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REGULAR ARTICLE

ASSESSMENT OF A HABITAT EQUIVALENCY ANALYSIS FOR FRESHWATER MUSSELS IN THE UPPER MISSISSIPPI RIVER

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ABSTRACT

The upper Mississippi River (UMR) contains diverse, dense, and reproducing assemblages of native freshwater mussels. In the case of an injury to mussels and their habitats, such as a hazardous material spill, train derailment, or barge grounding, resource managers have few restoration strategies. Resource managers need a means to document, quantify, and mitigate adverse effects on mussels resulting from injury. Habitat equivalency analysis (HEA), developed for use with a wide variety of habitat types, is a restoration scaling technique that compares ecological services lost from injury to ecological services gained through restoration actions. The U.S. Fish and Wildlife Service and Iowa Department of Natural Resources modified the HEA for use with native mussels. The mussel HEA has been applied within the UMR to estimate the quantity of restoration needed to compensate the public for injuries to mussels due to contaminant spills and construction projects. Our objective was to describe the UMR HEA for a general audience and assess if the four biological input variables used in the mussel HEA were reasonable based on literature values. We also evaluated the performance of HEA under a range of input scenarios. Although the input estimates used in HEA were within ranges reported in the peer-reviewed literature or were supported by professional judgment in the absence of peer-reviewed literature, outcomes of the mussel HEA were highly variable and would benefit from additional research to reduce uncertainty in the biological inputs. The application of HEA to mussels provides resource managers with a tool to quantify mussel-related ecological services lost from injury and to guide restoration efforts in the UMR.

KEY WORDS: freshwater mussels, habitat equivalency analysis, natural resource damage assessment, injury, sensitivity analysis

INTRODUCTION TO DAMAGE ASSESSMENTS

Resource managers in federal and state agencies must document, quantify, and mitigate ecological disturbances resulting from human activity (Bouska et al. 2018). In the event of a construction project, hazardous material spill, or other injury to a natural resource, environmental protection laws (e.g., Comprehensive Environmental Response, Compensation, and Liability Act) hold responsible parties accountable through recovery of monetary compensation (called damages) necessary to fund projects to offset environmental injuries. Through the Natural Resource Damage Assessment and Restoration Program (NRDAR), natural resource trustees (certain federal, state, or tribal government agencies) are authorized to assess and recover damages from potentially responsible parties to compensate the public for losses due to injury to natural resources (Table 1). Damage assessments typically have three components: (1) determine and quantify the extent of the injury, destruction, or loss (injury

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Table 1. Glossary of terms associated with natural resource damage assessments (definitions from NOAA 1997, except where otherwise indicated).

Term	Definition
Baseline	The condition of natural resources and services that would have existed had the incident not occurred.
Compensatory restoration	Any action taken to compensate for interim losses of natural resources and services that occur from the date of the incident until recovery of natural resources and services to baseline.
Damages	The amount of money sought by trustees as compensation for injury, destruction, or loss of natural resources (43 CFR[a] § 11.14).
Discount rate	The rate at which dollars or other valued items or services being provided in different time periods are converted into current time period equivalents. A discount rate is used to compensate for delayed provision of services.
Ecological services	The physical and biological functions performed by the resource including the human use of those functions (43 CFR[a] § 11.14).
Equivalency analysis	Process to determine the amount of ecological restoration required to mitigate or compensate for environmental injury or habitat loss (Strange et al. 2002).
Injury	A measurable adverse change in a resource such that the resource does not provide the same services as it would have in the absence of the unpermitted release of oil or a hazardous substance (Barnthouse and Stahl 2002).
Interim losses	The reduction in resources and the services they provide, relative to baseline levels, that occur from the onset of an incident until complete recovery of the injured resources.
Natural resources	Land, fish, wildlife, biota, air, water, ground water, drinking water supplies, and other such resources belonging to, managed by, held in trust by, appertaining to, or otherwise controlled by the United States, any State or local government or Indian tribe, or any foreign government.
Primary restoration	Any action, including natural recovery, that returns injured natural resources and services to baseline.
Restoration	Any action, or combination of actions, to restore, rehabilitate, replace, or acquire the equivalent of injured natural resources and services.
Scaling	The process of determining, for identified restoration actions, the size or scale of the actions that would be required to expedite recovery of injured resources to baseline and compensate the public for interim lost resources and services.
Service flows	Cumulative provision of services over time (Fonseca et al. 2000).
Service loss	The lost or reduced opportunity such as for fishing, nature viewing, hunting, or natural water treatment due to the injury to the resource, or basic life support (Barnthouse and Stahl 2002).

[a]Code of Federal Regulations.

quantification); (2) calculate and recover the damages needed to compensate for the injury (scaling and damages determination); and (3) use the recovered damages to restore, replace, or acquire the equivalent of the injured natural resources (restoration implementation; Baker et al. 2020). This paper addresses components 1 and 2.

