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REGULAR ARTICLE

PERSPECTIVES ON THE CONTROLLED PROPAGATION, AUGMENTATION, AND REINTRODUCTION OF FRESHWATER MUSSELS (MOLLUSCA: BIVALVIA: UNIONOIDA)

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ABSTRACT

Controlled propagation, augmentation, and reintroduction (PAR) of rare and endangered aquatic organisms has become a priority action for recovery and delisting, and in many cases is an action of "last resort" to either restore or maintain existing populations. The guiding principle of PAR efforts should be to avoid harming existing populations of congeneric or nontarget species and also minimize risks to extant populations and habitats. Controlled PAR of freshwater mussels should not be a long-term management strategy conducted in perpetuity and should not be used as a substitute for recovery tasks such as habitat restoration or addressing the causes of endangerment. The determination to pursue controlled PAR for freshwater mussels should follow a thorough evaluation of the status of existing wild populations, an agreement that PAR in the historic range is needed, and a conclusion that suitable habitat for long-term success is present. The primary purpose of any efforts to augment or reintroduce animals should be to establish free-ranging wild populations. Concomitant with this goal is the distinct possibility that these activities can represent appreciable genetic or ecological risks to resident animals, both nontarget taxa and wild conspecifics. To maintain the integrity of the fauna, communities, and ecosystems it is imperative that these risks be carefully considered before conducting controlled PAR. In this paper we pose several questions that we believe are important to consider before initiating PAR of freshwater mussels. We also recommend actions, some already used at individual facilities or by agencies, that we believe will aid in developing a more uniform approach to controlled PAR and safeguarding the ecological and genetic integrity of freshwater mussel communities.

KEY WORDS: Captive rearing, supplementation, population enhancement, restoration

INTRODUCTION

The history of North American conservation includes examples of population translocations, reintroductions, or augmentations that have had the desired effect of increasing the numbers, ranges, and genetic diversity of the target species (Heschel and Paige 1995; Westemeier et al. 1998; Madsen et al. 2004; Johnson et al. 2010). What should not be ignored, however, are examples in which these activities have either failed or had undesirable consequences for native species or habitats (e.g., Leberg and Ellsworth 1999; Kassler et al. 2002; Metcalfe et al. 2007; Hedrick et al. 2014). Controlled propagation, augmentation, and reintroduction (PAR) of rare and endangered aquatic organisms has become a priority action for the recovery of these animals and in many cases is an action of "last resort" to either restore or maintain existing populations, and prevent future listings, extirpations, or extinction (Ryman and Laikre 1991; IUCN 1996; Snyder et al. 1996). Although PAR is a valid and potentially useful tool for the management of species of conservation concern, a guiding principle of PAR efforts should be to avoid harming

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Table 1. The terminology used in controlled propagation, augmentation, and reintroduction is varied and often confusing. So in the context of this paper, we define the following terminology.

Term	Definition
Augmentation	The addition of individuals of a species within the geographic boundaries of an existing local population or metapopulation, often propagules from controlled propagation or translocated individuals (Ryman and Laikre 1991; IUCN 1996; George et al. 2009).
Captive population	An assemblage of a species maintained in a controlled environment for education and research purposes, for supplementation of wild populations, or as the vestige of the species (Lacy 2009).
Controlled propagation	Refers to any of the procedures discussed herein, including collection of gravid females or wild glochidia, inoculation of host fish, recovery and care of juveniles, captive grow-out, and captive breeding, usually within a controlled environment (Lacy 1995; USFWS and NMFS 2000; George et al. 2009).
Introduction	The deliberate movement of a species outside its historically accepted geographic boundaries (Fischer and Lindenmayer 2000; George et al. 2009).
Reintroduction	The release of a species at a location where it is not currently present and that is outside the geographic boundaries of existing local populations or metapopulations, but where there is evidence for the former presence of the species in historical times (IUCN 1996; George et al. 2009).
Relocation	The deliberate movement of individuals from one location to another often conducted under the premise of rescuing animals from some imminent anthropogenic threat (Dodd and Seigel 1991; Dunn et al. 2000; Fischer and Lindenmayer 2000). This includes collecting individuals and aggregating them in the same reach they were collected from.
Repatriation	The release of individuals of a species into occupied or unoccupied portions of that species' accepted range (Dodd and Seigel 1991).
Restoration	The successful re-establishment of a species into unoccupied portions of its historic range (Jones et al. 2006).
Translocation	The deliberate movement of individuals from the wild into a nonnatal location within the geographic boundaries of historic distribution with the intent to establish a reintroduced population (IUCN 1996; George et al. 2009).

existing populations of congeneric or nontarget species and minimize risks to extant populations and habitats (Snyder et al. 1996; George et al. 2009; Olden et al. 2010; FMCS 2016).

