Guadalupe Bass flow-ecology relationships; with emphasis on the impact of flow on recruitment

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GUADALUPE BASS FLOW-ECOLOGY RELATIONSHIPS; WITH EMPHASIS ON THE IMPACT OF FLOW ON RECRUITMENT

Final report to the Gulf Coast Prairie Landscape Conservation Cooperative and the Wildlife Management Institute
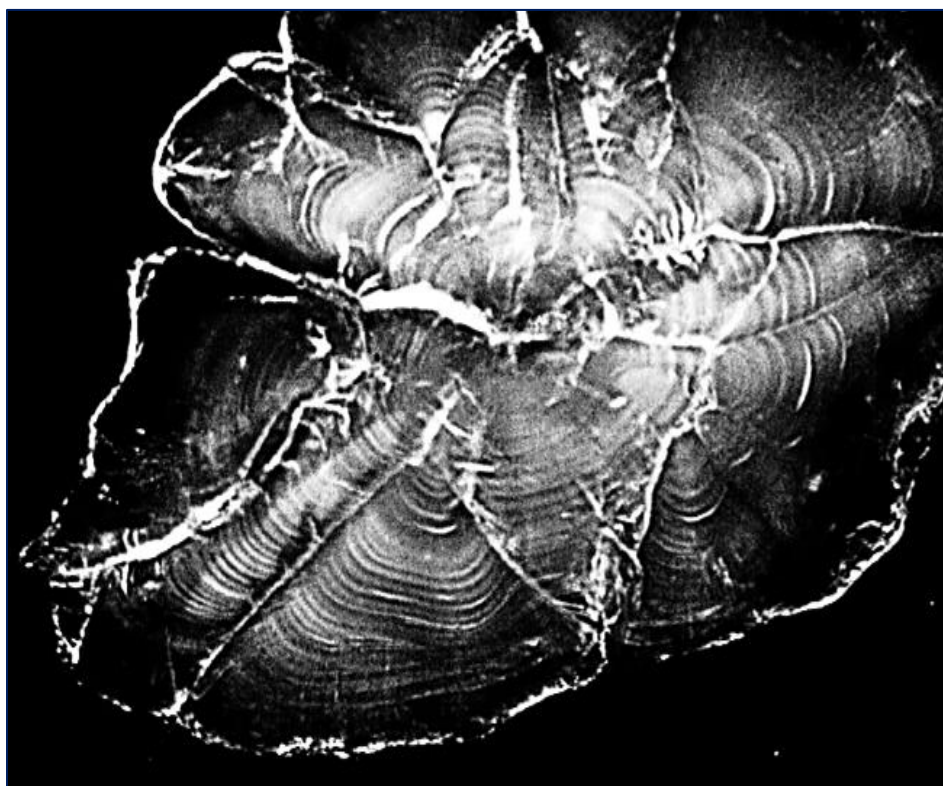
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Executive Summary

Guadalupe Bass *Micropterus treculii* is an economically and ecologically important black bass species endemic to the Edwards Plateau ecoregion and the lower portions of the Colorado River in central Texas. It is considered a fluvial specialist and as such, there are concerns that the increasing demands being placed upon the water resources of central Texas by growing human populations have the potential to negatively impact Guadalupe Bass populations. Therefore, this study assessed the relationship between Guadalupe Bass growth, feeding ecology, and streamflow. Sagittal otoliths were removed from Guadalupe Bass collected from throughout their range during 2015-2017 and used to estimate the age and back-calculate the growth trajectory of each individual. Additionally, young-of-year (YOY) Guadalupe Bass were collected every 10-14 days from two second-order streams, the North Llano River and South Llano River, in the Colorado Basin on the Edwards Plateau. Stomach contents of these individuals were identified and the effect of streamflow on the occurrence of the taxa comprising the stomach contents assessed.

Guadalupe Bass growth was greater in the Colorado and Guadalupe River basins, independent of stream order, and tended to increase with increasing stream order within a basin. Growth was higher in higher stream orders and during years with stable and lower spring and summer monthly median flows, lower minimum and maximum flows, slower rise and fall rates, and higher baseflows. Growth was not influenced by years with higher monthly median flows in winter. These results would seem to contradict previous research, but more likely represent a fuller picture of how Guadalupe Bass respond to flow conditions. The disagreement between the current study and past studies seem to be attributable, at least in part, to the fact that previous studies were conducted during a period of extensive drought, while the current study was conducted during relatively wet conditions. Taken together with previous studies, the current study suggests that Guadalupe Bass growth is sensitive to flow conditions and is lower in years with flow conditions that fall outside a basin- and stream order-specific optimal range for the species.

A total of 21 unique taxonomic groups were recovered from the stomachs of YOY Guadalupe Bass collected from the North Llano River and South Llano River. Aquatic insects, especially larval mayflies (Ephemeroptera), damselflies (Odanata: Zygoptera), and caddisflies (Trichoptera), were the most frequently encountered taxa. While there was no difference between the two rivers in stomach content composition, there was a strong longitudinal gradient in both systems with aquatic insects predominating at upstream sample sites and fishes being more common at downstream sites. Stream discharge during the 24 hours prior to collection did not have any influence on the probability of a taxa being found in Guadalupe Bass stomachs.

The results of this study support efforts to manage Guadalupe Bass populations at a sub-watershed scale and suggests that populations occupying the same stream order within a basin are likely to have similar responses to annual flow conditions. In addition, these results indicate that the lower Colorado River population may inhabit a unique set of conditions that has supported the development of a trophy Guadalupe Bass fishery. Further, this study highlights the need to incorporate a sufficient range of annual flow conditions to ensure that the influence of stream flow on fish growth is adequately assessed. While interannual variation in growth rates seem to be capable of serving as a proxy for recruitment and year-class strength, long-term monitoring of recruitment paired with assessment of growth is necessary to further clarify the relationship between population density, flow regime, recruitment and growth and allow the construction of predictive models.

Acknowledgements

Introduction

Recruitment, growth, and mortality are the three primary factors that determine the size and structure of fish populations, and unfortunately from a management perspective, all three factors are highly variable. Understanding the interplay of these factors and how environmental conditions and ecological interactions influence recruitment, growth, and mortality are critical for being able to predict and model population responses to environmental disturbances as well as developing conservation and management strategies. In riverine and stream fishes, there are numerous environmental factors and ecological interactions that can influence recruitment, growth, and mortality both directly and indirectly. While temperature and flow regime are likely to be the most important environmental factors influencing population dynamics for most stream fishes, developing direct relationships between environmental inputs, such as temperature and flow regime, and growth, recruitment, or mortality rates has proven challenging. However, without a thorough understanding of these relationships, it is difficult to develop recommendations for instream flows to benefit species of conservation concern.

Guadalupe Bass *Micropterus treculii* is an economically and ecologically important black bass species endemic to the Edwards Plateau ecoregion and the lower portions of the Colorado River in central Texas. The species distribution seems to be centered on the Colorado River Basin, but it is found throughout the portions of the Brazos River, Guadalupe River, and San Antonio River watersheds on the Edwards Plateau, including an introduced population in the Nueces River (Edwards 1980; Hubbs et al. 2008). Guadalupe Bass is one of the most abundant aquatic predators where it occurs (Edwards 1980; Bean et al. 2013; Cheek et al. 2016), is a potential indicator of stream health in the Edwards Plateau (Groeschel 2013), and is one of the primary targets of a recreational fishery that generates an estimated $76 million in economic activity in central Texas (Thomas et al. 2015). However, Guadalupe Bass is also listed as a Species of Greatest Conservation Need by Texas Parks and Wildlife Department due to a combination of acute and chronic threats (Birdsong et al. 2015). Smallmouth Bass *Micropterus dolomieu* was intensively stocked across the Edwards Plateau in the 1970's and the species rapidly hybridized with Guadalupe Bass (Whitmore and Butler 1982; Whitmore 1983; Garrett 1991; Morizot et al. 1991). Hybridization rates approached 100% in some drainages (Littrell et al. 2007; Bean et al. 2013), prompting extensive restoration efforts which seem to be having a positive impact on Guadalupe Bass populations (Birdsong et al. 2015; Fleming et al. 2015). While the efforts to control the threats posed by introgression and hybridization may ultimately prove successful, Guadalupe Bass face more chronic and diffuse threats due to changing land use patterns and flow regimes associated with the rapid urbanization occurring along the eastern edge of the Edwards Plateau, particularly within the Austin and San Antonio metropolitan areas (Birdsong et al. 2015). The human populations of these urban areas have increased dramatically since the 1980s and are predicted to continue growing (Murdock et al. 2002; Texas Water Development Board 2012). For example, the population of Austin has more than tripled since 1980 and is projected to grow by $\geq 3.0\%$ yr^{-1} during 2010-2020 (Murdock et al. 2002; U.S. Census Bureau 2010). This

increasing human population will place additional pressure on surface and groundwater supplies that are already struggling to meet current demands (Murdock et al. 2002; Ward 2011; Texas Water Development Board 2012) and will result in shifts in land-use patterns. For example, streams on the Edwards Plateau in the Colorado River Basin have seen significant changes in flow regime (Pease et al. 2018; Figure 1) and this pattern has undoubtedly been repeated in other systems across the region. Further alterations are likely due to not only water demands, but also changing climatic conditions (Ward 2011; Texas Water Development Board 2012).

Habitat degradation due to altered flow regimes and changing land-use patterns is thought to have been the major contributing factor to declines in abundance and local extirpations of Guadalupe Bass (Hurst et al. 1975, Edwards 1978, 1980, Garrett et al. 2015) and have the potential to impact populations in several ways (Grabowski 2014). Guadalupe Bass populations require a relatively undisturbed mosaic of instream habitats, as they exhibit both ontogenetic (Groeschel 2013), and seasonal and diel (Perkin et al. 2010; Pease 2018) shifts in habitat use. The species demonstrates a preference for higher-current velocity habitats (Perkin et al. 2010; Groeschel 2013; Pease 2018) and as such any hydrological alterations persistently reducing the productivity, availability, connectivity, or accessibility of riffles and runs are likely to negatively impact Guadalupe Bass populations (Grabowski 2014). Previous studies have found a negative correlation between low discharges and the growth of age-0 Guadalupe Bass (Groeschel 2013; Massure 2016). There is some evidence to suggest that year class strength exhibits a similar pattern (Groeschel 2013), but this relationship has not been well established.

The mechanisms driving these potential flow-growth and flow-recruitment relationship are not understood. Grabowski (2014) presented several hypotheses based on available data for Guadalupe Bass and other stream-dwelling black bass species, such as Smallmouth Bass and Shoal Bass *Micropterus cataractae*. The three hypotheses were 1) Guadalupe Bass growth, and ultimately recruitment, would be negatively correlated with the magnitude and duration of extreme low flow events, 2) Guadalupe Bass habitat quality and availability is negatively associated with both reduced base flow and the magnitude and duration of extreme high flow events, and 3) the nest success of Guadalupe Bass is negatively correlated to the duration and magnitude of high flow pulses during the spawning season. However, the data available to test and refine these hypotheses were not available. Therefore, the objectives of this study were to evaluate these hypotheses at both a range-wide scale and a much finer spatial and temporal scale to both evaluate broad trends and identify potential mechanisms driving such trends.

