Relations Between Shoal Bass and Sympatric Congeneric Basses in the Flint River, Georgia

by

Matthew Robert Goclowski

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Approved by

David Rouse, Chair, Professor of Fisheries and Allied Aquacultures
Steven Sammons, Research Fellow of Fisheries and Allied Aquacultures
Carol Johnston, Professor of Fisheries and Allied Aquacultures
Russell Wright, Associate Professor of Fisheries and Allied Aquacultures

Abstract

Shoal bass *Micropterus cataractae* is a fluvial specialist bass species endemic to the Apalachicola River drainage, which co-occurs with native largemouth bass *M. salmoides* throughout its range. Spotted bass *M. punctulatus* have been recently introduced to the upper Flint River in Georgia, causing concern among fisheries managers and anglers about the potential negative impacts the species may have on the population of shoal bass in the river. In this study, I investigated the potential for competitive interactions among the three species of basses in the Flint River at adult and juvenile life stages. In December 2008, 11 shoal bass, 10 largemouth bass, and 6 spotted bass were implanted with radio transmitters in the Flint River and were tracked for a period of one year. Basses exhibited habitat partitioning in this study; shoal bass were generally found near the fastest available water velocities in shoals with rocky substrates, largemouth bass were found almost exclusively near large woody debris in pools with sandy substrates and little to no flow, and spotted bass often showed habitat preferences intermediate to both species. Individuals of all three species were observed moving distances > 5 km to large shoal complexes during the spawning season; shoals may be important spawning and nursery areas for basses in the Flint River.

Age-0 basses were collected from piedmont and coastal plain segments of the Flint River in early summer during 2008 and 2009 to see if relative hatch timing would provide spotted bass with a competitive advantage over the two native basses in growth or size during juvenile life stages. Basses generally hatched from early April to mid-June at water temperatures ranging

from 20 to 25˚ C. Mean daily growth rates ranged from 0.822 to 1.07 mm/d across species and samples. Differences among species in mean hatch dates, mean growth rates, and mean total lengths were observed; however, these differences were not consistent across samples. Discharge varied widely between years and sampling sites and this may have contributed to the difficulty in detecting consistent patterns across samples. Relative hatch timing did not appear to convey any competitive advantage to spotted bass over the two native species.

Spotted bass were collected from the Flint River in Georgia and native Alabama bass were collected from the Tallapoosa River in Alabama to compare life history strategies among native and introduced bass populations. Males began maturing at 1 year and 168 mm in the Flint River and 2 years and 173 mm in the Tallapoosa River. Females began maturing at 2 years and 186 mm in the Flint River and 2 years and 200 mm in the Tallapoosa River. No differences in age or size at 50% maturity were evident between the two populations. The invasive success of spotted bass in the Flint River does not appear to be related to a shift in life history characteristics.

Competitive interactions between shoal bass and spotted bass do not appear to pose a large threat to the persistence of shoal bass in the upper Flint River. A potential for introgressive hybridization between the two species exists and warrants future investigation and monitoring. Fisheries managers must attempt to educate anglers about the dangers of moving species into new drainages, in order to prevent future invasions.

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Introduction

Shoal bass *Micropterus cataractae* is a recently described black bass species (*Micropterus spp.*), that is endemic to the Apalachicola River drainage in Alabama, Florida, and Georgia, including the Chattahoochee and Flint rivers (Williams and Burgess 1999). An introduced population has been established in the Ocmulgee River of the Altamaha River drainage in Georgia (Williams and Burgess 1999). Shoal bass are considered to be habitat specialists that prefer riffle and run habitats dominated by boulder and bedrock substrates in lotic systems (Wheeler and Allen 2003; Stormer and Maceina 2009). Shoal bass are capable of surviving and reproducing in ponds (Smitherman and Ramsey 1972), but they do not persist in impoundments (Williams and Burgess 1999). Johnston and Kennon (2007) suggested that shoal bass require complex shoal habitats with a variety of microhabitats to use at various life stages in order for the species to persist.

Populations of shoal bass are thought to be declining throughout much of their native range, and have been listed as a species of high conservation concern in Alabama (Mirarchi et al. 2004), threatened in Florida (Gilbert 1992), and a species of special concern over their entire range by the American Fisheries Society (Williams et al. 1989). Potential threats to shoal bass include habitat loss due to impoundment, siltation, and dredging, pollution, irregular flows, poor land use, and possible competition and hybridization with other bass species (Williams and Burgess 1999; Wheeler and Allen 2003; Stormer and Maceina 2008). In 2005-2006, a survey of several Alabama tributaries of the Chattahoochee River, where shoal bass historically occurred, found only one viable population, at Moffits Mill on Little Uchee Creek (Stormer and Maceina 2008). The researchers suggested that shoal bass populations may have been eliminated from streams where they were historically present by catastrophic events (e.g. droughts), and that habitat fragmentation due to impoundments on the Chattahoochee River may have prevented shoal bass from recolonizing these areas. Another factor that may have contributed to the decline of shoal bass is the introduction of spotted bass *M. punctulatus*, which appeared to dominate these Alabama streams that were formerly occupied by shoal bass (Stormer and Maceina 2008). Spotted bass were first introduced into the Apalachicola River system sometime around 1941, though no specimens were recorded above the fall line prior to 1968 (Williams and Burgess 1999). Alabama bass *M. henshalli*, formerly considered a subspecies of spotted bass (Baker et al. 2008), were also introduced to the upper Chattahoochee River system prior to 1970 (Williams and Burgess 1999). Hurst (1969) collected approximately equal numbers of shoal bass and spotted bass in Halawakee Creek, Alabama, during collections in 1968-1969; however Stormer and Maceina (2009) collected 53 spotted bass and only 3 shoal bass from the same areas in 2005-2006. It is possible that the more adaptive spotted bass was able to outcompete the shoal bass when faced with changing environmental conditions over time in the Alabama tributaries of the Chattahoochee River.

Shoal bass occur sympatrically with largemouth bass *M. salmoides* throughout their entire range (Williams and Burgess 1999). Wheeler and Allen (2003) found that adult shoal bass and largemouth bass in the Chipola River had very similar diets; however, they used different habitats and were able to coexist through habitat partitioning. Shoal bass were more abundant in the shallower, faster moving shoal areas while largemouth bass were more abundant in the deeper, slower moving pools and backwater areas. However, spotted bass appear to be more of a habitat generalist and are often found inhabiting a variety of areas, including the shallow rocky riffles and shoals that shoal bass prefer (Hurst 1969; Vogele 1975; Tillma et al. 1998). Horton and Guy (2002) found that spotted bass in Otter Creek, Kansas, used pool habitat located near large woody debris throughout much of the year. Spotted bass typically remained in one pool during the summer and winter but moved among pools, crossing over riffles and runs during the spring and fall. Stormer and Maceina (2009) found that shoal bass in Little Uchee Creek, Alabama, used shoal habitat near boulders throughout much of the year, except during low water periods in late summer and fall when they moved to deep-water refuge areas in pools. Although spotted bass in their native range have been shown to exist sympatrically with other black bass species through resource partitioning (Vogele 1975; Scott and Angermeier 1998; Sammons and Bettoli 1999), introductions of the species into streams containing shoal bass may have detrimental effects on shoal bass already present in those areas. Further research on the habitat use and movements of shoal bass and spotted bass occurring sympatrically is needed to provide insight on the degree of niche overlap and competition between the two species.

The relative spawning times of bass species can play an important role in determining the population dynamics of congeneric species (Sammons et al. 1999). Ludsin and DeVries (1997) found that cohorts of largemouth bass that hatched early in the year had a competitive advantage, leading to higher first-year recruitment rates than those experienced by cohorts that hatched later in the year. Smitherman and Ramsey (1972) found that shoal bass and spotted bass from Halawakee Creek both spawned around the same time in early May when held in hatchery ponds. Shoal bass and spotted bass may not spawn at the same time in all systems where they co-occur, and differences in relative hatch timing may lead to a competitive advantage in first year recruitment for one of the two species. Research on the hatching dates, growth, and weekly survival of young of the year shoal bass and spotted bass occurring sympatrically would aid in the understanding of the population dynamics between the two species.

In recent years, populations of introduced spotted bass have become established in the Flint and Ocmulgee rivers in Georgia. Spotted bass were first collected in the upper Flint River in 2005, and their numbers appear to be increasing rapidly (J. Evans, Georgia Department of Natural Resources, personal communication). It is likely that these fish were introduced from the Chattahoochee River system, where spotted bass, Alabama bass, and their intergrades are common. Four bass collected from the Flint River during 2009 were identified as spotted bass (C. Johnston, Auburn University, personal communication), however, it is possible that Alabama bass or intergrades may also have been introduced to the river. The introduction of spotted bass in the Flint River has caused great concern among anglers and fisheries managers about the potential negative impacts that spotted bass may have on shoal bass. In this study, I investigated the potential for competition among introduced spotted bass and native shoal bass and largemouth bass at adult and juvenile life stages in the Flint River. This study had two objectives: 1) describe the movement, behavior, and habitat use of the three bass species in the Flint River and 2) investigate the relative hatch timing of the three bass species to determine if hatch timing provides any of the species with a competitive advantage in growth or body size at early life stages.

Study Site

A major tributary of the Apalachicola River drainage, the Flint River flows 565 km from its headwaters near Atlanta, Georgia, to its confluence with the Chattahoochee River at Lake Seminole. The upper Flint River flows through the piedmont region of Georgia, which is characterized by a series of wide, granite shoal areas with shallow water and fast current interspersed with run and pool areas with deeper water and less flow. At the fall line, the river drops approximately 125 m over 80 km. Below the fall line the river becomes a typical coastal plain stream, characterized by a sandy substrate with some limestone outcroppings, greater amounts of woody debris present in the channel, and greater base flows, due to the addition of ground water from aquifers. The Flint River flows over 320 km before being impacted by the first of three mainstem impoundments, making it one of only 42 rivers in the U.S. with > 200 km of unimpeded flow (Benke 1990). The Flint River ecosystem is biologically diverse, containing numerous rare and/or protected species of flora and fauna, including the Halloween darter *Percina crypta*, Barbour's map turtle *Graptemys barbouri*, bluestripe shiner *Cyprinella callitaenia*, and shoal spider lily *Hymenocalis coronaria*. Major sport fish occurring in the Flint River include largemouth bass, shoal bass, striped bass *Morone saxatilis*, channel catfish *Ictalurus punctatus*, redbreast sunfish *Lepomis auritus*, flathead catfish *Pylodictus olivarus*, and the now introduced spotted bass.

Methods

Telemetry - In December 2007, a total of 27 basses (11 shoal bass, 6 spotted bass, and 10 largemouth bass) were collected with a boat-mounted DC electrofishing unit and fitted with Advanced Telemetry Systems (ATS) radio transmitters in the upper Flint River near the GA Highway 18 bridge (Figure 1). In June 2008, four additional shoal bass were fitted with radio transmitters in the same river section. Two size groups of fish were tagged in this study. Fish weighing between 180 g and 700 g were implanted with 3.6-g radio transmitters (ATS Model F1580) that had a 258-d battery life expectancy. Fish greater than 700 g were implanted with 14-g radio transmitters (ATS Model F1835) that had a 502-d battery life expectancy. Transmitter sizes were chosen to be less than 2% of a fish's body weight in order to ensure that movement and behavior would not be affected (Winter 1996). The larger transmitters were fitted with mortality sensors. If the transmitters were motionless for at least 24 h due to death or expulsion, then the mortality sensor caused the pulse rate to double. The smaller transmitters did not have a mortality sensor; if the fish with these transmitters were found in the same location for three consecutive tracking trips, they were considered to be dead.

Transmitters were implanted as described in Maceina et al. (1999). Fish were tracked approximately every 14 days, beginning about two weeks after surgery. Every other tracking session, fish were located once every 6 h over a 24 h period to assess diel movements (Sammons et al. 2003). Fish were located using an ATS Model R2000 signal receiver and a directional yagi antenna. The location of each fish was determined by moving along the stream in a boat until a signal was detected. Tracking would continue until the signal was strongest when the antenna was pointed at the water. At this point, the location of each fish was recorded using a global positioning system (GPS) unit. The mesohabitat type (pool, riffle, run, shoal, etc.) at the location of each fish was noted. The time, water depth, water velocity, and water temperature were recorded at each location. Additional data about river stage and discharge at the start of each tracking session were obtained from the United States Geological Survey. Fish were tracked on May 6, 2008, over approximately 120 river km from a fixed-wing aircraft fitted with two wing-mounted directional yagi antennae. Fish were tracked until they died, expelled the transmitter, or until the transmitter battery expired.

The daily movement rate of each fish was calculated in terms of minimum displacement per day (MDPD) by dividing the distance moved in meters between locations by the amount of time in days between locations (Colle et al. 1989; Wilkerson and Fisher 1997; Sammons et al. 2003). Similarly, the diel movement rate of each fish located on the 24 h tracking sessions was calculated in terms of minimum displacement per hour (MDPH) by dividing the distance moved in meters by the amount of time in hours between locations. Fish movement rates were compared among the four seasons, defined by water temperatures: winter, <12 °C; spring, increasing from 12-22 °C; summer, greater than >22 °C; and fall, decreasing from 22-12 °C (Todd and Rabeni 1989; Wilkerson and Fisher 1997; Sammons et al. 2003). Fish behavior was analyzed among four diel periods: dawn, day, dusk, and night. In order to increase the number of observations, diel movement rates were compared between two diel periods: day, the hours between sunrise and sunset; and night, the hours between sunset and sunrise. Mean daily and diel movement rates were compared among seasons, species, and diel periods using a repeated measures analysis of variance (ANOVA) with fixed and random effects (Maceina et al. 1994; Wilkerson and Fisher 1997; Bunnell et al. 1998; SAS Institute 2002; Sammons and Maceina 2005). Relations between movement rates and environmental variables were assessed with multiple regression models (Jones and Rogers 1998; SAS Institute 2002). Flow and depth use were compared among species, seasons, and diel periods using mixed-model ANOVAs (SAS Institute 2002). A Bonferroni correction ($P = 0.05/n$) was applied in all multiple comparisons of movements and habitat use among species, seasons, and diel periods.

On March 5, 2009, benthic sonar images were captured using a Humminbird® 981c Side Imaging Sonar unit along a 22-km section of the upper Flint River. This area encompassed virtually all of the locations of the radio-tagged bass. The images were captured during a high flow event so that they would cover the entire bankfull stream channel (Kaeser and Litts 2008). A GPS unit was used to collect reference location trackpoints during image capture. The sonar images and reference trackpoints were combined to create a detailed habitat map of the telemetry study area using the techniques described by Kaeser and Litts (2009). Each image was georeferenced using the appropriate trackpoint locations. The images were then stitched together into mosaics to create sonar image maps in ArcGIS 9.2 (ESRI 2007). Substrate type for the whole mapped area was classified as bedrock, rocky boulder, rocky fine, mixed rocky, sandy, or no data (Table 1). Classified substrates were digitized into a polygon shapefile using the sonar image maps in ArcGIS 9.2 (ESRI 2007). Substrate data was overlaid onto fish location waypoints in ArcGIS 9.2 (ESRI 2007). Mesohabitat types (eg. pool, run, etc.) were classified using satellite imagery and field observations and digitized into a polygon shapefile in ArcGIS 9.2 (ESRI 2007). The total available area (ha) was calculated for each substrate type and mesohabitat type within study area. Chi-squared tests and Manly selection ratios (Manly et al. 2002) were calculated using Fishtel 1.4 (Rogers and White 2007) to determine if fish were using habitat in proportion to its availability and determine which habitats fish were selecting for. Selection ratios with associated 95 % confidence intervals > 1 indicated that fish were selecting for a habitat type, selection ratios with associated 95 % confidence intervals < 1 indicated selection against a habitat type, and selection ratios with associated 95 % confidence intervals that contained a value = 1 indicated that fish were using habitat in proportion to its availability. Large woody debris was identified using the sonar image maps and digitized into a point shapefile in ArcGIS 9.2 (ESRI 2007). The nearest distance of each fish location to large woody debris and the stream bank was calculated using the Near tool in ArcGIS 9.2 (ESRI 2007). The number of pieces of large woody debris and the number of different substrate types (index of habitat complexity) found within a 15-m buffer zone surrounding each fish location were calculated using Joins in ArcGIS 9.2 (ESRI 2007). Mean distances to woody debris and the bank, and mean counts of woody debris and substrate types within 15 m of each fish location were compared among species using a mixed-model ANOVA (SAS Institute 2002).

Age-0 Study - During the summers of 2008 and 2009, age-0 bass were collected from the piedmont and coastal plain regions of the upper Flint River for hatch date estimation (Figure 2). Fish were collected using a seine, backpack electrofisher, or a DC electrofishing unit with a handheld anode. All bass collected in these samples were euthanized with MS-222, then placed on ice. All fish were measured for total length (TL, mm) and weighed (g). Sagittal otoliths from each fish were removed and mounted with thermoplastic cement, convex side down, on glass microscope slides (Miller and Storck 1982). Each otolith was read independently three times, and the mean of the three counts was considered as the age in days of each fish (DiCenzo and Bettoli 1995). Hatch dates of individual bass were determined using the equation modified by DiCenzo (1993):

Hatch = Date - Age - X, where

Hatch = estimated hatch date

Date = calendar day of capture

Age = mean number of growth rings counted

X = number of days between hatching and formation of first daily increment.

The first daily growth increment was assumed to form five days after hatching for all three black bass species (Miller and Storck 1982; DiCenzo and Bettoli 1995; Sammons et al. 1999). Daily growth rates for each fish were calculated by dividing total length (mm) by age (d). In 2009, temperature loggers were placed in the piedmont and coastal plain sections of the Flint River from March through June to determine temperature at hatch. Discharge data were obtained for both sampling years from United States Geological Survey (USGS) gauges in the piedmont (USGS 02344872) and the coastal plain (USGS 02347500). The relationships between abiotic variables (e.g. discharge, temperature) and biotic variables (e.g. growth rates) were examined using linear regression (SAS Institute 2002). One-way ANOVA was used to compare mean hatch date, mean total length, and mean growth rates among species and capture locations

(SAS Institute 2002). A Bonferroni correction ($P = 0.05/n$) was applied in all multiple comparisons among species. Only individuals captured during late June and early July were used in comparisons of total length. One early-hatching shoal bass from the coastal plain in 2009 was removed from analyses as it was an outlier.

Results

Telemetry

Radio-tagged basses were tracked between January 4, 2008 and December 16, 2008. A total of 27 radio-tracking surveys were conducted and 677 fish locations were obtained. When the study ended, three largemouth bass and one shoal bass had remained within the study area. The fates of the remaining fish were as follows: nine fish were tracked until tags expired, four fish were harvested by anglers, one fish was consumed by a bird, 10 fish died or expelled transmitters, and three fish were missing (Table 2).

Movement - All radio-tagged basses remained in close proximity to tagging locations until approximately two months after tagging. In late February and early March, several individuals of all three species (3 of 10 largemouth bass, 10 of 11 shoal bass, and 3 of 6 spotted bass) emigrated from the study area. Subsequent tracking trips and an aerial survey revealed that most fish had migrated between five and eight km to, or in close proximity to, major shoal complexes (Figure 3). Three largemouth bass moved upstream to the base of a large shoal complex that terminated approximately nine km upstream from the GA Highway 18 bridge. One spotted bass was observed approximately one km downstream from the shoal that the three largemouth bass migrated to, where it remained for about one week before returning to the tagging area. Five shoal bass and two spotted bass moved downstream into a large shoal complex that began about five km downstream from the GA Highway 18 bridge. One of these shoal bass returned to the tagging area in mid May, while the others remained in this area until their tags died or they were harvested. Two additional shoal bass tags were found with mortality sensors engaged in close proximity to this shoal. One shoal bass was found during the aerial tracking event in a shoal approximately 20 km downstream of its tagging location; that fish had returned to the area where it was originally tagged within 10 days. Two emigrating shoal bass could not be located outside of the tagging area, but they did return, one in early May, and one in July. All of the non-emigrating fish and all returning fish generally remained in close proximity to their tagging areas throughout the duration of the study.

