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FRESHWATER BIVALVES **Review Paper**

Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels

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Abstract The North America freshwater mussel fauna has suffered an inordinately high recent extinction rate, and the small size and isolation of many remaining populations portends a continued diminishment of this fauna. Causes of extinction and imperilment are varied but revolve around massive habitat loss, deterioration, and fragmentation. The National Strategy for the Conservation of Native Mussels, published in 1997, has guided efforts to address this crisis. Considerable progress has been made toward several of the Strategies' goals, particularly increasing our knowledge of mussel biology, promoting mussel conservation, and development of techniques for captive mussel propagation. However, mussel conservation should focus more directly on reducing fragmentation through bold and aggressive habitat restoration. In addition to dam removal, improvement in dam tailwater flows, and restoration of channelized streams, identification of factors that eliminated mussels from many otherwise intact streams is critical. Translocation and captive propagation will be key elements in reestablishing mussel assemblages in restored habitats, but these techniques should be used with caution and primarily to increase the occurrence of a species throughout its historical range. Conserving mussel diversity in an ever-changing world is dependent on promoting the natural, long-term sustainability and evolutionary potential of mussel populations.

Keywords Restoration · Fragmentation · Extinction · Propagation · Unionoida

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Introduction

North America is home to the world's richest freshwater mussel fauna (order Unionoida). About 300 species are recognized currently, but this number likely will increase as modern phylogenetic methods reveal previously unrecognized, cryptic diversity (e.g., Roe & Lydeard, 1998; Serb, 2006; Jones & Neves, 2010). To put this fauna in perspective, the Mississippi River basin alone supports 3–4 times as many mussel species as the Amazon-Orinoco or Congo river basins, which support the world's richest freshwater fish faunas, and in some parts of the eastern United States, more mussel species can be found in 1 m^2 of river bottom than occur on the entire continent of Europe (Haag, 2012). Mussels have been important to humans as a source of food, natural pearls, and raw material for button manufacturing, and they are the main source of shell bead nuclei for cultured pearls. Because mussels often dominate benthic biomass, they play an integral role in freshwater ecosystems. Filter feeding and burrowing may be critical in nutrient cycling by linking benthic and pelagic food webs and stimulating production across multiple trophic levels (Vaughn & Hakenkamp, 2001; Vaughn et al., 2008; Spooner et al., 2012). Dense mussel beds also can stabilize substrates and increase habitat heterogeneity, and the animals themselves are an important food source for fishes, mammals, and birds (Gutiérrez et al., 2003; Zimmerman & de Szalay, 2007; Haag, 2012).

This spectacular and ecologically important fauna also is distinguished by having among the highest extinction and imperilment rates of any group of organisms on the planet. About 30 North American taxa have become extinct in the last 100 years and 65% of remaining species are considered endangered, threatened, or vulnerable (Table 1). Many remaining species are on the brink of extinction, currently persisting only in one or two small, isolated populations that likely have a low probability of survival in the future (Haag, 2012). Projections of contemporary extinction rates forecast loss of as much as 50% of remaining species in the next century (Ricciardi & Rasmussen, 1999). In addition to a loss of diversity, sharp declines in mussel abundance in many places have doubtless resulted in serious impairment of ecosystem function, which may further hasten mussel declines and negatively affect many other organisms.

The vulnerability of freshwater mussels to human alteration of streams and lakes was recognized over 100 years ago (e.g., Simpson, 1899; Ortmann, 1909), but the magnitude of the current extinction crisis did not become apparent until the 1970s and has gained wide recognition only in the last 20 years (e.g., Stansbery, 1971; Bogan, 1993; Neves, 1993; Neves et al., 1997). The urgency of the situation has mobilized conservation action at the federal, state, and local levels, and from organizations such as The Nature Conservancy (TNC) and the World Wildlife Fund. In 1997, the National Strategy for the Conservation of Native Mussels (hereafter, National Strategy) was developed to focus and coordinate these efforts by providing an exhaustive list of action items and research needs (National Native Mussel Conservation Committee [NNMCC], 1997; Neves, 1997). Since that time, mussel conservation has continued to gain momentum, including major advances in captive propagation techniques, which hold great promise for restoration of extirpated mussel populations. Despite these and other encouraging signs, mussel declines continue in many places, and the proliferation of captive propagation and species translocation raises serious questions about the most appropriate use of these conservation tools. In recognition of the changing landscape of mussel conservation, the National Strategy is now undergoing revision (P. Morrison, personal communication). In this paper, we revisit the mussel extinction crisis and assess progress made in mussel conservation in the last 15 years, particularly with regard to the 10 goals of the National Strategy. Based on this assessment, we suggest ways that conservation and research programs can be focused further so as to have the greatest impact on reducing mussel extinction rates and maintaining and enhancing the ecological integrity of mussel assemblages and the services they provide.

