

FRESHWATER MOLLUSK BIOLOGY AND CONSERVATION

THE JOURNAL OF THE FRESHWATER
MOLLUSK CONSERVATION SOCIETY

VOLUME 26

NUMBER 1

MARCH 2023

Pages 1-10

Further bacteriological analysis of annual Pheasantshell (*Actinonaias pectorosa*) mussel mortality events in the Clinch River (Virginia/Tennessee), USA, reveals a consistent association with *Yokenella regensburgei*

Eric M. Leis, Sara Dziki, Jordan Richard, Rose Agbalog, Diane Waller, Joel Putnam, Susan Knowles, and Tony Goldberg

Pages 11-19

Changes in the mussel fauna of the Jacks Fork, Missouri over 35 years and relationships with species traits

Stephen E. McMurray and J. Scott Faiman

Pages 20-31

Gains and gaps in knowledge surrounding freshwater mollusk ecosystem services

Carla L. Atkinson, Garrett W. Hopper, Danielle A. Kreeger, Jonathan W. Lopez, Alexa N. Maine, Brandon J. Sansom, Astrid Schwalb, and Caryn C. Vaughn

Pages 32-44

Assessing potential habitat for freshwater mussels by transferring a habitat suitability model within the Ozark ecoregion, Missouri

Jordan H. Hartman, Amanda E. Rosenberger, Kayla N. Key, and Garth Lindner



REGULAR ARTICLE

FURTHER BACTERIOLOGICAL ANALYSIS OF ANNUAL PHEASANTSHELL (*ACTINONAIAS PECTOROSA*) MUSSEL MORTALITY EVENTS IN THE CLINCH RIVER (VIRGINIA/TENNESSEE), USA, REVEALS A CONSISTENT ASSOCIATION WITH *YOKENELLA REGENSBURGEI*

Eric M. Leis^{1*}, Sara Dziki¹, Jordan Richard^{2,3}, Rose Agbalog³, Diane Waller⁴, Joel Putnam⁴, Susan Knowles⁵, and Tony Goldberg³

¹ U.S. Fish and Wildlife Service, La Crosse Fish Health Center–Midwest Fisheries Center, Onalaska, WI 54650 USA

² U.S. Fish and Wildlife Service, Southwestern Virginia Field Office, Abingdon, VA 24210 USA

³ Department of Pathobiological Sciences and Freshwater & Marine Sciences Program, University of Wisconsin–Madison, Madison, WI 53706 USA

⁴ U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI 54603 USA

⁵ U.S. Geological Survey, National Wildlife Health Center, Madison, WI 53711 USA

ABSTRACT

Pheasantshell (*Actinonaias pectorosa*) mussels in the Clinch River (Tennessee/Virginia, USA) have declined dramatically in recent years. The bacterium *Yokenella regensburgei* was first isolated with high prevalence from Pheasantshells during the peak of a 2017 mortality event, but it was not identified after mortality subsided a few months later. Since 2017, Pheasantshell mortality in the Clinch River has occurred each autumn. We extended the investigation of culturable bacterial communities in the Clinch River during mussel mortality events in 2018, 2019, and 2020 and examined the spatial and temporal distribution of bacterial genera among Pheasantshells, as well as among other unionid mussels. We identified *Y. regensburgei* each year, almost exclusively during active mortality events. The significance of *Y. regensburgei* remains unclear, but the continued association of this bacterium with mussel mortality events warrants further study.

KEY WORDS: *Actinonaias pectorosa*, Pheasantshell mussel, Unionidae, *Yokenella regensburgei*, Clinch River, Virginia, mortality event

INTRODUCTION

Large-scale mortality events and declines in mussel populations have occurred with increasing frequency in recent decades (Strayer et al. 2004). Clear explanations, such as toxic spills, have been identified in some cases; in others, disease has been suspected, but not confirmed (Neves 1987; Haag 2019). Beginning in summer 2016, biologists observed a mass mortality event affecting numerous mussel species in the

Virginia and Tennessee portions of the Clinch River. Subsequent investigations revealed that mortality recurred seasonally from late summer to early autumn. Although many species were observed dead or moribund, the Pheasantshell (*Actinonaias pectorosa*) mussel was affected disproportionately. Pheasantshell initially was among the most abundant species in the Clinch River, but population sizes declined 50–80% across multiple sites after mortality events (Richard 2018). In response to the mortality event in the Clinch River and a contemporaneous multispecies mortality event in Big Darby Creek, Ohio, USA, a research group was formed to

*Corresponding Author: eric_leis@fws.gov

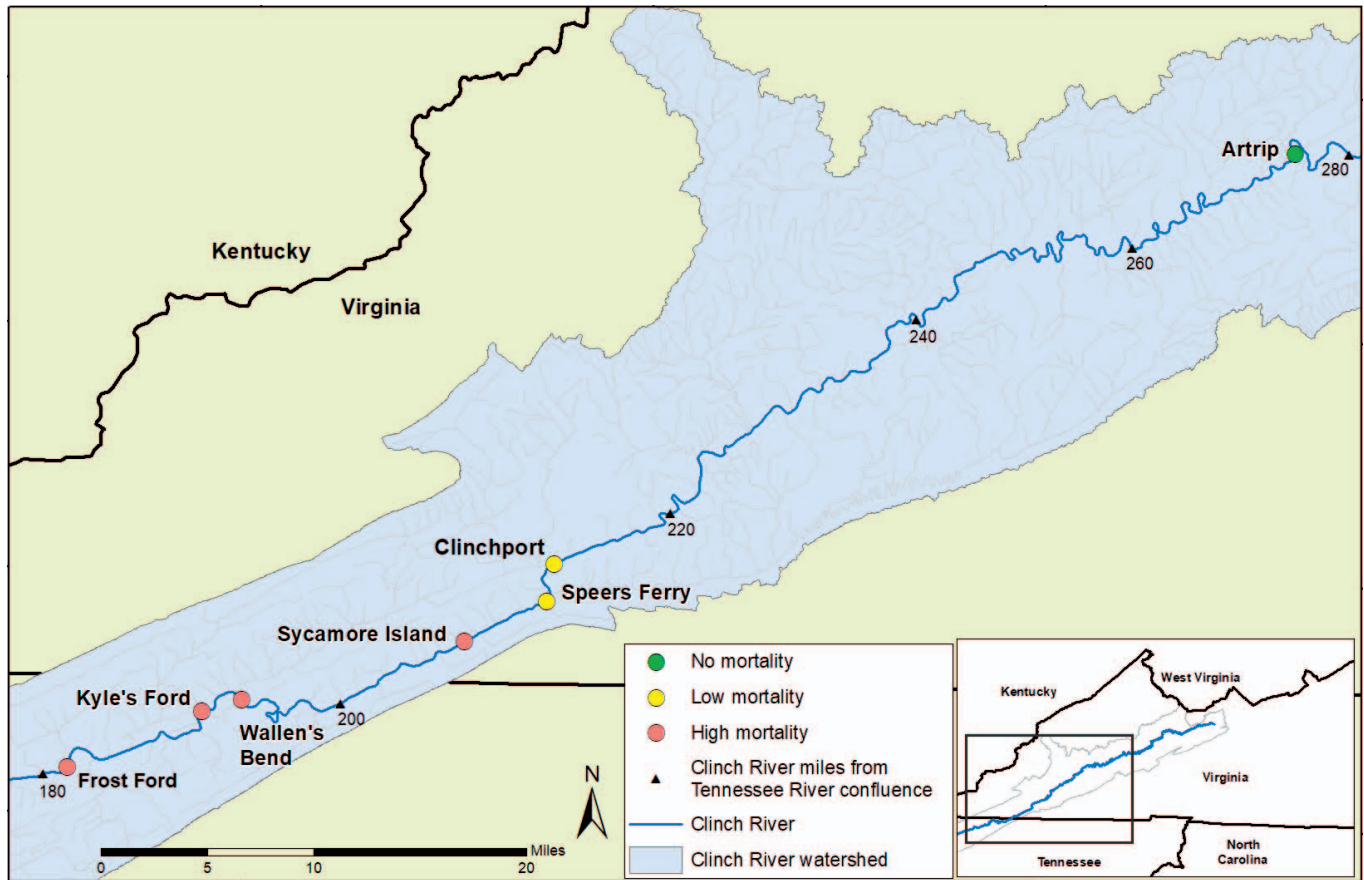


Figure 1. Locations where hemolymph samples were collected from mussels in the Clinch River, USA. Inset map shows location of the study area in southwestern Virginia and northeastern Tennessee.

study the events and gather baseline data to identify potential pathogens (Leis et al. 2018). The group reported a picorna-like virus from a Wabash Pigtoe (*Fusconaia flava*) in the upper Mississippi River (Goldberg et al. 2019); 17 novel viruses, including a densovirus associated with moribund mussels in the Clinch River (Richard et al. 2020); and a novel gonadotropic microsporidian (Knowles et al. 2022). They also conducted molecular and culture-based evaluations of the bacterial composition of mussel hemolymph from several river systems in the eastern United States (Leis et al. 2019; Richard et al. 2021).

In a previous study, we examined culturable bacteria associated with a 2017 mussel mortality event in the Clinch River (Leis et al. 2019). We identified many bacterial genera, but only *Yokenella regensburgei* was detected with high prevalence in Pheasantshells while mortalities were occurring, and it was not present a few months later after mortality subsided. This bacterium was previously identified from a mussel mortality event in the Tennessee River (Starliper et al. 2011), but whether it plays a direct role in such events remains unknown. Since 2017, episodic mortality of Pheasantshells has continued each autumn in the Clinch River. We investigated bacterial communities in the Clinch River during mussel mortality events in 2018, 2019, and 2020 and examined the

spatial and temporal prevalence of bacterial genera among Pheasantshell and other unionid species.

METHODS

We collected samples from live and moribund mussels at seven sites in the Clinch River in 2018, 2019, and 2020 (Fig. 1 and Table 1). After observing mussel mortality in autumn 2016 and 2017, we established a series of sampling sites within and upstream of the zone of observed mortality and began sampling in summer 2018. We sampled six sites monthly from August to October 2018. High rainfall forced us to abandon planned sampling events in November and December 2018. In 2018, we sampled Pheasantshell and Mucket (*Actinonaias ligamentina*); the annual Pheasantshell mortality event began in September and no moribund Muckets were observed (Table 1). In 2019, we observed a mortality event that began in September and sampling occurred at Sycamore Island while the event was ongoing in October. We sampled moribund Pheasantshells and apparently healthy individuals of Mucket, Pocketbook (*Lampsilis ovata*), Threeridge (*Amblema plicata*), Kidneyshell (*Ptychobranchus fasciolaris*), Wavyrayed Lampmussel (*Lampsilis fasciola*), and Purple Wartyback (*Cyclonaias tuberculata*). We observed

Table 1. Isolation and prevalence of *Yokenella regensburgei* in Clinch River, USA, mussels from 2018 to 2020. *A. ligamentina* = *Actinonaias ligamentina*; *A. pectorosa* = *Actinonaias pectorosa*; *A. plicata* = *Amblema plicata*; *P. fasciolaris* = *Ptychobranchus fasciolaris*; *L. fasciola* = *Lampsilis fasciola*; *C. tuberculata* = *Cyclonaias tuberculata*; *E. brevidens* = *Epioblasma brevidens*; *L. ovata* = *Lampsilis ovata*. *N* = number of individuals sampled.

Sampling Month and Year	Location	Mussel Species (<i>N</i>)	Active Mortality Observed	Prevalence of <i>Yokenella</i> (%)
August 2018	Sycamore Island	<i>A. pectorosa</i> (2)	No	0
		<i>A. ligamentina</i> (2)	No	0
	Wallen's Bend	<i>A. pectorosa</i> (2)	No	50
		<i>A. ligamentina</i> (2)	No	0
	Kyle's Ford	<i>A. pectorosa</i> (2)	No	0
		<i>A. ligamentina</i> (2)	No	0
Frost Ford	<i>A. pectorosa</i> (2)	No	0	
	<i>A. ligamentina</i> (2)	No	0	
September 2018	Artrip	<i>A. pectorosa</i> (3)	No	0
	Speers Ferry	<i>A. pectorosa</i> (3)	No	0
	Sycamore Island	<i>A. pectorosa</i> (5)	Yes	60
	Wallen's Bend	<i>A. pectorosa</i> (5)	Yes	40
	Kyle's Ford	<i>A. pectorosa</i> (6)	Yes	33
October 2018	Artrip	<i>A. pectorosa</i> (3)	No	0
		<i>A. pectorosa</i> (4)	Yes	25
	Sycamore Island	<i>A. ligamentina</i> (1)	No	0
		<i>A. pectorosa</i> (6)	Yes	0
October 2019	Kyle's Ford	<i>A. ligamentina</i> (1)	No	0
		<i>A. pectorosa</i> (6)	Yes	17
	Sycamore Island	<i>A. pectorosa</i> (2)	Yes	50
		<i>A. ligamentina</i> (4)	No	0
<i>L. ovata</i> (2)		No	0	
<i>A. plicata</i> (2)		No	0	
October 2020	Speers Ferry/Sycamore Island/Clinchport	<i>P. fasciolaris</i> (1)	No	0
		<i>L. fasciola</i> (2)	No	0
		<i>C. tuberculata</i> (1)	No	0
		<i>A. pectorosa</i> (7)	Yes	86
		<i>A. pectorosa</i> (9)	Yes	89
		<i>A. ligamentina</i> (1)	Yes	100
		<i>E. brevidens</i> (1)	Yes	100

mortality in October 2020 and collected targeted samples consisting of moribund Pheasant shells combined from three adjacent sites: Speers Ferry, Sycamore Island, and Clinchport. Later in the month, we also sampled moribund Pheasant shells, Muckets, and Cumberlandian Combshells (*Epioblasma brevidens*) from Sycamore Island.

In 2018 and 2019, we collected hemolymph from the anterior adductor muscle of each mussel by slightly opening the shell with a child nasal speculum, placing a stopper between the shells, and drawing out a hemolymph sample with a 1-mL syringe and 25-gauge needle. After collecting each sample, we immediately plated and streaked approximately 100 μ L of hemolymph onto sterile tryptic soy agar culture plates (Becton Dickinson, Le Pont de Claix, France). Plates were shipped overnight to the U.S. Fish and Wildlife Service, La Crosse Fish Health Center, La Crosse, Wisconsin. We incubated the plates at 21°C for 7–14 d. After incubation, we

used a sterile, disposable loop to remove morphologically unique colonies from each plate; placed them in a microcentrifuge tube; and extracted DNA by using the PrepMan™ Ultra Sample Preparation Reagent (Thermo Fisher Scientific, Waltham, MA, USA). We subjected the extracted DNA to 16S rRNA gene PCR by using the same primers used by Leis et al. (2019), followed by Sanger sequencing (Eton Biosciences, Union, NJ, USA). We then edited and assembled the sequences de novo by using the default parameters in Geneious v11.1.5 (<https://www.geneious.com/download/previous-versions/#geneious-r11-dot-1> [accessed August 19, 2022]), and we identified resulting contig sequences through megaBLAST searches in the National Center for Biotechnology Information database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi> [accessed August 19, 2022]). In 2020, moribund mussels were wrapped in wet towels and sent on ice to the La Crosse Fish Health Center for processing as described above. Because

Table 2. Prevalence of the six most common bacterial genera and samples yielding no bacterial isolates in moribund and healthy Pheasantshell (*Actinonaias pectorosa*) mussels collected in Clinch River, USA, from 2018 to 2020. An asterisk (*) indicates statistically significant differences in prevalence between healthy and moribund mussels (Fisher's exact test: $P \leq 0.002$). N = number of individuals sampled.

	<i>Yokenella</i> * (%)	<i>Aeromonas</i> * (%)	<i>Bacillus</i> (%)	<i>Pseudomonas</i> (%)	<i>Microbacterium</i> (%)	<i>Acinetobacter</i> (%)	No Isolates (%)
Healthy ($N = 33$)	9.1	0.0	24.2	21.2	21.2	9.1	27.3
Moribund ($N = 34$)	64.7	26.5	11.8	11.8	8.8	8.8	11.8

Pheasantshell was the primary species observed in moribund condition, we used Fisher's exact tests to examine whether there were nonrandom associations between frequently observed bacterial genera and healthy or moribund Pheasantshell samples. For each bacterial genus present in six or more Pheasantshells, as well as for the condition of "no bacterial growth observed," we set up a 2×2 contingency table with categories of bacteria presence/absence and healthy/moribund mussels. Pheasantshell samples within the moribund and healthy groups were pooled across all sites and dates from the study. The results of each Fisher's exact test indicate whether there was a statistically significant association between the presence of a particular bacterial genus and Pheasantshell health status.

RESULTS

We examined a total of 91 mussels (67 Pheasantshells, 15 Muckets, 1 Cumberlandian Combshell, 1 Purple Wartback, 2 Wavyrayed Lampmussels, 1 Kidneyshell, 2 Threeridges, and 2 Pocketbooks), including 49 healthy and 42 moribund individuals, from the Clinch River during 2018, 2019, and 2020. Bacteria were isolated from 80% (73 of 91) of the mussels sampled; 18 mussel samples yielded no bacterial isolates. All the cultured colonies were identifiable, except for two isolates from Muckets sampled on August 16, 2018, and October 25, 2018.

Across all sampling seasons, we identified 190 isolates belonging to 46 bacterial genera from 91 individual mussel hemolymph samples (49 apparently healthy, 42 moribund; Appendix A1). Most bacterial genera were observed only rarely, with 39 of the 46 genera present in three or fewer individual mussels and one present in four individuals (Appendix A1). The six most common genera identified were (in order of decreasing abundance) *Yokenella*, *Bacillus*, *Microbacterium*, *Pseudomonas*, *Aeromonas*, and *Acinetobacter*. The most common isolates for healthy mussels were *Bacillus* (27%; 13 of 49), *Microbacterium* (20%; 10 of 49), and *Pseudomonas* (16%; 8 of 49), with all other genera present in four or fewer individuals. The most common isolates for moribund mussels were *Yokenella* (57%; 24 of 42), *Aeromonas* (26%; 11 of 42), and *Bacillus* (14%; 6 of 42), with all other genera present in four or fewer individuals. *Yokenella* was observed in only three healthy individuals, whereas *Aeromonas* was never observed in healthy individuals. The prevalence of *Yokenella* and *Aeromonas* was significantly

higher in moribund than healthy Pheasantshells (Fisher's exact test: $P < 0.0001$ and $P = 0.0021$, respectively; Table 2). The prevalence of the other four most common genera and the prevalence of samples yielding no bacterial isolates were not significantly different between moribund and healthy Pheasantshells (Table 2).

We observed *Y. regensburgei* each year during active mortality events in the Clinch River. Sequences identified as *Y. regensburgei* shared >99.3% similarity and were between 636 and 1,375 bp (Appendix A1). In 2018, *Y. regensburgei* was present in Pheasantshells at Speers Ferry, Sycamore Island, Wallen's Bend, and Kyle's Ford, all of which are sites where moribund mussels were observed (Table 1). The bacterium was not isolated from apparently healthy Muckets sampled at these sites or from any samples collected at Artrip, an upstream site where Pheasantshell mass mortality has not been observed. All detections of *Y. regensburgei* in Pheasantshells occurred during periods of active mortality, except for one isolation from Wallen's Bend on August 16, 2018, which preceded our first observations of mortality by several weeks.

In 2019, *Y. regensburgei* was isolated from Pheasantshell, but not from six other mussel species; active mortality of Pheasantshells was also observed (Table 1). In 2020, during sampling that targeted moribund mussels, *Y. regensburgei* was isolated from 86% of Pheasantshells at three sites on October 7 and from 89% of Pheasantshells at Sycamore Island on October 20. *Yokenella regensburgei* also was isolated from moribund Muckets and Cumberlandian Combshell on October 20 (Table 1).

Aeromonas was detected only in 2020, when it was present in 11 of 18 moribund mussels collected. In one of these samples, two *Aeromonas* isolates were the only bacteria cultured, whereas in the remaining 10 samples containing *Aeromonas*, it co-occurred with *Yokenella*.

The prevalence of *Bacillus* spp. did not differ between apparently healthy mussels (44%; 16 of 36) and moribund mussels (17%; 6 of 36; Fisher's exact text: $P = 0.1986$).

DISCUSSION

The consistent association of *Y. regensburgei* with mussel mortality events and moribund mussels was one of the strongest and most conspicuous patterns of bacterial occurrence in our samples. We isolated *Y. regensburgei*, generally with high prevalence, during mortality events in every year of our study, and it was previously isolated during a mortality

event in 2017 (Leis et al. 2019). Furthermore, it was rarely identified when mortality events were not occurring or at sites where mortality has not been observed (Artrip). The only occurrence of *Y. regensburgei* outside of a mortality event was its detection in an apparently healthy Pheasantshell on August 16, 2018, at Wallen's Bend; this may have represented an incipient occurrence at the onset of mussel mortality, which was observed a few weeks later at this site.

Yokenella regensburgei, along with predominantly *Hafnia alvei*, was identified from Ebonyshell (*Reginaia eburnus*) during mortality events in the Tennessee River, Alabama (2006 and 2008), and *H. alvei* was previously identified from the Clinch River (Starliper et al. 2008, 2011). *Hafnia alvei* and *Y. regensburgei* both are enteric bacteria that share similar biochemical characteristics, making separation of the two species uncertain by using traditional laboratory diagnostic methods (Lo et al. 2011). It is unclear whether Starliper et al. (2011) used molecular or biochemical techniques to identify *Y. regensburgei* and *H. alvei*. Furthermore, the Analytical Profile Index database (Biomérieux, Marcy-l'Étoile, France; <https://www.biomerieux-diagnostics.com/sites/clinic/files/9308960-002-gb-b-apiweb-booklet.pdf> [accessed December 5, 2022]) used by Starliper et al. (2008) would have been unable to identify *Y. regensburgei* because that species is not included in the database, but *H. alvei* is included. Because of this limitation, it is possible that *Y. regensburgei* was present at higher prevalence during the Tennessee River mortality event. Our molecular methods should have allowed accurate separation of the two species, but neither we nor Richard et al. (2021) detected *H. alvei* in samples of mussel hemolymph from the Clinch River.

Despite the consistent association of *Y. regensburgei* with mussel mortality events, its role in these events is unclear. At least two scenarios could explain this association. The first scenario is that this bacterium is pathogenic. Preliminary histopathology work does not support pathogenicity (S. Knowles, unpublished data), but additional research is needed to confirm this result. The second scenario is that *Y. regensburgei* opportunistically colonizes mussels that are stressed and of compromised health due to a separate insult, such as exposure to environmental toxins or degraded water quality (see Leis et al. 2019). Richard et al. (2021) found a shift in bacterial communities of mussel hemolymph when mussels exhibit signs of apparent disease. An important question is whether there is a relationship between *Y. regensburgei* and Clinch densovirus 1 or other viruses identified from the Clinch River (Richard et al. 2020). For example, are these organisms pathogenic, or does a separate environmental factor (e.g., toxins, thermal stress, changes in water chemistry or algal communities) result in an immunocompromised state that allows unchecked bacterial growth and viral replication? Another important question is whether *Y. regensburgei* is consistently associated with mussel mortality events in other watersheds. Future work evaluating the importance of this bacterium would involve the development of a diagnostic assay to rapidly identify *Y. regensburgei* in

mussels, which could also be used to search for potential environmental sources or reservoirs and to better understand the seasonality of its occurrence. In addition, *in vivo* infection trials are needed to evaluate the pathogenicity of *Y. regensburgei* to Pheasantshell and other mussel species, alone and in combination with other factors.

Although the prevalence of *Bacillus* spp. did not differ significantly between healthy and moribund mussels, there was a suggestive trend of higher prevalence in healthy mussels, a trend also noted by Leis et al. (2019). Members of *Bacillus* have several characteristics that, hypothetically, could be considered beneficial to freshwater mussels (see Leis et al. 2019). The lack of a significant difference in the prevalence of *Bacillus* between healthy and moribund mussels could be due to the persistence of these bacteria in moribund mussels after the onset of disease. Additional studies are needed to evaluate potential associations of *Bacillus* spp. with mussel health.

The strong pattern of co-occurrence between *Aeromonas* and *Yokenella* in 2020 is intriguing because it also was observed by Richard et al. (2021) (their study included samples from Clinch River mussels in 2017–2018) and Leis et al. (2019) (their study included samples from Clinch River mussels in 2017). Both studies found high *Aeromonas* spp. and *Yokenella* prevalence associated with moribund mussels from mortality sites, and the two genera often co-occurred in samples. However, Richard et al. (2021) found high *Aeromonas* spp. prevalence in 2018 samples from Clinch River mussels, whereas we observed *Aeromonas* spp. only in samples collected in 2020. It is possible these discrepancies are due to differences between metagenomics and culture-based techniques, differences in sampling strategy, or other factors. Gill et al. (2022) observed an increase in potentially pathogenic *Aeromonas* in gut samples from Plain Pocketbook (*Lampsilis cardium*) after experimental exposure to mixed agricultural contaminants. It is possible that the *Aeromonas* represents late-stage opportunistic infections of individuals previously stressed by pathogens, contaminants, or other stressors. Future field studies and experimental infection challenges would aid our understanding of the role of these bacteria in mussel mortality events.

DATA AVAILABILITY STATEMENT

Data for this study are available in Leis et al. (2022) (<https://doi.org/10.5066/P9SARYP3> [accessed December 5, 2022]).

ACKNOWLEDGMENTS

We thank John Fisher from the National Conservation Training Center Library (Shepherdstown, WV, USA) for help locating references. All collections were conducted with required federal, state, and local permits. Samples of Cumberlandian Combshell were collected under the authority of 50 CR 17.21(c)(3)(iii). The use of trade, firm, or product

names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and the U.S. Geological Survey and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

LITERATURE CITED

- Gill, S. P., D. R. Learman, M. L. Annis, and D. A. Woolnough. 2022. Freshwater mussels and host fish gut microbe community composition shifts after agricultural contaminant exposure. *Journal of Applied Microbiology* 133:3645–3658.
- Goldberg, T. L., C. D. Dunn, E. Leis, and D. L. Waller. 2019. A novel picorna-like virus in a Wabash Pigtoe (*Fusconaia flava*) from the upper Mississippi River, USA. *Freshwater Mollusk Biology and Conservation* 22:81–84.
- Haag, W. R. 2019. Reassessing enigmatic mussel declines in the United States. *Freshwater Mollusk Biology and Conservation* 22:43–60.
- Knowles, S., E. M. Leis, J. C. Richard, R. Cole, R. E. Agbalog, J. G. Putnam, T. L. Goldberg, and D. L. Waller. 2022. A novel gonadotropic microsporidian parasite (*Microsporidium clinchi* n. sp.) infecting a declining population of Pheasantshell mussels (*Actinonaias pectorosa*) (Unionidae) from the Clinch River, USA. *Parasitologia* 2:1–12.
- Leis, E., S. Dziki, J. Richard, and D. L. Waller. 2022. Data release: Bacteria identified in freshwater mussels in the Clinch River, VA associated with mortality events from 2018 to 2020. U.S. Geological Survey data release. Available at <https://doi.org/10.5066/P9SARYP3> (accessed December 1, 2022).
- Leis, E., S. Erickson, D. Waller, J. Richard, and T. Goldberg. 2019. A comparison of bacteria cultured from unionid mussel hemolymph between stable populations in the upper Mississippi River basin and populations affected by a mortality event in the Clinch River. *Freshwater Mollusk Biology and Conservation* 22:70–80.
- Leis, E., D. Waller, S. Knowles, T. Goldberg, J. Putnam, J. Richard, S. Erickson, E. Blevins, and J. Weinzinger. 2018. Building a response network to investigate potential pathogens associated with unionid mortality events. *Ellipsaria* 20(4):44–45. Available at <https://molluskconservation.org/PUBLICATIONS/ELLIPSARIA/EllipsariaDec2018.pdf> (accessed December 1, 2022).
- Lo, Y. C., Y. W. Chuang, and Y. H. Lin. 2011. *Yokenella regensburgei* in an immunocompromised host: A case report and review of the literature. *Infection* 39:485–488.
- Neves, R. J. 1987. Recent die-offs of freshwater mussels in the United States: An overview. Pages 7–18 in R. J. Neves, editor. Proceedings of the workshop on die-offs of freshwater mussels in the United States. U.S. Fish and Wildlife Service and the Upper Mississippi River Conservation Committee, Davenport, Iowa.
- Richard, J. 2018. Clinch River mussel die-off. *Ellipsaria* 20:1–3. Available at <https://molluskconservation.org/PUBLICATIONS/ELLIPSARIA/EllipsariaMarch2018.pdf> (accessed December 1, 2022).
- Richard, J. C., L. J. Campbell, E. M. Leis, R. E. Agbalog, J. G. Putnam, C. D. Dunn, D. L. Waller, S. Knowles, and T. L. Goldberg. 2021. Mussel mass mortality and the microbiome: Evidence for shifts in the bacterial microbiome of a declining freshwater bivalve. *Microorganisms* 9:1976.
- Richard, J. C., E. Leis, C. D. Dunn, R. Agbalog, D. Waller, S. Knowles, J. Putnam, and T. L. Goldberg. 2020. Mass mortality in freshwater mussels (*Actinonaias pectorosa*) in the Clinch River, USA, linked to a novel densovirus. *Scientific Reports* 10:14498.
- Starliper, C. E., R. J. Neves, S. Hanlon, and P. Whittington. 2008. A survey of the indigenous microbiota (bacteria) in three species of mussels from the Clinch and Holston rivers, Virginia. *Journal of Shellfish Research* 27:1311–1317.
- Starliper, C. E., J. Powell, J. T. Garner, and W. B. Schill. 2011. Predominant bacteria isolated from moribund *Fusconaia ebena* Ebonyshells experiencing die-offs in Pickwick Reservoir, Tennessee River, Alabama. *Journal of Shellfish Research* 30:359–366.
- Strayer, D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton, and J. S. Nichols. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience* 54:429–439.

