Scale-Dependent Environmental Influences on Linked Mussel-Fish Assemblages in Big Darby Creek, OH

THESIS

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By

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Abstract

Freshwater mussels are considered to be the most imperiled group of animals in North America, yet the environmental factors that influence mussel assemblage structure and distribution are not fully resolved. The life cycle of freshwater mussels – whereby larvae are obligate ectoparasites on fishes and adults are benthic and sedentary – suggests that dispersal of mussels is linked to fish movement whereas growth and reproduction might be expected to be controlled by broad-scale environmental processes, thus adding to the complexity to mussel-environment relationships. A more thorough understanding of the responses of linked lotic mussel-fish assemblages to scale-dependent environmental characteristics is expected to improve both current ecological understanding as well as inform conservation and management.

To that end, my research investigated the relationships between (1) stream hydrogeomorphology and mussel and darter assemblages and (2) the relative influences of local- and catchment (i.e., landscape) -scale environmental factors on mussel assemblages in Big Darby Creek, OH. From July 2011 to October 2012, I surveyed mussel and fish assemblages, conducted geomorphic and habitat surveys, and measured water quality at twenty study reaches distributed over ~40 km of Big Darby Creek. For each stream reach, I also collected environmental data at local- (i.e., riparian land cover, stream hydrogeomorphic characteristics) and catchment- (i.e., drainage area; catchment land cover; modeled overland flow, sediment, and nutrient dynamics) scales. For the first
objective, principal component analysis (PCA) and stepwise multiple linear regressions were used to explore potential relationships between hydrogeomorphic variables and mussel and fish descriptors of the following assemblages: fish, darter, mussel, and mussels known to use darters as hosts. For the second objective, I used a partial constrained ordination approach to partition variation in the mussel assemblage dataset among fish, spatial, environmental, and shared (spatially-structured fish and environmental) factors.

At a coarse geomorphic resolution, density of the overall fish assemblage as well as the darter component of the fish assemblage \((p = 0.048, p = 0.024; \text{respectively})\) was greater at geomorphically adjusting reaches, whereas fish species richness was 1.2 times greater at equilibrium reaches \((p = 0.047)\). At a finer geomorphic resolution, eleven models emerged as significant. Across all models, hydrogeomorphic parameters explained from 20% (darter assemblage evenness) to 55% (density of mussels using darters as hosts) of the variation observed in mussel and fish assemblages. Drainage area was significant in almost every model. Other important variables included embeddedness, velocity, shear stress, roughness, channel dimensions, and sediment size.

I found that collectively, environmental, spatial, and fish datasets explained 99.2% of the variation observed in mussel assemblage structure. The shared component was the dominant predictor variable, explaining 40.1% of mussel assemblage variation, whereas fish density only accounted for 1.5%. The pure environmental component accounted for 31.5% of the variation, split relatively equally between local- (26.3%) and catchment- (32.4%) scale influences. Thus, although fish have been shown to be strong
predictors of mussel assemblages, in certain environmental contexts spatial and environmental factors at both fine and broad scales may be stronger determinants of mussel assemblage structure.

Overall, my results suggest that local-scale (i.e., reach level) environmental characteristics can be valuable in predicting linked mussel-fish assemblage distribution and structure. Whereas coarse-level geomorphic classifications may be meaningful for fish, they appear to be less so for mussels. Finer-resolution quantitative geomorphic variables provided substantially more information for both fish and mussel assemblages. However, findings from my thesis also indicate that a singular focus on local-scale environmental variables may underestimate the importance of broad-scale processes (e.g., dispersal, catchment-scale hydrology, land use and land cover). Collectively, my results show a strong influence of scale-dependent environmental factors on freshwater mussel assemblages, suggesting that conservation and management schemes including reintroduction efforts will benefit from approaches that combine reach- and catchment-level assessments, as well as the dynamics of cohabitating fish assemblages.
Dedication

I would like to dedicate this thesis to my loving husband, Daniel Bey, without whom I would never have made it this far. Thank you for putting up with my late nights of working, my monopolizing the computer, one never-ending yet unforgettable canoe trip, building my quadrats, and enduring my many days out in the field. Thank you for your support and your constant positive encouragement.
Acknowledgments

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Thanks to Dr. Thomas Watters, who as my boss and member of my committee has been very understanding of my situation and provided invaluable insight along the way. Thanks to Dr. Stephen Matthews, for serving on my committee and contributing appreciated advice.

Finally, many thanks and much appreciation to Dr. Mažeika Sullivan for the enormous amount of help and patience he has provided. This experience has been
priceless because of his encouragement and I hope that someday I will have even half of his knowledge and experience. Sincere thanks to all.
Vita

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Fields of Study

Major Field: Environment and Natural Resources
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Chapter 1: Background and Literature Review

Freshwater mussels are currently recognized by the US Fish and Wildlife Service as the most imperiled group of animals in North America (Master 1990, Williams 1993, Lydeard et al. 2004, Haag 2012). Of the approximately 80 species in Ohio, over half are endangered, extirpated, or extinct (Watters et al. 2009). Of the 44 species in Big Darby Creek, a National Wild and Scenic River of central OH, 23 are rare or declining throughout the state. Of the 12 species of the darters in the genus *Etheostoma* in OH, one is listed as state endangered, and two are listed as state threatened.

Multiple factors have contributed to declines in mussel populations. Mussels are especially sensitive to habitat impairment, water pollution, and increased sedimentation of stream and river channels (Diamond et al. 2002, Gillies et al. 2003, Gagnon et al. 2006, Gangloff and Feminella 2007, Strayer 2008, Gangloff et al. 2009, Hopkins and Burr 2009). Habitat fragmentation, including dams, is also a major factor leading to the decline of mussel populations (Vaughn and Taylor 1999, Doyle et al. 2005). Conversely, mussels have been shown to play a role in improving the quality of their habitat, including increasing stability of the substrate (Johnson and Brown 2000) and influencing water quality through feeding and respiration (Vaughn et al. 2004).

In their larval stage, freshwater mussels are obligate ectoparasites, and their host organism is almost always a fish (Watters et al. 2009). Some species of mussels are host-
generalists, while other species are host-specific such that they can only successfully parasitize one family or species of fish.

In order to best conserve freshwater mussels, a more complete understanding of how mussels respond to both local (i.e., reach-level) and landscape (i.e., catchment-level) changes in their physical environment is needed. Improved knowledge of the links among watershed attributes (e.g., land cover; timing and amounts of water, nutrient and sediment input); local stream hydrogeomorphic (e.g., channel adjustment, channel dimensions, substrate and flow dynamics) and riparian characteristics; and the quality, extent, location, and distribution of mussels and high-quality mussel habitat will be critical to fully integrate conservation and restoration efforts into a broader framework (Newton et al. 2008). Linking this work with host fish populations will also be crucial for long-term success of conservation efforts.

**Unionid Life History**

*General Life History*

Unionid bivalves, or freshwater mussels, have a unique life history that presents complex challenges to conservation and restoration efforts. Freshwater mussels are filter feeders that gather food from the water column. Primary food sources continue to be a source of debate, but they are thought to include diatoms, algae, zooplankton, and bacteria (Allen 1914, 1921, Churchill and Lewis 1924, Fikes 1972, Imlay and Paige 1972, Bisbee 1984, Nichols and Garling 1998). Mussels in North America lack true siphons, or tubes, for water intake and release and for food-gathering and respiration. The
lack of a siphon constrains their feeding activities to burrowing to the posterior edge of the shell, which increases their susceptibility to predators, desiccation, and temperature or other environmental extremes (Watters et al. 2009). Unionids are obligate ectoparasites as larvae, and almost always require a fish as the host organism. The Salamander Mussel (Simpsonaias ambigua) is the exception as its host is the common mudpuppy (Necturus maculosus) (Howard 1915, 1951). Hosts are infested with glochidia (larval mussels) when they come into contact with mussels or when attempting to ingest them (Watters et al. 2009) (Figure 1).
Figure 1. Freshwater Mussel Life Cycle, showing glochidia transferred from the female mussel to the host fish, and the metamorphosed juvenile mussels excysting and establishing themselves in the substrate to grow into adult mussels. (With permission from G.T. Watters).

Mussel species have varying methods of releasing glochidia and attracting host fishes. Some simply expel the glochidia along with waste products into the water. Others (e.g., Flat Floater [Anodonta suborbiculata], Cylindrical Papershell [Anodontoides ferussacianus], and Paper Pondshell [Utterbackia imbecillis]), release “webs” or “trot lines” of mucus containing glochidia that ensnare passing fishes (Hove 1995, Watters and O'Dee 1997b). Other mussels unite glochidia into matrices called conglutinates (Chamberlain 1934, Fuller 1971) and still other species combine conglutinates into a
single lure called a superconglutinate (Haag et al. 1995, Hartfield and Butler 1997). Glochidia clamp down on the host tissue subsequently using the host for food (Arey 1924, Blystad 1924, Arey 1932) and for dispersal for a period ranging from days to months (Watters et al. 2009), during which they metamorphose into juveniles (Schierholz 1889, Howard and Anson 1923) and later excyst, drop off the fish, and burrow into the substrate (Bauer 1986, Clarke 1986, Buddensieck et al. 1993) or attach to a larger object with a byssal thread (Watters et al. 2009).

Host specificity differs greatly among species of mussels. Some species are able to parasitize many species of fishes (Trdan 1981, Watters and O'Dee 1997a, 1998, Watters et al. 2009), and these mussel species are usually widespread and abundant (e.g., Giant Floater [Pyganodon grandis grandis], Fatmucket [Lampsilis radiata luteola]) (Watters et al. 2009). Other species of mussels (Scaleshell [Leptodea leptodon], Rayed Bean [Villosa fabalis]) may use only a few species of fish, and these species are usually localized and rare (Watters et al. 2009). This symbiosis, therefore, requires conservation and management efforts that consider host dynamics as well.

_Fishes as hosts_

Many correlations have been drawn between fish species richness and mussel species richness (Watters 1992, Vaughn and Taylor 2000). Haag and Warren (1998) found that fish species richness explained densities of mussels better than microhabitat variables did, as did the strategy used by the mussel for infesting host fishes. Some species of mussels are host generalists, whereas others are host specialists that can only
use one group of fishes, or in some cases only a single fish species (only reported host for Scaleshell is Freshwater Drum \textit{[Aplodinotus grunniens])} (Watters et al. 2009). Mussels have various ways of transferring the glochidia to the appropriate host. Mussel species have evolved an array of strategies by which the gravid females aid infestation of a host fish by glochidia, including modified mantle flaps and strands of mucus. In a study in Alabama, USA, Haag & Warren (1998) found that densities of host-specialist mussels with elaborate host-attracting mechanisms and host-generalist mussels were independent of host fish densities and these mussels were present throughout the drainage studied. However, densities of host-specialist mussels without elaborate host-attracting mechanisms were correlated positively with host fish densities and were absent or rare in headwater and mid-reach streams (Haag and Warren 1998).

\textbf{Ecogeomorphology}

Fluvial geomorphology has occupied a central role in the development of the field of stream ecology. The hydraulic and geomorphic stream channel adjustments along a river proposed by Leopold and his colleagues (Leopold and Maddock 1953, Leopold et al. 1964, Langbein and Leopold 1966), formed the basis for the physical construct of Vannote et al.’s (1980) River Continuum Concept (RCC) as well as an analog on which to frame their predictions of energy flow along the drainage network. In spite of the long-standing recognition of fluvial geomorphology as a physical driver of streams, explicit investigation and quantification of relationships between the form and physical processes of streams and their associated biota have only begun to receive significant attention in
recent years (Walters et al. 2003, Sullivan et al. 2006, Vaughan et al. 2009). Integrating fluvial geomorphology and stream ecology has the potential to go beyond describing the physical template of stream networks upon which lotic ecosystems organize themselves. Specifically, the linked structural-mechanistic potential among hydrology, geomorphology, and ecology has not been fully explored, but represents the essence of an ecogeomorphic approach and a powerful emerging ecological standard.

Streams are formed, maintained, and changed by the water and sediment they carry (FISRWG 1998). Channel size is controlled by four main factors: sediment discharge, bed sediment particle size, stream flow, and stream slope (Lane and Richards 1997). These variables interact across multiple dimensions (i.e., channel geometry is three dimensional; consisting of a longitudinal profile, a lateral cross-sectional profile, and plan view). Channel equilibrium occurs when all four factors are balanced. Equilibrium is lost when one of the variables changes, requiring one or more of the other variables to increase or decrease proportionally to maintain the equilibrium. When the channel loses equilibrium due to the formidable force of water and sediment, it can lead to significant changes in river channel form and structure (Pizzuto et al. 2000, Hession 2001). Many fluvial morphologists, consequently, divide streams into two categories:

1) *Equilibrium/Stable Rivers* (banks change very little, minimal alteration in course from year to year, move water and sediment load in balance, minor natural erosion, and

2) *Adjusting/Unstable Rivers* (change course by meters per year, often cut new channels, large sections of collapsing banks, widen and/or cut deeper into
channel, sand and sediment fill natural pools). The changes in a river that signify unstable rivers, or instability, can be divided into four categories: changes in planform, widening, degradation/incision, and aggradation (Table 1).

Table 1. Field indicators of geomorphic condition. (From Sullivan et al. [2006], with permission).

<table>
<thead>
<tr>
<th>Field indicators of lateral adjustment</th>
<th>Over-widening: erosion of banks creating a widened channel form</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change in planform: formation of new channel direction with change in slope</td>
<td>Over-widening: erosion of banks creating a widened channel form</td>
</tr>
<tr>
<td>Flood chutes or chute cut-offs</td>
<td>Leaning trees or trees falling into river</td>
</tr>
<tr>
<td>Evidence of channel avulsions</td>
<td>Erosion on both sides of the banks in a riffle section</td>
</tr>
<tr>
<td>Loss of structure and homogenization of form</td>
<td>Recently exposed tree roots</td>
</tr>
<tr>
<td>Multiple thread channels</td>
<td>Many bank overhangings</td>
</tr>
<tr>
<td>Formation of islands</td>
<td>Fracture lines at the top of the bank</td>
</tr>
<tr>
<td>Thalweg not aligned with planform</td>
<td>Deposition of mid-channel bars and shoals</td>
</tr>
<tr>
<td>Presence of berms and floodplain developments</td>
<td>High width to depth ratio</td>
</tr>
<tr>
<td>Meander pattern changes in reach</td>
<td>Moderately entrenched</td>
</tr>
<tr>
<td>Runs only or riffles that are partial or transverse</td>
<td>Presence of mid-channel bars</td>
</tr>
<tr>
<td>Atypical riffles spacing</td>
<td>Presence of channelization</td>
</tr>
<tr>
<td>Bank erosion on outside bends</td>
<td></td>
</tr>
<tr>
<td>Presence of channelization</td>
<td></td>
</tr>
</tbody>
</table>

Field indicators of vertical adjustment

| Degradation/incision: lowering of channel bed elevation through scour of channel bed | Aggradation: elevation of channel bed through sediment accumulation |
| Exposed till or fresh substrate in streambed | High degree of embeddedness |

Continued
Table 1 (cont’d). Field indicators of geomorphic condition. (From Sullivan et al. [2006], with permission).

| Recently abandoned terraces along the banks | Loss of diversity in velocity/depth regime & pool quality |
| Nickpoints or headcuts in the stream channel | Greater sediment deposition |
| Fresh vertical faces along the bank | Increased channel bed exposure during low flow periods |
| Alluvial sediments that are imbricated high in the bank | High width to depth ratio |
| Tributary rejuvenation | Partial riffles or runs only |
| Bar formation with steeply-cut faces | Plane bed stream type (in unconfined valleys) |
| Inactive floodplain | Homogenous gravel/sand substrates |
| Semi- to narrowly-confined channel | Regulated flow |
| Lack of grade controls | |
| Highly or moderately entrenched (<2.2) | Presence of mid-channel or diagonal bars |
| Flow regulated | Presence of chute cutoffs or channel avulsions |
| Presence of chute cutoffs | Evidence of gravel mining |
| Presence of nickpoints and headcuts, gravel mining, or channelization | |

To ecologists, fluvial geomorphology continues to provide insight into the complexity of physical, chemical, and hydraulic conditions of stream channels. However, the precise nature of many geomorphic-biotic associations remains elusive and largely undocumented (Urban and Daniels 2006). Developments thus far mostly contribute to an understanding of the relationships between fluvial geomorphology and structural aspects...
of stream assemblages (e.g., richness, diversity, composition, biomass, density, etc.). For example, numerous studies have now found strong associations between stream geomorphology and various descriptors of stream invertebrate (Brussock and Brown 1991, Olsen et al. 2001, Sullivan et al. 2004, Thomson et al. 2004, Wilcox et al. 2008) and fish (Peterson and Rabeni 2001, Walters et al. 2003, D'Ambrosio et al. 2009) assemblages.

