fowler et al. 1995). Therefore, analysis of otolith elemental patterns may be a viable method for differentiating between naturally-spawned and hatchery-reared individuals originating in the mid-upper Columbia River system.

The ability to distinguish hatchery-origin juveniles could be used to address ecological questions. Hatchery-reared and naturally-spawned fish may be affected differently by environmental conditions or may express different physiological responses. Atlantic salmon *Salmo salar* from hatcheries exhibited higher mortality than wild fish in the two years sampled (Saloniemi et al. 2004). Hatchery-origin

salmon can have lower reproductive fitness than their naturally-reared counterparts, and differences in fitness can manifest after just one generation (Araki et al. 2007). There is also variation between the rearing-types in traits and behaviors that may negatively influence fitness. For example, hatchery-reared coho salmon *O. kisutch* had slower freshwater and marine migration rates and lower physiological fitness in British Columbia, Canada (Chittenden et al. 2008) and yearling releases returned to the river as smaller adults with earlier migrations than wild fish in the Umpqua River, Oregon (Theriault et al. 2010). Additionally, hatchery fish may be more susceptible to predation after release. For example, Spring Chinook salmon juveniles from the Yakima River were significantly more susceptible to predation by both pelagic and benthic freshwater predators after just one generation of hatchery rearing (Fritts et al. 2007). Therefore, hatchery practices can influence factors that are related to survival and a technique for distinguishing hatchery-origin fish would be useful for investigating potential differences in response.

Certain hard structures have been used to identify fish of hatchery-origin. For example, otolith microstructure differs between naturally-spawned and hatchery-reared salmon and has been used to distinguish between the two rearing types for Chinook salmon in the Strait of Georgia (Zhang & Beamish 2000), from the Cowichan River, B.C. (Zhang et al. 1995), and California's Central Valley (Barnett-Johnson et al. 2007). Scale chemistry also varies between hatchery and wild fish. Atlantic salmon rearing type was successfully identified 98% of the time with discriminant function

analysis of scale chemistry; nine elements contributed to classification with manganese (Mn) and lithium (Li) being most influential (Adey et al. 2009).

Otolith chemistry also has a unique signature based on the environment experienced (e.g., Campana 1999, Kennedy et al. 2001, Campana and Thorrold 2001, Bacon et al. 2004, Kraus and Secor 2004, Miller et al. 2010). Certain elements, such as strontium (Sr) and barium (Ba), are substituted for calcium (Ca) in proportion to environmental availability as the otolith grows (Bath et al. 2000, Kraus & Secor 2004, Elsdon & Gillanders 2005). While the elemental composition of the otolith core is maternally influenced (Kalish 1990, Rieman et al. 1994, Volk et al. 2000), outside the core otolith composition is dependent on the water chemistry and food (Kennedy et al. 2000, Miller et al. 2010a). Water contributes a majority of the elements in the otolith but food contributes approximately 33% of the otolith Sr for salmonids (Gibson-Reinemer et al. 2009, Miller et al. 2010a). Incorporation of elements is also influenced by environmental and physiological factors such as salinity, temperature, ontogeny, and growth rate (Kalish 1989, Fowler et al. 1995, Zimmerman 2005).

Otolith elemental composition can be used to differentiate groups of fish that experienced chemically distinct environments. For example, hatchery-reared rainbow trout *O. mykiss* were correctly assigned to hatchery of origin based on otolith Sr:Ca, Ba:Ca, and ^{87}Sr:^{86}Sr (Gibson-Reinemer 2009). Rainbow trout and brook trout *Salvelinus fontinalis* rearing types were successfully differentiated in an Arkansas river system using element to calcium ratios: Sr and Ba for rainbow trout and magnesium (Mg), zinc (Zn), Mn, Sr, and Ba for brook trout (Coghlan et al. 2007).

I observed an increase in Sr:Ca in otoliths of hatchery-reared interior Columbia River spring Chinook salmon while evaluating the use of otolith chemistry to examine the timing of ocean entrance. The observed otolith Sr:Ca increase, hereafter termed 'pre-marine Sr:Ca peak' or 'Sr:Ca peak', approached marine levels and was associated with the exogenous feeding check (Figure 4.1). The Sr:Ca varied after the pre-marine peak but generally decreased around the time of hatchery release, shortly before the point of freshwater exit (Figure 4.1). I hypothesized that the Sr:Ca peak may be indicative of hatchery rearing and may be caused by elevated Sr:Ca in the rearing water, marine Sr:Ca levels in hatchery feed, or a combination of the water and feed. In this study, I: 1) determined whether the anomalous Sr:Ca peak was associated with hatchery produced individuals; 2) determined the classification error rate; 3) used the Sr:Ca pattern to categorize unknown individuals as hatchery-reared or naturally-spawned; and 4) evaluated mechanisms of elevated Sr:Ca.

