Articles

Population Viability of Endangered Lost River Sucker and Shortnose Sucker and the Effects of Assisted Rearing

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Abstract

The Lost River Sucker *Deltistes luxatus* and Shortnose Sucker *Chasmistes brevirostris* are two narrowly endemic fish species in the upper Klamath Basin of southern Oregon and northern California. Both species have been federally listed as endangered pursuant to the U.S. Endangered Species Act since 1988 because of dramatic declines in abundance and distribution. In Upper Klamath Lake, Oregon, both species have only recruited a single cohort to the adult populations since that time. Most individuals in this population are at or older than the expected life span of the species. Consequently, the U.S. Fish and Wildlife Service and the Klamath Tribes have initiated assisted rearing efforts to stabilize the population. However, it is unclear how quickly these populations might become extirpated and how assisted rearing might alter population trajectories. We modeled the potential for extinction and recovery of the populations of endangered Lost River Sucker and Shortnose Sucker in Upper Klamath Lake. We simulated population trajectories over the next 50y with a stochastic population viability assessment approach. Projections indicate that if population trajectories do not change, the Shortnose Sucker population may decline by 78% to number <5,000 in 10y and become completely extirpated within the next 30 (18.6% probability) to 40 y (99% probability). The two Lost River Sucker populations have a greater likelihood to remain extant after 50 y, with only 1% probability of extinction given our scenarios and assumptions, but the populations are likely to number fewer than 1,000 individuals. Our results also suggest that rearing of Klamath Lake sucker species in a controlled environment for augmenting the natural population will be effective in reducing extirpation probabilities over the next 50y if survival to recruitment can be achieved, but a long-term effort of at least 40 y will be required. The necessity of long-term augmentation to ensure population persistence in the absence of natural recruitment underscores the urgent need to determine and address the causes of recruitment failure in the wild.

Keywords: Catostomidae; Upper Klamath Lake; conservation propagation

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Introduction

Captive rearing is a common tool for the enhancement of wild populations of depleted species, but there is a trade-off between commitment of resources to captive rearing and habitat restoration or other in situ management actions (Dolman et al. 2015). Understanding and managing this trade-off is critical to successful species recovery because population augmentation is analogous to treating symptoms rather than the underlying disease and is unlikely to result in the recovery of self-sustaining populations alone (Meffe 1992; Snyder et al. 1996). However, in cases where populations are declining rapidly and there is either uncertainty about which
management actions will result in recovery of wild populations or a lag between implementation of conservation actions and the response of wild populations, captive rearing can be a necessary stopgap until conditions in the natural habitat improve (Molony et al. 2003; George et al. 2009; Lorenzen 2014).

To maximize the conservation benefit of captive rearing, the timing and scale of rearing activities should be targeted to conservation goals to avoid unnecessary diversion of resources from management activities that address the ultimate cause of population declines. One way to evaluate the appropriate timing and scale is to conduct a population viability analysis (PVA; Boyce 1992; Molony et al. 2003). Population viability analyses are demographic simulations of future scenarios to evaluate the probability of population persistence. In the context of captive rearing, PVA can be used to determine whether a program should be established and appropriate time lines to avoid unnecessary expenditures by implementing too early or extirpation by implementing too late (Molony et al. 2003). Further, PVA can be used to scale rearing efforts to conservation targets by evaluating expected population trajectories with varying scales of augmentation.

The goal of this study is to use PVA to simulate population trajectories for Lost River Sucker Deltistes luxatus and Shortnose Sucker Chasmistes breviceps in Upper Klamath Lake, Oregon with and without captive rearing and to evaluate the rates of natural production required to sustain populations. Both species are large (maximum sizes up to 600 to 800 mm fork length), long lived (maximum ages 33 to 57 y) fish (family Catostomidae) endemic to the lakes and reservoirs of the upper Klamath Basin in central Oregon and California. These species were concurrently listed as endangered under the U.S. Endangered Species Act (ESA 1973, as amended) by the U.S. Fish and Wildlife Service in 1988 (USFWS 1988). Historically, these species were extremely abundant despite being restricted to only a handful of lakes, all within roughly 3,000 km². Both species have now declined drastically in abundance across all populations and have been extirpated from one major growth habitat and several spawning locations (Rasmussen 2011).

