



Hydraulic requirements of freshwater mussels (Unionidae) and a conceptual framework for how they respond to high flows

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Abstract. Spatiotemporal variability in flow determines the physical structures of habitat. During low flows, aquatic organisms can be exposed to reduced dissolved oxygen concentrations, increased water temperature, and desiccation, whereas at high flows, increased velocity and hydraulic forces on the streambed can be equally detrimental. These constraints create a mosaic of habitat that influences the distribution and abundance of aquatic biota. This mosaic can change due to stochastic events or those mediated by humans. Understanding how low and high flow conditions affect aquatic organisms is critical not only for advancing ecological knowledge but also for protecting imperiled aquatic species such as unionid mussels. The overall goal of this project was to examine how substrate and hydrologic conditions affect mussel habitat and to then use the resulting information combined with life-history traits and shell morphology (i.e., sculpturing) to better understand how flow shapes mussel assemblage structure. Using quantile regression, we found that low values of relative shear stress (RSS), a measure of substrate stability, were associated with high mussel species richness and density. Change point analysis using threshold indicator taxa analysis (TITAN) indicated species-specific preferences for varying levels of bed stability. These preferences were best explained by life-history strategy and shell morphology based on the results of a principal component analysis. Using these results, we then present a conceptual model from which to derive expectations concerning taxonomic composition, life-history strategy, and shell sculpture type based on the degree of substrate mobility using RSS and variability in RSS.

Key words: e-flow; flow regime; habitat; life history; limiting factor; mussels; species traits.

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INTRODUCTION

Freshwater mussels (order Unionoida; hereafter “mussels”) are among the most imperiled faunal groups globally (Williams et al. 1993, Master et al. 2000, Strayer et al. 2004, Lopes-Lima et al. 2017). Mussel declines have been attributed to multiple causes, but loss of habitat because of impoundments and modified flow

regimes is among the most notable and pervasive impacts to mussels (Haag 2012). Unionid mussels provide essential ecosystem services such as nutrient cycling, water filtration, and habitat for other aquatic organisms (Vaughn and Hakenkamp 2001, Vaughn et al. 2008, Geist 2010, Lummer et al. 2016), and therefore, their decline will have long-term negative consequences for the ecological function of riverine systems.

Freshwater mussels can occur in dense multi-species aggregations, known as mussel beds, which are patchily distributed within streams and rivers. Complex hydraulic variables, such as shear stress, a measure of frictional force due to flow resistance along the stream bottom, are known to be important environmental determinants of this patchiness. For example, at high flows, mussel species richness and abundance are often maximized in areas where shear stress is low (Morales et al. 2006, Gangloff and Feminella 2007, Allen and Vaughn 2010, Stoeckl and Geist 2016). In contrast, at low flows, minimum velocity and depth along with complex hydraulic variables such as Froude and Reynolds Roughness numbers are known to be predictive of mussel occupancy and abundance (Gagnon et al. 2004, Steuer et al. 2008, Maloney et al. 2012). Taken together, these studies suggest that mussels are most likely to occur in areas of the stream bottom that remain stable during high flow events and wetted, and thermally buffered, during periods of low flow (Strayer 2008). A mismatch between these two constraints due to natural changes in the flow regime or those brought on by anthropogenic impacts can lead to scenarios in which a habitat patch is suitable for mussels only during low or high flows but not both. Such a mismatch can occur gradually, in the case of climate change or low-to-moderate land-use change, or suddenly such as with river impoundments or extensive changes in land use. In either case, the reduction in the availability, quality, and persistence of a given habitat patch can lead to population declines and eventually extirpation and/or extinction.

Conceptual frameworks that are able to predict how mussels respond to flow extremes (i.e., flood or drought) are lacking, due in part to the fact that mechanisms by which mussels are able to cope with either limiting event are not well known (but see Gates et al. 2015). As a consequence, conservationists and resource managers are unable to reliably predict how mussels may respond to changes in flow, natural, or man-made, or identify actions that would be successful in mitigating these changes. A potential solution to this issue is the use of species traits to understand how mussels cope with extreme disturbances. As pointed out by Mims and Olden (2012), there has been a growing movement

among ecologists to use species traits as a universal currency for studying flow-ecology relationships because they have evolved in response to a given flow regime. For freshwater fish, the Life History Continuum model (LHCM; Winemiller and Rose 1992) contrasts fish survivorship, generation time, and fecundity into three life-history strategies (opportunistic, periodic, and equilibrium) that respond in a predictable manner to specific changes in hydrologic conditions. Opportunistic strategists are characterized by life-history traits that allow them to occupy habitats defined by frequent and intense disturbance, 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 seasonal, periodically suitable environments with large spatial patchiness and temporal heterogeneity, such as seasonal flood pulses. Equilibrium strategists are those species with life-history traits that are maximized in more stable habitats with low environmental variation (Mims and Olden 2012). Haag (2012) adapted the LHCM model for mussels using life span, age at maturity, fecundity, maximum adult size, brooding strategy, and growth rate to assign species to the same three life-history strategies.

Another suite of traits that may also be important for determining how mussels cope with extreme flows is shell morphology (i.e., sculpture), which, similar to life-history traits, is hypothesized to be optimized to local hydrologic conditions, resulting in two general forms of shell ornamentation: unsculptured vs. sculptured (Stanley 1981). This idea is based on the premise that bivalves have adapted their morphology to cope with disruptive flows by inhibiting displacement (i.e., sculptured) or allowing for rapid reburial if dislodged from the sediment (i.e., unsculptured). Watters (1994) expanded these ideas to unionid mussels, suggesting there are two unsculptured morphologies (unsculptured [thin to thick shell, smooth exterior, no dorsal wing] and symphynote [thin to moderately thick shell, smooth exterior, dorsal wing present but may be reduced]) and four sculptured morphotypes (anti-scouring [pustules or ribs along dorsal end of shell], generalized [pustules throughout the shell surface], medial [pustules or ribs along the middle of the shell surface], and U2D2 [series

of ridges across the shell surface]). He further hypothesized that unsculptured species are likely more prevalent in areas with greater hydrological variability than sculptured forms because lack of ornamentation allows for easier burrowing following dislodgment than one that is ornate with sculpture (Watters 1994).

To date, there has been limited application of using life-history traits or shell sculpture types in evaluating general mussel-flow relationships, which could potentially be used to advance mussel focused environmental flow assessments. This is particularly important in places such as Texas, located in the southwestern USA, where water quantity and quality are always an issue and regulatory mechanisms to encourage ecologically sustainable water management are lacking (Randklev et al. 2018). Moreover, recent state and federal listings of mussels in Texas (USFWS 2009a, b, 2011, 2016, TPWD 2010) have raised questions about whether or not current environmental flows, and those under future climate change scenarios, will be able to sustain rare and threatened species. To begin addressing knowledge gaps, we evaluate how substrate and hydrologic conditions affect mussel habitat, specifically substrate stability. We use the resulting information combined with life-history traits and shell sculpture types to help explain how flow shapes mussel assemblage structure. Finally, we develop a conceptual framework (i.e., a niche scheme) that predicts which taxonomic groups, shell sculpture types, and life-history strategies are able to best cope with hydrologic extremes. This conceptual framework can serve as a basis for predicting the consequences of flow alteration and for informing flow-management recommendations across mussel taxonomies and geographies.

METHODS

Study area

This study took place in the Brazos and Trinity River basins of central Texas. Flow in the Brazos River basin is regulated by several mainstream and tributary flood control dams and reservoirs, concentrated mostly in the upper portion of the basin (Huser 2000, Gelwick and Li 2002, Osting et al. 2004). In the lower and middle Brazos River, where this study took place (Fig. 1), the

nearest major on-channel reservoir is Lake Whitney located several hundred kilometers upstream. Land use in the lower and middle Brazos River basin is predominately agricultural and open rangeland. The Trinity River is also heavily regulated by flood control dams and reservoirs, plus its headwaters are densely populated with ~6.9 million people as of 2010, the majority of which (~5.3 million) reside in the Dallas–Fort Worth metroplex (Perkin and Bonner 2016). This study was located in the middle Trinity River (Fig. 2), downstream of the Dallas–Fort Worth metroplex. Land use near our study reaches is predominately agricultural and open rangeland.