The explicit union of fluvial geomorphology and stream ecology (Figure 2) has only recently come to be recognized in its own right (e.g., biogeomorphology, ecohydraulics, ecogeomorphology, hydrogeomorphology) (Rice 1989, Sidle and Onda 2004, Stallins 2006, Vaughan et al. 2009, Poole 2010, Rice et al. 2010), but as such, has strong potential to make significant contributions to both ecological and applied aspects of stream and river science (Poole 2010). Particularly, the strong relationships between geomorphology and structural stream ecosystem characteristics suggest that functional linkages may be equally as strong. Sheldon and Thoms (2006) found that reduced geomorphic complexity in large rivers was related to decreased retention of in-stream organic matter. Richardson et al. (2009) modeled the interaction between leaf interception and entrainment processes in small streams in British Columbia, Canada. Recently, Sullivan (2013) found that stream geomorphic characteristics and δ¹³C of stream food webs were tightly linked in mountain streams of Idaho, USA.
Mussels are sensitive to a wide variety of environmental changes (Williams 1993) and intimately linked to channel hydraulics and sediment transport. Thus, mussels represent an appropriate taxonomic group to study the linkages among hydrology, geomorphology, and biology (Howard and Cuffey 2003). Whereas we know that local-scale hydrogeomorphic conditions can be important drivers of mussel assemblage characteristics, further research is necessary to resolve the nature of these relationships, especially considering linked responses with host fish communities.

Environmental influences across spatial scales
Because watersheds are thought to operate as a nested hierarchy of spatial scales (Allen and Starr 1982, Vaughn and Taylor 2000, Brierley et al. 2006), factors at the broader scale (e.g., catchment or landscape) influence those at the local scale (e.g., reach). The relative influences of local- and catchment-scale environmental characteristics on mussels will be an important step in further understanding mussel ecology and in informing conservation efforts.

SPATIAL VARIABILITY

DISPERsal Fish Hosts

LOCAL

Figure 3. Hypothesized hierarchy of constraints influencing mussel community structure. Adapted from Vaughn and Taylor (2000).

Figure 4. Conceptual view of spatial environmental levels affecting freshwater mussel assemblages.
Local-scale mussel-environment relationships

Table 2. Summary of local-scale mussel-environment relationships.

<table>
<thead>
<tr>
<th>Mussel Species</th>
<th>Study Area/System</th>
<th>Major Finding</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lampsilis radiata siliquoidea</em></td>
<td>Inner Long Point Bay, Lake Erie, Canada</td>
<td>Mussels in more exposed areas of the bay (more turbulence and sandier sediments) had thicker shells.</td>
<td>Bailey and Green 1988</td>
</tr>
<tr>
<td><em>Elliptio complanata, E. icterina, Toxolasma parvulus, Villosa lienosa, V. vibex</em></td>
<td>Apalachicola, Chattahoochee, and Flint river basins, southern USA</td>
<td>No associations among mussel presence and porosity, mean particle size, fraction of fine sediments, and sorting.</td>
<td>Box et al. 2002</td>
</tr>
<tr>
<td><em>Velesunio ambiguus, Hyridella depressa, H. australis</em></td>
<td>Hawkesbury-Nepean River (New S. Wales) Australia</td>
<td>River flow rates at sampling sites were not correlated with mussel distribution.</td>
<td>Brainwood et al. 2008</td>
</tr>
<tr>
<td><em>Elliptio complanata, Pyganodon grandis grandis</em></td>
<td>Experimental basins, Lac Croche water, Canada</td>
<td>In an experimental study, mussels migrated toward muddy patches, and the authors postulated that mussel distribution in lakes was influenced most strongly by factors other than sediment composition.</td>
<td>Downing et al. 2000</td>
</tr>
<tr>
<td>Multiple species</td>
<td>Coosa River catchment, Alabama, USA</td>
<td>Mussel abundance was related to stream geomorphology, whereas richness was related to stream size. Both measures were highly correlated with mean current velocity or stream size.</td>
<td>Gangloff and Feminella 2007</td>
</tr>
<tr>
<td>Multiple species</td>
<td>Chewacla Creek, Alabama, USA</td>
<td>Mussel abundance decreased with degraded habitat &amp; water quality downstream of highly urbanized tributaries.</td>
<td>Gangloff et al. 2009</td>
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<thead>
<tr>
<th>Mussel Species</th>
<th>Study Area/System</th>
<th>Major Finding</th>
<th>Citation</th>
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<tbody>
<tr>
<td>Multiple species</td>
<td>Sipsy Fork and Brushy Creek drainages, Alabama, USA</td>
<td>Mussel community composition was better explained by patterns in variability in the fish community and the type of strategy used by mussels for infecting host-fishes than by patterns of variability in microhabitat.</td>
<td>Haag and Warren 1998</td>
</tr>
<tr>
<td>Multiple species</td>
<td>Green, Rough, and Licking Rivers, Kentucky, USA</td>
<td>Water depth and mussel density were positively correlated in the Green River, negatively correlated in the Rough River, and not significantly correlated in the Licking River. Mussel density was negatively correlated in all rivers with shear velocity and FließWasserStammtisch (FST) hemisphere number.</td>
<td>Hardison and Layzer 2001</td>
</tr>
<tr>
<td><em>Margaritifera margaritifera</em></td>
<td>Spey River, Scotland</td>
<td>Mussels were found to be positively associated with boulder/cobble river bed substrates and channel flow types. Negative associations with gravel-pebble/silt substrates and emergent reeds/sedges/herbaceous were also found.</td>
<td>Hastie et al. 2003</td>
</tr>
<tr>
<td><em>Margaritifera falcata,</em></td>
<td>South Fork Eel River, California, USA</td>
<td>In all flow regimes, mussels were found in areas of lower boundary shear stresses and lower velocities.</td>
<td>Howard and Cuffey 2003</td>
</tr>
<tr>
<td><em>Anodonta californiensis</em></td>
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<tr>
<td><em>Margaritifera hembeli</em></td>
<td>Bayou Rigolette, Bayou Rapides, and Bayou Bouef drainages, Louisiana, USA</td>
<td>Mussel density was related to water depth, substrate size, substrate compaction, &amp; water velocity.</td>
<td>Johnson and Brown 2000</td>
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<tr>
<td>Multiple species</td>
<td>Horse Lick Creek, Kentucky, USA</td>
<td>High shear stress was strongly associated with low mussel densities. However the relationships between shear stress and density was more variable for shear stresses &lt; 40 dyn cm$^{-2}$.</td>
<td>Layzer and Madison 1995</td>
</tr>
<tr>
<td>Multiple species</td>
<td>River Raisin catchment, Michigan, USA</td>
<td>Sites with high mussel diversity were found to have higher habitat quality, less fine substratum, and higher flow stability.</td>
<td>McRae et al. 2004</td>
</tr>
<tr>
<td>Multiple species</td>
<td>Middle Allegheny River, Pennsylvania, USA</td>
<td>There were highly significant positive correlations between mussel density and instream cover, embeddedness, velocity/depth, and sediment deposits.</td>
<td>Nicklin and Balas 2007</td>
</tr>
<tr>
<td>35 Species</td>
<td>Multiple streams throughout Iowa, USA</td>
<td>Correlation analyses linked greatest declines to rarity of streamside woodlands, high siltation, and most intensive agricultural landscapes.</td>
<td>Poole and Downing 2004</td>
</tr>
<tr>
<td><em>Elliptio complanata</em>, <em>Alasmidonta varicosa</em>, <em>A. heterodon</em>, <em>Strophitus undulatus</em>, <em>Anodonta implicata</em>, <em>A. undulate</em></td>
<td>Neversink River, southeastern New York, USA</td>
<td>Weak associations were observed between mussel occurrence and microhabitat variables including water depth, roughness, % gravel, % coarse sand, % medium sand, % fine sand, and % silt/clay.</td>
<td>Strayer and Ralley 1993</td>
</tr>
<tr>
<td>34 Species</td>
<td>Clinton, Rouge, Huron, and Raisin River drainages, Michigan, USA</td>
<td>Stream size and surface geology were the two major environmental features that predicted the distribution of mussels.</td>
<td>Strayer 1983</td>
</tr>
<tr>
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<tr>
<td><em>Elliptio complanata,</em> <em>Strophitus undulatus,</em> <em>Alasmidonta undulata,</em> <em>Ligumia nasuta,</em> <em>Lampsilis radiata,</em> <em>Pyganodon cataracta,</em> <em>Alasmidonta varicosa,</em> <em>Alasmidonta heterodon,</em> <em>Anodonta implicate</em></td>
<td>Neversink River and Webatuck Creek, southeastern New York, USA</td>
<td>Mussels were found mainly in stable areas of the riverbed where hydraulic stresses during floods were low.</td>
<td>Strayer 1999</td>
</tr>
<tr>
<td>Multiple species</td>
<td>Red River drainage, Oklahoma, USA</td>
<td>Pure spatial and environmental effects accounted for 16.1% and 7.8% of the variation in mussel assemblages, respectively.</td>
<td>Vaughn and Taylor 2000</td>
</tr>
</tbody>
</table>
Although the composite influence of stream geomorphic characteristics (and stream geomorphic adjustment) on mussel assemblages is poorly resolved, recent studies have found strong relationships between geomorphology and fish assemblages. For example, Sullivan et al. (2006) found that geomorphic conditions of the stream were linked to diversity, production, and condition of fishes. Cianfrani et al. (2009) found that stream morphological type (i.e., pool-riffle, cascade, etc.) was related to fish assemblage diversity in VT streams. Given these established geomorphology-fish relationships, the potential for local-scale geomorphology-mussel relationships is strong.

*Catchment-scale mussel-environment relationships*

Despite strong relationships between mussels and local-scale environmental characteristics, many other studies have found links between variables at the catchment scale and descriptors of freshwater mussel assemblages. Catchment size and stream size have been linked to mussel richness (Strayer 1983, Watters 1992, Haag and Warren 1998, Gangloff and Feminella 2007). Multiple studies have linked mussel occurrence and density to land use and land cover (LULC) in the catchment. For example, Gagnon et al. (2006) found that LULC (i.e., wetland and catchment forest cover, average mid-channel depth, and drainage network position) explained abundance and richness of mussels in Georgia, USA. Poole and Downing (2004) found that landscape factors including streamside woodlands, high siltation, and intensive agricultural land uses better explained variation in mussel distribution than biotic factors in Iowa, USA. Areas with intensive agriculture tended to have fewer mussels and lower diversity (Hoggarth et al. 1995), and
contributed to mussel species richness decline (Poole and Downing 2004). Mynsberge et al. (2009) found that presence/absence of mussels differed according to the number of downstream dams and the catchment dam density. Hastie et al. (2003) found positive relationships with aquatic liverworts/mosses/lichens, broadleaf/mixed woodland/bankside tree cover, and a negative relationship with emergent reeds/sedges/herbs. In the Hawkesbury-Nepean River, Australia, areas of low human modification were linked to increased mussel density and disturbance of vegetation in the riparian zone was related to mussel abundance (Brainwood et al. 2008). Gillies et al. (2003) linked an increase in impervious surface area to an increase in mussel community impairment.

**Study system - Big Darby Creek**

Big Darby Creek drains approximately 1450 km² in central Ohio, and is a principal tributary of the Scioto River (Figure 5). Big Darby Creek flows for 127 km from its headwaters in Logan County, OH to its confluence with the Scioto River in Pickaway County, OH. There is one dam on the river, located in the upper half of the river system (39.93 N, 83.23 W). Land use in the basin is mostly row crop agricultural (73%), except for the catchment’s suburbanizing eastern edges along the borders of Madison and Franklin counties (2005). Groundwater feeds numerous tributaries at the headwaters and this cool water provides base flow in times of drought and buffers water chemistry and stream biology from some of the harsher impacts of human disturbances (EPA 2004). Coarse glacial deposits (gravels and cobbles) are common in the valleys of
lower Big Darby Creek. This material, combined with the natural stream gradient, creates excellent streambed habitat for a wide diversity of plants and animals (2006).

According to the Ohio EPA (EPA 2006), all sites sampled on the main stem of Big Darby Creek fully met all applicable biocriteria of the Total Maximum Daily Load (TMDL) report. Any causes of impairment in the catchment were listed as low dissolved oxygen (from groundwater, septic systems, and package plants), nutrients (from septic systems, row crop agriculture, suburban runoff, and package plants), siltation (from construction and hydro-modification), unionized ammonia (from package plants and septic systems), and sediment metals (from unknown sources). The most downstream portion of Big Darby Creek (from Darbydale to the Scioto River) has had an occurrence of conspicuous algal mats in recent years at locations where the stream canopy has permitted sunlight to reach the water’s surface, which suggests that lower Big Darby Creek receives increasing nutrient loads (EPA 2006). The report also mentioned that changes in hydrology have resulted in destabilization of the streambed making it hostile to bivalve molluscs.

The Ohio Department of Natural Resources (ODNR) has classified 82 miles of the Big and Little Darby Creeks (a major tributary of Big Darby Creek) as State and National Scenic Rivers. The Nature Conservancy has designated Big Darby Creek as one of the “Last Great Places” in the western hemisphere (Cormier and Smith 1996).

There are two parks in the Central Ohio Parks System located along Big Darby Creek (Prairie Oaks Metro Park [~2,000 acres] and Battelle Darby Metro Park [7,000 acres]; 2009). The catchment contains among the most biologically diverse streams of
similar size in the US Midwest (2005). There are ~ 100 species of fishes recorded from Big Darby Creek and ~ 44 species of freshwater mussels; many of both taxa are listed as ‘rare’ (Franklin County Metro Parks 2009). Among these rare species are the Spotted Darter (*Etheostoma maculatum*), Banded Darter (*E. caeruleum*), Tippecanoe Darter (*E. tippecanoe*), Northern Riffleshell (*Epioblasma torulosa rangiana*), Snuffbox (*E. triquetra*), and Rabbitsfoot (*Quadrula c. cylindrica*).

Figure 5. Big Darby Creek Watershed in central OH, USA. Dots represent study reaches.
Summary and Objectives

In order to conserve freshwater mussel populations, a more complete understanding of how mussels respond to changes in their physical environment across spatial scales is needed. The overarching goal of this research is to explore linkages between stream hydrogeomorphic characteristics and mussel assemblages within a model river system, Big Darby Creek. Because different factors and responses might be expected at different scales, I will explicitly address environmental-mussel and environmental-fish relationships both at the local, reach scale as well as at the broader, catchment scale. I will also consider responses to environmental characteristics of the linked fish communities on which mussels rely. In particular, this thesis addresses (i) the relationships between stream hydrogeomorphic characteristics and linked mussel-fish assemblage diversity, distribution, and density (Chapter 2) and (ii) the relative influences of catchment environmental characteristics (i.e., land use and land cover [LULC], catchment erosion, runoff, and nutrients) and local characteristics (i.e., stream geomorphology, habitat, riparian land cover), on mussel assemblage diversity, distribution, and density (Chapter 3). Chapters 2 and 3 represent manuscripts that will be submitted for publication in ecological journals. A subset of these data (geomorphology and fish datasets) was collected in collaboration with Kristi Harraman’s thesis work. This work was collected under animal use IACUC protocol numbers 2009A0215-R1 and 2010A0000172. I anticipate that this research will help resolve unknown relationships among both local- and catchment- scale environmental characteristics and linked freshwater mussel-fish assemblages across ecologically-meaningful spatial scales.
References


2006. Total Maximum Daily Loads for the Big Darby Creek Watershed. *in* Division of Surface Water, Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.


D'Ambrosio, J. L., L. R. Williams, J. D. Witter, and A. Ward. 2009. Effects of geomorphology, habitat, and spatial location on fish assemblages in a watershed in Ohio, USA. Environmental Monitoring and Assessment **148**:325-341.


Franklin County Metro Parks. 2009. Battelle Darby Creek. *in* Franklin County Metro Parks, editor., Ohio, USA.


Howard, A. D. 1915. Some exceptional cases of breeding among the Unionidae. The Nautilus 29:4-11.


OEPA. 2004. Darby at the Crossroads: A Summary of Ohio EPA's Work and Collaboration to Protect and Restore an Important Water Resource. in Division of Surface Water, Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.