Native freshwater mussels (Mollusca: Bivalvia: Unionoida) are one of the most imperiled faunas in North America. More than 1 in 10 species may have gone extinct during the past century, and over half of the North American species are in danger of extinction (Williams et al. 1993; Stein et al. 2000; Haag 2012). Despite the realized benefits from federal legislation such as the National Environmental Policy Act (NEPA 1970, as amended), the Clean Water Act (CWA 1972, as amended), and the Endangered Species Act (ESA) (ESA 1973, as amended), anthropogenic impacts continue to negatively affect freshwater mussel populations and many populations have declined to precarious levels. Despite tremendous progress, there remains an overall lack of knowledge about key ecological, biological, and life-history features of many freshwater mussel species that are critical to their management and conservation (Neves 2004; Jones et al. 2006; Haag 2012; FMCS 2016).

Controlled PAR of freshwater mussels to native habitats is an important component of plans to recover many species, as the establishment of new populations is often a requirement for recovery or down-listing of these species (NNMCC 1998; Neves 2004). Controlled PAR is also a prioritized action in regional and state freshwater mussel conservation and management plans (Posey 2001; UMRCC 2004; MDC 2008). In addition, the artificial propagation of many species has facilitated important toxicological research (e.g., Augspurger et al. 2007; Wang et al. 2010). The determination to pursue PAR actions for freshwater mussels should follow only after a thorough evaluation of the status of existing wild populations, an agreement that PAR in the historic range is needed, and a conclusion that suitable habitat and conditions for long-term success are present (George et al. 2009; Haag and Williams 2014). The particular recovery approach taken (i.e., augmentation vs. reintroduction; see Table 1) will be dependent upon the level of endangerment (e.g., rare but stable, rare and declining, currently rare but once common, etc.). These actions may be advisable when the population is judged to be at significant risk of extirpation or is extirpated and appears unlikely to recolonize formerly occupied areas by natural processes, is unable to naturally recolonize, or when the population represents a significant portion of the total population or genetic diversity of that species.

We acknowledge that controlled PAR is a valuable and useful tool to aid in recovery of freshwater mussels and to prevent extinctions, extirpations, and future listings. Our purpose in this paper is to discuss considerations that we believe should be addressed before initiating the controlled

Table 2. Careful consideration should be given to these prioritized questions, modified in part from Novinger (2002) and Jones et al. (2006). A negative or unsure response to any of these questions should prompt substantial justification to continue with any plan for controlled propagation, augmentation, and reintroduction (PAR)

1. Are reasons for a species' decline understood well enough to support reasonable odds for successful reintroduction into historic range?
2. Are recovery efforts such as habitat restoration or local translocation in the wild feasible means for meeting restoration goals? If not, will propagation and reintroduction be coordinated with such efforts?
3. Will PAR activities be conducted in accordance with existing guidelines and in coordination with other partners?
4. Has substantial or sufficient sampling been conducted to determine that PAR is necessary?
5. What are the objectives and protocols of propagation or reintroduction efforts and how will program success be evaluated?
6. Have the ecological and genetic ramifications of controlled PAR been carefully considered and researched to determine feasibility?
7. Will the proposed PAR action have a termination date, population size goal, and a stocking rate that is adaptive on the basis of population size?
8. What are the goals for restoration of the species – is a recovery plan in place?
9. Do suitable brood-stock source populations exist?
10. Has a plan for the disposition of individuals unfit for reintroduction or mortalities been devised, and will it be adhered to?

PAR of native freshwater mussels. These actions may be conducted to meet the objectives of endangered species recovery plans and other conservation efforts including preventing the extinction or extirpation of species, subspecies, and local populations; establishing new local populations or increasing extant local population sizes; maintaining the genetic resources of species and populations; facilitating research necessary for freshwater mussel restoration and recovery; or establishing refugia.

CONSIDERATIONS FOR THE PAR OF FRESHWATER MUSSELS

The primary purpose of any efforts to augment populations or reintroduce animals should be to establish viable, free-ranging, wild, self-sustaining populations (Dodd and Seigel 1991; IUCN 1996). Concomitant with this goal is the distinct possibility that these same activities can pose appreciable genetic or ecologic risks to resident animals, including nontarget taxa and wild conspecifics (Snyder et al. 1996; Olden et al. 2010; Haag and Williams 2014; Koppelman 2015). To maintain the integrity of the fauna, communities, and ecosystems it is therefore imperative that these risks be carefully considered before controlled PAR actions are initiated (Neves 2004; Jones et al. 2006; Haag and Williams 2014). Because of the possible risks posed by controlled PAR we believe careful consideration should be given to the following prioritized questions modified in part from Novinger (2002) and Jones et al. (2006) (Table 2). A negative or unsure response to any of these questions should require substantial justification to continue with plans for controlled PAR.