Appendix A1. Bacteria identified from mussels in the Clinch River, USA. Isolate refers to the number assigned to the mussel sample (number) and the isolate identification (letter). Location refers to the sampling locations as defined in Figure 1. Mussel species abbreviations are as follows: *A. ligamentina* = *Actinonaias ligamentina*; *A. pectorosa* = *Actinonaias pectorosa*; *A. plicata* = *Amblema plicata*; *P. fasciolaris* = *Ptychobranchus fasciolaris*; *L. fasciola* = *Lampsilis fasciola*; *C. tuberculata* = *Cyclonaias tuberculata*; *E. brevidens* = *Epioblasma brevidens*; *L. ovata* = *Lampsilis ovata*. Genus and species refer to the identifications of bacteria made through BLAST searches in the National Center for Biotechnology Information (NCBI) database (see text). Percent similarity represents the similarity of the isolate sequence to sequences in the NCBI database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi> [accessed August 19, 2022]). Length refers to the number of contiguous base pairs in the sequence for each isolate. Accession number refers to the top match or matches identified through the BLAST search of the NCBI database.

Isolate	Location	Mussel Species	Genus	Species	% Similarity	Length	Accession No(s).
August 16, 2018							
1B	Sycamore Island	<i>A. ligamentina</i>	<i>Microbacterium</i>	<i>testaceum</i>	100	901	MK618600.1
26A	Wallen's Bend	<i>A. ligamentina</i>	<i>Exiguobacterium</i>	<i>antarcticum/acetylicum</i>	100	817	MK478815.1/MH719376.1
26B	Wallen's Bend	<i>A. ligamentina</i>	Unidentifiable				
26C	Wallen's Bend	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>mycooides</i>	100	882	CP037992.1
26D	Wallen's Bend	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>pumilus/zhangzhouensis</i>	100	890	MK696261.1/MK131335.1
27A	Wallen's Bend	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>megaterium/aryabhatai</i>	100	893	MK027252.1/MK618612.1
45A	Kyle's Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>cereus/wiedmannii/thuringiensis</i>	100	778	MK696545.1/MK696254.1/MK696253.1
45C	Kyle's Ford	<i>A. ligamentina</i>	<i>Pseudoxanthomonas</i>	<i>japonensis/mexicana</i>	99.6	842	KX588601.1/KF135463.1
45D	Kyle's Ford	<i>A. ligamentina</i>	<i>Novosphingobium</i>	<i>barchaimii</i>	99.8	1212	KM019861.1
45E	Kyle's Ford	<i>A. ligamentina</i>	<i>Fictibacillus</i>	<i>phosphorivorans/nanhaiensis</i>	100	895	MG547923.1/MG049786.1
45F	Kyle's Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>cereus/mycooides/pseudomycooides/anthracis</i>	99.7	766	MK285635.1/MG694513.1/MG198676.1/MH261153.1
45G	Kyle's Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>mycooides</i>	99.9	816	MK719967.1
45I	Kyle's Ford	<i>A. ligamentina</i>	<i>Pseudomonas</i>	<i>rhodesiae</i>	100	907	MG571697.1
47A	Kyle's Ford	<i>A. ligamentina</i>	<i>Acinetobacter</i>	<i>guillouiae/lwoffii</i>	100	899	MK070050.1/MH930396.1
47B	Kyle's Ford	<i>A. ligamentina</i>	<i>Acinetobacter</i>	<i>guillouiae/johnsonii</i>	99.9	904	MH144279.1/MG788346.1
47C	Kyle's Ford	<i>A. ligamentina</i>	<i>Curtobacterium</i>	sp.	99.2	587	MK704290.1
47D	Kyle's Ford	<i>A. ligamentina</i>	<i>Microbacterium</i>	<i>oxydans</i>	99.7	906	KX083528.1
1D	Sycamore Island	<i>A. ligamentina</i>	<i>Streptomyces</i>	sp.	99.8	908	MH053444.1
2A	Sycamore Island	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>megaterium</i>	100	781	MH071287.1
2B	Sycamore Island	<i>A. ligamentina</i>	<i>Microbacterium</i>	<i>marinum</i>	99.8	901	MF373495.1
2D	Sycamore Island	<i>A. ligamentina</i>	<i>Agrococcus</i>	<i>terreus</i>	99.8	790	MH934923.1
10A	Sycamore Island	<i>A. pectorosa</i>	<i>Arthrobacter</i>	sp.	99.9	707	MG860243.1
10B	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudarthrobacter</i>	<i>defluviisiccitolerans/scleromae</i>	100	708	MH910272.1/MF681877.1/KY496253.1
13A	Sycamore Island	<i>A. pectorosa</i>	<i>Microbacterium</i>	sp.	90.4	463	HM352378.1
13B	Sycamore Island	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>pumilus/zhangzhouensis</i>	100	1413	MH045860.1/MG651573.1
17A	Wallen's Bend	<i>A. pectorosa</i>	<i>Pantoea</i>	sp.	99.9	900	MH769349.1
17B	Wallen's Bend	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.7	705	KR537290.1
17D	Wallen's Bend	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>oleivorans</i>	99.9	919	HF952706.1
17E	Wallen's Bend	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	788	LC383918.1
18A	Wallen's Bend	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>pumilus/zhangzhouensis</i>	100	810	MK696262.1/MK131335.1
18B	Wallen's Bend	<i>A. pectorosa</i>	<i>Curtobacterium</i>	<i>luteum/citreum</i>	100	845	MF959445.1/LT986192.1
18C	Wallen's Bend	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>pumilus/zhangzhouensis</i>	100	890	MK696261.1/MK131335.1
33A	Kyle's Ford	<i>A. pectorosa</i>	<i>Acinetobacter</i>	<i>solii</i>	100	823	MK241870.1
34A	Kyle's Ford	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>cereus/thuringiensis</i>	100	864	KT241012.1/FJ463780.1
34C	Kyle's Ford	<i>A. pectorosa</i>	<i>Pantoea</i>	<i>dispersa</i>	100	872	MF681826.1
34C	Kyle's Ford	<i>A. pectorosa</i>	<i>Erwinia</i>	sp.	100	872	MG681219.1
34D	Kyle's Ford	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>cereus/bingmayongensis/pseudomycooides</i>	100	875	MK285635.1/MK120869.1/MH578628.1
34E	Kyle's Ford	<i>A. pectorosa</i>	<i>Arthrobacter</i>	<i>pascens/globiformis</i>	99.9	902	HQ530516.1/HQ455821.1
August 23, 2018							
49A	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>megaterium</i>	99.3	667	LC269278.1
49B	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>toyonensis/cereus/thuringiensis</i>	100	816	MK611646.1/MK592620.1/MK583935.1
49C	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>cereus/mycooides/pseudomycooides</i>	99.9	1368	MK285635.1/MG694513.1/MG198676.1
49D	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>idriensis</i>	99.4	964	MK240437.1
49E	Frost Ford	<i>A. ligamentina</i>	<i>Lysinibacillus</i>	<i>sphaericus/xylanilyticus/boronitolerans</i>	99.9	893	MG928532.1/MG905851.1/MF111565.1
49F	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>thuringiensis</i>	98.5	1103	EU161995.1
49G	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>pumilus</i>	99.8	509	MK521054.1
49H	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>mycooides</i>	100	743	MK217080.1
49I	Frost Ford	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>altitudinis/pumilus/stratosphericus</i>	99.1	980	MK521060.1/MH118525.1/MH910298.1
63A	Frost Ford	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>thuringiensis</i>	99.3	1049	JF421247.1
63B	Frost Ford	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>thuringiensis</i>	98.5	1104	MK491010.1

Appendix A1, continued.

Isolate	Location	Mussel Species	Genus	Species	% Similarity	Length	Accession No(s).
63C	Frost Ford	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>megaterium/aryabhatai</i>	99.6	826	MH244337.1/MH177254.1
63D	Frost Ford	<i>A. pectorosa</i>	<i>Lysinibacillus</i>	<i>parviboronicapiens/sphaericus</i>	99.8	889	KY038722.1/MF111586.1
63E	Frost Ford	<i>A. pectorosa</i>	<i>Lysinibacillus</i>	<i>sphaericus/fusififormis</i>	98.3	514	JQ835283.1/JQ834699.1
63F	Frost Ford	<i>A. pectorosa</i>	<i>Exiguobacterium</i>	<i>acetylicum/indicum</i>	99.7	732	MK606065.1/MK294298.1
63G	Frost Ford	<i>A. pectorosa</i>	<i>Nocardopsis</i>	<i>alba</i>	100	802	MH333283.1
September 26, 2018							
15A	Speers Ferry	<i>A. pectorosa</i>	<i>Acinetobacter</i>	<i>radioresistens</i>	100	908	MK127547.1
15B	Speers Ferry	<i>A. pectorosa</i>	<i>Citricoccus/Micrococcus</i>	sp.	100	773	MF063312.1/JQ072036.1
15C	Speers Ferry	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>monteilii</i>	99.7	310	MH484604.1
15D	Speers Ferry	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>putida</i>	100	669	MK064155.1
17A	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>cereus/bingmayongensis/pseudomycooides</i>	99.9	878	MK285635.1/MK120869.1/MH578628.1
17B	Speers Ferry	<i>A. pectorosa</i>	<i>Novosphingobium</i>	<i>lindaniclasticum</i>	99.9	816	MK318596.1
17C	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>pseudomycooides</i>	100	1398	MG905900.1
17D	Speers Ferry	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>putida</i>	98.6	808	MK064155.1
26A	Sycamore Island	<i>A. pectorosa</i>	<i>Gordonia</i>	<i>hongkongensis/terrae</i>	100	1139	MK277458.1/MH518251.1
26B	Sycamore Island	<i>A. pectorosa</i>	<i>Pontibacter</i>	sp.	95.6	158	KY814729.1
32A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	808	LC383918.1
36A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	939	LC383918.1
37A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	882	LC383918.1
37B	Sycamore Island	<i>A. pectorosa</i>	<i>Gordonia</i>	<i>hongkongensis/terrae</i>	100	1163	MK277458.1/MH518251.1
37C	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	872	LC383918.1
44A	Wallen's Bend	<i>A. pectorosa</i>	<i>Hannaella</i>	<i>oryzae</i>	99.3	425	NG_063522.1
44B	Wallen's Bend	<i>A. pectorosa</i>	<i>Sphingobium</i>	sp.	99.8	1345	DQ413165.1
44C	Wallen's Bend	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>chocolatum</i>	100	639	MH748626.1
44D	Wallen's Bend	<i>A. pectorosa</i>	<i>Sphingobium</i>	<i>yanokuyae</i>	100	603	CP033230.1
46A	Wallen's Bend	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>toyonensis</i>	99.8	1225	KU179349.1
46B	Wallen's Bend	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>flavescens</i>	100	692	JQ958839.1
46C	Wallen's Bend	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>cereus/wiedmannii/thuringiensis</i>	100	718	MK696545.1/MK696254.1/MK696253.1
47A	Wallen's Bend	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	794	LC383918.1
49A	Wallen's Bend	<i>A. pectorosa</i>	<i>Oceanobacillus</i>	<i>massiliensis</i>	99.9	887	HQ586893.1
49B	Wallen's Bend	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>oxydans/foiorum</i>	99.5	894	MK696389.1/MK696388.1
49C	Wallen's Bend	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>putida/guariconensis</i>	100	794	MK534000.1/MK318649.1
50A	Wallen's Bend	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	694	LC383918.1
50B	Wallen's Bend	<i>A. pectorosa</i>	<i>Oceanobacillus</i>	<i>massiliensis</i>	100	766	KU727149.1
50C	Wallen's Bend	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>cichorii</i>	99.9	878	KU923374.1
59A	Kyle's Ford	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.3	947	KR537290.1
59B	Kyle's Ford	<i>A. pectorosa</i>	<i>Chromobacterium</i>	<i>haemolyticum</i>	99.4	869	LT628074.1
63A	Kyle's Ford	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>monteilii/plecoglossicida/putida</i>	100	863	MH997643.1/MH997642.1/MH997641.1
63B	Kyle's Ford	<i>A. pectorosa</i>	<i>Acinetobacter</i>	<i>schindleri</i>	100	1399	CP025618.2
63C	Kyle's Ford	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>parafulva</i>	99.9	1398	CP009747.1
63D	Kyle's Ford	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>monteilii/putida</i>	100	1384	KU862315.1/KT259326.1
64A	Kyle's Ford	<i>A. pectorosa</i>	<i>Acinetobacter</i>	<i>schindleri</i>	100	1201	MG461629.1
64B	Kyle's Ford	<i>A. pectorosa</i>	<i>Acinetobacter</i>	sp.	99.8	829	MG517420.1
64C	Kyle's Ford	<i>A. pectorosa</i>	<i>Serinibacter</i>	sp.	98.9	368	LC203065.1
66A	Kyle's Ford	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	891	KT260720.1
66B	Kyle's Ford	<i>A. pectorosa</i>	<i>Rhizobium/Agrobacterium</i>	sp./larrymoorei	99.2	1351	JQ660121.1/JN084151.1
67A	Kyle's Ford	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>proteolyticum</i>	99.9	903	MK281612.1
70A	Kyle's Ford	<i>A. pectorosa</i>	<i>Acinetobacter</i>	sp.	99.9	1385	MG517420.1
70B	Kyle's Ford	<i>A. pectorosa</i>	<i>Pseudomonas</i>	sp.	99.6	1333	MK680062.1
October 25, 2018							
006A	Artrip	<i>A. pectorosa</i>	<i>Knoellia</i>	<i>flava</i>	100	640	MG205530.1
016A	Speers Ferry	<i>A. pectorosa</i>	<i>Cellulosimicrobium</i>	<i>cellulans</i>	99.9	915	MH718838.1
016B	Speers Ferry	<i>A. pectorosa</i>	<i>Massilia</i>	<i>timonae</i>	100	901	MF592282.1
016C	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>pumilus/aerius/stratosphericus/altitudinis</i>	99.9	885	MH261170.1/MK629822.1/MH261171.1/MH261156.1
016D	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>safensis/altitudinis/pumilus</i>	100	1412	MK285608.1/MK241863.1/MG597491.1
021A	Speers Ferry	<i>A. ligamentina</i>	<i>Cutibacterium</i>	<i>acnes</i>	100	418	CP033842.1
023A	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>zhangzhouensis/pumilus</i>	100	881	MK583949.1/MH819709.1
027A	Speers Ferry	<i>A. pectorosa</i>	<i>Actinotalea</i>	<i>solisilvae</i>	100	832	NR_159882.1
028A	Speers Ferry	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	850	LC383918.1
028B	Speers Ferry	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>aerius/altitudinis/pumilus</i>	100	839	MG996801.1/MK521068.1/MK521063.1

Appendix A1, continued.

Isolate	Location	Mussel Species	Genus	Species	% Similarity	Length	Accession No(s).
028gA	Speers Ferry	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	831	LC383918.1
044A	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>kribbensis/protegens</i>	100	768	MK240439.1/LT628144.1
044B	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>kribbensis/reinekei/syringae/fluorescens</i>	100	819	MK240439.1/MK392138.1/CP024646.1/CP022313.1
049A	Sycamore Island	<i>A. ligamentina</i>	Unidentifiable				
049B	Sycamore Island	<i>A. ligamentina</i>	<i>Knoellia</i>	<i>flava</i>	99.9	845	MG205530.1
049C	Sycamore Island	<i>A. ligamentina</i>	<i>Pseudarthrobacter</i>	<i>oxydans/siccitolerans</i>	100	812	MG694475.1/MF681913.1
049D	Sycamore Island	<i>A. ligamentina</i>	<i>Microbacterium</i>	<i>phyllosphaerae</i>	98.7	832	KC355288.1
049E	Sycamore Island	<i>A. ligamentina</i>	<i>Bacillus</i>	<i>pumilus</i>	99	799	MH261008.1
051A	Sycamore Island	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>cereus/bingmayongensis/pseudomycooides/mycooides/subtilis</i>	100	793	MK285635.1/MK120869.1/MH578628.1/MH422001.1/MH422001.1
051B	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>putida</i>	99.6	550	MH298490.1
051C	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>taivanensis/putida/parafulva</i>	100	686	MK598329.1/CP030750.1/MH304303.1
057A	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>helmanticensis</i>	100	664	MK070159.1
057B	Sycamore Island	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>gibsonii</i>	100	759	MH910172.1
068A	Kyle's Ford	<i>A. pectorosa</i>	<i>Knoellia</i>	<i>flava</i>	99.7	770	MG205530.1
068B	Kyle's Ford	<i>A. pectorosa</i>	<i>Rhodococcus</i>	sp.	100	790	KY922741.1
068C	Kyle's Ford	<i>A. pectorosa</i>	<i>Arthrobacter</i>	<i>halodurans/laurens</i>	100	705	MK424278.1/KR611860.1
068D	Kyle's Ford	<i>A. pectorosa</i>	<i>Rhodococcus</i>	<i>gingshengii/erythropolis</i>	100	886	MH938043.1/MK371078.1
068E	Kyle's Ford	<i>A. pectorosa</i>	<i>Microbacterium</i>	sp.	99.4	1392	JQ977333.1
069A	Kyle's Ford	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>aureliae</i>	99.7	992	MK226317.1
069B	Kyle's Ford	<i>A. pectorosa</i>	<i>Terrabacter</i>	<i>terrigena/koreensis/tumescens</i>	100	732	MF681978.1/NR_134212.1/JQ342911.1
073A	Kyle's Ford	<i>A. pectorosa</i>	<i>Curtobacterium</i>	<i>oceanosedimentum/luteum/herbarum/citreum</i>	100	760	MK618608.1/MK618607.1/MK618606.1/MK618605.1
073B	Kyle's Ford	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>lemovicicum</i>	100	721	CP031423.1
074A	Kyle's Ford	<i>A. pectorosa</i>	<i>Leucobacter</i>	<i>tardus</i>	99.7	770	NR_042694.1
077A	Kyle's Ford	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	824	LC383918.1
077B	Kyle's Ford	<i>A. pectorosa</i>	<i>Plantibacter</i>	<i>flavus</i>	99.9	1230	LN774386.1
October 4, 2019							
16A	Sycamore Island	<i>P. fasciolaris</i>	<i>Lysinibacillus</i>	<i>fusiformis</i>	99.9	917	MT605500.1
19A	Sycamore Island	<i>L. fasciola</i>	<i>Curtobacterium</i>	<i>ammoniiigenes</i>	99.9	809	KP296215.1
21A	Sycamore Island	<i>A. ligamentina</i>	<i>Falsirhodobacter</i>	<i>halotolerans</i>	100	701	LN774250.1
26A	Sycamore Island	<i>A. plicata</i>	<i>Bacillus</i>	<i>paramycooides</i>	100	390	MT647568.1
26B	Sycamore Island	<i>A. plicata</i>	<i>Bacillus</i>	<i>cereus</i>	100	934	LR215149.1
28A	Sycamore Island	<i>A. pectorosa</i>	<i>Oerskovia</i>	<i>paurometabola</i>	100	1266	KX034798.1
28B	Sycamore Island	<i>A. pectorosa</i>	<i>Bacillus</i>	<i>aryabhatai</i>	99	1336	MK519060.1
28C	Sycamore Island	<i>A. pectorosa</i>	<i>Agrococcus</i>	<i>terreus</i>	99.9	856	MH934923.1
28D	Sycamore Island	<i>A. pectorosa</i>	<i>Microbacterium</i>	<i>paludicola</i>	99.8	536	MT733951.1
29A	Sycamore Island	<i>A. pectorosa</i>	<i>Acinetobacter</i>	sp.	75	803	AY922105.1
29B	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.6	1312	MT505131.1
29C	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	1345	MT505131.1
31A	Sycamore Island	<i>L. ovata</i>	<i>Staphylococcus</i>	<i>hominis</i> subsp. <i>novobiosepticus</i>	100	1262	MT585539.1
33A	Sycamore Island	<i>A. plicata</i>	<i>Micrococcus</i>	<i>yunnanensis</i>	100	855	MT033093.1
33B	Sycamore Island	<i>A. plicata</i>	<i>Staphylococcus</i>	<i>hominis</i> subsp. <i>novobiosepticus</i>	100	840	MT544813.1
33C	Sycamore Island	<i>A. plicata</i>	<i>Agrococcus</i>	<i>terreus</i>	99.5	913	JN585711.1
33D	Sycamore Island	<i>A. plicata</i>	<i>Micrococcus</i>	<i>yunnanensis</i>	100	836	LT978429.1
33E	Sycamore Island	<i>A. plicata</i>	<i>Staphylococcus</i>	<i>epidermidis</i>	99.4	883	KM972394.1
35A	Sycamore Island	<i>A. ligamentina</i>	<i>Micrococcus</i>	<i>yunnanensis</i>	99.9	828	KF758820.1
40A	Sycamore Island	<i>A. ligamentina</i>	<i>Exiguobacterium</i>	<i>aurantiacum</i>	99.4	837	MT225757.1
40B	Sycamore Island	<i>A. ligamentina</i>	<i>Staphylococcus</i>	<i>epidermidis</i>	100	1348	MT613456.1
40C	Sycamore Island	<i>A. ligamentina</i>	<i>Citricoccus</i>	<i>zhacaiensis</i>	100	1139	MG025801.1
40D	Sycamore Island	<i>A. ligamentina</i>	<i>Massilia</i>	<i>oculi</i>	99.9	1308	CP029343.1
October 7, 2020							
1A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	1335	MT505131.1
1B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Kocuria</i>	<i>rhizophila</i>	100	847	MT377849.1
2A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>veronii</i>	100	910	MT384380.1
2B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>allosaccharophila</i>	100	887	MN216261.1

Appendix A1, continued.

Isolate	Location	Mussel Species	Genus	Species	% Similarity	Length	Accession No(s).
3A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	1372	MT505131.1
3B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	819	MT505139.1
4A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	1342	MT505131.1
4B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>veronii</i>	100	1375	MT384380.1
5A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Chryseobacterium</i>	sp.	96.8	704	KU360139.1
5B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	1372	MT505131.1
5C	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	904	MT505139.1
6A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	1362	MT505131.1
6B	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.7	1362	MT505131.1
7A	Speers Ferry/Sycamore Island/Clinchport	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.7	1375	MT505131.1
October 20, 2020							
ALI-1A	Sycamore Island	<i>A. ligamentina</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	698	MT505139.1
ALI-1B	Sycamore Island	<i>A. ligamentina</i>	<i>Aeromonas</i>	<i>hydrophila</i>	100	387	MK880338.1
APE-1A	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>hydrophila</i>	100	549	MK880338.1
APE-1B	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	791	MT505139.1
APE-2A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	636	MT505139.1
APE-2B	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>poae</i>	100	758	MT631989.1
APE-2C	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>veronii</i>	100	760	MT384380.1
APE-3A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	700	MT505139.1
APE-3B	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>caviae</i>	100	578	MN481052.1
APE-4A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.7	762	MT505131.1
APE-4B	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>veronii</i>	97.7	303	CP012504.1
APE-6A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.7	653	MT505131.1
APE-6B	Sycamore Island	<i>A. pectorosa</i>	<i>Stenotrophomonas</i>	<i>pavanii</i>	95.6	484	MH810095.1
APE-6C	Sycamore Island	<i>A. pectorosa</i>	<i>Pseudomonas</i>	<i>putida</i>	100	811	CP050951.1
APE-7A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.8	1063	MT505131.1
APE-7B	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>hydrophila</i>	99.8	493	MK880338.1
APE-8A	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	100	751	MT505139.1
APE-8B	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>aquatilis</i>	100	765	LT630765.1
APE-9A	Sycamore Island	<i>A. pectorosa</i>	<i>Aeromonas</i>	<i>hydrophila</i>	100	452	MK880338.1
APE-9B	Sycamore Island	<i>A. pectorosa</i>	<i>Yokenella</i>	<i>regensburgei</i>	99.9	794	MT505139.1
EBR-1A	Sycamore Island	<i>E. brevidens</i>	<i>Yokenella</i>	<i>regensburgei</i>	88	673	MT505131.1
EBR-1B	Sycamore Island	<i>E. brevidens</i>	<i>Aeromonas</i>	<i>caviae</i>	100	467	MN481052.1
EBR-1C	Sycamore Island	<i>E. brevidens</i>	<i>Flavobacterium</i>	<i>tractae</i>	99.9	759	NR_133749.1

REGULAR ARTICLE

CHANGES IN THE MUSSEL FAUNA OF THE JACKS FORK, MISSOURI OVER 35 YEARS AND RELATIONSHIPS WITH SPECIES TRAITS

Stephen E. McMurray* and J. Scott Faiman

Missouri Department of Conservation, Central Regional Office and Conservation Research Center,
Columbia, MO 65201 USA

ABSTRACT

We conducted a mussel survey of the Jacks Fork, Missouri, an Outstanding National Resource Water, to document mussel diversity and distribution in the watershed, to determine if changes had occurred since a previous survey in 1982, and to relate observed changes to species traits. We surveyed mussels with timed tactile or visual searches at 28 sites during summer from 2017 to 2019 and compared our results with the 1982 survey. Catch per unit effort, number of live individuals, species richness, and diversity were significantly lower in 2017–19 than in 1982. The proportion of extirpation at the 11 resurveyed sites averaged 0.85 (range 0.50–1.00) among species, and the proportion of colonization was 0.0 for all species. There were no differences in the relative abundance of tribes, life-history strategies, or species of conservation concern between the two surveys, suggesting that the decline has occurred evenly across species, tribes, and life-history strategies. Ten species are possibly extirpated from the basin. Causes of the mussel decline in the Jacks Fork basin are unknown.

KEY WORDS: mussels, status, extirpation, colonization, decline, Missouri

INTRODUCTION

The mussel fauna of the Jacks Fork basin of Missouri is part of the Interior Highlands Province of the Mississippian Region (Haag 2010). This province covers two unique uplift areas, the Ozark Plateau and Ouachita Uplands, and it has a mussel fauna of over 70 species (Harris 1999; Haag 2010). Oesch (1995) reported 16 species from the Jacks Fork between 1967 and 1979 but did not report effort or the exact location of some sites (Table 1). Buchanan (1996) surveyed 11 sites in 1982 and observed 15 species, in addition to the invasive bivalve, *Corbicula fluminea*. A 2002 inventory of mussel resources within the Ozark National Scenic Riverways (OZAR) reported eight species from the Jacks Fork, but the survey was limited to only three sites (McClane Environmental Services 2004).

Documenting the distribution and status of mussel species and documenting faunal changes over time is important for conservation and management (MDC 2008; Haag and

Williams 2014; FMCS 2016). Species life-history traits and phylogenetic affinity can affect mussel responses to disturbance (Haag 2012; Lopes-Lima et al. 2017). We surveyed 28 sites (historical and new) in the Jacks Fork basin to document the diversity and distribution of the mussel fauna, we compare our results with the 1982 survey to determine if changes have occurred, and we examine those changes in regard to phylogenetic and life-history strategy composition.

METHODS

Study Area

The Jacks Fork is a 79-km-long (1,153 km² watershed area) easterly flowing tributary of the Current River (Black River system) in the Ozarks aquatic faunal region of Missouri. The uplifted and unglaciated Ozarks generally lie on Paleozoic sedimentary bedrock and have higher elevations and greater local relief than other regions in Missouri (Steyermark 1968; Pflieger 1989; Panfil and Jacobson 2001; Sowa et al. 2007). Ozark streams typically are high gradient and occupy narrow,

*Corresponding Author: Stephen.McMurray@mdc.mo.gov

Table 1. Freshwater mussels reported live or as shells (×) from the Jacks Fork basin, Missouri during 1967–79 (Oesch 1995), 1982 (Buchanan 1996), 2002 (McClane Environmental Services 2004), and 2017–19 (this study). A dash (—) indicates that a species was not observed.

