Spatial Ecology of Shoal Bass in Ichawaynochaway Creek, Georgia

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Abstract.—Shoal Bass (*Micropterus cataractae*) are fluvial specialists endemic to the Apalachicola-Chattahoochee-Flint River Basin that are considered to be in decline throughout their native range. Effective conservation requires a comprehensive understanding of the migratory behavior and multi-scale habitat associations of Shoal Bass with riverine shoals, the critical mesohabitat upon which the species depends. We assessed movement patterns and habitat use of Shoal Bass using radio telemetry in the lower 24 km of Ichawaynochaway Creek, a 6th-order tributary of the Flint River and one of the few relatively undisturbed streams inhabited by this species. In general, Shoal Bass exhibited relatively low movement rates with increased movement in the spring, and

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no tagged Shoal Bass migrated from the creek into the Flint River during the study period. Most study fish preferred moderate depths (<2 m) and swift velocities during the year, and higher velocities in the winter, potentially reflecting seasonal changes in flow. These conditions were routinely satisfied through occupation of a 9-km reach with a network of large shoal complexes. Shoal Bass exhibited a distinct preference for close proximity to large shoals, and an affinity for greater depth variability associated with edge and boundary conditions within discrete shoal complexes. Despite previous studies that have documented high movement of this species in other systems, these findings suggest that the Ichawaynochaway Creek Shoal Bass population may be relatively sedentary and associate to specific areas that provide suitable habitat. This may have implications for assessing the integrity, distribution, and abundance of suitable Shoal Bass habitat in small karst limestone streams, designing projects for restoration or enhancement of existing habitat, and gauging the species vulnerability to threats such as habitat loss, introgression, and hybridization.

Introduction

Shoal Bass *Micropterus cataractae* has been recognized as a unique riverine black bass for many years (Bailey and Hubbs 1949), but has only been formally described since 1999 (Williams and Burgess 1999). Shoal Bass are among a suite of aquatic species endemic to the Apalachicola-Chattahoochee-Flint (ACF) basin in Alabama, Florida, and Georgia (Couch et al. 1996; Brim Box and Williams 2000). Shoal Bass populations appear to be declining across parts of their range, and are nearly extirpated in the Chattahoochee River below Atlanta due to dam construction, habitat destruction, and introgressive hybridization with nonnative congeners (Sammons et al. 2015). Thus, with a growing emphasis on native black bass management and the rising popularity of Shoal Bass among anglers, attention has turned to species conservation. Effective Shoal Bass conservation requires knowledge of species movements and habitat use patterns to help identify priority management actions such as habitat restoration or enhancement and harvest regulations (Sammons et al. 2015).

Movements and habitat use of black bass (*Micropterus* spp.) can vary greatly depending on species and environmental conditions, supporting the need for inter- and intraspecific knowledge to inform management across the genus. For example, Smallmouth Bass *Micropterus dolomieu* are known to migrate substantial distances in large rivers and reservoirs at northern latitudes, but home ranges can be smaller in streams and more productive lakes (Langhurst and Schoenike 1990; Ridgway and Shuter 1996). Largemouth Bass *Micropterus salmoides* are usually more sedentary, with home ranges often <5 ha (Winter 1970; Mesing and Wicker 1986). Overall, Shoal Bass were thought to be relatively sedentary until recent studies revealed relatively large-scale movements (>5 km) occurred throughout the year (Goclowski et al. 2013; Ingram et al. 2013; Sammons and Earley 2015). Furthermore, the species exhibits potamodromy, or migration for reproduction within freshwater systems, in the upper Flint River in Georgia, moving up to 200 km to

access spawning habitat (Sammons 2015). Compared to mainstem rivers, Shoal Bass were observed to have limited movement within smaller tributaries (Stormer and Maceina 2009), but at times fish from mainstem rivers have been found to move up into tributaries during the spawning season (Sammons and Goclowski 2012; Sammons and Earley 2015). Given the observed range of movement behavior within mainstem rivers and between tributaries and mainstem rivers, understanding potential drivers of movements is imperative to informing management at the proper scale (Northcote 1997).

Shoal Bass are considered fluvial habitat specialists based on their common association with rocky substrates in swift flowing environments (Wheeler and Allen 2003; Goclowski et al. 2013). Individuals typically occur in larger rivers and streams that contain appropriate "shoal" habitat (i.e., shallow channel segments characterized by rocky substrates, swift current, and high gradient), but are rarely found in smaller streams (<4th order; Ramsey 1975; Katechis 2015). As habitat specialists, the entire life history of Shoal Bass is closely linked to shoal habitat. Shoals provide substrate for spawning, refuge from predators, and invertebrate (insect and crustacean) and vertebrate food items for all developmental stages (Wheeler and Allen 2003; Sammons 2012; Sammons et al. 2015). Shoal Bass are generally intolerant of reservoir conditions but have been documented moving through them to reach lotic habitat when translocated (Ingram et al. 2013), but not on their own initiative (Sammons and Earley 2015). Throughout their life history, use of shoal habitat may also be a mechanism for reducing interspecific competition and hybridization with native or introduced congeners (Wheeler and Allen 2003; Goclowski et al. 2013). Despite the importance of rocky, swift velocity habitats to Shoal Bass, little is known about differences between male and female habitat use, or the relative importance of shoal size and distribu-

tion within occupied streams. This knowledge is needed to assess the current state of Shoal Bass habitat at a scale relevant to its life history, and to assess population vulnerability and potential for restoration.

