

# Incorporating life history diversity in an integrated population model to inform viability analysis

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## Abstract

Life history diversity can significantly affect population dynamics and effects of management actions. For instance, variation in individual responses to environmental variability can reduce extirpation risk to populations, as the portfolio effect dampens temporal variability in abundance. Moreover, differences in habitat use may cause individuals to respond differently to habitat management and climate variability. To explore the role of life history diversity in population trajectories, population models need to incorporate within-population variation. Integrated population modeling (IPM) is a population modeling approach that offers several advantages for sharing information and propagating uncertainty across datasets. In this study, we developed an IPM for an endangered population of Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA, that accounts for diversity in juvenile life histories, spawning location, and return age. Our analysis revealed that diversity in the age of juvenile emigration from natal streams had a portfolio effect, resulting in a 20% reduction in year-to-year variability in adult abundance in population projections. Our population viability analysis suggests that management interventions may be necessary to meet recovery goals, and our model should be useful for simulating the outcomes of proposed actions.

**Key words:** chinook salmon (*Oncorhynchus tshawytscha*), endangered species, hatchery supplementation, life cycle model, portfolio effects, synchrony

## Introduction

Heterogeneity within a species or population, while often ignored or regarded as a nuisance in demographic parameter estimation, is an important biological phenomenon that influences and is influenced by life history trajectories, demography, and eco-evolutionary dynamics (Hamel et al. 2018). Heterogeneity can contribute to population stability when it results in asynchronous variability among individuals with different traits, a phenomenon known as the portfolio effect (Kendall and Fox 2002; Schindler et al. 2010). Some of this asynchrony may result from different demographic responses to environmental variability through time among individuals with unique traits (Gimenez et al. 2018; Forsythe et al. 2021). Furthermore, the distribution of heterogeneous life history traits such as growth, survival, and movement within a population may respond to population states (e.g., density dependence), which can in turn affect population trajectories (e.g., Martin et al. 2022). Therefore, considering within-population heterogeneity may be key to understand-

ing population-scale phenomena such as habitat use, population regulation, and response to environmental factors like anthropogenic climate change (Armstrong et al. 2021).

Increasingly, examples exist of ways in which within-population heterogeneity and its interaction with the environment can be accounted for in population models (Clark and Mangel 2000; Grimm et al. 2006; Plard et al. 2019a). Matrix population models often include effects of discrete traits (e.g., natal habitat patch and resident vs. migrant) on demographic rates, while integral projection models include effects of continuous traits (e.g., natal latitude/longitude and migration timing) on demographic rates (Doak et al. 2021). Models can account for different traits being favored under different habitat conditions or population states, which may affect the fitness of individuals and the relative expression of different traits in the population (e.g., Reid et al. 2020). Furthermore, heterogeneity that is not tied to a particular trait can be accounted for, such as by using individual random effects (Gimenez et al. 2018). An array of modeling techniques

accounting for different aspects of within-population heterogeneity is being developed and applied to answer fundamental questions in population biology and to guide management in a changing world, resulting in more accurate and informative predictions of population dynamics (Buoro et al. 2012; Forsythe et al. 2021).

In the past 20 years, integrated population models (IPMs) have become a critical tool for improving the accuracy and precision of population models (Besbeas et al. 2002). IPMs, which link multiple datasets through a common population process model via a joint likelihood, provide a framework for estimating population parameters from multiple data sources and are increasingly used in population management (Maunder and Punt 2013; Zipkin and Saunders 2018). While IPMs have greatly expanded our capabilities in population modeling, there have been relatively few examples illustrating how to effectively include within-population heterogeneity in IPMs, and how those models can be applied to assess the effects of heterogeneity on population dynamics, and the effects of management actions and environmental variability on population trajectories (though see Plard et al. 2019a).

Endangered spring Chinook salmon in the Wenatchee River Basin of Washington, USA, exhibit multiple dimensions of within-population heterogeneity, with important potential effects on population dynamics. First, each individual is hatched in, and as an adult returns to, one of several distinct spawning areas, and most but not all fish return to the same area where they were hatched (Honea et al. 2009). Second, individuals express different juvenile life history pathways (LHPs), determined by the timing of migration from the natal area; some juveniles rear within their natal tributary throughout their first year of life, while others disperse to downstream-rearing habitat at a few relatively distinct times during the year (Buchanan et al. 2015). After a full year in freshwater, all juveniles embark on a migration to the marine environment. A third dimension of heterogeneity is the number of years spent at sea, which varies between 1 and 3 years in this population, before returning to freshwater to spawn and then die. Multiple datasets exist from several long-running monitoring programs to inform IPMs for these and other salmon in the Columbia River Basin (Hillman et al. 2020), including data on spawner abundance, juvenile abundance, and survival through the dammed mainstem Columbia River during migration (Ford et al. 2013; Buchanan et al. 2015; Murdoch et al. 2019). Managers need tools to evaluate the effects of hatchery supplementation, habitat modification, hydroelectric dams, and fisheries on population status of spring Chinook salmon and other endangered salmonids in the Columbia River Basin.

We developed an IPM for the Wenatchee River spring Chinook salmon population that accounts for heterogeneity in spawning location, juvenile LHP, and return age. We used the model to evaluate population viability and the effect of juvenile life history diversity on temporal variance in abundance (portfolio effects). This IPM provides a template for development of IPMs of other populations exhibiting important forms of within-population heterogeneity. Our population viability analysis accounted for parametric uncertainty, environmental and demographic stochasticity, and density-

dependent survival and life history expression. We found that juvenile life history diversity and the existence of multiple spatially distinct spawning aggregations contribute to population stability. The portfolio effect provided by this life history diversity helped mitigate the risk of the entire population falling below the quasi-extinction threshold of 50 total spawners; however, abundance still did not meet recovery goals of a geometric mean of 2000 spawners (UCSRB and NMFS 2007). The model we developed provides a basis for evaluation of management scenarios in future work.

## Methods

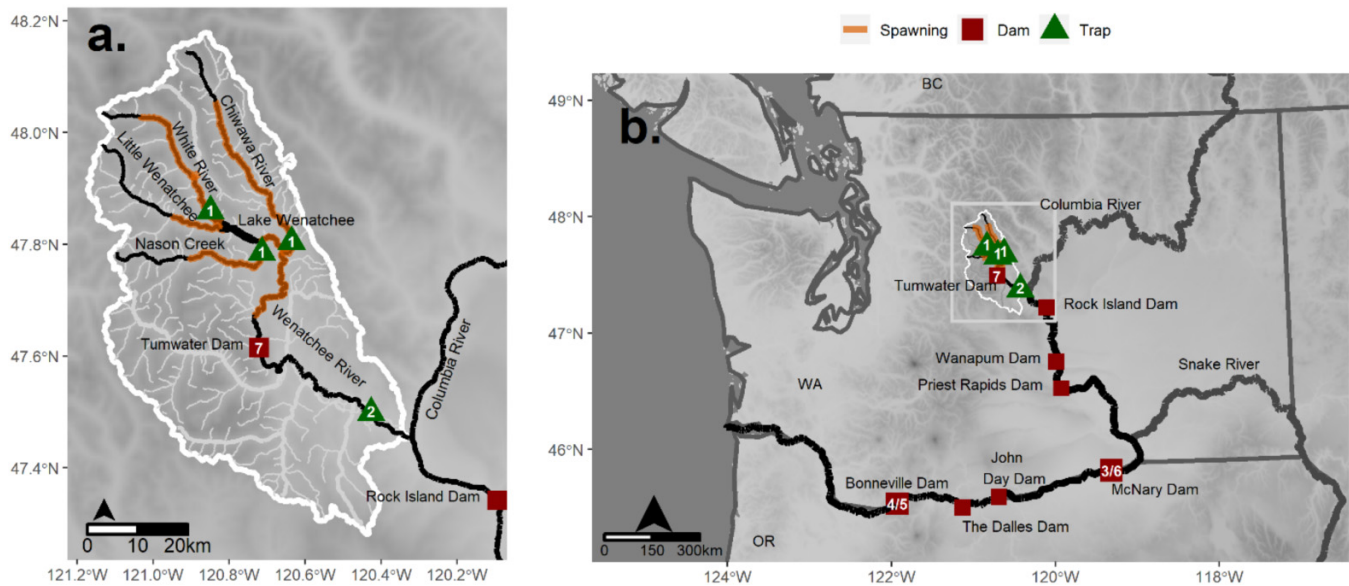
### Study species

The Wenatchee River drains from the east side of the Cascade Mountain Range in central Washington and meets the Columbia River at river kilometer 754 (Fig. 1). The population of spring Chinook salmon that spawns in the Wenatchee River Basin is part of the Upper Columbia River spring-run evolutionarily significant unit (ESU), designated as endangered under the U.S. Endangered Species Act (ESA) in 1999. This ESU is one of 29 threatened or endangered salmon and steelhead conservation units listed under the ESA.

