Watershed selection to support freshwater mussel restoration: an open-loop decision guide

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Photos: Ayla Skorupa

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Background

The global loss of freshwater mussel diversity has resulted in considering population augmentation and reintroduction as important tools for freshwater mussel conservation (FMCS 2016). The process of mussel population restoration broadly includes captive propagation followed by release of propagated juveniles into streams (Patterson et al. 2018). Despite the importance of propagation and restoration for freshwater mussel conservation (FMCS 2016), there are many risks associated with this conservation activity and factors to consider for responsible population restoration (Jones et al. 2006; Strayer et al. 2019).

The goal of mussel release is typically to either increase population numbers (augmentation) or create new populations (reintroduction) (McMurray and Roe 2017). The restoration watershed is relatively easy to select when considering an augmentation, because it must already contain the target species. However, deciding where to augment among existing populations may be challenging given a lack of information on potential stressors and success is often difficult to assess (Haag and Williams 2014). If the goal is to reintroduce mussels, there are likely a greater number of watersheds to consider and selecting among them may be unclear (Roy et al. 2022). Selecting watersheds for reintroduction that will support the target species through local catastrophic or climate-related events could reduce the effort needed for ongoing restoration (Haag and Williams 2014). Given the numerous factors that may affect population restoration success, a decision process to help select watersheds for mussel reintroduction may be useful for practitioners.

Here, we outline questions to help guide a practitioner when selecting potential watersheds for population restoration. The questions follow an open-loop process in a ‘yes’ or ‘no’ format (Figure 1), whereby the options are to either proceed to the next question if the disturbance in question is negligible to mussel persistence or end the loop; each question ignores previous answers. Many posed questions may be associated with a high degree of uncertainty because of insufficient information and thus answering each question as ‘yes’ or ‘no’ could be considered an extreme simplification of complex information. Given this simplification, if the uncertainty around any question is too great, it is at the practitioner’s discretion to either end the open-loop question process or skip the question and proceed. While this process identifies watersheds for potential restoration, it does not prioritize among them. If practitioners are interested in selecting among multiple watersheds that make it through the open-loop process, then watersheds can be subsequently compared by calculating metrics that assess the relative

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quality of the watershed for restoration or by comparing information gathered in the open loop process—this step is not described in this open-loop process. Once a watershed is selected for potential mussel restoration, further reach-scale characteristics would need to be considered before population augmentation or reintroduction (Zając et al. 2018).

Figure 1. The open loop process to identify potential watersheds for mussel population restoration. Proceeding in the loop occurs only if the impact is negligible to mussel persistence. Green arrows indicate moving to the next question within the open loop process while red arrows that point to the middle "do-not" symbol indicate ending the process. Photo of an Eastern Lampmussel (*Lampsilis radiatia*). Credit: Ayla Skorupa.

We test this open-loop process using the Dwarf Wedgemussel (*Alasmidonta heterodon*), a federally endangered freshwater mussel that regularly undergoes a five-year review by the U.S. Fish and Wildlife Service. The last review was completed in August 2019 and lays out the necessary requirements to downlist the species to threatened (USFWS 1993; USFWS 2019). To downlist the Dwarf Wedgemussel, four rivers listed in the recovery plan must have viable populations, and six additional rivers representative of the species range also must have viable populations (USFWS 2019).

Throughout this framework we reference different Hydrologic-Unit Codes (HUCs) that represent a hydrologic delineation (i.e., watershed boundary) that defines the extent of surface water that drains to a point (USGS 2019). In this document we reference HUC12s (subwatersheds) that are nested within HUC8s (subbasins). We worked within five Hydrologic-Unit Code 8 (HUC8) subbasins—in the states of Massachusetts, Connecticut, New York, Pennsylvania and New Jersey (Figure 2) —to explore potential for population restoration that may ultimately contribute to the recovery of Dwarf Wedgemussel.

Decision Framework

1. Does the watershed contain viable populations of target species?

A population's viability status—whereby viable populations contain a sufficient number of reproducing adults to maintain genetic variability and have adequate annual recruitment to maintain a stable population (USFWS 2019)—helps to identify restoration needs; watersheds with low population viability may be a good target for restoration. Parameters needed to calculate population viability include population size, population growth rate, recruitment, fecundity, and survival (Lane and Jones 2021). Given that these parameters are often unknown for many mussel populations, information on population size and/or recent recruitment (i.e., age-class distribution) may serve as a proxy for viability. For example, fertilization success was correlated with density of Eastern Elliptio (*Elliptio complanata*), where fertilization failure was found at local densities of <10 mussels/m^2 (Downing et al. 1993). However, minimum population sizes affecting viability are unknown for many species (Nunney and Campbell 1993), and the ability to use population size as a metric for viability is likely species-specific. Some species can exchange spermatozoa over long distances and are not as dependent on local density. For example, a Plain Pocketbook (*Lampsilis cardium*) male that was estimated to reside 16.2 km upstream of the female still contributed to fertilizing her brood (Ferguson et al. 2013). Species known to occur in low densities versus in aggregated beds likely contribute to mussels' ability to perform long-distance fertilization. For species where population size does not represent population viability, evidence of recent recruitment (i.e., smaller sized mussels present)—in addition to population size—may contribute to assessing if a population is viable (Hastie et al. 2010). Because recruitment often fails before adult mortality, presence of juveniles indicates populations may be viable and are thus not extant relict populations of larger individuals.

Treating species populations as individual management units is beneficial when there is genetic structure (Galbraith et al. 2015; McMurray and Roe 2017; Porto-Hannes et al. 2022; Wacker et al. 2019). Releasing mussels to watersheds that contain viable populations of the target species (augmentation) can result in outbreeding depression where decreased native mussel fitness is a result of mating among distantly-related individuals (Jones et al. 2006). Mussels with limited dispersal and exposed to local environmental selection pressures may have

