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REGULAR ARTICLE

WHAT ARE FRESHWATER MUSSELS WORTH?

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ABSTRACT

Historically, little thought was given to the value of freshwater mussels when making decisions that affected these animals and their habitats, even though these values may be considerable, and may be greatly changed by environmental alterations. Here, I review several kinds of values provided by freshwater mussels. Direct-use (market) values of mussels were substantial when the mussels were harvested to provide buttons and pearls, amounting to about $10 billion (2017 dollars) in the USA alone. Current harvests are much smaller but still valuable. Mussels also provide indirect-use value through the ecosystem functions that they provide (water clarification, nutrient cycling, pathogen suppression, etc.). The monetary value of these functions may be substantial, but has not yet been estimated. As interesting, rare creatures, freshwater mussels may also have existence value to society. This value probably is small at present, but could be increased greatly through outreach and education, as could their option and bequest values (the value of saving them for the future). The total value of a freshwater mussel community would be the sum of direct use, indirect use, existence, option, and bequest values, and has not yet been estimated for any real mussel community. Alternatively, one could calculate the replacement value of freshwater mussels (the cost of replacing a mussel community that was damaged or destroyed); procedures for estimating replacement costs have been published. Despite uncertainty about the precise value of freshwater mussels, it is clear that they have substantial value to humans, possibly many millions of dollars in individual ecosystems, which should be taken into account in environmental decision making. Mussel ecologists and biologists can play important roles in helping society better value freshwater mussels.

KEY WORDS: bequest value, ecosystem services, market value, option value, Unionoida, use value, valuation

INTRODUCTION

"What are they worth?" must rank with "What good are they?" and "Are they good to eat?" as the most common questions that mussel ecologists and biologists hear from the general public. Although "Are they good to eat?" has a clear answer (Haag 2012), the other two interrelated questions are surprisingly complicated to answer, ranging far from biology and ecology into matters of philosophy and economics. Nevertheless, these are important questions for mussel biologists and ecologists to be able to answer, because they determine how people—including decision makers—view mussels, and how they protect and manage mussels and the habitats that they live in.

In this essay, I briefly review some of the ways in which the question of what mussels are worth might be answered, and offer suggestions about how mussel biologists and ecologists might help society reach better answers. My intent is to stimulate discussion of, not provide definitive answers to, the important problem of valuing freshwater mussels. Unless I specify otherwise, I use "freshwater mussels" (or just "mussels") to refer to members of the order Unionoida.

What is "Value"?

"Value" has many meanings in both common and technical language. In particular, economists and philosophers have discussed the idea of value extensively (e.g., Goulder and Kennedy 1997; Millennium Ecosystem Assessment 2003, 2005; Daly and Farley 2010), and have offered several definitions. I will restrict myself here to the idea of "exchange value": an object has value in terms of what other objects you'd exchange it for (Goulder and Kennedy 1997). Exchange values are subjective and individual. Thus, although almost everyone would set a higher value on a new luxury car than a used cigarette butt (i.e., they would trade away the cigarette butt to get the car), the relative value of other items is less clear. Which has higher value: a cold beer or a hot chocolate? The answer differs across people, some of whom don't like beer or are allergic to chocolate, and even within a single person over time, depending on whether they've just mowed the lawn on a hot summer day or come in from the ski slope. Thus, people don't hold set, universally accepted values for mussels or anything else.

Furthermore, value is not the same as price. Economists recognize that price is the minimum value that a buyer would place on an item (i.e., you'd buy the item at any price at or below the value you place on it) (Goulder and Kennedy 1997; Daly and Farley 2010). For instance, a thirsty person in a desert might be willing to pay $1,000 for a cold bottle of water, even though the actual price is just $1.95. In addition, we value many things (a beautiful sunrise, a baby's smile) that are not for sale on the market, and thus have no price.

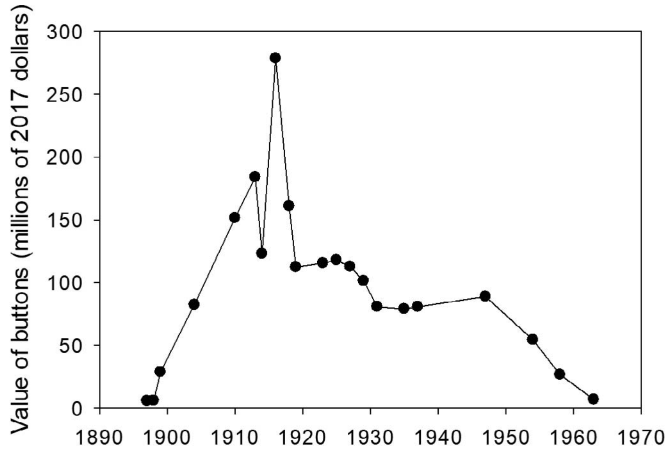

Figure 1. Value of finished buttons from the freshwater mussel fishery in the USA, 1897–1963, from data of Claassen (1994), converted to 2017 dollars using consumer price index (CPI) inflation calculator (https://data.bls.gov/cgi-bin/cpicalc.pl). The CPI inflation calculator goes back only to 1913; older data were corrected using 1913 figures and so are likely to be underestimates.

Why Might We Want to Set a Value on Freshwater Mussels?

