Freshwater Mollusk Biology and Conservation 00:000–000, 2025

DOI:10.31931/fmbc-d-23-00009

REGULAR ARTICLE

FINE-SCALE HABITAT AND CO-OCCURRENCE PATTERNS OF FISH, CRAYFISH, AND MUSSELS IN THE MUSKEGON RIVER, MICHIGAN, USA

Kiara C. Cushway[1,2,†] **and Daelynn A. Woolnough**[2,*]

[1] *Honors Program, Central Michigan University, 1200 S. Franklin Street, Mount Pleasant, MI 48859 USA*

[2] *Department of Biology and Institute for Great Lakes Research, Central Michigan University, 1200 S. Franklin Street, Mount Pleasant, MI 48859 USA*

ABSTRACT

Although the potential for species interaction at fine spatial scales is high, research on habitat and co-occurrence patterns for multifaunal groups at fine spatial scales is lacking. Video-recorded transect surveys provide the opportunity to examine abundance and distribution of multiple taxa at fine spatial scales to identify patterns in shared habitats. We examined habitat associations and patterns of species co-occurrence for fish, crayfish, and freshwater mussels by using video transect surveys at a site in the Muskegon River, Michigan, USA, in August 2020. Our results suggest that fine-scale habitat characteristics such as depth, substrate, estimated algal density, and siltation influence the distribution and abundance of fish, crayfish, and mussels at our site. Taxa co-occurrence was mostly random across transects, although there was some indication of segregated distribution of crayfish and mussels. Despite lack of strong patterns of transect-scale co-occurrence, we also found that several host fish species co-occurred with mussel species at our site, indicating that potential required life cycle interactions between mussels and host fish could still occur. Continued study of interactions and habitat requirements at fine spatial scales can inform restoration activities and elucidate the environmental and biological filters that influence the distribution of individual organisms and multifaunal communities.

KEY WORDS: assemblages, ecological interactions, multitaxa, macroinvertebrates, video

---

INTRODUCTION

Spatial scale is an essential consideration for ecological studies, given that organisms interact with each other and their environment differently at different scales (Levin 1992; Hernández 2020; DuBose et al. 2024). Unfortunately, research at fine spatial scales is frequently neglected in the scientific literature (Mehrabi et al. 2014), in part because observations at fine scales do not necessarily translate to larger habitats or ecosystems and may therefore be perceived as having limited value for solving problems that occur across larger scales (Schneider 2001). Despite the focus on larger scales, organisms are most directly impacted by (and conversely, most directly impact) the habitat conditions and species' interactions occurring in their immediate vicinity (Cushman and McGarigal 2004). Furthermore, restoration efforts are often most feasible (although not necessarily most effective) at finer spatial scales (Lake et al. 2007). Hence, understanding fine-scale habitat and species associations is important for management and restoration efforts that aim to promote species' persistence (Banks and Skilleter 2007; Rice et al. 2020).

Research at fine spatial scales has attempted to elucidate—with varying success—the distribution and habitat preferences of taxonomic groups such as freshwater mussels, fish, and crayfish (e.g., Vlach et al. 2009; Manna et al. 2017; Bird et al. 2022). Fine-scale distribution may be influenced by competition, predation or predator avoidance, and resource partitioning across species and taxa (Garvey et al. 1994; Pennock et al. 2018). However, few studies have attempted to quantify fine-scale patterns of co-occurrence and habitat

---

*Corresponding Author: wooln1d@cmich.edu

†Current Address: UIC Government Services, Bowhead Family of Companies, 6564 Loisdale Court, Suite 900, Springfield, VA 22150 USA

associations for all three groups, despite increasing recognition of the importance of cross-taxa interactions in ecological research (Noguiera et al. 2023). For example, fish, crayfish, and mussels are ecosystem engineers and can concurrently influence habitat availability and suitability (Reynolds 2011; Polvi and Sarneel 2017; DuBose et al. 2024). Fish alter habitat through nest digging or sediment disturbance during foraging (Moore 2006). Crayfish can influence base flow and sediment composition in aquatic habitats and impact resource availability for other organisms (Momot 1995; Statzner et al. 2000; Reynolds et al. 2013). Mussels influence nutrient availability, deposit organic material through excretion of pseudofeces, influence sediment stability through burrowing in substrate, and provide shelter and habitat for other organisms (Vaughn et al. 2004; Moore 2006; Zimmerman and de Szalay 2007). In addition, direct interactions of fish, crayfish, and mussel taxa can influence distribution and habitat use. Most freshwater mussels in the order Unionida require host fish during the larval reproductive stage, and at least one species of fish parasitizes freshwater mussels by laying eggs in mussel gills (Haag and Warren 1998; Reichard et al. 2010). Both crayfish and fish have been observed preying on freshwater mussels (Klocker and Strayer 2004; Clark et al. 2022). Some fish species prey on crayfish, and crayfish may eat fish eggs or compete with benthic fish for food or habitat (Garvey et al. 1994; Dorn and Mittelbach 1999).

Efficient methods are needed to quantify the prevalence of cross-taxa interactions; thus, our objectives were to (1) examine fine-scale (i.e., tens of meters) habitat associations for fish, crayfish, and mussels across a gradient of depths; and (2) investigate fine-scale patterns of co-occurrence for these three taxa within a single site in the Muskegon River, Michigan, USA, with comments on the efficacy of video recording for data collection in aquatic environments. We predicted that (1) fine-scale habitat conditions would influence the abundance of fish, crayfish, and mussels, but would be most important for mussels given their relatively sedentary nature; and (2) fish, crayfish, and mussels would have nonrandom patterns of co-occurrence due to important cross-taxa interactions that occur across the groups. Specifically, we predicted that mussels and fish and mussels and crayfish would exhibit aggregated co-occurrence patterns because of mussel-provided ecosystem services such as increased habitat cover and complexity, biodeposition, and nutrient cycling (Vaughn 2018; Hopper et al. 2019). In addition, because mussels often rely on close-up interactions with host fish to complete the mussel life cycle, we predicted that mussels would exhibit aggregated co-occurrence with fish. In contrast, we predicted that fish and crayfish would exhibit segregated co-occurrence patterns because of potential predation or competition for space. Our results can inform restoration activities and provide information, generally lacking, about the distribution of individual organisms and multifaunal communities and cross-taxa interactions.

METHODS

Study Area

We examined fish, crayfish, and mussel communities and microhabitat conditions at a site in the Muskegon River near Paris, Michigan, in August 2020 (Fig. 1). The Muskegon River is an ~341-km river in the Lake Michigan drainage system of the Laurentian Great Lakes (O'Neal 1997). The site was ~70 m wide and was in a rural residential area ~150 km upstream of Lake Michigan, bordered on one bank by a residential lawn and on the other bank by a mixed forest. Substrate at the site was relatively heterogenous, with interspersed sand, pebble, cobble, and boulder across much of the area. Prior observations indicated >10 mussel species, multiple fish species, and at least 1 crayfish species were present at the site (our personal observations). Water temperature at the time of data collection was ~21–22°C and air temperature varied between 24 and 28°C. Total dissolved solids Oakton Instruments (Vernon Hills, IL, USA) at the site were ~250–260 ppm during data collection.

