Hydrobiologia (2016) 770:173–191
DOI 10.1007/s10750-015-2586-5

PRIMARY RESEARCH PAPER

The influence of stream discontinuity and life history strategy on mussel community structure: a case study from the Sabine River, Texas

Charles R. Randklev · Neil Ford · Steve Wolverton · James H. Kennedy · Clint Robertson · Kevin Mayes · David Ford

Received: 21 May 2015 / Revised: 28 October 2015 / Accepted: 12 November 2015 / Published online: 30 November 2015

Abstract The impoundment of running waters is a threat to freshwater mussels and has only been cursorily examined in Texas. To address this, we evaluate mussel assemblage structure in the Sabine River downstream of a flood control and hydropower reservoir. We use the serial discontinuity concept (SDC) and the Life History Continuum model (LHCM) to explain relationships between stream position (i.e., downstream distance from either dam) and mussel species richness, catch-per-unit effort (CPUE), and life history strategy. Using 90th, 85th, and 80th quantile regression models, we observed that mussel species richness and abundance were reduced for stream segments located near Lake Tawakoni and Toledo Bend Reservoir and that these reductions decreased with distance from either reservoir. We also observed significant shifts in life history composition of mussel assemblages depending on stream position from either dam. Opportunistic strategists were more abundant in reaches located immediately downstream of Lake Tawakoni and Toledo Bend Reservoir whereas periodic and equilibrium strategists were most abundant in reaches located at intermediate distances from either reservoir. Findings from this study confirm the negative impact large impoundments have on downstream mussel populations and demonstrate the value of using the SDC and LHCM for evaluating mussel response to river impoundment.

Keywords Freshwater mussels · Unionidae · Flow regulation · Assemblage structure · Impoundment

---

Handling editor: Marcello Moretti

C. R. Randklev (✉)
Texas A&M Institute of Renewable Natural Resources,
1500 Research Parkway, Suite 110, College Station,
TX 77843, USA
e-mail: crandklev@ag.tamu.edu

N. Ford
Department of Biology, University of Texas at Tyler,
Tyler, TX 75799, USA

S. Wolverton
Department of Geography, University of North Texas,
Denton, TX 76203, USA

J. H. Kennedy
Department of Biology, University of North Texas,
Denton, TX 76203, USA

C. Robertson · K. Mayes
River Studies Program, Texas Parks and Wildlife,
San Marcos, TX 78667, USA

D. Ford
Halff Associates, Inc., Richardson, TX 75081, USA

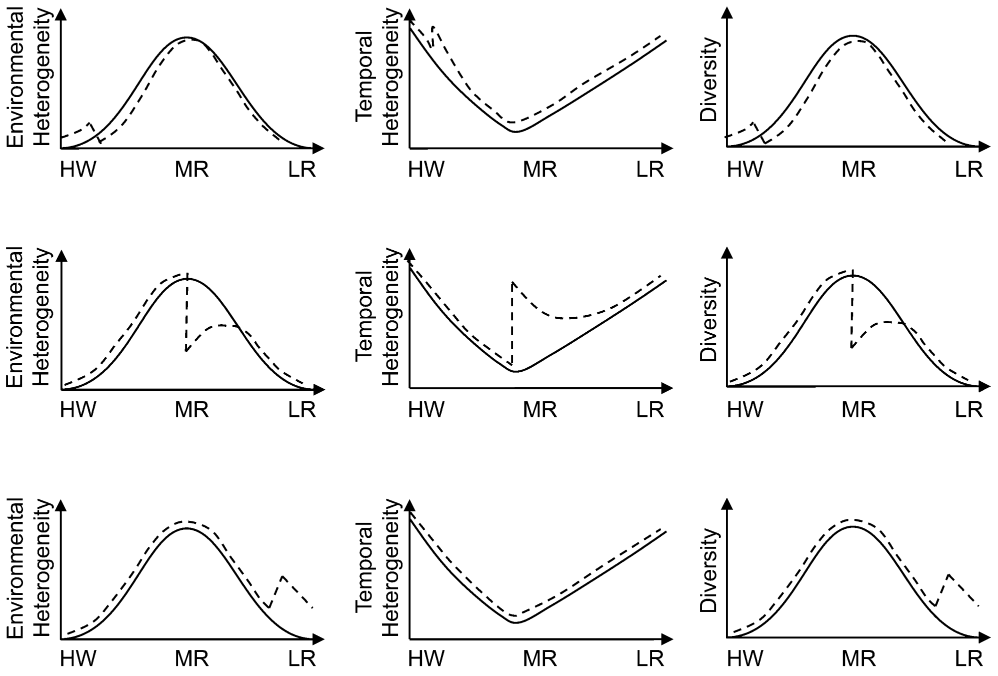
Introduction

Dams are typically constructed to help control flooding, provide water for cities and irrigation, produce hydropower, and provide recreational opportunities. Over 40,000 large dams have been constructed throughout the world, and hundreds of thousands of smaller structures impound water (McAllister et al., 2001). In the continental United States the exact number of dams is not known; however, there are approximately 87,076 dams listed on the U.S. Army Corps of Engineers National Inventory of Dams (NID), and 3606 are considered large as they exceed 10^7 m^3 in storage (Graf, 1999; NID, 2014). The massive proliferation of dams in the United States has resulted in irreversible changes to riverine ecosystems (Rosenberg et al., 2000; McAllister et al., 2001). Inundation following impoundment transforms reaches upstream into lentic habitats, whereas downstream impacts include altered hydrology, sediment transport as well as shifts in water clarity and temperature regimes (Baxter, 1977; Bunn & Arthington, 2002). Hydropower peaking operations are especially problematic because they can significantly alter the physiochemical characteristics of fluvial ecosystems, although reservoirs constructed for flood control or water supply may have similar effects (Bunn & Arthington, 2002; Magilligan & Nislow, 2005). In either case, alterations to flow, thermal, sediment and nutrient regimes can have broad effects on productivity and habitat structure and, ultimately, on the composition and distribution of aquatic biota (Baxter, 1977; Rosenberg et al., 2000; Bunn & Arthington, 2002). For unionid mussels, many (particularly riverine) species are threatened due to stream regulation (Haag, 2012), which is problematic since mussels can be important to nutrient dyamics and provide habitat for other benthic fauna in (Vaughn & Hakenkamp, 2001; Vaughn & Spooner, 2006; Vaughn et al., 2008; Strayer, 2014; Atkinson & Vaughn, 2015).

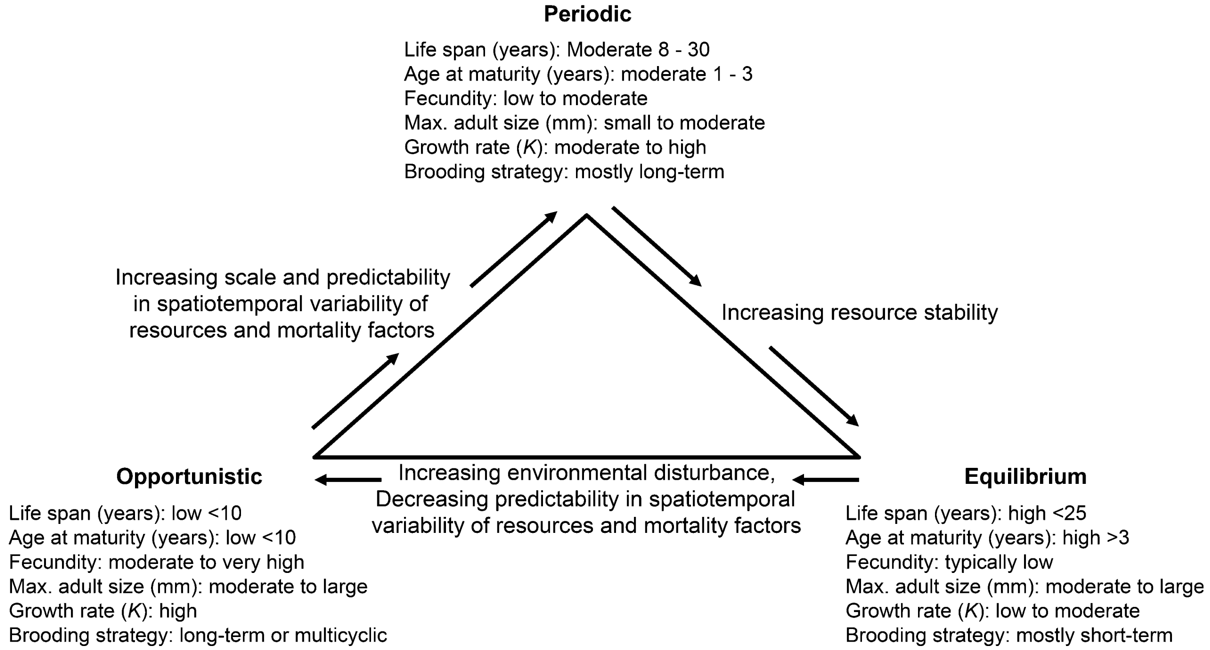
In freshwater systems, the hydrologic regime shapes abiotic and biotic attributes of rivers by "filtering" species based on their ability to cope with environmental variation at differing spatial and temporal scales (Southwood, 1977, 1988; Stearns, 1992; Poff, 1997). Life history theory seeks to explain these changes through a framework that examines how organism traits or resource allocation respond to environmental variation. One of the more notable models within this framework is that of Life History Continuum model [LHCM] (Winemiller & Rose, 1992), which is an adaptation of the theory of *r*- and *K*-selection (MacArthur & Wilson, 1967; Pianka, 1970) that contrasts juvenile fish survivorship, generation time, and fecundity for three life history strategies in response to environmental variation. In this model, opportunistic strategists, which mirror the *r*-selected strategy, are those species with short lifespans, small-bodies, and high fecundity, and are favored in habitats that are defined by frequent and intense disturbance. In contrast, equilibrium strategists, which align with the *K*-selected strategy, are large-bodied species with long lifespans that exhibit low fecundity, and are favored in stable, predictable habitats. Periodic species, typically characterized by large body size, high fecundity, late maturation, and low juvenile survivorship maximize fitness when environmental pressures are intermediate, cyclical, or both (Winemiller & Rose, 1992; Haag, 2012). For mussels, Haag (2012) adapted the model proposed by Winemiller & Rose (1992) to describe each endpoint based on five mussel life history traits: life span, age at maturity, fecundity, maximum adult size, brooding strategy, and growth rate (Fig. 1). Since impoundments can reshape physical and biological conditions, which in turn can influence mussel assemblage structure, Haag (2012) then used the LHCM to evaluate the relationship between tolerance to impoundment and life history traits of mussel species in the Cumberland, Tennessee, Ohio, Upper Mississippi and Illinois Rivers. However, his assessment focused only on navigation dams, not large flood control or hydropower reservoirs. As such, its unknown how flow alteration stemming from large dams shapes mussel life history strategies, or whether the LHCM can be combined with other models (e.g., serial discontinuity concept [SDC]; see below) to

