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Impact of Hydrologic Alteration on Brazos River Vertebrates

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Location(s):

Brazos River downstream from Possum Kingdom Lake.

Objective(s):

Conduct a comprehensive analysis of the flow regime and historical fish assemblages for the Brazos River system downstream from Possum Kingdom Lake to link patterns of fragmentation, flow behavior and biotic change to rates of population decline and extirpation for the endangered Brazos River minnows *Notropis buccula* (smalleye shiner) and *Notropis oxyrhynchus* (sharpnose shiner), and the state threatened *Nerodia harteri harteri* (Brazos water snake).

Significant Deviation(s):

N/A

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Executive Summary

The Brazos River downstream from Possum Kingdom Lake has been profoundly altered since the construction and operation of multiple impoundments. The resulting river regulation poses problems for organisms adapted to a natural flow regime and is thought to play a major role in the imperilment of the federally endangered smalleye Shiner (*Notropis buccula*) and sharpnose Shiner (*N. oxyrhynchus*), and the state threatened Brazos water snake (*Nerodia harteri harteri*). These two target fish species and five other minnows belong to the pelagic-broadcast spawning reproductive guild that synchronizes spawning during high flow pulses. These seven pelagophilic species appear to be variably affected by altered flows and all have exhibited declines through time, but not in the same time frame. To address the declines of these species, I constructed flow duration curves and used a range of variability approach to assess pre- and post-impoundment changes in flow regime from five localities across the entire lower Brazos River. Differences in flow duration curves and flow behavior were generally consistent with position in the drainage such that the greatest changes occurred in the highly fragmented upper reach of the study area. However, extensive hydrologic alteration was apparent at all five localities. None of the target species were collected or observed during sampling in 2017. The seven pelagophilic minnows exhibited a strong relationship between the year they were last documented in the lower river and their historical percent occurrence in the lower river. Thus, the extirpated pelagophils may have been more sensitive to altered flow regimes and accompanying geomorphic change, and/or were population sinks dependent on recolonization from upstream populations. Fish assemblages showed significant spatial and temporal differences with three generalist species accounting for approximately 50% of the overall assemblage change in space and time. The relationships between fish assemblage response

and natural flow regimes are complex, and non-flow variables such as population fragmentation, temperature, and geomorphology may be important when considering reasons for biodiversity loss. Likewise, the relationship between flows and population recruitment for the Brazos water snake are complicated, and a reduction of extreme high flow events has likely reduced flushing and scouring of the river channel, threatening habitat for neonates and juveniles. To manage flows to support species that require natural flow regimes, it will be necessary to not only better understand their reproductive life histories, but also the ecology and physiology of early life history stages.

Introduction

The Brazos River is the longest river in Texas and drains approximately 116,000 km^2 (Texas State Historical Association: Brazos River). This iconic Texas river also has the greatest discharge of any in the state and is one of the most impacted rivers in Texas (Anderson et al. 1983). Alterations to the natural flow regime are especially apparent in the highly regulated area between Possum Kingdom Lake and Lake Brazos (Texas Water Development Board: History of Reservoir Construction in Texas). Possum Kingdom Lake was the first water supply reservoir constructed on the Brazos River and was formed by the Morris Sheppard Dam in Palo Pinto County, which began impounding the river in 1941. A decade later (1951) and 142 river miles downstream, a flood control reservoir (Whitney Lake) was created by the construction of Whitney Dam in Hill and Bosque counties. Between Possum Kingdom and Whitney lakes, the De Cordova Bend Dam in Hood County was constructed (93 river miles above Whitney Dam) and began to impound water in 1969 resulting in Lake Granbury. Finally, in 1970 Lake Brazos Dam was built to form Lake Brazos in the city of Waco. The Lake Brazos Dam was replaced in

2005 after a drum gate malfunction.

These dams and impoundments, and others on tributary streams, have profoundly changed the Brazos River (defined hereafter as the river downstream of Possum Kingdom Lake) and its channel has been undergoing continual adjustment since the 1940s (Dunn and Raines 2001). These hydrologic and geomorphic changes have altered the native biota of the lower river and presumably led to the extirpation of four native minnows, two of which are endemic and federally endangered. Also accompanying these changes is a steep decline in the observed abundance of the endemic Brazos water snake (*Nerodia harteri harteri*), that historically occupied the highly regulated reach between Possum Kingdom Lake and Lake Granbury. The four reservoirs eliminate considerable riverine habitat and fragment the river, leading to problems for organisms that require long reaches of free-flowing habitat for successful population maintenance and recruitment.

This research emphasizes trends in the distribution and abundance of the federally endangered smalleye shiner (*Notropis buccula*) and sharpnose shiner (*N. oxyrhynchus*), and the state threatened Brazos water snake (*N. harteri harteri*). All three of these species have endured considerable declines in distribution and abundance since the largescale modification of natural flows began in the 1940s. Both shiner species are members of a pelagophilic reproductive guild of North American minnows that formerly inhabited much of the Great Plains. The group is of considerable conservation interest due to widespread imperilment associated with impoundments and altered hydrologic regimes. The Brazos water snake, while not completely confined to the aquatic environment, is endemic to the Brazos River watershed, including the upper reach of the study area to downstream near Glen Rose, TX (McBride 2009). The snake is patchily distributed along rocky shorelines of the river, and rocky banks of Possum Kingdom

Lake and Lake Granbury. Reasons for the Brazos water snake's decline in distribution and abundance are elusive, and its potential dependence on natural flows may be tied to the amount of rocky habitats available for juvenile recruitment (Scott et al. 1989). These essential habitats are associated with riffles, which are eliminated from large areas by impoundment. Based on much accumulated research, the pelagophilic minnows have life histories directly tied to the natural flow regime, whereas the Brazos water snake may be associated with natural flows to the extent that such flows provide and maintain habitat necessary for feeding and population recruitment.

An imperiled guild of fishes

The guild of pelagophilic minnows that is emblematic of the North American plains was historically ubiquitous and is phylogenetically diverse (Worthington et al. 2018). Because of their different evolutionary histories, members of the guild may differentially respond to variability in the natural flow regime. Likewise, their vulnerability to hydrologic alteration is certainly variable. Within the Brazos River, both target species are endangered, yet other members of the guild are not federally or state protected, despite geographic range contractions due to habitat fragmentation.

All members of this reproductive guild have life histories that are attuned to a natural flow regime (Poff et al. 1997), although nuanced differences in reproductive ecology likely interact with a modified flow regime to determine population vulnerability. Detailed life history information is available for three Brazos River pelagophils. *Notropis buccula*, *N. oxyrhynchus* and *Hybognathus placitus* (Plains Minnow) have been studied in detail in the upper Brazos River, and spawning in all three species was shown to be associated with discharge pulses (Urbanczyk 2012; Durham and Wilde 2008; 2009a,b; 2014). Though spawning was synchronous during periods of elevated streamflow, it was also asynchronous with small batches spawned throughout the reproductive season. *Hybognathus placitus* spawning was not only triggered by flood pulses, but also by small increases in base flow (Urbanczyk 2012). Other pelagophilic species likely respond to discharge in a similar way (Rodger et al. 2016). To date, all seven pelagophils addressed in this report have been found to live for one or two years, with most individuals spawning multiple batches for one season and dying (Taylor and Miller 1990; Durham 2007; Wilde and Durham 2008). Despite these life history similarities, variation in life history traits such as age at maturity, lifespan, fecundity, and number of clutches produced in a season is surely present given the phylogenetic diversity of the group, and likely associated with population vulnerability for a given river system. For example, a species living to age two would have a distinct advantage over an annual species in a particularly bad year, and a species that specializes on mainstem riverine habitats may be more susceptible to fragmentation than species with more generalist macrohabitat requirements that could sustain populations in tributary systems. Regardless, one or two years of failed or poor recruitment could threaten regional populations of all these Great Plains pelagophils.

Study area and Data Collection

The study area encompassed the spatial extent of the target species' geographic ranges in the Brazos River downstream of Possum Kingdom Lake, and 12 sites from the region were sampled by seine in 2017 (Figure 1; Table 1).

