

Variation and plasticity and their interaction with urbanization in Guadalupe Bass
populations on and off the Edwards Plateau

by

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A Dissertation

In

Wildlife, Aquatic, and Wildlands Science and Management

Submitted to the Graduate Faculty
of Texas Tech University in
Partial Fulfillment of
the Requirements for
the Degree of

DOCTORAL OF PHILOSOPHY

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August 2018

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ACKNOWLEDGEMENTS

I want to express my extreme gratitude to my advisors Dr. Tim Grabowski and Dr. Allison Pease for their continued efforts, mentorship, and support throughout this project. This research and the completion of my dissertation would not have been possible without their guidance and contributions. I would also like to thank my committee members Dr. Preston Bean and Dr. Adam Kaeser for their continued support and guidance throughout this project. Additionally, I want to thank all the individuals that have helped with both field and lab work over the past five years. A. Adams, C. Alejandrez, K. Aziz, P. Bean, M. Berlin, T. Birdsong, S. Boles, J. Botros, D. Bradsby, C. Carter, M. Casarez, D. Chilleri, A. Cohen, B. Cook, G. Cummings, M. DeJesus, J. East, S. Fritts, K. Garmany, D. Geeslin, M. Gilbert, D. Gossett, A. Grubh, R. Hawkenson, D. Hendrickson, S. Hill, A. Horn, F. Howell, L. Howell, M. Kelly, G. Kilcrease, K. Kolodziejczyk, T. Lane, D. Leavitt, K. Linner, C. Loeffler, D. Lutz-Carillo, S. Magnelia, K. Mayes, S. McClanahan, A. Nobles, C. Pavliska, S. Robinson, J. Salazar, S. San-Francisco, A. Stevens, C. Vaughan, and E. Verwys, thank you. I want to thank I want to express my sincerest thanks to my lab mates Q. Chen, J. East, J. Taylor, W. Massure, B. Roesler for their time and camaraderie. I want to especially thank my fellow lab mates M. Acre and H. Williams for their advice, support, and friendship for which I am forever grateful. I want to also thank R. Vickory and the staff of the Lower Colorado River Authority McKinney Roughs Nature Park, and T. Arsuffi, R. Stubblefield and K. Lopez at the Texas Tech University- Junction Campus

and Llano River Field Station provided accommodations and lab facilities while in the field. All Water Guides and their clients assisted with capturing Guadalupe Bass in the Lower Colorado River. D. Lutz-Carrilo and the staff at the A.E. Wood Lab for performing all genetic analyses. I also want to thank R. Katz for her efforts and guidance with my analyses in Chapter 4, as well as her assistance in R. R. Edwards and S. Magnelia who provided comments and suggestions on earlier revisions of this dissertation. I want to thank the U.S. Fish and Wildlife Service State Wildlife Grant, Texas Parks and Wildlife, and the Department of Natural Resources at Texas Tech University for funding this project. I also want to thank the entire staff and faculty of the Department of Natural Resources Management and the Texas Cooperative Fish and Wildlife Research Unit at Texas Tech University for all of their support and assistance. Finally, I cannot express how grateful for my friends and family who have showed continued encouragement and unwavering support throughout this entire process.

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ABSTRACT

The Colorado River Basin in Texas has experienced major alterations to its hydrologic regime due to changing land and water use patterns. These anthropogenic influences on hydrologic variability have had major implications for riparian and aquatic ecosystems and the species dependent upon them. However, these impacts are usually assessed at limited temporal and spatial scales, i.e., research tends to be focused on relatively short and discrete periods or portions of the river basin. It is not clear how basin-wide alterations occurring across decades affect species that maintain populations throughout a basin. Guadalupe Bass *Micropterus treculii* are endemic to central Texas and are typically associated with shallow runs and riffles in small streams. However, Guadalupe Bass are found throughout the Colorado River Basin, including the mainstem portion of the river downstream of Austin where they support a thriving trophy fishery. Because Guadalupe Bass exist across a wide range of stream orders within the Colorado Basin, it is unclear whether populations from different parts of the basin respond similarly to anthropogenic disturbances or to conservation and restoration activities. Therefore, my objectives were to 1) quantify the response of Guadalupe Bass to flow alteration and changing land use patterns throughout the Colorado River Basin, and 2) document differences between populations. To accomplish this, I used a combination of morphometric analyses, age and growth estimation, and radio telemetry.

Watershed variables were evaluated for percent difference in urban and agricultural land use as well as flow alteration using Indicators of Hydrologic

Alteration (IHA). I evaluated the influence of flow alteration on morphology, growth, recruitment, and movement of Guadalupe Bass. Relationships between hydrologic alteration and landscape changes were compared to shape variation determined using geometric morphometric for Guadalupe Bass in the late 1970s and present. I identified significant ecomorphological variation, as well as variation in standardized growth and recruitment, of Guadalupe Bass in response to flow alteration. Standardized growth was determined from Von Bertalanffy growth curves fit to the back-calculated length-at-age data for otoliths of contemporary Guadalupe Bass throughout the Colorado River Basin. In addition to life history traits, I evaluated the movement, habitat use, and behavior of Guadalupe Bass in the lower Colorado River. I used both radio telemetry and electrofishing surveys to describe the similarities and differences between tributary Guadalupe Bass populations and the unique mainstem population in the lower Colorado River. Radio telemetry allowed me to evaluate movement rates, home range size and the influence of habitat on activity levels.

This research revealed differences in Guadalupe Bass habitat associations and movements, contrasts in age and growth, and morphological variation across a gradient of disturbance throughout the Colorado River Basin. There was a longitudinal gradient in growth throughout the basin with individuals in the lower Colorado River growing faster than in tributaries. The highest growth rates occurred under moderate flow conditions throughout the basin and weaker year classes in the lower Colorado River were related to high and low flow conditions. Spatial differences in growth rates between mainstem and tributary populations were accompanied by temporal and

spatial morphological differences which were associated with altered flow regimes and landcover transitions. In addition to growth rate and morphological variability throughout the basin, there were differences in the movement and habitat associations of lower Colorado River in comparison to tributary individuals. The ability of the Guadalupe Bass population to not only persist but flourish downstream of a heavily populated urban area presented a unique opportunity to investigate the response of a native species to anthropogenic disturbance. Results of this work provide information on the potential effects of population growth and increased water withdrawals on Guadalupe Bass populations. Additionally, this work adds to an understanding of the unique Guadalupe Bass population found in the lower Colorado River and how it differs from upstream tributary populations. Providing more population-level information facilitates conservation actions critical to preserving preferred habitat and promoting growth rates for Guadalupe Bass in streams of different sizes and flow conditions while highlighting interpopulation differences that may warrant consideration for stocking programs and other management strategies.

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CHAPTER 1

INTRODUCTION

The Colorado River flows for approximately 967 kilometers across the state of Texas with a drainage area encompassing over 115,000 square kilometers. Intermittent headwaters begin in Dawson County, Texas, which borders the state of New Mexico in the northwestern corner of the state, and the river ends at Matagorda Bay on the Gulf of Mexico (Banks & Babcock, 1988; Clay & Kleiner, 2010). The Colorado River is unique in that a large part of the upper part of the watershed lies in the semi-arid High Plains ecoregion, which is mostly non-contributing, with average annual rainfall of 0.38 to 0.56 meters (Diamond & Elliott, 2015; Texas Natural Resource Conservation Commission, 1999). The majority of contribution to flow in the Colorado River is from rainfall and the spring-fed tributaries in the 93,000 km² karst ecoregion of the Edwards Plateau in central Texas (Heilman, McInnes, Kjelgaard, Keith Owens, & Schwinning, 2009).

The human population is expected to increase drastically in the Colorado Basin by 2050, with some areas expected to more than double in size, increasing demands on water resources (Colby & Ortman, 2015; Hoque, McNeill, & Granato, 2014). The mainstem Colorado River and its tributaries experience increasing urbanization as they flow through the Edwards Plateau ecoregion into Austin, Texas, and the extent of urbanization declines as the river progresses downstream. Altered land and water use patterns along the gradient of urbanization are accompanied by flow-regime alteration, including agricultural diversions, irrigation return flows and low-water dams. The

upper Colorado River watershed is comprised of spring-fed tributaries and withdrawals dominated by agricultural diversions. The middle of the Colorado flows through the densely urbanized city of Austin into the more rural, yet highly regulated downstream lower Colorado (Dahm, Edwards, & Gelwick, 2005). These impacts lead to fragmentation and homogenization of instream habitat in the mainstem and tributaries of the Colorado River. The compounding effects of urbanization place intense stressors on downstream aquatic populations that can be either acute, resulting in the rapid extirpation of local populations (Onorato, Marion, & Angus, 1998), or chronic and cumulative, changing population dynamics and increasing the vulnerability of local populations to environmental stressors or stochasticity (McDonnell & Hahs, 2008). Because many species are sensitive to stressors associated with landscape alteration, fishes are considered reliable indicators of urbanization and associated impacts, such as altered flow regimes (Helms, Feminella, & Pan, 2005; Mims, Olden, Shattuck, & Poff, 2010; Wang, Lyons, Kanehl, & Gatti, 1997). The gradient in urbanization throughout the Colorado River Basin provides an opportunity for determining the degree to which stream fishes exhibit plasticity in their behavior and biology in response to anthropogenic disturbance.

Understanding intraspecific variation, whether through genetic diversity or phenotypic plasticity, is critical in determining the resiliency of populations in rapidly changing environments (Chevin & Lande, 2010; Lande, 2009; Seebacher, White, & Franklin, 2014). This is especially true in the state of Texas, where climate change is likely to exacerbate demands for freshwater resources strained by changing land use

patterns and increasing population growth (Forsman, 2014; Sih, Ferrari, & Harris, 2011). Water withdrawal and use on the Colorado River makes the ecosystem more sensitive to the changing climate compared to river ecosystems where there is not major withdrawals for human consumption or irrigation (Gibson, Meyer, Poff, Hay, & Georgakakos, 2005; Jiang & Yang, 2012; Smith, David, Cardenas, & Yang, 2013; Vaughan et al., 2012). During periods of intense drought, habitat loss and degraded water quality impact stream fish populations, especially in aquatic communities downstream of major cities where water withdrawal and reservoir storage are a priority. Current land and water use patterns impacts on the Colorado River aquatic community will be further amplified by the lack of precipitation and increase in temperature that is expected throughout Texas with impending climate change (Jiang & Yang, 2012; Liu et al., 2012; Smith et al., 2013). These increases in temperature and decreases in the precipitation will directly influence aquifer recharge and discharge rates, while indirectly increasing the demand for water abstraction or storage in the upstream reservoirs (Chin, Laurencio, & Martinez, 2008; Yin, Yang, & Petts, 2012). These alterations to the instream discharge patterns impact the growth, spawning, feeding, and overall movement patterns of stream fish populations, especially those downstream of reservoirs and intense landcover transitions (Franssen, Harris, Clark, Schaefer, & Stewart, 2012; Lienesch, Lutterschmidt, & Schaefer, 2000).

Documenting inter-population trait variation in response to environmental change, as well as the consequences of these responses, is essential to the understanding of population resiliency and the success of management regimes for a

single species across systems (Storz, Scott, & Cheviron, 2010; Wennersten & Forsman, 2012). For example, two *Cyprinella* species, *C. lutrensis* and *C. venusta*, exhibit intraspecific trait divergence between reservoir and stream-residing populations (Franssen, 2011; Haas, Blum, & Heins, 2010). Under low flow conditions with high predator densities in reservoirs, *Cyprinella lutrensis* had smaller heads and deeper bodies. Increased predator evasion, swimming performance and maneuverability for feeding are all associated with increasing body depth and caudal fin area suggesting morphological shifts favor greater fitness for individuals residing in reservoirs (Franssen, 2011; Franssen et al., 2012). In addition to understanding of morphological divergence between reservoir and stream populations, there is a need to understand variation that may exist between populations upstream and downstream separated by barriers to movement. This is particularly important in central Texas, where increasing urbanization and demand for water resources has established a gradient of disturbance from upstream tributary systems to downstream mainstem populations.

Guadalupe Bass *Micropterus treculii* is a native black bass species endemic to central Texas. It is found primarily in the Edwards Plateau ecoregion, but its range also extends downstream into the Blackland Prairie and Coastal Plains ecoregions in the lower Colorado River Basin (Curtis, Perkin, Bean, Sullivan, & Bonner, 2015; Hubbs, Edwards, & Garrett, 1991; Koppelman & Garrett, 2002). Guadalupe Bass populations have declined across much of this range due to introgressive hybridization with introduced Smallmouth Bass *Micropterus dolomieu* (Bean, Lutz-Carrillo, &

Bonner, 2013; Littrell, Lutz-Carrillo, Bonner, & Fries, 2007; Whitmore, 1983). As a result, Guadalupe Bass has been identified as a species of greatest conservation need by Texas Parks and Wildlife Department and of special concern by Hubbs et al. (2008). Hybridization rates have exceeded 45% in some rivers (Garrett, 1991; Littrell et al., 2007) with non-introgressed Guadalupe Bass no longer occurring in the Blanco and Concho rivers. However, recent efforts to remove Smallmouth Bass and Guadalupe Bass X Smallmouth Bass hybrids or to stock large numbers of Guadalupe Bass fingerlings to reduce or eliminate hybridization are proving to be effective at reducing this acute threat (Bean et al., 2013; Birdsong et al., 2015; Fleming, Garrett, & Smith, 2015; Garrett, Birdsong, Bean, & McGillicuddy, 2015; Littrell et al., 2007) A more chronic threat currently facing Guadalupe Bass populations is habitat degradation and alteration resulting from changing land and water use patterns in central Texas (Anderson, Hubbs, Winemiller, & Edwards, 1995; Fitzhugh & Richter, 2004).

Guadalupe Bass are found across a wide range of habitats throughout the Edwards Plateau; a population also occurs in the lower Colorado River and has been documented as far downstream as Altair, Texas (Curtis et al., 2015; Hendrickson & Cohen, 2015). Despite the extensive range of Guadalupe Bass in Texas, they are considered fluvial habitat specialists, exhibiting both ontogenetic and seasonal shifts in habitat utilization (Groeschel, 2013; Perkin et al., 2010). Dependence on instream structure and variable habitats for different life history stages heightens the vulnerability of the population to habitat alteration (Birdsong et al., 2015; Garrett et

al., 2015). Seasonal shifts in habitat utilization range from deeper pools with some current for overwintering and shallow sheltered areas near flowing water for nest construction and spawning (Edwards, 1980; Enriquez, Gelwick, & Packard, 2016; Perkin et al., 2010). Ontogenetic habitat shifts occur throughout early life stages with movement toward increased current and depth following the juvenile stage (Edwards, 1980). Guadalupe Bass are listed as an 'intolerant' species in the regionalized Index of Biotic Integrity due to their dependence on an undisturbed heterogeneous habitat mosaic for the completion of their life history (Linam, Kleinsasser, & Mayes, 2002). Intolerant species are the first to disappear due to factors ranging from siltation to altered hydrology associated with human disturbance (Fausch, Karr, & Yant, 1984; Karr, 1981; Karr, Fausch, Angermeier, Yant, & Schlosser, 1986).

While the population dynamics of the species has been documented in tributary systems on Edwards Plateau, the populations in the lower Colorado and the Highland reservoirs immediately upstream of Austin, TX are relatively understudied. The ability of Guadalupe Bass to respond and tolerate a range of conditions is evident based on the capacity of these populations to thrive across a variety of habitats, as well as persistence in novel environments under altered conditions. Previous research has found that intra-population niche variation across nine Guadalupe Bass populations was mostly influenced by morphological variation. Individual specialization in wild Guadalupe Bass populations can occur at low levels of genetic diversity due to plasticity. Trophic diversity in Guadalupe Bass populations has been shown to be largely driven by plasticity in morphological characters in response to the differences

in flows and productivity across systems (Bean, 2012). Further, there is evidence that suggests that Guadalupe Bass are not as intolerant as previously conceived from studies conducted in smaller tributaries. Investigation of trait variation within Guadalupe Bass in response to changing environmental conditions would facilitate improved management and conservation of interpopulation variation. The inclusion of strategies for monitoring intraspecific variation is emerging as an important consideration for successful management of populations (Mimura et al., 2017). Understanding and monitoring intraspecific variation of Guadalupe Bass requires comprehensive knowledge on both genetic and phenotypic variation within the population. Texas Parks and Wildlife Department (TPWD) has committed a great deal of resources to monitoring and eliminating genetic threats to the population (Fleming et al., 2015; Koppelman & Garrett, 2002; Whitmore, 1983). A next step for the successful management of the population is to gain an understanding of the plasticity within the population and the ability to respond to environmental stressors permitting population persistence under variable conditions.

The overall objectives of this study were to 1) evaluate spatial variation in ecomorphology, 2) assess the effects of anthropogenic disturbance on Guadalupe Bass population structure and dynamics in the Colorado River Basin, 3) compare the habitat use and movement of Guadalupe Bass populations in the lower Colorado River to smaller Hill Country stream populations on the Edwards Plateau. In Chapter II, I evaluated spatial and temporal variation in Guadalupe Bass ecomorphology across environmental gradients in landcover and hydrology. The effects of flow regime on

Guadalupe Bass population structure and dynamics across the Colorado River Basin are evaluated in Chapter III. Chapter IV examines the habitat associations and movement patterns of Guadalupe Bass in the lower Colorado River. The final Chapter summarizes the results, conservation implications, and future directions of this research. Results of this work will assist in gaining an understanding of the response of Guadalupe Bass to anthropogenic disturbances, including increased urbanization in central Texas, and further assist in the conservation of the species.

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CHAPTER 2

CHANGING ENVIRONMENTAL GRADIENTS OVER FORTY YEARS ALTER ECOMORPHOLOGICAL VARIATION IN GUADALUPE BASS *MICROPTERUS TRECVLII* THROUGHOUT A RIVER BASIN

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ABSTRACT

Understanding the degree of intraspecific variation within and among populations is a key aspect of predicting the capacity of a species to respond to anthropogenic disturbances. However, intraspecific variation is usually assessed at either limited temporal, but broad spatial scales or vice versa, which can make assessing changes in response to long-term disturbances challenging. I evaluated the relationship between the longitudinal gradient of changing flow regimes and land use/land cover patterns since 1980 and morphological variation of Guadalupe Bass *Micropterus treculii* throughout the Colorado River Basin of central Texas. The Colorado River Basin in Texas has experienced major alterations to the hydrologic regime due to changing land and water-use patterns. Historical collections of Guadalupe Bass prior to rapid human-induced change present the unique opportunity to study the response of populations to varying environmental conditions through space and time. Morphological differentiation of Guadalupe Bass associated with temporal changes in flow regimes and land use/land cover patterns suggests that they are exhibiting intraspecific trait variability, with contemporary individuals showing increased body depth, in response to environmental alteration through time (specifically related to an increase in herbaceous land cover, maximum flows, and the

number of low pulses and high pulses). Additionally, individuals from tributaries with increased hydrologic alteration associated with urbanization or agricultural withdrawals tended to have a greater distance between the anal and caudal fin. These results reveal trait variation that may help to buffer populations under conditions of increased urbanization and sprawl, human population growth, and climate risk, all of which impose novel selective pressures, especially on endemic species like Guadalupe Bass. Overall results contribute an understanding of the adaptability and capacity of an endemic population to respond to expected future changes based on demographic or climatic projection.

INTRODUCTION

Intraspecific variation among populations allows a species to adapt to a range of environments along natural gradients in temperature, elevation, altitude, or precipitation, and such variation has been documented in terrestrial and aquatic species. For example, latitudinal gradients in temperature have influenced natural variability in the body size of lizards, with larger individuals being found in lower latitude environments with warmer temperatures (Pincheira-Donoso, Hodgson, & Tregenza, 2008; Zamora-Camacho, Reguera, & Moreno-Rueda, 2016). Plants have shown similar patterns across temperature gradients with increased metabolic rates, cell growth, and photosynthesis in warmer temperatures resulting in increased growth in species such as the flowering plant, *Arabidopsis thaliana* (Li, Suzuki, & Hara, 1998). However, anthropogenic disturbance has disrupted these natural gradients and established novel gradients along which populations must respond. Mechanisms of

response vary from shifting ranges (Case & Taper, 2000), dispersal across ranges (Kendall, Bjørnstad, Bascompte, Keitt, & Fagan, 2000; Horváth, Vad, & Ptacnik, 2016), adaptation (Jackson & Colmer, 2005), or plasticity in trait response (Bell & Sultan, 1999; Morris, 2014). However, anthropogenic disturbances often occur more rapidly than the pace of these mechanisms.

Plasticity in a given trait may permit rapid population response to environmental stochasticity through matching the phenotype with the fluctuation in optimum fitness imposed by a disturbance (Charmantier et al., 2009; Chevin & Lande, 2010; S. Richter et al., 2012). Therefore, gaining information on intraspecific variation provides an understanding of the capacity of a species to respond to environmental fluctuation. This is especially important when vulnerability is heightened in restricted or fragmented habitats where dispersal or range shifts are not feasible mechanisms of response (McInerny, Travis, & Dytham, 2007; Hodgson, Thomas, Dytham, Travis, & Cornell, 2012). The prevalence of fragmentation and natural restrictions to the stream channel make aquatic species in rivers especially vulnerable (Hugueny, Movellan, & Belliard, 2011; Braulik, Arshad, Noureen, & Northridge, 2014). Running-water habitats are restricted to mostly unidirectional natural gradients in abiotic and biotic influences within a dendritic network from headwaters to confluences with streams of increasing size (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980; Junk, Bayley, & Sparks, 1989; Fuller, Doyle, & Strayer, 2015). Variability within a species is expected to optimize fitness along these environmental gradients, and the extent of

variation dictates the range of local adaptations for populations within these freshwater systems (Langerhans, 2009a; Hietpas, Bank, Jensen, & Bolon, 2013).

Rapid, human-induced modifications to river ecosystems, through changes in flow regime and land use, can influence the fitness of individuals leading to population-level responses. These effects are usually assessed at relatively limited temporal and spatial scales; thus, it is not clear how basin-wide alterations occurring across decades affect species with populations distributed across large basins. Spatially, intraspecific trait divergence has been identified for multiple fish species in comparisons between reservoir- and stream-residing populations. For example, Black Shiner *Cyprinella venusta* individuals in reservoirs tended to have smaller heads, and deeper bodies in comparison to broader heads, and shallower bodies of stream individuals (Haas, Blum, & Heins, 2010). These traits are associated with occupying low current velocity habitats with high predator densities (Haas et al., 2010; Franssen, 2011). Increased predator evasion, swimming performance, and maneuverability for feeding are all associated with increasing body depth and caudal fin area suggesting such morphological shifts may be favored for individuals residing in reservoirs (Hambright, 1991; Holopainen, Aho, Vornanen, & Huuskonen, 1997; Langerhans, 2009b).

In addition to understanding of morphological divergence between reservoir and stream populations, there is a need to understand variation that may exist between populations separated by barriers to movement, such as in altered river networks. Population-level information documenting the capacity of fish populations to adopt

different morphologies in response to environmental change, as well as the consequences of these responses, assists in closing the gap in current understanding of population resiliency and identifies interpopulation differences critical to future management strategies. This is especially true for regions, such as central Texas, where human population growth has already strained on water supplies and climate projections are predicted to increase current extremes of temperature and precipitation resulting in prolonged drought and flooding conditions for which populations must respond (Jiang & Yang, 2012; Smith, David, Cardenas, & Yang, 2013).

Understanding population responses to rapid environmental change induced by human perturbation in central Texas will provide insight on future population persistence under environmental variability.

One of the major waterways in central Texas is the Colorado River, which flows through the heavily urbanized area of Austin, Texas. Human populations are expected to increase drastically in the Colorado River Basin by 2050. For instance, the population in the Austin metropolitan statistical area (MSA) is projected to continue to grow at a rate greater than 30% and potentially reach 5 million people by 2050, in comparison the Austin MSA population was less than 600,000 in 1980 (Hoque, McNeill, & Granato, 2014; The Office of the State Demographer, 2014; Colby & Ortman, 2015). The mainstem Colorado River and its tributaries experience increasing urbanization and regulation as they flow into Austin. While the extent of urbanization declines as the river progresses downstream, the lower Colorado River below Austin is one of the most highly regulated stretches of river within the basin. Flow regime

alterations throughout the basin due to urbanization are accompanied by agricultural diversions, irrigation return flows and low water dams all of which lead to fragmentation and homogenization of instream habitat in the mainstem and tributaries of the Colorado River Basin. Variation in urbanization impacts throughout the Colorado River Basin provides an opportunity for determining the degree to which stream fishes exhibit plasticity in their behavior and biology in response to anthropogenic disturbance. The inclusion of strategies for monitoring intraspecific variation is emerging as an important consideration for successful management of populations (Mimura et al., 2017). Understanding and monitoring intraspecific variation helps to ensure the persistence of species, as well as the community framework and ecosystem function of the systems where these representative species reside. For instance, population level trait variation in Trinidadian guppies *Poecilia reticulata* altered ecosystem structure through impacts on algal and invertebrate densities, and the function of the ecosystem by influencing the primary production (Bassar et al., 2010). Guadalupe Bass *Micropterus treculii* is a species endemic to Texas and can be found throughout the Colorado River Basin along the present gradient of urbanization (Curtis, Perkin, Bean, Sullivan, & Bonner, 2015; Hendrickson & Cohen, 2015). Guadalupe Bass are considered fluvial habitat specialists, exhibiting both ontogenetic and seasonal shifts in habitat utilization. The vulnerability of populations to habitat alterations is heightened by the dependence of this species on instream structure and variable habitats for different life history stages. Ontogenetic habitat shifts occur throughout early life stages with movement toward increased

current and depth following the juvenile stage (Edwards, 1980). The ability of Guadalupe Bass to respond and tolerate a range of conditions is evident based on the capacity of these populations to persist across a variety of habitats, as well as in novel environments under altered conditions. Previous research has found that intra-population niche variation across nine Guadalupe Bass populations was mostly influenced by morphological variation. Individual specialization in wild Guadalupe Bass populations can occur at low levels of genetic diversity due to plasticity (Bean, 2012). Trophic diversity in Guadalupe Bass wild populations has been shown to be largely driven by plasticity in morphological characters in response to the differences in flows and productivity across systems (Bean, 2012). Further study of trait variation within Guadalupe Bass in response to changing environmental conditions would facilitate improved management and conservation of intraspecific variation.

Here, I examined the morphological variation across an environmental gradient over a forty-year period throughout a large river basin by using an archived range-wide collection of Guadalupe Bass captured prior to major flow and land-use alterations to compare to individuals collected under present-day conditions. The objective of this study was to evaluate the effects of changing environmental gradients on ecomorphological variation in Guadalupe Bass populations across both temporal and spatial scales. Relationships between hydrologic alteration and landscape changes were compared to shape variation determined using geometric morphometric methods for Guadalupe Bass in the late 1970s and in contemporary conditions. Intensified landscape transitions are associated with flashier flow regimes and increased draw

downs (Paul & Meyer, 2001; Allan, 2004). In such conditions, increased body depth in fish allows for increased maneuverability and initial speed, as opposed to more streamlined (fusiform) body shape, which reduces drag and increases endurance in conditions where there is sustained flow (Blake, 2004; Collar & Wainwright, 2009; Langerhans & Reznick, 2010). I expected morphological differentiation over time in relation to altered landscapes and hydrologic regimes to result in less fusiform body shape in contemporary populations. Measuring population-level morphological response to anthropogenic changes across broad spatial and temporal scales allows for identification of plasticity within the species that has likely occurred with other physiological adjustments or adaptations through time. Understanding population-level morphological responses to environmental stressors provides a baseline for management in urbanizing watersheds with increasing water withdrawals and land alteration.

METHODS

Study Area

The Colorado River Basin drains an area of 103,341 km² and encompasses a large portion of Guadalupe Bass range. The majority (93,000 km²) of the basin lies within the karst ecoregion of the Edwards Plateau in central Texas where spring systems feed the Colorado's major tributaries: the Llano, Pedernales, San Saba, and Concho Rivers. I selected 30 sites corresponding to previous collections made by Edwards (1980) during 1975-1978. Sites spanned four different stream order categories: 1) three major tributaries (Llano, San Saba, and Pedernales), 2) smaller

tributaries of the three major tributaries, 3) smaller tributary streams in the highly urbanized area of Austin, and 4) the mainstem lower Colorado River (Figure 2.1 and Table A.1). Smaller tributaries in the upper watershed were classified as systems that were headwater streams originating with a stream order of 1 and not sharing a confluence with the mainstem Colorado River. The three major tributaries in the upper watershed were characterized as systems that shared a confluence with the mainstem of the Colorado River and sites were located within a stream order greater than 4. Smaller tributaries that shared a confluence with the mainstem Colorado River within the boundaries of the Austin metropolitan area and originated with a stream order of 1 were considered smaller tributaries in the urbanized area of Austin. Morphometric collections for the mainstem Colorado only included sites on the lower Colorado River below the city of Austin, with a Strahler stream order of 7.

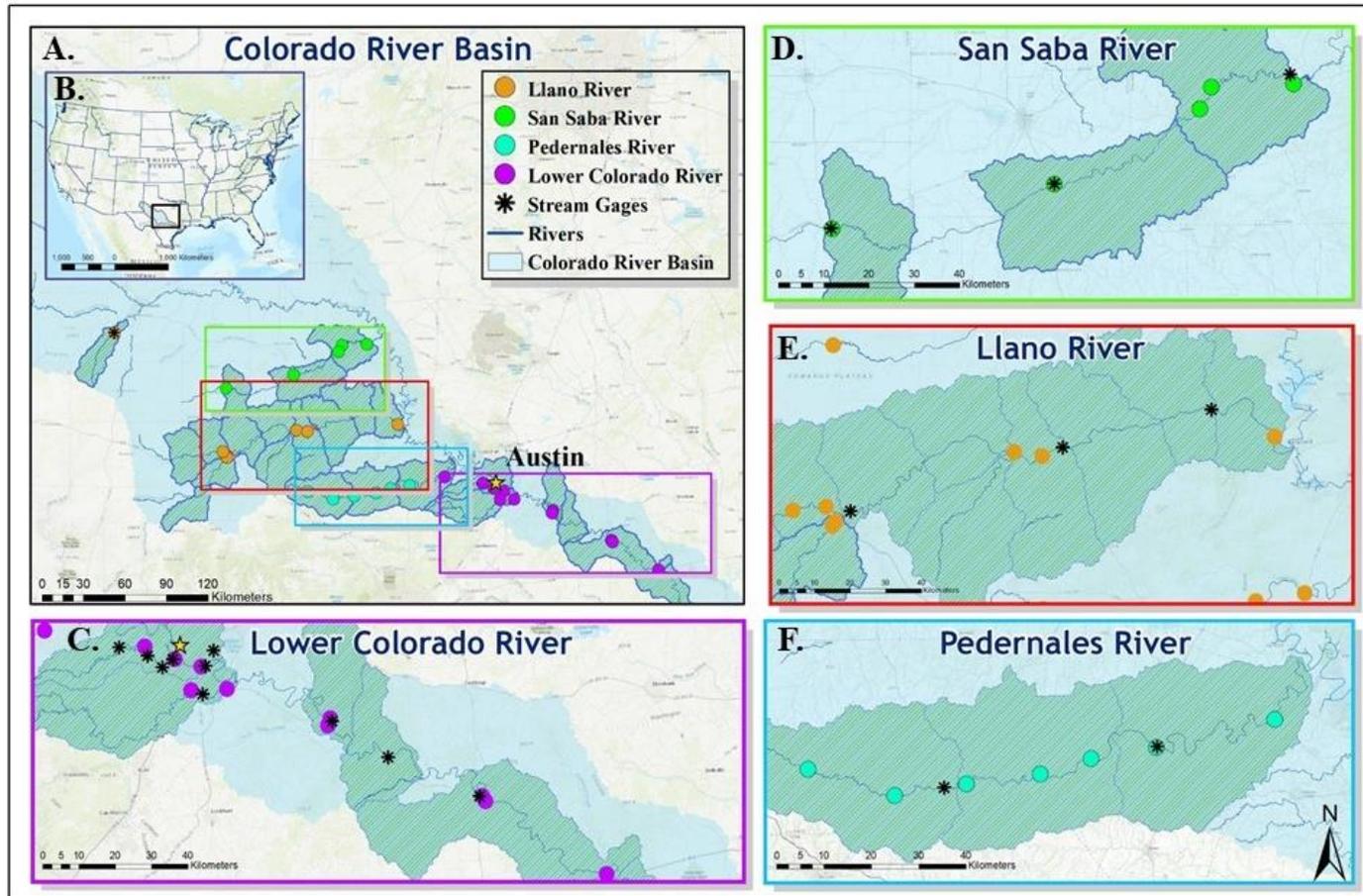


Figure 2.1: Map indicating the distribution of study sites and stream gages throughout the Colorado River Basin. Sites were chosen based on previous collections by Edwards (1980). Sites within each river system served as replicates representing the morphology of Guadalupe Bass within the mainstem and tributaries. A and B indicate the location of the Colorado River in Texas and the distribution of the sites. Inset D-F indicate major tributary sites and the associated gages. Inset C shows sites and gages in the Austin, Texas area and located on the lower Colorado River below Longhorn Dam in Austin, Texas. *Environmental datasets*

Historical and present geospatial data were used to determine land-use and land-cover (LULC) changes for the 30 Hydrologic Unit Code Level-10 (HUC-10) watersheds (Table A.2) which encompassed all study sites. Land-use and land-cover data from the 1970s and 1980s were obtained from the U.S. Geological Survey (USGS) National Water Quality Assessment (NAWQA) Program, which classified Landsat images (30-m resolution) collected from 1972 to 1976 using the 45 class Anderson II classification system for LULC (McMahan, Frye, & Brown, 1984). Current LULC data at 10-m resolution were obtained from the Texas Parks and Wildlife Department (TPWD) Ecological Systems of Texas (Diamond & Elliott, 2015), which used over 100 different LULC classes. Therefore, historical and present LULC data were reclassified into broad landscape classes of agriculture, barren, forested, herbaceous, water, urban high and urban low consistent between data sets in order to focus comparison on primary land conversion rather than vegetation types. Original LULC classes from both the historical and present datasets and the broader class within which each was reclassified into are defined in Table A.3. The percentages of each LULC class within individual sub-watersheds were quantified for both the historical and present datasets and used as the environmental variables for further analysis (Figure 2.2).