Fig. 1 Redrawn predictions of the serial discontinuity concept ▶ (Ward & Stanford, 1983; Ellis & Jones, 2013) and the Life History Continuum model from Winemiller (2005) and Winemiller & Rose (1992). Mussel life history traits are provided for each life strategy following Haag (2012). For the serial discontinuity concept, dashed lines indicate hypothesized changes to the variable with addition of an impoundment at the headwaters (HW), middle reach (MR), and lower reach (LR) along the river continuum

Serial-discontinuity concept



Life history continuum model



Periodic

Life span (years): Moderate 8 - 30
Age at maturity (years): moderate 1 - 3
Fecundity: low to moderate
Max. adult size (mm): small to moderate
Growth rate (*K*): moderate to high
Brooding strategy: mostly long-term

Increasing scale and predictability in spatiotemporal variability of resources and mortality factors

Increasing resource stability

Increasing environmental disturbance, Decreasing predictability in spatiotemporal variability of resources and mortality factors

Opportunistic

Life span (years): low <10
Age at maturity (years): low <10
Fecundity: moderate to very high
Max. adult size (mm): moderate to large
Growth rate (*K*): high
Brooding strategy: long-term or multicyclic

Equilibrium

Life span (years): high <25
Age at maturity (years): high >3
Fecundity: typically low
Max. adult size (mm): moderate to large
Growth rate (*K*): low to moderate
Brooding strategy: mostly short-term

provide a means for evaluating and explaining changes in mussel assemblage structure in response to river impoundment.

Analyzing biotic patterns along environmental gradients has been useful for examining the effects of flow regulation on community structure for aquatic invertebrates and fishes located downstream of dams (e.g., Voelz & Ward, 1990; Vaughn & Taylor, 1999; Quinn & Kwak, 2003; Suttkus & Mettee, 2009). Investigators have long realized that the occurrence and relative abundance of species in riverine systems is, in part, influenced by physical gradients that vary from the headwaters to the mouths of river systems (e.g., River Continuum Concept, Vannote et al., 1980; The Riverine Ecosystem Synthesis, Thorp et al., 2006, 2008; River Wave Concept, Humphries et al., 2014). These ideas provide the framework for the SDC, which proposes that dams at any position on a river system will alter physical parameters and that these changes (termed "discontinuity"), in turn modify biotic patterns and processes (Fig. 1; Ward & Stanford, 1983; Ellis & Jones, 2013). Recovery from these changes does occur, but often gradually and over long distances from the point of flow regulation and is dependent on position along the river and in many cases the operational type of the reservoir (Ward & Stanford, 1983; Poff & Hart, 2002). For mussels, the effects of large dams on mussel populations have been documented (e.g., Williams et al., 1992; Layzer et al., 1993) but detailed information on the spatial pattern of assemblage structure downstream of dams at a sufficient scale to document impacts and recovery, regardless of operational type, is rare (e.g., Vaughn & Taylor, 1999; Vaughn & Spooner, 2004; Randklev et al., 2013). Moreover, studies that examine community or ecological models such as the SDC and LHCM relative to changes in assemblage structure (e.g., life history strategies, richness, and abundance) brought about by river impoundments are uncommon (but see Vaughn & Taylor, 1999).

In Texas, there has been little consideration of the ecological risks posed by river impoundment on the 52 mussel species known to occur in the state despite the fact that Texas has the most dams of any state, with 7310, of which 235 are sizable enough to be characterized as large in the NID database (Graf, 1999; NID, 2014). Notable exceptions include assessments of the impacts associated with reservoir drawdown on unionid populations (Howells et al., 2000), characterization of mussel community composition within inundated reaches following river impoundment (e.g., White & White, 1977; Neck, 1986, 1990), surveys focused on documenting species presence/absence and distribution for mussel populations downstream of large reservoirs (e.g., Karatayev et al., 2012; Randklev et al., 2013), and studies of state-wide mussel distribution and factors responsible for their imperilment (Burlakova et al., 2011). To date, there have been no studies in Texas that have compared longitudinal patterns in mussel assemblage structure or life history composition for populations downstream of water supply vs. hydropower reservoirs on the same river system. This is problematic because there are 26 major reservoirs proposed for construction [each will exceed 6.2 10^6 m^3 in storage] (Texas Water Development Board [TWDB], 2012). For these projects, it is important that impacts to mussels and fish hosts be considered during environmental impact assessments or utilized to identify enhancement opportunities, especially given the recent state-listing of 15 mussel species (Texas Parks and Wildlife [TPWD], 2010) and the potential federal listing of 11 of these species under the Endangered Species Act by the U. S. Fish and Wildlife Service (USFWS, 2001, 2011).

The purpose of this study is to evaluate the structure and composition of mussel assemblages in the Sabine River, downstream of Lake Tawakoni (water supply reservoir) and Toledo Bend Reservoir (peaking hydropower reservoir), to observe how mussels respond to two different operations of large dams. We use the approach of quantile regressions to model the 90th, 85th, and 80th quantiles on species richness and abundance, and life history strategy in relation to distance downstream from the point of flow regulation. Drawing on the theory of SDC and LHCM for mussels, we predict that: (1) mussel species richness and abundance will be reduced in stream segments located immediately downstream of both reservoirs, but because biotic diversity, to include mussels (Haag, 2012), is often maximized in middle reaches of natural rivers, Toledo Bend Reservoir (hydropower reservoir) should then have the greatest reduction for mussel species richness and abundance compared to Lake Tawakoni (water supply reservoir) due to its stream position; (2) recovery (i.e., return to a reference condition) will occur with increased distance from both reservoirs, but it should be more attenuated downstream of Toledo Bend Reservoir because of its

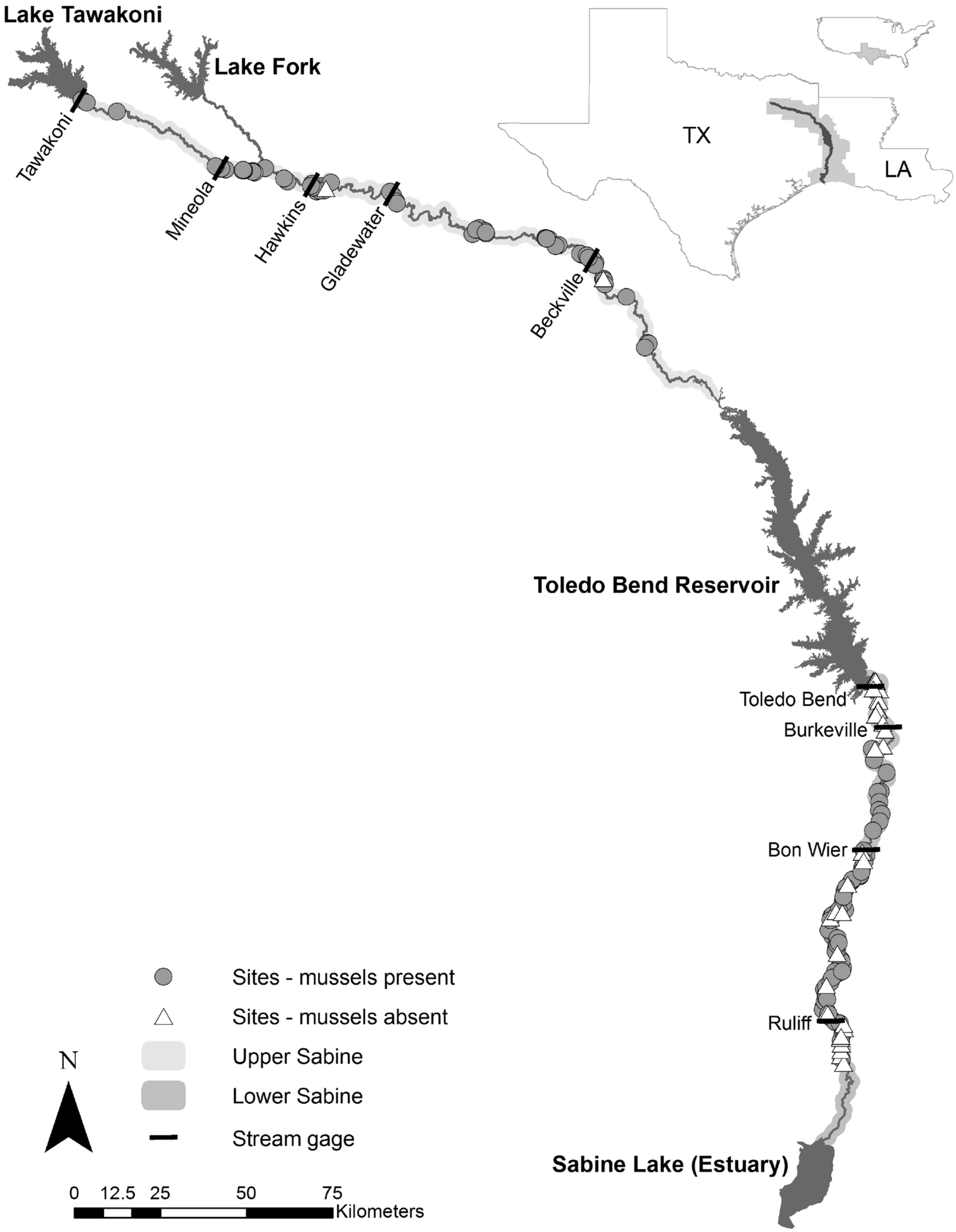


Fig. 2 Map of the Sabine River showing the study area, sampling locations, and USGS gaging stations

stream position and operational type; and (3) life history composition at any given point downstream of Lake Tawakoni or Toledo Bend Reservoir should be shaped by interactions between life history traits and the degree of flow alteration. As such, we expect opportunistic species will be proportionately more abundant in stream segments immediately downstream of Lake Tawakoni and Toledo Bend Reservoir where environmental variation is the greatest and habitat is frequently perturbed. By contrast, we predict equilibrium species will be proportionately most abundant in stream segments where dam-related impacts have been ameliorated and as a result habitat is less perturbed and therefore more stable. Periodic species should occupy reaches where dam-related impacts are present to the extent that they create environmental conditions that exclude equilibrium species, but are not so frequent or severe that they are unable to persist. In addition to advancing knowledge of how aquatic communities respond to impoundment of rivers the results from this study may help managers and conservationists predict the response of mussel assemblages to new reservoir construction and retrofitted dams.