Mussel, Fish, and Crayfish Assemblages

We recorded information about fish and crayfish abundance by using repeated video recordings of 20-m transects ($n = 12$) placed parallel to the river's flow (Fig. 1). We selected areas ~0.25, 0.5, 0.75, and 1 m in depth to capture the range of depths observed at the site. Whenever possible, we selected areas with relatively constant depth across the entire 20-m transect. We established transects by using rebar and rope marked at 1-m intervals. After laying transects, we left the transect location for ~5 min to avoid disturbance. After 5 min, one researcher holding a GoPro (GoPro Inc., San Mateo, CA, USA) recording device (Hero 6 Black or Hero 4 Silver) swam upstream at a speed of ~4 m min^{-1} along the side of the transect closest to the thalweg of the river, passively collecting video data regarding fish and crayfish communities (i.e., not directly seeking out organisms with the camera lens). We attempted to maintain a consistent field of view during data collection, capturing organisms on camera in the water column and near the substrate, resulting in a range of fish size classes. We repeated this process three times (i.e., three runs per transect) at 5-min intervals for each transect, and three different transects were completed for each depth ($n = 36$ recordings total).

After collecting the video data, we laid 1-m^2 quadrats centered at the meter mark every 5 m along each transect (0, 5, 10, 15, and 20 m). We measured water velocity (meters per second) in the center of the quadrat by using a Marsh McBirney Flow-Mate 2000 flowmeter (Marsh-McBirney Inc., Frederick, MD, USA). We also estimated substrate composition within each quadrat based on the Wentworth scale (Wentworth 1922) and recorded macrophyte presence and qualitative estimates of algae (i.e., none, slight [<1-cm-thick accumulation on substrate within the quadrat], medium [1–3-cm-thick accumulation], or high [>3-cm-thick accumulation]) and degree of siltation (i.e., none [>5-m visibility], slight [5- to 1-m visibility), medium (<1-m to 50-cm visibility), high [<50-cm

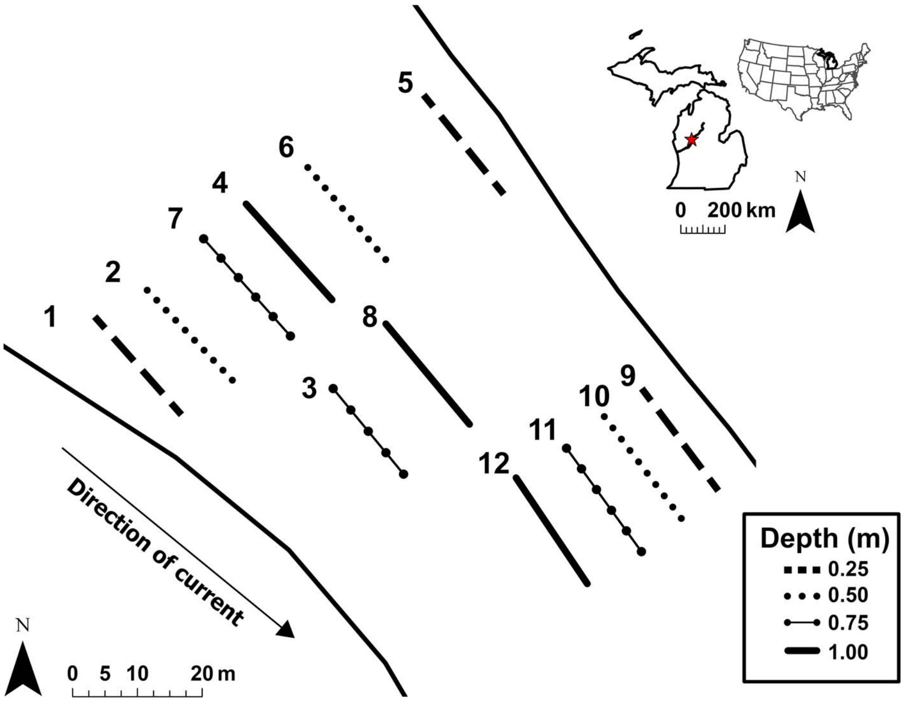

Figure 1. Locations of 12 transects of varying depths sampled for fish, crayfish, and mussels by using video recording and quadrat searches. Transect searches were conducted at a single site (indicated by star) in the Muskegon River, Michigan, USA, in August 2020.

visibility]). We then excavated each quadrat to a depth of ~10 cm and collected, measured (nearest millimeter), and identified (species level) any mussels found in quadrats by using a guidebook of mussel species in Michigan (Mulcrone and Rathbun 2020). We quantified mussel abundance as the cumulative abundance of mussels across quadrats from the same transect. We quantified habitat characteristics by averaging estimates from each quadrat within a transect.

Video Analysis

We analyzed the video recordings of transect runs ($n = 36$) by using BORIS 7.9.15 (Friard and Gamba 2016). Our video recordings ranged 3.3–5.9 min in length, with an average recording time of 4.8 ± 0.1 min. To facilitate recognition of organism presence, we reviewed videos at approximately one third to one fifth the original speed and recorded occurrences of fish and crayfish, for a total viewing time of ~15 min per video. We recorded the timestamp at which individual organisms were observed and identified each individual as a fish or crayfish. Whenever possible (based on image quality), we took screenshots of fish and crayfish that were reviewed by researchers with extensive knowledge of Michigan species to identify organisms to the genus or species level based on a list of species known to occur in the county (Appendix 1; Bailey et al. 2004). Sometimes, we observed mussels on the videos, but because mussels tend to burrow and rarely moved during the timeframe of videos, we used the quadrats (not the videos) to quantify mussel populations.

To enhance the accuracy of our abundance estimates, we reviewed each video three times. One researcher (K.C. Cushway) reviewed all video recordings initially; three additional researchers also rereviewed recordings for comparison (a total of three reviewers per video). We identified 16 additional individual organisms by reviewing videos multiple times after our initial analysis. Within runs, we quantified fish and crayfish abundance as the maximum count of individual observations of organisms (if a fish or crayfish was observed in the same location or moving upstream in the transect, it was counted one time even if it appeared in multiple frames). Hence, if a fish or crayfish moved outside of the camera frame and traveled upstream to another location on the transect, we may have recounted that organism within the same run. We recognize that this method of quantifying abundance may have resulted in double counting of some individuals, but using maximum number of individuals as a metric of abundance has been supported in other video-based studies and may lower sampling variability (Mallet and Pelletier 2014; Bruneel et al. 2022). Across runs, we quantified abundance at a given transect as the maximum number of individuals observed during any single run. For example, in transect 1, we observed 11 crayfish during run 1, 12 crayfish during run 2, and 3 crayfish during run 3, so the abundance of crayfish in transect 1 was set to 12 to account for the likelihood of double counting organisms during consecutive transect runs.

Analysis of Habitat Associations for Fish, Crayfish, and Mussels

We analyzed our data using R 4.2.2 (R Core Team 2022). Given the close spatial proximity of several of our transects within the site, fish or crayfish might have been counted in multiple transects, violating the assumption of independence.

Table 1. Variable groups used in multiple factor analysis, measured at 12 transects at a site in the Muskegon River, Michigan, USA, in August 2020.