Hatchery fish collected prior to release were used to investigate the prevalence of a hatchery signature in the otolith Sr:Ca and to create a classification baseline. Juveniles caught in the ocean that were coded-wire tagged (CWT) and adipose fin-clipped (ad-clipped) were used to assess accuracy of hatchery classification. Ocean-caught individuals of unknown origin were then designated as hatchery-reared or naturally-spawned.

METHODS

Fish Collection

Fish of hatchery- and unknown-origin were collected from the mid-upper Columbia River. The sample was comprised of: 1) hatchery-collected fish from Chiwawa and Tucannon hatcheries on the Wenatchee and Tucannon rivers in the Columbia River basin; 2) CWT ocean-caught juveniles originating from mid-upper Columbia River hatcheries; 3) ad-clipped ocean-caught juveniles of hatchery origin; and 4) ocean-caught juveniles with unknown rearing history and no tags or external markings (Table 4.1). The stock origin of the ocean-caught fish was determined using the Genetic Analysis of Pacific Salmon (GAPS) microsatellite baseline (D. Teel, National Oceanic and Atmospheric Administration Fisheries (NOAA), unpubl. data, Seeb et al. 2007). I collected rearing and release data on CWT individuals from the Regional Mark Information System (RMIS) online database (http://www.rmpc.org/external/rmis-standard-reporting.html).

Otolith Collection and Preparation

Sagittal otoliths were removed, cleaned of adhering tissue and stored dry. Left and right otoliths do not differ significantly in size or chemical composition (Gauldie 1996), but for consistency I used the left otolith if available. Otoliths were prepared using standard procedures for elemental analysis (described in Miller 2009). Each otolith was mounted onto a glass slide with the proximate side facing upwards using thermoplastic resin, ground to expose the primordia, then flipped and the distal side was polished with sandpaper (240-2500 grit) and lapping film (30-1 μm grit) to expose the dorsal-ventral axis from the core to the edge.

Otolith Chemical and Structural Analysis

I measured otolith Ca and Sr using laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS) in the W.M. Keck Collaboratory for Plasma Spectrometry at Oregon State University. The laser traced a path along the dorsal-ventral axis through the core. In half of the fish the scan extended from the otolith core to the dorsal edge and, in the other half the laser scanned the entire diameter, i.e. a life history profile. Diameter scans aided in chemical interpretation without affecting microstructure interpretation. The following laser settings were used: 8 Hz at 5 $\mu m \cdot s^{-1}$ with a spot size of 30 or 50 μm, depending on the instrument sensitivity. Accuracy of Sr:Ca was 2% based on a carbonate standard (MACS-1, n = 18). Precision was estimated using National Institute of Technology and Standards glass standards (NIST 612) and was 3.2% for Ca and 3.7% for Sr (n= 53). Normalized ion ratios were converted to elemental concentration ratios (described in Miller 2007) and then expressed as molar ratios based on the molar mass of Sr and Ca.

Hatchery Mark

I analyzed the otolith chemical composition in conjunction with the microstructure. I visually inspected the Sr:Ca of each otolith for the presence of a pre-marine Sr:Ca peak, which consists of Sr:Ca approaching marine levels (>1.4 $mmol \cdot mol^{-1}$: Miller et al. 2010b) near the exogenous feeding check (Figure 4.1). For ocean-caught fish, I also determined the location of freshwater exit near the edge of the otolith. Once identified chemically, the pre-marine Sr:Ca peak and freshwater exit were located on digital images of the otoliths. I captured otolith images with Leica

IM50 Image Manager ® image capture software using a Leica DC300 camera coupled with a Leica MZ95 stereoscope (20x) and a Leica DM1000 compound microscope (40x, 100x, 200x, and 400x) and performed image analysis with ImagePro ® Plus (Media Cybernetics).

I developed a method to quantitatively confirm the visually identified pre-marine Sr:Ca peak. Therefore, I calculated the difference between Sr:Ca levels at the pre-marine peak and background Sr:Ca immediately prior to that peak (Equation 1).

$$[(S_P / S_B) \cdot 100] - 100 \quad (1)$$

where S_P = peak Sr:Ca and S_B = background Sr:Ca.

The otolith chemistries of the pre-release hatchery fish were used to create a classification baseline. All 15 pre-release hatchery fish from Chiwawa and Tucannon hatcheries exhibited a pre-marine Sr:Ca peak near the exogenous feeding check. The Sr:Ca increase was ≥10% above background in all 15 fish and ≥20% above background in 14 fish (93%) (Table 4.2). Based on the pre-release hatchery fish baseline, classification criteria and thresholds were developed. To indicate hatchery origin the otolith Sr:Ca must: 1) exhibit a Sr:Ca peak associated with the exogenous feeding check; and 2) the peak must be a minimum of 10% above background levels. I used CWT and ad-clipped ocean-caught individuals to assess the accuracy of the baseline and then classified unknown-origin individuals. For ocean-caught fish, the Sr:Ca decline to freshwater levels at the approximate location of hatchery release contributed to visual classification (Figure 4.1).

