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Essay:

Making the most of recent advances in freshwater mussel propagation and restoration

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Abstract

Propagating and releasing freshwater mussels (Unionida) into the wild can contribute substantially to conservation and perhaps ecosystem restoration, but poorly conceived projects can waste money and public good will, and harm mussel populations and ecosystems. Moving from vague, emotional reactions about mussel restoration to more rigorous discussions and analyses can help focus efforts to where they do the most good. We suggest that: (i) projects to restore mussels for conservation goals to sites where known environmental problems have been eliminated or mitigated have good prospects for success; (ii) projects to restore mussels for conservation goals to sites where known environmental problems have not been eliminated or mitigated have poor prospects for success; (iii) projects to restore mussels for conservation goals to sites in the common situation in which the status of environmental problems is unknown have unknown prospects for success, but may be valuable as scientific experiments, if project performance is monitored properly; (iv) the value of population augmentation as a conservation tool is uncertain, and needs better theoretical and empirical analysis; (v) assisted migration of mussels as a conservation tool is controversial, and should be discussed thoroughly before we reach crises in which it is rejected or carried out carelessly; (vi) projects to restore ecosystem services face more stringent criteria for success than conservation projects, and some such projects being discussed seem unlikely to succeed. Monitoring data on how restoration projects perform typically are inadequately collected, reported, disseminated, and used to improve practice. This could be improved by setting up a clearinghouse to collect, hold, and disseminate

data; providing training to restorationists; and opening conversations between restorationists and data managers and statisticians.

The ability to propagate large numbers of freshwater mussels (Unionida) has been a major triumph for the conservation and management of these imperiled animals. Many species can now be raised by the thousands, thanks to recent advances in culture methods (summarized by Patterson et al. 2018b), and large-scale mussel hatcheries are now operating (Patterson et al. 2018b listed 18 from the United States alone). Propagation and reintroduction are now recommended activities in many species recovery plans (e.g., USFWS 2019). As a result, restoration projects that would have been unthinkable just a few years ago are now routinely considered or implemented. These advances arrived at a critical time for mussel conservation. Many freshwater mussel species are extinct or critically imperiled (e.g., Haag 2012; Lopes-Lima et al. 2017), and many surviving species probably will disappear without intervention. In addition, scientists and managers are coming to appreciate the important ecosystem functions and services that freshwater mussels may provide (e.g., Vaughn 2018). The ability to propagate large numbers of freshwater mussels gives managers a potentially powerful tool to restore freshwater mussel populations and the ecosystem services they provide.

But like any other restoration activity, mussel introductions (we will use the term “PARI” = propagation, augmentation, reintroduction, and introduction as the umbrella term for these activities, following McMurray and Roe (2017)) should be done only after carefully considering goals, feasibility, costs, efficiency, likelihood of success, and alternative actions. As recent

experience with the related fields of fish stocking and stream restoration have shown, projects that are poorly planned, executed, and evaluated are unlikely to meet their objectives or advance the field (e.g., Palmer et al. 2014; Geist & Hawkins 2016; Trushenski et al. 2018). In addition to direct damages caused by poor projects, failures of expensive projects can incur large opportunity costs, consuming resources that could have been spent on other projects with greater societal benefits. Further, repeated and conspicuous failures can erode the credibility of the discipline.

PARI has great potential as a conservation tool, but it is essential to consider carefully when and how it should be pursued, so as to avoid wasteful or harmful applications and achieve its highest potential. Previous publications have addressed aspects of these issues (e.g., Jones et al. 2006; Hoftyzer et al. 2008; Haag 2012; McMurray & Roe 2017; Patterson et al. 2018 a, b), but have focused mostly on technical biological issues (e.g., production methods, genetic concerns). Our intention here is to review more broadly the issues surrounding PARI of freshwater mussels as part of restoration programs, to spur critical discussion of these issues. Specifically, we (1) distinguish circumstances in which PARI is likely to be effective from those in which it is likely to be ineffective or harmful; (2) identify questions that should be answered before PARI is attempted; (3) extend the discussion of PARI into areas that have not yet received much attention from mussel conservationists (i.e., restoration of ecosystem services or assisted migration); and (4) make suggestions for better practices to accelerate progress in mussel restoration.

