

6-4-2016

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Recommended Citation

Roberts, James Henry, Paul L. Angermeier, Gregory B. Anderson. 2016. "Population Viability Analysis for Endangered Roanoke Logperch." *Journal of Fish and Wildlife Management*, 7 (1): 46-64. doi: 10.3996/032015-JFWM-026
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Articles

Population Viability Analysis for Endangered Roanoke Logperch

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Abstract

A common strategy for recovering endangered species is ensuring that populations exceed the minimum viable population size (MVP), a demographic benchmark that theoretically ensures low long-term extinction risk. One method of establishing MVP is population viability analysis, a modeling technique that simulates population trajectories and forecasts extinction risk based on a series of biological, environmental, and management assumptions. Such models also help identify key uncertainties that have a large influence on extinction risk. We used stochastic count-based simulation models to explore extinction risk, MVP, and the possible benefits of alternative management strategies in populations of Roanoke logperch *Percina rex*, an endangered stream fish. Estimates of extinction risk were sensitive to the assumed population growth rate and model type, carrying capacity, and catastrophe regime (frequency and severity of anthropogenic fish kills), whereas demographic augmentation did little to reduce extinction risk. Under density-dependent growth, the estimated MVP for Roanoke logperch ranged from 200 to 4200 individuals, depending on the assumed severity of catastrophes. Thus, depending on the MVP threshold, anywhere from two to all five of the logperch populations we assessed were projected to be viable. Despite this uncertainty, these results help identify populations with the greatest relative extinction risk, as well as management strategies that might reduce this risk the most, such as increasing carrying capacity and reducing fish kills. Better estimates of population growth parameters and catastrophe regimes would facilitate the refinement of MVP and extinction-risk estimates, and they should be a high priority for future research on Roanoke logperch and other imperiled stream-fish species.

Keywords: endangered species; extinction; fish; population viability analysis; risk

Received: March 20, 2015; Accepted: February 3, 2016; Published Online Early: February 2016; Published: June 2016

Citation: Roberts JH, Angermeier PL, Anderson GB. 2016. Population viability analysis for endangered Roanoke logperch. *Journal of Fish and Wildlife Management* 7(1):46-64; e1944-687X. doi: 10.3996/032015-JFWM-026

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Introduction

Population size is often considered the primary determinant of long-term viability (Shaffer 1981). This association results from a variety of intrinsic and extrinsic factors that have stronger effects when abundance is low.

Small populations are more susceptible to catastrophes; inbreeding depression; and environmental, demographic, and genetic stochasticity (Groom et al. 2006). Such risks are exacerbated in small populations with weak density dependence, a low exponential growth rate, or a small carrying capacity (K) (Hanski 1990; Lande 1993).





Figure 1. Photograph of an adult male Roanoke logperch *Percina rex*, approximately 135 mm in total length. Copyright Chris Crippen, Virginia Living Museum, November 2012.

In theory, there exists a minimum viable population size (MVP) above which a given population's risk of extinction from all of these factors is acceptably low (Shaffer 1981). Therefore, despite some criticisms (e.g., Flather et al. 2011), the MVP has long been a popular tool for setting quantitative abundance targets for recovery of poorly studied, nonexploited fish and wildlife species (Brook et al. 2011). The MVP of a focal species is expected to vary based on taxonomy, life history, and environmental variability (Gilpin and Soule 1986; but see Reed et al. 2003). Theoretical and empirical estimates of MVP range among species from hundreds to hundreds of thousands of individuals, numbers far greater than the actual current population sizes of many imperiled species (Allendorf et al. 1997; Reed et al. 2003; Traill et al. 2007), suggesting that many imperiled populations will not be viable over the long term.

The difficulty of accurately estimating species-specific MVP presents one of the biggest challenges to the broader use of the MVP concept in conservation planning. In some cases, time series of observed population extinctions can be used to model empirical relationships between population size, other ecological factors, and extinction risk (e.g., Newmark 1987; Pimm et al. 1988; Berger 1990; Morita and Yamamoto 2002) and thereby establish MVPs. However, such data are not available for the majority of species of conservation concern. For species for which population extinctions cannot be observed, population viability analysis (PVA) is a commonly used alternative tactic for modeling extinction probability (Morris and Doak 2002). In PVA, simulation models are parameterized based on assumptions about demography and life history, environmental variability, and management activities and then used to forecast population size over some time horizon into the future. This process is repeated thousands of times, to obtain a count of how often population size remained above zero (or some other threshold) for the duration of the simulation. By iteratively changing model input

parameters, we can assess the influence on extinction of demographic, life-history, environmental, and management factors, as well as uncertainty about these quantities. Model outputs can then be incorporated into conservation plans to enhance their cost-effectiveness.

Roanoke logperch *Percina rex* is a stream fish that persists in seven isolated populations in Virginia and North Carolina (Roberts et al. 2013; Figure 1). Within these populations, the species is patchily distributed among silt-free riffle habitats (Rosenberger and Angermeier 2003). Loss of silt-free habitat, habitat fragmentation by dams, and catastrophic fish kills from chemical spills are among the most serious ongoing threats to logperch populations (Rosenberger 2007). Due to these threats and perceived historical declines in the species' distribution, the species was listed as "endangered" in 1989, pursuant to the U.S. Endangered Species Act (ESA 1973, as amended). Various federal and state management agencies are involved with assessing the status and facilitating the recovery of the species. The success of these activities relies upon an understanding of current population sizes and their temporal variances, the MVP of the species and whether or not extant populations exceed this threshold, and the potential demographic consequences of alternative management tactics. However, population size has never been estimated for most populations, and the demographic data necessary to characterize population dynamics have not been previously compiled. Furthermore, threats and risks to Roanoke logperch populations have not been quantified, and there have been no previous attempts to characterize the relationship between population size and extinction risk, so no MVP thresholds exist. These knowledge gaps hamper the recovery of the species. Such gaps are common across the speciose darter group (Percidae: Etheostomatinae), despite the potential for PVA to provide insight into the demographic and environmental factors most closely tied to persistence of darter populations (e.g., Williams et al. 1999).

In this study, we conducted a PVA for Roanoke logperch based on available demographic data for this species and the environmental characteristics of the watersheds in which it lives. Models were constructed and evaluated under a stochastic count-based PVA framework (Morris and Doak 2002) that incorporated uncertainty in current population-size estimates, the form of density dependence, and the frequency and severity of catastrophes. We also simulated a variety of realistic alternative demographic-augmentation strategies. Our objectives were to use PVA models to 1) estimate the sensitivity of estimated extinction probabilities to model inputs and their uncertainty, 2) evaluate the possible benefits of alternative augmentation strategies, 3) estimate MVP for Roanoke logperch, 4) use MVP estimates to gauge the viability of extant logperch populations, and 5) identify important needs for future research.

Methods

Choice of modeling framework

There are various modeling frameworks within which to conduct a PVA. These models vary in complexity and realism, especially with regard to the number of required biological input parameters, degree of spatial explicitness, and assumptions about stochasticity (Beissinger and Westphal 1998; Morris and Doak 2002). “Demographic” PVA methods, for example, require the input of age- or stage-based survival and fecundity estimates (and their variance) in a Leslie or Lefkovich matrix. Such models can be based on a single panmictic population or a series of interconnected populations in a spatially explicit metapopulation (e.g., Akçakaya 1998). The disadvantage is that such models require detailed demographic knowledge and a large number of input parameters, which may be unavailable or poorly estimated for many taxa. Because we lacked reasonable estimates of age- or stage-based annual survival and fecundity for Roanoke logperch, we used a “count-based” approach to PVA. Count-based models ignore internal demographic details, focusing instead on their ultimate consequence: temporal variation in abundance. Although count-based models are relatively simple, they can provide valuable information on extinction risk and the potential effects of alternative management scenarios (Dennis et al. 1991; McGowan and Ryan 2010). This approach was appropriate for Roanoke logperch, because we had access to a relatively long (17-y) time series of population counts from the Roanoke River population and point estimates of population size in most other populations. These datasets allowed us to parameterize simulation models with estimates of initial population size, population growth rate, and the density dependence relationship, which are the primary features of a count-based model (Morris and Doak 2002). We opted to analyze each population in isolation and treat each as a demographically panmictic unit because genetic studies

have indicated that this accurately reflects contemporary population structure for the species (Roberts et al. 2013).

Our focal models simulated population dynamics and estimated extinction probabilities and MVPs over a time frame of 100 y, defining as viable those populations that exhibited a less than 0.05 probability of extinction over this period. All models assumed constant demographic and environmental conditions (growth rate, K , environmental stochasticity, and catastrophe probability) over the 100-y duration of simulations, as obtainable data (Anderson et al. 2014) indicate no temporal trends in these features. From a biological standpoint, a 100-y time frame is somewhat arbitrary, representing approximately 22 Roanoke logperch generations (Roberts 2012). However, we reasoned that from a management standpoint, achieving persistence over 100 y was long enough to be meaningful for conservation goal-setting, but short enough to avoid overextension of our predictions about future conditions. The 0.05 probability criterion is likewise biologically arbitrary as an “acceptable” risk, but both this criterion and the 100-y time frame are consistent with standards used by others to gauge the viability of threatened fish populations (Thompson 1991; Allendorf et al. 1997; Hilderbrand 2002). For comparison, we also conducted simulations using alternative time frames (50 and 200 y; see below), to evaluate the influence of this modeling choice on extinction estimates. We did not explore alternative acceptable-risk thresholds in the present analysis, but future users of these models could conduct such an analysis to determine the outcomes of alternative policy preferences. All models were written and implemented in R version 2.13.0 (R Development Core Team 2011); code is provided as Supplemental Material.

