

Linking life history strategies and historical baseline information shows effects of altered flow regimes and impoundments on freshwater mussel assemblages

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Abstract

- Human impacts on aquatic ecosystems are causing shifts in the composition and distribution of species, leading to subsequent changes in community structure. However, these changes may not be fully realised because of inadequate baseline information. In Texas, such baseline information is generally lacking for cryptic aquatic species such as unionid mussels, which will be likely to impede identification of impacted populations, potential causal factors, and the setting or achieving of management goals.
- The Navasota River, located in central Texas, is an exception, having been comprehensively surveyed more than 40 years ago, prior to large-scale impoundment of this system. Hierarchical cluster analysis, nonmetric multidimensional scaling, and fuzzy set ordination were performed to compare assemblage structure from the 1975 survey to that of a recent survey in 2016 at similar sampling locations.
- Comparing sites based on the presence–absence of mussel species, we found no significant differences between the number of taxa and species present; however, we did find significant filtering of mussel life history strategies. Specifically, prior to impoundment, we found that mussel assemblages were filtered based on longitudinal patterns in life history strategy from taxa that are adapted to disturbed habitats to those favoured in more stable habitats with low environmental variation.
- However, following large-scale impoundment after 1975, we saw a shift in the hydrologic regime towards consistent, homogenised flows and a shift in assemblage structure towards equilibrium species. This shift appears to represent a *discontinuity*, wherein river impoundment alters physical parameters of the hydrologic regime and these changes in turn modify biotic patterns and processes.
- Our results provide another example of how large dams can restructure mussel assemblages, highlight the importance of incorporating reference or baseline conditions wherever possible when evaluating the conservation status of aquatic biota, and provide further evidence for the use of life history theory and the serial discontinuity concept in predicting the consequences of flow alteration and river impoundment.

KEYWORDS

assemblage structure, conservation, history traits, life, shifting baseline, Unionidae

1 | INTRODUCTION

Flow alteration from human activities has resulted in significant alterations to aquatic ecosystems (Malmqvist & Rundle, 2002). In freshwater environments, spatial and temporal variability in the flow regime is the proximate driver determining the biophysical attributes of rivers, and thereby shaping community composition (Lytle & Poff, 2004). As a result, the types of species occurring and their relative abundances along the river continuum are a reflection of trade-offs (i.e. investments in one trait decreases resources available for investment in another) or spin-offs (i.e. investments in one trait reduces costs or increases benefits of investment in another trait) that enable an organism to cope with flow regimes and other environmental challenges (Olden & Kennard, 2010; Poff, 1997; Townsend & Hildrew, 1994; Vannote & Sweeney, 1980). Winemiller and Rose (1992) conceptualised these trade-offs for fishes into three strategies (i.e. opportunistic, periodic, and equilibrium) by contrasting variation in demographic patterns of survival, growth, and reproduction to environmental disturbances. This traits-based approach has subsequently been independently validated a number of times for flow–ecology relationships (e.g. Mims & Olden, 2012; Olden & Kennard, 2010). Opportunistic strategists are characterised by life history traits that allow them to occupy habitats defined by frequent and intense disturbances such as floods and droughts whose timing, frequency and duration are highly variable. Periodic strategists are those species with traits that enable them to persist in environments that change in a predictable manner such as seasonal flood pulses. Equilibrium strategists are those species with life history traits that are maximised in more stable habitats with low environmental variation (Winemiller, 2005).

Life history theory has the potential to provide stream ecologists with not only greater insight into causal mechanisms for various species–environment relationships but also more portability across taxa and geographies, which is important for drawing meaningful inferences. Despite its potential utility, life history theory has seen limited application to other faunal groups. Recently, Haag (2012) adapted the Winemiller and Rose (1992) framework to mussels, based on trade-offs among body size, age at maturity, growth rate, fecundity, brooding strategy, and life span. This adaptation of Winemiller and Rose (1992) resulted in a renewed examination of mussel–environmental relationships. For example, Daniel and Brown (2014) found higher abundances of opportunistic strategists in lower order streams where drying events were more frequent, but equilibrium strategists were dominant in higher order, more stable streams. Randklev et al. (2016) assessed life history strategies along a longitudinal river gradient and found significant shifts in life history composition based on proximity to a dam, with higher abundances of opportunistic strategists located immediately downstream of the dam while periodic and equilibrium strategists were most abundant

at intermediate distances. Collectively, these studies support life history theory as a framework for predicting the response of mussel species to hydrologic regimes and alterations to those regimes, such as impoundments and their associated impacts (e.g. changes to flow or thermal regimes, stream channel dewatering, and stream fragmentation; Allen, Galbraith, Vaughn, & Spooner, 2013; Shea, Peterson, Conroy, & Wisniewski, 2013; Watters, 1999). However, additional studies are needed to test predictions from life history theory against different mussel species under different environmental gradients.

Establishing baseline relationships is a critical step in conservation planning because identifying impacts (e.g. range reductions or changes to the flow regime) depends on clearly defined reference points that can serve as a model system for determining recovery (Humphries & Winemiller, 2009). A trait-based approach, such as life history theory, is particularly useful because it provides an ecological and evolutionary perspective to explain shifts in species composition within assemblages over time (Mims & Olden, 2012). It also allows managers to predict beyond well-studied taxa, to rare species of high conservation concern by describing how an environmental stressor might lead to predictable changes in assemblage structure based on life history strategies. For mussels, this is a critical need because this group is considered highly imperilled (Strayer et al., 2004). For example, Vaughn (2012) found that mussel life history traits could be used to predict extinction rates and long-term persistence of mussel populations. Similarly, Ries, Newton, Haro, Zigler, and Davis (2016) found that discharge patterns strongly influenced the degree of recruitment among species populations according to life history strategy. Because of their sensitivity to anthropogenic disturbance, mussels may serve as a model system to study ecological baselines and to determine whether *reference* conditions have changed over time.

