

Upriver Bright Density Dependence: Analyses of Existing Samples

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Chinook salmon otolith with laser ablation scar (L. Campbell)

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Abstract

Chinook salmon *Oncorhynchus tshawytscha* that spawn in the Hanford Reach of the Columbia River comprise the majority of the Columbia River Upriver Bright (URB) stock, which is a driver stock for several important commercial, tribal, and recreational fisheries. Previous research has suggested reduced productivity of this stock when escapement exceeded 42,000 adults. The very high URB Chinook salmon escapements to the Hanford Reach in 2013, 2014, and 2015 prompted examinations of possible mechanisms for reduced stock productivity of high escapement brood years. Further research indicated that the length of URB Chinook salmon smolts passing McNary Dam (the first of 4 Columbia River dams these fish encounter on their emigration to the ocean) was negatively correlated with prior year adult escapement. These results suggest possible density dependent effects within the Hanford Reach. To further test this hypothesis, we examined size at estuary/ocean entrance of returning adults from years of low (2007 and 2008) and high (2010 and 2013) parental spawning escapement to estimate growth during the juvenile phase of life. We used otolith microchemistry coupled with a fish size/otolith size relationship to predict juvenile size at contact with saline waters. A finding of increased size at estuary/ocean entrance with low parental spawning (or vice versa) would be taken as evidence of increased or decreased growth in the Hanford Reach and supporting the hypothesis that density dependent effects are at work in the Hanford Reach. The best-fitting multivariable model that included adult escapement (i.e., a density dependent effect) also included the duration of the emergence and rearing periods, measured as the number of days between the estimated beginning of emergence and the end of nearshore rearing ($R^2 = 0.988$; $P = 0.062$). This model predicts that at a given duration of the emergence and rearing period, size at ocean entry is reduced by 1 mm for each additional 15,920 adults that escape to spawn in the Hanford Reach. At a given adult escapement, the model predicts that size at ocean entry increases by 0.58 mm for each additional day between the start of emergence and the end of nearshore rearing in the Hanford Reach. Limitations in numbers of brood years (BY) examined ($n=4$) and number ($n=40-53$) and selection of samples (4 year old adults only) within each BY limit our ability to draw robust conclusions regarding density dependent effects regulating URB Chinook salmon production in the Hanford Reach. Examination of additional otoliths from returning adults from a larger number of BY as well as collection and analyses of otoliths from emigrating URB Chinook salmon smolts across a number of BY with varying escapement levels would improve the evaluation of this hypothesis.

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Introduction

Chinook salmon *Oncorhynchus tshawytscha* that spawn in the Hanford Reach of the Columbia River comprise the majority of the Upriver Bright (URB) stock, which is a driver stock for several fisheries that involve the Pacific Salmon Commission. The URB stock is perennially a primary driver for both southeast Alaska (SEAK) and northern British Columbia (NBC) Chinook salmon fisheries. This stock is an important contributor to all three aggregate abundance based management (AABM) fisheries and a primary contributor to Columbia River fisheries, as well as other fisheries along the coast. For example, in 2016 Interior Summer/Fall Chinook salmon (primarily URB stock) was the largest contributor to the SEAK troll (39%) and sport (25%) fisheries (Gilk-Baumer et al. 2018).

After a record low escapement in 2007, the Washington Department of Fish and Wildlife (WDFW) set an interim escapement goal for Hanford Reach URB Chinook salmon of 28,800 (Hoffarth 2016). Using stock-recruit analyses, Harnish et al. (2012, 2014) estimated the escapement level that produced the maximum sustained yield (S_{MSY}) to be 37,639 adults for the Hanford Reach URB Chinook salmon and found reduced productivity (estimated pre-smolts produced per egg deposited) for the stock when escapements were greater than about 42,000 adults. A subsequent analysis that included more recent years supported the earlier findings (Harnish 2017). The current minimum escapement goal set by the WDFW for the Hanford Reach URB Chinook salmon is 31,100 spawning adults, while the maximum escapement goal was set at 42,000 adults (i.e., for harvest management, sport fishing limits may be increased if escapement is expected to exceed 42,000 adults; Hoffarth 2016).

The adult URB escapement to the Hanford Reach was over 157,000 in 2013, over 152,000 in 2014, and over 233,000 in 2015. With escapement levels of this stock vastly exceeding the WDFW escapement goal between 2013 and 2015, there was interest in exploring mechanisms that may influence the productivity of this stock to inform future management actions intended to enhance productivity. This prompted investigations into the mechanisms that may help explain the relationship between high escapements and lower productivity. For example, McMichael and James (2015) performed a qualitative assessment of egg loss during the (then) record high escapement of URB Chinook salmon in the Hanford Reach in the fall of 2014 with the objective of determining whether there was a relationship between spawning density (and redd superimposition) and apparent egg loss. While redd density was very high in several survey areas in 2014, and redd margins overlapped to a great extent, widespread egg loss was not documented by McMichael and James (2015). Then, McMichael et al. (2015) examined the relationship between spawning density and URB Chinook salmon emergence timing and found that emergence was likely shifted later in areas of very high spawning density when compared to lower density spawning areas (putatively due to earlier constructed redds being dug up by later spawning fish) and predicted

emergence times based on accumulated thermal units. Further, McMichael et al. (2015) analyzed existing data for the period between 1995 and 2014 and found a significant negative relationship between Hanford Reach URB Chinook salmon escapement and subsequent smolt size in subyearling Chinook salmon measured emigrating through McNary Dam (the first dam encountered on the seaward migration from the Hanford Reach of the Columbia River); indicating possible density dependent effects on fry growth in freshwater rearing areas.