Species	Tribe ¹	Life-history Strategy ²	Adult Size ³	1967–79	1982	2002	2017–19
<i>Alasmidonta marginata</i> ⁴	Anodontini	P	Medium	×	×	—	—
<i>Alasmidonta viridis</i> ⁴	Anodontini	P	Small	×	×	—	×
<i>Lasmigona costata</i>	Anodontini	P	Large	×	×	—	—
<i>Pyganodon grandis</i>	Anodontini	O	Large	×	×	—	×
<i>Strophitus undulatus</i>	Anodontini	P	Medium	×	×	×	×
<i>Utterbackia imbecillis</i>	Anodontini	O	Medium	×	×	—	×
<i>Amblema plicata</i>	Amblemini	E	Large	×	—	—	—
<i>Cambarunio hesperus</i>	Lampsilini	P	Small	×	×	×	×
<i>Lampsilis reeveiana</i>	Lampsilini	P	Small	×	×	×	×
<i>Lampsilis teres</i>	Lampsilini	O	Large	×	—	—	—
<i>Leaunio lienosus</i> ⁴	Lampsilini	O	Small	—	—	×	—
<i>Leptodea fragilis</i>	Lampsilini	O	Large	—	×	—	—
<i>Ptychobranthus occidentalis</i> ⁴	Lampsilini	E	Medium	×	×	×	×
<i>Sagittunio subrostratus</i>	Lampsilini	O	Medium	×	×	×	×
<i>Toxolasma lividum</i> ⁴	Lampsilini	P	Small	×	—	×	—
<i>Toxolasma texasiense</i> ⁴	Lampsilini	P	Small	×	—	—	—
<i>Truncilla donaciformis</i>	Lampsilini	O	Small	—	×	—	—
<i>Eurynia dilatata</i>	Pleurobemini	E	Large	×	×	—	×
<i>Fusconaia ozarkensis</i>	Pleurobemini	E	Medium	×	×	×	×
<i>Pleurobema sintoxia</i>	Pleurobemini	E	Medium	—	×	—	—

¹Tribe designations from Lopes-Lima et al. (2017).

²Life-history strategy: P = periodic, O = opportunistic, E = equilibrium (Haag 2012, Moore et al. 2021).

³Small (≤ 7.6 cm), medium (7.7–15.1 cm), and large (≥ 15.2 cm) on the basis of maximum sizes reported in Oesch (1995).

⁴Missouri species of conservation concern (MDC 2022).

steep-sided valleys bordered by high bluffs, and base flows are often maintained by springs (Pflieger 1989; Panfil and Jacobson 2001). The Jacks Fork has an average gradient of 1.3 m/km, and the upper section (above the confluence with Leatherwood Creek, Fig. 1) flows through a narrow valley. The channel of the lower section is less confined, resulting in more extensive gravel bar areas than the upper river; however, stream reaches in the lower section can be less stable and provide less suitable mussel habitat. As a gravel-dominated river, the Jacks Fork is naturally active, with high flows mobilizing bed material, creating gravel bars and driving channel migration (Erwin et al. 2021).

Presettlement land cover in the basin consisted of oak (*Quercus* spp.) and oak/pine (*Pinus* spp.) woodlands, with occasional prairie and savannah openings and fens (Nigh and Schroeder 2002). Presently, land cover is dominated by forest with approximately one-third in grassland or cropland; there are only two urban centers with >500 people. Nearly 19% of the basin is in public ownership. Springs contribute a considerable portion of the base flow of the Jacks Fork, and Alley Spring, with a discharge of approximately 3.5 m³/s, is the largest of 48 known springs in the basin (Wilkerson 2001; Erwin et al. 2021). The Jacks Fork is designated an Outstanding National Resource Water, and since 1964 nearly its entire length has been managed by the National Park Service as part of OZAR (Wilkerson 2001).

Compared with rivers in other regions of Missouri, Ozark

streams such as the Jacks Fork overall are less affected by physical alterations such as agriculture and channelization (Sowa et al. 2007). Threats to water quality in the basin include gravel mining, livestock access to riparian zones, runoff from cleared land, and seven National Pollution Discharge Elimination System discharges in the basin (Wilkerson 2001). Water quality is also affected by periodically high fecal coliform levels, and an 11.3-km segment of the lower Jacks Fork is under a total maximum daily load for fecal coliform, assumed to originate from failing on-site septic systems (Wilkerson 2001; MDNR 2004).

Field Sampling

We surveyed mussels during summer low-flow conditions from 2017 to 2019 at 11 sites previously surveyed by Buchanan (1996; hereafter, “resurveyed” sites) and 17 previously unsurveyed sites encompassing 74.5 km of the Jacks Fork, 18.5 km of the North Prong Jacks Fork, and 15.5 km of the South Prong Jacks Fork (Fig. 1). We did not survey additional tributaries because they are too small to support substantial mussel faunas. New sites were selected on the basis of the presence of suitable mussel habitat (e.g., stable gravel or gravel/sand substrate, bluff pools) and to provide even spatial coverage throughout the watershed. We followed the survey methods used by Buchanan (1996) in his 1982 survey. At least two surveyors conducted timed tactile and visual searches in

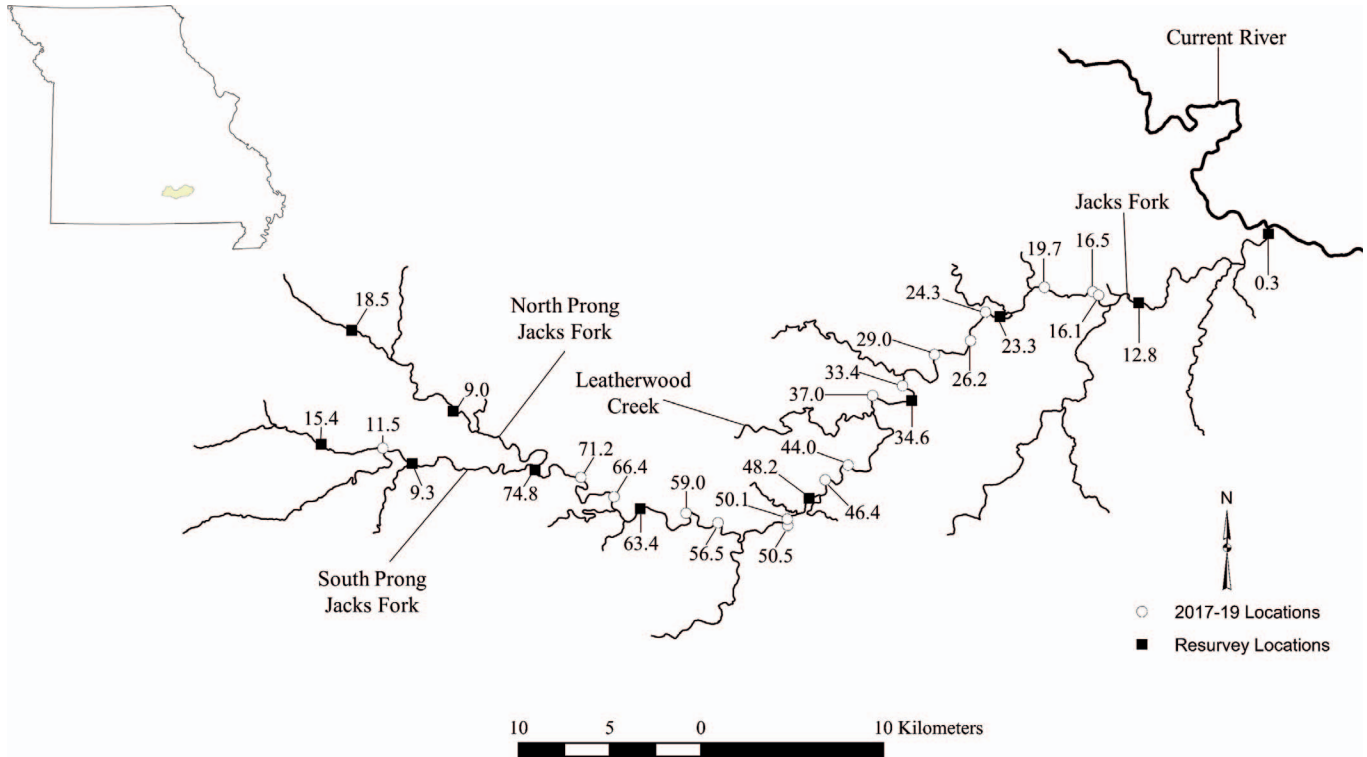


Figure 1. Sites surveyed for freshwater mussels in the Jacks Fork basin in 2017–19. Site numbers refer to river kilometer, measured from the stream mouth. Inset map shows the location of the Jacks Fork basin in Missouri, USA.

all available habitats at a site while wading or snorkeling. Search time at each site depended on the amount of available habitat.

Search time in our study averaged 2.4 person-hours/site across all sites (range 1.0–5.5; Table 2). At resurveyed sites,

we attempted to survey the same area surveyed in 1982, on the basis of Buchanan’s field notes (archived at Missouri Department of Conservation, Columbia). If field notes were not specific, or if the habitat at a site had changed to the extent that features could not be discerned, we surveyed represen-

Table 2. Sample effort and mussel community metrics in the Jacks Fork basin, Missouri at all 28 sites surveyed in 2017–19 and at 11 sites surveyed in 1982 (Buchanan 1996) and 2017–19 (resurveyed sites). All values are mean (SD). CPUE = catch per unit effort. Species richness is reported for live individuals or shells of any condition (live + shell), and live individuals or fresh dead shells (live + FD). H_B = Brillouin’s index of diversity, E = evenness, RA = relative abundance, and SOCC = Missouri species of conservation concern.

Parameter	2017–19			Resurveyed Sites	
	All Locations	Upper Jacks Fork	Lower Jacks Fork	1982	2017–19
Sample effort (person-hours)	2.4 (1.2)	2.6 (1.1)	2.6 (1.5)	1.8 (0.8)	3.1 (1.6)
CPUE (number of live mussels/person-hour)	14.6 (27.2)	30.0 (36.0)	6.0 (14.0)	28.2 (31.7)	5.5 (14.4)
Richness (live + shell)	2.5 (2.0)	4.2 (0.9)	2.0 (1.8)	4.4 (2.7)	2.1 (2.1)
Richness (live + FD)	2.1 (1.8)	3.8 (1.1)	1.3 (1.3)	3.9 (2.5)	1.4 (1.6)
Number of individuals	37.8 (73.2)	73.0 (92.0)	21.0 (58.0)	54.3 (59.4)	22.6 (60.3)
H_B	0.5 (0.3)	0.7 (0.3)	0.3 (0.3)	1.0 (0.5)	0.5 (0.4)
E	0.6 (0.2)	0.6 (0.2)	0.6 (0.3)	0.7 (0.2)	0.6 (0.2)
Anodontini RA	0.5 (1.6)	1.4 (2.4)	0.0 (0.0)	5.6 (13.0)	0.5 (1.6)
Lampsilini RA	48.6 (44.3)	69.0 (30.0)	50.0 (50.0)	58.2 (39.3)	34.2 (46.0)
Pleurobemini RA	15.1 (26.6)	29.0 (29.0)	8.0 (25.0)	18.0 (29.4)	10.8 (27.0)
Opportunistic RA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6.3 (18.3)	0.0 (0.0)
Periodic RA	22.9 (35.2)	21.0 (27.0)	34.0 (45.0)	41.8 (31.0)	20.4 (34.9)
Equilibrium RA	41.3 (43.9)	79.0 (27.0)	24.0 (40.0)	33.7 (31.4)	25.1 (38.8)
SOCC RA	26.4 (34.6)	50.0 (32.0)	16.0 (32.0)	16.8 (19.9)	14.3 (27.4)

tative mussel habitats at the site. Search time in 1982 averaged 1.8 person-hours/site (range 0.8–3.8; Table 2; Buchanan 1996). During both surveys, shells were collected during and outside of timed searches but were not included in estimates of abundance (see subsequent). We classified shells as fresh dead (FD; intact periostracum and lustrous nacre), weathered dead (WD; intact periostracum but weathered, chalky nacre), or subfossil (SF; shell chalky with no periostracum) following Southwick and Loftus (2003).

Data Analysis

We characterized species richness, diversity, abundance, and composition of the mussel communities at each site for both the 1982 and 2017–19 surveys. We calculated species richness in two ways: (1) the total number of species collected live and as FD shells (live + FD) and (2) the total number of species collected live and as shell material in any condition (live + shell). Because sites in both surveys were selected nonrandomly, and because visual and tactile techniques are often biased toward large or sculptured species, we calculated Brillouin's index of diversity (H_B) and Brillouin's evenness (E) with the R package *tabula* (version 4.1.3; Magurran 1996; Vaughn et al. 1997; Frerebeau 2019; R Core Team 2022). Brillouin's index of diversity describes only the known collection and is preferred when catchability of the study organism is not random; values for the index rarely exceed 4.5 (Magurran 1996). These are calculated as:

$$H_B = \frac{1}{N} \log \left(\frac{N!}{n_1!n_2!n_3!\dots} \right)$$

and

$$E = \frac{H_B}{H_{B\max}},$$

where N = total individuals collected, n_1, n_2, n_3 = number of individuals belonging to each species, and

$$H_{B\max} = \frac{1}{N} \times \ln \times \frac{N!}{\{[N/S]\}!^{s-r} \times \{([N/S] + 1)\}^r}$$

where S = species richness and

$$r = N - S[N/S].$$

We computed catch per unit effort (CPUE; number of live individuals/person-hour) as a measure of abundance. To describe the composition of the mussel community at each location, we calculated the relative abundances of individual species, life-history strategies (opportunistic, periodic, equilibrium), tribes (Anodontini, Lampsilini, Pleurobemini), and Missouri species of conservation concern (SOCC) that were detected live (Table 1). Opportunistic species exhibit a short life span with early sexual maturity, moderate-to-high fecundity, and moderate-to-large adult body size. Equilibrium species exhibit a longer life span, later sexual maturity, variable fecundity, and moderate-to-large adult size. Periodic

species exhibit an intermediate life span, early-to-moderate sexual maturity, low-to-moderate fecundity, and small-to-moderate-sized adults (Haag 2012; Moore et al. 2021). Within the Unionidae, tribes represent differing suites of morphological, life-history, and behavioral traits and their relative abundances within a community are hypothesized to reflect habitat or water-quality factors (Lopes-Lima et al. 2017; Dunn et al. 2020). Missouri SOCC are considered critically imperiled, imperiled, or vulnerable in the state and include state or federally endangered or threatened species (MDC 2022).

To examine colonization and extirpation since 1982, we calculated the colonization proportion (p_c) and extirpation proportion (p_e) for all 14 species, three tribes, and three life-history strategies that were detected live in either period from at least one of the resurveyed sites (Gotelli 2001). These proportions are calculated as:

$$p_c = \frac{\text{Number of times a location unoccupied in 1982 was occupied in 2017–19}}{\text{Total number of previously unoccupied locations}}$$

and

$$p_e = \frac{\text{Number of times a location occupied in 1982 was unoccupied in 2017–19}}{\text{Total number of occupied locations censused}}$$

We tested for significant differences in the relative abundances of tribes and life-history strategies among all sites surveyed in 2017–19 with a Kruskal–Wallis test (H) and Dunn's post hoc test (z) with Bonferroni adjustment using the R package *dunn.test* ($P \leq 0.05$; Dinno 2017; R Core Team 2022). To examine spatial differences between the upper (above Leatherwood Creek; sites 44.0–74.8; Fig. 1) and lower sections of Jacks Fork (sites 0.3–37.0), we tested for differences in community metrics between those sections with a Kruskal–Wallis test (R Core Team 2022). To determine if community changes had occurred since 1982, we tested for significant differences in community metrics between time periods for the 11 resurveyed sites and the calculated p_c and p_e values for all species with a Kruskal–Wallis test (R Core Team 2022). We also calculated species rank abundances for both time periods at the resurveyed sites with the R package *BiodiversityR* (Kindt and Coe 2005; Foster and Dunstan 2010; R Core Team 2022).

RESULTS

During 2017–19, we collected 1,058 live individuals of six species and shells only of four additional species, and we observed live individuals or shells at 18 of the 28 sites (Table 3). *Corbicula fluminea* was observed live or as shells at 16 sites. Catch per unit effort ranged from 0 to 132.4 live individuals/person-hour (mean = 14.6), and the mean number of live individuals/site was 37.8 (range 0–331; Table 2). Species richness ranged from 0 to 5/site for both live + shell (mean = 2.5) and live + FD (mean = 2.1). Diversity (H_B) ranged from 0.0 to 1.0 (mean = 0.5) and E from 0.3 to 1.0

Table 3. Results of mussel surveys in the Jacks Fork basin, Missouri, 2017–19. Site numbers refer to river kilometer, measured from the mouth. Numbers for each species represent the number of live individuals at a site; the presence of shells is indicated as FD = fresh dead, WD = weathered dead, SF = subfossil; CPUE = catch per unit effort. *Corbicula fluminea* presence is noted as live (L) or shells (FD or WD). SOCC = Missouri species of conservation concern. RA = relative abundance. An asterisk (*) indicates sites that were sampled in 1982. The division between the upper and lower Jacks Fork is between sites 37.0 and 44.0. A dash (—) indicates that a species was not observed live or as shells.

Genus/Species	North Prong		South Prong			Jacks Fork								
	18.5*	9.0*	15.4*	11.5	9.3*	74.8*	71.2	66.4	63.4*	59.0	56.5	50.5	50.1	48.2*
<i>Alasmidonta viridis</i>	—	—	—	—	—	—	—	—	—	2	—	—	—	—
<i>Pyganodon grandis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Strophitus undulatus</i>	—	—	—	—	—	—	1	—	1	—	—	—	—	—
<i>Utterbackia imbecillis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cambarunio hesperus</i>	—	—	—	—	—	1	2	2	—	4	3	3	1	—
<i>Lampsilis reeveiana</i>	—	—	—	—	—	1	SF	7	5	FD	8	3	4	2
<i>Ptychobranthus occidentalis</i>	—	—	—	—	—	WD	2	63	10	21	61	31	45	WD
<i>Sagittunio subrostratus</i>	—	—	—	—	—	WD	—	—	—	—	—	—	—	—
<i>Eurynia dilatata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Fusconaia ozarkensis</i>	—	—	—	—	—	19	17	39	3	11	22	12	13	—
<i>Corbicula fluminea</i>	—	—	—	—	—	L	L	WD	L	L	L	L	L	—
Species richness (live + shell)	0	0	0	0	0	5	5	4	4	5	4	4	4	2
Live species richness (live + FD)	0	0	0	0	0	3	4	4	4	5	4	4	4	1
Total live individuals	0	0	0	0	0	21	22	111	19	38	94	49	63	2
Sample effort (person-hours)	1.3	2.1	1.3	1.2	1.6	3.3	1.8	2.7	5.5	2.2	3.0	1.6	2.0	1.5
CPUE (mussels/person-hour)	0.0	0.0	0.0	0.0	0.0	6.4	12.2	41.1	3.5	17.3	31.3	30.6	31.5	1.3
Brillouin's index (H_B)	—	—	—	—	—	0.3	0.6	0.9	0.9	1.0	0.9	0.9	0.7	0.0
Evenness (E)	—	—	—	—	—	0.3	0.5	0.7	0.8	0.8	0.7	0.7	0.6	—
Anodontini RA	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.0	5.3	5.3	0.0	0.0	0.0	0.0
Lampsilini RA	0.0	0.0	0.0	0.0	0.0	9.5	18.2	64.9	78.9	65.8	76.6	75.5	79.4	100.0
Pleurobemini RA	0.0	0.0	0.0	0.0	0.0	90.5	77.3	35.1	15.8	28.9	23.4	24.5	20.6	0.0
Opportunistic RA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Periodic RA	0.0	0.0	0.0	0.0	0.0	9.5	13.6	8.1	31.6	15.8	11.7	12.2	7.9	100.0
Equilibrium RA	0.0	0.0	0.0	0.0	0.0	90.5	86.4	91.9	68.4	84.2	88.3	87.8	92.1	0.0
SOCC RA	0.0	0.0	0.0	0.0	0.0	0.0	9.1	56.8	52.6	60.5	64.9	63.3	71.4	0.0

(mean = 0.6). The relative abundances of SOCC ranged from 0.0% to 90.6% (mean = 26.4%). The relative abundance of Lampsilini ranged from 0.0% to 100.0% (mean = 48.6%) and Pleurobemini ranged from 0.0% to 90.5% (mean = 15.1%). Relative abundance differed among life-history strategies ($H = 20$, $df = 2$, $P < 0.0001$), and there were significantly fewer Anodontini (mean relative abundance = 0.5%) than Lampsilini ($z = -4.73$, $P < 0.0001$) or Pleurobemini ($z = -2.44$, $P = 0.02$), and significantly fewer Pleurobemini than Lampsilini ($z = 2.3$, $P = 0.03$). No Amblemini or Quadrulini were observed. The relative abundance of equilibrium strategists ranged from 0.0% to 93.1% (mean = 41.3%) and periodic strategists ranged from 0.0% to 100.0% (mean = 22.9%). Relative abundance differed among life-history strategies ($H = 20$, $df = 2$, $P < 0.0001$), and there were significantly fewer opportunistic strategists (mean relative abundance < 0.1%) than equilibrium ($z = -4.11$, $P = 0.0001$) or periodic strategists ($z = 4.32$, $P < 0.0001$). There was no difference in the relative abundance of equilibrium and periodic strategists ($z = 0.21$, $P = 1.00$).

Compared with the lower river, the upper Jacks Fork had significantly higher CPUE ($H = 8$, $df = 1$, $P = 0.004$), species

richness as both live + shell ($H = 8$, $df = 1$, $P = 0.005$) and live + FD ($H = 12$, $df = 1$, $P = 0.0006$), number of live individuals ($H = 9$, $df = 1$, $P = 0.003$), and H_B ($H = 4$, $df = 1$, $P = 0.03$) (Table 2). In addition, the upper Jacks Fork had significantly higher relative abundance of Pleurobemini ($H = 9$, $df = 1$, $P = 0.003$), equilibrium strategists ($H = 6$, $df = 1$, $P = 0.01$), and Missouri SOCC ($H = 5$, $df = 1$, $P = 0.03$) than did the lower Jacks Fork.

The SOCC *Ptychobranthus occidentalis* was the most abundant species, with 762 individuals observed (relative abundance = 72.0%), and it was observed live or as shells at 15 sites (Table 3). *Lampsilis reeveiana* was the most widely distributed species, with live individuals or shells occurring at 16 sites. We found 178 live individuals of *Fusconaia ozarkensis* (relative abundance = 16.8%), 45 *Cambarunio hesperus* (relative abundance = 4.3%), and two live individuals each of *Alasmidonta viridis* and *Strophitus undulatus*. *Pyganodon grandis*, *Sagittunio subrostratus*, and *Eurynia dilatata* were represented only by WD or SF shells, and *Utterbackia imbecillis* was represented only by FD shells. We found no live individuals or shells of 10 species previously

Table 3, extended.

Jacks Fork														Totals			
46.4	44.0	37.0	34.6*	33.4	29.0	26.2	24.3	23.3*	19.7	16.5	16.1	12.8*	0.3*	No. live	L + FD	L + shell	RA
—	FD	—	WD	—	—	—	—	—	—	—	—	—	—	2	2	3	0.2
—	—	—	—	—	—	—	—	—	—	—	—	—	SF	0	0	1	0.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	0.2
—	—	—	—	—	—	—	—	FD	—	—	—	—	—	0	1	1	0.0
4	7	3	7	WD	—	2	3	—	—	—	—	—	3	42	13	14	4.3
19	2	WD	9	1	—	—	3	—	5	—	—	—	—	69	14	16	6.5
300	43	23	162	WD	—	—	—	—	—	—	—	—	1	762	12	15	72.0
—	—	—	—	—	—	—	—	—	—	—	—	WD	—	0	0	2	0.0
—	—	—	—	—	—	—	—	—	—	—	—	—	WD	0	0	1	0.0
8	2	1	25	6	—	—	—	—	—	—	—	—	—	178	13	13	16.8
L	L	L	—	FD	L	WD	—	WD	L	—	—	WD	—	—	13	17	—
4	5	4	5	4	0	1	2	2	1	0	0	1	4				
4	5	3	4	2	0	1	2	1	1	0	0	0	2				
331	54	27	203	7	0	2	6	0	5	0	0	0	4				
2.5	2.0	2.0	4.2	3.0	1.2	1.0	1.5	5.3	2.5	1.5	1.0	3.3	4.5				
132.4	27.0	13.5	48.3	2.3	0.0	2.0	4.0	0.0	2.0	0.0	0.0	0.0	0.9				
0.4	0.6	0.4	0.7	0.3	—	0.0	0.5	—	0.0	—	—	—	0.4				
0.3	0.5	0.4	0.5	0.5	—	—	1.0	—	—	—	—	—	0.8				
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
97.6	96.3	96.3	87.7	14.3	0.0	100.0	100.0	0.0	100.0	0.0	0.0	0.0	100.0				
2.4	3.7	3.7	12.3	85.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
6.9	16.7	11.1	7.9	14.3	0.0	100.0	100.0	0.0	100.0	0.0	0.0	0.0	75.0				
93.1	83.3	88.9	92.1	85.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0				
90.6	79.6	85.2	79.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0				

reported from the basin (*Alasmidonta marginata*, *Lasmigona costata*, *Amblema plicata*, *Lampsilis teres*, *Leptodea fragilis*, *Toxolasma lividum*, *Toxolasma texasiense*, *Truncilla donaciformis*, *Leaunio lienosus*, *Pleurobema sintoxia*).

Values for most community metrics were lower in 2017–19 than 1982 (Table 2). There was a significant decline in CPUE ($H = 5$, $df = 1$, $P = 0.02$), number of live individuals ($H = 4$, $df = 1$, $P = 0.04$), live + shell richness ($H = 4$, $df = 1$, $P = 0.04$), live + FD richness ($H = 6$, $df = 1$, $P = 0.01$), and H_B ($H = 4$, $df = 1$, $P = 0.05$). Evenness was the only community metric that did not differ between time periods ($H = 1.4$, $df = 1$, $P = 0.23$). Faunal composition also differed between time periods. In 1982, 14 species were represented by live individuals, but only five species were represented by live individuals in 2017–19 (Fig. 2, Table 4). *Lampsilis reeveiana* was the most abundant species in 1982, representing 34.5% of live individuals, but it represented only 6.8% of individuals at the resurveyed sites in 2017–19. *Ptychobranthus occidentalis* was the most abundant species in 2017–19 (72.0% of individuals), but it represented only 30.8% of live individuals in 1982. There were no differences in proportional represen-

tation of tribes, life-history strategies, or SOCC between time periods ($H = 0.7$ – 3.3 , $df = 1$, $P = 0.07$ – 0.4).

Mean extirpation proportion (p_e) across the 14 species detected live in 1982 was 0.85 (range 0.50–1.00, Table 5). Colonization proportion (p_c) was 0.00 for all species, and p_e was significantly higher than p_c ($H = 20$, $df = 1$, $P < 0.0001$). Anodontini had the highest extirpation proportion ($p_e = 0.80$) of the three tribes, and opportunistic life-history strategists had the highest extirpation proportion ($p_e = 1.00$).

DISCUSSION

Our results suggest that mussel abundance, diversity, and richness have declined substantially in the Jacks Fork since 1982. Ten species present in 1982 may be extirpated in the basin. We cannot account for species nondetection but given that effort in 2017–19 was greater than in 1982, and no shells of these species were found in 2017–19, these species are, at best, extremely rare in the basin. In addition, three species reported in 1967–79 have not been seen since that time (*Amblema plicata*, *Lampsilis teres*, *Toxolasma texasiense*).

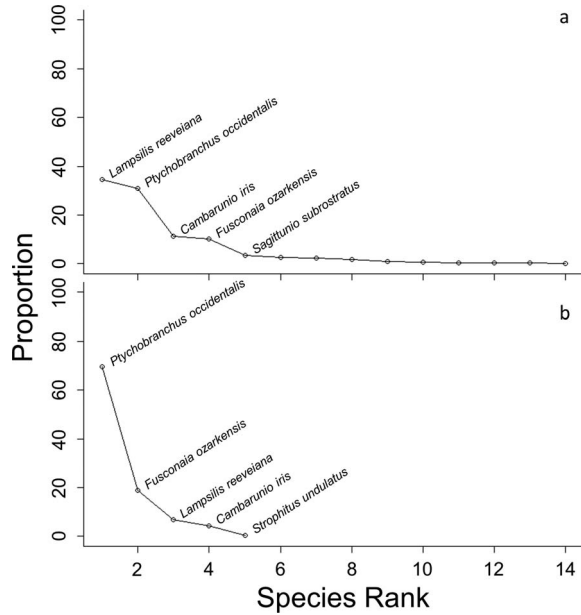


Figure 2. Species rank abundance plots for 11 sites surveyed in the Jacks Fork basin in (a) 1982 and (b) 2017–19.