Here, we use life history theory combined with long-term data to evaluate how mussels respond to environmental change over a 40-year period within the Navasota River, a tributary of the Brazos River, and a biodiversity hotspot within central Texas, U.S.A. Our specific objectives were to: (1) examine the status of freshwater mussels along the entire length of the Navasota River, focusing on locations where mussels had been historically surveyed; (2) use the resulting data to evaluate shifts in assemblage structure between historical and contemporary surveys; and (3) use life history theory to help explain the underlying mechanisms responsible for shifts in mussel assemblages. Drawing on life history theory and the natural flow paradigm, we predict that shifts in assemblage structure between historical and contemporary surveys will be greatest near points of flow regulation (i.e. such as impoundments) as periodic and equilibrium strategists are eliminated in favour of opportunistic species. In contrast, shifts in assemblage structure between historical and contemporary surveys should be minimal in reaches currently

located further from the nearest point of flow regulation. The dominant life history strategy in these unaffected reaches should be determined based on stream position, with periodic strategists being most prevalent in the middle reaches and equilibrium in the lower reaches of the Navasota River.

2 | METHODS

2.1 | Study area

The Navasota River, a tributary of the Brazos River, flows through the Southern Post Oak Savanna ecoregion of central Texas (Griffith, Bryce, Omernik, & Rogers, 2007), and drains an area of c. 5,800 km². Land cover is predominantly agriculture (particularly managed pastures or rangelands) and mixed deciduous forest with a small percentage characterised by urban land use (Griffith et al., 2007). The basin is characterised by a humid, subtropical climate and receives a mean annual precipitation of 750–1,300 mm (Clark, 1973; Phillips, 2006). Channel substrates range from sand and silt to compact clay but are generally characterised by highly mobile alluvial sediments (Phillips, 2006).

The Navasota River contains a high biodiversity of aquatic organisms (Clark, 1973), including 19 species of freshwater mussel (Howells, 1996; Littleton, 1979; Randklev, Kennedy, & Lundeen, 2010; Strecker, 1931), one of which is a Texas endemic. *Truncilla macrodon* is restricted to rivers of central Texas, including the Navasota River (Howells, Neck, & Murray, 1996) and is currently a state-listed species and a candidate for federal protection under the Endangered Species Act (ESA; USFWS, 2011). The Navasota River was intensively surveyed for mussels from 1972–1975 by Littleton (1979), who reported distributions and relative abundances of 16 species.

The mainstem of the Navasota River is influenced by three impoundments, Lake Mexia, Fort Parker Lake, and Lake Limestone, all of which occur in the headwaters of the Navasota River. Lake Mexia was completed in 1961 to provide water for municipal and industrial purposes and covers an area of 4.2 km² (TWDB, 2009). Fort Parker Lake, located downstream of Lake Mexia, was impounded in 1939 for public recreation and covers an area of 2.9 km² (Whisenant, Radloff, Bronson, & Contreras, 2010). Lake Limestone covers an area of 50.5 km² and is used primarily for municipal and industrial water supply (TWDB, 2014). Lake Limestone was impounded in 1978, and construction of the dam occurred from July 1975–October 1978 (TWDB, 2014), after the completion of Littleton's freshwater mussel surveys in May 1975.

Both Lake Mexia and Fort Parker Lake are impounded by earth-fill dams designed for unregulated discharge of overflow with a mean annual discharge of 5.5 m³/s (U.S. Geological Survey [USGS] Gage Station #08110325, Navasota River above Groesbeck, Texas) downstream of both lakes. Dissolved oxygen levels in Fort Parker Lake are below Texas Commission on Environmental Quality criteria for high aquatic life (Whisenant et al., 2010). Lake Limestone

is impounded by an earth-fill dam with a concrete channel spillway that releases from the middle of the dam. The average annual discharge below Lake Limestone is 12.0 m³/s (USGS Gage Station #08110500 Navasota River near Easterly, Texas). Additionally, the river segment below Lake Limestone is currently listed as impaired by Texas Commission on Environmental Quality due to high levels of *Escherichia coli* (TWRI, 2017). The high bacteria levels have been attributed to several sources, including feral hogs, livestock, and stormwater (TWRI, 2017).

2.2 | Survey design and sampling

We obtained historical mussel survey data from a comprehensive survey of the Navasota River basin that was completed in 1975 (Littleton, 1979). Of the 37 sites sampled by Littleton, 23 were located on the mainstem of the Navasota River (the remaining 14 were located in tributary streams or impoundments and were not included in our analysis or study design). Based on maps and site descriptions provided by Littleton (1979), historical survey sites were georeferenced using a combination of aerial photography and ArcGIS 10.3 (ESRI, Redlands, CA, U.S.A.). Contemporary survey sites were chosen using Littleton (1979) to position sites near historical collection localities. However, because the locality information provided by Littleton (1979) was approximate, we used the following random sampling design, based on Wisniewski, Rankin, Weiler, Strickland, and Chandler (2013) to provide adequate spatial coverage. Sites were at least 1 river km (rkm) apart and randomly selected using two strata to ensure sampling was representative of the mussel fauna at locations where historical surveys were likely performed: (1) river left or river right (except for riffle habitats which generally occur in the centre of a river channel); and (2) mesohabitat: banks, backwater, riffles, and pool. In total, 52 sites were selected along the entirety of the Navasota River, excluding impoundments (Figure 1). Approximately half of these correspond to sites previously sampled by Littleton ($n = 23$; Figure 1).