Mechanisms

The Sr:Ca pattern varied during hatchery residence; Sr:Ca peaked to marine levels at the exogenous feeding check, after which it decreased but generally remained elevated and variable. Additionally, Sr:Ca levels decreased to freshwater levels at the approximate time of hatchery release and remained low until emigration into marine waters (Figure 4.1b). To determine whether the pre-marine Sr:Ca peak could be explained by a combination of water chemistry and hatchery feed and whether medicated feed (which is used during only a portion of hatchery residence) could contribute to the variable pattern observed, I collected data on Sr:Ca levels in water and feed. Water Sr:Ca was compiled for ten locations in the Columbia River basin (National Quality Accounting Network: NASQAN; J. Miller, OSU, unpubl. data). Four samples of the feed used in many mid-upper Columbia River hatcheries (Bio-Vita feed) was provided by Ann Gannam, US Fish and Wildlife Service, Abernathy Fish Technology Laboratory. Sr:Ca levels were measured in Starter #0, Starter #2, Starter #2 medicated, and Fry 2mm to determine whether Sr:Ca varied with feed size and whether Sr:Ca was higher in feed treated with a common antibiotic (Aquamycin) than in regular feed.

I constructed a mixing model based on the findings of Kennedy et al.(2000), Gibson-Reinemer et al. (2009), and Miller et al. (2010a) (Equation 2).

$$Sr{:}Ca_{Otolith} = D_{Sr} \cdot [(1-f) \cdot Sr{:}Ca_{Water}] + (f \cdot Sr{:}Ca_{Feed}) \quad (2)$$

where D_{Sr} = the partition coefficient, and f = the Sr:Ca contribution from food. The partition coefficient is the proportion of Sr:Ca in the water that is incorporated into the otolith (Morse & Bender 1990). Reported mean values of D_{Sr} during freshwater

residence for five salmonid species including Chinook salmon were 0.25-0.27 in field studies (Bacon et al. 2004, Donohoe et al. 2008, Gibson-Reinemer et al. 2009) and ~0.38 in a laboratory study (Zimmerman 2005). I used the average of the reported field values: $D_{Sr} = 0.26$. The proportion of otolith Sr:Ca contributed by food (f) was assumed to be 33%, the mean value reported for juvenile salmonids (Gibson-Reinemer et al. 2009, Miller et al. 2010a). I assumed that the Sr:Ca in the feed was not biologically regulated or sequestered and was incorporated into the otolith in a 1:1 relationship ($D_{Sr} = 1$). The pre-marine Sr:Ca peak was associated with the exogenous feeding check; therefore, at the time of peak formation the fish were feeding on one of the two smallest feed sizes. I solved Equation 2 using the Sr:Ca values for Starter #0, starter #2, and Starter #2 medicated. I compared otolith peak Sr:Ca levels to water Sr:Ca values using water samples collected from the Columbia River and select tributaries in the mid-upper basin. Additionally, I compared otolith peak Sr:Ca from Methow Hatchery fish with Methow River, WA water Sr:Ca to determine whether predictions based on local water chemistry more closely matched observed otolith peak Sr:Ca levels.

I analyzed duplicate samples of each feed type to determine the Sr:Ca. I dissolved 0.125 g feed in 6.125 ml high purity nitric acid for 48 hours and diluted them to 250x, 500x, and 5000x concentrations. Standard calibrations were made using ULTRAgrade™ certified reference materials. Elemental concentrations of Sr and Ca were analyzed using inductively coupled-optical emission spectrometry (ICP-OES) in the W.M. Keck Collaboratory for Plasma Spectrometry at Oregon State University.

The precision and accuracy of the ICP-OES were determined as in Miller et al. (2010b) using reference material (NIST 1643e). Accuracy was >97% and precision was >99% for Sr and Ca (n = 5).

RESULTS

Fish Collection

A total of 257 fish (129 of known hatchery origin and 128 of unknown origin) were included. Some of the ocean-caught fish were tagged with coded-wire tags (CWTs) (n = 77), which allowed me to determine the hatchery of origin. Others were ad-clipped only, which identified them as hatchery origin but did not indicate which hatchery they originated from (n = 37). The remainder of the fish (n = 128) had no tags or markings. I categorized the hatchery fish by collection strategy (ocean-caught or hatchery-collected) and mark type (Table 4.1).

Hatchery Otolith Mark

The ocean-caught CWT and ad-clipped fish (n = 114) were used to assess the accuracy of the hatchery classification criteria. Of the 114 fish, 78.1% (n = 89) had a pre-marine Sr:Ca peak elevated ≥10% above background levels. An additional 7% (n = 8) had a visual pre-marine Sr:Ca peak <10% above background levels. The remaining 15% (n = 17) did not display any indication of a pre-marine Sr:Ca peak.

A portion of the unmarked ocean-caught fish (n = 128) displayed a pre-marine Sr:Ca peak near the exogenous feeding check. Based on the baseline threshold of Sr:Ca elevation ≥10% above background, I classified 46% (n=59) of the unmarked fish as hatchery-reared. An additional 11 (8.6%) of the unknown-origin fish displayed

a visual pre-marine Sr:Ca peak indicative of hatchery rearing. The remaining 58 fish (45.3%) did not have any otolith Sr:Ca evidence of hatchery-origin.