Once the injury has been quantified, trustees determine the type and quantity of restoration (scaling) that will adequately compensate the public for injuries to natural resources. Several tools have been developed to help NRDAR practitioners estimate the amount of restoration required. Habitat equivalency analysis (HEA; Unsworth and Bishop 1994) and resource equivalency analysis (REA; Sperduto et al. 2003) quantify compensation by equating ecological services (HEA) or species (REA) lost due to injury with those gained through restoration, without directly estimating economic values. The more recent habitat-based resource equivalency method (HaBREM) is a biomass-based REA with habitat scaling (Baker et al. 2020).

The principal concept underlying HEA is that the public can be compensated for past losses of habitat resources through habitat enhancement or replacement projects that provide additional resources of the same type as those injured. Habitat equivalency analysis has been used extensively in NRDAR (e.g., Ando et al. 2004; Roach and Wade 2006; Israel 2019). For example, a pipeline ruptured and released ~3 million L of tar sands oil into a tributary of the Kalamazoo River, Michigan, injuring numerous species, including freshwater mussels (USFWS et al. 2015). Natural resource trustees conducted an HEA that indicated that 5,790 discounted service acre years (i.e., the value of all ecological services provided by 1 acre [0.4047 ha] of the habitat in 1 yr) were lost due to the injury. Other examples include assessing environmental losses after forest fires (Hanson et al. 2013) and assessing the effects of the invasive lionfish (*Pterois volitans*) on Bahamian reef fish populations (Johnston et al. 2015).

In NRDAR, ecological services are defined as the physical and biological functions performed by the natural resource, including the human uses of those functions (Dunford et al. 2004). Restoration actions seek to fully recover the ecological services provided by a resource before injury. In other words, it is not the resource itself, but the services it would have provided in the absence of injury, that form the basis for damage assessments. To fully recover these services, trustees must estimate the services lost from a natural resource injury and develop restoration alternatives that will provide the same level of services to the public. The underlying assumption is that the public will accept a one-to-one trade-off between a unit of lost services and a unit of restored services. Because most ecological services have no market value, damage assessments use indicators of ecological services rather than measuring services directly (Ruiz-Jaen and Aide 2005). Furthermore, because it is not feasible to measure and quantify each of the individual services provided by mussel habitats, such as production, sediment stabilization, nutrient cycling, and improved water quality, a key consideration in HEA is identifying a sensitive indicator for the targeted ecological service (Dunford et al. 2004). Practitioners have several options for indicators depending on the type of ecosystem and the targeted services (Vaissière et al. 2013; Scemama and Levrel 2016). In salt marsh ecosystems, practitioners have used plant biomass as an indicator of primary production, vegetative canopy structure as an indicator of habitat, and organic matter content as an indicator of biogeochemical cycling (Strange et al. 2002). In marine systems, shellfish density has been used as an indicator of secondary production because it was correlated with the magnitude of ecological services provided by bivalves (McCay et al. 2003).

THE HEA MODEL APPLIED TO MUSSELS IN THE UMR

The upper Mississippi River (UMR, defined as the 1400-km reach from Minneapolis, Minnesota, to Cairo, Illinois) supports diverse and valuable natural resources, including federally endangered, threatened, and candidate species (USFWS 2006). However, the river is a major transportation artery, making natural resources vulnerable to toxic spills and other injury. More than 90 million metric tons (90 billion kg) of industrial and agricultural commodities are shipped annually by barge (UMRBA 2014), and many commodities, including hazardous materials, are shipped by railroads, which cross the UMR or run within 1.5 km of the river for at least 55% of its length (UMRBA 2014). In addition to spills of hazardous materials, natural resources in the UMR are at potential risk from construction (e.g., bridges, barge loading facilities), barge groundings, and many other human activities that affect shoreline and water resources.

The UMR supports a globally important native freshwater mussel resource (hereafter mussels; Newton et al. 2011; Haag 2012). Mussels reach their greatest diversity in North America but have among the highest extinction and imperilment rates of any group of organisms on the planet (Haag and Williams 2013). For example, about 60% of the 50 native species in the UMR are now extirpated or state or federally listed (Tucker and Thieling 1999). Long-lived mussels are keystone species with strong linkages to other ecosystem components and ecological processes (Vaughn 2018). Mussels provide important ecological services that benefit other aquatic species, such as nutrient cycling and storage, the creation and modification of riverine habitats, and biofiltration. However, research to quantify the ecological services performed by mussels is in its infancy, and the mechanisms by which short- and long-term losses of these services might affect ecosystems are largely undocumented (Vaughn and Hoellein 2018).

