Freshwater growth can provide a survival advantage to Interior Columbia River spring Chinook salmon after ocean entry

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ABSTRACT: ABSTRACT: A prerequisite to effectively managing fish populations is to understand what factors and processes, including predation and changing environments, affect the survival of individuals. In anadromous fishes, the transition from freshwater to marine habitats is considered a critical period regulating population abundance due to high and variable mortality rates. During this period, conditions experienced in freshwater may influence size- and growth-selective mortality in the ocean. To determine if size- or growth-selective mortality occurred in juvenile Interior Columbia River spring Chinook salmon *Oncorhynchus tshawytscha* as they migrated through the Lower Columbia River and Estuary (LCRE) and during early marine residence, we examined 2 cohorts in years with differing survival (2016 and 2017). We reconstructed the size and growth of individual Chinook salmon from otoliths and compared these attributes in fish caught at 4 sites in the LCRE to those caught in the ocean off Oregon and Washington. We observed evidence of growth-selective mortality in 2017 but not 2016. Specifically, in 2017, when overall survival was lower, individuals caught in the ocean grew significantly faster in freshwater than individuals caught in the estuary. Given that the fish had resided in the ocean for an average of 30 d, these results indicate growth-selective mortality in 2017 occurred soon after ocean entry. The finding that growth in freshwater may impact marine survival adds to the growing body of evidence that processes occurring both prior to and after ocean entry impact the marine survival of this species.

KEY WORDS: Growth selection · Otolith analysis · Pacific salmon · Columbia River · *Oncorhynchus tshawytscha* · Size selection

1. INTRODUCTION

Detailed knowledge of factors that affect survival of individuals is essential to the understanding of several key ecological and evolutionary processes, including phenotypic adaptation to changing environments, demographic responses to predation, and impacts of carryover effects (Swain et al. 2007, Beckerman et al. 2010, Moore & Martin 2019). Selective mortality is an important ecological process in which certain phenotypes confer a survival advantage relative to individuals that do not express these traits (Sogard 1997, Johnson et al. 2014). Information on the traits of survivors can provide insight into the phenotypes that may be linked to survival and thus affect population dynamics (Johnson et al. 2014).

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The life history stages of many marine animals include a critical period of high and variable mortality. Understanding factors affecting mortality during this period can help us recognise factors influencing future population abundance (Hjort 1914, Pearcy 1992, Beamish & Mahnken 2001, Khamassi et al. 2020). Size- or growth-selective mortality during this period is one such factor likely to be important in determining population abundance (Miller et al. 1988, Sogard 1997, Claiborne et al. 2014). Thus, a clear understanding of this process is essential to making predictions of future cohort strength. In addition to providing ecological insights, information on factors that regulate cohort strength is essential to the implementation of effective management plans for exploited or threatened species (Swain et al. 2007, Gamble et al. 2018).

Chinook salmon *Oncorhynchus tshawytscha* are an economically, ecologically, and culturally significant species in the north Pacific Ocean. The Columbia River is an important source of Chinook salmon, with individuals originating from this river found in the ocean from southern Oregon to the Bering Sea (Fisher et al. 2007, 2014, Weitkamp 2010). Populations of Chinook salmon in the Columbia River basin have decreased dramatically during the 20th century, with most evolutionarily significant units (ESUs) listed under the US Endangered Species Act (Northwest Fisheries Science Center 2015). Two of the 3 ESUs that comprise Interior Columbia River spring Chinook salmon runs, defined as runs that originate from above Bonneville Dam and return to spawning locations as adults in the spring and summer, are currently listed under the Endangered Species Act: the Upper Columbia River spring run ESU (endangered) and the Snake River spring/summer run ESU (threatened). Interior Columbia River spring runs also include the Mid-Columbia River spring run ESU, which is not currently listed. Several management strategies, therefore, exist to enhance populations of Columbia River Chinook salmon (Williams 2006, Upper Columbia Salmon Recovery Board 2007, NOAA Fisheries 2017). For management approaches to be successful, it is important to understand the drivers of survival, how those drivers influence population abundance, and the interactions between populations and the environment (Petrosky & Schaller 2010, Burke et al. 2013, Chasco et al. 2021).

Early marine residence is considered a critical period in the life history of salmon (Pearcy 1992, Beamish & Mahnken 2001). Several physical (temperature and large-scale climate processes such as the Pacific Decadal Oscillation), ecological (primary production and food chain structure), and individual (size and growth) factors and processes, as well as interactions among these components, affect survival during this critical phase (Beamish et al. 2004, Burke et al. 2013, J. A. Miller et al. 2014). Size and growth during this period are particularly important to survival (e.g. Sogard 1997, Tomaro et al. 2012, Claiborne et al. 2014). The growth–mortality hypothesis (Anderson 1988), which incorporates aspects of the bigger-is-better hypothesis (Miller et al. 1988), posits that larger individuals exhibit an enhanced ability to evade predators, are less susceptible to starvation, and can capture prey more efficiently. Thus, faster growing individuals that reach these sizes sooner and spend less time at more vulnerable sizes have a survival advantage (Anderson 1988, Miller et al. 1988). For example, Meekan et al. (2006) reported higher mortality in sprat *Spratelloides gracilis* with slower growing, smaller larvae, while Khamassi et al. (2020) observed that juvenile Atlantic mackerel *Scomber scombrus* with slower growth rates were more susceptible to predation. In juvenile Chinook salmon, positive correlations between growth rate, size, and survival during early marine residence also support these growth-mortality–bigger-is-better hypotheses (Tomaro et al. 2012, Woodson et al. 2013, Claiborne et al. 2014).

Size- and growth-related differences in predation risk during the transition from freshwater to the marine environment can have important impacts on survival and can play a critical role in limiting the recovery of Columbia River populations (Collis et al. 2001, Evans et al. 2012). As individuals migrate through the Lower Columbia River and Estuary (LCRE) and during early marine residence they are exposed to a suite of predators, including marine mammals (Wargo Rub et al. 2019, Sorel et al. 2021), birds (Collis et al. 2001, Wiese et al. 2008, Evans et al. 2012), and piscivorous fishes (Emmett & Sampson 2007, Brodeur et al. 2014). The recent recovery of marine mammal abundances has resulted in a coastwide increase in predation pressure (Chasco et al. 2017). Although the research on the predation of Chinook salmon by marine mammals has primarily focussed on impacts to returning adults (Wargo Rub et al. 2019, Sorel et al. 2021), juvenile Chinook salmon have been found in the diets of pinnipeds in Oregon and Washington (Szoboszlai et al. 2015, Adams et al. 2016). Avian predation also likely affects populations of juvenile Chinook salmon in the LCRE and during early marine residence. These juvenile Chinook salmon are regularly exposed to piscivorous seabirds in the Columbia River estuary (Collis et al. 2001, Evans et al. 2012, Good et al. 2022), the Columbia River plume (CRP)

(Zamon et al. 2014, Phillips et al. 2021), and along the Oregon and Washington coast (Phillips et al. 2021). Finally, piscivorous fishes including Pacific hake *Merluccius productus* and jack mackerel *Trachurus symmetricus*, which can be abundant in the CRP, are also known to prey on juvenile Chinook salmon (Emmett & Sampson 2007, Brodeur et al. 2014).

It is important to consider how an individual's experiences during an earlier life history stage (e.g. freshwater residency) can carry over to affect their survival when they reach the LCRE and enter the ocean. If size- or growth-selective mortality is occurring in the LCRE or during early marine residence, fish which grow faster or are larger in freshwater prior to reaching these locations may have a survival advantage. While the concept of carryover effects was initially developed to explain differential breeding success of migratory birds (reviewed by Harrison et al. 2011), the ecological definition of a carryover effect has expanded to describe any experience earlier in an individual's life that affects their future fitness (O'Connor et al. 2014). This definition has been applied to a wide range of taxa in several contexts; for example, to explore the effects of habitat differences in the natal environment (Saboret & Ingram 2019) or during migration (Norris 2005), maternal provisioning (Sopinka et al. 2014), and the impacts of stresses across life stages (Sopinka et al. 2014, Leung & McAfee 2020). In juvenile Chinook salmon, carryover effects have been observed with early ocean survival rates differing between fish subject to different transport histories (i.e. in-river vs. barged to the LCRE) (Brosnan et al. 2016, Gosselin et al. 2018), the timing of ocean entry (Chasco et al. 2021), and with hatchery practices (Beckman et al. 2017, Nelson et al. 2019). If carryover effects of size and growth exist for Interior Columbia River spring Chinook salmon, management actions that seek to maximise attributes related to survival, such as targeted hatchery actions or modification of existing habitat restoration programmes along the migratory corridor, may promote the survival of these stocks.

