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Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type

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ABSTRACT: The underlying causes of mortality during critical life stages of fish are not well understood, nor is it clear if these causes are similar for naturally versus artificially propagated (i.e. hatchery) individuals. To assess the importance of selective mortality related to production type (hatchery vs. naturally produced) and size at and timing of marine entry, we compared attributes of juvenile Chinook salmon *Oncorhynchus tshawytscha* from the upper Columbia River summer- and fall-run genetic stock group captured in the Columbia River estuary with back-calculated attributes of survivors captured in marine waters. We used genetic stock identification, otolith chemistry and structure, and physical tags to determine stock of origin, size at and timing of marine entry, and production type. Fish emigrated from fresh water in May to September and the majority of fish collected in the estuary (87%) had arrived within 3 d of capture. In 1 of 2 yr, timing of marine entry for both production types differed between the estuary and ocean: the ocean catch included a greater proportion of juveniles that emigrated in late July than the estuary catch. There was no evidence of selective mortality of smaller juveniles during early marine residence in hatchery or natural juveniles, but the mean percentage (±SE) of hatchery fish in ocean collections was 16 ± 5.8% less than in the estuary, which could indicate reduced survival compared to naturally produced fish. Results from this study highlight the need to understand the effects of hatchery rearing and how hatchery propagation may influence survival during later critical life-history transitions.

KEY WORDS: Chinook salmon · Early marine survival · Hatchery · Naturally propagated · Size-selective mortality · Otolith

INTRODUCTION

Understanding the factors influencing survival during critical life stages has been a primary focus of fisheries research, but it is not clear if those factors are similar for naturally propagated (hereafter 'natural fish') and artificially propagated individuals (hereafter 'hatchery fish') in many species. Chinook salmon *Oncorhynchus tshawytscha* is an ecologically and economically important anadromous species widely distributed along the West coast of the North America. In the Columbia River basin, average annual harvest

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of Chinook salmon is estimated to have declined by 80% since non-native exploitation began in the 1800s (Lichatowich 1999). Hatchery programs in the Columbia River basin release >100 million juvenile Chinook salmon annually (www.fpc.org). In many species there are clear negative effects of hatchery rearing including lower survival, behavioral disadvantages, and reduced reproductive success (reviewed by Araki & Schmid 2010). However, it is not clear if hatchery Chinook salmon negatively interact with, or have effects on, natural conspecifics, or if migratory patterns and survival consistently vary between hatchery and natural fish during the marine phase.

Several studies have demonstrated strong relationships between ocean conditions during the early marine phase and subsequent adult salmon survival (Mantua et al.1997, Peyronnet et al. 2008, Rupp et al. 2012, Burke et al. 2013). Additionally, marine mortality is likely greatest during the first summer at sea (Pearcy 1992, Pearcy & McKinnell 1997) although the mechanisms and the specific timing of mortality are not clear. Several factors during early marine residence are related to variation in survival of salmonids, including growth shortly after marine entry (Beamish et al. 2004, Peyronnet et al. 2007, Duffy & Beauchamp 2011, Tomaro et al. 2012), timing of marine entry (Scheuerell et al. 2009), and juvenile size at marine entry (Jokikokko et al. 2006, Bond et al. 2008, Claiborne et al. 2011). However, relatively few studies have examined these factors specific to production type (i.e. hatchery or naturally reared) (Levin & Williams 2002, Zabel & Achord 2004, Daly et al. 2012, Woodson et al. 2013, L. Weitkamp unpubl. data). Given that hatchery and natural salmonids can exhibit differential survival rates (Jonsson et al. 1991, Coronado & Hilborn 1998, Beamish et al. 2012) or could negatively interact during early marine residence (Levin & Williams 2002), it is important to understand the migratory behavior and the extent of spatial and temporal overlap between hatchery and natural juveniles during early marine residence.

The direct causes of mortality for salmon during their early marine residence likely include a combination of disease, starvation, and predation (Pearcy 1992), with the primary mechanism hypothesized to be predation (Beamish & Mahnken 2001). Predation rate is often inversely related to fish size (Ware 1975, Shepherd & Cushing 1980, Sogard 1997), with larger or faster-growing individuals surviving better than smaller or slower-growing individuals due to lower predation rates (Miller et al. 1988) and shorter stage duration (Houde 1987). Similarly, larger fish can have a survival advantage during periods of starvation or exhaustion (Sogard 1997, Beamish & Mahnken 2001, Beamish et al. 2004). As such, the disproportionate survival of larger individuals may occur during or between critical life stages (reviewed by Anderson 1988), such as when larvae transition to juveniles (Meekan et al. 2006) or during juvenile stages (Tsukamoto et al. 1989). Size-selective mortality of salmonids has been detected in several studies (Zabel & Williams 2002, Bond et al. 2008, Claiborne et al. 2011). However, for Columbia River Chinook salmon, it is not clear if this mortality occurs during emigration from the river, at marine entry when juveniles encounter a new suite of avian (Roby et al. 2003, Antolos et al. 2005, Sebring et al. 2013) and pelagic-fish (Emmett & Krutzikowsky 2008) predators, or sometime later in life before adults return to freshwater to reproduce. In addition, it is not clear if size-selective mortality affects hatchery and natural conspecifics similarly.

Natural fish are typically smaller than hatchery counterparts during seaward migration (Kallio-Nyberg et al. 2011) and early marine residence (Sweeting & Beamish 2009, Beamish et al. 2012, Daly et al. 2012). If mortality is biased towards smaller fish, then natural individuals may experience disproportionally higher mortality than hatchery fish. However, it is not clear if natural fish have behavioral advantages, such as increased ability to avoid predators (Johnsson & Abrahams 1991, Berejikian 1995, Chittenden et al. 2010) or feed successfully (Brown et al. 2003, Sweeting & Beamish 2009, Daly et al. 2012), which could balance or compensate for their smaller size. In a laboratory setting, natural fish have been observed to be less susceptible to predation than similarly sized hatchery fish (Fritts et al. 2007, Lee & Berejikian 2008). Therefore, it is possible that hatchery and natural fish do not experience size-selective mortality similarly. Recent field studies observed that natural fish were smaller during the early marine period yet experienced higher survival in both Chinook (Beamish et al. 2012) and Atlantic salmon *Salmo salar* (Jonsson et al. 2003).

The greater variation in size and migration timing exhibited by natural Chinook salmon is thought to provide a bet-hedging strategy that spreads the risk and increases survival in a seasonally variable marine ecosystem compared to hatchery fish (Bottom et al. 2009, Beamish et al. 2012). Timing of marine entry may differ between production types (L. Weitkamp unpubl. data) with natural juveniles emigrating over a more protracted period. In addition, environmental conditions, such as river flow, influence the initiation and duration of emigration in salmonids (Coutant &

Whitney 2006, Sykes et al. 2009), but hatchery fish cannot migrate until they are released. Therefore, it is possible that hatchery juveniles experience greater mortality, potentially due to size or time-dependent mortality, during emigration and early marine residence than natural juveniles.