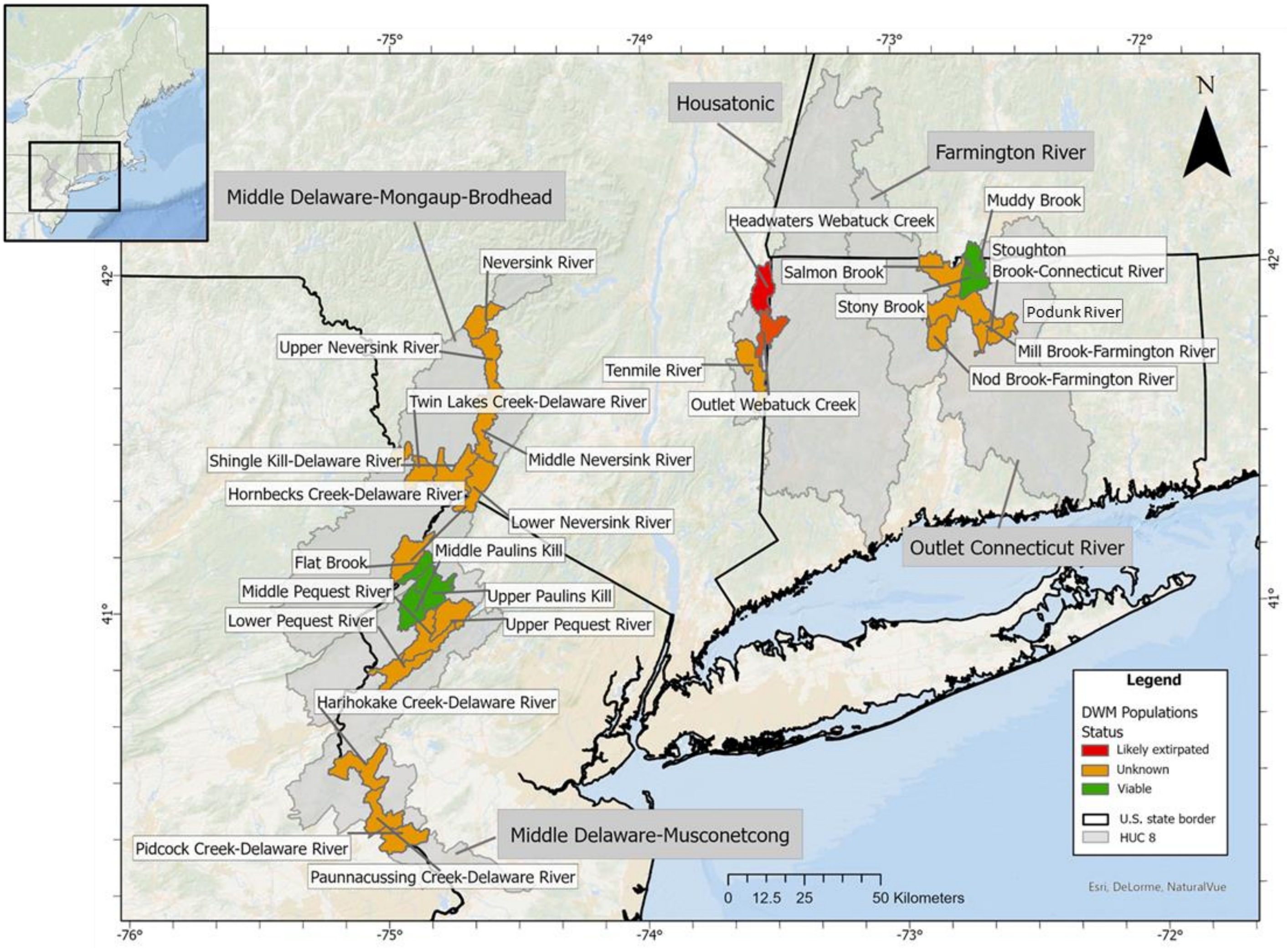

Figure 2. Map of the Hydrologic Unit Code (HUC) 8 subbasins (labels in gray) and HUC12 subwatersheds (labels in white) of Dwarf Wedgemussel (DWM) (*Alasmidonta heterodon)* population viability where populations are categorized as viable, likely extirpated, or unknown viability in the Connecticut and Delaware River Watersheds (USFWS 2019).

developed coadapted gene complexes specialized for their habitats (Lane et al. 2019), and use of local fish communities as hosts (Douda et al. 2017), thus mixing genetics among populations may exacerbate population declines. While we are unaware of evidence for outbreeding depression in freshwater mussels, it is documented in fishes (Gilk et al. 2004; Goldberg et al. 2005). For example, outbreeding increased the vulnerability of hybrid largemouth bass (*Micropterus salmoides*) to infectious disease; thus, a lowered fitness may create susceptibility to new diseases in the wild (Goldberg et al. 2005). However, increasing the genetic diversity within populations may be beneficial if it increases resiliency to extreme climactic events, as demonstrated in marine systems (Reusch et al. 2005). A different approach targets breeding across strains to produce heterosis hybrids with favorable traits (Crespel et al. 2012). Targeted release of species strains with traits that can withstand variable environmental conditions (e.g., temperature, drought tolerance) may further aid in resiliency to climate changes, a concept already under development with agricultural crops (Kilasi et al. 2018) and excluded from consideration in this decision framework.

Dwarf Wedgemussel

The watershed size used to represent a Dwarf Wedgemussel population status varied within the five-year review; thus, to complete the open-loop process at a consistent HUC12 watershed scale, we applied population statuses listed in the USFWS five-year review (USFWS 2019) to the HUC12s that comprised these larger and varying watershed sizes within the Connecticut and Delaware River basins (Table 1). We mapped all HUC12s (Figure 2) with their associated population statuses labeled as “viable”, “unknown” or “likely extirpated”. We eliminated watersheds containing viable populations, since they do not need restorations, and watersheds with an “unknown” population status. Unknown populations could be considered by practitioners in the future, but we did not have the information to warrant following these watersheds through the decision process. The remaining two watersheds (Outlet Webatuck Creek and Headwaters Webatuck Creek in the Housatonic River basin in the states of New York and Connecticut) that were “likely extirpated” were further evaluated within the open-loop process (Table 2).

2. Is the watershed outside the species indigenous range?

A watershed outside of the target species indigenous range (= the known or inferred distribution generated from historical written or verbal records, or physical evidence of the species’ occurrence; IUCN 2013) and without fundamental habitat needs would not be a candidate for mussel population restoration. It is at the discretion of the decision maker to determine the HUC size relevant to a reintroduction within the range of occurrence records. For example, occurrence records within a HUC12 or a HUC2 may be considered indigenous range dependent on the species local (endemic) or global distribution. Fundamental habitat includes specific water quantity, water chemistry, and sediment stability (Strayer 2008). While some mussel species can persist during dewatering events or droughts by burrowing vertically, all mussels require water to survive. Selecting watersheds that stochastically dewater or are devoid of habitat refuges (i.e., deeper pools that stay wetted) and require mussels to burrow vertically to survive may increase physiological demands and decrease overall mussel fitness (Archambault et al. 2013). Watersheds prone to dewatering events may be important to consider only if no other hydrologically stable watersheds are available. It is also critical that rivers have water chemistry that support mussel growth and survival. Mussels secrete a calcium shell; thus, water pH levels that dissolve shell material are not suitable habitats for mussels. For example, shell dissolution for the Duck Mussel (*Anodonta anatina*) occurred at pHs below 3.9 in a laboratory study in Finland (Mäkelä and Oikari 1992).

