ARTICLE

Freshwater Ecology

Riverscape heterogeneity in estimated Chinook Salmon emergence phenology and implications for size and growth

Matthew J. Kaylor[1] | **Jonathan B. Armstrong**[1] | **Joseph T. Lemanski**[2] | **Casey Justice**[3] | **Seth M. White**[3]

[1]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[2]Oregon Department of Fish and Wildlife, La Grande, Oregon, USA

[3]Columbia River Inter-Tribal Fish Commission, Portland, Oregon, USA

Correspondence
Matthew J. Kaylor
Email: matthew.kaylor@oregonstate.edu

Abstract

Many salmonid-bearing rivers exhibit thermal and hydrologic heterogeneity at multiple spatial and temporal scales, but how this translates into spatiotemporal patterns of fry emergence is poorly understood. Understanding this variability is important because emergence timing determines the biophysical conditions fish first experience (e.g., temperature, flow, and food supply), thereby influencing growth opportunities and survival during this critical life stage. We predicted spring Chinook Salmon (*Oncorhynchus tshawytscha*) emergence phenology across four northeastern Oregon subbasins over 5–9 years using empirical spawning and temperature data. We then related interannual emergence timing estimates to juvenile salmon size and growth rates at consistent sampling locations. There were clear longitudinal patterns of predicted emergence timing in each subbasin: The shape of these patterns was consistent among years, but not among subbasins. In two subbasins, emergence occurred progressively later with distance upstream, whereas in the other two subbasins emergence was earliest at upstream sites. Within each year, median emergence dates among sites within each subbasin ranged between 44 and 58 days. This spatial variation was comparable to interannual variation, with median emergence dates for a given location in each subbasin ranging between 47 and 74 days among years. Contrary to our expectations, juvenile salmon were not larger in years with earlier emergence, owing to slower estimated spring and summer growth rates compared to years with later emergence. Despite large interannual variation in estimated emergence dates, these results suggest that other factors (e.g., stream flow, temperature, and density-dependence) were more important than growth duration in determining juvenile salmon growth rates and size among years. We demonstrated considerable spatial and interannual variation in emergence phenology within these subbasins. Understanding how this variation translates to spatiotemporal patterns of juvenile salmon habitat use, growth, and survival has important implications for guiding restoration efforts and understanding how climate change may impact these populations.

INTRODUCTION

Temperature is a fundamental control on aquatic ecosystems, influencing physiological rates, animal behavior, species distributions, and community composition (Caissie, 2006). A key challenge is to understand how spatial and temporal patterns of temperature, that is, thermal regimes, mediate population processes. Temperature effects on salmonids have been well studied given the importance and sensitivity of these cold-adapted fishes (Beauchamp, 2009; Richter & Kolmes, 2005), with particular emphasis on relating responses such as distribution and survival to summer thermal regimes (Isaak et al., 2015; Lusardi et al., 2020). Yet, spatial temperature patterns during cooler seasons may shape important population responses such as growth rates, movement patterns, and incubation rates (Armstrong et al., 2021; Kaylor et al., 2021; McMeans et al., 2020), with effects carrying over to other seasons and life stages (Armstrong et al., 2010). Salmonid embryos typically incubate during this understudied portion of the thermal regime and development rates are largely controlled by temperature, thereby influencing the timing of hatching and emergence (Beacham & Murray, 1990). Emergence timing determines growth duration and the biophysical conditions (e.g., flow, food availability, and habitat access) experienced during early life stages, with important implications for survival and growth opportunities (Egglishaw & Shackley, 1977, Kaylor et al., 2021). While studies have compared emergence timing among rivers and populations (Adelfio et al., 2019; Austin et al., 2019; Campbell et al., 2019), it is unclear whether, and to what degree, emergence timing may vary at finer spatial scales such as within subbasins representing single populations.

Emergence timing has important, but context-dependent, implications for growth and survival (Skoglund et al., 2012). Earlier emerging individuals have more time to grow, and if conditions are suitable, they may achieve larger size than later emerging individuals (Egglishaw & Shackley, 1977). These early growth opportunities may have positive feedback on growth and survival in later life stages, for example, if there are size thresholds for consuming pulsed subsidies (Armstrong et al., 2010), if larger individuals have competitive advantages (Einum & Fleming, 2000), or if prior residence favors foraging opportunities (Harwood et al., 2003; O'Connor, 2000). However, there may also be disadvantages to emerging early. Emergence prior to high flows can reduce survival

of newly emerged fry (Jensen & Johnsen, 1999) as well as produce mismatches between emergence and optimal conditions for growth (i.e., temperature, prey availability, and foraging ability), which may further reduce survival (Jones et al., 2015). In addition, earlier emerging fish may experience stronger predation and thus reduced survival (Brannas, 1995). Given the advantages and risks associated with variation in emergence timing, adult spawn timing is thought to evolve to promote emergence aligned with local long-term average optimal conditions for juvenile fitness (Webb & Mclay, 1996).

Thermal heterogeneity across landscapes can generate spatial patterns of emergence phenology in multiple ways. For populations spawning in summer or fall, temperatures during this period can affect migration and spawning phenology, influencing when incubation begins (Beer & Anderson, 2001). Subsequent temperatures during the egg incubation period (generally fall–spring) determine development rates across landscapes. Lastly, temperatures in winter and spring influence juvenile rearing conditions and the profitability of emerging at different times. How these compounding thermal effects translate into spatial patterns of emergence depends on the relative strength of selection pressures across the spawning-to-juvenile life stages and how they vary across space. In theory, emergence timing matches peaks in juvenile rearing opportunity (Webb & Mclay, 1996). If the onset of optimal juvenile rearing conditions is homogenous across the landscape, then emergence phenology should be relatively synchronized, and spawning phenology should vary across space to compensate for heterogeneity in temperature and incubation rates (Campbell et al., 2019). Conversely, if juvenile rearing conditions peak asynchronously, or if there is high interannual variation in environmental conditions, emergence may be asynchronous, and patterns of spawning will depend on the correlation between incubation temperatures and juvenile rearing dynamics (Abrey, 2005). However, a third possibility is that emergence phenology is suboptimal due to overriding constraints on spawning phenology, for example, if avoidance of warm temperatures delays spawning such that emergence occurs after peak juvenile rearing conditions (Beer & Anderson, 2001; Crossin et al., 2008). Due to the logistical challenge of quantifying spawning and emergence phenology across landscapes, our understanding of these dynamics remains limited.

We characterized landscape heterogeneity in emergence phenology in temperate rivers where water

temperatures varied longitudinally throughout the adult spawning and subsequent incubation periods. Specifically, we estimated spring-run Chinook Salmon (*Oncorhynchus tshawytscha*) emergence phenology over 5–9 years within four northeastern Oregon subbasins using empirical spawning survey data, annual temperature data from multiple locations in each subbasin, and models relating incubation temperatures to development rates. We then used data from juvenile Chinook Salmon sampling in each year to relate interannual emergence timing predictions to fish size and growth rates. Our goals were to (1) evaluate spatial patterns of predicted emergence within and among subbasins, (2) evaluate interannual variation in emergence timing, and (3) relate interannual emergence estimates at defined locations to juvenile salmon size and growth.

METHODS

Study area

We conducted this study in four northeastern Oregon subbasins (Figure 1). Three of the subbasins—Catherine Creek (CC; 1051 km^2), the upper Grande Ronde River (UGR; 1896 km^2), and the Minam River (MIN; 618 km^2)—are tributaries of the Grande Ronde River, which flows northward to its confluence with the Snake River. The Middle Fork John Day River (MFJD; 2051 km^2), with its origins in close proximity to those of the Grande Ronde River, flows northwest into the John Day River before reaching the Columbia River. The region is characterized by hot, dry summers and cool, wet winters with the majority of precipitation occurring as snow during winter months, resulting in snowmelt-driven peak stream flows in spring. The drainages of MJFD (maximum elevation: 2478 m) and UGR (maximum elevation: 2414 m) originate from the lower elevation Blue Mountains, whereas CC (maximum elevation: 2640 m) and MIN (maximum elevation: 2791 m) drain higher elevations of the Wallowa Mountains. Snowmelt and associated peak flows typically occur earliest in MFJD, followed by UGR, CC, and MIN, respectively.

