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Role of maturation and mortality in portfolio effects and climate resilience

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Abstract

The portfolio effect plays a critical role in population productivity and stability. Age structure of spawning salmon represents an example of portfolio effects such that the risks of experiencing unfavorable conditions are spread across time. However, the distribution of maturation ages for Pacific salmon (*Oncorhynchus* spp.) is increasingly concentrated into fewer and younger ages, which may impact population resilience to climate change. We explored the population dynamics of Sacramento River fall-run Chinook salmon (*O. tshawytscha*) under different age structure scenarios using a life-cycle model and compared two mechanisms that can underlie these changes—mortality and maturation. In addition, we tested whether age structure promotes resilience to drought. We found that high age structure diversity increased the stability of population size and harvest compared with low diversity. However, mean population size responded differently depending on the underlying mechanism. Reduced mortality of adult fish ages 4–5 increased escapement, whereas delayed maturation decreased escapement. Overall, high age structure diversity was able to buffer against the adverse effects of droughts by reducing the variability of population size and harvest compared with low diversity. Our results suggest that age structure promotes stability of salmon in an increasingly variable climate.

Key words: Age structure, portfolio effects, climate change, salmon, population dynamics

Introduction

Intraspecific variation drives eco-evolutionary processes and plays a critical role in species and ecosystem resilience to climate change (Bolnick et al. 2011; Pauls et al. 2013; Des Roches et al. 2018; Cordoleani et al. 2021; Colombano et al. 2022). For example, phenotypic variation of temperature tolerance in corals can benefit management efforts and coral reef restoration programs by focusing effort on heat-tolerant phenotypes as sea surface temperatures rise (Bay et al. 2017; Morikawa and Palumbi 2019). Recent studies have demonstrated that ecological responses to intraspecific effects rival that of species effects, particularly for indirect responses such as trophic cascades (Des Roches et al. 2018). However, intraspecific variation is often overlooked in conservation planning despite declines in variation due to anthropogenic impacts such as habitat modification, climate change, and species introductions (Mimura et al. 2017). The consequences of such rapid loss of intraspecific diversity include species extinctions, simplified structure of ecological communities, constricted evolutionary potential, and reduced contributions to people such as economic value, cultural value, and ecosystem regulating processes (Oke et al. 2020; Des Roches et al. 2021).

One of the mechanisms by which intraspecific variation can affect ecological community structure and population dynamics is the portfolio effect (Tilman and Downing 1994; Doak et al. 1998; Bolnick et al. 2011). The portfolio effect, which is analogous to financial portfolio theory (Markowitz 1952), is the phenomenon that different phenotypic traits spread risk of experiencing adverse conditions across space and time. Thus, the portfolio effect can promote stability in species and ecosystem productivity, population size, and long-term viability of natural resource use (Greene et al. 2010; Stier et al. 2020). Pacific salmon (*Oncorhynchus* spp.) have become an important system for testing the strength of portfolio effects (Greene et al. 2010; Moore et al. 2010; Schindler et al. 2010; Carlson and Satterthwaite 2011; Thorson et al. 2014; Yamane et al. 2018; Cordoleani et al. 2021). Most studies on salmon have tested the effects of spatial structure of spawning populations, showing that diverse spawning populations serve to stabilize the variability in overall population size and fisheries harvest (Schindler et al. 2010; Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015). A recognized but less tested aspect of portfolio effects related to intraspecific variation is age structure—particularly the age at which individuals mature for semelparous species like salmon (Greene et al. 2010; Schindler et al. 2010). Whereas

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greater diversity of spawning locations serves to spread risk over space, greater age structure diversity serves to spread risk through time. This temporal risk spreading conferred by age structure may be critical for maintaining overall population stability in an increasingly variable climate (Greene et al. 2010; Buoro and Carlson 2014; Moore et al. 2014).

In this study, we examined the effects of age structure on the population dynamics of a harvested species under various climate change scenarios. We used fall-run Chinook salmon (*O. tshawytscha*) in the Sacramento River, California, as a case study because this population is particularly susceptible to climate change in the form of increasing severity of drought conditions (Notch et al. 2020; Munsch et al. 2022). In addition, Sacramento River fall Chinook (SRFC) contribute heavily to the California and southern Oregon salmon fisheries and have experienced high population variability and an overall declining trend in abundance in recent decades (Lindley et al. 2009; Munsch et al. 2022). For example, SRFC had historically high escapement in 2002 followed by population collapse in 2008 and 2009 (Lindley et al. 2009), and the National Marine Fisheries Service has designated Central Valley fall Chinook (for which SRFC is the dominant constituent) as a species of concern. Thus, understanding SRFC population dynamics in response to shifting age structure and climate change will provide insight into the impact of intraspecific variation on harvested populations in general and help identify management and conservation priorities for promoting stable populations and long-term viability of fisheries.

The spawner age distribution of Chinook salmon populations have been increasingly concentrated in fewer ages, and the oldest age classes of spawners are becoming very rare (Ohlberger et al. 2018; Oke et al. 2020). For example, age 4 fish composed the majority of spawners returning to the Central Valley of California a century ago, and there were even some age 6 fish returning to spawn (Clark 1929). However, age 6 fish are rarely observed today, and most fish return to spawn at age 3 (Satterthwaite et al. 2017). Shifts in the age structure of Chinook salmon are likely due to a combination of factors, including fisheries, warming environmental conditions, marine predation, competition, and hatchery practices (Barnett et al. 2017; Chasco et al. 2017; Ohlberger et al. 2018, 2019; Seitz et al. 2019; Oke et al. 2020; Manishin et al. 2021; Munsch et al. 2022).

Reduced age structure is influenced by both mortality (i.e., fewer old fish due to accumulated fishing and natural mortality) and maturation (i.e., fewer old fish due to accelerated maturation). In evolutionary terms, high mortality on older age classes in the short-term is expected to create selection driving the evolution of earlier age at maturation over the longer term (Reznick and Endler 1982; Stearns 2000). Thus, increased mortality can be thought of as an ecological precursor and selective driver of the evolution of earlier maturation. In addition, studies have demonstrated that size-at-age of young salmon has increased over time (i.e., faster growth rates at early ages), which may induce maturation at young ages (Vøllestad et al. 2004; Ohlberger et al. 2018). Random mating practices in hatcheries can also inadvertently select for earlier maturation schedules (Hankin et al. 2009). Prior examinations of the effects of age structure on portfolio effects have generally done so using empirical data by removing the non-dominant age classes from consideration or by calculating metrics of age diversity (Greene et al. 2010; Schindler et al. 2010; Price et al. 2021). However, these studies were unable to explore the roles of various mechanisms that can affect age structure. The mechanism driving degradation of age structure diversity may matter for the strength of portfolio effects because high mortality of old age classes simply eliminates individuals before getting a chance to reproduce (for semelparous species) while earlier maturation allows fish to spawn before being subject to additional fishing and natural mortality at older ages. Thus, delayed maturation comes at the cost of greater mortality risk (Andersen et al. 2007) when all else is equal, which is why fisheries may select for decreased age at maturation (the classic pattern in fisheries-induced evolution; Heino et al. 2015). In terms of portfolio effects, this may lead to a tradeoff between mean population abundance and population variability if populations with broad age structure spread risk across many age classes, but older age classes also experience high mortality and therefore fail to spawn altogether. To the best of our knowledge, no studies have examined the differential effects of mortality versus maturation on the strength of portfolio effects driven by age structure and how the effects of these drivers may interact with climate change.

There is growing consensus that California has entered a new climate regime, where severely hot and dry years increasingly coincide, leading to more severe droughts (Swain et al. 2016; Williams et al. 2020). Juvenile salmon require sufficient freshwater flow to successfully migrate to the ocean, and thus droughts can drastically reduce juvenile survival rates (Notch et al. 2020). Research on SRFC revealed that juvenile survival increased nonlinearly with flow and there was a 2.7-fold increase in survival from low to average flow levels (Michel et al. 2021). The 2012–2015 drought, for example, was the driest period in California for the past 1200 years and resulted in especially low juvenile Chinook salmon survival rates in the Sacramento River (Griffin and Anchukaitis 2014; Notch et al. 2020; Michel et al. 2021). Variation in the age of maturity may stabilize annual recruitment and escapement in the face of these highly variable flow conditions, yet the specific contributions of age structure to population stability under climate change has not been examined.

The effects of age structure and climate change on the population dynamics of harvested species can consequently impact management. SRFC are managed by a harvest control rule that sets exploitation rates based on preseason abundance forecasts, but also managed within a mixed stock fishery where the constraints to other stocks may affect harvest rates experienced by SRFC (Pacific Fisheries Management Council (PFMC) 2021*b*). In addition, low escapements create the risk of triggering overfished status (PFMC 2021*b*) that may lead to further constraints on the fishery. Previous research has shown that portfolio effects driven by spatial structure of Chinook salmon spawning populations can stabilize stock abundance and reduce the probability of falling below abundance thresholds (Yamane et al. 2018). However, the full effects of age structure on the management of this species remains uncertain.

Our first objective was to examine how variation in age structure impacts the population size, stability, and harvest of SRFC. We explicitly considered two processes that can affect age structure: (1) changes in mortality rates and (2) changes in maturation rates. The second objective of our study was to determine how drought impacts population dynamics under different age structure regimes. We considered four drought scenarios that are relevant to the California Central Valley: (1) contemporary drought conditions, (2) longer duration of drought events, (3) more frequent droughts, and (4) more intense droughts with higher probability of extremely low flow levels. Our third objective was to quantify the probability of triggering overfished status and resultant management restrictions (i.e., reduced allowable exploitation rate) for SRFC under various age structure and drought scenarios.

Methods

Population model

We developed a life cycle model for SRFC with similar structure to previous models created for Sacramento River winter Chinook (Winship et al. 2013, 2014). The model was structured by origin (natural or hatchery), sex, and age (Fig. S1). Density-dependent natural reproduction was modeled using a stochastic Beverton–Holt stock-recruitment relationship (Beverton and Holt 1957) for natural area spawners, and juvenile sex ratio was assumed to be 1:1 (Table 1, eqs. 1–4). Annual hatchery release of smolts (P_t) was randomly sampled with replacement from hatchery releases over the time period (1988–2012) for which the model was fit (Fig. S2; Huber and Carlson 2015).

Stochastic juvenile survival was a function of river flow (Table S1) during oceanward migration and ocean conditions experienced up to age 2 (Table 1, eqs. 5 and 9–11). The nonlinear relationship between survival and flow at Wilkins Slough (USGS station number 11 390 500) was adopted from Michel et al. (2021), which was represented by a step function with three thresholds (Table S1). Average survival below the minimum flow threshold (4259 cfs) was 0.03, 0.189 between the minimum and historical mean (10 712 cfs) thresholds, 0.508 between the historical mean and high flow (22 872 cfs) thresholds, and 0.353 above the high flow threshold (Michel et al. 2021). We modified this function with linear interpolation between each step to generate a smoother function because of undesirable properties in closed-loop simulations involving step functions and suspicion that a strict step function was unrealistic (Table S1; Fig. S3).

Early ocean survival was modeled as a function of the North Pacific Gyre Oscillation (NPGO) index (Table 1, eqs. 10–11). The NPGO index captures changes in circulation intensity of the North Pacific gyres and is significantly correlated with long-term trends in chlorophyll-a, salinity, and nutrients (Di Lorenzo et al. 2008). A preliminary analysis revealed that NPGO explained more variance in SRFC escapement than other indices of ocean and climate conditions (e.g., Pacific Decadal Oscillation (Mantua 2021), Biologically Effective Upwelling Transport Index (Jacox et al. 2018), and Coastal Upwelling Transport Index (Jacox et al. 2018)) for the time period that was used for model fitting (1988–2012). We acknowledge that the relationship between NPGO and early ocean survival may exhibit non-stationarity (Litzow et al. 2018, 2019), but our goal was to establish a reasonable model of SRFC population dynamics for the time period that was used to fit the model.

