





ARTICLE

Freshwater Ecology

Juvenile life history diversity is associated with lifetime individual heterogeneity in a migratory fish

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Funding information

National Oceanographic and Atmospheric Administration Northwest Fisheries Science Center; Washington Cooperative Fish and Wildlife Research Unit; Northwest Climate Adaptation Science Center; Grant County Public Utilities District; Chelan County Public Utilities District; Washington Department of Fish and Wildlife; Yakama Nation Fisheries; Bonneville Power Administration; Washington Department of Ecology; U.S. Geological Survey; U.S. National Weather Service

Handling Editor: Andrew Kramer

Abstract

Differences in the life history pathways (LHPs) of juvenile animals are often associated with differences in demographic rates in later life stages. For migratory animals, different LHPs often result in animals from the same population occupying distinct habitats subjected to different environmental drivers. Understanding how demographic rates differ among animals expressing different LHPs may reveal fitness trade-offs that drive the expression of alternative LHPs and enable better prediction of population dynamics in a changing environment. To understand how demographic outcomes and their relationships with environmental variables differ among animals with different LHPs, we analyzed a long-term (2006–2021) mark–recapture dataset for Chinook salmon (*Oncorhynchus tshawytscha*) from the Wenatchee River, Washington, USA. Distinct LHPs represented in this population include either remaining in the natal stream until emigrating to the ocean as a 1-year-old (natal-reach rearing) or emigrating from the natal stream and rearing in downstream habitats for several months before completing the emigration to the ocean as a 1-year-old (downstream rearing). We found that downstream-rearing fish emigrated to the ocean 19 days earlier on average and returned as adults from the ocean at higher rates. We detected a positive correlation between rate of return from the ocean by downstream-rearing fish and coastal upwelling in their spring of outmigration, whereas for natal-reach-rearing fish we detected a positive correlation with sea surface temperature during their first marine summer. Different responses to environmental variability should lead to asynchrony in adult abundance among juvenile LHPs. A higher proportion of downstream-rearing fish returned at younger ages compared with natal-reach-rearing fish, which contributed to variability in age at reproduction and greater mixing across generations. Our results demonstrate how diversity in juvenile LHPs is associated with heterogeneity in demographic rates during subsequent life stages, which can in turn affect variance in aggregate population abundance and response to environmental change.

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Our findings underscore the importance of considering life history diversity in demographic analyses and provide insights into the effects of life history diversity on population dynamics and trade-offs that contribute to the maintenance of life history diversity.

KEYWORDS

carryover effects, Chinook salmon, endangered species, individual heterogeneity, individual stochasticity, mark–recapture, maturation age, multistate model, survival, synchrony

INTRODUCTION

Individual heterogeneity in life history traits is often associated with individuals occupying distinct habitats and consequently experiencing differences in demographic rates throughout the life cycle (Clobert et al., 2009). This heterogeneity can result in important consequences for population dynamics and fitness (Forsythe et al., 2021; Kendall & Fox, 2002; Vindenes et al., 2008). Animals exhibiting alternative life history pathways (LHPs) defined by their timing of life-stage transitions (sensu Bourret et al., 2016) may have different survival rates, which have different environmental drivers. The resulting asynchronous variation through time in the abundance of animals expressing different LHPs dampens variability in total population abundance and may confer a level of resilience to environmental change known as the portfolio effect (Schindler et al., 2010). Life history diversity also contributes to population stability through variability in age at maturity and longevity (Lewin et al., 2017).

Trade-offs exist when life history events have both costs and benefits to fitness (Stearns, 1989). For example, reproduction increases immediate fitness, but may reduce survival, and therefore reproduction over an organism's lifetime (Oosthuizen et al., 2021). Thus, a trade-off exists between immediate and lifetime reproductive output in this example. Such trade-offs are believed to play a primary role in the evolution of life histories (Stearns, 1989). Furthermore, trade-offs can lead to heterogeneity within populations when multiple viable LHPs exist or when an organism's state determines which LHP will confer the greatest fitness (e.g., Oosthuizen et al., 2019).

A better understanding of how demographic rates differ among animals within populations that express different LHPs could help elucidate the trade-offs that maintain life history diversity within populations (Salguero-Gómez et al., 2018), while a better understanding of diversity in response to environmental variables could inform how life history diversity contributes to population stability (Hamel et al., 2018). Furthermore, information regarding how demographic rates and responses to environmental variability differ among organisms expressing alternative

LHPs could benefit conservation and management efforts by informing predictions of how populations will respond to management actions, climate change, and other sources of environmental change that may differentially affect LHPs (e.g., Lok et al., 2019). However, the lifetime demographic consequences of alternative LHPs, especially alternative pathways exhibited by young animals, are poorly studied because it is difficult to track individuals throughout their life cycles (Clutton-Brock & Sheldon, 2010). Above a certain age, it becomes difficult to distinguish individuals that exhibited different juvenile LHPs, yet those pathways may have lifetime effects on demographic rates and fitness.

Anadromous salmonids (*Salmonidae* spp.) exhibit considerable diversity of LHPs related to freshwater habitat use during juvenile life stages, and this diversity is associated with greater population stability (Bourret et al., 2016; Schroeder et al., 2015). However, the degree to which lifetime demographic rates and demographic responses to environmental conditions vary among juvenile LHPs within populations is not well understood (Bourret et al., 2016; Braun et al., 2016). To determine how lifetime demographic outcomes differ among animals with different juvenile LHPs, we analyzed a long-term (2006–2021) mark–recapture dataset for >150,000 Chinook salmon (*Oncorhynchus tshawytscha*) with known juvenile LHPs from a population in the Columbia River Basin listed under the Endangered Species Act. Fish were marked as juveniles when emigrating from their natal stream, the timing of which defined their juvenile LHP (Sorel, 2022a). They were subsequently detected when passing dams during their juvenile downstream and adult upstream migrations, allowing for estimation of survival, return rates from the ocean (reflecting at-sea survival and return age), and maturation age of fish expressing alternative juvenile LHPs. We identified differences in the rates and ages of return from the ocean as well as diversity in responses to environmental variables across LHPs. These results provide insights into the effects of life history diversity on population dynamics and trade-offs that may contribute to the maintenance of life history diversity.

METHODS

Study system

The Wenatchee River Basin lies in central Washington State, USA (Figure 1b) and supports a population of federally endangered spring Chinook salmon. As is common among Chinook salmon, juveniles exhibit a two-stage emigration from natal streams (Bourret et al., 2016; Copeland & Venditti, 2009; Schroeder et al., 2015); stage-one emigration is to downstream freshwater rearing areas and occurs at variable times but by their second spring, while stage-two emigration is to the ocean and occurs in the second spring (Buchanan et al., 2015; Favrot & Jonasson, 2020). One LHP is characterized by fish remaining in the natal stream until their second spring and initiating stage-two emigration directly after the first stage (natal-reach rearing). Other LHPs are characterized by fish carrying out stage-one emigration from natal streams in spring, summer, or fall of their first year of life, and rearing and overwintering in downstream reaches prior to initiating stage-two emigration the following spring (downstream rearing). Adults return from the ocean in spring at age three, four, or five, reside within the Wenatchee River Basin over summer, and spawn in late summer.