Numerous factors including habitat degradation, hydropower operations, altered predation, and overfishing have contributed to declines of returning spring Chinook Salmon in the Snake River basin (which includes the Grande Ronde basin), prompting the listing of this stock as threatened under the Endangered Species Act (NOAA, 2008). As part of recovery efforts, there is a history of hatchery supplementation in CC and UGR, with collection of local brood stock beginning in the late 1990s (Feldhaus et al., 2018). The Minam River flows through
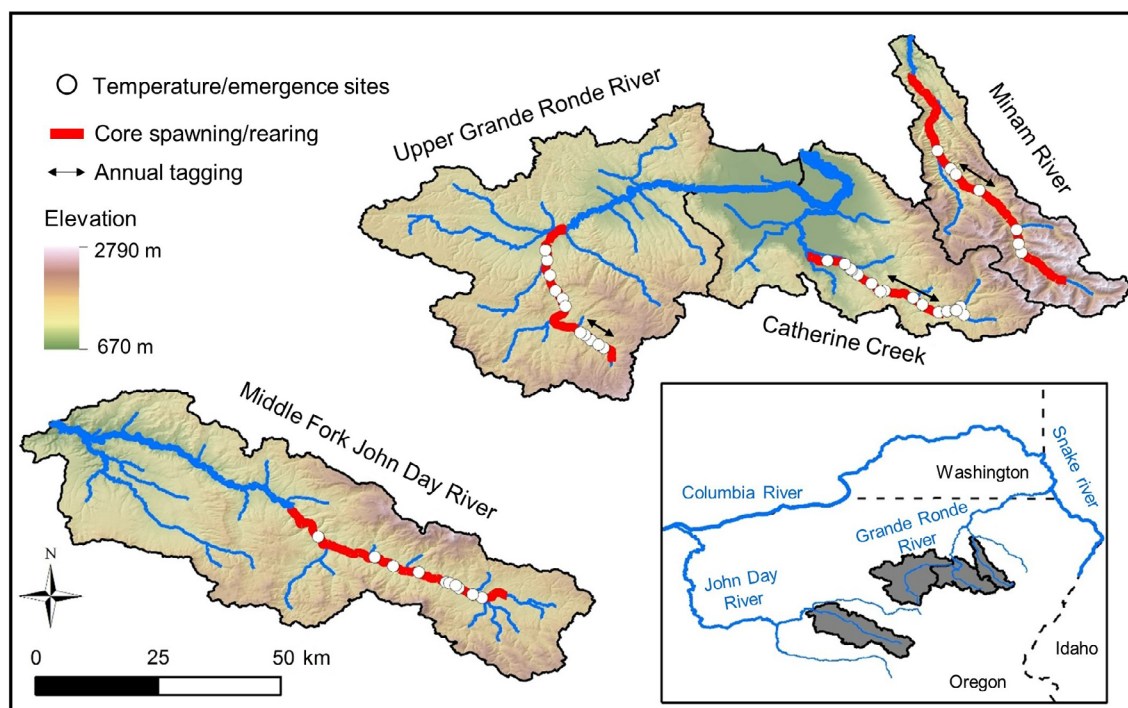

FIGURE 1 Map of study sites located within four northeastern Oregon subbasins. Open points represent sites with annual temperature data in which emergence timing was predicted (see Appendix S1: Table S1 for additional details). Areas indicated in red represent core spawning and rearing extents of each river. Arrows indicate areas in which annual capture and tagging of juvenile Chinook Salmon occurred (not available for the Middle Fork John Day River).

the Eagle Cap Wilderness and has undergone less habitat degradation (White et al., 2017) and no hatchery supplementation. Spring Chinook Salmon are not listed within the MFJD, and no hatchery supplementation has occurred. Across all four subbasins, adult Chinook Salmon enter natal tributaries from spring to early summer and spawn between mid-August and late September. Spawning typically occurs earlier in cooler, upstream sections and later in warmer downstream sections. Eggs incubate over the fall, winter, and spring and fry emerge from substrates from winter to spring (Kaylor et al., 2021; Lindsay et al., 1986).

Temperature conditions

We collected year-round water temperature data over 5–9 years from 6 to 12 sites spanning large portions of the core Chinook Salmon spawning and rearing extent in each subbasin (Figure 1; Appendix S1: Table S1). Temperature was collected using Onset Hobo Pro v2 and Tidbit data loggers recording at 60-minute intervals attached to the stream bottom (Dunham et al., 2005). Sufficient annual temperature data to estimate emergence timing were available for 9 years in CC and UGR (spawn years 2011–2019), 5 years in MIN (spawn years 2015–2019), and 7 years in MFJD (spawn years 2012–2018). We assumed that water temperatures measured by data loggers were representative of the incubation environment in the gravel below, as surveyors usually observed redds (i.e., spawning nests) in the tailouts of riffles, where localized downwelling of water oxygenates embryos (Baxter & Hauer, 2000).

Spawn timing

We modeled spawn timing using spawning survey data collected by a large collaborative group representing Oregon Department of Fish and Wildlife (ODFW) East Region Fish Research, Confederated Tribes of the Umatilla Indian Reservation, Nez Perce Tribe, Confederated Tribes of Warm Springs, and numerous other agencies and volunteers. Annual spawning surveys were conducted semi-continuously throughout each subbasin (some river sections were not accessible) and were typically repeated every 7–10 days over a 3–6-week period, resulting in 2–5 surveys per river section each year (Bare et al., 2015, Brandt et al., 2021; C. Bare, unpublished data). Surveyors recorded newly observed redds and their associated GPS location. Spawning surveys were conducted throughout tributaries of each subbasin, but our analyses only include mainstem survey data to be consistent with locations of

temperature sensors. To assess spatial and temporal patterns in spawn timing within each subbasin, we fit linear models with the observation date of each redd as the dependent variable and river kilometer (Rkm) and year as fixed effects for two separate models: one for Grande Ronde subbasins (UGR, CC, and MIN) and the other for MFJD. We included Grande Ronde subbasins in the same model as they are close in proximity and within the same Chinook Salmon evolutionary significant unit. This improved estimation in years in which redd data in some subbasins were sparse, unavailable in some sections (i.e., upper MIN in 2019 due to wildfires), or spatially clustered (Appendix S1: Figure S1; consistent with Austin et al., 2021). The Grande Ronde model included an interaction between each subbasin and Rkm to allow for different longitudinal patterns. Although longitudinal patterns of spawn timing may vary among years, limited spatial data in low return years (Appendix S1: Figure S1) prohibited us from rigorously evaluating interannual variation in these relationships. We therefore treated spawn year as a categorical fixed effect and did not include an interaction with Rkm (i.e., the intercept varied among years, but slope did not). Although spawning surveys are commonly used to evaluate spawn timing (Austin et al., 2021; Hughes & Murdoch, 2017; Webb & Mclay, 1996), it is important to note that redd observation dates differ from redd construction dates and are only as precise as the frequency of spawning surveys.

Emergence timing

We predicted emergence timing using the relationship between water temperature and incubation development rates developed by Beacham and Murray (1990), but with modifications suggested by Sparks et al. (2019) to better account for variable temperature exposure:

$$E_i = 1/\exp[\log_e a - \log_e(T_i - b)],$$

where E_i is the daily contribution to development (ranging from 0 to 1), T_i is the daily mean temperature (in degrees Celsius), and $\log_e a$ (6.872) and b (−0.332) are coefficients derived from Beacham and Murray (1990). For each location and year, the mean spawn date was predicted as described above. To account for intra-annual variation in spawn timing around the predicted mean spawn date, we used the residual standard error derived from the Grande Ronde (4.64 days) and MFJD (4.01 days) spawn timing models. This translated to 95% of simulated spawn dates at each site and year occurring within an 18-day window for Grande Ronde subbasins and a 16-day window for MFJD. We ran 1000 simulations for each site

and year combination by drawing a random spawn date for each simulation. Daily effective values (E_i) were summed from the selected spawn date, and the predicted emergence date was assumed to occur on the first day that the sum of E_i values exceeded 1.

We evaluated longitudinal patterns of emergence timing in each subbasin by fitting linear models with Rkm as the explanatory variable. Given the potential for nonlinear relationships, we fit simple linear, quadratic, and third-order polynomial models for each subbasin with year as an additive effect. Models were compared using Akaike information criterion adjusted for small sample size (AIC_c; Hurvich & Tsai, 1989), and we selected the model structure with the lowest AIC_c value (Burnham & Anderson, 2004). We then evaluated whether allowing the relationship between Rkm and emergence timing to vary among years improved model fit by fitting the selected models with interactions between year and Rkm.