Overview and timeline of the extinction crisis

The severity of the mussel extinction crisis is due to the apparently inordinate sensitivity of mussels to human alteration of aquatic ecosystems compared

Table 1 Box scores of extinct and imperiled freshwater species in the United States

Faunal group	Extinct species	Federally listed imperiled species	Imperiled species from independent assessments
Mussels	29 (10%)	83 (28%)	199 (65%)
Aquatic snails	67 (10%)	24 (4%)	452 (64%)
Fishes	30 (1%)	122 (5%)[a]	700 (39%)
Crayfishes	2 (<1%)	4 (1%)	172 (47%)

Data from Taylor et al. (2007), Jelks et al. (2008), USFWS (2012), Johnson et al. (in press), J. D. Williams et al., unpublished data

[a] Count excludes specific, local populations (e.g., runs) of salmonid fishes

with other organisms. Many streams that have lost nearly their entire mussel fauna continue to support diverse assemblages of fishes, crayfishes, snails, and aquatic insects (Haag, 2012). Extinction and imperilment rates for mussels eclipse those of other aquatic organisms, except for aquatic snails (Table 1), and several factors suggest an even wider disparity in imperilment between these groups. A large number of imperiled fish and snail taxa are endemic to springs or endorheic river systems in the western U.S. that lack mussels, and over half of extinct snails were endemic to a single river system (Coosa River, Alabama; Johnson et al., in press). Furthermore, many extinct or imperiled fishes are subspecies of otherwise widespread species. In contrast, many imperiled or extinct mussels were widespread historically, and because mussel systematics lags far behind that of fishes, the likely discovery of narrowly distributed cryptic species will increase extinction and imperilment rates. Clearly, mussels have suffered at the hands of humans to a much greater extent than most other aquatic organisms. Imperiled mussel species occur in all regions of North America, and we face an imminent diminishment of this fauna that is unprecedented in scope and magnitude.

The causes of the decline of the North American freshwater mussel fauna and the reasons for mussels' inordinate sensitivity have been discussed extensively, but typically only in general terms. The devastating effect of stream impoundment on mussels is widely acknowledged, but declines in unimpounded streams are attributed to a standard and often vague list of largely untested impacts such as sedimentation and "poor land use practices" (e.g., Bogan, 1993; Neves et al., 1997; Watters, 2000). Similarly, specific ecological attributes that render mussels more sensitive to these impacts than other organisms have not been widely examined. For example, development of the larvae (glochidia) of most species requires a brief period during which they are parasites on fishes, and many mussel species can parasitize only one or a few fish species, which are infected via highly developed lures or an array of other strategies (Haag, 2012; Fig. 1). This attribute is widely considered a conservation liability because mussels are vulnerable to reductions in fish populations (e.g., Neves, 1993). However, apart from well-documented declines of a few mussel species that are dependent on migratory fishes, which also have declined in response to impoundment (Smith, 1985; Kelner & Sietman, 2000; Fritts et al., 2012a), many imperiled species use common and widespread host fishes, and host relationships do not explain patterns of mussel declines in many cases (Haag, 2012). A more explicit examination of the chronology of mussel declines and assemblage responses to specific impacts is necessary to better understand the causes of mussel imperilment and to prescribe remedial actions.

Despite widespread but localized mussel declines in response to an array of severe, point-source impacts (e.g., Rhoads, 1899; Ortmann, 1909; Forbes & Richardson, 1913), mussel diversity remained largely undiminished by the 1920s. From the 1920s to the early 1980s, systematic destruction of riverine habitat throughout North America by dams and channelization

Fig. 1 Mussel interactions with fish hosts. Mussels are intimately enmeshed in the function of aquatic ecosystems, being dependent on fishes for reproduction but also providing essential ecosystem services that benefit many other organisms. *Top* Redeye Bass (*Micropterus coosae*) attacking lure of female Plain Pocketbook (*Lampsilis cardium*) (W.R. Haag, photo). *Bottom* Bluebreast Darter (*Etheostoma camurum*) captured by female Oystermussel (*Epioblasma capsaeformis*) after attacking the mussel's lure (David Herasimtschuk photo, courtesy Freshwaters Illustrated). In both cases, fishes became infected with parasitic mussel larvae during attacks

was directly responsible for the majority of mussel extinctions to date (Haag, 2012). Most of the species in this first extinction wave were restricted to large, mainstem rivers, which were dammed most extensively. These species were eliminated when their entire range was inundated by reservoirs and radically altered by chronically depressed water temperature, non-seasonal fluctuations in flow, and channel scour and entrenchment in dam tailwaters. Many species that survived systematic habitat destruction persisted only in a few small, isolated populations in unimpounded stream reaches, leaving them highly vulnerable to point-source impacts and natural, stochastic fluctuations in population size or environmental conditions. Species that adapted to impounded or channelized streams were a small, predictable subset of the fauna that shared a similar array of life history traits such as fast growth, early maturity, and use of host fishes that also were tolerant of radical habitat alteration (Haag, 2012).

Streams that escaped impoundment or channelization continued to be affected by localized, catastrophic impacts such as coal mining and chemical spills, which deepened the imperiled status of some species and resulted in extinction of several others whose range had been reduced previously by impoundment (Haag, 2012). However, on the whole, unimpounded streams across North America continued to support diverse and abundant mussel faunas throughout much of the twentieth century. Most intact streams were small or medium-sized tributaries, and they were inhabited by mussel assemblages characteristic of these habitats. Consequently, like extinct species, imperiled species during this time were composed predominantly of a subset of species restricted to large rivers or having very small initial ranges (e.g., Stansbery, 1971).

