Effect of Discharge on Hatching and Growth of Age-0 Black Bass in Two Southeastern U.S. Rivers

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Abstract

We examined the influence of variable discharge on hatching and age-0 growth for fluvial specialist and habitat generalist species of black bass *Micropterus* spp. in two southeastern U.S. rivers, the Flint River, Georgia (unregulated), and the Tallapoosa River, Alabama (regulated by several hydropower dams). Between 2008 and 2010, we collected 285 Largemouth Bass *M. salmoides* (generalist) and 254 Shoal Bass *M. cataractae* (specialist) from two reaches of the Flint River. In 2010–2011, we collected 309 Alabama Bass *M. henshalli* (generalist) and 216 Redeye Bass *M. coosae* (specialist) from two regulated reaches and one unregulated reach of the Tallapoosa River. Successful hatching of black bass in both rivers generally occurred from late March to early June when water levels were low and stable. Hatching distributions of all black bass were generally unimodal with little evidence of spawning disruption, except for Alabama Bass in the most-regulated reach of the Tallapoosa River, which appeared to be disrupted by large discharge events. Mean growth of both species in the Flint River varied from 0.64 to 0.82 mm/d across reaches and years; Shoal Bass generally grew faster than Largemouth Bass in all reach–year combinations. Largemouth Bass growth was inversely correlated to discharge variation in one reach, but Shoal Bass growth was not correlated to discharge variation in either reach. Alabama Bass and Redeye Bass growth rates in the Tallapoosa River were similar to rates observed for congeners in the Flint River; Alabama Bass grew faster than Redeye Bass. Growth of both species was inversely related to discharge variation in five of six reach–species combinations; the only exception was for Redeye Bass in the less-regulated reach. Results from this study suggest that variable discharge has less influence on successful reproduction of black bass than was reported for other fishes, but growth may be more affected by discharges resulting from anthropogenic sources than those associated with the natural regime.

Keywords: hydrology; spawning success; *Micropterus*; flow

Received: April 2021; Accepted: July 2021; Published Online Early: July 2021; Published: December 2021

Citation: Sammons SM, Earley LA, Goclowski MR. 2021. Effect of discharge on hatching and growth of age-0 Black Bass in two southeastern U.S. rivers. *Journal of Fish and Wildlife Management* X(X):xx-xx; e1944-687X. https://doi.org/10.3996/JFWM-21-021

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Introduction

Lotic ecosystems around the world have been manipulated, and many waterways suffer from low water quality due to pollution and a variety of land uses. Additionally, water from many rivers is diverted or impounded. Hydroelectric power dams provide numerous benefits to society in addition to electrical power, such as water supply, flood control, navigation, and recreational opportunities; however, they usually alter or influence downstream fisheries. Whereas upstream reservoirs often support economically important fisheries (Fisher et al. 1986; Riechers and Fedler 1996), nonsalmonid fisheries below dams are often ignored, despite their obvious economic values (Thomas et al. 2015). Tailwater fisheries are popular with anglers and can provide important spawning habitats and temperature refugia for certain fish species (Paragamian 1989; Pegg et al. 1996; Zale and Adornato 1996; Hutt and Bettoli 2007). However, changes in temperature and flow regimes below dams are often detrimental to native fishes, resulting in reduced abundance or extirpation of many species (Robinson et al. 1998; Freeman et al. 2001; Rolls et al. 2013). Where much work has been conducted on the effects of dams on fish populations and community dynamics (Kinsolving and Bain 1993; Shea and Peterson 2007; Jacobson and Galat 2008), less attention has focused on the dynamics of sportfish living under similar conditions. Recruitment of fishes is often related to variation in water discharge and levels in lotic systems (Tyus 1990; Lobon-Cervia 2004; Bonvechio and Allen 2005). For some species, floods and high-water events trigger spawning activities (Tyus 1990; Naesje et al. 1995; Baker et al. 2009), whereas for others, these same events can destroy nests and displace larvae through advection, resulting in lower recruitment (Jennings and Philipp 1994; Mallen-Cooper and Stuart 2003; Smith et al. 2005; Young et al. 2011). Variable water releases from upstream dams can complicate these relationships, interfering with spawning cues or introducing periodic high discharges during seasons when river discharges are normally low and stable, thereby increasing larval and juvenile mortality (Rulifson and Manooch 1990; Freeman et al. 2001; Young et al. 2011; Rolls et al. 2013).

Growth of fishes can be influenced by unnatural and natural flow regimes. Weisberg and Burton (1993) assessed growth of White Perch Morone americana before and after establishment of a minimum flow on the Susquehanna River, Maryland, and found that increasing the minimum flow increased first-year growth of White Perch. Larval growth rates of American Shad Alosa sapidissima in the Connecticut River increased asymptotically with declining discharges, but there was no relationship with juvenile growth rates (Crecco and Savoy 1985). Additionally, Jensen and Johnsen (2002) found that growth of Atlantic Salmon Salmo salar decreased in years with higher spring discharges in Norway. Many growth studies focused on larval and juvenile life stages, and important rearing habitats for these life stages are floodplains (Dudley 1974; Schlosser 1991; Sommer et al. 2001; Balcombe et al. 2007; Jeffres et al. 2008). Often, floodplain habitat is only connected to the stream during periods of higher discharges, and the lack of connectivity could influence growth (Sommer et al. 2001). These studies provide some evidence that fish growth can be influenced by river hydrology, but there is a need for similar research focused on warmwater sportfish.

