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The Role of Tributaries in Structuring Mussel Assemblages

Research Article

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Abstract

The influence of tributaries on mussel assemblages of the river mainstem are poorly understood. This paper aims to understand differences in mussel habitat associations between tributaries and the Neches River mainstem and if the mussel assemblages are nested in tributaries. During the months June through October in 2016, 28 tributaries and 22 mainstem sites were surveyed in the Neches River using tactile time search. A total of 3,620 individuals were collected, of which 44.5% were collected from tributaries. However, only eight of the 28 tributaries contained mussels, while every mainstem site sampled had mussels. Entrenchment ratio and sinuosity appear to be the variables most correlated with mussel habitat association, indicating that tributary complexity positively influences mussel populations and abundances. Mussel assemblages in tributaries were found to be significantly nested within the river mainstem sites.

Keywords: Freshwater mussel, mussel assemblages, nestedness, habitat association, Neches River

1.0 Introduction

Freshwater mussels (Bivalvia: Unionidae) are a unique group of animals that play a vital role in the world's ecosystems, such as aiding in nutrient cycling and storage (Atkinson et al., 2014). Of the 850 freshwater mussel species in the world, about 300 exist in North America (Strayer et al., 2004; Williams et al., 2017), of which about 90 species are federally listed (U.S. Fish and Wildlife Service, 2015). Approximately 50 species occur in Texas (Howells et al., 1996), and 14 of those species are state-listed (Texas Register 35, 2010). Human activities, such as dam construction and other river modification projects, which reduces suitable habitat, increases fragmentation and channelization, and contaminates water with harmful chemicals all have likely contributed to the decline of mussels. This degradation of habitat is believed to be the cause of extinction for 25 mussel species in the United States from the early 1900s to 1990s (Haag, 2012).

Adult mussels are sessile animals, settling into the river substrate as juveniles freshly fallen from their fish host, and they may not be able to change locations for a more favorable habitat if conditions change (Haag, 2012; Vaughn, 2012). While many studies have tried to address what habitat variables are more suitable for mussels, we are instead given a broad generalization of favorable macro and microhabitat factors in which mussels can live (Haag, 2012). Although several species can persist in lentic systems, most prefer lotic systems, where the habitat is considered stable in drought and flooding conditions, has more habitat and substrate variability, and favorable water chemistry (such as high dissolved oxygen; Atkinson et al., 2014; Haag and Warren, 2008; Strayer, 2008).

Most studies of mussel populations have been conducted in mid to large river systems, or in individual large tributaries, with few studies providing information about smaller tributaries and streams (Strayer, 1983; Haag, 2012; Ford et al. 2016). Only a handful of studies in the United States comprehensively surveyed mussels in tributaries. Two studies were conducted in Kansas and Alabama (Vanleeuwen and Arruda, 2001; Gangloff et al., 2009), and two studies were conducted in Texas (Arnold et al., 2016; Vaughn, 2012). Arnold et al. (2016) surveyed 41 sites on the tributaries of the lower Sabine River, of which only 17 had mussels; however, the authors did not describe habitat variables that could explain mussel presence/absence and distribution within these tributaries. Vaughn (2012) surveyed 14 streams in the Red River drainage of Oklahoma and Texas and found that local extinction rates exceeded local colonization rates, suggesting that habitat fragmentation (which inhibits the movement and ability of some host fish species to access ideal habitat areas) is a limit to mussel population dispersal. As mussels require a fish host to complete their reproductive life cycle, the distribution of fish hosts may also explain the distribution of mussel populations (Schwalb et al., 2013; Vaughn and Taylor, 2000).

Taylor and Warren (2001) showed evidence that fishes of the Red River drainage exhibit nested subset patterns (Atmar and Patterson, 1993). As extinction rate of fish assemblages increased, nestedness also increased; and as immigration rate increased, nestedness decreased. Nestedness (also known as nested subsets) is a measure of order and disorder where a species assemblage changes in a predictable extinction sequence the further they are from a species composition source pool (Atmar and Patterson, 1993). Vaughn (2012) showed that mussel populations exhibited higher extinction rates than colonization rates, but more research is needed to determine if mussel assemblages in tributaries are nested subsets of river mainstem communities. To our knowledge, there has not been a study that tested nestedness patterns for freshwater mussels. Because of their sessile nature and dependence on fish host for dispersal, we predicted that mussel assemblages in tributaries would highly nested within mainstem sites.