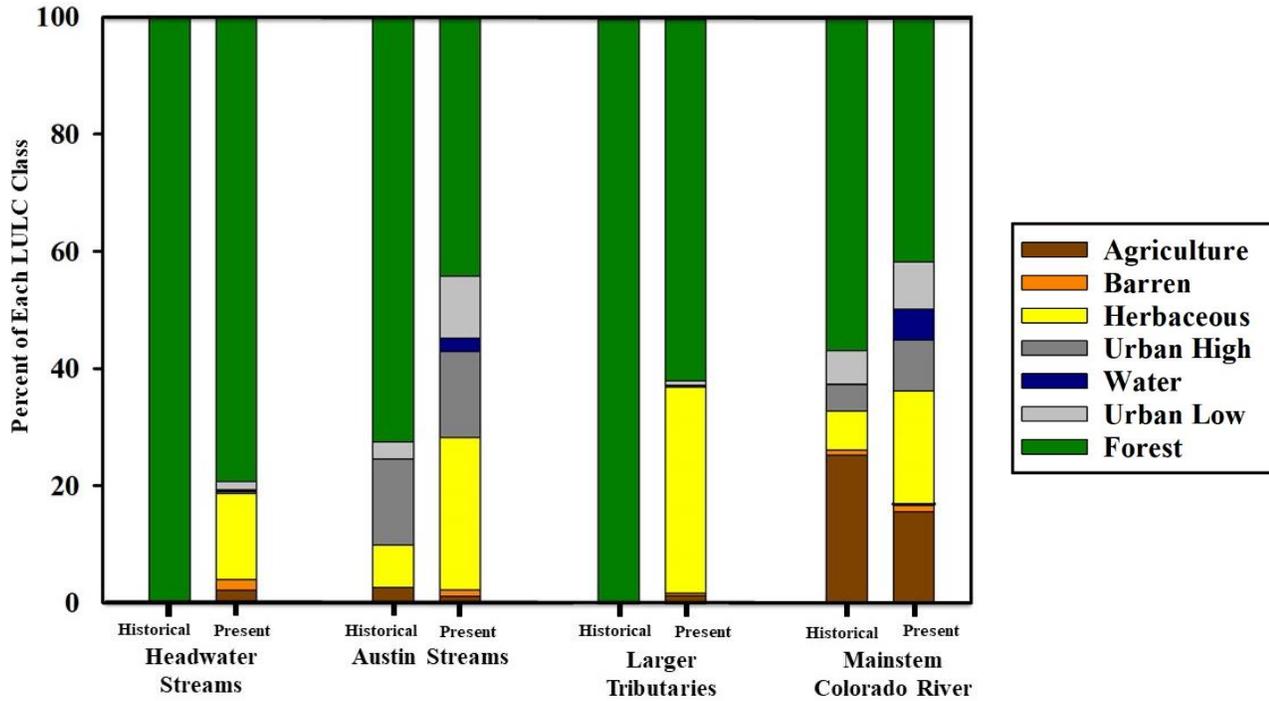


Figure 2.2 : Bar graph indicating the changes in land use and land cover (LULC) within the sub-watersheds in each of the four stream order classes. The four separate stream order classes represent 1) headwater streams (Dove Creek, North Llano River, South Llano River, James River), 2) larger tributaries (San Saba River, Pedernales River, Llano River), 3) lower-order Austin area streams (Barton Creek, Walnut Creek, Onion Creek), and 4) the mainstem Colorado River.

I evaluated changes in the variability of flow conditions across focal tributaries and the mainstem Colorado River between the 1970s and 1980s and present-day collection periods. Hydrological alteration was determined from the historic and present discharge records using USGS stream gages closest to each sampling location (Table A.4). Inter-annual hydrologic variability within the periods was assessed using Indicators of Hydrologic Alteration (IHA) software (B. D. Richter, Baumgartner, Powell, & Braun, 1996) for four separate groups of hydrologic parameters: 1) monthly average, 2) annual extremes in minimum and maximum flow, and baseflow index (7-day minimum flow/mean flow for year) 3) high and low pulse duration and frequency, and 4) overall change rate and frequency of water conditions. The coefficient of deviation (CD) for each of the hydrologic parameters was obtained for the given time period for further analysis. The CD measures the variability of individual hydrologic parameters as the (75th percentile – 25th percentile)/ 50th percentile.

Morphometric measurements

Guadalupe Bass (n=348) were collected throughout Colorado River Basin from March 2014 to May 2016 using backpack electroshocking and seining. Boat electroshocking was used when applicable on the mainstem Colorado River. Each site was sampled twice each year. Guadalupe Bass were euthanized using a > 400 mg/L aqueous solution of eugenol (Leary et al., 2013) and kept on ice until they were photographed. A digital camera (Nikon D3200, Melville, New York) was used to take a lateral left-side photo of each individual Guadalupe Bass collected during this study along with specimens (n=457) collected during 1975 – 1978 and housed at the Texas

Natural History Collection (see Table A.5 for accession numbers). Due to concerns about potential preservation effects confounding comparisons of freshly-caught and preserved fish (Sagnes, 1997; Berbel-Filho, Jacobina, & Martinez, 2013; Gaston, Jacquemin, & Lauer, 2013), a subset of Guadalupe Bass was photographed then fixed and held in 10% formalin similar to the specimens collected by Edwards (1980). Photos were taken with a reference scale. Landmarks, chosen based on previous fish morphological studies (Svanbäck & Eklöv, 2006; Langerhans, 2008; Arbour, Hardie, & Hutchings, 2011; Franssen, Stewart, & Schaefer, 2013) were digitized and the scale was set using tpsDig v. 2 (Rohlf, 2004a). The 15 digitized landmarks were: (1) anterior edge of the premaxillary, (2) caudal peduncle, (3) fork of the caudal fin, (4) center of the eye, (5) insertion of the last ventral ray on the pectoral fin, (6) anterior end of the dentary, (7) posterior-most point of maxillary, (8) origin of first dorsal fin, (9) origin of the second dorsal fin, (10) origin of the anal fin, (11) insertion of last anal fin ray, (12) dorsal origin of the caudal fin, (13) ventral origin of the caudal fin, (14) insertion of the last ray of second dorsal fin, and (15) insertion of the pelvic fin (Figure 2.3). All photographs were marked by a single observer for consistency, and TPSUtil v. 1.46 (Rohlf, 2004d) was used to randomize images after a landmark had been marked on each photograph in order to prevent sequence effects.

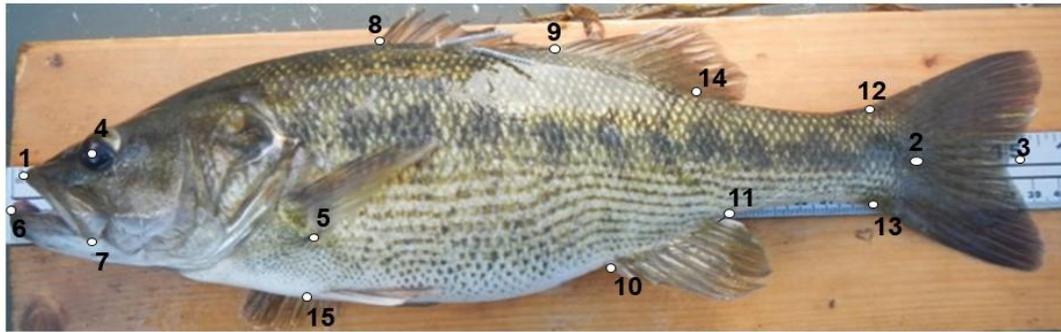


Figure 2.3: Location of the 15 landmarks used for morphological comparison of Guadalupe Bass *Micropterus treculii* throughout the Colorado River Basin, Texas. The 15 landmarks included in the analysis are: (1) anterior edge of the premaxillary, (2) caudal peduncle, (3) fork of the caudal fin, (4) center of the eye, (5) the insertion of the last ventral ray on the pectoral fin, (6) anterior end of the dentary, (7) posterior-most point of maxillary, (8) origin of first dorsal fin, (9) origin of the second dorsal fin, (10) origin of the anal fin, (11) insertion of last anal fin ray, (12) dorsal origin of the caudal fin, (13) ventral origin of the caudal fin, (14) insertion of the last ray of second dorsal fin, and (15) insertion of the pelvic fin.

Once morphometric images were landmarked, generalized Procrustes analysis (GPA) was used to account for the effects of translation, scale, and rotation on the spatial covariation of the landmarks using TPSRelw software (Rohlf, 2004c). TPSRelw was also used to calculate the square root of the sum of the squared distances from each landmark to the centroid for all 15 landmarks to determine centroid size, a metric for body size (Bookstein, 1984; Zelditch, Swiderski, Sheets, & Fink, 2004). While superimposition is useful for removing size differences in the shape variables, I also used centroid size as a covariate in further statistical analyses to account for allometric relationships between body size and shape differences (Krabbenhoft, Collyer, & Quattro, 2009; Mitteroecker & Gunz, 2009; Elmer, Kusche, Lehtonen, & Meyer, 2010; Webster & Sheets, 2010). Thin-plate spline transformation

grids were then used to visualize the individual variation in shape using TPSRegr software (Rohlf, 2004b).

Data Analysis

Spatial and temporal morphological variation across all rivers was detected using mixed-model multivariate analysis of covariance (MANCOVA) with 16 relative warps that explained 95.24% of the variance in the data as dependent shape variables (Hassell, Meyers, Billman, Rasmussen, & Belk, 2012; Kern & Langerhans, 2018). An *F*-test based on Wilks's λ was used to determine statistical significance for all terms in the model with the exception of time period for the temporal model and river for the spatial model. Significance of these terms was determined from an *F*-test that employed restricted maximum likelihood and the Kenward-Rogers degrees of freedom adjustment in SAS using the MIXED procedure (Hassell et al., 2012; Sharpe, Langerhans, Low-Décarie, & Chapman, 2015). The mixed procedure in SAS can effectively treat the population as a random effect, while also taking into consideration all relative warps at the same time. Following the methods of Hassell et al. (2012) I used an index variable to reflect the order of relative warps and treat the relative warps as repeated measures. Due to relative warps being treated as repeated measures on a single individual; individual and site within time period or river of origin were considered random variables in all models. Multivariate allometry was controlled for by including the centroid size, which is the square root of the sum of squared distance from each of the individual landmarks to the centroid, as a covariate. The partial

variance explained by each factor in the model was estimated using an F -test based on Wilks's n^2 (Langerhans & DeWitt, 2004).

To test for differences in body shape between historical and present-day individuals I modeled the main effects and interactions of time period and index variable with centroid size as a covariate. Interactions between the index variable and the main effect indicate the difference in shape for each of the relative warps independently and indicate morphological variation between the periods (following methods described in Wesner et al., 2011; Hassell et al., 2012; Heinen-Kay & Langerhans, 2013; Riesch et al., 2013).

To test for spatial differences in body shape variation in contemporary individuals I used river as a main effect, site nested within river as a random effect and log-transformed centroid size as a covariate. I visualized morphological variation between time periods and spatially across rivers by deriving and eigenvector of divergence (d) for each of the terms. Eigenvectors of divergence were obtained from a principal component analysis (PCA) on the sum of squares and cross-products matrix of the terms (Langerhans, 2009b). TPSRegr was used to generate thin-plate spline deformation grids visualizing the shape variation along the divergence vector for the term of interest (Rohlf, 2004b).

Heterogeneity of slopes was significant in all models and further influence on the statistical models were checked following Kern and Langerhans (2018). The importance of the interaction between centroid size and main effect was less than that of the main effect in all models. The partial variance (η_p^2) ranged from 4.6 – 14.5 %.

The statistical significance of morphological variability between time periods and between rivers was not altered by the inclusion of the interaction. The interaction term was removed from all models due to the fact that inclusion did not alter the correlation of divergent vectors.

Discriminant function analysis (DFA) was used for cross-validation and to determine assignment of individuals for river and time category based on size-corrected shape variables (relative warps). To correct for size in shape variables I used a MANCOVA with centroid size as the fixed factor and relative warps as the dependent variables then retained the residuals as size corrected shape variables in the DFA. DFA was also carried out to determine classification into stream order classes, with the four classes as 1) headwater tributaries (Dove Creek, North Llano River, South Llano River, James River), 2) upper watershed tributaries (San Saba River, Pedernales River, Llano River), 3) urbanized Austin area streams (Barton Creek, Walnut Creek, Onion Creek), and 4) the mainstem Colorado River. Canonical correlation analysis (CCA) was used to determine variation in body shape distinguishing between historical and present individuals in relation to the most informative flow and LULC variables determined by stepwise discriminant function analysis. All analyses were performed using SAS 9.4 (SAS Institute, Inc., Cary, North Carolina). Data used in my analyses are available through the Dryad Digital Repository (doi:10.5061/dryad.0n52027).

RESULTS

Historical and present-day landcover and land use in central Texas

During 1972-1976, the landscape within the HUC-10 watersheds of the headwater tributaries (South Llano River, North Llano River, James River, and Dove Creek) and the upper watershed tributaries (San Saba River, Llano River, and the Pedernales River) of the Colorado River Basin was dominated by forested land cover of juniper, mesquite, oak savannahs, and scrub oak. Similarly, the lower-order Austin urban watersheds (Barton Creek, Onion Creek, Walnut Creek) on the eastern edge of the Edwards Plateau ecoregion were dominated by forest land, in addition to 12-20% urban area, and to a lesser degree herbaceous and barren land cover. The mainstem Colorado River downstream of the Edwards Plateau flows through the westernmost extent of longleaf pines, contributing to the high percentage of forested land cover historically within the watersheds within the East Central Texas Plains ecoregion. Watersheds in closest proximity to Austin, Texas encompassed 5 to 15% high-intensity urban area, classified as greater than 70 % impervious surface, and from 3 to 11% low-intensity urban area, with less than 70% impervious surface (McMahan, Frye, & Brown, 1984; Diamond & Elliott, 2015). Historically, the second-most dominant landcover class in these watersheds was agriculture, with minimal amounts of barren or herbaceous land cover. In general, LULC changes in the Colorado River Basin since 1972-1976 were characterized by increased herbaceous land cover and decreased agriculture in increasingly urbanized watersheds. Similar transitions were documented between historical and present-day LULC in the lower and higher-order

tributaries in the upper Colorado River Basin, as well as in lower-order Austin streams and the lower mainstem Colorado River. All watersheds experienced a decrease in forested land cover and an increase in herbaceous land cover (Figure 2.2).

Hydrologic regime changes

Differences in hydrologic parameters between the two-time periods were greatest in the lower-order tributary systems in the upper Colorado River Basin and in the Austin urban streams (Figure A.1- A.2). Variation between the two periods for lower-order tributaries was related to decreases in the baseflow index and monthly summer flows and increases in the number of zero-flow days and minimum flows. Differences in flow in Austin urban streams were related to increasing minimum flows as well as an increase in the number of zero-flow days occurring per year. Additional differences between monthly flows were evident in Austin streams with present-day flows in February, April, October, and December decreasing on average (-17%) compared to the historical time period, while present-day flows were higher on average (21%) in June, July, September, and November. Lastly, baseflow index was greater than the mean in Austin streams during the present time period. Hydrologic changes in upper watershed rivers were related to increases in the baseflow index and monthly mean flows in August, and decreased minimum flows compared to historical regimes (Figure A.1-A.3). The mainstem Colorado River showed decreases in minimum flows and increases in maximum flows, as well as decreased flows in the late winter and early spring (Figure A.4). Throughout the Colorado River Basin, differences in the hydrologic regimes between the two-time periods indicated present-

day flows have increased flow variability, increased maximum flows, and diminished minimum flows. The small urban watersheds in Austin were an exception, with increasing average minimum flows, but the systems were flashier with more zero flow days (Figure A.2).

Preservation effects

No effects of preservation in formalin on Guadalupe Bass morphology based on the landmarks used in the current study were found after 18 months (Figure A.5). Although the study examining preservation effects was limited in duration relative to the length of time that fish collected by Edwards (1980) were held in formalin, previous studies have shown that preservation effects manifest relatively quickly after immersion in formalin (Sagnes, 1997; Jawad, 2003; Martinez, Berbel-Filho, & Jacobina, 2013).

Spatial and temporal morphological variation

Centroid size had a significant effect on morphological scores ($\eta^2p > 47\%$), indicating that RW scores and body size were correlated (Table 2.1). Time (i.e., whether the individual was collected between 1972 - 1980 as “historical” or between 2014 – 2016 as “present”) had the next strongest effect on morphological scores ($\eta^2p = 25.23$), indicating variability between the two-time periods regardless of river of origin. There were consistent morphological differences associated with river between the two-time periods ($\eta^2p = 7.40$). For example, relative warps for the mainstem Colorado River were significantly different between contemporary and historical individuals ($F_{4,61} = 14.97$, $P < 0.01$). Further, there were differences between rivers that

were independent of time period ($\eta^2p = 4.76$; interaction between stream order and time period). Historical and present-day Guadalupe Bass separated out along the first canonical axis ($F_{56,2799}=20.14$, $P<0.001$), which was related to the placement of the pelvic and pectoral fin, and the distance between the pre-maxillary and maxillary. Contemporary individuals exhibited deeper bodies and a more anterior placement of the pectoral and pelvic fin origins relative to previously collected individuals. The morphological divergence between the contemporary and historical samples was sufficient to allow a DFA to correctly assign fish to their time periods 79 % of the time using a single canonical dimension. The DFA based on river between the time periods was able to correctly assign historical individuals 48% of the time, while present individuals were correctly assigned to river of origin 26% of the time. The DFA based on stream order classes were able to correctly assign mainstem individuals 75%, major tributary individuals 74 % of the time, urbanized Austin stream individuals 67% of the time and the headwater tributary individuals 61% of the time.

Table 2.1: Results of MANCOVAs testing for body shape variation of contemporary Guadalupe Bass *Micropterus treculii* across all rivers and testing temporal shape variation. Time period indicates the difference between previously collected individuals (1975-1978) and individuals collected under current conditions (2014-2016).

Model	Model Term	F	df	P	η^2_p %
Spatial (only individuals collected from 2014-2016)	Log centroid size	21.01	16, 325	<.0001	47.44
	Site(River)	1.97	576, 4,831	<.0001	22.28
	River	3.04	160, 2,794	<.0001	9.60
	Log centroid size	62.34	16, 705	<.0001	58.59
Temporal (individuals collected from 1975- 1978 compared to individuals collected from 2014-2016)	Time Period	114.87	16, 705	<.0001	25.23
	River	3.56	160, 6,039	<.0001	7.40
	River x Time Period	2.21	64, 2,762	<.0001	4.76

Environment and morphological divergence

Morphological and environmental variables were related along two canonical functions for Guadalupe Bass over the forty-year time period. Morphological divergence between present and historical individuals was predicted by the first canonical variate ($R_c=0.81$, $F_{88,2493.7}=13.31$, $P<0.001$) with 67.0% of the variation in morphology being explained by the first environmental variate (Figure 2.4). The first morphological canonical variate primarily separated individuals based on the placement of the pelvic and pectoral fin, indicating body depth, and the distance between the pre-maxillary and maxillary, which is a measure of the head shape (Table A.6). The first environmental variate of the canonical correlation analysis was

associated with the increases in herbaceous land cover, decreases in forested land cover, and increasing maximum flows and the low pulse count (Table A.7). Onion Creek and Barton Creek, two urban streams, were the only exceptions to these trends with individuals under present conditions in both creeks separating out along the first canonical function gradient of morphological variation with historical individuals (Figure 2.4). All other present-day Guadalupe Bass tended to have increased body depth associated with a shift in the placement of the pelvic fin under increased maximum flow conditions. In comparison, historical individuals tended to have shallower body depths, with forested land cover and the number of low pulses contributing to the environmental canonical variate.

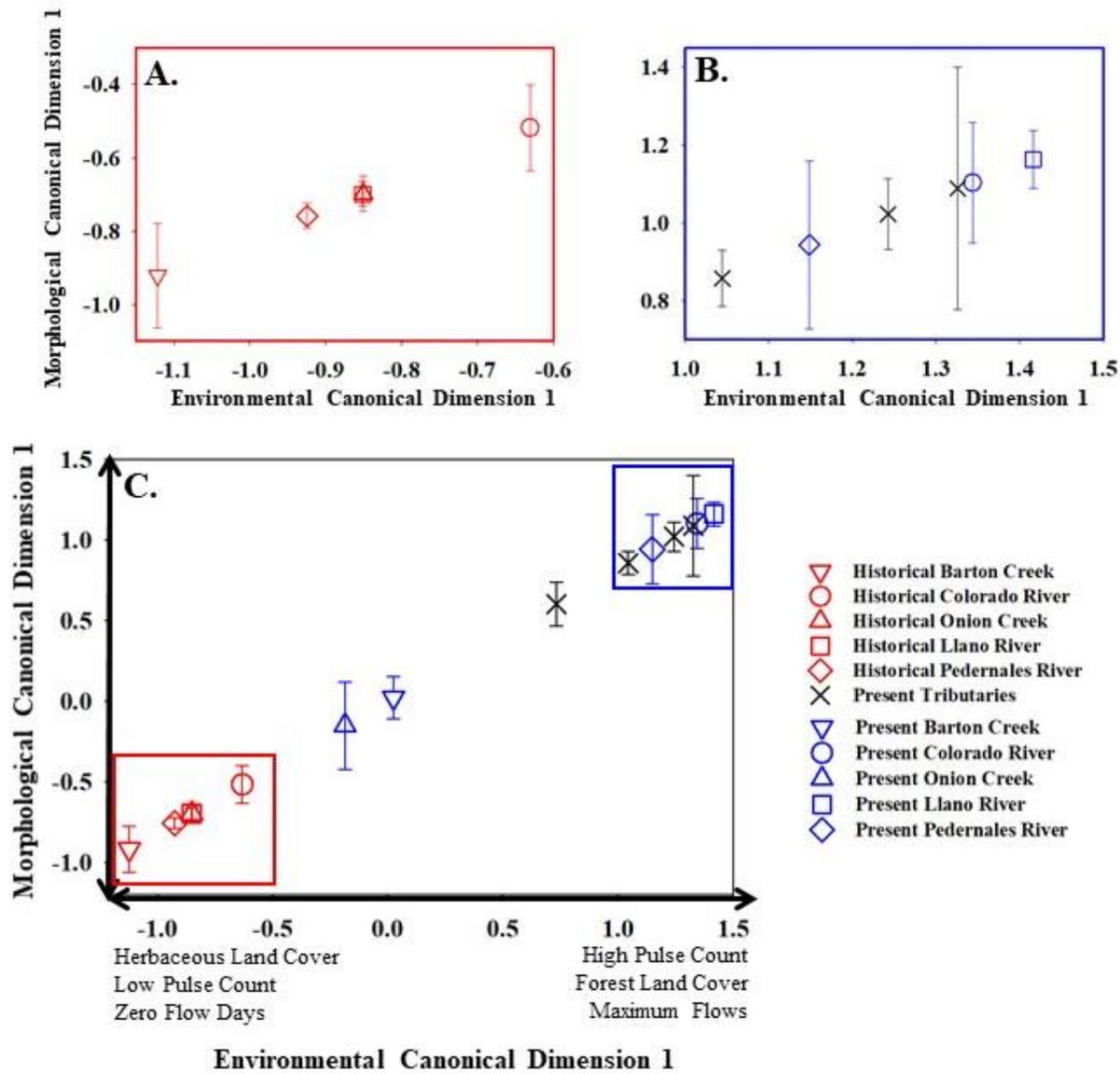


Figure 2.4: Mean morphological scores for historical and present-day collected Guadalupe Bass *Micropterus treculii* where red symbols represent historical morphological canonical scores and blue symbols represent present morphological canonical scores for the mainstem Colorado River and tributaries of the Colorado River. Historical specimens were obtained from Texas Natural Historical Museum for morphological analysis. Tributaries where historical specimens were not archived or available are indicated by black X's. The mainstem Colorado River and the three tributaries for which there were museum specimens are indicated by similar symbols with historical means represented in red and present means represented in blue. The first environmental canonical dimension representing hydrological and percentage difference in landscape is shown on the X axis. Inset A and B show the most closely related rivers from C.

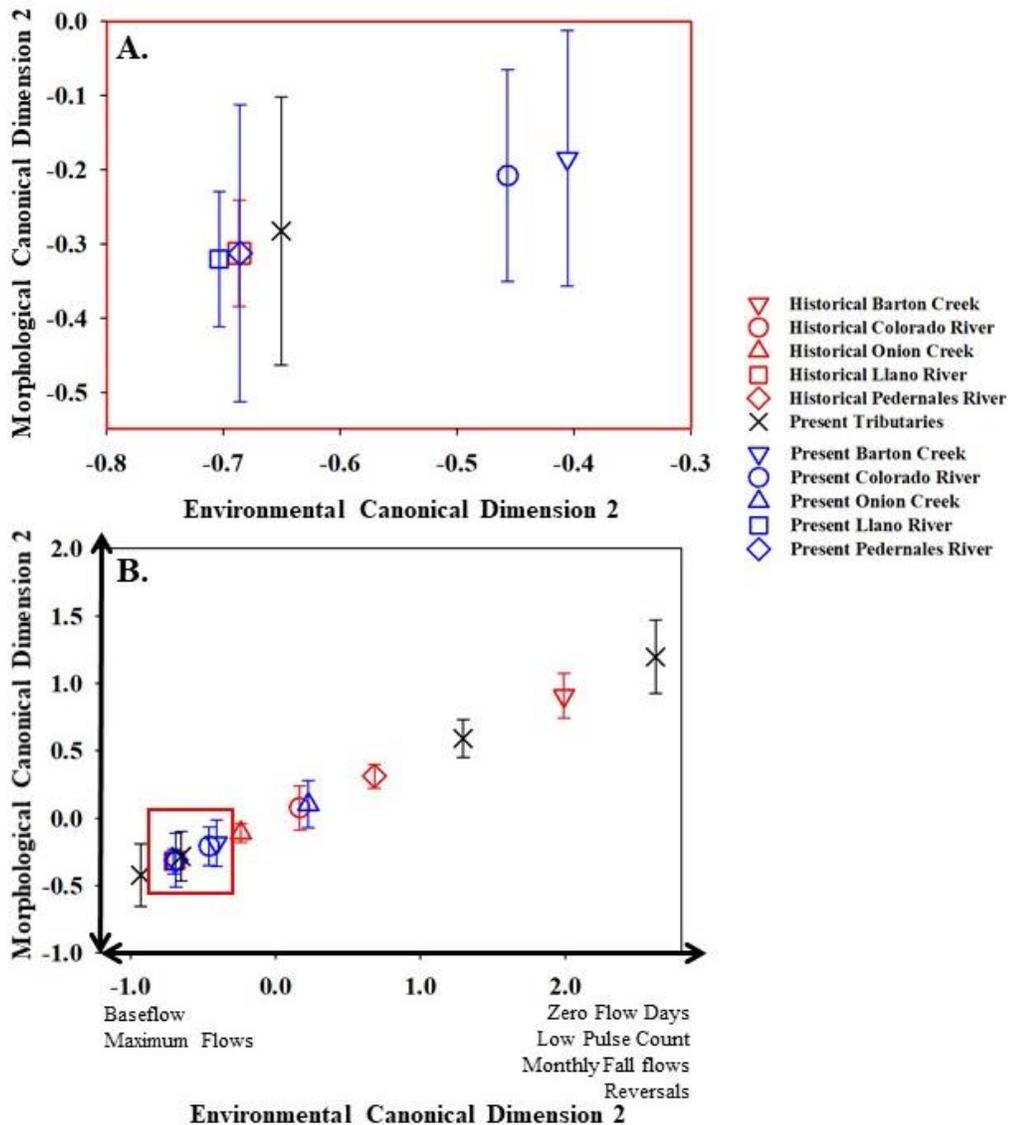


Figure 2.5: Mean morphological scores for historical and present-day collected Guadalupe Bass *Micropterus treculii* where red symbols represent historical morphological canonical scores and blue symbols represent present morphological canonical scores for the mainstem Colorado River and tributaries of the Colorado River. Historical specimens were obtained from Texas Natural Historical Museum for morphological analysis. Tributaries where historical specimens were not archived or available are indicated by black X's. The mainstem Colorado River and the three tributaries for which there were museum specimens are indicated by similar symbols with historical means represented in red and present means represented in blue. Environmental canonical scores representing hydrological and percentage difference in landscape are shown on the X axis. Inset A shows the most closely related sites from B.

The second morphological canonical variate represented morphological variation amongst and within sites throughout the Colorado River Basin (Figure 2.5). Differences were largely related to the distance between the caudal fin and anal fin, which represented a change in the length, as well as a shift dorsally of the caudal fin representing a change in depth (Figure 2.6). The main predictors loading the second environmental canonical variate were number of zero-flow days, baseflow index, low pulse count, thirty-day maximum flows, and monthly flows in in the fall. Present-day Guadalupe Bass showed an increased distance between the anal fin and the caudal fin. However, contemporary individuals collected in Onion Creek exhibited shorter distance between the anal fin and the caudal fin, more similar to individuals collected historically from Barton Creek.

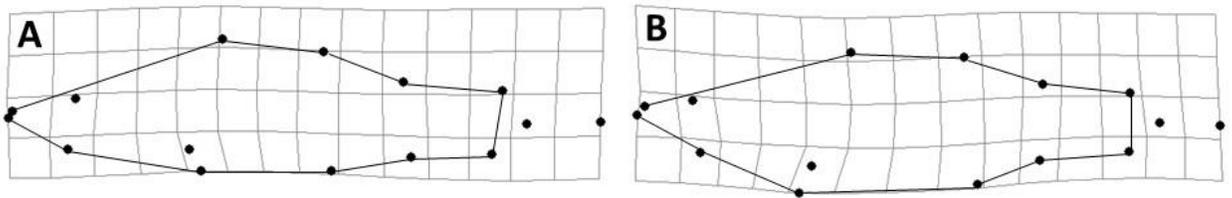


Figure 2.6: Thin-plate spline transformation grids illustrating the morphological variation in body shape between historical (A; pre-1980) and present-day (B; post-2012) Guadalupe Bass *Micropterus treculii*. Transformation grids are magnified 3x to better visualize the differences.

