

MOVEMENT AND HABITAT USE OF SHOAL BASS *Micropterus cataractae* IN TWO
CHATTAHOOCHEE RIVER TRIBUTARIES

by

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ABSTRACT

Shoal Bass *Micropterus cataractae* is a fluvial specialist endemic to the Apalachicola-Chattahoochee-Flint River basin in Alabama, Georgia, and Florida. Recent studies show there is a lot of variation in movement and habitat use across systems. Shoal Bass are imperiled throughout their entire native range with some populations facing severe declines, especially in areas highly impacted by impoundments, leading to habitat fragmentation and loss of connectivity. I studied the movement patterns and habitat associations of two isolated populations within the Fall-Line ecoregion of the Chattahoochee River, Georgia, using radio telemetry. This is a relatively understudy region with high population declines, though the studied populations are considered viable and self-supporting. Throughout the 18-month tracking survey, Shoal Bass exhibited higher mean daily movement rates in the spring compared to winter and autumn. Tagged fish used greater depths in the winter months, potentially reflective of available water levels. Fish used higher velocities in winter months than in spring on both creeks, though most fish were located in relatively swift velocities year round. Tagged fish in both creeks showed an affinity for rocky substrate, though type of substrate use varied across seasons and creeks. Fish in Flat Shoals Creek used shoal complexes during the spring and boulder substrate throughout rest of year. Fish in Mulberry Creek preferred boulder and bedrock substrates, but were often located in different areas throughout the year. Tagged fish selected rocky substrate. Results of this study suggest that habitat use of Shoal Bass may be determined by the amount and type of substrate available within the scope of movement. This study has

strong implications for managing these small populations in a highly imperiled region. Future studies should seek to investigate population dynamics and levels of reproductive success in order to predict habitat protection or restoration success.

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INTRODUCTION

Movement of individuals and populations across landscapes for different purposes is an essential component to the survival of a wide range of species (Gilliam and Fraser 2001). Understanding patterns of annual and seasonal movement at various scales is fundamental to our understanding of the ecology, life history and behavior of many species (Rubenstein and Hobson 2004). Rivers function as a common corridor for populations that would otherwise be ecologically and genetically isolated from movement between tributaries (Meffe and Vrijenhoek 1988). Movement within riverine systems is influenced by geomorphic features within individual reaches of the network (Rinaldo et al. 1991). Within riverine systems characterized by high habitat variability, species often occur as assemblages of local populations collectively called metapopulations, connected by migration of individuals among habitat patches (Hastings and Harrison 1994; Hanski and Gilpin 1997).

The characteristics of habitat required for populations to persist in a given system is garnering much attention in conservation biology (Marcot et al. 2012). Past studies have found that quantity and spatial arrangement of habitats can affect population abundance, distribution, and function (Loehle 2007; Keitt 2009). Smaller habitat patches and increased population isolation may act synergistically to increase extinction risk of species in fragmented landscapes (Fahrig and Merriam 1994). Long-term survival of these populations is possible only in networks of habitat patches, where subpopulation dynamics are asynchronous, making extinction

unlikely (Hanski et al. 1995). Hanski et al. (1995) found that the amount of occupied habitat patches declines as patch area and density decreases. In species that incorporate migratory behaviors, this effect is magnified.

Spatially influenced processes have received considerable attention in the study of dynamics and distribution of a variety of species, especially those that exhibit migration as a critical component to their life history (Rieman and McIntyre 1995). Many migratory fish species use fragmented habitats that may become increasingly fragmented by anthropogenic factors, including dam construction and habitat degradation (Dunham and Rieman 1999). The minimum size required for a habitat patch to support various species is highly variable and difficult to envision. Thus, applying minimum patch-size requirements derived for one species onto another has an unpredictable effect. It's also not recommended to apply these assumptions across a species endemic to regions with high environmental variation.

Shoal Bass *Micropterus cataractae*, endemic to the Apalachicola-Chattahoochee-Flint (ACF) River basin in Alabama, Georgia, and Florida, exhibit different migratory patterns that are likely affected by this varying environment. Within this river basin there are vast differences in landscape features, which can create problems when approaching management strategies throughout their native range. Though movement and habitat use of Shoal Bass has been studied before in the southern end of the ACF river basin (Bitz et al. 2015; Ingram et al. in press), the results are not applicable to managing populations in differing physiographic regions that are more typical throughout their range. These past studies have provided insight into the spatial ecology of Shoal Bass, though knowledge gaps remain in areas where they are more commonly found (but see Sammons and Goclowski 2012).

Shoal Bass are known fluvial specialists that exhibit potamodromous spawning migrations in connected river systems to rocky shoal habitat complexes (Sammons 2015). They

tend to congregate in these large, rocky shoal complexes when spawning, and high densities of age-0 fish are often found within these complexes during the summer, an indication that the shoal habitat also serves as an essential nursery habitat (Goclowski 2010). Although these complexes appear to be important spawning and nursery habitat for Shoal Bass, specific aspects of this use have been little studied (but see Johnston and Kennon 2007). In addition, timing and persistence of shoal habitat use by this species is unknown, likely due to its more recent description (Williams and Burgess 1999).

The Chattahoochee River system at one time likely contained a metapopulation of Shoal Bass, acting as a source-sink or drought refuge when tributary populations were reduced or eliminated by extreme weather events (Sammons and Maceina 2009). Individual shoal complexes within the mainstem river and its tributaries may have acted as separate habitat patches, separated by reaches of unsuitable habitat. However, 14 dams have been constructed on the Chattahoochee River over the last 150 years, nine of which are within the Fall-Line area, and have significantly altered and isolated riverine habitat. Construction of these dams also eliminated roughly half of the shoal habitat found above the Fall-Line in the Chattahoochee River basin (Sammons and Earley 2015). Smaller, recently isolated populations may become more prone to extinction through loss of habitat connectivity and access to these rocky shoal complexes. Isolated populations also increase the likelihood of limited genetic diversity and reduced recruitment of river fishes (Martinez et al. 1994; Jager et al. 2001; Sammons and Maceina 2009; Dakin et al. 2015; Sammons and Earley 2015). Remaining viable Shoal Bass populations in the Chattahoochee River persist in fragmented reaches of the mainstem and isolated larger tributary systems that were once all connected, however, these populations have been drastically understudied.

Because Shoal Bass appear to use different habitats for optimal growth and survival, involvement across multiple agencies and organizations may be necessary to improve the status of this imperiled species. Sammons (2015) suggested that because Shoal Bass appear to be highly migratory, management and conservation plans should transcend the local scale and encompass a wider range of habitat. Two of the more viable remaining populations of Shoal Bass in the Chattahoochee River basin persist on small tributary streams between Valley, AL, and Columbus, GA. Both of these tributaries contain habitat that Shoal Bass tend to associate with, yet differ in geomorphologic features, meaning that Shoal Bass may use habitat differently in each system. For conservation efforts to be successful, it is essential to accurately identify the habitat on which a species or population depends (Rosenfeld 2003).

The Native Black Bass Initiative (NBBI) is a new keystone initiative of the National Fish and Wildlife Foundation (NFWF), developed by multiple collaborators, including state and federal agencies, universities, non-governmental organizations, and corporations from across the southern United States (Birdsong et al. 2015). The focus of this initiative is to provide conservation strategies, objectives, and ecological targets to restore and preserve the environmental processes in the regional watersheds that support and promote stable populations of endemic black bass species. Shoal Bass is one of three high priority black bass species that are the initial focus of the NBBI, specifically in the Chattahoochee and Chipola rivers. The NBBI will continue to be successful as long as it involves all life history stages, as well as takes a conservation approach that is both cost-effective and sustainable for years to come (Birdsong et al. 2015). Prior to implementing large-scale conservation efforts, it is critical to gain a complete understanding of the complexity of Shoal Bass behavior within these smaller tributaries, in particular understanding the relationship between habitat size and frequency of use by Shoal

Bass. A more holistic characterization of spawning habitat, behavior, and annual movement patterns of populations in small tributaries is a necessary component in moving forward.

This research will consist of two hypotheses. First, I hypothesize that seasonal movements of two isolated shoal bass populations will differ across geomorphically distinct tributaries. Movement is considered to be one of the most important behavioral patterns in animals because it is directly related to their ability to respond to environmental conditions, consequently affecting growth, survival and reproductive success (Kahler et al. 2001; Albanese et al. 2004). Thus, movement behaviors are likely to differ in two geomorphically distinct tributaries. Second, I hypothesize Shoal bass will use habitat disproportionately to its availability across seasons and between creeks. Though there is little information regarding the scale or spatial aspects of necessary habitat for migratory fish, large-scale spatial geometry is considered important to the persistence of many species (Rieman and McIntyre 1995). Conservation efforts may be focused towards maintaining or restoring a critical amount or shape of habitat if it is proven to be beneficial (Simberloff 1988).

STUDY AREA

Flat Shoals Creek and Mulberry Creek (Figure 1) are two fifth-order tributaries of the Chattahoochee River, Georgia. Both creeks are located within the Piedmont region of Georgia and contain stable and abundant Shoal Bass populations (Katechis 2015). Flat Shoals Creek and Mulberry Creek both enter the Chattahoochee River near the Gulf Coast Fall-Line region, a transitional area approximately 32-km wide (Wharton 1977) that divides the Piedmont from the upper Coastal Plain. Similar to most streams in this area, Flat Shoals Creek and Mulberry Creek are characterized by areas of bedrock, boulder, and cobble substrates, high gradients, and high-velocity flows. Flat Shoals Creek flows 45 km southwestward through a heavily forested area with minimal urban development towards its confluence with the Chattahoochee River in northern Harris County. Flat Shoals Creek contains a large, continuous rocky shoal complex about 1.3 km in length. This complex is roughly 5 km upstream from the Chattahoochee River confluence, and is mostly bedrock in the upper portion of the river with frequent large deep pools. Substrate in the lower portion of the shoal complex is mostly boulder rock with scattered vegetation patches throughout. Mulberry Creek flows 42 km southwest towards the Chattahoochee River confluence, entering the Chattahoochee River within Goat Rock Reservoir. This watershed is also heavily forested with minimal urban development. Unlike Flat Shoals Creek, Mulberry Creek has multiple small rocky shoal complexes throughout the study area, ending in a series of waterfalls near the bottom of the study area; the river drops over 25 m in

less than 1 km prior to entering the reservoir, thus impeding upstream fish movement. The Chattahoochee River confluence of these streams is separated by 21 rkm, but the two Shoal Bass populations are isolated from each other by Bartlett's Ferry Lake and Dam (Figure 1). The Mulberry Creek population is further isolated by the series of waterfalls and Goat Rock Reservoir, which contains an effectively extinct population of Shoal Bass (Sammons and Maceina 2009). In contrast, the Flat Shoals Creek population is connected to the one found in the headwaters of Bartlett's Ferry Reservoir below Riverview Dam (Sammons and Earley 2015).

METHODS

Movement

Shoal Bass were collected using a boat-mounted DC electrofishing unit and angling from the Chattahoochee River confluence upstream to the County 219 bridge on Flat Shoals Creek, and from Mulberry Falls located 1.4 km up from the confluence to the Highway 27 bridge on Mulberry Creek. From December 2015 to March 2016, 39 Shoal Bass (19 in Flat Shoals Creek and 20 in Mulberry Creek) were surgically implanted with 14-g Model F1835 radio transmitters (Advanced Telemetry Systems, ATS; Isanti, Minnesota). These transmitters had a 502-d battery life expectancy and were equipped with mortality sensors, so that if they remained motionless for over 24 hours, the signal rate would increase from the alive pulse of 50 beats per minute (bpm) to a dead signal of 100 bpm (Gocłowski 2010). Just prior to the spawning period in 2016, 20 additional known male Shoal Bass were collected in the large shoal and tagged with 3.3-g Model F1580 radio transmitters (258-d life expectancy, no mortality sensor) in Flat Shoals Creek (Table 2). In March 2017, five additional Shoal Bass (three in Flat Shoals Creek and two in Mulberry Creek) were collected within each study reach and implanted with Model F1835 radio transmitters. In April 2017, 10 additional known male Shoal Bass were collected in the large shoal in Flat Shoals Creek and implanted with Model F1580 radio transmitters. In all cases, fish were selected to ensure that they did not exceed the 2% recommended tag burden, recommended

by Winter (1996). Fish in both streams were collected throughout the study reach and were tagged and released at the capture site (Table 1).

Fish were anesthetized using an electro-anesthesia table (Jennings and Looney 1998), and tags were inserted through a 1-3-cm incision made slightly to one side of the mid-ventral line just anterior to the pelvic girdle (Maceina et al. 1999). After the tags were inserted into the body cavity, the antenna was pulled through the body cavity wall posterior to the incision using a suture needle. The wound was closed with 2-3 monofilament sutures, and tissue adhesive (3M Vetbond, St. Paul, MN) was administered to ensure the opening was completely sealed. Post-surgery, fish were held underwater in the stream until they had recovered from the procedure and were capable of swimming away, which in most cases occurred within two minutes.

Fish were tracked biweekly from January 2016 to June 2017. During expected spawning seasons in both years (mid-March through mid-June), fish were tracked weekly. Tracking began roughly 14 days after tags were implanted to allow fish time to recover from the surgery process (Sammons and Earley 2015). Tracking was conducted from a canoe using an ATS R2000-receiver and a 4-element fixed yagi antenna. Fish were tracked once in an aircraft on September 29, 2016, to locate fish that were suspected to have moved beyond the study area. Under typical conditions, these tag models can be located within a 0.8-km radius from the boat and within a 1.6-km radius from a low-flying plane (T. Garin, ATS, personal communication).

Tracking was conducted throughout the study reach in both streams over a two-day period (Figure 1). The position of each fish was recorded using a Garmin eTrex 20 handheld GPS. Water depth (m), velocity (m/s), surface water temperature (°C), substrate type (boulder, bedrock, coarse rocky complex, sand) and cover type (% boulder, bedrock, coarse rocky complex, large woody debris (LWD), none) were measured at each fish location. Neither study

stream had a United States Geological Survey (USGS) stream gauge located on it; therefore, stream gauge 02338660 on the New River near Corinth, Georgia, was used as a surrogate for discharge data for both years. The New River is a fifth-order tributary of the Chattahoochee River and is relatively similar in watershed size. Prior to tracking, temperature loggers (Onset HOBO data loggers, Water Temp Pro v2) were deployed at two locations on each creek (Figure 1), and recorded water temperature data once every two hours for the duration of the study.

Habitat Use

During the spring of 2018, benthic sonar imagery was captured via video using a Humminbird 1198c Side Imaging Sonar system unit along the study reach in both streams. The scanning was conducted during high flows in order to capture all available instream channel habitat (Kaeser and Litts 2010). Two sonar-mounted kayaks were used to collect data. Water depth under each kayak and substrate composition were captured in sonar imagery. A GPS unit was used to collect reference location data during video capture. The sonar video and GPS location points were georeferenced in SonarTRX 17.1 (LEI 2017) and then used to create detailed habitat maps of the telemetry study area using techniques described by Kaeser et al. (2013). Digitized polygon shapefiles were created for each patch of classified substrate, then stitched together into a mosaic network representing the entire study area in ArcGIS 10.3.2 (ESRI 2016).

Fish locations obtained via telemetry were overlaid onto the complete substrate shapefile to characterize population-level habitat use within the study area. I used the distance-based approach as described by Sterrett et al. (2015) and Ingram et al. (in press) to associate each fish location with habitat data (Conner and Plowman 2001) across seasons. To compare habitat use to habitat availability, I generated an equal number of random location waypoints for each known

fish location to represent available habitat within the study reach using the Generated Random Tessellated Stratification (GRTS) sampling algorithm (Kincaid 2015). All random locations were assumed to be independently distributed. Because most fish exhibited large-scale movement patterns, all habitat within the study reach was considered available to all fish (Sterrett et al. 2015).

