AN ABSTRACT OF THE THESIS OF

Lance A. Campbell for the degree of Master of Science in Fisheries Science presented on March 9, 2010.
Title: Life Histories of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha)* in the Columbia River Estuary as Inferred from Scale and Otolith Microchemistry

Abstract approved:

_____

Ian A. Fleming                                    Daniel L. Bottom

Despite evidence that juvenile Chinook salmon (*Oncorhynchus tshawytscha)* utilize North Pacific estuaries for growth and salinity acclimation, research in the Columbia River estuary has lead to opposing hypotheses about the estuary's importance as a salmon rearing environment. Many contemporary tagging studies indicate that salmon residency within the estuary is short (< 1 week) and that mortality of estuarine migrants is a significant impediment to recovery of depressed salmon stocks. On the other hand, life history interpretations from fish scales collected early in the twentieth century suggest that juvenile Chinook salmon reared extensively in the estuary, leading some to hypothesize that life history variation has been constrained by anthropogenic changes in the Columbia River basin. To test these hypotheses we first validated previous methods of life history interpretation by comparing the results of otolith chemistry, scale chemistry, and scale morphology from juvenile salmon collected during monthly beach seine surveys in 2003. Although scale and otolith chemistry were strongly correlated, and scale chemistry was an accurate indicator of salt-water entry, scale morphometric characteristics did not coincide consistently with

the time of salmon entry into brackish water. We measured Strontium 86 and Calcium 43 in salmon otoliths collected in the lower Columbia River estuary in 2003-05 to quantify the period of salt-water residency of juvenile salmon and to back-calculate their size at salt-water entry. The estimated salt-water residency of juvenile Chinook ranged from 0-176 days with a mean residence time of 54, 67 and 30 days in 2003, 2004 and 2005, respectively. Chinook salmon that resided in salt water for more than 30 days comprised 55, 51 and 30% of the total estuary beach seine collections during each of these years. Forty to fifty percent of Chinook salmon had entered the saline portion of the estuary at a fork length < 60 mm. Furthermore we found a negative relationship between the size and time of entry with residency, where smaller earlier migrants on average resided for longer periods then larger late migrants. Peak migration times occurred in May, and 90% of the outmigration was completed by August 30 in all years. This pattern is substantially truncated relative to the results of a 1914-1916 salmon life-history survey, which showed that the historical outmigration period lasted well into the fall and was characterized by late pulses of new recruits into the lower estuary. Nonetheless, recent otolith results indicate that subyearling Chinook salmon use the saline portion of the estuary in a high proportion and for extended periods of time in contrast to short residency times reported by contemporary tagging and marking studies.

Life Histories of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha)* in the
Columbia River Estuary as Inferred from Scale and Otolith Microchemistry

by
Lance A. Campbell

A THESIS

Submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 9, 2010
Commencement June 2010

Master of Science thesis of <u>Lance A. Campbell</u>
presented on <u>March 09, 2010</u>.


APPROVED:


_____

Co-Major Professor, representing Fisheries Science


_____

Co-Major Professor, representing Fisheries Science


_____

Head of the Department of Fisheries and Wildlife


_____

Dean of the Graduate School


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.


_____

Lance A. Campbell, Author

# ACKNOWLEDGEMENTS

CONTRIBUTION OF AUTHORS

Daniel L. Bottom, Eric C. Volk and Ian A. Fleming contributed to Chapter Two, "*Correspondence Between Scale and Otolith Chemistry for Interpreting Life History Patterns of Juvenile Chinook Salmon (Oncorhynchus tshawytscha).*"

Daniel L. Bottom, Eric C. Volk and Ian A. Fleming contributed to Chapter Three "*Life history variation and growth of juvenile Chinook salmon (Oncorhynchus tshawytscha) in the Columbia River estuary.*"

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

*For my father who taught me to question.*

*For my professors, teachers and mentors who taught me how.*

**CHAPTER 1: GENERAL INTRODUCTION**

Many anadromous salmonid species depend upon estuaries for rearing and to make the physiological transition from fresh to salt water. This gateway is often described as a corridor connecting freshwater spawning and rearing habitat to productive ocean feeding grounds. It also links salmonids through evolutionary time by allowing for colonization of new and old habitats along the Pacific Rim (Lichatowich 1999). The use of estuaries by juvenile Pacific salmon was first described by Willis Rich (1920) in the Columbia River estuary in the early 20$^{th}$ century. Over the next 95 years our understanding of estuary use by Pacific salmonids has increased (Reimers 1973, Healey 1980, Healey 1982, Simenstad et al. 1982, Dawley et al. 1986, Healey 1991, Bottom et al. 2005a, Schreck et al. 2006, McComas et al. 2007, Hering et al. 2010, Volk et al. 2010) while, at the same time, estuarine habitats have been modified substantially by human impacts (Nicholas and Hankin 1988, Sherwood et al. 1990, Magnusson and Hilborn 2003, Bottom et al. 2005b). The use of a drastically altered Columbia River estuary by juvenile Chinook salmon is the focus of this thesis.

Juvenile Chinook salmon show the greatest diversity of estuarine life histories among Pacific salmon species. Gilbert (1913) originally classified juvenile Chinook salmon into two major types, ocean type and stream type. Ocean-type fish were those that migrate to sea within their first year of life and typically return to their natal streams in the fall. Conversely stream-type fish spend more than a year in freshwater before smolting and usually return to spawn in the spring. Spring/stream type

Chinook salmon have been described as the dominant race in the northern latitudes and in the upper reaches of large southern rivers such as the Columbia, Fraser, Sacramento, Klamath and Rogue. Fall/ocean type Chinook salmon are more commonly found in the lower reaches of large rivers and in smaller coastal rivers along southern British Columbia, Washington, Oregon and California coasts. However, the traditional fall/ocean type and spring/stream type dichotomy represents an overly simplistic interpretation of Chinook salmon life histories. We now know that both spring and fall spawners are capable of producing subyearling and yearling migrants, particularly in large river systems with complex habitats, where juvenile salmon often express a diversity of rearing and migratory behaviors (e.g. Healey 1991, Beckman 2002).

Life history has been defined as the critical periods of an organism's life cycle and the strategies it uses during these times to maximize survival and reproductive fitness (Stearns 1992). Life histories evolve in response to variation in fitness and underlying genetic differences among individuals. This variation allows for natural selection, a primary component of evolution (Darwin 1859). Given an organism's current circumstance, which is affected strongly by the environment, life history theory aims to predict the particular phenotype(s) likely to be expressed at equilibrium. Since environmental conditions constantly change, altering fitness of particular strategies, each species may express an array of life histories (Stearns 1976).

Understanding how life history traits in salmonids influence population stability and resilience has important implications for the management and recovery of

salmon species (Thorpe 1994, Hill et al. 2003, Einum et al 2003).  Hilborn et al (2003) reported that a diverse suite of juvenile and adult life histories contribute to the regional stability of the sockeye salmon (*O. nerka*) fishery in Bristol Bay, Alaska. Long-term catch records for sockeye salmon indicate that the fishery has been sustained by a complex of stream systems and local salmon populations that respond independently to environmental change (Hilborn et al. 2003).

Chinook salmon also exhibit a diversity of life history types, including juveniles that utilize the estuary for extended periods before migrating to the ocean.  In a study of hatchery Chinook salmon in 26 estuaries, Magnusson and Hilborn (2003) found that the juvenile-to-adult survival rate for salmon in river systems with an intact estuary was three times greater than that for more intensively modified estuaries. Together, these results suggest that diverse salmon life histories, including those linked to estuarine habitats, may increase population resilience to environmental perturbations and maintain long-term productivity.

Estuaries have been described as critical rearing areas that promote juvenile Chinook salmon growth and survival upon ocean entry.  In their review of returning adult Chinook data from coastal Oregon streams, Nicholas and Hankin (1988) concluded that juvenile Chinook salmon from Oregon coastal basins entered the ocean at sizes ranging from 100-160 mm, while their size at estuary entrance was much smaller, suggesting that the difference was due to estuary residency and growth. In Sixes River (Oregon), a disproportionate number of the adult survivors that returned to spawn in the basin had reared in the estuary as juveniles for an extended period in late

summer and then entered the ocean later in the fall at a large mean size (Reimers 1973).

Rich (1920) similarly reported that a significant proportion of juvenile Chinook salmon captured in the Columbia River estuary showed evidence of estuary rearing (~17%), as indicated by an "estuary check" recorded on their scales. Burke (2005) interpreted six life history types from Rich's historical sampling and, based on his scale measurements and various growth rate estimates from other estuaries, calculated an average residence time in the Columbia River estuary of 18.5 - 40 days (depending on the assumed growth rate). Published estuary residency estimates for juvenile Chinook salmon range from ~40 days or more in California's Sacramento River (Kjelson et al. 1982, MacFarlane and Norton 2002) and several Oregon coastal estuaries (Reimers 1973, Myers and Horton 1982, Volk et al. 2010) to 17-25 days in the Naniamo and Nitanat River estuaries of British Columbia (Healey 1982).

In contrast to these estimates, contemporary Chinook salmon tagging and marking studies in the Columbia River typically have reported estuary residence times that are < 1 week and often only a few days (Dawley et al. 1986, Schreck et al. 2006, McComas et al. 2007). These results coupled with significant mortality estimates in the lower river (Collis et al. 2001, Ryan et al. 2003) have contributed to the hypothesis that the estuary constitutes a hazardous corridor through which individuals must migrate rapidly to avoid being eaten by predatory birds that nest near the river mouth (Bottom et al. 2005a). Others have suggested, however, that short estuary residence times are more likely a symptom of historical changes in the basin rather than an

indicator of the estuary's potential function as a rearing area for juvenile salmon. Bottom et al. (2005a) and Burke (2005) hypothesized that Chinook salmon life histories have been simplified by anthropogenic changes throughout the basin—estuarine habitat losses, flow regulation, hatchery production, etc.—limiting the variety of juvenile rearing behaviors that are now expressed in the estuary. Regardless of the causal factors, several recent studies have speculated that estuary and early ocean mortality now constitute a significant impediment to the recovery of Columbia River salmon (Kareiva et al. 2000, Welch et al. 2008).

Unfortunately, no comprehensive life history surveys have been conducted on sub yearling Chinook in the Columbia River estuary since the initial characterization by Rich (1920). Despite various survival studies involving tagged groups of large yearling and subyearling fish (e.g., McComas et al. 2007) and periodic surveys monitoring salmon migrations through the lower river (e.g., Dawley et al. 1986), the estuarine life histories of contemporary Chinook salmon remain poorly understood. Opposing interpretations of the estuary's present-day function—hazardous corridor or productive nursery ground—cannot be resolved from the historical data.

In 2002 a research team organized by the National Marine Fisheries Service initiated a new study of the habitat associations and life histories of juvenile Chinook salmon in the lower Columbia River estuary (Roegner et al. 2008). The results reported here are derived from surveys conducted in 2003-05. The goal of this thesis is to describe the temporal patterns of estuary use by juvenile Chinook salmon in the Columbia River and to quantify life history attributes, including estuary residence

time, growth, and size and time of estuary entry (chapter 3). A sub-objective is to compare our findings with other contemporary and historical data to test the hypotheses that (1) contemporary estuary residence times for Chinook salmon are indeed short (i.e., measured in days not weeks or months), and (2) juvenile life history variation has been simplified in the Columbia River basin relative to the patterns that were observed near the turn of the twentieth century (Rich 1920).

Before we can quantify the life histories of Columbia River salmon or compare our results with those of Rich (1920), we must first verify whether his method for interpreting life histories from fish scales is accurate and reproducible. Although the patterns of circuli on scales have been used for nearly a century to infer the age, growth, and life histories of Pacific salmon (Dahl 1911, Gilbert 1913, Rich 1920, Shapovalov and Taft 1954, Bali 1959, Koo, 1962, Ward and Slaney 1988, Connor et al. 2005), such interpretations often have been subjective, and the results rarely have been validated (Beamish and MacFarlane 1983, Chilton and Bilton 1986, Hankin et al. 2005). Moreover, juvenile salmon scales have not been routinely collected in the lower Columbia River since the surveys of Rich (1920), and those scales are no longer available to verify his interpretations. To test whether the estuarine life histories of Columbia River Chinook salmon can be inferred from scale patterns, Chapter 2 of this thesis compares traditional scale morphometrics with new microchemical methods for analyzing scales and otoliths. From these results, we chose otolith microchemistry for the life history characterization in Chapter 3.

## LITERATURE CITED

Bali, J. M. 1959.  Scale analysis of steelhead trout *Salmo gairdnerii gairdneri* Richardson, from various coastal watersheds of Oregon. M.S. Thesis, Oregon State College, Corvallis, 117p

Beamish, R. J., and G. A. MacFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Beckman, B. R. 2002. Growth and plasticity of smolting in Chinook salmon. Ph.D Thesis, University of Washington, Seattle.

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005a. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. United States Department of Commerce, NOAA Technical Memo. NMFS-NWFSC-68.

Bottom, D. L., K. K.Jones, T. J.Cornwell, A. Gray and C. A.Simenstad. 2005b. Patterns of Chinook salmon migration and residency in the Salmon River Estuary (Oregon). Estuarine Coastal and Shelf Science 64: 79-93.

Burke, J. L. 2005. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to present. MS thesis, Oregon State University, Corvallis.

Chilton, D. E., and H. T. Bilton. 1986. New method for ageing Chinook salmon (Oncorhynchus tshawytscha) using dorsal fin rays, and evidence of its validity. Canadian Journal of Fisheries and Aquatic Sciences 43:1588–1594.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: Vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130: 385-396.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 134: 291- 304.

Dahl, K. 1911. The age and growth of salmon and trout in Norway, as shown by their scales. The Salmon and Trout Association, London.

Darwin, C.R. 1859. The origin of species. Oxford University Press, New York, N.Y. 439 pp.

Dawley, E. M., R. D. Ledgerwood, T.H. Blahm, C.W. Sims, J.T. Durkin, R.A. Kirn, G.E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. Coastal Zone and Estuarine Studies Division, NMFS-NOAA and Bonneville Power Administration. Contract No. DE-AI79-84-BP39652, Project No. 81-102. 256 pp.

Einum, S., I. A. Fleming, I. M. Cote, J. D. Reynolds. 2003. Population stability in salmon species: effects of population size and female reproduction allocation. Journal of Animal Ecology 72: 811-821.

Gilbert, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus Oncorhynchus. U.S. Bureau of Fisheries Bulletin, 32: 1-22.

Hankin, D. G., J. H. Clark, R. B. Deriso, J. C. Garza, G. S. Morishima, B. E. Riddell, C. Schwarz, and J. B. Scott. 2005. Report of the expert panel on the future of the coded wire tag program for Pacific salmon. Pacific Salmon Commission, Technical Report 18, Vancouver.

Healey, M.C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. United States Fisheries Bulletin 77: 653 – 668.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315 – 341 *in* B.R. Melteff and R.A. Nevé (editors). Estuarine comparisons. Academic Press, New York, N.Y.

Healey, M.C. 1991. Life history of Chinook salmon. Pages 313 – 393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, and I. A. Fleming. 2010. Tidal movements and residency of subyearling Chinook salmon (Onchorhynchus tshawytscha) in an Oregon salt marsh channel. Canadian Journal of Fisheries and Aquatic Sciences 67:524-533.

Hill, M.F., L. W. Botsford, A. Hastings. 2003. The effects of spawning age distribution on salmon persistence in fluctuating environments. Journal of Animal Ecology 72: 736-744.

Hilborn, R., T. P. Quinn, D. E. Schindler, D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100: 6564-6568.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fishery Bulletin 88: 657–666.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for Snake River spring/summer Chinook salmon in the Columbia River Basin. Science 290: 977-979.

Kjelson, M. A., P.F. Raquel, and F.W. Fisher. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California. Pages 393-411 *In* V. S. Kennedy, (editor), Estuarine comparisons, Academic Press, New York, N.Y.

Koo, T.S.Y. 1962. Age designation in salmon. Pages 41 – 48 *in* T.S.Y. Koo (editor). Studies of Alaska Red Salmon. University of Washington Press, Seattle, Wa.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C. 317 pp.

MacFarlane, R.B. and E.C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fisheries Bulletin 100: 244-257

Magnuson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries 26: 1094 – 1103.

McComas, R.L., L.G. Gilbreath, S.G. Smith, G.M. Matthews, J.W. Ferguson, G.A. McMichael, J.A. Vucelick, and T. Carlson. 2007. A study to estimate salmonids survival through the Columbia River estuary using acoustic tags, 2005. Report of the National Marine Fisheries Service to the U.S. Army Corps of Engineers, Portland, Oregon.

Myers, K.W., and H.F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. Pages 377 – 391 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, N.Y.

Nicholas, J. W., and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife Information Report. 88-1.

Reimers, P.E. 1973. The length of residence of juvenile fall Chinook salmon in the Sixes River, Oregon. Research Reports of the Fish Commission 4(2): 1-42.

Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers.  Bulletin of the United States Fish Commission 37 (DOC 887): 1-73.

Roegner, G.C.,  A. Baptista, D. L. Bottom, J. Burke, L. Campbell, C. Elliot, S. Hinton, D. Jay, M.A. Lott, T. Lundrigan, R. McNatt, P. Moran, C. A. Simenstad, D. Teel, E. Volk, J. Zamon, and E. Casillas. 2008. Estuarine habitat and juvenile salmon--current and historical linkages in the lower Columbia River and estuary, 2002-04. Fish Ecology Division, Northwest Fisheries Science Center, Seattle, WA.

Ryan, B.A., S.G. Smith, J.M. Butzerin, and J.M. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary 1998 – 2000. Transactions of the American Fisheries Society 132: 275 – 288.

Schreck, C.B., T.P. Stahl, L.E. Davis, D.D.. Roby, and B.J. Clemens. 2006. Mortality estimates of juvenile spring–summer Chinook salmon in the Lower Columbia River and estuary, 1992–1998: Evidence for delayed mortality? Transactions of the American Fisheries Society 135: 457-475.

Shapovalov, L., and A.C. Taft.  1954.  The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorynchus kisutch*) with special reference to Waddell Creek. California, and recommendations regarding their management.  California Depatment of Fish and Game Bulletin 98: 375 p.

Sherwood, C.R., D.A. Jay, R.B. Harvey, P. Hamilton, and C.A. Simenstad. 1990. Historical changes in the Columbia River estuary. Progress in Oceanography 25: 271-297.

Simenstad, C.A., K.L. Fresh, and E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343 – 364 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, N.Y.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51: 3-46.

Stearns, S.C. 1992. Evolutions of life histories. Oxford University Press, New York, NY. 249 pp.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17(1a):76-93.

Volk, E.C., D. L. Bottom, K.K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary (Oregon) using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139: 535-549.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (Salmo gairdneri) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45: 1110-1122

Welch D.W., E.L Rechisky, M.C. Melnychuk, A.D. Porter, C.J. Walters. 2008. Survival of migrating salmon smolts in large rivers with and without dams. Public Library of Science Biology 6(10): e265 doi:10.1371/journal.pbio.0060265

# CHAPTER TWO:

## Correspondence between scale and otolith chemistry for interpreting life history patterns of juvenile Chinook salmon (*Oncorhynchus tshawytscha)*

Lance A. Campbell[1,2*], Daniel L. Bottom[3], Eric C. Volk[2,4], and Ian A. Fleming[1,5]

[1] Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Corvallis, OR 97331

[2] current address: Washington Department of Fish and Wildlife, Science Division, Olympia, WA 98501

[3] NOAA Fisheries, Northwest Fisheries Science Center, Newport, OR  97365

[4] current address: Alaska Department of Fish and Game, Commercial Fisheries Division, Anchorage AK 99518

[5] current address: Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7 Canada

*corresponding author: campblac@dfw.wa.gov

# INTRODUCTION

For nearly a century, the morphometrics of scales have been used to reconstruct age, growth, and life history parameters of salmon (Dahl 1911, Gilbert 1913, Rich 1920, Shapovalov and Taft 1954, Koo 1962, Connor et al. 2005) and other fish species (Casselman 1983, Carlander 1987). This method relies on the assumption that circuli patterns recorded in scales reflect a fish's growth and corresponding rearing and migratory histories. Scales have a couple of key advantages over other methods for interpreting life histories: scales can be collected without sacrificing individuals, an important consideration for studies of small or at-risk populations; and many archival scale collections exist that could provide historical baselines for investigating life history changes in contemporary populations. Unfortunately, scale characteristics and growth patterns used to infer fish age and life history are seldom validated, and interpretations of life histories based on scale morphology are often subjective, raising questions about the accuracy and reproducibility of results. For example, scale characteristics have been used frequently to interpret life history events of diadromous fish as they migrate between freshwater and marine environments (Rich 1920, Reimers 1973, Schluchter and Lichatowich 1977, Burke 2005, Bottom et al. 2005a). Yet few study designs have incorporated independent life history measures to verify the scale interpretations. To test whether the estuarine life history of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, can be inferred from scale patterns, we compared scale morphometrics with independent microchemical analyses of scales and otoliths from fish collected within the Columbia River estuary.

Interpreting individual salmonid life histories from scale analysis often relies on changes in circuli patterns or other scale features, such as scale checks, that are believed to coincide with environmental transitions during juvenile salmon migrations. Generally, three types of salmon scale growth and circuli characteristics have been interpreted to reflect the fish's rearing environment: (1) narrow circuli spacing (freshwater growth), (2) intermediate circuli spacing (estuarine or reservoir/lake growth), and (3) wide circuli spacing (ocean growth) (Rich 1920, Reimers 1973, Schluchter and Lichatowich 1977, Connor et al. 2005). These interpretations rely on the direct positive relationship between fish size and scale size (Bilton and Robins 1971) and on the assumption that growth increases as salmon enter successively more productive feeding environments in the transition from river to estuary and from estuary to coastal ocean. The time of salmon entry into the estuary is often identified on scales as a region of changing circuli spacing marked by a distinct scale "check" designated by a few narrowly-spaced circuli, followed by an increase in circuli spacing (Rich 1920, Bilton 1975).

Scale checks have been produced experimentally with rapid increases and decreases in growth (Bilton 1975) and temperature (Boyce 1985) and are generally apparent after growth has resumed. In these laboratory studies, Bilton (1975) and Boyce (1985) described a "lag" between experimental treatments and the addition of scale material and the formation of checks. They estimated that two weeks to a month could lapse before physical evidence of environmental conditions is recorded on the scale. This lag effect, the lack of validation for observed scale patterns, and the

arbitrary criteria often used to identify scale features have led many biologists to question whether scale morphology is a trustworthy tool for reconstructing fish life histories or estimating age (Beamish and MacFarlane 1983, Carlander 1987).