Methods

Study area

The Edwards Plateau ecoregion encompasses just over 97,000 km^2 of central Texas in the area commonly referred to as the Texas Hill Country (Figure 1). The region comprises the majority of
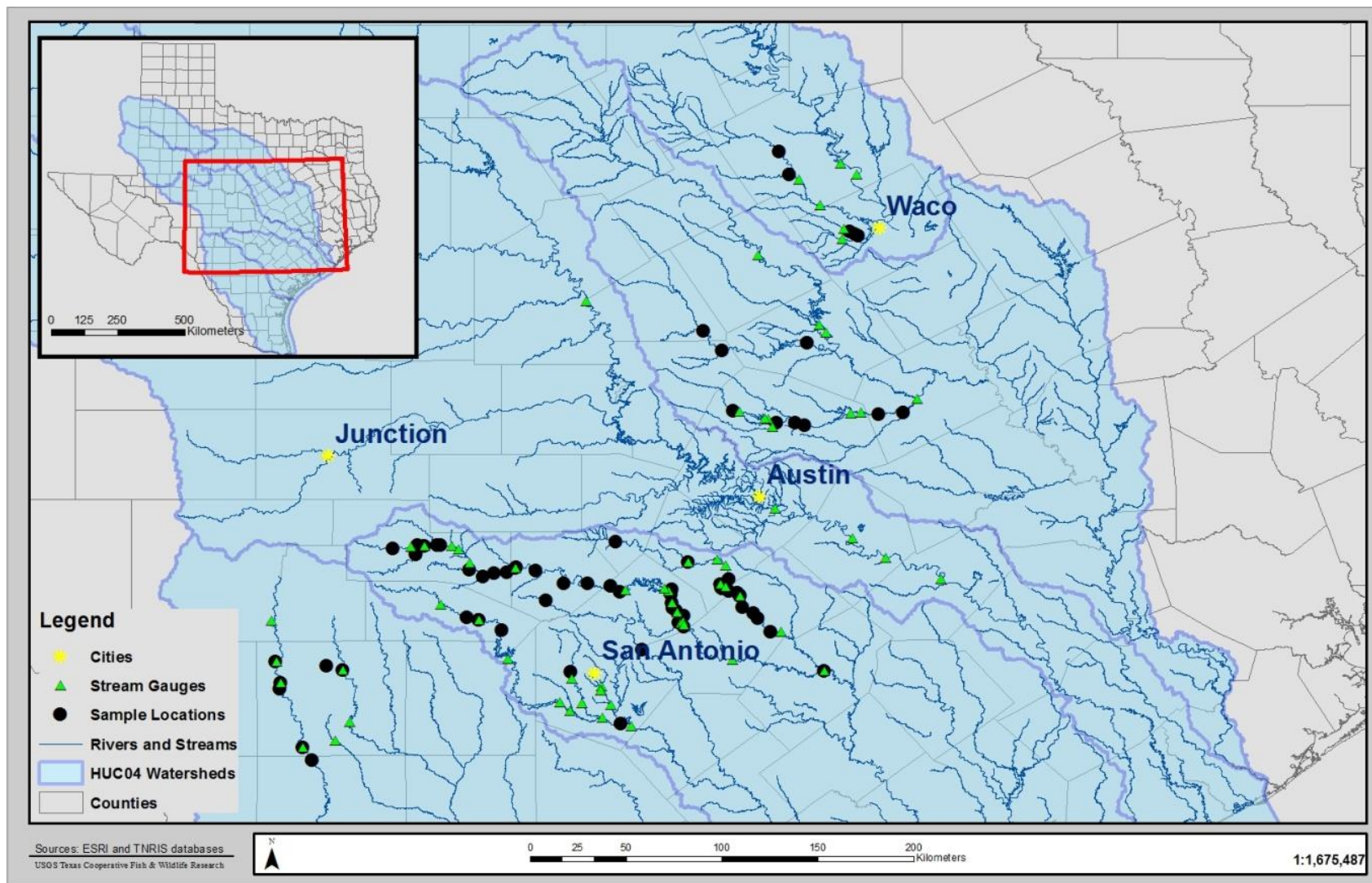
Figure 1. Map of the portions of the Brazos, Colorado, Guadalupe, San Antonio, and Nueces River Basins on the Edwards Plateau in central Texas with the locations sampled by Edwards (1980) and USGS gage stations indicated.

7

the range of Guadalupe Bass, with populations reported from the portions of the Brazos, Colorado, Guadalupe, San Antonio, Nueces, that flow on the Edwards Plateau. The rivers and streams of the Edwards Plateau are characterized by clear water, stable temperatures, high levels of dissolved solids, high aquatic macrophyte productivity, and high levels of biodiversity and endemism (Bowles and Arsuffi 1993). However, the hydrology of the rivers and streams on the Edwards Plateau have been heavily altered. A combination of groundwater and surface water withdrawals for agriculture and municipal use have reduced baseflows and impoundments have altered the timing, magnitude, and duration of high and low flow events (Bowles and Arsuffi 1993). Two of the fastest growing metropolitan areas in the United States, Austin and San Antonio, are both located within the Edwards Plateau ecoregion and their continuing growth will increase the demand placed on the streams and aquifers of the region.

The North Llano River (NLR) and South Llano River (SLR) are spring-fed, second-order streams that join near Junction, Texas approximately 180 km west of San Antonio to form the Llano River, a major tributary of the Colorado River. The NLR and SLR have watersheds of approximately equal size ($\approx$2,400km²), are similar in length (NLR= 93 km; SLR= 88 km), and share a similar geology and climate. The uppermost 50-60 km of both the NLR and SLR are intermittent before reaching more consistently flowing, spring-influenced portions. These rivers are representative of those found throughout the Edwards Plateau ecoregion of central Texas. Both are pool and drop rivers with karst bedrock substrates in the upstream reaches that transition to coarse gravel and cobble substrates in the downstream reaches (Broad 2012; SLWA 2012; Cheek et al. 2016). For most of their length, the NLR and SLR have open canopies. The NLR and SLR have different hydrologic characteristics and degree of anthropogenic disturbance (Edwards et al. 2004; Broad 2012). The SLR has a typical discharge rate that is about 4X that of the NLR. The NLR experiences 21–22 zero-flow days per year and is reduced to a series of isolated pools during most summers, while a zero-flow day has not been recorded in the SLR (TPWD 2005; Broad 2008; 2012; U.S. Geological Survey gage 08148500 and gage 08150000). Both rivers have experienced the same anthropogenic disturbances, but the degree of alteration through permanent and primitive road crossings, riparian alterations, dams, agricultural water withdrawals, and mining operations is greater on the NLR (SLWA 2012). Despite these disturbances, both the NLR and SLR are still considered relatively pristine (Hubbs et al. 1991; Curtis et al. 2015; Hendrickson and Cohen 2015).

Acquisition and analysis of stream discharge data

Discharge data was downloaded from the USGS National Water Information System (www.waterdata.usgs.gov/nwis) for the stream gage nearest to each sampling station. These data were summarized by year using Indicators of Hydrological Alteration v. 7.1 (Richter et al. 1996). The IHA software package calculates a suite of 32 hydrologic attributes across four broad categories describing the annual flow regime: magnitude of monthly median flows, magnitude and duration of flow extremes, timing of extreme flow conditions, and the frequency and duration of pulses (Richter et al. 1996; Table 2). A principal component analysis (PCA) was

performed on the resulting output of annual flow metrics for each gaging station to produce composite variables describing annual flow conditions (Jacquemin et al. 2015; Massure 2016; Pease 2018).

While discharge data for the NLR is readily available (stream gage 08148500), there is not a comparable gage on the SLR. Discharge for the SLR was estimated by subtracting the discharge of the NLR from that measured by the gage (gage station 08150000) on the Llano River < 2 km downstream of the confluence of the NLR and SLR (Groeschel 2013; Massure 2016). In addition to being used to calculate annual flow metrics as described above, these data were used to calculate the 24-hr mean discharge, in the SLR to evaluate the influence of discharge on diet of YOY Guadalupe Bass.

Range-wide assessment of flow effects on growth

A range-wide assessment of historical age structure and growth patterns relative to flow regime and land use was conducted using scales taken from specimens collected throughout the entire range of Guadalupe Bass, primarily during the late 1970s and deposited at the Ichthyology Collection at the Texas Natural History Collection (Edwards 1980; Hendrickson and Cohen 2010; Figure 1). However, the majority of individuals held in the collection were YOY and there was an insufficient number of fishes ≥ age 1 to conduct meaningful comparison to contemporary individuals. Therefore, no results of these comparisons are presented here. However, contemporary survey sites were selected prior to discovering the age structure of the Guadalupe Bass held in collections and thus were matched to the locations used by Edwards (1980) and for which stream gage data are available (Figure 1). Each location was surveyed for Guadalupe Bass using multiple pass electrofishing. All captured Guadalupe Bass were euthanized by immersion an a >250 mg L^{-1} aqueous solution of buffered tricaine methanesulfonate (MS-222; Leary et al. 2013) and stored on ice until they could be returned to the lab.

In the lab, each individual was measured to the nearest mm total length (TL). Fin clips were collected and sent to the Texas Parks and Wildlife Fish Health and Genetics Laboratory at A.E. Wood Fish Hatchery in San Marcos, Texas to be screened for Guadalupe Bass X Smallmouth Bass hybrids. Any hybrids that were identified were excluded from further analysis. Sagittal otoliths were extracted, cleaned of adhering tissue, and stored dry (Long and Grabowski 2018). Otoliths were mounted in epoxy resin and sectioned through the nucleus using a low-speed saw. The resulting thin sections were mounted to glass slides using thermoplastic cement and polished as needed to expose the nucleus. Each otolith section was photographed using a binocular dissecting microscope equipped with a digital camera (Long and Grabowski 2018). Age was assessed by two independent readers with a third reader resolving any discrepancies between the first two readers. The sample was excluded from further analysis if a resolution was not reached. Otolith radius and the radius to each annulus will be measured using ImageJ v. 1.48 (Abramoff et al. 2004) and length at age back-calculated using the Dahl-Lea direct proportion method (Campana 1990; Schramm et al. 1992):

$$TL_i = \frac{R_i}{R_c} \times TL_c$$

where TL_i is the back-calculated total length at age i, TL_c is the total length at capture, R_i is the otolith radius at age i, and R_c is the otolith radius at capture.

The mean back-calculated TL at each age was calculated for each basin separately and all basins pooled together and a Von Bertalanffy growth curve was fitted to these means. The Von Bertalanffy growth function is:

$$L_t = L_\infty \times (1 - e^{-k(t-t_0)})$$

where L_t is the predicted length at age t, L_∞ is the mean asymptotic TL, k is the growth rate coefficient, and t_0 is the theoretical age where TL = 0 mm. Due to the model failing to converge on realistic values of L_∞ (see Appendix 1), the value of L_∞ was set at 432 mm TL, the reported TL of the world record Guadalupe Bass recently captured from the Colorado River downstream of Austin, Texas, when fitting the Von Bertalanffy growth curves. All Von Bertalanffy growth curves were fit using PROC NLIN implemented in SAS 9.4 (SAS Institute Inc., Cary, North Carolina).

The relative growth index (RGI; Jackson et al. 2008) was calculated as the standardized residual of each back-calculated TL at age from the TL predicted by the Von Bertalanffy growth curve at that age using the following equation:

$$Z = \frac{TL_i - L_t}{L_t}$$

where TL_i is the back-calculated TL at age i, L_t is the length at age t predicted by the Von Bertalanffy growth curve, and $i = t$. The effect of annual flow metrics, stream order, and basin on RGI was evaluated using a mixed-effect model analysis of covariance (ANCOVA) implemented using PROC GLIMMIX in SAS 9.4 (SAS Institute Inc., Cary, North Carolina). Relative growth index was used as the dependent variable and river basin, stream order, and the first three principal components from the PCA conducted on the IHA variables were the fixed effects in the model. Age was treated as a random effect and grouped by individual fish to account for repeated, non-independent measures of RGI within individuals.

Back-calculated length at age were also compared across basins and stream orders using a mixed-effect model analysis of covariance (ANCOVA) implemented using PROC GLIMMIX in SAS 9.4 (SAS Institute Inc., Cary, North Carolina). Back-calculated TL at age was treated as the dependent variable while age, basin, and stream order were treated as fixed effects. Individual fish were treated as a subject effect in order to account for the repeated, non-independent measures of back-calculated TL made within each individual.

Assessment of flow effects on YOY Guadalupe Bass feeding

Young-of-year Guadalupe Bass were collected from transects established in the NLR and SLR at locations in the upper, middle, and lower thirds of the two rivers (Figure 1). Transect locations were primarily selected based on accessibility. Sampling was conducted every 10 days during June-August 2015-2016 using multiple pass electrofishing. The first ten YOY Guadalupe Bass captured from each location were euthanized and retained for further analysis as described below. All other Guadalupe Bass captured were measured to the nearest mm total length and a fin clip was taken prior to the fish being released. The euthanized fish were stored on ice and returned to the lab where stomachs and sagittal otoliths were removed. Stomach contents were preserved in a 70% ethanol solution.

Stomach contents were identified to the lowest taxonomic level possible in six broad prey categories, i.e., empty, aquatic insects, fishes, terrestrial arthropods, other aquatic invertebrates, and unidentified. Differences in the composition of stomach contents were evaluated using canonical correspondence analysis. Logistic regression was used to evaluate the influence of mean discharge 24 hrs prior to collection, the TL of the fish, location in the river, i.e., upper, middle, and lower, and river on the probability of encountering a fish with an empty stomach or containing each of the broad prey categories.

Results

Flow characteristics of central Texas rivers and streams

Streamflow data from 35 U.S. Geological Survey stream gages, representing 1,746 water years, were collected for analysis. Stream orders 3 and 4, particularly from rivers in the Colorado River and Guadalupe River basins, were best represented in the data set (Table 1). Conversely, data were far more limited from the tributaries of the Brazos River on the Edwards Plateau and the Nueces River.

Three principal components were needed to explain approximately 62.7% of the interannual variability in IHA variables across the study area. The first principal component (PC1) accounted for approximately 48.3% of the variation in the data set and was positively correlated with spring and summer monthly median flows, minimum and maximum flows, and rise rate (Table 2). The second (PC2) and third (PC3) principal components were negatively correlated with winter monthly median flows and baseflow, respectively, and together explained an additional 14.4% of the variation in the dataset (Table 2).