Model input parameters

Initial population size. Age-0 Roanoke logperch are difficult to reliably capture (Rosenberger and Angermeier 2003) and constitute a small percentage of the fish that are captured using the sampling methods on which the data used in this study are based (~6%; Anderson et al. 2014). Therefore, throughout this study, we focused only on catch and population size of age-1 or older fish (hereafter adults). All subsequent statements about population size and MVP refer only to the adult component of populations. For five of the seven known Roanoke logperch populations (Roanoke, Pigg, Otter, and upper Smith rivers and Goose Creek), we compiled available published and unpublished data on fish catch (raw number of adult fish captured per riffle during sampling events), abundance of suitable habitat patches (number of riffles per kilometer of stream), and known range extent (kilometer of stream), using these to derive estimates of initial population size (N_0). We focused on riffle habitats because, except in Nottoway River, logperch adults strongly prefer deep, fast riffles (Rosenberger and Angermeier 2003). For the other two populations (Nottoway and lower Smith rivers), no

comparable estimates of fish catch or patch spacing were available, so these populations were not analyzed. Fish catch estimates for the Roanoke River were obtained from Roberts (2003) and Anderson et al. (2014), estimates for the upper Smith River from Anderson et al. (2013), and estimates for the Pigg and Otter rivers and Goose Creek from Lahey and Angermeier (2007). For each population, we fit a negative binomial distribution to fish-catch-per-riffle data. We used the negative binomial in lieu of the Poisson because data were overdispersed. Estimates of riffle frequency and range extent were obtained from Roberts (2003, 2012) and used to estimate the mean total number of riffles available to be occupied by the population ($meanriffle = \text{riffle frequency times range extent}$). We had no empirical measures of uncertainty for these estimates, but assumed that the standard deviation of our estimates ($SDriffle$) was 10% of the mean (i.e., a coefficient of variation of 0.1, similar to rates of observation error in reach-scale habitat measurements determined by other studies; Roper et al. 2002).

To convert raw fish catch to a measure of population size (corrected for incomplete detection), we needed an estimate of capture probability ($p = \text{raw catch divided by abundance}$). Anderson et al. (2014) used an N -mixture model (Sólymos et al. 2012) to estimate abundance of Roanoke logperch at riffles from count data collected biannually for 17 y at 12 riffles in the Roanoke River. Based on 361 sampling events, the mean ($meanp$) and standard deviation (SDp) of p across riffles were 0.092 and 0.029, respectively. Mark-recapture studies of Roanoke logperch have observed similar capture probabilities by using this method (J. Roberts, personal communication). No estimates of p were available for other populations, but because all of the catch data described above were collected using the same method—electrofishing into a stationary seine net—we assumed that this estimate and variance of p were applicable to all populations.

We incorporated our uncertainty regarding the current abundance of fish and riffles via a Monte Carlo approach, by allowing the derived estimate of N_0 to vary stochastically among replicate model runs. For a given population (q) in a given replicate model run (i ; see below), N_{0qi} was determined based on a series of steps. First, we estimated the number of riffles (z_{qi}) in that population in that model run by drawing a random value from a normal distribution with mean = $meanriffle_q$ and standard deviation = $SDriffle_q$. Second, we assigned each riffle a fish catch by drawing a random value from a negative binomial distribution fit to population q 's fish-catch-per-riffle data (see above). Third, we assigned each riffle a p value by drawing a random value from a normal distribution with $meanp$ and SDp . If this calculation resulted in a value less than 0, a value of 0 was substituted instead. Fourth, for each riffle, we divided catch by p to calculate abundance at that riffle. Finally, abundances were summed across all z_{qi} riffles to obtain a

total population N_0 for that replicate model run. This process was repeated for each of the i model runs for each population. This provided a sample distribution from which a mean and variance estimate of current population size was developed for each of the five populations. These estimates were subsequently compared to MVP estimates to gauge the viability of each of the five populations. Estimates were also used to seed “downstream” PVA simulations with N_0 values (Figure 2).

Population growth. In PVA models, populations started at size N_0 in year 0. In each subsequent year (t), population size (N_t) was determined by population size in the previous year (N_{t-1}), a population growth model with environmental stochasticity, a catastrophe model, and an augmentation model. To determine the most appropriate population growth model for Roanoke logperch, we again analyzed the time series of abundance estimates of Anderson et al. (2014) for the Roanoke River (see Table S1). We averaged abundance across riffles within each of the two sampling seasons (summer and autumn) within each of the 17 y. Then, following Morris and Doak (2002), we estimated the natural logarithm of population growth rate [$\ln(\lambda)$] for each of the 14 summer and 14 autumn interannual intervals (some data were missing), as $\ln(\lambda_y) = \ln(N_{y+1}/N_y)$, where N is the abundance estimate and y is the sampling year. This resulted in a time series of 14 summer and 14 autumn $\ln(\lambda_y)$ estimates, which we pooled for further analyses.

We used nonlinear regression and an information-theoretic approach to evaluate the fit of alternative density dependence models to the time series of $\ln(\lambda_y)$ estimates. Three models were evaluated, featuring different assumptions about the form of density dependence: 1) density independent model, in which $\ln(\lambda_y) = r + \sigma^2$; 2) Ricker density-dependent model, in which $\ln(\lambda_y) = r[1 - (N_y/K)] + \sigma^2$; and 3) theta-logistic density-dependent model, in which $\ln(\lambda_y) = r[1 - (N_y/K)^\theta] + \sigma^2$. The r , K , and θ terms represent the exponential rate of increase, carrying capacity, and density dependence shape parameters, respectively, whereas the σ^2 term represents the model residual variance (Morris and Doak 2002). Ricker and theta-logistic models differ in that in the former, $\ln(\lambda_y)$ declines linearly as N_y increases, whereas in the latter, this relationship can be nonlinear. Models were fit using the nls function in R and ranked based on Akaike's Information Criterion adjusted for small sample size (AIC_c ; smaller values are better) and model weights (larger values are better; Burnham and Anderson 2004). The best-fitting (i.e., smallest AIC_c) model was assumed to be the best model of population growth, and these parameters were used to model growth in subsequent simulations. In modeling growth, we assumed that the r and θ estimates (if applicable) from the best-fitting Roanoke River model applied to other populations as well. We did not assume that the K for the Roanoke River was applicable to other populations, but we lacked empirical estimates of K for these

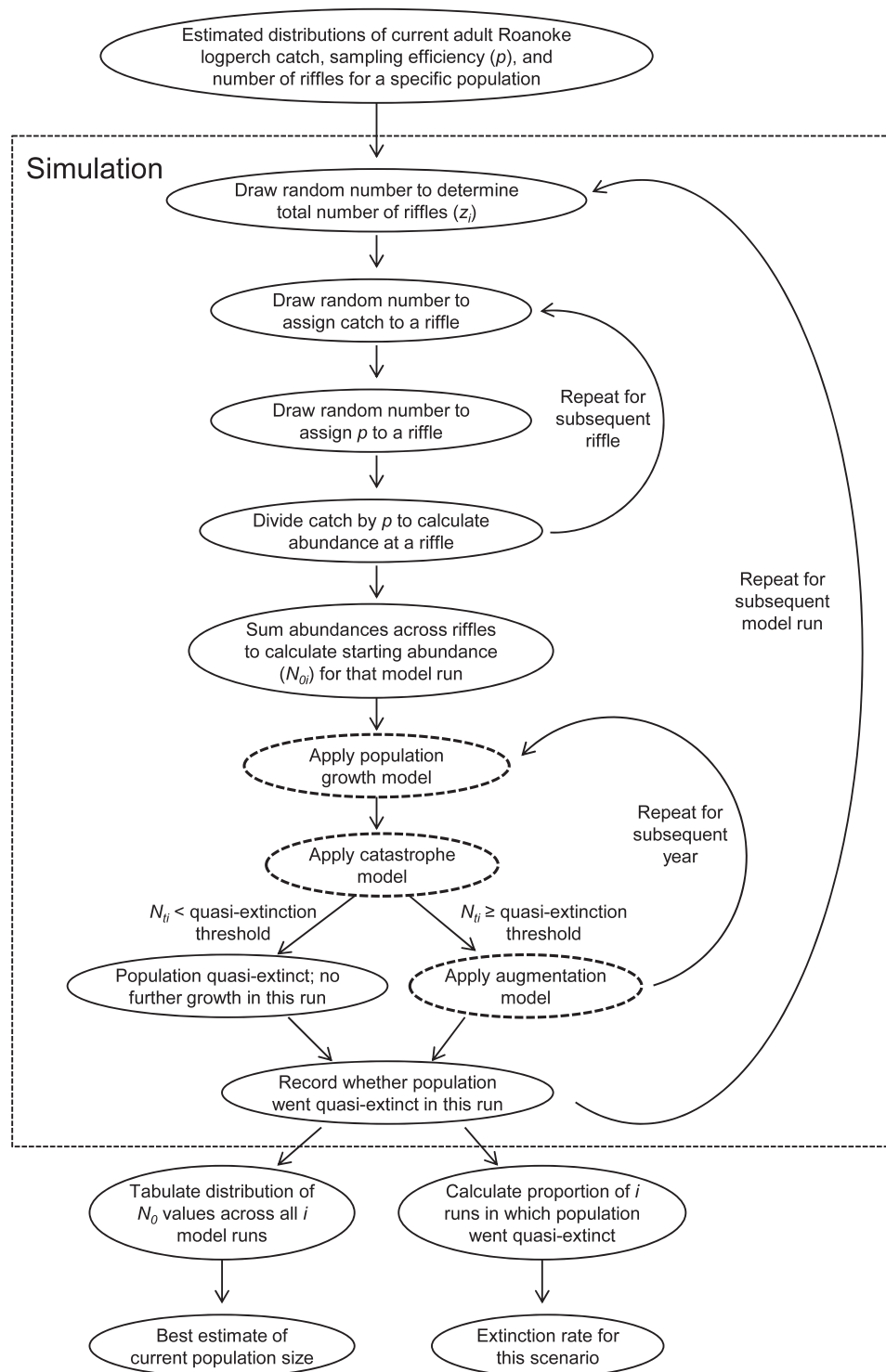


Figure 2. Conceptual diagram showing the workflow for estimating current population size and extinction risk for populations of Roanoke logperch *Percina rex*. Dotted ovals indicate the key factors that were varied among population viability analysis scenarios (i.e., the population growth, catastrophe, and augmentation models). Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

populations. We therefore assumed that $K = N_0$ for each population, in other words, that each population started at its K and that our estimate of N_0 was a reasonable expectation of K . The consequences of this assumption were evaluated during sensitivity analyses (see below).

