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Journal

The American naturalist, 192(2)

ISSN

0003-0147

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Publication Date

2018-08-01

DOI

10.1086/697581

Peer reviewed

E-ARTICLE

Integrating Genetic and Demographic Effects of Connectivity on Population Stability: The Case of Hatchery Trucking in Salmon

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Submitted September 12, 2017; Accepted January 25, 2018; Electronically published May 14, 2018

Online enhancements: appendixes, code files.

ABSTRACT: Connectivity among populations can have counteracting effects on population stability. Demographically, connectivity can rescue local populations but increase the synchrony across populations. Genetically, connectivity can counteract drift locally but homogenize genotypes across populations. Population independence and diversity underlies system-level buffering against environmental variability, termed the portfolio effect. The portfolio effect has declined in California fall-run Chinook salmon, possibly in part because of the trucking of juvenile hatchery-reared fish for downstream release, which reduces juvenile mortality but increases the connectivity between rivers. We use a dynamical population model to test whether this increased connectivity can explain the loss of the portfolio effect and quantify the relative demographic and genetic contributions to portfolio effect erosion. In the model, populations experience different within-population environmental conditions and the same time-variable ocean conditions, the response to which can depend on a quantitative genetic trait. We find that increased trucking for one population's hatchery can lead to a loss of the portfolio effect, with a system-level trade-off between increased average abundance and increased variability in abundance. This trade-off is much stronger when we include the effects of genetic homogenization than when we consider demographic synchronization alone. Therefore, genetic homogenization can outweigh demographic synchrony in determining the system-level effect of connectivity.

Keywords: *Oncorhynchus tshawytscha*, salmon hatcheries, Central Valley fall-run Chinook, portfolio effect, synchrony, quantitative genetic model.

Introduction

Connectivity can have counteracting effects on the stability of ecological systems—which affects the sustainable de-

livery of ecosystem services—through both genetic and demographic mechanisms. Demographically, by facilitating exchange, connectivity can revive small or declining local populations, which increases their stability and likelihood of persistence (e.g., Abbott 2011). However, increased exchange among spatially separated populations can synchronize their dynamics and result in similar fluctuations in population abundance over time (reviewed in Bjørnstad et al. 1999; Liebhold et al. 2004; Abbott 2011). Genetically, if small or declining populations experience loss of genetic diversity through drift or lack local diversity to respond to changing selection, then connectivity can supply local diversity in a genetic rescue effect (reviewed in Lenormand 2002). However, increased connectivity typically impedes local adaptation and homogenizes allele frequencies across populations (Lenormand 2002; Kawecki and Ebert 2004). This reduced diversity at the metapopulation level can decrease ecosystem stability and function across time and under changing conditions (e.g., Hughes and Stachowicz 2004; Reusch et al. 2005; Crutsinger et al. 2006; Hughes et al. 2008). Therefore, the overall consequences of increased connectivity on stability depend on the balance between local-level enhancement and system-level synchrony and homogenization.

At the population complex level, one concept that encapsulates this stability as it depends on the diversity and synchrony across populations is the portfolio effect. Under the portfolio effect, differences among individual population responses to variable environmental conditions drive greater stability in the population complex than in its individual components (Hilborn et al. 2003; Schindler et al. 2010). Ecologists borrowed the concept of a portfolio effect from finance, where investors invest in multiple stocks to stabilize returns through time (Markowitz 1952). Harvested natural systems—such as Atlantic cod (Hutchinson 2008; Olsen et al. 2008), Atlantic herring (Ruzzante et al. 2006; Secor et al. 2009), and salmon (e.g., Moore et al. 2010)—provide evidence of diverse subpopulations contributing to a

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Am. Nat. 2018. Vol. 192, pp. E000–E000. © 2018 by The University of Chicago. 0003-0147/2018/19202-57957\$15.00. All rights reserved.
DOI: 10.1086/697581

portfolio effect in ecological systems and their associated ecosystem services. A clearer understanding of what underlies such portfolio effects, such as the relative contribution of demographic independence and genetic diversity to system-wide stability, is therefore important to the sustainable management of systems exhibiting this effect as well as a basic understanding of their dynamics.

A key consideration of sustainably managing the portfolio effect in natural systems is anthropogenic impacts on connectivity. A common focus of conservation is anthropogenically driven reduced connectivity, such as habitat fragmentation (e.g., Fahrig and Merriam 1994; Opdam and Wascher 2004), but increased connectivity can occur (e.g., Crispo et al. 2011; Hudson et al. 2016) and pose conservation challenges as well. For example, the spread of invasive species can reduce beta diversity by making the species composition more similar across communities (Sax and Gaines 2003; Weiher et al. 2011). Here we raise an analogous consideration at the population complex level: that increased connectivity might degrade the portfolio effect and therefore decrease system-level stability through demographic synchrony and genetic homogenization.

Salmon provide a useful case study for examining the effect of anthropogenic changes to connectivity on the portfolio effect. Salmon populations exhibit a high degree of homing in a heterogeneous freshwater environment, which results in multiple demographically distinct and locally adapted runs (e.g., Taylor 1991; Fraser et al. 2011; Peterson et al. 2014). Independence and diversity among runs allow salmon to show a portfolio response to variable ocean conditions that affect their survival (Kilduff et al. 2015), growth (Wells et al. 2006), and productivity (Mantua et al. 1997; Hare et al. 1999). The Bristol Bay sockeye salmon fishery in Alaska provides a classic example of portfolio dynamics, where the stock that is dominant has shifted over the past century and the overall catch has remained more stable than the individual runs (Hilborn et al. 2003; Schindler et al. 2010), in part because of independence and diversity in migration timing among runs (Schindler et al. 2010).

In contrast to the Bristol Bay sockeye, the Central Valley fall-run Chinook (CVFC) in California show evidence of a weakened portfolio (increased covariation among streams through time; Carlson and Satterthwaite 2011), including a system-wide collapse and fishery closure in 2008–2009 (Lindley et al. 2009). While the proximate cause of the CVFC collapse was a mismatch between juvenile outmigration timing and the onset of ocean productivity, the ultimate cause is likely a variety of homogenizing and synchronizing forces (Lindley et al. 2009). Habitat destruction can exclude fish from their preferred spawning sites and mix runs on the remaining accessible spawning grounds (Garza et al. 2008). Hatcheries, intended to supplement salmon populations with captive-reared juveniles to alleviate historical declines

(Yoshiyama et al. 1998), can directly homogenize populations through practices such as mixing broodstocks or releasing fish into nonnatal watersheds. A key possible contributor to homogenization and synchrony in CVFC, though, is the practice of trucking the hatchery fish downstream to increase survival through outmigration, with the intention of boosting population size and fishery returns (Huber and Carlson 2015). Because trucked fish are unable to learn the scents of their stream during outmigration to guide their return as adults (Dittman and Quinn 1996), trucking increases straying—that is, adult fish returning to a nonnatal stream to breed—and therefore connectivity among runs both in the Central Valley (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013; Huber and Carlson 2015) and in other watersheds (e.g., the Columbia River basin; Bond et al. 2017). If trucking is a primary driver of the weakened portfolio in CVFC, then management actions and expectations for recovery of the portfolio effect will depend on the underlying causes. If the primary mechanism is demographic synchrony, where straying hatchery-reared fish dominate returning populations, and system-wide dynamics therefore depend on hatchery fish performance, then simply halting trucking might lead to rapid recovery of the CVFC portfolio. Alternatively, if the primary mechanism is genetic homogenization, where straying hatchery-reared fish have eroded local adaptation and therefore system-wide diversity, then recovery will likely take longer and might require actions to restore diversity.

