

Unionid Habitat and Assemblage Composition in Coastal Plain Tributaries of Flint River (Georgia)

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Abstract - Effective conservation of mussels in streams of the lower Flint River basin, southwest Georgia, requires more rigorous understanding of mussel-habitat associations and factors shaping assemblage composition in stream reaches. We surveyed mussels and habitat conditions at 46 locations, and used regression, correlation and multivariate direct gradient analysis (Canonical Correspondence Analyses) to identify species-habitat relationships and characteristic species-assemblage types in Flint basin streams. Riparian wetland and catchment forest cover, average mid-channel depth, and drainage network position accounted for 49% of the variability in mussel species richness, 36% of the variability in unionid abundance, and 32% of the variability observed in Shannon-Wiener diversity across survey sites. Species were grouped into four assemblage types based on their habitat associations: large-river-riffle associates, slackwater associates, habitat generalists, and stream-run associates. Results are broadly concordant with anecdotal reports of mussel-habitat relationships and provide insight into the habitat conservation needs of mussels.

Introduction

Freshwater mussels are among the most imperiled of North American fauna. About 70% of almost 300 native species are currently identified as endangered, threatened, or sensitive (Neves et al. 1997, Williams et al. 1993), with most species experiencing habitat loss across their ranges. Developing effective conservation and recovery strategies for unionids requires knowledge of habitat needs for mussels and environmental factors controlling distribution patterns. Prior studies indicate that unionid distribution and abundance is related to physical, chemical, and biotic factors across multiple scales (Bauer et al. 1991; Brim Box 1999; DiMaio and Corkum 1995; Haag and Warren 1998; Mamilton et al. 1997; Howard 1997; Morris and Corkum 1996; Strayer 1983, 1993; Strayer and Ralley 1993; Strayer et al. 1994; Vannote and Minshall 1982; Watters 1992, 1993). However, despite substantial anecdotal information about mussel habitat preferences, little empirical evidence currently exists to demonstrate links between habitat and particular mussel species and assemblages.

The objective of this study was twofold. First, we sought to identify patterns in species-assemblage composition across stream reaches in the

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tributary streams of the Coastal Plain portion of the Flint River Basin (lower FRB), and, if possible, characterize specific assemblage types based on the habitat associations of mussels. Second, we aimed to identify multiple-scale habitat conditions associated with the occurrence of freshwater mussel assemblages, and mussel community richness and diversity within 100-m stream segments in the lower FRB. We assessed habitat features at two spatial scales. Mesoscale (reach-scale) habitat conditions included composite measures of stream gradient, channel depth, hydrologic variability, stream ion content, and substrate composition. Macrohabitat (catchment-scale) variables included measures of stream size and drainage position (catchment area, d-link magnitude), predominant catchment landcover, riparian land use, and physiographic province type.

Methods

Study area and mussel surveys

Most of the streams in the lower FRB originate in the Fall Line Hills physiographic province, and are characterized by sandy mud bottoms and high turbidity. At the lower end of the drainage, streams flow into the Dougherty Plain physiographic province, a Coastal Plain region underlain by a shallow carbonate aquifer with direct links to surface water. Streams in the Dougherty Plain frequently dissect carbonate rocks and are relatively high in conductivity and alkalinity. Coastal Plain streams are generally naturally high in fine sand substrates and are low gradient throughout the entire system; large portions of the stream continuum, from headwaters to confluences, may anastomose and flow through marshy, slackwater, swampy areas.

In the lower FRB, agriculture and plantation forest are the predominant land-cover types, but stream-drainage networks are buffered by extensive forested floodplains (Houhoulis and Michener 2000, Lowrance et al. 1984), and marked by low levels of urban impacts, high water quality (Golladay et al. 2000), and relatively intact biotic communities. Most purported impacts likely result from agricultural practices and are not associated with point sources, except near urban areas.

Unionid communities derive from eastern Atlantic and western Gulf drainages (Johnson 1970). The FRB once supported 29 unionid species, seven of which were endemic to the Apalachicola drainage (Clench and Turner 1956). Currently, four federally endangered or threatened species persist in the lower FRB. Mussel communities within lower FRB streams represent the most diverse assemblages in the Apalachicola-Chatahoochee-Flint River Basin (Brim Box and Williams 2000). Although non-native *Dreissena* spp. have not been found in the basin, exotic *Corbicula* spp. are widespread and abundant.

During mid-June–late August, 1999, we conducted mussel surveys at 46 sites on 12 tributary streams in the lower FRB (Fig. 1). Survey sites were

located near bridge crossings at regular intervals along the longitudinal progression from headwaters to the Flint River confluence on each stream. At each site, we sampled a 100-m segment of stream bed beginning at 100 m and ending at 200 m upstream from the bridge. We sampled for mussels by visually searching the substrate and by sieving surface sediment with our fingers to a depth of about 5 cm. To standardize the amount of streambed sampled among various-sized streams, the following methodology was em-