OEPA. 2006. Total Maximum Daily Loads for the Big Darby Creek Watershed. in Division of Surface Water, Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.


Chapter 2: Associations between stream hydrogeomorphology and linked mussel-fish assemblages in central Ohio, USA

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Abstract

1. Understanding linkages among fluvial geomorphology, habitat, and aquatic biota is critical for effective stream ecosystem conservation. However, the composite effects of geomorphic adjustment and condition on freshwater mussel and stream fish assemblages remain unresolved.

2. Stream hydrogeomorphic characteristics (channel geometry, substrate composition, slope) were surveyed and linked to freshwater mussel and stream fish assemblages at 20 study stream reaches characterized by riffle-pool interfaces (RPI) in central Ohio, USA.

3. Principal component analysis (PCA) and multiple linear regression were used to explore correlations between hydrogeomorphic factors and descriptors of the following assemblages: fish, darter, mussel, and mussels known to use darters as hosts (mussel$_{darter}$).

4. At a coarse resolution using categorical classifications of equilibrium vs. adjusting RPIs, density of the overall fish assemblage ($p = 0.048$) as well as the darter assemblage ($p = 0.024$) were greater at adjusting RPIs. Conversely, fish species richness was 1.2x greater at equilibrium than adjusting RPIs ($p = 0.047$).

5. Analysis of detailed quantitative hydrogeomorphic data collected at a finer-resolution of geomorphic surveys revealed eleven significant models. Across all models, hydrogeomorphic parameters explained from 20% (darter assemblage evenness) to 55% (density of mussel$_{darter}$) of the variation observed in mussel and fish assemblages.

Drainage area was significant in most models but with variable influence: $R^2 = 0.10$ for
richness of darter assemblage to $R^2 = 0.41$ for Simpson’s index of mussel$_\text{darter}$. Other important predictor variables included embeddedness, velocity, shear stress, roughness, channel dimensions, and sediment size.

6. Collectively, our results suggest that fluvial geomorphic condition and characteristics can simultaneously influence interdependent stream biota. Whereas coarse-level geomorphic classifications may be meaningful for fish, they appear less so for mussels. Finer-resolution quantitative geomorphic variables provided substantially more information for both assemblages, although geomorphic-fish and geomorphic-mussel relationships were not consistent. Some of the strongest relationships related to components of the mussel community that use darters as hosts, suggesting that these species are particularly sensitive to hydrogeomorphic conditions.

**Keywords:**

Darters, channel equilibrium, hydrogeomorphology, freshwater mussel assemblages, riffle-pool interface, stream fish assemblages

**Introduction**

The integration of fluvial geomorphology, habitat, and aquatic biota is becoming increasingly recognized as a powerful framework for stream ecosystem science and conservation (reviewed in Vaughn et al. 2009, Poole 2010). Many studies have examined linkages between stream geomorphology and benthic macroinvertebrate density, diversity, and community composition (Sullivan et al. 2004, Sullivan and Watzin 2008,
Friberg et al. 2009). Multiple fluvial geomorphic features such as channel bedform, flow variability, and embeddedness have also been implicated as important factors governing fish assemblage diversity (Waters 1995, Cianfrani et al. 2009), composition (Berkman and Rabeni 1987, Sullivan et al. 2006), and distribution (Baxter and Hauer 2000, Fukushima 2001). Furthermore, stream geomorphic properties including substrate size, shear stress, and channel gradient have emerged as strong predictors of freshwater unionid mussel abundance (Strayer and Ralley 1993, Hastie et al. 2003, Gangloff and Feminella 2007), density (Layzer and Madison 1995, Johnson and Brown 2000), and species richness (Vaughn and Taylor 2000).

However, despite a developing understanding of the influence of geomorphic characteristics on stream biotic communities, the composite effects of geomorphic adjustment and condition remain unresolved (sensu Sullivan et al. 2006). Collectively, adjustment and condition describe channel stability (i.e., dynamic equilibrium) and may have serious consequences for stream biota that are intimately linked to their physical environment (Sullivan et al. 2004). Because of shared habitat requirements, trophic relationships, and life-history interdependencies, the influences of fluvial geomorphology on linked biotic assemblages are also likely, although this notion has received little attention to date (but see Wright and Li 2002, Sullivan and Watzin 2008).

Freshwater mussels may be especially susceptible to geomorphic change. As obligate ectoparasites in the larval stage, freshwater mussels require a host organism - almost always a fish (in one known case is the Common Mudpuppy, *Necturus maculosus*) (Watters et al. 2009). Their reliance on host fishes requires, therefore,
suitable environmental conditions for both mussel and host. Vaughn and Taylor (2000), for instance, found that species richness of cohabitating mussel and fish assemblages were positively correlated in the Red River Drainage of OK and TX, USA. For stream-dwelling mussels in the central United States, many species of darters serve as critical hosts: Rainbow Darter (*Etheostoma caeruleum*) for Spike (*Elliptio dilatata*); Rainbow, Fantail (*E. flabellare*), and Banded (*E. zonale*) Darters for Fluted Shell (*Lasmigona costata*); and Rainbow, Fantail, Banded, Greenside (*E. blennioides*) and Johnny (*E. nigrum*) Darters for Kidneyshell (*Ptychobranchus fasciolaris*) (Watters et al. 2009).

Both mussels and darters tend to be highly sensitive to habitat alterations and have experienced significant population declines (Williams 1993, Lydeard et al. 2004, Osier and Welsh 2007, Newton et al. 2008, Strayer 2008) in the US Midwest. In fact, freshwater mussels are the most endangered group of aquatic animals across North America. In Ohio, 54% of native freshwater mussel species are now endangered, extirpated, or extinct (Watters et al. 2009). In addition to requiring host fishes, other life-history characteristics including longevity and an extended time to reproductive maturity inhibit rapid recovery from environmental disturbance.

Within this context, the relationships between fluvial geomorphology and linked mussel-fish assemblages at twenty stream reaches in Big Darby Creek, OH, USA were investigated. We hypothesized that geomorphically-stable stream reaches (i.e., low channel adjustment, in a state of dynamic equilibrium) would be positively related to both mussel and fish density and diversity. It was anticipated that cobble embeddedness and flow variability would be the primary drivers of fish diversity, as these have been strong
predictors of fish-assemblage characteristics in other studies (Waters 1995, Sullivan et al. 2006, Walters et al. 2009). However, because of the reliance of mussels on host fish assemblages, we hypothesized that mussel diversity would be more strongly related to fish abundance and distribution than to geomorphic features.

**Materials and Methods**

*Study reaches*

We selected twenty study reaches in Big Darby Creek, a National and State Scenic River that drains 1,441 km$^2$ of central-southern OH, USA (Figure 1). Of the ~44 mussel species in Big Darby Creek, 23 have rare or declining state populations. Many darter species, including the state endangered Spotted Darter (*E. maculatum*), and the state threatened Tippecanoe (*E. tippecanoe*) and Bluebreast (*E. camarum*) Darters are also endemic to Big Darby Creek. Following a paired-study design, ten reaches were selected that represented equilibrium (i.e., stable) riffle-pool interfaces (RPI) and ten reaches that represented adjusting RPIs. To do this, coarse-resolution field indicators of channel stability were used to determine RPI conditions using signs of channel adjustment: channel degradation (e.g., exposed till or fresh substrate in streambed, recently abandoned terraces along the banks), aggradation (e.g., high degree of embeddedness, high width-to-depth ratio), change in planform (e.g., evidence of channel avulsions, newly formed channel bars), and over-widening (e.g., erosion on both sides of the banks in riffle section, presence of channelization) following Sullivan et al. (2006).
Each RPI constituted a study reach and consisted of the flow sequence from the top of the riffle to ~5m into the downstream pool, and represent critical habitat for both mussels and darters (Matthews 1985, Strayer 2008). On the average, study reaches spanned ~100 m. Reaches were selected so that each pair was located within the same larger stream segment to minimize differences the immediate near-shore zone (10 – 15 m) and water quality (Appendix 1, Table 1). Following study reach selection, coordinated surveys of quantitative geomorphic measurements, fish, and mussel assemblages were conducted in the summer and early autumn of 2011 and 2012.

**Geomorphic surveys**

Following the initial coarse equilibrium vs. adjusting characterizations of RPIs, quantitative geomorphic assessments were conducted for each of the twenty stream reaches following procedures outlined in Cianfrani et al. (2004) in order to generate a suite of 1st order geomorphic data (Table 1). The assessments included longitudinal and cross-sectional surveys of each RPI. Wolman’s (1954) pebble count method was used to estimate median bed grain size for each reach. Flow, turbidity, and embeddedness (% fine sediment surrounding 10 randomly-selected cobbles) were also measured. From these field data, 2nd order geomorphic variables were generated using the Reference Reach Spreadsheet developed by Mecklenburg (2006) (Table 1).

**Mussel and fish surveys**
At each study reach, mussel assemblages were sampled using a systematic sampling method with random starts (Strayer and Smith 2003). This method is easy to implement in the field, gives precise estimates for patchily distributed populations, and distributes sampling effort throughout study reach (Strayer and Smith 2003). A grid overlay of each RPI was first established, with each grid representing a 0.5 m² quadrat. Three random starts were then selected using the Quick Random Generator Application (CWE Software LLC). Subsequently, from 6 to 47 quadrats were established at each reach to ensure consistent representation of the mussel assemblage across study reaches of various sizes (Strayer and Smith 2003). To survey mussels, each quadrat was excavated to a depth of 10-15 cm, or until no more bivalves were found. All unionid mussels collected were identified and returned to the stream.

Fish assemblages were surveyed using a Smith-Root® LR-24 backpack electrofisher under normal flow conditions. Two passes of each site were conducted using dip nets (4.76 mm mesh) and a downstream blocknet with 3.175 mm mesh (given the high flow velocity, an upstream net was not necessary). After fish were collected, all individuals were identified to species and released.

Calculations

Mussel density (number m⁻²) was calculated based on substrate surface area (mean wetted width × reach length) of each study reach. Fish and darter density (number m⁻³) were calculated based on volume (mean wetted width × reach length × mean depth) of each study reach. The assemblage diversity of mussels, fish, darters, and mussels
known to use darters as hosts (hereafter, mussel darter) were measured using species richness ($S$); evenness:

$$ E = \frac{H'}{H_{max}} \text{ where } H' = -\sum_{i=1}^{R} p_i \ln p_i \text{ and } H_{max} = -\sum_{i=1}^{S} \frac{1}{S} \ln \frac{1}{S} = \ln S, $$ (1)

where $p_i$ is the proportion of individuals belonging to the $i$th species and $S$ is species richness; and Simpson’s Index:

$$ D = \frac{\sum n(n-1)}{N(N-1)}, $$ (2)

where $n$ = the total number of organisms of a particular species and $N$ = the total number of organisms of all species) (Simpson 1949). Simpson’s index measures dominance and quantifies the degree to which individuals are concentrated in a few species.

**Statistical analysis**

All statistical analyses were performed using JMP® Version 10 Statistical Discovery Software (SAS Institute, Cary, North Carolina). Logarithmic ($\log_{10}[x+1]$), square root ($\sqrt{x}$), or square ($x^2$) transformations were used where necessary to normalize data and eliminate heteroscedasticity prior to analysis (Zar 1984). Based on our paired-reach study design, our primary tool for analyzing differences seen in geomorphic condition and mussel and fish community measures between equilibrium and adjusting RPIs was the Student’s paired $t$-test. However, because anomalous geomorphic properties at two reaches (mid-channel islands, flood chutes, split channels) set them apart from their respective pairs, only 8 paired reaches were used in this phase of the analysis. All data were tested at $\alpha = 0.05$. 

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The goal of the second phase of the analysis was to explore the contribution of more detailed, quantitative geomorphic characteristics to patterns in mussel and fish assemblages. Because this component of the study was not based on a paired design, all twenty reaches were included. For this phase of the analysis, we considered RPIs sufficiently independent from each other given that study reaches were separated by at least one riffle-pool sequence and that fine-scale hydrogeomorphic controls on fish and mussel assemblages have been shown to be expressed at the site level (Sullivan et al. 2006). Principal component analysis (PCA) was performed on a suite of 1st and 2nd order geomorphic variables (D50, D95, channel slope, mean depth, maximum depth, width-depth ratio, embeddedness, cross-section area, velocity, discharge rate, Froude number, D’Arcy-Weisbach friction coefficient, relative roughness, and shear stress) that were identified a priori as potentially important characteristics to fish and mussel assemblages. Those PCA axes with eigenvalues >1 (Rencher 1995) were retained. Along with drainage area, which was used as a stand-alone variable given the documented associations between fish assemblage characteristics and catchment size (e.g., Matthews and Robinson 1998), the retained PCA axes were used in linear regression models as predictor variables. Mixed stepwise multiple linear regressions were used to select optimal predictors for each of our endpoint biological measures (S, E, D, density for fish and mussel assemblages). Variable additions proceeded until the F-statistic for the step change fell below the p < 0.05 significance threshold. We considered using an adjustment for multiple regression tests (e.g., Bonferroni adjustment, Wright 1992), however decided this was not necessary given that each assemblage type (mussels, fish, darters, mussels...
using darter species as hosts) represented a unique data set. Additionally, given the relatively small sample size in this and many other ecological studies, we were sensitive to the potential for multiple test corrections to add to the problem of low power (Holm 1979, Rice 1989).

**Results**

*Biotic assemblages*

Mussel species richness ranged from 0 to 12 ($\bar{x} = 3.6$). On the average, density was highest at upstream sites, where species common to small streams were numerically dominant (e.g., Spike and Creek Heelsplitter *Lasmigona compressa*). Species richness, on the other hand, was generally highest in the middle reaches, where a mixture of stream and river species were common (e.g., Fragile Papershell *Leptodea fragilis* and Pink Heelsplitter *Potamilus alatus*). However, we did not observe complete community turnover, with multiple species common across all study reaches (LIST A FEW). Mussels known to use darter species as their fish host ranged from 0 to 3 species ($\bar{x} = 1.0$).

Fish species richness ranged from 6 to 13 ($\bar{x} = 10.0$) and density ranged from 0.5 to 9.8 individuals m$^{-3}$ ($\bar{x} = 1.8$ individuals m$^{-3}$). Fish species diversity tended to be greater at downstream reaches. Across all reaches, Greenside Darters, Sand Shiners (*Notropis stramineus*), and Banded Darters were the most common, comprising 13.6%, 11.6%, and 11.5% of the assemblage, respectively. Darter species were observed at every study
reach, where species richness ranged from 3 to 7 (\( \bar{x} = 5.0 \)). The most common darter species included Greenside, Banded and Rainbow Darters, occurring at 20, 19, and 17 of the 20 reaches, respectively. The rarest darter species were \( E. nigrum \) and \( E. spectabile \) (Orangethroat Darter), each occurring at only one study reach.

There were no significant relationships found between the diversity \((S, E, D)\) of darters and mussel \( darter \) or between the density of darters and mussel \( darter \) \((p > 0.05)\).

\textit{Geomorphic variables}

Drainage area ranged from 531.6 km\(^2\) to 1437.3 km\(^2\) \((\bar{x} = 1270.9 \text{ km}^2)\), although differences in drainage area between each pair were minimal (Table 2). Channel slope (m \text{ m}^{-1}) was generally higher at the equilibrium RPIs \((0.004 \text{ to } 0.051 \text{ m m}^{-1}, \bar{x} = 0.016 \text{ m m}^{-1})\) compared to the adjusting RPIs \((0.003 \text{ to } 0.023 \text{ m m}^{-1}, \bar{x} = 0.009 \text{ m m}^{-1})\). Average \( D_{95} \) (mm) was also larger at the equilibrium RPIs \((\bar{x} = 110.6 \text{ mm})\) than at the adjusting RPIs \((\bar{x} = 92.8 \text{ mm})\). Conversely, width-to-depth ratio, a measure of channel dimension, was greater and more variable at the adjusting RPIs \((19.3 \text{ to } 91.2, \bar{x} = 44.8)\) than at equilibrium RPIs \((24.1 \text{ to } 48.2, \bar{x} = 36.8)\). Average velocity and discharge ranged from 1.3 to 4.5 m s\(^{-1}\) and 10.2 to 216.8 cms across all study reaches, respectively. On the whole, both average velocity (m s\(^{-1}\)) and discharge rate (cms) were greater at equilibrium RPIs (Table 2).