Evaluating the feasibility and success of different kinds of mussel restoration through PARI Goals of PARI. We recognize 2 broad classes of goals: (a) to increase the viability of one or more populations for conservation purposes (“conservation goals”); and (b) to restore or establish some desirable ecosystem service (“ecosystem service goals”). Of course, some projects aim to meet both classes of goals, but because the feasibility and evaluation of these 2 classes of goals can be very different, we treat them separately. Further, it seems useful to identify 3 variants of conservation goals (other than propagation for holding in zoo-like settings, which we do not discuss here). First, propagated mussels may be reintroduced to a site where a species was known to occur in the recent past (a “historical site”). Second, introductions may augment an existing population in an attempt to increase its long-term viability. Third, mussels could be introduced to a site where they did not occur in the recent past (“assisted migration”).

Reintroductions at historical sites. Conservation reintroductions at historical sites make 3 key assumptions: (i) the site was recently suitable for the species, as shown by historical records; (ii) the site was more recently unsuitable for the species, as shown by its subsequent disappearance; and (iii) environmental and biological conditions at the site have improved, so that the site is once again suitable. The first 2 assumptions seem uncontroversial, but the 3rd is more problematic. Sometimes we know the cause of a disappearance, and are confident that it has been eliminated (e.g., loss and restoration of a fish host, non-persistent point-source pollution). In other cases, we can identify likely suspects for the disappearance, and have at least some evidence that they have been eliminated. Many times, though, the causes of the disappearance

are unknown (“enigmatic” declines, Haag 2012), so we can have no confidence that they have been eliminated or moderated enough to allow the mussel population to return. This issue is especially problematic because the environmental quality of so many waters is impaired, frequently by multiple pollutants (e.g., USEPA 2016).

It is important to be clear about how well assumption (iii) is supported, and therefore how likely the reintroduction is to succeed. In cases where the cause has been identified and eliminated, it is reasonable to claim that the reintroduction is likely to succeed. However, if there is substantial uncertainty about the underlying problems and their reversal, it is more reasonable to present the reintroduction plan as a doctor presents the prospects for an experimental medical treatment – no guarantee of success but at least some evidence that the treatment might work. Finally, in cases of enigmatic disappearances, we have no idea whether the reintroduction will succeed (because we have little idea why the population disappeared, and therefore whether the harmful conditions have been eliminated). If the costs of propagation and stocking are low enough and the law allows it, it may be worth trying the reintroduction purely as an experiment, especially at a pilot scale. Such experiments might shed light on the causes of enigmatic mussel declines and provide important information for future restoration efforts (Haag & Williams 2014). However, in such cases it seems important to not claim that the project will succeed.

One aspect of reintroduction at historical sites may deserve more attention. Historical records represent a fraction (sometimes a small fraction) of sites where the species formerly lived, and so will always underestimate its historical range. The actual, unknown, historical

range could be construed narrowly as just the recorded sites, broadly as the entire polygon or drainage basins enclosing these sites, or the output of a formal model (e.g., Cao et al. 2017).

How should we consider reintroducing a species to sites where it probably or possibly occurred historically? Should we treat such projects as reintroductions at historical sites, or should they be subject to the more stringent evaluation required for assisted migration (see below)? Whatever the approach, it should balance the benefits of re-establishing historical populations against any risks of exceeding the historical range.

Population augmentation. Some projects attempt to increase the viability of a local population by augmenting it, either by releasing hatchery-raised animals or translocating wild animals from another site (e.g., animals moved out of the way of a construction or dredging project – Miller & Payne 2006). Such augmentation could increase the viability of a local population if (i) it increases genetic variation and thus adaptation potential into populations with low genetic diversity; or (b) it increases the size or density of a local population above a depensation threshold, thereby relieving Allee effects (i.e., positive density dependence below some threshold population density or size). Augmentation will not help if population size or density is set by and already in equilibrium with some environmental or biological factor. For instance, if population size is controlled by the number of fish hosts or the extent of suitable habitat, augmentation will increase population size only temporarily, after which it will return to the level set by the regulating factor. The circumstances under which population augmentation will increase population viability are thus narrowly restricted (Haag 2012). The few studies on Allee effects in

freshwater mussel populations have reported everything from severe effects (Downing et al. 1993), to mild or no effects at all (Mosley et al. 2014), to moderate, context-dependent effects (Terui et al. 2015). If augmentation projects are to be more than blind experiments, we need more information on depensation thresholds and Allee effects in mussel populations (whether they are rare or widespread, and at what densities and conditions), as well as pre-project analyses of proposed augmentation projects that justify their existence.