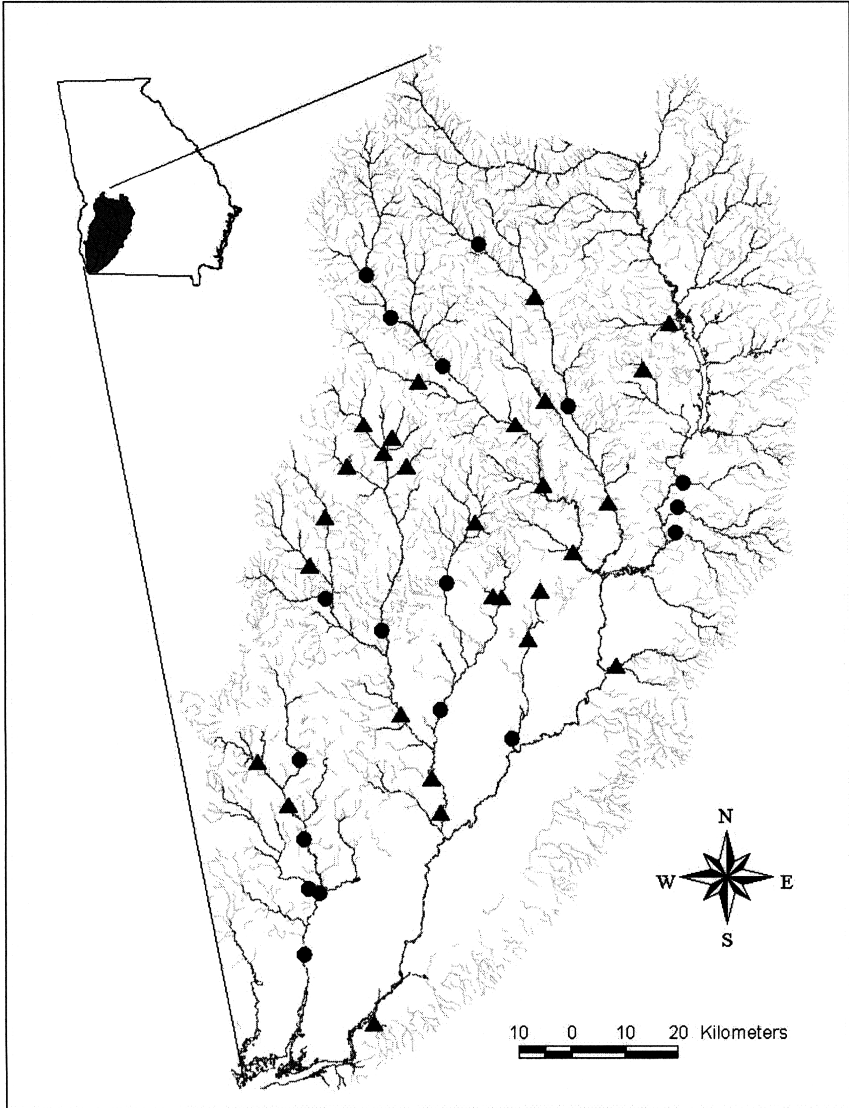


Figure 1. Locations (represented by circles and triangles) of mussel survey sites in the lower Flint River Basin (Coastal Plain portion), southwest Georgia. Circles indicate sites where endangered species were found.

ployed. In small streams (< 12 m wide), we surveyed the entire bed surface within the 100-m survey reach. In large streams (> 12 m wide), we conducted mussel searches along six transects placed parallel to stream flow along the length of the stream reach. Transects were two meters wide and evenly spaced across the width of the stream, with one transect in each bank. In both stream-size classes, we conducted surveys only in the main channel(s) of the stream; minor channels and ponded areas in floodplains were not searched.

We removed live mussels from the substrate, identified them, and then immediately returned them to the stream bottom. If more than 1000 individuals of any species were found before reaching the end of the sample area, we discontinued counting that species. Unionids were identified to species level, except *Elliptio complanata* (Lightfoot) and *Elliptio icterina* (Conrad), which were grouped together because of the difficulty in distinguishing the two species in the field. Dead shells found during the searches were collected, identified, and deposited at the Georgia Museum of Natural History.

Mesohabitat data

Habitat factors selected for this study were demonstrated to influence mussel distribution patterns elsewhere in North America (Bauer et al. 1991; Brim Box 1999; DiMaio and Corkum 1995; Haag and Warren 1998; Howard 1997; Morris and Corkum 1996; Strayer 1981, 1983, 1993; Strayer et al. 1994; Vannote and Minshall 1982; Watters 1992, 1993; Way et al. 1989), or were thought to be major habitat drivers in the Flint River basin (Brim Box 1999). We collected all mesohabitat data (except water samples) during baseflow conditions between July and August 1999 (Table 1).

We measured canopy openness (*canop*), coarse woody debris density (*cwdebris*) and average mid-channel depth (*avgdepth*) along a mid-channel transect extending the length of each 100-m survey reach. At 20-m intervals along the transects, we determined canopy openness by taking four spherical densiometer readings (upstream, downstream, left bank, right bank). At 10-m intervals we made water depth measurements. We estimated coarse woody debris density in the survey area by recording the size and number of logs > 10 cm in diameter intercepting the mid-channel transect.

At each site, we determined sediment bulk density (*bulkdens*), a measure of substrate porosity, from three substrate core samples collected using a 4.7-cm diameter PVC pipe inserted to a depth of 8.5 cm in the substrate at mid-channel at the beginning of each survey reach. Sediments captured in the core were removed, and samples were brought to the lab, dried for two months under ambient conditions, then weighed. Bulk density was calculated as sediment dry weight per unit wet volume.

We collected water samples from each survey site between August 31 and September 8 following several weeks of no rain. Samples were placed in plastic storage bottles and refrigerated until processed, 5–7 days after

Table 1. Physical habitat parameters collected within each survey reach (mesohabitat parameters), watershed and riparian zone landscape data (macrohabitat factors) determined for each study site, and mussel-community metrics employed in analyses.

Metric	Description	Collection method	Transformation	In reduced data set
Mesohabitat variables				
avgdepth	Average baseflow water depth at midchannel (m)	Longitudinal line transect	log 10	Yes
slope	Elevation change over 100 m survey reach (m)	Longitudinal profile survey	sqrt	Yes
flowstab	Base flow water level: bankfull water level	x-section profile survey		Yes
incision	Bankfull width: bankfull depth	x-section profile survey	log 10	Yes
mannn	Manning's n parameters	Visual	log 10	Yes
habdiv	Shannon index of microhabitat diversity	x-section line transect	log 10	No
pool	Frequency of pool microhabitat (%)	x-section line transect	-	No
riffle	Frequency of riffle microhabitat (%)	x-section line transect	-	No
finest	Frequency of fine sediment cover (%)	x-section line transect	arcsin-sqrt	Yes
bulkdens	Dry mass of sediment/mL of wet volume (g/mL)	Drying and weighing		Yes
detritus	Frequency of detritus on substrate surface (%)	x-section line transect		Yes
cwdebris	Frequency of logs > 10 cm diameter (#/10m)	Longitudinal line transect	arcsin-sqrt	Yes
cond	Water conductivity (mhos)	YSI meter	-	Yes
canop	Canopy openness at midchannel (%)	Longitudinal line transect	sqrt	Yes
Macrohabitat variables				
physio	Physiographic province type	1:2000 K Physiography map		No
catarea	Catchment area	1: 100 K DEMs	log 10	Yes
netpos	d-link magnitude	1:100 K DLGs	log 10	Yes
catrdens	Catchment road density (km/km ²)	1:100 K DLGs	-	No
caforest	Proportion of catchment in forest cover (%)	1998-90 Landsat TM		Yes
catwet	Proportion of catchment in wetland cover (%)	1998-90 Landsat TM		Yes
catag	Proportion of catchment in agriculture cover (%)	1998-90 Landsat TM		No
caturban	Proportion of catchment in urban cover (%)	1998-90 Landsat TM		No
ripddens	Riparian road density (km/km ²)	1:100 K DLGs	-	No
ripforest	Proportion of riparian area in forest cover (%)	1998-90 Landsat TM	arcsin-sqrt	Yes
ripwet	Proportion of riparian area in wetland cover (%)	1998-90 Landsat TM		Yes
ripag	Proportion of riparian area in agriculture cover (%)	1998-90 Landsat TM		No
ripurban	Proportion of riparian area in urban cover (%)	1998-90 Landsat TM		No
Mussel metric				
richness	Number of species at survey site	1999 survey		NA
abund	Number of live individuals at survey site	1999 survey	log 10	NA
swdiv	Shannon-Weiner diversity			

collection. Alkalinity (*alk*) was determined using a Mettler DL12 titrator (Mettler Electronics Corporation, Miami, FL). Conductivity (*cond*) measurements were made using a YSI® Meter #33 (YSI Incorporated, Yellow Springs, OH).

