

CHANGES IN THE FRESHWATER MUSSEL ASSEMBLAGE IN THE EAST FORK
TOMBIGBEE RIVER, MISSISSIPPI: 1988–2011

A Thesis
by
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Abstract

CHANGES IN THE FRESHWATER MUSSEL ASSEMBLAGE IN THE EAST FORK TOMBIGBEE RIVER, MISSISSIPPI: 1988–2011

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The Tennessee-Tombigbee Waterway is among the largest and most expensive environmental engineering projects of the 20th century. The waterway accommodates barge navigation between the Tennessee River drainage and Mobile River Basin through a series of locks, dams, canals, and dredged and diverted streams. These alterations have destroyed much riverine habitat and fragmented remaining aquatic habitats resulting in isolated freshwater mussel populations in patches of streams like the East Fork Tombigbee River, where 42 species were historically known. The first post-waterway mussel surveys in 1987 and 1988 reported 31 taxa (including 2 federally-listed species). I sampled 70 sites in 2010 and 2011 using both quadrats and timed searches and found 29 species to be extant. Though mussel richness was relatively unchanged, species composition shifted toward animals indicative of tributary systems rather than large rivers. Total abundance declined significantly. Relative abundance of 9 taxa decreased significantly; however, relative abundance increased for 11 species, 3 of them

federally listed. This dramatic shift in mussel species dominance suggests that present stream habitats and/or fish hosts in the East Fork Tombigbee River are apparently favoring smaller-bodied, ruderal taxa. Yet, changes in the host fish assemblage may be responsible for the increased abundance of some sensitive mussels. I found no live evidence for the 4th (*Quadrula verrucosa*) and 10th (*Lasmigona alabamensis*) most abundant species from 1988 surveys and my demographic data suggests that other historically dominant and currently rare species are at risk of extirpation from the river. Finally, I detected three non-native unionids—*Quadrula quadrula*, *Potamilus alatus*, and *Potamilus ohiensis*—which may have colonized the East Fork Tombigbee River from the Tennessee River drainage via the waterway. These results are among the first to document waterway-mediated shifts in mussel fauna and wide-spread assemblage changes linked to lock and dam river regulation. Resource managers should continue to monitor mussel and fish assemblages and changes to their habitat in the study area and throughout the upper Tombigbee River drainage.

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and the basis of its study design. Bob Butler (USFWS) provided extensive editorial assistance and invaluable career counsel.

Dedication

I dedicate this work to Braun, Theodora, Elwood, Elsie, and Zoe who introduced to me to the mystery and beauty of the natural world, and showed me the value of protecting it.

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Foreword

Work contained within this thesis will be submitted to *River Research and Applications*, an international peer-reviewed journal published by John Wiley & Sons, Ltd.; it has been formatted according to the style guide for that journal.

INTRODUCTION

Native freshwater mussel (Margaritiferidae and Unionidae) abundance and diversity declined abruptly during the past half-century on a global scale (Nalepa *et al.*, 1991; Bogan, 1993; Williams *et al.*, 1993; Neves *et al.*, 1997; Jones *et al.*, 2005). Williams *et al.* (1993) estimate that 72% of North America's ~300 native species are endangered, threatened, or of conservation concern because of anthropogenic modifications to river systems. However, historical quantitative data are few and monitoring programs rarely span sufficiently broad time intervals to reveal meaningful temporal patterns (Haag, 2012). Although degraded or impounded rivers generally support less diverse mussel assemblages (Jones *et al.*, 2001; Morowski *et al.*, 2009), some bivalves may benefit from changes in habitat conditions or from naive niche space (Bates, 1962; Houpp, 1993; Sickel *et al.*, 2007). Quantitative monitoring of historically species-rich mussel assemblages is important for understanding responses to stream alterations, and that need is critical in the southeastern United States where mussel diversity and imperilment are greatest (Williams *et al.*, 1993; Williams and Neves, 1995; Lydeard and Mayden, 1995; Neves *et al.*, 1997).

The Mobile River Basin (MRB) of Alabama, Georgia, Mississippi, and Tennessee once supported at least 73 mussel species, but extensive changes to fluvial habitats in the 20th century led to the loss of many taxa (Williams *et al.*, 2008). At least 10 of the 30+ mussel species endemic to the MRB are extinct (USFWS, 2000; Gangloff and Feminella, 2007; Williams *et al.*, 2008; Haag, 2009). The Tombigbee River (TR), Alabama and Mississippi,

historically harbored at least 52 mussel species, all but one species inhabiting the upper Tombigbee River (UTR), upstream of the confluence with the Black Warrior River. The construction (1972–1984) and maintenance of the Tennessee-Tombigbee Waterway (TTW) by the U.S. Army Corps of Engineers (USACE) coincides with the extinction of three mussel species endemic to the TR (Hartfield and Jones, 1989; Hartfield, 1993; Patrick and Dueitt, 1996; Jones *et al.*, 2005; Williams *et al.*, 2008). The TTW impounds and channelizes >300 km of the main stem TR, and conjoins the Mobile and Mississippi River Basins (at Whitten Lock near Bay Springs, MS) to facilitate barge navigation between the Gulf of Mexico and Ohio River drainage (Stine, 1993). For 240 km, the TTW flows within the banks of the original TR. The USACE maintains the TTW to a minimum bottom width of 92 m and dredge depth of ~3–4 m (McKee and McAnally, 2008). Additionally, because of river bendway cutoffs, the present TR is now >113 km shorter than before TTW construction (Stine, 1993; McKee and McAnally, 2008).

Historically, the UTR, like many Gulf Coastal Plain streams, supported a diverse aquatic community of 115 fish and 51 mussel taxa (Benz and Collins, 1997; Jones *et al.*, 2005; Taylor *et al.*, 2008; Williams *et al.*, 2008). Clemmer (1972, in Shultz, 1981) describes the UTR as having “deep pools, gravel and sand bars, swiftly flowing waters, undercut banks, and submerged trees.” However, channel modifications that promote hydraulically efficient barge navigation along the TTW have degraded habitats within channelized and disconnected reaches within the UTR drainage and led to geomorphic destabilization as the stream adjusts to a new dynamic equilibrium (Hartfield, 1993; Guegan *et al.*, 1998; Beisel *et al.*, 2000). River regulation and other hydrological processes associated with the TTW (e.g., dredging, channel straightening, stream diversion, wave-mediated erosion from barge traffic,

periodic releases at locks) modify important fluvial processes that structure benthic habitats, generally to the detriment of the native historical fauna.

Stream regulation typically elevates sediment deposition and turbidity. Mussels are generally sedentary and highly sensitive to habitat alterations resulting from stream regulation (Bogan, 1993; Watters, 2000; Garner and McGregor, 2001). However, habitat alteration may not affect all species similarly. Replacement of species in mussel assemblages is seldom documented but may have important implications for bivalve-mediated ecosystem services (Houp, 1993; Sickel *et al.*, 2007; Spooner and Vaughn, 2008; Morowski *et al.*, 2009; Jones and Byrne, 2010). Elevated concentrations of fine sediments may reduce available habitat, food availability, reproductive success, and mussel and fish production (Petts, 1984; Berkman and Rabeni, 1987; Carling and McCahon, 1987; Richards and Bacon, 1994; Wood and Armitage, 1997). Yet, some mussel species are tolerant of habitat degradation and may even thrive in recently impounded or overbank habitats characterized by low flows and fine substrates (Bates, 1962; Sickel *et al.*, 2007).

Several studies have modeled or otherwise use complex hydraulic and substrate parameters to identify mussel distribution patterns (Strayer, 1999; Gangloff and Feminella, 2007; Steuer *et al.*, 2008; Zigler *et al.*, 2008; Allen and Vaughn, 2010). Fewer studies have examined effects of habitat parameters and host fish presence on temporal mussel assemblage trends (see Vaughn and Taylor, 2000). Although shell characteristics (e.g., thickness, sculpture, dorsal wing) have been linked to preferential hydraulic and substrate conditions (Watters, 1994), few studies have shown empirical linkages between habitat changes and the proportion of shell morphologies within mussel assemblages. Data compiled by Haag (2012) also suggest that species grouped according to life history traits (e.g., growth

rate, age at maturity, fecundity, lifespan) and sharing similar life strategies may in part be indicative of stream stability and productivity.

In 1987, Miller and Hartfield (1988) sampled the East Fork Tombigbee River (EFTR), a major tributary of the UTR in northeastern Mississippi. They reported a diverse mussel assemblage comprised of 28 species but also observed high mussel mortalities apparently from stranding during attenuated flows following TTW construction (Miller and Hartfield, 1988; Hartfield and Jones, 1989). In 1988, Hartfield and Jones (1989) qualitatively and quantitatively sampled 68 sites on the EFTR from its confluences with the Lock B spillway to Mill Creek. The surveyors selected this reach for a comprehensive survey due to the high likelihood of supporting rare mussel species, as indicated by previous surveys (Stansbery, 1983a, b; Schultz, 1981; Miller and Hartfield, 1988; Hartfield and Jones, 1989). Additionally, this reach is currently USFWS-designated critical habitat for four federally-listed mussels: *Hamiota perovalis*, *Pleurobema decisum*, *P. perovatum*, and *Medionidus acutissimus*. Six other federally-listed mussels: *Epioblasma penita*, *Pleurobema curtum*, *P. marshalli*, *P. taitianum*, *Potamilus inflatus*, and *Quadrula stapes* historically occurred within the EFTR, or near its confluence with the main stem TR.

The goals of my study are threefold: quantify changes in the EFTR mussel assemblage that occurred between 1988 and 2011, examine associations between mussels and host-fish assemblage shifts, and determine changes to stream physical and hydraulic habitat parameters. I hypothesize that the EFTR mussel assemblage is adapting to habitat changes resulting from hydrologic and geomorphologic modifications associated with the construction and maintenance of the TTW. Specifically, I predict that the abundance of mussel species that have higher tolerances for flow instability and finer substrates will have

significantly increased since 1988. Moreover, I hypothesize that changes to the host-fish assemblage are also mediating changes to EFTR mussels. I predict that declines or gains in mussel species abundance mimic declines or gains in their respective host fishes.

MATERIALS AND METHODS

Study Area

The EFTR originates in Itawamba County, MS, formed by the confluence of Mackeys and Brown Creeks then flows south into the Tennessee-Tombigbee Waterway (TTW) at river km 589 in Monroe County, MS. The EFTR upstream of the TTW drains a catchment of ~2035 km². The EFTR is a moderate-gradient stream with alternating pool-riffle habitats. The US Army Corps of Engineers (USACE) did not incorporate ~100 km of the EFTR into the TTW as this reach (*viz.* Canal Section) was deemed too costly and environmentally detrimental to channelize (Stine, 1993). Instead, the navigation route lies just east and parallel to the EFTR, severing eastern tributaries, and diverting ~42% (855 km²) of the original catchment directly into the TTW, (Green, 1985; USGS gage 02433500). Severed eastern tributaries still contribute some stream flows to the EFTR, but the navigation canal, reservoir spillways, and minimum flow structures—including one at the Bull Mountain Creek (BMC) confluence—regulate base- and flood-flows. Historically, these eastern streams drained upland forests and well-developed floodplain swamps. Discharges from western tributaries remain relatively intact, but are eroding and unstable, and drain primarily agricultural lands (Hartfield and Jones, 1989).

The BMC reach is fragmented by the TTW and lies between the EFTR and TTW. Lower BMC is a sinuous medium-sized creek (mean wetted channel width of 14.3 m) during summer-fall base flow conditions. Stream channel geomorphology includes both gently-

sloping, well-vegetated and steep, and actively-eroding banks. Substrates in BMC are also heterogeneous, but dominated by cobble and gravel. The streambed is armored (larger substrate particles appear naturally cemented together), hyper-stable, and coated with manganese precipitate in some riffles and runs. However, deep deposits of unstable, coarse sand and silt pervade where current velocity is $<5 \text{ cm s}^{-1}$. Woody debris is also common in BMC and is critical to riffle formation and substrate stabilization. In addition to regulating flows in BMC, severance by and discharge from the TTW influence water chemistry (e.g., temperature, pH, DO, conductivity) and other habitat parameters in this reach.

Survey Methods

In fall 2010 and summer 2011, I re-sampled 68 sites on the EFTR initially surveyed in 1988 by Hartfield and Jones (1989) and added two additional sites (Figure 1). Of the 68 original sites, three were repositioned to accommodate for deviations in the stream's course since 1988 (Figure 1). Additionally, I surveyed nine sites in lower BMC in 2011, 0–1 km upstream of the EFTR confluence. Distance between my study sites ranged from 80–120 m. A transect line bisected the stream at each site, and was used to position five equidistantly spaced 0.25 m^2 quadrats in the substrate. Current velocity was recorded at mid-channel depth using a Marsh-McBirney™ Flo-Mate flow meter (Marsh-McBirney, Frederick, MD), and stream depth was measured with a meter stick or a stadia rod at each quadrat. Within each quadrat, 12 substrate particles were chosen randomly ($n=60$ particles site⁻¹). Non-lithic particles were classified as sand, silt, clay, claystone, organic matter (leaf pack or other decaying vegetation), woody debris, or bedrock. Lithic particles were measured at their

greatest diameter to the nearest mm. The sizes of fine sediments were approximated following ranges defined by Chang (1988). Respective sizes for sand, silt, and clay are 1.03, 0.032, and 0.002 mm, respectively. As a proxy for substrate stability, I quantified the proportion of lithic particles covered by ferromanganese precipitate by visually estimating to the nearest 5% areal coverage of the excavated material composed of black-stained particles.

Three to six personnel surveyed each site using mask and snorkel, or SCUBA in deeper or fast-flowing habitats. Quadrats were hand-excavated to a depth of 10–15 cm. Mussels were separated from substrate using 6.2 mm² wire mesh, wooden box sieves. Timed searches were conducted at all sites under low-flow conditions (<9.22 m³/s, USGS gage 02433500) in June and July 2011. Search areas extended 10 m up-and downstream from each site's central transect line. All wetted areas within this 20 m sub-reach were surveyed, although quadrat sample sites were avoided. I quantified search effort (surveyor-hours) and abundance (mussel catch per unit effort, mussels per person-hour⁻¹) for all sites. Mussels were identified to species, enumerated, and immediately returned to the streambed. I retained shells as vouchers whenever possible and deposited them in the Mississippi Museum of Natural Science (MMNS), Jackson.

Complex Hydraulic and Substrate Variables

I used mean depth, current velocity and substrate composition to calculate 38 variables to describe habitat conditions at each study site under low flows (LF, 9.22 m³/s) and high flows (HF, 131.96 m³/s). High flow conditions were estimated remotely using USGS gage data to establish a discharge-depth rating curve, and satellite imagery to establish

a discharge-wetted-width rating curve. The positive asymptotic relationship between the stream profile and discharge at the gage site was applied to the low-flow stream profile (derived from five equidistant depth and flow measurements along each transect) to back-calculate stream velocity and depth at each of my study sites. These calculations assume that the HF stream profiles at my 70 sites are similar to each other and to the HF profile at the gage. Indeed, my EFTR sites are all moderately to severely channelized and incised.

I calculated streambed roughness (k_s , cm), Froude number (Fr, dimensionless), Reynolds number (Re, dimensionless), boundary Reynolds number (Re*, dimensionless), shear velocity (U^* , cm/s), shear stress (SS, dynes/cm²), critical shear stress (CSS, dynes/cm²), and relative shear stress (RSS, dimensionless) following established formulae (Gordon *et al.*, 1992; Steuer *et al.*, 2008; Allen and Vaughn, 2010). Streambed roughness describes small-scale contour variations in the substrate surface and is proportional to particle-size heterogeneity. The Froude number is the ratio of inertial to gravitational forces and describes flow regime. Higher Fr values typically represent supercritical (fast) flows, and lower Fr values characterize subcritical (slow) flows. The Reynolds number describes if a fluid flow is laminar or turbulent, and is the ratio of inertial to viscous forces. Greater Re values indicate more turbulent flows. The Reynolds boundary number characterizes turbulence at the substratum. Shear stress is the tangential shearing frictional force on the substrate. The friction forces of shear stress are analogous to those created when one arm of a pair of shears passes the other. Critical shear stress is the minimum force required to set into motion a median-sized particle (D_{50}) at the site scale. Relative shear stress is the ratio of observed shear stress to critical shear stress. Relative shear stress values >1 indicate displacement of median-sized substrate particles, (i.e., bed-load erosion).