Mean annual daily movement rates of all three species ranged from 76 to 119 m/day (Table 3). Mean daily movement rates did not differ among species ($F = 2.77$; df = 2, 25; $P = 0.082$) or season ($F \leq 1.36$; df $\geq 3, 12$; $P \geq 0.21$; Figure 4). Mean annual diel movement rates of all three species ranged from 178 to 430 m/h (Table 3), and they did not differ among species ($F = 0.31$; df = 2, 24; $P = 0.7329$) or season ($F \leq 4.58$; df $\geq 2, 3$; $P \geq 0.06$; Figure 4). Diel movement rates were greater during daylight hours than at night for largemouth bass ($F = 6.44$; df = 1, 9; $P = 0.03$) but were similar between periods for shoal bass or spotted bass ($F \leq 3.20$; df $\geq 1, 6$; $P \geq 0.10$; Figure 5). The best model for predicting largemouth bass diel movement rates based on AIC selection criteria included temperature, discharge, and time of day and it was better by 1.2 AIC units than the second best model (Table 4):

$$\log_e(\text{MDPH}) = 1.07(\log_e(\text{temperature})) + 0.841(\log_e(\text{discharge})) + 3.64 * 10^{-6}(\text{time}) - 1.66$$

The best model for predicting shoal bass diel movement rates based on AIC selection criteria included only temperature and it was better by 2.2 AIC units than the second best model (Table 4):

$$\log_e(\text{MDPH}) = 0.509(\log_e(\text{temperature})) + 0.955$$

The best model for predicting spotted bass diel movement rates based on AIC selection criteria included both temperature and discharge and it was better by 1 AIC unit than the second best model (Table 4):

$$\log_e(\text{MDPH}) = 1.59(\log_e(\text{temperature})) + 0.771(\log_e(\text{discharge}) - 1.89$$

Habitat Use - No difference in mean depth use was detected among species during any season ($F \leq 2.37$; df $\geq 1, 8$; $P \geq 0.23$; Figure 6). Mean depth use of shoal bass was greater during winter than summer ($F = 13.96$; df = 2, 3; $P = 0.03$); mean depth use was similar among seasons within species for all other species-season combinations ($F \leq 2.95$; df $\geq 3, 5$; $P \geq 0.12$). Mean depth use within species was similar among diel periods for all species ($F \leq 1.68$; df $\geq 3, 15$; $P \geq 0.17$; Table 5). Mean flow use of shoal bass was greater than that of both largemouth bass and spotted bass during winter ($F = 11.01$; df = 2, 22; $P = 0.0005$; Figure 6). Mean flow use did not differ among species during the summer ($F = 2.35$; df = 2, 9; $P = 0.15$) or fall ($F = 0.91$; df = 2, 3; $P = 0.49$; Figure 6). No flow measurements were recorded during the spring due to equipment failure. Mean flow use did not differ among diel periods for any species ($F \leq 3.29$; df $\geq 3, 9$; $P \geq 0.052$; Table 5).

Analysis of the sonar image maps for the 22-km section of the upper Flint River revealed that sand was the most available substrate type, while mixed rocky was the least available substrate type (Table 6). Sand was the most frequently used substrate type by all three species. Largemouth bass generally selected against rocky habitats and selected for sandy substrates; whereas, shoal bass occasionally selected for bedrock and rocky boulder substrates, they selected against finer substrates such as mixed rocky, rocky fine, and sand (Figure 7). In contrast, spotted bass only displayed strong selection in winter, when they selected for sand and against mixed rocky and rocky boulder substrates; substrate selections were essentially nonexistent for spotted bass in spring or summer (Figure 7). Substrate selection was strongest in winter for largemouth bass and spotted bass and in spring for shoal bass; selection was least evident in the summer for all three species. Largemouth bass selected for pools and against shoals in three seasons, and runs were selected against in winter and summer (Figure 8). Shoal bass selected against pools in winter and spring, and showed no selection among mesohabitats in the summer; whereas, spotted bass selected against shoal habitat in all three seasons (Figure 8).

A total of 3,117 pieces of large woody debris were identified using the sonar image maps. Fish were located in close proximity (< 2m) to large woody debris in nearly 92% of all largemouth bass locations, 70% of all spotted bass locations, and 31% of all shoal bass locations. The mean distance of shoal bass from large woody debris was greater than that of both largemouth and spotted bass ($F = 9.36$; $df = 2, 27$; $P = 0.0008$; Figure 9). Largemouth bass had higher large woody debris counts within a 15-m radius than both shoal bass and spotted bass ($F = 16.33$; $df = 2, 27$; $P < 0.0001$; Figure 9). Shoal bass were found at greater distances from the bank than largemouth bass ($F = 5.28$; $df = 2, 27$; $P = 0.0116$; Figure 9), and spotted bass were intermediate and similar to both species. Shoal bass were found in more complex habitats with a greater mean number of substrate types found within a 15-m radius of fish locations than both largemouth bass and spotted bass ($F = 21.52$; $df = 2, 27$; $P < 0.0001$; Figure 9). Mean distances to the bank, mean distance to large woody debris, mean woody debris counts, and habitat complexity did not vary among diel periods ($F \leq 1.67$; $df = 3, 72$; $P \geq 0.18$).

Age-0 Study

In 2008, 141 basses were collected from the piedmont region and 142 basses were collected from the coastal plain region; total length ranged from 23 to 86 mm across all species and regions (Figure 10). Mean total length of shoal bass was greater than both largemouth bass and spotted bass in the piedmont ($F = 22.46$; $df = 2, 109$; $P < 0.0001$); whereas, mean total length of spotted bass was greater than that of largemouth bass in the coastal plain, and shoal bass were intermediate and similar to both species ($F = 6.53$; $df = 2, 135$; $P = 0.002$). In 2009, 154 basses were collected from the piedmont region and 164 basses were collected from the coastal plain region; total lengths ranged from 23 to 92 mm across all species and regions (Figure 11). Mean total length did not differ among species in the piedmont ($F = 1.7$; $df = 2, 149$; $P = 0.19$); whereas mean total length of largemouth bass was less than that of spotted bass in the coastal plain and mean total length of shoal bass was intermediate and similar to both species ($F = 9.26$; $df = 2, 160$; $P = 0.0002$).

Bass hatch dates ranged from April 1 to May 30 in 2008 (Figure 12). In the piedmont, largemouth bass first hatched on April 1, 18 days before spotted bass and 31 days before shoal bass (Table 7). Mean hatch dates of shoal bass were later than those of both largemouth bass and spotted bass in the piedmont ($F = 22.83$; $df = 2, 122$; $P < 0.0001$; Table 7). In the coastal plain, both largemouth bass and shoal bass first hatched on April 16, 15 days before spotted bass first hatched (Table 7). Mean hatch dates of largemouth bass were later than those of shoal bass (F = 3.10; df = 2, 138; P = 0.0482; Table 7), while mean hatch dates of spotted bass were intermediate and similar to both species. In 2009, bass hatch dates ranged from April 3 to June 16; however, most fish hatched from April 16 to June 16 (Figure 13). In the piedmont, both largemouth bass and shoal bass first hatched on April 16, 15 days before spotted bass, however, mean hatch dates did not differ among species (F = 0.09; df = 2, 149; P = 0.92; Table 7). In the coastal plain, largemouth bass first hatched on April 23, three days before spotted bass and six days before the majority of shoal bass began hatching, though a single shoal bass did hatch on April 3 (Table 7). Mean hatch dates of spotted bass and largemouth bass were similar and earlier than those of shoal bass (F = 6.59; df = 2, 160; P = 0.0018; Table 7).

In 2008, mean TL of shoal bass and spotted bass in the coastal plain were negatively correlated to hatch date; hatch date was not correlated to mean TL for any other species-area combination (Figure 14). In 2009, mean TL of largemouth bass in the piedmont and shoal bass in the coastal plain were negatively correlated to hatch date; however, the shoal bass relation was clearly driven by a single outlier, and removal of that one point eliminated the relation (R = 0.05; P = 0.11; Figure 15). No correlations between hatch date and TL were observed for any other species-area combination (Figure 15).

Mean growth rates of bass ranged from 0.82 to 1.07 mm/d across years and areas during the study (Table 7). In 2008, the mean growth rate of spotted bass was greater than that of largemouth bass in the piedmont, and the mean growth rate of shoal bass was greater than that of both species (F = 40.44; df = 2, 122; P < 0.0001; Table 7). In the coastal plain, mean growth rates of both largemouth bass and shoal bass were similar, however, both were lower than the mean growth rate of spotted bass (F = 10.76; df = 2, 138; P < 0.0001; Table 7). In 2009, the mean growth rate of shoal bass was greater than that of largemouth bass in the piedmont, and the mean growth rate of spotted bass was intermediate and similar to both species (F = 7.39; df = 2, 149; P = 0.0009). In the coastal plain, mean growth rates of shoal bass and spotted bass were similar and both were greater than the mean growth rate of largemouth bass (F = 11.99; df = 2, 160; P < 0.0001; Table 7).

In 2008, growth rates of largemouth bass from the piedmont and spotted bass from the coastal plain were positively correlated with hatch date (Figure 16); however, the relation for spotted bass was weak and driven by one outlier. No other relations between growth rate and hatch date were evident for any other species and area combination (Figure 16). However, in 2009 growth rates of shoal bass and spotted bass collected from the piedmont as well as those of all species collected from the coastal plain were positively correlated with hatch dates (Figure 17).

Flow regimes in the Flint River during the spawning period of both years were characterized by a series of high discharge events that occurred until early April, followed by a period of relatively stable discharge levels. Maximum discharge during the 2008 spawning season was 2,280 cfs in the piedmont and 3,230 cfs in the coastal plain (Figure 18). However, discharge was much greater during 2009, with discharge levels reaching 7,620 cfs in the piedmont and 32,200 cfs in the coastal plain (Figure 19). Except for largemouth bass in the piedmont during 2008 and shoal bass in the coastal plain during 2009, fish collected in mid-summer generally began hatching after high discharge events had passed (Figures 18 and 19).

Water temperatures were only collected in 2009, but in the piedmont, largemouth bass and shoal bass began hatching when water temperatures reached 16º C and spotted bass began hatching when water temperatures reached 20º C (Figure 20; Table 8). However, most species hatched at temperatures ranging from 20 to 25º C. Likewise, while largemouth bass began hatching at 18º C, shoal bass at 16º C, and spotted bass at 21º C in the coastal plain, the majority of the fish of all three species hatched at temperatures ranging between 21 and 25º C (Figure 20; Table 8).

Discussion

Movements and Habitat Use -Seasonal differences in movement rates have been observed for several species of stream dwelling black bass including shoal bass (Stormer and Maceina 2009), spotted bass (Horton and Guy 2002), and smallmouth bass (Montgomery et al. 1980; Todd and Rabeni 1989; Langhurst and Schoenike 1990). Though mean daily movement rates did not vary among species or season in this study, the highest observed mean daily movement rates occurred during the spring for all species. Individuals of all three species of bass moved large distances (> 5 km) during the spring, presumably to spawning areas. Spawning-related migrations have been reported for stream-dwelling basses in other studies. Montgomery et al. (1980) observed smallmouth bass moving up into sloughs off Columbia River, Washington, during mid-March where they remained until after spawning was completed in July or August. Todd and Rabeni (1989) reported that smallmouth bass emigrated out of their home pool just before spawning, and that 75% returned after spawning was completed. In this study, the bass that emigrated from the study area did so in early spring, at the beginning of what is considered the spawning season for black bass in the southeastern United States. All eight shoal bass and two of the spotted bass that were found outside of the study area during spring were located inside or in very close proximity to major shoal complexes. The three largemouth bass that emigrated outside of the study area were found at the base of another major shoal complex. Spawning aggregations of shoal bass have been observed in shoal habitats during spring in the lower Flint River below Albany (Travis Ingram, Georgia Department of Natural Resources, personal communication). Large shoal complexes may serve as important spawning and nursery areas for black bass in the upper Flint River. If all three species do use these shoal complexes as nursery areas, there is potential for competition among species at early life stages.

The largest observed displacement in this study was a shoal bass that was located approximately 20 km downstream from the study area during an aerial tracking survey. Within 10 days, that same fish had moved back up into the study area, very close to the area it had inhabited before moving downstream. This fish had not been located on tracking trips conducted through the same area as recently as two weeks earlier, indicating that the fish may have been further downstream. Large-scale movements have been observed for smallmouth bass in other river systems: up to 61 km in the Columbia river (Montgomery et al. 1980) and up to 109 km between the Embarrass and Wolf rivers (Langhurst and Schoenike 1990). Stormer and Maceina (2009) found that shoal bass were relatively sedentary in a small, isolated section of Little Uchee Creek in Alabama, but my data suggests that they are capable of making large-scale movements when in a free-flowing river system. The Flint River experienced a dry year during 2008 and thus, my observed movements may have been lower than normal. Low water conditions during drought years often reduce habitat connectivity and restrict fish movements (Lake 2003; Schrank and Rahel 2006). In a related study, tagged shoal bass were commonly recaptured by anglers 60-100 km away from where the fish were tagged (S. Sammons, Auburn University, unpublished data). Most of these movements were observed during the spring of 2009, which was characterized by frequent high-discharge events. In contrast, shoal bass recaptured by anglers in 2008, a much drier year, did not evidence this magnitude of movement. In my study, four of the emigrating shoal bass returned to the study area in late spring or early summer. Each fish moved back into areas approximately where they were located before emigrating; one of these fish actually moved back to the same exact rocky outcrop that it inhabited before leaving and it remained there for the duration of the study. Similar homing behavior has been observed for smallmouth bass in other studies (Langhurst and Schoenike 1990; VanArnum et al. 2004). Low flows in the Flint River during 2008 may have restricted shoal bass movements during summer and reduced the likelihood of additional fish exhibiting homing behavior during my study. A long-term telemetry study on a greater number of shoal bass may provide greater insight to the seasonal movement patterns and homing behavior of shoal bass in the Flint River.

Miller (1975) suggested that when found sympatrically, spotted bass showed habitat preferences between those of largemouth bass and smallmouth bass, where largemouth bass inhabit deep pools and quiet backwaters, smallmouth bass inhabit fast-moving waters, and spotted bass are found in intermediate areas in shallow pools near fast-moving water. I found a similar case of habitat partitioning in the Flint River, with shoal bass taking the place of smallmouth bass. In my study, shoal bass were commonly found in areas with greater than average current velocity, selecting for shoal and run mesohabitats and against pool mesohabitats, similar to what Wheeler and Allen (2003) observed. Stormer (2007) observed shoal bass using habitats with lower than average current velocity, but that study was conducted in a smaller stream under extreme drought conditions, when the only measurable current velocity occurred in areas too shallow to be inhabited by shoal bass. In this study, mean flow use of shoal bass was greater than that of largemouth bass and spotted bass only during the winter, but the trend was evident in other seasons as well. Prevailing drought conditions resulted in abnormally low discharge levels (up to 87% below mean monthly discharge at the USGS gauge 02347500) in the Flint River during the summer and fall of 2008. Low discharge levels may have reduced the heterogeneity of velocity levels throughout our study area, making it more difficult to detect differences in flow use among species during these seasons. Johnston and Kennon (2007) found that shoal bass in Little Uchee Creek, AL, used lower water velocities in summer during a dry year than they did during a wet year. If our study had been conducted during a wet year, we may have observed more pronounced differences in flow use among species during summer and fall.

Shoal bass were often found in shoals with coarse, rocky substrates such as bedrock and boulders, consistent with shoal bass behavior in other studies (Wheeler and Allen 2003; Johnston and Kennon 2007; Stormer and Maceina 2009). However, shoal bass were found in all mesohabitat types throughout the study, as in Wheeler and Allen (2003), but they appeared to select against pools and their associated sandy substrate throughout most of the year, despite the fact that they were the most abundant mesohabitat type and substrate type within our study area. In this study, although shoal bass were observed to select for shoal mesohabitats only in spring, both largemouth bass and spotted bass selected against shoal mesohabitats in all seasons. Shoal mesohabitats in the Flint River are highly complex habitats composed of a mix of bedrock and boulders interspersed with finer rocky substrates and sand. The relatively high use of shoal mesohabitats by shoal bass was reflected in the fact that shoal bass locations had a higher number of substrate types within a 15 m buffer than both largemouth bass and spotted bass. In the fall, when the lowest discharge levels of the year were observed, shoal bass were frequently observed in pools. Shoal bass in Little Uchee Creek, AL, were also observed moving to deep water refugia during times of low discharge (Johnston and Kennon 2007; Stormer and Maceina 2009).

Largemouth bass exhibited very different habitat preferences from shoal bass; they were found almost exclusively in pools with sandy substrates and little to no current velocity, similar to the behavior of riverine largemouth bass in other systems (Miller 1975; Wheeler and Allen 2003). Horton and Guy (2002) reported that spotted bass used pools far more often than runs and riffles and suggested that spotted bass preferred low velocity environments. Our observations of spotted bass habitat use were somewhat mixed; spotted bass selected against shoal mesohabitats, used pools about in proportion to their availability, and showed some selection for runs.

Large woody debris is an important component of many stream ecosystems, that can increase aquatic invertebrate production (Angermeir and Karr 1984; Benke et al. 1985), offer fish refuge from strong current velocities (Crook and Robertson 1999), provide fish with cover to hide from predators and ambush prey (Angermeir and Karr 1984; Crook and Robertson 1999), and can play a large role stream channel formation (Abbe and Montgomery 1996). Many studies have documented the importance of large woody debris to black bass in lotic environments (Todd and Rabeni 1989; Tillma et al. 1998; Horton and Guy 2002), although the relative importance of woody debris habitat does not appear to be consistent across species. Wheeler and Allen (2003) found that largemouth bass in the Chipola River, Florida, were associated with areas of higher than average woody debris index scores, whereas shoal bass presence was not related to woody debris index scores. Scott and Angermeier (1998) found that spotted bass in the New River, Virginia, occupied areas that featured woody cover, overhanging bank vegetation, and undercut banks, while smallmouth bass occupied rocky areas that lacked woody cover. In this study, I found that all three species of black bass used large woody debris as cover, though it appeared to be more important to largemouth bass and spotted bass than to shoal bass. My data suggests that largemouth bass used dense clusters of large woody debris located close to the stream bank, while spotted bass tended to use the outside edges of woody debris, closer to open water. Shoal bass were generally located further out in the stream channel than the other two species, where velocity was greater than along the stream banks. Woody debris was less abundant in the middle of the channel and shoal bass tended to rely on boulders and bedrock outcroppings for cover, though they still used woody debris as cover in approximately one third of all locations. In locations where rocky cover is scarce, woody debris becomes a very important cover type for shoal bass. Radio-tagged shoal bass from another study in the coastal plain area of the Flint River were nearly always found along the bank in the fastest flowing sections of the river channel using large woody debris as cover (personal observation). Proximity to flow appears to drive shoal bass habitat selection, regardless of cover type or distance to the bank.

Age-0 Hatch Dates and Growth Rates - Estimates of hatch dates and daily growth rates are dependent on the assumption that growth rings on age-0 fish otoliths are formed as daily increments. The formation of daily growth rings has been validated for several black bass species including largemouth bass (Miller and Stork 1982), smallmouth bass (Graham and Orth 1987), and spotted bass (DiCenzo and Bettoli 1995). Although daily growth rings have not been verified for age-0 shoal bass or Alabama bass, we assumed that increments were formed at daily intervals as in other black bass species (Long et al. 2004). Mean daily growth rates of shoal bass in this study were similar to growth rates of shoal bass observed in hatchery ponds (Smitherman and Ramsey 1972; Long et al. 2004; Table 9). Mean daily growth rates of largemouth bass and spotted bass in this study were much higher than those observed for largemouth bass, spotted bass, and Alabama bass in reservoirs (Sammons et al. 1996; Greene and Maceina 2000; Table 9).

