Articles

Growth and Habitat Use of Guadalupe Bass in the South Llano River, Texas

Jillian R. Groeschel-Taylor, Seiji Miyazono,* Timothy B. Grabowski, and Gary P. Garrett

J.R. Groeschel-Taylor, S. Miyazono
Texas Cooperative Fish and Wildlife Research Unit, Department of Natural Resources Management, Texas Tech University, Lubbock, Texas 79409

Present address of J.R. Groeschel Taylor: Metro Wastewater Reclamation District, Denver, Colorado 80022

Present address of S. Miyazono: Graduate School of Science and Technology for Innovation, Yamaguchi University, Yamaguchi, 755-8611, Japan

T.B. Grabowski
U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, Texas 79409

Present address: U.S. Geological Survey, Hawaii Cooperative Fishery Research Unit, University of Hawaii at Hilo, Hilo, Hawaii 96720

G.P. Garrett
Texas Natural History Collections and Department of Integrative Biology, University of Texas, Austin, Texas 78758

Abstract

Predicting how stream fishes may respond to habitat restoration efforts is difficult, in part because of an incomplete understanding of how basic biological parameters such as growth and ontogenetic habitat shifts interact with flow regime and riverscape ecology. We assessed age-specific Guadalupe Bass *Micropterus treculii* habitat associations at three different spatial scales in the South Llano River, a spring-fed stream on the Edwards Plateau of central Texas, and the influence of habitat and flow regime on growth. We classified substrates using a low-cost side-scan sonar system. We used scale microstructure to determine age and to back-calculate size at age. Over 65% of captured Guadalupe Bass were age 2 or age 3, but individuals ranged from 0 to 7 y of age. Habitat associations overlapped considerably among age classes 1–3+, but age-0 Guadalupe Bass tended to associate with greater proportions of pool and run mesohabitats with submerged aquatic vegetation. Although habitat metrics across multiple scales did not have a large effect on growth, river discharge was negatively correlated with growth rates. Understanding age-specific Guadalupe Bass habitat associations at multiple scales will increase the effectiveness of restoration efforts directed at the species by assisting in determining appropriate ecological requirements of each life-history stage and spatial scales for conservation actions.

Keywords: age-specific habitat use; habitat-specific growth; side-scan sonar habitat mapping

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* Corresponding author: seiji.miyazono@gmail.com

Introduction

Human-induced habitat degradation and alteration of flow regimes have been established as major stressors to the ecological integrity of rivers and streams (Poff et al. 1997; Poff and Zimmerman 2010) as well as major factors driving the decline of freshwater fish diversity in North America (Warren et al. 2000). Stream management depends on a solid understanding of biota–habitat relationships and, as such, specific habitat classifications and associations are critical components of stream science and management. For example, managers often rely on empirical descriptions of habitat use to infer factors that limit the growth, survival, and abundance of a species (Hawkins et al. 1993). The quantification of habitat as well as a species' associations with that habitat at different ontogenetic stages provides a basis for predicting response to changes in habitat availability. Both the quality and quantity of available habitat affect the structure and composition of resident biological communities and populations (Meffe and Sheldon 1988; Calow and Petts 1994; Maddock 1999). In addition, the species–habitat associations in lotic systems could vary with spatial scales (Cheek et al. 2016). Therefore, understanding age-specific habitat associations at multiple spatial scales may help predict how a species will respond to disturbance or degradation and assist in determining appropriate ecological requirements for each life-history stages and spatial scales for conservation actions.

The official Texas state freshwater fish, Guadalupe Bass *Micropterus treculii*, is endemic to the streams and rivers of the northern and eastern Edwards Plateau in central Texas, including portions of the Brazos, Colorado, Guadalupe, and San Antonio basins as well as portions of the lower Colorado River off the Edwards Plateau downstream of Austin (Koppelman and Garrett 2002; Hubbs et al. 2008). It is currently listed as a species of greatest conservation need by the state of Texas because of the chronic threats posed by hydrological alteration and habitat degradation (Birdsong et al. 2015), and the acute threat of introgression with introduced Smallmouth Bass *Micropterus dolomieu* (Edwards 1979; Whitmore and Butler 1982; Whitmore 1983; Bean et al. 2013).

Although the hybridization threats are managed through stocking and opportunistic removal of hybrids during droughts (Fleming et al. 2015), Guadalupe Bass face a more chronic and persistent threat in that the entirety of their range overlaps or is immediately upstream of some of the fastest-growing urban areas in Texas (Murdock et al. 2002). Habitat loss and degradation and decreased stream flow due to changing land-use patterns and increased water demands are thought to have contributed to declines in abundance and local extirpations (Hurst et al. 1975; Edwards 1979, 1980; Garrett et al.2015). However, detailed data on the relationship between Guadalupe Bass and their habitat at multiple spatial scales are lacking. In particular, the habitat associations of juveniles are poorly understood (Edwards 1980; Perkin et al. 2010). In addition, detailed description of growth rates of wild Guadalupe Bass and the relationships with flow regimes are limited.

Conservation efforts specifically dedicated to restoring habitat for Guadalupe Bass are currently underway in the South Llano River, located on the Edwards Plateau in central Texas (Birdsong et al. 2015). For example, the Texas Guadalupe Bass Restoration Initiative implemented by Texas Parks and Wildlife in 2010 is a conservation effort committed to conserving Guadalupe Bass populations by involving willing landowners in landscape conservation activities at watershed scales. These types of activities include reducing or eliminating actions that degrade riparian systems and water quality, reduce water quantity, favor nonnative species, and fragment the river (Birdsong et al. 2015; Garrett et al. 2015). However, there are no studies evaluating the effectiveness of the conservation efforts in the region. Understanding the factors controlling the habitat use and growth of Guadalupe Bass populations in the region is important to help to evaluate which conservation efforts are effective.

On the basis of these research gaps, the objectives of this study were to examine the influence of discharge on Guadalupe Bass growth rates and to determine age-specific habitat associations at three different spatial scales. The working hypotheses are 1) the Guadalupe Bass growth rates could be influenced by the amount and variability of the river discharge, 2) the habitat use could vary among the age classes, and 3) the age-specific habitat associations could change with spatial scales. Results of this work will help to develop conservation and management strategies (e.g., prioritizing conservation areas, developing flow recommendation, etc.) for Guadalupe Bass throughout their geographic distribution.