Increased understanding of the factors that affect the productivity of this important stock may lead to management improvements. To further investigate the possibility that density dependence mechanisms may affect growth of rearing URB Chinook salmon in the Hanford Reach, we received funding through the Northern Fund Committee of the Pacific Salmon Commission to evaluate metrics of growth in existing otolith samples of natural origin recruits (NOR) of the URB stock in the Hanford Reach of the Columbia River. To test the hypothesis that density dependent effects may be occurring during early freshwater residence in the Columbia River, we evaluated the mean size at seawater entry for returning Age 4 adult Chinook salmon from periods of low (2007 and 2008) and high (2010 and 2013) parental spawning abundance.

Methods

Otolith Sample Collection

As part of the Public Utility District of Grant County No. 2's (GPUD) Priest Rapids Hatchery monitoring (Richards and Pearsons 2018), otolith samples were collected from salmon carcasses in five sections of the Hanford Reach covering all spawning areas between November through the second week of December in 2011, 2012, 2014, and 2017. Carcass surveys in the Hanford Reach were generally performed by two to three boat crews of two to three staff operating seven days a week. All carcasses recovered were chopped in half after sampling to prevent the chance of double sampling during subsequent surveys. All recovered carcasses were examined for the presence of a coded wire tag (CWT). A systematic sample of carcasses encountered were sampled for scales (age), otoliths, gender, length, and egg retention. Otoliths were extracted in the field and placed in 95% ethanol filled vials for later analysis. Samples were screened to remove hatchery origin fish by excluding samples collected from fish with adipose fin absent, CWT, or thermally marked otolith. Samples were further refined by selecting only age 4 (generally the most abundant age class in the natural origin recruits (NOR) of the Hanford Reach stock) individuals in order to reduce overall sample size and costs for this analysis.

Otolith Chemical Analysis

Otolith chemistry was analyzed to estimate size at estuary /ocean entry of adult Chinook salmon sampled on the spawning grounds for brood years 2007, 2008, 2010, and 2013. Otoliths were prepared for chemical analysis by thin sectioning in the sagittal plane, where otolith material was removed from both the distal and proximal surfaces until primordia were clearly visible (Volk et al. 2010, Campbell et al. 2015, Claiborne and Campbell 2016). Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP MS) was used to collect otolith chemical data. Specific instrumentation consisted of a Thermo X series II ICPMS coupled with a Photon Machines G2 193-nm excimer laser. Ablated material was transported from the laser to the mass spectrometer using Helium as the carrier gas. The LA-ICPMS operating conditions were as follows: 13 L/min cooling gas, 0.95 L/min auxiliary gas, 0.75 L/min Helium. The laser beam diameter was set at 30 microns, scanned at 5 microns/second at a pulse rate of 8 Hz. Laser transects were analyzed from the otolith core to the otolith edge in the dorsal/posterior quadrant, ~25° off the midline (Figure 1). Normalized ion ratios were converted to elemental concentration using a glass standard from the National Institute of Standards and Technology (NIST 610 and 612) and finally converted to molar ratios for analysis. NIST scans were run every ten samples to quantify instrument drift. The point of estuary/ocean entrance for each otolith was determined as the point of inflection in ratio of Strontium to Calcium (Sr:Ca), defined here as the point of rapid Sr:Ca increase from a baseline freshwater signal (Figure 1). We used a fish size/otolith size relationship from juvenile Chinook salmon captured in the Columbia River estuary ($y = 0.1488x - 1.8822$, $n = 211$, Campbell 2010) and otolith radius at Sr:Ca inflection to back-calculate fish size at estuary/ocean entrance.