Body Morphology and Life History

Species were ranked into five groups using five morphological criteria (maximum body size, shell thickness, shell texture, body inflation, and extent of postero-dorsal wing), and four life history criteria (maximum age, mean annual fecundity, age at maturity, and glochidium length). I used species descriptions from Williams *et al.* (2008) and Parmalee and Bogan (1998) to classify morphological rankings, and Haag (2012) was used to classify species by life history criteria.

Fish Assemblage

I derived fish assemblage data from MMNS records. Numerous parties conducted 81 survey efforts in or nearby my study reach from 1972–2009, and recorded 70 species. Since sampling effort (e.g., crew size, person-hours, level of experience) and equipment (e.g., seine size, electro shocker) varied in the surveys, I summarized fish species abundance simply by presence or absence by year. Then, I grouped survey years into either pre- (1972–1981) or post-TTW construction (1989–2009) for nonlinear multidimensional scaling (NMS) ordination and multi-response permutation procedures (MRPP). The earliest available fish data were collected in 1972, but data were missing for several years during and post-construction of the TTW (1981–1989).

I compiled mussel/fish-host associations using records of natural infestation (NI) and laboratory transformation (LT) data compiled by the Molluscs Division of the Museum of

Biological Diversity at Ohio State University (<http://www.biosci.ohio-state.edu/~molluscs>) and Williams *et al.* (2008).

Data Analysis

I used timed-search data from 1988 and 2011 to examine differences in mussel assemblage structure, abundance, survey effort, CPUE, and relative abundance at EFTR sites as quadrat methodologies were not consistent between studies. However, I included quadrat data in species-richness estimates. CPUE data from seven of the original 68 EFTR sites were missing and excluded from abundance and effort analysis. I considered *Quadrula apiculata*, *Q. rumphiana*, and *Q. quadrula* a single taxon in assemblage analyses due to nomenclature changes and the potential for morphological ambiguity between species. However, these species were considered separately in richness analyses. I used paired *t*-tests (when data was normally distributed), and 1-way ANOVA on Ranks (for non-normally distributed data) to quantify statistical differences in relative abundance (SPSS, Inc., Chicago, IL). NMS models of species abundance-defined mussel assemblage structure were derived from timed-search data from three groups: the 1988 EFTR assemblage ($n=61$ sites), the 2011 EFTR assemblage ($n=70$ sites), and the 2011 BMC assemblage ($n=9$ sites) (PC-ORD v. 6.0, McCune and Mefford, 2006). My NMS response matrices were structured using Euclidean distances, as Sorensen measures cannot analyze sites that yielded no mussels into the model. MRPP analysis quantified statistical differences between mussel assemblage groups.

Thirty-eight habitat variables were analyzed using principal components analysis (PCA) and I employed a randomization test (999 iterations) to quantify significance of the

PCA solution (PC-ORD v. 6.0, McCune and Mefford, 2006). I performed nonlinear regressions to describe the associations between mussel distribution (richness and abundance metrics) and habitat variables deemed important by PCA (high-flow shear velocity and velocity-depth ratio). Additionally, NMS models of habitat-defined mussel assemblage structure were derived from the relationship of two groups across 66 2011 EFTR sites: sites that were abundant with declining mussel taxa in 1988 ($n=22$), and all other sites ($n=44$). NMS ordinations of morphological- and life history-defined assemblage structure were derived from the timed-search abundances of 36 species and 24 species, respectively. Differences between groups (1988 EFTR, 2011 EFTR, and 2011 BMC) were compared using MRPP.

RESULTS

Timed searches conducted in 1988 and 2011 on the EFTR produced 2246 and 2346 mussels, respectively. Mean mussel abundance was statistically similar: 36.8 and 38.5 mussels per site⁻¹ in 1988 and 2011, respectively (Figure 2). However, mean catch-per-unit-effort (CPUE) declined significantly from 34.6 mussels hour⁻¹ in 1988 to 17.8 hour⁻¹ in 2011 ($p=0.002$, $H=9.615$, $n=61$, Figure 2). Mean survey effort was significantly greater in 2011 (1.79 person-hours site⁻¹) than in 1988 (1.1 person-hours site⁻¹, $p<0.001$, $H=42.68$, $n=61$). To ensure that the significant difference in CPUE between surveys was not an artifact of unnecessary search effort in the 2011 survey, I compared species richness values from both studies using rarefaction in Estimate S (version 7.5.2, Colwell, 2005). Rarefaction curves for each survey show a high degree of overlap indicating that sampling regimes are comparably effective and differences in abundance measured by CPUE are not statistical anomalies (Figure 3).

Although mussel abundance declined sharply, mean species richness remained stable. Quadrat and timed searches found 31 species alive in 1988 and 29 species alive in 2010–2011. Mean species richness did not differ significantly between 1988 and 2010–2011 (6.72 species site⁻¹ in 1988 and 6.94 species site⁻¹ in 2010–2011, $p=0.490$, $n=67$ sites). Eight species observed in 1988 were not detected alive in my survey, and six species detected in 2010–2011 were not encountered in 1988 (Table I). Some species that were not detected in 2010–2011 (e.g., *Anodonta suborbiculata*) were represented by just one individual in 1988,

indicating persistent low detectability. However, *Quadrula verrucosa* declined from 340 animals in 1988 to zero in my EFTR timed-searches. Additionally, I found no *Lasmigona alabamensis* alive in 2010–2011, but 1988 surveys produced 54 individuals. Similarly, I found only nine *Elliptio crassidens* in 2010–2011. In 1988, *Elliptio crassidens* was the 10th most abundant species ($n=122$).

Federally Listed Mussels

Abundance of the federally-listed EFTR mussel fauna has increased since 1988. I found 90 federally-listed mussels (7 *H. perovalis*, 61 *P. decisum*, 1 *P. perovatum*, 21 *P. inflatus*) during 2010–2011 surveys in the EFTR, compared to 4 individuals (2 *H. perovalis*, 2 *P. decisum*) in 1988. I found a single weathered shell of a fifth federally-listed species—the endangered *Pleurobema curtum*—at a location ~400 m downstream from the BMC confluence with the EFTR. Of the additional six federally-listed species that historically occurred in the UTR (endangered *Epioblasma penita*, *Pleurobema marshalli*, *P. taitianum*, *P. curtum*, and *Quadrula stapes*; threatened *Medionidus acutissimus*), only *E. penita* and *P. curtum* were known to occur in the EFTR. The other taxa are primarily large river species, or in the case of the smaller-stream species *M. acutissimus*, outside of its range. *Pleurobema decisum* was the most frequently encountered federally listed species (61 individuals at 14 sites) in 2010–2011 EFTR sampling. This federally endangered mussel has significantly increased ($p=0.001$) in abundance in the EFTR since 1988 (Table II). All but one of the 61 *P. decisum* were collected downstream of the BMC confluence. At one site ~700 m downstream from BMC, *P. decisum* composed >50% of the total mussel sample (Table II). I

also observed a statistically significant ($p=0.001$) increase in *P. inflatus* abundance from 1988 to 2011 (Table I). The threatened *Potamilus inflatus* was found during timed-searches at 16 sites (21 individuals) and was the most widely distributed federally-listed mussel encountered during 2010–2011 surveys. The federally-threatened *Hamiota perovalis* remains rare in the EFTR. Only seven individuals were found at four sites distributed across 4.25 river km. A single individual of *Plerurbema perovatum* was found in 2011 during a timed search yet its abundance has increased significantly ($p=0.044$) in the EFTR since 1988 (Table II). *Potamilus inflatus* and the endangered *P. perovatum* were undetected during 1988 sampling.

Invasive Mussels

I detected individuals and one specimen resembling three invasive mussels during this survey. *Potamilus alatus*, *P. ohiensis*, and *Quadrula quadrula*—all native to the Mississippi River basin—were detected at several localities throughout the EFTR. *Potamilus ohiensis* ($n=8$) was encountered at eight sites spanning 6 km and *Q. quadrula* ($n=32$) was found at 20 sites. A single fresh dead shell of *Potamilus alatus* was also found. *Potamilus ohiensis* and *Q. quadrula* have not been reported from the EFTR to my knowledge, but are established in Pickwick Reservoir, an impoundment of the Tennessee River connected to the EFTR via the TTW since 1985. Both species appear to be recruiting in the EFTR as I found four *P. ohiensis* <78 mm and six *Q. quadrula* <42 mm in length. Though *Q. quadrula* and *P. ohiensis* sometimes bear strong morphological resemblance to native congeners (*Q. apiculata*, *Q. rumphiana*, and *P. inflatus*). Although *Q. quadrula* was integrated into the

Quadrula complex for assemblage analyses, *P. ohiensis* was treated as a unique taxon based on shell characters (e.g., relatively rounded opposed to obliquely truncated posterior shell margin, greater shell elongation and less completely re-curved dorsal wing are present in *P. ohiensis*).

Change in Assemblage Structure

Abundance of nine mussels has decreased significantly between 1988 and 2011: *Amblema plicata*, *Elliptio crassidens*, *Fusconaia cerina*, *Lasmigona alabamensis*, *Leptodea fragilis*, *Megalonaias nervosa*, *Pyganodon grandis*, *Quadrula verrucosa*, and *Truncilla donaciformis* (Table II). *Megalonaias nervosa*, *A. plicata* and *Q. verrucosa* were the 1st, 2nd, and 4th most abundant taxa during 1988 timed-searches at 61 EFTR sites. *Megalonaias nervosa* and *A. plicata* are now the 5th and 9th most abundant EFTR mussels, and *Q. verrucosa* was not detected in 2011 surveys (Tables I and II). The CPUE for eight species (*E. lineolata*, *H. perovalis*, *Plectomerus dombeyanus*, *P. decisum*, *P. inflatus*, *P. ohiensis*, *P. purpuratus*, and *Villosa lienosa*) increased significantly since 1988: and three species (*Lampsilis ornata*, *Obliquaria reflexa*, and *Q. asperata*) showed significant increases in relative abundance (Table II).

Changes in mussel relative abundance lead to a shift in species dominance and evenness among EFTR sites (Figures 4 and 5). Simpson's 1/D decreased from 7.41 in 1988 to 5.32 in 2011 timed-search surveys. *Quadrula asperata* and *L. ornata* remain among the most abundant species in 2011 (Table III). However, the dramatic increase in *Q. asperata* abundance has decreased species evenness throughout the EFTR mussel assemblage.

Megalonaias nervosa was the most dominant species in 1988 comprising 15.5% of the EFTR mussel assemblage, but the 2011 dominant species, *Q. asperata*, comprises >2x that proportion at 34.4%. Further, the two most-dominant species totaled 29.1% of the EFTR mussel assemblage in 1988 but 49.3% in 2011 (Table III).

Timed searches in nine BMC sites in 2011 detected 1354 mussels (16 species) and another 66 mussels (10 species) were detected in quadrat samples (total species richness=17). Mean mussel density in BMC sites was 12.1 mussels m⁻² (n=45 quadrats) and was significantly greater ($p < 0.001$) than the 5.11 mussels m⁻² (n=350 quadrats) measured in EFTR sites. The endangered *Pleurobema decisum* was the most abundant species at BMC sites (n=563), which comprised 41.6% of the total timed-search catch. *Quadrula asperata* (32.5%), *P. dombeyanus* (8.49%), and *O. reflexa* (6.43%), were the 2nd, 3rd, and 4th most abundant BMC taxa (Table III).

NMS and MRPP analysis of assemblage structure (using species abundance data) show three distinct mussel assemblages—EFTR 1988, EFTR 2011, and BMC 2011. I employed a two-dimensional NMS solution (final stress=7.102) after confirming consistency among five model iterations. The proportion of variance represented by axis 1 was 70.3%, and axis 2 added 26.7%. NMS modeling showed that the 1988 EFTR mussel assemblage was least similar to the 2011 BMC assemblage (Figure 6). Moreover, the 2011 EFTR mussel assemblage structure consistently ordinales between the other two surveys. MRPP analysis revealed that all differences in the model (including pair-wise) are significant ($p < 0.0001$, $A = 0.145$), and that sites differ along both axes. NMS axis 1 correlates negatively with abundances of the small-bodied *Q. asperata* ($R^2 = 0.645$) and *O. reflexa* ($R^2 = 0.434$), and the thin-shelled *L. ornata* ($R^2 = 0.315$). Axis 2 correlates negatively with the small-bodied and

heavy-shelled *P. decisum* ($R^2=0.70$), *Q. asperata* ($R^2=0.549$), and *O. reflexa* ($R^2=0.178$). Axis 2 also correlates positively with *M. nervosa* ($R^2=0.168$), *A. plicata* ($R^2=0.157$), *E. crassidens* ($R^2=0.096$), and *Q. verrucosa* ($R^2=0.090$). All four are large-bodied, thick-shelled animals characteristic of larger stream mussel assemblages.

Habitat-Mediated Change

PCA analysis of 38 habitat variables across 66 EFTR sites produced four significant ($p<0.05$) principal component (PC) solutions according to randomization tests (999 runs). However, comparison of the observed Eigen values to broken-stick Eigen values suggests that only the first three PCs are useful (Table IV). Broken-stick comparisons work well when variables are highly correlated, as is the case in my dataset (McCune and Mefford, 2006). The first, second, and third axes account for 51.6%, 8.9%, and 6.8% of the variance in physical habitat data (67.3% cumulative). PC1 is driven primarily by nine highly correlated HF and LF hydraulic variables with $r^2 \geq 0.88$, (HF and LF shear velocity (U^*), HF and LF Reynolds boundary number (Re^*), HF and LF mean current velocity (U), HF Froude number (Fr), LF current velocity to depth ratio ($U:d$), and HF shear stress (SS)). The proportion of gravel (lithic particles >2 mm) was highly correlated with PC1 ($R^2=0.787$), yet unrelated to the current velocity-dependant hydrologic variables above (Table IV; Figures 7, 8, and 9). PC2 was best correlated with substrate-dependent parameters like bed roughness (k_s , $R^2=0.291$), and mean particle size ($R^2=0.276$), though these associations were weak (Table IV; Figures 7, 8, and 9). HF and LF relative shear stress account for the majority of the

variation in PC3 ($R^2 = 0.466$ and 0.46 , respectively) and appear to be highly correlated with each other (Table IV; Figures 7, 8, and 9).

Nonlinear regression shows that mean mussel density (mussels m^{-2}) is greatest at sites characterized by moderate to high HF U^* (Figure 10). A Gaussian peak function best describes this distribution ($n=66$, $R^2=0.342$, $p<0.0001$, Figure 10). A similar Gaussian distribution is observed when mean mussel density is plotted against $U:d$ ratio ($n=66$, $R^2=0.3185$, $p<0.0001$, Figure 11). When I compared the abundance of only those species that had experienced significant declines or gains since 1988 with $U:d$ ratio and HF U^* , I found that species whose abundance has significantly increased show greater abundances at higher $U:d$ ratios compared to species that have significantly declined since 1988 (Figures 12 and 13). The data show a similar trend when abundance of recruiting species and declining species is expressed as a function of HF U^* (Figure 13).

NMS and MRPP analysis of habitat and mussel assemblage structure show that sites with historically high abundances of the nine species that have declined significantly since 1988 ($n=22$ sites) are statistically distinct ($p<0.0532$) from the 44 sites with low abundance of these species (Figure 14). I employed a two-dimensional NMS solution (final stress=0.012) after confirming consistency among five model iterations. NMS plots strongly differentiate site assemblage structure along hydraulic parameter-based axes. The proportion of variance represented by axis 1 was 96.2%, and the second axis added 3.8%. Axis 1 is strongly negatively correlated with HF and LF Re, and LF U ($R^2=0.988$, 0.966 , and 0.546 respectively). Axis 2 correlates positively with LF d , and LF Re ($R^2=0.396$, 0.293 respectively).

Morphological- and Life History-Mediated Change

The three mussel assemblages (1988 EFTR, 2011 EFTR, and 2011 BMC) are statistically distinct using MRPP analysis in terms of shell morphology ($p < 0.0001$, Figure 15) and life history variables ($p < 0.0001$, Figure 16). Moreover, all pair-wise differences between groups in both analyses are also highly significant ($p < 0.009$). Ordinations for these two analyses agree with the model produced by NMS species abundance-defined axes. In all three of these models, the 1988 EFTR mussel assemblage is least similar to that of 2011 BMC, and the 2011 EFTR assemblage consistently ordines between the other two assemblages.

