Movement and Microhabitat Associations of Guadalupe Bass in Two Texas Rivers

JOSHUAH S. PERKIN,*[1] ZACHARY R. SHATTUCK, PRESTON T. BEAN, AND TIMOTHY H. BONNER

Department of Biology, Aquatic Station, Texas State University–San Marcos, 601 University Drive,
San Marcos, Texas 78666, USA

EKATERINA SARAEVA AND THOMAS B. HARDY

Utah Water Research Laboratory, Utah State University, 1600 Canyon Road, Logan, Utah 84322, USA

Abstract.—The Guadalupe bass *Micropterus treculii* is endemic to Texas and is threatened by introgression with introduced smallmouth bass *M. dolomieu* as well as habitat degradation. This study described and quantified the movements and habitat associations of Guadalupe bass to assess the factors that may influence current populations. Radio-tagged adult Guadalupe bass were tracked in the Pedernales River ($n = 12$) and South Llano River ($n = 12$) from January through August 2008. Available microhabitats were measured and modeled in terms of depth, velocity, substrate, and cover for about 1.5 km in the Pedernales River and 1.2 km in the South Llano River. Rates of movement were greatest during the reproductive season, ranging from less than 1 to 9 m/d. Instream cover (such as undercut banks and woody debris) was preferred during daylight hours throughout the study period, although the distances from cover increased from January to August. Habitat shifts from cover to open water occurred at night and from woody structures to boulders and ledges during a large flood pulse. The habitats most suitable for adult Guadalupe bass had a depth of 1.0 m and a current velocity of 0.05 m/s, and habitat selection was strongest for eddy mesohabitats with smaller substrates. By July, the Guadalupe bass in the South Llano River were associated with runs with greater current velocities, whereas those in the Pedernales River were associated with pools with greater depths, largely owing to the low flows and reduced habitat availability in the Pedernales River. Environmental factors, including the availability and suitability of instream cover, are probably the strongest influences on the distribution and abundance of Guadalupe bass.

Movements among refuge, foraging, and spawning habitats are crucial to the completion of the life histories of many stream-dwelling fishes (Schlosser and Angermeier 1995), and quantification of such movements is important to developing management plans and conservation strategies for stream-dwelling micropterids (Horton and Guy 2002; VanArnum et al. 2004). Movements and habitat associations have been considered in the context of sport fish management (Bangham and Bennington 1939) and are well understood for micropterids with broad distributions and high sport fish value (e.g., largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, and spotted bass *M. punctulatus*). Only recently have the movements and habitat use of imperiled and rare species been considered. In response to the declines in abundance (e.g., spotted bass; Tillma et al. 1998) and the imperilment (e.g., shoal bass *M. cataractae*, redeye bass *M. coosae*, and Guadalupe bass *M. treculii*;

Warren et al. 2000) of several micropterids, there has been a growing body of research on the ecological and evolutionary significance of the movements and habitat use of stream-dwelling black basses (Horton and Guy 2002; Koppelman and Garrett 2002; Wheeler and Allen 2003; Stormer and Maceina 2009).

Members of the genus *Micropterus* inhabit lotic systems (Stormer and Maceina 2009), where habitat specialization has resulted in unique movement and reproductive habitat associations for each species (Koppelman and Garrett 2002). For example, large-mouth bass spawn on open nests in deep pools and move on the order of kilometers from overwintering to spawning habitats (Mesing and Wicker 1986; Raibley et al. 1997). Conversely, smallmouth bass spawn within overhead cover and generally remain within a single mesohabitat during spawning but exhibit migrations up to 24 km (Todd and Rabeni 1989; Lyons and Kanehl 2002; VanArnum et al. 2004). Spotted bass exhibit little movement (e.g., 18 m/h; Horton and Guy 2002) and generally remain within or close to a single pool, where spawning occurs on gravel bars (Viosca 1931; Horton and Guy 2002). Movement patterns and habitat associations are least understood for regionally endemic black bass species

---
* Corresponding author: jperkin@ksu.edu
[1] Present address: Division of Biology, Kansas State University, 232 Ackert Hall, Manhattan, Kansas 66506, USA.

(shoal bass, redeye bass, Suwannee bass *Micropterus notius*, and Guadalupe bass; Koppelman and Garrett 2002; but see Wheeler and Allen 2003 and Stormer and Maceina 2009). Koppelman and Garrett (2002) suggested that the paucity of data on the regionally endemic species has resulted in poor understanding of the competitive adaptations that allow the sympatric occurrence of allopatrically evolved species (Near et al. 2003). Furthermore, clear understanding of movements and habitat partitioning may be helpful in evaluating the consequences of micropterid introductions (Jackson 2002) as well as the ways in which anthropogenic stream regulation influences competition among sympatrically occurring species (Edwards 1980).

The Guadalupe bass is endemic to the western Gulf Slope drainages of central Texas, where it is currently listed as a species of special concern owing to introgression with introduced smallmouth bass and habitat degradation (Hubbs et al. 2008). Although introgression with smallmouth bass is the most immediate threat to the persistence of Guadalupe bass, habitat degradation is the most significant threat over the long term (Edwards 1980; Garrett 1991). Introgression with smallmouth bass was an unforeseen result of sport fish stockings, and the Texas Parks and Wildlife Department is currently combating genetic contamination in the upper Guadalupe River via supplemental stocking of pure-strain, hatchery-produced individuals (Carmichael and Williamson 1986; Garrett 1991; Koppelman and Garrett 2002). Habitat degradation has resulted in localized extirpations and declines in abundance throughout the Guadalupe bass's range, but the specific causes of these developments remain poorly understood (Edwards 1978, 1980). Furthermore, despite the longstanding recognition of the Guadalupe bass as a stream-adapted species (Hurst et al. 1975), there is a paucity of data pertaining to the autecology of this species in lotic systems (Garrett 1991).

To date, the ecology, geographic variation, reproduction, diet, and mesohabitat associations of Guadalupe bass have been investigated in only one study (Edwards 1980), which has been heavily relied on to develop the current management and conservation initiatives for the species (Garrett 1991). Its microhabitat associations and selection and movement patterns have not been considered, however. A more complete understanding of these factors will enhance our perspective on the mechanisms driving localized extirpations after habitat degradation, how future land use changes might impact Guadalupe bass habitat, and what microhabitats are essential for its life history (Orth and Newcomb 2002). The objectives of this study were to (1) determine the monthly and diel movement patterns of adult Guadalupe bass, (2) quantify their microhabitat associations, (3) measure their habitat preferences (i.e., selection versus avoidance), and (4) identify suitable habitat for them (i.e., the habitats most frequently used) throughout the primary reproductive period.

Study Area

Nonintrogressed, naturally occurring populations of Guadalupe bass exist in four western tributaries of the Colorado River drainage and the upper portions of the San Antonio River drainage in central Texas (Koppelman and Garrett 2002). The San Saba River, Pedernales River, Llano River, and Gorman Creek in the Colorado drainage and the Medina River in the upper San Antonio drainage remain free of smallmouth bass introductions and large-scale habitat alteration. For this study, two sites that are characteristic of the streams inhabited by Guadalupe bass were chosen.