Materials and Methods

Study area

The South Llano River is a second-order, spring-fed stream located on the Edwards Plateau within the Colorado River Basin, approximately 200 km west of San Antonio (Figure 1). It is approximately 175 km in length, but only the lower 53 km maintains year-round discharge because of the numerous springs that supply water to this portion of the river (Groeschel 2013). The remainder of the river is ephemeral, and contains flowing water only after heavy precipitation events (Groeschel 2013). Aquatic systems on the Edwards Plateau, such as the South Llano River, exhibit high levels of biodiversity and endemism (Conner and Suttkus 1986; Abell et al. 2000; Hubbs et al. 2008), but also face numerous threats that are ultimately related to the rapidly increasing human population of central Texas (Bowles and Arsuffi 1993). The changes in land use and increased demand for water associated with this rapidly increasing urban population is expected to result in altered water quality and quantity for the aquatic systems of central Texas (Bowles and Arsuffi 1993; O'Driscoll et al. 2010; Aitkenhead-Peterson et al. 2011).

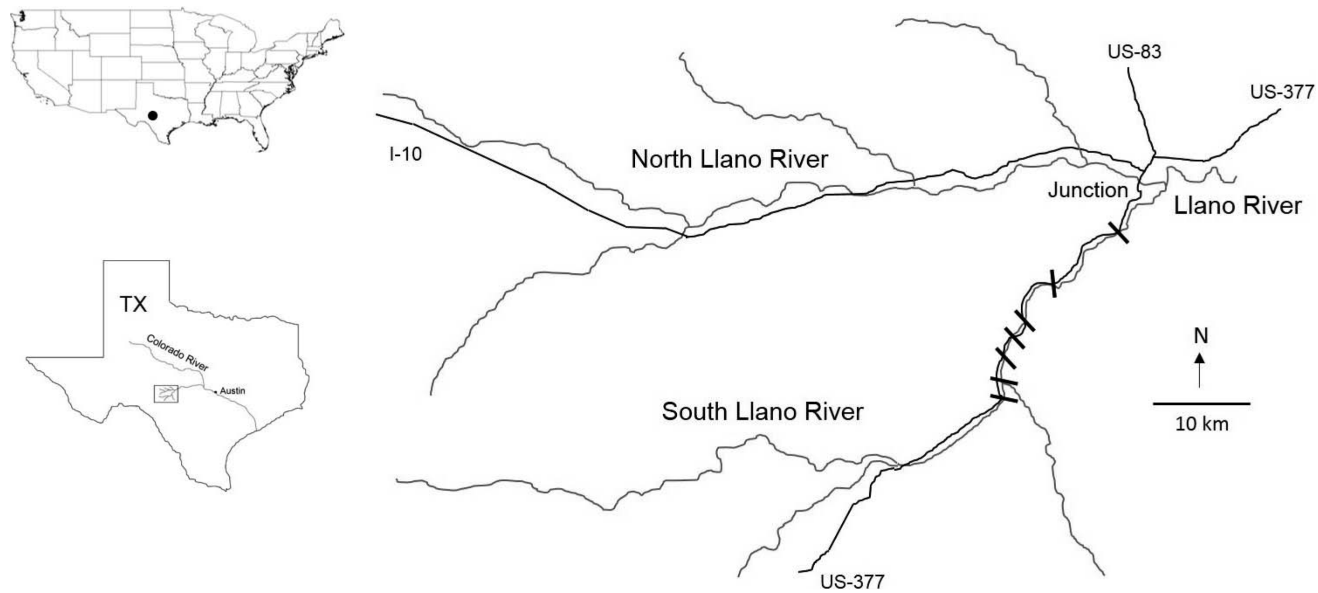

Figure 1. Map of the South Llano River study area in Kimble and Edwards counties, Texas in 2012. Road crossings and other barriers are indicated by lines crossing the river. The upper limit of the study area was approximately 1.5 km upstream of upstream-most barrier. Inset map shows location of the study area within Texas.

For example, changed land and water use along the increasing urban population may cause agricultural and municipal water supply diversions, irrigation and treated sewage effluent return flows, and changes in runoff dynamics associated with impervious surfaces (Pease et al. 2017). In addition, overgrazing and other land-use practices on some properties bordering the river have resulted in erosional banks and the potential for elevated sediment loads and altered channel morphology (Edwards et al. 2004). Because the aquatic faunas have high endemism in this region, these human activities may cause species extinctions. However, at present the South Llano River is considered to be a relatively pristine river with minimal human disturbance because of its relatively unaltered hydrological regime, good water quality, and diverse benthic macroinvertebrate and fish assemblages that are representative of the Edwards Plateau (Bayer et al. 1992; Broad et al. 2016; Cheek et al. 2016).

Age and growth

We captured Guadalupe Bass using a combination of angling, electrofishing, and seining during the spring, summer, and fall of 2012 (Table S1, *Supplemental Material*). We conducted angling along the entire river corridor, haphazardly from sunrise to sunset on the following dates in 2012: 21 April; 20, 28, 30 May; 25 June; 3 July; 4, 31 August; 14, 15, 16 September; 18 October. We conducted electrofishing with pulsed direct-current power at 120 pulses s^{-1} (Hz), with voltage and pulse width adjusted to maintain an output of approximately 4 A along 50-m transects. Electrofishing occurred from the northeast Hwy. 377 road crossing to the bridge at County Road 150 on 15 October 2012, and from the South Llano River State Park to the Flatrock Lane road crossing on 9, 10, and 20 November 2012. We surveyed fishes seasonally using a $3.96 \times 1.22 \times 2.00$ m bag seine with a 0.5-cm mesh pulled along a $\leq$ 25-m transect. We conducted seining at random locations from approximately 165 m upstream from the waterfall (30°18′30.44″N, 99°54′30.48″W) to the east edge of the South Llano River State Park property (30°27′11.84″N, 99°47′38.46″W) on 21–23 June 2012, 3 July 2012, 30 July 2012, 13–15 October 2012, and 17, 18 October 2012. We recorded capture locations using a wide-area augmentation system-enabled handheld global positioning system (GPS) unit (GPSMAP 78sc; Garmin International, Inc., Olathe, KS) with an accuracy of 3–5 m. We recorded capture locations of Guadalupe Bass caught by angling at the location of the angler and not directly where the bass was caught.

