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REGULAR ARTICLE

REASSESSING ENIGMATIC MUSSEL DECLINES IN THE UNITED STATES

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ABSTRACT

Freshwater mussels have disappeared from many U.S. streams since the 1960s. These declines are enigmatic: there are no clear causes and other components of aquatic communities appear unaffected. I review the characteristics, spatial occurrence, timing, and potential causes of enigmatic mussel declines. They share some or all of the following characteristics: (1) fauna-wide collapse, affecting all species; (2) recruitment failure, leading to a senescent fauna; (3) no well-documented impact sufficient to affect all species rapidly; (4) specific to mussels; (5) recent occurrence, since the 1960s; (6) rapid action, often leading to faunal collapse within 10 yr; and (7) upstream progression in some cases. Enigmatic declines are largely restricted to upland regions south of maximum Pleistocene glaciation and north or west of the Gulf and Atlantic coastal plains, and they appear restricted to small- to medium-sized streams. In contrast, mussel declines with different characteristics are reported nationwide. Their consistent characteristics, restricted spatial occurrence, and similar timing suggest that enigmatic declines represent a distinct, diagnosable phenomenon. Many commonly invoked factors are not plausible explanations for enigmatic declines, and others are vague or poorly supported. Other factors are plausible in some cases (e.g., agricultural effects) but cannot explain declines across the affected area. I identified only two factors that could broadly explain enigmatic declines: disease and introduction of *Corbicula fluminea*, but these factors are poorly understood. The occurrence of enigmatic declines overlies the region with the highest mussel species richness on Earth, but I believe their severity and importance are underappreciated. Streams affected by enigmatic declines are vital research and management opportunities, deserving of increased attention; I propose ways that research can be focused to rigorously evaluate the specific mechanisms for these declines. Until we understand the causes of enigmatic declines, mussel conservation in affected areas is substantially hamstrung.

KEY WORDS: Unionida, conservation, extinction, disease, invasive species, sediment, fragmentation

INTRODUCTION

The dramatic and widespread decline of North American freshwater mussels is well recognized. Many mussel declines in the first half of the 20th century are clearly attributable to massive habitat destruction, mainly by dams. In contrast, more recent declines are enigmatic: there are no clear causes, and other components of the aquatic communities in these streams are relatively unaffected (Haag 2012). Despite more than three decades of research, we are still far from understanding the causes of such declines. Enigmatic declines are rarely viewed as distinct events; rather, they usually are considered part of a

long, downward trend in mussel populations that began over 100 yr ago, and, as such, they are conflated with declines attributable to other, clearly supported causes. Explanations for enigmatic declines consist of a long list of potential threats or causal factors that has changed little over time. Hereafter, I refer to this body of explanations as “the conventional wisdom” (Table 1). Several factors in the conventional wisdom seem unrelated to enigmatic declines, the importance of many factors is untested, and the precise nature of other factors is unspecified. Nevertheless, much of the conventional wisdom has become accepted as proven fact.

Our understanding of enigmatic declines, and mussel declines in general, has been hampered by three related issues. First, a lack of clarity about the characteristics of enigmatic

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Table 1. The conventional wisdom: factors invoked to explain mussel declines. Adapted from Bogan (1993), Strayer et al. (2004), and FMCS (2016).

Dams and Impoundment

Dredging and channelization
 “Habitat degradation”
 “Poor land use practices”
 “Pollution,” water quality degradation, contaminants
 Sedimentation
 Loss of riparian buffers
 “Run-off,” impervious surfaces
 Eutrophication
 Coal mining, oil and gas extraction
 Exotic species
 Hydrologic change
 Overharvest
 Lack of fish hosts; changes in fish assemblages
 Climate change
 Endocrine disrupters
 Disease

declines makes it difficult to distinguish them from other types of declines and establish their spatial distribution and timing. Second, we are uncertain about whether enigmatic declines together represent a single, widespread phenomenon or a collection of largely unrelated events. Third, we have failed to critically evaluate the evidence for factors invoked to explain mussel declines and thus have tended to perpetuate poorly supported speculation about causes (see Downing et al. 2010). These issues have hampered the search for causes and may have encouraged management actions that have little chance of reversing declines.

I provide a critical analysis of enigmatic mussel declines and the factors invoked to explain them. First, I review the characteristics of enigmatic declines and assess their spatial occurrence and timing. Second, I evaluate how well the conventional wisdom explains these declines and discuss other potential explanations. Finally, I propose ways that mussel research and management can be focused to provide more specific information about the causes of enigmatic declines and more specific guidance for addressing them.

OVERVIEW OF ENIGMATIC MUSSEL DECLINES

In the first half of the 20th century, a frenzy of dam construction across the USA destroyed or radically altered thousands of kilometers of riverine habitat and profoundly affected aquatic communities. To date, most extinctions of North American mussel species are directly attributable to habitat destruction by dams (Haag 2012). Substantial mussel assemblages survived in some impounded streams, but they shifted to dominance of impoundment-tolerant species and now bear little resemblance to the pre-impoundment fauna (e.g., Garner and McGregor 2001). Fish assemblages and other aquatic organisms showed similar radical shifts after im-

poundment (Taylor et al. 2001). Throughout this period, mussels and other aquatic life also were nearly eliminated locally by severe water pollution or other specific, documented insults (Ortmann 1909; Forbes and Richardson 1913).

As late as the 1960s, many streams that escaped impoundment or other severe insults continued to support spectacular mussel faunas. We know about the condition of the fauna at that time in large part because of the efforts of two remarkable individuals, David H. Stansbery, of The Ohio State University, and Herbert D. Athearn, a private shell collector, both of whom collected mussels extensively across the eastern USA and whose large collections survive (Ohio State University Museum of Biological Diversity and North Carolina Museum of Natural Sciences, respectively). These and most other historical collections were not quantitative in any sense, and they have several potential sources of bias. First, sampling methods and effort are rarely recorded. Second, species that were common and widespread at the time (e.g., *Eurynia dilatata*) often appear to be underrepresented numerically in collections unlike rarer species for which most encountered individuals apparently were retained and catalogued (e.g., *Epioblasma* spp.). Third, many collections came mainly from muskrat middens, which may provide a biased depiction of the fauna that occurred at the site (Tyrrell and Hornbach 1998; Owen et al. 2011). Nevertheless, these collections clearly show that abundant, diverse, and largely intact mussel assemblages continued to exist across much of the USA (Table 2). Furthermore, these collections often contain a wide range of age classes, including juveniles.

Throughout this paper, I illustrate examples of enigmatic declines by comparing historical collections with contemporary survey data. Such comparisons must be made cautiously because of the unknown extent to which they are influenced by sampling artifacts at different times. To minimize this problem, the examples I provide consist of collections made at the same locations at different times, and I used only qualitative contemporary survey data. Contemporary qualitative survey methods are similar to methods used by Stansbery, Athearn, and others (Athearn 1969; J. Jenkinson, personal communication), and Stansbery trained or advised many contemporary mussel biologists. If anything, contemporary surveys probably are more exhaustive than historical surveys because today’s agency-supported mussel programs provide resources that were largely absent in the past (Haag and Williams 2014).

Even considering potential sampling artifacts, collections from the 1960s contrast starkly with contemporary survey data. These comparisons show that the condition of the mussel fauna in many streams has deteriorated dramatically since the 1960s. In the Red River, Tennessee, species richness declined 44% between 1966 and 1990, the total number of individuals reported declined 90%, and a subsequent survey showed further deterioration (Table 2). Furthermore, the 1966 collection contains multiple age classes, but the 1990 survey reported that all live individuals were “very old,” except for a

Table 2. Mussel assemblages in the Red River, Robertson County, Tennessee. Cell entries represent reported numbers of live individuals or recently dead shells. Sources: 1966, Ohio State University Museum of Biological Diversity, Division of Molluscs, Bivalve Collection Database (https://www.asc.ohio-state.edu/eeob/molluscs/terms_biv2.html, accessed February 14, 2019); 1990, Aquatic Resources Center (1993); 1998, Ray (1999).