A robust comparison of hatchery and natural fish requires the accurate identification of hatchery fish. Although many hatchery fish are marked with an adipose-fin clip or physical tag, the proportion of hatchery production in the Columbia River basin that is marked prior to release varies among hatcheries, and ranged from ~10 to 100% in 2010 and 2011 (www.fpc.org). Therefore, individual production type cannot be confidently determined by external markings in most Columbia River Chinook salmon, particularly for subyearling (0+) emigrants, which are marked at lower rates than yearling emigrants (1+). Otoliths provide natural tags that can be used to differentiate production type (Zhang et al. 1995, Zhang & Beamish 2000, Barnett-Johnson et al. 2007) because the different rearing environments experienced by hatchery and natural Chinook salmon are evident in their otoliths.

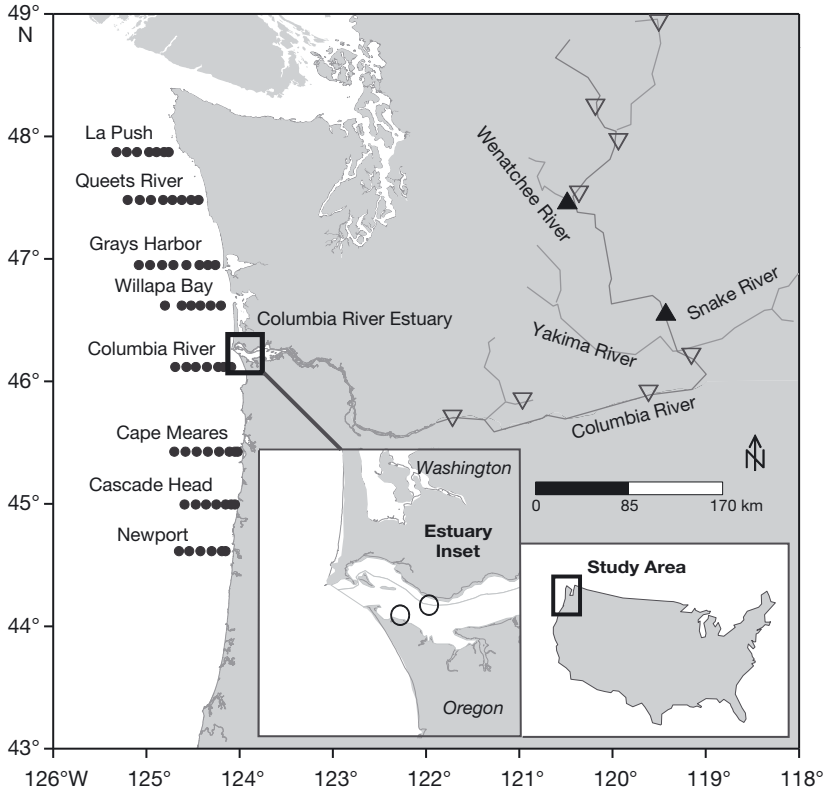

Fig. 1. (▽) Rearing location of known hatchery and (▲) naturally propagated Chinook salmon used to develop the otolith classification model. Capture sites: (●) off the coast of Oregon and Washington and (○, inset) Columbia River estuary, USA

To address the hypothesis that selective mortality is stronger in hatchery than natural juvenile Chinook salmon, we (1) developed a production-type classification model using otolith structure to differentiate hatchery and natural Chinook salmon; (2) directly compared migratory patterns of hatchery and natural individuals from the same genetic stock group; and (3) determined if there was evidence for selective mortality during early marine residence in both hatchery and natural Chinook salmon by comparing fish captured in the estuary to those captured later in the coastal ocean. We anticipated that migration size, timing, and distribution would consistently differ between production types. We expected that size-selective mortality would occur during early marine residence, but that natural fish would experience increased survival compared to hatchery fish

MATERIALS AND METHODS

We captured Chinook salmon in the estuary before their first summer at sea by repeatedly sampling at the mouth of the Columbia River during emigration (April to September) followed by juvenile collections in the marine waters of Oregon and Washington in late September (Fig. 1). We identified the genetic stock group and production type (hatchery or natural) and reconstructed migratory history of juvenile Chinook salmon using a combination of microsatellite genotyping, otolith analyses, and physical tags.

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 (Weitkamp et al. 2012; our Fig. 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 marine mortality. The Columbia River estuary was sampled twice monthly during April to June and monthly in July to Septem-

ber in 2010 and 2011 (apart from in August 2010, when no survey was conducted). Chinook salmon were collected using a 155 × 10.6 m purse seine with stretched 1.7 cm mesh and 1.7 cm knotless bunt mesh in approx. 9 to 10 m of water (described in Weitkamp et al. 2012). All individuals retained from each survey were measured (fork length, FL, in mm), frozen, and later thawed, re-measured, and weighed (to the nearest g). Otoliths were extracted, fish were examined for internal and external tags, and tissue samples were collected for genetic analysis.

Ocean-collected fish were used to quantify the size at and timing of freshwater emigration of those juveniles that survived their first ocean summer, and to determine the extent of spatial overlap of natural and hatchery juveniles in coastal waters. Ocean collections occurred during NOAA surveys in late September of 2010 and 2011 using a Nordic 264 rope trawl (Net Systems) fished at the surface directly astern of the research vessel. Eight transects from La Push, Washington to Newport, Oregon were sampled (Fig. 1). The trawl mouth had an opening 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). After capture, ocean-collected individuals were processed as described above.

Identification of genetic stock group

The upper Columbia River summer and fall (UCR Su/F) genetic stock group is composed of spawning populations in several rivers, including the mainstem Columbia, Yakima, Wenatchee, and Methow Rivers, with hatchery production within 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 fisheries resource (68% total exploitation rate) (Myers et al. 1998, Weitkamp 2010). The initial marine migrations of UCR Su/F subyearlings are limited, and most fish remain in coastal waters off Oregon and Washington during their first summer at sea (Teel 2004, Trudel et al. 2009, Tucker et al. 2012, Fisher et al. 2014). This local coastal residence of UCR Su/F subyearlings means the majority of the subyearlings remained in our study area through September, and we therefore assumed our sampling of ocean residents was representative of the overall population.