Introducing populations outside their current distribution may be considered in the context of assisted colonization. Assisted colonization is the planned introduction of a population beyond its current distribution where the climate is expected to become unsuitable into new locations where the taxon is expected to persist under future climatic conditions (Seddon 2010). Environmental variability can push species distributions to the edge of their known geographic range; thus, to avoid extinction, assisted colonization is a method to support species persistence. While assisted colonization is also considered for restoring ecosystem function (Lunt et al. 2013), we only consider it here for the purpose of rare species conservation.

Assisted colonization is a debated tactic to conserve biodiversity under changing climactic conditions (Brodie et al. 2021; Ricciardi and Simberloff 2009). Opponents to assisted colonization emphasize the limited understanding of total impacts caused by introduced species (Ricciardi and Simberloff 2009). Furthermore, assisted colonization may pay too little attention to evolution and place too much confidence in risk assessment (Ricciardi and Simberloff 2009). Potential negative effects from assisted colonization include species becoming invasive and competition for native species for resources (Purse et al. 2005). However, there may be more harm caused to species biodiversity by ignoring the option of assisted colonization and taking a route of inaction under the current changing climactic conditions (Brodie et al. 2021). Acknowledging uncertainty around assisted colonization for freshwater mussels is warranted given the lack of literature and case studies. The ongoing discussion around introduced fish (Vitule et al. 2009) may help to inform this field for freshwater mussels.

Dwarf Wedgemussel

We referenced the distribution of Dwarf Wedgemussel in the most current 5-year review (USFWS 2019). Records from the 5-year review indicate Outlet Webatuck Creek and Headwaters Webatuck Creek are both within the species indigenous range, thus we answered “no” to Question 2 (is the watershed outside the species indigenous range?) and continued to Question 4 (Table 2).

3. Are there mussels that co-occur with the target species (Skip question if answered “no” to Question 2)?

Mussels can occur in assemblages that are similar among rivers; a watershed may be a candidate for restoration if it has mussel species that are commonly found with the target species. Mussel assemblage composition may be related to shared host fish use (Haag and Warren 1998) or shared use of macrohabitat and biogeographical factors (Strayer 1993) including river size (Christian et al. 2021). Regardless of the underlying mechanism that contributes to supporting similar mussel assemblages, presence of mussels that co-occur with the target species may indicate habitat suitability.

Dwarf Wedgemussel

We skipped question three because we answered “no” to Question 2.

4. Does property ownership limit access?

Property ownership can limit stream access within a watershed; a watershed that lacks stream access may not be logistically feasible to conduct population restoration. Military operations, mining areas, or a drinking water supply area can prohibit trespassing and repeated site visits. If an agreement confirms that long-term access to a site is granted, then this concern may be negligible and potentially even beneficial since private property access could limit tampering from the public. Use of private property to access sites is at the discretion of the decision maker. In circumstances where logistics (e.g., long distance to access the stream from a road) or permission limit repeated or long-term access to sites, then logistically the watershed is not practical to include.

Dwarf Wedgemussel

To address watershed access in Outlet Webatuck Creek and Headwaters Webatuck Creek we inspected property ownership using the New York State Tax Parcel Access website (https://gis.dutchessny.gov/parcelaccess/) for Dutchess County. We further assessed road-stream crossings using Google Earth Engine. In the lower section of Outlet Webatuck Creek there is access around Leedsville, NY. Headwaters Webatuck Creek has river access along Mill Road in the town of North East, NY and there is a rail trail that crosses the creek several times. Thus, for both watersheds we answered “no” (property ownership does not limit access) and continued to Question 5 (Table 2).

5. Is the river flow controlled by dams?

Dams alter the natural flow regime, temperature, nutrient cycling, and sediment distribution both upstream and downstream of the infrastructure (Poff et al. 1997; Gabriela and Wüest 2002; Zaidel et al. 2021). When dams negatively affect ecological flows, they may not be adequate restoration watersheds. The differential impacts caused by dams may depend on the dam’s location in the watershed and underlying geology of the watershed (Poff et al. 1997). Likewise, how a dam is managed can greatly impact ecological effects to the aquatic community (Nagrodski et al. 2012).

Reservoir management and use directly impacts freshwater mussels. In one study, abundant and diverse mussel assemblages were compared downstream of reservoirs with different management objectives (Galbraith and Vaughn 2011). The Pine Creek reservoir in the Little River in southeastern Oklahoma mimics the natural flow regime and is used for flood control, municipal water supply, and recreation. The Broken Bow reservoir, also on the Little River in southeastern Oklahoma, is a hypolimnetic release dam that generates hydroelectric power and releases cold water during warmer months to support a stocked trout fishery. Lower mussel population density, higher hermaphroditism and parasitism rates, and reduced body condition were reported downstream of the dam with unnatural flow regimes (Broken Bow) compared to the reservoir that mimicked the natural flow regime (Pine Creek) (Galbraith and Vaughn 2011).

If reservoir management is modified to more closely mimic natural flow and better support the aquatic community, then the habitat may support mussel re-establishment. For example, adjustment to minimum flows at the Douglas Dam on the French Broad River (Tennessee River drainage system) and reaeration of discharged water improved habitat in the tailwater to support increases in fish diversity, and several mussel species naturally re-established following these management changes (Layzer and Scott 2006). Based on the mussel assemblage prior to dam installation and their lack of natural recolonization, an additional 19 species were translocated to the river. Multi-year follow up surveys indicated high survival and reproduction in at least one species (Layzer and Scott 2006). Therefore, rivers that have targeted dam management to support aquatic restoration may still provide habitat for mussel species.

The stable habitats created by dams may provide benefits to mussels. River reaches directly below or above dams can be colonized by rare or endangered mussel species and serve as habitat refuges (Gangloff 2013; Sousa et al. 2021). Habitat suitability likely varies among dam sites based on watershed and dam characteristics; thus, mussel assemblages around dam sites also may vary in species composition (Barnett and Woolnough 2021). Mussel translocations are regularly employed when removing a dam supporting rare species (Pires et al. 2021); however, if the dam is stable and has created unique habitat, (e.g., stable geomorphology, increased food availability; Singer and Gangloff 2013), it may provide conservation value if left in place or serve as unique experimental habitat for a population restoration.