The objectives of this study were to describe movement and habitat use of adult Shoal Bass in Ichawaynochaway Creek, a relatively undisturbed 6th-order tributary of the lower Flint River. Specifically, we set out to (1) quantify and assess variation in movement patterns among individuals, (2) to compare individual-level habitat associations across seasons and sexes, and (3) to assess population-level habitat preferences for local and neighboring shoal habitat characteristics within a habitat use versus availability framework.

Methods

Study Area

With a watershed area of 2,750 km², Ichawaynochaway Creek is one of the largest tributaries to the Flint River and is mainly fed by groundwater from the Floridan Aquifer during lower flow conditions (Golladay et al. 2007). Because of this karst geology, lower portions of Ichawaynochaway Creek contain numerous rocky shoals and limestone outcrops, unlike most coastal plain streams. This study was conducted on a 24-km reach in Baker County, where the creek flows through Ichauway, a 12,000-ha private reserve that is the research site of the Joseph W. Jones Ecological Research Center (Figure 1). This reach was bounded by a breached, 1920s-era power dam (RKM 23.6) and the confluence with the Flint River (RKM 0; Figure 1).

Fish Tagging and Tracking

Adult Shoal Bass were collected during the prespawning season (March–April 2015) by electrofishing (Figure 1). Equal effort was
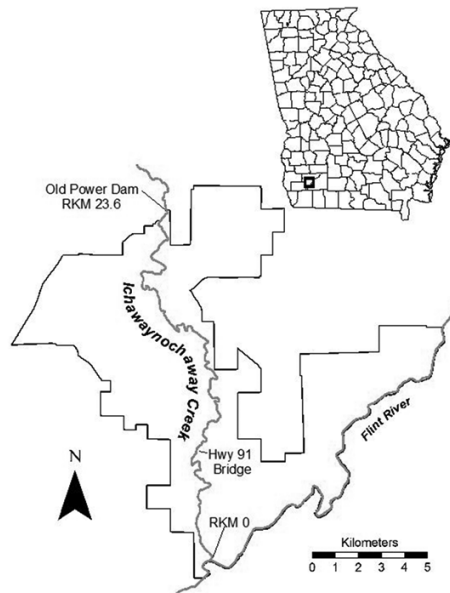
Figure 1. Ichauway reserve, located in Baker County, Georgia. The entire study reach of Ichawaynochaway Creek (RKM 0–23.6) flows through the center of the reserve and the Flint River forms the eastern border.

expended throughout the study area to minimize location bias, however few fish were captured below the Hwy 91 Bridge (Figure 1). Upon capture, the first 30 Shoal Bass that met the minimum 185-g weight requirements for the tags were measured (total length TL; mm) and weighed (g). Sex was visually determined during transmitter insertion. Fish were anesthetized using tricane methanesulfonate (150 mg/L) and surgically implanted with a 3.6-g transmitter with a battery life of 365 d (model F1580, Advanced Telemetry Systems) and an internal anchor tag (Floy Tag FM-84, Seattle, Washington, USA; Maceina et al. 1999). Shoal Bass were released at their capture location after regaining equilibrium. Although tricane methanesulfonate is regulated by a 21-d withdrawal period for use in public waters, public access is restricted at Ichauway and angling is not allowed in the study reach of Ichawaynochaway Creek.

Tracking began after a 14-d, postsurgery recovery period by either motorboat, kayak, or wading, and was conducted approximately every 14 d between April 2015 and April 2016. Tracking surveys of the entire study area were conducted using an ATS model R2000 receiver (Isanti, MN) and a directional yagi antenna. The signal range of transmitters was 0.8 km under normal conditions and may have been reduced in deeper water (>10 m; Sammons and Earley 2015); however, depths of the stream channel rarely exceeded 8 m. Daily streamflow ranged from 4.8 to 99.1 m^3/s during tracking (U.S. Geological Survey stream gauge site 02355350). When telemetered fish were not located in the study area, tracking was conducted in a 7-km reach above the dam, and within a reach of the Flint River ± 10 km from the Ichawaynochaway Creek confluence. In addition, a passive ATS model R4500 data-logger was deployed at river kilometer (RKM) 0 to detect any Shoal Bass leaving Ichawaynochaway Creek.

Fish locations were obtained as described by Sammons and Earley (2015) and marked using a Global Positioning System unit (Garmin GPSmap 78 s; Olathe, KS). Tracking

events were conducted downstream by boat until a signal was detected. A fish location was marked when the signal was strongest with the antenna pointed at the water's surface. At each fish location we recorded time and transmitter number, and measured water depth and midwater column velocity (via portable flowmeter model 2100, Swoffer Instruments, Seattle, Washington, USA). Fish locations obtained via telemetry were later used to associate each fish location with the substrate present at the location of the fish in a previously developed habitat map.

Investigating Habitat Associations

The instream habitat of Ichawaynochaway Creek was mapped using side scan sonar in 2008 (Kaeser and Litts 2008, 2010). The resulting map included classified substrates, mid-channel water depth, and large woody debris (defined as any piece of wood ≥10 cm diameter and ≥1.5 m in length; Figure 2). Substrate class descriptions, and details of field-assessed map accuracy are provided by Kaeser and Litts (2008, 2010). Because much of the substrate in Ichawaynochaway Creek
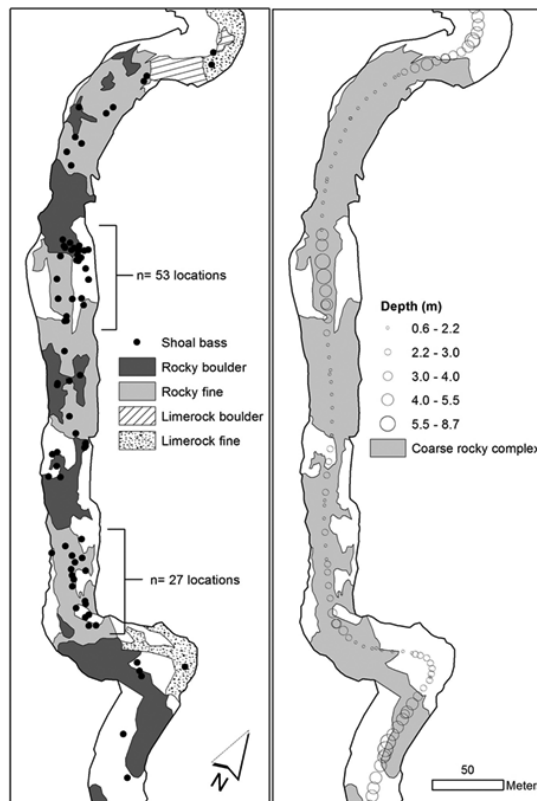