The Llano River originates in springs emerging from the Edwards–Trinity Aquifer that give rise to the 80-river-kilometer (rkm)-long North Llano River in Sutton County and the 89-rkm-long South Llano River in Edwards County. These tributaries converge in Kimble County to form the Llano River proper, which continues 161 rkm east through Mason and Llano counties into Lake Lyndon B. Johnson, an impoundment on the Colorado River (Figure 1). The mean annual discharge at Junction, Texas, just downstream of the confluence of the North and South Llano rivers, is 7.4 m^3/s (U.S. Geological Survey gauge 08150000). Guadalupe bass were radio-tagged along a 1-km stretch of the South Llano River (30°28'7″N, 99°47'07″W). During average flows, the movement of Guadalupe bass out of the study area was restricted by a low-water crossing at South Llano River State Park (30°27'0″N, 99°48'46″W) approximately 4 rkm upstream and a reservoir at Junction (30°29'21″N, 99°45'35″W) approximately 4 rkm downstream.

The Pedernales River originates in Kimble County and flows approximately 170 rkm northeastward through Gillespie, Blanco, Hays, and Travis counties, emptying into Lake Travis, an impoundment on the Colorado River (Figure 1). The upper reaches of the Pedernales River rise from spring discharges of the Edwards–Trinity Aquifer, producing a mean annual discharge of 3.4 m^3/s at Fredericksburg (gauge 08152900). Guadalupe bass were radio-tagged throughout a 1-km stretch of the Pedernales River near Fredericksburg (30°13'13″N, 98°54'1″W). During average flows, the movement of Guadalupe bass out of the study area was restricted by a low-water crossing near State Highway 16 (30°12'41″N, 98°56'30″W) approximately 8 rkm upstream and a low-head dam
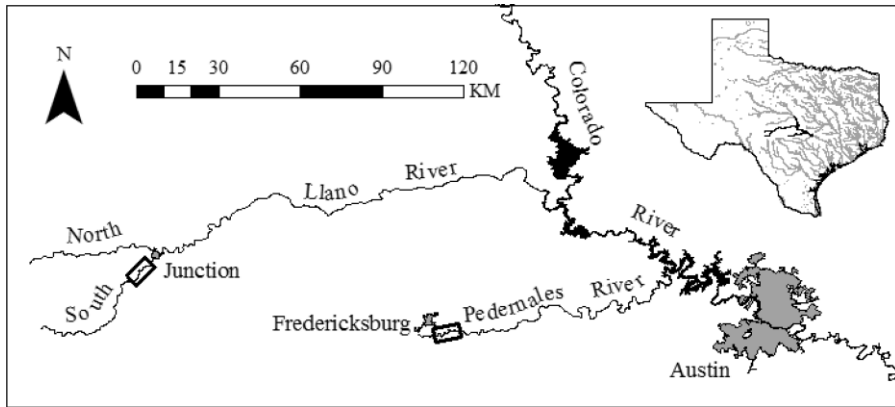
FIGURE 1.—Sites (rectangles) on the South Llano and Pedernales rivers at which Guadalupe bass were tracked from January to August 2008.

near Johnson City (30°17'25″N, 98°23'58″W) approximately 60 rkm downstream.

Methods

Transmitter attachment and tracking.—Twelve Guadalupe bass weighing more than 180 g each were collected from each river by electrofishing during December 2007. Radio transmitters (Advanced Telemetry Systems Model F1580) with a battery life of 250 d were surgically implanted following the anesthetization methods of Peake (1998; 60 mg/L clove oil) and the surgical methods of VanArnum et al. (2004). To improve retention, the tag antennae were inserted through a small puncture 10–15 mm behind the incision that was made with a modified hypodermic needle (Stormer and Maceina 2009). The fish were released at the site of collection after regaining equilibrium and normal swimming ability, and at least 7 d was allowed for them to adjust to the added weight of the radio transmitters (3.6 g, or <2% of body weight; Winter 1996) before tracking was conducted (January 6–August 16, 2008). Three-element, handheld directional Yagi antennae (Advanced Telemetry Systems) and Lotek Model SRX 400 (150-MHz) radio receivers were used to track the fish by walking along the shoreline in shallow areas and from kayaks in deep areas. Triangulation techniques and visual observation from the shoreline and by snorkeling (Winter 1996) improved radiolocation accuracy. When radio signals were not detected, multiple kayak passes were made from the upstream to the downstream boundary.

Movement and habitat associations.—Tracking was conducted biweekly during daylight hours, roughly every 11–16 d (Horton et al. 2004) throughout the primary reproductive season (March – June; Edwards 1980). Diel movement and habitat associations were assessed from a subset of individuals ($n = 5$) in the Pedernales River by conducting hourly tracking for a period of 15–24 consecutive hours on three occasions: March, May, and July. The biweekly and diel movements were analyzed independently (Horton et al. 2004) as the linear distance moved since the last tracking session (Stormer and Maceina 2009). The movement patterns of individuals were classified as sedentary (for fish that remained within the original capture mesohabitat), upstream, or downstream, and the maximum distances moved were measured from the original capture site (VanArnum et al. 2004). For each relocation, we recorded the Global Positioning System coordinates (Trimble Model XH units; accuracy, <1 m) and quantified numerous facets of the microhabitat (i.e., the environmental conditions at specific fish locations; Newcomb et al. 2007), including water temperature (°C), current velocity (m/s), depth (m), mesohabitat type, dominate substrate, and instream cover or distance to cover (Table 1).

Habitat availability.—We determined habitat suitability by calculating the amount of habitat used (from the tracking observations) in proportion to the total available habitat. Traditional transect sampling methods (Simonson et al. 1994) were inadequate for estimating the distribution and availability of all cover types (i.e., large woody debris and undercut banks) in our study streams. Thus, we utilized a novel approach to mapping and modeling the available habitat over a representative stretch of each river (i.e., 40× the mean channel width; Simonson et al. 1994). Trimble Model XH units were used to delineate polygons of available cover, mesohabitat, and dominant substrates within our study areas. Standard survey equipment was used to measure the topography (i.e., the elevation) within the annual wetted channel of each study site by means of a

TABLE 1.—Habitat variables measured or modeled for Guadalupe bass in the South Llano and Pedernales rivers.

Variable	Description
Temperature	Water temperature (°C)
Velocity	Current velocity (m/s)
Depth	Maximum depth (m)
Mesohabitat[a]	
Run	Moderate depth, moderate to swift current, dominated by bedrock or boulder substrate
Riffle	Shallow depth, moderate to swift current, dominated by gravel or cobble substrate
Pool	Greater depth, little to no current, dominated by silt or sand substrate
Eddy	Moderate depth, circular flow near run or riffle
Backwater	Moderate to shallow depth, little current, within-stream cover
Substrate[b]	
Bedrock	Unbroken stream bottom
Silt	Diameter less than 0.6 mm
Sand	Diameter 0.6–2 mm
Small gravel	Diameter 2–16 mm
Coarse gravel	Diameter 16–64 mm
Cobble	Diameter 64–256 mm
Boulder	Diameter 256–4,096 mm
Instream cover[c]	
Log	A single log of large diameter
Log complex	Two or more logs forming a single structure
Branches	Submerged branches or branches extending into the water
Vegetation	Submerged or emergent aquatic vegetation
Roots	Roots of deposited large woody debris or associated with bank overhang
Undercut bank	Eroding or overhanging banks without roots
Boulder/ledge	Crevices of large boulders and ledges formed by bedrock outcroppings
Open water	Water more than 0.33 m deep with no immediately adjacent cover
Distance to cover	Linear distance to the nearest cover (m)

[a] Box 4.3, McMahon et al. (1996).
[b] Table 4.2, McMahon et al. (1996).
[c] Snedden et al. (1999).

stratified random sampling design that incorporated all of the available heterogeneity in topography. The latitude (X), longitude (Y), topography (Z), and dominant substrate were recorded in Trimble data dictionaries for each point surveyed. Substrates were assigned specific roughness values (height in meters) based on Barton et al. (2005; silt = 0.00005 m, sand = 0.0037 m, fine gravel = 0.0159 m, coarse gravel = 0.0508 m, cobble = 0.1905 m, boulder = 0.762 m, and bedrock = 0.85 m). The water surface elevation (WSE) was recorded longitudinally for each river, encompassing the changes in WSE at each mesohabitat (i.e., at the upstream and downstream points). The survey data (X, Y, Z, and roughness) and the WSE data were loaded into the Multi-Dimensional Surface-Water Modeling System (MDSWMS; McDonald et al. 2005) to model the distribution and availability of current velocities and depths following the methods of Barton et al. (2005). Two-dimensional solution files for depths and current velocities were exported from MDSMWS and overlaid with the cover, substrate, and mesohabitat polygons in ArcView 9.2 to yield spatially explicit layouts of the mapped sections for each river.