Here, motivated by the CVFC example, we explore whether anthropogenic increases in connectivity can reduce stability by shifting the balance between local-scale population rescue and system-wide homogenization and synchronization. Specifically, we ask whether increased connectivity through trucking can degrade the portfolio effect and underlie a trade-off between mean population size and population stability. In addition, we compare the consequences of demographic effects of trucking, where high numbers of surviving and straying hatchery fish could synchronize runs, with genetic effects, where straying hatchery fish can homogenize the genetic diversity and environmental response across streams. We address these questions with a quantitative genetic model, analyzed across a range of trucking distances, that jointly follows trait diversity and demographics in multiple subpopulations, given environmental variation in space and time.

Methods

Motivating Study System

The California Central Valley is a highly modified system where harvest, habitat degradation and destruction, and hatcheries have heavily affected the salmon runs (Yoshiyama et al. 1998; Lindley et al. 2009). Historically, the Cen-

tral Valley Chinook (*Oncorhynchus tshawytscha*) complex contained considerable life-history diversity, with four runs (winter, spring, fall, and late fall) that supported spawning adults in the Sacramento River in the northern Central Valley almost year-round (Yoshiyama et al. 1998) and supported fisheries for centuries, especially since the mid-1800s (Yoshiyama et al. 1998). The fall-run Chinook currently dominates the ocean fishery (California HSRG 2012); it has been less affected by the construction of dams than the other runs because it spawns closer to the ocean (Yoshiyama et al. 1998). In the early 2000s, however, the population collapsed, prompting a fishery closure in 2008 and 2009. Delayed upwelling and ocean productivity in 2005 and 2006 were the proximate causes of the collapse (Barth et al. 2007), but a loss of life history and genetic diversity likely made the system more vulnerable to poor ocean conditions (Lindley et al. 2009).

Currently, five hatcheries that were built to maintain production after dams and water diversions eliminated and degraded habitat (Reynolds et al. 1993), release about 32 million CVFC juveniles a year into creeks and estuaries (Kormos et al. 2012; Huber and Carlson 2015). Hatchery fish have been the bulk of the harvested fish in recent years (Barnett-Johnson et al. 2007; Kormos et al. 2012) and so are important to maintaining the fishery. Hatchery fish also dominate returns to hatcheries and even some creeks without hatcheries (e.g., 79%–96% of returns to CVFC hatcheries in 2012 were hatchery origin; Palmer-Zwahlen and Kormos 2015). Fish were originally released upstream near the hatcheries, but since the 1980s, downstream release or direct release into an estuary later in the spring at larger sizes has become increasingly common (Huber and Carlson 2015). CVFC hatchery fish have high levels of straying (Palmer-Zwahlen and Kormos 2013, 2015) that could have contributed to the genetic homogeneity of the CVFC population complex (Garza et al. 2008), which is unusually homogeneous for its geographic size compared with other Chinook populations: on the basis of microsatellite data, the average Cavalli-Sforza and Edwards chord distance measure of genetic distance was 0.017 between CVFC populations as compared with 0.071 for ocean-type Chinook salmon populations in British Columbia, and CVFC had low average F_{ST} values (0.0013–0.0031 on a scale of 0–1, where 0 is no population structure), with only three of the pairwise comparisons among 13 populations that had a consistently significant $F_{ST} > 0$ through time (Williamson and May 2005). Although there is a long history of hatcheries in this system, the long-term viability of hatcheries in maintaining populations has been questioned (e.g., for pink salmon in Alaska; Hilborn and Eggers 2000).

CVFC spawn in creeks in the fall and fry emerge from the eggs 2–3 months later, usually between December and March (Merz and Setka 2004). Juveniles rear in freshwater until the spring, when they migrate out to the ocean over several

months, coinciding with high flow in streams and the onset of productivity in the ocean following upwelling (Satterthwaite et al. 2014). They spend 2–3 years in the ocean before returning to freshwater to spawn (Fisher 1994; Lindley et al. 2009).

Model Overview

We construct a simple, stylized model to represent the dynamics essential to the role of trucking hatchery fish in the portfolio effect rather than a full representation of the Central Valley system. We model two creeks, one with a hatchery and one without. The model tracks the population size and trait distribution in each creek (fig. 1). In each time step of the model, adults reproduce with density dependence; juveniles outmigrate and experience phenotype-dependent mortality; fish in the ocean experience natural and fishing mortality; and adult fish return to spawn, with the potential for adults to stray to the nonnatal stream. The hatchery on one of the creeks removes a fraction of the spawners from that stream for reproduction and can truck hatchery-reared fish downstream during outmigration. The greater the distance trucked, the greater the survival through outmigration, the weaker the within-stream selection in the genetic model, and the greater the straying above baseline natural levels for hatchery-reared fish (fig. 2).

The trait that drives phenotype-dependent mortality either depends on location of origin (demographic-only model) or evolves as a quantitative genetic trait under local selection (coupled genetic-demographic model). Each population experiences two phenotype-dependent mortality events, each of which incur stabilizing selection in the coupled genetic-demographic model. In the first mortality event, the optimum varies in space (i.e., creek dependent) to account for the population independence and differentiation that underlies the portfolio effect. In the second mortality event, the optimum is the same for both creeks and varies in time (i.e., ocean condition dependent) to capture the role of population independence and local adaptation in buffering against environmental variability. In the coupled genetic-demographic model, for generality we represent the trait as a generic quantitative genetic trait, where we assume that a large number of loci and environmental conditions contribute additively to the overall phenotype.

