

# *Diversity, abundance, and size structure of bivalve assemblages in the Sipsey River, Alabama<sup>†</sup>*

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## ABSTRACT

1. Patterns of mussel diversity and assemblage structure in the Sipsey River, Alabama, are described. Qualitative data were used to describe river-wide patterns of diversity. Quantitative data were used to describe the structure of mussel assemblages at several sites based on whole-substrate sampling that ensured all size classes were detected.

2. Major human impacts to the stream are limited to apparent effects of coal mining in the headwaters and the impoundment of the lower 9 km of the river by a dam on the Tombigbee River. These impacts resulted in a sharp decline in mussel diversity in the headwaters, and extirpation or decline of populations of several large-river species in the lower river that were probably dependent on colonization from the Tombigbee River.

3. Despite localized impacts, mussel assemblages throughout much of the river appear to be mostly intact and self-sustaining. These assemblages have several attributes that differ substantially from those in more degraded streams: (1) high retention of historical species richness; (2) gradual, longitudinal increase in species richness from upstream to downstream, resulting in distinctive headwater and downstream assemblages; (3) ubiquity of most species within particular river segments; (4) low dominance and high evenness with large populations of many species; and (5) frequent recruitment for most species resulting in occurrence of individuals in many size classes.

4. Few detailed and demographically unbiased descriptions of relatively intact mussel assemblages exist. We propose that characteristics described in the Sipsey River can be used as a baseline comparison for assessing relative degree of assemblage alteration in other streams and can serve as goals for restoration efforts.

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## INTRODUCTION

The structure and function of most freshwater mussel assemblages is altered by a wide variety of human impacts (Bogan, 1993; Neves *et al.*, 1997; Regnier *et al.*, 2009) in several characteristic ways: loss of a substantial portion of original species diversity, depressed population sizes, altered patterns of species relative abundance, and highly skewed size and age frequency distributions, usually with a preponderance of large, old individuals (Holland-Bartels, 1990; Layzer *et al.*, 1993; Ahlstedt and McDonough, 1993; Poole and Downing, 2004; Warren and Haag, 2005). Historical literature documents original mussel faunas of many regions (Clark and Wilson, 1912; Ortmann, 1918; Isely, 1924) but provide only presence/absence data or, at best, qualitative observations on species relative abundance. Consequently, knowledge of the

characteristics of mussel assemblages relatively uninfluenced by human impacts is limited.

Understanding the natural structure of mussel assemblages is important from ecological and conservation perspectives. Elucidation of mechanisms responsible for the origin and maintenance of diverse mussel assemblages can be confounded if observed assemblage structure is largely a legacy of human impacts. Similarly, lack of information about unaltered assemblages makes it difficult to specify desired assemblage attributes as goals for restoration efforts. The rarity of young age classes in many populations portends further, widespread declines, but demographic attributes of stable populations are unknown. Until population dynamics of mussels are better understood, assessments of population viability in degraded streams can be aided by using demographic data from relatively unaltered assemblages as a comparative baseline.

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In addition to the scarcity of unaltered assemblages available for study, accurately characterizing mussel assemblages is difficult and time consuming due to the burrowing habits of these animals. Most descriptions of mussel assemblage structure are based on visual sampling methods, which are biased against small species and size classes or species that burrow deeply (Miller and Payne, 1993; Hornbach and Deneka, 1996). The few studies that used methods to reduce this bias were conducted in highly modified habitats (Payne and Miller, 1989, 2000; Haag and Warren, 2007).

In this study, river-wide patterns of mussel diversity are evaluated in a relatively undisturbed river and related to major human impacts and geomorphic factors. In addition, assemblage structure is quantitatively described at several sites using data from whole-substrate samples to ensure all size classes were sampled. From this, differences in local assemblage structure are assessed, local population sizes are estimated, and patterns of size structure among sites and species are evaluated.

## METHODS

### Study area

The Sipsey River is a tributary of the Tombigbee River (Mobile Basin), draining an area of 2044 km<sup>2</sup> (McGregor and O'Neil, 1992). The headwaters, including the New and Little New Rivers, arise on uplands of the Cumberland Plateau physiographic province and flow through narrow floodplains (<1 km) in predominantly sandstone lithology. A short distance downstream of the confluence of the New and Little New Rivers, the Sipsey River enters the East Gulf Coastal Plain physiographic province and flows about 184 km to the Tombigbee River (Figure 1, McCullagh *et al.*, 2002). Within the East Gulf Coastal Plain, the river flows mostly through Cretaceous gravels of the Fall Line Hills district but enters the Black Prairie district about 25 km upstream from its mouth (Boschung and Mayden, 2004). In the Coastal Plain, the river occupies an increasingly broad alluvial floodplain averaging

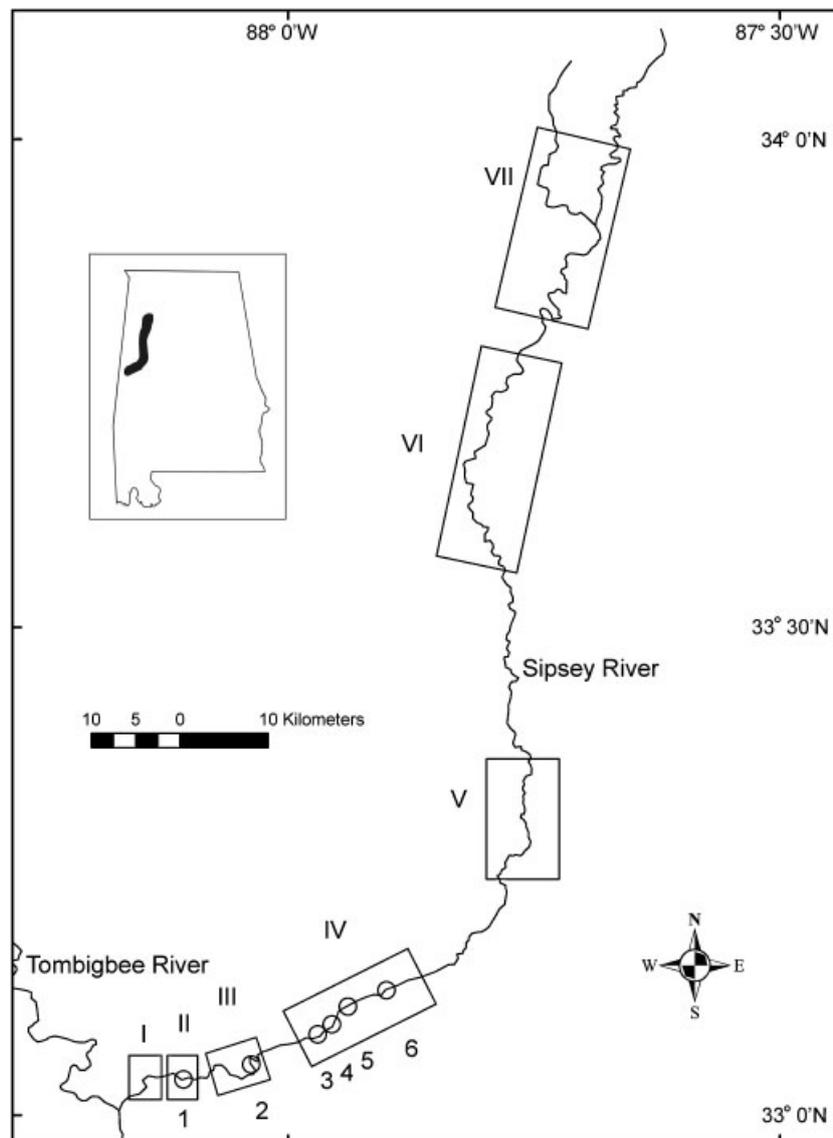


Figure 1. Map of Sipsey River, Alabama. Roman numerals indicate river reaches and numbered circles indicate location of quantitative study sites. Inset map shows location of the Sipsey River in Alabama, USA.

3–9 km wide in the middle and lower reaches (measured from 1:24,000 US Geological Survey topographic maps) and characterized by extensive, marginal wetlands including many secondary channels and oxbow lakes.