There was no evidence of colonization for any species in the Jacks Fork, and the extinction probability was ≥ 0.50 for all species, suggesting that local populations are not viable and hold an extinction debt from which additional extirpations should be expected in the future (Gotelli 2001; Vaughn 2012).

We found no differences in the composition of the Jacks Fork mussel assemblage between 1982 and 2017–19 with respect to tribe or life-history strategy, suggesting that the decline has occurred evenly across the fauna. However, most apparently extirpated species are short lived, and surviving species that declined in relative abundance also are short lived

Table 5. Colonization proportion (p_c) and extirpation proportion (p_e) for species, tribes, and life-history strategies detected live at 11 sites in the Jacks Fork, Missouri, during 1982 (Buchanan 1996) and 2017–19.

Species	p_e	p_c
<i>Alasmidonta viridis</i>	1.00	0.00
<i>Lasmigona costata</i>	1.00	0.00
<i>Pyganodon grandis</i>	1.00	0.00
<i>Strophitus undulatus</i>	0.67	0.00
<i>Utterbackia imbecillis</i>	1.00	0.00
<i>Cambarunio hesperus</i>	0.57	0.00
<i>Lampsilis reeveiana</i>	0.50	0.00
<i>Leptodea fragilis</i>	1.00	0.00
<i>Ptychobranthus occidentalis</i>	0.50	0.00
<i>Sagittunio subrostratus</i>	1.00	0.00
<i>Truncilla donaciformis</i>	1.00	0.00
<i>Eurynia dilatata</i>	1.00	0.00
<i>Fusconaia ozarkensis</i>	0.63	0.00
<i>Pleurobema sintoxia</i>	1.00	0.00
Mean	0.85	0.00
Anodontini	0.80	0.00
Lampsilini	0.38	0.00
Pleurobemini	0.63	0.00
Opportunistic	1.00	0.00
Periodic	0.38	0.00
Equilibrium	0.50	0.00

(*Strophitus undulatus*, *Cambarunio hesperus*, *L. reeveiana*). The only species that increased in relative abundance are relatively long lived (*Ptychobranthus occidentalis*, *Fusconaia ozarkensis*). Rapid disappearance of short-lived species and longer persistence of long-lived species is a common characteristic of enigmatic mussel declines or other changes in mussel assemblages (Haag 2012, 2019; Hornbach et al.

Table 4. Rank, catch per unit effort (CPUE), abundance, and proportion of species detected live at 11 sites in the Jacks Fork, Missouri during 1982 (Buchanan 1996) and 2017–19.

Species	1982				2017–19			
	Rank	CPUE	Abundance	Proportion	Rank	CPUE	Abundance	Proportion
<i>Alasmidonta viridis</i>	11	0.2	3	0.5	—	—	—	—
<i>Lasmigona costata</i>	14	0.1	1	0.2	—	—	—	—
<i>Pyganodon grandis</i>	8	0.5	10	1.7	—	—	—	—
<i>Strophitus undulatus</i>	7	0.7	13	2.2	5	0.03	1	0.4
<i>Utterbackia imbecillis</i>	9	0.3	6	1.0	—	—	—	—
<i>Cambarunio hesperus</i>	3	3.4	68	11.4	4	0.3	11	4.4
<i>Lampsilis reeveiana</i>	1	10.3	206	34.5	3	0.5	17	16.8
<i>Leptodea fragilis</i>	10	0.2	4	0.7	—	—	—	—
<i>Ptychobranthus occidentalis</i>	2	9.2	184	30.8	1	5.1	173	69.5
<i>Sagittunio subrostratus</i>	5	1.0	20	3.4	—	—	—	—
<i>Truncilla donaciformis</i>	13	0.1	2	0.3	—	—	—	—
<i>Eurynia dilatata</i>	6	0.8	16	2.7	—	—	—	—
<i>Fusconaia ozarkensis</i>	4	3.1	61	10.2	2	1.4	47	18.9
<i>Pleurobema sintoxia</i>	12	0.2	3	0.5	—	—	—	—

2017; Khan et al. 2020). The Jacks Fork does support a substantial population of the Missouri SOCC *P. occidentalis*. However, we have no information about size or age structure of mussel populations in the Jacks Fork or whether recruitment is occurring. Unless recruitment is occurring for *P. occidentalis* and *F. ozarkensis*, these species can be expected to decline in the future as remaining adults die.

We have no information about the causes of the mussel decline in the Jacks Fork. The stream experienced a 500-yr flood event during April–May 2017 that caused pronounced geomorphic changes in its channel (Heimann et al. 2018), but we do not know if this event is related to the mussel decline. If this flood event was the cause of the mussel decline, it means that the decline happened abruptly, immediately before our survey, rather than gradually since 1982. However, we did not observe large numbers of recently dead shells during our survey, and mussels are thought to be adapted to frequent bed disturbance from high-flow events (Sansom et al. 2018). The lower 11.3 km of the Jacks Fork is affected by high fecal coliform bacteria, presumably from failing on-site wastewater systems (MDNR 2004). Properly functioning on-site wastewater systems can have no measurable impacts on mussels, but failing systems can be a source of ammonia, which is harmful to mussels (Goudreau et al. 1993; Mummert et al. 2003; Grabarkiewicz and Davis 2008). However, we have no data on ammonia concentrations in the Jacks Fork and its potential linkage with mussel declines (Wilkerson 2001). As is the case for many streams in the USA, the mussel decline in the Jacks Fork is enigmatic and its causes are unknown (Haag and Williams 2014).

ACKNOWLEDGMENTS

We thank K. Corbett, T. Namoff, B. Stephens, and C. Thornberry for assistance in the field, and S. Erwin for providing additional literature. We thank J. Ackerson, S. Erwin, B. Sansom, and B. Stephens for reviewing an earlier version of this manuscript and providing helpful edits and suggestions, and W. Haag, C. Vaughn, and two anonymous reviewers for their critical review and improvement of the manuscript. Collections within the boundaries of the OZAR were permitted under Scientific Research and Collecting Permit OZAR-2017-SCI-0001. This survey was funded by the Missouri Department of Conservation, and shell voucher material has been retained in the Missouri Department of Conservation reference collection (Columbia).

LITERATURE CITED

- Buchanan, A. C. 1996. Distribution of naiades in select streams in southern Missouri: A survey conducted during 1981–1982. Technical Report, Missouri Department of Conservation, Columbia.
- Dinno, A. 2017. dunn.test: Dunn's test of multiple comparisons using rank sums. Available at <https://cran.r-project.org/package=dunn.test> (accessed November 18, 2022).
- Dunn, H. D., S. Zigler, and T. Newton. 2020. Mussel community assessment tool for the upper Mississippi River system. *Freshwater Mollusk Biology and Conservation* 23:109–123.
- Erwin, S. O., R. B. Jacobson, and J. C. Jones. 2021. Stream classification and gravel-bar inventory for Buffalo National River and Ozark National Scenic Riverways. U.S. Geological Survey Scientific Investigations Report 2020-5122. Available at <https://doi.org/10.3133/sir20205122> (accessed November 18, 2022).
- FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1–21.
- Foster, S. D., and P. K. Dunstan. 2010. The analysis of biodiversity using rank abundance distributions. *Biometrics* 66:186–195.
- Frerebeau, N. 2019. tabula: An R package for analysis, seriation, and visualization of archaeological count data. *Journal of Open Source Software* 4:1821. Available at <https://doi.org/10.21105/joss.01821> (accessed November 18, 2022).
- Gotelli, N. J. 2001. A primer of ecology, 3rd ed. Sinauer Associates, Sunderland, Massachusetts. 265 pp.
- Goudreau, S. E., R. J. Neves, and R. J. Sheehan. 1993. Effects of wastewater treatment plant effluents on freshwater mollusks in the upper Clinch River, Virginia, USA. *Hydrobiologia* 252:211–230.
- Grabarkiewicz, J., and W. Davis. 2008. An introduction to freshwater mussels as biological indicators. EPA-260-R-08-015. U.S. Environmental Protection Agency, Office of Environmental Information, Washington, DC. Available at https://www.waterboards.ca.gov/water_issues/programs/swamp/docs/cwt/guidance/445.pdf (accessed November 21, 2022).
- Haag, W. R. 2010. A hierarchical classification of freshwater mussel diversity in North America. *Journal of Biogeography* 37:12–26.
- Haag, W. R. 2012. North American freshwater mussels: Natural history, ecology, and conservation. Cambridge University Press, New York. 505 pp.
- Haag, W. R. 2019. Reassessing enigmatic declines in the United States. *Freshwater Mollusk Biology and Conservation* 22:43–60.
- Haag, W. R., and J. D. Williams. 2014. Biodiversity on the brink: An assessment of conservation strategies for North American freshwater mussels. *Hydrobiologia* 735:45–60.
- Harris, J. L. 1999. Diversity of mussels. Pages 115–132 in United States Department of Agriculture Forest Service, Southern Research Station. Ozark-Ouachita Highlands assessment: Aquatic conditions. General Technical Report SRS-33. Available at https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs033.pdf (accessed November 21, 2022).
- Heimann, D. C., R. R. Holmes, Jr., and T. E. Harris. 2018. Flooding in the southern Midwestern United States, April–May 2017. U.S. Geological Survey Open-File Report 2018-1004. Available at <https://doi.org/10.3133/ofr20181004> (accessed November 18, 2022).
- Hornbach, D. J., D. C. Allen, M. C. Hove, and K. R. MacGregor. 2017. Long-term decline of native freshwater mussel assemblages in a federally protected river. *Freshwater Biology* 2017:1–21.
- Khan, J. M., J. Dudding, M. Hart, E. Tsakiris, and C. R. Randklev. 2020. Linking life history strategies and historical baseline information shows effects of altered flow regimes and impoundments on freshwater mussel assemblages. *Freshwater Biology* 65:1950–1961.
- Kindt, R. and R. Coe. 2005. Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF). Nairobi, Kenya. Available at <https://www.worldagroforestry.org/output/tree-diversity-analysis> (accessed March 10, 2022).
- Lopes-Lima, M., E. Froufe, V. T. Do, M. Ghamizi, K. E. Mock, Ü. Kebapçı, O. Klishko, S. Kovitvadhi, U. Kovitvadhi, O. S. Paulo, J. M. Pfeiffer, III, M. Raley, N. Riccardi, H. Şereflişan, R. Sousa, A. Teixeira, S. Varandas, X. Wu, D. T. Zanatta, A. Zieritz, and A. E. Bogan. 2017. Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogenetics and Evolution* 106:174–191.
- Magurran, A. E. 1996. Ecological diversity and its measurement. Chapman and Hall, London. 179 pp.

- McClane Environmental Services. 2004. Ozark National Scenic Riverways 2002 freshwater mussel (Unionid) inventory. Final report completed for Heartland Inventory and Monitoring Network and National Park Service, Van Buren, Missouri. McClane Environmental Services, St. Louis, Missouri.
- MDC (Missouri Department of Conservation). 2008. Missouri mussel conservation and management plan. Missouri Department of Conservation, Columbia.
- MDC (Missouri Department of Conservation). 2022. Missouri species and communities of conservation concern checklist. Missouri Department of Conservation, Natural Heritage Program, Jefferson City. Available at https://mdc.mo.gov/sites/default/files/2022-02/Missouri%20SOCC%20Checklist_2022a.pdf (accessed November 21, 2022).
- MDNR (Missouri Department of Natural Resources). 2004. Total maximum daily loads (TMDLs) for Jacks Fork River, Shannon County, Missouri. Missouri Department of Natural Resources, Water Pollution Control Program, Jefferson City. Available at <https://dnr.mo.gov/document-search/jacks-fork-pathogen-total-maximum-daily-load> (accessed February 17, 2022).
- Moore, A. P., N. Galic, R. A. Brain, D. J. Hornbach, and V. E. Forbes. 2021. Validation of freshwater mussel life-history strategies: A database and multivariate analysis of freshwater mussel life-history traits. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2021:1–17.
- Mummert, A. K., R. J. Neves, T. J. Newcomb, and D. S. Cherry. 2003. Sensitivity of juvenile freshwater mussels (*Lampsilis fasciola*, *Villosa iris*) to total and un-ionized ammonia. *Environmental Toxicology and Chemistry* 22:2545–2553.
- Nigh, T. A., and W. A. Schroeder. 2002. Atlas of Missouri ecoregions. Missouri Department of Conservation, Jefferson City.
- Oesch, R. D. 1995. Missouri naiades: A guide to the mussels of Missouri. Missouri Department of Conservation, Jefferson City.
- Panfil, M. S., and R. B. Jacobson. 2001. Relations among geology, physiography, land use, and stream habitat conditions in the Buffalo and Current River systems, Missouri and Arkansas. U.S. Geological Survey, Biological Science Report USGS/BRD/BSR-2001-0005. Available at <https://pubs.usgs.gov/bsr/2001/0005/bsr20010005.pdf> (accessed November 21, 2022).
- Pfieger, W. L. 1989. Aquatic community classification system for Missouri. Aquatic Series No. 19, Missouri Department of Conservation, Jefferson City.
- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at www.R-project.org/ (accessed November 18, 2022).
- Sansom, B. J., S. J. Bennett, J. F. Atkinson, and C. C. Vaughn. 2018. Long-term persistence of freshwater mussel beds in labile river channels. *Freshwater Biology* 63:1469–1481.
- Southwick, R. I., and A. J. Loftus, editors. 2003. Investigation and monetary values of fish and freshwater mussel kills. American Fisheries Society, Special Publication 30, Bethesda, Maryland.
- Sowa, S. P., G. Annis, M. E. Morey, and D. D. Diamond. 2007. A GAP analysis and comprehensive conservation strategy for riverine ecosystems of Missouri. *Ecological Monographs* 77:301–334.
- Steyermark, J. J. 1968. Flora of Missouri. The Iowa State University Press, Ames.
- Vaughn, C. C. 2012. Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels. *Freshwater Biology* 57:982–992.
- Vaughn, C. C., C. M. Taylor, and K. J. Eberhard. 1997. A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. Pages 157–162 in K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo, editors. Conservation and Management of Freshwater Mussels II: Initiatives for the Future. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Wilkerson, T. F., Jr. 2001. Jacks Fork watershed inventory and assessment. Missouri Department of Conservation, West Plains. Available at https://mdc.mo.gov/sites/default/files/2021-12/160_2021_JacksFork.pdf (accessed November 21, 2022).

REGULAR ARTICLE

GAINS AND GAPS IN KNOWLEDGE SURROUNDING FRESHWATER MOLLUSK ECOSYSTEM SERVICES

Carla L. Atkinson^{1*}, Garrett W. Hopper¹, Danielle A. Kreeger²,
Jonathan W. Lopez³, Alexa N. Maine⁴, Brandon J. Sansom⁵, Astrid Schwalb⁶,
and Caryn C. Vaughn³

¹ Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487 USA

² Partnership for the Delaware Estuary, Wilmington, DE 19801 USA

³ Oklahoma Biological Survey and Department of Biology, University of Oklahoma, Norman, OK 73019 USA

⁴ Confederated Tribes of the Umatilla Indian Reservation, Fisheries Program, Freshwater Mussel Research and Restoration Project, Pendleton, OR 97801 USA

⁵ U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO 65201 USA

⁶ Department of Biology, Texas State University, San Marcos, TX 78666 USA

ABSTRACT

Ecosystems provide essential services to people including food, water, climate regulation, and aesthetic experiences. Biodiversity can enhance and stabilize ecosystem function and the resulting services natural systems provide. Freshwater mollusks are a diverse group that provide a variety of ecosystem services through their feeding habits (e.g., filter feeding, grazing), top-down and bottom-up effects on food webs, provisioning of habitat, use as a food resource by people, and cultural importance. Research focused on quantifying the direct and indirect ways mollusks influence ecosystem services may help inform policy makers and the public about the value of mollusk communities to society. The Freshwater Mollusk Conservation Society highlighted the need to evaluate mollusk ecosystem services in their 2016 National Strategy for the Conservation of Native Freshwater Mollusks, and, while significant progress has been made, considerable work remains across the research, management, and outreach communities. We briefly review the global status of native freshwater mollusks, assess the current state of knowledge regarding their ecosystem services, and highlight recent advances and knowledge gaps to guide further research and conservation actions. Our intention is to provide ecologists, conservationists, economists, and social scientists with information to improve science-based consideration of the social, ecological, and economic value of mollusk communities to healthy aquatic systems.

KEY WORDS: restoration, conservation, social valuation, provisioning, regulating, cultural, biodiversity

INTRODUCTION TO ECOSYSTEM SERVICES

Human societies obtain essential goods and services from natural ecosystems, including timber, food, water, and climate regulation, which are known as “ecosystem services” (Millennium Ecosystem Assessment 2005; Mace et al. 2012). Ecosystems provide such services in ways, both direct and

indirect, that underpin human well-being. For example, there is value in a clean river that can be used for human consumption while also providing habitat for fish communities and a place for people to recreate. Ecosystem services can be divided into four main categories, each of which can be valued to draw comparisons with human-engineered infrastructure and services to inform policy and decision makers (Millennium Ecosystem Assessment 2005).

*Corresponding Author: Carla.L.atkinson@ua.edu

This article has been contributed to by US Government employees, and their work is in the public domain in the USA.

(1) *Provisioning services* are those that provide goods such as food and water.

- (2) *Regulating services* are those that control various processes, such as water purification, flood control, climate regulation, or suppression of disease outbreaks.
- (3) *Supporting services* are those that maintain material and energy balances, such as nutrient recycling.
- (4) *Cultural services* are those that provide spiritual or aesthetic benefits.

A large body of work shows that higher biodiversity can enhance and stabilize ecosystem functioning (Tilman et al. 2001; Naeem and Wright 2003; Loreau and de Mazancourt 2013; Oliver et al. 2015), thus providing critical services. Therefore, biodiversity is considered an ecosystem service that is subject to valuation (Mace et al. 2012). Human-induced declines in biodiversity and biomass raise concerns about the deterioration of ecosystem functions and associated ecosystem services (Dirzo et al. 2014; Young et al. 2016). As such, the ecosystem service framework can improve understanding of how the existence of communities of abundant and diverse organisms enhances ecosystems.

Freshwater ecosystems and the organisms that inhabit them contribute to many important ecosystem services including provisioning of clean water, nutrient processing, recreation, and tourism (Brauman et al. 2007; Dodds et al. 2013). Freshwater mollusks (i.e., gastropods and bivalves) in rivers and lakes provide supporting services such as nutrient recycling and storage, provisioning services by acting as food for humans and other organisms, regulating services like water purification, and cultural services such as jewelry and art (FMCS 2016; Vaughn 2018; Zieritz et al. 2022; Table 1). Due to their ecological importance and potential role in provisioning ecosystem services, using mollusks to restore or establish desirable ecosystem services has been proposed (Strayer et al. 2019; Wood et al. 2021). Research that quantifies the direct and indirect ways mollusks provision ecosystem services is key to properly valuating these services and informing policy makers and the public about the value of mollusk communities to society (FMCS 2016). The Freshwater Mollusk Conservation Society identified understanding the role of freshwater mollusks and their habitats on ecosystem services as a high-priority need (FMCS 2016). Zieritz et al. (2022) recently synthesized knowledge on the services provided by and disrupted by bivalve mollusks. We expand on this synthesis by including freshwater bivalves and gastropods and identifying future research needs. We briefly review the status of native freshwater mollusks, assess the current state of knowledge regarding their ecosystem services, and highlight recent advances and knowledge gaps to guide further work describing and quantifying the role of these animals in sustaining ecosystem services. Our intention is to provide ecologists, conservationists, economists, and social scientists with information to improve science-based consideration of the social and economic values of mollusk communities and functioning aquatic systems.

FRESHWATER MOLLUSKS—A HIGHLY IMPERILED GROUP OF ORGANISMS

Freshwater mollusks are distributed globally, occurring on all continents except Antarctica (Graf and Cummings 2007; Strong et al. 2008). They provide valuable ecosystem services by improving water quality, enhancing nutrient cycling, and playing critical roles in aquatic food webs. However, biodiversity is declining at a greater rate in freshwaters globally than in terrestrial systems (Reid et al. 2019), and mollusks represent one of the most diverse aquatic groups with more than 6,000 species (Böhm et al. 2021). Extinction rates for North American freshwater fauna are estimated to be as high as 4% per decade, five times greater than species losses in terrestrial systems (Ricciardi and Rasmussen 1999). For example, of the species comprising potentially the most diverse freshwater mollusk assemblage in the world (the Mobile Basin in the southeastern USA), one-third are now extinct due to flow regulation and habitat alteration (Williams et al. 2008). More broadly, 44% of European (Cuttelod et al. 2011), 29% of African (Seddon et al. 2011), and 17% of Indo-Burman (Köhler et al. 2012) freshwater mollusks are threatened with extinction. Rates for less-studied regions and faunas may be as high or higher (Dudgeon et al. 2006; Böhm et al. 2021). Mollusk populations are extirpated or severely reduced in many freshwater systems globally due to significant and emerging anthropogenic stressors including habitat modification (e.g., dams and urbanization) and degraded water quality (Benson et al. 2021; Böhm et al. 2021). Globally, 40% of freshwater bivalves are considered threatened, with gastropods likely being more threatened, but this is probably an underestimate given the lack of data for many regions (Lopes-Lima et al. 2018; Böhm et al. 2021). In North America alone, an estimated 72% of freshwater mussels and 74% of freshwater gastropods are imperiled (Johnson et al. 2013). Therefore, it is critical to understand their role in the functioning of freshwater ecosystems and the resulting ecological services associated with them. Despite these and other anthropogenic pressures, some native freshwater mollusk populations remain intact or are being restored, and ecosystem services are a goal of some restoration efforts (FMCS 2016; Strayer 2017).

STATE OF OUR KNOWLEDGE REGARDING FRESHWATER MOLLUSK ECOSYSTEM SERVICES

Provisioning Services

Humans have used mollusks for food and as tools for millennia. Evidence of freshwater mollusks serving as a human food source dates to ~6000 years BP in northern Europe and to greater than 2800 years BP in North America (Haag 2012; Meadows et al. 2014; CTUIR 2020). The presence of large shell middens at human habitation sites shows that freshwater mussels were used as food extensively in prehistory by people in North America, Australia, Europe, and likely elsewhere (Parmalee and Klippel 1974; Nicodemus

Table 1. Examples of ecosystem services provided by freshwater mollusks. C = carbon, N = nitrogen, P = phosphorus.

Service Type	Use	Example	Selected References
Provisioning	Food	Freshwater mussels have been a food source as far back as the Stone Age in Europe and 800 BP for Native Americans.	Meadows et al. 2014; CTUIR 2020
		Mollusks are an important food commodity in southeast Asia.	Bolotov et al. 2014; Dee et al. 2019
	Medicinal uses	Freshwater clams, <i>Corbicula</i> , are used to treat liver disease and side effects of alcoholism.	Bai et al. 2020; Zieritz et al. 2022
	Buttons	Mussels were used extensively in the North American button industry from the mid-1800s to the mid-1990s.	Haag 2012; Strayer 2017
Regulating	Pearl culture	Beads from mussel shells are used as seeds in the pearl industry.	Jiale and Yingsen 2009
	Water purification	Water filtration: Freshwater mussels clear an extensive volume of water, but it depends on their density and the stream discharge.	Vaughn et al. 2004; Vaughn et al. 2015
		Nonnative snails filter a significant amount of particulates from the water column, and their filtration rates rival freshwater bivalves.	Olden et al. 2013
	Contaminant sequestration	Freshwater mussel filtration removes coliform bacteria, pharmaceuticals, personal care products, and algal toxins. Contaminants that are removed are sequestered by mollusks in the soft tissue and shell.	Downing et al. 2014; Ismail et al. 2014, 2015, 2016 Mersch and Johansson 1993; Zhang et al. 2012; Giari et al. 2017; Archambault 2020
Supporting	Algal control	Benthic grazing snails can remove and control algal biomass, including nuisance and toxic algae.	Lamberti et al. 1987; Hill et al. 1992; Rosemond et al. 1993; Fervier et al. 2020
		Filter-feeding mollusks can clear and control algal blooms including algal toxins.	Hwang et al. 2021
	Nutrient cycling and storage	Mussel soft tissue and shell act as long-term storage of nutrients such as C, N, and P as well as micronutrients.	Strayer and Malcolm 2007; Atkinson and Vaughn 2015; Atkinson et al. 2018; Hopper et al. 2021b
		Aggregations of mussels act as biogeochemical hotspots of dissolved organic matter and N and P.	Atkinson and Vaughn 2015; Vaughn et al. 2015; Hopper et al. 2021a
Denitrification	Algal grazing and excretion by freshwater gastropods enhance primary production and nutrient uptake rates.	Hall et al. 2003; Hill and Griffiths 2017	
Habitat provisioning	Mussels contribute to the permanent removal of N from aquatic ecosystems by enhancing denitrification rates.	Hoellein et al. 2017; Trentman et al. 2018; Nickerson et al. 2019	
	Mussels improve and create habitat by enhancing hydrodynamic habitat complexity and decreasing turbulent shear stresses	Sansom et al. 2018a, 2018b, 2020; Wu et al. 2020	
Food web support	Mollusk shells provide habitat for algae, macrophytes, macroinvertebrates, and fish.	Mollusk shells provide habitat for algae, macrophytes, macroinvertebrates, and fish.	Francoeur et al. 2002; Vaughn et al. 2002; Spooner and Vaughn 2006; Vaughn and Spooner 2006; Abbott and Bergey 2007; Lukens et al. 2017; Hopper et al. 2019
		Mussel excreta was found to support biomass accrual of primary producers and aquatic insects.	Atkinson et al. 2014, 2018
	Mussels enhance sediment organic matter and increase macroinvertebrate abundance and diversity.	Howard and Cuffey 2006; Spooner and Vaughn 2006; Simeone et al. 2021	
		Mollusks comprise the diet of many organisms including crayfish, fish, turtles, and muskrats.	Crowl and Covich 1990; Alexander and Covich 1991; Brown and Lydeard 2010; Haag 2012; Atkinson 2013

Table 1, continued.

Service Type	Use	Example	Selected References
Cultural	Ornamentation for rituals	Beads and other ornaments made from shells have been used in rituals and ceremonies. Shells are used to ornament burial sites.	Claassen 2008; CTUIR 2020 Haag 2012
	Heritage and sense of place	Locations with high abundances of mussels have been used in the names of locations within streams (e.g., Muscle Shoals, Alabama). There are multiple archeological and historical values from midden piles that have been discovered across Europe and North America.	Haag 2012; Hunn et al. 2015; Vaughn 2018 Parmalee and Klippel 1974; Bērziņš et al. 2014
	Education and research	Mollusks have been used to study water pollution, to set water quality criteria, to be set as biomonitors, and to reconnect people to nature.	Augspurger et al. 2003; Wang et al. 2007; Michel et al. 2019

2011; Haag 2012; Garvey 2017). Columbia Plateau tribes in northwestern North America, such as the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), historically harvested mussels in association with harvest of other food resources (e.g., salmon and plants; Quaempts et al. 2018; CTUIR 2020). The Umatilla named a site on the Columbia River Išáaxuyi, which means “covered with mussel shells,” due to the high abundance of mussels (Hunn et al. 2015). Freshwater mussels are still considered a first food, a food of significant cultural and ecological importance, by the CTUIR and are actively managed and protected (Quaempts et al. 2018; CTUIR 2020). Freshwater mollusks remain an important food resource in other parts of the world, especially Southeast Asia (Zieritz et al. 2018), where both freshwater mussels and gastropods are a common commodity in markets (Bolotov et al. 2014; Dee et al. 2019). Mollusks are also used for medicinal purposes, mainly in eastern Asia. For example, in its native range, *Corbicula fluminea* has long been a part of traditional Chinese medicine used to treat liver disease and the effects of alcoholism (Bai et al. 2020).

Historically, mollusk shells were important for tools, jewelry, and other uses. Native American tribes used mussel shells for tools and ground them to powder to temper pottery (Rafferty and Peacock 2008). In the Pacific Northwest, tribes collected mussels seasonally, stored shells in large piles, and later worked them into hooks, spoons, and adornment (Brim Box et al. 2006; CTUIR 2020; Peacock et al. 2020). Beginning in the mid-1800s and lasting through the mid-1900s, the mollusk shell button industry was a lucrative business in North America (Coker et al. 1919; Haag 2012). During the peak harvest in 1912, 50,000 tons of mussels were removed from North American rivers, and between 1897 and 1963, the total value of buttons was approximately \$6 billion U.S. dollars (Haag 2012; Strayer 2017). Subsequently, the Japanese pearl industry used beads made from freshwater mussel shells as nuclei to produce cultured pearls in marine bivalves (Haag 2012). Cultured pearls are also produced in freshwater mussels, and this is a large industry in Asia (Jiale and

Yingsen 2009). Additionally, many freshwater bivalves and gastropods have been harvested in Thailand for jewelry and artwork (Nagachinta et al. 2005; Allen et al. 2012a).