The timing and periodicity of hatching relative to the timing of other biotic events and abiotic conditions may play a large role in regulating the survival and recruitment of age-0 fishes. In this study, I attempted to determine if the relative hatch timing of spotted bass would provide them with a competitive advantage over shoal bass or largemouth bass during their first year of life. Early-hatched fish are exposed to a longer growing season than late-hatched fish, and therefore they may reach larger sizes and experience greater survival during their first year of life (Cargnelli and Gross 1996; Ludsin and DeVries 1997). Bass that hatch before other fish prey species are often able to undergo an early switch to piscivory, which allows for greater growth and survival (Olsen 1996; Ludsin and DeVries 1997). Body size has been shown to play a large role in determining age-0 survival and recruitment for many fish species (Miller et al. 1988; Houde 1994; Cargnelli and Gross 1996). Large body size may allow for greater foraging success and increased predator avoidance capabilities among larval and juvenile fishes (Miller et al. 1988; Post and Evans 1989; Lundvall et al. 1999). Total length was negatively related to hatch date in approximately 25% of species-section-year combinations in this study, lending support to the theory that earlier-hatched individuals attain larger sizes than late-hatched individuals. Whether this ultimately resulted in larger recruits by the end of their first year is unknown, as all fish were collected in this study during early summer. In contrast, growth rates were positively related to hatch dates in approximately 58% of all species-section-year combinations, indicating that later-hatched individuals were able to compensate for the shorter growing season with faster growth rates, a pattern consistent with that observed in other studies (Ludsin and DeVries 1997; Pine et al. 2000; Pine and Allen 2001; Sammons et al. 2001). The cause of these increased growth rates is unknown, though it is probably linked to increased water temperature and prey availability later in the spawning season (Ludsin and DeVries 1997; Phelps et al 2008).

The three black bass species in the Flint River exhibited differences among species in mean hatch dates, mean total lengths, and mean growth rates; however, these differences were generally not consistent across sections or years. The magnitude of peaks in early spring discharge varied widely among sites and years, which may account for some of these inconsistencies in differences among species across samples. Long-term datasets would likely be helpful in detecting patterns in hatching distributions among species across varying discharge levels. Mean hatch dates of spotted bass differed from those of shoal bass or largemouth bass in only two cases during this study, and there was no apparent advantage for spotted bass in either case. I found only one instance where differences in mean hatch dates coincided with differences in mean total length or mean growth rates among species, which was in the piedmont during 2008, when shoal bass hatched later than both largemouth bass and spotted bass. However, shoal bass exhibited faster mean growth rates than the other two species which resulted in greater mean total lengths. In this case, late hatching shoal bass appeared to have an advantage in both growth and size over the other two species.

Early hatching may have actually been disadvantageous for black bass in the Flint River, resulting in higher mortality due to harsh environmental conditions such as spring flooding events and variable water temperature. In the coastal plain during 2009, we collected one shoal bass that was estimated to have hatched on April 3, when discharge was approximately 30200 cfs. No other fish in our samples were estimated to have hatched until approximately two weeks later, when discharge fell to about 3000 cfs. It is likely that other fish within that fish's cohort and perhaps fish in other early cohorts of all three species suffered high mortality from the high discharge events that occurred during early spring 2009. Mion et al. (1998) found that larval walleye survival was strongly related to discharge levels, where walleye that hatched during high discharge events exhibited very low survival. Recruitment success of smallmouth bass in Virginia rivers was shown to be driven by discharge levels; years with very high or very low discharge levels during the spawning season produced poor year classes, whereas years with moderate discharge levels during the spawn produced strong year classes (Smith et al. 2005). Some largemouth bass in the piedmont hatched during flood pulse events in early spring during 2008. However, the magnitudes of these pulse events were the least severe of all that occurred during hatching of black bass in both years, peaking around 2280 cfs, therefore conditions may have been less severe for newly hatched fish. It is also possible that the early-hatching largemouth bass in the Flint River were spawned in one of several backwater areas that become available to fish in the piedmont as water levels rise, thus avoiding the detrimental effects of high discharge. Backwaters provide important spawning and nursery areas for largemouth bass in many fluvial systems (Nack et al. 1993; Slipke et al. 2005). It is also possible that these largemouth bass hatched in ponds within the watershed and that they were washed into the river during high discharge events.

Water temperatures declined rapidly just after the last major high discharge event in 2009, when water temperature dropped by approximately 3.5º C down to 12.5º C, and this could have caused high mortality of newly hatched fish during this time. Rutherford and Houde (1995) found that early-hatching cohorts of striped bass that were subjected to variable weather conditions and unstable water temperatures exhibited much higher mortality rates than later-hatched cohorts that experienced stable environmental conditions. Similarly, Pine and Allen (2001) found that early-hatching cohorts of black crappie *Pomoxis nigromaculatus* faced with unusually cool early spring temperatures suffered greater mortality rates than middle- and late-hatched cohorts.

Conclusions and Management Implications

In this study, I found little evidence to support the theory that spotted bass pose a competitive threat to the persistence of shoal bass in the upper Flint River. It appears that adult black bass in the Flint River may coexist through habitat partitioning, with spotted bass showing habitat preferences intermediate to those of shoal bass and largemouth bass. The Flint River is a relatively large river system in which habitat is probably not limiting for black bass. In a similar-sized river, the Ocmulgee River in Georgia, both shoal bass and spotted bass are introduced and they appear to coexist alongside native largemouth bass through resource partitioning (J. Evans, Georgia Department of Natural Resources, personal communication). However, a decline of native redeye bass *M. coosae* was associated with the introduction of shoal bass, possibly indicating some competitive interactions between those species. In smaller streams, habitat may be limiting, and the three species are probably more likely to interact and use similar habitats to each other, which may increase the potential of competition for resources among species. Competition may have played a large role in the decline of shoal bass populations in small tributaries of the Chattahoochee River in Alabama; however, in larger systems such as the Flint and Ocmulgee rivers, the potential of detrimental competitive impacts may be lessened.

Shoals appear to be a critical habitat type for shoal bass in Flint River and they may serve as an important spawning or nursery areas. Management efforts to protect shoal bass in the upper Flint River should be focused on conserving shoal habitat and preserving connectivity throughout this unimpounded river reach. Shoal bass appear to form spawning aggregations in shoals during the spring, further emphasizing the need to protect these habitats. A special regulations season with reduced harvest during the spring, when shoal bass form aggregations and become highly vulnerable to angling, may help to ensure successful recruitment and protect large spawning adults from overexploitation. Because both shoal bass and spotted bass were observed moving into shoal areas during the spawning season, future work should focus on determining the microhabitat scale spawning habitat requirements of both species. At early life stages, individuals of all three species were often collected in the same habitats, however, my research did not indicate that the relative timing of hatching provided spotted bass with any competitive advantage over either largemouth bass or shoal bass. Competition may not be a large threat to the recruitment of shoal bass in the Flint River, however, the fact that shoal bass and spotted bass appear to spawn in similar areas does increase the potential for introgressive hybridization between these species, which may pollute the shoal bass gene pool and threaten the persistence of native stocks of the species. Native stocks of Guadalupe bass *M. treculi* in Texas were threatened after the introduction of non-native smallmouth bass into several streams within the Guadalupe bass's range. Researchers identified introgressive hybridization between the two species as the primary threat to the continued persistence of Guadalupe bass (Whitmore 1983; Littrell et al. 2007). Similarly, native stocks of redeye bass in South Carolina are threatened by introgressive hybridization with non-native Alabama bass (Barwick et al. 2006). Introduced spotted bass may pose a similar threat to shoal bass as they have been found to hybridize with several of the black bass species including shoal bass and largemouth bass in tributaries of the Chattahoochee River (Maceina et al. 2007). Further sampling should be conducted in the upper Flint River to determine if all of the invading fish are actually spotted bass, Alabama bass, or intergrades, and to determine if any introgression with shoal bass is occurring.

In this study, I observed individuals of all three species making large movements during the spring. These findings, coupled with observations from an exploitation study and another telemetry study in the coastal plain (S. Sammons, Auburn University, unpublished data), highlight the importance of connectivity throughout the Flint River for shoal bass, as they appear to constitute one continuous metapopulation in this system. Measures should be taken to prevent any new impoundments from being constructed on the Flint River, as they would break up this metapopulation, reducing gene flow and likely restricting many fish from accessing prime spawning, nursery, or other critical habitats. Impoundments would also cause a drastic change in the river, from a natural flowing system to a large, lentic waterbody directly above the dam with an irregularly pulsed, likely cooler-temperature, tailwater below. Evidence of the effects of impoundments on shoal bass has been seen in the Chattahoochee River system, where spotted bass thrive in the reservoir habitat, and shoal bass persist in fragmented, relict populations below the dams (Sammons and Maceina 2009).

In recent years, water allocation has become a major topic of debate in the southeastern United States. Dams have been proposed on the Flint River, and while they are unlikely to ever be built, changes in water use throughout the Flint River watershed will likely still have some large impacts on shoal bass. During dry years in the Flint

River, water levels drop, water clarity increases, flow velocity is reduced, and lotic habitat is lost as the system becomes more lentic in nature. These conditions may favor the highly adaptable spotted bass over shoal bass. Shoal bass also become highly vulnerable to angling under these conditions and harvest can be quite high (S. Sammons, Auburn University, unpublished data). Increased water withdrawls from the Flint River watershed due to the ever-expanding human population in the Atlanta metro-area would likely cause drought-like conditions in the river even during years of normal rainfall. During dry years, these impacts may have severe impacts on the flora and fauna of the Flint River. Careful thought and planning by government officials should be directed towards developing a water allocation plan that uses conservation measures to meet the needs of the growing human population in this area, while retaining as much of the normal flow regime in the Flint River as possible

Spotted bass have become firmly established in the Flint River, and it is unlikely that they will ever be removed from the system. It does not appear as though spotted bass will displace shoal bass from the river in the near future, though it is likely still too early to detect the full impacts of their invasion. Close monitoring should be conducted in the coming years to see if trends in the spotted bass population correlate with changes in any other fish populations in the Flint River. Fisheries managers must attempt to educate anglers about the potential dangers of moving species into new drainages, in order to reduce the likelihood of future invasions. Despite the lack of direct interactions observed in this study between the introduced spotted bass and the native black bass species, the potential threat of introgressive hybridization between spotted bass and shoal bass remains high, and should be monitored in the future.

Chapter Two: The Role of Life History Plasticity in the Successful Invasion of Spotted Bass in the Flint River, Georgia

Introduction

Human-induced biological invasions are widespread and can have large impacts on ecosystem structure and function in the systems in which they occur (Kolar and Lodge 2001). In recent years, a large body of work has been conducted on invasions, however, the mechanisms underlying successful invasions are often poorly understood (Moyle and Light 1996; Kolar and Lodge 2001). Most successful invaders exhibit broad ecological niche requirements and are able to exploit vacant niches in their new environments (Olden et al 2006). Many invasive species also exhibit high phenotypic plasticity, which allows them to quickly adapt and persist under variable environmental conditions (Sultan 2000; Claridge and Franklin 2002). Life history traits such as growth, size at maturity, age at maturity, and fecundity can be highly plastic which may contribute to the invasiveness of a species (Sakai et al. 2001). Several studies have shown how life history plasticity may aid in the persistence of a species under changing environmental conditions (Reznick et al. 1990; Hutchings 1996; Casten and Johnston 2008).

Winemiller and Rose (1992) identified three life history strategies that are commonly used by fishes: 1) the opportunistic strategy, characterized by short generation length, low age-specific fecundity, and low age-specific survival; 2) the periodic strategy, characterized by long generation length, high age-specific fecundity, and low age-specific survival; 3) the equilibrium strategy, characterized by long generation length, low age-specific fecundity, and high age-specific survival. Olden et al (2006) found that the most successful invasive fish species in the Colorado River Basin exhibited characteristics of both opportunistic and equilibrium strategists. The authors hypothesized that these invasive species used equilibrium strategies during stable periods, yet they were able to adopt opportunistic strategies when faced with variable environmental conditions.

Spotted bass introduced to the Flint River likely experienced a strong change in environmental conditions, and it is possible that life history plasticity aided in their establishment and rapid expansion throughout the river system. In this study, I investigated life history characteristics of spotted bass from the Flint River, Georgia, and Alabama bass from the Tallapoosa River, Alabama, to determine if invasive spotted bass may have altered their life history strategies in response to being placed into a new environment.

Methods

During spring 2009, spotted bass were collected from the Flint River, GA, and Alabama bass were collected from the Tallapoosa River near Daviston, AL, to compare life history strategies between native and introduced bass populations. Although individuals from a sample of invasive bass from the Flint River were identified as spotted bass, they were believed to be introduced from the Chattahoochee River, where spotted bass – Alabama bass intergrades have been reported (J. Evans, Georgia Department of Natural Resources, personal communication), thus comparisons between populations in the Tallapoosa and Flint rivers were considered appropriate. Approximately 20 fish were collected from each river every two weeks over a six-week period during the spawning season. All bass collected in these samples were placed in a 300 mg/L solution of MS-222 until expired, then placed on ice. Each fish was measured for total length (mm) and weighed (g). Sagittal otoliths were removed from each fish for age determination. Ages were determined by counting annuli on each otolith in whole view by two independent readers. If disagreement occurred between readers, a concert read was conducted to determine fish age. Gonads were removed from each fish and weighed (g). Whole testes and 20-40 mm sections of ovaries were placed in Bouin's Fixative for approximately 24 h. The following day, the gonads were removed from the Bouin's Fixative and placed in 70% ethanol. After another 24 h, the ethanol was removed from each gonad and replaced with fresh 70% ethanol. Small sections were taken from each gonad and placed into plastic cassettes, which were filled with paraffin wax and allowed to dry. Thin sections were taken from gonads imbedded in paraffin wax using a microtome, and gonad sections were placed on glass microscope slides and stained. Sections were then viewed under a microscope to determine maturity stage. Average age at maturity and average size at maturity (TL, mm) were estimated for each sex and compared among rivers using logistic regression (SAS Institute 2002).

Results

Bass collected from the Flint and Tallapoosa rivers during spring 2009 ranged from 102 – 387 mm (Figure 21). Male spotted bass began maturing at age 1 and 168 mm in the Flint River and at age 2 and 173 mm in the Tallapoosa River (Table 10). Female spotted bass began maturing at age 2 and 186 mm in the Flint River and at age 2 and 200 mm in the Tallapoosa River (Table 10). Predicted age and size at 50% maturity did not differ between populations in the Flint and Tallapoosa Rivers for either males (age: $\chi^2 = 0.013$; df = 1; P= 0.91; size: $\chi^2 = 0.16$; df = 1; P = 0.69; Table 1) or females (age: $\chi^2 = 1.60$; df = 1; P = 0.21; size: $\chi^2 = 1.61$; df = 1; P = 0.21; Table 1). Predicted age and size at 50% maturity were 1.0 year and 155 mm for males and 2.0 years and 189 mm for females in the Flint River and 1.9 years and 169 mm for males and 2.3 years and 200 mm for females in the Tallapoosa River (Figures 22 and 23).

Discussion

Size and age at maturity were similar between rivers for both males and females, suggesting that spotted bass probably did not undergo a shift in life history traits after being introduced to the Flint River. While it is possible that life-history plasticity may have played a role in the rapid establishment of spotted bass in the Flint River, there are likely a number of interdependent factors that led to the invasive success of the species. Previous research has shown that it is often difficult to predict successful invasions of stream fishes based on life history characteristics alone (Rosecchi et al. 2001; Villa-Gispert et al. 2005). Olden et al. (2006) found that the invasion success of fishes in the Colorado River Basin could be predicted through models that incorporated both life history strategies as well as environmental niche requirements. Spotted bass are considered to be a generalist species with broad habitat requirements and it is likely that they were able to exploit a vacant ecological niche in the Flint River. Villa-Gispert et al. (2005) suggested that the timing of introduction, relative to flood events and other environmental conditions can play a large role in determining invasion success of stream fishes. Spotted bass were introduced into the Flint River around 2005, just prior to the onset of a major drought, where annual discharge levels at the USGS gauge 02347500 were $\leq$ 50% of the mean annual discharge levels during 2006 to 2008. The abnormally low water levels in the Flint River during the first few years of spotted bass invasion may have contributed to their successful establishment, as droughts and other disturbances may favor the establishment of invasive species (Chown et al. 2007). Flow velocities and lotic habitat were likely greatly reduced during the drought; these conditions may have given the highly adaptable spotted bass an advantage over the fluvial-specialist shoal bass during this time period, allowing spotted bass to become established.

The limited scope of this study, with only one sample of each population type within a single year, may have reduced my ability to detect differences between the two populations. The exact timing of spotted bass introduction into the Flint River is unknown, though the oldest fish collected from the Flint River was six years old. It is possible that my sampling missed the window where a shift in life history occurred, and that spotted bass have become naturalized, behaving as they would in their native range. I chose the Tallapoosa River between Harris Dam and Lake Martin as the reference site in this study as it was located in the piedmont ecoregion, and it had a similar size and a similar geomorphology to the piedmont section of the upper Flint River, and it supported a native population of Alabama bass. This section of the Tallapoosa River, however, is a regulated section; whereas the upper Flint River is a free flowing system. It is possible that Alabama bass may have responded to the stressors of living in a system where discharge levels are highly variable by undergoing a shift in life history traits, thus the population may have not represented a true, unaltered native population. However, I collected Alabama bass from the two riverine access points that were located farthest downstream from Harris Dam to minimize the impacts of flow regulation. Unfortunately most rivers similar in size to the Flint River that support native populations of Alabama bass are heavily impacted by impoundment and regulated water flows.

Tables

Table 1. Classification scheme and associated definitions developed for the Upper Flint River substrate map.

Substrate Class	Acronym	Definition
Sand	S	≥ 75% of area composed of particles < 2 mm diameter (sand, silt, clay or fine organic detritus)
Rocky fine	Rf	> 25% of area composed of rocks > 2 mm but < 500 mm diameter across the longest axis
Rocky boulder	Rb	An area that includes ≥ 3 boulders, each ≥ 500 mm diameter across longest axis, each boulder within 1.5 meters of the next adjacent boulder. Any area meeting these criteria, regardless of underlying substrate, is classified Rb.
Bedrock	Br	≥ 75% of area composed of bedrock or an outcropping with relatively smooth texture (not fractured into blocks ≥ 500mm diameter)
Mixed rocky	Mx	An area comprising 2 or more substrates classes (at least 1 being rocky) arranged such that no homogeneous portion is ≥ 10 m^2
No data	No	An area of the sonar map beyond sonar range but within the boundaries of the river channel

Table 2. Species, total length, weight, number of days at large, number of locations, and fate of fish tracked in the upper Flint River during 2008.