In this study, we determined the extent to which size- and growth-selective mortality was detected in juvenile Interior Columbia River spring Chinook salmon populations during their migration through the LCRE and into the ocean. Employing an approach that followed 2 out-migrating cohorts, we sampled fish at multiple sites in the LCRE and off the coast of Oregon and Washington in 2016 and 2017. We reconstructed size and growth history of individuals prior to ocean entry using otolith structural and chemical analyses to compare size and growth phenotypes

between successive sites, or regions of potential selection. This approach allowed us to determine which traits were related to survival through the LCRE and during early ocean residence. To test the hypothesis that larger, faster growing fish have a survival advantage during early marine residence, we addressed the following questions: (1) do we detect evidence for size- or growth-selection of juvenile Chinook salmon as they migrate through the LCRE and into the ocean; (2) if so, where did this selection occur; and (3) are there differences in apparent selection pressures among years?

2. MATERIALS AND METHODS

2.1. Fish collection

Juvenile Chinook salmon were collected in the ocean off the Oregon and Washington coast (hereafter 'the ocean') and in the LCRE in 2016 and 2017 (Fig. 1). Fish collections in the ocean were part of NOAA's Juvenile Salmon and Ocean Ecosystem Survey. Fish collections in the LCRE were part of the
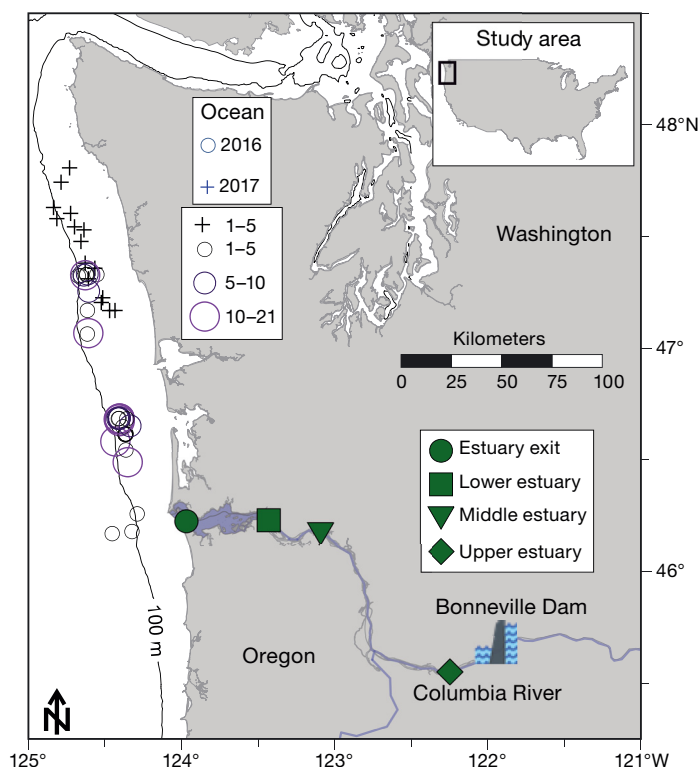

Fig. 1. Locations where Interior Columbia River spring Chinook salmon used in this study were caught as well as Bonneville Dam. Site marker size for ocean samples corresponds to the number of fish caught at each location

Action Effectiveness Monitoring and Research program (Weitkamp et al. 2020). Our samples included all ocean-caught fish, both hatchery and naturally produced, as this is representative of the population. More than 90% of Interior Columbia River spring Chinook salmon migrate as yearlings; therefore, all fish used in this study were identified as yearlings based on fork length (FL) and month of estuary and ocean capture. Length cut-offs were derived from known ages based on scale analysis and from tagged fish (Fisher & Pearcy 1995, Weitkamp et al. 2015).

In 2016 and 2017, Chinook salmon were collected monthly in April, May, and June at 5 sites in the LCRE (Fig. 1). These sites included an Upper Estuary site, located 210 km from the mouth of the Columbia River (river km [Rkm] 210); a Middle Estuary site (Rkm 92); a Lower Estuary site (Rkm 61); and 2 Estuary Exit sites (Rkms 17 and 13). A proportion of Snake River fish are transported downriver on barges and released below Bonneville Dam (32% of all Snake River spring/summer Chinook in 2017 and 33% in 2016; https://www.fpc.org/). However, the Upper Estuary site was located downstream of the release location of these fish and is therefore representative of the out-migrating population.

The methods used to collect fish in the LCRE were based on Weitkamp et al. (2015, unpubl. data). Briefly, 2 types of nets were used to collect Chinook salmon in the LCRE: a fine-mesh purse seine was used at the estuary sites and a 2-boat tow Kodiak surface trawl net was used at the remaining LCRE sites. The purse seine (10.6 m deep × 155 m long) was repeatedly set, retrieved, and the catch processed, starting at low tide and continuing throughout the incoming tide. The tow net measured 12.8 m long and had a 6.1 m wide × 2.9 m deep mouth. It was deployed in 10 min tows in an upstream direction using 2 boats spaced approximately 100 m apart. Each boat pulled a 70 m long tow rope attached to either side of the net. A different net was used in May and June of 2017; this net was 16 m long with a 7.6 m wide × 3.7 m deep mouth. As discussed by L. A. Weitkamp et al. (unpubl. data),where they describe the collection of the fish included in this study, we assumed that the different nets did not bias our catches of juvenile Chinook salmon. If biases in catches did exist, they would have likely been against larger fish such as juvenile steelhead.

Fish collections in the ocean occurred during the last 2 wk of May in 2016 and 2017. Fish were collected using a Nordic 264 rope trawl (Net Systems) fished at the surface directly astern of the F/V 'Frosti'. To fish the head-rope of the trawl at the sur-

face, a cluster of 2 meshed A-5 polyform buoys were tethered to each wing tip and 2 A-5 polyform floats were clipped at the centre of the head-rope. The trawl mouth was spread apart by a pair of 3.0 m Lite$^®$ trawl doors, creating a trawl opening of approximately 30 m wide × 20 m deep when fishing. Trawl mesh sizes ranged from 162.6 cm in the throat of the trawl near the jib lines to 8.9 cm in the cod end. At sea, all juvenile Chinook salmon were identified, FL measured (mm), and frozen after capture. In the laboratory, fish were thawed, remeasured, and weighed; a fin clip was taken for genetic analyses, and otoliths were removed for structural and elemental analyses. Fulton's condition factor was also calculated (100 × weight [g] / length [mm]^3).

2.2. Genetic analyses

To control for potential stock differences in size and growth, all fish included in this study were from interior spring Chinook salmon stocks. Genetic analyses were conducted to establish the stock grouping of each fish using genetic stock identification (GSI) methods. GSI was determined using single nucleotide polymorphisms (SNPs), which allow for automated, rapid genotyping (Campbell et al. 2015). A 'genotyping-in-thousands by sequencing' (GT-seq) method that uses next-generation sequencing of multiplexed PCR products to generate genotypes from relatively small panels (50–500) of targeted SNPs was used (Van Doornik et al. 2019). The focus of this study was on fish assigned to Interior Columbia River spring Chinook salmon stocks, which include Snake River spring and middle stocks as well as Upper Columbia River spring stocks. The average posterior probability of genetic assignment as Interior Columbia River spring Chinook salmon in this study was high (>0.8 for all fish; mean ± SD: 0.926 ± 0.124).

2.3. Otolith analysis

We performed structural and chemical analyses on one randomly selected otolith from each fish. Sagittae were mounted on a glass slide using thermoplastic resin and polished to expose the core using 3M trimite wet-or-dry paper (240–2000 grit) and diamond lapping film (1–30 μm). Digital images of each polished and mounted otolith were captured using a Levenhuk M1000 plus digital camera coupled to a Lecia DM1000 compound microscope. Images were captured at 40× and 400× magnification.