After capturing the fish, we measured individuals to the nearest millimeter total length (mm TL), and removed some scales and stored them dry in envelopes. We took a fin clip and stored it in 95% ethanol and later genotyped it following the protocols described by Lutz-Carrillo et al. (2006) to ensure that we used no Guadalupe Bass $\times$ Smallmouth Bass hybrids in our analyses. We released all captured Guadalupe Bass alive. Of the 291 Guadalupe Bass used for the age and growth analysis, we used a haphazard sample of 142 individuals stratified by age classes (age 1 through age 7) for genetic analysis. On the basis of small sample sizes, we used all fin clips from ages 1, 5, 6, and 7. We grouped together ages 2, 3, and 4 and randomly selected fin clips. We completed total genomic deoxyribonucleic acid (DNA) isolation and polymerase chain reactions at the Fish Health and Genetics Laboratory located at the A.E. Wood Fish Hatchery in San Marcos, Texas.

We prepared scales for reading by compressing them between two glass slides and placing them in a petri dish of water. We captured digital images of each scale using a compound microscope equipped with a camera (Olympus SZX16, Infinity 1, Olympus, Tokyo, Japan) and analyzed them using ImageJ (Abramoff et al. 2004) following descriptions for interpreting scale microstructure by DeVries and Frie (1996). We back-calculated TL at age for each annulus and corrected it (the size at scale formation above the pectoral fin, 26 mm TL, for Smallmouth Bass) using the direct proportion method (Everhart 1949; DeVries and Frie 1996). We aged all Guadalupe Bass assuming a birthdate of 1 January. We used second readers to assess the reliability of the age estimates from the first reader. We used a third reader to resolve disagreements between the first and second readers. If we determined no agreed-upon age from a scale, we did not include that scale in the data analysis ($n = 31$).

Although scales have been commonly used for estimating the age and growth of other *Micropterus* spp. (Carlander 1977; Maraldo and MacCrimmon 1979; Gaeta et al. 2011), scales tend to underestimate age in older fishes (Maceina and Sammons 2006; Sylvester and Berry 2006; Taylor and Weyl 2012). However, being able to release captured individuals alive was an important consideration in this study because of the conservation status of Guadalupe Bass and a concurrent population estimation study being conducted in the South Llano River. Currently specific references on age estimation accuracy for Guadalupe Bass do not exist. However, Largemouth Bass *Micropterus salmoides* ages estimated from scales and otoliths tend to be consistent for the first 6–8 y of life (Maraldo and MacCrimmon 1979; Maceina and Sammons 2006). Pease et al. (2017) did not report Guadalupe Bass older than age 8 from examination of the sagittal otoliths of 271 individuals collected from throughout the Colorado River Basin in central Texas).

Habitat mapping

We conducted side-scan sonar surveys in October 2011 and June 2012. We used the protocols described by Kaeser and Litts (2010) and Kaeser et al. (2012) to map instream habitats. Briefly, we used a Humminbird 998c SI side-scan sonar unit (Humminbird, Eufaula, AL) with the transducer mounted off the starboard bow of a canoe to capture georeferenced images of the river bottom substrate. We connected a wide-area augmentation system-enabled handheld GPS unit (Garmin) directly to the control head for generating a track plot of the course of the canoe during the survey. We set the handheld GPS to record a point at 3-s intervals and placed it near the transducer to ensure maximum accuracy, as recommended by Kaeser and Litts (2010).

We cropped the collected images with IrfanView v. 4.30 (Irfan Skiljan, Wiener Neustadt, Austria), imported into ArcGIS 10.0 (ESRI, Redland, CA) to form mosaics, or sonar image maps. We used georeferenced aerial images (96×96 dots per inch, 1 m^2 per pixel) of the study site collected by unmanned aerial vehicle flyovers in November 2011 to assist in creating the instream habitat map (Cheek et al. 2016). On each mosaic, we delineated substrate classes (Kaeser and Litts, 2010; Kaeser et al. 2012) and subclasses (Barnhardt et al. 1998) from resulting sonar imagery in ArcMap 10 (ESRI) on the basis of dominant ($> 50\%$) and subordinate ($< 50\%$) substrate types within a given area. Additionally, we identified instream structures $\geq$ 100 cm in length (e.g., boulders and large woody debris) and assigned them to separate classes. We delineated mesohabitat types (i.e., runs, riffles, and pools) from a combination of aerial images and side-scan sonar-generated depth profiles.

To complement and verify the side-scan sonar mosaic, we performed ground truthing at a total of 349 randomly selected sites. In shallow areas ($<$ 1 m) or areas with minimal turbidity, we either did sampling by hand to feel the bottom substrate, or we observed the bottom by sight. In turbid or deep areas, we used an underwater camera (Navroute Technologies, Miami, FL) to observe the substrate. We measured a subset (25%) of the large specific structures (i.e., large woody debris and boulders) to further ensure map scale accuracy. In addition, we calculated an accuracy rate (no. of incorrectly assigned points/total number of sites selected and sampled).

South Llano River discharge

The North and South Llano rivers are the only tributaries that contribute to the discharge measured at the Llano River gauge. However, stream gauge data were not available from the South Llano River before 16 May 2012. Therefore, we estimated discharge from 1915 through 2012 by obtaining gauge data from the North Llano River (U.S. Geological Survey gauge 08148500) and subtracting them from the data from the Llano River (U.S. Geological Survey gauge 08150000; approximately 4.5 km downstream of the confluence of the North and South Llano rivers). We then used these to calculate Q_{90}, Q_{low}, Q_{normal}, Q_{high}, and Q_{10} quantiles and the proportion of observations falling within each quantile annually. We defined Q_{low} as the discharge rates between the 75th and 90th percentiles of the total discharge observations for the South Llano River. We classified flows between the 25th and 75th percentiles as Q_{normal}, whereas we classified Q_{high} flows as those between the 10th and 25th percentile.