Data analysis.—The sample sizes for all statistical analyses were calculated as the number of individuals for which 12 or more locations were obtained over the course of the study; individuals with fewer than 12 locations were removed from the analyses. The distances moved during the biweekly and diel tracking were analyzed with ArcView 9.2. The mean movement rate (m/d) was calculated monthly as the grand mean of all individual mean movements within a given month (VanArnum et al. 2004). The diel movement rates (m/h) were calculated in a similar fashion, but the death of three fish (and the subsequent inclusion of three different ones) by July precluded a repeated-measures analysis of diel movement across months. As a result, only mean ± SD movement rates are reported for the diel movements. The factors commonly identified with black bass movement (i.e., water temperature, day number (day of the year), flow rate, and reproductive season; Railsback et al. 1999) were ordinated by means of principal components analysis (PCA; Microcomputer Power 2002) to identify those associated with movement by Guadalupe bass. The grand mean movement for each month was included in the PCA biplot to account for factors associated with greater movements. Biweekly habitat observations gathered from tracking data and all available habitats measured and mapped with ArcView and MDSWMS were ordinated by means of PCA to assess the changes in habitat associations during the study. Grand mean monthly PCA scores were calculated for each river to show the changes in habitat associations through time.

Observed habitat associations collected during diel tracking were ordinated by means of PCA and diel times, mean principal component scores, and collective variation (i.e., the 68% confidence interval, or ±1 SD) included in the PCA biplot to show habitat associations during the day and at night. For PCA, qualitative variables (reproductive season, cover, mesohabitat, substrate, and river) were represented by dummy variables, and quantitative variables (temperature, day number, flow, distance to cover, depth, and velocity) were z-score transformed (Krebs 1999; Williams and Bonner 2006).

Univariate statistical analyses were used to assess cover, substrate, and mesohabitat preference or avoidance as well as habitat suitability (i.e., the relative use of available habitats) for current velocity and depth by comparing the observed usage with the total available habitat. The total availability of each cover type was calculated as the area (m^2) of the polygons for that type within the mapped region of each river. The total availability of each substrate class was calculated from data collected during the stratified random sampling of each river. The total availability of each mesohabitat type was calculated as the area (m^2) of the polygons for that type within the mapped region of each river. For cover, substrate, and mesohabitat, the number of observations within a given class were figured for each individual and averaged across individuals to yield mean percent use. Preference or avoidance of cover, substrate, and mesohabitat were determined using the electivity index of Jacobs (1974), where 1 indicates complete preference and −1 indicates complete avoidance. Habitat suitability was calculated from all observations of Guadalupe bass associations with current velocity and depth, including observations made during the diel tracking events for individuals in the Pedernales River. The bin widths of the suitability curves were determined using the Sturges (1926) equation for all available depths and velocities (extracted from MDSWMS), and use was plotted versus availability (Newcomb et al. 2007).

Results

The total lengths of the radio-tagged Guadalupe bass ranged from 320 to 480 mm in the South Llano River and from 260 to 373 mm in the Pedernales River. Twenty-two of the 24 radio-tagged fish survived more than 5 months (for a minimum of 12 relocations per fish) and were retained for statistical analysis. The two individuals excluded from the analysis were radio-tagged in the South Llano River. A shed tag was found downstream in February, and the other fish was not relocated after March. Of the 22 tagged fish, 17 survived to the end of the study period in August 2008 and 5 died before that time (1 in May, 2 in June, and 2 in July). The causes of mortality included angler harvest ($n = 1$), predation by flathead catfish *Pylodictis olivaris* ($n = 1$), predation likely by great blue heron *Ardea herodias* or cormorant *Phalacrocorax* sp. ($n = 2$), and an undetermined cause ($n = 1$).

Monthly and Diel Movement

Of the 22 fish studied, 13 were sedentary (mean ± SD distance from the capture site = 16.6 ± 24.1 m), 6 moved upstream (1,026.8 ± 425.5 m), and 3 moved downstream (1,539.0 ± 1,641.3 m). Five of the upstream movements (maximum distance = 1,472 m) occurred in the Pedernales River during June. Only one fish moved upstream in the South Llano River (627 m during April). Three fish moved downstream (maximum distance = 3,420 m) in the South Llano River during April.

Movement rates ranged from 0.1 to 9 m/d and were primarily associated with the reproductive season. The first two principal component (PC) axes explained 82% of the total variation in the factors generally associated with Guadalupe bass movement (Table 2). The first principal component (which explained 56% of the total variation) represented a temperature, day number, and flow gradient (Figure 2). Months with the largest negative loadings along PC I were characterized by higher mean temperatures (loading = −1.30) and greater day number (−1.23), whereas months with the largest positive loadings were characterized by greater mean flow (0.86). The second principal component (which explained 26% of the total variation) primarily represented a reproductive period gradient. Months with the largest negative loadings along PC II were characterized by reproductive season (−1.90). The magnitude of fish movement was not associated with PC I ($r = 0.17$, $P = 0.51$) but was positively associated with PC II ($r = 0.77$, $P < 0.01$), specifically the reproductive season. Increases in movement rates were correlated with increases in temperature until the maximum movement rates occurred (January–April in the South Llano River; $r = 0.98$, $P < 0.01$; January–June in the Pedernales River; $r = 0.97$, $P < 0.01$).

Diel movement rates ranged from 0 to 35 m/h during the day and from 0 to 45 m/h at night. The mean ± SD movement rate during the day was 3.54 ± 3.21 m/h in March, 16.30 ± 16.35 m/h in May, and 5.28 ± 7.57 m/h in July. The corresponding rates at night were 6.35 ± 9.28 m/h in March, 13.67 ± 16.08 m/h in May, and 5.49 ± 6.30 m/h in July.

Habitat Associations

The first two principal components explained 30% of the total variation in available habitats within the

PERKIN ET AL.

TABLE 2.—Loadings and eigenvalues for variables on principal component (PC) axes I and II in three models (movement, monthly habitat, and diel habitat) for Guadalupe bass tracked in the South Llano and Pedernales rivers from January through August 2008. Values in bold italics are shown in PC biplots (Figures 2, 3, and 5).