Methods

Study area

The study was conducted on two reaches of the Sabine River in east Texas, U.S.A. (Fig. 2). The Sabine River has a total drainage area of 25,267 km^2, of which 18,591 km^2 (74%) is upstream from Toledo Bend Dam, and the remaining 6676 km^2 (26%) encompasses the area downstream from the reservoir to the Sabine Lake estuary (Fig. 2). In the upper reach, the Sabine River flows through the bottomlands of east central Texas and the south central plains ecoregions. In the lower reach, the Sabine River flows through the east central Texas and gulf coastal plains ecoregions. The study area has a humid subtropical climate and annual rainfall often exceeds 1000 mm per year, but drought often occurs in the late summer and fall. Land use within both reaches consists of commercial pine plantations, agriculture, oil production, and grazing lands (Federal Energy Regulatory Commission [FERC], 2013).

The mainstem of the Sabine River is influenced by two impoundments. Lake Tawakoni, located near the headwaters of the Sabine River in Hunt, Kaufman and Rains counties, was completed in 1960 to provide water for municipal and industrial purposes and covers an area of 153 km^2 (Sabine River Authority [SRA], 2014). The second is Toledo Bend Reservoir, which was completed in 1967 for the purpose of hydroelectric power generation and is located in Newton, Sabine and Shelby counties. The reservoir has a surface area of 735 km^2 and a capacity of 5.5×10^9 m^3 at normal water levels, making it the largest man-made body of water in the southern United States and the fifth largest in the United States (SRA, 2014).

Discharge in the Sabine River varies with stream flows being much lower downstream of Lake Tawakoni (median discharge is 13.6 m^3/s; USGS gaging station 08018500, Sabine River near Mineola, Texas) than those downstream of the Toledo Bend Reservoir (median discharge is 102.2 m^3/s; USGS gaging station 08028500, Sabine River near Bon Wier, Texas). Releases from Lake Tawakoni are not managed except for conservation and flood releases, and thus, the median monthly discharge is generally the same between pre- and post-impoundment periods, although large floods have been attenuated (Fig. 3). Water temperatures and dissolved oxygen are likely unaffected by Lake Tawakoni since discharge during non-flood events occurs via two 0.51 m-diameter pipes located midway up the dam at conservation pool elevation (SRA, 2014). By contrast, stream flows downstream of Toledo Bend Dam are managed and the effects of hydropower generation can be seen in gage data (Fig. 3) as far as 169 km from Toledo Bend Reservoir (USGS gaging station 08030500, Ruliff, Texas). Releases from Toledo Bend Reservoir have resulted in an altered flow regime where post-dam median monthly discharge during the winter and spring is lower than that during the pre-dam period, and stream flow during summer months is much higher than that during the pre-dam period. These changes are the effects of hydropower generation, as winter and spring rains are retained to maintain lake levels for power production during the summer months when demand for energy is at its highest (Fig. 3). Daily water levels also vary between the upper and lower Sabine, such that downstream of Lake Tawakoni, daily water levels are fairly consistent. By

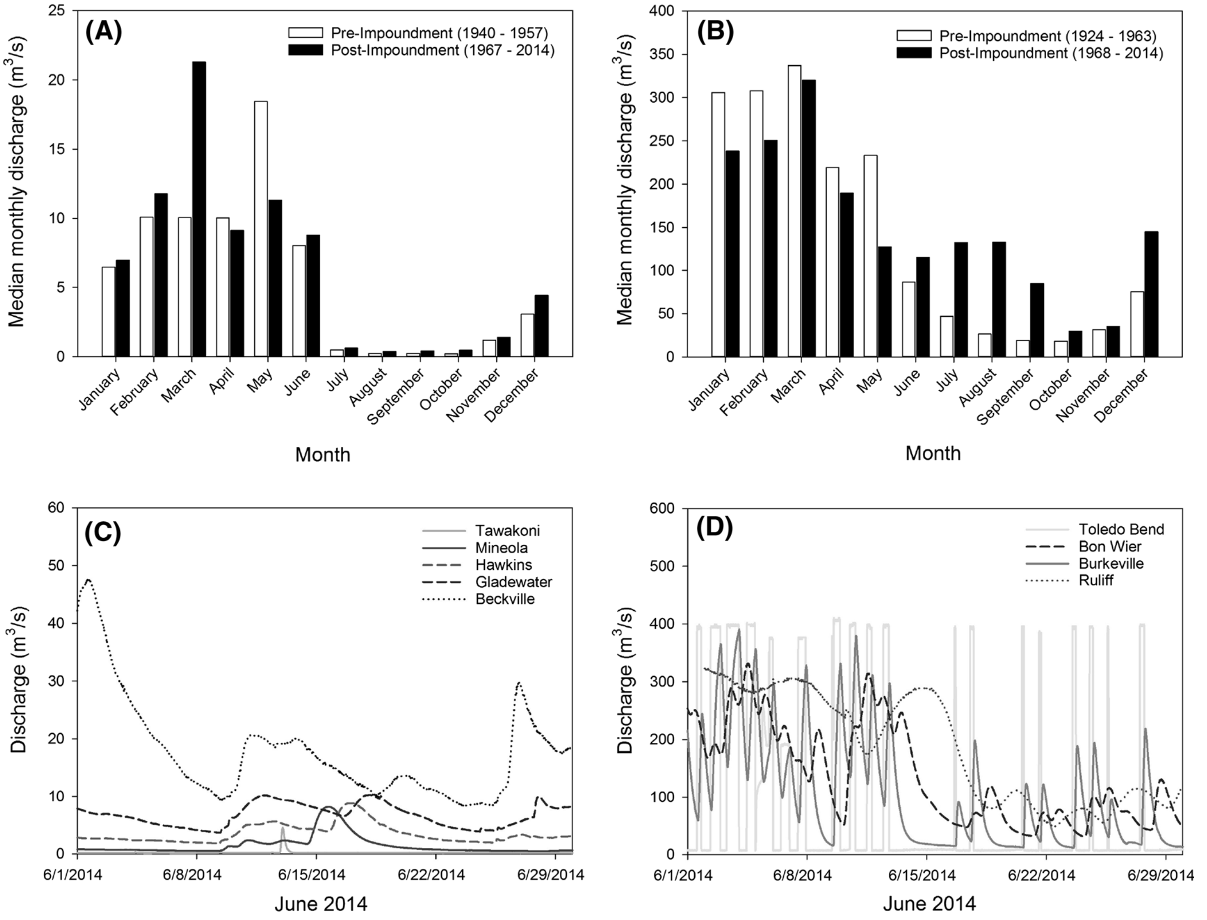


Fig. 3 A comparison of median monthly discharge for the pre- and post-impoundment periods on the (**A**) upper Sabine River downstream of Lake Tawakoni [USGS station name and number: Mineola, 08018500] and (**B**) lower Sabine River (*bottom*) downstream of Toledo Bend Reservoir [USGS station name and number: Bon Wier, 08028500]. A comparison of daily discharge at USGS gaging stations along the upper (**C**) and lower (**D**) Sabine River during June 2014; discharge data comes from the following USGS gages on the Sabine River: Wills Point (Tawakoni) 08017410; Mineola 08018500; Hawkins 08019200; Gladewater 08020000; Beckville 08022040; Toledo Bend 08025360; Burkeville 08026000; Bon Wier 08028500; and Ruliff 08030500. Figure 2 denotes the location of each gaging station in the upper and lower Sabine River

contrast, downstream of Toledo Bend Reservoir discontinuous water releases during periods of peak energy demand result in daily water-level fluctuations that often approach 3 m (USGS gaging station 08026000, Sabine River near Burkeville, Texas). Finally, water temperature in the spillway and in or near the tailrace range from 13 to 18°C and 20 to 33°C from May through September (when hydropower generation is occurring), respectively. Water temperatures do not approach ambient temperatures until flow reaches the USGS gaging station near Burkeville, Texas, located approximately 17 km from the reservoir, and it is unknown whether dissolved oxygen is impacted by flow releases from Toledo Bend Reservoir (FERC, 2013).

Mussel sampling

Upper Sabine River

The Sabine River between Lake Tawakoni and Toledo Bend Reservoir was sampled from April to October, 2005–2009 (Ford & Nicholson, 2006; Ford et al., 2009). River segments selected for sampling were chosen based on whether they could be reached from a public point of access. Each collection site was only sampled once and the area sampled varied from 50 to 200 m^2 and contained multiple geomorphic units (e.g., riffle, pool, run). Mussels were sampled using two to three person-hour tactile and visual searches in three or four sequential transects at each site. Deep-water habitats, those exceeding 2 m in depth were not sampled. Living and fresh-dead mussels, indicated by the presence of tissue, were identified to species, enumerated, and replaced, with the exception of voucher specimens.