Figure 2. Map of a single coarse rocky complex in Ichawaynochaway Creek, Georgia spanning river kilometer 16.5–17.1, where the largest number of telemetered Shoal Bass locations (*N* = 121) occurred. Figure denotes Shoal Bass telemetry locations (left panel) and center channel depth (right panel). The complex (14,700 m²) was composed of alternating patches of rocky boulder and rocky fine substrates; fish were frequently observed in proximity to the margins of these substrate patches, in areas of transition from shallow to deeper depths.

was large and coarse, and the channel was entrenched and highly stable, we did not expect any major changes in substrate distribution to have occurred between the habitat mapping and this study.

Fish locations obtained via telemetry were used to characterize population-level habitat use, as opposed to individual microhabitat use, within a 17.5-km focal reach of the study area. Among the 30 study fish, only 1 fish was ever located downstream of RKM 7.0; we chose to remove this individual (N = 9 locations) from the habitat-use analysis, and restricted the area for analysis to a focal reach spanning RKM 6.0–23.5. We used the distance-based approach, described in detail by Sterrett et al. (2015), to associate fish locations with map data (Conner and Plowman 2001; Conner et al. 2003). A 15-m buffer was generated around each fish location to represent the area in "use." To evaluate habitat use versus availability, we generated random locations (N = 475), one for each observed fish location (Northrup et al. 2013) that represented habitat available within the focal reach using the Generalized Random Tessellated Stratification (GRTS) sampling algorithm (Kincaid et al. 2013). We assumed all random availability locations were independent. We defined available habitat as habitat within a fish's potential home range (Johnson 1980) and assumed that habitat measured at the 18-km scale was proportionally similar to habitat available at the home-range scale (i.e., 1 km). To prevent overlap of used and random locations, buffered areas around used locations were excluded from the area available for random location assignment.

We identified a set of predictor variables representing local habitat and neighboring shoal habitat from the map that might explain patterns of habitat use by adult Shoal Bass in Ichawaynochaway Creek. To examine the influence of local features we used the NEAR tool in Arc GIS 10.2 and calculated the linear distances from all locations to the edge of the nearest representative of each of the following substrate features: (A) boulder (i.e., the nearest distance to either rocky boulder or limerock boulder substrates), (B) boulder-bedrock (i.e., nearest distance to either rocky boulder, limerock boulder, or limerock fine—a class of limestone bedrock substrate as defined in Kaeser and Litts (2010)), and (C) coarse rocky complex (CRC), a composite feature developed to represent potential shoal areas. We defined "coarse rocky complex" as an area spanning the creek channel composed of contiguous patches of rocky boulder, limerock boulder, and rocky fine substrates. Of note, our CRCs did not incorporate elements of depth and current velocity typically recognized as "shoal" habitat features. Patches of limerock fine substrate, narrow bands of rocky substrate along the river margins, and any complexes less than 200 m^2 in total area were excluded from the CRC class. Total counts of LWD were summarized within the 15-m buffer of all locations. To extract relevant water depth data, all used and random locations were snapped to the mid-channel line that represented the sonar survey track (Sterrett et al. 2015). At the snapped position, a 15 m buffer was generated around each location, and all depth measurements within the buffer ($n \geq 4$) were used to yield a measurement of average local depth and depth variability (standard deviation of depths) for each location (Sterrett et al. 2015).

To assess the influence of neighborhood habitat features, we calculated three variables representing near shoal-complex characteristics: total area (m^2) of the nearest CRC, distance (shortest channel length, m) to nearest neighboring CRC, and total area (m^2) of nearest neighboring CRC. If neighborhood habitats were found to be important, we inferred that features of the nearest shoal and instream, neighborhood context (i.e., shoal arrangement and sizes) influenced the likelihood of Shoal Bass occurring at any particular location in the stream channel.

Data Analyses

Mean daily movement rates of Shoal Bass were calculated as the distance moved between locations divided by elapsed time (Sammons et al. 2003). Mean daily movement (log-transformed), and stream velocity and depth at observed locations were compared among seasons (spring: March–May, summer: June–August, fall: September–November, and winter: December–February) and sexes using a mixed-model analysis of variance (ANOVA) (SAS Institute 2000). A Bonferroni correction ($P < 0.10$/number of comparisons) was used for multiple comparisons. Substrate use by male and female fish was compared among seasons (as percent use) using Z-tests (Sammons and Earley 2015). Significance for these tests was set $P = 0.10$, unless a Bonferroni correction was used as described above.