Site selection

Sample sites were chosen using a stratified random sampling design. In the Brazos, the following habitat types were randomly selected using satellite imagery and subsequently monitored under low and high flow conditions: (1) bank habitats (BH), (2) front of point bars (FPB), (3) behind point bars (BPB), (4) backwaters (BW), and (5) mid-channels (MC). Bank habitats were defined as the zone from the bank to the point in the channel where the slope of the bank leveled out, which indicated the beginning of the mid-channel habitat. Front of point bars and behind point bars were located in the up- or downstream portions of sand and gravel bars, respectively. Backwater habitats were areas typically out of the main channel current with minimal velocities and variable water depths. Mid-channel habitats were located in the middle of the river channel. For the Trinity, only bank and riffles were monitored, runs and pools were present but difficult to distinguish from backwaters, plus high-water velocity and extreme depth precluded our ability to safely and effectively sample these habitats. Bank habitats in the Trinity were identified similarly to those in the Brazos, and riffle habitat was defined as shallow areas with moderate to fast flows, where small hydraulic jumps over rough bed material caused small ripples, waves, and eddies that break the surface water tension.

Mussel surveys

At each randomly selected site (i.e., mesohabitat type), we confined our sample area to the

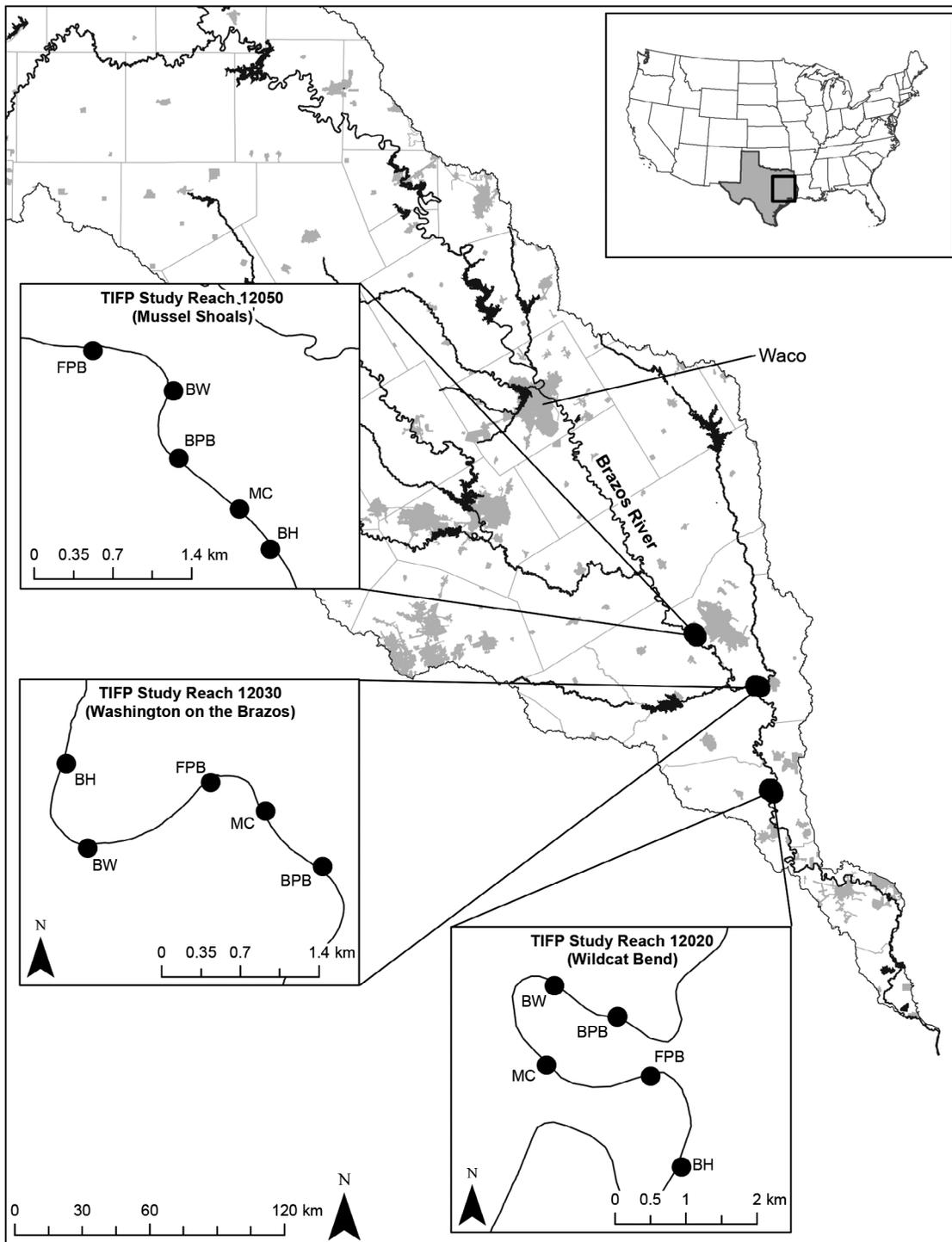


Fig. 1. Map of the study area showing specific Texas Instream Flow Project [TIFP#] reaches within the main-stem of the Brazos River where mussels were monitored during high flows. Habitat abbreviations denote the following: bank habitats (BH), front of point bars (FPB), behind point bars (BPB), backwaters (BW), and mid-channels (MC). Gray polygons denote urban areas.

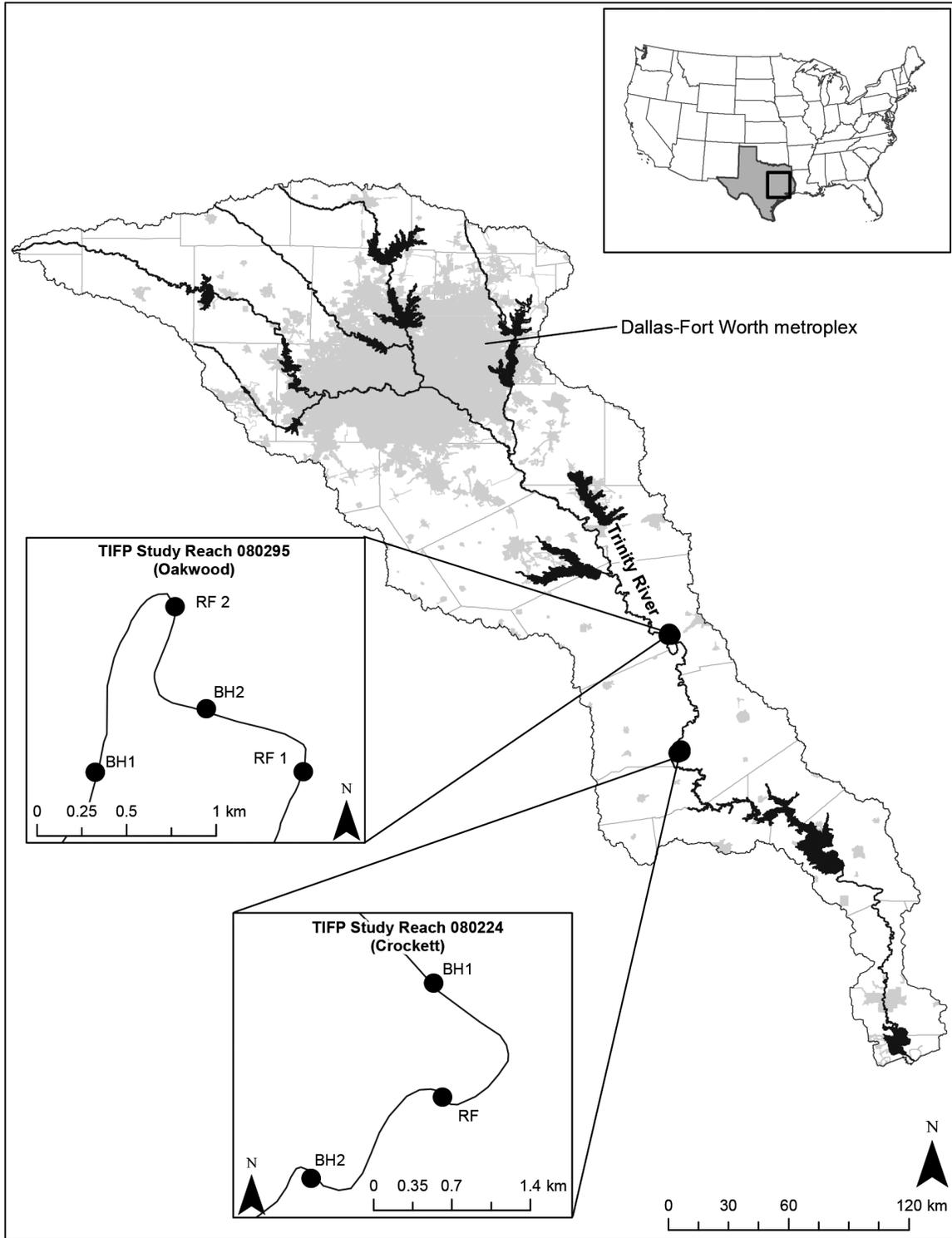


Fig. 2. Map of the study area showing specific Texas Instream Flow [TIFP#] reaches within the mainstem of the Trinity River where mussels were monitored during high flows. Habitat abbreviations denote the following: bank habitats (BH) and Riffles (RF).