NMS morphological axis 1 correlates positively with species that have a maximum body length of >175 mm and 151–175 mm ($R^2 = 0.859$ and 0.398 , respectively). Axis 1 also correlates positively with shell thicknesses classified as massive and thick-massive ($R^2 = 0.799$ and 0.388 , respectively). Axis 2 correlates negatively with the abundance of species that have a maximum body length of 51–100 mm, lack a posterior wing, are smooth in texture, and inflated ($R^2 = 0.967$, 0.945 , 0.828 , and 0.950 , respectively; Figure 15).

NMS ordination separated assemblages along axes of life history traits. Axis 1 correlates positively with the abundance of species that are longer-lived (>35 y, $R^2 = 0.553$), and have low fecundity ($<25,000$ glochidia year⁻¹, $R^2 = 0.898$). Axis 2 correlates negatively ($R^2 = 0.838$) with the abundance of species exhibiting delayed sexual maturity (>5 y) (Figure 16).

Host fish-Mediated Change

A three-dimensional solution best fit NMS ordination of annual fish presence/absence data, where axis 1, 2, and 3 explain 15.5%, 21.2%, and 45.4% of the variability in the data, respectively (final stress=7.302, Figures 17, 18, and 19). MRPP analysis showed that pre- and post-TTW fish assemblages are statistically distinct ($p < 0.001$). Axis 1 is positively correlated ($R^2 = 0.38$) with the presence of *Aplodinotus grunniens*, a host (NI) for *Potamilus* spp., *E. lineolata*, *M. nervosa*, and *A. plicata*, and also with *Luxilus chrysocephalus*, a host (LT) for *O. reflexa* and the endangered *P. decisum* ($R^2 = 0.326$). However, axis 1 is negatively associated ($R^2 = 0.21$) with the presence of *Lepomis gulosus*, a host (NI) for *A. plicata* and *M. nervosa*. Axis 2 is negatively correlated with the presence of *Campostoma anomalum* ($R^2 = 0.703$) and *Pylodictis olivaris* ($R^2 = 0.179$), which are known hosts for *M. nervosa* and *P. grandis*, and *M. nervosa* and *Q. verrucosa* respectively. *Micropterus punctulatus* associates positively with axis 3 ($R^2 = 0.503$). *Micropterus* spp. are known hosts (LT) for *L. ornata* and the threatened *H. perovalis*.

DISCUSSION

Though overall mussel abundance has decreased on the EFTR from 1988–2011, I still found a diverse assemblage composed of 29 species. Eight species found in 1988 went undetected in my survey, and it is likely that several historically abundant (e.g., *L. alabamensis*, *Q. verrucosa*) are extirpated from my study reach, others presumably extinct (e.g., *Pleurobema curtum*, *Quadrula stapes*) (Table I). In contrast, relative and total abundance of other mussels, including several federally-listed species (e.g., *P. decisum*, *P. perovatum*, *P. inflatus*) increased suggesting a shift in mussel assemblages as the EFTR adapts geomorphically and ecologically to post-TTW hydrology (Table II). EFTR assemblages are now more similar to those found in BMC. My analysis of habitat parameters suggests that changes to hydraulic conditions may be an important driver of mussel assemblage shifts. The implications of hydrologic changes on physical habitat conditions are unclear but reduced flows likely have the most substantial effect on deeper-water habitats typically occupied by larger-bodied taxa (and their fish hosts). Alternatively, reduced flows may lead to physical habitat conditions (i.e., reduced silt loads, lower near-bed shear forces) favoring smaller bodied species that typically occupy shallow riffle and run habitats.

Federally-listed Mussels

My data indicate that some federally-listed mussel populations are increasing in the EFTR. In 1988 Hartfield and Jones (1989) collected only four individuals of two listed species (*H. perovalis* and *P. decisum*). In contrast, 2010–2011 surveys revealed 90 individuals of four listed species (*H. perovalis*, *P. decisum*, *P. perovatum*, and *Potamilus inflatus*). Both *P. decisum* and *P. inflatus* populations appeared to be recruiting as >20% of specimens collected were assumed to be juveniles based on shell length and estimated age.

In 1988, only two *P. decisum* juveniles were collected and the source of these recruits was unclear. It is possible that EFTR *P. decisum* originated in lower BMC. However, 1988 surveys of lower BMC found only the non-native *Corbicula fluminea* (P. Hartfield, pers. comm.). Qualitative surveys conducted during the past decade found adult and juvenile *P. decisum* in lower BMC (Bob Jones, Mississippi Museum of Natural Science, pers. comm.). Subsequently, *P. decisum* was observed on EFTR shoals downstream from the BMC confluence. The nearest source populations of *P. decisum* occur in the severed BMC channel east of the TTW, and in Buttahatchee River. Both of these sources are isolated from the EFTR by extensive impoundments. Therefore, it appears likely that the source of the recruiting EFTR *P. decisum* encountered in both 1988 and in 2010–2011, was either a small overlooked, relict population surviving in the lower reaches of BMC, or nearby in the EFTR.

One federally-threatened species, *H. perovalis*, appears to have become marginally more abundant in the EFTR from 1988 to 2010–2011. Only two *H. perovalis* were collected alive in 1988 surveys, whereas seven *H. perovalis* were collected alive from four EFTR sites in 2010–2011. A single *P. perovatum* collected in 2010 is the first recent record for this

species in the EFTR and may indicate re-colonization from lower BMC or another nearby tributary.

Invasive Mussels

The TTW is a well-documented corridor for aquatic invasive species (Ferrer-Montano and Dibble, 2002; Taylor *et al.*, 2008; Strongin *et al.*, 2011). The invasive plant Eurasian milfoil (*Myriophyllum spicatum*) was known from Pickwick Reservoir prior to the completion of the TTW, and is now found throughout the Mobile Basin. Other recent plant invasions include hydrilla (*Hydrilla verticillata*), curly pondweed (*Potamogeton crispus*), and Coontail (*Ceratophyllum demersum*) (Ferrer-Montano and Dibble, 2002). *Anodonta suborbiculata* has a long history of exploiting modified rivers to expand its range (Williams *et al.*, 2008). It is possible that the TTW provided an avenue for its invasion into the Tombigbee River drainage. Hartfield and Jones (1989) made the first report of this species in the EFTR during their 1988 surveys. Though no records were known from the Mobile River basin prior to 1976, it has since been found in most of the basin's major drainages, which suggests recent invasion—in some cases (e.g., Coosa River) probably on host fishes (Williams *et al.*, 2008).

My surveys found evidence that three additional non-native mussels have invaded the EFTR via the TTW. *Potamilus ohiensis* prefers fine substrates in minimal flow and colonizes reservoirs where it may become abundant (Bates, 1962; Williams *et al.*, 2008). Bates (1962) reported that *Q. quadrula* was among the first mussels to colonize overbank habitat in Kentucky Reservoir, on the lower Tennessee River. Both *P. inflatus* and *P. ohiensis* prefer

similar habitats and may also compete for host fish. Natural *P. ohiensis* infestations have only been observed on *Pomoxis annularis* and *A. grunniens*. *Aplodinotus grunniens* is the only known host for *P. inflatus* (Roe et al., 1997). Internal shell characters are most reliable to distinguish these putative invaders from native congeners since externally *P. ohiensis* is morphologically similar to *P. inflatus* and *Q. quadrula* resembles numerous other native mussels (e.g., *Q. apiculata*, *Q. nobilis*, *Q. rumphiana*). Genetic analyses could be instrumental to diagnose the extent of the presence of these taxa in the EFTR.

Causes for Assemblage Change

My results seem to suggest that the EFTR mussel assemblage is transitioning from an assemblage composed of large river species to one dominated by taxa characteristic of tributaries (e.g., Bull Mountain Creek) or more lentic-like habitats (Figures 5–6, 15–16). Taxa characteristic of smaller streams, including *Q. asperata* and *O. reflexa*, are replacing large river species like *M. nervosa* and *A. plicata* (Figures 4–6). Of the nine species that have declined significantly, six are known primarily from large river habitats (Williams *et al.*, 2008; Figure 4). Conversely, 6 of the 11 species that significantly increased in abundance since 1988 are typically found in lentic habitats characterized by low flows, fine substrates, oxbow lakes, or overbank habitats (Williams *et al.*, 2008; Figure 5). Since some mussels may be long-lived, individuals may persist for decades despite changing conditions. The decline of large, thick-shelled taxa may have begun prior to 1988 since little to no recruitment was evident for most species except *Q. verrucosa* (Hartfield and Jones, 1989).

Present mussel assemblages likely reflect a system affected by elevated shearing flows, higher sediment loads, and low connectivity with natural large river habitats. These conditions appear to be favoring some mussel species over others. As hydrological and ecological conditions adapted to the TTW-related disturbances, it may be that mussels more resistant to greater seasonal extremes of low and high flows, and hydrological and geomorphic instability became more abundant. The gain in abundance of some disturbance-sensitive taxa (e.g., *H. perovalis*, *P. decisum* and *P. inflatus*) would seem unlikely under unstable conditions. However, the host fishes for these rare mussel species are more characteristic of the present fish assemblage (Figures 17–19).

Numerous studies show that complex hydrologic variables that describe HF conditions can be useful to describe patterns of mussel distribution (Gangloff and Feminella, 2007; Zigler *et al.*, 2008; Steuer *et al.*, 2008; Allen and Vaughn, 2010). My results show that HF shear velocity (HF U^*) and current velocity to depth ratio ($U:d$) are critical factors affecting mussel distributions in the EFTR (Figures 10–13). Gaussian functions best describe the relationship between these hydraulic variables and mussel density, suggesting that optimum HF U^* exist at $\sim 30 \text{ cm s}^{-1}$, and the optimum $U:d$ ratio for the current mussel assemblage is $\sim 7 \text{ cm s}^{-1} : 10 \text{ cm}$ (Figures 10–13). The pattern of median value optimization is consistent with studies suggesting that very high and very low discharges mediate physical hydraulic parameters that limit mussel distribution (Morales *et al.*, 2006; Zigler *et al.*, 2008). Moreover, sites with the highest abundance of significantly declining species have lower velocities but greater depths compared with sites that have the highest abundance for species whose abundance has increased significantly (Figures 12–13). These deeper and slower flowing habitats may serve as refugia from sediment-shearing flood flows for these large-

bodied, large-river taxa (Howard and Cuffey, 2003; Gangloff and Feminella, 2007).

However, reduced flows may also strongly affect flow and substrate conditions in deeper habitats.

EFTR sites that historically supported large numbers of locally rare species exhibited much higher current velocity and bed scouring potential (U^*) compared to other sites (Figure 14). In 1983, USACE established the East Fork Maintenance Project (EFMP) ostensibly to increase hydraulic efficiency of the EFTR via de-snagging and clearing banks and transitional zones. These sudden geomorphic changes likely resulted in the channelization and incision of the EFTR and its tributaries, producing increased stream velocities and bed movement (Hartfield and Jones, 1989; US Army Corps of Engineers (USACE), 1984). Some mussel taxa that have significantly declined since 1988 may have been displaced by major hydraulic changes in the river. However, it is possible that those sites had historically high velocities when mussels were abundant. Comprehensive historical habitat data were not available for this reach of the EFTR. Yet, photography, river course changes, and anecdotal accounts of past surveyors (J.D. Williams and P.D. Hartfield, pers. comm.) indicate that the geomorphology of the EFTR remains dynamic but may be stabilizing.

Present conditions in the EFTR appear to favor smaller, thinner-shelled animals that are laterally compressed and lack shell sculpture (Figure 15). Studies show that species with these morphological characteristics produce less drag in the sediment and burrow faster than species that are laterally inflated, sculptured, or heavy-shelled (Stanley, 1988; Watters, 1992; McLachlan *et al.*, 1995; Waller *et al.*, 1999; Haag, 2012). The 1998 and 2011 EFTR mussel assemblages also have higher proportions of species with dorsal wings compared with the 2011 BMC assemblage. Dorsal wing morphologies may aid buoyancy in softer substrates or

stabilize animals in the current (Watters, 1994; Haag, 2012). As the EFTR became more hydraulically efficient following the EFMP, it is likely that sediment and mussels became displaced more frequently. My data suggest that the modern EFTR mussel assemblage may be more resistant to scouring disturbances because many extant taxa appear to be fast burrowing. Furthermore, species with thin shells and dorsal wing morphology may be better suited for reaches of the EFTR where channel modifications now have increased fine sediment deposits.

Present habitat in the EFTR may select for longer-lived taxa with relatively low fecundity, and also a younger age of sexual maturity. These results are somewhat conflicting. It seems that the EFTR favors *K*-selective species employing an equilibrium life-history strategy (*sensu* Haag, 2012), which is indicative of stable, productive habitats. My results show that this strategy is indicative of the assemblage in BMC where mussel density is significantly greater ($p < 0.001$) than in the EFTR. Relatively high mussel density may be increasing competition for streambed, food, and reproductive (i.e., host fish) resources. It also appears that species that reach sexual maturity earlier (<6 y) are replacing species that mature more slowly. This implies that conditions on the EFTR are favoring a more periodic life strategy (*sensu* Haag, 2012), indicative of cyclical variations in productivity and geomorphology. However, the vast majority of unionid species reach sexual maturity before age six, suggesting that if the EFTR mussel assemblage is only weakly trending toward a more periodic life-history strategy (Haag, 2012).

Changes to the fish assemblage may also be partially responsible for observed changes in the mussel assemblage. It appears host fishes for mussels that became more abundant (*E. lineolata*, *L. ornata*, *P. inflatus*, *P. ohioensis*, and *P. purpuratus*) may be

replacing hosts of mussels that have declined significantly since 1988 (*A. plicata*, *M. nervosa*, *P. grandis*, and *Q. verrucosa*). Some fishes may serve as hosts for several mussel taxa. *Aplodinotus grunniens* is a host for several species that have become more abundant (e.g., *E. lineolata*, *L. ornata*, *Potamilus* spp.), as well as for several declining mussels (e.g., *A. plicata*, *M. nervosa*). However, *Potamilus* spp. are host specialists that use *A. grunniens* and may be outcompeting generalists like *A. plicata* and *M. nervosa*. The relative importance of host fishes remains unknown for the survival of generalists like *A. plicata*, *M. nervosa*, and *P. grandis*. However, 7 of the 11 mussels that have become more abundant are host specialists. (*H. perovalis*, *L. ornata*, *O. reflexa*, *P. decisum*, *P. inflatus*, *P. ohioensis*, and *P. purpuratus*). While the *Potamilus* spp. are true specialists that utilize a single fish species, *H. perovalis*, *L. ornata*, *O. reflexa*, and *P. decisum* are each known to exploit a few species by actively attracting them with mantle lures or conglutinates (Williams *et al.*, 2008; Haag, 2012; Vaughn, 2012).

Linkages between host fishes and mussel assemblage structure appear to vary greatly with the ecological and habitat requirements for individual species of each. However, the decline of the host specialist *E. crassidens* may be mimicking the abundance of its host fish *Alosa chrysochloris*. Small individuals of this migratory fish were found in the upper Tombigbee River before the construction of the TTW. However, no evidence suggests that *A. chrysochloris* is reproducing post-TTW (Boschung and Mayden, 2004). Alterations to channel connectivity due to several TTW locks and dams have vastly reduced *A. chrysochloris* runs and resulted in significant declines of *E. crassidens* in the EFTR. Changes in geomorphology, and water temperature from natural and anthropogenic sources have likely disrupted *A. chrysochloris* spawning behaviors and distribution. Even small disruptions

to *A. chrysochloris* spawning timing may desynchronize the reproductive cycle of *E. crassidens*.

Management Implications

EFTR mussel species composition, shell morphology, and life history consistently show that the EFTR mussel assemblage has become more similar to BMC mussel assemblages between 1988 and 2011. It is likely that EFTR habitats and fish assemblages have become more similar to conditions in BMC. The construction and operation of the TTW and subsequent channelization and de-snagging activities are likely responsible for changes to hydrology, geomorphology, and mussel assemblage structure in the EFTR. Flow diversion and periodic high flows from lock operation mimic hydrologic instability indicative of smaller streams. Small streams tend to be hydraulically inconsistent with episodic flows prone to extreme conditions of seasonal drought and flood (Gordon *et al.*, 1992). Conversely, large rivers have more consistent flows, and less turbulent flood spates due to higher streambed uniformity (Gordon *et al.*, 1992). Thus, large rivers tend to naturally ameliorate extremes in conditions that may profoundly affect smaller streams. It is likely that the hydrologic differences between small and large streams correlate to differences in the composition, shell morphology, and life history of the species that occupy them.