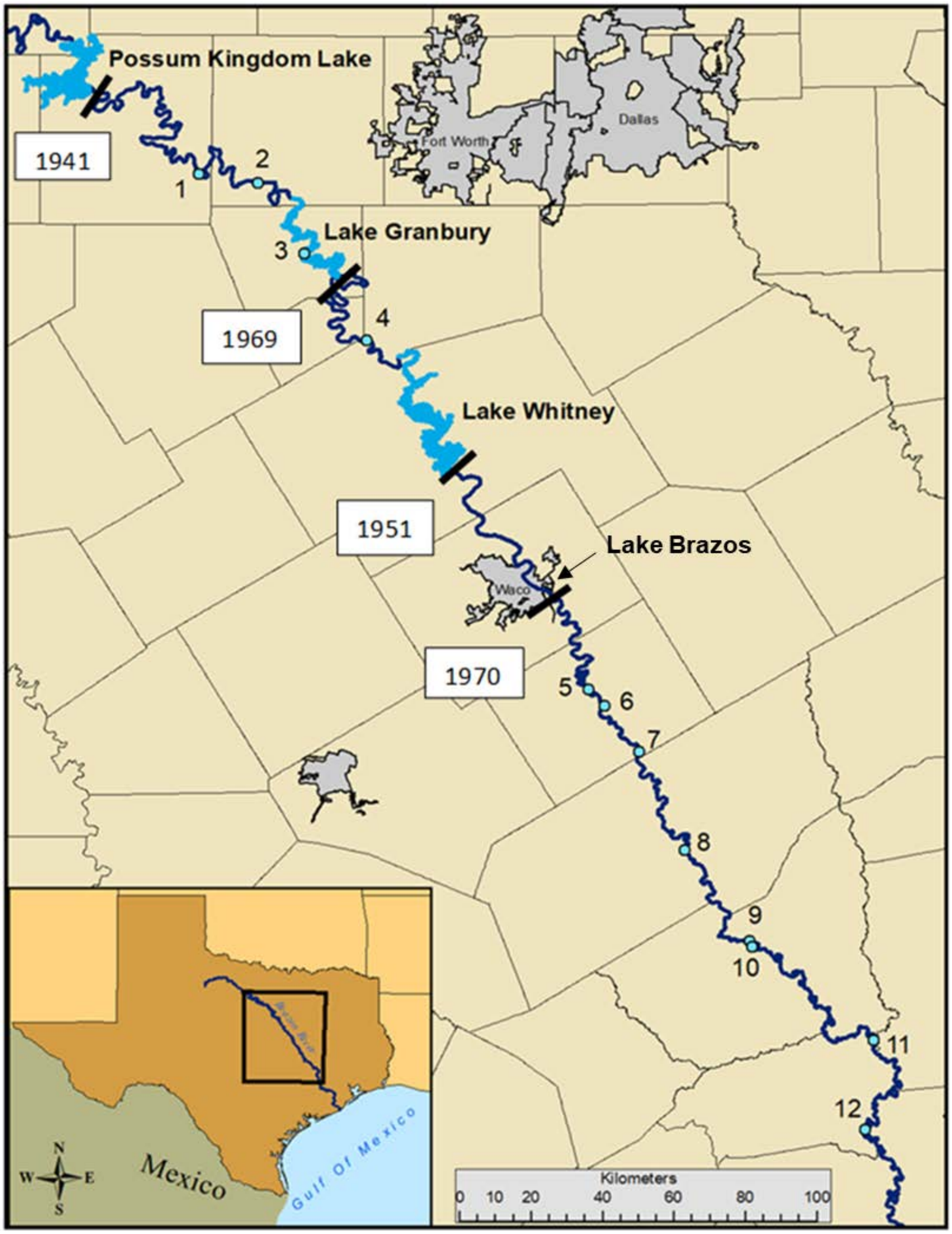

Figure 1. Map of the Brazos River (mainstem) study area. Blue dots indicate sampling localities for collections that were made in 2017, and black bars indicate dams with the year they were completed.

Table 1. Sample locality descriptions and dates for collections made in the Brazos River as a part of this study. Localities are listed in longitudinal order and correspond to Figure 1. Latitude, longitude, county, and proximity to mainstem dams are also given.

Site no.	Locality Description	Latitude	Longitude	County	Proximity to mainstem dams	Date sampled
1	State Highway 281, 12 mi S of Mineral Wells	32.64127	-98.10096	Palo Pinto	Below Possum Kingdom, above Granbury	11 July 2017
2	Farm to Market Rd 1189, 0.25 mi S of Dennis	32.61589	-97.92555	Parker	Below Possum Kingdom, above Granbury	12 July 2017
3	Farm to Market Rd 1175, 1.7 mi NE of Brazos Point	32.20374	-97.60620	Bosque	Below Granbury, above Whitney	12 July 2017
4	Farm to Market Rd 2114 (Smith's Bend), 7.9 mi SW of Aquilla	31.81188	-97.29729	Bosque	Below Whitney, above Waco	12 July 2017
5	State Highway 7, 4 mi W of Marlin	31.28800	-96.96851	Falls	Below Waco	12 July 2017
6	Farm to Market Rd 712, 4.5 mi SW of Marlin, at Falls on the Brazos Park (below the falls)	31.24518	-96.92065	Falls	Below Waco	25 July 2017
7	Farm to Market Rd 413, 4 mi ENE of Wilderville	31.13460	-96.82512	Falls	Below Waco	26 July 2017
8	Farm to Market Rd 485, 6 mi W of Hearne	30.86508	-96.69534	Robertson	Below Waco	13 July 2017
9	Confluence of Little River, 4 mi W of Hearne, access from private property	30.84266	-96.67844	Robertson	Below Waco	26 July 2017
10	8.5 mi W Texas A&M University, private access from Terry Stiles property	30.62062	-96.49015	Burleson	Below Waco	25 July 2017
11	State Highway 105, 4.3 mi W Navasota	30.36142	-96.15559	Brazos	Below Waco	13 July 2017
12	US Highway 290, 6.8 mi W Hempstead	30.12897	-96.18717	Waller	Below Waco	13 July 2017

There are five USGS discharge gages on the mainstem of the Brazos River that contain enough data to make adequate pre- and post-fragmentation flow regime comparisons (Table 2).

Table 2. Mainstem Brazos River USGS gages with pre- and post-impoundment discharge data that were used in this study. Post-impoundment start dates are based on nearest upstream dam that regulates flow.

Gage number	Gage name	County	Nearest upstream Reservoir	Pre-impoundment data	Post-impoundment data
08089000	Brazos R. near Palo Pinto	Palo Pinto	Possum Kingdom	1924-1940	1942-2016
08091000	Brazos R. near Glen Rose	Somervell	Granbury	1923-1940	1970-2016
08096500	Brazos R. at Waco	McLennan	Whitney	1898-1940	1952-2016
08109000	Brazos R. near Bryan*	Brazos	Whitney	1899-1940	1952-2016
08109000					
08114000	Brazos R. at Richmond	Fort Bend	Whitney	1903-1940	1952-2016

*Two gages five river miles apart used to provide complete pre- and post-impoundment data.

The first dam in the system was constructed in 1941 to form Possum Kingdom Lake. Because this dam potentially impacts the entire study reach, 1940 is the last year used as pre-impoundment data for all four gages in the hydrological analyses presented below. The Lake Brazos Dam is run-of-the-river and does not regulate flows, so gages at Waco, Bryan and Richmond have post-impoundment start dates of 1952 after construction of Whitney Lake.

All historical fish data used in analyses are readily available from a variety of sources. Historical fish species occurrence data for the Brazos River was obtained from the Fishes of Texas project website (Fishes of Texas; Hendrickson and Cohen 2015). Fish species abundance data for the Brazos River from below Possum Kingdom to near Hempstead, TX were obtained from the Texas Parks and Wildlife River Studies Program (TPWD: River Studies Program), a Texas Commission on Environmental Quality Report (Texas Commssion on Environmental Quality: Brazos River and Associated Bay and Estuary System, Appendix A, Fish Survey Summaries, which was compiled by Dr. Timothy Bonner), and Labay et al. (2013).

Fishes were sampled by seine (20ft x 6ft, 3/16in mesh) in July 2017 from 12 localities in the study area to provide a baseline for comparison with past sampling efforts. An effort was made to sample all habitat types available, and seining time was approximately one hour per site. All fishes less than 8 inches were preserved in a 10% formalin solution and returned to the lab. After approximately one week, specimens were washed for several days and stored in 70% ethanol. All preserved specimens were deposited in the Ichthyology Collection at the Texas Natural History Collections, Department of Integrative Biology, University of Texas at Austin.

Methods

Flow Regime Analyses

Data used in all flow regime analyses were daily mean streamflows (cubic feet per second, cfs) encompassing the reproductive season of the Brazos River pelagophils (Durham 2007, Urbanczyk 2012, Rodger et al. 2016), and defined herein as April 1–September 30. Flow duration curves (FDCs) for the spawning season were constructed for all gages, pre- and post-impoundment and visually assessed for differences. To identify changes in flow behavior (across 27 metrics) after fragmentation, a non-parametric range of variability approach (RVA) was used. To facilitate analyses, category boundaries were placed at 17 percentage points from the median yielding three categories of equal size: the lowest category contains all values less than or equal to the 33rd percentile; the middle category contains all values falling in the range of the 34th to 67th percentiles; and the highest category contains all values greater than the 67th percentile. The degree of non-attainment was determined and indicates the percentage of post-fragmentation years not meeting the RVA target (middle category). All flow analyses were conducted with Indicators of Hydrological Alteration (IHA) software, version 7.1 (The Nature Conservancy 2009).

Species and Assemblage Analyses

The Brazos water Snake population in the study area has been extensively surveyed twice in the past 40 years (Scott et al. 1989; McBride 2009) and it was beyond the scope of this project to resurvey the population. Instead, we take a retrospective approach and examine in detail how changes to the flow regime may be associated with population declines. There is enough knowledge of habitat use by the Brazos water snake to provide a general assessment of how that habitat has been modified due to anthropogenic impacts to the flow regime.

Pelagophilic species abundances from all lower Brazos River collections (historical and contemporary) were plotted across time to assess population trends and to identify potential time periods of rapid population decline. To assess the relationship between historical distribution in the Brazos River drainage and persistence in the lower river post-fragmentation, I determined the historical percentage occurrence (pre-1970) in the upper and lower river (above and below Possum Kingdom Lake) based on historical and contemporary data. I then plotted the year of last documented occurrence in the lower Brazos River (endpoint of 2017) as a function of the historical percent occurrence in the lower river. To assess changes in species assemblages in space and time, I used non-metric multidimensional scaling, implemented with PC-ORD (McCune and Mefford 2011), to ordinate historical and contemporary fish collections. Data were relativized to ameliorate sample-size differences. I did not use winter samples (December through February) for the assemblage-wide analyses because of sampling difficulty (detection) and I eliminated samples with less than 100 individuals or that appeared to be incomplete. Winter sampling is often difficult and fishes can be challenging to seine at this time, often seeking refuge in deeper waters (personal observation). Small samples were also eliminated because they may not represent the fish fauna well. I also scanned suspect collections from initial ordinations (outliers) and deleted one from 1967 that appeared to be a targeted sample or was otherwise incomplete. This resulted in 118 samples used for multivariate analyses. Samples were coded to visualize differences between the highly fragmented region upstream of Waco and remaining samples downstream of all dams. I then used Analysis of Similarities (ANOSIM) and Similarity Percentage (SIMPER) to identify spatial and temporal trends in the data set, and the species that were driving the trends (implemented with PAST, version 3.22; Past 3.x - the Past of the Future).