Regulating Services

Water filtration.—Through their filter feeding and grazing, mollusks provide important regulating services such as water purification and regulation of algal communities. Freshwater mussels are filter feeders that remove particles and associated nutrients from the water column and interstitial sediments, which can in turn decrease water treatment costs and improve water quality (Vaughn et al. 2008; Newton et al. 2011; Kreeger et al. 2018). Where mussel biomass is high in comparison to water volume, or where hydrologic residence times are long, mussels can filter a substantial amount of water (Vaughn et al. 2004). For example, mussels were able to clear the entire volume of a 440,000 m³ lake in less than a day, resulting in enhanced water clarity (Chowdhury et al. 2016). Efforts are underway to restore freshwater mussel filtration capacity to U.S. mid-Atlantic watersheds with the goal of improving water clarity and quality (Kreeger et al. 2018). Some groups of gastropods (e.g., Viviparidea and Bithynidae) also function as filter feeders in aquatic ecosystems (Brown and Lydeard 2010), thus likely providing similar benefits to water clarity (see Olden et al. 2013) and particulate nutrient removal. Future research on snail filtration capacity and their effects on water quality could broaden our understanding of the ecosystem services gastropods provide. Freshwater mussels also improve drinking water quality by filtering pathogens or contaminants such as coliform bacteria, pharmaceuticals, personal care products, and algal toxins (Mersch and Johansson 1993; Downing et al. 2014; Ismail et al. 2014, 2015; Hwang et al. 2021) and sequestering these contaminants in their soft tissue and shell (Giari et al. 2017; Archambault 2020). Less is known about filter-feeding gastropods, but based on work on bivalves (Roditi et al. 2000; Baines et al.

2005), we hypothesize that gastropods may be able to remove dissolved organic matter as well as materials such as heavy metals. Further work is needed to understand what mollusks can filter from the environment, what they sequester, the ultimate fate of sequestered materials, and how these aspects of filtration vary among species and environmental contexts.

Biofilm grazing.—Snails are important grazers that can substantially reduce algal and biofilm biomass (Lamberti et al. 1987; Hill et al. 1992; Rosemond et al. 1993). Nuisance and toxic algal blooms negatively affect wildlife and human health (Wurtsbaugh et al. 2019). Some work has shown that freshwater snails can help control algal blooms including nuisance cyanobacteria and toxic algae (Zhang et al. 2012; Groendahl and Fink 2017). More research is needed to better understand snails' ability to control algal blooms and their other functional roles in freshwater systems, particularly for detritivorous and filter-feeding snails.

Supporting Habitat Services

Nutrient storage and cycling.—Mollusks provide important supporting services such as nutrient recycling, translocation, and storage, and they may influence nutrient abatement (i.e., nutrient removal). As mollusks filter feed or graze, they convert energy and associated nutrients in their food into soft tissue, shell, and biodeposits (feces and pseudofeces), and they release bioavailable dissolved nutrients that support primary producers (Spooner and Vaughn 2006; Strayer 2014; Atkinson and Vaughn 2015) and detritus-based food webs (Atkinson et al. 2021; Hopper et al. 2021a).

Nutrient storage by mollusks is an overlooked, but potentially valuable, ecosystem service for nutrient abatement. For example, nitrogen (N)-trading programs in estuarine settings estimate the value of nitrogen assimilated by oysters at \$50 to \$181/kg N/year (Rose et al. 2021). Currently, similar programs to mitigate nutrient loading in freshwater environments do not exist, but they are being considered (Strayer et al. 2019; Wood et al. 2021). Freshwater mollusks assimilate nutrients into both their soft tissues and shells and can store kilograms of carbon (C), N, and phosphorus (P), as well as micronutrients, at a river reach (Atkinson and Vaughn 2015; Hopper et al. 2021b). Additionally, many species are relatively long-lived, and their shells can persist for decades (Strayer and Malcolm 2007; Atkinson et al. 2018), possibly providing long-term storage of nutrients such as calcium. Thus, long-term storage and sequestration via burial could be an important, but often overlooked, ecosystem service provided by freshwater mollusks.

Nutrients that are not assimilated into soft tissue and shell are egested as biodeposits or excreted as bioavailable dissolved nutrients (Strayer 2014; Atkinson and Vaughn 2015; Hopper et al. 2021a). Soluble nutrients excreted into the water column by mollusks are readily taken up by algae and heterotrophic bacteria (Evans-White and Lamberti 2005; Liess and Haglund 2007; Vaughn et al. 2008; Bril et al. 2014).

Snails (*Elimia* spp.) were an important source of recycled nitrogen in a U.S. stream, excreting 12 times more nitrogen than they accumulated in biomass during spring growth, and assimilating and excreting up to 50% of the nitrogen initially taken up by autotrophs and leaf microbes (Hill and Griffiths 2017). Thus, where mollusk biomass is locally high, mollusks can create “biogeochemical hotspots” where nutrient recycling and material flux are increased, leading to concentrations of nutrients that can exceed background ambient concentrations of bioavailable nutrients (Hall et al. 2003; Strayer 2014; Atkinson and Vaughn 2015; Hopper et al. 2021a). Mollusks also can affect nutrient cycling of entire ecosystems. In a small North American stream, nonnative New Zealand mud snails (*Potamopyrgus antipodarum*) dominated carbon sequestration and nitrogen excretion because of their high biomass and ubiquitous distribution (Hall et al. 2003). If bioavailable nutrients are limiting, fertilization by mollusk excreta can lead to spatial variation in algal community assemblages (Atkinson et al. 2013) and increases in biomass of benthic algae, macroinvertebrates, fishes, and riparian invertebrates and vertebrates (Allen et al. 2012b; Atkinson et al. 2014; Lopez et al. 2020; Simeone et al. 2021). Grazing by snails also can reduce macrophyte biomass. Most work on this topic focused on impacts of invasive snails on native aquatic plants (Yang et al. 2018; Bissattini et al. 2021), but native snails also can control invasive plants (Baker et al. 2010). Mollusks also have bottom-up food web effects as prey for other organisms such as crayfishes (Crowl and Covich 1990; Alexander and Covich 1991), fishes (Brown and Lydeard 2010), muskrats (Tyrrell and Hornbach 1998; Haag 2012), and turtles (Atkinson 2013).

Mollusks also have indirect effects on nutrient cycles by modifying biogeochemical reactivity, microbial communities, and redox gradients. Their interactions with the sediments alter oxygen profiles and fluxes of nutrients from the sediment and water column (Matisoff et al. 1985; Boeker et al. 2016). Due to their interactions with the benthic sediments and their high ammonia excretion and biodeposition rates, freshwater mussels enhance denitrification and anaerobic ammonium oxidation (anammox) rates in benthic sediments (Hoellein et al. 2017; Trentman et al. 2018; Nickerson et al. 2019; Atkinson and Forshay 2022). This is beneficial for water quality because denitrification results in the removal of nitrogen from the ecosystem; this service has received considerable attention in marine settings with oysters and other marine mollusks (Newell et al. 2005; Kellogg et al. 2018; Rose et al. 2021). Additional work examining how freshwater mollusks influence microbially mediated processes could increase our understanding of the breadth of ecosystem services mollusks provide. Such effects could be substantial given the high biomass of mollusks in some ecosystems and their important roles in nutrient cycling.

Habitat engineering.—Stream-dwelling organisms must cope with high flows (Lopez and Vaughn 2021). Mollusks physically engineer ecosystems through their shell production and movements across and within the benthic substrate, provisioning habitat for other organisms. Mollusk shells

generate complexity in benthic habitats that influence processes across trophic levels (Gutiérrez et al. 2003). Both living shells and spent shells enhance habitat complexity and provide a hard substrate for the settlement and establishment of organisms, including microscopic and macroscopic algae (Francoeur et al. 2002; Abbott and Bergey 2007; Lukens et al. 2017), macrophytes (Vaughn et al. 2002), macroinvertebrates (Spooner and Vaughn 2006; Vaughn and Spooner 2006; Simeone et al. 2021), and fishes (Hopper et al. 2019). Freshwater mussel aggregations can modulate near-bed velocities and turbulence in rivers over decadal time scales, which may enhance bed stability and create habitat for other stream-dwelling organisms by decreasing flow force and velocity (Sansom et al. 2018a, 2018b, 2020). As water flows past mussels, low-velocity refugia form behind them (Kumar et al. 2019), decreasing the hydrodynamic forces on the streambed downstream. Moreover, horseshoe vortices or complex wake structures are created around partially exposed mussels (Constantinescu et al. 2013; Sansom et al. 2018a; Wu et al. 2020), and such features are further modified when mussels are filtering (Wu et al. 2020). These hydraulic modifications can have important implications for other stream-dwelling organisms with specific microhabitat hydraulic preferences (e.g., Davis 1986; Bouckaert and Davis 1998). Overall, mussel aggregations have a reciprocal influence on near-bed flow because they both influence, and are constrained by, hydrodynamic forces at the streambed (Lopez and Vaughn 2021). In addition, shells provide spawning sites and serve as refugia for some fishes (Etnier and Starnes 1993; Aldridge 1999; Wisniewski et al. 2013). Locally high densities of shells, such as at mussel beds, increase the potential for strong hydraulic effects over extended spatial (tens to hundreds of meters) and temporal (decadal) scales (Strayer 2020). Much less is known about whether snails provide hydrodynamic refugia and/or stabilize sediments, but small stream invertebrates, such as caddisflies, can alter stream sediment dynamics and hydraulics when densities are high (Albertson and Allen 2015; Maguire et al. 2020; Mason and Sanders 2021; Mason et al. 2022). Thus, it is reasonable to expect that gastropods, with their sturdy shell, gripping foot, and mucus trails, also might stabilize sediment.

Beyond the obvious direct habitat provisioning of the shell, mollusks can increase habitat availability through their grazing and bioturbation activities. Filter-feeding bivalves increase the photic zone in lakes and rivers and enhance benthic substrate organic matter, allowing colonization by benthic macrophytes and aquatic insects (Strayer 2020). Grazing by invasive snails (*Pomacea canaliculata*) can have strong top-down effects by reducing biomass of aquatic plants, especially in shallow lakes with high nutrient loads (Gao et al. 2021; Liu et al. 2021), possibly leading to shifts from clear to turbid stable states. State shifts such as this can reduce light penetration in littoral zones and visibility for sight-feeding predators, with cascading effects on food webs. Overall, mollusks appear to have varied and sometimes strong effects on stream and lake habitats, which likely influence many other aquatic organisms.

Cultural Services

Freshwater mollusks provide many cultural services to humans. Large, durable freshwater mussel shells are particularly important for these services. Archaeological studies have shown that in Neolithic northern Europe, large mussel shell middens were used seasonally by pottery-using hunter-gatherer communities to temper pottery (Bērziņš et al. 2014). In North America, beads and other ornaments made from shells were used in rituals and ceremonies (Claassen 2008; CTUIR 2020). For example, the Winnebago tribe in Wisconsin, USA, used shell beads in rituals, produced utensils and fishing hooks from shells, and used powdered shell to temper pottery (Kuhm 2007). Currently, mollusk shells are sometimes used to ornament graves in the southern USA (Haag 2012). In the USA, the abundance of mussels in some areas invoked a sense of place that was translated into names of river reaches (e.g., Muscle Shoals and Išáaxuyi; Haag 2012; Hunn et al. 2015; Vaughn 2018). Living mollusks also bring humans enjoyment and are commonly sold internationally in the aquarium and ornamental pet trade (Ng et al. 2016; Patoka et al. 2017). In some cases, this practice has resulted in accidental introductions of mollusks into new ecosystems (Karatayev et al. 2009). Additionally, mollusks' regulating services (e.g., filtration, grazing) improve human perceptions of freshwater ecosystems by enhancing water clarity and other characteristics. For example, grazing by snails (*Haitia acuta*) reduces the occurrence of large algal mats (Parr et al. 2020), which can be unsightly to humans. Mollusks are also used in education and research to improve understanding of ecosystem health, and they are used as biomonitors for contaminants and pathogens (Mersch and Johansson 1993; Giari et al. 2017). Extensive toxicology research has evaluated mollusks' sensitivities to various contaminants, which have been used to evaluate water quality criteria (Augsburger 2003; Wang et al. 2007). Last, the bequest or existence value of mollusks is an important cultural service because people derive satisfaction from preserving the natural environment for future generations (Turner and Schaafsma 2015; Strayer 2017).

The Conundrum of Services and Disservices by Invasive Mollusks

The role of invasive mollusk species in providing ecosystem services has received attention primarily in terms of their negative effects or "disservices," but they can also enhance services (Charles and Dukes 2008; Limburg et al. 2010; Walsh et al. 2016; Zieritz et al. 2022). Invasive species often do not provide provisioning or cultural services in their introduced range because they have not been used traditionally for those purposes in the new area. However, some species may be introduced because of provisioning or cultural services they provide in their native range or elsewhere. For example, the bivalve *Corbicula fluminea* is thought to have been introduced into the USA in the 1930s by Chinese immigrants who used the species as a food item in its native range (Counts 1986). Thiarid snails have invaded freshwaters globally, and

they frequently are introduced through the aquarium trade, where their grazing services are used to keep aquaria clean (Padilla and Williams 2004; Preston et al. 2022). However, despite their use in the aquarium trade, invasive snails often provide disservices, as many are intermediate hosts for trematodes and other parasites that negatively affect the health of fishes, birds, and humans (e.g., Pinto and de Melo 2011; Lv et al. 2018; Valente et al. 2020).

Filtering and nutrient recycling by invasive mussels can provide important regulating and supporting services. Nutrient fluxes from high densities of *Corbicula* exceeded or equaled those from native mussels in two North American rivers (Hopper et al. 2022). Invasive dreissenid mussels can drastically change energy and nutrient fluxes in a system (Li et al. 2021; Zieritz et al. 2022). At high densities, their filtering activity reduces phytoplankton and redirects nutrients and energy from the water column to the benthos, causing a decrease in pelagic production and an increase in benthic production (Higgins and Vander Zanden 2010; Karatayev et al. 2015). This includes an increase in benthic algae and macrophytes, which are often perceived as nuisances that inhibit boating, swimming, and other recreational uses in lakes and reservoirs. Fouling of native mussels by dreissenid mussels causes high native mussel mortality through resource competition (Haag et al. 1993; Karatayev et al. 2015; Beason and Schwalb 2022), and *Corbicula* clams also are suspected to negatively affect native mussels (Ferreira-Rodríguez et al. 2018, 2022; Modesto et al. 2019). Both invasive species diminish ecosystem services provided by native mussels, but they also provide important benefits, especially in areas where the native mollusk filter-feeding community has been lost or severely degraded. For example, *Dreissena* can be used as biofilters to clear bioavailable contaminants from effluents before discharge (Binelli et al. 2015), and invasive *Corbicula* in Portugal assist in the remediation of acid mine drainage and other contaminants (Ismail et al. 2014; Rosa et al. 2014). Understanding how invasive mollusks provide and alter ecosystem services can give additional insight about services provided by native mollusks and how replacement of native species by invasive species ultimately affects ecosystem structure and long-term function.

DIRECTIONS FORWARD

A large body of work shows the foundational role of mollusks in freshwater ecosystems (Vaughn and Hakenkamp 2001; Vaughn and Hoellein 2018; Zieritz et al. 2022), but many research gaps and questions remain. Here we discuss research and information needed to better conceptualize mollusks in an ecosystem services framework, which will assist future conservation and management initiatives globally.

- Baseline information for ecosystem services. Information on the species richness, composition, and density of historical mollusk communities is needed to establish a baseline to guide restoration of ecosystem services. Generating this

information is especially important in understudied regions and likely will require combining reference site studies with modeling carrying capacity potential.

- Quantitative comparisons of the biomass distribution and ecosystem services provided by co-occurring native and invasive mollusks.
- Standardized methods that can be used to quantify ecosystem services of mollusks globally. For example, a standardized method for estimating filtration rates among and within species would help guide evaluation of the capacity for mollusks to influence water clarity. This gap could be addressed by globally coordinated research networks.
- The role of gastropods in provisioning ecosystem services. Snails can dominate benthic stream communities (Hawkins and Furnish 1987) and comprise >50% of invertebrate biomass in many systems (Brown et al. 2008; Brown and Lydeard 2010), but, apart from the effects of their grazing, little is known about their role in ecosystem processes. Quantitative assessments of gastropod abundance, functional feeding group status (algivorous and detritivores), nutrient excretion, and other physiological rates are needed.
- Understanding and acknowledging the role of traditional ecological knowledge in maintaining and restoring ecosystem services (e.g., Michel et al. 2019). Traditional knowledge regarding the distribution of mollusks and their uses is necessary for documenting their importance to ecosystem services.
- Understanding how factors such as carrying capacity and habitat suitability constrain mollusk populations and the ecosystem services they provide.
- Understanding how ecosystem services provided by mollusks vary along environmental gradients (e.g., eutrophic-oligotrophic), systems (e.g., river, lake, etc.), and both time and spatial scales.

In addition to research priorities, it is crucial that policy makers and the public recognize the value of and support restoration of mollusk-provided ecosystem services (“ecosystem service goals”; Wood et al. 2021). Disseminating research results and outreach is necessary to build this support, and outreach efforts should be focused on regions where mollusks are diverse and abundant or where they could be used to create a sense of place based on mollusks (e.g., areas where mollusks were once abundant). Building broad recognition of the value of mollusks is a major goal of the Freshwater Mollusk Conservation Society (FMCS 2016). We propose the following actions to meet these outreach and policy goals:

- Apply knowledge from work on ecosystem services provided by marine mollusks (i.e., successes and failures) to inform management and public outreach for freshwater mollusks.
- Examine how environmental, monetary, and institutional factors can both constrain and create opportunities for the

conservation and restoration of freshwater mollusks and the ecosystem services they provide.

- Increase outreach efforts to various stakeholders in regions where mollusks are diverse and abundant to create a sense of place within freshwater ecosystems and value for natural communities.
- Determine if research and management investments are being distributed to address actual needs (i.e., where people live and where services are needed) for enhanced ecosystem services. This could be determined using population census records coupled with evaluations of environmental degradation and public hearings and surveys.
- Encourage collaboration between biologists, social scientists, economists, outreach specialists, and policy makers to develop valuation guidelines for ecosystem services provided by freshwater mollusks and incorporate these guidelines into resource-management planning.

CONCLUSION

The loss of biodiversity is an urgent concern, one that threatens the ecological integrity of ecosystems along with the essential services they provide (Dudgeon et al. 2006; Oliver et al. 2015). Biodiversity loss is disproportionately high in freshwaters, particularly for mollusks (Lopes-Lima et al. 2018; Reid et al. 2019). Given their high diversity, global distribution, and, in some places, astounding biomass, it is critical to understand how restoration of mollusks fits into the framework of ecosystem services. Research that quantifies the functional importance of freshwater mollusks in ecosystems within a societal and policy context creates opportunities to value these animals and the services they provide as tangible benefits to society.

ACKNOWLEDGMENTS

We appreciate the input and discussions about this manuscript from members of the Freshwater Mollusk Conservation Society Ecosystem Service committee.

LITERATURE CITED

- Abbott, L. L., and E. A. Bergey. 2007. Why are there few algae on snail shells? The effects of grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*. *Freshwater Biology* 52:2112–2120.
- Albertson, L., and D. Allen. 2015. Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. *Ecology* 96:1329–1339.
- Aldridge, D. 1999. Development of European bitterling in the gills of freshwater mussels. *Journal of Fish Biology* 54:138–151.
- Alexander, J. E., and A. P. Covich. 1991. Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. *Oecologia* 87:435–442.
- Allen, D. J., K. G. Smith, and W. R. T. Darwall, compilers. 2012a. The status and distribution of freshwater biodiversity in Indo-Burma. International Union for Conservation of Nature and Natural Resources, Cambridge, UK, and Gland, Switzerland. 158 pp. Available at <https://www.iucn.org/>

- resources/publication/status-and-distribution-freshwater-biodiversity-indo-burma (accessed January 10, 2023).
- Allen, D. C., C. C. Vaughn, J. F. Kelly, J. T. Cooper, and M. Engel. 2012b. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. *Ecology* 93:2165–2174.
- Archambault, J. M. 2020. Contaminant-related ecosystem functions and services of freshwater mussels (Unionidae) and public views on nature's contributions to water quality. Doctoral dissertation, North Carolina State University, Raleigh.
- Atkinson, C. L. 2013. Razor-backed musk turtle (*Sternotherus carinatus*) diet across a gradient of invasion. *Herpetological Conservation and Biology* 8:561–570.
- Atkinson, C. L., and K. J. Forshay. 2022. Community patch dynamics governs direct and indirect nutrient recycling by aggregated animals across spatial scales. *Functional Ecology* 36:595–606.
- Atkinson, C. L., H. M. Halvorson, K. A. Kuehn, M. Winebarger, A. Hamid, and M. N. Waters. 2021. Filter-feeders have differential bottom-up impacts on green and brown food webs. *Oecologia* 195:187–198.
- Atkinson, C. L., J. F. Kelly, and C. C. Vaughn. 2014. Tracing consumer-derived nitrogen in riverine food webs. *Ecosystems* 17:485–496.
- Atkinson, C. L., B. J. Sansom, C. C. Vaughn, and K. J. Forshay. 2018. Consumer aggregations drive nutrient dynamics and ecosystem metabolism in nutrient-limited systems. *Ecosystems* 21:521–535.
- Atkinson, C. L., and C. C. Vaughn. 2015. Biogeochemical hotspots: Temporal and spatial scaling of the impact of freshwater mussels on ecosystem function. *Freshwater Biology* 60:563–574.
- Atkinson, C. L., C. C. Vaughn, K. J. Forshay, and J. T. Cooper. 2013. Aggregated filter-feeding consumers alter nutrient limitation: Consequences for ecosystem and community dynamics. *Ecology* 94:1359–1369.
- Augsburger, T., A. E. Keller, M. C. Black, W. G. Cope, and F. J. Dwyer. 2003. Water quality guidance for protection of freshwater mussels (Unionidae) from ammonia exposure. *Environmental Toxicology and Chemistry* 22:2569–2575.
- Bai, J., Y. Chen, Z. Ning, S. Liu, C. Xu, and J.-K. Yan. 2020. Proteoglycan isolated from *Corbicula fluminea* exerts hepato-protective effects against alcohol-induced liver injury in mice. *International Journal of Biological Macromolecules* 142:1–10.
- Baines, S. B., N. S. Fisher, and J. J. Cole. 2005. Uptake of dissolved organic matter (DOM) and its importance to metabolic requirements of the zebra mussel, *Dreissena polymorpha*. *Limnology and Oceanography* 50:36–47.
- Baker, P., F. Zimmanck, and S. M. Baker. 2010. Feeding rates of an introduced freshwater gastropod *Pomacea insularum* on native and nonindigenous aquatic plants in Florida. *Journal of Molluscan Studies* 76:138–143.
- Beason, E., and A. N. Schwalb. 2022. Impact of zebra mussels on physiological conditions of unionid mussels in Texas. *Aquatic Sciences* 84:21. <http://dx.doi.org/10.1007/s00027-022-00853-8>.
- Benson, J. A., B. A. Stewart, P. G. Close, and A. J. Lymbery. 2021. Freshwater mussels in Mediterranean-climate regions: Species richness, conservation status, threats, and conservation actions needed. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31:708–728.
- Bērziņš, V., U. Brinker, C. Klein, H. Lübke, J. Meadows, M. Rudzīte, U. Schmölcke, H. Stümpel, and I. Zagorska. 2014. New research at Rīņņukalna, a Neolithic freshwater shell midden in northern Latvia. *Antiquity* 88:715–732.
- Binelli, A., S. Magni, C. Della Torre, and M. Parolini. 2015. Toxicity decrease in urban wastewaters treated by a new biofiltration process. *Science of the Total Environment* 537:235–242.
- Bissattini, A. M., P. J. Haubrock, V. Buono, P. Balzani, N. Borgianni, L. Stellati, A. F. Inghilesi, L. Tancioni, M. Martinoli, and E. Tricarico. 2021. Trophic structure of a pond community dominated by an invasive alien species: Insights from stomach content and stable isotope analyses. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31:948–963.
- Boeker, C., T. Lueders, M. Mueller, J. Pander, and J. Geist. 2016. Alteration of

- physico-chemical and microbial properties in freshwater substrates by burrowing invertebrates. *Limnologia* 59:131–139.
- Böhm, M., N. I. Dewhurst-Richman, M. Seddon, S. E. H. Ledger, C. Albrecht, D. Allen, A. E. Bogan, J. Cordeiro, K. S. Cummings, A. Cuttelod, G. Darrigran, W. Darwall, Z. Fehér, C. Gibson, D. L. Graf, F. Köhler, M. Lopes-Lima, G. Pastorino, K. E. Perez, K. Smith, D. van Damme, M. V. Vinarski, T. von Proschwitz, T. von Rintelen, D. C. Aldridge, N. A. Aravind, P. B. Budha, C. Clavijo, D. Van Tu, O. Gargominy, M. Ghamizi, M. Haase, C. Hilton-Taylor, P. D. Johnson, Ü. Kebapçı, J. Lajtner, C. N. Lange, D. A. W. Lepitzki, A. Martínez-Ortí, E. A. Moorkens, E. Neubert, C. M. Pollock, V. Prié, C. Radea, R. Ramirez, M. A. Ramos, S. B. Santos, R. Slapnik, M. O. Son, A.-S. Stensgaard, and B. Collen. 2021. The conservation status of the world's freshwater mollusks. *Hydrobiologia* 848:3231–3254.
- Bolotov, I., I. Vikhrev, Y. Bespalaya, V. Artamonova, M. Gofarov, J. Kolosova, A. Kondakov, A. Makhrov, A. Frolov, and S. Tumpeesuwan. 2014. Ecology and conservation of the endangered Indochinese freshwater pearl mussel, *Margaritifera laosensis* (Lea, 1863) in the Nam Pe and Nam Long rivers, Northern Laos. *Tropical Conservation Science* 7:706–719.
- Bouckaert, F. W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology* 40:77–86.
- Brauman, K. A., G. C. Daily, T. K. Duarte, and H. A. Mooney. 2007. The nature and value of ecosystem services: An overview highlighting hydrologic services. *Annual Review of Environment and Resources* 32:67–98.
- Bril, J. S., J. J. Durst, B. M. Hurley, C. L. Just, and T. J. Newton. 2014. Sensor data as a measure of native freshwater mussel impact on nitrate formation and food digestion in continuous-flow mesocosms. *Freshwater Science* 33:417–424.
- Brim Box, J., J. Howard, D. Wolf, C. O. Brien, D. Nez, and D. Close. 2006. Freshwater mussels (Bivalvia: Unionoida) of the Umatilla and middle fork John Day rivers in eastern Oregon. *Northwest Science* 80:95.
- Brown, K. M., B. Lang, and K. E. Perez. 2008. The conservation ecology of North American pleurocerid and hydrobiid gastropods. *Freshwater Science* 27:484–495.
- Brown, K. M., and C. Lydeard. 2010. Mollusca: Gastropoda. Pages 207–306 in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, Cambridge, Massachusetts.
- Charles, H., and J. S. Dukes. 2008. Impacts of invasive species on ecosystem services. Pages 217–237 in W. Nentwig, editor. *Biological Invasions*. Springer, Berlin, Heidelberg.
- Chowdhury, G. W., A. Zieritz, and D. C. Aldridge. 2016. Ecosystem engineering by mussels supports biodiversity and water clarity in a heavily polluted lake in Dhaka, Bangladesh. *Freshwater Science* 35:188–199.
- Claassen, C. 2008. Shell symbolisms in pre-Columbian North America. Pages 207–306 in A. Antczak, and R. Cipriani, editors. *Early Human Impacts on Megamolluscs*. International Series 1865. British Archeological Reports Archeopress, Oxford, England.
- Coker, R. E. 1919. Fresh-water mussels and mussel industries of the United States. US Bulletin of the Bureau of Fisheries 36:13–89 [Issued separately as US Bureau of Fisheries Document 865].
- Constantinescu, G., S. Miyawaki, and Q. Liao. 2013. Flow and turbulence structure past a cluster of freshwater mussels. *Journal of Hydraulic Engineering* 139:347–358.
- Counts III, C. L. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *American Malacological Bulletin* 2:7–39.
- Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247:949–951.
- CTUIR (Confederated Tribes of the Umatilla Indian Reservation). 2020. Šáxu Siwáala Seewíŕs: River mussels through time. Lynx Group Publishing, Walla Walla, Washington.
- Cuttelod, A., M. Seddon, and E. Neubert. 2011. European Red List of non-marine Molluscs. Publications Office of the European Union, Luxembourg. Available at <https://portals.iucn.org/library/node/9981> (accessed November 3, 2022).
- Davis, J. 1986. Boundary layers, flow microenvironments and stream benthos. Pages 293–312 in P. De Deckker and W. D. Williams, editors. *Limnology in Australia*. Monographiae Biologicae, vol. 61. Springer, Dordrecht, the Netherlands.
- Dee, K. H., F. Abdullah, S. N. A. Md Nasir, S. Appalasamy, R. Mohd Ghazi, and A. Eh Rak. 2019. Health risk assessment of heavy metals from smoked *Corbicula fluminea* collected on roadside vendors at Kelantan, Malaysia. *BioMed Research International* 2019. <http://dx.doi.org/10.1155/2019/9596810>.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- Dodds, W. K., J. S. Perkin, and J. E. Gerken. 2013. Human impact on freshwater ecosystem services: A global perspective. *Environmental Science and Technology* 47:9061–9068.
- Downing, A. S., E. H. van Nes, J. S. Balirwa, J. Beuving, P. O. Bwathondi, L. J. Chapman, I. J. Cornelissen, I. G. Cowx, K. P. Goudswaard, and R. E. Hecky. 2014. Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecology and Society* 19:31.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status, and conservation challenges. *Biological Reviews* 81:163–182.
- Etnier, D. A., and W. C. Starnes. 1993. *The Fishes of Tennessee*. University of Tennessee Press, Knoxville.
- Evans-White, M. A., and G. A. Lamberti. 2005. Grazer species effects on epilithon nutrient composition. *Freshwater Biology* 50:1853–1863.
- Ferreira-Rodríguez, N., M. Gangloff, G. Shafer, and C. L. Atkinson. 2022. Drivers of ecosystem vulnerability to *Corbicula* invasions in southeastern North America. *Biological Invasions* 24:1677–1688.
- Ferreira-Rodríguez, N., R. Sousa, and I. Pardo. 2018. Negative effects of *Corbicula fluminea* over native freshwater mussels. *Hydrobiologia* 810:85–95.
- Fervier, V., P. Urrutia-Cordero, E. Piano, F. Bona, K. M. Persson, and L. A. Hansson. 2020. Evaluating nutrient reduction, grazing and barley straw as measures against algal growth. *Wetlands* 40:193–202.
- FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1–21.
- Francoeur, S. N., A. Pinowska, T. A. Clason, S. Makosky, and R. L. Lowe. 2002. Unionid bivalve influence on benthic algal community composition in a Michigan Lake. *Journal of Freshwater Ecology* 17:489–500.
- Gao, J., C. Yang, Z. Zhang, Z. Liu, and E. Jeppesen. 2021. Effects of co-occurrence of invading *Procambarus clarkii* and *Pomacea canaliculata* on *Vallisneria denseserrulata*-dominated clear-water ecosystems: A mesocosm approach. *Knowledge and Management of Aquatic Ecosystems* 422:1–7.
- Garvey, J. 2017. Australian aboriginal freshwater shell middens from late quaternary Northwest Victoria: Prey choice, economic variability and exploitation. *Quaternary International* 427:85–102.
- Giari, L., F. Vincenzi, E. A. Fano, I. Graldi, F. Gelli, and G. Castaldelli. 2017. Sensitivity to selected contaminants in a biological early warning system using *Anodonta woodiana* (Mollusca). *Water* 43:200–208.
- Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionida). *Journal of Molluscan Studies* 73:291–314.
- Groendahl, S., and P. Fink. 2017. High dietary quality of non-toxic