Stream gages tended to have similar principal component scores based on stream order and basin (Figure 2). Stream order was positively correlated with PC1, even when the observations from the gages on the mainstem Colorado River (stream order=6) were excluded ($F_{4,1528}=23.21$, $P<0.01$). While higher stream orders also tended to have higher values of PC2 ($F_{4,1528}=6.73$, $P<0.01$), there was a trend of increasing PC2 scores from the southernmost basin, the Nueces, through the northernmost basin, the Brazos ($F_{3,1528}=3.34$, $P=0.02$; Figure 2). There was not a

Table 1. Quantity and distribution of stream discharge data from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas. All stream gages represented are operated by the U.S. Geological Survey.

Basin	Stream order	Number of stream gages	Number of water years	Mean (±SE) number of water years per gage
Brazos		**8**	**187**	**23±9**
	2	4	68	17±11
	3	4	119	30±14
Colorado		**12**	**739**	**62±8**
	2	2	150	75
	3	3	226	75±23
	4	4	255	64±15
	6	3	108	36±11
Guadalupe		**13**	**717**	**55±8**
	2	3	173	58±7
	3	3	179	60±20
	4	7	365	52±14
Nueces		**2**	**103**	**51±43**
	3	1	94	—
	4	1	9	—
Overall		**35**	**1746**	**50±5**
	2	9	391	43±10
	3	11	618	56±11
	4	12	620	52±10
	6	3	108	36±11

Table 2. Indicators of hydrological alteration variables and variable classes with their eigenvector values. Eigenvector values were produced from a principal component analysis of all available discharge data collected from U.S. Geological Survey stream gages in the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas. Variables with eigenvector values ≥ |0.20| are highlighted with bold text.

IHA variable class	IHA variable	PC1	PC2	PC3
Magnitude of monthly median flows	January	0.17	**-0.34**	0.08
	February	0.14	**-0.39**	0.12
	March	0.19	**-0.30**	0.04
	April	**0.21**	**-0.24**	0.02
	May	**0.21**	-0.14	0.02
	June	**0.20**	-0.16	0.07
	July	0.16	0.02	-0.01
	August	**0.22**	0.01	-0.08
	September	**0.22**	0.04	-0.08
	October	0.19	**0.22**	-0.12
	November	0.17	**0.29**	-0.09
	December	0.19	**0.24**	-0.12
Magnitude and duration of flow extremes	1-day minimum	**0.22**	0.05	**-0.22**
	3-day minimum	**0.22**	0.05	**-0.22**
	7-day minimum	**0.22**	0.06	**-0.23**
	30-day minimum	**0.23**	0.08	**-0.21**
	90-day minimum	0.24	0.07	-0.15
	1-day maximum	0.14	**0.23**	**0.38**
	3-day maximum	0.17	0.19	**0.35**
	7-day maximum	**0.20**	0.13	**0.32**
	30-day maximum	**0.23**	-0.03	**0.24**
	90-day maximum	**0.23**	-0.12	0.18
	Number of zero-flow days	-0.03	-0.01	0.15
	Base flow	-0.02	-0.05	**-0.43**
Timing of extreme flow conditions	Date of minimum	-0.01	**-0.29**	-0.13
	Date of maximum	0.01	**0.29**	0.10
Frequency and duration of pulses	Low pulse number	-0.02	-0.04	0.04
	Low pulse duration	-0.02	-0.08	0.06
	High pulse number	0.07	0.14	0.01
	High pulse duration	0.01	0.10	0.07
Rate of change	Rise rate	**0.23**	-0.06	0.01
	Fall rate	**-0.24**	0.03	0.05
	Eigenvalue	15.44	2.38	2.21
	Percent variance explained	48.3	7.5	6.9

Figure 2. Biplots of the mean annual principal component scores from analysis of Indicators of Hydrological Alteration (IHA) variables calculated using stream discharge data from U.S. Geological Survey stream gages in the Brazos, Colorado, Guadalupe, and Nueces river basins of central Texas. Stream orders (SO) of 2-6 are included in this analysis. Eigenvector values of the IHA variables comprising the principal component scores are reported in Table 2. Error bars represent the 95% confidence intervals around the means.

clear relationship between PC3 and stream order, but gages in the Brazos and Colorado basins tended to have higher values of PC3 than those from the Guadalupe and Nueces basins ($F_{3,1528}$=4.10, P<0.01; Figure 2), suggesting that baseflow was higher in the Brazos and Colorado streams and was lower in the streams of the Guadalupe and Nueces basins.

Streamflow exhibited several consistent trends across all basins and stream orders in central Texas during the years encompassing the life spans of the Guadalupe Bass used in this study (2007–2017). Scores of PC1 tended to be lower during the drought of 2010–2013 relative to the other years (2007–2009, 2014–2017), and the effect of the drought, as measured by the change in PC1 scores, was more pronounced in higher-order streams ($F_{3,331}$≥7.10, P≤0.01; Figure 3) indicating lower summer monthly median flows, minimum and maximum flows, and rise rates. In contrast, scores for PC3 tended to be higher during the drought relative to the other years and experienced a greater change in higher-order streams ($F_{3,331}$≥5.77, P≤0.02; Figure 3) indicating lower winter monthly median flows and baseflows. There was no clear effect of drought on winter monthly median flows (PC2; $F_{3,331}$≥0.05, P≤0.82).

Guadalupe Bass growth – range wide

A total of 580 Guadalupe Bass were collected from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas (Table 3). An insufficient number of Guadalupe Bass were collected from the San Antonio River Basin to conduct meaningful analysis, so these individuals were excluded. There was relatively little variation in the mean TL or range of TL of fish collected from the different river basins (Table 3); however, mean age and the age range of the samples were more variable (Table 3). Mean back-calculated TL at age were similar across the four basins (Figure 4).

Mean back-calculated TL at age was variable across the Brazos, Colorado, Guadalupe, and Nueces river basins ($F_{4,626}$=2670.41, P < 0.01; Appendices 1-5) and covaried by stream order ($F_{4,578}$=32.41, P < 0.01; Figure 5). There was a positive relationship between mean back-calculated TL at age and stream order in both the Colorado and Guadalupe river basin (t_{598}≥2.01, P≤0.05), but this relationship was not consistently observed in the Brazos and Nueces river basins (t_{598}≤-1.37, P≥0.17; Figure 5). Mean back-calculated TL of age-1 individuals was similar across all four river basins (t_{578}≤0.00, P≥0.88). However, the mean back-calculated TL of individuals ≥ age-2 from the Colorado River Basin was greater than that of individuals from the Brazos River Basin and the mean back-calculated TL of individuals ≥ age-3 from the Colorado River Basin was greater than those other two basins (t_{578}≥2.68, P≤0.04; Figure 5). There were no meaningful differences in mean back-calculated TL at age among the Brazos, Guadalupe, and Nueces river basins (t_{578}≤0.42, P≥0.98).

Mean standardized growth of Guadalupe Bass varied by basin (Table 4), with individuals in the Brazos and Nueces river basins being, on average, about the size at age predicted by the range-wide Von Bertalanffy growth model and individuals from the Colorado and Guadalupe river
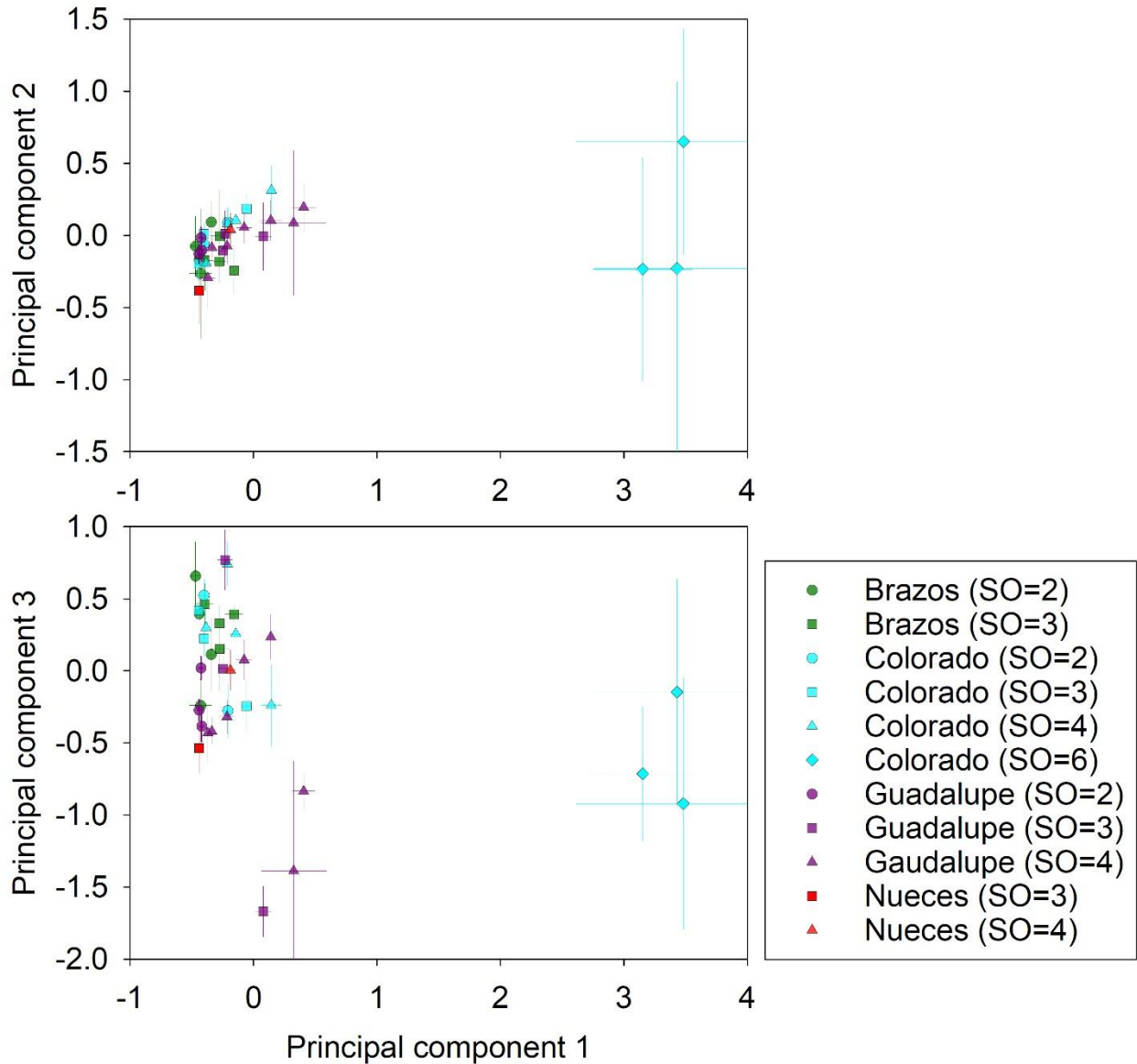
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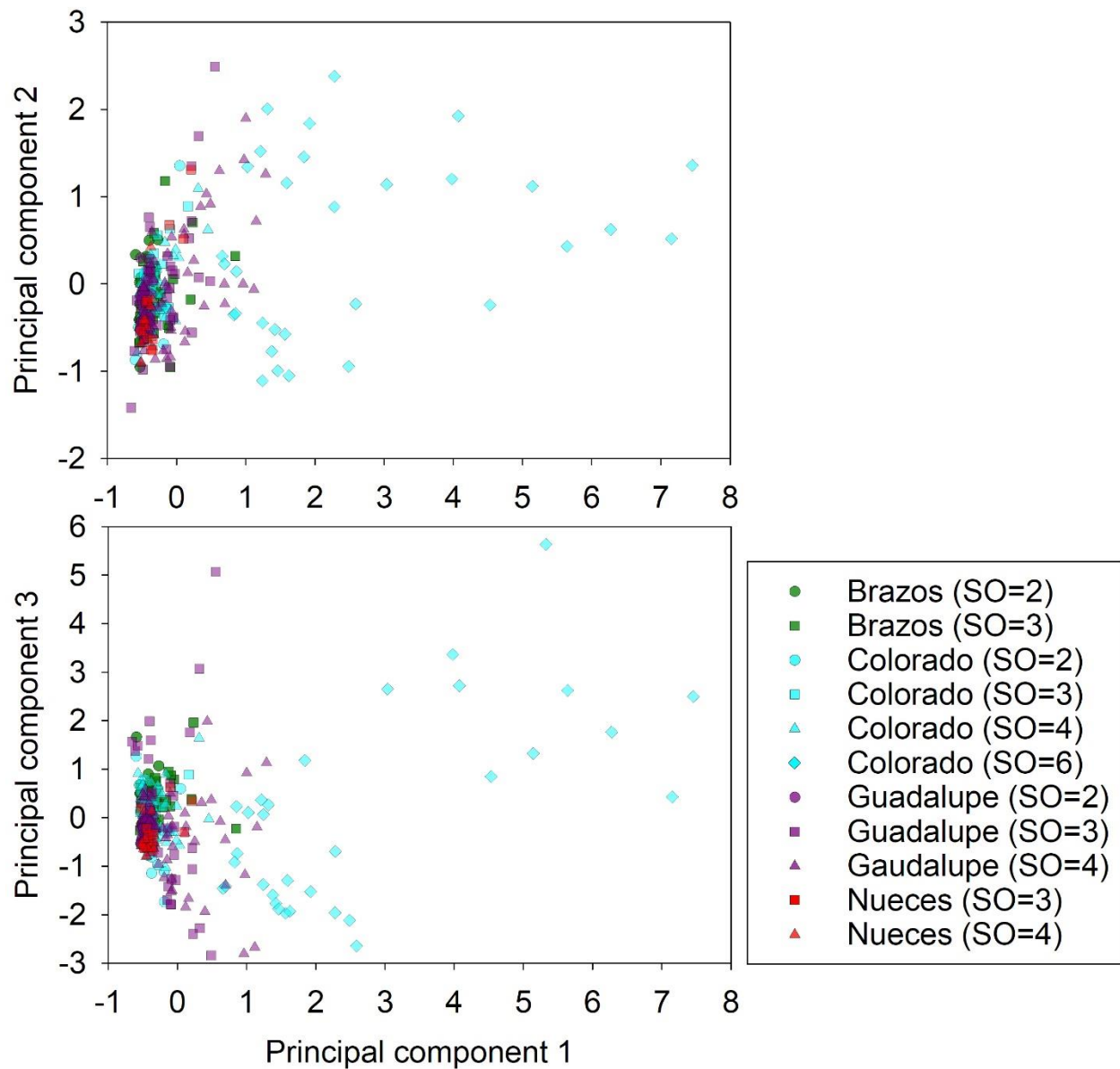
Figure 3. Biplots of the annual principal component scores from analysis of Indicators of Hydrological Alteration (IHA) variables calculated using stream discharge data from U.S. Geological Survey stream gages in the Brazos, Colorado, Guadalupe, and Nueces river basins of central Texas during the period encompassing the lifespans of the Guadalupe Bass *Micropterus treculii* used during the present study (2007–2017). Stream orders (SO) of 2-4 and 6 are included in this analysis. Eigenvector values of the IHA variables comprising the principal component scores are reported in Table 2.