Otolith structural analyses were used to determine otolith size and growth metrics for each fish. As otoliths grow in proportion to body length, otolith metrics are frequently used as a proxy for fish size and growth (e.g. Tomaro et al. 2012, Morrongiello et al. 2015, Chittaro et al. 2018). Otolith metrics collected included otolith radius (OR) (Fig. 2), which served as a proxy for fish size, and the width of daily increments, which served as a proxy for daily somatic growth. As increments are formed daily (Neilson & Geen 1982), combining these measurements with OR allows the size of fish prior to capture to be estimated.
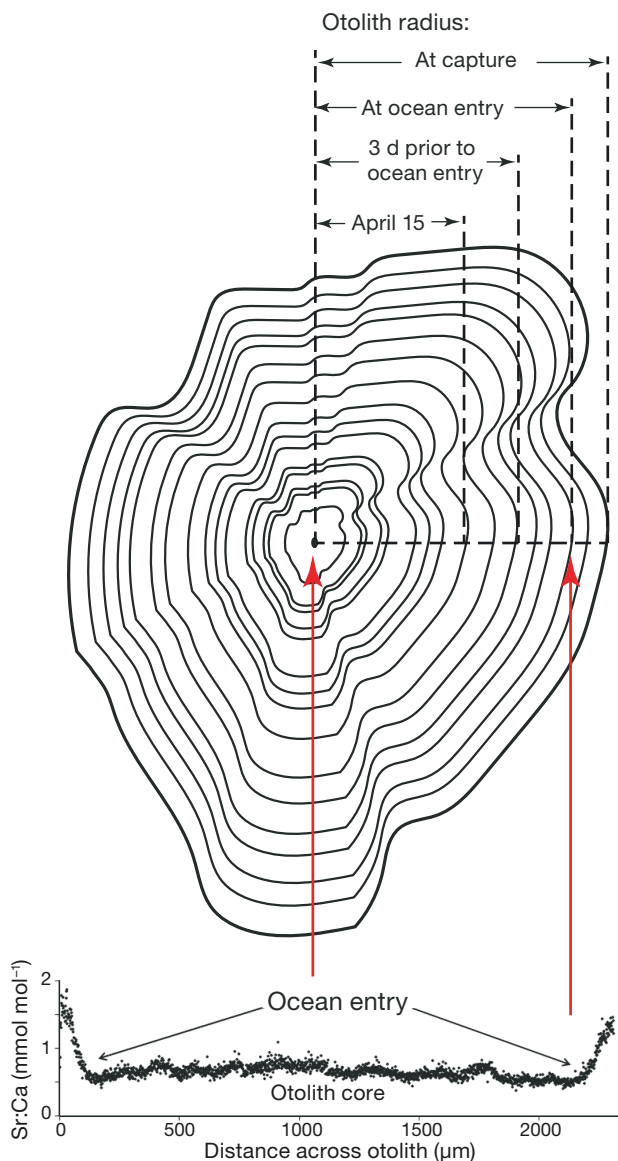

Fig. 2. Schematic of a representative Chinook salmon otolith. Examples of otolith radii measurements are displayed as well as an example Sr:Ca ratios across a transect of otolith for determining radius at ocean entry

Otolith images were analysed using Image Pro-Plus™ software (Media Cybernetics®). All otolith metrics were collected along a dorsal–ventral transect passing through the otolith core (Fig. 2). Otolith radii were measured from the core primordia to the dorsal edge using 40× magnification images. Daily increments were enumerated and measured from 400× magnification images along the same transect used to collect OR measurements. Daily increments from all otoliths were counted and measured to at least 15 April (the date of the first sampling event at the Upper Estuary site in 2016). Structural analysis on approximately 40% of the otoliths used in this study was performed twice by 2 different readers. Differences between readers were small (mean ± SD increment width: 2 ± 0.008%).

We used the strontium:calcium (Sr:Ca) ratio in otoliths to estimate the date of freshwater emigration for fish caught in the ocean. Otolith material deposited in marine environments is usually characterised by higher Sr:Ca ratios than that deposited in freshwater environments (Kraus & Secor 2004, Zimmerman 2005). Therefore, an increase in the Sr:Ca ratio to marine levels indicates residence in brackish or oceanic waters (Miller et al. 2010). As the salinity intrusion can reach up to 42.5 km from the mouth of the Columbia River (Chawla et al. 2008) the Sr:Ca ratio in otolith may begin to increase slightly before the estuary exit site. Hereafter, we refer to this transition from freshwater to brackish/ocean water as 'ocean entry'. Sr:Ca ratios were obtained through laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). Briefly, the laser was set with a pulse rate of 7 Hz and travelled at a speed of 5 μm s^{-1} across the sample. The spot size was either 30 or 50 μm, depending on instrument sensitivity. National Institute of Standards and Technology (NIST) 612 elemental glass standards were analysed repeatedly throughout analysis for standardisation and to calculate precision (%RSD ± SD: ^{43}Ca = 3.91 ± 1.22%; ^{86}Sr = 4.62 ± 1.48%; n = 13). Data was normalised to ^{43}Ca and standardised to NIST 612 standards and converted to molar ratios. Accuracy was determined using repeated analysis of the USGS calcium carbonate standard MACS-1 (mean ± SD for Sr:Ca = 85.3 ± 1%; n = 6).

2.4. Data analysis

All statistical analyses in this study were conducted in R v.4.2 (R Core Team 2020). Although efforts were made to include all fish caught in the analyses, some

otoliths were missing or damaged, resulting in differences in sample sizes between analyses. In addition to otolith analyses, we also compared Fulton's condition index, fish length, and fish mass across sites and between years using a 2-way ANOVA. Prior to this ANOVA, the data was inspected for normality and homogeneity of variance and met these assumptions.

2.4.1. Establishing common periods for size and growth comparisons

By examining the distributions of phenotypes in a population between successive potential selection events (sampling sites in this case), we can determine if, when, and where selection likely occurred (e.g. Woodson et al. 2013). Therefore, we established common points in time to compare body size and growth of fish collected at each of our sites. This method ensured that all fish caught were comparable. We examined body size and growth on specific calendar days to determine if fish which were larger and grew faster earlier in the year had a survival advantage. We examined these same metrics on dates relative to ocean entry to determine if fish which were larger or grew faster immediately prior to ocean entry had a survival advantage.

To estimate the date of ocean entry for fish caught in the LCRE, we calculated the distance from the location at which fish were caught to the river mouth and estimated the number of days required for a fish to travel this distance. These estimates were calculated from median migration rates reported for this stock group of 82 km d^{-1} in 2016 and 103 km d^{-1} in 2017 (Morris et al. 2017, 2018). These estimates were based on the time for fish tagged with passive integrated transponder (PIT) tags to travel from Bonneville Dam to a PIT-tag array towed in the mainstem of the LCRE between Rkm 66 and 84. Fish caught at the Upper Estuary (Rkm 210) were therefore deemed to be approximately 3 d from ocean entry, fish caught at the Middle Estuary (Rkm 92) and Lower Estuary (Rkm 61) were deemed to be 1 d from ocean entry, and fish caught in the Estuary Exit (Rkms 17 and 13) were deemed to be 0 d from ocean entry.

To estimate the date of ocean entry for fish caught in the ocean, we determined the OR at which the Sr:Ca ratio began to increase to marine levels (Miller et al. 2010, Claiborne et al. 2014). We then enumerated the daily otolith increments between the otolith edge and the otolith radii representing ocean entry. Although the Sr:Ca ratio in otoliths likely begins to increase immediately after a change in salinity, method-

ological constraints suggest that it can take up to 2–3 d until sufficient material has been deposited for this inflection to be measurable (Miller 2011). Therefore, fish caught in the ocean with otoliths without a clear Sr:Ca inflection point were estimated to have entered the ocean 3 d prior to capture.

2.4.2. Size selection

To determine if size-selective mortality was occurring in the LCRE or during early ocean residence, we compared otolith radii, a proxy for body size, across all sites on 15 April and 3 d prior to ocean entry. The date of 15 April was selected because this was the date of the first sampling event at the Upper Estuary site in 2016; 3 d prior to ocean entry was selected due to the estimated 3 d migration time from the Upper Estuary site to the ocean. An increase in average OR between successive sampling sites due to disproportionate loss of fish with smaller otoliths would indicate that selective mortality had occurred.

To determine if there was a shift in the mean otolith radii across sites within years and/or across years, we performed 2-way ANOVA for both points in time (i.e. 15 April and 3 d prior to ocean entry). We examined the main effects of year and sampling site as well as their interaction. Differences across sites were examined to determine if there was evidence for selection, whereas interannual differences were included to provide context for interannual differences in selection pressure. Tukey's post hoc tests were used to examine pairwise differences between sites and years. Prior to performing these analyses, the assumptions of normality and homogeneity of variance were checked using Shapiro-Wilk's test and Levene's tests. The data was ln-transformed, which improved normality and homogeneity of variance.

We used a linear mixed model approach in R (package 'lme4'; Pinheiro et al. 2021) to assess whether differences in otolith increment widths (as a proxy for growth rates) (Weisberg et al. 2010, Morrongiello et al. 2015, Fennie et al. 2020) existed among our fixed effects of sampling site and year. We included individual fish identity in the models as a random effect. We also fitted a random location slope and intercept term to the fish identity term, which allowed individual fish to have unique site-dependent growth trajectories (Morrongiello et al. 2015, Izzo et al. 2016). The most parsimonious model, based on having the lowest Akaike's information criterion values, did not include a random slope term, which was then excluded from the final model. Due

to the inherent autocorrelation of consecutive increment measurements on the same otolith, we incorporated a first-order autoregressive correlation structure into the model (Weisberg et al. 2010, Fennie et al. 2020). The structure of the model was: site + year + site × year | random intercept + autocorrelation. After fitting the model, we examined pairwise differences between sites and years using least squares means tests, which were adjusted for multiple comparisons using the Tukey method. As no pairwise differences in growth rate were observed between sites within the LCRE in either year (Table S1 in the Supplement at www.int-res.com/articles/suppl/m691 p131_supp.pdf), all fish caught in the LCRE were included as a single 'estuary' group for these analyses.

