Long life spans can mitigate the genetic effects of strays from temporary conservation hatchery programs

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Abstract

While conservation fish hatchery programs can be a valuable tool providing demographic support, they can also cause domestication, risking unintended fitness consequences to both target and connected populations. When conservation hatcheries are used over a fixed amount of time, the interaction between program duration and species life history might determine the scale of fitness effects and the effectiveness of mitigation measures. We develop a mathematical model to quantify the effectiveness of approaches to mitigate unintended fitness consequences in such temporary conservation hatchery programs. We parameterize our model to represent a conservation aquaculture-based recovery program for white sturgeon (*Acipenser transmontatus*) in the Nechako River (British Columbia), which might impose genetic risks on the adjacent populations within the Fraser River. We find that over a period spanning 50–200 years of hatchery operation, the life history characteristics of white sturgeon, particularly late age of maturity and longevity, reduce the genetic risks of conservation hatcheries when compared to shorter-lived species. The genetic impacts of the hatchery accumulate slowly increasing the potential for adaptive management in this system.

Key words: white sturgeon (*Acipenser transmontanus*), conservation hatchery, geneflow, domestication, quantitative genetics model

Introduction

Artificial propagation can be a valuable conservation and natural resource management tool that can help achieve a range of objectives. For example, artificial propagation in fish hatcheries has been to supplement harvested populations (Naish et al. 2007; Kitada 2020), maintain declining populations of threatened and endangered species (Naish et al. 2007; Lamothe et al. 2019), and re-introduce locally extirpated species into formerly occupied habitats (George et al. 2009; Lamothe et al. 2019). These practices, however, can have unintended consequences that threaten biodiversity through genetic and ecological mechanisms (Laikre et al. 2010). Artificial propagation in hatcheries can affect the fitness of supplemented populations through inadvertent domestication (Araki et al. 2007; Christie et al. 2012) and reduce genetic diversity in the population by increasing the reproductive output of the individuals reproducing in captivity (Ryman and Laikre 1991; Waples et al. 2016). Individuals released from hatchery programs can also have unintended ecological interactions with their wild counterparts through competition for scarce resources, increasing predator abundance, and the risk of disease (Kostow 2009).

Hatchery programs can also impact neighboring populations if hatchery-origin fish "stray" between adjacent locations. This dynamic creates the possibility that hatchery programs designed to support a single population can threaten the viability of neighboring groups and the collective metapopulation (Naish et al. 2007; McClure et al. 2008). In addition to the risks from domestication, genetic diversity, and ecological interactions analogous to the risks to the target population, straying poses additional risks to non-target populations. First, outbreeding depression can occur if straying leads to hybridization between populations with distinct local adaptations, thus reducing fitness (Gharrett et al. 1999; Naish et al. 2007; Rollinson et al. 2014). Second, straying can threaten diversity by homogenizing formerly distinct populations; when this includes homogenization of life

history traits that affect population responses to environmental variability, this loss of diversity among populations then undermines buffering capacity at the meta-population level and therefore can cause more synchronous, boom-and-bust dynamics (i.e., loss of "portfolio effects" Schindler et al. 2010; Carlson and Satterthwaite 2011; Dedrick and Baskett 2018).

Previous modeling studies suggest that even a small number of hatchery strays can have large effects on the long-term genetic and demographic state of wild populations (Ford 2002; Edmands and Timmerman 2003; Baskett and Waples 2013). For example, Ford (2002) showed that the equilibrium genetic state of the wild population can approach that of the hatchery population unless the rate of geneflow is very small (less than 5% of the spawning population is of hatchery origin). The models used to derive these results, however, describe the equilibrium impacts of permanent or longer term (more than tens of generations) hatchery programs, which might particularly apply to cases of harvest augmentation. As a result, these model findings might not hold if hatchery production is intended as a temporary conservation measure, which is often the case due to its high costs (Snyder et al. 1996) and used as a stop-gap measure until other measures address the root cause of the species decline (Naish et al. 2007; McMurray and Roe 2017). Furthermore, declines in fitness and genetic diversity caused by captive breeding can occur more slowly in longer-lived species (Willoughby and Christie 2019). Therefore, life history and duration of stocking could interact to mitigate the potential unintended consequences of shorter-term (less than 10 generations), temporary hatchery programs.

Species' life history and the duration of hatchery programs might also determine the effectiveness of management strategies designed to mitigate the genetic effects of strays. The genetic impacts of hatcheries can be controlled by limiting the domestication of hatchery fish by managing the genetics of the hatchery broodstock and minimizing domestication selection through rearing practices (e.g., shorter rearing duration, more natural rearing environment; Fraser 2008). They can also be controlled by limiting the amount of geneflow from individuals released from the hatchery to the wild. Geneflow can be limited by reducing the number of individuals released, removing individuals that have strayed to non-target populations, and limiting the duration of the stocking program. The relative efficacy of these methods for controlling geneflow, however, might depend on their interactions with one another. For example, the effect of reducing stray rates could depend on the duration of the stocking program because a longer duration would allow more time for fitness effects to accumulate in both the hatchery-raised and wild-origin populations. Furthermore, the effectiveness of removing hatchery-origin individuals might depend on when they are removed during their life cycle because of an individual's reproductive output and, thus, the potential for geneflow change through its life cycle.

An example of a temporary conservation hatchery with potential effects on connected populations is the conservation fish culture program for Nechako white sturgeon (*Acipenser*

transmontanus). White sturgeon are one of 27 species of sturgeon (Ascipenseridae), freshwater and anadromous fishes native to the Holarctic. Across this range, all sturgeon species have been assessed at some level of risk of extinction and all are characterized by a long-lived life history. For example, white sturgeon have an iteroparous life history with individuals maturing around 20 years of age and living in excess of 80 years in age (RL&L Environmental Services, Ltd. 2000). Populations in the upper Fraser River, British Columbia, form a genetically distinct designable unit (DU) and have been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada, and the DU awaits a listing decision under the Canadian Species at Risk Act (COSEWIC 2012). The Upper Fraser DU contains three groups that show a combination of genetic, demographic, and spatial distinctions: the Nechako River, mid-Fraser, and upper-Fraser (RL&L Environmental Services, Ltd. 2000; Schreier et al. 2012; DFO, Canada 2014). The two groups in the mainstem of the Fraser River (mid-Fraser and upper-Fraser) are near historical abundance levels (Smyth et al. 2016). The Nechako River group, however, has experienced a recruitment failure and a long-term decline in abundance caused by changes in river substrate that limit the survival of larval fish following the construction of the Kenny Dam.

To forestall further effects of the ongoing recruitment failure, a conservation hatchery program was established to supplement the population while research and restoration efforts address the root causes of the decline. Each year, the hatchery program collects up to 12 male and 12 female fish from the remaining Nechako River population, which are spawned in captivity and released (Nechako White Sturgeon Recovery Initiative 2005). The hatchery uses full factorial crosses (i.e., every possible combination of spawning pairs), resulting in up to 144 half-sibling crosses, although the broodstock collection goals are not met every year, resulting in a smaller number of crosses (Nechako White Sturgeon Recovery Initiative 2022). Juvenile releases began in the Nechako River in 2015 with the goal of releasing a sufficient number of juveniles to produce 50–60 mature adults per year class over a 45-year period (Nechako White Sturgeon Recovery Initiative 2005).

Since hatchery releases began, evidence has accumulated that hatchery-origin fish have emigrated from the Nechako River to the mid-Fraser, either permanently or temporarily. In some areas, hatchery fish comprise over half of the juveniles captured in monitoring programs in the mid-Fraser River (Nelson et al. 2021). This unexpectedly high proportion of hatchery-origin fish has raised concerns that the Nechako River hatchery might impact the neighboring populations in the mainstem of the Fraser River. Since its inception, the captive-rearing program has minimized genetic risks by using wild-origin brood stock from the Nechako River and maximizing genetic diversity by using every possible combination of spawning pairs. These steps, however, do not rule out the possibility that hatchery-origin fish that stray to the Fraser River could cause outbreeding depression. Declines in fitness could occur if the Nechako-origin fish dilute local adaptation in the mid-Fraser population or if they experience rapid adap-

tation to captivity, as documented in salmonids (Araki et al. 2007; Christie et al. 2012). The long-lived life history of white sturgeon and the intention to use the hatchery as a temporary conservation measure, however, might reduce genetic and ecological risks.