In recent years, otolith microchemistry has provided a more precise method for reconstructing fish life histories (Kalish 1990, Seccor et al. 1995, Thorrold et al. 1997, Campana 1999, Volk et al. 2000, Kennedy et al. 2002, Zimmerman and Reeves 2002, Wells et al. 2003) that does not require assumptions about changes in individual growth during environmental transitions or interpretations of scale morphometrics. Otoliths produce daily calcified material that reflects ambient water chemistry (Fowler et al. 1995). In addition, unlike bone, otoliths are not living tissue and therefore, calcified material and chemical signatures remain relatively stable after the material is deposited (Campana and Neilson 1985). The chemical composition of otoliths thus has been used successfully to determine fish migration routes, differentiate fish populations, distinguish anadromous from resident life histories, reconstruct water temperature profiles, and validate age interpretations (Campana et al. 1997).

The element strontium (Sr), which is generally found in low concentrations in fresh and high concentrations in marine water, has provided a useful marker for designating diadromous fish migrations (Kalish 1990, Volk et al 2000, Zimmerman and Reeves 2002, Zimmerman 2005, Brown and Severin 2009). Because Sr has a similar valence and ionic radius as calcium, it can be substituted in the calcium carbonate lattice of the otolith to represent the relative Sr concentrations in the environment (Kalish 1990). Chemical profiles across diadromous fish otoliths are

characterized by low strontium/calcium (Sr/Ca) ratios for periods of freshwater rearing and increased Sr/Ca ratios during periods of brackish and marine-water residency (Kalish 1990, Zimmerman 2005, Brenkman et al. 2006).

Several authors have suggested that the same geochemical record that is found in otoliths might also occur in scales, providing a potential method to validate traditional interpretations of scale patterns and to analyze juvenile life histories without having to sacrifice individuals for their otoliths (Wells et al. 2000a, Courtemanche et al. 2005). Scale chemistry has reportedly been used successfully to distinguish between resident and anadromous brown trout, *Salmo trutta* (Bagenal et al. 1973), brook trout, *Salvelinus fontinalis* (Courtemanche et al. 2005), and striped bass, *Morone saxatilis* (Coutant and Chen 1993); and to examine geographic variations in scale chemistry for juvenile weakfish, *Cynoscion regalis* (Wells et al. 2000b) and resident westslope cutthroat trout, *Oncorynchus clarki lewisi* (Wells et al. 2003). However, we are unaware of any studies that have compared scale and otolith chemistry with scale morphology to validate life history patterns derived from traditional scale-pattern analyses.

The reliability of scale chemistry as an index of current or past chemical environments used by fish may depend in part on the stability of the chemical signal through time. Unlike otoliths, which are isolated within a semi-permeable membrane (Lagler et al 1962, Campana 1999), scales are in direct contact with water and may be reabsorbed during periods of starvation or stress, eroding the scale edge and circuli (Wallin 1957, Bilton 1975). Although several studies have examined the stability of

trace elements in otoliths (Kalish 1990, Campana 1999), much less is known about scale chemistry and the stability of elements through time within the different regions of the scale. Wells et al. (2000b) found that Magnesium (Mg) and Manganese (Mn) concentrations recorded in weakfish scales during the first year of growth differed from those collected from adults, suggesting that these elements were not stable over time. On the other hand, Sr and Barium (Ba) concentrations remained relatively unchanged from juvenile to adult. In laboratory experiments, Wells et al. (2000a) found a linear relationship between scale Sr concentrations and the salinity levels experienced by juvenile spot (*Leistomus xanthurus*), but scale Sr and temperature were not correlated. These findings contrast with experimental studies that have shown nonlinear effects of both salinity and temperature on the incorporation of Sr into the aragonite lattice of the otolith (Wells et al. 2000a).

Otolith chemical analyses offer an independent method to validate whether juvenile salmon life histories can be determined reliably from measurements of either scale morphology or scale chemistry. Here we compare results of otolith chemistry, scale chemistry, and scale morphology for reconstructing the juvenile life histories of Columbia River Chinook salmon sampled within and above the saline portion of the estuary. More specifically, we test the hypothesis that scale checks and intermediate growth are accurate indicators of estuarine entry by testing: (1) whether scale checks from individual salmon were associated with significant transitions in scale Sr/Ca levels; and (2) whether these scale features and chemical transitions corresponded to similar chemical changes in their otoliths.

**METHODS**

*Study Area*

The Columbia River headwaters begin in British Columbia, Montana, Wyoming, Idaho, Nevada, Utah, Washington and Oregon, draining an area of 660,000 $km^2$ along a total network of 1,932 river km (Rkm) before entering the Pacific Ocean near Astoria, Oregon.  Maximum salt-water intrusion in the deepest portions of the river channel reaches ~Rkm 55, but tidal influence extends > 230 Rkm from the river mouth to the base of Bonneville Dam.

*Sample collection*

To validate whether juvenile Chinook salmon life histories can be determined reliably from measurements of scale morphology, scale chemistry, or otolith chemistry, samples were collected as part of an ongoing NOAA Fisheries research study. This research was initiated in 2002 to understand the role of estuarine habitat for juvenile Chinook salmon (*O. tshawytscha*) and to characterize life history variation among juveniles entering and leaving the Columbia River estuary.  Fish were collected monthly at four saline influenced estuarine sites and one tidal freshwater site (Fig. 2.1).  Fish were sampled at each site near low slack tide with a 50-meter beach seine (1.27 cm mesh in the wings and .95cm mesh in the bunt).  As many as ten samples from three size classes (fry 40-60 mm, sub-yearling 60-100mm, and yearling >100mm) were retained.  Paired otolith and scale samples were removed from individual fish in the laboratory, labeled, and stored until analysis.

We determined the frequency of scale checks and intermediate growth in the downstream migrant population from a random scale sample collected in 2003 at one tidal freshwater site at Lower Elochoman Slough (LES, n=119) and at one high-salinity site at Point Adams Boat Launch (PAB, n=108) (Fig. 2.1). We also compared otolith and scale samples from a non-random collection of individuals from the saline and tidal freshwater portions of the estuary to evaluate whether morphometric and chemical techniques for analyzing scales and otoliths yield consistent life history interpretations. For the non-random samples we selected fish based on the presence or absence of scale checks in order to test chemically the presence of elevated Sr. The saline samples (n=100) came primarily from PAB, but during months of low sample size, we included individuals from other lower estuary seining sites (Clatsop Spit, Point Ellice, and West Sand Island). All individuals from the tidal freshwater portion of the estuary were collected at LES (n=30).
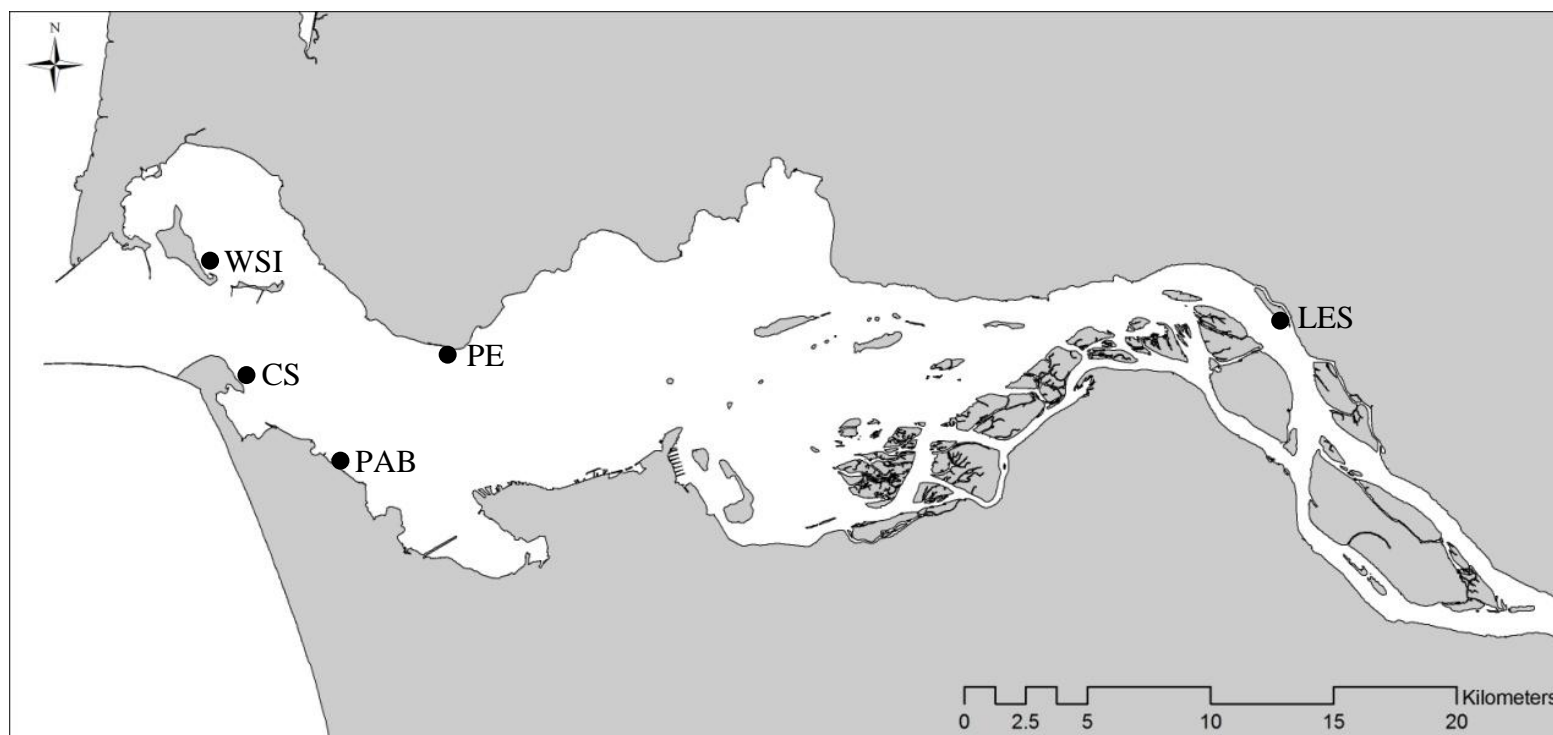
Figure 2.1. Map of the Lower Columbia Estuary. Freshwater site at Lower Elochoman Slough (LES) and marine/brackish water sites at Point Adams Boat Launch (PAB), Point Ellice (PE), Clatsop Spit (CS), and West Sand Island (WSI). Courtesy of Jen Burke, University of Washington.

*Sample analysis*

  To determine whether strontium (Sr) levels in juvenile Chinook salmon scales can be used to indicate time of estuary entrance, we analyzed otolith and scale chemistry from the same individuals.  All microchemical analyses were conducted at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. The analysis system consisted of New Wave DUV 193 nm ArF laser coupled with a Thermal Elemental PQ Excell quadropole inductively coupled plasma mass spectrometer (ICP-MS).  Helium was used as the carrier gas to transport the ablated material from the laser to the mass spectrometer.  Operating conditions for the LA-ICP-MS for both scales and otoliths are described in Table 2.1.

Table 2.1. General LA-ICP-MS operating conditions

| General operating conditions | | |
| --- | --- | --- |
| Cooling gas (L/min) | 13.00 | |
| Auxiliary gas (L/min) | 0.95 | |
| He carrier gas (L/min) | 0.75 | |
| | | |
| Detector mode | Pulse counting and analog | |
| Sweep mode | Peak hopping | |
| Dwell time (ms) | 10 | |
| Points per peak | 1 | |
| Analysis interval (sec) | 360 | |
| | | |
| **Specific operating conditions** | **Scales** | **Otoliths** |
| Laser ablation diameter (microns) | 40 | 30 |
| scanning speed (microns/sec) | 5 | 5 |
| Pulse rate (Hz) | 5 | 8 |

*Scales* – We sampled scales from frozen, subyearling Chinook salmon collected during the NOAA Fisheries Columbia River study. Scales were removed in an area a few scale rows above the lateral line between the anterior insertion of the anal fin and the posterior insertion of the dorsal fin. Scales were placed between clear acetate, labeled, and later examined for intermediate growth (IG) and scale checks under 10x magnification using a Micron 780® microfiche. We distinguished IG (wider circuli spacing) and scale checks using criteria similar to those of Rich (1920), Reimers (1973), and Bilton (1975) and classified each scale into one of four categories: (1) presence of intermediate growth (IG) on the scale margin or IG plus a check, (2) a clear check or check with additional growth but no IG, (3) presence of narrow circuli but no clear check or IG, and (4) no check or IG (Fig. 2.2).
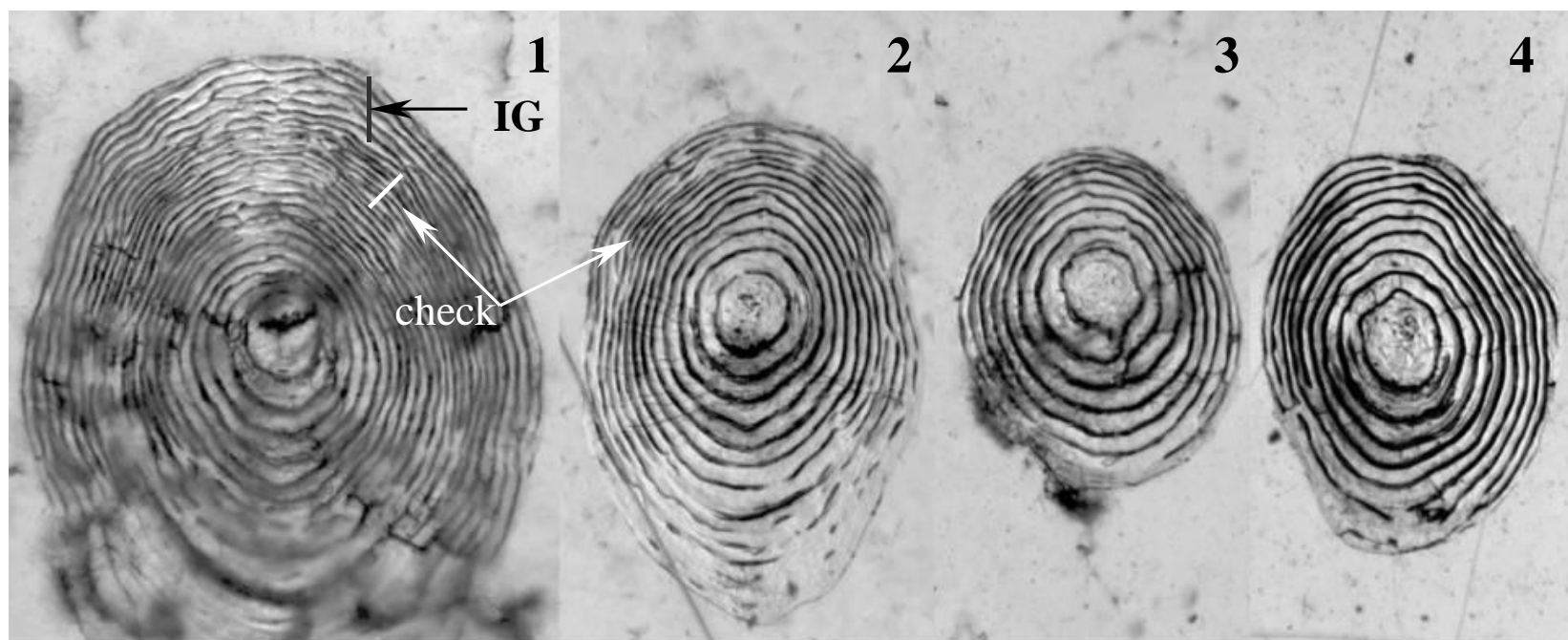
Figure 2.2. Morphometric classification of scales. From left to right: (1) presence of intermediate growth (IG) on the scale margin or IG plus a check, (2) a clear check or check with additional growth but no IG, (3) presence of narrow circuli but no clear check or IG, and (4) no check or IG.

Scales were carefully removed from the acetate under 10-40x magnification (Leica dissecting scope) and transferred to a petrographic slide prepared with mounting tape. We mounted approximately 4-10 scales per sample with both the distal (fibrillary) and proximal (osseous) sides facing up. To analyze scale chemistry, we traced a laser transect across each scale from the nucleus to just beyond the scale edge, approximately 20 degrees off the midline, in the anterior plane whenever possible (Fig. 2.3).

Of the 4-10 scales mounted from each fish sample, we analyzed both distal and proximal surfaces. However, because no noticeable difference could be detected and the distal side was difficult to view, we primarily analyzed the proximal side. In most cases, one distal side and two or three proximal sides were analyzed from each sample. To calibrate results for each scale transect, we analyzed a corresponding transect along a polished NIST (610) glass standard of known Sr and Ca concentrations. We transformed the raw counts to a smoothed atomic Sr/Ca ratio, plotted the results, and recorded points of interest (POI), such as start and end positions and points of Sr increase.

Figure 2.3. Juvenile Chinook salmon type 2 scale from the lower estuary showing laser scar/transect.

*Otoliths* – Sagiital otoliths were prepared for chemical and daily growth increment analysis by thin sectioning in the sagiital plane.  Petrographic slides were heated on a hot plate at approximately $275^oC$ with Crystal Bond 509™ added as a bonding medium for the otolith.  Otoliths were mounted sulcus side up and ground on a Buehler Ecomet 3™ grinder with 1200 grit, silicon carbide paper until the primordium was nearly exposed without sacrificing otolith edge integrity.  A fine polish was applied using 1 µm alumina slurry.  The half section was then warmed to melt the Crystal Bond and turned distal side up.  We repeated grinding until the primordium was exposed or until there was risk of obliterating the Daily Growth Increments (DGI) in the dorsal posterior region.   Again, a fine polish was added using 1 µm alumina paste.  Otolith thin sections were rinsed in deionized water and air dried (methodology modified from Volk et al. 2000 and Zimmerman and Reeves 2002).

A transect was drawn for laser ablation from the posterior visible primoridium to beyond the otolith edge in the dorsal/posterior quadrant (Fig. 2.4).  Each otolith transect was coupled with a transect along a polished NIST (610) glass standard with known concentrations of Sr and Ca for quantifying Sr/Ca atomic ratios.  Raw counts of Sr and Ca were plotted. Transect start and end points and the point of Sr inflection were recorded.  These points of interest on the chemical output were then related to actual location on the otolith by the equation (Brenkman et al. 2006, Volk et al. 2010):

$$otolith_{POI} \ (\mu m) = \left( \frac{laser_{POI} \ (ms) - laser_{start} \ (ms)}{1000} \right) * 5 \ \mu m/sec$$
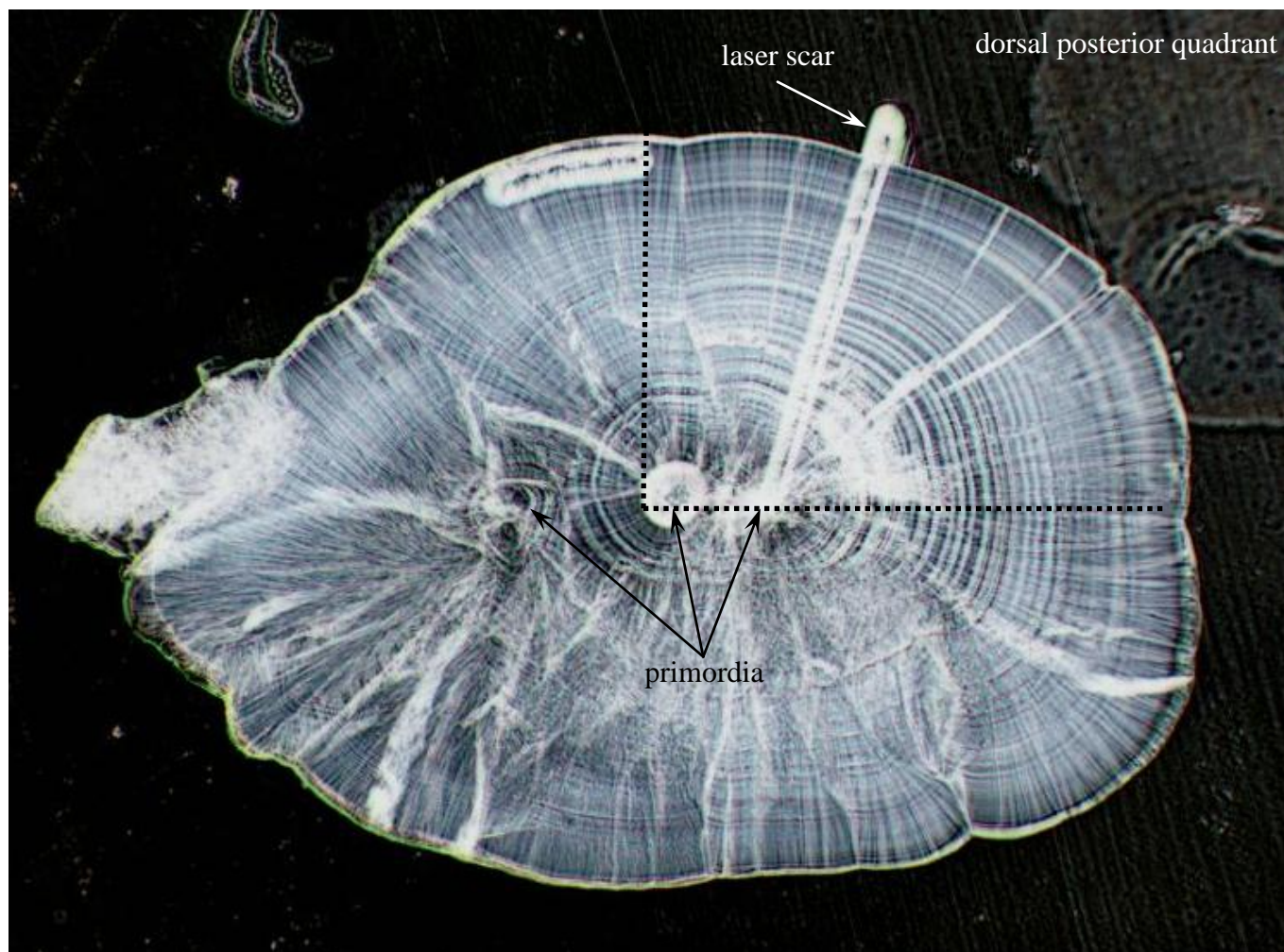
Figure 2.4. Juvenile Chinook salmon otolith showing laser ablation scar from the primordium to the dorsal posterior edge of the otolith.