Once the optimal population growth model was selected, we tested whether temporal autocorrelation in growth rates was significant and needed to be accounted for in PVA models. To do so, we calculated the Pearson correlation coefficient between the vector of

model residuals for year y and the vector of residuals for year $y+1$ (Morris and Doak 2002).

Environmental stochasticity. The effect of environmental stochasticity on population growth was simulated via a random variance term in the population growth equation. This term had a normal distribution with mean = 0 and variance = $[(j\sigma^2)/(j - 1)]$, where j is the sample size of observations and σ^2 is the residual variance of the best-fitting regression model (see above; Dennis et al. 1991; Morris and Doak 2002). This approach assumed that the 17-y Roanoke River dataset was sufficient for capturing the full range of population variability due to environmental stochasticity. Given that this study period encompassed some of the highest and lowest stream-flow events on record for the Roanoke River, this assumption seemed tenable. A more tenuous assumption was that population size was estimated without error and thus that all residual variance was due to the influence of environmental stochasticity on population growth. Confounding of these two sources of variance likely decreased the precision of model parameter estimates, resulting in wider estimates of population growth and more conservative assessments of extinction risk.

Catastrophes. Catastrophes reduce the size of populations below the range of variability due to year-in-year-out environmental stochasticity. We chose not to consider floods and droughts as catastrophes for Roanoke logperch, given that these events occur frequently and did not seem to dramatically affect population size within the 17-y Roanoke River dataset. However, we reasoned that anthropogenic disturbances such as chemical spills and discharges that cause fish kills could acutely and dramatically reduce the size of populations and therefore represent an important type of catastrophe. To estimate the frequency and severity of such catastrophes, we consulted published and unpublished reports and natural resource biologists to compile a list of known fish kills potentially affecting Roanoke logperch. The best available set of records was for the region surrounding Roanoke, Virginia, so we focused on the Roanoke River population and fish kills affecting water bodies therein. Based on these data, we estimated the per-year probability of a catastrophe occurring ($probcast$ = the number of fish kills divided by the number of years of observation). We assumed that this probability would be similar among populations, as would the typical length of stream affected. In most cases, data were available about the extent of the fish kill, in terms of stream length affected (kilometers), which is our measure of catastrophe severity. These data were used to estimate the proportion of the population affected by a given catastrophe (=mean stream length affected divided by total range extent of the population). This calculation accounted for the fact that a fish kill affecting a given length of stream would have a greater impact on population size in a geographically small population than a geographically large population. To

make catastrophe severity a random variable, we fit a beta distribution to the empirical distribution of population proportions affected by a catastrophe. In each year of PVA simulations, to determine whether a catastrophe occurred, a value was randomly drawn from a binomial distribution with probability = $probcast$. If the draw was a 1, a catastrophe was implemented. To determine the severity of this catastrophe ($severecast$), a value was then randomly drawn from the beta distribution described above. Population size was then reduced by multiplying N_t by one minus $severecast$.

Augmentation scenarios. We used simulation models to investigate the potential demographic benefits of four alternative augmentation strategies representing plausible scenarios of population variation and propagation capacity. Augmentation strategies involved either 1) no stocking, 2) one-time stocking of 1000 fish into the population in year 1, 3) stocking of 200 fish every 5 y, or 4) stocking of 200 fish in any year that population size was below 500 individuals. The latter strategy assumed that the population was monitored. We also simulated a variety of additional augmentation strategies involving alternative stocking densities and intervals, but results were qualitatively similar to results from models above and are not presented herein (results available from the authors upon request). These augmentation strategies were applied after N_t was determined by the stochastic population growth and catastrophe models, if N_t was still above the quasi-extinction threshold (N_x , see below). If, after population growth and catastrophes, N_t was below the quasi-extinction threshold, the population was considered extinct and no further augmentation was pursued for the remainder of that model run. Thus, each annual population “census” that described N_t occurred before augmentation and did not include any individuals that were subsequently stocked in year t , although it potentially included individuals that had been stocked in previous years. This approach assumed that augmented fish were functionally equivalent to naturally recruited fish.

Quasi-extinction threshold. In baseline models, we considered a population to be extinct if N_t dropped below an N_x of 50 individuals during any year within a given simulation run. We opted to use this N_x instead of a true extinction threshold (i.e., zero individuals remaining) because populations smaller than 50 individuals are known to be vulnerable to Allee effects, demographic stochasticity, and inbreeding depression (Lande 1988; Groom et al. 2006). We presumed that any population that had declined to such low levels would become trapped in an “extinction vortex” (Gilpin and Soulé 1986) and subsequently become extirpated. We had no way of empirically estimating an alternative, species-specific threshold for Roanoke logperch, given that we do not know enough about its breeding biology or genetic characteristics to pinpoint the onset of these deleterious factors. However, we view the threshold of 50 as reasonable, for three reasons. First, at population sizes

Table 1. Summary of conditions under which we assessed each model input variable's influence on estimates of extinction risk for the Otter River (Virginia) population of Roanoke logperch *Percina rex*. Extinction probability was estimated with each variable fixed at its “pessimistic” or “optimistic” value, while holding all other model inputs at their “baseline” values. Model sensitivity to each variable was then measured as the difference in extinction probability between pessimistic and optimistic models. Pessimistic parameter values for the exponential rate of increase and carrying capacity were based on the fitted Ricker model. Parameter ranges were based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

Parameter	Pessimistic	Baseline	Optimistic
Population growth model	Density independent	Ricker	Ricker
Exponential rate of increase	0.264	0.597	0.931
Carrying capacity	1473	2106	2916
Initial population size	1473 (constant)	2106 (variable)	2916 (constant)
Catastrophe regime	Yes	Yes	No
Augmentation regime	None	None	Scenario 4
Quasi-extinction threshold	100	50	10
Duration of simulations	200	100	50

of 50 or less, Allee effects, demographic stochasticity, and inbreeding depression can override environmental stochasticity in influencing persistence (Franklin 1980; Lande 1988), but these effects cannot be mathematically built into the models herein due to limited knowledge of how they affect Roanoke logperch. Second, given the geographic extent of these populations (see below), an abundance of 50 individuals represents an extraordinarily low fish density, comparable to other stream-fish populations that did not persist (e.g., Hilderbrand and Kershner 2000; Morita and Yamamoto 2002; Perkin and Gido 2011). Third, like previous investigators, we found it prudent to use a more conservative conservation target than “one or more individuals” for modeling viability of an endangered species (Thompson 1991; Allendorf et al. 1997). Nonetheless, to assess the influence of this modeling choice on estimates of extinction risk, we ran alternative simulations featuring lower (10) and higher (100) quasi-extinction thresholds and compared estimates to those from baseline models featuring a threshold of 50 individuals.

Calculation of extinction probability. For each unique model configuration, we simulated population dynamics across 10^4 replicate model runs. To estimate the probability of extinction under a given configuration, we counted the number of replicate runs in which N_t dropped below the N_x (50 individuals in most cases) during any point in the simulation (100 y long in most cases), and divided this count by 10^4 . This workflow is shown in Figure 2.

Sensitivity of extinction estimates to model inputs

We assessed the sensitivity of extinction-risk estimates to the influence of uncertainty in the following input variables or model choices: population growth model, r , K , N_0 , catastrophe regime, augmentation strategy, N_x , and duration of simulations (Table 1). Initially, we sought to measure sensitivity in two focal populations, those with the largest and smallest estimated mean N_0 , to bracket other populations. However, extinction risk was always near zero for the largest population (Roanoke River), so only results from the smallest population (Otter

River) are shown and discussed. Model sensitivity was assessed by first establishing “pessimistic,” “baseline,” and “optimistic” values for each input variable of interest (Table 1). Baseline values of variables included the best-fitting growth model, mean estimates of r and K from the best-fitting growth model, mean estimated N_0 for that population, empirically estimated catastrophe regime for that population, no augmentation, an N_x of 50, and simulation for 100 generations. Pessimistic values of variables included the density-independent growth model, lower 95% limits of r and K from the best-fitting growth model, lower 95% limit of N_0 for that population, more severe catastrophe regime, no augmentation, N_x of 100, and simulation of 200 generations. Optimistic values of variables included the Ricker growth model, upper 95% limits of r and K from the best-fitting growth model, upper 95% limit of N_0 for that population, no catastrophes, no augmentation, N_x of 10, and simulation of 50 generations. For each input variable in turn, we estimated the probability of extinction with that variable held at its pessimistic value, then with that variable held at its optimistic value, in each case holding all other variables at their baseline values. We then calculated a sensitivity score for each variable as the difference between these two extinction rates. Large sensitivity scores are thus indicative of variables for which uncertainty has a large effect on model estimates of extinction. Note that N_0 was a random variable (see above) when at its baseline value but was held constant at a low (pessimistic) or high (optimistic) value in those simulations that assessed the influence of N_0 on extinction.

