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Tamara J. Pandolfo, Thomas J. Kwak & W. Gregory Cope
ABSTRACT

Genetic and demographic modeling of two endangered mussel species, Epioblasma brevidens and E. capsaeformis, in the Clinch River, U.S.A., was conducted to determine quantitative criteria to evaluate performance of extant and reintroduced populations. Reintroduction modeling indicated that the initial population size created during a 5 y build-up phase greatly affected final population size at 25 y, being similar to the population size at the end of the build-up phase, especially when expected population growth rate was low (e.g., 1-2%). Excluding age-0 individuals, age-1 juveniles or recruits on average comprised approximately 11% and 15% of a stable population of each species, respectively. Age-class distribution of a stable or growing population was characterized by multiple cohorts, including juvenile recruits, sub-adults, and adults. Molecular genetic and demographic data indicated that the ratio of N0/Nc was ~5% for both species. Based on this ratio and predicted declines of genetic variation at different population sizes, reintroductions will play a prominent role in restoring populations in the United States.

INTRODUCTION

“There can be no purpose more inspiriting than to begin the age of restoration, re-weaving the wondrous diversity of life that still surrounds us.”

Edward O. Wilson, The Diversity of Life

The 19th and 20th centuries were periods of large-scale habitat loss, degradation and fragmentation caused by dam construction and operation, and severe pollution of aquatic ecosystems, with concomitant losses in biodiversity throughout the United States of America (U.S.A.). During this period, freshwater mussel populations declined greatly and are now considered one of the most imperiled groups of animals in the country (Neves et al., 1997). The passage of landmark environmental laws in the U.S.A., such as the Clean Water Act (1972), Endangered Species Act (1973), and Surface Mining Control and Reclamation Act (1977), have helped reduce impacts and raise public awareness toward proper environmental stewardship (Stein et al., 2000; Schwartz, 2008). More than thirty years later, some disturbed aquatic ecosystems are showing signs of improved water quality and physical habitat conditions. However, many mussel species cannot re-colonize previously occupied habitats because dams prevent dispersal of their host fishes. Reintroductions are recommended in the recovery plans of these endangered species (National Native Mussel Conservation Committee, 1998; USFWS, 2004). Establishing new populations or boosting declining ones meets recovery plan goals and helps to reduce risk to species survival.

The Clinch River in northeastern Tennessee (TN) and southwestern Virginia (VA) of the eastern U.S.A. contains a diverse mussel assemblage of 45 species, with numerous endangered mussel species to include the Cumberlandian combshell (Epioblasma brevidens (Lea, 1831)) and oyster mussel (E. capsaeformis (Lea, 1834)). Both species are endemic to the Tennessee...
and Cumberland river drainages, major tributaries of the Ohio River. These populations are large enough to support translocations of adults and for collecting pupae to use as broodstock at mussel hatcheries (Jones & Neves, 2011). Releasing translocated and hatchery-reared mussels allows biologists to augment and reintroduce populations to achieve species recovery (Miranda et al., 2009). Population densities in the Clinch River can serve as main sources to replenish and rebuild other populations throughout the Tennessee and Cumberland river systems.

While the federal recovery plans for E. brevidens and E. capsaeformis provide recovery criteria for both species, they are only marginally quantitative because demographic data are lacking to specifically define the criteria. When such data are unavailable, these plans recommend that the information be collected. For example, the plans specify that the demographic structure and effective size of a viable population of each species be determined (USFWS, 2004). The plans further state that, “A viable population is defined as a wild, naturally reproducing population that is large enough to maintain sufficient genetic variation to enable the species to evolve and respond to natural habitat changes without further intervention. Viable populations will therefore be stable and have multiple age classes, including newly recruited juveniles” (USFWS, 2004). Therefore, both demographic and genetic factors must be addressed to determine population viability, to include assessing age-class structure, recruitment level, and effective population size (Ne).

The recovery of E. brevidens and E. capsaeformis will depend upon sustainable populations be established in other rivers by releasing of translocated and/or hatchery-reared individuals. Ideally, re-introduced populations will be more than self-sustaining, but will grow in size to eventually expand to other sites. Thus, the purpose of this study was determine (1) how many individuals of each species are needed to create a self-sustaining, demographically viable population that is large enough to maintain sufficient genetic variation over time, and (2) practical quantitatively criterion to evaluate performance of reintroduced or recovering populations.