DATA ANALYSES

Movement

Mean daily movement rates were calculated for each individual as minimum displacement per day by dividing the distance moved (m) between locations by the amount of time in days between tracking locations (Wilkerson and Fisher 1997; Sammons et al. 2003). Movement rates were estimated for each season. Seasons were defined by water temperatures: spawn increasing from 12 – 22 C; autumn decreasing from 22 – 12 C; and winter < 12 C (Todd and Rabeni 1989).

A mixed model analysis of variance (ANOVA) was used to determine if there were seasonal differences in mean movement of individuals within each creek. A Tukey HSD post-hoc test was used to analyze pairwise comparisons of movement among all seasons. Time periods when fish were not relocated within three tracking periods were removed from the analysis until fish were consistently relocated again to reduce perceived daily movement estimation error (Laundre et al. 1987). Spatial distribution of tagged fish throughout the study reach in each stream was examined by expressing fish locations as river km (rkm) from the stream confluence with the Chattahoochee River. Frequency distributions of these locations were compared between the spawning season and the rest of the year using a Komolgorov-Smirnov test (Program R, 3.1.2).

A Poisson generalized linear model was used to evaluate the potential influence of environmental variables on seasonal movement of tagged Shoal Bass into the large shoal

complex during the spawning period on Flat Shoals Creek. Photo period (daylight hours), water temperature (°C), and discharge (m³/s) were used as environmental predictors, and separate models were run for each year. Residuals were normally distributed. The Poisson model used was as follows:

$$\ln(Y) = b_0 + b_1x_1 + b_2x_2 \dots + b_kx_k + E \sim N(0, \sigma_{\text{residual}})$$

Where Y = response variable; b₀ = intercept; b₁ = slope; x₁, x₂, x_n = explanatory variables; E = error term; N(0, σ_{residual}) = normally distributed with a mean of zero and standard deviation of sigma. σ = standard deviation in the error.

The time period covered by the analysis began 1 January of both years until the date when all fish were present in the large shoal complex. Predictors of large-scale springtime movement were identified using Akaike's Information Criterion (AIC) adjusted for small sample size (Burnham and Anderson 2002). I developed a set of six a priori candidate models that included combinations of photo period, water surface temperature (°C), and stream discharge (m³/s), and a global model that included all predictor variables. Models were developed to predict quantity of fish in shoal. I calculated AIC weights for each model, ranging from zero to one with the best approximating model having the highest weight. I used a multi-model inference using the MuMIn package in Program R to look at relative importance of each variable to the predictor model. Inferences were based on the importance of each habitat characteristic included in the top approximating models.

Habitat Use

Mean velocity and depth use of Shoal Bass were compared among seasons in each study stream using a fixed-effect multiple analysis of variance (MANOVA) (Program R 3.1.2, 2017).

Independent variables in the MANOVA were velocity and depth, with season as the dependent variable.

Distances from each known fish location point to each substrate type were calculated using the Locate Features Along Route tool and the NEAR tool in ArcGIS 10.3.2 (ESRI 2016). Known fish locations were compared seasonally and across years to the random location waypoints generated with the GRTS in Program R. A mixed model ANOVA was used to compare the mean distance to each substrate type for each fish location. A Tukey HSD post-hoc test was applied to analyze pairwise comparisons of distance to substrate type for all fish locations. A mixed model ANOVA was conducted to analyze these comparisons across seasons, with a Tukey HSD post-hoc test applied to analyze pairwise comparisons for all fish locations. A mixed model ANOVA was conducted to compare known fish locations to random location points across seasons as a proxy for habitat use vs. availability.

A Pearson's chi-square test of independence was used to assess whether substrate use was independent of availability across seasons. To test for independence across seasons, a chi-square test was performed between seasons in each year using the following equation:

$$\chi^2 = \sum_{\text{all cells}} \frac{(\text{observed} - \text{expected})^2}{\text{expected}}$$

Where observed is the proportion of substrate used by individual fish, expected is the proportion of substrate expected to be used by individuals.

Significance was set at $\alpha = 0.05$ for all analyses.

RESULTS

Telemetry

Radio-tagged Shoal Bass were tracked between January 11, 2016 and June 14, 2017. A total of 819 fish locations were obtained from 75 tracking surveys on Flat Shoals Creek. A total of 472 fish locations were obtained from 78 tracking surveys on Mulberry Creek. Of the 19 Shoal Bass implanted with Model F1835 tags on Flat Shoals Creek, nine were alive and accounted for by the end of 2016. Three tags were retrieved from the creek bed and implanted into fish prior to the spawning period of 2017, and by the end of the study, there were 11 tagged fish remaining in Flat Shoals Creek (Table 1). Fates of remaining fish in Flat Shoals Creek were as follows: eight fish died or expelled transmitters, one fish was harvested by an angler, 11 fish were tracked until tags expired, and 18 fish were missing (Tables 1 and 2). Of the 20 individuals implanted with Model F1835 transmitters on Mulberry Creek, 11 were alive and accounted for by the end of 2016. One tag that was expelled from a fish was retrieved from the creek bed and implanted into another fish prior to the spawning period of 2017. By the end of the study, there were nine fish remaining in Mulberry Creek. Fates of remaining fish in Mulberry Creek were as follows: 10 fish died or expelled transmitters, and three fish moved over a large waterfall, removing themselves from the study area (Table 1).

Movement

Radio-tagged individuals in Flat Shoals Creek began moving into the large shoal complex on March 22, 2016, and remained until May 27, 2016. Eighteen of the 20 tagged fish used the shoal complex during this time period. Tagged known males remained in the large shoal complex where they were tagged for seven weeks, but 16 of the 20 exited the shoal by May 27, 2016. Two known males perished in the shoal mid-July 2016, and two known males remained in the shoal until mid-August 2016. In 2017, individuals with the larger tags began moving into the large shoal complex on March 24 and remained until May 8. All ten known males tagged in the large shoal complex in 2017 remained there until tracking ceased on June 15th. Several tagged individuals made migrations to the large shoal complex late January to mid-February of both years, then returned to previous locations before migrating into them during the spawning period, where they stayed for multiple weeks. 14-g tagged individuals moved 3-13 km to, or from, the large shoal complex in the spring. Known males tagged in 2016 moved out of the large shoal complex in late May or early June and relocated 3-22 km away.

In Mulberry Creek, radio-tagged individuals began moving into rocky shoal complexes on March 15, 2016, and remained until May 25, 2016. Only 13 of the 20 tagged fish used shoal complexes during this time period; the remainder did not leave the reach where they were tagged. Fish that made large-scale migrations to shoal complexes moved 3 - 27 km. In 2017, only two tagged individuals moved into shoal complexes, and the remainder did not. The two individuals that migrated moved 1.5-7 km.

Mean daily movement rates varied across seasons from 0.00 to 2.56 km/day on Flat Shoals Creek in 2016, and from 0.00 to 1.82 km/day in 2017. Mean daily movement rates ranged from 0.00 to 2.31 km on Mulberry Creek in 2016, and from 0.00 to 1.82 km/day in 2017. Shoal

Bass mean daily movement in Flat Shoals Creek was greatest during the spawning period and least in fall and winter of 2016 ($F_{(2, 539)} = 5.757$; $p = 0.000702$), but was similar between winter and the spawning season in 2017 ($F_{(1, 159)} = 0.101$; $p = 0.751$; Table 3). Mean daily movement in Mulberry Creek was greatest during the spawning period and least in fall and winter in 2016 ($F_{(2, 286)} = 5.49$; $p = 0.00461$), but was similar between winter and spawning seasons in 2017 ($F_{(1, 108)} = 0.649$; $p = 0.422$; Table 3).

Radio-tagged individuals were located in different areas of Flat Shoals Creek during the spawning and non-spawning periods in 2016 (Kolmogorov-Smirnov test; $D = 0.257$; $p < 0.0001$) and 2017 ($D = 0.417$; $p < 0.0001$; Figure 2). This was also the case in Mulberry Creek in both 2016 (Kolmogorov-Smirnov test; $D = 0.274$; $p < 0.0001$) and 2017 ($D = 0.345$; $p < 0.0001$; Figure 3).

Habitat Use

Seasonal

In 2016, mean velocity use by tagged Shoal Bass in Flat Shoals Creek was lower in autumn than in spawning and winter seasons ($F_{(2, 532)} = 10.65$; $p < 0.0001$; Table 4; Figure 5). In 2017, mean flow use was lower in winter than in the spawning season. Shoal Bass used lower velocities in winter than they did during spawning season ($F_{(1, 249)} = 26.12$; $p < 0.0001$; Table 4; Figure 5). Similarly, Shoal Bass on Mulberry Creek used lower velocities in autumn than they did during spawning season in 2016 ($F_{(2, 291)} = 4.51$; $p = 0.0118$; Table 4; Figure 6), but velocity use in winter was intermediate and similar to either season. In 2017, fish used higher velocities in winter than they used during the spawning period ($F_{(1, 156)} = 6.41$; $p = 0.0125$; Table 4; Figure 6).

Mean velocity use on Flat Shoals Creek was higher during winter in 2016 than in 2017 ($F_{(2, 481)} = 15.41$; $p = 0.0001$) but was similar between years during spawn ($F_{(2, 481)} = 14.11$; $p = 0.1184$).

Mean velocity use on Mulberry Creek was different between years during winter ($F_{(3, 446)} = 3.17$; $p = 0.9991$) but was similar between years during spawn ($F_{(3, 446)} = 12.37$; $p = 0.0207$).

In 2016, mean velocity use by tagged Shoal Bass in Flat Shoals Creek was greatest in winter, intermediate during the spawning period, and lowest in autumn ($F_{(2, 532)} = 33.51$; $p < 0.0001$; Table 4; Figure 5). In 2017, mean depth use by tagged Shoal Bass was greatest in winter than during spawning period ($F_{(1, 249)} = 48.03$; $p < 0.0001$; Table 4; Figure 5). In 2016, mean depth use by tagged Shoal Bass on Mulberry Creek used greatest depths in winter and the spawning period and shallowest depths in autumn ($F_{(2, 291)} = 7.72$; $p = 0.0005$; Table 4; Figure 6). In 2017, mean depth use was greatest during winter compared to the spawning period ($F_{(1, 156)} = 9.47$; $p = 0.0024$; Table 4; Figure 6). Mean depth use on Flat Shoals Creek was similar between years during winter ($F_{(3, 490)} = 32.98$; $p = 0.9981$) but was different between years during spawning periods ($F_{(3, 490)} = 21.09$; $p = 0.0011$). Mean depth use on Mulberry Creek was similar between years during winter ($F_{(3, 453)} = 7.00$; $p = 0.2111$) but was different between spawning periods ($F_{(3, 453)} = 10.97$; $p = 0.0005$).

Shoal Presence

The best approximating model for predicting Shoal Bass presence in the large shoal complex on Flat Shoals Creek in 2016 contained photo period ($p < 0.0001$) and water discharge ($p = 0.0016$) (Figure 7). Water temperature was not a significant predictor of Shoal Bass presence ($p = 0.8222$). Photo period and water discharge were the best predictors of shoal

complex use by Shoal Bass when comparing best-fit models in 2016 (Table 5). This model was 3.11 AIC units larger than the second best-fit model. In 2017, the best approximating model for predicting Shoal Bass presence in the large shoal complex contained photo period ($p = 0.0084$) (Figure 7). There was no relationship between water temperature ($p = 0.8325$) or water discharge ($p = 0.6833$) and presence of Shoal Bass in the shoal complex in 2017. Photo period was the best predictor of shoal complex use by Shoal Bass when comparing best-fit models in 2017 (Table 6). This model was 1.92 AIC units larger than the second best-fit model.

Use vs. Availability

Shoal Bass were located closer to boulder and bedrock in the winter and autumn than they were during spawn ($F_{(2, 505)} = 59.42$; $p < 0.0001$), closer to coarse rocky complex during the spawning period than they were in the winter and autumn ($F_{(2, 505)} = 40.35$; $p < 0.0001$), and closer to sand in the winter and autumn than they were during spawn ($F_{(2, 505)} = 77.32$; $p < 0.0001$) on Flat Shoals Creek in 2016 (Figure 9). Shoal Bass were located closer to boulder and bedrock in winter than they were during the spawning period ($F_{(1, 250)} = 67.21$; $p < 0.0001$), closer to coarse rocky complex during the spawning period than they were in winter ($F_{(1, 250)} = 31.64$; $p < 0.0001$), and closer to sand in winter than they were during spawn ($F_{(1, 250)} = 148.30$; $p < 0.0001$) on Flat Shoals Creek in 2017 (Figure 10).

Shoal Bass were located further from boulder in the fall than they were in winter or spring ($F_{(2, 310)} = 6.17$; $p = 0.0023$), similar distances from bedrock across seasons ($F_{(2, 310)} = 1.57$; $p = 0.2091$), closer to coarse rocky complex in the spring than in the winter and fall ($F_{(2, 310)} = 9.26$; $p = 0.0001$), and further from sand in the spring than they were in the fall and winter

($F_{(2, 310)} = 4.74$; $p = 0.0094$) on Mulberry Creek in 2016 (Figure 11). Shoal Bass were located similar distances from all substrate types in winter and spring ($F_{(1, 142)} = 0.06$; $p = 0.8041$) on Mulberry Creek in 2017 (Figure 12).

Shoal Bass occurred closer to all substrate types when compared to random locations in winter of 2016 on Flat Shoals Creek ($F_{(7, 520)} = 59.26$; $p < 0.0001$; Figure 13). During the spawning period, Shoal Bass were found further from boulder, bedrock, and sand ($p < 0.0001$), and closer to coarse rocky complex ($p < 0.0001$) when compared to random locations ($F_{(1, 308)} = 58.65$; $p < 0.0001$). Individuals were found closer to boulder, bedrock, coarse rocky complex, and sand when compared to random locations during autumn ($F_{(1, 566)} = 36.73$; $p < 0.0001$).

Shoal Bass occurred closer to boulder, coarse rocky complex, and sand, and similar distances to bedrock ($p = 0.1181$) when compared to random location points in winter of 2017 on Flat Shoals Creek ($F_{(1, 250)} = 11.66$; $p < 0.0001$; Figure 14). Shoal Bass were found further from boulder, bedrock, and sand, and closer to coarse rocky complex when compared to random location points during the spawning period of 2017 on Flat Shoals Creek ($F_{(1, 238)} = 81.13$; $p < 0.0001$).

On Mulberry Creek, Shoal Bass were found closer to boulder, bedrock, coarse rocky complex, and sand when compared to random location points in winter of 2016 ($F_{(1, 120)} = 36.13$; $p < 0.0001$; Figure 15). During the spawning period, individuals were found closer to boulder and bedrock, similar distances to coarse rocky complex ($P =$), and further from sand when compared to random location points in 2016 on Mulberry Creek ($F_{(2, 297)} = 18.02$; $p = 0.0003$). Shoal Bass were found similar distances to boulder ($p = 0.3537$), closer to coarse rocky complex, and further from bedrock and sand when compared to random location points in during autumn of 2016 on Mulberry Creek ($F_{(1, 216)} = 14.02$; $p = 0.0021$). Shoal Bass were found closer to

boulder and coarse rocky complex, similar distances to bedrock ($p = 0.0668$), and further from sand in the winter of 2017 on Mulberry Creek ($F_{(1, 112)} = 8.99$; $p = 0.0033$; Figure 16).

Individuals were found similar distances to boulder ($p = 0.1224$), further from bedrock and sand, and closer to coarse rocky complex during the spawning period of 2017 on Mulberry Creek ($F_{(1, 173)} = 7.54$; $p = 0.0068$).

According to the chi-square test, tagged Shoal Bass on Flat Shoals Creek were using substrate disproportionately to what was available in both 2016 and 2017 ($p < 0.0001$; Table 7; Figure 17). To test which seasons were significantly different from each other, a chi-square test was performed for each combination of seasons based on 2x2 contingency tables. All pairwise tests between seasons for each year showed significant differences between seasons ($p < 0.0001$; Table 8; Figure 17). Tagged Shoal Bass on Mulberry Creek were using substrate disproportionately to what was available in both 2016 and 2017 ($p < 0.0001$; Table 7; Figure 17). Similarly, all pairwise tests between seasons for each year showed significant differences between seasons on Mulberry Creek in 2016 and 2017 ($p < 0.0001$; Table 8; Figure 17).

