

Genetic and demographic implications of aquaculture in white sturgeon (*Acipenser transmontanus*) conservation

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Abstract: This study uses a genetic individual-based model of white sturgeon (*Acipenser transmontanus*) populations in a river to examine the genetic and demographic trade-offs associated with operating a conservation hatchery. Simulation experiments evaluated three management practices: (i) setting quotas to equalize family contributions in an effort to prevent genetic swamping, (ii) an adaptive management scheme that interrupts stocking when introgression exceeds a specified threshold, and (iii) alternative broodstock selection strategies that influence domestication. The first set of simulations, designed to evaluate equalizing the genetic contribution of families, did not show the genetic benefits expected. The second set of simulations showed that simulated adaptive management was not successful in controlling introgression over the long term, especially with uncertain feedback. The third set of simulations compared the effects of three alternative broodstock selection strategies on domestication for hypothetical traits controlling early density-dependent survival. Simulated aquaculture selected for a density-tolerant phenotype when broodstock were taken from a genetically connected population. Using broodstock from an isolated population (i.e., above an upstream barrier or in a different watershed) was more effective at preventing domestication than using wild broodstock from a connected population.

Résumé : Un modèle génétique basé sur l'individu de populations d'esturgeons blancs (*Acipenser transmontanus*) dans une rivière permet d'étudier les compromis génétiques et démographiques associés à l'opération d'une pisciculture pour fins de conservation. Des expériences de simulation évaluent trois pratiques de gestion, (i) l'établissement de quotas pour équilibrer les contributions familiales afin d'essayer de prévenir la submersion génétique, (ii) un schéma d'aménagement adaptatif qui interrompt l'empoissonnement lorsque l'introgression dépasse un niveau prédéterminé et (iii) des stratégies de sélection de stocks reproducteurs de rechange qui influencent la domestication. La première série de simulations, destinée à évaluer l'équilibre des contributions familiales, ne démontre pas les bénéfices génétiques attendus. La deuxième série de simulations montre qu'un aménagement adaptatif simulé ne réussit pas à contrôler l'introgression à long terme, particulièrement avec une rétroaction incertaine. La troisième série de simulations compare les effets de trois stratégies de rechange de sélection des stocks reproducteurs sur la domestication en fonction de caractéristiques hypothétiques favorisant la survie précoce reliée à la densité. Une aquaculture simulée sélectionne un phénotype tolérant à la densité lorsque les stocks reproducteurs sont tirés d'une population possédant des liens génétiques. L'utilisation de stocks reproducteurs provenant d'une population isolée (c.-à-d., en amont d'une barrière en rivière ou dans un autre bassin hydrographique) est plus efficace pour prévenir la domestication que l'utilisation d'un stock reproducteur sauvage provenant d'une population apparentée.

[Traduit par la Rédaction]

Introduction

The original purpose of aquaculture was to increase fish harvest. Theoretical studies of hatchery operation predicted that stocking would increase sustainable levels of harvest (e.g., Botsford and Hobbs 1984). The authors concluded with the reminder that this result depends critically on the assumption that "stocked fish are identical to natural fish".

Today, aquaculture has acquired a new purpose: preventing the extinction of dwindling fish populations whose spawning habitat has been degraded. Conservation aquaculture is preventing the extinction of some fish populations. However,

aquaculture has failed to prevent declines in many stocks, particularly among Pacific salmon (*Oncorhynchus* spp.) (Meffe 1992; National Research Council 1996). This reflects failure to treat root causes of decline, such as habitat loss, which can be masked by stocking.

Perhaps the most significant long-term risk associated with aquaculture is that of evolving a domesticated animal with little in common with its wild precursor and subsequently losing the wild species. The idea that hatchery and wild fish are genetically different is controversial. In 2001, US District Judge Michael Hogan removed coho salmon (*Oncorhynchus kisutch*) along the Oregon coast from protection

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under the US Endangered Species Act claiming that hatchery and wild fish within the same region are genetically identical. Some scientific studies have shown genetic changes owing to aquaculture, including changes in gene frequency, and loss of unique, locally adapted phenotypes (Hansen and Loeschcke 1994; Reisenbichler et al. 2004).

Genetic differences in hatchery fish have also been shown to reduce fitness in the wild. For example, aquaculture has been shown to select for traits such as faster early growth in captivity (Reisenbichler et al. 2004), slower adult growth in the wild (Johnsson et al. 1996), reduced spawning success (Fleming and Gross 1994), poorer avoidance of predators (Berejikian et al. 1995; Jonsson et al. 2003; Yamamoto and Reinhardt 2003), increased fecundity, and smaller egg size (Heath et al. 2003).

Previous studies have studied the consequences of stocking fish with lower fitness for a single trait under selection using quantitative genetic models (e.g., McKenna 2000; Ford 2002). This study uses an individual-based model with genetics (IBM+G) to evaluate the demographic and genetic implications of several management practices in conservation aquaculture. The management practices considered include (i) equalizing family contributions from the hatchery, (ii) adaptive management, and (iii) three broodstock selection strategies. All are considered for a target river segment with and without natural recruitment. The main question of interest here is how hatchery operation contributes to demographic benefits and genetic costs to a population's viability. Second, this study seeks to find management practices that shift the balance to maximize demographic benefits and minimize genetic costs.

Aquaculture and white sturgeon (*Acipenser transmontanus*)

The effects of aquaculture have been extensively studied in salmonids. Extrapolating results from salmon to sturgeons, or other fishes with a dramatically different life history, may not be valid (Anders 1998). Studies of aquaculture effects on fishes with different life histories are therefore needed.

Efforts have been proposed worldwide to restore sturgeon populations through the use of hatcheries to supplement natural reproduction and to reintroduce sturgeon where they have become extinct (Stabile et al. 1996). Among white sturgeon, conservation aquaculture has been implemented in an effort to restore the Kootenai River population (Ireland et al. 2002) and those in the Upper Columbia River. Concerns about the genetic consequences are favoring caution and deliberation before instituting similar programs in other rivers, including the Snake River.

This study uses the Shoshone reach of the Snake River as a starting point and goes on to seek more general results. The Shoshone reach extends 56.5 km from Shoshone Falls, a natural barrier to upstream movement, to Upper Salmon Falls Dam and includes 46 km of free-flowing river. This reach evidently supports no natural recruitment, although it supports a population of between 574 and 1201 sturgeon (Lepla et al. 2002). The Shoshone population has a bimodal age distribution with a few wild adults and many subadult hatchery fish.

Two factors believed to limit this population are insufficient flow and lack of adult fish (Idaho Power Company 2003). Given enough spawners, successful recruitment will depend on whether habitat and flows are adequate to support natural reproduction in the river. Much of the flow is diverted for irrigation above Shoshone Falls. Spring recharge improves conditions in the lower part of the reach and should provide adequate flow conditions for spawning and rearing during high-flow years (Idaho Power Company 2003). As hatchery sturgeon reach maturity (circa 2008), we will discover whether suitable flows occur frequently enough to restore this population. If not, resource managers would consider the costs and benefits of operating a conservation hatchery. This study could help to guide decisions once the potential for natural recruitment is determined.