Because of their imperiled status and the ecological services that they provide, mussels are frequently the focus of restoration and mitigation efforts in the UMR. Resource managers from the Iowa Department of Natural Resources (IADNR) and the U.S. Fish and Wildlife Service (USFWS) have applied HEA to estimate the quantity of restoration needed to replace mussels lost from hazardous spills and construction activities in the UMR and to determine monetary damages. They used a three-step process to assess injury to mussel habitat. First, HEA was used to quantify the loss of habitat (component 1). Second, the amount of restoration required to offset the loss of habitat was estimated (scaling in component 2). Specifically, for every square meter of a mussel bed lost to injury, how many additional square meters (termed replacement habitat [RH]) are owed. Given that HEA is used to estimate the amount of habitat restoration needed to compensate for *ecological service losses over time*, HEA requires a proxy for ecological services. The mussel HEA uses the pre-injury density of mussels (in mussels/m^2) as an indicator of secondary production, assuming that production is correlated with the magnitude of ecological services provided by mussels (e.g., McCay et al. 2003). Third, resource managers use RH estimates from the HEA output and the pre-injury density of mussels to estimate how many mussels need to be replaced into the restored habitat to generate the same level of ecological services as the original habitat (damages in component 2). This is typically accomplished by estimating the propagation costs necessary to replace the quantity of mussels lost, while maintaining a similar species composition to the pre-injury bed. This aspect of the mussel HEA uses published propagation values (Southwick and Loftus 2017) and will not be discussed further.

The mussel HEA contains 11 input variables that influence estimates of the amount of RH needed to compensate for losses (i.e., square meters owed). The input variables were categorized into four site-specific variables, three standard variables, and four biological variables (Table 2). Our objectives were to assess (1) if the four biological input variables used by UMR resource managers in the mussel HEA were reasonable based on values in the literature and (2) the performance of HEA under a range of input scenarios.

PARAMETERIZATION OF THE HEA MODEL AND EVALUATION OF BIOLOGICAL INPUTS

A workshop was held with members of the IADNR, the USFWS, and the U.S. Geological Survey to evaluate how HEA was applied to mussels in the UMR, with an emphasis on the input variables used to generate estimates of RH owed. Seven input variables were not evaluated in our review. Three

Table 2. Habitat equivalency analysis input variables, description, category classification, and indication if a given input was assessed in this paper.

Input	Description	Category	Assessed?
Years to natural recovery	Length of time after recovery starts for the mussel bed to return to pre-injury condition	Biological	Yes
Relative productivity of created versus natural habitat	The fraction of natural productivity that the restored habitat will produce	Biological	Yes
Years to full-service flow after creation	Time lag for the new or reclaimed habitat to reach full service	Biological	Yes
Lifespan of the created habitat	The expected usable lifespan of the created or reclaimed habitat	Biological	Yes
Functional form of the recovery function	The form of the model used to compute the recovery function	Standard	No
Functional form of the maturity function	The form of the model used to compute the maturity function	Standard	No
Real discount rate (annual)	Discount or depreciable life in business is set at 3%	Standard	No
Year injury begins	The year in which the injury occurred	Site-specific	No
Area injured	The number of square meters injured	Site-specific	No
Percent of services lost	The percent of each mussel bed unit lost	Site-specific	No
Year restoration begins	The year that recovery could start	Site-specific	No

of these were categorized as standard HEA inputs: the real discount rate, the functional form of the recovery function, and the functional form of the maturity function (Table 2). The values of these inputs are relatively standard across most HEA applications and are consistent with a sensitivity analysis that found the shape of the recovery and maturity functions did not greatly affect model outcomes (Dunford et al. 2004). Four of the input variables were categorized as site-specific: the year injury began, area injured, percent of services lost, and the year restoration began (Table 2). These inputs have values that rely on site-specific information about an injury and would not benefit from a biological assessment.

The four biological inputs are years to natural recovery, relative productivity of created versus natural habitat, years to full-service flow after creation, and lifespan of the created habitat. These were identified as variables that are likely responsive and specific to the life history and ecology of mussels and would therefore benefit from scientific assessment (Table 2). At the workshop, IADNR and USFWS provided estimates they have used for each biological input based on their professional experience (Table 3). Our task was to assess if these estimates were reasonable based on values in the literature or on professional judgment in the absence of peer-reviewed data. For each of the four biological inputs, we completed a literature review, compiled a range of scientifically defensible estimates, and computed the minimum, maximum, and median values (Table 3). We consider each of the biological inputs in the subsequent sections.

Years to Natural Recovery

This input describes how long it takes an injured mussel bed to return to a pre-injury condition (used in component 1). This value depends largely on the severity of the injury. For example, if a chemical spill occurs directly over a mussel bed and kills most individuals, recovery may take considerable

Table 3. The four biologically based habitat equivalency analysis (HEA) input variables that we assessed. Range used by managers are the input values currently being used by resource managers in the mussel HEA for the upper Mississippi River. Also listed are the primary factors that influence the input values and the assessed range that was determined based on literature-derived data and professional judgment.