Assisted migration. The 3rd variant of introduction to meet conservation goals is assisted migration (= “managed relocation”, Schwartz et al. 2012) – deliberately establishing new populations outside the historical range of the species, primarily as a response to climate change. Assisted migration has been vigorously discussed by conservationists (e.g., Hoegh-Guldberg et al. 2008, Ricciardi & Simberloff 2009; Schwartz et al., 2012; Simler et al. 2018). Proponents argue that climate change and other factors are likely to eliminate many species from their existing ranges in this century, and that many species probably will not be able to reach suitable new ranges on their own (e.g., Hoegh-Guldberg et al. 2008; Schwartz et al., 2012). Deliberately moving these species into new ranges could save them from extinction. On the other hand, as the literature on invasive species shows, humans have had a disastrous history of moving species outside their native ranges, and have often failed to predict long-lasting negative consequences (e.g., Ricciardi & Simberloff 2009; Schwartz et al. 2012).

Assisted migration has not received much attention from mussel conservationists (a search of Web of Science on 18 Feb 2019 turned up 453 hits for “assisted migration” but none

for “assisted migration” plus “unionid*”, “margaritifer*”, or “mussel”). Nevertheless, freshwater mussels would seem to be strong candidates for assisted migration, according to conventional criteria (e.g., Hoegh-Guldberg et al. 2008; Dawson et al. 2011). Many species have small ranges, low dispersal rates across barriers such as drainage divides and dams, and are already imperiled. Thermal and hydrologic conditions in their ranges are likely to change substantially as a direct result of climate change as well as from human attempts to manage water resources under climate change (e.g., increased water withdrawals). Almost all mussel species depend on hosts (usually fishes), so environmental changes that affect either the mussels, their hosts, or their interactions could harm mussel populations. Even before humans altered the landscape, mussels were very slow in crossing drainage divides (e.g., van der Schalie 1945), and did not move freely across the landscape at a time-scale of decades (or even millennia). Humans have further fragmented freshwater systems (e.g., Fuller et al. 2015), so it seems unlikely that freshwater mussels (and their hosts) will be able to move across this altered landscape quickly enough to keep up with climate change. Thus, many mussel species may disappear unless we intervene.

At the same time, we know little about the impacts of establishing populations of freshwater mussels at new sites, whether on the mussel populations that already live at those sites or on other parts of the ecosystem. Many plants and animals that humans have moved outside of their native ranges have had large, negative, unexpected effects (e.g., Ricciardi & Simberloff 2009; Schwartz et al. 2012; Simler et al. 2018). Proponents of assisted migration argue that such problems can be avoided by careful analysis before translocation (e.g., Hoegh-Guldberg et al.

2008; Schwartz et al. 2012), but these authors appear to have been thinking mainly of well-studied species such as large mammals, birds, and British butterflies. Freshwater mussels (as well as many other small freshwater animals) are much less well studied (e.g., Strayer 2006). The entire scientific literature on such species may consist of just a handful of papers, and be insufficient to support a credible analysis of the likely need for, success of, and impacts of assisted migration. Thus, conversations and analyses about assisted migration for poorly known species such as freshwater mussels will have to follow a very different model from those for well studied species.

To be clear, we oppose moving mussels outside of their native ranges today (neither the needs nor the risks of such actions are sufficiently known), and we think that it is possible that the more careful analyses that we advocate will end up not supporting assisted migration. Nevertheless, questions like those raised in Box 1 of Schwartz et al. (2012) about whether and how to undertake assisted migration for freshwater mussels should be addressed now, before we are confronted with the choice between numerous, imminent climate-related extinctions and poorly planned and poorly executed emergency actions to prevent these extinctions. As Simler et al. (2018) noted, “These [challenges] should motivate, not deter, development of proactive comprehensive policy”. The alternative – reflexive decisions either to embrace or reject assisted migration as a conservation tool – is unlikely to maximize conservation benefits.

Ecosystem services. Freshwater mussels may be restored to increase ecosystem services.