We measured the remaining mesohabitat variables along two cross-section transects (at 10-m and 75-m points along each 100-m reach) mapped following Harrelson et al. (1994). We calculated stream incision (*incision*) as the ratio of bankfull (determined from visual estimates of bankfull level) width to bankfull depth measurements (therefore, a smaller number indicates a higher degree of streambed incision). Flow stability (*flowstab*), an approximation of the degree of hydrologic variability, was the ratio of average base-flow water depth to average bankfull water depth (a value of 1 indicates high flow stability; values less than 1 indicate flow instability). The proportion of survey area covered by detritus (*detritus*), fine sediments (*finest*), and slackwater/pool (*pool*) and riffle (*riffle*) habitat was estimated by recording the type of substrate and flow conditions at 1-m intervals along each cross-section transect. We classified substrate by visual identification according to a modified Wentworth scale (Cummins 1962). Slackwater/pool habitat was defined as areas of slow-moving to stagnant water greater than 10 cm deep with substrate consisting of mud, clay, or detritus. Riffle habitat was defined as areas of fast-moving water less than 10 cm in depth, with substrate consisting of gravel and cobble- and boulder-sized limestone. We determined the Shannon-Wiener index of habitat diversity (*habdiv*) from the number of unique combinations of substrate (7 classes: clay, sand, gravel, cobble, boulder, bedrock, detritus) and water depth (4 classes: 0–0.1m, 0.1–0.5m, 0.5–1.5m, > 1.5m) occurring along the cross-section transects.

Finally, we assessed channel roughness (*mannn*), a measure of streambed irregularity and frequency of flow obstructions and refuges, using Manning's *n* roughness coefficients. We determined the composite Manning's *n* value from scores we assigned to each of six stream roughness factors: substrate composition, channel irregularity, variation in channel cross section, obstructions, vegetation, and degree of meandering (Cowan 1956).

Macrohabitat data

Using a Geographical Information System (Environmental Systems Research Institute, Inc., 1999), we compiled all of the macrohabitat data (Table 1). We determined the physiographic province (*physio*) into which each site fell based on the 1:2,000,000 Georgia Geologic Survey Physiographic Province Map.

We characterized drainage network position (*netpos*) of each survey site using the 1:100,000 Digital Line Graphs (DLGs, US Geological Survey, Reston, VA) to calculate d-link magnitude. The d-link magnitude is the number of first-order streams draining into the point immediately below the

first confluence downstream from each survey reach (Osborne and Wiley 1992). Unlike stream order or link magnitude metrics, d-link magnitude approximates the functional size of a stream by adjusting for the effect of adjacent waterways and the position of the stream in the drainage network. For example, the d-link magnitude value for streams draining directly into large rivers is the sum of the link magnitude of the subject stream plus the link magnitude of the adjacent large river.

We identified catchment areas (*catarea*) for each survey site by using 1:100,000 Digital Elevation Models (US Geological Survey, Reston, VA) and the ArcView Hydrologic Modeling Extension (v1.0) to create polygons around the drainage area for each site. We delineated riparian zones adjacent to and upstream from each site by digitally creating a 250-m buffer polygon around 1 km of stream length above each survey location. To determine road density (*riprddens*; *catrddens*) upstream from each survey site we overlaid each catchment and riparian polygon on 1:100,000 DLGs. We determined the proportion of riparian zone and catchment area in forest (*ripforest*; *catforest*), agriculture, wetland, and urban landcover in the same manner as the roads using a landcover map prepared from Landsat TM imagery taken during the winters of 1988–1990 (Georgia Department of Natural Resources, Atlanta, GA).

Analysis methods

To quantify mussel communities in each survey reach, we calculated three metrics: unionid richness (*richness*; number of species), abundance (*abund*; number of individuals), and Shannon-Wiener diversity (*swdiv*). Where necessary, we transformed habitat measurements to normalize data (Table 1) and removed highly correlated variables and habitat factors that did not exhibit a wide range of variability across the survey sites. We also identified sources of multicollinearity by calculating Pearson correlations between all variables. We omitted variables if they were highly correlated with others ($r > 0.5$) and duplicated information provided by other variables (e.g., we omitted *catag* because it was highly negatively correlated to *catforest*).

We identified the strongest meso- and macrohabitat predictors of diversity, richness, and abundance using multiple regression with the maximum adjusted r^2 selection method (PROC REG, SAS v 8.1). We tested for patterns of mussel species and habitat associations using Canonical Correspondence Analysis (CCA; ter Braak 1986; PCord v 2.0) of species abundances and meso and macrohabitat variables across all survey sites.

To test the strength of habitat variables associated with each assemblage type, habitat variables at sites supporting each mussel assemblage type were compared to variables of non-supporting sites using the Mann-Whitney U test (PROC NPARIWAY, SAS v 8.1). Sites were classified as supporting a particular mussel assemblage type if 10 or more individuals of assemblage-type species were found at that site during our survey.