Two factors suggest that captive rearing may be an appropriate conservation strategy for Klamath Lake suckers in Upper Klamath Lake. First, the primary cause of decline appears to be a survival bottleneck within the first few years of life. Eggs and larvae are produced each year, but there appears to be consistent cohort collapse within the first 2 y on the basis of juvenile catches that fall to 0 during that period (Burdick and Martin 2017). However, annual survival of adults is relatively high, often around 90% (Hewitt et al. 2017), suggesting that reintroducing suckers that have been raised past the survival bottleneck could result in recruitment of new individuals to the adult spawning populations (Day et al. 2017).

Second, no in situ management actions have been demonstrated to result in recruitment. Alternative hypotheses for the cause of juvenile mortality include poor water quality, parasites, disease, predation, habitat loss, and a combination of these factors. Uncertainty about the true cause of mortality hinders implementation of management actions to address these issues (USFWS 2013). Even after the cause of mortality is identified, management actions addressing these issues are likely to take years or decades to yield benefits (Wherry and Wood 2018). Although Upper Klamath Lake is thought to harbor the most abundant populations of both species, its populations have declined by over 75% (Shortnose Sucker) or 50% (Lost River Sucker) since 2001 (Hewitt et al. 2017). Thus, captive rearing is likely necessary to sustain populations until the causes of juvenile mortality are determined and addressed (Day et al. 2017).

On the basis of these two factors and in response to the continued decline of these populations, the U.S. Fish and Wildlife Service initiated a pilot program to augment wild Lost River and Shortnose Sucker populations in Upper Klamath Lake (Day et al. 2017). Naturally spawned sucker larvae are collected in the wild and reared in seminatural ponds for subsequent reestablishment to Upper Klamath Lake (Day et al. 2017). In this study, we used a stochastic PVA model to evaluate the potential consequences of captive rearing on the three Lost River Sucker and Shortnose Sucker populations within Upper Klamath Lake, Oregon. By providing expected population trajectories, the PVA will help managers determine the appropriate timing of management actions such as increasing assisted rearing efforts, establishing refugial populations, and switching from collections of wild-hatched larvae to captive breeding. Additionally, this study evaluates the effects of different scales of assisted rearing efforts and will help managers scale assisted rearing efforts appropriately to meet conservation goals.

Methods

We developed a stochastic PVA to assess the probability of persistence and population trajectories of three spawning populations in Upper Klamath Lake, Oregon over 50 y: Lost River Sucker Williamson River spawning population, Lost River Sucker shoreline spring spawning population, and Shortnose Sucker. For the purposes of this study, we defined populations as groups of individuals that consistently spawn in the same location. Individuals from the two Lost River Sucker populations reside within the same lake; however, very few individuals switch from one spawning location to the other (Burdick et al. 2015). We chose 50 y as a relevant time reference on the basis of the revised Recovery Plan for these species, which concluded that recovery was likely to require 30–50 y (USFWS 2013). We did not treat age explicitly in any of the scenarios. There is no evidence of a trend in annual survival rates that would suggest senescence is increasing mortality. Therefore, we imposed no forced ageing out of individuals or elevated mortality rates given the lack of any empirical data related to senescence dynamics for these species. Instead, we gave all individuals of a given sex and population an equal probability of annual survival.
We assessed each population with the same model structure across three different scenario categories: status quo, rearing program, and natural recruitment. The status quo scenario models the current prevailing conditions of the natural populations within Upper Klamath Lake—consistent, widespread cohort failure each year resulting in negligible recruitment at best. Thus, the population trajectory of this modeling scenario depends exclusively on the survival of adults. The rearing program scenarios model the addition of captive-reared individuals to frame the potential effectiveness and efficiency of a range of rearing efforts. We simulated the number of released individuals and the duration of the program (i.e., the total number of years reared fish were actively stocked) across a range of values (described below). For the natural recruitment scenarios, we simulated natural production as following a lognormal distribution, which is the theoretical distribution for instances when there is nonindependence among individuals in early life survival (Shelton 1992). We incrementally increased the mean and standard deviation (SD) of per capita recruitment to determine recruitment levels necessary to achieve recovery or maintain a stable population. We conducted all analyses in Program R and code is available in Supplemental Material (R Core Team 2016; Text S1).

