



When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon

Londi M. Tomaro^{1*}, David J. Teel², William T. Peterson³, Jessica A. Miller¹

¹Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365, USA

²NOAA Fisheries, Northwest Fisheries Science Center, Manchester, Washington 98353, USA

³NOAA Fisheries, Northwest Fisheries Science Center, Newport, Oregon 97365, USA

ABSTRACT: Early ocean residence is considered a critical period for juvenile salmon although specific survival mechanisms are often unidentified and may vary by species or life stage. Columbia River spring-run Chinook salmon *Oncorhynchus tshawytscha* abundance has declined dramatically since the early 1900s. To elucidate mechanisms of early marine survival, we tested the 'bigger-is-better' and 'stage-duration' aspects of the 'growth-mortality' hypothesis, which posits that size and growth rate are important for future abundance. We tested the 'match-mismatch' hypothesis to determine whether early marine growth was related to indices related to regional productivity, including spring transition timing and copepod community composition. We generated estimates of individual size at ocean entry and capture, marine growth rate, early marine migration rate, and emigration timing using data from ocean surveys, genetic stock-assignment, and otolith analyses of juveniles collected across 8 yr between 1998 and 2008. Size at capture and marine growth rate after ~30 d marine residence were positively related to future adult returns, whereas size at marine entry was not. Growth rate was not significantly related to indices of secondary production, but size at capture was significantly greater when lipid-rich copepods dominated. Although future adult abundance was not related to emigration timing, juveniles migrated more slowly when copepod biomass was high, perhaps responding to foraging conditions. Overall, processes during early ocean residence appear to be more important for cohort size establishment than those at marine entry. Approaches that combine genetic and otolith analyses have great potential to provide information on stock-specific variation in survival mechanisms.

KEY WORDS: Survival mechanisms · Juvenile salmon · Columbia River · Ocean residence · Otolith back-calculation

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INTRODUCTION

Pacific salmon *Oncorhynchus* spp. are broadly distributed anadromous fishes. Early ocean residence is assumed to be a critical period for salmon based on several lines of evidence. For example, future adult abundance has been positively correlated with juvenile abundance after initial ocean residence (Pearcy 1992) and survival rates of several stocks were correlated regionally, i.e. at scales within ~500 km (Peter-

man et al. 1998, Hare et al. 1999, Pyper et al. 2005), which imply the establishment of cohort size soon after ocean entry. Survival has also been related to physical factors, such as river velocity, upwelling intensity, and water temperature (Scheuerell & Williams 2005, Petrosky & Schaller 2010), and biological factors, such as body size, primary production, and food chain structure (Henderson & Cass 1991, Beamish & Mahnken 2001, Peterson & Schwing 2003, Beamish et al. 2004, Peterson 2009), in both the fresh-

*Email: londi.tomaro@lifetime.oregonstate.edu

water and marine environment (for review, see Pearcy & McKinnell 2007). However, specific mechanisms of mortality are rarely identified and likely vary with species or life history. Overall, the relative importance of growth- versus predation-mediated processes (i.e. bottom-up versus top-down) during the early life history is not well understood.

Chinook salmon *Oncorhynchus tshawytscha* are distributed along the Pacific Rim and, in North America, spawn from central California to western Alaska (Beacham et al. 2006). Juveniles spend weeks, months, or over a year in freshwater before emigrating to the ocean (Taylor 1990), where most reside for 2 or more years (Quinn & Myers 2004). Marine distributions and migration patterns appear to vary by geographic origin and adult run time, i.e. spring, summer, or fall (Weitkamp 2010). The Columbia River is a major producer of Chinook salmon and supports numerous populations with diverse life-history and ecological characteristics (Waples et al. 2008). However, most populations have decreased substantially since the development of the hydropower system beginning in 1933. In particular, runs of spring Chinook salmon have declined throughout most of the basin, and certain populations, such as the upper Columbia River spring run, are listed as endangered (Good et al. 2005). A better understanding of the relative importance of freshwater versus marine mortality during the early life history of Columbia River spring Chinook salmon would aid conservation and management efforts.

Columbia River spring Chinook salmon generally emigrate after a year in freshwater (Rich 1920, Fryer 2009), migrate northward quickly (Trudel et al. 2009), and return to spawn as adults after 2 or more years at sea (Myers et al. 1998). Although the abundance of adults returning to the Columbia River is positively correlated with the abundance of precocial spawners the previous year (counts) and yearlings in coastal waters 2 yr earlier (fish km⁻¹), these relationships account for <35% of the variation in adult abundance ($r^2 = 0.26$, $p = 0.11$ and $r^2 = 0.34$, $p = 0.06$, respectively) over the last decade (National Oceanic and Atmospheric Administration [NOAA] unpubl. data, Columbia River Data Access in Real Time: www.cbr.washington.edu/dart/dart.html). Additionally, these relationships do not provide insight into mechanisms of survival. However, there is evidence that juvenile body size (Zabel & Williams 2002, Duffy & Beauchamp 2011) and timing of marine entry (Scheuerell et al. 2009) influence subsequent survival. The potential influences of body size and timing on subsequent survival are well-described in

the 'growth-mortality' and 'match-mismatch' hypotheses.

The growth-mortality hypothesis combines aspects of the 'bigger-is-better' and the 'stage-duration' hypotheses. The bigger-is-better hypothesis states that larger fish have higher survival because they more successfully avoid predators (Butler & Pickett 1988, Miller et al. 1988) and capture prey (Bailey & Batty 1983, Blaxter 1986). The stage-duration hypothesis posits that faster growing fish remain susceptible to predation for a shorter period (Houde 1987, 2008, Takasuka et al. 2004). Growth rate determines the span of a life stage (Chambers & Leggett 1987) and is often used as a proxy for stage duration (Takasuka et al. 2004). Therefore, larger size or faster growth rate may confer a survival advantage to juvenile salmon. However, it is not clear *when* size is important. Zabel & Achord (2004) found evidence for length-related mortality within populations of Chinook salmon but only examined juveniles, 50 to 100 mm in length, during their freshwater residence. Size variation within a population can result from growth variation or selective mortality at various points in the life history. For juvenile salmonids, it is not clear if size at marine entry, which may influence susceptibility to a new suite of predators (Pearcy 1992, Emmett et al. 2006, Emmett & Krutzikowsky 2008), is as important as size later in the life history such as after the first ocean summer, which may influence survival during the subsequent winter (Beamish & Mahnken 2001, Moss et al. 2005, Cross et al. 2009).