Data

From 2006 through 2017, juvenile spring Chinook salmon were sampled with rotary screw traps during stage-one emigration from three natal streams—the Chiwawa River, Nason Creek, and the White River (Figure 1a). The traps were installed in early spring and operated continuously through late fall. Captured juveniles >60 mm were implanted with passive integrated transponder (PIT) tags within their peritoneal cavity using a syringe. PIT tags transmitted a unique alphanumeric radio-frequency identification (RFID) code when triggered by an electromagnetic pulse from an RFID reader such that encounter histories unique to each tagged individual could be constructed. The dates and locations that marked fish were released and subsequently detected were downloaded from the Columbia Basin PIT Tag Information System (www.ptagis.org).

One of three possible LHPs was assigned to each fish based on their day of year (DOY) and age of emigration (corresponding to their DOY and age of first capture). LHPs were delineated based on the seasonality in average daily emigrant abundances (Sorel, 2022a): (1) summer subyearlings; (2) fall subyearlings; and (3) spring yearlings. Summer subyearlings were the youngest fish that were large enough to be marked with PIT tags. They

emigrated between DOY 141 and 262. Fall subyearlings emigrated between DOY 263 and when the traps were removed in early winter (\leq DOY 345). Spring yearlings emigrated in spring, between when traps were installed (\geq DOY 53) and DOY 179, and were distinguished from subyearlings based on a length–date cutoff rule (Sorel, 2022a).

Following initial capture, the first opportunity for detection (constituting the second capture occasion) occurred at a rotary screw trap operated near the confluence of the Wenatchee River and the Columbia River (lower Wenatchee screw trap) (Figure 1a). This trap was only operated from late winter through summer, but we assumed that downstream-rearing fish remained within the Wenatchee River Basin until their second spring of life, at which point surviving individuals could be recaptured when passing the lower Wenatchee screw trap during stage-two emigration. This assumption is supported by the very few recaptures of subyearling emigrants that have occurred during the summer prior to trap removal. However, it is possible that some fish passed the lower Wenatchee screw trap in late fall through winter prior to trap operations, which could introduce bias into survival estimates if these fish had different survival rates than fish that migrated during trap operations.

Subsequent detection occasions occurred as fish transited downstream on their way to the ocean and when they traveled back upstream as adults prior to spawning. The third and fourth detection occasions occurred at juvenile bypass systems at the McNary and Bonneville Dams within the Columbia River seaward migration corridor (Figure 1). Only juveniles that passed dams via the juvenile fish bypass systems were detected as there were no RFID readers in other passageways (i.e., spillways or turbines). After passing Bonneville Dam as juveniles, fish entered the marine environment and could not be detected until they returned to Bonneville Dam as adults 1–3 years later.

The fifth and sixth detection occasions occurred as returning adult fish ascended fish ladders at Bonneville and McNary Dams, which are the primary passage routes upstream through these dams. The seventh and final capture occasion occurred at the fish ladder at Tumwater Dam on the mainstem of the Wenatchee River, which all fish must transit to return to their natal streams.

We used data on several environmental variables as covariates in our analysis. Wenatchee River discharge data were recorded at USGS gauge 12,459,000 and obtained using the dataRetrieval package in R version 4.0.4 (De Cicco et al., 2018; R Core Team, 2021). Air temperature data were recorded at Wenatchee Pangborn Airport and obtained from the National Weather Service