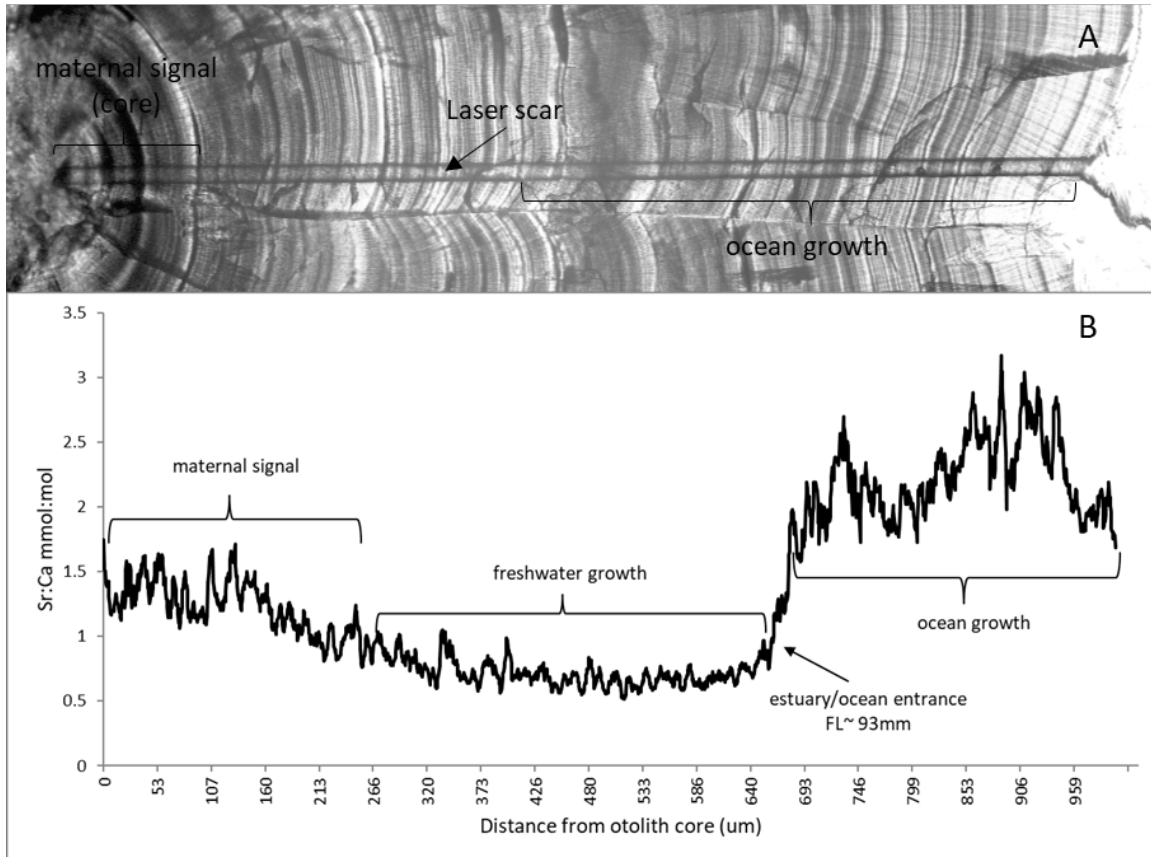


Figure 1. Sectioned adult Chinook salmon otolith with laser scar and approximate location of the maternal signal, freshwater and ocean phases noted (A). Life history transect (Sr:Ca) of a 4 year old adult Chinook salmon from brood year 2013 (B) sampled as a carcass on the Hanford Reach of the Columbia River.

Data Analyses

Histograms and quantile-quantile plots of estimated fork length at ocean entry data were examined for each brood year to determine whether or not the data were normally distributed. Normality was confirmed and pairwise comparisons of mean fork length were conducted using the Tukey-Kramer honestly significantly different (HSD) test ($\alpha = 0.05$).

A list of variables that could conceivably affect the size of Hanford Reach URB Chinook salmon smolts at the time of ocean entry was developed. Variables could be classified into one of four groups: 1) fish abundance (adult escapement), 2) life stage phenology, 3) environmental conditions (e.g., temperature and discharge) during specific life stages, and 4) characteristics of adults that produced each brood (e.g., age distribution, % hatchery origin).

Hanford Reach URB Chinook salmon adult escapement was estimated based on dam ladder counts, sport and tribal harvest, and tributary spawning populations (Richards and Pearsons 2018). Ladder counts at Priest Rapids (adjusted for fallback), Ice Harbor, and Prosser dams; Hanford Reach and Yakima River sport and tribal harvest; returns to Priest Rapids and Ringold Springs hatcheries; and spawning escapement in the hatchery discharge channel and the lower Yakima River (downstream of Prosser Dam) were subtracted from the ladder count at McNary Dam to estimate adult and jack URB Chinook salmon escapement to the Hanford Reach. The number of females of each age was estimated for each brood year by multiplying the adult escapement estimates by the proportion of each age, which was estimated from scales collected during carcass surveys. The number of females of each age was estimated for each brood year by multiplying the age-specific escapement estimates by the proportion of females from each age group during sport fishery creel surveys. The proportion of hatchery origin spawners (PHOS) was estimated from recoveries of CWT hatchery fish during spawning ground surveys (Richards and Pearsons 2018).

The timing of life stages was determined for each year using spawn timing and accumulated thermal units (ATUs). Water temperatures of the Priest Rapids Dam tailrace were simulated using MASS1 (Modular Aquatic Simulation System 1D), a one-dimensional, unsteady hydrodynamic model for river systems (Perkins and Richmond 2001). MASS1 utilizes cross-sectional averaged values of hydraulics and temperature to provide a single temperature value at a designated cross section. Inflow boundary conditions for MASS1 included daily discharge from USGS gauge 12472800, on the Columbia River below Priest Rapids Dam; daily scroll case temperature for Priest Rapids and Rock Island dams; and hourly meteorological data collected for the Hanford Reach (i.e., ambient air temperature, dew point temperature, wind speed, atmospheric pressure, and solar radiation). Temperatures were simulated hourly for the Priest Rapids Dam tailrace, from which daily averages were calculated.