The match-mismatch hypothesis, originally established for first-feeding larvae (Cushing 1974) and later expanded to other early life stages (Anderson 1988), states that young fish have higher survival if they experience spatiotemporal overlap with their food source (Cushing 1990). It is expected that year classes entering the ocean during periods with better foraging conditions will have higher survival. For example, pink salmon *Oncorhynchus gorbuscha* released into Prince William Sound during peak zooplankton abundance survived better than juveniles released during less favorable foraging conditions (Cross et al. 2008). Although juvenile Chinook salmon primarily consume juvenile fish, euphausiids, and decapod larvae (Daly et al. 2009), researchers hypothesized that their marine growth and survival would be enhanced during years in which the nutritional quality of lower trophic levels was enhanced due to the presence of a lipid-rich copepod community (Hooff & Peterson 2006, Litzow et al. 2006, Keister et al. 2011). The composition and abundance of the copepod community in the California Current

is influenced by upwelling frequency and intensity, and basin scale climate factors (Hooff & Peterson 2006). Furthermore, the timing of seasonal productivity along the west coast of the US is regulated by the spring transition, which is the switch from predominantly downwelling conditions in winter to predominantly upwelling conditions in summer (for review, see Checkley & Barth 2009). There is a lag of ~7 to 10 d between the onset of upwelling and increases in primary production (Henson & Thomas 2007), and copepod biomass increases during the upwelling season (Hooff & Peterson 2006). Juvenile salmon may encounter more productive waters if they enter the ocean later in the upwelling season. Therefore, if temporal and spatial overlap with certain trophic conditions during early marine residence is important, early marine growth should be related to indices of the timing, abundance, and composition of regional secondary production.

In salmonids, evaluations of the bigger-is-better hypothesis often rely on data from individuals released from hatcheries (e.g. Bilton et al. 1982, Unwin 1997) or sampled during passage over a particular dam (e.g. Zabel & Achord 2004). These approaches are biased towards hatchery fish or preclude a clear separation of size at marine entry from size at other points in the life history. Few studies on salmonids have effectively evaluated *when* bigger is actually better. Furthermore, more precise estimates of the date of marine entry would help evaluate the importance of emigration timing. Therefore, we combined data from ocean surveys, genetic stock identification, and otolith structural and chemical analysis to estimate individual size, timing of marine entry, and early marine growth and migration rates for Columbia River spring Chinook across 8 yr. Our samples included a mixture of all ocean-caught individuals, both hatchery and naturally produced, as this is representative of the population as a whole. We examined variation in juvenile size at 2 periods in the life history—marine entry and after ~30 d of marine residence—and growth during this early marine period to evaluate the growth-mortality hypothesis. We also compared juvenile size at capture, emigration timing, and growth rate and

migration rate after marine entry with indicators of the timing and relative magnitude of marine productivity to evaluate the match-mismatch hypothesis.

MATERIALS AND METHODS

Fish collection and processing

Juvenile salmon were collected during NOAA cruises off the coasts of Washington and Oregon during the last 2 wk of May and June from 1998 to 2008. The years 2001 and 2005 were removed from the analysis because there were inadequate numbers of fish and, therefore, otoliths collected (<20). Fish were collected using a 30 m wide by 20 m deep surface rope trawl (NET Systems Nordic 264) towed for 30 min at ~6 km h⁻¹ and frozen within 30 min of capture (Fig. 1; study area described in Daly et al. 2009). Salmon were later thawed, and each juvenile

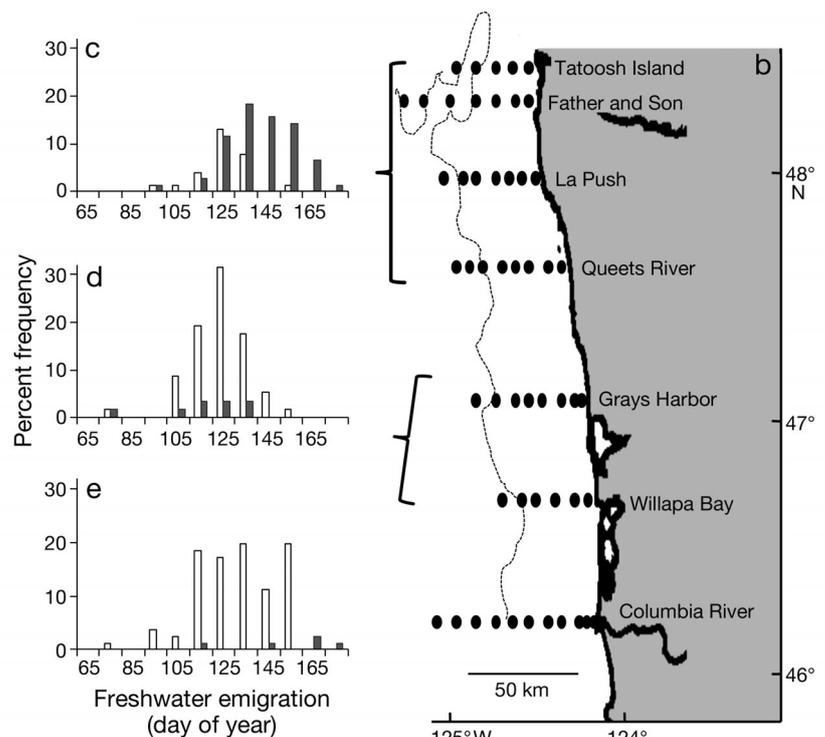


Fig. 1. (a) Sampling area relative to the west coast of North America. (b) Approximate position of transects and sample locations relative to the coast and shelf break (dotted line). Frequency distributions of freshwater emigration dates are included for fish collected at (c) Tatoosh Island, Father and Son, La Push, and Queets River ($n = 77$); (d) Grays Harbor and Willapa Bay ($n = 57$); and (e) Columbia River ($n = 81$) transects for all years combined. May (white bars) and June (gray bars) collections. Sample sizes include fish for which residence times could be estimated



was measured, weighed and checked for a coded-wire tag (CWT) and a passive integrated transponder (PIT) tag. Samples of fin tissues for genetic analysis and otoliths were removed.

All individuals included in this study were genotyped at 13 standardized microsatellite DNA loci following the procedures outlined in Teel et al. (2009) and assigned to the mid-upper Columbia River spring Chinook salmon stock group using baseline data from the genetic database described by Seeb et al. (2007). This stock group accounted for 23% of the spring-run Chinook salmon collected on the NOAA cruises between 1999 and 2008. Stock assignments were made with the genetic stock identification program ONCOR (Kalinowski et al. 2007) and the likelihood model of Rannala & Mountain (1997). The mid-upper Columbia River genetic stock group includes the Mid Columbia River spring-run and Upper Columbia River spring-run evolutionarily significant units (ESUs), which spawn in Columbia River tributaries east of the Cascade Mountains, excluding the Snake River (Myers et al. 1998). Seeb et al. (2007) found in evaluations of genetic baseline assignment accuracies that ~5.9% of individuals from other Columbia River spring-run stock groups (Snake River, Willamette River, and lower Columbia River) were incorrectly identified as belonging to the mid-upper Columbia River spring stock (D. J. Teel, NOAA, Manchester, WA, unpubl. data). In this study, 79%

of the individuals used had assignment probabilities >80%.