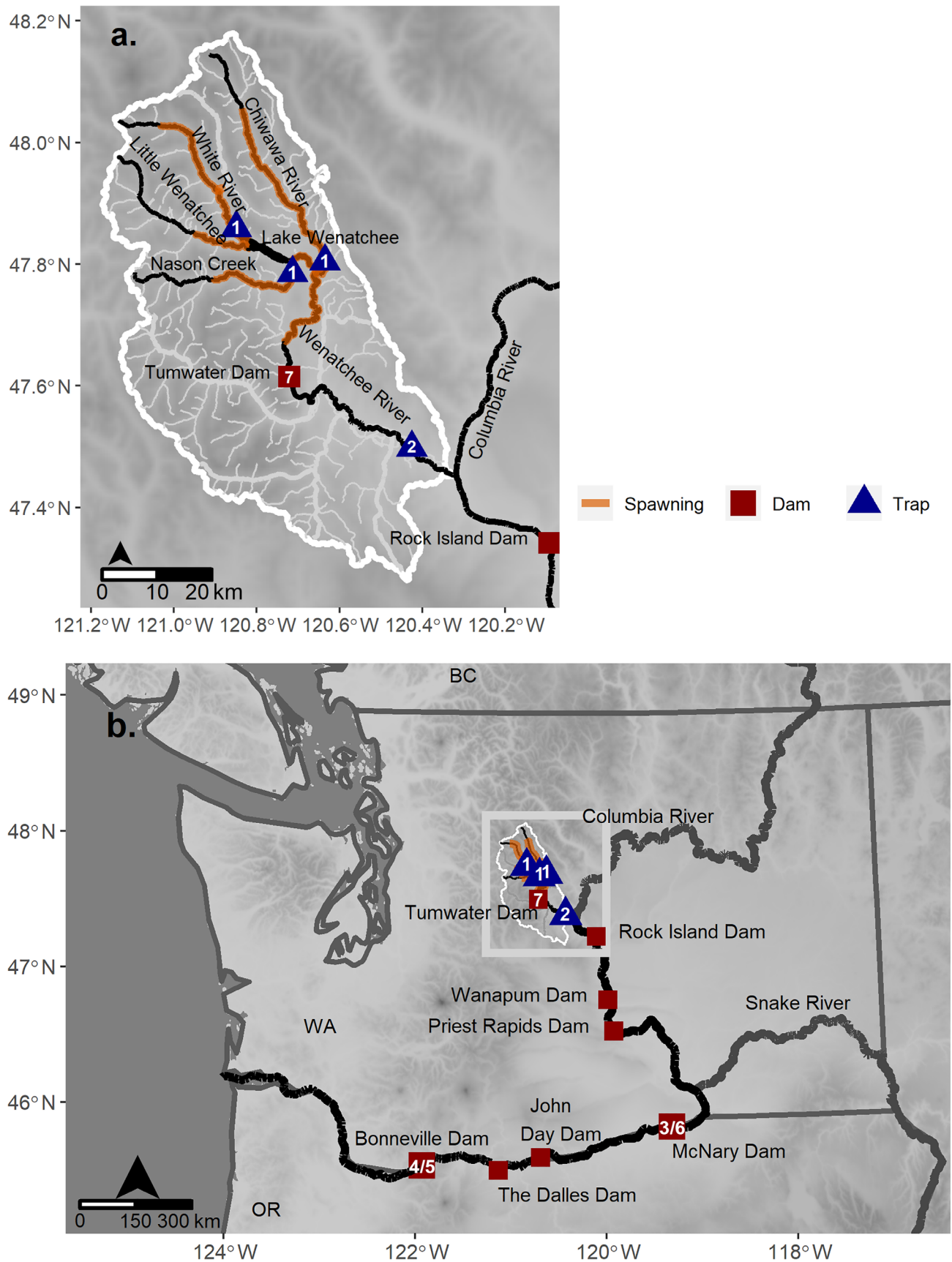


FIGURE 1 Maps of the Wenatchee River Basin (a) and the Columbia River migration corridor (b). The numbers on dams and traps represent the detection occasions corresponding with fish passing each location. Survival and return-rate intervals in the model represent the period between when fish pass different detection locations, with the first survival interval occurring between detection occasions one and two.

using the NOWData webtool (<https://w2.weather.gov/climate/xmacis.php?wfo=otx>). Data on discharge and spill percentage at mainstem Columbia River Dams were obtained using the Columbia Basin Research Data Access in real-time webtool (http://www.cbr.washington.edu/dart/query/river_graph_text). Processed data on seasonal sea surface temperature (<https://www1.ncdc.noaa.gov/pub/data/cmb/ersst/v5/netcdf/>) and coastal upwelling anomalies (<https://www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon>) were obtained from the github repository (bchasco/SAR_paper) associated with Chasco et al. (2021).

Model description

We used a multistate mark–recapture model to estimate downstream survival and ocean return rate ($\phi_{t,l,s,y}$) by interval (t , defined as the time between two detection occasions), juvenile LHP (l), natal stream (s), and year (y); upstream adult survival ($\phi_{t,y,a}$) by interval, year, and age (a); and maturation probabilities ($\psi_{l,y,a}$) by juvenile LHP, year, and age (Brownie et al., 1993; Neil Arnason, 1973). Because fish could not be observed after passing downstream of Bonneville Dam unless they returned to Bonneville Dam one to three years later (occasion five), annual marine survival and maturation (i.e., return) probabilities were confounded and not separately identifiable without making assumptions such as constant annual survival. Instead, we modeled the probability of return, at any age, for all fish entering the ocean each year, and conditional on return, the probabilities of fish spending 1, 2, or 3 years at sea (Buhle et al., 2018).

Survival and marine return rates

Juvenile survival and return rates (ϕ) were modeled as follows:

$$\begin{aligned} \text{logit}(\phi_{t,l,s,y}) &= \alpha_t + \mathbf{x}_{t,l,s,y}\boldsymbol{\beta} + \delta_{t,y} + \epsilon_{t,l,y} \\ \delta_{t,y} &\sim N(0, \sigma_t), \\ \epsilon_{t,l,y} &\sim N(0, \tau_{t,l}) \end{aligned} \quad (1)$$

where α_t is an interval-specific intercept, $\mathbf{x}_{t,l,s,y}$ is a row of the design matrix coding covariates and categorical effects, $\boldsymbol{\beta}$ is a vector of coefficients, $\delta_{t,y}$ are random effects of year specific to each survival interval, and $\epsilon_{t,y,l}$ are random effects of year specific to each survival interval and LHP (where certain LHPs were grouped in some intervals). The reasons for including the synchronous random effect of year, $\delta_{t,y}$, that affected all LHPs were so that the model could be used for prospective simulations that

account for synchrony, and to provide information about the degree of synchrony. The random effects of year were assumed to be normally distributed around zero with SD σ_t for effects modeled as synchronous across LHPs, and $\tau_{t,l}$ for effects modeled as asynchronous across individual LHPs. We did not include random effects of year that were specific to individual natal streams due to small sample sizes for some streams.

To improve parameter identifiability and increase model parsimony, we applied penalized-complexity priors (Simpson et al., 2017) on coefficients $\boldsymbol{\beta}$ and random effects of year. Each coefficient (β_n) was assumed to be drawn from a zero-centered normal distribution, $\beta_n \sim N(0, v_{\beta_n})$, with a SD (v_{β_n}) that was unique to each coefficient in the model. An exponential penalty was applied on each SD, $v_{\beta_n} \sim \exp(\lambda_t)$, where the rate parameter (λ_t) determined the strength of the penalty and was applied to all v_{β_n} within a given interval. In addition, to help with model fitting, a penalty-rate parameter (λ_t^{rand}) was fit and applied for random-effect SDs, $\sigma_t \sim \exp(\lambda_t^{\text{rand}})$, and $\tau_{t,l} \sim \exp(\lambda_t^{\text{rand}})$, in each interval t . We used a prior for the penalty-rate parameters, for example, $\lambda_t \sim \text{half-normal}(0, \text{SD} = 50)$, to constrain those that were not well informed by the data. The covariates, categorical effects, and random-effects structures included in each survival interval are presented in Table 1. We used sum-constraint coding for all categorical variables in the design vectors ($\mathbf{x}_{t,l,s,y}$) so that we penalized deviations from across-category averages.

During the first survival interval (from first capture to passage of the screw trap at the confluence of the Wenatchee and Columbia Rivers), we fit penalized effects of juvenile LHP, natal stream, and their interaction. In the second through fourth intervals, we grouped the two downstream-rearing LHPs (summer and fall subyearling emigrants; downstream rearing), to increase statistical power considering the relatively small sample size of summer subyearling emigrants. This decision was also supported by our observation that the two downstream-rearing LHPs had similar detection timing on occasions two through four (Appendix S1: Figure S2). In contrast, natal-reach-rearing emigrants had different detection timing on these occasions. Therefore, during the second through fourth survival intervals, we modeled penalized effects of grouped LHP (downstream vs. natal-reach rearing), natal stream, and their interaction.

During the first interval, we included the effects of average annual winter (November–February) air temperature and Wenatchee River discharge on survival of summer subyearling and fall subyearling LHPs (Favrot & Jonasson, 2020), allowing for separate effects by LHP but assuming common effects across natal streams. We did not include the effects of first-winter covariates on survival of yearlings

TABLE 1 Variables included in models of survival probabilities (ϕ) following each detection occasion, conditional probabilities of age at return from the ocean given survival (ψ), and detection probabilities (p) on each occasion.