Survival of hatchery-origin juveniles had an additional term, κ (Table 1, eq. 5), to incorporate a linear increase in survival advantage of trucked fish (transportation of hatchery fish in trucks or barges to release locations downstream) as a function of the average distance (rkm) between hatcheries and release sites in the Sacramento River Basin (Table 1, eq. 12). The average distance of trucked fish in a given year is mainly a function of the proportion of fish that are trucked all the way downstream (although some fish are only trucked partway) and which hatcheries the fish are trucked from, as some hatcheries are more distant from the bay/ocean than others. Hatcheries will increase the proportion of fish trucked all the way to the bay/ocean to increase the probability of survival during dry years (Sturrock et al. 2019). Thus, hatchery fish are expected to have a survival advantage, particularly during drought conditions. The annual average distance between hatcheries and release sites was simulated from a fitted Generalized Additive Model (GAM) with weighted average distance (weighted by total number of fish released) as the response variable and flow (cfs) at Wilkins Slough as the explanatory variable (Figure S4; Sturrock et al. 2019). We used a GAM to allow for a nonlinear relationship, and the number of basis functions was set to $k = 3$ to prevent overfitting (Zuur et al. 2009). In addition, the relationship between distance and flow was weak prior to the year 2000, thus we used transport distance and flow data post 1999 to fit the GAM (Sturrock et al. 2019). Flow at Wilkins Slough explained 72% of the variance in weighted mean distance between hatcheries and release sites, and the relationship was comparable to the results of mean transport distance and Sacramento Water Index presented in Sturrock et al. (2019). The simulated average distance, based on flow conditions, was then used to model a linear increase in survival of hatchery fish relative to naturally outmigrating juveniles and values for this function were selected to achieve a ratio of hatchery- to natural-origin fish within the range reported in literature (Table 1, eq. 12; Letvin et al. 2021 and reports in that series).

Natural mortality (Table 1, eq. 7) was implemented before fishing mortality (Table 1, eq. 8) because the SRFC fishery typically closes in the fall/late fall (soon after fish mature and return to freshwater) and opens in late spring (Prager and Mohr 2001). We considered fishing mortality to be the sum of total ocean and river harvest, which represents the proportion of fish at age a that died during the fishing season. The majority of harvest comprises ages 3 and 4 fish, and age 2 fish are often below minimum size limits during the fishing season. Thus, fishing morality at age 2 was scaled down with a fishery vulnerability parameter, ν (Table 2). Allowable exploitation rates were prescribed by the harvest control rule used for SRFC (Table S2), which depends on the preseason forecast of ocean abundance (Fig. 1; section 3.3.6 in PFMC

Table 1. Population model equations.

Natural reproduction	
(1)	$J_t \sim \text{round}\left(\text{Lognormal}\left[\log\left(\Sigma_a r_{a,t-1} F_{a,t-1}\right) - 0.5\sigma^2_{\log J}, \sigma^2_{\log J}\right]\right)$
(2–3)	$r_{a,t} = \frac{\theta_1 \gamma_a}{1+\theta_2 \gamma_a F_{a,t}}$; $F_{a,t} = S_{s=\mathrm{f},a,t}\left(1 - b_t\right)$
(4)	$\sigma^2_{\log J} = \log\left(1 + \mathrm{CV}^2_J\right)$
Age transitions	
(5)	$O_{o=\mathrm{n},s,a=2,t+1} \sim \text{Multinomial}\left(J_t, 0.5 j_t g_t\right)$; $O_{o=\mathrm{h},s,a=2,t+1} \sim \text{Multinomial}\left(P_t, 0.5 j_t g_t \kappa_t\right)$; $O_{o,s,a=\{3,4,5\},t+1} \sim \text{Multinomial}\left(E_{o,s,a-1,t}, \left[1 - \tau_{a-1}\right]\right)$
(6)	$E_{o,s,a,t} \sim \text{Multinomial}\left(X_{o,s,a,t}, \left[1 - i_t \nu_a\right]\right)$; fishing mortality
(7)	$X_{o,s,a,t} \sim \text{Multinomial}\left(O_{o,s,a,t-1}, \eta_a\right)$; natural mortality
(8)	$S_{o,s,a,t+1} \sim \text{Multinomial}\left(E_{o,s,a-1,t}, \tau_{a-1}\right)$
(9)	$j_t \sim z_t \alpha$; See Table S1 and Fig. S3
(10–11)	$g_t = \text{Inv.Logit}\left(u_t q_t\right)$; $q_t \sim \text{Lognormal}\left(\phi, \sigma^2_{q_t}\right)$
(12)	$\kappa_t = 2 + 7\left(\frac{d_t}{d_{max}}\right)$
Observation model	
(13)	$\widehat{N}_t \sim \text{round}\left(\text{Lognormal}\left[\log\left(\left[\Sigma_{o,s,a} S_{o,s,a,t}\right] - B_t\right) - 0.5\sigma^2_{\log \widehat{N}}, \sigma^2_{\log \widehat{N}}\right]\right) + B_t$
(14)	$\sigma^2_{\log \widehat{N}} = \log\left(1 + \mathrm{CV}^2_{\widehat{N}}\right)$
Forecast model	
(15–16)	$\widehat{O}_t = O_{a=\{3,4,5\},t} e^{\varepsilon}$; $\varepsilon \sim \text{Normal}\left(\mu, \sigma\right)$
Harvest rate	
(17)	$i_t \sim \text{Beta}\left(\alpha_c, \beta_c\right)$
(18–19)	$\alpha_c = \frac{1-c_t\left(1+\mathrm{CV}^2_c\right)}{\mathrm{CV}^2_c}$; $\beta_c = \frac{\frac{1}{c_t} - 2 + c_t + \mathrm{CV}^2_c\left(c_t - 1\right)}{\mathrm{CV}^2_c}$
Optimization	
(20)	$min\left(\sum_{t=1}^{n}\left[\widehat{N}_t - N_t\right]^2\right)$

2021*a*). The exploitation rate at maximum sustainable yield (F_{MSY}) for SRFC is assumed to be 0.78 (PFMC 2021*b*), which is buffered down to 0.7 (i.e., 0.78 × 0.9) because $F_{\mathrm{MSY}} = 0.78$ is the average F_{MSY} of other Chinook stocks with sufficient data (PFMC 2021*b*). For the most part, the goal of the harvest control rule is to achieve constant escapement (curved part of the control rule; Fig. 1), which is set equal to the reference point for escapement at MSY (S_{MSY}). Meeting the escapement reference point would require closing the fishery when the projected escapement in the absence of fishing is less than S_{MSY}. It would also require very low harvest rates when abundance is forecasted to be only slightly above S_{MSY}, and as a result "de minimis" provisions were implemented to allow for some fishing even though the escapement goal could not be met (Table S2; Fig. 1) or to allow fishing to drive the expected escapement below S_{MSY} in some cases. Section 3.3.6.1 of the Pacific Coast Salmon Fishery Management Plan (PFMC 2021*b*) provides a more detailed description of the harvest control rule.

To simulate forecast error, we obtained records of recent forecasts versus postseason abundance estimates from fishery management documents (PFMC 2021*b*) and reconstructed what the current forecast approach would have predicted for earlier years (back to 1995) with data available at the time (Winship et al. 2015). The logged ratio between the forecast and the postseason abundance estimate was well described by a lognormal distribution (Satterthwaite and Shelton 2022) with log-scale mean 0.132 and log-scale standard deviation 0.486 (Fig. S5). Thus, we modeled the forecast abundance as a function of the "true" model ocean abundance and log-scale error ε, which was drawn at random from the fitted normal distribution (Table 1, eqs. 15–16).

We simulated the process of estimating escapement as a function of the "true" model escapement plus observation error from postseason carcass surveys to maintain realism in our model (Table 1, eqs. 13–14). Estimated escapement was used for model fitting (see description below) and determining overfished status. In addition, we accounted for management implementation error and the reality of managing fisheries by using a realized exploitation rate that was a function of the allowable exploitation rate and error (Table 1, eqs. 17–19). Fishing mortality was assumed to have the same impact on natural- and hatchery-origin fish, since there are no mark-selective fisheries for Chinook salmon in California or the core of SRFC ocean distribution.

We conducted 20 000, 100 year stochastic simulations for each model scenario. The first 30 years of each simulation was considered the burn-in period to eliminate the influence of starting conditions on model outputs. Thus, simulation years 30–100 were used for calculating summary statistics for each scenario (performance metrics were calculated for the last 70 years of each simulation). The model outputs were the means and coefficients of variation (CVs) of estimated total spawner escapement and harvest. We focus on spawner

Table 2. Model indices, variables, and parameters.

Symbol	Value	Description
Indices		
o	{n = natural, h = hatchery}	Origin
s	{f = female, m = male}	Sex
a	{2, 3, 4, 5}	Age
t	{1, 2, …, 100}	Year
State variables		
$O_{o,s,a,t}$		Number of fish in the ocean
$S_{o,s,a,t}$		Number of spawners
$E_{o,s,a,t}$		Number of fish after fishing mortality
$X_{o,s,a,t}$		Number of fish after natural mortality
$F_{a,t}$		Number of female spawners
J_t		Number of natural-origin fry
P_t		Number of hatchery-origin smolts released
B_t		Number of spawners returning to hatcheries
C_t		Number of fish harvested
$\widehat{N}_t$		Simulated estimate of spawner abundance
$\widehat{O}_t$		Forecasted ocean abundance
Parameters		
τ_a	$\tau_{\{2,3,4,5\}}$ = {0.035, 0.55, 0.99, 1}	Maturation rate[a]
η_a	$\eta_{\{2,3,4,5\}}$ = {0.5, 0.8, 0.8, 0.8}	Natural adult survival rate[b]
γ_a	$\gamma_{\{2,3,4,5\}}$ = {4325, 5407, 5407, 6488}	Fecundity[c]
ν_a	$\nu_{\{2,3,4,5\}}$ = {0.02, 1, 1, 1}	Fishery vulnerability[d]
θ_1	0.4	Maximum egg-to-fry survival[e]
θ_2	1e-8	Strength of density dependence[e]
α	0.067	Residual juvenile survival[f]
ϕ	0.828[n]	Mean effect of NPGO on juvenile survival[f]
$\sigma^2_{q_t}$	0.131	Variance of NPGO effect on juvenile survival[f]
CV_j	0.215[n]	CV of recruitment stochasticity[f]
$\mathrm{CV}_{\widehat{N}}$	0.2	CV of observation error[g]
CV_c	0.32[n]	CV of realized harvest rate[h]
d_{max}	445	Distance (rkm) between Coleman National Fish Hatchery and Chipps Island in Suisun Bay[i]
μ	0.132	Log-scale mean ratio of preseason forecast and postseason estimate of escapement[j]
σ	0.486	Log-scale s.d. of preseason forecast and postseason estimate[j]
ε_t		Error in preseason forecast and postseason estimate at time t
Rate variables		
$r_{a,t}$		Mean number of fry per female spawner
j_t		Outmigration juvenile survival
z_t		Flow-dependent juvenile survival (see Table S1 and Fig. S3)
g_t		NPGO-dependent juvenile survival
κ_t		Relative hatchery-origin juvenile survival
c_t		Allowable exploitation rate
i_t		Realized exploitation rate
b_t		Proportion of spawners returning to hatcheries

escapement rather than total run size (escapement + harvest) as this is the metric used to determine whether the stock is overfished or rebuilt, and escapement is the driver of future natural production. We used the CV to quantify stability and portfolio effects as this metric is widely used for salmon stocks (Schindler et al. 2010; Connors et al. 2022), including SRFC (Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015; Yamane et al. 2018). Although the CV is not independent from the mean, the log transformed variance scales with log transformed mean for our model scenarios (slope = 2.15; Fig. S6) such that CV can be used to represent stability and portfolio effects in this study (Anderson et al. 2013). We also quantified management restrictions for simulation years 30–100 (see section on the

Table 2. (*concluded*).