DISSCUSSION

The Colorado River Basin has experienced a range of changes in LULC and flow conditions over the past four decades, and these changes were associated with temporal morphological shifts in Guadalupe Bass populations. Morphological differentiation

between the time periods showed a gradient in body depth with historical individuals being largely distinguished based on their shallower bodies compared to present-day, deeper-bodied Guadalupe Bass. In general, deeper bodied Guadalupe Bass in the contemporary, altered Colorado River Basin experienced more variable flows with higher maximum flows and lower minimum flows in comparison to historical flow conditions. These flashier flow regimes, characterized by short duration and high magnitude flow events, are commonly associated with urban areas (Paul & Meyer, 2001; Konrad & Booth, 2005; Walsh et al., 2005) due to increased impervious surface, preventing water infiltration and increasing surface runoff (Shuster, Bonta, Thurston, Warnemuende, & Smith, 2005; Yang, Bowling, Cherkauer, & Pijanowski, 2011).

While there is a well-established link between fish morphology and water velocity, the variability in the impact that urbanization and anthropogenic alteration of the landscape has on flow patterns through time has been shown to result in varying morphological responses (Leavy & Bonner, 2009; Franssen et al., 2013; Istead, Yavno, & Fox, 2015). Blacknose dace *Rhinichthys obtusus* in urbanized streams of North Carolina had more streamlined morphology, whereas Creek Chub *Semotilus atromaculatus* under the same environmental conditions showed deeper body morphology (Kern & Langerhans, 2018). In the Colorado River in Texas I found that Guadalupe Bass exhibited increased body depth in response to changes in hydrologic patterns associated with increased urbanization, as well as increased herbaceous cover in more rural watersheds. In the mainstem Colorado and Austin stream watersheds, there was an increase in urbanized area likely contributing to the increase in variability in these flow

regimes. However, the increased body depth of contemporary individuals residing in more rural upper watershed tributaries is potentially due to the transition of forested land to other cover types resulting in similar patterns of hydrologic change. Changes in LULC outside of these highly urbanized areas primarily involved loss of forest land cover and increasing herbaceous land cover. Increases in herbaceous land cover is likely due to the transition of forested land cover to grazing area for livestock (Paukert, Pitts, Whittier, & Olden, 2011), one of the primary land uses within the Colorado River Basin. Although herbaceous land cover is often associated with benefits of infiltration and decreased surface runoff, the grazing of livestock can cause soil compaction, which acts similarly to an impervious surface (Hamza & Anderson, 2005; Chyba, Kroulík, Křištof, Misiewicz, & Chaney, 2014). Deeper bodied individuals may be favored under these patterns in hydrological alteration associated with these landscape changes throughout the basin, due to the morphological advantages that increased body depth has on the maneuverability and increased bursts in swimming speed (Webb, 2006). Under decreased current or stagnant environments deeper bodied individuals have shown improved foraging ability and predator avoidance performance (Franssen et al., 2013; Santos & Araújo, 2015). For example, when Bluegill *Lepomis macrochirus* and Green Sunfish *Lepomis cyanellus* were compared between lotic and lentic habitats, which naturally represent two extremes in flow conditions, the individuals in the reservoir habitats tended to have deeper bodies, while streamlined individuals were found in lotic environments (Gaston & Lauer, 2015). Morphological differentiation in Guadalupe Bass was not compared across the extremes

of stream versus reservoir habitat; however, similar increases in body depth were observed between contrasting temporal flow conditions.

The observed trait changes were consistent with morphological variation observed in other fish species across spatial environmental gradients, but to our knowledge, such changes have rarely been identified over long temporal scales. Previous studies assessed spatial trait variation in fish populations between contrasting environmental conditions, such as the absence of a predator (Holopainen et al., 1997; Robinson, Januszkiewicz, & Koblitz, 2008) or between a lotic and lentic flow regime (Franssen, 2011; Franssen & Tobler, 2013). However, assessing temporal trait variability is challenging and often relies on extensive historical collections. Access to historical collections prior to rapid human-induced change presented the unique opportunity to study the response of populations to varying environmental conditions through space and time. Our results along with those of Kern and Langerhans (2018) suggest that anthropogenic alteration has the ability to alter fish morphology and this continued environmental change could impact ecosystem structure and function (Bassar et al., 2010; Crutsinger, 2016). These results contribute to an understanding of trait variation that may help to buffer populations under conditions of increased urbanization and sprawl, human population growth, and climate risk, all of which impose novel selective pressure on species (Nelson et al., 2009; Reed, Waples, Schindler, Hard, & Kinnison, 2010), especially endemic species like Guadalupe Bass (McDonald et al., 2011; Kwon et al., 2012).

The sensitivity of the Colorado River Basin to the changing climate combined with the narrow range and population declines of Guadalupe Bass associated with

fragmentation and hybridization with Smallmouth Bass necessitates investigating the ability of trait variation to buffer the Guadalupe Bass population (Koppelman & Garrett, 2002; Littrell, Lutz-Carrillo, Bonner, & Fries, 2007; Bean, Lutz-Carrillo, & Bonner, 2013; Curtis et al., 2015). In central Texas the persistent drawdown on the Ogallala Aquifer is currently occurring at an unsustainable rate (Vaughan et al., 2012). Increased population growth accompanied by climatic changes throughout the state of Texas have already reduced the amount of water available (Liu et al., 2012; Smith et al., 2013). Additional increases in temperature and decreased precipitation expected for the region will increase the demand for water abstraction and storage (Chin, Laurencio, & Martinez, 2008; Yin, Yang, & Petts, 2012). Continued anthropogenic alteration of flow regime will impact Guadalupe Bass and further drive variability in morphology. Understanding the limitations of intraspecific variability to buffer these populations will be crucial to future management under increased demographic and climatic changes (Garrett, Birdsong, Bean, & McGillicuddy, 2015; Mimura et al., 2017).

In addition to showing variable body depth, Guadalupe Bass also showed underlying spatial morphological variation in the caudal peduncle. There may be two possible mechanisms for these morphological differences across the Colorado River Basin. Firstly, a stouter and deeper caudal peduncle may permit an individual to remain in position (de Assumpção et al., 2012), especially under higher maximum flows and longer duration of high pulses. However, under contemporary conditions of decreased baseflow index, there may also be deeper and stouter caudal fins for maneuverability and increased foraging efficiency. The caudal peduncle plays a major role in fish movement and maneuverability

and both of these mechanisms have been shown to drive morphological variation (McLaughlin & Grant, 1994; Imre, McLaughlin, & Noakes, 2002). For example, in Brook Charr *Salvelinus fontinalis* high-velocity flows have been shown to increase the caudal fin height and depth of the caudal peduncle (Imre et al., 2002; Hendry et al., 2010; Istead et al., 2015); however, high-velocity flows have also been shown to favor slender narrower caudal peduncles with deeper caudal peduncles being favored in low-velocity flows (Vogel, 1994; Blake, 2004; Langerhans & Reznick, 2010). Understanding how Guadalupe Bass are changing in response to anthropogenic habitat disturbances throughout a basin provides an indication of the resiliency of this species and reveals issues that may impede future conservation and management efforts. When implementing restoration, consideration for population-specific responses to unique environmental stressors may also be crucial when managers are choosing the proper broodstock to combat introgression or repatriate populations. For example, stocking lower Colorado River individuals in the Pedernales River may not be as successful or result in similar recruitment success as if San Saba River broodstock fingerlings were stocked in the Pedernales river. Incorporating intraspecific variation into management efforts will assist managers in the continued effort to combat introgression and inform restoration efforts that are paired with the pace of phenotypic response time (e.g., Ensslin, Tschöpe, Burkart, & Joshi, 2015). Discerning the morphological response of species will allow managers to modify timing and efforts for populations that have adapted under altered environments, thus increasing the success of these management efforts.

The patterns in morphological variability of Guadalupe Bass in response to changes in the flow regime, whether natural or anthropogenic, suggest that intraspecific trait variation may support resilience of populations under fluctuating conditions. Population adaptive capabilities have been shown to enhance fitness under differing environmental demands (Reed et al., 2010; Laughlin & Messier, 2015). However, there are potentially a multitude of other environmental or interspecific interactions driving trait change in Guadalupe Bass, such as predation (Eklöv, Svanbak, Eklo, & Svanba, 2006; Hendry, Kelly, Kinnison, & Reznick, 2006), habitat use (Brinsmead & Fox, 2002; Langerhans, Layman, Langerhans, & Dewitt, 2003), and diet (Reimchen & Nosil, 2002; Ward-Campbell, Beamish, & Kongchaiya, 2005; O'Neill & Gibb, 2014). Our data do not permit us to determine the precise drivers, or whether observed intraspecific variation is due to genetic or phenotypic variation. However, I do show that population-level variation has possibly contributed to the persistence of Guadalupe Bass throughout the Colorado River Basin. Further study is warranted to determine if the trait differences I observed between tributary and mainstem populations are contributors to variable fitness of individuals and affect further population tolerance and dynamics. Persistence and resiliency of populations under hydrologic alteration and transitioning landscapes have also been seen in other aquatic and terrestrial animal populations (Ribera, Doledec, Downie, & Foster, 2001; Goodman, Miles, & Schwarzkopf, 2008; Craven, Peterson, Freeman, Kwak, & Irwin, 2010; Kolbe, Lockwood, & Hunt, 2011). In contrasting flow conditions between intermittent and permanent streams, the alpine caddisfly *Allogamus uncatatus* exhibits plasticity in life-history traits related to growth and emergence that

allowed *A. uncatus* to persist in streams where drying might occur multiple times a year (Shama & Robinson, 2006, 2009). Additionally, population resilience across landscapes has been observed in association with variation in morphological traits related to flying for female speckled wood butterfly *Pararge aegeria* under conditions of landcover transition from woodland to agriculture. *P. aegeria* females developed increased total dry mass and wing loading when offspring were transplanted to agricultural landscapes in comparison to woodland (Merckx & Dyck, 2006). Population resilience and persistence can become evident on a generational timescale in some organisms. Therefore, understanding the intraspecific variability enabling a population to maintain their distributional range is crucial as landscapes and flow regimes continue to undergo alteration disrupting the natural environmental gradients that originally established variation in population-level traits. For that reason, understanding the capacity of a population to persist due to intraspecific trait variation has implications in modern conservation that need to be addressed.

Environments naturally fluctuate; consequently, populations are never really at equilibrium due to the stressors imposed by the environment. If populations are continually driven in one direction by environmental change from anthropogenic influence, they may no longer have the adaptability and capacity to respond to future changes expected based on demographic or climatic projections. For example, desert-adapted spadefoot tadpole populations have developed accelerated metamorphosis to avoid desiccation, but continual pond drying has diminished the plasticity in metamorphosis timing of the desert population, in comparison to non-desert populations

(Gomez-Mestre & Buchholz, 2006; Kulkarni, Gomez-Mestre, Moskalik, Storz, & Buchholz, 2011). The preservation of variation within a population fortifies the species' ability to respond to environmental change and promotes persistence of populations in areas that are heavily disturbed or projected to have increased alteration. Continued research on species and population tolerance through the study of phenotypic plasticity will provide further information on the conservation of communities with impending anthropogenic alteration, and natural environmental fluctuations (Geist, 2011; Hendry et al., 2011).

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CHAPTER 3

VARIATION IN GROWTH AND RECRUITMENT OF GUADALUPE BASS *MICROPTERUS TRECULII* ACROSS GRADIENTS OF FLOW WITHIN A BASIN

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ABSTRACT

Gaining an understanding of the various environmental factors, such as flow regime, that dictate population dynamics facilitates the refinement of population-level management and conservation efforts under conditions of increasing human population and water demands. Understanding variability within species across fluvial gradients in environmental conditions is crucial for the refinement of range-wide management strategies. The objective of this study was to determine if growth and recruitment of Guadalupe Bass *Micropterus treculii* differed from observed growth in smaller tributaries in response to variations in flow conditions along the upstream-downstream gradient in a large river basin. Guadalupe Bass occur across multiple stream orders and a range of anthropogenic impacts from less disturbed headwater streams to the highly disturbed mainstem of the Colorado River. The mainstem Colorado River flows through the center of Austin, Texas and is highly regulated by a chain of reservoirs, in comparison to the spring-fed headwater streams. I found a longitudinal gradient in growth throughout the basin with slower growth in headwater streams and increasing growth downstream, with fastest growth in the mainstem Colorado River. The influence of flow on growth was consistent throughout the basin, with the greatest growth occurring under moderate flow conditions regardless of the

river of origin. Similarly, weaker year classes in the lower Colorado River occurred under flow conditions associated with high flows and low flows. My results provide an understanding of the population-level variation in growth and recruitment along the longitudinal gradient of a basin.

INTRODUCTION

Environmental changes occur along the longitudinal gradient from upstream to downstream within stream networks, and the effects on stream fishes are often considered from an assemblage perspective, e.g., shifts in trophic groups and species richness. However, a population perspective is also important when examining variability across fluvial gradients because abiotic and biotic factors that influence life history parameters can vary with the progression from headwater streams to large mainstem rivers (Goto, 1989; Lotrich, 1973; Tedesco, Sagnes, & Laroche, 2009). In a natural stream network, lower-order streams experience greater variability in flow and temperature that can lead to abiotic factors limiting growth within a fish population (Poff et al., 1997). As discharge increases moving downstream, so does the width and depth of the channel, modifying pool and riffle development, decreasing the slope and substrate size downstream (Hynes, 1970; Leopold, 1994). In downstream environments with more stable flow conditions, biotic factors, such as increased competition and predation due to shifting trophic groups, are more likely to limit growth rates (Horwitz, 1978; Jackson, Peres-Neto, & Olden, 2001). These different stressors throughout a watershed have variable impacts on the dynamics of a population. For example, in headwater streams in West Virginia Brook Trout

Salvelinus fontinalis growth was slower in comparison to mainstem populations due to consistent competition for food resources that did not occur in the mainstem environments where warmer temperatures, increased food availability and decreased density resulted in consistently higher growth (Petty et al. 2014). Data on how growth and other life history traits within species vary along longitudinal gradients within watersheds are relatively sparse and limited to coldwater species, such as salmonids (Logez & Pont, 2011; Rosenfeld, Post, Robins, & Hatfield, 2007). Determining growth rate at a population level within river networks is important due to the influence that growth has on the overall dynamics within populations, including maturity and recruitment rates. Growth is highly variable in response to changing environmental conditions, whether it is natural variation along the longitudinal gradient of the river or variability caused by anthropogenic impacts. Understanding population dynamics in size-structured fish populations requires determining the environmental conditions, such as changes in the flow regime, that influence growth (Schlosser, 1982, 1985).

Growth rates dictate the size structure of a population which largely regulates fecundity and mortality rate in a population (De Roos, Persson, & McCauley, 2003). Environmental conditions that result in slower individual growth can impact recruitment for multiple years through increased mortality of younger age classes during over-wintering (Shuter, Maclean, Fry, & Regier, 1980) or due to increased predation risk (Brenden & Murphy, 2004; Holbrook & Schmitt, 2002), as well as through delayed maturation and reduced fecundity (Cowan, Rose, & Houde, 1997;

Hutchings, 1997; Rice, Crowder, & Marschall, 1997). Decreased growth rate can also delay ontogenetic shifts in diet, such as the switch to piscivory for top-level predators, which in turn can have ramifications for the structure of an entire aquatic community (Persson & Brönmark, 2002; Takimoto, 2003). For example, the movement of Largemouth Bass *Micropterus salmoides* to a higher trophic level is regulated by individual growth, which varies within and among populations (Olson, 1996). In Paul Lake, Michigan, early piscivory was seen in Largemouth Bass when growth was greater than the mean for a given cohort, enabling individuals to switch and maintain piscivory in their first summer (Post, 2003). High growth rates in Largemouth Bass have often been related to abiotic factors, such as flooding in the spring (Raibley, O'Hara, Irons, Blodgett, & Sparks, 1997). For example, sustained floodplain inundation during the spring and summer was related to increased fish recruitment in the Apalachicola River, Florida, as well as having a positive influence on the growth of age-0 Largemouth Bass (Burgess, Pine, & Walsh, 2013; Dutterer et al., 2013).

When stream flow conditions are modified in regulated systems or by land use and land cover transitions associated with increased urbanization, the natural variability that stream fishes depend on for crucial life history stages, such as movement for spawning or increased food availability when rearing young, are disrupted (Schlosser, 1991, 1994). The relationship between flow regime and population dynamics reflects direct and indirect links between flow conditions and biological and physical mechanisms that dictate survival and recruitment in a population. For example, under high-flow conditions, there is an increase in the

amount of available habitat and food, which promotes the growth of juveniles and is presumed to increase the success of recruitment (Bunn & Arthington, 2002; Poff & Allan, 1995; Schlosser, 1991). Conversely, low-flow conditions have also been shown to provide nursery habitat and concentrate prey in some systems, therefore increasing availability of resources for growth and overall abundance (Freeman, Bowen, Bovee, & Irwin, 2001; Pease, Davis, Edwards, & Turner, 2006). Gaining an understanding of how variability in growth and recruitment influences population dynamics and how this varies with flow conditions across a range of stream orders will aid in assessing the impacts of anthropogenic disturbance that occur throughout a basin.

In this study, Guadalupe Bass *Micropterus treculii* in the Colorado River basin of Texas serve as a model system because they occur across a variety of stream orders and a range of anthropogenic impacts from the less disturbed headwater streams to the highly disturbed mainstem of the Colorado River, which flows through the heavily urbanized city of Austin, Texas. The spring-fed headwater streams of the Colorado River have relatively undeveloped riparian areas and dams present on tributaries are either smaller low-head or agricultural diversion dams (TPWD, 2005; U.S. Army Corps of Engineers, 2016). In comparison, the mainstem Colorado River flows through the highly urbanized center of Austin, Texas and is highly regulated by a chain of reservoirs. Increases in urbanized area and landcover transitions between forested land to herbaceous land cover, as well as changes to the flow regime have resulted in habitat degradation and population decline across much of the Guadalupe Bass range (Curtis, Perkin, Bean, Sullivan, & Bonner, 2015; Edwards, 1980;

Koppelman & Garrett, 2002). Increased knowledge of the differences between individuals in smaller tributary systems in comparison to mainstem individuals is necessary for the future refinement of restoration strategies and effective management of the lower Colorado River population found in habitat that is not considered “typical” for Guadalupe Bass. Filling this information gap is imperative with projected continuing human population increases, and with forecasted climatic changes likely to occur throughout the region. The objective of our study was to determine if the growth and recruitment of Guadalupe Bass in the Colorado River differed from previously observed growth in smaller tributaries and in response to variations in flow conditions. Gaining an understanding of the various environmental factors dictating population dynamics for a basin-wide, habitat specialist facilitates the refinement of population-level management and conservation efforts under conditions of increasing human population and water demands.

METHODS

Study Area

Guadalupe Bass are distributed throughout the Colorado River basin from small headwater streams to the mainstem lower Colorado (Curtis, Perkin, Bean, Sullivan, & Bonner, 2015; Edwards, 1980). Thirty-nine sites were selected along the mainstem Colorado River and its tributaries (Figure 3.1) based on previous collections made in the 1970s in order to make ecomorphological comparisons in a related study (Pease, Grabowski, Pease & Bean, 2018). Sites encompass the distinct upstream-downstream gradient in urbanization along the Colorado River and its major tributaries between

their headwaters and Austin, Texas (Pease, Grabowski, & Pease, 2017) with site accessibility also influencing site selection. Six spring-fed tributaries: North Llano River (n=7), South Llano River (n=6), San Saba River (n=4), Llano River (n=5), and Pedernales River (n=6), were sampled in the upper portion of the Colorado River Basin. While there are low-head dams present on the upper tributaries and headwater streams, their flows are largely unregulated in contrast to the five lower mainstem sites, which occur in a highly regulated reach of the Colorado River. Additional sites were sampled in Barton Creek (two sites), located within the rapidly growing, heavily populated metropolitan area of Austin, Texas. Guadalupe Bass were targeted in other urbanized streams in the Austin metropolitan area. However, these sites were ultimately not included in the analysis due to an inability to capture a sufficient number of individuals. The flow regimes of the urban tributaries are characterized by increased flashiness and draw-downs due to the intensified landscape transitions accompanying the increasing human population (Allan, 2004; Paul & Meyer, 2001; Pease et al., 2017). There is a decrease in the amount of urbanization moving downstream from the city of Austin (Pease et al. 2017); however, the amount of water moving through the system is highly regulated in comparison to the upper watershed streams due to a chain of reservoirs along the mainstem of the Colorado River immediately upstream of Austin.

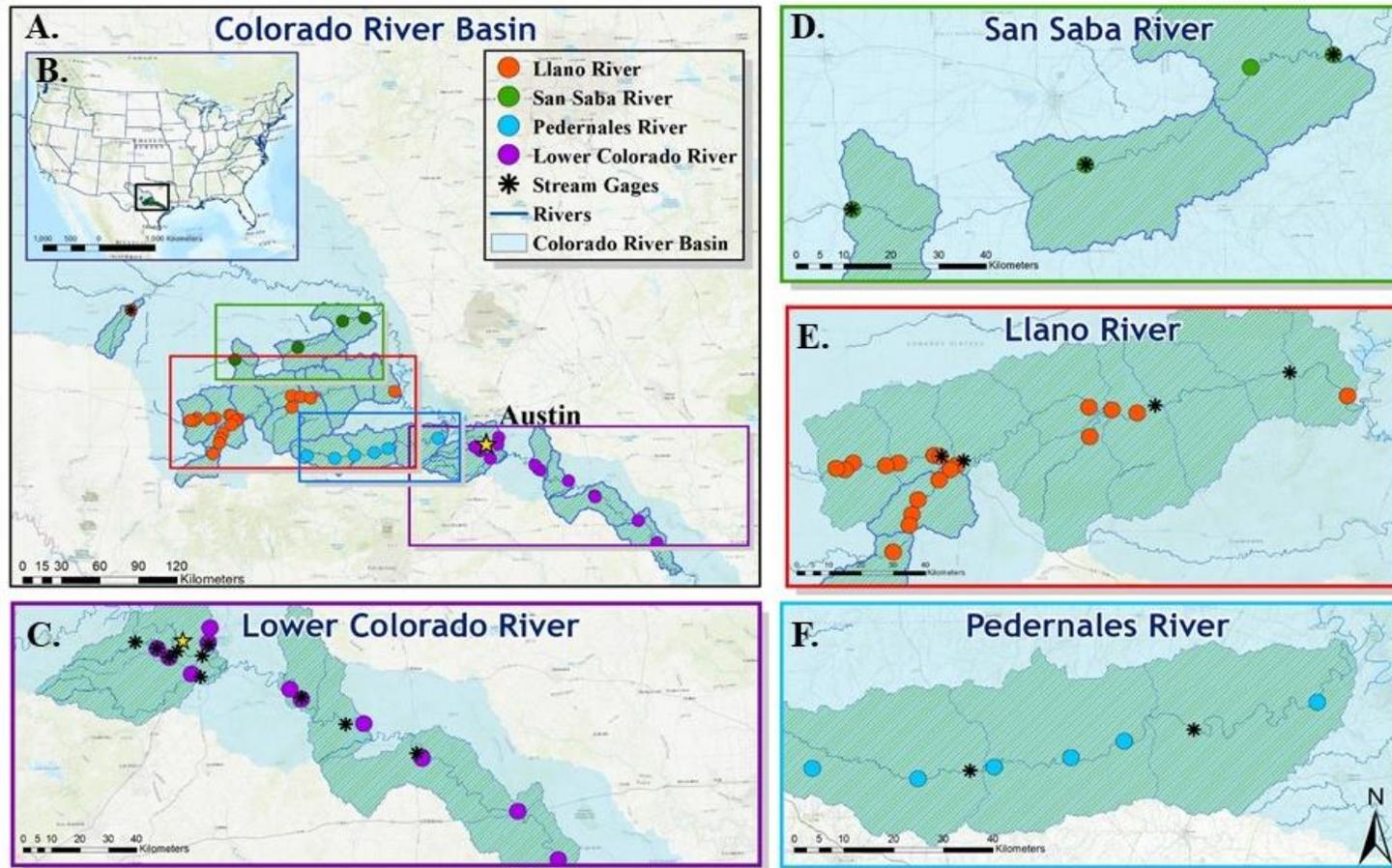


Figure 3.1: Map indicating the distribution of study sites and stream gages throughout the Colorado River Basin. A and B indicate the location of the Colorado River in Texas and the distribution of the sites. Inset D-F indicate major tributary sites and the associated gages. Inset C shows sites and gages in the Austin, Texas area and located on the lower Colorado River below Longhorn Dam in Austin, Texas.

Fish Collection

Guadalupe Bass were collected from a 100-m stream reach at each site using backpack electrofishing or boat electrofishing where applicable. Each site was sampled twice in 2014 and 2015 for approximately 1000 seconds. Total length (mm) was recorded for all individuals captured and euthanized with clove oil (eugenol) before transport to the lab where sagittal otoliths were removed. Otoliths were embedded in epoxy resin and a low-speed isometric saw (Bay Technology, San Clemente, California) was used to cut a transverse section (approximately 0.5-mm thick) from the otolith through its nucleus (Long & Grabowski, 2017). Digital images of otolith sections were captured using an Infinity 1-5C 5.0 MP digital camera (Lumenera Corporation, Ottawa, Ontario) attached to an Olympus SZX16 stereo microscope (Olympus Corporation, Tokyo, Japan). Image J v. 1.48 (Abràmoff, Magalhães, & Ram, 2005) was used to count annuli and measure otolith width and distance between each annulus. The formation of annuli has not been validated in Guadalupe Bass; however, annuli formation has been validated in multiple species of *Micropterus* across different locations (Buckmeier & Howells, 2003; Hoyer, Shireman, & Maceina, 1985). Age was determined by two readers working independently without knowledge of the age, origin, or length of the fish. Age estimates were compared between the two readers and any differences were resolved by a third reader. Back-calculated length of each annulus was determined using the Dahl-Lee method described by Devries and Frie (1996) and assuming a 01 January birthdate due to the protracted spawning season of Guadalupe Bass (Edwards, 1980;

Jones & Wells, 1998; Morgan, 1987). Back-calculated length-at-age data were used to fit a Von Bertalanffy growth curve ($L_t=L_\infty(1-e^{-k(t-t_0)})$) with the following parameters: L_∞ the asymptotic length, k for the growth coefficient and t_0 for the time where the length should theoretically be zeros (VonBertalanffy, 1938).

Hydrologic Analysis

Variability in stream discharge between years and sites was assessed using Indicators of Hydrologic Alteration software v. 7.1 (IHA; The Nature Conservancy) to calculate 33 parameters (Table 3.1; Richter, Baumgartner, Powell, & Braun, 1996) from the nearest USGS gage station to each site (Figure 3.1; Table A.4). Discharge data were not available until 01 October 2012 for the South Llano River, therefore prior years were estimated as the difference between the North Llano River gage and the downstream Llano River gage. The Llano River gage is located 5.33 km downstream of the confluence of the North Llano River and the South Llano River, which are the only contributing tributaries to the discharge rates recorded at the Llano River gage. The 33 IHA parameters describe the annual flow regime of a site based on stream gage data and are broadly grouped into four categories: 1) monthly averages, 2) annual extremes in minimum flows, maximum flows, and a baseflow index (7-day minimum flow/mean flow for year) 3) high and low pulse duration and frequency, and 4) overall change rate and frequency of water conditions (Richter, Baumgartner, Powell, & Braun, 1996). The parameters were normalized to a mean of zero with a standard deviation of one. Patterns in alteration of hydrologic parameters related to changing flow conditions can be identified using flow variables standardized across

the basin. Scaling flow parameters permits basin-wide comparisons but may inhibit the detection of an interaction between flows and river of origin. For instance, a substantial change in the flow conditions in one of the headwater rivers, such as the North Llano River, may be irrelevant in larger tributaries or the mainstem river. Redundancy in the 33 flow variables was accounted for using principal component analysis (PCA) to derive linearly uncorrelated components. Principal components were retained for further analysis based on the broken stick model (Jackson, 1993) and the proportion of variance explained by each component. The component scores of the hydrological parameters for each stream gage by year were associated with individual Guadalupe Bass growth in a given year based on proximity to collection site. I assume that movement of individuals between neighboring gages was unlikely based on telemetry studies (Perkin et al. 2010; Pease et al. 2017). or mark-recapture studies (Bean & Grabowski, 2015).

Data Analysis

The residual of each back-calculated length-at-age from the length-at-age predicted by the fitted Von Bertalanffy curve was calculated, then divided by the predicted length-at-age to generate departures from standardized growth (Quist, Pegg, & Devries, 2012). The influence of hydrologic parameters on the departures from standardized growth was evaluated using a mixed-model repeated-measures analysis of covariance (ANCOVA; Rutherford, 2011). Individual age and flow metrics represented by PC1, PC2, and PC3 were covariates in the model. River and back-calculated age were fixed effects. Individuals were treated as subject effects with

repeated measures back calculated for each year. Back-calculated measurements violate the assumption of independence because of the repeated nature of the observations on each individual. An autoregressive correlation covariance structure was used in the model to account for correlation between years and considers multiple measurements from one individual with a decrease in the correlation corresponding to an increasing age gap (Jacquemin, Doll, Pyron, Allen, & Owen, 2015).

In addition, I used catch-curve regression to estimate recruitment and mortality of the mainstem Colorado population (Maceina, 1997). Assessment of mortality in the lower Colorado River incorporated Guadalupe Bass collected in 2015 along the 260-river km between Webberville and Altair, TX as part of additional monitoring efforts. An additional 260 individuals collected over approximately 120 hours of electrofishing sampling were used to assess the mortality rates. An age-length key (Table S2) with 25-mm total length intervals was used to determine the probability that an individual in a length interval was a given age (Coggins, Gwinn, & Allen, 2013; Ricker, 1975). The age-frequency distribution for all individuals caught in the mainstem Colorado River was then used to construct a catch-curve for Guadalupe Bass collected in 2015 ($n=343$). Instantaneous mortality rate (Z) was estimated from the descending leg of the catch curve as described by Ricker (1975). The annual mortality rate corresponding to the instantaneous mortality rate for the population at a given time was then determined. The descending leg of the catch curve was also used to determine the relative recruitment as the residual of the cohort from the regression model as described by Ricker (1975) and Maceina (1997). Strong year classes are

indicated by a positive residual, and a negative residual represents a weaker year class in the population (Maceina & Pereira, 2007). Correlation was used to assess the influence of principal components for the hydrologic parameters on recruitment. Linear regression was also used to determine the relationship between relative recruitment and standardized growth. All analyses were performed using SAS 9.4 (SAS Institute, Inc., Cary, North Carolina).

RESULTS

Annual Stream Flow Metrics

The broken stick model selected a single significant axis indicating the variation in the hydrologic parameters between tributaries and the mainstem. Further examination of the scree plot (Cattell, 1966) and other stopping techniques (Jolliffe, 1986; Peres-Neto, Jackson, & Somers, 2005; Velicer, Eaton, & Fava, 2000) suggested multiple axes contributing to the variation in the hydrologic data. Therefore, the second and third principal component axes were also retained for interpretation of differences between tributaries. Cumulatively, the first three principal components explained 28% of the variation in the data (Table 3.1). The first principal component (PC1) separated the tributary systems from the mainstem Colorado River and was largely defined by increasing mean monthly flows (January, March, May, July, August, October, and December), number of reversals, number of high pulses, and duration and magnitude of one-day maximum flows (eigenvector: 5.45; proportion of variation: 0.16). Sites on the mainstem Colorado River had high scores on PC1, while tributary systems exhibited low PC1 scores. The second principal component (PC2)

contrasted years with higher minimum flows and those with more zero-flow days (eigenvector: 2.22; proportion of variation: 0.07). The third principal component (PC3) was also related to increasing December monthly flows and fall rate, as well as decreasing number of low pulses and the number of reversals (eigenvector: 1.85; proportion of variation: 0.06). Mainstem Colorado River sites were also separated from tributary sites along PC3 with the Colorado River having a negative PC3 scores and the tributaries having primarily positive PC3 scores (Table 3.2).

