

**Spawning and Early Ecology of Riverine  
Shoal Bass and Largemouth Bass**

By  
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## Abstract

Understanding fish movements and early life-history requirements is important for managing populations because they reflect changing resource needs across the life cycle. Riverine black basses (genus *Micropterus*) hold significant economic and ecological importance, but knowledge of their reproductive and early life-history requirements is lacking relative to rapidly evolving species designations. Thus, my study objectives were to determine seasonal movement patterns and the factors related to early life-history success of endemic Shoal Bass, *M. cataractae*, and native Largemouth Bass, *M. salmoides*, in the lower Flint River catchment, Georgia. Adult black basses were tagged and tracked for 15 months using radio telemetry. I used generalized additive mixed modelling to determine how biotic and environmental factors related to movement patterns. Both species included stationary and mobile individuals with some mobile bass moving greater than 70 km in one direction. Movements increased during the spring which was presumably related to spawning activity. There were numerous locations of fish aggregations during the spring, particularly below a hydropower dam. Shoal Bass females moved longer distances than males. Largemouth Bass moved less during periods of variable discharge. I also collected age-0 Shoal Bass and Largemouth Bass to analyze hatch success and growth using a hurdle model framework and linear regression. Largemouth Bass hatch success was negatively related to water temperature but positively related to increasing discharge. Shoal Bass hatch success was negatively related to discharge variability and was higher during relatively stable flows on the descending limb of the hydrograph. It appears that hydropeaking flows may have affected hatch success of both species, particularly Shoal Bass. Discharge and temperature conditions explained more variability in daily growth for Shoal Bass compared to Largemouth Bass. My results indicate important species-specific relationships that influence movement patterns and successful hatching and underscore the importance of maintaining components of a natural flow regime. If the goal is to promote recruitment in these populations, then consideration of dam operations and examining the level of angler exploitation during important spawning times may be worth consideration by managers.

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## Chapter I

### Introduction and Research Objectives

Rivers and associated wetlands represent diverse environments that provide important ecosystem services but are threatened by a myriad of human activities. Freshwaters support a significant portion of global biodiversity (6% of all described species; Hawksworth and Kalin-Arroyo 1995) relative to their surface area (0.8% of the Earth's surface; Gleick 1996). As much as one third of all vertebrate fauna is contained within freshwaters (Dudgeon et al. 2006) with an even larger proportion of fauna depending on them (Grosberg et al. 2012). Humans also depend heavily on rivers and wetlands for drinking water, power generation, food production, natural water treatment, flood control, transportation, and recreation (Aylward et al. 2005). Despite their significance to human livelihoods, riverine ecosystems are among the most imperiled by human activities. Reid et al. (2019) estimated that an 83% decline in freshwater vertebrate populations occurred between 1970 and 2014. Flow regulation, over exploitation, pollution, land-use change, invasive species, climate change and associated interactions are all considered major threats to freshwater ecosystems (Dudgeon 2019). Impoundments are one of the largest threats to natural flows, fragmenting river corridors and habitat for many stream fish (Poff et al. 1997; Poff and Zimmerman 2010).

Dam construction affects many attributes of river ecosystems including species phenology and the successful completion of life cycles. Dams alter natural flow regimes (Poff 1997) and reduce connectivity of almost half of global river volume (Grill et al. 2015). This, in turn, isolates aquatic populations, alters habitat, and degrades hydrologic conditions for all life stages (Ligon et al. 1995; Guenther and Spacie 2006; Freeman et al. 2007; Hastings et al. 2016; Reid et al. 2019).

Distributions and abundances of migrating species have declined worldwide in part due to artificial barriers such as dams (Jager et al. 2001; Flowers et al. 2009; Deinet et al. 2020). Changes in water quality (Ahearn et al. 2005), thermal regime (Caissie 2006), and channel morphology (Ligon et al. 1995) resulting from impoundments affect lotic fauna. For example, Kondolf et al. (2014) estimated a 51% decrease in sediment deposition in the Mekong River, China would occur downstream of current and future dams. Correspondingly, rivers in the Pacific Northwest after dam construction were markedly cooler during summer and warmer during fall and winter which was hypothesized to affect Chinook salmon *Oncorhynchus tshawytscha* spawning phenology (Angilletta et al. 2008). Additionally, many life history traits of lotic fishes are cued by or related to aspects of a natural flow regime such as magnitude, rate of change, frequency, and timing of flows (Lytle and Poff 2004; Taylor and Cooke 2012). Thus, alteration of natural variability and patterns can disrupt the timing and success of key life-history events (Bunn and Arthington 2002; Pennock et al. 2022). For example, alteration of the timing and magnitude of peak and low flows by river regulation can reduce juvenile fish abundance and favor species that have less stringent spawning requirements (Poff et al. 1997; Freeman et al. 2001; Craven et al. 2010; McManamay and Frimpong 2015). Despite these realizations, there is a lack of information on fish and flow relationships during important reproductive and early-life stages, particularly for narrow-range endemics (Cooke et al. 2012).

Black basses, *Micropterus* spp., are freshwater sportfish that are economically and ecologically important and occur over a wide range of habitats. There are 19 extant species of black bass in North America, with most restricted to relatively small ranges (Kim et al. 2022). Popularity as aggressive sportfishes has led to both riverine and reservoir populations of black bass conferring important economic benefits via recreational opportunities (Chen et al. 2003; Thomas et al. 2015;



Seguy and Long 2021). For instance, black basses are consistently ranked as the most sought-after fishes by freshwater anglers in the United States (USDOJ et al. 2016) and have been introduced to every continent except Antarctica (NatureServe 2019). As aggressive predators, black basses can confer top-down ecosystem effects (Power et al. 1985; Boschung and Mayden 2004), which can also result in introduced populations being problematic invasives (Jackson 2002). These sportfish occur in all sizes of streams, lakes, and impoundments and display a variety of behaviors depending on their environmental context (Nack et al. 1993; Waters and Noble 2004; Carter et al. 2012; Brewer and Long 2015). More widespread species such as Largemouth Bass *M. salmoides*, Smallmouth Bass *M. dolomieu*, and Spotted Bass *M. punctulatus* persist in a variety of environmental conditions and thus, appear more plastic in their ability to adapt to varying resource availability (Todd and Rabeni 1989; Greene and Maceina 2000; Richardson-Heft et al. 2000; Barthel et al. 2008). Narrow-range endemic black bass such as Shoal Bass *M. cataractae*, Guadalupe Bass *M. treculii*, and Suwannee Bass *M. notius* are restricted in their native distributions and may not be as tolerant to environmental changes (Birdsong et al. 2015; Shaw 2015). Despite their popularity and ecological importance, riverine black basses remain understudied compared to reservoir populations.

There are numerous threats to the persistence of riverine black bass populations. Habitat fragmentation and destruction appear to be primary threats for many populations. For example, 11 dams on the Chattahoochee River in Georgia appear to block Shoal Bass dispersal (Birdsong et al. 2015; Dakin et al. 2015; Taylor et al. 2018b), and similar fragmentation exists in the ranges of other narrow-range endemics including Neosho Bass *M. velox* (Brewer and Long 2015; Taylor et al. 2018a) and Bartram's Bass *M. cf coosae* (Peoples et al. 2021). Additionally, the Redeye Bass complex is negatively associated with landscape disturbance (Bartram's Bass, Peoples et al. 2021;

Warrior Bass *M. warriorensis*, Young 2022). The introduction of non-native congeners further threatens black bass populations through hybridization (Littrell et al. 2007; Alvarez et al. 2015; Koppelman 2015; Lewis et al. 2021; Judson et al. 2021) and competition (Sammons 2012). Hybridization results in the loss of genetically distinct populations, less-fit hybrid populations, and local extirpation (Rhymer and Simberloff 1996; Sinnatamby et al. 2020). Due to a combination of threats, some black bass populations have already been extirpated from portions of their range (e.g., Shoal Bass, Stormer and Maceina 2009; Sammons and Earley 2015; Bartram's Bass, Judson et al. 2021). Lastly, growing water demand for cities and agriculture has reduced aquifer levels across the country (Foster and Chilton 2003; Rugel et al. 2012; Haacker et al. 2016) which may also affect riverine black bass populations. For instance, higher abundance and growth potential of Smallmouth Bass was found in streams with higher groundwater input (Whitledge et al. 2006; Brewer 2013; Middaugh et al. 2018). Such a myriad of threats prompts the need for a better understanding of reproductive strategies and hatching dynamics so that populations can be better managed.

Populations of riverine Shoal Bass and Largemouth Bass in the Apalachicola-Chattahoochee-Flint (ACF) Basin in the southeast U.S. are of special interest to both scientists and managers, yet we lack information on many aspects of their life histories. Shoal Bass is endemic to this basin but was only recognized as a species in the late 1990s (Williams and Burgess 1999). Shoal Bass is commonly associated with swift-water shoal areas and rarely found in lentic conditions (Wheeler and Allen 2003; Gocłowski et al. 2013; Bitz et al. 2015). Movements of up to 200 km have been observed in un-impounded portions of its range, indicating that a mosaic of riverine habitats may be used (Gocłowski et al. 2013; Sammons 2015). However, little is known about relationships between abiotic conditions and its life history (Bitz et al. 2015; Woodside et al. 2015; Sammons

et al. 2021). Shoal Bass is popular among anglers due to their aggressive fight, picturesque habitats, and limited distribution (i.e., destination species; Sammons et al. 2015). Two major threats to the persistence of this species include habitat fragmentation (Stormer and Maceina 2009; Dakin et al. 2015) and hybridization with the invasive Spotted Bass and Alabama Bass *M. henshalli* (Alvarez et al. 2015; Tringali et al. 2015). Contrastingly, Largemouth Bass populations appear to be relatively stable within the ACF basin. Largemouth Bass are found in both lotic and lentic environments (Waters and Noble 2004; Bonvechio and Allen 2005), but research on reproductive and early life history in riverine ecosystems is also lacking (but see Nack et al. 1993; Raibley et al. 1997b; Wheeler and Allen 2003; Sammons et al. 2021). Information on how environmental conditions relate to seasonal movements, hatch success, and growth of juveniles will allow for the development of more informed management actions for these species.

Correspondingly, the goal of my thesis is to advance our understanding of riverine Shoal Bass and Largemouth Bass spawning and early life ecology, thereby informing the conservation and management of these species. Specifically, my first objective is to determine the seasonal movement patterns by adult Shoal Bass and Largemouth Bass in the lower Flint River. Understanding black bass movement can inform relevant management actions such as protecting river corridors and habitats that are important for fulfilling important life-history needs, particularly spawning. However, an understanding of reproductive dynamics is incomplete without considering what environmental factors are related to recruitment success. Thus, my second objective is to assess the environmental factors related to hatch date and daily growth of age-0 Shoal Bass and Largemouth Bass. Investigation of these dynamics in a partially regulated system like the lower Flint River catchment (LFRC) will provide managers with a better understanding of how riverine black bass species persist across a riverscape and what may threaten this persistence

in the future. More specifically, these data will aid in the identification of important spawning locations, habitats, and the environmental factors conducive to successful hatching and survival of young-of-year fish.

## **Study Area**

My study was conducted in the LFRC, within the Dougherty Plain and Fall Line Hills physiographic districts of Georgia (Figure 1). The Flint River begins in the Piedmont Province of Georgia and flows approximately 560 km south until it meets the Chattahoochee River to form the Apalachicola River at the GA-FL border (Couch et al. 1996). This confluence is impounded by Jim Woodruff Lock and Dam (JWLD), which forms Lake Seminole. The LFRC drains more than 21,900 km<sup>2</sup>, receives about 132 cm of annual precipitation, and is characterized by a warm and humid, temperate climate (Couch et al. 1996; Rugel et al. 2012). Streams in the Fall Line Hills begin as seeps and springs emanating from the Claiborne aquifer and are dominated by sand or silt substrates with meandering channels and wide floodplains (Golladay and Battle 2002). The Dougherty Plain is dominated by mantled karst topography with the Flint River and its tributaries flowing through exposed portions of Ocala Limestone lithology (Bacchus 2000; Opsahl et al. 2007). Streams in the LFRC are directly connected to the Upper Floridan Aquifer (UFA) with groundwater providing baseflows to many streams during times of low precipitation (Opsahl et al. 2007). Stream channels throughout the basin are characterized by limestone shoals and bluffs, sandbars, and abundant woody debris.

The LFRC is highly altered via land use and water allocations. Row-crop agriculture and pasture lands comprise more than 50% of land use and consumes approximately 5 million m<sup>3</sup> of water daily from regional aquifers and surface waters (Hook et al. 2005; Rugel et al. 2019). Remaining land use in the catchment consists of pine plantation, deciduous forest, and

geographically isolated wetlands. Two run-of-the-river reservoirs (Lake Blackshear and Lake Chehaw) lie along the lower Flint River formed by hydropower dams that produce hydropeaking flows (Couch et al. 1996) and along with JWLD have transformed 96 km of riverine habitat into more lentic conditions. The Flint River has been further altered by a 1-m low-water navigation channel from Albany to Bainbridge, Georgia, created in the late 1800s by the U.S. Army Corps of Engineers to facilitate commercial boat traffic on the river (Thurston 1973). This resulted in the loss of large portions of continuous shoal habitat, increased current velocities, and less areas of refugia.