2.4.3. OR–FL relationship

To verify that a positive relationship exists between OR and FL, we performed a linear regression. Although the primary focus of our analyses was on otolith metrics, we also used this relationship to estimate mean somatic growth rates (mm d^{-1}) to provide context to our results but did not perform statistical analyses to avoid the introduction of additional sources of error. We estimated somatic growth rates both between 15 and 29 April and immediately prior to ocean entry based on otolith growth rates. As we were estimating the growth rates of fish prior to marine entry, and the relationship between otolith growth and somatic growth may change after ocean entry due to a marked increase in somatic growth, we excluded fish from this analysis that had an ocean residence time of >5 d based on otolith Sr:Ca ratios.

2.5. Environmental conditions

Environmental conditions can influence the survival, growth, and behaviour of juvenile salmon (Quinn 2005, Petrosky & Schaller 2010). Higher survival rates are commonly associated with periods of lower water temperature and higher river flow, although the specific mechanisms are not yet clear (Burke et al. 2013, J. A. Miller et al. 2014). To characterise conditions during migration, we obtained river flow and temperature data from 'Columbia River Data Access in Real Time' (DART; www.cbr.washington. edu/dart/query/basin_conditions_hist). Temperature (°C) was measured below Bonneville Dam, while flow (m^3 s^{-1}) was measured at USGS Stn 14128870 below Bonneville Dam.

To understand the extent to which ocean conditions during our sampling years (2016 and 2017) compared to other years, we placed these 2 years into a broader context by comparing ocean conditions across a longer period (1998–2019). We collated information on daily sea surface temperatures from 5 buoys off the Oregon and Washington coasts (Stns 46229, 46211, 46041, 46029, and 46050; National Data Buoy Center https://www.ndbc.noaa.gov/). We also examined a multivariate index of ocean conditions related to salmon survival (Burke et al. 2013, https://www. fisheries.noaa.gov/west-coast/science-data/ocean-ecosystem-indicators-pacific-salmon-marine-survival-northern). This index includes metrics on physical and biological conditions, such as the timing of the physical spring transition and indicators of lower trophic level productivity.

We obtained smolt-to-adult-return ratios (SARs), which is the ratio of the number of PIT-tagged juvenile spring/summer Snake River Chinook salmon moving downstream past Bonneville Dam to the number of adults moving upstream past Bonneville Dam between 2000 and 2017 (www.cbr.washington. edu/dart). The SAR is a metric of survival during ocean residence.

3. RESULTS

The majority of Interior Columbia spring Chinook salmon were caught in the LCRE in May of both years (Table 1). In the LCRE, catch per unit effort (CPUE), although marginally higher in 2017 (1.89 fish haul^{-1}) than in 2016 (1.26 fish haul^{-1}), was relatively consistent between years. Conversely, CPUE in the ocean surveys was notably higher in 2016 (2.0 fish km^{-1} towed) than in 2017 (0.31 fish km^{-1} towed). Longer and heavier fish were caught in the ocean than in the LCRE in both years (Table 2). This difference was demonstrated by the significant main effect of site in the 2-way ANOVA (length $F_{1,501} = 113.6$, p < 0.01; mass $F_{1,501} = 175.3$, p = 0.01), but no significant interaction (length: $F_{1,501} = 2.9$, p = 0.08; mass $F_{1,501} = 0.7$, p = 0.63) or year (length: $F_{1,501} = 1.9$, p = 0.17; mass $F_{1,501} = 0.23$, p = 0.63) effects existed. The median day of ocean entry, as estimated from otolith chemistry, was 1 d earlier in 2016 (17 May, day-of-the-year [DOY] 139) than in 2017 (16 May, DOY 137) (Fig. 3C,D). In 2016, the period of ocean entry was more protracted (DOY 97–149) than in 2017 (DOY 108–146), and the mean residence time of fish caught in the ocean in 2016 (9.4 d) was nearly half that in 2017 (16.9 d). Mean

Table 1. Number of Interior Columbia River spring Chinook salmon caught in 2016 and 2017 in the Lower Columbia River and Estuary (LCRE) and the ocean by dates of capture. (−) indicates catch per unit effort (CPUE) for individual sites in the LCRE is not available and that no ocean samples were included from June

Site	2016					2017					Overall total
	11–22 April	9–20 May	9–20 June	Total	CPUE	18–28 April	5–16 May	13–21 June	Total	CPUE	
Upper Estuary	9	48	2	59	−	11	16	0	27	−	86
Middle Estuary	0	37	3	40	−	1	11	0	12	−	52
Lower Estuary	7	23	0	30	−	8	16	0	24	−	54
Estuary Exit	3	28	0	31	−	11	21	0	32	−	63
Estuary total	19	136	5	160	1.26	31	64	0	95	1.89	255
Ocean	−	214	−	214	2.0	−	35	−	35	0.31	249
Total	19	350	5	374		31	99	0	130		504

Table 2. Mean (±SE) fork length (FL), mass, Fulton's condition factor (K), and otolith radii (OR) of Interior Columbia River spring Chinook salmon caught at each of the sampling sites in this study. OE: ocean entry

Site	FL (mm)	Mass (g)	Fulton's K	OR (µm)	
				15 April	3 d before OE
2016					
Upper Estuary	136.2 ± 1.1	22.4 ± 0.7	0.87 ± 0.01	913 ± 10	955 ± 10
Mid Estuary	138.2 ± 1.3	23.4 ± 1.1	0.87 ± 0.01	934 ± 14	975 ± 14
Lower Estuary	144.4 ± 2.4	24.0 ± 0.8	0.83 ± 0.01	999 ± 18	1039 ± 18
Estuary Exit	145.7 ± 2.1	26.9 ± 1.1	0.87 ± 0.01	954 ± 26	1003 ± 23
Ocean	153.2 ± 1.0	36.8 ± 1.5	0.98 ± 0.01	944 ± 8	1006 ± 8
2017					
Upper Estuary	143.0 ± 2.5	28.1 ± 1.7	0.92 ± 0.02	968.30 ± 21	1006 ± 26
Mid Estuary	143.6 ± 3.3	28.4 ± 1.5	0.94 ± 0.02	894.46 ± 16	949 ± 15
Lower Estuary	140.8 ± 2.0	28.4 ± 1.2	0.93 ± 0.01	911.99 ± 27	966 ± 26
Estuary Exit	142.4 ± 1.5	27.1 ± 1.4	0.90 ± 0.01	933.69 ± 12	991 ± 12
Ocean	152.1 ± 2.5	38.9 ± 2.7	1.07 ± 0.01	911.65 ± 16	957 ± 16

Fulton's condition index was significantly higher in the ocean in both years relative to the LCRE and significantly lower at all sites in 2016 than in 2017 (Table 2). These differences in mean condition index between years are supported by the results of the 2-way ANOVA, which showed significant main effects of site ($F_{4,454} = 1.648$, p < 0.01) and year ($F_{1,454} = 0.066$, p < 0.01) but no significant interaction effects ($F_{4,454} = 0.0086$, p = 0.30).

3.1. FL–OR relationship

There was a significant positive relationship between FL at capture and OR at capture ($r^2 = 0.52$, p < 0.01; Fig. 4). The relationship between OR and FL at capture is shown in Eq. (1):

$$\ln(FL) = (0.183 \pm 0.313) + \ln(OR) \times (0.700 \pm 0.045) \quad (1)$$

The slope of this relationship was used to translate mean differences in otolith growth rate to mean differences in somatic growth rate over the periods investigated (15−29 April, 3−7 d prior to ocean entry, the 7 d immediately prior to ocean entry).

3.2. Size selection

We did not find significant differences in mean otolith radii on 15 April between years or across sites. The lack of differences in otolith size indicates no differences in fish size likely existed. Mean otolith radii on 15 April ranged from 894 ± 16 µm at the Middle Estuary site in 2017 to 999 ± 18 µm at the Lower Estuary in 2016 (Table 2, Fig. 5A). There was a significant site × year interaction ($F_{4,298} = 2.509$, p = 0.04), although Tukey's post hoc pairwise tests did not indicate significant pairwise differences existed between years or across sites. Similarly, significant differences were not observed in mean otolith radii 3 d prior to ocean entry between years or across sites. Mean otolith radii ranged from 949 ± 15 µm at the Middle Estuary in 2017 to 1039 ± 18 µm at Lower Estuary in 2016 (Table 2, Fig. 5B). There were no significant interactions ($F_{4,305} = 2.19$, p = 0.07), main effects of year ($F_{1,305} = 2.35$, p = 0.12), or main effects of site ($F_{4,305} = 0.64$, p = 0.64).