*Statistical methods:*

For its simplicity and accuracy, we used Campana's (1990) proportional Biological Intercept (BI) method to back calculate the fish size at a given otolith size based on the formula:

$$L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$

Where $L_c$ and $O_c$ are the size of the fish and otolith at the time of capture; $L_o$ and $O_o$ are the biological intercept for fish length and otolith size, respectively; and $L_a$ and $O_a$ are the size of the fish and the otolith at a particular point of interest, such as Sr inflection.

Scale chemistry inflection points were selected visually and the regions before and after the inflection point were tested for a difference using a two-sample t-test. An Arcsin square root transformation was used to normalize Sr/Ca atomic ratios for one-way ANOVA with a Holm-Sidak multicomparison test. Probability value for significance was < .05. Statistical analyses were undertaken using SYSTAT® 13 statistical package.

**RESULTS**

*Scale morphometrics*

Morphometric analysis of Chinook salmon scales suggested that many individuals collected near the river mouth had reared in the estuary before capture. Nearly half (49%) of 108 randomly-selected individuals collected at PAB exhibited

intermediate growth and scale checks compared with 24% of 119 samples collected at

a single station (LES) in the tidal fresh zone (Table 2.2).  As the season progressed,

the scale-check frequency increased at both the upper and lower sampling sites. Check

frequencies between April and June ranged from 15-33% at PAB and from 0-13% at

LES.  From July to October, the range in check frequencies at the two sites increased

to 52-100% and 21-100%, respectively.  By September, nearly all samples at both

sites showed evidence of checks, intermediate growth, or both (Table 2.2).

Table 2.2. Frequency of scale classes (1-4; see Fig. 2.2) by month for juvenile
Chinook salmon captured during beach seining in 2003 from a saline (PAB) and a
freshwater (LES) site in the lower Columbia River.

| | | | Scale Morphometric Classification | | | | | |
|------|-----------|-----|-----|-----|-----|-----|% with scale check|% without scale check|
| Site | Month | N | 1 | 2 | 3 | 4 | | |
| PAB | April | 22 | 5 | 1 | 2 | 14 | 27 | 73 |
| PAB | May | 13 | 2 | 0 | 1 | 10 | 15 | 85 |
| PAB | June | 21 | 2 | 5 | 6 | 8 | 33 | 67 |
| PAB | July | 23 | 8 | 4 | 4 | 7 | 52 | 48 |
| PAB | August | 10 | 3 | 4 | 1 | 2 | 70 | 30 |
| PAB | September | 10 | 5 | 5 | 0 | 0 | 100 | 0 |
| PAB | October | 9 | 7 | 2 | 0 | 0 | 100 | 0 |
| | N | 108 | 32 | 21 | 14 | 41 | 49 | 51 |
| LES | April | 32 | 0 | 0 | 2 | 30 | 0 | 100 |
| LES | May | 23 | 0 | 3 | 6 | 14 | 13 | 87 |
| LES | June | 17 | 0 | 2 | 6 | 9 | 12 | 88 |
| LES | July | 19 | 3 | 1 | 8 | 7 | 21 | 79 |
| LES | August | 10 | 1 | 4 | 3 | 2 | 50 | 50 |
| LES | September | 4 | 1 | 3 | 0 | 0 | 100 | 0 |
| LES | October | 14 | 7 | 3 | 3 | 1 | 71 | 29 |
| | N | 119 | 12 | 16 | 28 | 63 | 24 | 76 |

*Scale Chemistry*

We selected non-randomly 100 scale samples with and without checks at the brackish water site (PAB) and another 30 from the freshwater site (LES) to test whether scales with and without checks had a corresponding Sr signal on their scales and otoliths (Table 2.3). About half of the scale samples we selected from each site were classified as Types 3 or 4 (no scale check). Approximately one third were Type 2 (a clear check), while the remainder showed evidence of checks and intermediate growth (Type 1).

Table 2.3. Sample sizes for scale morphometric, scale chemistry (SC), and otolith chemistry (OC) types by location within the lower Columbia River.

| Scale Morphometric Types | | | | | |
|---|---|---|---|---|---|
| Location | N | 1 | 2 | 3 | 4 |
| PAB | 100 | 19 | 35 | 24 | 22 |
| LES | 30 | 2 | 12 | 9 | 7 |

| Scale Chemistry Types | | | | |
|---|---|---|---|---|
| Location | N | 1 | 2 | 3 |
| PAB | 100 | 34 | 32 | 34 |
| LES | 30 | 0 | 0 | 30 |

| Otolith Chemistry Types | | | | |
|---|---|---|---|---|
| Location | N | 1 | 2 | 3 |
| PAB | 100 | 43 | 31 | 26 |
| LES | 30 | 0 | 0 | 30 |

Chemical transects across (n=130) selected Chinook scale samples exhibited a more variable pattern than their corresponding otolith samples (see otolith section, Fig. 2.7), most likely due to the uneven surface of the scale circuli as the laser passed through (Fig. 2.5). Scale chemical (SC) profiles were grouped into three categories: SC Type 1, with a Sr inflection point; SC Type 2, no scale Sr inflection but an average scale Sr/Ca atomic ratio >.001; and SC Type 3, no Sr inflection and Sr/Ca atomic ratios < .001 (presumably a freshwater signal, since all samples collected at the freshwater site had this pattern). SC Type 2 fish were further split into two groups based on estuary residence times that were less than or greater than 30 days as inferred from their otolith microchemistry/microstructure (Fig. 2.6). All scale samples collected at the tidal freshwater site had a SC Type 3 pattern, whereas 35% and 33% of the scale samples collected near the river mouth (marine-brackish water) corresponded to SC Types 1 and 2, respectively (Table 2.3). A one way analysis of variance (ANOVA) found a statistically significant difference among the four scale chemistry types (including the two variants of SC Type 2 as defined by residence times) ($F_{3,122} = 148.5$, $P < .001$; Fig. 2.6). To compare between SC types, we used an average value collected in the portion of the scale after the Sr inflection point to the scale edge (SC Type 1) and an average values over the entire scale (SC Types 2-3). All scale chemistry types differed significantly in scale Sr/Ca from one another (Holm-Sidak, $P < .001$) except SC Types 1 and SC Types 2 (>30 days residency, $P=.305$) (Fig.2.6).
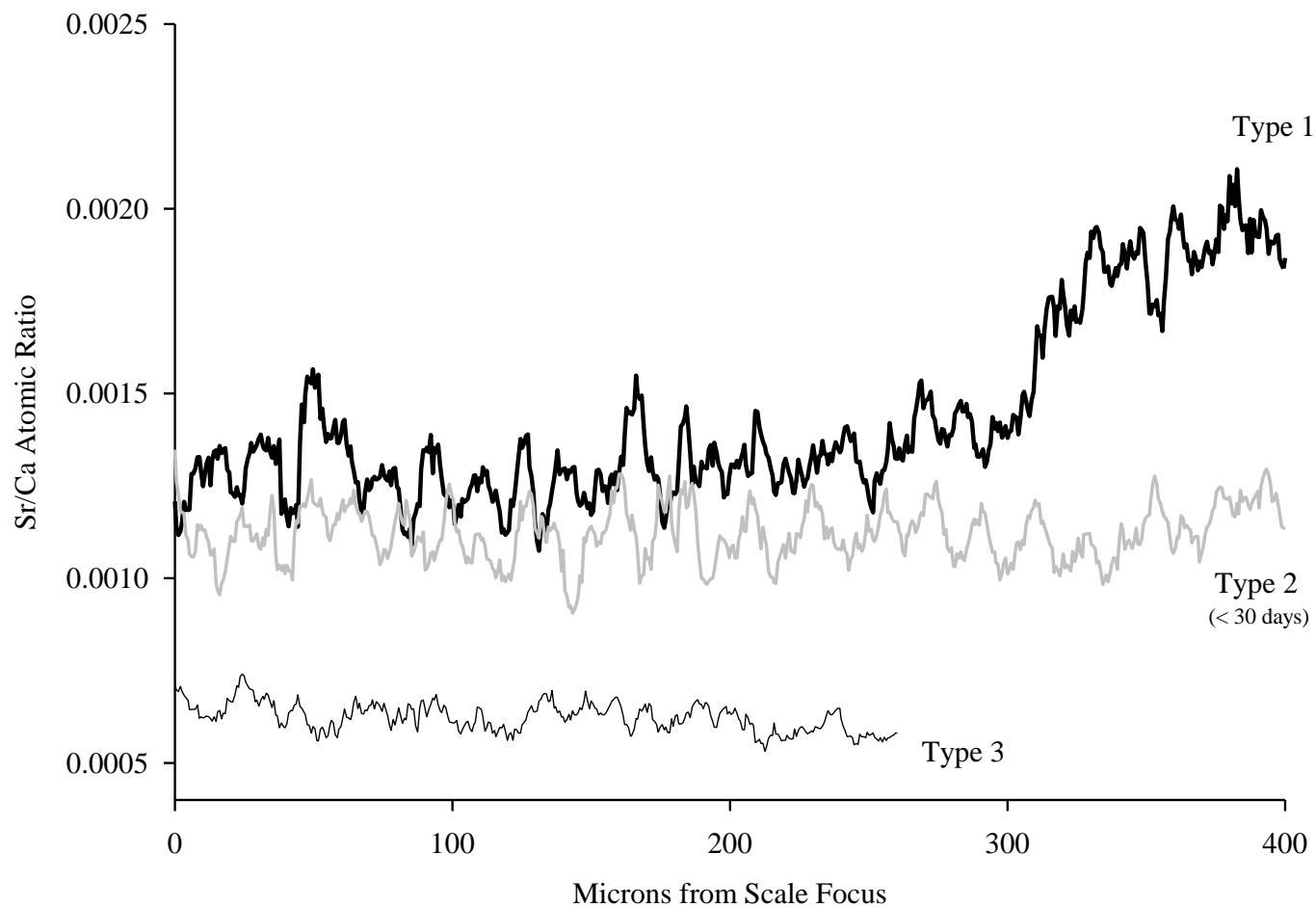
Figure 2.5. Scale Sr/Ca profiles for three individuals exhibiting scale chemistry (SC) Types 1-3: SC Type 1, Sr inflection; SC Type 2, elevated Sr but no inflection; and SC Type 3, assumed freshwater patterns.
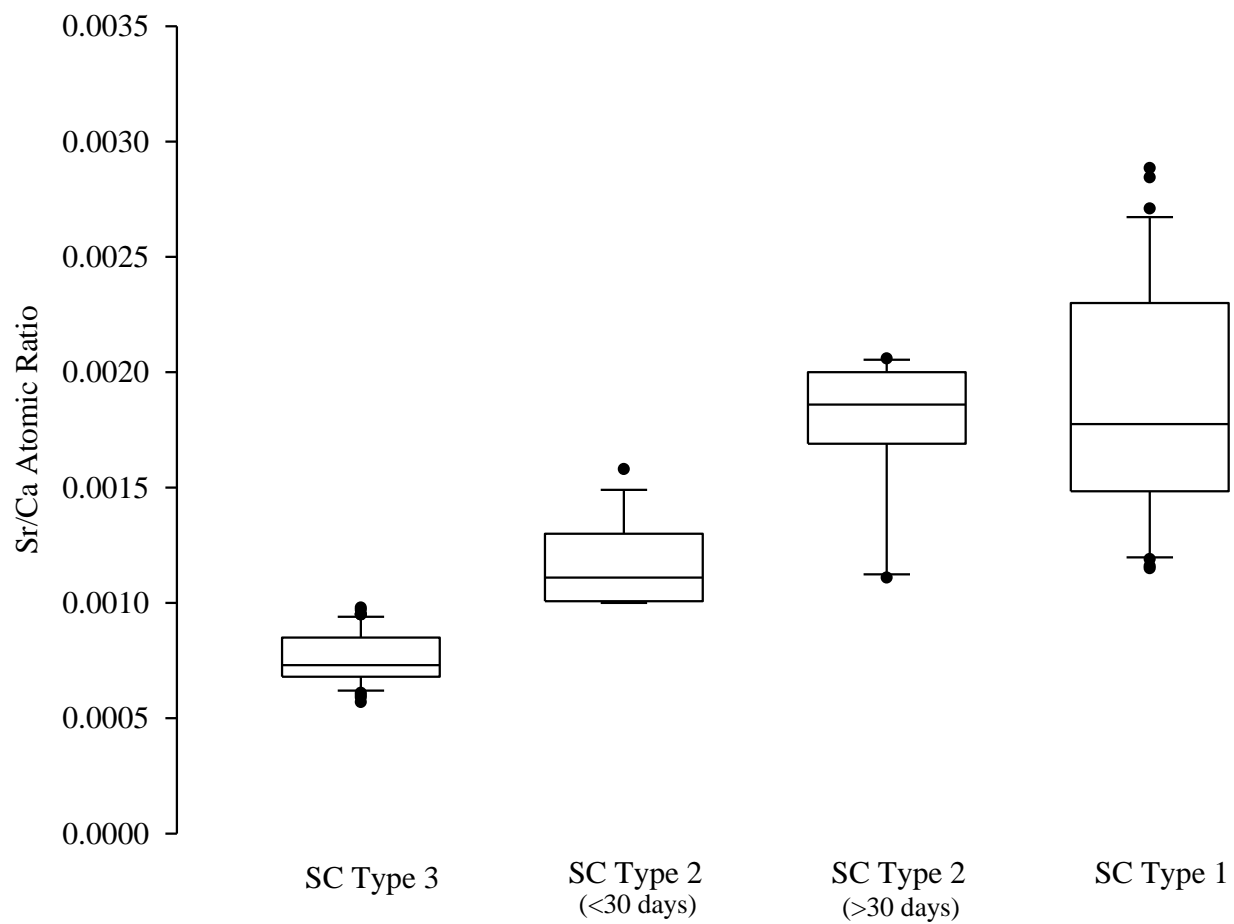
Figure 2.6. Scale Sr/Ca atomic ratios for each of the four scale chemistry (SC) patterns: SC type 3 (assumed freshwater), SC Type 2 (<30 days estimated residence time), SC type 2 (>30 days estimated residence time), and SC Type 1 (Sr inflection point).

### *Otolith chemistry*

Chemical transects across (n=130) selected Chinook otolith samples exhibited

patterns similar to those described for other anadromous salmonids (Kalish 1990, Volk

et al. 2000, Zimmerman and Reeves 2002). Generally, otolith Sr/Ca ratios were

relatively unchanged from an elevated core signal (due to Sr-rich marine water

experienced by the mothers and transferred to developing ova) to hatching, reflecting a

maternal signal. However, as fish came into contact with ambient water and used the

remainder of their Sr-rich yolk, Sr levels decreased gradually to low levels

corresponding to freshwater residence. Otolith Sr levels then rose again sharply,

presumably after the individual entered Sr-rich salt water (Fig. 2.7). We classified

otolith chemistry (OC) into one of three general patterns: OC Type 1, a pronounced

rise in Sr/Ca values sustained for a prolonged period (>30 days); OC Type 2, an

intermediate to pronounced increase in Sr/Ca (~ > ¼ of the maternal signal) values

with a short residency in salt water (<30days); OC Type 3, no appreciable Sr/Ca

increase above assumed freshwater levels (Fig. 2.7, Table 2.3).

Otolith Sr/Ca ratios were averaged from the primordium (.00154), assumed

freshwater zone (.00075), and in the region of elevated Sr in OC Types 1 and 2

(.00256 and .00152 respectively), and near the otolith edge in OC Type 3 (.00082)

(Fig 2.8). A one-way analysis of variance (ANOVA) indicated a significant difference

among the otolith chemistry types ($F_{4,385} = 274.8$, $P < .001$). A subsequent multiple

comparison test found no statistical difference between the freshwater Sr/Ca region in

all otolith samples and OC Type 3 (Holm-Sidak, $P = .657$) (Fig 2.8). Conversely, all

comparisons of OC Type 3 (freshwater) to OC Types 1 and 2 (elevated Sr) and

between OC Types 1 and 2 were significant (Holm-Sidak, $P < .001$) (Fig 2.8).   All

otolith samples collected at the fresh-water site (LES) were OC Type 3 fish, while

otolith samples collected at PAB or other sites near the mouth (marine-brackish water)

were 43% and 31% OC Types 1 and 2, respectively (Table 2.3).

Figure 2.7. Otolith Sr/Ca profiles showing three individuals exhibiting the three otolith chemistry (OC) patterns: OC Type 1, extended estuary residence; OC Type 2, short estuary residence; and OC Type 3, fresh-water residence only.
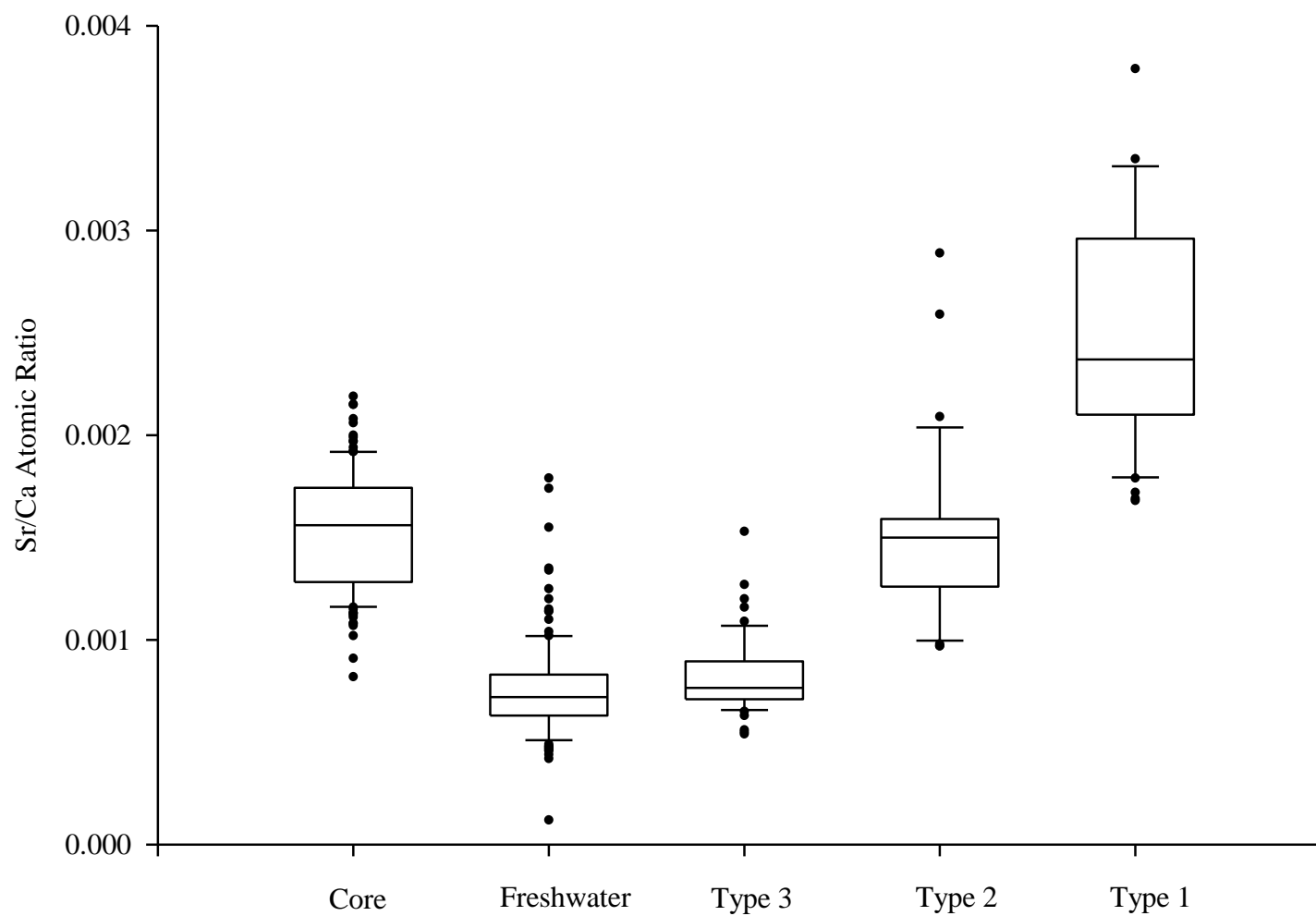
Figure 2.8. Otolith Sr/Ca atomic ratios for the core, assumed fresh-water values, and for regions of elevated Sr for otolith chemistry (OC) Types 1 and 2, and near the otolith edge for OC Type 3.

*Chemical validation of scale checks*

Life history interpretations based on scale morphometric characteristics (checks, intermediate growth [IG], or lack thereof) were validated by comparing the microchemistry of paired otoliths and scales from individual fish of the two major morphometric classifications, i.e. with (Types 1 and 2) and without checks (Types 3 and 4). Sixty-nine scale/otolith pairs from fish showing some form of check and/or IG on their scales (Types 1 and 2) were examined, and of these, 47% (n=32) had evidence of a Sr inflection on their scale. Sixty-one pairs of fish showing no recognizable IG or check on their scales (Types 3 and 4) were examined, and of these, 97% (n=59) were found to have no evidence of Sr inflection (Table 2.4). Using the broadest classification of scale checks (Types 1 and 2), we would have misclassified 53% of samples as estuary residents by scale morphology alone, when in fact there was no chemical evidence linking the scale check to a corresponding uptake of Sr. If we only used the most stringent classification (Type 1) we would have accurately linked the scale check with an uptake of Sr 67% of the time. However, this would have ignored another 26 samples (nearly double the sample size of Type 1) that had some form of Sr signal (either inflection or elevated Sr).