Much of the Sipsey River is relatively unmodified by human activities, and major impacts are restricted to the upper and extreme lower sections. The headwaters within the Cumberland Plateau are affected by coal extraction (Pierson, 1991a; see also Warren and Haag, 2005), and the greater relief and narrow floodplain results in increased sedimentation and channel instability from streambank clearing and other sources of erosion (Pierson, 1991a). Because these impacts are restricted to a small percentage of the river, their effects apparently are largely attenuated in the middle and lower river. Human impacts in the middle and lower river are associated mostly with timber harvest. Although commercial pine plantations and timber harvest occur throughout the basin, extensive marginal wetlands preclude most logging within much of the riparian zone and serve as a buffer from effects of more intensive timber harvest further from the stream. The lower *ca* 9 km of the river was impounded in 1976 by Howell Heflin Lock and Dam (Tennessee–Tombigbee Waterway) on the Tombigbee River. Effects of impoundment extend to about 1.5 km downstream of the Alabama Highway 14 bridge (Figure 1), but the upper portion of this section retains riverine characteristics, especially at low reservoir pool. Because of the few major human impacts compared with other streams, the Sipsey River supports one of most intact biological communities in the region (McGregor and O'Neil, 1992) including most of its historical mussel fauna (McCullagh *et al.*, 2002).

### Qualitative data

All freshwater mussel occurrences in the Sipsey River were compiled from Pierson (1991a; b), McGregor (1999), McCullagh *et al.* (2002), McGregor and Haag (2004), and our field work. Only species presence/absence data were extracted from previous surveys because sampling effort was not reported in most cases. Species occurrences were based on live, recently dead, or relic shells; however, shells decompose in <5 years in the poorly buffered waters of the river (Haag, unpublished data) so even relic shells indicate recent occurrence. Because of taxonomic confusion regarding *Quadrula apiculata*, *Quadrula aspera*, and *Quadrula rumphiana*, records for these species were combined as *Q. rumphiana*; specimens potentially referable to *Q. apiculata* or *Q. aspera* are rare in the river (only a single individual was encountered having characteristics of *Q. apiculata*), and the vast majority of individuals represent *Q. rumphiana* (see McCullagh *et al.*, 2002). To examine river-wide patterns of diversity, sample sites were grouped into seven reaches (Figure 1). These reaches were based on the seven zones described by McCullagh *et al.* (2002), except that their two adjacent headwater zones (their Zones VI and VII) were combined into a single reach (Reach VII), and a separate reach was created representing the lowermost portion of the river influenced by impoundment but retaining riverine characteristics (Reach I). Mussel occurrence data were available for two time periods, 1910–1911 and 1981–2000. Data for 1981–2000 were available for all reaches, but 1910–1911 data were limited to three sites in the upper river (one each in Reaches V–VII), two of which overlay

contemporary sites; no pre-1981 data exist for the lower river (McCullagh *et al.*, 2002, J. Williams personal communication, 7 June 2010). To examine diversity patterns unrelated to human impacts, a matrix of species presence/absence in each reach was created for both time periods combined. To examine temporal changes in diversity in the upper river, species occurrences were also compiled separately for the two time periods. Assemblage differences among reaches (both time periods combined) were tested with the multi-response permutation procedure (MRPP; PC-ORD, McCune and Mefford, 1999) (presence/absence, Euclidean distance, 34 sample sites  $\times$  41 species, sites grouped by seven reaches). Because the data matrix contained many zero entries, Beal's smoothing transformation was applied to the matrix to reduce problems of zero-inflated data (Beal, 1984; McCune, 1994). The transformation replaced each cell in the matrix with the probability of the target species occurring in that particular reach based on the joint occurrences of the target species with species actually occurring in the reach (McCune and Grace, 2002). For pairwise comparisons among reaches, *P*-values were adjusted to *P* < 0.05 using the sequential Bonferroni procedure for multiple comparisons (Holm, 1979). The chance-corrected within-group agreement statistic (*A*) was used to evaluate among-reach effect sizes. This statistic is independent of sample size and quantifies within-group (reach) homogeneity compared with the random expectation.

Quantitative data were unavailable for most sampling sites. To examine ubiquity of species in mussel assemblages throughout the river, the proportion of occurrence of each species was calculated across all sample sites within each reach. Assuming that more abundant species are more likely to be encountered given variation in sample effort and effectiveness among sites, ubiquity was used as a proxy for the relative abundance of mussel species in each reach. Similar to the analysis of species presence/absence, ubiquity was calculated for the 1910–1911 and 1981–2000 time periods combined to examine distributional patterns apart from recent changes in the fauna. However, because 1910–1911 data were limited to one site each in Reaches V–VII, omitting these data had little influence on ubiquity patterns. Patterns of species ubiquity among reaches were analysed with non-metric multidimensional scaling (NMS; PC-ORD, McCune and Mefford, 1999) (Euclidean distance, ubiquity arcsine square-root transformed, 7 reaches  $\times$  41 species). The influence of individual species on patterns of ubiquity was assessed using Pearson correlation coefficients (*r*) of species with ordination axes.

### Quantitative data

Mussel assemblages were sampled quantitatively at six sites in Reaches II–IV (Table 1, Figure 1). Each site encompassed a well-defined riffle/run complex. Sites were characterized by firm gravel and sand substrate within the main channel and sand and finer sediments along stream margins. Except for site 6, depths were <1 m; site 6 was a deep run (maximum depth about 2.5 m) at the upstream end gradually changing to a shallow riffle (depth <0.2 m). At each site, 6–8 randomly located transects were sampled across the stream. Within each transect, a 0.5 m<sup>2</sup> (sites 2 and 4) or 0.125 m<sup>2</sup> (all other sites) quadrat was sampled every 1 m; stream widths were relatively homogeneous within sites, resulting in similar numbers of quadrats within each transect. Sites 2 and 4 were sampled once

Table 1. Quantitative sample sites in the Sipsey River, Alabama. For sites 1, 3, 5, and 6, area sampled is for 1999 and 2000 combined. Site area was not determined for sites 2 and 4. Location of sites is shown on Figure 1

Site	Location	Site length (m)	Site area (m <sup>2</sup> )	Area sampled (m <sup>2</sup> )
1	33°02'03"N, 88°06'20"W	120	1952	16.8
2	33°02'47"N, 88°02'04"W	25	—	24.5
3	33°05'13"N, 87°57'43"W	60	995	18.9
4	33°05'18"N, 87°57'27"W	30	—	21.0
5	33°06'24"N, 87°56'49"W	100	1835	22.6
6	33°07'18"N, 87°54'40"W	60	823	18.1

(October and May 1998, respectively). Sites 1, 3, 5, and 6 were sampled in 1999 and 2000 (August or September). Sites 2 and 4 were sampled by visually examining the substrate using a mask and snorkel or surface air supply (hookah rig, Keene Engineering, Chatsworth, CA) then excavating substrate by hand to a depth of about 15 cm to find buried mussels. At sites 1, 3, 5, and 6, the substrate was excavated within each quadrat to about 15 cm using a portable diver-operated suction dredge (Keene Engineering, Chatsworth, CA). Substrate samples were processed across three sieves (smallest mesh = 2.5 mm), allowing detection of adult and small juvenile mussels. Live mussels were identified, measured (anterior-posterior axis, nearest 0.1 mm, dial calipers), and returned to the stream. In addition to mussels encountered in quantitative samples, the presence of other bivalve species was noted.

Mean mussel species abundance was calculated at each site (number of individuals m<sup>-2</sup>) as the average across transects; quadrats within each transect were combined due to the non-independence of these samples. Differences in mussel assemblages among sites were tested using MRPP (see previous) [Euclidean distance, log<sub>10</sub>(abundance + 0.2), 68 transects × 25 species, transects grouped by site], and were corrected for multiple comparisons (Holm, 1979). In this analysis, mean species abundance in 1999 and 2000 was used at sites 1, 3, 5, and 6. Population sizes of all species in quantitative samples in 2000 were estimated at sites 1, 3, 5, and 6 by extrapolating mean transect abundance and error estimates to the total area of the site. Population sizes were estimated only for 2000 to avoid having error at two levels (spatial variation among transects and temporal variation among years) and were meant to provide a representation of population size at a given time. However, population sizes were stable at these sites from 1999–2000 (Haag, 2002). Population sizes were not estimated at sites 2 and 4 because visual sampling probably underestimated abundance of small mussels.