Juvenile Chinook salmon were genotyped at 13 standardized microsatellite DNA loci (Seeb et al. 2007) following the methods outlined in Teel et al. (2009). A regional population baseline (Seeb et al. 2007, Moran et al. 2013, Hess et al. 2014) and the genetic stock identification software ONCOR (Kalinowski et al. 2007) were used to estimate the stock origin of individual fish. Fish were classified as subyearlings based on size at capture in the estuary (<115 mm before April 30, <120 mm May 1–15, <125 mm May 16–31, <130 mm June 1–15, <135 mm in June 16–30, any size after July 1; Weitkamp et al. 2012) and the ocean (<250 mm in September; Fisher et al. 2007). Only subyearling Chinook salmon assigned to the UCR Su/F genetic stock group were included in this study. Barnett-Johnson et al. (2010) used the same 13 microsatellite loci to identify UCR Su/F Chinook salmon, and reported that individuals with posterior assignment probabilities >90% were correctly assigned to the stock with 98% accuracy. There was a mean (±SD) genetic stock assignment probability of 96 ± 7.2% for the samples included in our study.

Production type classification

In 2010 and 2011, 63% of fish included in this study were unmarked (no adipose fin clip, or physical internal or external tag). These represent a combination of natural and unmarked hatchery fish, as significant natural production occurs in the UCR Su/F population (Myers et al. 1998), and a high percentage of unmarked hatchery individuals have also been released in recent years (www.fpc.org). In 2010 and 2011, >45 million hatchery subyearlings were released from the UCR Su/F stock, of which 32% were released unmarked (Table A1 in the Appendix). Hatchery individuals were released April to July in 2010 and 2011, and originated from 9 and 8 hatchery facilities, respectively (Table A1). Therefore, in order to develop an otolith structural baseline for determination of production type, known hatchery and natural fish were collected from several sources in the upper Columbia River, estuary and coastal waters (Table 1, Fig. 1).

Otoliths were mounted on glass slides using a thermoplastic resin, and ground on proximal then distal sides until core structure was evident and the edge maintained. Digital images were acquired and several metrics of otolith structure were recorded, including (1) the prominence of the exogenous feeding check (Barnett-Johnson et al. 2007); (2) otolith width (OW) at the hatch check; (3) OW at the exogenous feeding check; (4) mean increment width;

Table 1. Hatchery or rearing location, sample size (n), source (R = river, H = hatchery, CWT = coded wire tagged fish from estuary or ocean collections), adult run time (Su = Summer, Fa = Fall), mean ± SE fork length (FL) in mm at capture, emigration year, and production type (N = natural, H = hatchery) of upper Columbia River summer and fall Chinook salmon used to develop and test the production model. Sample sizes in parentheses indicate the individuals used to assess accuracy of the classification model

Rearing area	n	Source	Adult run time	FL	Emigration year	Production type
Lower Wenatchee River	40 (10)	R	Su	40 ± 0.5	2011	N
Hanford Reach Columbia River	17	R	Fa	44 ± 0.8	2012	N
Carlton Rearing Pond	9	H	Su	37 ± 1.4	2011	H
Priest Rapids Hatchery	2 (2)	CWT	Fa	167 ± 11.1	2010	H
Umatilla Hatchery	3 (2)	CWT	Fa	134 ± 17.8	2010 & 2011	H
Klickitat Hatchery	2 (2)	CWT	Fa	99 ± 13.9	2010 & 2011	H
Little White Salmon Hatchery	2 (2)	CWT	Fa	115 ± 14.8	2010 & 2011	H
Wells Hatchery	(2)	CWT	Su	114 ± 0.0	2010 & 2011	H
Similkameen Rearing Pond	7	H	Su	42 ± 1.6	2011	H
Wenatchee Rearing Pond	20	H	Su	43 ± 0.7	2011	H

and (5) coefficient of variation (CV) for the first 20 daily increments after the exogenous feeding check. A logistic approach was used to incorporate both continuous and non-continuous otolith metrics and predict a binary response, 'natural' or 'hatchery' origin (Ramsey & Schafer 2002). Akaike Information Criterion corrected for small sample size (AIC_C) (Hurvich & Tsai 1989) was used to measure relative goodness-of-fit of the 7 models examined (Table A2). The most parsimonious classification model (lowest AIC_C) incorporated the CV of the otolith increment widths for the first 20 d of post-exogenous feeding as the predictor of production type (Table A2):

$$P_{PT} = e^{\beta_0 + \beta_1 \times CVIW} / 1 + e^{\beta_0 + \beta_1 \times CVIW} \quad (1)$$

where P_{PT} is the probability of production type and the independent variable is the coefficient of variation of increment widths (CVIW). Model coefficients β_0 and β_1 are (coefficient ± SE) −14.32 ± 3.1, and 107.68 ± 23.53, respectively. The internal and jackknife accuracy of this classification model was 92%. Using a probability cutoff of 0.5, the classification model identified 'hatchery' individuals with 91% internal accuracy and 'natural' individuals with 93% internal accuracy. Ninety percent of the coded wire tag hatchery and natural individuals (n = 18 of 20) used to independently validate the classification model were classified correctly (Table 1). For a complete description of model development see Claiborne (2013).

To identify the production type of our unmarked, field-collected juveniles, we prepared their otoliths as described above and determined the mean and CV for the first 20 post-exogenous daily increment widths. We then used the classification model in Eq. (1) with a probability cutoff of ≥0.50 to assign natural fish, and <0.50 for hatchery individuals. This analysis provided individual assignments that could be directly compared between production types: the size at and timing of freshwater emigration, and marine growth. This statistical analysis was done using the software R (R Development Core Team 2013) and the programing package DAAG (Maindonald & Braun 2012).

We also wanted to compare the overall contributions of each production type within our collections. Therefore, we used 2 independent approaches, termed the 'otolith method' and 'marked method'. For the otolith method, we expanded the proportion of hatchery and natural fish as determined from otolith microstructure within each sample (estuary or ocean) and year to the total catch of UCR Su/F individuals.

$$\text{Hatchery contribution} = \{[(N_U \times P_H) + H_M] / n\} \times 100 \quad (2)$$

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

For the 'marked method' we estimated the proportion of hatchery and natural individuals in estuary and ocean collections based on the presence or absence of a physical tag and/or adipose fin clip, and reported hatchery marking rates. We determined the proportion of unmarked 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 with a

Table 2. Percent contribution (±SE) of natural (% N) and hatchery (% H) Chinook salmon captured at the mouth of Columbia River estuary (E) and in the coastal ocean (O) in 2010 and 2011 using the 'marked method' or the 'otolith method'. The total number of juveniles in each catch, the number of marked juveniles, the estimated mean proportion of the hatchery production that was marked in each year (marked hatchery releases), and the proportion of unmarked hatchery fish determined using the otolith method (unmarked hatchery correction) are included. See text for details on the 2 methods

Year	Study	Number marked in catch	Total in catch	Marked method			Otolith method		
				Marked hatchery releases	% H	% N	Unmarked hatchery correction	% H	% N
2010	E	23	53	0.69	63 ± 6.7	37	0.33	62 (6.7)	38
	O	26	92	0.69	41 ± 5.1	59	0.43	59 (5.1)	41
2011	E	39	75	0.68	76 ± 4.8	24	0.25	64 (5.5)	36
	O	40	124	0.68	47 ± 4.5	53	0.31	53 (4.5)	47

physical tag and/or adipose fin clip at hatcheries (Table 2) (www.fpc.org).

$$\text{Hatchery contribution} = [(H_M / P_M) / n] \times 100 \quad (3)$$

where H_M = number of marked hatchery subyearlings captured, P_M = the proportion of subyearling UCR Su/F hatchery production marked in a year, and n = the total number of subyearlings captured.