Group	Type	Variable
Velocity	Quantitative	Average transect velocity
Depth	Quantitative	Average transect depth
Substrate	Quantitative	% Sand, % pebble, % cobble, % boulder
Algae	Qualitative	Algae
Vegetation	Qualitative	Vegetation presence
Siltation	Qualitative	Degree of siltation

To account for this, we used residual randomization in permutation procedures (RRPP) to assess the influence of fine-scale habitat characteristics on fish, crayfish, and mussel abundance across transects (Collyer and Adams 2018). The RRPP method functions similarly to the 'lm' function in the 'stats' package in R, but constructs empirical distributions over many random permutations ($n = 1{,}000$) to estimate coefficients without requiring the stringent assumptions of a traditional linear regression (Collyer and Adams 2018).

Before conducting RRPP, we ran a multiple factor analysis (MFA) by using the 'FactoMineR' and 'Factoextra' packages in R to better understand the environmental variation explaining differences across transects and to group similar variables (Lê et al. 2008; Kassambara and Mundt 2020). The MFA ordination allows analysis of both quantitative and qualitative data simultaneously using groups of similar variables (Escofier and Pagès 1994). We grouped our data into six groups for the MFA (Table 1) and determined each group's contribution to MFA dimensions. We then used a broken stick model to determine the number of dimensions to retain based on whether a given dimension contributed more than expected to the amount of variation observed in the MFA (Frontier 1976; Jackson 1993). Based on the broken stick method, the expected contribution of a dimension can be calculated as

$$b_k = \sum_{i=k}^{p} \frac{1}{i}$$

where p is equal to the total number of variables used in the analysis and b_k is equal to the size of a given eigenvalue for the kth element of the broken stick model (Jackson 1993).

Following the MFA, we conducted bootstrap selection with the retained dimensions by using the 'FWDselect' package in R to determine what variables to include in our RRPP tests (Sestelo et al. 2015, 2016). Bootstrap selection identifies the number of variables (q) needed to minimize deviance in a model by increasing q one variable at a time and testing the null hypothesis that a given value of q is sufficient to minimize deviance in the model of interest (Sestelo et al. 2016). Using the dimensions selected by bootstrap selection, we used RRPP from the 'RRPP' package in R to run a nonparametric regression to determine how well the selected dimensions (habitat variables) could explain variation in fish, crayfish, or mussel abundance in transects (Collyer and Adams 2018). We conducted Spearman rank correlation tests with Bonferroni correction to determine whether the variables contributing significantly to the selected dimensions were positively or negatively correlated with fish, crayfish, or mussel abundance. We chose Spearman rank correlation because it can handle nonnormal data, and we applied Bonferroni correction to account for using multiple tests on the same dataset (Spearman 1904; Bonferroni 1936).

Analysis of Fish, Crayfish, and Mussel Co-occurrence

To test whether fish, crayfish, and mussel co-occurrence in transects was due to species interactions or random chance, we used randomized co-occurrence null models by using the 'EcoSimR' package in R (Gotelli et al. 2015). These tests work by repeatedly randomly permuting data ($n = 1{,}000$ permutations) in a presence–absence matrix and comparing the observed co-occurrence index with the expected co-occurrence index given random organism occurrence (Gotelli et al. 2015; Santangelo 2019). We used a randomization scheme that maintained the rarity of organismal groups, but allowed each transect equal chances of occurrence given the proximity of our transects ('sim2' algorithm from 'EcoSimR' package; Gotelli 2000). We used a checkerboard score, or "C-score" index, to assess aggregation of fish, crayfish, and mussels across transects. This index uses the concept of checkerboard distributions described by Diamond (1975) to determine whether average checkerboard patterns of species co-occurrence (or in this case taxa) differ from a random distribution (Stone and Roberts 1990). Higher than expected C-scores indicate segregation of organismal groups across transects, whereas lower than expected C-scores indicate aggregation (Gotelli et al. 2015). We constructed randomized null models for all taxa, fish and crayfish only, fish and mussels only, and crayfish and mussels only.

RESULTS

Mussel, Fish, and Crayfish Assemblages

We collected 39 live mussels of 8 different species during surveys (Table 2), with an additional 13 shells representing 5 species, one of which (*Alasmidonta marginata*) was not found alive in quadrats. Mussel density in transects ranged from 0 to 3.8 individuals m^{-2}, with an average of 0.7 ± 1.0 ($\bar{x} \pm \sigma$). Mussels ranged in size from 25 to 114 mm (Appendix 2). Forty-four live fish and 26 live crayfish were observed on video (Fig. 2). We could not identify all crayfish and fish to the species level, but we did identify at least 1 crayfish species (invasive *Faxonius rusticus*) and up to 10 genera of fish present in transects (Table 3; Appendix 1). Most of the individuals we observed were small fish or darters, but we did capture some larger fish (e.g., *Cyprinus carpio*) present in the water column during transect recordings. Across the site (all transects), several potential host fish species co-occurred with

Table 2. Freshwater mussel species collected in 1-m^2 quadrats during transect searches of 12 transects in the Muskegon River, Michigan, USA, in August 2020. Abundance denotes the total number of individuals found in all transects, and transects occupied refers to the specific transects in which each species was found. Species with an asterisk are considered threatened in the state of Michigan (Mulcrone and Rathbun 2020).

Species	Abundance	Transects Occupied
Cambarunio iris	1	1
Eurynia dilatata	17	1, 2, 4, 8, 11
Fusconaia flava	1	7
Lampsilis cardium	2	3, 8
Lampsilis siliquoidea	4	1, 10
Lasmigona costata	1	1
**Ligumia recta*	1	4
Ortmanniana ligamentina	12	1, 2, 3, 4, 9, 11, 12

mussel species (Table 3; Freshwater Mussel Host Database 2017).

Habitat Associations for Fish, Crayfish, and Mussels

The first seven dimensions of our MFA explained ~95% of the total variation across transects. Dimensions 1 and 2 alone explained ~45% of the overall variation, with velocity (dimension 1) and depth (dimension 2) being the primary quantitative variables contributing to these dimensions (Fig. 3). Based on the results of the broken stick model, however, we retained only dimensions 2–7, which explained ~71% of the total variation across transects (Table 4). Although dimension 1 explained ~24% of the overall variation, this was less than the amount of variation that would be expected based on the broken stick model, so it was not retained for further analysis.

Our bootstrap variable selection indicated that algae and transect depth (represented by dimension 3) were sufficient for explaining variation in fish abundance in response to habitat ($q = 1$, $T = 17.59$, $p = 0.566$, deviance = 205.16). Algae and depth explained ~30% of the variation in fish abundance across transects (df = 10, SS = 188.34, $F = 4.28$, $Z = 1.46$, Pr($>F$) = 0.05). Depth was negatively correlated with fish abundance, although this relationship was not statistically significant (Appendix 3). Algae, siltation, and substrate (represented by dimension 4) best explained crayfish abundance ($q = 1$, $T = 13.23$, $p = 0.339$, deviance = 40.26), accounting for ~28% of variation in abundance across transects (df = 10, SS = 39.24, $F = 3.83$, $Z = 1.38$, Pr($>F$) = 0.08), although the probability of obtaining a larger F value based on the empirical distribution was ~8%. Crayfish abundance tended to be weakly negatively related to sand and boulder substrate and weakly positively related to pebble and cobble substrate, although none of these relationships were statistically significant (Appendix 3). Algae, siltation, and depth (represented by dimension 2) best explained mussel abundance ($q = 1$, $T = 17.66$, $p = 0.531$, deviance = 99.58), accounting for ~35% of the variation in abundance across transects, although the probability of obtaining a larger F value based on the empirical distribution was ~9% (df = 10, SS = 100.15, $F = 5.27$, $Z = 1.55$, Pr($>F$) = 0.09). Depth alone was not strongly correlated with mussel abundance (Appendix 3).