## Chapter I Figure

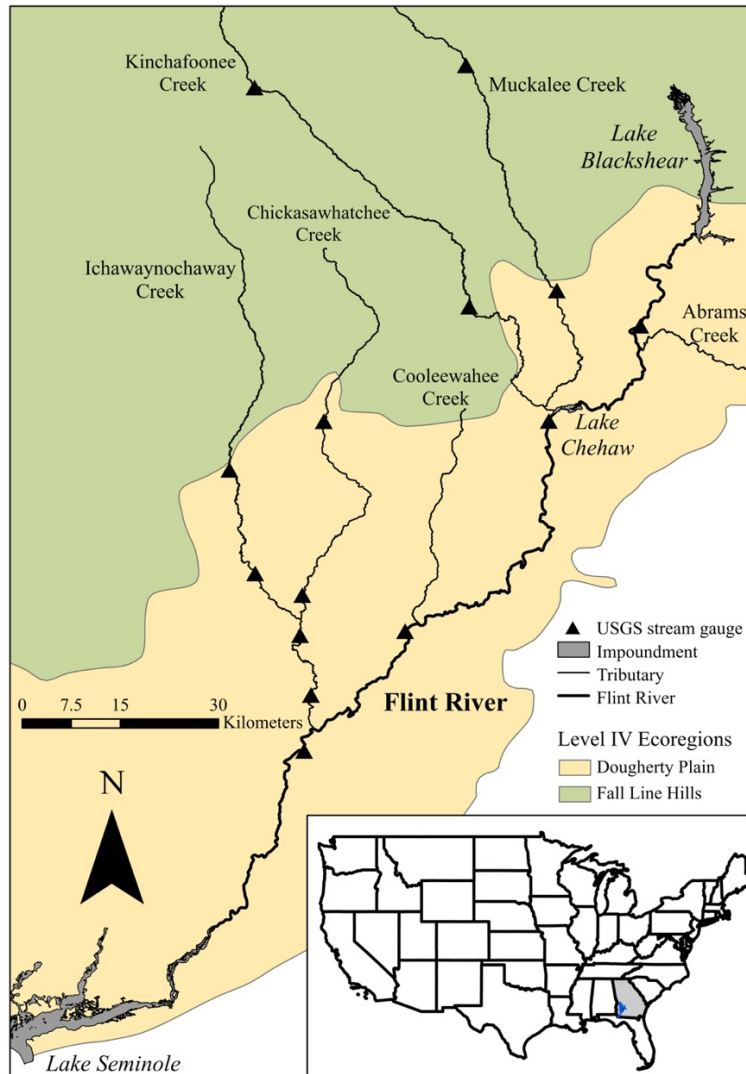


Figure 1. The lower Flint River catchment from Lake Blackshear to Lake Seminole within the Fall Line Hills (green) and Dougherty Plain (tan) ecoregions. The black triangles are U.S. Geological Survey stream gauges used in this study to obtain daily discharge data (from upstream to downstream by stream): Muckalee Creek: 02351500, 02351890, Kinchafoonee Creek: 02350600, 02350900, Chickasawhatchee Creek: 02354350, 02354500 Ichawaynochaway Creek: 02353265, 02353500, 02354800, 02355350, Flint River: 02350512, 02352500, 02353000, 02355662

## Chapter II

### Seasonal Movement Dynamics of Adult Shoal Bass and Largemouth Bass

#### Introduction

Fish movements allow populations to maintain genetic integrity, exploit or colonize environments, and meet their basic life needs. Movement can play an important role in reproductive strategies by enabling fish to be selective in spawning habitat and mate choice, thereby bolstering fish populations when spawning is successful (Lennox et al. 2019). Different portions of fish populations may exhibit divergent movement patterns (i.e., partial migration; Jonsson and Jonsson 1993; Chapman et al. 2012), suggesting the presence of both mobile and stationary components (Skalski and Gilliam 2000; Rodriguez 2002; Radinger and Wolter 2014). For example, both small-bodied fishes like Roach *Rutilus rutilus* and large salmonids such as Bull Trout *Salvelinus confluentus* can have migratory and resident components of their populations (Monnot et al. 2008; Chapman et al. 2011). The make-up of mobile and stationary fish in a population may be related to size, age, and the context of their environment (e.g., stream network, spatial-temporal variability of habitats; Schlosser 1991). Variation among individuals likely fulfills distinct roles within populations, with the mobile segment hypothesized to significantly contribute to genetic exchange, colonization, and recolonization (Barthel et al. 2008; Albanese et al. 2009; Chapman et al. 2012; Radinger and Wolter 2014). Prairie Chub *Macrhybopsis australis*, for example, are thought to recolonize habitats that cannot be used during droughts but benefit the population during wetter periods (Wedgeworth et al. 2022). Regardless of magnitude, movements enable fish to use diverse environments to meet their life-history needs (i.e., feeding, reproduction) and avoid physiological stress (Schlosser 1991). Annual movement cycles are often influenced by environmental cues such as temperature, photoperiod, discharge, and shifts in resource availability

(Bunn and Arthington 2002; Taylor and Cooke 2012). Therefore, disruption of these cues and habitats (e.g., natural flow regime; Poff et al. 1997) can lead to declines in lotic fish populations (Poff and Zimmerman 2010; Nagrodski et al. 2012).

Altering river habitats via damming can have significant consequences on fish populations including preventing successful migrations, but also altering downriver habitats. Disrupting connectivity of river ecosystems can negatively affect fish populations. Globally, artificial barriers, overexploitation, and pollution, are estimated to have decreased the abundance of freshwater migratory fishes by 76% between 1970 and 2016 (Deinet et al. 2020). Economically and culturally important fish populations like Pacific salmon *Oncorhynchus spp.* and sturgeon *Acipenseridae spp.* have declined, in part due to disconnection from their natal spawning grounds (Williot et al. 2002; Gustafson et al. 2007). Regulating flow regimes can disrupt thermal and discharge cues (Poff et al. 1997; Caissie 2006; Fullerton et al. 2010) and physically alter important stream fish habitats (e.g., sedimentation, channelization; Bunn and Arthington 2002; Poff and Zimmerman 2010). These alterations may force fish to seek alternative spawning destinations or, in some cases, result in reproductive failure (Poff and Zimmerman 2010; Ding et al. 2023). Identifying external cues associated with fish movement is thus important for mitigating the effects of human alteration to river corridors (Capra et al. 2017; Lennox et al. 2019).

North American black basses *Micropterus spp.* are both ecologically and economically important freshwater fishes, but our understanding of movement and reproductive ecology is limited for narrow-range endemics. There are 19 extant species of black bass in North America, with 12 species being restricted to relatively small ranges in the southeast United States (Kim et al. 2022). Functioning as top predators in their ecosystems, black basses' aggressive predatory behaviors also render them popular targets for recreational anglers in both reservoirs and streams



(Long et al. 2015). On an annual basis, it is estimated that approximately 9.6 million black bass anglers generate nearly \$30 billion dollars in economic activity in the United States (USDOJ et al. 2016). Black bass angling in 10 major Texas rivers was estimated to contribute \$71.5 million in annual economic benefits (Thomas et al. 2015). In contrast, reservoirs garner more support with single reservoirs contributing between \$9-46.7 million annually (Chen et al. 2003; Driscoll and Myers 2014). However, the ease of access and high popularity of reservoirs have skewed research efforts towards lentic populations for some species. Largemouth Bass *M. salmoides* movements, for example, have been studied in numerous reservoir and lake ecosystems (e.g., Mesing and Wicker 1986; Ridgway 2002; Slipke and Maceina 2007; Hanson et al. 2007; Hunter and Maceina 2008; Carter et al. 2012) but information on movements in riverine systems is lacking (but see Nack et al. 1993; Raibley et al. 1997a; Wallace and Hartman 2006; Gocłowski et al. 2013). Recent studies on riverine black bass movement and reproduction have revealed marked plasticity in the magnitude and patterns of movement (e.g., Guadalupe Bass *M. treculli*, Perkin et al. 2010, Smallmouth Bass *M. dolomieu*, Schall et al. 2019; Neosho Bass *M. velox*, Miller and Brewer 2022, Suwannee Bass *M. notius*, Yeager et al. 2023). Riverine populations of black bass may exhibit potamodromous behavior (Barthel et al. 2008; Bitz et al. 2015; Sammons 2015; Cottrell 2018), but our understanding of the frequency and drivers of this behavior across species and populations is lacking. Differences in movement magnitudes likely reflect varying resource availability and requirements among catchments and populations (Turner et al. 1995; Northcote 1997).

My study objective was to determine the seasonal movement dynamics of adult Shoal Bass *M. cataractae* and Largemouth Bass in the lower Flint River. Shoal Bass is a narrow range black bass that coexists with the more widespread Largemouth Bass in the Apalachicola-Chattahoochee-Flint (ACF) basin making this system ideal for examining black bass movement dynamics. Large-

scale movements (e.g.,  $\leq 200$  km) related to spawning have been indicated in some Shoal Bass populations (Ingram et al. 2013; Sammons 2015), but factors related to timing, frequency, and cues are poorly understood. Conversely, Largemouth Bass is often perceived as relatively sedentary in lentic settings (Minns 1995; Sammons et al. 2003; Wallace and Hartman 2006), but the species is understudied in riverine ecosystems (Moody 1960; Nack et al. 1993). Adding to our knowledge of lotic black bass movements will help us define key habitats (e.g., spawning), identify movement corridors, and better understand environmental cues and the relationship between river regulation and the management of riverine black bass (Birdsong et al. 2015). This is especially timely given local extirpations (Stormer and Maceina 2009; Birdsong et al. 2015; Bangs et al. 2018), extensive hybridization (Littrell et al. 2007; Alvarez et al. 2015; Koppelman 2015; Bangs et al. 2018; Lewis et al. 2021), habitat loss (Hurst et al. 1975; Perkin et al. 2010; Taylor et al. 2019), competition with invasive species (Pine et al. 2007; Sammons 2012; Sammons et al. 2023) and other threats facing our black bass populations.

## **Methods**

### *Study Area*

My study was conducted on the springfed lower Flint River, Georgia within the karstic Dougherty Plain physiographic district (see also Chapter 1). It is characterized by a stable, deeply incised channel constrained by steep sandy banks and limestone outcrops with rocky islands interspersed (Mueller 1990). Substrates include silt, sand, cobble, boulders, and bedrock (Kaeser et al. 2013). I tracked radio tagged fish in the 112 -km section of the Flint River between Albany Dam at Lake Chehaw (RKM 164) and Lake Seminole (RKM 52; Figure 1). Jim Woodruff Lock and Dam at the terminus of Lake Seminole was located at RKM 0. A 1-m low-water navigation channel was excavated in the 19<sup>th</sup> century (Thurston 1973). Dredge spoils from these operations

created numerous man-made islands and added to existing natural islands. Both channel form and hydrological conditions have been further altered due to hydropeaking flows from Albany Dam (Couch et al. 1996).

### *Fish Sampling and Tracking*

In cooperation with Georgia Department of Natural Resources (GADNR), I collected and tagged 30 adult Largemouth Bass and 30 adult Shoal Bass during February and March 2022. My five tagging locations were in the 95-km reach of the Flint River between Lake Chehaw Dam (RKM 164) and the Mitchell-Decatur County Line Boat Ramp (RKM 69; Figure 1). We boat electrofished for adult basses using a 40-amp Midwest Lakes Electrofishing Systems shocking unit (Polo, Michigan) powered by a 6,500-watt generator. We used standard American Fisheries Society electrofishing settings based on conductivity and standardized for generator power output with initial settings placed at pulsed DC current, 60Hz, 25% duty cycle, and 500 volts; settings were adjusted depending on catch success (Guy et al. 2009). I used 14-g Model F1835 radio transmitters (Advanced Telemetry Systems, ATS; Isanti, Minnesota) equipped with a 500-d battery life expectancy and mortality sensors. Mortality sensors increased the signal rate from 50 to 100 pulses per second if tags were motionless for at least 24 hours. Fish were measured (total length, TL, 1 mm) and weighed (1 g) prior to tagging. Only fish weighing more than 400 g were tagged (i.e., transmitter was  $\leq 4\%$  of body weight) conforming to the recommended limit of tag burden (Brown et al. 1999; Brownscombe et al. 2019). Fish were then anesthetized using electroanesthesia following Jennings and Looney (1998). Briefly, fish were placed on an electroanesthesia table that was immersed in water within a plastic container during surgery. Electricity safely immobilizes fish and has significantly faster induction and recovery time than chemical anesthesia (Kim et al. 2017). Once anesthetized, tags were inserted following Maceina

et al. (1999). Briefly, I created a 4-cm incision anterior to the pelvic fin along the ventral body cavity, then inserted the tag anteriorly so that the antenna trailed posteriorly out of the incision. I closed the incision with 2-3 sutures using Number 2 Prolene monofilament (Ethicon; Raritan, New Jersey; Appendix 1). Fish were released as soon as they regained equilibrium, usually within 3 min. Fish were tagged in groups of 5-10, allowed to recover, and then released within 2 km of the collection location.