Input parameter	Range used by managers	Factors influencing input values	Assessed range
Years to natural recovery	10–30 yr	Severity of injury, lifespan	Range: 10–30 yr, median: 20 yr
Relative productivity of created versus natural habitat	33–100%	Density, species richness	Range: 33–100%, median: 67%
Years to full-service flow after creation	10–30 yr	Lifespan, age at sexual maturity, physiological condition	Range: 10–30 yr, median: 20 yr
Lifespan of the created habitat	30–100 yr	Species composition, habitat type (specifically, hydraulic conditions at the site)	Range: 30–100 yr, median: 65 yr

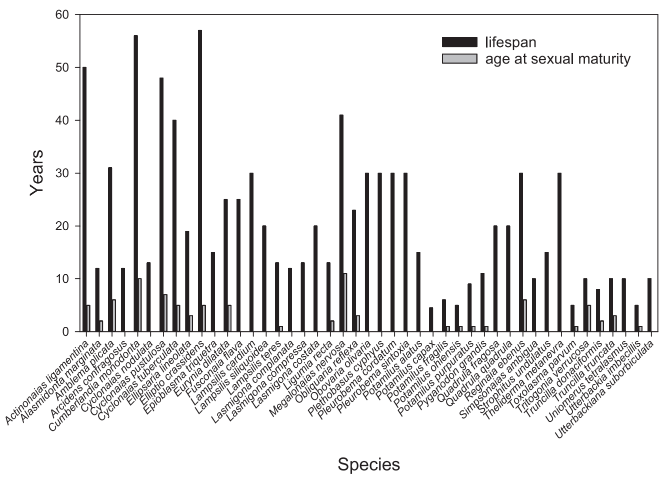

Figure 1. Estimates of maximum lifespans (Watters et al. 2009; Haag 2012) and age at sexual maturity (Payne and Miller 1989; Jirka and Neves 1992; Haag 2012) of select freshwater mussel species in the upper Mississippi River. Scientific names follow the 2021 Freshwater Mollusk Conservation Society checklist of freshwater mussels (FMCS 2021).

time because mussels will need to recolonize the area. In contrast, if a chemical spill occurs on the edge of a bed and kills only a fraction of the individuals, recovery should take less time. Larger affected areas also may take longer to recolonize, especially near the center of the area, because of limitations in the number of immigrants from nearby areas. The life-history traits of the resident species, specifically the lifespans of mussels in the original bed, may affect the years to natural recovery. For example, if a bed is dominated by longer-lived species, it will take longer to return to pre-injury conditions. In contrast, beds dominated by shorter-lived species may take less time to return to baseline. In the mussel HEA, UMR resource managers assigned values ranging from 10 yr (if >50% of the population is shorter-lived) to 30 yr (if >50% of the population is longer-lived) as the years to natural recovery.

To assess if the range of 10 to 30 yr was reasonable based on literature values, we compiled data on the lifespan of 45 species of mussels that reside in the UMR. The average lifespan was 21 yr but ranged from 5 to 57 yr (Fig. 1). This variation indicates that the number of years needed for a bed to return to its pre-injury condition could be highly variable depending on the lifespans of the individual species within the bed. Although the values used by resource managers are consistent with the literature, a more defensible estimate of this input can come only from population models or related approaches.

Relative Productivity of Created versus Natural Habitat

This input estimates the fraction of the natural productivity that the restored habitat will produce (used for scaling in component 2). For example, consider a wetland as the injured resource and primary productivity as the ecological service. If the restored wetland provides only 50% of the original productivity, twice as much restored wetland would be required to offset the losses, not accounting for any effects of time through discounting. Resource managers in the UMR assumed that productivity would vary as a function of mussel density. Using professional expertise, they assumed that if density in the original bed was low (~0–5 mussels/m^2), they might restore most (approaching 100%) of the original productivity; with moderate densities (~5–10 mussels/m^2) they might restore ~80%; and with high densities (>10 mussels/m^2), they might restore ~33% of the original productivity.

Because we know little about the productivity of natural mussel assemblages, this input was difficult to assess from either the literature or professional judgment. Although the ranges in density used by UMR resource managers are consistent with peer-reviewed data on mussels in the UMR (i.e., Newton et al. 2011; Dunn et al. 2020), we could find no data to support the level of productivity as a function of density. Because mussels in species-rich assemblages are often in better condition (Spooner and Vaughn 2009), productivity may be higher in diverse beds. Thus, species richness also may influence productivity of the restored bed. If restoration can capture the species richness of the original bed, its productivity should be comparable to the original assemblage (i.e., closer to 100% replacement). However, because propagation methods for many species are undeveloped, it may not be feasible to reintroduce some species into the restored bed. This would reduce the diversity of the restored bed and potentially reduce its productivity relative to the original bed. In the absence of peer-reviewed data, we were unable to assess this input. Thus, data to inform this input are a critical research need (see "Data Needed to Inform Mussel HEA Models").

Years to Full-Service Flow after Creation

This input addresses the time lag from establishment of a newly created or restored mussel bed to the time when it reaches its full ecological potential (used for scaling in component 2). It is influenced largely by the lifespan and age at maturity of the mussels in the original bed. For example, if a bed is dominated by a species that takes 5 yr to reach maturity and another 5 yr for their offspring to reach maturity, then the input value would be at least 10 yr. Because species in good condition contribute a greater magnitude of ecological services (Fridley 2001), the condition of species in the bed may also influence this input. Resource managers in the UMR assigned values ranging from 10 yr (if the original bed was dominated by shorter-lived species) to 30 yr (if the original bed was dominated by longer-lived species).