The scope and magnitude of the mussel extinction crisis increased dramatically from the 1970s to the 1990s. During this time, mussel populations crashed abruptly across much of North America, particularly in the central and southeastern U.S. These declines were enigmatic because they often occurred in otherwise intact streams unaffected by obvious catastrophic impacts and that continued to support diverse fish, snail, crayfish, and aquatic insect faunas (Haag, 2012). Unlike impoundment, which affected a predictable subset of the fauna, enigmatic declines typically affected all species in an assemblage, regardless of life history traits or other attributes, and survival probability was simply a function of initial abundance. Another conspicuous hallmark of enigmatic declines was that recruitment appeared to cease, leaving behind small, relict populations of aging individuals. The cause of these declines remains unknown, but their characteristic and rapid effects suggest an extremely virulent and widespread factor that is largely specific to mussels. Because of their wide occurrence, enigmatic declines had a devastating effect on the mussel fauna that remained after systematic habitat destruction. Furthermore, the non-selective nature of these declines broadened the representation of imperiled species to include a cross section of North American mussel diversity and life history strategies.

Systematic habitat destruction and enigmatic declines overlaid on a ceaseless array of catastrophic impacts and other factors such as invasive species have resulted in a highly fragmented stream landscape and mussel fauna. At least 40 species survive in only one or two isolated populations, many of which are exceedingly small and perhaps non-viable (Haag, 2012). A still larger number of species are apparently more secure, but the loss of one or two important populations could push these species to critically imperiled status. Hence, fragmentation and isolation have created a large extinction debt, which portends a second extinction wave that may eclipse the first in the numbers and breadth of species affected. In the short term, protection of remaining mussel populations is vital, but reduction of the extinction debt in the long run without additional species extinctions is dependent on directly addressing the factors responsible for fragmentation and isolation.

The National Strategy: successes and shortcomings

As mussel conservation efforts have expanded in the last 15 years, all of the 10 goals advocated by the National Strategy have been addressed in some way. In the following sections, we assess the progress made toward these goals and the effectiveness of the strategies designed to achieve them.

Goal 1 Increase coordination and information exchange among entities that study, manage, harvest, conserve, or recover native freshwater mussels.

Development of the National Strategy itself represented the first step toward this goal. The Strategy was developed through input from a broad cross section of the mussel conservation community, and its comprehensive nature makes it an extremely valuable resource. However, according to Google Scholar, the document has been cited only 50 times since 2000, or an average of <4 times/year, but the citation rate has remained steady over time. Given that an average of 136 scientific papers or reports relating to mussels appeared annually from 2005 to 2009 (Cummings et al., 2010), this citation rate is disappointingly low and suggests that the National Strategy is not being used extensively. In contrast, an assessment of conservation status of North American mussel species (Williams et al., 1993), which represents a companion to the National Strategy, has been cited 700 times, or 39 times/year. The National Strategy remains an essential document, and we encourage its use in guiding and coordinating conservation efforts.

The second major step toward this goal was the 1998 formation of the Freshwater Mollusk Conservation Society (FMCS), whose goal is to foster research and conservation of mussels and aquatic snails. The society has grown steadily and attendance at its biennial meetings averages nearly 300, making it an invaluable venue for information exchange. In addition to its quarterly newsletter, *Ellipsaria*, in 2012 the society launched its own journal, *Walkerana*, which provides an outlet for specialized research on mollusks. Another important development in the last 15 years was the creation of mussel biologist positions in most state and federal agencies and other conservation organizations. Previously, mussel conservation issues often were relegated to biologists with specialties and interests in other areas and who did not communicate widely with the mussel conservation community. Agency biologists dedicated to mussel issues now typically have specialized training and most are active members of FMCS.

Despite progress, coordination and information exchange needs improvement in several ways. Academic research on mussels has proliferated exponentially, and these results typically are disseminated and archived in scientific journals. On-the-ground management efforts are less well documented. Unlike researchers for whom journal publications are their primary currency, many managers have neither the time nor the impetus for publication, and the ongoing and adaptive nature of management activities makes it difficult to adapt them to the rigid format of a scientific paper. Consequently, these activities often are documented in agency reports or by word-of-mouth, sources which are difficult to obtain and may have a short life span. Documentation of management efforts is crucial to provide a body of case histories for use in evaluating the effectiveness of various approaches; this need is acknowledged in the National Strategy (item 2.2) but remains largely unfilled. The confines of state boundaries and agency jurisdictions also remain a barrier to coordination and information exchange. In addition to the FMCS, watershed-based (rather than state-based) conservation initiatives sponsored by organizations such as TNC and the U.S. Fish and Wildlife Service (USFWS) have helped transcend these boundaries, but entrenched barriers to communication remain.

Goal 2 Protect and reverse the decline of quality mussel habitat.

This is the single most important goal for mussel conservation, and most other elements of the National Strategy ultimately contribute to our ability to achieve this goal. Protection of remaining high quality stream reaches is obviously vital to prevent additional losses of mussel diversity in the short term. In addition to long-standing legislation such as the U.S. Clean Water, Endangered Species, and National Environmental Policy acts, our ability to protect remaining mussel diversity is greatly expanded by a large number of non-regulatory private landowner incentives available through the USFWS, Natural Resources Conservation Service, U.S. Department of Agriculture, TNC, and other organizations. The responsibility for stream protection ultimately falls to the agencies charged with implementing these policies and programs, but mussel biologists and groups like the FMCS have been strong advocates for conservation and have guided selection of specific stream reaches for protection.