	Movement		Monthly habitat		Diel habitat	
Variable	PC I	PC II	PC I	PC II	PC I	PC II
Temperature	*-1.2973*	-0.2141				
Day number	*-1.2262*	*0.2765*				
Flow	*0.8606*	*-0.5239*				
Reproductive season	-0.2698	*-1.8982*				
Cover			0.4017	*2.202*	-1.2489	*-1.6188*
Distance			0.1921	*-1.6458*	0.4886	*1.7892*
Velocity			*-1.5221*	-0.2776	*1.7605*	-0.2225
Depth			*1.4714*	*-1.0064*	-0.8171	*1.5026*
Eddy			-0.1055	1.2452	-0.1587	-0.0164
Backwater			0.4722	*1.3946*	-1.0615	*-1.5765*
Pool			*1.8568*	-0.7673	*-1.0868*	*1.7994*
Run			*-1.5715*	-0.7464	*1.5148*	-0.2711
Riffle			-0.6091	-0.356	0.8499	-0.0391
Bedrock			0.3035	*1.4822*	-0.0811	*-0.9656*
Boulder			0.0152	0.0603	-0.1187	-0.4859
Cobble			-0.897	*-0.8189*	*1.4114*	0.0442
Coarse gravel			*-1.1057*	0.453	0.5545	0.0028
Fine gravel			-0.1748	-0.2104	0.3203	0.1062
Sand			0.4778	-0.2412	-0.0813	0.8342
Silt			*1.6635*	-0.5344	*-1.6294*	0.4412
River			0.8074	0.3475		
Eigenvalue	0.56	0.26	0.18	0.12	0.22	0.16

South Llano and Pedernales rivers (Table 2). The first principal component (which explained 18% of the total variation) represented a velocity, depth, and substrate gradient (Figure 3). Habitats with large negative loadings along PC I were characterized by run mesohabitats (−1.57) with swift current velocity (−1.52) over coarse gravel substrate (−1.11); habitats with large positive loadings were characterized by pool mesohabitats (1.86) with silt substrate (1.66) and greater depths (1.47). The second principal component (which explained 12% of the total variation) represented primarily a cover gradient. Habitats with large
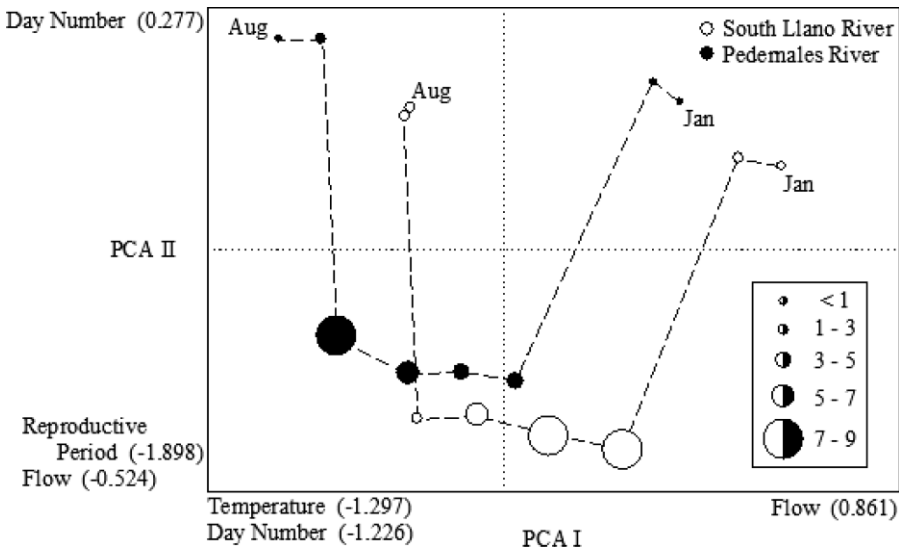

FIGURE 2.—Biplot of principal component axes (PCA) I and II for the factors associated with the mean monthly movements (m/d) of Guadalupe bass in the South Llano ($n = 10$) and Pedernales rivers ($n = 12$) from January to August 2008. The numbers in parentheses are the loadings for the different variables.
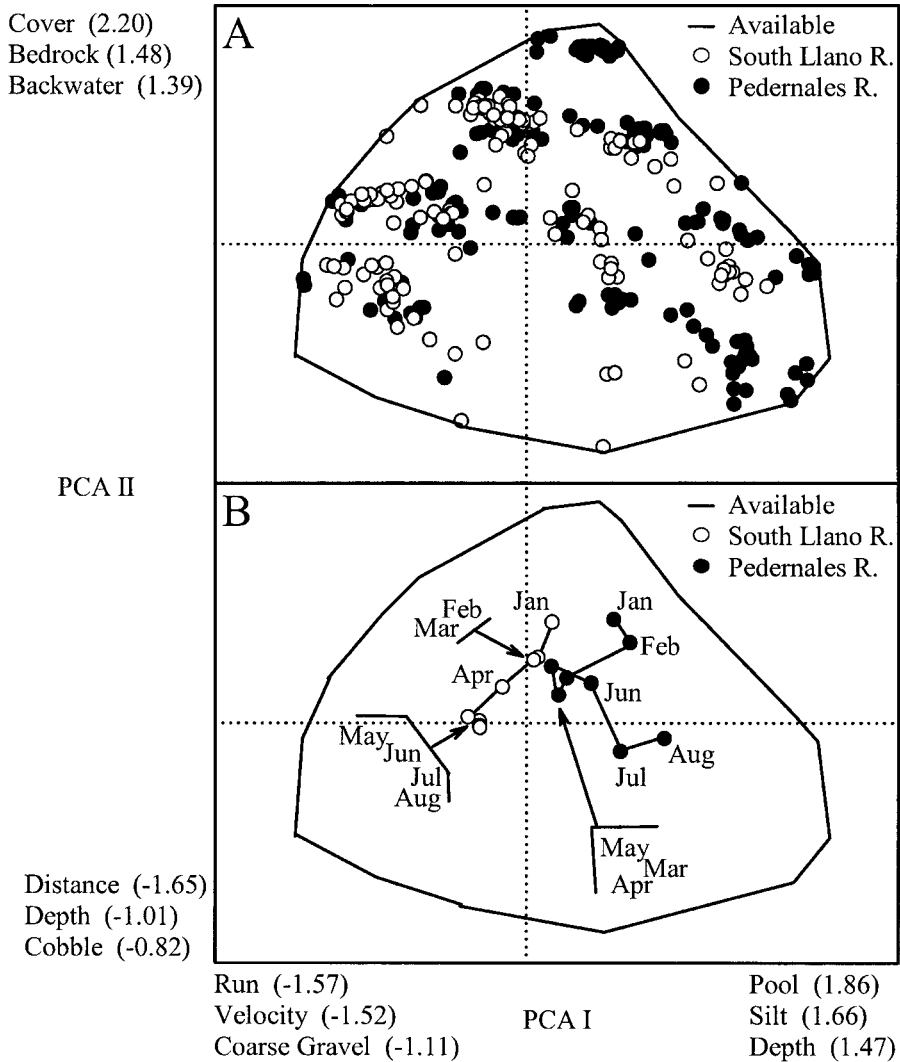
FIGURE 3.—Biplots of principal component axes (PCA) I and II for **(A)** all available habitat and all observations in the South Llano and Pedernales rivers and **(B)** monthly mean (grand mean of all individuals) PCA scores for 22 Guadalupe bass tracked from January to August 2008. The numbers in parentheses are the loadings for the different variables.

negative loadings along PC II were characterized by greater distances from cover (−1.65) and greater depths (−1.01) over cobble substrate (−0.82); habitats with large positive loadings were characterized by instream cover (2.20) over bedrock substrate (1.48) in backwater mesohabitats (1.39). Guadalupe bass were relocated at several mesohabitat types, depths, current velocities, and substrates (Figure 3A). Plotting the trajectory of mean PCA scores by month and across individual fish revealed that the associations with cover and bedrock substrates were stronger in the winter (the prereproductive season) in both rivers; thereafter the associations were with greater distance from cover and greater

depth (Figure 3B). With the onset of the reproductive season (March through June), the trajectories moved negatively along PC I for the South Llano River and positively along PC I for the Pedernales River. These contrasting shifts generally correspond to the declining flows in the Pedernales River (Figure 4).