We used 6 stock-specific juvenile metrics to test the growth-mortality and match-mismatch hypotheses, including fork length (FL; mm) at freshwater emigration and ocean capture; growth rate during initial marine residence; date of freshwater emigration relative to physical and biological indicators of the spring transition to predominantly upwelling conditions; and migration rate between the points of freshwater emigration and ocean capture. Otolith structural and chemical analyses were used to generate all of these metrics except for size at capture, which was determined from measurements of body size of all mid-upper Columbia River spring Chinook juveniles collected in the study. Otoliths were available for a subset of those juveniles.

Otolith preparation, analyses, and interpretation

Otolith Sr:Ca ratio is often used to reconstruct diadromous migrations when freshwater Sr:Ca ratio is distinct from marine waters (Secor 1992, Miller et al. 2010a). The Sr:Ca ratio in the Columbia River is lower than and, thus, distinguishable from oceanic waters (Miller et al. 2011). Therefore, we used otolith chemical and structural analyses to determine when juveniles left freshwater and entered brackish or oceanic habitats, i.e. 'freshwater emigration' (Miller et al. 2010a, 2011). Because variation in water Sr:Ca ratio is limited above salinities of 8 to 10 (Kraus & Secor 2004a, Zimmerman 2005, Miller et al. 2010a), we used otolith Sr:Ca ratio to identify transitions from fresh to brackish or oceanic waters but not to separate estuarine and ocean residence. Hereafter, we use 'marine' when referring to brackish and oceanic residence.

Sagittal otoliths were measured along the dorsal-ventral axis at the widest point using image analysis, and the left otolith was ground using wet-or-dry paper and lapping film to expose the dorsal-ventral growth axis (Fig. 2a). Otoliths were otherwise prepared with standard procedures for elemental analysis as described in Miller (2009). Otolith Sr and Ca were measured using laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS). Data were collected along a transect that

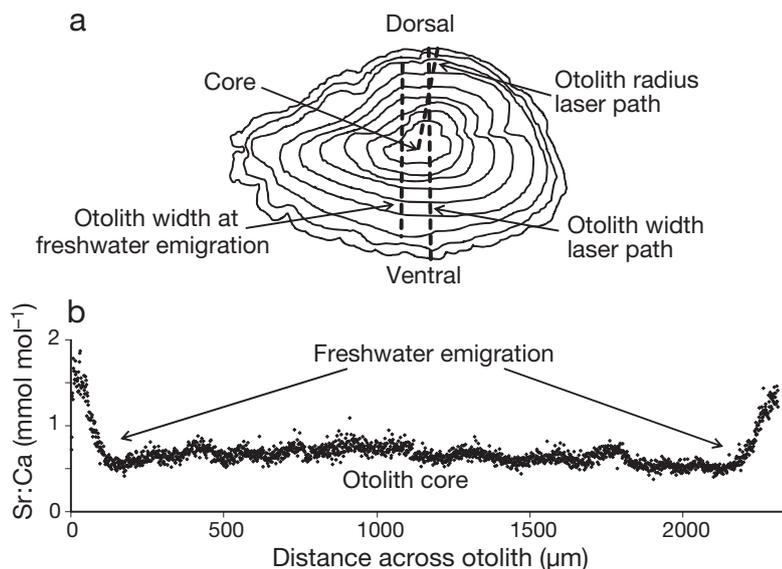


Fig. 2. *Oncorhynchus tshawytscha*. Schematic of a sagittal otolith and representative Sr:Ca ratio profile. (a) Core, otolith width at freshwater emigration, and laser path for otolith radius and width measurements are identified. (b) Sr:Ca ratio across otolith

included either the (1) otolith radius (OR) from core to dorsal edge (52% of otoliths) or (2) otolith width (OW) (48% of otoliths) (Fig. 2a). It was easier to interpret chemical data from scans of the entire growth axis; therefore, when analyzing otoliths from the second group of fish, data were collected along the otolith width rather than the radius. The laser was set at a pulse rate of 8 Hz and translated across the sample at $5 \mu\text{m s}^{-1}$ with a spot size of 30 or 50 μm . Normalized ion ratios were converted to elemental ratios using a glass standard from the National Institute of Standards and Technology (NIST 612) (Miller 2007) and converted to molar ratios. Instrument precision (mean percent relative standard deviation) based on NIST 612 was 3.2% for Ca and 3.7% for Sr across all samples and days ($n = 53$). We used a carbonate standard developed by the United States Geological Survey (MACS-1) to assess accuracy (Sr:Ca ratio = 2%, $n = 18$).

Structural analysis was combined with Sr:Ca ratio data to determine otolith size at freshwater emigration and estimate the date of freshwater emigration. After ablation, we captured digital images using a Leica DC300 camera coupled with a Leica MZ95 stereoscope (20 \times) or a Leica DM1000 compound microscope (40 \times , 100 \times , 200 \times , and 400 \times) and performed image analysis with ImagePro® Plus (Media Cybernetics). For each individual, the OR or OW at the time of freshwater emigration was determined by the initial and abrupt increase in otolith Sr:Ca ratio, which indicates exit from freshwaters, prior to stabilizing at marine values (Fig. 2b) (Miller et al. 2010a, 2011). In order to use a consistent metric (OW) for back-calculation of body size, we estimated OW for fish with OR scans. Juvenile Chinook salmon deposit otolith increments daily (Neilson & Geen 1982, 1985). Therefore, the paired opaque and translucent increments deposited after the initial and abrupt increase in Sr:Ca ratio were counted to determine duration of marine residence. Increment counts were completed twice at least 2 d apart and the error between counts was calculated.

Back-calculation of size and growth

We used 8 PIT-tagged juvenile Chinook salmon with known size and migration histories collected in the Columbia River estuary during 2008 to evaluate the assumption that otolith and somatic size are coupled (Campana & Jones 1992).

We compared direct and proportional back-calculation approaches for estimating size at tagging. For

direct back-calculation, we used a relationship based on yearling spring Chinook salmon from the interior Columbia River basin that were collected in coastal waters from 1999 to 2008 ($r^2 = 0.82$, $n = 362$, $p < 0.001$) (Eq. 1):

$$\ln(\text{FL}_T) = 1.126 (\pm 0.028 \text{ SE}) \times \ln(\text{OW}_T) - 3.69 (\pm 0.21 \text{ SE}) \quad (1)$$

where FL_T = fork length (mm) at tagging, and OW_T = otolith width (μm) at tagging. Overall, there was a small decline in otolith size for larger juvenile sizes, which resulted in underestimation of size for fish >165 mm FL by ~8%. Given that the majority of fish emigrate from the Columbia River at sizes <175 mm FL (Rich 1920, Giorgi et al. 1994, Tiffan et al. 2000), we felt that using Eq. (1) was warranted. For proportional back-calculation, we used Eq. (2) (Francis 1990):

$$\ln(\text{FL}_T) = \{ [1.126 \times \ln(\text{OW}_T) - 3.69] / [1.126 \times \ln(\text{OW}_C) - 3.69] \} \times \ln(\text{FL}_C) \quad (2)$$

where OW_C = otolith width at capture, and FL_C = fork length at capture.