Results

Flow duration curves

Flow duration curves were largely consistent with longitudinal position in the lower Brazos River. The upstream-most USGS gages, Palo Pinto and Glen Rose, exhibited the largest deviations from pre- and post-impoundment conditions (Fig. 2), with lower high flows (eco-deficits), higher low flows (eco-surpluses) and no zero flows post-impoundment (see Tables 4 and 5 for median flow values and number of zero flow days). In contrast, the downstream Waco, Bryan and Richmond flow duration curves were more similar between pre- and post-impoundment conditions (Fig. 2).

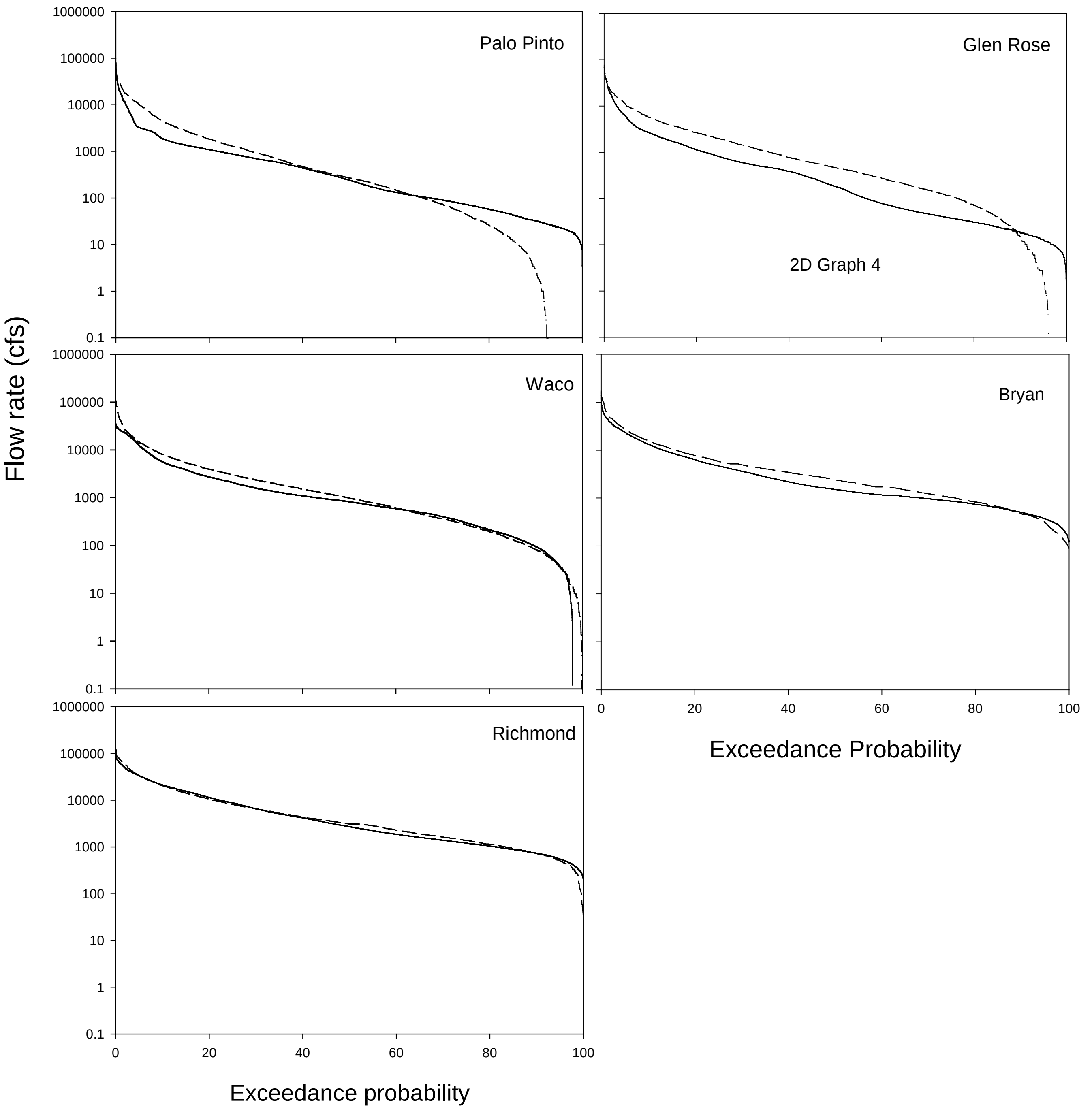

Figure 2. Flow duration curves for five Brazos River gages that have pre-impoundment discharge data. Dashed lines represent pre-impoundment data and solid lines represent post-impoundment data. Length of pre- and post-impoundment time intervals are provided in Table 2.

Range of Variability Analyses

Flow duration curves tell us about the percentage of time that flow in a river is likely to equal or exceed some specified value of interest, but very little about flow behavior across years. Range of variability analysis provided a means of assessing how flow behavior has changed across time, pre- and post-fragmentation, and reflected the general pattern exhibited by the FDCs with the greatest changes occurring in the upstream, highly fragmented reach. However, all five gages indicated strong, but variable disruption of the natural flow regime across the suite of 27 metrics from the following five categories: 1. magnitude of monthly water conditions (six months), 2. magnitude and duration of annual extreme conditions (12 variables), 3. timing of extreme water conditions (two variables), 4. frequency and duration of high and low flow pulses (four variables), and 5. rate/frequency of water condition changes (three variables).

Flow conditions at the uppermost Palo Pinto gage showed the most change post-fragmentation. Twenty-three of 27 parameters across all five categories were not attained (outside of the 34th-67th percentiles), and 13 of those had non-attainment rates greater than 50%. Three parameters had 100% non-attainment (7-day minimum, base-flow index, and number of reversals)(Table 4).

Table 4. Results of the range of variability analysis (RVA) for the USGS gage 08089000 Brazos River near Palo Pinto, TX. The degree of non-attainment indicates the percentage of post- years not meeting the RVA target (middle category).

	Pre-impoundment period: 1924-1940				Post-impoundment period: 1942-2016						
			Range limits				Range limits		RVA Boundaries		
	Medians	CD	Minimum	Maximum	Medians	CD	Minimum	Maximum	Low	High	Rate of non-attainment
Magnitude of monthly water conditions											
April	110.5	3.036	3.1	932	120	2.688	17	3510	52.13	182.2	**12%**
May	911	1.407	56	5750	206	3.303	19	33700	360.9	1347	**26%**
June	750.5	1.955	2.65	5585	476.5	2.128	16	8490	450.1	1522	**16%**
July	117	5.226	0	2400	442	1.787	13.9	3230	101.7	501.4	**9%**
August	170	2.218	0	1980	366	1.423	17.4	2090	24.46	350.7	0%
September	379	2.598	0	2945	241	2.159	16.5	3075	103.8	838.8	0%
Magnitude and duration of annual extreme conditions											
1-day minimum	0	0	0	66	23	1.209	3.4	119	0	6.052	**98%**
3-day minimum	0.2	68.33	0	75	25.33	1.118	5.067	153	0	6.633	**98%**
7-day minimum	1.829	8.789	0	133.4	34.57	1.14	8.057	372.1	0	7.802	**100%**
30-day minimum	32.64	2.783	0	780.8	104.8	1.425	15.19	666.8	13.55	79.94	**19%**
90-day minimum	403.7	3.854	0.1267	2321	388.3	1.157	24.24	2113	348.7	1126	0%
1-day maximum	30200	0.7781	2470	73000	8490	2.065	73.8	81700	14660	35060	**42%**
3-day maximum	21200	1.042	1857	47330	5980	2.577	73.66	76730	12520	26540	**55%**
7-day maximum	15560	0.9157	1446	29530	4056	2.763	73.39	62730	8957	18570	**48%**
30-day maximum	5192	1.342	487	11240	1903	2.305	71.82	34490	3316	7198	**58%**
90-day maximum	2574	1.173	350.3	6766	1058	1.896	64.21	16050	1959	3528	**48%**
Number of zero days	1	20.5	0	75	0	0	0	0	0	15.24	0%
Base flow index	0.00137	6.103	0	0.05667	0.0481	2.441	0.005509	0.8047	0	0.00313	**100%**
Timing of annual extreme water conditions											
Date of minimum	206	0.291	92	274	198	0.3989	92	274	177.6	230.2	**58%**
Date of maximum	211	0.2814	105	272	166	0.2213	92	274	167.2	244.5	**6%**
Frequency and duration of high flow pulses											
Low pulse count	3	1	0	8	5	1.8	0	16	1	3	**81%**
Low pulse duration	10	1.5	1	132	3	0.6667	1	31	5.61	15.78	**81%**
High pulse count	7	0.5	3	13	5	1.2	0	15	5	8	**55%**
High pulse duration	4.5	0.6667	1.5	9	3	1.333	1	27.5	4	6.06	**62%**
Rate/frequency of water condition changes											
Rise rate	270	1.996	33	1345	168.3	0.9086	1.8	416	193.9	390.7	**6%**
Fall rate	-51	-1.627	-268	-12	-69	-1.594	-340.5	-0.1362	-85.3	-47.64	**55%**
Number of reversals	40	0.3	27	58	75	0.2267	0	108	37.88	43.12	**100%**

Flow conditions at the Glen Rose gage also indicated severe hydrologic alteration post-fragmentation with 20 of 27 parameters not attained (outside of the 34th-67th percentiles), and eight with non-attainment rates greater than 50%. As with the Palo Pinto gage, all five categories of parameters were affected (Table 5).

Table 5. Results of the range of variability analysis (RVA, Indicators of Hydrologic Alteration software, version 7.1) for the USGS gage 08091000 Brazos River near Glen Rose, TX. The degree of non-attainment indicates the percentage of post-impoundment years not meeting the RVA target (middle category).