Literature-derived values of the lifespan (45 species) and age at sexual maturity (23 species) were used to estimate the years to full service after creation. The mean lifespan of mussels in the UMR was 21 yr and ranged from 5 to 57 yr, and the mean age at sexual maturity was 4 yr and ranged from 1 to 11 yr (Fig. 1). The longer it takes a mussel to reproduce, the longer the time lag from establishment of a restored bed to the time when it reaches its full ecological potential. Even if a regional supply of glochidia and newly released juveniles result in rapid settlement into the restored bed, mature stages could take decades to recover, especially since adults have limited mobility (Newton et al. 2008). If mussel lifespan is largely driving this input, the literature value of 21 yr is consistent with the range of values used by managers (10–30 yr). For age at sexual maturity, resource managers assumed a mean age of 5 yr, and our literature review indicated a mean of 4 yr. If physiological condition of mussels influences this input, then the restored bed should contain a sufficient quantity and quality of food to maintain species in good physiological condition to maximize performance of the entire assemblage (Spooner and Vaughn 2009). Although the input values used by resource managers are consistent with the literature review, more defensible estimates are needed. For example, age at sexual maturity is known for only a fraction of mussel species, and the error around these estimates is largely unknown. Similarly, the lack of robust data on what constitutes "good" physiological condition in mussels—and how this varies over time and space—limits assessment of this input.

Lifespan of the Created Habitat

This input seeks to describe the expected useable lifespan of the created or restored habitat (used for scaling in component 2). Resource managers have used estimates that ranged from 30 to 100 yr for this input, acknowledging that it could be shorter or longer if a bed was dominated by shorter-lived or longer-lived species, respectively. Mussel assemblages in the UMR are often dominated by longer-lived equilibrium and periodic species, with shorter-lived opportunistic species comprising $<25\%$ of assemblages (Newton et al. 2011). A review of 24 mussel beds across the United States indicated they remained intact for $\sim$62 yr (Sansom et al. 2018). In the UMR, some mussel beds have persisted for >70 yr (Scott Gritters, Iowa Department of Natural Resources, written communication, May 22, 2019). Thus, the range of input values used by managers is consistent with literature values. For reference, habitat restoration projects in the UMR are typically designed for a 50-yr project life (USACE 2012).

We propose that the lifespan of the restored habitat will depend on the hydraulic characteristics of the habitat to a much greater extent than the lifespan of mussels that inhabit it. If a bed is created in a dynamic habitat (e.g., shifting sand), the lifespan may be shorter than if the bed is created in a stable habitat. For example, in a hydraulically unstable area, beds can be ephemeral even if they are colonized by long-lived mussel species. Conversely, a hydraulically stable area could support a long-lived assemblage of short-lived mussel species (i.e., many generations). Some beds in the UMR are ephemeral (Ries et al. 2016), and extreme hydrologic events such as floods or droughts can influence persistence of beds in marginal areas (Zigler et al. 2008). For example, a 30- or 50-yr flood event could displace mussels in areas that have stable substrates during most years but experience high shear stress and mobile substrates at unusually high streamflow conditions. In the UMR, flow models indicated that high shear stress (resulting from high flows) negatively affects mussel abundance and can prevent juveniles from settling to the river bottom (Morales et al. 2006; Zigler et al. 2008). In contrast, empirical data reported no change in abundance or species richness of mussels after the 1993 flood in the UMR (Miller and Payne 1998).

SENSITIVITY ANALYSIS

We performed a sensitivity analysis on the four biological inputs to assess how uncertainties in the inputs contributed to uncertainty in HEA outputs. Managers from the IADNR and USFWS provided data from four locations in the UMR where they had previously applied the mussel HEA to address injuries to mussels (Table 4). In our sensitivity analysis, we created a baseline scenario for each dataset where each input was set to the median value from the literature. That is, the median values for the variable inputs were selected relative to the condition of the mussel beds absent the injury (also called relative productivity of restoration to baseline). First, the effect of each HEA input variable was assessed individually. Each input was modified, one at a time, to the minimum or the maximum value from the range to estimate the percent change in RH owed relative to the baseline condition (Dunford et al. 2004). Then the cumulative effect of simultaneously changing multiple input variables was evaluated by comparing the output (RH) of the baseline scenario to two bounding scenarios: the lowest possible RH estimate ("low scenario," least amount of restoration required) and the highest possible RH estimate ("high scenario," most amount of restoration required).

The individual and cumulative effects of changes in the input values resulted in substantial differences in loss estimates. Changing the values of inputs individually resulted in estimates that were –45% to 112% of the RH in the baseline scenario (Table 5). The loss estimates across the four UMR examples were most sensitive to the relative productivity of created versus natural habitat and the lifespan of the created habitat (Table 5).