METHODS
Predicting decline of genetic diversity
To predict declines in genetic diversity, the program EASYPOP (Balloux, 2001) was used to simulate changes in heterozygosity and allelic diversity over time based on different levels of Ne. Initial measures of allelic and genetic variability were obtained from Jones et al. (2004). Simulations were conducted assuming random mating among diploid individuals belonging to a single population, and with an equal sex ratio. Number of loci was set to ten, with free recombination between loci and the same mutation scheme and rate (1x10^-8) for all loci. The selected mutation model was a mixed model with a proportion of both single-step mutation events (90%) and infinite allele mutation events (10%), whereas the mutation scheme allows for equal probability to mutate to any of the possible allelic states (Garza & Williamson, 2001). The number of possible allelic states was set at seventeen for each locus. (Genetic) Variability of the initial population was set to maximum, meaning that alleles were randomly assigned to individual individuals. Simulations were conducted for 25 generations and replicated ten times to check for consistency of results.

Census and effective population sizes
Population sizes of Epiphrasma brevidens and E. capsaeformis in the Clinch River, TN were estimated in 2004 by collection of standard, 0.25 m^2 quadrat samples placed along transect lines (Jones & Neves, 2011). Sites sampled during the 2004 census included Wallen Bend [river kilometer (RKM) 309.9], Frost Ford (RKM 291.7) and Swan Island (RKM 277.2), which were selected because they represented the upper, middle and lower boundaries of the study reach, respectively. However, the entire sites areas at Wallen Bend and Frost Ford were not sampled in 2004, just the upper ~15% and 63% of each site, respectively. Thus, total population size at each site for both species was estimated by applying the 2004 density estimates to the entire measured site area. This section of river representing the upper, middle and lower boundaries of the study reach where the abundance of both species is adequate to estimate site-specific census sizes and to collect tissue samples for genetic analyses. In conjunction with 2004 censuses, tissues from 20-30 individuals per site were collected from both species and used to extract DNA and conduct analyses of DNA microsatellites. Contemporary effective population sizes (Ne) were estimated at each site using the linkage disequilibrium (LD) method of Hill (1981). The method is known to be downwardly biased, but the program LDNe corrects the bias and was used to estimate survival of newly metamorphosed juveniles from age-0 to 1 y old. Specifically, these are age-0 juveniles that upon excysting from fish hosts are considered viable based on observing metamorphosis, spawning and fertilization, production of glochidia, and ultimately metamorphosis and release of viable juveniles to the river bottom. Since these data are unavailable for most mussel species, it was solved iteratively in the model until a defined stable or increasing growth rate was obtained.

Demographic and environmental stochasticity
Both demographic and environmental stochasticity were included in the model because both sources of variation can alter the risk of population decline and extinction. Demographic stochasticity occurs when populations become very small and random fluctuations in mating and abundance can drive population size to zero. Demographic stochasticity was implemented by sampling abundance of age-1 or older survivors from a binomial probability distribution, and age-0 survivors from a Poisson probability distribution embedded in RAMAS. Fluctuations in environmental conditions, such as droughts and floods, can greatly affect population vital rates (Jones & Neves, 2011). E. brevidens and E. capsaeformis were extirpated from many locations and populations in RAMAS. Field study estimates of standard deviations (SD) for vital rates are sparse for most mussel species and when available, they are typically obscured by measurement error. Thus for both species, the SD (±1) was set at 33% of mean fecundity, 50% of mean survival of age-0 individuals, and 10% of mean survival of age-1 and older individuals. Fluctuations in SD based on known characteristics of mussel life history and demography, such as variable recruitment success of juveniles and annual survival of adults (Haag & Rypel, 2011; Jones & Neves, 2011). Survival and fecundity were assumed to be uncorrelated in the model. Extreme environmental variation such as catastrophes and bananzas (i.e., a period of very high recruitment and survival) were assumed to be rare and not included in the model.

Initial abundances and ages
Initial abundances for modeling reintroduction of mussel populations to a site, for example in the upper Clinch River, VA where both species have been extirpated, were based on the predetermined number of mussels to be reintroduced y^-1 for 5 y. Reintroduced mussels y^-1 ranged from 24-120 individuals for E. brevidens and from 50-400 individuals for E. capsaeformis (Table 1). Simulations were conducted based on reintroducing an equal number of individuals ages 4-11 for E. brevidens and ages 3-7 for E. capsaeformis. These cohorts are abundant...
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Clinch River, VA. Because populations of that was set too low, thus allowing for a wider range of values of $K$ for exponential population growth with a ceiling capacity ($N_c$) are unknown for mussel populations, it can be collected easily from the lower Clinch River, TN for reintroduction purposes.