specific habitat type, ensuring that the search area did not exceed 150 m². In the Brazos, 15–17 0.25-m² quadrats were randomly selected from each sample area (Appendix S1: Table S2). In the Trinity, 30 0.25-m² quadrats were sampled from a similar 150-m² area (Appendix S1: Table S3). We excavated each quadrat to a depth of 20 cm by hand in the Brazos and used a modified Surber sampler in the Trinity. Sediment excavated from quadrats was then examined for mussels by manually sorting in the case of the Brazos or passing it through a 0.25-inch sieve in the case of the Trinity. All collected mussels were stored in mesh bags submerged in water prior to identification.

Habitat sampling

Habitat from approximately the center of each quadrat was assessed during low flow conditions prior to mussel sampling. We recorded current velocity and water depth using an electromagnetic flow meter (OTT MF Pro). Water velocity was measured at $0.6 \times$ depth when water depth was <60 cm and as an average of velocity at 0.2 and $0.8 \times$ depth when water depth exceeded 60 cm. For sites in the Brazos, substrate type was determined by taking one sediment core per quadrat. Substrate samples were then taken back to the laboratory and dried for 24 h at 100°C in a convection oven. Dried samples were then passed through a series of sieves (4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm), and the sediment in each sieve was weighed. The resulting information was used to create cumulative frequency distribution curves to determine the median particle size (D_{50}) within each quadrat. For the Trinity, substrate was more complex than the Brazos, which was generally sand, and so we used a modified pebble count, wherein particles were handpicked from each quadrat. The intermediate axis of the substrate was then measured, and based on this assessment, the median particle size (D_{50}) was determined. For both the Brazos and Trinity study sites, the location of each quadrat was recorded using a Trimble GeoCollector so that each quadrat could be located and resampled during high flows.

We returned to each sampled location during periods of higher flows to measure water depth and velocity using either the OTT MF Pro or an Acoustic Doppler Current Profiler (ADCP). The

latter was used only in the Trinity study sites because sampled high flows were $\sim 413\text{--}484$ m³/s compared with the Brazos, which were $\sim 36\text{--}67$ m³/s and could be manually sampled. We did not reevaluate substrate type or mussel densities between low and high flow sampling events (see Table 1); however, we did evaluate whether mussels were still present and mesohabitats did not change following measured high flow events. We then calculated substrate and hydraulic variables from formulae in Table 2.

Data analyses

We used quantile regressions to examine the relationship between mussel species richness and density and substrate and complex hydraulic variables. Quantile regression is based on the least absolute deviation regression, which models the conditional median (50th quantile), but the approach can be applied to specific quantiles (or percentiles) of the response variable. Quantile regression can be applied to nonnormal datasets or to those with heterogeneous variances, which is common in ecological studies (Cade and Noon 2003). Following Allen and Vaughn (2010), we fit univariate models for the 95th, 90th, and 85th quantiles using linear, quadratic, Ricker, or negative exponential curves to the data (with and without y -intercepts) and chose the best fitting model for each quantile based on the Akaike information criterion (AIC) provided it gave non-zero parameter estimates for the model coefficients. The fit of each quantile regression model was evaluated with the AIC corrected for small sample size (AIC_c ; Burnham and Anderson 2002). We considered models to be plausible if their $\Delta AIC_c \leq 2$, which is the difference in AIC_c for a given model relative to that of the most parsimonious model. We also calculated a pseudo- R^2 for each model following Allen and Vaughn (2010), which provided an additional line of evidence for how well a particular function fit the data. Quantile regression analyses were performed using the QUANTREG package in R version 3.02 (R Foundation for Statistical Computing, Vienna, Austria).

Threshold Indicator Taxa Analysis (TITAN) was used to identify threshold-type responses between mussel community data and hydraulic variables. Threshold Indicator Taxa Analysis uses Indicator Species Analysis (Dufrene and

Table 1. Sampled low and high flows (m³/s) on the Brazos and Trinity Rivers.

Basin	USGS gauging station	TIFP Site no.	High flow—sampled (m ³ /s)	Date	Low flow—sampled (m ³ /s)	Date
Brazos	08108700 (Bryan)	12050	56.92 (Q42), 64.85 (Q39)	1 October 2013, 15 October 2013	12.37 (Q89)	5 August 2013
	08111500 (Hempstead)	12030	66.54 (Q38), 35.68 (Q54)	24 September 2013, 3 October 2013	12.58 (Q88)	17 December 2012, 10 September 2013
	08065350 (Crockett)	12020	54.93 (Q54), 60.31 (Q52)	1 October 2013	12.74 (Q93), 24.07 (Q94)	13 November 2012, 11 September 2013
Trinity	08065000 (Oakwood)	080295	413.43 (Q11)	17 April 2017	31.43 (Q59), 35.11 (Q55)	19 September 2016
	08065350 (Crockett)	080224	484.22 (Q10)	8 June 2017	31.15 (Q72), 34.55 (Q67)	22 September 2017, 5 October 2016

Notes: TIFP#s denote Texas Instream Flow study reaches. Exceedance probabilities are listed in parenthesis.

Table 2. Summary of habitat variables measured in the study.

Variable	Formula	Description	Source
D_{50} (cm)	See <i>Methods</i>	Median particle size of the sample	
Bed roughness (k_s , cm)	$6.8 \times D_{50}$	Topographic variation of the stream bottom	Bray (1980)
Boundary Reynolds number (Re^*)	$\frac{U_* k_s}{\nu}$	Roughness of flow near substrate	Statzner et al. (1988)
Shear stress (τ , dyn/cm ²)	$\rho(U_*^2)$	Force of friction on substrate	Statzner et al. (1988)
Shear velocity (U^* , cm/s)	$U/5.75 \log_{10} \left(\frac{12d}{k_s} \right)$	Friction velocity	Statzner et al. (1988)
Critical shear stress (τ_c , dyn/cm ²)	$\theta_c g D_{50} (\rho_s - \rho)$	Shear stress required to initiate substrate motion for a typical sample substrate size (D_{50})	Gordon et al. (2004)
Relative shear stress (RSS, dimensionless)	$\frac{\tau}{\tau_c}$	Ratio of observed to critical shear stress. Values >1 are thought to represent substrate movement for a typical sample substrate size (D_{50})	Morales et al. (2006)

Note: Abbreviations are U , average velocity ($0.6 \times d$ or the mean of 0.2 and $0.8 \times d$); d , water depth (cm); g , acceleration of gravity (980 cm/s^2); ν , kinematic viscosity of water ($0.01 \text{ cm}^2/\text{s}$); ρ_s , density of substrate (2.65 g/cm^3); ρ , density of water (0.998 g/cm^3); θ_c , Shield's parameter (0.065).