I can think of at least two reasons why we might want to estimate the value of freshwater mussels. First, mussel biologists and ecologists could use such a value to justify research and management of freshwater mussels (FMCS 2016). For example, someone who studies a sport fish might note that expenditures on recreational fisheries in the USA in 2011 were $42 billion, with an estimated economic impact of $115 billion (Hughes 2015), as a way to convince people that sport fisheries are worth protecting, and that research on sport fish is worth doing. It could be helpful to be able to quote a figure on the value of freshwater mussels to justify spending money and time on our research and management activities.

Perhaps more important, placing a value on freshwater mussels could help us make better decisions among alternative activities that might affect freshwater mussels. Many human activities (e.g., dam construction or removal, changes in dam release schedules, habitat restoration, climate or land use change) affect freshwater mussels. When we decide whether a proposed activity is a good idea or not, it seems reasonable to try to estimate the total values resulting from the various alternative actions, which would include the values of changes to freshwater mussel populations. The more complete and accurate our valuation, the more possible it is to make a good decision about alternative actions.

Approaches to Valuing Freshwater Mussels

Below, I briefly describe several ways by which the value of freshwater mussels might be calculated, describing the approach, illustrating it with real data (if they exist), and discussing its shortcomings. I will begin with the most obvious approaches, and will roughly follow the categories of values of Goulder and Kennedy (1997) from economics.

Market values and other direct-use values.—Probably the first thing that most people think of when they think of value is market value—how much can I sell freshwater mussels for? Unlike most other freshwater invertebrates, mussels sometimes have substantial direct market value, as a source of nacre and pearls (Kunz 1898; Claassen 1994; Anthony and Downing 2001; Haag 2012). These fisheries have been very valuable in various parts of the world, but I have been able to find good data only on the fishery in the USA. Between 1897 and 1963, when there was an active fishery in many rivers for nacre for buttons, the total value of buttons was about $6 billion (2017 dollars) (Fig. 1). I have not seen good figures on the value of the freshwater pearl fisheries in the USA, but according to Claassen (1994), they were about half as valuable as buttons during the years of the button fishery. However, the commercial pearl fishery extended over a longer time span than the button fishery, beginning in 1857 or earlier (Kunz 1898). It therefore seems reasonable to estimate that the total value of the fishery (buttons plus pearls) from 1857 to 1963 was in the neighborhood of $10 billion in today's dollars.

Modern fisheries are much smaller but still valuable. In Tennessee, which accounts for about 75% of the value of modern mussel fisheries in the USA (Olson 2007), the wholesale value of mussel fisheries has been in the range of a few million dollars per year, although highly variable depending on prices that year (Fig. 2). Estimated export value of the shell is three to five times higher than the wholesale price (Hubbs 2009). Most of this harvest comes from a single reservoir (Kentucky Lake).

One particular aspect of market pricing that can work against preservation of natural resources is the common use of discount rates to estimate the net present value of a resource in deciding whether to consume it or preserve it. The idea behind using a discount rate is that, in a growing economy, a dollar today is worth more than a dollar tomorrow. In practice, planners have often used discount rates of 3–7%/yr (Arrow et

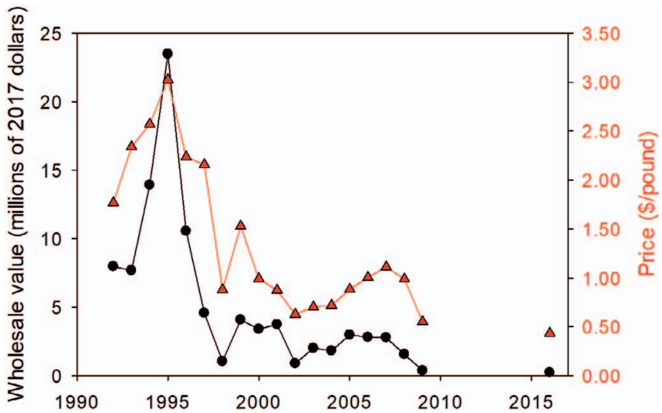

Figure 2. Wholesale value and price of mussel shells taken in the commercial fishery in Tennessee, 1992–2016, from data of Hubbs (2009) and Ganus (2016), converted to 2017 dollars using consumer price index inflation calculator (https://data.bls.gov/cgi-bin/cpicalc.pl).

al. 2013), which gives low value to benefits or costs that occur in the future, and almost no value to the distant future. In this worldview, it could have been economically sensible to harvest all of the mussels in the early 20th century, leaving none for the future. However, Arrow et al. (2013) made a compelling argument that uncertainty about future discount rates, declining population growth, and other factors should compel us to use declining discount rates, or at least use constant rates far lower than 3–7%, especially if we are considering long time horizons (> 10 yr). Either of these solutions would give much higher value to future benefits and costs, and tend to favor the preservation of natural resources rather than their immediate consumption or destruction.

At least one kind of direct-use value of mussels is not reflected in a market value, and that is their use as environmental indicators. Both the soft tissues and shells of mussels have been used as monitors of environmental conditions (e.g., water temperatures, concentrations of contaminants) in contemporary or past ecosystems (e.g., Schöne et al. 2004; Newton and Cope 2007), a use that has value to people. I don't know of any attempts to place a dollar value on this use.