We conducted surveys qualitatively using the timed search method in each randomly selected mesohabitat type. Search boundaries were confined to the specific habitat type, up to 150 m² if enough habitat was available. Each site was then surveyed tactilely for a total of 4 person-hours (p-h; for further details on this method, see Metcalfe-Smith, Di Maio, Staton, & Mackie, 2000).

2.3 | Flow regime

We obtained daily streamflow data from the USGS gage near Easterly, TX (USGS #08110400; c. 40 river km downstream of Limestone Lake) in the mainstem of the Navasota River to quantify changes in flow regime that might have contributed to changes in mussel assemblage composition. Daily flow data were downloaded for the period 1925–2018, such that 54 years of pre-impoundment and 40 years of post-impoundment data were used for analysis. We used the Indicators of Hydrologic Alteration (IHA), version 7.1

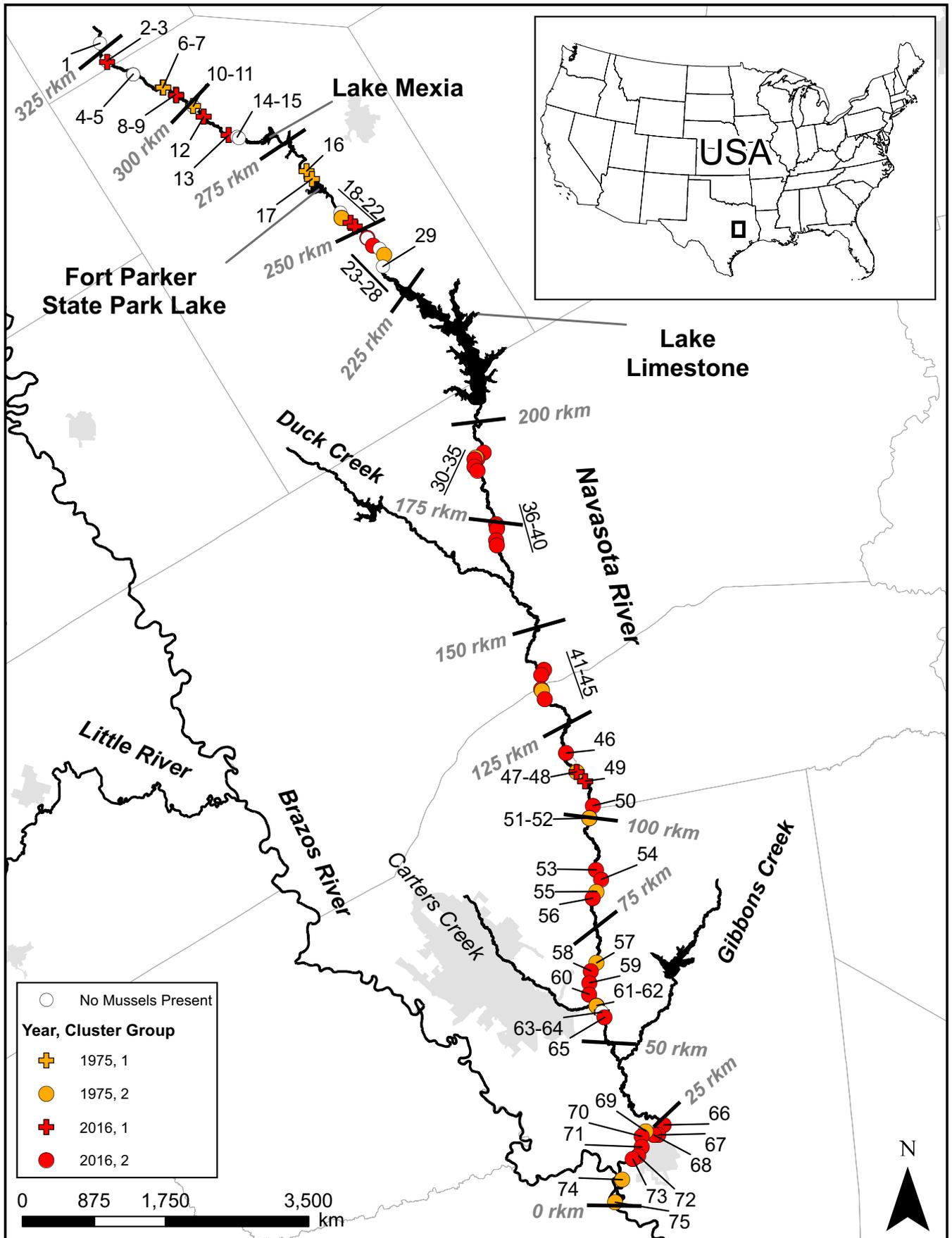


FIGURE 1 Map of the study area in central Texas showing historical (orange; Littleton, 1979) and contemporary (red; this study) sites in the Navasota River surveyed for mussels. Sites were assigned to groups by hierarchical cluster analysis and are denoted as follows: group 1 (plus symbol) and group 2 (circle). Groups primarily separate by river position with Group 1 occurring in the headwaters above Lake Limestone, while Group 2 is associated with the lower reaches downstream of the dam

TABLE 1 Records of live freshwater mussels collected in the Navasota River, Texas, including data from both Littleton (1979) and the present study