Species	Year		
	1966	1990	1998
<i>Amblema plicata</i>	49	66	25
<i>Cyclonaias tuberculata</i>	12	22	7
<i>Lampsilis cardium</i>	5	3	5
<i>Tritogonia verrucosa</i>	2	3	5
<i>Elliptio crassidens</i>	5	14	3
<i>Lampsilis fasciola</i>	24	1	2
<i>Eurynia dilatata</i>	209	13	1
<i>Potamilus alatus</i>	6	1	1
<i>Theliderma cylindrica</i>	1	3	1
<i>Alasmidonta marginata</i>	11	0	0
<i>Actinonaias pectorosa</i>	11	6	0
<i>Epioblasma triquetra</i>	5	0	0
<i>Epioblasma walkeri</i>	376	0	0
<i>Lasmigona costata</i>	57	2	0
<i>Leptodea fragilis</i>	5	0	0
<i>Medionidus conradicus</i>	18	0	0
<i>Obovaria subrotunda</i>	420	1	0
<i>Pleurobema oviforme</i>	0	1	0
<i>Pleurobema sintoxia</i>	1	0	0
<i>Pleuonaia dolabelloides</i>	3	0	0
<i>Ptychobranthus fasciolaris</i>	22	1	0
<i>Strophitus undulatus</i>	15	0	0
<i>Villosa iris</i>	10	0	0
<i>Villosa lienosa</i>	11	0	0
<i>Villosa taeniata</i>	32	0	0
<i>Villosa vanuxemensis</i>	69	0	0
Total species	25	14	9
Total individuals	1379	137	50

single individual estimated at 8 yr old. In the Conasauga River, Georgia, species richness declined 72% between 1961 and 2005, and the total number of individuals declined 97% (Table 3). These are, at best, coarse estimates of declines in abundance, but they are similar to quantitative estimates from other streams. The Embarras River, Illinois, is one of the few streams for which pre-1980 quantitative data are available (as catch-per-unit-effort [CPUE]); overall mussel abundance in that stream declined 86% from 1956 to 1987 (Cummings et al. 1988). More recent quantitative data from other streams also show declines of similar magnitude (see subsequent). In the absence of quantitative data, mussel declines are usually reported simply as declines in species richness, but this metric alone does not fully illustrate their severity. Examining museum collections helps to better illustrate the catastrophic nature of these declines.

Table 3. Mussel assemblages in the Conasauga River at Lower Kings Bridge, Murray County, Georgia. Cell entries represent reported numbers of live individuals or recently dead shells. Sources: 1916, Florida Museum of Natural History Invertebrate Zoology Collection Database (<http://specifyportal.flmnh.ufl.edu/fiz/>, accessed February 11, 2019); 1961, H. D. Athearn Museum of Fluvial Mollusks collection catalog, Volume 3, North Carolina Museum of Natural Sciences mollusk collection; 2005, Johnson et al. (2005).

Species	Year		
	1916	1961	2005
<i>Elliptio arca</i>	12	46	0
<i>Elliptio arctata</i>	10	3	0
<i>Epioblasma othcaloogensis</i>	6	42	0
<i>Epioblasma metastriata</i>	11	1	0
<i>Hamiota altilis</i>	0	8	1
<i>Lampsilis straminea</i>	0	1	0
<i>Lampsilis ornata</i>	9	6	0
<i>Leptodea fragilis</i>	0	0	2
<i>Medionidus parvulus</i>	18	18	0
<i>Pleurobema decisum</i>	1	8	1
<i>Pleurobema</i> spp. ¹	225	26	1
<i>Pyganodon grandis</i>	2	0	0
<i>Ptychobranthus foremanianus</i>	17	7	0
<i>Quadrula rumphiana</i>	3	2	0
<i>Strophitus connasaugensis</i>	1	1	0
<i>Toxolasma corvunculus</i>	1	6	0
<i>Tritogonia verrucosa</i>	2	2	2
<i>Villosa nebulosa</i>	2	11	0
<i>Villosa umbrans</i>	3	13	0
<i>Villosa vibex</i>	3	8	0
Total species	18	18	5
Total individuals	316	215	7

¹*Pleurobema* spp. includes *P. georgianum*, *P. hanleyanum*, and *P. stablile*.

CHARACTERISTICS OF ENIGMATIC MUSSEL DECLINES

Mussel declines or other changes in mussel assemblages can take many forms. I will begin this section by describing types of declines I do not consider “enigmatic declines.” Obviously, the elimination of mussels and most aquatic life by well-documented, acute impacts such as a major chemical spill are not enigmatic (e.g., Schmerfeld 2006). Impoundment typically results in the loss of half or more of the original mussel fauna, but impoundment-tolerant species often increase in abundance, and other impoundment-tolerant species not present historically may colonize the stream (Garner and McGregor 2001). Loss of a fish host can eliminate a particular mussel species while leaving the remainder of the fauna relatively unaffected (Smith 1985; Fritts et al. 2012). Many unimpounded streams have lost a substantial portion of their historical mussel species richness but continue to support large populations of apparently adaptable species (“opportunistic species”, Haag 2012; see “Fauna-Wide Collapse”). In one stream, overall mussel abundance declined slowly over 20 yr, but effects were disproportionate among species and recruitment continued (Hornbach et al. 2018). Some species have

Table 4. Characteristics of enigmatic mussel declines.

Fauna-wide collapse	Effects are not species-selective and result in loss of virtually the entire mussel assemblage.
Recruitment failure	Cessation of recruitment results in rapid loss of short-lived species followed by more gradual loss of long-lived species.
No smoking gun	Occurs in streams with no obvious, documented impacts even though a large number of factors may be invoked.
Specific to mussels	Other aquatic species, such as fishes, insects, snails and crayfishes, appear relatively unaffected.
Recent occurrence	Many began between the late 1960s and the 1990s, but some began more recently. However, there is little evidence of their occurrence prior to the 1960s.
Rapid action	Faunal collapse is evident within 10 yr.
Upstream progression	In some cases, faunal collapse proceeded upstream over 10–20 yr.

disappeared from nearly their entire historical range, even from streams that continue to support otherwise healthy mussel faunas (e.g., *Epioblasma rangiana*, *Pleurobema clava*, *P. rubrum*; Haag and Cicerello 2016; Stodola et al. 2017). These latter three types of declines are similar to enigmatic declines in that precise causes are unknown, but they differ in other ways, which I will describe subsequently. A final type of decline that I do not consider here is mussel die-offs. These remain truly enigmatic, and their relationship to enigmatic mussel declines—as I define them here—is unclear. However, die-offs often are relatively brief, transient events and may affect only certain species (Neves 1987; Jones and Neves 2007; J. Jones, personal communication).

Each of these types of declines have characteristics that distinguish them from other, unrelated declines and that may inform our understanding of causal factors and mechanisms. Similarly, enigmatic declines appear to be a distinct type of decline that share some or all of a group of consistent characteristics (Table 4).

Fauna-Wide Collapse

One of the most consistent characteristics of enigmatic declines is that they affect most or all species in the mussel

assemblage. This is a critical point. Mussel species often are viewed as “tolerant” or “sensitive” to various human impacts (e.g., Brim Box and Mossa 1999). Some mussel species adapt well to impoundment, while others do not (e.g., Garner and McGregor 2001; Haag 2012). Some species appear to tolerate other types of human degradation of streams, but the precise nature of degradation and mechanism for this tolerance are unknown. For example, about half of the 36 species reported historically from the Minnesota River, Minnesota, are now extirpated, but the river continues to support large populations of a few species (e.g., *Leptodea fragilis*, *Potamilus ohioensis*, *Truncilla truncata*, *Quadrula quadrula*, *Pyganodon grandis*; Sietman 2007).

Such differences in species’ responses are not evident in enigmatic declines. In the Embarras River, abundance of virtually all species declined 66–100% (overall decline = 86%) between 1956 and 1987, with the single exception of *Leptodea fragilis*, which was relatively uncommon in both time periods (Fig. 1). Species often categorized as “tolerant” to human impacts declined dramatically (e.g., *Lampsilis siliquoidea*, 66%; *Pyganodon grandis*, 86%; *Quadrula quadrula*, 96%). The two most abundant species in 1987, *Lampsilis cardium* and *Cyclonaias pustulosa*, declined 71% and 83%, respectively. Without quantitative historical data for this river, those

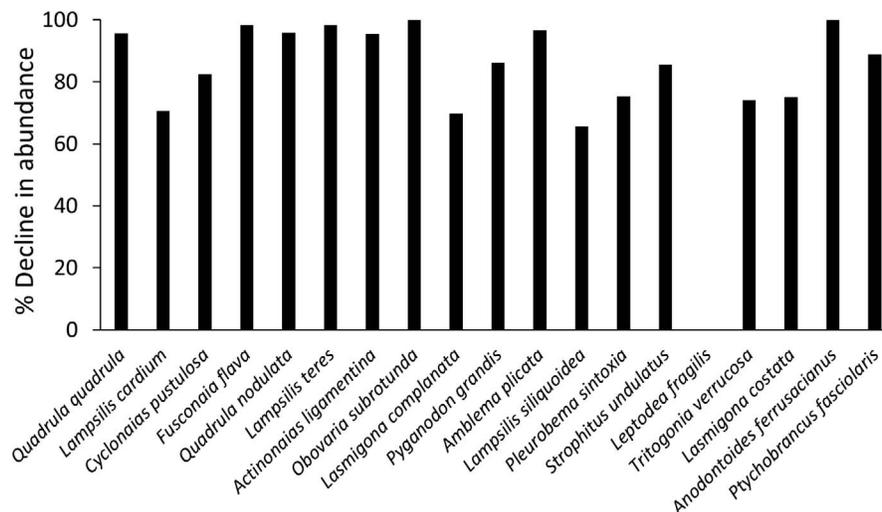


Figure 1. Percentage decline of mussel species in the Embarras River, Illinois, from 1956 to 1987. Thirty-nine species are reported from the river, but only the most abundant species are shown here. Data from Cummings et al. (1988).