Because information about the role of tributaries in structuring mussel assemblages is lacking, the objective of this study was to examine mussel assemblages in the mainstem and tributaries of the Neches River in Texas to determine: 1) habitat association for mussel assemblages in the tributaries versus the river mainstem, and 2) whether mussel populations in tributaries were nested in relation to the river mainstem.

2.0 Methods

2.1 Site characteristics

The study system selected was the Neches River in East Texas (Fig. 1). The headwaters begin in Smith County, TX, and the river flows for 683 km into the Gulf of Mexico. Two dams impound the river resulting in two reservoirs: Lake Palestine in the upper Neches and B.A. Steinhagen Lake in the lower Neches. A third low-head dam (height of 2 meters) is located in the middle Neches. The Neches River has numerous small to large tributaries along the river continuum, making it an ideal system to study mussels in the river mainstem and its tributaries.

Although frequent flooding is common in this river system, during the years 2015 and 2016 the Neches River experienced above average flooding with the highest annual discharge since 1946 (3,682cfs; USGS, gauge 08033000 near Diboll, TX). The Neches River was sampled during the receding flood of 2016 in the months June through October.

2.2 Site selection and data collection

All sample sites were in the section of the river between Lake Palestine and B.A. Steinhagen Lake (as indicated in Fig. 1). Tributaries were selected by proximity to river access from bridge crossings and public boat ramps, as the main mode of transportation to sites was by kayak. Tributaries and mainstems were sampled by conducting timed, tactile surveys (Strayer and Smith, 2003).

In each timed survey, the number of mussel species and individuals captured was recorded and released back into the river, except for specimens that required validation and/or confirmation. Dominant substrate type (clay, sand, woody debris, etc.) and any other physical characteristics (evidence of log jams, visual flow of water, etc.) of each site also were recorded.

The first sample of each tributary started at least 40 m from the mouth to reduce any bias of mainstem mussel movement into the tributaries. Because of the small size of the tributaries (width being approximately three meters), a 30-minute person-hour survey was conducted to determine presence or absence of mussels. If a mussel was found, then an additional 30-minute person-hour was completed at the same site, for a full 1-person-hour. A second sample was conducted at least 40 m from the first sample, with preference given towards habitat suitability (riffle, run, or shallow pool) and accessibility, for a full person-hour survey. If a new mussel species was recorded the above process was repeated for each additional site until no new mussel species were encountered. If no mussels were found in the first tributary sampling location and no evidence of mussel shells were found, then the survey of that tributary was concluded. When possible, each tributary had two mainstem samples, one below and one above the confluence, and they were each sampled for one person-hour. If parts of the river channel were too deep to sample, the mainstem sites were picked from the first suitable habitat that was easily sampled, with an ideal distance from the confluence both upstream and downstream being at least 40 m.

2.3 Data analysis

To examine habitat association with mussel assemblages, soil layers (SSURGO 2.1), USGS national elevation dataset, and National Hydrology Dataset (NHD) layers were collected from the Natural Resources Conservation Service (NRCS) Geospatial Data Gateway website (https://gdg.sc.egov.usda.gov/GDGOrder.aspx). Total drainage area (TDA), stream distance from Lake Palestine (SD), sinuosity (calculated 50 meters upstream of the sample site), slope, and percent organic matter, clay, and silt were extracted using ArcMap 10.5 software (ESRI). Entrenchment ratio (ER) was calculated using ArcMap 10.5 and ImageJ (Schindelin et al., 2012). Abundance data were square root transformed to normalize the data. To describe the relationship between habitat variables and mussel species associations a Canonical Correspondence Analysis (CCA) was used with the software package CANOCO 4.5 (Ter Braak and Smilauer, 2002). Monte Carlo permutation tests were run with 1,000 permutations on the full model to assess the probability that the model performed better than chance.