**Population growth rate and carrying capacity**

Although density-dependent regulation and carrying capacity ($K$) are unknown for mussel populations, it is unrealistic to expect indefinite growth. Thus, a model of exponential population growth with a ceiling, set by $K$, was implemented in RAMAS for both species. This strategy allowed exponential population growth at every time step, but if $N > K$, then $N$ was set equal to $K$. A general life-cycle diagram depicting the demography of a freshwater mussel species living to a maximum of 10 y, such as *Gastropus capsaeformis*. Species living longer can be accommodated in the model by adding age classes, such as five for *E. brevidens*. Nodes (circle and boxes) represent age-class stages, and arrows between nodes represent transitions (survival) between stages. Recruitment is shown as the number of age-0 individuals produced by adults in mature age classes.

Reproductive value

Reproductive value measures the worth of an individual in each age class by the total number of progeny it can be expected to produce, to include its immediate offspring and all future descendants (Fisher, 1930). It is expressed relative to the reproductive value of the first age class, which was set to age-1. Reproductive values were calculated in RAMAS and are a product of the projection matrix.

**Reintroduction simulation scenarios**

Simulations were conducted by reintroducing equal numbers of individuals per year from targeted age classes. Reintroductions occurred each year for a 5 y population build-up period, which then grew unassisted for the next 20 y. Population growth levels varied from low, intermediate, and high, and were chosen to explore scenarios relevant to the population management of each species (Table 1).

The uncertainty of mean population projections and probability of population decline were assessed for all modeled scenarios. However, not all data were reported because results were very similar for most projections and therefore redundant. Furthermore, because sample size ($N=10,000$) of mean trajectories was high, confidence intervals (CI) would be unrealistically narrow. Instead, uncertainty was explored using a small random sub-sample ($N=20$) of trajectories taken from reintroduction scenarios relevant to the population management of each species.

**RESULTS**

**Effective population size and loss of genetic diversity**

Estimates of contemporary $N_e$ ranged from 178 to 223 individuals for *E. brevidens* and from 294 to 2,917 individuals for *E. capsaeformis*, whereas estimates of the census size ($N_c$) were much higher and ranged from 2,304 to 4,730 individuals and from 3,840 to 176,665 individuals of each species, respectively (Table 3). Estimates of $N_c$ and $N_e$ generally varied congruently among sites for *E. capsaeformis*, whereas $N_c$ and $N_e$ were highest at Frost Ford and lowest at Swan Island. In contrast, variation of $N_c$ and $N_e$ for *E. brevidens* was similar among sites. Ratios of $N_c/N_e$ ranged from 0.0389 to 0.0773 for *E. brevidens* and from 0.0093 to 0.0766 for *E. capsaeformis*, with mean values at 0.0572 and 0.0342, respectively (Table 3).

**Reintroduction uncertainty for *E. capsaeformis***

Reintroduction uncertainty for *E. capsaeformis* was evaluated under a scenario of transplanting 300 individuals y$^{-1}$ and at a low growth rate ($\lambda=1.0125$). The sub-sampled mean was generally greater than the modeled mean, but the 95% CIs entirely contained the latter (Fig. 4). Seventeen of the sub-sampled population trajectories exhibited an increasing trend and finished greater than the post 5 y build-up population size. None of the sub-sampled trajectories declined to zero, and the minimum at 25 y was 105 individuals. Probability of decline was minimal (<5%) at all reintroduction levels, but slightly higher at only 50 individuals y$^{-1}$ (Fig. 5).

Although reintroduction uncertainty was evaluated only for the above scenarios, the same standard deviations for vital rates were used in all modeling scenarios. Hence, the uncertainty surrounding all modeling scenarios are qualitatively similar to the above results. The probability of a 100% decline was extremely low (<1%) for all reintroduction scenarios.

**Age class structure and reproductive value**

The stable age distributions (SAD) of *E. brevidens* and *E. capsaeformis* demonstrated that as survival of age-0 individuals increases, the proportion of individuals comprising younger age-classes increased (Fig. 6). Although at first glance such small proportional increases of 1-2% or less in the younger age-classes appear minimal, they allowed modeled populations to grow over time. A key feature of the SAD of a population with a positive growth rate was the presence of a high proportion of young individuals. Of course, natural populations rarely resemble the structure of an SAD over short time periods because of uneven recruitment, but if censuses are taken regularly, the mean cohort structure may reflect an SAD. Furthermore, because of...
FIGURE 2
Predicted decline in heterozygosity and allelic diversity over time is dependent on effective population size ($N_e$). Generation length of each species is 5 y.