We compared 2 approaches for estimating individual growth rate. (1) We examined the correlation between observed mean somatic growth rate and mean increment width from the time of tagging to capture for the 8 individuals. Increment width was measured twice and measurements had $\geq 94\%$ agreement. (2) We estimated mean growth rate by determining the difference between size at capture and back-calculated size at tagging and dividing by the days between tagging and capture as determined using tagging and capture dates. For ocean-caught individuals, growth is presented as percent body length per day (%bl d^{-1}) based on estimated size at freshwater emigration. To evaluate back-calculation methods, we used Pearson's correlation coefficient to compare (1) observed size at tagging with direct and proportional estimates of size at tagging and (2) observed growth rate with mean increment width and estimated growth rate.

Migratory characteristics

To determine individual date of freshwater emigration, the duration of marine residence was subtracted from the date of capture. We also estimated marine migration rate for each individual. Marine migration distance was conservatively estimated as the linear distance between the mouth of the Columbia River (46.253° N, 124.059° W) and the cap-

ture station plus 32.1 km to account for travel through the estuary (Chawla et al. 2008). We divided the migration distance (km) by the marine residence time (d) to calculate the mean migration rate (km d^{-1}) for each fish, which was converted to body lengths per second (bl s^{-1}) based on estimated size at freshwater emigration.

Indicators of survival

The smolt-to-adult ratio (SAR) is an indicator of overall survival of a population or stock group (Ward & Slaney 1988, Beckman et al. 1999). Determination of SARs requires extensive data on juvenile production and natural and fishing mortality rates. SARs estimates have been developed for 2 hatchery and 2 wild stocks of mid-upper Columbia River spring Chinook (Tuomikoski et al. 2011) but are not available for the other hatcheries and wild runs in the genetic stock group. Adult returns to Priest Rapids Dam (–2 yr lag), the first Columbia River mainstem dam upstream of the Snake River, were strongly correlated with the SARs for Cle Elum ($r = 0.91$, $n = 7$) and Leavenworth ($r = 0.93$, $n = 7$) hatcheries, and for Entiat and Methow ($r = 1.0$, $n = 3$) and Wenatchee wild runs ($r = 1.0$, $n = 2$). Therefore, because we were interested in all components of the genetic stock, we used spring run adult returns to Priest Rapids Dam (www.cbr.washington.edu/dart/) as an indicator of survival. Adult returns were lagged 2 yr because the majority of mid and upper Columbia River spring Chinook salmon return after 2 yr in the ocean (Myers et al. 1998). For example, in 2008 nearly all (98.9%) of the returning adults had emigrated after 1 yr in freshwater and most (77.5%) returned 2 yr after emigration (Fryer 2009).

Growth-mortality hypothesis

If interannual variation in size at the end of freshwater residence is consistently important to cohort success, then we expect size at freshwater emigration to be positively related to adult returns. However, if early marine growth or size-selective predation are consistently important to cohort success, size at capture after ~30 d marine residence would be more strongly related to adult returns than size at freshwater emigration. Furthermore, if early marine growth rate is important for future survival, then we expect marine growth rates to be positively correlated with adult returns. Therefore, we examined the correlations between adult returns and juvenile size

and growth. For those metrics that were correlated with future abundance, we quantified the relationships using simple linear regression. To further quantitatively evaluate the influence of the size and growth rate, we performed multiple linear regression to develop a hindcast model. Adult returns to Priest Rapids Dam were natural log-transformed, and all metrics had normal error distributions and were homoscedastic. We ranked the models according to their Akaike Information Criterion adjusted for small sample size (AICc) and the model with the lowest AICc was considered the most parsimonious.

Indices of production

To evaluate the match-mismatch hypothesis, we used 4 indicators of annual variation in productivity and temporal overlap between juvenile salmon and secondary production. For productivity we used 2 indicators of the copepod community that are based on data collected biweekly ~9 km offshore of Newport, Oregon (44.65°N, 124.18°W). We used (1) the anomaly of the total biomass of boreal copepods, which is the monthly logged biomass estimate (mg C m^{-3}) minus the 15-yr monthly mean averaged over May to September (W. T. Peterson, NOAA, Newport, OR, unpubl. data) and (2) an index of the copepod community structure (Keister et al. 2011). The Copepod Community Index (CCI) consists of the rotated Axis 1 scores of a non-metric multidimensional scaling ordination of species abundance by sample date from 1996 to 2010 (Keister et al. 2011). During spring and summer, positive anomalies of copepod biomass and negative CCI indicate the presence of a 'northern community', i.e. cold-water neritic (shelf-resident) taxa that are large and lipid-rich, as well as stronger equatorward transport and upwelling conditions (Hooff & Peterson 2006). Coastal copepod biomass is higher when cold, dense water is nearshore (Keister et al. 2009), and the CCI is lower when upwelling is more intense and regional and basin-scale water temperature anomalies are cooler (Keister et al. 2011). Although juvenile Chinook salmon do not directly consume copepods (Peterson et al. 1982, Brodeur & Pearcy 1990, Schabetsberger et al. 2003, Daly et al. 2009), these copepod metrics may be indicative of the nutritional quality of the food web supporting juvenile salmon and their prey.

To examine the influence of temporal overlap, we used indicators based on the physical and biological changes associated with the transition to upwelling conditions. The physical spring transition (T_p) is

defined as the 1st day that the 10-d average for upwelling indices was positive and sea level height was negative (Logerwell et al. 2003). The biological spring transition (T_B) is defined as the 1st day that zooplankton samples from 9 km offshore of Newport, Oregon contain an upwelling-associated copepod community that dominates in the summer (Peterson & Schwing 2003, Hooff & Peterson 2006). Therefore, we examined how interannual variation in emigration timing was related to these physical and biological transitions. We determined the number of days between juvenile emigration and the physical and biological spring transition dates, hereafter referred to as the physical transition lag ($FE-T_P$) and the biological transition lag ($FE-T_B$).

Match-mismatch hypothesis

We predicted that early marine growth rate would be positively related to (1) $FE-T_P$ and $FE-T_B$ because growth conditions are expected to improve as the upwelling season progresses; (2) the copepod biomass anomaly because higher copepod biomass is generally associated with the dominance of large, cold-water species with high lipid content; and (3) negative values of the CCI because they are also associated with the dominance of lipid-rich, cold-water copepod species. This approach allowed us to determine if juvenile growth is related to the timing of emigration relative to the onset of seasonal production, which we used because indices of Chinook salmon prey are not available, as well as formally evaluate the hypothesis that juvenile salmonid growth is enhanced during years in which the northern community dominates (Keister et al. 2011).