Fish growth rates

We evaluated relationships between interannual variation in emergence timing and juvenile Chinook Salmon size and growth using annual empirical fish sampling data collected by ODFW in three of the four subbasins where relevant data were available. Each year, juvenile Chinook Salmon were sampled during two time periods: mid-summer in natal rearing areas and in the fall at screw traps located downstream of summer sampling locations (Dowdy et al., 2019). ODFW crews captured and tagged fish within sections of CC (between Rkms 42–48), UGR (Rkms 319–326), and MIN (Rkms 33–38) at the same time of each year, providing consistent methods. However, specific sampling locations within these sections varied in accordance with interannual variation in fish distributions. During summer, juvenile salmon were captured using snorkel-herding in which snorkelers herded fish into a seine net (Tattam et al., 2017). Fish were anesthetized using MS-222 (tricaine methane sulfonate), and individuals larger than 55 mm were tagged with passive integrated transponder (PIT) tags. If undersized fish were captured, a minimum of 15 individuals were measured and the remainder were counted. In fall, fish were captured using rotary screw traps located downstream of tagging locations and checked for PIT tags.

We calculated mean summer and fall weight (including undersized, untagged fish) for all years in which emergence timing estimates were available. We then estimated mass-standardized growth rates (MSGRs; Ostrovsky, 1995) from emergence to summer (hereafter spring) and from summer to fall (hereafter summer):

$$\text{MSGR } (\%\text{day}^{-1}) = \left[\left(W_2{}^b - W_1{}^b \right) / (b \times t) \right] \times 100,$$

where W_1 and W_2 represent fish weight during the first and second sampling event, respectively, t is the number of days, and b is the allometric mass exponent for Chinook Salmon (0.338; Perry et al., 2015). To estimate spring growth rates, we measured W_2 directly, estimated W_1 as 0.5 g based on measured fry mass at emergence from Beacham and Murray (1990), and used the difference between W_2 and W_1 to calculate MSGR (see Kaylor et al., 2021). We used emergence timing estimates corresponding to the specific river sections where fish sampling occurred. To account for variation in emergence timing, we randomly resampled (with replacement) from our emergence estimates for each subbasin and year and calculated MSGR with these different values of t. When multiple temperature sensors, and thus sites of emergence timing predictions, were present within tagging sections, we combined these emergence predictions so that our random sampling occurred across the range of sites within tagging areas. We calculated summer growth rates empirically using summer-tagged individuals that were recaptured at screw traps. We present the mean MSGR and 95% confidence intervals (CIs) of all individuals recaptured between 1 October and 31 November of each year.

We evaluated relationships between annual emergence timing estimates and (1) summer mean size, (2) fall mean size, (3) spring MSGR, and (4) summer MSGR for each subbasin. We then used linear regression models to evaluate potential effects of density dependence and environmental conditions on MSGR. Because distributions of fry are logistically impractical to assess at the scale of our study, we instead used the total number redds from the previous year within tagging areas as a proxy for density dependence, as the number of redds should be strongly associated with the number of juveniles the following year (Pess & Jordan, 2019). We calculated mean spring and summer temperature in each subbasin and year using loggers located within tagging areas. Seasons were defined based on the historical timing of ODFW tagging efforts, with the transition between spring and summer corresponding to the start of the summer tagging event in each subbasin. Specifically, we defined spring as 1 April to 31 July in UGR and MIN, but from 1 April to 30 June in CC because CC parr are consistently tagged in July, whereas UGR and MIN parr are tagged in August. We represented fall as 1 August to 31 October in UGR and MIN and 1 July to 31 October in CC. Lastly, we obtained continuous discharge data from gauging stations in each subbasin (CC, USGS station 13320000; UGR, USGS station 13317850; MIN, USGS station 13331500) to

evaluate relationships between flow and growth rates. Similarly, we calculated mean flow in spring and summer for each subbasin. Given the low sample size (5–9 years in each subbasin), we did not attempt to include multiple covariates or interactions between covariates in linear models.

RESULTS

Temperature profiles

Longitudinal patterns of incubation temperatures varied among subbasins and seasons (Figure 2). For example, fall and spring temperatures decreased with distance upstream in CC and UGR, but winter temperature was relatively homogenous along the longitudinal profiles. In contrast, fall and spring temperatures in MFJD were comparatively more homogenous, whereas winter temperature increased with distance upstream. MIN exhibited a similar pattern, in which winter temperatures increased at the farthest

upstream locations, whereas fall and spring temperatures decreased slightly with distance upstream.

Within the four subbasins, seasonal mean temperatures varied considerably among years, but longitudinal trends were relatively consistent (Figure 2). In fall, spawn year 2019 (emergence year 2020) was consistently the coolest year, whereas 2014–2016 exhibited the warmest temperatures. In winter, spawn year 2014 was consistently the warmest year in which temperature was 1.0, 0.5, and 1.0°C greater than the mean temperature across all years in CC, UGR, and MFJD, respectively (no 2014 data for MIN). In spring, spawn years 2014 and 2015 exhibited the warmest temperatures, whereas 2018 and 2019 were coolest.

Spawn timing

Estimated mean spawn timing was earlier with distance upstream in each subbasin (Figure 3). However, the slope of the relationship between Rkm and mean spawn date
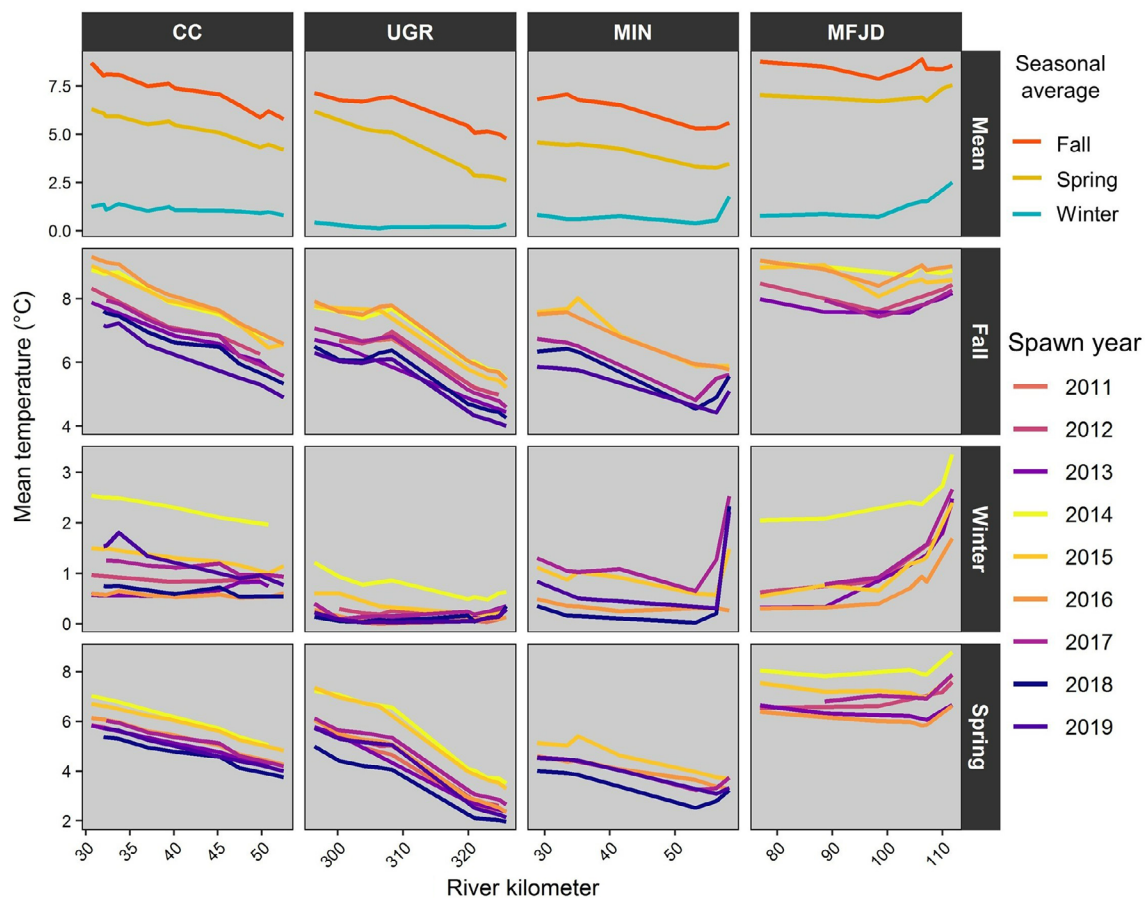