Although the market values of freshwater mussels are straightforward to understand, and have been substantial in particular times and places, it is unlikely that they represent the total value of these animals. To see this, apply the exchange test to mussel communities that contain no commercially valuable species, are too sparse to harvest, or occur in places where mussel harvesting is illegal, or to a rare species that is of no commercial value. These mussels have zero market value. If market value is the same as the total value of these mussels, you would gladly exchange them for a dollar, for example if a factory were proposed whose effluent would kill every mussel in the river. I doubt that many mussel ecologists or even ordinary people would make this exchange. Thus, however important market values of mussels may be, they do not represent the total value of these animals.

Indirect-use values of mussels: ecosystem services.— Mussels may also be valuable because they interact with other parts of the ecosystem that humans value, and thus indirectly increase human well-being. This could be through connections to consumptive uses, such as clean drinking water or commercially harvested fish, or nonconsumptive uses, such as clear water that is appreciated for its aesthetic or recreational value. Indirect-use values are related to the idea of ecosystem services. Recognizing the value of ecosystem services to human well-being has been a major recent advance in valuation of natural resources. The Millennium Ecosystem Assessment (2003, 2005) identified four broad classes of ecosystem services: provisioning services (where an ecosystem provides food, fresh water, wood, fuel, etc. directly to humans), regulating services (where an ecosystem regulates climate, flooding, diseases, water quality, etc.), cultural services (where an ecosystem provides aesthetic, spiritual, recreational, or educational opportunities to people), and supporting services (where an ecosystem provides structures or functions that support any of the other three classes of services; examples include soil formation and nutrient cycling). The direct-use value of mussels in providing nacre and pearls falls under provisioning services, and I will discuss cultural services in a later section on existence value, so this section corresponds roughly to supporting and regulating services.

One important contrast between direct-use value and indirect-use values is that the latter often are harder to estimate, because we cannot rely on markets to show their value. This is especially true if the direct use that is being supported is a nonconsumptive use such as water clarity, which does not have a market value. Nevertheless, the fact that indirect-use values can be hard to estimate does not mean that they are small and can be ignored, as was nicely illustrated in recent study (Walsh et al. 2016) of the costs of the invasion of Lake Mendota, Wisconsin by the nonnative cladoceran *Bythotrephes longimanus*. This predatory zooplankter substantially reduced populations of the grazer *Daphnia* in the lake, which allowed phytoplankton to proliferate, reducing water clarity by nearly 1 m. Surveys of the willingness to pay by local residents had shown that a change in water clarity of 1 m had a value of $140 million, which was almost exactly the same amount as the cost ($86–163 million) of phosphorus-reduction programs that would be needed to restore the invaded lake to its former clarity. This study showed that the indirect-use cost of this single species in a single lake was about $100 million, far from trivial.

Studies of the indirect-use values (regulating and supporting services) of freshwater mussels are relatively recent, so our knowledge of these services is still actively evolving. Vaughn (2017) provided an excellent review of this topic, so the following summary will be brief. Figure 3 summarizes what we know so far about the ecosystem services that freshwater mussels provide to humans. As suspension feeders, mussels remove particles from the water. This can increase water clarity, which can increase the recreational and aesthetic value

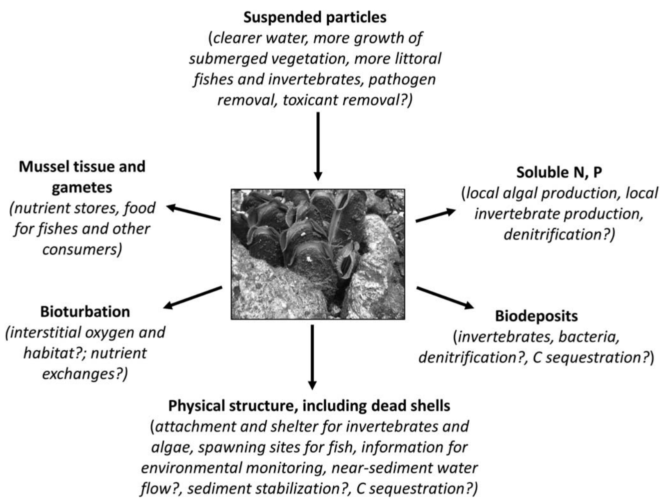

Figure 3. Summary of ecosystem services that might be provided by freshwater mussels, on the basis of the ideas of Vaughn and Hakenkamp (2001) and Vaughn (2010, 2017). Functions marked with a question mark probably occur but have not yet been definitively demonstrated. See text for further explanation. Photograph by Joel Berglund, from Wikimedia.

of a body of water and reduce treatment costs for drinking water. Increased water clarity can also lead to a whole range of subsequent effects in the ecosystem, including higher productivity of submersed plants and benthic algae, and higher productivity and diversity of littoral and benthic invertebrates, fishes, and waterfowl (Scheffer 2004), many of which may be valued by people.