3.3. Growth selection

3.3.1. Mid–late April (15–29 April)

Otolith growth rates during mid–late April were fastest for fish collected in the ocean in 2017. These results are supported by the significant year × site
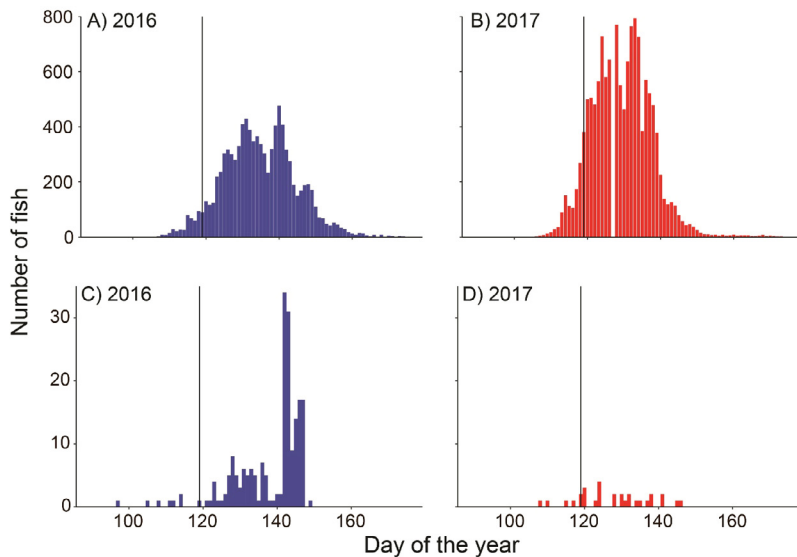
Fig. 3. (A,B) Total number of PIT-tagged Interior Columbia River spring Chinook salmon passing Bonneville Dam and (C,D) number of individuals caught in this study entering the ocean on each calendar day in 2016 and 2017. Dates of ocean entry were calculated from the Sr:Ca ratios in otoliths of fish caught in the ocean. Bonneville passage data was obtained from Columbia River DART (www.cbr.washington.edu/dart/query/pit_obs_hrt). Vertical lines: 15 April
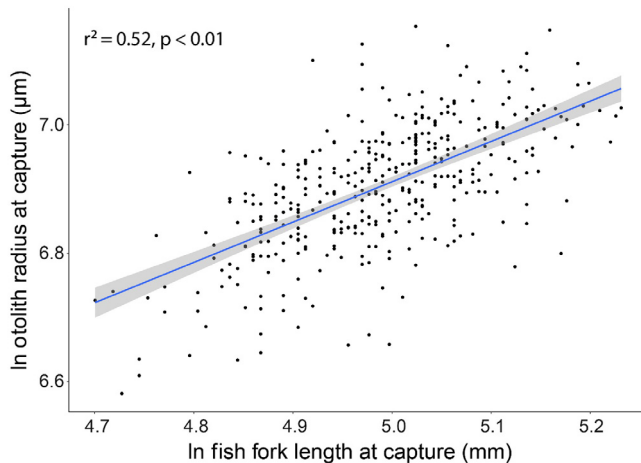

Fig. 4. Relationship between ln-transformed fork length at capture and ln-transformed otolith radius at capture of all Interior Columbia River spring Chinook salmon used in this study with an ocean residence time <5 d

interaction in the linear mixed model ($F_{1,328}$ = 12.3, p < 0.01; Table S2). Mean daily increment widths, a proxy for somatic growth, of fish caught in the ocean in 2017 were wider (2.08 ± 0.3 µm d^{-1}) than those caught in the LCRE (1.79 ± 0.02 µm d^{-1}) (p < 0.01; Table 3, Fig. 6, Table S3). In 2016, however, no significant differences in otolith growth rates existed between fish caught at each location (p = 0.84). Fish caught in the ocean in 2017 displayed significantly

faster otolith growth rates over this period than those caught in the ocean in 2016 (p < 0.01), whereas no differences in growth rates were observed between years in the LCRE (p = 1.0).

When somatic growth rate was estimated from differences in mean otolith growth between 15 and 19 April, we observed that fish caught in the LCRE in 2016 grew approximately 0.09 mm d^{-1} faster (1.54 mm d^{-1}) than fish caught in the ocean (1.45 mm d^{-1}). In 2017, estimated mean somatic growth rates of fish caught in the LCRE (1.40 mm d^{-1}) were 0.15 mm d^{-1} slower than fish caught in the ocean (1.65 mm d^{-1}).

3.3.2. Two weeks prior to ocean entry (17–3 d prior to ocean entry)

A significant interaction effect existed between year and site in the linear mixed model investigating otolith growth rates prior to ocean entry ($F_{1,323}$ = 19.20, p < 0.001; Table S2). In 2017, otoliths of fish caught in the ocean grew faster (2.08 ± 0.03 µm d^{-1}) over the 2 wk period prior to ocean entry than those caught in the LCRE (1.79 ± 0.02 µm d^{-1}; p < 0.01). In 2016, however, no differences in otolith growth rate were observed over this period (p = 0.99; Table 3, Fig. 6). Interannual comparisons of otoliths from fish caught in the ocean revealed that individuals grew significantly faster in 2017 than in 2016 (p < 0.01). Comparisons of otoliths of fish caught in the LCRE, however, did not exhibit any interannual differences in growth rate prior to ocean entry (p = 0.83).

In 2016, when mean otolith growth rate during this 2 wk period was translated to somatic growth rate, fish caught in the LCRE and the ocean displayed almost identical growth (1.42 and 1.43 mm d^{-1} respectively). In 2017, however, the estimated mean somatic growth rates of fish caught in the LCRE (1.49 mm d^{-1}) was 0.19 mm d^{-1} slower than fish caught in the ocean (1.68 mm d^{-1}).

3.3.3. Seven days prior to ocean entry

Fish caught in the ocean in 2017 exhibited faster otolith growth rates during the 7 d prior to ocean entry than fish caught in the Lower Estuary (Table 3, Fig. 7). In 2016, however, fish caught in the ocean
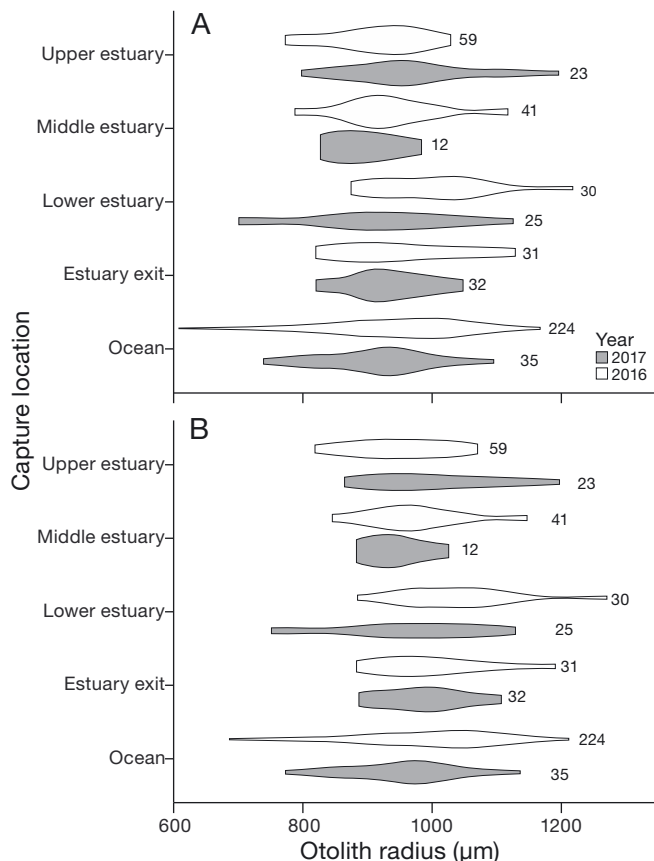
Fig. 5. Distribution of otolith radii of juvenile Interior Columbia River spring Chinook salmon (A) on 15 April and (B) 3 d prior to ocean entry. Fish were caught at sites in the Lower Columbia River and Estuary and in the ocean. Bar width represents the distribution of sizes; numbers adjacent to each bar: sample size

Between years, growth rates were similar for fish caught in the estuary in both years, but back-calculated estuary growth rates differed substantially for Chinook salmon caught in the ocean, with higher growth rates prior to ocean entry in 2017. Similar growth rates 7 d prior to ocean entry were observed between the ocean and the Lower Estuary in 2016.