Adult spring Chinook salmon return from the ocean to the Wenatchee River Basin in spring and spawn in autumn. Our model considers fish that spawn in three tributaries of the Wenatchee River—the Chiwawa River, Nason Creek, and the White River—which comprise approximately 90% of the population and which have been monitored for estimation of juvenile abundance as part of a hatchery-effectiveness monitoring program (Hillman et al. 2020). Juveniles emerge from nests in late winter and spend just over a year rearing within the Wenatchee River Basin or Columbia River before migrating to the ocean in their second spring of life. However, juveniles exhibit life history diversity: a portion rear within their natal tributary for the entirety of their freshwater juvenile rearing period, while others emigrate to downstream rearing areas at various times during their first year of life (Buchanan et al. 2015). Specifically, we consider the four juvenile LHPs identified in Sorel et al. (2023b): three LHPs that emigrate during their first year of life (*downstream-rearing LHPs*) in spring (*spr.0*), summer (*sum.0*), and fall (*fal.0*) and rear in mainstem habitats within the Wenatchee River system, and one LHP that emigrates at age 1 (*natal-reach-rearing LHP*) in spring (*spr.1*). All four LHPs migrate downstream through the Columbia River as 2-year-olds during the spring following hatching.

After migrating downstream through the mainstem Columbia River, which requires individuals to pass seven hydroelectric dams, fish enter the northeast Pacific Ocean where they rear for 1–3 years before maturing and returning through the Columbia River back to the Wenatchee River Basin to spawn. Fish pass Tumwater Dam, located on the Wenatchee River just downstream of the spawning habitat (Fig. 1), on their way to reproduce in the upper portions of the watershed. The population is supplemented by two integrated conservation hatchery programs, which use natural-origin fish in their broodstock to keep the hatchery popula-

**Fig. 1.** (a) Maps of the Wenatchee River Basin and the (b) Columbia River migration corridor. The numbers on dams (red squares) and traps (green triangles) represent the detection occasions corresponding with Chinook salmon passing each location. Detections of both juveniles moving downstream and adults moving upstream past McNary and Bonneville Dams were used. This map was created using projection EPSG:2856. Base map and data were obtained from the USGS National Hydrography Dataset (U.S. Geological Survey 2023a), the USGS Watershed Boundary Dataset (U.S. Geological Survey 2023b), PSMFC PTAGIS database (Pacific States Marine Fisheries Commission 2023), SRTM (CGIAR-CSI SRTM 2023), and Natural Earth.



tion more genetically related to the natural population. The programs release hatchery-origin juveniles in the Chiwawa River and Nason Creek, and a portion of returning adults from the hatchery population are allowed to pass upstream of Tumwater Dam to spawn with the natural population in the tributaries, contributing to natural production.

## Data sources

We used several data sources to develop our IPM (Fig. 2), including data from juvenile-migrant trapping to inform the abundance of juveniles expressing different LHPs, and mark-recapture data to inform juvenile survival rates, rates of return from the ocean (a function of survival and return age), and adult survival rates. We used data from surveys of the spawning grounds to inform female spawner abundance and the proportions of hatchery-origin spawners, and auxiliary data on the number of fish collected for hatchery broodstock and adult sex ratios. We also used information from the literature to develop informed priors on certain parameters.

**Screw traps**—we used estimates of the abundance of emigrants expressing different juvenile life history strategies generated from data collected at screw traps (Sorel et al. 2023b). A sample of juvenile emigrants from natal tributaries was captured in rotary screw traps operated downstream of spawning habitat. To estimate capture probability in the traps, mark-recapture trials were conducted wherein tagged fish were released upstream of traps and recaptures were recorded. The catch and mark-recapture data were used to estimate the abundance of daily emigrants (Sorel et al. 2023b).

Daily emigrant abundance estimates of each age were summed within discrete time periods each year that

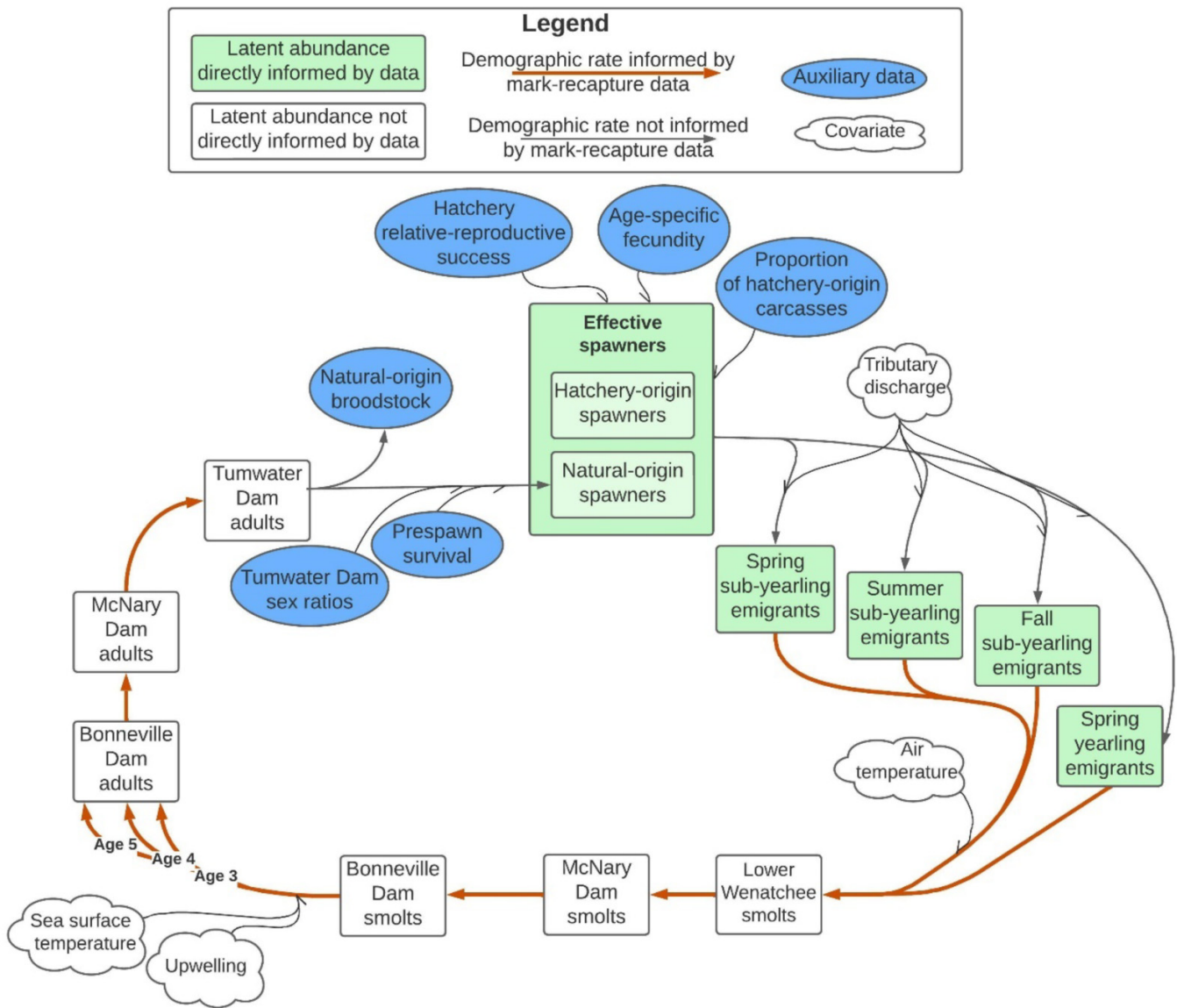
represented the four distinct juvenile LHPs—the three downstream-rearing LHPs (*spr.0*, *sum.0*, and *fal.0*) and the natal-reach-rearing LHP (*spr.1*; Sorel et al. 2023b). To account for uncertainty in estimates of the abundance of emigrants from each natal stream expressing each LHP each year, log-normal distributions were developed using a parametric bootstrap of daily abundance by LHP (Sorel et al. 2023b).