Estimating MVP

To estimate MVP for a “generic” Roanoke logperch population, we ran PVA models under a range of initial population sizes. To account for uncertainty in population growth and catastrophe regimes, we also estimated MVP under alternative assumptions about these factors. Based on preliminary analyses, for density-independent growth, we estimated the probability of extinction for each of 1000 different N_0 values that ranged from 10^3 to

10^6 individuals, in intervals of 1000 individuals. For density-dependent growth, we used a smaller range of values, estimating the probability of extinction for each of 100 different N_0 values that ranged from 10^2 to 10^4 individuals, in intervals of 100 individuals. Catastrophe scenarios included 1) no catastrophes; 2) a less severe catastrophe severity, in which *severecast* was set to the value of a geographically extensive population; and 3) a more severe catastrophe severity, in which *severecast* was set to the value of a geographically narrow population. Because we were interested in MVP in the absence of human intervention, we did not subject MVP simulations to augmentation. We defined MVP operationally as the smallest initial population size that resulted in a less than 0.05 probability of declining below 50 individuals over the 100-y simulation time frame. This workflow is shown in Figure 3.

Results

Current population size

Among the five Roanoke logperch populations for which we had fish-catch data, mean adult catch ranged from 0.33 fish per riffle (Otter River) to 2.35 fish per riffle (Roanoke River; Table 2). Because riffle spacing and range extent varied considerably among populations, the estimated total number of riffles within each population's range was likewise variable, ranging from 153 riffles (upper Smith River) to 1225 riffles (Pigg River; Table 2). Based on spatial variation and uncertainty in fish catch and riffle abundance, the estimated mean (95% confidence interval) of adult fish abundance ranged from 2106 (1473, 2916) in Otter River to 16875 (12 893, 21 928) in Roanoke River (Table 2). Because Roanoke and Otter populations bracketed the range of estimated population sizes, these two populations were used as the basis for defining less severe and more severe catastrophes, respectively, and were further used for exploring the sensitivity of extinction risk to uncertainty around model inputs.

Population growth

Based on AIC_c and associated model weights, the Ricker density-dependent model was the model of population growth that best fit the 17-y time series of Roanoke logperch abundances in the Roanoke River (Table 3). The theta-logistic model had substantially less support, and the density-independent model was least supported by the data (Table 3). The Ricker model exhibited good fit to the empirical data ($R^2 = 0.34$; Figure 4). Residual variance in this relationship was used to estimate environmental stochasticity. Based on residuals of the Ricker model, first-order autocorrelation between successive years was weak (Pearson's $r = 0.23$) and not statistically significant ($P = 0.27$), indicating that temporal autocorrelation was not a major driver of population dynamics. In other words, population growth of Roanoke logperch in a given year was not correlated with growth

in the preceding or subsequent years. We used the exponential growth rate ($r = 0.5967$) and environmental stochasticity ($\sigma^2 = 0.0745$) parameter values from the Ricker model as our best estimates of these parameters in subsequent baseline PVA simulations using Ricker population growth, but set K in such simulations equal to initial population size.

Although the density-independent model had relatively poor empirical support, we considered it prudent to take a conservative approach and also estimate extinction risk under density-independent growth, to complement estimates from better supported but more liberal models that assumed density dependence (Ginzburg et al. 1990). In simulations using density-independent population growth, we used the environmental stochasticity parameter value ($\sigma^2 = 0.1128$) from the fitted density-independent model (Table 3). However, we did not use the exponential growth parameter value ($r = -0.0099$) from this model because it was slightly negative and likely would have overestimated extinction risk. Moreover, the 95% confidence limits of this estimate overlapped zero. We assumed that slightly negative mean population growth in the Roanoke River was a chance occurrence, rather than a general feature of Roanoke logperch population dynamics. Therefore, in density-independent PVA simulations we assumed that the long-run average of r was zero (i.e., average λ was 1) and parameterized simulations as such.

Catastrophe regimes

Reliable data on the frequency and severity of anthropogenic fish kills were available only for the region surrounding the Roanoke River population of Roanoke logperch and were available only for two time periods: 1970–1982 and 1991–2013 (Table 4). Fish kill data for the former period were synthesized by Burkhead (1983). The latter period represents the time frame of modern, organized record keeping by state and federal resource agencies in the region (K. Smith, U.S. Fish and Wildlife Service, and M. Pinder, Virginia Department of Game and Inland Fisheries, personal communications). None of these fish kills overlapped spatially with any of sites of Anderson et al. (2014) during the time period of monitoring there; so, we presume that the data of Anderson et al. (2014) did not reflect the demographic effects of this type of catastrophe. Over the combined 35-y span, seven reported fish kills in total occurred in the Roanoke River watershed in streams containing logperch, for a probability of a fish kill of 0.2 per year. We used this estimate of catastrophe probability (*probcast*) in subsequent simulations. In six of the seven kills, the length of stream affected was reported, and this length averaged 10.1 km. This reach length equates to 8.6% of the known range extent of the Roanoke River logperch population (118 km) and 19.1% of the known range extent of the Otter River logperch population (53 km; Table 2). Assuming a total kill in the affected area, the average catastrophe reduced these two populations'



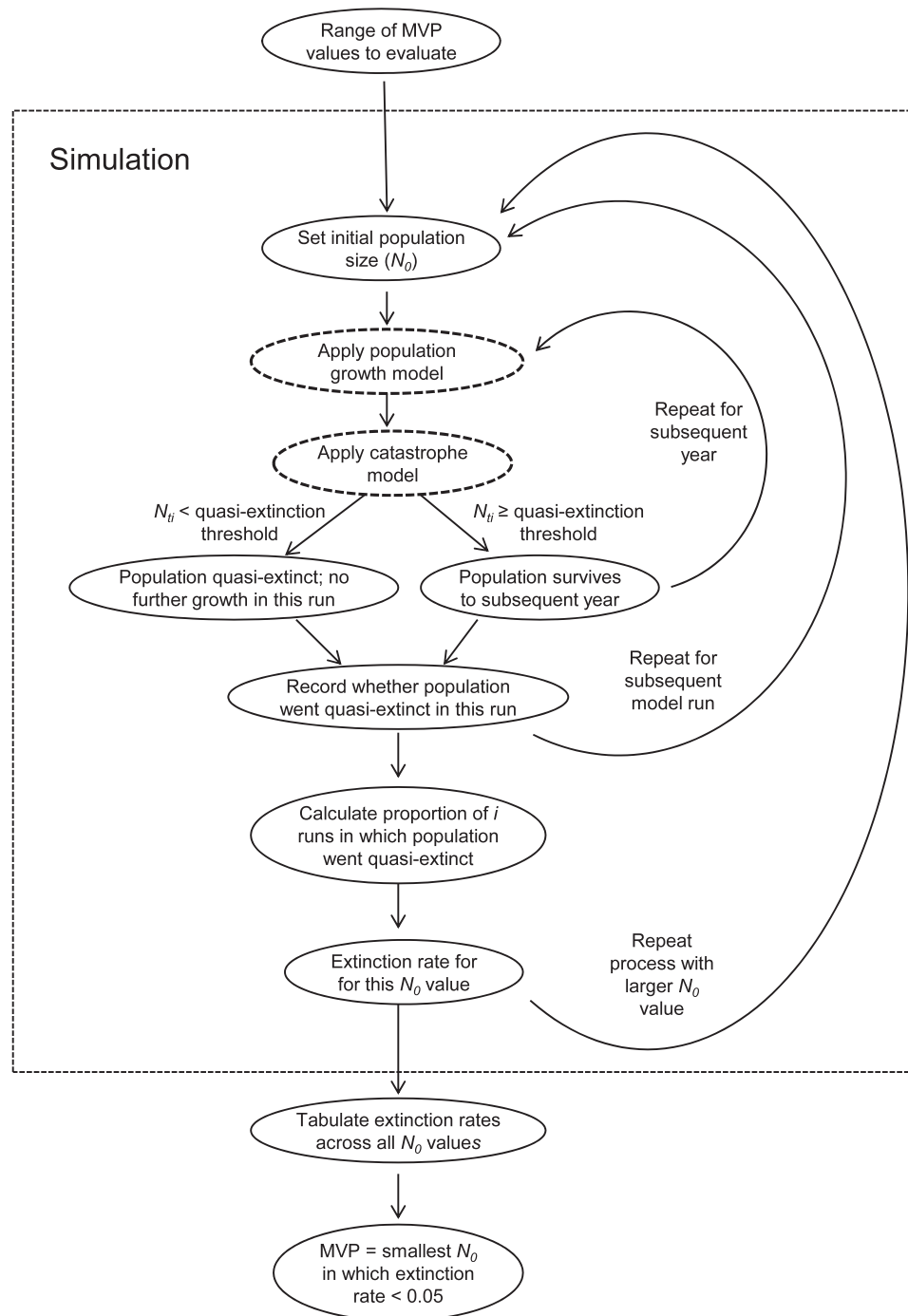


Figure 3. Conceptual diagram showing the workflow for estimating minimum viable population size (MVP) based on simulated “generic” populations of Roanoke logperch *Percina rex*. Dotted ovals indicate the key factors that were varied among population viability analysis scenarios (i.e., the population growth and catastrophe models). Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

abundances by 8.6 and 19.1%, respectively. To turn catastrophe severity into a random variable, we identified beta distributions that closely emulated the statistical properties of these relatively less severe (Roanoke-like) and more severe (Otter-like) catastrophe effects. The alpha and beta parameters for the less severe beta distribution were 0.5 and 2.8, respectively, and for

the more severe beta distribution were 0.5 and 1.3, respectively.