Additional tagging of Shoal Bass and Largemouth Bass was completed throughout the study using recovered transmitters. Transmitters were recovered from eight Shoal Bass and five Largemouth Bass that were harvested by anglers and one Shoal Bass that was killed via boat propeller during a separate GADNR sampling event. If recovered transmitters were in good condition, then they were cleaned and sterilized and implanted into new fish by GADNR personnel following the protocol described above.

I tracked tagged fish over different intervals depending on the season. Fish were tracked from March 2022 to May 2023 beginning 14 days after tag insertion to allow fish to recover from surgery (Sammons and Earley 2015). Fish were tracked weekly during the presumed spawning season each year (March-May; Johnson 1974; Nack et al. 1993; Bitz et al. 2015; Sammons et al. 2021) to identify spawning reaches. I tracked fish weekly because I hypothesized greater movement during this time. Due to water depth and turbidity, I could not visually confirm spawning, but I assumed fish that exhibited relative site fidelity during this time were likely spawning (Nack et al. 1993; Gocłowski et al. 2013; Bitz et al. 2015; Cottrell 2018; Ingram et al. 2019) and could be supported by age-0 fish detections (see Chapter 3). During the rest of the study (June-August and October-February), I tracked fish biweekly or monthly as black bass are typically more sedentary during summer and winter (Smallmouth Bass, Todd and Rabeni 1989;

Largemouth Bass, Karchesky and Bennett 2004; Largemouth Bass, Shoal Bass, and Spotted Bass *M. punctulatus*, Goclowski et al. 2013; Alabama Bass *M. henshalli* and Redeye Bass *M. coosae*, Earley and Sammons 2015).

Regular tracking was conducted from a boat using an ATS-R2000 receiver and 4-element fixed Yagi antenna following the methods of Eiler (2012). Each tracking event took three days and covered the area between Albany Dam (RKM 164) and Flint River Heights boat ramp (RKM 52; Figure 1). Briefly, I travelled downstream at a steady low speed while the receiver continually scanned frequencies. When a signal was detected, I used the directional Yagi antenna to sweep the area to determine the direction of strongest signal. I then used the homing method described by Koehn et al. (2012) to locate the tagged fish. I gradually reduced receiver gain to determine the area of strongest signal strength as I approached fish by boat. The fish location was determined by identifying the direction the antenna was pointed when the receiver gain was at the lowest setting while the strongest signal was detected. If fish moved due to a fright response, the initial point where fish location was determined was recorded. I used a handheld GPS (Garmin GPSMAP 64st) to record the position of each fish location on each tracking event. Before tracking, I determined the location accuracy of the homing method using dummy transmitters. An assistant hung a transmitter from an overhanging limb or tree root on the bank using fishing line (i.e., suspending the transmitter in the water column). I had no prior knowledge of the transmitter location. I then used the homing method to determine the point of the strongest signal and then measured the distance between my determined point and the actual transmitter location with a range finder. I repeated this three times at three unknown locations with an accuracy of approximately 15 m.

Additional surveys were completed outside of my study area to look for any missing tagged fish. During February 2023, an aerial tracking survey was completed to search for missing fish.

This survey covered the lower Flint River catchment (LFRC) from Lake Blackshear to Jim Woodruff Lock and Dam including Lake Chehaw, Ichawaynochaway Creek, Spring Creek, Lake Seminole, and the Chattahoochee River up to George W. Andrews Lock and Dam. During April 2023, Ichawaynochaway Creek (24-km long, located on The Jones Center at Ichauway property) was tracked via boat over 2 days to search for missing fish that were last observed near the Flint River-Ichawaynochaway Creek confluence. Our search terminated at a breached, 1920s-era power dam where fish passage is possible (Ingram et al. 2019), but boat passage is not. I did not observe any fish outside of the study area during these additional tracking events.

### *Environmental Measurements*

I accessed discharge data ( $1.0 \text{ m}^3/\text{s}$ ; USGS 2023) to relate flow conditions to patterns in bass movement (Table 1). Discharge patterns affect fish in many ways, and in combination with temperature changes, can cue fish movement (Taylor and Cooke 2012). Floods signal many freshwater fish species to move significant distances, particularly to spawn (Gordon et al. 1992; Taylor and Cooke 2012). Therefore, I hypothesized that movement in both species would be positively related to both mean discharge conditions and rate-of-change (ROC) in discharge conditions. I also wanted to examine variability in flows to see how increased variation (i.e., hydropeaking) may relate to riverine bass movement. To test these hypotheses, mean daily discharge data were obtained from four U.S. Geological Survey (USGS) stream gauges that span the study extent: Albany, Georgia (gauge 02352500), Newton, Georgia (gauge 02353000), and Hopeful, Georgia (gauge 02355662) (Figure 1). During the study period, pairwise correlations between mean daily discharge values for these gages were  $>0.93$ . Therefore, I averaged discharge data across stream gauges to calculate mean daily discharge, the coefficient-of-variation (CV;

mean/standard deviation) of instantaneous values (15-minute intervals) of discharge, and the ROC in discharge between fish relocations to relate to fish movements.

I also collected water temperature data (0.1°C) to relate thermal conditions to the timing and magnitude of fish movement (Table 1). Temperature cues fish to move to habitats that are more thermally suitable for their metabolic needs during a given stage of their life history, particularly reproduction (Shuter et al. 1980; Graham and Orth 1986; Peterson and Rabeni 1996; Northcote 1997). I hypothesized that both Shoal Bass and Largemouth Bass movement would have a quadratic relationship with water temperature, with higher movement rates occurring during periods of intermediate water temperatures (i.e., spring). Similarly, I also hypothesized that higher rates of movement would occur during periods of rising water temperature. To examine these hypotheses, water temperature was recorded at three locations throughout the study area. I used temperature data from the stream gauge located at RKM 43 in Bainbridge, Georgia (gauge 02356000), the National Ecological Observatory Network's (NEON) buoy-mounted sensor station (NEON Station: FLNT; Precision Measurement Engineering Inc. – T-Chain RS 232/485) located at RKM 86.5, and a continuous temperature logger (Onset Hobo MX2201, Bourne, Massachusetts) located at RKM 159 (0.1 °C; Figure 1). My temperature logger was attached to the inside of a cinderblock in a well-mixed and shaded area of river. Gaps in temperature logger data due to battery failure were estimated using least-squares regression with mean daily temperature values from the downstream USGS stream gage located in Bainbridge (gauge 02356000;  $R^2 = 0.99$ ). I averaged temperature data across these locations to calculate mean daily water temperature, CV of daily water temperature, and ROC in water temperature between fish relocations for comparison with fish movements.

I used my water temperature data to define my seasons. I used water temperature because temperature changes are variable between years (i.e., seasonal conditions may begin on different dates each year; Langan et al. 2001). Temperature can also be measured in any stream and similarly applied to compare this study to other black bass populations (Todd and Rabeni 1989). I defined the spring season as a period of increasing water temperatures. During this season, my water temperatures increased relatively quickly ranging 15-25 °C. I defined summer as a period of prolonged higher water temperatures over 25 °C. Lastly, I defined autumn as a time period when water temperatures decline appreciably. In the Flint River, water temperatures ranged 25-15 °C during autumn. Winter was the coldest period when water temperatures were less than 15 °C. Todd and Rabeni (1989) indicated these cold-water temperatures were associated with much lower movements by Smallmouth Bass in Missouri rivers. Based on mean-daily water temperature, I determined that categorical seasons began on the following dates: Spring- March 1, 2022, and February 22, 2023; Summer- May 14, 2022; Autumn- September 29, 2022; Winter- December 18, 2022.

### *Fish Home Range and Movement*

I inputted the tagged fish detections in geospatial software to calculate home ranges and movements. All geospatial methods were completed in ArcGIS Pro 3.3.1 (ESRI, Redlands, California 2024). First, I converted NHDFlowline stream data (National Hydrography Database plus V2- NHD+; USGS 2017) for the lower Flint River into a route. Then, I plotted observed fish locations collected in the field via GPS on top of this route. I used the “Locate Features Along Routes” tool to measure the distance from Jim Woodruff Lock and Dam (RKM 0) to each fish location (1 m). Locations with associated RKM values were then used to calculate home ranges and movement rates.



For each individual fish, I characterized both linear home range (LHR) and kernel density estimates. Linear home ranges were considered the entire stream area where an individual was observed. LHR was calculated as the distance between a fish's most upstream and most downstream relocation points (Vokoun 2003; Vokoun and Rabeni 2005a; Gilroy et al. 2010). These LHRs were then examined within each species to determine if heterogeneous movement patterns were present (Radinger and Wolter 2014; Yeager et al. 2023). I tested movement heterogeneity by examining the distribution and kurtosis of LHRs within each species using the `kurtosis()` function in the "moments" package (Komsta and Novomestky 2022) in the statistical software R (v4.3.2, R Core Team 2023). If the kurtosis of the LHR distribution was  $> 3$  (i.e., leptokurtic), the sample was characterized as exhibiting heterogeneous movement patterns (Fiori and Zenga 2009; Yeager et al. 2023). If LHR distribution was found to be leptokurtic within a species, individual fish were labelled as 'mobile' if that individual's LHR was greater than the mean LHR summed with one standard error of the mean, otherwise they were classified as 'stationary' (Yeager et al. 2023). For individual fish, I then calculated both 50% and 90% kernel home ranges. Kernel density estimates were based on use distributions calculated from the set of relocation points for each individual (Van Winkle 1975; Seaman and Powell 1996). These estimates are commonly used to define areas of use for individuals or populations and can be adjusted to delimit areas that have a higher probability of use (e.g., a 50% KDE predicts where an individual spent 50% of its time) or excludes portions of the LHR that may consist of outlier movements (e.g., outside of the 90% KDE; Seaman et al. 1999; Vokoun 2003). For these estimates, I followed procedures of Vokoun (2003) by creating kernel home range estimates of LHR (m) rather than area. With the statistical software R, I used the `density()` function to calculate both 50% and 90% kernel home ranges (m) per individual. Since time intervals between relocations varied

by season, I weighted relocations: spring = 0.15, summer = 0.25, autumn = 0.25, winter = 0.35. This corresponded to weekly tracking occurring during spring, biweekly tracking occurring during summer and autumn, and monthly tracking occurring during winter. Then weights were normalized per fish so that the sum of weights for all relocations for that fish equaled one. This allowed for more accurate estimates of time (%) spent in each portion of their home range.

I quantified movement rates of Shoal Bass and Largemouth Bass between detections. The RKM value of each fish's location was subtracted by the prior location's RKM value to determine distance moved (m). This was the minimum displacement of each fish because fish likely moved more than detected between discrete relocations. The absolute value of this distance was divided by the number of days between relocations to obtain movement rate (m/d; Wilkerson and Fisher 1997). Movement was analyzed as movement rates to account for uneven time intervals between relocations (Wilkerson and Fisher 1997; Goclowski et al. 2013). A small constant of 1 m/day was added to all movements to account for zero values in the data set. I also assumed it was unlikely that a fish did not move at all between relocations. Movement rates were then used as my response variable in subsequent statistical analyses. Any individual fish that had less than two relocations (i.e., no recorded movements) were not included in movement analyses ( $n = 2$ ).

### *Statistical Analyses*

Prior to my movement analyses, I made necessary variable calculations, transformations, and standardizations to predictor variables to meet the basic assumptions of linear regression. For each fish movement, I converted the final date of that movement to the day of the study (DOS, e.g., March 1<sup>st</sup> 2022 = Day 1, March 1<sup>st</sup> 2023 = Day 366) to account for time and season. In addition to DOS, I included the continuous covariates mean daily water temperature, the CV of mean daily water temperature, the ROC in mean daily water temperature, mean discharge, CV of discharge,

and the ROC in discharge. All flow and temperature variables were calculated over the time interval between fish relocations (i.e., during the movement). I log-transformed mean discharge and CV of discharge to account for skewness. Prior to model building and following transformations, I tested for multicollinearity among independent variables using Pearson's correlation coefficient and only retained variables in the models with  $r < 0.6$  (Roever et al. 2014). Mean daily water temperature and CV of water temperature were multicollinear ( $|r| = 0.62$ ; Table 2); therefore, I only retained mean daily water temperature. Retained continuous covariates were standardized to a mean of 0 and a standard deviation of 1 to aid in model interpretation and convergence (McCune et al. 2002). All analyses were conducted in R version 4.3.2 (R Core Team 2023).