Table 2.4. Comparison of scale morphometric types with scale and otolith chemistry classification.

| | | Scale Morphometric Type | | | | | | | |
| | | 1 | | 2 | | 3 | | 4 | |
| | | n | % | n | % | n | % | n | % |
|---|---|---|---|---|---|---|---|---|---|
| Scale chemistry type | 1 | 14 | 67 | 18 | 38 | 1 | 3 | 1 | 4 |
| | 2 | 4 | 19 | 8 | 17 | 11 | 33 | 10 | 36 |
| | 3 | 3 | 14 | 22 | 46 | 21 | 64 | 17 | 61 |
| | | | | | | | | | |
| Otolith chemistry type | 1 | 18 | 86 | 21 | 44 | 6 | 18 | 7 | 25 |
| | 2 | 0 | 0 | 8 | 17 | 4 | 12 | 7 | 25 |
| | 3 | 3 | 14 | 19 | 40 | 23 | 70 | 14 | 50 |
| | | | | | | | | | |
| Total paired samples | | 21 | | 48 | | 33 | | 28 | |

Of the 61 scale samples that were classified as having no checks or IG, 21 (37%) had Sr levels elevated above typical freshwater levels, but no Sr inflection.  In many of the scale samples without a noticeable rise in scale Sr (inflection), but with high average Sr, the otolith back-calculated size at estuary entrance occurred before or near the time of scale formation (i.e. at 35-40 mm fork length).

These scale chemistry and morphometric results indicate that fish entering Sr-rich estuary water do not necessarily lay down scale checks that correspond to estuary entrance.  Furthermore, many fish that were residing in the estuary showed no visual signs, in the form of scale checks, that they had entered the estuary.

*Comparison of scale and otolith chemistry*

Otolith and scale edge chemistry showed a strong positive relationship, explaining over 91% of the variation (Fig. 2.9).  All fish with a Sr inflection point on their scale chemical profile also had an inflection point on their otolith chemical

profile. Only four fish were found to have elevated otolith Sr (OC Types 1 and 2), but not elevated scale Sr. The earliest sample found with a detectable Sr inflection on its scales was estimated to have resided within the marine/brackish water portion of the estuary for 31 days. Of the fish that had Sr inflections in their otolith profile but not in their scale profile, all were either present in the estuary for less than 30 days or had entered the estuary between 35-40 mm (i.e. at or before scale formation). When samples with scale Sr/Ca inflection points were excluded from analysis and only specimens without inflection points were examined (SC Type 2 and 3; Fig. 2.10), we still found a linear relationship between otolith edge chemistry and the average scale chemistry across the entire scale. We found that otolith edge chemistry explained 86% of the variation in the average scale chemistry for fish that did not have any Sr inflection in their scale chemical profile ($P < .001$, Fig. 2.10). These results suggest that Sr is incorporated into the scale even before new scale material is deposited and calcified at the scale margin.
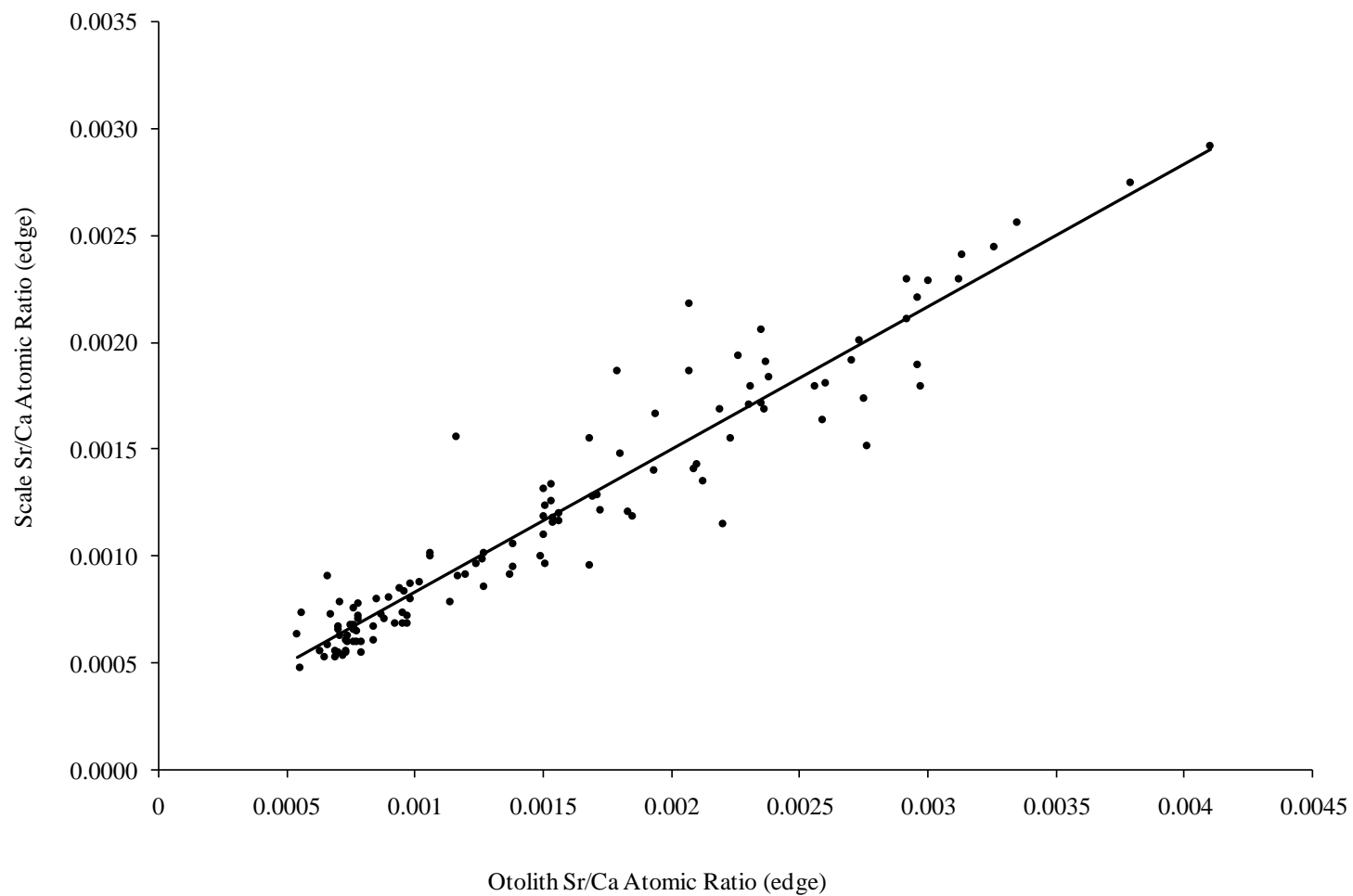
Figure 2.9. Relationship between otolith and scale Sr/Ca edge values from juvenile Chinook salmon within the Columbia River estuary ($y = 0.6674x + 0.0002$, $r^2 = 0.917$, $P < .001$).
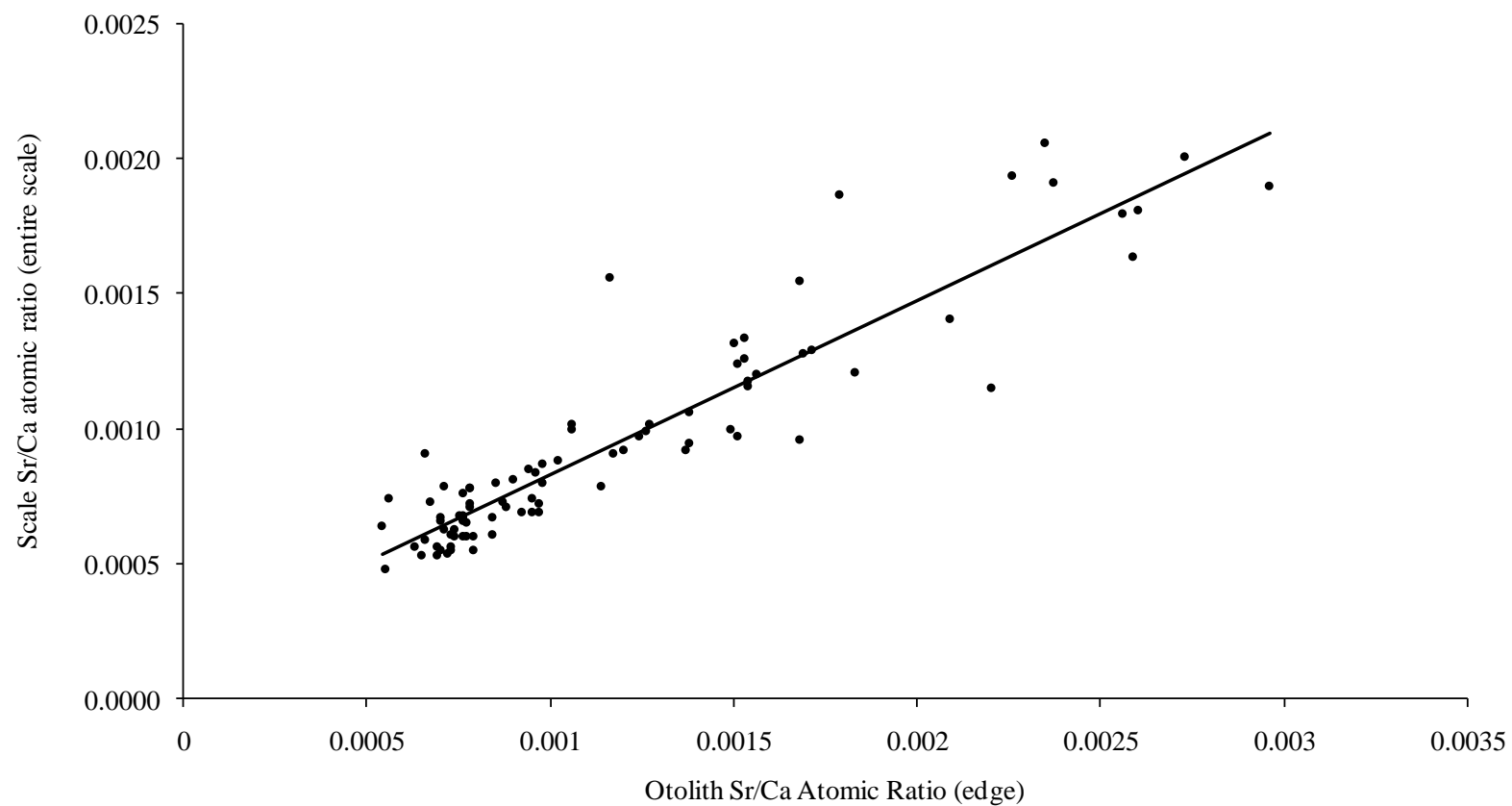
Figure 2.10. Comparison of average scale Sr/Ca with otolith edge Sr/Ca values for individuals classified as scale chemistry Types 2 and 3 (i.e., no Sr/Ca inflection point in their scale chemical profile).  (y=0.645x + 0.0002, $r^2$=0.855, *P* < .001).

## DISCUSSION

Scale checks and intermediate scale growth often have been used to identify individual anadromous salmon that have resided in estuaries and to calculate their growth and estuarine residency (Rich 1920, Reimers 1973, Schluchter and Lichatowich 1977, Burke 2005, Bottom et al. 2005a). However, the classification of fish life histories from scale morphometrics has been criticized for its subjectivity (Beamish and MacFarlane 1983, Chilton and Bilton 1986, Hankin et al. 2005), raising questions about the validity of life history interpretations and the accuracy of these results. Our comparison of scale features and scale and otolith chemistry for Columbia River Chinook salmon reinforces the concern that scale patterns may not always provide an accurate method for interpreting the life history transitions of migrating fish. We found that scale chemistry, although less sensitive than otolith chemistry, could offer a viable alternative for some life history studies, particularly where lethal sampling of at-risk fish populations is not an option, or archival scale collections are available to reconstruct historical life histories. However, our results show that all chemical methods based on Sr detection (otoliths or scales) may have limitations as indicators of fish entry or residency in large estuaries with long expanses of tidal fresh water.

Previous studies have linked the presence of scale checks and intermediate scale growth to fish entry into brackish water (Rich 1920; Reimers 1973), and these features also occurred most frequently among the Chinook salmon we captured in the lower, saline portion of the Columbia River estuary. Nonetheless, we found no

consistent correspondence between these features and indicators of estuary entry from scale or otolith chemical analyses. Scale checks underestimated the proportion of estuary residents among Columbia River Chinook salmon. Otolith Sr/Ca ratios suggested that 37% of the fish with no evidence of a scale check had resided in the saline portion of the estuary for an extended period of time prior to capture. We conclude that these individuals either (1) entered the estuary at a small size when their scales were just forming (~35-42 mm), or (2) had recently entered the estuary (<30days) before new scale material could be deposited and calcified.

When considering the factors that contribute to scale-check formation under experimental conditions, such as moderate to severe temperature and ration change (Bilton 1975, Boyce 1985), it is likely that any condition that alters growth may produce scale checks in natural populations. For example, among some individuals in our study, the Sr inflection within the scale coincided directly with the scale check and may have reflected increased growth related to increased estuarine food availability or water temperature changes. In other cases, fish with distinct scale checks showed no chemical evidence of estuary entry either on their scale or otolith. Here again a variety of growth altering factors (e.g., prey availability, temperature, smolting, metabolic stress, etc.) could have caused scale checks to form as individuals traveled downriver toward the brackish estuary. Of all the samples classified as having some form of scale check (Types 1 and 2), less than 50% had evidence of an increase in Sr denoting a transition from a low Sr environment to a high Sr environment.

Our results do not rule out the possibility that scale checks and intermediate growth may have been reliable indicators of estuary entry by juvenile Chinook salmon before the Columbia River basin was heavily modified.  Furthermore, scale-pattern analysis still may be a viable technique for studying salmon populations in other ecosystems.  For example, in Sixes River, Oregon, comprehensive sampling throughout the basin and mark-recapture studies verified that scale characteristics and growth transitions during downstream migration were closely linked and that scale checks accurately depicted estuary entrance.  However, the Sixes River estuary is quite small and tidal influence is limited relative to the Columbia River estuary, where tidal fresh water extends more than 230 km upriver from the mouth.  Our findings suggest that scale morphometrics must be applied cautiously because the parameters that influence fish growth and scale formation are likely to vary in each ecosystem. The environmental factors or gradients contributing to growth transitions and scale features therefore must be validated for each population before individual life histories can be inferred from the circuli patterns on fish scales.

Scale chemistry was a good indicator of entry into the saline portion of the lower Columbia River.  The majority of specimens that had elevated Sr in their otoliths also showed elevated Sr in their scales.  We found that the type of Sr signal in scales (SC Types 1 and 2) was related to the size of the fish at entry and residency within the estuary.  High Sr levels were present in the scales of fish that had encountered salt water near the time of scale formation (35-42mm), even when the chemical transects showed no significant transition from a low to a high Sr level (the

difference between SC Types 1 and 2). Scale samples of fish with low salt-water residency (<30 days) showed Sr levels intermediate between SC Type 2 (>30 days) and SC Type 1 samples. We hypothesize that this intermediate signal could reflect the permeable nature of the scale and the lag time between the time of entry into a new high Sr environment and the time of deposition and calcification of new scale circuli.

The factors that affect Sr uptake and persistence in fish scales are not well known. We hypothesize that our ability to detect a transition from low to high Sr within the scale may depend on the time elapsed since the individual entered brackish water and on the age of the fish and size of its scales. If scale circuli are deposited sequentially in a three-dimensional space, then fine layers of calcified material may override preexisting circuli, and the previous chemical signal would be altered by the current chemical environment. In a study of brook trout, *Salvelinus fontinalis*, Courtemanche et al. (2006) concluded that the entire scale was contaminated with elevated Sr once a fish entered a high Sr environment. Consequently, they could distinguish anadromous from resident brook trout, but could not reconstruct finer details of juvenile life history. Our results confirmed that total Sr/Ca levels were elevated in the scales of fish that had entered saline waters, even in portions of the scale that we believe were formed during freshwater residence. However, on some samples these regions were still discernable from even higher levels of Sr found near the scale margin. We conclude that this higher Sr region represents scale material that was deposited during fish residency in the saline portion of the estuary (SC Type 1 Fig. 2.5).

Otolith samples were a good indicator of entrance into brackish and marine waters. Samples collected at our freshwater site showed no evidence of elevated Sr unlike the chemical pattern of the samples we collected at mixed marine and brackish water sites. These findings are consistent with laboratory (Kalish 1990, Fowler et al. 1995, Zimmerman and Neilson 2003) and field (Volk et al. 2010) experiments indicating an increase in otolith Sr with an increase in salinity. Overall, the otolith Sr/Ca values were greater than scale values, but the relationship between the two was strongly positive, a result consistent with other scale and otolith chemistry comparisons (Wells 2000a).

Although scale and otolith chemistry were strongly correlated and scale chemistry was an accurate indicator of salt-water entry, scale morphometric characteristics did not coincide consistently with the proportion of individuals entering brackish water or their time of entry. These results raise concerns about traditional scale morphometric methods for reconstructing salmon life histories and reinforce the need to validate interpretations based on scale features. Scale chemistry was strongly and positively related to otolith chemistry, and thereby provided an accurate indicator of estuary entrance. However, the process by which Sr is incorporated into the scale and the stability of that chemical signal over time is poorly understood. Further examination of the Sr signal on returning adult fish is needed to determine whether the signal is altered over time.

Considering the limitations of scale-pattern analysis and the uncertainties about scale chemistry, we conclude that otolith chemistry offers the most reliable indicator

of estuary entrance by juvenile salmon. Otolith chemistry is also the most precise and sensitive life history indicator because otolith increments are added with daily periodicity, unlike our scale chemistry results which support the hypothesis that there is a lag between environmental conditions and scale formation. However, the Sr signal only measures salmon entry into salt water. It does not account for the entire complex of ecosystem gradients—from tidal-fluvial zone to the nearshore-ocean—that more broadly defines the "estuary" (Day et al. 1989, Fairbridge 1980, McClusky and Elliott 2004). In small coastal rivers, where the transition from tidal fresh to marine water occurs over short distances, Sr is an ideal indicator of salmon entry into the estuary (Volk et al. 2010). However, in large river-dominated ecosystems like the Columbia River, where tidal influence extends far upriver but salinity does not, otolith Sr can provide only a minimum estimate of estuary residency.

## LITERATURE CITED

Bagenal, T.B., MacKereth, F.J.H., and Heron, J. 1973. The distinction between brown trout and sea trout by the strontium content of their scales. Journal of Fish Biology 5: 555–557.

Beamish, R. J., and G. A. MacFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112: 735–743.

Bilton, H.T., and G.L. Robins. 1971. Effects of starvation, feeding, and light period on circulus formation on scales of young sockeye salmon Oncorhynchus nerka. Journal of the Fisheries Research Board of Canada 18: 1749–1755

Bilton, H. T. 1975. Factors influencing the formation of scale characteristics. International North Pacific Fisheries Commission., Bulletin. 32.

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. United States Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-68.

Boyce, R. R. 1985. Effects of feeding level, temperature, and photoperiod on growth and selected scale characteristics of juvenile steelhead trout. Masters Thesis, Oregon State University, Corvallis.

Brenkman, S. J., S. C. Corbett, and E.C. Volk. 2006. Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. Transactions of the American Fisheries Society 136: 1-11.

Brown, R.J., and K.P. Severin. 2009. Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Canadian Journal of Fisheries and Aquatic Sciences 66: 1790-1808.

Burke, J. L. 2005. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to present. MS thesis, Oregon State University, Corvallis.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47: 2219–2227.

Campana, S.E., Thorrold, S.R., Jones, C.M., Gunther, D., Tubrett, M., Longerich, H., Jackson, S., Halden, N.M., Kalish, J.M., Piccoli, P., de Pontual, H., Troadec, H., Panfili, J., Secor, D.H., Severin, K.P., Sie, S.H., Thresher, R., Teesdale, W.J., and Campbell, J.L. 1997. Comparison of accuracy, precision, and sensitivity in elemental assays of fish otoliths using the electron microprobe, proton-induced X-ray emission, and laser ablation inductively coupled plasma mass spectrometry. Canadian Journal of Fisheries and Aquatic Sciences 54: 2068–2079.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263–297.

Campana, S.E. and J.D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42: 1014-1032.

Carlander, K. D. 1987. A history of scale age and growth studies of North American freshwater fish. Pages 3-14 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Casselman, J.M. 1983 Age and growth assessment of fish from their calcified structures - techniques and tools. - U. S Department of Commerce, NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 8:1–17.

Chilton, D. E., and H. T. Bilton. 1986. New method for ageing Chinook salmon (Oncorhynchus tshawytscha) using dorsal fin rays, and evidence of its validity. Canadian Journal of Fisheries and Aquatic Sciences 43:1588–1594.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 134: 291- 304.

Courtemanche, D.A., F.G. Jr. Whoriskey, V. Bujold, and R.A. Curry. 2005. A nonlethal approach using strontium in scales to distinguish periods of marine and freshwater residency of anadromous species. Canadian Journal of Fisheries and Aquatic Sciences 62: 2443–2449.

Courtemanche, D.A., F.G. Jr. Whoriskey, V. Bujold, and R.A. Curry. 2006. Assessing anadromy of brook char (*Salvelinus fontinalis*) using scale microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 63:995-1006.

Coutant C.C., and C.H. Chen. 1993. Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. Canadian Journal of Fisheries and Aquatic Sciences 50:1318-1323

Dahl, K. 1911. The age and growth of salmon and trout in Norway, as shown by their scales. The Salmon and Trout Association, London.

Day, J. W. J., C. A. S. Hall, W. M. Kemp, and A. Yáñez-Arancibia. 1989. Estuarine ecology. Wiley, New York.

Fairbridge, R. W. 1980. The estuary: its definition and geochemical role. . Pages 1-35 in E. Olausson, and I. Cato, editors. Chemistry and geochemistry of estuaries. Wiley, New York.

Fowler, A.J., S.E. Campana, C.M. Jones, and S.R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Canadian Journal of Fisheries and Aquatic Sciences 52:1431-1441.

Gilbert, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus Oncorhynchus. U.S. Bureau of Fisheries Bulletin 32:1-22.

Hankin, D. G., J. H. Clark, R. B. Deriso, J. C. Garza, G. S. Morishima, B. E. Riddell, C. Schwarz, and J. B. Scott. 2005. Report of the expert panel on the future of the coded wire tag program for Pacific salmon. Pacific Salmon Commission, Technical Report 18, Vancouver.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fishery Bulletin. U.S. 88: 657–666.

Kennedy, B P., A. Klaue, J. D. Blum, C. L. Folt,  K. H. Nislow., 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences 59: 925-929.

Koo, T.S.Y. 1962. Age designation in salmon. Pages 41 – 48 *in* T.S.Y. Koo, editor. Studies of Alaska Red Salmon. Universtiy of Washington Press, Seattle.

Lagler, K.F., J.E. Bardach, and R.R. Miller. 1962. Ichthyology. John Wiley and Sons, Inc. New York.