Occasion/interval	Variables
ϕ	
1-Natal emigration	LHP + Stream + LHP \times Stream + DS \times Win.flow + DS \times Win.air + (1 Year) + (LHP Year)
2-Lower Wenatchee	NR.DS + Stream + NR.DS \times Stream + (1 Year) + (NR.DS Year)
3-McNary.juv	NR.DS + Stream + NR.DS \times Stream + (1 Year) + (NR.DS Year)
4-Bonneville.juv	NR.DS + Stream + NR.DS \times Stream + NR.DS \times SST.Arc.Win + NR.DS \times CUI.Spr + NR.DS \times SST.WA.Sum + (1 Year) + (NR.DS Year)
5-Bonneville.ad	Ad.age + (1 Year)
6-McNary.ad	Ad.age + (1 Year)
ψ	
4-Bonneville	NR.DS + (1 Year)
p	
2-Lower Wenatchee	LHP + Stream + LHP \times Stream + (1 Year) + (LHP Year)
3-McNary.juv	NR.DS + Stream + NR.DS \times Stream + NR.DS \times Flow + NR.DS \times Spill + (1 Year) + (NR.DS Year)
4-Bonneville.juv	NR.DS + Stream + NR.DS \times Stream + NR.DS \times Flow + NR.DS \times Spill + (1 Year) + (NR.DS Year)
5-Bonneville.ad	Ad.age + (1 Year)
6-McNary.ad	Ad.age + (1 Year)
7-Tumwater.ad	...

Note: Variables in parenthesis were random effects, where the term before the vertical bar was the grouping variable. Detection probability at Tumwater Dam for adults was assumed to be 1.0. Interval represents a period between two capture occasions during which survival, return rate, and return age were estimated, where the first interval is between occasions one and two.

Abbreviations: Ad.age, adult age; CUI.Spr, coastal upwelling off of the coast of Washington State in spring; DS, downstream-rearing LHPs (only summer and fall subyearlings); Flow, discharge measured at a dam of detection; LHP, juvenile life history pathway; NR.DS, juvenile life history pathways where summer and fall subyearlings are grouped (i.e., natal-reach vs. downstream rearing); Spill, percentage of water spilled at dam of detection; SST.Arc.Win, sea surface temperature in a broad area in the northeast Pacific Ocean defined by Johnstone and Mantua (2014) in winter; Stream, natal stream; SST.WA.Sum, sea surface temperature off the coast of Washington State in summer; Win.air, winter air temperature in the Wenatchee Basin; Win.flow, winter discharge in the Wenatchee River.

because they were not tagged until their second spring, so their first survival interval did not include overwinter survival. Based on relationships between Chinook salmon marine return rates and environmental covariates reported by Crozier et al. (2021), we evaluated the effects of three covariates on return rates (fourth interval): average sea surface temperature in an arc of the northeast Pacific Ocean defined by Johnstone and Mantua (2014) during December–February prior to the spring when fish entered the marine environment, coastal upwelling anomalies off the coast of Washington State at 45° longitude by –125° latitude from March through May in the spring when fish entered the ocean, and sea surface temperature in a 2° square bounded by 46° to 48° latitude and –124° to –126° longitude off the coast of Washington State during the summer (July–August) after fish entered. Coefficients for all environmental covariates on survival during intervals two through four were allowed to vary between natal-reach and downstream-rearing LHPs but were assumed to be common across natal streams to increase statistical power to detect relationships. All environmental covariate values were Z-score transformed prior to inclusion in the analysis.

In the fifth and sixth survival intervals, representing adult upstream migration, we did not model the effects of juvenile LHPs nor natal streams on survival, assuming that carryover effects from the juvenile life stage would be diminished by adulthood and due to the smaller numbers of detections of returning adults (Table 1). Instead, we modeled the effects of adult return age (a) on survival, as might result from age-specific migration timing differences and seasonality in fisheries or physical conditions in the river. Adult survival was modeled as follows:

$$\text{logit}(\phi_{t,y,a}) = \alpha_t + \mathbf{x}_{t,y,a}\boldsymbol{\beta} + \delta_{t,y}, \quad (2)$$

$$\delta_{t,y} \sim N(0, \sigma_t)$$

where α_t is an occasion-specific intercept, $\mathbf{x}_{t,y,a}$ is a row of the design matrix coding age effects, $\boldsymbol{\beta}$ is a vector of coefficients, and $\delta_{t,y}$ are random effects of year specific to each survival interval. No asynchronous year effects were included for upstream adult survival, due to the lower statistical power, given the smaller number of adult detections.

Return ages

The conditional probabilities ($\psi_{l,y}$) of returning at ages three, four, or five given that a fish returned from the ocean were modeled using a multinomial logit link (Aitchison, 1982),

$$\text{mlogit}(\psi_{l,y}) = \alpha^\psi + \mathbf{x}_{l,y}^\psi \boldsymbol{\beta}^\psi + \delta_y^\psi, \quad (3)$$

$$\delta_y^\psi \sim N(0, \boldsymbol{\Sigma}^\psi)$$

where α^ψ represents intercepts for ages three and five in multinomial logit space (age four is the reference age), $\mathbf{x}_{l,y}^\psi$ is a row of the design matrix coding effect of natal-reach and downstream-rearing LHP, and $\boldsymbol{\beta}^\psi$ is a vector of coefficients. These differences were penalized in the same fashion as coefficients in the model of survival, with penalty-rate parameter λ^ψ . We modeled only random effects of year that were synchronous across LHPs (δ_y^ψ) for adult return age probabilities due to limited power to fit asynchronous random effects of year. The synchronous random effects of year for the proportions returning at ages three and five relative to age four in logit space were bivariate normally distributed with covariance matrix $\boldsymbol{\Sigma}^\psi$ to account for the inherent correlation in the proportions of the population that returned at different ages each year (Buhle et al., 2018). The marginal SDs of the random effects of year, $\sigma^\psi = \text{diag}(\boldsymbol{\Sigma}^\psi)^{0.5}$, were penalized as described above for the random-effect SDs in the survival model, $\sigma^\psi \sim \exp(\lambda^\psi \text{rand})$.

Detection

Detection probabilities were modeled in logit space using the same specification of categorical effects and random effects of year as for survival (Table 1). However, different covariates were used, as described below. Coefficients and random effects of year were penalized in the same way as for survival, with unique penalty-rate parameters λ_t^p and $\lambda_t^{p\text{rand}}$ for each occasion.

On the third and fourth detection occasions (juvenile detection at McNary and Bonneville Dams), we included effects of average daily discharge and spill percentage in May–June at McNary and Bonneville Dams, as these could affect the proportion of fish going through the juvenile bypass systems, spillways, or turbines. Just as for survival probabilities, we allowed for different effects of environmental covariates—flow and spill—on detection probabilities of natal-reach and downstream-rearing LHPs, because of their different migration timing, but assumed common effects across natal streams.