Length–frequency distributions were constructed for the seven most common species (> 50 individuals across all sites) in 2000 at sites 1, 3, 5, and 6, based on 2 mm size classes. This analysis was not conducted for sites 2 and 4 because of probable underestimation of small individuals, or for 1999 because samples sizes in that year were smaller and few species were represented by > 50 individuals. Initially, separate length–frequencies were calculated for sites 5 and 6 (sites with the greatest sample sizes) for the four most abundant species (*Elliptio arca*, *Fusconaia cerina*, *Pleurobema decisum*, *Quadrula asperata*). For these species, differences in length–frequencies between sites were tested with RxC G-tests of independence (Sokal and Rohlf, 1995); these analyses used 10 mm size classes because 2 mm classes produced tables with many zeros.

Because length–frequencies did not differ among sites for any of these four species (see results), composite length–frequency histograms were constructed across sites 1, 3, 5, and 6 for these and all other species with sufficient samples sizes. The strength of recent recruitment was evaluated for the seven most common species and *Lampsilis ornata* and *Quadrula verrucosa* by calculating the proportion of populations composed of recruits (i.e. animals < 1 year old). The upper size limits for recruits were determined from the size range of well-defined cohorts on length–frequency histograms (Haag, 2002) and were corroborated by length at age data from validated shell-thin sections (Haag and Rypel, 2010).

## RESULTS

Diverse mussel assemblages occurred throughout the Sipsey River, and many species were distributed widely. Historically, 41 species were reported from the river (43 including *Quadrula apiculata* and *Q. aspera*), and 37 species were reported from 1981–2000 (Table 2). Eight species occurred in all reaches, including the reservoir-influenced Reach I, and of these, *Fusconaia cerina*, *Lampsilis straminea*, *Quadrula asperata*, *Q. verrucosa*, and *Villosa lienosa*, were present at an average of > 70% of sites in each reach (Table 2). Another 13 species occurred in ≥ 5 reaches, and most were ubiquitous within several reaches; only *Elliptio arctata* and *Strophitus subvexus* were distributed widely but occurred only sporadically within reaches. Most other species were restricted to the lower river, especially Reaches II–IV. Only *Anodontoïdes radiatus*, *Quadrula metanevra* (see Discussion), *Toxolasma parvum*, and *Unio merus tetralasmus* were restricted to the upper river, where they occurred only sporadically (Table 2). In Reaches II–IV, 92–100% of species in quantitative samples were found in previous surveys.

Sipsey River mussel assemblages showed strong longitudinal structure. Diversity was highest in free-flowing downstream Reaches II–IV (30–33 species), decreasing in an upstream direction; however, the reservoir-influenced Reach I had lower diversity than other downstream reaches (Table 2, Figure 2). A conspicuous faunal break occurred between Reaches IV and VI separating a headwater fauna (Reaches VI and VII) from a larger stream fauna (Reaches I–V). Patterns of species composition did not differ among Reaches II–V and between Reaches VI and VII but differed in three comparisons between headwater and large stream reaches (Table 3). Other comparisons of species composition between headwater and large stream reaches were not significantly different, but effect sizes showed a trend of increasing separation in an upstream direction except for comparisons involving the reservoir-influenced Reach I (Table 3). Patterns of species ubiquity from NMS were described by a two-dimensional solution accounting for 87% of variation among reaches. Axis 1 (75% of variation) revealed a longitudinal gradient with a transition between Reaches IV and VI but with Reach 1 as an outlier (Figure 3). This gradient described a general downstream trend of increasing ubiquity for many species including characteristic large-stream species (e.g. *Lampsilis teres*, *Lasmigona alabamensis*, *Megaloniais nervosa*, *Obliquaria reflexa*, *Truncilla donaciformis*), and species that occurred throughout the river (e.g. *Fusconaia cerina*, *Lampsilis straminea*, *Obovaria* spp., *Quadrula asperata*, *Villosa lienosa*) (Table 2). Species with negative correlations on axis 1 were those that occurred only in upstream Reaches V–VII

Table 2. Distribution of freshwater mussels in the Sipsey River, Alabama. Tabled values are the proportion of sites at which a species occurred in each reach; the number of sites in each reach is given in parentheses. Columns headed NMS are Pearson correlation coefficients ( $r$ ) of species with ordination axes from nonlinear multidimensional scaling. In reaches V–VII, species marked with a dagger were present in 1910–11 surveys, and those marked with an asterisk were present in 1981–2000 surveys. Occurrences in reaches I–IV are from 1981–2000

Species	Reach							NMS ( $r$ )	
	I (3)	II (3)	III (2)	IV (8)	V (5)	VI (5)	VII (8)	Axis 1	Axis 2
<i>Amblema plicata</i>	0	0.33	1.00	0.63	0.40 <sup>†*</sup>	0	0	0.738	-0.849
<i>Anodonta suborbiculata</i>	0	0	0	0.25	0.20 <sup>*</sup>	0	0	0.173	-0.533
<i>Anodontoides radiatus</i>	0	0	0	0	0.20 <sup>*</sup>	0	0.13 <sup>†</sup>	-0.600	0.147
<i>Arcidens confragosus</i>	0	0	0	0.13	0	0	0	0.383	-0.369
<i>Ellipsaria lineolata</i>	0	1.00	1.00	0.38	0	0	0.13 <sup>†</sup>	0.697	-0.612
<i>Elliptio arca</i>	0.33	1.00	1.00	1.00	0.40 <sup>†*</sup>	0.20 <sup>†</sup>	0	0.939	-0.839
<i>E. arctata</i>	0	0.33	0.50	0.38	0.20 <sup>†</sup>	0	0.13 <sup>†</sup>	0.562	-0.786
<i>E. crassidens</i>	0	0.67	0.50	0.88	0.40 <sup>†*</sup>	0	0	0.790	-0.958
<i>Fusconaia cerina</i>	0.67	1.00	1.00	1.00	1.00 <sup>†*</sup>	0.20 <sup>†*</sup>	0.13 <sup>†</sup>	0.842	-0.955
<i>F. ebena</i>	0	0.33	0.50	0.25	0	0	0.13 <sup>†</sup>	0.565	-0.509
<i>Hamiota perovalis</i>	0.67	1.00	0.50	0.88	0.60 <sup>†*</sup>	0	0	0.870	-0.741
<i>Lampsilis ornata</i>	0.33	1.00	1.00	1.00	0.60 <sup>†*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	0.910	-0.900
<i>L. straminea</i>	1.00	1.00	1.00	1.00	1.00 <sup>†*</sup>	0.20 <sup>†*</sup>	0.38 <sup>†*</sup>	0.840	-0.721
<i>L. teres</i>	1.00	1.00	1.00	0.88	0.80 <sup>†*</sup>	0.40 <sup>†*</sup>	0	0.850	-0.563
<i>Lasmigona alabamensis</i>	0.33	0.67	0.50	0.63	0	0	0	0.950	-0.574
<i>Leptodea fragilis</i>	0.33	1.00	0.50	1.00	0.80 <sup>†*</sup>	0.20 <sup>*</sup>	0	0.760	-0.837
<i>Ligumia recta</i>	0	0	0.50	0.25	0	0	0	0.625	-0.534
<i>Medionidus acutissimus</i>	0	1.00	1.00	0.75	0.40 <sup>†*</sup>	0	0.13 <sup>†</sup>	0.752	-0.860
<i>Megalaniais nervosa</i>	0	1.00	1.00	0.63	0.20 <sup>*</sup>	0	0	0.845	-0.858
<i>Obliquaria reflexa</i>	0.67	1.00	1.00	1.00	0.60 <sup>*</sup>	0	0	0.985	-0.836
<i>Obovaria jacksoniana</i>	0.67	0.67	1.00	0.75	0.60 <sup>†*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	0.852	-0.680
<i>O. unicolor</i>	0.67	1.00	1.00	1.00	0.60 <sup>†*</sup>	0	0.13 <sup>†</sup>	0.957	-0.816
<i>Plectomerus dombeyanus</i>	0	0.33	0.50	0	0	0	0	0.655	-0.553
<i>Pleurobema decisum</i>	0.33	1.00	1.00	1.00	0.80 <sup>*</sup>	0.20 <sup>†</sup>	0	0.899	-0.928
<i>P. perovatum</i>	0.67	0.67	1.00	1.00	1.00 <sup>*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	0.690	-0.826
<i>P. taitianum</i>	0	0	0.50	0	0	0	0	0.435	-0.344
<i>Potamilus inflatus</i>	0	0.33	0	0	0	0	0	0.417	-0.381
<i>P. purpuratus</i>	1.00	1.00	0.50	0.63	0.80 <sup>*</sup>	0	0	0.716	-0.477
<i>Pyganodon grandis</i>	0.33	0	0	0.13	0	0	0	0.273	0.234
<i>Quadrula asperata</i>	1.00	1.00	1.00	1.00	1.00 <sup>*</sup>	0.40 <sup>†*</sup>	0.25 <sup>*</sup>	0.855	-0.727
<i>Q. metanevra</i>	0	0	0	0	0	0	0.13 <sup>†</sup>	-0.560	0.462
<i>Q. rumphiana</i>	1.00	1.00	1.00	1.00	0.80 <sup>*</sup>	0.20 <sup>*</sup>	0	0.924	-0.652
<i>Q. stapes</i>	0	0	0.50	0	0	0	0	0.435	-0.344
<i>Q. verrucosa</i>	0.33	1.00	1.00	1.00	1.00 <sup>†*</sup>	0.40 <sup>†*</sup>	0.63 <sup>†*</sup>	0.611	-0.955
<i>Strophitus subvexus</i>	0	0.67	0.50	0.50	0.20 <sup>*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	0.486	-0.730
<i>Toxolasma parvum</i>	0	0	0	0	0.20 <sup>*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	-0.930	0.464
<i>Truncilla donaciformis</i>	0	0.67	0.50	0.50	0	0	0	0.867	-0.770
<i>Unio merus tetralasmus</i>	0	0	0	0	0	0.20 <sup>†</sup>	0	-0.548	0.483
<i>Utterbackia imbecillis</i>	0	0	0	0.13	0.20 <sup>*</sup>	0	0	0.090	-0.522
<i>Villosa lienosa</i>	1.00	1.00	1.00	1.00	0.80 <sup>†*</sup>	0.60 <sup>†*</sup>	0.75 <sup>†*</sup>	0.885	-0.464
<i>V. vibex</i>	0	1.00	1.00	0.75	0.80 <sup>†*</sup>	0.20 <sup>†</sup>	0.13 <sup>†</sup>	0.623	-0.901
Number of species	19	30	32	33	28	17	18		