We replicated each scenario (i.e., each combination of parameters) 100 times with the exception of the status quo, which we replicated 500 times. All scenarios shared the same underlying parameters (or draws from the same parameter distribution) for starting abundance and adult survival (Table 1), but scenarios varied in the mechanism and magnitude of recruitment. We took initial abundance from spawning population abundance estimates from a modified Bayesian Lincoln–Petersen estimator (E.C., unpublished data) using long-term mark–recapture data (Hewitt et al. 2017). The initial abundance of each replicate was randomly selected from the posterior distribution of abundance from the most recent year with available estimates, which was 2016 for the Lost River Sucker Williamson population and the Shortnose Sucker and 2017 for the Lost River Sucker springs population.

Table 1. Parameters used to initialize populations for each model run for the Lost River Sucker Deltistes luxatus Williamson River (Oregon) spawners, the Lost River Sucker spring spawners, and the Shortnose Sucker Chasmistes brevirostris populations that reside in Upper Klamath Lake, Oregon: mean initial population size (MIPS), the mean (MFS) and standard deviation (SDFS) of empirical data of female survival from 2002 to 2014 for Lost River Sucker and 2001 to 2014 for Shortnose Sucker (Hewitt et al. 2017), the coefficient of determination ($R^2$) from a linear model fit to predict male survival from female survival for each species on the basis of the same empirical data, the pseudoextinction level (PEL), the pseudorecovery level (PRL), and the male-to-female ratio (MFR).

| Population            | MIPS  | MFS   | SDFS  | $R^2$ | PEL  | PRL  | MFR |
|-----------------------|-------|-------|-------|-------|------|------|-----|
| Lost River Sucker Williamson | 90,944 | 0.931 | 0.574 | 0.11  | 100  | 300,000 | 1   |
| Lost River Sucker Springs   | 8,422  | 0.934 | 0.593 | 0.68  | 100  | 50,000 | 1   |
| Shortnose Sucker             | 19,586 | 0.869 | 0.638 | 0.25  | 100  | 100,000 | 1   |

*a* On the probability scale.

*b* On the logit scale.

Time steps began postspawn with the establishment of an annual cohort. We set the annual cohort for status quo to 0 for all time steps and replicates. We simulated annual cohorts for rearing program scenarios as a constant number of individuals reintroduced into the lake with randomly assigned sex from a binomial distribution (probability of being female = 0.5). We incremented the number of fish reintroduced into the lake annually from 500 individuals to 10,000 by 500. Similarly, the duration of active reintroduction ranged from 5 to 50 y with a step of 5 y. When we exceeded the active reintroduction period, we assumed all annual cohorts to be 0. We simulated recruitment and survival for these individuals identically to individuals in the natural recruitment scenarios described below.