	Pre-impoundment period: 1923-1940				Post-impoundment period: 1970-2016						
			Range limits				Range limits		RVA Boundaries		
	Medians	CD	Minimum	Maximum	Medians	CD	Minimum	Maximum	Low	High	Rate of non-attainment
Magnitude of monthly water conditions											
April	250	2.243	6.35	1870	225	3.664	8.3	4070	146.2	374.8	**95%**
May	1370	1.523	136	6680	349	3.53	13	9840	670.8	2512	**54%**
June	1270	1.893	25.5	6490	375.5	3.594	14	9670	645.5	2497	**59%**
July	356	2.706	0	3410	164	2.574	11	3310	106.3	669.6	**2%**
August	166	2.593	0	2890	58	7.897	9.2	1820	55.38	381.2	**43%**
September	500	2.883	0	4675	96.5	4.89	11.25	2910	198.7	1242	**2%**
Magnitude and duration of annual extreme conditions											
1-day minimum	3	11.03	0	166	12.3	1.203	0.17	54.4	0.988	25.06	0%
3-day minimum	3	13.87	0	182	15	1.238	1.49	131.3	1.489	29.66	0%
7-day minimum	13.43	3.44	0	241.7	21.2	1.474	4.143	294.2	2.681	37.13	0%
30-day minimum	116.4	1.454	0	1292	56.83	2.645	8.143	1084	16.38	141.7	0%
90-day minimum	626.1	3.252	1.048	2808	248.9	2.433	13.93	4041	425.6	1422	**22%**
1-day maximum	28000	1.073	3520	67400	10900	2.06	182	76800	14630	37380	**38%**
3-day maximum	22400	1.092	2803	54470	7277	2.091	119.9	65630	10830	30110	**38%**
7-day maximum	15200	1.05	1931	37440	5059	2.361	83.6	53040	9117	19010	**59%**
30-day maximum	5644	1.158	1232	15300	2669	1.477	38.69	26310	3779	7894	**54%**
90-day maximum	3076	0.963	506.7	8819	1297	1.466	31.44	11180	2242	4522	**59%**
Number of zero days	0	0	0	78	0	0	0	0	0	0	0%
Base flow index	0.005399	3.781	0	0.07378	0.0293	1.785	0.004562	0.4314	0.001	0.0204	**7%**
Timing of annual extreme water conditions											
Date of minimum	230	0.376	92	274	214	0.098	101	274	152.7	243.2	0%
Date of maximum	163	0.281	98	272	156	0.148	96	265	145.7	178.4	**17%**
Frequency and duration of high flow pulses											
Low pulse count	3	1.167	0	8	8	1	2	23	2	4.06	**41%**
Low pulse duration	10	2	1.5	62.5	5	1.5	1	154	8	19.6	**52%**
High pulse count	6	0.667	2	11	3	2	0	11	4.94	8	**49%**
High pulse duration	7	0.75	2	12.5	3	1.167	1	30	3.97	8.03	**48%**
Rate/frequency of water condition changes											
Rise rate	249	2.425	50.5	1346	148	1.718	1.75	595	151	594	0%
Fall rate	-72	-2.05	-430	-19.5	-40.5	-2.76	-350	-2.05	-141.2	-59.1	**48%**
Number of reversals	42	0.286	26	64	64	0.219	43	92	37.88	48	**96%**

For the Waco gage, 16 of 27 parameters across all five categories were not attained post-impoundment (outside of the 34th-67th percentiles), and four of those had non-attainment rates greater than 50% (Table 6).

Table 6. Results of the range of variability analysis (RVA) for the USGS gage 08096500 Brazos River at Waco, TX. The degree of non-attainment indicates the percentage of post-impoundment years not meeting the RVA target (middle category).

	Pre-impoundment period: 1898-1940				Post-impoundment period: 1952-2016						
			Range limits				Range limits		RVA Boundaries		
	Medians	CD	Minimun	Maximum	Medians	CD	Minimum	Maximum	Low	High	Rate of non-attainment
Magnitude of monthly water conditions											
April	803.3	2.192	14	9950	753.3	2.258	0	11750	498.8	1274	**31%**
May	2450	1.67	26	15800	1210	3.539	0	38200	1021	3366	**22%**
June	2108	1.134	14	7170	1036	3.792	0	38800	1456	3040	**68%**
July	561.5	2.857	12	4940	957	0.8665	0	28400	343.3	1268	0%
August	351.5	2.14	1.4	6880	753	0.5797	0	3270	172	725.8	0%
September	673	2.539	28.5	5055	545.5	0.9083	0	7100	230.5	1383	0%
Magnitude and duration of annual extreme conditions											
1-day minimum	56	2.862	0	475	57.55	1.82	0	1160	28.57	117.7	0%
3-day minimum	63	2.966	0	492	94.17	1.311	0	1433	32.79	150.6	0%
7-day minimum	70.14	**3.402**	0.1857	524.7	169.4	1.353	0	1600	37.58	191.5	0%
30-day minimum	166.6	2.786	1.667	3941	490.4	0.9333	0	3178	115.9	382.7	3%
90-day minimum	852.9	2.39	25.06	5337	806.7	1.059	0	11460	598.9	2172	0%
1-day maximum	35100	1.338	4590	158000	16200	1.295	0	65500	25050	47200	**17%**
3-day maximum	24700	1.327	3587	124600	12360	1.42	0	54170	18010	39210	0%
7-day maximum	16350	1.636	2247	70930	7542	2.164	0	52290	11720	26640	**3%**
30-day maximum	7667	1.41	1423	32590	4060	2.147	0	41660	5528	10360	**35%**
90-day maximum	4756	1.109	902.6	15770	2401	2.069	0	29340	3117	6862	**17%**
Number of zero days	0	0	0	5	0	0	0	183	0	0	0%
Base flow index	0.03003	1.672	9.40E-05	0.1466	0.08462	1.02	0	0.3414	0.0136	0.05359	**45%**
Timing of annual extreme water conditions											
Date of minimum	226.5	0.34	92	274	241.5	0.209	92	274	200.4	242.1	**31%**
Date of maximum	161.5	0.163	93	272	145	0.1346	92	272	142.2	180.5	**12%**
Frequency and duration of high flow pulses											
Low pulse count	4.5	1.111	0	10	9	1.139	0	30	2	5	**64%**
Low pulse duration	5.75	1.283	1	117	2	1	0	7	4.275	8.225	**68%**
High pulse count	6	0.5	3	16	3	1.333	0	13	5	7	**44%**
High pulse duration	3	1.333	1	16	4	1.75	0	69	2.095	4.81	**49%**
Rate/frequency of water condition changes											
Rise rate	534	1.344	21	2445	263	0.8232	31	932	357.7	774.3	**31%**
Fall rate	-157.5	-1.667	-560	-19	-214	-0.9638	-705	-20	-312.2	-95.14	0%
Number of reversals	54	0.241	36	69	85	0.1706	0	104	51.19	56.81	**95%**

For the two Bryan gages, 19 of 27 parameters were not attained and eight has non-attainment rates greater than 50%

Table 7. Results of the range of variability analysis (RVA) for the USGS gages 08109000 and 08108700 Brazos River at Bryan, TX. The degree of non-attainment indicates the percentage of post-impoundment years not meeting the RVA target (middle category). The two gages were approximately 5 river miles apart and together provide enough data for pre- and post-impoundment analysis.

	Pre-impoundment period: 1899-1950				Post-impoundment period: 1952-2016						
			Range limits				Range limits		RVA Boundaries		
	Medians	CD	Minimum	Maximum	Medians	CD	Minimum	Maximum	Low	High	Rate of non-attainment
Magnitude of monthly water conditions											
April	3298	1.24	151	30350	1810	2.224	381.5	23450	1748	4846	**29%**
May	4730	2.025	1200	51800	2830	2.648	364	48200	2957	7880	**42%**
June	4823	0.8245	458	19650	2240	2.99	229	48250	3170	5580	**54%**
July	1670	1.376	182	10700	1380	2.124	450	44300	1280	2540	**53%**
August	972.5	1.336	107	10500	1080	0.6866	270	16200	614.5	1408	0%
September	1445	1.701	261.5	11300	1020	0.8461	157	14650	841.9	2668	0%
Magnitude and duration of annual extreme conditions											
1-day minimum	425	1.084	89	1780	409	1.046	120	4380	327.4	586.3	**11%**
3-day minimum	425	1.141	91	1900	433.7	1.021	127.7	4900	336.1	606.7	**11%**
7-day minimum	461.8	1.142	94.43	2081	529.9	0.962	130.3	6330	350.8	696.7	0%
30-day minimum	818.3	1.051	102.3	7205	801.3	0.7824	212.7	13890	462.4	1060	0%
90-day minimum	1712	1.54	179.5	9483	1278	1.964	459.7	24840	1389	3187	**42%**
1-day maximum	48750	1.271	1700	172000	28600	1.575	1810	134000	29470	56770	**42%**
3-day maximum	41400	1.319	1700	140000	22470	1.792	1613	116300	27500	51940	**56%**
7-day maximum	30540	1.353	1700	111800	15310	2.079	1095	104400	21530	41940	**42%**
30-day maximum	14680	1.051	1700	72180	8444	1.994	815.7	63390	10780	19880	**56%**
90-day maximum	8541	0.9261	1700	35670	4529	2.217	640	46910	5484	10340	**78%**
Number of zero days	0	0	0	0	0	0	0	0	0	0	0%
Base flow index	0.08481	1.333	0.01582	1	0.1379	1.012	0.03266	0.9839	0.05895	0.1378	**2%**
Timing of annual extreme water conditions											
Date of minimum	238	0.1407	92	274	251	0.153	96	274	225.3	248.4	**60%**
Date of maximum	138	0.1277	92	274	142	0.123	92	272	120.7	150	0%
											0%
Frequency and duration of high flow pulses											0%
Low pulse count	3	1.667	0	10	8	0.6875	0	16	2	5	**71%**
Low pulse duration	9	2.528	1	94	4	0.9375	1	21	4.44	16.78	0%
High pulse count	5	0.6	0	10	2	1.5	0	9	4	6	**46%**
High pulse duration	6	1.146	1	59	4.75	2	1	162	4	9	**42%**
Rate/frequency of water condition changes											
Rise rate	517.5	1.766	19	5700	243	1.313	34	2335	283.1	991.9	0%
Fall rate	-260	-0.9904	-1230	-40	-230	-0.8587	-1100	-30	-371.4	-210	**20%**
Number of reversals	44.5	0.3708	0	66	60	0.175	4	76	36.74	49	**69%**

Finally, for the Richmond gage, 24 of 27 parameters across all five categories were not attained post-impoundment (outside of the 34th-67th percentiles), and 6 of those had non-attainment rates greater than 50% (Table 7).