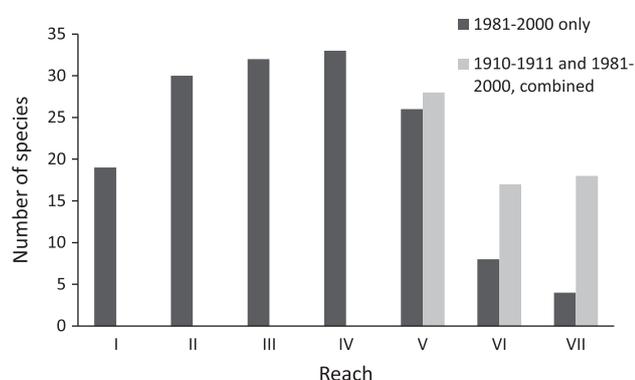


Figure 2. Freshwater mussel species diversity in seven reaches of the Sipsey River, Alabama. Reaches are numbered in longitudinal order from downstream (reach I) to upstream (reach VII).

(*Anodontoides radiatus*, *Toxolasma parvum*, *Quadrula metanevra*, and *Unio merus tetralasmus*). Axis 2 clustered Reaches II–V closely but separated upstream Reaches VI–VII and the reservoir-influenced Reach I (Figure 3). Although explaining less variation (12%), axis 2 emphasizes the high overall species richness in Reaches II–V (28–33 species) versus lower richness in Reaches I, VI, and VII (17–19 species).

Mussel assemblages in upstream reaches changed considerably between 1910–1911 and 1981–2000. Diversity in Reaches VI and VII declined 47% and 77%, respectively, between these time periods (Figure 2). Despite the greater number of sample sites in 1981–2000, only three species recorded in these reaches in 1981–2000 were not recorded in 1910–1911 (*Leptodea fragilis* and *Quadrula rumphiana*, Reach VI; *Quadrula asperata*, Reach VII), but 17 species recorded historically were absent in at least one upstream reach in

Table 3. Results of pairwise multi-response permutation procedure (MRPP) for mussel species presence/absence in seven reaches of the Sipsey River, Alabama. Tabled values are pairwise effect-sizes ( $A$ ) with observed  $P$ -values in parentheses (not corrected for multiple comparisons); asterisks indicate comparisons that were significant at  $P < 0.05$  after adjustment by the sequential Bonferroni procedure of Holm (1979). Reaches are numbered in longitudinal order from downstream (reach I) to upstream (reach VII)

Reach	Reach					
	II	III	IV	V	VI	VII
I	0.256 0.02489	0.197 0.00001*	0.170 0.00640	0.009 0.34908	0.121 0.05586	0.322 0.00986
II		-0.122 1.00000	-0.021 0.62110	0.136 0.03341	0.328 0.02355	0.465 0.00652
III			-0.054 0.81972	0.074 0.13246	0.262 <0.00001*	0.370 0.01452
IV				0.077 0.03860	0.297 0.00062*	0.501 0.00038*
V					0.160 0.02082	0.383 0.00401
VI						-0.034 0.61447

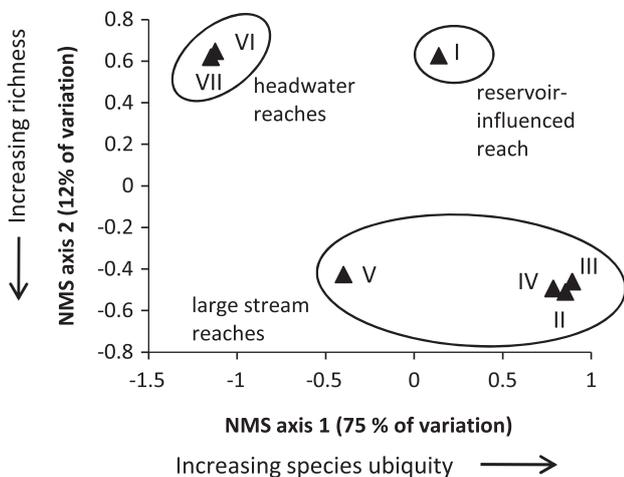


Figure 3. Non-metric multidimensional scaling (NMS) plot based on freshwater mussel species ubiquity values in seven reaches in the Sipsey River, Alabama. Roman numerals next to each point are reach numbers. Correlations of species with NMS axes are given in Table 2.

1981–2000 (Table 2). Only widely distributed species persisted in both upstream reaches (e.g. *Lampsilis straminea*, *Quadrula asperata*, *Quadrula verrucosa*, and *Villosa lienosa*). Except for *Q. verrucosa* and *V. lienosa*, all species were distributed sporadically ( $\leq 50\%$  of sites) in the upper river in 1981–2000. In contrast, diversity in Reach V appeared relatively unchanged between 1910–1911 and 1981–2000 (Figure 2). Recent collections found 27 species in Reach V, but only 16 were collected in 1910–1911; *Elliptio arcata* was the only species found historically but not in 1981–2000 (Table 2). Further, many species were ubiquitous ( $\geq 75\%$  of sites) within Reach V in 1981–2000 suggesting abundance of many species remained high.

Mussel assemblage structure varied among quantitative sites within and among Reaches II–IV. Mussel abundance was higher in Reach IV (10.8–38.4 mussels  $m^{-2}$ ) than in Reaches II (5.4  $m^{-2}$ ) and III (8.6  $m^{-2}$ ) (Table 4). Lower mussel abundance at sites 2 (Reach III) and 4 (Reach IV) could be due to lower efficiency of hand excavation used at these sites. However, the lowest observed abundance was at site 1 (Reach II) which was sampled with methods identical to higher abundance sites 3, 5, and 6

(Reach IV). Within-site homogeneity of mussel assemblages was significantly greater than expected by chance (MRPP,  $A = 0.170$ ,  $P < 0.00001$ ). Pairwise comparisons between site assemblages were all significantly different except between sites 2 and 4 which was only marginally significant (Table 5). Effect sizes showed a weak longitudinal gradient of increasing separation in assemblage structure between downstream and upstream sites; the highest effect size was between sites 1 and 6 (Table 5).