Though the 2011 mussel assemblage in the EFTR is structured differently than it was in 1988, it maintains high diversity, including several rare species. Future research should include periodic monitoring and documentation of mussel assemblage changes in the EFTR and other relict mussel assemblages in the Tombigbee River drainage (e.g., Buttahatchee,

Sipsey rivers; Bull Mountain, Luxapalila, Yellow creeks). BMC supports large populations of *P. decisum* and *P. perovatum*. Conservation measures should ensure that those populations remain intact and accessible to the EFTR. Western tributaries draining into the EFTR are highly impaired by geomorphic instability and erosion, and reaches of the EFTR above Mill Creek are degraded by high sediment from eroding tributaries. Any efforts to stabilize the geomorphology of these streams would likely benefit mussels and habitats in the EFTR.

The degree to which invasive mussel species have colonized the EFTR following the completion of the TTW remains uncertain. Genetic data are needed to confirm the identity of putative invasive species *P. alatus*, *P. ohioensis*, and *Q. quadrula*, determine their likely origins, and monitor their interactions (e.g., potential hybridization) with native species will be necessary. Resource managers should continue to monitor fish assemblage changes in the EFTR, BMC, and throughout the upper Tombigbee River drainage. Future efforts to quantify host fish use and the relative importance of host fish availability to the EFTR mussel assemblage may also be necessary to identify the drivers of assemblage changes.

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FIGURES AND TABLES

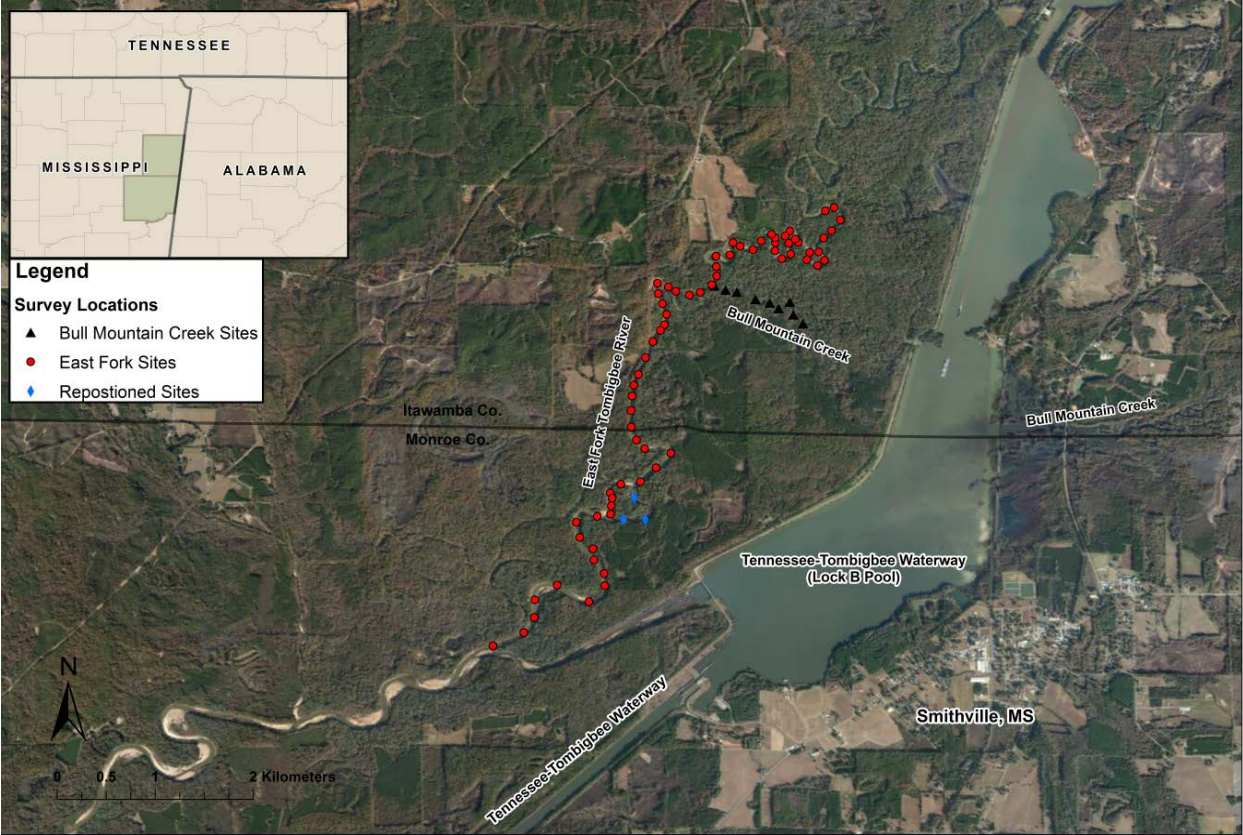


Figure 1. Map of 68 study sites on the East Fork Tombigbee River (EFTR, red circles) and 9 sites on Bull Mountain Creek (BMC, black triangles) in proximity to the Tennessee-Tombigbee Waterway. Three sites were repositioned from a dry stream meander (blue diamonds) to the newly straightened stream course to the west.

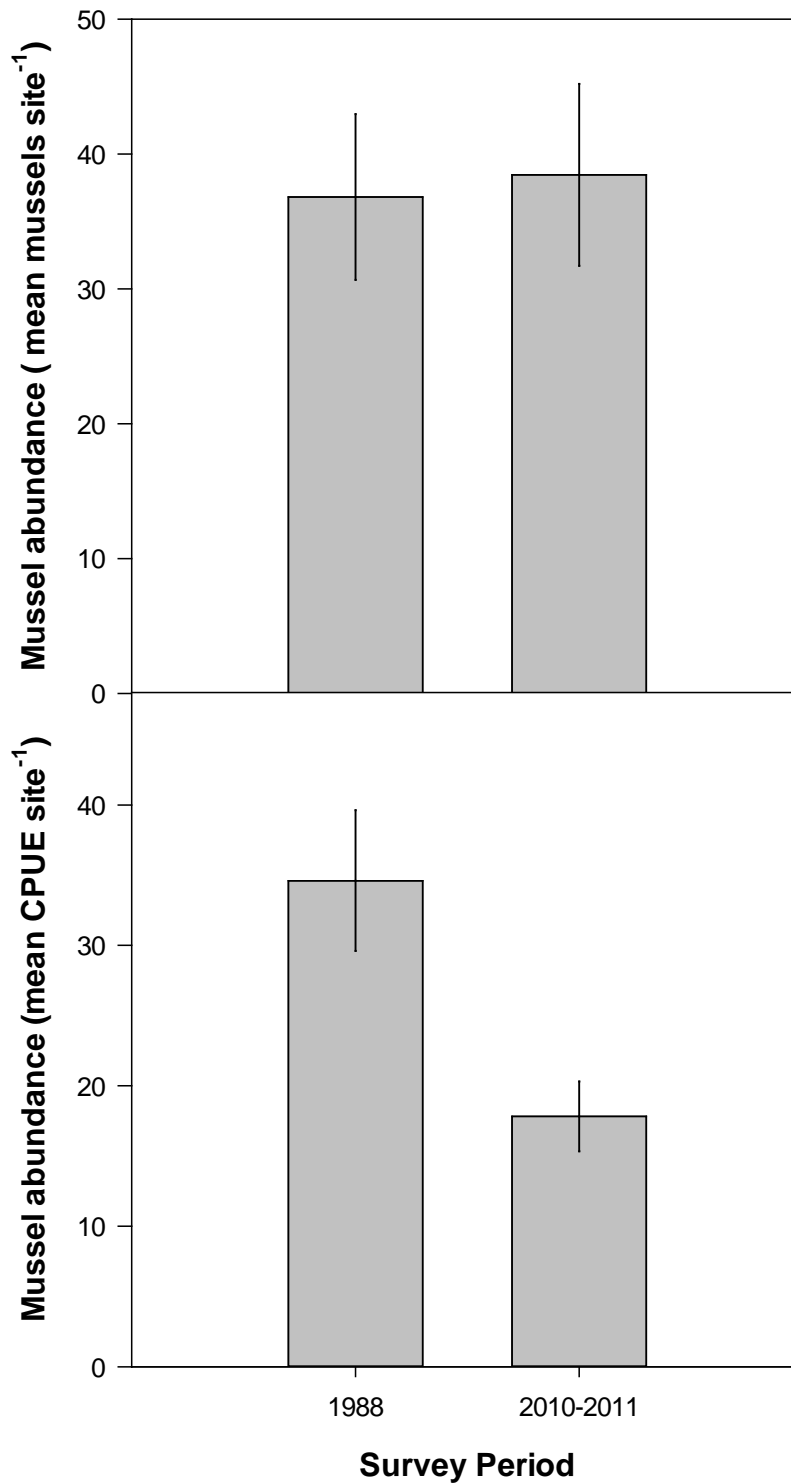


Figure 2. Change in freshwater mussel abundance from timed-searches at 61 sites on the East Fork Tombigbee River in 1988 and 2011. Differences in mean mussel abundance site⁻¹ (top) are not significant ($p=0.669$, $H=0.183$, $df=1$). Mean CPUE per site⁻¹ (bottom) was significantly less in 2011 than in 1988 ($p=0.002$, $H=9.615$, $df=1$).



Figure 3. Rarefaction curves showing cumulative species as a function of total mussels detected during 1988 (red) and 2010–2011 (black) sampling on the East Fork Tombigbee River.

Table I. Mussels known from the East Fork Tombigbee River. Eight mussel species were not detected in 2010/2011 surveys of the East Fork Tombigbee River, and 6 species were not observed in 1988 surveys. Asterisk (*) identifies federally listed species Federally threatened and endangered species are noted by T and E, respectively.

Species absent in 2010–2011 survey	Species absent in 1988 survey
<i>Anodonta suborbiculata</i>	<i>Pleurobema perovatum</i> E
<i>Elliptio arca</i>	<i>Potamilus inflatus</i> T
<i>Lasmigona alabamensis</i>	<i>Potamilus ohioensis</i>
<i>Obovaria jacksoniana</i>	<i>Quadrula metanevra</i>
<i>Pyganodon grandis</i>	<i>Quadrula quadrula</i>
<i>Quadrula verrucosa</i>	<i>Villosa vibex</i>
<i>Strophitus subvexus</i>	
<i>Toxolasma parvum</i>	

Table II. Change in mussel species composition from 1988 to 2011 at 61 timed-searched sites. Mean CPUE \pm SE is the mean abundance of a mussel species person-hour⁻¹ across 61 sites and the standard error. Significant statistical differences are described with p-values or are not significant (NS). Significant species losses and gains are represented by (Losses) and (Gains) respectively. Mean RA \pm SE is the mean relative abundance (% of mussel abundance site⁻¹) of a mussel species across 61 sites and the standard error. Federally threatened and endangered species are noted by T and E, respectively.

Taxon	Mean 1988 RA \pm SE	Mean 2010-11 RA \pm SE	Difference in RA
<i>Anodonta suborbiculata</i>	0.273 \pm 0.036	0	NS
<i>Amblema plicata</i>	13.586 \pm 0.233	1.735 \pm 0.050	<0.001 (Loss)
<i>Arcidens confragosus</i>	0.015 \pm 0.002	0.017 \pm 0.020	NS
<i>Elliptio arca</i>	0.086 \pm 0.011	0	NS
<i>Elliptio crassidens</i>	3.055 \pm 0.096	0.120 \pm 0.008	<0.001 (Loss)
<i>Ellipsaria lineolata</i>	0.065 \pm 0.005	1.992 \pm 0.083	<0.001 (Gain)
<i>Fusconaia cerina</i>	1.136 \pm 0.040	0.538 \pm 0.037	0.044 (Loss)
<i>Fusconaia ebena</i>	0.175 \pm 0.010	0.089 \pm 0.010	NS
<i>Hamiota perovalis</i> T	0	0.346 \pm 0.032	0.044 (Gain)
<i>Lampsilis ornata</i>	8.216 \pm 0.266	14.965 \pm 0.354	0.039 (Gain)
<i>Lampsilis straminea</i>	0.640 \pm 0.036	1.108 \pm 0.047	NS
<i>Lampsilis teres</i>	2.893 \pm 0.136	5.217 \pm 0.180	NS
<i>Lasmigona alabamensis</i>	2.400 \pm 0.113	0	<0.001 (Loss)
<i>Leptodea fragilis</i>	3.167 \pm 0.138	0.104 \pm 0.007	0.011 (Loss)

Taxon	Mean 1988 RA ± SE	Mean 2010-11 RA ± SE	Difference in RA
<i>Ligumia recta</i>	0.078 ± 0.010	0.072 ± 0.007	NS
<i>Megaloniaias nervosa</i>	15.511 ± 0.308	5.684 ± 0.167	0.003 (Loss)
<i>Obliquaria reflexa</i>	5.896 ± 0.126	11.226 ± 0.224	0.044 (Gain)
<i>Obovaria jacksoniana</i>	0.060 ± 0.006	0	NS
<i>Obovaria unicolor</i>	0.142 ± 0.009	0.404 ± 0.037	NS
<i>Plectomerus dombeyanus</i>	0.099 ± 0.009	0.612 ± 0.030	0.035 (Gain)
<i>Pleurobema decisum</i> E	0	0.503 ± 0.025	0.001 (Gain)
<i>Pleurobema perovatum</i> E	0	0.012 ± 0.002	NS
<i>Potamilus inflatus</i> T	0	1.656 ± 0.100	0.001 (Gain)
<i>Potamilus ohioensis</i>	0	0.398 ± 0.033	0.013 (Gain)
<i>Potamilus purpuratus</i>	4.060 ± 0.162	8.297 ± 0.256	<0.001 (Gain)
<i>Pyganodon grandis</i>	1.704 ± 0.109	0	0.007 (Loss)
<i>Quadrula</i> complex (i.e., <i>apiculata</i> , <i>quadrula</i> , <i>rumphiana</i>)	4.616 ± 0.158	2.713 ± 0.065	NS
<i>Quadrula asperata</i>	12.661 ± 0.268	34.351 ± 0.420	<0.001 (Gain)
<i>Quadrula metanevra</i>	0	0.035 ± 0.005	NS
<i>Quadrula verrucosa</i>	12.112 ± 0.217	0	<0.001 (Loss)
<i>Strophitus subvexus</i>	0.039 ± 0.004	0	NS

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Taxon	Mean 1988 RA ± SE	Mean 2010-11 RA ± SE	Difference in RA
<i>Toxalasma parvum</i>	0.321 ± 0.036	0	NS
<i>Truncilla donaciformis</i>	1.909 ± 0.069	0.077 ± 0.007	0.001 (Loss)
<i>Utterbackia imbecilis</i>	0.164 ± 0.021	0.546 ± 0.071	NS
<i>Villosa lienosa</i>	0.005 ± 0.001	0.595 ± 0.041	0.026 (Gain)
<i>Villosa vibex</i>	0	0.030 ± 0.004	NS

Table III. The four most abundant mussel species and their mean relative abundance (RA, % of total assemblage) for 61 timed-search sites on the East Fork Tombigbee River (EFTR) sampled in 1988 and 2011, and 9 sites on Bull Mountain Creek (BMC) sampled in 2011.

