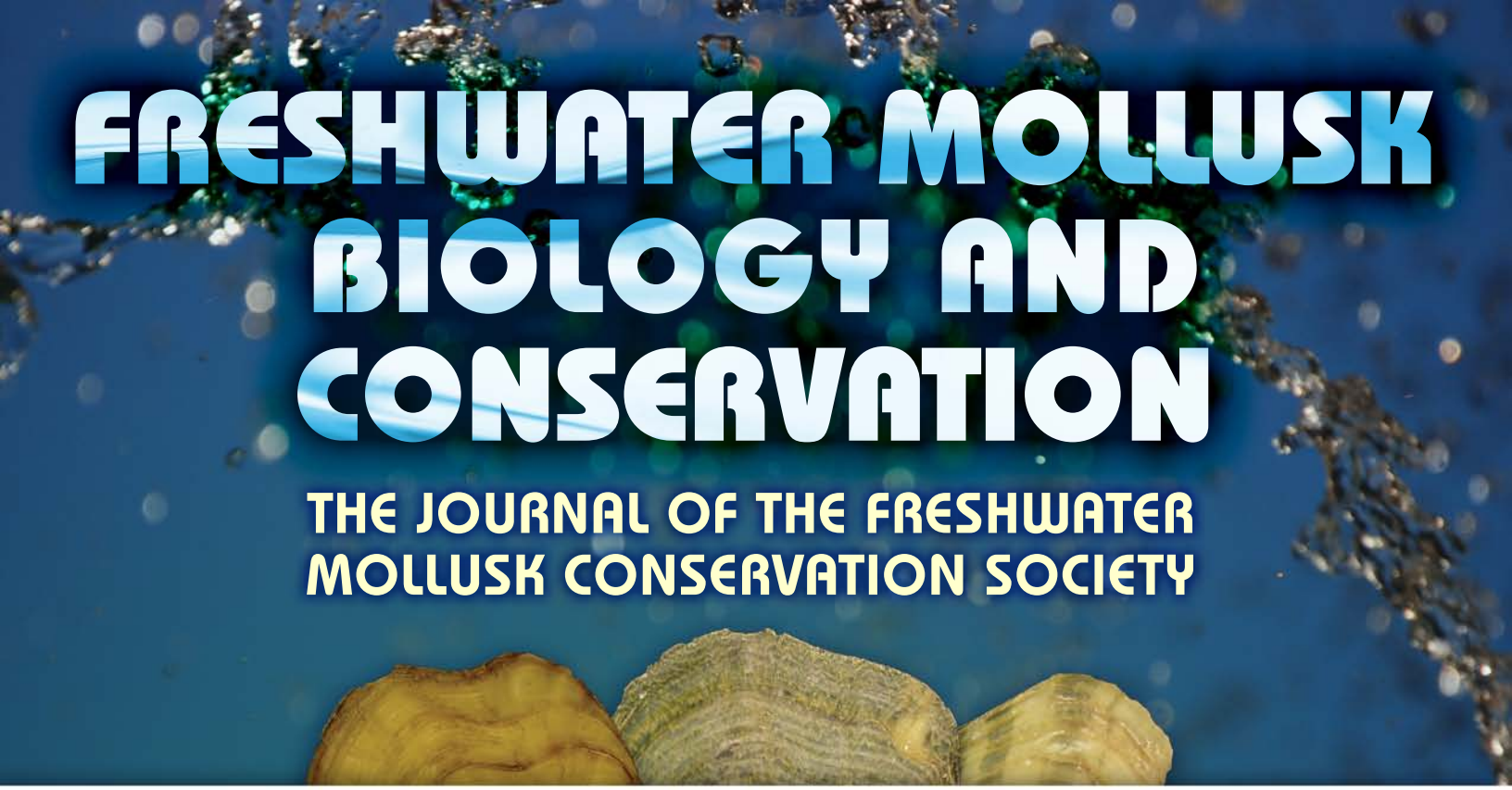

FRESHWATER MOLLUSK BIOLOGY AND CONSERVATION

THE JOURNAL OF THE FRESHWATER MOLLUSK CONSERVATION SOCIETY

VOLUME 20 NUMBER 1 MARCH 2017

Freshwater Mollusk Biology and Conservation 20:1–12, 2017

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).

ACKNOWLEDGMENTS

This manuscript resulted from and benefited from multiple discussions with J. Harris, P. Hartfield, and J. Koppelman. We thank P. Hartfield, P. Johnson, W. Cope, and an anonymous reviewer for reviewing the manuscript and providing helpful suggestions.

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Freshwater Mollusk Biology and Conservation 20:13–19, 2017

REGULAR ARTICLE

DECLINING OCCURRENCE AND LOW COLONIZATION PROBABILITY IN FRESHWATER MUSSEL ASSEMBLAGES: A DYNAMIC OCCURRENCE MODELING APPROACH

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ABSTRACT

Mussel monitoring data are abundant, but methods for analyzing long-term trends in these data are often uninformative or have low power to detect changes. We used a dynamic occurrence model, which accounted for imperfect species detection in surveys, to assess changes in species occurrence in a long-term data set (1986–2011) for the Tar River basin of North Carolina, USA. Occurrence of all species decreased steadily over the time period studied. Occurrence in 1986 ranged from 0.19 for *Utterbackia imbecillis* to 0.60 for *Fusconaia masoni*. Occurrence in 2010–2011 ranged from 0.10 for *Lampsilis radiata* to 0.40 for *F. masoni*. The maximum difference between occurrence in 1986 and 2011 was a decline of 0.30 for *Alasmidonta undulata*. Mean persistence for all species was high (0.97, 95% CI = 0.95–0.99); however, mean colonization probability was very low (<0.01, 95% CI = <0.01–0.01). These results indicate that mussels persisted at sites already occupied but that they have not colonized sites where they had not occurred previously. Our findings highlight the importance of modeling approaches that incorporate imperfect detection in estimating species occurrence and revealing temporal trends to inform conservation planning.

KEY WORDS: Unionidae, monitoring, Bayesian, existing data, Tar River, imperfect detection

INTRODUCTION

Mussel survey and monitoring data often are not collected or analyzed in a manner that allows strong inference about population trends over time (Downing and Downing 1992; Strayer and Smith 2003). A particular weakness of traditional approaches is an inability to account for imperfect species detection, which is inherent in all survey methods (MacKenzie et al. 2003; Royle and Kery 2007; Dorazio et al. 2010). Species detection has a large random component, and nondetection does not necessarily indicate species absence; failure to account for the probability of detection can lead to faulty conclusions about long-term assemblage changes (MacKenzie et al. 2002, 2003; Royle and Kery 2007; Wisniewski et al. 2013).

More robust analytical approaches that explicitly estimate

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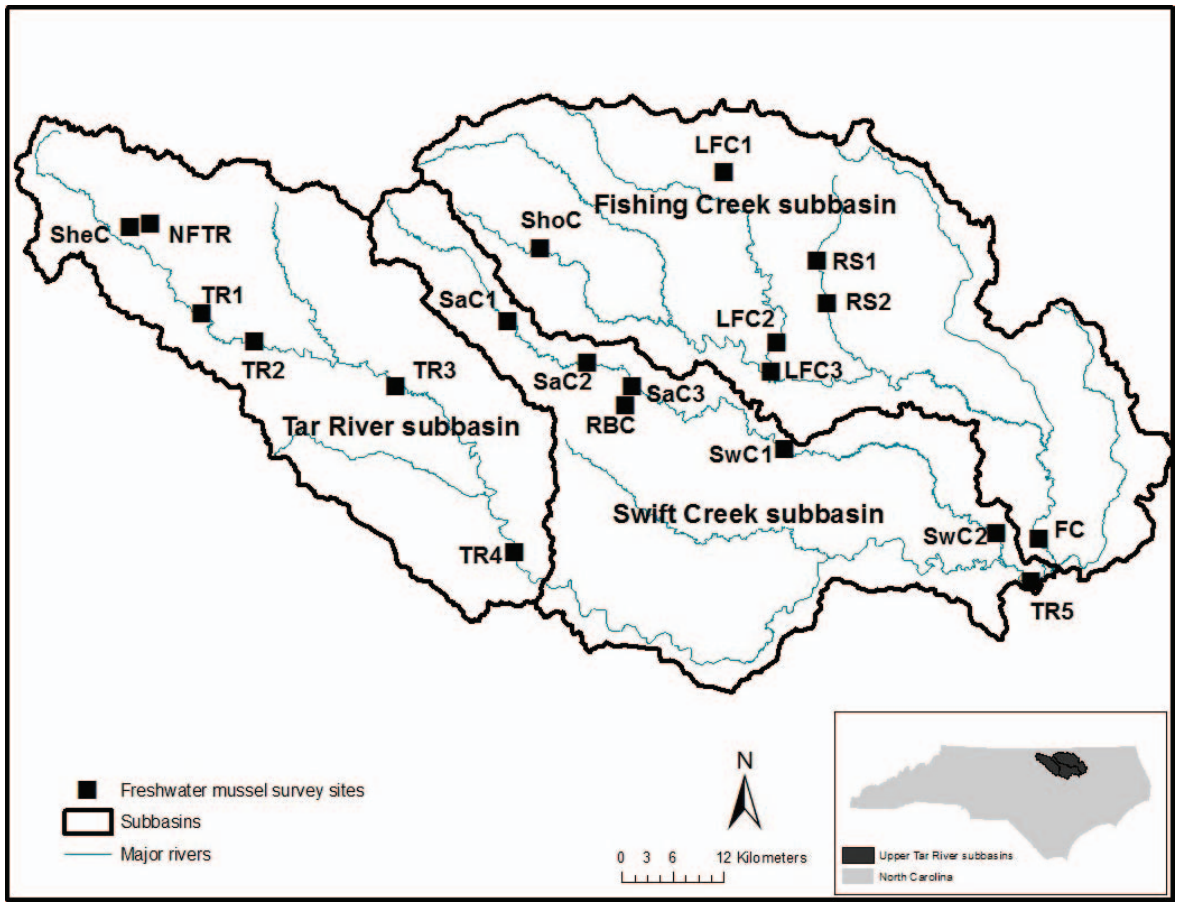

Figure 1. Location of 20 mussel survey sites in the Tar River basin, North Carolina, USA.

detection probability, such as occupancy modeling, provide more useful inference from survey data (Meador et al. 2011; Shea et al. 2013; Wisniewski et al. 2013). A related approach, dynamic occurrence modeling, can provide information on the processes that underlie population trends (Betts et al. 2008; Walls et al. 2011; Frey et al. 2012). In addition to accounting for imperfect detection, these models provide estimates of local colonization and extinction probabilities, which are often the focus of long-term monitoring projects (MacKenzie et al. 2003; Royle and Kery 2007).