Lower Sabine River

The Sabine River between Toledo Bend Reservoir and Orange, TX, was sampled from 2010 to 2013 (Randklev et al., 2011, 2014). Sites within the lower Sabine were selected either opportunistically (i.e., Randklev et al., 2011) or using a stratified random sampling design (i.e., Randklev et al., 2014; habitat and river left or right were the two strata). For both surveys, the following geomorphic units/cover types were sampled: banks, front-of-point bars, behind-point-bars, pools, backwaters, midchannel, and woody debris. Unlike the upper Sabine, sites were confined to the specific habitat type and the search area within each site was typically 50 m in length and did not exceed 15 m in width. Each site was surveyed tactilely and visually for a minimum of three person hours and SCUBA and snorkeling methods were used in areas deeper than 1 m. As with the upper Sabine River, each site was only sampled once and only mussels that were live or fresh-dead were collected and enumerated.

Biotic responses

The structure and composition of mussel assemblages downstream of Lake Tawakoni and Toledo Bend Reservoir were characterized based on mussel species richness, abundance, and life history strategy (Table 1). Mussel species richness was calculated as the total number of mussel species (live or fresh-dead) observed at a given site and abundance (catch-per-unit effort [CPUE]) was enumerated as the total number of individuals across all species collected per total amount of time spent searching a given site. Mussel life history strategies were evaluated according to the model of Haag (2012; which is adapted from Winemiller & Rose 1992 for fishes) that positions species along three primary life history axes defining the opportunistic, periodic, and equilibrium endpoints. For our analyses, mussel species were assigned to one of these three life history strategies based on general predictions by Haag (2012; Table 1). We then calculated the proportional composition of each strategy for each site by dividing the total number of individuals representing each strategy by the total number of individuals at that site.

Data analyses

Quantile regression was used to examine the relationship between mussel species richness, abundance, and life history strategy with respect to linear distance downstream from Lake Tawakoni and the Toledo Bend Reservoir. Quantile regression is a method used to investigate rates of change in all parts of the distribution of a response variable, which is particularly useful for ecological data where the mean response is likely to be unreliable due to heterogeneous distributions or unmeasured and unaccounted for factors (Koenker & Bassett, 1978). Unlike traditional least-square regression approaches, quantile regression is not sensitive to outliers, can be applied to non-normal datasets or those with heterogeneous variances, which is common in ecological studies (Cade & Noon, 2003; Hao & Naiman, 2007).

Relationships between distance downstream from Lake Tawakoni and Toledo Bend Reservoir and biological responses were modeled using the 90th, 85th, and 80th quantiles. These quantiles were chosen to ensure a more robust analysis and because they have been used in other ecological studies to evaluate limiting-factor relationships on a range of population and community characteristics for fishes and aquatic invertebrates (e.g., Konrad et al., 2008; Allen & Vaughn, 2010; Mims & Olden, 2012). Limiting-factor relationships are ecological constraints that limit the upper and lower bounds of a biological response such as richness or abundance. These factors are not always operative at all times or places, but when they are the biotic response cannot exceed the upper or lower limits for the constraining factor (Dunham et al., 2002; Konrad et al., 2008; Mims & Olden, 2012). In the present study, we fit individual univariate models from linear, asymptotic, polynomial, S-shaped, and Ricker functions (see Crawley, 2007, p. 662, Table 20.1). All functions were fitted to the data (with and without y-intercepts)

Table 1 Life history strategy for mussel species included in this study. Species are classified based on general predictions presented in Haag (2012)

Species	Common name	Location	Life history strategy
Amblema plicata	Threeridge	Upper/lower	Equilibrium
Arcidens confragosus	Rock pocketbook	Upper/lower	Opportunistic
Fusconaia askewi	Texas pigtoe	Upper/lower	Equilibrium
Glebula rotundata	Round pearlshell	Lower	Opportunistic
Lampsilis hydiana	Louisiana fatmucket	Upper/lower	Periodic
Lampsilis satura	Sandbank pocketbook	Upper/lower	Periodic
Lampsilis teres	Yellow sandshell	Upper/lower	Opportunistic
Leptodea fragilis	Fragile papershell	Upper/lower	Opportunistic
Megalonaias nervosa	Washboard	Upper	Equilibrium
Obliquaria reflexa	Threehorn wartyback	Upper/lower	Periodic
Plectomerus dombeyanus	Bankclimber	Upper/lower	Equilibrium
Potamilus amphichaenus	Texas heelsplitter	Upper	Opportunistic
Potamilus purpuratus	Bleufer	Upper/lower	Opportunistic
Pyganodon grandis	Giant floater	Upper/lower	Opportunistic
Quadrula apiculata	Southern mapleleaf	Upper/lower	Equilibrium
Quadrula mortoni	Western pimpleback	Upper/lower	Equilibrium
Quadrula nobilis	Gulf mapleleaf	Lower	Equilibrium
Quadrula verrucosa	Pistolgrip	Upper/lower	Equilibrium
Toxolasma parvus	Lilliput	Lower	Opportunistic
Toxolasma texasiensis	Texas lilliput	Lower	Periodic
Truncilla truncata	Deertoe	Upper	Opportunistic
Utterbackia imbecillis	Paper pondshell	Lower	Opportunistic
Villosa lienosa	Little spectaclecase	Lower	Opportunistic

Assignment of species not included in Haag (2012) are based on life span, age at maturity, fecundity, maximum adult size, brooding strategy, and growth rate, from multiple sources including Howells et al. (1996), Parmalee & Bogan (1998), Williams et al. (2008) and Williams et al. (2014)

and we chose the best-fitting model based on the Akaike information criterion (AIC), provided it gave non 0 parameter estimates for the model coefficients. We calculated AIC as equal to n x ln (deviance of the model of interest/n) + 2 *K*, where n is the total sample size, and *K* is the number of estimated variables + 2 (intercept and residual variance) (Vaz et al., 2008). In addition to the AIC, we calculated a pseudo-R^2 for each model, which provided an additional line of evidence for how well a particular function fit the data. Pseudo-R^2 was calculated as 1 – $(1 - R)^2$, where R is 1 – (deviance of the model of interest divided by the deviance of the intercept-only model) (Allen & Vaughn, 2010). Finally, because the range of extreme quantiles is dependent on sample size, we used the following guidelines proposed by Rogers (1992) to ensure reliable estimates of the 90th, 85th, and 80th quantiles: $n > 5/q$ and $n > 5/(1 - q)$, where q is the quantile proposed. Quantile regression analyses were performed using the QUANTREG package in R version 3.02 (R Core Development Team, 2011).

Results

Upper Sabine River

For the upper Sabine River, quantile regression analyses between mussel species richness, abundance, and life history strategy and distance downstream from Lake Tawakoni exhibited limiting-factor relationships for at least one of the 90th, 85th, and 80th quantiles. The response curves for all three biotic responses, regardless of the quantile, were best described by polynomial functions with slopes that were initially positive, but then become negative with distance from Lake Tawakoni (Table 2; Fig. 4B; Fig. 5B, C). The only exceptions were species richness and the proportion of opportunistic strategists, where the slope was initially negative and then becomes positive with increased distance from Lake Tawakoni; although for species richness the slope becomes negative again with increased proximity towards Toledo Bend Reservoir (Fig. 4A; Fig. 5A). For mussel species richness and abundance, both peak in stream segments located

Table 2 Relationships between mussel species richness, abundance, and proportional life history strategies with distance downstream from Lake Tawakoni and Toledo Bend Reservoir for the upper ($n = 72$ sites) and lower ($n = 110$) Sabine River

Variable	Location	Equation by Quantile	Quantile	*p* value for slope	SE for slope	*Pseudo-R*^{2}
Richness	Upper	=7.69 − 5.04e−2(Distance) + 2.89e−2(Distance)^2 − 1.27e−2(Distance)^3	0.90	<0.001/<0.001/<0.001/<0.001	2.15/0.02/2.56e−3/6.50e−4	0.56
Richness	Upper	=7.66 − 4.84e−2(Distance) + 2.84e−2(Distance)^2 − 1.26e−2(Distance)^3	0.85	<0.001/<0.001/<0.001/<0.001	1.59/0.02/2.76e−3/7.20e−4	0.54
Richness	Upper	=7.73 − 5.25e−2(Distance) + 2.88e−2(Distance)^2 − 1.26e−2(Distance)^3	0.80	<0.001/<0.001/<0.001/<0.001	1.85/0.02/3.13e−3/7.80e−4	0.49
Richness	Lower	=0.18(Distance) − 6.20e−4(Distance)^2	0.90	<0.001/<0.001	0.03/1.80e−4	0.36
Richness	Lower	=0.17(Distance) − 6.30e−4(Distance)^2	0.85	<0.001/<0.001	0.03/1.70e−4	0.36
Richness	Lower	=0.17(Distance) − 6.10e−4(Distance)^2	0.80	<0.001/<0.001	0.03/2.20e−4	0.34
Abundance	Upper	=2.12(Distance) − 6.00e−3(Distance)^2	0.90	<0.001/<0.001	0.66/2.14e−3	0.15
Abundance	Upper	=1.37(Distance) − 3.83e−3(Distance)^2	0.85	<0.001/0.02	0.51/1.65e−3	0.09
Abundance	Upper	=1.10(Distance) − 3.09e−3(Distance)^2	0.80	<0.001/<0.001	0.33/1.15e−3	0.09
Abundance	Lower	=−0.21(Distance) + 0.13(Distance)^2 − 4.33e−2(Distance)^3	0.90	0.09/<0.001/<0.001	0.13/0.01/2.33e−3	0.41
Abundance	Lower	=−0.23(Distance) + 0.13(Distance)^2 − 4.12e−2(Distance)^3	0.85	0.07/<0.001/<0.001	0.13/0.01/3.18e−3	0.39
Abundance	Lower	NS	0.80	NS	NS	NS
Opportunistic	Upper	NS	0.90	NS	NS	NS
Opportunistic	Upper	NS	0.85	NS	NS	NS
Opportunistic	Upper	=1.00 − 2.66e−3(Distance) + 7.59e−6(Distance)^2	0.80	<0.001/0.03/0.06	0.29/1.00e−3/1.00e−5	0.09
Opportunistic	Lower	=1.71e−2(Distance) − 7.00e−5(Distance)^2	0.90	<0.001/<0.001	2.33e−3/2.00e−5	0.42
Opportunistic	Lower	=1.60e−2(Distance) − 7.00e−5(Distance)^2	0.85	<0.001/<0.001	2.66e−3/2.00e−5	0.42
Opportunistic	Lower	=1.44e−2(Distance) − 7.00e−5(Distance)^2	0.80	<0.001/<0.001	2.42e−3/2.00e−5	0.41
Periodic	Upper	=1.50e−3(Distance) − 3.36e−6(Distance)^2	0.90	<0.001/0.02	4.20e−4/1.00e−5	0.16
Periodic	Upper	=1.43e−3(Distance) − 3.25e−6(Distance)^2	0.85	<0.001/0.02	4.00e−4/1.00e−5	0.13
Periodic	Upper	=1.06e−3(Distance) − 2.46e−6(Distance)^2	0.80	<0.001/0.08	4.00e−4/1.00e−5	0.11
Periodic	Lower	=2.72e−2(Distance)exp(−2.01e−2(Distance))	0.90	<0.001/<0.001	6.85e−3/2.97e−3	0.45
Periodic	Lower	=2.44e−2(Distance) exp(−2.03e−2(Distance))	0.85	<0.001/<0.001	7.56e−3/2.93e−3	0.43