Legendre 1997), which calculates an indicator value (IndVal) index based on differences among proportional occurrence and relative abundance of species within groups. In TITAN, groups represent incremental partitions along an environmental gradient (e.g., shear stress or relative shear stress [RSS]) and a taxon's IndVal is a function of its relative abundance on either side of a partition, weighted by its occurrence within each partition (i.e., the product of both). The larger IndVal on each side of a partition is retained and compared across partitions to find the greatest change in taxon abundance and frequency within the observed sample, which is the change point (King and Baker 2014). Threshold Indicator Taxa Analysis then standardizes the change point for each taxa to units of standard deviation to emphasize the change point relative to its own

pattern of variability in abundance and occurrence (Baker and King 2010). Taxa with negative z scores (z^-) are those that respond strongly in a negative direction relative to increases along an environmental gradient, whereas those with positive z scores (z^+) respond positively to increases along the same gradient. Uncertainty surrounding a taxon's change point is calculated using bootstrapping with replacement, which is then used to calculate confidence intervals and two metrics of uncertainty: purity and reliability. Purity is the proportion of times a taxon was assigned as a z^- or z^+ taxon in each bootstrap replicate scaled from 0 to 1. Reliability estimates the proportion of bootstrap replicates with a P -value <0.05 (King and Baker 2014). Taxa with a purity and reliability of ≤ 0.95 may be considered nonresponsive to a given environmental

gradient. We ran TITAN using the overall most parsimonious hydraulic variable across both river systems, identified from the quantile regression analysis. The minimum split size (minimum number of observations required on each side of a partition) was set to 5, the number of permutations was set to 250, and the number of bootstrap replicates was set to 1,000. Threshold Indicator Taxa Analysis analyses were performed using the TITAN2 package in R version 3.02 (R Foundation for Statistical Computing).

Based on the results from the TITAN analyses, we then evaluated the relationships between life-history traits, shell morphological types (i.e., sculpture vs. nonsculptured), and species change points, and their variability. In this study, life-history traits were obtained from Haag (2012) and shell sculpturing types following Watters (1994; Appendix S1: Table S1). Change point values were derived from the TITAN analysis, including the magnitude of variation for each estimate (i.e., subtracting the upper and lower CI limits and then dividing the resulting value by 2). These data were then used to construct a species-trait matrix, which was analyzed using principal component analysis (PCA). Principal component analysis is an ordination technique that helps simplify complex datasets while retaining trends and patterns (Lever et al. 2017). In our PCA, we used a correlation matrix because it can handle mixed data types and only the first two components are considered significant based on the broken-stick rule (Legendre and Legendre 1998). The resulting components were then visualized using a distance biplot. Principal component analysis was performed using the PRCOMP function in the STATS package in R version 3.02 (R Foundation for Statistical Computing).

RESULTS

Quantile regression

Brazos.—Quantile regression analyses showed limiting-factor relationships for the 95th, 90th, and 85th quantiles. The high flow RSS model performed the best across all three quantiles and accounted for as much as 38% and 42% of the variation in mussel species richness and density, respectively (Table 3, Fig. 3). The response curves for both species richness and density were

best described by a negative exponential function (Table 3) such that increases in RSS, particularly >1 , resulted in significant decreases in mussel species richness and density. However, the degree to which RSS became limiting varied by mesohabitat type. In near-shore littoral habitats (i.e., BH, BW, BPB), species richness and density were maximized at very low values of RSS and eventually reduced to zero at an RSS value slightly >1 . In near-shore lotic (i.e., FPB) and main channel (i.e., MC), habitats species richness and density were also maximized at very low RSS values, but unlike in near-shore littoral habitats, some mussel species were able to persist at RSS values >1 (Fig. 3).

Trinity.—Similar to the Brazos, we found limiting-factor relationships for the 95th, 90th, and 85th quantiles. For mussel species richness, the high flow RSS model performed best for the 95th quantile, explaining 46% of the variation in richness. The response curve for this model was best described by a negative exponential function (Table 3). For the other two quantiles, high flow shear stress models were the most explanatory, with each accounting for as much as 51% of the variation in mussel species richness (Table 3). Relative shear stress accounted for 42% and 48% in mussel species richness, depending on the quantile, despite not being the best approximating model (Table 3). The response curve for RSS at the 90th quantile was best described by a negative exponential function, while the 85th quantile was best described by the Ricker function (Table 3). For all three quantiles, mussel species richness was maximized in areas with low values of RSS, although this relationship varied by mesohabitat (Fig. 3), such that main channel habitat (i.e., riffles) had lower values of RSS, and higher species richness, compared with near-shore lotic habitats (i.e., banks; Fig. 3). For riffles, RSS values >1 appeared to be especially limiting to mussels species richness, whereas in bank habitats, RSS values needed to exceed ~ 4 before richness began to decline (Fig. 3).

For mussel density, high flow shear stress, substrate, and low flow boundary Reynolds number were the most important models and accounted for as much as 63%, 60%, and 59% of the variation in density, respectively (Table 3). The response curve for each was best described by a Ricker function. Relative shear stress for the 95th,

Table 3. Summary of quantile regression models for mussel species richness and abundance.

River	Indices	Quantile	Model	Equation	AIC _c	K	ΔAIC _c	w	R ²
Brazos	Richness	95	HF RSS	Negative exponential	1018.04	3	0.00	1.00	0.38
		90	HF RSS	Negative exponential	1059.66	3	0.00	0.99	0.25
		85	HF RSS	Negative exponential	921.28	3	0.00	0.99	0.27
	Density	95	HF RSS	Negative exponential	1411.95	3	0.00	1.00	0.42
		90	HF RSS	Negative exponential	1312.24	3	0.00	1.00	0.41
		85	HF RSS	Negative exponential	1252.66	3	0.00	0.99	0.39
Trinity	Richness	95	HF RSS	Negative exponential	870.27	3	0.00	0.99	0.46
		90	HF Shear stress	Ricker	786.58	3	0.00	0.99	0.51
		90	HF RSS*	Negative exponential	821.37	3	34.79	0.00	0.42
		85	HF Shear stress	Ricker	733.26	3	0.00	0.93	0.51
		85	HF RSS*	Ricker	747.14	3	13.88	0.00	0.48
		85	LF Boundary	Ricker	949.44	3	0.00	0.67	0.59
	Density	95	HF Shear stress	Ricker	1095.31	3	0.00	0.99	0.63
		95	HF RSS*	Negative exponential	1122.91	3	27.60	0.00	0.58
		90	Substrate	Ricker	1020.61	3	0.00	0.91	0.60
		90	HF RSS*	Ricker	1025.81	3	5.20	0.07	0.58
		85	Substrate	Ricker	951.29	3	1.84	0.27	0.59
		85	HF RSS*	Ricker	964.90	3	15.45	0.00	0.56

Notes: For each quantile, all univariate combinations of measured hydraulic variables (see Table 2) for each equation were tested. LF and HF designate whether the hydraulic variable was estimated at low or high flow conditions. Equation indicates shape of the response curve, AIC_c is small-sample Akaike information criterion, K is number of parameters in the model + 2, ΔAIC_c is the difference in AIC_c for a given model relative to that of the most parsimonious model, w is AIC_c weight and the model with the highest value is considered to be the most parsimonious, and R² is pseudo-R². Models with ΔAIC_c ≤ 2 were considered plausible. For the Trinity, the relative shear stress (RSS) model is shown (denoted by asterisks), even though in some cases it was not the most parsimonious model. We include these models for comparison purposes with the Brazos and because RSS integrates shear stress and particle size, thus providing a more synthetic approximation of habitat stability than shear stress or substrate by themselves.

90th, and 85th quantiles accounted for 58% and 56% of the variation in mussel density even though it was not the top model (Table 3). The response curves for RSS at these quantiles were best described by either Ricker or negative exponential functions (Table 3). For all three quantiles, increases in RSS values resulted in decreases in density, but the degree to which this occurred was related to mesohabitat type, mirroring our findings for species richness and our results in the Brazos. We found that riffles had lower values of RSS and higher density compared with bank habitats (Fig. 3) and that RSS values >1 were limiting at riffles but not at bank habitats until values exceeded 4 (Fig. 3).

TITAN: change point analysis

Brazos.—Threshold analysis (TITAN) identified nine mussel species that responded negatively (z– scores) to increasing values of RSS as follows (in order of increasing change point): *Amblema plicata* (Threeridge), *Toxolasma parvum* (Lilliput), *Potamilus streckersoni* (Brazos Heelsplitter),

Utterbackia imbecillis (Paper Pondshell), *Cyrtonaias tampicoensis* (Tampico Pearlymussel), *Quadrula quadrula* (Mapleleaf), *Lampsilis teres* (Yellow Sandshell), *Truncilla macrodon* (Texas Fawnsfoot), and *Cyclonaias pustulosa* (Pimpleback). *Potamilus streckersoni* had purity and reliability values that exceeded quality control criteria (Table 4), which could be the result of small sample size (n = 6) or its nonresponse to RSS. For these nine species, low change point values (0.00–0.50) and narrow confidence intervals (minimum of 0.00 to a maximum of 1.05 across all taxa) indicated sensitivity to RSS (Table 4, Fig. 4). In contrast, *Leptodea fragilis* (Fragile Papershell) responded positively (z+ scores) to increasing values of RSS, but purity and reliability values for this taxon exceed quality control criteria, which may indicate its nonresponse to RSS (i.e., may be tolerant of bed instability). The change point for this species was high (2.28), and confidence limits were broad (0.01–2.56), indicating occurrence over a wide range of RSS values (Table 4, Fig. 4).