Their small sizes (e.g., <5-10 mm) it is difficult to accurately census age-0 juvenile mussels in situ (Jones and Neves 2011). So, in practice, age-1 individuals usually are the youngest age-class in the census. Examining the SAD without age-0 individuals in the distribution allows for a more direct comparison of modeled data with field data. The SAD of an expanding, stable or declining population showed that age-class structure flattened as growth rate declined (Fig. 7). The SAD of an expanding population was characterized by a steep age-class structure with a high proportion and abundance of young individuals, whereas the SAD of a declining population was characterized by a flat age-class structure with a low abundance of young individuals.

For both species, reproductive values were highest for individuals in the 5 y age-class, when maturity is reached (Fig. 6). Reproductive values also were high for age-classes 1-2 years younger or older than 5 y, but declined thereafter, and values were lowest by comparison at the higher growth rates.

DISCUSSION
Effective population size and maintenance of genetic diversity

Effective population size ($N_e$) is a critical parameter in population biology because it determines the expected rate at which genetic diversity is lost per generation. The census size ($N_c$) is also important and together these two parameters can be used to evaluate the capacity of a population to maintain genetic diversity over time. Genetic diversity is needed for two primary reasons: (1) so populations can adapt to changing environmental conditions, such as diseases,
a high proportion (>95%) of molecular diversity could change (Frankham et al., 2002). The ability of populations to respond to environmental and declining population size, which can compromise more susceptible to loss of genetic diversity from geometric depression (Frankham, 1996; Reed & Frankham, 2003; Reid, 2005). It is well known that small populations are often too small to maintain sufficient genetic variation of populations as part of a species’ conservation program. Jones and Neves (2011) have shown that clear differences exist between the life-history traits and population demography of E. brevidens and E. capasaeformis, to include life span, population sizes, and recruitment. These differences undoubtedly influence the maintenance of genetic variation of each species. While a total Ne=500 is recommended here to maintain sufficient genetic variation for populations of E. brevidens and E. capasaeformis, it is critical that demographic and genetic methods be used together to set reintroduction targets and to monitor how populations are progressing over time. Periodic assessments of population size and genetic variation will be required to empirically validate whether targets are being met and sustained. Thus, a practical approach that seeks to maximize both abundance and genetic variation of populations is recommended.

Effect of reintroduction abundance on population restoration success

An important finding of the population reintroduction modeling was that the size of the initial population created during the 5 y build-up phase greatly affects final population size. If the expected growth rate of the reintroduced population was stable or even slightly positive (e.g., 1-2%), then final population size was very similar to size at the end of the build-up phase. In forecasting the expected outcomes of a reintroduction project, assuming a stable or low growth rate is probably the prudent and conservative approach. For example, the modeling results demonstrated that if 72 individuals of E. brevidens were transplanted y-1 to a total TN of 350, then 72 individuals would be present at the end of the build-up phase, assuming an annual growth rate of 0.5-1.25% (Fig. 3). Importantly, the final population size at 25 y also would be ~500 individuals or slightly larger depending on the specific growth rate employed. Therefore, it is critical that the intended target census size per site be similar to population size at the end of the build-up phase. Further, the target census size should be large enough to accommodate the Ne that meets established program goals.

Population growth during the build-up phase is enhanced by reintroducing a greater proportion of sub-adults and younger adults (e.g., ages 4-8) with higher reproductive potential (Fig. 6). When feasible, releasing young individuals with high reproductive value will likely be the most effective population reintroduction strategy. For example, translocations of adults proved to be the more effective strategy to restore populations of queen conch (Strombus gigas Linnaeus, 1758) in over-harvested areas of the Florida Keys, U.S.A., compared to releasing juveniles that had no immediate reproductive output and were susceptible to higher mortality (Delgado et al., 2004).

It is important to emphasize that the population trajectories presented in Fig. 3 are mean values calculated from thousands of stochastic population projections generated by the RAMAS computer program. While such programs are valuable tools in the field of conservation biology, the mean values they provide should be interpreted with caution. The input variables used for most species; e.g., survival and environmental stochasticity, are usually poorly understood. The trajectory of a real population is always singular and influenced by a unique and unpredictable set of variables over a specified time frame, and will ultimately look irregular and more like the individual trajectories presented in Fig. 4. Biologists are aware of how real populations can fluctuate and occasionally do so dramatically, due to stochastic effects from disease, competition, flood, drought, and other factors.