Table 3.1: Eigenvectors for discharge metrics of the Index of Hydrologic Alteration (Richter et al. 1996) resulting from a principle component analysis of the annual flow regime for the 17 U.S. Geological Survey (USGS) streamgages throughout the Colorado River Basin listed in (Table A.4). IHA metrics with bolded eigenvector values $\geq \pm 0.20$ were used to interpret principal component axis. Table located on page 86.

IHA Type	IHA Attribute	PC1	PC2	PC3
		Eigenvector	Eigenvector	Eigenvector
Magnitude of monthly flow conditions (mean for each month)	January	0.27	-0.15	0.18
	February	0.14	0.01	-0.17
	March	0.28	-0.13	0.10
	April	0.07	0.06	-0.23
	May	0.32	-0.14	-0.11
	June	0.06	0.17	-0.03
	July	0.25	-0.09	-0.11
	August	0.25	-0.10	-0.13
	September	0.03	0.11	-0.13
	October	0.28	-0.07	0.23
	November	0.15	0.09	-0.16
	December	0.29	-0.09	0.27
Magnitude and duration of annual extremes	1-day minimum	0.24	0.11	0.20
	3-day minimum	0.09	0.39	0.22
	7-day minimum	0.10	0.44	0.20
	30-day minimum	0.12	0.38	0.05
	90-day minimum	0.01	0.29	-0.21
	1-day maximum	0.26	-0.03	0.10
	3-day maximum	0.11	-0.18	0.15
	7-day maximum	-0.03	-0.16	0.14
	30-day maximum	-0.12	0.05	0.12
90-day maximum	-0.17	-0.01	0.11	
Frequency and duration of high- and low-flow pulses	Zero flow days	-0.12	-0.36	0.09
	Base flow	0.04	0.22	-0.03
	Date of minimum	0.00	-0.06	-0.20
	Date of maximum	0.06	-0.04	0.16
	Number of low pulses	0.13	-0.05	-0.40
	Low pulse duration	-0.05	-0.06	0.02
	Number of high pulses	0.24	0.02	0.03
Rate and frequency of changes in water conditions	High pulse duration	-0.01	-0.05	0.02
	Rise rate	0.09	-0.05	-0.19
	Fall rate	-0.09	0.06	0.26
	Reversals	0.27	0.07	-0.26

Table 3.2: Table of the mean standardized growth and mean principal component score for hydrological parameters by year for the individual rivers throughout the Colorado River Basin.

River	Year	Standardized Growth	PC 1	PC 2	PC 3
Barton Creek	2012	0.28	-0.63	-1.05	-0.20
	2013	0.15	-0.84	-0.50	-0.10
	2014	-0.07	-0.59	-0.23	-0.24
Colorado	2010	0.18	0.65	0.36	-0.58
	2011	0.28	0.28	0.23	-0.88
	2012	0.45	0.39	0.36	-1.51
	2013	0.34	0.19	0.24	-0.82
	2014	0.15	-0.14	0.06	-0.68
Llano	2012	0.08	-0.55	0.31	-0.66
	2013	0.14	-0.31	1.09	0.48
	2014	0.00	-0.49	0.67	-0.21
North Llano	2008	-0.09	-0.68	-0.58	0.82
	2009	-0.04	-0.32	0.92	-0.46
	2010	-0.12	-0.18	0.59	0.65
	2011	-0.19	-1.01	-1.59	-0.05
	2012	-0.17	-1.32	-1.71	0.34
	2013	-0.13	-0.74	-0.97	-0.03
	2014	-0.14	-0.65	-1.40	0.19
Pedernales	2011	0.40	-1.15	-1.92	-0.16
	2012	0.32	-0.69	-0.59	-0.51
	2013	0.19	-0.77	-1.15	-0.30
	2014	0.42	-0.91	-0.70	-0.46
San Saba	2011	0.28	-0.43	0.85	0.20
	2012	0.23	-0.46	0.21	-0.16
	2013	0.19	-0.70	-0.22	0.01
	2014	0.18	-0.92	-0.23	0.46
South Llano	2008	0.02	-1.07	0.43	0.07
	2009	-0.08	-1.35	0.05	1.39
	2010	-0.07	-1.46	0.39	-0.46
	2011	-0.13	-0.90	1.11	0.53
	2012	-0.11	-0.51	1.66	-0.37
	2013	-0.10	-0.52	-0.86	-0.69

Growth

A total of 234 Guadalupe Bass with a mean (\pm SE) age of 3 ± 2 years (range: 1 to 8 years) and a mean (\pm SE) TL of 223 ± 80 mm TL (range: 74–461 mm TL) were captured from the Colorado River Basin. The mean (\pm SE) catch rate (individuals per hour) in headwater streams (1.88 ± 1.79) was greater than that of the larger tributaries (0.99 ± 1.32) and urban streams (1.20 ± 0.32) where backpack electrofishing was used. The capture rate in the mainstem Colorado River (1.20 ± 0.58 individuals per hour) using boat electrofishing was not different ($F_{1,3}=1.18$, $P=0.33$) from the rate of Guadalupe Bass capture seen in the tributaries with backpack electrofishing.

The fitted Von Bertalanffy growth curve resulted in the following parameter estimates (\pm SE): $L_{\infty} = 635.7 \pm 141.0$, $k = 0.11 \pm 0.04$ and $t_0 = -0.46 \pm 0.14$ (Figure A.6-A.7). Guadalupe Bass in headwater streams grew slower than individuals in other habitats throughout the basin ($F_{1,227} \geq 12.46$, $P < 0.01$), while the growth of individuals within the mainstem Colorado River was comparable to that of individuals in the major tributaries, i.e., the Llano, San Saba and Pedernales Rivers ($F_{1,227}=0.22$, $P=0.64$). The growth of individuals inhabiting streams in the Austin metropolitan area did not differ from that of individuals in the adjacent mainstem Colorado River ($F_{1,227}=3.56$, $P=0.06$). Growth differed between urban streams and headwater streams ($F_{1,227}=12.46$, $P < 0.01$) with higher standardized growth in urban streams.

Elements of the flow regime had an overall influence on growth throughout the basin with standardized growth being related to hydrologic parameters associated with PC1 ($F_{1,207}=4.08$, $P=0.04$). The first principal component separated flow variability

between years and gage sites in the mainstem Colorado River from the other tributaries (Figure 3.2). The Colorado River had higher monthly flows, with higher maximum one-day flows, and a greater number of reversals in comparison to the flow conditions experienced in the tributary systems. Higher standardized growth in the Colorado River increased flow parameters represented by PC1. Standardized growth of Guadalupe Bass was greatest at moderate values along PC1 and lower at both high and low values along PC1 indicating that stable flow conditions result in the highest standardized growth. For instance, standardized growth was lower when monthly flows were lower and there were fewer reversals, as well as when monthly flows were a lot higher and there were a greater number of reversals. Similar relationships between PC1 flow parameters and standardized growth were seen for both larger tributaries and urban streams (Figure 3.2).

Flow conditions represented by PC2 were not related to standardized growth throughout the basin ($F_{1,207}=0.34$, $P=0.55$); however, the third principal component was related to basin-wide standardized growth ($F_{1,207}=5.22$, $P=0.02$). Higher standardized growth in both tributaries and urban streams was related to a reduced number of low pulses and number of reversals associated with PC3. Standardized growth in the mainstem, tributaries and urban streams was positively correlated with PC3, whereas in headwater streams standardized growth was negatively correlated with PC3 (Table 3.3). Positive standardized growth was related to maintained flows across the basin with the mainstem Colorado River showing increased standardized growth related to increasing monthly flow and decreasing fall rate in tributary systems.

The number of reversals separated the mainstem Colorado River from tributary systems along PC3, and a reduced number of reversals on PC3 was related to increased standardized growth in the mainstem Colorado River. Individual age was also a factor influencing growth regardless of the river of origin.

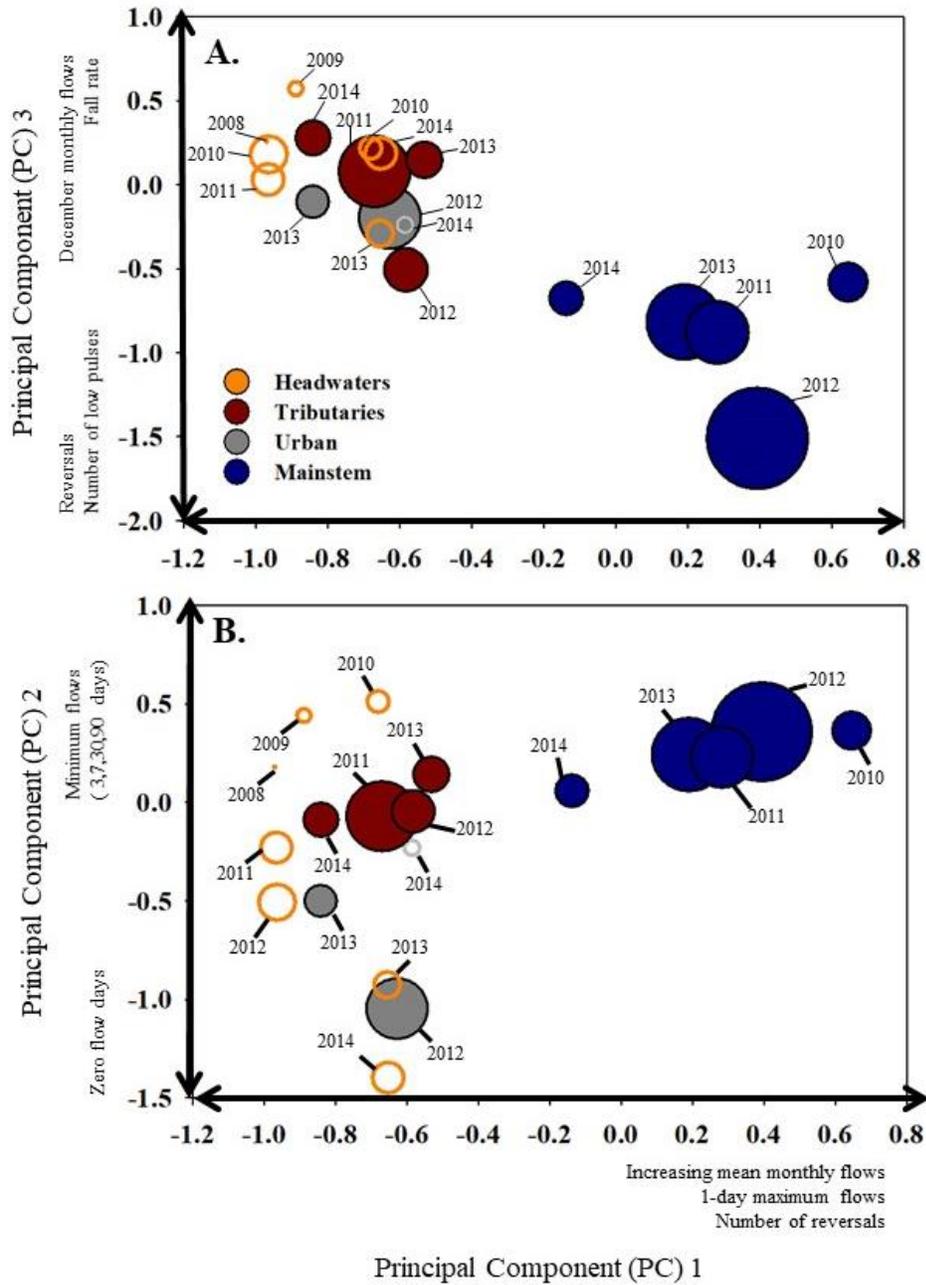


Figure 3.2: Standardized otolith growth for Guadalupe Bass captured throughout the Colorado River Basin, Texas from 2014-2015. The sizes of individual bubbles represent the magnitude of response in standardized growth to annual stream discharge metrics. Filled bubbles represent increased growth response, while unfilled bubbles represent a decreased growth response. Inset A and B represent the influence of annual stream discharge metrics for steams grouped by stream order throughout the Upper Colorado River Basin.

Table 3.3: Mixed-model repeated-measures ANCOVA results for Guadalupe Bass otoliths growth rate residuals for all ages. Annual stream flow metrics influences on growth rate residuals were evaluated for Guadalupe Bass collected between 2014 and 2016. Model effects with a P -value ≤ 0.05 were considered significant.

Effect	River	Value (\pmSE)	F	DF₁	DF₂	P
River	-	-	21.2	7	227	<0.01
	Barton	0.06 \pm 0.06	-	-	-	-
	Colorado	0.22 \pm 0.05	-	-	-	-
	Llano	0.14 \pm 0.04	-	-	-	-
	North Llano	-0.15 \pm 0.03	-	-	-	-
	Pedernales	0.22 \pm 0.05	-	-	-	-
	San Saba	0.21 \pm 0.05	-	-	-	-
	South Llano	-0.15 \pm 0.04	-	-	-	-
BC_Age	-	0.02 \pm 0.01	14.5	1	207	<0.01
PC1	-	0.05 \pm 0.02	4.08	1	207	0.04
PC2	-	-0.01 \pm 0.01	0.34	1	207	0.55
PC3	-	0.03 \pm 0.01	5.22	1	207	0.02

Mortality and Recruitment

Guadalupe Bass in the mainstem Colorado River were fully recruited to our sampling gear (boat-mounted electrofishing) at age-2 and exhibited an instantaneous mortality rate (Z ; \pm SE) of 0.34 ± 0.11 or annual mortality rate of 28.94% (Figure A.8). Recruitment was variable during 2009-2014, with relatively weaker year classes in 2009 and 2014 and stronger year classes during 2010-2013, with 2011 representing the strongest year class within the period examined. Mean annual standardized growth and relative recruitment were not correlated ($r=0.31$, $P=0.61$). Weaker year classes occurred in years when there were increased minimum flows.

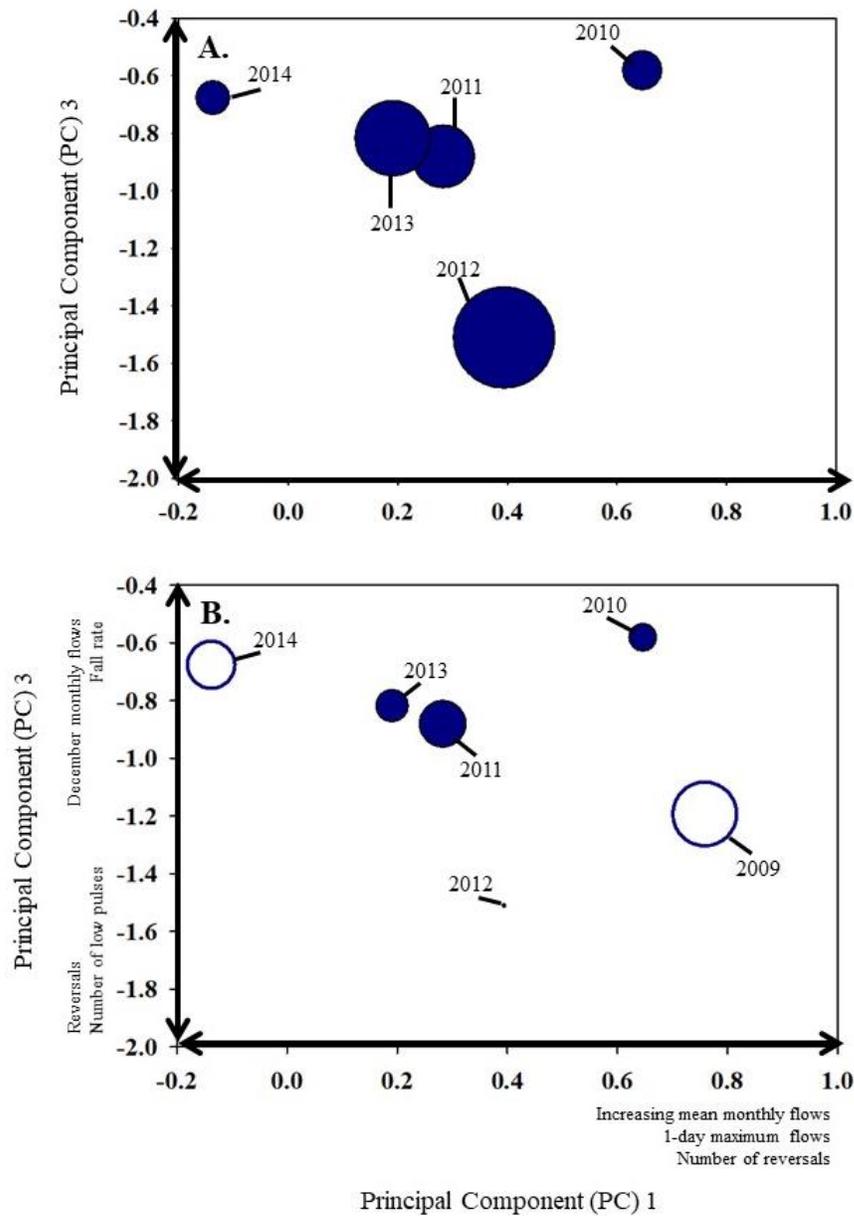


Figure 3.3: Relationship between annual Indicators of Hydrological Alteration metrics (Richter et al. 1996) as described by their first two principle components and Guadalupe Bass otolith growth (A) and recruitment (B) in the lower Colorado River downstream of Austin, Texas during 2009-2014. Relative recruitment was calculated as the residual of a cohort from the regression model of the descending leg of the catch curve for a sample of 234 Guadalupe Bass captured in 2015. The magnitude of relative recruitment is represented by the size of the bubbles. Filled blue bubbles indicate a positive residual or higher than predicted relative recruitment while empty bubbles indicate negative residuals or lower relative recruitment.

DISCUSSION

The upstream-to-downstream variation in abiotic and biotic factors has established a longitudinal gradient in Guadalupe Bass growth from the headwater streams to the mainstem lower Colorado River. Identifying the factors influencing these differences will assist in refining future basin-wide population management. Flow is one highly variable abiotic factor that has been found to influence the growth and structure of populations (Paragamian & Wiley, 1987; Sammons & Maceina, 2009), differs across stream orders, and is also influenced by the increasing anthropogenic changes occurring in the basin. Continued reductions in stream flows in the Colorado River Basin, whether due to persistent drought or increased anthropogenic water withdrawals, will likely result in lower Guadalupe Bass growth rates throughout the basin. Lower growth rates will potentially impact the size and composition of the population, as has been seen in Brook Trout *Salvelinus fontinalis* under drought conditions (Hakala & Hartman, 2004). Recruitment in the mainstem Colorado River downstream of Austin is also likely to be reduced, and I speculate that recruitment in other Guadalupe Bass populations would respond to flow variability in a similar fashion.

Guadalupe Bass in headwater streams exhibited slower growth in comparison to higher-order tributaries and the mainstem Colorado River. Several studies of stream fishes have shown increasing growth rate with stream order in relation to multiple factors ranging from prey availability, predation, competition, and several other potential abiotic and biotic factors (Blachuta & Witkowski, 1990; Lotrich, 1973;

Oberdorff, Guilbert, & Lucchetta, 1993; Schlosser, 1990). In two species of sculpin (*Cottus bairdi* and *C. cognatus*), for example, the density, fecundity, and growth of a population was found to be dictated by biotic factors related to variability in predation and prey productivity along a stream gradient with increased growth and fecundity in higher order streams (Anderson, 1985). The similar presence of a gradient in growth along the upstream-to-downstream gradient of the Colorado River suggests that local characteristics dictate variability and may need to be considered in range-wide management efforts.

Throughout the Colorado River basin there was a consistent response to altered flow conditions representing higher standardized growth and recruitment under stable flow conditions. Smallmouth Bass *Micropterus dolomieu* have shown similar flow-growth relationships, with increased growth and recruitment under stable, intermediate flow conditions and lower growth rates and weaker year classes in years with high and low flow conditions (Paragamian & Wiley, 1987; S. M. Smith, Odenkirk, & Reeser, 2005). Previous research on Guadalupe Bass growth rates throughout the Colorado River basin was conducted in the late 1970s, as well as in smaller tributary systems over the past five years. Our data, along with those of Groeschel (2013) and Massure (2016) indicate that there has been no appreciable change in the standardized growth rates of Guadalupe Bass in headwater streams since the late 1970s (Edwards 1980). In the North and South Llano Rivers annual variation in Guadalupe Bass growth was linked to mean monthly flows with lower growth rates during drought years

(Groeschel, 2013; Massure, 2016). I found similar relationships between flow conditions and growth rates in higher order tributaries and the mainstem.

Increased standardized growth in the mainstem Colorado River was attributed to flow variables, such as increasing monthly flows, reversals, and one-day maximum flows. The timing and magnitude of extreme high and low flows and the switch between the two conditions can be beneficial to growth and recruitment. For example, increased discharge during the spring to summer months in the Apalachicola River basin resulted in significantly positive recruitment of age-0 Largemouth Bass (Dutterer et al., 2013). Increased growth of salmonid populations has also been related to increased discharge, as well as the maintenance of minimum flows (Nislow, Sepulveda, & Folt, 2004; Teichert, Kvingedal, Forseth, Ugedal, & Finstad, 2010). High-magnitude flood pulses can not only positively influence growth, through floodplain inundation providing an influx of food resources, increased forging habitat, and nursery habitat, but can also protect and increase the oxygenation of developing eggs in nest building species resulting in increased young-of-year densities (Craven, Peterson, Freeman, Kwak, & Irwin, 2010). In addition to similarities in response to low-flow conditions compared to previous studies, I also found decreased standardized growth and recruitment related to high-flow conditions. Timing and magnitude of extreme high and low flows in flashier systems with an increasing number of reversals can also be detrimental to growth and recruitment. Weaker year classes may be linked to high flows wiping out nests or causing nest failure, as well as increased mortality due the displacement of juveniles, larvae, or eggs being washed downstream (Harvey,

1987; Lukas & Orth, 1995; Orth & Newcomb, 2002; Simonson & Swenson, 1990). Flow conditions in tributaries varied in minimum flows and the number of zero-flow days; however, these differences were not related to standardized growth of Guadalupe Bass. This relationship was not observed in headwater streams likely due to these systems being spring fed. Groundwater influences contribute to more stability in the flow regime of headwater streams in the Colorado River in comparison to headwater streams that are run-off fed (Davie, 2008). A negative correlation with the number of low pulses and the number of reversals further suggests that stable flow conditions with maintained flow levels that permit access to preferred habitat are beneficial to Guadalupe Bass growth throughout the Colorado River basin.

The Colorado River basin encompasses the semi-arid central Texas region where annual precipitation is less than the rate of evapotranspiration and runoff annually. Evapotranspiration and increased runoff projected in the Colorado River basin will outpace precipitation increasing the vulnerability of aquatic ecosystems to low flow and drought conditions (V. B. Smith, David, Cardenas, & Yang, 2013). The lower section of the basin is increasingly regulated and lies within a sub-humid region contributing to contrasting flow conditions (Lins, 1997; Poff, Bledsoe, & Cuhacyan, 2006). In the mainstem Colorado and urbanized tributaries in the Austin area, increased impervious cover associated with urbanization likely contributed to flow regimes with greater variability (Shuster, Bonta, Thurston, Warnemuende, & Smith, 2005). However, patterns of hydrologic change throughout the rest of the basin, including the upper watershed tributaries, are likely due to landcover transitions

associated with decreased agriculture and increases in urbanized or herbaceous land cover (Pease et al., 2017). In headwater streams Guadalupe Bass have been found to be more abundant in riffle and run habitats (Bean & Grabowski, 2015). In tributaries the availability of riffle and run habitats are linked to flow conditions. Under increased low-flow conditions, access to essential habitat may be inhibited. Restricted habitat and the timing of low flows play a central role in habitat availability influencing the level of competition and predation (Dutterer et al., 2013; Harvey, 1987; S. M. Smith et al., 2005). Size-dependent mortality from increased predation is elevated by the lack of refuge habitat under low flow conditions and has been shown to adversely affect recruitment (Devries, Garvey, & Wright, 2009; Garvey, Ostrand, & Wahl, 2004). Low-flow conditions are also associated with reduced invertebrate production, which can slow growth and influence survival of juveniles dependent upon drift feeding in riffles (Dewson, James, & Death, 2007; Paragamian & Wiley, 1987).

I expected standardized growth to be similar within stream orders, with headwaters and urban streams having similar growth. However, I found that urban stream growth was more like the mainstem Colorado in comparison to headwater streams, despite having a much smaller drainage area (Barton Creek: 281.5 km², North Llano River: 2,439 km², South Llano River: 2,432 km²) and being similar in length (Barton Creek: 79 km, North Llano River: 93 km, South Llano River: 88 km) to headwater streams (Broad, 2008). The similarities in stream order and drainage area between these headwater streams and other tributaries suggests that these differences are possibly related to density dependent factors in headwater streams, as evidenced by the higher

catch rate and intensive stocking efforts that have occurred in the upper Llano River watershed (Bean & Grabowski, 2015). This may also be due to movement occurring between the mainstem and the urban streams. Concurrent research on the Guadalupe Bass movement in the Colorado River found that during high-flow conditions individuals moved into from the mainstem Colorado into tributaries that were not impeded by a natural or artificial barrier (Pease et al., 2017). Under low-flow conditions the mainstem Colorado River may be providing refugia for tributary individuals. Movement into tributaries has also been seen in response to flooding conditions with stream fishes seeking refuge in tributary systems during high flow conditions. For example, Dolly Varden Char *Salvelinus malma* in the Satsunai River moved immediately into tributary systems following hydrological releases from an upstream dam in response to rapidly increasing flow conditions (Koizumi, Kanazawa, & Tanaka, 2013).

Consideration for the influence that flow-regime changes have on population dynamics is crucial in the management of freshwater systems under current demographic trends, like those occurring in the Colorado River basin. Accounting for the future impact of water abstraction and hydrologic alteration on aquatic ecosystems requires an understanding of the variability in life history characteristics of populations occurring along the longitudinal gradient of the basin (Merciai, Molons-Sierra, Sabater, & García-Berthou, 2017). Impacts of altered flow conditions, especially changes in the timing and magnitude of flows, across stream orders and degrees of disturbance is important for the management of streamflow in regulated

systems. For example, the severity of the effect of reduced baseflow on stream fish assemblages in the Flint River basin in Georgia varied seasonally and across stream orders, indicating the importance of understanding the impacts that timing and magnitude of flow conditions has on fish populations across river networks (McCargo & Peterson, 2010). Our results suggest that when managing a species throughout its range there needs to be consideration for the longitudinal gradient of local habitat variability to fully understand growth and recruitment of populations. This study contributes to an understanding of the impacts of modified flows on a non-migratory species residing across stream orders and under different disturbance regimes. Furthermore, our data suggest that conservation initiatives solely focused on physical instream or riparian habitat are unlikely to be as beneficial as those focused on restoring or maintaining adequate streamflow.

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CHAPTER 4

MOVEMENT PATTERNS AND HABITAT ASSOCIATIONS OF GUADALUPE BASS *MICROPTERUS TRECULII* IN THE LOWER COLORADO RIVER

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ABSTRACT

The degree to which a species exhibits variability in its behavior and biology across the longitudinal gradient in a river basin is important for understanding how the species responds to anthropogenic disturbance and for implementing effective conservation and management. Guadalupe Bass *Micropterus treculii* are endemic to small streams and rivers of the Colorado River Basin in central Texas, where they are associated with shallow runs and riffles. A thriving trophy fishery for the species also exists in the mainstem Colorado River downstream of Austin. It is unclear whether ongoing conservation and restoration activities in the upper portions of the Colorado River Basin are effective for the population in the mainstem of the river. Therefore, my objective was to determine if the habitat associations and movement patterns of Guadalupe Bass in the lower Colorado River downstream of Austin are similar to those described for counterparts in smaller tributaries upstream. Twenty-nine Guadalupe Bass were collected and surgically implanted with radio transmitters. Individuals were tracked and associated with substrate classifications and recorded habitat data. Overall, Guadalupe Bass in the lower Colorado River moved greater distances and utilized habitat differently than previously described for individuals tagged in tributaries of the upper Colorado River. I found that although Guadalupe Bass are ubiquitous throughout the

Colorado River Basin, their occurrence is more likely in close proximity to pool mesohabitat and fine substrate. Understanding habitat use and contrasting movement patterns of Guadalupe Bass in the lower Colorado River improves future management of the trophy fishery which contains larger individuals in comparison to tributary populations. Awareness of the differences in habitat use and movement patterns provides information that is necessary to assess the sensitivity of a population throughout the entire range and facilitates the implementation of strategies that are beneficial across stream sizes.

INTRODUCTION

Streams and landscapes are dynamic with an organizational hierarchy of patches through space and time, facilitating the necessity for movement in order for organisms to maximize fitness (Pringle et al. 1988; Fauchald and Tveraa 2006). A variety of ecological processes, such as population dynamics and predator-prey interactions, are largely influenced by animal movement (Railsback et al. 1999; Ng et al. 2007). For stream fishes, movement between habitats can be critical for foraging, reproduction and overwintering (Todd and Rabeni 1989; Lyons and Kanehl 2002; Karchesky and Bennett 2004; Goclowski et al. 2013). Knowledge of habitat requirements necessary for the completion of life history is important for successful management and conservation efforts to prevent decline of stream fish populations with increasing habitat fragmentation and anthropogenic alteration. Many studies on fish movement focus on movement in a single system within the range of a species and inform management throughout a broader region and across stream orders (Koppelman and Garrett 2002; Orth and Newcomb 2002;

Garvey et al. 2002). However, there is evidence that management of a population needs to be refined to consider differences in movement patterns and habitat associations of a species between smaller streams and larger rivers when the range extends throughout an entire basin (Merciai et al. 2017). A single species found along the longitudinal gradient of a river basin experiences differences in both population size and habitat characteristics. For instance, black bass are high-level predators that are widely-distributed throughout North America and occur across a broad range of stream sizes with substantial variation in the habitat associations and movement patterns across the longitudinal gradient within a basin (Warren 2009). These differences can result in contrasting movement patterns that may require different management strategies. For example, Smallmouth Bass in the Current River Basin have been found to undergo movements as great as 42.5 km (Todd and Rabeni 1989; Westhoff et al. 2016), whereas in the mainstem upper Mississippi River, Smallmouth Bass movements did not exceed 29 km (Altena 2003).

Understanding this variability is especially important for specialist endemic black bass species, which are of increasing conservation and management concern due to the wide range in habitats that are required for the completion of their life histories (Birdsong et al., 2010; Garrett, Birdsong, Bean, & McGillicuddy, 2015). There is increased recognition of the sensitivity of these species to anthropogenic disturbances, such as increased water withdrawals and altered flow regimes. While many of these endemic specialists, such as the Guadalupe Bass *Micropterus treculii* and Shoal Bass *Micropterus cataractae*, occur across a range of habitats within a basin, their populations have declined due to a variety of factors. Knowledge of the range of factors contributing to

these declines, from hybridization to flow alteration, and the variability in sensitivity across the broad spectrum of stream sizes is critical for successful management throughout the range of the species. For instance, Shoal Bass in the Chattahoochee River running between Alabama and Georgia and smaller tributary streams in Alabama have been found to be relatively sedentary with the largest movements not exceeding 10 km and site fidelity following seasonal movements for spawning (Stormer and Maceina 2009; Sammons and Earley 2015). In comparison, Shoal Bass in the larger Flint River in Georgia undergo movements > 120 km (Sammons 2015). Increased movement by the Flint River Shoal Bass suggests that individuals may be more sensitive to habitat fragmentation restricting these extensive movement corridors in comparison to the relatively sedentary Shoal Bass in the Chattahoochee River.

Movement patterns and habitat associations of black bass species have also showed spatial differences related to seasonal movements. Seasonal differences may involve movement associated with over-wintering habitat and spawning habitat (Wheeler et al. 2003; Warren 2009). However, within species there is evidence of dramatic differences in seasonal movements which emphasizes the need for management strategies that are specific to individual populations (Todd and Rabeni 1989; Stormer and Maceina 2009; Ettinger-Dietzel et al. 2016). For example, in the James Fork River in Missouri, Smallmouth Bass showed seasonal patterns in movement associated with favorable spawning habitat (Todd and Rabeni 1989). However, Ettinger-Dietzel et al. (2016) found no seasonal differences in movement patterns in Ozark streams over 24-hour tracking periods for Smallmouth Bass in Ozark streams comparable in size to the Jack's Fork

River. While there is a vast amount of information about the movement patterns and associations of broader ranging black basses, like the Smallmouth and Largemouth Bass, there is very little known about their endemic congeners with more restricted distributions (Warren 2009; Ettinger-Dietzel et al. 2016). Understanding the ability of habitat specialists, as opposed to more generalist species, to adapt to changing conditions is especially important under increased anthropogenic alterations and impending climatic changes.