In addition, freshwater mussels may improve the quality of drinking water by removing pathogens or contaminants, though this function is not yet well understood. We do know that they can remove a wide range of problematic particles and chemical compounds from the water column, including coliform bacteria, pharmaceuticals, personal care products, and algal toxins (Downing et al. 2014; Ismail et al. 2014, 2015, 2016). Freshwater mussels can capture a broad range of particle types (Vaughn et al. 2008), and we can expect from work on other bivalves (Roditi et al. 2000; Baines et al. 2005) that they may be able to remove many kinds of dissolved organic matter as well, including complexed materials such as heavy metals, so this function may be broad and important. However, for this function to be a useful service to humans, the materials removed from the water column by mussels must be quantitatively significant, and must stay out of the water column (i.e., be buried in the sediments, removed by harvesting the bivalves, or transformed into a harmless form) and not just returned to the water column upon the mussel's death.

The materials captured when mussels feed are routed to several fates, each having potential value to humans. Some of these materials are used to build mussel tissues, shells, and gametes, which can provide food to consumers and physical structure in the ecosystem. Some of the predators of juvenile and adult mussels (e.g., fishes, mammals, birds; Haag 2012) are of value to people, and little is known about the consumers of mussel sperm, glochidia, or dead mussels, even though large amounts of materials may be routed to these fates. It sometimes has been suggested that living mussels and spent shells can affect ecosystem function by serving as nutrient stores, but this will be important to the ecosystem only when the size of these stores is changing, resulting in net uptake from the ecosystem when stores are increasing and net release to the ecosystem when the stores are decreasing. The caveat also applies to the possible role of mussel shells in sequestering carbon or generating carbon dioxide (cf. Chauvaud et al. 2003). As long as spent shells are dissolving at the same rate as new shells are being formed, there will be no net effect on carbon sequestration or carbon dioxide generation; instead, spent shells must be permanently buried (which seems most likely to occur in fine-grained sediments or hard waters—Strayer and Malcom 2007), or the mass of live and dead shells must increase.

A large fraction of the material that mussels ingest ends up as wastes, either through excretion of dissolved materials (e.g., inorganic nitrogen or phosphorus) or egestion of biodeposits (feces and pseudofeces) (e.g., Christian et al. 2008; Atkinson and Vaughn 2015). The dissolved nutrients that mussels release can affect local production of algae (Atkinson et al. 2013), and this local algal production, together with the food provided by biodeposits and the shelter provided by the mussels, can likewise stimulate local production or diversity of animals (Howard and Cuffey 2006; Spooner and Vaughn 2006; Limm and Power 2011; Chowdhury et al. 2016). This local increase in productivity can extend far into the food web (Allen et al. 2012), presumably including fish. In addition, mussel beds may be sites where denitrification (the microbial conversion of nitrate to dinitrogen gas) occurs, which is an important ecosystem service in a time when many of our waters are polluted by inorganic nitrogen (e.g., Carpenter et al. 1998; Galloway et al. 2008). Denitrification requires ample nitrate and labile organic matter in a hypoxic or anoxic environment. All of these conditions could occur in dense mussel beds, and indeed denitrification occurs in beds of freshwater bivalves other than unionids (Bruesewitz et al. 2008, 2009; Turek and Hoellein 2015).

It has been suggested that unionids may stabilize sediments, but the few studies that have been done (Zimmerman and de Szalay 2007; Allen and Vaughn 2011) have provided mixed results. On the basis of work on other organisms in streams (Statzner 2012; Albertson and Allen 2015), it seems likely that mussels may either stabilize or destabilize sediments, depending on the species and densities of mussels, and the hydraulic and geomorphic setting.

The physical structures that mussels produce may have other value as well. In addition to sheltering invertebrates, mussels and their shells provide spawning sites and shelter for some fishes (Chatelain and Chabot 1983; Etnier and Starnes 1993; Aldridge 1999; Wisniewski et al. 2013). They presumably could alter near-bed and interstitial water flows as well, which could affect local habitat structure and

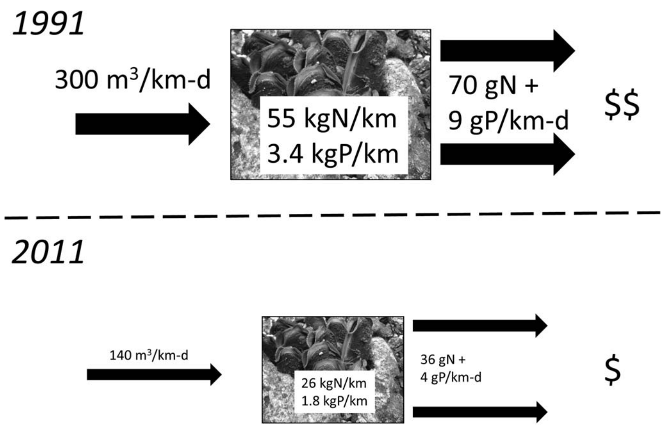

Figure 4. Changes in ecosystem functions provided by freshwater mussels in the Kiamichi River, Oklahoma after droughts between 1991 and 2011, on the basis of data of Vaughn et al. (2015). The width of arrows and the area of boxes are roughly proportional to the size of stores and flows (from left: volume of water filtered, size of stores of nitrogen and phosphorus in mussels and their shells, and excretion of inorganic nitrogen and phosphorus).

biogeochemical cycling, although this seems not to have been studied.

Sediment mixing (bioturbation) by freshwater mussels may also affect the structure of the interstitial habitat and sediment biogeochemistry, including sediment–water exchanges. This topic has received little attention (but see McCall et al. 1995).