Trinity.—Threshold analysis (TITAN) identified 10 mussel species that responded

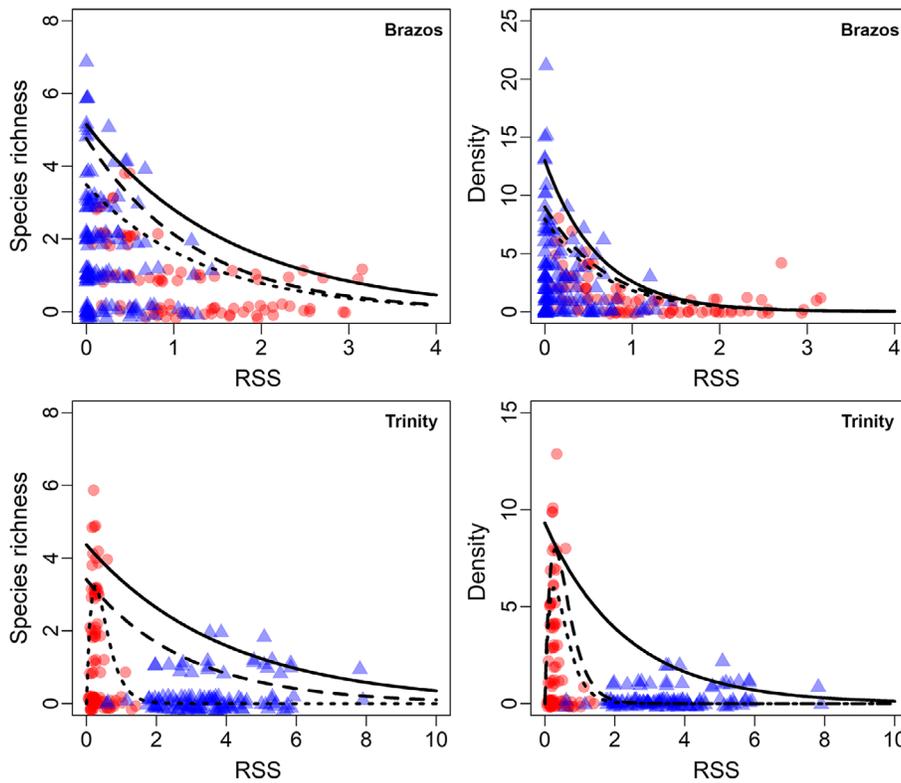


Fig. 3. Quantile regression models for mussel species richness and density for relative shear stress (RSS) across high flows at Texas Instream Flow monitoring sites on the Brazos (top graphs) and Trinity (bottom graphs) rivers. Species richness denotes number of species collected per 0.25-m² quadrat, and density refers to the total number of individual mussels collected per 0.25-m² quadrat. Black solid, dashed, and dotted lines represent 95th, 90th, and 85th quantile regression lines, respectively. Red shaded circles denote 0.25-m² quadrats from near-shore lotic (i.e., front of point bars [FPB]) and mid-channel habitats (i.e., mid-channels, riffles), and blue shaded triangles denote quadrats from near-shore littoral habitats (bank, behind point bars, and backwaters). Model parameters are provided in Table 3.

negatively (z- scores) to increasing values of RSS as follows (in order of increasing change point): *L. fragilis*, *Plectomerus dombeyanus* (Bankclimber), *Potamilus purpuratus* (Bleufer), *Obliquaria reflexa* (Threehorn Wartyback), *Cyclonaias pustulosa* (Pimpleback), *Fusconaia* sp. (either *Fusconaia flava* [Wabash Pigtoe], or *Fusconaia chunii* [Trinity Pigtoe]; see Pieri et al. 2018 for details regarding why these two species cannot be differentiated in the field), *Tritogonia verrucosa* (Pistolgrip), *Tritogonia nobilis* (Gulf Mapleleaf), *Megaloniais nervosa* (Washboard), and *T. macrodon*. Of these, three (*L. fragilis*, *P. purpuratus*, and *T. macrodon*) had purity and reliability values that exceeded quality control criteria, which could be the result of small sample sizes or

nonresponse to RSS. For these 10 species, all had low change point values (0.11–0.61) but some showed tolerance to a wide range in RSS (*L. fragilis*, *O. reflexa*, *P. purpuratus*) based on the width of the confidence intervals (Table 5). This suggests two different responses to RSS: those taxa that are sensitive with low change points (min/max: 0.20–0.61) and narrow confidence intervals (min/max: 0.17–1.46), and those that are moderately sensitive with low change points (min/max: 0.11–0.34) but wide confidence intervals (min/max: 0.10–5.15; Table 5, Fig. 4). In contrast, one mussel species, *L. teres*, responded positively (z+ scores) to increasing values of RSS. The change point for this species was high (4.69), and confidence limits were broad (2.35–

Table 4. Threshold Indicator Taxa Analysis (TITAN) results by species from the Brazos River for relative shear stress.

Species	Group	IndVal	Freq.	CP	5%	95%	Var.	Obs.Prob	Purity	Reliability
ANODONTINAE										
Anodotini										
<i>Utterbackia imbecillis</i>	-	16.69	11	0.04	0.00	0.06	0.03	< 0.001	1.00	1.00
AMBLEMINAE										
Amblemini										
<i>Amblyma plicata</i>	-	57.13	42	0.00	0.00	0.36	0.18	< 0.001	1.00	1.00
Lampsilini										
<i>Cyrtonaias tampicoensis</i>	-	31.06	52	0.19	0.02	0.25	0.11	< 0.001	1.00	1.00
<i>Lampsilis teres</i>	-	22.35	41	0.41	0.00	0.73	0.36	< 0.001	1.00	1.00
<i>Leptodea fragilis</i>	+	21.25	30	2.28	0.01	2.56	1.27	0.04	0.65	0.81
<i>Potamilus streckeri</i>	-	5.86	6	0.00	0.00	0.70	0.35	0.16	0.85	0.49
<i>Toxolasma parvum</i>	-	15.13	11	0.00	0.00	0.36	0.18	0.01	1.00	0.99
<i>Truncilla macrodon</i>	-	21.81	49	0.47	0.08	1.05	0.48	< 0.001	0.93	1.00
Quadrulini										
<i>Cyclonaias pustulosa</i>	-	24.64	55	0.50	0.09	0.83	0.37	< 0.001	0.94	1.00
<i>Quadrula quadrula</i>	-	8.25	10	0.20	0.00	0.23	0.11	< 0.001	0.99	0.96

Notes: Group indicates response direction (z+ or z-) along an environmental gradient. IndVal is the Indicator Species Analysis statistic (Dufrene and Legendre 1997) scaled from 0% to 100%. Freq. is the number of non-zero abundance values per taxon. CP is the environmental change point for each taxon based on z maximum. 5% and 95% are bootstrap confidence intervals. Var. is the product of subtracting the 95% from the 5% bootstrap confidence intervals and then dividing that value by 2. Obs.Prob is the probability of obtaining a larger IndVal Score from random data. Purity is the mean proportion of correct response-direction (z+ or z-) assignments, and reliability is the proportion of replicate Obs.Prob values ≤ 0.05.

5.74), indicating occurrence over a wide range of RSS values (Table 5, Fig. 4).

Principal component analysis: integrating life history, shell morphology, and RSS

Principal component analysis axes 1 and 2 explained 73% of the variation in life history, shell morphology, and RSS. Of this variation, PCA axis 1 explained 55% and PCA axis 2 accounted for 18% (Appendix S1: Table S4). Long-term brooding (-0.42) and high growth rate (-0.42) had the greatest negative loadings onto PCA 1, followed by unsculptured and symphyonote morphology (-0.20 and -0.22, respectively), RSS variability (-0.22), and then RSS change point (-0.14). Short-term brooding (0.42) and long life span (0.42) had the greatest positive loadings on PCA 1, closely followed by generalized and U2D2 morphotypes (0.37; Fig. 5; Appendix S1: Table S5). Relative shear stress variability (-0.52) had the greatest negative loading onto PCA 2, followed by symphyonote (-0.45) and then medial (-0.37) morphologies. Unsculptured morphology (0.61) was the only covariate that had a well supported positive loading on this axis (Fig. 5; Appendix S1: Table S5).