To explore how species life history and hatchery management measures might affect the potential for unintended fitness consequences of temporary hatchery programs, we developed a mathematical model of hatchery immigrating into a wild population. To build and parametrize our model, we use the Nechako River hatchery and neighboring population segments in the mainstem Fraser River as an example system. Building on previous work (Tufto 2001; Ford 2002; Baskett and Waples 2013), we use a coupled genetic–demographic model to describe the effects of the hatchery program on the abundance and fitness of neighboring wild populations. To capture the effects of the population's life history, we use an age-structured demographic model parameterized to match demographic rates of white sturgeon measured by a system-wide monitoring program (RL&L Environmental Services, Ltd. 2000). In addition, we develop a novel method to calibrate the genetic parameters of the model to match fitness declines observed in early-generation hatchery fish estimated by meta-analysis (Christie et al. 2014), which provides additional empirical grounding for our modeling framework.

Using this modeling framework, we test how interactions between the duration of the hatchery program and the species' longevity interact to determine the fitness and demographic effect of the hatchery program while accounting for feedback between these demographic and genetic changes. We also test how the life history and transient dynamics of temporary hatcheries determine the effectiveness of alternative strategies for limiting geneflow from hatchery strays and discuss the implications of our findings for adaptive management. Note that our focus on the effects of the Nechako strays on the Fraser River population complements existing work that quantitatively assesses the demographic impact of the hatchery on the Nechako River population (e.g., Smyth et al. 2016).

Methods

Model overview

Our model describes the genetic and demographic consequences of hatchery-origin immigrants on a neighboring wild population by tracking the abundance and genotypes of the wild population as it receives an influx of immigrants from a hatchery-raised population. We develop models for both the Nechako River hatchery population and a single wild population to represent the naturally occurring Fraser River populations. Given the recruitment failure in the Nechako River and the corresponding lack of natural production, we assume all reproduction in the system occurs in captivity. To date, the Nechako hatchery program has used wild-origin fish as broodstock and released all hatchery broodstock to the wild after spawning. In our model, the hatchery broodstock is

sampled at random from the Nechako River population, including wild-origin fish that have not been domesticated and hatchery-origin fish that have experienced domestication selection. Our model matches the current practices used by the program for the first 20 years of the simulations and allows hatchery operation to continue after the initial wild-origin fish die or reach their maximum age.

Following previous modeling studies (Ford 2002; Baskett and Waples 2013), we represent the effects of domestication with a single quantitative genetic trait. This trait represents a suite of phenotypes that can adapt to the natural or hatchery environment. We model domestication selection with stabilizing selection acting on the fecundity of adults and the viability of yearlings. We calibrate the strength of domestication selection to match fitness declines observed in early-generation hatchery fish (Christie et al. 2014). We also add a fixed reduction in the fecundity of hatchery-origin individuals in the wild to represent the plastic effects of captive breeding on fitness.

To capture the effects of the domestication of hatchery-origin stray on the Fraser population, we track the abundance and genotype distributions through five demographic events: reproduction, density-dependence, selection, immigration, and adult survival (Fig. 1). For reproduction, fecundity is a function of age and genotype to capture the effects of growth, maturation, senescence (reduced spawning frequency with age), and fecundity selection. Mating pairs form independently of their ages and phenotypes, and using the infinitesimal model of quantitative genetics (Barton et al. 2017), the genotypes of their offspring follow a normal distribution centered at the average of the parents genotypes. Yearlings experience density-dependent mortality and viability selection around an optimum phenotype, with selection events occurring before and after density-dependence. We chose to model selection in these two phases because the timing of selection relative to density-dependent mortality determines its impact on the abundance of the population (Débarre and Gandon 2011; Baskett and Waples 2013). After selection, we track each cohort as it ages and experiences growth, maturation, natural mortality, and senescence. We parameterized the vital rates of the population to match observations from a long-term monitoring study (RL&L Environmental Services, Ltd. 2000) and previous demographic analysis (Wood et al. 2007; Smyth et al. 2016).

To understand how hatchery operations affect the fitness and abundance of the wild population, we varied three factors: (1) the number of hatchery-origin individuals that immigrated into the wild population per year (immigration rate), (2) duration of hatchery releases, and (3) stray removal. The immigration rate captures the effect of the number of individuals released from the hatchery and factors influencing the probability of straying between river segments, such as acclimatization to the local environment before release. To test the effect of the duration of hatchery production and the system's dynamics, we vary the time over which immigration from the hatchery population occurs in our numerical simulations. For stray removal, we test the effect of removing post-release hatchery strays of different age classes and how

Fig. 1. The model is composed of two components: a model of the genotypes of the Nechako River population, which reproduces in captivity and experiences domestication selection, and a model of the genotypes and abundance of the wild Fraser River population as it receives immigrants from the Nechako hatchery population. Three selection events determine the effect of genotypes on the abundance of the Fraser River population: fecundity selection, which determines the reproductive success of adults, and two viability selection events that determine the survival of juveniles, one before and one after density-dependent mortality. Immigration from the Nechako River to the mainstem Fraser occurs before recruitment at age one, and immigrants remain in the mainstem or Nechako River population for the remainder of their life cycles. Each of these events affects the abundance $N_{i,j,a,t}$ and genotype distribution $\psi_{i,j,a,t}$ of the population of origin i in location j. The arrows indicate movement between demographic stages. Hash marks indicate transitions influenced by selection. All map data were sourced from rnaturalearth (Massicotte and South 2024) and presented in the Mercator projection.
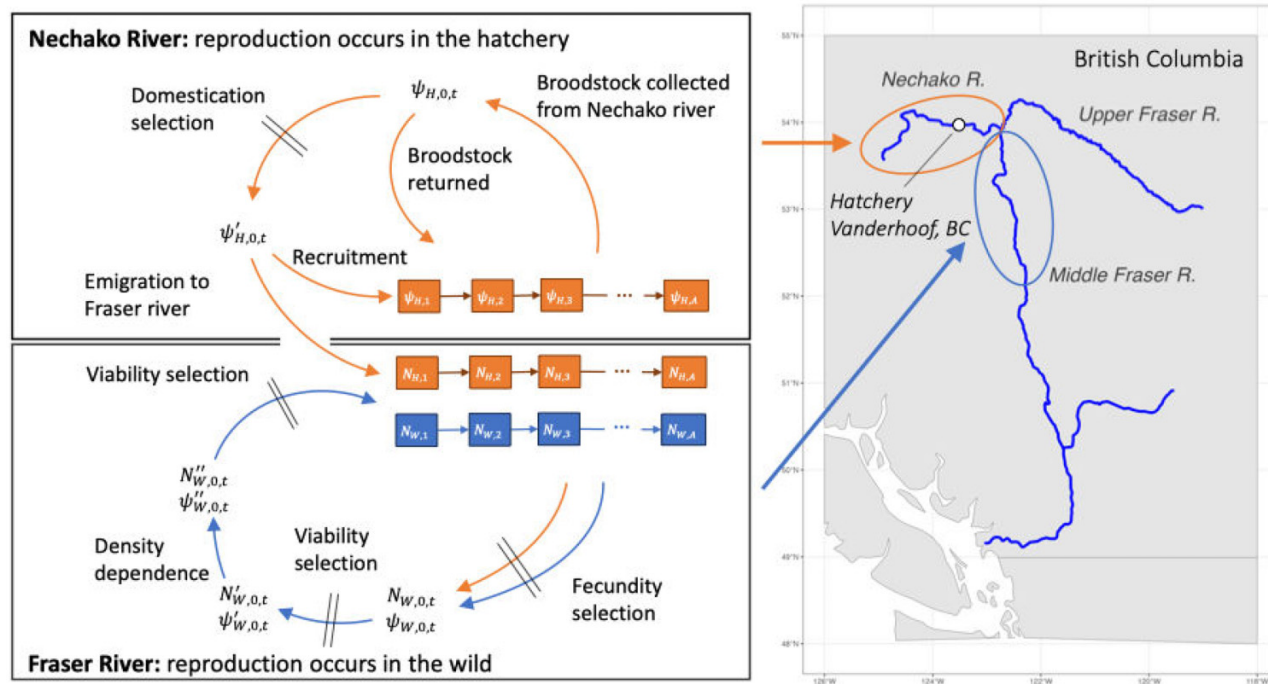
the effectiveness of removals changed as a function of the planned hatchery duration and immigration rate.