Table 7. Results of the range of variability analysis (RVA) for the USGS gage 08114000 Brazos River near Richmond, TX. The degree of non-attainment indicates the percentage of post-impoundment years not meeting the RVA target (middle category).

	Pre-impoundment period: 1903-1940				Post-impoundment period: 1952-2016						
			Range limits				Range limits		RVA Boundaries		
	Medians	CD	Minimum	Maximum	Medians	CD	Minimum	Maximum	Low	High	Rate of non-attainment
Magnitude of monthly water conditions											
April	3530	3.127	460	25400	4060	1.84	327.5	25150	2893	11700	0%
May	5665	1.417	1150	60500	5160	3	616	71000	3532	7603	**50%**
June	6723	0.8252	436	18250	4540	2.885	348	56200	4782	8470	**69%**
July	2355	1.59	264	12900	1710	2.579	473	60700	1429	3953	**13%**
August	1043	1.119	117	3580	1410	1.287	372	19500	752.5	1722	0%
September	1730	1.279	511.5	14250	1585	1.183	367	17100	1136	2056	**6%**
Magnitude and duration of annual extreme conditions											
1-day minimum	577.5	0.8649	35	1750	688	0.9826	55	8250	477.2	725	**25%**
3-day minimum	577.5	0.8612	43.33	1797	707	0.9783	87.33	8333	516.4	771.1	**19%**
7-day minimum	590.4	0.7975	47.86	1924	780.6	0.9614	93	9470	529.2	816	**6%**
30-day minimum	846.5	1.092	113	4069	1150	1.053	340.6	16650	658.8	1209	**13%**
90-day minimum	2221	1.84	234.3	7096	2051	1.747	436.6	31310	1578	4112	**25%**
1-day maximum	49750	0.9367	11600	123000	37800	1.196	1310	120000	41840	73480	0%
3-day maximum	46330	0.9971	10700	119300	33230	1.274	1177	117300	38590	71350	0%
7-day maximum	40980	1.063	9303	108800	27730	1.273	916.3	107400	28790	62790	0%
30-day maximum	20780	1.044	4533	55800	14600	1.434	749.9	80110	16540	26730	**31%**
90-day maximum	12650	0.8871	3345	28820	8472	1.675	655.7	55730	8268	15690	**38%**
Number of zero days	0	0	0	0	0	0	0	0	0	0	0%
Base flow index	0.1081	0.6741	0.01086	0.2107	0.1453	0.6641	0.03231	0.489	0.08395	0.1315	**25%**
Timing of annual extreme water conditions											
Date of minimum	239.5	0.06079	93	274	233	0.2104	92	274	236.5	249.7	**63%**
Date of maximum	150	0.1011	101	258	142	0.1148	92	267	135.4	153	**36%**
Frequency and duration of high flow pulses											
Low pulse count	2	1	0	6	4	1.5	0	11	2	3.73	**71%**
Low pulse duration	18.5	0.9189	2	56	6	1.333	1	149	8.26	20.36	**40%**
High pulse count	4	0.625	1	8	2	1.5	0	6	3.27	4	**79%**
High pulse duration	7	0.6071	2	20.5	8	1.625	1	152	5	8.23	**67%**
Rate/frequency of water condition changes											
Rise rate	850	1.296	89	1800	240	1.835	35	2400	329.5	1127	**19%**
Fall rate	-297.5	-1.462	-850	-94	-270	-1.259	-1500	-49	-465.7	-212.7	**25%**
Number of reversals	37.5	0.4467	19	51	46	0.2609	20	70	32.54	42.92	**38%**

Species abundances and persistence

During July 2017, we collected 31 species of fishes (Table 3) from 12 sites (Table 1) on the lower Brazos River.

Table 3. Fish collections from the Brazos River from summer 2017. Numbers correspond to locality descriptions in Table 1.

Species	1	2	3	4	5	6	7	8	9	10	11	12	Total
Aplodinotus grunniens	0	0	0	0	0	1	0	3	0	0	0	0	4
Campostoma anomalum	0	0	0	1	2	1	0	0	0	0	0	0	4
Carpiodes carpio	7	8	1	0	2	15	43	0	11	15	10	0	112
Cyprinella lutrensis	614	542	218	0	162	542	86	27	148	83	84	20	2526
Cyprinella venusta	33	128	446	117	1	0	1	0	0	0	0	0	726
Dorosoma cepedianum	0	0	0	0	60	4	12	1	0	3	41	3	124
Dorosoma petenense	0	4	0	2	0	1	1	0	0	4	6	0	18
Fundulus grandis	0	2	1	0	0	0	0	0	0	0	0	0	3
Fundulus notatus	0	1	2	0	0	0	0	0	0	0	0	0	3
Gambusia affinis	6	4	0	30	92	14	6	0	0	1	32	10	195
Hybognathus nuchalis	0	0	0	0	0	0	0	0	0	0	27	0	27
Ictalurus furcatus	0	0	0	0	0	6	0	1	1	2	34	38	82
Ictalurus punctatus	0	0	1	0	0	32	3	14	27	26	5	22	130
Labidesthes siculus	10	1	0	0	0	0	0	0	0	0	0	0	11
Lepisosteus osseus	0	1	5	0	0	21	1	0	0	1	4	2	35
Lepomis cyanellus	0	0	0	0	0	0	0	0	1	5	5	0	11
Lepomis humilis	0	0	1	0	8	0	0	1	0	2	17	4	33
Lepomis macrochirus	11	8	5	0	0	2	0	0	1	0	0	0	27
Lepomis megalotis	56	57	4	82	10	1	0	2	0	0	0	10	222
Macrhybopsis hyostoma	0	1	0	0	0	2	0	0	14	57	88	21	183
Macrhybopsis storeriana	0	0	0	0	0	0	0	0	0	0	3	4	7
Menidia beryllina	1	148	94	119	2	6	0	0	0	0	0	0	370
Micropterus punctulatus	12	8	4	0	6	0	0	0	1	2	0	0	33
Micropterus salmoides	7	1	1	7	1	0	0	0	0	0	0	1	18
Micropterus treculii *	0	0	0	1	4	0	0	0	0	0	0	1	6
Morone chrysops	0	1	3	0	0	0	0	0	0	0	0	0	4
Notropis buchanani	0	0	0	11	11	0	1	0	7	8	19	56	113
Notropis shumardi	0	0	0	0	0	0	0	1	3	2	9	15	30
Noturus gyrinus	0	0	0	2	0	0	0	0	0	0	0	0	2
Pimephales vigilax	29	89	30	1	33	32	543	16	144	147	86	169	1319
Pylodictis olivaris	0	0	0	0	0	0	0	0	0	1	0	0	1

*Possibly hybrids, but phenotypically resemble *Micropterus treculi*.

Neither of the fish target species were collected in 2017 and no Brazos water snakes were observed from the sites above Waco, where they are presumably still extant (McBride 2009, Paul Crump, pers. comm.). Regarding the pelagophilic minnow species, all exhibited tremendous declines through time but not in the same temporal window, suggesting differences in their vulnerability to hydrologic alteration (Fig. 3).