We lack information associated with natural recruitment processes within the populations. Therefore, we were unable to parameterize the numerous complex dynamics of early life stages (e.g., egg viability, fertilization rates, larval and juvenile survival). Instead, establishment of an annual cohort consisted of modeling the number of individuals achieving age 3 rather than modeling early life-stage dynamics directly. We selected this age because it is the earliest age at which individuals can become sexually mature (Perkins et al. 2000). We assumed that the number of individuals achieving age 3 per spawning female followed a lognormal distribution on the basis of empirical and theoretical studies on other species (Hennemuth et al. 1980; Myers et al. 1990; Shelton 1992). The lognormal distribution contains only positive real numbers and is positively skewed such that most years result in low production, but high-production years remain possible, particularly when the SD is high. Long-lived fish often display this pattern of numerous low-production years with occasional high-production years (Longhurst 2002). We assessed recruitment across a range of possible means and SDs from a lognormal distribution (range of means: $-5$ to $-1$ on the log scale with a step of 0.5; range of SD: 0.0 to 2.5 on the log scale with a step of 0.25) with all possible combinations replicated 100 times each. These values coincide with a range of means of $6.7 \times 10^{-3}$ to $3.7 \times 10^{-1}$ on the real scale. We simulated each annual cohort by a random draw from the lognormal distribution to generate per capita production multiplied by the number of females in the population and rounded to the nearest integer. We randomly assigned each individual a sex, with a probability of 0.5 for each sex. We assumed that cohorts survive at rates similar to the adult population beginning at age 3.
After the establishment of the annual cohort in the model, we simulated annual survival rates stochastically. We assumed that annual female survival followed a normal distribution on the logit scale using population-specific means and SDs derived from empirical estimates from long-term monitoring (12–14 y, depending on the population; Hewitt et al. 2017). We utilized reported survival estimates for 2002–2014 for both Lost River Sucker populations and for 2001–2014 for Shortnose Sucker. However, when at least one of the reported estimates for either male or female was unreliable because of proximity to the boundary or inordinately high error, we did not include these estimates. For example, we did not include 2004 survival rates for Lost River Sucker in our set because they were estimated to be at the boundary (1.0; Hewitt et al. 2017). For each time step, we randomly selected a single female survival rate from this assumed distribution. We took this approach to provide greater stochasticity in survival rates in the model rather than simply restrict rates to the limited set of empirical data.

To account for temporal correlation between male and female survival rates, we generated a linear model to predict male survival from female survival on the log scale. We then estimated male survival as the predicted value from the linear model given the randomly selected female survival (from the empirically derived distribution described above) for each time step, plus a random error value. We randomly drew this error from a normal distribution (N(0, linear model prediction error)). We then back-transformed estimates to the probability scale. The relationship between female and male survival was fairly weak in some cases, with $R^2 = 0.25$ for Shortnose Sucker, 0.11 for Lost River Sucker Williamson, and 0.68 for Lost River Sucker springs (Table 1). Thus, simulation of male survival rates included relatively large random variation in addition to the effect of female survival, particularly for Shortnose Sucker and Lost River Sucker Williamson populations.

The final process in a time step was the transition of subadults to the reproductive adult population. Little empirical information exists concerning the distribution of age at recruitment for either species, but the available information suggests that age at recruitment may be 4 to 5 y for Shortnose Sucker but somewhat later for Lost River Sucker (Buettner and Scoppettone 1990; Perkins et al. 2000). To avoid applying an overly detailed recruitment curve with little supporting data, we assumed that individuals would recruit into the spawning population at either age 4 or age 5. We randomly selected age-4 individuals to recruit to the spawning population on the basis of a binomial distribution ($P = 0.5$). Therefore, we recruited roughly half of each annual cohort into the spawning population at age 4, with the remaining recruiting in age 5. We limited annual cohorts to $1 \times 10^6$ total individuals at ages 4 and 5 to avoid scenarios that were unrealistically optimistic.