It is therefore clear that freshwater mussels could have large and varied indirect-use values. However, several issues will make it challenging to place a dollar value on these indirect-use values (but see EPA Science Advisory Board [2009] for a good overview on estimation methods). First, we do not yet know all of the pathways that link freshwater mussels to the things that humans value about freshwater ecosystems, although great progress has been made recently. Second, the strength of these pathways depends on the environmental context, in ways that are just beginning to be appreciated (Spooner and Vaughn 2006; Vaughn 2010, 2017; Spooner et al. 2013). Third, linkages between mussels and the rest of the ecosystem also depend on the species of mussel (Spooner and Vaughn 2008; Vaughn 2010, 2017; Atkinson et al. 2013; Atkinson and Vaughn 2015). Fourth, the value to humans of the ecosystem functions provided by freshwater mussels will also be strongly context-dependent. The value of increased water clarity, for instance, will depend on whether the body of water is used for recreation, drinking water, or neither, and whether increased growth of submerged plants is viewed as a boon or as a nuisance. These complications will make it challenging to estimate the indirect-use value of freshwater mussels for even a single ecosystem, and even more difficult to make regional or global estimates.

However, as the example of Walsh et al. (2016) on zooplankton invasions shows, it would be a mistake to assume that the indirect values of mussels are unimportant just because they are hard to estimate precisely. Furthermore, we can use indirect-use values in evaluating the attractiveness of environmental alternatives, even if we do not place a dollar value on the underlying functions. The analysis of Vaughn et al. (2015) of the effects of drought on freshwater mussels in the Kiamichi River, Oklahoma provides a good example (Fig. 4). Vaughn's group sampled mussel communities along the Kiamichi both before and after serious droughts that were exacerbated by water allocation programs. By combining these data with detailed laboratory measurements of the activities of mussels, they were able to quantify the ecosystem services provided by mussels before and after the drought. Although they did not try to put a dollar value on these services, it is clear that the indirect-use value provided by mussels was substantially reduced by the drought. That is, going back to the idea of exchange value, we would gladly trade away the mussel community of 2011 to get the mussel community of 1991 on the basis of their indirect-use values. Vaughn's analysis clearly could be useful in discussing alternative water allocation schemes for the future, even without being converted into dollars.

However, another example (Fig. 5) shows a potential limitation of relying solely on direct-use and indirect-use values in assessing the total value of freshwater mussels. In the Hudson River, New York, large populations of unionid mussels (1.1 billion animals, but without commercial value) were supplanted in the early 1990s by even larger populations of dreissenids (Strayer et al. 1994; Strayer and Malcom 2014). We were able to use published studies from other ecosystems to roughly estimate ecosystem functions provided by bivalves before and after the dreissenid invasion. Although approximate, these estimates clearly show that every ecosystem function that we could estimate increased, usually very substantially, after dreissenids invaded. Again without trying to place a dollar value on these direct- and indirect-use values, we would conclude that the value of the bivalve community increased considerably after the driessenid invasion. Yet I doubt that many mussel biologists and ecologists, and perhaps many members of the general public, would happily trade away the the unionid-filled Hudson to get the dreissenid-filled Hudson. Furthermore, there are many communities of freshwater mussels so sparse that they have negligible market value and negligible indirect-use value. This again could suggest that they have nearly zero value and that we would happily exchange them for a trivial amount of money, which does not feel right. These mismatches between our intuition and calculated values suggest that the total value of freshwater mussels is not adequately represented by direct-use values plus indirect-use values.

Existence value.—Existence value is the value that people place on an item merely to know that it exists, even if they do not use (or ever intend to use) that item (Goulder and Kennedy 1997; Millennium Ecosystem Assessment 2003). As an example, it is very unlikely that I will ever travel to Asia to see snow leopards in the wild, but I like to know that these beautiful animals are still around, stalking their prey through the mountains, and so would pay some amount of money to