Model details

State variables

We follow the population size of each cohort $N_{i,j,a,t}$ and their genotype g distribution $\psi_{i,a,t}(g)$ where i denotes the origin (hatchery H or wild W), j denotes their location (Nechako River n or Main-stem Fraser River m), a denotes age, and t denotes time. We follow the full genotype distribution rather than tracking the mean and variance of a normal distribution because geneflow between the populations can create departures from normality (Baskett and Waples 2013). We track the abundance of wild-origin yearlings $N_{W,m,0,t}$ through three life stages prior to recruitment, with each stage denoted by $N_{W,m,0,t}$, $N'_{W,m,0,t}$, and $N''_{W,m,0,t}$, along with the corresponding genotype distributions $\psi_{W,m,0,t}(g)$, $\psi'_{W,m,0,t}(g)$, and, $\psi''_{W,m,0,t}(g)$. We track the genotypes of hatchery-origin fish through two life stages prior to recruitment denoted by $\psi_{H,n,0,t}(g)$ and $\psi'_{H,n,0,t}(g)$. Furthermore, we only track the genotype distribution in the hatchery environment assuming a management-controlled constant population size.

Reproduction

The fecundity of individuals is determined by their age and genotype, and environmental effects of the hatchery, where the effect of age is given by a vector of age specific fecundities F_a, the effect of genotypes is given by a selection gradient $W_{f,j}(g)$, and environmental effects of the hatchery are given by a factor $\Delta < 1$. Fecundity selection is stabilizing around an optimum phenotype θ_j with strength $S_{f,j}$, both of which depend on the spawning environment $j \in \{ W, H \}$. Therefore, the fecundity of an individual in spawning environment j is the product of these three factors

(1) $\qquad F_{j,i,a}(g) = F_a \Delta^{I_{i=H}} e^{-0.5 s_{f,j}(g - \theta_j)}$

where $I_{i=H}$ is an indicator variable that takes the value of one for hatchery fish spawning in the wild and are zero otherwise. Following Wood et al. (2007) and Smyth et al. (2016), fecundity at age is proportional by a constant c to the amount weight at age exceeds the weight at maturation w_m. We also consider scenarios where spawning frequency declines with age, following Wood et al. (2007). We model this by multiplying the fecundity-at-age relationship by a decreasing function of age, with two parameters, μ_s, the age at 50% senescence,

and σ_s, the slope at the senescence-at-age relationship:

$$(2) \quad F_a = \begin{cases} c\left(w_a - w_m\right)\left(\dfrac{1}{1 + \mathrm{e}^{\frac{a - \mu_s}{\sigma_s}}}\right) & \text{if } w_a \geq w_m \\ 0 & \text{if } w_a < w_m \end{cases}$$

We model the weight at age w_a as an isometric function of length L_a with the average weight at 100 cm given by w_{100}.

$$(3) \quad w_a = w_{100} L_a^3 \times 100^{-6}$$

the factor of 100^{-6} is included to ensure $w_a = w_{100}$ when $L_a = 100$ cm. Length at age L_a follows a von Bertalanffy growth curve with asymptotic length L_∞, and growth rate k

$$(4) \quad L_a = L_\infty \left(1 - \mathrm{e}^{-ka}\right)$$

The total reproduction of the population is determined by the sum of age, genotype, and origin specific fecundities $F_{j,i,a}$ (g) weighted by abundance $N_{j,i,a,t}$

$$(5) \quad N_{j,j,0,t} = \sum_{i \in \{W,H\}} \sum_{a=1}^{A_{\max}} N_{j,i,a,t} \int_{-\infty}^{\infty} F_{j,i,a}(g)\,\mathrm{d}g$$

where $A_{\max} = 150$ is the oldest age class tracked by our model.

The genotype distribution of the yearlings is determined by the distribution of genotypes in the spawning population, the formation of mating pairs, and the transmission of genotypes from parents to offspring. The distribution of genotypes in the spawning population is the sum of genotypes for each age class weighted by their abundance and fecundity

$$(6) \quad \psi_{\mathrm{spawn},j,t}(g) = \frac{1}{Z_{j,t}} \sum_{i \in \{W,H\}} \sum_{a=1}^{A_{\max}} N_{j,i,a,t} F_{j,i,a}(g)\, \psi_{i,a}(g)$$

where $Z_{j,t}$ is a normalizing constant. Mating pairs form at random such that the genotypes g_1 and g_2 of the parents of each yearling can be treated as a random sample from the spawning population $\psi_{\mathrm{spawn},j,t}(g)$. The transmission of genotypes follows the infinitesimal model of quantitative genetics (Barton et al. 2017) that assumes genotypes are determined by small contribution from alleles at many loci. Given this model, the genotype g of yearlings with parent genotypes g_1 and g_2 are normally distributed around the mid-parental value with variance V_r. Combining these three assumptions yields an integral equation for the genotype distribution of yearlings

$$(7) \quad \psi_{j,0,t}(g) = \frac{1}{\sqrt{2\pi V_r}} \int_{-\infty}^{\infty} \int_{\infty}^{\infty} \mathrm{e}^{\frac{-(g - 0.5g_1 - 0.5g_2)^2}{2V_r}}$$
$$\times \psi_{\mathrm{spawn},j,t}(g_1)\, \psi_{\mathrm{spawn},j,t}(g_2)\,\mathrm{d}g_1\,\mathrm{d}g_2$$

(Slatkin 1970).

Selection

We model both natural and domesticating selection as viability selection events where the probability of survival is determined by a phenotype p. We assume that an individual's phenotype is determined by the sum of their genotype g and normally distributed environmental effects E, which have mean zero and variance V_E. Therefore, the joint genotype–phenotype distribution is $\phi_{j,a,t}(p,g) = \frac{1}{\sqrt{2\pi V_E}} \mathrm{e}^{-(p-g)^2/(2V_E)} \psi_{j,a,t}(g)$. The probability of surviving the selection event is a decreasing function of the distance between an individual's phenotype p and the optimum value θ_j, where selection strength $s_{k,j}$ for location selection event k in location j determines how quickly survival declines away from the optimum phenotype

$$(8) \quad W_{k,j}(p) = \mathrm{e}^{-\frac{s_{k,j}}{2}\left(p - \theta_j\right)^2}$$

following the stabilizing selection functional form used in previous models of hatchery effects (Tufto 2001; Ford 2002; Baskett and Waples 2013). To then determine how selection affects the genotype distribution, we integrate the post-selection population over all phenotypes:

$$(9) \quad \psi'_{j,a,t}(g) = \int_{-\infty}^{\infty} W(p)\, \phi_{j,a,t}(p,g)\,\mathrm{d}p = W_{\theta_j} W_{k,j}^*(g)\, \phi_{j,a,t}(g)$$

where the genotype-dependent fitness function is

$$(10) \quad W_{k,j}^*(g) = \mathrm{e}^{-\frac{s_{k,j}^*}{2}\left(g - \theta_j\right)^2}$$

and the effective selection strength $s_{k,j}^* = (V_E + 1/s_{k,j})^{-1}$ and the survival probably of an optimum phenotype $W_{\theta_j} = \sqrt{s_{k,j}/(1 + s_{k,j}V_E)}$ account for environmental variation of phenotypes around genotypes (see Supplemental material 1 for derivation). Because W_{θ_j} is a constant independent of the genotypic distribution at any given time, we consider it to be a component of the normalizing factors $Z_{v,j,t}$ in the equations for post-selection genotypic distributions and density-independent survival S_0 in the equations for post-selection population sizes below.