Table 2 continued

Variable	Location	Equation by Quantile	Quantile	*p* value for slope	SE for slope	*Pseudo-R^2*
Periodic	Lower	=2.25e−2(Distance) exp(−2.11e−2(Distance))	0.80	<0.001/<0.001	8.66e−3/3.55e−3	0.42
Equilibrium	Upper	=0.71 + 1.30e−3(Distance) − 4.09e−6(Distance)^2	0.90	<0.001/<0.001/0.01	0.11/3.50e−4/1.00e−5	0.12
Equilibrium	Upper	=0.71 + 1.27e−3(Distance) − 4.13e−6(Distance)^2	0.85	<0.001/<0.001/0.03	0.16/3.50e−4/1.00e−5	0.12
Equilibrium	Upper	=0.60 + 2.68e−3(Distance) − 8.76e−6(Distance)^2	0.80	0.01/<0.001/<0.001	0.21/5.00e−4/1.00e−5	0.14
Equilibrium	Lower	=1.03e−2(Distance) − 3.00e−5(Distance)^2	0.90	<0.001/0.03	2.00e−3/2.00e−5	0.23
Equilibrium	Lower	=1.15e−2(Distance) − 5.00e−5(Distance)^2	0.85	<0.001/<0.001	2.00e−3/1.00e−5	0.28
Equilibrium	Lower	=1.17e−2(Distance) − 5.00e−5(Distance)^2	0.80	<0.001/<0.001	2.00e−3/1.00e−5	0.30

NS denotes non-significant models, *SE* indicates ±1 standard error, and *p* values less than 0.10 are considered significant

at intermediate distances from Lake Tawakoni and Toledo Bend Reservoir and both showed limiting-factor relationships for the 90th, 85th, and 80th quantiles (Fig. 4A, B). Pseudo-R^2 values were highest for species richness, ranging from 0.56 to 0.49, depending on the quantile, whereas for abundance they were lower, ranging from 0.15 to 0.09 (Table 2). Proportional life history composition exhibited several, albeit weak, limiting-factor relationships that meet theoretical expectations. The proportion of opportunistic strategists was greatest in reaches located near Lake Tawakoni and Toledo Bend Reservoir, but decreased with distance from either reservoir (Fig. 5A). This association exhibited a limiting-factor relationship for only the 80th quantile (pseudo-$R^2 = 0.09$; Table 2). For periodic strategists, all three quantiles were significant (pseudo-R^2 ranged from 0.11 to 0.16, respectively; Table 2) and maximum limits on proportional abundance were lowest near Lake Tawakoni and Toledo Bend Reservoir, but increased with distance from either reservoir (Fig. 5B). For equilibrium strategists, there were significant limiting-factor relationships for all three quantiles (pseudo-R^2 ranged from 0.12 to 0.14, respectively; Table 2) and maximum limits on proportional abundance increased with distance from Lake Tawakoni and Toledo Bend Reservoir (Fig. 5C).

Lower Sabine River

For the lower Sabine River, quantile regression results between biotic responses and distance from Toledo Bend Reservoir revealed limiting-factor relationships that were highly significant. The threshold response between mussel species richness, abundance, and life history strategy were best described by polynomial or Ricker functions. Response curves for these functions were initially positive and then become negative with increased distance from Toledo Bend Reservoir (Table 2; Fig. 4C, D; Fig. 5D–F). Limiting-factor relationships for mussel species richness and abundance indicate that maximum limits on both were lowest at stream segments immediately downstream of Toledo Bend Reservoir and highest in the middle reaches of the lower Sabine (Fig. 4C, D). For mussel species richness, pseudo-R^2 values for 90th, 85th, and 80th quantiles were 0.36, 0.36, and 0.34, respectively. Models for mussel abundance explain slightly more variation (pseudo-R^2 values: 0.41–0.39) and only 90th

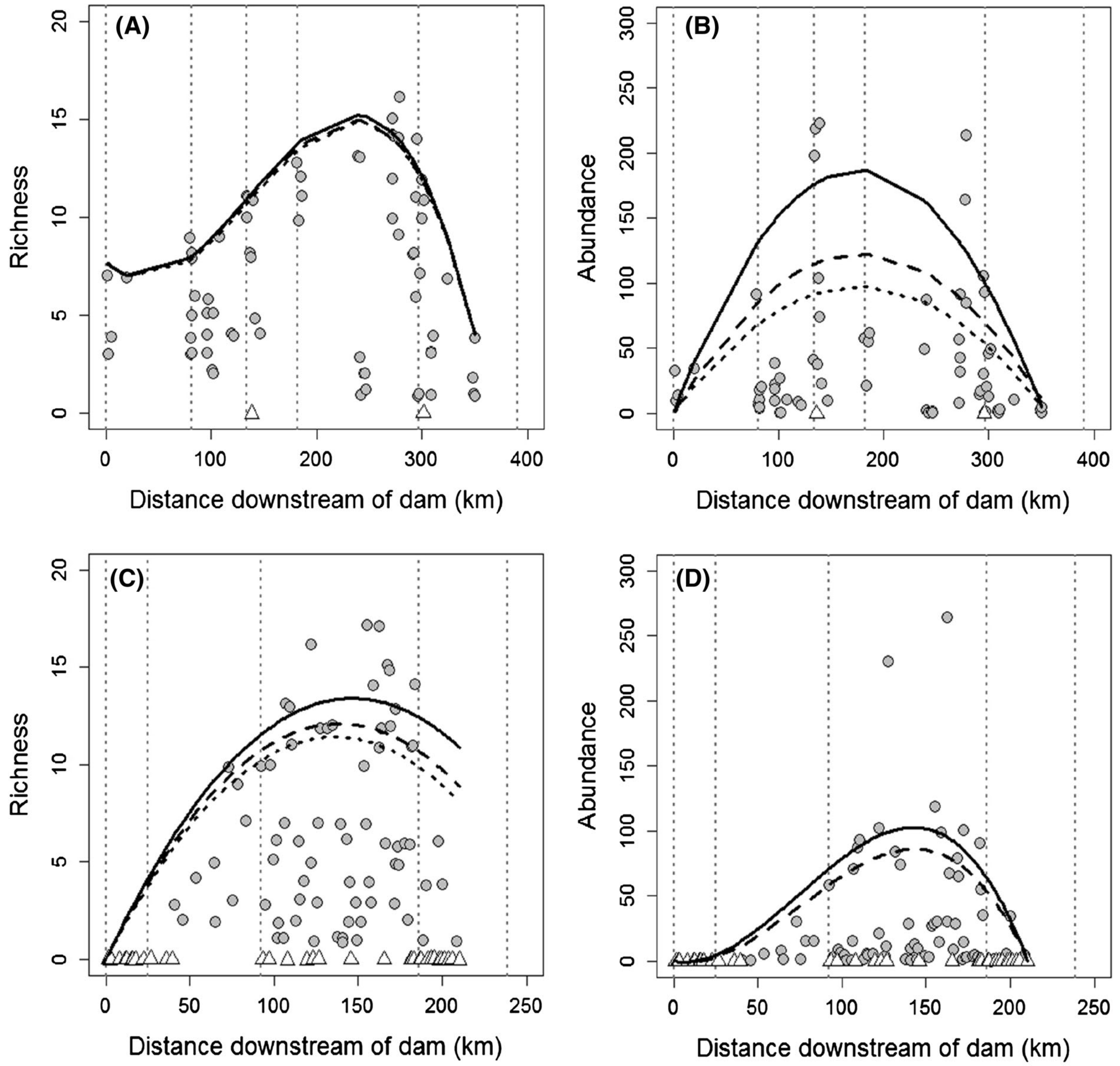


Fig. 4 Quantile regression results for relationships between distance downstream from Lake Tawakoni and Toledo Bend Reservoir and mussel species richness (**A**, **C**) and abundance (**B**, **D**) for the upper (*top*) and lower (*bottom*) Sabine River. *Solid, dashed*, and *dotted lines* represent the 90th, 85th, and 80th, quantile regression lines, respectively. *Vertical dashed lines* correspond to USGS gages or major water bodies in the upper (Wills Point 08017410; Mineola 08018500; Hawkins 08019200; Gladewater 08020000; Beckville 08022040; and confluence with Toledo Bend Reservoir) and lower (Toledo Bend 08025360; Burkeville 08026000; Bon Wier 08028500; Ruliff 08030500; and Sabine Lake) Sabine River

and 85th quantiles were significant (Table 2). For life history strategy, the shape of the response curves was generally the same for all three strategies such that maximum limits on proportional abundance increased with distance from Toledo Bend Reservoir and then decreased as the lower portion of the study area is approached (Fig. 5D, E, F). However, for periodic strategists the initial increase in the maximum limit for proportional abundance was more abrupt and occurred closer, in terms of stream position, to Toledo Bend Reservoir compared to the other two life history strategies (Fig. 5E). Models for all three life history