Table 3. Mean and range of total length (TL) and age and Von Bertalanffy growth curve parameter estimates of Guadalupe Bass *Micropterus treculii* populations sampled from streams within the Brazos, Colorado, Guadalupe, and Nueces River Basins in central Texas during 2015–2017. Von Bertalanffy growth curves were fitted to mean back-calculated lengths at age as estimated from sagittal otoliths and theoretical maximum length (L∞) was held constant at 432 mm TL.

Basin	Stream order	River	n	Mean (±SE) TL (mm)	TL range (mm)	Mean (±SE) age (yrs)	Age range (yrs)	Von Bertalanffy growth curve parameter estimates – k (±SE)	Von Bertalanffy growth curve parameter estimates – t_0 (±SE)
Brazos	**2–3**	**—**	**216**	**190±6**	**84–345**	**2.4±0.1**	**1–6**	**0.21±0.01**	**-0.16±0.16**
	2	Salado Creek	17	218±19	165–307	2.8±0.4	2–5		
	2	North Fork San Gabriel River	7	158±23	93–219	1.9±0.3	1–3		
	2	South Fork San Gabriel River	20	117±14	101–277	2.2±0.3	1–5		
	2,3	Brushy Creek	73	205±11	84–345	2.8±0.4	1–6		
	3	Lampasas River	14	170±21	93–305	2.1±0.4	1–4		
	3	San Gabriel River	85	182±9	103–292	2.0±0.2	1–4		
Colorado	**2–4,6**	**—**	**234**	**190±5**	**74–461**	**1.9±0.1**	**1–8**	**0.26±0.02**	**0.17±0.25**
	2	North Llano River	74	171±8	74–365	2.1±0.1	1–6		
	2	South Llano River	47	192±12	78-461	2.4±0.2	1–8		
	3	Barton Creek	12	178±15	87–237	1.8±0.2	1–3		
	3,4	San Saba River	47	192±12	141–318	1.4±0.2	1–4		
	3,4	Llano River	35	185±8	108–307	1.3±0.1	1–3		
	4	Pedernales River	21	199±11	116–311	1.3±0.1	1–3		
	6	Colorado River	20	262±19	79–380	2.3±0.4	1–5		
Guadalupe	**2–4**	**—**	**202**	**187±4**	**71–346**	**2.3±0.1**	**1–6**	**0.19±0.01**	**-0.33±0.22**
	2	Johnson Creek	19	206±16	81–330	2.9±0.4	1–5		
	2,3	North Fork Guadalupe River	17	171±10	96–277	2.1±0.2	1–4		
	2,3	South Fork Guadalupe River	6	203±23	142–285	2.7±0.6	1–5		
	3	Blanco River	22	158±11	86–251	2.0±0.2	1–4		
	3,4	San Marcos River	18	241±15	120–346	3.1±0.3	1–6		
	4	Guadalupe River	120	182±5	71–328	2.2±0.1	1–5		
Nueces	**3–4**	**Nueces River**	**42**	**179±9**	**85–306**	**2.3±0.2**	**1–5**	**0.17±0.01**	**-0.71±0.11**
		Total	**694**	**188±3**	**71–461**	**2.2±0.1**	**1–8**	**0.24±0.03**	**0.13±0.30**
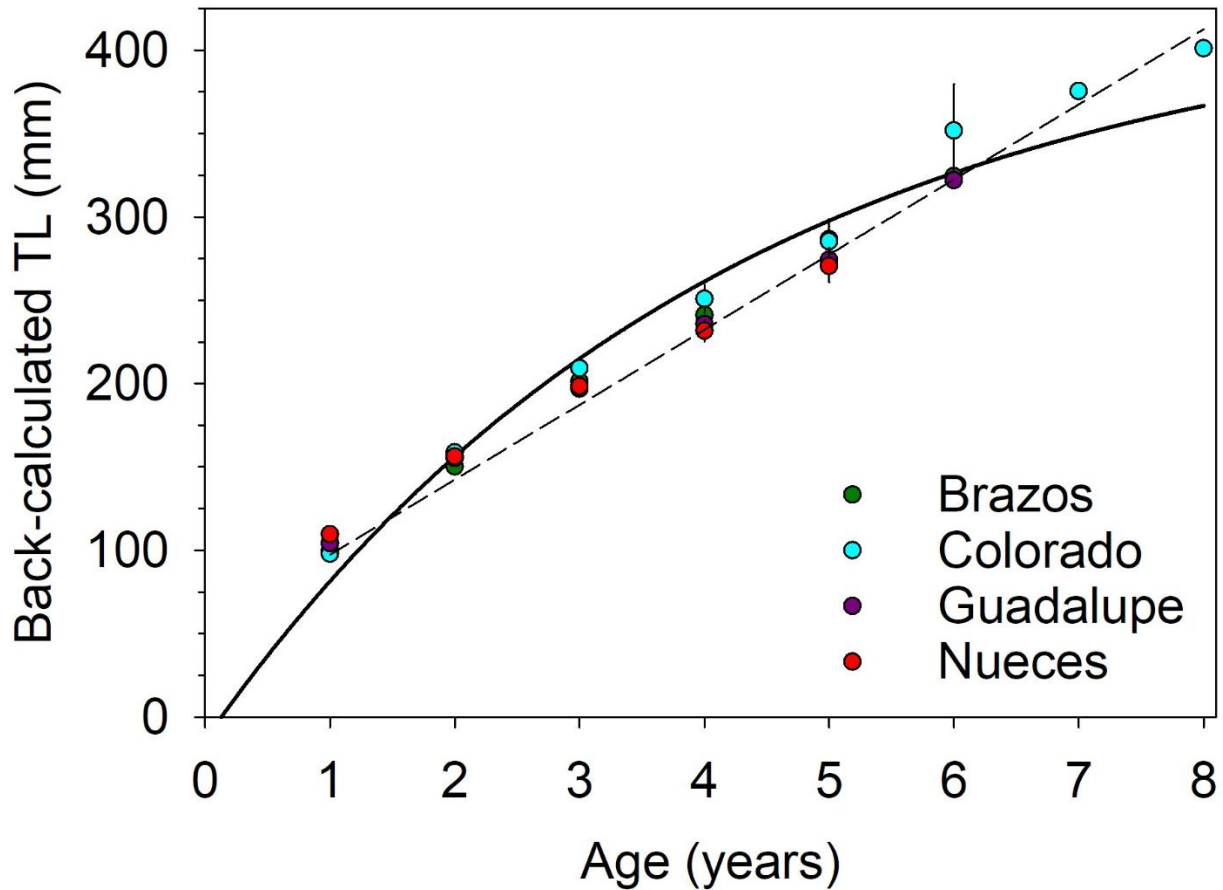
17

Figure 4. Mean back-calculated total length (TL) at age of Guadalupe Bass *Micropterus treculii* captured from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015–2017. Error bars represent standard error and the solid line is the predicted total length at age based on a Von Bertalanffy growth curve fitted to the mean back-calculated lengths at age for all basins pooled (see Table 3 for parameter estimates). Dashed line is a linear regression fitted to the mean length at age data and presented for comparison purposes.
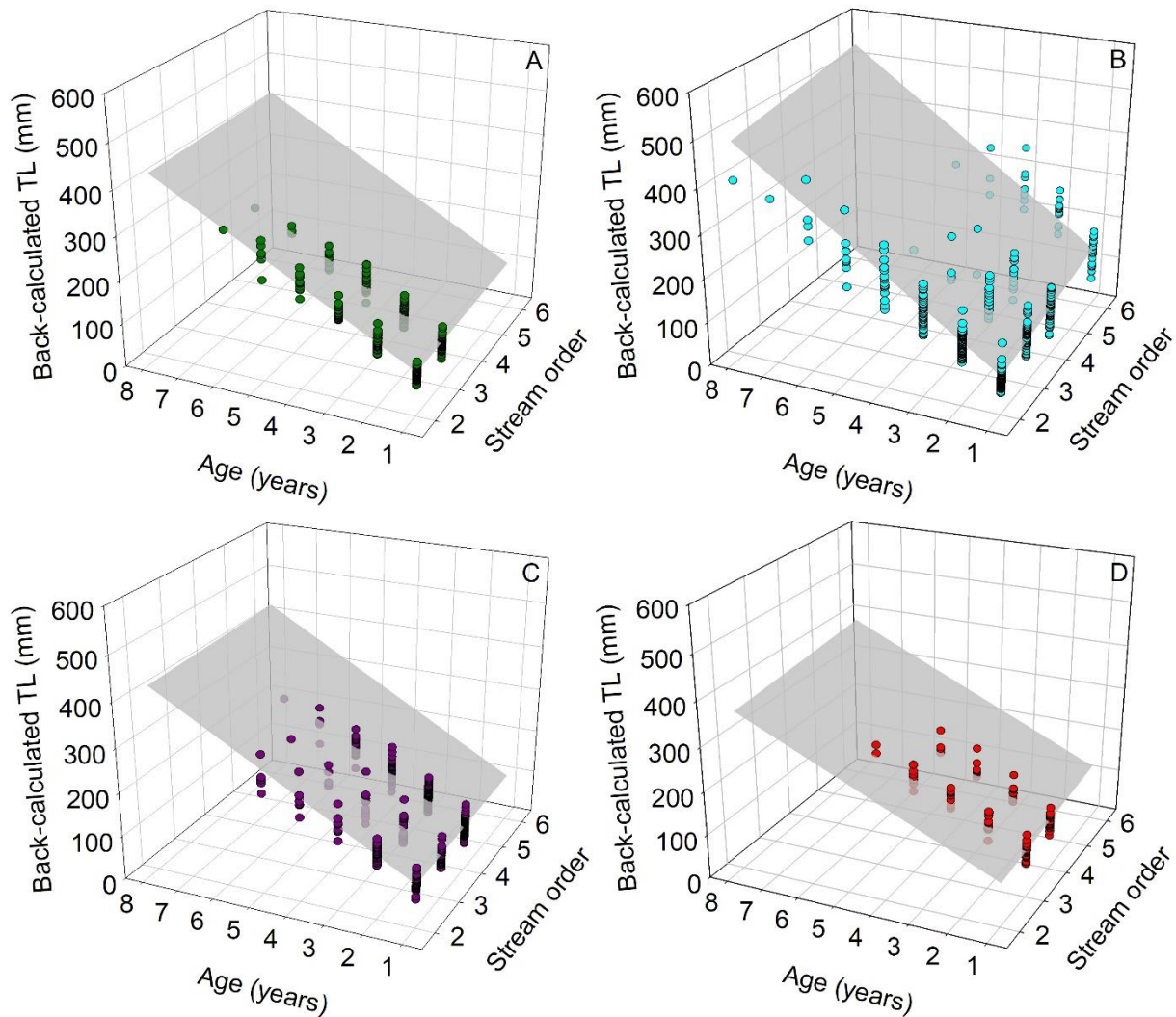
Figure 5. Back-calculated total length (TL) at age of Guadalupe Bass *Micropterus treculii* collected from different stream orders within the Brazos (A), Colorado (B), Guadalupe (C), and Nueces (D) river basins in central Texas during 2015–2017. The gray plane represents back-calculated lengths at age within each basin as predicted by a linear mixed-effects model.