Are Reasons for a Species' Decline Understood Well Enough to Support Reasonable Odds for Successful Reintroduction into Historic Range?

Many of the declines in freshwater mussel abundance and richness can be directly attributed to identifiable point source impacts or large-scale habitat modifications that left fragmented populations susceptible to stochastic events. However, many inexplicable population declines have also occurred. For example, many streams have lost almost their entire freshwater mussel fauna, but they still maintain viable populations of fish and other aquatic macroinvertebrates (Buchanan 1987; Haag 2009; Haag and Williams 2014). Often, the exact nature of the decline in a particular river is discussed in general terms or multiple causes are noted (Downing et al. 2010; Haag and Williams 2014). In a review of the causes of decline or extirpation of freshwater mussels, "pollution/water quality" and "habitat destruction or alteration" were by far the most common causes identified in the literature (Downing et al. 2010). Unfortunately, fewer than 50% of the studies analyzed in that review met high evidentiary standards. Therefore, determining whether the cause of the decline is still affecting the candidate river will be difficult at best, if not impossible. The decline in the abundance of species may not always be attributable to anthropogenic factors. Extirpation and extinction of species are normal processes and definitive evidence that a decline in the abundance of a species is related to human activities is important for designing a successful strategy. For example, competition for host fish, although not widely documented, has been offered as an explanation for the observed lack of recruitment in *Quadrula fragosa* (Roe and Boyer 2015).

Are Recovery Efforts Such as Habitat Restoration or Local Translocation in the Wild Feasible Means for Meeting Restoration Goals? If Not, Will Propagation and Reintroduction Be Coordinated with Such Efforts?

The long-term conservation of mussel diversity is dependent upon the protection and restoration of habitat. Therefore, controlled PAR should be viewed as secondary to recovery tasks such as habitat restoration or addressing the causes of endangerment and not as a substitute for those efforts (Neves 2004; Thomas et al. 2010; Haag and Williams 2014). The focus of the ESA is to recover species and the habitats on which they depend (ESA 1973, as amended). Mussels are intimately tied to their habitat, both physically and chemically, and the majority of the reasons for the decline of freshwater mussels is related to habitat degradation (Haag 2009; Downing et al. 2010). Reintroduction of propagated animals to areas that are still experiencing the anthropogenic threats that caused the decline in the first place are likely to be unsuccessful and a waste of resources (Thomas et al. 2010). If the proposed goal of PAR efforts is establishment of additional populations, the best available reintroduction sites within the historic range of the species should be determined. Translocation is another important tool that can be used to re-establish freshwater mussel populations (Villella et al. 1998; Dunn et al. 2000). However, translocation has its own drawbacks, including ecological and evolutionary concerns (Villella et al. 1998; Thomas et al. 2010).

Will PAR Activities Be Conducted in Accordance with Existing Guidelines and in Coordination with Other Partners?

Regulations, policies, and guidelines that affect and guide controlled PAR are likely to vary from state to state or region to region. For example, in Missouri, the Department of Conservation is the constitutionally mandated fish and wildlife agency and has sole responsibility for all wildlife in the state (§252.010, RSMo 2005 available at http://www.sos.mo.gov/adrules/csr/current/3csr/3csr.asp, accessed January 8, 2016). There are several important portions of the *Wildlife Code of Missouri* that are applicable to controlled PAR of freshwater mussels. In addition, there are policies on the conservation and interbasin transfer of aquatic organisms and invasive species, and published guidelines on controlled PAR that must be followed (McMurray 2015). Other states have their own guidelines for conducting controlled PAR of freshwater mussels (e.g., Davis 2005; McGregor 2005).

All directives and requirements for working with federally protected species must be closely adhered to. Guidance for animals that are afforded federal protection under the ESA and all requirements of federal collecting permits should be followed (USFWS and NMFS 2000). If there is no recovery plan in place or if controlled PAR is not specifically identified as a recovery strategy for a species, these actions require approval by the U.S. Fish and Wildlife Service (USFWS) Regional Director or Assistant Administrator and the state fisheries authority (USFWS and NMFS 2000; McMurray 2015). State fish and wildlife management or natural resource agencies are often authorized to conduct surveys, research, and recovery efforts for federally listed species via a cooperative agreement with the USFWS under Section 6 of the ESA (ESA 1973, as amended). Additional aspects of controlled PAR for federally listed species (capture, transport, release) are addressed under Section 10 of the ESA, via the Section 10(a)(1)(A) permitting process (ESA 1973, as amended; P.D. Johnson, Alabama Department of Conservation and Natural Resources, personal communication). Host fish for some mussels are unknown and could also have federal protection; special measures for these fish would also apply (e.g., Fritts et al. 2012).