- cyanobacteria for a benthic grazer and its implications for the control of cyanobacterial biofilms. *BMC Ecology* 17:20.
- Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos* 101:79–90.
- Haag, W. R. 2012. North American freshwater mussels: Ecology, natural history, and conservation. Cambridge University Press, New York.
- Haag, W. R., D. J. Berg, and D. W. Garton. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in Western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 50:13–19.
- Hall, R. O., J. L. Tank, and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1:407–411.
- Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? *Oikos* 49:209–220.
- Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: A meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 80:179–196.
- Hill, W. R., and N. A. Griffiths. 2017. Nitrogen processing by grazers in a headwater stream: Riparian connections. *Freshwater Biology* 62:17–29.
- Hill, W. R., S. C. Weber, and A. J. Stewart. 1992. Food limitation of two lotic grazers: Quantity, quality, and size-specificity. *Journal of the North American Benthological Society* 11:420–432.
- Hoellein, T. J., C. B. Zarnoch, D. A. Bruesewitz, and J. DeMartini. 2017. Contributions of freshwater mussels (Unionidae) to nutrient cycling in an urban river: Filtration, recycling, storage, and removal. *Biogeochemistry* 135:307–324.
- Hopper, G. W., J. K. Buchanan, I. Sánchez González, M. E. Kubala, J. R. Bucholz, M. B. Lodato, J. D. Lozier, and C. L. Atkinson. 2022. Little clams with big potential: Nutrient release by invasive *Corbicula fluminea* can exceed co-occurring freshwater mussel (Unionidae) assemblages. *Biological Invasions* 24:2529–2545.
- Hopper, G. W., S. Chen, I. Sánchez González, J. R. Bucholz, Y. Lu, and C. L. Atkinson. 2021a. Aggregated filter-feeders govern the flux and stoichiometry of locally available energy and nutrients in rivers. *Functional Ecology* 35:1183–1195.
- Hopper, G. W., G. K. Dickinson, and C. L. Atkinson. 2021b. Associations among elements in freshwater mussel shells (Unionidae) and their relation to morphology and life history. *Freshwater Biology* 66:1980–1991.
- Hopper, G. W., T. P. DuBose, K. B. Gido, and C. C. Vaughn. 2019. Freshwater mussels alter fish distributions through habitat modifications at fine spatial scales. *Freshwater Science* 38:702–712.
- Howard, J. K., and K. M. Cuffey. 2006. The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology* 51:460–474.
- Hunn, E. S., E. T. Morning Owl, P. E. Cash Cash, and J. Karson Engum. 2015. Čaw Pawá Láakni—They are not forgotten: Sahaptian place names atlas of the Cayuse, Umatilla, and Walla Walla. Tamástsklikt Cultural Institute, Pendleton, Oregon.
- Hwang, S.-J., Y.-J. Lee, M.-S. Kim, and B.-H. Kim. 2021. Filter feeding and carbon and nitrogen assimilation of a freshwater bivalve (*Unio douglasiae*) on a toxic cyanobacterium (*Microcystis aeruginosa*). *Applied Sciences* 11:9294.
- Ismail, N. S., H. Dodd, L. M. Sassoubre, A. J. Horne, A. B. Boehm, and R. G. Luthy. 2015. Improvement of urban lake water quality by removal of *Escherichia coli* through the action of the bivalve *Anodonta californiensis*. *Environmental Science and Technology* 49:1664–1672.
- Ismail, N. S., C. E. Müller, R. R. Morgan, and R. G. Luthy. 2014. Uptake of contaminants of emerging concern by the bivalves *Anodonta californiensis* and *Corbicula fluminea*. *Environmental Science and Technology* 48:9211–9219.
- Ismail, N. S., J. P. Tommerdahl, A. B. Boehm, and R. G. Luthy. 2016. *Escherichia coli* reduction by bivalves in an impaired river impacted by agricultural land use. *Environmental Science and Technology* 50:11025–11033.
- Jiale, L., and L. Yingsen. 2009. Aquaculture in China—Freshwater pearl culture. *World Aquaculture* 40:60.
- Johnson, P. D., A. E. Bogan, K. M. Brown, N. M. Burkhead, J. R. Cordeiro, J. T. Garner, P. D. Hartfield, D. A. Lepitzki, G. L. Mackie, and E. Pip. 2013. Conservation status of freshwater gastropods of Canada and the United States. *Fisheries* 38:247–282.
- Karatayev, A. Y., L. E. Burlakova, V. A. Karatayev, and D. K. Padilla. 2009. Introduction, distribution, spread, and impacts of exotic freshwater gastropods in Texas. *Hydrobiologia* 619:181–194.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2015. Zebra versus quagga mussels: A review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* 746:97–112.
- Kellogg, M. L., M. J. Brush, and J. Cornwell. 2018. An updated model for estimating the TMDL-related benefits of oyster reef restoration. Final report to The Nature Conservancy and Oyster Recovery Partnership. Available at https://www.conservationgateway.org/Documents/Harris_Creek_Model_and_Oyster_Reef_Restoration_Benefits.pdf (accessed October 28, 2022).
- Köhler, F., M. Seddon, A. E. Bogan, D. Van Tu, P. Sri-Aroon, and D. Allen. 2012. The status and distribution of freshwater molluscs of the Indo-Burma region. Pages 66–88 in D. J. Allen, K. G. Smith, and W. R. T. Darwall, editors. *The Status and Distribution of Freshwater Biodiversity in Indo-Burma*. IUCN, Cambridge, United Kingdom, and Gland, Switzerland.
- Kreeger, D. A., C. M. Gatenby, and P. W. Bergstrom. 2018. Restoration potential of several native species of bivalve mollusks for water quality improvement in mid-Atlantic watersheds. *Journal of Shellfish Research* 37:1121–1157.
- Kuhm, H. W. 2007. Aboriginal uses of shell. *Wisconsin Archeologist* 17:1–8.
- Kumar, S. S., J. Kozarek, D. Hornbach, M. Hondzo, and J. Hong. 2019. Experimental investigation of turbulent flow over live mussels. *Environmental Fluid Mechanics* 19:1417–1430.
- Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. *Journal of the North American Benthological Society* 6:92–104.
- Li, J., V. Ianaiev, A. Huff, J. Zalusky, T. Ozersky, and S. Katsev. 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. *Proceedings of the National Academy of Sciences U.S.A.* 118:e2008223118.
- Liess, A., and A. L. Haglund. 2007. Periphyton responds differentially to nutrients recycled in dissolved or faecal pellet form by the snail grazer *Theodoxus fluviatilis*. *Freshwater Biology* 52:1997–2008.
- Limburg, K. E., V. A. Luzadis, M. Ramsey, K. L. Schulz, and C. M. Mayer. 2010. The good, the bad, and the algae: Perceiving ecosystem services and disservices generated by zebra and quagga mussels. *Journal of Great Lakes Research* 36:86–92.
- Liu, Y., H. Liang, S. Hilt, R. Wang, H. Zhang, and G. Gang. 2021. Shallow lakes at risk: Nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails. *Freshwater Biology* 66:436–446.
- Lopes-Lima, M., L. E. Burlakova, A. Y. Karatayev, K. Mehler, M. Seddon, and R. Sousa. 2018. Conservation of freshwater bivalves at the global scale: Diversity, threats and research needs. *Hydrobiologia* 810:1–14.
- Lopez, J. W., T. B. Parr, D. C. Allen, and C. C. Vaughn. 2020. Animal aggregations promote emergent aquatic plant production at the aquatic-terrestrial interface. *Ecology* 101:e03126.
- Lopez, J. W., and C. C. Vaughn. 2021. A review and evaluation of the effects of hydrodynamic variables on freshwater mussel communities. *Freshwater Biology* 66:1665–1679.
- Loreau, M., and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters* 16:106–115.
- Lukens, N. R., B. M. Kraemer, V. Constant, E. J. Hamann, E. Michel, A. M.

- Socci, Y. Vadeboncoeur, and P. B. McIntyre. 2017. Animals and their epibiota as net autotrophs: Size scaling of epibiotic metabolism on snail shells. *Freshwater Science* 36:307–315.
- Lv, S., Y. H. Guo, H. M. Nguyen, M. Sinuon, S. Sayasone, N. C. Lo, X.-N. Zhou, and J. R. Andrews. 2018. Invasive Pomacea snails as important intermediate hosts of *Angiostrongylus cantonensis* in Laos, Cambodia and Vietnam: Implications for outbreaks of eosinophilic meningitis. *Acta Tropica* 183:32–35.
- Mace, G. M., K. Norris, and A. H. Fitter. 2012. Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology and Evolution* 27:19–26.
- Maguire, Z., B. B. Tumolo, and L. K. Albertson. 2020. Retreat but no surrender: Net-spinning caddisfly (Hydropsychidae) silk has enduring effects on stream channel hydraulics. *Hydrobiologia* 847:1539–1551.
- Mason, R. J., S. P. Rice, M. F. Johnson, P. Wood, and D. Vettori. 2022. Aquatic insect bioconstructions modify fine-sediment entrainment and mobility. *Earth and Space Science* 127:e2021JF006399
- Mason, R. J., and H. Sanders. 2021. Invertebrate zoogeomorphology: A review and conceptual framework for rivers. *WIREs Water* 8:e1540.
- Matisoff, G., J. B. Fisher, and S. Matis. 1985. Effects of benthic macroinvertebrates on the exchange of solutes between sediments and freshwater. *Hydrobiologia* 122:19–33.
- Meadows, J., H. Lubke, I. Zagorska, V. Berzins, A. Cerina, and I. Ozola. 2014. Potential freshwater reservoir effects in a Neolithic shell midden at Rinnukalns, Latvia. *Radiocarbon* 56:823–832.
- Mersch, J., and L. Johansson. 1993. Transplanted aquatic mosses and freshwater mussels to investigate the trace metal contamination in the rivers Meurthe and Plaine, France. *Environmental Technology* 14:1027–1036.
- Michel, P., A. Dobson-Waitere, H. Hohaia, A. McEwan, and D. F. Shanahan. 2019. The reconnection between mana whenua and urban freshwaters to restore the mouri/life force of the Kaiwharawhara. *New Zealand Journal of Ecology* 43:1–10.
- Millennium Ecosystem Assessment (MEA). 2005. *Ecosystems and human well-being: Synthesis*. Island Press, Washington, DC.
- Modesto, V., P. Castro, M. Lopes-Lima, C. Antunes, M. Ilarri, and R. Sousa. 2019. Potential impacts of the invasive species *Corbicula fluminea* on the survival of glochidia. *Science of the Total Environment* 673:157–164.
- Naem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6:567–579.
- Nagachinta, A., M. Piamtipmanus, J. Jivaluk, W. Punyaganok, and J. Totanapoka. 2005. Utilization of freshwater mollusks of Thailand. Department of Fisheries, Ministry of Agriculture and Cooperatives, 155 p. (In Thai, not seen; cited by Allen et al. 2012).
- Newell, R., T. Fisher, R. Holyoke, and J. Cornwell. 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. Pages 93–120 in R. F. Dame, and S. Olenin, editors. *The Comparative Roles of Suspension-Feeders in Ecosystems*. NATO Science Series IV: Earth and Environmental Series, vol. 47. Springer, Dordrecht, the Netherlands.
- Newton, T. J., S. J. Zigler, J. T. Rogala, B. R. Gray, and M. Davis. 2011. Population assessment and potential functional roles of native mussels in the Upper Mississippi River. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:122–131.
- Ng, T. H., S. K. Tan, W. H. Wong, R. Meier, S.-Y. Chan, H. H. Tan, and D. C. J. Yeo. 2016. Mollusks for sale: Assessment of freshwater gastropods and bivalves in the ornamental pet trade. *PLoS One* 11:e0161130.
- Nickerson, Z. L., B. Mortazavi, and C. L. Atkinson. 2019. Using functional traits to assess the influence of burrowing bivalves on nitrogen-removal in streams. *Biogeochemistry* 146:125–143.
- Nicodemus, A. 2011. The Bronze Age and Dacian fauna from new excavations at Pecica Santul Mare. *Analele Banatului, Serie Noua* 19:79–84.
- Olden, J. D., L. Ray, M. C. Mims, and M. C. Horner-Devine. 2013. Filtration rates of the non-native Chinese mystery snail (*Bellamya chinensis*) and potential impacts on microbial communities. *Limnética* 32:107–120.
- Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, B. A. Woodcock, and J. M. Bullock. 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution* 30:673–684.
- Padilla, D. K., and S. L. Williams. 2004. Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2:131–138.
- Parmalee, P. W., and W. E. Klippel. 1974. Freshwater mussels as a prehistoric food resource. *American Antiquity* 39:421–434.
- Parr, T. B., C. C. Vaughn, and K. B. Gido. 2020. Animal effects on dissolved organic carbon bioavailability in an algal controlled ecosystem. *Freshwater Biology* 65:1298–1310.
- Patoka, J., O. Kopecký, V. Vrabec, and L. Kalous. 2017. Aquarium mollusks as a case study in risk assessment of incidental freshwater fauna. *Biological Invasions* 19:2039–2046.
- Peacock, E., J. Mitchell, and B. Kirkland. 2020. Investigating freshwater mussel (Unionidae) shell diagenesis at an archaeological site on the Tombigbee River, Mississippi, southeastern U.S.A. *Journal of Archaeological Science: Reports* 31:102350.
- Pinto, H. A., and A. L. De Melo. 2011. A checklist of trematodes (Platyhelminthes) transmitted by *Melanoides tuberculata* (Mollusca: Thiaridae). *Zootaxa* 2799:15–28.
- Preston, D. L., E. R. Crone, A. Miller-ter Kuile, C. D. Lewis, E. L. Sauer, and D. C. Trovillion. 2022. Non-native freshwater snails: A global synthesis of invasion status, mechanisms of introduction, and interactions with natural enemies. *Freshwater Biology* 67:227–239.
- Quaempts, E. J., K. L. Jones, S. J. O'Daniel, T. J. Beechie, and G. C. Poole. 2018. Aligning environmental management with ecosystem resilience: A First Foods example from the Confederated Tribes of the Umatilla Indian Reservation, Oregon, USA. *Ecology and Society* 23:29.
- Rafferty, J., and E. Peacock. 2008. The spread of shell tempering in the Mississippi Black Prairie. *Southeastern Archaeology* 27:253–264.
- Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, and S. J. Cooke. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94:849–873.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:220–222.
- Roditi, H. A., N. S. Fisher, and S. A. Sañudo-Wilhelmy. 2000. Uptake of dissolved organic carbon and trace elements by zebra mussels. *Nature* 407:78–80.
- Rosa, I. C., R. Costa, F. Gonçalves, and J. L. Pereira. 2014. Bioremediation of metal-rich effluents: Could the invasive bivalve *Corbicula fluminea* work as a biofilter? *Journal of Environmental Quality* 43:1536–1545.
- Rose, J. M., J. S. Gosnell, S. Bricker, M. J. Brush, A. Colden, L. Harris, E. Karplus, A. Laferriere, N. H. Merrill, T. B. Murphy, J. Reitsma, J. Shockley, K. Stephenson, S. Theuerkauf, D. Ward, and R. W. Fulweiler. 2021. Opportunities and challenges for including oyster-mediated denitrification in nitrogen management plans. *Estuaries and Coasts* 44:2041–2055.
- Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: Effects of nutrients and herbivores. *Ecology* 74:1264–1280.
- Sansom, B. J., J. F. Atkinson, and S. J. Bennett. 2018a. Modulation of near-bed hydrodynamics by freshwater mussels in an experimental channel. *Hydrobiologia* 810:449–463.
- Sansom, B. J., S. J. Bennett, J. F. Atkinson, and C. C. Vaughn. 2018b. Long-term persistence of freshwater mussel beds in labile river channels. *Freshwater Biology* 63:1469–1481.

- Sansom, B. J., S. J. Bennett, J. F. Atkinson, and C. C. Vaughn. 2020. Emergent hydrodynamics and skimming flow over mussel covered beds in rivers. *Water Resources Research* 56:1–17.
- Seddon, M., C. Appleton, D. Van Damme, and D. Graf. 2011. Freshwater molluscs of Africa: Diversity, distribution, and conservation. Pages 92–125 in W. Darwall, D. Smith, D. Allen, R. Holland, I. Harrison, and E. Brooks, editors. *The Diversity of Life in African Freshwaters: Underwater, under Threat. An Analysis of the Status and Distribution of Freshwater Species throughout Mainland Africa*. IUCN, Cambridge, United Kingdom, and Gland, Switzerland.
- Simeone, D., C. H. Tagliaro, and C. R. Beasley. 2021. Filter and deposit: A potential role of freshwater mussels in ecosystem functioning associated with enhanced macroinvertebrate assemblage structure in a Neotropical river. *Hydrobiologia* 848:4211–4223.
- Spooner, D. E., and C. C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* 51:1016–1024.
- Strayer, D. L. 2014. Understanding how nutrient cycles and freshwater mussels (Unionoida) affect one another. *Hydrobiologia* 735:277–292.
- Strayer, D. L. 2017. What are freshwater mussels worth? *Freshwater Mollusk Biology and Conservation* 20:103–113.
- Strayer, D. L. 2020. Non-native species have multiple abundance–impact curves. *Ecology and Evolution* 10:6833–6843.
- Strayer, D. L., J. Geist, W. R. Haag, J. K. Jackson, and J. D. Newbold. 2019. Essay: Making the most of recent advances in freshwater mussel propagation and restoration. *Conservation Science and Practice* 1:10.1111/csp2.53
- Strayer, D. L., and H. M. Malcom. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. *Freshwater Biology* 52:1611–1617.
- Strong, E. E., O. Gargominy, W. F. Ponder, and P. Bouchet. 2008. Global diversity of gastropods (Gastropoda; Molluska) in freshwater. Pages 149–166 in E. V. Balian, C. Lévêque, H. Segers, and K. Martens, editors. *Freshwater Animal Diversity Assessment*. Springer, Dordrecht, the Netherlands.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Trentman, M. T., C. L. Atkinson, and J. D. Brant. 2018. Native freshwater mussel effects on nitrogen cycling: Impacts of nutrient limitation and biomass dependency. *Freshwater Science* 37:276–286.
- Turner, R. K., and M. Schaafsma, editors. 2015. *Coastal Zones Ecosystem Services: From Science to Values and Decision Making*. Springer International Publishing, Heidelberg.
- Tyrrill, M., and D. J. Hornbach. 1998. Selective predation by muskrats on freshwater mussels in 2 Minnesota rivers. *Journal of the North American Benthological Society* 17:301–310.
- Valente, R., M. R. Robles, and J. I. Diaz. 2020. Gastropods as intermediate hosts of *Angiostrongylus* spp. in the Americas: Bioecological characteristics and geographical distribution. *Memorias do Instituto Oswaldo Cruz* 115:e200236.
- Vaughn, C. C. 2018. Ecosystem services provided by freshwater mussels. *Hydrobiologia* 810:15–27.
- Vaughn, C. C., C. L. Atkinson, and J. P. Julian. 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. *Ecology and Evolution* 5:1291–1305.
- Vaughn, C. C., K. B. Gido, and D. E. Spooner. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: Species roles and effects of abundance. *Hydrobiologia* 527:35–47.
- Vaughn, C. C., and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46:1431–1446.
- Vaughn, C. C., and T. J. Hoellein. 2018. Bivalve impacts in freshwater and marine ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 49:183–208.
- Vaughn, C. C., S. J. Nichols, and D. E. Spooner. 2008. Community and foodweb ecology of freshwater mussels. *Journal of the North American Benthological Society* 27:409–423.
- Vaughn, C. C., and D. E. Spooner, D. E. 2006. Unionid mussels influence macroinvertebrate assemblage structure in streams. *Journal of the North American Benthological Society* 25:691–700.
- Vaughn, C. C., D. E. Spooner, and B. W. Hoagland. 2002. River weed growing epizoically on freshwater mussels. *Southwestern Naturalist* 47:604–605.
- Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences U.S.A.* 113:4081–4085.
- Wang, N., C. G. Ingersoll, D. K. Hardesty, C. D. Ivey, J. L. Kunz, T. W. May, F. J. Dwyer, A. D. Roberts, T. Augspurger, C. M. Kane, R. J. Neves, and M. C. Barnhart. 2007. Acute toxicity of copper, ammonia, and chlorine to glochidia and juveniles of freshwater mussels (Unionidae). *Environmental Toxicology and Chemistry* 26:2036–2047.
- Williams J. D., A. E. Bogan, and J. T. Garner 2008. *Freshwater Mussels of Alabama and the Mobile Basin in Georgia, Mississippi, and Tennessee*. University of Alabama Press, Tuscaloosa.
- Wisniewski, J. M., K. D. Bockrath, J. P. Wares, A. K. Fritts, and M. J. Hill. 2013. The mussel–fish relationship: A potential new twist in North America? *Transactions of the American Fisheries Society* 142:642–648.
- Wood, J., P. Bukaveckas, H. Galbraith, M. Gattis, M. Gray, T. Ihde, D. Kreeger, R. Mair, S. McLaughlin, S. Hahn, and A. Harvey. 2021. Incorporating freshwater mussels into the Chesapeake Bay restoration efforts. STAC Publication Number 21-004, Edgewater, Maryland. Available at https://www.chesapeake.org/stac/wp-content/uploads/2021/07/FINAL-Report_Freshwater-Mussels_21-004.pdf (accessed October 28, 2022).
- Wu, H., G. Constantinescu, and J. Zeng. 2020. Flow and entrainment mechanisms around a freshwater mussel aligned with the incoming flow. *Water Resources Research* 56:e2020WR027983.
- Wurtsbaugh, W. A., H. W. Paerl, and W. K. Dodds. 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *WIREs Water* 6:e1373.
- Yang, Q.-Q., S.-W. Liu, C. He, and X.-P. Yu. 2018. Distribution and the origin of invasive apple snails, *Pomacea canaliculata* and *P. maculata* (Gastropoda: Ampullariidae) in China. *Scientific Reports* 8:1185.
- Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, causes, and consequences of anthropocene defauna. *Annual Review of Ecology, Evolution, and Systematics* 47:333–358.
- Zhang, J., Z. Wang, Z. Song, Z. Xie, L. Li, and L. Song. 2012. Bioaccumulation of microcystins in two freshwater gastropods from a cyanobacteria-bloom plateau lake, Lake Dianchi. *Environmental Pollution* 164:227–234.
- Zieritz, A., A. E. Bogan, E. Froufe, O. Klishko, T. Kondo, U. Kovitvadhii, S. Kovitvadhii, J. H. Lee, M. Lopes-Lima, and J. M. Pfeiffer. 2018. Diversity, biogeography and conservation of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. *Hydrobiologia* 810:29–44.
- Zieritz, A., R. Sousa, D. C. Aldridge, K. Doua, E. Esteves, N. Ferreira-Rodríguez, J. H. Mageroy, D. Nizzoli, M. Osterling, and J. Reis. 2022. A global synthesis of ecosystem services provided and disrupted by freshwater bivalve molluscs. *Biological Reviews* 97: 1967–1998.

REGULAR ARTICLE

ASSESSING POTENTIAL HABITAT FOR FRESHWATER MUSSELS BY TRANSFERRING A HABITAT SUITABILITY MODEL WITHIN THE OZARK ECOREGION, MISSOURI

Jordan H. Hartman^{*†1}, Amanda E. Rosenberger², Kayla N. Key^{‡1}, and Garth Lindner^{§3}

¹ Tennessee Cooperative Fisheries Research Unit, Department of Biology, Tennessee Technological University, Cookeville, TN 38501 USA

² U.S. Geological Survey, Tennessee Cooperative Fisheries Research Unit, Department of Biology, Cookeville, TN 38501 USA

³ University of Missouri, Missouri Cooperative Fisheries Research Unit, School of Natural Resources, Columbia, MO 65211 USA

ABSTRACT

Habitat suitability models for freshwater mussels can inform conservation of these imperiled animals. Riverscape-scale hydrogeomorphic variables were previously used to predict suitable mussel habitat in the Meramec River basin, Missouri. We evaluated transferability of the Meramec River habitat suitability model to the Gasconade and Little Black rivers, in the Ozark Highlands ecoregion, Missouri. The best-fit models relied on transferring and adapting the original modeling framework to better represent the unique habitat characteristics of each river. Mussel bed occurrence in both rivers was associated with reaches that were classified as pools. Mussel beds in the Gasconade River were also associated with laterally stable reaches adjacent to small bluffs, distant from gravel bars, and with higher stream power indices. Mussel beds in the Little Black River were associated with reaches with higher surface water availability during low-flow conditions, lower stream power indices, and bluffs located downstream. Our results show that existing habitat models can be transferred to other streams with similar environmental conditions, but differences in watershed characteristics can affect transferability.

KEY WORDS: freshwater mussels, habitat suitability modeling, hydrogeomorphology, MaxEnt, riverscape scale, transferability

INTRODUCTION

Understanding habitat and environmental associations of freshwater mussels is essential for the conservation of these highly imperiled animals (FMCS 2016). The occurrence of

large, multispecies mussel aggregations, or mussel beds, suggests that common habitat preferences influence or limit mussel establishment and persistence across multiple species (Vaughn 1997). Reach-scale factors such as microhabitat characteristics and host-fish distributions typically have little explanatory power for predicting mussel distribution and abundance (Strayer and Ralley 1993; Johnson and Brown 2000; Vaughn 2012; Pandolfo et al. 2016; Randklev et al. 2019). Mussel occurrence can be predicted at watershed scales based on geology, soils, land use, and topography (Strayer 1993; Arbuckle and Downing 2002; Daniel and Brown 2014; Walters et al. 2017), but these factors are not tractable for

*Corresponding Author: Jnhnd@illinois.edu

†Current Address: University of Illinois, Department of Natural Resources and Environmental Science, Urbana-Champaign, Illinois 61829 USA

‡Current Address: West Tennessee River Basin Authority, Tennessee Department of Environment and Conservation, Humboldt, Tennessee 38343 USA

§Current Address: Indiana Department of Natural Resources, Indianapolis, Indiana 46204 USA

management actions (Fausch et al. 2002). More recently, hydrogeomorphic variables corresponding to in-channel stability (e.g., shear stress, hydraulic stability, and presence of refugia during high- and low-flow events) show promise for predicting mussel occurrence at the reach scale (Allen and Vaughn 2010; Drew et al. 2018). However, understanding mussel habitat associations at the riverscape scale may be most useful for prioritizing management efforts (Bouska et al. 2018).