The start and end of the spawning period was determined for each brood year from redd surveys conducted on Vernita Bar by GPUD, WDFW, and a HRF CPPA signatory fishery agency or tribe (Graf et al. 2018). The first day of egg incubation was estimated to be equivalent to the first day of spawning. The beginning of the hatching period was estimated as 500 ATUs from the first day of spawning. The beginning and end of the emergence period was estimated as 1,000 ATUs from the first and last day of spawning, respectively (Hoffarth et al. 2003, McMichael et al. 2005, Boyd et al. 2010, Graf et al. 2018). The last day of nearshore rearing was estimated to occur 1,400 ATUs from the last day of spawning (Hoffarth et al. 2003). Once the timing and duration of life stages were estimated for each brood year, environmental variables were calculated for each life stage.

The size of Hanford Reach URB Chinook salmon smolts that were included in our sample could be affected by variables outside of the Hanford Reach. Therefore, we also included discharge and temperature of the Columbia River during their downstream

migration and an indicator of conditions in the ocean during their first year of ocean residence. River conditions encountered by smolts during their seaward migration were estimated from temperatures and discharges measured at John Day Dam (http://www.cbr.washington.edu/dart/query/river_graph_text). Ocean conditions could affect the probability of small fish returning to the spawning grounds and was therefore included as a predictor variable. The sea surface temperature index for the northeast Pacific arc of Johnstone and Mantua (2014) during the first spring, summer, autumn, winter, and first year was used as an indicator of ocean conditions encountered by each brood year.

Each predictor variable was regressed against the estimated mean size of Hanford Reach fall Chinook salmon smolts at the time of ocean entry from each brood year using simple linear regression to evaluate the general strength and direction of each relationship. Next, adult escapement was included in a forward stepwise linear regression procedure to identify the best-fitting multivariable model that included an effect indicative of density dependence. Variables were added to the model that included adult escapement until the model with the lowest Bayesian Information Criterion (BIC) was established.

Results

Estimated Size at Ocean Entry

We estimated juvenile Chinook salmon size at estuary/ocean entrance for 4 brood years representing 2 years of low parental spawning escapement (2007 and 2008) and 2 years of high parental spawning escapement (2010 and 2013). Greater than 98% of all samples evaluated were estimated to be greater than 60 mm at ocean/estuary entrance (Figure 2). One adult Chinook salmon was estimated to have entered the estuary/ocean environment (high Sr) at ~ 45 mm in 2010 and no yearling life histories (overwintering in freshwater) were found in the 176 samples analyzed. We found size at estuary/ocean entry ranged from 45 to 109 mm with a mean size of 85 mm over the 4 brood years examined (Figure 3). We estimated an average juvenile outmigration size at ocean/estuary entrance of 87 mm and 82 mm during years of low (2007 and 2008) and high parental spawning abundance (2010 and 2013), respectively (Figure 3). However, pairwise comparisons of mean fork lengths at ocean entry among brood years revealed that smolts from brood year 2008 were significantly larger than those from brood years 2007, 2010, and 2013 ($P < 0.001$), which were all similar to one another ($P \geq 0.293$). These results suggest the two low spawning abundance years should not be pooled and may in fact be driven by other factors, such as the low overall survival of brood year 2008 (Table 1).