Black bass (Micropterus spp., Centrarchidae) are popular sportfish worldwide and the principal group sought by U.S. anglers. In 2011, anglers spent U.S. $456 million and $872 million on recreational fishing in Alabama and Georgia, respectively, and black bass species were the most targeted fish in both states (U.S. DOI et al. 2014). Both states support important river fisheries for black bass. In 2011, three times as many Americans participated in freshwater recreational fishing than marine recreational fishing (U.S. DOI et al. 2014). Of the estimated 516,000 people that fished Alabama’s freshwater systems in 2011, 45% fished rivers and streams, spending more than $205 million (U.S. DOI et al. 2014). Likewise, in Georgia, an estimated 829,000 anglers fished in freshwater in 2011, and 42% fished in rivers and streams, spending more than $366 million. Thus, recreational fishing on rivers and streams is important to the economies of both Alabama and Georgia, and understanding the dynamics of lotic sportfish populations is important to sustain these resources.

Black bass are nest spawners that continue to guard larvae for a period of 1–3 weeks after spawning (Boschung and Mayden 2004). As such, recruitment of these species is particularly vulnerable to hydrologic disturbance, whether due to high discharges in lotic systems or fluctuating water levels in reservoirs or natural lakes (Maceina and Betolli 1998; Sammons et al. 1999; Bonvechio and Allen 2005; Smith et al. 2005). Although Micropterus species are often associated with lentic environments, several species are obligate lotic specialists (Koppelman and Garrett 2002). However, the effects of dam operation on downstream black bass fisheries are rarely evaluated. Likewise, fluctuations in natural river discharges can also affect spawning dynamics of black bass but are rarely examined. Therefore, we evaluated the effects of variable river discharges on successful hatching and growth of age-0 black bass in two medium-sized rivers in the southeastern United States, one with an altered flow regime and the other with a natural flow regime. Both rivers support popular black bass fisheries. In each river, we examined growth and hatch-date distribution of a fluvial specialist and generalist black bass species. We hypothesized that growth and hatch date of age-0 black bass would be more influenced by discharges in the regulated river than in the unregulated river. Furthermore, we hypothesized that fish in the river with the altered flow regime that were collected in unregulated areas would have faster growth and more continuous hatch distributions than those collected in regulated areas. Finally, we hypothesized that discharges in each river would have
less of an effect on growth and hatch-date distribution in fluvial specialists than in generalists.

Study sites

The Flint River, a major tributary to the Apalachicola River, flows 565 km from its headwaters near Atlanta, Georgia, to its confluence with the Chattahoochee River at Lake Seminole (Figure 1). The upper reaches of the Flint River flow through the piedmont region of Georgia and are characterized by a series of wide, granite shoal areas with shallow water and fast current interspersed with narrower run and pool areas with deep water and low velocity. 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 sandy substrate with some limestone outcroppings, higher amounts of woody debris present in the channel, and high base discharges due to groundwater inputs. The Flint River flows over 320 km before the first of three mainstem impoundments, making it 1 of only 42 rivers in the United States with 200 km of unimpeded flow (Benke 1990). We conducted this research in the unregulated reach within both the piedmont (upper; Fup) and coastal plain (lower; Flow) ecoregions of Georgia (Figure 1). Discharge patterns in both areas approximated normal seasonal patterns, with discharges greater in the winter and spring and lower in the summer and fall. As expected, over all seasons, discharge was 5–10 times greater in the lower reach (Figure 2).

The Tallapoosa River originates in northwestern Georgia and flows 426 km southwest to its confluence with the Coosa River where it forms the Alabama River (Figure 1). The upper 172 km of river are unregulated before reaching Lake Wedowee formed by R. L. Harris Dam, the first of four hydroelectric dams on the Tallapoosa River. Harris Dam provides electricity, water supply, flood control, and recreational opportunities. Below Harris Dam, peaking hydropower discharge drastically alters the natural flow regime of the river, with discharge varying over tenfold. Hydropeaking usually occurs daily, depending on the availability of water. During the summer months, hydropower production from Harris Dam is less frequent due to a limited supply of water.

We conducted this research at two reaches in the 79-km regulated section of river between Harris Dam and Lake Martin and at a reference reach in the unregulated section of river above Lake Wedowee near the town of Heflin, Alabama (Figure 1). The upper regulated reach (middle; Tmid) was located 17–22 km downstream of Harris Dam and was characterized by highly variable discharges (Figure 2). The lower regulated reach (lower; Tlow) was located 42–46 km further downstream where dam releases had attenuated, and discharges were less variable. The unregulated reach (upper; Tup) was more than 50 km above the headwaters of Lake Wedowee (Figure 1) and was characterized by a relatively stable flow regime (Figure 2). All study sites were in the piedmont ecoregion of Alabama and had a relatively constant gradient of 0.64 m/km. However, stream geomorphology differed in each reach. The unregulated reach was characterized by a relatively narrow channel, approximately 15–50 m wide, with numerous sand and gravel bars. Substrate was mainly composed of coarse silt, gravel, and interspersed short stretches of bedrock and boulder. The two regulated reaches were characterized by large shoal complexes up to 1 km long, pools, and a wide channel (50–185 m). Substrate was predominately bedrock, boulder, and coarse silt. Discharge volumes steadily increased progressively downstream (Figure 2).