Data analyses

We fitted a von Bertalanffy growth curve, $L_t = L_\infty (1 - e^{-k(t-t0)})$, where L_t = length at time t (age), L_∞ = asymptotic length, k is a growth coefficient, and t_0 is a time coefficient where length would theoretically be zero (Ogle 2016), to both the length at age and mean back-calculated TL at age data separately using PROC NLIN in SAS 9.4 (SAS Institute, Cary, NC). We set the value of L_∞ at 432 mm TL, the reported TL of the world-record

Table 1. Most informative habitat variables selected from the discriminant function analysis that best discriminated among age classes (age 0, age 1, age 2, age 3+) of Guadalupe Bass *Micropterus treculii* captured in the South Llano River, Texas from April to November 2012. Bolded values indicate the most correlated variables for that axis.

Variable	Description	Axis 1	Axis 2
Channel unit buffer			
Riff GRsa P:A	Riffle gravel–sand habitat perimeter area ratio	**0.61**	0.17
Run GRco TE	Run gravel–cobble habitat total edge	**0.68**	0.03
Pool Bldr P:A	Pool boulder habitat perimeter area ratio	−0.06	**0.75**
Pool BR TE	Pool bedrock habitat total edge	**−0.77**	0.54
Riff SAV TE	Riffle submerged aquatic vegetation habitat total edge	**−0.65**	−0.06
Riff Bldr TE	Riffle boulder habitat total edge	−0.57	−0.30
Pool Bldr TE	Pool boulder habitat total edge	−0.50	−0.33
Riff GRco P:A	Riffle gravel–cobble habitat perimeter area ratio	−0.49	−0.30
250-m buffer			
%Riff BR	Percentage of riffle bedrock habitat	−0.57	−0.36
Run GRsa P:A	Run gravel–sand habitat perimeter area ratio	**−0.60**	−0.36
Run SAV TE	Total edge of submerged aquatic vegetation habitat in a run	**−0.67**	0.27
Run GRsa TE	Run gravel–sand habitat total edge	−0.31	**1.24**
Pool BR Contig	Pool bedrock habitat contiguity	0.18	**0.60**
Run LWD Contig	Run large woody debris habitat contiguity	0.44	0.17
% Rocky–fine	Percentage of rocky–fine substrate	**0.80**	−0.09
Pool Bldr Contig	Pool boulder habitat contiguity	0.35	−0.30
Run COgr TE	Run cobble–gravel habitat total edge	0.42	−0.44
50-m buffer			
% Pool	Percentageof pool mesohabitat	**1.57**	0.22
Run SAV Prop	Proportion of run submerged aquatic vegetation habitat	**1.45**	0.14
Pool Bldr Contig	Pool boulder habitat contiguity	−0.55	−0.21
% BR	Percentage of bedrock substrate	**−0.86**	−0.21
Run SAV TE	Run submerged aquatic vegetation habitat total edge	**−1.08**	−0.20
Run COgr P:A	Run cobble–gravel habitat perimeter area ratio	−0.50	0.39
% LWD	Percentage of large woody debris structures	−0.30	**0.77**

Guadalupe Bass recently captured from the main-stem Colorado River downstream of Austin, Texas (Texas Parks and Wildlife News 2014), because of the model failing to converge on realistic values of L_∞ when fitting the von Bertalanffy growth curves. We calculated the residuals from the mean back-calculated length-at-age growth curve across the growth history of each individual (Grabowski et al. 2012). We used the residuals to know whether an individual Guadalupe Bass reached a larger/smaller size at age than predicted size at age by the von Bertalanffy growth model (Grabowski et al. 2012). We classified discharge into quantiles, and we calculated the proportion of annual observations within each flow quantile for each year. We assessed the effects of the principal components of hydrological attributes as well as the South Llano River discharge quantiles on the residuals from the back-calculated length-at-age growth curve using a mixed linear model, with the flow quantiles as fixed effects, back-calculated age as a random effect, and individual Guadalupe Bass as a subject effect.

We assessed the habitat associated with captured Guadalupe Bass at three spatial scales: a fine scale within a 50-m radius surrounding the capture location, an intermediate scale within a 250-m radius surrounding the capture location, and a coarse scale of the stream unit in which the bass was caught, for example if we caught a bass in a riffle mesohabitat, we defined the stream unit area associated with that bass from its capture location to the adjacent upstream and downstream riffles. We selected these scales on the basis of the results of telemetry studies conducted on Guadalupe Bass movement, suggesting that most individuals were sedentary, moving on average $<$ 60 m over the course of a year (Perkin et al. 2010). We created the 50-m and 250-m scales using the circle buffer tool in ArcGIS 10.0, whereas we created the stream unit scale by using digitized lines. We then converted these scales to polygons and merged them with the underlying mesohabitat and substrate-type polygons. Once merged, we converted the scales to raster data sets and imported them into FRAGSTATS 4.1 (McGarigal et al. 2012). We used FRAGSTATS to compute patch and class metrics of the habitat types within each scale associated with each Guadalupe Bass (Table 1).

We used discriminant function analysis to assess age class-specific habitat associations at these three scales performed using PROC DISCRIM in SAS 9.4 (SAS Institute) as described by McGarigal et al. (2000). We grouped age-3 and older fish together into a single age class because of low sample sizes of older individuals and because these individuals were all likely to be sexually mature (Edwards 1980). We chose the habitat variables for the discriminant function analysis that best discriminated among age classes (ages 0, 1, 2, 3+) of Guadalupe Bass using a stepwise selection procedure (PROC STEPDISC) implemented in SAS 9.4 (SAS Institute). We assessed the effect of habitat type on Guadalupe Bass growth rates using analysis of covariance with habitat type as a covariate and age as the independent variable. We used

Table 2. Mean (± SE) back-calculated total length (TL) at each scale annulus of Guadalupe Bass *Micropterus treculii* from the South Llano River, Texas captured during April–November 2012.