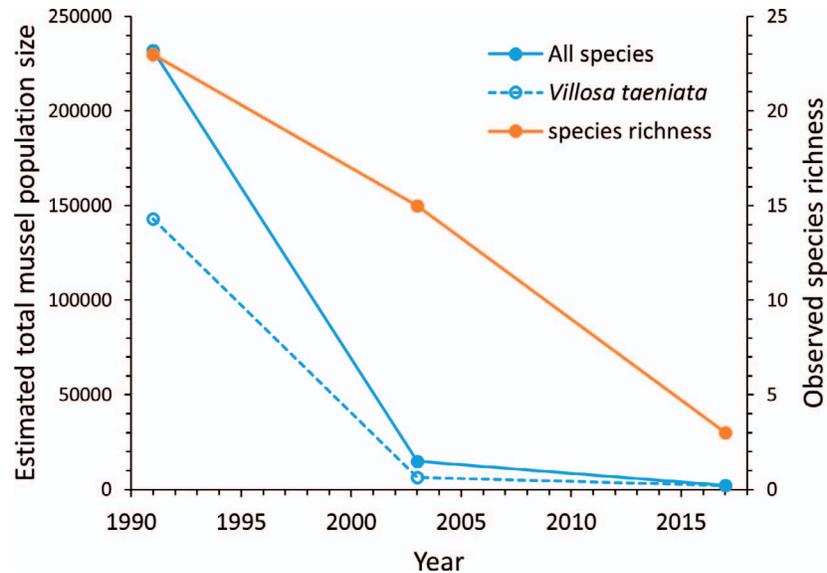


Figure 2. Declines in total mussel abundance; abundance of the dominant species, *Villosa taeniata*; and observed species richness in Horse Lick Creek, Kentucky, between 1991 and 2017. Data from Haag and Warren (2004) and W. Haag (unpublished data).

two species likely would have been viewed as “tolerant” based on their dominance in 1987, but this clearly was not the case. Similarly, *Villosa taeniata* was the most abundant species before and after an enigmatic decline in Horse Lick Creek, Kentucky, between 1991 and 2004, but its abundance declined 96%, similar to the overall mussel decline of 93% (Fig. 2). Because of the persistence of senescent adults (see subsequent), species richness typically declines more slowly than mussel abundance, initially masking the severity of the decline (Table 2 and Fig. 2). Despite the lack of quantitative historical baseline data in most streams, most well-documented examples of enigmatic declines show a near-complete collapse of the entire mussel fauna, ultimately resulting in a steep decline in species richness (e.g., Evans 2001; Warren and Haag 2005; Henley et al. 2013).

I found only two examples in which the mussel fauna survived a decline largely intact. Despite the 86% decline in mussel abundance in the Embarras River between 1956 and 1987, abundance appears to have stabilized subsequently, and species richness has changed little over time. CPUE and species richness were 47 individuals/h and 27, respectively, in 1956; 7/h and 25 in 1987; and 12/h and 26 in 2011 (Cummings et al. 1988; Shasteen et al. 2012b). Similarly, mussel abundance in the Sangamon River, Illinois, declined about 50% between 1956 and 1988, but abundance has stabilized and species richness has changed little (CPUE and richness, 1956: 22/h and 32; 1988: 9/h and 33; 2010: 13/h and 29; Schanzle and Cummings 1991; Price et al. 2012). I did not include the Sangamon River in my compilation of enigmatic declines (see “Spatial Occurrence of Enigmatic Mussel Declines”) because of the less severe nature of that decline. In any case, these two examples contrast with the near-complete faunal loss seen in most streams.

Recruitment Failure

A mechanism of enigmatic declines appears to be a cessation of recruitment for all species. A preponderance of large individuals and a conspicuous absence of smaller size classes is reported consistently for enigmatic declines (e.g., Isom and Yokely 1968; Pinder and Ferraro 2012; Henley et al. 2013; Irwin and Alford 2018). Consequently, short-lived species often are the first to disappear, but long-lived species may persist for several decades (Henley et al. 2013; Table 2). Recruitment often is difficult to assess from survey data, but I have observed two clues in these streams that seem to be associated with recruitment failure. First, remaining individuals frequently are highly eroded, in contrast to the pristine condition of shells in healthy streams or historical collections. Second, muskrat middens are composed exclusively of *Corbicula fluminea*, presumably because remaining native mussels are scarce and large, exceeding the handling capability of muskrats (see Warren and Haag 2005).

Although some adults typically survive enigmatic declines, patterns of adult mortality are poorly known because the onset of these events is rarely witnessed. In some cases, relatively large numbers of aging individuals may persist in affected streams (e.g., Henley et al. 2013; personal observations), but baseline data on abundance are rarely available. Large numbers of recently dead adult mussels were reported during the onset of an enigmatic decline in the Little South Fork Cumberland River, Kentucky, in the early 1980s (Warren and Haag 2005), and a more recent enigmatic decline in the Little Tennessee River, North Carolina, was accompanied by massive adult mortality (Jarvis 2011). Contemporaneous observations such as these are scarce, but I provide additional discussion of this issue under “Timing of Enigmatic Declines.” Regardless of their effects on adults, recruitment

failure in affected streams prevents recovery, ultimately leading to faunal collapse.

No Smoking Gun, Specific to Mussels

The most enigmatic characteristics of these declines are that they often occur in streams with no obvious impacts, and other aquatic species appear relatively unaffected. Aspects of the conventional wisdom typically are invoked to explain enigmatic declines, but conclusive evidence is rarely available. The decline in Horse Lick Creek was attributed to coal mining (Houslet and Layzer 1997; Haag and Warren 2004), but subsequent water and sediment sampling detected no evidence of coal mining effects (Haag et al. 2019). Furthermore, annual water quality sampling by the Kentucky Division of Water from 1998 to 2016 ranked the stream as “fully supporting aquatic life” (the highest possible ranking) in all years, and three assessments using the Kentucky Index of Biotic Integrity (IBI) during that period ranked the aquatic insect and fish assemblages as “good” or “excellent.” Despite a near complete loss of the mussel fauna in the Buffalo River, Tennessee, the snail fauna remained intact, and an IBI ranked the fish fauna as “excellent” (Ahlstedt et al. 2017). Similarly, IBIs for aquatic insects and fishes in the Embarras River consistently rank the stream as “good–excellent,” and it is widely used as a reference in bioassessments (Fausch et al. 1984).

Recent Occurrence, Rapid Action

I discuss aspects of the timing of enigmatic declines in more detail under “Timing of Enigmatic Declines.” For now, it is sufficient to point out two characteristics about timing. First, enigmatic declines appear to have begun abruptly during, or shortly after, the 1960s, and there is little evidence of their occurrence prior to that time. Many enigmatic declines occurred between the late 1960s and the 1990s, a fact that is emphatically apparent upon examination of Stansbery’s and Athearn’s collections and other historical sources, but declines occurred later in some areas. Second, enigmatic declines appear to act rapidly, often leading to faunal collapse within 10 yr.

Upstream Progression

I am aware of two examples of upstream progression of enigmatic declines. Declines in the lower portion of Horse Lick Creek were documented about 1985, but the fauna in the middle and upper creek remained intact. The decline moved steadily upstream, and by 2003, it had moved 20 km into the headwaters at an average rate of 1.1 km/yr (Houslet and Layzer 1997; Haag and Warren 2004). Similarly, declines began about 1982 in the lower section of Little South Fork Cumberland River, but they moved steadily upstream about 50 km into the headwaters by 1997 at a rate of about 3.3 km/yr (Warren and Haag 2005). These streams have an unusually

complete temporal and spatial sequence of survey data, which is available for few streams; consequently, it is unknown if upstream progression is a consistent characteristic of enigmatic declines.