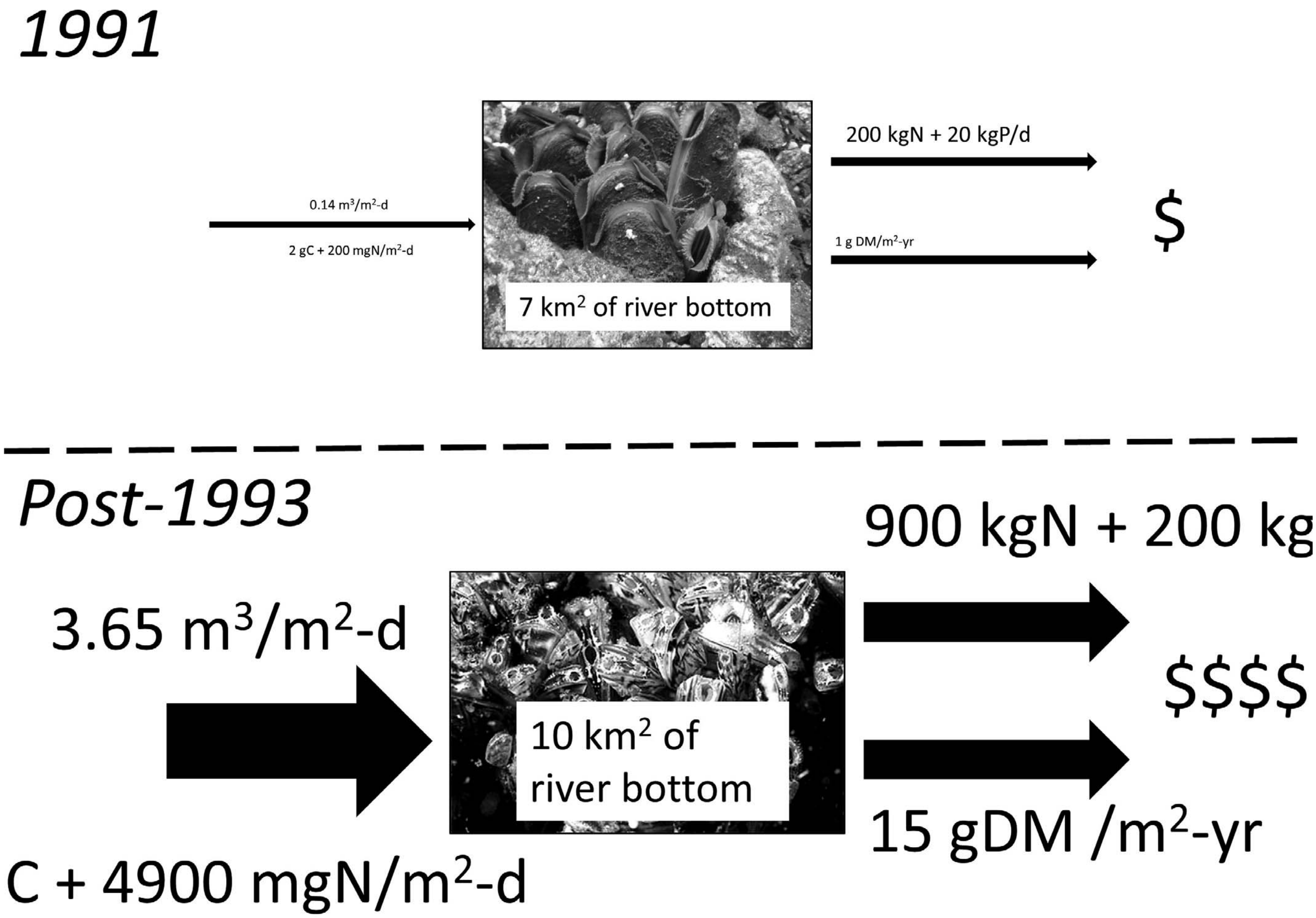

Figure 5. Changes in ecosystem functions provided by freshwater bivalves in the freshwater tidal Hudson River, New York after the invasion of the zebra mussel in the early 1990s, on the basis of the compilation of Strayer (2014) from multiple sources. The width of arrows and the area of boxes are roughly proportional to the size of stores and flows (from left: volume of water filtered [top], biodeposition of organic carbon and nitrogen in mussel beds [bottom], the spatial extent of mussel beds in the river, excretion of inorganic nitrogen and phosphorus [top], and production of bivalve tissue [bottom]).

help to preserve them. Existence value may have aesthetic, religious, or ethical foundations, and underlies many programs to conserve biodiversity or sites that are beautiful or culturally important. The large sums that people contribute to such programs show that existence value is real and can be large. People tend to assign higher existence value to things that are rare, unique, charismatic, or interesting (Goulder and Kennedy 1997), although some people have religious or ethical beliefs that assign value to the existence of all organisms or species. Surveys typically are used to estimate existence value, but it is difficult to measure accurately, and the resulting estimates tend to be controversial.

I know of no attempts to estimate the existence value of freshwater mussels. It seems likely that most people would give mussels an existence value near zero, because they don't know that freshwater mussels even exist, and know nothing about their rarity or interesting attributes. On the other hand, I suspect that many freshwater malacologists would assign a high existence value to unionids, because we know very well that they are rare and fascinating (e.g., Barnhart et al. 2008; Haag 2012; Lopes-Lima et al. 2017). Indeed, I suspect that it is a high existence value that would make many freshwater malacologists prefer a river full of unionids to the same river with a functionally similar (i.e., similar aggregate filtration rate) population of zebra mussels or *Corbicula*.

It also seems very likely that education and outreach about freshwater mussels could substantially increase their existence value outside the small community of freshwater malacologists. Kellert (1993) showed that people who knew little about invertebrates were likely to view them as unattractive and creepy, whereas people who knew a lot about invertebrates were more likely to see them as attractive and ecologically valuable. The more that people know that many freshwater mussels are rare, that some are unique or very unusual (e.g., *Epioblasma*), that many have fascinating life cycles, and that they may have direct economic or ecological utility, the higher the existence value that they are likely to give to them. Thus, websites such as the Unio Gallery (http://unionid.missouristate.edu/) and the many others that mussel biologists and their friends maintain (see http://molluskconservation.org/

Links.html for a partial list), and zoo exhibits about freshwater mussels (e.g., http://mnzoo.org/conservation/minnesota/freshwater-mussels/) may be critically important in increasing the existence value of freshwater mussels. They may even spur some additional element of nonconsumptive use value if people watch mussels in zoos or nature.