We used recent and existing survey data to assess changes in mussel occurrence in the Tar River basin, North Carolina, USA, over a 26-yr period with a dynamic occurrence model that estimated and incorporated detection probability. We then estimated persistence and colonization rates to examine processes driving changes in mussel occurrence.

METHODS

Study Sites

We conducted mussel surveys at 20 sites in the Tar River basin and analyzed previous survey data from those sites (Fig. 1). The Tar-Pamlico River basin is the fourth largest basin in North Carolina, with a 14,090-km^2 watershed and about 3,790 km of streams. Land use in the basin is primarily forest and wetland with areas of agriculture and urban development (NCDENR 2008). This river basin is among the most species rich of North Carolina, supporting a diverse mussel community of 24 species, 13 of which are imperiled (Bogan 2002). Sites were located among three subbasins (upper Tar River, Swift Creek, and Fishing Creek) and were selected to span a range of environmental conditions and include known occurrences of two U.S. federally endangered species, *Alasmidonta heterodon* and *Elliptio steinstansana*.

Mussel Surveys

We conducted timed snorkel and tactile search mussel surveys at all 20 sites during summer 2010 and at eight of those sites during summer 2011. Surveyed stream reaches were accessible at bridge crossings and coincided with known mussel beds or apparently suitable mussel habitat. Reaches extended for 200–500 m, approximately 20 times the average stream width of each site. A minimum of 6 person-hours of effort was expended at each site.

We compiled additional freshwater mussel survey data from the 26-yr period spanning 1986–2011 from the North

Table 1. Number of sites surveyed and number of sites with mussel detections for 14 freshwater mussel species in the Tar River basin, North Carolina, USA, from 1986 to 2011.

	Year																								
	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
No. of sites surveyed	4	1	6	2	1	2	1	3	4	4	4	6	5	8	1	4	6	2	8	9	4	6	3	5	20	8
Species																										
Alasmidonta heterodon	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	3	3	2	1	1	1	3	1
Alasmidonta undulata	0	0	0	0	0	1	0	2	0	0	1	3	1	0	0	1	0	0	0	0	0	0	1	1	1	1
Elliptio fisheriana	0	0	1	1	0	0	1	1	0	0	2	1	3	0	0	1	0	0	1	2	1	1	0	2	4	3
Elliptio lanceolata	2	1	3	1	0	1	0	1	1	1	1	1	0	1	0	0	0	1	1	2	0	0	0	0	2	0
Elliptio roanokensis	0	0	0	0	0	1	0	1	1	1	0	0	3	0	0	0	1	0	1	2	1	3	0	1	3	2
Elliptio steinstansana	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	2	0	0	0	3	1	1	1	1	2	1
Fusconaia masoni	0	1	4	1	0	1	1	1	2	0	2	3	1	0	0	1	3	1	2	4	1	4	1	2	7	3
Lampsilis cariosa	2	1	2	1	0	0	1	1	1	2	0	1	2	1	0	1	2	0	0	3	1	2	1	2	3	2
Lampsilis radiata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lampsilis sp.[a]	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0
Pyganodon cataracta	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Strophitus undulatus	0	0	1	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	2	1	1	1	1	0	1	0
Utterbackia imbecillis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Villosa constricta	0	0	3	0	0	1	0	1	1	1	1	3	4	2	0	1	2	0	1	4	1	2	1	2	5	3

[a]Undescribed *Lampsilis* species.

Carolina Wildlife Resources Commission (NCWRC) database. We included data from surveys that occurred within 500 m upstream or downstream of our 2010–2011 survey sites. We included only survey data that were collected or vetted by NCWRC staff to ensure appropriate survey techniques and accurate species identification. Sampling effort for these surveys was not recorded in the database. When database records included count data, we converted these records to detection/nondetection for each species.

Our survey data combined with NCWRC database records provided data from 127 surveys among our 20 sites (Table 1). We included all species detection/nondetection data from these surveys with the following exception. We excluded data for three *Elliptio* species—*E. complanata*, *E. icterina*, and *E. congaraea*—because these species are difficult to identify, and we were uncertain about the consistency of identifications in previous surveys. We did not pool these records (as *Elliptio* spp.), because *E. complanata* is extremely common in the Tar River basin and consistently present at all sites, and the lack of absence data would interfere with the ability of the occurrence model to accurately estimate parameters. We included all data for four other *Elliptio* that are more easily identified: *E. fisheriana*, *E. lanceolata*, *E. roanokensis*, and *E. steinstansana*.

Dynamic Occurrence Model

We developed a dynamic occurrence model using the detection/nondetection data from all 127 surveys to evaluate changes in species occurrence over the 26-yr period. We adopted a state-space representation of the model wherein we described two component processes: a submodel for the observations conditional on the unobserved state process and a submodel for the unobserved or partially observed state process. We followed an approach developed by Dorazio et al. (2010) and Walls et al. (2011) wherein the single-species model of Royle and Kery (2007) was extended to account for variation in model parameters among ecologically similar species. We modeled the entire species assemblage where each species' individual estimates influence the parameter estimates of every other species in the assemblage and inferences about one particular species are borrowed across all species. Essentially, the parameter estimates for one species are a compromise between the individual species estimates and the mean estimate of those parameters for the assemblage. This is referred to as "shrinkage" in the statistical literature (Gelman et al. 2003) because each species-specific estimate is shrunk in the direction of the estimated mean parameter value. The amount of shrinkage depends on the amount of information for each species and how closely it resembles the overall mean effect for a particular parameter. A major benefit of shrinkage is the ability to estimate parameters for species that are rarely detected. Such species may be critically imperiled species and are an important component of assemblage dynamics, but if analyzed individually there would be too few data to make relevant inference. Instead, these species can be included in the

analysis, and species-specific estimates can be obtained. Similarly, parameters may be estimated for years in which data are limited. For example, in years with no survey data, we obtained occurrence estimates by borrowing information from all other years and species through the estimated global mean and the prior distribution that we assigned to that year. In this case, we had noninformative priors indicating that the occurrence probabilities could take any value between 0 and 1, with most of the information drawn from other species and years.

Because sites were not surveyed multiple times per year, we were unable to estimate detection probability directly. However, a related study designed to explicitly estimate detection probability in the same streams found little evidence of species-specific detection rates (Pandolfo et al. 2016). Therefore, we focused on accounting for temporal (i.e., among-year) variability in detection rates. For each year, we randomly drew a single value for detection probability from a normal distribution with a mean of 0.42 (SD = 0.03), estimated previously from 14 Tar River basin mussel species (Pandolfo et al. 2016). This equated to using an informative prior on detection rates and allowed us to accommodate annual variability in detection. Although variable sampling effort across the 26-yr study period would be expected to contribute increased variability in occurrence estimates, our model accounted for this by allowing detection probabilities to vary from year to year. Therefore, unless there has been a systematic trend or bias through time that we have not accounted for explicitly, our estimates reflect the variable sampling effort across the study period.

Following Walls et al. (2011), we then specified a model using the randomly generated detection rates and conditional on the binary occurrence state (detected or not detected). We defined detection state as y_{ikt} for each combination of site (k), year (t), and species (i), where each binary observation indicates whether the species was detected ($y_{ikt} = 1$) or not detected ($y_{ikt} = 0$). We defined the occurrence state as z_{ikt} for species i, site k, and year t, such that $z_{ikt} = 1$ indicated species presence and $z_{ikt} = 0$ indicated absence of the species. It is noteworthy that if we observed no detections, there is ambiguity in defining the occurrence state because the site could be occupied and we failed to detect the species or the site could be unoccupied. Therefore, we defined the model for each element of the data as follows: $y_{ikt} \mid z_{ikt}, p_t \sim \text{Bernoulli}(z_{ikt} p_t)$, where p_t denotes the probability of detecting a species in year t given that the species is present. This implies that if the kth site is unoccupied by species i in year t, then $y_{ikt} = 0$ with probability 1 and otherwise the species is detected with probability p_t.

We modeled changes in occurrence state for each species by using a first-order Markov process (Royle and Kery 2007). We assumed the initial occurrence state for the ith species at site k is modeled as $z_{ik1} \mid \psi_{i1} \sim \text{Bernoulli}(\psi_{i1})$, where ψ_{i1} denotes the probability of occurrence for species i in year 1. Using a recursive relationship wherein occurrence states in subsequent years ($t+1, t+2, \ldots, T$) depend on the occurrence states 1 yr earlier, occurrence in subsequent years can be written as folows: $z_{ik,t+1} \mid z_{ik,t}, \varphi_{it}, \gamma_{it} \sim \text{Bernoulli}(z_{ik,t}, \varphi_{it} + \gamma_{it}(1 - z_{ikt}))$, where $\gamma_{it} = \Pr(z_{ik,t+1} = 1 \mid z_{ikt} = 0)$ denotes the probability of local colonization (i.e., a site unoccupied at time t will become occupied at time $t+1$), and $\varphi_{it} = \text{PR}(z_{ik,t+1} = 1 \mid z_{ikt} = 1)$ denotes the probability of local persistence (i.e., the probability of an occupied site at time t staying occupied at time $t+1$). We defined the probability of local extinction, ε_{it}, as the probability of an occupied site at time t becoming unoccupied at time $t+1$ and defined this as the complement of local persistence probability: $\varepsilon_{it} \equiv 1 - \varphi_{it}$. Colonization and persistence were fixed between years, with one colonization probability and one persistence probability modeled for each species and applied yearly throughout the 26-yr period.