SPATIAL OCCURRENCE OF ENIGMATIC MUSSEL DECLINES

I interviewed mussel biologists throughout the eastern USA and examined published literature and survey reports to compile a list of streams having the characteristics of enigmatic declines (Table 5). This list of streams is by no means comprehensive; rather, it is based on streams with which sources were familiar or for which published information was available. The confidence with which the severity, timing, and characteristics of declines in these streams can be assessed varies widely according to the nature of existing data. I omitted from this list streams where mussel declines are reasonably explained by a well-documented factor (e.g., major chemical spills, severe chronic pollution, direct impoundment-related effects), but undocumented insults of this nature may have occurred in some of the streams I do include. Despite these caveats, the occurrence of enigmatic declines showed a striking and surprising geographical pattern (Table 5 and Fig. 3).

Enigmatic mussel declines were largely restricted to uplands of the Interior Low Plateaus physiographic province, the Appalachian Highlands physiographic region south of the Ohio River (about 39° latitude), and the Ozark Plateaus and Ouachita physiographic provinces, mainly in northern and central Alabama, Arkansas, northern Georgia, Kentucky, Missouri, Tennessee, western Virginia, and West Virginia, with one example in southeastern Oklahoma. Enigmatic declines occurred throughout the Tennessee, Cumberland, Green, and Coosa river systems, other upland portions of the Mobile Basin (Black Warrior, Cahaba, and Tallapoosa river systems), portions of the Kanawha, Monongahela, and Kentucky river systems, and smaller tributaries of the Ohio River. West of the Mississippi River, enigmatic declines were reported in the White, Osage, Ouachita, Meramec, Red, and Arkansas river systems, and one smaller tributary of the Mississippi River (Salt River). Reports of enigmatic declines on the Atlantic Slope were limited mainly to streams in the Piedmont physiographic province in North Carolina, with two in the Potomac River system (Virginia and West Virginia). Outside of these areas, enigmatic declines were reported only in southern Illinois, northern Missouri, and eastern Iowa.

Enigmatic mussel declines were largely confined to areas south of the maximum extent of Pleistocene glaciation. With the exception of the Embarras, Salt, and Maquoketa rivers, enigmatic declines were not reported from the glaciated Central Lowlands physiographic province in Indiana, Illinois, Iowa, Ohio, Minnesota, or Wisconsin (B. Fisher, K. Cummings, J. Kurtz, B. Sietman, and T. Watters, personal communication). For example, mussel assemblages in the Little Wabash River, Illinois, remained relatively unchanged from 1956 to 2011. Mussel CPUE and species richness were

Table 5. Examples of potential enigmatic mussel declines in the eastern USA. Stream names are followed by the river system of which they are a part. Affiliations of individuals providing personal communications (pers. comm.) are provided in the Acknowledgments. Asterisks denote streams in which some recovery or stabilization has been documented.

Stream	Approximate Onset of Decline	Source
Alabama		
Terrapin Creek (Coosa)	1970–1990	Gangloff and Feminella 2007
Hatchet Creek (Coosa)	1970–1990	J. Moran, P. Johnson, pers. comm.
Shoal Creek (Coosa)	2000–2010	J. Moran, pers. comm.
Tallaseehatchee Creek (Coosa)	Before 2010	J. Moran, pers. comm.
Choctawhatchee Creek (Tallapoosa)	2000–2010	J. Moran, pers. comm.
Uphapee Creek (Tallapoosa)	2000–2010	J. Moran, pers. comm.
Little Cahaba River (Cahaba)	1970–1990	P. Johnson, pers. comm.
North River (Black Warrior)	1990–2000	O’Neil et al. 2011
Upper Black Warrior River tributaries	1990–2010	J. Moran, pers. comm.
Paint Rock River (Tennessee)	1970–1990*	P. Johnson, pers. comm.
Arkansas		
South Fork Ouachita River	1980–2000	J. Harris, pers. comm.
Upper Ouachita River	1990–2000	C. Davidson, pers. comm.
South Fork Saline River (Ouachita)	1990–2000	C. Davidson, pers. comm.
Middle Fork Saline River (Ouachita)	2000–2010	C. Davidson, pers. comm.
North Fork Saline River (Ouachita)	2000–2010	C. Davidson, pers. comm.
Alum Fork Saline River (Ouachita)	2000–2010	C. Davidson, pers. comm.
Caddo River (Ouachita)	1990–2000	C. Davidson, pers. comm.
Middle Fork Little Red River (White)	2000–2010	C. Davidson, pers. comm.
Illinois River (Arkansas)	2000–2010	C. Davidson, pers. comm.
Georgia		
Conasauga River (Coosa)	1970–1990	Evans 2001; Table 3
Etowah River tributaries (Coosa)	Before 1990	J. Wisniewski, pers. comm.
Coosawattee River tributaries (Coosa)	Before 1990	J. Wisniewski, pers. comm.
South Chickamauga Creek (Tennessee)	Before 1995*	P. Johnson, pers. comm.
Lookout Creek (Tennessee)	Before 1995*	J. Wisniewski, pers. comm.
Illinois		
Embarras River (Wabash)	1960–1985*	Cummings et al. 1988
Iowa		
Maquoketa River (Mississippi)	1980–1990	J. Kurth, pers. comm.
Kentucky		
Nolin River (Green)	1970–1990	Haag and Cicerello 2016
Drakes Creek (Green)	Before 1990	Haag and Cicerello 2016
Gaspar River (Green)	Before 1990	Haag and Cicerello 2016
Little River (Cumberland)	Before 1980	Haag and Cicerello 2016
Rockcastle River (Cumberland)	1970–1980	Cicerello 1993; Table 6
Horse Lick Creek (Cumberland)	1985–2000	Haag and Warren 2004
Roundstone Creek (Cumberland)	1970–1990	Haag and Cicerello 2016
Buck Creek (Cumberland)	1980–2000	M. Compton, pers. comm.
Little South Fork Cumberland River	1980–2000	Warren and Haag (2005)
Cumberland River	1970–1990	Cicerello and Laudermilk 1997, 2001; Table 7
Red River (Kentucky)	1980–2000	M. McGregor, pers. comm.
Tygarts Creek (Ohio)	1990–2010	M. McGregor, pers. comm.
Little Sandy River (Ohio)	1990–2010	Haag and Cicerello 2016
Missouri		
Niangua River (Osage)	Before 2010	McMurray et al. 2018
Bourbeuse (Meramec)	1980–2000	Hinck et al. 2012
Meramec	1980–2000	Hinck et al. 2012
Little Black River (White)	1980–1998	Bruenderman et al. 2001
North Fork White River (White)	1985–2010	S. McMurray, pers. comm.

Table 5, continued.

Stream	Approximate Onset of Decline	Source
Salt River system (Mississippi)	1985–2010	McMurray et al. 2017
Eleven Point River (White)	1985–2010	S. McMurray, pers. comm.
Jacks Fork River (White)	1985–2010	S. McMurray, pers. comm.
James River (White)	1985–2010	McMurray and Faiman 2018
North Carolina		
Little Tennessee River (Tennessee)	2003–2006	Jarvis 2011
Swift Creek (Tar)	1990–2000	S. McRae, pers. comm.
Tar River	1975–1990	S. McRae, pers. comm.
Swift Creek (Neuse)	1990–2000	S. McRae, pers. comm.
Little River (Neuse)	1990–2000	S. McRae, pers. comm.
Rocky River (Cape Fear)	1990–2000	S. McRae, pers. comm.
Waxhaw Creek (Catawba)	1980–2000	S. Fraley, pers. comm.
Oklahoma		
Blue River (Red)	1970–1990	Vaughn 1997
Tennessee		
Buffalo River (Tennessee)	Before 1965	Isom and Yokely 1968; Reed 2014
Duck River (Tennessee)	1970–1990*	Ahlstedt et al. 2017
Tellico River (Tennessee)	1980–2000	S. Fraley, pers. comm.
Harpeth River (Cumberland)	Before 1990	Irwin and Alford 2018
East Fork Stones River (Cumberland)	1970–1990	D. Hubbs, pers. comm.; Table 8
Red River (Cumberland)	1970–1990	Ray 1999; Table 2
Virginia		
Middle Fork Holston River (Tennessee)	1970–1990	Henley et al. 2013
North Fork Holston River (Tennessee)	2000–2010	J. Jones, pers. com
South Fork Holston River (Tennessee)	1980–2000	Pinder and Ferraro 2012
Copper Creek (Tennessee)	1980–2000*	Fraley and Ahlstedt 2000
Big Moccasin Creek (Tennessee)	1980–2000	J. Jones, pers. com
New River (Kanawha)	1970–1990	J. Jones, pers. com
Aquia Creek (Potomac)	1990–2010	J. Jones, pers. com
West Virginia		
Upper Elk River (Kanawha)	1990–2010	J. Clayton, pers. comm.
Patterson Creek (Potomac)	1990–2010	J. Clayton, pers. comm.
South Fork Hughes River (Little Kanawha)	Before 2005	J. Clayton, pers. comm.
Kincheloe Creek (Monongahela)	1990–2010	J. Clayton, pers. comm.
Tygart River headwaters (Monongahela)	Before 1990	J. Clayton, pers. comm.