Methods

This study uses an IBM+G developed for white sturgeon to simulate the effects of conservation hatchery operations on populations in the Middle Snake River. The model has an annual time step and represents connected populations in a series of adjacent river segments separated by dams. Only downstream migration is possible between segments. Within each segment, the model tracks individuals from age 1 onward, including survival and reproduction. The main features of the model are described elsewhere (Jager 2001; Jager et al. 2002). Here, I describe new model features and changes required for these simulation experiments (parameters are listed in Tables 1 and 2).

Various sources of mortality are represented in the model, including some caused by human activities. In these simulations, age-0 fish are exposed to four mortality risks: baseline, density-dependent, and temperature-related mortality and larval export. Simulated juvenile and adult fish are exposed to up to six mortality risks: baseline risk (S_j and S_a), turbine strike, mortality of broodstock ($S_{\text{hatch},a}$), mortality of excess hatchery juveniles, and hooking mortality (S_{hook}). Jager et al. (2002) described how these risks are modeled in more detail.

This study focuses specifically on juvenile density-dependent mortality, which is represented by parameters that differ among individuals. This mortality is applied in both the hatchery and river environment as described below.

Density-dependent juvenile survival

This paper focuses on hypothetical traits controlling density-dependent juvenile survival. This choice reflects the concern that hatchery supplementation alters the balance that has evolved between traits that enhance survival at high densities and those that enhance survival at low densities. Because densities reach higher levels in the hatchery environment, selection for traits that enhance fitness at high densities is likely. Specific traits are not simulated here, but disease resistance, starvation resistance, and aggressive feeding are three examples of traits that are likely to be more adaptive at high densities. Differences between some of these traits have been documented. For example, selection for competitive feeding ability has been observed among salmon (Berejikian et al. 1995; Yamamoto and Reinhardt 2003). Two studies of density effects on captive white

Table 1. Parameter values used in these simulations of the white sturgeon (*Acipenser transmontanus*) population viability analysis model.

Name	Parameter description	Baseline value
Hatch _{years}	Years juveniles in hatchery before release	2
T _{hatch}	Tank capacity inflated for high ration (km)	1.0
D _{max}	Fish·km ⁻¹ at which density-dependent mortality begins	100.0
S _{1st year}	First-year survival rate in river (year ⁻¹)	0.0002
S _j , S _a	Survival rate of juveniles and adults (year ⁻¹)	0.885
S _{hatch,j}	Survival rate of hatchery juveniles (year ⁻¹)	0.005
S _{hatch,a}	Survival rate for broodstock adults (year ⁻¹)	0.95
t _{0,survey}	Initial year of survey (years)	0
t _{int,survey}	Interval of surveys (years)	1
t _{effort,survey}	Effort for each pass 6 weeks × 3 days·week ⁻¹ × 8 h	144
N _{pass}	Number of passes in survey each year	4
Q	Quota, number of broodstock captured per year	6
S _{hook}	Survival of hooking mortality	0.98

sturgeon revealed that high density increases the incidence of iridovirus disease (Georgiadis et al. 2000), which lowers juvenile survival (LaPatra et al. 1994). A study by Georgiadis et al. (2001) suggested that genetic resistance to iridovirus was inherited.

The hypothesis adopted here is that density-dependent juvenile survival acts on age 1–2 juvenile sturgeon in both the river and hatchery environments. However, differences in food availability and predation permit considerably higher survival at the same absolute density in the hatchery environment. This is accounted for in the model by scaling effective density in the two environments. In the river, fish density, *D*, is calculated by dividing the number of age-1 and older fish by kilometres of free-flowing river between Shoshone Falls and Upper Salmon Falls Dam. In the hatchery, each family is quartered in one tank (Ireland et al. 2002). Because juveniles are smaller and feeding rations are higher in a hatchery than in the river, tank capacity must be scaled up to at least 0.5 km in the model to yield reasonable numbers of surviving juveniles. Density is calculated by dividing the number of juveniles in one family by the diameter of a hypothetical tank, *K_h*.

Density-dependent survival is represented by a function with two parameters. Similar relationships have been developed from empirical early survival data for other fish species (e.g., Nickelson and Lawson 1998). I simulate these parameters as two traits controlled in part by the genes of each individual sturgeon. The two parameters are *S**, the maximum survival at low density, and *D**, the density at which density-dependent survival begins to decline. Survival is highest at low *D* and declines after *D* reaches a threshold, *D** (Fig. 1):

$$(1) \quad S = S^* \times \begin{cases} 1, & D \leq D^* \\ D^*/D, & D > D^* \end{cases}$$

Values of the two parameters (traits) differ from individual to individual, controlled, in part, by their genes and, in part, by random variation. The genetic model for these two traits (see below) assumes that individuals that are genetically su-

perior in their ability to survive at low densities (high *S**) are inferior in their ability to tolerate high densities (low *D**).

Genetic model

The Acipenseriformes are believed to have evolved from ancestral species with 60 chromosomes 300 million years ago (Birstein et al. 1997). The evolutionary history of white sturgeons may have involved several hybridization and gene duplication events followed by long periods of diploidization. Some studies suggest that the white sturgeon genome is octoploid (Birstein and Vasiliev 1987; Smith et al. 2002), and others suggest it is tetraploid (Fontana et al. 2001; Ludwig et al. 2001).

The genetic component of the IBM+G used here is involved whenever new individuals are created. This model has the ability to simulate (i) population dynamics that depend on individual attributes as well as inheritance and genetic drift, (ii) traits controlled by an intermediate numbers of alleles with different effects, (iii) multiple pleiotropic traits, and (iv) polysomic (but not mixed) inheritance.

Because the actual genetic architecture underlying the traits in eq. 1 is not known, we make the following simplifying assumptions: genetic and environmental contributions to each trait are independent, with additive genetic variation contributing to each trait. Let *Z* be a vector of traits for a new offspring. The value of the *k*th trait, *z_k*, is the mean trait value, *μ_k*, plus a deviation from the mean trait value, *z_k - μ_k*. This deviation has both a genetic (*Z_G*) and an environmental (*Z_E*) component:

$$(2) \quad \mathbf{Z} = \boldsymbol{\mu} + \mathbf{Z}_E + \mathbf{Z}_G$$

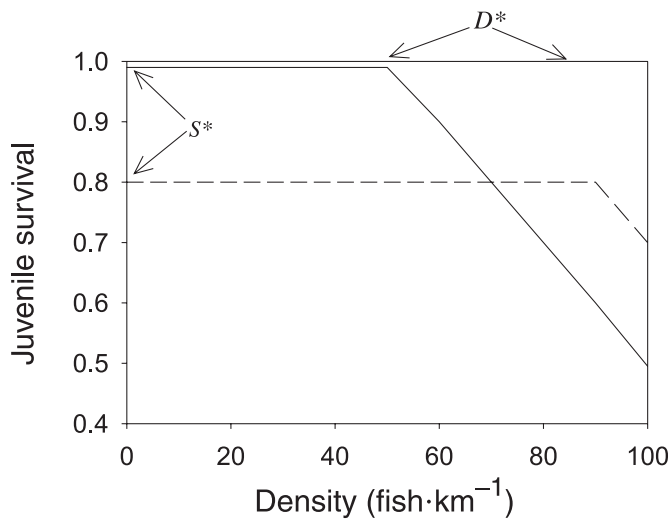
Individuals in the initial population derive their traits from a specified vector of trait means, *μ* = (0.9, 100.0), and standard deviations, *σ* = (0.05, 20.0). Heritability of each trait, *h²* = (0.3, 0.3), is also specified.