Species	Historic survey ^a	Recent survey ^b	Other surveys ^c	Life history strategy
Anodontini				
<i>Arcidens confragosus</i>	X	X	X	Opportunistic
<i>Pyganodon grandis</i>	X	X	X	Opportunistic
<i>Utterbackia imbecillis</i>	X	X	X	Opportunistic
Amblemini				
<i>Amblyma plicata</i>	X	X	X	Equilibrium
Lampsilini				
<i>Cyrtonaias tampicoensis</i>	X	X	X	Periodic
<i>Lampsilis hydiana</i>	-	X	X	Periodic
<i>Lampsilis teres</i>	X	X	X	Opportunistic
<i>Leptodea fragilis</i>	X	X	X	Opportunistic
<i>Ligumia subrostrata</i>	X	-	X	Opportunistic
<i>Potamilus streckeri</i>	X	X	X	Opportunistic
<i>Potamilus purpuratus</i>	X	X	X	Opportunistic
<i>Tritogonia verrucosa</i>	X	X	X	Equilibrium
<i>Toxolasma parvum</i>	-	X	X	Opportunistic
<i>Toxolasma texasiense</i>	X	X	X	Periodic
<i>Truncilla macrodon</i>	-	X	X	Opportunistic
Quadrulini				
<i>Cyclonaias pustulosa</i>	X	X	X	Equilibrium
<i>Megalonaias nervosa</i>	X	X	X	Equilibrium
<i>Quadrula apiculata</i>	X	X	X	Equilibrium
<i>Unio merus tetralasmus</i>	X	X	X	Periodic

^aLittleton (1979).

^bPresent Study.

^cSingley (1893), Strecker (1931), Calnan (1976), Howells (1996, 2000, 2001), Karatayev and Burlakova (2008), Randklev et al. (2010); Strecker (1931) also recorded *Fusconaia askewi*, which is probably erroneously reported

(Richter, Baumgartner, Powell, & Braun, 1996), to assess potential differences in hydrologic conditions prior to (1925–1978) and following (1979–2018) impoundment of Lake Limestone. The IHA method includes 33 ecologically relevant hydrologic parameters that describe five fundamental characteristics of the streamflow regime: magnitude, timing, frequency, duration, and rate of change of discharge (see Olden & Poff, 2003, for detailed descriptions of IHA parameters). We used the non-parametric statistics option within the IHA software to compare median and coefficient of variation values between pre- and post-impoundment periods and their *significance count*. The IHA software provides a significance count with values ranging from 0 to 1 based on a permutation procedure, which can be interpreted similarly to a *p*-value (The Nature Conservancy, 2009). For this study, values ≤ 0.05 were considered significant, and we

report only those IHA parameters that showed a significant difference between periods.

2.4 | Data analysis

To document changes in the mussel assemblage through time, we assessed patterns in observed species richness and assemblage composition. We used survey data to estimate species richness (total number of species) and, for contemporary sites, we also estimated catch-per-unit-effort (number of mussels/p-h) and species occurrence (percent of sites occupied by a species). For analysis of assemblage composition, we used a combination of hierarchical cluster analysis (HCA), non-metric multidimensional scaling

(NMDS), and fuzzy set ordination (FSO) to compare mussel assemblage composition between time periods and in a longitudinal gradient. Non-metric multidimensional scaling was used for unconstrained ordination of spatial locations of mussel assemblages, while FSO was used as constrained ordination to visualise the associations between each individual variable as well as their combination. Hierarchical cluster analysis was used to validate observed NMDS groupings.

Because Littleton (1979) did not provide abundance data by site, we transformed contemporary abundances to presence–absence for statistical analyses and constructed Bray–Curtis dissimilarity matrices based on these presence–absence data as the distance measure for all analyses. We used NMDS plots with minimum convex polygons based on distance matrices to illustrate differences in assemblage composition among study periods. Additionally, we included parameter vectors for life history strategies (proportion of species identified as either equilibrium, periodic, or opportunistic), river position (rkm), and year surveyed (1975 or 2016) to illustrate correlates for clusters identified in the NMDS plots. We assigned mussel species to one of three life history traits (equilibrium, periodic or opportunistic) based on Haag's (2012) classification (Table 1). River position was the number of rkm upstream from the confluence of the Brazos and Navasota rivers. Groupings observed in the NMDS plot were then validated by clustering sites on the basis of shared species using an unweighted pair group method with arithmetic mean hierarchical cluster analysis on the Bray–Curtis distance matrix. Groups were determined based on $\geq 95\%$ bootstrap support ($n = 1,000$ replicates). We then overlaid polygons constructed from the cluster analysis within the NMDS plot. If the polygons overlapped the NMDS groupings, then the ordination was considered a good representation of assemblage dissimilarities.

To further analyse the relationship between mussel assemblage composition (presence–absence data), spatial locations of mussels, and year surveyed, we used fuzzy set ordination (Roberts, 2008). The following variables, which were assumed to describe mussel assemblage structure, were used in the FSO: river position (rkm), year surveyed, proportion of life history strategies present at each site, and the dominant life history strategy present (i.e. largest proportional life history strategy). Fuzzy set ordination applies fuzzy logic to compare the community composition of each site and assign them a gradual membership (fuzzy) value ranging from 0 to 1 (Roberts, 2008), rather than exactly 0 or 1. Sites are ordered based on their species composition and assigned a membership value that indicates the probability of belonging to either end of the environmental variable gradient (e.g. river continuum). Fuzzy set ordination is expected to perform better than other models on more complex data sets, and it is insensitive to noise in environmental factors and rare species (Roberts, 2009). We used Spearman's rank correlation to determine whether the environmental variables were appropriate for predicting assemblage composition.