I used generalized additive mixed models (GAMMs) and a model selection approach to assess both linear and non-linear relationships between bass daily movement rate (m/d) and selected covariates. Candidate model sets were investigated separately by species to investigate species-specific relationships with covariates. For each species, I built 13 *a priori* GAMMS based on my hypothesized relationships between covariates (additive and interactions) and movement rates (Table 3). I fit GAMMs using the *mgcv* package in R (Wood 2023) including smooth thin-plate regression splines for continuous covariates and a restricted-maximum likelihood (REML) procedure (Mollenhauer et al. 2013; Wood 2017; Schall et al. 2019). I evaluated the strength of non-linear relationships for smoothed continuous covariates using the effective degrees of freedom (EDF). An EDF equal to one is a linear relationship whereas an EDF greater than one implies a non-linear relationship (Hunsicker et al. 2016; Wood 2017). Fixed effects considered in my candidate models included the continuous covariates listed above and the categorical effect of sex. I included individual fish as a random effect to account for unequal sampling of individuals (e.g.,

unequal number of locations between individuals) and autocorrelation among locations (Wilkerson and Fisher 1997; Otis and White 1999; Wagner et al. 2006). I assumed random effects were normally distributed as  $N(0, \sigma^2)$ , where  $\sigma^2$  represents the variance among individual fish (Gillies et al. 2006; Miller and Brewer 2022). The GAMM models built for each species can be expressed as:

$$Y_{i,j} = f_1(X_{1,ij}) + f_2(X_{2,ij}) + \dots + f_n(X_{n,ij}) + Z_{i,j}b + \epsilon_{i,j}$$

where  $Y_{ij}$  is the daily movement rate at relocation  $i$  for fish  $j$ ,  $X_1$  through  $X_N$  represent the values of the  $n$  covariates for that observation. The functions  $f_1$  to  $f_n$  represent the relationships between each covariate and the response variable (i.e., either linear or non-linear). The term  $Z_{i,j}$  is a matrix that specifies the random effects design for each observation,  $b$  is a vector of random effects coefficients, and  $\epsilon_{i,j}$  represents the error term for each observation. For each species, I ranked candidate model sets using Akaike's information criteria adjusted for small sample size ( $AIC_c$ ; Hurvich and Tsai 1991) and by assessing residual plots (Wood 2017; Schall et al. 2019). I ranked my models based on  $\Delta AIC_c$  values (i.e., difference between top ranked model and model at hand; Burnham and Anderson 2002). All models with  $\Delta AIC_c < 2$  were considered to have equal empirical support (i.e., competitor for drawing inference) if they contained the same number of or fewer parameters than the top model to avoid unnecessary model complexity and reduce the inclusion of uninformative parameters (Burnham and Anderson 2002; DeVries et al. 2008; Arnold 2010; Miller and Brewer 2022). I also reported deviance explained (%) for each considered model as the proportion of deviance (variance) in residuals that is explained by fixed and random effects (i.e., equivalent to unadjusted  $R^2$  in linear regression; Guisan and Zimmermann 2000; Guisan et al. 2002).

Before building a candidate set of models, I evaluated the assumption of temporal independence of residuals for each species with preliminary models. I compared a baseline model with only the covariate DOS to a model that explicitly models temporal autocorrelation (Table 3; Zuur et al. 2009; Mollenhauer et al. 2013). Temporal independence was assumed if the simpler model was preferred over the model with an autocorrelated error structure (based on  $AIC_c$ ) and if true, no correlation structure was carried forward in other competing models. I expected that movements would primarily be associated with season, due to seasonal spawning and overwintering movements being observed in many species of black bass (Todd and Rabeni 1989; Gocłowski et al. 2013; Bitz et al. 2015; Schall et al. 2019; Miller and Brewer 2022), therefore the effect of DOS was also included in all other subsequent models.

Subsequent hypotheses evaluated whether movement would primarily be predicted by the additive relationship of DOS with all other covariates, or by interactions between covariates (Table 3). I hypothesized that movement was positively related to mean discharge conditions due to fish commonly being cued by higher flows (Taylor and Cooke 2012; Mollenhauer et al. 2013). I hypothesized that movement would be quadratically related to mean water temperature, because movement of other black basses tends to be highest during spring water temperatures and then decreases (Graham and Orth 1986; Todd and Rabeni 1989; Peterson and Rabeni 1996; Northcote 1997). I also wanted to investigate how discharge variability was related to movement as fish behavior can be related to rapid changes in flow conditions downstream of dams (Bunt et al. 1999; Young et al. 2011). My next models were built to assess whether rates of change in water temperature and discharge patterns, rather than the averages of these conditions, may cue bass to move more (Olden and Poff 2003; Mollenhauer et al. 2013; Marshall et al. 2016). My last additive model was based on the hypothesis that sex may have a strong relationship with movement,

specifically with females of both species having significantly higher movement rates than males (Jonsson and Jonsson 1993; Waters and Noble 2004; Ingram et al. 2019). My final models tested interactions between flow, temperature, and sex covariates and DOS. Thus, I hypothesized that higher movements associated with these conditions only occurred at certain times of year.

## **Results**

### *Fish Sampling and Tracking*

We attempted to maintain an even distribution of size, sex, and species of tagged fish throughout the study (Table 4). Shoal Bass tagged in spring 2022 had a mean TL of 464 mm (SD: 53.34, range: 369 – 541 mm), and a mean weight of 1452.71 g (SD: 523.62, range: 634 -2536 g). Largemouth Bass tagged were slightly larger, on average, with a mean TL of 467.33 mm (SD: 77.62, range: 326 – 595 mm), and a mean weight of 1696.73 g (SD: 88.55, range: 474 – 3570 g). Over the duration of the study, 14 fish were either reported harvested or fatally wounded (n = 9 Shoal Bass, n = 5 Largemouth Bass), 13 transmitters were recovered from these fish, and I used 12 of these transmitters to tag new fish (n = 6 Shoal Bass, n = 6 Largemouth Bass). Over the 15-month study, I completed 33 tracking events and logged 1450 locations of 72 tagged fishes. I collected n = 765 individual locations of 37 Shoal Bass (16 female, 21 male) and n = 685 individual locations from 35 Largemouth Bass (23 female, 12 male). No mortalities were detected via mortality signal or otherwise assumed via limited movement between relocations. Eight Largemouth Bass and four Shoal Bass had an unknown fate at the end of the study (i.e., no longer detected).

### *Environmental Conditions*

Temperature and discharge conditions during the study period generally conformed to typical seasonal patterns of the region (Schoonover et al. 2006; Golladay et al. 2007; Figure 2;

Table 5). High flows occurred during spring both years and baseflow conditions occurred during the summer into autumn. Daily flow variability increased from late spring through autumn during baseflow conditions due to hydropeaking from Albany Dam (Figure 2). Average daily discharge throughout the study was 166.91 m<sup>3</sup>/s (SD: 127.94, range: 46.44 – 642.08 m<sup>3</sup>/s; Table 5). Water temperatures were highest in July and lowest in January. In late February and early March 2023, water temperatures were unusually high (20.7°C) but subsequently declined before the end of March (Figure 2). Mean daily-water temperature was 21.21°C (SD: 5.69, range: 8.54 – 30.82°C; Table 5).

### *Fish Home Ranges*

Home ranges were variable among and within species, reflecting heterogeneous movement patterns of my tagged fishes. Average LHRs for Shoal Bass and Largemouth Bass were 20.25 RKM (SD: 26.14, range: 0.009 – 92.1 RKM) and 12.35 RKM (SD: 21.99, range: 61.59 – 90.86 RKM), respectively (Table 6). The distributions of the dispersal kernels for both species were found to be leptokurtic (kurtosis = 3.35 (SHB) and 7.49 (LMB)) indicating heterogeneous movement patterns by the tagged fishes. Therefore, individual fish were identified as either mobile or stationary if their LHR was greater than one SE above the species mean LHR (SE of SHB: 4.36, SE of LMB: 3.7). This resulted in 28% of Shoal Bass being classified as mobile (10 out of 36 individuals) and 21% of Largemouth Bass classified as mobile (7 out of 34 individuals). Shoal Bass had larger KDEs than Largemouth Bass (Table 6) however, on average, mobile Largemouth Bass had larger core home ranges (50% KDE) than mobile Shoal Bass.

Both species demonstrated interesting spatial patterns where particular locations were used by multiple tagged fish during certain seasons. During the spring of both years, several tagged Shoal Bass and Largemouth Bass aggregated at Albany Dam (RKM 164) and near the shoal

complexes known as Goat Island (RKM 145) and Hell's Gate (RKM 79; Figures 3 and 4). These aggregations were denser (i.e., number of fish in an area) for Shoal Bass than Largemouth Bass. Only one fish (female Shoal Bass, Tag #482) was located near the river-reservoir interface at the downstream end of the study site (Figure 5), and it was not located thereafter. Lastly, there was a reach located RKM 120-135 where fish traversed during movements, but no tagged fish was located there during consecutive tracking events (Figures 3-6).

### *Fish Movement*

Both species exhibited movement variability with some tagged fish making extensive movements but not others. Shoal Bass movement rates (mean: 250 m/d, SD: 1103, CV: 440, range: 1-15,614 m/d) tended to be greater, on average, but also more variable than for Largemouth Bass (mean: 193 m/d, SD: 690, CV: 356, range: 1-8981 m/d; Table 7). Both species made movements > 70 km between consecutive locations. Moreover, many of the same fish exhibited large movements on multiple occasions (Figures 5 and 6). The maximum movement rates for Shoal Bass and Largemouth Bass were 15.61 km/d and 8.98 km/d, respectively.

Preliminary modeling related to movement of both species indicated that an autocorrelated error structure was not necessary. For my Shoal Bass models, the simpler model (AICc = 3446.1, log-likelihood = -1718.01, df = 5) was therefore chosen rather than the model with an autocorrelation structure (AICc = 3479.3, log-likelihood = -1732.56, df = 7). Likewise, my Largemouth Bass models showed a similar relationship (no autocorrelation structure: AICc = 2757.5, log-likelihood = -1373.71, df = 5; autocorrelation structure included: AICc = 2778.5, log-likelihood = -1382.16, df = 7). All subsequent models did not have an autocorrelated error structure.



The top-ranked Shoal Bass movement model contained an interaction between DOS and fish sex (Tables 8 and 9). This model explained 30.2% of deviance in my data. The other models considered were  $> 2 \Delta AIC_c$  from my top model indicating they had less support (Table 3). Both sexes of Shoal Bass moved more in the spring (i.e., presumed spawning season) than the rest of the year; however, females moved more in the spring compared to the males (Figure 7). Shoal Bass moved during the spring, on average, 380 m/d (SD: 1343), with females moving an average of 525 m/d (SD: 1622, range: 1 -15,614 m/d). Alternatively, males moved an average of 260 m/d (SD: 1050, range: 1-7715 m/d) during the spring. Both sexes were least active during the autumn, moving an average of 14 m/d (SD: 23, range: 1-161 m/d).

My top model related to Largemouth Bass movement rates included the main effects of DOS and discharge variability (i.e., CV) (Tables 8 and 9). This model explained 36.1% of the deviance in my data. No other models considered had as much support (Table 3). Similar to Shoal Bass, Largemouth Bass had higher movement rates in the spring, and lower movement rates during the rest of the year (Figure 8). Largemouth Bass movement rates during spring averaged 291 m/d (SD: 842, range: 1-8981 m/d). However, movement rates during autumn and early winter (DOS ~275) were higher than that of Shoal Bass, but less than spring Shoal Bass movements. Average Largemouth Bass movements in autumn and winter were 39 m/d (SD: 130, range: 1-1184 m/d) and 126 m/d (SD: 252, range: 1-1002 m/d), respectively. Movement rates by Largemouth Bass were also negatively related to discharge variability (Figure 8).

## **Discussion**

Large movements and home ranges were documented in both Largemouth Bass and Shoal Bass. In contrast, other studies observed small home ranges in Largemouth Bass populations (2.36 km - Mesing and Wicker 1986; 0.2 sq. km - Sammons et al. 2003), with few individuals exhibiting

unexplained longer-distance movements (Moody 1960; Nack et al. 1993). I show that Largemouth Bass is much more variable in movement behavior, with relatively large spring movements. This is an important first step towards understanding how Largemouth Bass successfully persists in riverine environments. Similarly, Shoal Bass display varying movement patterns across their native range (Stormer and Maceina 2009; Gocłowski et al. 2013; Cottrell 2018; Ingram et al. 2019) with greater movements in riverine systems that had longer river fragments between impoundments (Ingram et al. 2013; Sammons 2015). I add to this growing body of information where I observed some individuals moving long distances within the study area over multiple years. Variability in movement across studies may be attributed to a myriad of factors including food availability, predator competition, habitat quality, flow regime, and human alteration (Turner et al. 1995; Northcote 1997; Schoby and Keeley 2011). Thus, in rivers where local habitat conditions adequately meet their life-history requirements, there may be little need for extensive long-range movements by riverine black bass (e.g., tributaries; Stormer and Maceina 2009; Cottrell 2018; Ingram et al. 2019). Similar variation in movement dynamics has been noted by other black bass populations (e.g., Smallmouth Bass, Todd and Rabeni 1989; Schall et al. 2019; Neosho Bass, Miller and Brewer 2022) and in other riverine fishes (e.g., salmonids, Northcote 1997; Schoby and Keeley 2011; Mollenhauer et al. 2013), reflecting adaptations to diverse habitats.