Sensitivity of extinction risk to model inputs

The probability of extinction, defined as the proportion of replicate simulations in which N_t fell below the N_x , was almost always near zero for the Roanoke River

Table 2. Input parameters used to estimate current (i.e., initial) population size (N_0) for each of five Roanoke logperch *Percina rex* populations, all occurring in Virginia or North Carolina. Where available, estimates of standard deviation (SD) or confidence interval (CI) are given. Estimates were made during field studies conducted between 2003 and 2014.

Population	Empirical fish catch (fish riffle ⁻¹)		Empirical riffle spacing (riffles km ⁻¹)	Empirical range extent (km)	Estimated total no. of riffles		Estimated current population size (N_0)	
	Mean (SD)	Negative binomial probability of catch			Mean (SD)	Mean (95% CI)		
Roanoke River	2.35 (2.20)	0.299	4.57	118	539 (54)	16875 (12 893, 21 928)		
Pigg River	0.56 (1.04)	0.640	12.25	100	1225 (123)	9281 (6780, 12 011)		
Goose Creek	0.40 (0.58)	0.714	10.10	40	404 (40)	2111 (1466, 2904)		
Otter River	0.33 (0.42)	0.750	9.07	53	481 (48)	2106 (1473, 2916)		
Upper Smith River	1.63 (1.85)	0.380	5.47	28	153 (15)	3285 (2234, 4542)		

population. We therefore focused sensitivity analyses on the Otter River population, which exhibited a higher and more variable extinction probability that was more responsive to model inputs. By far the most influential model input was the population growth model. With all other variables held at baseline values, the estimated extinction probability for Otter was 11% under Ricker growth but 92% under density-independent growth (Figure 5). Thus, on a 0–1 scale, the sensitivity score of population growth model was 0.81.

Choices about N_x (baseline = 50 individuals, range = 10–100) and the duration of simulations (baseline = 100 y, range = 50–200) also had a substantial effect on estimates of extinction risk, with N_x being slightly more influential than duration (sensitivity scores of 0.23 vs. 0.16, respectively; Figure 5). These two factors also interacted, in that simulation duration had little effect if N_x was 10 but a strong effect if N_x was 100 (Figure 6).

Simulated uncertainty in the Ricker model parameters r and K had less influence on extinction than did uncertainty in the overall form of population growth (density dependent vs. density independent). Of the two parameters, r had a higher sensitivity score (0.16) than K (0.07), indicating that extinction estimates were more influenced by population growth rate than by K (Figure 5). Underestimation of r (e.g., use of baseline if optimistic was correct) seemed to have little effect on extinction, whereas overestimation of r (e.g., use of baseline if pessimistic was correct) would result in an 11–14% underestimation of extinction rate, depending on the K (Figure 6).

In contrast to r and K , initial population size had almost no effect on extinction (sensitivity score < 0.01; Figure 5). This indicates that setting N_0 much larger or

smaller than K had no effect on extinction because N quickly returned to K in density-dependent models. It also indicates that the assumption that $N_0 = K$ in baseline Ricker models had little influence on model results. The sensitivity score of catastrophe regime was 0.11, making this factor more influential than K , but less influential than r (Figure 5). In Ricker models, extinction probability of the Otter population ranged from 1% in the absence of catastrophes to 11% in the presence of more severe catastrophes, which were modeled after the presumed catastrophe regime in Otter River.

Influence of augmentation on extinction risk

Overall, augmentation was not effective at reducing estimated extinction probability for the Otter population of Roanoke logperch. The most intensive augmentation strategy was scenario 4: stocking 200 fish each year that N falls below 500 individuals. Under Ricker growth with more severe catastrophes (i.e., baseline conditions), this strategy reduced extinction rate from 11 to 9% (Figure 7). The effects of augmentation scenarios 2 and 3 were even weaker. Concomitantly, the sensitivity score of augmentation regime was only 0.02 (Figure 5). It is worth noting that in contrast to Ricker models, augmentation scenario 4 dramatically decreased extinction probability in density-independent models (Figure 7). However, as described previously, density-independent models were not well supported by empirical data.

Estimates of MVP and viability of specific populations

The MVP was defined as the smallest starting population size that resulted in a less than 0.05 probability of falling below 50 individuals over a 100-y

Table 3. Model fit and parameter estimates for three population growth models fit via nonlinear regression to population growth rates of adult Roanoke logperch *Percina rex* in the Roanoke River (Virginia) between 1997 and 2013. Lower Akaike’s Information Criterion corrected for small sample size (AIC_c) values and higher model weight values indicate better support for a model. Estimated parameters include the exponential rate of increase (r), carrying capacity (K), density dependence shape parameter (θ), and the model residual variance (σ^2). Estimates significantly different from zero are shown in bold and 95% confidence intervals (CIs) are in parentheses

Model	Residual sum-of-squares	AIC_c	Model weight	Parameter estimate			
				r	K	θ	σ^2
Ricker	0.9688	–6.328	0.717	0.597 (0.264, 0.931)	48.923 (43.045, 54.801)	—	0.075
Theta logistic	0.8987	–4.388	0.272	0.108 (–0.104, 0.321)	52.982 (41.745, 64.218)	4.312 (–1.542, 10.165)	0.069
Density independent	1.4660	1.964	0.011	–0.010 (–0.096, 0.076)	—	—	0.113

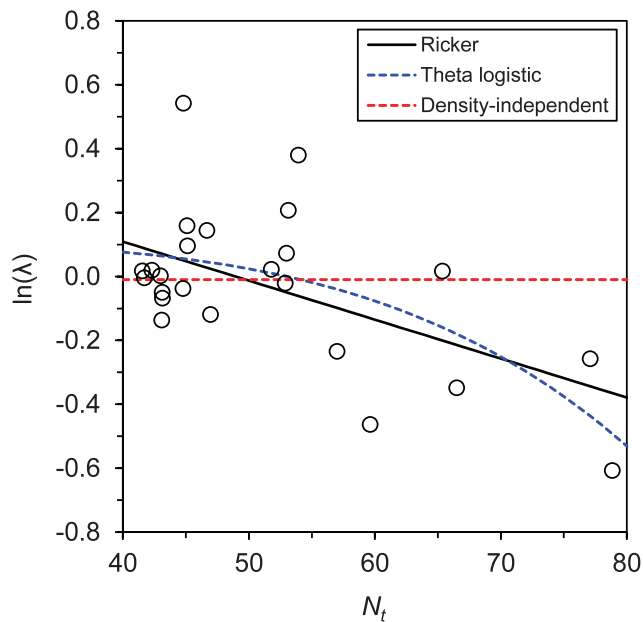


Figure 4. Fit of the Ricker, theta-logistic, and density-independent population growth models (regression lines) to observed interannual population growth rates of Roanoke logperch *Percina rex* in the Roanoke River (Virginia) between 1997 and 2013 (open circles).

simulation time frame. In Ricker models with no catastrophes, less severe (Roanoke-like) catastrophes, and more severe (Otter-like) catastrophes, MVP estimates were 200, 400, and 4200 adults, respectively (Figure 8). Because $N_0 = K$ in these models, these values can also be interpreted as estimates of minimum viable K . Although density-independent growth models were poorly supported by available data, as a conservative, limiting case, we also estimated MVP under density-independent growth with more severe catastrophes. We tested N_0 values as large as 10^6 and the extinction probability was still above 0.46 (Figure 8), so we did not continue testing larger N_0 values and could not estimate MVP for this scenario. Estimated MVP for density independence with no catastrophes was 31 000 adults (results not shown). Very large MVP sizes associated with the density-independent model indicate this growth model as parameterized here may not be biologically reasonable;

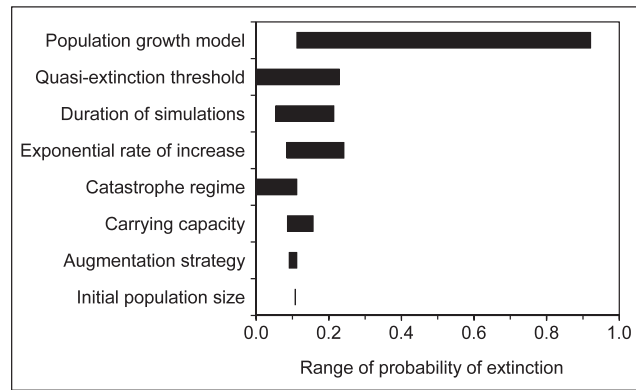


Figure 5. Results of the sensitivity analysis to measure each modeling input variable’s influence on estimates of extinction probability for the Otter River (Virginia) population of Roanoke logperch *Percina rex*. Each bar shows the range of estimated extinction probabilities over the range of input values used for each model variable or choice. Wider bars indicate greater sensitivity to that input. Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river populations between 1997 and 2014.

thus, results associated with this model should be interpreted with caution.