Symbol	Value	Description
Data		
N_t		Observed spawner escapement[l]
w_t		Flow (cfs) at Wilkins Slough[k]–calculate z_t.
u_t		NPGO index[m]
d_t		Mean distance between hatcheries and release sites[i]

[a] Values selected to generate an age composition that approximated empirical age compositions (Fig. S10).

[b] Assumed values consistent with current California salmon assessments (Prager and Mohr 2001; O'Farrell et al. 2012).

[c] Values for ages 3 and 4 adopted from (Friedman et al. 2019) SRFC model, and ages 2 and 5 values adjusted based on age-specific fecundity for Chinook salmon (Healey and Heard 1984; Kaufman et al. 2009).

[d] Values were selected to achieve reasonable age composition of catch (Palmer-Zwahlen et al. 2006).

[e] Natural production parameters were selected to achieve reasonable population dynamics for the 100 year simulations.

[f] Parameters that were calibrated by minimizing the sum of squared error between observed (PFMC 2021*b*) and simulated escapement.

[g] Pacific Fisheries Management Council 2019.

[h] Winship et al. 2013.

[i] Sturrock et al. 2019.

[j] Values from fitting a lognormal distribution to the logged ratio between the forecast and postseason abundance estimate from fishery management documents (PFMC 2021*b*; Satterthwaite and Shelton 2022).

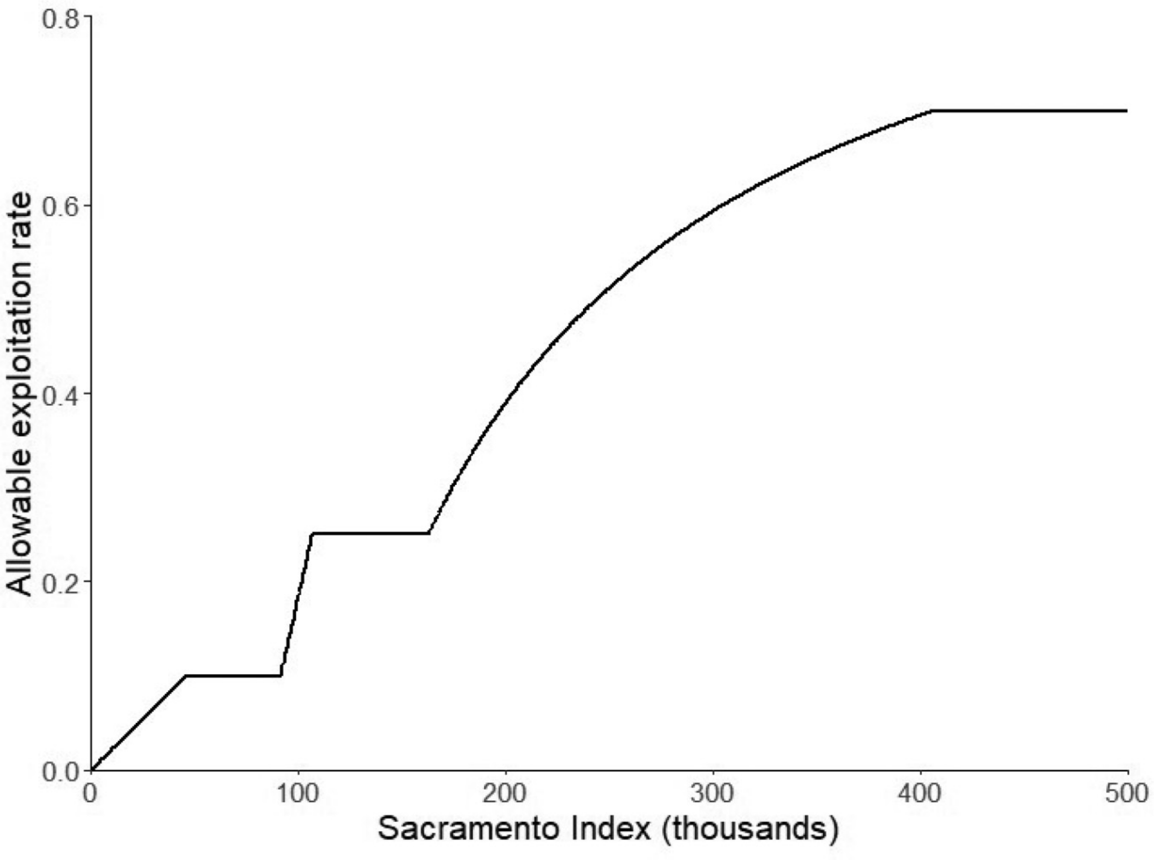
[k] USGS station number 11 390 500.

[l] PFMC 2021*b*.

[m] Di Lorenzo et al. 2008.

[n] Base values—see Supplementary material B for sensitivity analyses. CV: coefficient of variation; NPGO: North Pacific Gyre Oscillation.

Fig. 1. Harvest control rule for Sacramento River fall Chinook (PFMC 2021*b*). The control rule is defined in terms of the minimum stock size threshold (MSST; 91 500), adult spawners that achieve maximum sustainable yield (S_{MSY}; 122 000), and the annual exploitation rate associated with the acceptable biological catch (F_{ABC}; 0.7). The allowable exploitation rate is determined by the post-season estimate of the Sacramento Index, which is the sum of ocean fishery harvest, non-retention ocean fishery impacts, recreational fishery harvest in the Sacramento River, and spawner escapement (PFMC 2021*a*).



effects on management below for more details). In addition, we conducted sensitivity analyses to key model parameters (i.e., mean effect of NPGO on early ocean survival, CV of recruitment stochasticity, and CV of realized harvest rate) to test the robustness of our results (Supplementary material B).

Parameter estimation and model validation

The parameters for residual juvenile survival (i.e., all factors other than flow and NPGO), NPGO-dependent survival (mean and variance), and CV of recruitment stochasticity lacked empirical estimates and data to infer parameter values. Thus, we optimized these parameters to fit the empirical data by minimizing the sum of squared error between empirical and modeled estimates of annual adult spawner escapement for the years 1988–2012 (Table 1, eq. 20). Harvest was omitted from the model tuning process because estimates of harvest for SRFC are likely less reliable than estimates of escapement, this is especially true for recreational harvest. During the optimization procedure, spawner escapement at the beginning of each time step was set equal to observed escapement such that observed values were used as inputs to the stock-recruitment relationship. However, the modeled escapement at the end of each timestep was used for calculating the sum of squared error in the optimization routine. This approach was used to improve the overall model fit, and simulations for model validation and other scenarios were run without setting escapement equal to observed escapement at the beginning of each timestep. Following the optimization routine, minor adjustments were made to stock-recruitment parameter values to fine tune the model fit and ensure that the modeled long-term (100 year simulation) mean and median spawner escapement were <10% different from the observed mean and median (PFMC 2021*a*) for the time period used to fit the model. We validated the model by assessing: (1) the relationship between flow at Wilkins Slough and model estimated escapement, (2) the pattern of temporal autocorrelation in escapement (autocorrelation is a biologically expected property of time series of salmon abundance as demonstrated through observed escapement), (3) age-composition of escapement and harvest, and (4) ratio of natural-origin to hatchery-origin escapement. To assess the flow-escapement and NPGO-escapement relationships, we fit GAMs with escapement as the response variable and flow ($t-2$) and NPGO ($t-1$) as explanatory variables in separate models. We compared the variance in escapement explained by flow and NPGO and visually assessed the shape of these relationships (Fig. 2*b* and S7).

Age-structure scenarios

We modeled changes in two mechanisms that could affect the age structure of a population: mortality and maturation rates. In the base scenario, the natural mortality rate for ages 4 and 5 was 0.2 ($\eta_{a=4,5} = 0.8$, where η is the natural survival rate). The natural mortality rate for ages 4 and 5 fish was increased to 0.99 ($\eta_{a=4,5} = 0.01$) to simulate the loss of older fish. In addition, we simulated a lower natural mortality rate at 0.01 ($\eta_{a=4,5} = 0.99$) such that age 4 and 5 fish primarily experience fishing mortality and minimal natural mortality.

To model various age structure scenarios caused by different maturation rates, we modified only the maturation rate of age 3 fish as they compose the majority of harvest and spawner escapement for SRFC. Age 3 maturation in the base model scenario was $\tau_{a=3} = 0.5$, which generated an age-composition of spawners that approximated empirical estimates for SRFC (Fig. S8; Satterthwaite et al. 2017; Friedman et al. 2019). In the low age structure scenario, the age 3 maturation rate was $\tau_{a=3} = 0.99$ such that almost all fish matured at age 3, and very few fish progressed to ages 4 and 5 (Fig. S8). The age 3 maturation rate was $\tau_{a=3} = 0.25$ for the high age structure scenario, which produced an age-composition of spawners that was more even than the base and low age structure scenarios, and age 4 spawners were dominant (Fig. S8). Note that varying maturation rates while keeping natural mortality constant changes both age structure and the expected proportion of smolts that ultimately reach adulthood, as delayed maturation carries the risk of mortality in the meantime.

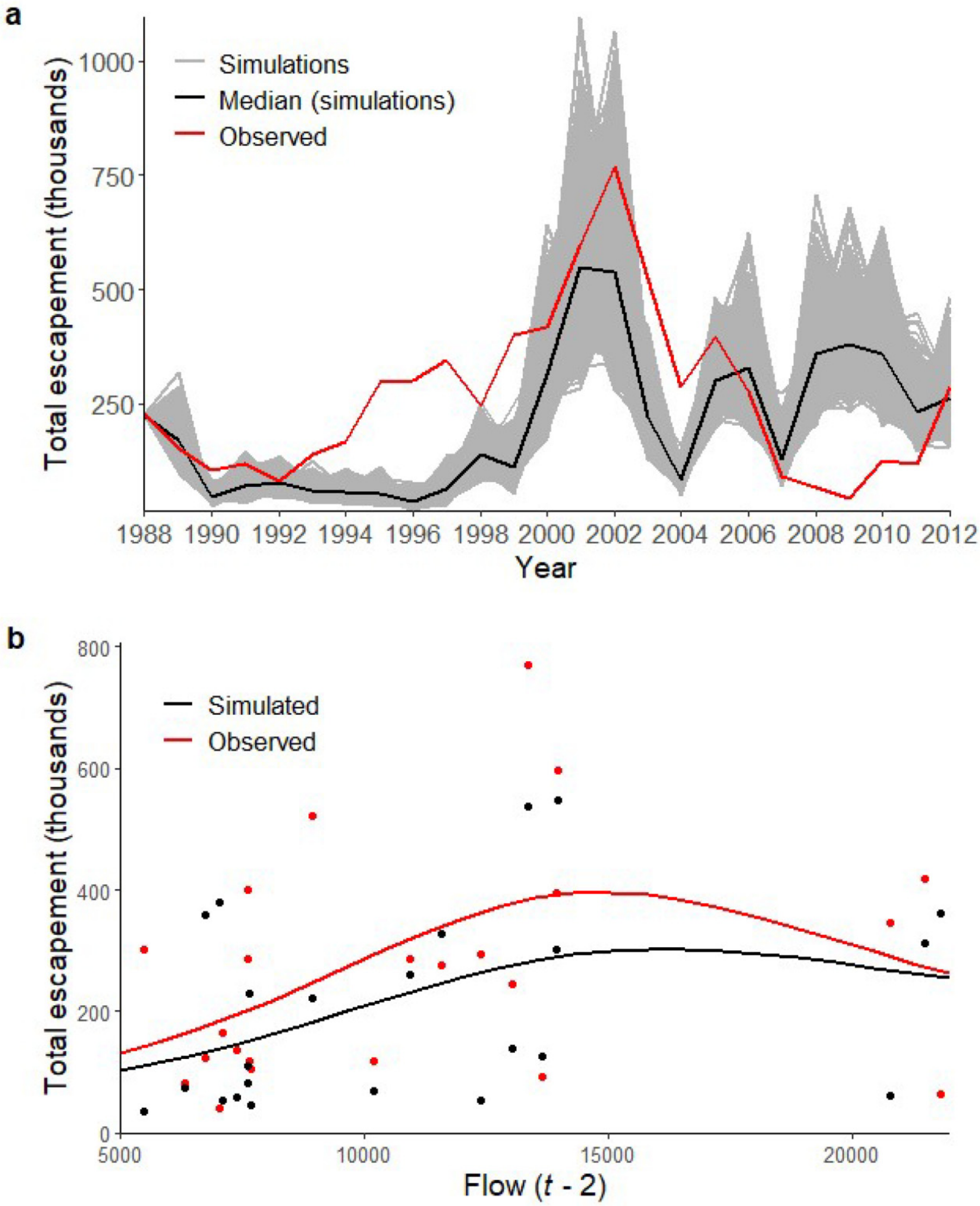
We used extreme values for alternative natural mortality and maturation rates to capture scenarios in which age structure was entirely driven by changes in natural mortality or entirely driven by maturation rates. Previous research on salmon age structure implicitly assumed extreme natural mortality by dropping non-dominant ages classes to represent “low age structure” scenarios (e.g., Schindler et al. 2010). However, in this study, we explicitly considered two mechanisms that can drive changes in age structure and compared the consequences of each one.