Abundance Rank	1988 EFTR	2011 EFTR	2011 BMC
1	<i>Megaloniaias nervosa</i> (15.51%)	<i>Quadrula asperata</i> (34.35%)	<i>Pleurobema decisum</i> (41.58%)
2	<i>Amblema plicata</i> (13.58%)	<i>Lampsilis ornata</i> (14.97%)	<i>Quadrula asperata</i> (32.50%)
3	<i>Quadrula asperata</i> (12.66%)	<i>Obliquaria reflexa</i> (11.23%)	<i>Plectomerus dombeyanus</i> (8.49%)
4	<i>Lampsilis ornata</i> (12.11%)	<i>Potamilus purpuratus</i> (8.30%)	<i>Obliquaria reflexa</i> (6.43%)

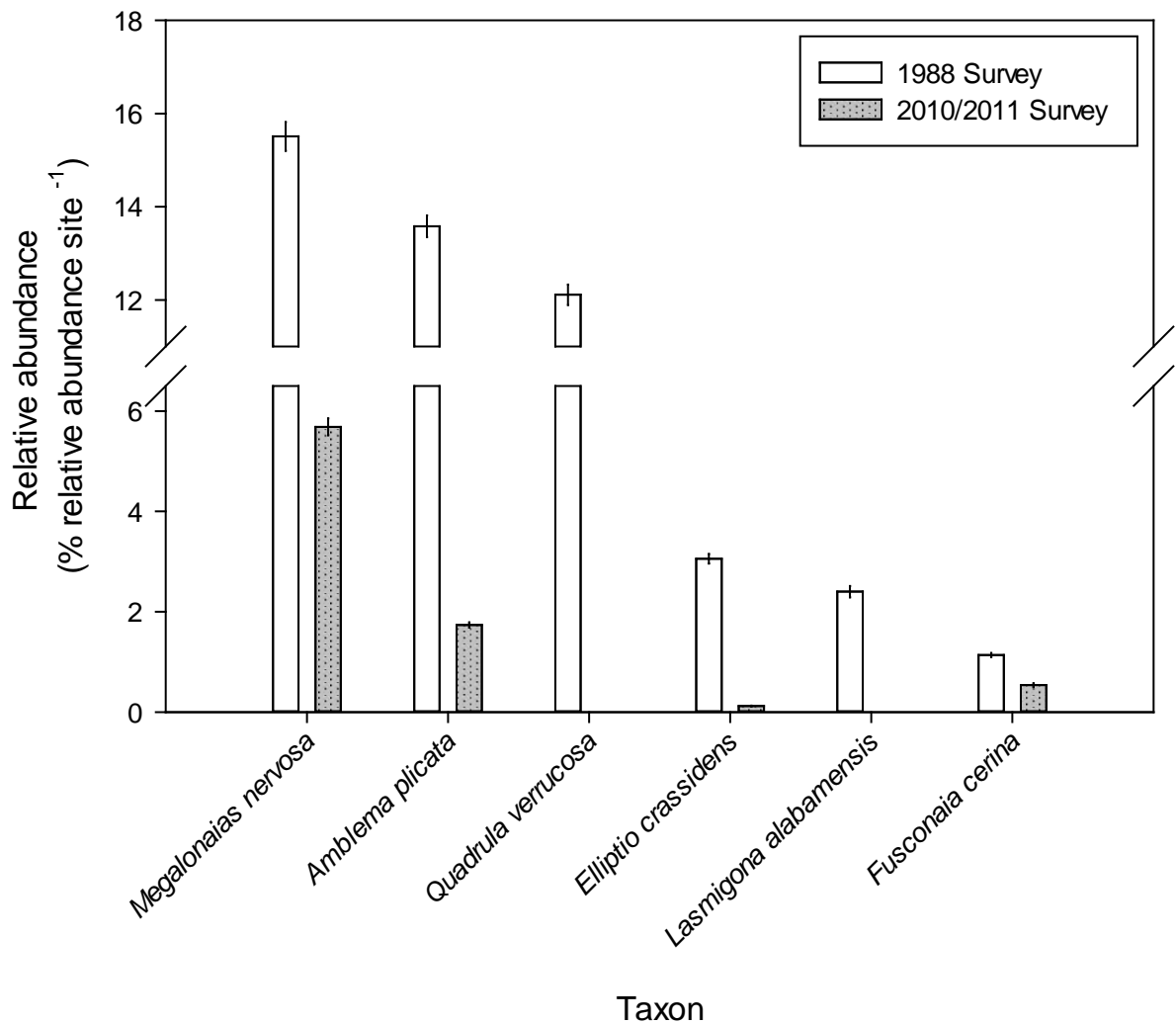


Figure 4. Significant declines ($p < 0.05$) in relative abundance of six mussel species according to timed-searches of 61 sites on the East Fork Tombigbee River between 1988 and 2011. These species are most commonly found in small to large rivers (Williams *et al.* 2008). No individuals of *Q. verrucosa* and *L. alabamensis* were found in the 2011 survey.

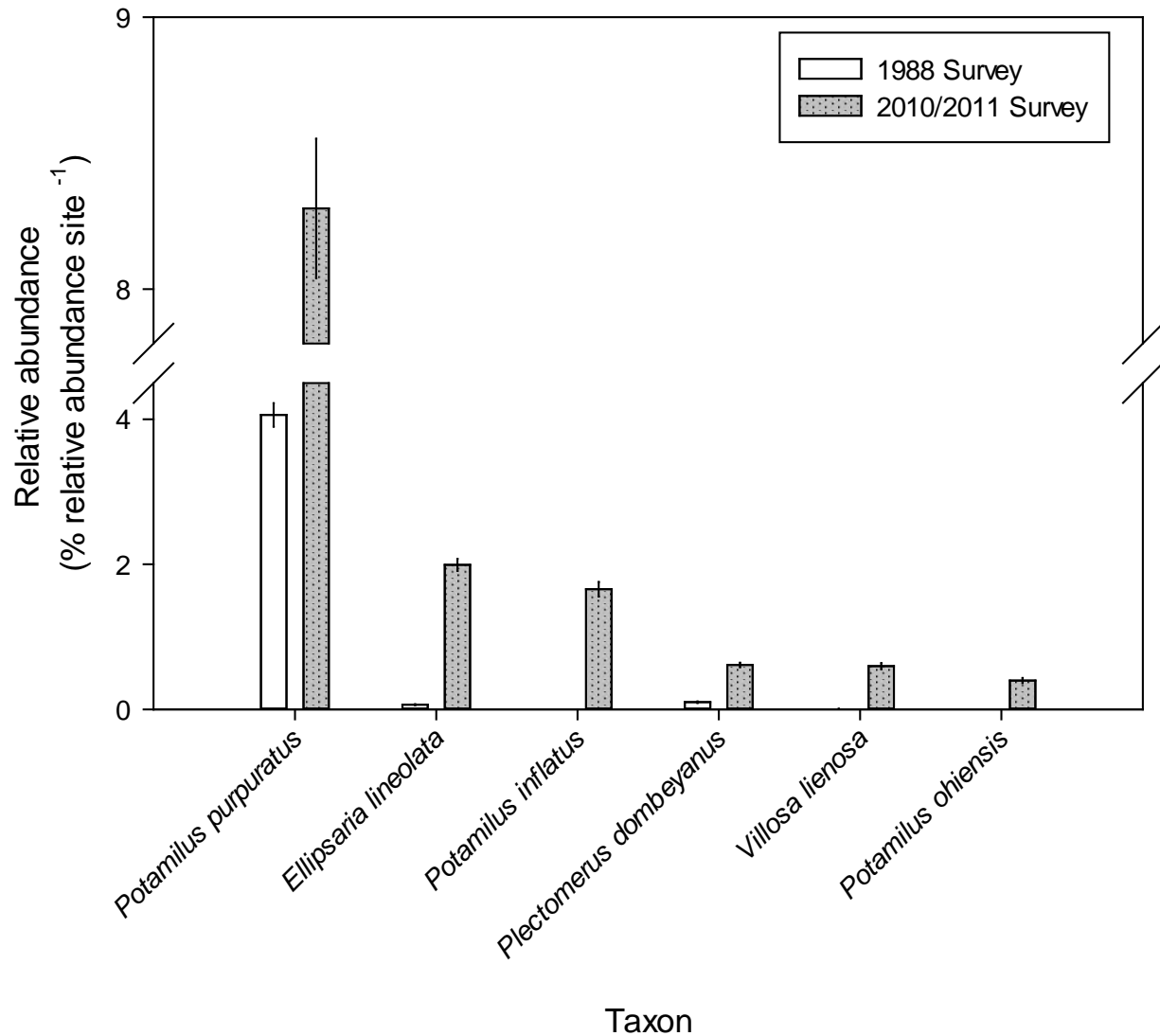


Figure 5. Significant gains ($p < 0.05$) in relative abundance of six mussel species according to timed-searches of 61 sites on the East Fork Tombigbee River between 1988 and 2011. These species are commonly found in lentic habitats (Williams *et al.* 2008). No individuals of *P. inflatus* and *P. ohioensis* were found in the 1988 survey.

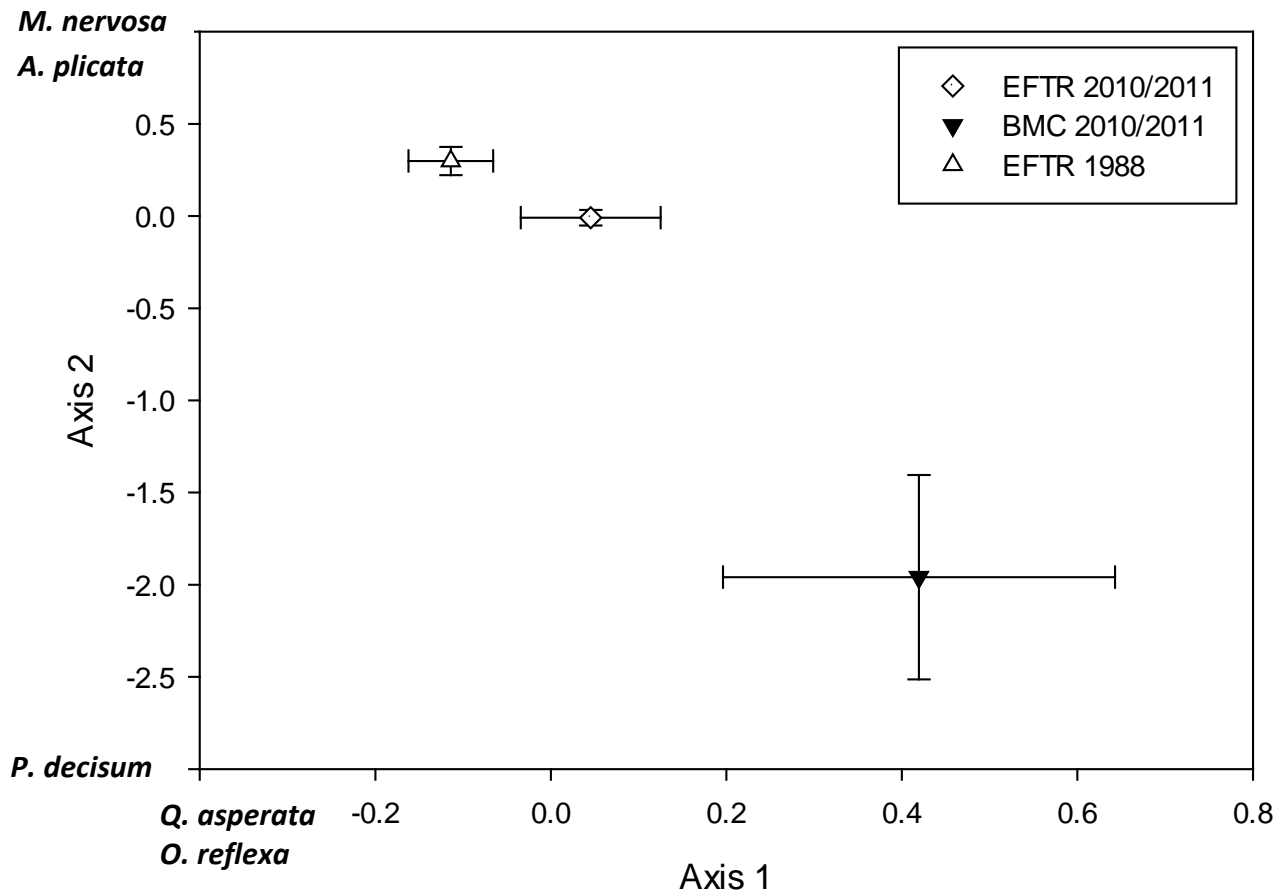


Figure 6. NMS ordination of the mussel assemblage structure of the East Fork Tombigbee River (EFTR) in 1988 (open triangle) and 2011 (solid triangle), and Bull Mountain Creek (BMC) in 2011 (open diamond) with bi-axis standard error bars about the centroid. All differences between and among mussel assemblages were statistically significant ($p < 0.0001$, $A = 0.145$). Axis 1 correlates negatively with abundances of *Q. asperata* and *O. reflexa*. Axis 2 correlates negatively with *P. decisum*, but positively with *M. nervosa* and *A. plicata*.

Table IV. Spearman’s correlations between principal components (PC) 1, 2, and 3 and 38 hydraulic and substrate variables (n=66 sites on the East Fork Tombigbee River). PC1, 2, and 3 explain 51.6%, 8.9%, and 6.8% of the variability in the data, respectively. See Methods for the code to abbreviations.

	PC 1			PC 2			PC 3	
	r	R ²		r	R ²		r	R ²
HF U^* (cm/s)	-0.970	0.941	k_s (cm)	0.539	0.291	LF RSS (dimensionless)	-0.683	0.466
HF Re^* (dimensionless)	-0.964	0.929	$(D_{16} + D_{50} + D_{84})/3$ (cm)	0.525	0.276	HF RSS (dimensionless)	-0.679	0.460
LF U^* (cm/s)	-0.960	0.922	LF Re (dimensionless)	-0.472	0.223	Proportion of clay substrate	-0.551	0.304
HF Fr , (dimensionless)	-0.953	0.909	CSS (dynes/cm ²)	0.450	0.202	LF wetted-width (m)	-0.465	0.216
LF Fr , (dimensionless)	-0.951	0.904	HF Re (dimensionless)	-0.449	0.202	LF Re (dimensionless)	0.446	0.199
LF Re^* (dimensionless)	-0.949	0.901	Proportion of sand substrate	-0.432	0.186	HF Re (dimensionless)	0.433	0.187
HF U (cm/s)	-0.949	0.901	Proportion of substrate >2mm	0.373	0.139	LF d range (cm)	0.413	0.171
LF U (cm/s)	-0.946	0.896	HF SS (dynes/cm ²)	-0.324	0.105	LF maximum d (cm)	0.385	0.148
$U:d$ ratio (cm/s:cm)	-0.938	0.880	LF SS (dynes cm ²)	-0.315	0.099	Proportion of silt substrate	-0.349	0.122
HF SS (dynes/cm ²)	-0.887	0.787	LF U (cm/s)	-0.304	0.093	LF mean d (cm)	0.302	0.091
Proportion of substrate >2mm	-0.874	0.764	Proportion of organic substrate	-0.305	0.093	HF mean d (cm)	0.302	0.091
LF SS (dynes cm ²)	-0.860	0.740	LF d Range (cm)	-0.292	0.085	CSS (dynes/cm ²)	0.275	0.076
LF maximum U (cm/s)	-0.859	0.738	HF U (cm/s)	-0.290	0.084	Proportion of wood substrate	0.199	0.040
LF mean d (cm)	0.820	0.673	LF Fr (dimensionless)	-0.278	0.077	Proportion of bedrock substrate	0.151	0.023
HF mean d (cm)	0.820	0.672	HF Fr (dimensionless)	-0.266	0.071	LF minimum U (cm/s)	0.148	0.022

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	PC 1		PC 2		PC 3			
	r	R ²		r	R ²		r	R ²
LF Specific mesohabitat type (fast riffle, riffle, fast run, run, slow run, pool)	0.810	0.656	<i>U:d</i> ratio (cm/s:cm)	-0.264	0.069	LF <i>U</i> Range (cm/s)	-0.122	0.015
CSS (dynes/cm ²)	-0.795	0.633	LF maximum <i>d</i> (cm)	-0.254	0.065	LF Specific mesohabitat type (fast riffle, riffle, fast run, run, slow run, pool)	0.108	0.012
LF General mesohabitat type (riffle, run, pool)	0.791	0.625	LF minimum <i>U</i> (cm/s)	-0.253	0.064	Proportion of substrate >2mm	0.111	0.012
(D ₁₆ + D ₅₀ + D ₈₄)/3 (cm)	-0.790	0.624	LF maximum <i>U</i> (cm/s)	-0.223	0.050	(D ₁₆ + D ₅₀ + D ₈₄)/3 (cm)	0.108	0.012
Proportion of substrate laden with ferromanganese	-0.771	0.595	HF <i>U</i> * (cm/s)	-0.196	0.038	Proportion of mudstone substrate	0.102	0.010
LF minimum <i>U</i> (cm/s)	-0.697	0.486	LF <i>U</i> * (cm/s)	-0.192	0.037	<i>U:d</i> ratio (cm/s:cm)	-0.089	0.008
LF maximum <i>d</i> (cm)	0.691	0.477	Proportion of wood substrate	-0.183	0.034	Proportion of substrate laden with ferromanganese	0.087	0.008
<i>k_s</i> (cm)	-0.686	0.471	Proportion of bedrock substrate	0.169	0.029	<i>k_s</i> (cm)	-0.075	0.006
Proportion of sand substrate	0.632	0.399	LF mean <i>d</i> (cm)	-0.157	0.025	LF General mesohabitat type (riffle, run, pool)	0.065	0.004
LF <i>U</i> Range (cm/s)	-0.581	0.338	HF mean <i>d</i> (cm)	-0.157	0.025	Proportion of organic substrate	-0.062	0.004
LF minimum <i>d</i> (cm)	0.561	0.315	Proportion of silt substrate	-0.143	0.020	LF Fr, (dimensionless)	-0.047	0.002
Proportion of silt substrate	0.556	0.309	LF General mesohabitat type (riffle, run, pool)	0.133	0.018	LF <i>U</i> * (cm/s)	-0.048	0.002
LF <i>d</i> range (cm)	0.512	0.263	LF Specific mesohabitat type (fast riffle, riffle, fast run, run, slow run, pool)	0.127	0.016	LF SS (dynes cm ²)	-0.045	0.002