We used a multivariate normal prior distribution to model species-specific deviations from the mean group-level parameter values (Dorazio et al. 2006; Kery and Royle 2008). We estimated parameters using a Bayesian approach with Markov chain Monte Carlo (MCMC) implemented using R statistical software (with the R2WinBUGS package; Sturtz et al. 2005) and WinBUGS (Lunn et al. 2000) using flat priors for each of the group-level parameters. The MCMC approach allowed us to explicitly measure uncertainty in parameter values by examining a posterior distribution for each parameter. We ran three chains of each model for 20,000 iterations, thinned by 5, after a burn-in of 10,000 iterations (resulting in 12,000 posterior samples for each parameter), and we assessed model convergence by examining trace plots and Gelman–Rubin statistics by using package CODA in R (Gelman et al. 2003). We estimated occurrence, persistence (1 – extinction), and colonization probabilities for the entire mussel assemblage.

RESULTS

Detection probabilities ranged from 0.39 to 0.45 among all species and years. The modeled overall occurrence for all 14 mussel species over 26 yr was 0.35 (95% CI = 0.20–0.51). Initial occurrence rates (1986) ranged from 0.19 for *Utterbackia imbecillis* to 0.60 for *Fusconaia masoni* (Table 2). Every species exhibited a decline in occurrence from 1986 to 2011, regardless of initial occurrence (Fig. 2). In 2011, occurrence ranged from 0.10 for *Lampsilis radiata* to 0.40 for *F. masoni*. The maximum difference between occurrence rates in 1986 and 2011 was a decline of 0.30 for *Alasmidonta undulata*. The mean persistence for all species was high (0.97, 95% CI = 0.95–0.99) and ranged from 0.93 for *L. radiata* to 0.98 for *A. heterodon*, *E. fisheriana*, *E. lanceolata*, *E. roanokensis*, *F. masoni*, and *V. constricta*. However, the mean colonization probability was very low (<0.01, 95% CI = <0.01–0.01). The modeled colonization probability for all 14 species was <0.01.

DISCUSSION

The dynamic modeling approach showed that the occurrence of all 14 mussel species in the study area declined

Table 2. Parameter estimates and SDs of occurrence, persistence, and colonization probabilities for 14 freshwater mussel species in the Tar River basin, North Carolina, USA, from 1986 to 2011.

	Occurrence				Persistence		Colonization	
Species	Ψ_{1986}[a]	SD	Ψ_{2011}[b]	SD	Φ[c]	SD	γ[d]	SD
Alasmidonta heterodon	0.30	0.12	0.24	0.08	0.98	0.01	<0.01	<0.01
Alasmidonta undulata	0.54	0.15	0.24	0.09	0.96	0.02	<0.01	<0.01
Elliptio fisheriana	0. 31	0.11	0.23	0.08	0.98	0.01	<0.01	<0.01
Elliptio lanceolata	0.34	0.11	0.22	0.08	0.98	0.02	<0.01	<0.01
Elliptio roanokensis	0.31	0.11	0.24	0.08	0.98	0.01	<0.01	<0.01
Elliptio steinstansana	0.32	0.12	0.20	0.08	0.97	0.02	<0.01	<0.01
Fusconaia masoni	0.60	0.15	0.40	0.11	0.98	0.01	<0.01	<0.01
Lampsilis cariosa	0.49	0.15	0.30	0.09	0.97	0.01	<0.01	<0.01
Lampsilis radiata	0.23	0.14	0.10	0.06	0.93	0.08	<0.01	<0.01
Lampsilis sp.[e]	0.22	0.12	0.13	0.06	0.97	0.03	<0.01	<0.01
Pyganodon cataracta	0.24	0.12	0.15	0.07	0.97	0.03	<0.01	<0.01
Strophitus undulatus	0.43	0.14	0.20	0.08	0.96	0.03	<0.01	0.01
Utterbackia imbecillis	0.19	0.11	0.12	0.07	0.96	0.05	<0.01	<0.01
Villosa constricta	0.51	0.12	0.39	0.11	0.98	0.01	<0.01	<0.01

[a]Occurrence probability in 1986.
[b]Occurrence probability in 2011.
[c]Persistence probability, 1986–2011.
[d]Colonization probability, 1986–2011.
[e]Undescribed *Lampsilis* species.

steadily over the 26-yr period. This finding is consistent with qualitative assessments of the region's fauna, which portray steep declines in mussel abundance and species richness (Alderman 1997). Although persistence probability was high among all species for every year in the study, it never reached a value of 1.0. This indicates that every year, there was at least one site where a mussel species was extirpated. Because persistence probability was accounted for annually, the effects of less than total persistence were compounded over the 26-yr period. This, combined with extremely low colonization probabilities, resulted in decreases in mussel occurrence probabilities over time.

A major advantage of our modeling approach was that it incorporated imperfect detection of mussels, and therefore we

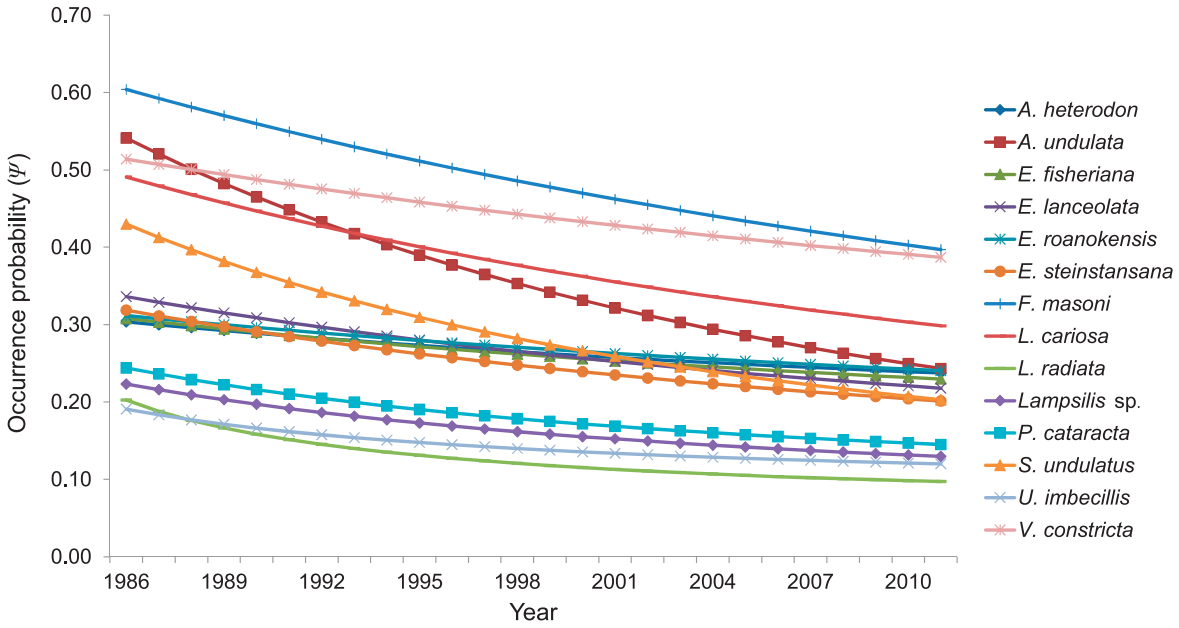

Figure 2. Estimated occurrence (Ψ) for 14 freshwater mussel species in the Tar River basin, North Carolina USA, from 1986 to 2011.

avoided basing inferences on biased data (MacKenzie et al. 2003; Kery and Schmidt 2008). For example, a cursory inspection of survey data (Table 1) might suggest that the federally endangered *A. heterodon* occurred at survey sites more frequently in later time periods than in earlier periods. However, dynamic modeling indicated that occurrence of *A. heterodon* declined steadily, and this finding is in agreement with regional mussel experts who infer that populations of *A. heterodon* are declining in the Tar River basin (R.B. Nichols, North Carolina Wildlife Resources Commission, personal communication). The apparent increase in the number of surveys in which *A. heterodon* was detected is most likely related to sampling effort and intensity or species detection issues. The species was federally listed as endangered in 1990, which led to expanded research interest in this species (Strayer et al. 1996). It is likely that survey efforts became more frequent and targeted for this species and surveyors became more adept at locating and identifying this small mussel (Strayer and Smith 2003; Meador et al. 2011). The apparent increase in species detections at survey sites could be misinterpreted as an increase in occurrence and perhaps misinform conservation planning.

Despite our finding of a steady decrease in mussel occurrence, the high persistence probabilities in the Tar River basin indicate that the majority of sites where mussels previously occurred have remained occupied. However, our analysis did not include a measure of abundance, and we have no information about changes in population size. Similarly, our analysis did not include individual size and provides no information about other changes in population status such as age structure or strength of recent recruitment.

The extremely low colonization probabilities that we modeled for mussels in the Tar River basin cannot be conclusively attributed to a particular cause. Other studies found that colonization rate depends on mussel density and distribution and larval dispersal traits (McClain and Ross 2005; Vaughn 2012). Habitat requirements of newly settled and established juvenile mussels may also influence colonization success. For example, juvenile mussels may not be able to settle during high velocity or shear stress conditions (Payne and Miller 2000). We have no information about changes in mussel density or habitat conditions that may influence colonization in the Tar River basin. However, it is likely that, to a large extent, unoccupied sites are not being colonized simply because mussels have reached a steady state in which all species suited for the habitat and resources at a particular site have already colonized that site.

Our analyses were constrained by the data available in the existing database. Most records in the database did not report sampling effort, which limited our analyses to presence/absence. Including sampling effort in survey records can greatly enhance their utility by allowing assessment of long-term trends in abundance. Also, our data were not collected specifically for application in an occurrence model, so results should be interpreted with a degree of caution. For example, methods of estimating detection probability are data intensive, and we were unable to model it using survey data from the database. Instead, we relied on detection probability estimates derived from a complementary study in the same river basin (Pandolfo et al. 2016). These detection probabilities were estimated for the same species at the same sites examined in this study, and our model included annual variation around the mean detection probability from the complementary study. However, we were unable to empirically estimate changes in detection probability over time. Therefore, our modeled occurrence probabilities over the study period may not reflect actual changes in detection probability that may have occurred during that time. For example, our model cannot conclusively address the presumption that detection of *A. heterodon* has increased during the study period due to increased focus on this species (see above). In addition, because our modeling approach uses shrinkage (i.e., it borrows data across all species), the parameter estimates are influenced by the mean estimates for the entire assemblage (Gelman et al. 2003). Thus, if one species is more data rich than others in the assemblage, it may influence the parameter estimates of the other species.