The need for consultation, consensus, and coordinated effort among specialists both within and outside agencies and universities during PAR activities cannot be overemphasized. After the determination that controlled PAR should be undertaken, an advisory committee or recovery team to guide and coordinate efforts should be assembled, if one does not already exist (Neves 2004; George et al. 2009). Partners from the areas where brood stock will be acquired and the areas where propagated mussels will be stocked should be involved, as appropriate. Any actions involving federally protected species should be coordinated with USFWS staff.

Has Substantial or Sufficient Sampling Been Conducted to Determine that PAR Is Necessary?

Any number of habitat, ecological, and life-history variables can affect the detectability and capture probability of freshwater mussels (Strayer and Smith 2003; MacKenzie et al. 2006; Meador et al. 2011). This is especially true for species of conservation concern, which because of their rareness are difficult to detect. Nondetection of species occurrence is unavoidable and can be substantial, leading to erroneous assumptions about the occupancy of a site simply because of a species rarity (Gu and Swihart 2004; George et al. 2009). This error would then affect the decision to reintroduce a species or augment an existing population, especially when populations can persist for an extended period of time.

Mussel populations can increase in size after undetected improvements in water quality and habitat (Miller and Lynott 2006; Haag 2012). Whereas some rivers in North America have been surveyed at regular intervals for over a century (e.g., the Duck River in Tennessee), other river systems have either never been surveyed or haven't been surveyed in decades (FMCS 2016; Hubbs 2016). Species thought extinct or extirpated have been rediscovered after dedicated, targeted efforts to locate specimens or when sampling conditions have improved such that species are collected in rivers in which they haven't been documented in over 100 yr and were presumed extirpated (Randklev et al. 2012; K.S. Cummings, Illinois Natural History Survey, personal communication). For these reasons we recommend that adequate targeted surveys for controlled PAR candidates be conducted before initiating any actions for specific river basins.

What Are the Objectives and Protocols of Propagation or Reintroduction Efforts and How Will Program Success Be Evaluated?

Since the initial publication of a U.S. national strategy for the conservation of native freshwater mussels, programs to propagate freshwater mussels have rapidly increased in number (NNMCC 1998; FMCS 2016). Multiple federal, state, or university facilities in the U.S. are now propagating freshwater mussels and releasing an estimated 1 million or more juvenile mussels (Neves et al. 2007; Haag and Williams 2014). Propagation facilities include those that use recirculated river or pond water, or dechlorinated municipal water (O'Beirn et al. 1998; Beaty and Neves 2004; Mummert et al. 2006). In addition, there are programs that use *in situ* cages placed in rivers or compact recirculating systems (Barnhart 2005; Brady et al. 2011). Along with the variety of facilities and techniques available to produce freshwater mussels is the diversity of methods used to release propagules into the wild. Although the release of newly transformed juveniles or infested host fish has resulted in some success, albeit possibly circumstantial, the translocation of adults and release of laboratory-propagated subadults have been shown to be the most effective techniques (Thomas et al. 2010; Haag 2012; Carey et al. 2015). In reality, it does not matter which methods are used for propagation and release, but rather that the methods are refined, work for the species in question, and are documented.

Proposals to conduct controlled PAR should explicitly define what constitutes "success" of the actions. In practice, there are several intermediate and near-term hierarchical measures of success that are being used, such as releasing individuals, monitoring released individuals, and assessing growth and survival. Ultimately, however, because the primary purpose of controlled PAR is to establish viable, free-ranging, wild, self-sustaining populations, the action of releasing propagated mussels is in and of itself not a measure of success. Success of controlled PAR should be measured in terms of juvenile recruitment into an established population (Dodd and Seigel 1991; IUCN 1996; Thomas et al. 2010).

Monitoring of controlled PAR actions, when implemented with a scientific foundation, is paramount to documenting success of the effort (IUCN 1996; Jones et al. 2006; George et al. 2009; FMCS 2016). Monitoring should evaluate both acute and chronic effects of controlled PAR, including genetics, and, importantly, determine when the actions can be discontinued (Hard et al. 1992; Laikre et al. 2010; Jones et al. 2012). Depending on the age class released, species, nature of the stocking, and the monitoring approach, the probability of finding stocked freshwater mussels at a release site is often much greater than for fish or other mobile species (Waller et al. 1993). The design of any plan for monitoring stocked freshwater mussels should take into account the biology and life history of the species, what will be released (infested host fish, newly transformed juveniles, older juveniles), and how the release will be conducted. Because of the large variations in longevity, age to sexual maturity, and recruitment exhibited by freshwater mussels, monitoring efforts can, and likely should be, long term and quantitative to measure demographic information (Haag 2012; Lane et al. 2014; FMCS 2016).