Despite significant differences in assemblage structure among sites, general patterns of species abundance were similar (Table 4). Across all six sites, dominance was relatively low (0.239 to 0.336) and evenness high (0.815 to 0.876). *Pleurobema decisum* and *Quadrula asperata* were among the five most abundant species at all sites, and *P. decisum* was the most abundant species at half of the sites. Three additional species were consistently prominent components of the assemblages, ranking within the top five species at four or more sites (*Elliptio arca*, *Fusconaia cerina*, and *Medionidus acutissimus*). Eleven other species occurred at all sites but were at low to moderate densities or below levels detectable by quantitative methods.

Freshwater mussel assemblages in the lower Sipsey River were large, ranging from about 11 000–40 000 individuals/site for all species combined (Table 6). Population estimates for the most abundant species exceeded 1500 individuals at most sites but were as high as 10 000–17 000 for *Pleurobema decisum* at site 5. Confidence intervals for most rare species included zero, but the estimates suggested that even these species were present in considerable numbers if viewed at a river-wide scale. Except at site 1, unionid numbers were comparable with or only slightly smaller ( $> 50\%$ ) than population sizes of the invasive bivalve, *Corbicula fluminea* (Table 6). Interestingly, *Corbicula* abundance appeared to be highest at the site with the lowest unionid abundance (site 1); however, due to their patchy distribution, confidence intervals around estimated *Corbicula* population sizes were comparatively wider than for unionids.

Populations of most species comprised individuals in many size classes, including recent recruits ( $< 1$  year old), and no populations were dominated by a single size class (Figures 4 and 5). Length–frequency distributions were not significantly different ( $P > 0.05$ ) between sites 5 and 6 for *Elliptio arca* ( $G = 6.85$ , 7 df), *Fusconaia cerina* ( $G = 11.65$ , 6 df), *Pleurobema decisum* ( $G = 8.50$ , 6 df), or *Quadrula asperata* ( $G = 1.14$ , 6 df).

Table 4. Freshwater mussel abundance (number m<sup>-2</sup>) at six sites in the lower Sipsey River, Alabama. *P* denotes that a species was present at the site but not detected in quantitative samples. Dominance was estimated as the proportion of the most abundant species and evenness was calculated as the probability of an interspecific encounter (Hurlbert, 1971)

Species	Reach					
	II		III		IV	
	Site					
	1	2	3	4	5	6
<i>Amblema plicata</i>	<i>P</i>	0.04	0.51	<i>P</i>	—	—
<i>Anodonta suborbiculata</i>	—	—	—	<i>P</i>	—	—
<i>Elliptio arca</i>	0.07	0.78	1.79	2.90	2.61	3.38
<i>E. arctata</i>	<i>P</i>	—	—	<i>P</i>	—	—
<i>E. crassidens</i>	<i>P</i>	—	0.19	0.29	<i>P</i>	<i>P</i>
<i>Ellipsaria lineolata</i>	<i>P</i>	0.04	—	<i>P</i>	—	—
<i>Fusconaia cerina</i>	0.15	0.69	1.99	1.14	3.43	9.48
<i>F. ebena</i>	—	—	—	0.10	—	0.07
<i>Hamiota perovalis</i>	<i>P</i>	—	—	<i>P</i>	<i>P</i>	0.18
<i>Lampsilis ornata</i>	0.59	0.65	0.92	0.86	0.52	0.60
<i>L. straminea</i>	0.07	<i>P</i>	0.42	<i>P</i>	0.20	<i>P</i>
<i>L. teres</i>	<i>P</i>	<i>P</i>	0.09	<i>P</i>	0.07	0.19
<i>Lasmigona alabamensis</i>	—	—	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
<i>Leptodea fragilis</i>	0.11	—	0.27	<i>P</i>	0.25	0.24
<i>Ligumia recta</i>	—	—	—	<i>P</i>	—	<i>P</i>
<i>Medionidus acutissimus</i>	0.52	1.76	1.85	<i>P</i>	1.47	1.67
<i>Megaloniaias nervosa</i>	—	0.04	<i>P</i>	<i>P</i>	<i>P</i>	0.10
<i>Obliquaria reflexa</i>	0.41	0.33	1.46	0.24	0.19	0.64
<i>Obovaria jacksoniana</i>	—	<i>P</i>	—	<i>P</i>	<i>P</i>	<i>P</i>
<i>O. unicolor</i>	0.74	0.33	1.03	0.43	0.37	2.04
<i>Pleurobema decisum</i>	0.86	2.33	5.30	1.48	6.51	8.18
<i>P. perovatium</i>	<i>P</i>	0.08	0.14	0.05	0.06	0.21
<i>P. purpuratus</i>	<i>P</i>	—	—	0.05	<i>P</i>	0.05
<i>Pyganodon grandis</i>	—	—	—	<i>P</i>	—	—
<i>Quadrula asperata</i>	1.30	1.14	4.72	2.29	2.18	6.08
<i>Q. rumphiana</i>	0.26	0.04	0.36	0.19	0.29	3.82
<i>Q. verrucosa</i>	0.26	0.08	1.76	0.67	0.94	1.36
<i>Strophitus subvexus</i>	—	—	—	<i>P</i>	0.04	<i>P</i>
<i>Truncilla donaciformis</i>	0.04	<i>P</i>	0.63	<i>P</i>	<i>P</i>	<i>P</i>
<i>Utterbackia imbecillis</i>	—	—	—	—	<i>P</i>	—
<i>Villosa lienosa</i>	0.04	<i>P</i>	0.14	0.10	0.09	0.07
<i>V. vibex</i>	<i>P</i>	<i>P</i>	—	<i>P</i>	0.15	0.05
Number of species	23	20	20	31	25	26
Total unionid abundance	5.43	8.33	23.58	10.76	19.37	38.41
Dominance	0.239	0.280	0.225	0.269	0.336	0.247
Evenness	0.867	0.834	0.876	0.840	0.815	0.845
<i>Corbicula fluminea</i>	45.73	<i>P</i>	27.75	<i>P</i>	30.20	29.25

In most populations, multiple peaks were evident on length–frequency histograms suggesting the presence of multiple age cohorts (Figures 4 and 5). For several species (e.g., *E. arca*, *Medionidus acutissimus*, *P. decisum*, *Quadrula rumphiana*), recruits and age-1 individuals were distinguishable as two distinct cohorts that corresponded to length-at-age data for these species (Haag and Rypel, 2010); larger size classes probably included multiple cohorts due to individual variation in growth. In contrast to most species, *M. acutissimus* had only three apparent cohorts because of its short life span ( $\leq 5$  years, Haag and Rypel, 2010). Recruits composed a large part of populations of *E. arca*, *Lampsilis ornata*, and *Obovaria unicolor* (22–37%, Table 7), and especially *M. acutissimus*, for which nearly half of the individuals were recruits. Populations of *F. cerina*, *P. decisum*, and *Quadrula* spp. also

Table 5. Results of pairwise multi-response permutation procedure (MRPP) for mussel assemblages at six sites in the Sipsey River, Alabama. Tabled values are pairwise effect-sizes (*A*) with observed *P*-values in parentheses (not corrected for multiple comparisons); asterisks indicate comparisons that were significant at  $P < 0.05$  after adjustment by the sequential Bonferroni procedure of Holm (1979). Sites are numbered in longitudinal order from downstream (site 1) to upstream (site 6)

Site	Site				
	2	3	4	5	6
1	0.047 (0.01649)*	0.120 ( $<0.00001$ )*	0.067 (0.00253)*	0.157 ( $<0.00001$ )*	0.241 ( $<0.00001$ )*
2		0.067 (0.00076)*	0.063 (0.05684)	0.062 (0.00407)*	0.178 ( $<0.00001$ )*
3			0.074 (0.00069)*	0.044 (0.00007)*	0.081 ( $<0.00001$ )*
4				0.086 (0.00134)*	0.167 (0.00003)*
5					0.093 ( $<0.00001$ )*

had strong, but lower recruitment (11–20%, Table 7). In addition to recruits, all of these species were represented by individuals spanning a wide size range (Figures 4 and 5). Recruits or juvenile individuals ( $< 2$  years estimated age) of most other species were observed, including *Amblema plicata*, *Hamiota perovalis*, *Lampsilis straminea*, *L. teres*, *Lasmigona alabamensis*, *Leptodea fragilis*, *Megaloniaias nervosa*, *Obliquaria reflexa*, *Pleurobema perovatium*, *Potamilus purpuratus*, *Strophitus subvexus*, *Truncilla donaciformis*, *Utterbackia imbecillis*, *Villosa lienosa*, and *Villosa vibex*. Apart from very rare species, only *Elliptio crassidens* and *Fusconaia ebena* were not represented by juveniles in these samples.