Finally, to illustrate changes between life history strategies present and detected during each study period, we calculated diversity metrics (Shannon diversity index, evenness, and abundance) using

life history strategies as proxies for species. Since abundance information was not available for the historic sites, the proportion of life history strategies based on presence–absence data was used in place of species abundances. Thus, the maximum number of species that could be present at a site was 3 (i.e. equilibrium, periodic, or opportunistic species).

All statistical analyses were performed in the R statistical language and environment (Version 3.5.1, R Core Team, 2018); the *stats* and *recluster* packages were used to compute HCA (Dapporto et al., 2015), the *vegan* package was used to compute NMDS (Oksanen et al., 2018), and the *fso* and *LabDSV* packages were used to compute FSO (Roberts, 2016, 2018).

3 | RESULTS

3.1 | Recent and historical survey overview

During recent surveys, 10,899 live individuals of 18 species were found ($n = 52$ sites), while in historical surveys, 16 species were found ($n = 23$ sites). State-threatened and ESA candidate *T. macrodon*, which is historically known from the Navasota River (Table 1), was not recorded by Littleton (1979) but was observed in the present study. The three most abundant species were *Amblema plicata*, *Lampsilis teres*, and *Cyclonaias pustulosa*. While Littleton (1979) did not report absolute abundance data by site, relative abundances were reported for the entire study, and a similar pattern was observed with *A. plicata*, *Quadrula apiculata*, and *C. pustulosa* being the most abundant. Contemporary mussel species richness and catch-per-unit-effort across sites ranged from 0 to 12 species (5.4 ± 0.6 ; mean \pm SE) and 0 to 329.8 mussels/p-h (49.2 ± 9.4), respectively, and species occurrence ranged from 3.8 to 61.5% ($30.2 \pm 5.2\%$) across the study area. Historical species richness ranged from 0 to 11 (4.8 ± 0.8 ; Littleton, 1979), and a Student *t*-test indicated that average species richness was not significantly different between historical and contemporary surveys ($t = -0.6$, $df = 48$, $p = 0.5$).

3.2 | Assemblage structure changes

The fuzzy ordination found a significant effect of both rkm and year surveyed on mussel assemblage composition, indicating both rkm and survey year were predictive of assemblage composition (Figure 2). However, the longitudinal position of the sites (i.e. rkm) had a greater effect on assemblage composition than year surveyed ($r = 0.75$ and $r = 0.28$, respectively).

Survey sites were classified into two groups according to similarities in their species composition through HCA (Figure 3). Sites from Group 1 mainly occurred in the headwaters of the Navasota River while sites from Group 2 mostly occurred in the middle and lower reaches of the river (Figure 1). The results of the NMDS analysis (Figure 4) were consistent with those of the HCA. There was a significant relationship between NMDS 1 and rkm ($r^2 = 0.42$, $p < 0.01$);

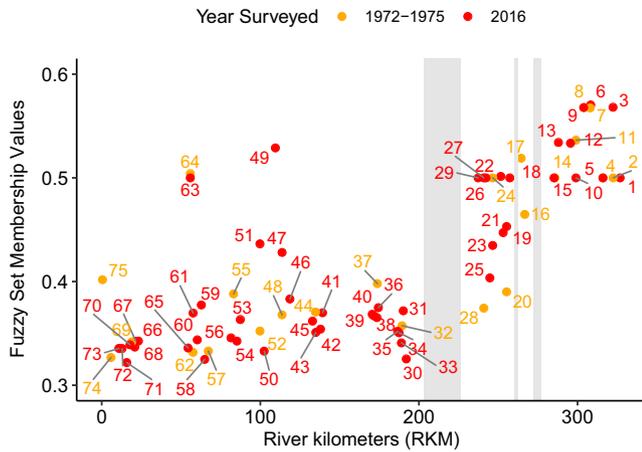


FIGURE 2 Fuzzy set ordination showing the similarity of mussel assemblage structure at each site within the Navasota River by longitudinal position (river km). Longitudinal position was determined by the distance upstream from the confluence of the Navasota and Brazos rivers (0 river km). Site numbers (ordered upstream to downstream) are given for each point. Vertical grey bars demarcate the footprint of the three lakes located on the mainstem (Lake Limestone, Fort Parker Lake, and Lake Mexia)

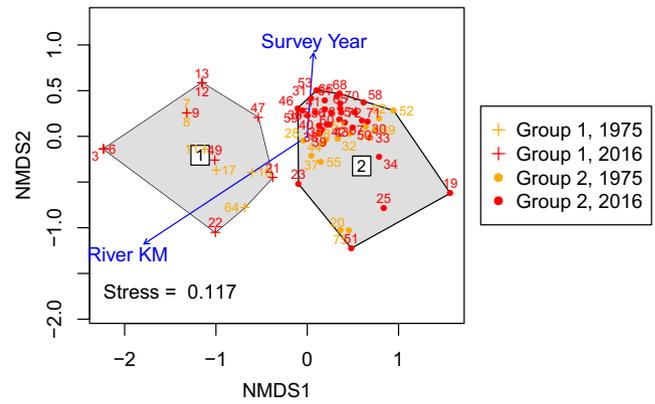


FIGURE 4 Two-dimensional non-metric multidimensional scaling (NMDS) biplots illustrating ordinated distances for mussel assemblage structure by site during historical (orange) and contemporary (red) with significant ($p \leq 0.05$) parameter vectors. Sites were assigned to groups by hierarchical cluster analysis and are denoted as follows: group 1 (plus symbol) and group 2 (circle). Groups primarily separate by river position with Group 1 occurring in the headwaters above Lake Limestone, while Group 2 is associated with the lower reaches downstream of the dam. River km is the distance upstream from the confluence of the Navasota and Brazos rivers (0 rkm). Survey year was the year mussel surveys were conducted (1972–1975 or 2016)