\textit{Adjusting v. equilibrium RPIs}
Density was not significantly different between equilibrium and adjusting RPIs for assemblages of mussels or mussel\textsubscript{darter} ($p > 0.05$). However, for both fish ($t = -0.73$, $df = 14$, $p = 0.048$) and darter assemblages ($t = -1.25$, $df = 14$, $p = 0.024$), density was higher at adjusting RPIs. Fish $S$ was greater at equilibrium than at adjusting RPIs ($t = 1.79$, $df = 14$, $p = 0.047$). Evenness was not significantly different between equilibrium and adjusting RPIs for any of the assemblages considered ($p > 0.05$). $D$ was 1.4 times lower for darter assemblages at equilibrium ($\bar{x} = 0.30$, $SD = 0.09$) vs. adjusting RPIs ($\bar{x} = 0.43$, $SD = 0.13$) ($t = -2.42$, $df = 14$, $p = 0.030$; Figure 3).

**Influences of quantitative geomorphic characteristics**

The PCA of hydrogeomorphic and in-stream habitat characteristics identified four axes with eigenvalues $>1$, explaining 87% of the total variance (Table 3). PC1 explained ~39% of the variance. Because this axis was predominantly driven by factors related to channel dimensions (maximum depth [$r^2 = 0.84$], mean depth [$r^2 = 0.82$], cross-sectional area [$r^2 = 0.76$], discharge rate [$r^2 = 0.71$]; + correlations) and roughness elements (relative roughness [$r^2 = 0.72$], D’arcy-Weisbach friction coefficient [$r^2 = 0.54$]; + correlation), we named this PC “Channel Dimensions & Roughness Axis”. PC2 was chiefly driven by velocity ($r^2 = 0.95$; + correlation) and shear stress ($r^2 = 0.84$; + correlation) and therefore it was named “Velocity and Shear Stress Axis”. PC3, “Sediment Size Axis”, explained about 14% of the variance and was dominated by sediment size factors ($D_{95}$ [$r^2 = 0.89$] and $D_{50}$ [$r^2 = 0.87$]; + correlations). Finally, PC4
was predominantly driven by embeddedness \( r^2 = 0.72; + \) correlation, thus represented an “Embeddedness Axis”.

Eleven models emerged as significant, illustrating that hydrogeomorphic characteristics were influential to a suite of linked mussel-fish characteristics (Table 4). Across all models, the strength of the models ranged from \( R^2 \) of 0.20 (Darter \( E \)) to 0.54 (Mussel_darter \( D \)) and 0.55 (Mussel_darter density). Drainage Area was significant in ten of the eleven models, explaining from 10% of the observed variation in Darter \( S \) to 39 and 41% in Fish \( S \) and Mussel_darter \( S \), respectively. However, Drainage Area exerted a positive influence in some models (e.g., fish and darter \( S \)) and negative in others (mussel_darter \( S \) and \( D \)). Embeddedness Axis was also a common predictor variable (7 models), with \( R^2 \) values ranging from 0.08 (Mussel_darter density) to 0.31 (Mussel_darter \( E \)). The Velocity & Shear Stress and the Channel Dimensions & Roughness Axes also contributed to significant models for Mussel_darter density, \( S \), and \( D \). For darter \( E \) and \( D \), the Sediment Size Axis was a key explanatory variable (Table 4).

Discussion

Although multiple studies have linked geomorphic characteristics to aquatic biota (Sullivan et al. 2006, Gangloff and Feminella 2007, reviewed by Vaughan et al. 2009 and Poole 2010), few have considered the composite effects of stream channel geomorphic adjustment on linked biotic assemblages (but see Wright and Li 2002, Sullivan and Watzin 2008). In this study, freshwater mussels and stream fish were used as model assemblages to more fully integrate fluvial geomorphology and aquatic biota within an
ecogeomorphic context (Sheldon and Thoms 2006, Vaughan et al. 2009, Sullivan 2012). Coarse-level geomorphic classifications (i.e., geomorphic “stability” of riffle-pool interfaces) discriminated between select measures of abundance and diversity of fish assemblages, but not mussels. Finer-resolution quantitative geomorphic variables provided substantially more information for both mussel and fish assemblages, but geomorphic-fish and geomorphic-mussel relationships were not consistent in either direction or magnitude. Some of the strongest relationships related to the component of the mussel community that uses darter species as hosts, suggesting that these mussel species are particularly sensitive to hydrogeomorphic conditions. Additionally, given that the current list of potential host fishes may be incomplete for the region, additional mussel species may utilize darters as hosts and may also be highly sensitive to hydrogeomorphic change. Taken as a whole, our results illustrate that geomorphic condition and characteristics can simultaneously influence interdependent stream biota. Conservation and management strategies that include a geomorphic component may have substantial benefits for stream biotic communities, which is particularly important given the threatened status of North American mussel populations.

*Geomorphic condition – adjusting vs. equilibrium RPIs*

Both the densities of the overall fish assemblage (1.9x) as well as the darter component of the fish assemblage (1.7x) were greater at adjusting RPIs than at equilibrium RPIs. Greater fish $S$ was observed at equilibrium RPIs but lower darter assemblage $D$ was observed at equilibrium RPIs (Figure 3). The lack of relationships
observed between RPI geomorphic condition and mussel assemblage descriptors may relate to the difference in mobility between the two taxa. Fish, being more mobile and thereby integrating a broader area of the stream may reflect the composite, reach-level effects of stream geomorphic condition and have been shown to be associated with coarse-level measurements of channel change. Gorman and Karr (1978), for example, observed that the stability of the fish community was lower in modified streams as opposed to natural streams. Sullivan et al. (2006) observed that fish community diversity, density, and condition were related to composite geomorphic adjustment in VT, USA streams. However, the density of the overall fish assemblages as well as the darter assemblage was lower at more stable reaches whereas Sullivan et al. (2006) found the opposite pattern. In their study, the reach lengths were orders of magnitude larger (250 – 3000 km) than our reaches (~100 m on average), and therefore fish responses were not limited to only a subset of the fish assemblage, as was the case in the current study where primarily riffle species were sampled, which are not typically found in high densities (Langeani et al., 2005).

Consistent with our hypotheses, greater fish $S$ was observed at equilibrium RPIs, although this was not the case with the darter assemblage. In our study system, equilibrium RPIs were characterized by multiple physical habitat features thought to promote high fish diversity including unembedded cobbles, a mixture of velocity-depth regimes (e.g., deep-fast, shallow-fast, etc.), and heterogeneous cover (large wood, overhanging vegetation, etc.) (Waite and Carpenter 2000, Sullivan et al. 2006, Casatti et al. 2009). Darter assemblage $D$ was found to be lower at equilibrium than adjusting RPIs
(Figure 3), likely because of the dominance of a few species within the assemblage including Greenside, Rainbow, and Banded Darters.

Our categorical stability assessments failed to discriminate mussel assemblage descriptors, suggesting that composite geomorphic evaluations that synthesize reach-level geomorphic adjustment may not be of sufficient resolution. Because mussels are restricted in movement, they likely experience their environment at the microhabitat scale rather than integrating habitat across the entire RPI. However, this does not preclude the potential for mussels to respond to changes in overall channel stability. For example, Johnson and Brown (2000) found that mussel beds were more common in sections of their study stream where the substrate was more stable through time. Greater understanding of the potential effects of channel adjustment on mussel assemblages will require further investigation.

Fine-resolution geomorphic variables influencing fish and mussel assemblages

Drainage area was important in ten of the eleven significant models (Table 4). Drainage area has been shown to be positively related to fish assemblages in multiple studies (Sepkoski and Rex 1974, Watters 1992, Newall and Magnuson 1999, Park et al. 2006). Mussel assemblage descriptors have been linked to drainage area as well. For instance, Watters (1992) found that the number of unionid species was positively related to drainage area. Sepkoski and Rex (1974) found that area of drainage basins was the best predictor of the number of species.
We hypothesized that mussel assemblage diversity would be more strongly related to host fish assemblages than to hydrogeomorphic features. However, the lack of significant relationships between both density and diversity of darter and mussel_darter assemblages indicated that this may not be the case. Indeed, it was found that assemblages of darters as well as mussels known to use darters as their hosts were both influenced by hydrogeomorphic PC axes. Embeddedness, for example, was an influential predictor variable for descriptors of the mussel_darter assemblage ($R^2 = 0.18$ for $S$, $R^2 = 0.31$ for $E$) as well as the darter assemblage ($R^2 = 0.26$ for $S$, $R^2 = 0.08$ for $D$).

Embeddedness was also an important variable for $S$, $E$, and $D$ of the entire fish assemblage. Embeddedness has been widely shown to be negatively related to fish assemblages via multiple mechanisms (Nerbonne and Vondracek 2001, Walters et al. 2009). For example, embeddedness can depress benthic insect populations (Lemly 1982, Nerbonne and Vondracek 2001, Kochersberger et al. 2012), and limit food availability to benthic insectivores such as the darter species found in our study system (Lemly 1982, Osmundson et al. 2002, Walters et al. 2009). For fish and darter $D$, our results were consistent with these findings. However, for other measures of fish and darter diversity, a positive relationship was found with the Embeddedness Axis. A significant relationship was also found between Embeddedness Axis and darter density, but no relationship between embeddedness and mussel_darter. Although filter-feeding mussels are not tied to benthic food resources, embeddedness was positively related to mussel_darter density, $S$, and $E$ in our study system. Strayer (2008) suggests that when the interstitial habitat is missing (i.e., increased embeddedness), juvenile mussels may be exposed to increased
predation rates. For adult mussels, however, our results indicate that a degree of embeddedness (\(\bar{x} = 35\%\) across our study reaches) may be important in order to provide a sufficiently stable substrate. It is likely that extreme levels of embeddedness would be detrimental to mussels, as reported in other studies (Strayer 2008).

Velocity and Shear Stress Axis negatively influenced mussel \(darter\) density, \(S\), and \(D\), although the relationships were relatively weak \((R^2 = 0.07, R^2 = 0.10, \text{ and } R^2 = 0.06\) respectively). Shear stress and velocity could be limiting to density and diversity because these factors collectively inhibit mussels from persisting within a reach via multiple mechanisms. For example, juvenile mussels require low shear stress for settlement, whereas adult mussels require sufficiently slow currents to prevent interference with feeding and to minimize likelihood of being washed downstream (Strayer 2008).

The Sediment Size Axis was an important variable in models for darter \(E\) \((R^2 = 0.20)\) and \(D\) \((R^2 = 0.13)\), although the relationship was negative for \(E\) and positive for \(D\). Substrate size has also been shown to be of considerable importance to stream fish by limiting food sources (Berkman and Rabeni 1987, Osmundson et al. 2002), reproduction (Peters 1967, Muncy et al. 1979), and growth rates (Shields et al. 1994). In some cases, bed composition has been shown to be the dominant factor explaining fish assemblage characteristics. For example, Walters et al. (2003) found that fish richness and density were correlated with basin area, but species composition was best predicted by reach-level geomorphic variables (stream slope, bed texture, bed mobility, and tractive force) that were unrelated to stream size. In general, increases in substrate size from fines to gravel and cobble is positively correlated with measures of fish diversity (Berkman and
Rabeni 1987, Waters 1995, Jones III et al. 1999). The contrasting directionality of the relationships between Sediment Size Axis and darter $E$ and $D$ may in part reflect an artifact of stream size, whereby fine substrates (e.g., silt-sand) small substrate profiles were typically found lower in the watershed, where fish evenness also tended to increase.

Conclusions

Coarse-level geomorphic classifications (i.e., geomorphic condition of riffle-pool interfaces) were found to discriminate between select measures of density and diversity of fish assemblages, but not mussels. Finer-resolution quantitative geomorphic variables provided substantially more information for both mussel and fish assemblages, but geomorphic-fish and geomorphic-mussel relationships were not consistent. Some of the strongest relationships related to the component of the mussel community that use darters as hosts, suggesting that these species are particularly sensitive to hydrogeomorphic conditions including embeddedness, velocity/bed stress, and channel adjustment.

In spite of many strong relationships, there remains significant unexplained variation in our models, stemming from the myriad factors that influence fish and mussel assemblages that were not measured in this study. Linking our results with broader-scale factors, such as influences of land use and land cover and spatial variability would strengthen our mechanistic understanding of the impacts of hydrogeomorphic factors on fish and mussel assemblages. For example, studies by Esselman & Allen (2010) and Kautza and Sullivan (2012a) illustrated that local, landscape, and spatial factors contributed to patterns seen in fish assemblage characteristics. Further understanding the
impacts of hydrogeomorphic conditions on linked mussel-fish assemblages will require investigations that target geomorphic influences on the various life stages of both mussels and fish. However, taken as a whole, our results provide initial evidence that fluvial geomorphic condition and characteristics can simultaneously influence interdependent stream biota. Conservation and management strategies that include a geomorphic component may have substantial benefits for stream biotic communities, which is of critical importance given the threatened status of North American mussel populations. The few significant relationships that resulted from the paired design are an indication that coarse level analyses may be helpful, especially for management and conservation ends.

Acknowledgements

This research was supported by The Ohio Division of Wildlife through the State Wildlife Grants Program and the Ohio Biodiversity Conservation Partnership. We extend our thanks to Kristi Harraman, Adam Kautza, Brittany Gunther, Marty Chance Jr., Dan Bey, Jen Cecil, Peggy Lawlis, Timothy Lawlis, Lyndsey Lawlis, Barrett Lawlis, Lindsey Boaz, Lars Meyer, Ben Rubinoff, Mik Berzins, Kristen Shearer, Leslie Reick, Tagwie Paradzayi, Amy Barrett, Jacqualyn Halmbacher, Kody Kuehnl, and Megan Patterson for their assistance in the field. We are grateful to Franklin County Metro Parks and Howard “Mae” Albin for their cooperation and access to study reaches. Finally, thanks Dr. G. Thomas Watters and Dr. Stephen Matthews for reviews of earlier manuscript drafts.
Table 3 (Chapter 2 Table 1). Measured (1\textsuperscript{st} order) and calculated (2\textsuperscript{nd} order) geomorphic characteristics of riffle-pool interface (RPI) study reaches. 2\textsuperscript{nd} order variables were generated using the Reference Reach Spreadsheet developed by Mecklenburg (2006)

<table>
<thead>
<tr>
<th>Geomorphic Characteristics</th>
<th>1\textsuperscript{st} order</th>
<th>2\textsuperscript{nd} order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bankfull width (m)</td>
<td>D’Arcy-Weisbach friction coefficient</td>
<td></td>
</tr>
<tr>
<td>Channel slope (m m\textsuperscript{-1})</td>
<td>Discharge rate (cms)</td>
<td></td>
</tr>
<tr>
<td>Cross-sectional area (m)</td>
<td>Froude number</td>
<td></td>
</tr>
<tr>
<td>D\textsubscript{50} (mm)</td>
<td>Relative roughness</td>
<td></td>
</tr>
<tr>
<td>D\textsubscript{95} (mm)</td>
<td>Shear stress (kg m\textsuperscript{-2})</td>
<td></td>
</tr>
<tr>
<td>Drainage area (km\textsuperscript{2})</td>
<td>Velocity (m s\textsuperscript{-1})</td>
<td></td>
</tr>
<tr>
<td>Embeddedness (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width-depth ratio</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4 (Chapter 2 Table 2). Descriptive statistics for mussel assemblages, fish assemblages, and geomorphic characteristics of riffle-pool interfaces (RPIs) from the 20 study reaches in Big Darby Creek, Ohio, USA.