Nestedness calculations were performed using Nestedness software program (Ulrich, 2006). We decided to use the metrics matrix temperature (MT), overlap and decreasing fills (NODF), and discrepancy (BR) because they test for species composition and species incidence within the matrix (Ulrich et al., 2009). Matrix temperature is a modified version of the original nestedness model, nestedness temperature calculator (NTC) developed by Atmar and Patterson (1993). It measures nestedness by calculating distances of absences and presences above and below an isocline of a perfectly nested matrix (Rodríguez-Gironés and Santamaría, 2006; Ulrich et al., 2009). This produces a temperature gradient (T), where at T=0 the matrix is perfectly nested while at T=100 the matrix is completely random and not nested. NODF quantifies whether less common species and assemblages are found as subsets of richer sites (Almeida-Neto et al., 2008). A high NODF value indicates nestedness. The BR index counts the number of species absences and presences that if removed from the matrix, would produce a perfectly nested matrix (Brualdi and Sanderson, 1999). A low BR value indicates nestedness. To guard against Type I error, the null model Fixed-Fixed (FF) was used with all three matrices (Ulrich and Gotelli, 2007). Fixed-Fixed is a conservative model that constrains the matrix row and column totals, keeping the integrity of the original matrix. To quantify the metrics, we used Z-scores and index values; a negative Z-score and a low index value indicates a more nested matrix (Ulrich, 2006; Ulrich and Gotelli, 2007). All of the mainstem sites across the entire length of the river were condensed as a single site and treated as the source pool in the nestedness matrix. Tributaries that had at least one mussel present were condensed down to a single site.

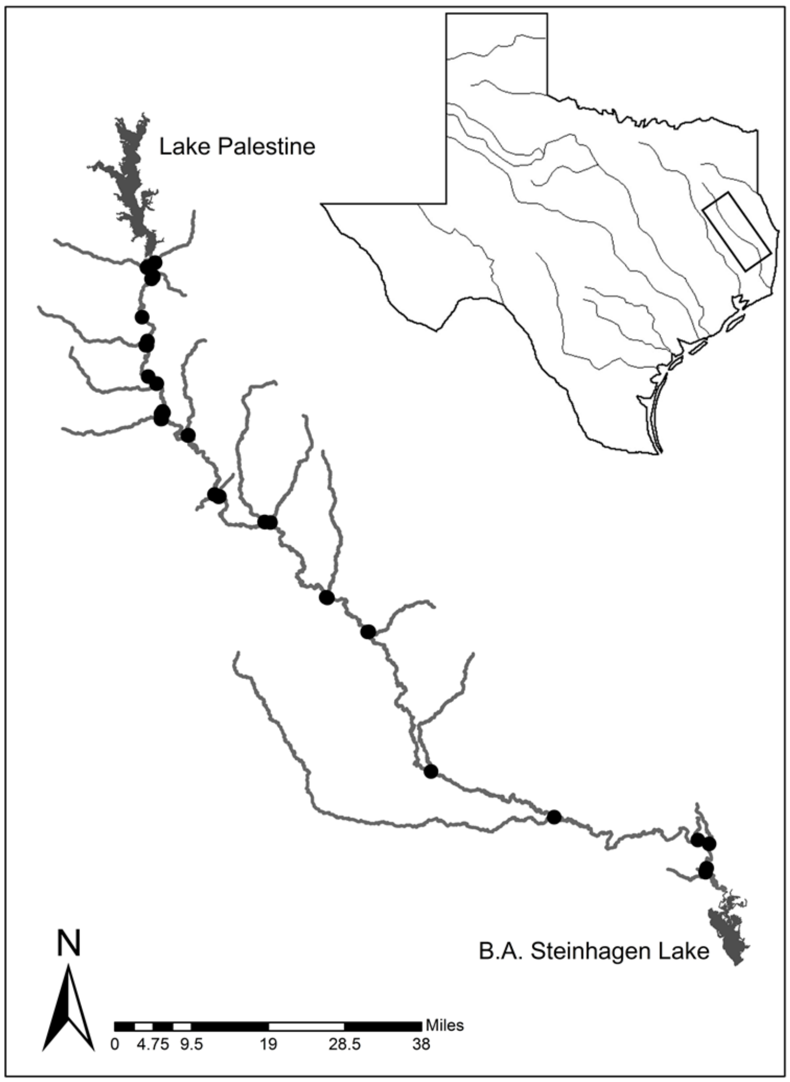

Figure 1. Map of the Neches River in Texas between Lake Palestine and B.A. Steinhagen Lake. Only the tributaries sampled are shown on the map. The black circles represent sample locations for each mainstem and tributary sample sites.