Option and bequest values.—Finally, two other kinds of values may be important but are hard to estimate. Option value is the value placed on something that you're not using today, but which you might want to use in the future (Goulder and Kennedy 1997; Gascon et al. 2015): that extra rocking chair in the attic or the can of nuts and bolts in the basement. Bequest value is similar, except that you're retaining something to give to your descendants—your grandmother's table that you are never going to use yourself, but which you'd like to pass along to a child or grandchild as a family heirloom.

We might assign option or bequest values to freshwater mussels for several reasons. We might recognize that our understanding of the practical uses or indirect-use values of mussels is incomplete, and so give them value higher than the direct- and indirect-use values that we know about today. This often is given as a reason for preserving species, whose uses in medicines or other commercial products, or roles in ecosystems, remain to be discovered (e.g., Gascon et al. 2015). We might also recognize that tomorrow's world will be different from today's as a result of climate change, species invasions, and so on, and that mussels may thus have different uses and values than they have today. In any case, it may be valuable to us to preserve mussels so that we and our descendants can use them in the future.

Option and bequest values can be estimated through surveys of people's willingness to pay to keep mussels for the future, but the resulting estimates often are uncertain and controversial. These values are also easily underestimated, especially by those who haven't thought much about them, and could be increased by education about the current and possible future utility of mussels. I am not aware of any attempts to estimate the option and bequest values of freshwater mussels.

Replacement value.—An alternative approach to valuing freshwater mussels is based on their replacement cost (Southwick and Loftus 2003). The approach, intended to restore mussel populations after an accidental kill, estimates the costs associated with propagating (or translocating) enough mussels to replace the animals that were killed, allowing for mortality between the time that the new mussels are stocked and the time they reach the size or age of the mussels that were killed. These costs can be substantial: the estimated cost of replacing a population of 15,000 *Lasmigona complanata* (a species of average propagation difficulty) was $122,312–150,312 (2003 dollars; Southwick and Loftus 2003). This is not an especially large mussel population nor an expensive species to handle, so it is apparent that replacement value of freshwater mussels could easily reach into the millions of dollars or more. Furthermore, updated estimates of replacement costs will soon appear, resulting in values that generally are substantially higher than the 2003 estimates (R. Hoch, North Carolina Wildlife Resources Commission, personal communication).

Replacement value is not easily related to the other kinds of values that have been discussed: it could be very much larger than the sum of other values if the species is of little economic or ecological significance but is hard to propagate, or it could be far smaller than the sum of other values if these are substantial and the species is easy to propagate.

What is the total value of mussels?—Depending on the purpose of the estimate, the total value of freshwater mussels could be estimated either as the sum of direct-use value, indirect-use value, existence value, option value, and bequest value across all stakeholders, or as replacement value. I am not aware of any attempts to estimate the total value of real mussel communities using either approach. Nevertheless, it should be obvious that the total value of mussel communities could be large (easily millions of dollars or more for an individual body of water), because we know from the examples I've presented that the values of the individual components that contribute to total value can be in the millions of dollars or more.

If total values are estimated correctly, they should match our intuition about what we would be willing to exchange a community of mussels for, whether in terms of dollars or in terms of other benefits to be produced by the ecosystem (e.g., electric power production, recreational angling, irrigation water, etc.). This is, after all, the definition of exchange value. Furthermore, even though we have not yet been able to estimate the total value of mussels in monetary terms, I suggest that even a narrative discussion about the total value of mussels, extending beyond their obvious market values to indirect-use, existence, option, and bequest values, may help us make better decisions about management actions that concern freshwater mussels.

Complications and Caveats

Several complications or caveats concerning valuation of freshwater mussels are worth discussing. The following is not intended to be comprehensive, but includes a few important considerations.

Whose values matter?—When we talk about adding up values of freshwater mussels across all stakeholders to estimate the total value of mussels to society, we gloss over the question of who the stakeholders are. We rarely would mean every human being on the planet, but there are several logical answers as to whom to include, and whom we include in the calculation can critically influence the calculation of societal value. For instance, do we include only those with legal standing (e.g., the property owners, the voting-age citizens of the political unit that claims authority over the decision), even if they are not geographically close to or directly involved with the target ecosystem (cf. Braumann et al. 2014)? Or might we recognize that natural resources belong to a broader constituency? Who should have a voice in determining the value of the last wild *Epioblasma obliquata* on the planet?

Second, does everybody's value carry the same weight, or do we give the values of some people greater weight? For example, if we are considering building a dam for hydropower, should the opinions of people who live right along the river or who benefit directly from the electricity get extra weight? What about experts? Should the opinion of economists or mussel biologists or ecologists be given special weight?

Because different groups of people often hold very different values (e.g., Hostmann et al. 2005; Castro et al. 2016), the choice of whose values are counted (and how they are counted) can be critically important in determining the value of alternative actions, and therefore the choice of the "best" alternative.

What aspect of value should we optimize?—What parameter do we attempt to optimize in a society whose members disagree on values? It is perhaps most natural to simply calculate the total value of each alternative, then choose the one with the highest value; that is, to maximize societal value. However, other alternatives may be equally reasonable. For instance, instead of maximizing value to society as a whole, one might choose to minimize the number of people who hold very negative values of each alternative (i.e., minimize total unhappiness). Hostmann et al. (2005) described such a situation, in which different groups of stakeholders were asked to rate different alternatives for the purpose of finding an alternative that provided reasonably acceptable outcomes for all stakeholder groups. On the other hand, knowing that the outcomes of many management actions are highly uncertain, and that estimates of values often are also imprecise, we may choose to minimize the chance of a catastrophic outcome. Again, the choice of the metric to be optimized may strongly affect which alternative is chosen as best.