Tag #	Species	TL (mm)	Weight (g)	Days at Large	# Locations	Fate
252	LMB	380	660	273	36	Tag Expired
262	LMB	337	461	146	13	Harvested by Angler
262B	SHB	354	470	102	15	Tag Expired
272	SHB	258	212	273	17	Tag Expired
282	SPB	323	447	273	31	Tag Expired
292	SHB	294	300	273	17	Harvested by Angler
303	SHB	345	471	168	18	Died
312	SPB	261	210	224	26	Died
322	SHB	279	252	25	1	Died
333	LMB	275	222	168	13	Consumed by Bird
342	LMB	324	367	253	35	Died
352	SHB	342	520	273	30	Tag Expired
361	SPB	281	202	302	41	Tag Expired
373	SHB	300	300	226	15	Harvested by Angler
381	LMB	247	180	168	22	Died
392	SPB	286	240	272	17	Tag Expired
402	SPB	260	207	271	36	Tag Expired
423	SPB	290	254	272	17	Tag Expired
434	SHB	508	2040	156	4	Missing
444	LMB	394	850	370	46	Study Ended
454	SHB	467	1483	155	15	Died
464	SHB	493	1562	25	1	Died
493	LMB	478	1389	370	45	Study Ended
503	SHB	492	1409	145	10	Died
514	LMB	426	937	369	45	Study Ended
523	SHB	409	863	301	18	Missing
553	LMB	392	770	167	16	Missing
563	SHB	392	875	126	13	Harvested by Angler
563B	SHB	415	851	169	19	Study Ended
572	LMB	462	1594	225	27	Died
584	SHB	499	1872	224	18	Died

Table 3. Annual mean movement rates, depth use, and flow use of radio-tagged black bass in the Flint River, Georgia during 2008.

	Largemouth Bass		Shoal Bass		Spotted Bass	
	Mean (n)	SE	Mean (n)	SE	Mean (n)	SE
Diel Movement (m/hr)	119 (10)	43.6	97 (11)	30.8	76 (6)	17.6
Daily Movement (m/d)	288 (10)	74	430 (11)	210	178 (6)	83.7
Depth (m)	1.6 (10)	0.08	1.6 (11)	0.02	1.7 (6)	0.069
Flow (m/s)	0.03 (10)	0.009	0.15 (11)	0.03	0.06 (6)	0.012

Table 4. Akaike's Infromation Criteria (AIC) model selection for predicting the effects of environmental variables on $\log_e$MDPH of largemouth bass, shoal bass, and spotted bass. The smallest AIC value represents the best fitting model.

Model	AIC value
Largemouth Bass	
$\log_e$(temperature) Time $\log_e$(discharge)	280.1
$\log_e$(temperature) $\log_e$(discharge)	281.3
Time $\log_e$(discharge)	286.4
$\log_e$(discharge)	289
Time	289.2
$\log_e$(temperature) Time	293
$\log_e$(temperature)	296.5
Shoal Bass	
$\log_e$(temperature)	147
$\log_e$(temperature) $\log_e$(discharge)	149.2
Time $\log_e$(discharge)	149.2
$\log_e$(discharge)	150.6
Time	150.6
$\log_e$(temperature) Time $\log_e$(discharge)	286.4
$\log_e$(temperature) Time	286.4
Spotted Bass	
$\log_e$(temperature) $\log_e$(discharge)	125.2
$\log_e$(temperature) Time $\log_e$(discharge)	126.2
$\log_e$(temperature)	132.7
$\log_e$(temperature) Time	132.9
Time	136.5
$\log_e$(discharge)	138.2
Time $\log_e$(discharge)	138.5

Table 5. Mean depth and flow use of black bass among diel tracking periods in the Flint River, Georgia during 2008. The numbers in parentheses (n) represent the number of fish used in each analysis.

	Largemouth Bass		Shoal Bass		Spotted Bass	
	Mean (n)	SE	Mean (n)	SE	Mean (n)	SE
			Dawn			
Depth (m)	1.47 (10)	0.086	1.47 (11)	0.18	1.55 (6)	0.14
Flow (m/s)	0.006 (5)	0.002	0.03 (4)	0.018	0.018 (3)	0.008
			Day			
Depth (m)	1.66 (10)	0.11	1.73 (11)	0.25	1.57 (6)	0.18
Flow (m/s)	0.041 (10)	0.018	0.12 (10)	0.03	0.07 (6)	0.017
			Dusk			
Depth (m)	1.71 (10)	0.14	1.42 (11)	0.16	1.83 (6)	0.195
Flow (m/s)	0.049 (10)	0.009	0.12 (11)	0.018	0.06 (6)	0.025
			Night			
Depth (m)	1.60 (10)	0.12	1.52 (11)	0.16	1.75 (6)	0.184
Flow (m/s)	0.014 (5)	0.003	0.012 (4)	0.006	0.022 (3)	0.011

Table 6. Available area (ha) of substrate types within the 22 km sonar mapping section of the upper Flint River.

Type	Availability (ha)
Substrate	
Sand	52
Rocky fine	18
Rocky boulder	23
Bedrock	1
Mixed rocky	10
No data	5
Mesohabitat	
Pool	81
Run	14
Shoal	38

Table 7. Initial hatch dates, mean hatch dates, and mean growth rates for age-0 black bass collected from the Flint River during 2008 and 2009. Superscripts a, b, and c represent differences among species within a particular year and section.

Species	Section	First Hatch Date	Mean Hatch Date	Hatch Duration (d)	Mean Growth Rate (mm/d)
		2008			
LMB	Piedmont	1-Apr	28-Apr	59	0.822[c]
SHB	Piedmont	2-May	14-May	21	1.07[a]
SPB	Piedmont	19-Apr	4-May	35	0.944[b]
LMB	Coastal Plain	25-Apr	6-May	21	0.874[b]
SHB	Coastal Plain	20-Apr	2-May	26	0.888[b]
SPB	Coastal Plain	20-Apr	4-May	38	0.994[a]
		2009			
LMB	Piedmont	16-Apr	12-May	60	0.953[b]
SHB	Piedmont	16-Apr	12-May	45	1.06[a]
SPB	Piedmont	1-May	12-May	23	0.999[ab]
LMB	Coastal Plain	23-Apr	10-May	37	0.875[b]
SHB	Coastal Plain	3-Apr*	13-May	56	0.965[a]
SPB	Coastal Plain	26-Apr	10-May	27	0.993[a]

* Only one shoal bass hatched on April 3, the rest of the shoal bass began hatching on April 29.

Table 8. First, mean, and final hatch dates and associated temperatures for age-0 black bass collected in the Flint River, Georgia during 2009. Temperatures are reported in degrees C.

Species	First Hatch	(Temp)	Mean Hatch	(Temp)	Final Hatch	(Temp)	75% Temp Range
			Piedmont				
LMB	16-Apr	(16)	12-May	(22.4)	16-Jun	(27.7)	20.1 - 25.4
SHB	16-Apr	(16)	12-May	(22.4)	31-May	(24.6)	20.2 - 23.1
SPB	1-May	(22.2)	12-May	(22.4)	24-May	(21.0)	20.5 - 23
			Coastal Plain				
LMB	23-Apr	(18.4)	10-May	(25)	29-May	(24.8)	21 - 25
SHB	3-Apr	(15.9)	13-May	(22.6)	29-May	(24.8)	21.2 - 24.9
SPB	26-Apr	(21.9)	10-May	(25)	24-May	(22)	22 - 25

Table 9. Mean daily growth rates of age-0 black bass from other studies.

Mean Growth Rate (mm/d)	Waterbody Type	Authors
	Shoal Bass	
0.85	Hatchery Pond	Long et al. 2004
0.95 - 1.14	Hatchery Pond	Smitherman and Ramsey 1972
	Largemouth Bass	
0.55 - 0.70	Reservoir	Greene and Maceina 2000
0.67 - 0.74	Reservoir	Sammons et al. 1999
	Alabama Bass	
0.58 - 0.71	Reservoir	Greene and Maceina 2000
	Spotted Bass	
0.61 - 0.75	Reservoir	Sammons et al. 1999

Table 10. Life history parameters of spotted bass collected from the Flint River, Georgia and Alabama bass collected from the Tallapoosa River, Alabama during spring 2009.

River	N	Age at First Maturity	Size at First Maturity (mm)	Age at 50% Maturity	Size at 50% Maturity (mm)
			Males		
Flint	35	1	168	1	155
Tallapoosa	49	2	173	1.87	169
			Females		
Flint	36	2	186	2	189
Tallapoosa	32	2	200	2.28	200

Figures

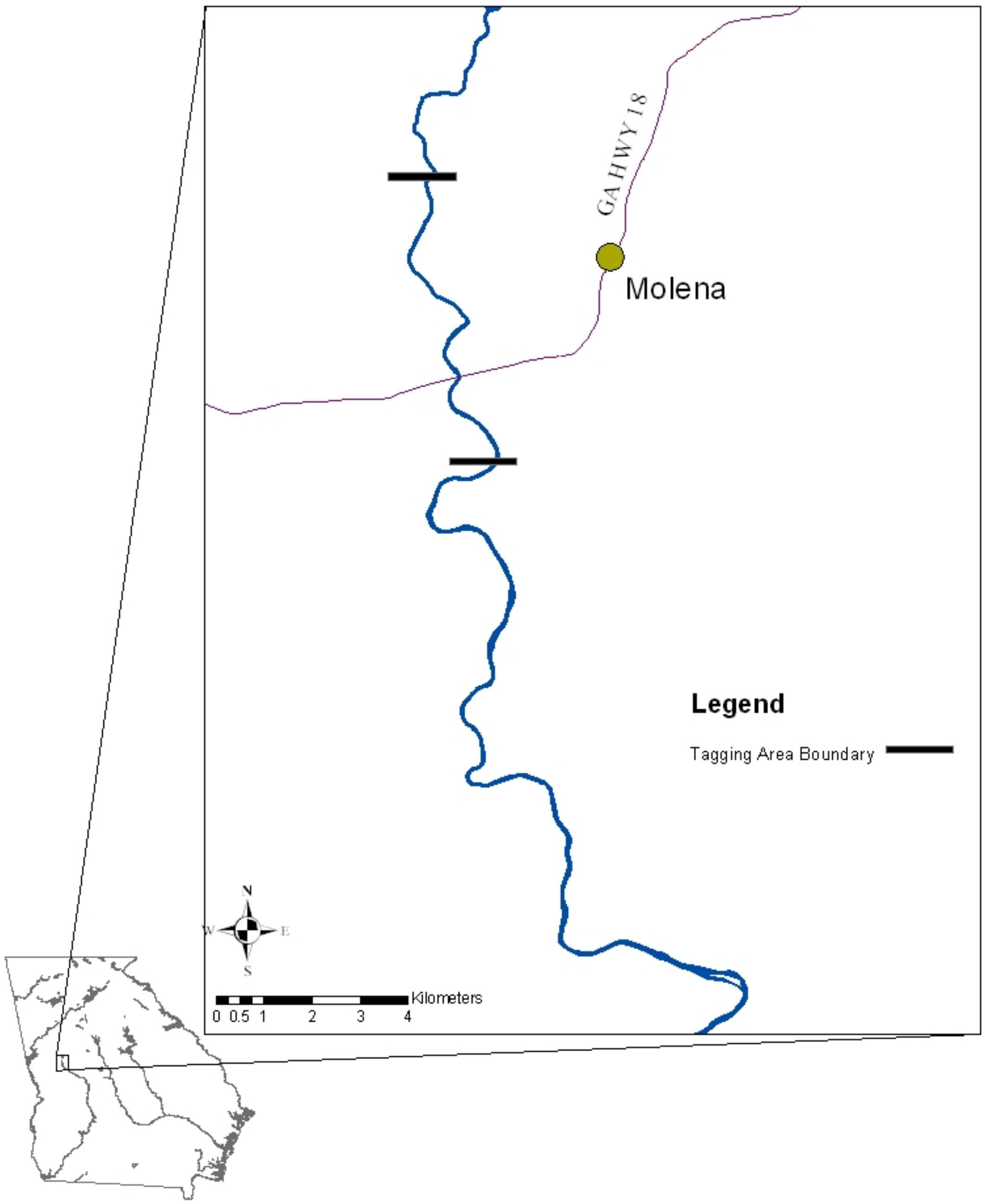

Figure 1. Map of fish radio telemetry tagging location in the upper Flint River, Georgia, near Georgia Highway 18 in December 2007.

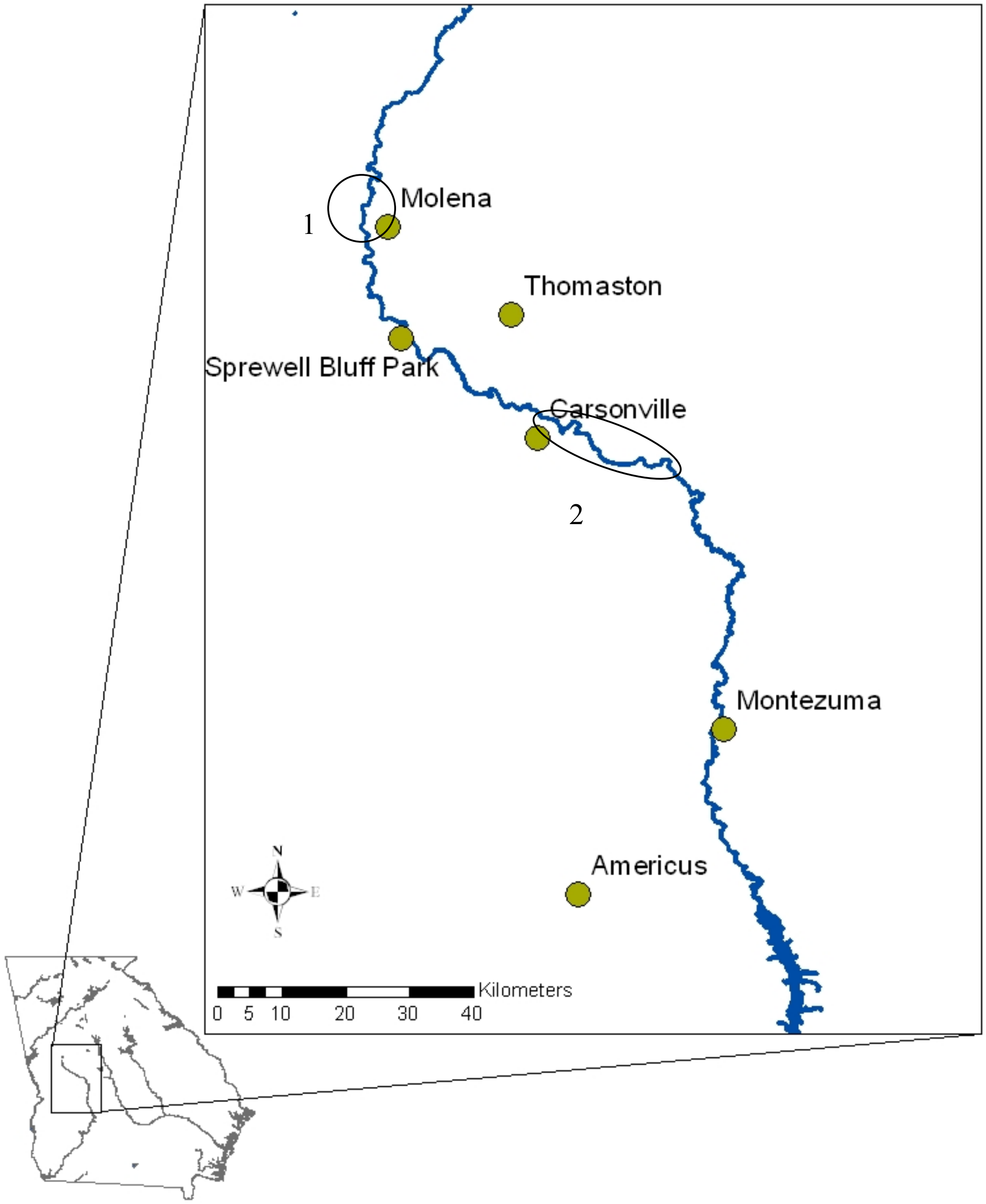

Figure 2. Map of upper Flint River above Lake Blackshear in Georgia. Age-0 collection sites in the piedmont (1) and coastal plain (2) are shown circled.

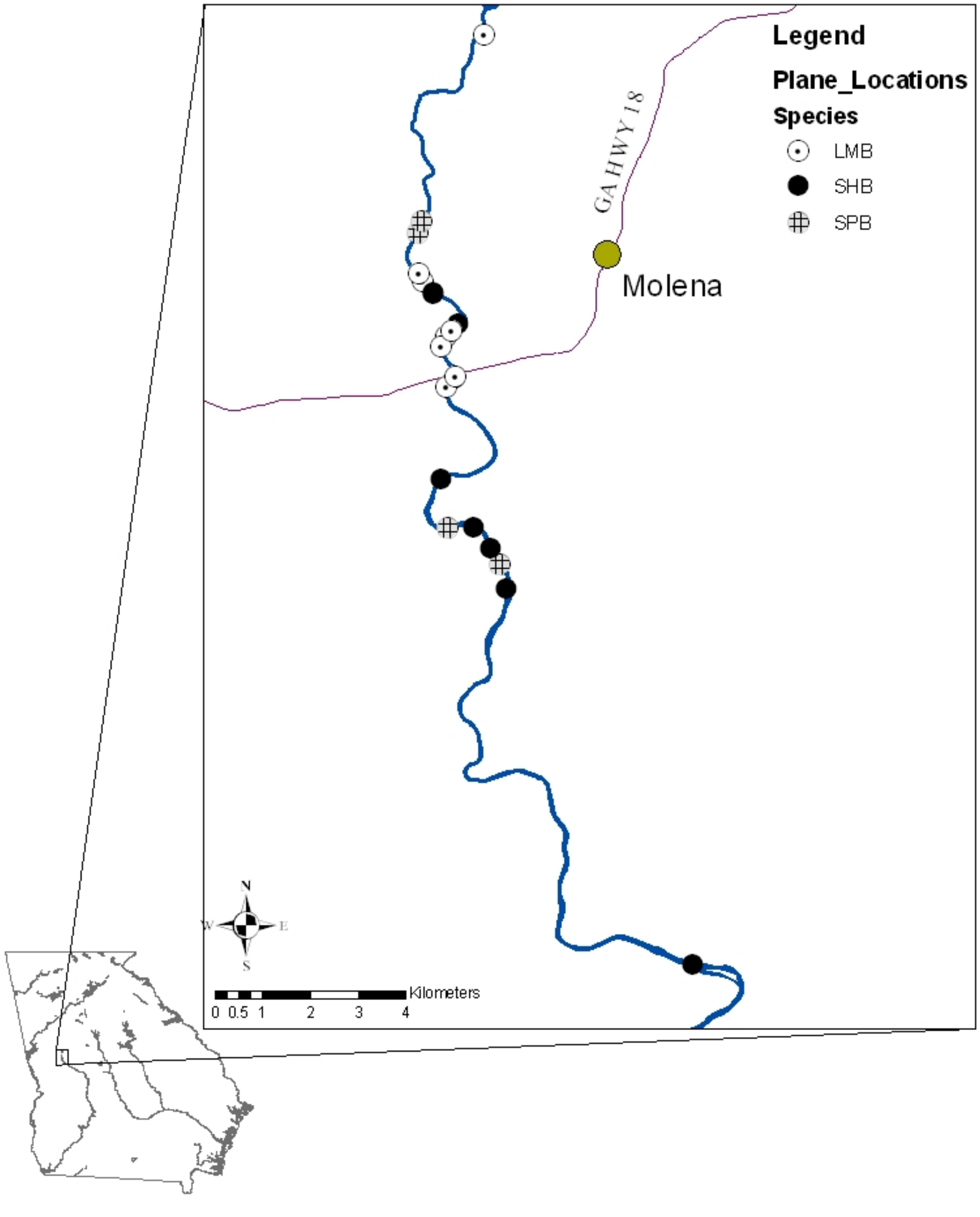

Figure 3. Map of fish locations recorded during a plane telemetry survey of the upper Flint River, Georgia, on May 6 2008.