Domestication selection

After reproduction hatchery juveniles experience stabilizing viability selection with effective strength $s_{v,H}^*$ and optimum phenotype θ_H, such that $W_{v,H}^*(g) = \mathrm{e}^{-\frac{s_{v,H}^*}{2}(g - \theta_H)^2}$. The effect of selection on the genotype distribution of the population is the product of the initial genotype distribution and the survival probability, normalized by $Z_{v,H,t}$

$$(11) \quad \psi'_{H,n,0,t}(g) = \frac{1}{Z_{v,H,t}} \psi_{H,0,t}(g)\, W_{v,H}^*(g)$$

Can. J. Fish. Aquat. Sci. **82**: 1–15 (2025) | dx.doi.org/10.1139/cjfas-2023-0355

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Natural selection

The wild population experiences two viability selection events in their first year of life: one before and one after density-dependent mortality with survival probabilities determined by stabilizing selection gradients $W^*_{v_1,W}(g)$ and $W^*_{v_2,W}(g)$. Following Dédarre and Gandon (2011), selection before density-dependence has a smaller effect on the abundance of the population and is called "soft" selection, while selection after density-dependence or "hard" selection has a larger demographic effect. We model these two separate selection events to capture both types of selectivity and approximate, within our discrete-time dynamics, the reality that both selection and density-dependence are likely continually co-occurring. These two selection events have the same optimum phenotype θ_W, but different selection strengths $s^*_{v_1,W}$ and $s^*_{v_2,W}$, respectively. The survival probability integrated over all genotypes determines the proportion of the population that survives selection and therefore the abundance after the first $N'_{W,0,t}$ and second selection events $N'''_{W,0,t}$

$$(12) \quad N'_{W,0,t} = N_{W,0,t} \int_{-\infty}^{\infty} \psi_{W,0,t}(g) W^*_{v_1,W}(g)\, dg$$

$$(13) \quad N'''_{W,0,t} = N''_{W,0,t} \int_{-\infty}^{\infty} \psi''_{W,0,t}(g) W^*_{v_2,W}(g)\, dg$$

where density-dependence (described in the next sub-section below) occurs between these two selection events to determine $N''_{W,0,t}$. The genotype distribution after natural selection is given by the product of the fitness function and genotype distribution, normalized by $Z_{v_x,t}$

$$(14) \quad \psi'_{W,0,t}(g) = \frac{1}{Z_{v_1,t}} \psi_{W,0,t}(g) W^*_{v_1,W}(g)$$

$$(15) \quad \psi'''_{W,0,t}(g) = \frac{1}{Z_{v_2,t}} \psi''_{W,0,t}(g) W^*_{v_2,W}(g)$$

where again, density-dependence determines $\psi''_{W,0,t}$ as described below.

Density-dependence

In white sturgeon, there is evidence that yearlings are most sensitive to density-dependent mortality (Justice et al. 2009). Therefore, we model density-dependence with a single mortality event acting on yearlings between the two selection events. Survival is a decreasing function of abundance, consistent with a Beverton Holt stock recruit relationship $f\left(N'_{W,0,t}\right) = \frac{S_0}{1+\beta N'_{W,0,t}}$, where β determines the strength of density-dependence and S_0 is the density-independent survival. The abundance of the wild population after density-dependent mortality is

$$(16) \quad N''_{W,0,t} = \frac{S_0 N'_{W,0,t}}{1 + \beta N'_{W,0,t}}$$

Finally, we assume, density-dependent survival is independent of genotype, so the genotype distribution is unchanged $\psi''_{W,0,t}(g) = \psi'_{W,0,t}(g)$.

Immigration

After density-dependence and selection, hatchery-origin individuals emigrate. The number of hatchery-origin fish emigrating from the Nechako River population is subject to uncertainty and is determined by many factors including the number of releases, rearing strategies, and variable environmental conditions. To accommodate this uncertainty, we test a range of scenarios determined by a fixed number of immigrants each year when the hatchery is in operation

$$(17) \quad N'''_{H,f,0,t} = \bar{N}_{H,0}$$

We represent the immigration rate as a proportion of natural recruitment at equilibrium $r_H = \bar{N}_{H,0}/N^*_{W,f,1}$ in our results to account for the effect of the wild population size on the rate of geneflow.

Transitions between age classes

After selection, density-dependence, and immigration, yearlings enter the first age class such that

$$(18) \quad N_{i,1,t+1} = N'''_{i,0,t}$$

$$(19) \quad \psi_{i,1,t+1}(g) = \psi'''_{i,0,t}(g)$$

All age classes 1 year and older experience density-independent mortality with survival probability S_a before transitioning to the next age class

$$(20) \quad N_{i,a+1,t+1} = S_a N_{i,a,t} \quad \text{for } a > 0$$

Survival between age classes does not depend on genotype; therefore, the genotype distribution of all cohorts (accept yearlings) is unchanged after each time step

$$(21) \quad \psi_{i,a+1,t+1}(g) = \psi_{i,a,t}(g) \quad \text{for } a > 0$$

Genetic parameters

There is a significant body of evidence linking hatchery cultivation to rapid declines in fitness in the wild (Christie et al. 2014). These studies measure the relative reproductive success of hatchery-origin and wild-origin fish in the wild by comparing the performance of individuals with mixed wild and hatchery ancestry in the wild and hatchery environments, respectively. These studies, however, all require multiple generations of data and, therefore, have only been conducted in short-lived species like salmonids (Christie et al. 2012). Acknowledging the uncertainty associated with using these estimates in a longer-lived species, we calibrate the range of genetic parameters of the model (Table 1) to match the fitness declines in early-generation hatchery fish estimated by the meta-analysis by Christie et al. (2014), as the best available data on the range of plausible values. Christie

Table 1. Genetic parameters.

Parameter	Interpretation	Value	Range
Q_{g_1}	Relative fitness of first generation hatchery fish genetic component	0.85	(0.7, 1.0)
Δ	Relative fitness of first generation hatchery fish environmental component	0.85	(0.7,1.0)
S_f	Effect of fecundity selection on first generation hatchery fish	0.1	
S_v	Fraction of fish generation hatchery fish that survival viability selection	0.01	(0.05, 0.005)
V_r	Recombination variance	0.5	
θ_W	Optimal genotype in the wild	0.0	
θ_H	Optimal genotype in hatchery	10.0	
s_W	Total strength of natural selection	0.25	(0.18,0.61)
$s_{f,W}$	Strength of natural fecundity selection	$0.25s_W$	$(0.0s_W, 1.0s_W)$
$s_{v_1,W}$	Strength of soft viability selection	$0.25s_W$	$(0.0s_W,1.0s_W)$
$s_{v_2,W}$	Strength of hard viability selection	$0.5s_W$	$(0.0s_W,1.0s_W)$
$s_{v,H}$	Strength of domesticating viability selection	0.10	(0.06, 0.13)
$s_{f,H}$	Strength of domesticating fecundity selection	0.05	

et al. (2014) observed fitness declines between 30% and 60% in a single generation. These declines are attributed to both genetic (adaptation) and environmental effects (plasticity). The relative contribution of genetic and environmental effects varies by program and species (Araki et al. 2007; Williamson et al. 2010). We follow a prior modeling study (Willoughby and Christie 2019) and consider a range of fitness declines caused by genetic effects between 0.0% and 30% per generation, with a baseline value of 15%.

We calculate the relative fitness of hatchery-origin fish after one generation of hatchery production by first solving for the equilibrium genotype distribution of the population at birth under natural selection $\psi_W^*(g)$. We then calculate the genotype distribution of the first generation of hatchery fish $\psi_{g_1}(g)$ by applying the model of reproduction and domestication selection to the equilibrium genotype distribution after natural selection $\psi_W'''^*(g)$. We compute the relative fitness in the wild by comparing the average fitness of each population under natural selection.

$$(22) \quad Q_{g1} = \frac{\int_{-\infty}^{\infty} e^{-\frac{s_W}{2}(g-\theta_W)^2} \psi_{g_1}(g)\,dg}{\int_{-\infty}^{\infty} e^{-\frac{s}{2}(g-\theta_W)^2} \psi_W^*(g)\,dg}$$

where $s_W = s_{f,W} + s_{v_1} + s_{v,2}$ is the total strength of selection summed across the three selection events.