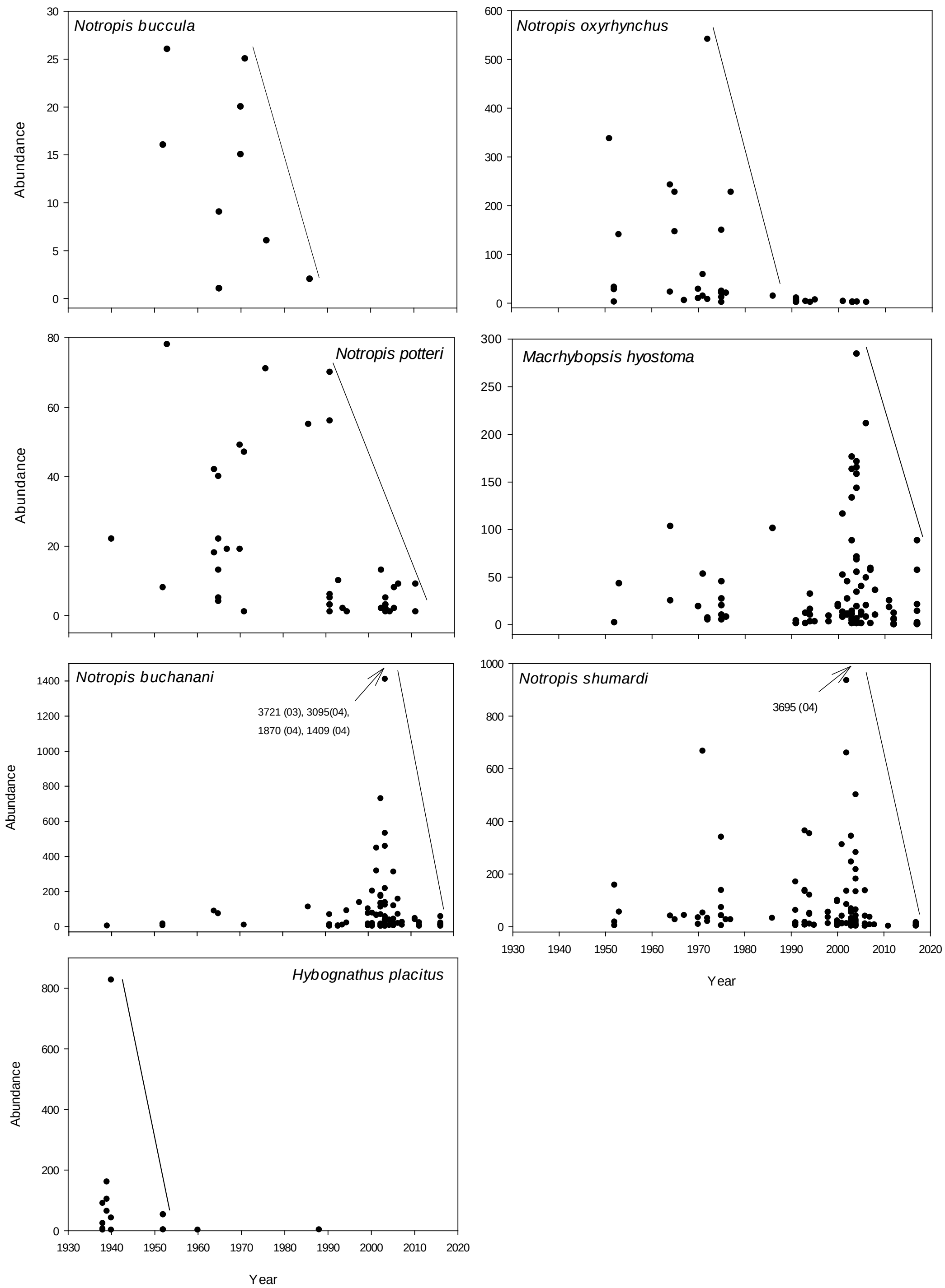

Figure 3. Pelagophilic species abundances across time in the lower Brazos River (downstream from Possum Kingdom Lake). Diagonal lines indicate time period of rapid declines for species. Inserts and arrow indicate numbers off the scale and the year of collection. Only species occurrences where abundance data were available are shown.

Notropis buccula and *N. oxyrhynchus* both show a very similar pattern of steep decline that began in the 1970s, with *N. buccula* presumably becoming extirpated by the early 1980s, while *N. oxyrhynchus* persisted at low numbers well into the 2000s before apparent extirpation. Chub Shiner *Notropis potteri* showed a similar decline, but starting in the 1990s and persisting until 2011. Shoal Chub *Macrhybopsis hyostoma*, Ghost Shiner *N. buchanani* and Silverband Shiner *N. shumardi* all exhibited spikes in abundance in the early to mid-2000s, with all three species strongly declining thereafter. As of my sampling in 2017, *M. hyostoma*, *N. buchanani* and *N. shumardi* were still extant in the mainstem of the lower Brazos River (Table 3). *Hybognathus placitus* showed the earliest and most precipitous drop, but persisted until 1988, when two individuals were collected by Moss and Mayes (1993).

Pelagophilic minnows in the Brazos River are variable in their distributional extent, with some species thriving in the high salinity and drought-prone upper river, while others are well-adapted to large river conditions found in the lower basin. There was a significant relationship between the year of last documented occurrence in the lower Brazos River (endpoint is 2017) and the historical percent occurrence in the lower river (Fig. 4). Thus, species well-adapted to the large, lower river environment were less likely to become extirpated after fragmentation, whereas species with high occurrences in the upper river were the first to be lost from the lower river after fragmentation and hydrologic alteration.

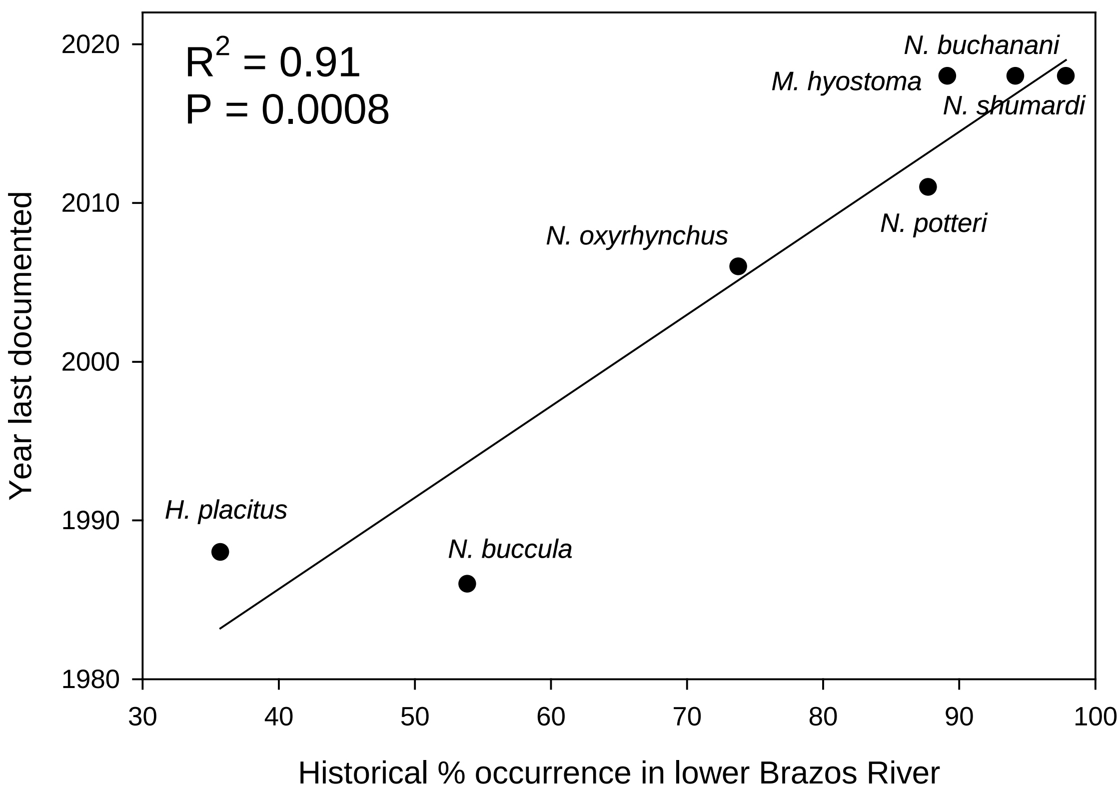

Figure 4. For Brazos River pelagophilic minnows, the year of last documented occurrence in the lower Brazos River is plotted as a function of the historical percent occurrence in the lower river. Percent occurrence is based on pre-1970 records from throughout the Brazos River basin. Occurrence data were assembled from the Fishes of Texas Project database (http://www.fishesoftexas.org/home/).

Fish assemblage change

The non-metric multidimensional scaling analysis provided a qualitative visual picture of fish assemblages across space and time, and illustrated differences between samples from the highly fragmented region above Waco and the downstream samples below Waco (Fig. 5).

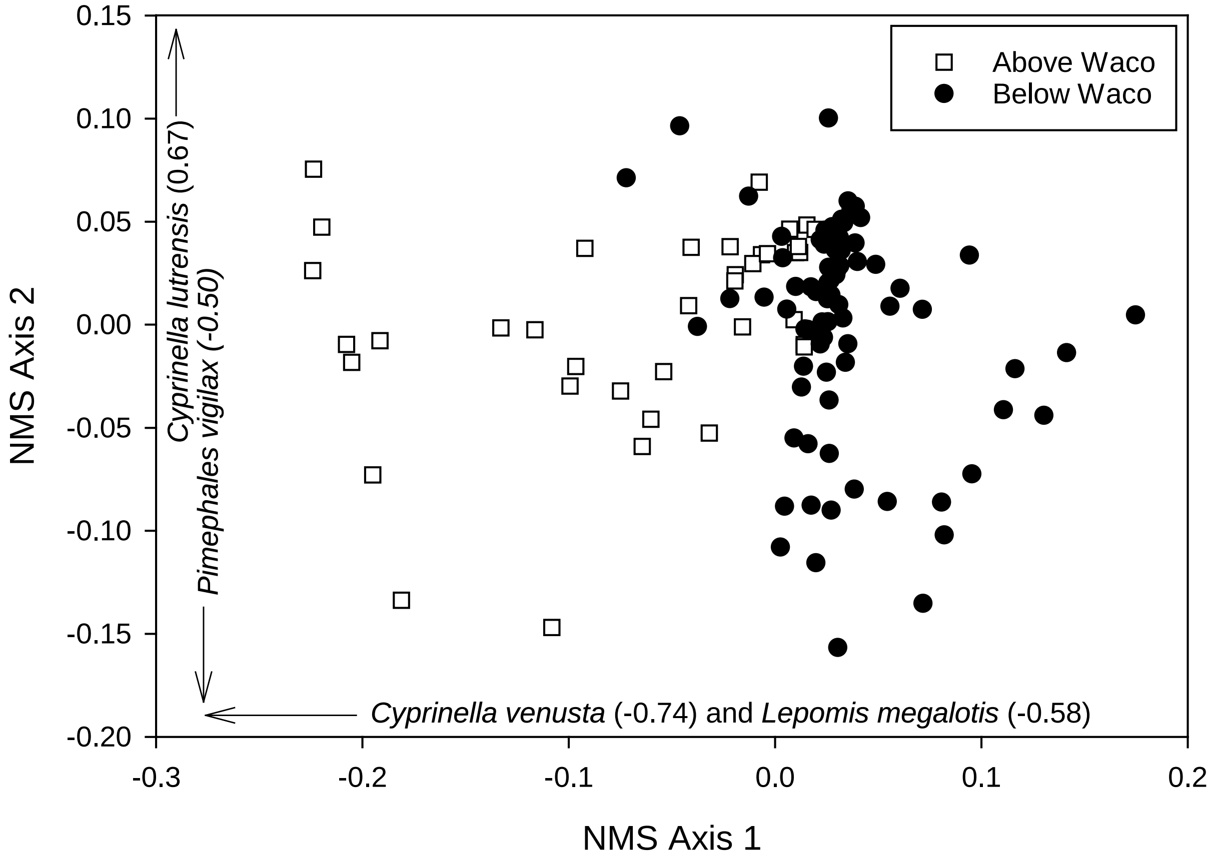

Figure 5. Result from a non-metric multidimensional scaling analysis of 118 samples from the Brazos River downstream from Possum Kingdom Lake across 65 years (1952 – 2017). Open squares represent sites above Waco, closed circles represent sites below Waco. Numbers in parentheses indicate species correlations (> |0.50|) with NMS axes.