Even with multiple layers of protection, isolated stream reaches will continue to experience catastrophic impacts or gradual deterioration (e.g., Warren & Haag, 2005; Schmerfeld, 2006; Hanlon et al., 2009), and small, isolated populations are vulnerable to extinction from natural stochastic effects even in high quality habitats. Long-term conservation of mussel diversity therefore is dependent on an increase in available habitat through restoration. Habitat restoration is alluded to in several places in the National Strategy, but it is curiously underemphasized. There is a small but growing body of successful mussel recovery or restoration stories resulting from programs focused on mussels as well as appurtenant responses to more general improvements in habitat quality (e.g., Miller & Lynott, 2006). Restoration of more natural flows in dam tailwaters is one of the most promising opportunities in the short term because it could restore hundreds of kilometers of critical large river habitat, and recent examples show the viability and effectiveness of this strategy (Ahlstedt et al., 2004; Hubbs et al., 2011; Konrad et al., 2012). In the long run, restoration of stream habitat and watershed connectivity is dependent on more expensive and contentious strategies such as dam removal and restoration of channelized streams. However, dam removal has accelerated in recent years, both for ecological and public safety reasons, and a few dams already have been removed specifically to benefit mussels (Baldigo et al., 2003–2004; USFWS, 2010a; Fig. 2). Opportunities for habitat restoration will increase as the value of ecosystem services becomes more widely recognized (Bernhardt et al., 2005), and the mussel conservation community should be a vocal and organized supporter of these efforts.

Goal 3 Increase fundamental knowledge of basic biology and habitat requirements of mussels.

Along with Goal 8, more progress has been made in this area than perhaps any other. The proliferation of researchers focusing on mussels has dramatically increased our knowledge of fundamental topics such as diet, reproduction, life history, and habitat requirements (for reviews, see Strayer, 2008; Haag, 2012). For example, researchers have deemphasized the unrealistic goal of developing detailed, predictive habitat models for mussels in favor of more generally applicable measures of habitat suitability such as substrate stability (Strayer & Ralley, 1993; Layzer & Madison, 1995). Nevertheless, we still have much to learn about all of these topics. Information about host use is available for only about one-third of the North American fauna, and much of this information is incomplete or poorly supported. Host studies are in danger of becoming passé, but they remain vital for mussel conservation and can reveal specific management needs (e.g., Fritts et al., 2012a). Particularly valuable are replicated studies that provide a clear picture of the breadth of host use by assessing suitability of a broad cross section of the co-occurring fish fauna (e.g., Hove et al., 2011; Fritts et al., 2012b). Studies of mussel population dynamics have only recently begun to appear (e.g., Jones & Neves, 2011; Haag, 2012), and we still have little information about such critical topics as population growth rate and the levels of survivorship and recruitment necessary to sustain populations.

Fig. 2 Demolition of Embrey Dam on the Rappahannock River, Virginia, 2004 (U.S. Department of Defense photo, courtesy Integration and Application Network image library, http://ian.umces.edu/imagelibrary/)

Goal 4 Increase knowledge of status and trends of native mussel populations.

Our knowledge of the geographic distribution of species and the location of remaining populations is relatively comprehensive due to intensive surveys by state mussel biologists and others and the widespread use of diving and standardized sampling protocols. These efforts have uncovered additional populations of rare species and even have relocated species thought to be extinct (USFWS, 2009; Simmons, 2011; Randklev et al., 2012). On the basis of this information, the conservation status of all North American species now has been evaluated, in contrast to earlier efforts that were hampered by a lack of information about some species (Williams et al., 1993; J. D. Williams et al., unpublished data). However, our ability to assess the status of populations and monitor trends in their abundance remains poor for several reasons. First, it is difficult or impossible to obtain precise estimates of abundance of rare species that can provide statistically defensible inference about changes in abundance over time. Second, our poor knowledge of population dynamics precludes useful assessments of population health or viability, and demographic data needed to inform these assessments are difficult to obtain, especially for rare species. Even for apparently secure species, we have little information about population stability or long-term viability. A widespread species may be in jeopardy if few populations are viable; this problem is especially serious for long-lived species that may persist for decades after a decline in recruitment. In addition, we have little information about minimum viable population size or minimum density required for egg fertilization. Finally, the potential for undiscovered cryptic diversity can lead to erroneous conclusions about a species' status. For example, *Epioblasma capsaeformis* previously was thought to exist in several streams in the Tennessee and Cumberland river systems, but genetic work showed that these populations represent at least three distinct and highly imperiled taxa (Jones & Neves, 2010).

Goal 5 Determine how various perturbations impact mussels.

Our knowledge of how various perturbations affect mussels varies widely depending on the type of impact, and this disparity underscores the danger of uncritically invoking and conflating the standard list of impacts traditionally used to explain mussel declines. The effects of major impacts such as dams and introduction of zebra mussels (*Dreissena* spp.) are relatively well understood (but see Goal 6). For example, chronically low temperatures and altered flows in dam tailwaters are known to interfere with mussel reproduction, providing clear management recommendations (Heinricher & Layzer, 1999; Konrad et al., 2012). In contrast, the causes of enigmatic mussel declines remain largely unknown, and because of the broad scope of these declines, this is currently one of the greatest impediments to mussel conservation. Until the causes of these declines are understood, we have minimal ability to protect streams from future declines or to prescribe remedial actions for restoration of affected streams. Commonly invoked explanations for these declines are largely untested and some, such as sedimentation, may not be directly responsible (Haag, 2012; Strayer & Malcom, 2012). However, we may be nearing a breakthrough on this topic. A growing body of evidence shows that two pervasive environmental contaminants, pesticides and ammonia, are acutely toxic to mussels, particularly juveniles, and mussel sensitivity to these compounds is greater than that of other stream organisms (e.g., Bringolf et al., 2007; Newton & Bartsch, 2007; Wang et al., 2008; Strayer & Malcom, 2012). These results may explain both the lack of recruitment in affected streams and the inordinate effects on mussels compared with other organisms, but further testing of these relationships in an array of environmentally relevant contexts is urgently needed. In addition, other factors in these declines need to be examined. For example, the potential role of disease has received little research attention (see Starliper et al., 2008; Grizzle & Brunner, 2009).