Understanding inheritance patterns in white sturgeon is an active area of research. Van Eenennaam et al. (1998) suggested that the species is functionally diploid based on the observation of bivalent pairing during meiosis in males.

Table 2. Relevant segment-specific parameters of the white sturgeon (*Acipenser transmontanus*) population viability analysis model.

Parameter	Hydrologic year	River segment below dam listed				
		Shoshone Falls	Upper Salmon	Lower Salmon	Bliss	C.J. Strike
Dam location (km)	All	989.26	932.75	922.13	901.69	794.99
Segment length (km)	All	56.51	10.62	20.44	106.7	58.41
Free flowing (km)	All	46.02	0.17	11.58	60.83	38.62
Average width (km)	All	0.134	0.21	0.13	0.22	0.28
Initial density (fish·km ⁻¹)	All	13.75	0.0	2.45	24.95	12.43
Initial % < 43 cm	All	57.9	0.0	71.0	8.0	16.4
Initial % = 43–183 cm	All	24.0	0.0	29.0	71.0	68.0
Initial % > 183 cm	All	18.1	0.0	0.0	13.0	15.0
Harvest effort (days·km ⁻¹)	All	7.72	7.72	7.72	30.44	45.09
Probability of release	All	1.0	1.0	1.0	1.0	1.0
Trashrack spacing (cm)	All	23	23	23	22.2	13.3
Probability of entrainment	Dry	0.96	1.0	1.0	1.0	1.0
	Normal	0.78	0.99	0.97	0.98	0.99
	Wet	0.52	0.95	0.86	0.87	0.94
Probability of strike	All	0.011	0.0048	0.0104	0.0111	0.0053
Retention time (days)	Dry	0.07	1.04	0.57	18.78	0.52
	Normal	0.05	0.76	0.47	15.57	0.41
	Wet	0.05	0.41	0.28	10.46	0.23
Temperature survival	Dry	0.981	0.990	0.987	0.983	0.984
	Normal	0.982	0.988	0.981	0.986	0.979
	Wet	0.975	0.942	0.969	0.940	0.944
Recruitment possible	Dry	0	1	1	1	1
	Normal	0	1	1	1	0
	Wet	0 or 1	1	1	0	0

Fig. 1. The trade-off between juvenile white sturgeon (*Acipenser transmontanus*) survival at low and high densities is represented as a function of two parameters: postulated relationships that would evolve in the river (solid line) and hatchery (broken line) environments.



Rodzen and May (2002) discovered residual polysomic inheritance at some loci, but they also determined that individual parental alleles were transmitted to roughly half of their progeny. A diploid model is therefore used here to approxi-

mate white sturgeon inheritance. Vector \mathbf{Z}_E describes the environmental component and vector \mathbf{Z}_G contains the genetic component of each trait. The \mathbf{Z}_E is assumed to be independent Gaussian with mean vector zero and variance-covariance matrix

$$(3) \quad \mathbf{V}_E = \begin{bmatrix} \frac{\sigma_1^2(1-h_1^2)}{\sqrt{M}} & 0 \\ 0 & \frac{\sigma_2^2(1-h_2^2)}{\sqrt{M}} \end{bmatrix}$$

Following Bulmer (1980) and others, the average genetic component is built from the additive effects, x_k , of alleles at M loci on trait k . For a particular locus, independent effects of each allele on each trait, z_k , are drawn from a standard normal distribution.

The genetic architecture assigned to these two traits assumes that individuals that are genetically superior for high-density, hatchery environment are inferior for the low-density river environment and vice versa. The specified genetic correlation, $\rho = -0.5$ (antagonistic pleiotropy), between the two traits is imposed on the vector of independent effects, \mathbf{z} , to obtain a vector of correlated allelic effects, $\mathbf{x} = \mathbf{L}\mathbf{z}$, where $\mathbf{V}_G = \mathbf{L}\mathbf{L}'$ (lower triangular matrix \mathbf{L} is the Cholesky decomposition of \mathbf{V}_G). Thus, allelic effects at each locus have variance-covariance matrix

$$(4) \quad \mathbf{V}_G = \begin{bmatrix} \sigma_1^2 h_1^2 & \rho \sigma_1 \sigma_2 \\ \rho \sigma_1 \sigma_2 & \sigma_2^2 h_2^2 \end{bmatrix}$$

Allelic effects are initially assigned for all simulated alleles, including those not present at the start of the simulation.

Vector \mathbf{Z}_G contains the additive genetic contributions to the two traits of each offspring:

$$(5) \quad \mathbf{Z}_G = \begin{bmatrix} \sum_{i=1}^M (x_{1,A(pa)} + x_{1,A(ma)}) \\ \sum_{i=1}^M (x_{2,A(pa)} + x_{2,A(ma)}) \end{bmatrix}$$

where A(pa) is the allele contributed to an offspring by the father and A(ma) is the allele contributed by the mother at locus i .

Initialization

Simulated individuals have a hypothetical genome containing 10 loci, each with an upper limit of 64 possible alleles. At the start of the simulation, the effects of each allele on each trait are drawn from a standard normal distribution. However, each initial population contains a restricted subset of alleles at each locus.

Each individual in an initial population draws a vector of alleles for each locus from a multinomial distribution of initial alleles in which all alleles are equally likely. Simulated populations in each river segment were assigned genomes with eight alleles, each with an initial frequency of 0.125. These frequencies change over time in response to selection, mutation, drift, and migration.

Four of the alleles present in the population are private, meaning that they occur only in one of the segments. The 56 remaining alleles may enter the population later through mutation.