Dwarf Wedgemussel

We used the National Inventory of Dam (NID) website (https://nid.usace.army.mil/#/; accessed September, 2022) to inspect the Outlet Webatuck Creek and Headwaters Webatuck Creek watersheds for dams that may impact flows. Based on the NID website, neither watershed had mapped dams (although there are likely small, unmapped dams; Magilligan et al. 2016). We answered “no”—indicating that both watersheds are not flow controlled by dams—and continued to Question 6 (Table 2).

6. Are there known water pollutants?

Watersheds where there are known chemical stressors, such as point source discharges or pollution inputs, may be locations to avoid during mussel restoration. Examples of contaminants include sewage, mining waste, and industrial effluents (Armon and Starosvetsky 2015). Effluent discharged from municipal wastewater treatment plants (WWTPs) (Yu et al. 2013), stormwater sewers (Zgheib et al. 2012), and failed septic systems (James et al. 2016), can contain contaminants that are known to affect mussels’ growth and survival (Gillis et al. 2014; Nobles and Zhang 2015). For example, effluents may contain metals, pharmaceuticals, personal care products, macronutrients, and endocrine disrupters. The diversity of compounds and concentrations can affect toxicity to organisms through impairing biological functioning and altering the overall water chemistry that can cause shifts in aquatic communities (Eggen et al. 2014). Point source effluents, like those from WWTPs can be linked to mussel abundance or condition. In the Grand River in Ontario, Canada there were lower mussel abundances below point source WWTP effluent relative to above the source (Gillis et al. 2017) and in the same river, after 4 weeks, caged Flutedshell (*Lasmigona costata*) exhibited higher stress and alterations to biological functioning downstream of a WWTP (Gillis et al. 2014). In Wilbarger Creek in the state of Texas, Caged Threeridge (*Amblema plicata*) demonstrated reduced survivorship and growth downstream of effluent compared to upstream (Nobles and Zhang 2015). While contaminants from WWTPs vary by point source, correlations generally indicate negative mussel responses to effluent exposure.

Ammonia (NH_3), which naturally degrades from nitrogenous organic matter, is common in outfalls from wastewater and WWTPs (Goudreau et al. 1993) and is particularly toxic to multiple life stages of freshwater mussels (Wang et al. 2007; Wang et al. 2008; Kleinhenz et al. 2018). Because of freshwater mussels’ sensitivity to ammonia, a database was developed to compile ammonia toxicity for glochidia and juveniles of 10 species across 8 genera, including 30 LC50s (median lethal concentration) for acute (24-96 h) ammonia exposure (Augspurger et al. 2009). Acute values that were combined for mussel genera ranged from a mean of 2.56 to 8.97 mg/L total ammonia as N (Augspurger et al. 2009); however, some species were more sensitive to ammonia than others. A separate study found the LC50 of unionized ammonia for Rainbow mussel [*Cambarunio (Villosa) iris*] was 0.11 mg/L NH_3-N and for Wavyrayed Lampmussel (*Lampsilis fasciola)* was 0.26 mg/L NH_3-N (Mummert et al. 2003). If available, information on ammonia levels may be particularly important to understanding a watersheds potential to support mussel population restoration.

Organic compounds like endocrine disrupters found in effluent from stormwater sewers, failed septic systems, and WWTPs, can negatively affect aquatic organisms by altering fertilization and survival rates, as shown for fishes (Harris et al. 2011; Jobling 2012). While effects of endocrine disrupters are less studied on freshwater mussels, these chemicals have resulted in severe biological stress responses that alter mussels’ physiological functioning (Falfushynska et al. 2014). Research with Fluoxetine (a common antidepressant) caused nonviable larvae in female Eastern Elliptio, stimulated lure display in Wavyrayed Lampmussel and Plain Pocketbook, and stimulated release of spermatozeugmata in Eastern Elliptio (Bringolf et al. 2010).

Dwarf Wedgemussel

Although neither watershed has WWTP effluent (based on inspection of EPA StreamCat data for National Pollutant Discharge Elimination Systems; Table 2), pollutants from wastewater (i.e., failed septic tanks with leach fields) and storm sewers may degrade water quality in the Headwaters Webatuck Creek and reduce habitat quality for Dwarf Wedgemussel. In the Ten Mile River Watershed Management Plan (HVA 2018), a water quality assessment found slightly higher nitrate levels in the Headwaters Webatuck Creek than most other sampled areas in the larger Ten-Mile River watershed (HVA 2018). The site in Headwaters Webatuck Creek also had relatively high ammonia (0.73 mg/L) as compared to other sites sampled in July 2018. Because of the complicated nature of ammonia toxicity (dependent on water hardness, temperature, and pH), it is difficult to determine if this ammonia concentration is acutely toxic to Dwarf Wedgemussel but is approaching the 1.9 mg/L continuous water quality criterion and the chronic (28 day) mean lethal concentrations for two freshwater mussel genera (*Lampsilis*, *Villosa*; US EPA 2013). Given the lack of information on ammonia toxicity to Dwarf Wedgemussel or the genus *Alasmidonta*, we referenced reported chronic juvenile mussel survival data (US EPA 2013; Wang et al. 2007) and determined this ammonia level (0.73 mg/L) is too close to the 28-day chronic lethal threshold for freshwater mussels and would likely cause chronic physiological affects to Dwarf Wedgemussel. Because the samples in Headwaters Webatuck Creek posed a high level of ammonia, we eliminated this watershed, and moved on to Question 7 in the open-loop process with only Outlet Webatuck Creek.

7. Does watershed land use negatively impact habitat?

Stocking mussels in watersheds with a high proportion of anthropogenic land use can result in acute mussel mortality or chronic effects that influence long-term survival of individuals, thus reducing the feasibility for watershed restoration (Gillis 2012; Gillis et al. 2014). Urban or residential growth, deforestation, and agriculture are known threats to freshwater mussels. Although urban development and agricultural land use can affect streams differently, both types of land use can alter mussel habitat to a state that negatively affects mussel populations persistence (Brown et al. 2010; Poole and Downing 2004).

Agricultural land use can negatively affect mussel richness, abundance (Daniel and Brown 2013), and growth (Haag et al. 2019), suggesting that a high amount of agricultural land use in a watershed may be problematic for restoration. During a resurvey of streams in Iowa, where the landscape was converted from prairies and riparian woodlands to intensive agriculture, there was a loss of 7 species (from 22 species down to 15 species) and all mussel species were extirpated from 47% of the river reaches surveyed (Poole and Downing 2004). Watersheds that had higher habitat conversion to farmland exhibited greater losses in mussel richness, potentially related to high siltation and the lack of wooded riparian buffers (Poole and Downing 2004). As such, high levels of agricultural land use can limit watershed restoration potential.