Age class	Year class	*n*	TL (mm) at capture		Back-calculated TL (mm) at age						
			Mean	Range	1	2	3	4	5	6	7
0	2012	79	56 ± 2	35–91							
I	2011	14	107 ± 8	69–171	85 ± 6						
II	2010	55	167 ± 4	106–211	78 ± 3	138 ± 3					
III	2009	79	216 ± 3	152–293	81 ± 2	142 ± 3	188 ± 3				
IV	2008	49	244 ± 4	200–310	88 ± 4	137 ± 4	184 ± 4	220 ± 4			
V	2007	11	294 ± 8	248–330	99 ± 8	160 ± 5	204 ± 78	240 ± 10	271 ± 9		
VI	2006	1	341	—	133	183	231	271	296	318	
VII	2005	3	365 ± 19	333–397	130 ± 13	180 ± 13	227 ± 14	256 ± 14	289 ± 17	321 ± 13	344 ± 14
Mean TL (mm) at age					84 ± 2	142 ± 2	189 ± 2	226 ± 4	276 ± 7	320 ± 10	344 ± 14
Mean annual growth (mm)					84 ± 2	58 ± 1	46 ± 1	35 ± 1	30 ± 2	30 ± 4	23 ± 5

only individuals less than age 6 in the analysis because of the small sample sizes of age-6 ($n = 1$) and age-7 ($n = 3$) bass. We analyzed only growth rates from the most recent year, 2012, to avoid assuming that Guadalupe Bass remain in their location of capture throughout their entire lives. We did this analysis by assessing instream habitat at the three different spatial scales.

We assessed all parametric assumptions of normality and independence, and made transformations as appropriate; in particular, many of the habitat variables generated by FRAGSTATS needed to undergo a square-root transformation to approximate a normal distribution. We performed all statistical analyses using SAS 9.4 (SAS Institute). We used a significance level of $\alpha = 0.05$ for all hypothesis tests and the Holm–Bonferroni method (Holm 1979) to correct for multiple comparisons.

Results

We used scales from 291 Guadalupe Bass for age and growth analysis. We detected eight hybrids from the sample of 142 Guadalupe Bass, or a hybridization rate of 5.6%. Age-0 and age-3 bass constituted approximately 54% of captured Guadalupe Bass; however, we encountered individuals as old as 7 (Table 2). The von Bertalanffy growth curve fitted to the back-calculated length-at-age data for Guadalupe Bass yielded parameter estimates (± SE) for $k = 0.20 \pm 0.01$ and $t_0 = -0.04 \pm 0.09$ that were not appreciably different from the curve fitted to the length-at-capture data ($k = 0.20 \pm 0.01$; $t_0 = -0.46 \pm 0.14$; Figure 2). Individuals tend to reach approximately 84 mm TL by age 1, with growth decreasing to about 60 mm per year from age 1 to age 2 (Table 2).

At the stream unit scale, age-0 Guadalupe Bass tended to be associated with an increase in the size of gravel substrate habitat patches in runs (Figure 3a; Table S2, *Supplemental Material*). Both age-1 individuals and older fish were associated with the availability of edge habitats along patches of boulders and submerged aquatic vegetation in riffles at the stream unit scale. Age-1 fish were also associated with patches of boulder habitats with relatively high perimeter-to-area ratios, suggestive of larger numbers of smaller boulders (Figure 3a). The association with larger patches of gravel in runs was also evident at the 250-m spatial scale, but age-0 individuals also exhibited an association with an increase in edge habitat adjacent to submerged aquatic vegetation in runs and the availability of bedrock habitat in riffles (Figure 3b). At the 250-m spatial scale, Guadalupe Bass ages 1–3+ y were associated with areas of greater contiguity of large woody debris and boulders in runs and pools as well as relatively higher proportions of rocky–fine substrates. However, the amount of edge habitat associated with gravel–sand patches in runs was also important to age-1 individuals (Figure 3b; Table S3, *Supplemental Material*). At the 50-m spatial scale, the proportion of pool habitat and submerged aquatic vegetation in runs were most closely associated with age-0 individuals (Figure 3c; Table S4, *Supplemental Material*). At the 50-m spatial scale, there was no appreciable difference between individuals ages 1, 2, and 3+ y, as all three groups were associated with the availability of edge habitat along patches of submerged

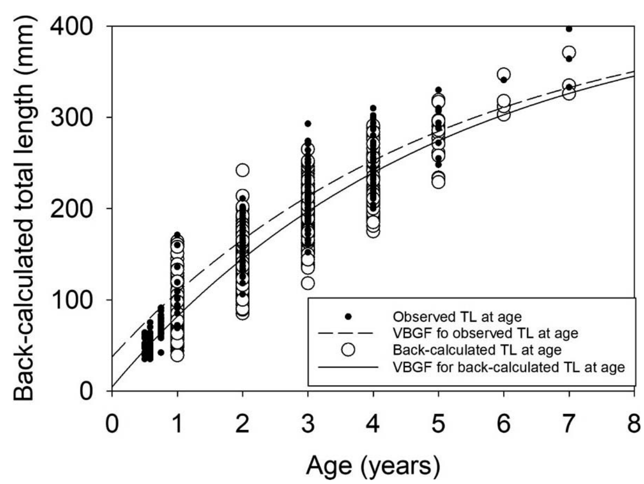

Figure 2. The von Bertalanffy growth curve fitted to observed and back-calculated lengths at age of Guadalupe Bass *Micropterus treculii* captured from the South Llano River, Texas during April–November 2012.