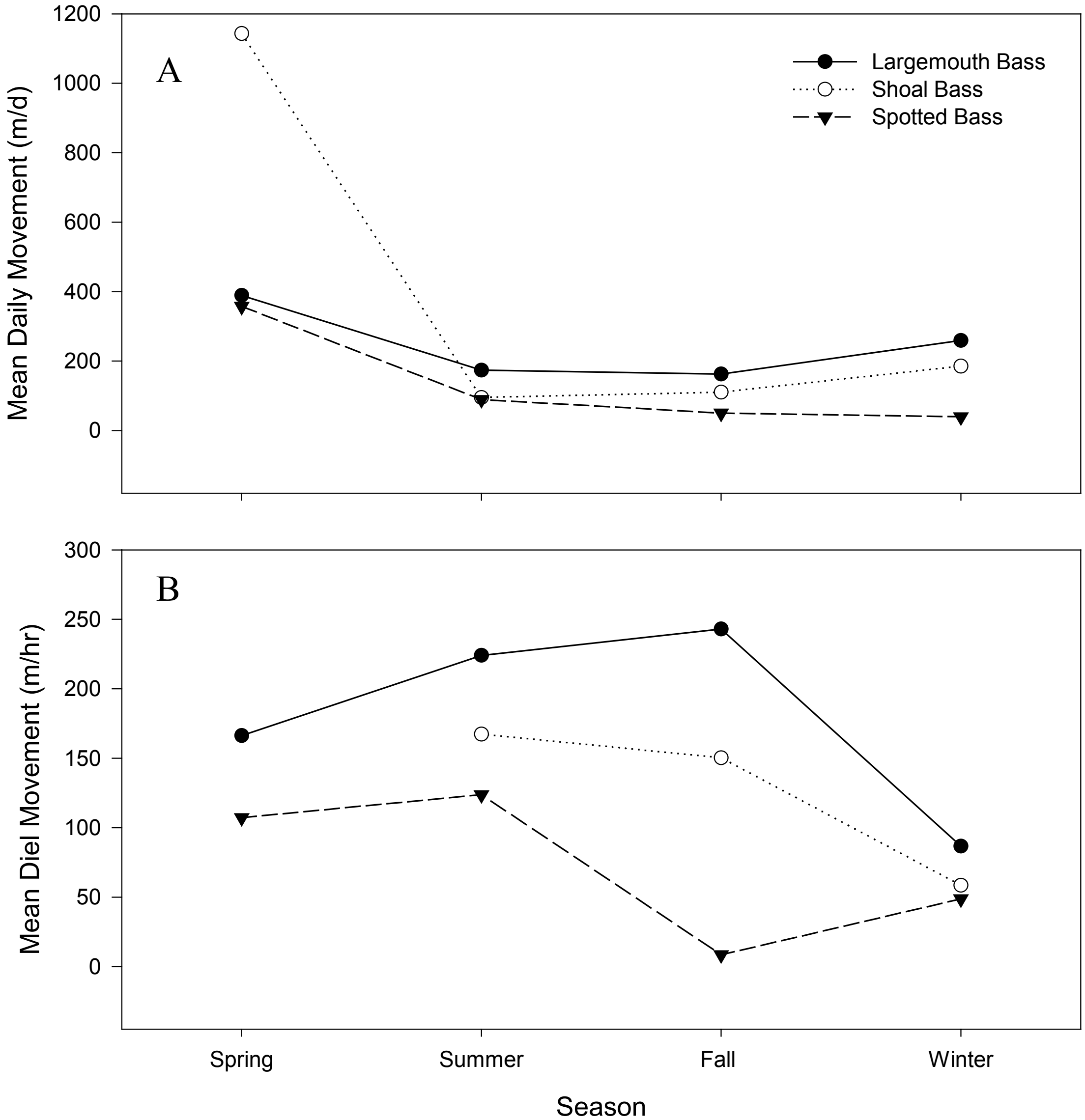

Figure 4. Seasonal mean daily (A) and diel (B) movement rates of largemouth bass, shoal bass, and spotted bass in the upper Flint River, Georgia, in 2008. No shoal bass were observed on 24 h tracking events during the spring because they had all migrated out of the diel tracking area.

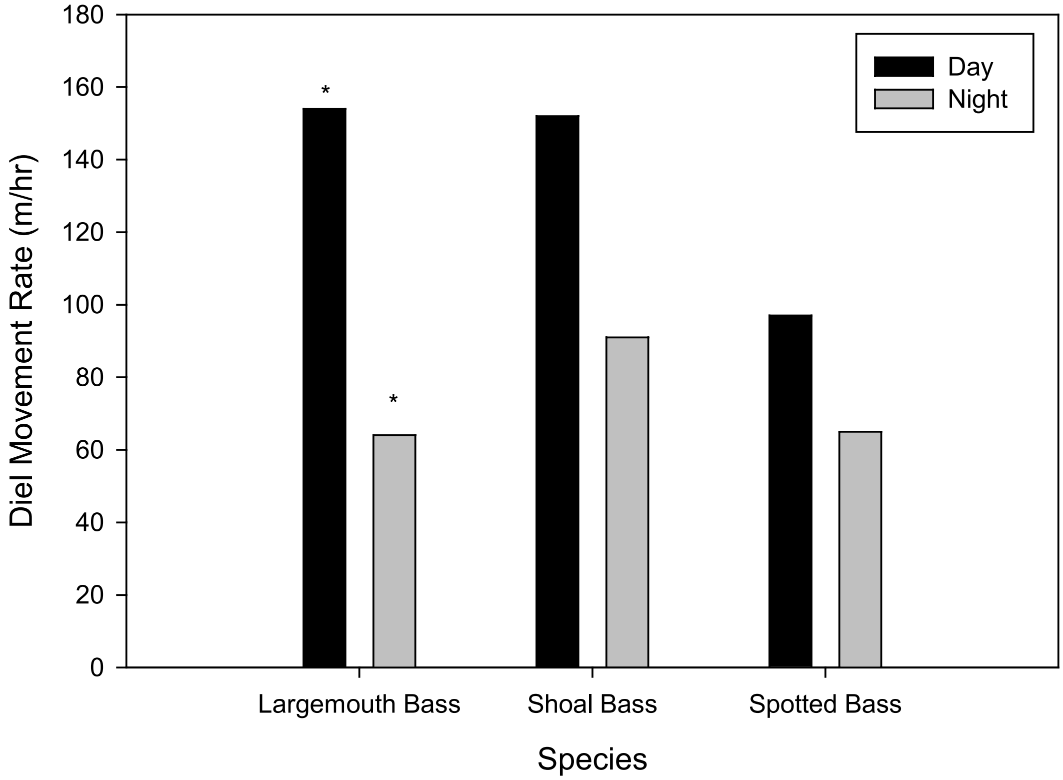

Figure 5. Diel movement rates of black bass in among diel periods in the Flint River, Georgia during 2008. An asterisk denotes a difference in diel periods within a species ($P \leq 0.05$).

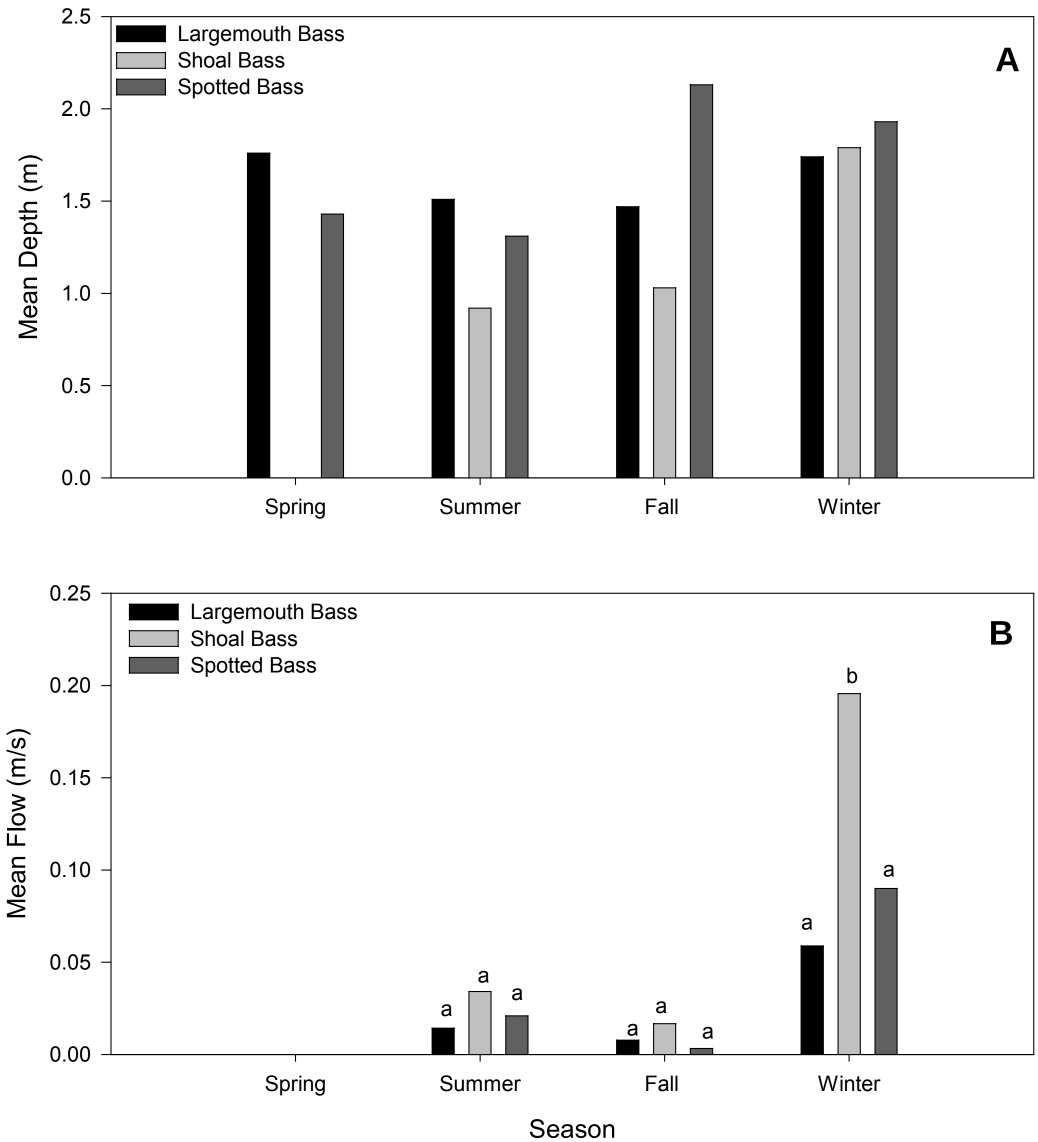

Figure 6. Seasonal mean depth (A) and flow (B) use of radio-tracked black bass in the upper Flint River, Georgia, in 2008. No shoal bass depths were observed on tracking events during the spring. No flow measurements were taken during the spring due to equipment malfunction. Different letters represent significant differences (Bonnferoni adjusted $P < 0.05$) among species within a season.

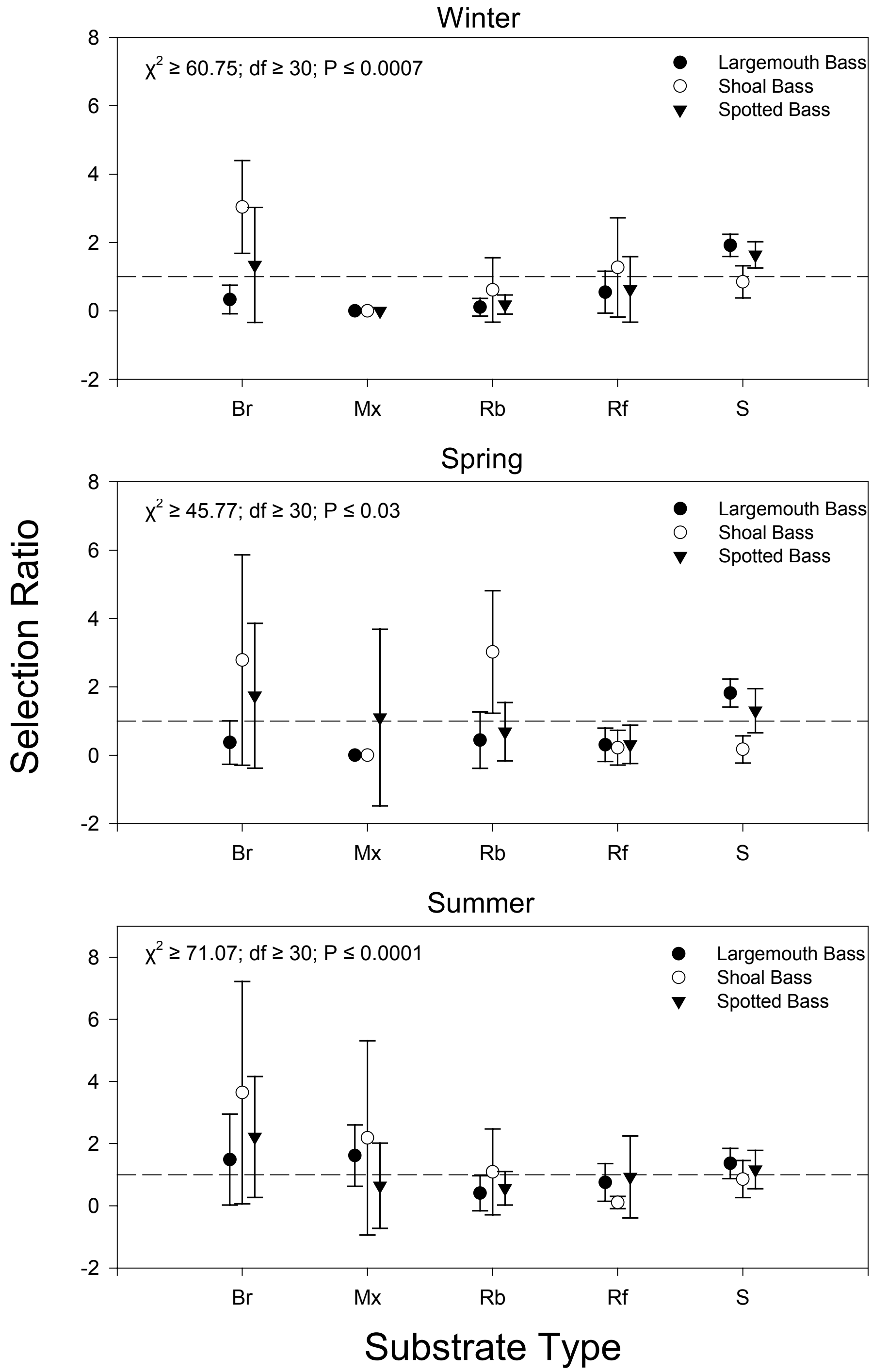

Figure 7. Seasonal selection ratios and 95% simultaneous Bonferroni confidence intervals of substrate types (Br = bedrock, Mx = mixed rocky, Rb = rocky boulder, Rf = rocky fine, S = sandy) for largemouth bass, shoal bass, and spotted bass in the upper Flint River, Georgia, 2008. Values greater than 1 (dashed line) indicate positive selection, values less than 1 indicate negative selection, and values of 1 indicate selection in proportion to availability.

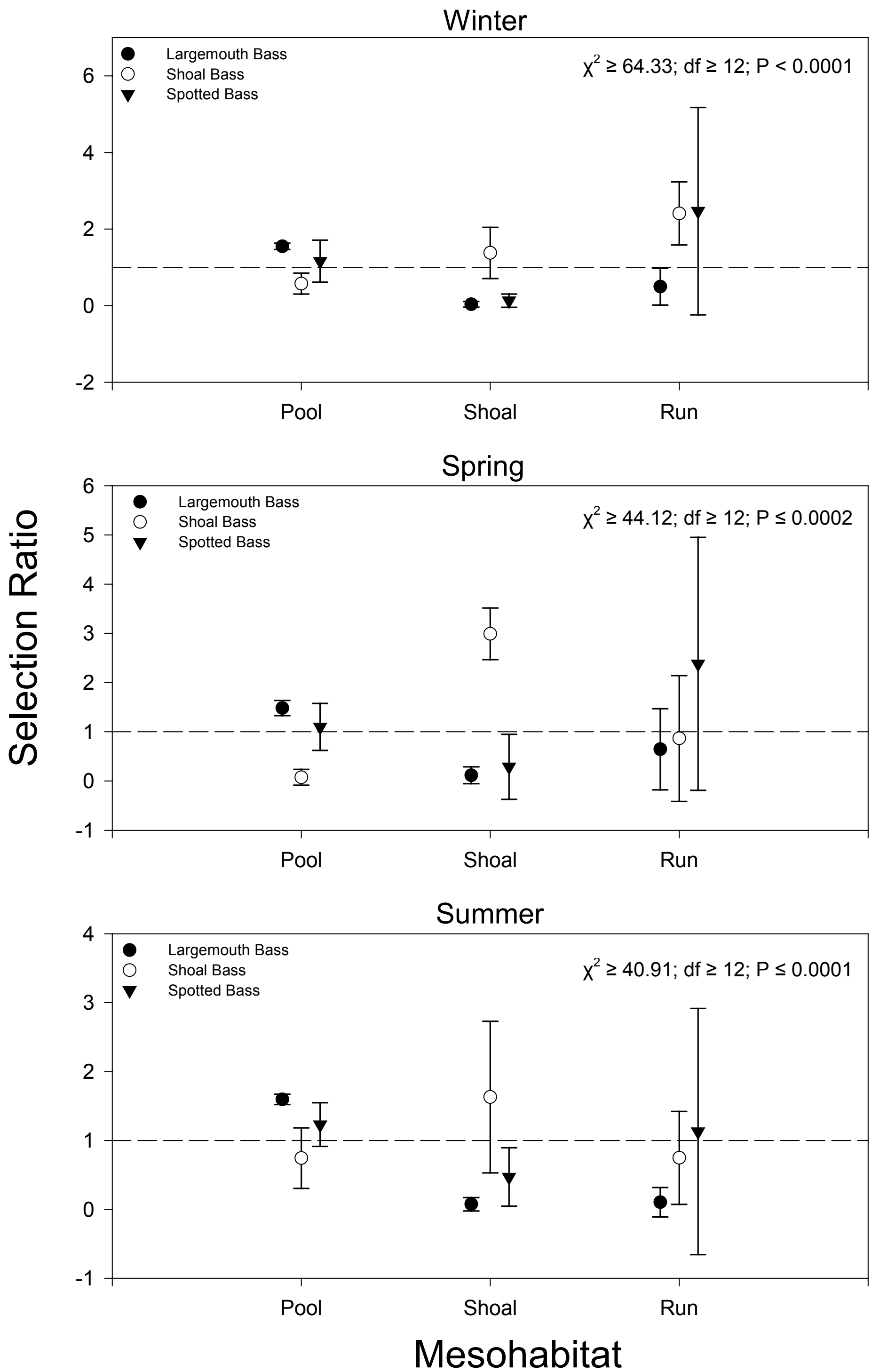

Figure 8. Seasonal selection ratios and 95% simultaneous Bonferroni confidence intervals of mesohabitat types for largemouth bass, shoal bass, and spotted bass in the upper Flint River, Georgia during 2008. Values greater than 1 (dashed line) indicate positive selection, values less than 1 indicate negative selection, and values of 1 indicate selection in proportion to availability.