One possible interpretation of the trait underlying phenotype-dependent mortality—which we use below to develop biological intuition and because of its suggested importance in CVFC portfolio dynamics (Satterthwaite et al. 2014)—is outmigration timing, when the fish leave their natal creek and swim out to the ocean. In this interpretation, the first phenotype-dependent mortality event represents optimal outmigration time as it depends on watershed characteristics, such as timing of high flows that ease

Figure 1: Adult spawning fish reproduce, with inheritance in the coupled genetic-demographic model (A), in two creeks, one with a hatchery and one without a hatchery. The offspring rear in fresh water and experience density dependence in the creeks (B). Depending on their phenotypes, which vary around genotypes in the coupled genetic-demographic model (C) or depend on location in the demographic-only model, individuals undergo both instream (D) and ocean (E) selection. The fish experience natural and fishing mortality while in the ocean and return to freshwater as mature adults to spawn. The middle column shows the dynamics occurring at each stage, and the right column shows sample trait distributions in the coupled genetic-demographic model for the two wild populations without a hatchery at the spawner stage (F) and the juvenile stage (G).

Figure 2: By reducing their exposure to the freshwater outmigration route, trucking affects hatchery fish in three ways: increasing their density- and phenotype-independent survival through outmigration (A), weakening the freshwater selection they experience (B), and increasing the rate at which they stray as returning spawners (C).

outmigration or dropping water levels near the dry season. The second phenotype-dependent mortality event then represents optimal ocean arrival date as it depends on inter-annual variation in upwelling onset and subsequent establishment of trophic levels (Bograd et al. 2009; Wells et al. 2012, 2016; Woodson et al. 2013; Satterthwaite et al. 2014), where fish arriving too early experience higher mortality because of lack of food (Barth et al. 2007) or high estuarine predation if they linger in the estuary to delay ocean arrival (Hearn et al. 2014; Michel et al. 2015), and fish arriving too late face higher ocean predation (Pearcy 1992). Phenological traits in salmon such as outmigration and ocean arrival timing are often heritable and highly genetically correlated (Carlson and Seamons 2008), and Pacific salmon display sub-population divergence in outmigration timing at both large (e.g., across latitudinal clines) and small (e.g., within a reach) spatial scales (Quinn 2005).

In reality, outmigration is likely one of many traits that underlie the portfolio effect in CVFC, and salmon outmigration timing—as with any migration or dispersal trait (Dingle and Drake 2007)—depends on multiple morphological, physiological, and life-history traits, environmental conditions, and their interaction (Quinn 2005). For example, three interrelated factors that all influence outmigration timing are size, temperature, and flow, where flow can influence temperature and temperature can influence size, and size affects multiple aspects of survivorship and reproduction beyond those dependent on outmigration timing (Quinn 2005; Kallio-Nyberg et al. 2011; Irvine et al. 2013; Sturrock et al. 2015). Given our focus on the qualitative

questions of whether increased connectivity alone can drive a loss of portfolio effects and, if so, what are the relative genetic and demographic contributions to that loss, we choose a phenomenological approach of modeling a generic trait in order to focus our model on the dynamics essential to how connectivity and local adaptation influence the portfolio effect in isolation of the many confounding factors that occur in reality (e.g., direct effects of hatchery rearing on growth and size in addition to the indirect effects through trucking-dependent straying; Reisenbichler and Rubin 1999; Kostow 2004; Kallio-Nyberg et al. 2011). In other words, we construct a general model focused on differentiating qualitative outcomes as compared with a realistic model focused on quantitatively precise predictions, such as predicting the full suite of hatchery and trucking effects on CVFC (i.e., a strategic as opposed to a tactical model sensu May 2001). Therefore, the applied utility of our model is in identifying which dynamics (e.g., trucking effects on connectivity and the genetics of local adaptation) might be necessary to include in a more mechanistic, tactical model that could quantitatively inform management decisions in CVFC.

To assess the potential for trucking to increase production but weaken the portfolio effect, we analyze total population abundance and variability, given many stochastic runs for a range of trucking distances. To explore the effects of genetic homogenization versus the effects of demographic synchronization from trucking, we compare the hypothesized abundance-variability trade-off for the coupled genetic-demographic model versus the demographic-only model.

Model Details

Coupled Genetic-Demographic Model. The genetic-demographic model (fig. 1) tracks the population density distribution $n_{i,t}(g)$ of genotypes g in each population i (C1 for the creek with the hatchery, C2 for the creek without a hatchery, and H for the hatchery) at generation t across life stages, denoted sequentially with superscripts (e.g., n'). The total population size at a given time is $N_{i,t} = \int n_{i,t}(g)dg$ and the genotype probability density is $\psi_{i,t}(g) = n_{i,t}(g)/N_{i,t}$.

For reproduction with inheritance, we use the infinitesimal model of quantitative genetics (Turelli and Barton 1994), which assumes that many unlinked loci contribute additively to the genotype. We assume random mating within each stream and within the hatchery to calculate the probability of each possible combination of parents and distribute the offspring genotypes around the midparental mean with the variance at linkage equilibrium (V_{LE} ; fig. 1A). We multiply the offspring genotype distribution by the number of returning adults and the production per adult ($\rho_i(N_{i,t})$) to obtain the juvenile population density of genotypes $n'_{i,t}(g)$:

$$n'_{i,t}(g) = N_{i,t}\rho_i(N_{i,t}) \iint \psi_{i,t}(g_1)\psi_{i,t}(g_2) \frac{1}{\sqrt{\pi V_{LE}}} e^{-\{[g-(g_1+g_2)/2]^2\}/V_{LE}} dg_1 dg_2. \quad (1)$$

We then incorporate Beverton-Holt density dependence, where R_i is fecundity in terms of smolts produced per spawner and K_i is the carrying capacity of each creek, applied to the two wild populations (fig. 1B):

$$\rho_i = \begin{cases} \frac{R_i}{1 + R_i N_{i,t}/K_i}, & i = \text{C1, C2} \\ R_i, & i = \text{H}. \end{cases} \quad (2)$$

We place density dependence in the juvenile stage, where habitat constraints can provide limited cover for juveniles (Johnson et al. 2005; Honea et al. 2009), although density dependence could occur throughout the life cycle.

Wild fish leave for the ocean as smolts in each creek and experience three mortality events: (1) density- and phenotype-independent mortality, (2) within-stream selection with an optimal value that varies across locations, and (3) ocean selection with an optimal value that varies across years. The survivorship and within-stream selection that hatchery fish experience depend on the proportion of the total outmigration distance that they are trucked τ (fig. 2A, 2B). If we interpret the genotype as the propensity to outmigrate at a particular time and the phenotype as the outmigration time, then the within-stream selection represents local selection on outmigration time, and the ocean selection represents selection on ocean arrival time, assuming that fish take a fixed amount of time to outmigrate to the ocean so the outmigration timing trait also determines the ocean arrival date.

In the first mortality event, fish experience density- and phenotype-independent mortality (with survivorship ν) from freshwater hazards such as predators. Wild fish have a survival of ν_{wild} , which is also the survival of untrucked hatchery fish. Trucked hatchery fish encounter fewer river hazards so experience higher phenotype-independent freshwater survival ν_H . Given a maximum phenotype-independent survival ν_{max} for fish trucked all the way to the ocean, phenotype-independent survival for hatchery fish increases linearly with trucking distance τ (fig. 2A): $\nu_H = \nu_{\text{wild}} + (\nu_{\text{max}} - \nu_{\text{wild}})\tau$.