Detection probability on the final occasion (Tumwater Dam) was fixed at 1.0, which ensured identifiability of

the final interval-specific survival rate. This detection probability was supported by the auxiliary observation that out of 465 fish that were known to have passed Tumwater Dam as adults because they were detected at downstream dams on the mainstem Columbia River and then on PIT detection arrays in natal tributaries upstream of Tumwater Dam, 464 (99.78%) were detected in adult fish ladders in Tumwater Dam.

Model fitting

The likelihood of the data for a given set of parameters was calculated using the forward algorithm (McClintock et al., 2020; Zucchini et al., 2016) and the Laplace approximation of the marginal log-likelihood integrated over random effects by the package TMB in R (Kristensen et al., 2016; R Core Team, 2021). We fit the model by minimizing the negative marginal log-likelihood, which was conducted in R using the `TMBhelper::fit_tmb` function, which relies on the `base::nlminb` optimization algorithm (Gay, 1990; Thorson, 2020). Fixed effects were intercepts, SDs, covariance, and penalty-rate parameters. The random effects were the regression coefficients and all random effects of year. To calculate 95% CIs for derived quantities, we conducted a parametric bootstrap where we sampled 10,000 fixed and random effects from a multivariate normal distribution defined by the maximum marginal likelihood estimates and the inverse Hessian matrix returned by TMB, then calculated derived quantities with each sample parameter set and found the quantiles corresponding with the 95% CI.

Goodness of fit

We assessed goodness of fit by examining scaled quantile residuals (Dunn & Smyth, 1996; Gelman, 2006). We simulated 250 datasets of the same size as the observed data by sampling from binomial distributions for survival and detection, and multinomial distributions for return age, conditional on the marginal maximum likelihood estimates (MLEs) of parameters. Conditional simulations were conducted using the MLEs of model parameters and random effects of year, while marginal simulations were conducted using the MLEs of model parameters (including coefficients) but simulating random effects of year based on the mean and SD of their distributions (Conn et al., 2018). We summarized, simulated, and observed datasets by the number of detections on each occasion from each release group (LHP by stream by year) and adult age for adult detection occasions. We used the DHARMA package (Hartig, 2021) to calculate

scaled quantile residuals for the summarized numbers of detections and to interrogate the residuals for outliers and departures from uniformity.

In addition, we calculated p values by sampling 500 parameter sets from the multivariate normal distribution defined by the MLEs and inverted Hessian matrix and calculating the Freeman–Tukey fit statistic, $\sum_t \sum_l \sum_s \sum_y \sum_a \left(\sqrt{d_{t,l,s,y,a}} - \sqrt{E[d_{t,l,s,y,a}]} \right)^2$ for observed and simulated data generated with each parameter set (Conn et al., 2018). Here, $d_{t,l,s,y,a}$ is the summarized number of detections at a given occasion for fish of a given juvenile LHP, natal stream, year, and age, and $E[d_{t,l,s,y,a}]$ is the expectation of that number of detections given the model and a particular parameter set. The p value was then calculated as the proportion of parameter sets in which the Freeman–Tukey fit statistic for the simulated data was greater than the statistic for the observed data. We calculated p values either conditionally given the fitted random effects of year or marginally by sampling random effects of year from their hyper-distributions (Conn et al., 2018).

RESULTS

Average survival of fish from the White River during the first interval, which included migration through a lake,

was lower than the average across all three natal streams (effect size = -0.786 ; 95% CI = $-1.117, -0.451$) (Figure 2, Appendix S1: Table S1). Here and in the remainder of the Results section, effect size refers to the magnitude of the effect on the logit-scale parameter estimate. Winter air temperature was negatively associated with survival of summer (-0.435 ; 95% CI = $-0.641, -0.228$) and fall (-0.289 ; 95% CI = $-0.511, -0.068$) subyearling LHPs (Appendix S1: Figure S1).

Both the timing of detection on the second occasion (the mouth of the Wenatchee River) and third occasion (McNary Dam), and survival of fish during the interval, differed between natal-reach and downstream-rearing life histories. The median detection day at the mouth of the Wenatchee River was 19 days earlier for downstream-rearing fish than natal-reach-rearing fish across natal streams, and 9 days earlier at McNary Dam (Appendix S1: Figure S2). Between the mouth of the Wenatchee River and McNary Dam (second survival interval), there was some evidence that downstream-rearing fish from the Chiwawa River had lower survival than natal-stream-rearing fish (-0.367 ; 95% CI = $-0.539, 0.139$), whereas there was little evidence of this for fish from Nason Creek (-0.033 ; 95% CI = $-0.295, 0.220$) or the White River (0.286 ; 95% CI = $-0.272, 0.520$; Figure 3, Appendix S1: Table S1). We did not detect survival differences among LHPs during the third interval, which