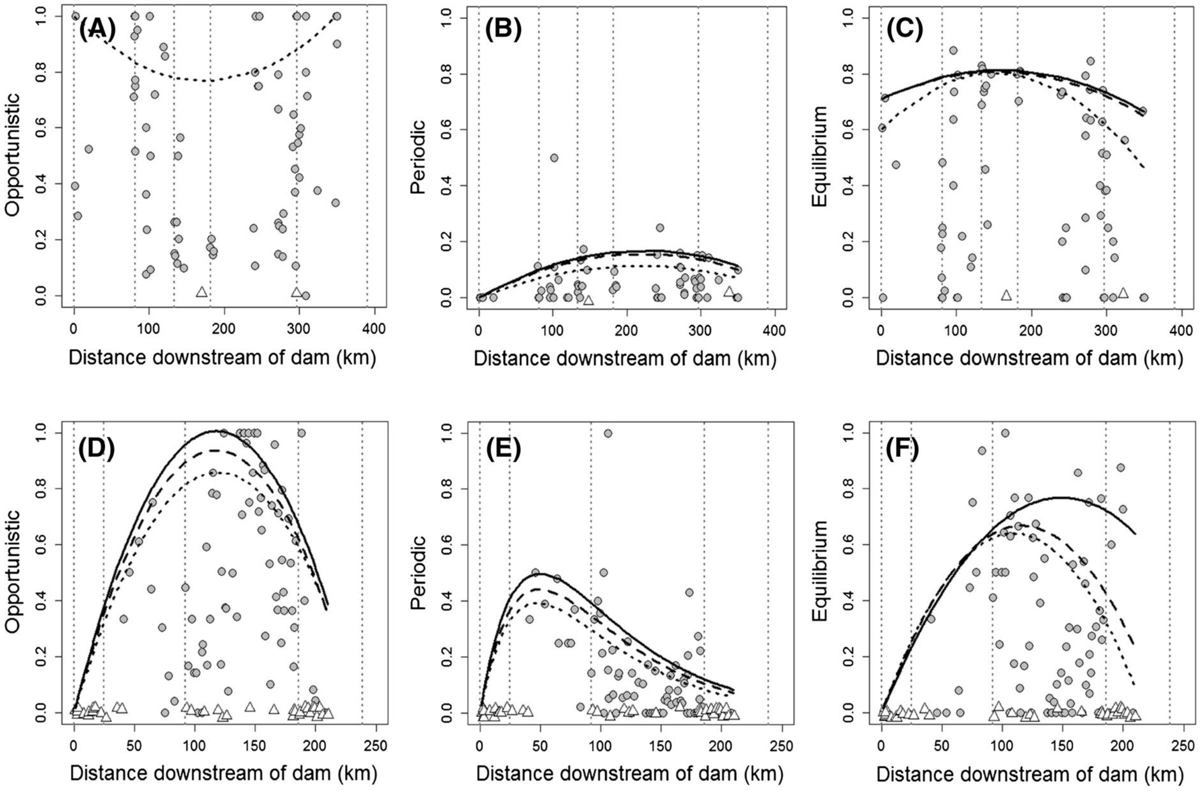


Fig. 5 Quantile regression results for relationships between distance downstream from Lake Tawakoni and Toledo Bend Reservoir and proportional life history composition (opportunistic: **A**, **D**; periodic: **B**, **E**; equilibrium: **C**, **F**) for the upper (*top*) and lower (*bottom*) Sabine River. Solid, dashed, and dotted lines represent the 90th, 85th, and 80th, quantile regression lines, respectively. Vertical dashed lines correspond to USGS gages or major water bodies in the upper (Wills Point 08017410; Mineola 08018500; Hawkins 08019200; Gladewater 08020000; Beckville 08022040; and confluence with Toledo Bend Reservoir) and lower (Toledo Bend 08025360; Burkeville 08026000; Bon Wier 08028500; Ruliff 08030500; and Sabine Lake) Sabine River

strategies showed significant relationships for the 90th, 85th, and 80th quantiles and pseudo-R^2 values ranged from 0.45 to 0.23 depending on the strategy (Table 2).

Discussion

Ward & Stanford (1983) predicted that biotic diversity should be reduced immediately downstream of impoundments and the magnitude of those reductions should be greatest for reservoirs located in middle reaches along the river continuum. Although the effect size of some of the relationships we observed is weak (particularly those related to distribution of life history types in the upper Sabine River), in general our results match Ward & Stanford's (1983) expectation. We observed that mussel species richness and abundance (for which effect sizes are stronger) are most limited for stream segments located in close proximity to Lake Tawakoni and Toledo Bend Reservoir and these declines decreased with increased distance from either reservoir. We also found that when comparing the two reservoirs, reductions in richness and abundance were most severe for Toledo Bend Reservoir and recovery more protracted (i.e., larger discontinuity) compared to Lake Tawakoni. These observations also generally meet theoretical expectations predicted by the SDC, but may be explained by varying characteristics of each reservoir.

It is important to note the patterns we observed in this study could be an artifact of differences in sampling methodologies between the upper and lower Sabine. For the upper Sabine River, each site contained multiple geomorphic units/cover types and the search area, on average, was larger. In contrast, the same habitats were sampled in the lower Sabine River, but the search area at each site was confined to a specific habitat type. Since effort, (i.e., total amount of time spent searching for mussels within a given site) was generally the same between the upper and lower Sabine (~2 to 3 person hours) combined with the large number of sites surveyed in each river (upper Sabine River, $n = 72$; lower Sabine River, $n = 110$), we feel it is doubtful that lumping or splitting geomorphic units/cover types is driving our results. Another potential bias is that deeper waters in the upper Sabine River were searched less rigorously than shallow areas because SCUBA or surface supplied air were not used during those surveys, which may have had consequences for mussel detection and therefore biased our results. This limitation is likely not a problem because the upper Sabine River is generally wadeable throughout most of its length, particularly in the upper and middle portions of the river where most of our surveys occurred. Although we cannot completely rule out these potential biases, to include not accounting for imperfect detectability (see Huang et al., 2011; Wisniewski et al., 2013), the fact that the functional response (i.e., reduction in mussel species richness and abundance and change in proportional life history) and the magnitude of change between the two rivers generally followed theoretical expectations demonstrates that dam-induced impacts, not sampling bias, are most likely responsible for the patterns we observed in this study.

Generally, dam size, storage volume, and operation type are important factors mediating a dam's ecological impact (Poff & Hart, 2002). In our study, the two reservoirs examined not only differed in operation type (flood control vs. hydropower generation) but also in size (Toledo Bend Reservoir is nearly five times as large as Lake Tawakoni) as well as flow releases. For the latter, impoundment releases from Toledo Bend Reservoir range from 4 m^3/s (low flow) to either 198 m^3/s or 396 m^3/s (high flow) on a daily basis to meet peak electrical demand (FERC, 2013). By contrast, flows from Lake Tawakoni are not managed, except during conservation releases (0.2 m^3/s; Sabine-Neches Basin and Bay Expert Science Team [Sabine-Neches BBEST], 2009) and floodwater releases (up to 1415 m^3/s; Dowell & Breeding, 1967). The data presented here indicate that both factors (location and operational type) are influencing mussel species richness and abundance, although it is likely that operational type is playing a much greater role given the magnitude of change in mussel assemblage structure downstream of Toledo Bend Reservoir compared to Lake Tawakoni. This is not entirely unexpected as hydropower operations usually have a greater impact on flow, temperature, and sediment regimes compared to water supply reservoirs (Poff & Hart, 2002); which Ward & Stanford (1983) noted in their original publication of the SDC. However, for water supply reservoirs where environmental flows are lacking changes to the flow regime during periods of low rainfall can be as dramatic and detrimental to mussels as those observed downstream of hydropower reservoirs (Randklev et al., 2013; Vaughn et al., 2015).

In addition to declines in richness and abundance immediately downstream of Lake Tawakoni and Toledo Bend Reservoir, we also observed reductions for both responses in the lower reaches of the upper and lower Sabine. In general, the effects of dams are thought to extend in up-and-downstream directions until new equilibria are reached. Attenuation of dam-induced impacts may be interrupted in systems where there are multiple dams such that upstream–downstream impacts interact and overlap—essentially segmenting what was previously one system into multiple smaller river continua (Haag, 2012; Skalak et al., 2013). For the upper Sabine River, it is plausible that reductions in mussel diversity and shifts in assemblage structure near Lake Tawakoni (i.e., downstream effects) and Toledo Bend Reservoir (i.e., upstream effects) are the consequences of multiple impoundments on the same river.

In the lower Sabine River, a similar pattern is observed, but likely relates to tidal influences from the Gulf of Mexico. In a geomorphological survey of the Sabine River, Phillips (2008) reported strong tidal signals and coastal backwater effects ~50 rkm upstream from Sabine Lake and moderate influences up to ~90 rkm from the estuary. Within this tidally influenced zone, we observed shifts in life history strategy from equilibrium to opportunistic strategists. These shifts coincided with major changes in assemblage structure such that species like *Glebula rotundata* (Lamarck, 1819), round pearlshell, which is known to be tolerant of brackish conditions (Williams et al., 2008), were dominant. In general, salinity, even at low levels, has been shown to negatively impact unionid mussel reproduction, physiology, and survival (Blakeslee et al., 2013).

Although the SDC is informative for evaluating impacts to mussel richness and abundance and the response curves generally meet theoretical expectations, we did observe several subtle exceptions for the upper Sabine River that may relate to land use/land cover differences between the upper and lower Sabine. Specifically, limiting-factor relationships between mussel abundance and stream position were weak (pseudo-R^2 ranged from 0.09 to 0.15) compared to models for the lower Sabine River (pseudo-R^2 ranged from 0.39 to 0.41). This may be explained, in part, by the fact that the shape of the response distribution (i.e., abundance) appears to be multimodal, indicating that other factors could also be constraining abundance. For reaches located approximately 130 and 275 rkm downstream from Lake Tawakoni there were two prominent modes. The first (~130 rkm) likely represents recovery from Lake Tawakoni, while the second (~275 rkm) may represent recovery from impacts associated from urbanization and mining activities. Longview, Texas, located between rkms 130 and 275 is the largest city in the Sabine River basin, with a population over 80,000 and within the same area are a number of oil and gas fields, near-surface mines for lignite, and industrial mines for construction materials (FERC, 2013). Generally, urban centers and mining activities can directly and indirectly impact mussels by eliminating habitat or fish hosts (Brim & Mossa, 1999; Lyons et al., 2007). For the lower Sabine River, the response distribution does not show a multimodal pattern, which we interpret as further evidence that Toledo Bend Reservoir is the primary, large-scale, factor impacting downstream mussel communities and as such the single mode observed at ~150 rkm likely represents recovery from dam-induced impacts.