The National Strategy also recommended development of biomonitoring protocols using mussels to complement existing protocols using fish and aquatic insects to assess the ecological integrity of streams (item 5.6). The development of such protocols may be difficult because it will require extensive calibration to account for the patchy and clumped distribution of mussels and the large faunal differences related to stream size, including naturally low mussel diversity and abundance in small streams (Haag, 2012). Furthermore, most biomonitoring metrics are based on functional guilds or other ecological attributes, which are poorly understood for mussels, and accurate assessments of stream health may require estimation of size structure or other measures of population viability, which may be beyond the scope of a biomonitoring protocol. Most seriously, a mussel biomonitoring protocol would not allow assessment of the degree to which a stream that previously lost its mussel fauna may have recovered from those impacts. As an alternative, we encourage a more direct assessment of the ability of a stream to support mussels by using in situ survival trials with propagated juveniles housed in silos or other enclosures (e.g., Gagné et al., 2004). Silos are small versions of a flow-through system developed for juvenile culture in the laboratory (Barnhart, 2006) that can be deployed in streams in a replicated fashion (Fig. 3). Silo survival trials are being used by several labs in the U.S. (C. Barnhart, P. Johnson, personal communication), but published guidance and evaluation of this method is not currently available. In addition to assessing the suitability of potential reintroduction sites (see Goals 8 and 9), silo trials could provide important information about causes of enigmatic mussel declines. Because all species appear to be affected by these declines, readily available, non-imperiled species could be used informatively in such trials. However, it is important that juveniles be ecologically and genetically suitable for the stream in question—as for species reintroductions or augmentations—because silos are vulnerable to damage by environmental events or vandalism, potentially resulting in release of test animals. One disadvantage of silos is that contact with potentially contaminated natural sediments is limited, but this method represents perhaps our most powerful tool to assess stream health from a mussel perspective, and its use should be disseminated and promoted.

Goal 6 Develop management options to eliminate or reduce the threat of zebra mussels to native mussels.

The National Strategy was written about 10 years after the appearance of Eurasian zebra mussels in North America when these species were rapidly expanding their range. Fouling by zebra mussels virtually eliminated native mussels in many areas in the northern U.S. and southern Canada, and the spread of this species was predicted to result in widespread mussel extinctions throughout the continent (Ricciardi et al., 1998). However, in the mid-late 1990s the expansion slowed, and zebra mussels have been largely unsuccessful in colonizing the southern U.S. or free-flowing streams. Furthermore, zebra mussel populations in some areas have crashed after the initial outbreak phase, allowing recovery and coexistence of native mussels as seen widely in Europe (Strayer & Malcom, 2007; Strayer et al., 2011). Zebra mussels aggravated the fragmentation of the North American mussel fauna, and natural recovery of native mussels in some affected water bodies may be difficult due to extremely low post-invasion population sizes. Nevertheless, no species extinctions are attributed to the zebra mussel invasion, and its most severe effects may be behind us.

Invasive species remain an ever-present and ever-increasing threat to native mussels. Of particular concern is the Black Carp (*Mylopharyngodon piceus*), a large, specialized molluscivore native to China. Black Carp appear to be established in the U.S., but they are not yet widely distributed (Nico et al., 2005); proliferation of this fish could be the final nail in the coffin for several mussel species. Surprisingly, we still know little about the effects on native mussels of well-established invasive species such as the Asian Clam (*Corbicula fluminea*) and Common Carp (*Cyprinus carpio*). These species have coexisted with native mussels in North America for decades, but the introduction of Asian Clams coincided closely with the advent of enigmatic mussel declines, and more study of these issues is needed (Haag, 2012). As in all species interactions, the effects of invasive species on native biota vary in time and space. Apart from advocating aggressive measures to prevent the introduction and spread of invasive species, conservation efforts that strengthen the natural resilience of mussel populations, such as increasing population size and connectivity, will be most effective in allowing them to weather these and other human-caused impacts.

Fig. 3 Silos for testing in situ survival of juvenile mussels. *Top* Silo prior to deployment. *Middle* Juvenile mussels in holding chamber for placement in silo. *Bottom* Silo deployed in stream bottom (Alabama Aquatic Biodiversity Center, Marion, Alabama, photos, courtesy Paul D. Johnson)

Goal 7 Enhance public and government understanding and support for programs that protect and enhance natural stream ecosystems for the benefit of freshwater mussels.

Previously unsung freshwater mussels have emerged from the shadows to a remarkable degree in the last two decades. The establishment of mussel biologist positions and conservation initiatives by many agencies and the growth of groups such as the FMCS have both resulted from and furthered outreach efforts to raise awareness of mussels' desperate conservation plight. Recent discoveries about fascinating aspects of mussel life history also have helped to increase interest in these animals. As a result, mussels have received considerable coverage in scientific and popular media (e.g., *National Geographic*, *Natural History*, *Nature*, *Science*, *Smithsonian*), and this attention has helped to increase support for mussel conservation programs from local watershed groups to national initiatives.