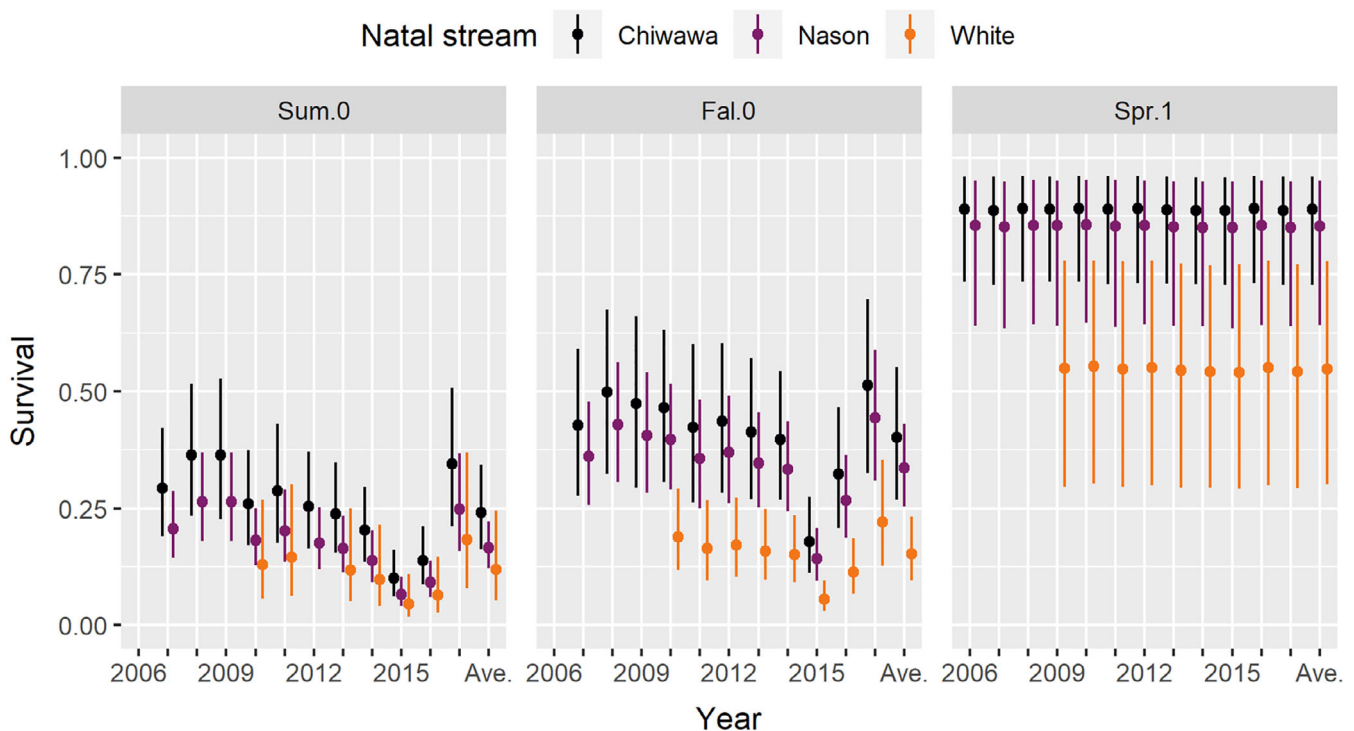


FIGURE 2 Annual survival estimates between release near the mouths of three natal streams, Chiwawa River, Nason Creek, and White River, and passing the mouth of the Wenatchee River en route to the ocean, for fish expressing three different juvenile life history pathways (LHPs). The three juvenile LHPs are fish that emigrated from their natal stream as subyearlings in summer (Sum.0) or fall (Fal.0), or as yearlings in spring (Spr.1). Points represent median estimates and lines span 95% CIs. The final points on the x -axis represent across-year medians. Ave., Average.

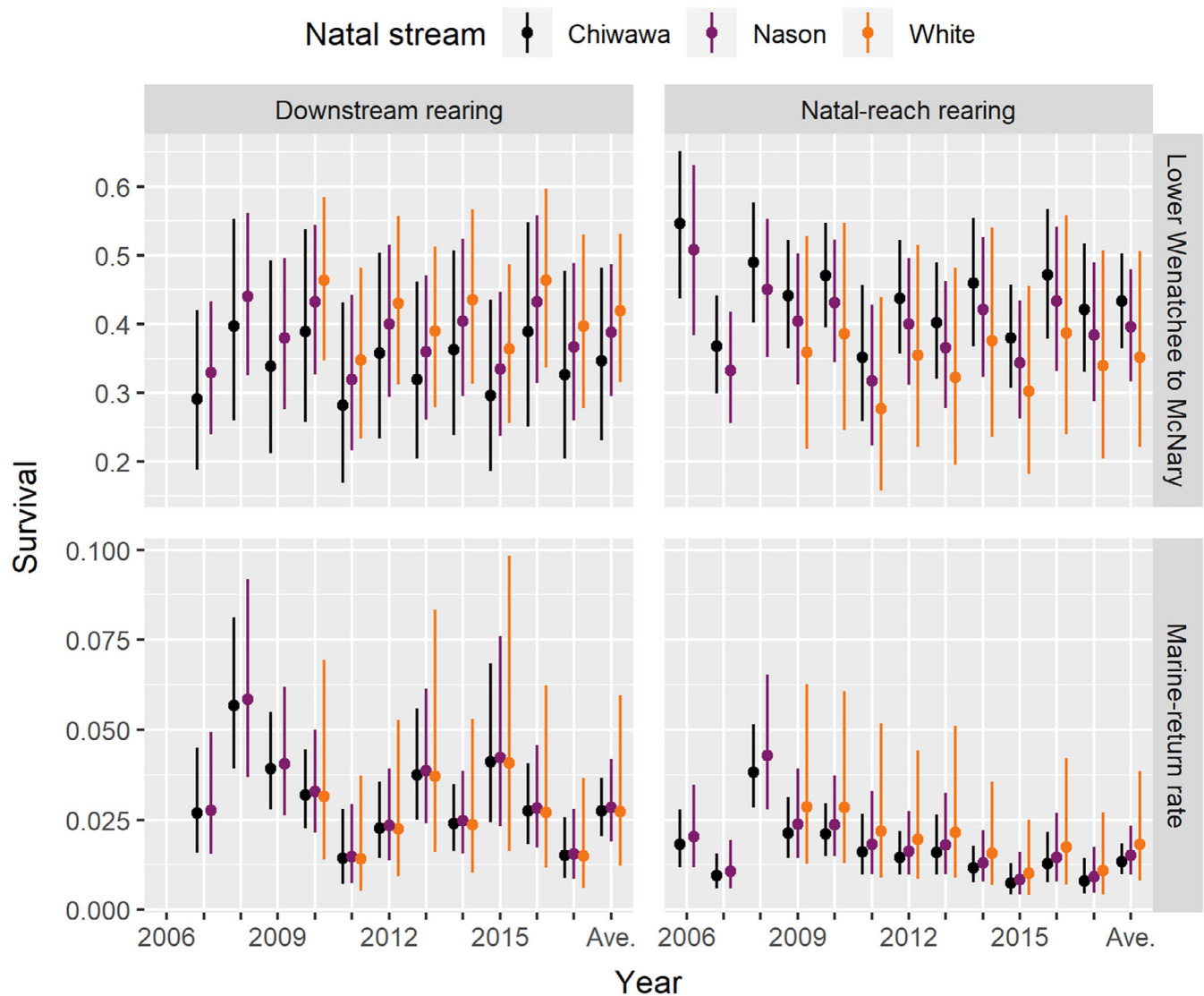


FIGURE 3 Annual survival estimates between the mouth of the Wenatchee River and McNary Dam (top row) and marine return rates between passing downstream of Bonneville Dam as a juvenile and returning to Bonneville Dam as an adult between 1 and 3 years later (bottom row). Different juvenile life history pathways (LHPs) are shown in different columns of panels and natal streams are indicated by color. Points represent median estimates and lines span 95% CIs. The final points on the *x*-axis represent across-year medians. Ave., Average.

represented the second stretch of the downstream migration (Appendix S1: Table S1).

We identified differences among LHPs in timing of ocean entry, return rates (a function of survival and return age), and relationships between return rates and sea surface temperature and upwelling covariates. Downstream-rearing fish passed Bonneville Dam 10 days earlier as juveniles on average than natal-reach-rearing fish and returned at a higher rate on average than natal-reach-rearing fish (0.597; 95% CI = 0.117, 1.078; Figure 3, Appendix S1: Table S1). Return rates of downstream-rearing fish were positively associated with coastal upwelling in spring (0.327; 95% CI = 0.080, 0.574), but we did not detect the same relationship for natal-reach-rearing fish (−0.001; 95% CI = −0.133, 0.131; Appendix S1: Figure S1).