Fish, Crayfish, and Mussel Co-occurrence

Based on our randomized co-occurrence null model for all taxa, the C-score for fish, crayfish, and mussel distribution across transects was not significantly different from the randomly simulated C-score (Fig. 4A; Table 5). This result indicated that, on average, the three organismal groups were not significantly aggregated or segregated across transects. Similarly, we found that fish and crayfish and fish and mussels co-

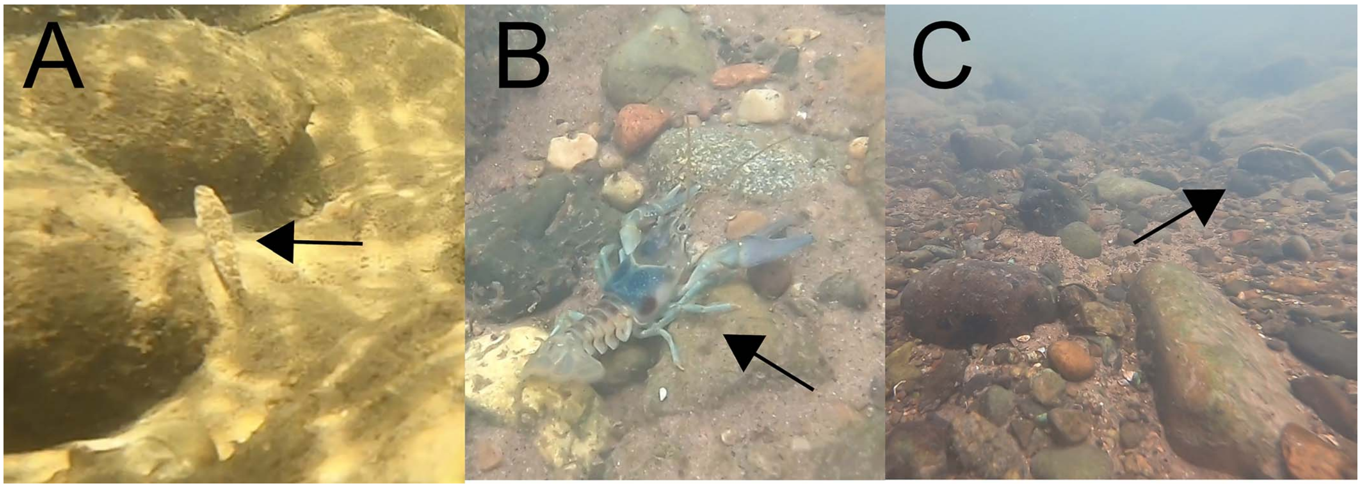

Figure 2. Examples of (A) fish, (B) crayfish, and (C) mussels captured during video-recorded transect surveys of 12 transects at a site in the Muskegon River, Michigan, USA, sampled in August 2020. Note that although mussels were sometimes captured in video recordings, mussels were sampled only by using quadrats placed along transects.

Table 3. Potential host fish species co-occurring with mussel species at a site in the Muskegon River, Michigan, USA, in August 2020. Evidence of host potential was obtained from the Freshwater Mussel Host Database (2017) and included successful infestation or transformation in natural and laboratory settings, including unspecified infestation types. Fish species marked ZT were tested as host fish, but did not support successful transformation of that particular mussel species (Freshwater Mussel Host Database 2017). Species with one asterisk in front of the genus name were identified by experienced researchers from still images obtained using GoPro video recordings along twelve 20-m-long transects at ∼0.25-, 0.5-, 0.75-, and 1.0-m depths (n = 3 for each depth). Species with two asterisks were also identified as potentially being present at the site and were historically found in the Muskegon River watershed, but not within Mecosta County.

Fish Species			Mussel Species							
Genus	Specific Epithet	Common Name	*Cambarunio iris*	*Eurynia dilatata*	*Fusconaia flava*	*Lampsilis cardium*	*Lampsilis siliquoidea*	*Lasmigona costata*	*Ligumia recta*	*Ortmanniana ligamentina*
***Cyprinus*	*carpio*	Common Carp						X	X	X
***Dorosoma*	*cepedianum*	Gizzard Shad		X				X		
**Etheostoma*	*caeruleum*	Rainbow Darter	X	X	ZT		ZT	X		
**Etheostoma*	*exile*	Iowa Darter		X			X			
**Etheostoma*	*nigrum*	Johnny Darter		X	ZT		X	X		
**Micropterus*	*salmoides*	Largemouth Bass	X	X	X	X	X	X	X	X
***Neogobius*	*melanostomus*	Round Goby	X				X		X	X
***Notropis*	*atherinoides*	Emerald Shiner			X					
**Perca*	*flavescens*	Yellow Perch	X	X		X	X	X	X	X
***Percina*	*caprodes*	Logperch	ZT	X	ZT		ZT	X		
**Percina*	*maculata*	Blackside Darter		X	ZT		ZT	X		
**Rhinichthys*	*obtusus*	Western Blacknose Dace			X					
**Semotilus*	*atromaculatus*	Creek Chub	ZT		X		ZT	X		X

occurred randomly across transects (Fig. 4B, C; Table 5). Crayfish and mussels exhibited some indication of segregation (i.e., the observed C-score was always higher or equal to the simulated C-score), but this pattern was not statistically significant (Fig. 4D; Table 5).

DISCUSSION

Mussel, Fish, and Crayfish Assemblages

As the technology improves, video recording methods for data collection are becoming increasingly popular (Mallet and Pelletier 2014). Our study demonstrated a unique way to use video analysis to assess habitat associations and co-occurrence of multifaunal groups at fine spatial scales. Although we focused on fish, crayfish, and mussels, our methodology could easily be expanded to include other organisms such as gastropods and other macroinvertebrates, providing a quick and relatively straightforward method of assessing multiple taxa simultaneously. In addition, use of video recordings can decrease the time and training needed to conduct field surveys and help reduce species' misidentification while increasing organism detection (Bruneel et al. 2022). Repeated review of our video recordings (after our initial review) helped us detect an additional 16 organisms and allowed us to consult subject experts for help with crayfish and fish identification.