The two selection events act on the phenotypes f of the fish, which are normally distributed around their genotypes g with environmental variance E to account for imperfect heritability (fig. 1C):

$$P(f|g) = \frac{1}{\sqrt{2\pi E}} e^{-(f-g)^2/2E}. \quad (3)$$

After applying selection as phenotype-dependent survival in the joint phenotype-genotype distribution $P(f|g)n'_{i,t}(g)$, we integrate over phenotypes to determine the resulting population density distribution over genotypes.

For the within-stream selection, fish experience stabilizing selection $\omega_i(f)$ with selectional variance S_i , which is the inverse of selection strength, on their phenotype f compared with the optimal value for their creek χ_i : $\omega_i(f) = e^{-(f-\chi_i)^2/2S_i}$ (fig. 1D). In reality, for outmigration time, the optimal time to leave the freshwater environment is likely to vary across years, but we consider it to be constant through time for each creek for simplicity. Hatchery fish experience weaker freshwater selection the farther they are trucked, with $S_H = S_{C1}e^{\tau/\theta}$, where S_{C1} is the freshwater selection variance in the creek with the hatchery and θ is a tuning parameter (fig. 2B).

For the ocean selection, fish experience stabilizing selection $\omega_o(f)$ with selectional variance S_o on their phenotype compared with the optimal value for that year ϵ_t : $\omega_o(f) = e^{-(f-\epsilon_t)^2/2S_o}$ (fig. 1E). We assume that the distance hatchery fish are trucked does not change the ocean selection they experience, as might occur if the outmigration phenotype (and therefore ocean arrival date) instead depends on developmental progress.

We randomly draw optimal ocean values from a normal distribution with mean μ_o and variance V_o ($\epsilon_t \sim N(\mu_o, \sqrt{V_o})$), as might represent variability in the timing of upwelling within a particular regime of the Pacific Decadal Oscillation. When a regime shift happens, even a population with a full portfolio would likely experience a few years of low population size, such as the Bristol Bay stocks in the mid-1970s (e.g., Hilborn et al. 2003); therefore, here we consider the portfolio effect within a regime (as measured in Carlson and Satterthwaite 2011) rather than looking at how it responds to an oceanic regime shift.

Given these three mortality events, after outmigration the new population density distribution becomes

$$n''_{i,t}(g) = \int \nu_i \omega_i(f) \omega_t(f) P(f|g) n'_{i,t}(g) df. \quad (4)$$

Once in the ocean, fish undergo density- and phenotype-independent natural mortality at a rate M and fishing mortality at a rate F . When the fish return to the creeks to spawn, some fish stray and return to the other creek instead of their natal creek. We use a linear function of the outmigration trucking distance to determine the proportion of hatchery fish that stray $r(\tau)$ (California HSRG 2012), ranging from a base value σ for wild fish and hatchery fish released at the hatchery site to 0.5 (i.e., randomly choosing a spawning stream) for hatchery fish trucked all the way to the ocean ($\tau = 1$; fig. 2C). When adults return to the creeks, the hatchery takes in a fraction h_t of the adults returning to the creek with the hatchery for broodstock, unless that exceeds the maximum hatchery capacity:

$$N_{H,t} = \begin{cases} h_t N_{C1,t} & \text{if } h_t N_{C1,t} < H_{\max} \\ H_{\max} & \text{otherwise.} \end{cases} \quad (5)$$

The resulting genotype probability distributions in each creek are

$$n_{C1,t+1}(g) = (1 - h_t) e^{-(M+F)} [n''_{C1,t}(g)(1 - \sigma) + n''_{C2,t}(g)\sigma + n''_{H,t}(g)(1 - r(\tau))], \quad (6)$$

$$n_{C2,t+1}(g) = e^{-(M+F)} [n''_{C1,t}(g)\sigma + n''_{C2,t}(g)(1 - \sigma) + n''_{H,t}(g)r(\tau)], \quad (7)$$

and the hatchery distribution is

$$n_{H,t+1}(g) = h_t e^{-(M+F)} [n''_{C1,t}(g)(1 - \sigma) + n''_{C2,t}(g)\sigma + n''_{H,t}(g)(1 - r(\tau))]. \quad (8)$$

Demographic-Only Model. The demographic-only version of the model has no heredity and has location-dependent phenotypes, as might occur if the outmigration phenotypes depend entirely on the streamflow conditions in each creek. The number of spawning fish affects the level of juvenile production, but the phenotype distributions of the parents do not affect the phenotypes of the offspring. Instead, in each generation, the phenotypes of the juveniles in each creek and the hatchery have a static phenotype distribution with mean μ_{D_i} and variance X_{D_i} . Assuming a normal distribution of phenotypes, the juvenile population density of phenotypes for the demographic-only model is

$$n'_{i,t}(f) = N_{i,t} \rho_i(N_{i,t}) \int \frac{1}{\sqrt{\pi X_{D_i}}} e^{-(f - \mu_{D_i})^2 / X_{D_i}} df, \quad (9)$$

as compared with equation (1) for the genetic-demographic model.

After reproduction, the juveniles undergo density dependence in the same way as in the genetic-demographic model (i.e., $\rho_i(N_{i,t})$ in eq. [9] given by eq. [2]) and then outmigrate, during which they experience mortality in both freshwater and the ocean on the basis of their phenotype, as in the coupled genetic-demographic model. Here, the difference between the models is that the phenotype distribution that underlies these mortality events is constant in time in the demographic-only model and depends on only location of origin, while it can evolve depending on both selection and gene flow in the coupled genetic-demographic model. Given phenotype-independent outmigration survival ν_i , phenotype-dependent within-creek survival $\omega_i(f)$, and phenotype-dependent ocean survival $\omega_t(f)$ with environmental stochasticity as in the coupled genetic-demographic model, the population size after outmigration is

$$N''_{i,t} = \int \nu_i \omega_i(f) \omega_t(f) n'_{i,t}(f) df, \quad (10)$$

as compared with equation (4) in the genetic-demographic model (for the postintegration expression for population size dynamics, see app. A). As before, hatchery outmigration survival (ν_H and $\omega_H(f)$) increases with increased trucking distance. After ocean natural and fishing mortality, the population sizes returning to each creek to spawn are

$$N_{C1,t+1} = (1 - h_t) e^{-(M+F)} [N''_{C1,t}(1 - \sigma) + N''_{C2,t}\sigma + N''_{H,t}(1 - r(\tau))], \quad (11)$$

$$N_{C2,t+1} = e^{-(M+F)} [N''_{C1,t}\sigma + N''_{C2,t}(1 - \sigma) + N''_{H,t}r(\tau)], \quad (12)$$

and the number of fish taken in by the hatchery to spawn is

$$N_{H,t+1} = h_t e^{-(M+F)} [N''_{C1,t}(1 - \sigma) + N''_{C2,t}\sigma + N''_{H,t}(1 - r(\tau))]. \quad (13)$$

as compared with equations (6)–(8).