Age class structure and recruitment

Natural populations rarely resemble the cohort structure of a SAD over short time periods, especially when data are from a single census. However, if censuses are taken at regular intervals (e.g., annually), then the mean cohort structure should begin to resemble the SAD. The SAD provides a portrait of the average cohort structure given key input variables, such as survival, fecundity, age at maturation, and maximum age. The SAD can be used to evaluate cohort structure of natural populations and determine whether they are recruiting and surviving at sustainable levels. Populations that are stable or growing will be characterized by a predominance of younger individuals and cohort structure will be skewed to the left, whereas declining and older populations will be characterized by middle to older-aged individuals and cohort structure will be skewed to the right.
FIGURE 5
Probability of observing a decline from initial abundance over a 25 y period for *Epioblasma brevidens* and *E. capsaeformis*, based on various reintroduction scenarios. All probabilities were computed using the stable growth rate (λ=1.005), which represents the high risk scenario investigated in the study. Probabilities of decline at higher growth rates are lower.

**FIGURE 6**
Stable-age distributions (SAD) and reproductive values for *Epioblasma brevidens* and *E. capsaeformis*; SADs at higher growth rates were similar to those computed using a stable growth rate, increasing only ~1-2% in younger age-classes (≤5 y).

Skewed to the right. Obviously, for a population to grow, the birth rate must exceed the death rate and the longer-lived a species, the less frequently it needs to experience above-average recruitment. Freshwater mussels are typically long-lived (>20 y) animals, and many species do not exhibit high annual recruitment, but rather sporadic recruitment that is occasionally punctuated by exceptional year classes (Payne & Miller, 2000; Strayer et al., 2004). However, shorter-lived species such as *E. capsaeformis* must recruit more often and at greater levels to sustain viable populations, and therefore are more vulnerable to decline and ultimately to extinction, especially if population or habitat disturbances are long-lasting (Jones & Neves, 2011).

Two key demographic questions, then, are to determine the cohort structure and annual recruitment levels needed to sustain a stable or growing population of *E. brevidens* and *E. capsaeformis* (USFWS, 2004). The SAD histograms in Fig. 6 show profiles of three cohort structures for each species based on stable, low and moderate growth rates, illustrating that the cohort structure of a stable or growing population should be dominated by immature individuals and young adults. The histograms also indicate that age-0 individuals should make up about 26-27% of the population for *E. brevidens* and about 31-34% of the population for *E. capsaeformis*, depending on the growth rate examined. These percentages are a product of the Leslie matrices, which were parameterized with input variables to include the age-0 survival rate, which in this study was approximately 30% (Table 2). While these input variables represent areas of uncertainty in the model, the SADs generated for each species are similar to cohort data obtained from field collections. The mean cohort structure (2004-2008) of *E. brevidens* and *E. capsaeformis* in the Clinch River, TN, is currently dominated by younger age groups, indicating that these populations are stable or expanding, respectively (Jones & Neves, 2011). During this period, both populations exhibited strong and weak year-classes, but recruitment was always a measurable feature of the population. Of course, age-frequency histograms produced from real populations in the river are more uneven, but they do match expectations based on the computer-generated SAD. It is difficult to accurately census age-0 individuals in mussel populations because of their small size (typically <10 mm), so age-1 is usually the first age-class assessed as a measure of recruitment. Therefore, if age-0 individuals are removed from the SAD.
FIGURE 7

Stable-age distributions generated in RAMAS depicting declining (front), stable (middle) and expanding (back) populations of each species. Population sizes (N) given on the Z-axis represent mean abundance (10,000 simulations) after 25 y. Age-0 individuals are not shown or included in total N. Typically, this cohort is too difficult to sample reliably for freshwater mussels. Instead, age-1 individuals are the first cohort shown along with its percentage of total N. Starting population sizes were N=4,500 and N=152,000 for each species, respectively.