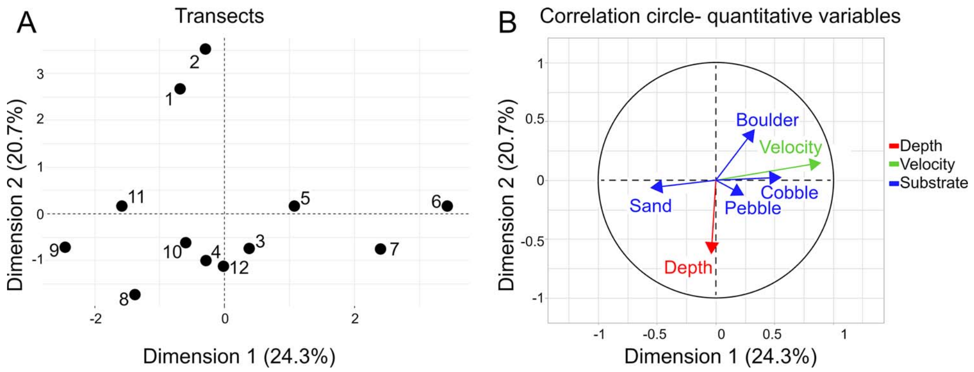

Figure 3. Position of (A) transects and (B) quantitative variables on the primary axes of a multiple factor analysis (MFA) evaluating variation in habitat characteristics across a site in the Muskegon River, Michigan, USA. Transects were sampled for fish, crayfish, and mussels in August 2020. Direction of arrows in B indicate relationships between variables (arrows pointing in opposite directions are negatively correlated), and length of arrows represents the importance of each variable in the MFA. Variables are colored by group.

Table 4. Multiple factor analysis dimensions (along with explained variance) retained for bootstrap variable selection based on the results of a broken stick model. Groups included in each dimension contributed more than expected given uniform contribution from all possible groups (Kassambara 2017).

Dimension	% Variance Explained	Groups Included	Group Contribution to Dimension (%)
2	20.7	Algae	42
		Siltation	35.4
		Depth	17.3
3	15.3	Algae	53.8
		Depth	24.3
4	12	Algae	33.3
		Siltation	31.8
		Substrate	22.5
5	9.2	Algae	52.2
		Siltation	39.3
6	7.9	Substrate	59.2
		Algae	24.2
7	5.6	Algae	47.9
		Vegetation	27.2

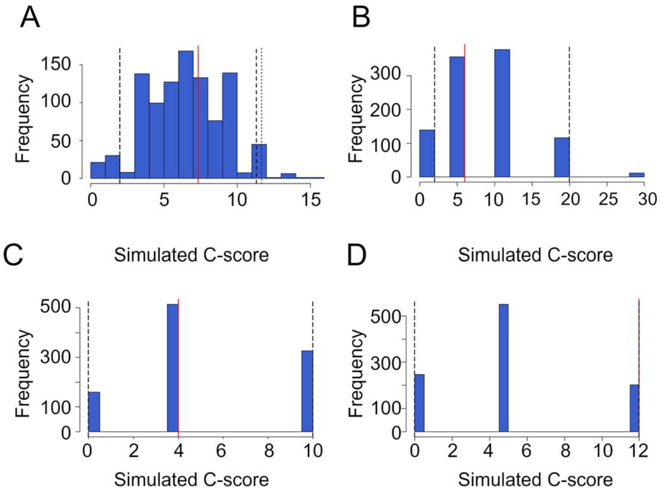

Figure 4. Frequency distribution of simulated checkerboard scores (C-scores) for randomized species co-occurrence null models for (A) fish, crayfish, and mussels, (B) fish and crayfish only, (C) fish and mussels only, and (D) crayfish and mussels only. The red vertical line represents the observed C-score for taxa co-occurrence across 12 transects sampled at a site in the Muskegon River, Michigan, USA, in August 2020. Vertical dashed lines represent one-tailed (long dash) and two-tailed (short dash) 95% confidence intervals. Where only one set of dashed lines is visible, one- and two-tailed confidence intervals were equivalent.

Habitat Associations for Fish, Crayfish, and Mussels

Our results suggest that fine-scale habitat characteristics were related to the abundance and distribution of fish, crayfish, and mussels at our site, although statistical support was rather low for crayfish and mussels. Increased sampling would likely strengthen the statistical power of our results, but even with our small sample sizes, we observed some interesting patterns in taxa occurrence. As we predicted, habitat conditions were most explanatory for mussels. Although mussels can move short distances to seek suitable habitat, they are much less mobile than fish or crayfish and were likely relatively stationary at the timescale we examined (Schwalb and Pusch 2007). By contrast, fish and crayfish can move in and out of suitable areas relatively quickly and could have been influenced by observer presence in transects, which may be why habitat was slightly less important for predicting their abundance (Bruneel et al. 2022).

Estimated algal density appeared as an important factor of the MFA dimensions used in all models, which could be related to trophic interactions and prey density. We identified several species of darters in our transects, and both darters and crayfish prey on macroinvertebrates that eat periphyton (Stelzer and Lamberti 1999). Mussels also influence periphyton abundance through biodeposition and excretion, although the density of mussels observed in our transects was relatively low compared with mussel density in southern streams where these effects have been measured (densities as high as 64 individuals m^{-2} in southern study system; Spooner and Vaughn 2006). In addition, some species of crayfish (including *F. rusticus*), fish (e.g., *C. carpio*), and mussels consume algae and periphyton, which may be why it appeared ubiquitously across all models (Lodge et al. 1994; Matsuzaki et al. 2007; Vaughn et al. 2008). Similarly, degree of siltation was included in influential dimensions for both crayfish and mussels, which may be related to the influence of both taxa on stream bioturbation (Statzner et al. 2000; Vaughn et al. 2004).

Depth was an important factor in the dimensions explaining fish and mussel abundance, whereas substrate was an important factor in the dimension explaining crayfish abundance. Fish abundance tended to decrease with increasing depth, which may be because many of the fish we observed were small darters that use shallow habitats as refuges from predation by larger fish (Schlosser 1987). Mussel abundance was not strongly correlated with depth on its own, which aligns with several studies that suggest complex hydraulic characteristics may be more important for influencing mussel distribution (Allen and Vaughn 2010; Pandolfo et al. 2016). However, mussels in a study in Kentucky were observed preferentially occupying depths between 7 and 30 cm during base flow periods, which falls into the range of observed depths at our study site (Layzer and Madison 1995). Depth preferences may be stronger in southern streams where drought and subsequent stream drying poses a threat to mussels, and species-specific depth preferences may also influence mussel abundance at different depths (Hart 1995; Cushway et al. 2024). Substrate was an important group in the dimension selected for the crayfish model, which aligns with past research suggesting that substrate influences crayfish distribution (e.g., Smith et al. 2019). Many nonburrowing crayfish species prefer cobble or boulder substrates for shelter and as refuge from predation (Smith et al. 2019). We did not find very strong relationships with individual substrate variables, but there

Table 5. Results of randomized species co-occurrence null models ($n = 1{,}000$ permutations; Gotelli et al. 2015) for fish, crayfish, and mussels found in 12 transects at a site in the Muskegon River, Michigan, USA, in August 2020. Results include observed (Obs.) and simulated (Sim.) checkerboard scores (C-score); variance of the simulated C-score; upper bound (UB) and lower bound (LB) of one- and two-tailed confidence intervals; *p* values for upper and lower tails; standard effect size; and the percent of simulated C-scores less than, greater than, or equal to the observed C-score.