Climate scenarios

We tested four climate scenarios characterized by alternative flow regimes at Wilkins Slough, which affected juvenile survival rates. First, we modeled the base scenario where flow resembled contemporary conditions. Flow values for non-drought years were randomly sampled, with replacement, from Wilkins Slough flow data for years 1993–2006, 2010–2011, and 2017–2019 (Fig. S9). However, values were constrained such that a maximum of two consecutive years were allowed to be below the mean historical threshold (10 712 cfs; Michel et al. 2021) because we considered periods with flow below this threshold for more than two consecutive years to be drought events (Fig. S9). The flow values for drought years were randomly drawn from recent notable drought events (1988–1992, 2007–2009, and 2012–2016; note that the first drought event started in 1987, but flow data at Wilkins Slough were unavailable prior to 1988), and all values from droughts were below the mean historical threshold (Fig. S9). The duration of each drought event was 3–5 years, which was randomly sampled for each event. The time interval between drought events was assumed to follow a Poisson distribution, with $\lambda = 12$ years, the mean number of years between initial drought years for recent events (Fig. S9).

For the second scenario (“longer duration”), we followed the same procedure as the base scenario but increased the range of drought duration to 3–7 years. In the third scenario (“more frequent”), we simulated more frequent droughts by reducing λ to 6 years and followed the other procedures of the base scenario (Fig. S10). Last (“more intense”), we

Fig. 2. Total spawner escapement (*a*) for observed (red line, PFMC 2021*b*) and simulated (gray and black lines) data, and the effect of flow on escapement (*b*). Total escapement includes natural and hatchery origin populations. The effect of flow on escapement was estimated using Generalized Additive Models, and flow was lagged two years as that is when age 3 (dominant age class) was affected by freshwater conditions during outmigration.



simulated increased drought intensity by doubling the probability of drawing the lowest flow value, which was below the minimum flow threshold of the juvenile survival function (Michel et al. 2021) and followed the base scenario procedures for drought duration and frequency (Fig. S10).

Effects on management

We quantified the effects of climate change and age structure on several metrics of SRFC management including the proportion of years with overfished status and proportion of years with fisheries restrictions. SRFC are designated as overfished by U.S. fisheries management law when the most recent three-year geometric mean for adult (ages 3 or older) spawner escapement is less than the minimum stock size threshold (91 500; PFMC 2021*b*). The term "overfished" is not to be confused with "overfishing", for which the latter term is linked to harvest mortality (i.e., harvest mortality above the rate assumed to achieve maximum sustainable yield is considered overfishing). In addition, we calculated the proportion of years with abundance forecasts that resulted in allowable exploitation rates of 10% (very heavily restricted fisheries), 25% (heavily restricted fisheries), and 70% (maximum allowable exploitation, with the only constraint in this case being the Magnuson–Stevens Fishery Conservation and Management Act prohibition on overfishing that applies regardless of stock size).

Results

Model validation

The simulated total spawner escapement for SRFC had the same magnitude as the observed data and encompassed about 50% of the observed escapement (Fig. 2*a*). The simulated relationship between total spawner escapement and flow (lagged 2 years) matched well with the observed relationship (Fig. 2*b* and 2*c*). Flow explained 22% of the variance in observed total spawner escapement and 17% of the simulated escapement (Fig. 2*b* and 2*c*). A single year lag in NPGO explained the most variance in observed total spawner escapement compared with alternative time lags, and the variance explained for observed data was 51% and 41% for simulated data. In addition, the observed and simulated (calculated as annual means) Sacramento Index (harvest + escapement) exhibited similar trends in temporal autocorrelation (Fig. S11), and the age composition of spawner escapement and harvest was comparable to observed age compositions (Fig. S12; Palmer-Zwahlen et al. 2006; Satterthwaite et al. 2017).

Age structure scenarios

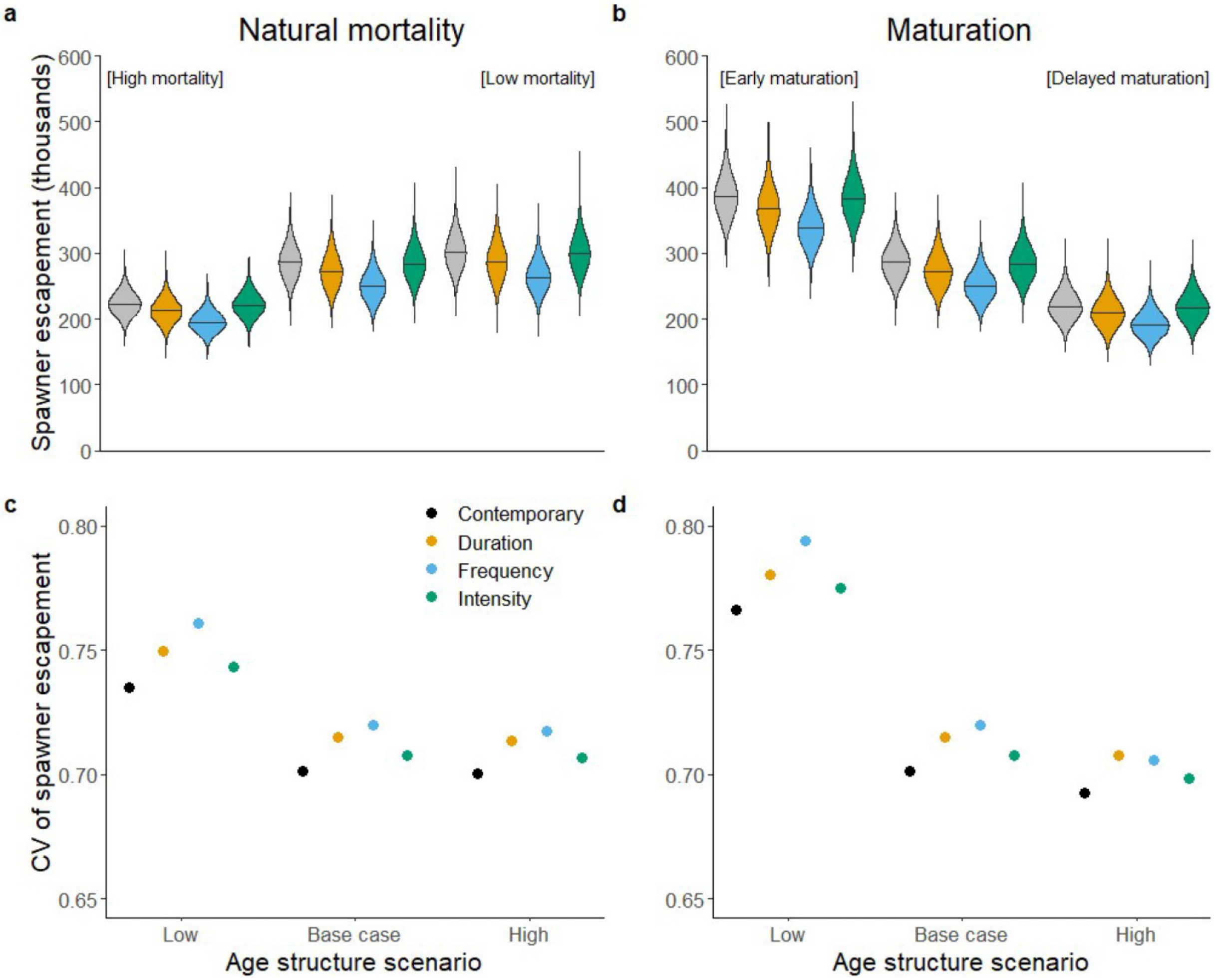
Effects on spawner escapement—mean spawner escapement increased with more diverse age structure when driven by reduced natural mortality rates but decreased when diverse age structure was driven by delayed maturation (contemporary flow conditions in Fig. 3*a* and 3*b*). However, the temporal variability (CV) of spawner escapement decreased when diverse age structure was driven by either reduced natural mortality or delayed maturation, although decrease in variability was small from base case to high age structure diversity (Fig. 3*c* and 3*d*). Escapement increased when we lowered natural mortality rates and, thus, increased the population's age structure (35% increase in escapement from low to high age structure) because there were more fish at older ages that survived and returned to spawn (Fig. 3*a*). Lowering the age 3 maturation rate to increase diversity of age structure had the opposite effect on spawner escapement because fish that delayed maturation were exposed to additional natural and fishing mortality (43% decrease in escapement from low to high age structure scenarios; Fig. 3*b*). The diverse age structure scenarios, regardless of the mechanism driving changes in age structure (reduced natural mortality or delayed maturation), had lower variability of escapement and increased temporal buffering (i.e., stronger portfolio effect) compared with less diverse age structure scenarios. Maturation rates, however, had a greater impact on the variability of escapement than natural mortality rates (Fig. 3*c* and 3*d*). Natural mortality, particularly lower mortality rates, had a lower impact than maturation rates because of the high exploitation rates that resulted in only a modest increase in age structure diversity (see section below on the effects on management for the distribution of exploitation rates across scenarios). The CV of escapement ranged from 0.74 (low age structure) to 0.7 (high age structure) for alternative natural mortality rates and 0.77 (low age structure) to 0.69 (high age structure) for alternative maturation rates (Fig. 3*c* and 3*d*).

Effects on harvest—assuming that the harvest control rule remains the same, more diverse age structure driven by either lower natural mortality rates or delayed maturation rates resulted in increased mean harvest and decreased variability of harvest (contemporary flow conditions in Fig. 4*a* and 4*b*). For alternative natural mortality rates, there was a 23% increase in mean harvest from low to high age structure (Fig. 4*a* and 4*c*). When age structure was modified by maturation rates, there was a 26% increase in mean harvest from low to high age structure (Fig. 4*b*). Harvest increased with more diverse age structure because fish escaped sources of natural mortality and were available to the fishery the next year or they escaped harvest, delayed maturation, and were available to catch the following year. Thus, the decrease in escapement caused by delayed maturation (described above) is primarily because more fish are being caught in the fishery. Also, the CV of harvest under alternative natural mortality rates was 0.78 (high mortality, low age structure diversity) to 0.73 (low mortality, high age structure diversity). Under alternative maturation rates, CV of harvest was 0.78 (high maturation rate, low age structure) to 0.73 (low maturation rate, high age structure; Fig. 4*d*). The qualitative results for escapement and harvest with respect to age structure scenarios were robust to different values for key model parameters (Fig. S13–S15). In addition, the main qualitative results held when we considered total run size (escapement + harvest) rather than escapement and harvest separately (Fig. S16).