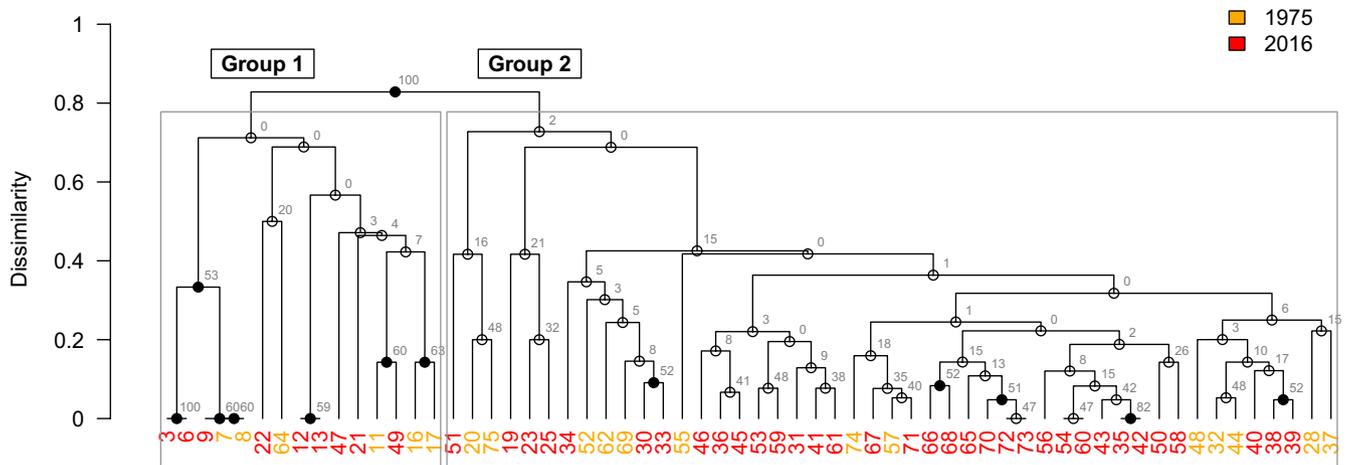


FIGURE 3 Dendrogram derived from hierarchical cluster analysis of similarity in mussel assemblage structure in the Navasota River at sites surveyed either from 1972–1975 (orange) or 2016 (red). Filled circles represent >50% support at a node based on bootstrapping ($n = 1,000$ permutations)

however, survey year which was positively correlated with NMDS 2 did not have a significant effect ($r^2 = 0.07$, $p = 0.11$; Figure 4).

3.3 | Life history trait composition

Results from the FSO analyses on life history strategy indicated that assemblage structure was significantly different among locations. We found the proportion of equilibrium species ($r = 0.85$, $p < 0.01$), periodic species ($r = 0.82$, $p < 0.01$), and opportunistic species ($r = 0.77$, $p < 0.01$) had significant effects on predicting mussel assemblage composition. We also found significant effects of the dominant

life history strategy at each site ($r = 0.67$, $p < 0.01$) on predicting mussel assemblage composition. Fuzzy set ordination plots of the dominant life history strategy for sites in 1975 (Figure 5a) and 2016 (Figure 5b) show equilibrium strategists became the dominant strategy at sites directly upstream and downstream of Lake Limestone after impoundment. Using life history strategy in place of taxa for diversity metrics, Shannon's diversity index decreased while species evenness increased in upstream sites compared to downstream sites (Figure S1). This trend was visible in both historic and contemporary data, but in the contemporary data, diversity decreased much more rapidly in the upstream sites as compared to the historic data. Sites within c. 50 rkm of the upstream boundaries and c. 100 rkm of the

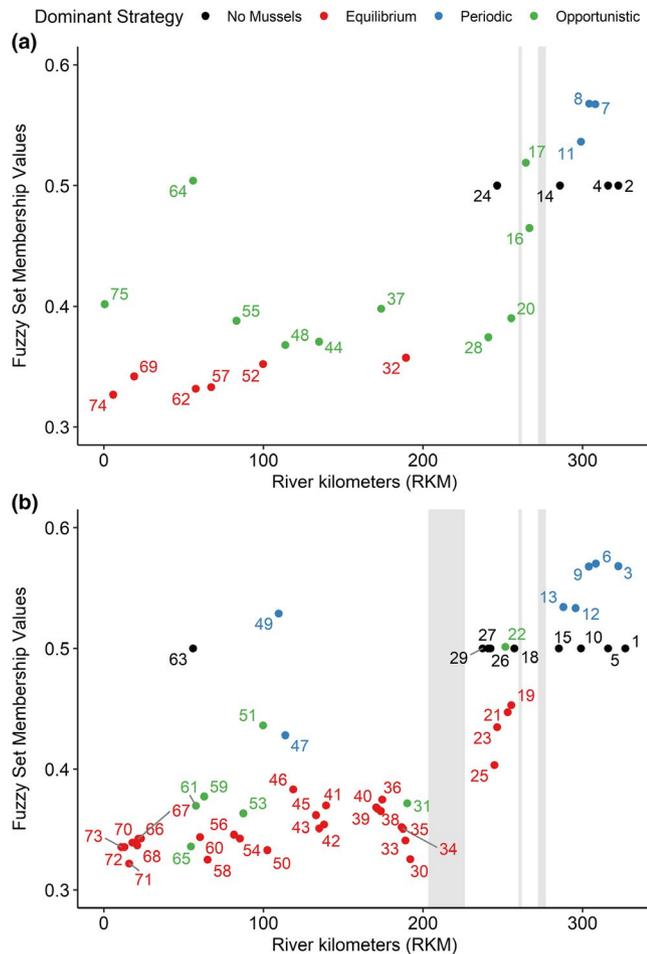


FIGURE 5 Fuzzy set ordination showing the relationship between sites based on the similarity of mussel assemblage structure, longitudinal position (rkm), and dominant life history strategy for (a) historical and (b) contemporary surveys. Longitudinal position was determined by the distance upstream from the confluence of the Navasota and Brazos rivers (0 rkm). Dominant strategies are determined by the largest proportional life history strategy present at each site. Vertical grey bars demarcate the footprint of the three lakes located on the mainstem (Lake Limestone, Fort Parker Lake, and Lake Mexia)