For the diel habitat associations, the first two principal components explained 38% of the total variation in available habitats in the Pedernales River (Table 2). The first principal component (which explained 22% of the total variation) represented a mesohabitat, velocity, and cover gradient. Location events with large negative loadings were characterized
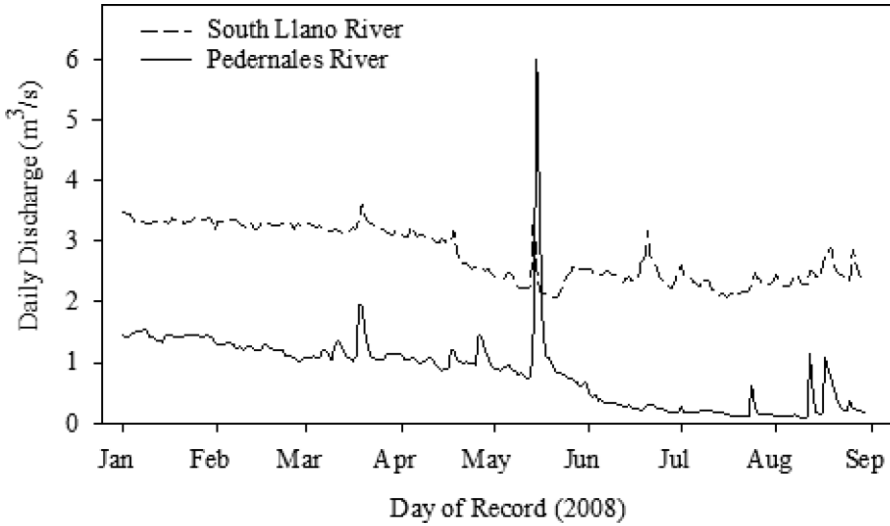
FIGURE 4.—Daily discharge for the Pedernales River near Fredericksburg, Texas (U.S. Geological Survey gauge 08152900), and the South Llano River near Junction, Texas (inferred from the discharges for the North Llano River [gauge 08148500] and Llano River proper [gauge 08150000]).

by silt substrate (−1.63) and instream cover (−1.25) in pool mesohabitats (−1.09; Figure 5); location events with large positive loadings were characterized by higher current velocities (1.76) in run mesohabitats (1.51) with cobble substrate (1.41). The second principal component (which explained 16% of the total variation) represented a mesohabitat, cover, and depth gradient. Location events with large negative loadings were characterized by instream cover (−1.62) in backwater mesohabitats (−1.58) over bedrock substrate (−0.97); location events with large positive loadings were characterized by pool mesohabitats
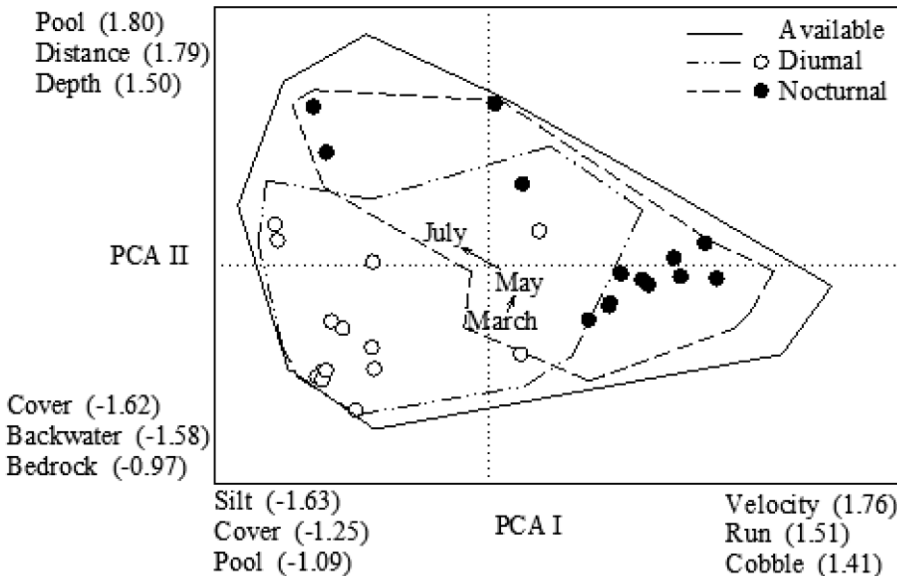

FIGURE 5.—Biplot of principal component axes (PCA) I and II for all available habitat and the mean PC scores and 68% confidence intervals (±1 SD) for individuals observed during the day and at night in the Pedernales River during March, May, and July 2008. The monthly values represent the mean PC scores of all individuals tracked in that month both during the day and at night. The numbers in parentheses are the loadings for the different variables.
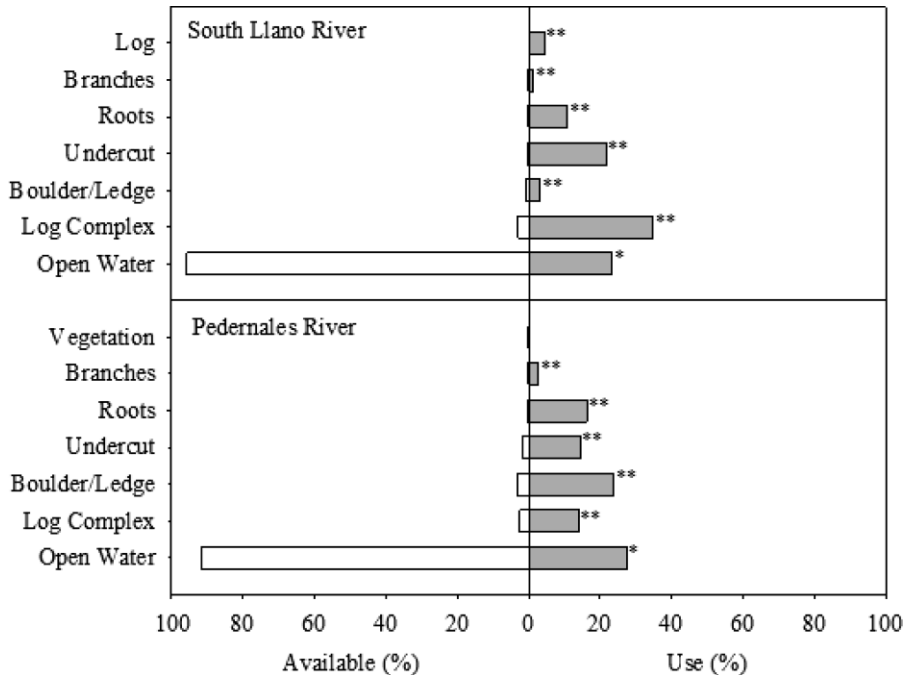
FIGURE 6.—Frequency of occurrence of habitat types (white bars) and mean percent use (gray bars) in the South Llano and Pedernales rivers for 22 Guadalupe bass tracked from January to August 2008. Single asterisks indicate avoidance (Jacobs' electivity values less than −0.9), double asterisks preference (Jacobs' electivity values more than 0.7).