	PC 1		PC 2		PC 3		r	R ²
	r	R ²	r	R ²	r	R ²		
HF Re (dimensionless)	-0.509	0.259	LF RSS (dimensionless)	-0.121	0.015	HF Fr, (dimensionless)	-0.048	0.002
LF Re (dimensionless)	-0.484	0.234	LF <i>U</i> range (cm/s)	-0.112	0.013	LF <i>U</i> (cm/s)	0.035	0.001
Proportion of organic substrate	0.396	0.157	LF Re* (dimensionless)	-0.111	0.012	LF maximum <i>U</i> (cm/s)	-0.038	0.001
Proportion of wood substrate	0.370	0.137	HF Re* (dimensionless)	-0.093	0.009	LF Re* (dimensionless)	-0.035	0.001
Proportion of clay substrate	0.258	0.067	HF RSS (dimensionless)	-0.085	0.007	HF <i>U</i> (cm/s)	0.030	0.001
Proportion of mudstone substrate	0.180	0.032	Proportion of clay substrate	0.069	0.005	HF <i>U</i> * (cm/s)	-0.031	0.001
Proportion of bedrock substrate	0.147	0.022	LF minimum <i>d</i> (cm)	0.040	0.002	HF SS (dynes/cm ²)	-0.025	0.001
LF RSS (dimensionless)	-0.106	0.011	LF wetted-width (m)	-0.025	0.001	LF minimum <i>d</i> (cm)	0.007	0
LF wetted-width (m)	-0.021	0	Proportion of substrate laden with ferromanganese	0.035	0.001	Proportion of sand substrate	0.010	0
HF RSS (dimensionless)	-0.009	0	Proportion of mudstone substrate	0.013	0	HF Re* (dimensionless)	-0.020	0

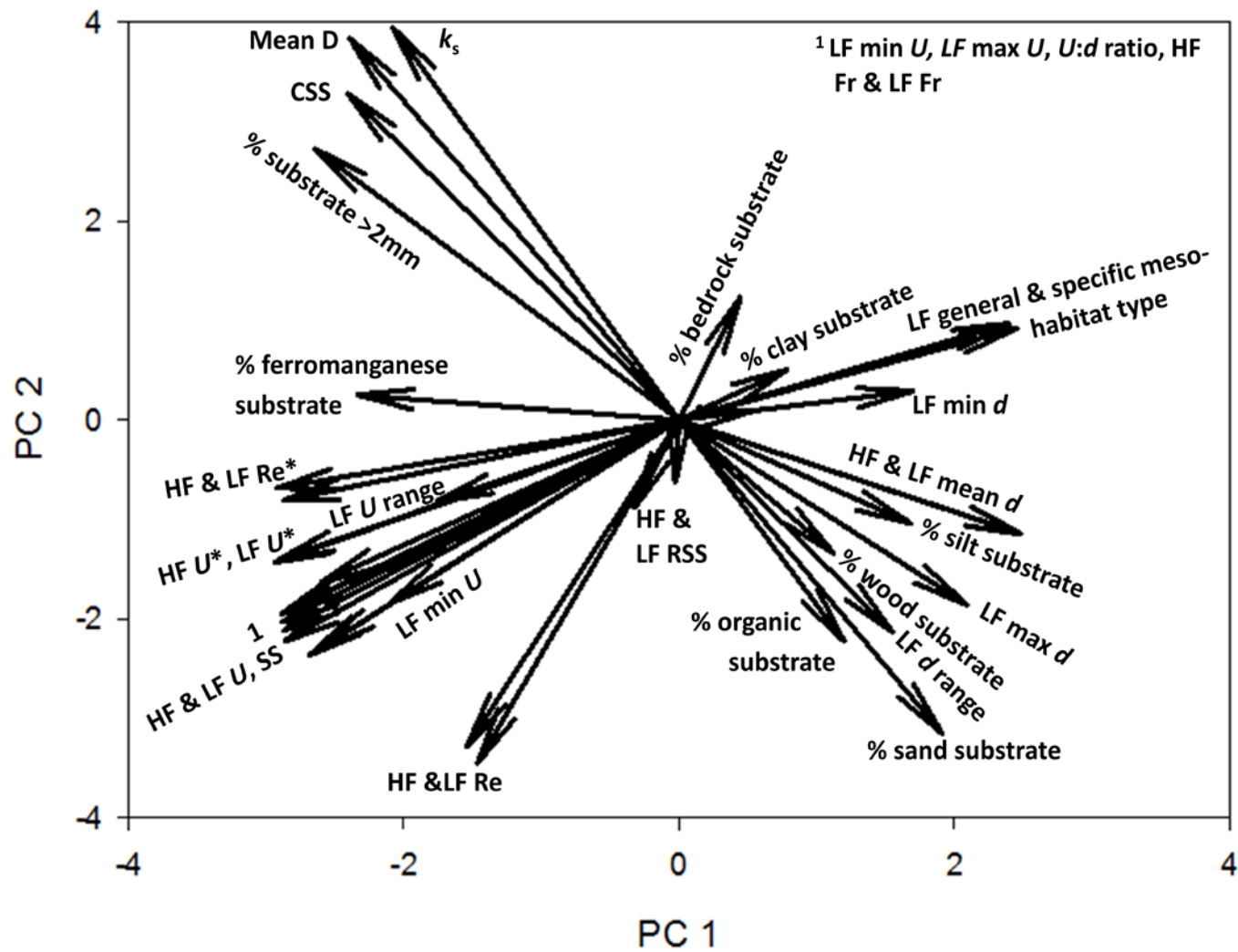


Figure 7. Principal components analysis vector plot showing the relationship between 38 hydrologic and substrate variables and PC1 and PC2 ($n=66$ sites on the East Fork Tombigbee River). The length of each line is proportional to that variable's correlation to PC1 and PC2.

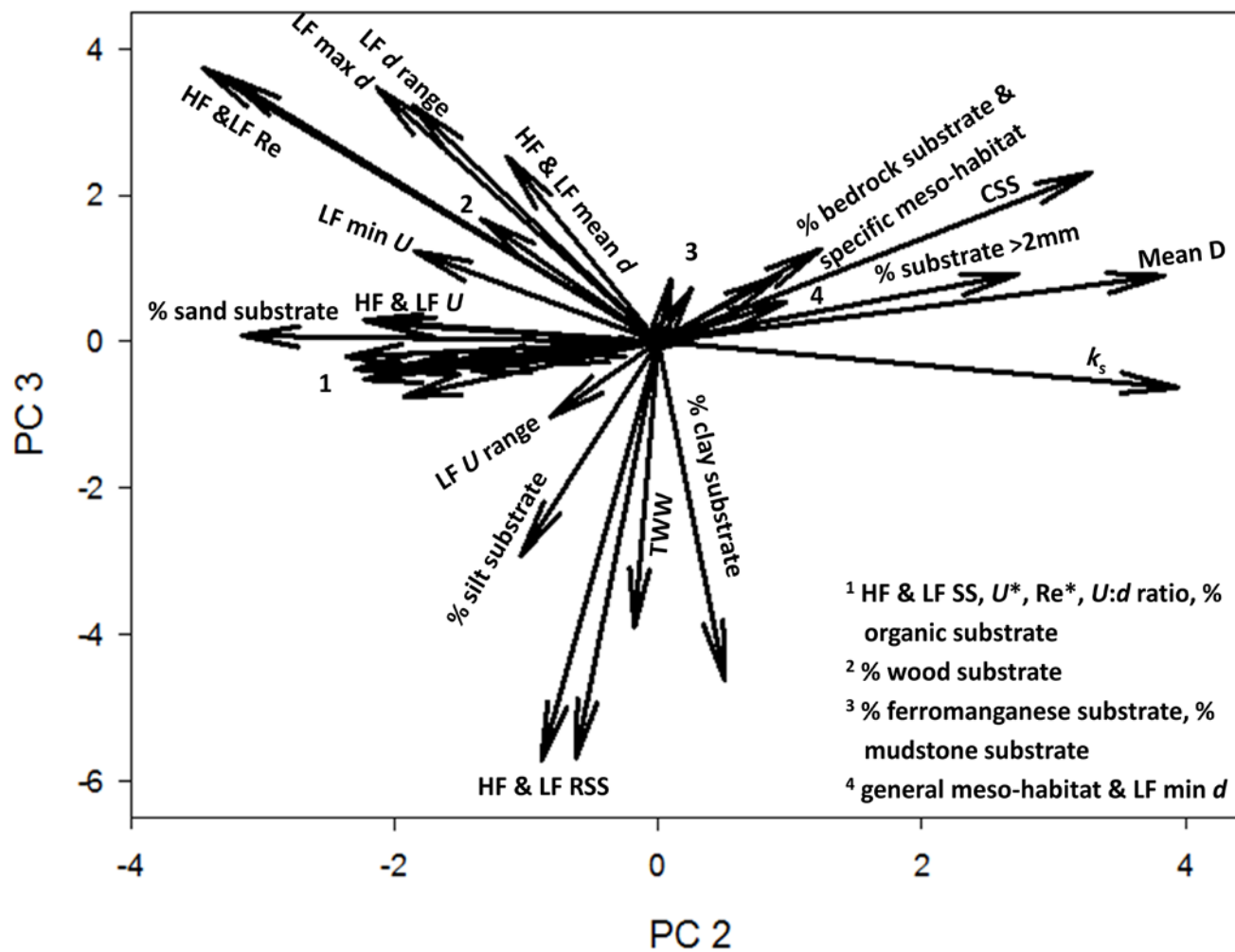


Figure 9. Principal components analysis vector plot showing the relationship between 38 hydrologic and substrate variables and PC2 and PC3 ($n=66$ sites on the East Fork Tombigbee River). The length of each line is proportional to that variable's correlation to PC2 and PC3.

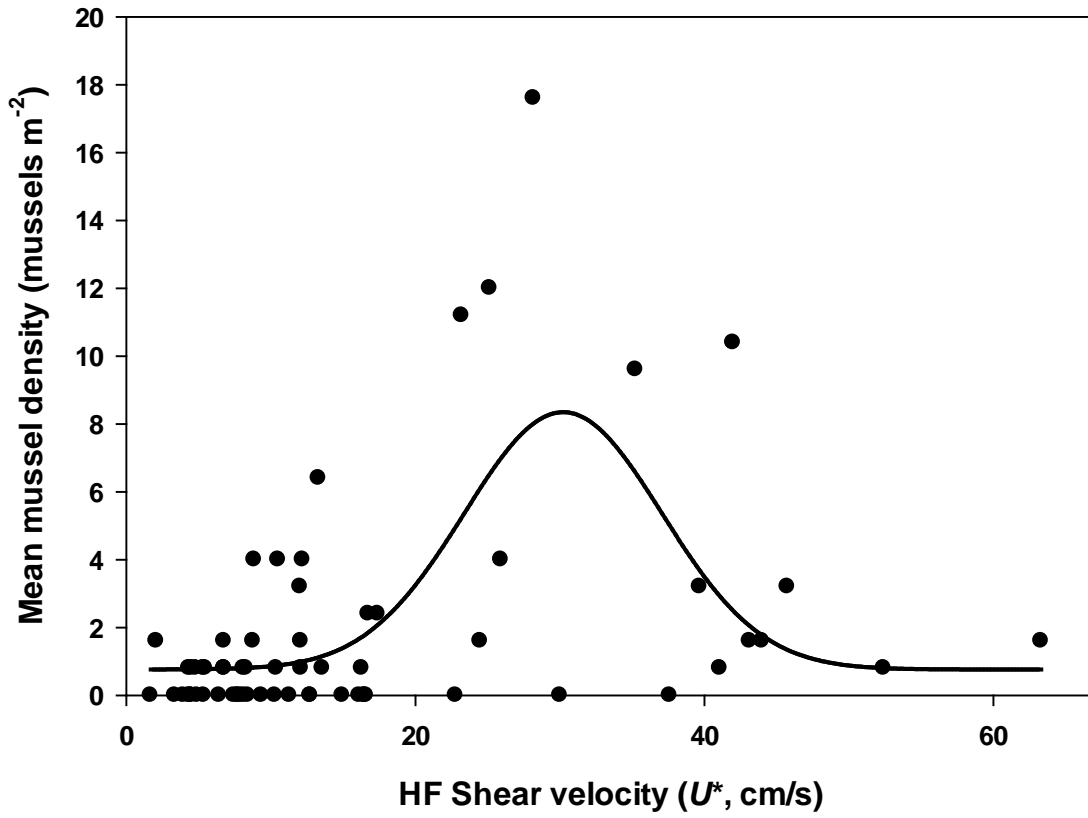


Figure 10. The relationship between shear velocity (U^*) under high flow (HF) conditions and mean mussel density from 66 sites on the East Fork Tombigbee River ($R^2=0.342$, $p<0.0001$).

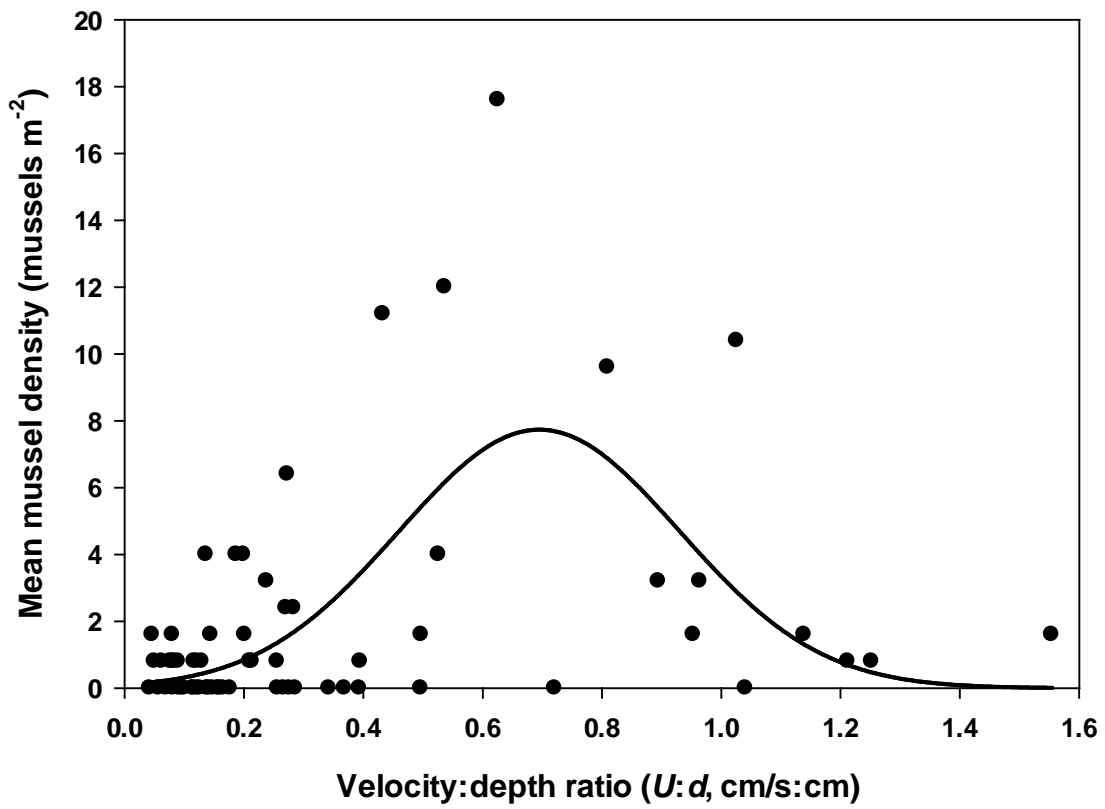


Figure 11. The relationship between velocity (U) to depth (d) ratio and mean mussel density from 66 sites on the East Fork Tombigbee River ($R^2=0.319$, $p<0.0001$).