The propagation of freshwater mussels has been conducted for well over 100 yrs (Lefevre and Curtis 1908). Given the relative infancy of modern-day efforts and the overall lack of information on the effects of these actions on a variety of adaptive traits in freshwater mussels, the monitoring and evaluation of controlled PAR actions should utilize an adaptive management approach where knowledge gained from previous experiences is incorporated into programs to advance conservation goals (Nichols et al. 1995; IUCN 1996; Peterson et al. 2007). This approach has been successfully used in the management of other animal groups such as salmonids and waterfowl, and can be useful in the management of rare and endangered species (Walters et al. 1993; Nichols et al. 1995; Runge 2011).

Have the Ecological and Genetic Ramifications of Controlled PAR Been Carefully Considered and Researched to Determine Feasibility?

Freshwater mussels use a wide variety of life-history strategies (Barnhart et al. 2008; Cummings and Graf 2010). Possible intraspecific or population differences in host suitability, age and growth, spawning, seasonality, and physiology should be considered and, if necessary, investigated before choosing brood stock and initiating controlled PAR activities (Jones et al. 2006; Haag 2012; Zanatta and Wilson 2011).

Mussel species richness is incompletely documented and possible species complexes and taxonomic problems remain (Neves 2004). Recent taxonomic and phylogenetic research acknowledges that formerly wide-ranging species, rare species, or even species that are often considered common and widely distributed may in fact include lineages that represent hidden biodiversity (e.g., Zanatta and Murphy 2008; Moyer et al. 2011; Zanatta and Wilson 2011; Campbell and Lydeard 2012; Gangloff et al. 2013; Inoue et al. 2013; Zanatta and Harris 2013; Chong et al. 2016, among others). The accurate identification of the species being propagated is critical and may require an a priori taxonomic assessment, especially when species misidentification may occur because of shell homoplasy or researcher inexperience (IUCN 1996; Roe and Lydeard 1998; Shea et al. 2011). It is often recognized that taxonomic species should not be the minimal unit for conservation. Conservation units such as "distinct population segments" and "evolutionarily significant units" (ESUs) do not prioritize which population segments are important, but in essence represent frameworks for the conservation of genetic diversity such that evolution of the species continues (Waples 1995; Fraser and Bernatchez 2001).

Although use of the ESU concept is restricted to vertebrate taxa under the ESA, there is ample evidence that populations of many freshwater mussel species should be treated, if not as distinct species, then at the very least as separate management units (Roe and Lydeard 1998; Zanatta and Murphy 2008; Moyer et al. 2011; Inoue et al. 2013; Zanatta and Harris 2013; Jones et al. 2015).

Since their introduction to North America, Zebra Mussels (*Dreissena polymorpha*) have quickly spread among multiple river systems and have had devastating effects on native freshwater mussels (Haag 2012). These and other invasive species could very easily be inadvertently moved during controlled PAR activities, and their possible transport into new waters or into state, university, federal, or private facilities warrants serious consideration before initiating controlled PAR (Villella et al. 1998; Cope et al. 2003). In addition, controlled PAR presents the distinct possibility that nontargets such as filamentous algae, *Chara* spp., *Myriophyllum spicatum*, or even other native freshwater mussels could be inadvertently introduced into new systems and potentially become invasive (Olden et al. 2010).

The potential that diseases, bacteria, or other etiological agents could be spread to host fish, facilities, or new waters should be considered before initiating controlled PAR actions (Cunningham 1996; Snyder et al. 1996; Villella et al. 1998). Unfortunately, there is a dearth of information on possible diseases, viruses, bacteria, or other etiological agents associated with freshwater mussels, and it is often unknown what effect these pathogens would have on freshwater mussels (Villella et al. 1998; Grizzle and Brunner 2009; Müller et al. 2015; McElwain et al. 2016). This is partly due to a lack of research, limitations of detection methods, and the fact that seemingly healthy bivalves can support a diverse assemblage of bacteria including *Aeromonas salmonicida* and *Flavobacterium columnare*, pathogens of warm- and cool-water fishes (Starliper 2008; Starliper et al. 2008, 2011). Although both *A. salmonicida* and *F. columnare* are ubiquitous and common in aquatic systems and infect a wide variety of fish species, outbreaks of the diseases they cause are still economically important in fish production facilities (Lasee 1995; Welker et al. 2005; Bullard et al. 2013).

