



AN ABSTRACT OF THE THESIS OF

Andrew M. Claiborne for the degree of Master of Science in Fisheries Science  
presented on March 12, 2013.

Title: A Comparison of Early Marine Residence in Hatchery and Natural Chinook  
Salmon (*Oncorhynchus tshawytscha*)

Abstract approved:

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Jessica A. Miller

The mechanisms of mortality during critical life stages of fish are not well-understood and, for many species, it is not clear if the mechanisms are similar for naturally and artificially propagated individuals. For Chinook salmon (*Oncorhynchus tshawytscha*), natural fish potentially face negative interactions, such as competition, and survival disadvantages, such as smaller size, that may limit survival when in association with hatchery fish. To better understand the mechanisms of mortality for hatchery and natural Chinook salmon during the critical early marine residence stage, I: (1) developed a model to discriminate between hatchery and natural juveniles using otolith structure; (2) directly compared migratory patterns of hatchery and natural juveniles; and (3) determined if there was evidence for selective mortality during early marine residence. I followed two cohorts through space and time by collecting juveniles from May-September in the Columbia River estuary and off the coast in September of 2010 and 2011. I compared attributes of those juveniles when they first

entered marine waters with those of survivors after their first summer at sea. I used a combination of genetic stock identification, otolith chemistry and structure, and physical tags to determine stock of origin, size at and timing of freshwater emigration, marine growth, and production type (hatchery or natural). I focused on the subyearling life history of a federally managed genetic stock group (upper Columbia River summer and fall Chinook salmon, UCR Su/F) because: 1) it is an abundant stock group; 2) subyearlings may be more vulnerable to size-selective mortality than yearlings; and 3) it is currently impossible to assess impacts of hatchery production due to low rates of marking the hatchery fish within this stock group. The classification model included two metrics, the presence or absence of a previously unreported transfer check associated with hatchery rearing and variability in otolith increment width, and predicted production type with a 92% jack-knifed accuracy.

Overall, timing of marine entry was similar for hatchery and natural UCR Su/F juveniles, which entered marine waters from May-September with a peak in July and August in both years. Estuarine residence times were brief: 80% of the individuals captured in the estuary had resided in saline waters for < 3 days and mean estuarine residence was significantly greater ( $7 \pm 1.3$  d) in 2010 than 2011 ( $1 \pm 0.3$  d). The only clear difference was that natural individuals captured in the estuary in 2011 migrated to saline waters earlier (July  $13^{\text{th}} \pm 4$  d) than hatchery conspecifics (August  $10^{\text{th}} \pm 6$  d). However, the timing of marine entry was similar (July  $27^{\text{th}} \pm 1$  d) between hatchery and natural fish collected later in the ocean. This observation could be due to differential survival related to the timing of marine entry. Alternatively, estuarine

collections may not have adequately represented the emigrating population due to rapid emigration.

I documented clear spatial overlap between production types during early marine residence but no difference in median size at marine entry ( $100 \pm 3.5$  mm), size at capture ( $152 \pm 4.0$  mm), or marine growth ( $0.94 \pm 0.1$  % b l d<sup>-1</sup>). There were also no significant differences in size at marine entry between estuary and ocean collections, which indicates that size-selective mortality had not occurred. Based on both external tags and the otolith classification model, the mean percentage of natural fish in ocean collections was 17% ( $\pm 4.8$ ) greater than in the Columbia River estuary; this finding may indicate that estuarine collections are biased to hatchery fish or, more likely, that natural fish survived at higher rates than hatchery fish. Increased survival of natural fish may be related to greater selection pressure during freshwater rearing and prior experience with predators. This study provides the first direct stock-specific comparison of juvenile migratory behavior in natural and hatchery juvenile Columbia River Chinook salmon during early marine residence. Further research is needed to determine if natural fish consistently survive better than hatchery conspecifics and, if so, determine the specific traits and behaviors that afford a survival advantage.

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A Comparison of Early Marine Residence in Hatchery and Natural Chinook Salmon  
(*Oncorhynchus tshawytscha*)

by  
Andrew M. Claiborne

A THESIS

Submitted to  
Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Presented March 12, 2013  
Commencement June 2013

Master of Science thesis of Andrew M. Claiborne  
Presented on March 12, 2013.

APPROVED:

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Major Professor, representing Fisheries Science

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Head of the Department of Fisheries and Wildlife

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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.

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Andrew M. Claiborne, Author

## ACKNOWLEDGEMENTS

This research was supported by the Bonneville Power Administration; National Oceanic and Atmospheric Administration (NOAA) Fisheries; The Mamie Markham Research Award; Washington County Flyfishers; and the Flyfishers Club of Oregon. I am especially indebted to Robert Emmett for giving me the chance to work with an amazing group of researchers and for his steadfast support and guidance through the years.

I would first like to thank my committee members Jessica Miller, Laurie Weitkamp, Daniel Bottom, and Daniel Roby for critique, advice, and perspective through this process. This work would have not been possible without otolith collections from Cindy Bucher and Laurie Weitkamp to whom I am grateful. I cannot stress enough that this work would not have been possible without the plume and estuary group that meticulously collected these data and captain and crew of FV Frosti. I would like to thank Andy Stephens for statistical advice and David Teel for providing genetic stock identification and Curtis Roegner for providing perspective and data from an intertidal estuary site. I would like to thank Paul Hoffarth and Todd Miller of WDFW, and numerous hatchery personnel for providing fish. I am truly indebted to Jessica Miller for walking me through this process and helping me further my ability as a biologist. Finally, I would like to thank my father for engraining in me an interest in the sea and my family and friends for their unwavering support.



## CONTRIBUTION OF AUTHORS

Dr. Robert Emmett assisted with fish collection and design of Chapter 3.

Dr. Laurie Weitkamp assisted with the fish collection, interpretation, design, and writing of Chapter 3.

David Teel provided genetic stock identification for fish used in Chapter 3, as well as interpretation, and design of Chapter 3.

Dr. Jessica Miller assisted with the otolith structure and elemental analysis, interpretation, design, and writing of Chapter 3.

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## CHAPTER 1: GENERAL INTRODUCTION

Fish culture has existed in Asia for over 2000 years and intensive artificial propagation has occurred for over 600 years (Sharp 2000). In many cases, artificial propagation consists of rearing fish during early life stages and then stocking juveniles into natural environments. Many hatchery programs focus on the supplementation of harvestable biomass, but conservation of natural stocks can also be a goal (Araki and Schmid 2010). Efforts to understand the effects of artificial propagation have increased exponentially since the mid-1990s (for review, see Araki and Schmid 2010). Over the last two decades, research has largely focused on differences in behavior, lifetime fitness, and survival between production types (hatchery or natural). In many species there are clear negative effects of artificial propagation, including lower survival (Iglesias et al. 2003), behavioral disadvantages (Stunz and Minello 2001; Schroder et al. 2010), and reduced reproductive success of hatchery fish (Flemming et al. 1997). There are also potential negative impacts to natural populations, such as reduced fitness if hatchery fish reproduce in the wild (Araki et al. 2007), reduced survival via density dependence (Kitada and Kishino 2006) when food resources are limited, and increased transmission of diseases (Naish et al. 2008). However, for many species and stocks, the direct effects of artificial propagation on natural populations are not clear.

Chinook salmon (*Oncorhynchus tshawytscha*) is a culturally and economically valuable species that has experienced precipitous declines in the abundance of many populations across its geographic range from Big Sur, California to Alaska (Myers et al. 1998). Population declines have resulted in the establishment

of hatchery programs to increase harvestable stocks. Chinook salmon are anadromous, and these programs have focused on reducing freshwater mortality prior to migration to the sea. Historically, some of the largest runs of Chinook salmon occurred within the Columbia River basin (Lichatowich 1999). In the Columbia River, juvenile Chinook salmon emigrate to sea either as yearlings (after their first winter) or as subyearlings (before their first winter). Today, > 90% of the subyearling and yearling migrants captured in the estuary (Weitkamp et al. 2012) and > 80% of returning adults (Williams et al. 1999) are estimated to be hatchery individuals. Advances in genetic stock identification have been combined with ecological field studies to examine factors influencing juvenile migratory behavior and early marine survival on a stock-specific basis (Daly et al. 2012; Tomaro et al. 2012; Miller et al. in press). However, few studies have evaluated if factors influencing juvenile migratory behavior and early marine survival are similar between natural and hatchery fish within a stock (Daly et al. 2012).

A robust comparison of hatchery and natural fish requires the accurate identification of hatchery fish. Although many hatchery fish are marked with a fin clip or other tag, the proportions of juveniles produced that are marked prior to release vary among hatcheries i.e. from ~10-100% in 2010-2011 (Appendix Table 1; [www.fpc.org](http://www.fpc.org)). Therefore, individual production type cannot be confidently determined by external markings in most Columbia River stocks, particularly for subyearling emigrants, which are marked at lower rates than yearlings. Natural tags, such as otoliths, can be used to differentiate production type (Zhang and Beamish 2000; Barnett-Johnson et al. 2007) because hatchery and natural Chinook salmon



experience different rearing environments during early life stages. Variation in temperature and/or growth rates of juveniles is reflected in otoliths, which produce daily growth increments (Neilson and Geen 1982). Therefore, otolith structure after the onset of exogenous feeding can be used to differentiate production type in juvenile and adult Chinook salmon (Zhang and Beamish 2000; Barnett-Johnson et al. 2007). However, a regional baseline that characterizes the variation in otolith growth between natural and hatchery fish is required and has not been developed within the Columbia River basin. Therefore, in Chapter Two, I develop a classification baseline using otolith structure of known hatchery and natural Chinook salmon from the Columbia River.

Marine survival (smolt-to-adult) has been estimated to range from < 1- 5% for hatchery and natural Chinook salmon (Cross et al. 1991; Bradford 1995; [www.fpc.org](http://www.fpc.org)), and marine mortality rates are hypothesized to be highest shortly after freshwater emigration during the first year at sea (Pearcy and McKinell 1997). Marine survival of salmon can be influenced by a variety of factors, including ocean conditions (Mantua et al. 1997), predation pressure (Emmett and Kruzikowsky 2008), prey abundance (Weitkamp et al. 2008), migration timing (Scheuerell et al. 2009), inter- and intra-specific competition (Miller et al. in press), juvenile growth (Duffy and Beauchamp 2011), and health (Jacobson et al. 2008). Larger or faster growing individuals often have increased survival, and predation rate can be inversely related to fish size (Sogard 1997; Ware 1975; Sheperd and Cushing 1980). Similarly, larger fishes can have a survival advantage during periods of starvation or exhaustion (Sogard 1997; Beamish and Mahnken 2001; Beamish et al. 2004) because larger fish

deplete energy reserves at slower rates than smaller individuals (Schultz and Conover 1999). This concept is here after referred to as “negative size-selective mortality”.

Most tests of size-selective mortality in salmonids compare size at two periods, once at the emigration and again when a cohort returns as adults (Zabel and Williams 2002; Scheuerell et al. 2009; Claiborne et al 2011). While studies have reported that larger individuals experienced higher survival (Zabel and Williams 2002; Claiborne et al. 2011), few studies explicitly examine natural fish (Zabel and Williams 2002). The question of whether size-selective mortality occurs within each production type is critical to address because natural fish are often smaller than hatchery fish (Beamish et al. 2012; Daly et al. 2012) and, thus may have a survival disadvantage. Negative size-selective mortality has been observed in yearling migrants from the Columbia River (Zabel and Williams 2002; Claiborne et al. 2011), and given that predation can be inversely related to size (Sogard 1997), we expect subyearling Chinook salmon may also experience negative size-selective mortality. A study of subyearling hatchery Chinook salmon in Puget Sound indicated that mortality during summer was consistently size-dependent (Duffy and Beauchamp 2011), but no studies have evaluated size-selective mortality of Columbia River subyearlings during the first summer at sea.

Over 100 million hatchery Chinook salmon are released each year in the Columbia River basin ([www.fpc.org](http://www.fpc.org)). There is concern of potential direct and indirect impacts of hatchery individuals on natural salmon populations via density dependence and competition between production types (National Research Council 1996; Rand et al. 2012). For example, high abundances of hatchery fish have been

hypothesized to limit the marine survival of natural fish due to food limitation, particularly during periods of poor ocean productivity (Levin et al. 2001). Similarly, Miller et al. (in press) observed that a mix of hatchery and natural juveniles had lower condition during the early marine period in higher survival years, which indicates inter- or intra-specific competition or selective mortality. On the other hand, recent mesocosm (Chittenden et al. 2010) and ecological field studies (Beamish et al. 2012) suggest that natural fish may have survival advantages over hatchery fish due to behavioral differences. For example, it is possible that an increased ability to avoid predators by natural juveniles may compensate for their smaller size.

It is possible that natural fish display greater diversity in migration size and timing than hatchery fish, which could lead to increased cohort survival in a variable marine ecosystem (Bottom et al. 2009). Migration timing in salmonids is, in part, influenced by environmental conditions (i.e. river flow) (Coutant and Whitney 2006; Sykes et al. 2009), and hatchery fish cannot migrate until after release. Therefore, it is possible that timing of marine entry may differ by production type and fish entering the marine environment at different times may exhibit differential survival (Scheuerell et al. 2009). However, no studies in the Columbia River have compared juvenile migration, i.e., the size at and timing of marine entry, in hatchery and natural Chinook salmon. A direct comparison will determine the spatial and temporal overlap of hatchery and natural fish during a critical life stage, and determine if there is potential for negative interactions, such as competition, between production types.

In Chapter Three, I tested four hypotheses: (1) there is spatial overlap between natural and hatchery Chinook salmon during early marine residence; (2) the timing of

marine entry will be more protracted for natural Chinook salmon; (3) hatchery fish experience negative size selection during early marine residence; and (4) natural fish will be smaller than hatchery conspecifics at marine entry but do not experience negative size-selective mortality. I combined info from genetic stock identification, otolith chemistry and structure, and physical tags to determine genetic stock of origin, juvenile size at and timing of freshwater emigration, marine residence, and production type (hatchery or natural). I focused on the subyearling life history of a federally managed genetic stock group (upper Columbia River summer and fall Chinook salmon) because it is one of the most abundant stocks and low rates of marking hatchery fish have made it difficult to assess impacts of hatchery production.

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**DIFFERENTIATING HATCHERY AND NATURAL UPPER COLUMBIA RIVER SUMMER AND FALL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*): APPROACHES AND APPLICATIONS**

**ABSTRACT**

Successful conservation and management of natural populations of Chinook salmon (*Oncorhynchus tshawytscha*) relies on understanding the interactions between production types (hatchery or natural) in the marine environment and determining if early marine survival varies between production types. However, studies specific to each production type are few because of the difficulty associated with identifying unmarked hatchery fish. I developed a model to classify fish to production type based on variation in otolith structure. Natural fish had a significantly wider median otolith width at hatching ( $240 \pm 26.9$ ) and at the onset of exogenous feeding ( $543 \pm 47.0$ ) than hatchery fish ( $229 \pm 17.2$  and  $518 \pm 35.0$  respectively). This may indicate that natural individuals experienced a greater duration between fertilization and the onset of exogenous feeding. The coefficient of variation of daily increment widths of natural fish ( $0.18 \pm .04$ ) immediately post exogenous feeding was significantly greater than the more uniform pattern observed in hatchery individuals ( $0.13 \pm .06$ ). In some hatchery individuals, a distinct check was observed that corresponded to an abrupt rearing tank transfer and change in water temperature. Multi-model selection criteria were used to identify the most appropriate model for classification, which included the coefficient of variation of increment widths, and the presence of a transfer check. Jack-knifed classification success was 92% indicating this tool may be useful in discriminating upper Columbia River Chinook salmon of unknown origin later during their lifecycle.

## INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) possess substantial ecological, cultural, and economic value and are captured in commercial, recreational, and subsistence fisheries. Historically, the Columbia River basin had several of the largest runs throughout the species' range from Big Sur, California to Alaska (Myers et al. 1998) and initial harvests in the late 1860s averaged over 11 million kilograms each year (Lichatowich 1999). By the late 1880s it was clear that runs were declining and hatchery programs became the primary solution for maintaining fisheries (Lichatowich 1999). There are potentially negative effects of artificial propagation for natural stocks such as reduced fitness via reproduction of less fit hatchery fish in the wild, and competition for food resources between production types (hatchery or natural) (reviewed by Araki and Schmid 2010). However, despite over a century of artificial propagation, the ecological impacts of hatchery production on many natural populations of Chinook salmon remain poorly understood (National Research Council 1996). Furthermore, there are relatively few field studies focused on understanding the interactions between production types of Chinook salmon in the marine environment (Levin et al. 2001; Daly et al. 2012; Beamish et al. 2012). In many cases, studies of some commercially important stocks from the Columbia River are limited by uncertainty in identifying unmarked hatchery individuals.