Mechanisms

Previous research has shown that water and food contribute to otolith composition. Water Sr:Ca ranged from 2.0 to 3.3 mmol·mol^{-1} across the mid-upper Columbia River basin (Table 4.3) and the mean was 2.4 ± 0.2 mmol·mol^{-1} (mean ± SE). Based on water alone, predicted otolith Sr:Ca levels ranged from 0.5 to 0.8 mmol·mol^{-1} (Figure 4.2). With food included, the mean potential water contribution to otolith Sr:Ca was 0.4 ± 0.04 mmol·mol^{-1} (mean ± SE). The amount of Sr:Ca in the food samples decreased with increasing feed size from 1.7 mmol·mol^{-1} in the Starter #0 to 1.4 mmol·mol^{-1} in the 2 mm but was lowest (1.2 mmol·mol^{-1}) in the Starter #2 medicated (Table 4 .4). Therefore, the potential contribution from food ranged from 0.4 to 0.6 mmol·mol^{-1} (Table 4.4). Predicted otolith Sr:Ca levels based on water and food contributions ranged from 0.8 to 1.1 mmol·mol^{-1} (Table 4.4).

I compared observed pre-marine peak Sr:Ca to predicted otolith Sr:Ca. All but one fish had pre-marine peak Sr:Ca higher than predicted from water alone. However, water and food contributions did not entirely explain the otolith Sr:Ca peak levels. Most of the fish had pre-marine Sr:Ca peak greater than or equal to the water and feed predictions, and many had pre-marine Sr:Ca peaks much higher than predictions based on water and food (Figure 4.3).

To determine whether otolith Sr:Ca was related to water chemistry on a smaller scale, I compared predictions based on local water Sr:Ca levels to pre-marine peak values for five fish from the Methow Hatchery. All five fish had pre-marine peak Sr:Ca above the level predicted by water alone (>14%). Three fish matched the water and food predictions for Starter #0 and Starter #2, one was intermediate between predictions for the Starter feeds and the 2mm feed, and one matched the Sr:Ca prediction using Starter #2 medicated (Figure 4.4).

DISCUSSION

This study demonstrated that Columbia River spring Chinook salmon have a discernable peak in otolith Sr:Ca formed during freshwater residence that is indicative of hatchery rearing and likely influenced by hatchery feed and local water chemistry. Other studies have used otolith elemental composition to determine rearing type or identify hatchery of origin. To my knowledge, this is the first study to use the Sr:Ca pattern to classify fish as hatchery-reared. Although the results are promising, the technique should be applied cautiously. The study included no definitely known wild fish from the same geographic region. Therefore, I could not validate the presumed absence of a pre-marine Sr:Ca peak at the exogenous feeding check in naturally-spawned individuals. Future studies should examine otolith Sr:Ca of naturally-spawned fish.

Hatchery otolith mark

The otolith Sr:Ca peak may be unique to mid-upper Columbia River and this technique cannot yet be used for other stocks or species. The Sr:Ca pattern, including

the pre-marine peak and subsequent decline toward freshwater levels has not been observed in other runs; however, it is too soon to tell if it is limited to the mid-upper Columbia River. For mid-upper Columbia River and selected Snake River spring Chinook salmon populations, a discernable Sr:Ca peak occurs at exogenous feeding. Based on my results, the Sr:Ca peak in juvenile Columbia River spring Chinook salmon otoliths was not fully explained by the contribution of water alone or a combination of water and food. However, the declining pattern after the pre-marine peak suggests that additional factors influence otolith Sr:Ca during freshwater residence.

The otolith Sr:Ca pattern of mid-upper Columbia River hatchery spring Chinook salmon can be used to determine the proportion of individuals that originated in hatcheries. Based on Sr:Ca peak ≥10% above background levels 22% of the known hatchery-reared fish were not correctly classified. Based on the visual classification, 15% of hatchery-origin fish were classified as non-hatchery. This technique can be used to collect data that can be used to address important ecological questions regarding differential response to environmental or biological factors between hatchery-reared and naturally-spawned fish.

If individual identification is not necessary, the error rates can also be used to extrapolate the actual number of hatchery-origin fish in a sample. If an additional 15% of the unmarked fish were actually hatchery fish but did not exhibit the Sr:Ca mark, as many as 85% (n = 218) of the fish could have been hatchery origin. This is similar to other estimates of the proportion of hatchery-origin Chinook salmon in the Columbia

River. Likewise, based on the ≥10% Sr:Ca, as many 84% (n = 216) of the fish could have been hatchery-reared.