Despite the limitations of our data set, our dynamic occurrence modeling approach incorporated imperfect detection to generate parameter estimates for an entire mussel assemblage, including rare species that are more data limited. This approach enabled us to document gradual declines in occurrence for all species in this region since 1986. The specific causes of these declines are unknown, but species life history traits, agricultural land use, and stream power influence occurrence of mussels in this region (Pandolfo et al. 2016). In addition, this region is experiencing intensive climate and land use changes, rendering the aquatic fauna vulnerable (Ingram et al. 2013). A wealth of mussel survey data exist among individuals, agencies, and universities, and more effective analytical approaches can increase the value of these data for assessing long-term trends in mussel populations and the causes of mussel declines (Burgman et al. 1995; Reichman et al. 2011). Our ability to assess long-term trends can be enhanced further by recording sampling effort and population measures such as individual size in future surveys.

ACKNOWLEDGMENTS

We thank T. Black, B. Jones, E. Buttermore, D. Weaver, J. Archambault, A. White, B. Cope, and M. Fisk for mussel field survey assistance and support and A. Drew for a constructive manuscript review. This research was funded by the U.S. Geological Survey, National Climate Change and Wildlife Science Center, through Research Work Order 171. The North Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Freshwater Mollusk Biology and Conservation 20:20–31, 2017

REGULAR ARTICLE

ESTIMATION OF APPARENT SURVIVAL, DETECTABILITY, AND DENSITY OF THREE FEDERALLY THREATENED MUSSEL SPECIES IN A SMALL WATERSHED

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ABSTRACT

Almost half of the mussel species in North America are imperiled, and eight species found in the eastern Gulf Coastal Plain drainages were recently federally listed. Information regarding the status of known populations of these species is either limited or outdated. Three sites in the Choctawhatchee River watershed (southeast Alabama), where federally threatened mussel species were known to occur, were sampled for mussels eight times each over 4 mo. Three federally threatened species, *Fusconaia burkei*, *Hamiota australis*, and *Pleurobema strodeanum*, and one common species, *Elliptio pullata*, were individually tagged and released using a robust mark-recapture sampling design. Each species-site combination having sufficient sample sizes was analyzed using a set of six candidate mark-recapture models chosen a priori, and estimates of apparent survival, detectability, and density were derived using the computer program MARK to average models. A total of 820 mussels, 427 of which are listed as federally threatened or endangered, were tagged over eight sampling occasions at three sites. Apparent survival of *E. pullata* varied among sampling occasions (0.96–0.99), while threatened species tended to have nearly constant survival. Detectability increased with mussel length for *E. pullata* at all sites (0.07–0.82), but with the exception of *P. strodeanum* at 8M1, length did not affect detectability of threatened species (0.11–0.52). Densities of threatened species (0.05–1.0 individuals/m^2) were typically lower than those of *E. pullata* (0.15–1.78 individuals/m^2) at each site. These data offer insights into the current status of known populations of threatened species at three sites in the Choctawhatchee watershed and will serve as a baseline against which the future status of these populations can be measured. These data also demonstrate the potential viability of using these methods for long-term monitoring of these populations.

KEY WORDS: mark-recapture, freshwater mussels, Akaike's Information Criterion (AIC), robust design, conservation, multimodel inference

INTRODUCTION

Unionid mussels are among the fastest declining groups of freshwater organisms in North America (Vaughn and Taylor 1999). About 30 of the approximately 300 species now recognized are believed extinct. Of those remaining, 65% are either endangered, threatened, or vulnerable (Haag and Williams 2014). In November 2012, eight mussel species endemic to the Gulf drainages of southeast Alabama were listed under the Endangered Species Act (U.S. Fish and Wildlife Service 2012). *Margaritifera marrianae* Johnson, 1983; *Fusconaia rotulata* (Wright, 1899); *Ptychobranchus jonesi* (van der Schalie, 1934); and *Obovaria choctawensis* (Athearn, 1964) were listed as endangered, and *Fusconaia burkei* (Walker in Ortmann and Walker, 1922); *Fusconaia escambia* Clench and Turner, 1956; *Hamiota australis* (Simpson, 1900); and *Pleurobema strodeanum* (Wright, 1898) were listed as threatened. Information regarding the local population status of many of these protected species

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indicates areas where conservation efforts should be focused to prevent further decline and extirpation. Such information is also useful when comparing current population levels to those historically reported and serves as a baseline against which future assessments of these populations can be compared. Further, known populations of threatened mussels may serve as future sources of gravid females for captive propagation of these species, making knowledge of their status of vital importance. The population parameters of interest in this study were apparent survival, detectability, and population size, all of which can be estimated using mark-recapture models (Hart et al. 2001).

Detectability is the probability of detecting (or finding) an individual or species at a site if present (MacKenzie et al. 2006). Imperfect species detectability is a major source of bias in estimating parameters such as population size and survival (Mazerolle et al. 2007). Mark-recapture models are able to account for detectability when estimating population parameters of interest, producing relatively unbiased estimates compared to other methods. Mark-recapture models generally fall under one of two categories: (1) closed population models or (2) open population models. Sampling in a closed population model occurs over a short enough period that changes in population due to births, deaths, or migration are assumed to be negligible (Kendall 1999). Closed population models are primarily used to estimate population size and generally have only one parameter: the probability p that an individual is detected given that it is available for capture (i.e., detectability). In open population models, sampling occurs over a period during which the population is vulnerable to change. Open models have an additional parameter (Φ), which is the probability that a marked individual survives between sampling periods (Amstrup et al. 2010). Open models, such as Cormack-Jolly-Seber, are commonly used to estimate apparent survival and recruitment (Meador et al. 2011). Apparent survival is the probability of a marked individual both surviving in the interval between primary sampling periods and not emigrating from the sample area.

Pollock's robust design is a combination of closed and open population models (Pollock 1982). The robust design consists of a number of secondary sampling occasions (closed), each taking place over a short period (usually consecutive days). These secondary sampling occasions are nested within primary sampling periods (open) with much longer intervals. Survival, population size, and capture probabilities (detectability) can be simultaneously estimated by combining open and closed models.

To estimate parameters such as survival, a model with a given set of assumptions (e.g., constant recapture probability) is chosen. This model is applied to the data, and estimates of the desired parameters, such as population size or survival, are calculated. Estimates will vary depending on the model chosen. To ensure that an appropriate model is used, a set of candidate models are chosen a priori and tested to determine which best explains the underlying process given the data collected. Akaike's Information Criterion is a method of choosing the model that best fits the data using the fewest number of parameters. The most likely model is one that best balances bias (fit of data) and variance (number of parameters) (Burnham and Anderson 2002). Akaike weights can then be used to determine the relative level of support for each model in a given set of candidate models. When no single model is well supported, parameter estimates can be derived from the entire candidate model set using multimodel inference (Burnham and Anderson 2002). A mean of each individual parameter can be calculated using Akaike weights of all models in the candidate set.

The objective of this study was to use a robust mark-recapture design to sample three federally threatened and one common mussel species at three sites in the southeastern Coastal Plains (Choctawhatchee River watershed). We used an initial set of six candidate models to calculate estimates of detectability, apparent survival, and density for the federally threatened species *Fusconaia burkei, Hamiota australis,* and *Pleurobema strodeanum,* and a common species, *Elliptio pullata*. Results were then compared among species and among sites. Few studies have used these methods on mussels in general (Villella et al. 2004; Meador et al. 2011), and an in-depth search of the literature failed to reveal any studies that used the robust design on federally threatened mussel species in particular.

METHODS AND MATERIALS

Study Area

The Choctawhatchee River watershed lies in the Southeastern Plains level III ecoregion and covers about 12,297 km^2 (Heath et al. 2010). Three sites from the Choctawhatchee River watershed were selected based on previous knowledge of species composition (Pilarczyk et al. 2006; Reátegui-Zirena et al. 2013) and were sampled from June to October 2012 (Fig. 1). The first site (BS, 31°39′49.6″N, 85°30′18.8″W) was located on the West Fork of the Choctawhatchee River and is a fourth-order stream near Blue Springs State Park, in Barbour County, Alabama. The remaining two sites (8M1, 30°58′50.3″N, 86°10′45.5″W; 8M2, 30°58′46.7″N, 86°10′45.4″W) were located at Eightmile Creek, a second-order stream in Walton County, Florida.

Field Methods

We captured and tagged mussels between June and October 2012 using Pollock's robust design (Pollock 1982). We sampled each site during four primary periods, each of which was approximately 1 mo apart. Each primary period consisted of two secondary sampling days as close to each other as possible (usually consecutive). The length of intervals between primary sampling periods varied slightly both within and among sites. A combination of tactile and visual searching was used to sample the stream, generally following Georgia/Florida qualitative/semiquantitative protocols (Carlson et al.