Precise conclusions about the viability of the five real-world populations we examined were impossible due to uncertainty about the MVP for Roanoke logperch. Assuming Ricker growth with no to less severe catastrophes, 95% lower bounds of current population-size estimates are above the MVP threshold of 400 individuals for all five populations (Table 2), so all five populations would be considered viable. In contrast, assuming Ricker growth with more severe catastrophes, only the Roanoke and Pigg populations have a 95% lower bound of N_0 that is greater than 4200 individuals, so only these two populations would be considered viable. Moreover, the 95% upper bounds of N_0 in Goose and Otter are less than 4200 individuals. None of the five populations would be considered viable under any density-independent scenario.

Discussion

Factors affecting extinction risk for Roanoke logperch

Population size typically is presumed to be the best predictor of extinction risk (Shaffer 1981; Reed et al.

Table 4. Summary of all known fish kills reported in the portion of the upper Roanoke River watershed (Virginia) occupied by Roanoke logperch *Percina rex* during two periods (1970–1982 and 1991–2013). Personal communication with the U.S. Fish and Wildlife Service (USFWS) and Virginia Department of Game and Inland Fisheries (VDGIF) occurred during July 2013.

Date of fish kill	Water body	Substance	Stream length affected (km)	Source
October 1970	Roanoke River near Salem	Ethyl benzene-creosote	11.3	Burkhead (1983)
June 1975	Roanoke River near Salem	Unidentified	12.1	Burkhead (1983)
July 1975	Roanoke River near Roanoke	Toluene	Unknown	Burkhead (1983)
June 1976	Roanoke River near Roanoke	Sodium cyanide	12.1	Burkhead (1983)
October 1991	Elliott Creek and South Fork Roanoke River near Shawsville	Liquid manure	19.0	Ensign et al. (1997)
August 2003	Roanoke River near Salem	Various chlorine derivatives	3.8	Kimberly Smith, USFWS
July 2007	North Fork Roanoke River near Blacksburg	Fungicide	2.3	Michael Pinder, VDGIF

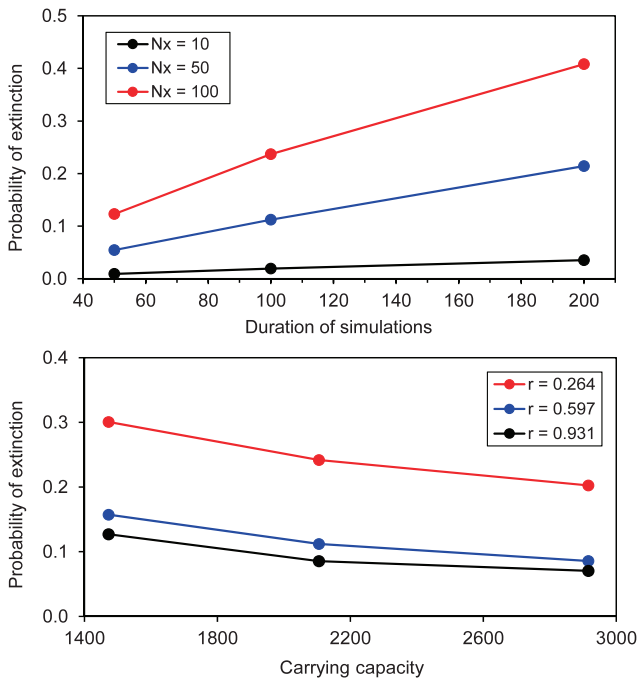


Figure 6. Estimates of extinction probability for the Otter River population of Roanoke logperch *Percina rex* under variable modeling assumptions. Input variables that were varied included the quasi-extinction threshold (N_x) and the number of generations being simulated (top), and the exponential rate of increase (r) and carrying capacity of Ricker population growth models (bottom). In each case, all other parameters were held at their baseline values. Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

2003). Although we found expected negative relationships between current population size and estimated extinction risk of Roanoke logperch populations, this relationship was mediated by other important modeling assumptions and choices. In fact, one of the most salient findings from this analysis was the importance of these “other factors” in determining extinction risk. Based on sensitivity analyses, the most influential of these model features was the form of population growth. We contrasted density-independent and density-dependent models and found that density dependence had a strong stabilizing influence on population size and dramatically increased the probability of persistence, consistent with previous studies of population biology (Hanski 1990; but see Dochterman and Peacock 2013). Even the smallest population (Otter River) undergoing the most severe catastrophe regime exhibited an extinction risk of less than 12% under Ricker growth, compared to an extinction risk of more than 90% under density-independent growth.

Although simulated uncertainty in the population growth model had a large effect on extinction risk, we had considerable evidence that the Ricker density-dependent model was the best representation of

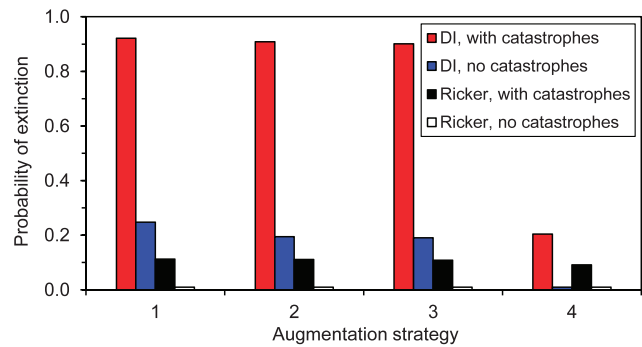


Figure 7. Estimates of extinction probability for the Otter River population of Roanoke logperch *Percina rex* under variable modeling assumptions. Input variables that were varied included the population growth model (Ricker vs. density independent [DI]) the demographic augmentation strategy. Augmentation strategies involved either no stocking (1), stocking 1000 fish in the first year (2), stocking 200 fish every 5 y (3), or stocking 200 fish in any year population size fell below 500 individuals (4). In each case, all other parameters were held at their baseline values. Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

population regulation for Roanoke logperch. Empirical abundance data from the Roanoke River strongly supported this model over all others and further suggested a K of about 49 adult fish per riffle in that population. Negative density dependence has been observed in various other stream-dwelling fishes, including trout and salmon (Strange et al. 1992; Grossman et al. 2012; Dochtermann and Peacock 2013), sculpin (Grossman et al. 2006), and minnows (Schlosser 1998;

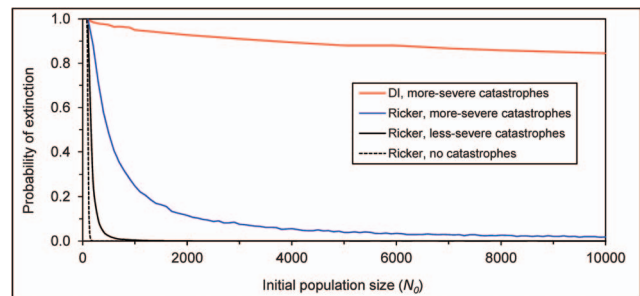


Figure 8. Results of population viability analysis models investigating the influence of varying starting population sizes (N_0 values) on the estimated probability of extinction for Roanoke logperch *Percina rex*, given alternative assumptions about whether population growth follows a density independent (DI) vs. Ricker model, and whether catastrophes are more severe (Otter like), less severe (Roanoke like), or nonexistent. We considered the minimum viable population size (MVP) to be the smallest N_0 value for which the extinction probability was less than 0.05. For the red, blue, solid black, and dotted black curves, these MVP values were $> 10^6$, 4200, 400, and 200 individuals, respectively. Simulation models were parameterized based on empirical data collected in the Roanoke and Otter river (Virginia) populations between 1997 and 2014.

Matthews et al. 2001). Moreover, density dependence matches intuitive expectations based on the biology of Roanoke logperch. The species is a feeding and spawning microhabitat specialist (Rosenberger and Angermeier 2003), and the prevalence of suitable microhabitats (i.e., silt-free, moderate- to high-velocity patches of coarse substrate) varies widely from year to year, presumably due to annual variation in hydrologic regimes (Anderson et al. 2014). This potentially creates competition for feeding and spawning habitat, forcing inferior competitors into less optimal patches and lowering their probability of survival and subsequent reproduction. Yet the large r of the fitted Ricker model indicates that logperch populations have high growth potential to rebound when N falls well below K , for example after a year of particularly harsh hydrologic conditions or particularly severe density-dependent mortality.

Although it was not surprising that Roanoke logperch would exhibit density dependence in general, it was more surprising that we would observe strong density dependence on an annual time step. Roanoke logperch exhibit life-history characteristics toward the “periodic” end of the life-history continuum (Winemiller and Rose 1992), including delayed maturity (2–3 y), little parental investment, and long life span (5–6 y; Jenkins and Burkhead 1994). Such traits are expected to produce temporal autocorrelation in abundance, in that a single cohort can dominate the population for multiple years and high-recruitment years may be followed by a string of consecutive low-recruitment years. Lagged population growth responses to low- or high-abundance years should weaken the apparent strength of density dependence and produce temporal autocorrelation in growth rates. However, we saw no temporal autocorrelation or lagged relationships in the Roanoke River dataset. Thus, this analysis of growth rate has provided a signal of density dependence that was not evident from previous analyses of population size alone, which have primarily indicated the importance of density-independent influences such as hydrologic variability (Anderson et al. 2014). Presumably, both density-dependent and density-independent factors interact to regulate the abundance of Roanoke logperch, as has been documented for other stream fishes (Strange et al. 1992; Dochtermann and Peacock 2013).