Despite increased awareness, and similar to biodiversity conservation in general, mussel conservation has lacked a strong, pragmatic imperative, but recent research may provide a solution to this problem. Through filter feeding, burrowing, and other activities, mussels are increasingly recognized as keystone organisms that provide multiple ecological services essential for the health of streams and lakes (e.g., Gutiérrez et al., 2003; Vaughn, 2010; Spooner & Vaughn, 2012). These findings have far-reaching implications for humans and therefore provide a concrete imperative for mussel conservation that is vastly more compelling to policy makers and the public at large than a simple need to conserve mussel biodiversity for its own sake. In addition to their astounding diversity, the ecological role of mussels should be a centerpiece of outreach efforts, and further work that quantifies the value and magnitude of these services is needed. An effective outreach approach may be to turn this goal on its head: that is, to protect mussels for the benefit of stream ecosystems, rather than vice versa.

Goal 8 Develop, evaluate, and use the technology necessary to propagate and reintroduce juvenile mussels on a large scale.

Captive propagation has been a goal of mussel conservation for over 100 years. It was originally proposed to replenish mussel stocks depleted by overharvest (e.g., Lefevre & Curtis, 1910), but it is now emphasized as a primary conservation strategy for imperiled species (Neves, 1997). Until recently, juvenile mussels could be produced easily in the laboratory on host fishes artificially infected with glochidia, but it was difficult to culture juveniles to a larger size suitable for release. Extensive research in the last 15 years has largely solved these problems, and large numbers of juvenile mussels can now be produced and reared in captivity for more than 1 year (e.g., Henley et al., 2001; Jones et al., 2005; Barnhart, 2006; Owen et al., 2010). Captive propagation may be the only way to save species teetering on the brink of extinction, and the near perfection of these methods is one of the most important developments in the history of mussel conservation.

Captive propagation programs are now underway in at least 12 U.S. states and in Canada, and several federal and state fish hatcheries have been retooled for intensive mussel production (Neves, 2004). At two of the largest facilities, over six million mussels had been produced and over one million had been released into the wild by 2010 (Gum et al., 2011). To date, the success of most of these efforts is unknown, but in some cases, propagated individuals have survived and grown in the wild (e.g., Barnhart, 2002; Davis, 2005). The full extent of propagation efforts and their success are difficult to evaluate because this information is not widely disseminated.

Despite its great promise, the rapid proliferation of propagation raises serious concerns about the appropriate use of this technology. Genetic issues such as mixing of genetic stocks, reduction of genetic variation, and hatchery selection have been addressed by the conservation community (USFWS & NMFS, 2000; Jones et al., 2006), and for species near extinction many of these issues are moot. However, for species that remain more widespread, comprehensive assessments of genetic structure needed to guide selection of source stock and release sites are largely unavailable (but see Grobler et al., 2006). Advances in captive propagation methods have rapidly outpaced habitat restoration, and for many propagated species suitable reintroduction sites either do not exist or have not been specifically identified. As a result, the urgency of the mussel extinction crisis and the appeal of propagation as a direct solution appear to have initiated many propagation programs before development of specific plans for their implementation. For example, an 87-page document reporting the establishment of a propagation facility and production of 60,000 juveniles of 10 mussel species, included only one sentence, near the end of the document, that addressed the ultimate destination for propagated juveniles, and it stated only that site selection was underway (Eads et al., 2007). Even formal recovery plans for federally endangered species that emphasize propagation as a high priority action item typically do not provide well-supported, prioritized lists of specific stream reaches for receipt of propagated juveniles (e.g., USFWS, 2010b).

Because of the scarcity of suitable reintroduction sites, the great majority of propagated mussels now go toward augmenting existing populations, often the population from which source stock was obtained. Augmentation of extremely rare species may be necessary to prevent short-term extinction, but the rationale for augmentation and the likelihood of its success are often unclear. Augmentation typically occurs at sites where mussels are declining but where the factors responsible for the decline remain unknown, and augmentation often occurs even when evidence of natural recruitment is documented. In these cases, it is difficult to objectively determine when population size or recruitment is "too low", and thus requires augmentation, and continuing human impacts or natural constraints on population size will likely limit its effectiveness. Even with awareness of genetic concerns, augmentation of existing populations carries unavoidable risks, and the broader ecological effects of augmentation have not been evaluated or even widely considered (see Haag, 2012). The most fundamental concern is that the considerable effort spent on augmentation does not directly address species extinction risk by establishing additional populations within its range.

The focus on augmentation has limited progress toward Goal 8, which correctly emphasizes *reintroduction* of mussel species on a large scale. As stated earlier, reintroduction is hampered by uncertainty about the ability of candidate streams to support mussels, but these uncertainties also plague augmentation efforts. It is therefore curious that managers are willing to use untested strategies for augmentation but appear less willing to take bolder measures toward reintroduction that have a similar degree of uncertainty but a much greater potential for long-term species recovery. Widespread reintroduction of propagated juveniles into historically occupied habitats has several positive aspects, even when these habitats are not fully restored (e.g., USFWS, 2001). First, widespread reintroductions will increase the probability of establishing additional populations necessary for species survival. A commonly invoked argument against reintroductions into degraded streams is that propagated juveniles will simply die, representing wasted effort, but in reality, we know little about the extent to which these streams may have recovered. Reintroduction of propagated juveniles represents a relatively low-cost and risk-free assessment of stream health, and the probability of successful reintroductions will be proportional to the extent to which they are attempted. Second, even unsuccessful efforts will provide valuable lessons for future reintroductions and may represent short-term repositories for species in the event of loss of the source population. Finally and critically, reintroduction has a much lower potential for negative effects on existing populations. It is vital that we aggressively use all available technologies for mussel conservation, but it is equally vital that we avoid unintentional harm to the few remaining high quality mussel populations and assemblages.