Mechanisms

Some of the unexplained variability in otolith Sr:Ca may be due to differences in rearing water Sr:Ca or the feed consumed at exogenous feeding. For this analysis I used average water values from 10 sites to represent the Sr:Ca over the portion of the Columbia River basin in which the study fish reared. The standard error among sites was 6%; however, the water chemistry among hatcheries may differ enough to cause some of the variation observed in this study. For example, predictions using Methow River water Sr:Ca matched the pre-marine Sr:Ca peak in fish from the Methow Hatchery better than the predictions using the mean Columbia River basin water Sr:Ca. Additionally, Sr:Ca of medicated feed was considerably lower than regular feed so fish being medicated at exogenous feeding ingest lower Sr:Ca and likely do not display a pre-marine Sr:Ca peak.

Previous research has shown that water and food contribute to otolith composition. Variable water chemistry likely contributed to the inconstancy in otolith Sr:Ca pattern along the growth axis. Additionally, the declining Sr:Ca pattern may have been due to the decreasing Sr:Ca levels as feed size increased. The peak Sr:Ca in juvenile Columbia River spring Chinook salmon otoliths was not fully explained by the contribution of water alone or a combination of water and food (Figure 4.3). Despite this, the visual and quantitative Sr:Ca patterns were unusual and they appear to be useful for identifying hatchery-reared individuals.

Hatchery conditions, such as water temperature, may influence the Sr:Ca composition of the otoliths throughout residence. Temperature can influence the rate of otolith incorporation of Sr:Ca (for example, Radtke 1989, Bath et al. 2000). Otolith Sr:Ca increased linearly with water temperature in spot *Leiostomus xanthurus* (Bath et al. 2000) and goldfish *Carassius auratus* (Mugiya & Tanaka 1995). However, there may be a limit to the positive effect of temperature on otolith Sr:Ca; incorporation was inhibited at high temperatures in the goldfish (Mugiya & Tanaka 1995). Exogenous feeding occurs in late winter or early spring, when water temperatures increase. If juveniles experienced a temperature increase at the time of exogenous feeding, it may contribute to the Sr:Ca pattern observed in this study.

It is possible that juvenile fish respond to available Sr:Ca differently during the transition to exogenous feeding. I observed small Sr:Ca increases near the edge of the core in presumptively wild fish. The peaks in hatchery fish may have been larger because the increase caused by developmental stage was enhanced by hatchery conditions (e.g. feed, temperature). It may be possible that incorporation of otolith Sr:Ca was altered by a physiological change, such as protein synthesis during rapid growth following exogenous feeding, and the hatchery feed contribution emphasized or inflated the effect.

Temperature, ontogeny, and hatchery feed may influence the pre-marine Sr:Ca peak, as described above. The otolith Sr:Ca generally remained elevated, but at a lower level and in some fish gradually declined to freshwater levels. This may be caused by the pattern of decreasing Sr:Ca as feed size increases. Additionally, the

otolith Sr:Ca dropped near the end of freshwater residence, at about the time of hatchery release.

Future research should determine the prevalence of the pre-marine Sr:Ca peak to evaluate whether the otolith Sr:Ca pattern is indicative of hatchery-origin in other salmon stocks. Additionally, research should be focused on determining the causes of the pre-marine peak and the hatchery otolith Sr:Ca pattern. By understanding the mechanisms of Sr:Ca incorporation into salmon otoliths, we may gain a valuable tool for investigating salmon ecology.

TABLES

Table 4.1. Fish used in this study were categorized by their collection type and their mark status. The mean size for each category is displayed with the standard error.

Group	n	Mean Size	Size Range	Collection Dates	Origin and Rearing
1) Hatchery-collected	15	90 ± 9	70-100	10/2007	Tucannon and Chiwawa hatcheries (Tucannon and Chiwawa rivers)
2) CWT ocean-caught	78	164 ± 3	108-249	5/21-6/29 1999–2008	Columbia River hatcheries[1]
3) Ad-clipped ocean-caught	37	161 ± 4	132-241	5/23-6/29 1999–2008	Mid-upper Columbia River hatcheries or spawning areas
4) Unknown origin ocean-caught	129	161 ± 3	102-250	5/21-6/29 1999-2008	Unknown - natural or hatchery rearing

[1] Carson Hatchery – Columbia River, Carson, WA; Chiwawa Hatchery – Chiwawa River, WA; Cle Elum Hatchery – Yakima River, WA; Dryden Pond – Wenatchee River, WA; Dworshak National Fish Hatchery – Clearwater River, ID; Entiat,National Fish Hatchery – Entiat River, WA; Kooskia National Fish Hatchery – Clearwater River, WA; Leavenworth National Fish Hatchery – Wenatchee River, WA; Lewis River Hatchery – Lewis River, WA; Lookingglass Hatchery – Grand Ronde River, OR; Lyons Ferry – Snake River, WA; Methow Hatchery – Methow River, WA; Rapid River Hatchery – Rapid River, ID; Round Butte Hatchery – Deschutes River, OR; Similkameen Hatchery – Similkameen River, WA; Turtle Rock Hatchery – Columbia River, WA; Umatilla Hatchery – Columbia River, OR; Warm Springs National Fish Hatchery – Warm Springs River, OR; Willard National Fish Hatchery – Little White Salmon River, WA; Winthrop National Fish Hatchery – Methow River, WA.