Model Analysis

Numerical Implementation. Given the complexity of our model, including stochastic environmental conditions (optimal ocean phenotype), we analyze the model numerically. For computational efficiency, we assume that the genotype distributions are normal and follow only the means ($\mu_{g_{i,t}} = \int g \psi_{i,t}(g) dg$), variances ($G_{i,t} = \int (g - \mu_{g_{i,t}})^2 \psi_{i,t}(g) dg$), and total population sizes ($N_{i,t}$) in each creek rather than tracking the full genotype distributions (derivation in app. A; eqq. A1–A16). In appendix A, we verify that assuming normality does not alter the results presented here (fig. A1).

Because many of the parameter values are difficult to estimate empirically and highly uncertain, we base parameter values on those that produce the relevant dynamics to our central questions and are within a possible range for CVFC (table 1, including the range of outmigration values reported by Merz et al. 2013). Specifically, we choose values that lead to persistent, locally adapted, and demographically independent populations in simulations without a hatchery, which allows us to explore the effect of having a hatchery with trucking on the portfolio effect in such population complexes. We also test the sensitivity of our results to all parameter values (see “Results”; app. B; figs. B1–B3).

For each analysis, we run 100 simulations with different sequences of ocean conditions for 1,000 generations (sample partial time series in fig. 3). The first 10 time steps in each simulation have optimal ocean arrival times that are the mean of the ocean arrival time distribution (μ_o) to prevent an extreme ocean event before the distributions have time to settle from the initial conditions. We use the first half

of the simulation as a burn-in period and measure the outputs over the second half. We initialize each creek mean genotype at the average value between the optimum for that creek and the average ocean optimum ($\mu_{C1,0} = 45$, $\mu_{C2,0} = 55$), initialize the genotypic variances at $2V_{LE}$ ($G_{i,0} = 10$), and initialize the population size at $N_{i,0} = 50,000$ returning adults, which is the approximate average return population size of fall-run Chinook to the larger tributaries in the Central Valley system (Azat 2016). Code for all analyses was written and run using MATLAB (MATLAB 2016).

We consider two methods of trucking: (1) truck all of the hatchery fish and vary the distance trucked and (2) vary the proportion of hatchery fish trucked and truck the full outmigration distance (app. D; eqq. [D1]–[D9]). In reality, the trucking strategy is a combination, with both distance and proportion of fish changing over time. Both methods give the same results; we present the results of varying the trucking distance here and those of varying the proportion trucked in appendix D (figs. D1, D2).

Table 1: Table of parameter values

Symbol	Parameter	Units	Base value
μ_o	Mean optimal ocean phenotype (e.g., arrival date)	Julian day	50 ^a
V_o	Variance in optimal ocean phenotype ^b	day ²	15
χ_{C1}	Optimal phenotype (e.g., outmigration date) for the creek with the hatchery	Julian day	40
χ_{C2}	Optimal phenotype for the creek without a hatchery	Julian day	60
V_{LE}	Genetic variance at linkage equilibrium	day ²	5
θ	Tuning parameter for calibrating freshwater selection by distance traveled		.5
S_i	Freshwater selection variance (inversely related to selection strength)	day ²	20
S_o	Ocean selection variance (inversely related to selection strength)	day ²	20
E	Environmental variance	day ²	10
R_i	Fecundity	smolts per spawner	200
K_i	Freshwater juvenile carrying capacity	smolts	500,000
v_{max}	Maximum phenotype-independent freshwater outmigration survival ^c		1
v_{wild}	Phenotype-independent freshwater outmigration survival for wild and untrucked fish		.7
h_i	Fraction of adults taken for hatchery broodstock from creek with hatchery		.25
H_{max}	Maximum hatchery capacity	spawners	1,000
τ	Proportion distance trucked		0–1
σ	Baseline proportion straying for wild fish		.05 ^d
r_{max}	Maximum straying proportion for hatchery fish trucked to the ocean		.5
M	Natural ocean mortality	time ⁻¹	.45 ^e
F	Ocean fishery harvest mortality	time ⁻¹	.7 ^f
$\mu_{D,i}$	Mean of static phenotype distributions for demographic-only model	Julian day	$\mu_{D,C1} = 46.5922$, $\mu_{D,C2} = 53.4078^g$
$X_{D,i}$	Variance of static phenotype distributions for demographic-only model	day ²	16.2401 ^g

^a Mean date of spring transition index at 39°N from 1967 to 2007 (Bograd et al. 2009).

^b Variance within an environmental regime.

^c For hatchery fish trucked the full outmigration distance.

^d Quinn 2005.

^e Corresponds to 2 years of 20% annual natural mortality (O’Farrell et al. 2012).

^f Corresponds to 1 year (O’Farrell et al. 2013) of approximately 50% ocean harvest mortality.

^g Equilibrium values from simulations of the coupled genetic-demographic model with no hatchery at constant ocean conditions (optimal ocean arrival time ϵ_i set to μ_o for all time steps).

Figure 3: Example time series of genetic means (e.g., outmigration time propensity) in each of the two wild populations (solid line, creek with hatchery; dotted line, creek without hatchery) from one simulation with no hatchery (A), a hatchery with no trucking (B), and a hatchery with trucking the full outmigration distance (C) in the coupled genetic-demographic model. The sequence for ocean conditions (i.e., optimal trait in the ocean; red line with stars) is the same for all three simulations. The ocean optimum for the first 10 time steps in each simulation is set to the mean ocean value to allow the distributions in the creeks to settle from the initial conditions.

Analyses. We investigate whether trucking can homogenize the trait distributions across the creeks by comparing the genetic mean and variance in each creek and for the population as a whole over the range of trucking distances. To measure the portfolio effect and determine whether there is a trade-off in the mean and variability of the return popu-

lation size as trucking increases, we compare the mean number of fish returning to spawn in both creeks and a measure of the variability in run sizes across the range of trucking distances. For population variability, we consider both the variance and the coefficient of variation (CV), which considers the variance in the context of the mean

as used in previous analyses of the portfolio effect in CVFC (e.g., Carlson and Satterthwaite 2011). If the portfolio effect is weakened, we would expect the variance and the CV of the return population size to increase as the returns in the two creeks become more synchronous and less able to compensate for one another as ocean conditions fluctuate. Finally, we compare the potential trade-off between mean population size and variability in the demographic-only model to that in the genetic-demographic model in order to investigate the effect of demographic synchrony on the portfolio effect compared with both genetic homogenization and demographic synchrony.