FIGURE 2 Seasonal temperature profiles within each subbasin during seasons that incubating Chinook Salmon experience prior to emergence—fall: September–November; winter: December–February; and spring: March–May. CC, Catherine Creek; MFJD, the Middle Fork John Day River; MIN, the Minam River; UGR, the upper Grande Ronde River.
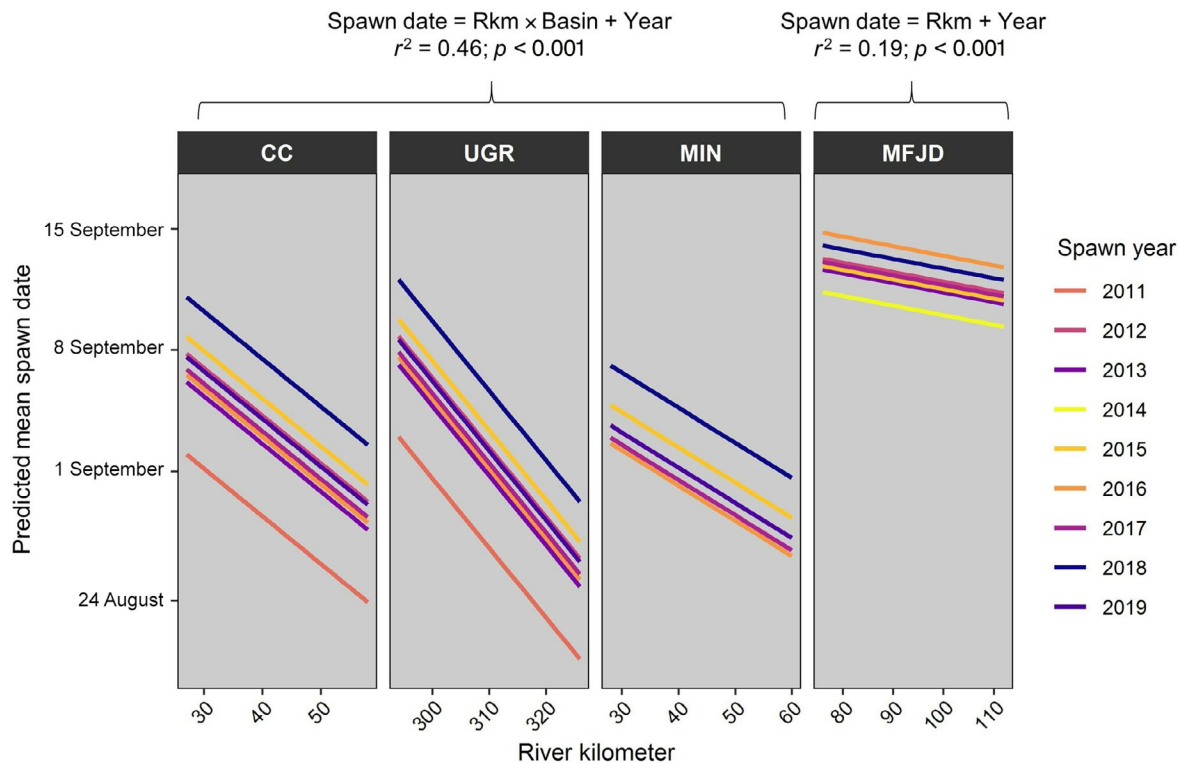
FIGURE 3 Modeled relationship between river kilometer (Rkm) and mean spawn date in each subbasin. Rivers within the Grande Ronde River basin (i.e., Catherine Creek [CC], the upper Grande Ronde River [UGR], and the Minam River [MIN]) were included in a single model to allow for estimation in data poor years. The Middle Fork John Day River (MFJD), located in the John Day River basin, was analyzed separately due to geographic isolation because Chinook Salmon are in a separate evolutionary significant unit.

differed among subbasins: -0.43 days km^{-1} in UGR (95% CI $= -0.46, -0.40$; $p < 0.001$); -0.29 days km^{-1} in CC ($-0.33, -0.26$; $p < 0.001$); -0.22 days km^{-1} in MIN ($-0.24, -0.19$; $p < 0.001$); and -0.06 days km^{-1} in MFJD ($-0.08, -0.04$; $p < 0.001$). The inclusion of spawn year as a covariate improved model explanatory power for the Grande Ronde subbasins model ($r^2 = 0.46$ vs. 0.28) and the MFJD model ($r^2 = 0.18$ vs. 0.02), and models were ranked higher than those without spawn year (Grande Ronde subbasins $\Delta AIC_c = 1046$; MFJD $\Delta AIC_c = 400$).

Emergence timing

Predicted emergence timing exhibited clear longitudinal patterns in each subbasin, but patterns differed among subbasins (Figure 4). Predicted emergence timing was progressively later with distance upstream in CC and UGR, whereas emergence timing exhibited a dome-shaped pattern with distance upstream in MIN and MFJD, with the earliest predicted emergence at the farthest upstream sites. All models with year as an additive effect produced lower AIC_c values ($\Delta AIC_c > 20$) than models with an interaction between Rkm and year, and patterns were relatively

consistent even when allowing relationships to vary among years (Appendix S1: Figure S2), suggesting that models with year as an additive effect appropriately characterized emergence patterns. Within years, the range of predicted median emergence dates among sites (i.e., spatial variation) averaged 58 days in CC, 44 days in UGR, 49 days in MIN, and 46 days in MFJD. Among years, the range in estimated median emergence timing for a given location (i.e., interannual variation) was 73 days in CC, 54 days in UGR, 47 days in MIN, and 74 days in MFJD. Predicted emergence was earliest in 2015 (spawn year 2014) and latest in 2018 (spawn year 2017).

Fish size and growth

Contrary to our expectations, earlier emergence did not result in larger parr in summer or fall (Figure 5a,b). In contrast, later emergence was positively correlated with mean parr size in fall in CC and UGR (Figure 5b), but this was not the case for summer size in which no relationships were evident (Figure 5a). Additionally, spring and summer growth rates were both positively correlated with later emergence (Figure 5c,d). Thus, although fish
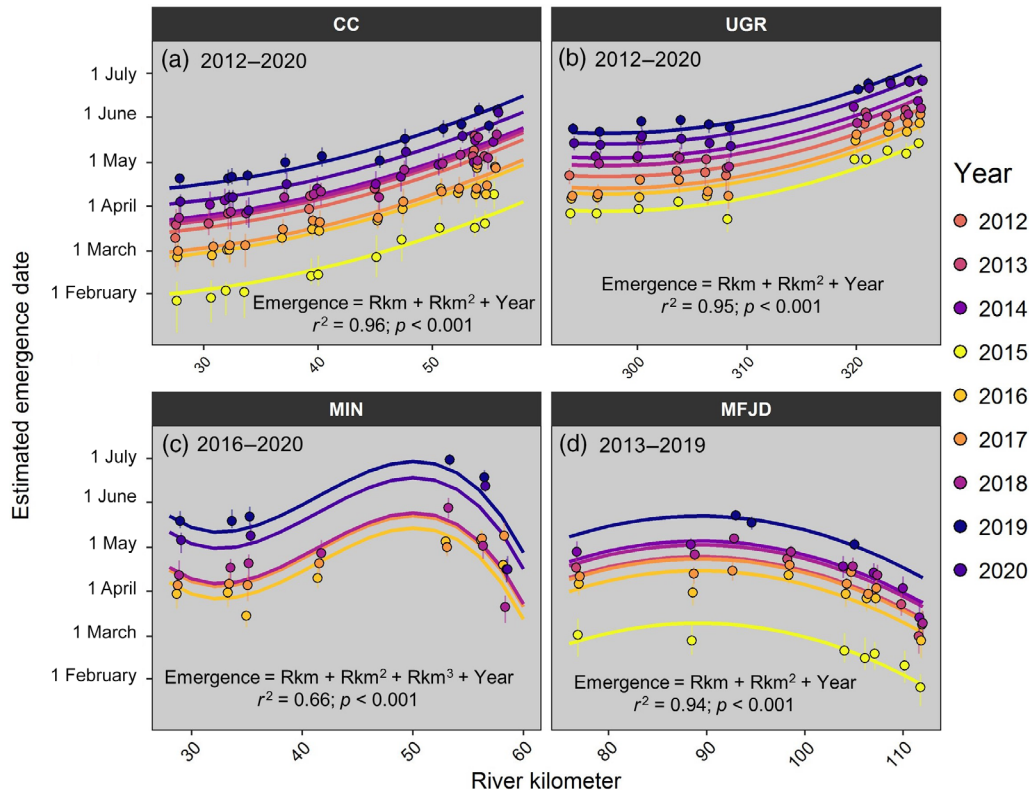
FIGURE 4 Spatial and temporal patterns of predicted Chinook Salmon emergence timing in each subbasin. Points indicate sites in which emergence was predicted using annual empirical temperature data; vertical lines indicate the 25th and 75th percentile of simulated emergence estimates based on variability in spawn timing; and lines indicate model fit. Warmer colors represent years with earlier emergence, and cooler colors represent years with later emergence. CC, Catherine Creek; MFJD, the Middle Fork John Day River; MIN, the Minam River; Rkm, river kilometer; UGR, the upper Grande Ronde River.

in years exhibiting early emergence had a longer estimated growth duration, their growth rates were slower, negating effects on interannual size patterns.