Certain populations of Chinook salmon are managed under the Endangered Species Act (ESA) as reproductively isolated groups termed Evolutionary Significant Units (ESU) which possess similar life-history characteristics such as adult run timing (Myers et al. 1998). In the Columbia River basin, there are eight ESUs of Chinook

salmon and five are listed under the ESA as either threatened or endangered, including the upper Columbia River spring, Snake River spring and summer, Snake River fall, upper Willamette River spring, and lower Columbia River. The upper Columbia River summer and fall, mid Columbia River spring, and Deschutes River summer and fall are not listed (Ford et al. 2011). Over 100 million hatchery Chinook salmon from these ESUs are released in the Columbia River basin each year ([www.fpc.org](http://www.fpc.org)). The percentage of unmarked hatchery Chinook salmon varies by year, ESU, and between life history type, i.e., subyearling (migrate to sea before first winter) and yearling (migrate to sea after first winter) migrants. Over the last decade, the marking rate of hatchery subyearling Chinook (an adipose fin clip or Coded Wire Tag) in some ESUs has been as low as 10% (Figure 2.1). In recent years, mark rates of hatchery individuals increased substantially to nearly 70% in some ESUs (Fig. 2.1; Appendix Table 1). However, the current inability to accurately identify all hatchery fish in current and historical collections precludes robust comparisons between hatchery and natural fish (Fig. 2.1). Methods to distinguish between unmarked hatchery and natural individuals could contribute novel insights regarding variation in stage-specific survival, competition, and variation in size at and timing of freshwater emigration between these two production types.

Several approaches have been used to distinguish hatchery and natural Chinook salmon, including scale morphology (Connor et al. 2005), size at estuary entrance (Campbell 2010), otolith chemistry (Tomaro 2010; Johnson et al. 2012) and structure (Volk et al. 1990; Zhang et al. 1995; Barnett-Johnson et al. 2007), and external and internal tags (Daly et al. 2012). Tradeoffs between accuracy and cost

exist among the various methods. For example, otolith thermal marking is less expensive than other individual tags and may be used to distinguish the production type, hatchery of origin, and brood year of an individual fish (Volk et al. 1990; Volk et al. 1999). However, not all hatcheries in the Columbia River basin thermally mark their juveniles (WDFW, pers. comm.) and thus only some of the hatchery production can be identified. External tags, such as adipose fin clips are easily identifiable in field studies and estimates of the number of unmarked hatchery individuals present in a sample can be simply calculated if the clip rate within hatcheries is known (Daly et al. 2012). However, there is error associated with this method because it relies on the mean mark rate across numerous hatcheries, and mark rates and post-release survival can vary among hatcheries (Weitkamp et al. 2012). Furthermore, this method only produces a proportional estimate of each production type; one cannot determine the production type of individuals, thus preventing comparisons among individuals. Conversely, chemistry techniques, such as comparison of sulfur isotope values near the exogenous feeding check, have been shown to classify production type with ~100% accuracy (Webber et al. 2002; Johnson et al. 2012). This is because  $^{34}\text{S} / ^{32}\text{S}$  is incorporated in otoliths from the diet, and  $^{34}\text{S} / ^{32}\text{S}$  values do not typically overlap between dietary items of natural (aquatic insects) and hatchery individuals (marine protein) (Webber et al. 2002). However, the high cost associated with quantifying  $^{34}\text{S} / ^{32}\text{S}$  with an ion microprobe (~\$100 / fish after otolith preparation) is not practical for all studies. Otolith structure has been shown to provide a relatively simple, low cost, and accurate method of classifying production type (Zhang et al. 1995; Barnett-Johnson et al. 2007; Volkoff and Titus 2007).

Chinook salmon otoliths are formed in daily increments and their structure has been shown to mark life-history transitions, such as the initiation of exogenous feeding. Therefore, they provide a robust retrospective tool that persists throughout a fish's lifecycle (Marshall and Parker 1982; Campana and Neilson 1985). For example, hatchery and natural individuals experience dissimilar rearing conditions between initiation of exogenous feeding and freshwater emigration (or hatchery release) that can result in significant differences in otolith structure.

The width of otolith daily increments can vary depending on food abundance, feeding frequency, and temperature (Neilson and Geen 1982; Campana and Neilson 1985). Uniform rearing conditions, such as constant temperature and food ration, can result in lower variance in otolith increment width in hatchery fish compared with those reared naturally (Zhang et al. 1995). Natural fish can also have a more prominent exogenous feeding check (Barnett-Johnson et al. 2007). Using variance in increment width and prominence of the exogenous feeding check Barnett-Johnson et al. (2007) was able to classify the production type of known hatchery adult Chinook salmon from the Central Valley of California with 90% accuracy and adults from the Gulf of Alaska with 90% and 75% accuracy (hatchery and natural, respectively). Therefore, otolith structure may be useful in determining production type in field studies of Columbia River Chinook salmon with unknown rearing history.

Stocks of Chinook salmon are reproductively isolated and in turn are genetically distinct (Waples et al. 2004). An approach to accurately determine production type within a stock of juveniles could provide novel insights into factors limiting marine survival. For example, studies have observed that hatchery fish are

often larger than natural conspecifics (Daly et al. 2012; Beamish et al. 2012), and larger fish may experience greater survival to adulthood than smaller individuals (Zabel and Willimas 2002; Claiborne et al. 2011). Thus, natural fish may have survival disadvantages during critical life-history transitions in the marine environment. The development and evaluation of a production type classification model based on otolith structure would allow direct comparisons of hatchery and natural individuals collected in field studies at various stages after release. Therefore, I determined if otolith structure consistently and predictably varies between hatchery and natural Chinook salmon from the upper Columbia River summer and fall (UCR Su/F) stock.

## METHODS

### *Collection of Hatchery and Natural Fish*

Hatchery fish were collected from several sources in the upper Columbia River to develop a classification baseline. In 2011, Washington Department of Fish and Wildlife (WDFW) personnel collected individuals from the summer component of the UCR Su/F stock from: the Eastbank Hatchery, Similkameen Pond, Carlton Pond, and Wells Hatchery (Fig. 2.2; Table 2.1). Individuals from these four locations represent summer-run broodstock from the Wenatchee, Methow, Okanogan, and Columbia (at Wells Hatchery) rivers. Hatchery individuals were collected between 30-50 days after yolk-sac absorption or at the onset of exogenous feeding when fish were transferred to ponds.

Additional hatchery fish were collected during National Oceanic and Atmospheric Administration (NOAA) research surveys targeting juvenile salmonids

at the mouth of the Columbia River and off the coasts of Oregon and Washington. Collection of coded wire tagged (CWT) individuals from the UCR Su/F stock provided information on production type (hatchery or natural), hatchery of origin, and brood stock river origin (Regional Mark Processing Center; [www.rmpec.org](http://www.rmpec.org)). CWT hatchery individuals from the fall-run component of the UCR Su/F stock ( $n = 9$ ) were used to expand hatchery representation in the baseline (Fig. 2.2; Table 2.1). The remaining 10 CWT individuals were used to independently validate the accuracy of our baseline assignments (Fig. 2.2; Table 2.1).

Natural summer Chinook salmon from the UCR Su/F stock were collected from two sources: (1) the Wenatchee River at Monitor, WA in 2011, and (2) along the Hanford Reach on the main stem Columbia River in 2012 (Fig. 2.2; Table 2.1). Fish were collected using a dip-net in 2011 and beach seine in 2012 and assumed to be natural based on date collected (i.e., before the majority of hatchery releases in the region), size (Table 2.1), and the presence of an intact adipose fin. Natural individuals captured on the Wenatchee River represent summer-run individuals and those collected in the Hanford Reach represent fall-run individuals (Myers et al. 1998).

#### *Otolith Preparation*

Sagittal otoliths were extracted, washed in deionized water, and stored dry. The left otolith, or right when left was unavailable, was mounted on a glass slide with thermoplastic resin and ground using successive grits of lapping film (Buehler ®) and polished using an aluminum oxide slurry. Both sides of each otolith were polished until the primordia and exogenous feeding check were evident. Digital images of

each otolith were taken using a compound microscope (Leica DM1000; 100X, 200X, and 400X) with a mounted camera (Leica DC30).

#### *Otolith Structural Analysis*

Six metrics were collected from each otolith. Qualitative measurements included (1) the prominence of the exogenous feeding check and (2) the presence or absence of a transfer check. The exogenous feeding check was ranked from (1) to (3): (1) characterized by several faint, non-distinct checks that are not present along the entire circumference of the otolith; (2) one to several distinct narrow checks, clear on all portions of otolith; or (3) a prominent distinct, wide check that was clear on all portions of otolith. In some individuals, there was a prominent and distinct exogenous feeding check followed by a second prominent check approximately 30 days after the exogenous feeding check (Fig. 2.3), which I refer to as the transfer check. The transfer check was only observed in individuals from the Wells Hatchery and is likely related to stress caused by their source water system (WDFW, pers. comm.). Specifically, individuals were reared at temperature ~6 C° warmer than other hatcheries producing UCR Su/F in this study. This has been associated with high rates of mortality during yolk-sac absorption and subsequent transfers (WDFW, pers. comm.).

Quantitative measurements included: (3) otolith width at the hatch check; (4) otolith width at the exogenous feeding check; (5) mean increment width for the first 20 days after the exogenous feeding check (MIW); and (6) coefficient of variation of first 20 daily increments after the exogenous feeding check. Twenty days was selected because most natural individuals used to develop the baseline displayed 20-



36 daily increments after the exogenous feed check. Otolith width at the hatch and exogenous feeding checks represent the distance across each otolith through the primordia at the widest point for each respective check mark (Fig. 2.3). The hatch check was identified as described by Marshall and Parker (1982). The exogenous feeding check was identified as described by Zhang et al. (1995) and validated with individuals with known rearing and feeding history.

#### *Statistical Analysis*

Six metrics were generated for each fish including otolith width at the hatch and exogenous feeding checks, prominence of the exogenous feeding check, presence or absence of a transfer check, and the mean width and coefficient of variation of the first 20 daily increments after the exogenous feeding check (Fig. 2.3). I compared the six metrics between hatchery and natural individuals using one of three approaches, depending on the distributional characteristics of the metrics. (1) Comparisons of non-continuous data (prominence of the exogenous feeding check and presence or absence of a transfer check) were made using the Chi-square test. (2) Comparisons between non-parametric variables (otolith width at the exogenous feeding check and coefficient of variation of daily increments) were made using the Wilcoxon rank sum test. (3) Comparisons between variables that met the assumptions of normality and homogenous variance (otolith width at the hatch check, and mean increment width) were made with Welch's t-test.

A logistic regression approach was used to generate a classification model. A logistic approach was chosen to incorporate both continuous and non-continuous metrics and predict a binary response, natural or hatchery (Ramsey and Schafer 2002).

Logistic regression also allows fitted values from the model to be expressed as probabilities of production type, which allow for evaluation of assignment accuracy across a range of probabilities. Akaike Information Criterion ( $AIC_C$ ) corrected for small sample size (Hurvich and Tsai 1989) was used to measure relative goodness-of-fit of models and the model with the lowest  $AIC_C$  was retained as the final model (Table 2.3).

Accuracy of the final model was evaluated using three approaches. First, I generated an estimate of internal accuracy, i.e. the number of known hatchery and natural individuals classified incorrectly using a probability cutoff of 0.5. Second, I used a jack-knife estimate, which provides a robust estimate of accuracy by removing each individual and evaluating the model for each case. Third, I used the final classification model to predict production type of UCR Su/F hatchery individuals that were collected in the estuary and ocean and had CWTs but were not used to develop the logistic model (Table 2.1). All statistical analysis was done using the software R (R Development Core Team 2012) and the programming package DAAG (Maindonald and Braun 2012).

## RESULTS

### *Otolith Structure*

Hatchery individuals had a significantly smaller mean otolith width at the hatch check (Fig. 2.4 and Table 2.2.; Welch's t-test:  $p = 0.02$ ) and a smaller median otolith width at the exogenous feeding check than natural individuals (Fig. 2.4; Table 2.2; Wilcoxon rank sum test:  $p < 0.01$ ). Hatchery individuals had similar mean increment width as natural individuals (Fig. 2.4; Table 2.2; Welch's t-test:  $p = 0.17$ ).

Natural individuals exhibited greater variation in mean increment width and had a significantly higher coefficient of variation in increment widths (Fig. 2.4; Table 2.2; Wilcoxon rank sum test:  $p < 0.01$ ). The transfer check was only present in Wells Hatchery fish (Table 2.2) and effectively separated this group from the rest of the fish (Chi-square test:  $p < 0.01$ ). The transfer check was observed in 92% of hatchery fish from the Wells Hatchery that were used in the development of the classification model. Two of the ten individuals used to independently validate the classification model originated from the Wells Hatchery and the transfer check was observed in one of these individuals. The prominence of the exogenous feeding check did not differ between natural and hatchery individuals (Table 2.2; Chi-square test:  $p = 0.63$ ).

#### *Classification Model*

The most parsimonious classification model incorporated the coefficient of variation of increment widths and the presence or absence of a transfer check as predictors of production type (Table 2.3). The internal and jack-knife accuracy of this classification model was 93% and 92%, respectively. A relative frequency histogram of fitted values indicated a distinct separation between production types using a probability cutoff of 0.5 (Fig. 2.5). The classification model determined hatchery individuals with 91% internal accuracy and natural with 94%. Ninety percent of CWT hatchery individuals ( $n = 10$ ) used to independently validate the classification model were classified correctly. These CWT fish were from two emigration years (2010 and 2011), which indicates that the model correctly classified hatchery individuals collected in the ocean and estuary from multiple outmigration years.

## DISCUSSION

A critical step in the conservation of natural Chinook salmon is to develop an understanding of the biotic and abiotic factors related to survival during specific life stages, including the impact of hatchery conspecifics. Currently, our understanding is hindered by the release of large numbers of unmarked hatchery individuals. Several studies have observed that differences in rearing environment result in distinct patterns of otolith formation that are useful in identifying hatchery and natural individuals. This is the first study to determine that similar otolith metrics can be used to classify production type of Chinook salmon in the Columbia River with a high degree of accuracy (92% jack-knife accuracy). The ability to distinguish production type during the early marine phase, which is a stage characterized by high mortality, should increase our understanding of the impacts of artificial propagation on natural individuals and populations.

Temperature and food ration are likely the most influential factors related to otolith structure (Campana and Neilson 1985). The results of this study are consistent with previous observations that natural Chinook salmon display more variable increment width after initiation of exogenous feeding than hatchery fish (Zhang et al. 1995; Barnett-Johnson et al. 2007). This consistency is likely attributable to the relatively constant ration and temperature environment experienced by hatchery individuals compared with more variable environments experienced by natural individuals. However, I observed a smaller mean increment width in natural individuals (2.02  $\mu\text{m}$ ) than did Zhang et al. 1995 (2.37  $\mu\text{m}$ ) and Barnett-Johnson et al. 2007 (2.49 and 2.50  $\mu\text{m}$ ). Similarly, mean increment width was smaller in hatchery

individuals from this study (Table 2.2; Zhang et al. 1995; Barnett-Johnson et al. 2007). It is likely that differences in temperature, food availability and composition, and photoperiod among these study systems, such as the colder climate of the upper Columbia River, may account for the observed differences in increment width. For example, in March 2011, temperature of the Columbia River at McNary Dam, Washington ranged from 3.74 and 6.27 C° while temperature over the same period on the American River at Fair Oaks California ranged between 7.90 and 10.80 C° ([www.cbr.washington.edu](http://www.cbr.washington.edu); [www.nwis.waterdata.usgs.gov](http://www.nwis.waterdata.usgs.gov)). I observed a similar coefficient of variation for increment width in natural individuals (0.18) as Zhang et al. 1995 (0.16) and Barnett-Johnson et al. 2007 (0.19). However, I documented more variation in increment width of hatchery individuals (CV = 0.05-0.32) than did Zhang et al. (1995) (CV = 0.06-0.17). The higher variation in increment widths in our study can be accounted for by the Wells Hatchery fish (CV = 0.08-0.32), which were more variable than any other hatchery source (CV = 0.05-0.16).

Otolith daily increments consist of one opaque zone and one translucent zone. However, discontinuity in formation does occur and the occurrence of several concurrent translucent zones, referred to as checks, can occur as a result of stress, or ontogenetic events such as hatching and the onset of exogenous feeding (Marshall and Parker 1982; Campana et al. 1985; Zhang and Runham 1992). Barnett-Johnson et al. (2007) found that natural Chinook salmon from the Central Valley, California had a more prominent exogenous feeding check than hatchery individuals. I did not observe a similar pattern, which could be related to variation in hatchery practices and rearing conditions throughout the upper Columbia River. For example, individuals from the

Wells Creek Hatchery had a mean prominence of the exogenous feeding check score of 2.8 while all other hatchery individuals had a score of 1.8. When Wells Creek Hatchery individuals are removed from the analysis, natural individuals had slightly more prominent exogenous feeding checks (mean = 2.00 vs. 1.82, for natural and hatchery individuals respectively) although the difference was not significant (Chi-square test:  $p = 0.36$ ).