Mussel populations downstream of cities can exhibit physiological oxidative stress (Gillis et al. 2014) and a lower body condition (Gillis 2012) when compared to mussels upstream of cities. Physical modification of in-stream channels associated with urbanization through channelization can harm mussels by creating flow alterations. Mussels' complex life cycle lends both adult and juvenile mussel adaptations to flows that not only sustain their food and oxygen, but also provide suitable habitat for their host fish (Gates et al. 2015). Freshwater mussel survival may be negatively impacted by salinization resulting from road runoff of deicers or eutrophication caused from overland runoff of fertilizers (Patzner and Müller 2001; Beggel and Geist 2015). Identifying specific reasons behind urbanization impacts to freshwater biotic integrity is challenging, but in watersheds where practitioners consider urbanization to negatively impact mussel persistence, freshwater mussel restoration may be impractical.

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We assessed agricultural land use and urban development in Outlet Webatuck Creek by referencing the Ten Mile River Watershed Management Plan (HVA 2018) and by calculating watershed land cover using the 2019 National Land Cover Database (NLCD) (Dewitz 2021). The HVA plan labeled waters within Outlet Webatuck Creek as impaired for recreational use due to elevated *Escherichia coli* bacteria concentrations, specifically within Mill Brook tributary. *Escherichia coli* can indicate high levels of agriculture. We summarized development area over the four classifications in NLCD (high, medium, and low intensity; open space; see NLCD for definitions) and summarized agricultural area in two classifications (hay/pasture, cultivated crops; see NLCD for definitions). The percent development in the watershed was 5.3 while the percent agriculture was 24.8, supporting the HVA Plan's description of agricultural land use in the watershed. Because of the described *E. coli* levels and agricultural practices within river floodplains, we answered 'yes' that watershed land use negatively impacts habitat, thereby eliminating Outlet Webatuck Creek from further consideration for mussel restoration (Table 2). This land use and associated impaired water quality would likely not support Dwarf Wedgemussel persistence.

8. Are there detrimental invasive species?

Watersheds with a high number or abundance of invasive or nonnative species including crayfishes, the Zebra Mussel (*Dreissena polymorpha*), and Asian clams (*Corbicula* spp.) may negatively affect the survival of native mussels and the watersheds restoration potential. In a laboratory experiment the European invasive Signal Crayfish (*Pacifastacus leniusculus*) caused greater shell damage during predation on freshwater mussels than the native Noble Crayfish (*Astacus astacus*) (Dobler and Geist 2022). Invasive crayfish can also predate on juvenile mussels by cracking their shell, shown from laboratory experiments and *in situ* at field sites (Machida and Akiyama 2013; Sousa et al. 2019). Invasive crayfish may preferably predate on different species of adult mussel (regardless of mussel thickness; Dobler and Geist 2022) based on the crayfish's ability to hold the mussel; in this way the crayfish damage the adult mussel's tissue at the shell margin, resulting in injury and possible mortality (Machida and Akiyama 2013). In a different study conducted in a laboratory, non-native Rusty Crayfish (*Faxonius* (*Orconectes*) *rusticus*; collected from Webatuck Creek, Dutchess County, NY) outcompeted native Spinycheek Crayfish (*Faxonius* (*Orconectes*) *limosus*; collected from the Neversink River, Orange County, NY and the East Branch of the Wappinger Creek, Dutchess County, NY) for shelter and bivalve food (Klocker and Strayer 2004), further suggesting that displacement of native crayfish species to invasive crayfish species may result in higher freshwater mussel mortality.

The Zebra Mussel is a biofouling organism that attaches to the shells of native mussels impacting feeding and respiration, eventually causing a lower physiological condition and mortality (Haag et al. 1993). In addition to physically fouling native mussels, Zebra Mussels are more efficient than Unionidae in extracting nutritious particles, leaving lower quality food sources for native mussels (Baker and Levinton 2003). Lakes and streams in the U.S. with high Zebra Mussel densities (>3200 m^2), have experienced extirpation of native mussel populations within 4–8 years (Ricciardi et al. 1998). Zebra Mussels may be limited in range because of their calcium requirements; they may be unable to establish at calcium levels under 12 mg/L and in areas of hard water where pH is under 7.4 (Strayer 1991; Neary and Leach 1992; Cohen and Weinstein 2001), so they are likely only a concern in some areas.

Asian clams (*Corbicula* spp.) were introduced to the U.S. around 1950 and have since spread throughout South America, Europe, and North Africa where they impact benthic communities in streams and rivers (Ferreria-Rodríguez et al. 2018). The level of impact of Asian clams on native mussels is likely dependent on the abundance of both fauna groups (Vaughn and Spooner 2006; Haag et al. 2020). A negative relationship existed between Asian clam abundance and native mussel abundance within small habitat patches (0.25 m^2), whereby high abundances of native mussels occurred at low abundances of Asian clams (Vaughn and Spooner 2006). The ability for Asian clams to establish likely decreases as abundance of native mussels increases (Vaughn and Spooner 2006). A separate study found that a native mussel species, *Unio delphinus*, had lower growth, physiological condition, and higher locomotor activity at higher densities of Asian clams (Ferreria-Rodríguez et al. 2018). Similarly, Asian clam abundance negatively impacted growth across four freshwater mussel species in a Kentucky stream (Haag et al. 2021). Asian clam populations can exhibit rapid die-offs due to silt loading from flooding, temperature extremes, and low dissolved oxygen during low water flows (Strayer 1999). During Asian clam die-offs, low dissolved oxygen and high ammonia associated with decaying tissue can cause toxic conditions for native mussels (Cherry et al. 2005).

9. Are there host fish?

Host fish are essential for most mussel species to complete their life cycle, and thus their presence and abundance may be vital when considering watershed restoration. Mussels' specialization toward host fish varies; some species can use multiple fish species to metamorphose their glochidia into juveniles while other mussels specialize on one or a few fish species (Barnhart et al. 2008). The co-existence of mussels with their hosts is essential for their survival. For example, the extirpation of the federally endangered Dwarf Wedgemussel in Canada is attributed to the construction of the Moncton-Riverview causeway that resulted in loss of one of the mussels' potential hosts in the Petitcodiac River system in New Brunswick, the American Shad (*Alosa sapidissima*) (Department of Fisheries and Oceans Canada 2007).