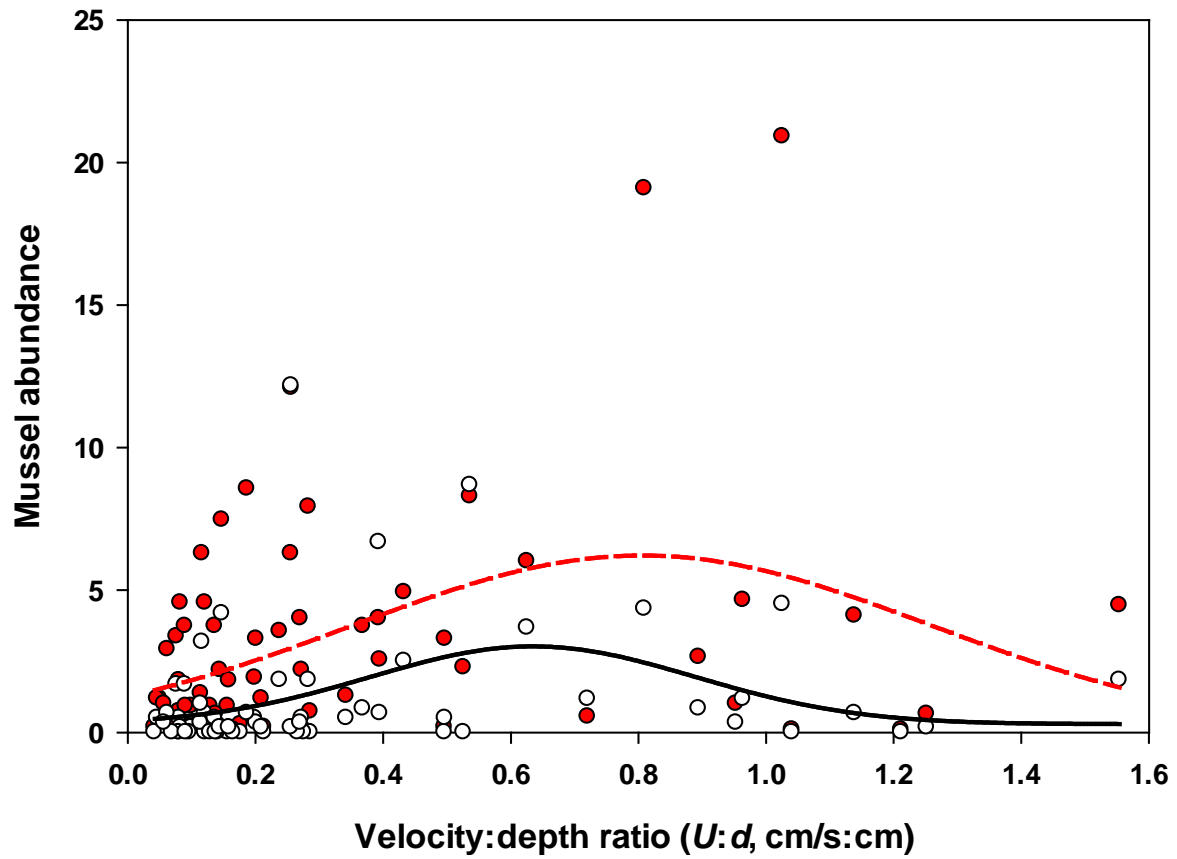


Figure 12. The relationship between velocity (U) to depth (d) ratio and abundance of 11 species that have become significantly more abundant (red hashed line) and less abundant (black solid) from 1988–2011 at 66 sites on the East Fork Tombigbee River (significant gains: $R^2=0.126$, $p<0.0145$, significant losses: $R^2=0.138$, $F=3.315$, $p<0.0256$).

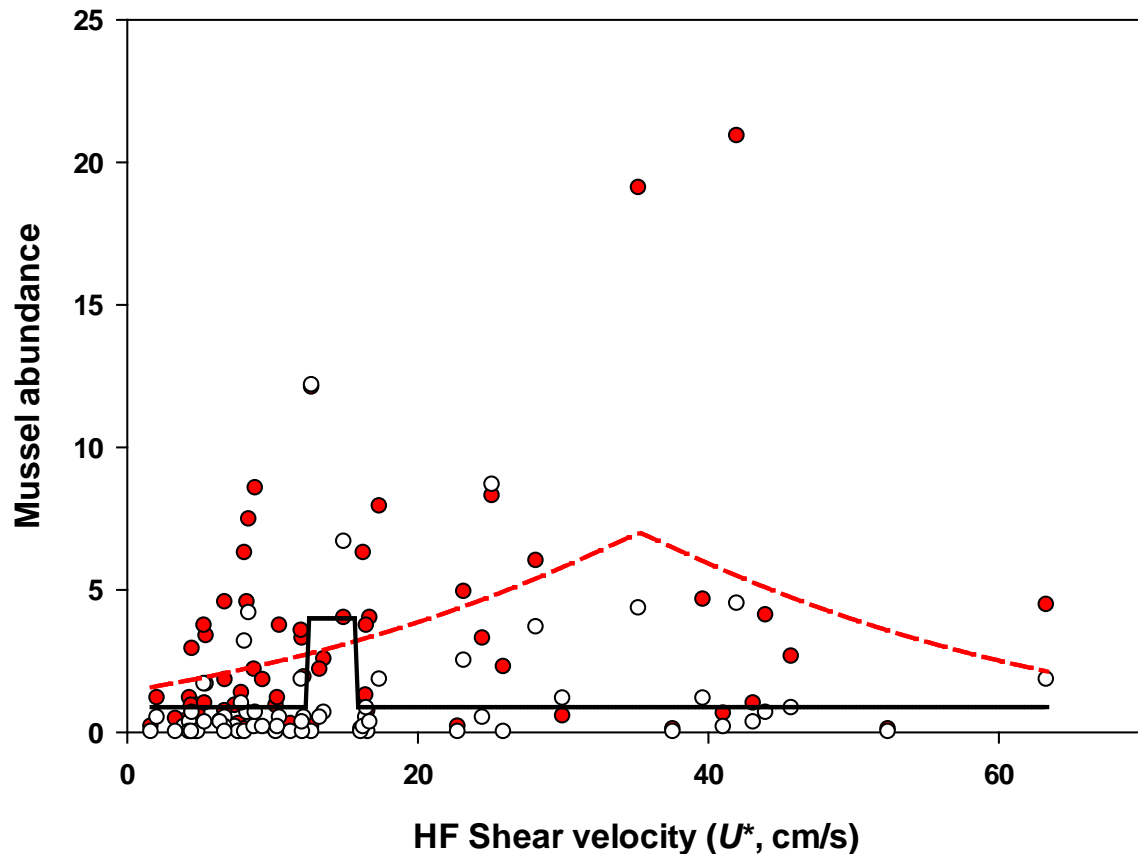


Figure 13. The relationship between velocity (U) to depth (d) ratio and abundance of 11 species that have become significantly more abundant (red hashed line) and less abundant (black solid) from 1988-2011 from 66 sites on the East Fork Tombigbee River. (significant gains: $R^2=0.151$, $p<0.038$, significant losses: $R^2=0.151$, $p<0.0376$).

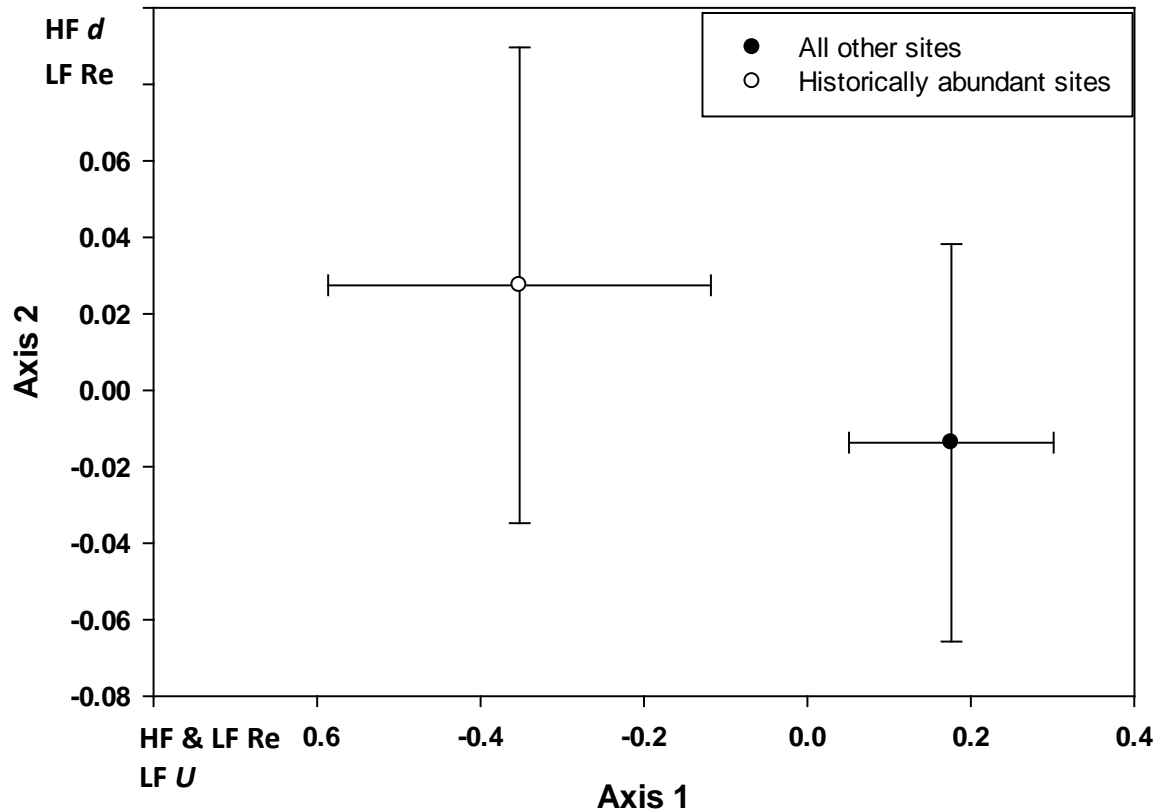


Figure 14. NMS ordination of 22 East Fork Tombigbee River sites (open circle) with high historical abundances of mussel species that have declined significantly from 1988-2011, and all other 44 sites (closed circle) surveyed with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by 38 hydrologic and substrate parameters. Differences between mussel assemblages were statistically significant ($p < 0.0532$, $A = 0.145$). Axis 1 correlates negatively with sites that have large high and low flow (HF and LF) Reynolds number (Re), and LF current velocity U . Axis 2 correlates positively with sites that have high HF mean water depth (d) and LF Reynolds number (Re).

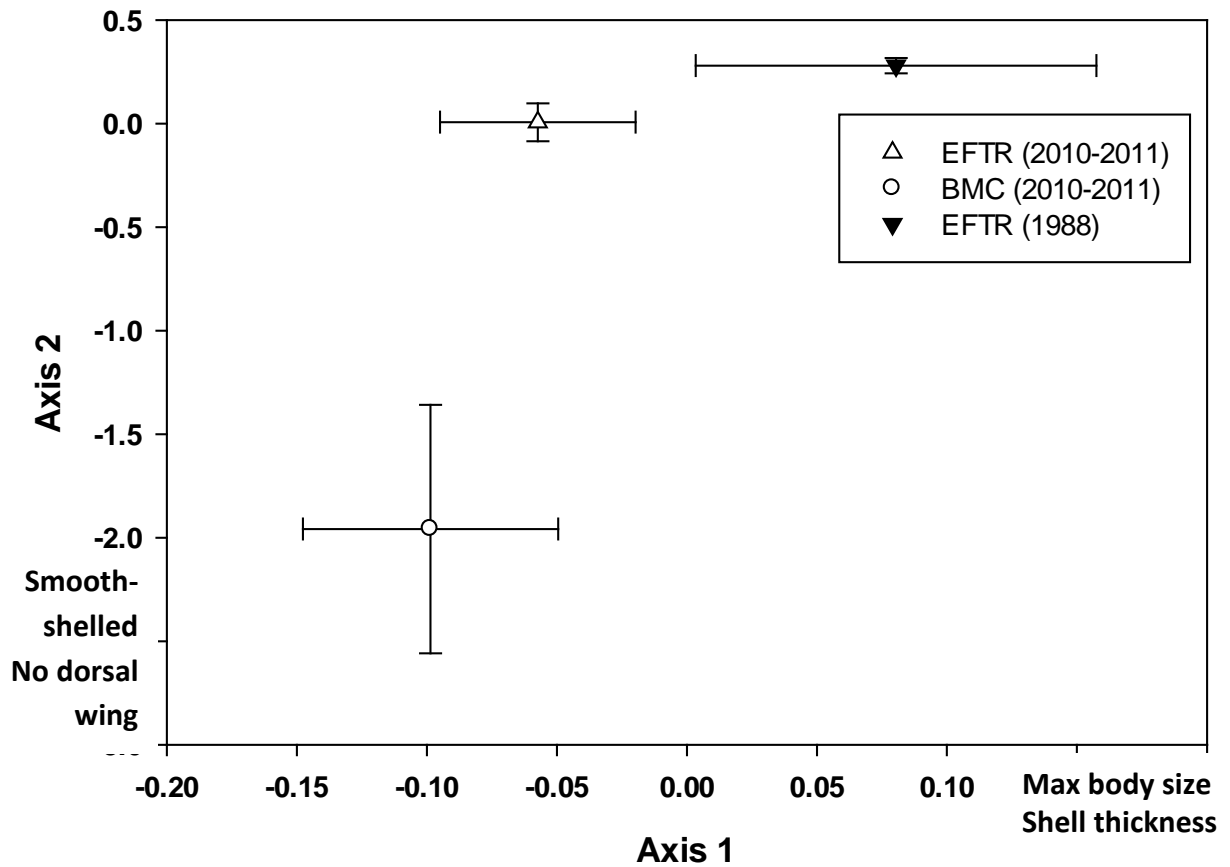


Figure 15. NMS ordination of the mussel assemblage structure of the East Fork Tombigbee River (EFTR) in 1988 (open triangle) and 2011 (solid triangle), and Bull Mountain Creek (BMC) in 2011 (open circle) with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by five shell morphology parameters. All differences between and among mussel assemblages were statistically significant ($p < 0.0001$, $A = 0.134$). Axis 1 correlates positively with the abundance of mussels with large maximum body size and thick shells. Axis 2 correlates negatively with the abundance of mussel species that are smooth-shelled and those lacking a dorsal wing.