When mean otolith growth rates over the 7 d prior to ocean entry were translated to somatic growth rates, fish caught at Estuary Exit in 2016 displayed mean growth rates of 0.10 mm d^{-1} faster (1.51 mm d^{-1}) than those caught in the ocean (1.41 mm d^{-1}). In 2017, however, fish caught in the LCRE displayed somatic growth rates which were approximately 0.16 mm d^{-1} slower (1.42 mm d^{-1}) than fish caught in the ocean (1.68 mm d^{-1}).

3.4. Environmental conditions

3.4.1. River conditions

The 2016 river temperatures were above the long-term averages (1995–2015) (Fig. 8A), whereas in 2017 temperatures were similar to or below this average. During juvenile migration, between 9 April and 30 June, temperatures in the river averaged 1.7°C higher in 2016 (14.7°C) than in 2017 (13.0°C). River flow rates in 2016 were lower than in 2017. In 2016, flow rates were below the long-term average (1969–2015), whereas in 2017 they were above these averages (Fig. 8B).

3.4.2. Ocean conditions

Overall, indicators of ocean condition were similarly poor for salmon survival in both years, including copepod community composition, the biomass of northern copepods, and the ichthyoplankton assem-

had the same pre-ocean entry growth rate as those caught in the Lower Estuary. These differences are demonstrated by the presence of significant interactions between site and year in the linear mixed model ($F_{1,221} = 14.18$, p < 0.01; Table S2) and significant pairwise least squared means comparisons (Table S4).

Table 3. Mean (±SE) daily otolith growth (µm) of yearling Interior Columbia River spring Chinook salmon in early April (15–29), prior to ocean entry (from 17–3 d before ocean entry [OE]) and during Lower Columbia River and Estuary (LCRE) residence (7 d prior to OE) in 2016 and 2017. (–) not applicable

| Site	15–29 April		17–3 d before OE		7 d before OE	
	2016	2017	2016	2017	2016	2017
Upper Estuary	1.88 ± 0.08	1.86 ± 0.12	1.70 ± 0.08	1.66 ± 0.12	–	–
Middle Estuary	1.70 ± 0.10	1.73 ± 0.17	1.59 ± 0.10	1.73 ± 0.15	–	–
Lower Estuary	1.74 ± 0.12	1.95 ± 0.12	1.61 ± 0.11	1.87 ± 0.12	–	–
Estuary Exit	1.72 ± 0.13	1.71 ± 0.09	1.81 ± 0.15	1.69 ± 0.15	1.81 ± 0.14	1.65 ± 0.01
Combined LCRE caught fish	1.82 ± 0.01	1.79 ± 0.02	1.68 ± 0.02	1.76 ± 0.01		
Ocean	1.70 ± 0.01	2.08 ± 0.30	1.66 ± 0.04	2.09 ± 0.10	1.64 ± 0.04	2.09 ± 0.11
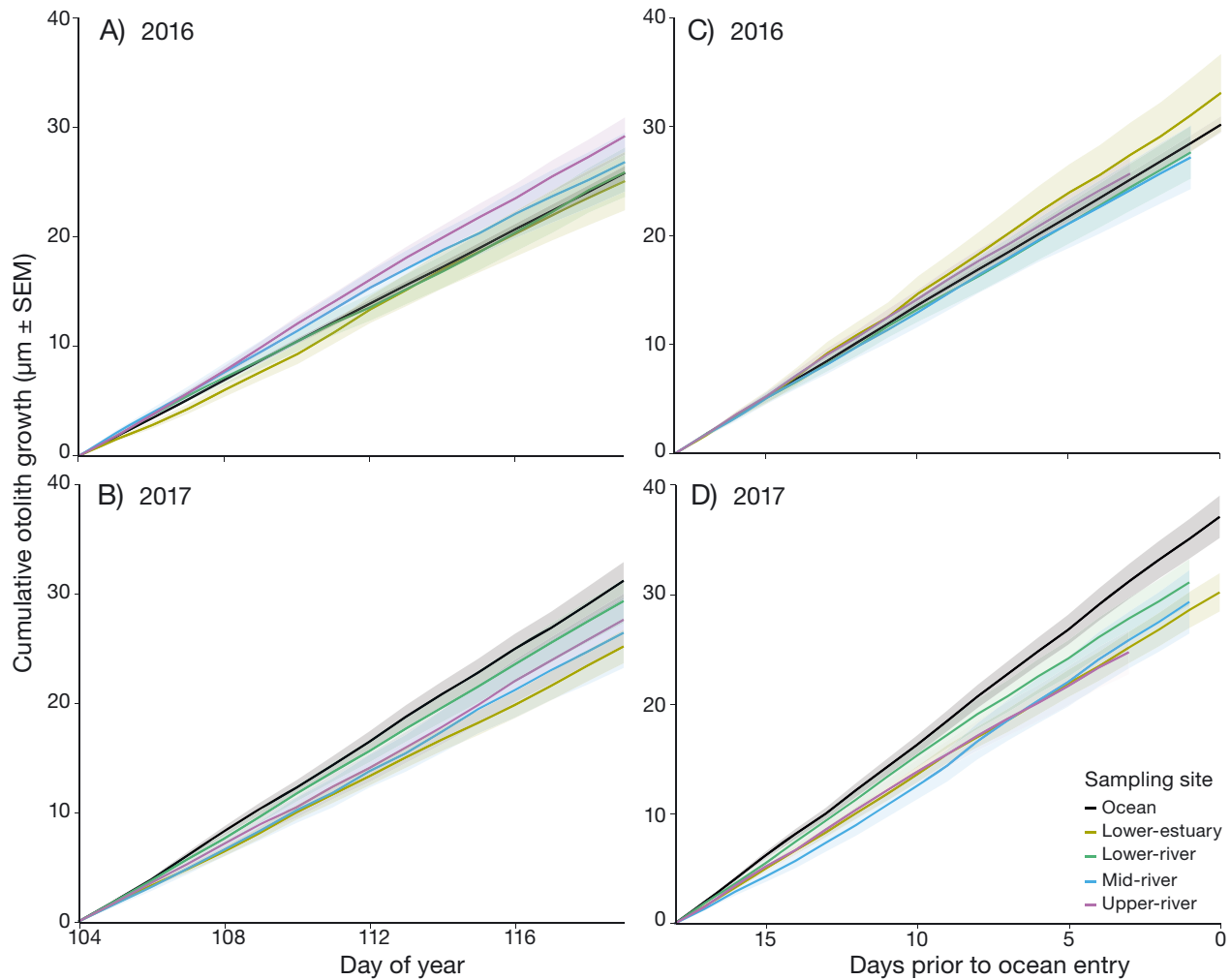
Fig. 6. Cumulative otolith growth of juvenile Interior Columbia River spring Chinook salmon caught in the Lower Columbia River and Estuary and ocean in early April (15–29) (A) 2016 and (B) 2017 and 17 d prior to marine entry in (C) 2016 and (D) 2017. On average, fish were (A) 23 d prior to ocean entry (range: 41 d prior to 11 d post) and (B) 28 d prior to ocean entry (range: 44 d prior to 22 d post)

blage. Over the 23 yr time series monitoring ocean conditions (Peterson et al. 2019), the overall rank of ocean conditions was lower in 2016, at 19th, compared to 2017, which was 17th. The greatest difference observed during the spring of 2016 and 2017 was the mean CPUE (fish km^{-1} towed) of yearling Chinook salmon in late June: 2017 had the lowest CPUE for all yearling Chinook salmon stocks combined for the prior 22 yr. For Interior Columbia River Chinook salmon, mean CPUE was an order of magnitude higher in 2016 (2.0 ind. km^{-1} towed) than in 2017 (0.3 ind. km^{-1} towed). However, stock-specific catches within the LCRE were similar in 2016 and 2017.

Between 2000 and 2019, SARs for wild Snake River spring/summer Chinook salmon ranged from 0.40–4.94%, whereas for hatchery populations, SARs ranged from 0.15–8.4%. Although SARs were low for both wild and hatchery fish in 2016 and 2017, survival was consistently greater in 2016 (wild: 0.69%; hatchery: 1.39%) than 2017 (wild: 0.42%; hatchery: 0.90%).