Results

In the coupled genetic-demographic model, higher trucking leads to genetic homogenization across the population (fig. 4A, 4B). Because trucking causes more hatchery fish to stray and they originate from the same trait distribution as the fish in the creek with the hatchery, the genetic mean of the creek without the hatchery approaches the mean ge-

notype in the creek with the hatchery as trucking increases (figs. 3C, 4A). The genetic variance within each creek declines with trucking (fig. 4B) as they become more similar because the strays they exchange are less different and so bring less diversity. The variance starts and stays higher in the creek without the hatchery because it receives more strays overall as a result of the straying hatchery fish, even when they stray at the wild rate. The largest loss of genetic variance occurs at the total population level (fig. 4B). As the two creeks' genetic compositions become more similar to each other, there is less overall genetic diversity in the population as a whole. The reduction of total genetic variance in the system with increased trucking occurs across a wide range of population parameters, although the exact trajectory of the decline can shift (app. B; figs. B4, B5).

Demographically, trucking creates a trade-off between the average population size and its variance. The mean total population size, censused at the returning spawner stage, increases with higher levels of trucking (fig. 4C) because trucked hatchery fish bypass freshwater selection and mortality. The variance of the total population size also in-

Figure 4: In the coupled genetic-demographic model, genetic mean (A), genetic variance (B), population size (C), and population variance (D) in the creek with the hatchery (black line), the creek without the hatchery (blue circles), and the total population (red X's) shown across trucking distances. We calculate each metric from the last 500 time steps of 1,000-year simulations and show the mean (solid lines) and standard deviations (dashed lines) of 100 simulations with different sequences of optimal ocean values.

creases with higher levels of trucking (fig. 4D). Although the variance of the return population size in each individual creek does not change substantially with trucking, the variance of the total return population size increases throughout. The shape and strength of the trade-off between population size and variance depend on the metric used to characterize the portfolio effect (fig. 5). The mean and variance of the total return increase throughout the range of trucking (fig. 5A), while the CV increases until midlevels of trucking and then declines (fig. 5B). The homogenization of the trait distributions—and therefore similar responses to variable ocean conditions—occurs faster in the first half of the range of trucking distances, contributing to a higher CV, but the population size increases throughout trucking, driving a CV decline at the larger trucking distances.

The loss of the portfolio effect due to trucking is primarily due to genetic homogenization because the genetic-demographic model shows a much larger response in mean and variance to trucking than the demographic-only model (fig. 5A). Note that the two models do not have the same population mean and variance when the trucking distance is zero because without trucking, the hatchery increases the number of fish in the creek with the hatchery and therefore the total number of fish that can stray to the other creek at

the natural rate, with different consequences in the two models (app. C; fig. C1).

In our sensitivity analyses, the qualitative trend of an increase in mean returns and an initial increase and then a decrease in CV with increasing trucking is consistent across most parameter values (figs. 6, B1). Exceptions to this qualitative trend occur primarily in two types of cases: when the population size is low or the portfolio is weak at the start. For parameter combinations that generate a low population size (e.g., high ocean mortality, strong selection in either freshwater or the ocean, or low juvenile carrying capacity) or a low ability to sustain a portfolio even without trucking (e.g., large difference between optimal freshwater traits, high wild straying rate, or high ocean variance relative to the base case), the CV declines monotonically as trucking increases. In these cases, the positive effect on mean population size of trucking outweighs the increase in variance, resulting in a declining CV. In two cases (low ocean selection and low wild straying rate), the mean population size initially drops with trucking before increasing at higher trucking values (fig. 6C, 6E). In appendix B (fig. B1), we show sensitivity to parameters that lead to the same qualitative trend as in figure 5 but differ quantitatively in the location and presence of the inflection point and the relative CV at the no-trucking

Figure 5: Mean and variance (A) and mean and coefficient of variation (CV; B) of total population size across both creeks at the spawner stage shown for 100 ocean sequences run for 1,000 time steps across the range of trucking values. Each point is the mean value over the second half of one simulation, with circles for runs with the genetic-demographic model and X's for runs with the demographic-only model. Color indicates the distance trucked, with the darkest color for no trucking and the lightest color indicating trucking the full outmigration distance.

Figure 6: Sensitivity of the trade-off between mean total population size and the coefficient of variation (CV) of total population size to the parameter values in cases where the qualitative shape of the trade-off changes. The mean trade-off between mean return population size and CV is calculated over the last 500 time steps in a 1,000-step run across 100 runs of different ocean sequences in the coupled genetic-demographic model. We show the sensitivity of the trade-off to the remaining parameter values, where the qualitative trend is consistent, in appendix B (fig. B1).

and full-trucking extremes. The qualitative trend of increasing variance of the return population size with trucking is insensitive to the parameter values explored (figs. B2, B3).

Discussion

We find that increased population connectivity, such as occurs with trucking hatchery-reared fish, can produce a trade-off between average population abundance and the ability of the population to display a portfolio effect (fig. 4), where genetic homogenization across populations plays a stronger role in eroding the portfolio effect than demographic synchronization (fig. 5). Our result that increased connectivity from trucking can homogenize traits across creeks suggests that trucking could have contributed to the genetic homogeneity of the CVFC (Williamson and May 2005) and the weakened portfolio effect observed (Carlson and Satterthwaite 2011). More generally, our results suggest that observations of demographic synchrony under high connectivity might arise as much, if not more, from genetic as compared with demographic effects of connectivity. In other words, the capacity for dispersal to lead to population synchrony is greater than might be expected from theory focused on the demographic effects of dispersal alone (reviewed in Bjørnstad et al. 1999; Liebhold et al. 2004; Abbott 2011), given the additional potential for genetic homogenization and the erosion of local adaptation to traits that influence population response to environmental variability in both space and time. The increased capacity for synchrony with genetic dynamics might also shift expectations from demographic-only models where system-level stability can increase concurrent with synchrony because both stability and synchrony are enhanced by increased dispersal (Abbott 2011) to a system where high dispersal erodes system-level stability by reducing total genetic variation across locations.

One reason genetic homogenization plays a crucial role in synchrony in our model is that we assumed that the same trait affects response to both local-scale environmental variability in space and larger-scale environmental variability in time. Therefore, the genetic dynamics of our model lead to a synergistic interaction between two of the three potential drivers of synchrony: dispersal and a shared environmental forcing factor (where the third potential driver is trophic interactions with mobile species; Bjørnstad et al. 1999; Liebhold et al. 2004). Response to both a shared environmental factor and local conditions dependent on the same trait or suite of traits might apply not only to migration phenology (as in our motivating example) but also to phenological traits more generally, given their influence on exposure to both microclimatic conditions and larger-scale weather patterns. For example, theory predicts the potential for optimal flowering time in annual plants to depend on growing season length, which in turn depends

on both local-scale conditions, such as the local water table and soil richness, and larger-scale weather patterns, such as drought conditions (Weis et al. 2014). Another potential trait of broad relevance to the dynamics modeled here is body size, given its role in mediating the influence of an array of environmental factors on multiple aspects of demography and therefore fitness (Sæther 1997; including migration, as noted in “Model Overview”). In cases when the traits that influence response to local conditions and larger-scale environmental variability are distinct, the degree to which dispersal might drive synchronous dynamics through genetic homogenization will inevitably depend on the amount of linkage and pleiotropy between the two sets of traits.