(1.80) with greater distances from cover (1.79) and greater depths (1.50). Diurnal observations generally had negative mean values for PC I and II and were characterized by instream cover in backwaters or pools over silt or bedrock. Nocturnal observations generally had positive mean values for PC I and II and were characterized by either pool mesohabitats with greater depths or run mesohabitats with greater velocities, but the overall distances from cover were greatest during nocturnal hours. Nocturnal associations with run mesohabitats dominated the observations in March, but a gradual shift toward pool mesohabitats occurred in May and July.

Habitat use by Guadalupe bass in comparison with habitat availability varied among univariate gradients. Open water constituted more than 90% of the available habitat in both rivers, but mean percent use across fish indicated that open water was avoided (Jacobs' electivity index < −0.9 for both rivers; Figure 6). Jacobs' electivity values were more than 0.7 for all instream cover types except vegetation, which was the least available cover in the Pedernales River (<0.1%) and was not used, resulting in a Jacobs' electivity value of −1. Electivity values were positive for silt, sand, fine gravel, and coarse gravel in the South Llano River and for silt, coarse gravel, and bedrock in the Pedernales

River (Figure 7). Electivity values were positive for backwater and eddy mesohabitats in the South Llano River and for pool, backwater, and eddy mesohabitats in the Pedernales River. Available depths ranged from 0 to 6 m, and suitability was highest (1.0) at a depth of 1.0 m in both rivers; use was correlated with availability for depths exceeding 1.0 m (South Llano River: $r = 0.90$, $P < 0.01$; Pedernales River: $r = 0.88$, $P < 0.01$; Figure 8). Available velocities ranged from 0 to 0.6 m/s, and suitability was highest (1.0) at 0.05 m/s in both rivers; use was correlated with availability for velocities exceeding 0.05 m/s (South Llano River: $r = 0.91$, $P < 0.01$; Pedernales River: $r = 0.97$, $P < 0.01$), although the observed values of velocity were consistently less than those available in the South Llano River.

Discussion

Guadalupe bass were associated with eddy mesohabitats created by instream cover within or adjacent to run mesohabitats; small to medium-size substrates; depths of 1.0 m; and current velocities less than 0.1 m/s. Log complexes, boulders, and ledges were used often, whereas open water was generally avoided. The microhabitats used by Guadalupe bass in this study are similar to those reported for other stream-dwelling
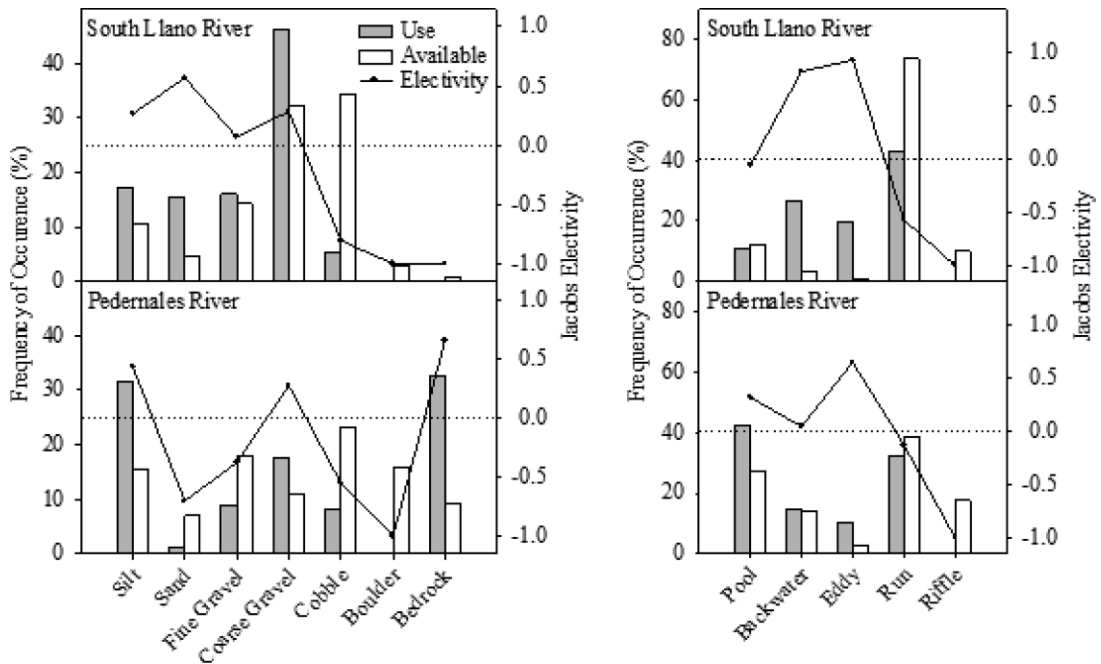
FIGURE 7.—Frequency of occurrence, mean percent use, and Jacobs' electivity values for the substrates (left panel) and mesohabitats (right panel) available to Guadalupe bass in the South Llano and Pedernales rivers from January to August 2008. Positive electivity values indicate preference and negative values avoidance.

members of the genus *Micropterus*. Smallmouth bass in rivers are associated with large woody debris and boulders, depths ranging from 1 to 2 m, and current velocities less than 0.2 m/s, and they avoid open water during daylight hours (Todd and Rabeni 1989; Orth and Newcomb 2002). Similarly, riverine spotted bass were associated with woody debris and avoided open water (Horton and Guy 2002), and shoal bass were associated with depths ranging from 0.4 to 1.4 m and current velocities less than 0.35 m/s and preferred boulder cover types while avoiding open water (Stormer and Maceina 2009).

The movement patterns of Guadalupe bass during the 8 months of tracking ranged from no movement (i.e., remaining within a single mesohabitat) to moving 3.4 km from the point of initial capture. Of the 22 fish studied, 13 moved less than 58 m and remained within the mesohabitat of initial capture, whereas 9 moved into other mesohabitats with similar microhabitats. *Micropterus* spp. are primarily sedentary in streams and rivers (movement <1.6 km; Funk 1957), but more mobile largemouth and smallmouth bass individuals travel up to 24 km (Funk 1957; Raibley et al. 1997; Lyons and Kanehl 2002; VanArnum et al. 2004). Intraspecific variation in movement is known for several riverine-type fishes (Funk 1957; Gerking 1959; Hill and Grossman 1987; Gatz and Adams

1994; Smithson and Johnston 1999) and is probably attributable to both biotic (e.g., genetics, ontogeny, and population size) and abiotic conditions (e.g., habitat availability and suitability, spates, and drying) (Funk 1957; Raibley et al. 1997; VanArnum et al. 2004; Cooke et al. 2008; Remshardt and Fisher 2009; Stormer and Maceina 2009).