4. DISCUSSION

Due to the inherent logistical challenges of repeatedly sampling cohorts of migratory fish populations over broad spatial scales, our study is one of few to directly examine selective mortality in a salmon population as fish move from freshwater through estuarine habitats to early marine residence. Our 'follow the cohort' approach is the first to directly examine how
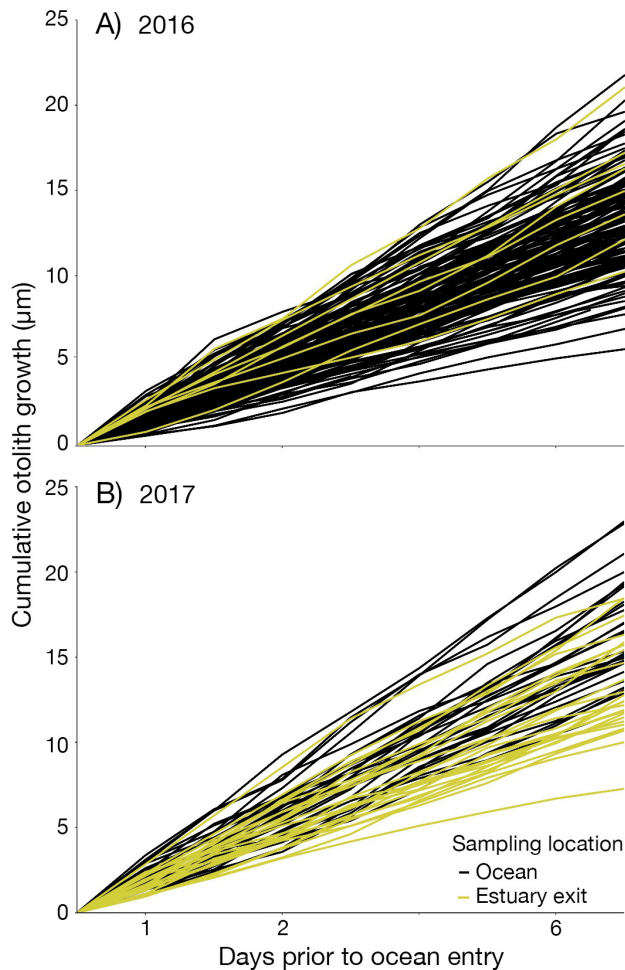
Fig. 7. Individual otolith growth of Interior Columbia River spring Chinook salmon over the 7 d prior to ocean entry of individuals caught in the lower estuary and in the ocean in (A) 2016 and (B) 2017
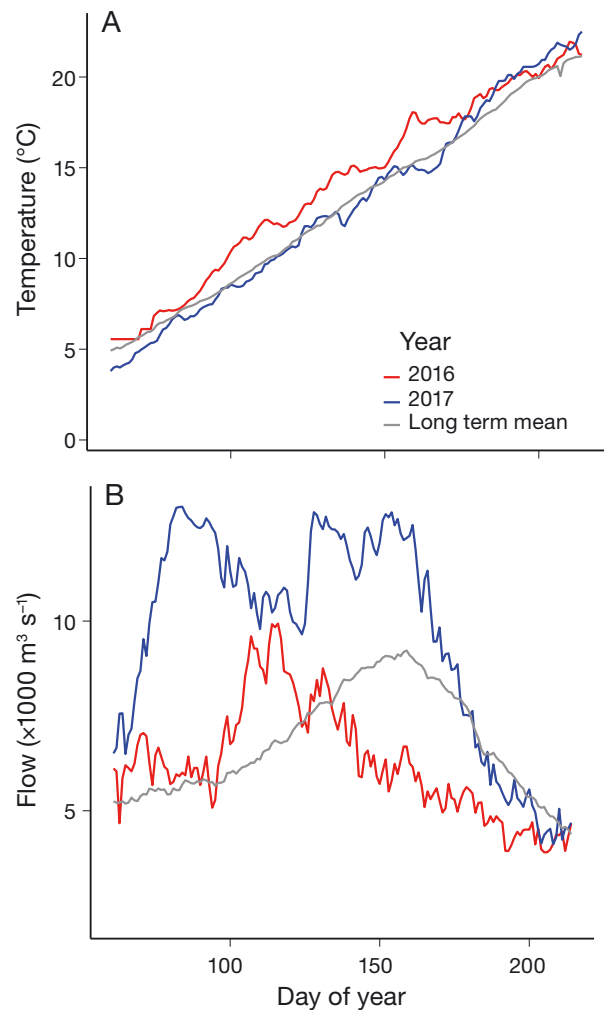

Fig. 8. Daily (A) temperature and (B) flow rates as measured below Bonneville Dam in 2016 and 2017 compared to long-term means for temperature (1995–2015) and flow (1969–2015) at this site

growth- and size-selective mortality may affect threatened and endangered juvenile Interior Columbia River spring Chinook salmon during this transition from freshwater to marine residence. Our study builds upon previous work that focussed on a single location within the LCRE or only in the ocean (e.g. Tomaro et al. 2012, Claiborne et al. 2014, J. A. Miller et al. 2014). We posit that our results demonstrate selective mortality of fish during early ocean residence in 2017 but not in 2016. Specifically, fish caught in the ocean in 2017 grew significantly faster prior to ocean entry than those caught in 2016. The finding that selection occurred in the marine environment, but was related to growth rates in freshwater, demonstrates the existence of potential freshwater–marine carryover effects. These results highlight the importance of considering both marine and freshwater factors in management plans for this species.

A parsimonious explanation for our results is that in 2017, fish that were growing slower during freshwater residence experienced increased mortality during early marine residence, which resulted in higher mean apparent growth rates of the surviving sampled population. This hypothesis is supported by differences in CPUE between years and in SARs. CPUE, which is an indicator of the abundance of individuals, in the LCRE was relatively stable between 2016 (mean: 2.7 fish haul^{-1}) and 2017 (mean: 1.9 fish haul^{-1}) (Weitkamp et al. 2020). CPUE in the ocean, however, was notably lower in 2017 (0.3 fish m^{-2}) than in 2016 (2.1 fish km^{-1} towed). These differences in ocean CPUE between years indicate that higher mortality, possibly driven by predation, occurred during early marine residence in 2017 (Beamish & Mahnken 2001, Emmett & Sampson

2007, Phillips et al. 2021). The differences in mean growth rate prior to ocean entry between years indicate that this mortality disproportionately affected slower growing individuals. While differences in CPUE may be due to other factors — such as ocean residence time, with fish being present in the ocean longer in 2017, or migration behaviour, with fish of different sizes migrating at different times — low CPUE occurred in the same year as low SARs were observed. The relationship between low CPUE and low SARs supports the hypothesis that significant mortality occurred during early ocean residence. Although it is not possible to directly attribute low survival to selective mortality, the finding of evidence for growth-selective mortality in 2017, which also had lower overall survival, adds to previous research suggesting that the demographic impacts of selective mortality are clearer when overall survival is lower (Emmett & Sampson 2007, Woodson et al. 2013).

The finding that growth-selective mortality occurred during early ocean residence, but that this selection was related to growth in freshwater, illustrates the potential for freshwater–marine carryover effects of growth. This study is the first to demonstrate potential carryover effects from growth in freshwater immediately prior to ocean entry in Interior Columbia River spring Chinook salmon. Our results add to a growing body of evidence indicating that conditions experienced in freshwater, such as migration history (in-stream vs. barged), ocean arrival time, or size at ocean entry, can affect survival in the ocean (Russell et al. 2012, Brosnan et al. 2016, Chasco et al. 2021). Our results also support previous findings that indicate the strength of carryover effects can vary based on both extrinsic and intrinsic factors. Chasco et al. (2021), for example, used PIT-tag-based ocean entry and survival data to demonstrate that wild Snake River spring/summer runs of Chinook salmon that passed over Bonneville Dam earlier, and thus were assumed to have entered the ocean earlier, experienced higher survival. Clear correlations between the arrival timing and ocean survival of individuals originating from hatcheries, however, did not exist. Similarly, Gosselin et al. (2018) showed that interacting environmental (Pacific Decadal Oscillation) and individual (hatchery vs. wild) factors modulated the impact of carryover effects from migration history on survival in the marine environment. These varying effects highlight the importance of a clear understanding of environmental factors that may result in carryover effects of size and growth and emphasise the importance of examining these effects over multiple years.

Growth before and after ocean entry are likely to positively covary. This covariance in growth rates may be the mechanism by which faster growth in freshwater carries over to higher survival during early marine residence. The preferential survival of faster growing individuals is often attributed to the survival advantage gained by reaching larger sizes sooner (Takahashi et al. 2012, Fennie et al. 2020, Khamassi et al. 2020). Thus, if fish are able to attain faster growth rates in freshwater and maintain these growth rates in the marine environment, size in the ocean may be the trait on which selection pressures directly act. However, faster growing individuals do not always have a size advantage, with negative size-selective mortality or selection for growth in the absence of size being observed in some cases (Sponaugle et al. 2011, Takahashi et al. 2012). While a size advantage gained during early marine residence from faster growth in freshwater could have resulted in the observed differences in ocean survival, we did not directly detect evidence of size selection in mid-April or immediately prior to ocean entry. This lack of evidence for size selection indicates that growth rate selection likely occurred independently of size.