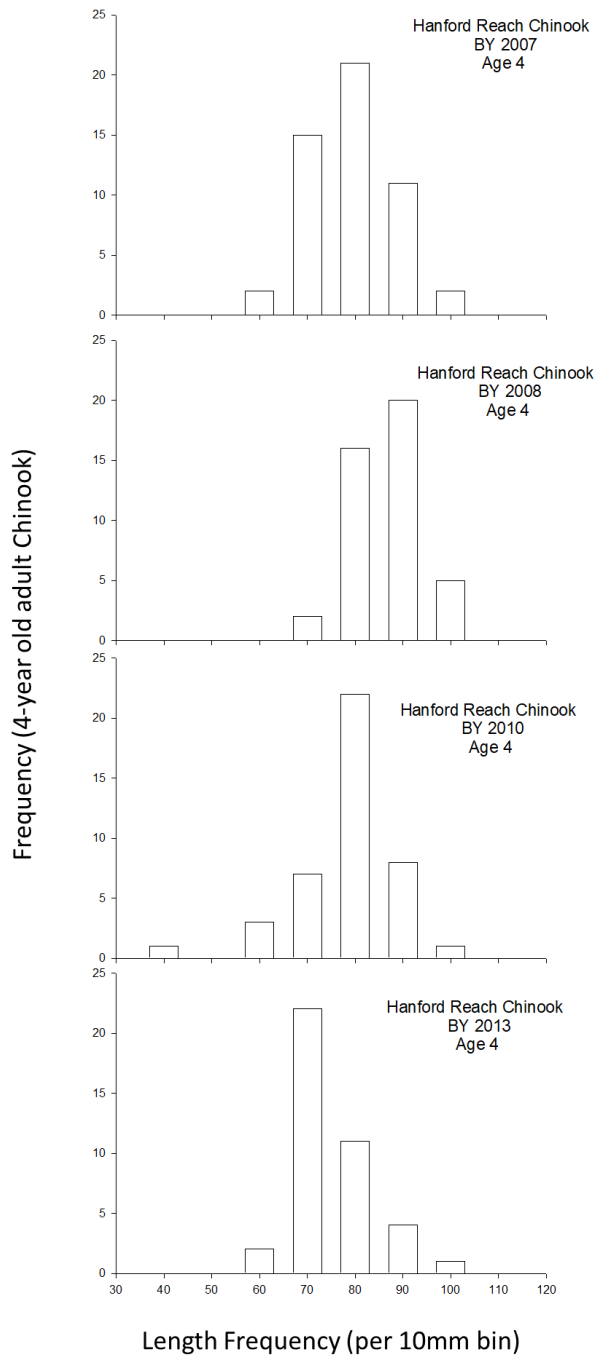


Figure 2. Length frequency histogram(s) of estimated size at ocean/estuary entrance during the juvenile outmigration of returning adult (natural origin) Chinook salmon to the Hanford Reach (survivors). Brood years standardized by 4-year-old returns from two low parental escapement years (2007 and 2008) and two high parental escapements years (2010 and 2013) to the Hanford Reach of the Columbia River.

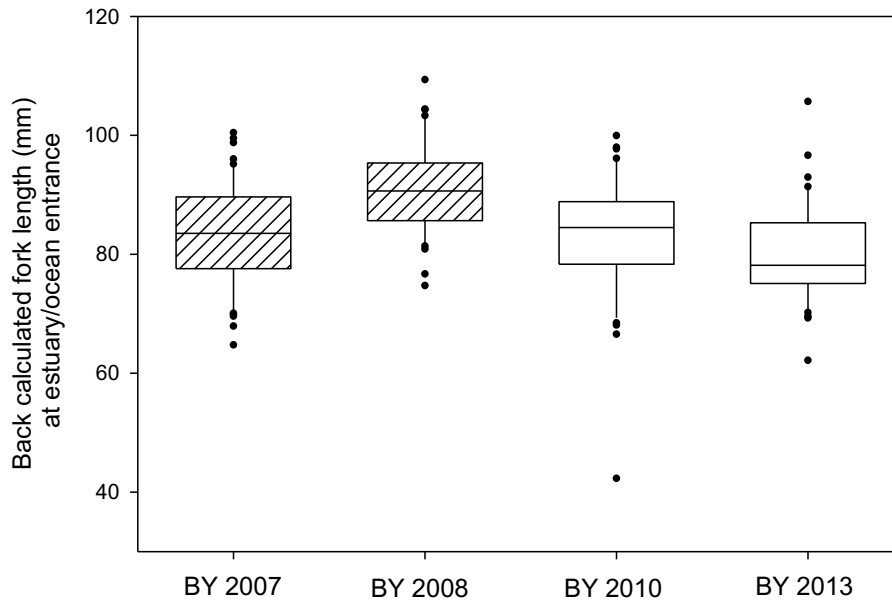


Figure 3. Box and Whisker Plot for back calculated fork length of juvenile Chinook salmon at estuary/ocean entrance for low parental spawning abundance (dashed boxes) vs high parental spawning abundance (clear boxes).

Table 1. Numbers of otoliths from Hanford Reach fall Chinook salmon adults sampled (n) to estimate fork length (FL) at ocean entry for brood years 2007, 2008, 2010, 2013. 1Stdev = standard deviation. Smolt to Adult Survival estimates (%) for unmarked juvenile Chinook salmon tagged in the Hanford Reach and estimated survival of the Priest Rapids Hatchery group for brood years 2007, 2008, 2010 and 2013 from the Regional Mark Information System (<http://www.rmhc.org>).

Hanford Reach Natural Origin Chinook (Age 4)						
Parental spawning escapement	Brood Year	presmolt abundance	n	estuary/ocean entry-FL (1Stdev)	Smolt to Adult Survival (SAR)	
					Hanford Reach (W*)	Priest Rapids Hatchery
13,977	2007	19,792,089	51	83 (8)	0.83	1.10
23,361	2008	26,421,704	43	91 (8)	0.27	0.30
80,408	2010	57,669,968	42	83 (11)	1.77	2.91
157,484	2013	65,817,816	40	80 (8)	0.25	0.73

Of all the variables regressed against fork length at ocean entry, the day of year (DOY) that marked the end of nearshore rearing within the Hanford Reach was the only variable that was significantly correlated (Table 2). The end of nearshore rearing DOY was highly correlated with the mean length at ocean entry data ($R^2 = 0.997$; $P = 0.001$). However, the range of observed predictor variable values was extremely narrow, ranging from DOY 169 to 172, therefore it is possible this correlation is spurious.