Following the habitat use-availability analyses of Sterrett et al. (2015), we used logistic regression (Hosmer and Lemeshow 2000) and an information theoretic approach (Burnham and Anderson 2002) to evaluate Shoal Bass habitat use at the population level given the habitat available measured by random locations (Gillies et al. 2006; Beyer et al. 2010). We developed a set of 11 a priori candidate models to explore hypotheses related to local habitat features and six a priori candidate models to explore additional hypotheses related to neighborhood habitat features (Table 1). Local habitat models examined combinations of distance to boulder, boulder-bedrock, and CRC, mid-channel depth, and mid-channel depth variability. Although LWD was measured during the habitat survey, we did not include LWD in any candidate model because Shoal Bass are not known to use LWD in rocky habitats (Goclowski et al. 2013) and variation in LWD among fish and random locations was low. Correlated variables ($r^2 > 0.50$) were never

included in the same candidate model. We also included a global model that contained all local and neighborhood habitat variables to evaluate model fit. We included an individual random effect in all models to account for nonindependence among repeat observations of habitat used by the same fish and unequal number of observations per fish. The random effect was centered on zero with a large variance in each candidate model, which allowed for robust population-level inference in habitat use (Gillies et al. 2006). We used all random locations ($N = 475$) to represent available habitat to each individual and assumed that actual habitat availability (i.e., within each fish's home range) was proportional to habitat available in the study area.

We evaluated the relative support of each local and neighborhood habitat use-availability model using Akaike's Information Criterion (AIC) with a small-sample bias adjustment (AICc) (Burnham and Anderson 2002). The number of parameters (K) for each candidate model included the number of variables in the model and an additional three parameters representing the intercept, error term, and variance of the random effect. We calculated Akaike weights (w) for each model, which ranged from zero to one with the best approximating model having the highest weight; models with delta AICc of less than two were considered equally plausible (Burnham and Anderson 2002). We first identified a plausible candidate set of local habitat models, then evaluated relative support for the addition of neighborhood shoal habitat variables in a second candidate model set. We based inferences on variables included in the top approximating model(s) to understand the importance of local habitat and neighborhood features. The precision of each parameter was estimated using 95% credibility intervals. We calculated scaled odds ratios for each predictor in top model(s) to facilitate interpretation of habitat and neighborhood variables (Hosmer and Lemeshow 2000).

Ingram et al.

Table 1. Total length (TL, mm), weight (WT, g), number of times relocated (LOC), maximum range (Max range, km), days at large during the study (Days), and the fate of each male (M) and female (F) Shoal Bass tracked from April 2015–April 2016 in Ichawaynochaway Creek, Georgia. Maximum range was defined as the distance between the farthest upstream and farthest downstream location a fish was relocated.

Transmitter	Sex	TL	WT	LOC	Max range	Days	Fate
8010	M	321	409	4	2.30	331	Tag Died
8028	F	360	640	21	4.63	364	Alive
8052	M	356	667	18	8.49	364	Alive
8071	F	351	563	18	0.46	316	Tag Died
8090	F	538	620	24	14.70	345	Tag Died
8110	M	335	552	9	9.32	100	Fish Died
8131	M	390	820	19	0.63	331	Tag Died
8151	M	431	1110	19	8.11	345	Tag Died
8170	F	378	800	17	0.30	364	Alive
8191	F	397	932	14	0.56	330	Tag Died
9001	M	319	361	20	0.50	345	Tag Died
9014	M	315	389	17	5.66	304	Tag Died
9023	F	322	373	17	7.93	148	Unknown
9031	F	356	456	14	0.32	304	Tag Died
9044	F	375	803	18	0.15	345	Tag Died
9052	M	331	501	17	0.27	345	Tag Died
9063	M	374	612	21	0.30	364	Alive
9073	M	466	1367	10	0.08	321	Tag Died
9082	F	312	352	24	11.12	364	Alive
9091	F	353	631	12	12.55	203	Unknown
9104	M	350	606	17	1.47	364	Alive
9112	M	340	602	18	0.11	364	Alive
9120	M	338	560	9	5.12	330	Tag Died
9130	M	360	675	17	0.21	330	Tag Died
9142	M	328	487	19	0.74	364	Alive
9151	F	315	398	22	4.90	345	Tag Died
9159	F	348	617	10	0.23	345	Tag Died
9171	F	340	575	18	1.41	364	Alive
9183	M	382	710	12	2.45	286	Unknown
9192	F	362	631	16	0.47	364	Alive

All models used Markov chain Monte Carlo (MCMC) sampling implemented in JAGS (version 3.4.0) using the Rjags package in R (version 3.3.1), and models were fit using 5,000 iterations, a 500 burn-in, a thinning rate of three to reduce autocorrelation among samples, three chains, and diffuse priors. Model convergence was assessed using visual inspection of chains and Gelman-Rubin's convergence diagnostic (R-hat <1.1; Gelman and Rubin 1992). We evaluated model fit of the global model using a posterior predictive check and a Bayesian *P*-value based on the sums of squares discrepancy metric, where a fit model has a *P*-value near 0.5 (Gelman and Hill 2007).

Results

We captured and implanted transmitters in 16 male and 14 female adult Shoal Bass ranging from 312 to 466 mm TL and 352–1,367 g (Table 2). Twenty-one tracking events were conducted after initial capture from April 14, 2015 to April 12, 2016, with individual fish at large for 100–364 d and relocated 4–24 times, resulting in a total of 484 fish locations (Table 2). Of the 30 telemetered fish, one fish was relocated downstream past the Hwy 91bridge after initial capture, and remained at RKM 1.5–1.6 for the duration of the study. Two fish emigrated upstream of the breached power dam during the study (one in May and one in March). The fish located in May later returned to the study area and remained for the entirety of the study. The fish located in March remained upstream of the study area until the study ended. No fish were located in a 5.3-km section below the Hwy 91 bridge (i.e., between RKM 1.6 and 7.0). This section was deeper with slower average velocity than other sections of the study area. No fish were detected by the passive data logger located near the confluence of the Flint River, indicating that all study fish remained in Ichawaynochaway Creek for the duration of the study.