DISCUSSION

Springtime movement patterns of Shoal Bass in both streams emulated those described in the Flint River, Georgia, and the Chipola River, Florida (Goclowksi et al. 2013; Bitz et al. 2015), and conformed to the proposed potamodromy of the species as theorized by Sammons (2015). In contrast, Ingram et al. (in press) found that Shoal Bass exhibited relatively low movement rates in a Flint River tributary. This tributary was characterized by much deeper depths (> 8 m) than either of my study streams, which may have allowed Shoal Bass in that stream to fulfill all their requirements in a relatively small area (Beyer et al. 2010). Spring movement patterns of Shoal Bass in Flat Shoals Creek were similar in both years, but in Mulberry Creek fish moved shorter distances and less often in 2017 compared to 2016.

Migratory fish respond to environmental cues that act as triggers to stimulate large-scale movement (Jonsson 1991). Limited movement seen in the wintering seasons of black bass has previously been linked to decreases in water temperature (Hunter and Maceina 2008; Goclowksi et al. 2013). Additionally, a lot of variation in distance moved and frequency of movement has been reported in other black bass species. For example, Dauwalter and Fisher (2008) found that Smallmouth Bass in the Ozark Highlands ecoregion exhibited seasonal differences in movement, with more movement occurring between wintering and summer months. However, within the same ecoregion, Todd and Rabeni (1989) found that Smallmouth Bass movement was minimal, even when there was seasonal flooding. This supports the suggestion by Lyons and Kanehl (2002) that degree of movement is often population-specific regardless of system size.

Tagged fish on both study creeks tended to move between two distinct locations, depending on whether they were spawning or not. While home ranges were not calculated for these two streams, home range of Shoal Bass within a confined 600-m reach in an eastern

Alabama tributary was estimated to be 0.47-ha within a 1.7-ha study area (Stormer and Maceina 2009). Knight (2011) suggested that more frequented areas may be more important than home range limits because this is where fish spend the majority of their time. Some areas within a home range are not visited often because they do not provide a service, and thus attention should be centered on spaces that are used repetitively (Powell 2000). Several fish in Flat Shoals Creek made brief late-winter movements into the shoal complex, to which they then returned in mid-spring. Additionally, although the large shoal complex usually had enough water to allow passage, tagged fish were never observed traversing the entire shoal and relocating on the opposite side (i.e., fish tagged in the upstream section moved into the shoal complex but were never located downstream of it). This may indicate that Shoal Bass in Flat Shoals Creek were separated into independent population units.

Although movement patterns were unique to each population, I also observed a lot of variation in individual movement on both creeks, although fish on Flat Shoals Creek exhibited more consistent movement patterns. In Mulberry Creek, Shoal Bass exhibited much more individual variation in movement. Tagged fish typically frequented three to four distinct locations and exhibited a lot more movement throughout the year. Fish did not return to wintering areas after the spawning period, although the new areas they were using consisted of similar characteristics. Although Shoal Bass in Mulberry Creek moved among similar types of substrate, because they moved to new areas between winter and autumn, habitat requirements may differ seasonally. Previous studies on potamodromous salmonids suggested that salmonids annually migrate amongst three prime habitat types used for feeding, wintering, and spawning (Flick and Webster 1975; Gowan and Fausch 1996), and site fidelity among these specific habitats has also been documented (Bachman 1984; Northcote 1984; West et al. 1992).

Movement among smaller habitat patches, as documented in Mulberry Creek, may also increase potential for intra- and interspecific competition, particularly between Shoal Bass and non-native congeneric Spotted Bass (*Micropterus punctulatus*) (Sammons 2012; Goclowski et al. 2013).

No individuals in either population moved into the mainstem Chattahoochee River. Mulberry Creek fish are naturally isolated due to the high gradient waterfall near the confluence that prevents upstream movement. However, four individuals tagged below Riverview Dam on the Chattahoochee River were relocated in Flat Shoals Creek in a previous study, with two individuals located in the large shoal complex during spring months (Sammons and Earley 2015). This suggests potential genetic mixing between mainstem and local tributary populations. However, though Shoal Bass in Flat Shoals Creek may have historically interacted with the mainstem population, I did not observe tagged fish moving out of Flat Shoals Creek in this study. Similarly, Ingram et al. (in press) also did not document fish moving between a sixth-order tributary and the mainstem Flint River. Since both mainstem populations located near these tributary confluences are considered viable, tributary and mainstem populations likely exist independently of one another.

Telemetry studies typically suffer from low sample sizes and short durations due to limitations in cost and technology (Nams 1989; Lindberg and Walker 2007). Individuals in this study were tracked over multiple spawning periods, which presented a rare opportunity to observe consistencies in behavior by comparing movement patterns of the same individuals over two seasons in response to environmental cues. Photoperiod and velocity were both significant predictors of the number of fish occupying the shoal complex in Flat Shoals Creek during the spawning season, although velocity was only significant when there was high variation in flow and more peak flow events. Photoperiod is often considered an indicator of season for fishes

because it is predictive and quite consistent across years (Northcote 1992). Secondary cues like water temperature and water velocity are dynamic and influence timing of movement within the season (Northcote 1997). Fish respond to both, but when the secondary cues are absent, fish rely on initial cues for movement (Jonsson 1991). This hierarchy has been shown across multiple species (Schafer 2001; Albanese et al. 2004). Tyus and Karp (1990) found that Razorback Suckers (*Xyrauchen texanus*) spawned during ascending and highest spring flows when water temperatures reached 14 °C. Variation in water velocity has been demonstrated to be an important factor in stimulating upstream movement in adults of numerous anadromous species (Webb and Hawkins 1989; Jonsson et al. 1990), and in stimulating downstream migration of salmonid smolt (Hesthagen and Garnas 1986). Unlike these other species that respond to peak flow events, I didn't detect an effect of flow on movement of Shoal Bass during spring months. My reliance on a surrogate stream gauge for flow data may be driving the inability to observe a relationship between flow and movement. Thus, this study cannot conclusively demonstrate that Shoal Bass did not respond to peak flow events. Shoal Bass typically did associate with relatively high velocities year-round, with an increase in high-velocity use during spring months (Stormer and Maceina 2009; Gocłowski et al. 2013; this study). Future studies on gauged streams may be more successful investigating factors that may be driving these large-scale movements.

My tagged fish used the deepest water in winter and transitioned to shallower water in summer and autumn. My findings show that Shoal Bass shifted from deeper to shallow water throughout the year appears to agree with previous studies on *Micropterus* species. Lyons and Kanehl (2002) found Smallmouth Bass inhabited areas of receding depths as the year progressed. Smallmouth Bass were found in deeper areas during winter months compared to summer and fall

months in the Pend Oreille River, Idaho (Karchesky and Bennett 2004). Earley (2012) also found that depth of Alabama Bass *Micropterus henshalli* and Redeye Bass *Micropterus coosae* in the Tallapoosa River, Alabama, declined throughout the year, likely coinciding with reduced water levels. The use of shallow depths in autumn of 2016 was certainly driven by the amount of available water in both streams. The study region experienced a six-week drought during this period, causing water levels and velocity to drop well below mean values. Although depth availability and use varied across seasons, fish were consistently located in relatively similar velocities across seasons, suggesting that higher velocities are used regardless of depth. During a drought period in the fall of 2006, Stormer and Maceina (2009) found most fish stranded between a 100-m stretch of dry shoal bed and a downstream waterfall, a slack-water region containing habitats that were avoided by fish earlier in the year. This movement restriction and decrease in water levels likely limited their ability to find more suitable velocities. Regardless, selection for higher velocities may stimulate movement during periods of reduced water levels when movement is not restricted.

Increased movement frequency increases the probability of encountering discrete habitat patches. Tagged Shoal Bass in both creeks used substrate disproportionately to what was available, though type of substrate used varied across seasons and between the two study streams. Fish in Flat Shoals Creek typically associated with boulder substrate during winter and autumn periods, and shifted to coarse rocky complexes during spawning period. Use may be reflective of availability, as most of the rocky substrate available in Flat Shoals Creek was boulder and coarse rocky complex. In contrast, Shoal Bass in Mulberry Creek associated with boulder and bedrock throughout all seasons in both years. Although 60% of fish associated with coarse rocky complexes during the spawning period of 2016 on Mulberry Creek, this was the

only time fish were found in these areas. Most studies have found that Shoal Bass associated with rocky substrate year-round, with increased use of shoal complexes during spring months (Stormer and Maceina 2009; Gocłowski et al. 2013; Ingram et al. in press). According to the distance-based approach analysis used in my study, habitat use was considered non-random, as Shoal Bass were selecting for specific types of rocky substrate (Sterrett et al. 2015; Ingram et al. in press). However, further investigation should be pursued in order to classify whether selected habitat was optimal. Establishing the value of a habitat to an organism requires both a measurement of fitness and identifying whether that value was received (Gaillard et al. 2010). Considering Shoal Bass are using distinct areas to spawn, and consequently rear their young, measuring recruitment levels as a proxy for spawning and nursery habitat quality is crucial (Beyer et al. 2010).

Spatial patterns of fishes are driven by proximity to optimal habitat, and the measurement of spatial value changes depending on the life-history process driving movement (Collinge 2010). Optimality is also known to change within a species across populations if habitat is available in differing proportions (Collinge 2009). Thus, distance travelled to reach these habitats increases when suitable habitats are less frequent (Wiens 2001). Available habitat is limited to the individual tributary boundaries, so isolated populations in the Fall-Line region of the Chattahoochee River basin may be artificially denied access to seasonally optimal habitats if they occur outside that boundary. Measuring reproductive success in selected areas would increase understanding of habitat value. Negative consequences resulting from loss of connectivity would be exaggerated if reproduction and thus recruitment were unmeasurable. During this study, I observed drastic differences in Shoal Bass recruitment levels between years and both streams. Age-0 Shoal Bass were easily collected in 2016 in shoal complexes, but few

age-0 fish were collected in 2017. Reasons behind the almost complete reproduction failure of Shoal Bass observed in both streams in 2017 are unclear but could have been related to abnormally low flows and high temperatures occurring from January to March. Suppressed environmental cues that play a role in timing of movement may be responsible, as past studies show decreases in recruitment of other species when conditions are not optimal (Kayes and Calbert 1979; Hansen et al. 1998; Hokanson 2011).

Reduced connectivity may be preventing Shoal Bass in the Chattahoochee River basin from accessing alternative spawning and nest sites when conditions are not optimal, thus lowering annual recruitment success. Eliminating access to other Chattahoochee River populations through fragmentation not only limits genetic integrity, but also removes the ability of these fish to optimize their fitness. However, genetic isolation has occurred naturally in Mulberry Creek, where there is a natural barrier to downstream movement at the confluence. The fact that this population never relied on interactions with other populations suggests that these fish may be using their habitat in a more optimal manner. Northcote (1997) suggests that small isolated populations are often maintained in marginal habitats if growth and fecundity are balanced, similar to salmonids that get trapped in headwater streams above waterfalls when postglacial lakes are lowered. Identifying unique habitat features and verifying reproductive success of this population should be done to determine viability.

CONCLUSION

Though isolated populations are considered extinction-prone, they often persist with the presence of favorable habitat patches (Thomas and Harrison 1992; Thomas and Jones 1993). Rocky shoal complexes, quite prevalent in Fall-Line streams, are known to be important landscape features for Shoal Bass: they act as spawning and nesting sites, provide nurseries for offspring, refuge from predators, and foraging opportunities for all life stages (Wheeler and Allen 2003; Sammons et al. 2015). Even though immense knowledge gaps remain pertaining to the life history of Shoal Bass in this region, identification of spawning areas and associated movement patterns is an important precursor to further investigations of specific features of selected patches that may appear to be imperative to spawning and rearing success. Consistently tracking unique individuals through a multi-year telemetry study provides critical information regarding the scale and frequency of movement and habitat interactions. This project allowed us to document baseline habitat interactions for two isolated populations persisting in geomorphically distinct tributaries, which is a critical first step in protecting and restoring populations in this area.

Effective conservation and management of these small isolated populations will require a comprehensive understanding of the migratory behavior and multi-habitat associations of Shoal Bass across seasons and across tributaries. To achieve the goal of restoring and preventing further decline of this imperiled sportfish, management agencies should gravitate towards the more conservative approach and attempt to protect large expanses of connected habitat in order

to account for maximum spatial use by most individuals. Movement and habitat use of *Micropterus* spp. is known to vary greatly across species and populations (Birdsong et al. 2015). Because movement and habitat use varied at the second-order of selection in this study (Johnson 1980), management within the Fall-Line region should be population-specific until further similarities are found that can be applied across systems. Spatial and temporal variation at the individual level are also important considerations when determining appropriate habitat restoration or protection efforts.

Taylor et al. (2018) reported that tributary populations fragmented from mainstem populations provide the best opportunity for restoring populations of Shoal Bass. Although Smallmouth Bass are known to exhibit homing tendencies towards particular habitats, stocked Smallmouth Bass typically show low site fidelity, with individuals dispersing long distances from the stocking location (Brown 1961). Though recent measurements of success are variable (P. O'Rourke, personal communication; T. Ingram, personal communication; Porta and Long 2015), reintroducing or stocking Shoal Bass in these Fall-Line tributaries may be necessary and a supportive management practice. In doing so, management agencies should consider the origin of parental source prior to reintroduction efforts and consider the ecological effects of transferring genomes (Taylor et al. 2018).

Fishing regulations, if applicable, should be considered for the entire range of movement of the population to account for as large a regulation area as possible. While Sammons (2016) found that more than half of harvested fish were caught in known spawning areas, my study further suggests that Shoal Bass exhibit spawning aggregations. Therefore, regulation limits should include known spawning areas and scale of movement (Lyons and Kanehl 2002; Erisman et al. 2017). Restrictions are often placed within known spawning areas to reduce fishing

mortality (Murawski et al 2000), and research within marine reserves demonstrates an increase in recruitment potential as population exploitation decreases (Roberts et al. 2001). Although there is no fishery for Shoal Bass in eastern Alabama, strict creel limits and size limits in areas where populations are considered viable may help to reduce population declines. This practice is considered successful in areas where populations are viable enough (Woodside et al. 2015; Sammons 2016).