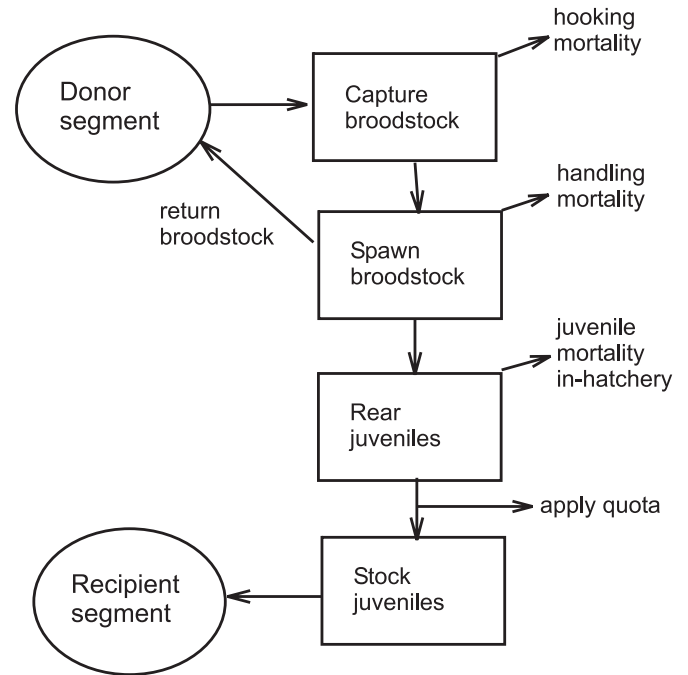
Mutation

Mutation is the only source of new genetic information for closed populations. Mutation rates for white sturgeon have been reported to be low (Birstein et al. 1997). The population model simulates genetic changes according to the stepwise mutation model of Kimura and Ohta (1978) with a mutation frequency of 10^{-5} per locus and generation. Each mutation increases or decreases the allele index by one unit. Because the order of allele indices is unrelated to their effects on a trait, the allelic effect resulting from mutation is unrelated to the effect of its wild precursor. Although included in the model, mutation plays an insignificant role in these simulations, which span a relatively short time period.

Conservation hatchery

Hatchery operation is represented by a submodule in the IBM+G that simulates four processes: (i) broodstock capture, (ii) spawning, (iii) juvenile rearing, and (iv) stocking juveniles (Fig. 2).

Fig. 2. Flow diagram showing the simulation of conservation hatchery operation.



Broodstock capture

Broodstock are captured from a specified river segment with a 1-year interval between attempts. The probabilities of capture and release are calculated using the same functions that simulate harvest. Captured individuals are subjected to a hooking mortality (survival, $S_{hook} = 0.98$) and a handling mortality (survival, $S_{hatch,a} = 0.95$). As with angling, either a quota, Q , or fishing effort can be specified for obtaining broodstock. These simulations used an annual quota of six adults, which could be any possible combination of males and females. Individuals not ready to spawn in the year that they are captured are released. In these simulations, individuals that survived hooking mortality were returned to the river segment of origin after breeding. Because so few adults are permanently removed, simulated quota-based removal did not significantly reduce the population lending broodstock.

Spawning

The model makes the simplifying assumption that all possible broodstock females are mated with all possible males and each cross is considered a family. For each family, the model calculates how many eggs survive to the end of the 1st year in the hatchery. Eggs produced by each female are divided equally among males to be fertilized. Average survival in the hatchery, $S_{hatch,j}$, is assumed to be 25 times greater than that of age-0 sturgeon in the river. The number of juveniles in each family is a binomial proportion of the family's eggs, with mean fraction $S_{hatch,j}$. This survival includes egg viability and other sources of mortality not explicitly modeled. As a result, some families have higher survival than others. Thus, at the end of the 1st year, variation in the number of juveniles among families is due to

variation in the female parent's survival and fecundity and juvenile survival in the hatchery.

Juvenile rearing

Juveniles are added to the main list of individuals tracked in the model. Each individual is assigned attributes, just as is done for offspring produced by natural reproduction, including information about its parents and its genes. Juveniles remain in the hatchery until they are stocked. After the 1st year, juveniles are exposed to a density-dependent mortality that increases with the size of the family. Density-dependent mortality is calculated based on family size because fry from different families are reared in separate tanks in the Kootenai hatchery (Ireland et al. 2002). Fry are kept in circular tanks with a 1- to 1.2-m radius, whereas age-1+ juveniles are kept in larger tanks (1.38- to 1.64-m radius). Mims et al. (2002) suggested a rearing density for juvenile sturgeon between 133 and 762 juveniles per metre radius.

Stocking juveniles

The hatchery submodel plants juveniles at a specified age. In these simulations, juveniles are kept in the hatchery for 2 years following the protocols of the Kootenai Conservation Aquaculture Program (Ireland et al. 2002). All hatchery juveniles in these simulations are stocked in the Shoshone Falls reach. The maximum number of individuals that may be planted per family cross is N_j ; excess juveniles are killed.

Simulated adaptive management

Adaptive management is a trial-and-error approach to managing populations when population responses to management changes are uncertain (Walters 1986). When large enough changes in policy are compared (Van Winkle et al. 1997), including both in the direction expected to benefit the population and in the direction expected to harm the population, this approach can facilitate learning about the relationships between management policies and population status. Sequential changes in the decision variable(s) are guided by feedback from empirical monitoring data.

Here, I use a model to simulate adaptive management with hatchery operation as the control knob. The management goal is to prevent harm to the donor and recipient populations by suspending hatchery operation when "bad" events are detected. Management is adaptive in the sense that the management action (i.e., to collect adults for supplementation or not) depends on feedback about the populations in the simulated river. When an event occurs that suggests that hatchery operation is adversely affecting the populations involved, operation of the hatchery is suspended.

In this demonstration, hatchery operation is suspended when (i) the density of the donor population falls below D_{adapt} or (ii) the proportion of alleles in the recipient population not present in the initial population, P , exceeds the threshold value of P , P_{alien} . In a year when either of these events occurs, no broodstock are captured but 2-year-old hatchery juveniles are planted.

Both population size and the proportion of alien alleles are estimated for the population from individuals sampled as a part of a simulated four-pass ($N_{\text{pass}} = 4$) annual survey. Surveys begin in year $t_{0,\text{survey}}$ and continue at $t_{\text{int},\text{survey}}$ inter-

vals with effort $t_{\text{effort},\text{survey}}$. Population size (used to estimate density) is estimated using a Schnabel estimate. Allele frequencies of the population are assumed to be the same as those in the sample (sturgeon captured as part of the mark-recapture survey, excluding recaptures). Simulations used for this comparison did not impose a quota on the number of juveniles released per family. These are neutral-genetic simulations: traits are assumed not to be heritable.

Simulation experiments

Initial conditions are the population densities and length structure for five segments between Shoshone Falls and Brownlee Dam based on recent surveys. The initial density in the Shoshone segment is $13.75 \text{ fish}\cdot\text{km}^{-1}$. Simulations were run for 500 years with initial conditions and parameters shown in Tables 1 and 2. I simulate a baseline scenario with no stocking for each scenario described below. The population between Bliss and C.J. Strike dams (the C.J. Strike reach) is the only one in this stretch of river that is potentially large enough to use as a source of broodstock adults. It also has the most reliable natural recruitment upstream of Hell's Canyon Dam (Coutant 2004). Therefore, this population is used as the donor of broodstock adults in most simulations.

Two types of simulations are presented: neutral simulations that do not involve evolution of density-dependent survival ($h_1^2 = h_2^2 = 0.0$) and evolution experiments that do ($h_1^2 = h_2^2 = 0.3$). For the neutral experiments, I examine genetic effects on neutral alleles, such as genetic diversity within and among populations, and alien versus original alleles and retention of private alleles that may control unique adaptations to a particular site. For simulations involving hatchery operations, broodstock were collected annually.