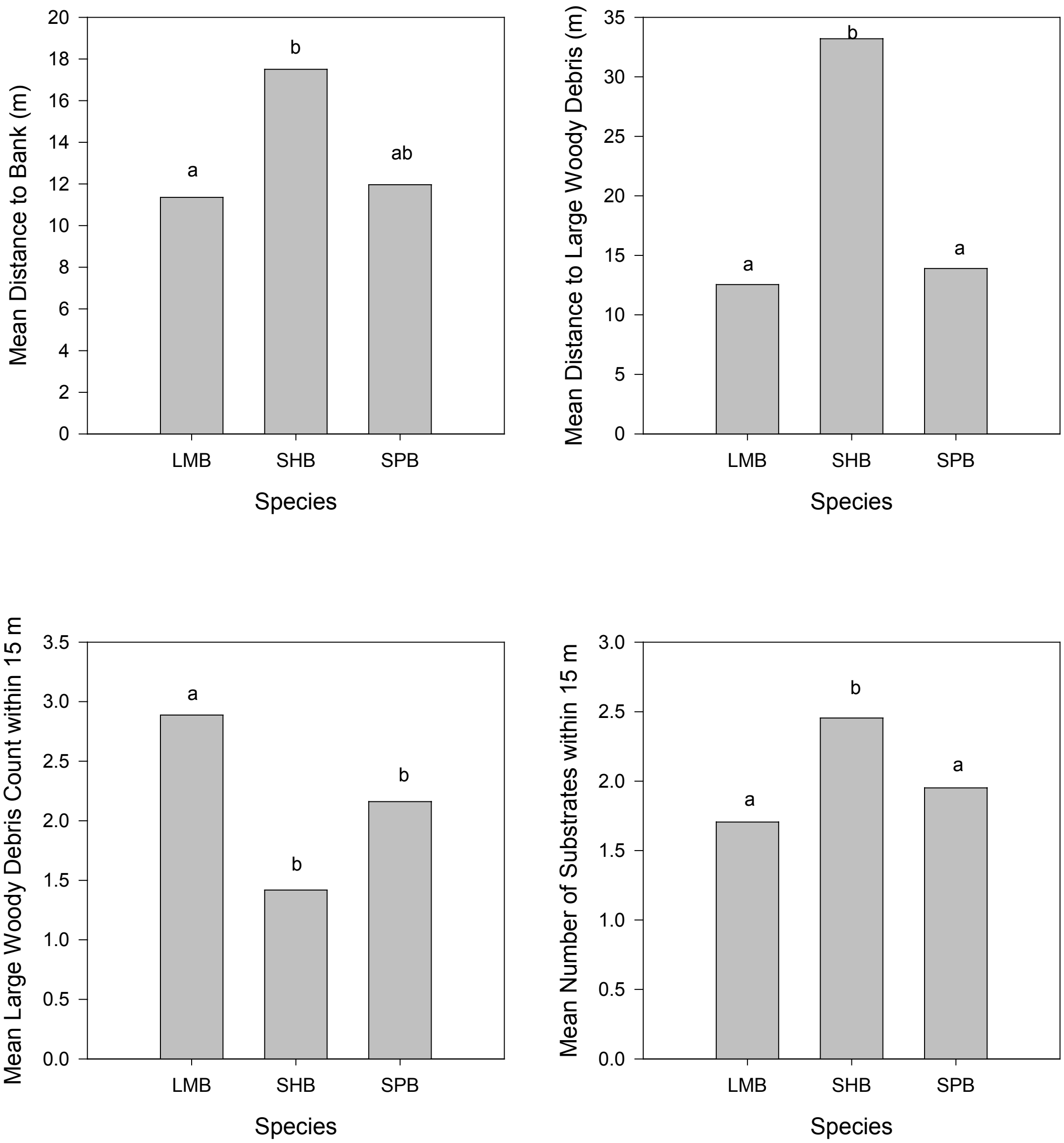

Figure 9. Mean distances to stream bank, mean distances to large woody debris, mean counts of large woody debris within 15 m of fish locations, and mean number of substrate types within 15 m of fish locations for largemouth bass (LMB), shoal bass (SHB), and spotted bass (SPB) in the Flint River, Georgia, in 2008. Different letters represent significant differences (Bonnferoni adjusted $P \leq 0.0376$) among species.

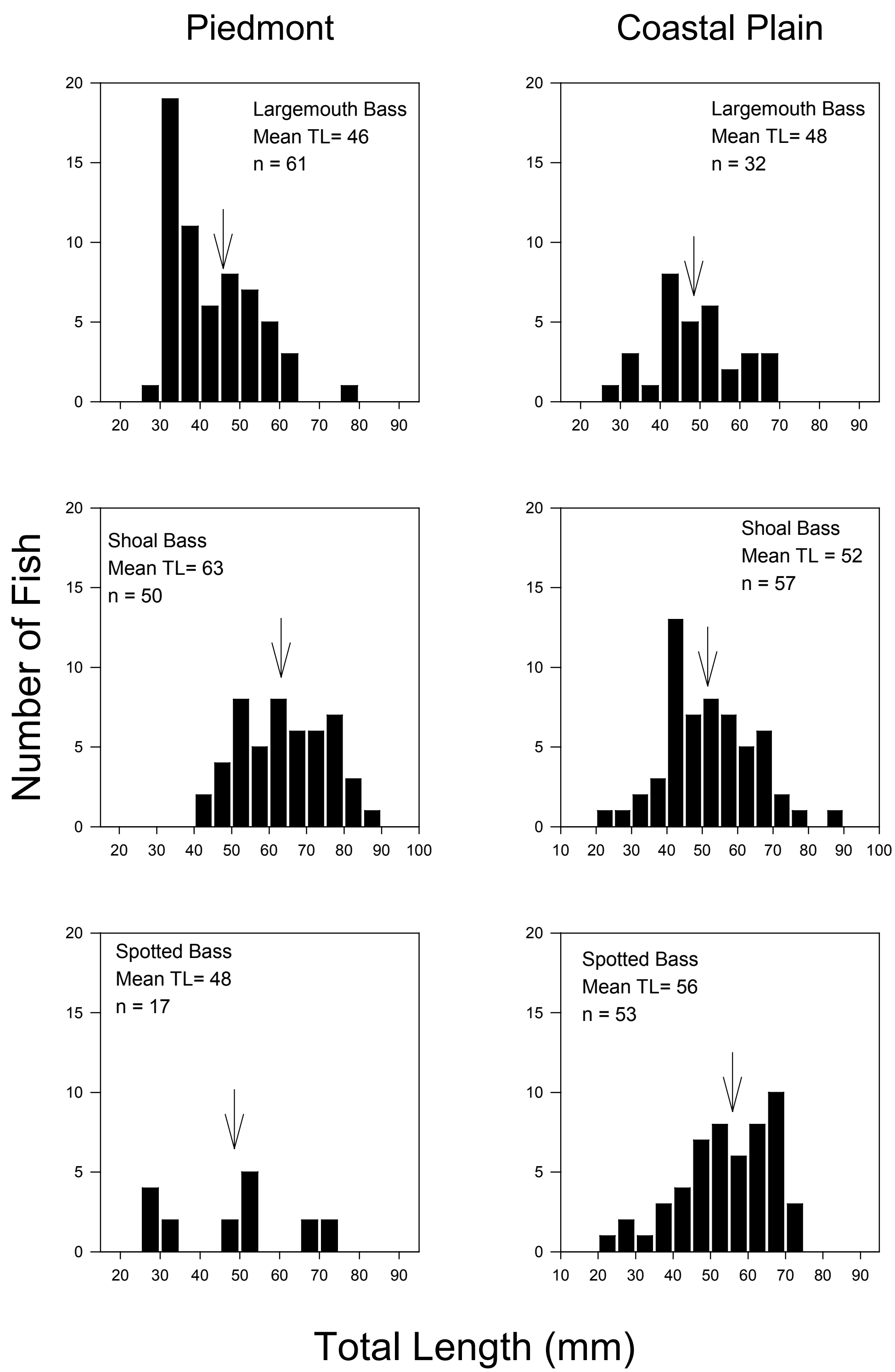

Figure 10. Length-frequency histograms for age-0 largemouth bass, shoal bass, and spotted bass collected in the upper Flint River, Georgia, in 2008. Arrows denote mean total length of basses in each sample.

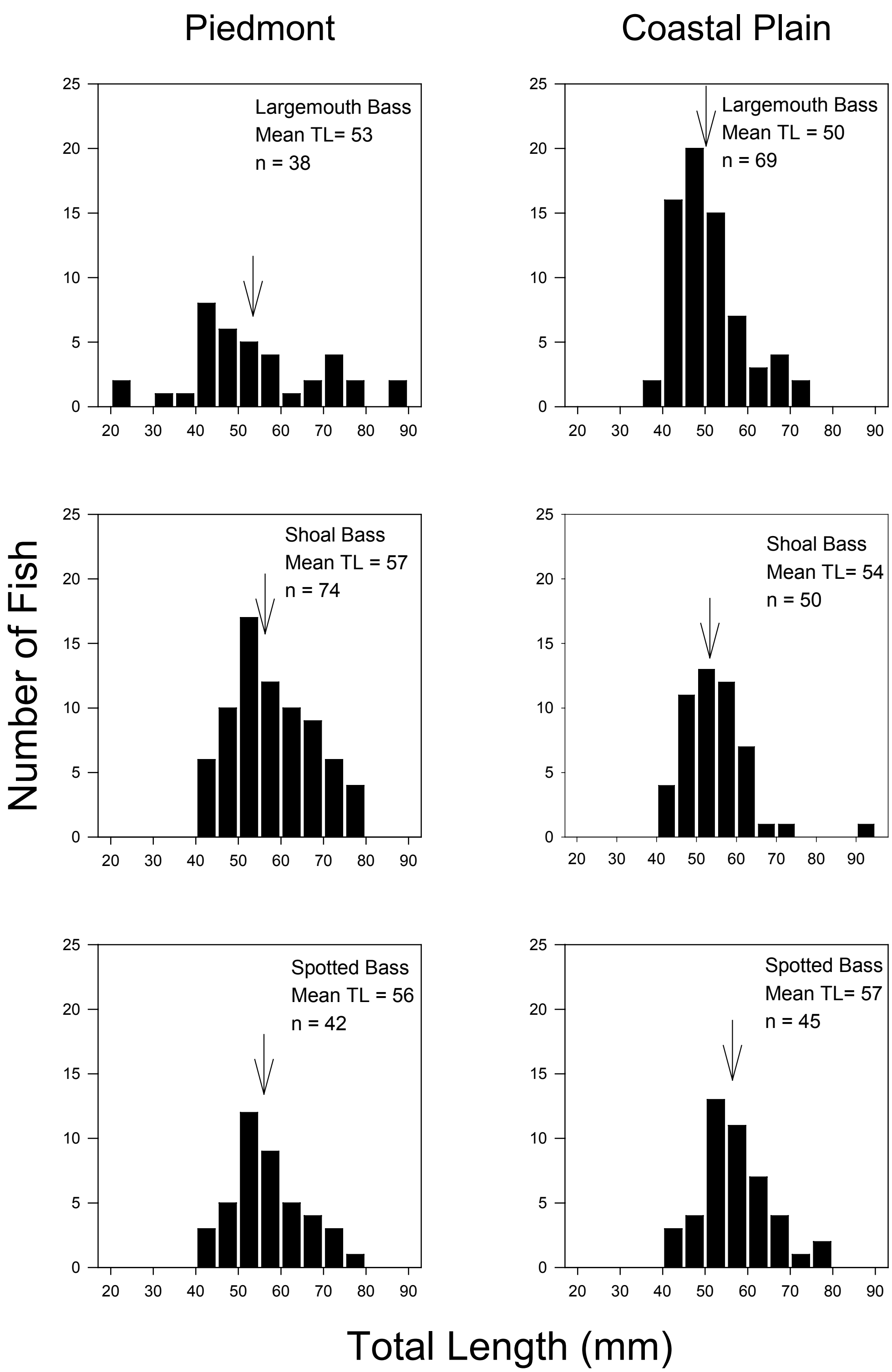

Figure 11. Length-frequency histograms for age-0 largemouth bass, shoal bass, and spotted bass collected in the upper Flint River, Georgia, in 2009. Arrows denote mean total length of basses in each sample.

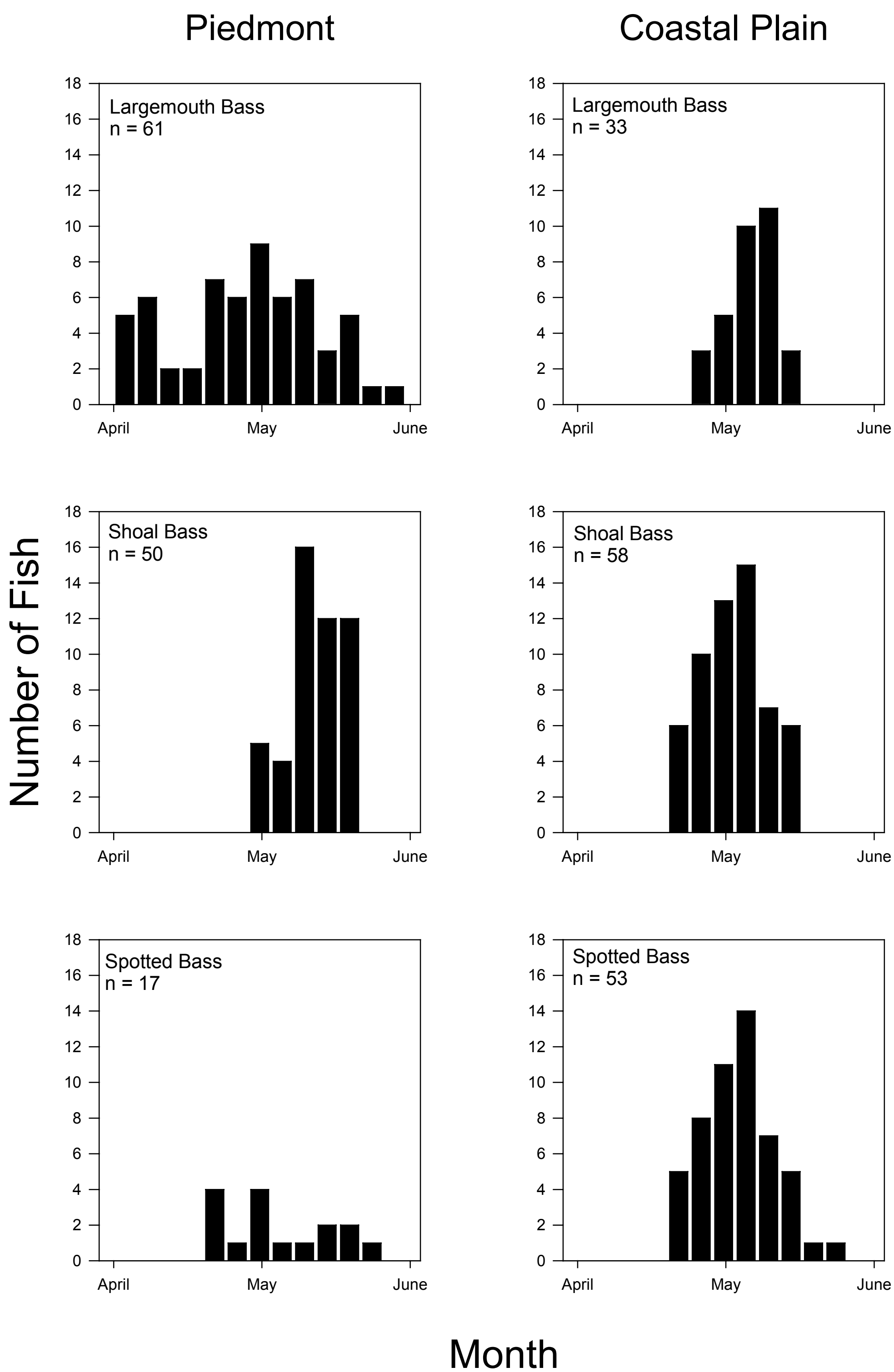

Figure 12. Hatch-date frequencies of age-0 largemouth bass, shoal bass, and spotted bass collected in the upper Flint River, Georgia, in 2008. Month labels on the x-axis represent the first day of each month.

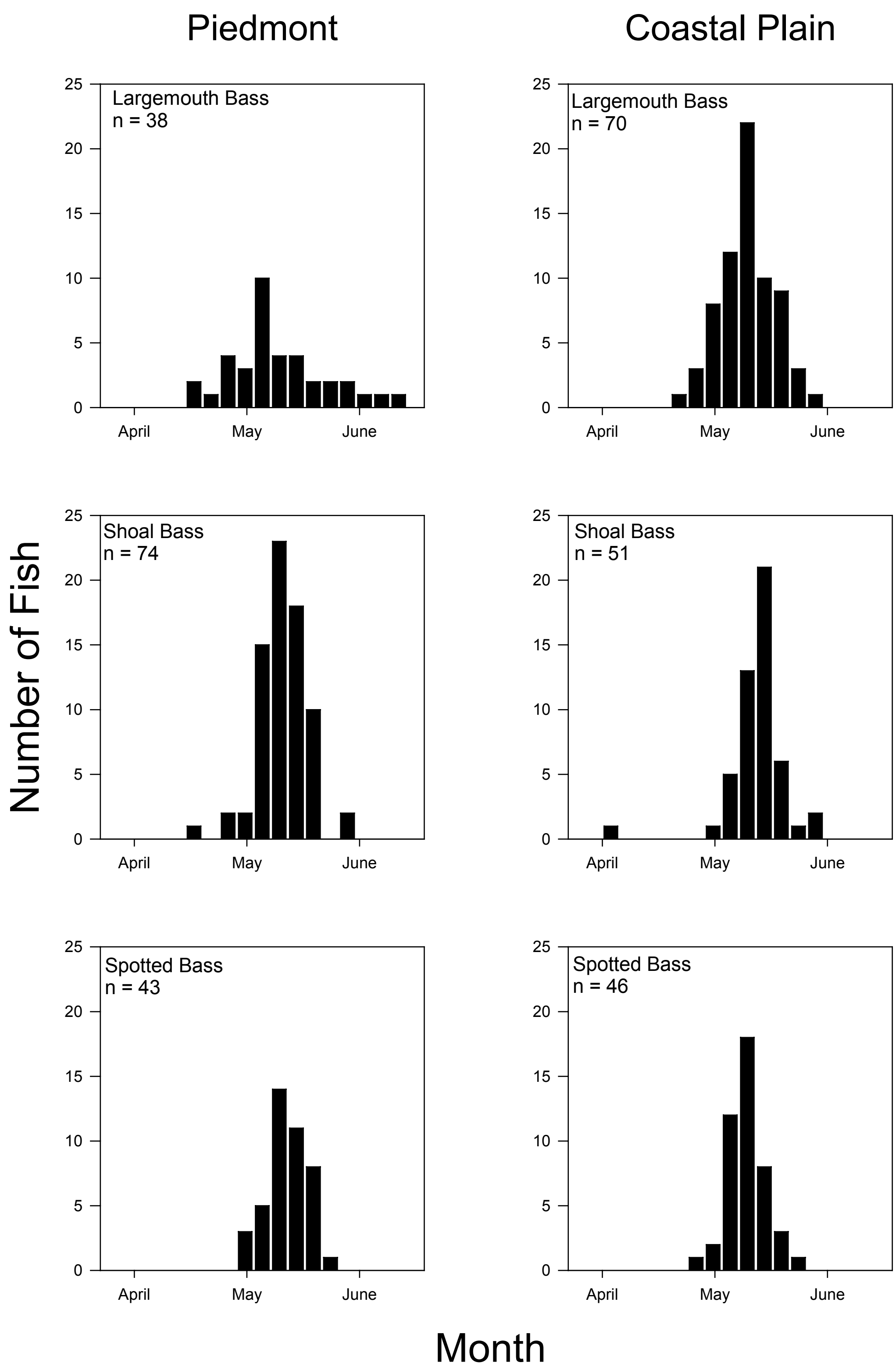

Figure 13. Hatch-date frequencies of age-0 largemouth bass, shoal bass, and spotted bass collected in the upper Flint River, Georgia, in 2009. Month labels on the x-axis represent the first day of each month.