TABLES AND FIGURES

Table 1. Length (TL, mm), weight (WT, g), and tagging date of Shoal Bass implanted with radio tags in two Georgia streams to examine annual movement and habitat use. Last date located, number of days at large, number of locations over this period (N), and fate of each fish by study end are also provided. Fate: (Alive = pulse rate 50 bpm, fish moving; Dead = fish found dead (mortality signal) or tag found on bank; Harvested = angler harvest; Lost = fish disappeared and tag).

| | Tag | TL | WT | Tag Date | Last Date | Days at Large | N | Fate |
|-------------------|------------------|-----|------|-----------|------------|---------------|----|-----------|
| Flat Shoals Creek | 394 | 546 | 2410 | 1/13/2016 | 6/30/2016 | 169 | 14 | Dead |
| | 410 | 404 | 1060 | 1/13/2016 | 6/9/2017 | 513 | 34 | Alive |
| | 433 | 400 | 890 | 1/13/2016 | 3/27/2017 | 439 | 29 | Lost |
| | 492 | 438 | 1290 | 1/13/2016 | 6/9/2017 | 513 | 32 | Alive |
| | 511 | 485 | 1630 | 3/17/2016 | 5/12/2016 | 56 | 6 | Dead |
| | 531 ^a | . | . | 1/14/2016 | 5/26/2017 | 498 | 35 | Alive |
| | 553 | 450 | 1292 | 1/13/2016 | 9/8/2016 | 239 | 22 | Dead |
| | 591 | 382 | 814 | 1/13/2016 | 5/16/2017 | 489 | 27 | Lost |
| | 612 ^a | . | . | 1/12/2016 | 8/27/2016 | 228 | 20 | Dead |
| | 652 ^a | . | . | 1/12/2016 | 4/15/2017 | 459 | 22 | Lost |
| | 672 ^a | . | . | 1/13/2016 | 1/3/2017 | 356 | 18 | Lost |
| | 691 ^a | . | . | 1/12/2016 | 6/9/2017 | 514 | 38 | Alive |
| | 732 | 408 | 883 | 1/13/2016 | 8/26/2016 | 226 | 21 | Dead |
| | 793 ^a | . | . | 1/13/2016 | 3/14/2017 | 426 | 28 | Harvested |
| | 812 ^a | . | . | 1/12/2016 | 5/8/2017 | 482 | 18 | Lost |
| | 832 ^a | . | . | 3/22/2016 | 5/8/2017 | 412 | 17 | Lost |
| | 891 ^a | . | . | 1/13/2016 | 5/16/2017 | 489 | 30 | Tag died |
| | 932 ^a | . | . | 1/12/2016 | 12/20/2016 | 343 | 23 | Dead |
| | 952 | . | . | 1/12/2016 | 8/11/2016 | 212 | 15 | Dead |
| | 732 ^b | 408 | 883 | 3/2/2017 | 5/26/2017 | 85 | 8 | Alive |
| Mulberry Creek | 235 | 392 | 798 | 3/16/2016 | 6/2/2017 | 443 | 21 | Alive |
| | 254 | 452 | 1383 | 3/10/2016 | 12/12/2016 | 277 | 18 | Dead |
| | 273 | 449 | 1145 | 3/16/2016 | 12/12/2016 | 271 | 17 | Dead |
| | 291 | 399 | 878 | 2/1/2016 | 6/14/2017 | 499 | 38 | Alive |

| | | | | | | | |
|------------------|-----|------|------------|------------|-----|----|-------|
| 314 | 429 | 1045 | 3/16/2016 | 8/15/2016 | 152 | 13 | Dead |
| 335 | 482 | 1504 | 3/16/2016 | 3/25/2017 | 374 | 22 | Dead |
| 353 | 420 | 948 | 3/16/2016 | 6/14/2017 | 455 | 33 | Alive |
| 374 | 379 | 738 | 3/10/2016 | 5/26/2016 | 77 | 9 | Lost |
| 454 | 393 | 855 | 3/10/2016 | 5/26/2016 | 77 | 5 | Lost |
| 471 | 389 | 660 | 12/12/2015 | 5/17/2017 | 522 | 36 | Dead |
| 572 ^a | . | . | 1/7/2016 | 5/30/2017 | 509 | 39 | Alive |
| 632 | . | 693 | 12/11/2015 | 4/14/2016 | 125 | 9 | Dead |
| 712 ^a | . | . | 1/7/2016 | 5/3/2016 | 117 | 12 | Dead |
| 753 | 397 | 757 | 12/15/2015 | 12/12/2016 | 363 | 21 | Dead |
| 773 | | 1797 | 12/11/2015 | 6/2/2017 | 539 | 38 | Alive |
| 852 | 419 | 921 | 12/12/2015 | 6/2/2017 | 538 | 35 | Alive |
| 872 ^a | . | . | 1/7/2016 | 6/14/2017 | 524 | 33 | Alive |
| 913 | 525 | 1939 | 12/15/2015 | 3/30/2016 | 106 | 7 | Dead |
| 973 ^a | . | . | 1/7/2016 | 5/3/2016 | 117 | 11 | Lost |
| 991 | 412 | 856 | 12/12/2015 | 6/14/2017 | 550 | 35 | Alive |
| 394 ^b | 390 | 704 | 2/14/2017 | 5/17/2017 | 92 | 10 | Alive |
| 952 ^b | 402 | 781 | 2/14/2017 | 4/11/2017 | 56 | 5 | Dead |

^a Tagging data were lost for these fish; thus, no length or weight data were available and the first track date was used to calculate days at large.

^b Expelled tags that were implanted in new individuals in 2017.

Table 2. Length (TL, mm), weight (WT, g), and tagging date of male Shoal Bass implanted with radio tags in Flat Shoal Creek, Georgia, to examine spawning habitat. Last date was the final time the fish were located; number of days the fish were at large, number of locations over this period (N), and fate of each fish by the end of the study are also provided.

| Tag | TL | WT | Tag Date | Last Date | Days at Large | N | Fate |
|-----|-----|------|-----------|-----------|---------------|----|----------|
| 1 | 343 | 588 | 3/17/2016 | 7/27/2016 | 132 | 12 | Dead |
| 11 | 388 | 818 | 4/11/2016 | 3/14/2017 | 331 | 20 | Tag died |
| 23 | 402 | 837 | 3/17/2016 | 9/6/2016 | 173 | 10 | Lost |
| 31 | 380 | 801 | 4/11/2016 | 2/28/2017 | 317 | 21 | Tag died |
| 40 | 391 | 783 | 3/17/2016 | 3/17/2017 | 360 | 18 | Tag died |
| 51 | 324 | 445 | 4/21/2016 | 3/21/2017 | 328 | 16 | Tag died |
| 61 | 429 | 1035 | 4/11/2016 | 6/2/2016 | 52 | 7 | Lost |
| 70 | 418 | 1036 | 4/21/2016 | 2/28/2017 | 307 | 16 | Lost |
| 80 | 392 | 777 | 4/11/2016 | 2/14/2017 | 303 | 14 | Tag died |
| 91 | 359 | 605 | 3/17/2016 | 3/2/2017 | 345 | 23 | Tag died |
| 100 | 351 | 511 | 3/17/2016 | 9/6/2016 | 173 | 15 | Dead |
| 110 | 389 | 858 | 3/17/2016 | 3/14/2017 | 362 | 18 | Tag died |
| 143 | 345 | 588 | 3/17/2016 | 4/21/2016 | 35 | 4 | Lost |
| 151 | 364 | 607 | 4/11/2016 | 3/14/2017 | 337 | 16 | Tag died |
| 162 | 348 | 555 | 4/11/2016 | 2/28/2017 | 323 | 16 | Lost |
| 171 | 399 | 825 | 3/17/2016 | 4/27/2016 | 41 | 5 | Lost |
| 182 | 428 | 1057 | 3/17/2016 | 5/26/2017 | 435 | 23 | Alive |
| 193 | 437 | 1215 | 3/17/2016 | 3/21/2017 | 369 | 20 | Tag died |
| 215 | 539 | 2176 | 4/11/2016 | 3/17/2017 | 340 | 13 | Tag died |
| 233 | 375 | 696 | 3/21/2017 | 5/26/2017 | 66 | 6 | Alive |
| 241 | 354 | 556 | 4/8/2017 | 6/9/2017 | 62 | 6 | Alive |
| 252 | 310 | 326 | 3/2/2017 | 6/9/2017 | 99 | 8 | Alive |
| 261 | 383 | 706 | 3/21/2017 | 5/16/2017 | 56 | 8 | Lost |
| 271 | 296 | 349 | 3/21/2017 | 6/9/2017 | 80 | 9 | Alive |
| 282 | 389 | 712 | 4/8/2017 | 5/8/2017 | 30 | 4 | Lost |
| 290 | 338 | 464 | 4/8/2017 | 5/16/2017 | 38 | 5 | Lost |
| 300 | 411 | 882 | 4/8/2017 | 5/8/2017 | 30 | 4 | Lost |
| 312 | 372 | 663 | 3/21/2017 | 6/9/2017 | 80 | 7 | Alive |
| 321 | 344 | 462 | 4/8/2017 | 4/29/2017 | 21 | 3 | Lost |

Table 3. Mean daily movement (m/d) of Shoal Bass across seasons in Flat Shoals Creek and Mulberry Creek in 2016 and 2017. Means followed by the same letter were similar among seasons (Tukey's post-hoc test; $p \leq 0.05$).

| Year | Creek | N | Winter | | Spawn | | Autumn |
|------|----------------------|----|--------------------------|-----|--------------------------|-----|-------------------------|
| | | | Mean (SE) | N | Mean (SE) | N | Mean (SE) |
| 2016 | Flat Shoals Creek | 97 | 63 ^a (14) | 275 | 127 ^b (19) | 170 | 35 ^c (10) |
| 2016 | Mulberry Creek | 72 | 178 (36) | 106 | 211 (32) | 111 | 79 (24) |
| 2017 | Flat Shoals Creek | 76 | 90 ^a (25) | 83 | 105 ^a (31) | | |
| 2017 | Mulberry Creek | 43 | 125 ^a (18) | 67 | 112 ^a (45) | | |

Table 4. Mean depth and velocity of Shoal Bass between seasons in Flat Shoals Creek and Mulberry Creek in 2016 and 2017. Means followed by the same letter were similar among seasons (Tukey's post-hoc test; $p \leq 0.05$).

| Year | Creek | Parameter | N | Winter | N | Spawn | N | Autumn |
|------|-------------------|----------------|----|--------------------------------|-----|-------------------------------|-----|-------------------------------|
| | | | | Mean (SE) | | Mean (SE) | | Mean (SE) |
| 2016 | Flat Shoals Creek | Depth (m) | 98 | 1.02 ^a (0.04) | 288 | 0.85 ^b (0.01) | 183 | 0.71 ^c (0.01) |
| | | Velocity (m/s) | 89 | 0.277 ^a (0.026) | 285 | 0.290 ^a (0.013) | 183 | 0.204 ^b (0.011) |
| | Mulberry Creek | Depth (m) | 56 | 1.11 ^b (0.062) | 113 | 1.04 ^b (0.048) | 131 | 0.86 ^a (0.035) |
| | | Velocity (m/s) | 56 | 0.209 ^{ab} (0.024) | 113 | 0.23 ^a (0.0056) | 125 | 0.17 ^b (0.014) |
| 2017 | Flat Shoals Creek | Depth (m) | 98 | 1.10 ^a (0.29) | 131 | 0.68 ^b (0.03) | | |
| | | Velocity (m/s) | 98 | 0.398 ^a (0.176) | 131 | 0.243 ^b (0.015) | | |
| | Mulberry Creek | Depth (m) | 62 | 0.99 ^a (0.06) | 97 | 0.78 ^b (0.04) | | |
| | | Velocity (m/s) | 61 | 0.209 ^a (0.029) | 97 | 0.157 ^b (0.015) | | |

Table 5. Candidate models projecting degrees of freedom (df), log-likelihood, AICc value, delta value, and model weight (w) from the top four best approximating Poisson GLM models of environmental predictors of shoal complex use by Shoal Bass in Flat Shoals Creek in 2016.

| Model | df | log-Likelihood | AICc | delta | w |
|---------------------------------------|----|----------------|-------|-------|------|
| Photo period, flow | 3 | -14.53 | 62.65 | 0 | 0.79 |
| Photo period, flow, water temperature | 4 | -14.19 | 65.76 | 2.39 | 0.17 |
| Photo period | 2 | -14.52 | 69.00 | 3.05 | 0.03 |
| Photo period, water temperature | 3 | -14.19 | 71.93 | 6.02 | 0.01 |

| Model-averaged coefficients | | | | | |
|-----------------------------|----------|---------|-------------|---------|----------|
| | Estimate | SE | Adjusted SE | z value | Pr > z |
| Photo period | 1.149 | 0.2509 | 0.272 | 4.22 | < 0.0001 |
| Discharge | -0.00942 | 0.00394 | 0.00423 | 2.22 | 0.026 |
| Water temperature | -0.0137 | 0.0573 | 0.061 | 0.224 | 0.822 |

Table 6. Candidate models projecting degrees of freedom (df), log-likelihood, AICc value, delta value, and model weight (w) from the top four best approximating Poisson GLM models of environmental predictors of shoal complex use by Shoal Bass in Flat Shoals Creek in 2017.

| Model | df | log-likelihood | AICc | delta | w |
|--|----|----------------|-------|-------|------|
| Photo period | 2 | -21.49 | 47.73 | 0.00 | 0.57 |
| Photo period, discharge | 3 | -21.03 | 49.65 | 1.93 | 0.22 |
| Photo period, water temperature | 3 | -21.32 | 50.23 | 2.51 | 0.16 |
| Photo period, discharge, water temperature | 4 | -20.93 | 52.73 | 5.00 | 0.05 |

| Model-averaged coefficients | | | | | |
|-----------------------------|----------|---------|-------------|---------|---------|
| | Estimate | SE | Adjusted SE | z value | Pr > z |
| Photo period | 4.064 | 1.407 | 1.54 | 2.634 | 0.00844 |
| Discharge | 0.000249 | 0.00411 | 0.00453 | 0.055 | 0.956 |
| Water temperature | 0.0178 | 0.0573 | 0.0613 | 0.291 | 0.7707 |

Table 7. Summary of Pearson's chi-square results comparing available habitat to used habitat on Flat Shoals Creek and Mulberry Creek in 2016 and 2017.

| Year | Creek | Season | Chi-Square value | df | p value |
|------|-------------------|--------|------------------|----|----------|
| 2016 | Flat Shoals Creek | Winter | 79.72 | 3 | < 0.0001 |
| | | Spring | 1098.88 | 3 | < 0.0001 |
| | | Autumn | 657.83 | 3 | < 0.0001 |
| 2016 | Mulberry Creek | Winter | 76.32 | 3 | < 0.0001 |
| | | Spring | 236.705 | 3 | < 0.0001 |
| | | Autumn | 58.19 | 3 | 0.0014 |
| 2017 | Flat Shoals Creek | Winter | 497.96 | 3 | < 0.0001 |
| | | Spring | 791.06 | 3 | < 0.0001 |
| 2017 | Mulberry Creek | Winter | 11.65 | 3 | 0.0086 |
| | | Spring | 173.73 | 3 | < 0.0001 |

Table 8. Summary of Pearson's chi-square results comparing seasonal differences in proportional habitat use on Flat Shoals Creek and Mulberry Creek in 2016 and 2017.

| Year | Creek | Season | Chi-Square value | df | p value |
|------|-------------------|---------------|------------------|----|----------|
| 2016 | Flat Shoals Creek | Winter-Spring | 1154.65 | 3 | < 0.0001 |
| | | Spring-Autumn | 742.36 | 3 | < 0.0001 |
| | | Autumn-Winter | 1205.87 | 3 | < 0.0001 |
| 2016 | Mulberry Creek | Winter-Spring | 981.36 | 3 | < 0.0001 |
| | | Spring-Autumn | 227.66 | 3 | < 0.0001 |
| | | Autumn-Winter | 32.32 | 3 | 0.0004 |
| 2017 | Flat Shoals Creek | Winter-Spring | 3903.33 | 3 | < 0.0001 |
| 2017 | Mulberry Creek | Winter-Spring | 61.26 | 3 | 0.0032 |

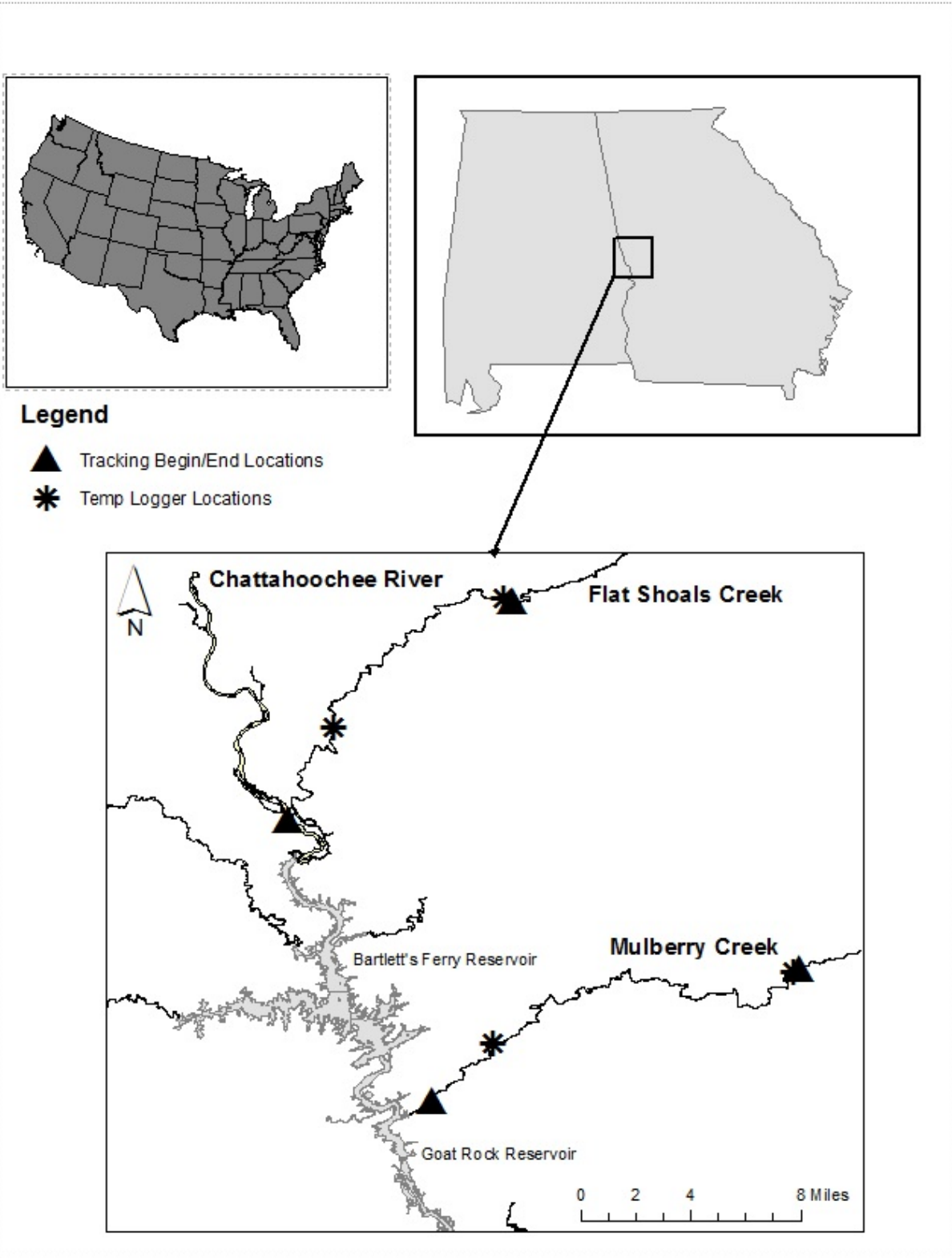


Figure 1. Map of Flat Shoals Creek and Mulberry Creek, Georgia, USA. Triangles represent tracking routes within our study reach; stars represent the locations of temperature loggers in both streams.