We used both a pseudoextinction value (all scenarios) and a pseudorecovery value (natural recruitment scenarios only) to manage model runs. We assumed populations to go extinct, and we subsequently terminated the run if at the beginning of a time step the population was less than or equal to the pseudoequilibrium value of 100 individuals. Similarly, we terminated a run if at the beginning of a time step the population was greater than or equal to the pseudorecovery value. This value varied depending on the population in question: Lost River Sucker Williamson = 300,000; Lost River Sucker springs = 50,000; Shortnose Sucker = 100,000. These values equate to roughly three to five times the current estimates of population densities. The current recovery criteria for the species do not include a specific abundance target, but rather a metric of realized population growth over at least 25 y (USFWS 2013). Our pseudorecovery values do not directly relate to the recovery criteria but we chose them to be broad enough to incorporate population growth dynamics that would achieve specified recovery criteria as well as permit model runs to continue to better evaluate long-term stability.

In addition to examining the population size after 50 y, we evaluated the effects of varying stocking levels on two other metrics: short-term population growth rate and long-term equilibrium population size. We estimated the short-term effect on population growth rate for years 2 to 6 of the simulations. We discarded year 1 because not all individuals from the first cohort recruit in the first year, and we discarded trajectories after 6 y to minimize the effect of approaching the equilibrium population size on population growth rate. We estimated average population growth rate as the natural exponential of the slope of a linear regression between natural logarithm of population size and year. We used replicate simulations to characterize the uncertainty in population growth rate. We calculated the effect on long-term equilibrium population size directly from the empirical survival estimates assuming no natural recruitment. We estimated the effect of one additional stocked individual annually on long-term equilibrium population size as the inverse of the mean mortality rate assuming that annual mortality rate was normally distributed on the logit scale. We calculated confidence intervals (CIs) on the mean mortality rate using the t-distribution.

We assumed survival and reproduction to be density independent. Although density dependence is likely to act on these populations when they are close to carrying capacity, the strength of density dependence at the current population levels is likely negligible. Current population levels are very low compared with historical levels and are thus likely to be well below carrying capacity potential of the habitat, assuming that a drastic reduction in carrying capacity has not also occurred given that the lake remains highly productive in general. Additionally, we did not model density-dependent dynamics of low population sizes (e.g., Allee effect) because the magnitude and distribution of such effects would be essentially speculative at this point.

**Results**

**Shortnose Sucker**

Simulated Shortnose Sucker populations in Upper Klamath Lake assuming no change to the current
dynamics (i.e., status quo scenario) went extinct between 2042 (1% probability) and 2054 (99% probability; Figure 1a). However, males had a 47% probability of extinction by 2040 and a > 99% probability of extinction by 2046 (Figure 1b), whereas females remained in the system longer, with a probability of extinction of 42% by 2046 and > 99% by 2054. Projected Shortnose Sucker populations declined an average of 78% (95% CI: 66–87%) to a median projected population size of 4,273 (95% CI 2,608–6,621) in 10 y.

Figure 1. Projected population trajectories (a, c, e) and probability of extinction (b, d, f) for Shortnose Sucker Chasmistes brevirostris (a, b), Lost River Sucker Deltistes luxatus, spawning at shoreline springs in Upper Klamath Lake, Oregon (c, d), and Lost River Sucker spawning in the Williamson River, Oregon (e, f) assuming no recruitment to the spawning populations, which is currently thought to be the case (status quo). The simulation starting year in all cases was 2017.
Projected extinction risk for Shortnose Sucker within 50 y (2066) was substantially reduced in the rearing program scenarios compared with the status quo scenario. Duration of the rearing program had a stronger effect on the number of individuals remaining in the population and the probability of extinction than the numbers of individuals stocked annually, particularly when at least 3,000 individuals were stocked annually (Figures 2a and 2b). The minimum stocking rate that achieved a short-term population growth rate \( \geq 1 \) was 2,500 individuals annually (Figure 3a), and stocking at that rate annually sustained the 2016 population abundance through 2066 in simulations (Figure 2). Although higher stocking rates for a shorter duration achieved the same result, stocking 10,000 individuals annually for approximately 40 y was required to sustain the population at 2016 levels. A larger population in 2066 only resulted from efforts greater than these boundaries (Figure 2). Nevertheless, the probability of extinction within 50 y was practically eliminated for Shortnose Sucker in Upper Klamath Lake when the rearing program was continued for at least 40 y regardless of the numbers stocked, although some scenarios resulted in very low numbers (Figure 2). Reducing the duration of stocking to approximately 25 y with greater than 5,000 individuals stocked each year achieved similar results (i.e., projected probability of extinction in 50 y < 0.01). Stocking additional Shortnose Sucker individuals beyond 5,000 annually did not appreciably reduce the projected probability of extinction. Increasing the stocking rate by one male and one female annually increased the projected long-term