22 individuals/h and 29, respectively, in 1956, 20/h and 26 in 1988, and 18/h and 27 in 2011 (Cummings et al. 1989; Shasteen et al. 2012a). Similarly, enigmatic declines were not evident in the northeastern USA, including Pennsylvania, New York, and New England (R. Anderson and D. Strayer, personal communication; Strayer and Fetterman 1999; Raithel and Hartenstine 2006; Nedeau et al. 2000; Nedeau 2008).

Most surprisingly, enigmatic declines were not reported in most of the Gulf or Atlantic coastal plains, despite multiple reports of declines in adjacent upland regions. Many coastal plain streams in Alabama, Georgia, North Carolina, and South Carolina continue to support diverse and abundant mussel assemblages (J. Garner, J. Moran, T. Savidge, J. Wisniewski, personal communication). Streams in all of these areas have experienced changes in the mussel fauna or species losses due to various factors, known and unknown, but examples of

unexplained, rapid, and complete faunal collapse are rare or nonexistent.

Assessing the occurrence of enigmatic declines is particularly difficult in Texas. Patterns of mussel declines in Texas are strikingly similar to those in the east: Coastal Plain streams continue to support diverse and abundant faunas, but many upland streams (e.g., those on the Edwards Plateau) now are essentially defaunated, despite having supported diverse faunas prior to the 1980s (Howells et al. 1997; C. Randklev, personal communication). However, these declines coincide with dramatic increases in water abstraction and aquifer depletion, leaving streams highly vulnerable to drought. Major hydrologic change is a plausible mechanism for mussel declines in Texas, but causal factors remain poorly understood.

Mussel declines are less well documented in the western USA, and this region has a limited mussel fauna. A recent

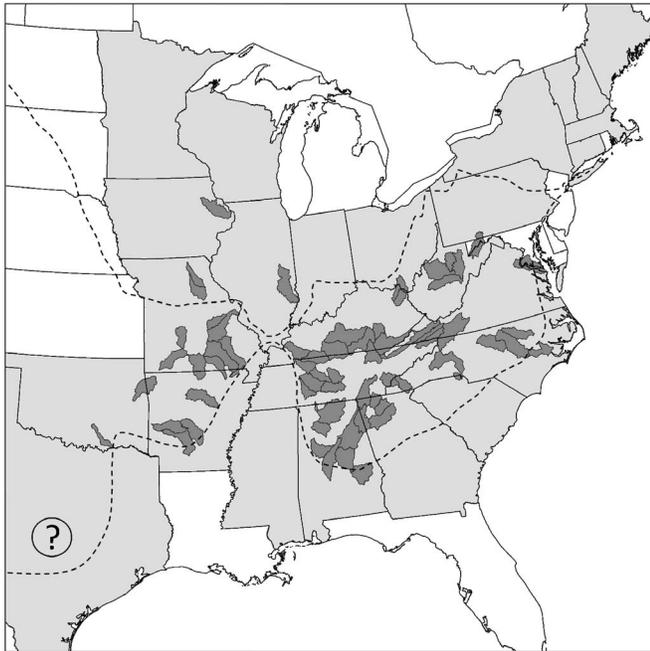


Figure 3. Map of the eastern United States showing the occurrence of enigmatic mussel declines. Shaded states are those for which the occurrence of enigmatic declines was assessed. Shaded polygons are eight-digit hydrologic units in which potential enigmatic declines are reported (see Table 5). The upper dashed line represents the maximum extent of Pleistocene glaciation; the lower dashed line represents the boundaries of the Gulf and Atlantic coastal plains. The question mark in Texas shows the approximate location of the Edwards Plateau and other upland regions that may have experienced enigmatic declines (see text).

assessment of Pacific coast river systems showed mussel declines in some areas (Blevins et al. 2017), but the characteristics of these declines, and the extent to which they are enigmatic or attributable to specific factors, remain unclear.

In addition to their restricted geographic scope, enigmatic declines are notable for their apparent occurrence only in small- to medium-sized streams. Few of the streams listed in Table 5 have watershed areas $>2,000$ km² (e.g., Conasauga, Embarras, Meramec, and Red [Tennessee] rivers), and some have watersheds <100 km² (e.g., Horse Lick Creek). Some that are depicted as separate events may reflect a single, larger phenomenon. For example, mussels have declined throughout the Rockcastle River system, including its tributaries Horse Lick and Roundstone creeks, and declines are evident throughout the upper Coosa and Ouachita river systems. Nevertheless, enigmatic declines are not reported from large rivers within the affected geographical area. Mussel species richness in the Ohio and Tennessee rivers is greatly reduced compared with historical richness, but these rivers continue to support large mussel populations (Payne and Miller 2000; Garner and McGregor 2001). The upper reaches of several watersheds have experienced widespread enigmatic declines, but their lower mainstem rivers continue to support extraordinary mussel assemblages, particularly beyond the point where those rivers flow off of uplands onto the Coastal Plain

(e.g., Ouachita, Saline, and White rivers; Posey 1997; Davidson and Clem 2004).

Because of their severity, enigmatic declines in most affected streams are evident even from coarse, qualitative data. Declines in the Embarras and Sangamon rivers appear to be comparatively less severe (see “Fauna-Wide Collapse”). These declines are evident because of the unusual availability of historical abundance estimates, but they would not be detectable based on historical changes in species richness. It is possible that similar, less severe declines have occurred in other regions, but detecting them is difficult because of the lack of historical abundance estimates. Regardless, it seems clear that severe, enigmatic declines are restricted in distribution, but the reason for this is unknown.

TIMING OF ENIGMATIC MUSSEL DECLINES

Establishing the exact timing of enigmatic declines is usually impossible due to the nature of available data. Unusually complete collecting records from the Rockcastle and Cumberland rivers, Kentucky, and the East Fork Stones River, Tennessee, provide more precise assessments of the timing of these declines (Tables 6–8). Despite the qualitative nature of these data, they clearly show abrupt faunal collapse within 10 yr between the 1960s and the 1970s. In all three streams, the stark differences in the results of two surveys conducted only 10 yr apart likely cannot be explained solely by recruitment failure; rather, they suggest that high adult mortality also occurred during that period. These declines did not go unnoticed at the time. When I was a student of David Stansbery’s in the 1980s, he once mused rhetorically, “Whatever happened to the East Fork Stones River?” Similarly, Herbert Athearn was aware of the decline in the Conasauga River. After a visit to the river in 1971, he recorded in his collection catalog, “This may be the last station I collect on this ailing stream” (H. D. Athearn Museum of Fluvial Mollusks collection catalog, Volume 6, North Carolina Museum of Natural Sciences mollusk collection). This comment, made 10 yr after his 1961 collection (Table 3), also suggests the decline in the Conasauga River was rapid. Such precise estimates of timing are unavailable for most streams, but many experienced faunal collapse within a similar time period between the 1960s and 1990s (Table 5).

Other enigmatic declines appear to have begun substantially later, particularly in smaller streams. The decline in Horse Lick Creek, a tributary of the Rockcastle River, began in the 1980s, 10–15 yr after the decline began in the main stem (Tables 5 and 6). Mussel abundance (as CPUE) in the Little Black River, Missouri, declined about 80% between 1980 and 1998 (Bruenderman et al. 2001). Other recent declines are reported in Alabama, Arkansas, North Carolina, Missouri, and West Virginia. An unusually well-documented recent example is the Little Tennessee River, North Carolina, where the mussel fauna collapsed rapidly between 2003 and 2006 (Jarvis 2011). This example differs from others in Table 5 in that the decline appeared to have been most severe for *Alasmidonta*

Table 6. Mussel assemblages in the Rockcastle River at Livingston, Rockcastle County, Kentucky. A total of 29 species are reported from the site, but only the most abundant species are reported here. Cell entries represent reported numbers of live individuals or recently dead shells; dashes indicate that the species was not reported, but presence or absence is unclear. Sources: 1910, Wilson and Clark (1914); 1947, Neel and Allen (1964); 1963–1975, Ohio State University Museum of Biological Diversity, Division of Molluscs, Bivalve Collection Database (https://www.asc.ohio-state.edu/eeob/molluscs/terms_biv2.html, accessed February 14, 2019); 1982, Thompson (1985); 1990, Cicerello (1993).