## DISCUSSION

The Sipsey River is a rare example of a large stream with a nearly intact mussel assemblage. Only two species, *Quadrula metanevra* and *Unio merus tetralasmus*, were reported historically from the river but not in recent surveys. *Quadrula metanevra*, a large river species, was reported only from the upper river (Reach VII) in 1910–1911. Two other large river species, *Ellipsaria lineolata* and *Fusconaia ebena*, were reported from Reach VII in 1910–1911 but not recorded there since, but they still occur in the lower river. These three species rarely, if ever, occur in headwater streams (Williams *et al.*, 2008), and records from the upper river may be based on incorrect locality information or misidentification of specimens (McCullagh *et al.*, 2002, J. Williams personal communication, 7 June 2010). *Unio merus tetralasmus* is often absent in main channel mussel assemblages of larger rivers, occurring primarily in small streams and wetlands (Williams *et al.*, 2008), which were not sampled extensively in recent surveys (McCullagh *et al.*, 2002). This species remains widespread in the Tombigbee River system (McGregor and Haag, 2004) and probably occurs in tributaries or floodplain wetlands of the Sipsey River along with other species that were rare in recent main channel surveys (e.g. *Anodontooides radiatus*, *Pyganodon grandis*, *Utterbackia imbecillis*). Another species characteristic of lentic habitats, *Toxolasma parvum*, was reported in 1910–1911 but not in a recent survey (McCullagh *et al.*, 2002); however, it was reported recently from Reach V (McGregor

Table 6. Estimated bivalve population size (95% confidence intervals) at four sites in the Sipsey River, Alabama in 2000

Species	Site 1	Site 3	Site 5	Site 6
<i>Amblema plicata</i>	—	447 (59–836)	—	—
<i>Elliptio arca</i>	292 (–115–699)	2236 (1290–3182)	5872 (3772–7972)	3840 (1956–5725)
<i>E. crassidens</i>	—	89 (–88–267)	—	—
<i>Fusconaia cerina</i>	584 (13–1154)	1789 (960–2618)	6806 (4409–9204)	7837 (5716–9958)
<i>Hamiota perovalis</i>	—	—	—	78 (–78–234)
<i>Lampsilis ornata</i>	584 (13–1154)	1163 (516–1810)	1068 (344–1792)	549 (94–1004)
<i>L. straminea</i>	292 (–115–699)	358 (8–707)	534 (–109–1177)	—
<i>L. teres</i>	—	89 (–88–267)	267 (–106–639)	313 (7–620)
<i>Leptodea fragilis</i>	438 (–59–934)	537 (114–960)	934 (254–1615)	392 (52–732)
<i>Medionidus acutissimus</i>	1459 (584–2335)	1968 (1082–2854)	3737 (2037–5436)	1567 (811–2323)
<i>Megalonaia nervosa</i>	—	—	—	157 (–62–376)
<i>Obliquaria reflexa</i>	1022 (78–1966)	2057 (1029–3085)	267 (–106–639)	627 (150–1104)
<i>Obovaria unicolor</i>	1168 (376–1959)	626 (172–1080)	934 (157–1712)	1959 (1051–2868)
<i>Pleurobema decisum</i>	1605 (604–2607)	5724 (4086–7363)	13746 (10057–17434)	7210 (5064–9356)
<i>P. perovatum</i>	—	89 (–88–267)	—	235 (–32–502)
<i>Potamilus purpuratus</i>	—	—	—	78 (–78–234)
<i>Quadrula asperata</i>	2189 (1067–3311)	4740 (3535–5945)	3870 (2290–5451)	5251 (4169–6332)
<i>Q. rumphiana</i>	1022 (278–1765)	537 (114–960)	667 (87–1248)	3057 (1681–4432)
<i>Q. verrucosa</i>	438 (–59–934)	1520 (726–2315)	1601 (655–2548)	627 (205–1049)
<i>Strophitus subvexus</i>	—	—	133 (–131–398)	—
<i>Truncilla donaciformis</i>	146 (–143–435)	1073 (497–1649)	—	—
<i>Villosa lienosa</i>	146 (–143–435)	—	133 (–131–398)	—
<i>V. vibex</i>	—	—	534 (12–1056)	78 (–78–234)
Total unionids	11530 (8309–14750)	25848 (22036–29660)	42038 (34862–49215)	34092 (27874–40310)
<i>Corbicula fluminea</i>	150760 (80745–220775)	43467 (29192–57742)	75268 (55074–98463)	36913 (19690–54136)

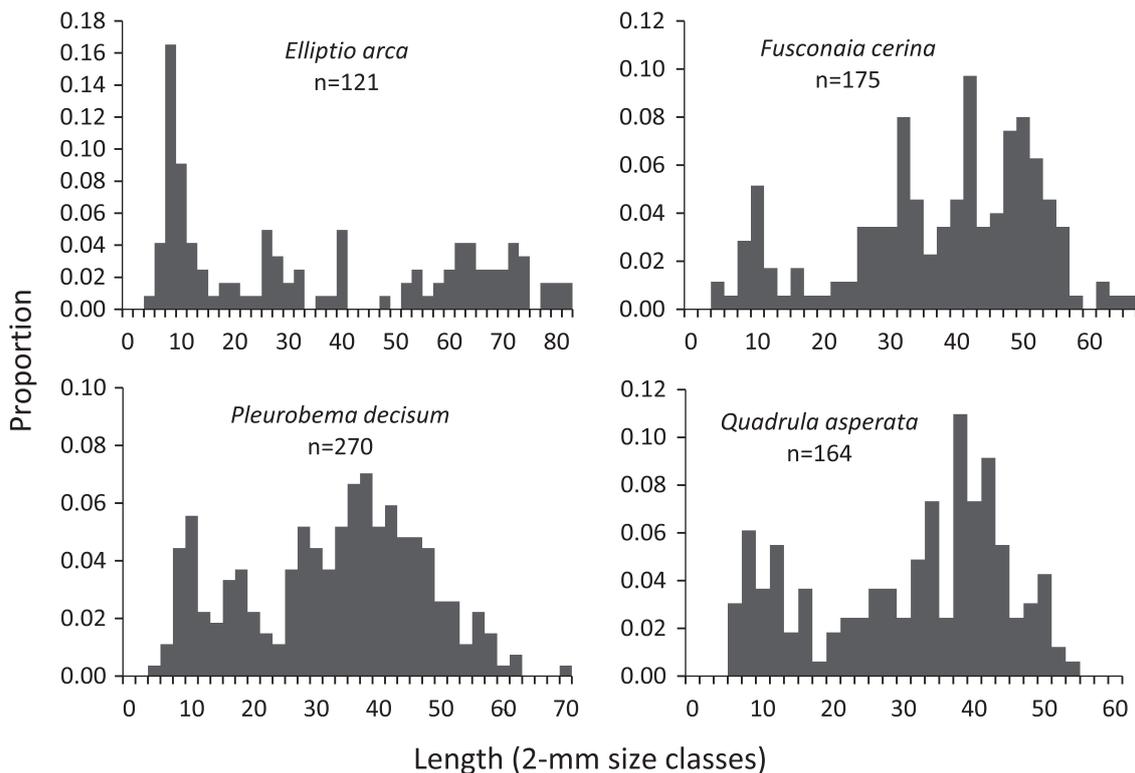


Figure 4. Length–frequency histograms for the four most common mussel species in the Sipsey River in 2000. Data are composites across sites 1, 3, 5, and 6 (see text).

and Haag, 2004). *Elliptio arctata* and *Ligumia recta* were each known previously from single occurrences in the river (McCullagh *et al.*, 2002); we provide two additional records of both species showing that, although rare, these species are more widely distributed in the river than previously thought. Intensive whole-substrate sampling also revealed that other

species formerly considered rare (McCullagh *et al.*, 2002) were more common, particularly small-bodied species like *Medionidus acutissimus* and *Truncilla donaciformis*.