19

Table 4. Parameter estimates (±SE) and test statistics of fixed effects from a linear mixed effects model evaluating the relationship between standardized growth of Guadalupe Bass *Micropterus treculii* captured from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015-2017 and the basin of capture, stream order or capture, and principal component scores from analysis of Indicators of Hydrological Alteration (IHA) variables calculated using stream discharge data from U.S. Geological Survey stream gages. Eigenvector values of the IHA variables comprising the principal component scores are reported in Table 2.

Parameter	Basin	Estimate (±SE)	*df1,df2*	*F*	*P*
Intercept		-0.76 ± 0.26	3, 598	4.16	0.01
Basin			4, 598	35.12	<0.01
	Brazos	0.43 ± 0.29			
	Colorado	0.32 ± 0.27			
	Guadalupe	0.61 ± 0.27			
	Nueces	0			
Stream order (Basin)			4, 598	35.12	<0.01
	Brazos	0.09 ± 0.04			
	Colorado	0.18 ± 0.02			
	Guadalupe	0.07 ± 0.02			
	Nueces	0.21 ± 0.07			
PC1(Basin)			4, 649	13.89	<0.01
	Brazos	-0.11 ± 0.03			
	Colorado	-0.03 ± 0.01			
	Guadalupe	-0.04 ± 0.01			
	Nueces	-0.14 ± 0.04			
PC2		-0.005 ± 0.010	1, 649	0.26	0.61
PC3		0.02 ± 0.01	1, 649	7.42	0.01

basins being larger than predicted (Figure 6). However, both stream order and annual flow conditions influenced standardized growth. Similar to mean back-calculated TL, standardized growth exhibited a positive relationship with stream order across all of the basins ($F_{4,598}=35.12$, $P<0.01$; Figure 7). Standardized growth was negatively associated with PC1 ($F_{4,649}=13.89$, $P<0.01$; Figure 7) in every basin. Standardized growth was greater in higher-order streams and during years with lower spring and summer monthly median flows, lower minimum and maximum flows, and slower rise and fall rates. Standardized growth was not influenced by years with higher monthly median flows in winter as evidenced by the lack of a relationship between standardized growth and PC2 in all four river basins ($F_{1,649}=0.26$, $P=0.61$; Figure 8). There was a positive relationship between baseflow (PC3) and the standardized growth of Guadalupe Bass in all of the river basins ($F_{1,649}=7.42$, $P=0.01$; Figure 8).

Effect of streamflow on young-of-year Guadalupe Bass feeding ecology

The stomach contents of a total of 1,243 YOY Guadalupe Bass collected from the NLR and SLR were examined (Table 5). While aquatic insects, especially larval mayflies (Ephemeroptera), damselflies (Odanata: Zygoptera), and caddisflies (Trichoptera), were the most frequently encountered taxa in Guadalupe Bass stomachs, a total of 21 unique taxonomic groups were recovered and identified (Table 5). Percid darters and cyprinid minnows were the most common fish taxa found in Guadalupe Bass stomachs, and terrestrial arthropods were found relatively infrequently (Table 5). Only 36% of the individuals examined had more than one prey item type in their stomach and various combinations of Ephemeroptera, Zygoptera, Hemiptera, and unidentified insects constituted the contents of most of these stomachs.

There was no difference between the NLR and SLR in the composition of the stomach contents; however, there were consistent differences between the upper, middle, and lower portions of the two rivers (Mahalanobis distance ≥ 0.50, $F_{27,1214}\geq3.34$, $P\leq0.01$; Table 5, Figure 9). Only two canonical axes were necessary to account for the variability in stomach contents of Guadalupe Bass from the upper, middle, and lower reaches of the NLR and SLR (eigenvalue ≤ 0.22; $F_{26,1215}\geq1.81$, $P\leq0.01$). However, there was considerable overlap among stream reaches in the composition of Guadalupe Bass stomach contents as the linear discriminant functions constructed from these canonical axes produced an error rate of approximately 51%.

Guadalupe Bass with empty stomachs comprised 22% of the individuals examined (Table 5). While there was no difference between the NLR and SLR in the probability of encountering an individual with an empty stomach ($F_{1,1234}=0.95$, $P=0.33$), the chances of encountering a Guadalupe Bass with an empty stomach increased from upper reaches to lower reaches ($F_{2,1234}=6.39$, $P<0.01$; Figure 10). Day of year, mean discharge on the day of capture, and TL had no effect on the probability of capturing a Guadalupe Bass with an empty stomach ($F_{1,1234}\leq1.76$, $P\geq0.19$).

21
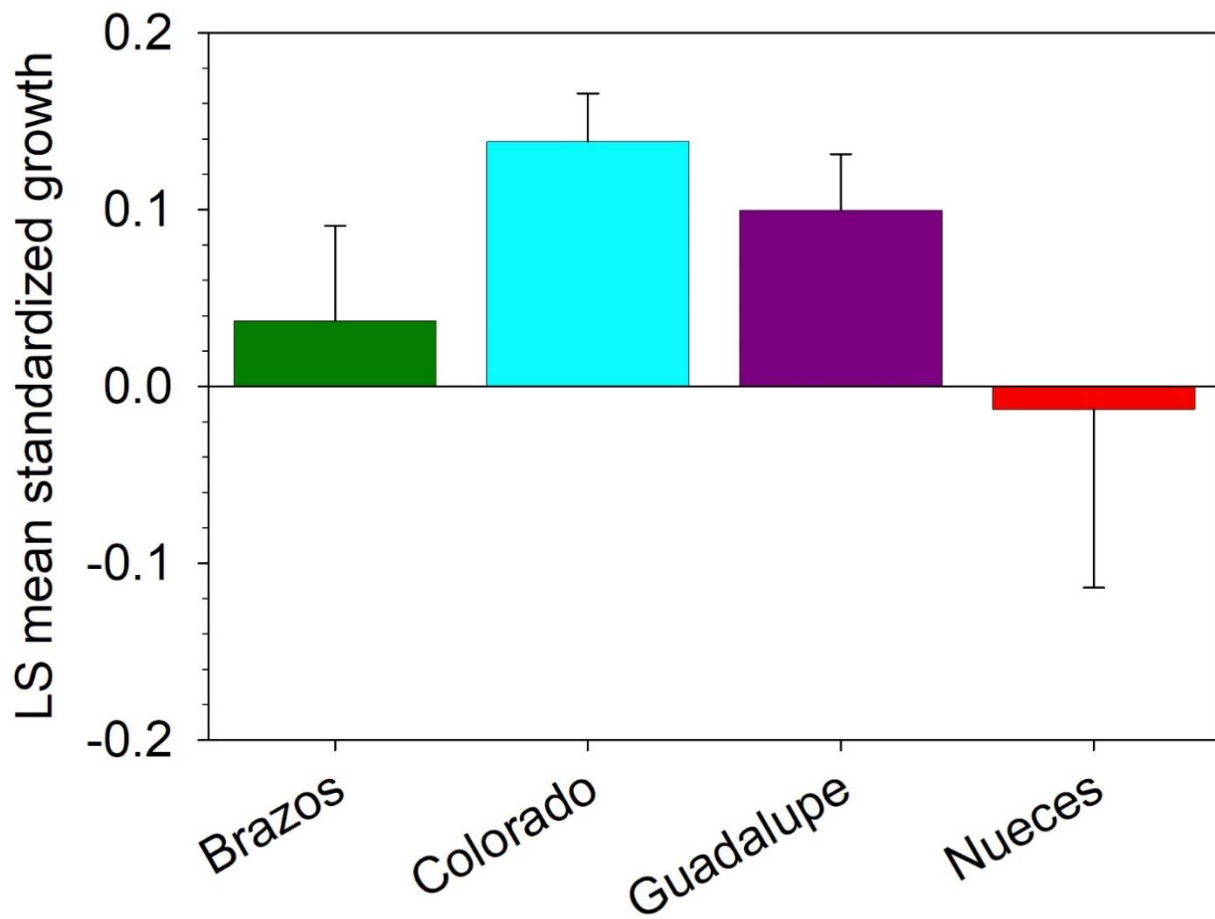
Figure 6. Least-squares (LS) mean standardized growth of Guadalupe Bass *Micropterus treculii* collected from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015–2017. Error bars represent 95% confidence intervals around the LS means.
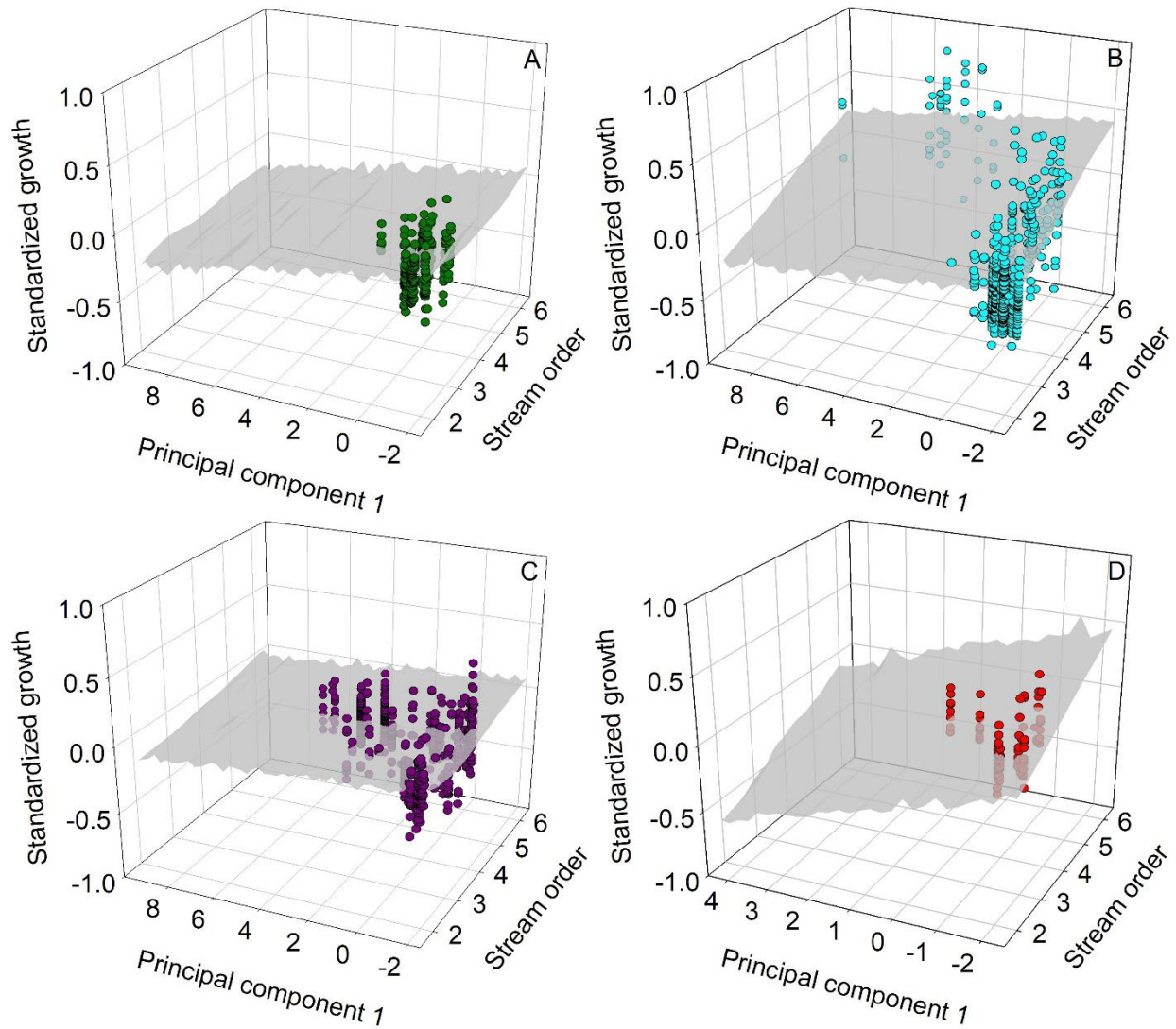
Figure 7. Relationship between standardized growth of Guadalupe Bass *Micropterus treculii*, stream order, and stream discharge as represented by a principal component of annual flow metrics in the Brazos (A), Colorado (B), Guadalupe (C), and Nueces (D) river basins in central Texas during 2015–2017. Principal component 1 is positively correlated with lower spring and summer monthly median flows, lower minimum and maximum flows, and slower rise and fall rates. The variables contributing to principal component 1 and their associated eigenvectors are listed in Table 2. The gray plane represents standardized growth within each basin as predicted by a linear mixed-effects model.
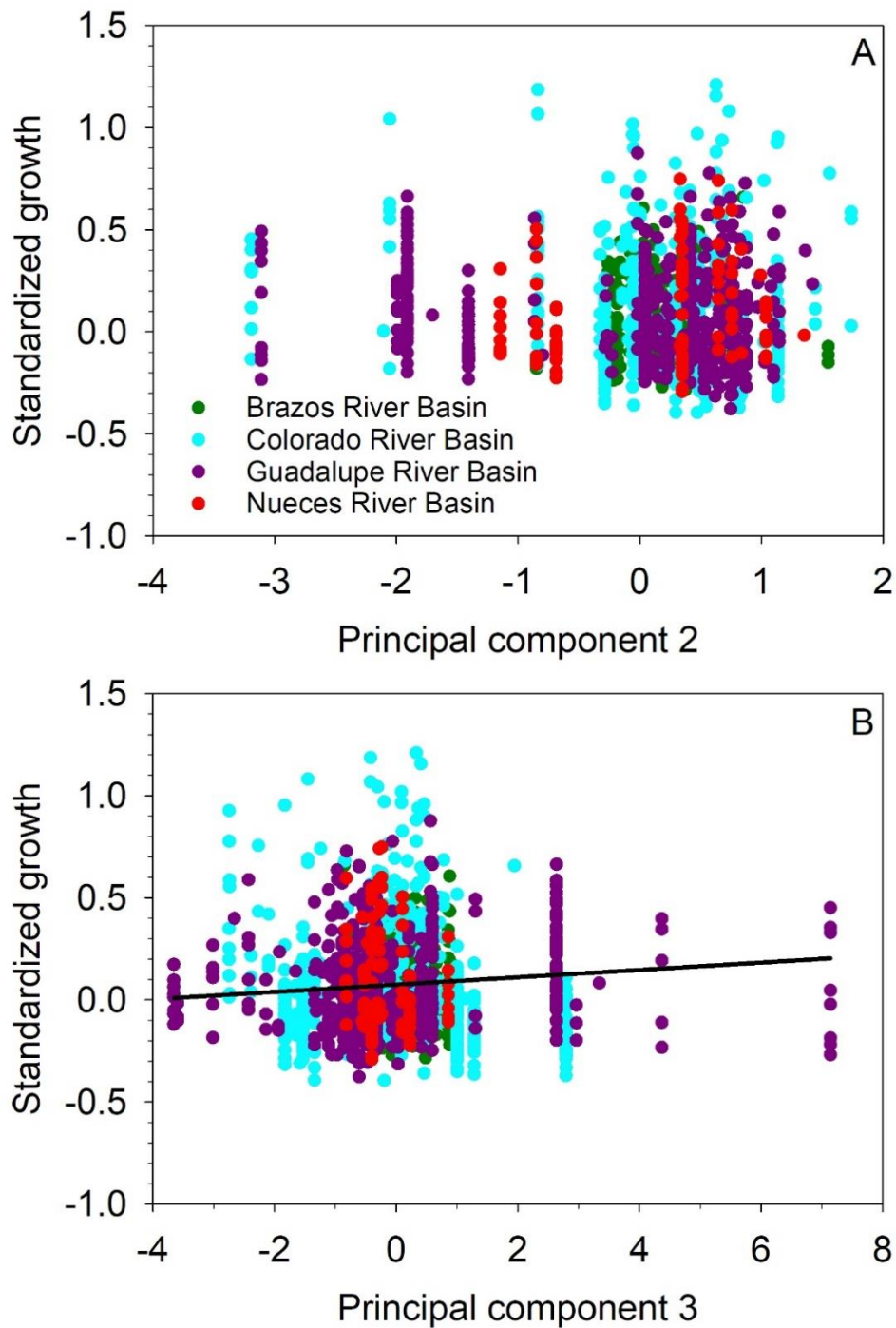
Figure 8. Relationship between standardized growth of Guadalupe Bass *Micropterus treculii* and stream discharge as represented by the second (A) and third (B) principal components of annual flow metrics in the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015–2017. Principal component 2 is positively correlated with higher monthly median flows in winter, while principal component 3 is positively correlated with baseflow. The variables contributing to principal components 2 and 3, as well as their associated eigenvectors, are listed in Table 2.