<table>
<thead>
<tr>
<th></th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biotic Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mussels</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Density (individuals m⁻²)</strong></td>
<td>0.00</td>
<td>0.84</td>
<td>0.13</td>
<td>0.23</td>
</tr>
<tr>
<td><strong>Evenness</strong></td>
<td>0.00</td>
<td>1.00</td>
<td>0.38</td>
<td>0.44</td>
</tr>
<tr>
<td><strong>Simpson's index</strong></td>
<td>0.00</td>
<td>0.95</td>
<td>0.27</td>
<td>0.37</td>
</tr>
<tr>
<td><strong>Species richness</strong></td>
<td>0.0</td>
<td>12.0</td>
<td>2.7</td>
<td>3.6</td>
</tr>
<tr>
<td><strong>Mussel-darter density (individuals m⁻³)</strong></td>
<td>0.00</td>
<td>0.27</td>
<td>0.04</td>
<td>0.07</td>
</tr>
<tr>
<td><strong>Mussel-darter evenness</strong></td>
<td>0.00</td>
<td>0.97</td>
<td>0.24</td>
<td>0.40</td>
</tr>
<tr>
<td><strong>Mussel-darter Simpson's index</strong></td>
<td>0.00</td>
<td>1.00</td>
<td>0.21</td>
<td>0.32</td>
</tr>
<tr>
<td><strong>Mussel-darter species richness</strong></td>
<td>0.0</td>
<td>3.0</td>
<td>0.8</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Fish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Density (individuals m⁻³)</strong></td>
<td>0.5</td>
<td>9.8</td>
<td>2.5</td>
<td>2.1</td>
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<tr>
<td><strong>Evenness</strong></td>
<td>0.54</td>
<td>2.94</td>
<td>1.23</td>
<td>0.79</td>
</tr>
<tr>
<td><strong>Simpson's index</strong></td>
<td>0.13</td>
<td>0.55</td>
<td>0.21</td>
<td>0.09</td>
</tr>
<tr>
<td><strong>Species richness</strong></td>
<td>6.0</td>
<td>19.0</td>
<td>10.6</td>
<td>3.0</td>
</tr>
<tr>
<td><strong>Darter density (individuals m⁻³)</strong></td>
<td>0.3</td>
<td>5.0</td>
<td>1.6</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>Darter evenness</strong></td>
<td>0.50</td>
<td>0.93</td>
<td>0.78</td>
<td>0.10</td>
</tr>
<tr>
<td><strong>Darter Simpson's index</strong></td>
<td>0.21</td>
<td>0.71</td>
<td>0.35</td>
<td>0.12</td>
</tr>
<tr>
<td><strong>Darter species richness</strong></td>
<td>3.0</td>
<td>8.0</td>
<td>5.1</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>Geomorphology</strong></td>
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<td></td>
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<tr>
<td><strong>1st order</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Bankfull Width (m)</strong></td>
<td>15.4</td>
<td>35.7</td>
<td>34.5</td>
<td>10.8</td>
</tr>
<tr>
<td><strong>Channel Slope (m m⁻¹)</strong></td>
<td>0.003</td>
<td>0.051</td>
<td>0.013</td>
<td>0.012</td>
</tr>
<tr>
<td><strong>D₅₀ (mm)</strong></td>
<td>21.0</td>
<td>98.0</td>
<td>43.3</td>
<td>21.0</td>
</tr>
<tr>
<td><strong>D₉₅ (mm)</strong></td>
<td>53.0</td>
<td>300.0</td>
<td>101.7</td>
<td>56.5</td>
</tr>
<tr>
<td><strong>Drainage Area (km²)</strong></td>
<td>531.7</td>
<td>1437.3</td>
<td>1122.0</td>
<td>305.2</td>
</tr>
<tr>
<td><strong>Embeddedness (%)</strong></td>
<td>11.2</td>
<td>70.0</td>
<td>35.3</td>
<td>16.2</td>
</tr>
<tr>
<td><strong>Maximum Depth (m)</strong></td>
<td>0.6</td>
<td>2.6</td>
<td>1.3</td>
<td>0.5</td>
</tr>
<tr>
<td><strong>Mean Depth (m)</strong></td>
<td>0.3</td>
<td>1.2</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td><strong>Width-Depth Ratio</strong></td>
<td>19.3</td>
<td>91.2</td>
<td>40.8</td>
<td>16.4</td>
</tr>
<tr>
<td><strong>2nd order</strong></td>
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</table>

Continued
Table 4 Continued  (Chapter 2 Table 2).

<table>
<thead>
<tr>
<th></th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>D'Arcy-Weisbach Friction Coefficient</td>
<td>0.08</td>
<td>0.14</td>
<td>0.10</td>
<td>0.02</td>
</tr>
<tr>
<td>Discharge Rate (cms)</td>
<td>10.2</td>
<td>216.8</td>
<td>73.9</td>
<td>52.3</td>
</tr>
<tr>
<td>Froude Number</td>
<td>0.46</td>
<td>1.83</td>
<td>0.76</td>
<td>0.29</td>
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<tr>
<td>Relative Roughness</td>
<td>6.0</td>
<td>73.2</td>
<td>23.3</td>
<td>14.7</td>
</tr>
<tr>
<td>Shear Stress (kg m$^{-2}$)</td>
<td>1.39</td>
<td>27.01</td>
<td>6.56</td>
<td>5.47</td>
</tr>
<tr>
<td>Velocity (m s$^{-1}$)</td>
<td>1.25</td>
<td>4.51</td>
<td>2.18</td>
<td>0.76</td>
</tr>
</tbody>
</table>

*Mussel$_{darter}$ refers to mussels that use the species of darters found in our reaches as a host fish.
Table 5 (Chapter 2 Table 3). Eigenvalues (>1.0) and the percent variance captured by the principal components, along with each principal component's loadings and the proportion of the variance ($r^2 = \text{loading}^2 \times \text{eigenvalue}$) shared with the PCA axes.

<table>
<thead>
<tr>
<th>Eigenvectors</th>
<th>PC1 - Channel Dimensions &amp; Roughness</th>
<th>PC2 - Velocity &amp; Stress</th>
<th>PC3 - Sediment Size</th>
<th>PC4 - Embeddedness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Loading $r^2$</td>
<td>Loading $r^2$</td>
<td>Loading $r^2$</td>
<td>Loading $r^2$</td>
</tr>
<tr>
<td>Bankfull width (m)</td>
<td>0.29 0.50</td>
<td>-0.17 0.12</td>
<td>-0.08 0.01</td>
<td>0.28 0.08</td>
</tr>
<tr>
<td>Channel Slope (m m$^{-1}$)</td>
<td>-0.21 0.27</td>
<td>0.37 0.56</td>
<td>-0.20 0.08</td>
<td>0.08 0.01</td>
</tr>
<tr>
<td>Cross-sectional area (m)</td>
<td>0.36 0.76</td>
<td>-0.05 0.01</td>
<td>-0.02 0.00</td>
<td>-0.09 0.01</td>
</tr>
<tr>
<td>$D_{50}$ (mm)</td>
<td>-0.10 0.05</td>
<td>0.02 0.00</td>
<td>0.64 0.87</td>
<td>0.00 0.00</td>
</tr>
<tr>
<td>$D_{95}$ (mm)</td>
<td>-0.04 0.01</td>
<td>0.04 0.01</td>
<td>0.65 0.89</td>
<td>0.03 0.00</td>
</tr>
<tr>
<td>D'Arcy-Weisbach friction coefficient</td>
<td>-0.30 0.54</td>
<td>-0.16 0.10</td>
<td>-0.09 0.02</td>
<td>-0.26 0.07</td>
</tr>
<tr>
<td>Discharge rate (cms)</td>
<td>0.35 0.71</td>
<td>0.19 0.14</td>
<td>0.05 0.00</td>
<td>-0.08 0.01</td>
</tr>
<tr>
<td>Embeddedness (%)</td>
<td>0.18 0.19</td>
<td>0.04 0.01</td>
<td>-0.02 0.00</td>
<td>0.84 0.72</td>
</tr>
<tr>
<td>Froude number</td>
<td>-0.21 0.27</td>
<td>0.40 0.65</td>
<td>-0.11 0.02</td>
<td>0.05 0.00</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>0.38 0.84</td>
<td>0.12 0.06</td>
<td>0.00 0.00</td>
<td>-0.17 0.03</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>0.37 0.82</td>
<td>0.16 0.10</td>
<td>0.10 0.02</td>
<td>-0.12 0.02</td>
</tr>
<tr>
<td>Relative roughness</td>
<td>0.35 0.72</td>
<td>0.13 0.07</td>
<td>-0.18 0.07</td>
<td>-0.28 0.08</td>
</tr>
<tr>
<td>Shear stress (kg m$^{-2}$)</td>
<td>-0.13 0.09</td>
<td>0.45 0.84</td>
<td>-0.07 0.01</td>
<td>0.04 0.00</td>
</tr>
<tr>
<td>Velocity (m s$^{-1}$)</td>
<td>-0.03 0.01</td>
<td>0.48 0.95</td>
<td>0.00 0.00</td>
<td>0.03 0.00</td>
</tr>
<tr>
<td>Width-depth ratio</td>
<td>-0.12 0.09</td>
<td>-0.35 0.50</td>
<td>-0.24 0.12</td>
<td>0.09 0.01</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>5.87</td>
<td>4.11</td>
<td>2.13</td>
<td>1.03</td>
</tr>
<tr>
<td>% Variance</td>
<td>39.14</td>
<td>27.39</td>
<td>14.18</td>
<td>6.85</td>
</tr>
</tbody>
</table>
Table 6 (Chapter 2 Table 4). Explanatory variables and their coefficients in the significant multiple regression models for characteristics of mussel assemblages, assemblages of mussels known to use darters as hosts (mussel$_{darters}$), fish assemblages, and darter assemblages.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>Coefficient</th>
<th>$R^2$</th>
<th>$F$-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mussel density (# ind. m$^{-2}$; $p = 0.015$)</td>
<td>Intercept</td>
<td>0.7966</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0005</td>
<td>0.29</td>
<td>0.015</td>
</tr>
<tr>
<td>Mussel$_{darter}$ density (# ind. m$^{-2}$; $p = 0.013$)</td>
<td>Intercept</td>
<td>0.6305</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0004</td>
<td>0.36</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>0.0510</td>
<td>0.08</td>
<td>0.098</td>
</tr>
<tr>
<td></td>
<td>Velocity &amp; Stress Axis</td>
<td>-0.0256</td>
<td>0.07</td>
<td>0.108</td>
</tr>
<tr>
<td></td>
<td>Channel Dimensions &amp; Roughness Axis</td>
<td>0.0159</td>
<td>0.04</td>
<td>0.249</td>
</tr>
<tr>
<td>Mussel$_{darter}$ richness ($S$; $p = 0.035$)</td>
<td>Intercept</td>
<td>2.7010</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0017</td>
<td>0.14</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>0.4308</td>
<td>0.18</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>Velocity &amp; Stress Axis</td>
<td>-0.1610</td>
<td>0.10</td>
<td>0.124</td>
</tr>
<tr>
<td>Mussel$_{darter}$ evenness ($E$; $p = 0.006$)</td>
<td>Intercept</td>
<td>0.7859</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>0.2378</td>
<td>0.31</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0005</td>
<td>0.14</td>
<td>0.056</td>
</tr>
<tr>
<td>Mussel$_{darter}$ Simpson's index ($D$; $p = 0.006$)</td>
<td>Intercept</td>
<td>1.1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0009</td>
<td>0.41</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Velocity &amp; Stress Axis</td>
<td>-0.0455</td>
<td>0.06</td>
<td>0.126</td>
</tr>
<tr>
<td></td>
<td>Channel Dimensions &amp; Roughness Axis</td>
<td>0.0397</td>
<td>0.07</td>
<td>0.131</td>
</tr>
<tr>
<td>Fish richness ($S$; $p = 0.018$)</td>
<td>Intercept</td>
<td>6.1654</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>1.2126</td>
<td>0.22</td>
<td>0.046</td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>0.0039</td>
<td>0.16</td>
<td>0.053</td>
</tr>
<tr>
<td>Fish evenness ($E$; $p = 0.013$)</td>
<td>Intercept</td>
<td>2.4721</td>
<td></td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>0.0007</td>
<td>0.26</td>
<td></td>
</tr>
</tbody>
</table>

Continued
### Table 6 Continued (Chapter 2 Table 4).

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>Coefficient</th>
<th>$R^2$</th>
<th>F-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish Simpson's index ($D; p = 0.004$)</td>
<td>Intercept</td>
<td>-0.3974</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0003</td>
<td>0.39</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>-0.0436</td>
<td>0.09</td>
<td>0.103</td>
</tr>
<tr>
<td>Darter richness ($S; p = 0.022$)</td>
<td>Intercept</td>
<td>3.6254</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>0.5801</td>
<td>0.26</td>
<td>0.028</td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>0.0013</td>
<td>0.10</td>
<td>0.119</td>
</tr>
<tr>
<td>Darter evenness ($E; p = 0.043$)</td>
<td>Intercept</td>
<td>0.7585</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sediment Size</td>
<td>-0.0337</td>
<td>0.20</td>
<td>0.043</td>
</tr>
<tr>
<td>Darter Simpson's index ($D; p = 0.045$)</td>
<td>Intercept</td>
<td>-0.2909</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sediment Size</td>
<td>0.0326</td>
<td>0.18</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>Drainage Area</td>
<td>-0.0001</td>
<td>0.13</td>
<td>0.113</td>
</tr>
<tr>
<td></td>
<td>Embeddedness Axis</td>
<td>-0.0370</td>
<td>0.08</td>
<td>0.180</td>
</tr>
</tbody>
</table>
Figure 6 (Chapter 2 Figure 1) 2011 and 2012 study reaches ($n = 20$) in Big Darby Creek, Ohio, USA. Solid dots indicate equilibrium study reaches and open dots indicate adjusting study reaches.
Figure 7 (Chapter 2 Figure 2). Species richness of mussel assemblages, assemblages of mussels known to use darters as hosts, fish assemblages, and darter assemblages at equilibrium and adjusting RPIs ($n=16$). Different letters represent significant differences based on paired t-tests ($p < 0.05$). Error bars are ± 1 SE from the mean.
Figure 8 (Chapter 2 Figure 3). Simpson's index of mussel assemblages, assemblages of mussels known to use darters as hosts, fish assemblages, and darter assemblages at equilibrium and adjusting riffle-pool interfaces (RPIs) in Big Darby Creek, OH, USA ($n=16$). Different letters represent significant differences based on paired t-tests ($p < 0.05$). Error bars are ± 1 SE from the mean.
Table 7 (Chapter 2 Table 5). Water-quality parameters of riffle-pool interface (RPI) study reaches.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Median</th>
<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>10.7</td>
<td>18.0</td>
<td>27.8</td>
<td>19.8</td>
<td>5.3</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.48</td>
<td>0.84</td>
<td>0.92</td>
<td>0.78</td>
<td>0.12</td>
</tr>
<tr>
<td>DO %</td>
<td>80.0</td>
<td>136.3</td>
<td>287.0</td>
<td>156.8</td>
<td>66.7</td>
</tr>
<tr>
<td>pH</td>
<td>8.3</td>
<td>8.6</td>
<td>9.2</td>
<td>8.6</td>
<td>0.2</td>
</tr>
</tbody>
</table>
References


Rencher, A. C. Methods of multivariate analysis. John Wiley and Sons, Inc. New York, NY, USA.


Chapter 3: Scale-dependent environmental factors influence freshwater mussel assemblages in an Ohio river system

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Abstract

Untangling the relative influences of hierarchically-structured environmental characteristics on riverine biota has proven challenging, in spite of significant research on the subject. For freshwater mussels, whose larvae are obligate ectoparasites on fishes, mussel assemblage characteristics should also be influenced by the distribution and abundance of cohabitating fish assemblages. We conducted coordinated surveys of fish and mussel assemblages at twenty reaches in Big Darby Creek, OH. For each reach, we also collected environmental data at local- (i.e., riparian land cover, stream hydrogeomorphic characteristics) and catchment- (drainage area; catchment land cover; modeled overland flow, sediment, nutrient dynamics) scales. Using a partial constrained ordination approach, we found that collectively, environmental, spatial, and fish datasets explained 99.2% of the variation observed in mussel assemblage structure. The shared (spatially-structured fish and environmental) component was the dominant predictor variable (40.1%). Fish density only accounted for 1.5% of the mussel assemblage variation. The pure environmental component explained 31.5% of the variation, with local- (26.3%) and catchment-scale factors (32.4%) contributing roughly equally. Thus, although fish have been shown to be strong predictors of mussel assemblages, in certain environmental contexts, spatial and environmental factors at both fine and broad scales may be the strongest determinant of mussel assemblage structure. Our results reinforce the notion that conservation and management efforts of freshwater mussels should consider a hierarchical suite of environmental factors.
Keywords
Fish assemblages, freshwater mussel assemblages, pure environmental factors, shared environmental variables, Soil and Water Assessment Tool, spatial patterns

Introduction
River ecosystems are largely thought to be hierarchical in nature, whereby physical and biological features are spatially nested from smaller to larger units (Vannote et al. 1980, Allen and Starr 1982, Frissell et al. 1986). For example, Frissell et al. (1986) and Dent et al. (2001) proposed a riverine hierarchical scaling system consisting of (from smallest to largest) microhabitats, individual patch habitats, river reaches, river segments, and the river network. Others (Poff 1997, Burcher et al. 2007) have described spatial hierarchies at the catchment scale, implicating a suite of increasingly finer-scale hierarchical filters that constrain biotic and abiotic processes.