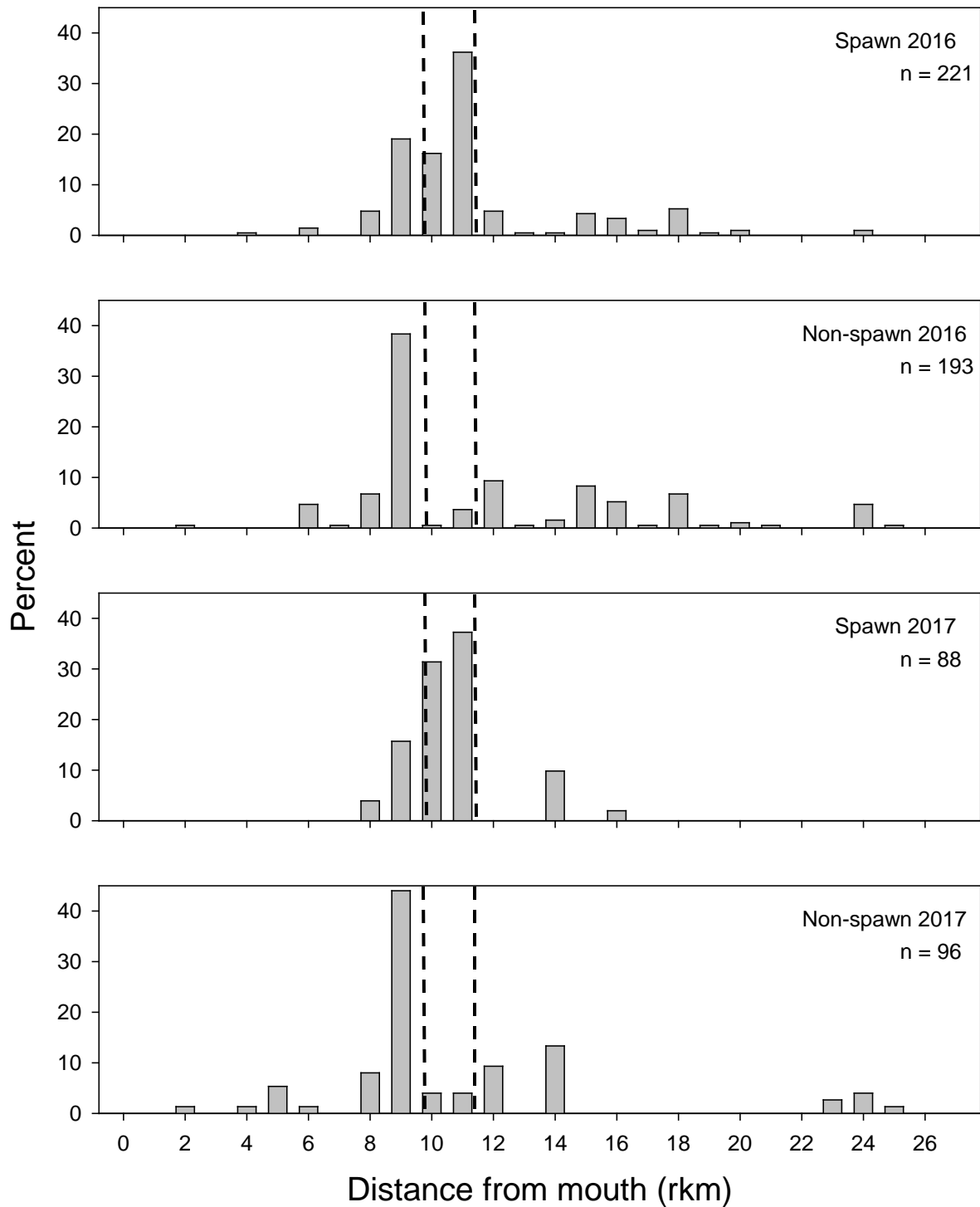


Figure 2. Frequency distribution showing location of radio-tagged Shoal Bass along Flat Shoals Creek study reach during spawning and non-spawning season in 2016 and 2017. Dashed lines represent the upper and lower portion of the large shoal complex. N = number of relocations.

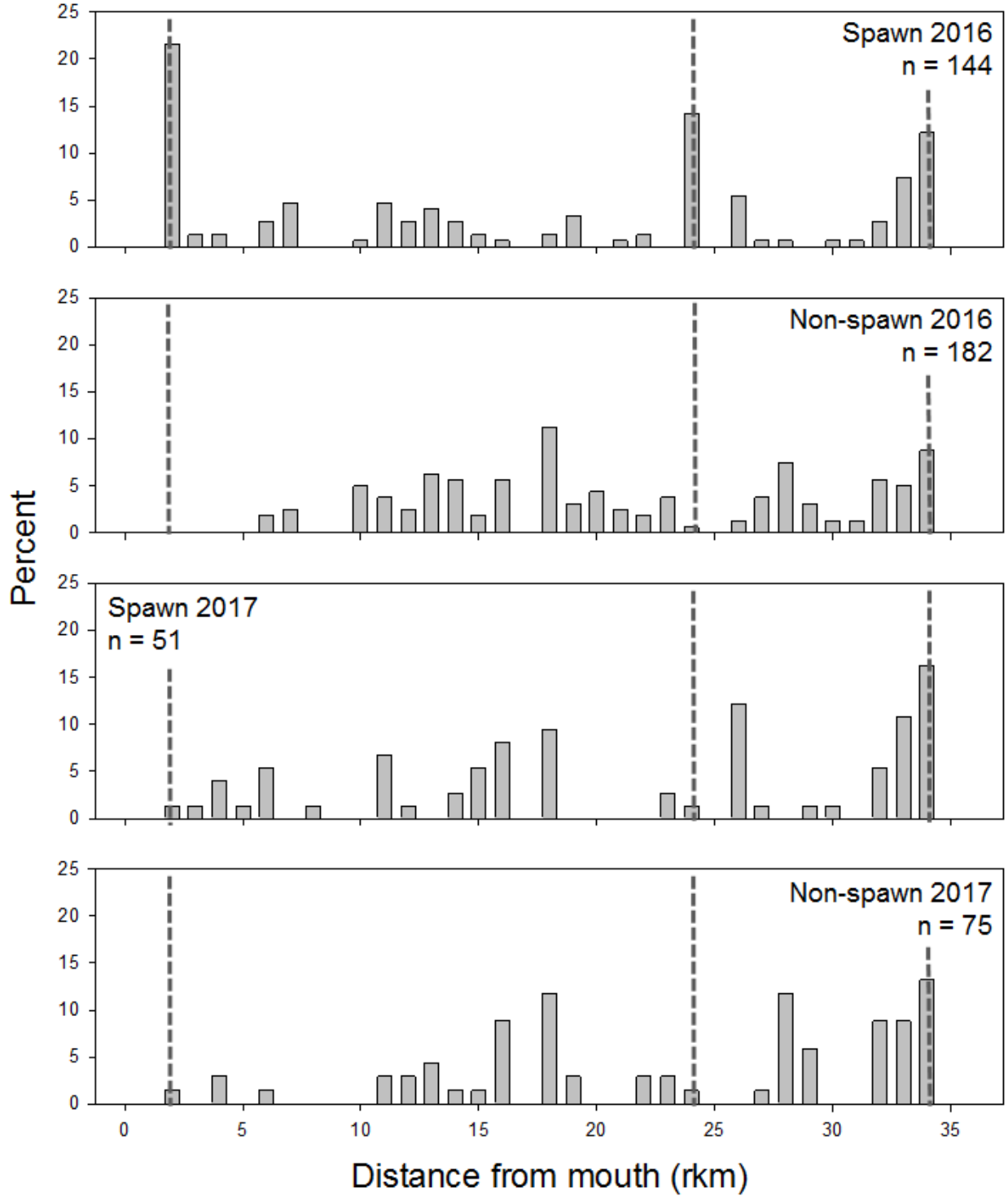


Figure 3. Frequency distribution showing location of radio-tagged shoal bass along Mulberry Creek study reach during spawning and non-spawning season in 2016 and 2017. Dashed lines represent shoal complexes. N = number of relocations.

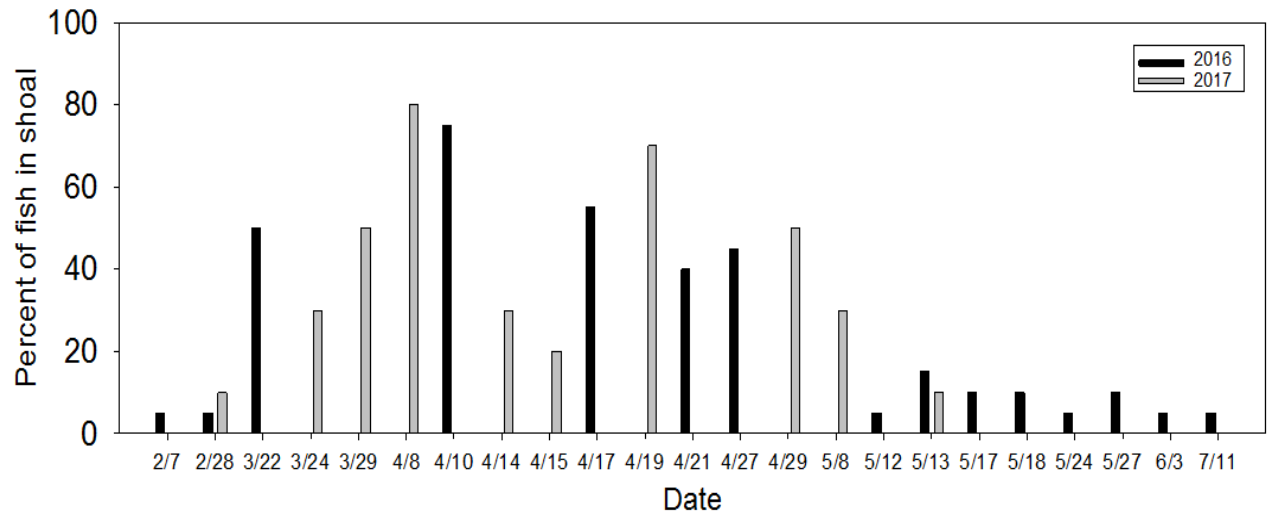


Figure 4. Percent of tagged individuals located within shoal complex on tracking locations in Flat Shoals Creek in both 2016 and 2017.

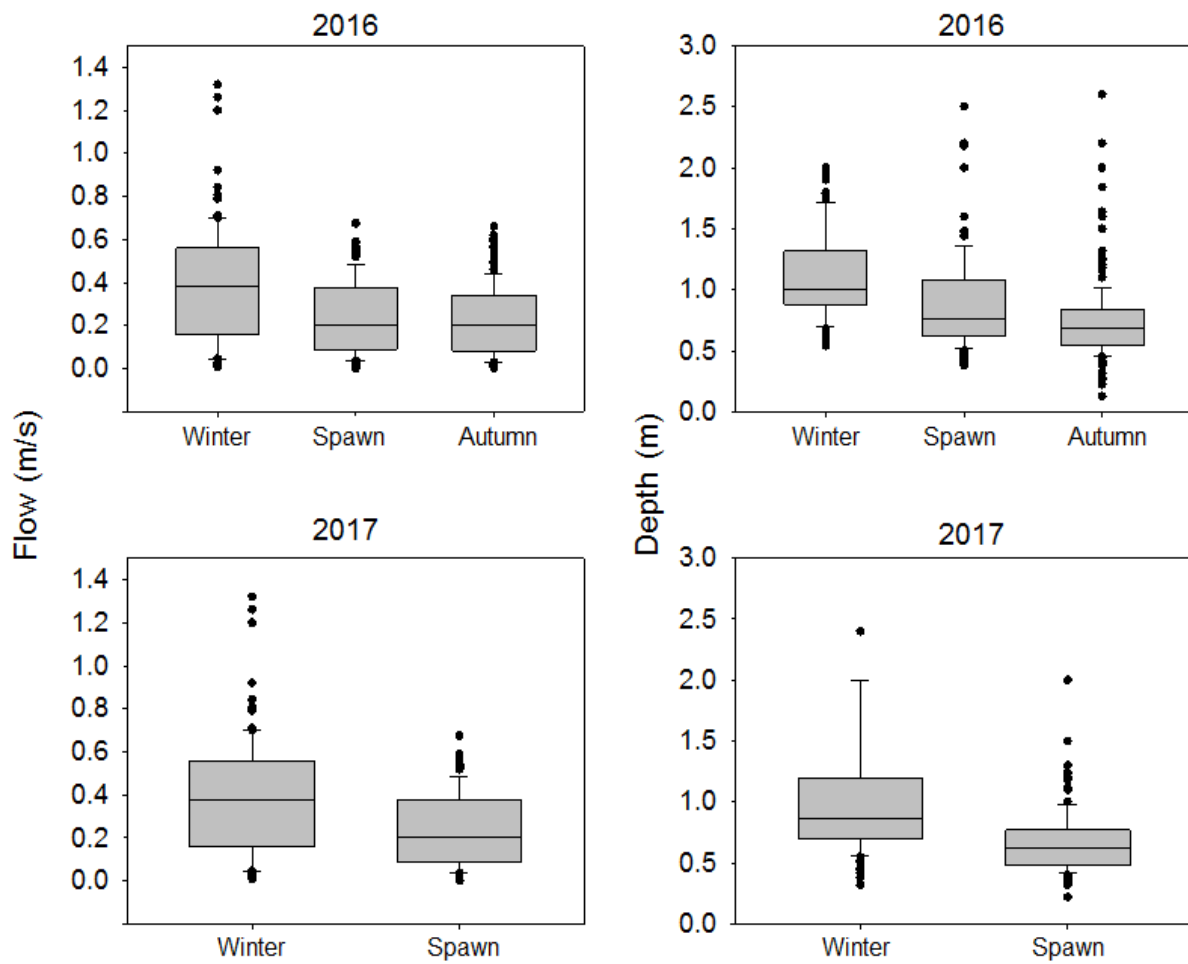


Figure 5. Seasonal velocity and depth use on Flat Shoals Creek in 2016 and 2017.