I observed a previously unreported check mark that I called the “transfer check”. A second prominent check approximately 30 days later was only observed in hatchery individuals from the Wells Hatchery. I conclude that the transfer check is related to physiological stress and change in rearing water temperature that individuals experience when being transferred from rearing tanks to raceways approximately 30-45 day after the initiation of exogenous feeding. The distinct and prominent exogenous feeding check is likely related to this facility’s well-water system which results in warmer water that causes unusually high mortality as result of yolk-sac coagulation (WDFW, pers. comm.). I obtained two Wells Hatchery CWT individuals emigrating from freshwater captured at the mouth of the Columbia River and identified the transfer check in 1 of the 2 individuals emigrating in 2011 indicating the transfer check is useful for separating Well Hatchery fish in field studies. When Wells Hatchery fish were removed from the classification model the coefficient of variation alone classified production type with 91% jack-knife accuracy (not shown). This finding indicates that most hatcheries had rearing conditions that resulted in uniform increment formation and could be accurately classified using only the coefficient of variation of daily increments.

Natural Chinook salmon can have larger otoliths at hatching and at the onset of exogenous feeding compared with hatchery individuals (Zhang et al. 1995; Volkoff and Titus 2007). Similarly, in this study natural individuals had larger otolith widths at the hatch and exogenous feeding checks. Slower growing fish can have larger otoliths than faster growing individuals at similar ages (Reznick et al. 1989). Both temperature and food ration were likely higher for hatchery Chinook salmon in this study thus they may have experienced higher somatic growth rates. Differences in otolith size at exogenous feeding have been used to differentiate production type in Chinook salmon (Volkoff and Titus 2007). Volkoff and Titus (2007) predicted production type of Central Valley Chinook salmon with nearly 80% accuracy based primarily on otolith size at exogenous feeding. Conversely, I observed an internal accuracy of 60% and 61% for models with independent variables EOW and both EOW and HOW, respectively (not shown). Our study indicates that although both EOW and HOW differed significantly between production types, they alone may not be accurate predictors of production type for individuals from the upper Columbia River.

One potential deficiency of the classification model is the limited spatial representation of natural individuals. However, Wenatchee River summer run and Hanford Reach Columbia River fall run Chinook salmon are primary contributors to natural production in the UCR Su/F ESU (Myers et al. 1998) and thus likely account for a substantial portion of the natural individuals in this stock group. Furthermore, natural fish from both rivers had a similar coefficient of variation of daily increments (0.18), although Hanford Reach fish had larger increment widths (2.82  $\mu\text{m}$ ) than

natural fish from the Wenatchee River (1.74  $\mu\text{m}$ ). This may indicate that there is variability in abiotic conditions (i.e. temperature) between rearing sites that influences daily increment formation, but higher variation in formation may be consistent in fish rearing in the wild. I was unable to confirm this by independently validating our classification model with additional natural individuals, but this could be completed with future collections. I observed relatively similar accuracy in classifying CWT hatchery fish (90%), and hatchery fish incorporated in the model (91%) but a slightly higher accuracy in classifying natural fish (94%). Because I have lower accuracy in classifying hatchery fish, and some hatcheries may have rearing conditions that result in similar CVIW as observed in natural fish, I may expect a limited bias towards classifying unknown hatchery fish as natural. This could be further evaluated in field studies because some externally unmarked hatchery individuals from the UCR Su/F stock have been thermally marked.

Thermal marking of otoliths involves manipulating rearing water temperature to produce distinct patterns of otolith increment formation (Volk et al. 1990; Volk et al. 1999). These patterns can be used to identify the production type of unmarked hatchery fish in later stages (Volk et al. 1999). Fish are generally marked during yolk sac absorption and/or after fish are feeding exogenously (Volk et al. 1999). In 2010 and 2011 100% hatchery individuals from the Priest Rapids Hatchery were thermally marked (WDFW pers. comm.). Unmarked hatchery individuals from the Priest Rapids Hatchery account for 14% and 17% of unmarked hatchery releases of UCR Su/F in the Columbia River basin in 2010 and 2011, respectively. Therefore, any unmarked fish from this hatchery captured in field studies could provide an additional



assessment of accuracy by determining production type based on the classification model developed in this study and the presence or absence of a thermal mark.

In conclusion, I show that several measurements of otolith structure differ among hatchery and natural UCR Su/F Chinook salmon. However, only two variables, the variation in increment width and presence of a transfer check, were in the most parsimonious classification model. Our one way independent validation indicated that hatchery individuals were accurately (90%) identified using our classification model. In the Columbia River, marking rates of hatchery Chinook salmon have fluctuated markedly in the last decade and are still well below 100% in some hatcheries (Fig. 2.1; Appendix Table 1). Our results indicate that a robust determination of production type is possible. Accurate identification of genetic stock of origin and production type (hatchery or natural), will allow workers to estimate the relative survival of natural fish, if competition between production types is occurring, or generate basic biological information, such as size at and timing of marine entry. Furthermore, unmarked hatchery fish that return to spawning grounds confound estimates of natural escapement and can inflate growth estimates for natural populations (Johnson et al. 2012). Therefore, this classification model and similar approaches could be useful for determining the degree to which hatchery stray rates are subsidizing natural production. Future studies should utilize natural tags, such as otolith structure, to address these and other question to inform management decisions and ultimately aid in the conservation of natural Chinook salmon.

## TABLES

Table 2.1. Hatchery or rearing site, sample size ( $n$ ), source (R = in river, H = hatchery, CWT = CWT-fish from estuary or ocean) adult run time (Su = Summer, Fa=Fall), mean fork length (FL) at capture ( $\pm$  SD), emigration year, and production type (N = Natural, H = Hatchery) of upper Columbia River summer and fall Chinook salmon used in this study. Rearing information for field-collected individuals captured during their marine migration was determined from Coded Wire Tags. Sample sizes in parentheses indicate the CWT individuals used to assess model accuracy.

Rearing Area	$n$	Source	Adult Run Time	FL (mm)	Emigration Year	Production type
Lower Wenatchee River	50	R	Su	40 (3.6)	2011	N
Hanford Reach Columbia River	17	R	Fa	44 (3.3)	2012	N
Carlton Rearing Pond	9	H	Su	37 (4.1)	2011	H
Priest Rapids Hatchery	2 (2)	CWT	Fa	167 (22.1)	2010	H
Umatilla Hatchery	3 (2)	CWT	Fa	134 (39.7)	2010 & 2011	H
Klickitat Hatchery	2 (2)	CWT	Fa	99 (27.7)	2010 & 2011	H
Little White Salmon Hatchery	2 (2)	CWT	Fa	115 (29.5)	2010 & 2011	H
Wells Hatchery	13 (2)	H & CWT	Su	49 (2.7)	2010 & 2011	H
Similkameen Rearing Pond	7	H	Su	42 (4.3)	2011	H
Wenatchee Rearing Pond	20	H	Su	43 (3.1)	2011	H

Table 2.2. Median, standard deviation (in parentheses), and sample sizes ( $n_H$  = hatchery,  $n_N$  = natural) for otolith analysis of hatchery and natural Chinook salmon. EOW = otolith width at exogenous feeding; HOW = otolith width at hatching; MIW = otolith increment width; CVIW = coefficient of variation of increment widths; PE = prominence of the exogenous feeding check; and TC = transfer check. Also shown are results (p-values) from statistical comparisons and bold indicates significant at  $\alpha = 0.05$ . A “\*” denotes Wilcoxon rank sum test was used, “\*\*” denotes a Welch’s t-test was used and “\*\*\*” denotes a Chi-square test was used.

Otolith Metric	Natural	Hatchery	$n_H$	$n_N$	$p$ -value
EOW ( $\mu\text{m}$ )*	543.41 (46.99)	518.34 (35.01)	58	67	< <b>0.01</b>
HOW ( $\mu\text{m}$ )*	240.26 (26.87)	228.93 (17.21)	58	67	<b>0.02</b>
MIW ( $\mu\text{m}$ )**	2.02 (0.53)	2.15 (0.52)	58	67	0.17
CVIW*	0.18 0(.04)	0.13 (0.06)	58	67	< <b>0.01</b>
PE (1-3)***	2.0 (0.74)	2.09 (0.78)	58	67	0.63
TC (0,1)***	0.0 (0.0)	0.21 (0.41)	58	67	< <b>0.01</b>

Table 2.3. Model selection including number of independent variables ( $k$ ), sample size ( $n$ ), Akaike Information Criterion corrected for small sample size ( $AIC_C$ ), delta ( $\Delta$ ) $AIC_C$ , and accuracy of each classification model. Independent variables are coefficient of variation of increment width (CVIW), transfer check (TC), hatch check otolith width (HOW), and exogenous feeding check otolith width (EOW).

Model	$k$	$n$	$AIC_C$	$\Delta AIC_C$	Accuracy (%)
CVIW + TC	2	125	50.88	0.00	92.8
HOW + CVIW + TC	3	125	51.47	0.59	91.2
EOW + CVIW + TC	3	125	52.69	1.81	92.0
EOW + HOW + CVIW + TC	4	125	53.47	2.59	91.2
HOW + CVIW	2	125	142.79	91.91	77.6
EOW + HOW + CVIW	3	125	144.48	93.60	74.4
CVIW	1	125	145.32	94.44	81.6
EOW + HOW + TC	3	125	146.45	95.57	64.0
HOW + TC	2	125	151.29	100.41	64.8
TC	1	125	156.76	105.88	63.2

## FIGURE LEGENDS

Figure 2.1. The proportion of marked and unmarked subyearling upper Columbia River summer and fall (UCR Su/F) Chinook salmon juveniles released from hatcheries in the mid- and upper Columbia River from 2002-2011. The UCR Su/F are described in Myers et al. (1998) as originating above McNary Dam but hatchery production extends into the mid- Columbia River above Bonneville Dam. Light grey bars indicate the proportion of unmarked hatchery individuals released and dark grey bars indicate the proportion of marked hatchery individuals released in each year. Overall, 114,693,274 unmarked and 86,814,977 marked hatchery individuals were released in Columbia River basin from 2002-2011. Data source: The Fish Passage Center ([www.fpc.org](http://www.fpc.org)).

Figure 2.2. Map of the Columbia River basin indicating the rearing location of upper Columbia River summer and fall (UCR Su/F) Chinook salmon used in this study. Filled circles indicate rearing locations of hatchery individuals while open triangles indicate collection locations for natural juveniles. The dark grey outline represents the geographic extent of UCR Su/F stock group.

Figure 2.3. A) Schematic of an otolith from a hatchery individual showing uniform daily increment widths indicative of a stable rearing environment; B) Schematic of an otolith from a natural individual with variable increment widths indicative of a stochastic rearing environment. EOW = otolith width at exogenous feeding; HOW = otolith width at hatching; MIW = otolith increment width; CVIW = coefficient of variation of increment widths; PE = prominence of the exogenous feeding check; and TC = transfer check.

Figure 2.4. Boxplots of metrics of otolith structure of hatchery and natural individuals compared in this study. EOW = otolith width at exogenous feeding; HOW = otolith width at hatching; MIW = otolith increment width; CVIW = coefficient of variation of increment widths. Open boxes indicate natural and filled boxes indicate hatchery. Black lines indicate median values and box and whiskers show 95% confidence intervals. Values outside the 95% confidence intervals are shown as black circles and asterisk above boxes denote significant differences ( $\alpha \leq 0.05$ ).

Figure 2.5. Histogram of fitted values of the production type classification model (hatchery or natural). Open bars indicate natural and filled bars indicate hatchery production type. Fitted < 0.5 indicate classification as hatchery and > 0.5 indicate classification as natural.