Figure 2. Projected population size after 50 y (a, c, e) and probability of extinction (b, d, f) for Shortnose Sucker *Chasmistes brevirostris* (a, b), Lost River Sucker *Deltistes luxatus* spawning at shoreline springs (c, d), and Lost River Sucker spawning in the Williamson River (e, f) in simulations with varying numbers of captive-reared individuals surviving to age 3 and recruiting to spawning populations after having been stocked into Upper Klamath Lake, Oregon (x-axis) for varying durations (y-axis). The simulation starting year in all cases was 2017.
Lost River Sucker lakeshore springs population

The simulated Lost River Sucker springs populations under the status quo scenario were all functionally extinct after 50 y (2067) because of the complete loss of males; however, only 1% of projected populations were completely extinct. A small number of females survived through 2067, with an average projection of 150 individuals (range: 0–295). However, the lower annual survival rates for males led to an earlier disappearance, with a 48% probability of disappearance by 2047 and 99% probability by 2052. The median projected Lost River Sucker springs population after 10 y was 3,976 (95% CI: 3,236–4,790), which represents a decline of 52.8% from the starting abundance. Additionally, given the higher mortality rates of males, fewer than 500 males existed in the simulated populations within 20 y (median 350 [95% CI: 247–464]).

In the rearing program scenarios, Lost River Sucker springs population required much lower stocking levels than Shortnose Sucker to sustain the population. Stocking 500 individuals annually for 50 y sustained the population at current levels. Furthermore, stocking 500 individuals achieved an average short-term (years 2–6) population growth rate ≥ 1 (Figure 3b). Stocking 10,000 individuals for 20 y resulted in a similar final population size but generated highly dynamic population trajectories, with large increases followed by steep decline. To achieve probabilities of extinction ≤ 0.5, stocking generally needed to occur for more than 10 y or consist of more than 2,000 individuals.

Lost River Sucker Williamson River population

The simulated Lost River Sucker Williamson populations did not go extinct after 50 y (2066) in any model projections, even in the absence of recruitment (Figure 1d). However, the average projected population size for the status quo scenario in 2066 was 1,341 females (range: 824–1,972) and 317 males (range: 80–904). Overall, this represents a 98% decline from the current estimated population size.

In the rearing program scenarios, Lost River Sucker Williamson population stocking levels needed to be at least 6,000 individuals annually for 50 y to maintain current population sizes, and stocking cohorts of at least 10,000 individuals produced similar final population sizes if the program was terminated at 40 y (Figures 2e and 2f). Stocking any number of individuals for any period of time eliminated any risk of complete extirpation within 50 y of this population, but significant stocking effort was required to maintain a population of more than 2,500 individuals. Achieving short-term population growth ≥ 1 required a minimum of 5,000 individuals stocked annually.

Natural recruitment scenarios

Given the model framework of 9 possible mean values, 11 possible SD values, 50 time steps, and 100 replicates, we could simulate a possible total of 450,000 annual
recruitment values per population. Once pseudoextinction or pseudorecovery rates were reached, we terminated runs. This resulted in a range of approximately 310,000 to 350,000 values being simulated per population. Median simulated recruitment rates (number of age-3 individuals per female) ranged from 0.054 to 0.095 across the three populations. Simulated values varied across five orders of magnitude, but the vast majority (99.9%) were ≤ 12.6 per female annually. This equates to roughly 350 instances per population where the simulated value was greater than 12.6 recruiting individuals per female. The maximum per population ranged from 34.6 to 197.3, and the minimum in each case was 0.