Model predictions

For each simulation experiment, I report the average and standard error of model predictions obtained from 100 replicate simulations. In most cases, the final value at the end of 500 years is reported. The main predictions of interest in simulations of family equalization and adaptive management practices include (i) final sturgeon density, (ii) introgression as measured by final number of alien alleles, (iii) preservation of original alleles, and (iv) genetic swamping as measured by maximum gene frequency, P_{max} . The main model prediction of interest in the evolution experiments is the change (evolution) in the average value and variation among individuals in the two traits controlling juvenile density-dependent survival.

The genetic responses deserve some further explanation. Original alleles are those initially present in the Shoshone population, whereas those not initially present are alien alleles. These might originate from mutation or they may be private alleles of the population donating broodstock. Because Shoshone is the river segment farthest upstream, these are the only two options. Introgression is measured by the decrease in the proportion of alleles originally present in the Shoshone population and an increase in the number of alien alleles.

Genetic swamping is indicated by dominance by a few alleles with high frequencies. Average P_{max} , the frequency of

the dominant allele among loci of individuals in the Shoshone population at the end of the simulation, is used here as an index of genetic swamping. For example, if an allele at one locus became fixed in the population (i.e., all individuals have the same value), then P_{\max} would be 1.

Family quota experiment

Conventional wisdom in aquaculture suggests that limiting the contribution from any one family will prevent genetic swamping. At the outset, the expectation is that lower values of the juvenile quota per family, N_j , will reduce genetic swamping, but perhaps also reduce the size of the Shoshone population. This experiment is designed to test whether this pattern will appear in a simulated hatchery setting.

In aquaculture parlance, a “family” consists of offspring from a male–female pairing. Variation among families, in how many individuals, hence, genes, each family contributes, is controlled by a quota or maximum number of juveniles stocked per family, N_j , which is a management decision. When the N_j quota is small, families are more equally represented (illustrated by Fig. 3). Unless some families experience 100% mortality, all families in the hatchery contribute exactly N_j juveniles (i.e., zero variance among families). As N_j increases, variance in the number of juveniles contributed by families tends to increase because some families produce fewer than N_j juveniles (see Fig. 3), and this subset of families will contribute different numbers of juveniles.

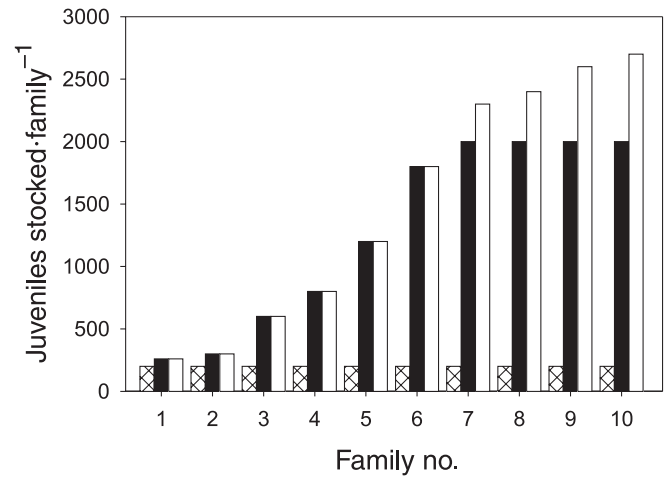
In this simulation experiment, I compare release levels of 500, 1000, 1250, 1500, 1750, 2000, and 2250 juveniles per family. In addition, results are shown for simulations with no stocking and no limit on the number of juveniles per family. These simulations use the neutral version of the model, which focuses on neutral genetics rather than on the fitness-related differences among families. Each year, six broodstock adults are captured from the Bliss reach, mated in the hatchery, and their offspring stocked into the Shoshone reach. To better understand the effects of parameter values used, I compared simulations with and without density-dependent mortality acting on juveniles and adults in the river.

The demographic benefits of stocking are expected to be greatest when no natural reproduction is possible in the recipient segment (the Shoshone reach). I therefore compared two scenarios: a supplementation scenario in which recruitment is possible just during wet years (approximately one in 5 years) and a stocking scenario in which recruitment is never possible.

Simulated adaptive management

Adaptive management was simulated with two goals: (i) to prevent genetic introgression and loss of alleles in the population receiving hatchery sturgeon and (ii) to prevent demographic harm to the population lending broodstock. I compared the results of simulations with no hatchery, with hatchery always in operation, and with adaptive management of hatchery operation. In addition, I compared adaptive management simulations with the following threshold values: P_{alien} (0.1, 0.3, 0.5, 0.7, and 0.9) and D_{adapt} (0, 25, and 50 fish·km⁻¹).

Fig. 3. An example with 10 families illustrates that variance in the numbers of juveniles stocked per family increases as the juvenile quota per family (N_j) increases from 200 (cross-hatched bars) to 2000 (solid bars) to no quota (open bars).



The situation considered here is the one with individuals from a different river segment (Bliss) used as broodstock for the Shoshone population. In each case, 100 replicates were simulated with supplementation of wet-year natural recruitment in the Shoshone reach.

Supplementation occurred every year, except when disallowed by one of the two specified criteria. I compared demographic (final densities of donor and recipient populations) and genetic results (final proportion of alien alleles in the recipient reach).

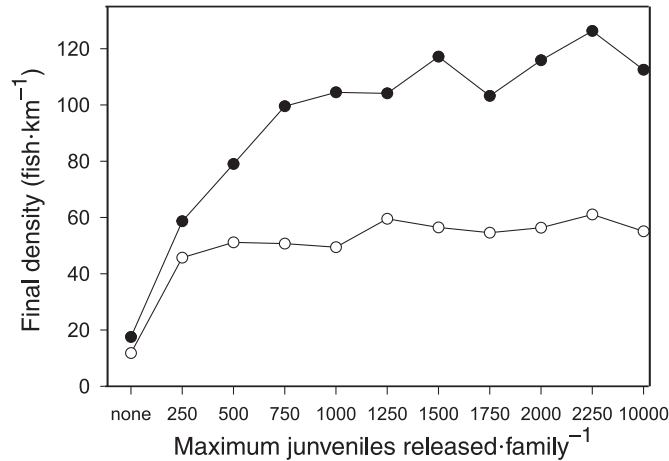
Evolution experiments

For the evolution experiments, I examined changes in gene frequencies and the evolution of traits associated with density-dependent survival. All scenarios with selection assumed that recruitment was possible in Shoshone during wet years.

I specified initial average values for S^* and D^* of 0.8 (SD = 0.10) and 50 fish·km⁻¹ (SD = 20), respectively. Because trajectories of the three management scenarios follow essentially the same pattern relative to one another from different starting points, I chose arbitrary initial values bounded away from the extremes.

I compared the simulated evolutionary trajectory of S^* and D^* for three scenarios with hatchery operation and for the scenario with no hatchery operation. In one hatchery scenario, the segment receiving stocked sturgeon (the Shoshone reach) also provided broodstock adults, i.e., the donor was connected to the recipient. In a second scenario, the same donor reach was used, but only wild fish were used as broodstock. In a third scenario, a segment isolated from the segment receiving stocked sturgeon provided broodstock adults (all wild). In the latter case, broodstock were obtained from the Bliss reach. (Although there is a downstream connection between the Shoshone and Bliss segments, few sturgeon successfully emigrate from Shoshone to Bliss because the two segments are separated by short reservoirs, Upper and Lower Salmon Falls Reservoirs, that lack spawning habitat.)