Juvenile emigration and growth

The size at, and timing of, freshwater emigration (Campbell 2010, Miller et al. 2011, Tomaro et al. 2012) and marine growth (Tomaro et al. 2012, Miller et al. 2014) have been estimated for Chinook salmon using the combination of otolith chemistry, structure, and back-calculation models. Sr:Ca levels are consistently lower in freshwater (i.e. 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). For estuary collections, we used all otoliths from UCR Su/F subyearlings captured in 2010 and 2011. For ocean collections, we subsampled otoliths from the total catch of UCR Su/F to represent all transects and maintain representative size at capture and proportion of marked fish.

Otoliths were prepared as described above using standard methods for trace element analysis (Miller et al. 2011, Tomaro et al. 2012). Otolith Sr and Ca was measured 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, Corvallis, Oregon. Data were collected along a ventral–dorsal transect through the core at the widest point (Fig. 2). The laser was set at a pulse rate of 7 Hz traveling across the sample at 5

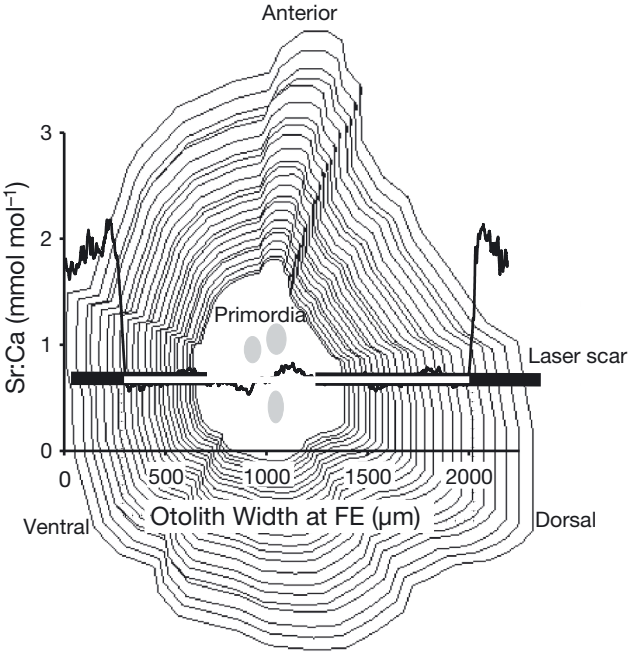

Fig. 2. Schematic of an otolith with the laser path and otolith width at freshwater emigration of a Chinook salmon and corresponding otolith Sr:Ca. White line: otolith width at freshwater emigration (FE)

or 7 µm s^{-1} with a spot size of 30 µm. 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. OW at freshwater emigration was defined as the distance between points of inflection in the Sr:Ca profile along the dorsal-ventral axis (Fig. 2; Miller et al. 2011, Tomaro et al. 2012). Mean precision (% relative SD) determined from NIST 612 was 5.7% for ^{43}Ca and 4.9% for ^{86}Sr (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).

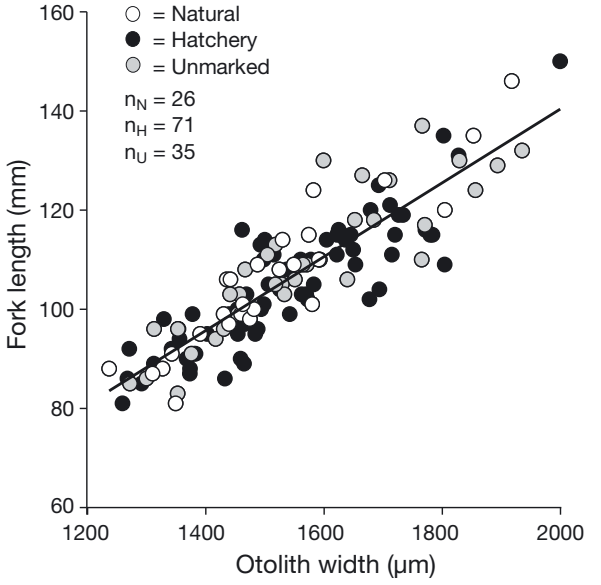

Fig. 3. Relationship between otolith width and fork length at capture ($r^2 = 0.77$, n = 132, $p < 0.01$) for Chinook salmon sampled in 2010 and 2011 in Oregon and Washington, USA. Number of samples for natural (n_N) (open circles), hatchery-reared (n_H) (filled black circles), and unmarked and unknown (n_U) (filled grey circles)

We estimated fish size at freshwater emigration using a stock-specific relationship between FL (mm) and OW (µm) (Fig. 3):

$$FL_{FE} = OW_{FE} \times 0.07\ (\pm 0.004\ SE) - 7.22\ (\pm 5.44\ SE) \quad (4)$$

where FL_{FE} is the estimated fork length at freshwater emigration and OW_{FE} is the OW at freshwater emigration as determined from otolith Sr:Ca. We only included estuary- and ocean-captured individuals that had recently emigrated from freshwater (≤10 d) in the model because we were predicting size at freshwater emigration ($r^2 = 0.77$, n = 132, $p < 0.01$). We note that for hatchery and natural fish there was a difference in the relationship between FL and OW (Fig. 3; ANCOVA, $p < 0.01$). For example, at larger sizes (e.g. 120 mm) natural fish had 5% smaller otoliths than hatchery fish (Fig. 3). However, estimates of size at freshwater emigration using production type-specific relationships and the stock-specific relationship above were not significantly different (Wilcoxon-rank sum: $p > 0.41$); thus, we used Eq. (4) for all fish. Of the individuals captured in the estuary in 2010 and 2011, 87% exhibited no increase in otolith Sr:Ca, indicating entrance into saline waters within the last 1 to 3 d (Miller 2011). For these individuals, size at capture was assumed to represent size at freshwater emigration.