downstream boundaries of the reservoir showed the most change and this was largely driven by an increase in the proportion (i.e. species abundance) of equilibrium strategists in contemporary surveys (Figure S2). The proportion of sites where equilibrium strategists were the dominant strategy, increased from 31.6% in 1975 to 67.4% in 2016. Conversely, periodic strategists remained relatively flat at 15.8 and 16.3%, respectively, while opportunistic strategists decreased from being the dominant strategy in 52.6% of sites in 1977 to only 16.3% in 2016.

3.4 | Flow regime changes

Mean annual discharge at the Easterly USGS Gage Station was not significantly different pre- and post-impoundment; however,

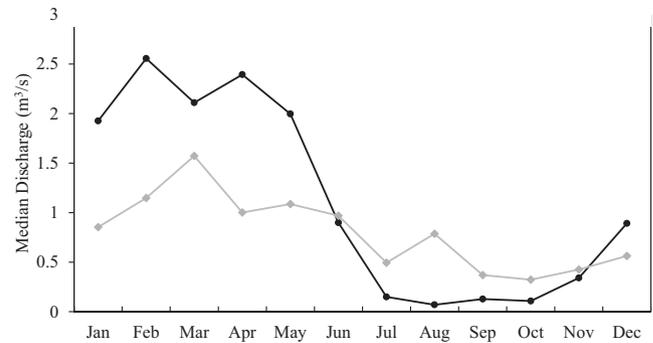


FIGURE 6 Monthly median discharge (in m^3/s) for pre-impoundment (black line; 1925–1978) and post-impoundment (grey line; 1979–2018) recorded at the U.S. Geological Survey gaging station near Easterly, TX (USGS #08110400; c. 40 river km downstream of Limestone Lake) in the Navasota River

the late-summer to early-fall monthly magnitudes (July, August, September, and October) were all significantly higher in the post-dam period compared to pre-dam (significance count ≤ 0.001 ; Figure 6). Consequently, the low pulse count significantly decreased while baseflow significantly increased after impoundment (significance count ≤ 0.001). Furthermore, the median monthly flows from winter to early summer (December–May) decreased during the post-impoundment period, though these changes were not significant. Overall, the flow regime at the Easterly gage following impoundment showed reduced variability with flows characterised by higher low flows, lower high flows, and augmented base flows.

4 | DISCUSSION

We observed that overall assemblage composition and species richness of the Navasota River remained similar across the 40-year period. Despite this similarity, we found shifts in mussel assemblage structure and dominant life history strategies among reaches near Lake Limestone. Based on life history theory, we predicted that opportunistic strategists would be favoured following impoundment due to environmental disturbance and flow alteration. However, the dominant life history strategies observed at sites near Lake Limestone were equilibrium strategists, which are predicted to occur in stable, productive habitats. This unexpected shift may be explained by attributes of the dams in the Navasota River, which determine their ecological effects. This shift may also be explained by the scarcity of empirical knowledge on mussel life history, which might preclude appropriate classification of various taxa to specific endpoints and hinder the ability to accurately predict species and assemblage response to environmental change.

The location, size, and operational type of dams influence how they impact river ecosystems. This observation, well known to ecologists, led to the development of the serial discontinuity concept, which provides a framework for describing how biotic patterns shift based on the stream position of a dam and the magnitude of downstream

alteration (hereafter *discontinuities*; Ellis & Jones, 2013; Ward & Stanford, 1983). Generally, reservoirs located in middle reaches along the river continuum are expected to have a far greater impact than dams located in the upper or lower reaches of a river system because biotic diversity is often maximised in middle portions of a river system (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980; Ward & Stanford, 1983). The magnitude and length of discontinuity from a dam, regardless of its position, is related to dam size and operational type. Because of this, large impoundments tend to be more impactful than small ones, and those that generate hydropower can lead to greater impairment than projects used solely for drinking water and/or flood control (Poff & Hart, 2002; Ward & Stanford, 1983). In our study, all three impoundments are located in the headwaters of the Navasota River, are relatively small, ranging from 2.9 to 50 km², and are used primarily for municipal and industrial water supply (TWDB, 2014). These factors, plus minimal land use changes in the basin, probably explain why overall changes in mussel assemblage composition along the Navasota River were minimal over the past 40 years.