## FIGURES

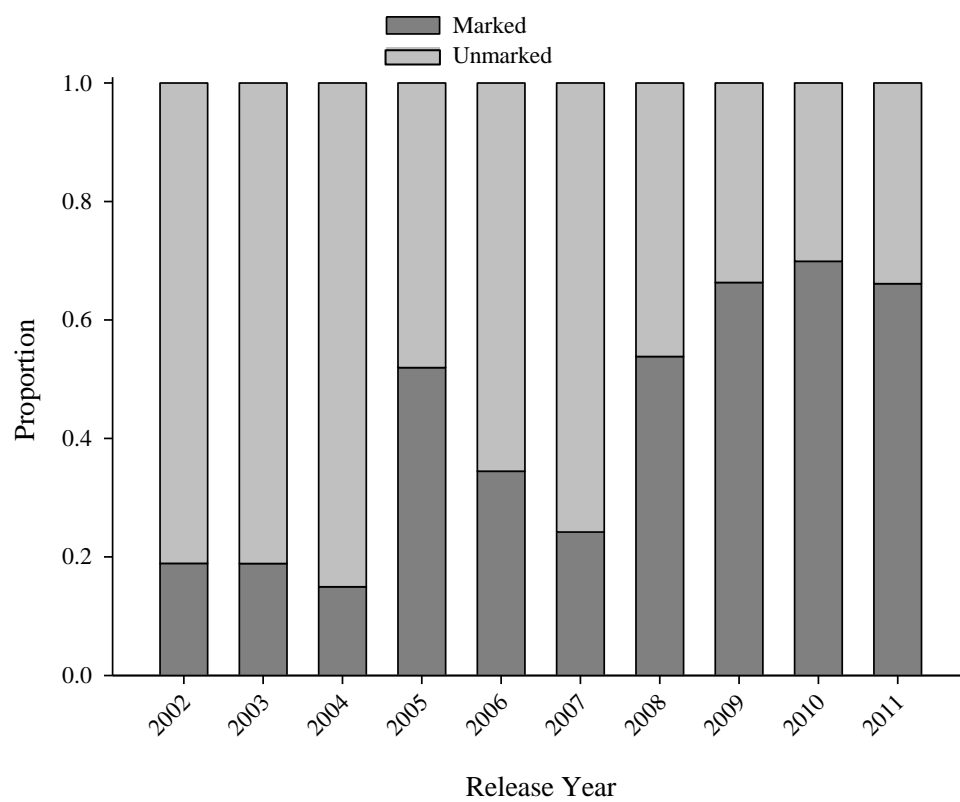


Figure 2.1

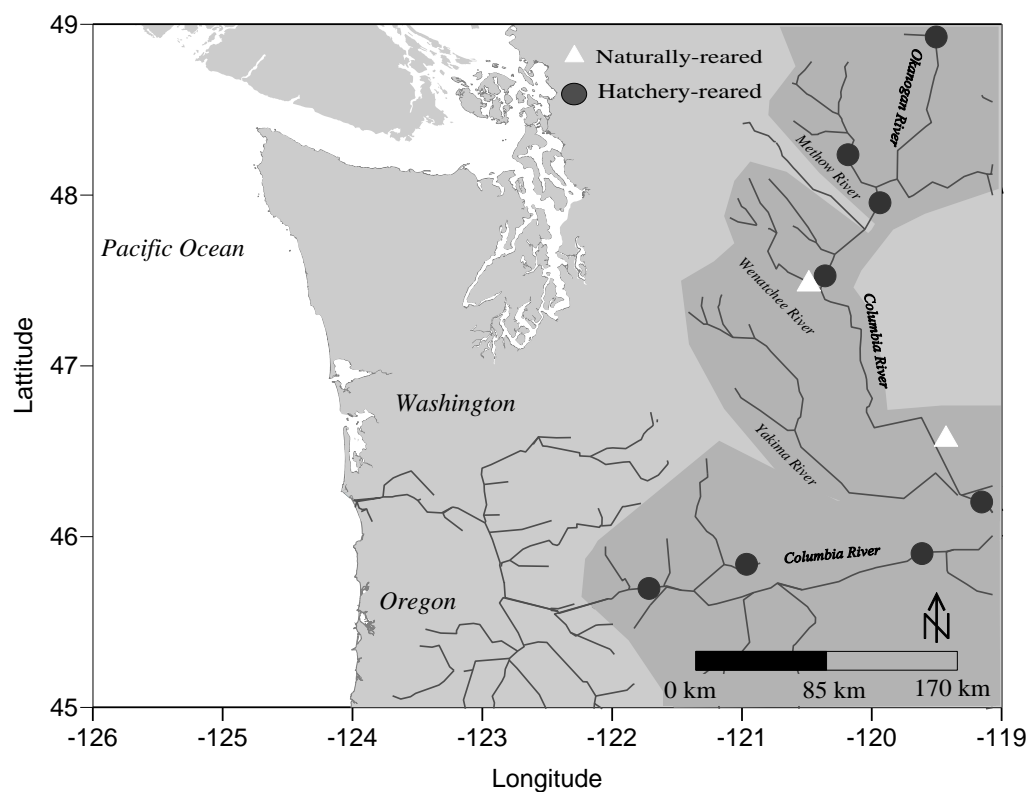


Figure 2.2

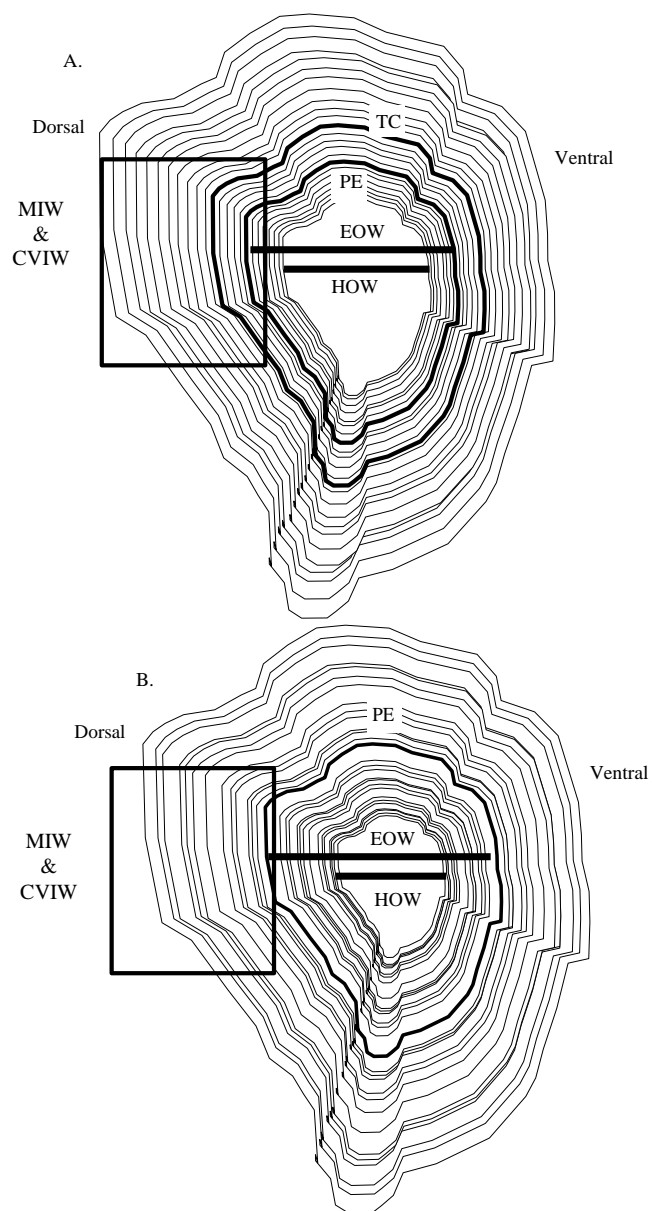


Figure 2.3



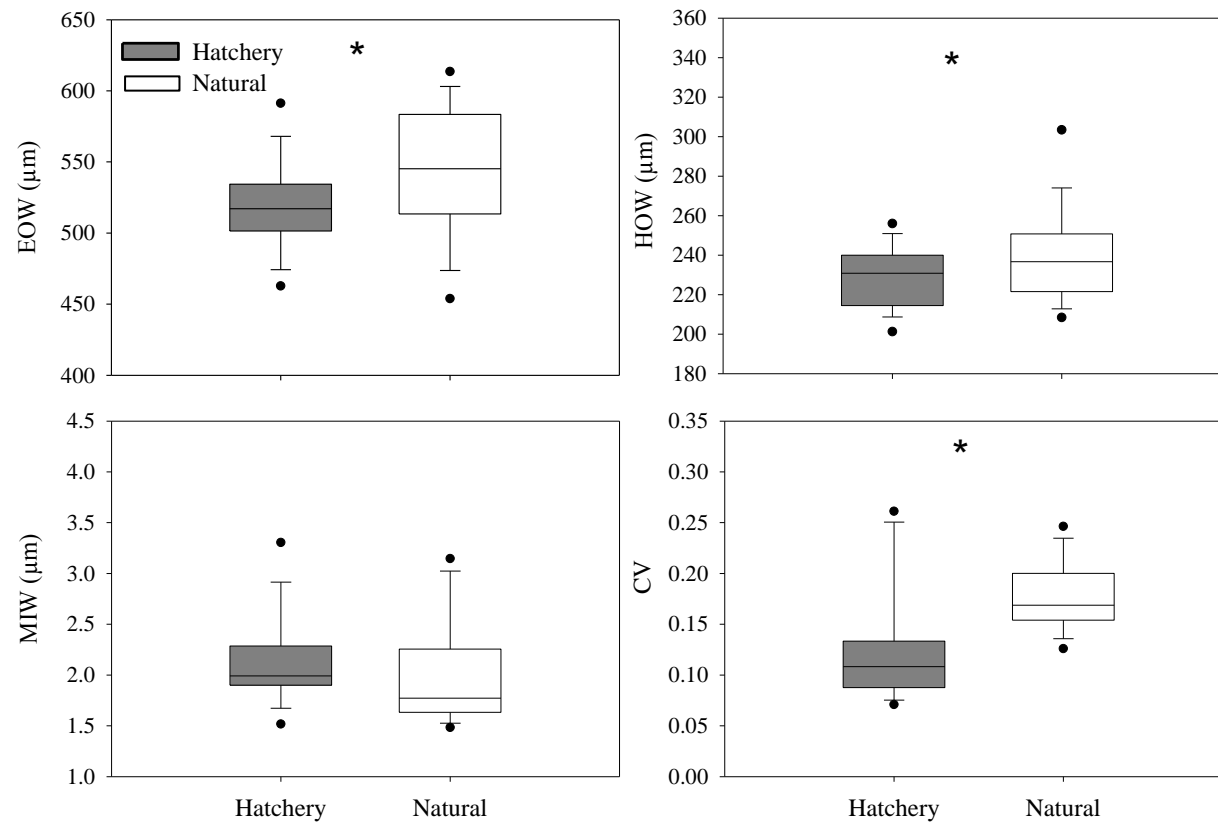


Figure 2.4

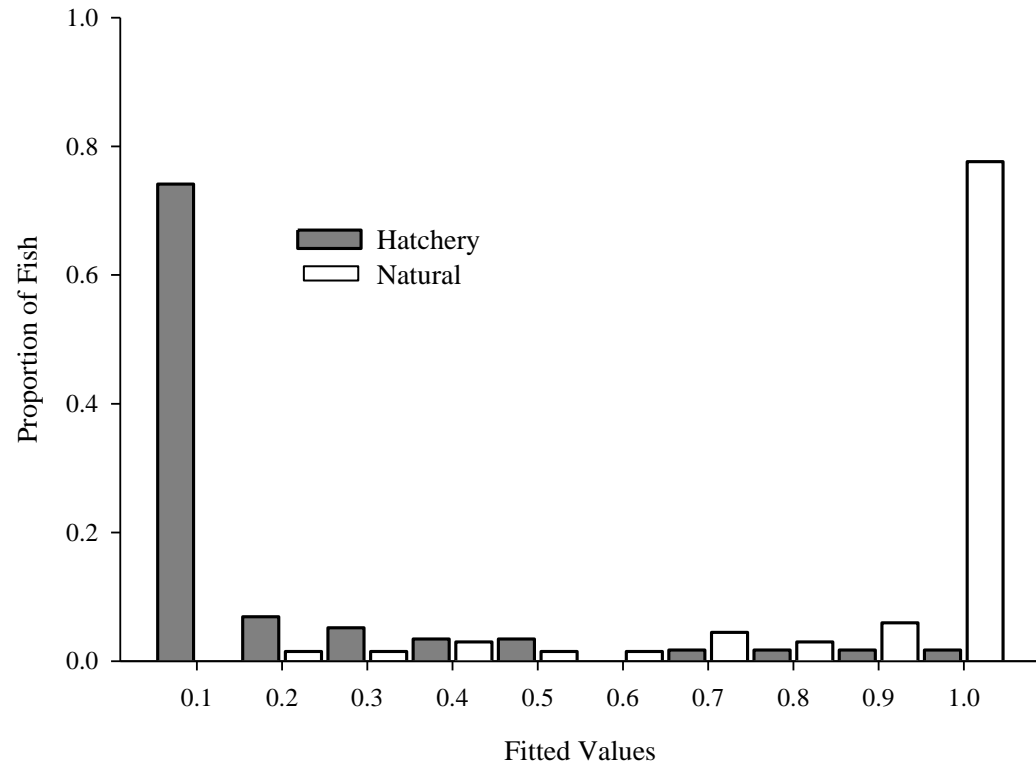


Figure 2.5

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### **CHAPTER THREE: A COMPARISON OF EARLY MARINE RESIDENCE IN HATCHERY AND NATURAL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)**

#### **ABSTRACT**

For many fish species, it is not clear if the mechanisms of mortality are similar for naturally and artificially propagated individuals. For Chinook salmon (*Oncorhynchus tshawytscha*) survival advantages for either production type (hatchery or natural) are often inferred, but seldom shown. Furthermore, high levels of mortality are often associated with marine entrance and early ocean life. To determine if mechanisms of mortality were similar for each production type, we compared attributes of juveniles from the upper Columbia River summer and fall population segment captured in the estuary with survivors captured later off the coast in 2010 and 2011. We determine stock of origin, size and timing of marine entry and production type (hatchery or natural) using genetic stock identification, otolith chemistry and structure, and physical tags. Overall the timing of marine entry (May-September) was similar among production types and 80% of fish captured in the estuary had resided in saline waters for < 3 days before capture, but residence varied interannually. In the ocean, there was clear spatial overlap between hatchery and natural fish, and no difference in growth, size at capture, or back calculated size at marine entry between production types. Comparisons between juveniles in the estuary and ocean provided no evidence for size-selective mortality, but the mean percentage of natural fish in ocean collections was 17% ( $\pm 4.8$ ) greater than in the estuary, which may suggest enhanced survival of natural fish. Further research is

needed to examine sampling bias and to elucidate potential survival advantages of natural fish over hatchery individuals.

## INTRODUCTION

Management of anadromous fishes is inherently difficult because population abundances fluctuate in relation to anthropogenic, environmental, and biotic factors in freshwater, estuarine, and marine habitats. Chinook salmon (*Oncorhynchus tshawytscha*) is an ecological and economically important anadromous species in the Pacific Northwest, USA. In the Columbia River basin, average annual harvest of Chinook salmon is estimated to have declined by 80% since initial western exploitation (Lichatowich 1999). Due to continuing declines, several stocks of Chinook salmon were listed under the U.S. Endangered Species Act in the 1990s. However, five of eight federally managed population segments remain listed as either threatened or endangered (Myers et al. 1998; Ford et al. 2011). Hatchery programs in the Columbia River basin release > 100 million Chinook salmon annually, primarily to increase harvestable biomass ([www.fpc.org](http://www.fpc.org)). Despite negative effects associated with hatchery rearing observed in many other species (reviewed by Araki and Schmid 2010), it is not clear if hatchery Chinook salmon negatively interact with or impact natural conspecifics, i.e. competing for resources or reproducing in the wild, which is a primary concern in recovery plans (National Research Council 1996; Fresh et al. 1997; Rand et al. 2012).

Several studies have demonstrated strong relationships between ocean conditions during juvenile emigration and adult survival (Mantua et al. 1997; Rupp et al. 2012; Burke et al. 2013) and marine mortality is likely greatest during the first

summer at sea (Pearcy 1992; Percy and McKinnell 1997). However, the mechanisms regulating survival and the timing of mortality during the first year at sea are not clear. Several factors during early marine residence are related to variation in adult survival of Chinook salmon including; growth shortly after marine entry (Duffy and Beauchamp 2011; Tomaro et al. 2012), timing of marine entry (Scheuerell et al. 2009), and juvenile size at marine entry (Claiborne et al. 2011) and in freshwater (Zabel and Williams 2002). However, few studies have examined these factors specific to production type (hatchery or natural) (Levin and Williams 2002; Zabel and Achord 2004; Daly et al. 2012). Therefore, information on size at and timing of marine entry and marine growth, and marine distribution exist for only a few genetic stock groups in the Columbia River and have not been compared between production types. Given that hatchery and natural Chinook salmon can experience differential survival rates (Beamish et al. 2012) or negatively interact (i.e. density dependence) during early marine residence (Levin and Williams 2002), it is important to understand the migrator behavior and the extent of spatial and temporal overlap between hatchery and natural juveniles during early marine residence.

The direct causes of mortality for hatchery and natural Chinook salmon during the early marine residence likely include a combination of disease, starvation, and predation. However, it is hypothesized that mortality during early marine residence is primarily related to predation (Beamish and Mahnken 2001). Predation rate is often inversely related to fish size (Ware 1975; Sheperd and Cushing 1980; Sogard 1997), with larger or faster growing individuals surviving better than slower-growing or smaller individuals. Similarly, larger fish have been hypothesized to have



a survival advantage during periods of starvation or exhaustion (Sogard 1997; Beamish and Mahnken 2001; Beamish et al. 2004). As such, the disproportionate survival of larger fishes (negative size-selectivity mortality) may occur during or between critical life stages (reviewed by Anderson 1988) such as when larvae transition to juveniles (Meekan et al. 2006) or later during juvenile to adult stages (Tsukamoto et al 1989). Similarly, in Chinook salmon, negative size-selective mortality has been observed between juvenile and adult stages; from freshwater (Zabel and Williams 2002) and marine entry (Claiborne et al. 2011) to adulthood. However, the importance of size, specific to early marine survival, is not clear despite juveniles encountering a new suite of avian (Roby et al. 2003; Antolos et al. 2005) and pelagic fish predators (Emmett and Krutzikowsky 2008) at marine entry.

Natural Chinook salmon are often smaller than hatchery counterparts during early marine residence (Daly et al. 2012; Beamish et al. 2012). If selective mortality is biased towards smaller fish, then natural individuals may experience disproportionately higher mortality. However, it is not clear if natural fish have behavioral advantages that may balance or overcompensate for their smaller size such as increased ability to avoid predators (Chittenden et al. 2010) or feed successfully. A recent study observed that natural fish were smaller during the early marine period yet experienced higher survival (Beamish et al. 2012). This has been similarly observed in Atlantic salmon (*Salmo salar*) (Jonsson et al. 2003). Furthermore, researchers have noted that natural Chinook salmon may have enhanced survival over hatchery fish due to greater diversity in size and migration timing, which could increase survival in a seasonally variable marine ecosystem (Bottom et al. 2009; Beamish et al. 2012).

Similarly, fish entering the marine environment at different times may exhibit differential survival to adulthood, potentially as a result of variability in the marine ecosystem (Scheuerell et al. 2009). Timing of marine entry and marine distribution vary between population segments of Chinook salmon (Trudel et al. 2009; Fisher et al. in review). Therefore it is important to directly compare hatchery and natural fish from the same population segment. Environmental conditions (i.e. river flow) influence migration timing in salmonids (Coutant and Whitney 2006; Sykes et al 2009), and hatchery fish cannot migrate until they are released. Therefore, it is possible that the timing of marine entry differ between production types.

The extent of variation in size and timing of marine entry between natural and hatchery juveniles within specific population segments is not well-documented. Furthermore, it is not yet clear if hatchery and natural fish experience similar patterns and rates of survival during early marine residence. Therefore we: (1) directly compared migratory patterns of hatchery and natural individuals from the same genetic stock group; (2) determined if size-selective mortality during early marine residence occurs in hatchery and natural Chinook salmon. Specifically, we tested four hypotheses: (1) there is spatial overlap between natural and hatchery Chinook salmon during early marine residence; (2) the timing of marine entry will be more protracted for natural Chinook salmon; (3) hatchery fish experience negative size selection during early marine residence; and (4) natural fish will be smaller than hatchery conspecifics at marine entry but do not experience negative size-selective mortality.

## METHODS

We reconstruct genetic stock group, migratory history, and production type (hatchery or natural) of juvenile Chinook salmon using a combination of microsatellite genotyping, otolith analyses, and physical tags. We captured fish in 2010 and 2011 by repeatedly sampling Chinook salmon at the mouth of the Columbia River during emigration and later in September off the coast of Oregon and Washington (Appendix Table 2; Figure 3.1). Estuary fish collections were used to quantify size at and timing of freshwater emigration and to determine the relative proportion of each production type prior to ocean entry and subsequent mortality (Appendix Table 2; Fig. 3.1). In the Columbia River, salinity intrusion extends ~55 km from the river mouth in the deepest portions of the river channel: we define the estuary as the extent of salinity intrusion. Ocean-collected fish were used to determine the extent of spatial overlap of natural and hatchery juveniles and quantify the size at and timing of freshwater emigration of those juveniles that survived their first ocean summer. By comparing the characteristics (size at and timing of freshwater emigration) and the relative proportions of hatchery and natural fish before and after their first summer at sea, we were able to determine if size at marine entry, timing of marine entry, and production type were factors related to early marine survival (Appendix Table 2; Fig. 3.1).