Climate scenarios

Effects on spawner escapement—climate change (i.e., longer duration, more frequent, or more intense droughts) reduced mean escapement and increased variability of escapement across all age structure scenarios (Fig. 3). More frequent droughts had the largest impact on mean (13% lower than contemporary drought conditions) and variability (3% higher mean CV than contemporary conditions—for example, 0.73–0.76 for contemporary and more frequent drought scenarios, respectively) of escapement for both alternative mortality and maturation rates (Fig. 3). More intense droughts (i.e., higher probability of extremely low flow levels) had the smallest impact on escapement with a 1% difference in mean and variability compared with contemporary conditions (Fig. 3). Longer duration, more frequent, and more intense droughts decreased escapement and increased variability because juvenile survival rates were reduced during low flow drought conditions. Increased age structure diversity driven by lower natural mortality and delayed maturation rates decreased escapement variability across all drought scenarios (Fig. 3*c* and 3*d*). However, the simulated effects of natural

Fig. 3. Total spawner escapement (*a* and *b*) and coefficients of variation (CV; *c* and *d*) under various age structure and drought scenarios (longer duration, more frequent, and more intense droughts). Age structure scenarios are arranged from lowest (left) to highest (right) diversity and modified by natural mortality rates (*a* and *c*) or maturation rates (*b* and *d*). Horizontal lines in the violin plots (*a* and *b*) indicate mean spawner escapement.



mortality and maturation had a slightly greater impact on escapement variability under more frequent droughts (i.e., the % difference for the CV of escapement between contemporary conditions and more frequent droughts decreased as age structure increased) than longer or more intense droughts (Fig. 3*c* and 3*d*). Importantly, the variability of escapement with low age structure and contemporary drought conditions was still greater than the variability of escapement for higher age structure and future drought scenarios (Fig. 3*c* and 3*d*).

Effects on harvest—assuming that the harvest control rule remains the same, the effects of drought on harvest were similar to escapement such that drought decreased the mean and increased the variability of harvest across all age structure scenarios (Fig. 4). Also, more frequent droughts had the largest impact on mean (13% lower than contemporary drought conditions) and variability (3% higher mean CV than contemporary conditions—for example, 0.74–.77 under contemporary and more frequent drought conditions, respectively) of harvest for both alternative mortality and maturation rates (Fig. 4). Reduced natural mortality and delayed maturation rates (i.e., increased age structure diversity) increased mean harvest and decreased variability of harvest across all drought scenarios (Fig. 4*b* and 4*d*). The variability of harvest under low age structure scenarios with contemporary drought conditions was greater than variability of harvest under higher age structure scenarios with drought conditions (Fig. 4*d*). A sensitivity analysis showed that our results on the effects of drought on populations with different age structures were robust to alternative values of key model parameters and that our qualitative results remained consistent (Fig. S13–S15).

Effects on management

The percentage of years with overfished status decreased as age structure increased via natural mortality rates because lower natural mortality at ages 4 and 5 resulted in more fish surviving to spawn per juvenile entering the ocean (Fig. 5*a*). However, the percentage of years with overfished status increased with greater age structure driven by delayed maturation because fish spent more time exposed to natu-

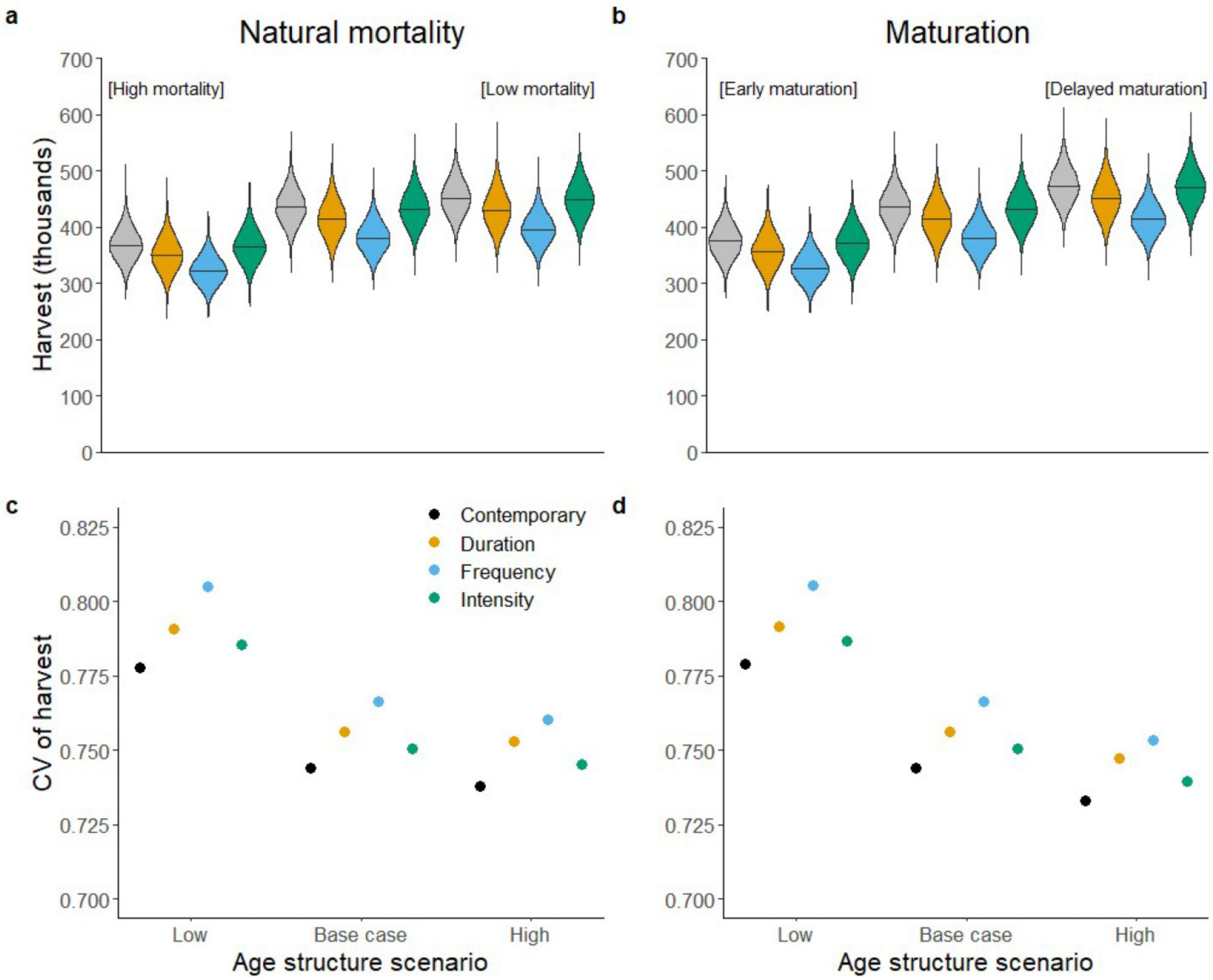


Fig. 4. Harvest (*a* and *b*) and coefficients of variation (CV; *c* and *d*) under various age structure and drought scenarios (longer duration, more frequent, and more intense droughts). Age structure scenarios are arranged from lowest (left) to highest (right) diversity and modified by natural mortality rates (*a* and *c*) or maturation rates (*b* and *d*). Horizontal lines in the violin plots (*a* and *b*) indicate mean spawner escapement.

ral and fishing mortality while in the ocean (Fig. 5*b*). Thus, for a given level of juvenile production there were fewer fish that survive to spawn when maturation was delayed (i.e., high age structure), and consequently there was a greater risk of spawner escapement below the overfished threshold with delayed maturation while holding mortality rates constant.

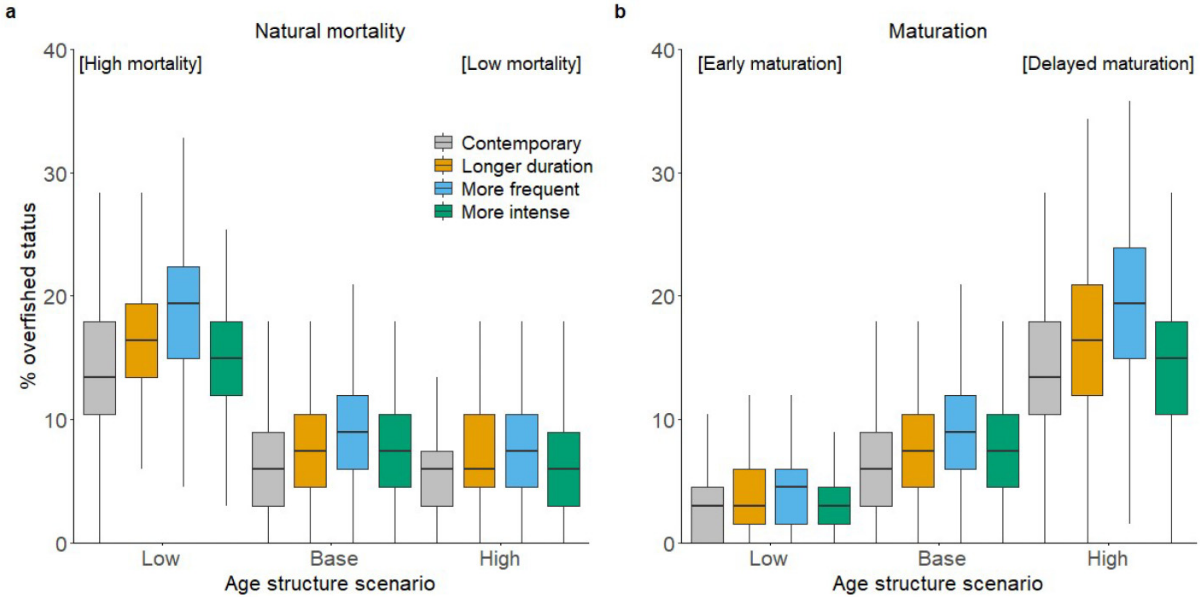
Climate change increased the percentage of years with overfished status across all age structure scenarios and more frequent droughts had the highest impact (Fig. 5). In addition, increased age structure via natural mortality rates dampened the effects of climate change on overfished status such that the difference in percentage of years with overfished status between contemporary conditions and more frequent droughts was smaller for high age structure scenarios (Fig. 5*a*). The percentage of years with overfished status under contemporary conditions and low age structure was greater than climate change scenarios with higher age structure (Fig. 5*a*). However, delayed maturation (high age structure diversity) exacerbated the impact of climate change on overfished status (Fig. 5*b*).

Fisheries were less restricted under lower natural mortality and delayed maturation rates (i.e., high age structure diversity) such that the percentage of years with maximum allowable exploitation rate ($c = 0.7$) increased under high age structure scenarios (Fig. 6). When mortality was low or maturation was delayed the "true" model ocean abundance was high and, thus, increased the forecasted abundance that is used to prescribe allowable exploitation rates (Fig. 6). Climate change scenarios increased fisheries restrictions across all age structure scenarios for both natural mortality and maturation rates, and more frequent droughts had the highest impact (Fig. 6). In addition, there were more fisheries restrictions under the low age structure scenarios with contemporary drought conditions than higher age structure scenarios and potential future drought conditions (Fig. 6*c*–6*f*).

Discussion

Our results show that maintaining or even restoring age structure diversity by either reduced natural mortality of

Fig. 5. Percentage of years with overfished status for various age structure and drought scenarios (longer duration, more frequent, and more intense droughts). The horizontal lines represent median values. Age structure scenarios are arranged from lowest (left) to highest (right) diversity, which includes alternative ages 4 and 5 natural mortality rates (*a*) and alternative age 3 maturation rates (*b*). Sacramento River fall Chinook are considered overfished when the most recent three-year geometric mean of the adult spawner escapement estimate is less than 91 500.