Having mobile and stationary members within a population confers advantages to population persistence. The percentages of mobile fish represented in my tagged population of Shoal Bass and Largemouth Bass (28% versus 21%, respectively) were slightly lower than in Suwannee Bass (34% mobile; Yeager et al. 2023) and across 62 freshwater fish species (34% mobile; Radinger and Wolter 2014). Populations with a lower proportion of mobile fish may take longer to respond to habitat change, disperse slower, and have lower genetic diversity compared

to populations with more mobile individuals (Gowan et al. 1994; Radinger and Wolter 2014; Shelley et al. 2022). Having both mobile and less mobile members of a population can represent an important strategy in cases of catastrophic population events (Kokko and López-Sepulcre 2006; Albanese et al. 2009; Radinger and Wolter 2014). For example, some minnow species have a highly migratory portion of populations that are suspected to aid recolonization of habitats (Chase et al. 2015), whereas more stationary individuals may be important for population persistence in some areas (Meka et al. 2003). Shoal Bass movements may still exceed those of Largemouth Bass to meet their life-history needs, though it is curious why Largemouth Bass would have larger core home ranges (i.e., 50% KDE). This could relate to density-dependent factors (Marco-Rius et al. 2013). It is increasingly apparent that there is variation in movement and home range exhibited by these species across their ranges. Thus, examination of the proportion and role of mobile individuals (independent of movement magnitude) in other Shoal Bass and Largemouth Bass populations would help inform these populations' potential to recover from natural and human disturbance (Radinger and Wolter 2014). Additionally, similar investigation of the mobility potential of invasive congeners (e.g., Alabama Bass, Spotted Bass) may aid in the understanding of the mechanisms of such invasions (Dakin et al. 2015; Peoples et al. 2021).

As hypothesized, larger movements by both species were presumably associated with spring spawning. Larger movements in spring than other seasons by Flint River populations mirror observations in other black bass populations, and typically coincide with spawning (Goclowski et al. 2013; Cottrell 2018; Schall et al. 2019; Miller and Brewer 2022; Yeager et al. 2023). Support for spawning during that time is evidenced by movement synchronicity between years and my observed timing of age-0 bass hatches (see Chapter 3). Spring movements tend to be associated with the search for suitable spawning habitats (e.g., nesting and rearing), which may not fulfill

adult foraging and growth needs, necessitating adult movement to other locations (Northcote 1997; Lucas et al. 2001). Migrations within freshwater (i.e., potamodromy) are common by a variety of fishes (e.g., salmonids, Northcote 1997; Channel Catfish *Ictalurus punctatus*, Pellett et al. 1998; Colorado Pikeminnow *Ptychocheilus lucius*, Irving and Modde 2000; Paddlefish *Polyodon spathula*, Simcox et al. 2015) including black basses (Barthel et al. 2008; Sammons 2015; Cottrell 2018; Schall et al. 2019; Miller and Brewer 2022). The spawning season for Largemouth Bass appears to occur sooner than spawning for Shoal Bass (see also Chapter 3). Protracted spawning by Largemouth Bass (Isely et al. 1987; Goodgame and Miranda 1993; Rogers and Allen 2009) and earlier hatch timing compared to Shoal Bass (Sammons et al. 2021) has been previously reported. This temporal difference is hypothesized to be related to habitat partitioning and divergent life-history strategies enabling sympatric species occurrence (Wheeler and Allen 2003; Sammons et al. 2021).

Greater movements by females during the spawning season may be related to morphological, energetic, and behavioral differences between the sexes. Interestingly, Shoal Bass movement was related to DOS and sex but none of the environmental covariates I measured. This sex-related movement disparity was observed on Ichawaynochaway Creek (Ingram et al. 2019) and has been observed in several freshwater fish species (salmonids, Lambert and Dodson 1990; Northcote 1997; Largemouth Bass, Waters and Noble 2004; Paddlefish, Miller and Scarnecchia 2011). In my study, adult Shoal Bass females were generally larger than males, a trait commonly associated with increased movement due to greater overall fitness (Minns 1995; Mollenhauer et al. 2013; Radinger and Wolter 2014; Miller and Brewer 2022). Additionally, females may move further in search of optimal feeding habitats to enhance fecundity (e.g., post-spawn), as egg production typically increases with body size (Jonsson and Jonsson 1993; Northcote 1997) and is

often more energetically costly than sperm production in fishes (Wootton 1985; Hayward and Gillooly 2011). Movement magnitude may also relate to the presence (or absence) of males (Brown et al. 2019) and choices associated with mate selection (e.g., females being choosier; Hanson and Cooke 2009; Franckowiak et al. 2017). A better understanding of Shoal Bass mate choice may help elucidate this relationship and could also inform patterns of introgression with non-native congeners (e.g., preference for conspecifics versus heterospecifics; Kozak et al. 2009; Enriquez et al. 2016). Furthermore, investigating differences in habitat selection between sexes during spawning and non-spawning times may help explain these movement behaviors.

In contrast, discharge variability associated with dam operations was negatively related to Largemouth Bass movement. Discharge patterns in the study area are primarily governed by a hydropower dam upstream. Operating as a "run-of-the-river" facility (Couch et al. 1996), this dam maintains some level of natural flow variability within the study area. However, during the study period, CV of discharge was highest during hydropeaking flow releases from Albany Dam rather than natural flood pulses. Thus, the negative relationship may be attributed to unnatural flow fluctuations, potentially reducing habitat connectivity in some locations (Bradford and Heinonen 2008). Moreover, flow fluctuations may relate to behavioral changes where bass are seeking local refuge rather than moving (Liao 2007; Costa et al. 2018). Deviations from natural flow patterns can have negative effects on fish populations (Poff and Allan 1995; Poff and Zimmerman 2010; Young et al. 2011). Examination of the behavioral mechanisms associated with this relationship would be beneficial to see if growth or survival are affected (Costa et al. 2017). Thus, this relationship may be related to Largemouth Bass in the lower Flint River having lower growth rates than both Shoal Bass and reservoir Largemouth Bass in the same system (Sammons et al 2019).

There is a growing body of literature that demonstrates individual variability within movement studies. These phenomena are common in fish movement studies, highlighting the challenge of capturing patterns when movements are influenced by many internal (e.g., genetic, physiological, homing) and external (e.g., abiotic factors, food availability, territoriality, presence of mates) cues (Lucas et al. 2001; Rasmussen and Belk 2017). Under similar generalized additive mixed modeling frameworks, there is 13-47% of deviance explained in fish movements related to both environmental and individual predictors (Dance and Rooker 2015; Becker et al. 2016; Hughes et al. 2022; Pedaccini et al. 2023). Similarly, studies on black bass observe high levels of individual variability that may relate factors such as to body condition and/or reproductive status (Barthel et al. 2008; Sammons 2015; Schall et al. 2019; Miller and Brewer 2021; Yeager et al. 2023). Individual variation in fish movement behaviors is assumed to contribute to population-level robustness and adaptability (e.g., gene flow, recolonization, species turnover; Albanese et al. 2009; Radinger and Wolter 2014).

Missing fish from my study may be attributed to angler exploitation, fish leaving the study area, or predation. Anglers harvested 18% of my tagged fish and many others were caught-and-released by anglers which may affect their movement behavior (Cooke et al. 2002; Halttunen et al. 2010). Unreported exploitation may account for the disappearance of several fish from the study area that were not located via aerial or tributary surveys. Other possibilities include transmitter failure, predation (e.g., alligators, Saalfeld et al. 2011; osprey, eagles, Goclowski et al. 2013; otters Roberts et al. 2008) or some fish left the study area and were undetected on the single aerial flight. It is interesting that one Shoal Bass was detected in the river-reservoir interface and then not detected thereafter suggesting it may have moved downstream out of the study area. Although Shoal Bass are considered riverine fishes, a variety of other black bass species can tolerate

reservoir conditions (Sammons et al. 1999; Hunter and Maceina 2008; Barthel et al. 2008). Despite the high exploitation and some missing tagged fish, I was able to detect a large number of fish, thereby limiting significant effects on my study results.

The majority of my tagged fish appeared to remain in my study area during my 15-month study. It is not uncommon for some populations to be observed to stay primarily in mainstem rivers or tributaries (e.g., Rainbow Trout *Oncorhynchus mykiss*, Meka et al. 2003; Flathead Catfish *Pylodictis olivaris*, Vokoun and Rabeni 2005b). For example, Neosho Bass avoided reservoirs or river-reservoir interfaces despite connectivity (Miller and Brewer 2022). Likewise, Ingram et al. (2019) observed no telemetered Shoal Bass leaving Ichawaynochaway Creek (i.e., entering the lower Flint River), although that study also occurred over a 1-year period. These patterns are restricted to our observational period which tends to be a few years or less. Genetics studies reveal population mixing often occurs (Stepien et al. 2007; Underwood et al. 2016), but the temporal scale is much larger than the period over which tracking studies typically occur (Underwood et al. 2016). A future study addressing population mixing via genetic testing may be beneficial to our understanding of how these populations interact (Fontaine et al. 1997; Schall et al. 2017).

I observed locations where my tagged fish commonly aggregated suggesting they may be important to spawning or barriers to upstream movements (or both). Shoal Bass had denser aggregations compared to Largemouth Bass, reflecting differences in spawning habitat requirements or behaviors (Wheeler and Allen 2003; Bitz et al. 2015; Sammons et al. 2021). Individuals of both species congregated below Albany Dam (RKM 164) during the spring seasons of both years but were rarely present there during other periods. This observation is supported by the high numbers of age-0 bass collected here during this study (see Chapter 3). These observations suggests that Albany Dam may be an upstream barrier to movement even though we observed

some successful spawning at those locations. Additional areas of heavy spring use by both species included the shoal complexes known as Goat Island and Hell's Gate. These areas are characterized by rocky shoals, mid-channel islands, and channel complexity (i.e., areas of current refugia, diversity of channel units; Jungwirth et al. 1993; O'Neill and Thorp 2011) and appear similar to areas of spawning aggregation in other portions of the Shoal Bass's range (Gocłowski et al. 2013; Bitz et al. 2015; Cottrell 2018). However, many other areas within my study area share similar characteristics. There is a shoal complex located at RKM 125 which was rarely used by tagged fish during my study, except via upstream and downstream movements. However, Ingram et al. (2013) documented this location as important for spawning fishes, so such locations may vary over time. There may be spatial and temporal variation in black bass spawning habitats within these populations. Interannual variation in spawning locations is not uncommon in freshwater fishes (e.g., Bluehead chub *Nocomis leptocephalus*, Bolton et al. 2015; darters *Etheostoma* spp., Roberts and Angermeier 2007; Chinook Salmon *Oncorhynchus tshawytscha*, Cram et al. 2017) and may relate to flow, temperature, and sediment patterns (Beechie and Moir 2008; Flowers et al. 2009; Kemp et al. 2011; Qiu et al. 2023), and the behaviors of fish as the presence of spawning partners and behaviors cue spawning for many species (Kekäläinen et al. 2011; Brown et al. 2019). Moreover, riverine habitat changes over time (Frissell et al. 1986; Ward 1989; Thorp et al. 2006) such that habitat that is suitable for spawning may vary. Efforts to understand longer-term patterns in spawning success would benefit our ability to conserve Shoal Bass (Humphries et al. 2002; Krabbenhoft et al. 2014) given stocking has been used to supplement successful spawning in some years (T. Ingram, GADNR, personal communication).

My results indicate there are several management and conservation possibilities that could be considered to improve Largemouth Bass and Shoal Bass and populations. Because I observed



successful hatches by Largemouth Bass across the catchment (see Chapter 3), the primary concern for the population appears to be exploitation that can be managed through regulations. Shoal Bass populations, however, face a myriad of threats. Fish congregating during critical times of the year leave these fish vulnerable to exploitation. An ongoing study on the lower Flint River has observed high exploitation, especially at the dam during the spawning period (S. Brewer, USGS, personal communication). Moreover, aggregation behavior that I and others have observed by endemic black basses (Goclowksi et al. 2013; Bitz et al. 2015; Cottrell 2018; Miller et al. 2021) suggests increased vulnerability to overexploitation at specific locations and times (Erisman et al. 2017). Management strategies such as protected areas or closed seasons (i.e., catch-and-release only) could mitigate potential angling pressure (Suski et al. 2002; Suski and Cooke 2007; Sammons 2019), as successfully implemented in other black bass populations (e.g., black bass closed season in the Ozark Highlands of Missouri; catch-and-release only areas and times in Pennsylvania). This may be especially important to consider for Shoal Bass given agencies have had to stock fish during some years to bolster recruitment (T. Ingram, GADNR, personal communication). Although it is unlikely that large dam removal is a viable option, examining possible passage strategies have been done on several large rivers (Bunt et al. 2012; Simcox et al. 2015) and may be an option. Moreover, revisiting dam operations such that hatching success increases is another consideration (see Chapter 3). Lastly, maintaining the current structure of shoals for spawning seems prudent; consideration for restoring shoals is possible though estimated to be very costly (Dobes et al. 2013; Williams 2015; Bakke et al. 2020).

## Chapter II Tables

Table 1. Environmental covariates that influence black bass movement with their associated units, data source, and ecological importance.

<i>Covariate</i>	<i>Unit</i>	<i>Gear/Source</i>	<i>Justification and citation</i>
Temperature	°C	Hobo Pendant Logger, NEON buoy, U.S. Geological Survey stream gauge	Temperature changes cue stream fish movement for varying life history stages, particularly reproduction <sup>1,2,3</sup>
Discharge	m <sup>3</sup> /s	USGS stream gauge	Streamflow is correlated with migratory and non-migratory fish movement <sup>4</sup>
Day of year	1 d	Calendar day	Movement by black bass varies seasonally and with photoperiod <sup>5,6,7,8</sup>

1. (Graham and Orth 1986) 2. (Peterson and Rabeni 1996) 3. (Northcote 1997) 4. (Taylor and Cooke 2012) 5. (Gocłowski et al. 2013) 6. (Ingram et al. 2019) 7. (Todd and Rabeni 1989) 8. (Miller and Brewer 2022)

Table 2. Pearson's Correlation matrix (rho values) for environmental covariates used for movement analysis. All covariates were calculated between relocations for each movement value. DOS = day of study, Mean Q = mean daily discharge (m<sup>3</sup>/s), Mean Temp = mean daily temperature (°C), CV Q = coefficient of variation in instantaneous (15 minute) values of discharge, CV Temp = coefficient of variation in mean daily values of temperature, ROC Temp = rate of change in mean daily temperature, ROC Q = rate of change in mean daily discharge.