Goal 9 Develop, evaluate, and use the techniques necessary to hold and translocate large numbers of adult mussels.

Similar to propagation, translocation of mussels from one place to another has been used in conservation for over 100 years, and methods for holding and moving mussels have been improved (e.g., Henley et al., 2001; Cope et al., 2003; Boyles, 2004). Translocation is used in four major ways: (1) to move mussels from impacts of dredging or construction to nearby, unaffected sites, (2) to augment declining or small populations, (3) to reintroduce or establish additional populations, and (4) to hold "ark" populations of critically imperiled species in captivity until release to the wild is appropriate. Like propagation, translocation is an important conservation tool, but there are a number of concerns about its most appropriate use.

Translocation from construction impacts is intuitively appealing as a way of reducing mussel mortality, but if animals are returned to other locations in the same stream it is of dubious mitigation value because neither the total population size nor number of populations for a species is likely to be increased

(Haag, 2012). Translocation efforts are often expensive, and funds allocated for these efforts may be used more productively in other ways, such as supporting habitat restoration, propagation, or research. Alternatively, mussels moved from impacted areas could be used to reestablish mussel populations in other streams that have previously lost their mussel faunas. Translocation of even "common" species into previously defaunated streams may hasten recovery by restoring facilitative feeding interactions and other ecosystem services (e.g., Vaughn, 2010) and would provide valuable, low-risk lessons for reintroduction of imperiled species.

Augmentation using translocated individuals has the same pitfalls and risks as augmentation with propagated juveniles. However, because translocated individuals necessarily originate from another stream, as opposed to originating from broodstock from the same stream, careful assessment of genetic suitability is paramount. For example, individuals of several species from the Tennessee River system have been used to augment small populations in the Big South Fork Cumberland River without assessment of genetic variation in these populations. This is worrisome because several mussels and fishes that were previously considered widespread in these two river systems recently have been shown to represent distinct taxa endemic to each system (Kinziger et al., 2001; Powers et al., 2004; Blanton & Jenkins, 2008; Jones & Neves, 2010), and mixing of these stocks could result in the extinction of endemic Cumberland River taxa. The potential for disease transmission also should be a concern with translocation for augmentation purposes. Translocated mussels typically are not screened for disease, in part because our poor understanding of mussel diseases precludes effective screening at this time.

Translocation is of limited use for reintroduction of very rare species because source populations cannot sustain removal of the large numbers of individuals necessary for successful establishment. However, translocation to appropriate streams may represent the fastest and cheapest way to reestablish populations of more common species. This approach has the additional benefit of capturing a much higher percentage of the genetic variation in the source population compared with reintroduction with juveniles propagated from relatively few female mussels. Despite improvement in holding methods, maintenance of critically imperiled species in captive ark populations remains risky and should be considered a strategy of last resort. For example, temporary removal of large numbers of mussels from streams affected by drought could also result in high captive mortality and may have negative long-term consequences because recruitment of many species is dependent on low-water conditions (Jones & Neves, 2011). In contrast, extremely rare species that exist only as non-viable populations may be saved only by bringing individuals into captivity for propagation.

Goal 10 Increase available funding levels and develop other means to increase mussel conservation efforts.

Efforts by organizations such as FMCS to publicize the mussel extinction crisis have been successful at increasing funding for mussel conservation. For example, the large number of mussel biologist positions established by state agencies in the last 15 years represents a considerable investment in mussel conservation and is evidence of a sea change in attitudes toward non-game species. Establishment of the State Wildlife Grant Program and an array of other conservation initiatives also have provided much-needed funding for mussel conservation and research. As for Goal 7, one of the most effective ways to further increase funding for mussel conservation is to focus on the critical ecosystem services provided by healthy mussel assemblages. A useful parallel here is the successful effort to increase awareness for the wildlife and societal value of wetlands, which culminated in The North American Wetlands Conservation Act of 1989 and subsequent legislation. Programs under this legislation provide matching grants of up to $75 million annually to support wetlands conservation. As issues relating to fresh water quality and quantity continue to gain prominence, aggressive promotion of the positive influence of mussels on water quality could lead to similar legislation to support mussel and stream restoration under a broader and more politically effective umbrella.

Most important future actions

All of the goals of the National Strategy continue to be relevant and important to freshwater mussel conservation. Efforts to increase our understanding of basic mussel biology and to promote awareness of freshwater mussel conservation are vital and ongoing. Many of the strategy's goals will need to be expanded to address emerging issues such as increasing environmental prevalence of pharmaceuticals and other endocrine disrupters, saline intrusion in coastal streams, and invasive species such as Black Carp. One of the most important emerging issues is increased human water demand, which portends widespread stream dewatering, aquifer depletion, and resurgence in the construction of storage reservoirs, and this and all other threats are compounded by the specter of global climate change. Addressing these and other future threats can be easily accommodated within the National Strategy, particularly a revised version that more specifically emphasizes stream and mussel population restoration. We provide the following recommendations about how mussel conservation efforts can be focused further to more effectively address long-term species survival in an ever-changing world.