Multiple investigations have examined the influences of environmental characteristics at different spatial scales on stream biota. Catchment and stream size have consistently been related to species richness of both fish (Newall and Magnuson 1999, Smith and Kraft 2005) and unionid mussel (Strayer 1983, Watters 1992, Haag and Warren 1998, Gangloff and Feminella 2007) assemblages. Fish and freshwater mussel assemblages have also been linked to land use and land cover (LULC). For example, Hoggarth et al. (1995) observed that intensive agriculture on the landscape was correlated with lower mussel abundance and community diversity. Walters et al. (2009) found that stream fish assemblage characteristics including an Index of Biotic Integrity (IBI) and the
ratio of endemic species to endemic and cosmopolitan species richness were positively associated with forest cover at the catchment level. Wang et al. (1997) observed a negative association between watershed urban land use and a fish community coldwater IBI (Lyons et al. 1996).

Local, reach-scale environmental variables can also exert strong influences on fish and mussel assemblages. In particular, hydrogeomorphic variables have been shown to strongly influence biotic communities in streams (Wright and Li 2002, Sullivan et al. 2006, Cianfrani et al. 2009). Gangloff and Feminella (2007), for instance, found that both mussel abundance and richness were negatively correlated with mean current velocity. Johnson and Brown (2000) observed that mussel abundance was positively related to water depth, substrate size, sediment compaction, and water velocity. Bey and Sullivan (Chapter 2) found negative relationships between streamflow velocity and shear stress and density, richness, and evenness of the component of the mussel assemblages using darters as hosts, and positive relationships between this assemblage and embeddedness.

In spite of significant research investigating the influence of environmental factors at different spatial scales on stream biotic assemblages, the precise nature of these relationships remains elusive (see Allan et al. 1997, Vaughn and Taylor 2000, Townsend et al. 2003). Additionally, the influence of spatial factors (i.e., spatial position of assemblages as well as the underlying spatial structure of environmental conditions) is increasingly recognized in the literature. For example, Kautza and Sullivan (2012a) found that a combination of environmental and spatial factors influenced fish assemblages differently in distinct landscape settings.
Additionally, the complex life history of freshwater mussels suggests that biotic factors (i.e., cohabitating fish assemblage characteristics) may also be critical in explaining mussel community dynamics. As mussels are obligate ectoparasites in their larval stage, they require a host organism, which is almost always a fish (Watters et al. 2009). This dependence on host fish suggests that fish community dynamics are a critical factor in governing mussel assemblages. Indeed, many studies have demonstrated the influence of host fish assemblages on mussels (Watters 1992). Haag and Warren (1998) found that freshwater mussel community composition within two drainage basins in AL, USA, was better explained by patterns of variability in the fish community than by variability in the microhabitat. Vaughn and Taylor (2000) found that of the variation in the mussel assemblages in the Red River Drainage, >50% was explained by the distribution and abundance of the fish assemblage.

Therefore, a combination of both spatially-explicit environmental characteristics and host fish dynamics might be expected to drive patterns of mussel assemblages in river systems. Within this framework, we investigated the effects of (1) spatial influences (i.e., distribution of study sites and underlying spatial structure of environmental factors), (2) environmental characteristics at both broad (i.e., catchment/landscape, \(10^3\) m) and fine (i.e., reach and riparian, \(\sim10^2\) m) spatial scales, and (3) host fish assemblages on mussel assemblages at twenty stream reaches in Big Darby Creek, OH, USA. We predicted that a hierarchy of broad-scale environmental features (drainage area, land cover) and local hydrogeomorphic and riparian land-cover characteristics would collectively exert the greatest influence on mussel assemblage structure. However,
because of the expected spatial autocorrelation among fish, mussels, and the environment (Vaughn and Taylor 2000), we anticipated that spatial factors would also be strongly predictive. Because the distribution and abundance of fishes have been shown to be a strong determinant of mussel assemblage structure (Watters 1992, Haag and Warren 1998, Vaughn and Taylor 2000), we anticipated that fish would play a complementary role in structuring mussel assemblages.

Methods

Study reaches

We selected twenty stream reaches in Big Darby Creek, a largely free-flowing National and State Scenic River that drains 1,441 km² of central-southern OH, USA (Figure 1). Of the ~44 mussel species in Big Darby Creek, 23 have rare or declining state populations. Many darter species, including the state endangered Spotted Darter (*Etheostoma maculatum*) and the state threatened Tippecanoe (*E. tippecanoe*) and Bluebreast (*E. camarum*) Darters are also native to Big Darby Creek. Each study reach consisted of a pool-riffle sequence (i.e., the flow sequence from the top of the riffle to ~5m into the downstream pool) and thus represented critical habitat for mussels (Strayer 2008). Following study reach selection, we conducted coordinated surveys of habitat assessments, geomorphic measurements, and fish and mussel assemblages in the summer and early autumn of 2011 and 2012.

Mussel and fish surveys
At each study reach, we sampled mussel assemblages using a systematic sampling method with random starts (Strayer and Smith 2003). This method is easy to implement in the field, gives precise estimates for patchily distributed populations, and distributes sampling effort throughout the study reach. A grid overlay of each study reach was first established, with each grid representing a 0.5 m$^2$ quadrat. Three random starts were then selected using a random number generator (CWE Software LLC). Subsequently, from 6 to 47 quadrats were established at each reach to ensure consistent representation of the mussel assemblage across study reaches of various sizes (Strayer and Smith 2003). To survey mussels, we excavated each quadrat to a depth of 10-15 cm, or until no more bivalves were found. All unionid mussels were identified and returned to the stream.

We surveyed fish assemblages using a Smith-Root® LR-24 backpack electrofisher under normal flow conditions. Two passes of each study reach were conducted using dip nets (4.76 mm mesh) and a downstream blocknet with 3.175 mm mesh (given the high flow velocity at these study reaches, an upstream net was not necessary). All individual fish were identified to species and released.

_Habitat and geomorphology_

We conducted habitat and geomorphic assessments for each of the twenty stream reaches following procedures outlined in Kautza and Sullivan (2012a) and Cianfrani et al. (2004), respectively. We measured water temperature, conductivity, dissolved oxygen, pH, and turbidity at three points (left-bank, mid-channel, right-bank) at the bottom, middle, and top of each study reach using a YSI 650 MDS® with a 600 R® sonde. From
these sub-sampling locations, we generated mean estimates for each study reach (Appendix 1). Geomorphologic assessments included longitudinal and cross-sectional surveys at three transects per reach. Wolman’s (1954) pebble count method was used to estimate median grain size for each reach. Flow, mean wetted width, and embeddedness (% fine sediment surrounding ten randomly selected cobbles) was also measured. From the geomorphic field data, velocity (m s\textsuperscript{-1}) and shear stress (kg m\textsuperscript{-2}) were generated using the Reference Reach Spreadsheet developed by Mecklenburg (2006).

**Land use/Land cover**

We calculated drainage area and land-cover variables using ArcGIS® 10.1 (ESRI, Redlands, CA, USA). We used land-cover data from the National Land Cover Dataset (Fry et al. 2011) to quantify the following land-cover categories, which represent the major land uses of the study basin: % agriculture (i.e., % pasture/hay + % cultivated crops), % forest (i.e., % deciduous forest + % evergreen forest + % mixed forest), % developed (% developed open space + % developed low intensity + % developed medium intensity + % developed high intensity), and % wetlands (% woody wetlands + % emergent herbaceous wetlands). We calculated these land-cover metrics at buffers with a radius of 100 m and 1000 m from the center of each study reach to account for both riparian and landscape-scale catchment characteristics, respectively, as both have been shown to influence aquatic biotic communities (Hopkins and Burr 2009, Brown et al. 2010).
Soil and Water Assessment Tool (SWAT)

The minimum, maximum, mean, and standard deviation (SD) of organic N (kg N ha\(^{-1}\)), organic P (kg P ha\(^{-1}\)), flow in (m\(^3\) s\(^{-1}\)), flow out (m\(^3\) s\(^{-1}\)), sediment in (metric tons), sediment out (metric tons), sediment concentration (mg L\(^{-1}\)), and sediment yield (mm) were modeled for each study reach catchment using SWAT. This catchment model functions on a continuous daily time-step simulating precipitation, infiltration, surface runoff, evapotranspiration, lateral flow, and percolation processes (Neitsch et al., 2002). A 30m digital elevation model and National Land Cover Dataset from the United States Geological Survey (Fry et al. 2011) as well as a soils database obtained from the United States Department of Agriculture National Resource Conservation Service (STATSGO; http://soildatamart.nrcs.usda.gov) were used in the SWAT-modeling procedure. To enhance the likelihood of accurate modeling results, detailed daily precipitation data from a nearby weather station in Marysville, OH were put into the SWAT weather generator.

We performed basic parameterization and a preliminary calibration of the SWAT models were performed using techniques described in Neitsch et al. (2002). Region-specific suggestions from a detailed SWAT-modeling study performed in a central Ohio watershed by Witter (2006) were used to better inform the parameterization and calibration of the models. We calibrated the model for hydrology with respect to flow, which is consistent with other studies (Cianfrani et al. 2010, Kautza and Sullivan 2012b). Table 1 outlines the parameters changed and the original (default) values. The altered parameters were altered consistently for all study reaches.
Preliminary calibration was performed by comparing mean daily stream flow for each month as generated by SWAT to observed stream flow from the USGS stream gauge located on Big Darby Creek in Darbyville, OH. The time-period of calibration for climate data was 1 January 2008 through 31 October 2012. The first year (2008) was used as a warm-up period to allow for model stabilization. To assess performance, the deviation of flow volume ($D_v$) was used to express the difference of observed and predicted flow volumes as a percentage of measured flow over a particular time period:

$$D_v (\%) = \frac{\sum_{i=1}^{n} |O_i - P_i|}{\sum_{i=1}^{n} O_i} \times 100$$  \hspace{1cm} (1)$$

where $O_i$ was the observed discharge for the time period $i$, $P_i$ was the predicted discharge for time period $i$, and $n$ was the number of intervals or units in the time period of interest (Witter 2006).

**Spatial characteristics**

We used a Principal Coordinates of Neighbors Matrix (PCNM) approach to produce a set of spatial variables, following Esselman and Allan (2010) and Kautza and Sullivan (2012a). The PCNM is created from a Euclidean distance matrix based on the latitudinal and longitudinal coordinates of each study reach. These axes provide a method to explicitly investigate the underlying spatial structure of all study reaches included in the investigation, and can be used to discover significant spatial relationships among sample sites and biological data.

**Calculations**
We calculated mussel and fish density (number m$^{-2}$, and number m$^{-3}$, respectively) for each study reach (mean wetted width x reach length, and mean wetted width x reach length x mean depth, respectively). Mussel and fish assemblage diversity was measured using species richness (S); Shannon-Weiner’s Informational Index ($H'$):

$$H' = -\sum_{i=1}^{R} p_i \ln p_i,$$

(2)

where $p_i$ is the proportion of individuals belonging to the $i$th species in the dataset (Shannon and Weaver 1949); evenness ($E$):

$$E = \frac{H'}{H'_{\text{max}}},$$

(3)

where $H'$ is the number derived from the Shannon Weiner Information index, and $H'_{\text{max}}$ is the maximum value of $H'$, equal to:

$$H'_{\text{max}} = -\sum_{i=1}^{S} \frac{1}{S} \ln \frac{1}{S} = \ln S,$$

(4)

where $S$ is species richness; and Simpson’s index ($D$):

$$D = \frac{\sum n(n-1)}{N(N-1)},$$

(5)

where $n$ is the total number of organisms of a particular species, and $N$ is the total number of organisms of all species (Simpson 1949). Shannon-Weiner’s Information index ($H'$) is a measure of diversity, but also accounts for the relative density of each species. Evenness ($E$) is a measure of the relative abundance of each species that contributes to the richness of given area. Simpson’s index is a measure of dominance, and measures the probability that two individuals randomly selected from a sample belong to the same species.
**Statistical Analysis**

In order to minimize the number of highly correlated variables, we generated pairwise multivariate correlations matrices for the fish, local, and catchment datasets and identified pairs with Pearson correlation coefficients \( r \) > 0.80. When significant pairs were found, only one variable was retained, which we selected based on our judgment of its relative explanatory importance. From this analysis, we removed Fish \( H' \), % agriculture (1000 m), shear stress and SWAT-generated FLOW_IN, SED_CONC, and Organic N from the partial constrained ordination analysis.

We arranged our four sets (fish, local, catchment, and spatial [derived from PCNM]) of explanatory variables into separate matrices for use in a partial constrained ordination analysis, similar to the procedure used by Kautza and Sullivan (2012a). Local variables consisted of reach-scale hydrogeomorphic and habitat characteristics, as well as land-cover (100 m). Because of the lack of variability in water quality parameters (Appendix 1), we decided to exclude these from the set of local variables. Catchment variables consisted of land cover (1000 m), drainage area, and SWAT-generated estimates. Using partial constrained ordination allowed us to partition out the value of the effect of pure and shared environmental descriptors while controlling for spatial influences and vice versa (Borcard et al. 1992). In partial constrained ordination, either canonical correspondence analysis (CCA) or redundancy analysis (RDA) are used based on the relationship between the observed biological variables and environmental gradients; unimodal responses require CCA and linear relationships call for RDA. We ran detrended correspondence analysis (DCA) with our environmental, fish, and mussel data.

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to decide which constrained ordination analysis to use (ter Braak and Verdonschot 1995). Results of gradient lengths along the first DCA axis were <2 standard deviations, indicating that RDA was the appropriate ordination analysis (ter Braak and Verdonschot 1995).

We used forward selection to identify significant predictors (Blanchet et al., 2008) and ran 1000 permutations of Monte Carlo tests to identify an appropriate number of significant predictors (i.e., sample size – 1) in four explanatory matrices (fish, catchment, local, and spatial). We retained one of four fish assemblage descriptors (fish density), five of five catchment variables (% forest 1000 m, % developed 1000 m, % wetland 1000 m, drainage area, and SWAT-generated organic P), six of nine local variables (% developed 100 m, embeddedness, $D_{50}$, velocity, channel slope, and mean depth), and seven of the eleven PCNM-generated spatial variables.

Variance partitioning required 14 runs ([run] constraining variable (covariables)): [1] environment; [2] spatial; [3] fish; [4] environment (spatial); [5] environment (fish); [6] environment (spatial + fish); [7] spatial (environment); [8] spatial (fish); [9] spatial (environment + fish); [10] fish (environment); [11] fish (spatial); [12] fish (environment + spatial); [13] local (catchment + spatial + fish); and [14] catchment (local + spatial + fish). This method partitions out the total variation of the mussel assemblage dataset into components that are explained by fish, environment (catchment and local), and spatial predictors, as well as the relative amount explained by each matrix when one or more matrix is partialled out as covariables (Anderson and Gribble 1998). Using this approach, we partitioned total variation in mussel assemblage composition into five components:
pure environmental, pure fish, pure spatial, shared (i.e., spatially-structured fish and spatially-structured environmental), and unexplained. To quantify the influence of environmental factors at local and catchment scales, we partitioned out the three components of pure environmental variation (i.e., local, catchment, and joint). We visually displayed select ordination results by creating biplots for environment- and fish-mussel datasets.

Because all measures of fish diversity were removed during the data reduction procedures, and because of the strong relationships between fish and mussel diversity reported in other investigations (Haag and Warren 1998, Vaughn and Taylor 2000), we independently performed linear regression analysis to test for potential associations between measures of diversity between fish and mussel assemblages.

We used JMP 10.0 (SAS Institute Inc., Cary, NC) for correlation analysis, summary statistics, and regression analysis; Canoco 4.5 (Microcomputer Power, Ithaca, NY) for the ordination analysis; and CanoDraw 4.5 (Microcomputer Power, Ithica, NY) for the biplots.

**Results**

*Preliminary SWAT modeling*

Following calibration, simulations were run for the catchment of each of our study reaches using preliminarily calibrated model parameters (Table 1). Organic P was the only variable that emerged as significant for use in the partial constrained ordinations, and ranged from 14.15 to 15.09 kg ha\(^{-1}\) (\(\bar{x} = 15.01 \text{ kg ha}^{-1}\)). Organic N was found to be
highly correlated with organic P and was less variable, ranging from 85.0 to 92.7 kg ha\(^{-1}\) (\(\bar{x} = 87.8\) kg ha\(^{-1}\)). FLOW\(_{IN}\) (m\(^3\) s\(^{-1}\)) was the average daily streamflow into the study reach during each time step, and ranged from 13.3 to 37.1 m\(^3\) s\(^{-1}\) (\(\bar{x} = 25.7\)). SEDCONC, defined as the concentration of sediment in the study reach during the times step, ranged from 928.3 to 4673.6 mg L\(^{-1}\) (\(\bar{x} = 2008.2\) mg L\(^{-1}\)). Both FLOW\(_{IN}\) and SEDCONC were highly correlated with drainage area.