Table 5. Percent of stomachs containing various categories of prey taxa, number of stomachs examined, the mean and range of total lengths of the young-of-year Guadalupe Bass collected from the upper, middle, and lower portions of the North Llano River and South Llano River in central Texas during 2016–2017 from which the stomachs were removed. UID = unidentifiable.

		Upper North Llano River	Middle North Llano River	Lower North Llano River	Upper South Llano River	Middle South Llano River	Lower South Llano River
N		169	191	283	144	257	199
TL (mm)	Mean (±SE)	71±1	69±1	65±1	76±1	66±1	59±1
	Range	37–105	39–121	25–144	36–119	38–113	24–111
Empty		12.4	28.3	30.0	9.7	14.8	31.7
Aquatic insects	Anisoptera	3.6	3.1	2.8	6.3	4.3	1.5
	Diptera	5.9	3.7	1.8	1.4	6.6	9.0
	Ephemeroptera	66.9	30.9	29.7	72.2	54.1	27.1
	Hemiptera	17.8	20.4	9.5	13.9	18.3	11.1
	Megaloptera	1.2	0.5	0.4	1.4	1.2	0.0
	Trichoptera	14.8	3.1	2.5	16.7	7.8	3.0
	Zygoptera	23.7	24.1	23.7	20.8	19.5	16.6
Fishes	Centrarchidae	0.6	0.0	1.4	0.0	0.8	0.0
	Cichlidae	0.6	0.0	1.1	0.0	0.4	1.5
	Cyprinidae	0.0	0.5	1.8	0.0	0.4	2.0
	Ictaluridae	0.0	0.0	0.4	0.0	0.8	0.5
	Poeciliidae	0.0	0.0	0.4	0.0	0.8	0.5
	Percidae	0.0	0.5	3.5	0.0	0.0	4.0
	UID Fish	1.2	9.9	6.7	6.3	4.3	14.1
Terrestrial arthropods	Araneae	0.0	1.6	0.4	0.7	0.8	1.0
	Hymenoptera	0.0	0.5	0.0	0.0	1.2	0.0
	Lepidoptera	2.4	0.0	0.4	1.4	0.0	0.5
	Orthoptera	0.0	0.0	0.4	0.0	0.0	0.0
	UID winged insect	0.6	1.6	0.7	0.0	2.3	0.5
Other invertebrates	Amphipod	0.6	0.0	0.7	0.0	0.0	0.0
	Annelid	0.0	0.5	0.0	0.0	0.0	0.5
	Cambaridae	0.0	0.0	0.4	0.0	0.0	0.5
Unidentified	Object	0.0	1.0	0.7	1.4	0.0	0.5
	Insect	16.0	13.1	10.2	6.9	24.5	12.1
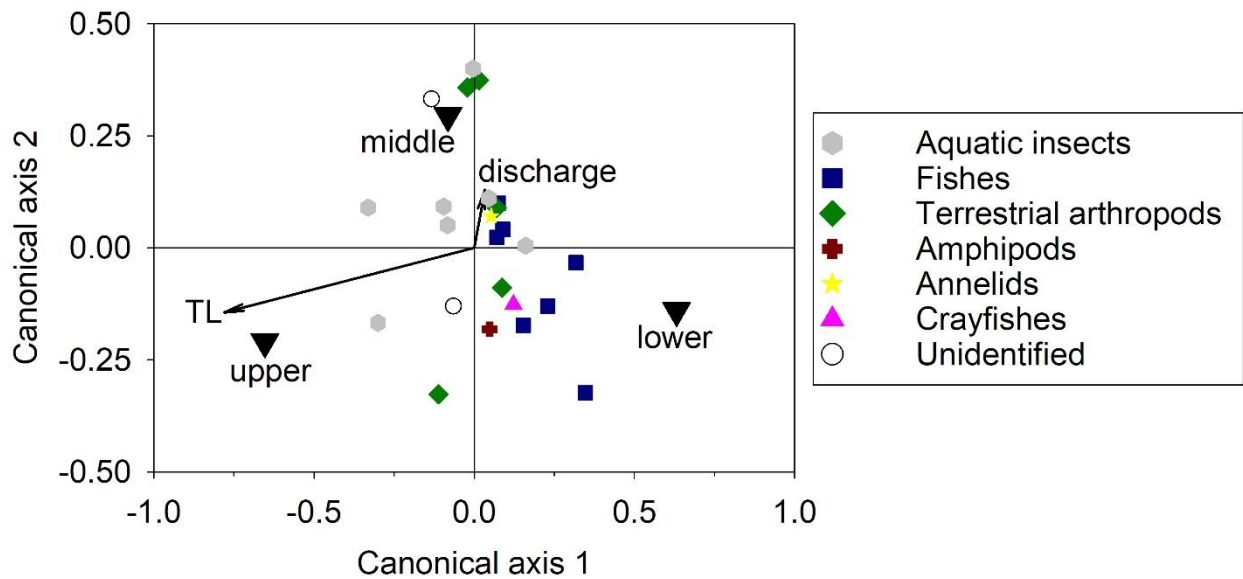
Figure 9. Biplot of the taxa found in the stomachs of young-of-year Guadalupe Bass *Micropterus treculii* collected from study reaches in the upper, middle, and lower North Llano River and South Llano River in central Texas during May-August 2016 and 2017. Total length (TL) and the mean stream discharge recorded during the 24 hours prior to collection were the only variables identified as influential. Canonical axis 1 had an eigenvalue of 0.22 and explained approximately 85% of the variation in the dataset, while canonical axis 2 explained the remaining 15% of the variability and had an eigenvalue of 0.04. The taxa comprising each of the prey categories are listed in Table 4.

The probability of encountering an individual with terrestrial insects in its stomach was relatively low, i.e.,< 5%, and did not differ between the two rivers ($F_{1,1227}=1.6$, $P=0.21$). Nor did the occurrence of empty stomachs vary between the three reaches ($F_{2,1227}=1.01$, $P=0.36$; Figure 10). Furthermore, the probability of occurrence of terrestrial insects in Guadalupe Bass stomachs was independent of discharge, day of year, and TL ($F_{1,1227}\leq2.84$, $P\geq0.09$).

In contrast, the probability of occurrence of aquatic insects in Guadalupe Bass stomachs was dependent upon both reach ($F_{2,1227}=12.36$, $P<0.01$) and the TL of the individual ($F_{1,1227}=9.16$, $P<0.01$; Figure 11). Individuals captured from the upper reaches of the NLR and SLR had a higher probability of having aquatic insects in their stomachs compared to counterparts in the middle and lower reaches ($t_{1227}\leq-3.37$, $P<0.01$). Further, the probability of an individual having aquatic insects in their stomach was inversely related to its TL (Figure 11). Stream discharge and day of the year did not influence the probability of Guadalupe Bass stomachs containing aquatic insects ($F_{1,227}\leq0.90$, $P\geq0.34$).

While aquatic insects were more commonly encountered in the stomachs of smaller Guadalupe Bass captured from the upper reaches of the NLR and SLR, fishes were more commonly encountered in larger individuals captured from farther downstream (Figure 12). The probability of fishes occurring in the stomachs of Guadalupe Bass increased from the upper reaches to the lower reaches of both the NLR and SLR ($F_{2,1227}=19.23$, $P<0.01$), but there were no differences between the two rivers ($F_{1,1227}<0.01$, $P=0.99$). Fishes were more likely to be observed in the stomachs of Guadalupe Bass with increasing TL ($F_{1,1227}=31.35$, $P<0.01$) and increasing mean discharge during the 24 hrs prior to capture ($F_{1,1227}=5.78$, $P=0.02$).