**Mark-recapture data**—a subset of emigrants captured in the screw traps that were >60 mm was marked with passive integrated transponder (PIT) tags prior to release (Fig. 1). These fish could be recaptured at a screw trap near the confluence of the Wenatchee River and the Columbia River and could be detected in PIT-tag detection arrays when migrating downstream past McNary and Bonneville Dams as juveniles and again when migrating upstream as adults. Fish that survived to return to the Wenatchee River were detected when passing Tumwater Dam, just below the spawning grounds.

**Hatchery removals and sex ratios**—some returning natural-origin adults were collected at Tumwater Dam and at weirs within spawning tributaries to serve as conservation hatchery broodstock. The abundance and age composition of natural-origin adults collected for broodstock were recorded. Age was determined using the presence of a PIT tag that the fish received as a juvenile or, in the absence of a tag, by analysis of scales (Hillman et al. 2020). The sex of fish that were handled at Tumwater Dam and weirs was determined by examining external features visually and internal anatomy with a portable ultrasound and used to inform sex ratios for the population.

**Spawning-ground surveys**—all known spawning habitat was walked by surveyors from the Washington Department of

**Fig. 2.** Conceptual diagram of population model for spring Chinook salmon in the Wenatchee River Basin, Washington, USA. Square boxes represent population states (i.e., life stage abundances) and arrows connecting boxes represent demographic rates (i.e., juvenile production, survival, and maturation). Green boxes are directly informed by abundance data, whereas white boxes are not. Orange arrows are directly informed by mark-recapture data, whereas black lines are not. Blue ovals represent auxiliary data that inform population states and demographic rates, and white clouds represent environmental covariate data.



Fish and Wildlife and Chelan County Public Utilities District at 7–10-day intervals in August and September each year. Redds (nests) were counted and marked with flagging to avoid double counting in subsequent surveys. In addition, the origin (hatchery vs. natural) of salmon carcasses recovered by surveyors was determined based on the presence of coded wire tags and clipped fins in hatchery-origin fish to inform the proportion of hatchery-origin spawners in each of the three natal reaches.

### Population process model

The population process model described below consisted of the following components: functions for density-dependent juvenile production, survival rates, return rates from the

ocean, return ages from the ocean, adult sex ratios, proportions of hatchery- and natural-origin spawners, a scalar for the number of eggs in 5-year-old females relative to 4-year-old females, and a scalar for the production of juveniles by hatchery-origin spawners relative to natural-origin spawners (Fig. 2). Environmental covariates were included on demographic parameters governing juvenile production and survival (see below) to account for environmental variability that affects the population.

### Juvenile production

The functional form of the relationship between the abundance of juvenile emigrants,  $Juv_{h,y,s}$ , expressing LHP  $h$  and emigrating in year  $y$  from stream  $s$  and the effective number of

female spawners,  $S_{y(h),s}$  (defined in eq. 8 below), in year  $y_h$ , which is 1 year before the emigration year for downstream-rearing LHPs and 2 years before for natal-reach-rearing LHPs, was informed by Sorel et al. (2023b) (Table 1). To allow for both positive and negative density dependence in the production of juvenile emigrants, we modeled juvenile production using the modified Beverton–Holt model of Myers et al. (1995),

$$(1) \quad Juv_{h,y,s} = \frac{\alpha_{h,s}(S_{y_h,s})^{\gamma_{h,s}}}{1 + \frac{\alpha_{h,s}(S_{y_h,s})^{\gamma_{h,s}}}{J_{h,s}^{max}}} \exp(\epsilon_{h,y,s})$$

with shape parameters  $\alpha_{h,s}$ ,  $\gamma_{h,s}$ , and  $J_{h,s}^{max}$ , specific to each LHP  $h$  and stream  $s$ , and process error  $\epsilon_{h,y,s}$  specific to each LHP, year  $y$ , and stream (Supplementary material A; Sorel et al. 2023b). This model simplifies to the traditional Beverton–Holt model when  $\gamma_{h,s}$  is equal to one, in which case  $\alpha_{h,s}$  is interpretable as the asymptotic maximum production rate. However, when  $\gamma_{h,s}$  is greater than one, it induces positive density dependence, and when it is less than one, it induces negative density dependence. In either case,  $\alpha_{h,s}$  is no longer interpretable as the asymptotic maximum juvenile production rate when  $\gamma_{h,s} \neq 1$ , but does affect predicted productivity. As in the traditional Beverton–Holt model, the  $J_{h,s}^{max}$  parameter is the asymptotic maximum expected juvenile abundance.

The shape parameters of the modified Beverton–Holt function were modeled hierarchically across streams, and penalties were applied to avoid overfitting (Supplementary material A; Sorel et al. 2023b). The lognormal process errors in juvenile abundance,  $\epsilon_{h,y,s}$ , for each LHP  $h$ , year  $y$ , and stream  $s$ , were modeled as a function of annual streamflow covariates, a latent variable that each LHP and stream loaded onto uniquely, and random effects of year that were unique to each LHP and stream.

### Survival and adult return

Modeling of survival and adult return rates was informed by Sorel et al. (2023a) and is detailed in Supplementary material B. The abundance of juvenile smolts (2-year olds) passing Bonneville Dam,  $Smolts_{h,y,s}$ , in year  $y$  from stream  $s$  that had expressed LHP  $h$  was the product of the number of emigrants and their survival rates  $\phi_{h,y,s}^r$  over three intervals,  $r$ , between emigration from natal streams and passing Bonneville Dam,

$$(2) \quad Smolts_{h,y,s} = Juv_{h,y,s} \prod_{r=1}^3 \phi_{h,y,s}^r$$

The three intervals were (1) from natal-stream emigration to the lower Wenatchee River screw trap, (2) from the lower Wenatchee to McNary Dam, and (3) from McNary Dam to Bonneville Dam (Fig. 1). For downstream-rearing LHPs, the year of downstream migration was the year following emigration from the natal stream, whereas the natal-reach-rearing LHP initiated seaward migration in the same year as emigration from the natal stream.

During the first survival interval, we fit unique survival rate intercepts for each LHP in each stream, synchronous random effects of year that were common to all LHPs and stream, and asynchronous random effects that were unique to LHPs but

common across streams (Sorel et al. 2023a, Supplementary material B). In the first survival interval, we included effects of winter air temperature on the survival of downstream-rearing LHPs (Sorel et al. 2023a). In the second and third survival intervals, we assumed that the three downstream-rearing LHPs from each natal stream had the same survival rates, which were allowed to differ from the natal-reach-rearing LHP in each stream.