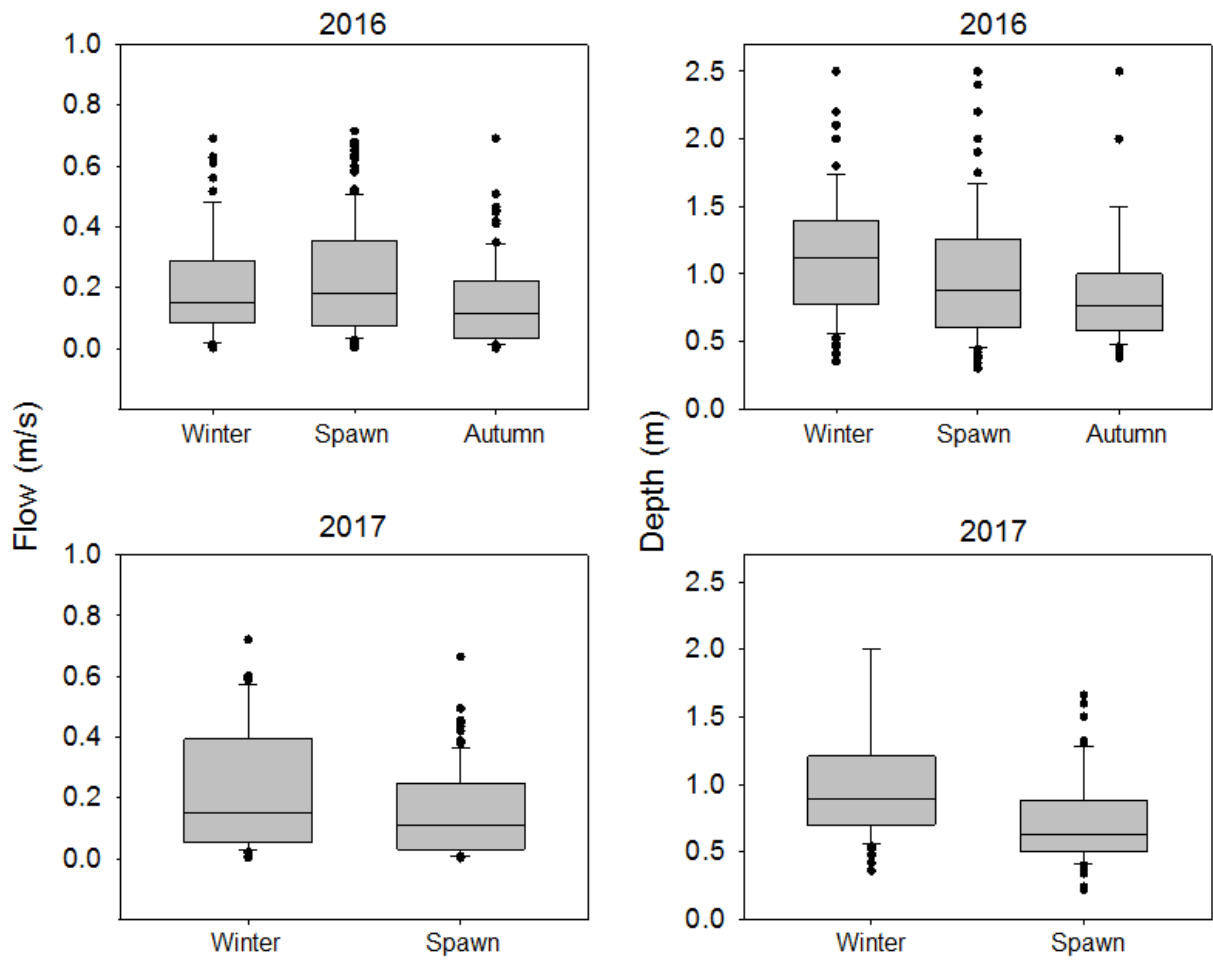


Figure 6. Seasonal velocity and depth use on Mulberry Creek in 2016 and 2017.

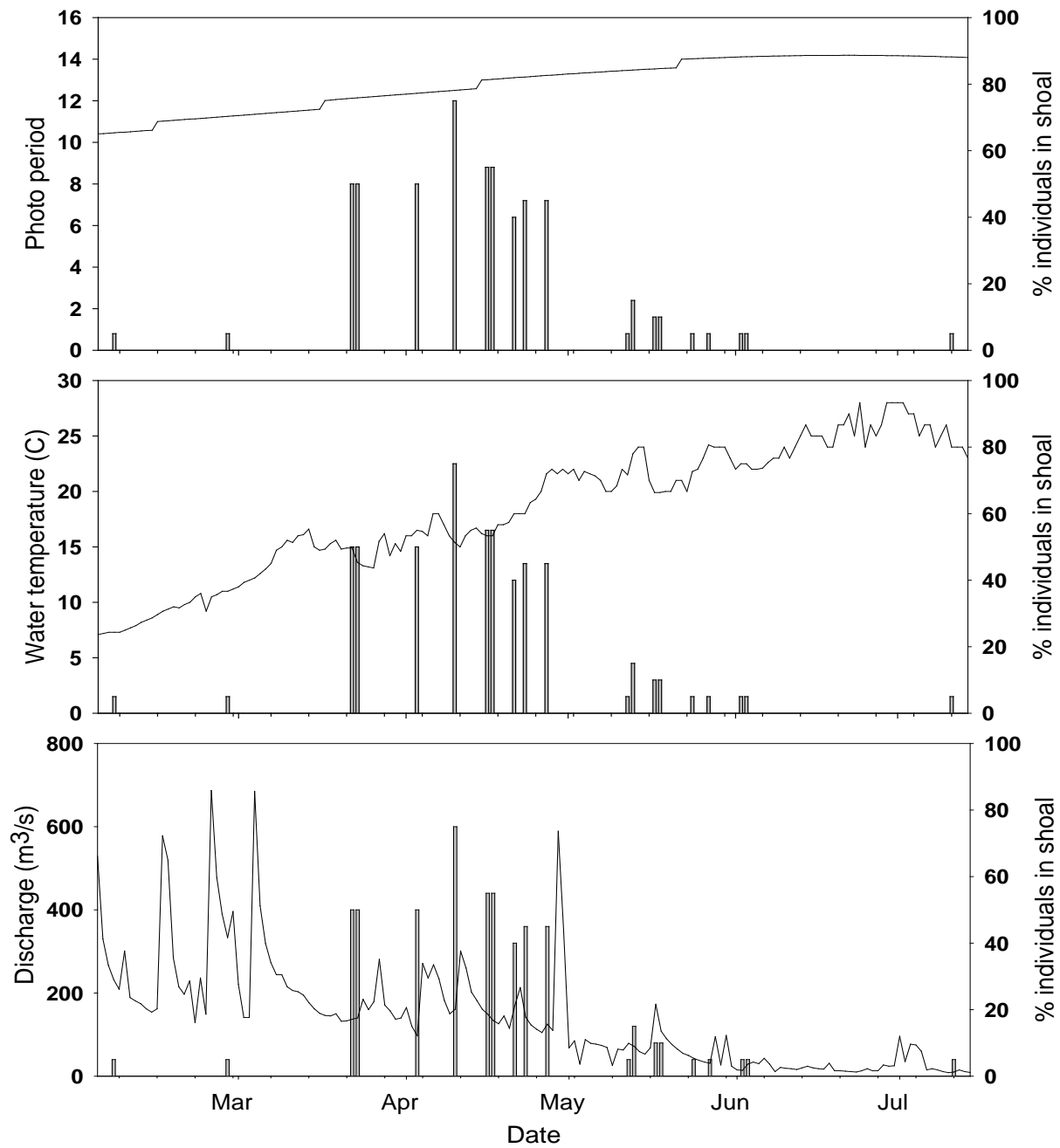


Figure 7. Percent of radio-tagged individuals (bars) located in the large shoal complex on Flat Shoals Creek in 2016 in relation to different environmental variables (lines); photo period, water temperature (°C), and water discharge m³/s.

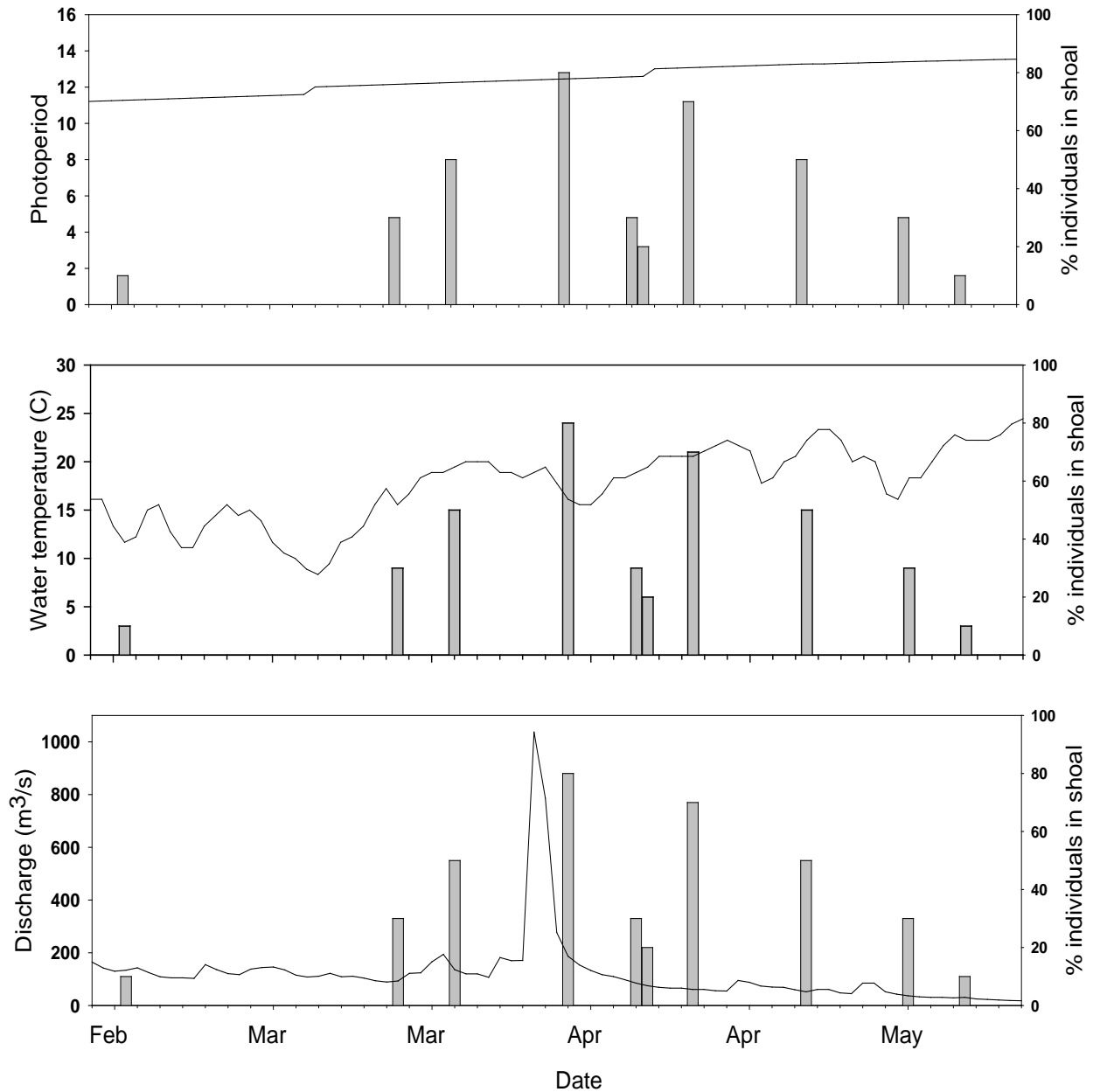


Figure 8. Percent of radio-tagged individuals (bars) located in the large shoal complex on Flat Shoals Creek in 2017 in relation to different environmental variables (lines); photoperiod, water temperature (°C), and water discharge m³/s.

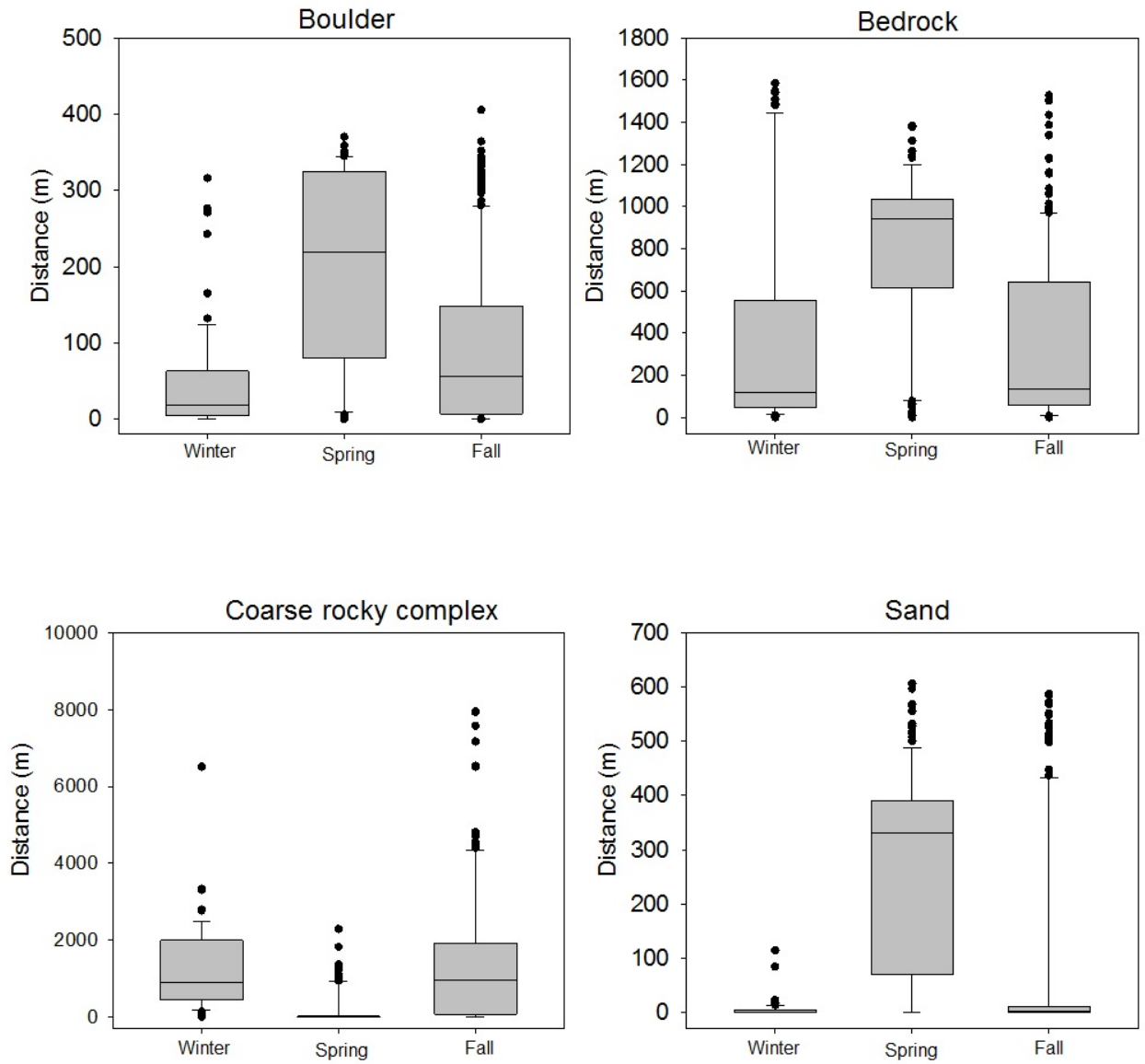


Figure 9. Distance of individual fish locations to boulder, bedrock, coarse rocky complex, and sand substrates across seasons in 2016 on Flat Shoals Creek, Georgia. Note the different Y axes.