Most fish locations (446 of 484; 92%) occurred in a 9-km reach spanning RKM 14–22. A total of 24 CRCs existed within this reach, representing 54% of the total channel area. The ratio of rocky boulder to rocky fine substrates in this reach was nearly 50:50 (i.e., 82,300:83,800 m2). Eleven study fish were consistently located in a single, large (14,700 m2) shoal complex spanning RKM 16.5–17.1 (Figure 2).

Table 2. Seasonal mean and standard error (SE) daily movement rates (m/d), depth (m), and velocity (m/s) at capture locations of male and female Shoal Bass in Ichawaynochaway Creek, Georgia (April 2015–April 2016). Means of each variable followed by the same letter were similar among seasons ($P \geq 0.1$).

Sex	Parameter	Spring	Summer	Fall	Winter
Male	Movement	134.0y (64.8)	9.1z (4.0)	5.6z (4.0)	3.2z (0.7)
	Depth	2.4y (0.2)	1.5z (0.1)	2.1y (0.2)	3.2yz (0.2)
	Velocity	0.3z (0.0)	0.3z (0.0)	0.3z (0.0)	0.8y (0.1)
Female	Movement	131.1y (56.3)	104.9yz (71.3)	5.25z (1.3)	24.7yz (20.5)
	Depth	2.3y (0.2)	1.5z (0.1)	1.8z (0.2)	2.9yz (0.2)
	Velocity	0.3z (0.0)	0.3z (0.0)	0.3z (0.0)	0.8y (0.1)

Movement Patterns

All locations for each of nearly half of the study fish (16 of 30) fell within a reach of creek spanning less than 1 km per individual. Thirteen of these limited-range fish appeared to remain in a reach <500 m long for the duration of the study (Figure 4). Shoal Bass daily movement was higher for females (mean = 73.8 m/d) compared to males (mean = 35.9 m/d; F = 3.86; df = 1, 454; P = 0.04; Table 1) and females, on average, had greater maximum movement distances (mean = 7.23 km; SE = 2.7; maximum = 15.00 km) compared to males (mean = 4.07 km; SE = 1.4;

maximum = 9.00 km; Table 2). In general, average daily movement was less than 150 m for both sexes throughout the year (Table 1; Figure 3). Daily movements of both sexes were higher in the spring compared to the fall and winter (F = 2.62; df = 3, 98; P < 0.01; Table 1; Figure 3). Daily movement of males was 14–44 times greater in spring than movement in the other seasons. However, female movement was similar between spring and summer, and 4–24 times greater in spring and summer compared to fall and winter. Mean movement was similar between the sexes across seasons (F = 1.26; df = 4, 20; P = 0.32; Figure 3).
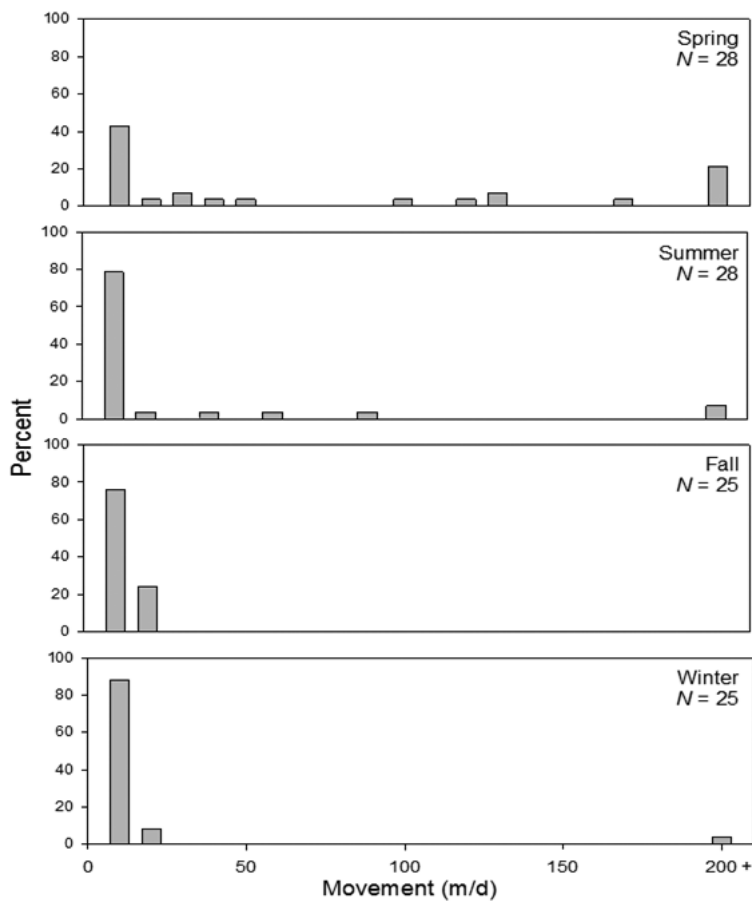