McLusky, D. S., and M. Elliott. 2004. The estuarine ecosystem: ecology, threats, and management, 3rd edition. Oxford University Press, Oxford.

Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in the Sixes River, Oregon. Research Reports of the Fish Commission. 4(2): 1-42.

Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers. Bulletin of the United States Fish Commission 37 (DOC 887): 1-73.

Schluchter, M. D. and J.A Lichatowich. 1977. Juvenile life histories of spring Chinook salmon *Oncorhynchus tshawytscha,* as determined by scale analysis. Oregon Department of Fish and Wildlife Information Report 77-5.

Shapovalov, L., and A.C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorynchus kisutch*) with special reference to Waddell Creek. California, and recommendations regarding their management. California Department of Fish and Game Bulletin 98: 375 p.

Secor, D.H., A. Henderson-Arzapalo, and P.M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology 192:15–33.

Thorrold, S. R., C. M. Jones, and S. E. Campana. 1997. Response of otolith microchemistry to environmental variations experienced by larval and juvenile Atlantic croaker (*Micropogonias undulatus*). Limnology and Oceanography 42:102– 11.

Volk, E.C, A. Blakley, S.L. Schroder and S.M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and fresh waters. Fisheries Research 46: 251-266.

Volk, E.C., D. L. Bottom, K.K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary (Oregon) using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139: 535-549.

Wallin, O. 1957. On the growth structure and development of the scales of fish. Institute of Freshwater Research 38: 385-447.

Wells, B. K., G. E. Bath, S. R. Thorrold, and C. M. Jones. 2000a. Incorporation of strontium, cadmium, and barium in juvenile spot, *Leistomus xanthurus*, reflects water chemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2122–2129.

Wells, B. K., S. R. Thorrold, and C. M. Jones. 2000b. Geographic variation in trace element composition of juvenile weakfish scales. Transactions of the American Fisheries Society 129: 889–900.

Wells, B. K., and B. E. Rieman, J. L. Clayton, D. L. Horan, C. M. Jones. 2003. Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: The potential application of hard-part chemistry to describe movements in freshwater. Transactions of the American Fisheries Society 132: 409–424.

Zimmerman, C. E., and G. H. Reeves. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 135: 457-475. 131:986-993.

Zimmerman, C. E., and R. L. Nielsen. 2003. Effect of analytical conditions on the measurement of strontium to calcium (Sr/Ca) ratios in otoliths of anadromous salmonids using wavelength dispersive electron microprobe analysis. Fishery Bulletin 101: 712-718.

Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62: 88-97.

# CHAPTER THREE:

Life history variation and growth of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary

Lance A. Campbell[1, 2*], Daniel L. Bottom[3], Eric C. Volk[2,4], and Ian A. Fleming[1,5]

[1] Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Corvallis, OR 97331

[2] current address: Washington Department of Fish and Wildlife, Science Division, Olympia, WA 98501

[3] NOAA Fisheries, Northwest Fisheries Science Center, Newport, OR  97365

[4] current address: Alaska Department of Fish and Game, Commercial Fisheries Division, Anchorage AK 99518

[5] current address: Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7 Canada

*corresponding author: campblac@dfw.wa.gov

**INTRODUCTION**

Estuaries provide the link between the upriver spawning and rearing habitats of Pacific salmon and their feeding grounds in the ocean. Despite evidence that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) utilize estuaries for growth and salinity acclimation (Rich 1920, Reimers 1973, Schluchter and Lichatowich 1977, Simenstad et al. 1982, Bottom et al. 2005a, Volk et al. 2010), the Columbia River estuary often has been viewed as a hazardous environment (Schreck et al. 2006, McComas et al. 2007) that creates a significant bottleneck for salmon survival and recovery (Kareiva et al. 2000, Welch et al. 2008). In contrast to most other estuaries where juvenile Chinook salmon reside for weeks or months before migrating to sea (Reimers 1973, Healey 1980, Myers and Horton et al. 1982, Simenstad et al. 1982, Nicholas and Hankin 1988, Healey 1991, Magnusson and Hilborn 2003, Bottom et al. 2005b, Hering et al. 2010, Volk et al 2010), recent tagging studies in the Columbia River have documented rapid estuarine migration rates, raising questions about the role of the estuary as a salmon rearing habitat. One recent study, for example, estimated migration times for tagged yearling and subyearling Chinook salmon through the Columbia River estuary—a distance of more than 230 km from Bonneville Dam to the river mouth—at only 2.9 d and 4.1 d, respectively (McComas et al. 2007).

The Columbia River was once the world's largest producer of Chinook salmon (estimated between 8-10 million returning fish annually) although contemporary runs now account for only a fraction of the historical abundance (Lichatowich 1999). Thirteen stocks of Columbia River salmon have been added to the federal list of

threatened or endangered species (http://www.nwr.noaa.gov/ESA-Salmon-Listings).

Recent analyses have concluded that improved estuary and early ocean survival could

substantially benefit salmon recovery (Kareiva et al. 2000, Welch et al. 2008). These

findings and widespread habitat loss in the estuary (Sherwood et al. 1990, Bottom et

al. 2005a) have generated considerable interest in habitat restoration despite continued

uncertainty about the estuary's role in salmon life history: Is the estuary a hazardous

corridor through which fish must migrate as rapidly as possible to avoid predators? Or

do young salmon depend on the estuary to rear and grow for extended periods before

entering the ocean?

The lower Columbia River and estuary was the site of one of the first Pacific

salmon life history studies. During a series of expeditions to the lower river and

estuary in 1914-16, Rich (1920) monitored the relative abundance of juvenile Chinook

salmon and reconstructed the freshwater and estuarine rearing histories of individuals

by analyzing the circuli patterns on their scales. However, few other salmon surveys

were conducted in the Columbia River estuary again until the 1960's, after numerous

main-stem dams had been constructed and hatchery programs were releasing

approximately 100 million Chinook salmon to mitigate for lost habitat and fish

production (Dawley et al. 1986, Bottom et al. 2005a). From 1966 to 1983 several

studies examined the diel migration patterns, size and time of estuary entrance, and

survival of marked groups of hatchery fish entering and migrating through the estuary

(McCabe et al. 1986, Dawley et al. 1986, Ledgerwood et al. 1991). More recent

tagging experiments have examined salmon mortality and residency through the lower

river and estuary by implanting individuals with Passive Integrated Transponder (PIT)

(Schreck et al. 2006) or acoustic (McComas et al. 2007) tags. Most of these studies

have targeted large juveniles, often produced in hatcheries, that are of sufficient size to

accept large PIT tags (i.e., fish $> \sim 60$ mm) or acoustic tags (i.e., fish $> \sim 90$ mm)

However, because estuary residency and habitat use has been linked to fish size

(Healey 1982, Healey 1991, Levy and Northcote 1982), it is unclear whether the

tagging results can be applied to other size classes of unmarked fish.

A recent analysis compared survey results in the 1960s and 1980s with the

historical surveys of Rich (1920) and concluded that juvenile Chinook salmon on

average were smaller and more variable in length during the early decades of the

twentieth century (Burke 2005, Bottom et al. 2005a). These investigators

hypothesized that estuarine habitat losses, intensive hatchery production, and other

changes upriver had simplified salmon life histories. However, this interpretation

remains speculative because the historical and contemporary fish surveys employed

different sampling methods, and again, present-day residency studies may depict

primarily the behaviors of relatively large reared juveniles.

Fish otoliths provide an independent method to reconstruct juvenile salmon life

histories, including those of small fry and fingerling size classes that are unaccounted

for in most tagging studies (Volk et al. 2000, Zimmerman and Reeves 2002, Volk et

al. 2010). Otoliths produce daily calcified material (Pannella 1971) that reflects the

ambient water chemistry (Fowler et al. 1995, Zimmerman 2005, Brown and Severin

2009, Volk et al. 2010) and retains a stable chemical signal after the calcified material

is deposited (Campana and Neilson 1985, Campana 1999).  Specifically otolith

microchemistry can distinguish between periods of growth in marine/brackish and

freshwater environments because concentrations of the element strontium (Sr) are high

in marine water but generally low in freshwater.  Thus, chemical profiles across

diadromous fish otoliths are characterized by low strontium/calcium (Sr/Ca) ratios for

periods of freshwater rearing and increased Sr/Ca ratios during periods of residency in

brackish and marine waters residency (Kalish 1990, Zimmerman 2005, Brenkman et

al. 2006, Volk et al. 2010, Chapter 2).

In 2002, the National Marine Fisheries Service initiated a series of monthly

surveys to determine salmon distribution, habitat use, and life history in the lower

Columbia River estuary.  Here we use otolith microchemistry to reconstruct the life

history patterns of subyearling Chinook salmon collected from selected estuary survey

sites in 2003-05.  The objectives of this study are to: (1) quantify the proportion of

juvenile migrants that reside in the estuary; (2) estimate their mean estuary residence

times, size and time of estuary entry, and growth; and (3) compare these and other

contemporary results with the historical survey data (Rich 1920) to re-examine the

hypothesis that salmon life history diversity in the estuary has declined during the last

century.

**METHODS**.

*Study Area*

The Columbia River drains 660,000 km$^2$ and runs approximately 1,932 river km (Rkm) through portions of seven states (Montana, Wyoming, Idaho, Nevada, Utah, Washington and Oregon) and one Canadian province (British Columbia) en route to the Pacific Ocean. River flows in the basin are highly regulated by a series of 23 hydropower and flood control dams on the main-stem Columbia and Snake Rivers, and more than 300 smaller dams distributed on tributaries throughout the U.S. portion of the basin (Bottom et al. 2005a). Tidal influence of the Columbia River estuary extends ~233 km from the river mouth to the lowermost mainstem dam (Bonneville Dam), maximum salt-water intrusion is limited to approximately Rkm 55, where salt-water intrusion is limited to the deepest portions of the ship channel (Fig. 3.1).
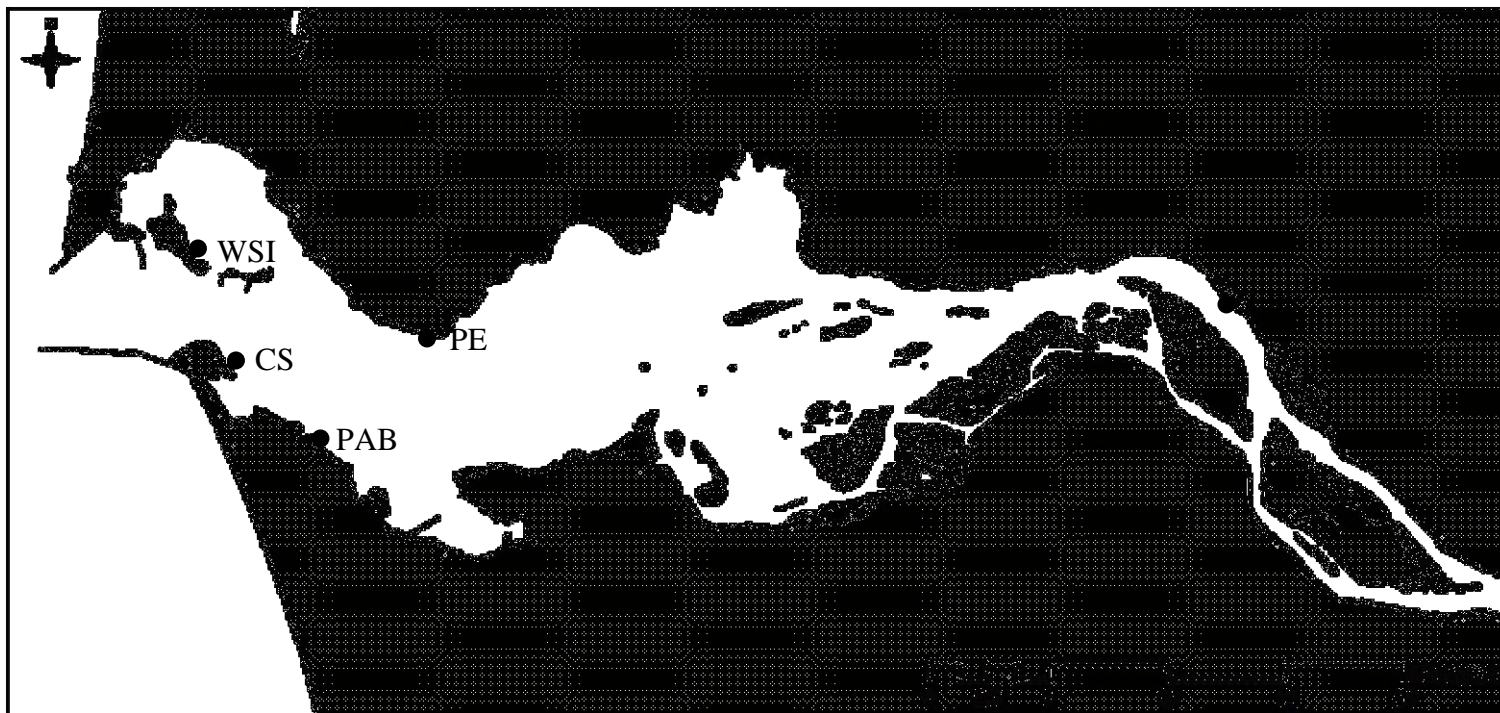
Figure 3.1. Map of the Lower Columbia Estuary. Lower Elochoman Slough (LES) a fully freshwater site. Point Adams Boat Launch (PAB), and three other lower estuary sites are within the zone of salinity intrusion: Point Ellice (PE), Clatsop Spit (CS), and West Sand Island (WSI). Courtesy of Jen Burke, University of Washington.

Four species of semelparous Pacific salmon: Chinook, sockeye (*O. nerka),* chum (*O. keta*) and coho salmon (*O. kisutch*) are native to the Columbia River. The total annual run of these species prior to European settlement has been estimated at 10 to 16 million fish (Northwest Power Planning Council 1986). Present-day returns of salmon to the Columbia River average approximately one million fish each year, of which 80% or more are produced in hatcheries (National Research Council 1996, Williams 2006).

### *Sample collection*

Samples for this study were collected as part of an ongoing NOAA Fisheries research project that was initiated in 2002 to understand the role of estuarine habitat for juvenile Chinook salmon and to characterize life history variation among juveniles entering and leaving the lower estuary. The NOAA survey collected fish samples monthly at four saline sites and one tidal freshwater site (Fig. 3.1). Tidal freshwater habitat in this study is defined as the region of the river and associated habitat that is influenced by tidal fluctuations but not by salt water. Most otolith samples from the saline portion of the estuary were collected at Point Adams Boat Launch (PAB), but during periods of low salmon catch, these were occasionally augmented with samples from other lower estuary sites (Fig. 3.1). Fish were sampled at each site near low slack tide with a 50-meter beach seine (1.27 cm mesh in the wings and .95 cm mesh in the bunt). Ten samples of as many as three Chinook salmon size classes (35-60 mm, 60-100 mm, >100 mm) were retained during each sample date, killed with an

overdose of Tricaine methanesulfonate, and placed on ice until their return to the

laboratory, where they were stored frozen until necropsy.

*Sample analysis:* All otolith chemistry analyses were conducted at the Keck

Collaboratory for Plasma Mass Spectrometry at Oregon State University. The

analysis system consisted of New Wave™ DUV 193 nm ArF laser coupled with a

Thermal Elemental PQ Excell ™ quadropole inductively coupled plasma mass

spectrometer (ICP-MS). Helium was used as the carrier gas to transport the ablated

material from the laser to the mass spectrometer. Operating conditions for the LA-

ICP-MS are described in Table 3.1.

Table 3.1 Operating conditions for LA-ICP-MS.

| **General operating conditions** | |
| --- | --- |
| Cooling gas (L/min) | 13.00 |
| Auxiliary gas (L/min) | 0.95 |
| He carrier gas (L/min) | 0.75 |
| | |
| Detector mode | Pulse counting and analog |
| Sweep mode | Peak hopping |
| Dwell time (ms) | 10 |
| Points per peak | 1 |
| Analysis interval (sec) | 360 |
| | |
| Laser ablation diameter (microns) | 30 |
| scanning speed (microns/sec) | 5 |
| Pulse rate (Hz) | 8 |

Sagittal otoliths were prepared for chemical and daily growth increment analysis by thin sectioning in the sagittal plane. Petrographic slides were heated on a hot plate at approximately 275 $^{o}$C, with Crystal Bond 509® added as a bonding medium for the otolith. Otoliths were mounted sulcus (medial) side up and ground on a Buehler Ecomet 3® grinder with 1200 grit silicon carbide paper until the primordium was nearly exposed without sacrificing otolith edge integrity. A fine polish was applied using 1 μm alumina slurry. The otolith half section was then warmed to melt the Crystal Bond and turned distal side up. We repeated grinding until the primordium was exposed or until there was risk of obliterating the Daily Growth Increments (DGI) in the dorsal posterior region. Again, a fine polish was added using 1 μm alumina paste. Otolith thin sections were rinsed in deionized water and air dried (methodology modified from Volk et al. 2000, Zimmerman and Reeves 2002).

A fish otolith forms concentric layers of calcium carbonate each day, providing a chemical and temporal record of a fish's life. Chemical and microstructural analyses of the sectioned otoliths were usually completed 20 degrees off the midline in the dorsal posterior quadrant. Laser paths were selected from the most posterior primordium to the otolith edge. We deviated from the preferred transect on samples with severe pitting or cracking. Each otolith analysis was coupled with a transect along a polished National Institute of Standards and Technology glass standard (NIST 610). Atomic ratios of Sr/Ca were calculated by the equation:

$$= \left(\frac{Sr}{Ca}\right) otolith\ sample \left( \left( \frac{1}{\frac{Sr}{Ca} NIST\ sample} \right) \left( \frac{\frac{Sr\ ppm}{Ca\ ppm} NIST}{\frac{Sr\ atomic\ weight}{Ca\ atomic\ weight}} \right) \right)$$

Raw counts of Sr and Ca were plotted, and points of interest (POI) were recorded for transect start and end points, and the point of Sr inflection. Strontium inflection was determined visually and defined as the region immediately prior to a rapid increase in Sr. Rapid increases in Sr were assumed to correspond to contact with salinity because we found no such rapid elevations in Sr in our samples from freshwater sites (see Chapter 2). This pattern is consistent with results from published laboratory (Zimmerman 2005) and field experiments (Volk et al. 2010) examining otolith and water chemistry. Points of interest on the chemical output were related to the location on the otolith by the equation (similar to Brenkman et al. 2006, Volk et al. 2010):

$$otolith_{POI}\ (\mu m) = \left( \frac{laser_{POI}\ (ms) - laser_{start}\ (ms)}{1000} \right) * 5\ \mu m/sec$$

For its simplicity and accuracy, we used Campana's (1990) proportional Biological Intercept (BI) method to back calculate the fish size at a given otolith size based on the formula:

$$L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$

where $L_c$ and $O_c$ are the size of the fish and otolith at the time of capture; $L_o$ and $O_o$ are the biological intercept for fish length and otolith size, respectively (fig 3.2); and $L_a$ and $O_a$ are the size of the fish and the otolith at a particular point of interest, such as Sr inflection. All subsequent references to estuary entry or estuary residence time herein apply to the saline portion of the estuary, as calculated from the Sr inflection point. These chemical measurements do not account for fish entry or residency in the tidal freshwater reaches of the Columbia River estuary (Chapter 2).

Otolith daily growth increments were measured and counted from the otolith edge parallel to the LA-ICPMS chemical transect using light microscopy and were enumerated as far towards the core as possible. Increments were initially annotated from Image-Pro 6.0® software using a peak/valley luminescence algorithm and then adjusted by eye to remove or add obvious increments. In cases where DGI were not discernable due to otolith preparation or clarity, an average increment width of 2.58 μm (mean increment width of all measurable otoliths in 2003) was used to estimate residence times.
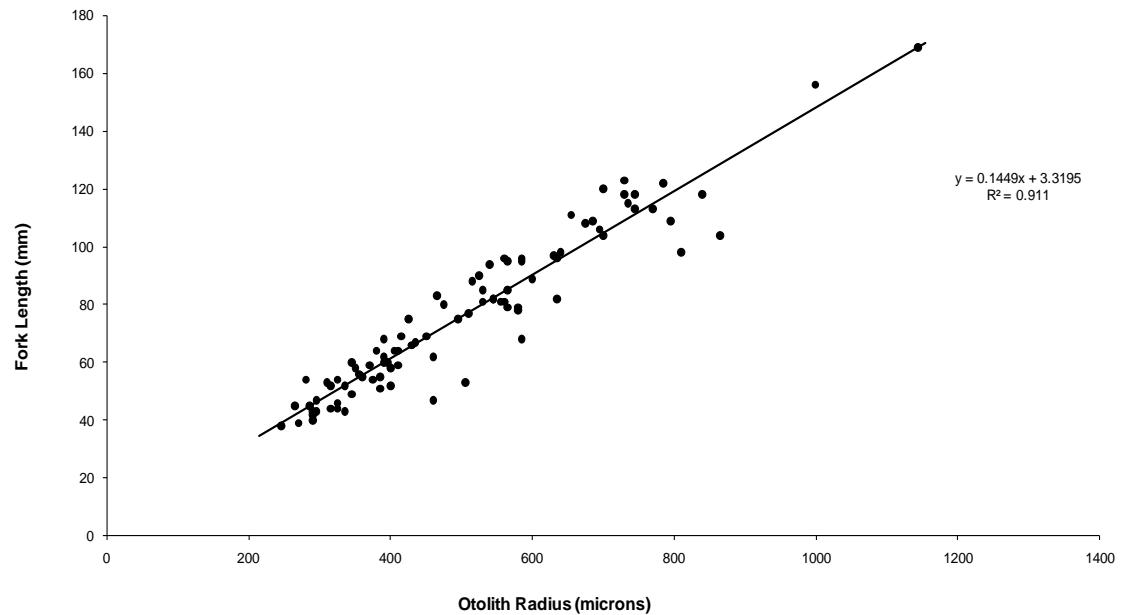
Figure 3.2. Fish size-otolith size relationship for juvenile Chinook salmon within the Columbia River estuary. Otolith size was measured as a radius along the sagittal plane from the most anterior primordia to the dorsal/posterior edge approximately 20º off the midline.