Both rivers occupy similar physiographic areas and have similar drainage areas (Table 1). Five-year mean discharge of the Flint River was generally lower than the Tallapoosa River, possibly due to pervasive water withdrawals for municipal and agricultural use (Viger et al. 2011). As expected, mean daily discharge variability was higher in the regulated reaches of the Tallapoosa River than in the unregulated reach of the Tallapoosa River or any reach of the Flint River (Table 1). Discharges during the putative spawning period for the study species followed a typical rise and fall pattern in the two regulated reaches of the Tallapoosa River, whereas
Figure 2. Discharge (m³/s) from April 1, 2010, to June 1, 2010, from two U.S. Geological Survey gauges on the Flint River (15-min intervals), Georgia, and three gauges on the Tallapoosa River (30-min intervals), Alabama.
Discharges were more stable in the unregulated reach above Lake Wedowee (Figure 2). Discharge variation in Flint River was much lower than that found in the regulated reaches of the Tallapoosa River and was greater in Fup than in Flow.

### Methods

#### Study species

In this work, we focused on the principal native black bass species found in each river that are important to the recreational fishery in each area. Alabama Bass *Micropterus henshalli* (Figure 3) are endemic to the Mobile Basin, including the Tallapoosa River (Baker et al. 2008). They are widely distributed throughout the system in both lotic and reservoir systems. Redeye Bass *M. coosae* (Figure 3) are fluvial specialists endemic to the Mobile Basin, are primarily distributed above the Fall Line in small- to medium-sized upland streams, and are intolerant of reservoirs (Boschung and Mayden 2004; Leitner and Earley 2015). Shoal Bass *M. cataractae* (Figure 3) is a species endemic to the Apalachicola drainage, including the Chattahoochee and Flint river systems in Alabama, Florida, and Georgia. They are fluvial specialists, occupying shallow rocky areas in medium- to large-sized streams and rivers, and are intolerant of reservoir conditions (Boschung and Mayden 2004; Sammons et al. 2015). Largemouth Bass *M. salmoides* has the broadest distribution of the genus, with a native range stretching from the Great Lakes to the southeastern United States and westward to Texas (Boschung and Mayden 2004). The species has also been stocked far outside its native range throughout North America and around the world (Jackson 2002). Largemouth Bass are highly adaptable and occupy a wide diversity of habitats, from slow streams to large reservoirs and natural lakes (Boschung and Mayden 2004).

#### Fish collection and processing

We collected fish from the two regulated areas on the Tallapoosa River and all areas on the Flint River within a <5-km reach; however, we collected fish in T_{up} over a 25-km reach of river due to low catch rates. We collected all fish over a 3-wk period in July–August each year using a DC backpack electrofishing unit, seine, or a boat electrofishing unit with a hand-held anode (Sammons et al. 1999). We determined the timing of sampling to ensure that all fish were less than 90 d old to lessen the chance of aging errors (Buckmeier et al. 2017). We made collections of Shoal Bass and Largemouth Bass on the Flint River in 2008–2010, whereas we made collections of...
Table 2. Mean total length, hatch dates (first, mean, and last), hatching duration, mean incremental growth, and standard error of Largemouth Bass Micropterus salmoides and Shoal Bass M. cataractae in two reaches (upper and lower) of the Flint River, Georgia, over 3 y. Mean hatch dates and incremental growth rates with the same letter were similar (t-test, \( P > 0.05 \)) among reaches within each species in 2008 and 2009. Only the lower reach was sampled in 2010.

| Year | Species | Area | N  | TL (mm) | First | Mean  | Last | Dur (d) | Growth (mm/d) | SE  |
|------|---------|------|----|---------|-------|-------|------|---------|--------------|-----|
| 2008 | LMB     | UP   | 59 | 46      | March 21 | April 17 a | May 19 | 59      | 0.64 b       | 0.01|
|      |         | LO   | 33 | 48      | April 16  | April 27 b | May 16 | 30      | 0.69 a       | 0.02|
|      | SHB     | UP   | 49 | 63      | April 21  | May 2 b    | May 19 | 26      | 0.82 a       | 0.02|
|      |         | LO   | 56 | 52      | April 9   | April 26 a | May 10 | 31      | 0.74 b       | 0.02|
| 2009 | LMB     | UP   | 37 | 53      | March 17  | April 26 a | June 5  | 80      | 0.68 a       | 0.02|
|      |         | LO   | 69 | 50      | March 27  | April 26 a | May 23 | 57      | 0.64 a       | 0.01|
|      | SHB     | UP   | 73 | 58      | April 4   | April 30 a | May 12 | 38      | 0.79 a       | 0.01|
|      |         | LO   | 19 | 54      | April 24  | May 3 b    | May 14 | 20      | 0.73 b       | 0.01|
| 2010 | LMB     | UP   | 87 | 54      | March 23  | April 14   | May 18 | 56      | 0.69         | 0.01|
|      |         | LO   | 57 | 57      | March 24  | April 13   | May 8  | 45      | 0.72         | 0.01|

Dur = hatching duration; LMB = Largemouth Bass Micropterus salmoides; LO = lower; SE = standard error; SHB = Shoal Bass M. cataractae; TL = total length; UP = upper.

Data analyses

We examined hatch-date distributions for each species–reach–year combination in each river and compared them with the flow regime during hatching. We assessed differences in mean hatch date and mean growth rates among reaches for each species–year combination using analysis of variance tests or t-tests (SAS Institute 2012). We examined relations between incremental growth and hatch date for each species–reach combination using linear regression (SAS Institute 2012). We calculated discharge variation (variance of discharge) for the interval beginning at the estimated hatch date and ending the day before capture for each fish. Due to instances of low sample sizes in certain species–reach–year combinations, we pooled data across years. Also, we standardized variances of discharge to vary from 0 to 1 to better assess discharge variations across years, rivers, and reaches. We plotted relations between daily growth rate (mm/d) and discharge variation experienced by each fish from hatch until collection and examined the data for all species in each reach–year combination using Pearson correlations (SAS Institute 2012). We conducted all statistical analyses using \( P = 0.05 \) for significance.