We used an optimization algorithm to solve for the strength of the domestication section events ($s_{f,H}$, $s_{v,H}$), optimum phenotype in the hatchery (θ_H), and the total strength of natural selection (s_W), which produced the target value of fitness decline. This optimization problem is over determined because we are tuning four variables to achieve one outcome. Therefore, we add additional constrains by specifying the expected effect of fecundity selection on the average fitness of wild-origin fish in the hatchery ($S_f = \int \psi_W^*(g) W_{f,H}(g)\,dg$), and the expected survival of the domesticating viability selection event ($S_v = \int \psi_{g_1}(g) W_{v,H}(g)\,dg$). We select the parameter combination that met these three constraints with the minimum strength of natural selection s_W, and distance between the optimum hatchery geno-

type θ_H and a target value $\bar{\theta}_H$. We solve the optimization problem using the Nelder–Mead algorithm implemented in the Optimization.jl package in Julia programming language (Bezanson et al. 2017).

The contribution of each natural selection event to the total selection strength s_W determines the effect of selection on demographic outcomes and geneflow. For the base parameter set we fix the value of the soft selection and fecundity selection event at $s_{f,W} = s_{v_1,W} = 0.25s_w$ with the rest contributed by the hard selection event $s_{v_2,W} = 0.5s_w$. We consider the effects of alternative parameter choices in the Supplemental material 2.

Demographic parameters

We chose the demographic parameters in our analysis (Table 2) to represent the life history characteristics of the mid-Fraser River white sturgeon population. We obtained information on growth, survival, maturation, and fecundity from population monitoring studies and previous demographic modeling exercises (RL&L Environmental Services, Ltd. 2000; Wood et al. 2007; Smyth et al. 2016). No information was available to estimate yearling survival rates or the strength of density-dependence. We tuned these parameters to fix equilibrium recruitment at 100 individuals per year, using the equilibrium conditions given in Supplemental material 3, and varied the strength of density-dependence to test the effects of uncertainty over this quantity on our results (Supplemental material 2).

We tuned the strength of density-dependence β and the yearling survival S_0 to adjust the strength of density-dependence without changing equilibrium recruitment (Supplemental material 4). These two changes, in turn, change the basic reproductive number of the population R_0 (i.e., the expected number of offspring produced in an individual's lifetime in the absence of density-dependence), with larger values of R_0 implying greater density-dependence (higher values of β). To improve the interpretability of our results we report these values of R_0 to represent the strength of density-dependence.

Table 2. Demographic parameters.

Parameter	Interpretation	Value	Range	Source
L_∞	Asymptotic or maximum length	300 cm		Smyth et al. (2016)
k	Von Bertlanffy growth coefficient	0.034		Smyth et al. (2016)
a_0	Length at age zero	0.0		
w_{100}	Weight at 100 cm	9.3 kg		Smyth et al. (2016)
w_m	Weight at maturation	33 kg		Smyth et al. (2016)
c	Size to fecundity conversion factor			Smyth et al. (2016)
μ_s	Age at 50% senescence	N.A.[a]	80	Wood et al. (2007)
σ_s	Slope of senescence at age relationship	N.A.	5	Wood et al. (2007)
S_a	Survival from age a to age $a+1$	0.96		Smyth et al. (2016)
R_0	Basic reproductive number	3.0	(1.5–9.0)	
N^*	Equilibrium population density	100		
S_0	Natural mortality of yearlings	N.A.		Determined by R_0 and N^*
β	Strength of density-dependence	N.A.		Determined by R_0 and N^*
b_a	Age dependent competition	Fig. S2.1		
$A_{\max}$	Maximum age	150		

[a]Set to values so that senescence does not influence the fecundity-at-age relationship.

Table 3. Simulation parameters.

Parameter	Interpretation	Value	Range
r_H	Annual proportional hatchery immigration	0.5	(0.0, 1.0)
T	Hatchery duration	100	(0, 250)

Simulations

We numerically iterated eqs. 1–18 to characterize the recipient population's response to immigration by hatchery-origin fish. We developed numerical procedures to approximate the genotype distribution in the Julia programming language (Bezanson et al. 2017). A detailed description of these methods is in Supplemental material 5. We initiated each simulation with the population at equilibrium without a hatchery, iterated forward in time for $T \in (0, 250]$ years with annual proportional immigration from the hatchery of $r_H \in (0, 1]$. We then simulated another 20 generations without immigration to evaluate the recovery dynamics, where generation times are calculated from the fecundity and natural mortality parameters (Supplemental material 6). For each simulation, we tracked four statistics that summarized the genetic and demographic state of the population: (1) we characterized changes in abundance by tracking annual recruitment $N_{1, W, t}$, and we described changes in the genotype distribution with (2) the average fitness $\bar{W}_{W, t}$, (3) the mean genotype $\bar{g}_{1, W, t}$, and (4) the genetic variance $V_{1, W, t}$. We extracted the minimum fitness $\bar{W}_{\min}$, minimum abundance $N_{\min}$, and cumulative immigration $r_H \times T$ from each simulation to characterize the maximum effect of the hatchery program.

Sensitivity analysis

We used a local sensitivity analysis to identify the effects of the genetic and life history parameters on the cumulative fitness effects of straying by hatchery-origin fish. To account for the effects of immigration rate r_H and the duration of the hatchery program in years T we calculated the difference between the equilibrium fitness and the minimum fitness $\Delta \bar{W}(r_H, T) = \bar{W}_W^* - \bar{W}_{\min}$ across the range of values of r_H and T. We found this was well approximated by a log-linear function $\Delta \bar{W}(r_H, T) \approx \alpha r_H T^2$, where the parameter α determined the magnitude of the genetic effects for a given combination of r_H and T. We tested the sensitivity of the parameter α to the genetic and life history parameters of the model using a local sensitivity analysis where the elasticity of α to a parameter θ is defined as $\lambda_\alpha(\theta) = \frac{\theta}{\alpha} \frac{\partial \alpha}{\partial \theta}$. We computed the slope coefficient α of the log-linear relationship using the GLM package in Julia and the partial derivatives with finite differences (Bezanson et al. 2017).

Mitigation measures

We evaluated the effectiveness of three approaches to reducing the fitness effects of the hatchery: (1) reducing the annual proportion of the hatchery-origin fish r_H, (2) reducing the duration of hatchery supplementation T, and (3) removing hatchery-origin individuals after they have immigrated. For hatchery emigration and duration, we characterized the effect of a small reduction in each factor on the minimum fitness $(\bar{W}_{\min})$ by calculating the elasticity of $\bar{W}_{\min}$ to r_H and T $\left(\text{i.e. } \frac{r_H}{\bar{W}_{\min}} \frac{\partial \bar{W}_{\min}}{\partial r_H}, \frac{T}{\bar{W}_{\min}} \frac{\partial \bar{W}_{\min}}{\partial T}\right)$ across the range of r_H and T values given in Table 3. We calculated the derivatives for these elasticity values using the finite difference method (Khan and Ohba 2000). For removal of hatchery-origin strays, we solved for the number of removals required to reduce the fitness loss by 50%. To this end, we defined a function that returns the maximum fitness loss $\mathcal{L}(E, \boldsymbol{q}) = \bar{W}_w^*(E, \boldsymbol{q}) - \bar{W}_{\min}$ as a function of the total removal effort E and the catchability of each age class $\boldsymbol{q}$. We applied the bisection algorithm (Roots.jl package) to solve for the level of removal effort E^* required to reduce $\mathcal{L}$ by 50% for a given vector of catchabilities a. We then calculated the total removals by simulating the model with removal effort E^* summing the total removals in each period. The effect of removing individuals was largely determined by