Adult escapement of Hanford Reach URB Chinook salmon was negatively correlated with size at ocean entry; however, as mentioned, the correlation was not significant. Adult escapement regressed against estimated size at ocean entry provided an R^2 of 0.483 ($P = 0.305$; Figure 4). The best-fitting multivariable model that included adult escapement (i.e., a density dependent effect) also included the duration of the emergence and rearing periods, measured as the number of days between the estimated beginning of emergence and the end of nearshore rearing ($R^2 = 0.988$; $P = 0.062$). This model predicts that at a given duration of the emergence and rearing period, size at ocean entry is reduced by 1 mm for each additional 15,920 adults that escape to spawn in the Hanford Reach. At a given adult escapement, the model predicts that size at ocean entry increases by 0.58 mm for each additional day between the start of emergence and the end of nearshore rearing. In other words, an additional 2 days of rearing in the Hanford Reach would increase the estimated length at ocean entry of juvenile URB Chinook salmon by 1.16 mm (2 days x 0.58 mm/day, assuming the same adult escapement levels).

Brood year 2007 had the lowest adult escapement ($N = 13,977$) of the four brood years examined; however, this brood year also had the shortest nearshore rearing period (78 d). These two factors may have contributed to produce the relatively low estimated 83.4 mm mean fork length at ocean entry. Brood year 2008 was also a year of low escapement ($N = 23,361$) but experienced an extended nearshore rearing period (92 d), which may have contributed to producing the largest mean fork length at ocean entry of the four brood years (91.1 mm). Brood year 2013 had the highest escapement of the four years examined ($N = 157,484$) but a relatively long rearing period (88 d), producing a mean fork length at ocean entry of 80.2 mm.

Table 2. Summary of linear regression model results constructed to identify variables that could potentially affect the size (fork length) of Hanford Reach fall Chinook salmon smolts at the time of ocean entry. DOY = day of year; BY = brood year; PRD = Priest Rapids Dam; ATU = accumulated thermal units; PHOS = proportion hatchery-origin spawners; NE = northeast; SST = sea surface temperature; SD = standard deviation; JDA = John Day Dam.

Variable(s)	Intercept β_0	Slope β_1	Slope β_2	R^2	Prob > F
End of nearshore rearing (DOY)	-540.53	3.67	.	0.997	0.001
Adult escapement + days between beginning of emergence and end of nearshore rearing	39.52	-6.28×10 ⁻⁵	0.58	0.988	0.062
Proportion of BY females age-5+	77.35	23.97	.	0.605	0.222
Adult escapement	87.87	-4.87×10 ⁻⁵	.	0.483	0.305
End of emergence (DOY)	-42.35	0.92	.	0.395	0.372
Days between beginning of hatch and end of nearshore rearing	-42.48	0.64	.	0.372	0.390
PRD mean discharge from beginning of hatch through 31 July	98.32	-0.10	.	0.340	0.417
ATUs between beginning of hatch to beginning of emergence	846.67	-1.50	.	0.329	0.426
BY PHOS	87.66	-24.60	.	0.317	0.437
Proportion of BY females age-3	87.89	-20.23	.	0.316	0.438
Proportion of BY females age-4	99.67	-28.42	.	0.274	0.476
Days between beginning of emergence and end of nearshore rearing	51.26	0.39	.	0.252	0.498
NE Pacific arc SST SD 1 st autumn	84.53	-2.44	.	0.224	0.527
Days between beginning and end of emergence	70.91	0.26	.	0.206	0.547
NE Pacific arc SST SD 1 st spring	84.44	-2.14	.	0.183	0.572
JDA mean temperature from 5 June through 10 August	55.86	1.59	.	0.168	0.591
JDA mean discharge from 5 June through 10 August	91.16	-0.03	.	0.165	0.594

NE Pacific arc SST SD 1 st year (June–May)	84.57	-2.05	.	0.154	0.608
NE Pacific arc SST SD 1 st winter	84.63	-1.88	.	0.134	0.634
Beginning of emergence (DOY)	107.31	-0.27	.	0.100	0.684
ATUs between end of emergence and end of nearshore rearing	-78.54	0.40	.	0.098	0.686
NE Pacific arc SST SD 1 st summer	84.64	-1.60	.	0.082	0.713
ATUs between beginning of emergence and end of nearshore rearing	65.14	0.02	.	0.073	0.729
Beginning of hatch (DOY)	205.88	-0.36	.	0.070	0.736
ATUs between beginning of hatch and end of nearshore rearing	54.80	0.02	.	0.064	0.746
End of spawning (DOY)	-46.01	0.40	.	0.062	0.751
ATUs between beginning and end of emergence	76.52	0.02	.	0.056	0.762
Hanford Reach SAR	85.66	-1.49	.	0.053	0.770
PRD mean temperature from beginning of hatch through 31 July	124.19	-4.83	.	0.052	0.772
ATUs between beginning of hatch and end of emergence	67.41	0.02	.	0.049	0.779
Beginning of spawning (DOY)	243.97	-0.54	.	0.048	0.781