Fish density may affect successful glochidia attachment, depending on the mussel's mode of glochidia transfer. In the Sipsey Fork and Brushy Creek drainages in the state of Alabama, densities of mussels without elaborate host attracting mechanisms (but species that do not freely broadcast glochidia) were positively correlated with host fish densities (Haag and Warren 1998). In the same study densities of host specialist mussels with elaborate host-attracting mechanisms (i.e., display lures that imitate fish prey) and broadcasting host-generalist mussels were independent of host fish densities (Haag and Warren 1998). In some areas, non-native fish species are stocked to rivers with mussels for recreational purposes, potentially increasing overall fish density and glochidia encounter. However, stocking of fish may not result in higher overall glochidia attachment. For example, the Duck Mussel, which can use multiple species as hosts, was able to attach to native fish species better than non-native fish species (Douda et al. 2013). Therefore, increasing the density of non-native fish species may negatively impact overall mussel recruitment.

The absence of host fish from a watershed may prevent mussels from completing their life cycle, creating unsuitable mussel stocking conditions (Watters 1996; Brainwood et al. 2008). A reduced probability of mussel-host encounter could result from in-stream barrier impediments limiting the distribution of long-distance dispersal fish hosts or disturbances that result in local extinctions of fish hosts (Fritts et al. 2012; Vaughn 2012; Galbraith et al. 2018). In a study that analyzed mussel traits related to larval dispersal, local extinction rates were partly predicted by the primary host group (=most frequent host from the literature; Vaughn 2012). Mussels with highest extinction rates used Gar (*Lepisosteidae* spp.), Drum (*Sciaenidae* spp.), and Tessellated Darter (*Etheostoma olmstedi*) as hosts. Mussels dependent on Gar and Drum may have higher extinction rates because these fish swim long distances and barriers prohibit travel throughout the stream (Vaughn 2012). For mussels that use Tessellated Darter as hosts, high extinction rates may be from the small home range of darters that limits their recolonization (Vaughn 2012).

10. Are there mussel pathogens?

Mussel diseases are understudied in the literature and thus difficult to identify (Waller and Cope 2019); however, speculation that mussel die-offs are related to disease outbreaks suggests that the presence of mussel pathogens are an important consideration prior to stocking. Mortality events affecting mussels (and no other aquatic fauna) with no link to water quality and no preemptive mussel stress response suggest potential mussel pathogens. Unexplained mortality events were reported in six U.S. rivers between 1977 and 1986, and more recently (2014 and 2018) there are reports of mussel declines in the Pacific Northwest within the states of Oregon, Washington, California, and Idaho (Waller and Cope 2019). The Western Pearlshell (*Margeritifera falcata*) mussel experienced die offs in the state of Washington (Brenner 2005; Thomas 2008) and mussels relocated from unaffected sites to affected sites died similarly with no sign of stress (Thomas 2008). Similar unexplained mortality events occurred in Sweden with the Eastern Pearlshell (*Margaritifera margaritifera*) (Wengström et al. 2019). Potential pathogens that cause mussel disease outbreaks include viruses, fungi, protozoa, and metazoans (Carella et al. 2016). In China one viral disease was identified in farmed *Hyriopsis cumingii* referred to as Lea Plague Virus (HcPV) (Zhong et al. 2011). In the Clinch River (within the states of Virginia and Tennessee) a study assessed the cause of mass mortality in wild populations of Pheasantshell (*Actinonaias pectorosa*; syn: *Ortmanniana pectorosa*) and out of 17 viruses tested, only *Clinch densovirus* 1 had higher prevalence and load in an experimental case group relative to a control group (Richard et al. 2020). The uncertainty around mussel diseases stems from their understudied nature and lack of baseline pathogens that mussels host in the wild (Richard et al. 2020). Some documented die-offs were associated with increased water temperature or gravidity (Waller and Cope 2019), instigating hypotheses that other factors (e.g., changing environmental conditions) could physiologically stress mussels, thus enhancing susceptibility to infection and allowing common pathogens to cause infectious disease and mortality (Richard et al. 2020).

11. Is there planned watershed development?

As described previously (Question 7), alteration of land use within a watershed is a primary driver affecting loss of mussel populations through habitat degradation (Downing et al. 2010); thus, proposed plans to urbanize a watershed may be a reason not to stock mussels. Urban development alters river hydrology and increases concentrations of nutrients, sediments, and pollutants (Paul and Meyer 2001; Walsh et al. 2005). In the Line Creek watershed in Atlanta, Georgia, an increase in impervious surface was associated with mussel habitat degradation and a 50–70% species loss (Gillies et al. 2003). While urbanization (as area of impervious surface) alone does not cause mussel mortality, it serves as a proxy for multiple factors that can cause mussel species loss (Gillies et al. 2003).

12. Do climate forecasts negatively impact mussel habitat?

Climate change can impact the natural flow and thermal regimes of a river, which in turn can affect mussel survival (Luck and Ackerman 2022; Said and Nassar 2022). Forecast modeling predicts changes in temperature and flow associated with precipitation, runoff, groundwater, and evapotranspiration; areas predicted to have adverse climate-induced changes to mussel habitat may not be good stocking locations. Assessing variation in sub-watersheds across a larger HUC unit may be beneficial to compare where climate-predicted changes are most extreme. For example, in the Connecticut River watershed, evapotranspiration attributed to rising temperatures had no change in some subbasins, whereas other subbasins exhibited increases of up to 62 mm (Tsvetkova and Randhir 2019). Almost half of the Connecticut River's watershed area is expected to have a decrease in groundwater discharge (-480 to 0 mm) from years 1960 to 2100, yet there are areas where groundwater is projected to increase (by up to 389 mm) (Tsvetkova and Randhir 2019). Climate-induced hydrological changes may be particularly problematic for freshwater mussels by destabilizing sediment during floods or drying river reaches during droughts.

If climate-induced stream temperature predictions exceed the thermal tolerance of mussels, the watershed may not be suitable for restoration. Temperature is fundamental to mussel growth and reproduction (Pandolfo et al. 2010; Schneider et al. 2018), and climate predictions indicate temperature increases in some watersheds (Morrison et al. 2002; Tsvetkova and Randhir 2019; Hosen et al. 2019). While temperature needs to meet thresholds that support glochidia release (Schneider et al. 2018), if rivers approach or exceed thermal tolerance for any life stage of the mussel—glochidia (Khan et al. 2019), juvenile (Sangsawang et al. 2019), or adult (Ganser et al. 2015)—then risk of thermal stress to the mussel or mussel mortality increases. Regional information on predicted future stream water temperature may be helpful for assessing watersheds for restoration.