Results

Flint River Largemouth Bass and Shoal Bass

During this study, in the Flint River we collected 287 Shoal Bass, with TL values ranging from 24 to 92 mm (mean = 57 mm), and a total of 288 Largemouth Bass, with TL values ranging from 23 to 86 mm (mean = 51 mm). Mean TL varied across years and areas from 52 to 63 mm for Shoal Bass and from 46 to 54 mm for Largemouth Bass (Table 2). We met the sample goal of at least 50 fish collected per reach per year in most instances, although we collected only 19 Shoal Bass from Flow in 2009 (Table 2; Data S1, Supplemental Material). Black bass hatch dates ranged across species and reaches from March 21 to May 19, March 17 to June 5, and March...
23 to May 18 in 2008, 2009, and 2010, respectively. Other than Shoal Bass in 2008, both species began hatching earlier in Fup than in Flow. Mean hatch date was earlier in Fup for Largemouth Bass in 2008 and Shoal Bass in 2009 (t = 3.40 to 4.35, P < 0.01), but the reverse was true for Shoal Bass in 2008 (t = 4.70, P < 0.01), and mean hatch dates were similar among reaches for Largemouth Bass in 2009 (Table 2; t = 0.11, P = 0.91). Largemouth Bass usually began hatching 3–4 weeks earlier than Shoal Bass in both areas in 2008 and 2009. Hatch duration of Largemouth Bass was more than twice that of Shoal Bass in Fup and Flow in 2009 and 24% longer in Flow in 2010, but hatch duration was essentially equal between the species in Flow in 2008 (Table 2). Also, hatching duration of Largemouth Bass was considerably longer in Fup than in Flow in 2008 and 2009. The same was true for Shoal Bass in 2009 but was 5 d longer in Flow in 2008 (Table 2).

Hatch distribution of Largemouth Bass generally indicated that successful hatching occurred once water levels stabilized in most areas and years (Figure 4). However, successful hatching occasionally occurred during spates, particularly in Flow. By contrast, successful hatching of Shoal Bass rarely occurred during spates, and almost all Shoal Bass hatched after water levels stabilized (Figure 4). Hatch distribution of both species was generally continuous; thus, few instances of spawning disruption were detected during this study. However, we observed significant discontinuity in the Largemouth Bass hatching distribution at Fup in 2009, including both during and after large water spates moved through the system. We found that one Shoal Bass hatched in early April 2009 in Fup during a high discharge event, followed by several more hatching in mid- to late April during a smaller spate, but the majority of the fish hatched once water levels stabilized later in the year (Figure 4).

Mean daily incremental growth of both species varied between 0.64 and 0.82 mm/d across reaches and years, and generally Shoal Bass growth was greater than Largemouth Bass. Shoal Bass growth was higher in Fup than Flow in both years (t = 3.39 to 3.63, P < 0.01), whereas for Largemouth Bass, the reverse was true in 2008 (t = 2.54, P = 0.01) and was similar between reaches in 2009 (Table 2; t = 1.94, P = 0.06). Incremental growth was not related to hatch date (r² ≤ 0.03, P ≥ 0.09) for seven of ten species–year–reach combinations; however, later-hatched fish showed small increases in growth for Largemouth Bass in Fup in 2008 (r² = 0.35, P < 0.001) and in Flow in 2009 (r² = 0.22, P < 0.0001) and for Shoal Bass in Flow in 2010 (r² = 0.21, P = 0.0003). Daily growth of age-0 Largemouth Bass in Fup was highly variable at low discharge variances but was characterized by lower than average growth at higher discharge variability (Figure 5). No such pattern was observed in Flow. Growth was inversely correlated to variance of discharge in Fup but not in Flow (Figure 5). Shoal Bass growth was variable but displayed no consistent patterns with discharge variation and was not correlated with discharge variance in either reach.

**Tallapoosa River Alabama Bass and Redeye Bass**

In the Tallapoosa River, we collected 311 Alabama Bass from 33 to 95 mm in TL (mean = 60 mm) and 221 Redeye Bass from 32 to 79 mm in TL (mean = 51 mm). Mean TL varied across years and areas from 55 to 68 mm for Alabama Bass and from 48 to 59 for Redeye Bass (Table 3). It was more difficult for us to collect age-0 black bass in the Tallapoosa River than in the Flint River; thus, we reached the sampling goal of at least 50 fish per reach and year only 6 of 12 times (Table 3; Data S1, Supplemental Material). It was especially difficult for us to collect Redeye Bass in Tmid, where discharge was most variable (Figure 2). Nonetheless, age-0 black bass hatched across areas and species from April 5 to June 28 and from April 24 to June 8 in 2010 and 2011, respectively (Table 3). Both species hatched later in Tup than the two regulated reaches (Tmid and Tlow) in 2010, but this was not the case in 2011. In 2010, mean hatch date of Alabama Bass was almost a month later in Tup than Tlow and almost 20 d later than in Tmid (Table 3; F = 15.69, df = 2,87, P < 0.01). Likewise, the Redeye Bass mean hatch date was earliest in Tlow and progressively later in Tmid and Tup (F = 137.95, df = 2,85, P < 0.01). However, in 2011, the mean hatch date of Alabama Bass in Tmid was 4 and 7 d later than those in Tlow or Tup, respectively (Table 3; F = 8.46, df = 2,218, P < 0.01). Also in 2011, the Redeye Bass mean hatch date was 9 d earlier in Tlow than in Tmid or Tup (F = 14.22, df = 2,130, P < 0.01). Hatch duration varied from 18 to 80 d across reaches, years, and species, but were between 34 and 52 d for most individuals (Table 3). There were no obvious differences between species or reaches.