Although the Ricker model provided the best fit to the Roanoke River dataset, we had no comparable time series of fish counts from other populations. We therefore made the key assumption that the same growth model governed the dynamics of all populations. It seems reasonable to assume that all Roanoke logperch populations are limited in density by the availability of suitable habitat (Lahey and Angermeier 2007), but it is more tenuous to assume that all populations exhibit the same r and K , and that all populations currently are at K (i.e., $N_0 = K$). For example, Dochtermann and Peacock (2013) found significant intraspecific variation in the

strength of density dependence across populations of various salmonid species, and such variation could characterize logperch populations as well. Sensitivity analyses allowed us to evaluate potential consequences of misspecification of these input variables in PVA models. On the basis of these analyses, we conclude that the most costly error would be underestimating r ; in other words, using the r estimate from the Roanoke River population when a lower r value was more appropriate. Under these circumstances, we may have underestimated extinction risk in other populations by 11–14%. We were less likely to have overestimated extinction risk by setting r too high (Figure 6). Misspecification of K had less effect on estimates of extinction, and the *difference* between N_0 and K had almost no effect on extinction, presumably because the strength of density dependence was so strong that population size rapidly returned to K after an initial overshoot or undershoot. Because K overwhelms N_0 as a predictor of extinction risk, another way of exploring the effect of misspecifying K is to examine MVP curves (Figure 8). Under density dependence, all of these curves have an “elbow” beyond which further increases in K ($= N_0$) have minimal effect on extinction risk. In models with no, less severe, and more severe catastrophes, these thresholds occur at approximately 150, 500, and 4000 individuals, respectively. Thus, within a wide range of the modeled parameter space, uncertainty about K did not affect model results as much as the growth model itself, r , and the catastrophe regime

Results of the sensitivity analyses gave us greater confidence about generalizing density-dependent models and parameters across populations. Nonetheless, we considered it prudent to also consider extinction projections under a more conservative model of population dynamics that assumed all interannual variation in growth rate to be due to the action of stochastic, density-independent factors. Density-independent models can be thought of as a limiting case of density dependence with an extremely large K ($\gg N$) and small r . Such models feature much less population stability and make it harder for a population to remain viable (Ginzburg et al. 1990). Adoption of such models would mean setting higher abundance thresholds for MVP and the initiation of management actions. As expected, when we analyzed extinction risk by using such models, the picture changed dramatically. In density-independent models, not even the Roanoke River population was deemed viable (i.e., with a <0.05 probability of extinction over the next 100 y), even in the absence of catastrophes. In our judgment, this finding seems too pessimistic to be true for a population as large as that occupying the Roanoke River. This implausible finding, along with empirical evidence from model fitting to Roanoke River data, corroborates the hypothesis that extinction-risk estimates from density-independent models are inaccurate. However, the large influence of assumptions about population growth models and parameter values on conclusions about population

viability reveals a clear need for better understanding of the temporal dynamics of additional Roanoke logperch populations, beyond the one occupying the Roanoke River. In fact, sensitivity analyses indicate that characterizing these dynamics may be more important than estimating average population sizes, if the goal is to forecast extinction risk.

Another key determinant of extinction risk in PVA models was the frequency and severity of catastrophes, in the form of anthropogenic fish kills. Fish kills were frequent in the Roanoke River watershed over the 35-y period of available data, occurring every 5 y on average, or with a 20% chance in any given year. The average fish kill affected 10.1 km of stream, which we assumed removed roughly 9% of the Roanoke River population. This may seem overly frequent and severe, but is less so than estimates of catastrophe frequency and severity in the Global Population Dynamics Database would suggest (NERC 1999). Reed et al. (2003) analyzed these data for 88 vertebrate species (including fishes) and found that for species with a generation length similar to that of Roanoke logperch (i.e., 4.5 y), catastrophes causing a 33 or 50% reduction in population size occurred with an average chance of 14 or 5%, respectively, in any given year. If we assume a logarithmic relationship between severity and frequency and fit a regression line to these estimates, then the chance of a 9% decline (as assumed in the Roanoke River population) is 42% per year. This suggests that our estimates of catastrophe frequency and severity were conservative.

The influence of simulated catastrophes on extinction was intermediate to the influences of r and K . Furthermore, catastrophes had less influence on extinction risk in Ricker models than in density-independent models, presumably because density dependence allowed populations to rebound quicker from sudden declines. However, even in Ricker models, the catastrophe regime meant the difference between whether Otter River was considered viable or not, as models with and without catastrophes featured extinction risks of 11 and 0%, respectively. Despite the moderate influence of catastrophes in sensitivity analyses, we reason that a better understanding and characterization of fish kills affecting Roanoke logperch would enhance conservation planning, for three reasons. First, relatively small changes in catastrophe severity (Otter like vs. Roanoke like) had large effects on MVP, so refining estimates of catastrophe parameters is a key to accurate estimation of MVP. Second, estimates of fish kill frequency and severity were based solely on data from the Roanoke River watershed, which may or may not be applicable to other watersheds. For example, these values could overestimate catastrophe effects, given that the Roanoke watershed is more urbanized, industrialized, and bisected by roads than other watersheds and may therefore be more susceptible to chemical spills. In contrast, the values could underestimate catastrophe effects, given that fish kills are more likely to go undetected in less populated,

more remote watersheds such as the Goose Creek and Otter, upper Smith, and Nottoway river watersheds. Furthermore, streams differ in discharge rates, which could cause the effect of a given volume of spilled contaminant to vary among populations. Third, our finding that the catastrophe regime has more impact than the augmentation regime on logperch persistence (see below) implies that catastrophe management could be a more effective recovery tactic than augmentation activities.

All of the above-mentioned findings stemmed from simulations with an N_x of 50 individuals, conducted over a time horizon of 100 y. For reasons previously described, these choices seemed to us biologically and practically reasonable, and were consistent with modeling choices made by previous PVA practitioners (Thompson 1991; Allendorf et al. 1997; Hilderbrand 2002). An infinite number of alternative choices could have been made; our analysis of a small subset of these choices indicates that such choices could have a large effect on estimates of extinction risk. Requiring viability over longer time frames increases the risk of extinction, as does requiring population size to remain above a higher N_x . It is important to recognize that the choice of a time frame is a policy decision with no biological basis, whereas the choice of N_x should be based in data and theory about the biology of the focal organism. In the case of Roanoke logperch, we lacked information necessary to develop a species-specific N_x that accounted for the effects of demographic stochasticity, inbreeding depression, and Allee effects, opting instead to use a value of 50 based on previous research on other species (Gilpin and Soulé 1986; Lande 1988; Groom et al. 2006). However, to improve the accuracy of future viability projections for Roanoke logperch, better knowledge of these small-population phenomena would be valuable.

Efficacy of augmentation for reducing extinction risk

Stocking is a long-standing, often effective tool for increasing the size of populations of game and nongame fishes (Trushenski et al. 2010). However, we found that demographic augmentation was ineffective at reducing extinction risk for populations of Roanoke logperch. We developed four realistic, simulated augmentation scenarios based on assumptions about how many fish it would be feasible to collect, propagate, and stock and how often it would be feasible to perform augmentation efforts, monitoring efforts, or both. However, results of PVA models and sensitivity analyses indicate that these resources would be better spent on other research and management priorities.

In Ricker models with catastrophes for the Otter River, the estimated extinction rate was nearly constant regardless of augmentation. This probably is because augmented individuals could increase population size above K for only a short period before negative density-dependent growth brought population size below K again. In density-dependent populations, the average

upper limit of population size can only be as large as K , regardless how many individuals are stocked into that population. Density-independent populations, in contrast, theoretically have no upper limit to population size, so additional stocking always translates into increased population size. As such, the augmentation strategy involving sustained monitoring and stocking (scenario 4) substantially reduced extinction risk in models assuming density independence. However, as previously discussed, these models likely are a poor representation of population regulation in Roanoke logperch. Therefore, instead of focusing on demographic augmentation, a more effective tactic for improving viability of logperch populations might focus on increasing K , for example through habitat restoration. Once K is larger, augmentation might become a more effective tactic for increasing N to the new, higher level of K .

It is important to distinguish that this analysis investigated the ability of augmentation activities to provide a positive *demographic* impact to populations, in the form of decreased extinction risk. An alternative use of augmentation, which we did not explore, is to provide a positive *genetic* impact, in the form of increased genetic diversity and effective population size. Theoretical considerations and studies of other species indicate that relatively few stocked individuals are necessary to restore significant gene flow and effect genetic restoration in recipient populations (Minckley et al. 2003; Yamamoto et al. 2006; George et al. 2009; Hedrick and Fredrickson 2010). Although the present study indicates that demographic augmentation is unlikely to be effective at this time, to the extent that Roanoke logperch populations could benefit from genetic restoration (e.g., Roberts 2012; Roberts et al. 2013), genetic augmentation may be a useful tool for this purpose (Weeks et al. 2011).

Estimation of MVP for Roanoke logperch

How many adult individuals are necessary to maintain a self-sustaining population of Roanoke logperch for the next 100 y? This was the key question of this study, and the answer is subject to considerable uncertainty due to limitations on available empirical data. Revealing key biological uncertainties is among the most useful outcomes of PVA (Beissinger and Westphal 1998; Morris and Doak 2002). In this case, we gained greater understanding of the competing models of population growth and catastrophe intensity that need testing to further hone estimates of MVP. By far the best available dataset for understanding both of these processes comes from the upper Roanoke River. Obtaining comparable demographic and fish kill datasets from other populations would enhance our ability to confidently answer the question posed above.