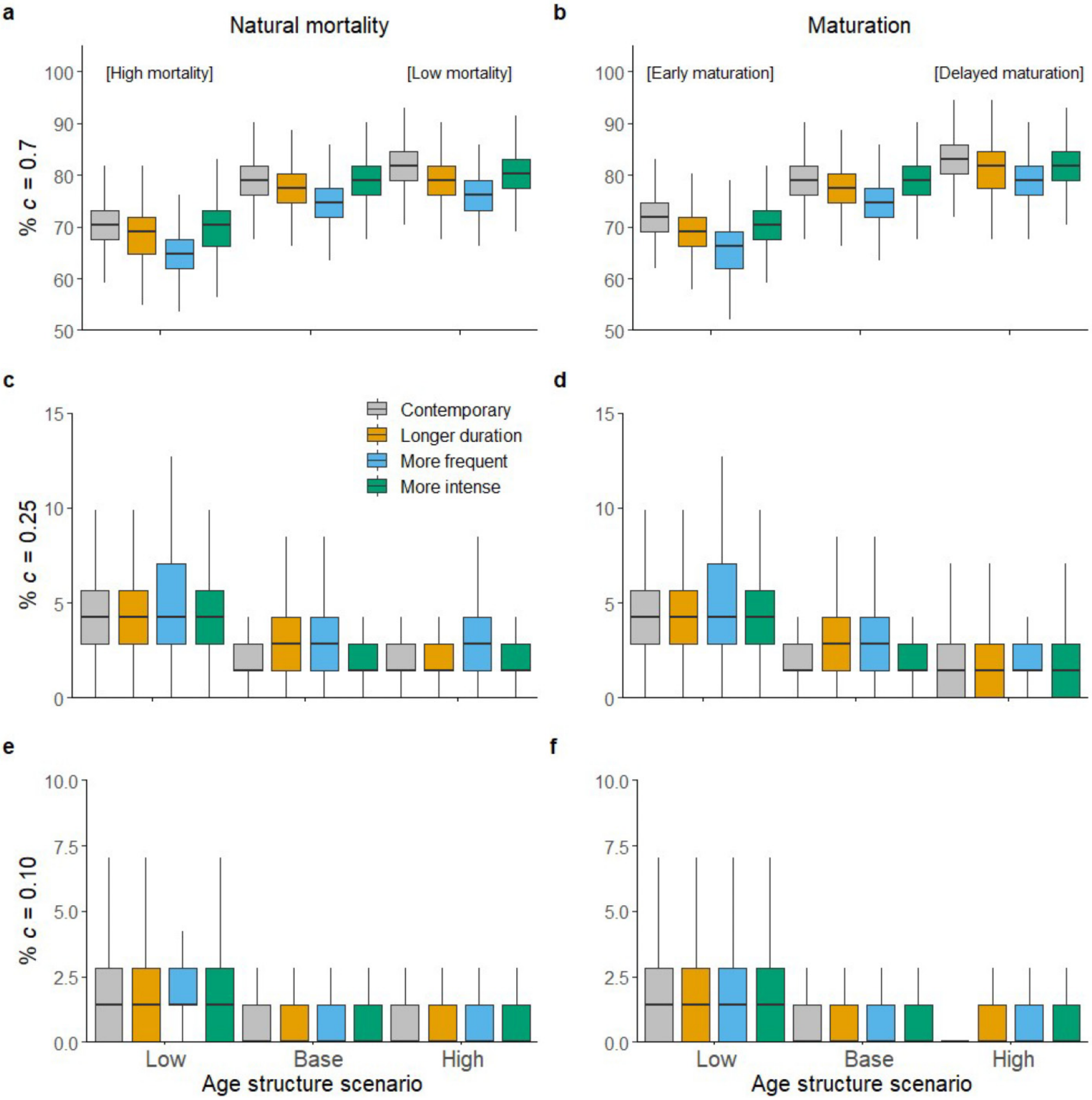
adult fish or delayed maturation of age-3 fish would serve to stabilize the Sacramento River fall-run Chinook (SRFC) population. In contrast, the mean population size responded differently depending on the mechanism driving changes in age structure. Reduced mortality increased escapement whereas delayed maturation decreased escapement. We found that drought decreased means and increased variabilities of both escapement and harvest, but reduced natural mortality and delayed maturation (i.e., diverse age structure) were able to buffer the adverse effects of climate change on variability of both escapement and harvest. Finally, the percentage of years with overfished status decreased with greater age structure diversity driven by reduced natural mortality. Reduced natural mortality was able to reduce the frequency of overfished status even when the system experienced the effects of climate change. However, we observed the opposite pattern for percentage of years overfished when delayed maturation was responsible for changes in age structure.

Results show that population stability was higher (i.e., lower CV) for base case and more diverse age structure scenarios than less diverse scenarios because of the benefits from the portfolio effect such that the risk of experiencing adverse environmental conditions was spread across time and multiple age classes. Our findings corroborate empirical studies that observed increased population stability with age structure for sockeye salmon (*O. nerka*; Greene et al. 2010; Schindler et al. 2010) and expand on these studies by explicitly comparing the effects of mortality and maturation rates. Greater age structure driven by reduced natural mortality increased escapement because more fish at ages 4 and 5 were surviving and returning to spawn. Although we simulated different natural mortality rates for older individuals, alternative exploitation rates on these age classes would generate the same response. Greater age structure driven by delayed maturation decreased escapement because older fish were exposed to additional natural and fishing mortality while in the ocean. This result shows that delayed maturation is not demographically free and would likely need to be managed alongside strategies to reduce fishing and/or natural mortality. If such strategies are implemented, greater stability of populations and higher escapement could be achieved.

Harvest increased and variability decreased with greater age structure driven by either reduced natural mortality or delayed maturation rates. While the reduction in the CV of harvest is relatively small, a change in harvest of ∼100 000 from low (∼375 k) to high (∼475 k) age structure diversity is consequential and enhances nature's contributions to people through increased economic and cultural value (Oke et al. 2020; Des Roches et al. 2021). Diverse age structure can also benefit people's livelihoods through more stable annual harvest and income. In addition, fisheries would harvest more of the older, larger individuals that delay maturation, which typically have higher commercial and recreational fisheries value (Arlinghaus 2006; Lew and Larson 2012). For example, Oke et al. (2020) estimated that declines in body size, which were primarily attributed to shifts in age structure, of Chinook salmon populations in Alaska between 1990 and 2010 resulted in ∼25% loss in commercial value and ∼26% loss in subsistence meals provided for rural people.

The magnitude of differences in CV of escapement and harvest between age structure scenarios in this study (5%–

Fig. 6. Percentage of years when the allowable exploitation rate (*c*) was 0.7 (*a* and *b*), 0.25 (*c* and *d*), and 0.1 (*e* and *f*) for various age structure and drought scenarios (longer duration, more frequent, and more intense droughts). The horizontal lines represent median values. Note that some of these lines are at the lower edge of the boxes. Age structure scenarios are arranged from lowest (left) to highest (right) diversity, which includes alternative ages 4 and 5 natural mortality rates (*a*, *c*, and *e*) and alternative age 3 maturation rates (*b*, *d*, and *f*). Allowable exploitation of 0.7 represents the highest rate allowed under the control rule, 0.25 represents heavily constrained fisheries, and 0.1 represents very heavily constrained fisheries (Fig. 1).



10%) were smaller than the results from previous research on age structure and portfolio effects. For example, Schindler et al. (2010) found differences in CVs of escapement between age structure scenarios to be > 20%, and Carlson and Satterthwaite (2011) found 27%–38% differences in CVs of escapement from portfolio effects of pooling together rivers in the San Joaquin and Sacramento River basins. Part of the difference in these findings is the result of simulating a system that manages towards the goal of constant escapement, which adjusts harvest rates upward when abundance is expected to be high and downward when expected to be low. In addition, the harvest control rule is currently applied to modeled ocean abundance with the expectation that all unfished adults would return in the same year (i.e., assumes 100% maturation rate), and we did not model adjustments to the control rule such that it would apply only to an expected escapement that reflected a reduced maturation rate. Scaling harvest rates with forecasted abundance acts to stabilize escapement and partially dilute the effect of age structure. However, even a 5%–10% change in harvest would be taken seriously by management and fishers because there can be consequences for fishing opportunity. For example, buffers of 5%–10% are used to account for different levels of uncertainty in F_{MSY} reference points (PFMC 2021*b*).

The effects of climate change were consistent across age structure scenarios such that longer duration, more frequent, and more intense droughts decreased mean escapement and harvest and increased variability. This was due to reduced juvenile survival rates under drought (i.e., low river flow) conditions (Notch et al. 2020; Michel et al. 2021). More frequent droughts had the greatest impact on escapement and harvest because there was a higher proportion of years with flow below the historical mean threshold (10 712 cfs), which resulted in a large drop in juvenile survival (Michel et al. 2021). In addition, the population was sensitive to both juvenile survival and generation length such that under more frequent and longer duration droughts there was a higher probability of low flow impacting consecutive generations and cohorts. Thus, the population had less time to recover between drought events. Importantly, maintaining or increasing age structure through reduced mortality and delayed maturation rates was able to mitigate the adverse effects of climate change by reducing the variability of escapement and harvest. This result strengthens previous findings on the benefits of life-history diversity and the portfolio effect on population stability in variable environmental conditions (Schindler et al. 2015; Cordoleani et al. 2021; Munsch et al. 2022). Droughts can also limit access to temperature refuges for adult salmon migrating to spawning grounds and lead to premature mortality (von Biela et al. 2022), so the drought effects presented here are likely conservative. Thus, age structure is an important management consideration for salmon as droughts are expected to increase in frequency and severity (Chou et al. 2013; Dai 2013; Trenberth et al. 2014).

The percentage of years with overfished status decreased as age structure increased via reduced natural mortality rates because more fish survived and contributed to natural production, which also stabilized the population. Other studies have demonstrated that among population diversity across space for SRFC can reduce the probability of fisheries restrictions (Yamane et al. 2018), but our study extends this to within population diversity across time through age structure. In addition, we show that the decrease in overfished status can buffer against the harmful effects of climate change as natural mortality rates decrease and age structure diversity increases. However, our results with respect to maturation rates challenge the way portfolio effects are typically viewed because high age structure and life-history diversity through delayed maturation increased the percentage of years overfished. This result highlights the mean versus variability tradeoff under delayed maturation rates such that high age structure reduced mean escapement, increased percentage of years overfished, but also reduced variability and increased harvest. Given the tradeoff that stems from earlier maturation, future research and management (particularly with respect to hatchery practices) should consider the implications of different mechanisms that can alter age structure of a population. Changing adult natural mortality rates will likely have minimal impacts on a population that exhibits early maturation because fish return before they are exposed to additional mortality or before most of the adult population can benefit from reduced mortality. On the other hand, if maturation rates are delayed and the population has high age structure diversity, changing natural mortality rates will have a greater impact as fish will experience the increase or decrease in mortality as they remain in the ocean. However, altering natural mortality rates (e.g., by culling predators or boosting predator's alternate prey) of adult salmon in practice may not be a feasible option. In the case of delayed maturation, exploitation rates can be co-managed with delayed maturation to increase escapement (via reducing total mortality of adults), decrease the probability of reaching overfished status, increase stability, and maintain harvest at a level similar to that under the base age structure scenario.

Our results focus on mean and variability of escapement and harvest, but there are additional benefits of older, larger fish that we did not consider in this study. Older, larger fish likely increase the productivity of populations through allometric relationships with fecundity and egg mass (Kinnison et al. 2001; Ohlberger et al. 2020; Staton et al. 2021). Larger salmon also transport more marine-derived nutrients to freshwater and terrestrial ecosystems (Carlson et al. 2011; Hocking and Reynolds 2011) and provide more energy to large predators such as Southern Resident Killer Whales (*Orcinus orca*; Ford and Ellis 2006). Direct benefits for people, including increased cultural, economic, and subsistence value also increase with fish size (Oke et al. 2020). Thus, a population with diverse age structure may be able to provide higher quality ecosystem services that are also less variable than low age structure populations regardless of the mechanism.

In our model, only the SRFC population was used for determining exploitation rates. However, ocean salmon fisheries off the U.S. west coast are mixed stock fisheries, and our model assumes that SRFC are always the limiting stock (PFMC 2021*b*). This may not be the case in reality because of constraints arising from co-occurring Sacramento River winter run Chinook (endangered), California Coastal Chinook (threatened), and Klamath River fall run Chinook, which can be more limiting at times (appendix C in PFMC 2019). Thus, our model was unable to capture potential fishery constraints due to limiting stocks other than SRFC that may also be affected by climate change and declining age structure. In addition, while our simulation modeling approach represents our best attempt to capture the observed dynamics of SRFC, the inherent challenges in forecasting population dynamics means that our results do not represent quantitative predictions of SRFC abundance or fishery performance in the near-term.