Interannual variability in growth rates was explained by both abiotic and biotic factors; however, the strength of these relationships varied by subbasin and growth interval (Figure 6). The number of redds from the previous year—a proxy for juvenile abundance in the growth year of interest—was negatively correlated with spring ($r^2 = 0.52$; $p = 0.03$) and summer growth rates in CC ($r^2 = 0.37$; $p = 0.07$), but relationships were not evident in UGR and MIN ($r^2 = 0$). However, a single outlier in UGR (rearing year 2012) exhibited high leverage given the small sample size (8 years). With this year excluded, the number of redds from the previous year explained more variation in spring ($r^2 = 0.52$; $p = 0.04$) and summer ($r^2 = 0.29$; $p = 0.12$) growth rates. Mean spring temperature was negatively associated with spring growth rates in all three subbasins, but these relationships were not significant at the $\alpha = 0.05$ level. Mean summer temperature was negatively correlated with summer growth rates in CC ($r^2 = 0.73$; $p < 0.01$), but not in UGR or MIN ($p > 0.05$). Mean spring discharge and mean summer

discharge were both positively related to spring and summer growth rates in CC and UGR ($p < 0.05$), but not in MIN.

DISCUSSION

Temperate rivers exhibit diverse temperature profiles during summer (Fullerton et al., 2015), which have important implications for fish physiology, growth, and distribution within watersheds (Isaak & Hubert, 2004; Kaylor et al., 2021). However, the spatial patterning and implications of temperature on fish in non-summer months remains understudied. We characterized variation in longitudinal thermal profiles from fall through spring to explore how landscapes differ in their patterns of spring Chinook Salmon emergence phenology. Two subbasins exhibited progressively later emergence upstream, whereas two basins exhibited the opposite, with the earliest predicted emergence at upstream sites. The shape of these longitudinal patterns remained consistent among years, despite large interannual variation in seasonal water temperatures and emergence dates.
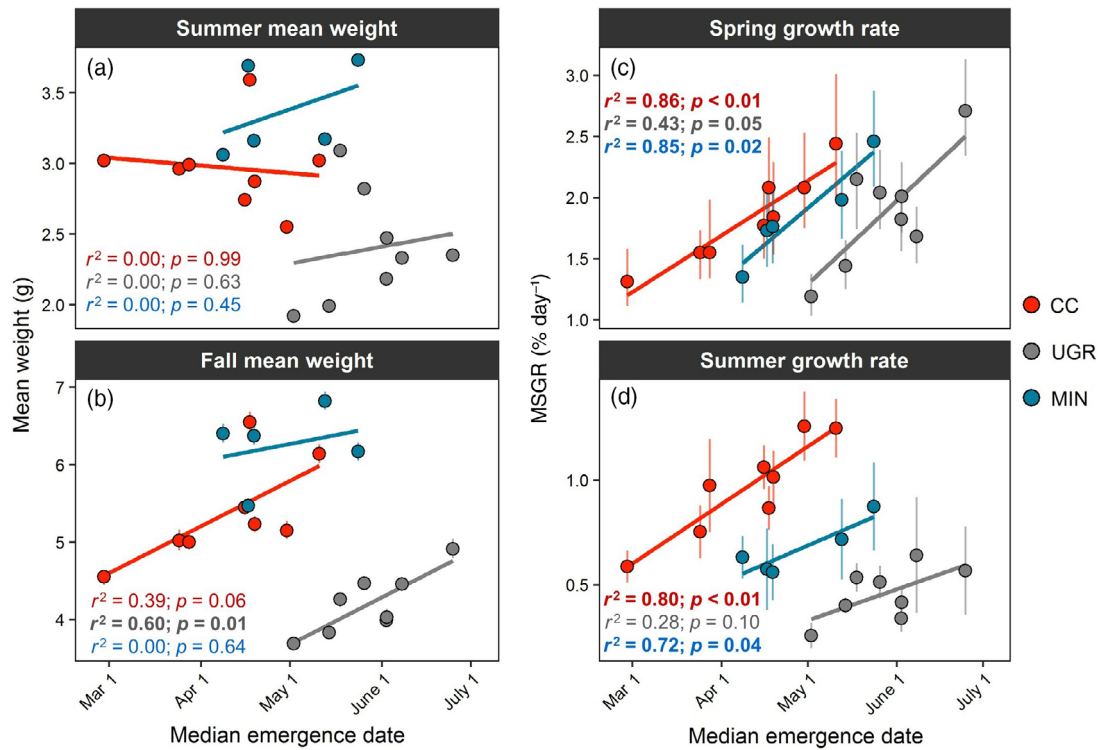
FIGURE 5 Relationships between estimated median emergence date and summer mean weight (a), fall mean weight (b), estimated mass-standardized growth rates from emergence to summer (c), and empirical growth rates from summer to fall (d). Each point represents a year, and vertical error bars represent 95% confidence intervals. Among years, fish were sampled in consistent locations within each subbasin and at approximately the same dates. CC, Catherine Creek; MIN, the Minam River; MSGR, mass-standardized growth rate; UGR, the upper Grande Ronde River.
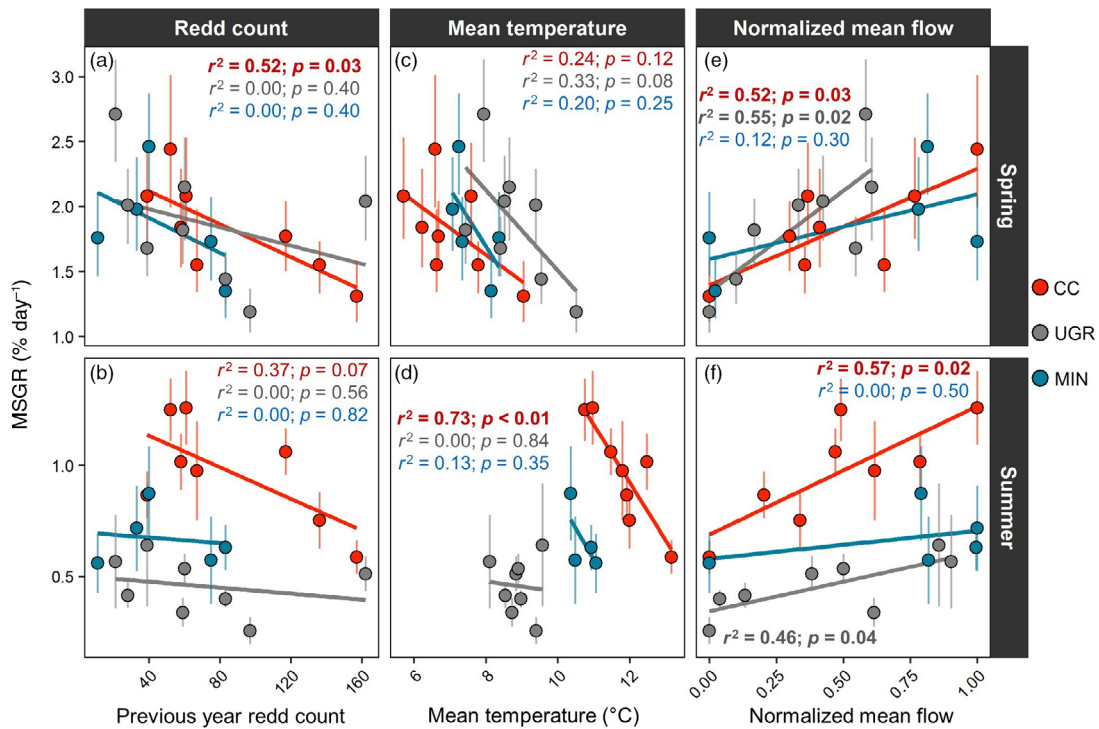

FIGURE 6 Estimated mass-standardized growth rates from emergence to mid-summer (a, c, and e) and from mid-summer to fall (b, d, and f) relative to the number of redds from the previous year (a and b), mean spring (c) and summer (d) water temperature, and mean spring (e) and summer (f) flow. CC, Catherine Creek; MIN, the Minam River; MSGR, mass-standardized growth rate; UGR, the upper Grande Ronde River.