Based on our best estimates of density dependence parameters and environmental stochasticity, the MVP for Roanoke logperch is estimated to be 200, 400, or 4200 individuals, depending upon whether catastrophes are

nonexistent, less severe, or more severe, respectively. This range of values is based partly on our uncertainty about the catastrophe regime affecting a given population and partly due to actual variance in the catastrophe regime between populations. As discussed previously, interpopulation variation in geographic extent, land use, and road density are likely to drive interpopulation variation in fish kills. Regardless, the true MVP probably lies closer to the upper end of this range, given that an abundance of 200–400 individuals would equate to a density of only two to four fish per kilometer in a geographically extensive population such as the one occupying the Roanoke River, which does not seem to us a biologically realistic density for this species. These MVP estimates are based on a Ricker model, whereas estimates from a density-independent model range from 31 000 to well over a million individuals, which also is implausible and provides further support for the appropriateness of the Ricker model for this species. On the basis of these considerations and the precautionary principle, we think 4200 adult individuals might be considered a tentative MVP for the species, subject to revision on the basis of new data and models. This figure is remarkably similar to that of Traill et al. (2007) that 4102 individuals was the median MVP in a meta-analysis of 182 published estimates from other vertebrate species (including fishes). It also is broadly consistent with the criterion of Allendorf et al. (1997) that salmonid populations containing less than 2500 individuals should be considered at high risk of extinction (see also Hilderbrand 2002).

Viability of Roanoke logperch populations

Uncertainty about the MVP for Roanoke logperch clouded our conclusions about the viability of the five real-world populations we examined. Assuming less severe catastrophes, all populations have a greater than 95% probability of persisting for the next 100 y, whereas if we assume more severe catastrophes and the more strongly supported MVP threshold of 4200 individuals, only the Roanoke and Pigg populations can be considered truly viable. Conclusions also were limited by the precision of N_0 estimates for specific populations. Our estimates of N_0 were imperfect, as they were based on the simplifying assumptions that 1) fish capture probability follows the same underlying distribution across all populations, locations, and sampling dates; and 2) fish density varies among populations, but follows the same underlying distribution across all riffles within a population. These assumptions were necessitated by limits to available fish and habitat data, and their violation could bias our estimates of N_0 and extinction risk for individual populations. For example, estimates of capture probability were developed from fish surveys conducted at mainstem sites on the Roanoke River. This may underestimate capture probability at headwater sites in the Roanoke River, resulting in an overestimate of N_0 for this population. Conversely, it may overestimate

capture probability in other rivers (many of which are turbid and difficult to sample), resulting in underestimated N_0 for these populations. Furthermore, fish survey data for all populations were biased toward downstream sites where density of fish may be greater. This could result in overestimation of fish density in upstream areas and therefore systematic overestimation of N_0 across populations. Obtaining better field-based estimates of population size has been cited as a high priority for future research on Roanoke logperch (Rosenberger 2007). Our findings support this notion, particularly the need for information about present abundances to evaluate the status of populations relative to MVP reference points. However, our findings also indicate the importance of estimating other factors that play a similarly large role in conclusions about viability and MVP estimates, including the population growth rate, K , and catastrophe regime. As these improved estimates are developed, they can be incorporated into PVA models to improve predictions of extinction risk for individual populations.

Current data limitations notwithstanding, these PVA results should help managers target populations in greatest need of conservation and activities that might reduce extinction risk the most. For example, numerically and geographically small populations in Goose Creek and Otter and upper Smith rivers are susceptible to extirpation from environmental stochasticity and catastrophes, whereas numerically large and geographically extensive populations in Roanoke and Pigg rivers are at lower risk for these factors. These demographic risks correlate with small-population genetic risks previously estimated for these populations (Roberts 2012). Demographic augmentation evidently is not an effective option for decreasing extinction risk in these populations. Alternative tactics for increasing population size could seek to reduce the frequency and severity of fish kills and increase the K . Attempts to increase K might focus on increasing the geographic extent of populations, for example by removing barriers to range expansion and dispersal between fragmented subpopulations (e.g., dams; Roberts et al. 2013), or increasing the quantity and quality of suitable habitat configurations within already occupied areas. Progress toward the latter task could be accomplished via habitat restoration projects and stricter sediment controls in watersheds containing logperch (Rosenberger 2007).

Directions for future research

This analysis indicates the importance of moving beyond population size when estimating extinction risk for Roanoke logperch, a finding that likely is generalizable to other species (Flather et al. 2011). Factors such as the population growth rate, K , N_x , and catastrophe regime mediate the relationship between population size, extinction risk, and MVP and therefore merit additional research in Roanoke logperch. Collection of time-series datasets on abundance in additional popu-

lations would allow future investigators to assess the fit of alternative population growth models, estimate K and r for these populations, and test the generality of our findings from the Roanoke River. These data would be most useful if collected in a way that allows correction for capture probability. Geographically extensive trend data, when combined with datasets on chemical spills and fish kills, would enable the refinement of catastrophe models, perhaps further enabling managers to target efforts toward fish-kill abatement in those watersheds where kills are most prevalent or pernicious.

The logical next step for modeling population viability in Roanoke logperch arguably is to make the leap from count-based to demographic or individual-based PVA models. Although this would add realism, and potentially accuracy, to simulated population dynamics and estimates of extinction risk, it is important to recognize that this would come with trade-offs. The *intensive*, within-population study necessary to build stage-based survival and fecundity schedules and individual movement functions could force a trade-off of the *extensive* study necessary to characterize abundance dynamics across populations. It might be possible to generalize survival, fecundity, and movement estimates across logperch populations, in the way that we generalized population growth functions across populations in this study. However, these assumptions and trade-offs should be taken into account by managers when deciding how to allocate limited resources toward recovery of this species. For many endangered species such as Roanoke logperch, count-based PVA and MVP thresholds may be the best tools available for demographic recovery planning.

Supplemental Material

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Table S1. Population size estimates for age-1 or older Roanoke logperch *Percina rex* found by Anderson et al. (2014) at 12 riffles in the Roanoke River (Virginia) between 1997 and 2013, averaged over riffles within year \times season sampling periods and converted to interannual population growth rates (λ). Dashes indicated unsampled years or inestimable quantities.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S1> (200 KB PDF).

Table S2. Estimates of extinction risk for each of 208 population viability analysis models investigating the effect of 13 alternative demographic augmentation strategies in the Roanoke and Otter river (Virginia) populations of Roanoke logperch *Percina rex*, based on empirical data collected from these rivers between 1997 and 2013.



Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S2> (200 KB PDF).

Table S3. Estimates of extinction risk in population viability analysis models used to estimate minimum viable population size for a generic population of Roanoke logperch *Percina rex*, based on empirical data collected from the Roanoke and Otter river (Virginia) populations between 1997 and 2013.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S3> (200 KB PDF).

File S1. R code for a count-based population viability analysis for Roanoke logperch *Percina rex*, a species investigated in Virginia and North Carolina between 1997 and 2013.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S4> (200 KB PDF).

File S2. R code to estimate the minimum viability population size for Roanoke logperch *Percina rex*, a species investigated in Virginia and North Carolina between 1997 and 2013.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S5> (200 KB PDF).

Reference S1. Anderson GB, Roberts JH, Angermeier PL. 2013. Monitoring of endangered Roanoke logperch in Smith River upstream of Philpott Reservoir. Report of Virginia Tech to U.S. Army Corps of Engineers, Wilmington, North Carolina.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S6> (200 KB PDF).

Reference S2. Anderson GB, Roberts JH, Angermeier PL. 2014. Assessing impacts of the Roanoke River Flood Reduction Project on the endangered Roanoke logperch. Report of Virginia Tech to U.S. Army Corps of Engineers, Wilmington, North Carolina.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S7> (200 KB PDF).

Reference S3. Burkhead NM. 1983. Ecological studies of two potentially threatened fishes (the orangefin madtom, *Noturus gilberti* and the Roanoke logperch, *Percina rex*) endemic to the Roanoke River drainage. Report from Roanoke College to U.S. Army Corps of Engineers, Wilmington, North Carolina.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S8> (200 KB PDF).

Reference S4. Lahey AM, Angermeier PL. 2007. Range-wide assessment of habitat suitability for Roanoke logperch (*Percina rex*). Report from Virginia Tech to Virginia Transportation Research Council, Charlottesville, Virginia.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S9> (200 KB PDF).

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Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S10> (200 KB PDF).

Reference S6. Thompson GG. 1991. Determining minimum viable populations under the Endangered Species Act. Seattle, Washington: National Marine Fisheries Service. National Oceanic and Atmospheric Administration Technical Memorandum NMFS F/NWC-198.

Found at DOI: <http://dx.doi.org/10.3996/032015-JFWM-026.S11> (200 KB PDF).

Acknowledgments

We thank K. Smith and W. Hester for helping to bring this project to fruition and K. Smith, J. Jones, the Associate Editor, and three anonymous reviewers for helpful comments on the manuscript. B. Blood assisted with R programming. The Virginia Cooperative Fish and Wildlife Research Unit is jointly sponsored by the U.S. Geological Survey, Virginia Polytechnic Institute and State University, Virginia Department of Game and Inland Fisheries, and Wildlife Management Institute.

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