DISCUSSION

Quantile regression: modeling mussel species richness and abundance

We found that substrate stability models at high flow were generally the most predictive of mussel species richness and abundance, which mirrors other mussel-flow studies (Morales et al. 2006, Gangloff and Feminella 2007, Allen and Vaughn 2010, Stoeckl and Geist 2016). We also found that mussel occupancy and abundance were often maximized in areas where RSS < 1. Morales et al. (2006) hypothesized that such areas represent places along the streambed with little to no bed mobility. Strayer (1999) and then later Stoeckl and Geist (2016) suggested stable areas in river systems (i.e., low entrainment potential) should be where mussels are chiefly found because individuals are not washed away during floods. Our results and those of Allen and Vaughn (2010), who used a similar experimental approach, generally support both hypotheses, but there were exceptions as RSS values > 1 did not completely eliminate mussels.

These exceptions may stem from the fact that critical shear stress is considered, at best, a

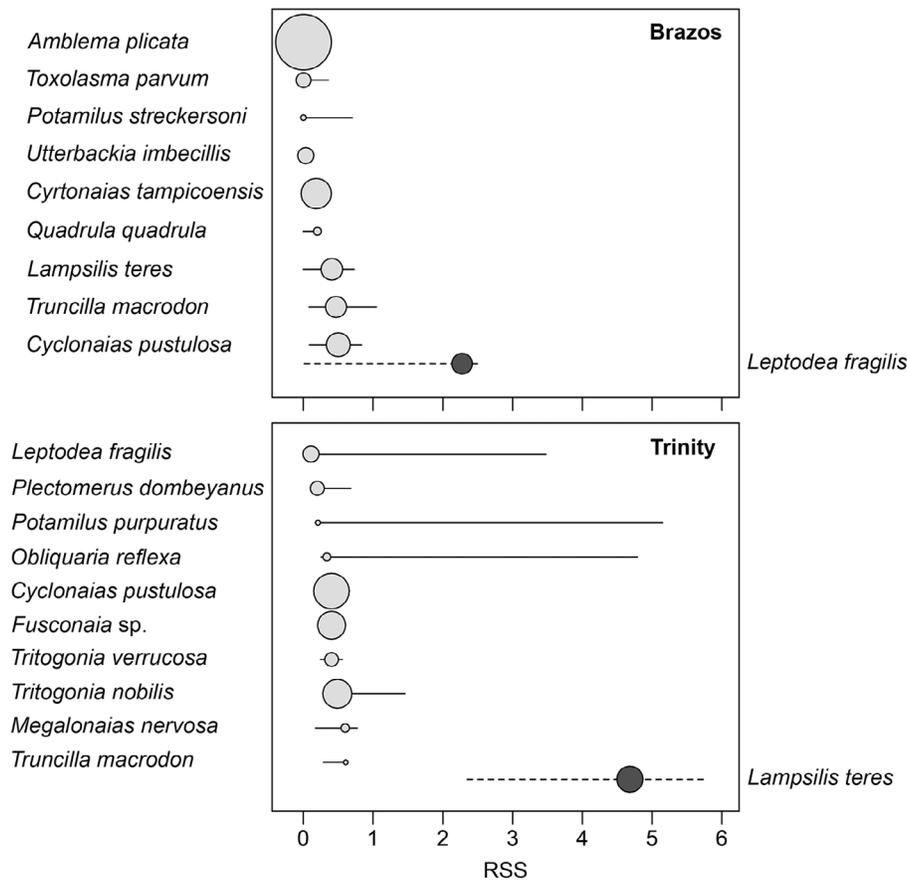


Fig. 4. Change points by mussel species identified by Threshold Indicator Taxa Analysis (TITAN) in response to relative shear stress (RSS) during high flows. Taxa are plotted in increasing order with respect to their change point (Tables 4 and 5) and horizontal lines represent 5th and 95th percentiles among 1,000 bootstrap replicates. Circles on the left-hand side denote taxa that respond strongly (z^-) in a negative direction relative to increases in RSS, whereas those on the right-hand side of each graph respond positively (z^+) to increases in RSS. The size of the circles denotes the relative magnitude of the Indictor Species Analysis statistic (Dufrene and Legendre 1997) at the change point for a given taxon.

minimum estimate of sediment entrainment potential (Elliott 2002), and therefore, it is not unexpected that mussel species richness and abundance persist at RSS values beyond 1. Allen and Vaughn (2010) made a similar point, arguing that because RSS is calculated using particle size D (e.g., D_{50} or D_{84}), resulting RSS values could over- or underestimate substrate movement depending on how representative D is of the bed surface. Mussels themselves could also stabilize substrates by forcing tight particle interlocking of the surrounding substrate via their physical presence and burrowing (Zimmerman and De Szalay 2007, May and Pryor 2016), but this seems likely only in areas

with high densities. In our study, areas of the streambed with high entrainment potential generally had low abundance. Another potential explanation is that mussels occurring in high RSS areas are transient, occupying these patches for only a short period of time before being dislodged during extreme high flow events (May and Pryor 2016). However, species traits for these transient taxa, at least in our study, suggest that morphological and behavioral adaptations, for adults, may allow some species to cope with areas of the streambed that have high potential for bed disturbance.

We also found that how well bed stability mediates mussel species richness and abundance

Table 5. Threshold Indicator Taxa Analysis (TITAN) results by species from the Trinity River for relative shear stress.

Species	Group	IndVal	Freq.	CP	5%	95%	Var.	Obs.Prob	Purity	Reliability
AMBLEMENAE										
Lampsilini										
<i>Lampsilis teres</i>	+	26.68	15	4.69	2.35	5.74	1.70	<0.001	1.00	0.99
<i>Leptodea fragilis</i>	-	16.73	8	0.11	0.10	3.48	1.69	0.15	0.77	0.52
<i>Plectomerus dombeyanus</i>	-	14.46	7	0.20	0.19	0.68	0.25	<0.001	1.00	0.99
<i>Potamilus purpuratus</i>	-	5.19	3	0.21	0.17	5.15	2.49	0.06	0.65	0.66
<i>Obliquaria reflexa</i>	-	8.18	8	0.34	0.26	4.79	2.27	0.01	0.94	0.94
<i>Truncilla macrondon</i>	-	5.00	4	0.61	0.29	0.60	0.15	<0.001	0.98	0.77
Pleurobemini										
<i>Fusconaia</i> sp.	-	28.57	20	0.40	0.35	0.60	0.12	<0.001	1.00	1.00
Quadrulini										
<i>Cyclonaias pustulosa</i>	-	36.54	34	0.40	0.35	0.66	0.16	<0.001	1.00	1.00
<i>Megalonaias nervosa</i>	-	8.86	7	0.60	0.17	0.77	0.30	<0.001	1.00	0.98
<i>Tritogonia nobilis</i>	-	29.65	25	0.49	0.36	1.46	0.55	<0.001	1.00	1.00
<i>Tritogonia verrucosa</i>	-	14.08	10	0.40	0.25	0.56	0.16	<0.001	1.00	1.00

Notes: Group indicates response direction (z+ or z-) along an environmental gradient. IndVal is the Indicator Species Analysis statistic (Dufrene and Legendre 1997) scaled from 0% to 100%. Freq. is the number of non-zero abundance values per taxon. CP is the environmental change point for each taxon based on z maximum. 5% and 95% are bootstrap confidence intervals. Var. is the product of subtracting the 95% from the 5% bootstrap confidence intervals and then dividing that value by 2. Obs.Prob is the probability of obtaining a larger IndVal Score from random data. Purity is the mean proportion of correct response-direction (z+ or z-) assignments, and reliability is the proportion of replicate Obs.Prob values ≤0.05.

depends on whether measured flows are actually limiting. For example, we found that our quantile regression models from the Trinity had greater support in terms of pseudo- R^2 values (min/max; richness 0.42–0.51; density 0.56–0.63) than those from the Brazos (richness 0.25–0.38; density 0.39–0.42). In the Brazos study sites, sampling occurred primarily at flows between 56 and 66 m³/s, with exceedance values ranging from Q42 to Q38, and the river remained wadeable in places. In the Trinity, sampling occurred when discharge was between 413 and 484 m³/s, or Q11 to Q12, which was nearing overbank flow. Allen and Vaughn (2010) made a similar observation, reporting pseudo- R^2 values ranging from 0.14 to 0.20 for mussel species richness and 0.17 to 0.22 for abundance, depending on the quantile. Sampling in their study occurred at 53.07 m³/s, or Q30, which is similar to sampled high flows in the Brazos Rivers, and was unlikely near overbank flow. Zigler et al. (2008) observed similar results for a reach of the upper Mississippi River, concluding that hydraulic variables would be most predictive during high flows (i.e., Q5) than average flows (i.e., Q50), and therefore, more extreme discharges might lead to further insight into mussel-habitat relationships.