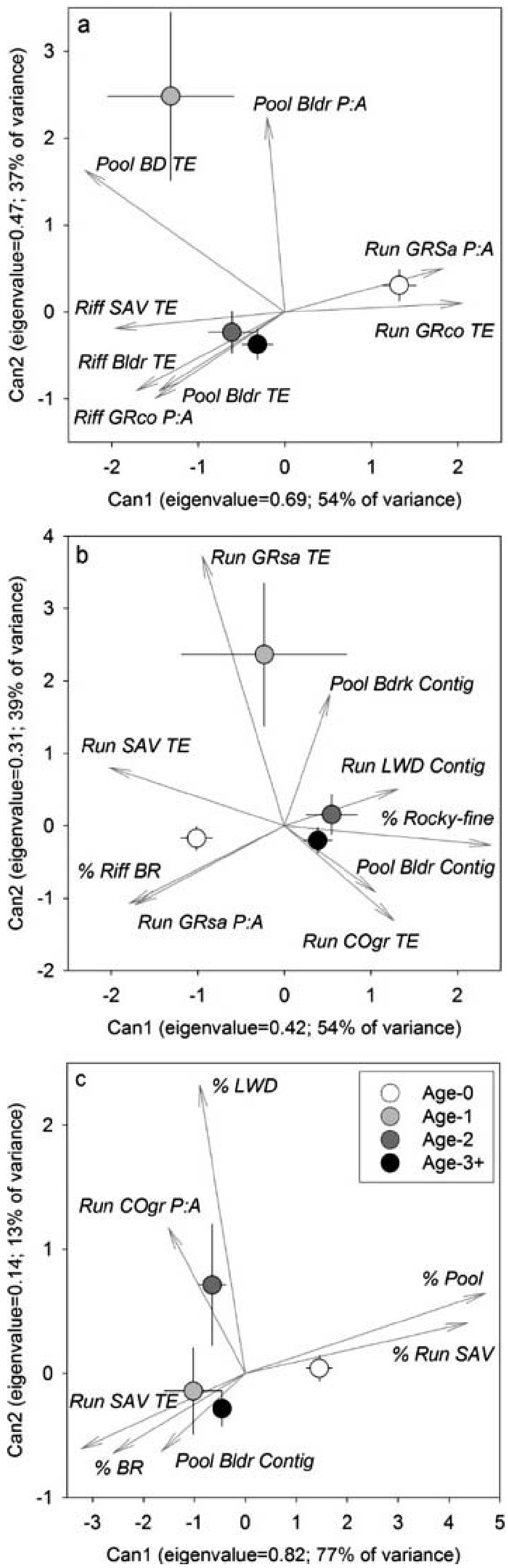

Figure 3. Discriminant function analysis biplots of age-specific habitat associations of Guadalupe Bass *Micropterus treculii* at three different spatial scales in the South Llano River, Texas during April–November 2012. The stream unit scale, that is, the riffle–run–pool complex from which the individual was captured, is presented (**a**), whereas the characteristics of the river in a 250-m (**b**) and 50-m (**c**) buffer around the capture location of the fish are presented in the remaining panels.

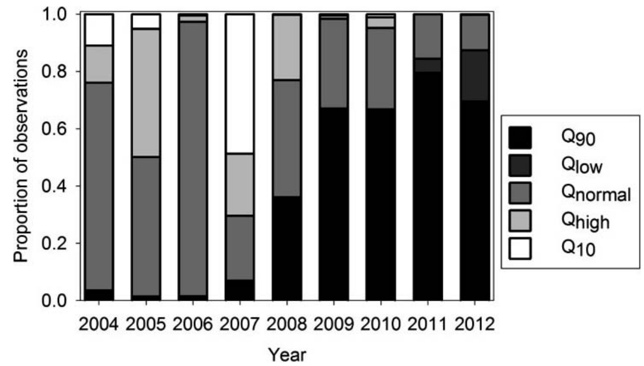

Figure 4. Annual proportion of observations of discharge within flow quantiles from the South Llano River, Texas during 2004–2012.

aquatic vegetation in runs, the distance between boulders in pools, and the proportion of bedrock (Figure 3c).

Even though there was clear separation among most of the age classes in their habitat associations at different spatial scales, we did not detect a strong influence of any of the measured habitat characteristics on the most recent year of growth. Age alone explained most of the variation in the most recent year of Guadalupe Bass growth at all spatial scales. At the stream unit scale, growth was also positively correlated with riffle cobble–gravel contiguity ($F_{1,265} = 16.87$, $P < 0.01$); however, this variable alone explained just 4% of the variation. At the 250-m scale, growth was positively correlated with pool bedrock contiguity ($F_{1,270} = 7.24$, $P < 0.01$) and negatively correlated with pool submerged aquatic vegetation perimeter-area ratios, explaining 2% and 1% of the variation respectively. Growth rates were positively correlated with three habitat variables at the 50-m scale: riffle gravel–cobble total edge ($F_{1,269} = 5.59$, $P = 0.02$), riffle boulders perimeter-area ratios ($F_{1,269} = 6.16$, $P = 0.01$), and run bedrock perimeter-area ratios ($F_{1,269} = 12.80$, $P < 0.01$), but together only explained about 3% of the variation in growth.

In contrast, stream discharge explained a much greater proportion of the variability in growth. The hydrologic profile of the South Llano River during the period encompassed by the life spans of the Guadalupe Bass used in this study (2004–2012) can be roughly divided into three periods (Figure 4). A period of "typical" discharges during 2004–2006 that were dominated by flows within the 25–75th percentiles was followed by a high flow year in 2007. The remaining years were characterized by moderate to severe drought and extreme low flows (2008–2012). Overall, the proportion of discharge observations falling in the Q_{90} range in a given year had the greatest influence on Guadalupe Bass growth rates. Residuals from the von Bertalanffy model were negatively correlated to the

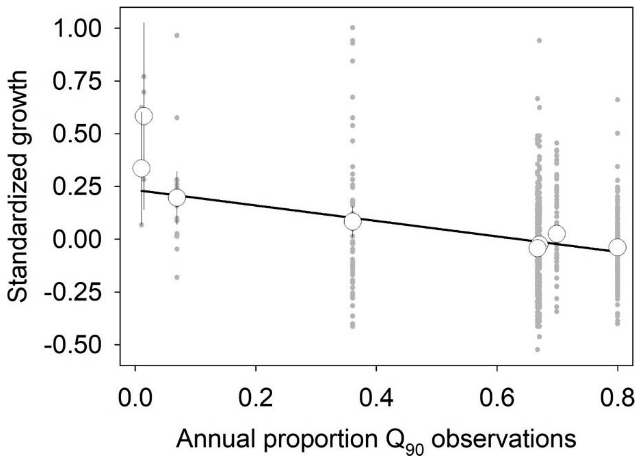

Figure 5. Regression of mean residuals by cohort from the von Bertalanffy model of back-calculated lengths at age against the proportion of Q_{90} discharge rates observed during that year for Guadalupe Bass *Micropterus treculii* captured from the South Llano River, Texas during 2011–2012. The period represented by the individuals presented in this figure encompasses 2004–2012. Error bars represent 95% confidence intervals around the mean residuals. Individual observations are represented by gray-filled circles.

proportion of Q_{90} discharge rates observed during a particular year over the first 3 y of growth ($F_{1,339} = 48.83$, $P < 0.01$; Figure 5; Table S5, *Supplemental Material*).