This pattern generally conforms to expectation based on longitudinal zonation of fish assemblages, as numerous studies from a wide range of Great Plains stream systems have shown (Taylor et al. 1993, Matthews 1998). It is harder to depict temporal change in the ordination, but there was a significant relationship between the primary fish assemblage gradient and time (Fig. 6).

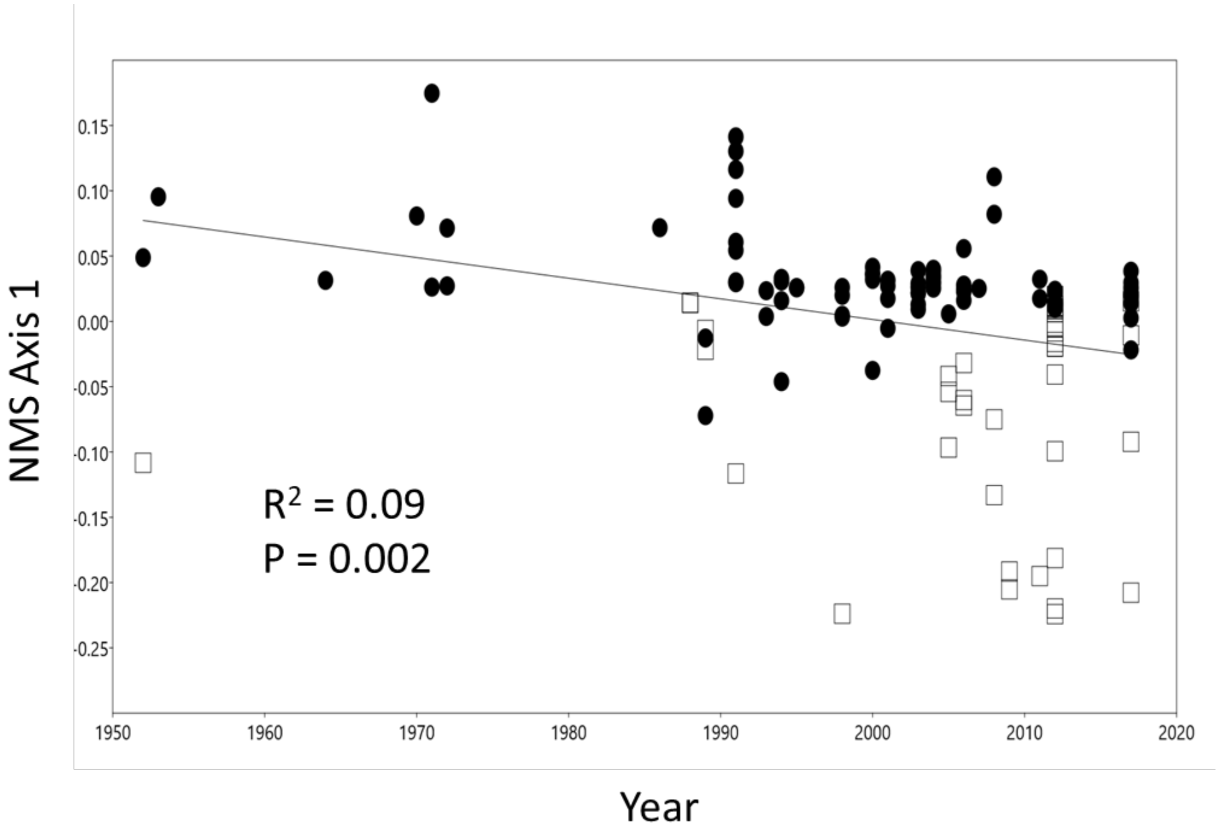

Figure 6. Fish assemblages in the lower Brazos River are correlated with time. Open squares represent sites above Waco, closed circles represent sites below Waco. Although the linear relationship is weak, it is highly significant.

Analysis of similarity (ANOSIM) and similarity percentage analysis (SIMPER) provided a quantitative assessment of spatial and temporal change. Results from a two-way ANOSIM indicated a significant difference between upper (above Waco) and lower (below Waco) fish assemblages (R = 0.49, P = 0.0001) and a significant difference between time periods (R = 0.23, P = 0.0002)(Table 4). Similarity Percentage Analysis (SIMPER) provided a means of determining which taxa are primarily responsible for differences between groups of samples. I arbitrarily used a 60% cutoff meaning that species shown in Table 4 account for 60% of the differences in similarity between the two spatial groups, and among the five temporal groups. Interestingly, the same three species accounted for approximately 50% of the differences in similarity for both the spatial and temporal groups, although they ranked differently. *Cyprinella lutrensis* was the primary contributor to change both spatially and temporally. *Pimephales vigilax* and *C. venusta* both played secondary or tertiary roles depending on the analysis. Thus, increased relative abundances of three tolerant and generalist species are largely responsible for differences in lower Brazos River fish assemblages above and below Waco, and across more than 60 years of time, and these results were consistent with the initial ordination (Fig. 5) and Bonner and Runyan's (2007) previous work.

Table 4. Similarity Percentage Analysis (SIMPER) to assess which taxa are primarily responsible for differences between groups of samples. Cumulative percent contributions by taxa, and mean relative abundances are shown. Time periods are as follows: t_1 = 1950-1969, t_2 = 1970-1989, t_3 = 1990-1999, t_4=2000-2009, and t_5 = 2010-2017. Parentheses indicate the sample size for the time period. Time periods are of unequal length because of differences in sampling frequency through time, and contributions up to 60% similarity difference are shown.

Species	Cumulative % contribution	Mean Relative Abundance Through Time				
		t_1 (4)	t_2 (12)	t_3 (23)	t_4 (44)	t_5 (35)
Cyprinella lutrensis	26.2	37.9	34.3	42.5	50.1	44.4
Pimephales vigilax	40.8	6.9	18.5	16.3	18.1	13.9
Cyprinella venusta	49.9	1.4	4.9	5.9	4.9	9.9
Notropis shumardi	55.1	9.3	8.5	6.6	1.8	0.3
Gambusia affinis	59.9	1.0	0.8	2.4	2.0	8.0
		Mean Relative Abundance Across Space				
		Above Waco (38)		Below Waco (80)		
Cyprinella lutrensis	25.3	32.9		50.6		
Cyprinella venusta	39.0	18.1		0.9		
Pimephales vigilax	51.5	10.2		19.0		
Lepomis megalotis	56.8	7.0		0.7		

Discussion

The lower Brazos River has undergone considerable physical and biological change over the past century after fragmentation by a series of dams that have altered its hydrologic and geomorphic characteristics. The two target pelagophilic minnow species have been extirpated and the Brazos water snake has undergone considerable population contraction (McBride 2011). In addition, two other pelagophilic minnows appear to have been extirpated from the study area, and the remaining three species have declining populations that will need monitoring in the future. Specific mechanisms leading to species declines and/or loss from the lower river remain elusive, but in addition to fragmentation by the series of dams, I have identified largescale alteration to the flow regime across the entire lower river, which spans approximately 580 river miles.

It is difficult to generalize regional hydrologic change from pre- to post-fragmentation, because of the variability seen from upstream to downstream across the five USGS gages. The magnitude of monthly spawning season median flows varied from month to month and was not consistently different between pre- and post-fragmentation time periods except at the Glen Rose gage, where median flows were lower for all months post-fragmentation. Minimum flows were generally attained, or higher, and base flows were always higher post-fragmentation. The timing of the annual extremes (low and high) differed with maximum flows occurring earlier in the spawning season post-fragmentation for all gages except at Bryan. The frequency of low pulse counts was consistently higher and high pulse counts were always lower at all gages post-impoundment. Low pulse durations also decreased at all gages. High pulse durations decreased at Palo Pinto Glen Rose and Bryan gages, but increased at Waco and Richmond gages. The rate/frequency of water condition changes also differed pre- and post-fragmentation. Rise rates declined across all gages, but fall rates varied. The one remarkable difference that stood out for all streamflow gages was the number of flow reversals, which increased dramatically post-fragmentation, even at the Richmond gage within 100 river miles from the Gulf of Mexico.