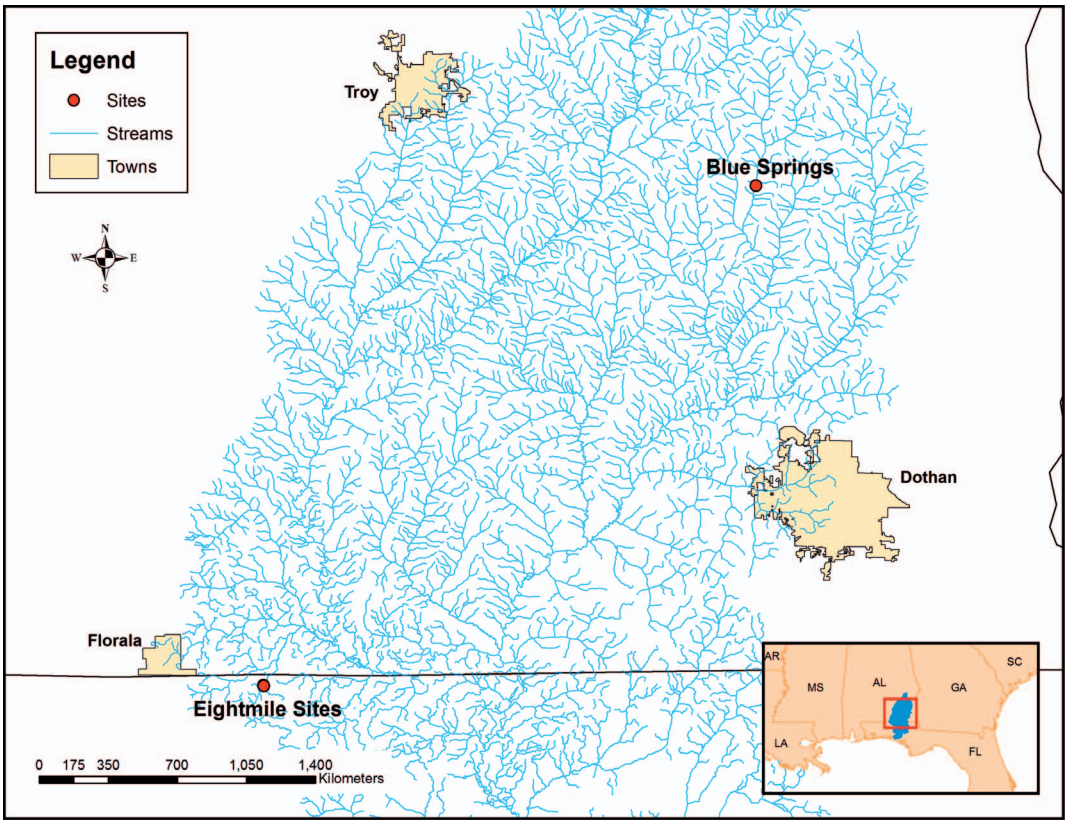

Figure 1. Location of three sites in the Choctawhatchee River watershed sampled from June to October 2012.

2008). We did not excavate quadrats because of its time-intensive nature, rarity of the species of interest, and greater disturbance to the habitat. We sampled the same reach for approximately five man-hours at each site per sampling event (Metcalfe-Smith et al. 2000). Mussels were identified to species on site using Williams et al. (2008). All listed mussels encountered in the study sites were tagged during the first sampling event, and all untagged (not previously collected) individuals encountered on subsequent sampling events were also tagged. Because of their abundance, the first 30 *E. pullata* encountered within each site were tagged during the first sampling event. Subsequent sampling for this species was limited to the segment of each site where these individuals were found. Untagged *E. pullata* found within that segment were tagged in subsequent sampling events. *Elliptio pullata* found outside this segment of each site were counted but were not tagged and were not included in modeling. Listed mussels were tagged throughout the entire site reach. Tag numbers of any previously captured mussels were recorded for each sampling event.

Target mussels were tagged using Hallprint glue-on shellfish tags (available from www.hallprint.com). No juveniles of federally threatened species and few juveniles of *E. pullata* were captured during this study, which were not tagged due to their small size. Consequently, estimates of apparent survival, detectability, and population size calculated for these populations apply only to adult mussels that exceeded a minimum size (26.2 mm in length). We removed a small section of the periostracum with a file and cleaned and dried the area with a cotton swab and isopropyl alcohol. Tags were attached using forceps and cyanoacrylate glue (superglue). Mussels were kept out of the water for at least 2 min to allow the glue to dry (Lemarie et al. 2000). We returned mussels to the general area from which they were collected by an individual not involved in the collection to avoid bias during subsequent sampling events. None of the current federally threatened species we sampled were listed at the time of sampling, before November 2012 (U.S. Fish and Wildlife Service 2012).

Model Description

A set of six candidate models were developed for each site and species combination. These models contained the following parameters:

S_i = apparent survival during primary period i
γ' = probability of not being available for capture during primary period i, given that an individual was not available for capture during primary period i–1 (i.e., the probability of not immigrating back into the study area)
γ'' = probability of not being available for capture during primary period i, given that an individual was available for

Table 1. Reference table for models used to estimate apparent survival, detectability, and population size for mussel species at three sites in the Choctawhatchee River watershed. Capture probabilities are denoted by p and recapture probabilities are denoted by c, (t) indicates a given parameter varies with time, (·) indicates that a parameter is constant across all sampling periods, and (length) indicates that that a parameter varied with the length of an individual mussel. Models where p and c are equal indicate no behavioral response to initial capture; models where p and c are not equal indicate a behavioral response.

Model
1. $p(t) \neq c(t)$
2. $p(t) = c(t)$
3. $p(\cdot) = c(\cdot)$
4. $p(\cdot) \neq c(\cdot)$
5. p(length) = c(length)
6. p(length) ≠ c(length)

capture during period i–1 (i.e., the probability of temporarily emigrating)

p_{ij} = probability of being captured during secondary sampling occasion j of primary period i

c_{ij} = probability of being recaptured during secondary sampling occasion j of primary period i.

All models assumed that capture probability was constant within a primary period but varied among primary periods (i.e., $[p_{11} = p_{12}] \neq [p_{21} = p_{22}]$). Temporary emigration was assumed to be constant and random (i.e., $\gamma'[\cdot] = \gamma''[\cdot]$). Finally, all models assumed that apparent survival varied with time ($S[t]$).

Model 1 was the most general model, allowing both initial capture (p) and recapture (c) probabilities to vary with time between primary periods (interval between primary sampling period) and not be equal to each other between secondary sampling occasions within each primary period (i.e., a behavior response to being captured initially) (Table 1). Model 2 still allowed capture and recapture probabilities to vary with time (interval between primary sampling periods), but they were equal between secondary sampling occasions within a primary period (i.e., no behavior response). Capture and recapture were constant between primary sampling periods in models 3 and 4, but model 3 had no behavior response and model 4 had a behavior response. Finally, models 5 and 6 allowed capture and recapture to vary based on length of individual mussels. Model 5 had no behavior response, and model 6 had a behavior response.

Data Analysis

To ensure that models adequately fit the data, some form of goodness-of-fit testing is necessary. In cases where the most general model in a candidate model set does not fit the data, a correction factor, $\hat{c}$, can be estimated and applied to the model set (Burnham and Anderson 2002). We tested goodness of fit for each site-species combination by collapsing encounter histories to primary sampling periods and using the live encounter Cormack-Jolly-Seber model in the computer program MARK. One thousand bootstrap simulations were run using a fully time-dependent model. We estimated $\hat{c}$ using two methods: (1) by dividing the deviance of the time-dependent model by the mean deviance of the simulations and (2) dividing the $\hat{c}$ of the model by the mean $\hat{c}$ of the simulations. We used the higher $\hat{c}$ as a correction factor when analyzing our candidate model set (Table 1). In cases where the estimated $\hat{c}$ was less than one, we used a $\hat{c}$ of one for analysis.

We analyzed our candidate model sets using MARK to determine the model with the highest likelihood (Villella et al. 2004; Meador et al. 2011). The same set of candidate models was used for all site-species combinations. Likelihood estimates were based on Akaike's Information Criterion (AIC) (Akaike 1973) modified for small sample sizes (AIC_c) (Sugiura 1978):

$$AIC_c = -2\log\left(L(\widehat{\theta})\right) + \frac{2K(K+1)}{n-K-1}$$

where $L(\hat{\theta})$ is the likelihood of the parameter estimates, given the data, K is the number of parameters, and n is the sample size. In cases where we used a $\hat{c}$ correction, likelihood estimates were based on $QAIC_c$ by dividing the likelihood by the $\hat{c}$ correction (Burnham and Anderson 2002):

$$QAIC_c = \frac{-2\log\left(L(\widehat{\theta})\right)}{\hat{c}} + \frac{2K(K+1)}{n-K-1}$$

where $\hat{c}$ is the calculated correction factor (see above). Akaike weights (w) are used to normalize the relative likelihoods of models in a candidate set. For a given candidate set of models, Akaike weights sum to 1 and can be thought of as the weight of evidence for each model.

After analysis of the initial candidate set, we added subsets of the top models where apparent survival was constrained to be constant to see if there was support for survival being constant across our primary sampling periods. For example, if model 3 of a given site-species combination was one of the top models, we ran the same model with constant apparent survival. If this model had a substantially lower AIC, then there was evidence that apparent survival was indeed constant rather than varying among primary sampling periods. This also helped improve our estimates and the precision of parameter estimates in cases where the data were sparse. If these post hoc models were not improvements, we removed them and used the original model set for subsequent analyses.

There is often substantial uncertainty when selecting the best model from a candidate set (Burnham and Anderson 2002). Ignoring this uncertainty can overestimate the precision of parameter estimates. Consequently, we estimated parameters using the model averaging function of MARK to obtain estimates of apparent survival, probability of capture and recapture, and population size during each primary period for each species. To facilitate comparisons among sites, popula-

Table 2. Number of tagged mussels by species and site for mussel species at three sites in the Choctawhatchee River watershed.

Site	*Elliptio pullata*	*Fusconaia burkei*	*Hamiota australis*	*Pleurobema strodeanum*	*Obovaria choctawensis*	Total
BS	133	1	13	24	1	172
8M1	94	30	5	57	-	186
8M2	166	99	11	186	-	462
Total	393	130	29	267	1	820

tion sizes were converted to density using the length of stream sampled and the mean width of the stream.

RESULTS

A total of 820 mussels, 427 of which were either federally threatened or endangered, were tagged over eight sampling occasions at three sites (Table 2). Relative abundance was highest at 8M2 with 462 total tagged mussels and 296 threatened mussels tagged, and lowest at BS (172 total and 38 threatened tagged). Based on poor goodness-of-fit results (possibly due to low recapture rates) we did not analyze *H. australis* at any site or *F. burkei* at 8M1. Nor did we analyze *F. burkei* or *O. choctawensis* at BS due to low sample sizes ($n = 1$) (Table 2). Finally, estimates of parameters of *P. strodeanum* at BS were highly suspect (e.g., high standard errors of population size, poor convergence on estimates of *S*), even for the top models (i.e., those with the lowest AIC values).