Species	Year							
	1910 ¹	1947	1963	1964	1967	1975	1982	1990
<i>Eurynia dilatata</i>	33	Common	209	139	35 ²	23	3	15
<i>Villosa taeniata</i>	6	Common	378	166	28	4	4	0
<i>Medionidus conradicus</i>	31 ¹	Common	28	95	23	0	0	0
<i>Venustaconcha troostensis</i>	—	Common	44	24	7	2	0	0
<i>Ligumia recta</i>	1	Common	22	15	14	3	0	3
<i>Lasmigona costata</i>	8	Common	14	15	13	0	1	0
<i>Ptychobranthus fasciolaris</i>	1	Common	70	34	23	6	0	1
<i>Actinonaias pectorosa</i>	—	Common	15	14	8	1	0	0
<i>Amblema plicata</i>	1	Common	20	7	15	0	1	2
<i>Lampsilis cardium</i>	—	Common	48	13	1	0	2	2
<i>Toxolasma lividus</i>	—	—	22	6	1	0	0	0
Total species	18	18	24	20	17	10	10	9
Total individuals	458	—	1,056	573	184 ²	47	11	31

¹Mussels overall described as “excessively abundant,” and “in favored localities . . . *Medionidus conradicus* covered the entire bottom.” Note that the sum of individuals reported for each species (including those not shown here) does not match the total individuals reported in this survey.

²Field notes report the species as “abundant” and most individuals were not retained; total individuals for this date does not include released *E. dilatata*.

spp., but these species dominated the fauna, and I include this example here despite the potential for selective effects.

Affected streams typically show little or no evidence of recovery. Two remarkable exceptions are the Duck River, Tennessee, and the Paint Rock River, Alabama, where mussel abundance has increased dramatically since a low point in the late 1970s and 1980s (Ahlstedt et al. 2017; P. Johnson, personal communication), and some recovery is evident in Copper Creek, Virginia (Hanlon et al. 2009). Apart from the Embarras River (see “Fauna-Wide Collapse”), I found no

other documented examples of mussel recovery or stabilization after an enigmatic decline. The mussel faunas of Horse Lick Creek and the Cumberland, Red, Rockcastle, and East Fork Stones rivers continue to disappear (Fig. 2 and Tables 6–8), and other streams in Kentucky that experienced enigmatic declines in the 1970s or 1980s now are essentially defaunated (e.g., Little River, Nolin River; Haag and Cicerello 2016).

A critical question about enigmatic declines is whether they began abruptly after the 1960s, or if they are part of a longer, more gradual decline beginning in the early 1900s.

Table 7. Mussel assemblages in the Cumberland River below Cumberland Falls, McCreary County, Kentucky. A total of 22 species are reported from the site, but only the most abundant species are reported here. Cell entries represent reported numbers of live individuals or recently dead shells. Sources: 1910 and 1987, Cicerello and Laudermilk (1997); 1961 and 1972, Ohio State University Museum of Biological Diversity, Division of Molluscs, Bivalve Collection Database (https://www.asc.ohio-state.edu/eeob/molluscs/terms_biv2.html, accessed February 14, 2019).

Species	Year			
	1910	1961	1972	1987
<i>Eurynia dilatata</i>	122	113	2	7
<i>Actinonaias pectorosa</i>	73	161	1	~50
<i>Lampsilis fasciola</i>	16	20	0	0
<i>Medionidus conradicus</i>	Present	154	0	0
<i>Ptychobranthus fasciolaris</i>	81	35	1	5
<i>Cyclonaias pustulosa</i>	49	122	2	10
<i>Tritogonia verrucosa</i>	32	75	0	4
<i>Villosa iris</i>	0	27	0	0
<i>Venustaconcha troostensis</i>	5	7	1	0
Total species	20	16	5	10
Total individuals	810	810	7	88

Table 8. Mussel assemblages in the East Fork Stones River at Walterhill, Rutherford County, Tennessee. A total of 31 species are reported from the site, but only the most abundant species are reported here. Cell entries represent reported numbers of live individuals or recently dead shells; dashes indicate that the species was not reported, but presence or absence is unclear. Sources: 1911, Wilson and Clark (1914); 1965–1981, Ohio State University Museum of Biological Diversity, Division of Molluscs, Bivalve Collection Database (https://www.asc.ohio-state.edu/eob/molluscs/terms_biv2.html, accessed February 14, 2019); 2002, D. Hubbs, personal communication.

Species	Year						
	1911 ¹	1964	1965	1966	1976	1981	2002
<i>Villosa taeniata</i>	—	57	112	107	2	2	0
<i>Lasmigona costata</i>	8	27	93	5	25	34	0
<i>Obovaria subrotunda</i>	2	38	64	51	1	0	0
<i>Epioblasma walkeri</i>	70	18	39	84	0	0	0
<i>Lampsilis fasciola</i>	2	26	30	23	1	2	0
<i>Amblema plicata</i>	5	24	26	3	8	7	0
<i>Pyganodon grandis</i>	1	9	25	6	1	1	0
<i>Fusconaia flava</i>	5	15	22	4	2	0	0
<i>Leptodea fragilis</i>	—	5	12	0	0	1	0
<i>Eurynia dilatata</i>	—	7	10	0	6	1	0
<i>Ptychobranchus fasciolaris</i>	—	9	10	1	8	8	0
<i>Lasmigona complanata</i>	—	9	9	0	2	0	0
Total species	13	27	24	16	13	10	0
Total individuals	194	309	500	298	63	58	0

¹Note that the sum of individuals reported for each species (including those not shown here) does not match the total individuals reported in this survey.

Collections from many streams in the 1960s and 1970s are remarkably similar in species composition to collections from the early 1900s (e.g., Hurd 1974; Jones and Neves 2007; Henley et al. 2013), but even crude historical estimates of abundance are scarce. The qualitative data in Tables 3 and 6–8 show considerable variation in mussel abundance among surveys attributable to river condition, collector efficiency, etc. For example, the higher abundance of *Pleurobema* in the Conasauga River in 1916 compared with 1961 is noteworthy. Overall, however, in all four examples, collections from the 1960s are remarkably similar to those from the early 1900s when compared with the major changes that occurred after the 1960s. Historical data such as these are available for few streams, but the spectacular museum collections from the 1960s strongly suggest that the mussel fauna in many places remained essentially intact until that time.

EXPLAINING ENIGMATIC MUSSEL DECLINES

An attempt to evaluate causes of enigmatic declines can benefit by placing these events in a broad context. I propose that enigmatic declines collectively represent a discrete, widespread phenomenon. This assertion is based on (1) the consistent characteristics shared by enigmatic declines, particularly the highly virulent, fauna-wide effects; (2) the restriction of these events to particular geographic regions and to small- to medium-sized streams, but their widespread occurrence within those regions; and (3) the rapid pace of declines and their sudden occurrence within a relatively narrow time frame since the 1960s. I further propose that enigmatic declines are largely unrelated to other factors that

affect mussels, but they may occur in concert with those factors. I will elaborate on this assertion subsequently. This context is useful for evaluating the causes of enigmatic declines, but its validity is not necessarily a prerequisite for evaluating how well the conventional wisdom explains them.

Regardless of whether enigmatic declines are a distinct phenomenon, we can quickly eliminate several factors in the conventional wisdom (Table 1). Clearly, loss of fish hosts cannot explain enigmatic declines because the fish fauna in affected streams usually remains intact, as discussed previously. Even if changes in the fish fauna occur, these changes would have selective effects on particular species instead of fauna-wide effects including host generalists and specialists on many different fishes. Overharvest cannot explain enigmatic declines because few affected streams experienced commercial harvest of any kind, which was restricted mainly to large rivers, particularly since the 1960s (Haag 2012). Radical habitat alteration, such as channelization and dams, is eliminated by definition (no smoking gun), but indirect effects of dams are possible (see subsequent). The effects of climate change on mussels are poorly known, but those factors are expected to have selective effects depending on differences in thermal sensitivity among species (Galbraith et al. 2010).

Two major problems with the conventional wisdom for explaining any type of mussel decline is that many factors are vague, and the importance of some prominent factors is not well tested. Factors such as “habitat degradation,” “poor land use,” “pollution,” and “run-off” are cited repeatedly in studies of mussel declines (Strayer et al. 2004; Downing et al. 2010), but these terms provide neither a specific mechanism for those declines nor specific guidance for conservation. Sedimentation

is perhaps the most frequently cited explanation for mussel declines (e.g., Brim Box and Mossa 1999). Recent experimental or modeling studies support a role of elevated suspended sediment in mussel reproductive failure or population declines (Gascho Landis 2016; Hansen et al. 2016), but studies in the wild are conflicting. Increases in deposited fine sediment and substrate embeddedness are associated with recruitment failure of *Margaritifera margaritifera* in oligotrophic streams (Geist and Auerswald 2007; Denic and Geist 2015), but no such relationships have been found for unionids in eutrophic, warmwater streams (Strayer and Malcom 2012; Denic et al. 2014), which describes most or all streams in Table 5. At this time, the role of sedimentation in mussel declines remains poorly understood (reviewed by Haag 2012).