All individuals retained from each survey were frozen after capture and later thawed, re-measured, and weighed. Otoliths were extracted and fish checked for internal and external tags, and tissue samples collected for genetic analysis. Chinook salmon were genotyped at 13 microsatellite DNA loci that have been standardized

among genetics laboratories (Seeb et al. 2007) following the methods outlined in Teel et al. (2009). A regional baseline of population data from the genetic databases described by Seeb et al. (2007) and Moran et al. (In press) and the genetic stock identification software ONCOR (Kalinowski et al. 2007) were used to estimate the stock origins of individual fish. The upper Columbia River summer and fall (UCR Su/F) stock group is made up of spawning populations on several rivers including the Columbia, Yakima, Wenatchee, and Methow Rivers and hatchery production extends geographically in the mid and upper Columbia River basin above Bonneville Dam. The UCR Su/F stock group is relatively abundant in the Columbia River basin and a valuable resource in fisheries (68% harvest annually) from the Pacific Northwest to Alaska (Myers et al. 1998; Weitkamp 2010). Furthermore, significant natural production is observed in this stock (Myers et al. 1998), yet a high percentage of unmarked hatchery individuals have been released in recent years (Appendix Table 1; [www.fpc.org](http://www.fpc.org)). In 2010 and 2011 over 45,000,000 hatchery fish from the UCR Su/F stock were released in the Columbia River basin and 32% were released unmarked (Appendix Table 1; [www.fpc.org](http://www.fpc.org)).

Based on a previous mark recapture studies, there is strong evidence that the vast majority of subyearlings (migrate before their first winter) from the UCR Su/F stock group remain in local marine waters during summer while yearlings migrate quickly northward (Trudel et al. 2009; Tucker et al. 2012; Fisher et al. in review). Therefore, subyearlings from the UCR Su/F stock provide a unique opportunity to investigate mortality during early marine residence. We classified fish as subyearlings based on size at capture in the estuary (Weitkamp et al. 2012) and the

ocean (< 250 mm in September). Subyearling Chinook salmon assigned to the UCR Su/F genetic stock group were included in this study. Overall, 94% of individuals we selected had an assignment probability  $\geq 90\%$  with a mean assignment of 96% (7.2% SD).

#### *Estuary Fish Collections*

Chinook salmon were collected in 2010 and 2011 during National Oceanic and Atmospheric Administration (NOAA) surveys in the mainstem channel of the Columbia River estuary (Appendix Table 2; Fig. 3.1). The Columbia River estuary was sampled bi-monthly during April–June and monthly in July–September in 2010 and 2011, except no survey was conducted in August of 2010. Chinook salmon were collected using a 155-m by 10.6-m purse seine with a 1.7-cm mesh and 1.7-cm knotless bunt mesh in approximately 9–10 m of water (described in Weitkamp et al. 2012).

Previous research has noted that size in Chinook salmon is positively related to depth captured (Weitkamp et al. 2012; Roegner et al. 2013) and that 40–50% of migrants captured in intertidal estuarine habitats are < 60 mm FL at marine entry (Campbell 2010). Juvenile salmon were collected in shallow, intertidal areas in the lower Columbia River estuary, but otoliths from these individuals were unavailable. Thus, we were unable to complete similar analyses for this group of fish. However, size at capture, the presence of a physical tag, and genetic stock group were available (Curtis Roegner unpublished data). To assess potential bias in purse seine collections from the main channel we compared information on UCR Su/F subyearlings captured in the intertidal and the main channel habitat, including the percent marked, percent of

subyearling catch, and size at capture (Table 3.1). UCR Su/F Chinook salmon constituted a greater percentage of the subyearling catch in the channel compared with intertidal collections (mean of 29% vs. 6%, respectively). However, the percentage of tagged UCR Su/F subyearlings was similar between locations (48% in channel and 50% in intertidal; Table 3.1). There was no clear size bias: individuals in intertidal habitats were smaller than channel collections in 2011 (77 vs 106 mm; Wilcoxon rank sum test:  $p < 0.01$ ), but not in 2010 (118 vs 110 mm; Wilcoxon rank sum test:  $p > 0.05$ ) (Table 3.1). Thus, we conclude that our channel collections may miss some smaller migrants but appear to adequately represent UCR Su/F subyearlings in the lower Columbia River estuary.

#### *Ocean Fish Collections*

Ocean collections occurred during NOAA surveys using a Nordic 264 rope trawl (Net Systems, Bainbridge Island, WA) fished at the surface directly astern of the research vessel. Eight transects from La Push, Washington to Newport, Oregon were sampled (Fig. 3.1). The trawl mouth has an opening of 30 m wide by 20 m deep when fishing, with a mesh size range from 162.6 cm in the throat of the trawl near the jib lines to 0.8 cm in a knotless liner sewn into the cod end (described in Brodeur et al. 2005). In 2010-2011, 51% of subyearling Chinook salmon captured in the ocean were assigned to the UCR Su/F stock group.

#### *Otolith Preparation and Elemental Analysis*

We used otoliths from individuals collected in the estuary and ocean to estimate size at and timing of freshwater emigration, production type (hatchery or natural), and marine growth. We used all otoliths from UCR Su/F subyearlings

captured in the estuary in 2010 and 2011. In the ocean, we subsampled otoliths from the total catch to represent all transects and maintain representative size at capture and proportion of marked fish.

Otoliths provide a natural tag in fishes because they grow throughout a fish's life (Marshall and Parker 1982; Campana and Neilson 1985). Otolith Sr:Ca is useful for reconstructing migratory history in anadromous fishes because Sr is incorporated in the otolith in proportion to its abundance in the environment (Kraus and Secor 2004). Sr:Ca levels are consistently lower in freshwater of the Columbia River than in marine waters; thus variation in otolith Sr:Ca can be used to reconstruct the seaward migration of Columbia River Chinook salmon (Miller et al. 2011; Tomaro et al. 2012). The relationship between salinity and water Sr:Ca is non-linear (Krause and Secor 2004), and there is minimal variation in water Sr:Ca at salinities greater than ~8 (Kraus and Secor 2004; Miller et al. 2010). Therefore, otolith Sr:Ca is a useful tool in determining juvenile movement to brackish/marine waters, which we refer to as "freshwater emigration" (Miller et al. 2011; Tomaro et al. 2012).

Otoliths were cleaned, dried and the left sagittal otolith, when available, was measured along growth axis through the core at the widest point (Fig. 3.2). Otoliths were mounted on a glass slide with thermoplastic resin and then ground using successive grits of lapping film (Buehler® grits) and polished using an aluminum oxide slurry. We measured otolith Sr and Ca using a Thermo X series II inductively coupled mass spectrometer (LA-ICPMS) coupled with a Photon Machines G2 193 nm excimer laser at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. Scans were completed along a ventral-dorsal transect through the

core at the widest point (Fig. 3.2). The laser was set at a pulse rate of 7 Hz traveling across the sample at 5 or 7  $\mu\text{m s}^{-1}$  with a spot size of 30  $\mu\text{m}$ . Normalized ion ratios were converted to elemental concentration using a glass standard from the National Institute of Standards and Technology (NIST 612) and finally converted to molar ratios for analysis. Otolith width (OW) at freshwater emigration was defined as the distance between points of inflection in the Sr:Ca profile along the dorsal-ventral axis (Fig. 3.2; Miller et al. 2011; Tomaro et al. 2012). Mean precision (percent relative standard deviation) determined from NIST 612 was 5.7% for  $^{43}\text{Ca}$  and 4.9% ( $n = 10$ ). Accuracy (92% for Sr:Ca;  $n = 20$ ) was determined using a carbonate standard developed by the United States Geological Survey (USGS MACS-1).

#### *Size and Timing of Freshwater Emigration and Marine Growth*

Size at freshwater emigration was estimated using a stock-specific relationship between fork length (FL, mm) and OW ( $\mu\text{m}$ ). We included individuals that had recently emigrated from freshwater ( $\leq 10$  d) because we were predicting size at freshwater emigration (Fig 3.3;  $R^2 = 0.77$ ,  $n = 133$ ,  $p < 0.01$ ):

$$L_{\text{FE}} = \text{OW}_{\text{FE}} * 0.07 (\pm 0.004) - 7.22 (\pm 5.44)$$

where  $L_{\text{FE}}$  is the estimated fork length at freshwater emigration and  $\text{OW}_{\text{FE}}$  is the OW at freshwater emigration as determined from otolith Sr:Ca. We note that for hatchery and natural fish there was a difference in relationships between fork length (FL, mm) and OW ( $\mu\text{m}$ ) (ANCOVA:  $p < 0.05$ ; Fig. 3.3). However, estimates of size at freshwater emigration using the production type specific relationships and the stock specific relationship above were not significantly different (Wilcoxon-rank sum:  $p > 0.05$ ) thus, to increase sample size, we used the stock specific relationship.



Chinook salmon otoliths are formed in daily increments (Campana and Neilson 1985). Therefore, after determining  $OW_{FE}$  using Sr:Ca (Fig. 3.2), we enumerated daily increments to estimate the date of freshwater emigration and brackish/marine growth and residence, here after termed “marine growth and marine residence”. Note marine residence refers to residence in brackish/marine waters of the estuary and ocean. Digital images of each otolith were acquired using a compound microscope (Leica DM 1000; 200X, and 400X) with a mounted camera (Leica DC30). The width and number of daily increments from the point of freshwater emigration on the dorsal side to the edge of each otolith were enumerated and verified by hand (Fig. 3.2). The date of freshwater emigration was calculated by subtracting the number of increments after freshwater emigration from the date of capture. Therefore, we define marine residence as the number of days between freshwater emigration and capture in the brackish/marine waters of the estuary and ocean. Individuals captured at the mouth of Columbia River exhibiting no inflection in otolith Sr:Ca ratio were assumed to have entered the estuary on the day of capture (Miller 2011). Marine growth was calculated as percent body length per day:

$$\text{Growth (\% mm d}^{-1}\text{)} = (((L_C - L_{FE}) / D_{FE}) * L_{FE}) * 100$$

where  $L_C$  indicates fork length at capture,  $L_{FE}$  indicates fork length at freshwater emigration, and  $D_{FE}$  indicates days since freshwater emigration.

#### *Juvenile Production type*

We used two independent methods to estimate the proportion of hatchery and natural individuals. First, we determined the proportion of unmarked (no physical external or internal tag) and marked fish in each year and for ocean and estuary

collections separately. The total percentage of hatchery fish for each collection was estimated based on the mean annual proportion of UCR Su/F hatchery fish that were marked (Table 3.2). This approach is referred to as the “tag method”:

$$\text{Hatchery contribution} = ((H_M / P_M) / n) * 100$$

where  $H_M$  = number of marked hatchery individuals captured,  $P_M$  = the proportion of subyearling UCR Su/F hatchery production marked in a year ([www.fpc.org](http://www.fpc.org)), and  $n$  = the total number of fish captured.

Hatchery and natural individuals experience different temperature and feeding regimes. Given that the rate of otolith deposition is primarily related to water temperature and food ration (Neilson and Geen 1982), the stable rearing environment experienced by hatchery individuals can result in more regular daily increment formation than in natural individuals (Zhang et al. 1995; Chapter 2 this study). Differences in otolith structure during early life stages have allowed researchers to determine production type of unmarked individuals (Zhang and Beamish 2000). Therefore, we used otolith structure and the classification model developed in Chapter 2 of this study, hereafter referred to as the “otolith method”, as a second approach to estimate the proportion of hatchery fish (Fig. 3.4). The tag method cannot be used to determine the production type of an individual fish. Therefore, the otolith method provided individual assignments allowing direct comparisons of size at and timing of freshwater emigration and marine growth, between production types.

After completing initial chemical and structural analyses, otoliths from unmarked individuals, which include both hatchery and natural juveniles, were further polished until the primordia and structure near the exogenous feeding check were

evident. Additional polishing was necessary at this stage because the edges of the otoliths, which are required to determine timing of freshwater emigration and marine growth rates, are typically “polished away” when the core region is clearly exposed. The classification model relies on two metrics, the presence of a transfer check (TC) and the coefficient of variation of the first 20 daily increments after the exogenous feeding check. The TC was only observed in fish from the Wells Hatchery and occurred during the transfer of fish from rearing tanks to raceways, likely due to a change in water temperature (Chapter 2). For each unmarked individual, production type was then determined by:

$$RT = e^{\beta_0 + \beta_1 * CVIW + \beta_2 * TC} / e^{\beta_0 + \beta_1 * CVIW + \beta_2 * TC} + 1$$

where RT is the probability of production type (0-1) and the independent variables are CVIW = the coefficient of variation of increment width and TC = the presence or absence of a transfer check. Model coefficients  $\beta_0$ ,  $\beta_1$ ,  $\beta_2$  are -14.60 ( $\pm 3.1$  SE), 110.96 ( $\pm 23.3$  SE), and -37.18 ( $\pm 19.1$  SE) respectively. We used a probability cutoff of  $\geq 0.50$  to assign natural fish and  $< 0.50$  for hatchery individuals (Fig. 3.4).

Microstructure immediately after exogenous feeding was not interpretable in all otoliths due to variation in formation or sample preparation. Thus, only 57% of the otoliths from unmarked individuals were classified to production type (86 of 150). Note that direct comparison between hatchery and natural fish were made only for fish successfully assigned to production type, thus unmarked and unknown fish were not included. Therefore, the percentage of each production type in our sample was extrapolated to the total catch (Table 3.2):

$$\text{Hatchery contribution} = ((N_U * H_O) + H_M) / n * 100$$

Where  $N_U$  = number of unmarked individuals captured,  $H_O$  = proportion of hatchery fish determined from the otolith classification model,  $H_M$  = number of marked hatchery fish, and  $n$  = total number of fish captured.

### *Statistical Analysis*

To address the objectives and hypotheses of this study we: 1) describe overall migratory patterns in the estuary and ocean distribution; 2) compare size at and timing of freshwater emigration, growth, and size at capture between hatchery and natural fish; and 3) compare size at and timing of freshwater emigration and contribution of hatchery and natural fish captured in the estuary and ocean. First, we describe the timing of freshwater emigration and marine residence in the estuary and ocean. We compare the mean marine residence between years in the estuary and ocean using a two-sample permutation test. We qualitatively describe the ocean distribution of hatchery and natural Chinook salmon at the spatial scale of transect (Fig. 3.1). Secondly, we test for differences in size at, and timing of, freshwater emigration, size at capture, and marine growth between production types using the Wilcoxon rank sum test separately for fish captured in the estuary and in the ocean. These comparisons were done separately because fish captured in estuary represented the size at and timing of freshwater emigration prior to any mortality that occurred in the coastal ocean. Finally, to test for differences in the distribution of size at and timing of freshwater emigration over summer, we compared these metrics for hatchery and natural individuals captured in the estuary and ocean. We evaluated annual distributions of size at and timing of freshwater emigration using the Kolmogorov-Smirnov test because parametric assumptions were not met even after transformation.

We compared the proportion of natural and hatchery fish between the estuary and ocean using Fisher's exact tests. We evaluated the proportions estimated using the tag, and otolith method separately.

## RESULTS

### *Classification Model*

Using the otolith method we successfully determined the rearing production type of 57% of the unmarked individuals (86/150) captured in the estuary and ocean in 2010 and 2011. Overall, 69% were classified as natural and 31% as hatchery origin (Fig. 3.4): only these individuals were used for direct comparisons between production types. The contribution of each production type was estimated by expanding the proportion of hatchery and natural fish classified in each sample (estuary or ocean) and year to the total catch of UCR Su/F individuals.

### *Migratory Patterns*

Overall, the timing of freshwater emigration ranged from late May to late September and peaked in July through August in both 2010 and 2011 (Fig. 3.6). All hatchery and natural fish emigrated after the onset of hatchery releases in 2010 and 2011 and freshwater emigration continued ~2 months after hatchery individuals were last released (Fig. 3.6). For estuary collections, juveniles emigrated from freshwaters between May 5<sup>th</sup> and September 14<sup>th</sup> and had resided in marine waters for  $4 (\pm 1.4 \text{ SE})$  days prior to capture. Mean residence was  $7 (\pm 1.3 \text{ SE})$  days in 2010 and  $1 (\pm 0.3 \text{ SE})$  in 2011 (Fig. 3.6) and was significantly longer in 2010 than 2011 (two-sample permutation:  $p < 0.05$ ) and there was some evidence that hatchery fish resided longer and entered earlier than hatchery fish (Fig. 3.6). For ocean collections, juveniles

emigrated from freshwater between June 19<sup>th</sup> and September 18<sup>th</sup> and had resided in marine waters for 59 ( $\pm 1.8$  SE) days. Mean residence was 62 ( $\pm 2.0$  SE) days in 2010 and 56 ( $\pm 1.7$  SE) in 2011 (two-sample permutation:  $p > 0.05$ ; Fig. 3.6). For fish captured in the ocean, both production types were present at all transects sampled except no natural fish were captured in La Push in 2011 (Fig. 3.6).