The riverscape scale represents the continuous, longitudinal river gradient as intermediate between reach-scale microhabitat characteristics and watershed-scale factors. Therefore, the riverscape scale is small enough to be influenced by management actions but large enough to encompass the continuous, hierarchical, and heterogeneous river system in its entirety (Schlosser and Angermeier 1995; Fausch et al. 2002; Bouska et al. 2018). However, at a riverscape scale, it is time-consuming and expensive to generate hydrogeomorphic data needed to predict mussel occurrence while providing inferences relevant to management (Bouska et al. 2018).

Key et al. (2021) developed a habitat suitability model using open-source, remotely sensed data to predict mussel bed occurrence at the riverscape scale in the Meramec River basin, Missouri. The Meramec River habitat suitability model (MRHSM) assessed the association of mussel beds with hydrogeomorphic variables reflecting water availability, channel stability, and the presence of stable gravel substrate. Habitat suitability models, such as the MRHSM, may be transferred to other areas with similar environmental conditions by obtaining remotely sensed data for those areas (Randin et al. 2006; Barbosa et al. 2009; Werkowska et al. 2016).

We investigated the transferability of the MRHSM (Key et al. 2021) to the Gasconade and Little Black rivers, two other Ozark rivers in Missouri. Transferring the MRHSM could inform mussel conservation throughout the Ozark region and provide more information about mussel habitat associations in general. Our objectives were to derive a dataset of spatial layers for our study streams that represent hydrogeomorphic variables used in the MRHSM and determine the best method for transferring the MRHSM to the Gasconade and Little Black rivers. We discuss how well the MRHSM can be transferred to the Gasconade and Little Black rivers and how the hydrogeomorphology of those watersheds affects transferability.

METHODS

Study Areas

The Meramec, Gasconade, and Little Black river basins are within the Ozark Highlands ecoregion of Missouri (Fig. 1) and share similar physiographic and watershed features. In the interior of the region, dolomite and sandstone comprise the dominant bedrock, while the western outer regions are

dominated by Mississippian limestone (Ozark Ecoregional Assessment Team 2003). All three watersheds have steep bluffs along streams, narrow valleys, and karst features, and many of their streams are spring-fed. Seasonal patterns of discharge are similar among all three streams (Fig. 2), but discharge in the Little Black River is much lower than the Gasconade and Meramec rivers because of its smaller watershed (990 km² and 7,268 km² for the Little Black and Gasconade rivers, respectively). We describe additional features of the Gasconade and Little Black rivers below; a description of the Meramec River basin can be found in Key et al. (2021).

Gasconade River.—The mainstem Gasconade River flows north for 436 river-km (rkm) before joining the Missouri River (Blanc 2001). Our habitat suitability models included about 800 rkm including the mainstem Gasconade River and three of its tributaries, Osage Fork, Big Piney River, and Roubidoux Creek (Fig. 1). These streams are not channelized or impounded, but in-channel gravel mining has altered and destabilized some segments (Blanc 2001), and decreased riparian vegetation has also contributed to channel instability and erosion (Jacobson and Primm 1997). Forty-six mussel species are reported from the Gasconade River basin (Blanc 2001).

Little Black River.—The mainstem Little Black River flows south 137 rkm into Arkansas before joining the Current River. Most of the Little Black River and its tributaries are within the Ozark Highlands, but the downstream portion of the mainstem flows through the Mississippi Alluvial Plains (Fig. 1; Wilkerson 2003). Because of the physiographic differences between the Ozark Highlands and Mississippi Alluvial Plains, we did not include that portion of the stream in our habitat suitability models. Our habitat suitability models included 120 rkm comprising the mainstem Little Black River and three of its tributaries, North and South prongs and Beaverdam Creek (Fig. 1). The Little Black River is highly altered with 13 impoundments and about 98 rkm of channelized streams (Wilkerson 2003). Thirty-nine mussel species are reported from the Little Black River basin (Wilkerson 2003).

Mussel Survey Dataset

We determined mussel bed locations in the Gasconade and Little Black rivers from the Missouri Department of Conservation mussel database (data available upon request to and subject to the approval of the Missouri Department of Conservation, 3500 East Gans Road, Columbia, MO 65201). This database includes mussel survey information for specific locations across Missouri, including GPS points, survey methods, lists of species found, and numbers of individuals found. We used mussel survey data from 1994 to 2013, following the MRHSM (Key et al. 2021). We filtered the data to include only timed-search samples; incidental collections, collections using a groping technique, or entries with missing sampling method were excluded. We considered sites within 180 m of each other to represent the same mussel bed

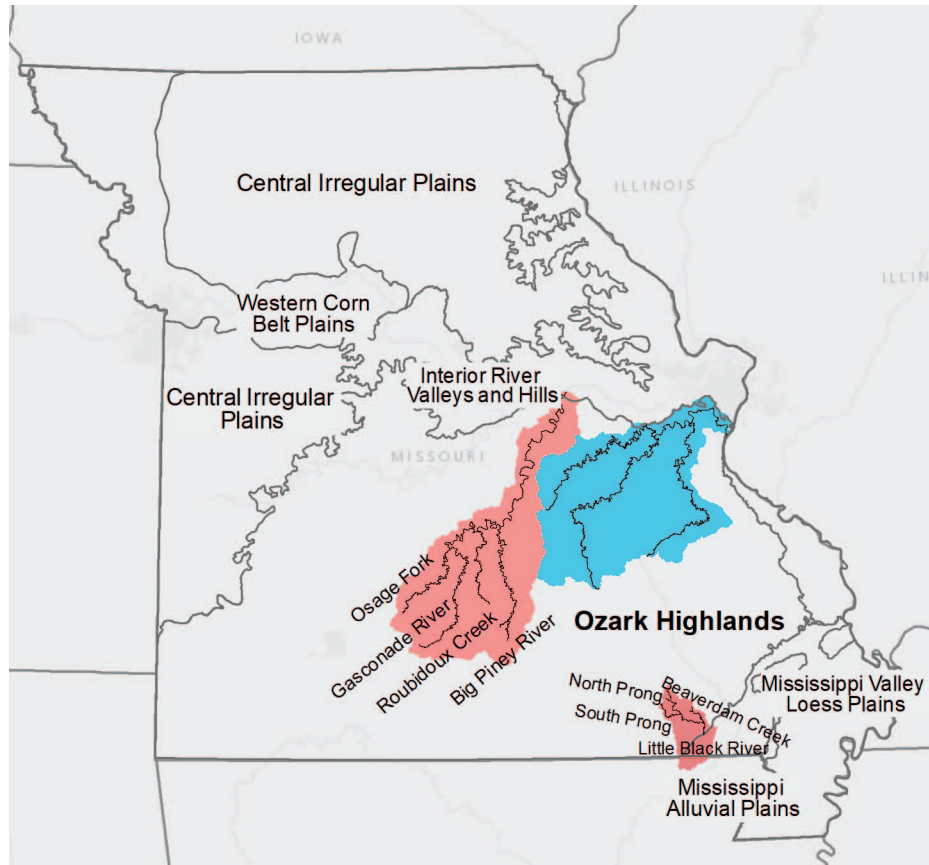


Figure 1. Map of Missouri, USA, showing the Gasconade (pink), Little Black (dark pink), and Meramec (blue) river watersheds and major streams included in habitat suitability models. Other text and boundaries within the state boundary are Level IV ecoregions.

(Lueckenhoff 2015; Schrum 2017; Key et al. 2021). Our resulting dataset included 130 unique mussel bed locations. We selected a subset of 85 mussel beds that had the highest species richness (hereafter species-rich mussel beds; Key et al. 2021) to develop our habitat suitability models. The remaining 45 mussel beds (hereafter validation mussel beds) were used to validate our models by determining how many of these beds fell within habitat deemed suitable by our model.

Generation of Hydrogeomorphic Variables

We derived 12 hydrogeomorphic variables for the Gasconade and Little Black rivers, including all 10 variables used in the MRHSM and two additional variables that we created (see below; Table 1). These variables represent habitat characteristics thought to correspond to suitable habitat for mussels at a riverscape scale, including bluff adjacency, presence of and proximity to gravel bars, lateral channel stability, low-flow surface water availability, and stream power index (Table 1; Key et al. 2021). Mussel beds in Ozark rivers are often found in the vicinity of bluffs, possibly because bluffs exert channel control and stabilization that is amenable to mussel establishment and persistence (Vannote and Minshall 1982; Key et al. 2021). Mussel beds often are

associated with gravel bars, and the presence of persistent gravel bars after high-flow events can indicate channel stability (Bates 1962; Peck 2005; Zigler et al. 2008; Key et al. 2021). Lateral channel movement is indicative of bank erosion and sediment deposition, which can destabilize substrate and limit mussel occurrence (Strayer 1999; Strayer et al. 2004). Low-flow surface water availability is intended to represent a proxy for the existence of permanently watered areas that serve as refugia during drought periods (Table 1; Golladay et al. 2004; Key et al. 2021). Stream power is an index of potential energy in the channel and influences channel erosion and stability.

We derived estimates for the hydrogeomorphic variables from high-resolution, open-source datasets of aerial imagery and topography following Key et al. (2021) and summarized as follows. We began our workflow by defining the stream dimensions and location of the river channel and subsequently creating a stream centerline. We then generated points on the stream centerline at 10-m cross sections to create a spatially continuous dataset. After we defined our stream dimensions and stream centerline, we derived our 12 hydrogeomorphic variables and assigned the data to each point on the stream centerline. The 10-m points were then interpolated using natural neighbors into continuous grids representing our final

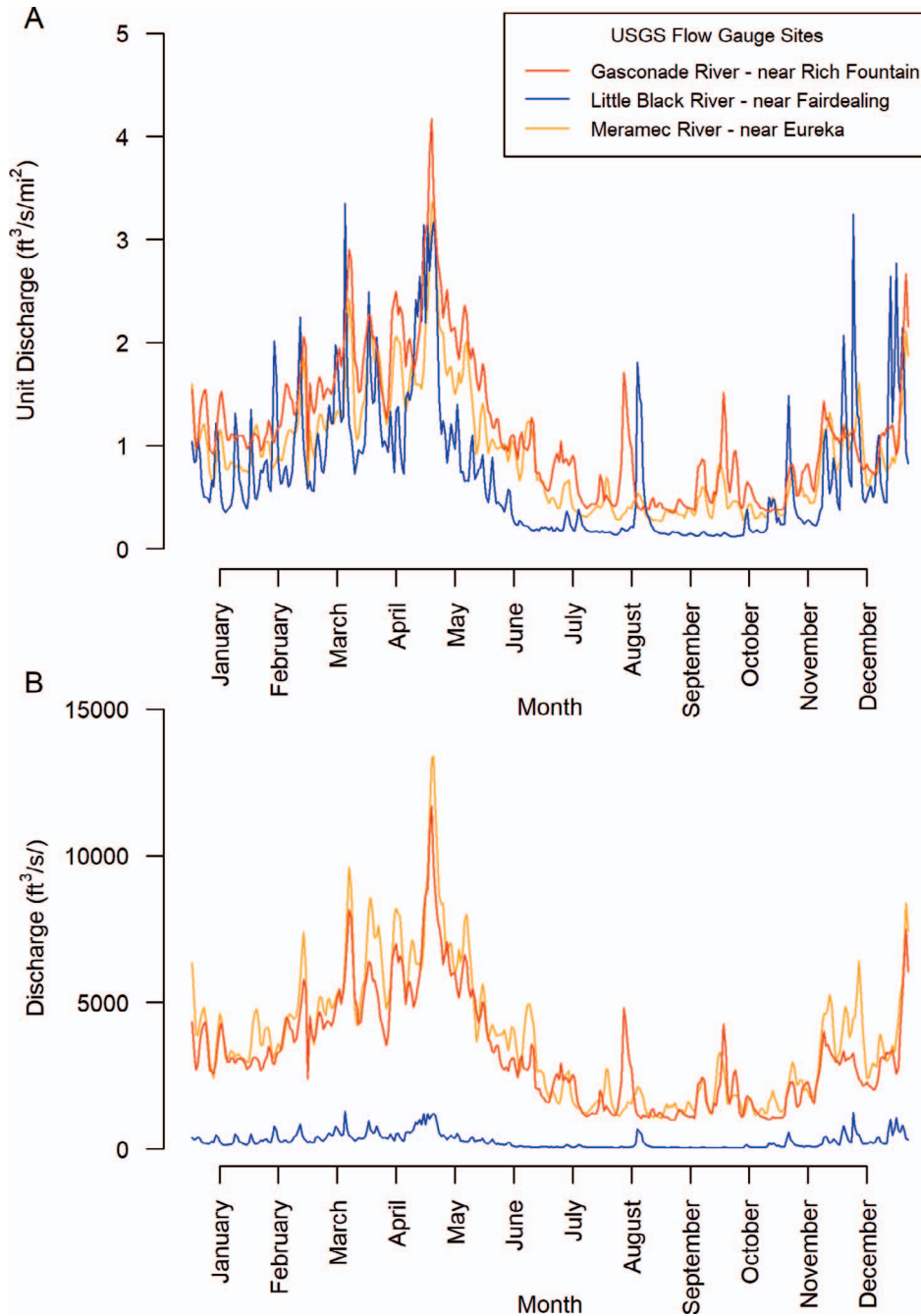


Figure 2. (A) Mean monthly unit discharge (ft³/s/mi²) and (B) mean monthly discharge (ft³/s) for the Meramec, Gasconade, and Little Black rivers. Flow data are from <https://waterdata.usgs.gov/mo/nwis/rt> (accessed January 23, 2023).

hydrogeomorphic variables. All spatial analyses were performed in ArcGIS and projected to NAD 1983 UTM zone 15N (ESRI 2011; Key et al. 2021).

We used a combination of 1-m light detection and ranging (LiDAR) and 10-m digital elevation model (DEM) coverage of both study areas (MSDIS 2011) to generate six hydrogeomorphic variables related to bluff adjacency and stream power. Two bluff adjacency variables represented whether a bluff is present within one channel width of each bank from a mussel bed (binary variable) and, if so, the total bluff area

(continuous variable). In addition to the bluff adjacency variables from the MRHSM, we generated two new variables representing the total bluff area within 500 m upstream or downstream of a mussel bed. We added these variables to explore whether bluffs located upstream or downstream, versus directly adjacent to the stream channel, are associated with mussel bed occurrence. Because of the limited availability of LiDAR for the Gasconade River, we used 10-m DEMs to extend the remotely sensed data across the entire drainage area. The 1-m horizontal resolution LiDAR tiles and 10-m

Table 1. Justification and description of hydrogeomorphic variables evaluated in habitat suitability models for the Meramec, Gasconade, and Little Black rivers. Variables that were included in the final, best-fit models differed among streams and transferability levels (see text). “Type” refers to whether the variable was continuous or binary.

Habitat Characteristic: Type	Justification	Description
Bluff adjacency area: continuous	Mussel beds are usually found in the vicinity of bluffs adjacent to the stream channel.	Total bluff area (m ²) within one channel width of each bank
Bluff adjacency: binary		Whether there is a bluff within one channel width of each bank
Longitudinal bluff adjacency area upstream: continuous	Stream power influences oxygen, food supply, successful host infestation, and offspring dispersal.	Total bluff area (m ²) within 500 m upstream
Longitudinal bluff adjacency area downstream: continuous		Total bluff area (m ²) within 500 m downstream
Stream power index: continuous		Index of potential energy of water in the channel, using $SPI = \ln(A_d) * S_{500}$
Stream power class: binary		Potential energy of water in the stream channel, classed as either high or low using the mean
Lateral channel stability: binary	Lateral channel movement can disrupt habitat condition.	Lateral channel movement of > 10 m between 1990–95 and 2015, classed as unstable, all else classed as stable
Gravel/pool class: binary	Reaches with persistent gravel bars can indicate in-stream stability after high-flow events. In smaller streams, however, they can also indicate reaches that dry during low-flow events.	Reaches dominated by gravel are classed at gravel, all else classed as pool reaches
Gravel bar proximity: binary		All locations within 100 m of a gravel bar are classed as adjacent to a gravel bar
Distance to gravel bar: continuous	Refuge during drought periods is necessary for mussel survival.	Euclidean distance (m) to nearest gravel bar
Low-flow surface water availability index: continuous		The number of water pixels surrounding each cell
Low-flow surface water availability class: binary		The number of water pixels surrounding each cell, classed as high or low using the mean

DEMs were mosaicked into a single DEM and resampled to 10-m resolution for analysis (Key et al. 2021). We then used a slope and range criteria to define bluffs in the watersheds and performed a zonal search at each point on the stream centerline.

For the stream power variables, we estimated the watershed area at each stream centerline point and estimated the stream power index (SPI) using the bankfull elevation (see Key et al. 2021 for methods to determine bankfull elevation) as $SPI = S \times \ln(A_d)$, where, for any location along the stream centerline, SPI is the stream power index, S is the channel slope, and A_d is the watershed area (Moore et al. 1991). Slope was averaged over a 500-m interval, 250 m upstream and 250 m downstream from each point on the stream centerline, and then smoothed using a 50-m moving average. The binary stream power variable was derived by classifying each pixel as either high or low stream power using the mean value as the break between the two classes.

We used National Agriculture Imagery Program leaf-off aerial imagery to generate the six remaining hydrogeomorphic variables related to gravel bars, lateral channel stability, and low-flow surface water availability. We derived three variables reflecting the presence of or proximity to gravel bars for each

mussel bed (Table 1). We classified mussel bed locations as “gravel” if the stream reach was dominated by persistent gravel before and after a high-flow year, and as “pool” if the reach was dominated by water (binary variable). We then determined whether each mussel bed was located within 100 m of a gravel bar (binary variable), and we created a continuous variable representing the Euclidean distance from a mussel bed to the nearest gravel bar. We derived these variables with a differencing technique between two sets of aerial imagery. In the Little Black River, 2007 and 2015 were low-water years, while 2013 was a high-water year. In the Gasconade River, 2012 and 2014 were low-water years, and 2013 was a high-water year. Pixels that changed state (water or gravel) between the two images were classified as a pool, and pixels that did not change state were classified as either gravel or a pool. The gravel/pool class therefore does not represent the underlying sediment (gravel versus depositional sediments) but rather areas that had persistently exposed gravel bar versus areas that were predominantly water during low-flow conditions. Without ground-truthing, we cannot differentiate whether the areas classified as pools had gravel or depositional sediments.

For the lateral channel stability variable, we created two polygons representing the stream banks based on visual cues

such as shadow, vegetation, and scour lines in the leaf-off imagery from 1990–95 and 2015. We defined each point on the stream centerline as unstable if the channel moved > 10 m between the two time periods or stable if the channel moved ≤ 10 m (binary variable; Key et al. 2021).

We derived two variables for low-flow surface water availability index using imagery taken at the time of lowest discharge available (2007 for the Little Black River and 2012 for the Gasconade River). We performed a focal search to estimate the number of pixels classified as water that were adjacent to the focal pixel (continuous variable). We then used the median value to categorize high- and low-surface water availability in a low-flow period to create the binary variable. We acknowledge that these variables do not directly represent vulnerability to drying because water depth is not accounted for (see Key et al. 2021). However, we used these variables as proxies for drought refugia because bathymetric data were not available from our imagery.

Habitat Suitability Models

We used maximum entropy modeling (MaxEnt; Phillips and Dudík 2008) to generate habitat suitability models for mussels in the Meramec, Gasconade, and Little Black rivers. This method uses presence-only occurrence data in combination with environmental data layers to produce a model of habitat suitability spanning a specified geographic area (Phillips and Dudík 2008). For models that included the Meramec River, we used the presence-only occurrence data and environmental layers created by Key et al. (2021). We spatially constricted our habitat suitability models to each drainage and used the location of species-rich mussel beds in each river system in combination with the hydrogeomorphic variables determined for those locations. We used the same settings in MaxEnt as used for the MRHSM (Key et al. 2021). Specifically, we set the run type to bootstrap to generate training and test occurrence data (80% and 20% of the species-rich mussel bed locations, respectively), and we ran models with 10,000 background points and 5,000 iterations. None of the hydrogeomorphic variables included in each model were correlated with each other (correlation coefficient < 0.40).

We converted the raw model results to a binary map of suitable and unsuitable reaches based on the equal test sensitivity and specificity logistic threshold of each model (Key et al. 2021). The equal test sensitivity and specificity logistic threshold is a commonly used threshold that sets the sensitivity equal to the specificity (Cao et al. 2013; Phillips 2017; Key et al. 2021). After suitable and unsuitable reaches were delineated, we used a buffer of 40 m to separate the suitable and unsuitable habitats to account for areas of transition (following Key et al. 2021). We then used jackknife analysis and the test gain values to assess the relative contribution of each hydrogeomorphic variable and to determine which variables were most important for model fit (Phillips 2017; Key et al. 2021). We used a stepwise model selection approach of our hydrogeomorphic variables to select

the best-fit model. The area under the receiver operating curve (AUC) values from MaxEnt provided relative values for comparing the performance of models that were built with the same data (Phillips et al. 2006). Therefore, we selected variables that led to higher AUC values and contained hydrogeomorphic variables with sizeable individual effects on model results when others were removed (following Elith 2002 and Key et al. 2021). We also created response curves to investigate the relationships between suitable and unsuitable habitats (y-axis) and our hydrogeomorphic variables (x-axis). The results for our continuous hydrogeomorphic variables were presented as curves spanning the range of values for that layer, whereas the binary hydrogeomorphic variables were presented as two bars representing the binary. The range in values of the continuous—or bars of the binary—hydrogeomorphic variables were classified as suitable if they were equal to or above the equal test sensitivity and specificity logistic threshold on the response curves. For low-flow surface water availability and stream power, higher values in the response curves represented more contiguous surface water availability during low-flow conditions and higher stream power, respectively. Although AUC values provided comparisons of model performance, they did not provide a measure of the accuracy of habitat suitability (Jiménez-Valverde and Lobo 2006). Therefore, we used the location of the validation mussel beds (not used in model development) to assess the accuracy of our best-fit models. We calculated the percentage of the validation mussel beds that fell within a reach predicted to be suitable by the best-fit models across the entire spatial extent. For models that included the Meramec and Gasconade rivers or the Meramec and Little Black rivers, we also calculated validation per drainage as the proportion of validation mussel bed locations that fell within a reach predicted to be suitable for each drainage, separately.

Transferability

We separated our methods of transferability into three categories representing different levels of dependence on the original MRHSM: Level 1, transferring the original model; Level 2, transferring the modeling framework; and Level 3, adapting the modeling framework (Fig. 3).

Level 1: Transferring the original model.—To transfer the original model from the Meramec River to the Gasconade and Little Black rivers, we utilized the species-rich mussel bed locations and hydrogeomorphic variables used in the MRHSM (Key et al. 2021) and species-rich mussel bed locations and hydrogeomorphic variables that we derived for the Gasconade and Little Black rivers. Specifically, we combined the species-rich mussel bed locations and hydrogeomorphic variables to include the spatial extent of both the Meramec and Gasconade rivers or the Meramec and Little Black rivers. We started this level of transferability with all 10 hydrogeomorphic variables from the MRHSM (Fig. 3). We then used the jackknife analysis and stepwise model selection approach as described previously to find the best-fit model. The results from the best-

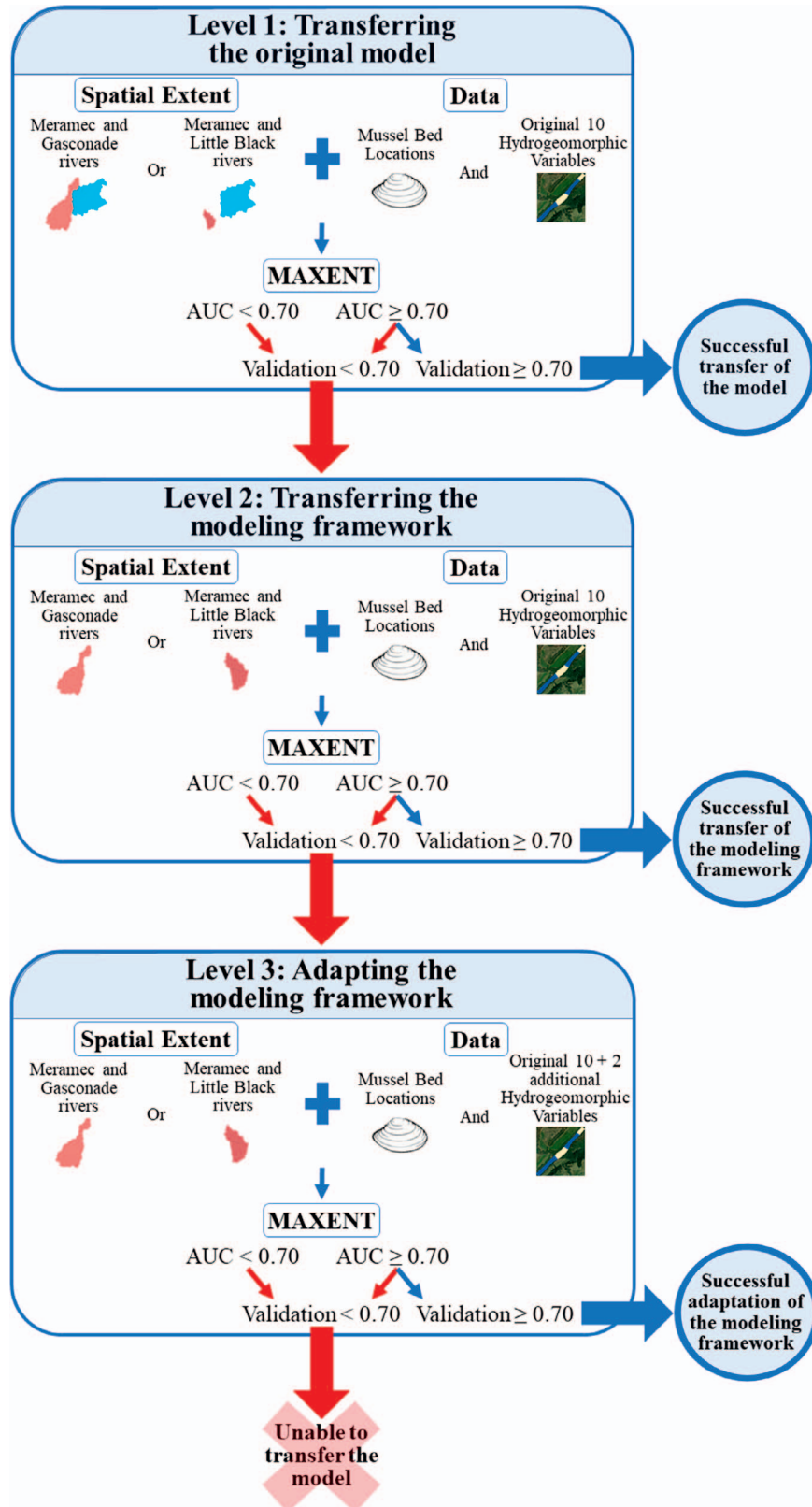


Figure 3. General framework used to test the transferability of the Meramec River habitat suitability model to the Gasconade and Little Black rivers, including three levels of transferability and the spatial extent, required data, and evaluation criteria for each level.

Table 2. Results for the Meramec River habitat suitability model (Key et al. 2021) and evaluation of transferability of that model to the Gasconade and Little Black rivers. All models are best-fit models for each river and level of transferability. We considered model transfer successful if the best-fit model had a test AUC ≥ 0.70 and total validation ≥ 0.70 . Equal test sensitivity and specificity logistic threshold is the value used to delineate suitable and unsuitable habitats for all variables in each model. Total validation is the proportion of validation mussel bed locations that were identified by the model as suitable habitat across all rivers in the model. Validation/drainage is the proportion of validation mussel-bed locations identified as suitable habitat within each river.

River(s)	Level of Transferability	Test AUC	Equal Test Sensitivity and Specificity Logistic Threshold	Total Validation	Validation/ Drainage
Meramec River	Original model	0.62	0.45	0.90	—
Meramec and Gasconade rivers	Level 1	0.69	0.41	0.68	Meramec: 1.00 Gasconade: 0.24
Gasconade River	Level 2	0.70	0.34	0.82	—
Meramec and Little Black rivers	Level 1	0.64	0.42	0.64	Meramec: 0.65 Little Black: 0.60
Little Black River	Level 2	0.74	0.48	0.60	—
Little Black River	Level 3	0.72	0.44	0.80	—

fit model were converted to a binary map and validated using the validation mussel bed locations. We considered model transfer to be successful if the best-fit model had a test AUC ≥ 0.70 and total validation ≥ 0.70 (Fig. 3). If either the test AUC or model validation was < 0.70 , we progressed to Level 2 (Fig. 3).