Instead, return rates of natal-reach-rearing fish were negatively correlated with sea surface temperature off the coast of Washington State during summer (−0.311; 95% CI = −0.554, −0.069). There was relatively little evidence of such a correlation for downstream-rearing fish (−0.119; 95% CI = −0.329, 0.092). Spring upwelling and summer sea surface temperature were not meaningfully correlated with each other (0.25 Pearson correlation).

Most adult fish returned at 4 years of age in both natal-reach (0.739 probability of returning at age four; 95% CI = 0.660, 0.801) and downstream-rearing fish (0.750; 95% CI = 0.680, 0.803), but there were differences between LHPs in proportions returning at ages three and five (Figure 4, Appendix S1: Table S2). The proportion of age-three returning adults was higher among

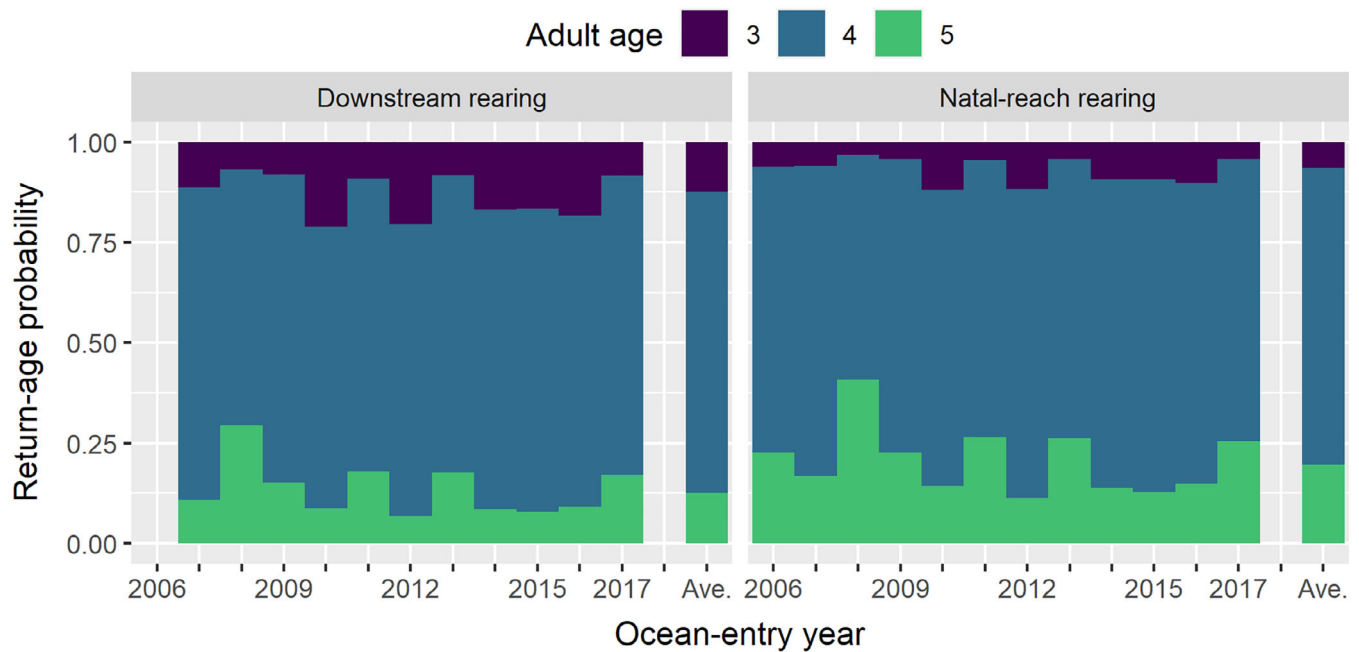


FIGURE 4 Maximum likelihood estimates of probabilities of surviving adult salmon returning from the ocean at different ages by juvenile life history pathway and year. The final bars on the x-axis represent across-year medians. Ave., Average.

downstream-rearing fish (0.123; 95% CI = 0.075, 0.192) than natal-reach-rearing fish (0.065; 95% CI = 0.035, 0.117). The proportion of age-five returning adults was lower among downstream-rearing fish (0.126; 95% CI = 0.078, 0.193) than natal-reach-rearing fish (0.195; 95% CI = 0.131, 0.277).

Goodness of fit indicated that the model adequately fit the data. Scaled quantile residuals were approximately uniformly distributed based on examination of Q–Q plots and plots of simulated residuals versus observations, and the numbers of outliers did not exceed the range of expectations (Appendix S1: Figures S8–10). The p value conditional on the fitted random effects of year was 0.312, and when we sampled the random effects of year from their hyper-distributions, it was 0.700, neither of which indicated a lack of fit.

DISCUSSION

We found that marine return rates of the distinct life history types (defined by their behavior as juveniles) responded differently to environmental drivers in the marine environment. These results should contribute to asynchronous year-to-year variability in return rates among LHPs within populations, which should dampen the variance in return rates of the aggregate population (Elmqvist et al., 2003; Kendall & Fox, 2002). This is akin to differential responses to environmental variability that has previously been observed among populations of

Chinook salmon (Braun et al., 2016) and sockeye salmon (*Oncorhynchus nerka*) (Freshwater et al., 2017) that exhibit different ages at ocean entry and behave differently upon ocean entry. The different relationships between marine return rates and environmental variables that we identified may have been facilitated in part by differences in ocean-entry timing that we observed. Additionally, differences among LHPs in habitat use and feeding behavior in the ocean, or body condition, might have contributed to different relationships with environmental variables.

We found that downstream-rearing fish entered the marine environment earlier and returned from the ocean at a higher rate than natal-reach-rearing fish. Earlier marine entry timing has been associated with higher rates of return from the ocean in multiple populations and species of salmon in the Columbia River Basin (Chasco et al., 2021; Scheuerell et al., 2009; Wilson et al., 2021), suggesting that earlier downstream migration may have contributed to the higher return rates of downstream-rearing LHPs. The downstream-rearing LHPs were detected entering the downstream-migration corridor 19 days earlier than natal-reach-rearing LHPs but were detected only 10 days earlier on the final occasion before ocean entry, suggesting that migration was slower for downstream-rearing LHPs. This suggests a potential survival trade-off wherein earlier seaward departure is associated with slower migration and potentially lower migration survival for downstream-rearing LHPs but confers the benefit of earlier ocean entry and higher marine survival. However, our analysis provided

evidence of lower downstream-migration survival in downstream-rearing LHPs from only one of three natal streams.

Salmon smolt survival has also been shown to be positively associated with growth rate and size (Norrie et al., 2022; Tomaro et al., 2012), which presumably affect predation risk, as well as the degree of physiological preparedness for the transition to the marine environment (i.e., smoltification; Wedemeyer et al., 1980). Therefore, differences in growth rate, size, and smoltification among the LHPs may also have contributed to differences in return rates.