#### *Hatchery and Natural Comparison*

Overall, median size of hatchery and natural fish at freshwater emigration was 101 mm, and varied by less than  $\leq 10$  mm between production types and years (Table 3.4). There was no evidence that size at freshwater emigration was different between hatchery and natural individuals in 2010 or 2011 in the estuary or ocean (Table 3.4; Wilcoxon-rank sum:  $p > 0.05$ ). There was also no difference in the timing of freshwater emigration between production types captured in the estuary or in the ocean in 2010 (Fig. 3.7; Table 3.4; Wilcoxon-rank sum:  $p > 0.05$ ). For juveniles collected in the estuary in 2011, however, natural individuals emigrated significantly later ( $\sim 1$  month) than hatchery conspecifics (Wilcoxon-rank sum:  $p < 0.05$ ; Fig. 3.7). However, there was no difference in timing of freshwater emigration between production types for juveniles collected later in the ocean in 2011 (Fig. 3.7; Table 3.4; Wilcoxon-rank sum:  $p > 0.05$ ). There were no other significant differences in size at capture or marine growth rate between production types (Table 3.4).

#### *Estuary and Ocean Comparison*

We observed no difference in the distributions of size at freshwater emigration between the estuary and ocean for hatchery or natural fish in 2010 or 2011 (Table 3.3; Fig. 3.5; Kolmogorov-Smirnov test:  $p > 0.05$ ). Similarly, there was no

difference in the distribution of timing of freshwater emigration between estuary and ocean for hatchery or natural fish in 2010 (Table 3.3; Fig. 3.5; Kolmogorov-Smirnov test:  $p > 0.05$ ). However, for hatchery and natural fish in 2011, the distribution of timing of freshwater emigration varied between estuary and ocean (Table 3.3; Fig. 3.5; Kolmogorov-Smirnov test:  $p < 0.05$ ) and migrants emigrating in late July were most represented while earlier and later migrants were not (Table 3.3; Fig. 3.5).

We also compared the proportion of hatchery and natural fish from the estuary to ocean to estimate any changes in the contribution of each rearing production type over the summer. Overall, the proportion of natural production type-fish collected in the ocean increased by 17% compared to estuary collections (Table 3.2). The otolith method indicated a non-significant increase in the proportion of natural fish in ocean collections compared with the estuary (6% in 2010 and 14% in 2011; Fisher's exact:  $p > 0.05$ ; Table 3.2). The tag method indicated that there was a significantly greater proportion of natural fish in ocean collections compared with the estuary (22% in 2010 and 29% in 2011; Fisher's exact:  $p < 0.05$ ; Table 3.2)

## DISCUSSION

There is substantial evidence that the first summer at sea is a critical life stage for hatchery and natural Chinook salmon, because juvenile condition (Miller et al. In press), growth (Duffy and Beauchamp 2011), and size (Tomaro et al. 2012) during early marine residence, as well as emigration timing (Scheuerell et al. 2009) are highly correlated to adult survival. However, to our knowledge, no other study has determined the size at and timing of marine entry for hatchery and natural fish independently to examine the potential for selective mortality during the first summer

at sea. We observed no differences in size at marine entry between hatchery and natural fish, and there was no evidence of size-selective mortality at the time of marine entry. Overall, there was spatial and temporal overlap in the emigration of hatchery and natural fish and spatial overlap later in the ocean. We also determined that the proportion of natural individuals was consistently higher in the ocean compared with estuary collections. There are two likely explanations for this observation: 1) the estuary site is biased to capturing hatchery fish; or 2) natural fish survived at greater rates.

A recent study of UCR Su/F Chinook salmon demonstrated that variability in adult survival was significantly and negatively related to juvenile condition at the end of the first summer at sea (Miller et al. in press). The authors postulate that lower condition of juveniles in higher survival years may be result of inter- or intra-specific competition. For competition to occur, potential competitors must overlap in space and time. We documented spatial and temporal overlap between hatchery and natural Chinook salmon in the estuary and coastal ocean. Both production types were captured at most all of ocean transects from Newport, OR to La Push, Washington and resided in coastal waters throughout summer, consistent with previous observations of primarily hatchery fish (Trudel et al. 2009; Fisher et al. in review). Competition is difficult to directly evaluate in field studies, but indirect measures, such as growth, or condition, may be used to infer competitive advantages when species or production types overlap (Daly et al. 2012). We did not directly assess competition between production types, but we observed that early marine growth and condition (data not shown) did not differ between production types within a year.



Contrary to our expectations, we observed no evidence of size-selective mortality at the time of marine entry. We hypothesized that negative size-selective mortality would occur in hatchery fish because: 1) negative size-selective mortality has been observed in yearling hatchery Chinook salmon (Zabel and Williams et al. 2002; Claiborne et al. 2011) and; 2) subyearlings are smaller at marine entry than yearling migrants, and predation rate is expected to increase with decreasing size (Sogard et al. 1997). Size-selective mortality of smaller salmonids has been observed during freshwater stages (Zabel and Achord 2004) and during the first winter at sea (Beamish et al. 2004). Therefore, it is possible that, for the study population, selection against smaller slower growing individuals already occurred in freshwater or had yet to occur in the marine environment (i.e. the first winter at sea). Conversely, there may be disruptive selection, where the smallest and largest salmonids are not targeted by predators and are less susceptible to predation (Hostetter et al. 2012). We observed no evidence of disruptive selection in this study, but we note that disruptive selection of steelhead (*Oncorhynchus mykiss*) by Caspian terns in the Columbia River has been documented (Hostetter et al. 2012).

In this study, we identified three potential biases that warrant consideration. First, we were not able to include individuals from the shallow intertidal estuary, which may include smaller individuals than the channel collections. However, there is little evidence that the UCR Su/F juveniles use the shallow intertidal habitats (Roegner et al. 2013). Secondly, the purse seine collections in the main channel may be biased towards capturing hatchery fish. However, mark rates were similar between intertidal estuarine collections and the channel collections used in this study (Table

3.1; C. Roegner unpublished data.). Finally, it is possible that the frequency of estuary sampling (bi-weekly, then monthly) does not fully capture the out-migrating population due to short estuary residence (80% of fish < 3d). For example, UCR Su/F individuals may rear in freshwater portions of Columbia River below Bonneville Dam (Teel et al. 2009) and migrate quickly through the brackish/marine portions of the estuary between sampling events. Based on this evidence, we suspect our sample adequately represents the UCR Su/F stock, but more frequent sampling across a broader depth range in the estuary is warranted to address these considerations.

We observed that there were higher proportions of natural juveniles in ocean collections compared with the estuary in 2010 and 2011. This could indicate that natural fish survived better than hatchery conspecifics. Natural individuals exhibited higher marine survival than hatchery individuals in several species of salmonids (Coronado and Hilborn 1998; Jonsson et al. 2003; Beamish et al. 2012). For example, Beamish et al. (2012) observed that natural Chinook salmon survived better (6-24x) than hatchery individuals captured during their first summer at sea in Gulf Islands of British Columbia. Beamish et al. (2012) hypothesized that increased survival of natural individuals may be related, in part, to increased diversity in size and timing of marine entry and nearshore residency and thus resilience to changing marine conditions. In this study, the only difference between production types was that the timing of marine entry of natural fish captured in the estuary was later than hatchery conspecifics in 2011.

Behavioral traits, such as migration timing (Quinn et al. 2000), and predator-prey interactions (Jackson and Brown 2011) in fishes are influenced by genetic and

environmental factors. In addition, migration timing has been correlated to differential survival in salmonids (Scheuerell et al. 2009). For example, Scheuerell et al. (2009) found that Chinook salmon and steelhead that entered marine waters earlier in May survived at greater rates (4-50x) than those that migrated in June, although peak survival varied annually. These authors attributed this difference to interannual changes in ocean conditions (e.g. upwelling & temperature) and trophic dynamics. In this study, we observed some evidence of intra-annual variation in early marine survival related to the timing of marine entry in 2011. This finding indicated that migrants emigrating at the end of July were most represented while earlier and later migrants were not.

There could be differences in behavioral responses to predators between production types (Chittenden et al. 2010; Jackson and Brown 2011) that lead to differential mortality of hatchery and natural production type fish (Fraser 2008). For example, using a mesocosm approach, Chittenden et al. (2010) observed that individuals reared under pseudo-natural conditions had a greater tendency to seek refuge in the presence of simulated avian predators. Similarly, one generation of hatchery rearing was related to selection of negative predatory response behaviors, such as reduced time spent moving, and increased foraging attempts, in offspring of Atlantic salmon (*Salmo salar*) (Jackson and Brown 2011). Because of the high rates of predation on salmonids by piscivorous fish (Emmett et al. 2006; Emmett and Kruzikowsky 2008), and colonial seabirds (Roby et al. 2003; Lyons et al. 2005), it is possible that natural individuals that have experienced natural selection pressures

prior to freshwater emigration may exhibit behavioral differences, such as predator avoidance, that provide a survival advantage compared with hatchery individuals.

Our findings of higher proportions of natural fish in the ocean than estuary were based on two independent estimation methods. The tag and otolith method produced similar conclusions, but variation between estimates varied ~15% in 2010 and 2011. We suspect that this error is related to differences in survival and mark rates between hatcheries and the ~10% classification error of hatchery fish we observed using our classification model (Chapter 2). In 2010 and 2011, 100% of unclipped hatchery individuals from the Priest Rapids Hatchery were thermally marked (WDFW pers. comm.). These thermally-marked individuals accounted for 14% and 17% of unclipped hatchery releases of UCR Su/F in the Columbia River basin in 2010 and 2011, respectively. Therefore, to further evaluate our production type classifications model, we determined if any unmarked fish classified as “natural production type” had been thermally marked. Based on vouchers of thermally marked fish, 3% of individuals (2 of 59) classified as natural were potentially hatchery fish from the Priest Rapids Hatchery (WDFW pers. comm.). If our classification model had similar error among hatcheries, our classification error would be double (22%) what we expected. However, there is error associated with recognizing thermal marks particularly for each hatchery. For example, 1-45% of the voucher specimens of non-marked and marked fish were incorrectly classified (Volk et al. 1999). Therefore, we suspect our classifications are largely valid, although independent validation using known hatchery and natural fish is warranted.

For Chinook salmon, estuaries serve as both a migration corridor connecting freshwater and marine habitats and also as a productive rearing habitat for some individuals (Healey 1991). Campbell (2010) observed that 70-80% of primarily subyearling migrants from lower Columbia River stocks had elevated Sr: Ca in shallow ( $< 3$  m) portions of the estuary indicating residence in brackish/marine waters for at least 3 days (Miller 2011). Furthermore 30-55% of lower Columbia River juveniles (primarily subyearlings) captured in the lower estuary had resided in brackish/marine waters for  $> 30$  days (Campbell 2010). Our results indicate that individuals from the upper Columbia River may rely more on deeper portions of estuary for shorter periods of time ( $\sim 5\%$  resided in brackish/marine waters for  $>$  than 30 days). Residence in the Columbia River estuary may differ among subyearling stocks in Columbia River basin and warrants further investigation. It is important to note that our study defined the Columbia River estuary as the extent of salinity intrusion  $< 55$  (km) from the mouth. However, UCR Su/F subyearlings, which originate from sources above Bonneville Dam, have been observed to utilize tidal fresh portions of the Columbia River estuary below Bonneville Dam (Teel et al. 2009). Future studies should attempt to quantify residence in freshwater portions of the Columbia River estuary specific to the UCR Su/F stock.

Similar to Campbell (2010), we observed interannual and individual variation in the length of marine residency of Chinook salmon captured in the Columbia River estuary. This is not surprising as the Columbia River estuary is a highly dynamic environment and fish assemblages can vary on daily to annual time scales (Weitkamp et al. 2012). Notably, we observed that the proportion of fish that resided for  $> 3$  d

was 18% in 2010 and 6% in 2011. Interestingly, this decrease in residence was concurrent with a 25% increase in flows May-July in 2011 than 2010, and the highest flows since 2004 (the first year of available data) at Cascade Island below Bonneville Dam ([www.cbr.washington.edu](http://www.cbr.washington.edu)). This observation supports recent observations that juveniles may migrate more quickly through the estuary in years with higher flows (Weitkamp et al. 2012).

In conclusion, there was no evidence of selective mortality for size during early marine residence for either hatchery or natural fish UCR Su/F Chinook salmon subyearlings. Future studies should estimate size at freshwater emigration in returning adults that emigrated in 2010 and 2011 to determine the importance of size at freshwater emigration later in marine life. In 2011 the timing of marine entry differed between production types in the estuary but not in the ocean, and future studies should evaluate the alternative explanations we outlined for this finding. We expected that size at and timing of freshwater emigration would consistently differ between hatchery and natural fish. Interestingly, we observed few differences between origins, except that natural individuals emigrated later than hatchery fish in 2011. This may indicate that timing of marine entry may vary between hatchery and natural juveniles vary in response to differences in their freshwater rearing environments. It is noteworthy that the proportion of natural individuals consistently increased between the estuary and the ocean. Beamish et al. (2012) suggested that, although hatchery individuals experience higher survival rates than natural populations during early freshwater life stages, higher survival of natural populations at sea may minimize the effectiveness of artificial propagation to increase harvestable

biomass. Future studies should examine survival by production types whenever possible to determine if natural fish consistently survive at higher rates.

## TABLES

Table 3.1. Comparison of fork length at capture ( $L_c$ ), percent of subyearling catch (% Catch), percent marked (% Marked), and sample size ( $n$ ) of upper Columbia River summer and fall Chinook salmon captured in the Columbia River channel (this study) and intertidal (Curtis Roegner unpublished data) estuary.

Study	Year	Months Sampled	$n$	$L_c$ (mm)	% Catch	% Marked
Estuary Channel	2010	April-July, September	53	110	25	43
Estuary Intertidal	2010	April-September	5	118	4	50
Estuary Channel	2011	April-September	75	106	33	52
Estuary Intertidal	2011	April-September	14	77	7	50



Table 3.2. The estimated percent contribution of natural (%N) and hatchery (%H) upper Columbia River summer and fall Chinook salmon captured at the mouth of Columbia River (CR) and off the coast in September (O) in 2010 and 2011 using the tag and otolith method. Standard error shown in parentheses.

Tag Method	Study	Number Marked in Catch	Total in Catch	Marked Hatchery Releases	% H	% N
2010	CR	23	53	0.69	63 (6.7)	37
	O	26	92	0.69	41 (5.1)	59
2011	CR	39	75	0.68	76 (4.8)	24
	O	40	124	0.68	47 (4.5)	53

Otolith Method	Study	Number Unmarked in Catch	Total in Catch	Unmarked Hatchery Correction	% H	% N
2010	CR	30	53	0.35	63 (6.6)	37
	O	66	92	0.40	57 (5.2)	43
2011	CR	36	75	0.25	64 (5.5)	36
	O	84	124	0.27	51 (4.5)	50

Table 3.3. Median size at freshwater emigration and mean standard error for upper Columbia River summer and fall Chinook salmon captured at the mouth of Columbia River ( $FE_{CR}$ ) and off the coast in September ( $FE_O$ ) in 2010 and 2011 by production type and regardless of production type (All). Also shown are sample sizes of individuals captured at the mouth of Columbia River ( $n_{CR}$ ) and off the coast ( $n_O$ ).

Year	Production type	Size at $FE_{CR}$	$n_{CR}$	Size at $FE_O$	$n_O$
2010	All	103 (2.0)	53	101 (1.7)	52
	Hatchery	100 (2.9)	28	100 (3.3)	23
	Natural	108 (4.8)	14	107 (2.3)	12
2011	All	103 (1.8)	65	98 (1.3)	73
	Hatchery	102 (1.7)	33	101 (2.0)	33
	Natural	106 (4.0)	15	96 (2.1)	20

Table 3.4. Median and mean standard error of metrics compared between hatchery and natural upper Columbia River summer and fall Chinook salmon captured off the coast in 2010 and 2011. FE indicates freshwater emigration. Sample sizes are shown as a range because not all metrics were able to be calculated for each individual.