Only two species, *Pleurobema taitianum* and *Quadrula stapes*, appear to be extirpated from the river, but these were probably waifs from the Tombigbee River and may have never

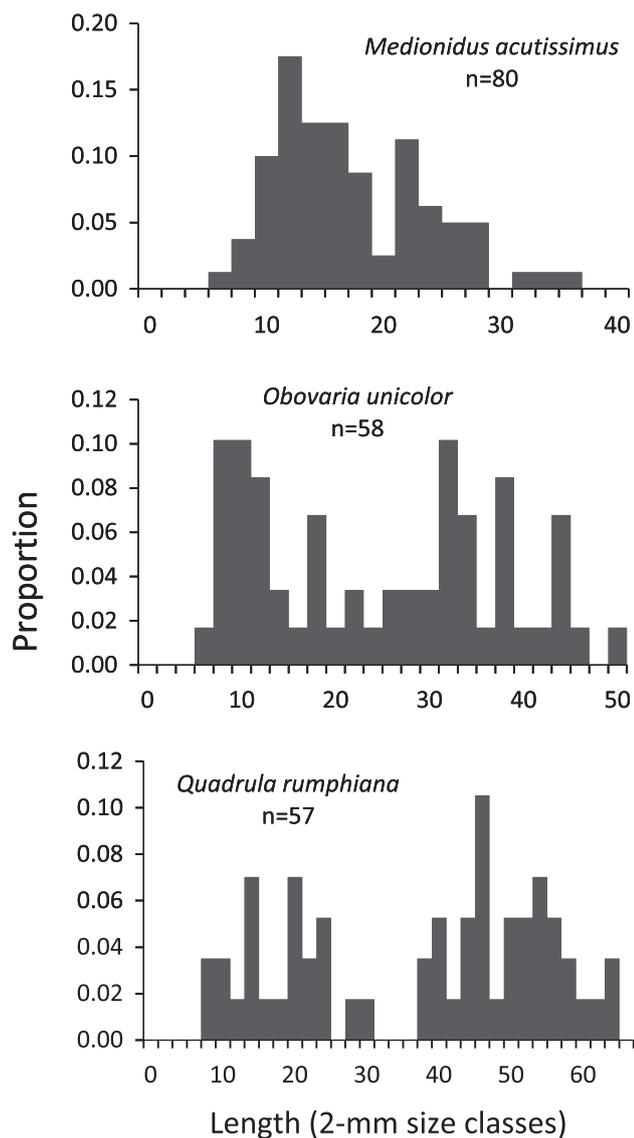


Figure 5. Length–frequency histograms for three mussel species in the Sipsey River Alabama in 2000. Data are composites across sites 1, 3, 5, and 6 (see text).

Table 7. Proportion of mussel populations composed of recruits in the Sipsey River, Alabama, in 2000 at sites 1, 3, 5, and 6, combined. Recruits are defined as individuals <1 year old (see text)

Species	Maximum size of recruits (mm)	Proportion of population
<i>Elliptio arca</i>	14.9	0.37
<i>Fusconaia cerina</i>	12.4	0.11
<i>Pleurobema decisum</i>	11.9	0.14
<i>Lampsilis ornata</i>	30.5	0.22
<i>Medionidus acutissimus</i>	13.5	0.45
<i>Obovaria unicolor</i>	12.0	0.36
<i>Quadrula asperata</i>	9.4	0.13
<i>Q. rumphiana</i>	11.0	0.09
<i>Q. verrucosa</i>	13.1	0.20

been important components of the Sipsey fauna (see below). No historical information exists on mussel assemblages in the lower river (Reaches I–IV). However, the lower river currently

supports nearly all species that occur in large streams in the western Mobile Basin, except those that were largely restricted to the main channel of the Tombigbee River (*Epioblasma penita*, *Pleurobema marshalli*, *P. taitianum*, *Quadrula metanevra*, and *Q. stapes*; Williams *et al.*, 1992). *Epioblasma penita* occurs rarely in the lower Buttahatchee River, a tributary of the Tombigbee River that is similar to the Sipsey (McGregor and Haag, 2004), and we cannot explain its absence in the Sipsey River. Although *E. penita* is a federally endangered species considered highly sensitive to habitat alteration (Williams *et al.*, 2008), several other threatened or endangered species currently thrive in the Sipsey River (e.g. *Medionidus acutissimus*, *Pleurobema decisum*, *P. perovatium*) demonstrating that the quality of mussel habitat in the river is not limiting.

In addition to retaining much of its original diversity, the Sipsey River mussel assemblage has other attributes that suggest a high degree of ecological integrity. Most obviously, the river supports large mussel populations including several Mobile Basin endemic species that have declined precipitously elsewhere across their range (e.g. *Elliptio arca*, *Medionidus acutissimus*, *Obovaria unicolor*, *Pleurobema decisum*; Mirarchi *et al.*, 2004). These species not only persist in the river, they are among the most abundant species and these populations are undoubtedly the largest remaining worldwide (Mirarchi *et al.*, 2004; Williams *et al.*, 2008). Although our quantitative sites may represent habitats supporting particularly high mussel abundance, the high ubiquity values for most species indicate that mussels are distributed continuously throughout much of the middle and lower river. Extensive sections of Reaches II–IV were surveyed qualitatively by boat and canoe during study site selection in 1998–1999 and it was found that most shoal habitats supported large and diverse mussel assemblages similar to the study sites. These sites were chosen for accessibility as well as mussel presence so it is unlikely that they support unusually high abundance. Moreover, other habitats that are not typically considered optimal for mussels or are rarely sampled (e.g. deep runs and flowing pools) often supported high mussel abundance; for example, the highest mussel abundance in this study occurred at site 6, much of which was a deep run (2.5 m deep). Consequently, for most species this section of the river probably functions as a single, large population with local patches that frequently exchange immigrants via sperm and glochidial drift and transport of encysted glochidia on fishes. Local population sizes in the Sipsey River are comparable with similarly-sized sites in other high quality streams (Smith *et al.*, 2001; Crabtree and Smith, 2009). However, even highly degraded streams may continue to harbour large mussel populations (Ahlstedt and McDonough, 1993), but these assemblages have attributes indicative of compromised viability and ecological functioning.

Mussel assemblages in degraded streams are often dominated by a single species comprising >60% of total individuals and only two or three species may constitute >90% of the assemblage (Miller *et al.*, 1986, 1992; Ahlstedt and McDonough, 1995–1996; Haag and Warren, 2007). In contrast, low dominance and high evenness characterized mussel assemblages in the Sipsey River. Across sites, the most abundant species comprised only 24–34% of total unionids and the three most abundant species together constituted ≤65% of assemblages. The apparent rarity of some species in

the river is because they occur primarily in fine sediments along the stream margin or in backwater habitats, which were not sampled extensively in this study (e.g. *Lampsilis straminea*, *L. teres*, *Obovaria jacksoniana*, *Pleurobema perovatum*, *Pyganodon grandis*, *Villosa lienosa*; Haag, 2002). Other species occurring widely in main-channel habitats were consistently rare or absent in our samples and in previous surveys (e.g., *Elliptio arcata*, *Hamiota perovalis*, *Lasmigona alabamensis*, *Strophitus subvexus*, *Villosa vibex*; McCullagh *et al.*, 2002). Rarity may indicate that the Sipsey River is marginal habitat for some of these species or may be a historical artefact of random fluctuations in population size. For example, although extremely rare in the Sipsey River, *Strophitus subvexus* is relatively common in the neighbouring and physically similar Buttahatchee River (Hartfield and Jones, 1990). Rare species are a feature of any biological community (Rabinowitz, 1981; Gaston, 1994); however, dominance of only one or a few species in mussel assemblages may often be indicative of human impacts or other stressors. Similar to these findings in the Sipsey River, other relatively intact mussel assemblages are characterized by the prominent occurrence of a large number of species rather than dominance by one or a few species (Ahlstedt and Tuberville, 1997; Hornbach, 2001; Smith *et al.*, 2001). Dominance and evenness therefore appear to be useful measures of the relative health of a mussel assemblage.