“Ecosystem services” covers a broad range of benefits to humans (e.g., Costanza et al. 2017),

many of which could be provided by freshwater mussels (Vaughn 2018). Nevertheless, in discussions of freshwater mussel restoration, “ecosystem services” usually has meant improvements in some aspect of water quality – clearer water, lower concentrations of sediments, nutrients, or other chemical pollutants, or fewer human or wildlife pathogens, for example. We focus here on water quality, while recognizing that freshwater mussels may be restored to improve other ecosystem services. As for water quality, though, restoration for other ecosystem services should be supported by critical analyses about whether mussel restoration is the best way to provide these services.

A requirement for success in restoring mussel populations to improve water quality is that the restored mussel population is adequate to improve water quality enough to meet regulatory or other goals. We highlight 4 elements that should be included when evaluating whether a proposed restoration project will meet this requirement: (i) identifying specific water quality goals; (ii) focusing on the net functions of mussels rather than their gross functions; (iii) considering other ecosystem processes that affect water quality; and (iv) determining whether a mussel population large enough to meet the water quality goals can be sustained.

Water quality goals should specifically identify the variable(s) being targeted (e.g., mean phytoplankton biomass, annual phosphorus load, maximum daily nitrate concentration) and the desired numerical value for that variable. Specifying the water quality goal matters because the ability of mussel restoration to reach the goal can differ greatly among water quality variables and ecosystem characteristics.

We illustrate the critical difference between net and gross functions with a trivial example. Could mussels perform an ecosystem service by reducing the water flow in a stream? Even though mussels take in a lot of water, the answer is obviously “no”. Any water that a mussel takes in through its incurrent siphon (gross water intake) is immediately balanced by an equal amount of water released through its excurrent siphon (gross water release), resulting in a net water flux of zero. No matter how large the mussel population, it will not affect the amount of water flowing down a stream.

Similar considerations apply to other substances taken up by mussels, including organic matter, suspended sediment, nutrients, and other pollutants. Unless a substance is destroyed by the mussel (or mussels are removed from the ecosystem), the material that it takes up is later returned to the ecosystem when excreta or egesta (feces and pseudofeces) are released and decomposed, sperm and glochidia are released and decomposed, or the mussel dies and its body and shell decay. In the long run, these return flows back to the ecosystem partially or wholly balance the gross uptake of materials by mussels. As a result, gross uptake rates can vastly overstate the effects of mussel activities on water quality. Indeed, as the water flow example shows, if mussels do not contribute to the loss of a material from the ecosystem, they might have no effect at all on water quality, no matter how large their population.

Examples of how mussels might contribute to net loss of materials from an ecosystem include digestion or immobilization of pathogens (Ismail et al. 2015), phytoplankton (Welker and Walz 1998), or toxins (Downing et al. 2014), provision of food or habitat to microbes that

transform or destroy materials (e.g., denitrification, Hoellein et al. 2017), or enhancement of long-term burial of materials in mussel shells or sediments trapped in a mussel bed. Even in these cases, the term of interest is net losses from the ecosystem, which are likely to be far smaller than gross uptake rates.

Nevertheless, there are 2 interesting cases in which short-term uptake rates might be relevant. First, if the biomass of the bivalve population is growing rapidly, pollutants and other materials may be sequestered into mussel biomass. If the sequestration rate is fast enough, water quality will temporarily improve. This benefit will disappear once the mussel population reaches steady state and biomass stops growing. (Declining mussel biomass will produce the opposite effect, and so temporarily degrade water quality.) Second, short-term storage of pollutants by mussels could be beneficial if pollutant uptake occurs during a season in which the pollutant is especially harmful, but release occurs at a time of year when the pollutant causes less severe problems. (Again, mussels will degrade water quality if the seasonal timing of uptake and release is the opposite of what was just described.)

The 3rd element to be considered is how mussel activities fit with other processes in the ecosystem that determine water quality. Processes such as allochthonous inputs into the target area, autochthonous production (e.g., of algae), hydrologic loss, export to floodplains, burial, resuspension, and activities of consumers other than mussels all affect water quality. For mussels to affect water quality, the net effects of mussels must be large compared to these other activities. For instance, losses of phytoplankton from bivalve feeding must be large compared with

phytoplankton growth rates. Such growth rates often are 10% to >100%/day during the growing season, meaning that mussel feeding rates must be of this order or larger to control phytoplankton. Analyses by Strayer et al. (1999) and Vaughn et al. (2004) suggested that lotic mussel populations rarely are dense enough to compete with algal growth and advection as controllers of phytoplankton, although it does occur (e.g., Welker & Walz 1998). Similar considerations apply to other ecosystem processes. If losses to mussels are small compared to inputs (e.g., allochthonous inputs, autochthonous production, resuspension) or losses to other processes (e.g., sedimentation, advection, and uptake by consumers other than mussels), mussel populations probably will have little effect on water quality. For instance, Roditi et al. (1997) found that zebra mussels removed 8400 tons/day of silt from the water column of the Hudson River (75% of the silt in the water), depositing this material into the sediments, yet concentrations of suspended sediment in the river did not decline (Strayer et al. 1999), presumably because resuspension rates were so high.