RESULTS

Fish collection

All juveniles were captured between 21 May and 29 June and most (80%) emigrated from freshwater between 18 April and 30 May (Fig. 1). Size at capture ranged from 102 to 261 mm with an overall mean \pm SE of 161 ± 1 mm. Nearly three-quarters of the fish (74%) were collected along 3 transects: LaPush, Grays Harbor, and the Columbia River (Appendix 1). In general, the fish collected in June were farther north of the Columbia River than those collected in May (Appendix 1). The CWT prevalence was 36% for all mid-upper Columbia River spring Chinook salmon collected and 28% for the subset used for otolith analyses. The actual proportion of hatchery origin fish is likely higher than the CWT prevalence because just 50 to 78% of the hatchery-reared fish in this stock were CWT and 53 to 80% were marked (adipose fin-clipped) during the years of this study. We had no way to definitively group untagged and unmarked fish as 'wild' or 'hatchery'.

Migratory characteristics

Some fish ($n = 20$) had no discernable elevation of Sr within their otolith. Laboratory studies indicate an increase in otolith Sr occurs within 2 to 4 d of exposure to salinity (Miller 2011). Therefore, we used a 1 d marine residence time for those fish, which were included in analyses of freshwater emigration but not migration rate.

Size at freshwater emigration, size at capture, date of freshwater emigration, marine migration rate, and $FE-T_P$ and $FE-T_B$ varied among years (Table 1)

Table 1. *Oncorhynchus tshawytscha*. Juvenile metrics (mean \pm SE) and adult returns to Priest Rapids Dam for each juvenile emigration year. Number of days between freshwater emigration (FE) and the physical (T_P) and biological (T_B) spring transitions = $FE-T_P$ and $FE-T_B$, respectively. Range of sample sizes (n) are presented for each otolith-derived metric (sample size used to calculate fish size at capture in parentheses). Sample sizes for otolith-derived metrics were low in 2004 because 13 fish showed no sign of freshwater emigration. FL: fork length, bl: body length

Emi- gration (yr)	Size (FL, mm) at FE	Size (FL, mm) at capture	Marine residence (d)	Marine growth rate (%bl d ⁻¹)	Marine migration rate (bl s ⁻¹)	FE date (day of year)	$FE-T_P$ (d)	$FE-T_B$ (d)	Adult returns	n
1999	140 \pm 3	167 \pm 2	37 \pm 3	0.80 \pm 0.10	0.59 \pm 0.09	131 \pm 3	40 \pm 3	-3 \pm 3	51 133	26-30 (140)
2000	141 \pm 4	165 \pm 3	23 \pm 2	0.90 \pm 0.11	0.37 \pm 0.02	121 \pm 2	49 \pm 2	24 \pm 2	34 066	22-25 (62)
2002	156 \pm 5	160 \pm 4	21 \pm 3	0.45 \pm 0.10	0.40 \pm 0.14	122 \pm 3	42 \pm 3	14 \pm 3	13 521	16-21 (41)
2003	126 \pm 4	155 \pm 2	31 \pm 3	0.87 \pm 0.16	0.71 \pm 0.09	146 \pm 3	34 \pm 3	-10 \pm 3	14 148	24-25 (72)
2004	142 \pm 4	147 \pm 3	16 \pm 4	0.38 \pm 0.10	0.28 \pm 0.05	134 \pm 4	24 \pm 4	-12 \pm 4	8 535	9-24 (38)
2006	135 \pm 5	152 \pm 2	26 \pm 2	0.73 \pm 0.08	0.64 \pm 0.08	130 \pm 3	18 \pm 3	-50 \pm 3	12 178	24-29 (111)
2007	143 \pm 4	158 \pm 3	25 \pm 3	0.67 \pm 0.10	0.50 \pm 0.06	122 \pm 2	48 \pm 2	41 \pm 2	13 469	26-31 (85)
2008	145 \pm 4	169 \pm 2	26 \pm 3	0.71 \pm 0.12	0.39 \pm 0.10	120 \pm 3	31 \pm 3	56 \pm 3	30 539	26-30 (207)

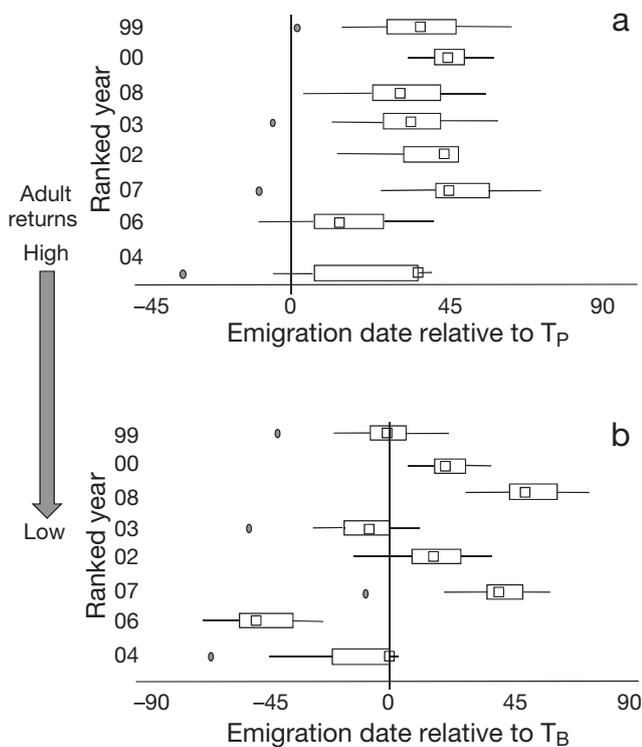


Fig. 3. *Oncorhynchus tshawytscha*. Dates of freshwater emigration (FE) relative to (a) physical (T_P) and (b) biological (T_B) spring transitions. Years ranked from highest to lowest adult returns and labeled by juvenile emigration year. Boxes = middle 50%, internal squares = median, whiskers = smallest and largest values within 1.5 \times the interquartile range of rectangle edge, ellipses = outliers

(ANOVA: $F_{7, >166} > 2.2$, $p < 0.01$). Marine growth rate also varied among years ($F_{7, 165} = 1.8$, $p = 0.09$). Size (mean \pm SE) ranged from 126 ± 4 to 156 ± 5 mm at freshwater emigration and from 147 ± 3 to 168 ± 2 mm at capture (Table 1). Marine growth rate ranged from 0.38 ± 0.10 to 0.90 ± 0.11 %bl d^{-1} (Table 1). Overall, the mean date of emigration ranged from 29 April to 26 May and occurred after the physical spring transition in every year (Fig. 3a) and after the biological spring transition in 4 of the 8 yr (Fig. 3b). Marine migration rate ranged from 0.28 ± 0.05 to 0.71 ± 0.09 bl s^{-1} (Table 1), which is equivalent to 3.7 ± 0.6 to 7.3 ± 0.9 km d^{-1} .