Results

General mussel survey data

Across all survey sites, we found 14,873 unionids, including 19 of the 29 species historically inhabiting the lower FRB. Four species comprised 85%

Table 2. Relative abundance of each species across all survey sites. Total abundance of species in all survey sites was 14,786. Current conservation status (Brim Box and Williams 2000) is indicated next to the species name: * = currently stable; # = special concern; ## = federally endangered

Species	Relative abundance (%)
<i>Elliptio complanata/icterina</i> (eastern elliptio and variable spike) *	57.70
<i>Villosa lienosa</i> (little spectaclecase) *	14.92
<i>Elliptio crassidens</i> (elephantear) *	13.51
<i>Villosa vibex</i> (southern rainbow) *	3.20
<i>Toxolasma paulus</i> (iridescent lilliput) *	3.18
<i>Quincuncina infucata</i> (sculptured pigtoe) #	3.01
<i>Lampsilis subangulata</i> (shiny-rayed pocketbook) ##	1.16
<i>Elliptio purpurella</i> (inflated spike) #	1.03
<i>Unio merus carolinianus</i> (Florida pondhorn) *	0.79
<i>Pleurobema pyriforme</i> (oval pigtoe) ##	0.34
<i>Utterbackia imbecillis</i> (paper pondshell) *	0.28
<i>Villosa villosa</i> (downy rainbow) #	0.21
<i>Lampsilis straminea claibornensis</i> (southern fatmucket) #	0.20
<i>Elliptio arctata</i> (delicate spike) #	0.18
<i>Medionidus pencillatus</i> (gulf moccasinshell) ##	0.07
<i>Pyganodon grandis</i> (giant floater) *	0.07
<i>Strophitus subvexus</i> (southern creekmussel) #	0.07
<i>Megaloniaias nervosa</i> (washboard) *	0.04
<i>Utterbackia peggyae</i> (Florida floater) *	0.03

Table 3. Models of mussel community diversity (Shannon-Wiener), species richness and unionid abundance selected through stepwise regression analysis using meso and macrohabitat predictor variables. (Mussel abundance, avgdepth, and netpos were log10 transformed prior to analyses.)

Variables		R ²	F	Prob > F
Dependent	Independent			
Macrohabitat variables only				
Diversity	0.12 + 1.78(ripwet) ^{◊◊} + 0.27(netpos) [◊]	0.16	3.98	0.02
Richness	-1.71 + 16.89(ripwet) [◊] + 2.76(netpos) [◊]	0.37	12.57	0.00
Abundance	0.34 + 5.88(ripwet) [◊] + 0.45(netpos) [◊]	0.25	5.36	0.00
Mesohabitat variables only				
Diversity	1.97-0.63(flowstab) ^{◊◊} -3.21(bulkdens) [◊] + 1.91(avgdepth) [◊]	0.27	4.79	0.01
Richness	1.76 + 21.86(mann) [◊] + 12.95(avgdepth) [◊]	0.28	7.74	0.00
Abundance	No significant model			
Meso- and Macrohabitat variables combined				
Diversity	0.88 + 0.70(avgdepth) [◊] + 0.25(netpos*ripwet) ^{◊◊}	0.32	9.94	0.00
Richness	3.43 + 3.67(avgdepth) [◊] + 2.17(netpos*ripwet) [◊] + 2.14(netpos*catforest) [◊]	0.49	13.59	0.00
Abundance	0.18 + 0.80(avgdepth) [◊] + 1.70(netpos) [◊] + 4.31(ripwet) [◊] - 1.36(netpos*ripwet) [◊]	0.36	5.72	0.00

[◊]p < 0.05; ^{◊◊}p < 0.10

of the individuals encountered, and nine species accounted for 96% of the mussels surveyed (Table 2). Three federally endangered species, *Lampsilis subangulata* (Lea), *Pleurobema pyriforme* (Lea), and *Medionidus pencillatus* (Lea) were found in isolated locations throughout the basin, usually in very low numbers (Fig. 1). Species richness ranged from 0 to 11 species per site, averaging 6 per site, and unionid abundance ranged from 0 to 1723 individuals per site, averaging 323 native mussels per site. *Corbicula* numbers ranged from 0 to > 1000 per site.

Mussel assemblage-habitat associations

The reduced habitat data set included 11 mesohabitat and 7 macrohabitat variables (Table 1). Average mid-channel depth, drainage network position, riparian wetland cover, and catchment forest cover were the best predictors of mussel richness, abundance, and diversity (Table 3). These habitat variables accounted for 32–49% of the variance observed in mussel community metrics. When only macrohabitat variables were included in the regression analysis, riparian wetland cover and drainage network position were consistently selected as the best predictors, explaining 16–37% of the variance in the three mussel metrics. In a regression analysis consisting only of mesohabitat variables, flow stability, bulk density, average mid-channel depth, and channel roughness (*mannn*) were selected as the variables that best explained diversity and richness.

Table 4. Canonical correspondence analysis variance scores, species-habitat Pearson correlations, Monte Carlo test results (for 99 runs of species-habitat correlations), and correlation scores (bottom portion of table) for habitat variables and CCA axes.

	Meso- + macrohabitat CCA		Macrohabitat CCA		Mesohabitat CCA	
% variance explained	16.3	12.6	13.2	8.1	14.6	7.3
Species-habitat correlation	0.829	0.838	0.762	0.698	0.792	0.705
Monte-Carlo test	p < 0.07	p < 0.07	p < 0.01	p < 0.01	p < 0.03	p < 0.07
Variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
avgdepth	-0.485	-0.132	-	-	-0.538	0.533
slope	-0.039	-0.133	-	-	-0.016	-0.017
flowstab	-0.131	-0.310	-	-	-0.129	0.529
incision	-0.057	-0.158	-	-	-0.028	0.130
mannn	0.054	-0.189	-	-	0.079	0.058
finest	0.708	-0.252	-	-	0.754	0.374
bulkdens	-0.293	-0.137	-	-	-0.295	0.043
detritus	0.475	-0.216	-	-	0.515	0.068
cwdebris	0.345	-0.438	-	-	0.380	0.598
cond	-0.110	0.201	-	-	-0.103	-0.501
canop	-0.405	-0.047	-	-	-0.453	0.168
catarea	-0.637	-0.403	-0.796	-0.401	-	-
netpos	-0.377	0.394	-0.374	0.501	-	-
catforest	0.150	0.135	0.157	0.030	-	-
catwet	-0.184	0.089	-0.207	0.237	-	-
ripforest	0.247	-0.041	0.265	-0.129	-	-
ripwet	0.421	-0.515	0.358	-0.755	-	-

Overall, macro- and mesohabitat variables accounted for up to 28.9% of the variation observed in mussel community composition across the sites (Table 4). The macrohabitat-only CCA had a total explained variance of 21.3% (Table 4, Fig. 2). Two axes were significant. The first axis was correlated with catchment area and the second was most closely correlated with riparian wetland cover. The CCA considering only mesohabitat