Finally, we found that likelihood of bed disturbance varied by mesohabitat, which indicates the importance of considering hydraulic properties of sampled habitats, which are determined by channel morphology and underlying substrate (Frissel et al. 1986). Howard and Cuffey (2003) examining occurrence and habitat associations within a continuous 8-km section of the South Fork Eel River in California made a similar point, noting that mussel occurrence varied along bank habitats such that prevalence and abundance were maximized in near-bank environments where channel form did not accelerate flow. May and Pryor (2016) similarly found that mussels often occurred in areas where geomorphology enhanced bed stability but also noted that habitats with increased roughness or cover types (e.g., root wads, bedrock crevices, or sedge mats) were important to increased bed stability.

TITAN: modeling mussel species thresholds

We found that most mussel taxa responded negatively to increasing values of RSS. This finding corroborates the results of our quantile regression analysis, which showed that mussel species richness and abundance were maximized at low values of RSS. However, in using TITAN,

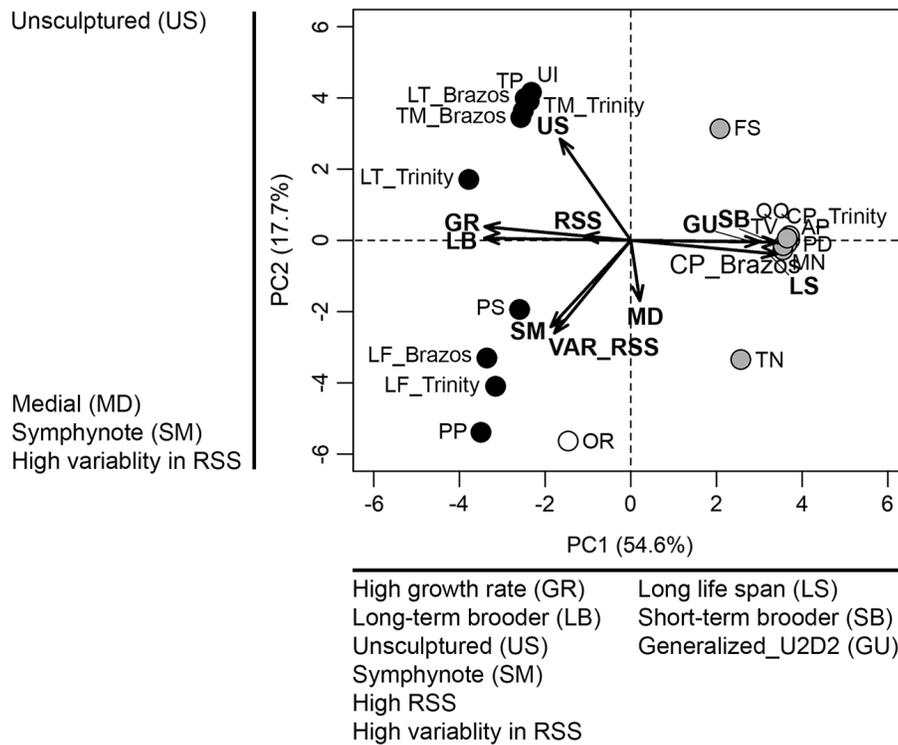


Fig. 5. Principal component analysis (PCA) distance biplot showing the relationship between life-history traits (growth rate, brooding strategy, and life span), shell morphology (unsculptured, symphynote, medial, generalized, and U2D2), and the change point of relative shear stress (RSS) and its variability, by species. The contribution and direction of a given trait are described based on its vector and listing below a given component. Species-trait assignments are given in Appendix S1: Table S1 and specific contributions to a given component are listed in Appendix S1: Tables S4 and S5. The overall variation explained by component 1 or 2 is listed in parenthesis. Circles denote the following life-history categories: Dark shaded circles represent opportunistic species, gray circles denote equilibrium species, and white circles denote periodic species. Species abbreviations are the following: *Amblyma plicata* (AP), *Cyclonaias pustulosa* (CP), *Fusconaia* sp. (FS), *Lampsilis teres* (LT), *Leptodea fragilis* (LF), *Megaloniais nervosa* (MM), *Obliquaria reflexa* (OR), *Plectomerus dombeyanus* (PD), *Potamilus purpuratus* (PP), *Potamilus streckeri* (PS), *Quadrula quadrula* (QQ), *Toxolasma parvum* (TP), *Tritogonia nobilis* (TN), *Tritogonia verrucosa* (TV), *Truncilla macrodon* (TM), and *Utterbackia imbecillis* (UI).

we were able to identify specific species thresholds (i.e., change points) across a suite of taxa contributing to this response, which is rarely assessed (but see Steuer et al. 2008). We found that for all of the species that responded negatively to RSS, the change point values, where occurrence and abundance began to decline, were <1. Confidence intervals around change point estimates for many of these taxa (e.g., *A. plicata*, *C. pustulosa*, and *M. nervosa*) were also <1. However, there were some negatively responding taxa (e.g., *L. fragilis*, *P. purpuratus*, and *O. reflexa*) that had broad confidence intervals that

exceeded an RSS value of 1, in some cases reaching values >5. These species-specific differences along with those taxa that responded positively to RSS explain why mussel species richness and abundance were never reduced to zero at RSS values >1 in our quantile regression analysis. This result highlights that RSS <1 may identify hydraulic refuge for some species, but for others, it may have little practical application. Because of this variation, species-specific RSS change points and their confidence intervals should be determined to ensure that habitat availability is accurately characterized. Failing to do so will

likely lead to cases of over- and underestimation of available habitat depending on the species in question, which may hinder environmental flow recommendations and confound conservation status assessments that seek to determine whether altered flows are responsible for a species decline.

Principal component analysis: integrating life history, shell morphology, and RSS

We show that species with certain morphologies (smooth and/or thin shells) plus demographic traits (i.e., short life spans, high fecundity, and high growth rates) were more associated with high RSS habitats than species that lacked these traits, which would suggest biological mechanisms for coping with high flows. Sansom et al. (2018) examining persistence of mussel assemblages to bed load transport made a similar observation. The authors found that mussel beds within modeled rivers persisted over a 20-yr time span despite evidence that bed mobilization had occurred frequently (at least once every 2 yr or less) over that same time period. The authors argued based on this result that sediment stability by itself provides only a partial explanation for mussel occurrence and hypothesized that species traits may also contribute to persistence, even in stable habitats. Thus, our results appear to provide validation of Sansom's et al. (2018) hypothesis and a potential mechanistic understanding for how mussels are able to persist in habitats with varying levels of entrainment potential.

High flow conceptual model

Using the results of our PCA, we formulate a conceptual model (Fig. 6) contrasting life-history strategy, taxonomic composition, and shell sculpturing type with bed stability inferred using RSS, which is based on change point estimates (i.e., species thresholds) and their corresponding confidence intervals. Interpretation of this model is then based on position of a given species along the gradient of decreasing bed stability, its life-history strategy, and sculpture type. For example, as one moves toward the upper right corner of the graph, the likelihood of bed instability is high because RSS and variability in RSS are maximized (Fig. 6). For this area of the graph, we predict opportunistic strategists (*Leptodea*, *Potamilus*) with

symphyonote shells. Species belonging to these genera are characterized by short life spans, early onset of sexual maturity, high fecundity, and high growth rates, which are traits considered adaptations for rapid colonization and persistence in disturbed but productive habitats (Haag 2012). The symphyonote morphology, which is characterized by an unsculptured, compressed, shell with a posterior wing, is considered an adaptation to prevent individuals from being washed away, obtain a favorable position when righted following dislodgement, and prevent sinking when deposited in soft substrates (Watters 1994). *Lampsilis teres*, which does not belong to either genera or possess a symphyonote morphology, is grouped in this area of the graph. This species shares similar demographic traits with *Leptodea* and *Potamilus*, and its unsculptured morphology, which comprises of a smooth shell without a wing or ornamentation, is also considered an adaptation to entrainment by allowing individuals to rapidly reburrow following dislodgement.