Thus, restoring mussels is most likely to benefit water quality when the pollutant does not grow on its own (e.g., chemical pollutants, biological populations such as intestinal bacteria that are poorly adapted to the aquatic environment), the activities of the mussel destroy or bury the pollutant rather than simply recycle it, and competing loss processes in the ecosystem are relatively small (e.g., standing rather than running waters). However, plans for mussel restoration to improve water quality must go beyond such generalities and actually estimate how many

mussels would be needed in a specific ecosystem to reduce a specific water quality problem to a specific target level.

This brings us to the 4th element in assessing whether mussel restoration will improve water quality: will PARI be able to increase mussel populations enough to meet water quality goals? As was the case for restoring mussel populations for conservation, we have to ask – why don't large mussel populations already exist at the restoration site? If the mussels are entirely absent, there is no natural source of colonists to repopulate the site, and environmental and biological conditions are suitable to support a sufficiently large population of mussels, then PARI may be able to improve water quality. Note that this is a more stringent condition (“a sufficiently large population”) than for conservation reintroduction, which required only a viable population to be established. As in the case of conservation reintroductions, introductions to sites with inadequate environmental conditions will result in failure and waste time and money.

One special case worth considering is whether it would ever be sensible to maintain dense mussel populations to improve water quality solely by continuous stocking. We have in mind a situation in which mussels might be able to survive at high density but not reproduce well enough to sustain the population, or where occasional disturbances eliminate the mussel population. Such a project could be beneficial if the costs of propagating and releasing mussels were more than offset by the ecosystem service benefits. However, it can be expensive to propagate and release large numbers of mussels (Southwick & Loftus 2017).

Costs of restoration programs

But is all of this analysis really necessary? Even if it does not always work, how could PARI reduce the viability of mussel populations or diminish ecosystem services? Shouldn't it be regarded as a "no regrets" option that should be pursued whenever possible?

There are several reasons to be cautious about trying to restore mussel populations by PARI and using it only when it is justified. First, as others have pointed out (e.g., Jones et al. 2006; Haag 2012), PARI may cause genetic problems (swamping of locally adapted genotypes, outbreeding depression) if not done carefully, and thereby reduce long-term population viability. Likewise, careless culture methods or translocations of wild stocks can introduce diseases or parasites. These issues have been discussed, and can be avoided through careful planning and protocols (Jones et al. 2006; Patterson et al. 2018a; Mair 2018).

Perhaps more importantly, one must consider the opportunity costs of any PARI project – money spent on PARI is money that is not available for other projects (unless a funder will pay for PARI but not for other projects). If we wish to improve the viability of mussel populations or increase the ecosystem services that a river provides, many actions are available. To name just a few, we could pay for fences to keep livestock out of streams, pay farmers to leave buffer strips of riparian vegetation or apply less fertilizer to their fields, restore physical habitats within the stream channel for mussels or their hosts, add fish passage to dams (or remove dams), modify release schedules for hydropower dams, build ponds for stormwater retention or infiltration, and so on. It is essential to ask which of these activities, alone or in combination, most increases mussel population viability or ecosystem services, given a certain expenditure of resources. It is

possible that PARI is part of the most efficient way to reach our goals, but this is not self-evident, and should be supported by careful analysis (cf. Geist & Hawkins 2016; Trushenski et al. 2018). Otherwise, we will be spending more money and achieving smaller benefits than we could by pursuing other activities. These considerations are especially important because most budgets for mussel restoration are very small (Strayer 2006, Bouska et al. 2018).

Furthermore, at this early stage in the development of the field of mussel restoration, there is a substantial risk that any project, no matter how carefully planned and executed, may fail. Failures are likely to disappoint funders and supporters of mussel restoration, and repeated failures may disillusion them altogether. This is especially likely if project planners have oversold the project and not clearly explained the possibility of failure.