Figure 3. Seasonal movement distribution of telemetered Shoal Bass in the study reach of Ichawaynochaway Creek, Georgia.
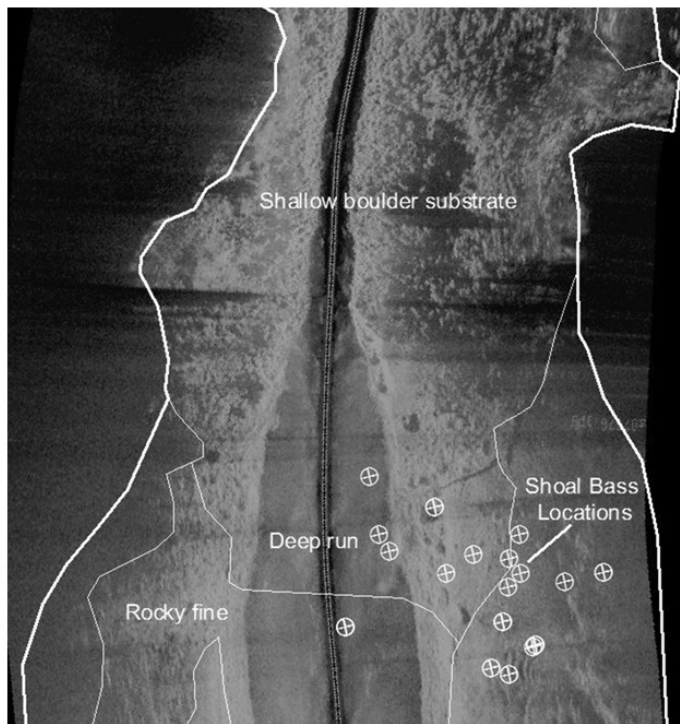
Figure 4. A close-up look at a high use area in Ichawaynochaway Creek, Georgia, within the coarse rocky complex at river kilometer 16.9, as it appeared in sonar imagery. A total of 33 Shoal Bass locations (white circle with crosshairs; many overlapping) were observed in the area shown. Here, fish occupied a 6-m deep run immediately downstream of a shallow, boulder outcrop that spanned the river channel. Water flow over the boulders and into the run created much turbulence, a phenomenon that is manifest in the sonar imagery as a fuzzy, whitish tone to the otherwise dark, water column region in the center of the image.

Individual-level Habitat Associations

Both male and female Shoal Bass occurred in areas with similar, moderate stream velocity (i.e., 0.5 m/s; $F = 3.86$; df = 1, 484; $P = 0.95$), except during the winter, when both sexes occurred in higher velocities (i.e., 0.8 m/s; $F = 2.47$; df = 4, 92; $P < 0.01$; Table 1). Mean depth was also similar among sexes ($F = 3.86$; df = 1, 484; $P = 0.12$), but it differed across seasons ($F = 2.47$; df = 4, 92; $P < 0.01$) with fish of both sexes located in deeper depths in the winter (Table 1).

Shoal Bass were located in all substrate classes over the duration of the study (Table 3). Percent limerock substrates (limerock fine and limerock boulder) and rocky fine substrates were similar among sexes ($Z = –0.68$; $P > 0.05$, $Z = 0.45$; $P > 0.05$, $Z = 0.78$; $P \geq 0.05$, respectively; Table 3). Male and female substrate use slightly differed in the fall and winter months with females utilizing a higher percentage of rocky fine substrate ($Z = –6.51$; $P < 0.05$ and $Z = –1.73$; $P < 0.05$, respectively; Table 3). Both sexes were found in similar substrates during the summer and spring spawning season (Z range –0.40 to –0.93; $P > 0.05$, respectively). During the summer, Shoal Bass were located in areas with lower percentages (23–37%) of rocky fine substrates compared to the winter and fall and in areas with higher percentages

Table 3. Percentage of fish locations associated with each mapped substrate class for male and female Shoal Bass during each season of the study in Ichawaynochaway Creek. Substrate class acronyms represent: sand (S), rocky fine (Rf), rocky boulder (Rb), rocky limerock fine (Lf), and limerock boulder (Lb).

		Substrate				
Sex	Season	S	Rf	Rb	Lf	Lb
Male	Spring	37	29	25	4	6
	Summer	27	24	39	5	5
	Fall	22	48	18	10	2
	Winter	29	36	22	12	2
Female	Spring	31	46	20	3	0
	Summer	19	37	37	5	2
	Fall	15	55	28	2	0
	Winter	13	67	20	0	0

(37–39%) of rocky boulder (Table 3). In the spring, fish were found in areas with higher percentages (31–37%) of sandy substrates compared to other substrates, and this was similar between sexes ($Z = -1.54$; $P > 0.05$). Use of sandy substrates was low during other seasons, and again, this was similar between sexes ($Z = 1.65$; $P > 0.05$; Table 3).

Population-level Habitat Use

Local and neighborhood habitat variables examined for use-availability analysis varied among fish and random locations (Table 4). Frequently relocated individuals had similar ranges in habitat-use variables compared to individuals observed less often, suggesting a limited influence of unequal location on habitat use.

The best-approximating local habitat model contained all of the model support (wi), included the variables distance to CRC and depth variability, and it was 5.4 times more likely to be the best approximating model than the second best model ($\Delta AICc = 3.4$), which included the interaction between CRC and depth variability (Table 5). Neighborhood habitat variables improved the best-approximating local habitat model and included the area of the nearest and nearest neighboring CRC (Table 5). This model was 5.7 times more likely the best neighborhood model than the next model ($\Delta AICc = 3.5$) which additionally included distance to the nearest neighboring CRC. Parameter estimates (scaled odds ratio) from the top neighborhood model indicated that Shoal Bass were, on average, 68 times less likely to occur with every 20-m increase in distance from the nearest CRC, and 15 times more likely to occur with every 5,000-m^2 increase in the area of the nearest CRC (Table 6). Additionally, Shoal Bass were 43 times more likely to occur with every 0.5-m increase in depth variability (standard deviation in mid-channel depths) and less likely to occur as the size of the nearest neighboring shoal increased (Table 6). The intra-class correlation coefficient (a measure of consistency among individuals) was high (0.71), suggesting similar habitat use-availability responses within and among individuals. Bayesian *P*-values indicated that the global and best-approximating models adequately fit the observed data ($P = 0.51$ and 0.51, respectively).