	DOS	Mean Q	Mean Temp	CV Q	CV Temp	ROC Temp	ROC Q
DOS	1.00						
Mean Q	0.29	1.00					
Mean Temp	-0.51	-0.59	1.00				
CV Q	0.01	0.34	-0.21	1.00			
CV Temp	0.16	0.26	-0.62	0.41	1.00		
ROC Temp	-0.10	0.22	0.14	0.09	-0.17	1.00	
ROC Q	0.04	-0.04	-0.02	0.11	0.01	-0.29	1.00

Table 3. Summary of considered *a priori* generalized additive mixed models for assessing linear and non-linear relationships between Largemouth Bass and Shoal Bass daily movement rate (m/d). All covariates were calculated between relocations for each movement value. DOS = day of study, Mean Q = mean daily discharge (m<sup>3</sup>/s), Mean Temp = mean daily temperature (°C), CV Q = coefficient of variation in instantaneous (15 minute) values of discharge, ROC Temp = rate of change in mean daily temperature, ROC Q = rate of change in mean daily discharge. Sex = sex of individual fish (categorical where female was the reference). s() denotes smoothed terms. The random effect of individual was included in all models. Preliminary models to assess temporal autocorrelation are denoted with “\*”.

Model Description
~ s(DOS)*
~ s(DOS) + corSpher(~DOS FishID)*
~ s(DOS) + s(Mean Q)
~ s(DOS) + s(Mean T)
~ s(DOS) + s(CV Q)
~ s(DOS) + s(ROC T)
~ s(DOS) + s(ROC Q)
~ s(DOS) + Sex
~ s(DOS) x s(Mean Q)
~ s(DOS) x s(Mean T)
~ s(DOS) x s(CV Q)
~ s(DOS) x s(ROC T)
~ s(DOS) x s(ROC Q)
~ s(DOY) x Sex

Table 4. Summary of tagged fish demographics, tagging dates, and fate of the tagged fish if known. Tag number, sex (Male (M) or Female (F)), length (TL, mm), weight (WT, g), tagging date, last date located (or harvested), and number of relocations (N) of adult Shoal Bass and Largemouth Bass implanted with radio tags in the lower Flint River are provided. Fate is defined as: Alive = Located on final tracking event; Harvested = angler harvest; Lost = fish no longer detected; Fatality = fish was killed via boat propeller during a separate DNR sampling event. Tag numbers with letters associated indicate transmitter was used again to tag another fish post-harvest or mortality.

	Tag	Sex	TL	WT	Tag Date	Last Date	Days at Large	N	Fate
Largemouth Bass	11	F	488	1900	2/16/2022	8/4/2022	169	12	Lost
	43b	F	509	1644	3/30/2022	5/10/2023	406	26	Alive
	52a	M	408	976	2/17/2022	7/22/2022	155	12	Harvested
	52b	M	383	718	9/27/2022	12/21/2022	85	5	Lost
	72	F	421	1190	2/15/2022	5/9/2023	448	33	Alive
	112	M	434	2074	2/15/2022	5/9/2023	448	32	Alive
	121	M	410	1016	2/17/2022	12/21/2022	307	15	Lost
	132	F	590	3570	2/17/2022	5/10/2023	447	28	Alive
	153	F	516	2534	2/16/2022	5/9/2023	447	28	Alive
	162	F	540	2450	2/16/2022	5/9/2023	447	30	Alive
182	M	395	894	2/16/2022	5/9/2023	447	31	Alive	

203b	M	427	1158	9/26/2022	12/21/2022	86	5	Lost
241	F	554	2818	2/15/2022	5/10/2023	449	29	Alive
292	F	399	776	2/16/2022	5/11/2023	449	27	Alive
313	F	570	2958	4/6/2022	5/9/2023	398	24	Alive
332	M	489	1492	3/30/2022	5/9/2023	405	29	Alive
381	F	565	2674	4/6/2022	8/10/2022	126	11	Lost
392	F	595	3214	3/30/2022	5/9/2023	405	26	Alive
401a	M	378	620	3/30/2022	6/13/2022	75	8	Harvested
401b	M	486	1540	8/8/2022	5/10/2023	275	14	Alive
451	M	326	474	3/30/2022	8/2/2022	490	12	Lost
460	F	541	2764	4/6/2022	5/5/2022	29	3	Lost
471a	F	393	758	3/30/2022	5/20/2022	51	5	Harvested
471b	F	405	992	6/6/2022	8/1/2022	56	3	Harvested
471c	F	515	2138	8/8/2022	5/10/2023	275	17	Alive
492	F	509	1850	3/30/2022	5/9/2023	405	26	Alive
503	F	408	970	3/30/2022	4/26/2023	392	24	Alive
522	F	471	1880	4/6/2022	5/9/2023	398	28	Alive
542	F	551	2286	4/6/2022	4/12/2022	6	1	Lost
552	M	443	1140	4/4/2022	6/3/2022	60	6	Harvested
562	F	403	992	4/4/2022	5/11/2023	402	27	Alive
571	F	514	2128	4/6/2022	5/10/2023	399	27	Alive

## Shoal Bass

582	M	495	1678	3/30/2022	5/10/2023	406	27	Alive
591	F	365	654	4/4/2022	5/10/2023	401	27	Alive
602	F	340	528	3/30/2022	5/10/2023	406	28	Alive
22	F	506	2028	2/15/2022	5/9/2023	448	27	Alive
32	M	524	2032	2/16/2022	5/9/2023	447	33	Alive
43a	M	453	1446	2/16/2022	3/23/2022	35	1	Harvested
63	F	486	1720	2/15/2022	5/9/2023	448	31	Alive
82	M	452	1222	2/16/2022	3/30/2023	407	26	Lost
91	M	472	1530	2/16/2022	5/10/2023	448	32	Alive
100	M	449	1080	2/17/2022	5/10/2023	447	33	Alive
140a	F	433	1124	2/16/2022	5/9/2022	82	8	Fatality
140b	F	453	1438	5/9/2022	5/9/2023	365	24	Alive
172	M	454	1270	2/16/2022	9/1/2022	197	16	Harvested
191a	F	541	2270	2/17/2022	8/13/2022	177	13	Harvested
191b	M	383	580	10/27/2022	5/10/2023	195	14	Alive
203a	F	532	2174	2/17/2022	7/18/2022	151	12	Harvested
211a	M	450	1292	2/17/2022	9/12/2022	207	14	Harvested
211b	M	344	528	11/2/2022	5/9/2023	188	14	Alive
223	F	540	2536	2/16/2022	5/9/2023	447	33	Alive
233	M	397	832	2/15/2022	4/21/2022	65	6	Lost
252	M	496	1520	3/30/2022	5/10/2023	406	26	Alive

262	M	521	1756	2/15/2022	5/9/2023	448	29	Alive
274	F	525	2240	2/16/2022	5/9/2023	447	33	Alive
282	M	430	1022	2/17/2022	5/10/2023	447	31	Alive
302	M	481	1482	2/17/2022	4/13/2023	420	28	Alive
322	F	533	2164	4/4/2022	5/10/2023	401	33	Alive
341	M	369	804	4/4/2022	11/22/2022	232	12	Lost
352	M	370	634	4/4/2022	5/10/2023	401	27	Alive
361	F	452	1298	4/4/2022	5/10/2023	401	28	Alive
371a	F	441	1214	4/4/2022	10/4/2022	183	10	Harvested
371b	F	383	696	10/27/2022	5/11/2023	196	15	Alive
412a	M	403	904	4/4/2022	8/1/2022	119	9	Harvested
412b	M	498	1604	8/8/2022	5/10/2023	275	17	Alive
421	M	388	776	3/30/2022	5/10/2023	406	23	Alive
432	F	433	1194	4/1/2022	5/9/2023	403	23	Alive
442	F	537	2040	4/4/2022	5/10/2023	401	29	Alive
482	F	428	1004	4/1/2022	6/3/2022	63	8	Lost
513a	M	377	674	3/30/2022	5/3/2022	34	3	Harvested
513b	M	498	2122	6/6/2022	5/9/2023	337	21	Alive
532	F	511	1752	3/30/2022	5/10/2023	406	29	Alive



Table 5. Movement analysis covariate means, standard deviations (SD), and ranges (minimum and maximum values). All covariates were measured over the time interval of the movement (i.e., between relocations) unless noted otherwise. DOS = day of study (recorded on last day of each movement), Mean Q = mean daily discharge (m<sup>3</sup>/s), CV Q = coefficient of variation of instantaneous (15 min) values of discharge, ROC Q = rate of change in mean daily discharge, Mean Temp = mean daily temperature (°C), CV Temp = coefficient of variation of mean daily temperature, ROC Temp = rate of change in mean daily temperature.

Covariate	Mean	SD	Min	Max
DOS	233.26	144.5	24	437
Mean Q	166.91	127.94	46.44	848.56
CV Q	21.98	11.62	3.42	59.3
ROC Q	-1.48	16.7	-65.45	91.08
Mean Temp	21.21	5.69	8.54	30.82
CV Temp	4.67	3.81	0.79	20.39
ROC Temp	0.04	0.24	-0.69	0.63

Table 6. Summary statistics of estimated linear, 50% kernel-density estimated, and 90% kernel-density estimated home ranges for adult telemetered Shoal Bass and Largemouth Bass in the lower Flint River. Mean, standard-errors ( $\pm$ ), and ranges (in parentheses) for each group of fish is presented. Linear home range is the distance between the most upstream and most downstream locations. Kernel estimates were produced by a univariate, fixed kernel density estimate that was calculated on the distribution of relocations for each individual. Two individuals (one per species) were not included in estimates due to only being relocated once. Mobile Largemouth Bass and Shoal Bass were individuals with  $\geq 16.0$  or  $\geq 24.6$  km long linear home ranges, respectively.

Predictor	N	Linear home range (m)	Kernel estimate (km)	
			90%	50%
Largemouth Bass	34	12345.22 $\pm$ 3700.95	11.76 $\pm$ 4.16	5.67 $\pm$ 2.89
Mobile	7	47130.35 $\pm$ 10801.69 (18056.78 - 90855.14)	45.25 $\pm$ 14.54 (0.54 - 101.96)	23.80 $\pm$ 12.34 (0.18 - 78.32)
Stationary	27	3326.85 $\pm$ 743.95 (61.59 - 15293.6)	3.08 $\pm$ 0.95 (0.06 - 19.35)	0.97 $\pm$ 0.32 (0.02 - 7.09)
Shoal Bass	36	20249.98 $\pm$ 4356.23	21.72 $\pm$ 5.6	4.42 $\pm$ 1.59
Mobile	10	58005.00 $\pm$ 6002.63 (24662 - 92090)	64.09 $\pm$ 12.26 (0.83 - 125.33)	11.3 $\pm$ 4.77 (0.14 - 35.48)
Stationary	26	5728.82 $\pm$ 1196.78 (9.38 - 22570)	5.42 $\pm$ 1.35 (0.26 - 31.02)	1.77 $\pm$ 0.86 (0.08 - 21.58)
All fish	70	16410.53 $\pm$ 2912.04	16.88 $\pm$ 3.54	5.03 $\pm$ 1.61

Table 7. Summary statistics for movement rates of radio-tagged adult Largemouth Bass and Shoal Bass. Movement rates were calculated as the fluvial distance moved between relocations divided by the duration of time between relocations. Means, standard-errors ( $\pm$ ), coefficients of variation (CV), max movement rate, and max movement are reported. Max Movement = longest recorded movement one way (upstream or downstream; duration of movement in days in parentheses).

Species	Sex	N	Mean movement rate (m/d)	CV of movement rate	Max movement rate (m/d)	Max movement (m)
Largemouth Bass		35	193.77 $\pm$ 27.06	356.11		
	F	21	200.5 $\pm$ 34.55	371.99	8,981.22	90,531.42 (12)
	M	12	176.71 $\pm$ 38.63	296.58	4,058.25	50,380.12 (20)
Shoal Bass		37	250.7 $\pm$ 40.87	440.18		
	F	16	323.16 $\pm$ 70.69	400.43	15,614.37	88,453.04 (19)
	M	21	189.1 $\pm$ 45.74	480.17	7,715.31	50,380.12 (7)

Table 8. Top ranked generalized additive mixed models describing the relationship between movement of adult Shoal Bass (SHB) and Largemouth Bass (LMB) and my covariates. Only one model per species met the criteria for being considered my top model. The random effect of individual was included in all models. Model description = covariates included: + indicates the covariates are additive in the model; x indicates an interaction between two covariates; CV Q =  $\log_e$  transformation of the coefficient of variation for discharge measured between relocations. s() denotes smoothed terms.  $AIC_c$  = AIC corrected for small sample size,  $\Delta AIC_c$  = the difference of between each model and the top ranked model,  $w_i$  = Akaike weight, df = degrees of freedom, logLik = log-likelihood, Deviance explained = proportion of the deviance in residuals that is explained by fixed and random effects.