As freshwater mussel propagation programs have become more prolific and the number of propagules produced has increased, the possibility of harmful genetic effects of controlled PAR must be carefully considered (Jones et al. 2006; Laikre et al. 2010; Haag and Williams 2014). Understanding and preserving genetic diversity in freshwater mussel populations is critical to the management and conservation of the fauna (IUCN 1996; Villella et al. 1998; Zanatta and Murphy 2008). Evidence indicates that high genetic diversity increases resilience of species (Reusch et al. 2005), and heterozygous bivalves have higher survivorship, greater resistance to stress, and faster growth rates (e.g., Launey and Hedgecock 2001). Although freshwater mussels may have a wide range of resistance to inbreeding depression, they are a highly fecund group such that propagation produces large groups of full or half siblings that will possess a reduced within-population genetic diversity relative to the wild population (Villella et al. 1998; Ferguson et al. 2013). Conversely, outbreeding depression could be an important issue for freshwater mussels because of local adaptations of species to particular populations of host fishes, and ecological conditions can be disrupted by the introduction of alleles from other drainages that lack the same adaptive value as the local alleles (Neves 2004).

Local allele frequencies can be changed and rare alleles can be lost by genetic drift in small populations or by exaggerating the reproductive success of a few individuals, and founder effects may become an issue if a limited number of females are used, eventually resulting in a reduction in heterozygosity, making the population more susceptible to extirpation (Hoftyzer et al. 2008; George et al. 2009). Artificial selection may occur as a result of controlled PAR of freshwater mussels, but the effects in mussels are unknown (Jones et al. 2006; Hoftyzer et al. 2008). Domestication from selection regimes imposed by captive rearing can result in the differential survival of individuals that are genetically adapted to artificial conditions and not those found in the site where they will be introduced (Lynch and O'Hely 2001). Inadvertent domestication is known to occur in fishes and some invertebrates, and can occur rapidly because of their short generation time and high fecundity (Snyder et al. 1996). For example, reduced reproductive success in the wild has been documented in hatchery-raised *Oncorhynchus mykiss* and *O. kisutch* (Araki et al. 2007; Thériault et al. 2011). For freshwater mussels, these unintended selective forces may include selection for artificial foods or transformation on host fish species that are maladaptive in their natal habitat.

Unfortunately, the extent that inbreeding, outbreeding, founder effect, and domestication could affect freshwater mussel populations is unknown because of the lack of studies documenting the amount of genetic diversity in populations or the presence of rare alleles that should be conserved (Villella et al. 1998; Jones et al. 2006). Facilitating the survival of large numbers of juveniles from the same cohort in a hatchery setting does not always result in high numbers of fit individuals, and this accentuates the need for genetic data and management plans before initiating restorative propagation.

Although typically not used in hatcheries, genetic management plans represent a mechanism for possibly mitigating the negative effects of artificially propagated animals (Fisch et al. 2013). Although pedigree information is often, if not always, unknown for freshwater mussels selected as brood stock, the lack of individual pedigree should not hinder the development of a genetic management plan (Wang 2004; George et al. 2009; Ferguson et al. 2013). If the need arises to maintain captive populations of freshwater mussels or a need to utilize descendants from captive populations, a genetic management plan should certainly be developed. These plans should include pedigree analysis, provide for the periodic incorporation of wild individuals, and should prevent or minimize the effects of domestication (Lacy 2009; Fisch et al. 2013). Genetic population viability analysis models can provide information on preserving genetic variation in propagated freshwater mussels (D.J. Berg, Miami University, personal communication).

Maintenance of the genetic effective population size (N_e) of rare and endangered species is an important consideration in conserving overall genetic diversity and ultimately the recovery of a species (Frankham et al. 2002; Jones et al. 2006, 2012; Laikre et al. 2010). Many factors can affect N_e, but one of particular importance to controlled PAR in freshwater mussels is variation in family size (lifetime production of offspring per individual). Diversification in family size results when one or a few individuals leave many more offspring relative to other individuals. When the deviation in family size exceeds that of a random distribution, N_e is reduced to less than the number of adults in the population (Frankham 1995). Equalizing family size has the effect of minimizing inbreeding and the distortion of allele frequencies while maximizing the amount of heterozygosity that is passed on to the next generation.

Will the Proposed PAR Action Have a Termination Date, Population Size Goal, and a Stocking Rate That Is Adaptive Based on Population Size?

Controlled PAR is not intended to be a management strategy conducted in perpetuity (USFWS and NMFS 2000; George et al. 2009; Haag and Williams 2014). To that end, proposals for controlled PAR actions should identify the point at which they will be terminated. Although a chosen calendar date is likely not feasible or appropriate, identifying a targeted population size goal is achievable (Jones et al. 2012; FMCS 2016). Initial post-release monitoring should be used to confirm if repeated actions are feasible or if the actions should be discontinued. Freshwater mussels often form highly dense aggregations of >100 individuals/m^2 (Strayer 2008). Unfortunately, little is known about the effects of overcrowding, or even what density of mussels is considered to be overcrowding, when releasing artificially propagated freshwater mussels. On the basis of previous relocations, stockings were limited such that they did not increase density in the existing mussel community more than 2×, and release areas that had evidence of recent recruitment (individuals <5 yr old) were chosen (Dunn et al. 2000). Stocking densities for *Unio tigridis* of 40–60 individuals/m^2 in a lake were preferred for promoting growth; however, little research has been conducted on the effect of stocking densities in lotic systems (Şereflişan and Yilmaz 2011).