	C-Score			Confidence Interval				*p* Value			% of Permutations		
Taxa	Obs.	Sim.	Sim. variance	One-tailed LB	One-tailed UB	Two-tailed LB	Two-tailed UB	Lower tail	Upper tail	Standard effect size	Sim. < Obs.	Sim. > Obs.	Sim. = Obs.
All	7.3	7	6.7	2	11	2	11.7	0.7	0.41	0.26	59.1	31.3	9.6
Fish/crayfish	6	9.2	30.08	2	20	2	20	0.53	0.86	−0.58	14.2	47.1	38.7
Fish/mussels	4	5.27	12.22	0	10	0	10	0.69	0.85	−0.36	15.5	31.5	53
Crayfish/mussels	12	5.63	17.33	0	12	0	12	1	0.25	1.53	75.2	0	24.8

were weak tendencies for lower crayfish abundances in sandy habitats, which does not provide much cover from predators.

Fish, Crayfish, and Mussel Co-occurrence

Contrary to our expectations, we did not see strong patterns of co-occurrence across taxa, particularly for fish and crayfish or fish and mussels, indicating potential limited cross-taxa interactions. This may be due, in part, to our sampling representing a short snapshot in time. Because most mussels require a host fish to reproduce, fine-scale interactions of fish and mussels are required for successful host infestation and mussel reproduction (Haag 2012). In addition, host fish are often the primary means of mussel dispersal during the glochidial life stage and influence mussel distribution at larger scales, but they also may influence fine-scale distribution if host fish have particular habitat preferences that influence their time spent in specific habitats (which could increase the probability of a juvenile mussel dropping off and settling in that habitat; Schwalb et al. 2015). However, because fish are relatively mobile, there may be stronger patterns of fine-scale co-occurrence over longer time scales and repeated sampling, or with experiments designed more appropriately to detect these types of cross-taxa interactions. Because mussels use several strategies, such as mantle lures or conglutinates that resemble prey items, to attract host fish during spawning, stronger co-occurrence patterns also may be observed during mussel reproductive periods (Haag 2012). We did observe that several host fish species co-occurred with mussels at the site, indicating the potential for interaction to occur, which is essential for completion of the mussel life cycle.

Our results provided some evidence of segregation of mussels and crayfish in transects that could become more apparent with additional sampling. Most research regarding mussel and crayfish interactions have focused on crayfish predation of mussels, which is unlikely to have influenced the individuals in our transects given the size classes observed during sampling (e.g., Klocker and Strayer 2004; Meira et al. 2019). Furthermore, mussels can increase macroinvertebrate prey abundance, stabilize substrate, and provide shelter or habitat which are all beneficial for crayfish (Vaughn 2018). Additional sampling could help clarify this relationship and its potential causes, and whether native crayfish species might exhibit contrasting patterns of co-occurrence with mussels. In addition, our methodology and lack of a control treatment make it difficult to separate the effects of habitat (i.e., shared habitat preferences) from the direct impact of taxa co-occurrence, which could also influence our ability to recognize clear patterns of co-occurrence.

Our use of video recording to capture abundance patterns is particularly suited to understanding co-occurrence and cross-taxa interaction, although we did not observe strong patterns of co-occurrence across fish, crayfish, and mussels. Sampling mobile taxa such as fish and crayfish simultaneously allows investigators to document the presence of organisms at the same point in time and space, which would be difficult or impossible with other sampling methods targeting individual taxa. As a result, this study provides a better understanding of how different organisms may directly share resources in habitats where they are observed together.

CONCLUSION

Although research at fine scales is lacking, the potential for interactions between taxa (and between organisms and their environment) is high at fine scales (Cushman and McGarigal 2004; Mehrabi et al. 2014). Hence, understanding fine-scale distribution patterns in relation to habitat and co-occurring organisms can help clarify important environmental or biological filters acting on multitaxa assemblages occurring in proximity. Our study demonstrated the utility of video-recorded transects for assessing multifaunal habitat and taxa associations, and our methods could be expanded easily to increase the accuracy and scope of riverine studies at fine spatial scales. Even with relatively limited sample sizes, our approach allowed us to detect fine-scale habitat associations for fish, crayfish, and mussels and investigate co-occurrence patterns across taxa. Understanding the patterns that occur at fine spatial scales can help inform management strategies that account for both the habitat requirements and species interactions that influence organism persistence in their immediate environment.

ACKNOWLEDGMENTS

Special thanks to Hanna Muntz (HM), Shay Keretz (SK), Michael Chatterton, Nathan Ring (NR), Scott LaValley, Alex Frankila (AF), and Meghan Martinski (MM) for assistance in organism collection and to HM, AF, and MM for assistance in video analyses. Thanks to SK and MM for assisting in fieldwork preparation. This study happened during the very beginning of the

COVID pandemic, and all work was successfully performed with the highest concern for researchers' health. Thanks to Mael Glon, Kevin Pangle, Kevin Keretz, SK, John Matousek, and NR for assistance with organism identification and to Kelly and Karen Cushway for access to the site. Mussels were collected under Michigan Scientific Collection permits obtained from the Michigan Department of Natural Resources. Finally, thank you to the Central Michigan University Honors Program and the Central Michigan University Department of Biology for providing funding for this project. Thank you to the FMBC editor, associate editor, and anonymous reviewers for their comments, all of which improved this manuscript. This paper is contribution #210 of the Central Michigan University Institute for Great Lakes Research.

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.

Bailey, R. M., W. C. Latta, and G. R. Smith. 2004. Fish Distribution Maps and Illustrations. Pp. 56–208 *in* J. B. Burch, J. Pappas, and K. Stefano, editors. An Atlas of Michigan Fishes with Keys and Illustrations for Their Identification. Miscellaneous Publication 192. Museum of Zoology, University of Michigan, Ann Arbor.

Banks, S. A., and G. A. Skilleter. 2007. The importance of incorporating fine-scale habitat data into the design of an intertidal marine reserve system. Biological Conservation 138:13–29.

Bird, C. T., M. D. Kaller, T. E. Pasco, and W. E. Kelso. 2022. Microhabitat and landscape drivers of richness and abundance of freshwater mussels (Unionida: Unionidae) in a coastal plain river. Applied Sciences 12:10300.

Bonferroni, C. E. 1936. Teoria statistica delle classi e calcolo delle probabilità. Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commerciali di Firenze 8:3–62.

Bruneel, S., L. Ho, W. Van Echelpoel, A. Schoeters, H. Raat, T. Moens, R. Bermudez, S. Luca, and P. Goethals. 2022. Sampling errors and variability in video transects for assessment of reef fish assemblage structure and diversity. PLoS One 17:e0271043.

Clark, K. H., D. D. Iwanowicz, L. R. Iwanowicz, S. J. Mueller, J. M. Wisor, C. Bradshaw-Wilson, W. B. Schill, J. R. Stauffer, Jr., and E. W. Boyer. 2022. Freshwater unionid mussels threatened by predation of round goby (*Neogobius melanostomus*). Scientific Reports 12:12859.

Collyer, M. L., and D. C. Adams. 2018. RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. Methods in Ecology and Evolution 9:1772–1779.

Cushman, S. A., and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon coast range. Ecological Applications 14:1090–1105.