The length of free-flowing river or stream, or fragment length (Wilde and Urbanczyk 2013), available for life history needs has been implicated as being important to pelagophil persistence (Winston et al. 1991, Perkins and Gido 2011, Wilde and Urbanczyk 2013), and a challenge to successful repatriation efforts in the fragmented river reaches between Possum Kingdom Lake and Lake Brazos (Wilde and Urbanczyk 2013), presumably even if prescriptive environmental flows could be managed to support imperiled fish populations. Winston et al. (1991) suggested that pelagophilic species loss above a reservoir in southwestern Oklahoma was likely due to the barrier preventing movement of individuals that were more common in downstream reaches, but that utilized the upper river sporadically or on a more temporary basis. At face value, this seems to support a ‘fragment length hypothesis’, but Winston et al. (1991) also noted a general shift in the fish assemblage above the reservoir, with the presence of many reservoir-associated species that could have played a role in species extirpations. Wilde and Ostrand (1999) documented a similar phenomenon from the Double Mountain Fork Brazos River upstream from Lake Alan Henry, where *N. buccula* and *H. placitus* have become extirpated (Wilde 2015). However, fragment length alone may only be a surrogate variable for the actual mechanism(s) involved in determining pelagophil persistence. Hoagstrom (2014) disputed this ‘fragment length’ hypothesis based on a lack of evidence that propagules must drift as they develop, and Cheek and Taylor (2016) emphasized the importance of habitat, and water quality and quantity that may override the importance of fragment length. Furthermore, the lower Brazos River is very different than that of the fragmented North Fork of the Red River or Double

Mountain Fork Brazos River. The lower Brazos River below the last dam at Waco contains approximately 382 free-flowing river miles, yet the reach shows considerable hydrologic alteration due to regulation by the upstream dams.

Despite our lack of understanding of the actual mechanism(s) responsible for species loss in fragmented rivers, pelagic-broadcast spawning appears to be an adaptation that takes advantage of a flow-recession environment (Hoagstrom 2014) where propagule retention occurs on the descending limb of the hydrograph (Dudley and Platania 2007). Floods create nursery habitats, deliver propagules to them, and provide relief from predators and competitors (Moore 1944; Hoagstrom and Turner 2014). Propagule transport and retention rates are influenced by channel shape and complexity, hydrograph magnitude and shape, and river floodplain connectivity (Dudley and Platania, 2007; Medley et al., 2007) such that complex river reaches will efficiently retain eggs in low (or zero) velocity habitats (Dudley and Platania 2007). Recruitment to populations occurs during flow recession (Durham and Wilde 2009a) with larvae ending up in backwaters and other low-velocity habitats (actively or passively) along river margins, where conditions are favorable for survival, feeding, and growth of early life stages (Taylor and Miller 1990; Dudley and Platania 1999; Hoagstrom 2014).

It may be possible to regulate flows that mimic the natural flow regime and species-specific flow-biota relationships are increasingly being used to determine environmental flow needs and manage their use, but these relationships are complicated and variable among species (King et al. 2016). Much of what we know is based on a coarse conceptual understanding of these relationships (Arthington 2012). For example, flow-triggered spawning behavior is common among pelagophils, but the physiological basis for this phenomenon is elusive, and the cues elicited by rising or declining flows are not well understood. However, we do know that important environmental factors affecting fish reproduction are interrelated and difficult to tease apart. Synchronous spawning of North American pelagophilic minnows on flow pulses is well known, yet we do not understand why this group of species shows wide variation in success in the face of hydrologic alteration. Surely this variation is tied to differences in life history attributes and their interaction with the environment, which ultimately results in the cascade of physiological events that elicit spawning when the right conditions occur.

Fish physiologists are keenly aware that temperature is extremely important in the early life history of fishes (Helfman et al. 1997), and it is well-known to hydrologists that a change in discharge is accompanied by a change in water temperature (Gu 1998; Gu et al. 2009). Water temperature in a river is proportional to discharge and the amount of heat energy present. For a given level of solar radiation or heat, stream temperature is inversely proportional to stream discharge (Brown 1972). Thus, in the hypothetical situation where discharge increases without any change in heat energy or surface area, there will be a corresponding decline in water temperature. The thermal characteristics of the dominant source of water are an important consideration, whether from heavy rainfall events or dam releases, as is channel morphology (Sinokrot and Gulliver 2000). The use of streamflow management in regulated rivers to improve river water quality and to moderate high river temperature in the summer is an emerging issue. For example, in the Platte River, Nebraska, a clear relationship was found between river water temperatures and river flow-rate, providing a feasible way to moderate high summer river temperatures via management of reservoir discharge (Sinokrot and Gulliver 2000). Olden and Naiman (2010) suggested that research should focus on characterizing variability in stream temperatures in relation to the temporal and spatial impacts of dam operations on thermal regimes to elucidate the relative roles of altered flow and temperature in shaping ecological patterns and processes in rivers. A river’s thermal regime is an important and often neglected component of environmental flows, and non-flow environmental features (e.g. temperature, sediments) should be incorporated into environmental flow assessments (Poff 2018). Because a flow pulse or a flow decline will be accompanied by a change in water temperature, it seems likely that temperature change is a reliable physiological cue to initiate synchronized spawning in pelagophils. In an Australian river system, principally temperature, and flow as a secondary variable, influenced the timing and strength of fish spawning intensity for seven native species (King et al. 2016).

For the lower Brazos River, the range of variability analyses indicated many flow regime changes pre- and post-fragmentation, but there were ample flow pulses present to trigger spawning in the pelagophils. Furthermore, the lower Brazos river has not lost all pelagophilic species and there are differences in habitat use and suitability that occur among the seven species (Bonner and Runyan 2007). For example, *N. buchanani* is adapted to several habitat types in the river and in smaller tributary streams (Gilbert 1980, Rose and Echelle 1981), and has been successful in the lower river after impoundment. Additionally, *N. shumardi* and *M. hyostoma* appear to maintain stable populations in the lower Brazos river. Differences among species regarding their historical distribution above and below Possum Kingdom Lake was a strong predictor of species persistence in the lower river (Fig. 4). It is possible that extant and primarily lower river-adapted species such *N. buchanani*, *N. shumardi* and *M. hyostoma* may require a less prescriptive set of flow events than the target minnow species, and *H. placitus* and *N. potteri*. Nuanced differences in life history are likely to occur among species and may explain some differential response to the altered flow regime. The extirpated pelagophils may be more sensitive to altered flow regimes and the accompanying geomorphic change that has occurred (Dunn and Raines 2001), and/or individuals in the lower river may have been population sinks dependent on extensive populations upstream. Once disconnected from these population sources, it would only be a matter of time before extirpation.

Another consideration regarding declines in all three target species are the unpredictable and devastating consequences of golden algae (*Prymnesium parvum*) in the Brazos River. In 2001, a winter bloom of golden alga in Possum Kingdom Lake, subsequently spread downstream to Lake Granbury, then finally to Whitney Lake, causing massive fish kills along the way (TPWD: The History of Golden Alga in Texas) and recurring blooms caused fish kills for the next seven years. Although not confirmed, fish kills in the upper Brazos River in 1981-1982 (and variably persisting throughout the decade) are thought to have been due to golden alga (TPWD 2007). The direct effects of *P. parvum* on fishes are evident, but impacted fish populations may affect the Brazos water snake, particularly during crucial feeding periods (e.g., after spring emergence or after parturition in the fall) (McBride 2009).

Unfortunately, recent population survey data for the Brazos water snake is lacking. However, a detailed survey of extant populations was completed during 2006–2008 by McBride (2009). Before this work, Scott et al. (1989) conducted extensive surveys between 1979 and 1987. Scott et al. (1989) found the range of *N. h. harteri* to encompass approximately 700 km in the Brazos River drainage, but within this range the snake was found to inhabit only 300 km of river corridor and portions of shoreline on Possum Kingdom Lake and Lake Granbury. The patchy distribution was thought to be due to a lack of suitable juvenile habitat, especially the presence of medium (>10 cm) to large flat rocks on unshaded shoreline for cover and adjacent rocky shallows for foraging, habitat typically associated with riffles. Reservoir populations occupy shoreline habitat with similar features (Scott et al., 1989). McBride (2009) found that the range of *N. h. harteri* and suitable habitat remain intact, but that the snake was rare throughout its range with an overall paucity of juveniles, suggesting population contraction. McBride (2009) speculated that the reduction of extreme high flow events has likely reduced flushing and scouring of the river channel and threatening juvenile *N. h. harteri* habitat. I found that all five gages had reduced high pulse counts post-fragmentation. McBride (2009) also noted an increase in flow reversals, and that altered timing and frequency of short bursts of flow from the dams, may affect successful recruitment, reduce foraging opportunities for neonates and increase the risks of predation by forcing snakes to frequently move out from under rocks when the river rises. My RVA analysis indicated a 100% non-attainment of pre-fragmentation flow reversal numbers (all exceeding the upper boundary threshold) at the Palo Pinto gage, and a 96% and 95% non-attainment at Glen Rose and Waco gages (respectively). Other potential threats to the Brazos water snake include invasive plants that can choke riffles and increase sedimentation, and fire ants that were observed at several Brazos River riffles where they were prevalent under virtually all suitable rocks with no snakes of any species found (McBride 2009). A lack of flushing and scouring flows is likely to exacerbate the negative influence of these invasive species.

It is likely not just one component of the flow regime that is important for maintaining aquatic biodiversity in the lower Brazos River, and non-flow variables such as temperature and sedimentation may be significant factors. For managing flow regimes to support species that cue their spawning to flow events, it will be necessary to not only better understand pelagophil reproductive life histories, but also the physiology and ecology of early life history stages that may be susceptible to abrupt temperature changes that would accompany the high frequency of post-fragmentation flow reversals. Flow reversals also alter the succession of larval habitat formation and availability along the river margins and backwaters, with nursery habitats blinking in and out at a more rapid pace. For the Brazos water snake, altered flows may directly impact populations or indirectly affect them through alterations to the fish assemblages that they depend on. Finally, Arthington et al. (2018) noted that a more robust, dynamic and predictive approach to environmental water science is emerging that encourages the measurement of biological process rates (e.g. colonization, extirpation), species traits (e.g. physiological requirements, adaptations) and community attributes (e.g. species richness, assemblage structure) that represent ecological responses to hydrologic alteration. River flow behavior is complex and closely associated with channel geometry and changes in the suspended sediment loads (Dunn and Raines 2001). Linking the physical characteristics of a river to the biological attributes of river-associated organisms will help us to better understand the variability in species' responses to anthropogenic flow regime change.

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