It has been proposed that California hatchery production should increase in hopes of compensating (at least in part) for the adverse effects of climate change on salmon populations (CDWR 2021). While increased production in our model would result in higher escapement and harvest, increased hatchery production and trucking of hatchery fish downstream has a suite of biological and ecological ramifications including further loss of life-history diversity, degradation of the portfolio effect, and earlier maturation schedules (Hankin et al. 2009; Vainikka et al. 2010; California HSRG (California Hatchery Scientific Review Group) 2012; Huber and Carlson 2015; Satterthwaite and Carlson 2015; Sturrock et al. 2019). In addition, there is evidence that hatchery practices that accelerate growth or release fish at a large juvenile size can lead to earlier maturation (Vøllestad et al. 2004; Ohlberger et al. 2018). This can result in a tradeoff between juvenile survival and degraded age structure diversity. As the SRFC population is already dominated by hatchery-produced fish, hatchery practices should focus on restoring life-history diversity and age structure (instead of simply increasing production) to enhance population resilience to climate change and combat recent trends of increasing variability and decreasing population size (Lindley et al. 2009; Munsch et al. 2022).

Decreases in maturation age suggest that the alleles underlying delayed maturation are likely being lost from populations, as shown for Atlantic salmon (*Salmo salar*) which have also undergone rapid evolution of earlier maturation age (Czorlich et al. 2018, 2022). The heritability of age at maturation (Hankin et al. 1993; McKinney et al. 2020) suggests that broodstock selection programs could implement nonrandom mating practices to mimic natural mating patterns that would prevent further loss of, or even restore, age structure diversity. In addition, this approach to preserving or restoring age structure diversity for SRFC is much more feasible than reducing natural mortality rates of adult fish (e.g., culling predators or boosting populations of predators' alternate prey). Managing hatchery practices to promote a diversity of juvenile and adult life histories will be an increasingly important management strategy as SRFC face more extreme climates. Finally, reducing fishing mortality, especially during droughts, will likely be needed to allow sufficient escapement to maintain sustainable populations and the ecosystem services they provide.

We show that intraspecific variation (here in the form of age structure) can stabilize populations, maintain consistent harvest, and in some cases increase population size and productivity. In addition, age structure contributed to the portfolio effect and was able to buffer against the unfavorable effects of drought on population size and harvest. Thus, the loss of intraspecific variation has important implications for the ecological, economic, and cultural value of natural resources. Age structure preservation and restoration will likely be increasingly important for long term sustainability of natural resources in a rapidly changing climate.

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Competing interests

The authors declare that 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-2022-0171.

References

Andersen, K.H., Farnsworth, K.D., Thygesen, U.H., and Beyer, J.E. 2007. The evolutionary pressure from fishing on size at maturation of Baltic cod. Ecol. Model. **204**(1–2): 246–252. doi:10.1016/j.ecolmodel.2007.01.002.

Anderson, S.C., Cooper, A.B., and Dulvy, N.K. 2013. Ecological prophets: quantifying metapopulation portfolio effects. Methods Ecol. Evol. **4**(10): 971–981. doi:10.1111/2041-210X.12093.

Arlinghaus, R. 2006. On the apparently striking disconnect between motivation and satisfaction in recreational fishing: the case of catch orientation of German anglers. N. Am. J. Fish. Manag. **26**(3): 592–605. Taylor & Francis. doi:10.1577/M04-220.1.

Barnett, L.A.K., Branch, T.A., Ranasinghe, R.A., and Essington, T.E. 2017. Old-growth fishes become scarce under fishing. Curr. Biol. **27**(18): 2843–2848. e2. doi:10.1016/j.cub.2017.07.069.

Bay, R.A., Rose, N.H., Logan, C.A., and Palumbi, S.R. 2017. Genomic models predict successful coral adaptation if future ocean warming rates are reduced. Sci. Adv. **3**(11): e1701413. doi:10.1126/sciadv.1701413.

Beverton, R.J.H., and Holt, S.J. 1957. *On the Dynamics of Exploited Fish Populations*. Chapman and Hall, London, UK.

von Biela, V.R., Sergeant, C.J., Carey, M.P., Liller, Z., Russell, C., Quinn-Davidson, S., et al. 2022. Premature mortality observations among Alaska's Pacific Salmon during record heat and drought in 2019. Fisheries **47**(4): 157–168. doi:10.1002/fsh.10705.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., et al. 2011. Why intraspecific trait variation matters in community ecology. Trends Ecol. Evol. **26**(4): 183–192. doi:10.1016/j.tree.2011.01.009.

Buoro, M., and Carlson, S.M. 2014. Life-history syndromes: integrating dispersal through space and time. Ecol. Lett. **17**(6): 756–767. doi:10.1111/ele.12275.

California HSRG (California Hatchery Scientific Review Group). 2012. *California Hatchery Review Report*. Prepared for the U.S. Fish and Wildlife Service and Pacific States Marine Fisheries Commission.

Carlson, S.M., Quinn, T.P., and Hendry, A.P. 2011. Eco-evolutionary dynamics in Pacific salmon. Heredity **106**(3): 438–447. doi:10.1038/hdy.2010.163.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. **68**(9): 1579–1589. doi:10.1139/f2011-084.

CDWR (California Department of Water Resources). 2021, October 4. *Feather River Fish Hatchery Seeks to Increase Production, Offset Drought Impacts to Feather River Chinook Salmon Populations*. California Department of Water Resources: 715 P St, Sacramento, CA 95814. Available from https://water.ca.gov/News/News-Releases/2021/Oct-21/Feather-River-Fish-Hatchery-Seeks-to-Increase-Production.

Chasco, B., Kaplan, I.C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M.J., et al. 2017. Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. Can. J. Fish. Aquat. Sci. **74**(8): 1173–1194. doi:10.1139/cjfas-2016-0203.

Chou, C., Chiang, J.C.H., Lan, C.-W., Chung, C.-H., Liao, Y.-C., and Lee, C.-J. 2013. Increase in the range between wet and dry season precipitation. Nat. Geosci. **6**(4): 263–267. doi:10.1038/ngeo1744.

Clark, G.H. 1929. *Fish Bulletin No. 17. Sacramento-San Joaquin Salmon (Oncorhynchus tshawytscha) Fishery of California*. Division of Fish and Game of California: UC San Diego: Library - Scripps Digital Collection.

Colombano, D.D., Carlson, S.M., Hobbs, J.A., and Ruhi, A. 2022. Four decades of climatic fluctuations and fish recruitment stability across a marine-freshwater gradient. Glob. Change Biol. **28**(17): 5104–5120. doi:10.1111/gcb.16266.

Connors, B.M., Siegle, M.R., Harding, J., Rossi, S., Staton, B.A., Jones, M.L., et al. 2022. Chinook salmon diversity contributes to fishery stability and trade-offs with mixed-stock harvest. Ecol. Appl. **32**(8): e2709. doi:10.1002/eap.2709.

Cordoleani, F., Phillis, C.C., Sturrock, A.M., FitzGerald, A.M., Malkassian, A., Whitman, G.E., et al. 2021. Threatened salmon rely on a rare life history strategy in a warming landscape. Nat. Clim. Change **11**(11): 982–988. doi:10.1038/s41558-021-01186-4.

Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., and Primmer, C.R. 2018. Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. Nat. Ecol. Evol. **2**(11): 1800–1807. doi:10.1038/s41559-018-0681-5.

Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., and Primmer, C.R. 2022. Rapid evolution in salmon life history induced by direct and indirect effects of fishing. Science **376**(6591): 420–423. doi:10.1126/science.abg5980.

Dai, A. 2013. Increasing drought under global warming in observations and models. Nat. Clim. Change **3**(1): 52–58. doi:10.1038/nclimate1633.

Des Roches, S., Pendleton, L.H., Shapiro, B., and Palkovacs, E.P. 2021. Conserving intraspecific variation for nature's contributions to people. Nat. Ecol. Evol. **5**(5): 574–582. doi:10.1038/s41559-021-01403-5.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., et al. 2018. The ecological importance of intraspecific variation. Nat. Ecol. Evol. **2**(1): 57–64. doi:10.1038/s41559-017-0402-5.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., et al. 2008. North Pacific Gyre oscillation links ocean climate and ecosystem change. Geophys. Res. Lett. **35**(8): L08607. doi:10.1029/2007GL032838.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., and Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. Am. Nat. **151**(3): 264–276. doi:10.1086/286117.

Ford, J., and Ellis, G. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Mar. Ecol. Prog. Ser. **316**: 185–199. doi:10.3354/meps316185.

Friedman, W.R., Martin, B.T., Wells, B.K., Warzybok, P., Michel, C.J., Danner, E.M., and Lindley, S.T. 2019. Modeling composite effects of marine and freshwater processes on migratory species. Ecosphere **10**(7): e02743. doi:10.1002/ecs2.2743.

Greene, C.M., Hall, J.E., Guilbault, K.R., and Quinn, T.P. 2010. Improved viability of populations with diverse life-history portfolios. Biol. Lett. **6**(3): 382–386. Royal Society. doi:10.1098/rsbl.2009.0780.

Griffin, D., and Anchukaitis, K.J. 2014. How unusual is the 2012–2014 California drought? Geophys. Res. Lett. **41**(24): 9017–9023. doi:10.1002/2014GL062433.

Hankin, D.G., Fitzgibbons, J., and Chen, Y. 2009. Unnatural random mating policies select for younger age at maturity in hatchery Chinook salmon (*Oncorhynchus tshawytscha*) populations. Can. J. Fish. Aquat. Sci. **66**(9): 1505–1521. doi:10.1139/F09-085.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**(2): 347–358. doi:10.1139/f93-040.

Healey, M.C., and Heard, W.R. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Can. J. Fish. Aquat. Sci. **41**(3): 476–483. doi:10.1139/f84-057.

Heino, M., Díaz Pauli, B., and Dieckmann, U. 2015. Fisheries-induced evolution. Annu. Rev. Ecol. Evol. Syst. **46**(1): 461–480. doi:10.1146/annurev-ecolsys-112414-054339.

Hocking, M.D., and Reynolds, J.D. 2011. Impacts of salmon on riparian plant diversity. Science **331**(6024): 1609–1612. doi:10.1126/science.1201079.

Huber, E.R., and Carlson, S.M. 2015. Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley. San Franc. Estuary Watershed Sci. **13**(2).

Jacox, M.G., Edwards, C.A., Hazen, E.L., and Bograd, S.J. 2018. Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the U.S. West Coast. J. Geophys. Res. Oceans **123**(10): 7332–7350. doi:10.1029/2018JC014187.

Kaufman, R.C., Houck, A.G., Workman, M., and Cech, J.J. 2009. Chinook salmon length/fecundity: a regression model for the Mokelumne River, California. Calif. Fish Game **95**(2): 88–105.

Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution **55**(8): 1656–1667. doi:10.1111/j.0014-3820.2001.tb00685.x.

Letvin, A., Palmer-Zwahlen, M., Kormos, B., and McHugh, P. 2021. *Recovery of Coded-Wire Tags from Chinook Salmon in California's Central Valley Escapement, Inland Harvest, and Ocean Harvest in 2019*. Joint PSMFC-CDFW Report, Santa Rosa, CA.

Lew, D.K., and Larson, D.M. 2012. Economic values for saltwater sport fishing in Alaska: a stated preference analysis. N. Am. J. Fish. Manag. **32**(4): 745–759. doi:10.1080/02755947.2012.681012.

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T., et al. 2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Tech Memo. Available from https://repository.library.noaa.gov/view/noaa/3664/noaa_3664_DS1.pdf [accessed 13 April 2022].

Litzow, M.A., Ciannelli, L., Cunningham, C.J., Johnson, B., and Puerta, P. 2019. Nonstationary effects of ocean temperature on Pacific salmon productivity. Can. J. Fish. Aquat. Sci. **76**(11): 1923–1928. doi:10.1139/cjfas-2019-0120.