The Guadalupe Bass is a valued sport fish and the official state freshwater fish of Texas, but is listed as a species of special concern and as such, is a priority for conservation and management (Hubbs et al. 1991). Guadalupe Bass primarily reside in central Texas in the streams of the Edwards Plateau ecoregion. There is an additional Guadalupe population off of the Edwards Plateau in the lower Colorado River below highly urbanized Austin and in habitat not considered “typical” Guadalupe Bass habitat. Continued human population growth is expected to increase demands on water resources in a region that is plagued by periods of intense drought and sporadic flooding (TWDB 2012; Jiang and Yang 2012). With impending climate change, aquatic communities downstream of these highly urbanized areas could face detrimental low flows that may threaten the ability of these downstream habitats to support the developing trophy Guadalupe Bass sport fishery (Smith et al. 2013). Therefore, understanding differences in the movement and habitat use patterns of Guadalupe Bass found in the smaller tributaries in comparison to populations in the lower Colorado River is crucial for informing future conservation and management decisions.

In smaller tributary systems of the Colorado River Basin, Guadalupe Bass have been found to exhibit minimal movement (<3.5 km per year) associated with faster current velocities in eddy mesohabitats containing structure, such as boulders and woody debris (Perkin et al. 2010). Perkin et al. (2010) found that Guadalupe Bass movements in both the Pedernales (4th order tributary) and South Llano (5th order tributary) tributary systems were associated with the spawning season. Guadalupe Bass have been shown to favor eddy mesohabitats when available and to shift from woody structures to more secure refuge, such as ledges or boulders. In the Pedernales River where flows are commonly reduced and habitat availability is limited, individuals were more commonly found in deeper pool habitats. In tributary systems, where there are often barriers limiting movement, Guadalupe Bass are driven by availability and suitability of habitat (Perkin et al. 2010). In the mainstem Colorado River, a wider range of barriers limit movement, providing a distinct system for further understanding of habitat selection and utilization of this black bass species in large river systems.

My objective was to assess the movement patterns and habitat associations of Guadalupe Bass in the mainstem Colorado River and compare these habitat associations with those found for Guadalupe Bass in smaller tributary systems. Guadalupe Bass is a fluvial specialist, that can be found in low-order streams and large rivers throughout its range in central Texas; however, the majority of studies on this species focused on smaller systems. An understanding of the variation in movement patterns and habitat associations across stream sizes is important when refining management practices throughout the basin. Secondly, I assessed home range sizes and habitat selection

compared to availability along the upstream to downstream fluvial gradient of the lower Colorado River to determine habitat preference and areas of optimal habitat for Guadalupe Bass in the mainstem. Gaining information on habitat utilization of the population will facilitate the development of management strategies and habitat protection encompassing overwintering and spawning habitat. Refinement of management practices that pertain to the unique larger river population is especially important in the maintenance of this trophy fishery under projected demographic and climatic changes.

METHODS

Study area

The lower Colorado River, a 6th-order stream, starts where the Colorado River drops off the Edwards Plateau and into the Blackland Prairie ecoregion and is the easternmost extent of the Guadalupe Bass range (Curtis et al. 2015). The study area on the lower Colorado River extends approximately 285 river kilometers (rkm) ranging from 76.2 to 243.8 meters above sea level between from Longhorn Dam in Austin to the Garwood Dam downstream of Altair, Texas (Figure 4.1). Four reaches were determined based on tagging location and distance from the mouth of the Colorado River with Matagorda Bay (Bastrop: 415-355 rkm, Smithville: 350-300 rkm, LaGrange: 300-240 rkm, Altair: 220-160 rkm). The Bastrop reach has the greatest elevational difference along a single reach, as the Colorado River runs off the Edwards Plateau at the Balcones Escarpment Fault Line (LCWRPG 2011). Reaches were determined based on variability physiographic regions along the elevational gradient of lower Colorado River Basin

(TNRCC 1999). The width of the Colorado River at baseflow varies from approximately 8.0 km at the most upstream reach to 16.0 km at the most downstream reach. This lower section of the Colorado River is highly regulated due to the two-large flood-control dams and three smaller hydropower dams located immediately upstream (Vaughan et al. 2012). Flow conditions in the lower Colorado River vary with precipitation and upstream regulation. Agricultural releases occur from March to October and a substantial amount of flows are contributed from upstream wastewater treatment facilities. The lower section of the Colorado River basin drains an approximate area of 4,506 square kilometers with precipitation varying from 0.76 - 1.02 m yr⁻¹ (TNRCC 1999). There are typically two peaks in rainfall, the first occurring in May of each year, with a second peak during autumn between September and October. Land use within the watershed is primarily rangeland, agricultural, and forest land, with the exception of the metropolitan area surrounding the city of Austin in the uppermost part of the study reach (LCWRPG 2011).

Radio tagging and tracking

Guadalupe Bass weighing more than 220 g each were collected from within each of the stream reaches described above, along the Colorado River using a boat-mounted electrofisher in December 2014 (Figure 4.1; Table 4.1). Prior to the surgical implantation of radio transmitter individuals were anesthetized using a 40 mg/L eugenol (clove oil) solution (Murphy and Willis 1996; Peake 1998). Once the fish exhibited a loss of equilibrium, they were placed in a surgical cradle and the incision site was wiped with gauze soaked in a topical iodine antiseptic solution (Betadine Solution, Johnson Distributors, Gastonia, North Carolina). A 2-cm incision was made into the peritoneal

cavity and a Lotek MCFT2-3BM (11 x 43mm, 8.0 g in air) radio transmitter tag (Lotek Wireless Inc., Newmarket, Ontario) with an estimated battery life of 184 - 306 days was then inserted into the body cavity. The wire antenna was then threaded through a separate opening in the body wall made approximately 1.5 -2.0 cm posterior of the incision using the shielded needle technique described by Ross and Kleiner (1982). One to two non-absorbable, polypropylene sutures were used to close the incision and approximately 0.5 g of powdered oxytetracycline was placed on the incision site (Grabowski & Jennings, 2009; Walsh, Bjorgo, & Isely, 2000). The mean time from the placement of the fish in the cradle to placement in the recovery tank was 4.14 minutes (range: 3-6 minutes). Following surgery all fish were held in a holding tank (approximately 10-20 minutes) until they regained equilibrium and were behaving normally. Fish were then released within a 100 m of their capture site.

Tracking began in January 2015 and was conducted once every two weeks during spring (March, April, May) and monthly during other seasons, weather permitting, for the life of the transmitter batteries. Fish were relocated along the approximate 285-river km (rkm) reach between Webberville and Altair, Texas (Figure 4.1). Tracking was conducted along the center of the channel using SRX800-M-1 receivers (Lotek Wireless Inc., Newmarket, Ontario) with a three-element yagi antennae. Individuals were tracked using triangulation techniques and multiple passes to identify the strongest signal with the antennae pointed at the water surface. The location of the fish was recorded using a global positioning system (GPS) unit with an accuracy of three meters. Water temperature, conductivity, turbidity, time, coordinates, mesohabitat and substrate type

were recorded at each relocation. Water quality parameters were recorded using an YSI Model 95 handheld water quality meter (YSI, Yellow Springs, Ohio) and an Oakton TN-100 portable turbidimeter (Oakton, Vernon Hills, Illinois).

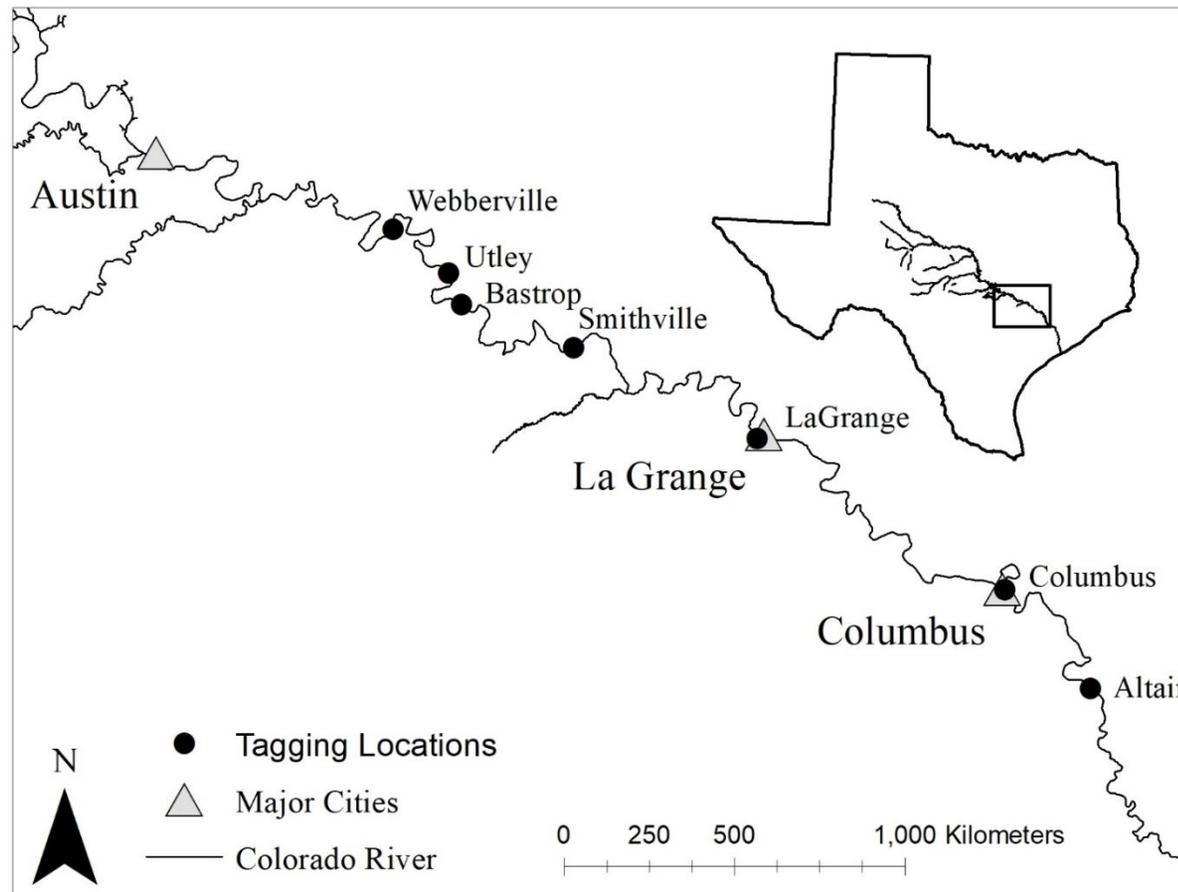


Figure 4.1: Original capture locations of Guadalupe Bass implanted with radio transmitters ($n = 29$) during December 2014 and December 2015 in the lower Colorado River downstream of Austin, Texas. Guadalupe Bass ($n = 24$) were tagged in December 2014 at the Bastrop, Smithville, LaGrange and Altair reaches. Five additional Guadalupe Bass were tagged in December 2015 in between Webberville and Utley. Individuals tagged in December 2015 were used to extend predictions of habitat use and occurrence of Guadalupe Bass upstream of Bastrop, Texas.

Table 4.1: Tagging location, total length (TL), tag identification number, number of relocation events, linear home range, core area of home range and home range for twenty-three Guadalupe Bass (>5 relocations) implanted with MCFT2-3BM radio transmitter tags (Lotek Wireless Inc., Newmarket, Ontario, Canada) during December 2014 in the lower Colorado River, downstream of Austin, Texas. The linear home range is defined as the distance measured along the middle of the river channel between the most upstream and the most downstream relocation. Core area is the high use area defined as area where a fish is likely to be located 50% of the time. The home range is defined as the area where there is a 90% probability of located an individual. Location of tagging reaches are listed from the most upstream reach to the most downstream reach. Exact locations are shown in Figure 4.1.

Tagging reach	TL (mm)	Tag identification	Number of relocations	Linear Home Range (km)	Core Area (ha)	Home Range (ha)
Bastrop (<i>n</i> = 6)	279	31	9	21.52	100.95	130.18
	357	32	6	3.02	14.01	19.15
	331	39	17	46.73	133.28	247.21
	336	40	11	21.12	115.16	123.07
	415	43	20	35.98	155.45	213.68
	401	47	17	2.61	14.13	14.13
Smithville (<i>n</i> = 8)	385	11	17	11.10	52.33	56.30
	277	12	11	11.18	46.00	56.13
	290	14	18	6.08	30.13	35.37
	281	18	17	2.49	16.41	16.41
	400	20	13	9.07	282.71	312.00
	264	33	9	2.60	11.90	17.43
	266	35	10	19.97	69.22	108.95
	285	38	18	1.18	6.88	9.98
	323	25	13	9.74	47.70	61.42
La Grange (<i>n</i> = 3)	279	26	18	1.90	11.23	11.23
	266	27	11	2.30	11.77	18.09
	249	15	16	31.42	134.71	147.69
Altair (<i>n</i> = 6)	317	19	16	4.22	24.73	27.30
	351	23	8	3.43	16.00	22.01
	324	24	7	25.85	106.72	119.52
	262	28	11	2.96	13.72	16.00
	319	30	7	5.89	25.02	37.65

Characterizing instream habitat availability

Instream substrate in the lower Colorado River between TX- 130 highway crossing (30°12'37.9" N, 97° 37'19.8" W) and the agricultural dam in Garwood, Texas (29°30'53.7" N, 96° 24'30.0" W) was identified using recordings of sonar data of the river bottom recorded using a Humminbird 998cSI side scan sonar unit (Humminbird, Eufaula, Alabama) with a starboard-rail mounted transducer. SonarTRX v. 16.1 (Leerand Engineering Inc., Honolulu, Hawaii) was used to process all recorded sonar data in preparation for classifying instream substrate along the study reach in the lower Colorado River. Raw sonar data recordings were converted into georeferenced images, the water column was removed, and corrections were made for altitude of the transducer and beam angle. Images were then imported into ArcGIS 10.5 (ESRI, Redland, California), and polygons were digitized to distinguish substrate classes and mesohabitats. Dominant substrate classifications were: bedrock, cobble, gravel, sand, mud and silt, submerged aquatic vegetation (SAV), and unidentifiable substrates (Table 4.2) (Kaeser and Litts 2010; Groeschel 2013; Kaeser et al. 2013).

Table 4.2: Classification of substrate types using side scan sonar imagery along the 285 river kilometers (rkm) reach of the lower Colorado River between from Longhorn Dam in Austin to the Garwood Dam downstream of Altair, Texas.

Substrate Type	Classification
Bedrock	Karst limestone bedrock
Boulder	Particles greater than 300 mm in size
Cobble	Particles less than 300 mm and greater than 60 mm in size
Gravel	Particles smaller than 60 mm in size and greater than 2 mm
Sand	Particles less than 2 mm
Fine sediment	Substrate is composed of undistinguishable grain less than 2 mm
Unidentified substrates	Large woody debris, anthropogenic artifacts (i.e. tires)
Submerged aquatic vegetation (SAV)	Submerged aquatic vegetation

In addition to substrate classes, mesohabitats (riffles, runs, and pools) were also classified (Barnhardt et al. 1998; Kaeser et al. 2013). Mesohabitats were delineated using high resolution aerial imagery available on Google Earth and provided by the United States Department of Agriculture (USDA). Shallow areas where the side-scan sonar could not be deployed were characterized as riffle habitats. Runs were characterized as the areas upstream or downstream of riffles where the water's surface is not broken at baseflow conditions as observed in the aerial imagery. Deeper areas with slower current were classified as pools. Mesohabitat classifications were confirmed visually on-site while conducting relocation surveys. Riffle boundaries were marked by GPS in the field to refine the classification of riffle mesohabitat and ensure accurate delineation. Substrate was ground-truthed at 212 random locations throughout the study area and the substrate was recorded and described at each of the GPS locations. Ground-truthed locations were compared to the completed habitat map to determine accuracy rate of substrate classifications.

Habitat use and availability

Habitat use and availability were assessed using Guadalupe Bass relocations and the generated substrate map using a distance-based approach (Conner et al. 2003) following the methods of Sterrett et al. (2015). Habitat substrate and mesohabitat in “use” were determined from a 15-m radius buffer around each relocation to account for uncertainty in GPS location and tracking. The 15-m relocation buffers were omitted from the river substrate map prior to determining a set of equivalent random locations with a 15-m buffer to avoid overlap. There was a total of 356 relocations throughout the study period. Similar substrate and mesohabitat associations were seen within single tracking events for individuals tracked fewer than 15 times and individuals tracked more than 15 times. Therefore, I assume that variation in the number of relocations does not have a large amount of influence on habitat use variables. An additional 356 random locations were generated within the study area in ArcGIS 10.5 with a 15-m buffer as a representation of the habitat available throughout the study area. All random locations were assumed to be independent and representative of the habitat available. Predictor variables were used to assess both substrate and mesohabitat associations. Proximity to nearest substrate and mesohabitat class was determined using the NEAR tool in ArcGIS 10.5, which determines the distance to the nearest edge for each relocation and randomly generated point.

Data analysis

Guadalupe Bass individuals were considered as primary sampling units and statistical inference was based on the individual as replicates. Movement data was non-normally distributed, therefore prior to analysis all data was transformed using the natural log (Guy and Brown 2007). Global Positioning System (GPS) data was visualized in ArcGIS using network analysis to determine distance moved by each individual. The movement rates, home range size,

site fidelity and the influence of discharge and habitat on the activity levels of Guadalupe Bass in the lower Colorado River Basin through weekly and monthly tracking were evaluated. Substrate and mesohabitat comparisons were made using goodness-of-fit χ^2 tests. Comparisons were used to determine if mesohabitat and substrate proportions differed between reaches and seasons. Individual displacement was quantified as the minimum movement from the previous location divided by the time in between relocations (Sammons et al. 2003). Net upstream movement is indicated by positive displacement values, while negative values indicate downstream movement. Mean absolute movement was determined as the total movement from tagging location divided by the time in between relocations when there is no associated upstream or downstream value. Variation in mean displacement and absolute movement across reach and season was determined using mixed model analysis. Seasons were classified by the meteorological full three-month groupings determined from annual temperature cycles (spring: March 1-April 30, summer: June 1-August 31, autumn: September 1 – November 30, winter: December 1 -February 28). Linear home range was calculated as the distance between the most upstream and downstream relocation following the middle of the river channel. In addition, kernel density estimates (KDE) for home range were determined using the FishTracker toolbox in ArcGIS following the methods of Laffan and Taylor (2013). I calculated the 90% isopleth for home range, indicated the area in which an individual can be located 90% of the time, and then the subset 50% high use core area (Laffan and Taylor 2013). Home range analysis was done in ArcGIS 10.5 (ESRI, Redland, California). The relationship between home range and individual total length was determined using a linear regression.

Habitat model development

Habitat suitability was assessed throughout the lower Colorado River to predict the probability of Guadalupe Bass occurrence based on proximity habitat variables. Submerged aquatic vegetation and objects, such as woody debris and sunken human artifacts were not included in the models due to the low frequency of the substrate classes occurrence throughout the river. Bedrock and fine sediment encompassed less than 10% of the total habitat area, therefore fine sediment and sand were combined to represent fine sediment and boulder and bedrock were combined to represent coarse substrate. Habitat variables included in the model were fine substrate (sand and fine sediment), coarse substrate (boulder or bedrock), cobble substrate, and gravel substrate. Mesohabitat variables included pool and run or riffle, which were combined into a single mesohabitat for comparison to tributary systems where Guadalupe Bass have been associated with faster moving water in riffles, runs, and eddies (Birdsong et al. 2015; Garrett et al. 2015).

Habitat suitability for Guadalupe Bass throughout the Colorado River Basin was assessed using logistic regression (Hosmer and Lemeshow 2000; Sterrett et al. 2015) and an information theoretic approach (Anderson 2008) to select the top model for predicting the probability of occurrence as a function of the independent variables in the model. Differences between habitat use and the availability of habitat were based on randomly generated locations. Candidate models were developed *a priori* to examine combinations of the proximity to large rocky (boulder-bedrock), coarse (cobble-gravel), or fine (sand-fine sediment) to determine if habitat associations in the lower mainstem Colorado River differed from habitat associations in tributary systems. Additional candidate models were developed to evaluate the distance to mesohabitats types. Habitat variables that were correlated were not included in the same candidate model in

the analysis ($r^2 > 0.50$). Model fit was evaluated using a global model containing both substrate and mesohabitat variables. The non-independence of repeated measurements of an individual was accounted for with the incorporation of an individual random effect that was centered on zero. Inclusion of the individual random effect allows for the strong inference of population level habitat use (Gillies et al. 2006).

Table 4.3: Mean and standard error (SE) in meters of the substrate and mesohabitat variables quantified for each Guadalupe Bass relocation ($N = 356$) and pseudo-absence points that cannot fall within the “use” area occupied by relocations ($N = 356$) throughout the 285 rkm study reach of the mainstem Colorado River, Texas. All measures represent the proximity from the position of the relocation or random location to the nearest substrate or mesohabitat type.

Habitat Variables		Random		Relocations	
		Mean (m)	SE	Mean (m)	SE
Substrate	Proximity to boulder or bedrock substrate	0.30	0.02	2.60	0.26
	Proximity to fine sediment or sand substrate	0.06	0.01	0.16	0.02
	Proximity to gravel or cobble substrate	0.04	0.01	0.37	0.07
Mesohabitat	Distance to the nearest run or riffle mesohabitat	0.88	0.08	1.89	0.32
	Distance to pool mesohabitat	0.44	0.06	1.48	0.17

The support for each of the candidate models was determined using Akaike’s Information Criterion for small sample sizes (AIC_c). The highest (w) was considered the best approximating model, with values of ΔAIC_c of less than two (Burnham and Anderson 2002). The candidate models were evaluated for the substrate variables and then a second set of candidate models was developed for the mesohabitat variables. JAGS v. 3.4.0 (Plummer 2003) was used in R v. 3.4.1 (R Development Core Team 2008) with the Rjags package (Su and Yajima 2012) to implement Markov chain Monte Carlo (MCMC) sampling. All models were fit with three chains, 5,000 iterations, a 500 burn-in, autocorrelation reduction thinning parameter of three, and diffuse priors. Gelman-Rubin’s convergence diagnostic ($\hat{R} < 1.1$; Gelman & Rubin, 1992) and visual inspection of the three chains were used to assess model convergence. Adequate model fit was determined based on a Bayesian P -value near 0.50 based on the sums of squares discrepancy metric (Gelman and Rubin 1992; Gelman and Hill 2007). The importance of individual variables and selection of habitat variables in the top model was estimated based on the 95% credibility

interval and further interpretation of habitat variable avoidance or selection was facilitated by the calculation of the odds ratios.

RESULTS

Twenty-four Guadalupe Bass ranging from 249-436 mm TL and 226 – 1134 g, were tracked over a total of 21 tracking events, and individuals were relocated 13 ± 4 times (mean \pm STD; range: 3 – 20 times) during January 2015 – May 2016 (Table 4.1). One individual tagged in Altair was only tracked initially after tagging and was presumed to have passed the low head dam that delineated the downstream extent of the study reach. Individuals tagged in Webberville, Texas in December 2015 had too few relocations to be included in the home range analysis, but tracking data was included in the habitat-use availability logistic regression analysis. Guadalupe Bass in the Colorado River were mostly sedentary, rarely exhibiting displacement movements > 75 m between tracking events. Furthermore, TL of tagged individuals did not affect overall displacement ($F_{22,302} = 1.88, P = 0.70$). The largest movements were made by individuals tagged at Bastrop and Altair that moved ≤ 31 km up/downstream during large flood pulses that occurred in March and June of 2015.

Fine substrate (sand and fine sediment; 39.0%) and gravel substrate (37.0%) were the dominant substrates throughout the study reach. The remaining percentage of the substrate throughout the study reach was cobble (12.6%), coarse (boulder and bedrock; 9.17%), and other (submerged human artifacts, large woody structure, SAV; $<2.0\%$). Substrate was classified with an 82% accuracy rate with the majority of misclassified substrate was due to the intermixing of substrates and determination of the dominant and subordinate substrate at the sampling location. Out of all the substrate types, distinguishing the dominant substrate from intermixed gravel and sand substrate and distinguishing between cobble and gravel substrate resulted in the most error

in classification. Errors occurred where the boundaries shifted between substrates and lead to reduced classification accuracy.

Seasonal movement and habitat use

Guadalupe Bass mean (\pm SD) absolute movement between relocation events was greatest in summer (3.38 ± 1.42 km) and least in autumn (0.21 ± 0.12 km). Overall, both the absolute movement ($F_{3,82}=8.99$, $P < 0.01$) and the displacement (upstream-downstream direction; $F_{3,82}=6.81$, $P < 0.01$) were different across seasons, but not different based on location in the river (displacement: $F_{3,19}=1.57$, $P=0.23$, absolute $F_{3,19}=1.27$, $P=0.31$; Figure 4.2). Seasonal differences in the directionality of movement showed downstream movements in the summer and upstream movements in the spring and winter. Seasonal differences in utilization occurred in the spring and summer with individuals showing a greater association with fine substrates (sand and fine sediment ($F_{3,352} \leq 3.03$, $P \leq 0.03$). There was no other evidence of seasonal differences in substrate selection ($F_{3,12} \leq 0.96$, $P \geq 0.45$; Table 4.4).

Table 4.4: Summary of the percentage of fish relocations within each substrate class and mesohabitat classes by reach and season for Guadalupe Bass in the lower Colorado River between January 2015 and May of 2016. Where seasons were classified by the meteorological full three-month groupings determined from annual temperature cycles (spring: March 1-April 30, summer: June 1-August 31, autumn: September 1 – November 30, winter: December 1 - February 28). Table located on page 132.

Reach	Season	Boulder	Bedrock	Cobble	Sediment	Gravel	Other	Sand	Pool	Riffle	Run
Altair		0.21	0.00	2.43	6.57	14.93	0.02	54.86	55.36	21.71	22.93
	Spring	5.88	0.00	0.00	8.88	27.29	0.06	57.88	47.06	6.82	46.12
	Summer	7.75	0.00	4.08	15.25	6.67	0.00	66.25	66.67	8.33	25.00
	Fall	0.00	0.00	20.25	7.75	0.00	0.00	72.00	75.00	0.00	25.00
	Winter	27.44	0.00	0.33	0.17	16.22	0.00	55.83	66.67	27.78	5.56
Bastrop		20.97	1.63	4.27	0.43	42.10	0.01	30.60	25.43	43.69	30.88
	Spring	23.27	0.78	3.39	1.02	48.76	0.02	22.73	21.15	45.12	33.73
	Summer	14.29	0.00	4.43	0.00	32.79	0.00	48.64	50.00	37.50	12.50
	Fall	3.80	0.00	6.60	0.00	44.60	0.00	44.90	50.00	36.00	14.00
	Winter	33.68	5.04	3.92	0.00	35.44	0.00	21.96	16.00	60.12	23.88
LaGrange		1.49	41.58	6.36	0.00	41.82	0.09	8.51	52.09	27.38	20.53
	Spring	1.69	42.75	12.44	0.00	29.81	0.19	12.88	63.06	12.06	24.88
	Summer	0.71	42.14	0.00	0.00	53.14	0.00	4.00	36.14	56.57	7.29
	Fall	1.40	18.80	3.60	0.00	74.40	0.00	1.60	80.00	20.00	0.00
	Winter	2.00	57.00	4.93	0.00	25.79	0.07	10.07	48.71	17.36	33.93
Smithville		0.79	9.11	6.88	2.20	32.81	1.17	47.07	59.40	29.24	11.36
	Spring	1.00	1.70	7.15	0.63	42.41	1.78	45.41	66.13	24.76	9.11
	Summer	0.00	0.95	2.57	7.38	21.48	1.38	66.33	65.81	31.57	2.62
	Fall	0.21	2.93	11.57	5.21	33.57	0.14	46.29	61.71	16.86	21.43
	Winter	1.47	5.09	9.00	0.28	34.31	0.91	48.94	59.38	21.88	18.75
Webberville		24.35	1.78	13.30	0.00	46.27	0.00	14.22	33.65	15.95	50.41
	Spring	29.67	0.00	6.00	0.00	47.96	0.00	16.26	38.70	21.85	39.44
	Winter	20.00	13.20	3.00	0.00	46.40	0.00	17.40	40.00	0.00	60.00
Grand Total		12.04	8.98	6.07	1.90	35.07	0.42	35.52	45.91	30.38	23.71

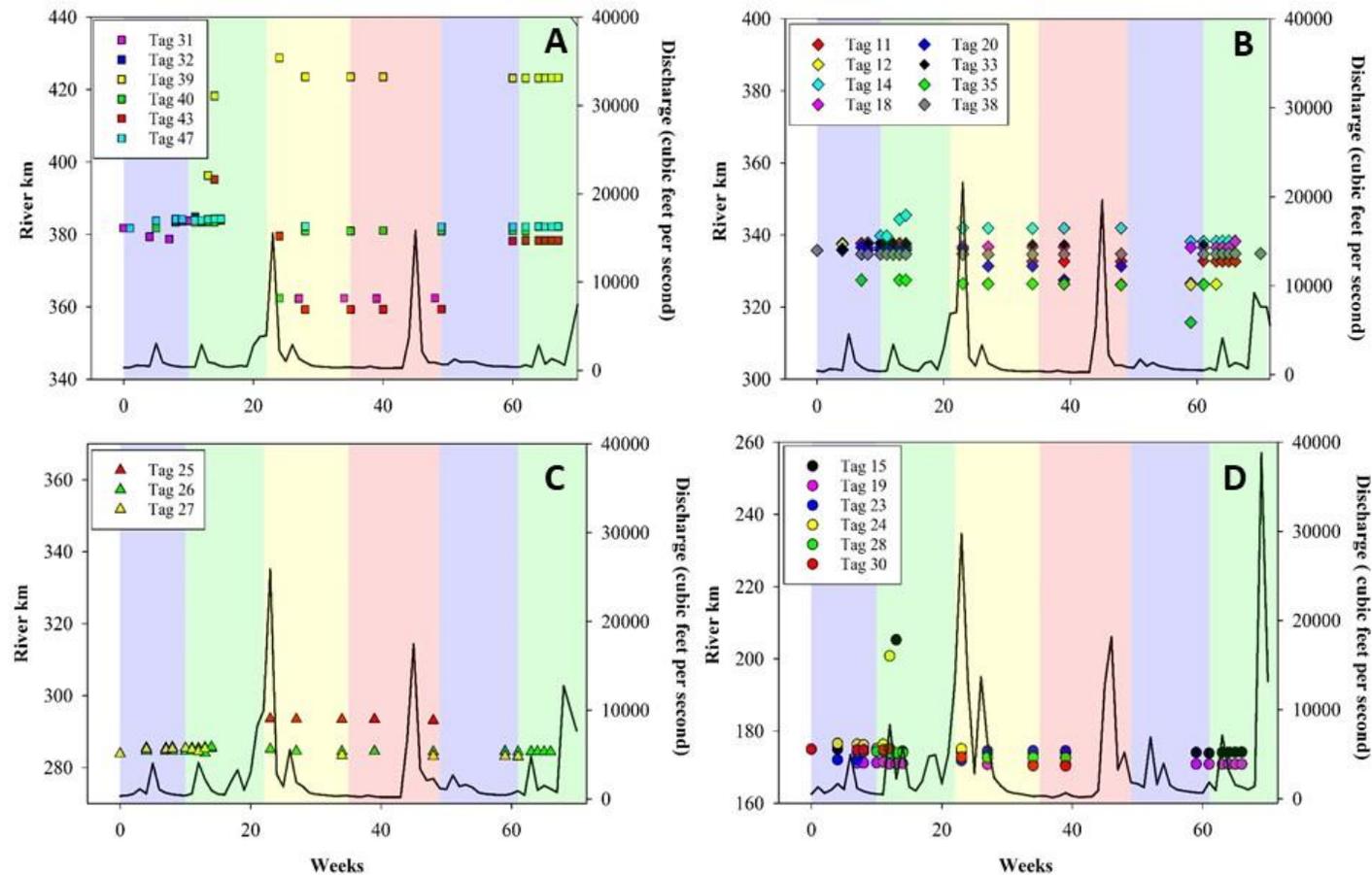


Figure 4.2: Scatter plots (A-D) of individual Guadalupe Bass movements at each complete tagging location. The first Y-axis is the distance (km) moved in river kilometers from the mouth of the Colorado River with Matagorda Bay. The second Y-axis on the left of the figures shows the discharge in cubic feet per second. The X-axis shows the number of weeks from initial tagging. Background colors indicate seasons where blue is winter (weeks 1-11, 50-62), spring is green (weeks 11-23, 62-71), summer is yellow (weeks 23-36), and fall is red (weeks 36-50).