The habitat associations and movement patterns of Guadalupe bass were influenced by season. During winter, associations with undercut banks were strong and movement rates ranged from less than 1 to 3 m/d. During spring and the reproductive season, habitat associations were weaker and included a heterogeneous mix of habitats, and movement rates ranged from 3 to 9 m/d. During late summer, associations with run mesohabitats (South Llano River) and pool mesohabitats (Pedernales River) were strong, and movement rates ranged from less than 1 to 3 m/d. Inhabiting undercut banks or areas with instream cover requires minimal energy expenditure with respect to abiotic (e.g., current velocity) or biotic (e.g., predatory) conditions during a time of low prey availability (Edwards 1980; Raibley et al. 1997; Allouche 2002). Daily movements typically increase more than 200% in *Micropterus* spp. as spring approaches and are related to foraging activities and reproduction (Edwards 1980; Mesing and Wicker 1986; Todd and Rabeni 1989;
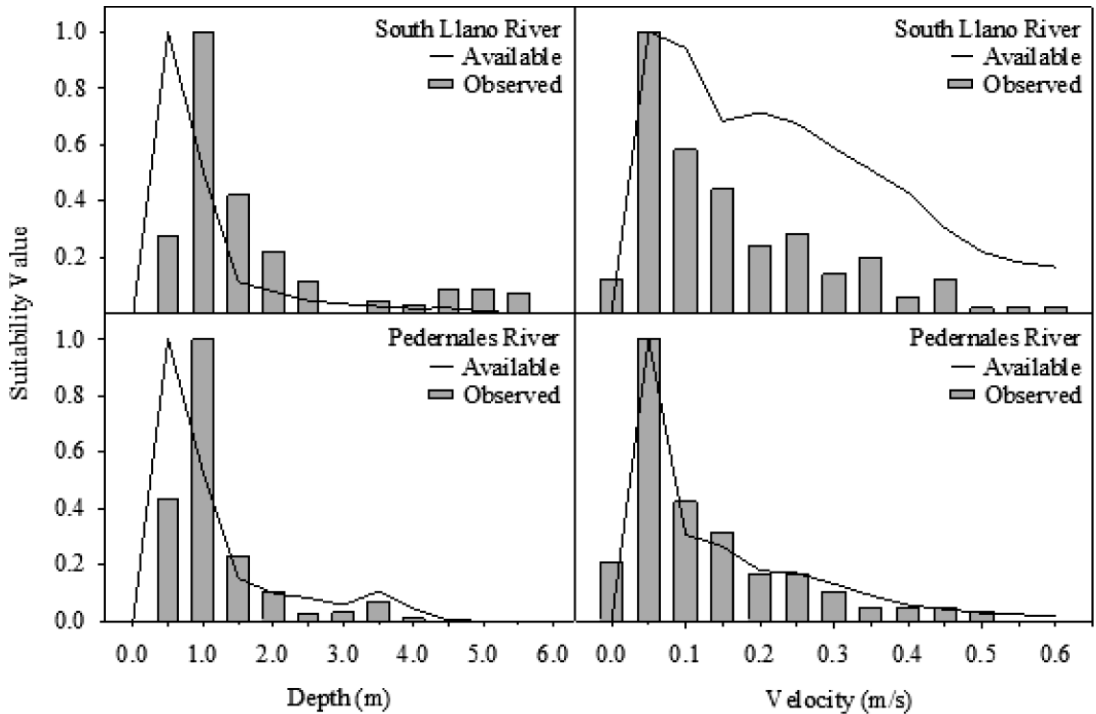
FIGURE 8.—Suitability curves for Guadalupe bass in the South Llano ($n = 162$ observations) and Pedernales rivers ($n = 393$ observations) between January and August 2008 in terms of the available depths and velocities and those observed to have been used by the fish.

Horton and Guy 2002; Stormer and Maceina 2009). Consequently, habitat associations are weaker and home range sizes increase during the spring (Todd and Rabeni 1989; Raibley et al. 1997). Even so, Guadalupe bass, like many other stream-dwelling fishes (Schlosser and Angermeier 1995), were not involved in long-range spawning migrations.

Additional environmental factors related to the movement, and consequently the habitat associations, of Guadalupe bass were time of day and flow regime. Guadalupe bass often shifted from habitats with cover during the day to open water at night. Associating with cover during the day probably reduces predation risks (Horton and Guy 2002; this study), and movement into open water is probably for nocturnal foraging (Todd and Rabeni 1989). In addition to undertaking diel movements, Guadalupe bass were readily responsive to changes in the flow regime. During the May 2008 diel tracking period, Guadalupe bass in the Pedernales River shifted from branches and roots along the stream bank to an area downstream of boulders or bedrock ledges during a rapid rise in flow caused by a flash flood event during which flows increased from about 1 to 6 m³/s over the course of 1 d. The use of instream structures as refugia is suspected in stream-adapted

fishes (Minckley and Mefee 1987) as a way to resist downstream displacement. To date, telemetry studies have only tracked smallmouth bass to eddy mesohabitats with lower current velocities during a flood event (Todd and Rabeni 1989). Also in the Pedernales River, Guadalupe bass gradually shifted toward pools with greater depths during a period of extreme low flow in summer. Responding to periods of stream drying by moving from preferred habitats is common in other stream fishes (Matthews 1996) as well as *Micropterus* spp. (Stormer and Maceina 2009).

Habitat degradation is the most significant threat to the persistence of Guadalupe bass (Edwards 1980). In our study, habitat for Guadalupe bass more than 260 mm long consisted of a heterogeneous mix of run and open-water pool habitats with undercut banks and instream woody debris. The extirpation of the Guadalupe bass in the Concho River of Texas (Edwards 1980) is probably attributable to changes in available habitats because of dam construction, which typically reduces flood pulses, undercut banks, habitat heterogeneity, and the deposition of large woody debris (Poff et al. 1997; Crook and Robertson 1999). Similar habitat changes from dam construction and the mismanagement of watersheds probably caused population

declines and localized extirpations in shoal bass (Stormer and Maceina 2009). Future concerns regarding the persistence of Guadalupe bass include stream dewatering (Hurst et al. 1975) and aquifer drawdowns (Bowles and Arsuffi 1993) as well as impoundment (Edwards 1978) and competition with lacustrine-adapted species (Koppelman and Garrett 2002), all of which may contribute to the reduction of the Guadalupe bass's range (Jelks et al. 2008). Such negative impacts of anthropogenic stream alteration occur worldwide and may be mitigated by watershed management practices that favor sustainable management and ecological integrity (Richter et al. 2003). For example, watershed management approaches that include mimicry of natural flow regimes favor the recruitment of native fish (Propst and Gido 2004), naturally occurring assemblage compositions (Marchetti and Moyle 2001), and the restoration of habitat heterogeneity (Aadland 1993). Furthermore, future watershed management approaches should consider the effects of surrounding land use on aquatic biodiversity (Sutherland et al. 2002; Allan 2004). The consequences of anthropogenic alteration remain poorly understood; however, continued research on ecosystem and species responses to restoration efforts will provide more complete understanding of aquatic biodiversity conservation (Bunn and Arthington 2002).

Acknowledgments

References

Aadland, L. P. 1993. Stream habitat types: their fish assemblages and relationship to flow. North American Journal of Fisheries Management 13:790–806.

Allan, J. D. 2004. Landscapes and riverscapes: the influences of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35:257–284.

Allouche, S. 2002. Nature and functions of cover for riverine fish. Bulletin Français de la Peche et de la Pisciculture 365/366:297–324.

Bangham, R. V., and N. L. Bennington. 1939. Movement of fish in streams. Transactions of the American Fisheries Society 68:256–262.

Barton, G. J., R. R. McDonald, J. M. Nelson, and R. L. Dinehart. 2005. Simulation of flow and sediment mobility using a multidimensional flow model for the white sturgeon critical habitat reach, Kootenai River near Bonners Ferry, Idaho. U.S. Geological Survey, Scientific Investigations Report 2005–5230, Reston, Virginia.

Bowles, D. E., and T. L. Arsuffi. 1993. Karst aquatic ecosystems of the Edwards Plateau region of central Texas, USA: a consideration of their importance, threats to their existence, and efforts for their conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 3:317–329.

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

Carmichael, G. J., and J. H. Williamson. 1986. Intensive production of Guadalupe bass. Progressive Fish-Culturist 48:133–136.