Successful hatching of Alabama Bass in Tup generally began after water levels were low and stable (Figure 6). A small spate came through the system just after hatching began in 2010, which may have resulted in a short disruption of successful hatching, but low sample size makes this conclusion tenuous. In 2010, hatching of Alabama Bass in Tmid was extended and discontinuous, which matched the variable discharge pattern observed during that time (Figure 6). Water levels were more stable in 2011, and hatching distribution was more continuous; however, all successful hatching occurred after water levels stabilized. By contrast, Alabama Bass hatching distributions were mostly continuous in Tlow in both years, even during sudden spates moving through the system (Figure 6). Redeye Bass hatching distributions followed a similar pattern to those described above for Alabama Bass. Hatching was more or less continuous in all reaches both years, although few age-0 Redeye Bass were collected in Tmid either year, making assessment difficult (Figure 7). Like Alabama Bass, the sudden spate of water moving through Tlow in 2010 did not appear to affect hatching distribution of Redeye Bass. However, virtually all successful Redeye Bass hatching occurred during stable water periods in all three reaches and in both years, similar to Alabama Bass (Figure 7).
Figure 4. Hatch-date distributions (5-d groups) of Largemouth Bass *Micropterus salmoides* and Shoal Bass *M. cataractae* in two reaches of the Flint River, Georgia, in 2008–2010. Lines represent mean daily discharge recorded by U.S. Geological Survey gauges near the collection sites in each area. Note different scales on discharge axes.
Figure 5. Daily incremental growth versus variance of discharge from hatch date until the day before collection of Largemouth Bass *Micropterus salmoides* and Shoal Bass *M. cataractae* from two reaches of the Flint River, Georgia, in 2008–2009. The dotted line denotes overall mean growth for that reach–species combination.
Table 3. Mean total length, hatch dates (first, mean, and last), hatching duration, mean incremental growth, and standard error of Alabama Bass Micropterus henshalli and Redeye Bass M. coosae in three reaches (unregulated, upper regulated, and lower regulated) of the Tallapoosa River, Alabama, over 2 y. Mean hatch dates and incremental growth rates with the same letter were similar (Tukey’s test, $P > 0.05$) among reaches within each year and species combination.

| Year | Species | Area    | N  | TL (mm) | First    | Mean   | Last   | Dur (d) | Growth (mm/d) | SE   |
|------|---------|---------|----|---------|----------|--------|--------|---------|---------------|------|
| 2010 | ALB     | UNR     | 13 | 55      | May 25   | June 7 b| June 17| 23      | 0.88 a        | 0.02 |
|      |         | URE     | 24 | 68      | April 5  | May 18 a| June 24| 80      | 0.82 ab       | 0.01 |
|      |         | LRE     | 50 | 64      | April 15 | May 11 a| June 6 | 52      | 0.76 b        | 0.02 |
|      |         | REB     | 34 | 49      | June 1   | June 8 c| June 19| 18      | 0.76 a        | 0.01 |
|      |         | URE     | 11 | 48      | May 10   | June 3 b| June 28| 49      | 0.76 a        | 0.02 |
|      |         | LRE     | 38 | 59      | April 15 | May 11 a| May 21 | 36      | 0.75 a        | 0.01 |
|      | ALB     | UNR     | 78 | 57      | April 26 | May 14 a| June 6 | 41      | 0.72 ab       | 0.01 |
|      |         | URE     | 62 | 59      | May 4    | May 20 b| June 8 | 35      | 0.74 a        | 0.01 |
|      |         | LRE     | 82 | 58      | April 26 | May 16 a| June 6 | 41      | 0.69 b        | 0.01 |
|      |         | REB     | 47 | 48      | April 24 | May 18 b| June 6 | 43      | 0.63 b        | 0.01 |
|      |         | URE     | 19 | 56      | May 2    | May 18 b| June 5 | 34      | 0.70 a        | 0.02 |
|      |         | LRE     | 67 | 50      | April 9  | May 9 a | June 5 | 57      | 0.61 b        | 0.01 |

ALB = Alabama Bass Micropterus henshalli; Dur = hatching duration; LRE = lower regulated; REB = Redeye Bass M. coosae; SE = standard error; TL = total length; UNR = unregulated; URE = upper regulated.