Addressing modeling uncertainty

In this study, the two areas of modeling uncertainty that deserve further consideration are: (1) predicting declines of genetic diversity based on effective population size, and (2) the species-specific demographic input variables used for the Leslie-matrices. First, the simulations conducted in EASYPOP to predict declines of genetic diversity did not account for effects of hermaphroditic reproduction, fluctuating population size, or overlapping generations due to extended life span. The first two demographic factors would act to increase the rate of loss of genetic variation, while the last demographic factor would act to decrease the rate of loss of genetic variation. The program can simulate effects of different levels of hermaphroditic mating, but the incidence or rate of hermaphroditism is unknown for either E. brevidens or E. capsaeformis. Until studies are conducted to examine rates of hermaphroditic reproduction across a range of mussel taxonomic groups, modeling its effect on maintenance of genetic diversity will remain too speculative to be of predictive value. In addition, population size is held constant during program simulations; therefore, effects of fluctuating population size on genetic diversity are not considered, which would be important for species such as E. capsaeformis, especially at small population sizes. Also not accounted for in the model was increased life span and overlapping generations, which would act to decrease the loss of genetic diversity. Thus, for species such as E. brevidens that exhibit longer life span and perhaps a more stable population size over time, such species would contain a greater number of overlapping generations, and therefore a higher ratio of Nm/Ns and capacity to retain genetic variation over time. Again, the mean ratio of Nm/Ns for E. brevidens was slightly higher than that for E. capsaeformis (Table 3). Other areas of modeling uncertainty include the mutation rate for molecular markers used in simulations, which in this study was based on a commonly reported rate for microsatellites in the literature, but higher or lower rates would slow down or accelerate loss of genetic variation, respectively.

The input variables used to parameterize each species Leslie-matrix are another source of uncertainty, including: (1) survival of age-0 individuals and other cohorts, (2) maximum age, (3) average age or size at maturation, (4) average fecundity of females, and (5) effects of density-dependence. The survival rates used in this study were derived using a combination of empirical data, anecdotal observations, and professional judgment. Survival rate of individuals ≥1 y old is high (>90% y-1) for mussel species early in life (e.g., ages 1-5), but then decreases as mussels become reproductively active, due to predation, physiological stress of reproduction and other factors. The shape and slope of a species or population survival curve will vary and be influenced by both environmental conditions and longevity. However, the estimated survival rate of age-0 individuals is the least certain. Although set at 30% for each species in this study (Table 1), field and laboratory studies are needed to better quantify the mean rate and variance of these parameters.

Maximum age of E. brevidens and E. capsaeformis in the Leslie-matrices was set at 15 and 10 y, respectively, based on ages of collected females. It is possible that maximum age of the former species was set too low. Males of the species in the Clinch River can live to at least 28 y; suggesting that females also live longer than 15 y (Jones and Neves 2011). Increasing maximum age in either species’ matrix would change modeling results. Importantly, it would act to decrease the recruitment rate needed to maintain stable or growing populations. Thus, the maximum ages used here provide higher, but arguably more conservative estimates of recruitment for reintroduction and recovery purposes. Additional sampling and thinning of collections of shells could possibly identify the presence of older females in the population of both species, but setting the maximum age based on older, perhaps se-
nescent individuals may not reflect average population dynamics for the species. Age at maturation was set at 5 y for both species, but favorable environmental conditions could enhance growth and allow some individuals in the population to mature at younger ages, perhaps in 3 or 4 y. Accounting for a proportion of earlier maturing individuals (<5 y) would increase population recruitment and growth.

Density-dependent factors are not well understood for freshwater mussel population growth and cannot go unchecked indefinitely. Limiting factors such as competition for physical space, fish hosts, food, predation and other factors will eventually limit population growth. However, most mussel species occur at sufficiently low densities that density-dependent factors likely would not affect population growth. Hence, setting carrying capacity (K) or a population ceiling for most species may be arbitrary, but likely one that is useful to prevent unrealistically high trajectories from occurring during simulations. Time series data on population sizes across a range of sites could help inform such decisions. In this study, population ceilings were set at sufficiently high levels as to minimally influence mean trajectories, and were based on time-series data from multiple sites in the Clinch River (Ahlstedt et al., 2005; Jones & Neves, 2011).

Finally, as more data become available, the modeling assumption of a closed population at restoration sites should be revisited for species utilizing host fishes with high capabilities, such as E. brevidens. It is likely that a percentage of local fish hosts infested with glochidia from released mussels would disperse away from the site. However, an equal number of infected fish hosts would not disperse to the site because nearby or adjacent sites would lack established populations. Therefore, the site emigration rate would likely exceed the immigration rate depending on the dispersal ability of the fish hosts. The net effect would be to decrease juvenile recruitment and the local population growth rate.