Cooke, S. J., S. G. Hinch, A. P. Farrell, D. A. Patterson, K. Miller-Saunders, D. W. Welch, M. R. Donaldson, K. C. Hanson, G. T. Crossin, M. T. Mathes, A. G. Lotto, K. A. Hruska, I. C. Olsson, G. N. Wagner, R. Thomson, R. Hourston, K. K. English, S. Larsson, J. M. Shrimpton, and G. Van der Kraak. 2008. Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: an interdisciplinary case study of adult Fraser River sockeye salmon. Fisheries 33(7):321–338.

Crook, D. A., and A. I. Robertson. 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. Marine and Freshwater Resources 50:941–953.

Edwards, R. J. 1978. The effect of hypolimnion reservoir releases on fish distribution and species diversity. Transactions of the American Fisheries Society 107:71–77.

Edwards, R. J. 1980. The ecology and geographic variation of the Guadalupe bass, *Micropterus treculii*. Doctoral dissertation. University of Texas, Austin.

Funk, J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85:39–57.

Garrett, G. P. 1991. Guidelines for the management of Guadalupe bass. Texas Parks and Wildlife Department, PWD-RP-N3200-367-11/91, Kerrville.

Gatz, A. J., and S. M. Adams. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecology of Freshwater Fish 3:35–48.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews 34:221–242.

Hill, J., and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. Copeia 1987:376–380.

Horton, T. B., and C. S. Guy. 2002. Habitat and movement of spotted bass in Otter Creek, Kansas. Pages 161–171 *in* D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Horton, T. B., C. S. Guy, and J. S. Pontius. 2004. Influence of time interval on estimates of movement and habitat use. North American Journal of Fisheries Management 24:690–696.

Hubbs, C., R. J. Edwards, and G. P. Garrett. 2008. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. Texas Academy of Science, Austin. Available: www.texasacademyofscience.org/. (May 2009).

Hurst, H., G. Bass, and C. Hubbs. 1975. The biology of the Guadalupe, Suwannee, and redeye basses. Pages 47–53 in R. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Jackson, D. A. 2002. Ecological effects of Micropterus introductions: the dark side of black bass. Pages 221–232 in D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev electivity index. Oecologia 14:413–417.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Conteras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33(8):372–407.

Koppelman, J. B., and G. P. Garrett. 2002. Distribution, biology, and conservation of the rare black bass species. Pages 333–341 in D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Krebs, C. J. 1999. Ecological methodology, 2nd edition. Addison-Welsey, Menlo Park, California.

Lyons, J., and P. Kanehl. 2002. Seasonal movements of smallmouth bass in streams. Pages 149–160 in D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11:530–539.

Matthews, K. R. 1996. Habitat selection and movement patterns of California golden trout in degraded and recovering sections of the Golden Trout Wilderness, California. North American Journal of Fisheries Management 16:579–590.

McDonald, R. R., J. M. Nelson, and J. P. Bennett. 2005. Multi-dimensional surface-water modeling system user's guide. U.S. Geological Survey, Techniques and Methods, 6-B2, Reston, Virginia.

McMahon, T. E., A. V. Zale, and D. J. Orth. 1996. Aquatic habitat measurements. Pages 83–115 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Mesing, C. L., and A. M. Wicker. 1986. Home range, spawning migrations, and homing of radio-tagged largemouth bass in two central Florida lakes. Transactions of the American Fisheries Society 100:29–32.

Microcomputer Power. 2002. CANOCO (Canonical Community Ordination), version 4.5. Microcomputer Power, Ithaca, New York.

Minckley, W. L., and G. K Mefee. 1987. Differential selection by flooding in stream fish communities of the arid American Southwest. Pages 93–104 in W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Near, T. J., T. W. Kassler, J. B. Koppelman, C. B. Dillman, and D. P. Philipp. 2003. Speciation in North American black basses, Micropterus (Actinopterygii: Centrarchidae). Evolution 57:1610–1621.

Newcomb, T. J., D. J. Orth, and D. F. Stauffer. 2007. Habitat evaluation. Pages 843–886 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Orth, D. J., and T. J. Newcomb. 2002. Certainties and uncertainties in defining essential habitats for riverine smallmouth bass. Pages 251–264 in D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Peake, S. 1998. Sodium bicarbonate and clove oil as potential anesthetics for nonsalmonid fishes. North American Journal of Fisheries Management 18:919–924.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Propst, D. L., and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society 133:922–931.

Raibley, P. T., K. S. Irons, T. M. O'Hara, and K. D. Blodgett. 1997. Winter habitats used by largemouth bass in the Illinois River, a large-floodplain ecosystem. North American Journal of Fisheries Management 17:401–412.

Railsback, S. F., R. H. Lamberson, B. C. Harvey, and W. E. Duffy. 1999. Movement rules for individual-based models of stream fish. Ecological Modeling 123:73–89.

Remshardt, W. J., and W. L. Fisher. 2009. Effects of variation in streamflow and channel structure on smallmouth bass habitat in an alluvial stream. River Research and Applications 25:661–674.

Richter, B. D., R. Mathews, D. L. Harrison, and R. Wigington. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. Ecological Applications 13:206–224.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes in lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing,

sample size, and a proposed framework. North American Journal of Fisheries Management 14:607–615.

Smithson, E. B., and C. E. Johnston. 1999. Movement patterns of stream fishes in an Ouachita Highlands stream: an examination of the restricted-movement paradigm. Transactions of the American Fisheries Society 128:847–853.

Snedden, G. A., W. E. Kelso, and D. A. Rutherford. 1999. Diel and seasonal patterns of spotted gar movement and habitat use in the lower Atchafalaya River basin, Louisiana. Transactions of the American Fisheries Society 128:144–154.

Sutherland, A. B., J. L. Meyer, and D. P Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. Freshwater Biology 47:1791–1805.

Stormer, D. G., and M. J. Maceina. 2009. Habitat use, home range, and movement of shoal bass in Alabama. North American Journal of Fisheries Management 29:604–613.

Sturges, H. A. 1926. The choice of a class interval. Journal of the American Statistical Association 21:65–66.

Tillma, J. S., C. S. Guy, and C. S. Mammoliti. 1998. Relations among habitat and population characteristics of spotted bass in Kansas streams. North American Journal of Fisheries Management 18:866–893.

Todd, B. L., and C. F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Transactions of the American Fisheries Society 118:229–242.

VanArnum, C. J. G., G. L. Buynak, and J. R. Ross. 2004. Movement of smallmouth bass in Elkhorn Creek, Kentucky. North American Journal of Fisheries Management 24:311–315.

Viosca, P. Jr. 1931. The southern small-mouthed black-bass, *Micropterus pseudaplites* Hubbs. Transactions of the American Fisheries Society 61:95–98.

Warren, M. L. Jr., B. M. Burr, S. J. Walsh, H. L. Bart Jr., R. C. Cashner, D. A. Etnier, B. J. Freeman, B. R. Kuhajda, R. L. Mayden, H. W. Robison, S. T. Ross, and W. C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern Unites States. Fisheries 25(10):7–31.

Wheeler, A. P., and M. S. Allen. 2003. Habitat and diet partitioning between shoal bass and largemouth bass in the Chipola River, Florida. Transactions of the American Fisheries Society 132:438–449.

Williams, C. S., and T. H. Bonner. 2006. Habitat associations, life history, and diet of the Sabine shiner *Notropis sabinae* in an East Texas stream. American Midland Naturalist 155:84–102.

Winter, J. D. 1996. Advances in underwater biotelemetry. Pages 572–575 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.