Discussion

Reflection on the open-loop process

We found making assessments in the open-loop process was relatively straightforward, except when there were varying levels of impact from a stressor within one question. For these questions (e.g., land use in Question 7), it was challenging to know at what level the impact will negatively affect mussel persistence, resulting in uncertainty in the decision process about whether to continue in the loop or eliminate the watershed. Despite this uncertainty, the open-loop process allowed us to advance and ultimately eliminate both subwatersheds based on gathered information that indicated poor habitat for Dwarf Wedgemussel.

We began this process by compiling resources that were nationally available, but upon further investigation, we found local resources to be the most helpful when assessing the subwatersheds. While moving through the open loop we were surprised at the number of local resources and the number of collaborators already invested in the watersheds and their recovery. The amount of information this provided was likely a best-case scenario for moving through the process and we realize the extent of available information at the local level could be lacking for other watersheds. Most of the local resources we found by searching the internet to better understand the area and the stakeholders (e.g., The Ten Mile River Collaborative, Cary Institute for Ecosystem Studies, Housatonic Valley Association, New York State Department of Environmental Conservation, Connecticut Department of Energy and Environmental Protection, Dutchess County Planning Department, and Northwest Hills Council of Governments) involved in restoration.

Using local resources may also provide insight towards future opportunities to collaborate with stakeholders. Understanding stakeholder objectives for watershed restoration may result in opportunities to combine available resources for restoration. For example, the Ten Mile River Management Plan (that contains Outlet Webatuck Creek and Headwaters Webatuck Creek) acknowledged habitat needs for the Bog Turtle (*Glyptemys muhlenbergii*) (HVA 2018), yet nowhere in the plan was Dwarf Wedgemussel mentioned. If the Housatonic Valley Association knew Dwarf Wedgemussel historically occurred in the watershed, then it may facilitate restoration efforts targeted at the species' habitat and its host fish. Discovering and capitalizing on opportunities to work with the numerous stakeholders in a watershed (like the Housatonic Valley Association) may be ideal when looking to combine resources to further restoration in a watershed.

While the open-loop process includes multiple questions that are important to consider before mussel population restoration within a HUC12, it omits other temporal aspects, such as mitigated threats, legacy effects, and planned conservation activities. The Ten Mile River Watershed Management Plan references numerous planned activities aimed at restoring the watershed, including implementing best management practices for farming and riparian planting (HVA 2018). Given that Headwaters Webatuck Creek was eliminated as a potential restoration site due to impaired water quality, successful management of the impacts may be a good reason to reconsider this watershed for mussel population restoration. Furthermore, some threats in the watershed have already been mitigated; for example, moving a highway department salt supply pile out of the river floodplain (HVA 2018). Although threats may be mitigated in watersheds, there still could be legacy effects that persist that negatively impact habitat or water quality. However, determining the cause of population declines or extirpations is sometimes infeasible. In a meta-analysis with geographically international coverage, 48% of studies could identify a cause behind mussel population declines, but in most studies, there was no causal mechanism (Downing et al. 2010). Thus, it is left to the discretion of the manager to determine whether known mitigated threats are sufficient to proceed with restoration. Continued restoration in the two example watersheds we considered in this framework, Outlet Webatuck Creek and Headwaters Webatuck Creek, may create suitable Dwarf Wedgemussel habitat within the coming years and thus both watersheds may be important to consider in the next 5-year review.

Meeting legal requirements for freshwater mussel population restoration is an important aspect not considered in this document. Legal requirements may depend on species listing status (i.e., federal or state), individual state regulations, and management within the specific watershed (i.e., drinking water supply area, conservation land, public land). While we are unable to discuss all varying legal aspects, we acknowledge that acquiring permits and approvals to reach legal compliance may be important prior to beginning the watershed selection process, or after selecting a watershed in instances where specific geographic requirements are necessary.

Watershed prioritization and river reach identification

If multiple watersheds are considered acceptable for mussel restoration (i.e., no problems are revealed in the 12 questions), then prioritizing among them may be necessary. To prioritize watersheds the quality of the watershed could be assessed using information from the 12 questions. For example, proportions of intact, forested land cover could be compared across watersheds. Alternatively, other factors like comparing the connectivity among free flow river reaches (i.e., dam density) or logistic feasibility may be included to prioritize watersheds.

Selecting a watershed geographically that is most efficient for sampling logistics (i.e., distance to travel) or to maximize resources available among multiple stakeholders may be the most reasonable method in selecting a watershed to move forward with restoration.

Once a watershed is selected for restoration, the next step is locating a section within the river to collect data or potentially release mussels. Ideal reaches would stay watered, exhibit low or moderate flows that lack streambed scour, and sediment that supports mussel burrowing yet is non-mobile. Furthermore, river reaches for successful restoration must have adequate food quantity to support a population and be connected to areas with potential host fishes. Useful information on species habitat may include the stream order (i.e., big river versus small tributary), flow (i.e., riffle or pool), substrate type (i.e., cobble or sand), or information on mussel species that co-occur with the target species and may indicate potential habitat. Habitat information on suitable river reaches for restoration could be collected using a rapid habitat assessment protocol (e.g., Sterrett et al. 2018; Skorupa 2022). Once a river section is located, other site-specific information could be collected, like the fish assemblage, water quality, and temperature variability. Prior to freely releasing mussels, they may be housed in silos or cages to collect information on growth and survival (Haag et al. 2019) and food availability for growth (Skorupa 2022). It may be necessary to test multiple river reaches within a HUC12 to determine the best area for release. Site selection within a watershed is equally as important as the watershed selection.

Two primary limitations to rare mussel reintroductions are a lack of information and monetary resources. The process outlined above, although relatively basic, may inform restoration of a rare species because it works within these bounds of limited information and monetary resources. Furthermore, because the Dwarf Wedgemussel is federally endangered, its rarity limits understanding of potentially useful information (e.g., habitat, host fishes) when selecting a watershed for restoration. Despite information constraints, we found that by applying this simple process using freely available resources, we were able to obtain a general understanding of two watersheds and their potential for restoration. We stress that a lack of information encountered during this process does not derail an individual’s ability to move forward with restoration; this open loop is intended as a guide and individuals may apply best professional judgement when considering decisions and determining whether to move forward. This simple process may be useful when applied or adapted to other rare mussels and aquatic species.