We estimated the average size of hatchery Chinook salmon at release from a fish per pound measure for 52 hatcheries within the Columbia River Basin, 2003-2005 (http://www.fpc.org/hatchery/Hatchery_Queries.html).  For these estimates, we converted the number of fish per pound at the time of hatchery release to a mean fork length based on a length: weight relationship for fish captured in the beach seine:

$$\ln(y) = .3086x + 5.7467$$

Where fork length in mm was substituted for $y$ and weight in grams was substituted for $x$ ($P < .001$, n=6520, r²=.979).

**RESULTS**

*Abundance and size at capture in the estuary*

The size distribution of juvenile Chinook salmon sampled at four lower estuary beach seining sites increased gradually throughout the year for all years of sampling. Small fish (< 60 mm) dominated the collection before April each year. Annual trends in mean size at capture increased during late winter and early spring, leveled off in late spring and early summer, and increased again in late summer and fall (Fig. 3.3). Fry (< 60 mm) were most prevalent early in the year, but still were present as late as June in 2004 and 2005.
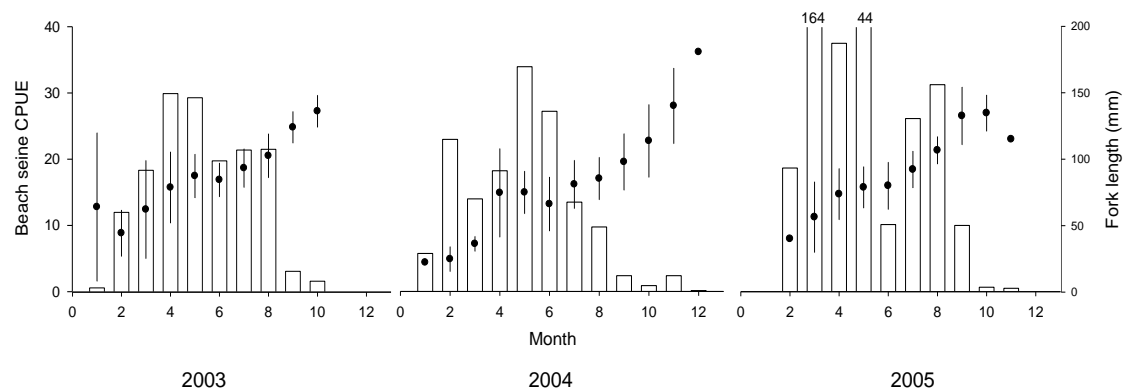


Figure 3.3. Catch per unit of effort (bars) and mean fork length (black circles $\pm$ 1 SD) for juvenile Chinook salmon sampled in the lower estuary from 2003 through 2005.

*Estuarine residency*

We analyzed approximately 100 otolith samples per year from PAB and surrounding brackish water sites, and approximately 50 per year from the fresh-water site at LES (Table 3.2). The percentage of samples with an obvious inflection and elevated Sr levels, indicating contact with salt water, varied at PAB and was generally lower during months of peak migration (Fig. 3.3, Table 3.2). Samples collected at LES generally showed no evidence of elevated Sr. However, a few samples indicated that individuals had entered a high Sr environment previously, but had recently moved back into a low Sr environment. Quantifying this type of migration is not suited to our methodology because: (1) the body burden of Sr in an individual fish slowly dissipates with time, and (2) the speed of the laser and clearing of material through the mass spectrometer likely bias Sr values measured at the otolith edge.

Table 3.2. Otoliths examined at Point Adams Boat Launch (PAB) and Lower Elochoman Slough (LES) for elevated Sr indicative of entrance into the saline portion of the estuary. * In 2003 and 2005, samples from other lower estuary sites were included with those of PAB.

| | | 2003 | | | | 2004 | | | | 2005 | | | |
| | | PAB * | | LES | | PAB | | LES | | PAB * | | LES | |
| Month | | N | % with Sr signal | N | % with Sr signal | N | % with Sr signal | N | % with Sr signal | N | % with Sr signal | N | % with Sr signal |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| January | **5** | | | | | 4 | 0 | | | | | 1 | 0 |
| February | **23** | | | | | 9 | 44 | | | 8 | 100 | 6 | 0 |
| March | **22** | | | | | | | | | 17 | 94 | 5 | 0 |
| April | **52** | 6 | 100 | | | 11 | 100 | 9 | 0 | 20 | 75 | 6 | 0 |
| May | **90** | 31 | 77 | 8 | 0 | 16 | 31 | 10 | 0 | 20 | 70 | 5 | 0 |
| June | **35** | 10 | 60 | | | 10 | 90 | 10 | 0 | | | 5 | 0 |
| July | **73** | 29 | 62 | 12 | 0 | 3 | 100 | 10 | 0 | 14 | 79 | 5 | 0 |
| August | **40** | 3 | 100 | 1 | 0 | 11 | 73 | 4 | 0 | 16 | 88 | 5 | 0 |
| September | **30** | 9 | 89 | | | 9 | 89 | 8 | 0 | 4 | 100 | | |
| October | **22** | 6 | 100 | 9 | 0 | 6 | 100 | 1 | 0 | | | | |
| November | **19** | | | | | 14 | 86 | 5 | 0 | | | | |
| December | **0** | | | | | | | | | | | | |
| N | 411 | 94 | | 30 | | 93 | | 57 | | 99 | | 38 | |

Most otoliths of juvenile Chinook salmon collected at PAB or at nearby lower estuary sites showed evidence of a rapid increase in Sr, indicating contact with salinity 72%, 68%, and 86% for 2003, 2004, and 2005, respectively. The estimated residency of all juvenile Chinook salmon collected in the lower estuary ranged from 0- 176 days. Residence duration (count data) was normalized by a square root transformation, and a one-way analysis of variance (ANOVA) indicated a significant difference between years ($F_{2,215}$ = 22.6, P < .001). Generally residence times were greater in 2004 (mean $\pm$ SD = 67.3 $\pm$ 43.5 days) than in 2003 (53.6 $\pm$ 41.0 days; P = .021) or 2005 (29.7 $\pm$ 23.7 days; P < .001, Holm-Sidak multiple comparison test). Residence times in 2003 were greater than those in 2005 (P < .001). Juvenile Chinook salmon with more than 30 days of estuary residency comprised 55, 51, and 30 % of the samples collected in 2003, 2004, and 2005, respectively.

### *Size at estuary entrance*

For all Chinook salmon sampled for otolith microchemistry from 2003-2005, the sizes at estuary entrance ranged from 34 – 178 mm. A one-way ANOVA found a significant difference between years ($F_{2,289}$ = 6.15, P = .002). A Holm-Sidak multiple comparison test found a significant difference between the size of individuals at estuary entry in 2003 (mean $\pm$ SD = 79.6 $\pm$ 23.1 mm) and 2004 (71.0 $\pm$ 26.5 mm; P = .025) and in 2003 and 2005 (66.7 $\pm$ 29.6 mm; P < .001), but not between 2004 and 2005 (P > .05).

We estimated that nearly half of all the samples collected in 2004 and 2005 were composed of individuals that had entered the estuary at sizes < 60 mm (Table 3.3). This total includes fry that had recently entered the estuary (and therefore showed no Sr signal), as well as earlier migrants with back-calculated sizes at entry < 60 mm. Larger fish in the 61-90 mm and > 90 mm size ranges made up a smaller, but significant proportion of all individuals that entered the estuary in 2004 and 2005 (Table 3.3). A larger proportion of 61-90 mm fish was estimated in the 2003 sample collection relative to the other years. However, because the 2003 otolith samples were chosen to represent individuals with and, without scale checks as part of a scale chemistry study (see Chapter 2), the 2003 results are likely biased for larger fish. Scale formation does not occur until fish are at least ~38-42 mm, and in 2003, all individuals chosen for scale and otolith microchemistry comparisons were $\geq$ 50 mm.

Table 3.3. Proportion of juvenile Chinook salmon by size class entering the Columbia River estuary each year.  Size at entry in 2003 could be biased toward larger individuals because otolith samples were chosen for a scale chemistry study that targeted fish $\geq$ 50 mm.

| Size at Estuary Entrance | 2003* (n = 101) | 2004 (n = 93) | 2005 (n = 98) |
|---|---|---|---|
| < 60 mm | 0.17 | 0.41 | 0.53 |
| 61 - 90 mm | 0.64 | 0.37 | 0.23 |
| > 91 mm | 0.19 | 0.23 | 0.23 |

Approximately 32 and 45% of the Chinook salmon collected in the beach seine in 2004 and 2005, respectively, entered the saline portion of the estuary at sizes < 45

mm (i.e. 0-3 weeks post emergence). Despite the sampling bias in 2003, we still estimated that 13% of the individuals in the sample had entered at sizes < 45 mm. Fry with unabsorbed yolk were present occasionally, indicating that some individuals moved into the estuary immediately after emergence. Pooling all sampling years and estimating back-calculated size and season of estuary entrance indicated that progressively larger fish entered and resided in the estuary during the rearing season. Small migrants (< 60 mm) that dominated early in the year were primarily comprised of newly emerged fry, indicating that these small individuals survive and contribute to larger sizes classes (Table 3.4).

Table 3.4. Estimated mean residency in days (± 1 SD) of juvenile Chinook salmon for all years combined (2003-2005) by estimated size and season at first entry into the estuary (N=218). Bold indicates the dominate size class by season. The < 45 mm size class is a sub-group of the < 60 mm.

| | Jan-April | | | May-Aug | | | Sept-Dec | | |
|---|---|---|---|---|---|---|---|---|---|
| | Residency (days) | N | % | Residency (days) | N | % | Residency (days) | N | % |
| < 45 mm | 52 (36.2) | 60 | 21 | 79 (39.1) | 7 | 2 | | | 0 |
| < 60 mm | **54 (34.7)** | **75** | **26** | 59 (44.6) | 14 | 5 | | | 0 |
| 61-90 mm | 50 (35.5) | 28 | 10 | **46 (45.8)** | **56** | **19** | 33 (n/a) | 1 | 0 |
| > 90 mm | 31 (13.6) | 11 | 4 | 45 (44.2) | 34 | 12 | **20 (16.1)** | **4** | **1** |

### *Time of estuary entrance*

From counts/measurements of daily growth increments we back-calculated the time of estuary entrance based on the location of the Sr inflection point on otolith chemical transects. We also used the date of capture as the time of estuary entrance for samples that showed no Sr signal. Together we used all samples collected to test

the mean date of estuary entrance by year.  A difference was detected amongst the three years of sampling (one-way ANOVA ($F_{2,291}$ = 3.41, P = .035), but was only significant between 2003 (mean $\pm$ SD = 5/22/2003 $\pm$ 58.1 days ) and 2005 (5/1/2003 $\pm$ 70.7 days; P > .05).  No significant difference was found between 2003 and 2004 (5/16/2003 $\pm$ 74.4 days; P > .05) or between 2004 and 2005(P > .05).

### *Effects of size and time of entry on estuarine residency*

To examine whether early migrating fish reside in the estuary longer then late migrants, we categorized fish by season of estuary entry: January-April, May-August, and September-December.  A one-way ANOVA indicated a significant difference in estimated residency among fish entering the estuary during each of the three seasonal periods in 2003 ($F_{2,68}$ = 3.78, P = .028) and 2005 ($F_{1,78}$ = 15.01, P < .001), but not in 2004 ($F_{2,64}$ = 1.75, P > .05).  Early migrating fish (Jan-April) in 2003 spent more time in the estuary (mean $\pm$ SD = 58.8 days $\pm$ 6.1 days) than fish migrating in May-August (36.0 days $\pm$ 7.7 days; P = .009).  The residence duration for early migrants in 2005 (32.6 days $\pm$ 4.2 days) was greater than that of May-August migrants (17.6 days $\pm$ 2.5 days; P < .001).  No significant differences were found in residency between any season and fish entering after September 1 (P > .05; Fig. 3.4), likely a result of the low number of fish captured after September 1.
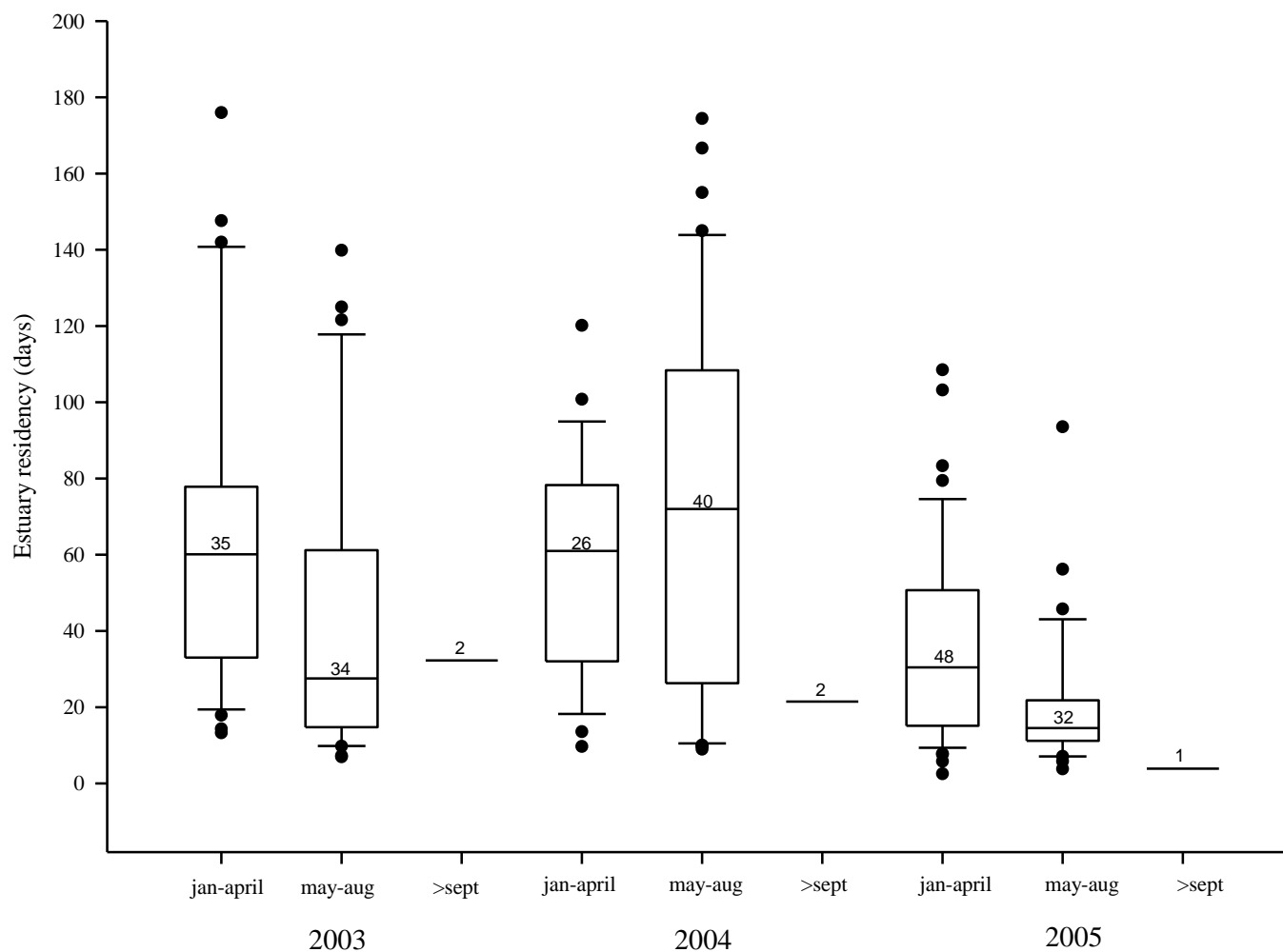
Figure 3.4. Box and whisker plot for residency of juvenile Chinook salmon within the saline portion of the Columbia River estuary by time period of entry and year. The box represents the 25th and the 75th percentile and whiskers represent the 10th and 90th percentile, sample size included above the median.  Dots indicate outliers.

The size of juvenile Chinook salmon as they entered the estuary explained 20% of the variation in estuary residence time in 2003 (P < .001) and 18% in 2005 (P < .001), but was not statistically significant in 2004.  However, a significant negative relationship between size and residency was apparent for spring and summer months (May – August, in all years) when a wide range of size classes and estuary residence times were represented in the estuary population (Table 3.5, Fig. 3.5).   During May-August, the fork length at estuary entrance explained 46% of the variation in residency in 2003 (P < .001), 47% in 2004 (P < .001), and 35% in 2005 (P < .001).  There were, however, no significant relationships between size at estuary entrance and residency during January-April and during September-December (P > .05), except in 2003 (P < .001, $y = -1.4879x + 152.18$; Table 3.5).

Table 3.5. The negative relationship between Chinook salmon size at capture and residency time within the Columbia River estuary for three time periods from 2003 through 2005.

| Year | Time of capture | N | Mean fork length (mm) | SD | Mean residency (days) | SD | $R^2$ | P-value |
|------|-----------------|---|-----------------------|-----|-----------------------|-----|-------|---------|
|      | Jan-April | 6 | 106.0 | 35.7 | 35.5 | 11.3 | 0.20 | 0.37 |
| 2003 | May-Aug | 51 | 87.6 | 14.3 | 49.0 | 38.8 | 0.46 | <.001 |
|      | Sept-Dec | 14 | 128.4 | 12.3 | 78.3 | 48.3 | 0.68 | <.001 |
|      | Jan-April | 15 | 68.5 | 18.5 | 51.5 | 26.1 | 0.02 | 0.61 |
| 2004 | May-Aug | 25 | 80.5 | 15.8 | 47.2 | 32.6 | 0.47 | <.001 |
|      | Sept-Dec | 26 | 129.0 | 30.5 | 97.9 | 44.7 | 0.02 | 0.51 |
|      | Jan-April | 39 | 59.3 | 26.4 | 32.5 | 22.9 | 0.09 | 0.07 |
| 2005 | May-Aug | 38 | 90.6 | 20.2 | 25.4 | 22.5 | 0.35 | <.001 |
|      | Sept-Dec | 4 | 118.0 | 15.0 | 43.7 | 39.7 | 0.62 | 0.21 |
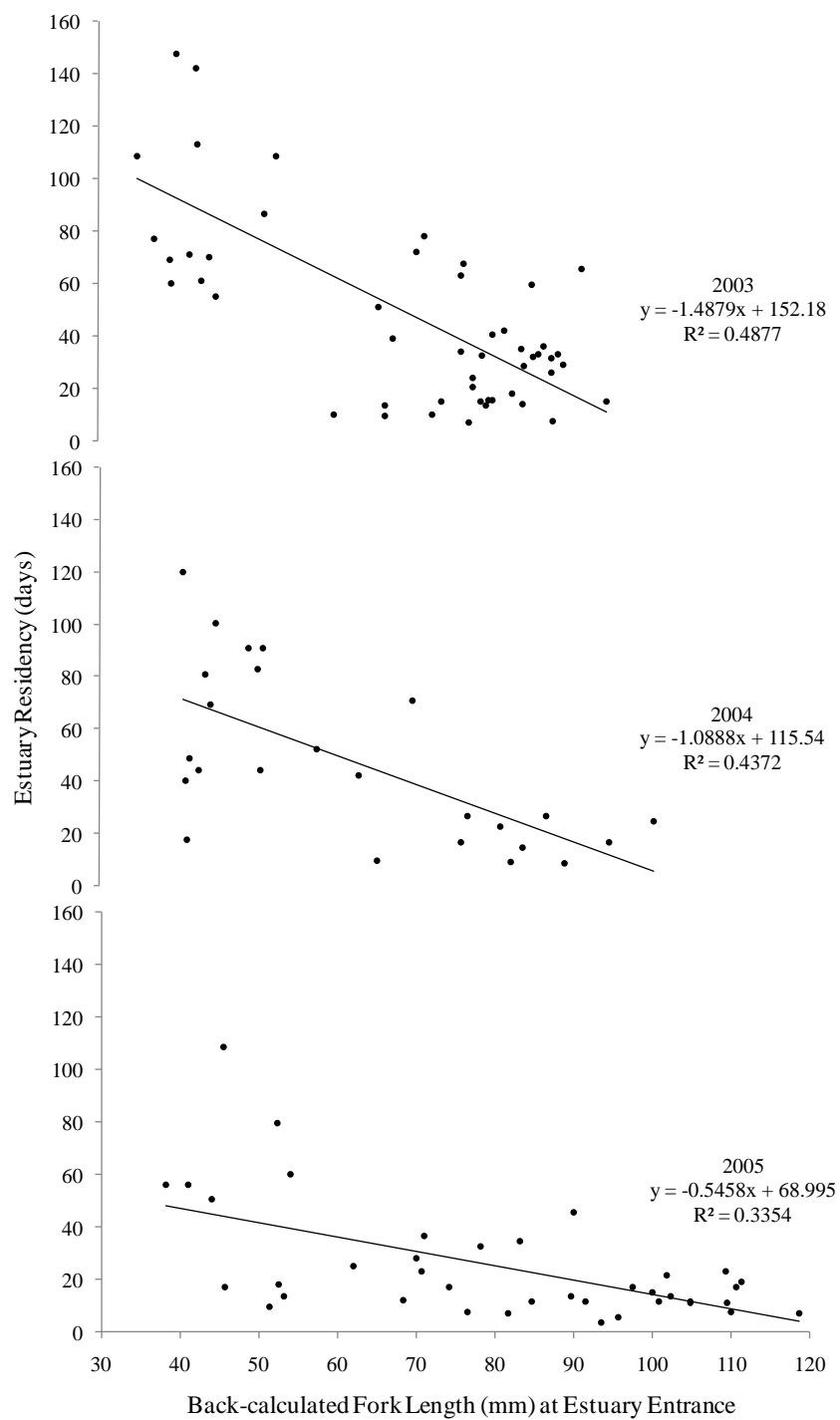
Figure 3.5. Relationship between back-calculated fork length at estuary entrance and the residence time of juvenile Chinook salmon in the Columbia River estuary during May-August, 2003-2005.

Furthermore, a two-way ANOVA on the square root transformed residence data (to normalize count data) by size class of estuary entrance (< 60 mm, 61-90 mm, and > 91 mm) indicated a significant effect of size class on estuary residence when accounting for year of collection ($F_{2,105} = 30.8$, $P < .001$). In general, smaller fish (< 60 mm) resided in the saline portion of the estuary longer (mean $\pm$ SD = 62.4 $\pm$ 6.1 days) than fish in the 61-90 mm (24.0 $\pm$ 2.6 days) and >91 mm size ranges (22.0 $\pm$ 1.7 days). No significant difference in mean residence time was found between the 61-90 mm and > 91 mm size categories ($P = .124$). These results indicate that the length of residency in the estuary is related to both the time and size of fish at estuary entrance and is variable between years.