Model Results

The top models (i.e., those with lowest AIC values) for *E. pullata* at 8M1 were models 5 and 6. The combined weight of these models ($\omega \approx 0.99$) strongly suggests that length affected capture probability of this species at this site. Although the top model (5) showed no effect on capture probability due to sampling (i.e., behavior response) ($\omega \approx 0.60$), the second best model (6) suggested otherwise ($\omega \approx 0.40$). The high ranking of this second model may be due more to the importance of length as a variable, although there was evidence for a small behavioral response. Constrained versions of models 5 and 6 with constant apparent survival had less support (AIC) than the original models. These two post hoc models were therefore discarded before averaging models for parameter estimation.

The top models for *P. strodeanum* at 8M1 were 5, 3, and 6. Initial post hoc analysis of models 5, 3, and 6 suggested strong evidence for apparent survival being constant. Therefore, we included a total of six post hoc models corresponding to the original model set but with apparent survival constrained as constant. This resulted in the final model set used for analysis having 12 models. Based on this model set, the strongest evidence was for no behavior effect ($\omega \approx 0.77$), followed by constant survival ($\omega \approx 0.67$), and then capture rate varying by length of individual ($\omega \approx 0.59$).

We found models 5, 3, and 6 to be the top models for *E. pullata* at 8M2 ($\omega \approx 0.84$). A post hoc analysis of models 5 and 3 with survival constrained to be constant showed these models had lower $QAIC_c$ values. However, the estimates of the temporary emigration parameters for these models were suspect (zero with zero standard error), so we discarded these models and used the original model set for subsequent analysis. Using these models, there was evidence for no behavior effect ($\omega \approx 0.71$). Length had the most effect on capture probabilities ($\omega \approx 0.57$), and there was very little evidence for a time effect on capture ($\omega \approx 0.07$).

Model 2 was the only model with any support for both *F. burkei* ($\omega \approx 0.93$) and *P. strodeanum* ($\omega \approx 0.99$) at 8M2, suggesting that capture and recapture probabilities varied with time and that there was no behavior effect. Models with length as a covariate of capture had the least support. Constraining apparent survival in model 2 to be constant resulted in a lower $QAIC_c$ in both cases, suggesting that survival was constant over the course of our study. This model was included in the final model set for parameter estimation of both species.

Models 5 and 6 had almost all the support for *E. pullata* at BS ($\omega \approx 0.99$), which suggests that length as a covariate affecting capture was the most important variable ($\omega \approx 0.99$) followed by no behavior effect ($\omega \approx 0.56$). We ran a post hoc analysis on models 5 and 6, constraining survival to be constant. Both models had substantially higher AIC_c values and were thus discarded. We used the original model set for parameter estimation.

Parameter Estimates

The lowest apparent survival estimates were 0.96 (95% CI [0.94, 0.97]) for *E. pullata* at BS during the second sampling interval and 0.98 (95% CI [0.95, 0.98]) for *E. pullata* at 8M1 during the third sampling interval (Figs. 2 and 3). Otherwise, apparent survival rates for all target species were in the 0.98–0.99 range with generally more precise estimates for threatened species at 8M2 (Fig. 4).

The lowest densities were found at BS. The estimated densities of *E. pullata* were less than $1.0/m^2$ on all sampling occasions, and no other species at this site occurred in sufficient numbers to estimate density (Fig. 5). Estimated densities were higher at 8M2 than 8M1 for both *E. pullata* and *P. strodeanum*, although estimates at 8M2 had wider confidence intervals (Figs. 6 and 7). Presumably 8M2 had a higher density of *F. burkei* as well, since this species did not occur in sufficient numbers to estimate density at 8M1. Overall, densities of *E. pullata* (0.15–1.78) were higher at all sites than any threatened species (0.1–1.0).

Detectability increased with mussel length for *E. pullata*

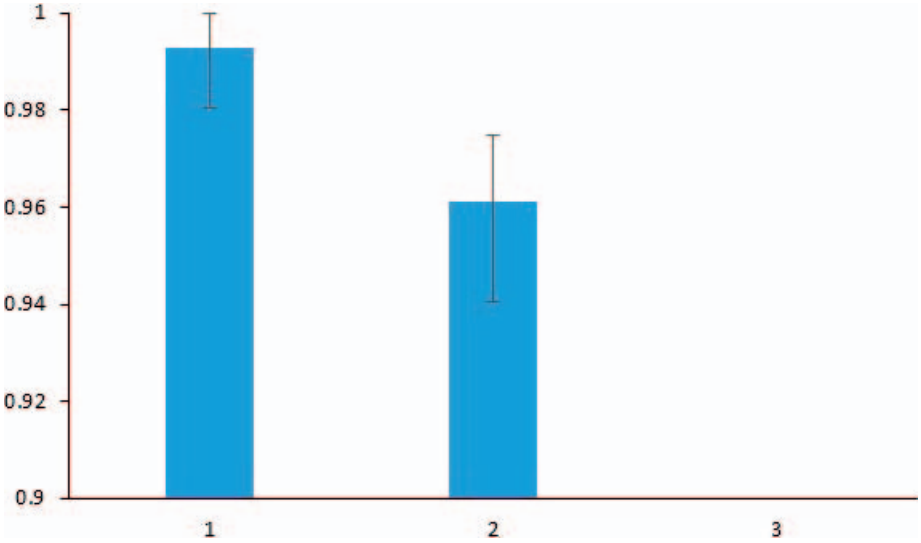

Figure 2. Apparent survival estimates with 95% confidence intervals for *Elliptio pullata* at BS during two intervals among primary sampling periods. Apparent survival during the third interval could not be estimated.

at all three sites. This relationship was strong at 8M1 and BS but weaker at 8M2 (Figs. 8, 9, and 10). This is due to the lower support for length as a covariate at 8M2 ($\omega \approx 0.57$) as compared to 8M1 and BS ($\omega \approx 0.99$). Detectability increased with mussel length for *P. strodeanum* at 8M1 as well (Fig. 11), although the relationship was also not as strong as *E. pullata* at 8M1 and BS because of lower support for length as a covariate ($\omega \approx 0.59$). Overall, detectability ranged from 0.07–0.82 for *E. pullata* and from 0.11 to 0.52 for threatened species.

Length had no effect on detectability of either *P. strodeanum* or *F. burkei* at 8M2. There was strong support that detectability varied with time in these cases ($\omega \approx 0.99$). *Fusconaia burkei* appeared to have slightly higher detectability on a given occasion than *P. strodeanum* (Fig. 12). Detectability was highest on the first and last sampling occasions with a decrease during the two intervening occasions.

DISCUSSION

Apparent survival is the probability of both surviving between primary sampling periods and not permanently emigrating (i.e., remaining in the superpopulation). Thus, apparent survival estimates will typically underestimate actual survival. As permanent emigration increases, apparent survival estimates become more negatively biased compared to true

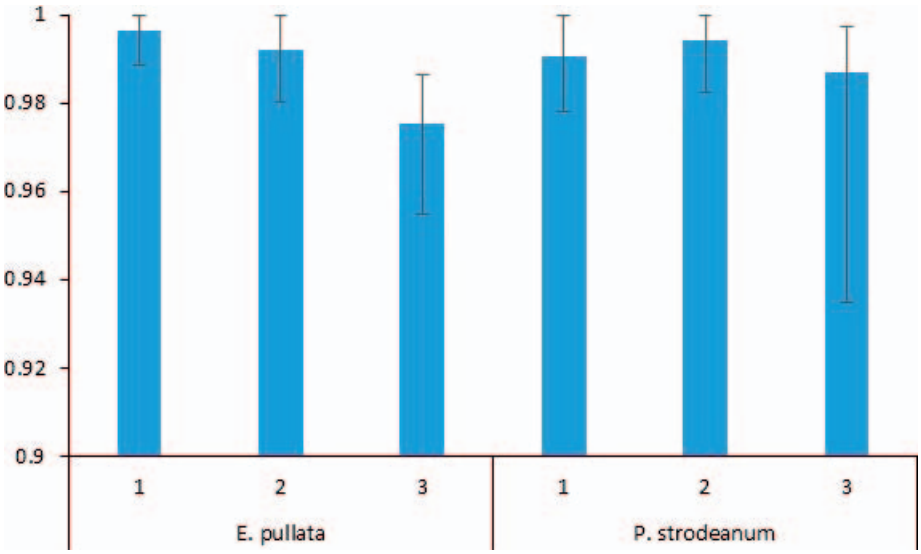

Figure 3. Apparent survival estimates with 95% confidence intervals for *Elliptio pullata* and *Pleurobema strodeanum* at 8M1 during three intervals among primary sampling periods.