Since impoundments are predicted to reset physical and biological conditions (Ward & Stanford, 1983) that can influence mussel habitat then the LHCM provides a means for interpreting changes in assemblage structure in response to river impoundment. In our study, opportunistic strategists were proportionately more abundant in reaches where adverse effects of dams (or tidal influences) are prominent. For the upper Sabine River, this pattern is subtle, as indicated by the low pseudo-R^2 value, but the shape of the response curve does meet theoretical expectations set forth by the LHCM. Reaches immediately downstream of Toledo Bend Reservoir are an exception as mussels (even opportunists) are generally absent (Randklev et al., 2011). In general, opportunistic strategists are characterized by rapid growth, early maturity, short life span, and high reproductive output. These traits allow rapid colonization and persistence in unpredictable environmental settings dominated by density-independent, ecological influences (Winemiller, 2005; Haag, 2012). Thus, the absence of opportunists in reaches immediately downstream of Toledo Bend Reservoir is informative because it indicates that even with traits that lead to a large intrinsic rate of population increase, dam-induced impacts are so extreme that mussels utilizing this strategy are unable to maintain large enough populations to guarantee some level of reproductive success to offset continuous and high mortality during the adult stage. For the upper Sabine River, opportunistic species that characterize sites near Lake Tawakoni include *Potamilus purpuratus* (Lamarck, 1819), bleufer, and *Pyganodon grandis* (Say, 1829), giant floater (Ford & Nicholson, 2006; Ford et al., 2009), which are considered lentic species and are host generalists or use reservoir-adapted host fishes (Haag, 2012). For the lower Sabine River, *Lampsilis teres* (Rafinesque, 1820), yellow sandshell, and *Leptodea fragilis* (Rafinesque, 1820), fragile papershell (Randklev et al., 2011, 2014) are the dominant species at sites in close proximity to Toledo Bend Reservoir. These species are lentic microhabitat specialists and use host fishes that are tolerant of disturbed habitats (Haag, 2012).

Equilibrium strategists are characterized as having slow growth, late maturity, long life span, and typically low fecundity. These traits are favored in stable, predictable environments, with density-dependent or resource limited influences (Winemiller & Rose, 1992; Winemiller, 2005; Haag, 2012). We found that the proportion of equilibrium strategists increases with distance from both dams, and tidal influences in the lower Sabine River. Shifts in life history strategy from opportunistic to equilibrium likely coincide with longitudinal attenuation of dam-induced impacts as predicted by the SDC. Equilibrium species that characterize the middle reaches of the upper Sabine River, where dam-related impacts are likely ameliorated, include *Fusconaia askewi* (Marsh, 1896), Texas pigtoe, and *Quadrula verrucosa* (Rafinesque, 1820), pistolgrip (Ford & Nicholson, 2006; Ford et al., 2009). These species typically occur in main-channel habitats and likely use minnows, *Cyprinidae*, and catfish, *Ictaluridae* as hosts, respectively (Williams et al., 2008; Haag, 2012). Species tending toward the equilibrium strategy in the lower Sabine River are rare, which underscores our point regarding the severity of dam-induced impacts from Toledo Bend Reservoir, but include *Plectomerus dombeyanus* (Valenciennes, 1827), bankclimber, and *Quadrula mortoni* (Conrad, 1835), western pimpleback (Randklev et al., 2011, 2014). These species are considered lentic microhabitat specialists and they utilize host species that are tolerant of disturbed habitats (Howells et al., 1996; Randklev et al., 2014; B. Bosman, pers. comm.).

Periodic strategists are characterized by small to moderate body size, moderate to high growth rate, low to intermediate life span, age at maturity, and fecundity (Haag, 2012). They are often found in disturbed habitats that are more stable and predictable than those occupied by opportunistic strategists or that are subject to cyclical environmental variation or stress (Haag, 2012). This strategy is characterized as a form of bet-hedging, whereby reproductive effort is either spread across multiple years or is synchronized to coincide with specific interannual time periods or habitats that favor growth and survival of juveniles (Winemiller & Rose, 1992; Winemiller, 2005; Haag, 2012). For the upper Sabine, periodic strategists are proportionately abundant in stream reaches located at intermediate distances from Lake Tawakoni (though statistically weak in terms of effect size), which meets theoretical expectations as periodic strategists typically occupy an intermediate position along a gradient of disturbance (Winemiller & Rose, 1992; Winemiller, 2005; Haag, 2012). For the lower Sabine, a similar pattern is observed and may be explained by the timing of hydropower generation and brooding strategy of periodic strategists. In general, peaking flows from Toledo Bend Reservoir occur from June to October and during this time hydropower generation typically occurs 5–6 days a week, and discharge varies from 4 m^3/s to either 198 m^3/s or 396 m^3/s daily (FERC, 2013). Periodic strategists typically spawn in the spring and then brood mature larvae over winter, or the larvae remain attached to the host over winter, and then transform to juveniles the following spring (Barnhart et al., 2008). Thus, this strategy may allow periodic mussel species to not only sidestep peaking flows during reproduction but also provide more time for juvenile growth. Finally, many periodic strategists use lures to facilitate mussel-host contact, which is important when mussel densities are low and encounters are infrequent (Haag & Warren, 1998). The decline in periodic strategists with increased distance from Toledo Bend Reservoir is likely the result of density-dependent interactions, which periodic strategists are likely ill-equipped to handle based on their life history traits (Winemiller & Rose, 1992; Winemiller, 2005; Haag, 2012). Periodic species that are characteristic of the upper Sabine River include *Lampsilis satura* (I. Lea, 1852), sandbank pocketbook, and *Obliquaria reflexa* (Rafinesque, 1820), threehorn wartyback (Ford & Nicholson, 2006; Ford et al., 2009). These species typically occur in main-channel or lentic habitats and likely utilize host species tolerant of disturbed habitats (Haag, 2012; Randklev et al., 2014). For the lower Sabine River, *Lampsilis hydiana* (I. Lea, 1838), Louisiana fatmucket, and *L. satura* characterize periodic strategists found in reaches near Toledo Bend Reservoir and in the brackish zone (Randklev et al., 2011, 2014). These species occur primarily in lentic habitats and likely use centrarchids for hosts (Howells et al., 1996; Haag, 2012; Randklev et al., 2014).

In conclusion, we found that expectations concerning habitat gradients related to proximity to dams from the SDC and life history characteristics of unionids framed under the LHCM were useful for evaluating mussel response to river impoundment. Specifically, we found that location of the dam along the stream profile and operational type were important for explaining reductions in diversity and shifts in life history composition of mussel assemblages. These changes, in turn, likely have long-term negative ecological consequences due to losses in mussel-provided ecosystem services (Vaughn et al., 2015). Our results demonstrate that linking predictions by the SDC and LHCM provides a means to connect changes in assemblage structure (i.e., LHCM) with dam-induced environmental gradients (SDC). For regions like Texas, where water resources at times are limited and where human demands for water are growing, it is important to recognize the value of environmental flows for sustaining ecosystems and the impacts impoundments pose to those systems.

Acknowledgments We thank Mark Cordova, Joe Skorupski, Ben Lundeen, Eric Tsakiris, Melissa Broderick, Ashley Walters, and Bryan Sowards for their assistance in the field. We gratefully acknowledge Ben Bosman and Wendell Haag for valuable comments on earlier drafts of this manuscript. Funding for this project was provided in part by the Texas Parks and Wildlife Department, the United States Fish and Wildlife Service, and the Sabine River Authority.

References

Allen, D. C. & C. C. Vaughn, 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. Journal of the North American Benthological Society 29: 383–394.

Atkinson, C. L. & C. C. Vaughn, 2015. Biogeochemical hotspots: temporal and spatial scaling of the impact of freshwater mussels on ecosystem function. Freshwater Biology 60: 563–574.

Barnhart, C. M., W. R. Haag & W. N. Roston, 2008. Adaptations to host infection and larval parasitism in Unionoida. Journal of North American Benthological Soceity 27: 370–394.

Baxter, R. M., 1977. Environmental effects of dams and impoundments. Annual Review of Ecological Systematics 8: 225–283.

Blakeslee, C. J., H. S. Galbraith, L. S. Robertson & J. White, 2013. The effects of salinity exposure on multiple life stages of a common freshwater mussel, *Elliptio complanata*. Environmental Toxicology and Chemistry 32: 2849–2854.

Brim, B. J. & J. Mossa, 1999. Sediment, land use, and freshwater mussels: prospects and problems. Journal of the North American Benthological Society 18: 99–117.

Burlakova, L. E., A. Y. Karatayev, V. A. Karatayev, M. E. May, D. L. Bennett & M. J. Cook, 2011. Biogeography and conservation of freshwater mussels (Bivalvia: Unionidae) in Texas: patterns of diversity and threats. Diversity and Distributions 17: 393–407.

Bunn, S. E. & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Cade, B. S. & B. R. Noon, 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and the Environment 1: 412–420.

Crawley, M. J., 2007. The R Book. John Wiley & Sons Limited, West Sussex.

Dowell, C. L. & S. D. Breeding, 1967. Dams and Reservoirs in Texas: Historical and Descriptive Information. Texas Water Development Board Report No. 48: 274 pp.

Dunham, J. B., B. S. Clad & J. W. Terrell, 2002. Influences of spatial and temporal variation on fish-habitat relationships defined by regression quantiles. Transactions of the American Fisheries Society 131: 86–98.

Ellis, L. C. & N. E. Jones, 2013. Longitudinal trends in regulated rivers: a review and synthesis within the context of the serial discontinuity concept. Environmental Reviews 21: 136–148.

Federal Energy Regulatory Commission (FERC), 2013. Final environmental impact statement for hydropower license. Toledo Bend Hydroelectric Project No. 2305-036, 304 pp.