Table 4. Mean and standard error (SE) of local and neighborhood habitat variables quantified at capture ($N = 475$) location of Shoal Bass and random locations ($N = 475$) throughout the 24-km Ichawaynochaway Creek study area. The variables large woody debris (LWD), mid-channel depth, and mid-channel depth variability represent conditions within a 15-m buffer located mid-channel and adjacent to the position of the fish and proximity metrics represent distance to nearest substrate type. CRC = coarse rocky complex.

	Random Locations		Capture Locations	
Local Habitat Variables	Mean	SE	Mean	SE
Depth (m)	3.0	0.04	3.1	0.06
Depth variability (SD)	0.35	0.02	0.52	0.02
proximity to bedrock outcrop substrate (m)	14.8	1.3	8.7	0.70
proximity to boulder substrate (m)	41.7	2.70	12.0	0.95
proximity to nearest CRC (m)	24.7	2.12	2.9	0.37
Neighborhood Habitat Variables				
area of nearest CRC (m^2)	7093	340	11708	336
proximity to nearest neighbor CRC (m)	52.5	2.1	38.3	1.1
area of nearest neighbor CRC (m^2)	4194	204	3520	172

Discussion

Shoal Bass in Ichawaynochaway Creek were sedentary, with few large movement events occurring during the study period. When long-range movements did occur, Shoal Bass moved during the spring, most likely in relation to spawning activity (Bitz et al. 2015). Shoal Bass in a Chattahoochee River tributary were observed to have extremely low movement rates (<7 m/week), but these fish were confined to a 600-m reach of shoal habitat between two natural barriers (Stormer and Maceina 2009). Similarly, Shoal Bass in a 2-km reach of the Chattahoochee River bounded by an upstream dam and a downstream large reservoir also exhibited low movement (Sammons and Earley 2015). In contrast, Shoal Bass in the Flint River have been documented to move longer distances (>10 km), especially during the spring spawning period, when fish have been documented to move up to 200 km (Goclowski et al. 2013; Sammons 2015; T. Ingram, unpublished data). Similar to our study, Bitz et al. (2015) found low movements for Shoal Bass in the Chipola River, Florida, which, like Ichawaynochaway Creek, is a karst limestone stream with no movement barriers near the southern limit of the species' range. Movement of Shoal Bass may be at least in part dictated by geomorphology and hydrology of streams, combined with the quality and distribution of shoal habitats (Goclowski et al. 2013; Ingram et al. 2013; Sammons 2015). Thus, it is possible that behavior of this species in streams with abundant deep and complex shoal habitat (i.e., karst limestone features) and high groundwater influence may differ from those living in more typical lotic systems, similar to what has been found for Smallmouth Bass (Ettinger-Dietzel et al. 2016; Westhoff et al. 2016). Consistent and strong effects of rocky substrate and shoal area, along with movement patterns, suggest that a relatively small reach containing large

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Table 5. Candidate habitat use-availability models with mean deviance (Dev), effective number of parameters (K), AIC, AICc, the difference between the best model (bold type) and each subsequent model (delta-AICc), model weight (wi), and the standard deviation of the individual random effects (RE SD) for habitat selection of Shoal Bass in Ichawaynochaway Creek, Georgia, from April 14 2015 to April 12 2015. CRC = coarse rocky complex.

Local Habitat Model	Dev	K	AICc	ΔAICc	wi	RE SD
Proximity to CRC, depth variability	3828.9	5.0	3839.0	0.0	1.00	0.07
Proximity to CRC x depth variability	3830.2	6.0	3842.4	3.4	0.18	0.06
Proximity to CRC x depth	3868.3	6.0	3880.5	41.5	0.00	0.07
Proximity to CRC, depth	3872.8	5.0	3883.0	44.0	0.00	0.07
Proximity to CRC	3887.3	4.0	3895.4	56.4	0.00	0.06
Proximity to boulder, depth variability	3904.2	5.0	3914.3	75.3	0.00	0.07
Proximity to boulder	3943.3	4.0	3951.4	112.4	0.00	0.07
Proximity to boulder, depth	3941.9	5.0	3952.1	113.1	0.00	0.08
Proximity to boulder-bedrock, depth variability	4060.5	5.0	4070.6	231.6	0.00	0.06
Proximity to boulder-bedrock	4130.8	4.0	4138.9	299.9	0.00	0.07
Proximity to boulder-bedrock	4130.4	5.0	4140.5	301.5	0.00	0.07

Neighborhood Habitat Candidate Models	Dev	K	AICc	ΔAICc	wi	RE SD
Proximity to CRC, depth variability, area of the nearest CRC, area of the nearest neighboring CRC	3783.3	7.0	3793.5	0.0	1.00	0.07
Proximity to CRC, depth variability, area of the nearest CRC, area of the nearest neighboring CRC, proximity of the nearest CRC	3784.8	8.0	3796.9	3.5	0.17	0.06
Proximity to CRC, depth variability, area of the nearest CRC	3802.7	6.0	3810.8	17.4	0.00	0.06
Proximity to CRC, depth variability, area of the nearest neighboring CRC	3807.6	6.0	3815.6	22.2	0.00	0.07
Proximity to CRC, depth variability, depth variability	3828.9	5.0	3834.9	41.5	0.00	0.07
Proximity to CRC, depth variability, proximity of the nearest neighboring CRC	3830.4	6.0	3838.5	45.0	0.00	0.07

Table 6. Parameter estimates and scaled-odds ratios (mean and 95% credible intervals, CI) from top supported neighborhood habitat use-availability model for proximity to CRC, depth variability (standard deviation of mid-channel depth), area of the nearest CRC, area of the nearest neighboring CRC). Scaled odds ratios less than 1 represent decreased odds of habitat use and values greater than 1 represent increased odds of habitat use with every 1 increase in the corresponding unit scalar. CRC = coarse rocky complex.