In natural recruitment scenarios, lower average recruitment rates sustained populations only if the variance around those averages was relatively high (Figure 4). For each population, a per capita recruitment rate of $e^{-1.0} = 0.368$ always resulted in recovery regardless of the associated distribution SD. Each population required a mean per capita recruitment rate slightly higher than the average annual mortality rate (replacement) to achieve a mean probability of recovery of at least 0.5 across all SD values. This value was $e^{-2.0} = 0.135$ for Shortnose Sucker and $e^{-2.5} = 0.082$ for both Lost River Sucker populations. Furthermore, at this “replacement rate” a SD of 1.25 on the log scale was required to achieve a probability of recovery higher than 0.5 for each population. For example, the estimated probability of recovery for Shortnose Sucker in a 50-y period with a mean annual per capita recruitment rate of $e^{-2.0} = 0.135$ and a SD on the log scale of 1.0 is 0.15, but this increases to 0.53 with a SD of 1.25.

**Discussion**

Declines in populations in Upper Klamath Lake have been well documented (Hewitt et al. 2017), but we are not aware of any estimates of the probability of complete population extirpation within a given time period for these species before this effort. Our results provide expected population trajectories that can assist conservation planners to determine appropriate time and scale of actions to stave off population extirpation and manage trade-offs. Our results indicate that if population trajectories continue as they have over the past 15 y, two of three endangered sucker populations may be lost from Upper Klamath Lake within the next 50 y, with the third as a much reduced remnant population. Assisted rearing is projected to have potential to sustain the populations, but efforts of at least 40 y will be needed to sustain populations near their current abundance in the absence of natural recruitment. Results also demonstrate that the populations could persist with rare but strong natural cohorts, but achieving even sporadic natural recruitment is likely to require substantial habitat restoration.

Our estimates of time to extirpation for Lost River and Shortnose Sucker in Upper Klamath Lake may in fact be optimistic given that we did not model senescence scenarios. For all of the scenarios explored in this analysis
we assumed stationarity in adult survival, but an age-related reduction in survival rates could accelerate the time to extinction estimates, possibly substantially. Decreased survival and fecundity with age appear to be widespread among vertebrates (Nussey et al. 2013), and there is some theoretical support for the evolution of this process among fish (Reznick et al. 2002). Sucker populations in Upper Klamath Lake have had only two spawning cohorts recruit substantial numbers to the adult population in the last 25 y. The 1991 and 1993 juvenile cohorts apparently recruited in the late 1990s (Perkins et al. 2000). Thus, nearly all individuals in the populations have exceeded the average life span of their species (Terwilliger et al. 2010; USFWS 2013). However, to date there is no evidence of a systematic decline in annual survival rates of adults that would indicate that senescence is occurring (Hewitt et al. 2017). If senescence does indeed occur, then we can expect an accelerated rate of the loss of individuals relative to our projections. Similarly, large-scale fish die-offs could increase the rate of decline toward extinction compared with projections presented here. Such events have been known to occur in Upper Klamath Lake. The empirical survival data used to parameterize our simulations included to some extent estimates of such events (Hewitt et al. 2017). Nevertheless, more severe and frequent die-offs apparently occurred in the 1990s (Perkins et al. 2000) before the availability of robust annual survival estimates.