3.0 Results

A total of 28 tributaries and 22 mainstem sites were sampled during the months of late June to early October in 2016. Of the 28 tributaries, only eight had mussels while all 22 mainstem sites had mussels. A total of 3,620 individuals were collected. Of those individuals, 1,614 were collected from eight tributaries (44.5% of total), of which 1,093 were collected from a single tributary (30.2% of total). A total of 26 mussel species were collected, the most abundant being western pimpleback (*Cyclonaias mortoni*; 1,039 individuals), threeridge (*Amblema plicata*; 538 individuals), and bankclimber (*Plectomerus dombeyanus*; 363 individuals). Threeridge (404 individuals), western pimpleback (324 individuals), and bankclimber (221 individuals) were the most abundant in tributary sites. Western pimpleback (715 individuals), pistolgrip (*Tritogonia verrucosa*; 171 individuals), and bankclimber (142 individuals) were the most abundant in the river mainstem sites. Five of the six state-listed East Texas mussel species were collected in this study: Louisiana pigtoe (*Pleurobema riddelli*), Texas pigtoe (*Fusconaia askewi*), sandbank pocketbook (*Lampsilis satura*), Texas heelsplitter (*Potamilus amphichaenus*), and the southern hickorynut (*Obovaria arkansasensis*).

3.1 Habitat Associations

The first two CCA axes showed a significant relationship ($p<0.002$) between mussel species and habitat variables, explaining 36.7% of the variance. Tributaries were associated with axis 1 ($\lambda=0.136$) and weakly associated with axis 2 ($\lambda=0.085$), while mainstems were positively correlated with axis 2 and neutral in axis 1. Percent clay, organic matter (OM), and silt were positively associated with the second axis. Cedar Creek (TCeC) contained a high percentage of organic matter and was one of the two sites that the state-listed Texas heelsplitter was found (Figure 2). The Texas heelsplitter was also found in site M5, which was also correlated with organic matter but to a lesser degree. Louisiana pigtoes were negatively correlated with organic matter, and were typically found in gravel beds. Stream distance from Lake Palestine (SD) and total drainage area (TDA) were positively associated with both axes. State-listed species Texas pigtoe and sandbank pocketbook were typically found in larger tributaries with a larger drainage area. Entrenchment ratio (ER) and sinuosity were negatively correlated with both axes (Fig. 2). All seven sites (M14, M18, M19, M17, T4, T7, and TSC) located near Hwy 84 (Rusk, TX) were clustered together, with the majority being positively associated with entrenchment ratio and sinuosity. These sites also had the highest species richness (M14=16, M18=18, M19=15, M17=15, T4=16, T7=21, and TSC=18) of all the sites in this study, and contained 54.7% of all individuals collected. The state listed southern hickorynut was only found in this area (Fig. 2).

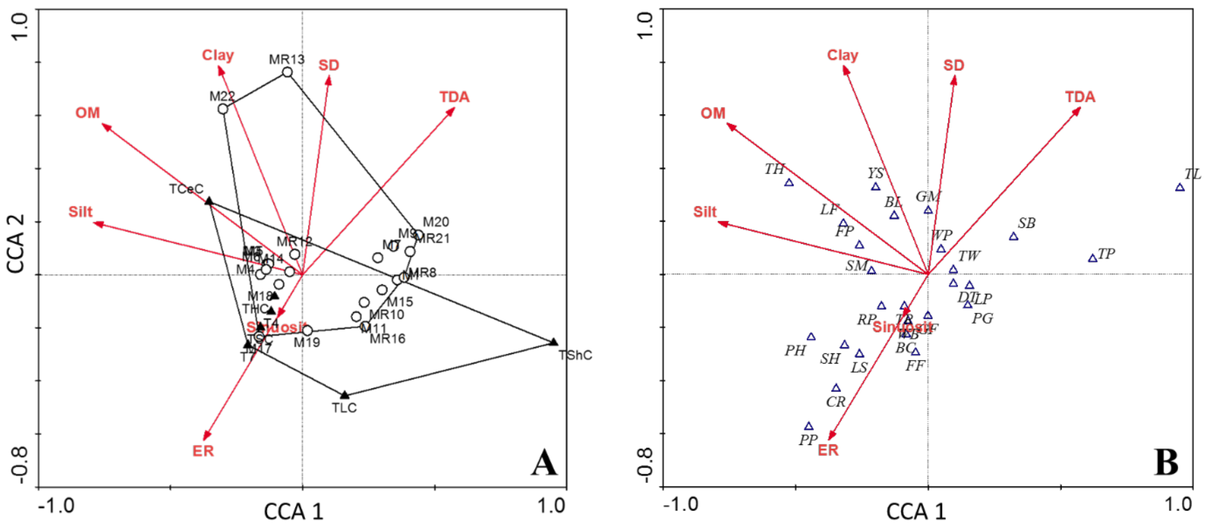

Figure 2. CCA analyses of habitat associations between species and sites. Habitat variables include percent organic matter (OM), percent clay (Clay), percent silt (Silt), stream distance (in meters) from Lake Palestine (SD), total drainage area (TDA), sinuosity (Sinuosity), and entrenchment ratio (ER). (A) Filled triangles indicate tributary sites, while open circles indicate mainstem sites. An envelope is drawn around both classes to show distinctions between habitat variables. (B) Open triangles indicate mussel species.