Aquatic habitats and ecosystems doubtless are degraded by sediment and other results of human land use (e.g., Waters 1995), but there are two logical flaws in using them to explain enigmatic mussel declines. First, these factors are expected to have long-term, cumulative, and broad-based effects on aquatic ecosystems corresponding to well over a century of intensive human alteration of the landscape. For example, over 75% of conversion of forest lands to other uses occurred prior to 1900, and many watersheds in areas affected by enigmatic declines were clear cut prior to 1920 but are now reforested (Clark 1984; USDA Forest Service 2001). Long-term, cumulative, and broad-based effects are not concordant with the abrupt, rapid decline of mussel populations seen since the 1960s and the lack of similarly rapid effects on other components of those ecosystems. Second, long-term degradation of stream habitats should have predictably selective effects on aquatic species, resulting in a homogenization of those faunas (McKinney and Lockwood 1999). Such homogenization is seen in impounded streams, where mussel faunas are dominated by a highly predictable group of impoundment-tolerant species with similar life history traits (Haag 2012). Similarly, mussel species losses in Midwestern rivers are attributed to long-term increases in sediment loads, but those rivers continue to support large populations of a characteristic group of species that apparently can thrive under such conditions (Sietman 2007). Outcomes of enigmatic declines also are highly predictable, but only in the characteristic decline or loss of the entire fauna, including species that typically tolerate habitat degradation.

Other, more specific factors in the conventional wisdom remain highly plausible explanations for enigmatic declines. Inputs of agricultural contaminants such as pesticides and nitrogenous fertilizers increased exponentially since the 1960s, coincident with the advent of enigmatic declines (Vitousek et al. 1997; Nowell et al. 1999). Research suggests an especially important role of unionized ammonia, which is acutely toxic to mussels but less toxic to other aquatic organisms, potentially explaining the mussel-specific effects of enigmatic declines (Augsburger et al. 2003; Wang et al. 2007; see also Strayer and Malcom 2012). This is a compelling mechanism in some cases. For example, the Red River, Tennessee, the Little and

Nolin rivers in Kentucky, and the Conasauga River in Georgia are in intensely agricultural regions and show elevated nitrogen loading, which creates conditions favorable for ammonia formation; pesticide contamination is also prevalent in these streams (Sharpe and Nichols 2007; Haag et al. 2019).

Despite the compelling case for a role of agricultural contaminants, intensive agriculture is of limited occurrence in many affected streams, particularly in the Appalachian, Ozark, and Ouachita highlands. Horse Lick Creek and the Little South Fork have little row-crop agriculture in their largely forested watersheds, and agricultural contaminants are absent or present at low concentrations (Haag et al. 2019). Initially, declines in these two streams were attributed to coal mining, which was plausible because of the advent of mining activity in the lower portions of both watersheds in the late 1970s and 1980s (Houslet and Layzer 1997; Warren and Haag 2005). However, mining became a more tenuous explanation in these streams as the declines moved upstream beyond mined areas (see “Upstream Progression”). Coal mining is a likely cause of mussel declines in some areas, particularly those affected by severe pollution such as acid-mine drainage (e.g., Clayton et al. 2015), but I did not consider declines in streams with documented coal mine pollution as enigmatic (e.g., Powell River, Virginia; Zipper et al. 2016). The lack of satisfactory explanations for enigmatic declines in many streams such as Horse Lick Creek and the Little South Fork calls into question the veracity of factors used to explain similar declines at similar times in other streams.

An important implication of viewing enigmatic declines as a distinct phenomenon is that it compels us to search for factors common to all affected streams. Even though enigmatic declines appear restricted to specific regions, the affected areas encompass a wide diversity of landscapes and land uses. Consequently, enigmatic declines typically are explained by invoking whichever factors from the conventional wisdom appear plausible in a particular stream, whether or not supporting information is available. Enigmatic declines in agricultural regions typically are attributed to agricultural contaminants, sediment, and related effects, while declines in urbanizing watersheds are explained by issues such as proliferation of impervious surfaces. Enigmatic declines without obvious or satisfactory explanations often are attributed to multiple, often vague factors. Haag and Warren (2004) explained the mussel decline in Horse Lick Creek as “likely a result of ongoing contamination from reclaimed and abandoned coal mines, as well as possible contamination from other, unidentified sources.” Out of 45 peer-reviewed papers dealing with mussel declines, more than half invoked multiple factors, and up to eight factors were invoked in a single paper (Strayer et al. 2004).

We cannot rule out the possibility that enigmatic declines are caused by multiple, varying factors in different streams. However, the multiple-factor explanation seems unlikely for two reasons. First, most or all of the factors in the conventional wisdom are present throughout much of the USA, and it is difficult to imagine how they could be so harmful in the

affected region but not in others. Second, the probability of all of these factors coming into play to produce such disastrous effects suddenly and virtually simultaneously across a large, heterogeneous area seems very low.

If we assume that enigmatic declines are caused by a single factor, this leads us to consider if any factors in the conventional wisdom or elsewhere can reasonably explain enigmatic declines in all affected streams. Such a factor needs to satisfy two requirements: (1) it is present in all affected streams and (2) it was absent prior to the 1960s.

Stream fragmentation and associated effects of isolation and small population size are not usually considered in the conventional wisdom. However, nearly all streams affected by enigmatic declines are isolated to some extent by impoundments or other stretches of highly modified stream habitats, and fragmentation generally occurred prior to the 1960s, thus potentially satisfying both requirements. Fragmentation is a likely mechanism for the selective disappearance of large river species in the lower reaches of smaller streams because these populations were probably sustained by immigration from mainstem rivers, which are now impounded (Haag 2009). In contrast, for several reasons, fragmentation is an unlikely explanation for the rapid, fauna-wide collapse characteristic of enigmatic declines. First, mussel assemblages eliminated from mainstem rivers by impoundment differed substantially from assemblages in unimpounded tributaries. Assemblages in Cumberland River tributaries such as the Rockcastle and Stones rivers were dominated by or included *Villosa taeniata*, *Lampilis fasciola*, *Medionidus conradicus*, and other species that were rare or absent in the mainstem (Wilson and Clark 1914; Neel and Allen 1964), making it unlikely that they were sustained by mainstem populations. Second, a biogeographic analysis of the Cumberland River system based on regional species-area relationships showed that tributaries should have been large enough to support nearly their entire historical mussel assemblage even after loss of mainstem populations (Haag 2012); these streams have largely maintained their fish and snail faunas after isolation. Third, like long-term habitat degradation, effects of fragmentation should be gradual and selective. Initially abundant species, particularly those not sustained by mainstem populations, should decline more slowly (or not at all) than species initially present as small populations; such patterns are not seen in enigmatic declines. Finally, nearly all streams in the United States are fragmented and isolated to some extent (Benke 1990), begging the question: why are enigmatic declines restricted to certain regions?

I am aware of only two factors that fit the requirements stated above. The first is disease. Disease is rarely considered as a factor in mussel declines, except for its potential role in mussel die-offs (Neves 1987). At this time, few potential pathogens of freshwater mussels have been identified in North America, and none have been linked conclusively to mussel declines or die-offs (reviewed in Grizzle and Brunner 2009 and Haag 2012). Disease could explain the rapid pace of enigmatic declines, but several important issues about this

explanation need to be examined. First, most identified bivalve pathogens are highly species-specific (e.g., Allam et al. 2006). To explain enigmatic declines, a pathogen would need to be both highly virulent to all unionid species and nonvirulent to nonnative *Corbicula fluminea*, which persists in affected streams. Second, the persistence of aging, adult mussels suggests that a pathogen would need to be particularly virulent to younger life stages. Third, and importantly, there would need to be a mechanism that restricts the effects or occurrence of a pathogen to the affected geographic regions. Even within those regions, some streams continue to support apparently healthy mussel populations, including large, impounded streams that receive flow from affected streams (e.g., Garner and McGregor 2001). Nevertheless, disease is an understudied factor that deserves more attention. Raising these issues here is not meant to discount disease as a potential factor; rather, these issues should be viewed as the basis for testable hypotheses about their mode of action.