The number of adults  $Ad.Bon_{h,y,s}$  that had expressed each LHP  $h$  from stream  $s$  returning to Bonneville Dam from the ocean in year  $y$  at adult age  $a$  was a product of smolt abundance, smolt-to-adult return rate in year  $y-a$ ,  $\phi_{h,y-a,s}^{SAR}$ , and the conditional probability,  $\psi_{h,y-a,a}$ , of a smolt that entered the ocean in year  $y-a$  returning at age  $a$ , given that it returned:

$$(3) \quad Ad.Bon_{h,y,s,a} = Smolts_{h,y-a,s} \phi_{h,y-a,s}^{SAR} \psi_{h,y-a,a}$$

We modeled  $\phi^{SAR}$  similarly to survival during the second and third survival intervals, such that downstream-rearing LHPs were assumed to have common rates that differed from the natal-reach-rearing LHP, and we included random effects of year that were synchronous and other random effects that were asynchronous between LHP types (Supplementary material B). We included effects of upwelling during the spring of ocean entry and sea surface temperature during a fish’s first marine summer as covariates on  $\phi^{SAR}$ , allowing for unique effects on each LHP type (downstream- and natal-reach-rearing) but assuming common effects across natal streams. We allowed for different return age intercept parameter,  $\psi_{h,y-a,a}$ , values for LHP types and fit random effects of year that were synchronous across LHPs and natal streams (Supplementary material B).

### Abundance of female spawners

The abundance of adults returning to Tumwater Dam,  $Ad.Tum_{h,y,s,a}$ , was the product of the number of adults returning to Bonneville Dam and their upstream survival rates,

$$(4) \quad Ad.Tum_{h,y,s,a} = Ad.Bon_{h,y,s,a} \prod_{r=4}^5 \phi_{y,a}^r$$

where the two upstream survival occasions,  $r$ , were (5) from Bonneville Dam to McNary Dam, and (6) from McNary Dam to Tumwater Dam. We allowed upstream survival to vary by adult age but assumed that it was common across LHPs and natal streams (Supplementary material B). We included random year effects that were synchronous across all fish for upstream survival.

The total number of natural-origin adults passing upstream of Tumwater Dam,  $Ad.Tum_{y,s,a}$ , from stream  $s$  in year  $y$ , was the sum of returning adults across juvenile LHPs  $h$  less fish removed for hatchery broodstock,  $B_{y,s,a}^{Rem}$ :  $Ad.Tum_{y,s,a} = (\sum_h Ad.Tum_{h,y,s,a}) - B_{y,s,a}^{Rem}$ . The total abundance of natural-origin female spawners,  $S.NO_{y,s}$ , was the abundance of adults that returned to Tumwater Dam summed across ages and multiplied by the proportion of returning adults that were female  $p_{y,s}^F$  and survived from Tumwater Dam to

**Table 1.** Terms used in the description of the model.

Term	Description
<b>Indices</b>	
$h$	Juvenile life history pathway
$y$	Year
$s$	Natal stream
$a$	Age
$r$	Survival interval
<b>Juvenile production</b>	
$J_{uv}^{h,y,s}$	Abundance of juvenile emigrants
$S_{y(h),s}$	Effective number of female spawners
$\alpha_{h,s}$	Productivity parameter
$\gamma_{h,s}$	Density dependence parameter
$J_{h,s}^{\max}$	Asymptotic maximum juvenile production
$\epsilon_{h,y,s}$	Process error
<b>Survival and return</b>	
$Smolts_{h,y,s}$	Abundance of juvenile smolts (2-year olds) passing Bonneville Dam
$\phi_{h,y,s}^r$	Survival rates
$\phi_{h,y,s}^{SAR}$	Smolt-to-adult return rate
$\psi_{h,y-a,a}$	Conditional probability of a smolt that entered the ocean in year $y-a$ returning at age $a$ , given that it returned
<b>Abundance of female spawners</b>	
$Ad.Bon_{h,y,s,a}$	Number of adults returning to Bonneville Dam
$Ad.Tum_{h,y,s,a}$	Number of adults returning to Tumwater Dam
$B_{y,s,a}^{Rem}$	Adults removed for hatchery broodstock
$S.NO_{y,s}$	Abundance of natural-origin female spawners
$S.HO_{y,s}$	Female spawners of hatchery origin that spawned in the wild
$p_{y,s}^F$	Proportion of returning adults that were female
$\phi^{PS}$	Survival from Tumwater Dam to spawning
$B_{y,a,Nason}^{obs}$	Observed total number of fish of age $a$ collected for the Nason Creek program broodstock from either stream
$B_{y,a,Chiwawa}^{obs}$	Observed abundance of adults returning from the Chiwawa River collected for the Chiwawa River hatchery program broodstock
$B_{y,a,Nason}^{Nason}$	Abundance of natural-origin returns collected for the Nason Creek program broodstock that originated from Nason Creek
$B_{y,a,Nason}^{Chiwawa}$	Abundance of natural-origin returns collected for the Nason Creek program broodstock that originated from the Chiwawa River
$p_{y,s}^{HO}$	Proportion of females spawning in the wild that were of hatchery origin
$p^{RRS}$	Productivity of hatchery-origin female spawners relative to 4-year old natural-origin females
$\delta$	Percent difference between the productivity of 5- and 4-year-old natural-origin spawners
<b>Joint likelihood</b>	
$\overline{M}_{h,y,s}^r$	Mean of log of estimated juvenile abundance from observation model
$\sigma_{h,y,s}^M$	Standard deviation of log of estimated juvenile abundance from observation model
$\sigma_S$	Observation standard error for log of redd counts
$S.obs_{y,s}$	Observed count of redds
$p_y^{Fobs}$	Observations of the proportion of natural- and hatchery-origin adults that were female
$\mu_{p^F}$	Hyper mean proportion female
$\sigma_{p^F}$	Hyper standard deviation proportion female
$C_{y,s}^H$	Observed number of hatchery-origin carcasses
$C_{y,s}$	Total number of observed carcasses
$\mu_{p^{HO}}$	Hyper mean proportion of hatchery-origin spawners
$\sigma_{p^{HO}}$	Hyper standard deviation proportion of hatchery-origin spawners

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spawning,  $\phi^{PS}$ .

$$(5) \quad S.NO_{y,s} = \sum_{a=3}^5 Ad.Tum_{y,s,a} p_{y,s}^F \phi^{PS}$$

Fish are collected for the Chiwawa River hatchery broodstock either at a weir in the Chiwawa River or at Tumwater Dam if they can be identified as having originated from the Chiwawa River based on PIT tags inserted as juveniles, so all fish for the Chiwawa Broodstock originate in the Chiwawa River (NMFS 2015). However, for the Nason Creek broodstock, natural-origin fish of unknown origin are collected at Tumwater Dam because of the difficulty of trapping fish without a weir in Nason Creek. Fish from the White River are not collected because they can be differentiated based on genetics. To reflect this in the model, the broodstock for the Nason Creek supplementation program was composed of fish originating from the Chiwawa River and Nason Creek in proportion to their abundance. The abundance of natural-origin returns collected for the Nason Creek program broodstock that originated from Nason Creek,  $B_{y,a,Nason}^{Nason}$ , was calculated as

$$(6) \quad B_{y,a,Nason}^{Nason} = B_{y,a,Nason}^{obs} Ad.Tum_{y,Nason} / \left( Ad.Tum_{y,Chiwawa} - B_{y,a,Chiwawa}^{obs} + Ad.Tum_{y,Nason} \right)$$

where  $B_{y,a,Nason}^{obs}$  is the observed total number of fish of age  $a$  collected for the Nason Creek program broodstock from both streams,  $Ad.Tum_{y,Nason}$  is the latent abundance of adults from Nason Creek returning to Tumwater Dam,  $Ad.Tum_{y,Chiwawa}$  is the latent abundance of adults from the Chiwawa River returning to Tumwater Dam, and  $B_{y,a,Chiwawa}^{obs}$  is the observed abundance of adults returning from the Chiwawa River collected for the Chiwawa River hatchery program broodstock. The abundance of natural-origin returns from the Chiwawa River collected for the Nason Creek hatchery broodstock was,  $B_{y,a,Nason}^{Chiwawa} = B_{y,a,Nason}^{obs} - B_{y,a,Nason}^{Nason}$ . The total number of adults from the Chiwawa River collected for broodstock,  $B_{y,a,Chiwawa}^{em}$  (used in eq. 5) was therefore  $B_{y,a,Chiwawa}^{obs} + B_{y,a,Nason}^{Chiwawa}$  and for Nason Creek, it was simply  $B_{y,a,Nason}^{Nason}$ .