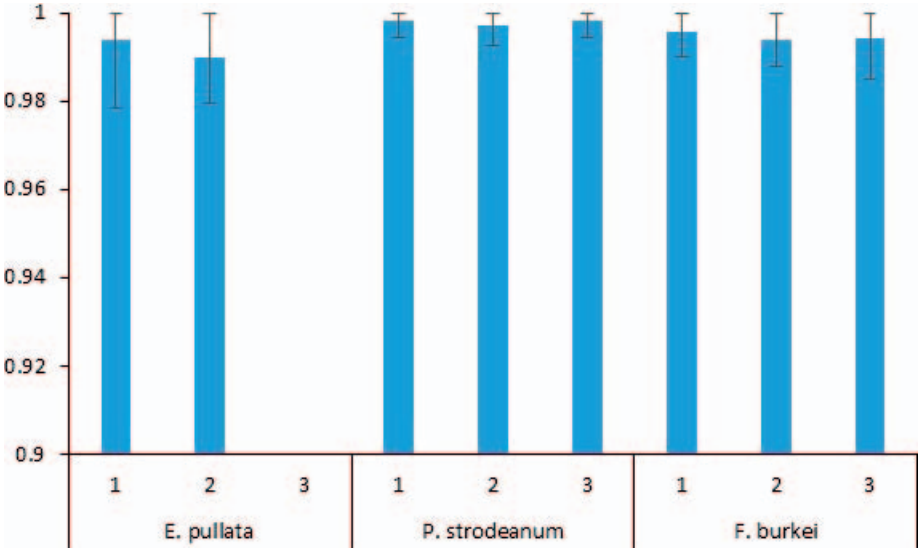

Figure 4. Apparent survival estimates with 95% confidence intervals for *Elliptio pullata*, *Pleurobema strodeanum*, and *Fusconaia burkei* at 8M2 during three intervals among primary sampling periods. Apparent survival of *E. pullata* during the third interval could not be estimated.

survival estimates (Gilroy et al. 2012). However, as our estimates were all relatively high (all but two were at least 0.98), permanent emigration was likely not very high at our sites. Given the relatively sedentary nature of mussels, this should not be surprising. Villela et al. (2004) found evidence of very little movement of mussels in their study. Another study found that *Elliptio complanata* moved a mean of 27 cm downstream over the course of 1 yr (Balfour and Smock 1995). Additionally, Reátegui-Zirena et al. (2013) were able to recover 17% of tagged mussels released 7 yr before from a previous study located at our Eightmile sites.

We found evidence that apparent survival of *E. pullata* varied with time at all sites, and apparent survival was constant for *P. strodeanum* at 8M1 and 8M2 and *F. burkei* at 8M2. Villella et al. (2004) found that apparent survival varied with time in three species of mussels (including two *Elliptio* species) in the Cacapon River, West Virginia, although their study took place over 3 yr, with sampling occurring throughout the year, while our study took place over only 4 mo. To extrapolate these estimates to annual survival, we would have to assume that apparent survival is the same during the rest of the year in which we did not sample. Given that Villela et al. (2004) found much lower survival estimates during the fall and winter months, this seems unwarranted. Most of the species in our study were in the Tribe Pleurobemini, which often live at least 20 yr (Haag and Rypel 2011). Because of this, apparent survival estimates are likely to be high for all of our species over

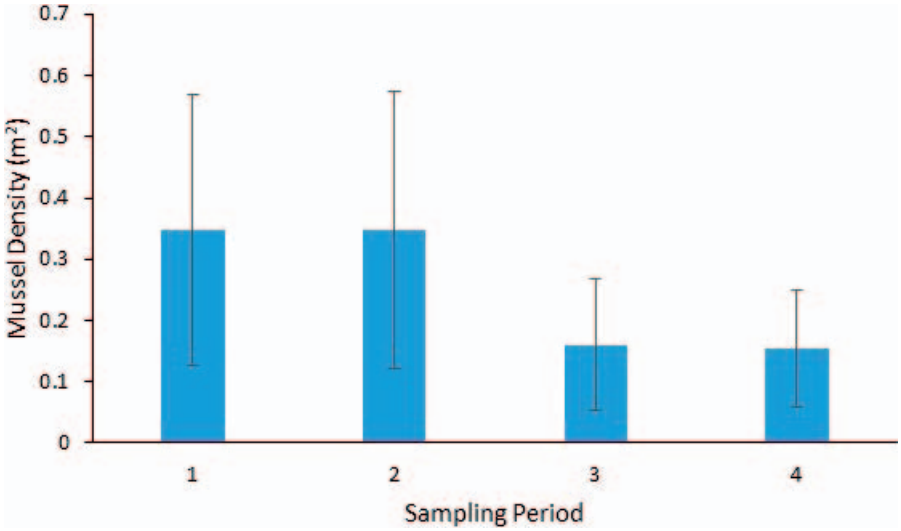

Figure 5. Density (m^2) estimates with 95% confidence intervals for *Elliptio pullata* at BS during four primary sampling periods.

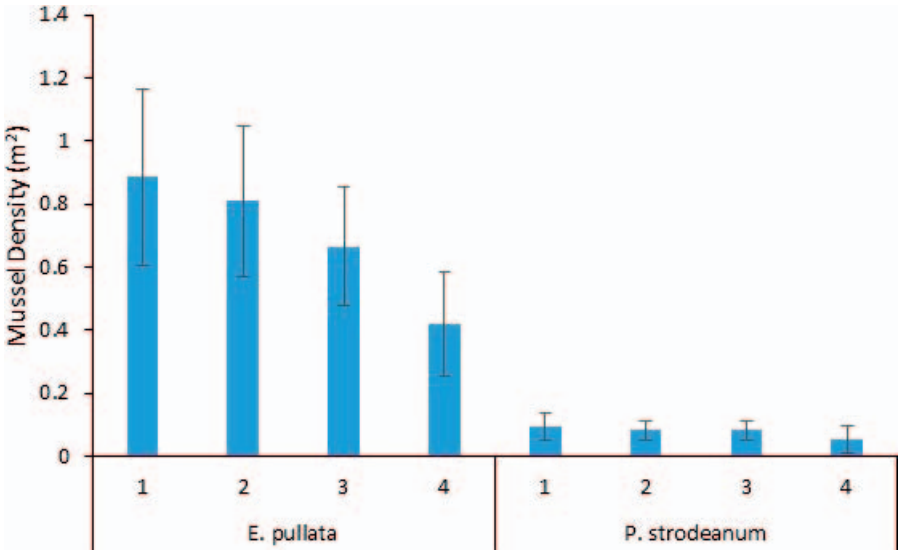

Figure 6. Density (m^2) estimates with 95% confidence intervals for *Elliptio pullata* and *Pleurobema strodeanum* at 8M1 during four primary sampling periods.

such a short period, regardless of actual differences in survival. Indeed, the lowest survival estimate we found was 0.95 (95% CI [0.94, 0.97], while most other estimates were at least 0.98. Despite these shortcomings, we were able to successfully estimate apparent survival over the time frame of our study. This suggests that using these methods for long-term monitoring of these populations, with a larger interval between primary periods, could potentially allow more robust estimates of annual apparent survival, allow trends in apparent survival to be tracked over time, and allow differences in apparent survival among species to be found.

Detectability is seldom 100% and may vary over time and space due to choice of sampling method, habitat, weather conditions, experience of collectors, and other variables (Bailey et al. 2004; Wisniewski et al. 2014). Reproductive condition can also affect detectability, as a larger proportion of the adult population is at the surface during the breeding season (Balfour and Smock 1995; Villella et al. 2004). We found that detectability increased with mussel length for *E. pullata* at all three sites, although this relationship was relatively weak at 8M2. Length seemed less important for *P. strodeanum* at 8M1 and not important at all for *P. strodeanum* and *F. burkei* at 8M2. Meador et al. (2011) found that length had a positive effect on detectability of mussels in all habitat types. Length's lack of influence on detectability at 8M2 may

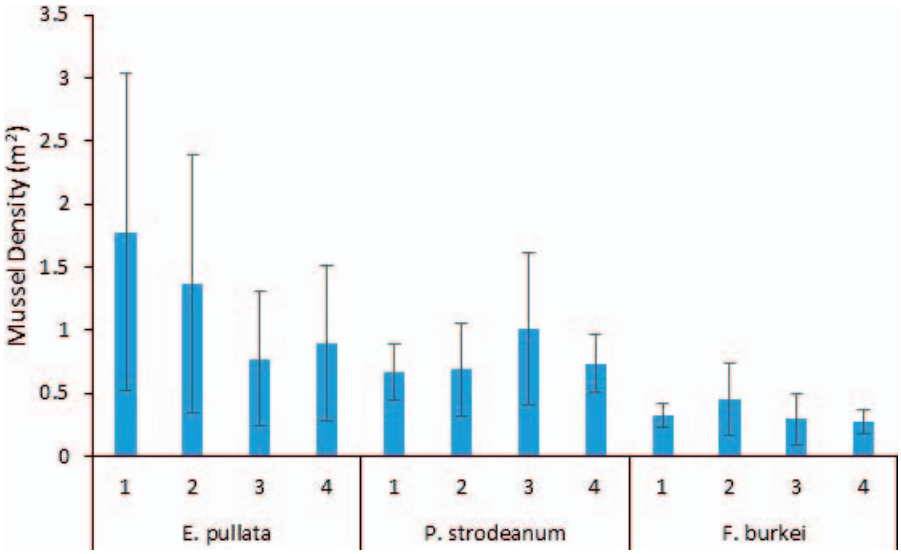

Figure 7. Density (m^2) estimates with 95% confidence intervals of *Elliptio pullata*, *Pleurobema strodeanum*, and *Fusconaia burkei* at 8M2 during four primary sampling periods.

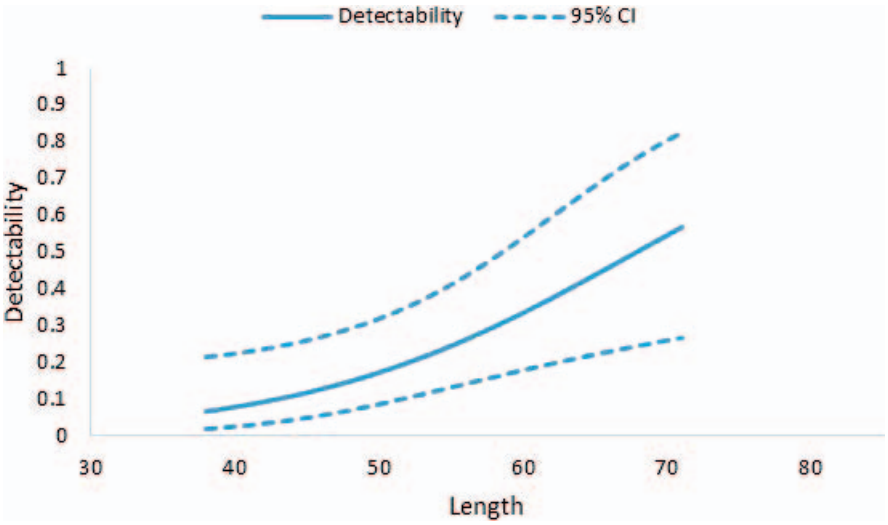

Figure 8. Model-averaged detectability with 95% confidence intervals as a function of length for *Elliptio pullata* at BS.

be due to environmental factors being far more diverse and important at this site, as well as 8M2 being generally more difficult to sample due to depth. Because of rain, water levels were also higher during the second and third primary sampling periods at 8M2, resulting in reduced detectability. Wisniewski et al. (2013) found that detectability of *E. nigella* decreased with increasing depth, and Schwalb and Pusch (2007) found that the surface density of three species of mussels decreased as river discharge increased due to vertical mussel migration. The time effect on detectability observed at 8M2 may have been a result of these environmental variables (either by causing vertical migration or by decreasing searcher efficiency) and could have masked any length effect (if present) on *P. strodeanum* and *F. burkei* and made length less important for *E. pullata* compared to 8M1 and BS. It is also possible that length is less important for *P. strodeanum* and *F. burkei* in general because of their smaller maximum lengths. *Elliptio pullata* had a maximum length of 81.7 mm in this study and thus a larger range of lengths over which detectability could vary. In contrast, the maximum lengths of *P. strodeanum* and *F. burkei* were 57.1 mm and 61.7 mm, respectively. In addition to finding that detectability increased with length, Meador et al. (2011) found that habitat type affected capture. Specifically, detectability was higher in slackwater habitats (zones with low velocities and deposition) than pool and swiftwater habitats. This is consistent with the lower detectability at 8M2, which was deeper with greater habitat heterogeneity, compared to 8M1.