As one moves toward the lower left corner of the graph, the likelihood of bed instability decreases because RSS and its variability are minimized (Fig. 6). For this portion of the graph, we predict equilibrium strategists (*Amblema*, *Cyclonaias*, *Fusconaia*, *Megalonaias*, *Plectomerus*, *Quadrula*, and *Tritogonia*) with generalized or U2D2 shell sculpturing. *Fusconaia*, and presumably *Pleurobema*, are exceptions as both genera are unsculptured but show longitudinal changes in shell morphology wherein headwater specimens tend to be compressed, thin shelled, and more elongate compared with downstream specimens which are thicker shelled, inflated and globose shaped, with elevated umbos and a developed sulcus (Watters 1994). These differing features are thought to reflect differences in dealing with dislodgment with the headwater form adapted to burrowing and the downstream form to anchoring. Species belonging to the lower left corner of the graph are characterized by long life span, delayed onset of sexual maturity, typically low fecundity, and low growth rates, which are traits considered adaptations for stable, productive habitats (Haag 2012). Similarly, the generalized or U2D2 morphologies are considered adaptations to aid in anchoring within the substrate, which may inhibit quick reburrowing following dislodgment (Watters 1994).

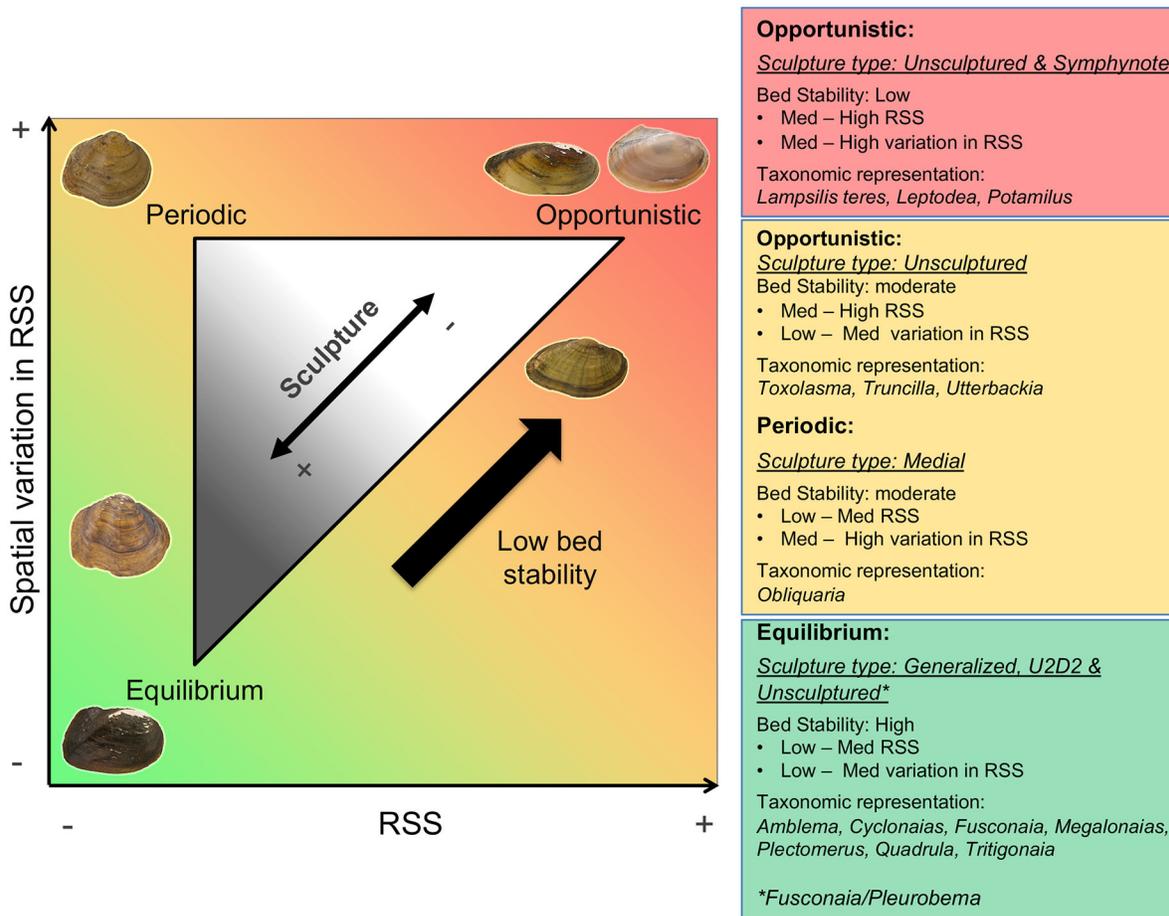


Fig. 6. A conceptual model for predicting mussel community composition, life-history traits, and sculpture type relative to bed stability (Relative shear stress [RSS] and variation in RSS) using the life-history triangle model, overlaid with a linear gradient depicting sculptured (black) vs. unsculptured (white). Probability of bed stability decreases moving from the lower left to the upper right quadrant, which is shown by a gradient of green to red. Boxes corresponding to these colors provide our predictions by life-history strategy regarding bed stability, sculpture type, and taxonomic composition. The following representative species are overlaid for each life-history endpoint: *Plectomerus dombeyanus* (Bankclimber) and *Tritogonia nobilis* (Gulf Mapleleaf), equilibrium strategists; *Obliquaria reflexa* (Threehorn Wartyback), periodic strategist; and *Lampsilis teres* (Yellow Sandshell), *Truncilla macrodon* (Texas Fawnsfoot), and *Potamilus streckersoni* (Brazos Heelsplitter), opportunistic strategists.

The remaining two areas of the graph (upper left and lower right-hand) represent intermediate conditions where either RSS or variability in RSS, but not both, can be high, and therefore, the likelihood of bed instability is low to moderate (Fig. 6). For the upper left portion of the graph, RSS is predicted to be low, while spatial variation in RSS is high, and we predict periodic strategists (*Obliquaria*) with medial shell sculpturing. The periodic strategy is hypothesized to be an

adaptation to moderately disturbed habitats or those that are seasonal or periodically suitable with high temporal and spatial variability (Haag 2012, Mims and Olden 2012). Medial sculpturing is considered an adaptation to strong currents (Watters 1994). For the lower right portion of the graph, RSS is predicted to be high with low variation. We predict that species within this quadrant are opportunistic strategists (*Toxolasma, Truncilla, and Utterbackia*) with unsculptured

shells. The opportunistic strategy is adapted for unstable environments, which elevated RSS represents, but this habitat is not nearly as unstable as those that are also highly variable (i.e., the upper right corner of the graph). Thus, partitioning of the opportunistic strategy between the upper (i.e., *L. teres*) and lower right portions of the graph represents a continuum of taxa based on their ability to cope with unstable environments (Fig. 6). The unsculptured morphology is adapted to unstable environments allowing for quick burial in fast currents following dislodgment (Watters 1994, Haag 2012).

It is important to point out that this model is limited to only predicting how species will respond to high flows, which to date is considered a proximate factor in mussel bed formation (Strayer 1999, Gangloff and Feminella 2007, Allen and Vaughn 2010). Examining how life-history and morphological traits relate to other dimensions of flow, such as subsistence flows, or including nonadult life stages will likely improve efforts to conceptualize mussel habitat in a way that can be used to both guide management and enhance understanding of the mechanisms driving mussel distribution. Winemiller et al. (2015) made a similar point, proposing that creation of niche schemes, such as the one we present, should be useful for advancing ecological knowledge and its applications. However, the authors also argued that the complexity of these models is predicated on functional traits and performance datasets, which are lacking for mussels as a group. Thus, we envision in the future a suite of niche schemes that are developed to address not only abiotic requirements of mussels but also their biotic needs (i.e., host-fish) with respect to multiple dimensions of flow.

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