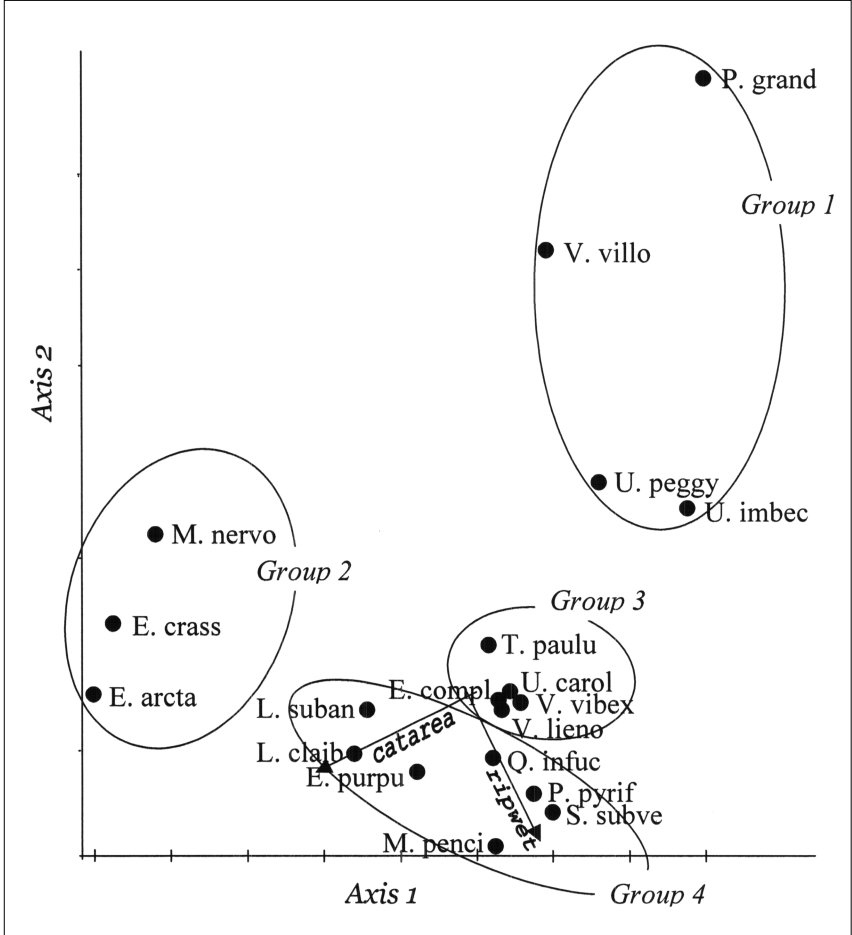


Figure 2. Biplot of species scores and macrohabitat variable vectors for CCA axes one and two from the CCA ordination of the 1999 survey data. Site scores have been omitted for clarity. Species names are abbreviated by indicating the first name of the genus and the first four letters of the epithet. Species groups have been manually encircled on the biplot. Arrows represent the habitat variables most highly correlated with each ordination axis. The length and direction of each arrow corresponds to the magnitude and direction of positive change for the habitat variable. Variable names correspond to abbreviations in Table 1. Table 4 details the correlation scores between habitat variables and CCA axes. Group 1 = slackwater associates; Group 2 = large river riffle associates; Group 3 = generalists; Group 4 = stream run associates.

variables resulted in 21.9% of the observed variance explained by the habitat variables (Table 4, Fig. 3). Only Axis 1 was significant, with multiple habitat variables, including average mid-channel depth, percent fines, and detritus cover demonstrating similar levels of correlation with the axis. In the combined macrohabitat plus mesohabitat CCA, no axis was significant (Table 4, Fig. 4).

In all of the CCAs, species were arrayed in similar clusters in habitat space. Accordingly, four assemblage types were identified from CCAs (Figs. 2–4): slackwater associates, large-river riffle associates, habitat generalists, and stream-run associates. Mann-Whitney U tests largely confirmed habitat differences among sites supporting different assemblage types (Table 5).

The slackwater associates included *Utterbackia peggyae* (Johnson), *Utterbackia imbecillis* (Say), *Villosa villosa* (Wright) and *Pyganodon grandis* (Say). CCA indicated these species were associated with small, shallow streams high in conductivity, fine sediment cover, and detritus (Table 4, Figs. 2–4). These physical conditions are indicative of pool

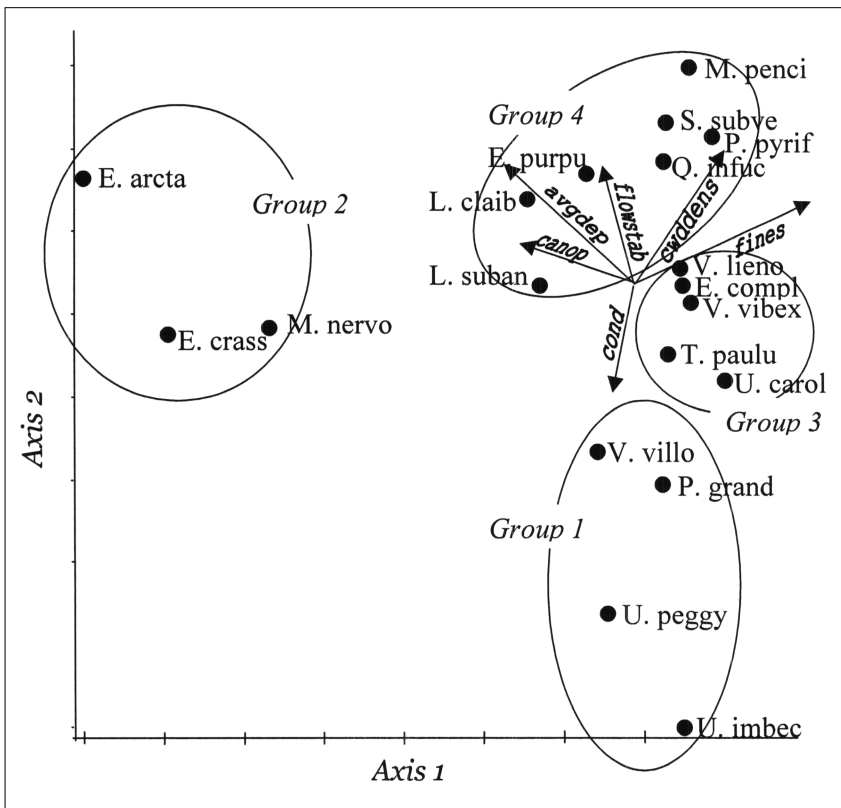


Figure 3. Biplot of species scores and mesohabitat variable vectors for CCA axes one and two. See Figure 2 legend for explanation.

environs, stream margins and backwater areas, and small headwater creeks in marshes. Sites supporting slackwater associates had significantly more pool habitat and were lower in riparian wetland cover than sites not supporting slackwater species (Table 5).