Back-calculation of size and growth

The 8 juveniles had been PIT-tagged 20 to 124 d prior to capture and were released 19 to 104 d before capture. For these fish, direct and proportional estimates of fish size at tagging were positively correla-

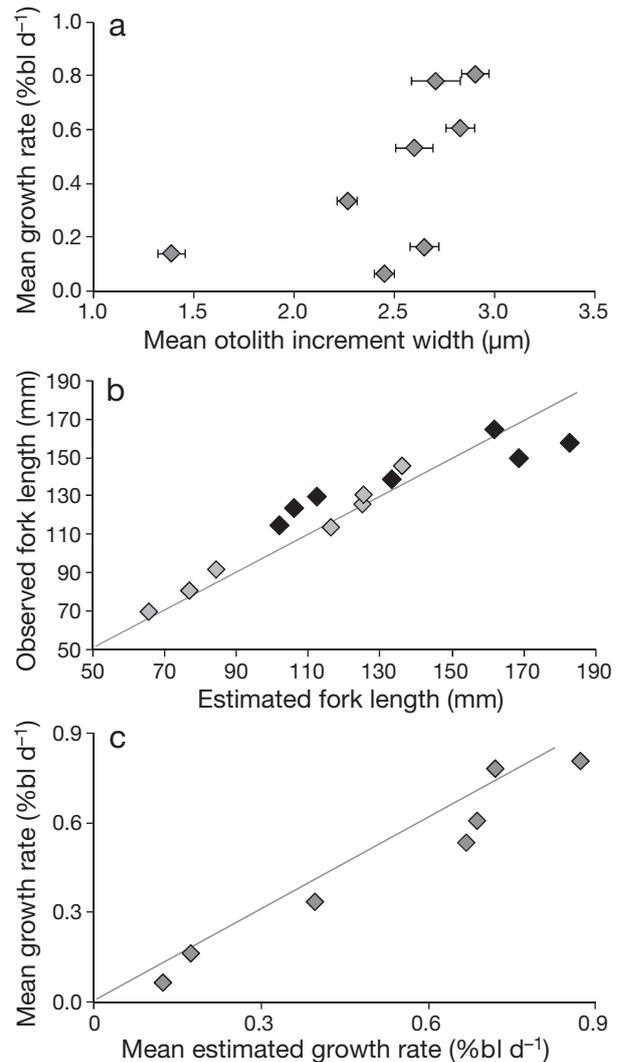


Fig. 4. *Oncorhynchus tshawytscha*. Relationships between fish and otolith size for interior Columbia River Chinook salmon juveniles with known tagging, size and migration history. (a) Mean somatic growth rate (%body length [bl] d^{-1}) vs. mean \pm SE increment width. (b) Observed vs. estimated fork length at tagging (grey; $r^2 = 0.98$, $p < 0.001$) and capture (black; $r^2 = 0.86$, $p = 0.002$). (c) Observed vs. estimated mean growth rate ($r = 0.97$, $p < 0.001$). Estimated growth rate was calculated as: (estimated size at tagging – size at capture) \div days since tagging

ted with observed size at tagging ($r = 0.99$, $p < 0.001$ and $r = 0.90$, $p = 0.006$, respectively). However, the accuracy was slightly better and the variation was smaller for direct back-calculation. Therefore, we estimated size at freshwater emigration for the remaining individuals using direct back-calculation (Eq. 1). All estimated lengths at PIT-tagging were within 7% of observed lengths. For the fish that was most recently tagged, i.e. 20 d prior to capture, tagging size was overestimated by 5%, which made the

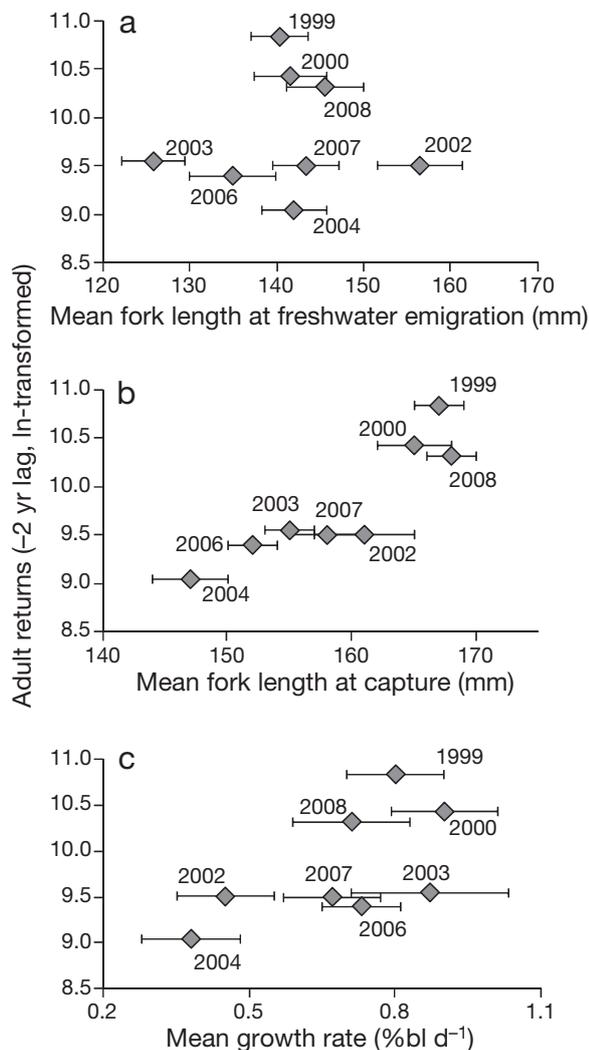
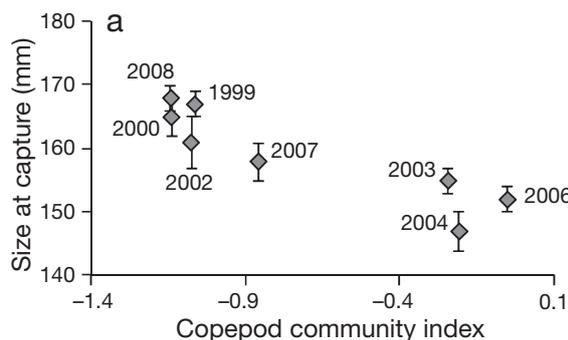


Fig. 5. *Oncorhynchus tshawytscha*. Adult returns to Priest Rapids Dam (–2 yr lag) vs. juvenile fork length (mean \pm SE) at (a) freshwater emigration ($r^2 = 0.001$, $df = 6$, $p = 0.93$) and (b) capture ($r^2 = 0.80$, $df = 6$, $p = 0.003$), and (c) marine growth rate (mean \pm SE; $r^2 = 0.39$, $df = 6$, $p = 0.10$). bl = body length; labels = juvenile emigration year



Match-mismatch hypothesis

Contrary to our predictions, marine growth rate was not significantly correlated with copepod biomass anomalies ($r = -0.24$, $p = 0.56$), the CCI ($r = -0.15$, $p = 0.72$), FE- T_P or FE- T_B (Table 3), although the trends for these pairwise comparisons were in the expected direction. However, size at capture was greater in years with negative values of the CCI, which is indicative of the lipid-rich copepod community (Fig. 6a; $r = -0.90$, $p = 0.002$) and earlier biological transitions, i.e. a greater FE- T_B (Fig. 6b; $r = 0.64$, $p = 0.09$). Size at capture was not related to the copepod biomass anomaly ($r = 0.49$, $p = 0.22$) or FE- T_P (Table 3).