Mesohabitat associations of fish relocations were dominated by pool-classed mesohabitat (45.91 %) and were different between reaches ($F_{4,352} \geq 5.64$, $P \leq 0.01$). Individuals at the most downstream reaches of Smithville, LaGrange, and Altair were primarily associated with pool mesohabitat (range: 59.4-52.09 %). Guadalupe Bass in upstream reaches (Bastrop and Webberville) had a greater association with riffle ($F_{4,351}=9.36$, $P < 0.01$) and run ($F_{4,351}=5.36$, $P < 0.01$) mesohabitat in comparison to other sampling locations. Guadalupe Bass relocations were mostly within habitats dominated by boulder, gravel, and sand substrate classes ($\chi^2 \leq 299.15$; $df=6$; $P \leq 0.01$). Guadalupe Bass were more commonly located in gravel substrate (range: 14.93- 46.27%) across all reaches. In the spring Guadalupe Bass relocations were commonly associated with gravel substrate (range: 27.29 – 48.76%). Guadalupe Bass in the most upstream reaches of Bastrop and Webberville had different substrate associations in comparison to downstream reaches ($> 24.35\%$; $\chi^2= 59.25$; $df=9$; $P \leq 0.01$), utilizing a higher percentage of boulder habitat ($F_{4,351}=18.36$, $P < 0.01$). Relocations within bedrock differed across reaches ($F_{4,351}=43.07$, $P < 0.01$) with individuals being rarely relocated in bedrock substrate except for in LaGrange. In Altair, individual relocations were more commonly associated with sand substrate (72.00-55.83%) in comparison to all other reaches ($F_{1,354}=36.67$, $P < 0.01$).

Home range

Guadalupe Bass in the lower Colorado River had a mean (\pm SD) linear home range of 12.27 ± 12.70 rkm (range: 1.18 - 46.73 rkm), which varied by tagging location ($F_{4,18}=7.69$, $P < 0.01$) with Altair and Bastrop individuals having linear home ranges

greater than those of LaGrange and Smithville. However, linear home ranges did not vary by total length ($F_{1,21}=3.37$, $P=0.41$). Within this home range, the mean (\pm SD) 50% core area was 62.62 ± 67.52 ha (range: 6.88 – 282.71 ha) and the mean (\pm SD) 90% home range was 79.17 ± 84.20 ha (range: 9.98 – 312.00 ha). Mean 50% core areas ($F_{4,18}=5.18$, $P<0.01$) and 90% home ranges differ between tagging locations ($F_{4,18}=5.85$, $P<0.01$; Table 4.1). While there was evidence to suggest that the size of the 50% core area ($r=0.40$; $p=0.06$) and total 90% home range ($r=0.38$; $p=0.07$) were positively correlated to the total length of the individual Guadalupe Bass. The relationship between the core area and the home range with the total length of the individual Guadalupe Bass suggest that the home range and core area of the individual tends to increase with total length. Gravel dominated the largest proportion of the area in Guadalupe Bass home ranges (mean: $> 0.43 \pm 0.04$), followed by sand (mean: $> 0.26 \pm 0.06$). Mesohabitat and substrate proportions did not differ by size of home range or core area ($\chi^2 \leq 1.29$; $df=22$; $p \leq 1.00$).

Habitat selection and availability

The global model was fully supported and the best approximating model (w_i) included all substrate and mesohabitat parameters ($AIC_w > 0.90$; Table 4.5). The beta coefficients for the top competing model were used without model averaging. Scaled odds ratios suggested that Guadalupe Bass were on average 70 times more likely to occur with every 50-m increase in the distance to a pool habitat. With every 50-m increase in the distance to boulder or bedrock Guadalupe Bass were 151 times more likely to occur. In contrast, for every 50-m increase in the distance from fine substrate, Guadalupe Bass were 16 times less likely to occur (Table 4.6).

Table 4.5 : The mean deviance, number of parameters (K), AIC_c values, Δ AIC_c values, Akaike weights (*w_i*), and the standard deviation of the individual random effect (RE SD). for each candidate habitat use availability models. The best model is in bold for habitat selection of Guadalupe Bass in the lower Colorado River, Texas from January 2015 to May 2016.

Local Habitat Model	Deviance	K	AIC _c	Δ AIC _c	<i>w_i</i>	RE SD
Global	2402.1	11	2424.6	0.0	1.00	
Substrate	2452.1	7	2466.3	41.7	0.00	0.08
Proximity of fine substrate, proximity to boulder or bedrock	2464.9	5	2475.1	50.4	0.00	0.08
Proximity to run or riffle mesohabitat and proximity to boulder or bedrock	2568.3	5	2578.4	153.8	0.00	0.08
Proximity to boulder or bedrock substrate	2590.1	3	2596.1	171.5	0.00	0.08
Proximity to cobble or gravel substrate	2911.6	3	2917.7	493.0	0.00	0.08
Proximity to cobble or gravel substrate and riffle mesohabitat	2912.1	5	2922.2	497.6	0.00	0.08
Proximity to pool mesohabitat	2974.7	2	2978.7	554.1	0.00	0.10
Proximity to fine sediment or sand substrate	3018.9	3	3024.9	600.3	0.00	0.11
Proximity to run or riffle mesohabitat	3038.2	3	3044.2	619.6	0.00	0.08

Table 4.6: Parameter estimates, scaled odds ratios, and credible intervals (95% CI) from the global model. The global model was the top supported model for determining Guadalupe Bass habitat use based on availability of both substrate and mesohabitat for the lower Colorado River, Texas. Decreased odds of habitat use are represented by scaled odds ratios less than 1. Increased odds of habitat use for every single unit increase in the unit scalar by an individual are represented by scaled odds ratios less than 1. Increased odds of habitat use for every single unit increase in the unit scalar by an individual are represented by values greater than 1.

Parameter	Estimate	SD	Unit Scalar	Scaled Odds Ratio	Lower 95% CI	Upper 95% CI
Proximity to pool	0.03	0.07	50 m	1.70	0.15	15.57
Proximity to the run or riffle mesohabitat	0.05	0.06	50 m	3.00	0.18	38.90
Proximity to sand or fine sediment	-0.07	0.06	50 m	0.84	0.60	1.12
Proximity to gravel substrate	0.00	0.00	50 m	0.99	0.99	1.00
Proximity to cobble substrate	0.00	0.00	50 m	0.97	0.96	0.98
Proximity to boulder or bedrock substrate	0.14	0.05	50 m	2.52	1.23	4.92

DISCUSSION

I found that Guadalupe Bass exhibited different behavioral patterns in both habitat use and movement in comparison to tributary populations. Guadalupe Bass movement, home ranges, and habitat associations in the lower Colorado River indicated increased mobility with stream size and patterns in movement possibly associated with spawning and overwintering. Habitat associations of tagged individuals in the lower Colorado River suggest that Guadalupe Bass have the potential to be ubiquitous throughout the study area. Guadalupe Bass movement patterns, habitat associations and home ranges have been studied in smaller tributary systems (Perkin et al. 2010; Groeschel 2013), but there is limited information on the differences between tributary and mainstem populations. While there were similarities in movement patterns and habitat associations between the mainstem and upper watershed tributary individuals, there were also differences that could potentially influence the outcome of conservation and management actions. Understanding these differences provides managers with the ability to predict presence and assess the potential threats of future habitat loss on the population in the mainstem Colorado River. In addition, understanding behavioral differences improves the ability target future restoration or management practices for the long-term viability of the trophy Guadalupe Bass fishery in the lower Colorado River.

Overall movement patterns showed similar variability to tributary populations with some individuals being relatively stationary, while other individuals exhibited greater movements or higher mobility. Individuals in the Pedernales and South Llano River moved a maximum of 3.4 rkm (Perkin et al. 2010), while I found that Guadalupe

Bass in the lower Colorado River moved a maximum of 44 rkm. In the lower Colorado River movements greater than 10 km were not uncommon. However, some individuals were relatively sedentary, moving less than 10 km in total throughout the study period. Guadalupe Bass in the lower Colorado River are capable of moving greater distances to find habitat that maximizes the individual fitness, whether that is spawning or overwintering habitat. In addition to variability in individual movement within the population, there were also seasonal differences in movement. The largest individual movements, regardless of directionality, occurred in March and June which coincides with the months in which Guadalupe Bass spawning has been observed (Edwards 1980; Warren 2009). Given their timing, these large movements were likely associated with finding suitable nesting habitat and returning to their feeding areas. Seasonal variability in movement has been exhibited in other black bass species (Langhurst and Schoenike 1990; Horton and Guy 2002; Lyons and Kanehl 2002), as well as by tributary populations of Guadalupe Bass to a lesser magnitude (Perkin et al. 2010; Groeschel 2013). Shoal Bass (Stormer and Maceina 2009; Taylor et al. 2013; Taylor and Peterson 2015), Spotted Bass (Horton and Guy 2002), Smallmouth Bass (Gerber and Haynes 1988; Tabor et al. 2012) and Largemouth Bass (Hanson et al. 2007) have all exhibited seasonal differences in movements. Smallmouth Bass, for example, have exhibited large overwintering movements (69-87 km) in streams in Wisconsin (Langhurst and Schoenike 1990). Shoal Bass in the Flint River in Georgia have exhibited movements up to 200 km during spring to reach optimal spawning habitat (Sammons and Goclowski 2012). Understanding contrasting movement patterns and habitat associations of Guadalupe Bass across both

seasons and stream sizes will enable managers to implement practices that protect the habitat within the extensive home ranges of the mainstem population, permitting the continued development of the trophy fishery in the lower Colorado River, as well as maintain the stability of tributary populations.

Guadalupe Bass are reported to favor swifter currents, woody debris, and gravel/cobble substrates with strong associations with instream cover in tributary systems of the upper Colorado River Basin (Edwards 1980; Garrett 1991; Hubbs et al. 1991; Koppelman and Garrett 2002; Perkin et al. 2010; Bean and Grabowski 2015; Curtis et al. 2015). Guadalupe Bass in both the mainstem and tributaries of the Colorado River have been observed in areas where there was instream cover, commonly associated with woody debris or boulder habitat (Edwards 1980; Perkin et al. 2010; Curtis et al. 2015). Mesohabitat associations in the lower Colorado River differed from those of tributary systems. Pool-classed mesohabitat was the dominant mesohabitat used by Guadalupe Bass downstream of Bastrop, while in Bastrop, riffle was the dominant mesohabitat for Guadalupe Bass in the lower Colorado River. In contrast, the dominant mesohabitat used by Guadalupe Bass is typically eddy mesohabitat located near a run in tributary systems; however, seasonal associations with pool mesohabitat do occur in the late summer and winter (Edwards 1980; Perkin et al. 2010). Similarly, Spotted Bass have shown variation in habitat associations across regions with populations favoring pool mesohabitats in Kansas streams, and other populations found to show preference for riffles and shoal habitats in streams in Alabama (Horton and Guy 2002). Goclowksi et al. (2013) found that Spotted Bass tended to show high variation in habitat use in association with

proportion of available habitat. Differences in mesohabitat availability between the reaches within the Colorado River network may have driven the observed differences in mesohabitat associations between tributary and mainstem Guadalupe Bass populations. Perkin et al. (2010) found that in the South Llano River and the Pedernales River, habitat availability played a role in Guadalupe Bass distribution, abundance and habitat associations. In the late summer Guadalupe Bass in the South Llano River were associated with run mesohabitats, while in the Pedernales River pool mesohabitat was favored under conditions of low flow and limited habitat availability. Along the Colorado River fluvial gradient, the proportion of fine substrates increases as the slope of the stream bed decreases, which leads to a decrease in the availability of riffle habitat the further downstream from Longhorn Dam in Austin, Texas. The gradient in habitat availability and habitat preference of Guadalupe Bass may be driving the observed mobility and increased movements observed in the mainstem population.

The population of Guadalupe Bass in the lower Colorado River exhibits larger movements, suggesting that a longer stretch of river and extended movement between essential habitats are required to complete their life history in comparison to smaller tributary populations. Smallmouth Bass in Kentucky showed similar increases in movement and home range size when comparing mainstem and tributary populations. Median 95% kernel home ranges increased to 0.7 km² for Smallmouth Bass individuals residing in the larger Buffalo River system, and when both Bear Creek and Buffalo River were utilized by an individual the median home range increased drastically to 3.2 km² (Bare 2005). I found increases in linear home ranges in comparison to previously

determined movements of Guadalupe Bass in smaller tributary systems (Perkin et al. 2010). Guadalupe Bass linear home range across all reaches was 10.71 km (0.68-46.73 km) and was greatest in Bastrop and Altair, but overall core area home ranges were greater in Bastrop and Smithville. Increased movement and home range size in the lower Colorado may possibly be due to the presence of a larger length class that is not present in tributary systems. For example, Bean and Grabowski (2012) found that Guadalupe Bass in the South Llano River very seldomly exceeded 310 mm. In contrast, I found that in the lower Colorado River individuals commonly exceeded 310 mm and multiple individuals were greater than 400 mm (Pease et al. 2017). Individuals in this larger length class have larger home ranges and may possibly be utilizing habitat differently than smaller individuals found in tributaries.

Increased downstream home ranges and movement may also be associated with availability of habitat, as well as differences in flow regimes, between the lower Colorado and its headwater tributaries. Zero-flow days are a very rare occurrence in the lower Colorado River, whereas in tributary systems zero-flow days occur more often limiting movements and potentially isolating individuals (Saunders 2006; Vaughan et al. 2012). However, extended movements to optimal spawning and overwintering habitat may be required under low flow conditions and altered flow regimes that change the quantity and location of mesohabitat. Understanding the movement patterns of this developing trophy fishery and the habitat associations driving these movements is important, especially in the lower Colorado River where there is an entire length class not present in tributary systems. Larger individuals may possibly be utilizing habitat more similar to congener

species, such as the Largemouth Bass, therefore further evaluation of these differences may be warranted in order to maintain the habitat complexity that is suitable for Guadalupe Bass and congener species. Maintaining suitable habitat for black bass populations is especially crucial in rivers, such as the lower Colorado River where black bass fisheries are economically important (Thomas et al. 2014).

The logistic regression model indicated that the proximity to fine substrate and proximity to pool habitat were the most important habitat variables determining the predictability of locating Guadalupe Bass in the lower Colorado River. Guadalupe Bass in tributary systems have been associated with shallower and higher velocity riffle and run habitats, as well as with boulder structures (Perkin et al. 2010; Groeschel 2013). Habitat selection near these areas is likely due to resource availability and foraging, as well as shelter from predators. The diets of both juvenile and adult Guadalupe Bass contain large amounts benthic macroinvertebrates that are in highest abundance in riffle or run habitats with flowing water (Pridmore and Roper 1985). Following the switch to piscivory, Guadalupe Bass adult diets are dominated crayfish and small fish that are associated with flowing waters, yet macroinvertebrates still make up a significant portion of the adult diet (Edwards 1980; Warren 2009). The significant portion of macroinvertebrates throughout all life history stages of Guadalupe Bass suggests that the proximity to flowing water is important for successful foraging at every life history stage (Edwards 1980). However, Guadalupe Bass diet was assessed in the late 1970s prior to extensive landcover transitions and flow alteration in the Colorado River Basin surround the growing Austin metropolitan area. My results found that the habitat associations of

Guadalupe Bass are flexible and contrasting habitat associations suggests that there could also be a possible shift in the diets of Guadalupe Bass in the lower Colorado River Basin in comparison to tributary populations. Further research on the differences in Guadalupe Bass diets between tributary and mainstem populations, as well as the diets of the larger length class of Guadalupe Bass present in the lower Colorado River would assist in determining if Guadalupe Bass diets are becoming more similar to their congeners under increased anthropogenic alteration and determine whether the flexibility in habitat associations related to changing environmental variables may possibly lead to higher rates of competition with other *Micropterus* species.

Overall, I determined that Guadalupe Bass exhibit differences in movement patterns and habitat associations across stream orders. There were similarities in the seasonality of movements and the variability in mobility among individuals within a population with both stationary and mobile individuals being represented. However, the extended mobility of individuals in the lower Colorado River potentially increases the population's sensitivity to flow alteration and vulnerability to habitat fragmentation. Individuals in the mainstem population have larger home ranges requiring maintained connection with nesting and overwintering habitat for successful life history completion. Differences in habitat preferences related to the proximity to pool habitat and fine substrate habitat possibly contribute to movement differences between Guadalupe Bass mainstem and tributary populations. Further research on the mechanistic drivers guiding contrasting movement patterns within populations will facilitate management efforts that account for both mobile and stationary individuals. Further, an understanding of the observed

differences between mainstem and tributary populations informs managers of the contrasting population-level utilization patterns and movements that could potentially influence the response of the Guadalupe Bass to conservation and management actions. Broader-scale restoration that considers access and availability of habitat for seasonal movements may be more effective if managers consider the difference in habitat associations across stream orders and habitat connectivity for both mobile and stationary individuals comprising a population.

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CHAPTER 5

CONCLUSIONS AND CONSERVATION IMPLICATIONS

The Guadalupe Bass is the state fish of Texas and a popular sport fish throughout the Edwards Plateau. The total economic impact of angling over this 24-county region was estimated to be approximately \$71 million. Over half of the anglers throughout the region targeted black bass species, while 42% of anglers specifically targeted Guadalupe Bass (Thomas, Arsuffi, & Magnelia, 2014). In addition to being a highly sought-after sport fish, Guadalupe Bass are considered a species of special concern (Hubbs, Edwards, & Garrett, 1991) and an ‘intolerant’ or sensitive indicator of habitat alteration for the regional Index of Biological Integrity for Texas (Linam, Kleinsasser, & Mayes, 2002). The biggest threats to Guadalupe Bass are introgressive hybridization with Smallmouth Bass and habitat degradation (Curtis, Perkin, Bean, Sullivan, & Bonner, 2015). Successful restoration efforts have reduced the introgression rates throughout Guadalupe Bass range (Bean, Lutz-Carrillo, & Bonner, 2013; Fleming, Garrett, & Smith, 2015). Therefore, understanding the effects that habitat degradation has on Guadalupe Bass populations throughout the Colorado River Basin, which encompasses a large majority of their range, is critical for continued management. Differences in LULC and flow regime were assessed to determine the gradient of disturbance that occurs between upstream tributaries to the mainstem downstream of the Austin area. Mainstem Guadalupe Bass in the lower Colorado River were found to reside in different habitats than previously noted as “typical” for upstream tributary populations. I also identified differences in the lower Colorado

River Guadalupe Bass in terms of age and growth, movement patterns, as well as morphological variation from upstream populations that occur in more “typical” habitat.

Understanding the ability of Guadalupe Bass to respond to alterations to the hydrologic regime and LULC throughout the basin is critical for successful management and conservation. For example, managers choosing the proper broodstock in the continuing effort to combat introgression throughout Guadalupe Bass range may need to take into consideration population-specific responses to unique environmental stressors. Altered hydrologic and LULC regimes have the potential to impact populations differently, possibly resulting in plastic responses to environmental variables. Different behavioral patterns in movement and habitat use, and morphological variation between tributary populations and mainstem Guadalupe Bass populations, suggest that site-specific restoration or conservation strategies, such as stocking plans, are important for the continued management success of Guadalupe Bass throughout the state of Texas. Introgression of tributary populations with lower Colorado River Guadalupe Bass may potentially reduce the fitness of those adapted individuals and increase the chances of population decline. For example, stocking lower Colorado River individuals in the Pedernales River may not be as successful or result in similar recruitment success as if San Saba River broodstock fingerlings were stocked in the Pedernales River.

Guadalupe Bass plasticity in response to disturbance is especially important in the Edwards Plateau region where population growth is expected to more than double in

the next 25-50 years. Local plasticity and adaptation to environmental stressors are possible across the range of habitats for which Guadalupe Bass reside in the Colorado River Basin. Morphological response to LULC and flow alteration throughout the Colorado River Basin indicated that Guadalupe Bass can be variable in their response to disturbance. While my results suggest that there is some morphological differentiation between historical and present Guadalupe Bass located in the lower Colorado River, the drivers of these variations is still unclear. Further research on prey availability and temperature environmental drivers may aid in identifying drivers of morphological variation in Guadalupe Bass.

Additionally, I found that lower Colorado River Guadalupe Bass have higher rates of growth than their counterparts in tributary systems, as well as showing greater overall movement in the larger Colorado River system when not inhibited by natural and artificial barriers to movement. The growth patterns under variable flows throughout the system may be applicable to other ecologically similar species, and identifying the flows required to promote optimum recruitment and growth for Guadalupe Bass may help in understanding requirements for flow conditions and cohort success in other species. It would be beneficial to investigate growth patterns of species occupying different ecological niches in response to variable flow conditions in order to manage aquatic communities throughout the Colorado River Basin. Additional studies on the influence of productivity on growth differences in flow altered systems would need to be conducted in order to elucidate whether prey availability drives differences in growth rate.

Mainstem population individuals are capable of thriving under present-day development within the watershed and regulated flow conditions of the Highland Lakes, but effects of continued environmental change are unknown. Basin-wide variation in the population dynamics of Guadalupe Bass support further watershed scale approaches to management and conservation planning to maintain the ecological processes and natural habitat that support distinct populations. When planning for the conservation of the unique mainstem population under current projected population growth and further urbanization within the watershed, managers could consider increasing releases prior to and immediately following spawning in the lower Colorado River. Watershed-scale restoration and management of the population would not only be beneficial to Guadalupe Bass, but has the potential to also benefit other focal or endemic species, such as the Guadalupe Roundnose Minnow *Dionda nigrotaeniata*, Texas Logperch *Percina carbonaria*, as well as sympatric state-threatened species, such as Blue Sucker *Cycleptus elongatus* (Birdsong et al., 2010; Garrett, 1991). In addition to the community level benefits of range wide management of Guadalupe Bass understanding the differences between the mainstem and the tributary ecology will facilitate the development of the trophy fishery in the lower Colorado and increase the economic value of Guadalupe Bass for Central Texas.

Overall this study contributes to the understanding of population-level variation in ecological traits associated with urbanization, water withdrawals and other anthropogenic stressors. Environments naturally fluctuate; consequently, populations are never really at equilibrium due to the stressors imposed by the environment. If

populations are continually driven in one direction by environmental change from anthropogenic influence, they may no longer have the adaptability and capacity to respond to future changes expected based on demographic or climatic projections. My results not only emphasize the importance of understanding population-level ecological response to flow and land use alterations, but also the importance of taking into consideration stream order effects on movement and growth rate when managing a population.

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APPENDICES**Table A.1:** Summary table of site locations and the associated ten-digit hydrologic unit code (HUC) and United States Geological Survey stream gage number.

Site	River	River	Latitude	Longitude	HUC 10	USGS Gage	Watershed
Barton Creek Greenbelt S Capital of Texas Hwy 360	1	BART	30.244703	-97.8022	1209020503	8155240	22
Lost Creek Access to Barton Creek Greenbelt off Lost Creek Blvd.	1	BART	30.2743	-97.8444	1209020503	8155240	22
South of US 90 Alt Boat Ramp in Eagle Lake	2	COLO	29.5532	-96.4008	1209030201	8161000	30
South of Fisherman's Park Boat Launch in Bastrop	2	COLO	30.0994	-97.3211	1209030102	8159200	27
South of Webberville Park	2	COLO	30.2019	-97.4868	1209030102	8159200	27
North of Fisherman's Park Boat Launch in Bastrop	2	COLO	30.1333	-97.3614	1209030102	8159200	27
South of the Fannin St. TX 71 Business Boat Ramp	2	COLO	29.7158	-96.5416	1209030107	8160400	29

State Highway 71	2	COLO	29.9012	-96.8870	1209030107	8160400	29
South of State Highway 71 Boat Ramp	2	COLO	29.8957	-96.8843	1209030107	8160400	29
South of the State Hwy 71 crossing in Smithville	2	COLO	30.0145	-97.0942	1209030104	8159200	28
FM 2335 outside Knickerbocker	3	DOVE	31.2738	-100.6308	1209010203	8130500	3
James River Rd. crossing north of Eckert James River Bat Cave Preserve	4	JAME	30.5725	-99.3233	1209020404	8150700	17
RR 1871	5	LLAN	30.6579	-99.3246	1209020402	8150000	16
RR 2389 James River and Llano River confluence.	5	LLAN	30.6502	-99.2507	1209020405	8150700	17
South Llano and North Llano confluence off Camino Rio St.	5	LLAN	30.4926	-99.7567	1209020202	8148500	15
FM 3404 in Kingland, Texas	5	LLAN	30.6824	-98.4835	1209020408	8151500	21
Simonsville Rd.	5	LLAN	30.64002	-99.168097	1209020405	8150700	18

Bear Creek at Interstate 10	6	NLR	30.5210	-99.8293	1209020203	8148500	12
CR260	6	NLR	30.4986	-100.0927	1209020203	8148500	11
CR271	6	NLR	30.5181	-99.8102	1209020203	8148500	12
CR274	6	NLR	30.4981	-99.9448	1209020203	8148500	12
CR275	6	NLR	30.4909	-99.9864	1209020203	8148500	11
CR260 at River Rd in Roosevelt	6	NLR	30.4796	-100.1195	1209020203	8148500	11
CR310 to River Rd. in Sonora	6	NLR	30.4826	-100.1474	1209020203	8148500	11
McKinney Falls State Park	7	ONIO N	30.1885	-97.7205	1209020504	8159000	23
RR 1320	8	PEDE	30.2726	-98.5455	1209020602	8153500	25
Texas Hwy 16	8	PEDE	30.2070	-98.9790	1209020601	8153500	24

Hamilton Pool Rd. (FM 3238) Crossing	8	PEDE	30.3399	-98.1392	1209020504	8152900	26
U.S. Route 290	8	PEDE	30.2276	-98.8188	1209020602	8153500	25
Fiedler Rd.	8	PEDE	30.2277	-99.2001	1209020601	8152900	24
RR 1623	8	PEDE	30.2433	-98.6572	1209020602	8153500	25
Decker St. off TX Hwy 83 in Menard	9	SABA	30.9190	-99.7840	1209010905	8144500	8
FM 340 / S. Cotton Belt Rd.	9	SABA	31.1910	-98.9026	1209010908	8146000	10
Texas Hwy 16 at the intersection with FM 1480	9	SABA	31.2133	-98.7199	1209010908	8146000	10
US Hwy 377/87 outside Brady	9	SABA	31.0040	-99.2695	1209010907	8146000	9
Flatrock Ln. off US 377	10	SLR	30.4790	-99.7779	1209020302	1111111	14
CR150	10	SLR	30.3936	-99.8820	1209020302	1111111	14

CR408	10	SLR	30.2419	-99.9628	1209020302	1111111	13
US Hwy 377 at the first crossing south of Junction	10	SLR	30.3504	-99.9017	1209020302	1111111	14
South Llano State Park (State Park Rd. 73)	10	SLR	30.4502	-99.8128	1209020302	1111111	14
Stevenson RR in Telegraph	10	SLR	30.3199	-99.9109	1209020302	1111111	14
Springdale Rd.	11	WC	30.3375	-97.6502	1209020503	8158600	22
Walnut Creek Bike Trail off FM 969	11	WC	30.2906	-97.6567	1209020503	8158600	22

Table A.2: Summary table of Hydrologic Unit Codes for Sub-watersheds (Figure 2.1; Figure 3.1) encompassing study sites of interest. HUC 10 watersheds were accessed through USGS.

SUBBASIN	HUC_10	HU_10_NAME	Area_km
Austin-Travis Lakes			
	1209020503	City of Austin-Colorado River	848.77
	1209020504	Onion Creek-Colorado River	944.14
Llano			
	1209020402	Big Saline Creek-Llano River	787.56
	1209020403	Honey Creek-Llano River	731.25
	1209020404	Little Devils River-James River	879.60
	1209020405	Comanche Creek-Llano River	958.23
	1209020406	Hickory Creek-Llano River	1092.77
	1209020407	San Fernando Creek-Llano River	870.56
	1209020408	Little Llano River-Llano River	616.74
Lower Colorado			
	1209030201	Skull Creek-Colorado River	890.35
Lower Colorado- Cummins			
	1209030102	Piney Creek-Colorado River	497.75
	1209030104	Alum Creek-Colorado River	482.73
	1209030107	Buckners Creek-Colorado River	1316.76
Middle Colorado			
	1209010606	San Saba River-Colorado River	758.23
North Llano			
	1209020202	Middle North Llano River	803.70
	1209020203	Lower North Llano River	560.22
Pedernales			
	1209020601	Headwaters Pedernales	1095.37

		River	
	1209020602	North Grape Creek- Pedernales River	1094.16
	1209020603	Pedernales River-Lake Travis	1127.10
San Saba			
	1209010905	Elm Creek-San Saba River	534.72
	1209010907	Tiger Creek-San Saba River	1043.93
South Concho	1209010908	Richland Springs Creek-San Saba River	923.85
	1209010203	Dove Creek	689.75
South Llano			
	1209020302	Middle South Llano River	564.39
	1209020304	Lower South Llano River	494.04

Table A.3: Broad land cover classes used to reclassify historical and current land use and land cover (LULC) dataset within HUC 10 watersheds (Figure 2.1; Figure 3.1) within the Colorado River Basin, Texas. Historical LULC data was re-classified from the Anderson II classification system used to classify Landsat images from the 1970's ad 1980's. Current LULC was reclassified from remote sensing data collected in 2011 and classified by Texas Parks and Wildlife Ecological Systems of Texas.

Broad Reclassified Classes	Historical	Current
Agriculture	Cropland, pasture, orchards, groves, vineyards, nurseries, ornamental horticultural, confined feeding operations, other agricultural land	Agriculture
Barren	Dry salt flats, Beaches, Sandy areas not beaches, bare exposed rock, strip mines, quarries, gravel pits, transitional areas, mixed barren land, bare ground	Barren, Cliff
Deciduous	Deciduous forest land	Deciduous Forest, Deciduous Shrubland, Floodplain CD Forest, Floodplain Deciduous Shrubland, Floodplain Live Oak Forest, Live Oak Forest, Mesquite Shrubland, Post Oak Forest, Riparian CD Forest, Riparian Deciduous Shrubland, Riparian Live Oak Forest, Sandy Oak Forest, Slope Cold Deciduous Forest, Slope Deciduous Shrubland, Slope Live Oak Forest Evergreen Shrubland, Floodplain Juniper Forest, Floodplain Juniper Shrubland, Juniper Forest, Juniper Shrubland, Pine Forest, Riparian Juniper Forest, Riparian Juniper Shrubland, Slope Evergreen Shrubland, Slope Juniper Forest
Evergreen	Evergreen forest land	
Herbaceous	Herbaceous rangeland, Shrub and Brush rangeland, Mixed rangeland, Shrub and brush tundra, Herbaceous tundra	Floodplain Herbaceous, Grassland, Marsh, Riparian Herbaceous

Mixed	Mixed forest land	Floodplain Mixed Forest, Mixed Forest, Riparian Mixed Forest, Slope Mixed Forest
Water	Streams and Canals, Lakes, Reservoirs	Open Water
Urban High	Commercial and Services, Industrial, Transportation, communication, utilities, Industrial and commercial complexes, Mixed urban or built- up land, other urban or built-up land	Urban High
Urban Low	Residential	Urban Low
Wetland	Forested wetland, Non-forested wetland	Swamp

Table A.4: Summary table of USGS gage numbers for study sites of interest. USGS gage data was accessed through USGS.