Differential survival of faster growing fish could be related to traits that positively covary with growth. For example, fish caught in the ocean in 2017 exhibited higher Fulton's condition index than those caught in 2016. Faster growing fish may be able to better avoid predators by being in better physiological condition (Takasuka et al. 2003, 2007) or by exhibiting behavioural differences (Jørgensen et al. 2014). Selective predation on fish in lower condition has previously been observed in migrating salmon, both in conjunction with size selection and regardless of individual size (Hostetter et al. 2012, Tucker et al. 2016). The physiological condition of an individual may affect predation vulnerability by altering swimming behaviour, responses to predation attempts, or escape activities (Chick & Van Den Avyle 2000, Grorud-Colvert & Sponaugle 2006, Silva et al. 2014). Behavioural differences between fish growing at different rates may include differences in risk taking or differences in schooling behaviour (Hoare et al. 2000, Jørgensen et al. 2014). Lower condition may also be a sign of infection, which may reduce individual fitness (K. M. Miller et al. 2014, Furey et al. 2021). Thus, interannual differences in predation pressure combined with the selection for faster growing individuals, which were in better condition, may have contributed to our observed differences in presumed selective mortality.

Predation pressure on juvenile salmon during early marine residence may be influenced by several factors, including the availability of alternative prey for predators such as seabirds and piscivorous fish, and the dynamics of the CRP (Emmett & Sampson 2007, Brosnan et al. 2014, Phillips et al. 2021). The alternative prey hypothesis proposes that there is a negative relationship between the availability of species such as coastal pelagic forage fish, juvenile rockfish, or squid and predation pressure on juvenile salmon (Emmett & Sampson 2007, Phillips et al. 2017). Salmon comprise a smaller proportion of predators' diets when the abundance of these species is higher, therefore reducing pressure on salmon smolts, which are of a similar size to these species (Emmett & Sampson 2007, Emmett & Krutzikowsky 2008, Phillips et al. 2021). Although potential alternative prey in the LCRE was an order of magnitude lower in 2016 than in 2017 (Weitkamp et al. 2020), catches of alternative prey in the ocean such as California market squid, juvenile rockfish, and Pacific herring in the marine surveys were all significantly higher in 2016 than in 2017 (Morgan et al. 2019). This lack of alternative prey in 2017 may have increased predation pressure on juvenile Chinook salmon, thereby resulting in selection for faster growing individuals.

The dynamics of the CRP can also influence predation pressure on juvenile salmon. Although the turbid nature of the CRP may provide refugia from visual predators (Vogel & Beauchamp 1999, Hansen et al. 2013), it may also attract and aggregate predators (Brosnan et al. 2014, Zamon et al. 2014). As the morphology and orientation of the CRP can vary over short temporal scales (Hickey et al. 1998, Jay et al. 2009), it is important to understand the CRP at the time of ocean entry of juvenile salmon. The high river flows in 2017 resulted in a large plume, which is thought FF spread predators over larger spatial scales and therefore reduce predation pressure on juvenile salmon (Zamon et al. 2014, Phillips et al. 2017). Our results, however, suggest high predation pressure may have existed in 2017. At the time of ocean entry, the CRP may have been oriented northwards and along the Washington coast due to southwest winds and downwelling conditions (Hickey et al. 2005, Thomas & Weatherbee 2006). These conditions would have resulted in individuals spending more time in the CRP as they moved north, which increases the length of time exposed to predators in the CRP and increased predation pressure (Brosnan et al. 2014, Phillips et al. 2021).

There are several possible interacting environmental and individual factors that may have contributed to the differences in observed growth between individuals that survived and those that did not. Intrinsic differences in growth rates between individuals or populations, for example, can be driven by factors such as variation in metabolic rates, maternal provisioning, and genetic differences (Arnott et al. 2006, Beldade et al. 2012, Garrido et al. 2015). Environmental conditions such as temperature and food availability as well as hatchery practices may also affect freshwater growth rates (Todd et al. 2008, Russell et al. 2012, Beckman et al. 2017). Interactions between these intrinsic differences in growth and environmental conditions, however, likely drove observed differences in growth rates (Beckman et al. 1999, Connor & Tiffan 2012, Nelson et al. 2019). Variation in habitat utilisation as individuals moved downriver may have impacted observed differences in growth rates. The difference in selection intensity, defined as differences in growth rates between the survivors and non-survivors (Takahashi et al. 2012), was greater in the 2 wk prior to ocean entry than over the period in mid–late April. This finding implies that while growth rates early in downstream migration were important in 2017, growth in the period immediately prior to ocean entry likely had a larger impact on survival during early marine residence. During the 2 wk period prior to ocean entry, fish were likely to be in the mainstem of the Columbia River. This location estimate is based on median migration rates from Lower Granite Dam (in the lower Snake River) to Bonneville Dam, which ranged from 10–17 d in both years (Faulkner et al. 2017, Widener et al. 2018). The majority of the 7 d period prior to ocean entry likely consists of residence in the LCRE (Morris et al. 2017, 2018, Morrice et al. 2020).

As the location inhabited by juvenile salmon has a large impact on their growth rates (Chittaro et al. 2018), management actions that promote growth of individuals in the mainstem of the Columbia River may enhance their survival during early ocean residence. The restoration of hydrological connectivity of tidal wetland in the LCRE, for example, is the target of intensive efforts to benefit juvenile salmon (Naiman et al. 2012, Bond et al. 2019). This restoration has been shown to improve the quantity and quality of prey exported to the mainstem, therefore providing more opportunities for growth (L. A. Weitkamp et al. unpubl. data). In years with low survival and apparently intense selection, such as 2017, small differences in growth or body condition due to more favourable habitat in the mainstem Columbia River could confer a survival advantage for these vulnerable interior spring Chinook salmon populations.

It is important to interpret the results of this study in the context of environmental differences between years. Although SARs were higher in 2016 (1.18%) than in 2017 (0.76%), both years were below the rebuilding target of 2–6% set by the Northwest Power and Conservation Council's Fish and Wildlife Program for the recovery of these populations (McCann et al. 2018). As we only detected evidence for selective mortality in 2017, a year with some of the lowest SARs on record, this underscores questions of which environmental conditions affect the survival of individuals and what impacts are important. While conditions in the ocean were relatively consistent and poor between years, conditions in the LCRE differed significantly. Higher river flow rates and lower water temperatures existed in 2017, which are considered more favourable conditions for the survival of smolts (Quinn 2005, Morrice et al. 2020). Stomach fullness of fish caught in the LCRE was also higher in 2017 than 2016, and the levels of insulin-like growth factor 1, which is positively related to growth, were also higher in 2017 (L. A. Weitkamp et al. unpubl. data). Despite the favourable conditions in the LCRE in 2017, overall survival (as measured by SARs) was 30% lower than in 2016, and there was evidence for growth-selective mortality soon after ocean entry. These interannual differences highlight the fact that good river conditions are necessary, but not wholly sufficient, for high juvenile Chinook salmon survival. Our results indicate that in a year with very poor ocean survival, an individual's prior experience (growth in this case) could influence their early marine survival.

4.1. Caveats

This study relied on several important assumptions. It is important that fish caught in the ocean accurately reflect the same portion of the out-migrating population as fish caught in the LCRE. In 2017, ocean fish were caught further north and entered the ocean earlier, thus resided in the ocean longer than fish caught in 2016. This longer ocean residence time may have provided more opportunity for selective mortality to occur through longer exposure to selective pressures. However, in 2016 there was no spatial pattern in freshwater growth rates of fish collected in the ocean. Combined with the similar CPUE in the LCRE and lower SARs in 2017, this supports our conclusion that interannual differences in selection pressure occurred. It is also important to consider that although CPUE is considered a metric of juvenile abundance in the area covered by the oceanic sur-

veys, these surveys are snapshots in large landscapes. Thus, CPUE may be impacted by variations in migration patterns and sampling locations.

4.2. Conclusions

This research demonstrates that yearling Interior Columbia River spring Chinook salmon that grew faster during downriver migration were more likely to survive early ocean residence in 2017. However, in 2016 we did not observe evidence of a survival advantage associated with faster growth over this period. Several factors contribute to the conclusion that selection for faster growth prior to ocean entry occurred in 2017 but not in 2016: (1) faster growth prior to ocean entry was observed in fish that were caught in the ocean relative to those caught in the LCRE in 2017, but not 2016; (2) CPUE during the LCRE surveys was similar in both years but CPUE during 2017 ocean surveys was the lowest of the prior 22 yr, which suggests high mortality occurred soon after ocean entry; (3) overall survival (SARs) was lower in 2017 than 2016. The finding that survival in the ocean was at a record low in 2017 despite freshwater conditions that were favourable for salmon survival (e.g. high flow, low temperatures) highlights the need to understand the influence of conditions both before and after ocean entry on the survival of threatened Chinook salmon. Overall, these results stress the relationships between freshwater growth and ocean survival and add to evidence that freshwater–marine carryover effects exist for this species.

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