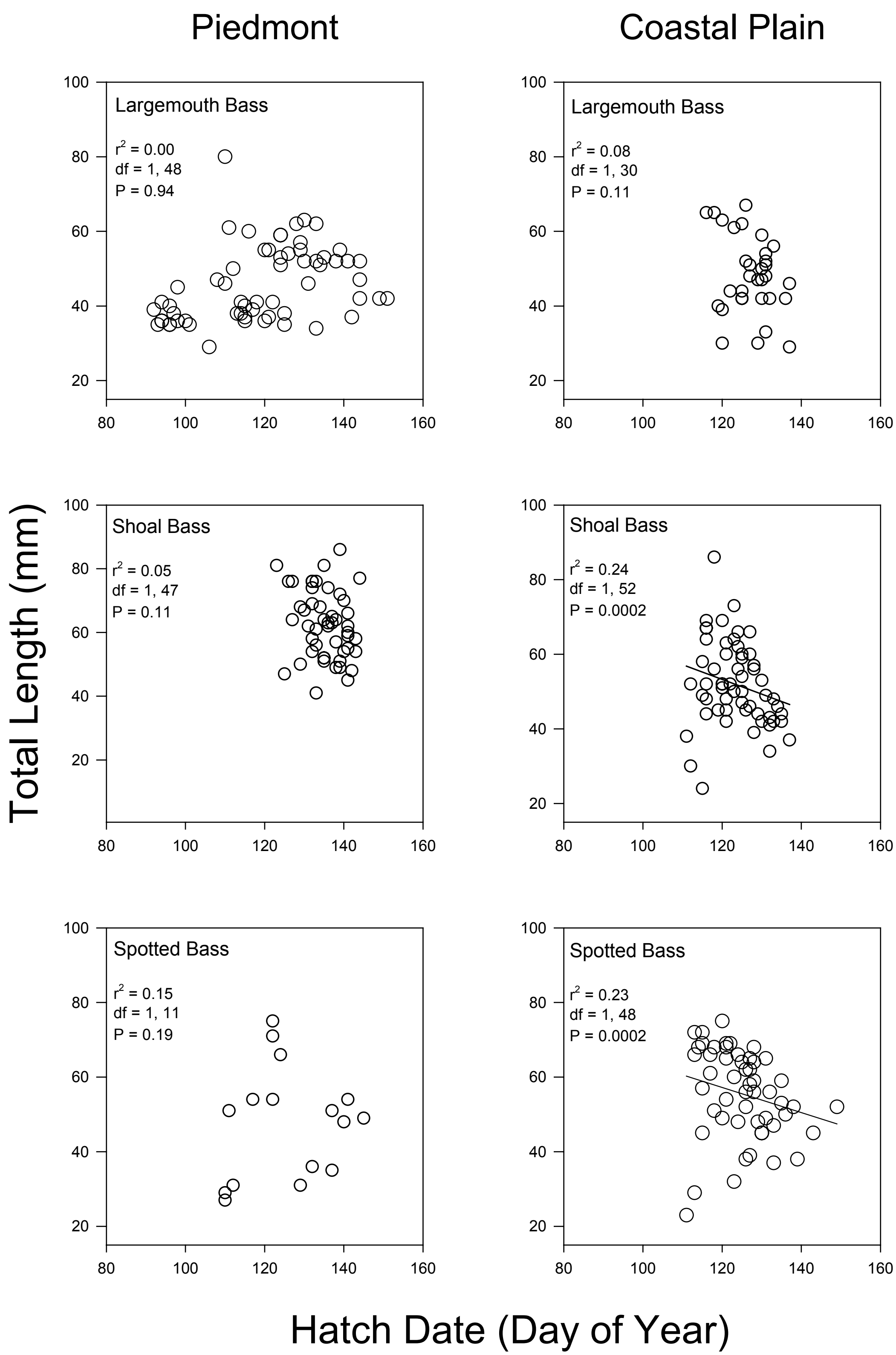

Figure 14. Total length (mm) versus hatch date of age-0 largemouth bass, shoal bass, and spotted bass collected in the Flint River, Georgia, during 2008.

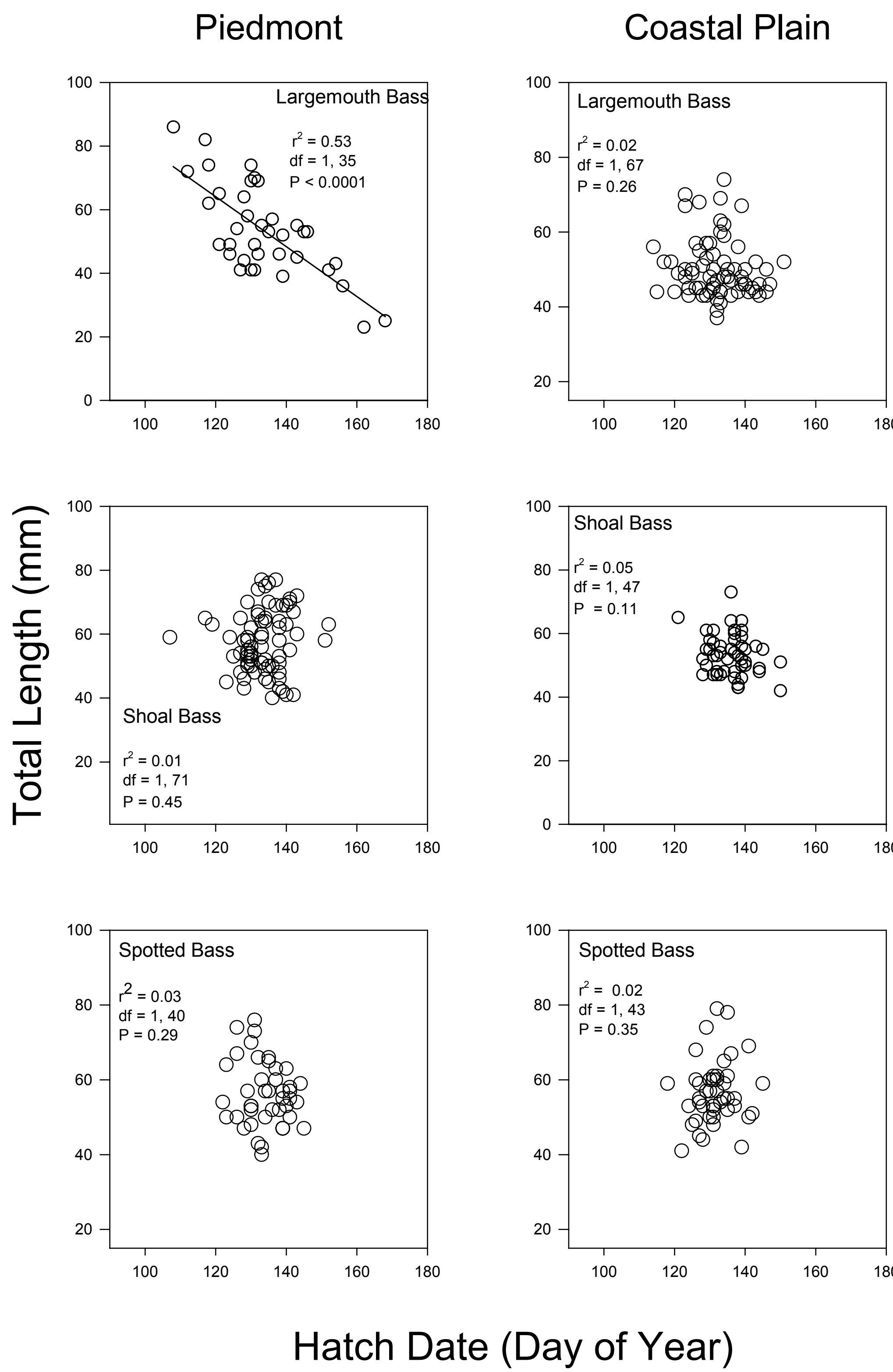

Figure 15. Total length (mm) versus hatch date of age-0 largemouth bass, shoal bass, and spotted bass collected in the Flint River, Georgia, during 2009.

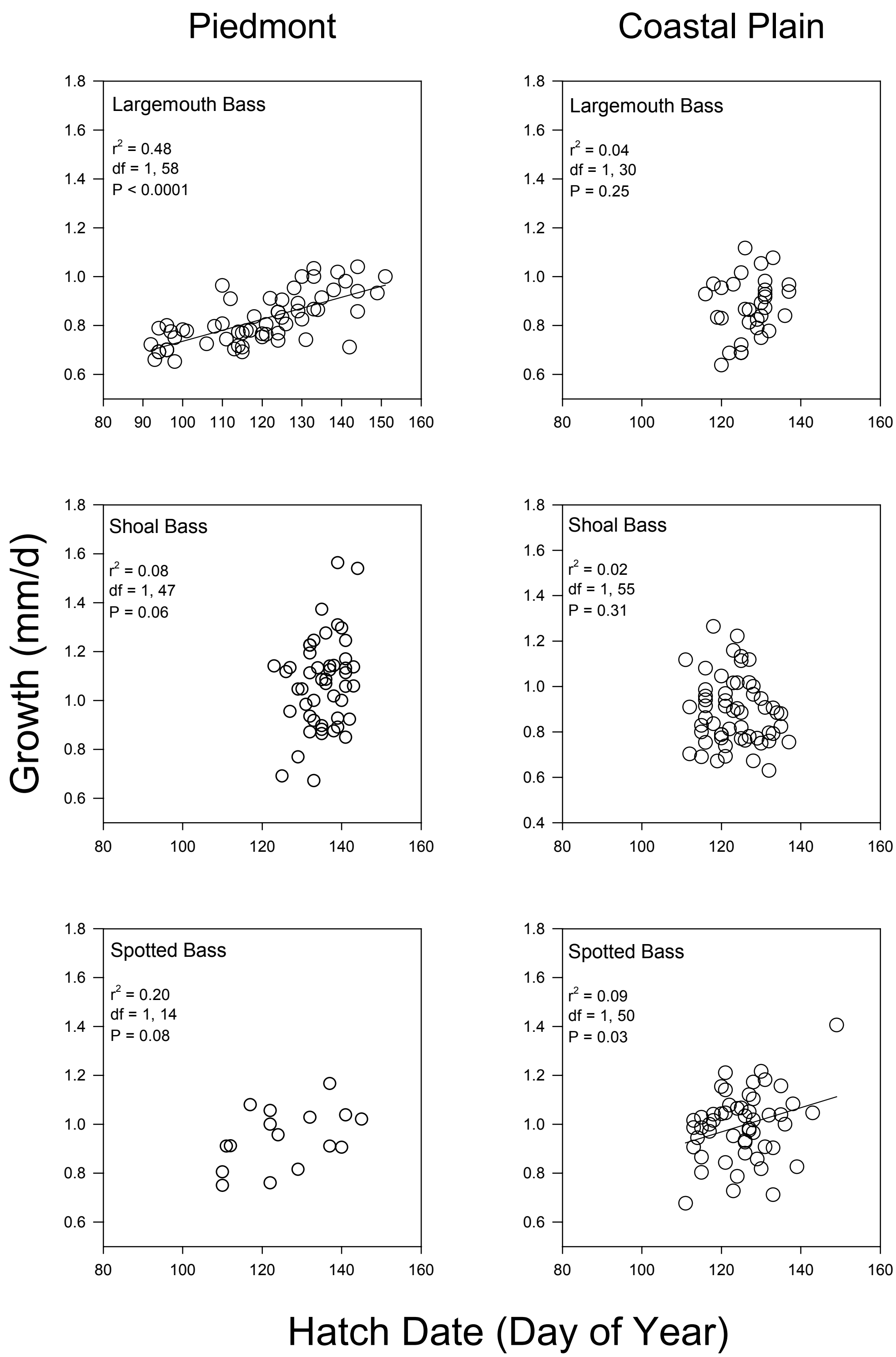

Figure 16. Growth (mm/d) versus hatch date of age-0 largemouth bass, shoal bass, and spotted bass collected in the Flint River, Georgia, during 2008.

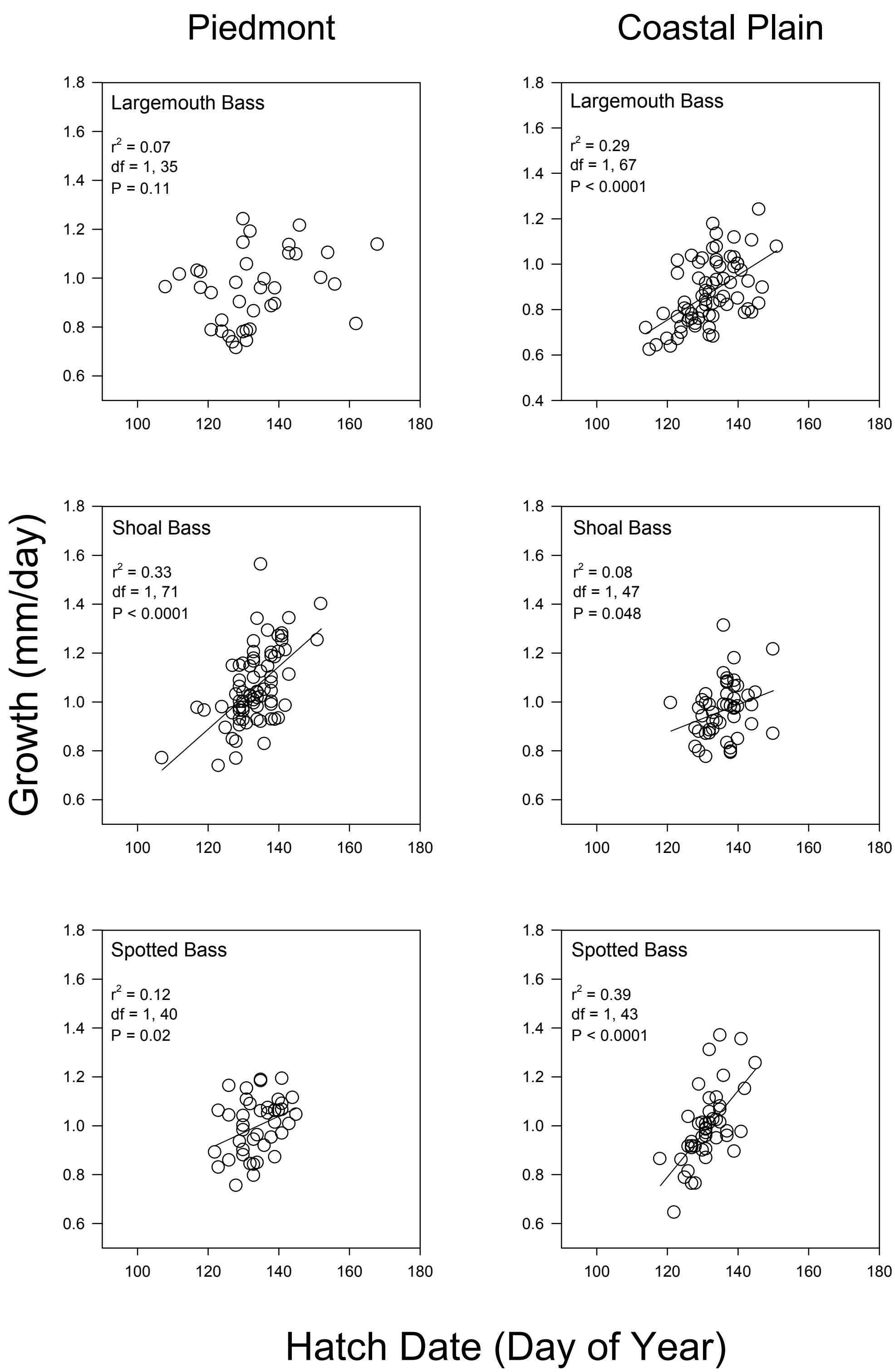

Figure 17. Growth (mm/d) versus hatch date of age-0 largemouth bass, shoal bass, and spotted bass collected in the Flint River, Georgia, during 2009.

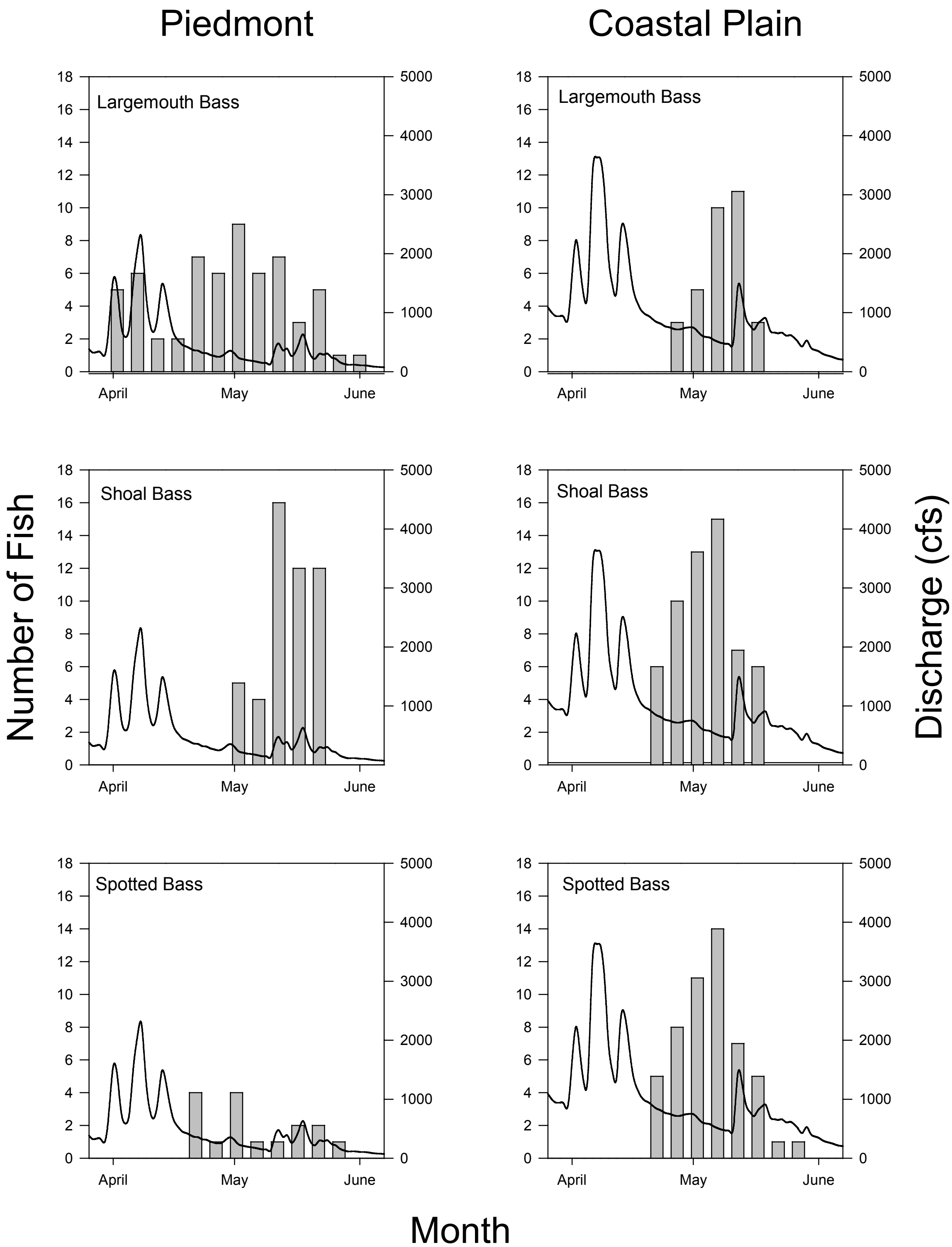

Figure 18. Black bass hatch dates relative to discharge levels in the Flint River, Georgia. during 2008.