Differences in collector experience may have affected detectability during this study. For example, sites were sampled with four people during the first primary sampling period and with only two people on all subsequent sampling

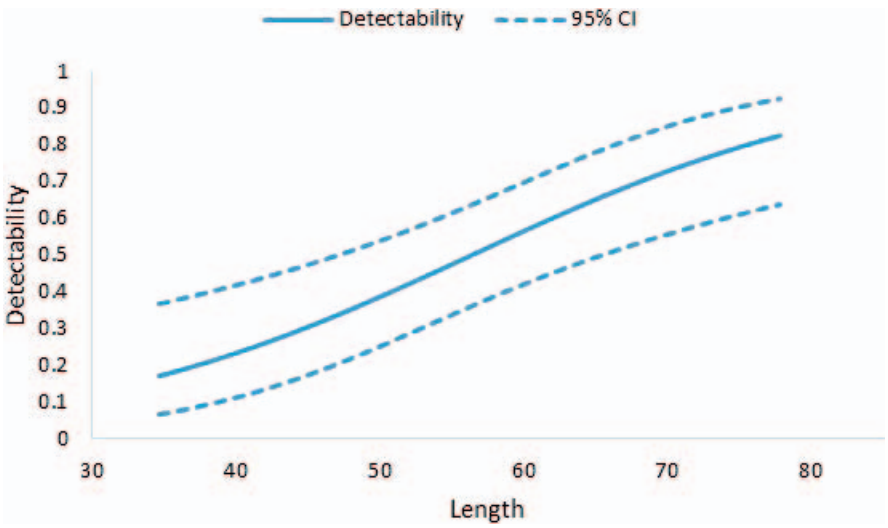

Figure 9. Model-averaged detectability with 95% confidence intervals as a function of length for *Elliptio pullata* at 8M1.

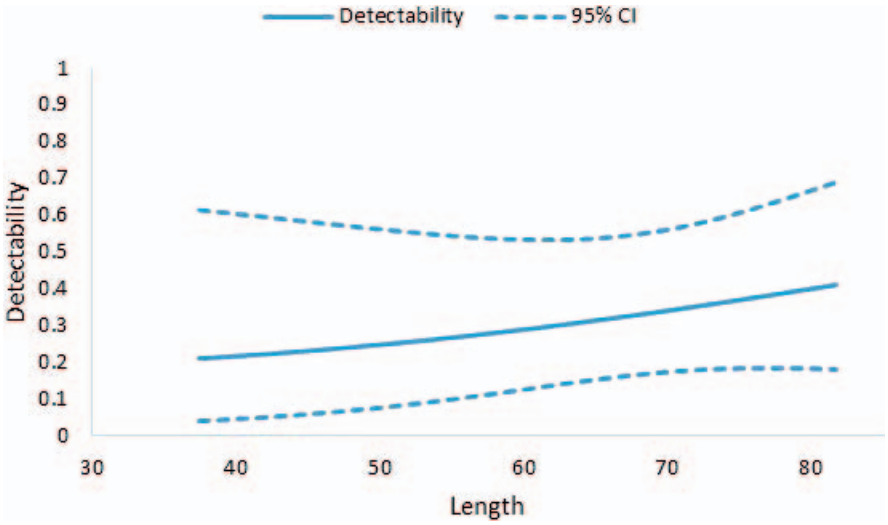

Figure 10. Model-averaged detectability with 95% confidence intervals as a function of length for *Elliptio pullata* at 8M2.

events. Further, although the same two people sampled on all occasions, their efficiency likely increased over time. However, even if detectability varied due to these issues, the final parameter estimates should not have been affected. Detectability in our models was explicitly estimated based on actual data collected. If detectability varied from one primary period to another, parameter estimates such as density and apparent survival accounted for this, even if the causes (collector experience, environmental conditions, etc.) of differences in detectability were not explicitly modeled.

In conclusion, the apparent survivability and detectability calculated from our models serve as repeatable baseline data. These models provide robust data that can be used in long-term monitoring studies to evaluate the status of these species over time. These sites were previously qualitatively sampled. For example, Pilarcyzk et al. (2006), in a single sample, found 13 individuals of *Hamiota australis* at BS, but the most we found in a single sampling event was five (although they sampled 150 m instead of our 100 m). Pilarcyzk et al. (2006) also found 47 *P. strodeanum* and 18 *O. choctawensis* at BS, but we found only 11 *P. strodeanum* and one *O. choctawensis* during a single sampling event. This superficially suggests that Eightmile Creek is a stronghold and species are declining at other sites. However, previous data were qualitatively collected and could be biased by detectability (sampling conditions, reproductive condition, collector experience) and are not directly comparable. Using the mark-recapture methods suggested in this study in the future could provide a robust means of determining population trends of these species over time. However, the 4 mo sampling period used in this study is fairly short compared to the long life span of these species. For example, *P. strodeanum* can live at least 70 yr

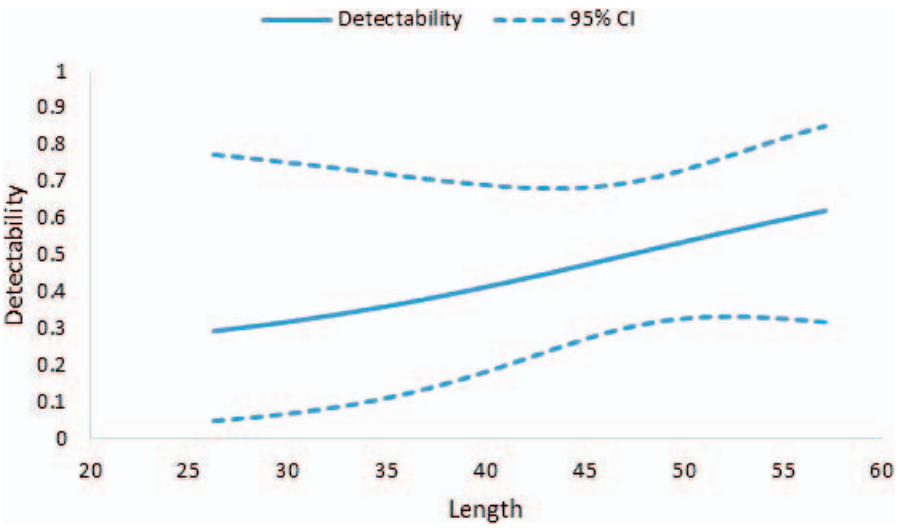

Figure 11. Model-averaged detectability with 95% confidence intervals as a function of length for *Pleurobema strodeanum* at 8M1.

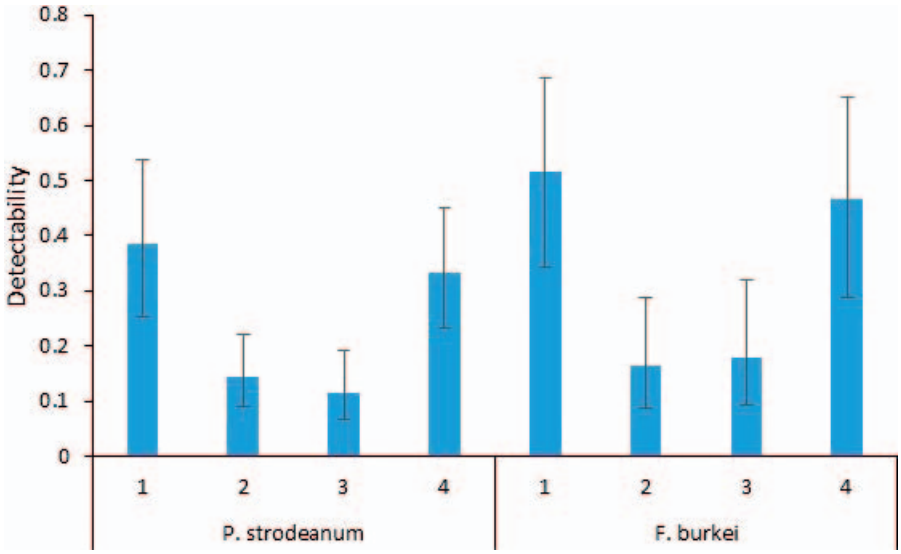

Figure 12. Model-averaged estimates of detectability of *Pleurobema strodeanum* and *Fusconaia burkei* at 8M2 during four primary sampling periods.

(Reátegui-Zirnea et al. 2013). Testing these methods over several years is needed to evaluate their efficacy.

ACKNOWLEDGMENTS

We thank Evelyn Reátegui-Zirena and Miluska Olivera Hyde for their assistance in the field. Financial support for this project was provided by the ALFA Fellowship.

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Freshwater Mollusk Biology and Conservation

ISSN 2472-2944

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