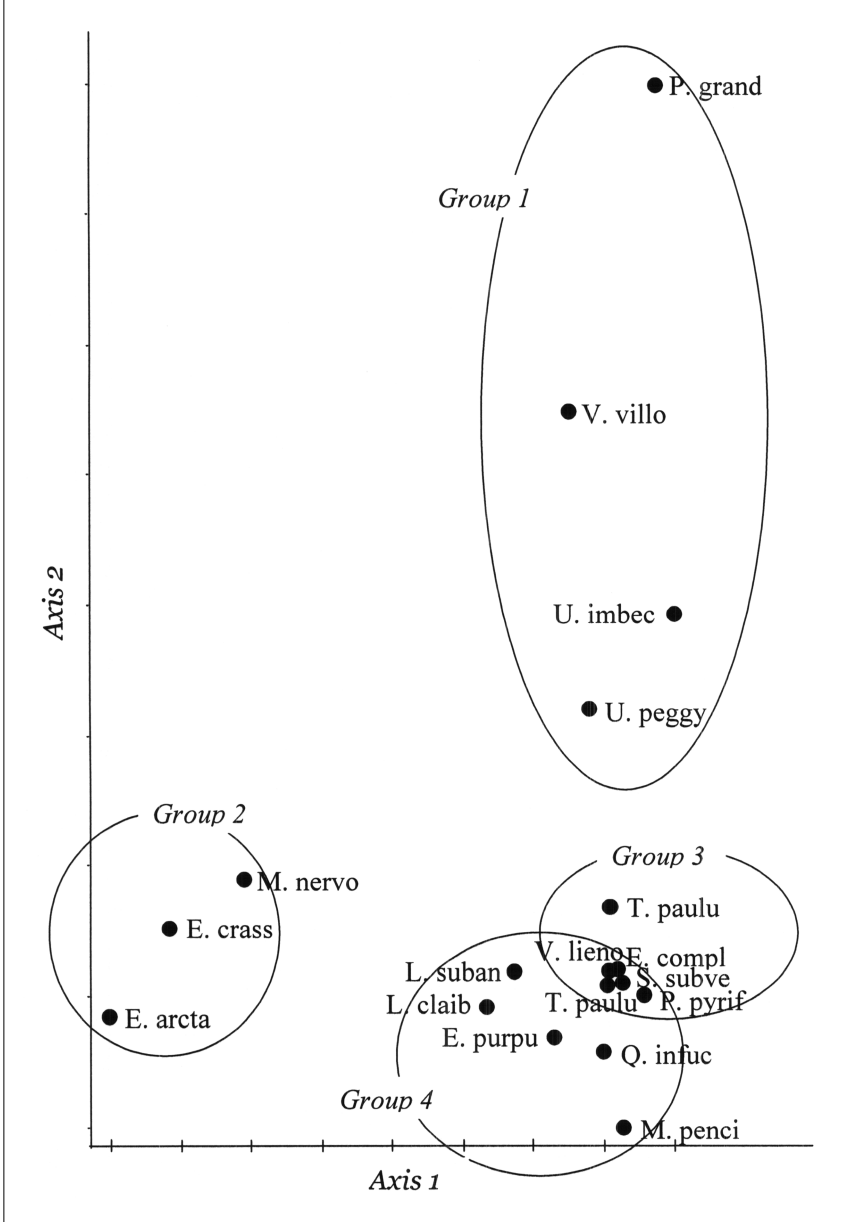


Figure 4. Biplot of species scores and meso- and macrohabitat variable vectors for CCA axes one and two. See Figure 2 legend for explanation.

Elliptio arctata (Conrad), *Megaloniaias nervosa* (Rafinesque), and *Elliptio crassidens* (Lamarck) comprised the group of large-river riffle associates. These taxa were associated with streams having large catchments, deeper flow, high levels of coarse wood debris density and flow stability, and low levels of fine sediments and detritus (Figs. 2–4; Table 4). Sites inhabited by large-river riffle species were significantly larger and deeper, and had more riffle habitat and lower amounts of detritus, fines, and coarse wood debris than non-supporting sites. Large-river riffle type species were also found in areas with lower riparian forest and riparian wetland cover (Table 5).

The most abundant and widespread species in the basin, *Elliptio complanata/ icterina*, *Villosa lienosa* (Conrad), *Villosa vibex* (Conrad), *Toxolasma paulus* (Lea), *Uniomerus carolinianus* (Bosc), were clustered into the generalist group. Sites supporting generalist species had few distinguishing features: significantly more pool habitat and riparian wetland cover, but lower sediment bulk density than non-supporting sites (Table 5).

Table 5. Mann-Whitney U (Wilcoxon rank-sum) test results comparing habitat differences between sites supporting and not supporting each assemblage type.

	Supporting sites		Non-supporting sites		Z	p > Z
	Mean	StdError	Mean	Std Error		
Slackwater	(n = 2)		(n = 44)			
pool	0.35	0.31	0.06	0.01	1.39	0.08
netpos*	2.62	0.59	1.79	0.09	1.43	0.07
catarea*	3.82	0.21	4.37	0.08	-1.43	0.08
ripwet*	-0.83	0.25	-0.52	0.05	-1.54	0.06
Large river/riffle	(n = 5)		(n = 41)			
detritus	0.15	0.04	0.39	0.04	-2.29	0.01
cwdens**	0.27	0.08	0.45	0.03	-1.71	0.04
fines**	0.84	0.20	1.41	0.04	-2.77	0.01
pool	0.00	0.00	0.09	0.02	-1.79	0.04
riffle	0.35	0.15	0.03	0.01	2.37	0.01
avgdepth*	-0.01	0.05	-0.30	0.05	2.29	0.01
netpos*	2.43	0.20	1.75	0.09	2.33	0.01
catarea*	4.98	0.16	4.27	0.08	2.57	0.01
ripwet*	-0.76	0.19	-0.50	0.05	-1.55	0.06
ripforest**	0.90	0.11	1.11	0.03	-1.87	0.03
Generalist	(n = 36)		(n = 10)			
bulkdens	1.44	0.04	1.64	0.05	2.63	0.01
pool	0.09	0.02	0.02	0.02	-2.21	0.01
ripwet*	-0.44	0.04	-0.85	0.14	-3.02	0.00
Stream/run	(n = 16)		(n = 30)			
cond	87.7	18.56	162.7	17.44	-2.71	0.01
flowstab	0.45	0.03	0.36	0.04	1.93	0.03
avgdepth*	-0.15	0.04	-0.34	0.07	2.07	0.02
netpos*	1.98	0.12	1.73	0.13	1.46	0.07
catarea*	4.59	0.10	4.22	0.12	2.32	0.01
ripwet*	-0.36	0.05	-0.62	0.07	2.33	0.01
catforest	0.49	0.03	0.41	0.02	2.25	0.01

*Values not back-transformed from log₁₀ transformation.