The number of female spawners of hatchery origin that spawned in the wild in year  $y$  and stream  $s$ ,  $S.HO_{y,s}$ , was calculated based on the number of natural-origin spawners,  $S.NO_{y,s}$ , and the proportion of hatchery-origin spawners,  $p_{y,s}^{HO}$ ,

$$(7) \quad S.HO_{y,s} = \frac{S.NO_{y,s} p_{y,s}^{HO}}{1 - p_{y,s}^{HO}}$$

To calculate the effective number of female spawners,  $S_{y,s}$ , used in eq. 1, we weighted the numbers of spawners to account for the greater number of eggs in older natural-origin fish relative to younger natural-origin fish and the lower production of juvenile emigrants by hatchery-origin relative to natural-origin spawners (relative reproductive success;

Ford et al. 2013).

$$(8) \quad S_{y,s} = \left[ S.NO_{y,s} \left( 1 + \frac{Ad.Tum_{h,y,s,5}}{Ad.Tum_{h,y,s,4} + Ad.Tum_{h,y,s,5}} \delta \right) \right] + S.HO_{y,s} p^{RRS}$$

where  $\delta$  is the percent difference between the productivity of 5- and 4-year-old natural-origin spawners and is restricted to be positive, and  $p^{RRS}$  is the productivity of hatchery-origin female spawners relative to 4-year old natural-origin females and is restricted to be between 0 and 1. We did not explicitly model the age structure of hatchery-origin fish, assuming that their mean per capita reproductive potential was approximately constant. We assumed that all 3-year-old spawners were male, whereas all female spawners were either 4-year-olds or 5-year-olds (Hillman et al. 2020). We assumed that the sex ratios for 4- and 5-year-old adults were the same as one another.

Because abundance in the first 5 years is needed to calculate abundance in the sixth year and beyond, we fit parameters for natural-origin female spawner abundance in the first 5 years, which differed among natal streams due to different years of available juvenile abundance data. We assumed that the population age structure in the first 5 years was equal to the expected value of the age structure of adults returning from the ocean across downstream- and natal-reach-rearing LHPs, which was necessary to calculate the effective number of spawners in eq. 8. The abundances of spawners in the sixth year and beyond were calculated from the effective number of spawners in the first 5 years and the population process model.

### Joint likelihood

The observed abundances of juvenile emigrants and total female spawners were assumed to be lognormally distributed around the latent values from the population process model,

$$(9) \quad \overline{M}_{h,y,s}^* \left( \log (Juv_{h,y,s}), \sigma_{h,y,s}^* \right), \log (S.obs_{y,s}) \left( \log (S.NO_{y,s} + S.HO_{y,s}), \sigma_S \right)$$

where  $\overline{M}_{h,y,s}^*$  and  $\sigma_{h,y,s}^*$  are the log mean and standard deviation, respectively, of juvenile abundance in LHP  $h$ , year  $y$ , and natal stream  $s$  estimated from a model of daily abundance fit to screw trap data (Sorel et al. 2023b),  $S.obs_{y,s}$  is the observed count of redds, and  $\sigma_S$  is the observation standard error for redd counts. We applied an informed lognormal prior on the observation standard error for redd counts,  $\log (\sigma_S) \sim N(\log (0.10), 0.25)$  based on published estimates of observation error in redd counts (Chasco et al. 2014; Murdoch et al. 2019).

The multistate model likelihood for each PIT-tagged fish released from a rotary screw trap was calculated with the forward algorithm (McClintock et al. 2020; see Zucchini et al. 2016), while accounting for imperfect detection. Details of the observation model for the multistate model are included in Supplementary material B and Sorel et al. (2023a). We did not have data to directly inform the survival of spr.0 emigrants, because they were almost all too small to be

tagged (<60 mm) upon emigration. We therefore used a relationship between fork length at emigration and survival during the first interval for sum.0 emigrants, as well as the mean fork lengths of the spr.0 and sum.0 emigrants, to estimate the difference in survival between the spr.0 and sum.0 LHPs during the first interval (Supplementary material B). All downstream-rearing LHPs were assumed to have common demographic rates after the first interval.

Data on the sex ratio of adults came from an examination of a composite of fish from all spawning areas upstream of Tumwater dam, including those not considered in the IPM. We therefore assumed that observations of the proportion of natural- and hatchery-origin adults that were female,  $p_y^{F,obs}$ , in year  $y$  were a noisy measure of the true proportion of adults that were female within each stream  $s$  and year  $y$ ,  $\text{logit}(p_y^{F,obs}) \sim N(\text{logit}(p_{s,y}^F), 0.25)$ , with an observation SE of 0.25. We also assumed that the annual proportions of returning adults that were female were normally distributed on the logit scale,  $\text{logit}(p_{s,t}^F) \sim N(\mu_{p^F}, \sigma_{p^F})$ , with mean  $\mu_{p^F}$  and standard deviation  $\sigma_{p^F}$  across streams and years.

We did not have annual data on the pre-spawn survival rates between when fish pass Tumwater Dam as adults and when they spawn. We therefore assumed a constant rate,  $\phi^{PS}$  across years and streams, which was informed by a prior:  $\text{logit}(\phi^{PS}) \sim N(\text{logit}(0.85), 0.50)$ , with parameters based on a meta-analysis of pre-spawn survival rates for spring Chinook in tributaries of the upper Columbia River (Bowerman et al. 2016, 2021).

The percent difference in the number of eggs between 4- and 5-year-old females,  $\delta$ , was based on counts of eggs within natural-origin females used in hatchery broodstock between 1997 and 2020. The mean fecundity of natural-origin 4-year-old spawners was 4437 eggs ( $n = 519$ ,  $sd = 682$ ), and for 5-year-old females, it was 5507 ( $n = 133$ ,  $sd = 897$ ) (Hillman et al. 2020). Based on this information, we applied an informative prior on  $\delta$ ,

$$\log(\delta) \sim N\left(\log\left(\frac{5,507}{4,437} - 1\right), 0.1\right)$$

The proportion of hatchery-origin spawners,  $p_{y,s}^{HO}$ , was informed by the numbers of hatchery-origin carcasses recovered on the spawning grounds,  $C_{y,s}^H$ , out of the total number of carcasses,  $C_{y,s}$ , recovered. However, Murdoch et al. (2010) found that carcass recovery probabilities were affected by fish sex and length, which induced observation error in the proportion of hatchery-origin carcasses recovered above that of a binomial sample. We therefore modeled the number of hatchery-origin carcasses as Poisson distributed, with rate equal to the product of the total number of carcasses and the proportion of hatchery-origin spawners,  $C_{y,s}^H \sim \text{Poisson}(C_{y,s} p_{y,s}^{HO})$ . To regularize  $p_{y,s}^{HO}$  values away from boundaries at 0 and 1, we assumed that they were normally distributed around a mean,  $\mu_{p^{HO}}$ , on the logit scale,  $\text{logit}(p_{y,s}^{HO}) \sim N(\mu_{p^{HO}}, \sigma_{p^{HO}})$  with standard deviation  $\sigma_{p^{HO}}$ . We applied an informative prior on the relative reproductive suc-

cess of hatchery-origin spawners,  $\text{logit}(p^{RRS}) \sim N(\text{logit}(0.53), 1.0)$  based on the results of Ford et al. (2013).