We enumerated daily increments after the increase in Sr:Ca to estimate the date of freshwater emigration and brackish/marine growth, hereafter termed 'marine growth' (Fig. 2). Individuals captured at the mouth of Columbia River and in the ocean exhibiting no increase in otolith Sr:Ca were assumed to have entered the saline waters on the day of capture. Marine growth was calculated as percent body length (bl) per day:

$$\text{Growth (\% mm d}^{-1}) = \{[(FL_C - FL_{FE})/D_{FE}]/FL_{FE}\} \times 100 \quad (5)$$

where FL_C indicates fork length at capture, FL_{FE} indicates fork length at freshwater emigration, and D_{FE} indicates days since freshwater emigration.

Statistical analysis: hatchery and natural comparison

To address our objective of directly comparing migratory patterns of hatchery and natural fish, we compared marine distribution, size at and timing of freshwater emigration, and marine growth between production types. (1) We qualitatively compared the timing of freshwater emigration and marine residence for estuary and ocean collections between years. We did not statistically compare marine residence for fish captured in the estuary because 87% had only recently entered the estuary. (2) We determined if there were differences in the spatial distribution between production types captured in the ocean using the Cramér-von Mises test (Syrjala 1996) with the software R (R Development Core Team 2013) and programming package ecespa (De la Cruz 2008). We calculated catch per unit effort (i.e. abundance) as the number of hatchery and natural fish captured per km trawled for each transect. The Cramér-von Mises test compares a measure of abundance by latitude and longitude coordinates, and is resistant to differences in abundance between 2 groups, but is sensitive to the way 2 groups are distributed across the study area (Syrjala 1996). A single test statistic (Ψ) is computed for the square of the difference between 2 cumulative distribution functions, and the significance level of the statistic is determined using a randomization test (n = 1000 permutations) (Syrjala 1996). Thus, ocean spatial distributions were compared between production types in each year at the spatial level of transect (n = 8 transects). Our subsample of UCR Su/F was assumed to be representative (n = 35 and 53 in 2010 and 2011, respectively) because its spatial distribution did not differ from the distribution of the total catch of UCR Su/F in 2010 (n = 92) or 2011 (n = 124) at the spatial level of

Table 3. Median (±SE) of metrics compared between natural and hatchery Chinook salmon captured in estuary and in the coastal ocean in 2010 and 2011. Values for 'marine residence' and 'estuarine residence' is the mean (±SE). FE = freshwater emigration, FL = fork length, bl = body length. Sample sizes are shown as a range because all individuals could not be included for each metric. '*w*' = the sum of ranks of each metric for hatchery fish; (–) = no data

Metric	2010				2011			
	Hatchery	Natural	*w*	p	Hatchery	Natural	*w*	p
Estuary								
Size at FE (FL, mm)	100 (2.9)	108 (4.8)	165	0.32	101 (1.7)	106 (4.0)	192	0.16
Day of FE (day of the year)	207 (4.9)	207 (8.7)	201	0.96	194 (4.0)	222 (6.6)	106	<0.01
Estuarine residence (d)	13 (5.4)	1 (0.8)	–	–	1.0 (0.9)	0 (0.0)	–	–
n	28	14	–	–	36	15	–	–
Coastal ocean								
Size at FE (FL, mm)	100 (3.3)	107 (2.3)	98	0.17	101 (2.0)	95 (2.1)	189	0.02
Size at capture (FL, mm)	155 (4.6)	154 (3.4)	135	0.94	159 (4.5)	148 (3.2)	209	0.05
Marine growth rate (% bl d^{-1})	0.88 (0.1)	0.81 (0.1)	128	0.59	0.95 (0.1)	1.03 (0.1)	264	0.58
Day of FE (day of the year)	200 (4.4)	215 (6.4)	108	0.82	210 (4.0)	208 (4.5)	230	0.82
Marine residence (d)	66 (4.2)	61 (6.1)	–	–	58 (4.0)	56 (4.1)	–	–
n	19–23	12	–	–	30–35	16–18	–	–

transect (Cramér-von Mises test, $\Psi > 0.01$, $p > 0.42$). (3) We tested 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.

Statistical analysis: estuary and ocean comparison

To test for selective mortality between estuarine residence and ocean capture, we compared distributions of size at and timing of freshwater emigration for individuals captured in the estuary and ocean. In each year, we compared hatchery and natural distributions separately using the Kolmogorov-Smirnov test in order to identify differences in selective mortality between production types. Finally, to test for selective mortality related to production type we compared the proportion of natural and hatchery fish between the estuary and ocean using Fisher's exact tests, and for the marked and otolith method separately.

RESULTS

Using the classification model, we successfully determined the production type of 57% of the unmarked individuals (86 of 150) captured in the estuary and ocean in 2010 and 2011. For the remaining 43% (64 of 150) of unmarked samples, otolith structure near the exogenous feeding check was unable to be quantified due to damage caused by preparation. Overall, 69% of unmarked fish were classified as natural and 31% as hatchery origin: only these unmarked individuals and those marked with an adipose fin clip or physical tag were used for comparisons between production types. In total, 59 natural and 122 hatchery individuals from the estuary and ocean in 2010 and 2011 were used in comparisons (Table 3).

Hatchery and natural comparison

Overall, we observed few phenotypic differences between hatchery and natural fish captured in the estuary and ocean in 2010 and 2011. The timing of freshwater emigration ranged from late May to late September and peaked in July and August in both 2010 and 2011. All hatchery and natural fish emigrated after the onset of hatchery releases in 2010 and 2011 and freshwater emigration continued for approx. 2 mo after hatchery individuals were last released (www.fpc.org). For estuary collections from 2010 and 2011, 87% of fish captured had resided in brackish/marine water for <3 d, and 11% had resided for >7 d, before capture. Estuarine residence (mean ± SE) of hatchery fish was 12 d longer in 2010 (13 ± 5.4 d) than 2011 (1 ± 0.9 d), primarily due to 5 hatchery individuals which resided in the estuary for 40 to 111 d before capture in 2010. Natural fish resided 1 ± 0.8 d in 2010 and 0 ± 0.0 d in 2011 (Table 3). For ocean collections, juveniles had resided in marine waters for 62 ± 2.0 d in 2010 and 56 ± 1.7 d in 2011 (Table 3, Fig. 4).