ACKNOWLEDGEMENTS

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LITERATURE CITED


**Performance Criteria to Evaluate Mussel Populations**

<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>Summary of the Leslie matrix model parameters used in RAMAS to simulate population growth and reintroduction of the Cumberlandian combshell (<em>Epioblasma brevidens</em>) and oyster mussel (<em>E. capsaeformis</em>). Simulations were conducted using an exponential growth model, where standard deviation (SD) represents environmental variation and was sampled from a log-normal distribution.</th>
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</thead>
<tbody>
<tr>
<td><strong>Parameter</strong></td>
<td><strong>E. brevidens</strong></td>
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<tr>
<td><strong>Age at first reproduction</strong></td>
<td>Males and females</td>
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<tr>
<td>Population growth rate ((\lambda))</td>
<td>Stable population</td>
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<td>Low growth</td>
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<td>Moderate growth</td>
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<td>Survival rate (S) of Age-0 juveniles controls (\lambda)</td>
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<td>Initial population size (N)</td>
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<td>(number released (y^{-1}) for 5 y)</td>
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<td>Age of adults (y)</td>
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<td>Carrying capacity (A)</td>
<td>Reintroduced population</td>
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<td>Type of density dependence</td>
<td>Ceiling (=K)</td>
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</table>

**TABLE 2** Age-structured Leslie matrices of survival and fecundity values used to simulate population growth and reintroduction of Cumberlandian combshell (*Epioblasma brevidens*) and oyster mussel (*E. capsaeformis*). The three different survival values of juvenile mussels in the first column (0-1*) correspond to stable, low and moderate population growth simulated in the study (see Table 1).

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**Epioblasma brevidens**: |

<table>
<thead>
<tr>
<th>Immature Age Classes (0-4)</th>
<th>Mature Age Classes (5-10)</th>
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<tbody>
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<td>0-1</td>
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<tr>
<td>5-6</td>
<td>0.95</td>
</tr>
<tr>
<td>6-7</td>
<td>0.85</td>
</tr>
<tr>
<td>7-8</td>
<td>0.95</td>
</tr>
<tr>
<td>8-9</td>
<td>0.95</td>
</tr>
<tr>
<td>9-10</td>
<td>0.95</td>
</tr>
</tbody>
</table>

**E. capsaeformis**: |

<table>
<thead>
<tr>
<th>Immature Age Classes (0-4)</th>
<th>Mature Age Classes (5-10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1</td>
<td>0.30</td>
</tr>
<tr>
<td>1-2</td>
<td>0.50</td>
</tr>
<tr>
<td>2-3</td>
<td>0.95</td>
</tr>
<tr>
<td>3-4</td>
<td>0.95</td>
</tr>
<tr>
<td>4-5</td>
<td>0.95</td>
</tr>
<tr>
<td>5-6</td>
<td>0.95</td>
</tr>
<tr>
<td>6-7</td>
<td>0.95</td>
</tr>
<tr>
<td>7-8</td>
<td>0.95</td>
</tr>
<tr>
<td>8-9</td>
<td>0.95</td>
</tr>
<tr>
<td>9-10</td>
<td>0.95</td>
</tr>
</tbody>
</table>
TABLE 3

Effective population sizes ($N_e$) and census sizes ($N_c$) for *Epiblasma brevidens* and *E. capsaeformis* in the Clinch River, TN at Wallen Bend (WB), Frost Ford (FF) and Swan Island (SI). The 95% confidence intervals are given in parentheses. Sampling was conducted in 2004.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>$N_e$</th>
<th>$N_c$</th>
<th>$N_e/N_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Epiblasma brevidens</em></td>
<td>WB</td>
<td>223 (49; infinity)</td>
<td>4,023 (1*; 8,495)</td>
<td>0.0554</td>
</tr>
<tr>
<td></td>
<td>FF</td>
<td>184 (60; infinity)</td>
<td>4,770 (1*; 9,998)</td>
<td>0.0389</td>
</tr>
<tr>
<td></td>
<td>SI</td>
<td>178 (37; infinity)</td>
<td>2,306 (34; 4,067)</td>
<td>0.0773</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td></td>
<td></td>
<td>0.0372</td>
</tr>
<tr>
<td><em>Epiblasma capsaeformis</em></td>
<td>WB</td>
<td>320 (124; infinity)</td>
<td>57,615 (23,294; 51,798)</td>
<td>0.0093</td>
</tr>
<tr>
<td></td>
<td>FF</td>
<td>2,617 (128; infinity)</td>
<td>178,685 (140,670; 212,472)</td>
<td>0.0108</td>
</tr>
<tr>
<td></td>
<td>SI</td>
<td>294 (94; infinity)</td>
<td>3,840 (1,401; 6,278)</td>
<td>0.0766</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td></td>
<td></td>
<td>0.0342</td>
</tr>
</tbody>
</table>