Fig. 2. Time series of the (A) fitness, (B) recruitment, (C) mean genotype, and (D) genotype variance of the wild population under the default parameter values in Tables 1–3. The red shading indicates the period of hatchery operation. Note that the *y*-axis scale for both fitness (A) and recruitment (B) have high minimum values.
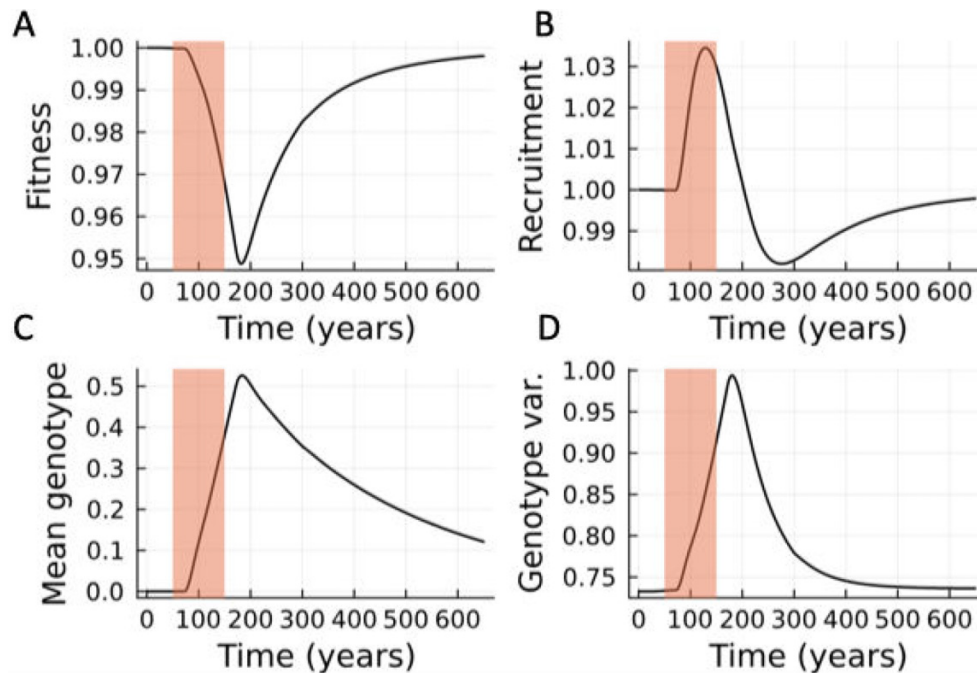
their age class. To help interpret these results, we calculated the expected geneflow caused by a single hatchery-origin individual from each age class (Supplemental material 7).

Results

Transient dynamics in fitness effects and demographic outcomes

Our model captures a small decline in recruitment of the wild population (∼2%) after 100 years of hatchery production (Fig. 2B) owing to a decline (∼5%) in fitness (Fig. 2A). Geneflow from the hatchery shifts the genotype distribution of the wild population away from the local optimum and increased the genetic variance, which together reduces the average fitness (Figs. 2C and 2D). We found a substantial delay between when hatchery production occurred and the eventual decline in abundance (Fig. 2B). Hatchery stocking can create a demographic boost that leads to increased abundance in the short run, followed by a decline caused by the reduction in fitness. The minimum abundance often occurred over 100 years after hatchery production ended. This delay between the end of hatchery production and the eventual decline in abundance depended on the strength of density-dependence measured by the basic reproductive number. Smaller values of R_0 lead to longer delays between the decline in fitness and the eventual demographic response (SI Fig. S1) because density-dependence is weaker, which strengthens the feedback between the population's reproductive potential and future population sizes.

The decline in abundance also depends on the timing of selection, relative contribution of genetic and plastic environ-

mental effects to the fitness declines of hatchery fish, and the effective strength of natural selection on genotypes (Figs. S2–S4). The largest declines in abundance occur when viability selection acts after density-dependent mortality (Fig. S2), because selection before density-dependence has a minimal effect on population sizes if the post-selection population is near or above carrying capacity, while selection after density-dependence always affects population size. The contribution of environmental factors to the fitness declines of hatchery fish (Δ) mitigates the abundance declines in the wild population by reducing geneflow from the hatchery (Fig. S3). Finally, lower effective selection strengths on genotypes $(s^*_{v,W})$ increase the abundance declines by increasing the amount of time required for the population to adapt back to the optimum phenotype after hatchery releases ends (Fig. S4). These differences in effective selection strength $(s^*_{v,W})$ could either represent weaker selection on the phenotype or greater environmental variation contributing to the phenotype (lower heritability of the trait).

Effect of immigration rate and hatchery duration

Minimum fitness and recruitment decreased with increasing hatchery duration (T) and immigration (r_H), and the smallest values of fitness and abundance occurred when both parameters (T and r_H) were large (Figs. 3A and 3B). Based on the simulations, the effect on fitness increased linearly with the rate of immigration and with the 3/2 power of the duration of the hatchery program ($T^{3/2}$), while the effect on recruitment increased linearly with the rate of immigration (r_H) and with the square of duration (T^2; Figs. 3C and 3D). These exponents have values greater than one which implies that increasing

Can. J. Fish. Aquat. Sci. **82**: 1–15 (2025) | dx.doi.org/10.1139/cjfas-2023-0355

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Fig. 3. Effects of the immigration rate and duration of hatchery production on fitness and recruitment in the wild population. Panels (A) and (C) are heat maps showing the minimum fitness values and recruitment as a function of immigration proportion r_H and hatchery duration T. Panels (B) and (D) plot the same data as a function of the production of r_H and T^α. This illustrates that the fitness and demographic effects of the hatchery depend on the interaction effect of immigration proportion r_H and duration T with duration playing a larger role. Panel (E) shows the effect of the biological parameters of on the minimum fitness of the wild population from the local sensitivity analysis.
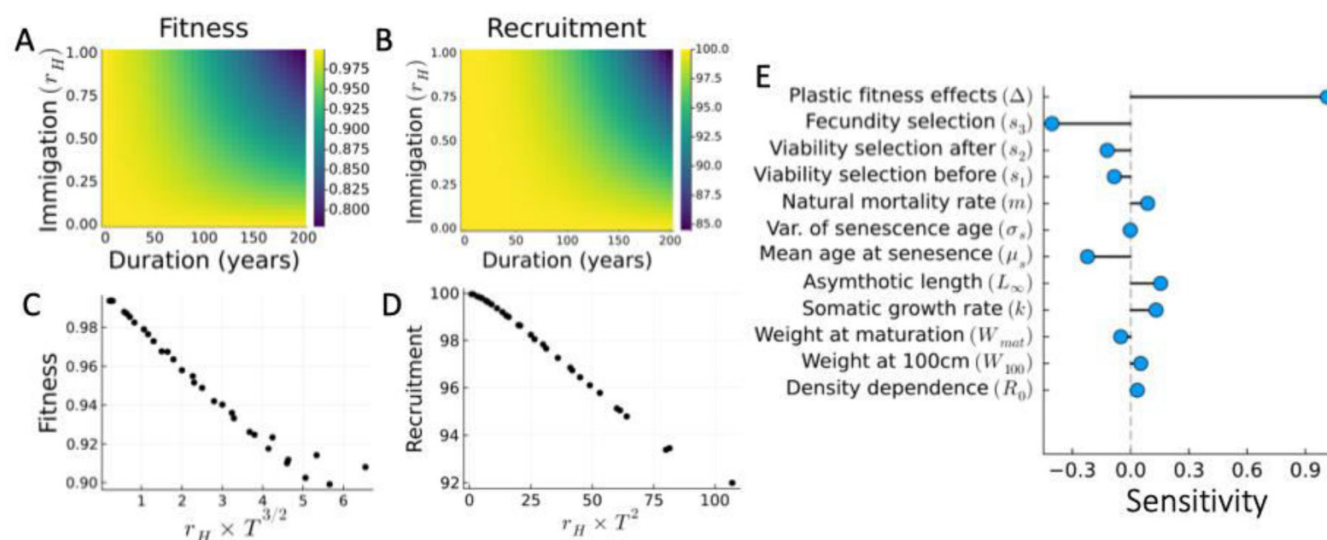
duration disproportionally affects outcomes. The convex relationship between hatchery duration and fitness effects occurs because the duration of the program determines the number of generations in captivity and, therefore, the level of domestication as well as the cumulative number of immigrants and geneflow to the wild population. In contrast, the rate of immigration only affects the amount of geneflow from the hatchery.