The other factor that could explain enigmatic declines is the invasive Asian Clam, *Corbicula fluminea*. Several mechanisms by which *Corbicula* could negatively affect native mussels have been proposed, including food competition; ingestion of mussel sperm, glochidia, and juveniles; habitat disturbance by burrowing; and water quality degradation associated with periodic, mass *Corbicula* die-offs (reviewed by Strayer 1999). Even if *Corbicula* does not directly affect native mussels, it could be a vector for disease. Compared with another invasive bivalve, *Dreissena polymorpha*, *Corbicula* has received little attention as a possible explanation for mussel declines, and some authors have effectively dismissed this possibility (e.g., Vaughn and Spooner 2006; Haag 2012). *Dreissena* does not occur in most streams affected by enigmatic declines, but *Corbicula* occurs throughout the affected region (Foster et al. 2019).

The arrival of *Corbicula* coincides remarkably closely with the advent of enigmatic declines. *Corbicula* first appeared in Stansbery's collections from the Rockcastle, Cumberland, and East Fork Stones rivers in 1967, 1972 and 1970, respectively, almost precisely at the time that native mussel populations crashed in those streams (Tables 6–8). *Corbicula* was first reported in the Conasauga River in 1970, one year before Athearn described the stream as “ailing” (Foster et al. 2019). In the Little South Fork Cumberland River, *Corbicula* moved upstream about 20 km between 1981 and 1987, which closely followed the upstream progression of the native mussel decline (data from Starnes and Bogan 1982; Anderson et al. 1991). Arrival of *Corbicula* in the Little Tennessee River, between 2002 and 2004, was followed immediately by an abrupt decline in mussel abundance, including an 80% decline in *Alasmidonta raveneliana* by 2006 (Jarvis 2011; S. Fraley personal communication). Most studies of *Corbicula*–native mussel interactions are dated and anecdotal (see Strayer 1999), but a growing body of experimental evidence shows a strong potential for food competition with native mussels (Hakenkamp and Palmer 1999; Yeager et al. 2000; Ferreira-Rodríguez and Pardo 2017; Ferreira-Rodríguez et al. 2018).

Finally, *Corbicula* is mostly absent in the northern USA, which could explain the absence of enigmatic declines in that region (but see subsequent).

There are at least two issues related to invoking *Corbicula* as a mechanism for enigmatic declines. Competition with *Corbicula* should be stronger for juvenile mussels than adults to explain adult persistence in affected streams; such selective effects are plausible if juveniles have higher energetic requirements than adults. As with disease, the most important issue is that *Corbicula* occurs throughout the Coastal Plain, where enigmatic declines are not documented, and in streams in affected areas that continue to support mussel populations (e.g., Miller et al. 1986; Garner and McGregor 2001). To my knowledge, a mechanism by which native mussels could co-occur with *Corbicula* in some areas but not in others has not been proposed. One possibility is that smaller or less productive upland streams may have lower food resources, and mussels in these streams may be more vulnerable to food competition with *Corbicula*. Again, as with disease, these issues can form the basis of testable hypotheses. In my opinion, *Corbicula* is the most compelling single explanation for enigmatic mussel declines, and this potential factor deserves increased attention.

MOVING FORWARD: FOCUSING RESEARCH AND MANAGEMENT EFFORTS

Below I provide my perspective on how research and management can be focused to better understand and address mussel declines. My suggestions pertain most specifically to enigmatic declines, but they are relevant to any poorly understood decline or change in mussel assemblages.

Deemphasize the Conventional Wisdom

The most important initial step toward better understanding mussel declines is to acknowledge explicitly that we do not understand the causes of those declines in many cases. Mussel biologists should refrain from speculating about the causes of declines when no specific mechanisms are proposed and little or no supporting evidence is available. The conventional wisdom can provide a basis for testable hypotheses, but I believe that habitual recitation of vague or untested factors has hampered mussel conservation for two reasons. First, apart from propagation, most mussel conservation actions involve addressing “poor land use,” sedimentation, or related factors. These actions are likely to benefit streams broadly, but the precise role of these factors in mussel declines is poorly known, and they are unlikely causes of enigmatic declines. Second, habitual recitation of the conventional wisdom either has convinced policy-makers (and even many mussel biologists) that causes of mussel declines are understood, or it has confused them due to the myriad factors that are often invoked. A frank acknowledgment that causes remain largely unknown is more likely to encourage funding and creative

research, ultimately leading to more effective and targeted conservation strategies.

Revisit Previously Ignored or Poorly Understood Factors

An important need is for more research on potentially widespread, but largely ignored factors such as disease and *Corbicula*. It is also important that other poorly studied factors receive more critical evaluation. I have argued that sedimentation is an unlikely factor in enigmatic declines, but this assertion needs evaluation, and sedimentation may be important in other contexts. The prominence of sedimentation in the conventional wisdom may have discouraged additional research because investigators have the impression that its effects on mussels are well understood. Given the widespread increases in sediment in streams, this factor sorely deserves a fresh look.

Develop Better Assessment Approaches

Most existing information about potential causes of mussel declines comes from either (1) correlative or observational field studies or (2) laboratory toxicological studies. Field studies nearly always focus on correlations or qualitative associations of assemblage- or population-level responses with various factors. For example, a study may correlate land use at a specific time with species richness in a watershed. Such approaches are informative, but they rarely provide concrete information about specific factors or mechanisms, and they are not repeatable or replicable. They also are limited by the potentially long response time of mussel assemblages and populations to various factors; current assemblage condition may be a function of past events, and recovery may be a slow process. Another weakness of these approaches is that they do not allow us to assess present conditions in streams that have lost their mussel fauna and whether the causal factor for the decline is still in effect. Results of toxicological studies can be readily applied to the field by assessing exceedance of a contaminant above a critical level, but contaminant effects in the wild may be influenced by many environmental factors.

These approaches represent two opposite ends of the research spectrum, and both are essential, but the link between these approaches is underrepresented in our knowledge base. The link is measuring specific responses (e.g., survival, growth, physiological condition) of individual mussels to ambient conditions in the wild (e.g., Bartsch et al. 2003; Gagné et al. 2004; Nobles and Zhang 2015; Haag et al. 2019). This approach also may be correlative, but it provides a real-time assessment of mussel responses to current conditions (whether or not wild mussel populations exist), it is repeatable and replicable to a much greater extent than assemblage- or population-focused approaches, and it allows evaluation of toxicological results in a natural context. The availability of large numbers of propagated juvenile mussels makes this approach feasible with a minimal impact on wild populations. Studies of this nature typically are conducted by housing

mussels in enclosures. However, detailed monitoring of wild or reintroduced individuals and their responses to ambient conditions also provides opportunities to evaluate specific hypotheses about causes of mussel declines (e.g., Jones et al. 2012; Clayton et al. 2015; Stodola et al. 2017). For example, assessing changes in individual mussel performance over time in response to management actions meant to reduce sediment could provide valuable information about the effectiveness of such actions.

Don't Abandon Degraded Streams

The focus of much mussel research and management is on remaining high-quality mussel assemblages. It is essential to protect these assemblages, but degraded streams, particularly those with no clear source of impairment, are vital opportunities for research and conservation. For research, these streams are opportunities to identify and study factors that have severe, negative effects on mussel assemblages. For conservation, these streams represent hundreds of kilometers of potentially recoverable habitat. Recovery plans for nearly all threatened and endangered species stipulate creation of additional populations, and indeed, this is the only way to significantly reduce extinction risk. For many species, suitable locations for establishing additional populations do not exist unless streams affected by enigmatic declines can be rehabilitated. Mussel biologists (myself included) have tended to walk away from streams after loss of the mussel fauna. Horse Lick Creek and the Little South Fork have received little attention since the early 2000s, in contrast to the intense activity that occurred in those streams when they supported important mussel faunas. The elimination of the mussel fauna from a stream for unknown or poorly understood reasons should spur intensified research and management activity, not abandonment.

SUMMARY

Although mussel declines in general are well recognized, the severity and importance of enigmatic declines are underappreciated by the conservation community. One reason for this may be their restriction to specific regions, which are unfamiliar to many biologists. However, their occurrence closely overlies the region with the most species-rich mussel fauna on Earth. Enigmatic declines throughout that region have profoundly deepened the mussel conservation crisis in a few decades. For example, nearly all unimpounded tributaries of the Cumberland River have experienced enigmatic declines, placing that system's unique species and assemblages in imminent danger of extinction. Another reason for the underappreciation of enigmatic declines may be our failure to recognize them as a distinct, diagnosable phenomenon. I make the case that characteristics of enigmatic declines support such a view, but this assertion needs further evaluation. Regardless, it is essential that we discover the causes of these declines, including the reasons for their

puzzling restriction to smaller streams and specific geographic areas. Until enigmatic declines are better understood, mussel conservation in affected areas is substantially hamstrung, and conservation in other areas faces the possibility that the scope of enigmatic declines will expand.

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