Cushway, K. C., A. E. Harris, C. D. Piercy, Z. A. Mitchell, and A. N. Schwalb. 2024. Go with the flow: impacts of high and low flow conditions on freshwater mussel assemblages and distribution. PLoS One 19:e0296861.

Diamond, J. M. 1975. Assembly of species communities. Pp. 342–444 *in* M. L. Cody and J. M. Diamond, editors. Ecology and Evolution of Communities. Harvard University Press, Cambridge, Massachusetts.

Dorn, N. J., and G. G. Mittelbach. 1999. More than a predator and prey: A review of interactions between fish and crayfish. Vie et Milieu 49:229–237.

DuBose, T. P., C. C. Vaughn, G. W. Hopper, K. B. Gido, and T. B. Parr. 2024. Habitat engineering effects of freshwater mussels in rivers vary across spatial scales. Hydrobiologia 851:3897–3910.

Escofier, B., and J. Pagès. 1994. Multiple factor analysis (AFMULT package). Computational Statistics and Data Analysis 18:121–140.

Freshwater Mussel Host Database. 2017. The freshwater mussel host database, Illinois Natural History Survey & Ohio State University Museum of Biological Diversity, 2017. Available at http://wwx.inhs.illinois.edu/collections/mollusk/data/freshwater-mussel-host-database (accessed June 2024).

Friard, O., and M. Gamba. 2016. BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7:1325–1330.

Frontier, S. 1976. Etude de la decroisissance des valeurs propres dans une analyze en composantes principals: Comparison avec le modele de baton brise. Journal of Experimental Marine Biology and Ecology 25:67–75.

Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75:532–547.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621.

Gotelli, N. J., E. M. Hart, and A. M. Ellison. 2015. EcoSimR: Null model analysis for ecological data. R package version 0.1.0. Available at http://github.com/gotellilab/EcoSimR (accessed February 20, 2025).

Haag, W. R. 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge, United Kingdom.

Haag, W. R., and M. L. Warren, Jr. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. Canadian Journal of Fisheries and Aquatic Sciences 55:297–306.

Hart, R. A. 1995. Mussel (Bivalvia: Unionidae) habitat suitability criteria for the Otter Trail River, Minnesota. Master's thesis, North Dakota State University, Fargo.

Hernández, F. 2020. Ecological discord and the importance of scale in scientific inquiry. Journal of Wildlife Management 84:1427–1434.

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.

Jackson, D. A. 1993. Stopping rules in principal component analysis: A comparison of heuristical and statistical approaches. Ecology 74:2204–2214.

Kassambara, A. 2017. MFA-multiple factor analysis in R: Essentials. Available at http://www.sthda.com/english/articles/31-principal-component-methods-in-r-practical-guide/116-mfa-multiple-factor-analysis-in-r-essentials/ (accessed February 20, 2025).

Kassambara, A., and F. Mundt. 2020. Factoextra: Extract and visualize the results of multivariate data analyses. Available at https://CRAN.R-project.org/package=factoextra (accessed February 20, 2025).

Klocker, C. A., and D. L. Strayer. 2004. Interactions among an invasive crayfish (*Orconectes rusticus*), a native crayfish (*Orconectes limosus*), and native bivalves (Sphaeriidae and Unionidae). Northeastern Naturalist 11:167–178.

Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. Freshwater Biology 52:597–615.

Layzer, J. B., and L. M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regulated Rivers: Research and Management 10:329–345.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25:1–18.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lodge, D. M., M. W. Kershner, J. E. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral foodweb. Ecology 75:1265–1281.

Mallet, D., and D. Pelletier. 2014. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). Fisheries Research 154:44–62.

Manna, L. R., C. F. Rezende, and R. Mazzoni. 2017. Effect of body size on microhabitat preferences in stream-dwelling fishes. Journal of Applied Ichthyology 33:193–202.

Matsuzaki, S. S., N. Usio, N. Takamura, and I. Washitani. 2007. Effects of common carp on nutrient dynamics and littoral community composition: Roles of excretion and bioturbation. Fundamental and Applied Limnology 168:27–38.

Mehrabi, Z., E. M. Slade, A. Solis, and D. J. Mann. 2014. The importance of microhabitat for biodiversity sampling. PLoS One 9:e114015.

Meira, A., M. Lopes-Lima, S. Varandas, A. Teixeira, F. Arenas, and R. Sousa. 2019. Invasive crayfishes as a threat to freshwater bivalves: Interspecific differences and conservation implications. Science of the Total Environment 649:938–948.

Momot, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science 3:33–63.

Moore, J. W. 2006. Animal ecosystem engineers in streams. Bioscience 56:237–246.

Mulcrone, R. S., and J. E. Rathbun. 2020. Pocket Field Guide to the Freshwater Mussels of Michigan, 2nd ed. Michigan Department of Natural Resources, Lansing. 78 pp.

Noguiera, J. G., M. Lopes-Lima, P. Beja, A. F. Filipe, E. Froufe, D. V. Gonçalves, J. P. da Silva, R. Sousa, A. Teixeira, S. Varandas, and V. Hermoso. 2023. Identifying freshwater priority areas for cross-taxa interactions. Science of the Total Environment 864:161073.

O'Neal, R. P. 1997. Muskegon River watershed assessment. Fisheries Special Report 19. Michigan Department of Natural Resources, Lansing.

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.

Pennock, C. A., C. N. Cathcart, S. C. Hedden, R. E. Weber, and K. B. Gido. 2018. Fine-scale movement and habitat use of a prairie stream fish assemblage. Oecologia 186:831–842.

Polvi, L. E., and J. M. Sarneel. 2017. Ecosystem engineers in rivers: An introduction to how and where organisms create positive biogeomorphic feedbacks. WIREs Water 5:e1271.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichard, M., M. Polačik, A. Serhan Tarkan, R. Spence, O. Gaygusuz, E. Ercan, M. Ondračkova, and C. Smith. 2010. The bitterling-mussel coevolutionary relationship in areas of recent and ancient sympatry. Evolution 64:3047–3056.

Reynolds, J. D. 2011. A review of ecological interactions between crayfish and fish, indigenous and introduced. Knowledge and Management of Aquatic Ecosystems 401:102–1021.

Reynolds, J. D., C. Souty-Grosset, and A. Richardson. 2013. Ecological roles of crayfish in freshwater and terrestrial habitats. Freshwater Crayfish 19:197–218.

Rice, C. J., C. A. Taylor, D. A. Swedberg, and R. J. DiStefano. 2020. Targeted microhabitat sampling and its role in conserving endemic freshwater taxa. Freshwater Science 39:334–346.

Santangelo, J. S. 2019. Data simulation and randomization tests. NEON Faculty Mentoring Network, QUBES Educational Resources.

Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68:651–659.

Schneider, D. C. 2001. The rise of the concept of scale in ecology: The concept of scale is evolving from verbal expression to quantitative expression. BioScience 51:545–553.

Schwalb, A. N., and M. T. Pusch. 2007. Horizontal and vertical movement of unionid mussels in a lowland river. Journal of the North American Benthological Society 26:261–272.

Schwalb, A. N., T. J. Morris, and K. Cottenie. 2015. Dispersal abilities of riverine freshwater mussels influence metacommunity structure. Freshwater Biology 50:911–921.