How should we recognize the rights of future generations?—It seems reasonable to acknowledge that future generations have some rights, and that we should not leave them a useless planet. Bequest values deal partly with this problem, but are inevitably based on our values (what we think is valuable enough to leave to our descendants) rather than the values of our descendants, which are unknowable. We do know that values can change greatly from generation to generation, so it seems safe to assume that our grandchildren's values will be different from ours. For example, just a few generations ago, wetlands were largely regarded as wasteland, not as habitats that are valuable for supporting plants and animals, recharging aquifers, preventing floods, and protecting water quality. It is therefore unlikely that your great-grandparents would have thought to leave a wetland for you. Consequently, about half of the area of wetlands in the lower 48 states (and 90% of wetlands in places like Ohio and California) were destroyed (Mitsch and Gosselink 2015).

Since the values of future generations are unknowable, this problem is to some extent unsolvable. However, recognizing that future generations may value things that we do not, we might want to be very careful about making any decisions with consequences that are irreversible or even very difficult to reverse (e.g., extinction, habitat destruction). The recent emphasis on sustainability (leaving as many options open for the future as possible—e.g., United Nations 1987) seems like a step in the right direction to protect the rights of future generations.

Which alternatives should be taken off the table?—It is widely recognized that some management options may be unacceptable, regardless of their calculated value to society, because they violate an absolute right or taboo. The most familiar example probably is human life. An option that kills people usually is not chosen (or even seriously considered), regardless of its value to society, so we instead choose a highly valued option that does not kill people. Societies often recognize other taboos (e.g., desecration of sacred sites), and individuals often recognize absolute rights that are not universally recognized by the society as a whole (e.g., avoidance of animal suffering or species extinction). Which of these taboos should we recognize when evaluating possible management actions? When we are comparing the values of multiple management alternatives, which do we take off the table because they violate some absolute right?

How should we deal with uncertainty?—Some kinds of values (direct-use market values) can be estimated precisely, whereas others (e.g., indirect-use, existence, option, and bequest values) can be estimated only very approximately, and the estimates are likely to be controversial. This differential uncertainty has at least two important consequences. First, we may tend to ignore the values that are difficult to estimate, and pretend that they are not real. However, it is clear that these values can be substantial, so ignoring them could greatly underestimate the value of freshwater mussels and other items that play important roles in ecosystems, have high existence value, etc. Further, avoiding the hard-to-measure values will bias actions away from those with public benefits, because these often are harder to measure precisely than private benefits (Goulder and Kennedy 1997).

Second, large uncertainty means that highly negative and highly positive outcomes are possible, even if the expected outcome is close to neutral. People often are risk averse and choose to avoid the possibility of very negative outcomes. Thus, we may want to explicitly include the uncertainty of our value estimates when choosing among options. Specifically, we may wish to choose the option that minimizes the probability of disaster (e.g., if there is a small possibility that losing freshwater mussels would lead to toxic algae in a drinking water supply, we may want to keep the mussels).

It will not always be easy to include all classes of values when evaluating management alternatives, but simply excluding those that are hard to estimate will lead to bad choices, especially for public interests. All classes of values can at least be included at the conceptual level, even if they cannot be precisely valued in monetary terms. Further, it may be easier to estimate the difference in value between two management options than the total value of either state of the ecosystem.

How can Mussel Biologists and Ecologists Help Society Better Value Freshwater Mussels?

Freshwater mussels are valuable, even if only occasionally bought and sold these days, and their value should be taken into account in environmental decision making. Even though methods to estimate all the values provided by freshwater mussels are still in development, and it probably isn't yet possible to assign a firm monetary value to mussel populations, there are nevertheless several ways by which mussel biologists and ecologists can help society better value freshwater mussels (a point that was also made in the recent National Strategy for the Conservation of Native Freshwater Mollusks—FMCS 2016).

To begin with, we can increase people's awareness, understanding, and appreciation of freshwater mussels. Most of the people I meet, including many of the anglers and boaters I meet out on the water, don't even know that freshwater mussels exist, and they certainly don't know about their peril, fascinating biology, commercial value, or potential roles in freshwater ecosystems. Outreach and education of all kinds can help people understand why freshwater mussels might reasonably be included in decision making about environmental management. In addition, a better appreciation of freshwater mussels will almost certainly substantially increase their existence, option, and bequest values among the public.

Even if we cannot yet provide an accurate monetary value for freshwater mussel communities, we certainly can provide a narrative account of the multiple values that they provide to society. Clear and compelling narratives or diagrams of some or all of these values could increase the frequency and effectiveness with which mussels are included in environmental decision making.

As I noted earlier, our understanding of the roles of freshwater mussels in ecosystems (and their indirect-use value) still is developing. We still need research that identifies and quantifies these roles, and how they vary across different kinds of ecosystems. Although this is an obvious point, estimation of the values of freshwater mussels will require mussel ecologists (who can estimate ecosystem functions) to collaborate with social scientists (who can estimate the values of those functions) and educators (who can help us increase the existence value of mussels, as well as transmit the existence and values of mussels to the public).

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