3.2 Nestedness

The resulting nestedness matrix consists of nine sites (the mainstem and eight tributaries that had mussels) and 26 mussel species (Fig. 3). The matrix is highly nested across two of the three metrics. The matrix temperature (MT) was not significant despite the low temperature (T = 13.11, Z-score = 1.7). NODF showed significant nestedness (NODF = 71.98, Z-score = -3.1, index value = -0.13) as well as BR (BR = 8, Z-score = -2.85, index value = -3.65).

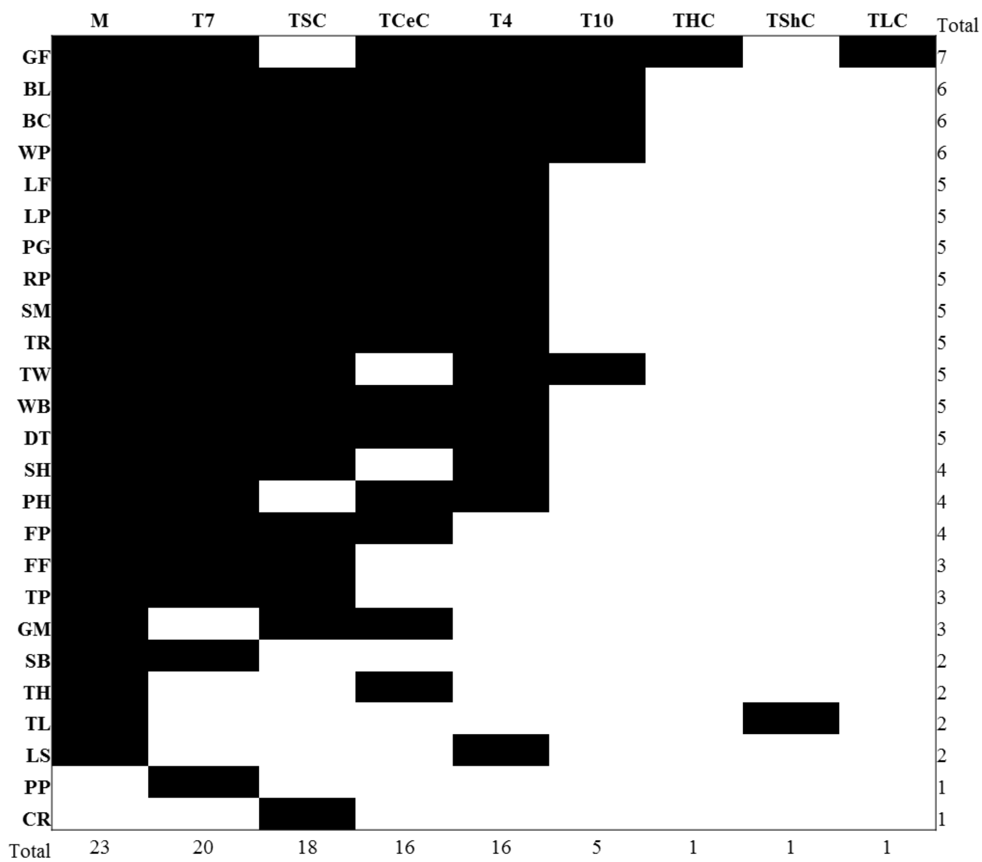

Figure 3. Nestedness matrix of mussels in the Neches River mainstem (M) and eight tributaries. The filled squares represent species presence in the site, while white squares represent species absence. The y-axis is species collected and x-axis is sites sampled. The total of rows and columns are shown.