1. Dissemination of information about management efforts. A body of readily available case histories (successful and unsuccessful) of mussel management and recovery efforts is sorely needed to guide future efforts. In particular, detailed records of propagation and translocation projects will be invaluable to future workers. In addition to outlets such as *Ellipsaria* and *Walkerana*, a clearing house or repository, perhaps sponsored by FMCS, could be established to disseminate and preserve these records.
2. Identification of factors responsible for enigmatic declines. Hundreds, if not thousands, of stream kilometers in North America have experienced enigmatic mussel declines and without knowledge of their causes other streams remain vulnerable. Because the physical habitat of affected streams often remains intact, they represent prime candidates for restoration. The role of pervasive factors such as pesticides and ammonia should receive special attention, but declines should be evaluated on a case-by-case basis to avoid conflating unrelated impacts. Such studies also are important in providing guidance for revision of water quality standards, which in many cases clearly are not protective of mussels (e.g., Wang et al., 2008). We may never know the cause of enigmatic mussel declines in many streams, but in these cases it is more important to assess simply whether or not streams can now support mussels. In lieu of identification of specific causes, pilot reintroductions of propagated juveniles or translocated adult mussels can provide important information about current-day ecological integrity.
3. Assessment of cryptic diversity and geographic patterns of genetic variation within species. Phylogenetic relationships among genera and species groups are becoming better understood through the use of molecular techniques, but fine-scale patterns of genetic variation remain poorly known. For species that survive only in one or two populations, genetic issues are of relatively low priority. For others, comprehensive assessments of genetic variation (e.g., Grobler et al., 2006) are needed to identify cryptic species that may be in need of immediate conservation action and to guide propagation and translocation efforts.
4. Increased emphasis on population reintroduction and decreased emphasis on augmentation. Establishment of additional populations of imperiled species is the only way to reduce their extinction risk in the long run. Consequently, the focus of propagation and translocation efforts should be on restoration of mussel assemblages in previously impacted streams, rather than augmenting remaining populations. In some cases, critically endangered species may warrant augmentation, but augmentation should be approached with extreme caution and restraint, especially in relatively intact assemblages and when global species survival is not in immediate jeopardy. Supposed reintroductions also need to be approached with caution because existing mussel populations can persist for years at undetectable levels, and these populations have the potential to rebound naturally after improvement in stream conditions (Haag, 2012; Randklev et al., 2012). Determining whether a proposed effort represents reintroduction or augmentation should be based on exhaustive surveys with a level of effort sufficient to address any reasonable doubt that native populations still exist; this is especially important when a lack of appropriate source stock necessitates cross-drainage basin transfer of propagated or translocated individuals. Finally, all propagation efforts should have clear, well-supported

objectives. It is necessary to conduct pilot propagation studies during establishment of new facilities, but large-scale propagation should occur only after specific and well-supported plans for dispersal of juveniles have been developed.

5. Primary emphasis on habitat and mussel assemblage restoration. The most fundamental long-term goal of mussel conservation is to increase the amount of occupied mussel habitat and stream connectivity so species can sustain localized catastrophic events and adapt to more subtle but longer-term environmental changes. As such, stream restoration and reintroduction of mussel assemblages should be a primary focus. In addition to providing habitat for imperiled species, habitat and assemblage restoration is essential for other reasons. First, reestablishment of even relatively common species in restored streams may hasten stream recovery and can prevent these species from reaching imperiled status in the future. Second, reintroduction of mussels into previously degraded habitats carries far fewer risks than augmentation in relatively intact streams, and these efforts can provide valuable lessons to inform our limited knowledge of how best to carry out reintroductions. Finally, as the dependence of humans on healthy aquatic ecosystems becomes more fully appreciated, mussels and the ecosystem services they provide can be legitimately and effectively promoted as centerpieces in restoration efforts.

A critical first step in restoration is development of a prioritized list of candidate stream reaches. This was recommended by the National Strategy, but a coordinated, widely available list has not been developed. In many cases restoration is opportunistic, but long-range plans are needed to maximize the effects of restoration on reducing fragmentation and increasing effective population size. Such a list should be realistic but bold. For example, removal of navigation dams essential to commerce (e.g., upper Mississippi and Ohio rivers) is unlikely, but specific recommendations can be made about how operation of these dams can be modified to support aquatic ecosystem values. In contrast, streams affected by non-functional or aging and unsound dams should be high priority for restoration. Similarly, stream reaches affected by enigmatic declines but with otherwise intact habitat should be high priority for restoration, especially if they have the potential to serve as dispersal corridors between mussel populations in unaffected tributaries. A bold vision that is not limited by perceived feasibility in the short term is needed to allow for unanticipated opportunities in the future, and the mussel conservation community should be ready to capitalize on the growing momentum and necessity for ecological restoration.

In the last 25 years, mussel conservation and the study of mussel ecology have grown and matured to become diverse, vital fields. Strategies for mussel conservation, including the National Strategy, need revision and refocusing to take into account lessons learned during this time and to address emerging issues that threaten the fauna. The extent to which these strategies will be effective in preventing further mussel extinctions requires not only coordination but a more specific focus on conservation strategies that promote long-term population survival and evolutionary potential.

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