Fig. 4. Demographic response of a simulated white sturgeon (*Acipenser transmontanus*) population in the Shoshone reach to the maximum number of hatchery juveniles released per family with (solid circles) and without (open circles) density-dependent mortality. Simulations permitted natural recruitment during wet years.



Results

Results for three simulation experiments are presented below. The experiments were designed to (i) evaluate the demographic and genetic effects of equalizing family contributions, (ii) evaluate adaptive management as a tool for preventing adverse consequences of stocking, and (iii) assess the potential for artificial selection on juvenile density-dependent survival in the hatchery setting.

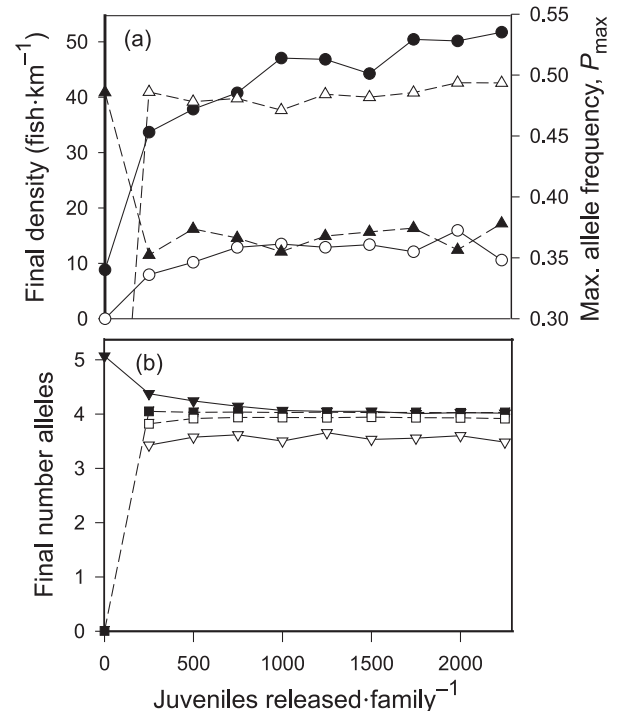
Family quota experiment

The final density in the recipient reach increased with the maximum number of juveniles released per family (family quota), N_j , up to a point (Fig. 4). Beyond this point, increasing the N_j quota did not increase the total number of fish stocked because of density-dependent mortality in the hatchery. Final density was higher with stocking than without, but increasing N_j did not provide as much of a demographic benefit as expected.

Parameter explorations showed that the demographic response to N_j is sensitive to parameters that influence density dependence in the hatchery and river. Decreasing the capacity of the hatchery caused final population sizes to reach a plateau at a lower N_j value (Fig. 4). Increasing density-dependent mortality in the river caused final population sizes to reach a plateau at a lower quota (Fig. 4).

All genetic responses changed when stocking was added, but none changed in response to the N_j quota (Fig. 5). In simulations with recruitment in wet years, stocking decreased average P_{\max} from 0.486 (SE = 0.032) to between 0.352 and 0.378 (SE ~ 0.010). In simulations with no recruitment, average P_{\max} values also showed no apparent trend with increasing N_j , ranging from 0.461 to 0.536 (SE ~ 0.015). In the case of no hatchery, no populations persisted, and thus, it makes no sense to discuss genetic responses.

Fig. 5. Responses of final averages to the number of hatchery juveniles released per family for two cases: natural recruitment during wet years (open symbols) and no natural recruitment in the Shoshone reach. Responses include (a) fish density (circles) and P_{\max} (triangles) and (b) number of alleles retained from the original population (inverted triangles) and number of alien alleles (squares).



In short, genetic swamping decreased in response to stocking but showed no trend in response to N_j . Note that individuals with genes from a different segment introduce new alleles and are, therefore, likely to lower the frequencies of original alleles. This result probably would not hold if broodstock were taken from the same (or a connected) segment instead of an isolated one.

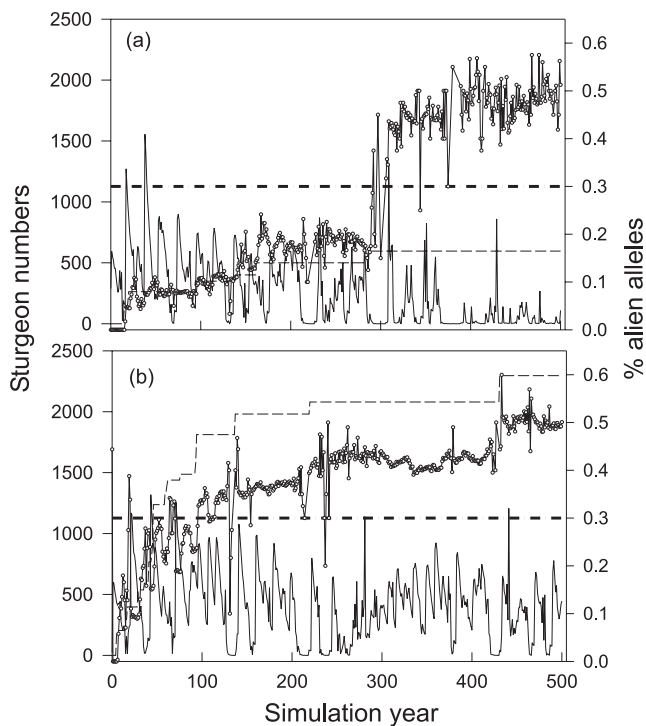
Similarly, the proportion of original alleles within the recipient reach changed in response to hatchery operation (Fig. 5) but showed no trend in response to the number of juveniles released. When natural recruitment was possible, stocking decreased the proportion of original alleles; when no recruitment was possible, stocking increased the proportion. In the latter case, stocking increased the retention of original (including locally private) alleles because (i) the increased size of the Shoshone population protected it from loss of alleles through genetic drift and (ii) the original Shoshone population had a subset of alleles in common with the broodstock population, providing a genetic rescue effect.

In summary, the simulated genetic benefits of culling larger families were too subtle to detect. Stocking had similar genetic effects (swamping, retention of local alleles, and introgression by alien alleles) regardless of the release quota placed on families.

Simulation of adaptive management

Simulated adaptive management was not effective at controlling introgression over the long term. This was true both

Fig. 6. Change over time in survey estimated proportion of alien alleles (open circles), population size (solid line), and the number of stocked fish (broken line) in one adaptive management simulation with (a) perfect and (b) uncertain feedback for threshold values $P_{\text{alien}} = 0.3$ (horizontal reference line) and $D_{\text{adapt}} = 25$.