All four HEA datasets reflected a similar sensitivity in RH between the bounded scenarios (greatest amount of RH, least amount of RH). Thus, we will discuss only one example in detail (Appendix A contains the results of the other three examples). Example 1 concerns a mussel bed that was affected by a train derailment in 2011 (Table 4). Seven cars of a train containing coal derailed into the UMR at Keokuk, Iowa, and resource managers estimated $\sim$17,000–25,000 mussels were injured. The constant inputs used by resource managers were the injured area units (353 m^2), the percent of services lost initially (25%), and the real discount rate (3%). The percent of services lost initially was estimated by resource managers who assumed that 25% of the bed was injured by coal smothering the mussels. The variable inputs were years to natural recovery (10–30 yr), relative productivity of created versus natural habitat (33–100%), years to full-service flow after creation (10–30 yr), and lifespan of the created habitat (30–100 yr).

Table 4. Descriptions of habitat equivalency analyses that have been conducted in the upper Mississippi River and that were used in the assessment process.

Example	Description	Location	Year	Outcome
1	Seven cars of a coal train derailed into the upper Mississippi River; an estimated 17,000-25,000 mussels were affected	Keokuk, Iowa	2011	Settled in 2013 for $137,000
2	Train derailment that covered 301 m^2 of a mussel bed with ~28 mussels/m^2	Guttenberg, Iowa	2008	Settled in 2014 for $625,000
3	A company wanted to construct a barge loading facility on top of a 113-m^2 mussel bed with densities of ~16 mussels/m^2	Davenport, Iowa	2010	Active case
4	Derailment of a train containing ethanol	Balltown, Iowa	2015	Active case

The baseline scenario for HEA estimated the RH as 57 m^2 owed (Table 6). The highest bound, which was based on simultaneous changes to inputs, resulted in an RH estimate of 485 m^2—a 751% change from the baseline scenario. The inputs for this scenario included setting the years to natural recovery and the years to full-service flow after creation to the maximum value in their range (both 30 yr) and setting the relative productivity of created versus natural habitat and lifespan of created habitat to the minimum values in the assessed range (33% and 30 yr, respectively). Changing the inputs to the lowest bound resulted in an estimated RH of 15 m^2—a –74% change from the baseline scenario (Table 6). The inputs for this scenario included setting the years to natural recovery and the years to full-service flow after creation to the minimum value in their range (both 10 yr) and setting the relative productivity of created versus natural habitat and lifespan of the created habitat to the maximum values in the validated range (100% and 100 yr, respectively). Across all four UMR examples, the percent change in RH from baseline ranged from –73% in the low scenario to +759% in the high scenario (Table 6 and Appendix A).

MODEL LIMITATIONS AS APPLIED TO MUSSELS

In our opinion, the most serious limitation of the mussel HEA is that robust, peer-reviewed data are not available for accurate estimates of the input parameters. When peer-reviewed data are available, they are highly variable, and selecting an appropriate value is difficult without population models or more detailed empirical studies. These limitations can introduce considerable uncertainty in the amount of RH required to restore inured habitats. When empirical data were lacking, input values in the mussel HEA were estimated based on professional judgment. Experts often differ substantially in professional judgment, which can lead to uncertainty in input values. The uncertainty in professional judgment does not preclude its use in NRDAR, and several methods are available to produce consensus in a group of experts. The Delphi technique is an iterative structured elicitation process used to gather and evaluate professional opinions (Mukherjee et al. 2015). This technique was recently applied on the UMR to compare outputs from a mussel community assessment tool with professional judgment of resource managers (Dunn et al. 2020). The Delphi method provided a consistent evaluation

Table 5. Sensitivity analysis of input variables in a habitat equivalency analysis (HEA) for native mussels in the upper Mississippi River (UMR). The baseline scenario describes conditions where all input values were set to the median value based on data in the peer-reviewed literature. The alternative scenarios change one parameter at a time (bolded text) to the minimum or maximum value from the literature range (first four rows). The last five rows illustrate how the replacement habitat (RH in m^2) changed in four example HEAs that have been conducted in the UMR. The mean percent of baseline (the percent change in service losses) across the four examples was also calculated.

	Baseline scenario	Years to natural recovery		Relative productivity of created versus natural habitat		Years to full-service flow after creation		Lifespan of the created habitat	
		Min	Max	Min	Max	Min	Max	Min	Max
Years to natural recovery	20	**10**	**30**	20	20	20	20	20	20
Productivity of created versus natural habitat (%)	67	67	67	**33**	**100**	67	67	67	67
Years to full-service flow	20	20	20	20	20	**10**	**30**	20	20
Lifespan of created habitat (yr)	65	65	65	65	65	65	65	**100**	**30**
RH example 1	57	31	78	115	38	48	67	120	48
RH example 2	218	119	300	443	146	183	259	460	184
RH example 3	77	42	106	157	52	65	91	163	65
RH example 4	81	45	112	165	55	69	97	172	69
Mean change from baseline (%)	–	−45	38	103	−33	−16	19	112	−16

Table 6. An example habitat equivalency analysis for native mussels in the upper Mississippi River used to assess the cumulative effect of simultaneously changing multiple input variables. This sensitivity analysis compares estimates of replacement habitat (RH) from a baseline scenario (all variable inputs were set to the median values derived from the literature) to two bounded scenarios: the lowest possible RH (low scenario) and the highest possible RH (high scenario). This example corresponds to Example 1 in Table 4.