*The lower confidence interval was set based on the number of mussels collected in quadrat samples at each site.*

TABLE 4

Proposed population performance criteria to evaluate reintroduction and recovery of two endangered mussel species. Values are intended as overall targets to evaluate a contiguous riverine population comprised of multiple demes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total $N_e$</th>
<th>Mean recruitment $^b$ of age-1 juveniles</th>
<th>Mean age-class structure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Epiblasma brevidens</em></td>
<td>≥100</td>
<td>≥10,000</td>
<td>≥11%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Age-classes ranging from 1-12+ yrs.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Age-classes 1-4 comprise ~40% of $N$</td>
</tr>
<tr>
<td><em>Epiblasma capsaeformis</em></td>
<td>≥100</td>
<td>≥10,000</td>
<td>≥15%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Age-classes ranging from 1-14+ yrs.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Age-classes 1-4 comprise ~50% of $N$</td>
</tr>
</tbody>
</table>

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**OUR PURPOSE**

The Freshwater Mollusk Conservation Society (FMCS) is dedicated to the conservation of and advocacy of freshwater mussels, North America’s most imperiled animals. Membership in the society is open to anyone interested in freshwater mussels who supports the stated purposes of the Society which are as follows:

1) Advocate conservation of freshwater molluscan resources;
2) Serve as a conduit for information about freshwater mussels;
3) Promote science-based management of freshwater mussels;
4) Promote and facilitate education and awareness about freshwater mussels and their function in freshwater ecosystems;
5) Assist with the facilitation of the National Strategy for the Conservation of Native Freshwater Mussels (Journal of Shellfish Research, 1999, Volume 17, Number 5), and a similar strategy under development for freshwater gastropods.

**OUR HISTORY**

The FMCS traces its origins to 1992 when a symposium sponsored by the Upper Mississippi River Conservation Committee, USFWS, Mussel Mitigation Trust, and Tennessee Shell Company brought concerned people to St. Louis, Missouri to discuss the status, conservation, and management of freshwater mussels. This meeting resulted in the formation of a working group to develop the National Strategy for the Conservation of Native Freshwater Mussels and set the ground work for another freshwater mussel symposium. In 1995, the next symposium was also held in St. Louis, and both the 1992 and 1995 symposia had published proceedings. Then in March 1996, the Mississippi Interstate Cooperative Research Association (MICRA) formed a mussel committee. It was this committee (National Native Mussel Conservation Committee) whose function it was to implement the National Strategy for the Conservation of Native Freshwater Mussels by organizing a group of state, federal, and academic biologists, along with individuals from the commercial mussel industry. In March 1998, the NNMCC and attendees of the Conservation, Captive Care and Propagation of Freshwater Mussels Symposium held in Columbus, OH, voted to form the Freshwater Mollusk Conservation Society. In November 1998, the executive board drafted a society constitution and voted to incorporate the FMCS as a not-for-profit society. In March 1999, the FMCS held its first symposium "Musseling in on Biodiversity" in Chattanooga, Tennessee. The symposium attracted 280 attendees; proceedings from that meeting are available for purchase. The second symposium was held in March 2001 in Pittsburgh, Pennsylvania, the third in March 2003 in Raleigh, North Carolina, the fourth in St. Paul, Minnesota in May 2005, the fifth in Little Rock, Arkansas in March 2007, and the sixth in Baltimore, Maryland in April 2009. The society also holds workshops on alternating years, and produces a newsletter three times a year.

**FMCS SOCIETY COMMITTEES**

Participation in any of the standing committees is open to any FMCS member. Committees include:

- Awards
- Environmental Quality and Affairs
- Gastropod Distribution and Status
- Genetics
- Guidelines and Techniques
- Information Exchange - Walkerana and Ellipsaria
- Mussel Distribution and Status
- Outreach
- Propagation and Restoration

**TO JOIN FMCS OR SUBMIT A PAPER**

Please visit our website for more information at [http://www.molluskconservation.org](http://www.molluskconservation.org)

Or contact any of our board members or editors of WALKERANA to talk to someone of your needs. You’ll find contact information on the back cover of this publication.
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