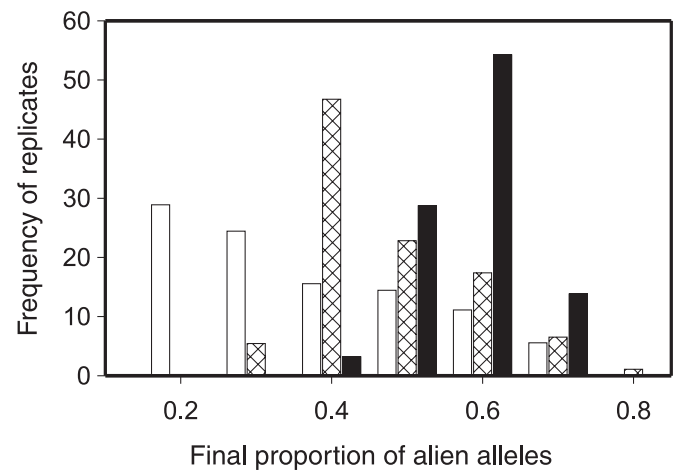
in simulations with perfect feedback (the actual proportion of alien alleles) (Fig. 6a) and in simulations with uncertain feedback (survey estimates) (Fig. 6b). The proportion of alien alleles present in the final Shoshone population exceeds the P_{alien} threshold in many cases and is not that much lower in simulations with a lower threshold (Table 2). However, the proportion does climb more slowly in simulations with a lower threshold (Fig. 7).

The reason that introgression is not controlled very well can be seen by observing the patterns in Fig. 6. Once the proportion of alien alleles falls below P_{alien} and supplementation occurs, natural reproduction increases the frequency of these alleles until they represent about 50% of the alleles in the population (Fig. 6). After a few supplementation events, it is too late to put the genie back in the bottle. The equilibrium proportion is likely determined by what proportion of alleles the two populations share.

In real life, uncertain survey estimates would be used for feedback. This leaves little room for error: if the proportion is underestimated in a given year's survey because only a few sturgeon, all of wild ancestry, happened to be captured, then the hatchery operates and ratchets up the proportion of alien alleles permanently. Survey estimates improve with the size of the survey sample and are therefore much less certain when the population, or sampling effort, is small.

Because temporary removal of broodstock had such a small effect on the donor population, varying the D_{adapt} threshold had little effect on the final size of the donor population (between 41 and 44 fish·km⁻¹). Nevertheless, adaptive manage-

Fig. 7. Frequency distribution of final proportion of alleles after 500 years among 100 replicate simulations for three threshold values: $P_{\text{alien}} = 0.1$ (open bars), 0.3 (cross-hatched bars), and 0.5 (solid bars).



ment might be an effective means of preventing harm in situations with a smaller population donating broodstock.

These adaptive management results demonstrate a trade-off between genetics (i.e., minimizing introgression) and demography (i.e., maximizing population size). Permitting a higher level of introgression (increasing P_{alien}) resulted in higher final population sizes in the Shoshone reach (Table 3).

Evolution experiments

Simulations without hatchery operation showed an increase in average S^* and a decrease in average D^* over time (Fig. 8). The S^* tended to increase over time, approaching 1. In the lower density environment of the river, selection appeared to favor higher juvenile survival at lower densities, as one would expect (compare the no-hatchery case in Fig. 8 with Fig. 1). Average D^* tracked the decline in population density, probably as a result of upward selection pressure on S^* (Fig. 8). In simulations with hatchery operation (open and solid circles in Fig. 8), S^* increased more slowly than in the case without hatchery operation, but D^* appeared not to be under directional selection.

Genetic variance is expected to decrease under a constant selection regime. In simulations with no hatchery, the variation among individuals, measured by the SD in each trait, decreased over time for S^* (from 0.26 at 0 time to 0.05 after 500 years). Variation in D^* did not decrease as consistently over time: it decreased from an initial value of 23.5 but varied between 17.5 and 19.4 in later years. In simulations with hatchery operation using a connected broodstock, variation in S^* declined more slowly with hatchery operation to 0.11. Variation in D^* also declined but leveled out near 19.2. Variation in trait D^* remained higher over time than that in trait S^* , consistent with the idea that genetic polymorphism is maintained in density-dependent traits, i.e., those under soft selection (Mueller 1997).

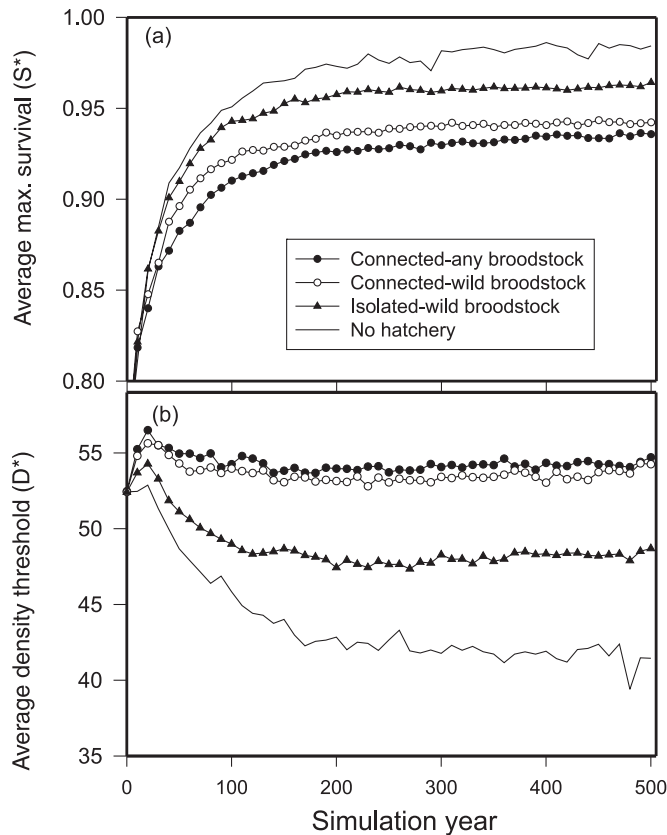
Hatchery simulations with broodstock collected from the same reach (Shoshone) (solid circles in Fig. 8) followed an evolutionary trajectory different from that of simulations with

Table 3. Results of simulated adaptive management with survey (uncertain) feedback and two criteria for interrupting hatchery operations.