We also observed that downstream-rearing LHPs returned from the ocean at younger ages on average, reducing time at sea to grow but also reducing exposure to marine mortality. This likely contributed to the higher return rates of downstream-rearing LHPs. Females that return at younger ages are generally smaller and have fewer eggs (Healey & Heard, 1984), and the smaller size of early returning males makes them less effective at competing for mates (Berejikian et al., 2010). Thus, there is a trade-off between return rate and fecundity or fertility (Gross, 1985), which the alternative LHPs navigate differently. The differences in return ages between LHPs should contribute to population stability by spreading the reproductive effort of each individual generation more uniformly across future generations (Schindler et al., 2010).

The younger return age of downstream-rearing LHPs relative to natal-reach-rearing LHPs may be influenced by both environmental and genetic factors (Waters et al., 2021). Tréhin et al. (2021) found that marine growth rates during the first year at sea were positively associated with the probability of maturation after only one year at sea in Atlantic salmon (*Salmo salar*). A number of studies have found that larger salmon smolts tend to return at younger ages (Gregory et al., 2019; Scheuerell, 2005; Tattam et al., 2015). Additionally, genetic and environmental factors experienced early in life may have set downstream-rearing fish on a trajectory for a faster life history wherein they initiated emigration from natal streams, seaward migration, and marine return all at younger ages than did natal-reach-rearing fish.

For downstream-rearing LHPs in our system, survival while rearing in downstream habitats of the Wenatchee River Basin was negatively associated with winter air temperature. Winters are warming in this region and are projected to continue to do so (Mantua et al., 2010; Masson-Delmotte et al., 2021), suggesting that survival rates of fish overwintering in downstream habitats may decline. Warmer air temperature is associated with warmer water temperature, which may increase metabolic demand during winter when food is scarce. This may lead to starvation or increased time spent foraging

and associated predation risk (Favrot & Jonasson, 2020). We were not able to estimate the overwinter survival of natal-reach-rearing fish within the natal reach because fish were not tagged until emigration. However, knowing how average overwinter survival differed between natal-reach and downstream-rearing fish, and whether they exhibit different responses to winter air temperature, could reveal further trade-offs and asynchrony among LHPs.

The dataset that we analyzed contained limited information to assess some parameters of interest. It only included fish that were >60 mm upon emigration from the natal stream and therefore excluded approximately 13% of all emigrants. Most of these small fish emigrate in a pulse during the spring considerably earlier than the summer subyearling LHP, and consequently can be assumed to represent an additional LHP that is not considered in this study (Sorel, 2022a, 2022b). Additionally, recapture probabilities were particularly low during the second capture occasion at the lower Wenatchee screw trap, which contributed to uncertainty in estimates of survival, especially during the first and second intervals. This contributed to uncertainty about survival during the first two intervals and limited our ability to identify differences in survival between LHPs during downstream migration.

Combining our model with a model of the production of juvenile emigrants expressing alternative LHPs as a function of adults returning to the basin within an integrated population model (Buhle et al., 2018; Plard et al., 2019; Schaub & Abadi, 2011) would allow for population projection and assessment of the contribution of alternative LHPs to population productivity and stability (Sorel, 2022a). Because our multistate model includes both synchronous (common among LHPs) and asynchronous variability in demographic rates as functions of ecological variables and unidentified sources of stochasticity (through random effects of year), it can be used to simulate population trajectories that reflect this variability in vital rates (Kendall & Fox, 2002). A population model accounting for differences in demographic rates between LHPs would be able to capture differential effects on LHPs of alternative management strategies such as restoration of habitat in natal streams versus restoration in downstream areas. Lastly, the relationships that we identified between environmental variables and demographic rates could be used to simulate the effects of projected climate change on demographic rates and population trajectories (e.g., Crozier et al., 2021).

Our model allowed us to identify sources of demographic asynchrony and adult life history diversity among fish exhibiting different juvenile LHPs, which have important implications for conservation and natural resource management in a changing world. Population

traits that contribute to stability in variable environments may be important for reducing the impact of changing environmental conditions and increasing environmental variability on population dynamics (Mantua et al., 2010; Masson-Delmotte et al., 2021; Moran et al., 2016). Therefore, conserving juvenile life history diversity is one tool that can be used to conserve populations and the sustainable provisioning of ecosystem services (Cordoleani et al., 2021).

As long-term population-monitoring datasets continue to grow and more complex modeling techniques are developed and refined, there should be new opportunities to assess individual heterogeneity in populations and understand its consequences for population dynamics (Gimenez et al., 2018). One advantage of this type of modeling is that it allows assessment of asynchronous variability through time in demographic rates and abundance among groups of individuals (Kendall & Fox, 2002; van Daalen & Caswell, 2020). Further, considering population components individually allows for the detection of relationships between demographic rates and environmental variables that may not be detectable when considering an entire population in aggregate (Guéry et al., 2017). These relationships may enable better prediction of population responses to environmental change when that change differentially affects population components (Moran et al., 2016; Vindenes et al., 2008). For these reasons, we see models that account for individual heterogeneity in demographic rates as valuable tools for learning about drivers of population dynamics and effectively managing populations.

ACKNOWLEDGMENTS

Funding for this research was provided by the National Oceanographic and Atmospheric Administration Northwest Fisheries Science Center, the Washington Cooperative Fish and Wildlife Research Unit, and the Northwest Climate Adaptation Science Center. Data collection was funded by Grant County Public Utilities District, Chelan County Public Utilities District, the Washington Department of Fish and Wildlife, Yakama Nation Fisheries, Bonneville Power Administration, Washington Department of Ecology, the U.S. Geological Survey, the U.S. National Weather Service, and others. We thank the many biologists and technicians who have tagged juvenile Chinook salmon in the Wenatchee River Basin and who maintain and operate recapture and detection locations on the Columbia River. We also thank the organizations and individuals who maintain databases for accessing data, including the Pacific States Marine Fisheries Commission and Columbia Basin Research. We are grateful for helpful reviews of previous versions of this manuscript by Abby Bratt, Brielle Thompson, Nathan Hostetter, and two

anonymous reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.


DATA AVAILABILITY STATEMENT

Data and code (Sorel, 2022b) are available from Zenodo: <https://doi.org/10.5281/zenodo.7328840>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sorel, Mark H., Andrew R. Murdoch, Richard W. Zabel, Jeffrey C. Jorgensen, Cory M. Kamphaus, and Sarah J. Converse. 2023. "Juvenile Life History Diversity is Associated with Lifetime Individual Heterogeneity in a Migratory Fish." *Ecosphere* 14(1): e4366. <https://doi.org/10.1002/ecs2.4366>