## Model fitting

The model was developed in Template Model Builder (Kristensen et al. 2016) in R version 4.1.2 (R Core Team 2021) and fit by minimizing the negative marginal log-likelihood using the TMBhelper package (Thorson 2020). Convergence was evaluated by ensuring the gradient of the log-likelihood function was  $<1e-6$  with respect to all parameters and by optimizing the model with several different sets of initial parameter values. A complete table of all model parameters that were treated as fixed effects or marginalized out of the likelihood using the Laplace approximation is included in Table SF.1.

## Population viability analysis

To evaluate population viability, we projected the population into the future for 50 years. Future demographic rates were based on realizations of random processes (i.e., random effects of year), environmental covariates, and hatchery management decisions. All random effects of year other than  $p_{y,s}^{HO}$  were sampled from their hyper distributions when simulating demographic rates for projections. Rather than calculating the number of hatchery-origin spawners based on  $p_{y,s}^{HO}$ , as we did when fitting the model (eq. 7), the number of hatchery-origin spawners in projections was determined by an abundance-based control rule designed to meet the constraints in the hatchery genetic management plans (HGMPs; Supplementary material C; Chelan PUD and WDFW 2009, Grant PUD et al. 2009). Management decisions about the abundance of natural-origin returns to collect for hatchery broodstock in projections also followed abundance-based control rules defined in the HGMPs.

*Environmental covariate simulation*—to generate future times series of environmental covariates with similar temporal and among-variable correlation structure as the historical covariate values, we fit multivariate autoregressive state-space models to the historical time series of the environmental covariates used in the IPM, which we then sampled from to simulate covariates to calculate demographic parameters during the projection period. We used longer time series of covariates to fit the models than were used to estimate demographic parameters to maximize the information used to inform future covariate trajectories. We assessed whether there were trends in the historical time series of covariates, which might reflect climate change. Covariate model fitting and simulation were conducted using the MARSS package in R (Holmes et al. 2012). Additional details on covariate modeling and simulation are provided in Supplementary material D.

*Hatchery supplementation*—management decisions regarding hatchery supplementation were simulated based on control rules that satisfied the constraints outlined in HGMPs (Chelan PUD and WDFW 2009; Grant PUD et al. 2009) and the Biological Opinion (NMFS 2015) for the programs (Supplementary material C). The two decisions that were made annually in the model for each program were the number of natural-



origin adults collected for hatchery broodstock and the number of hatchery-origin adults released to spawn in the natural environment. Each of these decisions was made based on the forecasted number of natural-origin adults returning to Tumwater Dam, because no more than 30% of forecasted natural-origin returns were collected for broodstock and the number of hatchery-origin adults released onto the spawning grounds decreased with increasing natural-origin adult abundance. Details of the implementation of hatchery management rules in the model are in Supplementary material C.

**Population viability metrics**—we projected the population forward for 50 years to determine viability. To account for parametric uncertainty and stochasticity, we simulated 100 prospective population trajectories for each of 200 parameter sets drawn from a multivariate normal posterior distribution defined by the maximum a posteriori estimate of parameters and the inverted Hessian matrix. We predicted future abundance based on the geometric mean of natural-origin female spawner abundance over the 50 projected years (2020–2069). We also predicted the probability of the population declining to a low abundance, where risks of inbreeding depression and reduced mate finding success increase. This has often been referred to as the probability of falling below a quasi-extinction threshold (Buhle et al. 2018; Crozier et al. 2021). We defined  $p^{\text{QET}}$  as the probability of the 4-year mean natural-origin spawner abundance falling below 50 fish to be consistent with the Interior Columbia Technical Recovery Team (Buhle et al. 2018). To evaluate parametric uncertainty around  $p^{\text{QET}}$ , we calculated the proportion of the 100 simulations conducted with each parameter set in which the 4-year mean fell below 50 spawners. As a metric to describe the genetic effects of introgression with the hatchery population, we calculated the across-year mean proportionate natural influence (PNI; Paquet et al. 2011),  $\text{PNI}_{y,s} = p_{y,s}^{\text{NOB}} / (p_{y,s}^{\text{NOB}} + p_{y,s}^{\text{HO}})$ , where  $p_{y,s}^{\text{NOB}}$  is the proportion of the broodstock for the hatchery program in stream  $s$  in year  $y$  composed of natural-origin spawners, and  $p_{y,s}^{\text{HO}}$  is the proportion of fish spawning in the natural environment that are of hatchery origin. When calculating  $p_{y,s}^{\text{NOB}}$ , we assumed that the difference between the number of natural-origin adults collected and the broodstock target size would be made up of hatchery-origin adults. Higher PNI is associated with a lower effect of hatchery supplementation on the natural adaptations of fish to their environment (Paquet et al. 2011).

We conducted a sensitivity analysis to evaluate the effect of parametric uncertainty on projected abundance. This entailed assessing the correlation between parameter values from posterior samples and the geometric mean abundance in projections based on those parameter values. Detailed methods and results of the sensitivity analysis are included in Supplementary material E.

**Portfolio effects**—we calculated portfolio effects attributable to asynchrony among LHPs and natal streams. To do so, we calculated the coefficients of variation (CV) of natural-origin adults returning to Tumwater Dam for each juvenile LHP and natal stream as well as for the total spawner abundance across LHPs within each natal stream and for the total

spawner abundance across natal streams and LHPs. We calculated portfolio effects as  $1 - \frac{\text{CV}^{\text{Total}}}{\text{CV}^{\text{Mean}}}$  where  $\text{CV}^{\text{Total}}$  was the CV of the aggregate return across LHPs or natal streams and  $\text{CV}^{\text{Mean}}$  was the mean of the CVs of individual LHPs or natal streams, weighted by their relative abundance (Schindler et al. 2010; Carlson and Satterthwaite 2011).

## Results

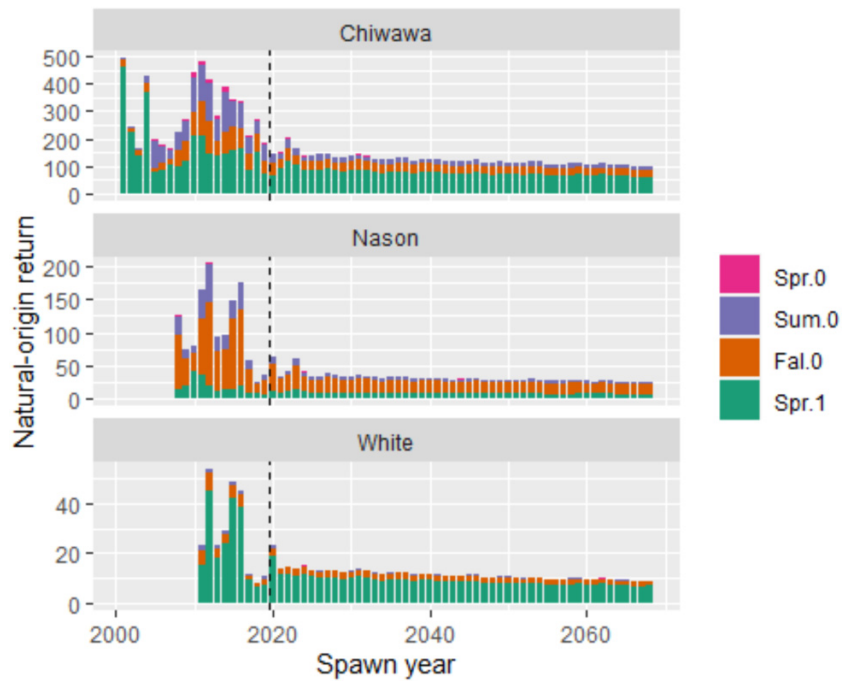
Most adults returning to Tumwater Dam had expressed the natal-reach-rearing (*spr.1*) or fall subyearling emigrating (*fal.0*) LHPs. The mean proportion of projected natural-origin adults returning to Tumwater that had expressed the natal-reach-rearing LHP (*spr.1*) as juveniles was 0.58 (90% quantile = 0.42–0.70) in the Chiwawa River, 0.31 (0.16–0.51) in Nason Creek, 0.71 (0.40–0.88) in the White River, and 0.53 (0.34–0.67) across all three streams (Fig. 3). The proportion that had expressed the *fal.0* LHP was 0.24 (90% quantile = 0.16–0.37) in the Chiwawa River, 0.54 (0.36–0.68) in Nason Creek, 0.23 (0.09–0.53) in the White River, and 0.31 (0.19–0.48) across all three streams. The remaining adults had expressed the *spr.0* and *sum.0* LHPs as juveniles. The *spr.0* LHP contributed a considerably smaller amount toward total abundance than other LHPs.