Species	Model description	df	logLik	$AIC_c$	$\Delta AIC_c$	$w_i$	Deviance explained
SHB	s(Day of study) x Sex	45	-3511.64	7119.38	0	0.99	30.2%
LMB	s(Day of study) + CV Q	46	-3161.07	6421.79	0	0.98	36.1%

Table 9. Estimates of each covariate included in the top generalized additive mixed models related to the movement rates of Shoal Bass (SHB) and Largemouth Bass (LMB). For non-linear smoothed s() terms: edf = effective degrees of freedom, F = F-statistic, P = p-value. For linear terms: the standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Individual = random effect of individual fish, DOS = day of study, Male/Female = categorical fixed effect of sex interacting with DOS (day of study), CV Q = the coefficient of variation for discharge measured between relocations.

<i>Non-linear terms</i>				
Species	Covariate	edf	F	P
SHB	s(DOS) x Female	6.21	6.71	<0.0001
	s(DOS) x Male	7.78	18.05	<0.0001
	s(Individual)	23.72	5.44	<0.0001
LMB	s(DOY)	12.04	19.63	<0.0001
	s(Individual)	26.74	20.65	<0.0001

<i>Linear terms</i>					
	Covariate	Estimate	SE	95% CI	P
LMB	Intercept	4.04	0.22	(3.62, 4.47)	<0.0001
	CV Q	-0.21	0.06	(-0.32, -0.10)	0.0003

## Chapter II Figures

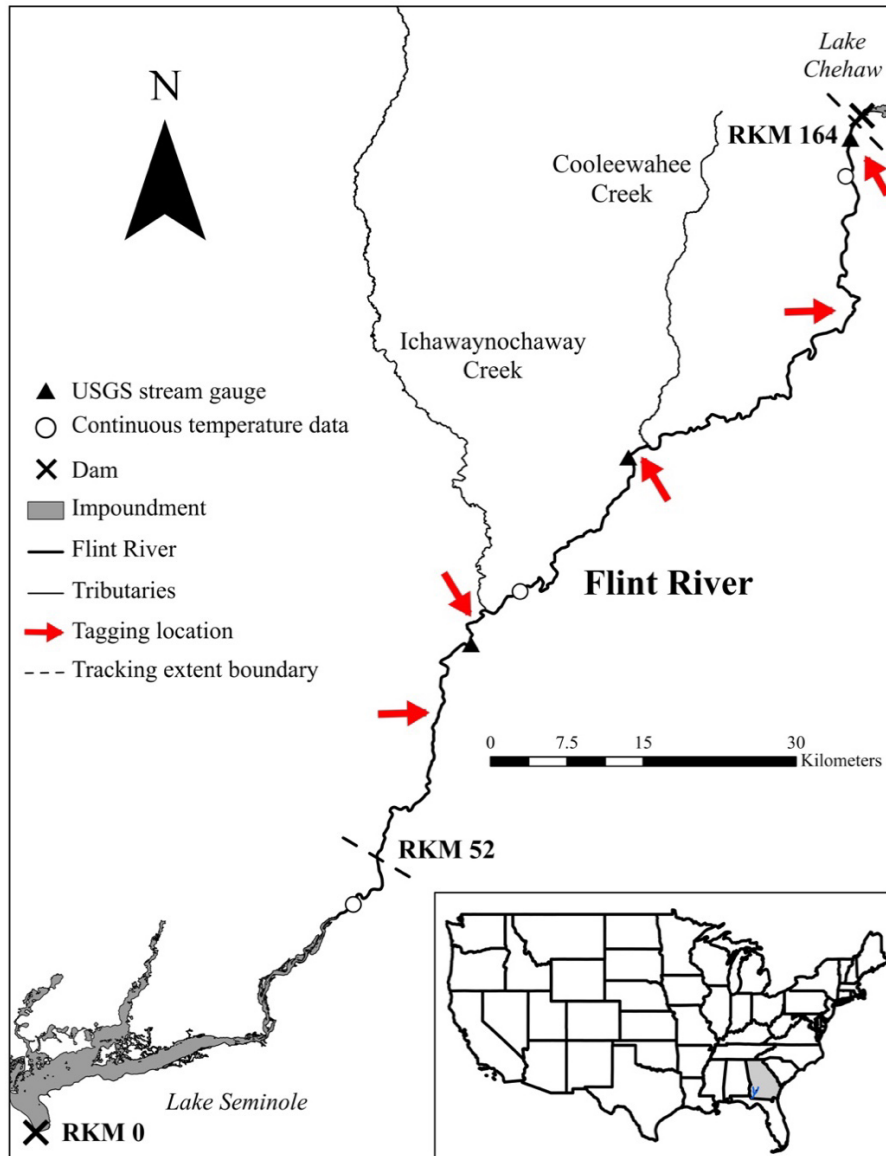


Figure 1: The lower Flint River catchment showing the study extent for movement analysis. Dashed lines indicate the section of river that was scanned during each tracking event from Albany Dam to Flint River Heights Boat Ramp. Black x's represent reservoir dams, black triangles are U.S. Geological Survey stream gauge locations, white circles are locations of continuous temperature data. The black line is the lower Flint River, light gray lines are major tributaries, and gray polygons are impoundments. Red arrows indicate areas where fish were captured, tagged, and released.

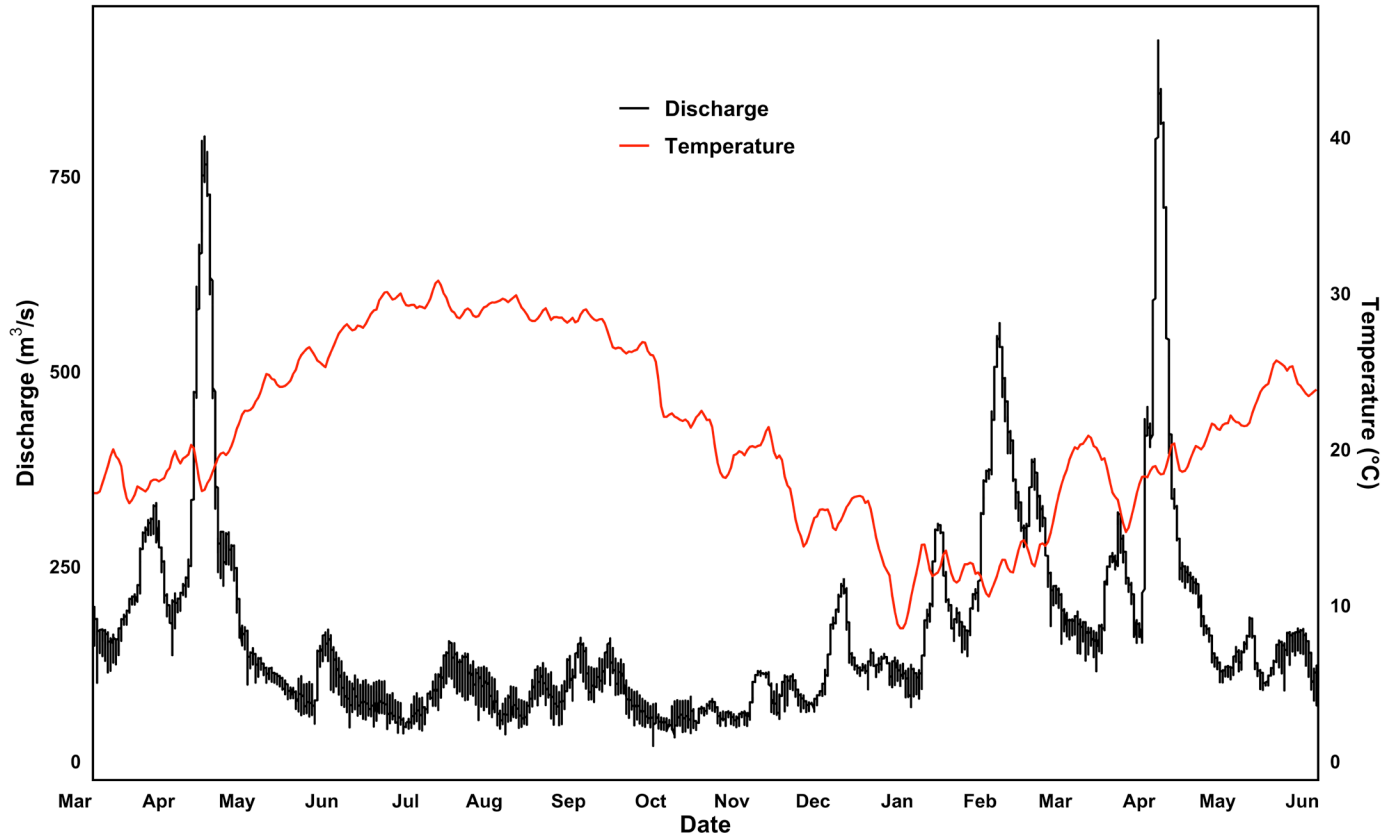


Figure 2. Water discharge (black) and temperature (red) conditions for the lower Flint River during the March 2022-May 2023 study of adult Shoal Bass and Largemouth Bass movement and habitat selection. Temperature values are averaged daily across data collected from continuous Hobo temperature logger (RKM 159), NEON station (RKM 86.5), and a U.S. Geological Survey stream gauge (02356000; RKM 43). Discharge values are averaged at 15-min intervals across data from three USGS stream gauges (02352500, 02353000, 02355662).

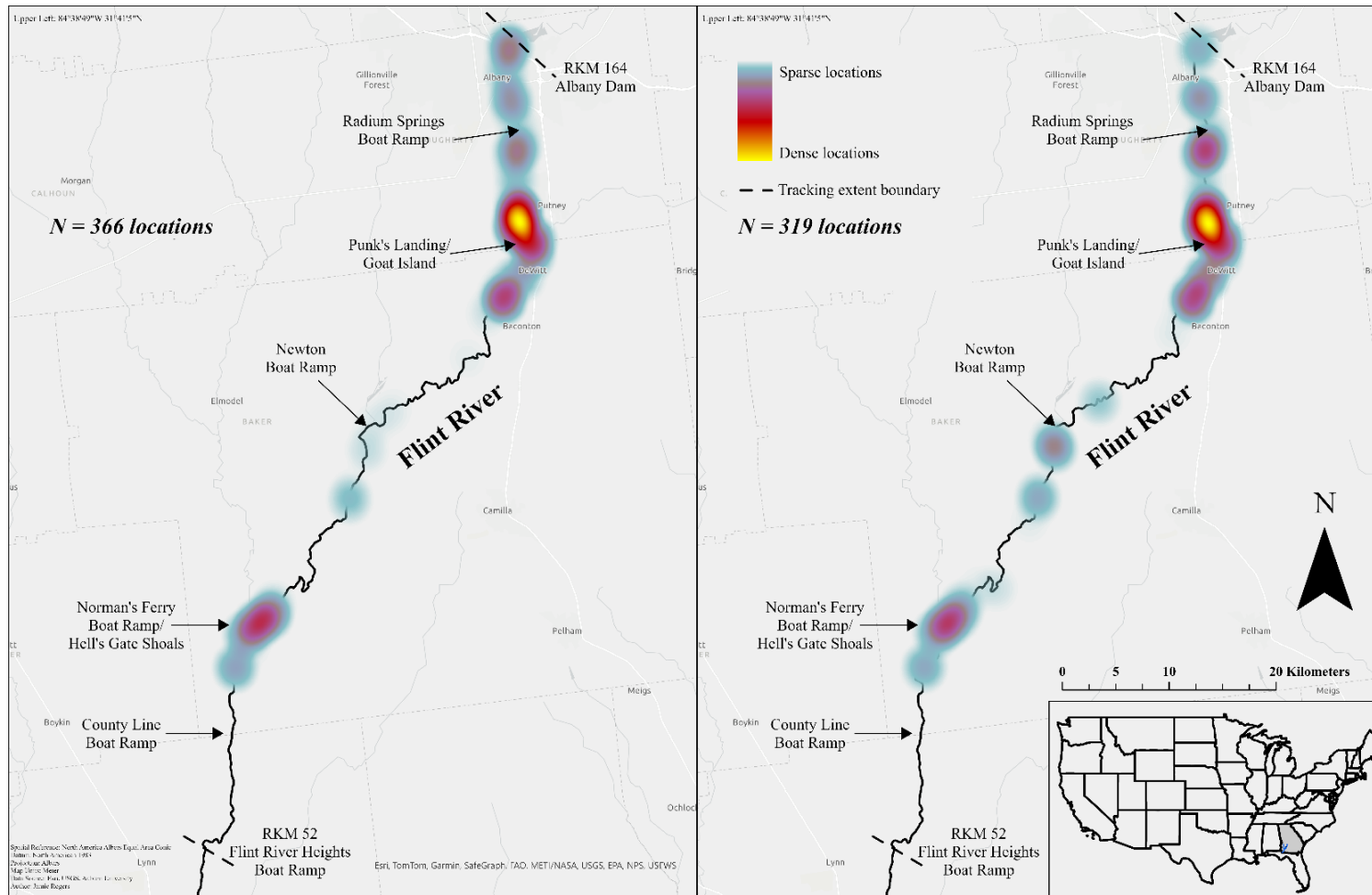


Figure 3. Aggregations of tagged Largemouth Bass during study period (March 2022 – May 2023). The left panel is during spring of both years and the right panel is during summer, autumn, and winter. Yellow denotes denser aggregation while blue indicates fewer fish in the same area. The black line is the lower Flint River and dashed lines indicate the section of river that was scanned during each tracking event from Albany Dam to Flint River Heights Boat Ramp. Notable landmarks are pointed out. Number of locations (N) is how many fish relocations were recorded for each period of time.