4.0 Conclusion and Discussion

Habitat associations were positively associated with high entrenchment ratio and sinuosity. High entrenchment ratio appears to be an important association for several mussel species. Entrenchment ratio measures the connectedness of the river to its flood plain, which is important for energy dispersion in a flood event (Rosgen, 1994). Sinuosity, which is a measure of curvature in a river channel, was positively correlated with entrenchment ratio in the CCA analyses. This pattern is consistent with Rosgen's (1994) classification of natural rivers, where an increase in entrenchment ratio results in an increase in sinuosity because the river is more connected to its floodplain. However, with an increase in sinuosity there is also an increase in shear stress on the outer beds of the river (Bryant, 2016). High shear stress levels limit mussel abundance because high velocity causes sediment transport, dislodging mussels from the substrate and preventing settlement of juvenile mussel (Allen and Vaughn, 2010). The sites with the highest values of entrenchment ratio and sinuosity, sites below Hwy 84 (Near Rusk, TX), encompass a complex system of tributaries. The river in this reach is well connected to its floodplain because of its geomorphology (Troia et al., 2015). During high flow events, excess water volume can spread into these tributary systems and reduce the magnitude of the sheer stresses.

Tributaries in the middle reaches (Troia et al., 2015) adjoin Davy Crockett National Forest and had high mussel abundance and stream complexity. In the lower reaches (Troia et al., 2015) the river channel begins to braid and tributaries have an increased influence. However, unlike the middle reaches, entrenchment ratio and sinuosity are not highly associated; rather, these sites were associated with total drainage area size. This is because of the increase in tributaries and the fact that they are located in the lower reach of the Neches River and farther from the influence of Lake Palestine. It is possible that with an increase in drainage area, there is also an increase in sediment and/or woody debris deposition.

Two of the three metrics showed significant nestedness of the matrix of mussel presence in the Neches River mainstem and tributaries. It should be noted that the matrix temperature (MT) showed significant nestedness for EE, EF, and FE null models in *Nestedness*. Although MT is a classic model in determining nestedness, previous studies showed that the MT metric is not an accurate measurement of nestedness because of its liberal algorithms (Ulrich and Gotelli, 2007). In contrast, the BR and NODF metrics are more conservative and less biased for matrix shape and fill. The Z-score produced by the BR index when used with the FF null model is least affected by matrix properties and size when compared to other indices, and because of its conservative nature, indicates a significant nested matrix less frequently than other metrics and null models (Ulrich and Gotelli, 2007; Brualdi and Sanderson, 1999). As a result, we feel confident in saying that the mussel assemblages in the tributaries of the Neches River are nested subsets of the mainstem mussel communities.

In a perfectly nested community, the mainland would have all the species present. As predicted, the mainstem acting as the “mainland,” with all but two species being present. Tributaries that were nested within the mainstem, such as Tributary 7, Stills Creek, and Tributary 4, were located in the middle reach of the river and were some of the more abundant sites with a similar species composition to the mainstem. Cedar Creek is located just upstream from B.A. Steinhagen Lake, and was the next most abundant site for mussel species and individuals. Tributary 10, Hurricane Creek, Shearwood Creek, and Larrison Creek had only a handful of mussel individuals and one to two species. In this study, only eight of the 28 tributaries contained mussels. The lack of mussel presence in tributaries is not uncommon in East Texas river systems. Of 41 tributary sites surveyed on the lower Sabine River, only 17 had mussels present (Arnold et al., 2016).

In the nestedness matrix the giant floater was found in most sites, followed by the bluefer, bankclimber, and western pimpleback. Coincidently, these species are located around or close to the node in the CCA graph. This could suggest that species that are tolerant of a wide range of habitat conditions are found in more sites. The giant floater, though preferring sand and mud can be found in a wide variety of substrates (Oesch, 1984; Howells et al., 1996). Bleufers and western pimplebacks are also found in a variety of habitats, and can be found in small to large water bodies, with slow to moderate flows, and sandy to gravel substrates. Bankclimbers are found in similar habitats, but closer to banks and in shallow waters. Rare species, such as the southern hickorynut and Texas heelsplitter, are nested in fewer sites in the nestedness matrix.

Connectivity to the river floodplain is important for mussel persistence in the Neches River. Because of the complexity of the habitat and rich mussel abundance in the middle reaches of the river (near Texas Hwy 84), this area should be protected from potential anthropogenic influences that could possibly degrade and negatively impact mussels. The mussel assemblages within tributaries are nested in the Neches River, and the patterns of this nestedness matrix are following the same trends that was seen in the ordination habitat associations.

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Software Availability

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