The mean proportion of hatchery-origin spawners ( $p^{\text{HOS}}$ ) over the 50 projected years was 0.54 (90% quantile range = 0.23–0.73) in the Chiwawa River, 0.52 (0.18–0.75) in Nason Creek, and 0.21 (0.06–0.52) in the White River (Fig. SF.1). The mean proportion of broodstock that was of natural origin ( $p^{\text{NOB}}$ ) was 0.69 (0.47–0.91) in the Chiwawa River and 0.20 (0.04–0.62) in Nason Creek (Fig. SF.2). The mean PNI for the Chiwawa River supplementation program was 0.57 (0.38–0.82) and for the Nason Creek program, it was 0.21 (0.04–0.61; Fig. SF.3).

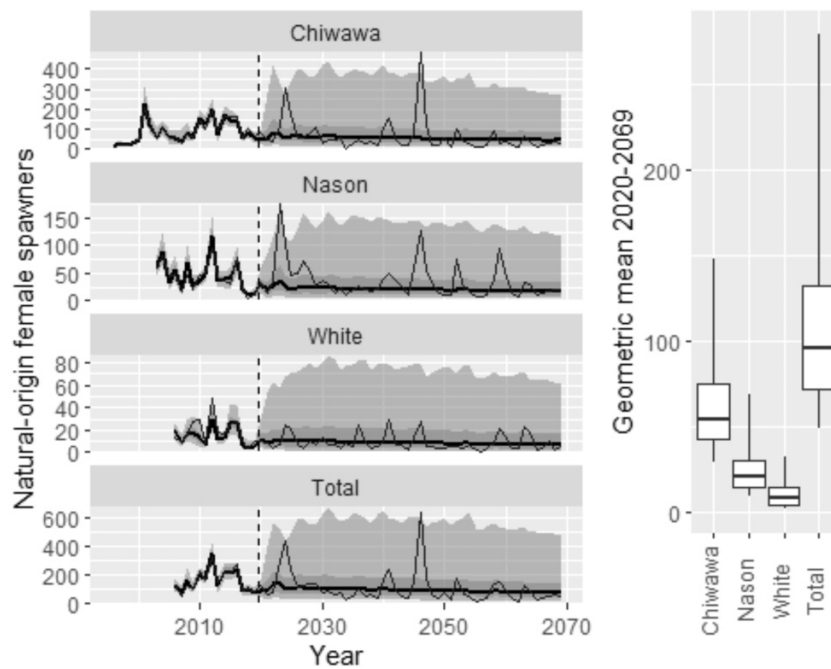
The median annual abundances across individual simulations indicated that population equilibria with current hatchery supplementation were somewhat less than their recent historical abundances, although abundance varied inter-annually in individual projections (Fig. 4). The median across simulations of the geometric mean abundance of natural-origin female spawners over the 50 projected years was 55 (90% quantile range = 30–149) in the Chiwawa River, 21 (10–69) in Nason Creek, 9 (2–33) in the White River, and 96 (49–279) in total across all three streams (Fig. 4). The probability that the 4-year running mean of natural-origin spawner abundance dropped below 50 in the projection was 0.00 (0.00–0.00) for the three streams combined (Fig. 3).

We examined the percent reduction in the CV of projected natural-origin adult returns to Tumwater Dam relative to the weighted mean of CVs across LHPs (i.e., portfolio effects), where a larger reduction is indicative of a larger portfolio effect. Across simulations, the mean percent reduction was 19% (90% quantile = 9%–29%) in the Chiwawa River, 21% (8%–33%) in Nason Creek, 10% (2%–25%) in the White River, and 20% (9%–31%) for the aggregate abundance across streams (Fig. 5). The CV of the aggregate abundance across LHPs and streams was 28% (15%–40%) lower than the weighted mean of CVs across individual LHPs and natal streams, and 6% (2%–14%)

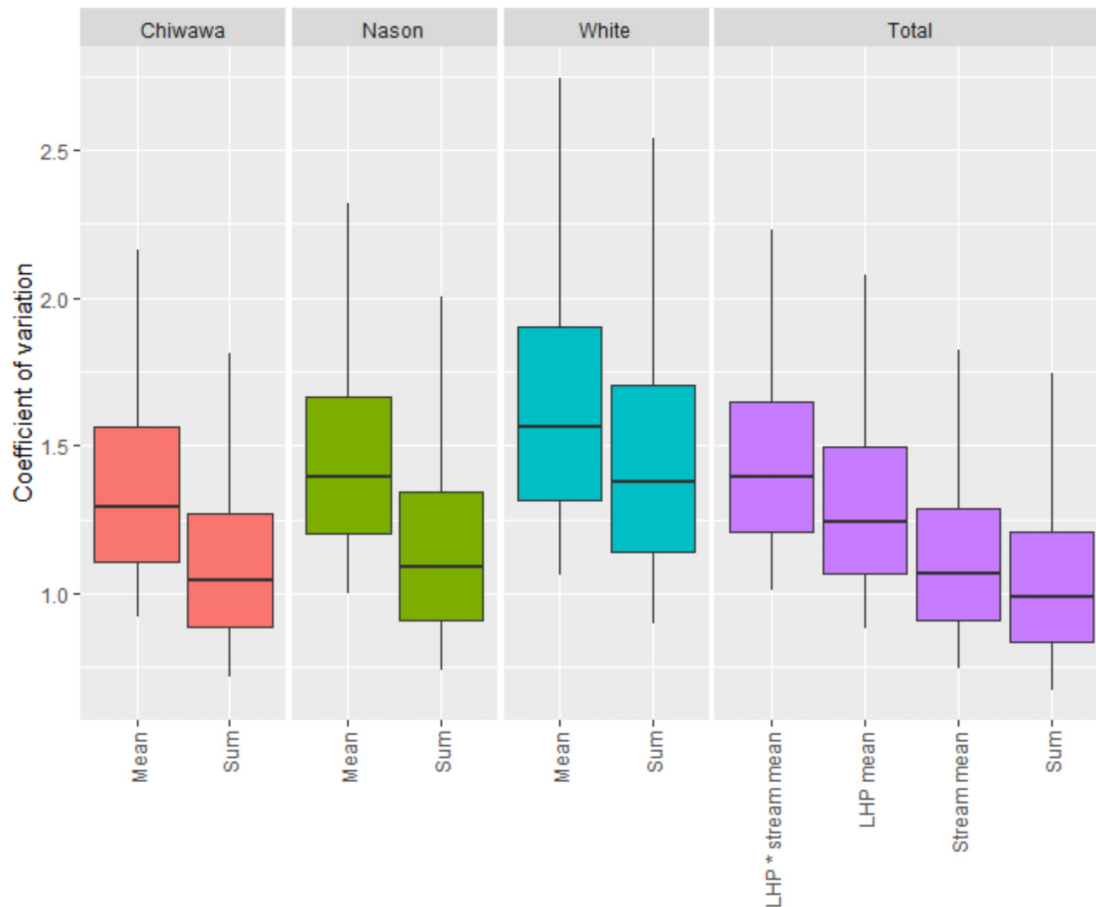
**Fig. 3.** Median abundance of natural-origin spring Chinook salmon adults returning to Tumwater Dam, Washington, USA by year and juvenile life history pathway (LHP; color) for three natal streams and the total across streams. Years to the left of the dotted line were fit to data, and years to the right of the dotted line were projected.