Sestelo, M., N. M. Villanueva, and L. Roca-Pardinas. 2015. FWDselect: Selecting variables in regression models. R package version 2.1.0. Available at https://CRAN.R-project.org/package=FWDselect (accessed February 20, 2025).

Sestelo, M., N. M. Villanueva, L. F. Meira-Machado, and J. Roca. 2016. FWDselect: An R package for variable selection in regression models. R Journal 8:132–148.

Smith, K. R., B. M. Roth, M. L. Jones, D. B. Hayes, S. J. Herbst, and N. Popoff. 2019. Changes in the distribution of Michigan crayfishes and the influence of invasive rusty crayfish (*Faxonius rusticus*) on native crayfish substrate associations. Biological Invasions 21:637–656.

Spearman, C. 1904. The proof and measurement of association between two things. American Journal of Psychology 15:72–101.

Spooner, D. E., and C. C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. Freshwater Biology 51:1016–1024.

Statzner, B., E. Fievet, J. Y. Champagne, R. Morel, and E. Herouin. 2000. Crayfish as geomorphic agents and ecosystem engineers: Biological behavior affects sand and gravel erosion in experimental streams. Limnology and Oceanography 45:1030–1040.

Stelzer, R. S., and G. A. Lamberti. 1999. Independent and interactive effects of crayfish and darters on a stream benthic community. Journal of the North American Benthological Society 18:524–532.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia 85:74–79.

Vaughn, C. C. 2018. Ecosystem services provided by freshwater mussels. Hydrobiologia 810:15–27.

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., 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.

Vlach, P., D. Fischer, and L. Hulec. 2009. Microhabitat preferences of the stone crayfish *Austropotamobius torrentium* (Schrank, 1803). Knowledge and Management of Aquatic Ecosystems 15:394–395.

Wentworth, C. K. 1922. A scale of grade and class terms for classic sediments. Journal of Geology 30:377–392.

Zimmerman, G. F., and F. A. de Szalay. 2007. Influence of unionid mussels (Mollusca: Unionidae) on sediment stability: An artificial stream study. Fundamental and Applied Limnology 168:299–306.

Appendix 1. Species of fish identified as being present in Mecosta County, Michigan (the county containing the study site; Bailey et al. 2004). Species with one asterisk in front of the genus name were identified by experienced researchers from still images obtained using GoPro video recordings along twelve 20-m-long transects at ~0.25-, 0.5-, 0.75-, and 1.0-m depths ($n = 3$ for each depth) surveyed at a site in the Muskegon River, Michigan, USA, in August 2020. Species with two asterisks also were identified as potentially being present at the site and were historically found in the Muskegon River watershed, but not within Mecosta County. Not all organisms found along transects could be identified due to limitations in visual clarity or organism visibility.

Genus	Specific Epithet	Common Name
Ambloplites	*rupestris*	Rock Bass
Ameiurus	*melas*	Black Bullhead
Ameiurus	*natalis*	Yellow Bullhead
Ameiurus	*nebulosus*	Brown Bullhead
Campostoma	*anomalum pullum*	Central Stoneroller
Catostomus	*commersonii*	White Sucker
Cottus	*bairdii*	Mottled Sculpin
Culaea	*inconstans*	Brook Stickleback
***Cyprinus*	*carpio*	Common Carp
***Dorosoma*	*cepedianum*	Gizzard Shad
Esox	*americanus vermiculatus*	Grass Pickerel
Esox	*lucius*	Northern Pike
Etheostoma	*flabellare flabellare*	Barred Fantail Darter
**Etheostoma*	*caeruleum*	Rainbow Darter
**Etheostoma*	*exile*	Iowa Darter
Etheostoma	*microperca*	Least Darter
**Etheostoma*	*nigrum*	Johnny Darter
Hybognathus	*hankinsoni*	Brassy Minnow
Hypentelium	*nigricans*	Northern Hog Sucker
Ichthyomyzon	*castaneus*	Chestnut Lamprey
Lethenteron	*appendix*	American Brook Lamprey
Lepisosteus	*osseus*	Longnose Gar
Lepomis	*cyanellus*	Green Sunfish
Lepomis	*gibbosus*	Pumpkinseed
Lepomis	*macrochirus*	Bluegill
Lepomis	*peltastes*	Northern Longear Sunfish
Luxilus	*cornutus*	Common Shiner
Margariscus	*nachtriebi*	Northern Pearl Dace
**Micropterus*	*salmoides*	Largemouth Bass
***Neogobius*	*melanostomus*	Round Goby
Nocomis	*biguttatus*	Hornyhead Chub
Nocomis	*micropogon*	River Chub
Notemigonus	*crysoleucas*	Golden Shiner
Notropis	*anogenus*	Pugnose Shiner
***Notropis*	*atherinoides*	Emerald Shiner
Notropis	*dorsalis*	Bigmouth Shiner
Notropis	*heterodon*	Blackchin Shiner
Notropis	*heterolepis*	Blacknose Shiner
Notropis	*rubellus*	Rosyface Shiner
Notropis	*volucellus*	Mimic Shiner
Noturus	*flavus*	Stonecat
Noturus	*gyrinus*	Tadpole Madtom
Oncorhynchus	*mykiss*	Rainbow Trout
**Perca*	*flavescens*	Yellow Perch
***Percina*	*caprodes*	Logperch
**Percina*	*maculata*	Blackside Darter
Phoxinus	*eos*	Northern Redbelly Dace
Pimephales	*notatus*	Bluntnose Minnow
Pimephales	*promelas*	Fathead Minnow
Pomoxis	*nigromaculatus*	Black Crappie
**Rhinichthys*	*obtusus*	Western Blacknose Dace
Salmo	*trutta*	Brown Trout
Salvelinus	*fontinalis*	Brook Trout
Salvelinus	*namaycush*	Lake Trout
**Semotilus*	*atromaculatus*	Creek Chub
Umbra	*limi*	Central Mudminnow

Appendix 2. Length statistics for mussel species collected during transect sampling at a site in the Muskegon River, Michigan, USA, in August 2020. Species were measured to the nearest millimeter by using calipers.

Species	No. of Individuals	Minimum Length (mm)	Mean Length (mm)	Median Length (mm)	Maximum Length (mm)
Actinonaias ligamentina	12	57	89.3	89	107
Cambarunio iris	1	41	41	41	41
Eurynia dilatata	17	43	63.4	63	81
Fusconaia flava	1	56	56	56	56
Lampsilis cardium	2	25	45	45	65
Lampsilis siliquoidea	4	42	57	55.5	75
Lasmigona costata	1	75	75	75	75
Ligumia recta	1	114	114	114	114

Appendix 3. Spearman rank correlations of quantitative habitat variables with fish, crayfish, or mussel abundance observed in transects in the Muskegon River, Michigan, USA, in August 2020. The α value for tests for crayfish was corrected to 0.01, with Bonferroni correction due to multiple comparisons.

Taxa	Habitat Variable	S	*r*	*p*
Fish	Depth	434.84	−0.52	0.08
Crayfish	Sand	342.69	−0.20	0.54
	Pebble	225.36	0.21	0.51
	Cobble	271	0.05	0.87
	Boulder	316.59	−0.11	0.74
Mussels	Depth	280.91	0.018	0.96