What Are the Goals for Restoration of the Species – Is a Recovery Plan in Place?

Currently, 88 North American freshwater mussel species are listed in the United States as threatened or endangered. Of these, 71 have finalized recovery plans (plans are available at http://www.fws.gov/endangered/species/recovery-plans.html, accessed November 15, 2015; MRBMRC 2010). In a review of these plans, four species (*Alasmidonta heterodon*, *Lampsilis abrupta*, *Pleurobema collina*, and *Potamilus capax*) did not have controlled PAR identified as a recovery strategy. Most of these plans were authored before controlled PAR became more widely used as a conservation strategy for freshwater mussels. Of the plans that listed controlled PAR as a recovery strategy for freshwater mussels, several older plans merely stated that the actions should be evaluated, developed, or investigated as a means to conserve the species, and not necessarily that the action should be undertaken. Recently authored recovery plans often emphasize controlled PAR as a useful recovery tool and specify the number and geographical extent of populations required for down-listing or delisting.

Species limited to a few recruiting populations such as *P. collina* are likely viable candidates for controlled PAR, whereas more wide-ranging endangered species such as *L. abrupta* may not be suitable (USFWS 1990; Bogan 2002; Williams et al. 2008). Regional planning and prioritization efforts throughout a species range are key in determining whether controlled PAR should be implemented as a recovery strategy (e.g., CRMRC 2010; MRBMRC 2010). Many wide-ranging species are considered rare in some portions of their range, but are considered relatively common in others. In addition, species considered common throughout their ranges are propagated for a variety of research purposes. Few states require the development of species recovery plans for state rare species. In those situations, the state agency responsible for management of fisheries and wildlife should convene a panel of species and genetic experts to determine the feasibility of initiating controlled PAR.

Do Suitable Brood-Stock Source Populations Exist?

Selection of the appropriate brood stock is one of the most critical decisions that should be made before initiating controlled PAR. Given the general lack of genetic information at the taxonomic and population level for many mussel species, it should be assumed that each river basin (using an eight-digit hydrologic unit code) is at least a metapopulation and possibly contains several local populations. The proximity of populations or phenotypic similarity does not necessarily preclude the need for genetic studies (Neves 2004; Jones et al. 2006). When trying to establish a new population or to augment an existing one, it is important that an adequate number of individual brood stock be used to approximate the entire gene pool. Brood stock should be selected following a combination of genetic and morphological studies. These studies would assist with identifying the best source population or populations for augmentations or reintroductions (George et al. 2009). It is often assumed that wild-caught brood stock are not related; however, closely related individual freshwater mussels have been found as far as 16.2 km apart (Ferguson et al. 2013; Fisch et al. 2013). This suggests that brood stock selected from the same reach of river, let alone the same location, could be closely related.

Efforts should be made to select new individuals each year to reduce the effects of artificial selection, inbreeding, or founder effects, and the number of progeny released from each female should be equalized (Neves 2004; Jones et al. 2006; George et al. 2009). Where it can be sustained by larger populations, >50 females should be targeted to serve as brood stock (Jones et al. 2006). Populations of most rare freshwater mussel species could not sustain this amount of removal (FMCS 2016). Therefore, brood stock should contain as many females as possible or females from multiple locations. Care must be taken to prevent depletion of the source population(s) as well, so the removal of mussels from donor populations should affect <5% of the donor population, thus requiring preliminary population size estimates (Jones et al. 2006; George et al. 2009).

Has a Plan for the Disposition of Individuals Unfit for Reintroduction or Mortalities Been Devised, and Will It Be Adhered to?

Because of the large number of juveniles that can be produced through controlled propagation, there may be times when there is an excess of progeny produced. The disposition of excess progeny should not be an afterthought and should be given ample consideration before beginning controlled PAR activities. These individuals should be disposed of following guidelines described in the PAR plan. Possible uses of excess progeny include additional augmentation opportunities, use in toxicity studies or other similar research, genetic studies, or euthanized and deposited in a natural history museum collection. A subset of all propagules should be retained as vouchers for genetic assessments (USFWS and NMFS 2000). For federally listed species, these activities are typically addressed as part of the Section 10 permitting process (P.D. Johnson, Alabama Department of Conservation and Natural Resources, personal communication). Because there are species propagated for which there is no federal nexus, the disposition of excess propagules should be clarified before initiating PAR actions.