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Data Availability

No data were created for this project. Information on Dwarf Wedgemussel populations used in this report came from: U.S. Fish and Wildlife Service, 2019, Dwarf Wedgemussel (*Alasmidonta heterodon*) 5-Year Review: Summary and Evaluation, available at: https://www.nrc.gov/docs/ML1428/ML14286A003.pdf.

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Tables

Table 1: The population status of Dwarf Wedgemussel (*Alasmidonta heterodon)* for each Hydrologic Unit Code 12 (HUC12) subwatershed and larger Hydrologic Unit Code 8 (HUC8) subbasin in the Connecticut and Delaware River basins, based on USFWS (2019). A population status of "extirpated" indicates "likely extirpated". In the "State" column, CT = Connecticut, MA = Massachusetts, NY = New York, PA = Pennsylvania, and NJ= New Jersey.

5 Year review waterbody	Referenced HUC12 in Figure 2	HUC 8	Population status	State
Farmington River	Nod Brook-Farmington River	Farmington	Unknown	CT
Farmington River	Mill Brook-Farmington River	Farmington	Unknown	CT
Farmington River	Salmon Brook	Farmington	Unknown	CT,MA
Neversink	Middle Neversink River	Middle Delaware-Mongaup-Brodhead	Unknown	NY
Middle Delaware	Twin Lakes Creek-Delaware River	Middle Delaware-Mongaup-Brodhead	Unknown	NY,PA
Neversink	Neversink River	Middle Delaware-Mongaup-Brodhead	Unknown	NY
Neversink	Upper Neversink River	Middle Delaware-Mongaup-Brodhead	Unknown	NY
Neversink	Lower Neversink River	Middle Delaware-Mongaup-Brodhead	Unknown	NJ,NY
Middle Delaware	Harihokake Creek-Delaware River	Middle Delaware-Musconetcong	Unknown	NJ,PA
Pequest River, Lake Aeroflex (syn: New Wawayanda Lake)	Upper Pequest River	Middle Delaware-Musconetcong	Unknown	NJ
Pequest River, Lake Aeroflex (syn: New Wawayanda Lake)	Middle Pequest River	Middle Delaware-Musconetcong	Unknown	NJ
Pequest River, Lake Aeroflex (syn: New Wawayanda Lake)	Lower Pequest River	Middle Delaware-Musconetcong	Unknown	NJ
Middle Delaware	Shingle Kill-Delaware River	Middle Delaware-Mongaup-Brodhead	Unknown	NJ,NY,PA
Middle Delaware	Hornbecks Creek-Delaware River	Middle Delaware-Mongaup-Brodhead	Unknown	NJ,PA

Middle Delaware	Paunnacussing Creek-Delaware River	Middle Delaware-Musconetcong	Unknown	NJ,PA
Middle Delaware	Pidcock Creek-Delaware River	Middle Delaware-Musconetcong	Unknown	NJ,PA
Webatuk Creek	Headwaters Webatuck Creek	Housatonic	Extirpated	CT,NY
Connecticut River	Stoughton Brook-Connecticut River	Outlet Connecticut River	Unknown	CT
Webatuck Creek	Outlet Webatuck Creek	Housatonic	Extirpated	CT,NY
Podunk River	Podunk River	Outlet Connecticut River	Unknown	CT
Webatuck Creek	Ten Mile River	Housatonic	Unknown	CT,NY
Paulins Kill	Upper Paulins Kill	Middle Delaware-Musconetcong	Viable	NJ
Paulins Kill	Middle Paulins Kill	Middle Delaware-Musconetcong	Viable	NJ
Big/Little Flat Brook	Flat Brook	Middle Delaware-Mongaup-Brodhead	Viable	NJ
Muddy Brook, Philo Brook	Muddy Brook	Outlet Connecticut River	Viable	CT,MA
Stony Brook, Philo Brook	Stony Brook	Outlet Connecticut River	Viable	CT

Table 2: Table with questions that relate to the open loop process in Figure 1, and associated answers for the Outlet Webatuck Creek and Headwaters Webatuck Creek in Dutchess County, in the states of New York and Connecticut (Figure 2; watersheds in red with the label "likely extirpated"). Sources are local to the watersheds or are available nationally.

Question No.	**Outlet Webatuck Creek**	**Headwaters Webatuck Creek**	**Sources**
1. Does the watershed contain viable populations of target species?	No	No	5-year review (USFWS 2019)
2. Is the watershed outside the species indigenous range?	No	No	5-year review (USFWS 2019)
3. Are there mussels that co-occur with the target species (Skip question if answered "no" to Question 2)	Skip	Skip	Skip question
4. Does property ownership limit access?	No	No	NYS Tax Parcels www.gis.ny.gov/parcels/ | Google search the watershed name
5. Is the river flow controlled by dams?	No	No	National Inventory of Dams (NID) www.nid.usace.army.mil/#/ | USDOT Dam Layer www.data-usdot.opendata.arcgis.com
6. Are there known water pollutants?	No	Yes	NYS State Pollution www.dec.ny.gov/25.html | Google for each watershed "point source discharge" OR "wastewater treatment plant" | EPA StreamCat Dataset documenting National Pollutant Discharge Elimination Systems https://www.epa.gov/national-aquatic-resource-surveys/streamcat-dataset | NYS DEC State Pollutant Discharge Elimination System www.dec.ny.gov/permits/6054.html | Ten Mile River Watershed Management Plan (HVA 2018)
7. Does watershed land use negatively impact habitat?	Yes	-	National Land Cover Dataset (CONUS) www.mrlc.gov/data/nlcd-land-cover-conus-all-years| Ten Mile River Watershed Management Plan (HVA 2018)
8. Are there detrimental invasive species?			USGS Nonindigenous Aquatic Species Database (Specify species) www.nas.er.usgs.gov/

9. Are there host fish?			Digital Distribution of Native U.S. Fishes by Watershed on NatureServe www.natureserve.org/products/digital-distribution-native-us-fishes-watershed | NY DEC Region 3 Fish Stocking www.dec.ny.gov/outdoor/7739.html | state fish database (requested upon state approval)
10. Are there mussel pathogens?			Google search "mussel pathogens" OR "mussel die off" in the watershed name
11. Is there planned watershed development?			Google search "development" OR "infrastructure projects"
12. Do climate forecasts negatively impact mussel habitat?			WorldClim www.worldclim.org/ | peer reviewed literature search | EcoSHEDS www.usgs.gov/apps/ecosheds/#/