Level 2: Transferring the modeling framework.—To reduce our dependence on the MRHSM, we transferred only the modeling framework by building our MaxEnt models without data from the Meramec River. Specifically, we used only species-rich mussel bed locations and 10 hydrogeomorphic variables in either the Gasconade River or Little Black River (Fig. 3). Following the same methodology as Level 1, we determined the best-fit model and validated those results with the validation mussel bed locations. Again, if the best-fit model had a test AUC ≥ 0.70 and total validation ≥ 0.70 , it was considered a successful transfer of the modeling framework. If either the test AUC or model validation was < 0.70 , we progressed to Level 3 (Fig. 3).

Level 3: Adapting the model.—If neither of the previous transferability methods produced an adequate model, we adapted the modeling framework used in the MRHSM by including two additional hydrogeomorphic variables, longitudinal bluff adjacency upstream and downstream. Similar to Level 2, models were built only with the species-rich mussel bed locations and hydrogeomorphic variables from the Gasconade or Little Black rivers. We started this level with the 10 original hydrogeomorphic variables plus the two additional bluff adjacency variables that we created. We followed the same stepwise model selection approach as Levels 1 and 2 to find the best-fit model and then created the binary suitability map and validated the results with the locations of the validation mussel beds. If the best-fit model had a test AUC ≥ 0.70 and total validation ≥ 0.70 , we considered this a successful adaptation to the modeling framework (Fig. 3). If either the test AUC or total validation was < 0.70 , we considered model transfer unsuccessful (Fig. 3).

RESULTS

Gasconade River

Level 1: Transferring the original model.—The best-fit habitat suitability model for Level 1 had a test AUC of 0.69 (Table 2). The best-fit model included six hydrogeomorphic variables: lateral channel stability, distance to gravel bar, gravel/pool class, stream power index, bluff adjacency area, and low-flow surface water availability index. Jackknife analysis indicated that bluff adjacency area, distance to gravel bar, gravel/pool class, and lateral channel stability contributed significantly to the final model (Table 3).

An equal test sensitivity and specificity logistic threshold of 0.41 separated habitats into suitable and unsuitable. Response curves indicated that suitable habitat was represented by reaches with small bluffs, 0–700 m or $> 1,500$ m from gravel bars, areas with a low-flow surface water availability index > 0 but < 10 , and intermediate stream power. While 68% of our validation mussel bed locations were found in areas identified as suitable in both the Meramec and Gasconade rivers, only 24% of the validation mussel beds were found in areas identified as suitable in the Gasconade River alone. Because the test AUC and total validation were < 0.70 , we considered model transfer to the Gasconade River unsuccessful at this level and continued to Level 2 (Table 2).

Level 2: Transferring the modeling framework.—The best-fit habitat suitability model for Level 2 had a test AUC of 0.82 (Table 2). The best-fit model included six hydrogeomorphic variables: lateral channel stability, distance to gravel bar, gravel/pool class, stream power index, bluff adjacency area, and low-flow surface water availability index. Jackknife analysis indicated that bluff adjacency area, distance to gravel bars, gravel/pool class, and low-flow surface water availability contributed significantly to the model (Table 3).

An equal test sensitivity and specificity logistic threshold of 0.34 separated habitats into suitable and unsuitable. Response curves indicated that suitable habitat was represent-

Table 3. Results of the jackknife analyses for the final, best-fit models of the original Meramec River habitat suitability model and transfer of that model to the Gasconade River and Little Black rivers. An asterisk (*) indicates hydrogeomorphic variables that contributed significantly to the model based on the jackknife analyses.

Variable	Gasconade River	Meramec River	Little Black River
Bluff adjacency area	Near small bluffs*	Near small bluffs	—
Distance to gravel bar	Farther than 1,250 m*	Less than 400 m*	Any distance outside the reach*
Gravel/pool class	Pool*	—	Pool*
Low-flow surface water availability index	Greater than 0*	Greater than 3*	Greater than 7*
Stream power index	Greater than 0	Greater than 0*	Less than 0.05*
Lateral channel stability	Laterally stable	Laterally stable*	—
Bluff adjacency area downstream	—	—	Any amount of bluff area downstream*

ed by reaches classified as pools, near small bluffs, 100–300 m or > 1,250 m from persistent gravel bars, with low-flow surface water availability and stream power indices > 0, and laterally stable channels (Fig. 4 and Table 3). Because the test AUC was > 0.70 and total validation was 0.82, we concluded that transfer of the modeling framework to the Gasconade River was successful, and we did not evaluate Level 3 transferability (Table 2).

Little Black River

Level 1: Transferring the original model.—The best-fit habitat suitability model for Level 1 had a test AUC of 0.64 (Table 2). The best-fit model included the same six hydrogeomorphic variables as for the Gasconade River: lateral channel stability, distance to gravel bar, gravel/pool class, stream power index, bluff adjacency area, and low-flow

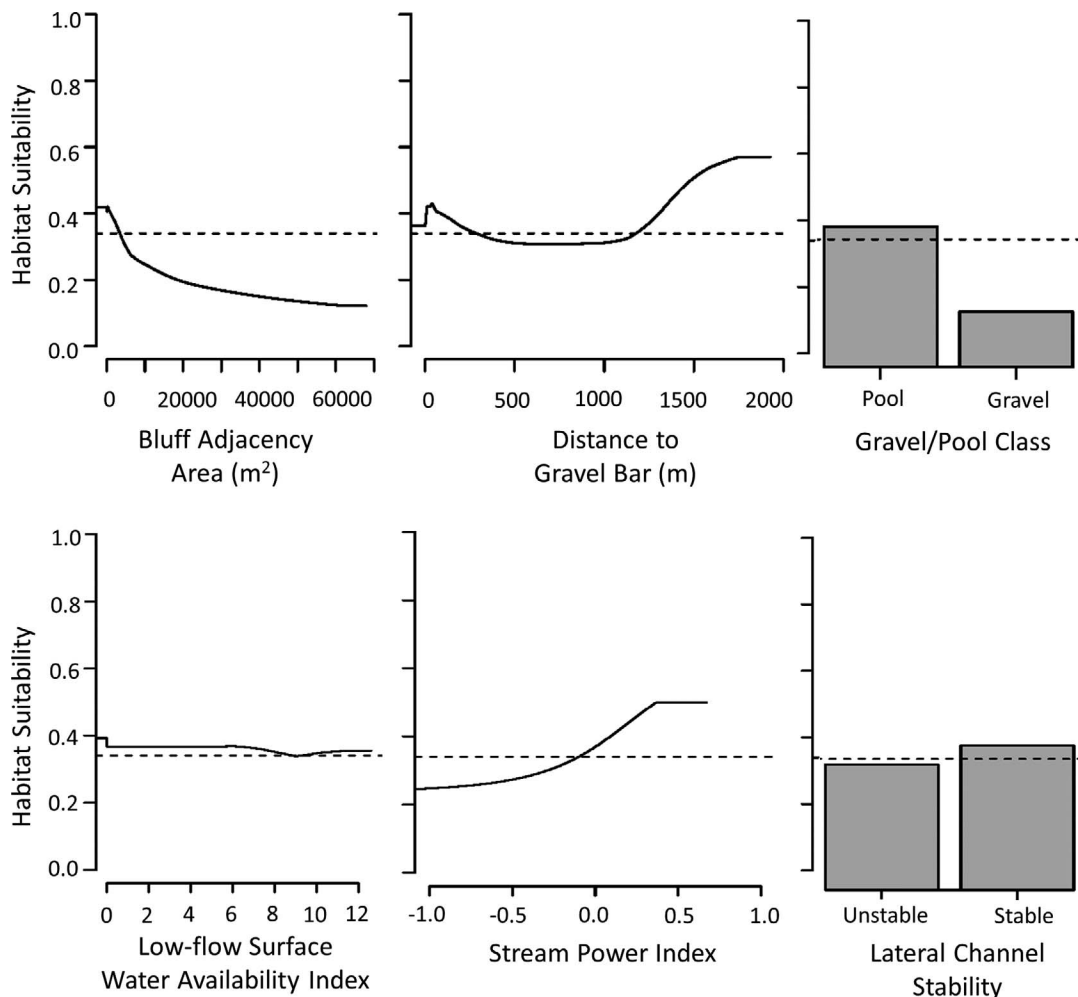


Figure 4. Response curves for hydrogeomorphic variables that contributed significantly to transferring the Meramec River modeling framework to the Gasconade River at Level 2. The dashed line represents the equal sensitivity and specificity logistic threshold used to delineate suitable and unsuitable habitats.

surface water availability index. Jackknife analysis indicated that distance to gravel bar, gravel/pool class, low-flow surface water availability index, stream power index, and lateral channel stability contributed significantly to the final model.

An equal test sensitivity and specificity logistic threshold of 0.42 separated habitats into suitable and unsuitable. Response curves indicated that suitable habitat was represented by reaches near small bluffs, 0–500 m or > 2,000 m from gravel bars, with higher low-flow surface water availability, low-intermediate stream power indices, and laterally unstable channels. Sixty-four percent of validation mussel bed locations were found in areas identified as suitable by the model, and validation in the Little Black River was 60% (Table 2). Because the test AUC and total validation were < 0.70, we considered model transfer to the Little Black River unsuccessful at this level and continued to Level 2.

Level 2: Transferring the modeling framework.—The best-fit habitat suitability model for Level 2 had a test AUC of 0.74 (Table 2). The best-fit model included the same six hydrogeomorphic variables as Level 1. Jackknife analysis indicated that distance to gravel bar, gravel/pool class, stream power index, and lateral channel stability contributed significantly to the final model.

An equal test sensitivity and specificity logistic threshold of 0.48 separated habitats into suitable and unsuitable. Response curves indicated that suitable habitat was represented by reaches near small bluffs, with high water availability, lower stream power indices, and areas classified as pools. The test AUC was > 0.70, but because total validation was only 60%, we concluded that transfer of the modeling framework to the Little Black River was unsuccessful and continued to Level 3 (Table 2).

Level 3: Adapting the model.—The best-fit model for Level 3 had a test AUC of 0.72 (Table 2). The best-fit model included downstream bluff adjacency area, distance to gravel bar, gravel/pool class, low-flow surface water availability, and stream power index. Jackknife analysis indicated that downstream bluff adjacency area, gravel/pool class, low-flow surface water availability, and stream power index contributed significantly to the final model (Table 3).

An equal test sensitivity and specificity logistic threshold of 0.44 separated habitats into suitable and unsuitable. Response curves indicated that suitable habitat was represented by reaches classified as pools, with higher surface water availability and lower stream power indices (Fig. 5 and Table 3). Suitable habitat also was represented by reaches with any amount of downstream bluff area and persistent gravel bars at any distance. The best-fit model at this level had a total validation of 0.80 (Table 2). Because the test AUC was > 0.70 and total validation was 0.80, we concluded that transfer of the model to the Little Black River at this level was successful.

DISCUSSION

Our study successfully identified suitable habitat for freshwater mussels in the Gasconade and Little Black rivers.

Mussel beds in both rivers were associated with reaches classified as pools based on the absence of exposed gravel bars. In the Gasconade River, laterally stable reaches near small bluffs, with gravel bars farther than 1,250 m away and higher stream power indices, were considered more suitable. In the Little Black River, suitable habitat was related to reaches with higher surface water availability during low-flow conditions, lower stream power indices, and bluffs located downstream.

In the MRHSM, distance to gravel bars, low-flow surface water availability index, stream power index, and lateral channel stability contributed significantly to the final model based on jackknife analysis (Table 3; Key et al. 2021). An equal test sensitivity and specificity logistic threshold of 0.45 separated habitats into suitable and unsuitable. Based on the response curves, locations identified as suitable were in reaches close to small bluffs, near persistent gravel bars, with higher stream power indices, laterally stable channels, and in reaches with greater low-flow surface water availability (Key et al. 2021).

The similarity of some features of our models to the original MRHSM suggests that mussel beds in the Gasconade and Little Black rivers are associated with some of the same habitat characteristics as those in the Meramec River. This is not surprising because the Meramec, Gasconade, and Little Black rivers all are in the Ozark Highlands ecoregion and share similar physiographic and watershed features. Most conspicuously, the best-fit habitat suitability model for all three rivers included a hydrogeomorphic variable representing bluff adjacency. Response curves show similar trends in increased habitat suitability associated with smaller bluffs (in relation to the amount of bluff area in the system) and decreased habitat suitability associated with larger bluffs. While bluffs can exert lateral channel control (Vannote and Minshall 1982), larger bluffs could reduce flow and sediment transport causing areas of unstable gravel deposition (Jacobson and Gran 1999; Owen et al. 2011). The best-fit model for the Little Black River included the bluff area downstream of mussel beds, but we do not necessarily know how downstream bluffs may influence channel stability or other habitat features.

Differences in other aspects of our models between all three rivers suggest that factors associated with mussel bed location differ according to watershed characteristics specific to each system. We were unable to transfer the MRHSM to either river at Level 1, which shows that direct transfer of the MRHSM was not possible. We were able to transfer the MRHSM to the Gasconade River at Level 2 and able to adapt it to the Little Black River at Level 3. Our results suggest that the unique features of each watershed affect model transferability, and additional variables (e.g., downstream bluff adjacency) may be needed to predict mussel occurrence in some streams.

Although the Meramec, Gasconade, and Little Black river watersheds share features characteristic of the Ozark Highlands ecoregion, each stream has unique features that may influence mussel bed habitat associations. Stream drying is an important factor in the disturbance regime of many rivers in

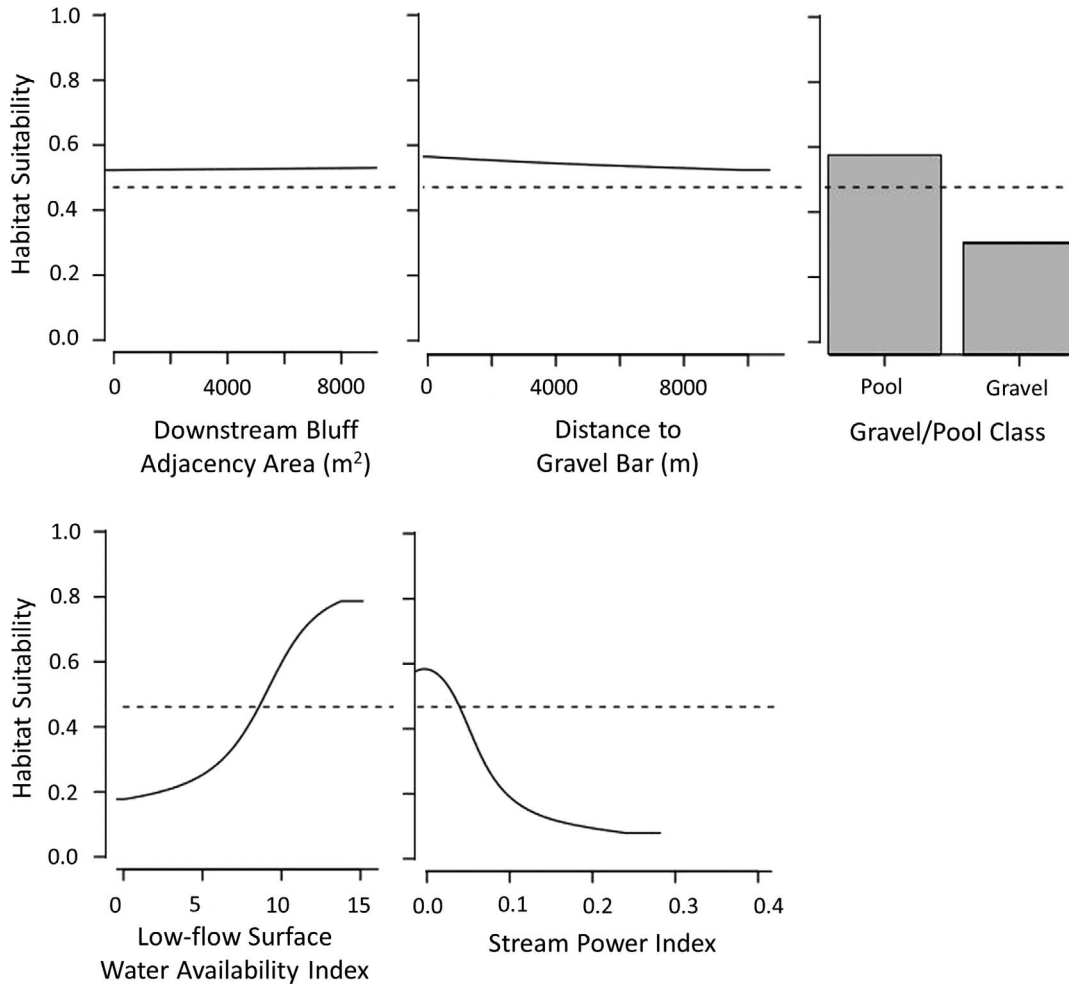


Figure 5. Response curves for hydrogeomorphic variables that contributed significantly to adapting the Meramec River modeling framework to the Little Black River at Level 3. The dashed line represents the equal sensitivity and specificity logistic threshold used to delineate suitable and unsuitable habitats.

the Ozark Highlands (Lynch et al. 2018). We observed numerous large, dry stretches of streambed during low-flow conditions in the aerial imagery for both the Gasconade and Little Black rivers. In contrast, we did not observe streambed drying throughout the Meramec River, even during low-flow conditions. The association of mussel beds in the Gasconade and Little Black rivers with reaches classified as pools, at greater distances from gravel bars, and with higher surface water availability may indicate mussel occurrence in reaches that are less prone to drying during drought (Gagnon et al. 2004; Haag and Warren 2008; Atkinson et al. 2014).

Our use of remotely sensed, large-scale hydrogeomorphic data instead of direct measurements of stream habitat characteristics affects the interpretation of our habitat suitability models. We showed an association of mussel beds with areas classified as pools. However, our aerial imagery did not provide bathymetric or flow data necessary to differentiate between low-flow, depositional pools and gravel-bottomed runs with no exposed gravel. Typically, mussel beds do not occur in depositional pools, but gravel-bottomed runs can be optimal mussel habitat (Vannote and Minshall 1982; Vaughn

and Taylor 1999). Similarly, without bathymetric data we cannot fully evaluate the extent to which low-flow surface water availability represents vulnerability to emersion during drought. Nevertheless, these variables provide useful information with which to broadly characterize reaches that support mussel beds in our study streams.

Many other factors that influence mussel presence were not included in our model, including species-specific differences in habitat requirements, anthropogenic factors, and fish-host relationships. However, at the riverscape scale, our hydrogeomorphic variables can identify broad habitat characteristics necessary to support mussels. By providing longitudinally continuous characterization of habitat suitability at the riverscape scale, our models provide a baseline that can allow evaluation of the effects of other factors on mussel occurrence (Bouska et al. 2018; Key et al. 2021).

ACKNOWLEDGMENTS

Data on freshwater mussel distributions were provided by the Missouri Department of Conservation (MDC) and

Matthew Schrum, who is working on a related project in the Little Black River with support from the MDC. Funding for this research was provided by the MDC, Tennessee Technological University Water Center, and Tennessee Technological University Department of Biology. As data were acquired from existing sources, no federal, state, or Animal Care permits were required for completion of this study. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We also would like to thank Kristin Womble for editing the manuscript prior to submission, as well as an anonymous reviewer and Wendell Haag for constructive reviews of the manuscript.

LITERATURE CITED

- Allen, D. C., and C. C. Vaughn. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. *Journal of the North American Benthological Society* 29:383–394.
- Arbuckle, K. E., and J. A. Downing. 2002. Freshwater mussel abundance and species richness; GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* 59:310–316.
- Atkinson, C. L., J. P. Julian, and C. C. Vaughn. 2014. Species and function lost: Role of drought in structuring stream communities. *Biological Conservation* 176:30–38.
- Barbosa, A. M., R. Real, and J. Mario Vargas. 2009. Transferability of environmental favourability models in geographic space: The case of the Iberian desman (*Galemys pyrenaicus*) in Portugal and Spain. *Ecological Modelling* 220:747–754.
- Bates, J. M. 1962. The impact of impoundment on the mussel fauna of Kentucky Reservoir, Tennessee River. *American Midland Naturalist* 68:232–236.
- Blanc, T. J. 2001. Gasconade River watershed inventory and assessment. Missouri Department of Conservation Fisheries Division, Jefferson City. Available at https://mdc.mo.gov/sites/default/files/2021-12/130_2021_GasconadeRiver.pdf (accessed January 31, 2023).
- Bouska, K. L., A. Rosenberger, S. E. McMurray, G. A. Lindner, and K. N. Key. 2018. State-level freshwater mussel programs: Current status and a research framework to aid in mussel management and conservation. *Fisheries* 43:345–360.
- Cao, Y., E. R. DeWalt, J. L. Robinson, T. Tweddale, L. Hinz, and M. Pessino. 2013. Using Maxent to model the historic distributions of stonefly species in Illinois streams: The effects of regularization and threshold selections. *Ecological Modelling* 259:30–39.
- Daniel, W., and K. M. Brown. 2014. The role of life history and behavior in explaining unionid mussel distributions. *Hydrobiologia* 734:57–68.
- Drew, C. A., M. Eddy, T. J. Kwak, W. G. Cope, and T. Augspurger. 2018. Hydrologic characteristics of freshwater mussel habitat: novel insights from modeled flows. *Freshwater Science* 37:343–356.
- Elith, J. 2002. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. Pages 39–59 in S. Ferson and M. Burgman, editors. *Quantitative Methods for Conservation Biology*. Springer, New York.
- ESRI (Environmental Systems Research Institute). 2011. ArcGIS Desktop: Release 10.8. Environmental Systems Research Institute, Redlands, CA.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–498.
- FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1–21.
- Gagnon, P. M., S. W. Golladay, W. K. Michener, and M. C. Freeman. 2004. Drought responses of freshwater mussels (Unionidae) in Coastal Plain tributaries of the Flint River Basin, Georgia. *Journal of Freshwater Ecology* 19:667–679.
- Golladay, S. W., P. Gagnon, M. Kerans, J. M. Battle, and D. W. Hicks. 2004. Response of freshwater assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. *Journal of the North American Benthological Society* 23:494–506.
- Haag, W. R., and M. L. Warren. 2008. Effects of severe drought on freshwater mussel assemblages. *Transactions of the American Fisheries Society* 137:1165–1178.
- Jacobson, R. B., and K. B. Gran. 1999. Gravel sediment routing from widespread, low-intensity landscape disturbance, Current River Basin, Missouri. *Earth Surface Processes and Landforms* 24:897–917.
- Jacobson, R. B., and A. T. Primm. 1997. Historical land-use changes and potential effects on stream disturbance in the Ozark Plateaus, Missouri. US Geological Survey. Available at <https://pubs.usgs.gov/wsp/2484/report.pdf> (accessed January 31, 2023).
- Jiménez-Valverde, A., and J. M. Lobo. 2006. The ghost of unbalanced species distribution data in geographical model predictions. *Diversity and Distributions* 12:521–524.
- Johnson, P. D., and K. M. Brown. 2000. The importance of microhabitat factors and habitat stability to the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad). *Canadian Journal of Zoology* 78:271–277.
- Key, K. N., A. E. Rosenberger, G. A. Lindner, K. Bouska, and S. E. McMurray. 2021. Riverscape-scale modeling of fundamentally suitable habitat for mussel assemblages in an Ozark River System, Missouri. *Freshwater Mollusk Biology and Conservation* 24:43–58.
- Lueckenhoff, L. 2015. Development of standardized visual sampling methods for assessing community metrics of unionoid mussel species and tribal groups in Missouri. Master's thesis, University of Missouri, Columbia.
- Lynch, D. T., D. R. Leasure, and D. D. Magoulick. 2018. The influence of drought on flow-ecology relationships in Ozark Highland streams. *Freshwater Biology* 63:946–968.
- Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. *Hydrological Processes* 5:3–30.
- MSDIS (Missouri Spatial Data Information Service). 2011. Curators of the University of Missouri-Columbia. Available at <http://msdis.missouri.edu> (accessed January 31, 2023).
- Owen, M. R., R. T. Pavlowsky, and P. J. Womble. 2011. Historical disturbance and contemporary floodplain development along an Ozark river, southwest Missouri. *Physical Geography* 32:423–444.
- Ozark Ecoregional Assessment Team. 2003. Ozarks ecoregional conservation assessment. The Nature Conservancy, Midwestern Resource Office, Minneapolis, Minneapolis.
- Pandolfo, T. J., T. J. Kwak, and W. G. Cope. 2016. Microhabitat suitability and niche breadth of common and imperiled Atlantic Slope freshwater mussels. *Freshwater Mollusk Biology and Conservation* 19:27–50.
- Peck, A. J. 2005. A reach scale comparison of fluvial geomorphological conditions between current and historic freshwater mussel beds in the White River, Arkansas. Master's thesis, Arkansas State University, Jonesboro.
- Phillips, S. J. 2017. A brief tutorial on MaxEnt. Available at http://biodiversityinformatics.amnh.org/open_source/maxent/ (accessed January 31, 2023).
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with MaxEnt: New extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmermann, M. Zappa, and

- A. Guisan. 2006. Are niche-based species distribution models transferable in space? *Journal of Biogeography* 33:1689–1703.
- Randklev, C. R., M. A. Hart, J. M. Khan, E. T. Tsakiris, and C. R. Robertson. 2019. Hydraulic requirements of freshwater mussels (Unionidae) and a conceptual framework for how they respond to high flows. *Ecosphere* 10:e02975. doi: 10.1002/ecs2.297
- Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: Conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. *Evolution and the Aquatic Ecosystem symposia proceedings, Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation*. American Fisheries Society, New York.
- Schrum, M. C. 2017. Development and validation of standardized sampling protocols for assessing freshwater mussel populations in Missouri. Master's thesis. University of Missouri, Columbia.
- Strayer, D. L. 1993. Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the Northern Atlantic Slope. *Journal of the North American Benthological Society* 12:236–246.
- Strayer, D. L. 1999. Use of flow refuges by Unionid mussels in rivers. *Journal of the North American Benthological Society* 18:468–476.
- Strayer, D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton, and S. Jerrine Nichols. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *Bioscience* 54:429–439.
- Strayer, D. L., and J. Ralley. 1993. Microhabitat use by an assemblage of stream-dwelling Unionaceans (Bivalvia), including two rare species of Alasmidonta. *Journal of the North American Benthological Society* 12:247–258.
- Vannote, R. L., and G. W. Minshall. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences* 79:4103–4107.
- Vaughn, C. C. 1997. Regional patterns of mussel species distributions in North American rivers. *Ecography* 20:107–115.
- Vaughn, C. C. 2012. Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels. *Freshwater Biology* 57:982–992.
- Vaughn, C. C., and C. M. Taylor. 1999. Impoundments and the decline of freshwater mussels: A case study of an extinction gradient. *Conservation Biology* 13:912–920.
- Walters, A. D., D. Ford, E. R. Chong, M. G. Williams, N. B. Ford, L. R. Williams, and J. A. Banta. 2017. High-resolution ecological niche modeling of threatened freshwater mussels in east Texas, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27:1251–1260.
- Werkowska, W., A. L. Márquez, R. Real, and P. Acevedo. 2016. A practical overview of transferability in species distribution modeling. *Environmental Reviews* 25:127–133.
- Wilkerson, T. F. 2003. Current River watershed inventory and assessment. Missouri Department of Conservation Fisheries Division, Jefferson City. Available at <https://mdc.mo.gov/sites/default/files/mdcd7/downloads/page/080Current%20River.pdf> (accessed January 31, 2023).
- Zigler, S. J., T. J. Newton, J. J. Steuer, M. R. Bartsch, and J. S. Sauer. 2008. Importance of physical and hydraulic characteristics to unionid mussels: A retrospective analysis in a reach of large river. *Hydrobiologia* 598:343–360.

Freshwater Mollusk Biology and Conservation

©2023

ISSN 2472-2944

Editorial Board

EDITOR IN CHIEF

Wendell Haag, U.S. Department of Agriculture, Forest Service

MANAGING EDITOR

Ani Escobar, Georgia Department of Natural Resources

ASSOCIATE EDITORS

David Berg, Miami University, Ohio

Robert Bringolf, University of Georgia

Serena Ciparis, U.S. Fish & Wildlife Service

Traci DuBose, ORISE post-doctoral fellow, U.S. Forest Service

Daniel Hornbach, Macalester College

Caryn Vaughn, University of Oklahoma

Alexandra Zieritz, University of Nottingham