	Baseline scenario	Low scenario	High scenario
Constant inputs			
Injured area units (m^2)	353	353	353
Percent of services lost initially (%)	25	25	25
Real discount rate (%)	3	3	3
Variable inputs			
Years to natural recovery	20	10	30
Relative productivity of created versus natural habitat (%)	67	100	33
Years to full-service flow after creation	20	10	30
Lifespan of the created habitat (yr)	65	100	30
Performance measure			
RH (m^2)	57	15	485
Percent change from baseline (%)		−74	751

technique with uniform definitions that managers could use to evaluate mussel assemblages.

The mussel HEA was most sensitive to the relative productivity of the created versus natural habitat and lifespan of the created habitat; thus, users should carefully consider inputs for these variables. The cumulative effects of changing multiple input variables on the estimate of RH required was substantial. However, this level of difference is based on bounded examples that used only the minimum and maximum values for the input variables regardless of any relevant biological and local information. In the absence of empirical data, objective professional judgment will be essential for fair evaluations. One approach might be to start with median values and then adjust inputs up or down based on a priori information such as species composition, life history, density, and age structure. Peer-reviewed information might help assess how the injured bed compares to other beds. The mussel community assessment tool (Dunn et al. 2020) might provide useful context for evaluating the relative qualities of individual beds.

DATA NEEDED TO INFORM MUSSEL HEA MODELS

Although HEA shows promise as a tool to restore mussels after injury, substantial data gaps must be addressed. We identified four areas where additional research could benefit HEA: formal demographic modeling to predict years to natural recovery, the need to address habitat quality and quantity to inform lifespan of the created habitat, the identification of representative indicators for ecological services to inform relative productivity of created versus natural habitat, and the development of a relationship between services and species richness to produce more comprehensive measures of service losses and gains. Tools (e.g., population and production models) are lacking for using existing data to make robust estimates of the four inputs.

Both HEA and REA would benefit from development of demographic data on basic biological processes in mussels (i.e., rates of mortality, growth, and reproduction) across species, habitats, and ecosystems. For example, natural variation in vital rates of four species of mussels over a 4-yr period in the UMR varied considerably (survival varied six-fold, growth varied two-fold) and was related to life history, habitat quality, and hydrologic events (Newton et al. 2020). Similarly, recruitment rate and population growth rates of two species of mussels varied considerably in the Clinch River, Tennessee, and were strongly associated with stream discharge (Lane et al. 2021). Studies such as these, which quantify natural variation in population vital rates and the physical conditions that influence them, may reduce uncertainty in mussel HEA input values. Equivalency analyses also would benefit from development of Leslie matrix population models and associated life tables. Leslie matrix models are discrete, age-structured models of population growth often used in population ecology (e.g., Vindenes et al. 2021). This information can inform HEA and REA by documenting how many mussels are lost over time by age class based on survival and longevity. These models can help determine the restoration needed to replace what was lost to injury (e.g., Jones et al. 2012).

In HEA, managers seek to estimate the quantity of habitat restoration needed to compensate for ecological service losses over time. However, habitat quality may be as (or more) important than habitat quantity or configuration in enhancing species richness and persistence (Summerville and Crist 2004). Although habitat quantity can be measured directly, habitat quality remains elusive. Recently a few metrics have been proposed to assess habitat quality. For example, measures of substrate stability (as an indicator of habitat quality) might allow meaningful inference about the potential lifespan of a mussel bed at a particular location (Newton et al. 2020). Combined measures of substrate resistance (a measure of consolidation of surface sediments), redox potential (as a proxy for oxygen penetration), and substrate texture were strong indicators of mussel recruitment (Geist and Auerswald 2007). The amount of fine sediment in interstitial spaces largely explained the decline of *Margaritifera margaritifera* in German streams (Stoeckl et al. 2020). In a mark-recapture study in the UMR, survival of mussels was consistently higher in areas with stable substrate, relative to areas where the substrate was less stable (Newton et al. 2020). Importantly, habitat quality and quantity are not mutually exclusive and should be considered interactively. It is likely that there are locations where high-quality habitats (i.e., those where survival, growth, and reproduction are optimized) are present only in low quantity, or, conversely, locations where quantity is large but quality is uniformly low. Further complicating the assessment of habitat quality is that it likely varies temporally. Research that identifies habitat attributes that optimize biological processes will provide valuable information for damage assessments.