Predicted emergence timing was earlier in warmer years (such as 2015), yet juvenile salmon were not larger in summer and fall despite longer growth durations. Instead, earlier emergence was associated with slower growth rates during spring and summer. Conditions that promoted earlier emergence such as warmer winter air temperatures and reduced snowpack (Adelfio et al., 2019) may have had carryover effects that resulted in poorer growth conditions after emergence including reduced summer streamflow and higher temperatures that counteracted longer growth intervals. Understanding the mechanisms driving relationships between emergence and subsequent rearing conditions has important implications for predicting climate change impacts on juvenile salmon growth and survival (Crozier et al., 2008).

Adult spawn timing is thought to be selected upon to promote emergence aligned with long-term average optimal conditions for juvenile growth and survival (Quinn, 2005; Webb & Mclay, 1996). Across landscapes with heterogeneous thermal regimes, there are multiple mechanisms thought to increase emergence synchrony including earlier spawning in cooler sections to compensate for longer incubation durations (Campbell et al., 2019; Quinn, 2005), and the dome-shaped relationship between mean incubation temperature and the required degree days to emerge, with fewer degree days required at lower or higher temperatures (Beacham & Murray, 1990). While we observed earlier spawning in cooler upstream sections of each subbasin, predicted emergence was not synchronous within or among subbasins, nor were longitudinal patterns consistent among subbasins. This asynchronous emergence may reflect variation in the timing of optimal emergence and rearing conditions within subbasins. For example, warmer spring temperatures in downstream sections of CC and UGR or warmer winter temperatures in upstream sections of MFJD may provide earlier favorable growth conditions. Alternatively, adults may have to wait for rivers to cool before they spawn because embryos have a low thermal tolerance (Beer & Anderson, 2001; Crossin et al., 2008). Thus, emergence phenology may be influenced by constraints on spawning phenology, which vary longitudinally. Regardless of the mechanisms driving asynchronous emergence in these populations, altered spawn timing and spawning locations stemming from climate change (Austin et al., 2021), continued hatchery supplementation (Hoffnagle et al., 2008; Hughes & Murdoch, 2017), and additional habitat degradation (McClure et al., 2008) would further disconnect spatiotemporal patterns of emergence phenology that these populations have adapted to.

Longitudinal temperature trends varied among subbasins, but also among seasons within each subbasin, resulting in different longitudinal patterns of emergence phenology. For example, temperature generally increased with distance downstream across all seasons in CC and UGR (to a lesser degree in winter) leading to earlier downstream emergence. In contrast, the longitudinal temperature profile of MFJD was relatively homogenous in fall and spring, but was warmer upstream in winter, resulting in earlier emergence at upstream sites. Warmer winter temperatures in upstream sections of MFJD suggest localized inputs of warmer (in winter) groundwater that dissipated downstream, which is consistent with previous characterization of groundwater sources in MFJD (Torgersen et al., 2006). In contrast, the thermal profiles of CC and UGR suggest minimal or more spatially homogeneous groundwater inputs. However, other factors such as localized air temperatures, thermal insulation, stream shading, and tributary inputs may also shape seasonal temperature patterns in these subbasins (Minder et al., 2010). Further understanding of the drivers of temperature patterns during the incubation period is needed to more accurately project climate change effects on salmonid emergence phenology (Adelfio et al., 2019; Sparks et al., 2019; Steele et al., 2016).

Spatial variation in emergence phenology has important implications for juvenile salmon ecology. For example, Kaylor et al. (2021) found that within a single year juvenile Chinook Salmon in downstream sections of CC and UGR emerged earlier, exhibited higher spring growth rates, and were larger in summer compared to fish from upstream locations. Earlier emergence may further lead to greater survival over conspecifics due to size- and foraging-based competitive advantages (Einum & Fleming, 2000; Harwood et al., 2003). Variation in emergence timing also influences the environmental conditions to which newly emerged fry are exposed. In particular, emergence timing relative to snowmelt-driven spring peak flows has potential consequences for survival, dispersal, and habitat use. The coincidence of high flows and emergence can result in lower survival (Jensen & Johnsen, 1999) and may also increase downstream dispersal (Saltveit et al., 1995). Streamflow also controls the accessibility and profitability of floodplain habitats (Baldock et al., 2016), which can provide velocity refuge and enhanced growth opportunities for juvenile salmon (Jeffres et al., 2008; Sommer et al., 2001). Thus, the timing of emergence relative to floodplain inundation may influence habitat use and the benefits floodplains provide to juvenile salmon. Evaluating how emergence phenology variation influences these aspects of juvenile salmon ecology is an important avenue of future research.

In contrast to our expectations, juvenile Chinook Salmon were not larger in years with earlier emergence, despite longer growth durations. This result contrasts with Egglishaw and Shackley (1977), who found that

age-0 salmonids were larger in years with earlier emergence. Further, they found similar seasonal growth rates among years, and attributed greater size in years with earlier emergence to a longer growth period. In contrast, we found greater estimated emergence-to-summer growth rates and empirical summer-to-fall growth rates in years with later emergence. There are several potential explanations for why earlier emergence did not lead to greater size. First, later emerging fish may have exhibited compensatory growth. However, compensatory growth typically occurs after a period of growth suppression (Ali et al., 2003), and later emergence was associated with higher initial (i.e., spring) growth rates. It is unclear whether delayed emergence may lead to compensatory growth. Second, growth rates and size may have been more strongly controlled by density dependence than growth duration in years exhibiting earlier emergence. Our proxy of intraspecific competitor density (i.e., the number of redds contributing to the following year's abundance) was negatively correlated with spring and summer growth rates, but just one of the six relationships were statistically significant. However, sample size was low (5–8 years) and trends were consistent among subbasins and between the two growth periods, suggesting density dependence may have contributed to observed growth rates. Lastly, the environmental conditions influencing water temperature and emergence timing may be correlated with growth conditions after emergence. For example, warm winters with sparse snowpack accumulation may lead to faster development rate and earlier emergence (Adelfio et al., 2019), but also earlier onset and prolonged duration of low-flow conditions, which have been experimentally linked to lower growth rates in drift-feeding salmonids (Harvey et al., 2006). If conditions resulting in earlier emergence are correlated with poorer conditions for juvenile growth, earlier emergence anticipated with climate change (Adelfio et al., 2019; Sparks et al., 2019) may not benefit juvenile salmon size and growth through longer growth durations.

There are a number of caveats and limitations of our study. First, although we attempted to account for variability in spawn timing, we were not able to capture other sources of variability influencing emergence timing. For example, families within the same population can exhibit different development rates (Beer & Steel, 2018) and variation in dissolved oxygen can influence incubation duration (Geist et al., 2006). Additionally, we modeled median emergence timing, but individual fry emergence can occur over a period of weeks to months (Campbell et al., 2019) and at varying levels of development and yolk absorption (Beer & Anderson, 2001). Thus, the range in realized emergence is likely greater than we modeled. Second, spawn timing was

modeled and may differ from realized spawn timing. Redd construction dates were not known with certainty due to limited redd counts in some years and locations (Appendix S1: Figure S1) and because surveys documenting new redd formation were conducted 7–10 days apart. Obtaining more precise redd construction dates at these spatial scales is logistically challenging but would improve emergence prediction accuracy. Third, when evaluating relationships between interannual conditions and growth rates, our sample size was low (5–8 years depending on subbasin), limiting evaluation of interactions between covariates. It is likely that environmental factors (i.e., flow and temperature) interacted with biotic factors (i.e., density dependence) to shape interannual patterns of growth rates. This highlights the importance of and need for long-term data collection to understand drivers of population dynamics, especially under changing climatic conditions.