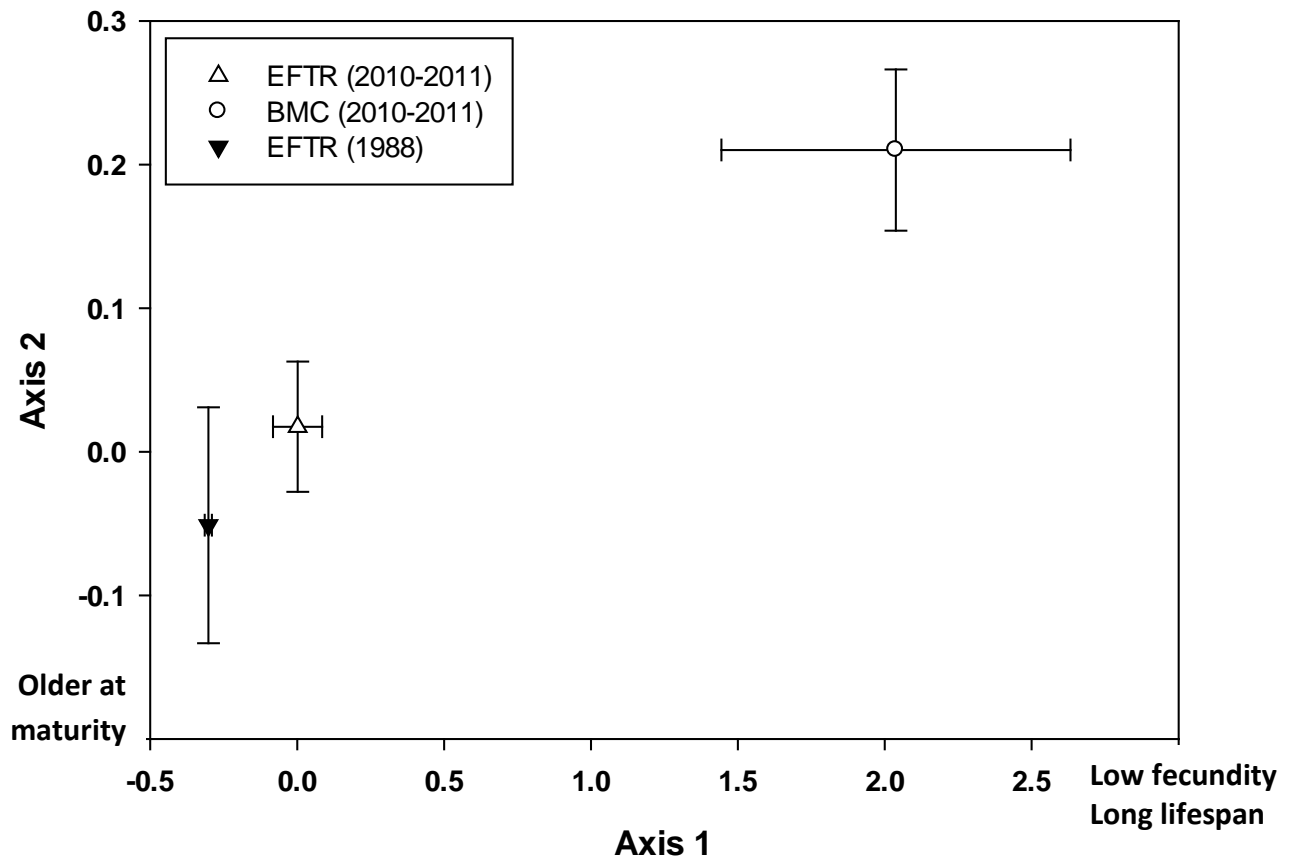


Figure 16. NMS ordination of the mussel assemblage structure of the East Fork Tombigbee River (EFTR) in 1988 (open triangle) and 2011 (solid triangle), and Bull Mountain Creek (BMC) in 2011 (open circle) with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by four life history parameters. All differences between and among mussel assemblages were statistically significant ($p < 0.0001$, $A = 0.153$). Axis 1 correlates positively with the abundance of mussel taxa that have low fecundity and longer lifespans. Axis 2 correlates negatively with the abundance of mussel species that are older at maturity.

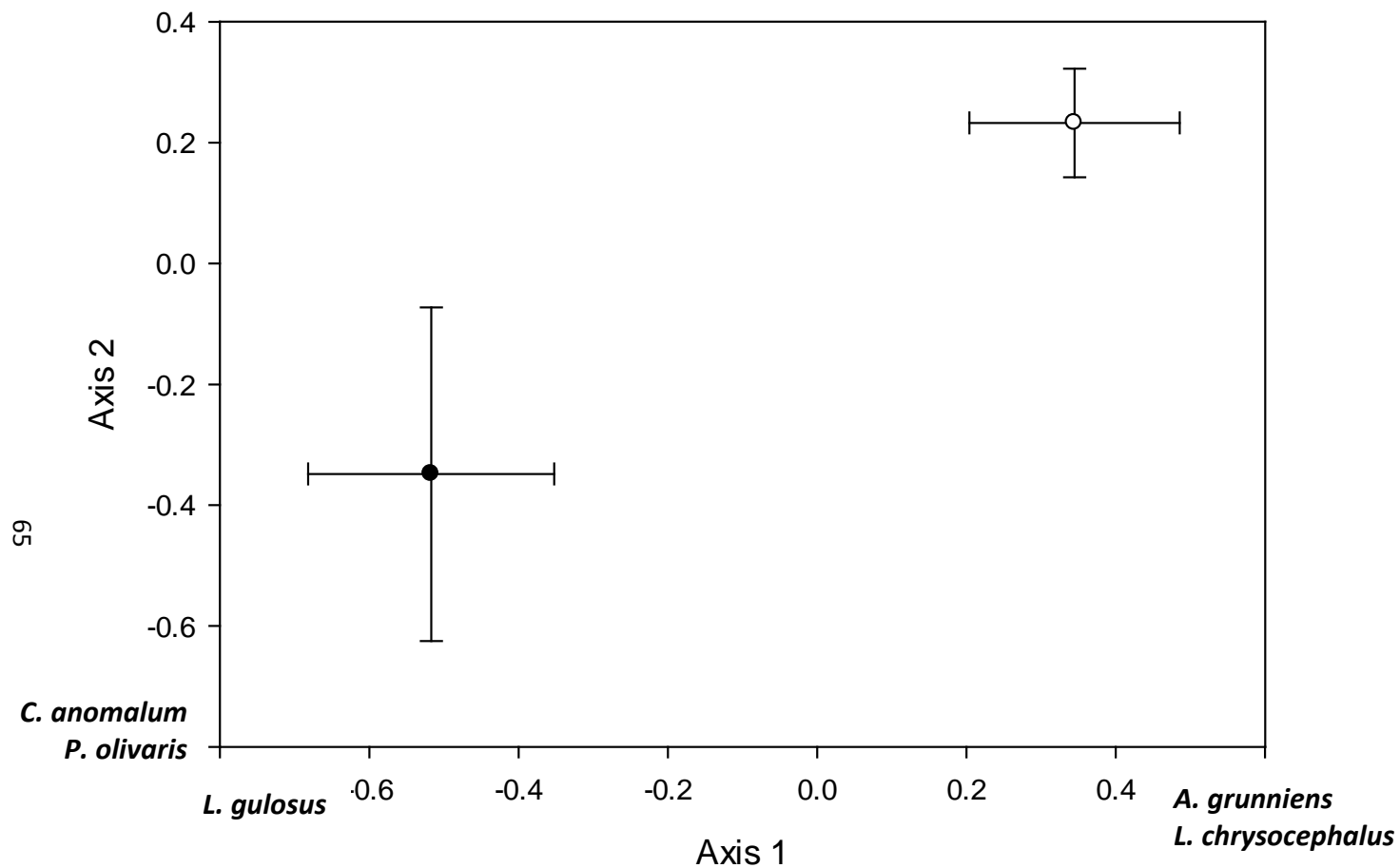


Figure 17. NMS ordination of the fish assemblage structure near the East Fork Tombigbee River (EFTR) pre- (closed circle) and post-construction of the Tennessee-Tombigbee Waterway (open circle) with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by annual presence or absence of 70 fish species from 81 surveys. All differences between and among mussel assemblages were statistically significant ($p < 0.001$, $A = 0.073$). Axis 1 correlates positively with the annual presence of *A. grunniens*, (host for *Potamilus* spp. and *E. lineolata*) and *L. chrysocephalus* (host for *O. reflexa* and *P. decisum*), and negatively with the presence of *L. gulosus* (host for *A. plicata* and *M. nervosa*). Axis 2 correlates negatively with the annual presence of *C. anomalum* and *P. olivaris* (hosts for *M. nervosa*, *Q. verrucosa*, and *P. grandis*).

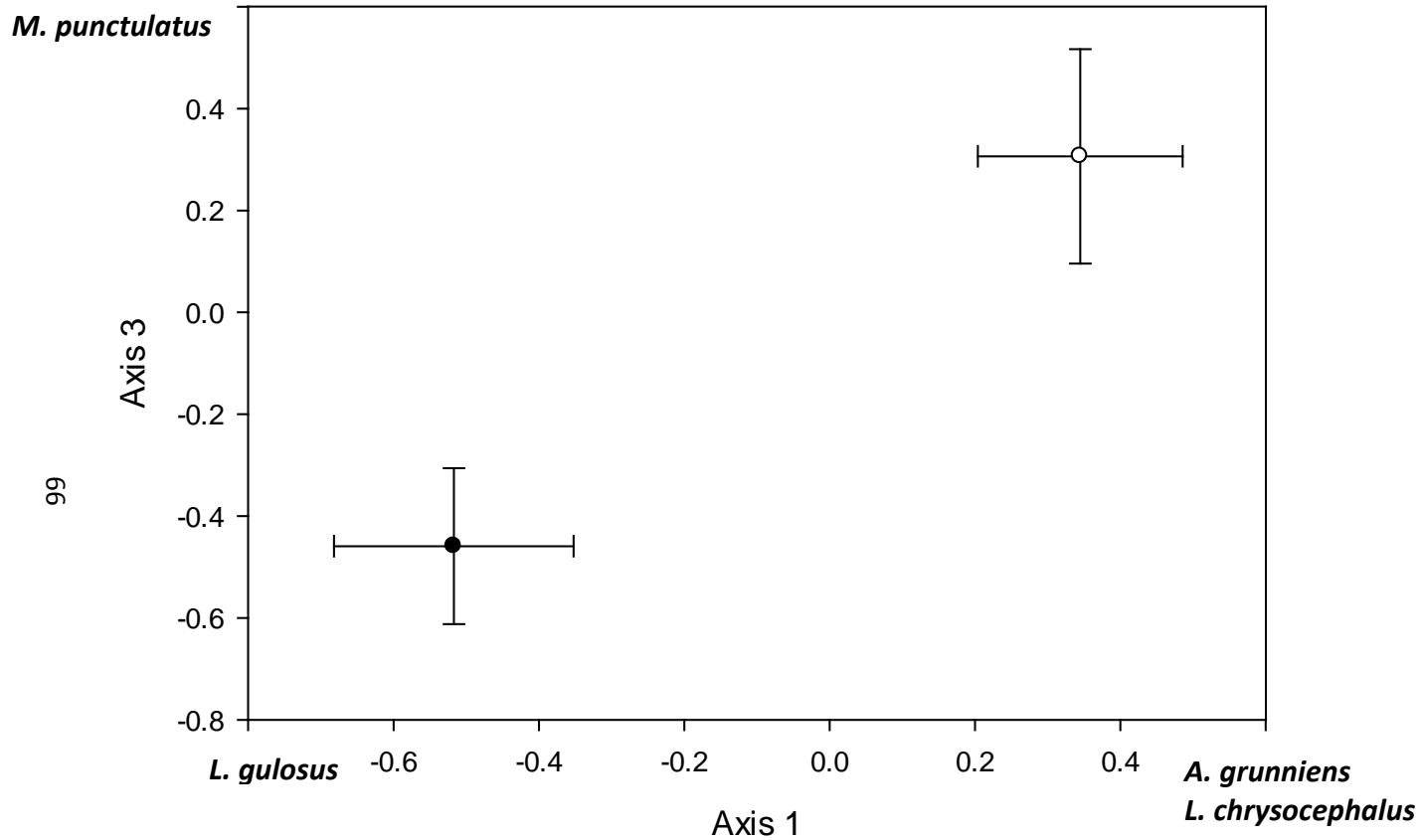


Figure 18. NMS ordination of the fish assemblage structure near the East Fork Tombigbee River (EFTR) pre- (closed circle) and post-construction of the Tennessee-Tombigbee Waterway (open circle) with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by annual presence or absence of 70 fish species from 81 surveys. All differences between and among mussel assemblages were statistically significant ($p < 0.001$, $A = 0.073$). Axis 1 correlates positively with the annual presence of *A. grunniens*, (host for *Potamilus* spp. and *E. lineolata*) and *L. chrysocephalus* (host for *O. reflexa* and *P. decisum*), and negatively with the presence of *L. gulosus* (host for *A. plicata* and *M. nervosa*). Axis 3 correlates positively with the annual presence of *Micropterus punctulatus* (hosts for *L. ornata* and *H. perovalis*).

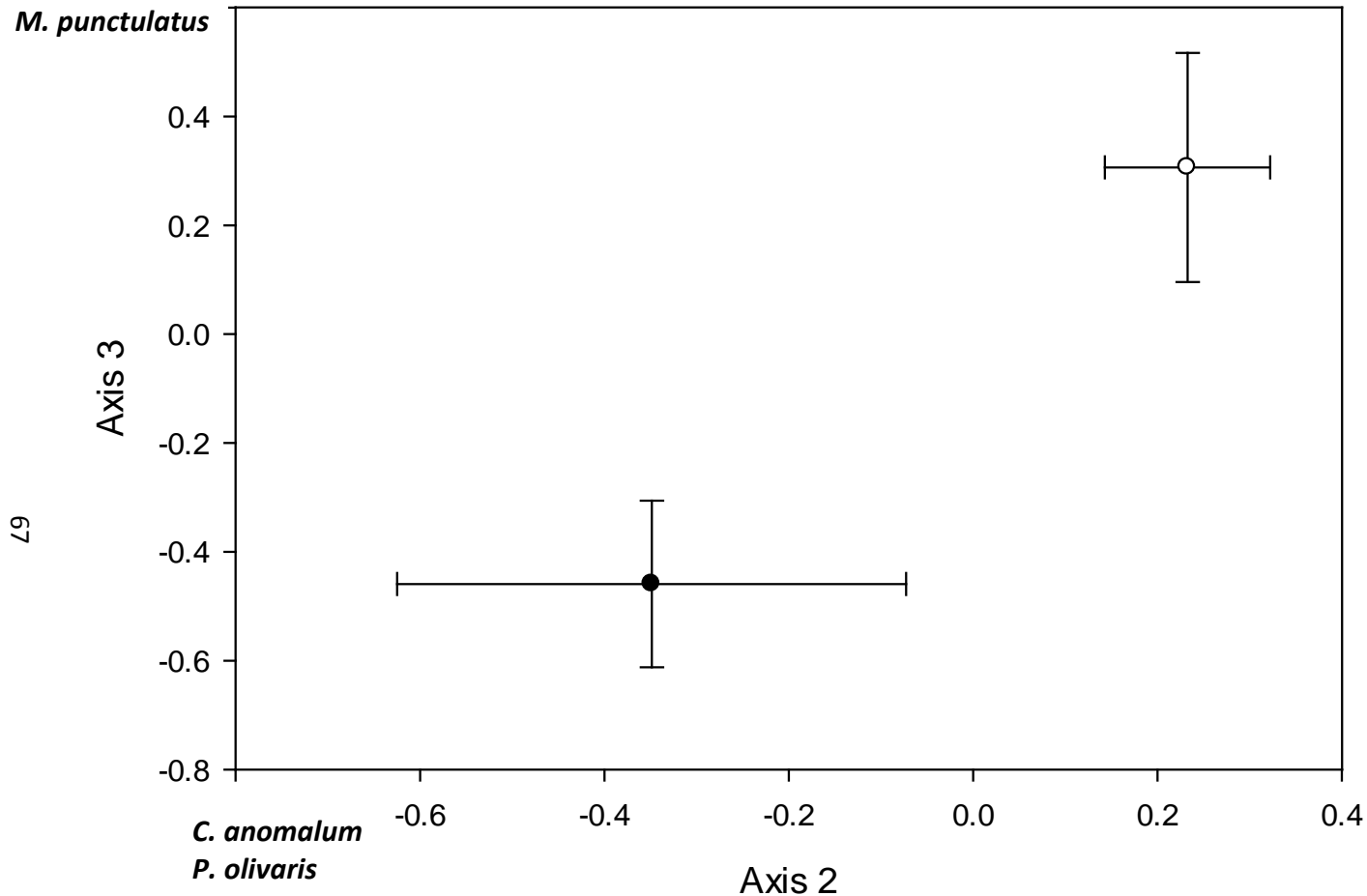


Figure 19. NMS ordination of the fish assemblage structure near the East Fork Tombigbee River (EFTR) pre- (closed circle) and post-construction of the Tennessee-Tombigbee Waterway (open circle) with bi-axis standard error bars about the centroid. Ordination is plotted on axes defined by annual presence or absence of 70 fish species from 81 surveys. All differences between and among mussel assemblages were statistically significant ($p < 0.001$, $A = 0.073$). Axis 2 correlates negatively with the annual presence of *C. anomalum* and *P. olivaris* (hosts for *M. nervosa*, *Q. verrucosa*, and *P. grandis*). Axis 3 correlates positively with the annual presence of *Micropterus punctulatus* (hosts for *L. ornata* and *H. perovalis*).

Vita

Byron Adam Hamstead was born to Theodora and Braun in 1986 in Kearneysville, WV. He attended Leesville Road High School in Raleigh, NC from 2000-2004, and graduated from Saint Maria Goretti High School in Hagerstown MD in 2004. He earned a Bachelor of Science from Appalachian State University in 2008. In August 2013 he was awarded the Master of Science.