### *Growth*

Growth in the estuary was estimated by measuring otolith daily growth increments (DGI) for the previous 30 days of estuary residence and then averaged over the time periods (January-April, May-August, and September-December) to produce a mean increment width (MIW) by season and year. A one-way ANOVA found no significant difference between MIW for 2003 (mean $\pm$ SD = 2.53 μm $\pm$ .55 μm), 2004 (2.76μm $\pm$ .50 μm), and 2005 (2.61μm $\pm$ .54 μm) ($F_{2, 88} = 1.14$, $P > .05$). Moreover, there were no significant differences in MIW among time periods (January-April, May-August, and September-December) within a year, except in 2005 ($F_{1, 37} = 25.07$, $P < .001$) when the MIW was greater during May-August than January-April ($P <$ .001; Table 3.6). Examining time period between years only found a significant

difference between 2003 and 2005 (May-August, $F_{2, 39} = 5.47$, P = .008) (Table 3.6).

A two-way ANOVA on the MIW growth data by year and season (January-April,

May-August, and September-December) indicated a significant effect of season on

growth (MIW) when accounting for year ($F_{2,82} = 8.0$, P < .001). In general, fish

entering the estuary in May-August (3.08 µm $\pm$ .46 µm) grew more rapidly than fish

entering in January-April (2.36 µm $\pm$ .39 µm; P < .001; Holm-Sidak multiple

comparison test). No effects of year on growth ($F_{2,82} = 2.2$, P = .116) or of season and

year on growth ($F_{4,82} = .584$, P = .675) were detected.

Table 3.6. Mean otolith increment widths by year and time period and estimated growth rates within the Columbia River estuary.

| Year | Time of Capture | N | Mean increment width | SD | Growth rate ($mm\ d^{-1}$) | SD | Statistically significant with: |
|---|---|---|---|---|---|---|---|
| | Jan-April | 3 | 2.13 | 0.17 | 0.35 | 0.06 | none |
| 2003 | May-Aug | 22 | 2.57 | 0.52 | 0.36 | 0.1 | 2005 May-Aug |
| | Sept-Dec | 7 | 2.57 | 0.72 | 0.39 | 0.07 | none |
| | Jan-April | 5 | 2.47 | 0.16 | 0.48 | 0.05 | none |
| 2004 | May-Aug | 7 | 3.07 | 0.56 | 0.4 | 0.1 | none |
| | Sept-Dec | 7 | 2.67 | 0.49 | 0.43 | 0.09 | none |
| | Jan-April | 26 | 2.37 | 0.43 | 0.36 | 0.12 | 2005 May-Aug |
| 2005 | May-Aug | 13 | 3.09 | 0.43 | 0.49 | 0.09 | 2003 May-Aug |
| | Sept-Dec | 1 | 2.78 | n/a | 0.43 | n/a | none |

The mean growth rate of juvenile Chinook salmon residing in the Columbia

River estuary was approximately .4 mm $d^{-1}$ and ranged from .11 - .67 mm $d^{-1}$. In

general, growth rate increased steadily from January (.19 mm $d^{-1}$) and February (.36

mm $d^{-1}$) through the spring and summer, reaching a peak in August (.55 mm $d^{-1}$).

These results indicate that there are seasonal differences in growth within the estuary, and to a lesser extent annual differences.

### *Estimates of wild and hatchery fish in beach seined data*

The contemporary life histories of juvenile Chinook salmon may be influenced strongly by the large number of hatchery fish released into the Columbia River and its tributaries.  Marked hatchery fish (fin clipped and coded wire tagged fish) composed 3 %, 4 %, and 15 % of the Chinook salmon collected in 2003, 2004, and 2005, respectively.  However, because only a small fraction of the approximately 100 million hatchery fish released into the Columbia River each year were marked ((http://www.fpc.org/hatchery/Hatchery_Queries.html), these values may underestimate greatly the proportion of hatchery fish in our otolith samples.

From the back-calculated sizes at estuary entrance of the juvenile Chinook salmon we analyzed, we estimate that approximately 40 % of the fish we collected in 2004 and 50 % in 2005 had entered the estuary at a size (< 60 mm) smaller than the average size of Chinook salmon released from Columbia River hatcheries (Fig. 3.6). A bimodal distribution occurred in the back-calculated size at estuary entrance for the samples collected in 2004 and 2005.  Both size distributions were characterized by one peak at less than 45mm (i.e. natural origin recruits) and a second peak at a mean size similar to the peak length of Chinook salmon released from hatcheries (Fig. 3.6). These results indicate that juvenile Chinook salmon captured in the beach seine may be composed of a disproportionate number of natural-origin recruits.
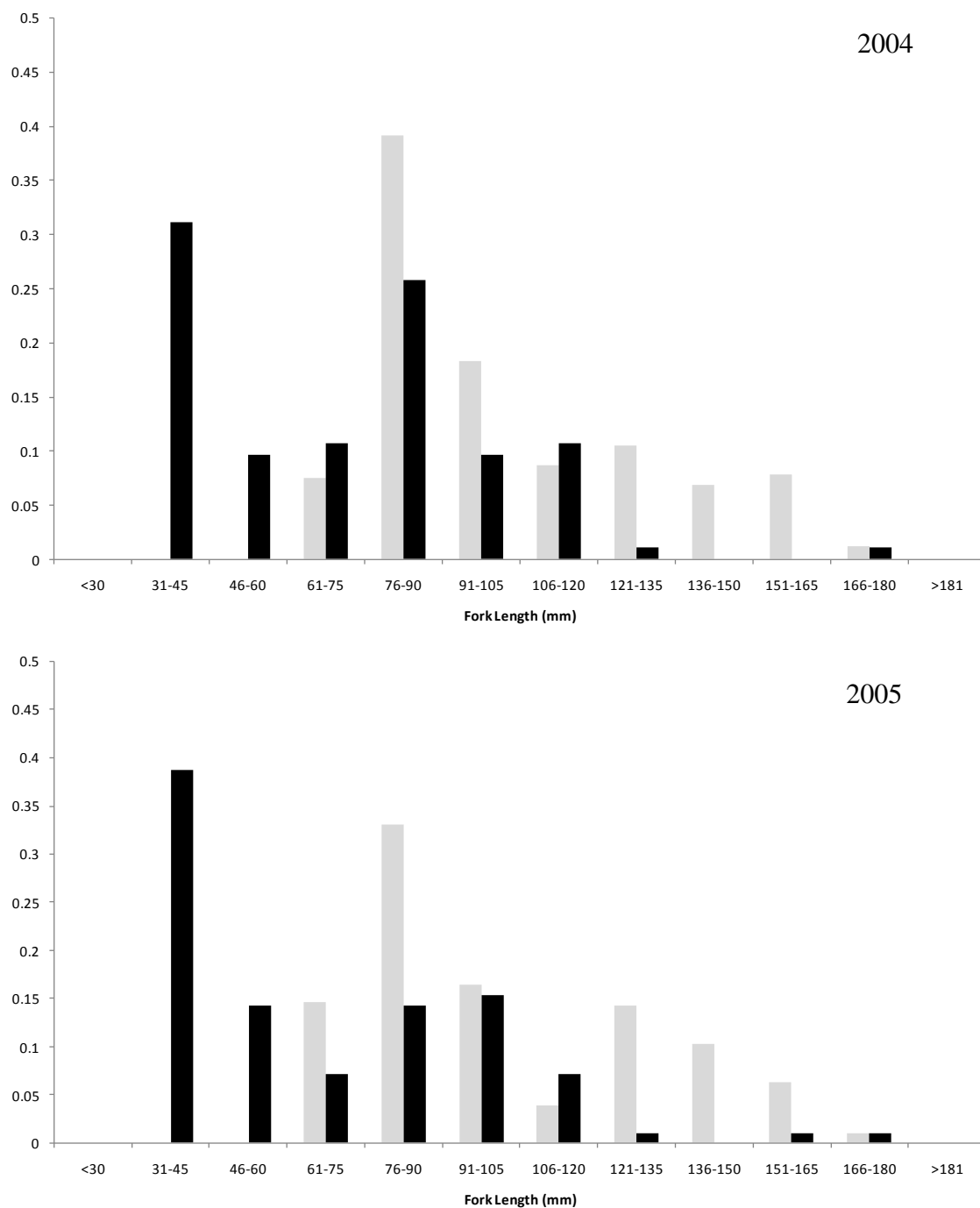
Figure 3.6. Comparison of the estimated size classes at release of hatchery-reared Columbia Basin Chinook salmon (light gray bars) with back-calculated sizes at estuary entrance for juvenile Chinook salmon captured in the lower estuary (black bars). 2003 not included due to sampling bias (chapter 2).

### *Historic versus contemporary run timing*

A comparison of Rich's 1914-1916 samples (Rich 1920) to our 2003-2005 surveys suggests that the seasonal abundance and migration timing of Chinook salmon in the Columbia River estuary may have changed significantly since early in the twentieth century. While contemporary abundances now peak in May and decline rapidly by July or August, a much broader period of estuary use is shown in the historical salmon data. Historical abundances also peaked in May but large pulses of juvenile Chinook salmon occurred in July and again in September and October (Fig. 3.7).
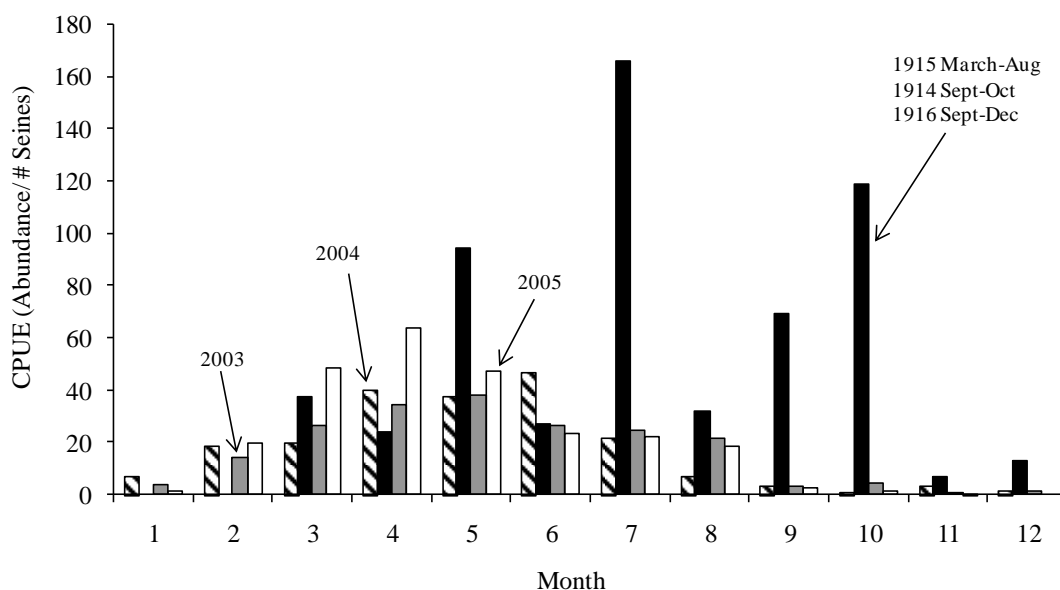


Figure 3.7. CPUE of juvenile Chinook in the Lower Columbia River and estuary. The solid dark bars represent Rich's 1914-1916 collections (Sept-Oct 1914, March-Aug 1915, and Sept-Dec 1916), while the gray bars, dashed bars and clear bars represent our 2003, 2004, and 2005 collections, respectively.

## DISCUSSION

This is the first study since Willis Rich's surveys in 1914-1916 that has reconstructed the life histories of juvenile Chinook salmon in the lower Columbia River estuary. We used otolith microchemistry and microstructure to quantify key attributes of estuary residency, size and time at estuary entrance, and growth. In each of three survey years, a large proportion of the Chinook salmon that we collected in shallow, near-shore habitats had resided in the brackish portion of the estuary for extended periods prior to capture. Although our estimates varied amongst years, average salt-water residency ranged from weeks to months (30 to 67 days), contrasting sharply with the findings of tagging studies that have shown salmon migrating through the Columbia River estuary in a matter of days (Dawley et al. 1986, Schreck et al. 2006, McComas et al 2007). The otolith results revealed considerable variation in estuary entrance times and sizes, and contradicted the premise that Columbia River Chinook salmon now rarely express estuarine-resident life histories (Burke 2005, Bottom et al. 2005a). Nonetheless, we documented limited use of the estuary by juvenile salmon during late summer and fall, supporting the broader hypothesis that life history diversity among Chinook salmon stocks has declined since the first decades of the twentieth century (Rich 1920).

Our estimates of estuary residency for subyearling Chinook salmon in the Columbia River are similar to those reported for other Pacific Coast estuaries from California to British Columbia. Two types of methods have been used to calculate estuary residency: (1) indirect measures for groups of fish, including the time elapsed

in the downstream movement of abundance peaks or between the release of large marked groups and the subsequent recapture of individuals from a group (Rich 1920, Reimers 1973, Healey 1980, Healey 1982, Kjelson et al. 1982, Myers and Horton 1982, Dawley et al 1986, MacFarlane and Norton 2002, Bottom et al. 2005a); and (2) direct measures for individual fish, including chemical signals that mark the estuary entry time on otoliths (Chapter 2, Volk et al. 2010) or implanted tags that track the migration routes and rates of marked individuals (Schreck et al. 2006, McComas et al 2007). Reported residence times have ranged from 17-25 days in the Naniamo and Nitanat River estuaries in British Columbia (Healey 1982); 30-45 days in the Sixes River (Reimers 1973) and 45 days in the Yaquina River estuaries in Oregon (Myers and Horton 1982); and 40-60 days in the Sacramento River estuary in California (Kjelson et al. 1982, MacFarlane and Norton 2002).

In contrast to these results, estimated residence times for juvenile Chinook salmon have varied widely in the Columbia River. Applying a range of literature values for estuary growth rates, Burke (2005) estimated that historical salmon residence times during the Rich (1920) surveys were from 18 to 40 days. Yet various tagging methods employed since the 1980's have reported residence times less than one week (Dawley et al. 1986), including estimated migration times for the entire estuary from Bonneville Dam to near the river mouth (Schreck et al. 2006, McComas et al. 2007). These findings differ substantially from our otolith results, which estimated that 70-80% of the individuals from the beach-seine catches were estuary

residents, and 30-50% of these fish had remained in the estuary for > 30 days prior to capture.

Such wide variations in residency estimates likely reflect differences in the specific segment of the estuary population that has been targeted by different survey methods. Estuary habitat use by juvenile Chinook salmon is often size-related with small size classes frequenting shallow, near-shore and off-channel habitats, while larger subyearlings and yearlings often move into deeper channel areas further from the shoreline (Ledgerwood et al. 1991, Healey 1991, Bottom et al. 2005a). Our beach seine surveys, like those of Rich (1920), thus targeted substantial proportions of fry ($\leq$ 60 mm) and fingerling (60 – 90 mm) size classes. Because Chinook salmon residence times decrease as fish size increases (Figure 3.5), it is not surprising that tagging studies have yielded considerably shorter estuary residence times than those estimated from beach-seine collections. For example, the smallest fish size that can accommodate the newest generation of acoustic tags is ~ 90 mm, and the average subyearling size for a recent tagging experiment was 109.4 mm (McComas et al. 2007). We estimated that the mean estuary residence times for a 110 mm fish in 2003-05 ranged from 0 to 8.9 days, depending on the year of sampling. In contrast we estimated that a 60 mm fish may reside in the estuary for 30-60 days.

Juvenile Chinook salmon occurred in the Columbia River estuary during every month of the year. However, unlike some Oregon populations dominated by fingerlings that enter in the summer and remain until September or October (Reimers 1973, Myers and Horton 1982, Nicholas and Hankin 1988), recently-emerged fry

began entering the Columbia River estuary in late winter and early spring. Larger fingerlings (> 60 mm) later appeared as the season advanced. Similar sizes and times of estuary entrance have been reported for the Fraser, Nanaimo, and Nitanat Rivers (Healey 1982, Healey 1991); the Salmon River (Oregon) (Bottom et al. 2005b); and the Sacramento River (Kjelson et al 1982, MacFarlane and Norton 2002). Healey (1991) termed the progressive pattern of salmon entry as "alternation", hypothesizing that one life history strategy replaces another or occupies habitat vacated as others migrate seaward.

Biologists have debated whether the large number of newly-emerged fry that enter many estuaries is an adaptive life history strategy or simply lost production that exceeds the carrying capacity of natal streams (Healey 1991, Volk et al. 2010). Several studies provide evidence that fry mortality in estuaries is relatively high, as indicated by a large migration of emergent fry into upper estuary reaches with little evidence of recruitment into lower estuary habitats (Healey 1982, Bottom et al 2005b). Our results confirmed that 21 % of the fingerling Chinook salmon sampled in the near-shore areas of the lower Columbia River estuary were composed of "hold-over" emergent fry migrants (< 45 mm)—i.e., fry that had entered the estuary in the spring and were later counted among fingerlings sampled during mid-summer. Similar results were reported in the Salmon River estuary, where ~17% of all fingerlings captured near the river mouth had entered the estuary as fry earlier in the year (Volk et al. 2010). The growth and survival of fry migrants in the lower Columbia River estuary

is consistent with the assumption that the fry-migrant pattern is an adaptive life-history strategy (Healey 1991).

Burke (2005) and Bottom et al. (2005a) hypothesized that life history diversity of Chinook salmon has been constrained by development activities in the Columbia River Basin during the last century. Incorporating results from previous tagging, beach seine, and purse seine surveys, they suggested that the proportion of fry migrants and the relative contributions of estuary-resident life histories among Columbia River Chinook salmon have declined. However, the mean sizes of juvenile salmon at the time of capture during our beach seine surveys were not statistically different from the beach seine results reported by Rich (1920) in 1914-16, and most of the fish we sampled in shallow habitats were estuary residents. By targeting nearshore habitats, our survey results likely over-represented the proportions of small, naturally-produced juveniles that currently rear in the estuary and under-represented the contributions by larger hatchery-reared juveniles that account for the largest percentage of the fish now produced in the Columbia River basin (Williams et al. 2006). For example, ~ 40% of our catch consisted of juveniles that had entered the estuary at sizes smaller than the estimated mean minimum size of Chinook salmon released from Columbia River hatcheries. Furthermore, we accounted for few fish that had entered the estuary at sizes >120mm, a size range that constitutes a significant proportion of the total hatchery production (Fig. 3.6).

Despite similarities to the historical life history patterns observed by Rich (1920), our survey results are consistent with the general hypothesis that life history

diversity among juvenile Chinook salmon has been simplified (Burke 2005, Bottom et al. 2005a). Most notably, we found a much smaller proportion of large juvenile migrants entering or remaining in the estuary during mid-summer and fall compared with the protracted period of estuary use observed by Rich (1920). Although juvenile Chinook salmon still occur in near-shore habitats of the lower estuary every month of the year, the vast majority of the fish are now present from February through August (Fig. 3.7). In 1914 and 1916, Rich (1920) recorded as many or more salmon in September and October than he estimated in April and May, 1915 (Rich 1920). Many factors could account for the apparent shift in temporal distribution, including the decline and extinction of many upper Columbia River populations that historically may have entered the estuary later in the rearing season; the replacement of wild production with hatchery fish that are released over a relatively narrow range of sizes and times; and increasing river temperatures or other habitat changes that could affect late-season rearing opportunities for downstream migrants (Brannon et al. 2004, Bottom et al. 2005a, Roegner et al. 2008).

We conclude that a significant component of fish from near-shore habitats do not use the lower Columbia River as a simple corridor for migrating rapidly seaward, but rear and grow for considerable periods before leaving the estuary. We cannot determine from these results whether delay in the lower estuary for additional rearing and growth improves marine survival of Columbia River salmon or, as some tagging studies suggest (Collis et al. 2001, Ryan et al. 2003, McComas et al. 2007), contributes to additional mortality from lower-estuary predators. However, because

the various methods for measuring salmon residency target fish of different size classes and rearing histories (i.e., hatchery vs. wild), opposing perceptions of the estuary as a hazardous corridor and as an important nursery ground may not be mutually exclusive. Future Columbia River studies should examine the otoliths from selected spawning populations to determine the relative contributions of different juvenile rearing behaviors to the surviving adults.

## LITERATURE CITED

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005a. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. United States Department of Commerce, NOAA Technical Memorandum. NMFS-NWFSC-68.

Bottom, D. L., K. K. Jones, T. J.Cornwell, A. Gray and C. A.Simenstad. 2005b. Patterns of Chinook salmon migration and residency in the Salmon River Estuary (Oregon). Estuarine Coastal and Shelf Science 64:79-93.

Brannon, E L., M.S. Powell, T.P. Quinn, and A.J. Talbot. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science. 12: 99-232.

Brenkman, S. J., S. C. Corbett, and E.C. Volk. 2006. Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. Transactions of the American Fisheries Society. 136: 1-11

Brown, R.J., and K.P. Severin. 2009. Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Canadian Journal of Fisheries and Aquatic Sciences 66: 1790-1808.

Burke, J. L. 2005. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to present. MS thesis, Oregon State University, Corvallis.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47: 2219–2227.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263–297.

Campana, S.E. and J.D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42: 1014-1032.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: Vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130: 385-396.

Dawley, E. M., R. D. Ledgerwood, T.H. Blahm, C.W. Sims, J.T. Durkin, R.A. Kirn, G.E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. Coastal Zone and Estuarine Studies Division, NMFS-NOAA and Bonneville Power Administration. Contract No. DE-AI79-84-BP39652, Project No. 81-102. 256 pp.

Fowler, A.J., S.E. Campana, C.M. Jones, and S.R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Canadian Journal of Fisheries and Aquatic Sciences 52: 1431-1441.

Healey, M.C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. United States Fisheries Bulletin 77: 653 – 668.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315 – 341 *in* B.R. Melteff and R.A. Nevé (editors). Estuarine comparisons. Academic Press, New York.

Healey, M.C. 1991. Life history of Chinook salmon. Pages 313 – 393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, I. A. Fleming. 2010. Tidal movement and residency of subyearling Chinook salmon (*Onchorhynchus tshawytscha*) in an Oregon salt march channel. Canadian Journal of Fisheries and Aquatic Sciences 67: 524-533

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fishery Bulletin. U.S. 88: 657–666.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for Snake River spring/summer Chinook salmon in the Columbia River Basin. Science 290: 977-979.