Discussion

The annual flow metrics derived from stream gage data from the Brazos, Colorado, Guadalupe, and Nueces river basins reflect expected patterns associated with stream order and regional climatic gradients. On the Edwards Plateau, low-order headwater streams are primarily spring-fed from the underlying Trinity and Edwards Aquifers (Bowles and Arsuffi 1993). While there were differences in principal component scores of low-order streams between the river basins, these streams generally exhibited less interannual and between-stream variability than higher-order streams in the same basins. The increasing human population density from west to east across the Edwards Plateau also was likely contributing to higher interannual variability of flow metrics in higher-order streams. This human population gradient follows the direction of flow in each of the four basins examined in this study, culminating in the highly urbanized corridor between Austin and San Antonio along the Balcones Escarpment that constitutes the eastern edge of the Edwards Plateau. However, human population density is not the only gradient relevant to streamflow on the Edwards Plateau. The portions of the Brazos, Colorado, Guadalupe, and Nueces river basins flowing across the Edwards Plateau occur along a strong east-west precipitation gradient influencing differences in a particular stream order across basins. It also may contribute to the observed between-basin variability in the annual flow metrics
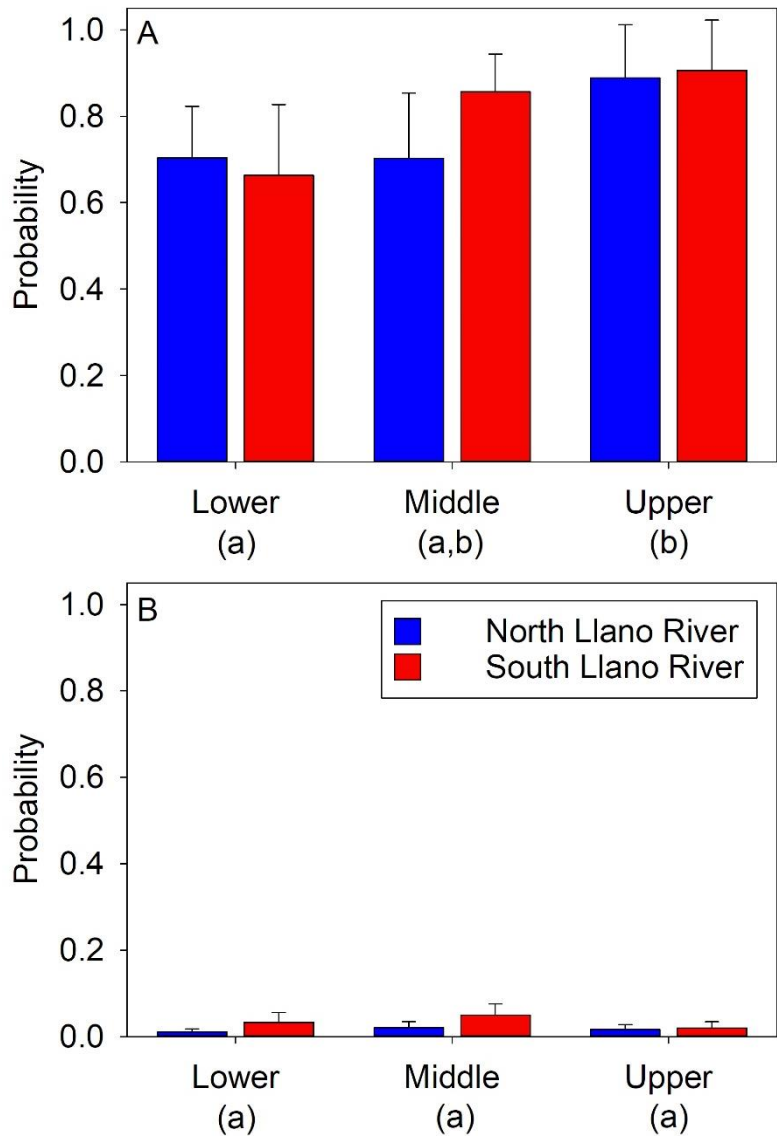
Figure 10. Probability of occurrence of full stomachs (A) and stomachs containing terrestrial insects (B) from young-of-year Guadalupe Bass *Micropterus treculii* sampled from study reaches in the upper, middle, and lower portions of the North Llano River and South Llano River in central Texas during May-August 2016 and 2017. Differences between reaches in the upper, middle, and lower portions of the two rivers are indicated by letters in parentheses along the axis. There was no difference detected between the North Llano River and the South Llano River. The taxa comprising terrestrial insects are listed in Table 4.

28
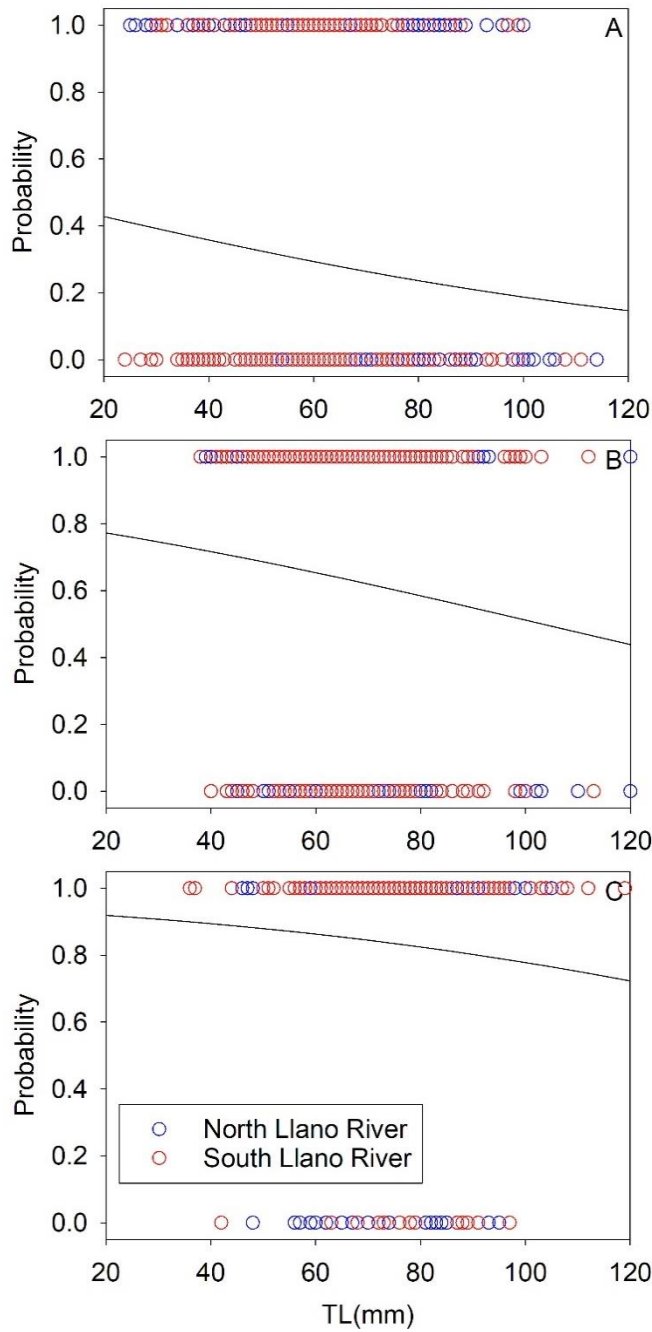
Figure 11. Probability of occurrence of aquatic insects in the stomachs of young-of-year Guadalupe Bass *Micropterus treculii* sampled from study reaches in the lower (A), middle (B), and upper (C) portions of the North Llano River and South Llano River in central Texas during May-August 2016 and 2017. There was no difference detected between the North Llano River and the South Llano River. The taxa comprising aquatic insects are listed in Table 4.
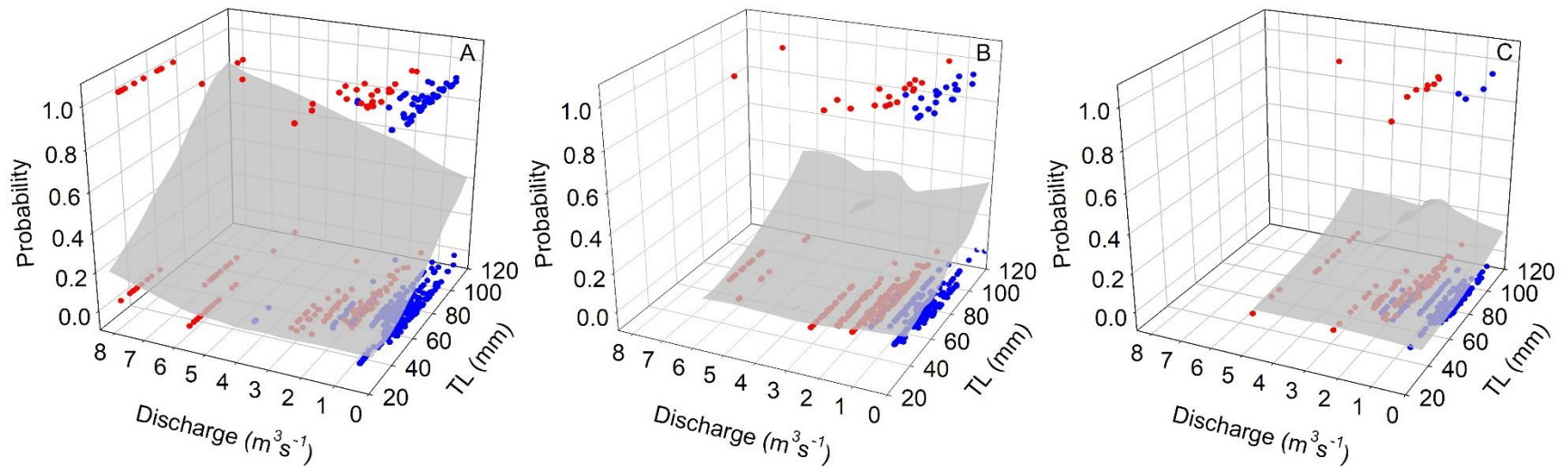
Figure 12. Relationship between total length (TL), mean stream discharge during the 24 hours prior to sampling and the probability of occurrence of fishes in the stomachs of young-of-year Guadalupe Bass *Micropterus treculii* sampled from study reaches in the lower (A), middle (B), and upper (C) portions of the North Llano River (blue) and South Llano River (red) in central Texas during May-August 2016 and 2017. The gray plane represents the probability of the occurrence of fishes in stomachs from Guadalupe Bass as predicted by a linear mixed-effects model. There was no difference detected between the North Llano River and the South Llano River. The taxa comprising fishes are listed in Table 4.

recorded at the gaging stations within higher-order streams that are less directly influenced by groundwater discharge.

The interannual variability in streamflow between basins and across different order streams within a basin was influential on the growth rates of Guadalupe Bass. On average and independent of stream order and annual flow metrics, Guadalupe Bass growth in the Colorado and Guadalupe river basins tended to be greater than that predicted by the Von Bertalanffy growth function. In contrast, growth of Guadalupe Bass in the Brazos and Nueces generally matched predicted values. There are a number of potential explanations for this higher growth rate in the Colorado and Guadalupe river basins. Guadalupe Bass exhibit a relatively high degree of genetic population structuring between basins (Bean 2012), raising the possibility that the different growth rates are due to underlying genetic differences between the populations in the four river basins. While the levels of genetic diversity of populations in the Brazos River Basin are comparable to those in the Colorado and Guadalupe river basins, the Nueces River Basin population is more homogenous (Bean 2012), likely due to a founder effect stemming from the introduction of the species to the Nueces River in the 1970s (Hubbs et al. 2008; Curtis et al. 2015). The Colorado and Guadalupe river basins also constitute the center of the range of Guadalupe Bass and therefore may potentially represent optimal habitat conditions for the species while the Brazos and Nueces river basins represent the northeastern and southwestern extents of the distribution, respectively. Furthermore, climatic variation on even relatively small spatial scales can result in interpopulation differences in growth patterns. For example, Largemouth Bass *Micropterus salmoides* populations can exhibit differences in growth rates associated with climatic variability and gradients, such as precipitation and temperature gradients and El Niño/Southern Oscillation events (Rypel 2009).

Within a basin, Guadalupe Bass growth rate increased with increasing stream order. Longitudinal studies through a river basin on fish growth are rare in the literature. However, the conditions that would support faster growth rates for a high trophic level predatory fish, such as Guadalupe Bass, are more likely to occur in larger streams (Lotrich 1973; Goto 1989; Tedesco et al. 2009; Olden and Kennard 2010). Habitat area, available cover, and primary production all tend to increase with increasing stream order within a river basin (Hynes 1970; Leopold 1994) and may result in dietary shifts associated with increased availability and quality of prey species. While the present study only examined the stomach contents of YOY Guadalupe Bass from two relatively short streams of the same order, there was a clear change in the probabilities of aquatic insects and fishes occurring in stomachs along an upstream-downstream gradient. An increasing degree of piscivory is associated with faster growth rates in other species of black basses (Olson 1996; Post 2003; Steinhart et al. 2004). Therefore, if the observed pattern from the NLR and SLR holds across a wider spatial scale and age range, then it may provide an explanation for the increased growth rates observed in higher stream orders, particularly in the mainstem Colorado River downstream of Austin, Texas.