CONTROLLED PAR PLANS AND REVIEW

Controlled PAR plans should be specific, set goals, and considered as dynamic documents that can be amended or updated as new information becomes available. Plans should be coordinated with USFWS and all state agencies within the jurisdictional reach of the plan (e.g., CRMRC 2010; MRBMRC 2010). Regional prioritization of controlled PAR targets (rivers and species) is preferred to state-level propagation planning (CRMRC 2010; MRBMRC 2010; FMCS 2016). Plans need to identify protocols for the monitoring and evaluation of stocked propagules, existing mussel communities, and overall program effectiveness. This monitoring should include, at minimum, evaluation of the population at the release site(s) within 1 yr after the release, annually for 4 yr, and again after year 10. Monitoring should match PAR objectives and follow clearly defined plans that establish what constitutes success, scope, frequency, duration, and appropriate repeatable methods.

Plans for controlled PAR must set carefully established guidelines to minimize artificial selection, inbreeding, and loss of natural diversity, with the intent to mimic natural patterns of diversity and gene flow (Jones et al. 2006; George et al. 2009). Attempts should be made to preserve genetic diversity when establishing a new population or augmenting an existing one by using an adequate number of individuals to approximate the entire gene pool. Permit considerations (federal and state) may limit this level of sampling for brood stock. Considerations of effective population size generally dictate that the offspring of dozens of females be represented to thoroughly encompass the genetic diversity of a population. Host fish should support a high rate of transformation and should ideally be either from, or genetically similar to, the hosts available at the release sites. Avoid inbreeding by dispersing offspring of particular females among multiple sites. These sites should have other, less closely related individuals of the same species. Conversely, inbreeding could be lessened by selecting brood stock from multiple locations (Ferguson et al. 2013). Individuals should not be moved outside of their metapopulation, if there is any reason to suspect local adaptations. In addition, consideration should be given to the likelihood of river basin or regional endemism (e.g., Ozarks, Cumberlandian, Mobile; Haag 2012) and species should not be moved outside of their respective faunal regions or basin. As much as possible, progeny should be equalized among females used for producing juveniles to maintain N_e and reduce the distortion of allele frequencies in subsequent generations.

To prevent the unwanted movement and possible introduction of diseases or nontarget and possibly invasive organisms, cooperators conducting controlled PAR should consider all necessary decontamination and quarantine procedures that will need to be followed for gear, boats, and animals, especially when brood stock or release sites are located in infested or potentially infested waters (Cope et al. 2003). One method to manage the risk of spreading invasive species is to implement a hazard analysis and critical control point plan to address all invasive species or disease avoidance steps to limit the possible transfer of diseases and nontarget organisms (Britton et al. 2011).

The identification of suitable reintroduction sites within the historic range of the species is paramount to the long-term success of efforts to augment or reintroduce freshwater mussels from propagated animals. Sites should be free from the original cause of decline or at least lacking significant threats and provide suitable habitat and host fish (IUCN 1996; Haag and Williams 2014). In addition to suitable host fish populations and stable mussel communities, aspects of physical habitat that should be examined for suitability of sustaining restored mussel populations are water quality, substrate stability and composition, and water velocities and depths, especially during extreme hydrologic events (Sheehan et al. 1989; Villella et al. 1998; Zanatta and Wilson 2011). Priority should be given to sites located on protected public lands or private lands with minimal public access (George et al. 2009).

CONCLUSIONS

Any controlled propagation of freshwater mussels, regardless of species status or the nature of the action, including both stocking into the wild or using brood stock to produce mussels for research, should require the development of a plan for controlled PAR. Although the use of propagated mussels in laboratory research is important to the continued protection and conservation of the fauna, the use of brood stock collected from the wild also represents a loss of those particular individuals' genetic material. As with laboratory research projects, research in natural systems is important to the survival and conservation of the fauna. In addition to the removal of potential year classes or genetic material from the brood-stock river, the placement of mussels into cages, silos, etc., or directly into a stream as part of in situ research presents the possibility that these animals or their gametes could be released into a nonnatal system due to vandalism or natural events.

As required for federally endangered or threatened species, all controlled PAR plans should have well-supported objectives (IUCN 1996; George et al. 2009; Haag and Williams 2014). Plans may be written for single species or multispecies assemblages, and should, at a minimum, incorporate each of the subjects required by the USFWS and National Marine Fisheries Service policy on controlled propagation of species listed under the ESA (USFWS and NMFS 2000). Additionally, plans should identify and address the transport of stock to the release site so as to minimize stress and increase the welfare of animals that are being released, establish the release strategy, timing, and techniques that will be utilized, identify target densities that will be achieved, and specifically identify site selection for release of mussels on the basis of consultation between the partners (IUCN 1996).

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