Metric	Study	2010		2011	
		Hatchery	Natural	Hatchery	Natural
Size at FE (FL mm)	CR	100 (2.9)	108 (4.8)	102 (1.7)	106 (4.0)
Day of FE	CR	207 (4.9)	207 (8.7)	194 (4.0)	222 (6.6)
<i>n</i>	CR	28	14	33	15
Size at FE (FL mm)	O	100 (3.3)	107 (2.3)	101 (2.0)	96 (2.1)
Size at Capture (FL mm)	O	155 (4.6)	154 (3.4)	159 (4.5)	148 (3.2)
Marine Growth Rate (%bl d <sup>-1</sup> )	O	0.88 (0.1)	0.81 (0.1)	0.95 (0.1)	1.03 (0.1)
Day of FE	O	200 (4.4)	215 (6.4)	209 (4.0)	208 (4.5)
<i>n</i>	O	19-23	12	28-33	18-20

## FIGURE LEGENDS

Figure 3.1. Map of study area and sites where upper Columbia River summer and fall Chinook salmon were captured off the coast of Oregon and Washington in 2010 and 2011. Insert indicates sites sampled in the Columbia River estuary.

Figure 3.2. A) Schematic of an otolith with the laser path and otolith width at freshwater emigration and B) corresponding otolith Sr:Ca. Arrows indicate otolith width at freshwater emigration.

Figure 3.3. Relationship between otolith width ( $\mu\text{m}$ ) and fork length at capture (mm) for upper Columbia River summer and fall Chinook salmon in the Columbia River estuary and coastal ocean in 2010 and 2011 ( $R^2 = 0.77$ ,  $n = 133$ ,  $p < 0.01$ ). Natural fish are shown as filled grey, hatchery as filled black, and unmarked and unknown as open.

Figure 3.4. Production type classification of juvenile Chinook salmon collected in the Columbia River estuary and coastal ocean. Histogram of fitted values for the model developed to classify unmarked fish to production type (hatchery or natural) (see Chapter 2 for details). Open bars indicate known natural and dark filled bars indicate known hatchery individuals. Grey filled bars indicate the fit of unmarked individuals captured in the Columbia River estuary and coastal waters in 2010 and 2011. Fitted values  $< 0.5$  indicate model classification as hatchery and  $\geq 0.5$  indicate model classification as natural individuals. The number of classified individuals is shown in Table 3.3

Figure 3.5. Histogram of size at freshwater emigration for upper Columbia River summer and fall Chinook salmon captured in the Columbia River estuary (black line) and coastal ocean (dotted line) for A) all fish combined in 2010; B) all fish combined in 2011; C) natural fish in 2010; D) 2011 natural; E) 2010 hatchery; F) 2011 hatchery. Sample sizes are in Table 3.3.

Figure 3.6. Day of capture and freshwater emigration for upper Columbia River summer and fall Chinook salmon captured in the Columbia River estuary A) 2010 and B) 2011, and in the ocean in C) 2010 and D) 2011. Note that C) and D) are arranged by transects sampled North to South. Each row of dots represents the day of year from freshwater emigration to capture for an individual fish. Red indicates natural, black indicates hatchery, and grey indicates unmarked and unknown. Open bars are a histogram of hatchery releases by day of year ([www.fpc.org](http://www.fpc.org)). LP = La Push, QR = Queets River, GH = Grays Harbor, WB = Willapa Bay, CR = Columbia River,

CM = Cape Meares, CH = Cascade Head, and NP = Newport. Sample sizes are shown in Table 3.4.

Figure 3.7. Histogram of the day of freshwater emigration for upper Columbia River summer and fall Chinook salmon captured at the mouth of the Columbia River estuary (black filled bars) and off the coast in September (grey filled bars) for A) 2010 natural; B) 2011 natural; C) 2010 hatchery; D) hatchery 2011. Sample sizes are shown in Table 3.4.