Accounting for genetic homogenization also reveals the role of background diversity in determining the relative balance of the impeditory (synchronizing and homogenizing) and supportive (genetic and demographic rescue) roles of connectivity (fig. 5B). At low levels of trucking, the erosion of the portfolio outweighs the small survival boost, leading to an overall negative effect of increased connectivity. At higher levels of trucking, with the portfolio already eroded to some extent, the positive effects of demographic enhancement and higher survival counteract any remaining loss of overall population diversity, and the CV declines along with an increase in mean population size with increased connectivity. This finding is in line with the theory of gene flow and local adaptation, where exceptions to the paradigm of gene flow impeding local adaptation typically occur with small, declining, or poorly adapted local populations such that dispersal provides genetic and demographic support (reviewed in Lenormand 2002). Note that our model accounts for one aspect of genetic rescue—the supply of local genetic diversity for response to variability in larger-scale (ocean) conditions—but does not account for local-scale environmental variability, drift, or inbreeding. While accounting for such dynamics might increase the positive local genetic supply role of dispersal as compared with the negative effect of system-wide genetic homogenization, theory suggests that this counterbalancing effect typically occurs at low levels of dispersal (e.g., in the model with genetic drift of Alleaume-Benharira et al. 2006; note that our model has low levels of connectivity without trucking through natural straying). Our results indicate that a comprehensive theory of genetic rescue, with multiple drivers of local diversity loss or local maladaptation, would require accounting for the effect of dispersal on genetic homogenization across locations and therefore the total amount of background diversity available for local supply.

Management and Conservation Implications

The trade-off trucking can drive between average population size and variability can present a trade-off between

management outcomes. Both higher total population size and lower variability through time support possible management goals: population size sets the level of sustainable catch the fishery can support, while stability in population size (and therefore catch) can help maintain incomes and employment for those in the fishing industry. Managers' goals (e.g., maximizing catch, stabilizing catch, or conserving wild runs), relative values, and tolerance for risk will affect which management strategy is optimal. We find that the relative variance (CV; fig. 5B) is highest at intermediate levels of trucking, suggesting that managers might prefer to truck fish either not at all or completely, either trying to preserve diversity within the system as a buffer or relying on hatchery fish to maintain population sizes. Elsewhere, we use optimal control analysis to better understand the balance between these multiple objectives (M. Springborn, A. Faig, M. Baskett, and A. Dedrick, unpublished manuscript). Studies in other ecological systems (e.g., Kellner et al. 2011; Lester et al. 2013) use the concept of efficiency frontiers to quantify the optimal outcomes for multiple metrics representing different management goals, such as fish biomass and fishery profit (Lester et al. 2013). While efficiency frontiers provide a potential next step for exploring questions of mean returns versus stability in returns from a natural resource exhibiting the portfolio effect, a key consideration would be whether genetic diversity is valuable only in its stabilizing role or has value in and of itself to realize biodiversity conservation goals (e.g., as suggested by separate listings of different evolutionary significant units of salmon populations under the Endangered Species Act; Waples 1991).

Any precise quantification of the trade-offs inherent to trucking and other hatchery practices in salmon as well as any quantification of the role of trucking relative to other homogenizing influences in CVFC would require a more detailed, mechanistic model that incorporates a variety of dynamics ignored here for generality and tractability (see "Assumptions and Simplifications"). Our results indicate that capturing the effects of hatcheries and trucking on the CVFC portfolio in such a model would require accounting for genetic drivers of outmigration dynamics because they affect response to environmental heterogeneity in both space and time. In addition, our sensitivity analysis indicates which parameter values, such as the strength of freshwater and ocean selection, would be most important to resolve for quantitatively precise predictions (fig. 6). Constructing and parameterizing a model that more mechanistically and realistically represents the genetic drivers of CVFC outmigration dynamics (e.g., one that accounts for the role of size, as mentioned in "Model Overview") will require a deeper understanding of which traits drive survival throughout the freshwater and ocean life cycle stages. Existing and recently implemented data collection programs,

such as the Constant Fractional Marking program (marks 25% of hatchery-produced CVFC with coded-wire tags since 2007; e.g., Buttars 2014), smolt trap records (e.g., Watry et al. 2012), and the ocean salmon survey run by the National Marine Fisheries Service (e.g., Hassrick et al. 2016) are offering emerging insight into the traits driving survival at each stage.

Given the influence of genetic homogenization on portfolio effect erosion in our model, a goal of restoring the portfolio effect in CVFC would likely rely on an array of management approaches to protect or restore diversity in the system (Waples et al. 2008). Hatchery strays could be reduced through actions such as mimicking the natural selective environment as much as possible in the hatchery (e.g., California HSRG 2012), which can also help promote olfactory imprinting (Keefer and Caudill 2014), or releasing hatchery fish earlier and farther upstream (Huber and Carlson 2015). Barging rather than trucking fish to expose them to freshwater scents during transport has not reduced straying rates in other systems (Bond et al. 2017), possibly because the conditions are not suitable for successful imprinting. Additionally, hatchery managers can select breeders to represent the range of phenotypes in the wild stock (Ford 2002; California HSRG 2012). Habitat restoration (e.g., juveniles rearing on floodplains; Jeffres et al. 2008), with the goal of boosting the other Chinook runs that respond to environmental conditions differently (Lindley et al. 2009), could provide space for local adaptation to re-emerge. However, there might be limits to how much diversity can regenerate in the Central Valley system today without major changes such as dam removals or a reconfiguration of the Delta (Yamane et al. 2018). In addition to a loss of buffering against interannual environmental variation, loss of genetic diversity in the population could limit the ability for CVFC to respond to larger-scale changes in both the marine and freshwater environments, such as shifts in the Pacific Decadal Oscillation and climate change effects on upwelling and precipitation.