CONCLUSION

Within these watersheds, spatial structuring of emergence timing may be an overlooked aspect of intrapopulation variability that may contribute to stability and resilience. Interannual variation in environmental conditions may favor earlier emergence in some years and later emergence in others, translating to shifting locations of optimal rearing conditions and productivity within subbasins, as has been observed across watersheds (Brennan et al., 2019). Habitat degradation (McClure et al., 2008), declining adult returns (Flitcroft et al., 2014), stream warming (Crozier et al., 2008), and hatchery integration (Hoffnagle et al., 2008; Hughes & Murdoch, 2017) can shift or contract spawning ranges, thereby reducing population-level variability in emergence timing and the range of biophysical conditions experienced by newly emerged fry. Similarly, limiting habitat restoration efforts to relatively short stretches of rivers within core spawning habitat may not result in conservation of the complete range of conditions populations were historically exposed to. However, further research is needed to empirically link spatiotemporal emergence patterns to key aspects of juvenile salmon ecology including habitat use (e.g., floodplains), growth, survival, and productivity, which has important implications for guiding restoration efforts and understanding how changing conditions may influence juvenile salmon ecology (Crozier et al., 2008).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw data and descriptions of how to access publicly available data used in this study (Kaylor et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.6512250.

ORCID

Matthew J. Kaylor https://orcid.org/0000-0001-5331-9830
Jonathan B. Armstrong https://orcid.org/0000-0003-3360-0523
Seth M. White https://orcid.org/0000-0003-4918-6865

REFERENCES

Abrey, C. A. 2005. "Variation in the Early Life History of Sockeye Salmon (*Oncorhychus nerka*): Emergence Timing, an Ontogenetic Shift, and Population Productivity." MS thesis. University of Washington.

Adelfio, L. A., S. M. Wondzell, N. J. Mantua, and G. H. Reeves. 2019. "Warm Winters Reduce Landscape-Scale Variability in the Duration of Egg Incubation for Coho Salmon (*Oncorhynchus kisutch*) on the Copper River Delta, Alaska." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 1362–75.

Ali, M., A. Nicieza, and R. J. Wootton. 2003. "Compensatory Growth in Fishes: A Response to Growth Depression." *Fish and Fisheries* 4: 147–90.

Armstrong, J. B., A. H. Fullerton, C. E. Jordan, J. L. Ebersole, J. R. Bellmore, I. Arismendi, B. E. Penaluna, and G. H. Reeves. 2021. "The Importance of Warm Habitat to the Growth Regime of Cold-Water Fishes." *Nature Climate Change* 11: 354–61.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. "Thermal Heterogeneity Mediates the Effects of Pulsed Subsidies across a Landscape." *Ecology* 91: 1445–54.

Austin, C. S., T. E. Essington, and T. P. Quinn. 2019. "Spawning and Emergence Phenology of Bull Trout *Salvelinus confluentus* under Differing Thermal Regimes." *Journal of Fish Biology* 94: 191–5.

Austin, C. S., T. E. Essington, and T. P. Quinn. 2021. "In a Warming River, Natural-Origin Chinook Salmon Spawn Later but Hatchery-Origin Conspecifics Do Not." *Canadian Journal of Fisheries and Aquatic Sciences* 78: 68–77.

Baldock, J. R., J. B. Armstrong, D. E. Schindler, and J. L. Carter. 2016. "Juvenile Coho Salmon Track a Seasonally Shifting Thermal Mosaic across a River Floodplain." *Freshwater Biology* 61: 1454–65.

Bare, C. M., J. J. Rogers, I. A. Tattam, J. R. Ruzycki, and R. W. Carmichael. 2015. Chinook Salmon Productivity and Escapement Monitoring in the John Day River Basin Annual Technical Report. John Day, OR.

Baxter, C. V., and F. R. Hauer. 2000. "Geomorphology, Hyporheic Exchange, and Selection of Spawning Habitat by Bull Trout (*Salvelinus confluentus*)." *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1470–81.

Beacham, T. D., and C. B. Murray. 1990. "Temperature, Egg Size, and Development of Embryos and Alevins of Five Species of Pacific Salmon: A Comparative Analysis." *Transactions of the American Fisheries Society* 119: 927–45.

Beauchamp, D. A. 2009. "Bioenergetic Ontogeny: Linking Climate and Mass-Specific Feeding to Life-Cycle Growth and Survival of Salmon." *American Fisheries Society Symposium* 70: 1–19.

Beer, W. N., and J. J. Anderson. 2001. "Effect of Spawning Day and Temperature on Salmon Emergence: Interpretations of a Growth Model for Methow River Chinook." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 943–9.

Beer, W. N., and E. A. Steel. 2018. "Impacts and Implications of Temperature Variability on Chinook Salmon Egg Development and Emergence Phenology." *Transactions of the American Fisheries Society* 147: 3–15.

Brandt, E., J. Smith, J. Feldhaus, and J. Ruzycki. 2021. *Lower Snake River Compensation Plan: Oregon Spring Chinook Salmon Evaluation Studies 2019 Annual Progress Report*. La Grande, OR: Oregon Department of Fisheries and Wildlife.

Brannas, E. 1995. "First Access to Territorial Space and Exposure to Strong Predation Pressure: A Conflict in Early Emerging Atlantic Salmon (*Salmo salar* L.) Fry." *Evolutionary Ecology* 9: 411–20.

Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019. "Shifting Habitat Mosaics and Fish Production across River Basins." *Science* 364: 783–6.

Burnham, K. P., and D. R. Anderson. 2004. "Multimodel Inference: Understanding AIC and BIC in Model Selection." *Sociological Methods & Research* 33: 261–304.

Caissie, D. 2006. "The Thermal Regime of Rivers: A Review." *Freshwater Biology* 51: 1389–406.

Campbell, E. Y., J. B. Dunham, G. H. Reeves, and S. M. Wondzell. 2019. "Phenology of Hatching, Emergence, and End-of-Season Body Size in Young-of-Year Coho Salmon in Thermally Contrasting Streams Draining the Copper River Delta, Alaska." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 185–91.

Crossin, G. T., S. G. Hinch, S. J. Cooke, D. W. Welch, D. A. Patterson, S. R. M. Jones, A. G. Lotto, et al. 2008. "Exposure to High Temperature Influences the Behaviour, Physiology, and Survival of Sockeye Salmon during Spawning Migration." *Canadian Journal of Zoology* 86: 127–40.

Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. "Potential Responses to Climate Change in Organisms with Complex Life Histories: Evolution and Plasticity in Pacific Salmon." *Evolutionary Applications* 1: 252–70.

Dowdy, J. W., B. C. Power, G. A. McMichael, E. N. Branigan, K. J. Wauhkonen, C. R. Warnock, O. C. Davis, S. D. Favrot, E. R. Sedell, and J. R. Ruzycki. 2019. *Investigations into the Early Life History of Naturally Produced Spring Chinook Salmon and Summer Steelhead in the Grande Ronde River Subbasin: Annual Report 2018*. La Grande, OR: Oregon Department of Fisheries and Wildlife.

Dunham, J., G. Chandler, B. Rieman, and D. Martin. 2005. *Measuring Stream Temperature with Digital Data Loggers: A User's Guide*. Gen. Tech. Rep. RMRS- GTR-150. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Egglishaw, H. J., and P. E. Shackley. 1977. "Growth, Survival and Production of Juvenile Salmon and Trout in a Scottish Stream, 1966–75." *Journal of Fish Biology* 11: 647–72.

Einum, S., and I. A. Fleming. 2000. "Selection against Late Emergence and Small Offspring in Atlantic Salmon (*Salmo salar*)." *Evolution* 54: 628–39.

Feldhaus, J. W., D. L. Eddy, P. J. Keniry, and J. R. Ruzycki. 2018. *Lower Snake River Compensation Plan: Oregon Spring Chinook Salmon Evaluation Studies. 2016 Annual Progress Report*. Salem, OR: Oregon Department of Fish and Wildlife.

Flitcroft, R., K. Burnett, J. Snyder, G. Reeves, and L. Ganio. 2014. "Riverscape Patterns among Years of Juvenile Coho Salmon in Midcoastal Oregon: Implications for Conservation." *Transactions of the American Fisheries Society* 143: 26–38.

Fullerton, A. H., C. E. Torgersen, J. J. Lawler, R. N. Faux, E. A. Steel, T. J. Beechie, J. L. Ebersole, and S. G. Leibowitz. 2015. "Rethinking the Longitudinal Stream Temperature Paradigm: Region-Wide Comparison of Thermal Infrared Imagery Reveals Unexpected Complexity of River Temperatures." *Hydrological Processes* 29: 4719–37.