Mean daily incremental growth varied between 0.61 and 0.88 mm/d across reaches, years, and species and was generally greater for Alabama Bass than for Redeye Bass within each year–reach combination (Table 3). Alabama Bass growth in 2010 was highest in $T_{up}$ and lowest in $T_{low}$ ($F = 11.68$, df = 2,85, $P < 0.01$), whereas growth in 2011 was highest in $T_{mid}$ and lowest in $T_{low}$ ($F = 4.90$, df = $2,218$, $P < 0.01$). Redeye Bass growth was similar among reaches in 2010 ($F = 0.55$, df = 2,85, $P = 0.58$) but was higher in $T_{mid}$ than $T_{up}$ and $T_{low}$ in 2011 (Table 3; $F = 12.72$, df = 2,130, $P < 0.01$). Alabama Bass growth was not related to hatch date at $T_{up}$ and $T_{mid}$ in either year ($r^2 = 0.09–0.16$, $P > 0.05$) but was slightly higher for later-hatched fish at $T_{low}$ in both years ($r^2 = 0.28–0.46$, $P < 0.0001$). Redeye Bass growth followed a similar pattern with no relation with hatch date at $T_{up}$ and $T_{mid}$ in either year ($r^2 < 0.05$, $P > 0.21$) but was slightly higher for later-hatched fish at $T_{low}$ in both years ($r^2 = 0.09–0.16$, $P = 0.0245$). Alabama Bass growth in $T_{up}$ and $T_{mid}$ displayed similar patterns of variable growth at high discharge variation but faster than average growth at lower variation (Figure 8). Conversely, in $T_{low}$, Alabama Bass growth was variable at lower discharge variation and was lower than average at higher variation. Redeye Bass growth at $T_{up}$ was highest than average at lower discharge variation and lower than average at higher variation (Figure 8). A similar pattern was evident at $T_{mid}$ although that sample suffered from low sample sizes. Conversely, no growth pattern was evident in relation to discharge variability at $T_{low}$. Overall, black bass growth was negatively correlated with discharge variance in five of six reach–species combinations (Figure 8).

Discussion

Accurate estimates of daily growth and hatch dates depend on the assumption that growth rings on age-0 fish otoliths are formed as daily increments. The formation of daily growth rings was validated for several centarchid species, including Largemouth Bass (Miller and Stork 1982), Smallmouth Bass Micropterus dolomieu (Graham and Orth 1987), Spotted Bass Micropterus punctulatus (DiCenzo and Bettoli 1995), and Redspotted Sunfish Lepomis miniatus (Roberts et al. 2004). Long et al. (2006) likewise assumed daily ring formation for Shoal Bass collected from hatchery ponds in Georgia; further study demonstrated relatively accurate age determination for daily ages of Shoal Bass up to 60 d old (Long and Porta 2019). Although daily growth rings have not been verified for age-0 Alabama Bass or Redeye Bass, we assumed that increments were formed at daily intervals as in other centarchid species. Further, like most studies on age-0 black bass, we assumed ring formation in our study species began at swim up (i.e., 5 d), following Graham and Orth (1987). However, Hill and Bestgen (2014) reported the first ring to form at hatch for Smallmouth Bass. The timing of first ring formation obviously has implications for estimating hatch dates and calculating incremental growth (Buckmeier et al. 2017), and further study is needed to better understand the timing of first ring deposition in black bass.

Successful hatching of Micropterus species in both rivers generally occurred in mid- to late spring when water levels became low and stable. We would expect this for nest-spawning species, such as black bass, and similar results were observed for lotic populations of Smallmouth Bass (Reynolds and O’Bara 1991; Lukas and Orth 1995; Dauwalter and Fisher 2007). Sabo and Orth (1995) noted that Smallmouth Bass in the North Anna River, Virginia, spawned later during a wet year than during a dry year. Early hatched fry are exposed to a longer growing season than late-hatched fry, 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). However, Smallmouth Bass in the North Anna River, Virginia, exhibited compensatory growth, wherein later-hatched individuals grew faster than those who hatched earlier in cooler temperatures; thus, by mid-summer, individuals from all cohorts were characterized by similar lengths.
Figure 6. Hatch-date distributions (5-d groups) of Alabama Bass *Micropterus henshalli* in three reaches of the Tallapoosa River, Alabama, in 2010 and 2011. Lines represent mean daily discharge recorded by U.S. Geological Survey gauges near the collection sites in each reach. Note different scales on discharge axes.
Figure 7. Hatch-date distributions (5-d groups) of Redeye Bass *Micropterus coosae* in three reaches of the Tallapoosa River, Alabama, in 2010 and 2011. Lines represent mean daily discharge recorded by U.S. Geological Survey gauges near the collection sites in each area. Note different scales on discharge axes.
Figure 8. Daily incremental growth versus variance of discharge from hatch date until the day before collection of Alabama Bass *Micropterus henshalli* and Redeye Bass *M. coosae* from three reaches of the Tallapoosa River, Alabama, in 2010 and 2011. The dotted line denotes overall mean growth for that reach–species combination.
(Sabo and Orth 1995). Likewise, variable weather patterns or cold water temperatures during the spawning season can result in greater mortality of early hatched fry (Kramer and Smith 1962; Siefert 1968; Sabo and Orth 1995; Mion et al. 1998; Garvey et al. 2002). Thus, early hatching may be disadvantageous for black bass in the unregulated Flint River, resulting in higher mortality due to environmental conditions, such as spring flooding events and variable water temperature. Mion et al. (1998) found that larval Walleye *Sander vitreus* survival was strongly related to discharge levels; Walleye that hatched during high discharge events exhibited low survival. Most successful spawning of Smallmouth Bass in the North Anna River, Virginia, occurred during low-discharge periods following large spates (Sabo and Orth 1995), similar to what we observed in our study.

In contrast to the other species, Largemouth Bass in the Flint River often hatched during flooding, especially in *T*up. Largemouth Bass usually spawn in protected areas characterized by firm substrate and vegetation or woody debris cover (Kramer and Smith 1962; Bruno et al. 1990; Nack et al. 1993). Gocłowski et al. (2013) noted that Largemouth Bass and Shoal Bass in the Flint River migrated to shoal habitats during the spawning season, although only Shoal Bass appeared to spawn within the shoals. Largemouth Bass commonly spawn in backwaters and off-channel pockets in rivers (Nack et al. 1993; Raibley et al. 1997) and thus may be able to successfully spawn during floods. However, the other three black bass species that we examined in this study spawn in the main channel and are therefore vulnerable to spates disrupting successful spawning events (Bitz et al. 2015; Earley and Sammons 2015). This may be a strategy to minimize predation on nests, as main-channel habitats typically contain lower densities of potential egg and larval predators (Dauwalter and Fisher 2007).