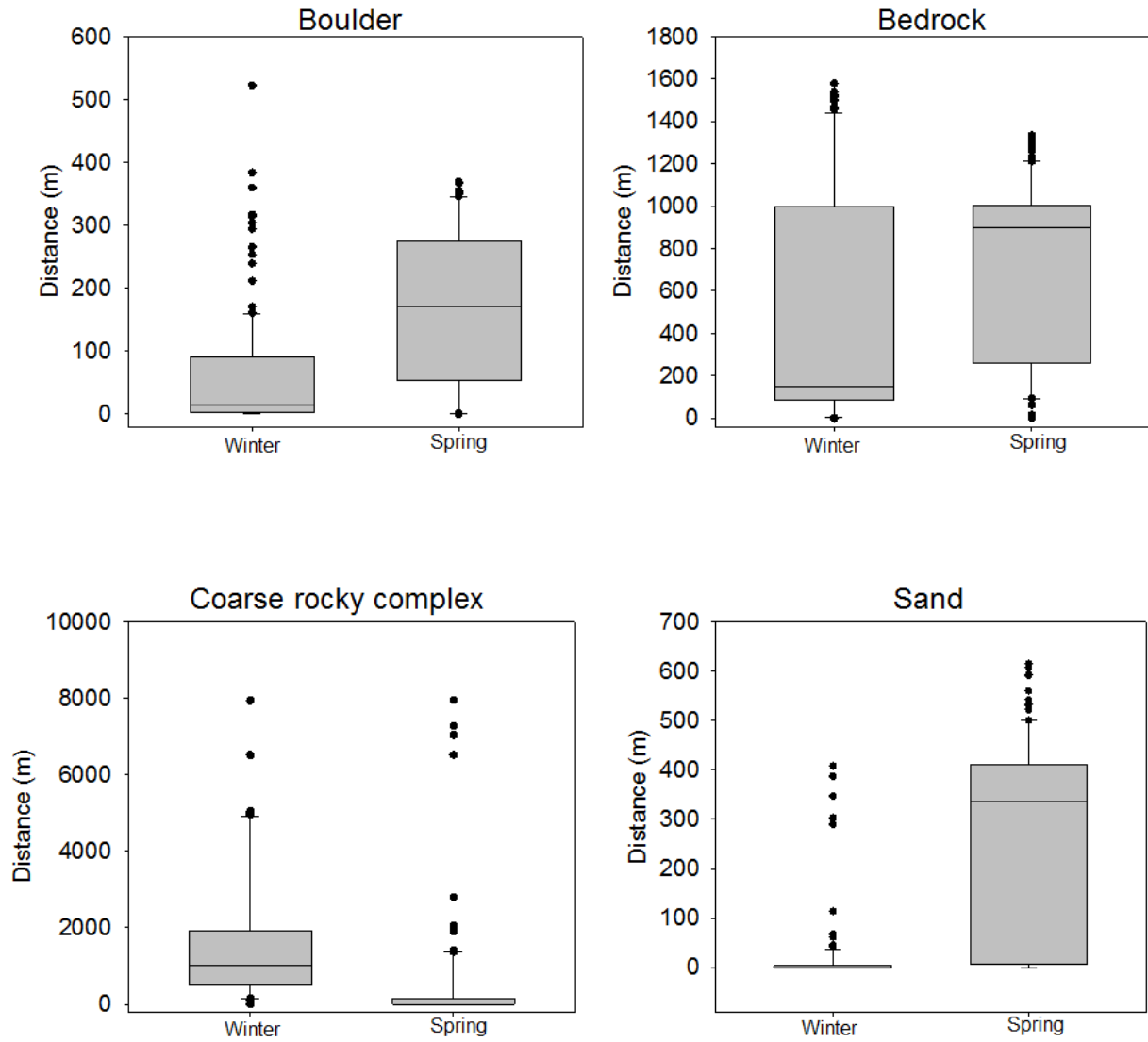


Figure 10. Distance of individual fish locations to boulder, bedrock, coarse rocky complex, and sand substrates across seasons in 2017 on Flat Shoals Creek, Georgia. Note the different Y axes.

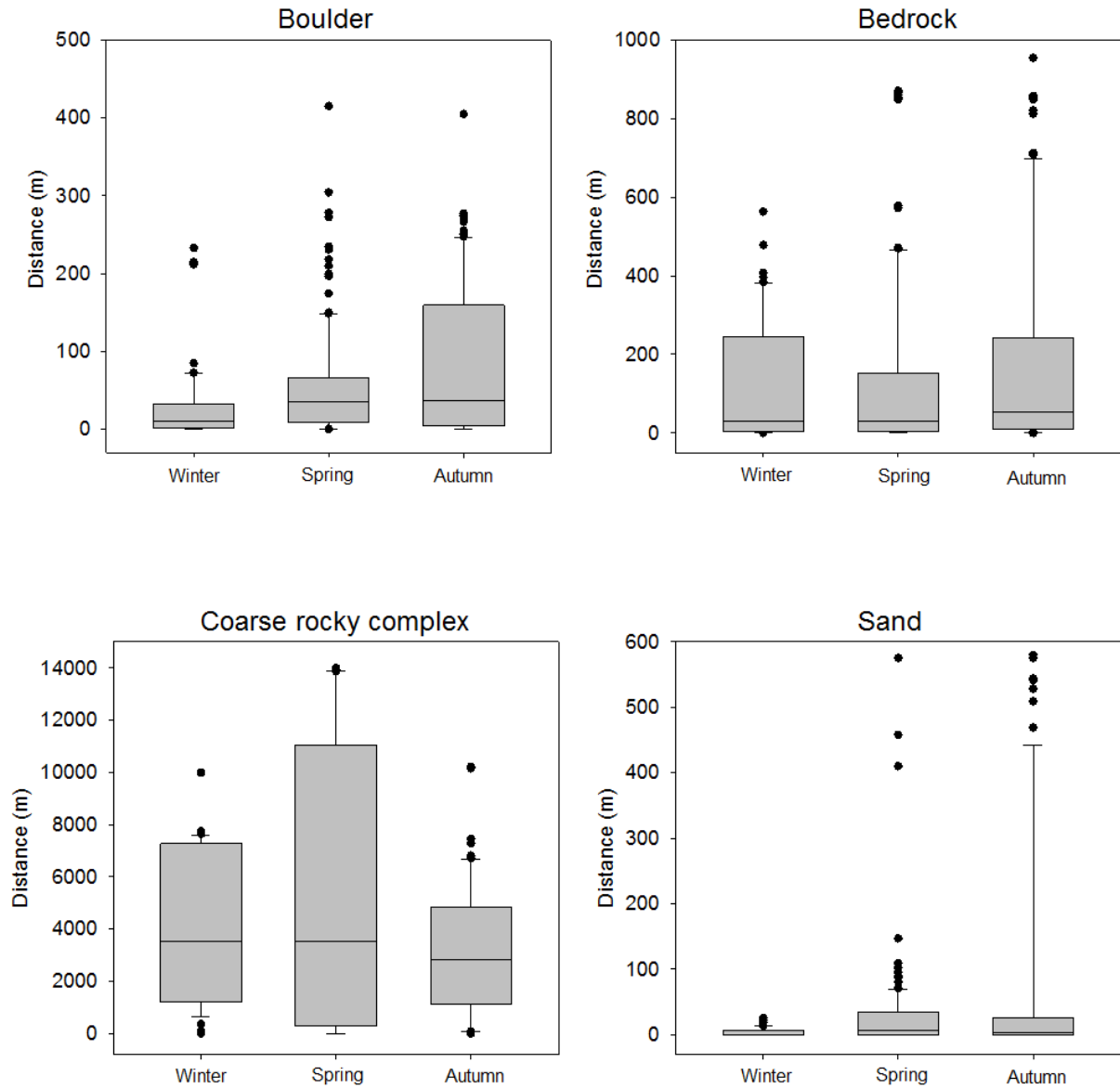


Figure 11. Distance of individual fish locations to boulder, bedrock, coarse rocky complex, and sand substrates across seasons in 2016 on Mulberry Creek, Georgia. Note the different Y axes.

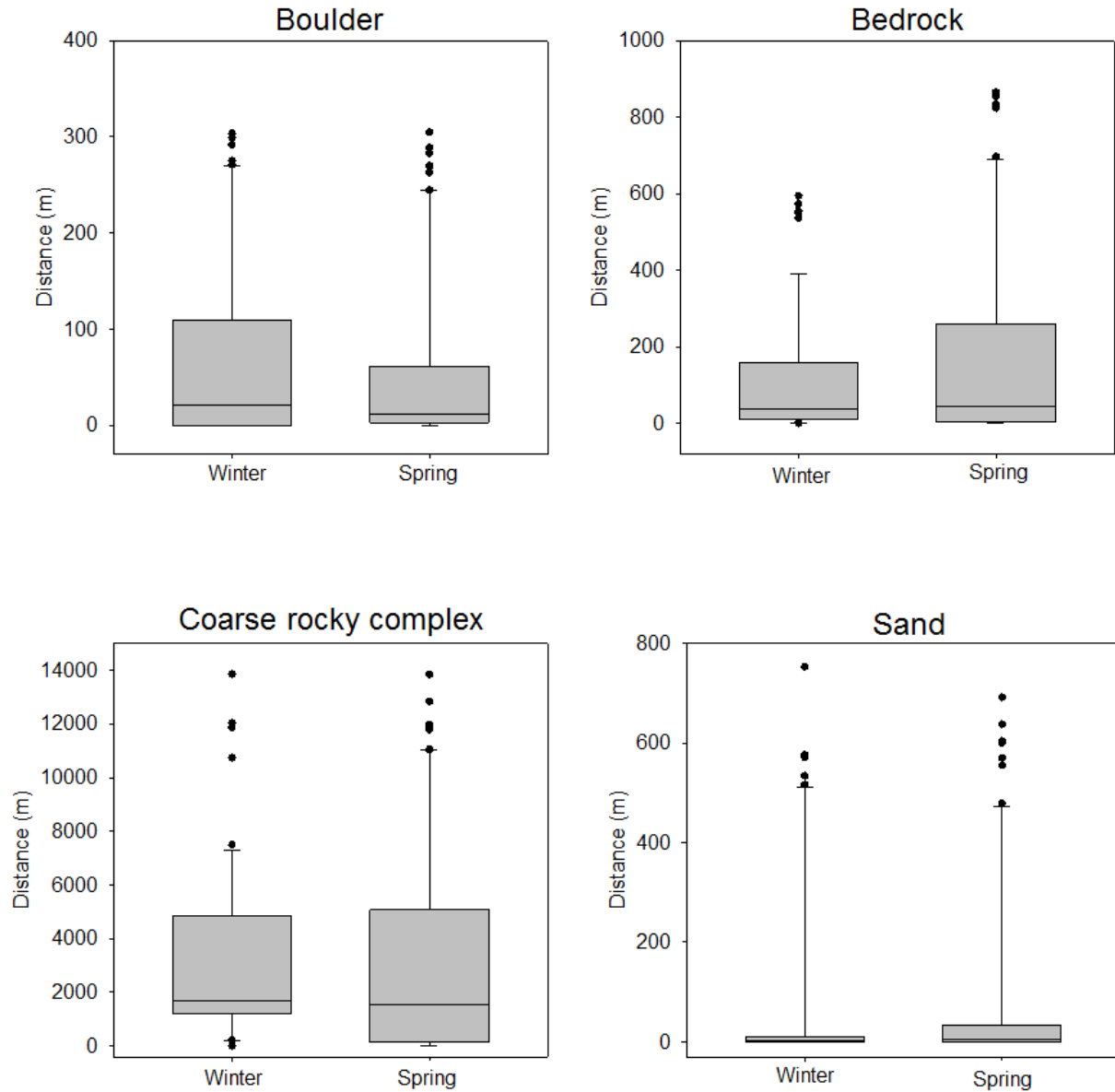


Figure 12. Distance of individual fish locations to boulder, bedrock, coarse rocky complex, and sand substrates across seasons in 2017 on Mulberry Creek, Georgia. Note the different Y axes.

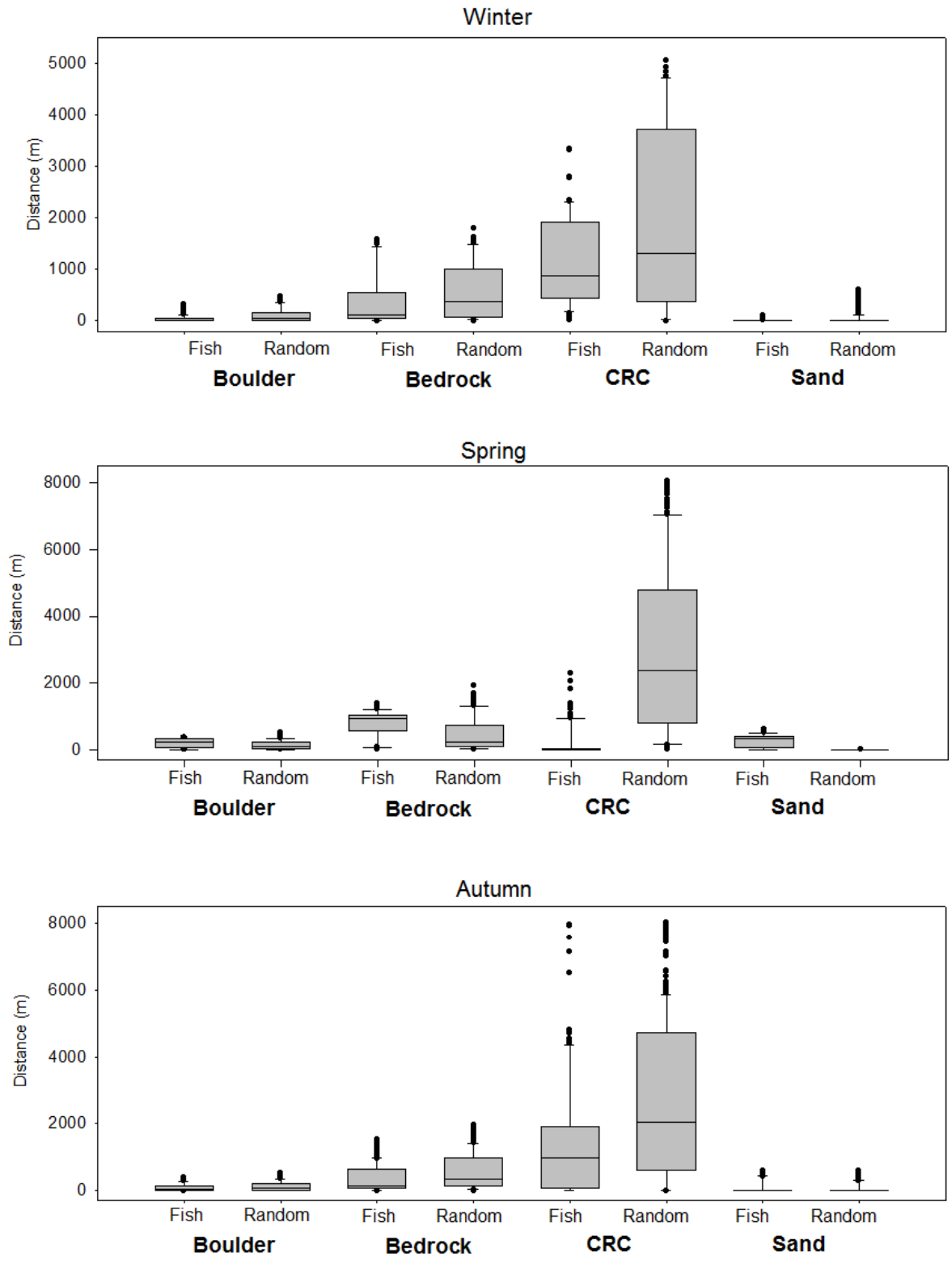


Figure 13. Distance of known fish locations to boulder, bedrock, coarse rocky complex, and sand substrates compared to random location points across seasons in 2016 on Flat Shoals Creek, Georgia.