Parameter	Estimate	SD	Unit Scaler	Scaled Odds Ratio	Lower 95% CI	Upper 95% CI
Intercept	–3.7096	0.1576	–	–	–	–
Proximity to CRC	–2.0143	0.4133	20 m	0.3158	0.2426	0.6852
Depth variability	0.2991	0.0450	0.50 SD	1.4348	1.2894	1.5837
Area of nearest CRC	0.2159	0.0427	5000 m^2	1.1503	1.0916	1.2174
Area of nearest neighboring CRC	–0.1930	0.0483	5000 m^2	0.7911	0.7050	0.8889

continuous shoals provided suitable spawning and year-round habitat for Shoal Bass in Ichawaynochaway Creek, Georgia.

Potamodromy is well documented in salmonids (Northcote 1997) but has only recently been described in Shoal Bass (Sammons 2015). Shoal Bass in the Chattahoochee and Flint rivers have been found to migrate into tributary streams during the spawning season, presumably to access spawning habitat (Sammons and Goclowski 2012; Sammons and Earley 2015). Furthermore, several studies have demonstrated spawning potamodromy behavior of this species within the mainstem Flint River (Goclowski et al. 2013; Ingram et al. 2013; Sammons 2015), and to a lesser extent in the Chipola River, Florida (Bitz et al. 2015). Both male and female Shoal Bass in Ichawaynochaway Creek exhibited an increase in daily movement rates in the spring that may have been linked to spawning migrations. Females exhibited ten times greater movement than males in the summer that may be attributed to postspawning migration. This behavior has been documented in salmonids with males making short-distance migrations and females undertaking longer migrations (Jonsson and Jonsson 1993; Northcote 1997).

However, Sammons (2015) suggested both sexes of Shoal Bass exhibited similar migratory behavior in the Flint River.

Habitat use-availability analyses indicated that not all rocky habitat in the creek was utilized equally by Shoal Bass. Previous studies used proximity to various coarse rocky substrate classes, such as rocky boulder and bedrock, as indicators of shoal association (Goclowski et al. 2013; Sterrett et al. 2015). However, we found that the best substrate-based predictor of Shoal Bass habitat use in Ichawaynochaway Creek was proximity to CRCs—a variable we synthesized that combined contiguous, coarse rocky substrates into a single, composite shoal unit. Proximity to limerock fine did not improve our ability to predict habitat use, unlike other rocky substrates. Although Shoal Bass have been associated with bedrock substrate in other studies (Stormer and Maceina 2009; Goclowski et al. 2013; Bitz et al. 2015; Sammons and Earley 2015), these results generally indicate that bedrock associations likely differ according to type of bedrock, stream context, and hydrogeomorphic setting. In Ichawaynochaway Creek, limerock fine bedrock outcroppings typically occur in runs, and areas of low

bathymetric relief (i.e., uniformly shallow or deep reaches). The lack of surface complexity of this bedrock type may limit its attractiveness for foraging or cover.

Habitat use-availability analyses further indicated that not all shoal habitat in the creek was utilized equally by Shoal Bass. Coarse rocky complexes, particularly the larger complexes, were used in higher proportion than their availability. High site fidelity of Shoal Bass observed between RKM 14 and 22 suggests an underlying benefit to occupation of reaches with numerous, large shoals arranged in series. Moreover, we found no evidence that reaches composed of smaller, scattered shoals with similar total area were used by Shoal Bass as often as larger continuous shoals. Levels of benthic organic matter and macroinvertebrates are higher in shoals than in pools (O'Connell and Campbell 1953; Bogan et al. 1995; Grubaugh et al. 1997; Marcinek et al. 2005). As islands of biological productivity, large shoals in series may trap and retain allochthonous material being carried downstream, thereby improving overall utilization of organic carbon, and supporting the development of trophic complexity (Elwood et al. 1983). The availability of prey, substrate complexity for shelter, and substrate stability for macrophyte production likely support large numbers of crayfish and benthic fish such as darters and madtoms, key prey items for adult shoal bass (Wheeler and Allen 2003; Marcinek et al. 2005; Sammons 2012).

If typical of other years, our results suggested that migration may be minimal between the mainstem and Ichawaynochaway Creek, which has implications for management and conservation. Limited migration between the mainstem and tributaries can result in reduced dispersal among populations, which can act as vectors for gene flow and increase overall fitness of a population (Northcote 1997). Fitness can further be reduced because of hybridization among species, which has been documented in Ichawaynochaway Creek, with Shoal Bass hybridizing with nonnative Spotted Bass *Micropterus punctulatus* (Alvarez et al. 2015). Because Shoal Bass in Ichawaynochaway Creek appear to be segregated to some degree from the mainstem Flint River population, opportunities may exist for specific regulations and/or management for each stock if warranted or desired. Overharvest of disjunct and vulnerable fish populations can have severe impacts by minimizing potential for genetic rescue (if migration does occur) and increasing potential for genetic bottlenecks (Diaz et al. 2000). Catch and harvest rates of Shoal Bass in the nearby Flint River have been documented in excess of 20%, and population dynamics models demonstrate harvest at this level can affect size structure of these populations (Ingram and Kilpatrick 2015; Sammons 2016). If harvest rates in smaller streams are similar, there may be need for more restrictive harvest regulations relative to larger mainstem stocks.

Acknowledgments

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