Assumptions and Simplifications

In order to balance tractability with capturing the essential dynamics relevant to the portfolio effect as it depends on connectivity, we make a number of assumptions in our model construction. For the genetic dynamics, for generality we use the infinitesimal model to track the genotypes, ignoring genes of major and minor effects (e.g., Yeaman and Guillaume 2009; Gomulkiewicz et al. 2010), which could increase the rate of evolution. More rapid evolution might make the populations track the varying ocean conditions even more tightly and therefore increase the effects of straying and homogenization on population variability. Accurately modeling genes of major and minor effects in a

mechanistic model would require knowledge of the genetic architecture of the evolving trait, which is rarely (but increasingly) available. Also, we focus on a single generic trait that is either genetically determined with random environmental effects (coupled genetic-demographic model) or entirely environmentally determined (demographic-only model). In reality, multiple traits with both genetic and environmental influences determine complex outcomes such as outmigration and ocean arrival timing, including complicated outmigration journeys that could enhance survival of juveniles that might otherwise be mismatched with ocean conditions (e.g., Sturrock et al. 2015). Both adaptive plasticity in and separate determination of freshwater outmigration and ocean arrival timing would increase the system-level buffering against environmental variability, depending on cue reliability and the amount of genetic or phenotypic correlation between the traits underlying outmigration. Furthermore, as described in “Model Overview,” the traits that underlie outmigration (e.g., body size) affect multiple aspects of fitness beyond outmigration and ocean arrival survivorship (e.g., size-dependent reproduction) and depend on rearing in the hatchery environment. Accounting for such additional fitness and hatchery consequences would likely increase the demographic consequences of trucking.

The stylized two-population representation of the portfolio we use is simplistic compared with most real populations in both space and time. Spatially, straying hatchery fish in our two-creek system can only go to the creek without the hatchery rather than being spread across multiple creeks (e.g., CVFC inhabit two large river systems each with numerous tributaries and basins; Williams 2006). This simplification likely leads us to underestimate the starting strength of the portfolio without trucking and the potential amount of genetic homogenization with trucking. While spread across multiple creeks might reduce the load on a particular creek, it might also increase the chance that strays will end up in a location with an optimum much different than their natal environment, with greater homogenization consequences to the overall genetic variation. This greater homogenization potential could be counterbalanced by stronger selection with greater differences in local conditions, but theory suggests that this counterbalancing effect requires particularly strong local selection occurring after straying and before reproduction (as opposed to after reproduction and before straying, as modeled here) such that essentially no straying hatchery-reared fish survive to reproduce (Baskett and Waples 2013). Note that the CVFC also has multiple hatcheries producing potential strays and many more hatchery fish than wild, such that hatchery returns dominate populations across creeks (Palmer-Zwahlen and Kormos 2013) comparable to what we model here. Temporally, we simplify variation in both salmon (e.g., Central Valley Chinook show overlapping generations and have

four seasonal runs; Yoshiyama et al. 1998) and the environment. Specifically, as compared with our static optimal freshwater traits in each creek in the model, in reality freshwater conditions vary across years. Accounting for temporal heterogeneity in freshwater conditions could increase selection for trait variance (given great enough environmental variability, selection strength, and generational overlap; Ellner and Hairston 1994), with the potential for increased importance of genetic variation on the portfolio effect, depending on the relative range of optimal traits across the two creeks and the ocean.

Finally, we ignore other homogenizing and hatchery influences in CVFC populations. Beyond trucking, anthropogenic activities that homogenize habitats (e.g., habitat loss [particularly of upstream tributaries and floodplains], changes in water temperatures below dams, and changes in flow from dams and diversions) might also drive a loss of the portfolio effect in CVFC (Lindley et al. 2009). Hatchery impacts also extend beyond trucking to include domestication selection in the hatchery for traits that are maladaptive in the wild (McClure et al. 2008) and environmentally driven phenotypic differences that affect survival (e.g., Kostow 2004). Ignoring these effects means we might both overestimate the ability of hatchery fish to survive in the wild and their contribution to productivity and underestimate the fitness consequences of hatchery fish reproducing in the wild, if those that do survive have maladaptive traits that depress the fitness of wild populations (e.g., Araki et al. 2007). A key next step for understanding and managing the CVFC portfolio is to integrate multiple hatchery and homogenizing influences in a mechanistic model to quantify their relative roles in population dynamics and therefore the efficacy of alternate management approaches that differentially affect each.

Conclusions

The importance of genetic homogenization to demographic synchrony found here provides an example of evolutionary change on ecological timescales and with ecological consequences. The expanding field of coupled ecological-evolutionary dynamics indicates the potential for ecological consequences of evolutionary dynamics at scales ranging from populations to communities and ecosystems (e.g., Carroll et al. 2007; Bailey et al. 2009a; Schoener 2011), including cases where gene flow and dispersal can interact with and drive coupled ecological-evolutionary dynamics to affect metapopulation persistence (e.g., Garant et al. 2007; Kinnison and Hairston 2007). As compared with the typical focus on mean effects and outcomes (e.g., Bailey et al. 2009b; Palkovacs et al. 2009; with exceptions, e.g., the role of eco-evolutionary feedbacks in predator-prey oscillations; Yoshida et al. 2003; Cortez and Weitz 2014), our results demonstrate that evolutionary-driven changes to population variability

can be as ecologically consequential as those to the mean state.

As with coupled ecological-evolutionary dynamics in general, our results highlight the role of variability in understanding the conservation consequences of anthropogenic effects on connectivity in an eco-evolutionary context. Much like anthropogenic disruption to connectivity (with effects such as drift, inbreeding depression, and demographic stochasticity; e.g., Oostermeijer et al. 2003; Yamamoto et al. 2004; Honnay and Jacquemyn 2007), we show that anthropogenically driven increases in connectivity can also have combined genetic and demographic consequences that can reduce population stability. Previous work on negative population-level effects of increased connectivity through outbreeding depression and gene swamping has tended to assess change in population size or growth rate through metrics that are proxies for fitness, such as fecundity and survival (e.g., Gharrett et al. 1999; Edmands 2007). Our analysis extends beyond the consequences of increasing connectivity for overall fitness and population size to also consider effects on population variability through time. Our results indicate that increased variability in population size over time can be an additional conservation challenge of increased connectivity if a population complex becomes unable to maintain a portfolio of locally adapted subpopulations.

Acknowledgments

We thank Stephanie Carlson (University of California, Berkeley), Amanda Faig (National Oceanic and Atmospheric Administration [NOAA] Fisheries), Steve Lindley (NOAA Fisheries), Will Satterthwaite (NOAA Fisheries), Mike Springborn (University of California, Davis), Anna Sturrock (University of California, Berkeley), and Robin Waples (NOAA Fisheries) for insightful discussions and comments. In addition, we thank two anonymous reviewers for their insightful feedback on an early version of the manuscript. Funding support for this article is from the California Department of Fish and Wildlife Ecosystem Restoration Program (E1383002 to M.L.B.), the University of California Davis Graduate Group in Ecology Fellowship (to A.G.D.), and NOAA grant NA14OAR4170202 (to A.G.D.), California Sea Grant College Program Project E/PD-12, through NOAA's National Sea Grant College Program, US Department of Commerce. The statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of California Sea Grant, NOAA, or the US Department of Commerce.

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Associate Editor: Robin E. Snyder
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Fall-run Chinook salmon (*Oncorhynchus tshawytscha*). Photo credit: Lauren Yamane.