**Fig. 4.** *Left panel:* natural-origin female spawner abundance in three natal streams and the total across streams, for spring Chinook salmon in the Wenatchee River, Washington, USA. Years to the left of the dotted line were fit to data and years to the right of the dotted line were projected. Thick lines represent medians across simulations, thin lines represent single example simulations, dark shaded envelopes represent interquartile ranges, and light shaded envelopes represents 90% quantile ranges. *Y-axis scales differ across streams.* *Right panel:* boxplots are of the geometric mean abundance in years 2020–2069 across projections. Horizontal lines represent medians, boxes span interquartile ranges, and whiskers span 90% quantile ranges.



**Fig. 5.** Boxplots of the coefficients of variation (CV) of simulated abundance of natural-origin Chinook salmon adults returning to Tumwater Dam, Washington, USA, in 2020–2069. Means for Chiwawa, Nason, White, and Total represent mean CVs across life history pathways (LHPs) within each stream or for the total abundance across streams. Sums represent the CV of the sum of returns across LHPs. The *LPH \* stream mean* is the mean CV across LHPs and natal streams, and the *Stream mean* is the mean of the CVs of the total returns (across LHPs) to each stream. *Total sum* is the CV of the aggregate return across streams and LHPs. For each box, the thick line represents the median CV across 50 000 projections, the boxes span the interquartile range, and the whiskers span the 90% quantile range.



lower than the weighted mean of the CVs of the total returns to individual streams. Returns of fish that had expressed the *fal.0* LHP had the lowest CV in each stream (Fig. SF.4).

## Discussion

In our simulations, the productivity of the endangered Chinook salmon population in the Wenatchee River did not appear sufficient to meet recovery goals for abundance of 2000 natural-origin adults (UCSRB and NMFS 2007). However, when accounting for diversity in juvenile LHPs in our model, we were able to identify that asynchronous variability among LHPs dampened the variance in overall abundance, which reduced the risk of it falling below a quasi-extinction threshold. Our model provides an example of how life history diversity influences populations due to the differential effects of environmental conditions on demographic performance of different traits (i.e., LHPs) and density dependence in the relative frequency of alternative traits.

In our population projections, the geometric mean abundance of spawners was less than the recovery goal of 2000 adults in 94% of simulations. There is some production from spawning habitat that we did not model, but the unmodeled production generally only makes up about 10% of the population (Hillman et al. 2020). Considerable numbers of hatchery-origin fish also spawned in the wild in our simulations (59–157 per year; 90% interval of mean total across streams). The average projected PNIs of both supplementation programs were below the 0.67 minimum level suggested in the Biological Opinions for the programs (NMFS 2015), indicating a higher than preferred effect of supplementation on the genetic adaptations of the population to its habitat.

Our population viability analysis indicated a 0.0 probability of the population dropping below a quasi-extinction threshold of a mean of 50 spawners over a 4-year period given the current productivity of the natural population, trends in environmental variables, and the current rate of hatchery supplementation. However, the projected geometric mean abundances of wild female spawners were only 21 and 9 in two of

the spawning streams. This raises questions about the risk of extirpation for individual spawning streams and how demographically connected the spawning streams are. Previous studies of this population have found that natural-origin adults disperse between natal streams at relatively low rates (2%–7%; Ford et al. 2015; Pearsons and O'Connor 2020), but future population models could account for dispersal to evaluate the effects of dispersal on population viability.

We also examined the role of life history diversity in dampening population variability (i.e., portfolio effects). Intuitively, the greatest dampening of variability of abundance in natal streams was found in the streams that had more juvenile life history diversity, based on their more nearly equal proportions of natal-reach- and downstream-rearing LHPs. Abundance of the *fal.0* LHP was the least variable through time of the four LHPs but was the numerically dominant LHP in only one of three natal streams. We also documented portfolio effects of multiple distinct spawning aggregations, although the structure of the model, wherein random effects of year on survival and return were assumed to be synchronous among natal streams, somewhat limited our ability to fully evaluate these portfolio effects. It may be possible to effectively estimate random effects of year on survival unique to each stream, but that would likely require more years of data. The maintenance of multiple spatially distinct spawning aggregations and life history diversity within the population are commonly considered to be conservation objectives for at-risk salmon populations due to their benefits for population stability (Phillis et al. 2018; Cordoleani et al. 2021), and our results provide a quantitative assessment of this benefit.

Our population viability analysis suggests that management interventions may be necessary to meet recovery goals for abundance, and our model will be useful for simulating the outcomes of proposed actions in future work. For example, population trajectories may be simulated under alternative hatchery-control rules and with modified demographic parameters to represent habitat management actions (Honea et al. 2009; Saunders et al. 2018; Nater et al. 2022; Sorel 2022). This will provide policy makers with estimates of expected population viability metrics (e.g., abundance,  $p^{QET}$ , and PNI) across a range of different management scenarios to help inform decisions. There is also interest in better understanding the effects of climate change on the population under alternative management actions (e.g., Crozier et al. 2021), which our projections accounted for by including trends of decreasing spring upwelling and increasing summer sea surface temperature and the (negative) effects of those trends on return rates. Our model's ability to account for unique effects of environmental conditions and population abundance on the productivity of different population components may improve predictions of responses to management and climate change relative to a model where this heterogeneity is ignored (Plard et al. 2019a; Armstrong et al. 2021).

A challenge of accounting for demographic heterogeneity as a function of individual traits is that it requires fitting more parameters, which generally increases parametric uncertainty. But statistical methods are available to efficiently share information about parameter values across discrete (e.g., natal habitat patch and resident vs. migrant) or continu-

ous (e.g., natal latitude/longitude and migration timing) trait values (Schaub and Kéry 2012). Specifically, random effects can be used to share information across groups or across the range of continuous variables (Pedersen et al. 2019) and can be fit within fully Bayesian or marginal maximum likelihood frameworks (Herliansyah et al. 2022). Our model provides an example of how these techniques can be used to share information about demographic rates and their variance through time.

A primary goal of accounting for life history diversity in population models is to capture how the distribution of traits within a population interacts with environmental factors to shape population trajectories (Fox and Kendall 2002; Hamel et al. 2018; Plard et al. 2019a). This may include modeling how environmental factors affect the distribution of traits, including both plastic and evolutionarily fixed responses to factors like population density and habitat conditions (Vindenes and Langangen 2015; Plard et al. 2019b). Accounting for heterogeneity allows for modeling different effects of environmental conditions on vital rates among individuals (e.g., Henn et al. 2018), which can help with predicting population responses to climate change, management, and other environmental changes that may favor particular life history traits over others (Vindenes and Langangen 2015; Johnston et al. 2019). Understanding how variability in life history traits translates to reduced variability in population abundance through time provides insights into the implications of the loss of life history diversity for the extinction risk of small populations and the sustainable provisioning of ecosystem services (Kendall and Fox 2002; Schindler et al. 2010; van Daalen and Caswell 2020; Armstrong et al. 2021).

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## Data availability

All data and code used in the analysis are available from Zenodo: doi:10.5281/zenodo.8336612.

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### Competing interests

The authors declare there are no competing interests.

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## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2023-0118>.

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