Extreme water-level fluctuations disrupt black bass spawning in reservoirs and rivers (Summerfelt 1975; Reynolds and O’Bara 1991; Kohler et al. 1993; Lukas and Orth 1995; Sabo and Orth 1995; Knotek and Orth 1998). Hatching distributions of Largemouth Bass and Shoal Bass in the Flint River and Redeye Bass in the Tallapoosa River were generally unimodal, with few if any disruptions of successful hatching noted, even during spates moving through the system. However, hatch distribution of Alabama Bass in the most-regulated reach of the Tallapoosa River (i.e., *T*mid) appeared to be disrupted by large spates of water moving through the system in 2010, leading to a bimodal distribution. By contrast, hatch distribution of this species was more continuous in the other reaches in 2010 and in all reaches in 2011, when discharges were lower and more stable. Similarly, spring and summer discharges in the Flint River were also generally below average during all 3 y of the study due to extended drought conditions. In earlier studies on the Tallapoosa River, Andress (2001) and Martin (2008) observed spawning disruptions of two centrarchid species due to hydropoaking operations during years of more normal rainfall. During years of extensive flooding, water discharges may exert a greater influence on hatching distributions of black bass in both rivers (Reynolds and O’Bara 1991; Lukas and Orth 1995; Sabo and Orth 1995). However, our data indicated that only large discharges occurring during the spawning season are likely to result in population-level impacts in the hatching of these species. Successful recruitment of riverine fishes is commonly tied to water levels, with low recruitment noted in years with high-water events occurring during or immediately after the spawning period (Mason et al. 1991; Mallen-Cooper and Stuart 2003; Bonvechio and Allen 2005; Smith et al. 2005). By contrast, recruitment of Alabama Bass, Shoal Bass, and Redeye Bass was generally unaffected by discharge in these rivers, whereas Largemouth Bass recruitment in the Flint River was negatively related to higher discharges during the spawning season (Sammons et al. 2013; Sammons et al. 2019).

Growth of black bass in the Flint and Tallapoosa rivers was similar to those observed for other *Micropterus* species in lentic systems (Phillips et al. 1995; Sammons et al. 1999; Greene and Maceina 2000; Long and Fisher 2003). Daily growth rates of black bass species other than Largemouth Bass are little studied, but growth rates of age-0 Shoal Bass, Redeye Bass, and Alabama Bass documented in our study appeared to be relatively high compared with estimates reported for Spotted Bass and Smallmouth Bass (Sabo and Orth 1995; Sammons et al. 1999). It is somewhat surprising that daily growth of age-0 black bass in a river would approximate or exceed those found in lentic systems given the added metabolic costs of existing in flowing water; however, this matches the annual growth observed for these species in both rivers (Earley and Sammons 2018; Sammons et al. 2019). Johnston and Kennon (2007) found that larval and juvenile Shoal Bass commonly used current refuges and areas of low current in an Alabama stream. Similarly, Earley and Sammons (2015) showed that adult Redeye Bass and Alabama Bass in the Tallapoosa River were in areas of low current even during base flow and commonly used current refugia during hydropoaking discharges from Harris Dam. Possibly, these species use feeding strategies of using current refuge as ambush areas to take advantage of macroinvertebrate drift, thereby minimizing metabolic costs, as has been described for other riverine species (MacDonald et al. 1987; Simonson and Swenson 1990; Childs et al. 1998).

Flow regulation through Harris Dam on the Tallapoosa River would be expected to disrupt natural patterns in productivity, fish densities, and growth (Young et al. 2011; Rolls et al. 2013). We expected slower growth of age-0 black bass at the regulated sites due to reduced feeding opportunities, physiological stress due to rapidly changing water depth, velocity, and temperature (Martin 2008) and an impoverished macroinvertebrate community in terms of abundance and diversity (Haxton and Findlay 2008). In 2010, the mean daily growth rate of Alabama Bass was greater in *T*up than in the two regulated reaches, whereas Redeye Bass growth was similar across reaches. However, in 2011, growth of both black bass species was highest in *T*mid, which could have been caused by density-dependent mechanisms as catch rates of juvenile black bass in that reach were low.
compared with the other reaches (Sammons et al. 2013). Also, the low discharges that characterized 2011 may have minimized the impacts of Harris Dam releases on the aquatic community, as theorized by Freeman et al. (2001), resulting in the differences in spatial patterns in growth of these species observed between 2010 and 2011. Sabo and Orth (1995) noted that annual variation in temperature and discharge can override other ecological factors governing growth of age-0 fishes.

Temperature data were not available for these study areas during the years of our study, but temperature is a well-known environmental variable that impacts growth of fishes (Beitinger and Fitzpatrick 1979; Imsland et al. 1996; Deegan et al. 1999). Irwin and Freeman (2002) documented that water temperatures in the Tallapoosa River below Harris Dam can fluctuate up to 10°C during generation events; however, 2019–2020 data from the USGS gauges demonstrated that water temperatures only varied an average of 3°C over a 24-h period over April–July at Tmid. Water temperatures only varied an average of 2°C at Tlow, during this same period. Similar data are not available from the Flint River, but given the natural flow regime in that river, 24-h temperature differences were likely smaller than in the Tallapoosa River. Therefore, we believe that undescribed temperature variation among sites and years in our study was likely only a minor confounding variable. However, future studies of this type should make every effort to account for temperature fluctuations in the study systems, even if the researchers must measure temperatures themselves.