Effect of biological parameters on changes in fitness

In the local sensitivity analysis, both the genetic and demographic parameters determine the genetic impacts of the hatchery program (Fig. 3E). Of the genetic parameters, the plastic effects of the hatchery (Δ) and the strength of fecundity selection (s_3) have the largest effect on the accumulation of fitness effects because these two mechanisms determined the efficiency of geneflow from the hatchery to the wild population. The strength of the viability selection also reduced the genetic impacts of the hatchery by limiting geneflow. They do so to a lesser degree, however, because viability selection does not act directly on hatchery-origin fish; rather, it affects their progeny.

The fitness effects of the immigration by hatchery-origin fish are also determined by the generation time of the population. The demographic parameters with the largest impact were the somatic growth rate (k), asymptotic length (L_∞), age at senescence (μ_s), and the natural mortality rate (m), which interact to determine the generation time. Longer generation times lead to smaller fitness effects. This can be explained in two ways. First, fitness effects accumulate more slowly in long-lived species. Therefore, given a fixed duration of hatch-

ery operation, we expect lower total impacts in longer lives species. Second, in longer-lived populations, the age structure acts as a buffer, reducing the genetic impact because each year class contributes less (in proportional terms) to the total reproductive potential of the population.

Effects of alternative mitigation strategies

We found that reducing the duration of hatchery operation and reducing the immigration rate of hatchery-origin fish were similarly effective strategies for mitigating the genetic effects of hatchery production (Figs. 4A and 4B), but the effects of a small change in each depended on both the immigration rate and the planned duration of the program. Reducing the immigration rate resulted in the largest increase in fitness when the planned duration of the program was long and when the initial immigration rate was low (Fig. 4A). The relationship between the initial immigration rate and the effect of a small change is caused by a saturating relationship between the immigration rate and the minimum fitness of the wild population. As the immigration rate increases, the fitness effects approach a maximum value. Near this point, small reductions in geneflow have a limited impact on the wild population. In contrast, we found that reducing the duration of the hatchery program was most effective when immigration rates were high (Fig. 4B). This is likely because when geneflow is high, the domestication of the hatchery population (which increases over time) more directly impacts the wild population.

Translocating or removing hatchery-origin individuals can also mitigate the fitness effect of hatchery releases, but the strategy's effectiveness depends on the age of the removed individuals (Figs. 4C and 4D). Removing older individuals had

Fig. 4. The effects of mitigation strategies. The marginal effect of reducing the immigration rate from the hatchery (A) and the duration of the hatchery (B) on the minimum fitness of the wild population. (C) The total number of adults (age 20 and over) and (D) juveniles (age 19 and under) removed to achieve a reduction in the genetic load by 50%. (E) The expected reduction in reproductive success of an individual, and thus reduction in geneflow, caused by caused by removing a hatchery-origin individual as a function of its age for two alternative sets of demographic parameters, one with senescence (dashed line) and one without senescence (solid line).
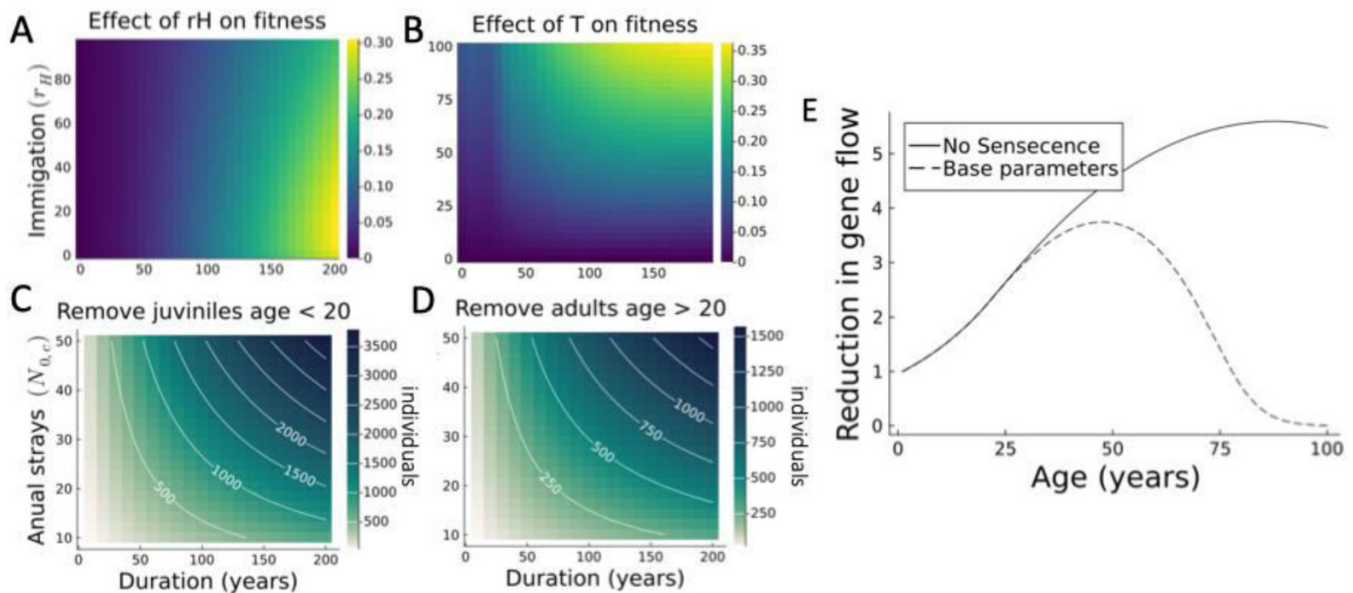
a larger effect because they had higher expected lifetime reproductive potential (Fig. 4E). An older mature individual is more likely to reproduce successfully, affecting the genetic state of the population. In contrast, a young individual that is removed would have had a higher probability of dying before it reproduced (Fig. 4E). Removing very old individuals also had a small effect if they had reached the age of senescence.

Discussion

Our model shows that even temporary hatchery programs can create long-lasting effects on the fitness and abundance of wild populations, but the longevity of the species, strength of domestication selection, and duration of the program strongly influence the magnitude of those impacts. In our model, geneflow from hatchery-origin individuals that immigrate results in a decline in fitness in the adjacent wild population, an expected outcome given the parameterization based on evidence for domestication and a decline in relative fitness of hatchery populations (Christie et al. 2014). Once hatchery operations end, natural selection causes the fitness of the wild population to eventually recover back to the optimum, given the available genetic variance in our model. Over the range of parameter values we considered, geneflow is a stronger force than selection, causing genetic effects to accumulate quickly in the wild population and recover more slowly back to the original fitness, resulting in long-lasting impacts. Furthermore, the age-structured dynamics of the population caused the maximum demographic impacts on

the wild population to occur long after the hatchery program ended, which might make it difficult to detect the negative impacts of the hatchery program before the consequences are baked in.

Despite this potential for long-term impacts, we found that the maximum genetic effects of temporary hatchery programs in our long-lived example species were much smaller than the potential long-run impacts if stocking continued indefinitely (Ford 2002; Baskett and Waples 2013). Therefore, limiting the duration of captive breeding programs can be an effective strategy for mitigating unintended fitness consequences. Doing so reduces the time required for domestication to occur in the hatchery environment and the total amount of geneflow from the hatchery population to the wild, limiting the overall genetic load.

The duration of captive breeding is one of several interacting risk factors identified in the case study of Nechako white sturgeon. The combined effects of the relative fitness of hatchery-origin individuals, the immigration rate, the program duration, and the population's generation time determine the scale of genetic risks. Risks from each of these factors roughly combine in a roughly multiplicative fashion, which means that low levels of risk from only one factor can offset high values of the other three. For example, careful genetic management and cultivation practices can reduce domestication (Hess et al. 2012; Janowitz-Koch et al. 2019). In these cases, the genetic risk of captive breeding can be small even if it lasts for many generations and straying is high. Conversely, reducing the duration of captive breeding can offset cultivation practices that increase the risk of do-

mestication. For example, currently (in 2024), Nechako River hatchery sturgeon are released at 2 years of age to increase survival. While this practice might increase domestication selection, the long generation time of the species (white sturgeon mature between age 20–40 years on average) acts to offset these risks. Finally, if logistically feasible, removals from non-target populations can also reduce the rate of geneflow, offsetting high values of immigration, domestication, and duration. We found that the effectiveness of removing individuals increased with their age because the expected reproductive success (and thus geneflow) tends to increase through an individual's life cycle.