USGS Gage Number	Gage Name
08130500	Dove Ck at Knickerbocker, TX
08144500	San Saba Rv at Menard, TX
08144600	San Saba Rv nr Brady, TX
08146000	San Saba Rv at San Saba, TX
08148500	N Llano Rv nr Junction, TX
08149900	S Llano Rv at Flat Rock Ln at Junction, TX
08150000	Llano Rv nr Junction, TX
08150700	Llano Rv nr Mason, TX
08151500	Llano Rv at Llano, TX
08152900	Pedernales Rv nr Fredericksburg, TX
08153500	Pedernales Rv nr Johnson City, TX
08155240	Barton Ck at Lost Ck Blvd nr Austin, TX
08155300	Barton Ck at Loop 360, Austin, TX
08158000	Colorado Rv at Austin, TX
08158700	Onion Ck nr Driftwood, TX
08159000	Onion Ck at US Hwy 183, Austin, TX
08159200	Colorado Rv at Bastrop, TX
08159500	Colorado Rv at Smithville, TX
08160400	Colorado Rv abv La Grange, TX
08161000	Colorado Rv at Columbus, TX

Table A.5: Catalog ID numbers for all Guadalupe Bass used in the morphometric analysis. These specimens were accessed at the Texas Natural History Collection in the Biodiversity Collections of the Department of Integrative Biology at The University of Texas at Austin.

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<i>Catalog ID</i>	<i>Specimens</i>	<i>River</i>	<i>County</i>	<i>Location</i>	<i>Collecting Date</i>	<i>Collector</i>	<i>Coordinates</i>
<u>TNHC10349</u>	6	Llano	Llano	Llano River 1 km NE Kingsland off Highway 1431	18-Jul-77	Edwards	30.65119252, -98.48866364
<u>TNHC10110</u>	6	Onion Creek	Travis	Onion Creek, 12 km. SE Austin, State Hwy 183	19-Mar-78	Edwards	30.17791123, -97.68897812
<u>TNHC10114</u>	4	Barton Creek	Travis	Barton Creek, 21 km. SW Austin at State Hwy 71	9-Oct-77	Edwards	30.296277, -97.925624
<u>TNHC10117</u>	34	Onion Creek	Travis	Onion Creek, 12 km. SE Austin, State Hwy 183	18-Jun-77	Edwards	30.17791123, -97.68897812
<u>TNHC10192</u>	42	Llano	Llano	Llano River, 19 km. W Llano off Hwy 152	16-Jul-78	Edwards	30.71027191, -98.86003926
<u>TNHC10194</u>	1	Llano	Llano	Llano River, Kingsland near Kingsland Estates	24-Apr-77	Edwards	30.64016489, -98.47570928
<u>TNHC10198</u>	4	Pedernales	Gillespie	Pedernales River, 6.4 km. S Fredericksburg, State Hwy 16	16-Dec-78	Edwards	30.20919787, -98.94879018
<u>TNHC10200</u>	15	Llano	Llano	Llano River, Llano near Hwy 16	11-Jun-78	Edwards	30.75243093, -98.67581467
<u>TNHC10205</u>	2	Llano	Llano	Llano River, Llano near Hwy 16	18-Nov-78	Edwards	30.75243093, -98.67581467
<u>TNHC10206</u>	4	Llano	Llano	Llano River, Llano near Hwy 17	18-Nov-78	Edwards	30.75243093, -98.67581467
<u>TNHC10207</u>	39	Onion Creek	Travis	Onion Creek, 12 km. SE Austin, State Hwy 183	4-Jul-77	Edwards	30.17791123, -97.68897812

<u>TNHC10213</u>	43	Pedernales	Travis	Pedernales River, 40 km. E Johnson City, State Hwy 962	21-Jun-77	Edwards	30.33990517, - 98.13912996
<u>TNHC10218</u>	52	Pedernales	Gillespie	Pedernales River, 6.5 km. SE Fredericksburg, US Hwy 290	6-Aug-77	Edwards	30.22709728, - 98.94879023
<u>TNHC10225</u>	3	Pedernales	Blanco	Pedernales River, 12 km. W Johnson City, State Hwy 1320	3-Dec-77	Edwards	30.2722066, - 98.54552012
<u>TNHC10229</u>	13	Colorado	Colorado	Colorado River, Columbus, State Hwy 90	10-Jul-77	Edwards	29.70625864, - 96.53656784
<u>TNHC10232</u>	1	Pedernales	Gillespie	Pedernales River, 6.5 km. SE Fredericksburg, US Hwy 290	5-Mar-78	Edwards	30.22709728, - 98.94879023
<u>TNHC10233</u>	1	Pedernales	Gillespie	Pedernales River, State Hwy 1 Immediately Downstream from Lbj Ranch	3-Dec-77	Edwards	30.2445474, - 98.59765137
<u>TNHC10239</u>	18	Llano	Llano	Llano River, .2 km. N Castell, State Hwy 2768	28-Aug-76	Edwards	30.70380192, - 98.95863175
<u>TNHC10241</u>	13	Llano	Llano	Llano River, Llano near Hwy 16	15-Oct-77	Edwards	30.75243093, - 98.67581467
<u>TNHC10247</u>	5	Colorado	Colorado	Colorado River, 7.2 km. NE Altair, US Hwy 90A	10-Jul-77	Edwards	29.58034302, - 96.41714457
<u>TNHC10327</u>	4	Colorado	Travis	Colorado River, 14.5 km. E Austin, Hwy 973	31-Oct-76	Edwards	30.20818034, - 97.6380769
<u>TNHC10330</u>	2	Llano	Kimble	Llano River, 32 km. NE Junction, State Hwy 385	20-Feb-77	Edwards	30.6587426, - 99.32412093
<u>TNHC10113</u>	46	Llano	Mason	14.5 km. SE Mason, State Hwy 87	17-Jun-77	Edwards	30.66117297, - 99.10949548
<u>TNHC17318</u>	1	Dove Creek	Irion	Dove Creek at first crossing	22-Feb-86	Hubbs, Marsh-Matthews, and Scott	31.15589373, - 100.7527988
<u>TNHC17355</u>	3	Llano	Kimble	Llano River at Junction	25-Jun-86	Hubbs and Morales	30.49784685, - 99.75186133

<u>TNHC17356</u>	1	Llano	Kimble	Llano River at Junction	25-Jun-86	Hubbs and Morales	30.49784685, - 99.75186133
<u>TNHC2072</u>	2	San Saba	Menard	San Saba River, 1 mi. N Ft. McKavitt	10-Feb-52	Hubbs and Strawn	30.83592528, - 100.1050113
<u>TNHC2525</u>	1	San Saba	Menard	San Saba River, 1 mi. E Ft. McKavitt	10-Feb-52	Hubbs and Strawn	30.83461535, - 100.093721
<u>TNHC2599</u>	1	North Concho	Tom Green	N Fork Concho River, near dam, San Angelo	9-Feb-52	Hubbs, Strawn, Henderson, and Pyburn	31.46714483, - 100.450052
<u>TNHC3068</u>	1	South Llano	Kimble	S Fork Llano River, 14.5 mi. SW Junction	27-Dec-52	Hubbs and Strawn	30.38543019, - 99.88780445
<u>TNHC3102</u>	3	Dove Creek	Irion	Dove Creek, headsprings, 7 mi. SW Knickerbocker	21-Feb-53	Hubbs and Strawn	31.20565229, - 100.7065677
<u>TNHC3276</u>	1	Colorado	Bastrop	Colorado River at SH969 Southeast of Utley	13-Mar-53	Hubbs	30.16746206, - 97.40291082
<u>TNHC5419</u>	1	San Saba	Menard	San Saba River north of Fort McKavett	16-Jul-56	Hubbs and Strawn	30.83592528, - 100.1050113
<u>TNHC8008</u>	1	San Saba	Menard	San Saba River at SH 864 (first crossing north-northeast of Fort McKavett)	16-Jul-56	Hubbs and Strawn	30.83461535, - 100.093721
<u>TNHC5419</u>	1	San Saba	Menard	N Valley Prong San Saba River, 1 mi. N Ft. McKavitt	17-Jul-56	Hubbs and Strawn	30.83592528, - 100.1050113
<u>TCWC235.01</u>	3	Colorado River	Colordao	Colorado River drainage; 6.0 mi NE Columbus on Cummings Creek	24-Oct-59	Jones	29.73585769, - 96.5089472
<u>TCWC6670.03</u>	2	Llano	Llano	Llano River; Llano River: 4 mi W Llano.	30-May-86	WFS 300 Class	30.74395108, - 98.73857625

<u>TCWC7826.06</u>	5	Dove Creek	Tom Green	Dove Creek.; Dove Creek, 0.5 mi NW Knickerbocker at FR 2335.	21-May-91	Brown and Smith	31.27377036, -100.630536
<u>TCWC8925.08</u>	3	Colorado River	Concho	Colorado River; Colorado River, FM 1929 downstream from Freese Dam	14-Oct-96	Brown and Smith	31.49830568, -99.66221199
<u>TNHC10536</u>	6	Onion Creek	Travis	State Hwy 183 crossing, 5 km. SE Austin	6-Aug-80	Pezold	30.17791123, -97.68897812
<u>TNHC11233</u>	1	Colorado River	Travis	Colorado River near SH 71 in vicinity of Del Valle	4-Oct-81	Winemiller	30.21226018, -97.64852718
<u>TNHC21719</u>	2	Barton Creek	Travis	Barton Creek at Lost Creek Blvd.	18-May-93	Warren and Freeman	30.27412783, -97.8444023
<u>TNHC10536</u>	6	Onion Creek	Travis	Onion Creek, State Hwy 183 crossing, 5 km. SE Austin	6-Aug-80	Pezold	30.17791123, -97.68897812
<u>TNHC1428</u>	1	Pedernales River	Travis	Pedernales River at Cypress Creek	11-May-51	Jameson and Phillips	30.35100481, -98.13701993
<u>TNHC21746</u>	1	Barton Creek	Travis	Barton Creek at SH 71	15-Feb-93	Warren and Wright	30.29627697, -97.92562442
<u>TNHC21806</u>	5	Barton Creek	Travis	Barton Creek at Barton West subdivision off Bee Cave drive	7-Jul-88	Kleinsasser and Linam	30.29889697, -97.87623317
<u>TNHC22059</u>	1	South Llano Little Barton Creek	Kimble	South Llano River at first FM 377 crossing SW of Junction	21-Jun-89	Kleinsasser and Sager	30.36201094, -99.88930442
<u>TNHC22323</u>	1	South Llano Little Barton Creek	Travis	Little Barton Creek at private road off SH 71 W of Austin near confluence with Barton Creek	15-Mar-89	Linam and Sauders	30.29586698, -97.92731446
<u>TNHC22797</u>	3	Barton Creek	Travis	Barton Creek, 13.8 mi SW of Austin on St. Hwy. 71	7-Jun-93	Warren and Freeman	30.29627697, -97.92562442

<u>TNHC22817</u>	79	Barton Creek	Travis	Barton Creek, Austin, 0.8 mi E of Lost Creek Blvd. on Plumbrook Road	11-Jul-93	Warren and Freeman	30.269878, -97.82928191
<u>TNHC22819</u>	5	Barton Creek	Travis	Barton Creek, Austin, below Barton Springs Pool at Zilker Park	29-Jul-93	Warren and Freeman	30.26495827, -97.76569028
<u>TNHC22841</u>	4	Barton Creek	Travis	Barton Creek, Austin, 1.7 mi S of Loop 360 on Lost Creek Blvd.	24-Aug-93	Warren and Freeman	30.27412783, -97.8444023
<u>TNHC22848</u>	1	Barton Creek	Travis	Barton Creek, Austin, below Barton Springs Pool at Zilker Park	20-Nov-93	Warren and Freeman	30.26495827, -97.76569028
<u>TNHC22866</u>	1	Barton Creek	Travis	Barton Creek, Austin, 1.7 mi S of Loop 360 on Lost Creek Blvd.	19-Dec-93	Warren and Freeman	30.27412783, -97.8444023
<u>TNHC22915</u>	9	Barton Creek	Travis	Barton Creek. 1.4 mi S of Bee Cave Road on Crystal Creek Drive	17-Jun-94	Warren and Freeman	30.30145691, -97.86433287
<u>TNHC22928</u>	30	Barton Creek	Travis	Barton Creek, 1.4 mi SW of Loop 360 on Plumbrook road below Lost Creek subdivision	28-Aug-93	Warren, Freeman, and Hiers	30.269878, -97.82928191
<u>TNHC22973</u>	1	Little Barton Creek	Travis	Little Barton Creek at private road off SH 71 W of Austin at Fandango Way	7-Jul-88	Kleinsasser and Linam	30.29586698, -97.92731446
<u>TNHC22989</u>	1	Barton Creek	Travis	Barton Creek, 1.4 mi SW of Loop 360 on Plumbrook road below Lost Creek subdivision	25-Aug-93	Warren and Freeman	30.269878, -97.82928191
<u>TNHC230</u>	5	Onion Creek	Travis	10 mi. SE on Onion Creek, near del Valle	17-Sep-47	Blair	30.18925098, -97.6201864
<u>TNHC23004</u>	7	Barton Creek	Travis	Barton Creek, 13.8 mi SW of Austin on St. Hwy. 71	23-Aug-93	Warren and Freeman	30.29627697, -97.92562442
<u>TNHC23015</u>	2	Barton Creek	Travis	Barton Creek, 7.0 mi NE of Dripping Springs on Co. Rd. 185 (or	24-Aug-93	Warren and Freeman	30.23644873, -98.0248168

Trautwein Road)

<u>TNHC23116</u>	7	Colorado River	Bastrop	Colorado River in town of Bastrop at loop 150 river crossing	Jul-87	Morales	30.10989408, - 97.32286866
<u>TNHC23120</u>	1	Colorado River	Bastrop	Colorado River in town of Bastrop at loop 150 river crossing	Oct-86	Morales	30.10989408, - 97.32286866
<u>TNHC23122</u>	8	Colorado River	Bastrop	Colorado River in town of Bastrop at loop 150 river crossing	Jun-87	Morales	30.10989408, - 97.32286866
<u>TNHC23146</u>	1	Colorado River	Bastrop	Colorado River in town of Bastrop at loop 150 river crossing	Nov-86	Morales	30.10989408, - 97.32286866
<u>TNHC23155</u>	7	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	May-86	Morales	30.18786136, - 97.42345139
<u>TNHC23163</u>	3	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	Jul-87	Morales	30.18786136, - 97.42345139
<u>TNHC23173</u>	3	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	Sep-86	Morales	30.18786136, - 97.42345139
<u>TNHC23181</u>	1	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	August - September 1986	Morales	30.18786136, - 97.42345139
<u>TNHC23196</u>	15	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	Jun-87	Morales	30.18786136, - 97.42345139
<u>TNHC23203</u>	1	Colorado River	Travis	Colorado River at FM 973 highway crossing	Sep-86	Morales	30.20816034, - 97.6379969
<u>TNHC23233</u>	2	Colorado River	Travis	Colorado River at Longhorn Dam	May-86	Morales	30.25036883, - 97.71344891

<u>TNHC23244</u>	3	Colorado River	Travis	Colorado River at Longhorn Dam	Jun-87	Morales Hendrickson , Mosier, and Southwest Texas State University Class	30.25036883, - 97.71344891
<u>TNHC23605</u>	5	Colorado River	Colorado	Colorado River at Smithville from about 50m below St. Hwy. 95 to 400m below St. Hwy. 71	29-Jun-96		30.02294702, - 97.26388697
<u>TNHC23645</u>	4	Colorado River	Travis	Colorado River at FM 973 highway crossing	Jul-87	Morales	30.20816034, - 97.6379969
<u>TNHC23648</u>	2	Colorado River	Travis	Colorado River at FM 973 highway crossing	Jul-87	Morales	30.20816034, - 97.6379969
<u>TNHC23651</u>	2	Colorado River	Travis	Colorado River at Longhorn Dam	Jun-87	Morales	30.25036883, - 97.71344891
<u>TNHC23658</u>	3	Colorado River	Bastrop	Colorado River at Pope Bend off of FM 969 approx 7 mi E of its jct with SH71	August - September 1986	Morales	30.18786136, - 97.42345139
<u>TNHC2525</u>	1	San Saba	Menard	San Saba River at SH 864 (first crossing north-northeast of Fort McKavett)	10-Feb-52	Hubbs and Strawn Hubbs, Strawn, Henderson, and Pyburn Hendrickson	30.83461535, - 100.093721
<u>TNHC2599</u>	1	N Fork Concho River	Tom Green	North Concho River downstream of O. C. Fisher Dam	9-Feb-52		31.46714483, - 100.450052
<u>TNHC29916</u>	3	Walnut Creek	Travis	Walnut Creek, reach from Springdale Road upstream to Sprinkle Cutoff Road	20-Mar-03	, Hendrickson , and Hicks	30.35145566, - 97.65306761

<u>TNHC29926</u>	3	Walnut Creek	Travis	Walnut Creek, reach from Springdale Road upstream to Sprinkle Cutoff Road	30-Mar-03	Hendrickson , Hendrickson , and Hicks Hendrickson	30.35145566, - 97.65306761
<u>TNHC29947</u>	3	Walnut Creek	Travis	Walnut Creek, reach from Springdale Road upstream to Sprinkle Cutoff Road	30-Mar-03	Hendrickson , Hendrickson , and Hicks	30.35145566, - 97.65306761
<u>TNHC5076</u>	1	Pedernales River	Travis	Pedernales River at confluence of Cypress Creek and Hamilton Creek	6-May-55	McCoy	30.34975485, - 98.13725993
<u>TNHC538</u>	2	Colorado River	Travis	Colorado River at Waller Street Llano River, near Submerged bridge	3-Oct-47	Blair and Class	30.25068878, - 97.73535947
<u>TNHC7313</u>	1	Llano	Llano	Past Kingsland to The Left of Fr 1431	8-Mar-68	Rogers and Leach	30.68206354, - 98.4841796
<u>TNHC8200</u>	1	Llano	Kimble	Llano River at Junction	28-Apr-68	Eddleman	30.49784685, - 99.75186133

Table A.6: Canonical structure coefficients for the first three canonical variates for relative warp scores used in the canonical correlation analysis of Guadalupe Bass morphology related to altered flow and land cover throughout the Colorado River Basin, Texas. Historical individuals were collected by Edwards (1980) and stored at the Texas Natural Historical Museum collection where morphological photos were taken for analysis (Table A.5). Present-day individuals were collected between March 2014 and September 2016. Location of landmarks comprising relative warps are illustrated in

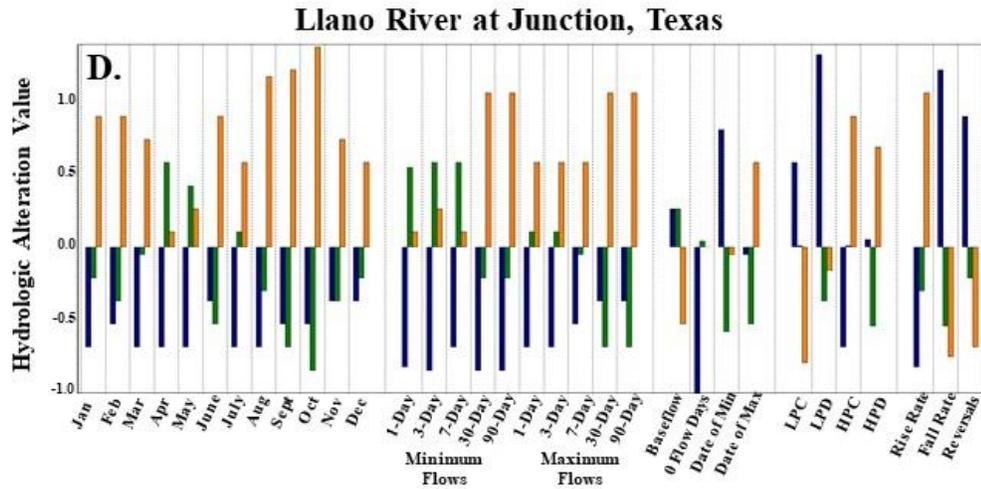
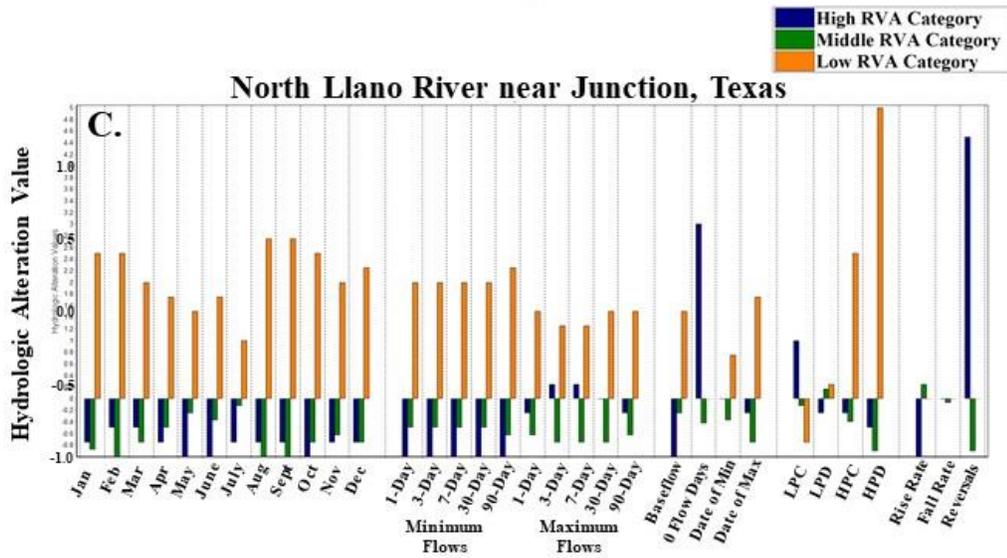
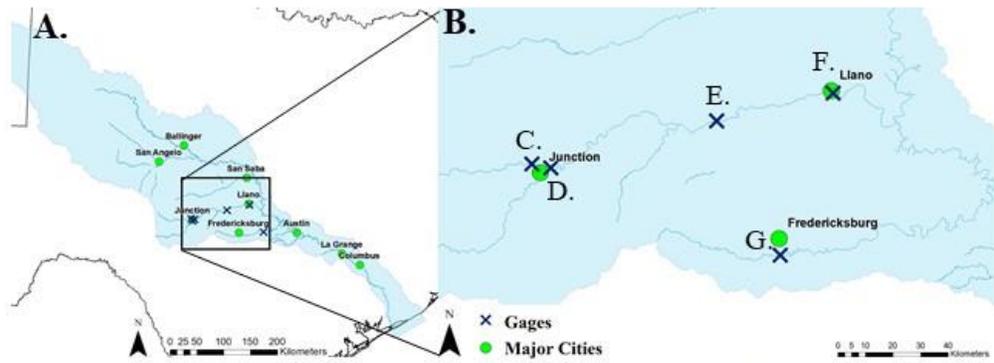
Variable	morphology1	morphology2
RW1	-0.9358	-0.0647
RW2	0.3221	0.0253
RW3	0.0682	-0.9797
RW4	0.0686	0.2135

Table A.7: Canonical structure coefficients for the first three canonical variates for environmental variables (land use and landcover (LULC) changes and indicators of hydrologic alteration (IHA) used in the canonical correlation analysis of Guadalupe Bass morphology related to altered flow and LULC throughout the Colorado River Basin, Texas. Historical individuals were collected by Edwards (1980) and stored at the Texas Natural Historical Museum collection where morphological photos were taken for analysis (Table A.5) Present-day individuals were collected between March 2014 and September 2016. Location of landmarks comprising relative warps are illustrated in Figure 2.3. Bolded values indicate the most correlated variables for the particular morphological variable.

Variable	Environment 1	Environment 2
Herbaceous	0.6782	-0.0738
Barren	0.2873	0.335
Reversals	-0.0237	0.4426
0 Flow Days	0.3997	0.4912
7-Day Max	0.5264	0.2509
30-Day Max	0.4017	0.3919
Baseflow	-0.2404	-0.2579
3-Day Max	0.3725	0.1466
Forested	-0.5197	0.0854
90-Day Max	0.445	0.3848
Fall Rate	0.2696	-0.0207
7-Day Min	-0.3672	0.082
Low Pulse Count	-0.4104	0.4601
November	0.0172	-0.0114
Agriculture	-0.0028	0.0427
Date of Minimum	0.2782	0.2662
December	-0.1988	0.0404
30-Day Min	0.0773	0.1674
High Pulse Count	0.3944	0.039

Table A.8: Age-length key for Guadalupe Bass in the mainstem Colorado River, Texas based on otolith age at capture and total length (TL) at age of collection between 2014-2015. Rows indicate the percent probability that with the given 25-mm length interval a Guadalupe Bass individual is a certain age.

TL(mm)	Age						
	1	2	3	4	5	6	
75-99	100	0	0	0	0	0	
100-124	33.33	66.67	0	0	0	0	
124-149	25	75	0	0	0	0	
150-174	12.5	62.5	25	0	0	0	
175-199	0	62.5	12.5	25	0	0	
200-224	0	40	40	20	0	0	
225-249	0	40	0	60	0	0	
250-274	0	0	42.86	28.57	14.29	14.29	
275-299	0	0	57.14	28.57	14.29	0	
300-324	0	0	0	66.67	33.33	0	
325-349	0	0	0	44.44	44.44	11.11	
350-374	0	0	0	0	100	0	
375-399	0	0	0	0	0	100	
400+	0	0	0	0	0	100	
Total	9	19	12	18	11	4	73



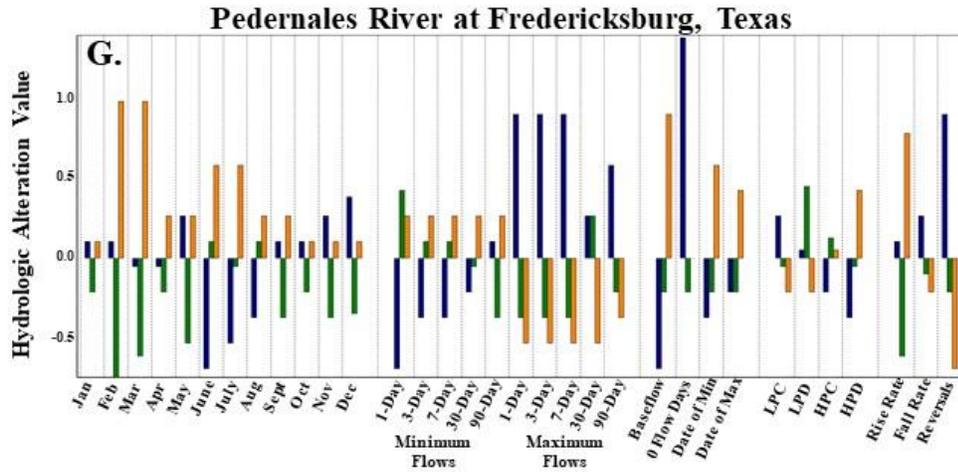
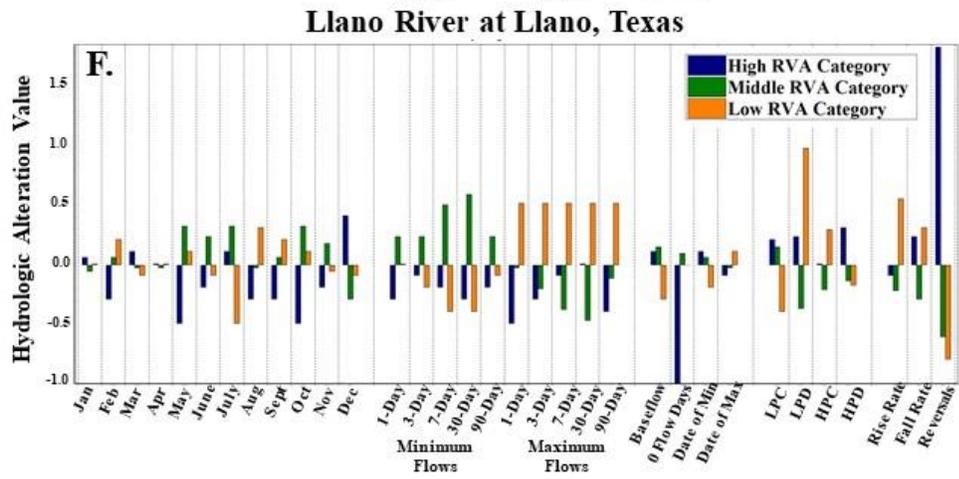
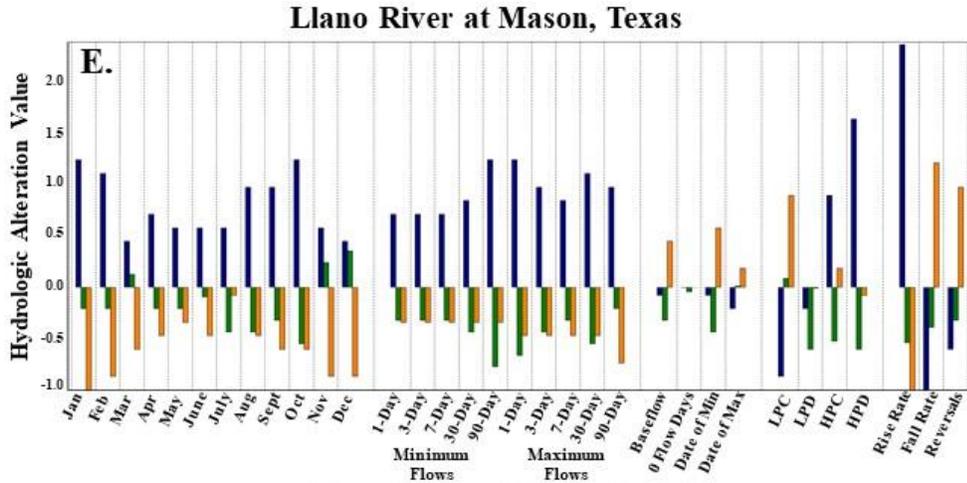
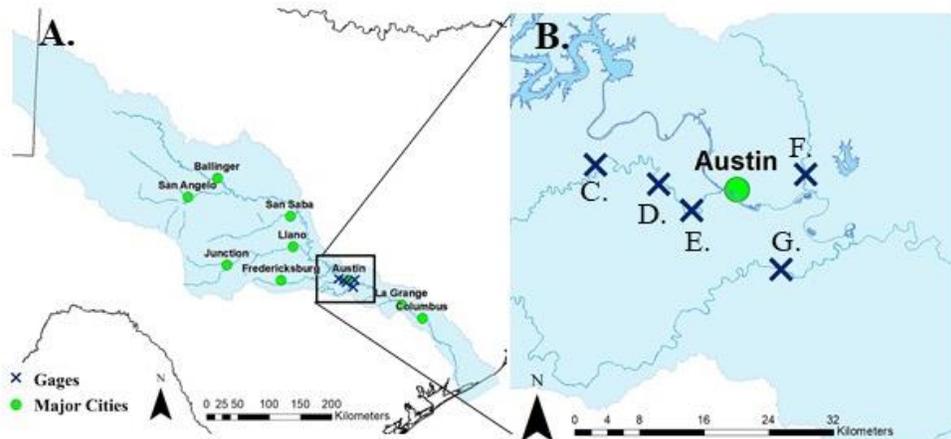
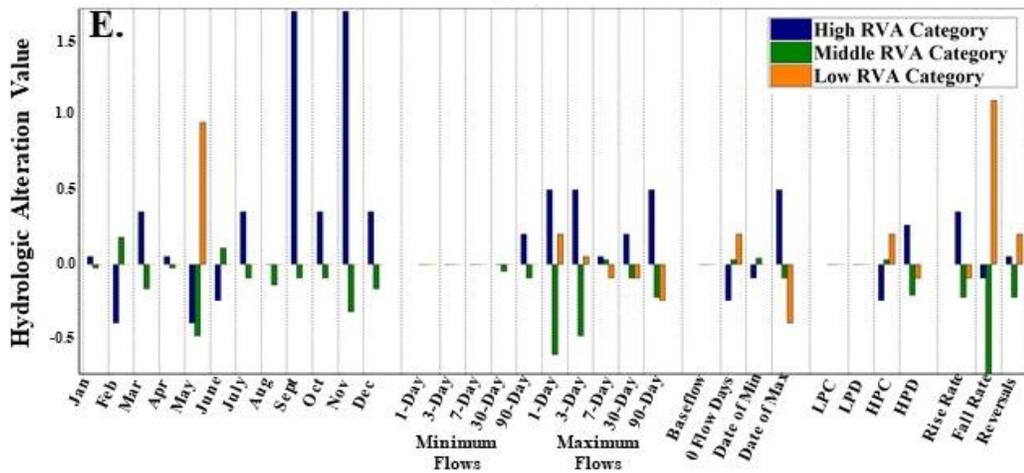


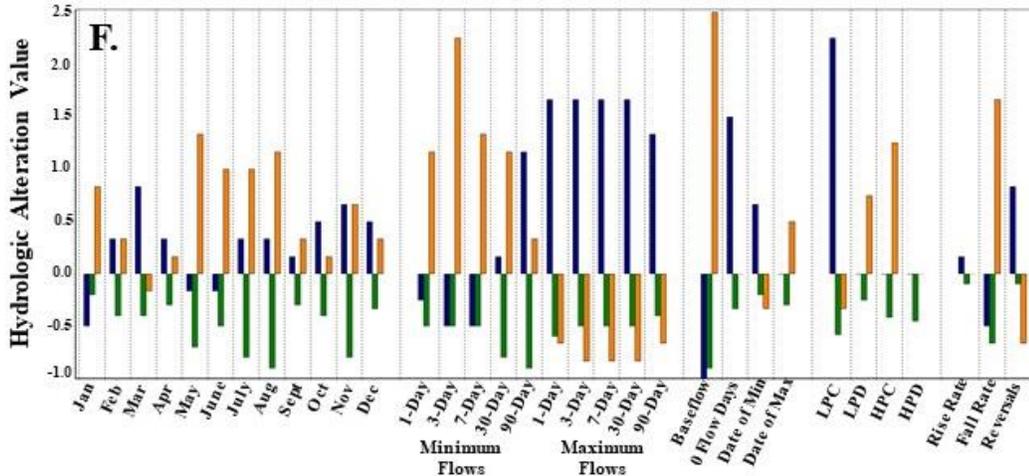
Figure A.1: Map and bar graphs representing hydrologic alteration between pre-1980 and post-1995 for the U.S. Geological Survey (USGS) gaging stations closest to the sampling locations on the Llano River and Pedernales River in Texas with historic and current discharge records. Hydrologic alteration was assessed using the range of variability approach (RVA) as described by Richter et al. (1997). RVA scores have a maximum value of infinity and a minimum value of -1. The 33rd and 67th percentiles are used to determine the three distinct categories (High, Medium, Low). Positive values indicate an increase in the frequency; negative values indicate a decrease in the frequency of the parameter values between the two-time periods within a given category. Map A and B represent the location of the stream gages (Gauges:08148500 North Llano River near Junction, Texas (C),08150000 Llano River Near Junction, Texas (D), 08150700 Llano River near Mason, Texas (E), 08151500 Llano River at Llano, Texas (F), and 08152900 Pedernales River near Fredericksburg, Texas (G)) used to determine the flow conditions an individual Guadalupe Bass experienced.