Adaptive management criteria		Years hatchery operation interrupted by reason (SE)		Final population attributes, average (SE): average density (D) (fish·km ⁻¹), number of original alleles (N_{orig}), or proportion of alien alleles (P)			
D_{adapt}	P_{alien}	$D < D_{adapt}$	$P > P_{alien}$	Shoshone D	Bliss D	Shoshone N_{orig}	Shoshone P
0	0.1	0 (0.0)	102.9 (6)	10.5 (1.0)	42.9 (0.6)	4.32 (0.13)	0.37
0	0.3	0 (0.0)	217.4 (10)	12.2 (1.2)	43.3 (0.6)	4.36 (0.14)	0.43
0	0.5	0 (0.0)	365.9 (11)	18.6 (1.8)	43.7 (0.5)	4.04 (0.11)	0.48
0	0.7	0 (0.0)	499.8 (0)	22.6 (1.4)	43.0 (0.5)	4.22 (0.10)	0.48
0	0.9	0 (0.0)	500.0 (0)	20.9 (1.4)	42.8 (0.7)	4.19 (0.11)	0.49
25	0.1	11.8 (0)	385.3 (6)	10.4 (1.0)	43.2 (0.6)	4.36 (0.14)	0.38
25	0.3	11.7 (0)	273.1 (9)	14.0 (1.3)	42.8 (0.7)	4.26 (0.14)	0.44
25	0.5	12.2 (0)	103.4 (10)	14.9 (1.2)	43.5 (0.6)	4.23 (0.13)	0.47
25	0.7	12.3 (0)	0.0 (0)	19.7 (1.2)	42.5 (0.6)	4.21 (0.10)	0.49
25	0.9	12.0 (0)	0.0 (0)	20.6 (1.7)	42.8 (0.6)	4.20 (0.11)	0.48
50	0.1	472.7 (1)	3.9 (1)	7.8 (0.9)	43.2 (0.6)	4.54 (0.20)	0.19
50	0.3	472.6 (1)	1.8 (0)	8.7 (1.1)	43.6 (0.6)	4.53 (0.20)	0.19
50	0.5	472.1 (1)	0.5 (0)	7.3 (1.1)	42.0 (0.7)	4.32 (0.21)	0.24
50	0.7	474.3 (2)	0.0 (0)	8.3 (1.1)	43.3 (0.6)	4.66 (0.17)	0.24
50	0.9	474.0 (1)	0 (0)	7.8 (1.1)	43.0 (0.6)	4.66 (0.17)	0.22
Hatchery always		na	na	21.1 (1.4)	41.6 (0.6)	3.99 (0.09)	0.50
Hatchery never		na	na	9.5 (1.2)	43.7 (0.6)	5.03 (0.15)	0.0

Note: na, not applicable.

Fig. 8. Simulated evolution over time of (a) S^* and (b) D^* for four scenarios: no hatchery influence, an isolated broodstock, a connected broodstock, and a connected broodstock consisting of wild individuals.



no hatchery operation. After 500 years, hatchery simulations with broodstock collected from the Shoshone reach evolved to an end point with lower maximum survival S^* (Fig. 8a) and higher threshold density D^* (Fig. 8b) than simulations with no hatchery and those with an isolated donor.

The mean trajectories of the two traits in simulations that restricted broodstock to wild adults in Shoshone, although slightly closer to the no-hatchery trajectories, were similar to those in simulations with no restriction on adults used as broodstock (Fig. 8).

Discussion

Simulation results presented here suggest that management efforts designed to reduce genetic risk may not only fail but could, in some cases, reduce population size. These results support Lande’s (1988) advice to focus on demography (i.e., increasing population size) and not to allow recovery efforts to be upstaged by concerns about genetic risk.

Model limitations

This study used an IBM+G model to study the demographic and genetic effects of alternative conservation hatchery management practices. This required a number of assumptions and parameter choices that are not exactly true for the Shoshone population of white sturgeon or any other. However, these simplifying assumptions make it possible to generate qualitative predictions of population response that advance our intuitive understanding of the system. A modeling approach is especially valuable when managing a long-lived species like the white sturgeon because field experiments would take much too long.

In future, it will be important to study how robust these predictions are to model assumptions. For example, whether the predictions about family equalization hold up when survival rates among families are very different, if the same

broodstock are kept and reused, or if the proportion of private alleles is higher or lower than those simulated here. Another question of interest is how these results would change if private alleles were used to simulate local adaptation rather than having a neutral effect on fitness.

Inheritance is poorly understood for sturgeons, and residual polysomic inheritance may characterize a fraction of loci. This raises the issue of whether these simulation results differ significantly from those that would be obtained using a mixed polysomic–disomic model of inheritance. Polysomic inheritance at a fraction of loci would increase genetic variation and might therefore increase rates of evolution but would be less likely to alter the trajectories followed by traits under selection. Polysomic inheritance would not have a large influence on model predictions of introduced alien allele frequencies. Once the segregation mechanisms are better understood for sturgeons, it might be possible to refine the modeling approach (e.g., Allendorf and Danzmann 1997).

For the evolution experiments, we do not know if different traits, subject to selective differences in the hatchery and river, show the same response to broodstock choices as the ones simulated here, but there is no reason to believe that they would not. One interesting question raised here is whether the mathematical constraints in how we represent traits are mirrored in nature. For example, survival S^* has an upper (and lower) limit, and most mathematical functions chosen to represent this trait would result in low variation among individuals near the extremes.

Family quota experiment

In the first experiment, simulations suggest that, if the level of density-dependent mortality acting on sturgeon in the river is low, equalizing families can reduce population size, with no decrease in genetic swamping. I can envision two situations in which these results may not hold. First, variation in survival among families may be larger, for some species and situations, than that simulated here (a more skewed distribution than the binomial). If survival was much higher for some families than others, swamping might be a greater concern. Second, genetic dominance by a few individuals might be higher if broodstock were kept rather than returned and if the source of broodstock were connected to the supplemented reach.

Simulation of adaptive management

Adaptive management, as simulated here, turned out not to be an effective means of minimizing introgression in the recipient population. This experiment was better carried out *in silico* than in the field because populations in simulations that halted hatchery operation to prevent introgression suffered a demographic cost. Overall, results suggest that choosing an isolated broodstock would be a more effective means of controlling introgression than dynamic control of hatchery operation.

Evolution experiments

The second type of concern addressed in this study is that hatchery operation will select for phenotypes poorly adapted to the river environment. Results of this study suggest that

this concern is more pressing when broodstock are collected from the same river segment or from a connected segment that receives immigrants from the target segment. Such a connection is required to close the evolutionary feedback loop over multiple generations.

Adaptation to hatchery conditions can be avoided by choosing a broodstock source isolated from the recipient population. In rivers, this could be an upstream reach above a dam or one from another watershed. For a locally adapted broodstock (i.e., a species with high geographic spawning fidelity), it would also be important to follow the precautionary conservation practice of using broodstock from a source geographically as close as possible to the recipient segment (Busack and Currens 1995).

If it is not possible to find an isolated broodstock source, results here suggest that restricting broodstock to wild individuals would slow the rate of domestication while other measures, such as habitat restoration, are implemented. Simulated benefits here were smaller than those obtained by two other theoretical studies. Ford (2002) and Goodman (2005), using single-trait models of salmon populations, found that requiring all hatchery broodstock to be withdrawn from the naturally spawned component of the population was an effective means of preventing domestication and loss of fitness in the wild. However, Ford (2002) found that considerable phenotypic evolution occurred even when a small proportion of broodstock were hatchery spawned. The predicted rate of phenotypic change was higher in populations that were declining than in those that were increasing (Ford 2002). Together, theoretical results suggest that using wild broodstock may be able to slow, but not prevent, domestication, especially if adult origins are uncertain. Meanwhile, one can hope that efforts will be devoted to restoring spawning habitat, which remains the only long-term solution for maintaining river-adapted species.

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