**Values not back-transformed from arcsine squareroot transformation.

Table 6. Comparison of historic accounts of species-habitat relationships and findings of this study. Numbered references given in parentheses represent the following sources: 1 = Headlee 1906, 2 = Clench and Turner 1956, 3 = Johnson 1965, 4 = Johnson 1970, 5 = Jenkinson 1973, 6 = Heard 1975, 7 = Heard 1979, 8 = Huehner 1987, 9 = Butler 1989, 10 = Counts et al. 1991, 11 = Cummings and Mayer 1992, 12 = Williams and Butler 1994, 13 = Brim Box and Williams 2000, 14 = www.inhs.uiuc.edu/cbd/flspecies/mollusks_list.htm.

Species	Reported mesohabitat	Reported substrate	Habitat preference identified in this study
Slackwater			
<i>Pyganodon grandis</i>	Ponds, lakes, impoundments, mud-bottomed creeks and rivers (13,1,14)	Sand, mud (13,1,8)	Pool mesohabitat; fine sediments; low flow stability, stream incision, detritus cover, and sediment bulk density;
<i>Utterbackia imbecillis</i>	Slackwater, banks of large rivers, ponds, reservoirs (4,13,2)	Sand, mud (13,2)	closed canopy; smaller streams
<i>Utterbackia peggyae</i>	Sluggish streams and ponds (3)	Sand, mud (13,3)	
<i>Villosa villosa</i>	Slackwater, banks of large rivers, ponds, reservoirs, spring-fed streams and clear rivers (2,4,7,9)	Mud, silt, clay, sand, vegetation, limestone (7,9,13)	
Large-river riffle			
<i>Elliptio arctata</i>	Shore; swift current (4,13)	Sand, gravel, limestone, vegetation (7,13)	Riffle mesohabitat; low levels of fine sediments, detritus, and coarse woody debris; high
<i>Elliptio crassidens</i>	Moderate to strong current; sandbars (7,4)	Sand, limestone, rock, muddy sand (7,13)	incision ratio; large streams and rivers
<i>Megaloniata nervosa</i>	Large rivers; main channel (13,7,2)	Sand, limestone, rock, muddy sand (7,13,2)	
Generalist			
<i>Elliptio complanata</i>	All types (5,7,10,13)	All types (5,7,10,13)	General stream habitat and pool habitat; low sediment bulk
<i>Elliptio icterina</i>	Streams, lakes, reservoirs, ponds, large rivers; swift to moderate current (4,7,13)	Mud, clay, sand, gravel, limestone (13,5)	density; riparian wetland cover

Table 6, continued.

Species	Reported mesohabitat	Reported substrate	Habitat preference identified in this study
Generalist, cont.			
<i>Toxolasma paulus</i>	Small streams with slight current; lakes; banks (7,2)	Mud, clay, sand, vegetation, rock (5,7,13)	
<i>Unimerus carolinianus</i>	Slight current; lakes (4,13)	Sand, mud, clay, limestone (7,13)	
<i>Villosa lienosa</i>	Slight to moderate current; small to large streams (5,7,13,2)	Mud, silt, clay, sand, limestone (5,7,13,2)	
<i>Villosa vibex</i>	Small rivers, creeks and lakes; slight to moderate current (4,7,12)	Mud, silt, clay, sand, limestone (4,7,12,13)	
Stream-run			Intermediate stream habitat; low conductivity; high flow stability; larger streams and rivers; riparian wetland cover
<i>Lampsilis straminea clabornensis</i>	Main channel and banks of large creeks and rivers, slow to moderate current (13,2,7)	Sand, sandy mud bottom, limestone (7,2,13)	
<i>Elliptio purpurella</i>	Sand-bottomed pools, rocky areas with swift current, small to large streams (5,2,7,6)	Sand and limestone (14)	
<i>Medionidus pencillatus</i>	Streams and rivers with moderate current, sandy areas with slight current (5,2,6,7,13)	Sand, mud, fine gravel, limestone, detritus (6,7,13)	
<i>Pleurobema pyriforme</i>	Small to large streams with moderate current, clean substrate; midchannel (6,7,12,13)	Mud, clay, sand, gravel, cobble, limestone (5,2,6,7,13)	
<i>Strophitus subvexus</i>	Backwater, slow to moderate currents, large creeks and rivers (12,2,7,13)	Mud, sand, clay, cobble (5,6,7,12,13)	
<i>Lampsilis subangulata</i>	Small creeks to large rivers; slow to moderate current (12,2,7)	Sand, mud (12,13,7)	
		Sand, clay, rock (6,7,13)	

The final group, the stream-run associates, included the federally endangered *Lampsilis subangulata*, *Medionidus pencillatus*, and *Pleurobema pyriforme*, and species of special concern in the FRB: *Elliptio purpurella* (Lea), *Lampsilis straminea claibornensis* (Lea), *Quincuncina infucata* (Conrad), and *Strophitus subvexus* (Conrad) (Brim Box and Williams 2000). Although the CCA biplot placed these species close to generalist species in habitat space, Mann-Whitney U-tests demonstrated that these taxa were found in larger streams (greater drainage network position, catchment area, and average mid-channel depth) that had significantly lower levels of conductivity, greater flow stability, and catchment forest and riparian wetland cover in comparison to non-supporting (Figs. 2–4, Tables 4 and 5). Because these taxa occupied “intermediate” habitat space on the CCA biplot (i.e., they fell between riffle habitat and slackwater habitat—presumably in a habitat space akin to stream runs), we labeled them as stream-run associates.

Comparisons of the findings of this study and historic anecdotal and experimental evidence of mussel-habitat associations for Flint basin mussels are provided in Table 6. Our results conform well to the habitats identified with slackwater and large-river riffle associates. In our study, generalist species showed no strong patterns of habitat associations, a situation which is also suggested in the reported habitat conditions tied to these taxa in other locations. Similarities between the habitats identified for stream-run associates in our study and those reported from other studies were not strong.

Discussion

Freshwater mussels of the FRB appear to be significantly influenced and structured by both meso- and macroscale habitat conditions. Primary macrohabitat drivers include drainage network position, riparian wetland and catchment forest cover, and mesohabitat complexes such as riffles and slackwater areas. Multiple species demonstrated similar habitat preferences, and could be grouped into assemblage types based on patterns of co-occurrence and habitat use.