Hatchery and natural fish were captured throughout our study area north and south of the Columbia

River — from La Push, Washington to Newport, Oregon (Fig. 4). There was no difference in ocean distributions between hatchery and natural fish during early marine residence in 2010 (hatchery n = 23, natural n = 12) (Cramér-von Mises test, $\Psi = 0.13$, $p = 0.28$) or 2011 (hatchery n = 35, natural n = 18) (Cramér-von Mises test, $\Psi = 0.06$, $p = 0.57$) or between years for either production type (Cramér-von Mises test, $\Psi > 0.21$, $p > 0.68$).

Overall, median size of hatchery and natural fish at freshwater emigration was 101 mm, and varied by <8 mm between production types and years (Table 3). For estuary collections, there were no differences in size at freshwater emigration between hatchery and natural juveniles in 2010 or 2011 (Table 3; Wilcoxon rank sum test, $p > 0.10$). For ocean collections, back-calculated size at freshwater emigration for hatchery and natural fish was similar in 2010 (Table 3; Wilcoxon rank sum test, $p = 0.17$), but hatchery fish were larger at freshwater emigration (Table 3; Wilcoxon rank sum test, $p = 0.02$) and at capture (Table 3; Wilcoxon rank sum test, $p = 0.05$) in 2011.

Ocean growth rates did not differ between hatchery and natural fish in 2010 or 2011 (Table 3; Wilcoxon rank sum test, $p > 0.58$). Median growth rates for hatchery fish were 0.88 and 0.95 (% bl d^{-1}) in 2010 and 2011, respectively (Table 3). Median growth rates for natural fish were 0.81 and 1.03 (% bl d^{-1}) in 2010 and 2011, respectively (Table 3).

There was no difference in the estimated timing of freshwater emigration between production types captured in the estuary or in the ocean in 2010 (Table 3, Wilcoxon rank sum test: $p > 0.80$). In 2011, however, estuary collections indicated that natural individuals emigrated significantly later (~1 mo) than hatchery conspecifics (Table 3; Wilcoxon rank sum test, $p < 0.01$), but there was no difference in timing for fish caught in marine waters (Table 3; Wilcoxon rank sum test, $p = 0.82$).

Estuary and ocean comparison

We observed no evidence of negative size-selective mortality in 2010 or 2011 for either production type. Size at freshwater emigration did not differ between the estuary and ocean catches for hatchery or natural fish in 2010, or hatchery fish in 2011 (Fig. 5; Kolmogorov-Smirnov test, $p > 0.40$). Unexpectedly, in 2011, natural fish in the estuary were 10 mm larger at freshwater emigration than natural fish collected later in the ocean (Fig. 5; Kolmogorov-Smirnov test,

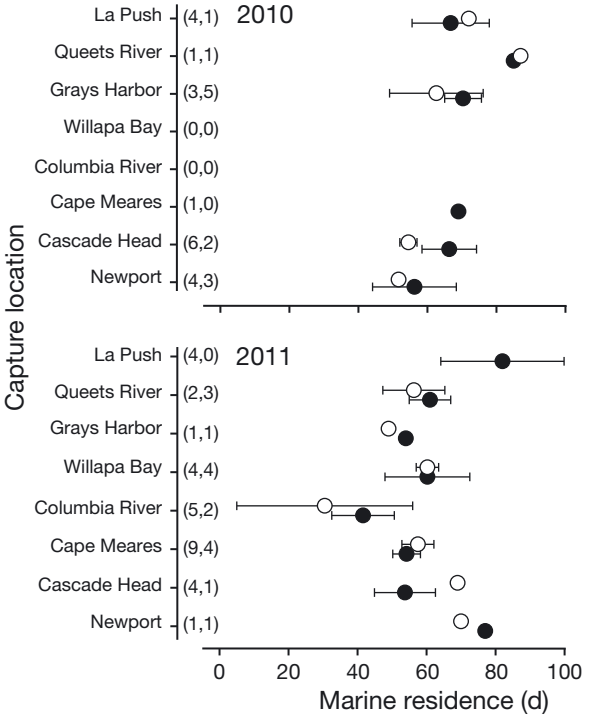

Fig. 4. Mean (±SE) marine residence for Chinook salmon sampled along each ocean transect: hatchery-reared (●) and naturally propagated (○). Sample sizes (in parentheses) are indicated for each transect (hatchery, natural). See Fig. 1 for transect locations

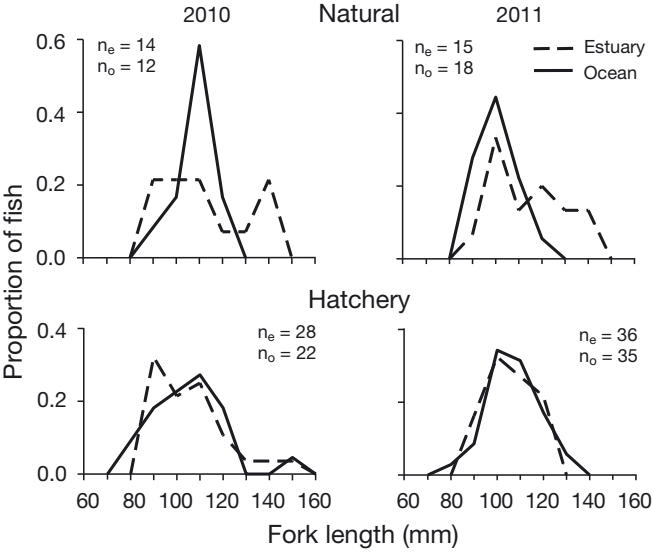

Fig. 5. Frequency distribution for size (10 mm bins) at freshwater emigration for juvenile Chinook salmon that were classified as 'natural' or 'hatchery' based on otolith structure. Juveniles were captured in the Columbia River estuary (dashed line) and coastal ocean (black line) in 2010 and 2011; 'n_e' and 'n_o' indicate the number of estuary and ocean fish, respectively