Evaluating performance

Mussel restoration, whether to improve population viability or ecosystem services, is still more or less experimental. It is therefore essential to track how well projects meet their goals, disseminate this information widely, and use it to improve mussel restoration in the future (Geist & Hawkins 2016). Funding for monitoring and dissemination of results should be included in project budgets. Given the long generation time of many mussels (years to decades) and the high temporal variability of mussel populations and ecosystems, this monitoring will usually need to extend for many years. Unfortunately, plans and funding for monitoring often are not included in restoration plans (e.g., Pander & Geist 2013; Simmons et al. 2018), or are later cut as budgets

tighten. This prevents scientists and managers from benefiting from the lessons of both successful and unsuccessful projects, and slows progress in the field.

The monitoring program should be matched to the design and goals of the restoration project, but might include the following elements. First, the goals (e.g., Jones et al. 2012) and design of the project should be quantitatively stated, and as actually implemented. Most projects should monitor the size and demography of the mussel population, over a spatial extent that will depend on the size of the project area and the biology of the mussel and its hosts (see Boon et al., 2019 for an example). The amount of demographic detail to be monitored will vary, but should include at least the presence or density of juveniles (to verify that recruitment is occurring), which may require special sampling methods (Strayer & Smith 2003). The frequency of sampling also depends on the goals and resources of the project, but might include regular sampling (e.g., every 3-5 years) coupled with event-based sampling after major events such as floods and droughts that might affect project success. Care should be taken that the monitoring itself does not harm the mussels. For example, surveys should minimize handling time, place mussels promptly back into the site in the streambed from which they were taken, and avoid handling animals at critical times of the year (e.g., during high temperatures or just before glochidia are released) (Strayer & Smith 2003). To the extent practicable, such monitoring efforts should be harmonized across projects (see Boon et al. 2019 for an example).

If the purpose of the restoration project is to increase ecosystem services, then these services or underlying ecosystem functions should be included in project goals and monitored as

well. Examples might include algal chlorophyll, suspended particles, or nutrient concentrations. Such variables typically are more variable temporally than mussel populations, and may need to be monitored more frequently than mussel populations.

Further, it often will be useful to monitor key environmental variables that might affect the project performance, such as streamflow or water temperature. Data on such variables often are available through government monitoring programs (e.g., USGS stream gages) or can be monitored at modest cost. Indeed, when choosing sites for mussel restoration, it may be worth trying to use sites where environmental variables (or better yet, mussel populations) are already monitored.

Depending on the goals of the project, and on the specific factors that may affect its performance, it may be worthwhile to monitor additional variables (Boon et al. 2019). Examples include fish populations, concentrations of current or legacy pollutants, or human use of and attitudes about the restoration site or its mussels.

Finally, monitoring should extend for long enough to provide a fair and reasonably complete assessment of project performance. In view of the multiyear life cycles of mussels, often-irregular reproduction, mortality, and site disturbance, and a possible need for multiple introductions, monitoring often will need to extend for >10 years.

Although good analyses of project performance sometimes are reported in the peer-reviewed scientific literature (e.g., Carey et al. 2015), this is rare, and any data that are collected often are buried so deeply in gray-literature reports or computer hard drives that they contribute

little to improving practice. We suggest 3 steps to improve the collection, dissemination, and use of monitoring data. First, set up an international clearinghouse to collect, hold, and disseminate data on mussel restoration projects (see also Haag & Williams 2014). Second, offer training to mussel restorationists on how to collect, report, disseminate, and use data from their projects so that they have the tools to contribute to the clearinghouse. Third, hold ongoing conversations between in-the-stream restorationists and statisticians and data managers to develop standards for data collection and reporting that are both scientifically sound and practical for practitioners to collect. These activities could be housed in an existing organization (e.g., the Freshwater Mollusk Conservation Society), or in a purpose-built organization. Regardless of the details, it is unrealistic to expect substantial progress on monitoring and data sharing without some kind of institutional and educational support.

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Authors' contributions

J.K.J., J.D.N., and D.L.S. conceived the paper, and D.L.S. led the writing. All of the authors decided on the content of the paper, contributed to writing, and edited drafts of the paper.

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Data Accessibility Statement

Not applicable; no data sets are associated with this essay.

Conflict of Interest

The authors declare no conflicts of interest.

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