One of the most conspicuous features of Sipsey River mussel assemblages is the presence of individuals in a wide range of size classes for most species. Many mussel populations are dominated by large, old individuals because human impacts have curtailed recent recruitment (Miller *et al.*, 1992; Ahlstedt and McDonough, 1993; Houslet and Layzer, 1997; Vaughn and Spooner, 2004). In most studies, accurate estimates of size distributions and recent recruitment strength could not be made because of sample bias against small individuals. In a previous study using whole-substrate sampling to reduce this bias, a population of *Fusconaia ebena* in the lower Ohio River experienced strong recruitment in only 2 of 16 years with low or no recruitment in intervening years (Payne and Miller, 1989, 2000). Based on this single result, intermittent recruitment is widely invoked as a general characteristic of mussel populations (Garner *et al.*, 1999; Curole *et al.*, 2004; Vaughn and Spooner, 2004; Berg *et al.*, 2008). The results of this study show a different picture of mussel population dynamics. Although 2000 possibly represented an exceptional recruitment year, the presence of multiple size classes for most species suggests that, although varying among species, substantial recruitment occurs frequently. Distinct peaks in length–frequency histograms representing recruits and age-1 individuals indicate that strong recruitment occurred for these species in at least two consecutive years. Other recent studies showed evidence of frequent recruitment (Villella *et al.*, 2004; Haag and Warren, 2007; Crabtree and Smith, 2009). Consequently, intermittent recruitment may be another manifestation of human impacts to mussel assemblages.

Despite the intact nature of mussel assemblages in much of the Sipsey River, human impacts have had measurable effects on the fauna in the upper and extreme lower river. Diversity in the extreme lower river is reduced by the effects of impoundment. Although no historical data exist for Reach I, diversity was probably similar to Reaches II–IV, or higher because of additional large river species from the Tombigbee

River. In the upper river, mussel diversity and probably abundance have been reduced substantially since 1910–1911. The prevalence of coal extraction in the headwaters suggests this activity has had effects similar to those associated with dramatic declines in mussel populations elsewhere on the Cumberland Plateau (Anderson *et al.*, 1991; Houslet and Layzer, 1997; Warren and Haag, 2005). The pattern of mussel decline in the upper river is similar to other streams affected by coal extraction in that surviving species are primarily those that were historically widespread, suggesting that all species in the assemblage have declined at similar rates (Warren and Haag, 2005). Before declines in the upper river, assemblages changed along a longitudinal gradient from the headwaters to the lower river. Headwaters supported a distinctive assemblage, but longitudinal changes were gradual, including an increase in species richness in a downstream direction and a broad transitional zone in patterns of species ubiquity between Reaches IV and VI. The form of this gradient could be an artefact of the low intensity of historical sampling in the upper river resulting in an underestimation of diversity before recent human impacts and an underestimation of the extent of species loss. However, similar gradual patterns of longitudinal change are characteristic of many riverine mussel assemblages (Strayer, 1983, 1993; Warren *et al.*, 1984). Human impacts in the upper river and extreme lower river have clearly disrupted longitudinal patterns, with the result that there are now abrupt and major changes in species richness and ubiquity between Reaches V and VI and Reaches I and II.

The effects of coal extraction and other human impacts in the upper river appear to be largely attenuated in the middle and lower river. To an extent, attenuation may be a simple function of distance from the impacts. However, extensive forested wetlands adjacent to the stream throughout much of its length probably also play a large role in maintaining the high quality of the middle and lower reaches. Wetlands, particularly riverine wetlands, can dramatically improve water quality and hydrological stability of associated streams (Brinson, 1988; Johnston *et al.*, 1990). In an agricultural landscape, low-gradient streams flowing through extensive alluvial deposits retained higher mussel richness and abundance than high-gradient streams, an effect attributed to increased groundwater flux in alluvial deposits resulting in greater hydrologic stability (Arbuckle and Downing, 2002). In addition to their potential role in attenuation of impacts from the headwaters, wetlands in the Sipsey River floodplain may also buffer human impacts in the middle and lower basin (e.g. timber harvest, row-crop agriculture).

Lower mussel abundance was observed at quantitative sites in downstream Reaches II and III than in Reach IV. In Reach III, the river enters the Black Prairie physiographic district. The Black Prairie is underlain by relatively impermeable calcareous chalk, and streams are more hydrologically flashy and deeply entrenched than those in the Fall Line Hills (Boschung and Mayden, 2004). As a result, this section of the river has fewer energy dissipating meanders and wetlands adjacent to the stream relative to Reach IV. Lower mussel abundance in the Black Prairie may reflect the lack of wetland buffers against impacts on the landscape or may be a natural feature reflecting greater hydrologic instability. However, species richness and composition of Reaches II and III was similar to Reach IV, and recruitment of most species was observed at these sites, suggesting that, despite lower mussel

abundance, the Black Prairie section of the river maintains high ecological integrity.

Apart from direct loss of riverine habitat in the impounded lower 9 km, human impacts in the lower and middle river appear limited to indirect effects of isolation and loss of source populations for large-river species. Several characteristic large-river species (*Elliptio crassidens*, *Ellipsaria lineolata*, *Fusconaia ebena*, *Ligumia recta*) were restricted to the lower river and were rare. As noted, two other large-river species, *Pleurobema taitianum* and *Quadrula stapes*, occurred in the Sipsey River as late as the 1980s but now apparently are extirpated (McCullagh *et al.*, 2002). Before impoundment, all these species were abundant or widespread in the Tombigbee River (especially *E. lineolata* and *F. ebena*, Williams *et al.*, 1992), and populations in the Sipsey River were probably sustained largely by immigration from the Tombigbee River. In the Sipsey River, some remaining large-river species may now represent non-viable, relict populations following loss of source populations or potential loss of large-river host fishes. We observed no recruitment of *E. crassidens* or *F. ebena*. Hosts for these species are thought to be skipjack herring (*Alosa chrysochloris*; Surber, 1913; Howard, 1914), a migratory species restricted primarily to the main channel of large rivers (Etnier and Starnes, 1993). The effect of impoundment on populations of skipjacks in the Tombigbee River is unknown, but dams are likely to impede migrations and their movement may be restricted further through the impounded lower reaches of the Sipsey River. Similarly, host fishes for *L. recta* are walleye and sauger (*Sander vitreus* and *S. canadensis*, Khym and Layzer, 2000). Sauger do not occur in the Mobile Basin, and walleye populations there are reduced by impoundment (Ross, 1991; Boschung and Mayden, 2004). Consequently, *L. recta* is nearly extirpated from the Mobile Basin (Herod, 2004). In contrast, large-river species that are host-generalists (e.g. *Amblema plicata*, *Lasmigona alabamensis*, *Megaloniais nervosa*) or use widespread host species (e.g. freshwater drum, *Aplodinotus grunniens*; *Truncilla donaciformis*) remain more common in the Sipsey River and are reproducing. Nevertheless, because of their restriction to the lower river, population sizes of these species are relatively small and their isolation from sources of recolonization makes them vulnerable to human impacts or stochastic effects.

The Sipsey River supports a rare example of a large stream mussel assemblage that appears to retain much of its original ecological function. Because of their rarity, few detailed descriptions exist of the attributes of relatively intact mussel assemblages. Characteristics of the Sipsey River fauna suggest that intact, self-sustaining mussel assemblages exhibit: (1) high retention of their historical species richness; (2) a gradual, longitudinal increase in species richness from upstream to downstream, resulting in distinctive headwater and downstream assemblages; (3) widespread occurrence of most species within particular river segments; (4) low dominance and high evenness with high abundance of many species; and (5) frequent recruitment for all species resulting in occurrence of individuals in many size classes. These characteristics can be used as a baseline comparison for assessing the relative degree of assemblage alteration in other streams and can serve as goals for restoration efforts.

Exceptions to these characteristics in the Sipsey River are the result of localized human impacts to the stream itself or larger impacts beyond the river. Impacts in the upper river and

impoundment of the lower river have disrupted longitudinal patterns in richness. At a larger scale, the lack of recent recruitment for *Elliptio crassidens* and *Fusconaia ebena* and loss of other large-river species is attributable to indirect effects of impoundment in the Tombigbee River. In other streams, the extent of deviations from these characteristics can be useful in conservation assessments. Despite localized human impacts, the Sipsey River is vitally important as a conservation refuge and supports globally important mussel populations many of which are stable or potentially increasing (Haag, 2002). These populations together represent a globally unique laboratory in which to study freshwater mussel assemblages.

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