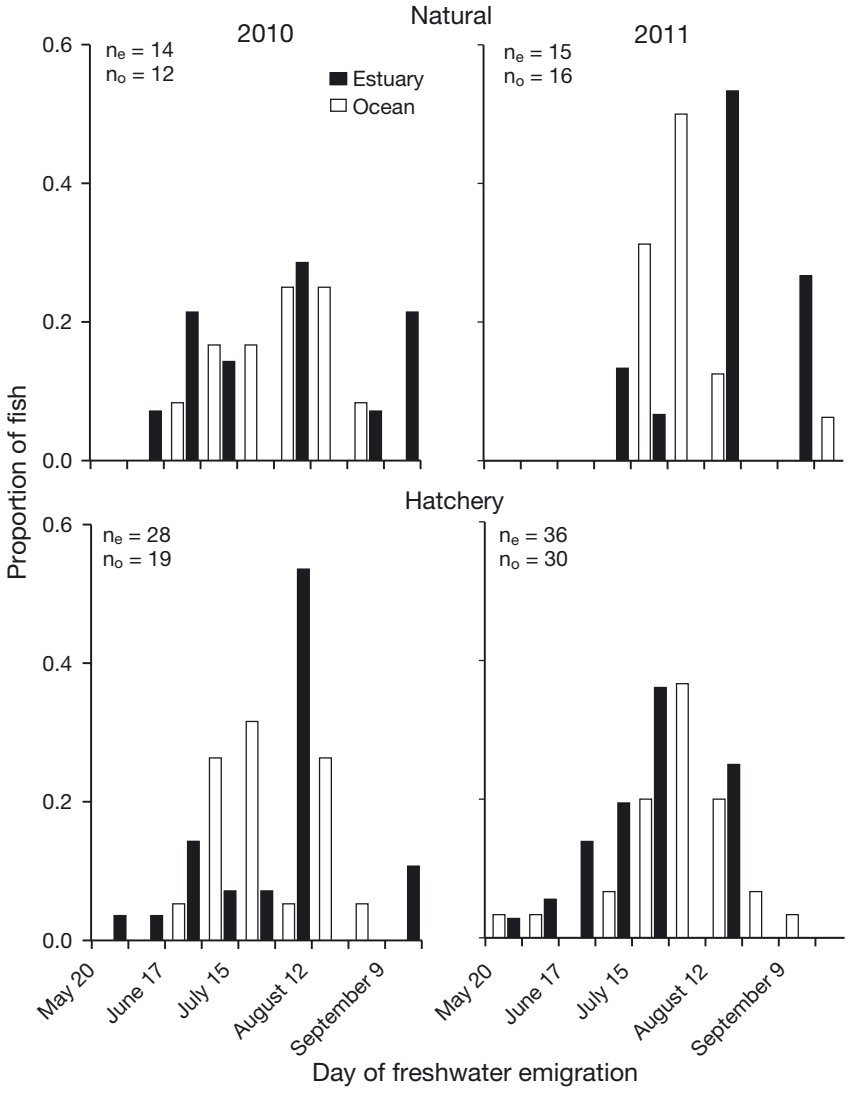

Fig. 6. Histogram of the day (14 d bins) of freshwater emigration for natural and hatchery Chinook salmon captured at the mouth of the Columbia River estuary (black bars) and in the coastal ocean in September (white bars) in 2010 and 2011; 'n_e' and 'n_o' indicate the number of estuary and ocean fish, respectively

p = 0.06) due to the absence of large (>120 mm) natural emigrants in ocean collections.

There was no evidence for selective mortality related to the timing of freshwater emigration for either production type in 2010 (Fig. 6; Kolmogorov-Smirnov test, $p > 0.10$), but there was evidence for it in 2011 (Fig. 6; Kolmogorov-Smirnov test, $p < 0.01$). In 2011, earlier migrating hatchery fish and later migrating natural fish captured in the estuary were under-represented in ocean catches and juveniles of both production types emigrating between late July and August were over-represented (Fig. 6).

We did observe evidence for selective mortality by production type. Overall the proportion of hatchery produced fish collected in the ocean decreased by 16% (± 5.8 SE) compared to estuary collections (Table 2). The otolith method indicated a non-significant increase in the proportion of natural fish in ocean collections compared with the estuary (3% in 2010 and 11% in 2011) (Table 2; Fisher's exact, $p > 0.20$). The marked 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) (Table 2; Fisher's exact, $p < 0.02$).

DISCUSSION

We present one of the first stock-specific estimates of the size at and timing of marine entry for hatchery and natural fish to determine if there were differences between production types, and if selective mortality due to size, timing, or production type occurred during the first summer at sea. We observed temporal overlap in the emigration of hatchery and natural fish and spatial overlap in the ocean. Although there were differences in size at marine entry between hatchery and natural fish, there was no evidence of negative size selection during the first weeks of ocean life. However, we observed decreases in the proportion of hatchery fish from the estuary to ocean, which suggests hatchery fish may have experienced greater mortality during early marine residence than natural fish.

Contrary to our expectations, we observed no evidence for selective mortality of juveniles that were smaller at the time of marine entry. We believe this lack of size selection was due in part to ecosystem conditions that were moderate to favorable for salmon survival in 2010 and 2011, including cooler ocean temperatures and higher productivity (Bjorkstedt et al. 2012). A recent study on Chinook salmon from the Central Valley, California observed that size-selective mortality during early marine residence was associated with periods of very poor overall survival, but was not observed during periods of

high survival (Woodson et al. 2013). Woodson et al. (2013) suggest that the size-selective mortality observed in a poor survival year, 2005, may have been related to delayed coastal upwelling and a mismatch between food availability and emigration timing of juveniles. Furthermore, Miller et al. (2013) determined that UCR Su/F subyearlings had a higher body condition index during years with poor ocean condition and low salmon survival (1998-2008), which would be expected if selective mortality was stronger in poor survival years. Estimates of survival for UCR Su/F Chinook salmon are not yet available for the full cohorts examined in our study. However, counts of fall Chinook (age-1) passing above Bonneville Dam are available for outmigration years 2010 and 2011, and were 31 and 95% higher respectively than the average for outmigration years 1999 to 2012 (www.fpc.org). Therefore, it is plausible that selective mortality of juveniles that are smaller at marine entry only occurs in very poor survival years.

Unexpectedly, although we observed few phenotypic differences between fish of different production types, natural fish appeared to have survived at higher rates. Natural populations have exhibited greater marine survival than hatchery populations in several species of salmonids (Jonsson et al. 1991, 2003, Coronado & Hilborn 1998, Jokikokko et al. 2006, Beamish et al. 2012). For example, Beamish et al. (2012) observed that natural Chinook salmon survived 6 to 24 times better than hatchery salmon captured during their first ocean summer in the Gulf Islands of British Columbia. Beamish et al. (2012) hypothesized that increased survival of natural individuals may be related, in part, to their increased diversity in size and timing of marine entry, which could provide resilience to changing marine conditions at the population level. Our results suggest that despite few differences in size at and timing of marine entry between production types, hatchery fish may experience reduced survival during early marine residence.

One explanation of our finding of differential mortality between production types is that behavioral responses to predators may differ between production types (Chittenden et al. 2010, Jackson & Brown 2011) which may lead to differential mortality (Fraser 2008). Natural individuals have experienced natural selection pressures prior to freshwater emigration, which may provide a survival advantage compared with hatchery individuals. For example, using a mesocosm approach, Chittenden et al. (2010) observed that coho 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 & Brown 2011).