**Mussel assemblages**

The density of mussels at our study reaches ranged from 0 to 0.84 mussels m\(^{-2}\) (\(\bar{x} = 0.13\)) (Table 2). Mussel species richness was more variable, ranging from 0 to 12 (\(\bar{x} = 2.7\)). Mussel density tended to be higher at upstream reaches, where numerically dominant species included Spike (*Elliptio dilatata*), Wabash Pigtoe (*Fusconaia flava*), and Kidneyshell (*Ptychobranchus fasciolaris*). Species richness was greater at our mid-catchment reaches, where Spike, Wavy-rayed Lamp Mussel (*Lampsilis fasciola*), and Pistolgrip (*Tritogonia verrucosa*) were the most common species.

**Fish-mussel relationships**

Fish density ranged from 0.5 to 9.8 individuals m\(^{-3}\) (\(\bar{x} = 1.8\) individuals m\(^{-3}\)) (Table 3). In contrast to mussel density (greatest at our upstream reaches), fish species diversity tended to be greater at downstream reaches. Across all study reaches, Greenside darters (*E. blennioides*), Sand Shiners (*Notropis stramineus*), and Banded darters (*E.*
zonale) were the most common species in the fish assemblages sampled. Common species used by mussels as hosts included Bluegill (*Lepomis macrochirus*), Smallmouth Bass (*Micropterus dolomieu*), Green Sunfish (*Lepomis cyanellus*), and Rainbow Darters (*E. caeruleum*), and represented between 2.6 to 80.0% (̅ = 29.9%) of the fish assemblage.

Partial constrained ordination results indicated that the pure fish component explained only 1.5% of the variation in the mussel assemblages. However, fish assemblage properties also contributed to the 40.1% of the variation in mussel assemblages explained by the shared factors (i.e., variation shared by fish, spatial, and environmental characteristics). The fish-mussel ordination biplot suggested that fish density was negatively related to multiple measures of mussel assemblage diversity, although the relationships were not strong (Figure 3a). Linear regression between measures of fish and mussel assemblage diversity revealed no significant relationships (p > 0.05).

*Environmental-fish relationships*

Our dataset accounted for almost the total variation in the mussel assemblages (Figure 2). The proportion of assemblage variation accounted for by pure spatial influences (i.e., spatial patterns not shared by environmental data) was 26.0%. Pure environmental factors (i.e., local and catchment variables with spatial and fish influences partialled-out) accounted for 31.5% of the variation in mussel assemblages. Catchment- (32.4%) and local- (26.3%) scale variables contributed roughly equally to the
environmental component (Figure 2), whereas the joint influence was the most dominant (41.3%).

We illustrated key influences of environment-mussel relationships at both fine and broad spatial extents in our ordination biplots. At the local-scale, we found that mussel assemblage $S$, $H'$, $D$, and $E$ was positively aligned with mean depth but was negatively related to $D_{50}$ and % developed (100 m). Mussel density exhibited a positive relationship with velocity and channel slope, and a weakly negative relationship with embeddedness. At the catchment-scale (Figure 3c), mussel assemblage density, $E$, and $D$ were closely aligned with % forest (1000 m). Mussel density was most closely aligned with % wetland (1000 m) and % forest (1000 m), and all mussel descriptors were negatively related to drainage area.

Discussion

Consistent with hierarchical theory of ecological patterns (Frissell et al. 1986, Levins 1992), both spatial levels (i.e., local and catchment) considered in our study contributed to explaining variation in mussel assemblage structure. Although we anticipated that fish assemblages would contribute to predicting mussel assemblage structure, we found that fish density only explained a small percentage of the variation (1.5%). However, the composite effects of fish, the environment, and underlying spatial structure are difficult to decipher, compounded by the spatial autocorrelation expected among fish, mussels, and the environment. In fact, pure spatial factors – representing
factors such as biogeographic history, underlying geology, topology, and climate – emerged as important explanatory variables in our study system.

Variance partitioning enabled us to statistically account for the influences of the pure spatial factors (26.0%) as well as the shared spatial structure that occurred in the observed environmental, fish, and mussel assemblage variables (40.1%). Multiple investigators have reported comparable influences of pure spatial factors (e.g., 16.1% [Vaughn and Taylor 2000]; 17.5 - 25.5% [Kautza and Sullivan 2012a]) on aquatic biota, in spite of spanning multiple catchments or incorporating greater spatial extents (whereas our study was constrained to a single, relatively small catchment). Thus, although spatial variability was more restricted in our study, variability in topography, biogeography, and other underlying factors were strongly predictive.

The shared variation that could not be partitioned into independent effects represented the dominant predictor in our study. This finding is consistent with those of Esselman and Allen (2010), who proposed that a strong shared influence could indicate that the aquatic community data (in their case, fish assemblage) and the environmental data have fairly similar spatial structures that may imply similar responses to common underlying mechanisms, although not all these mechanisms have been identified in our study. Marzin et al. (2013) found that shared factors (shared physiographic and human pressure variables across spatial scales) strongly predicted invertebrate and fish assemblages (41 - 47% of the variation). Thus, our results contribute to the growing understanding that a complex suite of factors influence the structure and distribution of aquatic biotic assemblages.
For mussels, the interaction of environmental and fish assemblage characteristics may play a significant role, even when the pure effect of fish is minimal. This may be the case in our study, where we found that the pure fish component was not strongly predictive (1.5%) of mussel assemblage structure. This result contrasts that of others, who have reported fish to be an important predictor of mussel assemblages. For example, Haag and Warren (1998) and Vaughn and Taylor (2000) showed strong macroecological relationships between mussels and fish, implicating the importance of the regional abundance and distribution of fishes to mussel dispersal, among other factors. Although the variability in fish assemblage structure in our study was similar to that reported in other studies (e.g., 6-19 species in current study, 6-20 species reported in Vaughn and Taylor [2000]), fish density emerged as the only salient variable from our forward selection procedure, and thus diversity measures were not included in the ordination analysis. However, subsequent regression analysis showed no relationships between fish and mussel assemblage diversity in our study system.

In contrast to the variability in fish assemblage diversity, fish density was less variable (0.5 to 9.8, \( \bar{x} = 2.5 \)) and was potentially not sufficiently low or high to prompt a shift in mussel assemblage characteristics. Additionally, we surveyed the entire fish community, irrespective of whether fish were hosts or not. For most systems, fish-host requirements are unknown or questionable (McMahon 1991, Watters 1994) and this information is anticipated to improve our ability to fully understand the influence of fish on mussel assemblages.
The relative influence of local- vs. broad-scale factors on mussels remains an open question (Strayer and Ralley 1993, Vaughn and Taylor 2000, Strayer 2008). Local factors were driven by strong correlations between mussel assemblage diversity measures and mean depth (+), $D_{50}$ (-), and % developed (100 m) (-); as well as between mussel density and embeddedness (-), channel slope (+), and velocity (+). Although multiple published studies suggest a decreasing ability to predict mussel distributions as the scale of observation decreases (Strayer 1981, Holland-Bartels 1990, Strayer and Ralley 1993, Vaughn and Pryon 1995), others support local-scale relationships (e.g., Diamond et al.[2002], and Gagnon et al. [2006]). For example, Strayer (2008) suggests that interstitial space may be especially critical for mussels in their juvenile stage. As embeddedness increases, the amount of interstitial space between substrate decreases, which reduces the amount of habitat available for mussels. Channel slope and velocity would be expected to have similar effects on mussels; as channel slope increases, so does velocity. This increase in velocity could dislodge mussels (Strayer 2008), especially at high flows, which could explain the negative relationships demonstrated in our biplots. An intact buffer zone has also been shown to be critical to mussel assemblages through mediating effects on water temperature and inputs of sediment and pollutants (Brainwood et al. 2006, Richardson et al. 2010).

The strongest associations at the 1000 m scale (Figure 3c) were between mussel assemblage $E$ and $D$ and % forest (1000 m) (+) and between mussel density and % wetland (1000 m) (+) and drainage area (-). These relationships are in agreement with previous studies (Hoggarth et al. 1995, Poole and Downing 2004, Mynsberge et al. 2009).
Although a negative relationship with drainage area does not align with some reports (e.g., Watters 1992,) greater density and diversity at our upstream sites is consistent with previous surveys in the study catchment (personal communication, Watters 2012). Land-cover influences could also be influencing this observation, as our upstream study reaches were dominated by forest, whereas many of our downstream reaches were located in agriculture landscape matrices, thus potentially limiting mussel diversity (Hoggarth et al. 1995, Poole and Downing 2004).

Our dataset accounted for almost the total variation in the mussel assemblages, pointing to potential overparameterization and/or insufficient truncation during the ordination procedures, particularly in terms of the spatial matrix. Therefore, although we have confidence in the overall patterns, we offer this caveat in fully interpreting some of the specific results.

This study contributes to a growing understanding of the multiple mechanisms that structure freshwater mussel assemblages. In particular, a singular focus on local-scale environmental variables may underestimate the importance of broad-scale processes (e.g., dispersal, catchment-scale hydrology, land use and land cover; Palmer et al. 1996, Mynsberge et al. 2009, Marzin et al. 2013), and vice versa, whereby fine-scale variables may be critical in predicting mussel assemblage structure (Layzer and Madison 1995, Gangloff and Feminella 2007, Bey and Sullivan Chapter 2)., The significant influence of variation shared by both local- and landscape-scale variables (i.e., joint) suggests that cross-scale interaction effects may be an important factor governing freshwater mussel assemblages. Catchment context also appears to be of considerable importance, as
significant variability exists relative to the precise nature of the influences of environmental factors across spatial scales in differing physiographic and land-use regimes (Esselman and Allen 2010, Cunico et al. 2012, Kautza and Sullivan 2012a). Furthermore, teasing out the independent effects of the shared component will be an important step in targeting influential environmental factors. Collectively, our results show a strong influence of scale-dependent environmental factors on freshwater mussel assemblages, suggesting that conservation and management schemes will benefit from approaches that combine reach- and catchment-level assessments.

Acknowledgements

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References


Environmental Resources Congress. American Society of Civil Engineers, Reston, VA, Salt Lake City.


Witter, J. D. 2006. Water quality, geomorphology, and aquatic life assessments for the Olentangy River TMDL evaluation. The Ohio State University, Columbus, Ohio.


Table 8 (Chapter 3 Table 1). Soil and Water Assessment Tool (SWAT) input parameters that were modified for model calibration using Big Darby Creek catchment, OH USA.

The baseflow alpha number is a model parameter that estimates the change in groundwater in response to recharge. The Soil Conservation Curve (SCS) number is a model parameter that estimates surface runoff based on soil and land use characteristics.

<table>
<thead>
<tr>
<th>Calibration variable</th>
<th>Original/default value</th>
<th>Calibrated value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manning's $n$ for main channel</td>
<td>0.014</td>
<td>0.050</td>
</tr>
<tr>
<td>Baseflow alpha factor</td>
<td>0.048</td>
<td>0.020</td>
</tr>
<tr>
<td>SCS curve default</td>
<td></td>
<td>+ 10%</td>
</tr>
<tr>
<td>Surface runoff lag coefficient</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Manning's $n$ for tributary channels</td>
<td>0.014</td>
<td>0.044</td>
</tr>
</tbody>
</table>
Table 9 (Chapter 3 Table 2). Summary statistics for predictor variables (fish, local-scale, and catchment-scale) from the 20 study reaches in Big Darby Creek, OH. Variables in italics were removed following pairwise multivariate correlations for Pearson correlation coefficients ($r > 0.80$). Variables in bold were the 19 ($n - 1$) variables selected by forward selection to be significant predictors.

<table>
<thead>
<tr>
<th></th>
<th>Minimum m</th>
<th>Median</th>
<th>Maximum m</th>
<th>Mean</th>
<th>SD</th>
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</thead>
<tbody>
<tr>
<td><strong>Fish assemblages</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density (individuals m$^{-3}$)</td>
<td>0.5</td>
<td>2.1</td>
<td>9.8</td>
<td>2.5</td>
<td>2.1</td>
</tr>
<tr>
<td>Species richness ($S$)</td>
<td>6.0</td>
<td>10.5</td>
<td>19.0</td>
<td>10.6</td>
<td>3.0</td>
</tr>
<tr>
<td>Evenness ($E$)</td>
<td>0.5</td>
<td>0.8</td>
<td>2.9</td>
<td>1.2</td>
<td>0.8</td>
</tr>
<tr>
<td>Simpson's Index ($D$)</td>
<td>0.13</td>
<td>0.19</td>
<td>0.55</td>
<td>0.21</td>
<td>0.09</td>
</tr>
<tr>
<td>Shannon-Weiner Index ($H'$)</td>
<td>1.0</td>
<td>1.9</td>
<td>2.4</td>
<td>1.8</td>
<td>0.3</td>
</tr>
<tr>
<td><strong>Local-scale environmental variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Channel slope (m m$^{-1}$)</td>
<td>0.003</td>
<td>0.009</td>
<td>0.051</td>
<td>0.013</td>
<td>0.012</td>
</tr>
<tr>
<td>$D_{50}$ (mm)</td>
<td>21.0</td>
<td>35.0</td>
<td>98.0</td>
<td>43.3</td>
<td>21.0</td>
</tr>
<tr>
<td>Embeddedness (%)</td>
<td>11</td>
<td>34</td>
<td>70</td>
<td>35</td>
<td>16</td>
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<tr>
<td>Mean depth (m)</td>
<td>0.3</td>
<td>0.8</td>
<td>1.2</td>
<td>0.8</td>
<td>0.3</td>
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<tr>
<td>Shear stress (kg m$^{-2}$)</td>
<td>1.39</td>
<td>6.04</td>
<td>27.01</td>
<td>6.56</td>
<td>5.47</td>
</tr>
<tr>
<td>Velocity (m s$^{-1}$)</td>
<td>1.2</td>
<td>2.2</td>
<td>4.5</td>
<td>2.2</td>
<td>0.8</td>
</tr>
<tr>
<td>% Agriculture 100 m buffer</td>
<td>0.0%</td>
<td>15.9%</td>
<td>78.3%</td>
<td>19.2%</td>
<td>19.5%</td>
</tr>
<tr>
<td>% Developed 100 m buffer</td>
<td>0.0%</td>
<td>0.0%</td>
<td>34.8%</td>
<td>6.6%</td>
<td>11.1%</td>
</tr>
<tr>
<td>% Wetland 100 m buffer</td>
<td>0.0%</td>
<td>2.9%</td>
<td>32.5%</td>
<td>7.1%</td>
<td>8.9%</td>
</tr>
<tr>
<td>% Forest 100 m buffer</td>
<td>0.0%</td>
<td>40.4%</td>
<td>87.8%</td>
<td>41.6%</td>
<td>25.9%</td>
</tr>
<tr>
<td><strong>Catchment-scale environmental variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Agriculture 1000 m buffer</td>
<td>24.9%</td>
<td>62.5%</td>
<td>85.6%</td>
<td>58.2%</td>
<td>20.8%</td>
</tr>
<tr>
<td>% Developed 1000 m buffer</td>
<td>1.7%</td>
<td>5.9%</td>
<td>23.9%</td>
<td>9.3%</td>
<td>7.4%</td>
</tr>
<tr>
<td>% Forest 1000 m buffer</td>
<td>7.0%</td>
<td>22.1%</td>
<td>62.4%</td>
<td>25.7%</td>
<td>16.6%</td>
</tr>
<tr>
<td>% Wetland 1000 m buffer</td>
<td>0.0%</td>
<td>0.9%</td>
<td>1.6%</td>
<td>0.8%</td>
<td>0.4%</td>
</tr>
<tr>
<td>Drainage area (km$^2$)</td>
<td>531.68</td>
<td>1194.95</td>
<td>1437.30</td>
<td>1121.97</td>
<td>305.15</td>
</tr>
<tr>
<td>$FLOW_{IN}$ (m$^3$ s$^{-1}$)</td>
<td>13.25</td>
<td>23.99</td>
<td>37.08</td>
<td>25.66</td>
<td>9.18</td>
</tr>
<tr>
<td>Organic N (kg ha$^{-1}$)</td>
<td>84.99</td>
<td>87.76</td>
<td>92.73</td>
<td>87.84</td>
<td>1.94</td>
</tr>
<tr>
<td>Organic P (kg ha$^{-1}$)</td>
<td>14.15</td>
<td>15.01</td>
<td>15.09</td>
<td>15.01</td>
<td>0.47</td>
</tr>
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Table 9 Continued (Chapter 3 Table 2).