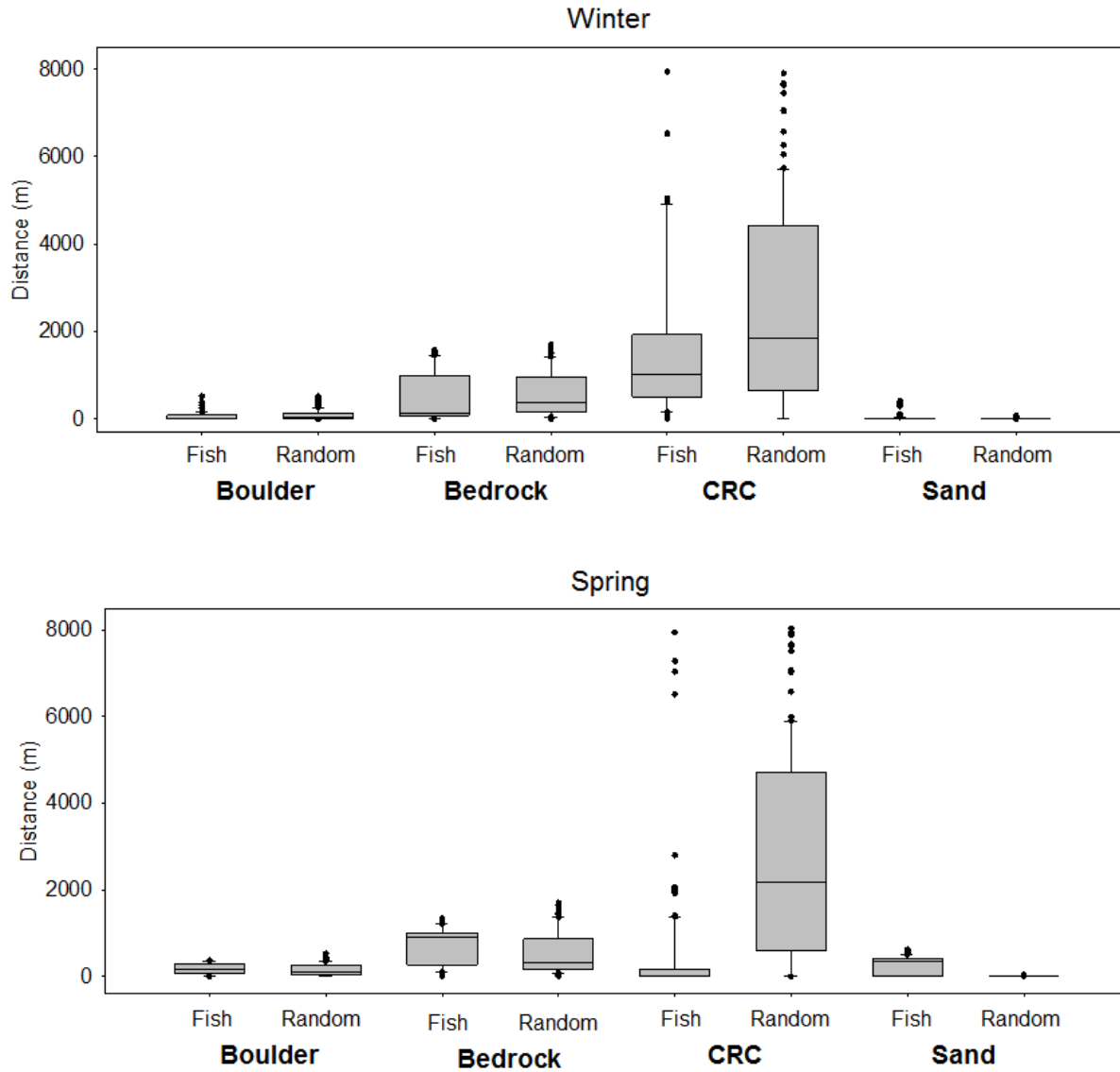


Figure 14. Distance of known fish locations to boulder, bedrock, coarse rocky complex, and sand substrates compared to random location points across seasons in 2017 on Flat Shoals Creek, Georgia.

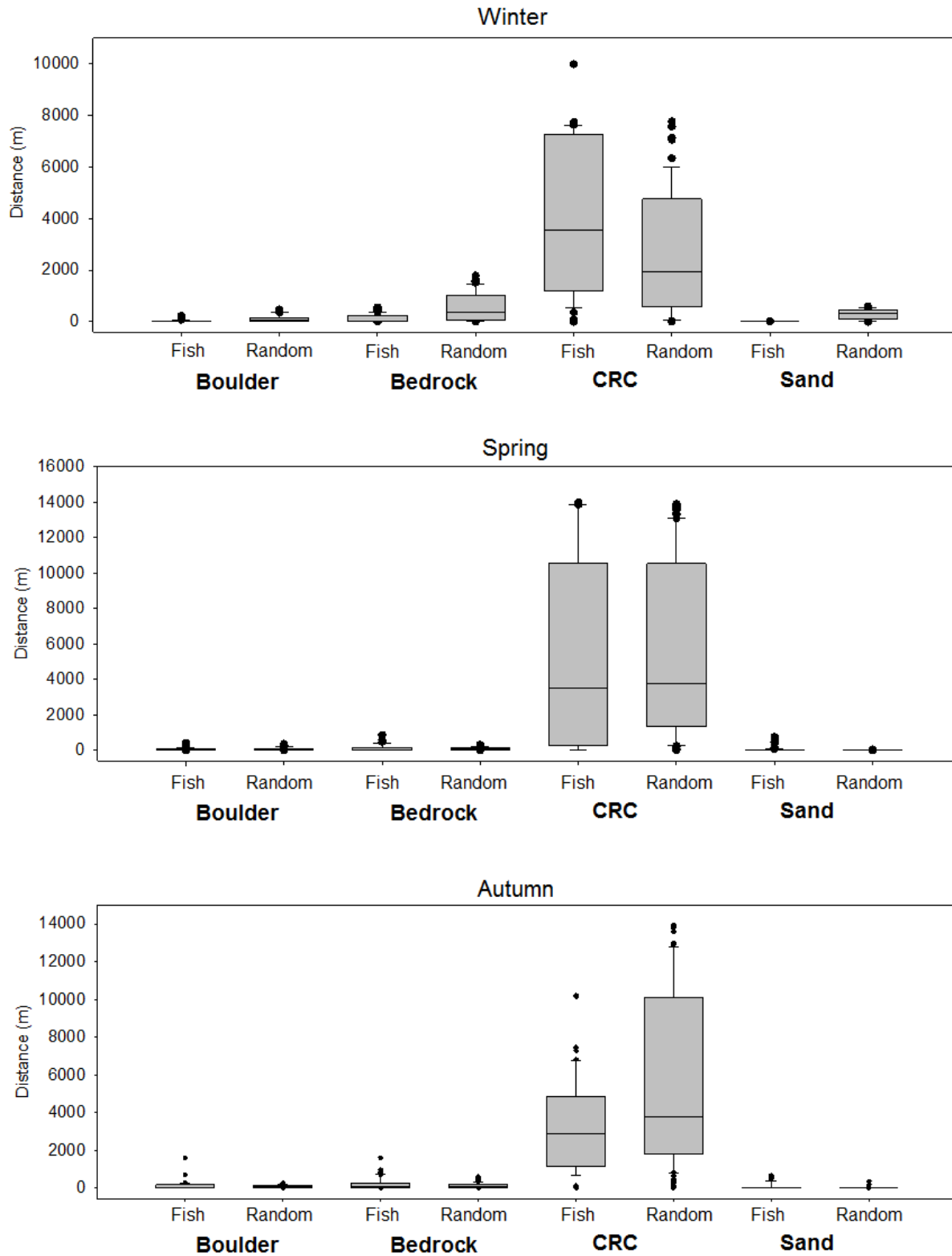


Figure 15. Distance of known fish locations to boulder, bedrock, coarse rocky complex, and sand substrates compared to random location points across seasons in 2016 on Mulberry Creek, Georgia.

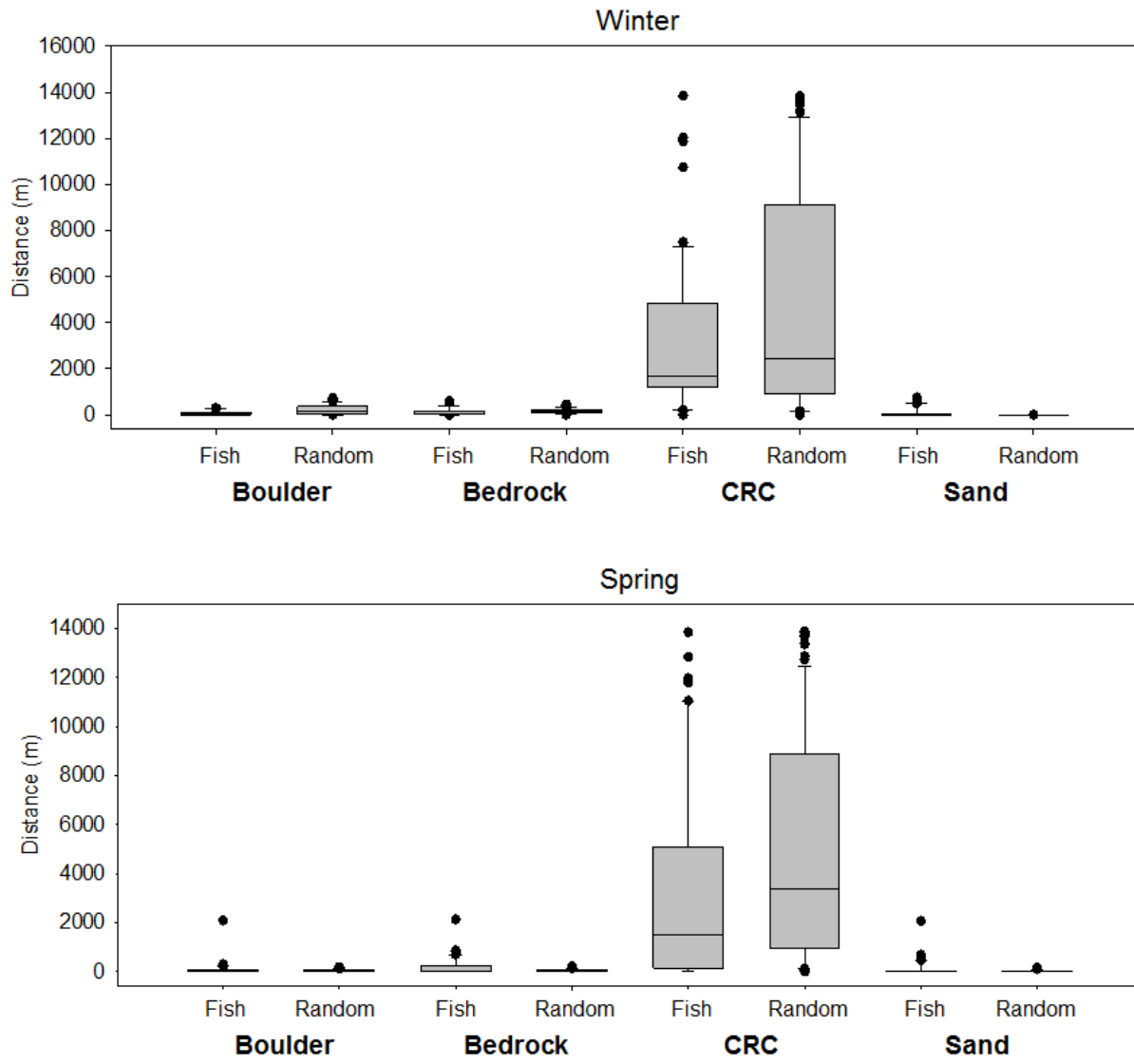


Figure 16. Distance of known fish locations to boulder, bedrock, coarse rocky complex, and sand substrates compared to random location points across seasons in 2017 on Mulberry Creek, Georgia.

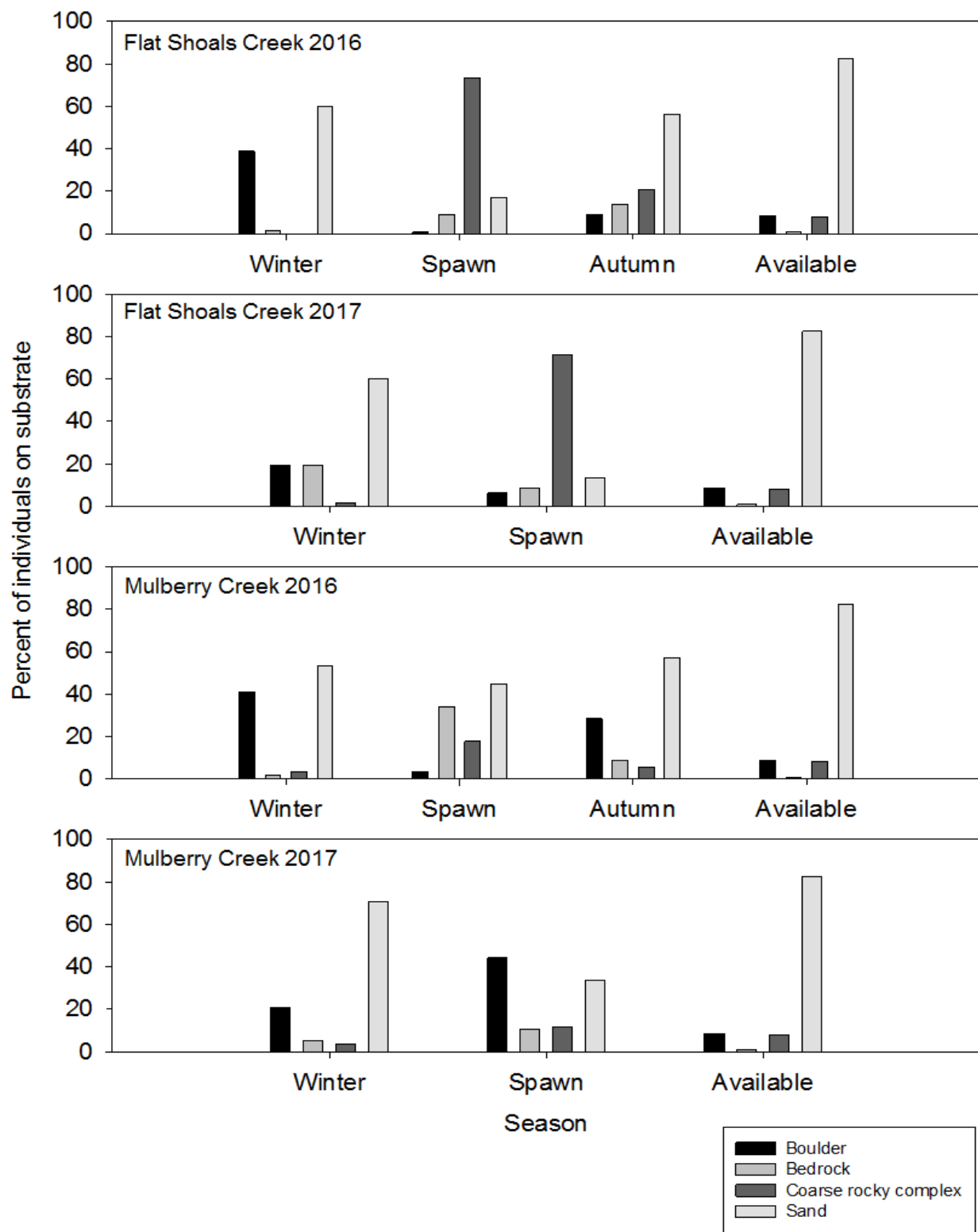


Figure 17. Substrate use by tagged individuals compared to substrate availability for each season on Flat Shoals Creek and Mulberry Creek in 2016 and 2017.

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