The population's life history characteristics determined outcomes by changing the time scale of the population dynamics. We found that both the rate of accumulation of genetic load and the rate of recovery are a function of the population's generation time. Willoughby and Christie (2019) found a similar result for the effects of hatcheries on fitness and genetic diversity with an individual-based model by comparing species with different life histories. Measuring the duration of captive breeding in terms of generations (rather than years) can largely account for these effects of life history and the difference between species. For example, all else equal, 40 years of hatchery production of white sturgeon would have a similar effect to 4 years for Chinook salmon (*Oncorhynchus tshawytscha*), given the differences in the species generation times (the numbers of years chosen roughly corresponds to one generation for each species). Re-scaling time in this way allows us to draw a rough equivalence between the dynamics of populations with very different life histories. Interestingly, models of the long-term effects of aquaculture escapees show that long-lived species can be more sensitive to the fitness consequences of geneflow due to greater total accumulation of fitness effects over their lifespan (Yang et al. 2019), further emphasizing the differences between the long-run and transient dynamics of the system.

Implications for adaptive management

The time scale of population dynamics relative to the time scale of management interventions can determine the effectiveness of such interventions. In the case of the Nechako River white sturgeon system, a mismatch in these time scales might provide an opportunity. Because fitness effects accumulate slowly, captive breeding can maintain recruitment in the Nechako River population for a long period with relatively low risks to neighboring populations, thus providing time to identify and address the root causes of the recruitment failure. In shorter-lived species, restoration efforts might take the same amount of time as they would for longer-lived species due to similar levels of scientific uncertainty and bureaucratic delays. The genetic effect of captive breeding, however, would accumulate more quickly. Longevity, therefore, can strongly affect the balance between conservation benefits from hatchery production and genetic risks.

The time scale of population dynamics can also determine the ability of managers to learn and adapt. In this system, managers face the dual goals of promoting recovery in the Nechako River (the focus of Smyth et al. 2016) while mit-

igating unintended consequences for the Fraser River (our focus here), with potential trade-offs between the two. In the first years of operation, the Nechako River hatchery released large numbers of yearling sturgeon, observed high natural mortality, and detected emigration to the mid-Fraser River. In response, the program shifted to releasing fewer larger individuals, causing an apparent decline in both mortality and emigration. In a short-lived population, these initial year classes could have caused larger decreases in fitness in the mid-Fraser River, if they interbred before managers could have observed and responded to the event. In the Nechako River Sturgeon system, however, the impact of these cohorts is likely to be relatively small because each year class contributes less to the total reproductive potential of the population. In this case, each year provides an opportunity to learn, and because the population dynamics are slow, adaptive management approaches (sensu; Walters and Holling 1990) can be employed quickly relative to the rate at which impacts accumulate.

The spatial ecology of the population is a particular promising direction for adaptive management of the Nechako sturgeon population because the causes of emigration from the Nechako are uncertain. Emigration may be a direct consequence of hatchery production (due to developmental effects or transport of hatchery-reared fish affecting imprinting ability and opportunities; Keefer and Caudill 2014), a density-dependent response to the large numbers of individuals released from the hatchery in the initial cohorts (Berdahl et al. 2016), or a previously unknown natural aspect of the population's migratory patterns. Which mechanism is the most relevant will affect management approaches to mitigating emigration. If cultivation practices cause strays, then more acclimation of fish before release or closer mimicking the natural environment in the hatchery might effectively mitigate emigration. If staying is a density-dependent response, then managing the number of individuals released might be more effective. However, such approaches are only relevant if hatchery rearing affects emigration rather than if emigration occurs as a natural part of the population's life history.

Limitations and assumptions

As with all modeling studies, ours involves simplifying assumptions, and the interpretation of our results depends on this context. The quantitative results of our model are sensitive to the value chosen for the fitness declines of hatchery-origin fish in the natural environment. There is a substantial body of evidence suggesting that differences in relative fitness can arise from both domestication selection and plastic environmental effects (Araki et al. 2007; Christie et al. 2012). However, the cumulative fitness declines and the relative contribution of genetic and environmental effects vary between systems (Christie et al. 2014), and measurements of these quantitates are not available in our study system. This limits the quantitative precision of our model estimates. Our qualitative findings about the relative effectiveness of the alternative mitigation measures and the effects of life history traits, however, are robust to this source of uncertainty. Furthermore, the scenarios with high estimated fitness effects

likely represent an upper bound on the potential impact of the program, given that much of the uncertainty is associated with mitigating factors such as the timing of natural selection and the relative contribution of environmental effects on fitness.

In addition to parametric uncertainty, our model uses a simplified representation of the population's genetics. We assume the effects of domestication can be represented by a single quantitative trait. This model captures the additive fitness effects of domestication selection, but it also assumes there is sufficient genetic variation for the population to recover back to the wild phenotypic optimum once hatchery production ends. In a small population, however, unfavorable alleles might reach fixation through genetic drift, permanently limiting the population's ability to recover (Lande 1998; Castellani et al. 2018). These mechanisms related to a finite population size could be incorporated by using an individual-based modeling framework (e.g., Jager 2005). Furthermore, if multiple traits are under selection, differences in selection strengths and heritability between these traits can result in quantitative changes in the accumulation of genetic load accumulation and recovery. However, our single-trait model likely captures the essential qualitative features of these processes (Tufto 2010, 2017).

Our model also makes several simplifying assumptions about the population's ecology. We assume that the primary ecological interactions between hatchery and individuals of natural origin occur before recruitment. This is consistent with a meta-analysis that shows density-dependent mortality declines in fish populations with age (Lorenzen and Camp 2019). It does not, however, account for other interactions that might operate throughout the life cycle. For example, competition between juveniles and adults could reduce growth, maturation rates, and fecundity. The presence of hatchery-origin fish in a population can also increase the risk of disease and attract predators (Kostow 2009). Incorporating these processes was beyond the scope of our study, but they might play an important role in the demographic effects of hatchery production.

Finally, our model presents a highly simplified representation of the spatial and movement ecology of our study organism. We represent the hatchery and wild populations in our model as two distinct populations separated by a clearly defined boundary; however, these boundaries might be less clear in many real-world systems with multiple populations characterized by patterns such as isolation by distance. Furthermore, we assume that all movement occurs before maturation and that fish do not exhibit homing behaviors, returning to their river of origin to reproduce. It is currently unknown whether the hatchery-origin fish that have emigrated from the Nechako River will remain in the mid-Fraser River throughout their life cycle or return to the Nechako to reproduce. If some hatchery fish do return to the Nechako River, geneflow impacts will be reduced; however, ecological impacts from hatchery fish using the mid-Fraser River habitat would remain. More detailed information about habitat uses and spawning behavior would help reduce uncertainty about the extent of the genetic and ecological effects of the hatchery program.

Conclusions

In our modeled case study, the long-lived life history of white sturgeon caused the genetic effects of hatchery production to accumulate slowly over time. Given that captive breeding is expected to be a temporary measure in this system, the slow time scale of the population's dynamics is a dominant factor determining the level of genetic risks. This highlights the general importance of time scales and the management of ecological systems. Models that only account for a population's biology often explicitly ignore the time scale of the system's dynamics by studying equilibrium behaviors and rescaling (non-dimensionalizing) the units of time. Although these can be useful methods in some cases, in an applied setting, the time scale of the ecological system's dynamics can influence the options available to managers. In our case study, the relatively slow time scale of the population's dynamics provides a long window of time for managers to learn and address the root causes of the population's decline, with a relatively limited risk of unintended genetic consequences compared to shorter-lived species. In effect, the time scale of the biological system becomes important in an applied context because of its interaction with the time scale of the management system.

Acknowledgements

Article information

History dates

Copyright

Data availability

Code to run the genetic–demographic model and reproduce the simulation analysis is available on GitHub: https://github.com/Jack-H-Buckner/Nechako-Sturgeon-Hatchery-Model.

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Competing interests

The authors have no competing interests to declare.

Funding information

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0355.

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