<table>
<thead>
<tr>
<th></th>
<th>Minimum (mg L$^{-1}$)</th>
<th>Median (mg L$^{-1}$)</th>
<th>Maximum (mg L$^{-1}$)</th>
<th>Mean (mg L$^{-1}$)</th>
<th>SD (mg L$^{-1}$)</th>
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<tr>
<td>SED_CONC (mg L$^{-1}$)</td>
<td>928.28</td>
<td>1501.68</td>
<td>4673.57</td>
<td>2008.19</td>
<td>1261.40</td>
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Table 10 (Chapter 3 Table 3). Summary statistics for the mussel assemblage at study reaches in Big Darby Creek, OH, USA.

<table>
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<tr>
<th>Mussel assemblages</th>
<th>Minimum</th>
<th>Median</th>
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<tbody>
<tr>
<td>Density (individuals m$^{-2}$)</td>
<td>0.00</td>
<td>0.03</td>
<td>0.84</td>
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<td>Evenness ($E$)</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
<td>0.38</td>
<td>0.44</td>
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<td>Shannon-Weiner informational index ($H'$)</td>
<td>0.00</td>
<td>0.00</td>
<td>2.14</td>
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</tr>
<tr>
<td>Simpson's index ($D$)</td>
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<td>0.00</td>
<td>0.95</td>
<td>0.27</td>
<td>0.37</td>
</tr>
<tr>
<td>Species richness ($S$)</td>
<td>0.0</td>
<td>1.0</td>
<td>12.0</td>
<td>2.7</td>
<td>3.6</td>
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</tbody>
</table>
Figure 9 (Chapter 3 Figure 1). Study reaches within Big Darby Creek catchment, OH, USA. 'Open Water' is areas of open water. 'Developed' is a combination of areas of developed open space and low, medium, and high intensities of development. 'Barren Land’ is areas of earthen materials with vegetation accounting for less than 15% of total cover. ‘Forest’ is a combination of deciduous, evergreen, and mixed forests. ‘Grassland/Herbaceous’ is areas dominated by herbaceous vegetation. ‘Agriculture’ is a combination of woody wetlands and emergent herbaceous wetlands. Landuse was downloaded from the 2006 Multi-Resolution Land Characteristics Consortium (Fry et al. 2011)
Figure 10 (Chapter 3 Figure 2). The proportion of variation in mussel assemblage characteristics accounted for by pure spatial factors (derived from a principal coordinates of neighbor matrices approach), shared (spatially-structured) fish-environmental variables, pure (non-spatial) fish variables, and pure (non-spatial) environmental variables. Proportions of explained variation were obtained from variance partitioning procedures in partial RDA. Also illustrated, (in call-out) are the relative amounts of the pure, non-spatial environmental variation accounted for by local, catchment, and joint (i.e., variation shared by both local- and catchment-scale variables) influences.
Figure 11 (Chapter 3 Figure 3). RDA biplots illustrating relationships between (a) fish assemblage density and mussel assemblage characteristics, (b) local-scale environmental variables and mussel assemblage characteristics, and (c) catchment-scale environmental variables and mussel assemblage characteristics. Thin arrows represent the direction of increase for the mussel assemblage variables and the bold arrows indicate how the environmental variables were oriented.
Figure 11 continued (Chapter 3 Figure 3).
Figure 11 continued (Chapter 3 Figure 3).
Table 11 (Chapter 3 Table 4). Water-quality parameters of study reaches.

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
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<tr>
<td>Temperature</td>
<td>10.7</td>
<td>18.0</td>
<td>27.8</td>
<td>19.8</td>
<td>5.3</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.48</td>
<td>0.84</td>
<td>0.92</td>
<td>0.78</td>
<td>0.12</td>
</tr>
<tr>
<td>DO %</td>
<td>80.0</td>
<td>136.3</td>
<td>287.0</td>
<td>156.8</td>
<td>66.7</td>
</tr>
<tr>
<td>pH</td>
<td>8.3</td>
<td>8.6</td>
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References

2005. Big Darby Creek Watershed Draft TMDL Report. in Division of Surface Water, State of Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.

2006. Total Maximum Daily Loads for the Big Darby Creek Watershed. in Division of Surface Water, Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.


D' Ambrosio, J. L., L. R. Williams, J. D. Witter, and A. Ward. 2009. Effects of geomorphology, habitat, and spatial location on fish assemblages in a watershed in Ohio, USA. Environmental Monitoring and Assessment 148:325-341.


Franklin County Metro Parks. 2009. Battelle Darby Creek. in Franklin County Metro Parks, editor., Ohio, USA.


Howard, A. D. 1915. Some exceptional cases of breeding among the Unionidae. The Nautilus 29:4-11.


OEPA. 2006. Total Maximum Daily Loads for the Big Darby Creek Watershed. *in* Division of Surface Water, Ohio Environmental Protection Agency, editor., Columbus, Ohio, USA.


Watters, G. T. 2012. Conversation about Big Darby Creek mussel populations. in C. R. Bey, editor.


Witter, J. D. 2006. Water quality, geomorphology, and aquatic life assessments for the Olentangy River TMDL evaluation. The Ohio State University, Columbus, Ohio.


Appendix A. Latitude and longitude coordinates for study reaches

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## Appendix C. Summary of geomorology data for all study reaches

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Appendix D. 2011 Permits

Division of Wildlife Headquarters
2045 Morse Road, Bldg. G
Columbus, Ohio 43229-6693
1-800-WILDLIFE

WILD ANIMAL PERMIT:  12-11

MAZEKA SP. SULLIVAN
OHIO STATE UNIVERSITY
SCHOOL OF ENVIRONMENTAL & NAT. RES., 210 KOTTMA
COLUMBUS, OH 43210

SPECIAL SECURITY NUMBER: XXX-XX-2071

is hereby granted permission to take, possess, and transport at any time and in any manner specimens of wild animals, subject to the conditions and restrictions listed below or any documents accompanying this permit.

This permit, unless revoked earlier by the Chief, Division of Wildlife, is effective
from:  3/16/2009  to:  3/15/2012

This permit must be carried while collecting wild animals and be exhibited to any person on demand.

THIS PERMIT IS RESTRICTED TO THE FOLLOWING:

1. PERMITTEE MUST NOTIFY THE DIVISION OF WILDLIFE OF EACH STUDY SITE LOCATION AND RECEIVE PRIOR APPROVAL BEFORE CONDUCTING COLLECTION ACTIVITIES.
2. PERMITTEE MAY COLLECT FISH, BIRDS, REPTILES, AMPHIBIANS, AND MACRO INVERTEBRATES FOR SURVEY AND INVENTORY. NO SPORT FISH OVER SIX (6) INCHES MAY BE RETAINED.
3. PERMITTEE MAY COLLECT BLOOD AND FEATHER SAMPLES FROM BIRDS. A USFWS PERMIT MAY BE REQUIRED IF COLLECTING MIGRATORY BIRD SPECIES.
4. ANY SPECIMEN HELD LONGER THAN 30-DAYS MUST BE HUMANELY EUTHANIZED OR RETAINED.
5. PERMITTEE MUST CONTACT THE DIVISION OF WILDLIFE IF UNDOCUMENTED AQUATIC INVASIVE SPECIES ARE DISCOVERED.
6. TWENTY-FOUR HOURS PRIOR TO COLLECTING ACTIVITIES, PERMITTEE MUST CONTACT THE LOCAL WILDLIFE OFFICER OR NEAREST WILDLIFE DISTRICT OFFICE TO ADVISE LOCATIONS AND DURATION OF SAMPLING.
7. ALL VOUCHER SPECIMENS ARE TO BE DEPOSITED AT THE OHIO STATE UNIVERSITY, MUSEUM OF BIOLOGICAL DIVERSITY OR THE CLEVELAND MUSEUM OF NATURAL HISTORY.
8. COLLECTION IS PROHIBITED IN THE KILLBUCK, BIG DARBY AND LITTLE DARBY, CHAGRIN RIVER, FISH CREEK (WILLIAMS COUNTY) AND DIVISION OF WILDLIFE PROPERTIES WITHOUT EXPEDITED WRITTEN PERMISSION FROM THE DIVISION OF WILDLIFE. ELECTROSHOCKING ONLY PERMITTED ON THE BIG DARBY WITH THIS PERMIT.
9. PERMITTEE MUST PROVIDE AN ANNUAL REPORT OF COLLECTING ACTIVITIES TO THE DIVISION OF WILDLIFE. REPORT SHALL PROVIDE SPECIES, QUANTITY AND LOCATIONS OF COLLECTION.

Locations of Collecting
STATEWIDE WITH PRIOR WRITTEN APPROVAL

Equipment and method used in collection:
ELECTROSHOCKERS, SEINES, BLOCK NETS, DIP NETS, HOOP NETS, MINNOW TRAPS, SURBER SAMPLES, MIST NETS, HAND NETS, AND ROCKET NETS

Name and number of each species to be collected:
FISH, BIRDS, MACRO-INVERTEBRATES, REPTILES, AND AMPHIBIANS. SAMPLING BY ELECTROSHOCKING ONLY IS PERMITTED ON THE BIG DARBY.
RESTRICTIVE DOCUMENTS ACCOMPANYING THIS PERMIT? NO
This permit is not valid for collecting migratory birds, their nests, or eggs unless a current permit from
the U.S. Fish and Wildlife Service has been obtained.

NO ENDANGERED SPECIES MAY BE TAKEN WITHOUT WRITTEN PERMISSION FROM THE CHIEF

ATTACHMENT
This attachment to Scientific Collecting Permit # 13-11 authorizes the following persons to
conduct the activities listed on the permit, within the conditions and restrictions set forth. Each person
must carry and exhibit upon request, a copy of the permit and this attachment when conducting any of the
listed activities. The person named on the permit assumes full responsibility for the actions of the persons
on this list and for completing and submitting all required reports.

<table>
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<tr>
<td>ADAM KAUTZA</td>
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<td>JEREMY ALBERTS</td>
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Appendix E. 2012 Permits

DIVISION OF WILDLIFE
Ohio Department of Natural Resources

WILD ANIMAL PERMIT: 15-49
SCIENTIFIC COLLECTION

MAESEIKI P. SULLIVAN
OHIO STATE UNIVERSITY
SCHOOL OF ENVIRONMENTAL & NAT. RES., 210 KOTTM
COLUMBUS, OH 43210

DATE ISSUED: 3/29/2012

SPECIAL CONDITION:

This permit, unless revoked earlier by the Chief, Division of Wildlife, is effective from:
3/16/2012 to: 3/15/2015

This permit must be carried while collecting wild animals and be exhibited to any person on demand.

THE PERMIT IS RESTRICTED TO THE FOLLOWING:

1. PERMITTEE MUST NOTIFY THE DIVISION OF WILDLIFE (DOW) OF EACH STUDY SITE LOCATION AND RECEIVE PRIOR APPROVAL BEFORE CONDUCTING COLLECTION ACTIVITIES.
2. PERMITTEE MAY COLLECT FISH, BIRDS, REPTILES, AMPHIBIANS, MOLLUSKS, AND MACROINVERTEBRATES FOR SURVEY AND INVENTORY. RACCOONS MAY ALSO BE LIVE TRAPPED FOR RESEARCH. NO SPORT FISH OVER SIX (6) INCHES MAY BE RETAINED. MOLLUSKS MAY NOT BE REMOVED FROM THE SITE AND MUST BE IMMEDIATELY RETURNED TO THE COLLECTION LOCATION UPON IDENTIFICATION.

3. AREAS WHERE THE NORTHERN RIFFLE SHELL AND CLUB SHELL HAVE BEEN REINTRODUCED MUST BE AVOIDED.
4. PERMITTEE MAY COLLECT BLOOD AND FEATHER SAMPLES FROM BIRDS. A USFWS PERMIT MAY BE REQUIRED IF COLLECTING MIGRATORY BIRD SPECIES.
5. ANY SPECIMEN HELD LONGER THAN 30 DAYS MUST BE HUMANELY EUTHANIZED OR RETAINED.
6. PERMITTEE MUST CONTACT THE DOW IF UNDOCUMENTED AQUATIC INVERTEBRATE SPECIES ARE DISCOVERED.
7. TWENTY-FOUR HOURS PRIOR TO COLLECTING ACTIVITIES, PERMITTEE MUST CONTACT THE LOCAL WILDLIFE OFFICER OR NEAREST WILDLIFE DISTRICT OFFICE TO ADVISE LOCATIONS AND DURATION OF SAMPLING.
8. ALL TRAPS MUST BE CLEARLY LABELED WITH THE CONTACT INFORMATION OF THE RESPONSIBLE PERSON. TRAPS MUST BE CHECKED WITHIN 24 HOURS OF DEPLOYMENT.
9. ALL VOUCHER SPECIMENS ARE TO BE DEPOSITED AT THE OSU, MUSEUM OF BIOLOGICAL DIVERSITY.
10. COLLECTION IS PROHIBITED IN THE KILLBUCK, TRIBUTARIES TO AND EAST BRANCH OF THE CHAGRIN RIVER NORTH OF 480, FISH CREEK (WILLIAMS COUNTY) AND DIVISION OF WILDLIFE PROPERTIES WITHOUT EXPLICIT WRITTEN PERMISSION FROM THE DOW. PERMISSION IS GRANTED FOR MUSSEL WORK IN THE DARYS WATERSHED. ELECTROSHOCKING ONLY IS PERMITTED IN THE BIG DARYS WITH THIS PERMIT.
11. PERMITTEE MUST PROVIDE AN ANNUAL REPORT OF COLLECTING ACTIVITIES TO THE DOW IN THE DIVERSITY DATABASE EXCEL SPREADSHEET (PROVIDED WITH PERMIT). A COPY OF ANY PUBLISHED REPORTS FROM THIS PROJECT SHOULD ALSO BE SENT TO THE DOW.

Locations of Collecting:
STATEWIDE WITH NOTED EXCEPTIONS

Equipment and method used in collection:
ELECTROSHOCKER, BINES, BLOCK NETS, DIP NETS, HOOP NETS, MINNOW TRAPS, SURGER SAMPLES,
MIST NETS, HAND NETS, BOX TRAPS AND ROCKET NETS
ATTACHMENT

This attachment to Scientific Collecting Permit #15-49 authorizes the following persons to conduct the activities listed on the permit, within the conditions and restrictions set forth. Each person must carry and exhibit upon request, a copy of the permit and this attachment when conducting any of the listed activities. The person named on the permit assumes full responsibility for the actions of the persons on this list and for completing and submitting all required reports.

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<tr>
<th>Name</th>
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<td>MATTHE MCFARLAND</td>
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<td>CLARISSA BEY</td>
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July 20, 2012

Dr. Mazenka S.P. Sullivan
School of Environment and Natural Resources
The Ohio State University
2021 Coffey Road
Columbus, OH 43210

Dear Dr. Mazenka:

This letter shall serve as your permit to continue your study of changes in geomorphology as they relate to darter and mussel populations in Big Darby Creek at Battelle Darby Creek Metro Park and Prairie Oaks Metro Park. This information will be helpful in OSU’s and the Columbus Zoo’s effort in propagating darters and mussels to be released into Ohio streams, possibly including some Metro Parks stream reaches. As discussed in your conversation with Mac Albin, great care will be taken in capturing and releasing the darters unharmed on site using your backpack electro-fishing gear. Your students and yourself will also follow accepted safety precautions in the use of the gear, and when you might come into contact with the public. In addition:

1) Please notify the Park Managers (Battelle Darby Creek - Kevin Kasnyik, 878-1076; Prairie Oaks - Tom Cochran, 879-0020) before you or your graduate students visit the park for your research. If you have a schedule of visits, you can submit that (please notify in case of changes). Carry this permit or a copy with you (or graduate students) on your visits.

2) Please submit a summary or progress report of your study to Mac Albin (albin@metroparks.net) before July 31, 2013.

3) You will be limited to 4 sampling sites at Prairie Oaks and 6 sites at Battelle Darby Creek.

Good luck with your research.

Sincerely,

[Signature]

John O’Meara
Executive Director

cc: Kasnyik, Cochran, Albin