Barton Creek at Loop 360 in Austin, Texas



Walnut Creek at Webberville Rd. in Austin, Texas



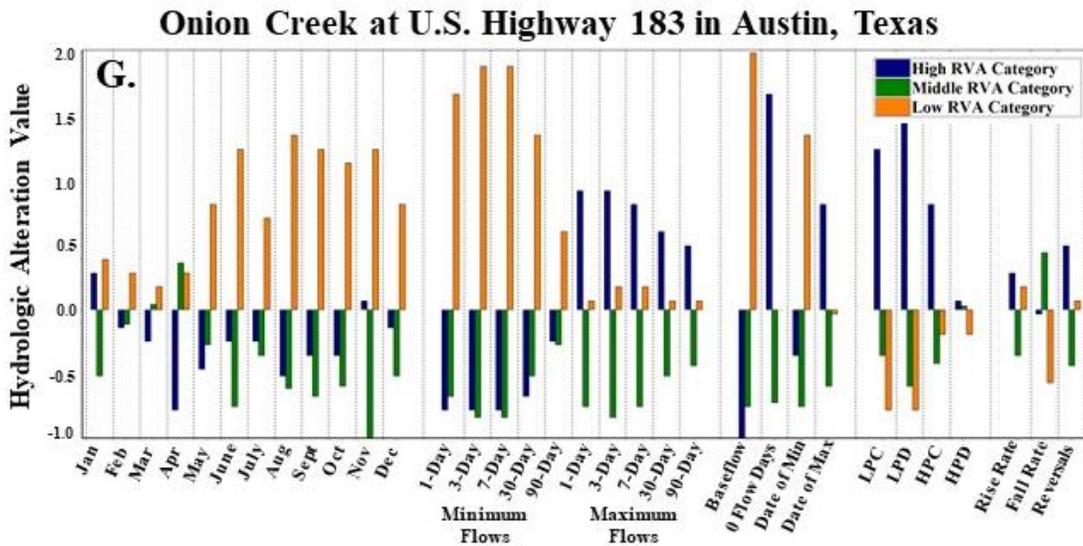
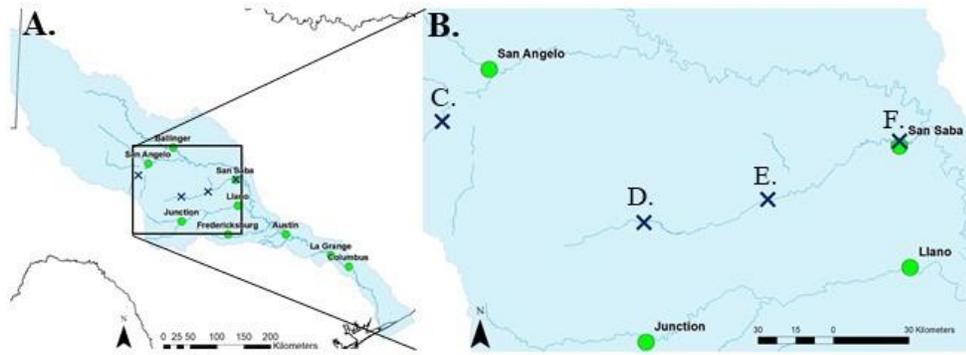
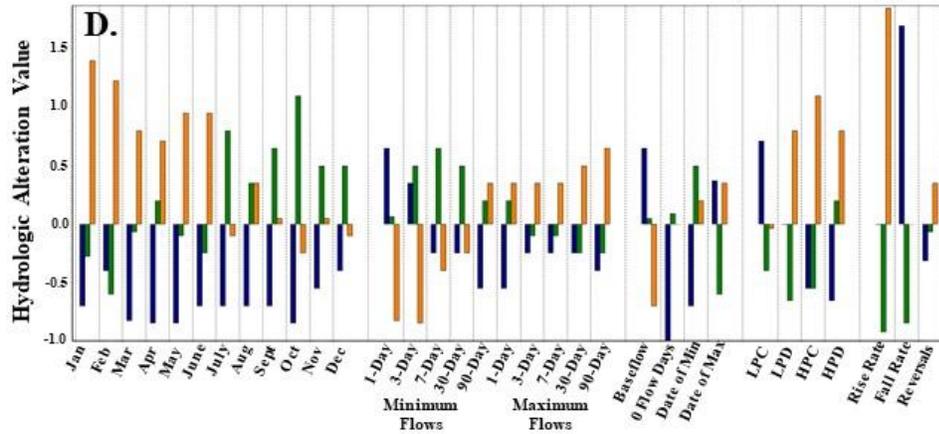


Figure A.2: Map and bar graphs representing hydrologic alteration between pre-1980 and post-1995 for the U.S. Geological Survey (USGS) gaging stations closest to the sampling locations on the Llano River and Pedernales River in Texas with historic and current discharge records. Hydrologic alteration was assessed using the range of variability approach (RVA) as described by Richter et al. (1997). RVA scores have a maximum value of infinity and a minimum value of -1. The 33rd and 67th percentiles are used to determine the three distinct categories (High, Medium, Low). Positive values indicate an increase in the frequency; negative values indicate a decrease in the frequency of the parameter values between the two-time periods within a given category. Map A and B represent the location of the stream gages (Gauges: 08155200 Barton Creek at State Highway 71 near Oak Hill, Texas (C), 08155240 Barton Creek at Lost Creek Boulevard near Austin, Texas (D), 08155300 Barton Creek at Loop 360, Austin, Texas (E), 08159000 Onion Creek at U.S. Highway 183, Austin, Texas (F), 08158600 Walnut Creek at Webberville Road, Austin, Texas (G)) used to determine the flow conditions an individual Guadalupe Bass experienced. Historical discharge records were not sufficient enough to conduct RVA analysis for Barton Creek at Lost Creek or Barton Creek at State Highway 71, therefore RVA analysis is not shown for these gages.



San Saba River at Menard, Texas



San Saba River at San Saba, Texas

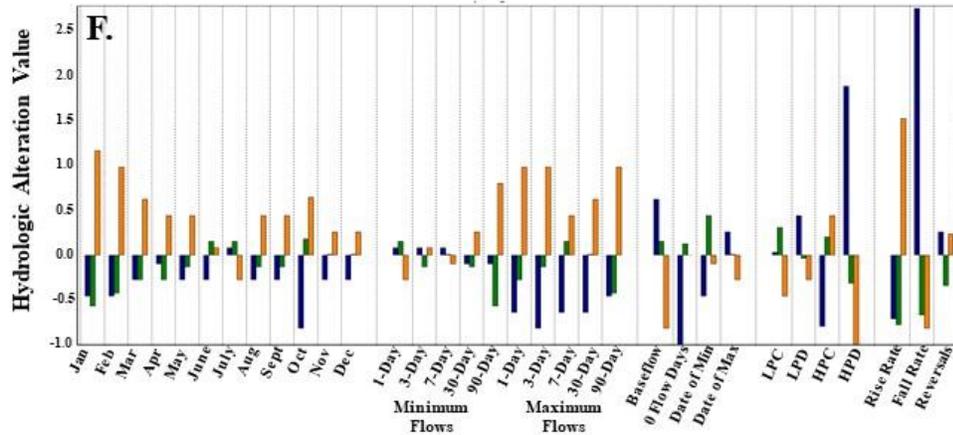
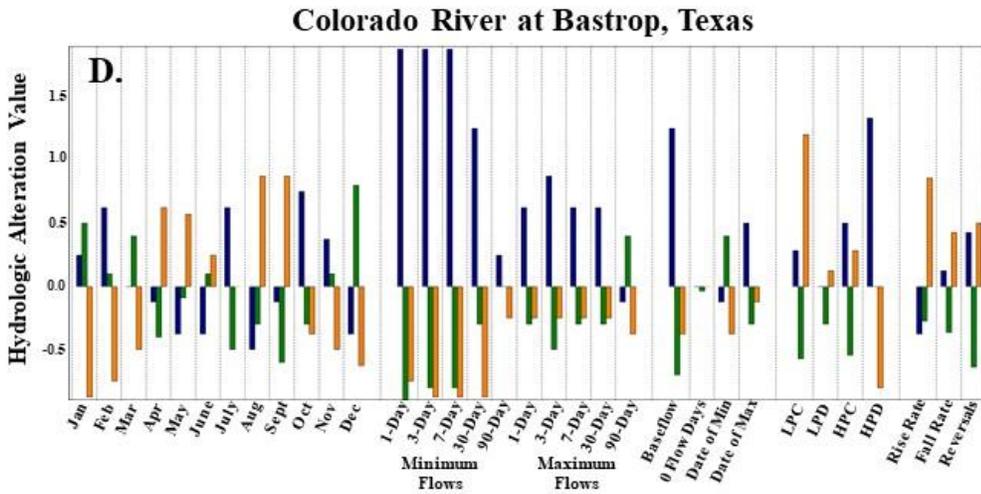
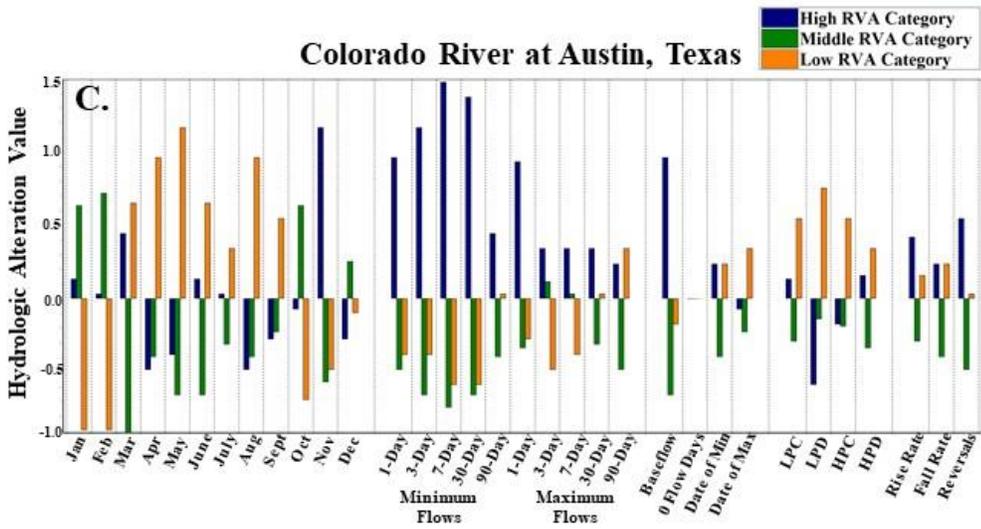
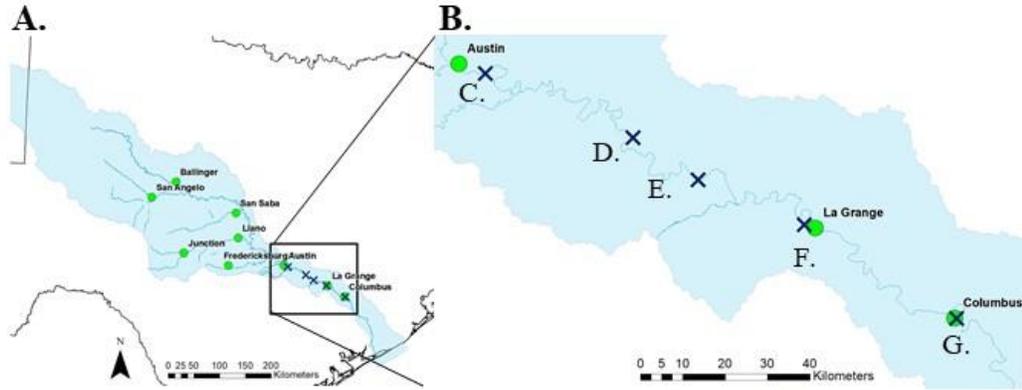


Figure A.3: Map and bar graphs representing hydrologic alteration between pre-1980 and post-1995 for the U.S. Geological Survey (USGS) gaging stations closest to the sampling locations on the San Saba River in Texas with historic and current discharge records. Hydrologic alteration was assessed using the range of variability approach (RVA) as described by Richter et al. (1997). RVA scores have a maximum value of infinity and a minimum value of -1. The 33rd and 67th percentiles are used to determine the three distinct categories (High, Medium, Low). Positive values indicate an increase in the frequency; negative values indicate a decrease in the frequency of the parameter values between the two-time periods within a given category. Map A and B represent the location of the stream gages (Gauges: 08144500 San Saba River at Menard, Texas (C), 08144600 San Saba River near Brady (D), Texas, 08146000 San Saba at San Saba, Texas (E)) used to determine the flow conditions an individual Guadalupe Bass experienced. Historical discharge records were not sufficient enough to conduct RVA analysis for the San Saba River at Brady, Texas, therefore RVA analysis is only shown for the San Saba River at Menard, Texas (C) and for the San Saba River at San Saba, Texas (E).



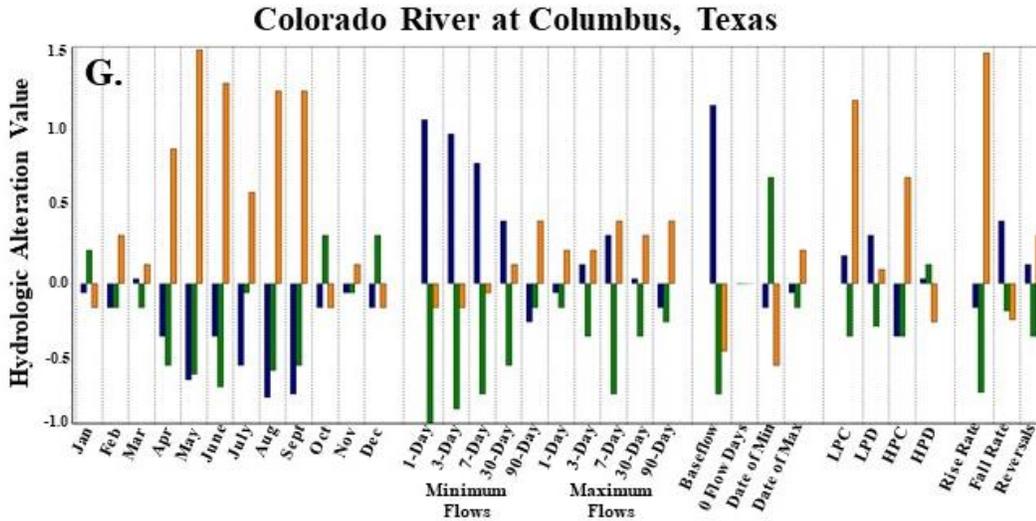
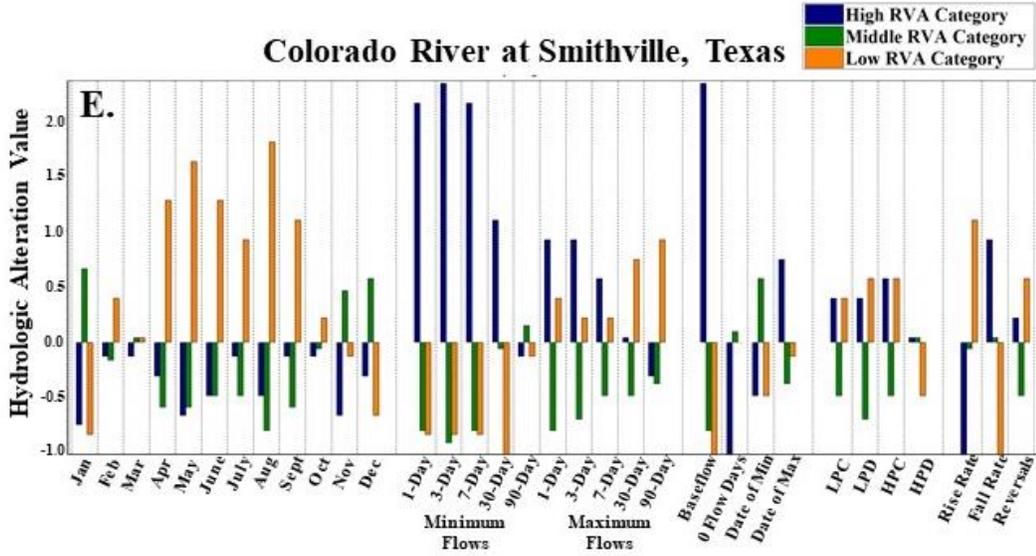


Figure A.4: Map and bar graphs representing hydrologic alteration between pre-1980 and post-1995 for the U.S. Geological Survey (USGS) gaging stations closest to the sampling locations on the lower Colorado River in Texas with historic and current discharge records. Hydrologic alteration was assessed using the range of variability approach (RVA) as described by Richter et al. (1997). RVA scores have a maximum value of infinity and a minimum value of -1. The 33rd and 67th percentiles are used to determine the three distinct categories (High, Medium, Low). Positive values indicate an increase in the frequency; negative values indicate a decrease in the frequency of the parameter values between the two-time periods within a given category. Map A and B represent the location of the stream gages (Gauges:08158000 Colorado River at Austin, Texas (C), 08159200 Colorado River at Bastrop, Texas (D), 8159500 Colorado River at Smithville, Texas (E), 8160400 Colorado River at LaGrange, Texas (F), 8161000 Colorado River at Columbus, Texas (G)) used to determine the flow conditions an individual Guadalupe Bass experienced. Historical discharge records were not sufficient enough to conduct RVA analysis for the Colorado River at La Grange, Texas, therefore RVA analysis is not shown for this gage.

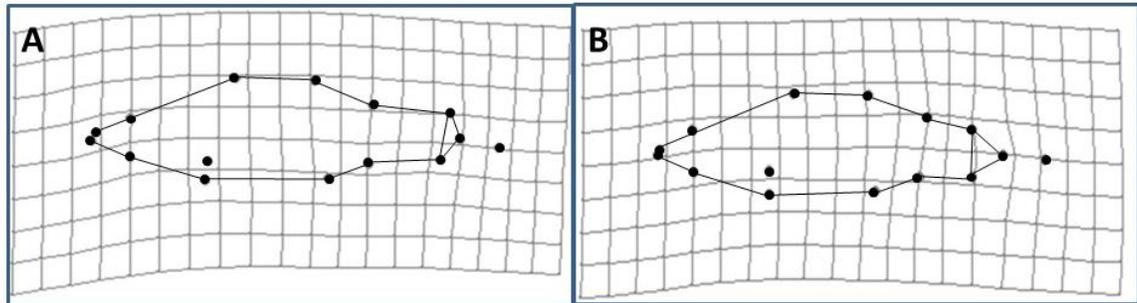


Figure A.5: Thin-plate splines representing morphological variation between the average or consensus shape of Guadalupe Bass initial capture morphology (A) and following 18-month period of preservation in formalin for 23 individual Guadalupe Bass.

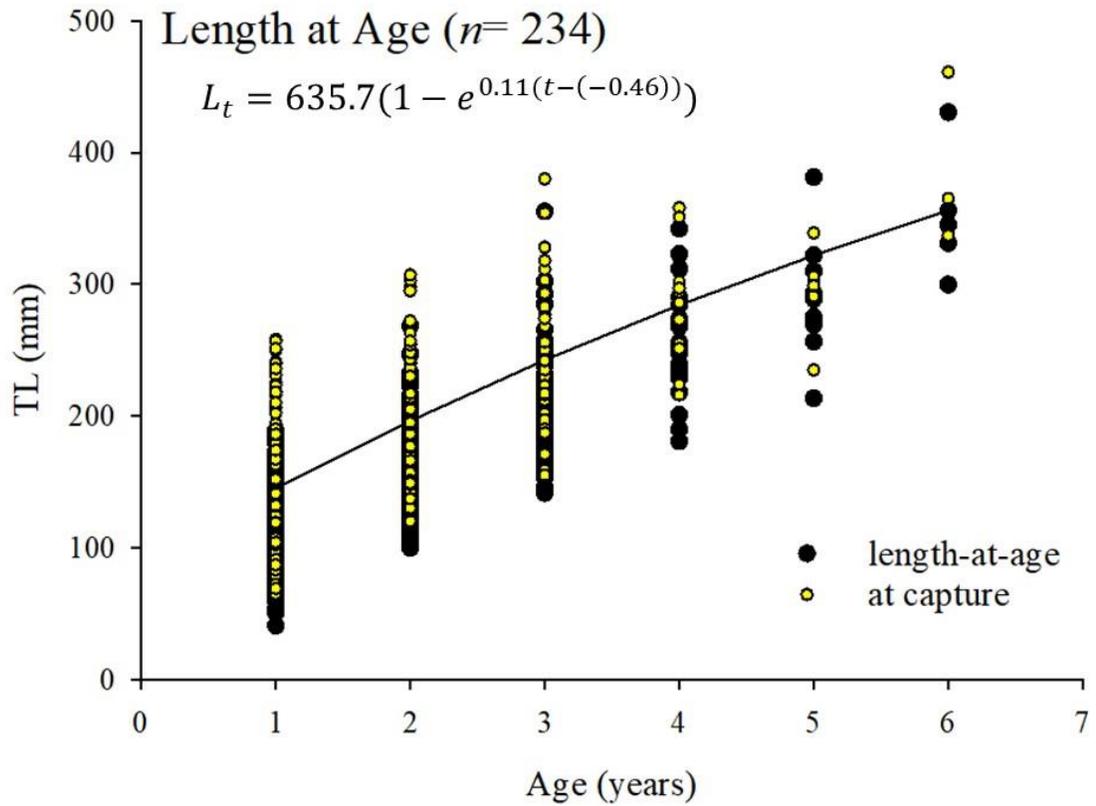


Figure A.6: Von Bertalanffy growth curve based on back-calculated total length at age of Guadalupe Bass ($n=234$) otoliths collected throughout the Colorado River Basin, Texas from March 2014 to August 2015. Back-calculated total lengths (TL) at age are represented by black circles and the total length at initial capture is represented by yellow circles.

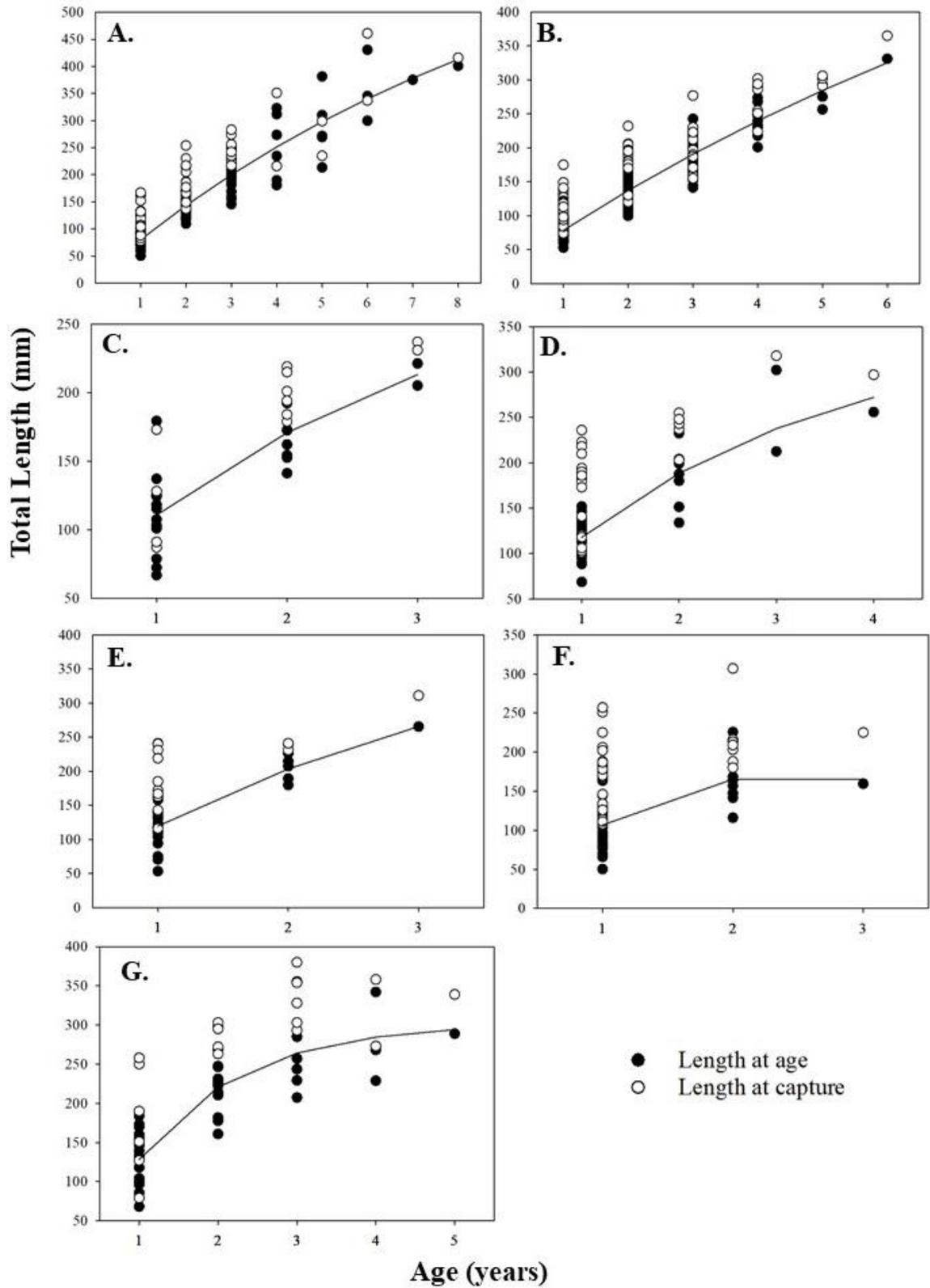


Figure A.7: Von Bertalanffy growth for Guadalupe Bass in the tributaries and mainstem Colorado River basin. Growth curves are based on the back-calculated total length-at-age for Guadalupe Bass collected from March 2014 to August 2015. Tributaries included the South Llano River (A), North Llano River (B), Barton Creek (C), San Saba River (D), Pedernales River (E), and Llano River (F). Guadalupe Bass growth in the mainstem Colorado south of Austin, Texas is shown in Inset G.

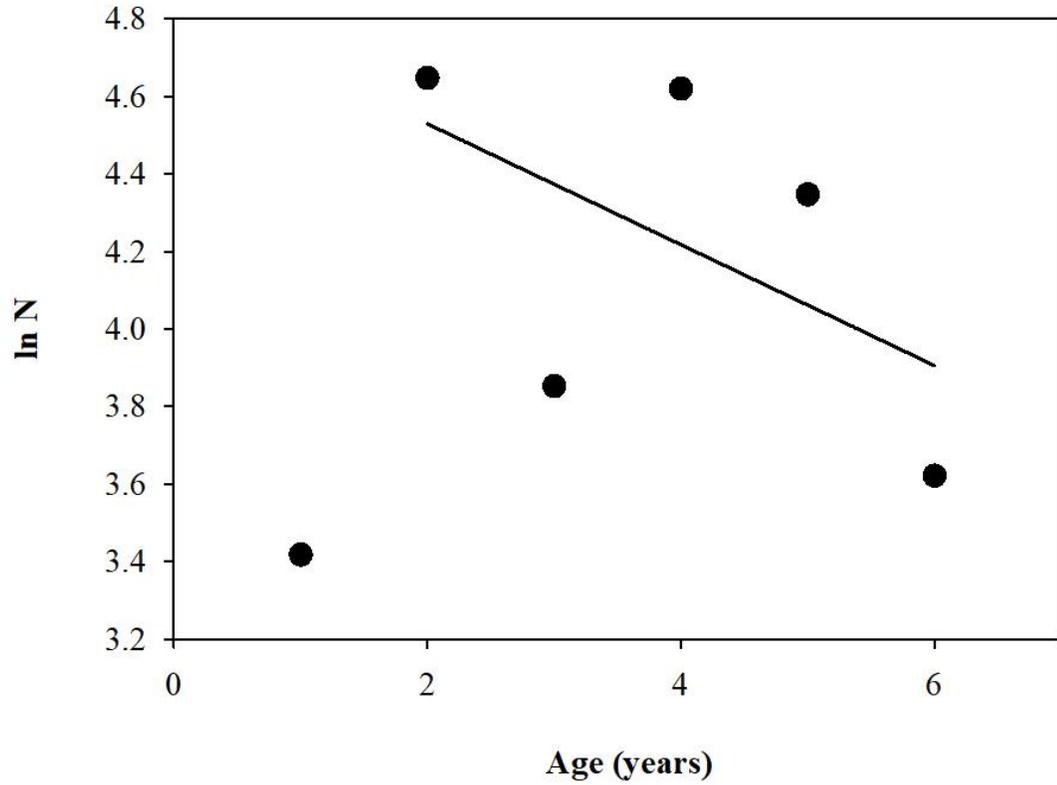


Figure A.8: Catch curve illustration for Guadalupe Bass in the mainstem Colorado River from 2014 to 2016. Instantaneous mortality rate of Guadalupe Bass in the mainstem was 0.34 ± 0.11 ($Z; \pm SE$) with an annual mortality rate of 28.94%.