We observed that juveniles migrated more slowly during periods when the copepod biomass was relatively high (Fig. 7a; $r = -0.68$, $p = 0.06$). Migration rate was not significantly correlated with FE- T_P or FE- T_B (Table 3), or CCI ($r = 0.38$, $p = 0.36$), although the trends for all 3 variables were in the expected direction if spatiotemporal overlap with highly productive conditions influenced the time spent in coastal waters. Additionally, we observed that marine migration rate was positively related to the date of freshwater emigration for individual fish collected in both May ($r = 0.59$, $p < 0.0001$) and June ($r = 0.67$, $p < 0.0001$) (Fig. 7b). Fish emigrating from the Columbia River later in the year tended to move northward more quickly than those emigrating earlier in the year.

DISCUSSION

We combined genetic and otolith chemical and structural approaches to generate individual data for juvenile spring Chinook salmon across 8 yr. This

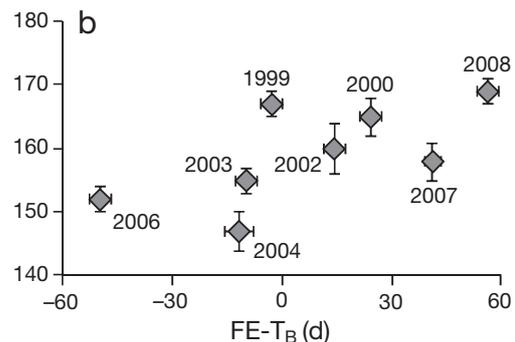


Fig. 6. *Oncorhynchus tshawytscha*. Relationships between juvenile size at capture and indices of ocean productivity. Fork length at capture (mean \pm SE) vs. (a) copepod community index (CCI; $r = -0.90$, $p = 0.002$) and (b) time between freshwater emigration and the biological spring transition (FE- T_B , d; $r = 0.64$, $p = 0.09$). Labels = juvenile emigration year

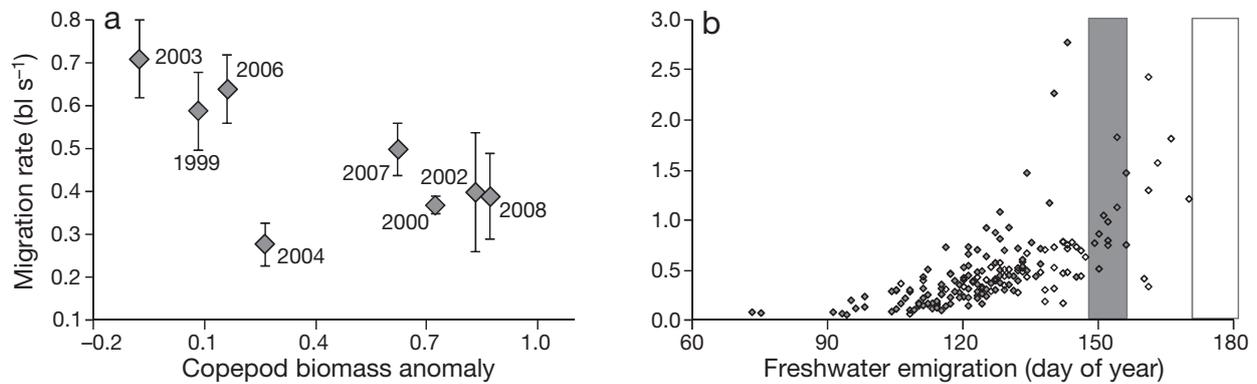


Fig. 7. *Oncorhynchus tshawytscha*. (a) Migration rate (mean \pm SE) vs. copepod biomass anomaly ($r = -0.68$, $p = 0.06$). Labels = juvenile emigration year. (b) Marine migration rate (mean \pm SE) vs. date of freshwater emigration for fish collected in May (\blacklozenge : $r = 0.59$, $df = 126$, $p < 0.001$) and June (\circ : $r = 0.67$, $df = 67$, $p < 0.001$). bl = body length. Boxes = May (grey) and June (open) collection dates

integrated approach allowed us to evaluate factors that can influence survival during early ocean residence and, therefore, may regulate future adult abundance. We excluded 2 low-catch years, 2001 and 2005, from our analysis; ocean conditions during these years were also poor. The physical spring transition was late in both years and in 2005 cumulative upwelling was anomalously low and sea surface temperature was anomalously high (Pierce et al. 2006). Our results provide strong support for the cumulative growth (size) and growth rate mechanisms of the growth-mortality hypothesis. Although results for the match-mismatch hypothesis were less clear, there was some evidence that juvenile size is related to interannual variation in the timing and composition of production in lower trophic levels. Furthermore, we observed seasonal and interannual variation in migratory behavior that may be related, in part, to foraging conditions.

Body size has previously been demonstrated to be important for survival of juvenile salmonids (Bilton et al. 1982, Henderson & Cass 1991) and many other fishes (for reviews, see Anderson 1988, Sogard 1997). For Chinook salmon, the relative importance of size at freshwater emigration compared with other periods in the life history has been difficult to evaluate. Studies often compare size at release from hatcheries, which is biased and does not provide information on the specific size at marine entry. Our results provide no evidence that interannual variation in size at freshwater emigration, based on our Sr:Ca ratio work, was related to future adult abundance. Variation in size at capture may be caused by growth rate-dependent or size-dependent mortality or a combination of these factors. Similar to Duffy & Beauchamp (2011), we observed that size shortly after marine

residence was positively related to adult returns (or survival). Given that we also observed positive (although weaker) relationships between marine growth rate and future adult returns, it is plausible that a combination of interannual variation in marine growth rate and size-selective survival influenced body size by May and June. If there was strong size-selective mortality when juveniles initially entered the marine environment, we may not be able to detect it because we only sampled individuals that survived 1 to 75 d of marine residence. However, for the 8 yr examined in this study, size at marine entry did not account for any of the subsequent variation in adult returns whereas size after an average of 30 d of marine residence accounted for ~80% of that variation. This observation indicates that processes shortly after initial marine entry play a larger role in determination of cohort strength than those occurring at the time of marine entry.