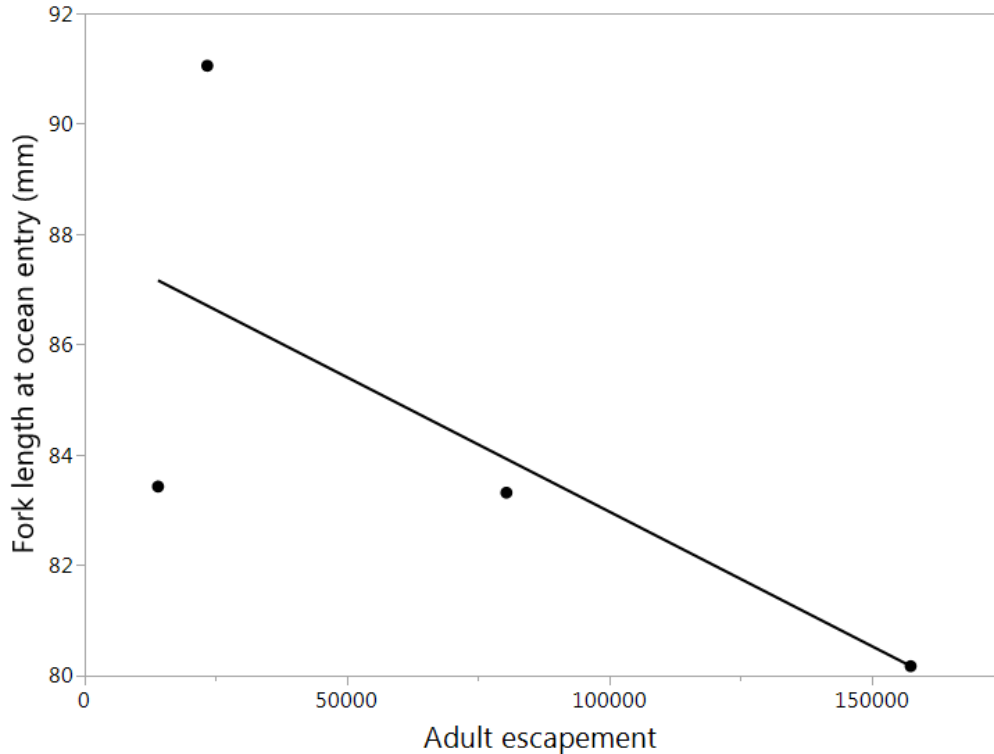


Figure 4. Linear relationship between adult escapement and estimated fork length at the time of ocean entry for Hanford Reach fall Chinook salmon.

Discussion

This inspiration for this investigation was a consequence of the findings of previous analyses and observations. First, recent work on the productivity of the Hanford Reach fall Chinook salmon (URB stock) suggested that productivity was lower when adult escapement exceeded about 42,000 adults (Harnish et al. 2017). Second, an analysis of outmigration data on juvenile fish collected at McNary Dam (the first dam downstream of the Hanford Reach) showed a strong negative relationship between prior-year adult escapement and size of juvenile URB Chinook salmon migrating seaward from areas upstream of McNary Dam (McMichael et al. 2015). Finally, very high escapements of adult URB Chinook salmon in 2013, 2014, and 2015 spurred interest in increasing our understanding of the mechanisms that may be responsible for the reduced productivity of this population at these higher escapement levels.

Factors we thought were important in the development of the hypothesis for this work were based on the conceptual model that density dependent effects in the freshwater rearing area would reduce growth or prompt earlier emigration from the freshwater rearing areas (e.g., Connor et al. 2013). The net effect would be that smaller

juvenile fish would enter the ocean following escapements over some threshold value. Further, we assumed that smaller size at ocean entry would reduce survival to adult return. While our simple concept seemed plausible, the work we have completed to date does not provide compelling evidence to support it.

Our work provides an initial attempt at answering the question of whether there is a strong density dependent force acting in early juvenile freshwater rearing or migration that affects the growth and size of emigrating fall Chinook salmon from the Hanford Reach of the Columbia River to the ocean. Our results indicate that lower adult escapement levels and longer rearing periods in freshwater were associated with larger size at ocean entry. However, our results should be viewed with caution for the following reasons:

1. There are a number of factors which may have influenced our results including low sample size, our methods, and/or density dependence in freshwater rearing may have been weak or non-existent in the years that we examined. Low sample size (4 years) limits the conclusions we can draw from this analysis, as the effect of each year is substantial when the sample size is so low. We also relied on using the otoliths from surviving age 4 adults which may have obscured relationships that occurred in freshwater. It is difficult for us to know whether the size of juvenile fish at ocean entry (of adults that returned to spawn) was influenced primarily by forces acting in freshwater, saltwater, or a combination of both.
2. The large variation in juvenile fish size that survived to age 4 (45-109 mm) and the approximate normal distribution of juvenile fish size suggest that juvenile fish size may not have had a strong effect on survival to age 4 for the years we examined. In addition, the size of juvenile fish and SARs to age 4 were not well correlated, suggesting that factors besides juvenile fish size were important in determining survival to age 4.
3. Juvenile salmonids that begin their ocean residence at a larger size are thought to be more likely to survive to return as adults due the advantages of being larger with respect to vulnerability to predators and the relative fish size to prey size (Ivlev 1961; Mittelbach and Persson 1998). However, Claiborne et al. (2014) found no evidence of selective mortality against smaller juveniles during early marine residence in hatchery or natural juvenile Columbia River summer-fall Chinook salmon. This is consistent with our findings in terms of the relatively high estimated smolt-to-adult survival of the 2010 brood year which had below-average estimated mean length at ocean entry (83 mm) and the largest mean size at ocean entry (BY2009; 91 mm) experienced the lowest smolt-to-adult survival rate.

4. Fish from BY 2007 (83 mean FL) experienced the coolest sea surface temperatures (SSTs) in the NE Pacific arc (Johnstone and Mantua 2014), followed closely by 2010. BY 2008 experienced neutral SSTs and BY 2013 the warmest. 1st year (June through May) SST anomalies were: BY 2007 = -0.57, BY 2008 = -0.05, BY 2010 = -0.53, BY 2013 = 1.32. Therefore, it is possible that the relatively small fish from BY07 had a higher probability of surviving to adulthood due to good ocean conditions. However, the small difference in mean size between survivors from good (BY2007) and poor (BY2013) ocean conditions indicates this may not have had a strong influence.

5. We do not know the size of the juvenile fall Chinook salmon that emigrated from the primary spawning and rearing area in the year of their outmigration. We are limited to the estimated length of fish when they entered seawater on their seaward migration for fish that survived to age 4 and successfully returned to spawn in the Hanford Reach. Interestingly, McMichael et al. (2015) reported a strong negative relationship between adult URB escapement and lengths of juvenile subyearling Chinook salmon emigrating past McNary Dam the following year. Also, the estimated mean lengths McMichael et al. (2015) reported for fish beginning their seaward migration were larger (e.g., 92-110 mm) than those estimated at the time ocean entry from the current study (80-91 mm). It is possible that inclusion of unmarked Chinook salmon in the McNary Dam samples considered by McMichael et al. (2015) were unmarked hatchery origin Chinook salmon, which would bias the mean sizes upward. In addition, the estimates of size derived from otoliths in this study were not well correlated with size of fish sampled during the same year at McNary Dam.

Previous research on factors related to the productivity of the Hanford Reach fall Chinook salmon found limited egg loss during a year of very high spawning escapement, indicating that spawning habitat doesn't appear to be limiting (McMichael and James (2015). Also, there is limited evidence suggesting higher egg retention in females (a form of pre-spawn mortality) associated with spawner abundance (Richards and Pearsons 2018). McMichael et al. (2015) found a possible shift to later emergence in higher density spawning areas, possibly due to effects of redd superimposition resulting in later built redds producing more fry than redds built earlier in the spawning season. As mentioned previously, McMichael et al. (2015) also performed historical data analysis showing smaller fish emigrating through McNary after high escapement years, however it is possible that inclusion of unmarked hatchery origin fish may have influenced those analyses.

Harnish et al. (2014) reported that the fall Chinook salmon in the Hanford Reach of the Columbia River are among the most productive in the species' range, and the productivity of this stock was improved by flow constraints on the operation of dams upstream of the Hanford Reach. Further, Langshaw et al. (2017) reported relatively high

survival rates at many life-stages and high spawning flows (i.e., increased spawning habitat area) relative to historic conditions.

While previous research and the current study have increased our understanding of this issue, the relative influence of specific mechanisms responsible for reduced productivity from high escapements remain uncertain. It is also likely that the mechanisms controlling productivity are temporally and spatially complex and variable, and even more so with the unmarked (natural origin) Chinook salmon we choose to examine in this study. To further understand forces regulating Chinook salmon production in the Hanford Reach as it relates to growth and survival, we would suggest three things: 1.) Include juvenile sampling in the Hanford Reach or at McNary Dam, estuary and offshore (if possible) to describe residency, survival and life history of out-migrants. 2.) Increase the sample size to include all major adult age classes per brood and 3.) Increase the number of brood years (currently $n=4$) to appropriately describe trends regulating production in the Hanford Reach.

The increased sample sizes should improve the utility of the multivariate methods for understanding the relative influence of the various factors that may affect fish size at ocean entry. To better understand the relative size at emigration from the Hanford Reach to estimated size at ocean entry would require that samples of juvenile fish be collected and measured at McNary Dam or Bonneville Dam. These fish would need to be sacrificed and their otoliths could be sampled to distinguish unmarked hatchery fish from natural origin fish. Further, it would be possible to distinguish between natural origin Chinook salmon from the Columbia River above McNary Dam and their counterparts from the Snake River using Strontium isotope ratios. By collecting data from emigrating fish as well as from the survivors that return as adults, we may be able to better understand the relative influence of any density dependent forces that may exist in freshwater.

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