Size-selective mortality of salmonids has been observed during freshwater stages (Zabel & Achord 2004), early marine residence (Woodson et al. 2013), and during the first winter at sea (Beamish et al. 2004). Therefore, it is possible that, for the study population, selection against smaller or slower growing individuals occurred in freshwater, prior to marine entry, 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 disruptive selection of steelhead *Oncorhynchus mykiss* by Caspian terns in the Columbia River has been documented (Hostetter et al. 2012). Surprisingly, we did observe a negative shift in the size of natural fish from the estuary to the ocean in 2011 but this result is closely related to emigration timing and is discussed below.

For fish captured in the estuary in 2011, hatchery fish emigrated approx. 1 mo earlier than natural fish, which has been observed in this and other stocks of subyearling Chinook salmon (L. Weitkamp unpubl. data). However, for juveniles collected at the end of September in the ocean, emigration timing was similar between production types, but there was an overrepresentation of juveniles that emigrated at the end of July and beginning of August in comparison with estuarine collections. In particular, larger (>120 mm) and later (late August and September) natural emigrants collected in the estuary were not proportionally represented in the ocean collections, resulting in a 10 mm decrease in median size of natural fish from the estuary to the ocean in 2011. This may be evidence of intra-annual variation in early marine survival related to the timing of marine entry but, emigration behavior and sampling methodology (i.e. frequency, timing, and location) cannot be completely discounted.

Analysis caveats

We identified 4 potential biases in our analyses that warrant discussion. (1) We note that our comparisons between hatchery and natural fish were based on

2 yr of data, relatively small sample sizes, and limited temporal sampling in the ocean (September only). Additional sampling is needed to determine if the results of our study are consistent within and across years. (2) We were unable to include individuals from the shallow intertidal estuary (depth = 1 to 3 m of water) where smaller UCR Su/F individuals may reside (Roegner et al. 2012). However, this does not explain the absence of large natural individuals in ocean catches in 2011. (3) Our estuary collections may be biased towards capturing hatchery fish (Weitkamp et al. 2012, Roegner et al. 2012). However, the percentage of tagged UCR Su/F salmon was similar between our estuary site and an adjacent intertidal site sampled over the same period (48% and 50% respectively, C. Roegner unpubl. data). (4) It is possible that the frequency of estuary sampling (biweekly, then monthly) did not fully capture the emigrating population due to short (<3 d) estuary residence observed in 87% of individuals included in this study. For example, some 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. More frequent estuarine sampling across a broader depth range could address these considerations.

Our finding of higher proportions of natural fish in the ocean than estuary were based on 2 independent estimation methods. The 'marked method' and 'otolith method' yielded similar conclusions, but the estimated hatchery contribution varied from 1 to 18% between the 2 methods. We suspect that this variation is related to differential mark rates and survival among hatcheries, CWT retention, adipose fin regeneration, and the classification error of our otolith method. Regeneration of adipose fin-clips has been observed to vary from 3 to 8% (Eames & Hino 1983), CWT tag loss from 1 to 7% (Knudsen et al. 2009), and we observed a ~10% classification error in our model. The classification model could be expanded with additional collections of hatchery and natural samples from other years and locations, which could increase its accuracy. Our intention was to identify production type in order to determine if hatchery and natural fish display phenotypic variation or display different migration patterns. Therefore, although determining production type using the otolith method is a time-intensive method with minimal equipment costs, it was necessary to classify individuals by production type. There was only 1 additional emigration year (2012) in which adequate numbers of juveniles were collected to compare estuary and ocean catches. Interestingly, based on the 'marked method', in 2012 we observed a 14% increase in the proportion of natural fish from the estuary (H = 48%, N = 52%) to the end of the first summer at sea (H = 34%, N = 66%), a finding very similar to 2010 and 2011. This study demonstrated that otolith structure is a useful tool to discriminate production type of Columbia River Chinook salmon, and may have utility for other population segments where high rates of unmarked hatchery fish are released.

CONCLUSIONS

In conclusion, we found no evidence of negative size-selective mortality for either hatchery or natural UCR Su/F Chinook salmon subyearlings. Although we expected that size at and timing of freshwater emigration would consistently differ between hatchery and natural fish, we observed few differences. In contrast, the proportion of hatchery fish decreased from the estuary to ocean in both years, which indicates reduced survival of hatchery relative to natural fish during the first summer at sea. If natural populations consistently experience higher survival rates during early marine residence than hatchery populations, the benefits of reduced mortality during early freshwater life stages within hatcheries may be negated and minimize the effectiveness of artificial propagation (Beamish et al. 2012). Future studies should examine survival by production types across more years and different populations to determine if natural fish consistently survive at higher rates.

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Appendix. Additional data

Table A1. Hatchery production of upper Columbia River summer and fall subyearling Chinook salmon. The hatchery, year of release, number released unmarked (n, unmarked), marked (n, marked), hatchery mark rate (% marked), and percent unmarked (% unmarked total) relative to the total number released (www.fpc.org) are presented

Hatchery	n, unmarked	n, marked	% marked	% unmarked total
2010				
Prosser	299542	13685	4.4	1.3
Turtle Rock	534847	178283	25.0	2.3
Klickitat	3023113	1129623	27.2	12.8
Priest Rapids	3412348	3364303	49.6	14.4
Ringold Springs	44365	3354194	98.7	0.2
Chelan	2909	710221	99.6	0.0
Wells	1122	670911	99.8	0.0
Little White Salmon	0	6231304	100.0	0.0
Umatilla	0	645488	100.0	0.0
Total	7318246	16298012	69.0	31.0
2011				
Prosser	597981	22985	3.7	2.6
Klickitat	2830294	1145883	28.8	12.4
Priest Rapids	3887631	3414531	46.8	17.1
Ringold Springs	23621	3453333	99.3	0.1
Little White Salmon	2200	6173612	100.0	0.0
Eastbank	0	177357	100.0	0.0
Umatilla	0	562855	100.0	0.0
Wells	0	482227	100.0	0.0
Total	7341727	15432783	67.8	32.2

Table A2. Model selection including number of independent variables (k), sample size (n), Akaike Information Criterion corrected for small sample size (AIC_C), delta (Δ) AIC_C, and jackknife accuracy of each classification model. Independent variables are coefficient of variation of increment widths (CVIW), otolith width at hatch (HOW), and otolith width at exogenous feeding (EOW)

Model	k	n	AIC_C	ΔAIC_C	Accuracy (%)
CVIW	1	102	46.11	0.00	92
HOW + CVIW	2	102	46.59	0.48	90
EOW + CVIW	2	102	47.27	1.16	91
EOW + HOW + CVIW	3	102	48.35	2.24	89
EOW	1	102	125.42	79.31	68
HOW + EOW	2	102	126.41	80.30	66
HOW	1	102	135.96	89.85	59

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