Early marine growth was not related to the timing of the physical and biological transition in relation to marine entry. The consistent observation that juveniles emigrated after the spring transition suggests that the emigration timing of mid-upper Columbia River spring Chinook salmon may be an adaptation to the long-term pattern of seasonal upwelling (Taylor 1990, Via et al. 1995). Additionally, the similarity in emigration timing across years may also be influenced by the similar timing of hatchery release across years (~3.5 wk) (Regional Mark Information System, www.rmipc.org). Previous studies found that, for hatchery Chinook salmon, subyearling juveniles that emigrated earlier in the year had higher survival (Duffy & Beauchamp 2011) and individual survival probability was highest for yearling fish migrating during the first half of May (Scheuerell et al. 2009).

These 2 previous studies examined intra-annual variation in migration timing while we focused on inter-annual variability. While relative interannual stability in emigration timing may be adaptive for the population as a whole, intra-annual variation in migration timing may result in differential survival within a year-class, i.e. an early migrating contingent of the stock may experience relatively higher survival (Kraus & Secor 2004b).

We did find evidence that juvenile size at capture was related to ocean conditions during early marine residence. Juvenile size at capture was related to the community structure of copepods in coastal shelf waters. Body size was greater when the CCI indicated that cold-water copepods were dominant. Juvenile Chinook salmon do not eat copepods (Peterson et al. 1982, Schabetsberger et al. 2003, Daly et al. 2009, Miller et al. 2010b), so this obviously does not demonstrate a direct link to prey. However, it does suggest that foraging conditions are related to the structure of the zooplankton community. One potential mechanism for the link between juvenile size and the CCI is that variation in the nutritional quality of secondary producers influences yearling Chinook salmon prey, which is usually dominated by larval fishes and decapods (Daly et al. 2009, 2011). There is some evidence that the lipid composition of potential prey varies with ocean conditions (Litzow et al. 2006, Litz et al. 2010). Alternatively, the CCI may provide a relative indicator of larger-scale ocean conditions that are beneficial to juvenile salmon survival rather than indicate a direct trophic linkage.

Interannual variation in growth rate was not related to the copepod community structure. If size was related to the copepod community via trophic linkages then one might expect growth rate to also be higher when the CCI indicates that lipid-rich copepods are present. The relationship between growth rate and the CCI trended the same direction as the relationship between capture size and the CCI, but was not significant. Potential explanations for this unexpected finding deserve some exploration. Size at capture was based on all fish caught in each year while growth rate was based on a subsample for which otoliths were available. It is possible that a derived metric of growth rate based on a smaller sample may not represent interannual variation as well as body size at capture. Additionally, there is some indication that the juveniles from the mid-upper Columbia River stock group included in this study may represent a subset of slower migrating individuals. For example, the mean migration rates observed in this study (3.7 to 7.3 km d⁻¹) were slower

than some previous estimates based on fish with CWTs (9.7 to 10.4 and 10 to 20 km d⁻¹) (Trudel et al. 2009, J. P. Fisher, Oregon State University, Newport, OR, unpubl. data). The mean date of marine entry observed in this study was prior to May 13th in all but one year. Therefore, it is likely that faster migrants were northward of our sampling grid before the cruise at the end of May. The fish that were collected during the late May and June collections may represent slower migrating individuals with somewhat different growth characteristics than the overall population. Growth can be related to temperature and one might expect ocean temperature to influence the marine growth rate; however, we found no evidence that growth rate was related to sea surface temperature in the study region (data not shown).

The observation that the mean migration rate was slower when copepod biomass anomalies were higher demonstrates interannual variability in migratory behavior. Migration rate may be a response to foraging conditions. Fish may migrate more slowly when foraging conditions are good. Alternatively, high biomass anomalies correspond to periods of upwelling (Hooff & Peterson 2006), which usually correspond to enhanced southward, alongshore transport (Strub et al. 1987). Therefore, the net migration rate of juvenile salmon may be slower during periods with high biomass anomalies. Coastal sea level height is related to the intensity of equatorward current and offshore advection (Strub et al. 1987, Checkley & Barth 2009). However, we found no relationships between migration rate and interannual variation in sea level height or alongshore transport during spring and early summer (data not shown). Nevertheless, regardless of the underlying mechanism, it appears that at least some juveniles migrate northward more slowly and, thus, spend more time in the local coastal waters during periods of greater copepod biomass.

The relationship between migration rate and emigration timing indicates consistent intra-annual patterns in migration rate. Later emigrants migrated faster across all years, which suggests that migratory behavior may be partially a seasonal response. One potential explanation is that individual migration rate may be influenced by some type of circadian rhythm (Gibson et al. 1978, Meseguer et al. 2008, Lopez-Olmeda & Sanchez-Vazquez 2009).

We were able to successfully isolate an important period in the life history of spring Chinook salmon—marine entry—to evaluate the relative importance of the size and timing of juvenile Chinook salmon upon marine entry. Across 8 yr, we found no

evidence that the annual variation in mean size at marine entry was related to subsequent abundance. However, size after ~1 mo of marine residence was highly correlated with adult abundance, which suggests that processes occurring shortly after marine entry may be more important for understanding mechanisms that establish cohort size. Furthermore, we were able to provide data on migratory characteristics at the individual level that highlight interannual and seasonal variation that may be influenced by foraging conditions. Overall, combined approaches that incorporate genetic analyses to estimate stock-of-origin with individual-level otolith analyses hold great promise to provide detailed information at the necessary scales to understand stock-specific adaptation and identify mechanisms regulating interannual variation in population size.

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Appendix 1.

Table A1. *Oncorhynchus tshawytscha*. Numbers of fish whose otoliths were used in this study by collection transect, month, and year. Otolith samples were selected in proportion to number of fish collected at each transect. See Fig. 1 for transect locations

	Year	May (n)	June (n)	Transect total		Year	May (n)	June (n)	Transect total
Tatoosh Island	2003		1	<u>1</u>	Willapa Bay	2003		1	
Father and Son	2006		4			2006	6		
	2007	3		<u>7</u>		2007	14		
La Push	1999		26			2008	4		<u>25</u>
	2003		12		Columbia River	2000	12		
	2006	5	5			2002	17		
	2007		1	<u>49</u>		2003		6	
Queets River	2003		9			2004	20		
	2004		2			2006	3	2	
	2006	5	1			2007	4		
	2007	6				2008	22		<u>86</u>
	2008	4		<u>27</u>					
Grays Harbor	1999		6						
	2000	14							
	2002	5							
	2004	4	1						
	2006	2							
	2007	4		<u>36</u>					

Editorial responsibility: Edward Durbin,
Narragansett, Rhode Island, USA

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