Table 4.2. Number of fish with a visual otolith Sr:Ca peak in each category and the number also displaying a Sr:Ca peak >10% and >20% above background.

Group	Total	Visual mark	Sr:Ca Increase ≥10%	Sr:Ca Increase ≥20%
Pre-release hatchery	15	15	15	14
CWT ocean-caught	77	66	65	50
Ad-clipped ocean-caught	37	31	24	20
Unknown origin	128	70	59	44

Table 4.3. Water Sr:Ca from sites in the mid-upper Columbia River basin.

Collection Site	Year Collected	Sr:Ca $mmol \cdot mol^{-1}$
Columbia River mainstem and most tributaries	1998-2000, 2008	2.0 – 2.6
Methow R. at rkm 35	2008	3.2
Okanogan R. at rkm 25	2008	3.3

Table 4.4. Predicted amount of otolith Sr:Ca ($mmol \cdot mol^{-1}$) contributed by water and food. Predictions use $D_{Sr} = 0.26$ and a feed contribution of 33%. Predictions for each water value are listed below the underlined water Sr:Ca.

Predicted otolith Sr:Ca at varying water Sr:Ca levels and feed sizes

Feed Size	Feed Sr:Ca	Water Sr:Ca					
		2.00	2.25	2.50	2.75	3.00	3.25
Starter #0	0.57	0.92	0.97	1.01	1.05	1.10	1.14
Starter #2	0.56	0.90	0.95	0.99	1.03	1.08	1.12
Starter #2 med	0.41	0.75	0.80	0.84	0.88	0.93	0.97
Fry 2 mm	0.45	0.80	0.84	0.88	0.93	0.97	1.02

FIGURE LEGENDS

Figure 4.1. Otolith schematic (a) and representative Sr:Ca profile (b). . The core, pre-marine Sr:Ca peak, and dorsal and ventral otolith edges are noted on the a) otolith schematic, which also shows the laser path, and exogenous feeding check, and b) Sr:Ca plotted against distance across the otolith.

Figure 4.2. Predicted otolith Sr:Ca mmol·mol^{-1} at various water Sr:Ca levels. Water partition coefficient is 0.26 and food contribution is 33%. The four food types were Starter # 2 medicated (solid line), 2mm, (dot-dash line), Starter #2 (dashed line), and Starter #0 (dotted line). The grey line is based on water with no food contribution.

Figure 4.3. Predicted otolith Sr:Ca mmol·mol^{-1} at water Sr:Ca levels found in the mid-upper Columbia River basin. Individual pre-marine Sr:Ca peak levels are shown for reference and were arbitrarily distributed across the water Sr:Ca levels.

Figure 4.4. Observed (diamonds) and predicted (lines) otolith Sr:Ca for Methow River fish.. Pre-marine Sr:Ca peak levels (mean ± SD) for Methow Hatchery fish compared to predictions based on Methow River Sr:Ca levels. The grey line is the prediction with no food contribution; the black lines include 33% food contribution of Starter #0 (dashed), Starter #2 (dotted), Fry 2mm (solid), and Starter #2 medicated (double).