Kjelson, M. A., P.F. Raquel, and F.W. Fisher. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California.Pages 393-411 *In* V. S. Kennedy, editor, Estuarine comparisons, Academic Press, New York, NY.

Ledgerwood, R. D., F. P. Thrower, E.M. Dawley. 1991. Diel samplingof migratory juvenile salmonids in the Columbia River estuary. Fishery Bulletin, U.S. 89: 69-78.

Levy, D. A., and T. G. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Canadian Journal of Fisheries and Aquatic Sciences 39: 270-276.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C. 333 pp.

MacFarlane, R.B. and E.C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fisheries Bulletin 100: 244-257.

Magnuson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries 26: 1094 – 1103.

McCabe Jr., G. T., R. L. Emmett, W. D. Muir, and T. H. Blahm. 1986. Utilization of the Columbia River estuary by subyearling Chinook salmon. Northwest Science 60(2): 113-124.

McComas, R.L., L.G. Gilbreath, S.G. Smith, G.M. Matthews, J.W. Ferguson, G.A. McMichael, J.A. Vucelick, and T. Carlson. 2007. A study to estimate salmonids survival through the Columbia River estuary using acoustic tags, 2005. Report of the National Marine Fisheries Service to the U.S. Army Corps of Engineers, Portland, Oregon.

Myers, K.W., and H.F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. Pages 377 – 391 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Research Council. National Academy Press, Washington, D.C.

Nicholas, J. W., and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife Information Report. 88-1.

Northwest Power Planning Council. 1986. Compilation of information on salmon and steelhead losses in the Columbia River basin. Appendix D of the 1987 Columbia River Basin Fish and Wildlife Program. Portland, OR.

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173: 1124-1 127.

Reimers, P.E. 1973. The length of residence of juvenile fall Chinook salmon in the Sixes River, Oregon. Research Reports of the Fish Commission. 4(2): 1-42.

Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers.  Bulletin of the United States Fish Commission 37 (DOC 887): 1-73.

Roegner, G.C.,  A. Baptista, D. L. Bottom, J. Burke, L. Campbell, C. Elliot, S. Hinton, D. Jay, M.A. Lott, T. Lundrigan, R. McNatt, P. Moran, C. A. Simenstad, D. Teel, E. Volk, J. Zamon, and E. Casillas. 2008. Estuarine habitat and juvenile salmon--current and historical linkages in the lower Columbia River and estuary, 2002-04. Fish Ecology Division, Northwest Fisheries Science Center, Seattle, WA.

Ryan, B.A., S.G. Smith, J.M. Butzerin, and J.M. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary 1998 – 2000. Transactions of the American Fisheries Society 132: 275 – 288.

Schluchter, M. D. and J.A Lichatowich. 1977. Juvenile Life histories of spring Chinook salmon  *Oncorhynchus tshawytscha,* as determined by scale analysis. Oregon Department of Fish and Wildlife Information Report 77-5.

Schreck, C.B., T.P. Stahl, L.E. Davis, D.D.. Roby, and B.J. Clemens. 2006. Mortality estimates of juvenile spring–summer Chinook salmon in the Lower Columbia River and estuary, 1992–1998: Evidence for delayed mortality? Transactions of the American Fisheries Society 135: 457-475.

Sherwood, C.R., D.A. Jay, R.B. Harvey, P. Hamilton, and C.A. Simenstad. 1990. Historical changes in the Columbia River estuary. Progress in Oceanography 25: 271-297.

Simenstad, C.A., K.L. Fresh, and E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343 – 364 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Volk, E.C, A. Blakley, S.L. Schroder and S.M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and fresh waters. Fisheries Research 46: 251-266.

Volk, E.C., D. L. Bottom, K.K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary (Oregon) using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139:535-549.

Welch D. W., Rechisky E.L., Melnychuk M.C., Porter A.D., Walters C.J. 2008. Survival of migrating salmon smolts in large rivers with and without dams. Public Library of Science Biology 6(10): e265 doi:10.1371/journal.pbio.0060265

Williams, R. N., editor. 2006. Return to the River: restoring salmon to the Columbia River. Elsevier, San Diego.

Zimmerman, C. E., and G. H. Reeves. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 135: 457-475.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios to salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62(1): 88–97.

**CHAPTER 4: GENERAL DISCUSSION**

Despite evidence that juvenile Chinook salmon utilize other North Pacific estuaries for weeks to months, contemporary tagging studies in the Columbia River have indicated that salmon residency in the estuary is short (< 1 week) and mortality is high. This has led some investigators to hypothesize that extended estuary residency is hazardous for juvenile salmon and may impede recovery of at-risk salmon stocks. Others have hypothesized that the estuary is an important salmon rearing ground, and that any reduction in contemporary estuary use is an artifact of changes that have reduced estuarine rearing opportunities and simplified life history diversity over time. To examine these interpretations, we first compared alternative methods for reconstructing the estuarine life histories of juvenile Chinook salmon. We then used otolith microchemistry to quantify various salmon life history attributes in the Columbia River estuary, including growth, size and time of estuary entry, and estuary residency. Our survey results indicated that many juvenile Chinook salmon utilize the Columbia River estuary in a high frequency and for extended periods of time.

Chapter Two tests the validity of using scale morphometric characteristics, scale chemistry and otolith chemistry to identify estuary residing Chinook salmon. Although scale and otolith chemistry were both accurate indicators of estuary entry, scale morphometric characteristics did not coincide consistently with entry into brackish water. Scale morphometric features were a poor indicator of salmon entry into the Columbia River estuary. Although we cannot draw conclusions about the utility of scale-pattern analysis for studying other river basins, our results suggest that

careful validation is necessary before salmon life histories can be interpreted from the morphometric features of scales. We found that scale chemistry was a good indicator of estuary entry by juvenile salmon. However, it was not as precise a method as otolith chemistry because otolith increments form daily, while scale material is added less frequently (i.e., over weeks). How Sr is incorporated into scales and the consistency of that chemical signal over time is relatively unknown and will require further study. Although otolith chemistry proved to be the most reliable indicator of estuary entrance by juvenile salmon, it can only measure entry into the saline portion of the estuary where Sr is elevated. This does not account for salmon residency in the long tidal freshwater portions of many large estuaries.

The otolith chemistry results presented in Chapter Three demonstrate that juvenile subyearling Chinook salmon utilized shallow, near-shore habitats of the lower Columbia River estuary in a high frequency (70-80%) and for extended periods of time (30- 67days). These results contrast with those of contemporary tagging studies, which found that juvenile Chinook salmon move rapidly through the estuary (<1 week). Our results suggest that the size of fish used in the two sample populations may account for these differences. Tagging studies in the Columbia River are restricted to size classes of salmon that can accommodate large tags (i.e., $\geq$ 90 mm fish for acoustic tags; ~55 or 60 mm for PIT tags). Our analysis of otoliths was not constrained by a particular size range. The otolith method allowed us to quantify residence times for many small fry and fingerlings that are otherwise impossible to tag.

Our results indicated that size and time of estuary entry were negatively related to estuary residency.  Generally, small and early migrating fish resided in the estuary for longer periods than those of large late migrants.  Importantly we found that a significant proportion of the sample population had entered the estuary at a size < 45 mm (0-3 weeks post emergence).  These results support the hypothesis that newly emerged fry leaving their natal streams are not "lost" to a population but survive in the estuary, grow, and likely contribute to the outmigrating population of Chinook salmon.

Historical evidence suggests that juvenile Chinook salmon migrated into and resided in the Columbia River estuary in large number during late summer through fall. We were unable to document this migration strategy to any significant degree in three years of monthly beach seining. This suggests that changes in habitat or fish population structure in the basin now may limit opportunities for salmon to access or occupy the estuary during the late summer and fall months.  The apparent reductions in estuarine rearing potential and their causes are important considerations for future salmon recovery efforts.

This thesis has examined the use of estuary habitat by juvenile Chinook salmon and has shown that residence times can be long and recruitment of fry to larger sizes classes is significant.  Additional research should examine the occurrence and proportion of estuary-resident juvenile life histories in representative populations of returning adults.  To better quantify patterns of habitat use and residency, otolith studies should evaluate alternative chemical indicators that may reflect freshwater

portions of the estuary and its tributaries. Future laboratory experiments should focus on optimal instrument conditions to detect chemical signals, as well as the formulas used to determine points of interest on otoliths. Finally, the factors influencing contemporary patterns of estuary use by juvenile salmon and the relative effects of genetic or habitat losses on life history expression are poorly understood. Quantifying variations in life history by basin/population for both outmigrating juveniles and returning adults will provide valuable information on the types of habitats that are critical and in need of protection today. In addition, understanding alternative or unsuccessful life history strategies today may guide us to the types of restoration that are needed in the future to connect lost strategies with historically robust populations.

The findings of this study suggest that, not unlike other North Pacific estuaries, juvenile Chinook salmon in the Columbia River utilize the estuarine environment in a high proportion and for extended periods of time. The degree of use appears to be related to size, which may explain the differences between our results and that of other contemporary studies that have relied on estimates from larger fish. This research supports the hypothesis that estuarine habitats and their links to other salmon rearing habitats may be important for population viability and resiliency.

**BIBLIOGRAPHY**

Bali, J. M. 1959.  Scale analysis of steelhead trout *Salmo gairdnerii gairdneri* Richardson, from various coastal watersheds of Oregon. M.S. Thesis, Oregon State College, Corvallis, 117p

Bagenal, T.B., MacKereth, F.J.H., and Heron, J. 1973. The distinction between brown trout and sea trout by the strontium content of their scales. Journal of Fish Biology 5: 555–557.

Beamish, R. J., and G. A. MacFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112: 735–743.

Beckman, B. R. 2002. Growth and plasticity of smolting in Chinook salmon. Ph.D Thesis, University of Washington, Seattle.

Bilton, H.T., and G.L. Robins. 1971. Effects of starvation, feeding, and light period on circulus formation on scales of young sockeye salmon Oncorhynchus nerka. Journal of the Fisheries Research Board of Canada 18: 1749–1755.

Bilton, H. T. 1975. Factors influencing the formation of scale characteristics. International North Pacific Fisheries Commission., Bulletin. 32.

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005a. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. United States Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-68.

Bottom, D. L., K. K.Jones, T. J.Cornwell, A. Gray and C. A.Simenstad. 2005b. Patterns of Chinook salmon migration and residency in the Salmon River Estuary (Oregon). Estuarine Coastal and Shelf Science 64: 79-93.

Boyce, R. R. 1985. Effects of feeding level, temperature, and photoperiod on growth and selected scale characteristics of juvenile steelhead trout.  Masters Thesis, Oregon State University, Corvallis.

Brannon, E L., M.S. Powell, T.P. Quinn, and A.J. Talbot. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science. 12: 99-232.

Brenkman, S. J., S. C. Corbett, and E.C. Volk. 2006. Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. Transactions of the American Fisheries Society 136: 1-11.

Brown, R.J., and K.P. Severin. 2009. Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Canadian Journal of Fisheries and Aquatic Sciences 66: 1790-1808.

Burke, J. L. 2005. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to present. MS thesis, Oregon State University, Corvallis.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47: 2219–2227.

Campana, S.E., Thorrold, S.R., Jones, C.M., Gunther, D., Tubrett, M., Longerich, H., Jackson, S., Halden, N.M., Kalish, J.M., Piccoli, P., de Pontual, H., Troadec, H., Panfili, J., Secor, D.H., Severin, K.P., Sie, S.H., Thresher, R., Teesdale, W.J., and Campbell, J.L. 1997. Comparison of accuracy, precision, and sensitivity in elemental assays of fish otoliths using the electron microprobe, proton-induced X-ray emission, and laser ablation inductively coupled plasma mass spectrometry. Canadian Journal of Fisheries and Aquatic Sciences 54: 2068–2079.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263–297.

Campana, S.E. and J.D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42: 1014-1032.

Carlander, K. D. 1987. A history of scale age and growth studies of North American freshwater fish. Pages 3-14 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Casselman, J.M. 1983 Age and growth assessment of fish from their calcified structures - techniques and tools. - U. S Department of Commerce, NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 8:1–17.

Chilton, D. E., and H. T. Bilton. 1986. New method for ageing Chinook salmon (Oncorhynchus tshawytscha) using dorsal fin rays, and evidence of its validity. Canadian Journal of Fisheries and Aquatic Sciences 43:1588–1594.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: Vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130: 385-396.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 134: 291- 304.

Courtemanche, D.A., F.G. Jr. Whoriskey, V. Bujold, and R.A. Curry. 2005. A nonlethal approach using strontium in scales to distinguish periods of marine and freshwater residency of anadromous species. Canadian Journal of Fisheries and Aquatic Sciences 62: 2443–2449.

Courtemanche, D.A., F.G. Jr. Whoriskey, V. Bujold, and R.A. Curry. 2006. Assessing anadromy of brook char (*Salvelinus fontinalis*) using scale microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 63:995-1006.

Coutant C.C., and C.H. Chen. 1993. Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. Canadian Journal of Fisheries and Aquatic Sciences 50:1318-1323.

Dahl, K. 1911. The age and growth of salmon and trout in Norway, as shown by their scales. The Salmon and Trout Association, London.

Darwin, C.R. 1859. The origin of species. Oxford University Press, New York, N.Y. 439 pp.

Dawley, E. M., R. D. Ledgerwood, T.H. Blahm, C.W. Sims, J.T. Durkin, R.A. Kirn, G.E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. Coastal Zone and Estuarine Studies Division, NMFS-NOAA and Bonneville Power Administration. Contract No. DE-AI79-84-BP39652, Project No. 81-102. 256 pp.

Day, J. W. J., C. A. S. Hall, W. M. Kemp, and A. Yáñez-Arancibia. 1989. Estuarine ecology. Wiley, New York.

Einum, S., I. A. Fleming, I. M. Cote, J. D. Reynolds. 2003. Population stability in salmon species: effects of population size and female reproduction allocation. Journal of Animal Ecology 72: 811-821.

Fairbridge, R. W. 1980. The estuary: its definition and geochemical role. Pages 1-35 in E. Olausson, and I. Cato, editors. Chemistry and geochemistry of estuaries. Wiley, New York.

Fowler, A.J., S.E. Campana, C.M. Jones, and S.R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Canadian Journal of Fisheries and Aquatic Sciences 52:1431-1441.

Gilbert, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus Oncorhynchus. U.S. Bureau of Fisheries Bulletin 32:1-22.

Hankin, D. G., J. H. Clark, R. B. Deriso, J. C. Garza, G. S. Morishima, B. E. Riddell, C. Schwarz, and J. B. Scott. 2005. Report of the expert panel on the future of the coded wire tag program for Pacific salmon. Pacific Salmon Commission, Technical Report 18, Vancouver.

Healey, M.C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. United States Fisheries Bulletin 77: 653 – 668.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315 – 341 *in* B.R. Melteff and R.A. Nevé (editors). Estuarine comparisons. Academic Press, New York, N.Y.

Healey, M.C. 1991. Life history of Chinook salmon. Pages 313 – 393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, and I. A. Fleming. 2010. Tidal movements and residency of subyearling Chinook salmon (Onchorhynchus tshawytscha) in an Oregon salt marsh channel. Canadian Journal of Fisheries and Aquatic Sciences 67:524-533.

Hill, M.F., L. W. Botsford, A. Hastings. 2003. The effects of spawning age distribution on salmon persistence in fluctuating environments. Journal of Animal Ecology 72: 736-744.

Hilborn, R., T. P. Quinn, D. E. Schindler, D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100: 6564-6568.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fishery Bulletin. U.S. 88: 657–666.

Kennedy, B P., A. Klaue, J. D. Blum, C. L. Folt, K. H. Nislow., 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences 59: 925-929.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for Snake River spring/summer Chinook salmon in the Columbia River Basin. Science 290: 977-979.

Kjelson, M. A., P.F. Raquel, and F.W. Fisher. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytsch*a, in the Sacramento-San Joaquin estuary, California. Pages 393-411 *In* V. S. Kennedy, editor, Estuarine comparisons, Academic Press, New York, N.Y.

Koo, T.S.Y. 1962. Age designation in salmon. Pages 41 – 48 *in* T.S.Y. Koo editor. Studies of Alaska Red Salmon. Universtiy of Washington Press, Seattle.

Lagler, K.F., J.E. Bardach, and R.R. Miller. 1962. Ichthyology. John Wiley and Sons, Inc. New York.

Ledgerwood, R. D., F. P. Thrower, E.M. Dawley. 1991. Diel samplingof migratory juvenile salmonids in the Columbia River estuary. Fishery Bulletin, U.S. 89: 69-78.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C. 317 pp.

MacFarlane, R.B. and E.C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fisheries Bulletin 100: 244-257.

Magnuson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries 26: 1094 – 1103.

McCabe Jr., G. T., R. L. Emmett, W. D. Muir, and T. H. Blahm. 1986. Utilization of the Columbia River estuary by subyearling Chinook salmon. Northwest Science 60(2): 113-124.

McComas, R.L., L.G. Gilbreath, S.G. Smith, G.M. Matthews, J.W. Ferguson, G.A. McMichael, J.A. Vucelick, and T. Carlson. 2007. A study to estimate salmonids survival through the Columbia River estuary using acoustic tags, 2005. Report of the National Marine Fisheries Service to the U.S. Army Corps of Engineers, Portland, Oregon.

McLusky, D. S., and M. Elliott. 2004. The estuarine ecosystem: ecology, threats, and management, 3rd edition. Oxford University Press, Oxford.

Myers, K.W., and H.F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. Pages 377 – 391 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, N.Y.

Nicholas, J. W., and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife Information Report. 88-1.

Northwest Power Planning Council. 1986. Compilation of information on salmon and steelhead losses in the Columbia River basin. Appendix D of the 1987 Columbia River Basin Fish and Wildlife Program. Portland, OR.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Research Council. National Academy Press, Washington, D.C.

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173: 1124-1 127.

Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in the Sixes River, Oregon. Research Reports of the Fish Commission. 4(2): 1-42.

Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers. Bulletin of the United States Fish Commission 37 (DOC 887): 1-73.

Roegner, G.C., A. Baptista, D. L. Bottom, J. Burke, L. Campbell, C. Elliot, S. Hinton, D. Jay, M.A. Lott, T. Lundrigan, R. McNatt, P. Moran, C. A. Simenstad, D. Teel, E. Volk, J. Zamon, and E. Casillas. 2008. Estuarine habitat and juvenile salmon--current and historical linkages in the lower Columbia River and estuary, 2002-04. Fish Ecology Division, Northwest Fisheries Science Center, Seattle, WA.

Ryan, B.A., S.G. Smith, J.M. Butzerin, and J.M. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary 1998 – 2000. Transactions of the American Fisheries Society 132: 275 – 288.Schluchter, M. D. and J.A Lichatowich. 1977. Juvenile Life histories of spring Chinook salmon *Oncorhynchus tshawytscha,* as determined by scale analysis. Oregon Department of Fish and Wildlife Information Report 77-5

Schluchter, M. D. and J.A Lichatowich. 1977. Juvenile life histories of spring Chinook salmon *Oncorhynchus tshawytscha,* as determined by scale analysis. Oregon Department of Fish and Wildlife Information Report 77-5.

Schreck, C.B., T.P. Stahl, L.E. Davis, D.D.. Roby, and B.J. Clemens. 2006. Mortality estimates of juvenile spring–summer Chinook salmon in the Lower Columbia River and estuary, 1992–1998: Evidence for delayed mortality? Transactions of the American Fisheries Society 135: 457-475.

Secor, D.H., A. Henderson-Arzapalo, and P.M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology 192:15–33.

Shapovalov, L., and A.C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorynchus kisutch*) with special reference to Waddell Creek. California, and recommendations regarding their management. California Department of Fish and Game Bulletin 98: 375 p.

Sherwood, C.R., D.A. Jay, R.B. Harvey, P. Hamilton, and C.A. Simenstad. 1990. Historical changes in the Columbia River estuary. Progress in Oceanography 25: 271-297.

Simenstad, C.A., K.L. Fresh, and E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343 – 364 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, N.Y.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51: 3-46.

Stearns, S.C. 1992. Evolutions of life histories. Oxford University Press, New York, NY. 249 pp.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17(1a):76-93.

Thorrold, S. R., C. M. Jones, and S. E. Campana. 1997. Response of otolith microchemistry to environmental variations experienced by larval and juvenile Atlantic croaker (*Micropogonias undulatus*). Limnology and Oceanography 42:102– 11.

Van Oosten, J. 1957. The skin and scales. Pages 207-244 *in* M. E. Brown (editor) the physiology of fishes. Academic Press, New York, N.Y.

Volk, E.C, A. Blakley, S.L. Schroder and S.M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and fresh waters. Fisheries Research 46: 251-266.

Volk, E.C., D. L. Bottom, K.K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary (Oregon) using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139: 535-549.

Wallin, O. 1957. On the growth structure and development of the scales of fish. Institute of Freshwater Research (38): 385-447.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (Salmo gairdneri) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45: 1110-1122

Welch D.W., E.L Rechisky, M.C. Melnychuk, A.D. Porter, C.J. Walters. 2008. Survival of migrating salmon smolts in large rivers with and without dams. Public Library of Science Biology 6(10): e265 doi:10.1371/journal.pbio.0060265

Wells, B. K., G. E. Bath, S. R. Thorrold, and C. M. Jones. 2000a. Incorporation of strontium, cadmium, and barium in juvenile spot, *Leistomus xanthurus*, reflects water chemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2122–2129.

Wells, B. K., and B. E. Rieman, J. L. Clayton, D. L. Horan, C. M. Jones. 2003. Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: The potential application of hard-part chemistry to describe movements in freshwater. Transactions of the American Fisheries Society 132: 409–424.

Williams, R. N., editor. 2006. Return to the River: restoring salmon to the Columbia River. Elsevier, San Diego.

Zimmerman, C. E., and G. H. Reeves. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 135: 457-475. 131:986-993.

Zimmerman, C. E., and R. L. Nielsen. 2003. Effect of analytical conditions on the measurement of strontium to calcium (Sr/Ca) ratios in otoliths of anadromous salmonids using wavelength dispersive electron microprobe analysis. Fishery Bulletin 101: 712-718.Wells, B. K., S. R. Thorrold, and C. M. Jones. 2000b. Geographic variation in trace element composition of juvenile weakfish scales. Transactions of the American Fisheries Society 129: 889–900.