Discussion

This study represents the first detailed description of growth rates of wild Guadalupe Bass, and our results suggest that the habitat use could vary among the age classes. The association of age-0 Guadalupe Bass with run mesohabitats at all three spatial scales suggests that higher current velocities or environmental factors associated with higher current velocities are important to their survival. Current velocity has been demonstrated to influence first-year growth and survival of Smallmouth Bass, by possibly influencing feeding activities and swimming performance (Simonson and Swenson 1990; Livingstone and Rabeni 1991; Brewer 2011). Furthermore, runs in the South Llano River are typically shallower and warmer than pools during summer and fall (Cheek and Grabowski 2014) and thus may offer a more optimal temperature regime for age-0 Guadalupe Bass (27–28°C, Sullivan et al. 2013). Thermally driven habitat preferences have been noted in stream-dwelling age-0 Smallmouth Bass, which tend to use habitat with the warmest temperature available < 32°C (Brewer 2008). Moreover, the proportion of submerged aquatic vegetation, as well as the availability of edge habitat around it, seemed to be important factors associated with the presence of age-0 Guadalupe Bass at the finest spatial scales.

There was greater overlap in the habitat associations among older age classes of Guadalupe Bass than with age-0 counterparts and the availability of edge habitats seemed to be an important factor at multiple spatial scales for these older fish. Edge effects on the distribution and abundance of species have been known since Leopold (1933) coined the term to describe an increase in game species in patchy landscapes. For older age classes of Guadalupe Bass, edges likely provide access to resources that are spatially separated by a boundary (Ries et al. 2004), such as prey and refuge from current velocity or predators. Furthermore, the contiguity, or spatial proximity of instream structures or habitat features, such as large woody debris, boulders, and submerged aquatic vegetation, to each other also became more influential for older age classes. This may reflect a change in the perception of available habitat with increasing body size, that is, larger fish may be more likely to move between patches of structure within a certain distance, elevating the importance of the spatial arrangements of these patches, whereas smaller fish may be more likely to remain in a single habitat patch, rendering the total size of the habitat more important.

Although the size-selective habitat associations exhibited by Guadalupe Bass were expected, the minimal influence of habitat on recent growth observed in this study was not. The literature suggests that fish should associate with habitat that maximizes somatic or gonadal growth while minimizing the risk of mortality (Gilliam and Fraser 1987; Gotceitas 1990). Since Guadalupe Bass are drift feeders at younger ages and feed primarily on benthic macroinvertebrates as they age (Edwards 1980), certain habitat variables such as the contiguity of riffle cobble–gravel habitats were expected to positively influence growth. The resulting low influence of habitat on growth observed in this study could be attributed, in part, to a few factors. The year of growth evaluated in this study coincided with an extreme drought in Texas. It is possible that changes in habitat availability or suitability effectively equalized all habitats in terms of ability to support Guadalupe Bass growth. However, we based the three spatial scales used in our analysis on telemetry studies indicating that Guadalupe Bass typically do not move great distances (< 60 m; Perkin et al. 2010). Still, movement could have been underestimated as individuals may have been more mobile because of the drought (see Matthews and Marsh-Matthews 2003 for review). Alternatively, factors at scales coarser than those encompassed by this study, such as those at the watershed scale, may have a greater influence on growth than those at finer scales. However, a replication of our study design across several watersheds would be required to address this possibility.

Although we did not detect a strong relationship between habitat and growth, the growth rates of young (ages 1–3) Guadalupe Bass were negatively correlated to the proportion of Q_{90} discharge observations during that year of growth. This is in contrast to riverine populations of Largemouth Bass in the southeastern United States (Rypel 2009) and Smallmouth Bass in the midwestern United States (Paragamian and Wiley 1987) that exhibited higher growth rates during periods of drought. Edwards (1980) reported a strong preference by Guadalupe Bass for moving water habitats during most of the year. Similarly, Perkin et al. (2010) found that Guadalupe

Bass were responsive to changes in the flow regime, gradually shifting toward pools with greater depths during a summer period of extreme low flow in the Pedernales River. Although we captured individuals outside of pools even during extreme low flows on the South Llano River, it is possible that the productivity of riffles and runs was reduced. Periods of low discharge can reduce the growth rates of drift-feeding fishes (Rimmer 1985; Hakala and Hartman 2004; Nislow et al. 2004; Harvey et al. 2006), potentially reducing the efficacy of a feeding strategy often used by young Guadalupe Bass (Edwards 1980) and not typically used by Largemouth Bass or Smallmouth Bass. Our results suggest that Guadalupe Bass could be flow dependent, but high flow extreme could negatively affect the growth.

The results of this study are relevant to the advancement of our current understanding of lotic fish conservation. Age-0 Guadalupe Bass tended to associate with greater proportions of pool and run mesohabitats with submerged aquatic vegetation. This suggests the importance of riparian vegetation management for the recruitment of Guadalupe Bass in riverine systems. The ontogenetic shifts in habitat association at multiple spatial scales exhibited by Guadalupe Bass render it difficult to assign an appropriate scale at which to target conservation efforts. However, identifying the habitat features and qualities with which fish species associate at different points in their life history combined with a thorough habitat inventory and understanding of the population structure would offer the potential to create an adaptive approach that can be customized to work in specific watersheds. In addition, our results suggest that hydrologic alterations such as significant flow release from dams and extreme decrease in river discharge would negatively affect the growth of Guadalupe Bass because the extreme high and low flow conditions were negatively related to the Guadalupe Bass growth in our study. These conservation implications may be useful for not only Guadalupe Bass but also other fish species with similar life-history traits in different lotic systems.