FIGURES

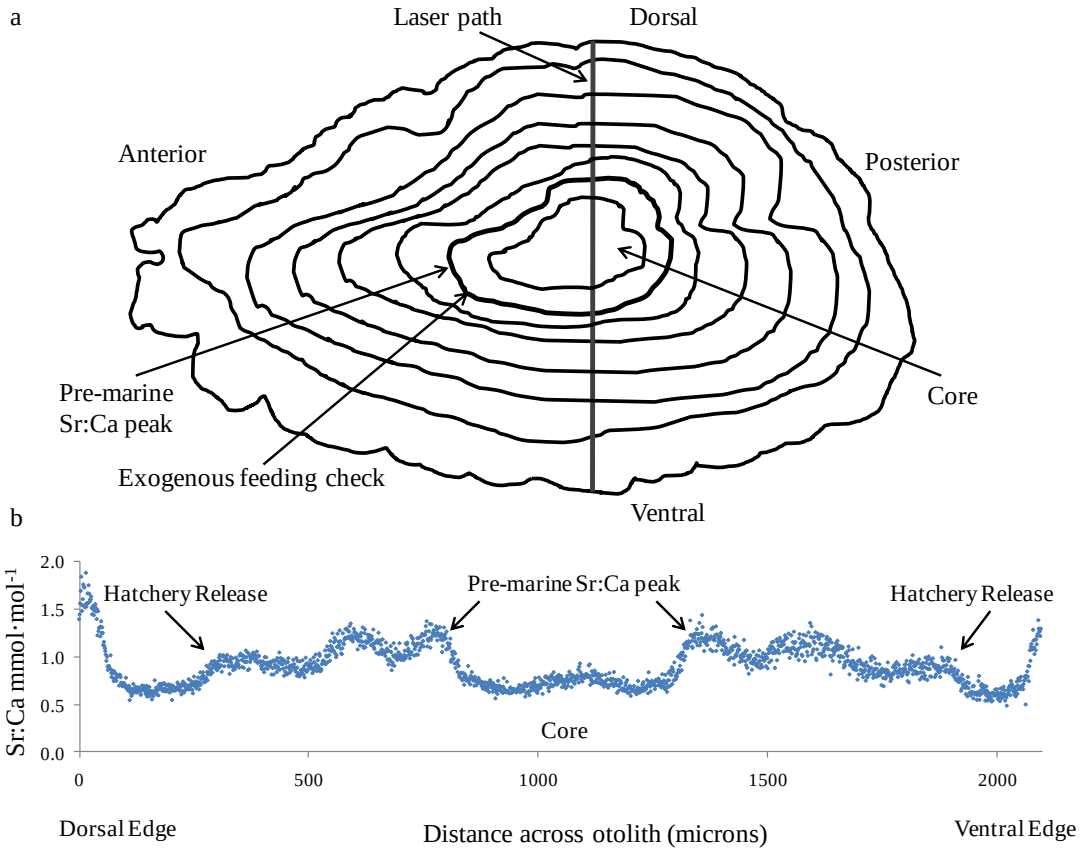


Figure 4.1.

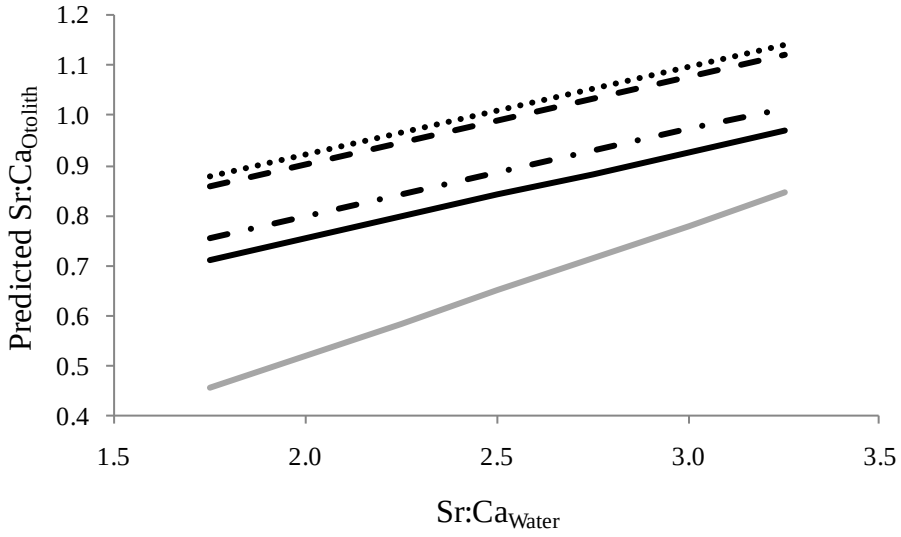

1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Predicted Sr:Ca$_{Otolith}$
1.5
2.0
2.5
3.0
3.5
Sr:Ca$_{Water}$

Figure 4.2

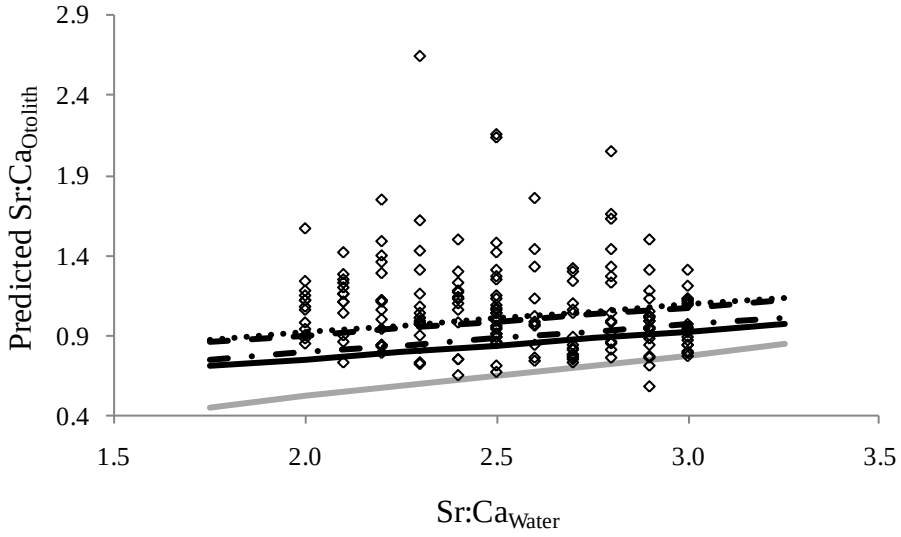

2.9
2.4
1.9
1.4
0.9
0.4
Predicted Sr:Ca Otolith
1.5
2.0
2.5
3.0
3.5
Sr:Ca Water

Figure 4.3.