Among the habitat variables we examined, two emerge as important indicators of FRB mussel community richness, diversity, and abundance metrics. The first of these is stream drainage network position, which has also been positively correlated with mussel richness across North America: in central Alabama, the Ohio basin, southeastern Michigan, and northern Atlantic Slope streams (Haag and Warren 1998; Strayer 1983, 1993; Watters 1992, 1993). Possible mechanisms driving this pattern are greater flow stability, lower environmental stochasticity, as well as higher habitat heterogeneity and host fish abundance in larger streams (Haag and Warren 1998, Strayer 1993). In the lower FRB, the persistence of perennial flows may be one of the greatest factors contributing to the increased diversity of larger stream habitats, as extensive amounts of headwater and low-order stream reaches stagnate and dry up during

drought conditions, and most basin species do not tolerate hypoxic and desiccating conditions (Johnson 2001).

The second habitat variable important in predicting mussel richness, abundance, and diversity in the FRB is riparian wetland and catchment forest cover. Again, this pattern of mussel association with forested areas has been observed elsewhere in North America (Howard 1997, Morris and Corkum 1996). The influence of catchment forest and riparian wetland cover on unionid assemblages is likely due to the capacity of these land cover types to retain sediments from overland flow, and chemically filter water before entering streams in Coastal Plain ecosystems (Lowrance et al. 1984, 1986), particularly since mussels are thought to be very sensitive to pollution and sedimentation (for summaries, see Brim Box and Mossa 1999, Fuller 1974).

While patterns of diversity and richness are related more to catchment-scale features, site-level assemblage compositions in the lower FRB seem to be constrained by a combination of mesohabitat parameters. In particular, factors such as water depth, coarse wood debris, detritus cover, sediment bulk density and riparian wetland cover combine to create mesohabitat complexes (e.g., riffles, slackwater areas) that support predictable combinations of basin unionid species.

Two groups of species occupy extreme ends of the mesohabitat continuum from riffle and slackwater environs, while two other species groups, the generalists and stream-run associates, occupy intermediate conditions between these two extremes. Despite their close proximity in the CCA diagram, the two intermediary species groups display different patterns of habitat associations. Based on the results of the Mann-Whitney U tests, we conclude that the intermediary placement of generalist species represents the widespread, non-specific habitats of component species. In contrast, the placement of stream-run species on the CCA plot seems to be an indication that these species primarily occupy habitats that are truly intermediate between riffle and slackwater environs. Although limited due to the paucity of locations where stream-run species were found, our data suggest that the habitats of stream-run species include areas of relatively low conductivity, and high flow stability, water depth, coarse woody debris density, and canopy openness.

Features of unionid shell morphology and respiratory physiology have been hypothesized as factors governing species-habitat relationships and may prove to be the mechanistic link between mussels and their preferred habitats (Chen et al. 1997, Sheldon and Walker 1989, Watters 1994). For example, heavy valve structure is thought to confer "anchorage" against shear forces (Sheldon and Walker 1989), resistance to lethal abrasion and desiccation, and protection against predators (McMahon 1991, Watters 1994). Consequently, thick-shelled species may inhabit more abrasive riffle environments and large river systems. Thin shells provide fewer defenses against predators, abrasion

and desiccation, but allow for faster growth, earlier maturation (McMahon 1991), and buoyancy in soft sediments. Thin-shelled species are thought to be adapted to pool environments, and soft-bottom, slow-moving backwater areas of large rivers and streams.

Respiratory response under hypoxia may also be a key physiological determinant of unionid distribution potential. Some mussels (particularly pool and lake dwellers, which experience seasonal hypoxic conditions) demonstrate the ability to regulate oxygen uptake in response to declining levels of dissolved oxygen. Other species (particularly riffle and riverine species) are unable to regulate oxygen uptake, and cannot tolerate hypoxic conditions (Chen et al. 1997, Sheldon and Walker 1989).

Available data on the hypoxia-related mortality and shell characteristics of FRB mussels align with the results that hypotheses described in the previous paragraphs would predict (Table 7). Among mussels that were measured and monitored (Johnson 2001), slackwater species had the thinnest shells, while large river riffle species had the thickest. Stream-run and generalist species had intermediate shell thickness. Mortality under hypoxia also varied with habitat association: generalist species were relatively tolerant of hypoxia; stream-run species had higher mortality under hypoxia; and the highest mortality under hypoxic conditions was observed with one large-river riffle species.

Table 7. Comparison of hypoxia tolerance, shell thickness, and conservation status of species in each assemblage type. "NA" means data were not available. Hypoxia data were originally reported in Johnson 2001.

Species	Average mortality under hypoxia (DO < 5 mg/L)	Average shell thickness:length
Slackwater		
<i>Pyganodon grandis</i>	na	1.01
<i>Utterbackia imbecillis</i>	na	0.64
Large-river riffle		
<i>Elliptio arctata</i>	na	na
<i>Elliptio crassidens</i>	82% ± 9%	5.94
<i>Megaloniaias nervosa</i>	na	6.74
Generalist		
<i>Elliptio complanatalicterina</i>	9% ± 2%	2.23
<i>Toxolasma paulus</i>	23% ± 12%	3.83
<i>Unio merus carolinianus</i>	0% ± 0%	2.82
<i>Villosa lienosa</i>	9% ± 5%	2.64
<i>Villosa vibex</i>	3% ± 1%	1.62
Stream-run		
<i>Lampsilis straminea claibornensis</i>	na	5.17
<i>Elliptio purpurella</i>	na	3.01
<i>Quincuncina infucata</i>	na	5.18
<i>Medionidus pencillatus</i>	50% ± 29%	3.25
<i>Pleurobema pyriforme</i>	15% ± 7%	3.76
<i>Lampsilis subangulata</i>	28% ± 10%	2.62

The results of this study provide further insight into the habitat associations of FRB mussels, but do not offer a complete picture of mussel-habitat requirements. We were able to identify several habitat and landscape variables that accounted for a moderate amount of variation in mussel richness, abundance, and diversity in the basin. Furthermore, we elucidated distinct mussel assemblage groups and habitat associations that are broadly concordant with previous qualitative descriptions for these species. However, numerous habitat variables remain to be examined and much still needs to be done to identify the habitat needs and conservation requirements of FRB mussels, in general, and rare species (the stream-run associates), in particular. Such research would be critical to successful conservation of mussel diversity in this region.

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