Supplemental Material

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Table S1. Mean size (mm) ± SD of Guadalupe Bass *Micropterus treculli* collected by three sampling techniques (angling, electrofishing, and seining) in each month in 2012 from the South Llano River, Texas. The numbers in parentheses indicate the captured number of Guadalupe Bass.

Found at DOI: https://doi.org/10.3996/022018-JFWM-015.S1 (1 KB TXT).

Table S2. Fish identification number, total length (mm TL), age (y), and variables describing habitat within the riffle–run–pool complex containing the capture location of Guadalupe Bass *Micropterus treculli* sampled during April–November 2012 from the South Llano River, Texas. The habitat variables include the proportion of area encompassed by gravel–cobble substrate in riffle (%riff_COgr) and pool (%pool_COgr) habitat and boulders in run habitat (%run_bldr); the perimeter:area ratio of boulders in pool habitat (pool_bldr_P:A) and gravel–cobble (riffle_GRco_P:A), gravel–sand (riffle_GRsa_P:A) and cobble–gravel (riffle_COgr_P:A) substrates in riffle habitat; the total edge (m) of gravel–cobble substrate in run habitat (run_GRco_TE), bedrock substrate (riff_BR_TE), boulders (riff_bldr_TE), and submerged aquatic vegetation (riff_SAV_TE) in riffle habitat, boulders (pool_bldr_TE) and cobble–gravel substrate (pool_-COgr_TE) in pool habitat, and all submerged aquatic vegetation (total_SAV_TE); and the contiguity of gravel–sand substrate (pool_GRsa_contig) and submerged aquatic vegetation (pool_SAV_contig) in pool habitat, boulders in riffle habitat (riff_bldr_contig), bedrock substrate in run habitat (run_BR_contig), cobble–gravel substrate in riffle habitat (riff_COgr_contig), large woody debris in run habitat (run_LWD_contig), and bedrock substrate in riffle habitat (riff_BR_contig).

Found at DOI: https://doi.org/10.3996/022018-JFWM-015.S2 (67 KB TXT).

Table S3. Fish identification number, total length (mm TL), age (y), and variables describing habitat within a 250-m radius of the point of capture of Guadalupe Bass *Micropterus treculli* sampled during April–November 2012 from the South Llano River, Texas. The habitat variables include the proportion of area encompassed by riffle habitat with bedrock substrate (%riff_BR) and rocky–fine substrate (%rocky–fine); the perimeter:area ratio of submerged aquatic vegetation in riffle habitat (riffle_SAV_P:A), gravel–sand substrate in riffle (riffle_GR-sa_P:A) and run (run_GRsa_P:A) habitats, and submerged aquatic vegetation in run habitat (run_SAV_P:A); the total edge (m) of submerged aquatic vegetation in run (run_SAV_TE) and pool (pool_SAV_TE) habitats, cobble–gravel substrate in pool habitat (pool_COgr_TE), and gravel–sand (run_GRsa_TE), gravel–cobble (run_-GRco_TE), and cobble–gravel (run_COgr_TE) substrates in run habitat; the contiguity of large woody debris in run habitat (run_LWD_contig), bedrock substrate in pool habitat (pool_BR_contig), boulders in pool habitat (pool_bldr_contig), and gravel–sand substrate in run habitat (run_GRsa_contig); and the landscape contagion index (contag).

Found at DOI: https://doi.org/10.3996/022018-JFWM-015.S3 (28 KB TXT).

Table S4. Fish identification number, total length (mm TL), age (y), and variables describing habitat within a 50-m radius of the point of capture of Guadalupe Bass *Micropterus treculli* sampled during April–November 2012 from the South Llano River, Texas. The habitat variables include the proportion of area encompassed by pool habitat (%pool), bedrock substrate (%BR), large woody debris (%LWD), submerged aquatic vegetation in run habitat (run_SAV_prop), cobble–gravel substrate in run habitat (run_COgr_prop), and boulders in riffle habitat (riffle_bldr_run); the total edge (m) of submerged aquatic vegetation in run habitat (run_SAV_TE); the perimeter:area ratio of cobble–gravel substrate in run habitat (run_COgr_P:A) and gravel–sand substrate in riffle habitat (riffle_GRsa_P:A); and the contiguity of boulders in run habitat (run_bldr_contig) and gravel–sand substrate (pool_GRsa_contig), cobble–gravel substrate (pool_COgr_contig), and boulders (pool_bldr_contig) in pool habitat.

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Table S5. Identification number, total length (mm TL), age (y), cohort, age at back-calculated length, back-calculated TLh (mm), growth (mm/y), and proportion of stream discharge observations falling below *Q*90, between *Q*90 and *Q*75 (Q_{low}), between *Q*75and *Q*25 (Q_{normal}), between *Q*25 and *Q*10 (Q_{high}), and above *Q*10 during the year of the back-calculated length estimate for Guadalupe Bass *Micropterus treculli* captured during April–November 2012 from the South Llano River, Texas.

Found at DOI: https://doi.org/10.3996/022018-JFWM-015.S5 (72 KB TXT).

Reference S1. Cheek BD, Grabowski TB. 2014. Evaluating habitat associations of a fish assemblage at multiple scales in a minimally disturbed stream on the Edwards Plateau, central Texas. Washington, D.C.: U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-104-2014.

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Reference S2. Pease JE, Grabowski GB, Pease AA. 2017. Variation and plasticity and their interaction with urbanization in Guadalupe Bass populations on and off the Edwards Plateau. Washington, D.C.: U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-125-2017.

Found at DOI: https://doi.org/10.3996/022018-JFWM-015.S7 (6.11 MB PDF); also available at https://usgs-cru-individual-data.s3.amazonaws.com/t.grabowski/intellcont/CSS-125_Pease_etal_2017-1.pdf

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