Highly variable discharges, whether from natural or anthropogenic sources, disrupt feeding and food supplies and can cause direct mortality through physical trauma (Bunn and Arthington 2002; Young et al. 2011; Rolls et al. 2013). Large discharge variation negatively affected the growth of age-0 black bass in both rivers, but to a lesser extent than we expected. In the Flint River, low to moderate discharge variation did not have an appreciable effect on the growth of black bass, but slower growth of Largemouth Bass in Fup appeared to be associated with high discharge variation. This corresponded with hatch distributions of the species, as Largemouth Bass was the only species that we found hatched during high-water events. However, in the Tallapoosa River, growth of both species was negatively affected by highly variable river discharges, and we often observed higher than average growth at lower discharge variances. Although feeding habits of most of the study species are not well studied, based on studies of other black bass species, it seems likely that these age-0 fish were mostly insectivores (George and Hadley 1979; Easton and Orth 1992; Sutton and Ney 2002; Dauwalter and Fisher 2008; Sammons 2012). Variable discharges resulting from hydropower operation can reduce abundance and diversity of benthic macroinvertebrates in streams (Cushman 1985; Shaw and Richardson 2001), ultimately leading to reduced growth of fishes (Young et al. 2011; Rolls et al. 2013).

Hydropower discharges in the Tallapoosa River likely influenced hatch distribution and first-year growth of Alabama Bass and Redeye Bass to some degree. In Tmid, there was a greater effect on hatching distribution and growth of both species than what was observed in Tlow where discharge variation was more muted. Further, hatching distribution of both species in 2010 (the wetter of the two years) followed a more typical pattern in Tup and Tlow with a single mode and generally narrow duration compared with the more regulated Tmid where hatching was characterized by broader, disjointed, and bimodal distributions. These patterns may indicate that the attenuated discharges that characterize the farther downstream Tlow reach more closely resemble the unregulated Lup reach above Lake Wedowee and provide better spawning conditions than the more variable discharges experienced in the highly regulated Tmid reach close to Harris Dam.

Our results suggested that growth of Shoal Bass, a fluvial specialist, was unaffected by natural discharge variation in the Flint River during our study, but growth of Largemouth Bass, a less flow-adapted species, can be lower when fish were exposed to highly variable discharges. By contrast, highly variable discharge in the Tallapoosa River negatively affected the growth of both Redeye Bass, a fluvial specialist, and Alabama Bass, a generalist species. In the regulated reaches of the river, this was more apparent in the reach with the greater amount of discharge variability. However, the fact that we observed the largest discharge effects on growth for both Alabama Bass and Redeye Bass in the unregulated reach suggests that possibly neither species are as flow adapted as Shoal Bass. Regardless, these negative growth effects were likely too small to alter population-level growth rates of these species in either river, as most individuals were hatched once water levels declined and were more stable. Whether this was due to active selection on the part of the parents or a product of earlier-spawned fish suffering high mortality or nest failure (Lukas and Orth 1995; Knotek and Orth 1998; Dauwalter and Fisher 2007) was beyond the scope of our study. Finally, results from this study suggest that variable discharge has less of an impact on successful reproduction of black bass than was reported for other fishes (Freeman et al. 2001; Mallen-Cooper and Stuart 2003; Shea and Peterson 2007; Young et al. 2011), but growth may be more affected by discharges resulting from anthropogenic sources than those associated with more natural flow regimes.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Supplemental data for all the analyses detailed in this study can be found in the file “Age-0 Bass and Discharge Relations Supplemental Data.xlsx”. This file contains the sample river, year (YY), species (SPP; LMB, Largemouth Bass Micropterus salmoides; SHB, Shoal Bass M. cataractae; ALB, Alabama Bass M. henshalli; REB,
Redeye Bass *M. coosae*), reach (as abbreviated in text), incremental growth (IN GROW; mm/d), hatch date, and the standardized variance of discharge experienced by each fish sampled (STD VAR of Q). This study was conducted on the Flint River, Georgia, from 2008 to 2010, and on the Tallapoosa River, Alabama, from 2010 to 2011.

Found at DOI: [https://doi.org/10.3996/JFWM-21-021.S1](https://doi.org/10.3996/JFWM-21-021.S1) (59 KB XLSX).

**Reference S1.** Sammons SM, Earley LA, McKee CE. 2013. Sportfish dynamics in the regulated portion of the Tallapoosa River between Harris Dam and Lake Martin, Alabama. Montgomery, Alabama: Final Report to Alabama Department of Conservation and Natural Resources.

Found at DOI: [https://doi.org/10.3996/JFWM-21-021.S2](https://doi.org/10.3996/JFWM-21-021.S2) (1.42 GB PDF).

**Acknowledgments**

Field and lab assistance was provided by Ryan Hunter, Matthew Marshall, Michael Shepherd, Tyler Thomas, Ian Palmer, Benjamin Hutto, Chris McKee, Alexandra Christopher, and Colin Dinken. Also, Jonathan Brown provided training and a second read of the otoliths that helped increase the accuracy of these data. Funding for this project was provided by the Alabama Department of Conservation and Natural Resources and Georgia Department of Natural Resources (Wildlife Resources Division). Comments by Michael Quist, two anonymous reviewers, and the Associate Editor improved this manuscript.

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