31

Guadalupe Bass growth, regardless of basin or stream order, was greater during years with relatively low and stable flow conditions. Growth was positively associated with lower minimum flows, maximum flows, and median monthly flows during spring and summer. This response was consistent across all four basins, but its magnitude was greatest in the Brazos and Nueces river basins. This response to lower discharges was not anticipated given that Guadalupe Bass is widely considered a fluvial specialist (Curtis 2015) and is typically associated with high current velocity habitats (Perkin et al. 2010; Groschel 2013; Pease 2018). Furthermore, previous work done in the NLR and SLR, 2nd order streams in the Colorado Basin, indicated that relative growth was greater in years with higher spring and summer median monthly flows and minimum flows (Massure 2016) or a larger proportion of discharge observations above the 90th percentile (Q_{90}; Groeschel 2013). However, in both of those studies a large proportion of the individuals sampled experienced the extreme drought conditions that occurred throughout Texas during 2010-2013. In contrast, the individuals collected as part of the current study experienced conditions that ranged from average in most of the lower-order streams to the extreme flood events that occurred in the main stems of the Colorado and Brazos Rivers during 2014-2015. Only a relatively small proportion of the individuals sampled for the present study were alive during 2011, considered the worst year of the 2010-2013 drought (Nielsen-Gammon 2012). While the data collected by Groeschel (2013) are not directly comparable to the present study because scales were used as the structure for age estimation, Massure (2016) used otoliths following the same procedures as used in the present study. Therefore, the effect of a fuller range of annual flow conditions on growth was examined by incorporating the data from the 121 fish collected from the NLR and SLR during the present study with the data from the 115 individuals collected by Massure (2016). The same mixed-model analysis described above was performed on the pooled data set and indicated a positive relationship between Guadalupe Bass growth in the NLR and SLR and spring and summer monthly median flows and minimum and maximum flows (β_{PC1}=0.28, $F_{1,260}$=6.99; P=0.01). These findings support the conclusion that a sufficient range of annual flow conditions must be encompassed to adequately assess the influence of stream flow on fish growth. Taken together with previous studies, the current study suggests that Guadalupe Bass growth is sensitive to flow conditions and is lower in years with flow conditions that fall outside a basin- and stream order-specific optimal range for the species.

The sensitivity of Guadalupe Bass growth to annual flow conditions does not seem to be directly associated with its feeding. The stomach content data collected from YOY Guadalupe Bass in the NLR and SLR indicated that fishes were the only category of prey whose probability of occurrence in Guadalupe Bass stomachs was influenced by discharge and there was no relationship between the probability of encountering a fish with an empty stomach and discharge. While macroinvertebrates are important component of Guadalupe Bass diets, feeding on macroinvertebrate drift does not seem to be the primary means by which these prey items are acquired. This largely decouples the feeding ecology of Guadalupe Bass to stream discharge as macroinvertebrate drift tends to exhibit a positive relationship with discharge rates (Corrarino and Brusven 1983). If Guadalupe Bass are drift feeding, the data suggest that it may constitute a

relatively minor component of their feeding ecology or that insect drift in low-order spring-fed Texas streams is independent of discharge under the conditions observed in this study.

Instead directly effecting the feeding of Guadalupe Bass, the influence of annual flow conditions on growth likely operate via Guadalupe Bass trophic ecology through a less direct route, namely by influencing habitat availability and quality. Guadalupe Bass are strongly associated with higher current velocity habitats, such as riffles and runs (Perkin et al. 2010; Groeschel 2013; Pease 2018). The quantity and accessibility of riffles and runs are strongly influenced by discharge (Stewart et al. 2005; Clark et al. 2008). For example, riffle area can rapidly decrease under low-flow conditions, reducing the amount of habitat available to aquatic invertebrates and the ability of fish to forage within these habitats (Freeman et al. 2001; Bradford and Heinonen 2008; Rosenfeld 2017). Furthermore, temperatures with riffles and runs can become extreme and experience a high level of diel variability under low flow conditions (Arismendi et al. 2013; Rosenfeld 2017). In contrast, high flow conditions can render riffles and runs energetically expensive for fish to occupy (Hughes and Dill 1990; Nislow et al. 2000), reducing the energetic benefits of foraging in these habitats. The relationship between discharge, foraging ecology, and growth would also potentially explain the basin- and stream order-specific effects on growth observed in the current study.

While growth rates are generally indicative of conditions that are conducive to strong year class strength (Houde 1987, 1989; Campana 1996; Houde 2008), there is also the potential for there to be an inverse relationship between growth and year class strength due to density-dependent effects on growth (DeAngelis et al. 1991; Lorenzen and Enberg 2002). For example, growth can be inhibited due to intraspecific competition for food resources in habitats with high abundance, resulting in a high risk of overwinter mortality (DeAngelis et al. 1991). While this renders growth as a reasonable proxy for predicting relative year class strength, overwinter mortality is not likely a significant factor influencing Guadalupe Bass populations possibly resulting in a decoupling between growth rate and year-class strength. It is likely that mortality rates are lower and year class strength is greater during years supporting higher growth rates, particularly of YOY, this statement cannot be made unequivocally. Therefore, developing an understanding of the relationship between population density, growth rates, and recruitment in Guadalupe Bass is necessary before measuring growth rates alone will serve as a proxy for year class strength in this species. Theoretically, developing a better understanding of the relationship between growth and year-class strength could be achieved through an examination of the population age structure but this approach poses challenges in relatively short-lived species, such as Guadalupe Bass. For example, the short life span of Guadalupe Bass means that any given study is unlikely to encapsulate a sufficient range of environmental variation to fully examine their influence on recruitment, and as discussed above in the apparent disagreement between the current studies and previous studies on the response to low flow conditions. Furthermore, developing indices of relative recruitment constructed from catch-curve data can require relatively large samples. This may be problematic for Guadalupe Bass as there were difficulties in acquiring the modest sample

sizes in this study from many of the locations surveyed, particularly those outside the Colorado River Basin. Therefore, a monitoring program, in which YOY and juvenile Guadalupe Bass are annually surveyed from fixed stations scattered throughout the species range using a standardized sampling methodology is likely to prove a more effective method of clarifying the relationship between growth, year class strength, and annual flow conditions.

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Appendix 1. Estimates (±SE) of the Von Bertalanffy growth curve parameters fitted to back-calculated length at age data from Guadalupe Bass *Micropterus treculii* collected from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015-2017. In contrast to the results presented in the main paper, the parameter L_∞ was not held constant.

	L_∞	k	t_0
Brazos	818 ± 70	0.08 ± 0.01	-0.74 ± 0.06
Colorado	754 ± 176	0.09 ± 0.03	-0.56 ± 0.29
Guadalupe	1867 ± 2186	0.03 ± 0.03	-1.29 ± 0.34
Nueces	635 ± 174	0.09 ± 0.04	-1.11 ± 0.24
Pooled	1141 ± 385	0.05 ± 0.02	-0.89 ± 0.25

Appendix 2. Mean back-calculated total length (TL) at age by cohort of Guadalupe Bass *Micropterus treculii* **captured from the Brazos, Colorado, Guadalupe, and Nueces river basins in central Texas during 2015-2017. Standard errors are reported in parentheses, where a period (.) indicates where standard error could not be calculated due to insufficient sample size.**

Cohort	*n*	Mean back-calculated TL (mm) at age							
		1	2	3	4	5	6	7	8
2016	116	97 (2)	—	—	—	—	—	—	—
2015	154	105 (1)	153 (2)	—	—	—	—	—	—
2014	103	105 (2)	155 (3)	199 (3)	—	—	—	—	—
2013	185	103 (2)	159 (3)	201 (3)	237 (3)	—	—	—	—
2012	80	99 (4)	158 (4)	194 (6)	235 (5)	274 (6)	—.	—	—
2011	35	89 (5)	155 (7)	210 (9)	238 (10)	293 (7)	324 (1)	—	—
2010	12	89 (6)	146 (9)	207 (12)	256 (13)	289 (.)	—	—	—
2009	5	87 (8)	146 (11)	190 (12)	229 (13)	262 (13)	—	—	—
2008	3	94 (4)	152 (9)	219 (18)	270 (27)	315 (34)	354 (39)	—	—
2007	0	—	—	—	—	—	—	—	—
2006	1	73 (.)	160 (.)	226 (.)	274 (.)	310 (.)	345 (.)	375 (.)	401 (.)
Overall	694	101 (1)	155 (1)	202 (2)	240 (3)	280 (5)	340 (16)	375 (.)	401 (.)

Appendix 3. Mean back-calculated total length (TL) at age by cohort of Guadalupe Bass *Micropterus treculii* **captured from the Brazos River Basin in central Texas during 2016-2017. Standard errors are reported in parentheses.**

Cohort	*n*	Age 1	2	3	4	5	6	7	8
2016	54	95 (1)	—	—	—	—	—	—	—
2015	77	104 (1)	149 (3)	—	—	—	—	—	—
2014	38	97 (3)	151 (5)	197 (4)	—	—	—	—	—
2013	37	104 (2)	153 (4)	204 (2)	244 (3)	—	—	—	—
2012	6	100 (4)	141 (2)	191 (4)	233 (5)	276 (8)	—	—	—
2011	4	97 (6)	155 (7)	214 (14)	266 (8)	300 (5)	324 (1)	—	—
2010	0	—	—	—	—	—	—	—	—
2009	0	—	—	—	—	—	—	—	—
2008	0	—	—	—	—	—	—	—	—
2007	0	—	—	—	—	—	—	—	—
2006	0	—	—	—	—	—	—	—	—
Overall	216	100 (1)	151 (1)	201 (2)	243 (3)	287 (6)	324 (1)	—	—

Appendix 4. Mean back-calculated total length (TL) at age by cohort of Guadalupe Bass
Micropterus treculii **captured from the Colorado River Basin in central Texas during 2015-2017. Standard errors are reported in parentheses, where a period (.) indicates where standard error could not be calculated due to insufficient sample size.**

Cohort	*n*	1	2	3	4	5	6	7	8
					Age				
2016	0	—	—	—	—	—	—	—	—
2015	0	—	—	—	—	—	—	—	—
2014	19	108 (6)	—	—	—	—	—	—	—
2013	107	100 (3)	180 (11)	—	—	—	—	—	—
2012	58	98 (5)	161 (5)	211 (20)	—	—	—	—	—
2011	29	88 (5)	155 (8)	211 (9)	237 (19)	—	—	—	—
2010	12	89 (6)	146 (9)	207 (12)	256 (13)	289 (.)	—	—	—
2009	5	87 (8)	146 (11)	190 (12)	229 (13)	262 (13)	—	—	—
2008	3	94 (4)	152 (9)	219 (18)	270 (27)	315 (34)	354 (39)	—	—
2007	0	—	—	—	—	—	—	—	—
2006	1	73 (.)	160 (.)	226 (.)	274 (.)	310 (.)	345 (.)	375 (.)	401 (.)
Overall	234	98 (2)	159 (3)	209 (6)	251 (8)	285 (14)	352 (28)	375 (.)	401 (.)

Appendix 5. Mean back-calculated total length (TL) at age by cohort of Guadalupe Bass *Micropterus treculii* captured from the Guadalupe River Basin in central Texas during 2016-2017. Standard errors are reported in parentheses, where a period (.) indicates where standard error could not be calculated due to insufficient sample size.

Cohort	*n*	1	2	3	4	5	6	7	8
		Age							
2016	44	94 (2)	—	—	—	—	—	—	—
2015	72	106 (2)	156 (2)	—	—	—	—	—	—
2014	42	109 (3)	158 (3)	200 (4)	—	—	—	—	—
2013	29	108 (4)	152 (5)	198 (5)	236 (4)	—	—	—	—
2012	14	102 (4)	147 (5)	189 (8)	236 (8)	274 (8)	—	—	—
2011	1	103 (.)	147 (.)	193 (.)	225 (.)	277 (.)	322 (.)	—	—
2010	0	—	—	—	—	—	—	—	—
2009	0	—	—	—	—	—	—	—	—
2008	0	—	—	—	—	—	—	—	—
2007	0	—	—	—	—	—	—	—	—
2006	0	—	—	—	—	—	—	—	—
Overall	202	104 (1)	155 (2)	197 (3)	236 (4)	274 (8)	322 (.)	—	—

Appendix 6. Mean back-calculated total length (TL) at age by cohort of Guadalupe Bass *Micropterus treculii* **captured from the Nueces River Basin in central Texas during 2016-2017. Standard errors are reported in parentheses, where a period (.) indicates where standard error could not be calculated due to insufficient sample size.**

		Age							
Cohort	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
2016	18	108 (4)	—	—	—	—	—	—	—
2015	5	93 (4)	131 (9)	—	—	—	—	—	—
2014	4	110 (8)	150 (5)	192 (12)	—	—	—	—	—
2013	12	120 (5)	166 (5)	200 (6)	228 (8)	—	—	—	—
2012	2	112 (5)	151 (4)	200 (8)	237 (0)	261 (.)	—	—	—
2011	1	82 (.)	142 (.)	199 (.)	252 (.)	280 (.)	—	—	—
2010	0	—	—	—	—	—	—	—	—
2009	0	—	—	—	—	—	—	—	—
2008	0	—	—	—	—	—	—	—	—
2007	0	—	—	—	—	—	—	—	—
2006	0	—	—	—	—	—	—	—	—
Overall	42	109 (3)	156 (4)	198 (4)	232 (6)	270 (10)	—	—	—