Geist, D. R., C. S. Abernethy, K. D. Hand, V. I. Cullinan, J. A. Chandler, and P. A. Groves. 2006. "Survival, Development, and Growth of Fall Chinook Salmon Embryos, Alevins, and Fry Exposed to Variable Thermal and Dissolved Oxygen Regimes." *Transactions of the American Fisheries Society* 135: 1462–77.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 2006. "Streamflow Lowers Dry-Season Growth of Rainbow Trout in a Small Stream." *Transactions of the American Fisheries Society* 135: 998–1005.

Harwood, A. J., S. W. Griffiths, N. B. Metcalfe, and J. D. Armstrong. 2003. "The Relative Influence of Prior Residency and Dominance on the Early Feeding Behaviour of Juvenile Atlantic Salmon." *Animal Behaviour* 65: 1141–9.

Hoffnagle, T. L., R. W. Carmichael, K. A. Frenyea, and P. J. Keniry. 2008. "Run Timing, Spawn Timing, and Spawning Distribution of Hatchery- and Natural-Origin spring Chinook Salmon in the Imnaha River, Oregon." *North American Journal of Fisheries Management* 28: 148–64.

Hughes, M. S., and A. R. Murdoch. 2017. "Spawning Habitat of Hatchery Spring Chinook Salmon and Possible Mechanisms Contributing to Lower Reproductive Success." *Transactions of the American Fisheries Society* 146: 1016–27.

Hurvich, C. M., and C. L. Tsai. 1989. "Regression and Time Series Model Selection in Small Samples." *Biometrika* 76: 297–307.

Isaak, D. J., and W. A. Hubert. 2004. "Nonlinear Response of Trout Abundance to Summer Stream Temperatures across a Thermally Diverse Montane Landscape." *Transactions of the American Fisheries Society* 133: 1254–9.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. "The Cold-Water Climate Shield: Delineating Refugia for Preserving Salmonid Fishes through the 21st Century." *Global Change Biology* 21: 2540–53.

Jeffres, C. A., J. J. Opperman, and P. B. Moyle. 2008. "Ephemeral Floodplain Habitats Provide Best Growth Conditions for Juvenile Chinook Salmon in a California River." *Environmental Biology of Fishes* 83: 449–58.

Jensen, A. J., and B. O. Johnsen. 1999. "The Functional Relationship between Peak Spring Floods and Survival and Growth of Juvenile Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*)." *Functional Ecology* 13: 778–85.

Jones, M. H., J. E. Seeb, K. I. Warheit, T. R. Seamons, T. P. Quinn, and L. W. Seeb. 2015. "Consequences of Emergence Timing for the Growth and Relative Survival of Steelhead Fry from Naturally Spawning Wild and Hatchery Parents." *Transactions of the American Fisheries Society* 144: 977–89.

Kaylor, M. J., J. B. Armstrong, J. Lemanski, C. Justice, and S. M. White. 2022. "Riverscape Heterogeneity in Estimated Chinook Salmon Emergence Phenology and Implications for Size and Growth." Zenodo. Dataset. https://doi.org/10.5281/zenodo.6512250.

Kaylor, M. J., C. Justice, J. B. Armstrong, B. A. Staton, L. A. Burns, E. Sedell, and S. M. White. 2021. "Temperature, Emergence Phenology and Consumption Drive Seasonal Shifts in Fish Growth and Production across Riverscapes." *Journal of Animal Ecology* 90: 1727–41.

Lindsay, R. B., W. J. Knox, M. W. Flesher, B. J. Smith, E. A. Olsen, and L. S. Lutz. 1986. *Study of Wild Spring Chinook Salmon in the John Day River System. 1985 Final Report*. Portland, OR: Oregon Department of Fish and Wildlife.

Lusardi, R. A., B. G. Hammock, C. A. Jeffres, R. A. Dahlgren, and J. D. Kiernan. 2020. "Oversummer Growth and Survival of Juvenile Coho Salmon (*Oncorhynchus kisutch*) across a Natural Gradient of Stream Water Temperature and Prey Availability: An In Situ Enclosure Experiment." *Canadian Journal of Fisheries and Aquatic Sciences* 424: 413–24.

McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Pess, J. C. Jorgensen, S. M. Sogard, S. E. Sultan, et al. 2008. "Evolutionary Consequences of Habitat Loss for Pacific Anadromous Salmonids." *Evolutionary Applications* 1: 300–18.

McMeans, B. C., K. S. McCann, M. M. Guzzo, T. J. Bartley, C. Bieg, P. J. Blanchfield, T. Fernandes, et al. 2020. "Winter in Water: Differential Responses and the Maintenance of Biodiversity." *Ecology Letters* 23: 922–38.

Minder, J. R., P. W. Mote, and J. D. Lundquist. 2010. "Surface Temperature Lapse Rates over Complex Terrain: Lessons from the Cascade Mountains." *Journal of Geophysical Research* 115: 1–13.

NOAA. 2008. *Supplemental Comprehensive Analysis of the Federal Columbia River Power System and Mainstem Effects of the Upper Snake and Other Tributary Actions*. Washington, DC: NOAA.

O'Connor, K. I. 2000. "The Effects of Prior Residence on Behavior and Growth Rates in Juvenile Atlantic Salmon (*Salmo salar*)." *Behavioral Ecology* 11: 13–8.

Ostrovsky, I. 1995. "The Parabolic Pattern of Animal Growth: Determination of Equation Parameters and their Temperature Dependencies." *Freshwater Biology* 33: 357–71.

Perry, R. W., J. M. Plumb, and C. W. Huntington. 2015. "Using a Laboratory-Based Growth Model to Estimate Mass-and Temperature-Dependent Growth Parameters across Populations of Juvenile Chinook Salmon." *Transactions of the American Fisheries Society* 144: 331–6.

Pess, G., and C. E. Jordan. 2019. *Characterizing Watershed-Scale Effects of Habitat Restoration Actions to Inform Life Cycle Models: Case Studies Using Data-Rich vs. Data-Poor Approaches*. NOAA Technical Memorandum NMFS-NWFSC-151. Washington, DC: U.S. Department of Commerce.

Quinn, T. P. 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. Seattle, WA: University Press.

Richter, A., and S. A. Kolmes. 2005. "Maximum Temperature Limits for Chinook, Coho, and Chum Salmon, and Steelhead Trout in the Pacific Northwest." *Reviews in Fisheries Science* 13: 23–49.

Saltveit, S. J., T. Bremnes, and O. R. Lindå. 1995. "Effect of Sudden Increase in Discharge in a Large River on Newly Emerged Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*) Fry." *Ecology of Freshwater Fish* 4: 168–74.

Skoglund, H., S. Einum, T. Forseth, and B. T. Barlaup. 2012. "The Penalty for Arriving Late in Emerging Salmonid Juveniles: Differences between Species Correspond to their Interspecific Competitive Ability." *Functional Ecology* 26: 104–11.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. "Floodplain Rearing of Juvenile Chinook Salmon: Evidence of Enhanced Growth and Survival." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 325–33.

Sparks, M. M., J. A. Falke, T. P. Quinn, M. D. Adkison, D. E. Schindler, K. Bartz, D. Young, and P. A. H. Westley. 2019. "Influences of Spawning Timing, Water Temperature, and Climatic Warming on Early Life History Phenology in Western Alaska Sockeye Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 123–35.

Steele, E. A., C. Sowder, and E. Peterson. 2016. "Spatial and Temporal Variation of Water Temperature Regimes of the Snoqualmie River Network." *Journal of the American Water Resources Association* 52: 769–87.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. "Seasonal Changes in Spatial Patterns of *Oncorhynchus mykiss* Growth Require Year-Round Monitoring." *Ecology of Freshwater Fish* 26: 434–43.

Torgersen, C. E., C. V. Baxter, H. W. Li, and B. A. McIntosh. 2006. "Landscape Influences on Longitudinal Patterns of River Fishes: Spatially Continuous Analysis of Fish–Habitat Relationships." *American Fisheries Society Symposium* 48: 473–92.

Webb, J. H., and H. A. Mclay. 1996. "Variation in the Time of Spawning of Atlantic Salmon (*Salmo salar*) and its Relationship to Temperature in the Aberdeenshire Dee, Scotland." *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2739–44.

White, S. M., C. Justice, D. A. Kelsey, D. A. McCullough, and T. Smith. 2017. "Legacies of Stream Channel Modification Revealed Using General Land Office Surveys, with Implications for Water Temperature and Aquatic Life." *Elementa: Science of the Anthropocene* 5: 1–18.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.