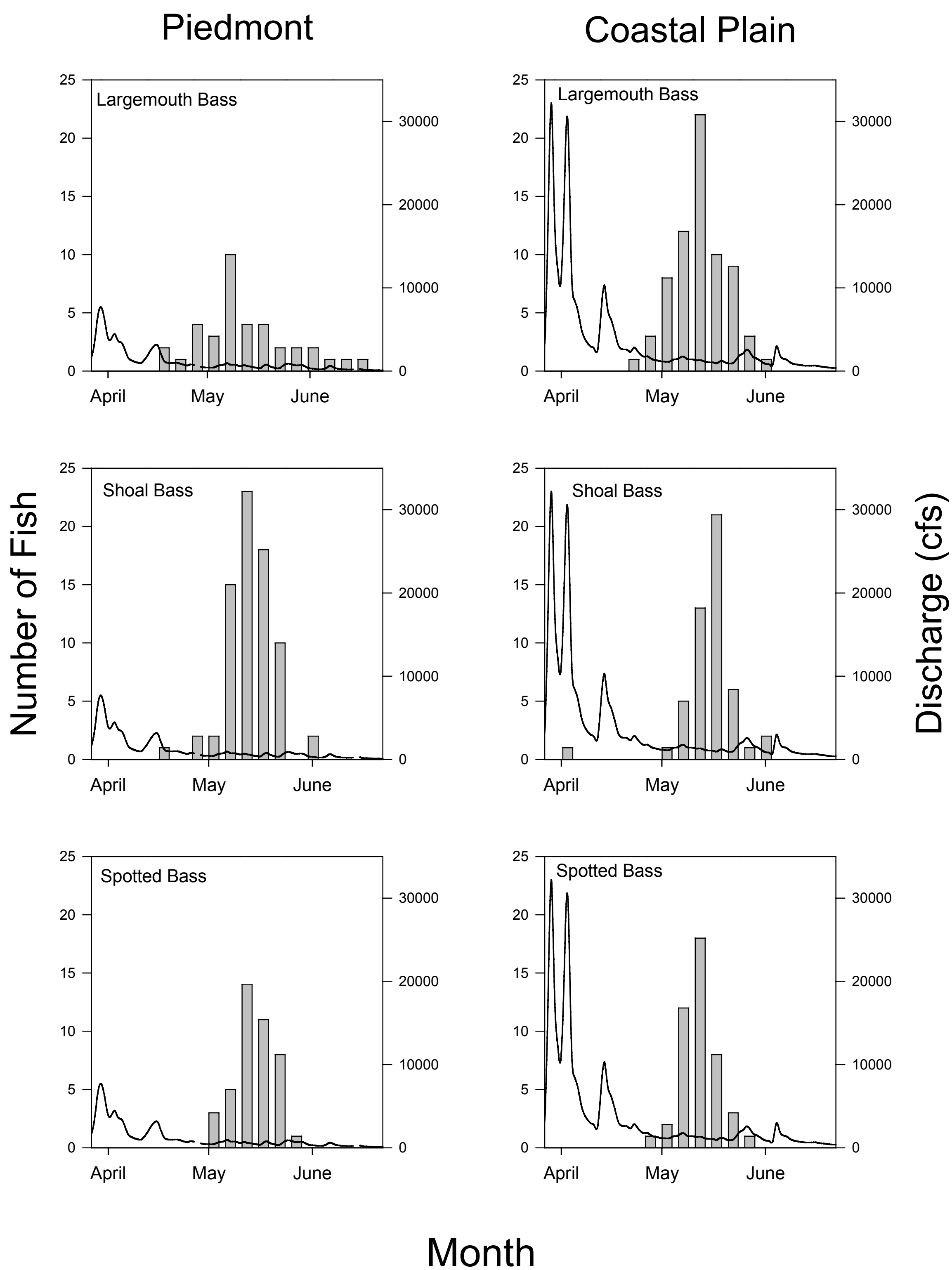

Figure 19. Black bass hatch dates relative to discharge levels in the Flint River, Georgia, during 2009.

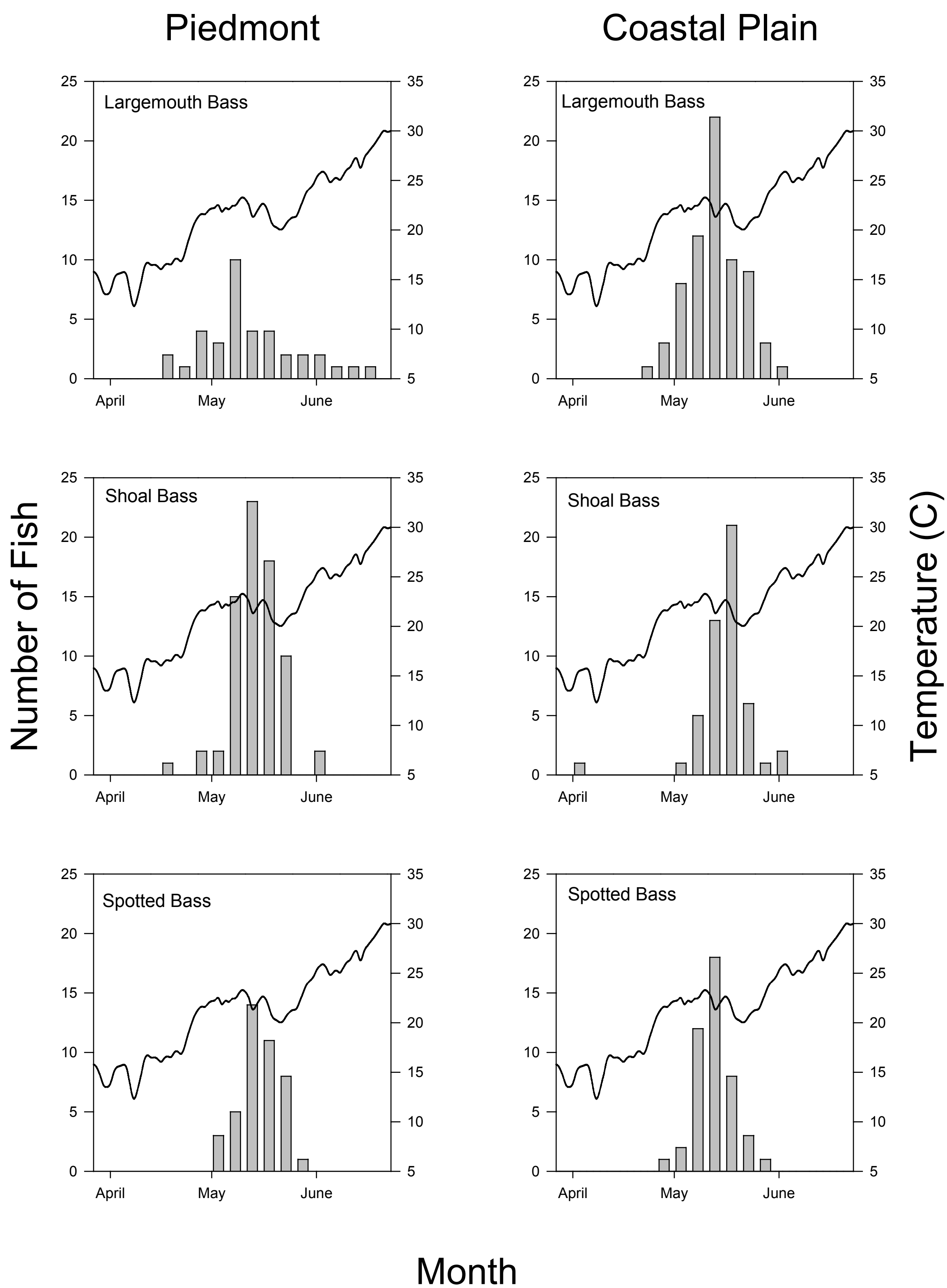

Figure 20. Black bass hatch dates relative to temperature in the Flint River, Georgia, during 2009.

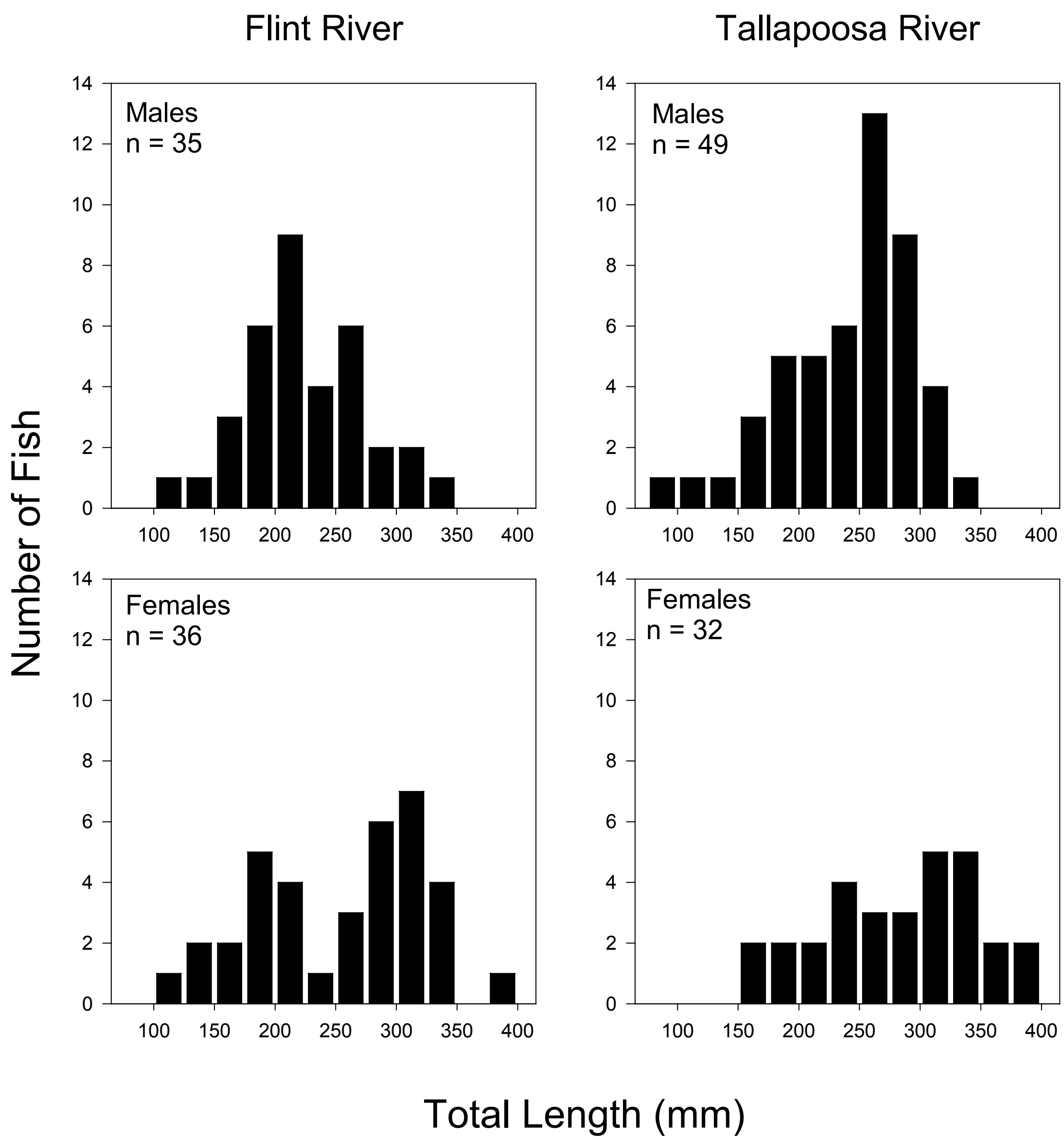

Figure 21. Length frequency of spotted bass collected from the Flint River, Georgia, and Alabama bass collected in the Tallapoosa River, Alabama, for life history analysis.

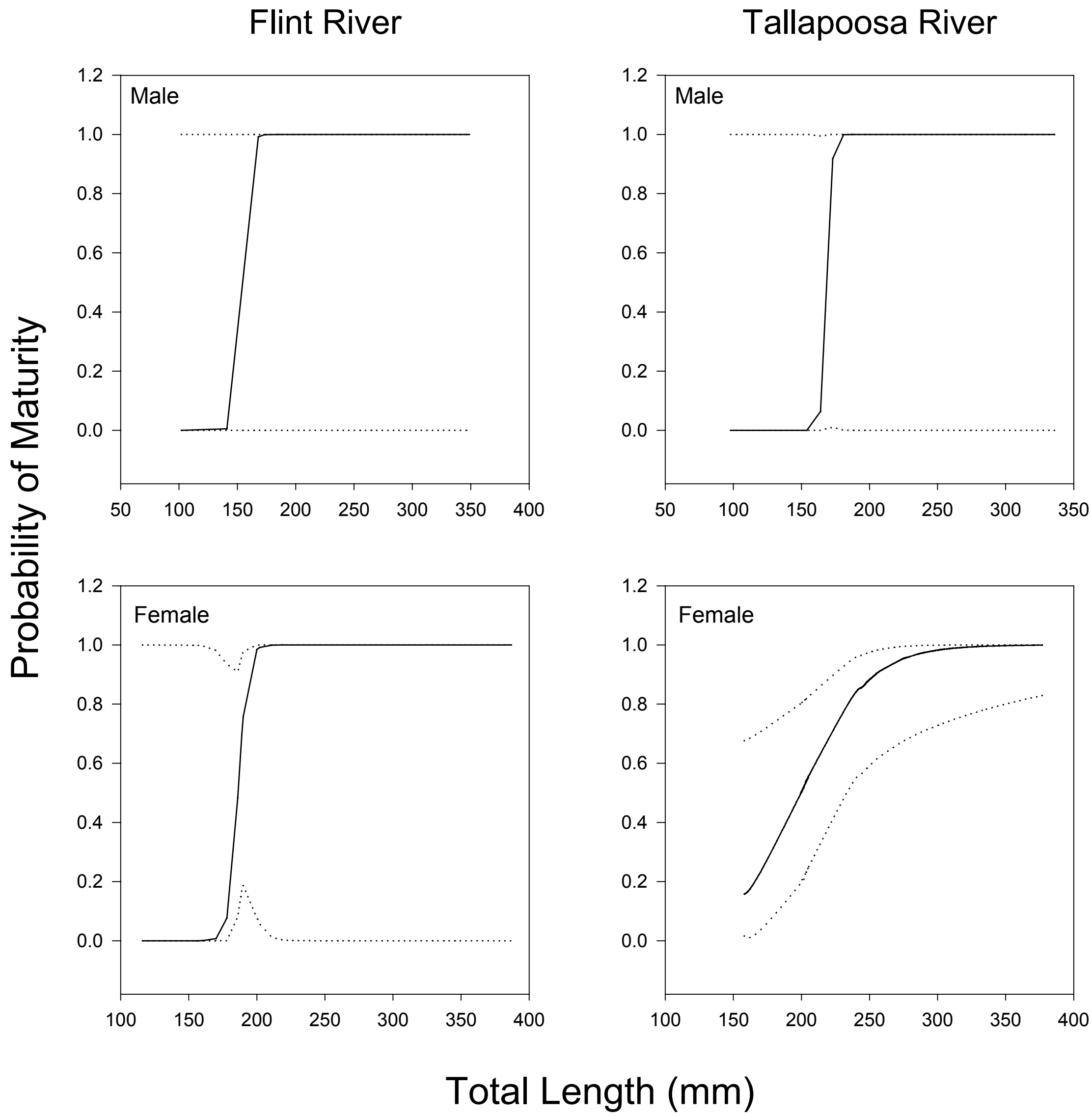

Figure 22. Probability of maturity versus total length (mm) for spotted bass collected in the Flint River, Georgia, and Alabama bass collected in the Tallapoosa River, Alabama, during spring 2009. The solid line represents the probability of a fish being mature at a given length. The dotted lines represent the 95% confidence intervals for the probability of maturation function.

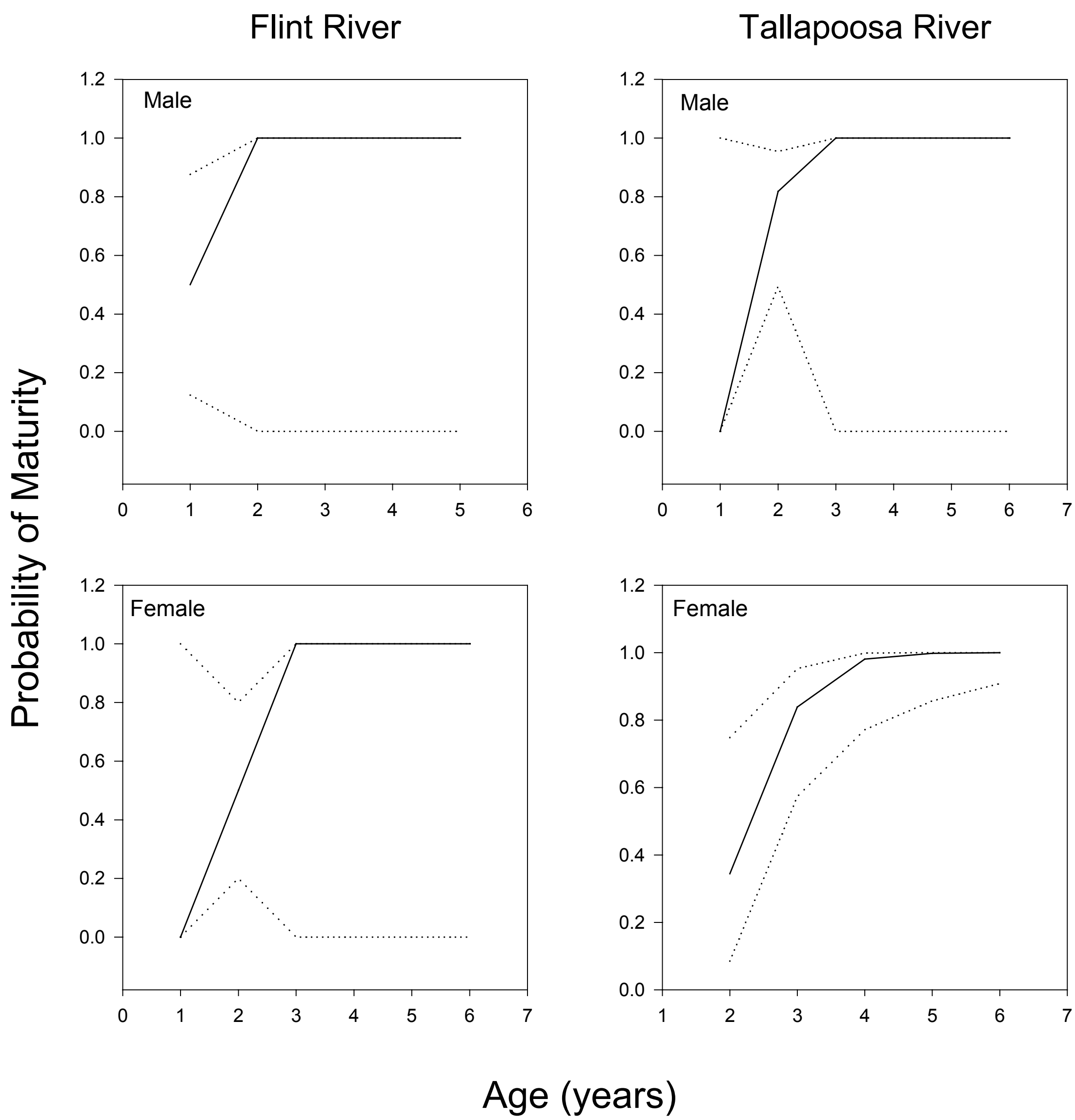

Figure 23. Probability of maturity versus age (years) for spotted bass collected in the Flint River, Georgia, and Alabama bass collected in the Tallapoosa River, Alabama, during spring 2009. The solid line represents the probability of a fish being mature at a given length. The dotted lines represent the 95% confidence intervals for the probability of maturation function.

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