FIGURES

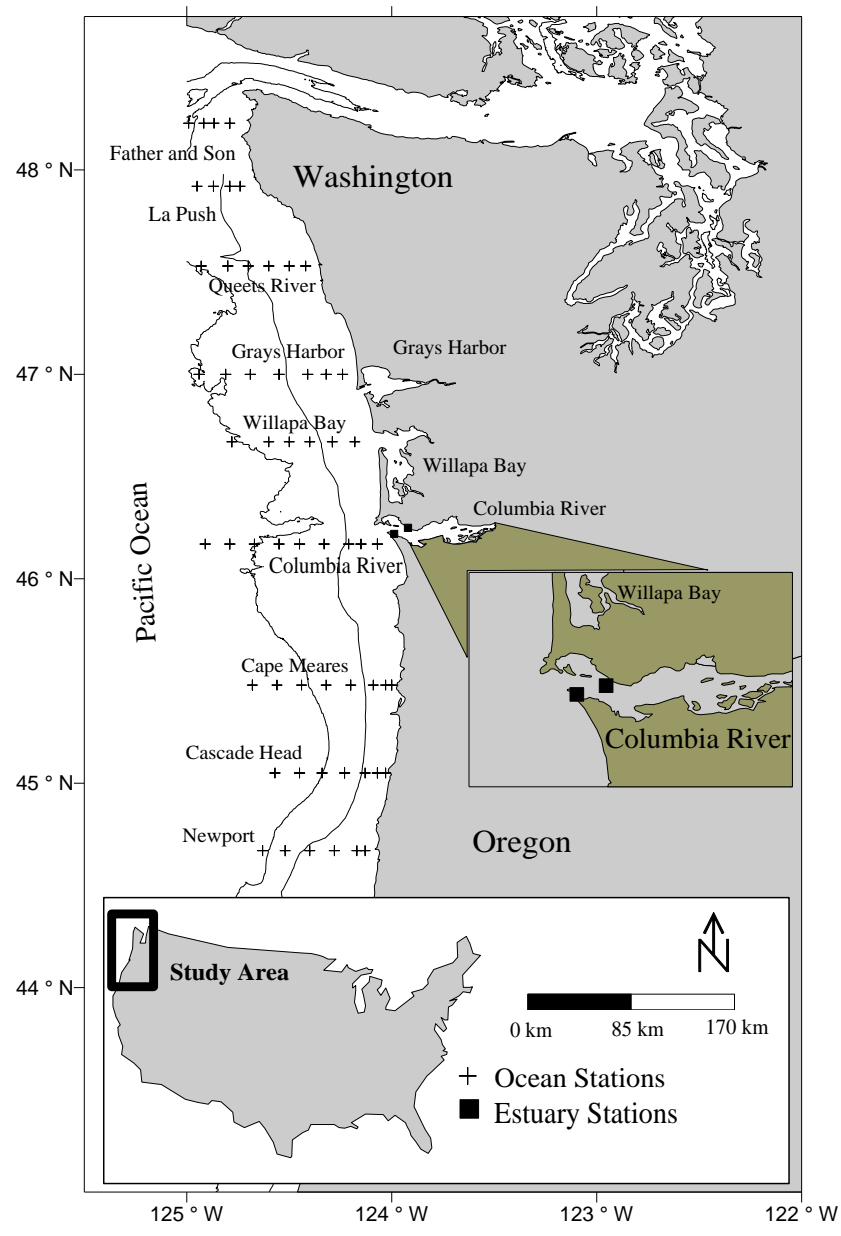


Figure 3.1

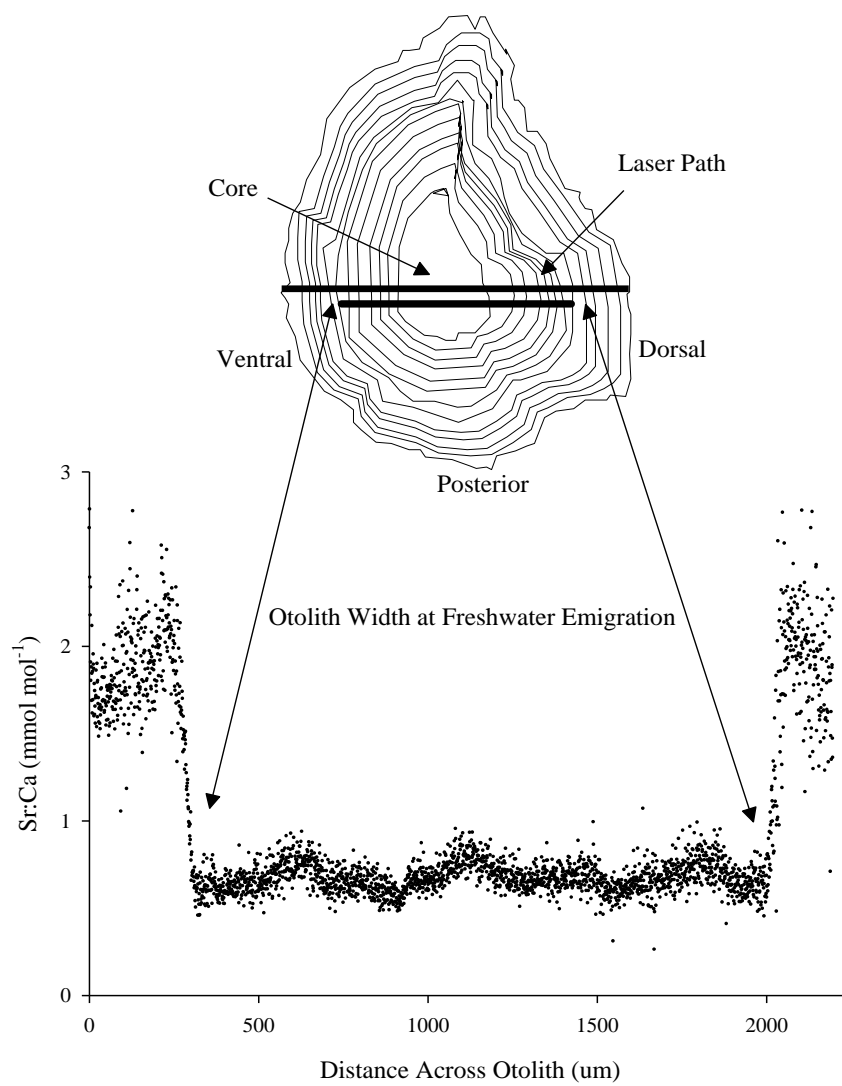


Figure 3.2

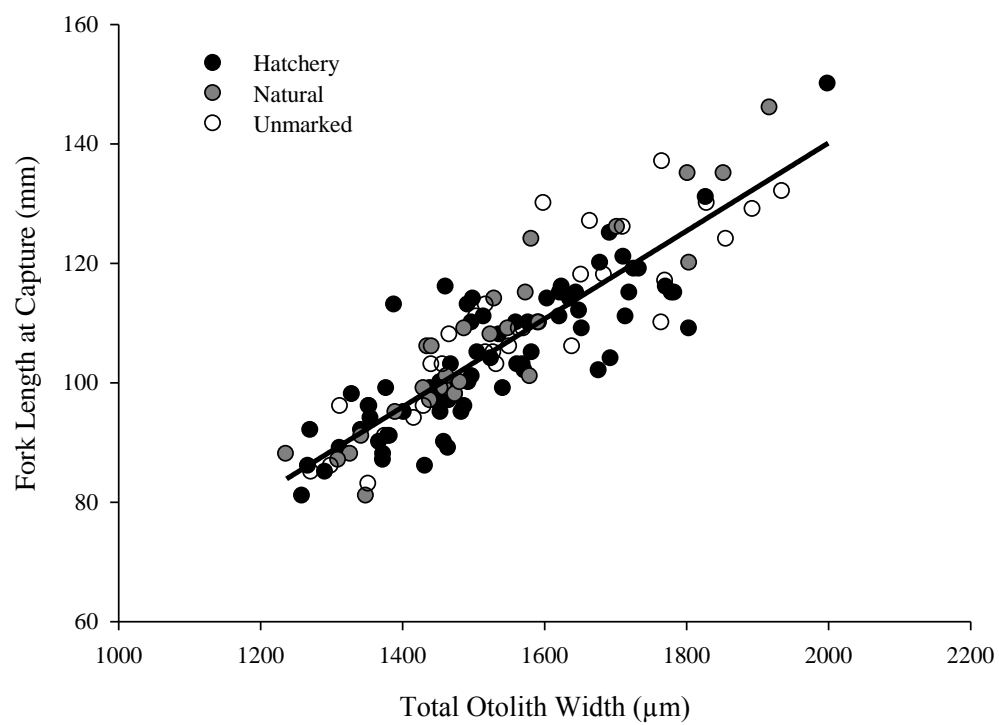


Figure 3.3



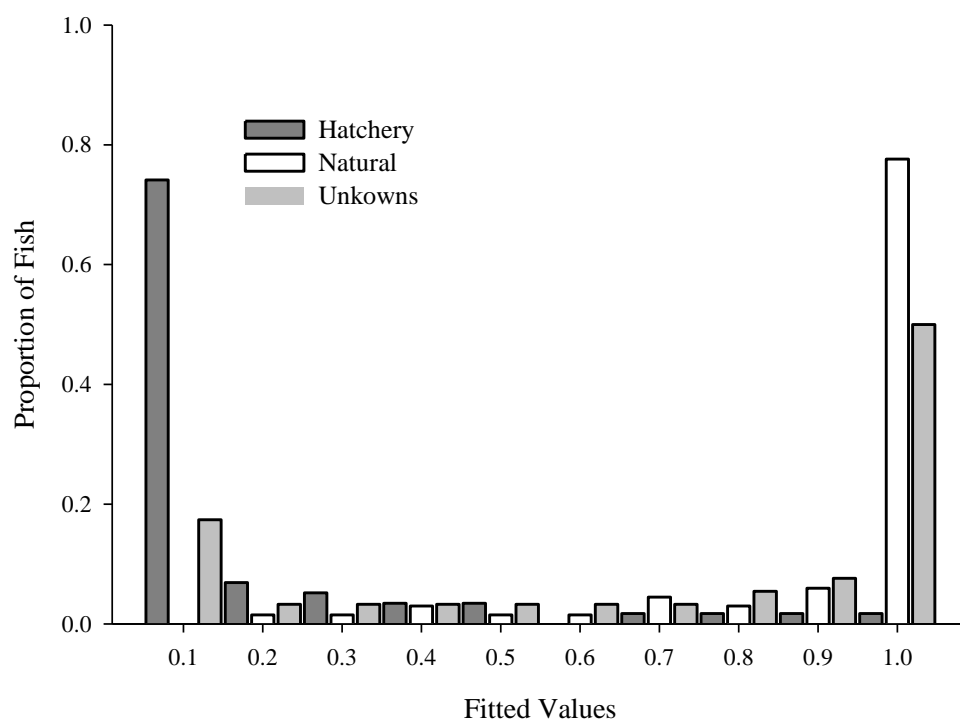


Figure 3.4

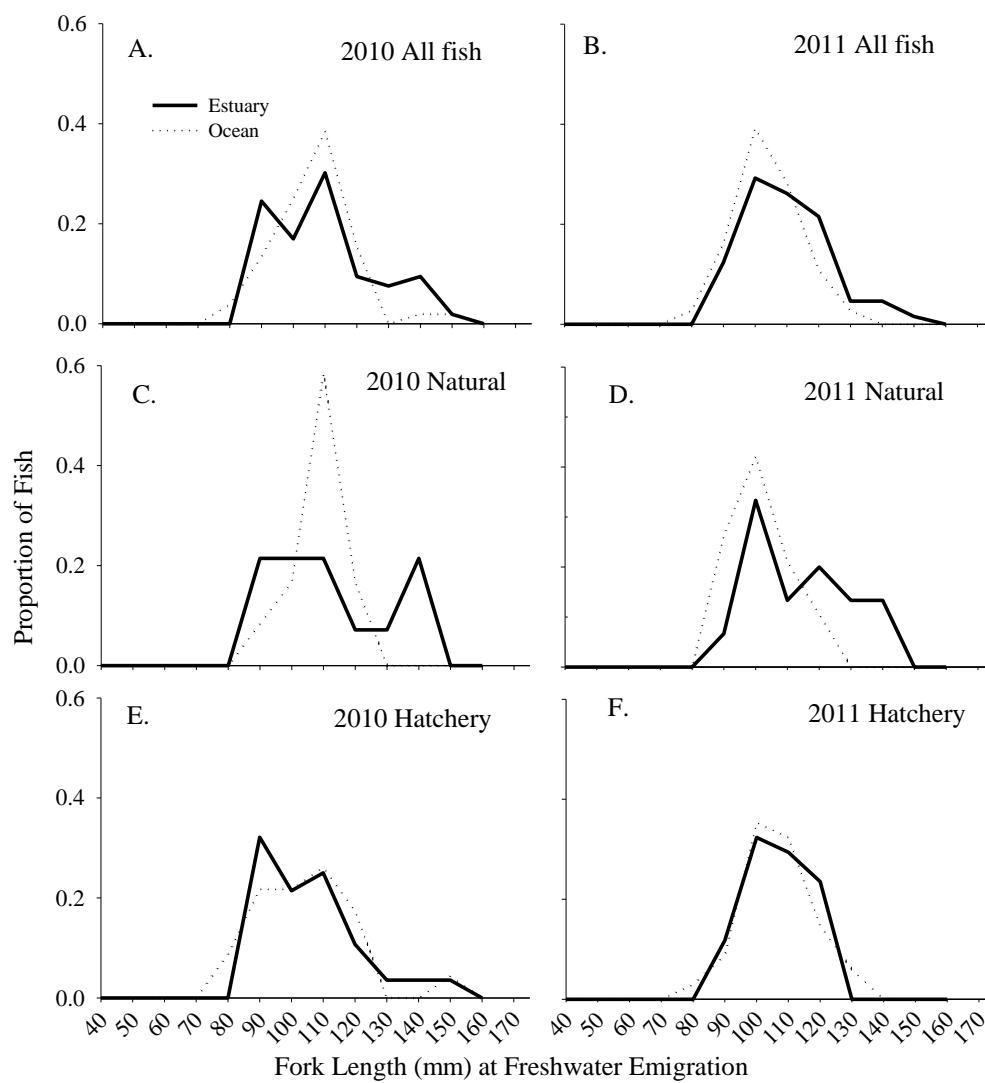


Figure 3.5

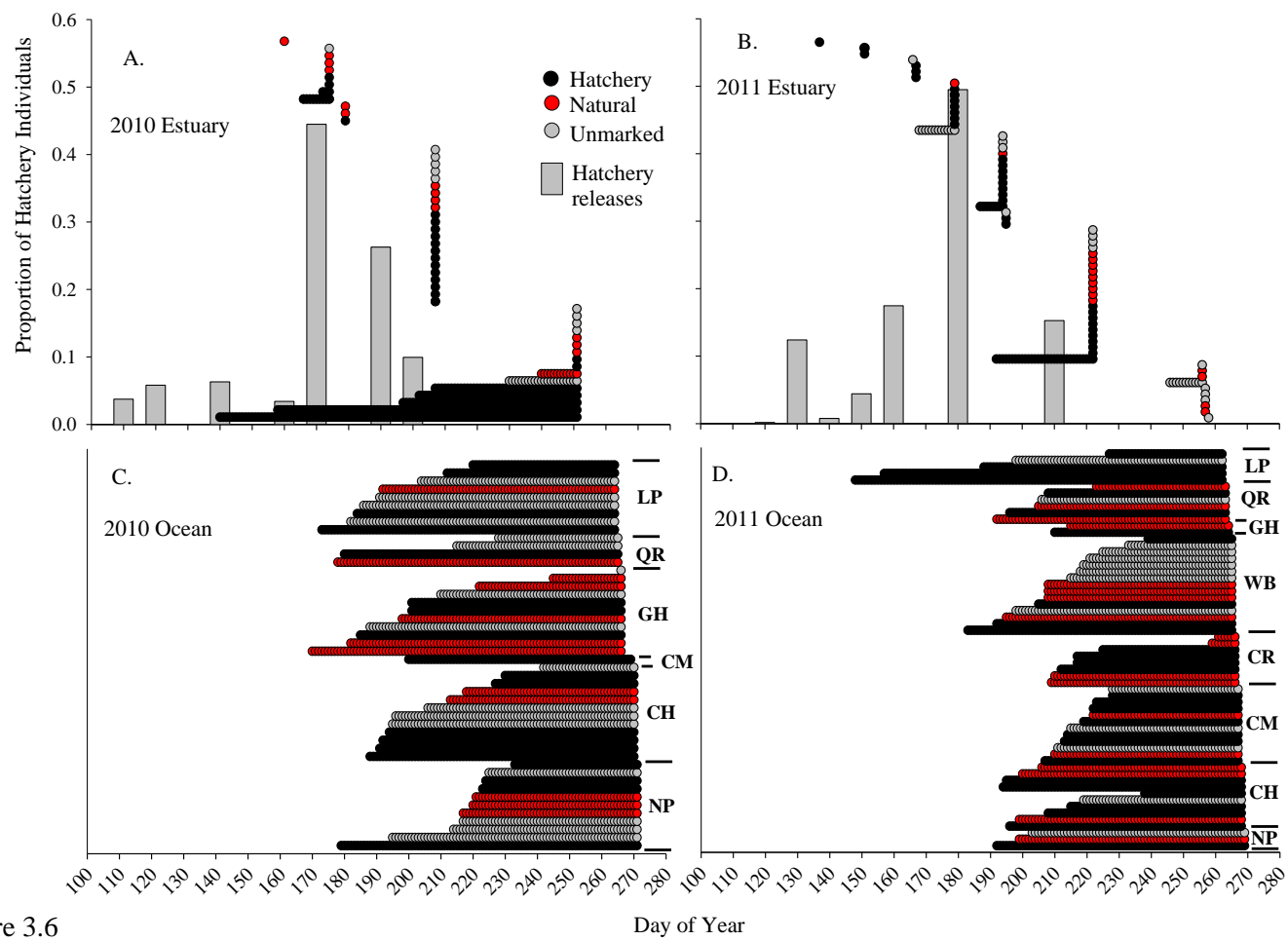


Figure 3.6

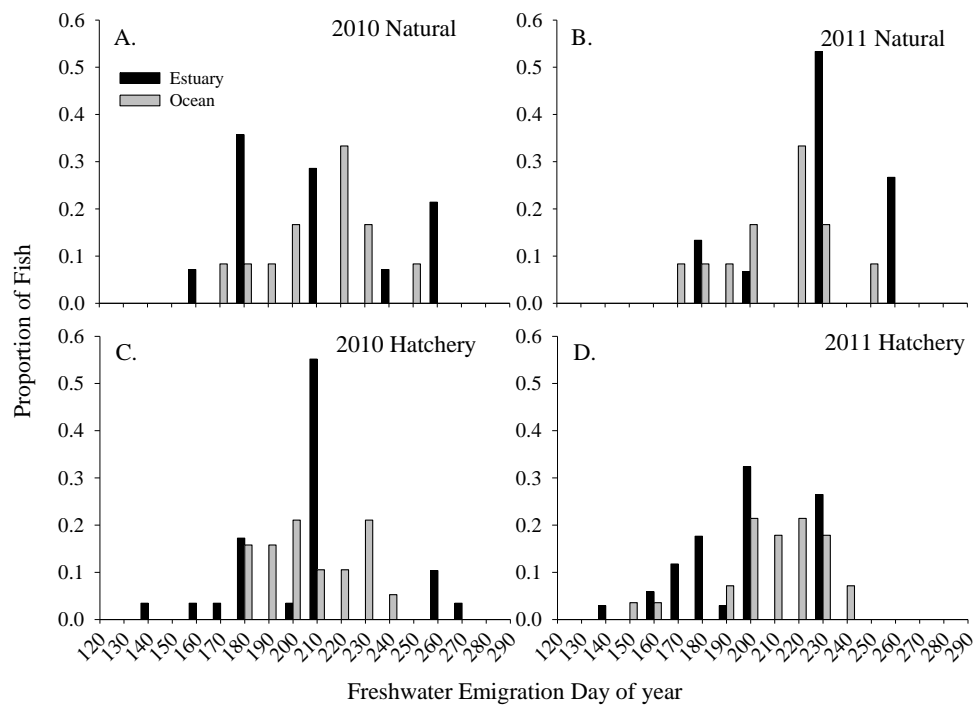


Figure 3.7

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## CHAPTER 4: GENERAL CONCLUSION

Understanding the factors influencing survival during critical life stages has been a primary focus of fisheries research, but it is not clear if they are similar for natural and artificially propagated individuals in many species. In addition, there are clear negative effects of artificial propagation, including lower survival (Iglesias et al. 2003), behavioral disadvantages (Stunz and Minello 2001) and reduced reproductive success (Flemming et al. 1997) of hatchery fish. However, in many species it is not clear how hatchery fish interact with or impact natural populations (for review, see Araki and Schmid 2010). Chinook salmon is a culturally and economically valuable anadromous species in the Pacific Northwest. In the Columbia River, declines in harvestable biomass have resulted in hatchery programs which currently release > 100 million Chinook salmon annually ([www.fpc.org](http://www.fpc.org)). For many genetic stock groups in the Columbia River, interactions between production types and factors limiting early marine survival of natural fish are not clear (National Research Council 1996; Rand et al. 2012). Furthermore, basic biological information such as size and growth, do not exist for natural fish from many stock groups within the Columbia River basin.

A robust comparison of hatchery and natural fish requires the accurate identification of hatchery individuals. For some commercially valuable stocks of Chinook salmon in Columbia River, our ability to make valid comparisons between production types (hatchery or natural) is inhibited by large numbers of unmarked hatchery fish released each year. Natural tags, such as otoliths, can be used to differentiate production type (Zhang and Beamish 2000; Barnett-Johnson et al. 2007) because hatchery and natural juveniles experience different rearing environments.

Therefore, in Chapter Two, I evaluated the use of otolith structure to differentiate between hatchery and natural Columbia River Chinook salmon and developed a classification model to differentiate production type of unmarked fish. In Chapter Three, I used this model to compare juvenile migratory behavior between hatchery- and naturally-produced fish from the same genetic stock group, the upper Columbia summer and fall Chinook salmon (UCR Su/F), and determine if there was evidence of selective mortality during early marine residence. Specifically, I followed two cohorts through emigration by collecting juveniles in the Columbia River estuary during spring and summer and in the coastal ocean in September, after their first summer at sea. I then compared the size at and timing of freshwater emigration of juveniles at initial entry into marine water (estuary collections) with the survivors (ocean collections) for evidence of selective mortality based on size at or timing of marine entry.

I determined that otolith structure varied between hatchery fish, which are reared in relatively stable environments, and natural fish, which rear in the variable natural environment. Several metrics of otolith structure varied between hatchery and natural juvenile Chinook salmon and I documented a previously unreported “transfer check” in some hatchery fish. The presence or absence of the transfer check and the coefficient of variation of daily increments predicted production type with 92% accuracy (jackknife accuracy). Independent validation using hatchery juveniles with Coded Wire Tags (CWTs) captured in the ocean indicated accuracy may be slightly lower (90% accuracy), at least for identification of hatchery fish. Therefore, I used this classification model to provide the first direct comparisons of size at and timing

of marine entry, marine growth, residence, and marine distribution of hatchery and natural UCR Su/F Chinook salmon during a critical life stage.

I observed that natural and hatchery UCR Su/F Chinook salmon emigrated from freshwater from May-September, and my results support the observation that they remain off the coast throughout their first summer at sea (Trudel et al. 2009; Fisher et al. in review). Overall, 80% of the individuals captured in estuary had resided in marine waters for  $< 3$  days and mean residence was significantly greater ( $7 \pm 1.3$  d) in 2010 than 2011 ( $1 \pm 0.3$  d). The shorter residence times in 2011 may be related to higher river flows in 2011 than 2010 ([www.cbr.washington.edu](http://www.cbr.washington.edu)), as recent observations indicate that fish migrate more quickly through the estuary channel in years of high flow (Weitkamp et al. 2012). Hatchery and natural fish were captured at similar locations and times in the ocean indicating there is spatial and temporal overlap between production types. Futures studies should further assess interactions between production types and the potential for competition.

Survival during critical life stages is influenced by many factors. For many fish species, increased growth and greater size is related to increased survival through critical life stages (for review see Anderson 1988). For Chinook salmon, size (Tomaro et al. 2012) and timing of marine entry (Scheuerell et al. 2009) and body condition (Miller et al. In press) and growth (Duffy and Beauchamp 2011) after initial marine residence have been related to adult survival, but the mechanisms and timing of mortality in marine environment are not clear. I determined that distributions of size at marine entry did not differ between individuals captured in the estuary and in the ocean for both production types. This indicates that the mechanism of mortality

during the first critical summer may not be size-selective. In 2011, I observed distributions of timing of marine entry for both production types significantly differed between the estuary and ocean such that fish emigrating in late July were more represented in the ocean than estuary. This may indicate: 1) differential survival related to the timing of marine entry; 2) an undetected bias in sample collection. Although I cannot discount sampling bias, the timing of marine entry was similar in 2010 from the estuary to the ocean indicating that our sample is representative in some years.

I observed few differences between hatchery and natural fish during their marine residence with the exception that natural individuals in the estuary emigrated later than hatchery fish in 2011 (~28 days). This finding may indicate that migratory behavior may differ between production types in some years, which may be related to the timing of hatchery releases and river conditions. Otherwise, size at marine entry and at capture, timing of marine entry, and marine growth did not significantly differ between hatchery and natural individuals in 2010 or 2011. I also determined that the proportion of natural individuals was consistently higher in the ocean compared with the estuary collections. There are two likely explanations for this observation: 1) the estuary site is biased to capturing hatchery fish; or 2) natural fish survived at greater rates. I cannot discount this bias but note that the proportion of marked fish in the intertidal collections was similar to the channel collections. Thus it is likely that, for the UCR Su/F stock group, the in-channel purse seine collections are not greatly underestimating natural fish. It is plausible that natural individuals experienced increased survival, compared with hatchery fish, during their first summer at sea in

2010 and 2011. Further research is needed to evaluate if natural fish consistently survive better than hatchery conspecifics and to determine what traits and behaviors may increase survival. The possibility that hatchery fish experience lower survival during early marine residence than natural fish is consistent with observations that hatchery fish have reduced lifetime fitness.

Considerable mortality occurs during early life stages of all fish species. However, the factors regulating survival may vary temporally, spatially, among life stages, species, and between artificially propagated and natural fish. I adopted a novel approach to evaluating selective mortality and migratory patterns of a depleted species during a critical life stage while also specifically comparing hatchery and natural fish. To my knowledge, this is the first study to compare size at and timing of marine entry for natural and hatchery Chinook salmon from the Columbia River. Future studies should increase sampling effort in the estuary to determine the frequency of sampling required to accurately characterize the timing of marine entry. Similarly, the possibility of differential survival related to migration timing warrants further research. Further investigations characterizing timing of marine entry and early marine growth may provide insight. Finally, physically marking all hatchery fish prior to release would be a logical step to facilitating comparisons between production types and would tremendously increase our understanding of the potential negative effects of artificial propagation.



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## APPENDIX

Appendix Table 1. Hatchery, year released, number released unmarked (*n* unmarked), marked (*n* marked), hatchery mark rate (% marked), and percent unmarked (% unmarked total) relative to the total number of upper Columbia River summer and fall subyearling Chinook salmon released in the mid- and upper Columbia River ([www.fpc.org](http://www.fpc.org)).

Hatchery	Year	<i>n</i> unmarked	<i>n</i> marked	% marked	% unmarked total
Prosser	2010	299,542	13,685	4.37	1.27
Turtle Rock	2010	534,847	178,283	25.00	2.26
Klickitat	2010	3,023,113	1,129,623	27.20	12.80
Priest Rapids	2010	3,412,348	3,364,303	49.65	14.45
Ringold Springs	2010	44,365	3,354,194	98.69	0.19
Chelan	2010	2,909	710,221	99.59	0.01
Wells	2010	1,122	670,911	99.83	0.00
Little White Salmon	2010	0	623,1304	100.00	0.00
Umatilla	2010	0	645,488	100.00	0.00
Prosser	2011	597,981	22,985	3.70	2.63
Klickitat	2011	2,830,294	1,145,883	28.82	12.43
Priest Rapids	2011	3,887,631	3,414,531	46.76	17.07
Ringold Springs	2011	23,621	3,453,333	99.32	0.10
Little White Salmon	2011	2,200	6,173,612	99.96	0.01
Eastbank	2011	0	177,357	100.00	0.00
Umatilla	2011	0	562,855	100.00	0.00
Wells	2011	0	482,227	100.00	0.00

Appendix Table 2. Collection date and number of upper Columbia River summer and fall Chinook salmon captured at the mouth of Columbia River ( $N_{CR}$ ) and off the coast in September ( $N_O$ ) used in tests of selective mortality. Dashes indicate no sampling occurred.

Year	Collection Date	$N_{CR}$	$N_O$
2010	9-Jun	1	-
	23-Jun	8	-
	28-Jun	4	-
	26-Jul	24	-
	8-Sep	16	-
	21-Sep	-	9
	22-Sep	-	4
	23-Sep	-	13
	26-Sep	-	1
	27-Sep	-	14
	28-Sep	-	11
2011	17-May	1	-
	31-May	2	-
	15-Jun	1	-
	16-Jun	4	-
	28-Jun	9	-
	13-Jul	13	-
	14-Jul	3	-
	10-Aug	22	-
	13-Sep	4	-
	14-Sep	6	-
	19-Sep	-	8
	20-Sep	-	6
	21-Sep	-	2
	22-Sep	-	17
	23-Sep	-	10
	24-Sep	-	18
	25-Sep	-	9
	26-Sep	-	3