Litzow, M.A., Ciannelli, L., Puerta, P., Wettstein, J.J., Rykaczewski, R.R., and Opiekun, M. 2018. Non-stationary climate–salmon relationships in the Gulf of Alaska. Proc. R. Soc. B Biol. Sci. **285**(1890): 20181855. doi:10.1098/rspb.2018.1855.

Manishin, K.A., Cunningham, C.J., Westley, P.A.H., and Seitz, A.C. 2021. Can late stage marine mortality explain observed shifts in age structure of Chinook salmon? PLoS ONE **16**(2): e0247370. Public Library of Science. doi:10.1371/journal.pone.0247370.

Mantua, N.J. 2021. The Pacific Decadal Oscillation (PDO). Available from http://research.jisao.washington.edu/pdo [accessed 1 December 2021].

Markowitz, H. 1952. Portfolio selection. J. Finance **7**(1): 77–91.

McKinney, G.J., Seeb, J.E., Pascal, C.E., Schindler, D.E., Gilk-Baumer, S.E., and Seeb, L.W. 2020. Y-chromosome haplotypes are associated with variation in size and age at maturity in male Chinook salmon. Evol. Appl. **13**(10): 2791–2806. doi:10.1111/eva.13084.

Michel, C.J., Notch, J.J., Cordoleani, F., Ammann, A.J., and Danner, E.M. 2021. Nonlinear survival of imperiled fish informs managed flows in a highly modified river. Ecosphere **12**(5): e03498. doi:10.1002/ecs2.3498.

Mimura, M., Yahara, T., Faith, D.P., Vázquez-Domínguez, E., Colautti, R.I., Araki, H., et al. 2017. Understanding and monitoring the consequences of human impacts on intraspecific variation. Evol. Appl. **10**(2): 121–139. doi:10.1111/eva.12436.

Moore, J.W., McClure, M., Rogers, L.A., and Schindler, D.E. 2010. Synchronization and portfolio performance of threatened salmon. Conserv. Lett. **3**(5): 340–348. doi:10.1111/j.1755-263X.2010.00119.x.

Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. J. Anim. Ecol. **83**(5): 1035–1046. doi:10.1111/1365-2656.12212.

Morikawa, M.K., and Palumbi, S.R. 2019. Using naturally occurring climate resilient corals to construct bleaching-resistant nurseries. Proc. Natl. Acad. Sci. U. S. A. **116**(21): 10586–10591. doi:10.1073/pnas.1721415116.

Munsch, S.H., Greene, C.M., Mantua, N.J., and Satterthwaite, W.H. 2022. One hundred-seventy years of stressors erode salmon fishery climate resilience in California's warming landscape. Glob. Change Biol. **28**(7): 2183–2201. doi:10.1111/gcb.16029.

Notch, J.J., McHuron, A.S., Michel, C.J., Cordoleani, F., Johnson, M., Henderson, M.J., and Ammann, A.J. 2020. Outmigration survival of wild Chinook salmon smolts through the Sacramento River during historic drought and high water conditions. Environ. Biol. Fishes **103**(5): 561–576. doi:10.1007/s10641-020-00952-1.

O'Farrell, M.R., Mohr, M.S., Grover, A.M., and Satterthwaite, W.H. 2012. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. NOAA Tech Memo NMFS **NOAA-TM-NMFS-SWFSC-491**. Available from https://repository.library.noaa.gov/view/noaa/4474/noaa_4474_DS1.pdf?download-document-submit=Download [accessed 13 April 2022].

Ohlberger, J., Schindler, D.E., Brown, R.J., Harding, J.M.S., Adkison, M.D., Munro, A.R., et al. 2020. The reproductive value of large females: consequences of shifts in demographic structure for population reproductive potential in Chinook salmon. Can. J. Fish. Aquat. Sci. **77**(8): 1292–1301. NRC Research Press. doi:10.1139/cjfas-2020-0012.

Ohlberger, J., Schindler, D.E., Ward, E.J., Walsworth, T.E., and Essington, T.E. 2019. Resurgence of an apex marine predator and the decline in prey body size. Proc. Natl. Acad. Sci. U. S. A. **116**(52): 26 682–26 689. National Academy of Sciences. doi:10.1073/pnas.1910930116.

Ohlberger, J., Ward, E.J., Schindler, D.E., and Lewis, B. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. Fish Fish. **19**(3): 533–546. Wiley-Blackwell. doi:10.1111/faf.12272.

Oke, K.B., Cunningham, C.J., Westley, P.A.H., Baskett, M.L., Carlson, S.M., Clark, J., et al. 2020. Recent declines in salmon body size impact ecosystems and fisheries. Nat. Commun. **11**(1): 4155. doi:10.1038/s41467-020-17726-z.

Pacific Fisheries Management Council. 2019. *Salmon Rebuilding Plan for Sacramento River fall Chinook*. Pacific Fishery Management Council, Portland, Oregon. Available from https://www.pcouncil.org/documents/2019/07/sacramento-river-fall-chinook-salmon-rebuilding-plan-regulatory-identifier-number-0648-bi04-july-2019.pdf/.

Pacific Fisheries Management Council. 2021*a*.*Preseason* Report I: Stock Abundance Analysis and Environmental Assessment Part 1 for 2021 Ocean Salmon Fishery Regulations. Pacific Fishery Management Council, Portland, Oregon. pp. 97 220–91 384.

Pacific Fisheries Management Council. 2021*b*. *Pacific Coast Salmon Fishery Management Plan for Commercial and Recreational Salmon Fisheries Off the Coasts of Washington, Oregon, and California as Revised Through Amendment 21*. PFMC, Portland, OR. Available from https://www.pcouncil.org/documents/2016/03/salmon-fmp-through-amendment-20.pdf/.

Palmer-Zwahlen, M.L., Grover, A.M., and Duran, J.A. 2006. *Feather River Chinook Cohort Reconstruction Brood Years 1998 and 1999 Fall and Spring Runs*. California Department of Fish and Game, Marine Region, Ocean Salmon Project: Santa Rosa, California.

Pauls, S.U., Nowak, C., Bálint, M., and Pfenninger, M. 2013. The impact of global climate change on genetic diversity within populations and species. Mol. Ecol. **22**(4): 925–946. doi:10.1111/mec.12152.

Prager, M.H., and Mohr, M.S. 2001. The harvest rate model for Klamath River fall Chinook salmon, with management applications and comments on model development and documentation. N. Am. J. Fish. Manag. **21**(3): 533–547. doi:10.1577/1548-8675(2001)021⟨0533:THRMFK⟩2.0.CO;2.

Price, M.H.H., Moore, J.W., Connors, B.M., Wilson, K.L., and Reynolds, J.D. 2021. Portfolio simplification arising from a century of change in salmon population diversity and artificial production. J. Appl. Ecol. **58**(7): 1477–1486. doi:10.1111/1365-2664.13835.

Reznick, D., and Endler, J.A. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution **36**(1): 160–177.

Satterthwaite, W.H., and Carlson, S.M. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. Can. J. Fish. Aquat. Sci. **72**(12): 1860–1875. doi:10.1139/cjfas-2015-0169.

Satterthwaite, W.H., Carlson, S.M., and Criss, A. 2017. Ocean size and corresponding life history diversity among the four run timings of California Central Valley Chinook salmon. Trans. Am. Fish. Soc. **146**(4): 594–610. Taylor & Francis. doi:10.1080/00028487.2017.1293562.

Satterthwaite, W.H., and Shelton, A.O. 2022. Methods for assessing and responding to bias and uncertainty in U.S. West Coast salmon abundance forecasts. Fish. Res. **257**: 106502. doi:10.1016/j.fishres.2022.106502.

Schindler, D.E., Armstrong, J.B., and Reed, T.E. 2015. The portfolio concept in ecology and evolution. Front. Ecol. Environ. **13**(5): 257–263. doi:10.1890/140275.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**(7298): 609–612. doi:10.1038/nature09060.

Seitz, A.C., Courtney, M.B., Evans, M.D., and Manishin, K. 2019. Pop-up satellite archival tags reveal evidence of intense predation on large immature Chinook salmon *Oncorhynchus tshawytscha* in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. **76**(9): 1608–1615. doi:10.1139/cjfas-2018-0490.

Staton, B.A., Catalano, M.J., Fleischman, S.J., and Ohlberger, J. 2021. Incorporating demographic information into spawner–recruit analyses alters biological reference point estimates for a western Alaska salmon population. Can. J. Fish. Aquat. Sci. **78**(12): 1755–1769. NRC Research Press. doi:10.1139/cjfas-2020-0478.

Stearns, S.C. 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften **87**(11): 476–486. doi:10.1007/s001140050763.

Stier, A.C., Shelton, A.O., Samhouri, J.F., Feist, B.E., and Levin, P.S. 2020. Fishing, environment, and the erosion of a population portfolio. Ecosphere **11**(11). doi:10.1002/ecs2.3283.

Sturrock, A.M., Satterthwaite, W.H., Cervantes-Yoshida, K.M., Huber, E.R., Sturrock, H.J.W., Nusslé, S., and Carlson, S.M. 2019. Eight decades of hatchery salmon releases in the California Central Valley: factors influencing straying and resilience. Fisheries **44**(9): 433–444. doi:10.1002/fsh.10267.

Swain, D.L., Horton, D.E., Singh, D., and Diffenbaugh, N.S. 2016. Trends in atmospheric patterns conducive to seasonal precipitation and temperature extremes in California. Sci. Adv. **2**(4): e1501344. doi:10.1126/sciadv.1501344.

Thorson, J.T., Scheuerell, M.D., Buhle, E.R., and Copeland, T. 2014. Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon. J. Anim. Ecol. **83**(1): 157–167. doi:10.1111/1365-2656.12117.

Tilman, D., and Downing, J.A. 1994. Biodiversity and stability in grasslands. Nature **367**: 363–365. doi:10.1038/367363a0.

Trenberth, K.E., Dai, A., van der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R., and Sheffield, J. 2014. Global warming and changes in drought. Nat. Clim. Change **4**(1): 17–22. doi:10.1038/nclimate2067.

Vainikka, A., Kallio-Nyberg, I., Heino, M., and Koljonen, M.-L. 2010. Divergent trends in life-history traits between Atlantic salmon *Salmo* *salar* of wild and hatchery origin in the Baltic Sea. J. Fish Biol. **76**(3): 622–640. doi:10.1111/j.1095-8649.2009.02520.x.

Vøllestad, L.A., Peterson, J., and Quinn, T.P. 2004. Effects of freshwater and marine growth rates on early maturity in male Coho and Chinook salmon. Trans. Am. Fish. Soc. **133**(3): 495–503. doi:10.1577/T03-033.1.

Williams, A.P., Cook, E.R., Smerdon, J.E., Cook, B.I., Abatzoglou, J.T., Bolles, K., et al. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science **368**(6488): 314–318. doi:10.1126/science.aaz9600.

Winship, A.J., O'Farrell, M.R., and Mohr, M.S. 2013. Management strategy evaluation applied to the conservation of an endangered population subject to incidental take. Biol. Conserv. **158**: 155–166. doi:10.1016/j.biocon.2012.08.031.

Winship, A.J., O'Farrell, M.R., and Mohr, M.S. 2014. Fishery and hatchery effects on an endangered salmon population with low productivity. Trans. Am. Fish. Soc. **143**(4): 957–971. doi:10.1080/00028487.2014.892532.

Winship, A.J., O'Farrell, M.R., Satterthwaite, W.H., Wells, B.K., and Mohr, M.S. 2015. Expected future performance of salmon abundance forecast models with varying complexity. Can. J. Fish. Aquat. Sci. **72**(4): 557–569. doi:10.1139/cjfas-2014-0247.

Yamane, L., Botsford, L.W., and Kilduff, D.P. 2018. Tracking restoration of population diversity via the portfolio effect. J. Appl. Ecol. **55**(2): 472–481. doi:10.1111/1365-2664.12978.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.