The unexpected shift in life history composition near Lake Limestone is probably a function of dam size and operational type. Lake Mexia and Fort Parker Lake cover an area of 4.2 and 2.9 km², which compared to Lake Limestone (50.5 km²) are c. 12 and 17 times smaller, respectively. During Littleton's (1979) surveys, mussel assemblage structure downstream of Lake Mexia and Fort Parker Lake resembled theoretical expectations regarding life history composition along the river continuum – assemblages in the headwaters were dominated by opportunistic and periodic species, which then gradually changed to assemblages dominated by equilibrium strategists in middle and lower reaches (Haag, 2012). The IHA results comparing pre- and post-flow following construction of Lake Limestone reveal a homogenisation (i.e. less variable) of the flow regime, wherein there is a shift from high winter and low summer flows to augmented base flows with increased summer flows. Life history theory predicts that under scenarios where habitat becomes more stable, equilibrium strategists should be favoured over opportunistic and periodic species (Mims & Olden, 2012; Olden & Kennard, 2010; Winemiller & Rose, 1992). Thus, the unexpected shift in assemblage composition towards equilibrium species (e.g. *Q. apiculata*) is likely to be in response to increases in base flow and reductions in low flows. Tsakiris and Randklev (2016) surveying Yegua Creek, also a tributary of the Brazos River, made a similar observation, noting that mussel diversity was higher than expected immediately downstream of Lake Somerville, a large flood control reservoir, and included equilibrium species (e.g. *Q. apiculata*). Analysis of the flow regime downstream of Lake Somerville showed a similar reduction in flow variability post-reservoir construction with a decrease in annual peak flows and increase in mean annual flows that resulted in a reduction of the number of zero flow days (Tsakiris & Randklev, 2016). The authors argued that this change had increased habitat stability, allowing some equilibrium species to persist. Taken together, our findings show that changes in the flow regime brought about by river impoundment are reflected in shifts in life history and the magnitude and extent of these shifts can be explained by the location, size, and operational type of dams. Randklev et al. (2016) made

a similar observation and advocated using both life history theory and serial discontinuity concept to predict the effect of dams on downstream mussel assemblages.

Life history traits vary greatly among mussel species and this variation has been used to categorise mussels into groups based on similar traits, which led to the development of a life history framework for mussels (Haag, 2012). An important feature of this framework is that it generalises trade-offs between variations in demographic patterns to density-independent (e.g. floods and droughts) and density-dependent processes (e.g. competition, predation) (Haag, 2012), which can be used to make predictions about population and assemblage response to environmental changes. However, life history information remains unavailable or overly generalised for most mussel species (Haag, 2012), which may lead to scenarios where empirical data do not meet theoretical expectations. In this study, the occurrence of some equilibrium species in areas directly impacted by river impoundment may be an example of this mismatch. For example, we found that *Q. apiculata* was the dominant equilibrium strategist near Lake Limestone. Tsakiris and Randklev (2016) made a similar observation in reaches impacted by Lake Somerville on Yegua Creek. *Quadrula apiculata* is considered an equilibrium strategist but is known to persist in reservoirs and other man-made habitats (Howells et al., 1996; Williams, Bogan, & Garner, 2008), which that implies this species is tolerant to environmental disturbance and runs counter to expectations for the equilibrium endpoint.

The periodic strategy for mussels is also a conundrum relative to the opportunistic and equilibrium strategies, which typically align with *r*- and *K*-selected strategies (MacArthur & Wilson, 1967; Pianka, 1970). Haag (2012) described periodic strategists as those species that are characterised by low to intermediate life-span, maturation, and fecundity and are expected to be favoured in unproductive habitats or habitats where environmental variation is large-scale and predictable due to cyclical or seasonal variation. However, it is unclear how mussel periodic life history traits, as currently defined, maximise persistence under such variation or why prevalence for periodic strategists is expected to be higher in small streams and headwaters than opportunistic strategists, who are adapted to cope with environmental extremes. For periodic fish strategists, locomotive and reproductive cues are aligned with seasonal changes in habitat, such as the flow regime, and thus are linked to ecological and environmental endpoints (Mims & Olden, 2012; Olden & Kennard, 2010; Winemiller & Rose, 1992), but for mussels, such relationships have yet to be identified. We suspect that the issue for some mussel species classified as equilibrium or periodic strategists is that the selected demographic traits are not well defined and/or lack information on intraspecific variability of demographic traits across populations. This is not to say the mussel life history framework is not useful but that additional information is needed to refine the model so that it more accurately generalises trade-offs among basic demographic patterns to density-independent and density-dependent processes.

Information on the status and trends of species and their populations is a cornerstone of effective conservation planning for mussels (Haag & Williams, 2014). Because mussels are long-lived, changes to assemblage structure may not be obvious without

long-term monitoring or comparison against detailed, historical records. However, long-term data are often lacking, and so, in the absence of reliable historical information, conservation and recovery targets can be biased because environmental conditions of the recent past may be assumed to be similar to those of more distant, historical baselines. This type of *shifting* baseline is a major concern when assessing long-term change of ecosystems because it can lead to erroneous conclusions regarding environmental factors responsible for species or population declines (Humphries & Winemiller, 2009). In this study, we highlight the importance of incorporating reference or baseline conditions wherever possible when evaluating changes in species occurrence and community structure of mussels. Although overall assemblage composition and species richness of the river remained similar across the 40-year period, our comparison of contemporary data with detailed historic records showed altered mussel assemblage composition both upstream and downstream of Lake Limestone with sites within c. 50 rkm of the upstream and downstream boundaries of the reservoir showing the most change. Comparing the pre- and post-impoundment periods following completion of Lake Limestone, we also observed flow homogenisation of the reaches downstream of Lake Limestone, which is likely to be responsible for the downstream changes in assemblage structure by favouring equilibrium strategists over opportunistic species. Without the ability to compare detailed historic records to the current conditions in the river, it is likely that some of these effects would have been overlooked due to the bias of a shifting baseline. Thus, if possible, it is essential to gather baseline information pertaining to the number and structure of communities that exist in a river so that managers can assess the status and trends of those communities over time.

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CONFLICT OF INTEREST

No conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gmsbcc2jr>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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