We believe it is probable that achieving recruitment of Lost River Sucker and Shortnose Sucker through a captive-rearing program to a wild spawning population will be effective in delaying or preventing extirpation of the populations in the wild. However, on the basis of our results, sustained rearing and stocking efforts will be required to maintain populations until natural recruitment is restored. Similar propagation efforts have been part of recovery programs for three other closely related species for at least 35 y: June Sucker *Chasmistes liorus*, Cui-ui Sucker *Chasmistes cujus*, and Razorback Sucker *Xyrauchen texanus* (Cooke et al. 2005; Schooley and Marsh 2007; Day et al. 2017). These species continue to be listed as endangered under the ESA despite substantial augmentation efforts, but all three species are extant, potentially due in part to augmentation. Trends from these propagation programs coupled with the long-term stocking required to maintain populations in our simulations highlight the need for concurrent ecosystem recovery because sustaining the populations through augmentation appears to be a stopgap resolution (Snyder et al. 1996).

The analysis presented here relies on numbers of recruiting individuals, so actual releases will need to be higher because not all individuals will survive and recruit. Information on early life survival and on the probability of recruitment for reared fish is lacking for both Shortnose Sucker and Lost River Sucker. Estimates of recruitment rates for stocked June Sucker suggest that rates will be highly variable, potentially very low, and depend to a large degree on the rearing methods utilized (Rasmussen et al. 2009; Billman et al. 2011). Some estimates of Razorback Sucker survival over the first year are as low as 1% (Schooley and Marsh 2007). The high uncertainty of these demographic rates precluded their inclusion in the analysis presented here; however, development of empirical estimates of these rates is critically important for improving the estimates of effects of rearing efforts on population trajectories. Updating the analyses presented here regularly as new data become available will allow for adaptive management of rearing efforts to achieve conservation objectives.

Our results indicate that assisted rearing will be required until significant natural recruitment occurs. Short-term stocking reduced the probability of extinction after 50 y in the simulations; however, when stocking ceases, the populations are expected to decline rapidly. Thus, ongoing stocking will likely be required until habitat conditions improve and natural recruitment is able to sustain the populations. The necessity of sustained augmentation in the absence of natural recruitment underscores the urgent need to resolve the uncertainty around the cause of juvenile mortality to minimize the long-term cost of recovery.

**Supplemental Material**

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

**Text S1.** The entire annotated code for the stochastic simulation model. We developed a stochastic population viability analysis to assess the probability of persistence and population trajectories of three spawning populations in Upper Klamath Lake, Oregon over 50 y: Lost River Sucker *Deltistes luxatus* Williamson River spawning population, Lost River Sucker shoreline spring spawning populations, and Shortnose Sucker *Chasmistes brevirostris*. The model was implemented in Program R using the R programming language.

Found at DOI: [https://doi.org/10.3996/032018-JFWM-018.S1](https://doi.org/10.3996/032018-JFWM-018.S1) (81 KB PDF).

**Reference S1.** Buettner M, Scoppettone G. 1990. Life history and status of Catostomids in Upper Klamath Lake, Oregon: completion report. Reno Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, U.S. Department of Interior, Reno, Nevada.

Found at DOI: [https://doi.org/10.3996/032018-JFWM-018.S2](https://doi.org/10.3996/032018-JFWM-018.S2) (2.54 MB PDF).

**Reference S2.** Myers RA, Blanchard W, Thompson KR. 1990. Summary of North Atlantic fish recruitment, 1942–1987. Canadian Technical Report of Fisheries and Aquatic Sciences 1743, Department of Fisheries and Oceans, Science Branch.

Found at DOI: [https://doi.org/10.3996/032018-JFWM-018.S3](https://doi.org/10.3996/032018-JFWM-018.S3) (3.75 MB PDF).

**Reference S3.** Perkins DL, Scoppettone GG. The role of poor water quality and fish kills in the decline of...
endangered Lost River and shortnose suckers in Upper Klamath Lake. U.S. Geological Survey, Reno, Nevada.

Found at DOI: https://doi.org/10.3996/032018-JFWM-018.S4 (583 KB PDF).

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