Ford, N. B. & M. L. Nicholson, 2006. A survey of freshwater mussels (Unionidae) of the Old Sabine Wildlife Management Area, Smith County, Texas. Texas Journal of Science 58: 243–254.

Ford, N. B., J. Gullett & M. E. May, 2009. Diversity and abundance of unionid mussels in three sanctuaries on the Sabine River in northeast Texas. Texas Journal of Science 61: 279–294.

Graf, W. L., 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research 35: 1305–1311.

Haag, W. R., 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge.

Haag, W. R. & M. L. Warren, 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. Canadian Journal of Fisheries and Aquatic Sciences 55: 297–306.

Hao, L. & D. Q. Naiman, 2007. Quantile Regression. Sage Publications, Thousand Oaks.

Howells, R. G., R. W. Neck & H. D. Murray, 1996. Freshwater Mussels of Texas. Texas Parks and Wildlife Press, Austin.

Howells, R. G., C. M. Mather & J. A. M. Bergmann, 2000. Impacts of dewatering and cold on freshwater mussels (Unionidae) in B.A. Steinhagen Reservoir. Texas. The Texas Journal of Science 52: 93–104.

Huang, J., Y. Cao & K. S. Cummings, 2011. Assessing sampling adequacy of mussel diversity surveys in wadeable Illinois streams. Journal of the North American Benthological Society 30: 932–934.

Humphries, P., H. Keckeis & B. Finlayson, 2014. The river wave concept: integrating river ecosystem models. BioScience 64: 870–882.

Karatayev, A. Y., T. D. Miller & L. E. Burlakova, 2012. Long-term changes in unionid assemblages in the Rio Grande, one of the World's top 10 rivers at risk. Aquatic Conservation: Marine and Freshwater Ecosystems 22: 206–219.

Koenker, R. & G. Bassett Jr, 1978. Regression quantiles. Econometrica 46: 33–50.

Konrad, C. P., M. D. Brasher & J. T. May, 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. Freshwater Biology 53: 1983–1998.

Layzer, J. B., M. E. Gordon & R. M. Anderson, 1993. Mussels: the forgotten fauna of regulated rivers. A case study of the Caney Fork River. Regulated Rivers: Research & Management 8: 63–71.

Lyons, M. S., R. A. Krebs, J. P. Holt, L. J. Rundo & W. Zawiski, 2007. Assessing causes of change in freshwater mussels (Bivalvia: Unionidae) in the Black River, Ohio. American Midland Naturalist 158: 1–15.

McAllister, D., J. Craig, N. Davidson, D. Murray & M. Seddon, 2001. Biodiversity impacts of large dams. Background Paper No. 1. In The International Union for Conservation of Nature, and United Nations Environmental Programme. Gland: 63 pp.

MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Monographs in Population Biology, Vol. 1. Princeton University Press, Princeton.

Magilligan, F. J. & K. H. Nislow, 2005. Changes in hydrologic regime by dams. Geomorphology 71: 61–78.

Mims, M. C. & J. D. Olden, 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 93: 35–45.

Neck, R. W., 1986. Freshwater bivalves of Lake Tawakoni, Sabine River, Texas. The Texas Journal of Science 38: 241–249.

Neck, R. W., 1990. Geologic substrate and human impact on bivalves of Lake Lewisville, Trinity River, Texas. The Nautilus 104: 16–25.

National Inventory of Dams (NID), 2014. U. S. Army Corps of Engineers National Inventory of Dams. http://geo.usace.army.mil/pgis/f?p=397:1:0::NO:::.

Parmalee, P. W. & A. E. Bogan, 1998. The Freshwater Mussels of Tennessee. The University of Tennessee Press, Knoxville.

Phillips, J. D., 2008. Geomorphic controls and transition zones in the lower Sabine River. Hydrological Processes 22: 2424–2437.

Pianka, E. R., 1970. On *r*- and *K*-selection. American Midland Naturalist 104: 592–597.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society 16: 391–409.

Poff, N. L. & D. D. Hart, 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52: 659–668.

Quinn, J. W. & T. J. Kwak, 2003. Fish assemblage changes in an Ozark River after impoundment: a long-term perspective. Transactions of the American Fisheries Society 132: 110–119.

R Core Development Team, 2011. R (version 2.11.2): A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Randklev, C. R., B. J. Lundeen, J. Skorupski, J. H. Kennedy & S. Wolverton, 2011. Toledo Bend relicensing project: Lower Sabine River mussel study. Final report to Sabine River Authority: 19 pp.

Randklev, C. R., M. S. Johnson, E. T. Tsakiris, J. Groce & N. Wilkins, 2013. Status of the freshwater mussel (Family: Unionidae) fauna in the mainstem of the Leon River, Texas. Aquatic Conservation: Marine and Freshwater Ecosystems 23: 390–404.

Randklev, C. R., M. Cordova, J. Groce, E. Tsakiris & B. Sowards, 2014. Freshwater mussel survey (Family: Unionidae) of the lower Sabine River between U. S. Hwy 190 and Orange, Texas. Final report to Texas Parks and Wildlife :37 pp.

Rogers, W. H., 1992. Quantile regression standard errors. Stata Technical Bulletin 9: 16–19.

Rosenberg, D. M., P. McCully & C. M. Pringle, 2000. Globalscale environmental effects of hydrological alterations: introduction. Bioscience 50: 746–751.

Sabine-Neches Basin and Bay Expert Science Team (Sabine-Neches BBEST), 2009. Environmental flows recommendations report. Final report to Sabine and Neches Rivers and Sabine Lake Bay and Basin and Bay Area Stakeholder Committee, Environmental Flows Advisory Group, and Texas Commission on Environmental Quality, 1215 pp.

Sabine River Authority (SRA), 2014. Sabine River Authority Projects. www.sratx.org/projects/ibp.asp.

Skalak, K. J., A. J. Benthem, E. R. Schenk, C. R. Hupp, J. M. Galloway, R. A. Nustad & G. J. Wiche, 2013. Large dams and alluvial rivers in the Anthropocene: the impacts of the Garrison and Oahe Dams on the upper Missouri River. Anthropocene 2: 51–64.

Southwood, T. R. E., 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337–365.

Southwood, T. R. E., 1988. Tactics, strategies and templates. Oikos 52: 3–18.

Stearns, S. C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Strayer, D. L., 2014. Understanding how nutrient cycles and freshwater mussels (Unionoida) affect one another. Hydrobiologia 735: 277–292.

Suttkus, R. D. & M. F. Mettee, 2009. Post-impoundment changes in the Cyprinid fauna of the lower Sabine River, Louisiana and Texas. Southeastern Fishes Council Proceedings 51: 1–8.

Texas Parks and Wildlife Department (TPWD), 2010. Threatened and endangered nongame species. Texas Register 35: 249–251.

Texas Water Development Board (TWDB), 2012. State water plan. Texas Water Development Board, 314 pp. www.twdb.texas.gov/publications/state_water_plan/2012/2012_SWP.pdf.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: bio complexity in river networks across space and time. River and Research Applications 22: 123–147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Academic Press, London.

U. S. Fish and Wildlife Service (USFWS), 2001. Endangered and threatened wildlife and plants: Review of plant and animal species that are candidates or proposed for listing as endangered or threatened, annual notice of findings on recycled petitions, and annual description of progress on listing actions; proposed rule. Federal Register 66: 54808–54832.

U. S. Fish and Wildlife Service (USFWS), 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list Texas fatmucket, golden orb, smooth pimpleback, Texas pimpleback, and Texas fawnsfoot as threatened or endangered. Federal Register 76: 62166–62212.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Vaughn, C. C. & C. M. Taylor, 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conservation Biology 13: 912–920.

Vaughn, C. C. & C. C. Hakenkamp, 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biology 46: 1431–1446.

Vaughn, C. C. & D. E. Spooner, 2004. Status of the mussel fauna of the Poteau River and implications for commercial harvest. American Midland Naturalist 152: 336–346.

Vaughn, C. C. & D. E. Spooner, 2006. Unionid mussels influence macroinvertebrate assemblage structure in streams. Journal of the North American Benthological Society 25: 691–700.

Vaughn, C. C., S. J. Nichols & D. E. Spooner, 2008. Community and foodweb ecology of freshwater mussels. Journal of the North American Benthological Society 27: 409–423.

Vaughn, C. C., C. L. Atkinson & J. P. Julian, 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. Ecology and Evolution 5: 1291–1305.

Vaz, S., C. S. Martin, P. D. Eastwood, B. Ernande, A. Carpentier, G. J. Meaden & F. Coppin, 2008. Modelling species distributions using regression quantiles. Journal of Applied Ecology 45: 204–217.

Voelz, N. J. & J. V. Ward, 1990. Macroinvertebrate responses along a complex regulated stream environmental gradient. Regulated Rivers: Research & Management 5: 365–374.

Ward, J. V. & J. A. Stanford, 1983. The serial discontinuity concept of lotic ecosystems. In Fontaine, T. D. & S. M. Bartell (eds.), Dynamics of Lotic Ecosystems. Ann Arbor Science Publishers, Ann Arbor: 29–42.

White, D. S. & S. J. White, 1977. Observations on the pelecypods of Lake Texoma, Texas and Oklahoma, after more than thirty years of impoundment. The Southwestern Naturalist 22: 235–254.

Williams, J. D., S. L. H. Fuller & R. Grace, 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee Rivers in western Alabama. Bulletin of the Alabama Museum of Natural History 13: 1–10.

Williams, J. D., J. T. Garner & A. E. Bogan, 2008. Freshwater Mussels of Alabama and the Mobile Basin in Georgia. The University of Alabama Press, Tuscaloosa, Mississippi and Tennessee.

Williams, J. D., R. S. Butler, G. L. Warren & N. A. Johnson, 2014. Freshwater Mussels of Florida. The University of Alabama Press, Tuscaloosa.

Winemiller, K. O., 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 62: 872–885.

Winemiller, K. O. & K. A. Rose, 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Science 49: 2196–2218.

Wisniewski, J. M., N. M. Rankin, D. A. Weiler, B. A. Strickland & H. C. Chandler, 2013. Occupancy and detection of benthic macroinvertebrates in the lower Flint River, Georgia, USA. Freshwater Science 32: 1122–1135.