Habitat equivalency analysis uses the percent of ecological services lost as part of the scaling process (see Table 2). HEA practitioners urgently need data on representative indicators for ecological services to inform the relative productivity of created versus natural habitat. Prior studies indicated that HEA results are sensitive to the choice of indicator used to assess ecological services lost (Strange et al. 2002; Vaissière et al. 2013). For example, the years to natural recovery in salt marsh ecosystems was highly dependent on which ecological indicator (i.e., primary production, soil development and biogeochemical cycling, invertebrate food supply, and secondary production) was used as a proxy for ecological services (Strange et al. 2002). It is not feasible to measure and quantify each of the ecological services provided by mussels and their habitats. The use of HEA to scale restoration is warranted only when the loss of ecological services can be quantified through a scientifically robust indicator that is representative of the damaged habitats and/or natural resource. In the mussel HEA, the pre-injury density of mussels (in mussels/m^2) was used as an indicator of secondary production (the ecological service), assuming that production is correlated with the magnitude of ecological services provided by mussels (e.g., McCay et al. 2003). However, estimates of secondary production in mussels in rivers are limited to a few studies (Strayer et al. 1994; Newton et al. 2011). Future mussel HEAs should consider other indicators such as abundance as a surrogate for population size, the number of live species as a surrogate for biodiversity, or stability of river substrates as a surrogate for habitat longevity. Regardless of the chosen indicator, sufficient data on the input values either need to exist or be cost-effective to obtain. Given the current state of research on quantifying ecological services provided by mussels and their habitats, this will be challenging.

The lack of an established relationship between services and species richness is a critical data gap in mussel HEAs. Although we know that the ecological services performed by mussels vary across species and environmental contexts (Spooner and Vaughn 2008), we do not know the degree to which restoration is dependent on recovering the original species richness. If reestablishing the original species assemblage is not possible or cost-effective, is restoration of species with similar functional traits sufficient? Also the relationship between services and species richness may depend on the mussel-provided ecological service of interest. For services such as biofiltration and nutrient cycling, those species that dominate the biomass typically provide most of the services (Vaughn 2018). However, there may be existence values for biodiversity (the value that people place on an item merely to know it exists, even if they do not use or ever intend to use that item; Strayer 2017) that would support restoration of all mussel species. Thus, although our assessment of the biological inputs to HEA was reasonable based on the literature or professional expertise, practitioners must recognize that conclusions about the amount of restoration needed depend on the data and assumptions that are used in the mussel HEA calculations.

FUTURE CONSIDERATIONS

As equivalency models continue to be applied to mussels, practitioners might consider the following points when trying to restore mussels, their habitats, and the ecological services they provide. Where practical, practitioners should ensure that conservation goals are inclusive of all life stages. Because the ecological services performed by mussels often scale with biomass, habitats that are restored with hatchery-reared juveniles may approach the same level of productivity as the original bed only when a size distribution similar to the original bed is achieved. Restoration efforts would benefit from re-creating a species composition similar to the original assemblage. This will be challenging because propagation methods are available for only a fraction of mussel species, and it may be difficult to propagate enough mussels to have a tangible effect on ecological services at large scales. If a similar species composition cannot be attained, practitioners should try to use species with similar life history strategies (i.e., equilibrium, opportunistic, periodic; Haag 2012). It also would be beneficial to ensure that appropriate hosts are available in the vicinity of the restored habitat. In conclusion, restoring mussels in large complex rivers like the UMR will be challenging and will not occur solely by stocking captively propagated individuals. Restoration of mussels will require a multifaceted approach that may include stocking captively propagated individuals, translocating mussels, protecting habitats that support both a high density and a high diversity of mussels, and aggressively re-creating habitats of sufficient quantity and quality to facilitate natural recolonization.

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Appendix A. Three examples of the habitat equivalency analysis for native mussels in the upper Mississippi River used to assess the cumulative effect of simultaneously changing multiple input variables. This sensitivity analysis compares estimates of replacement habitat (RH) from a baseline scenario (all variable inputs were set to the median values derived from the literature) to two bounded scenarios: the lowest possible RH (low scenario) and highest possible RH (high scenario).

	Baseline scenario	Low scenario	High scenario
Example 2			
Constant inputs			
Injured area units (m^2)	301	301	301
Percent of services lost initially (%)	100	100	100
Real discount rate (%)	3	3	3
Variable inputs			
Years to natural recovery	20	10	30
Relative productivity of created versus natural habitat (%)	67	100	33
Years to full-service flow after creation	20	10	30
Lifespan of the created habitat (yr)	65	100	30
Performance measure			
RH (m^2)	218	58	1,863
Percentage change from baseline (%)		−73	755
Example 3			
Constant inputs			
Injured area units (m^2)	113	113	113
Percent of services lost initially (%)	100	100	100
Real discount rate (%)	3	3	3
Variable inputs			
Years to natural recovery	20	10	30
Relative productivity of created versus natural habitat (%)	67	100	33
Years to full-service flow after creation	20	10	30
Lifespan of the created habitat (yr)	65	100	30
Performance measure			
RH (m^2)	77	21	659
Percentage change from baseline (%)		−73	756
Example 4			
Constant inputs			
Injured area units (m^2)	7500	7500	7500
Percent of services lost initially (%)	1.5	1.5	1.5
Real discount rate (%)	3	3	3
Variable inputs			
Years to natural recovery	20	10	30
Relative productivity of created versus natural habitat (%)	67	100	33
Years to full-service flow after creation	20	10	30
Lifespan of the created habitat (yr)	65	100	30
Performance measure			
RH (m^2)	81	22	696
Percentage change from baseline (%)		-73	759