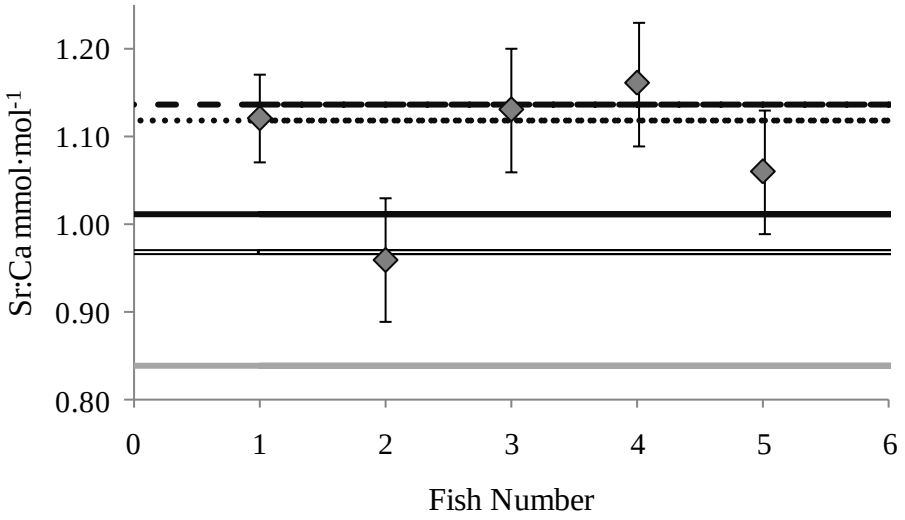


Figure 4.4.

CHAPTER 5: GENERAL CONCLUSIONS

Salmon stock abundance fluctuates interannually and is influenced by factors throughout life history. Spring Chinook salmon *Oncorhynchus tshawytscha* populations from the interior Columbia River are less abundant than they were historically and are federally listed as 'endangered'. Columbia River spring Chinook salmon generally over winter in freshwater and migrate to the ocean as yearlings. The mechanisms acting to regulate population size are not known; however, evidence is accumulating that the early ocean period is important. I tested the 'bigger is better' (size), 'stage duration' (growth rate), and 'match-mismatch' (predator/prey overlap) hypotheses to evaluate potential mechanisms regulating adult abundance. In Chapter 2, I presented a validation that otolith and somatic growth rates are proportional. In Chapter 3, I applied my approach to examine how size, growth rate, and migration timing were related to adult returns, a proxy for survival. Finally, in Chapter 4, I evaluated the otolith Sr:Ca pattern as a novel marker for differentiating between naturally-spawned and hatchery-reared individuals.

Growth rate calculated from the difference in back-calculated sizes was positively correlated with actual growth rate ($r = 0.96$) of juvenile Chinook salmon. Otolith width was positively correlated with fish length at tagging ($r = 0.98$) and capture ($r = 0.93$), and the data indicated that proportional back-calculation adequately estimated size of juvenile Columbia River Chinook salmon <165 mm. With this technique, it is possible to collect size data from individual fish at distinct times and to examine size and growth through time to investigate ecological hypotheses.

The results presented in Chapter 3 provide support for the 'bigger is better' hypothesis. Fish size at freshwater exit and at capture were the only metrics related to survival. Mean fish length was related to adult returns at tagging ($r^2 = 0.56$) and at capture ($r^2 = 0.60$). The size rank by year changed minimally between freshwater exit and capture. Growth during the first few months in the ocean was not related to survival. However, particularly slow growth rates may negatively affect adult returns if there is a size or growth threshold for good survival.

Mid-upper Columbia River spring Chinook salmon use the coastal ocean habitat prior to and during their migration northward. Most fish sampled (93%) resided in the brackish ocean for less than two months and over half (57%) for one to two months prior to capture. Therefore, environmental conditions during early ocean residence may influence survival and may be related to the ~40% of interannual variation in adult returns not explained by fish size at emigration.

In Chapter 4, I determined that it was possible to differentiate between hatchery-reared and naturally-spawned individuals using a peak in the Sr:Ca pattern along the dorsal-ventral growth axis. Visual and quantitative inspection of the Sr:Ca peak resulted in 15% and 22% misclassification rates of hatchery-origin fish. I used these error rates to estimate the number of hatchery-origin fish in a sample of juveniles of unknown-origin and determined that 78 – 85% of the fish I examined in Chapter 3 (Relating juvenile size, growth rate, and migration timing to adult returns of mid-upper Columbia River spring Chinook salmon *Oncorhynchus tshawytscha*) were hatchery-origin fish.

Various factors influence salmon growth and survival across life stages. The data presented here indicate that factors during both the freshwater life stage and the first ocean months are important determinants of year-class abundance of mid-upper Columbia River spring Chinook salmon. Size at emigration, which is obviously influenced by freshwater conditions, explained ~60% of the variation in adult returns and ocean conditions during the first few months at sea may explain some of the remaining 40%. Although the specific factors in each environment have yet to be identified, this study provided valuable insight into the spring Chinook salmon juvenile life stage and the mechanisms influencing survival.

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