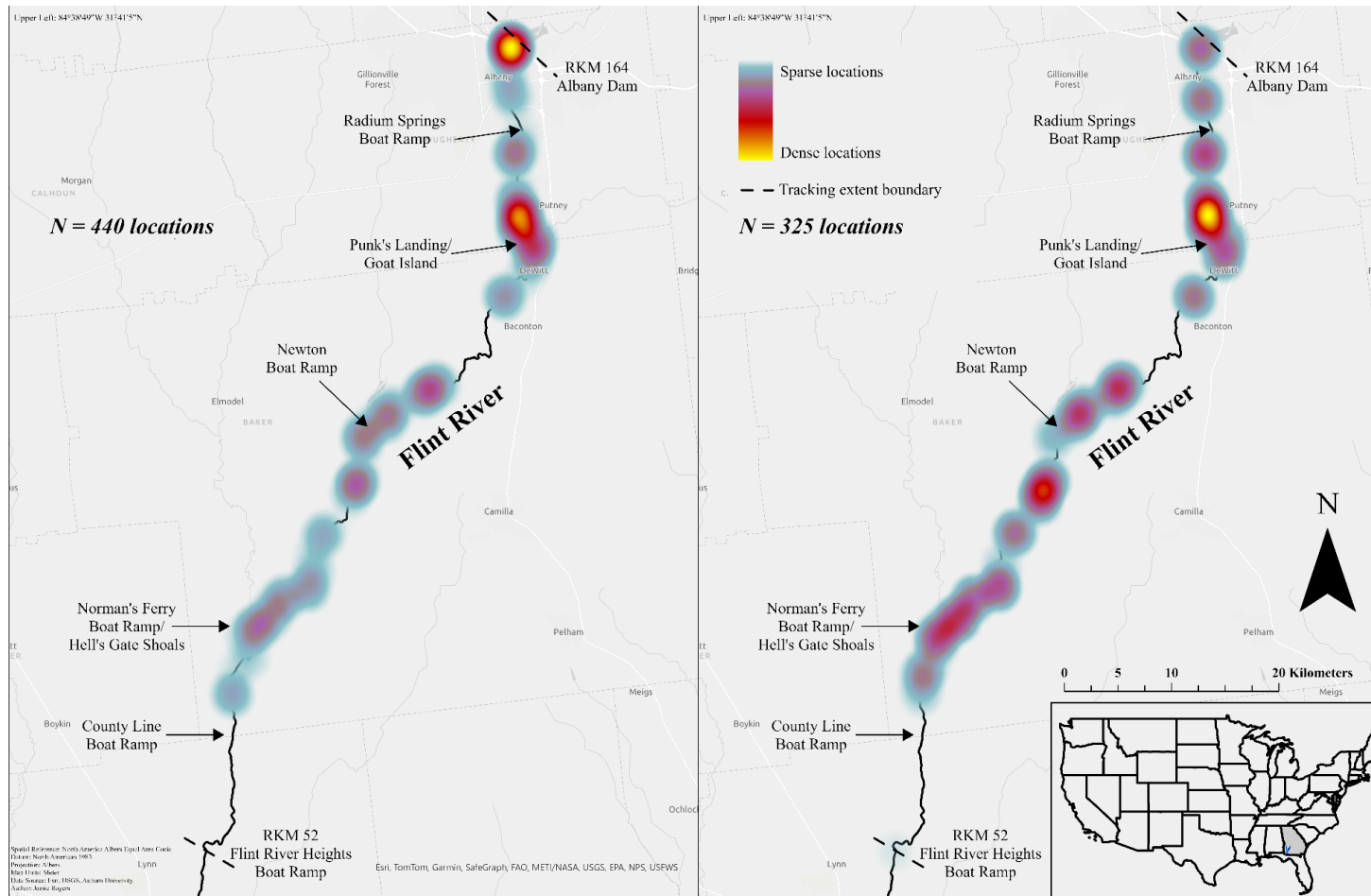


Figure 4. Aggregations of tagged Shoal Bass during study period (March 2022 – May 2023). The left panel is during spring of both years and the right panel is during summer, autumn, and winter. Yellow denotes denser aggregation while blue indicates fewer fish in the same area. The black line is the lower Flint River and dashed lines indicate the section of river that was scanned during each tracking event from Albany Dam to Flint River Heights Boat Ramp. Notable landmarks are pointed out. Number of locations (N) is how many fish relocations were recorded for each period of time.

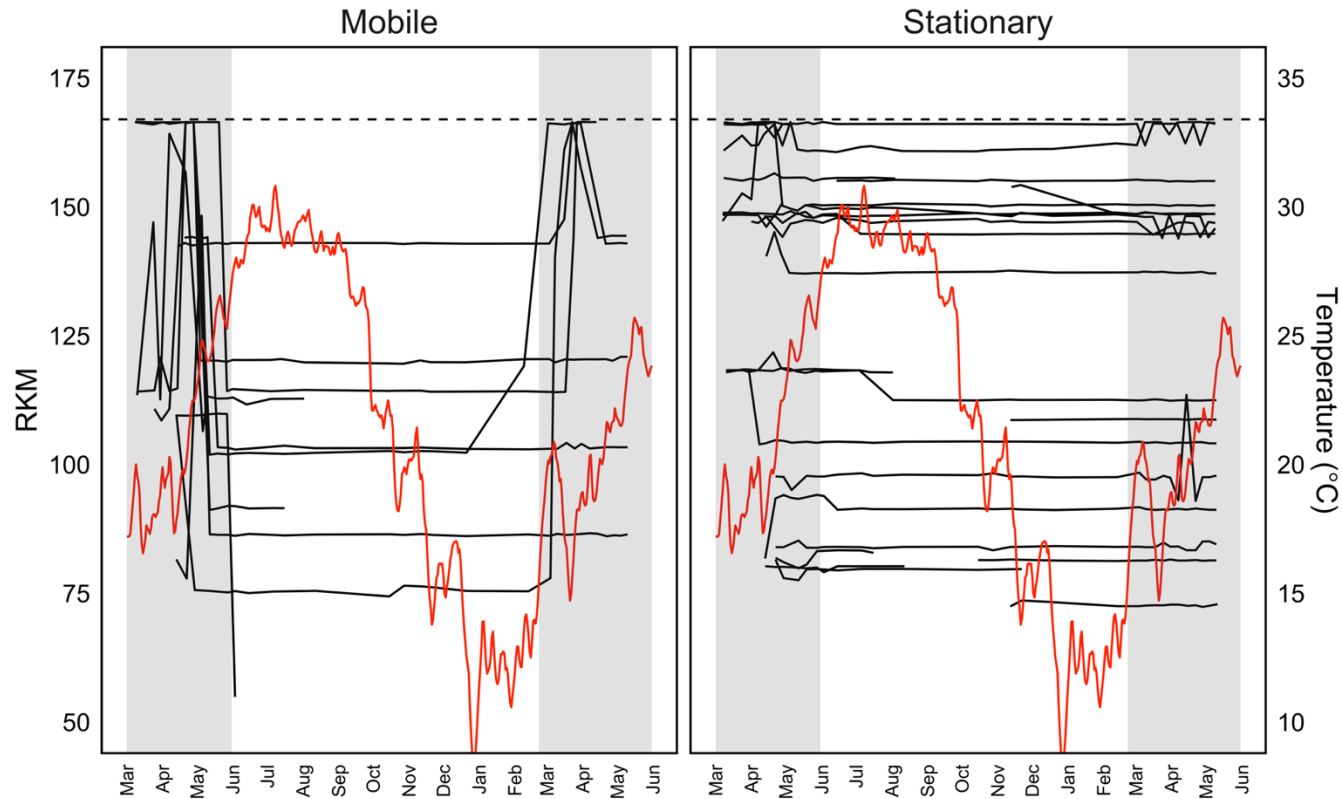


Figure 5. Mobile and stationary adult Shoal Bass movement patterns during study period (March 2022 – May 2023). Left y-axis is river kilometers going downstream to upstream (bottom to top) with RKM 0 being Jim Woodruff Lock and Dam and RKM 164 being Albany Dam (dashed horizontal line). Right y-axis is temperature (red line, °C). Black lines indicate individual fish locations connected between relocations. Lines that end abruptly indicate fish was harvested or no longer located at subsequent tracking events. Mobile fish (Shoal Bass with linear home ranges  $\geq 24.6$  RKM long) are displayed on the left panel, stationary fish (Shoal Bass with linear home ranges  $< 24.6$  RKM long) are displayed on the right panel. Gray shaded regions indicate the spring seasons (i.e., presumed spawning season; temperature increasing from 15-25°C).

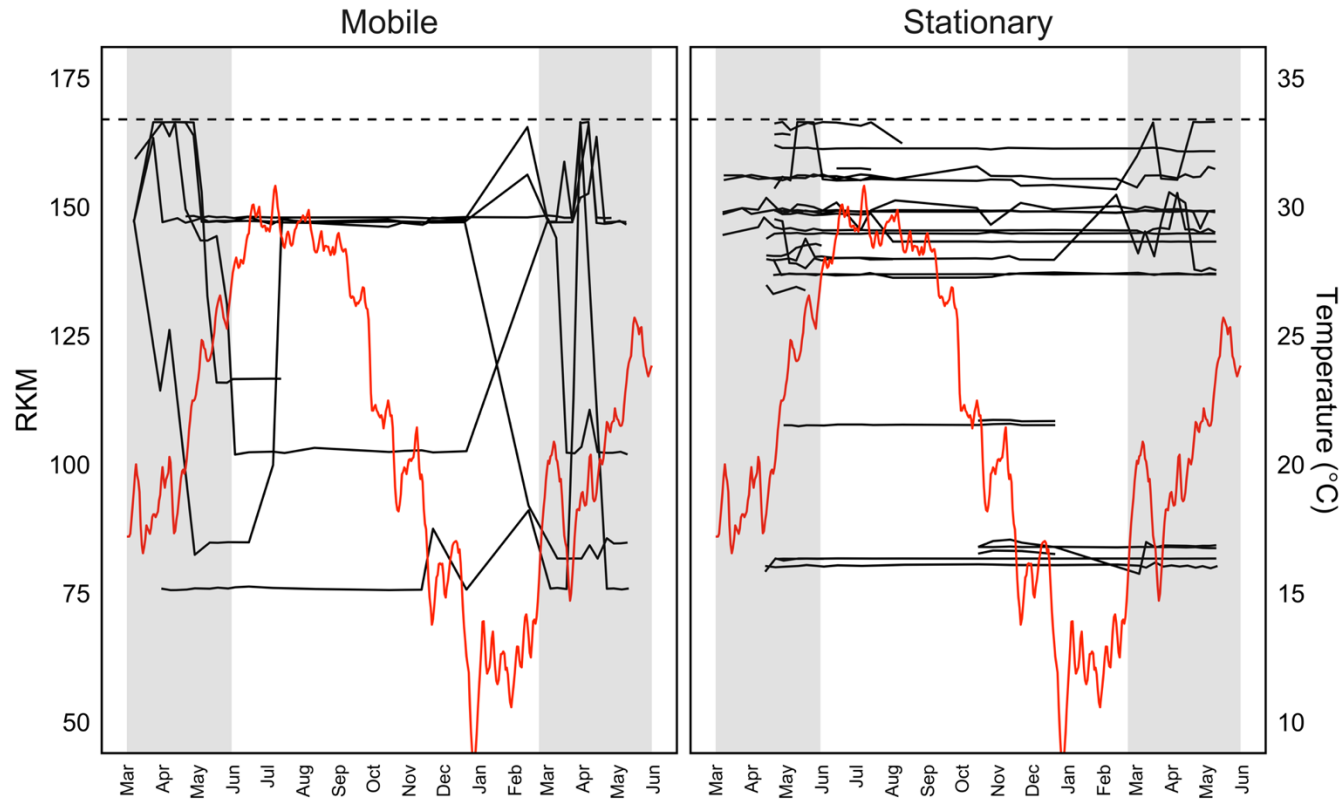


Figure 6. Mobile and stationary adult Largemouth Bass movement patterns during study period (March 2022 – May 2023). Left y-axis is river kilometers going downstream to upstream (bottom to top) with RKM 0 being Jim Woodruff Lock and Dam and RKM 164 being Albany Dam (dashed horizontal line). Right y-axis is temperature (red line, °C). Black lines indicate individual fish locations connected between relocations. Lines that end abruptly indicate fish was harvested or no longer located at subsequent tracking events. Mobile fish (Largemouth Bass with linear home ranges  $\geq 16.0$  RKM long) are displayed on the left panel, stationary fish (Largemouth Bass with linear home ranges  $< 16.0$  RKM long) are displayed on the right panel. Gray shaded regions indicate the spring seasons (i.e., presumed spawning season; temperature increasing from 15-25°C).

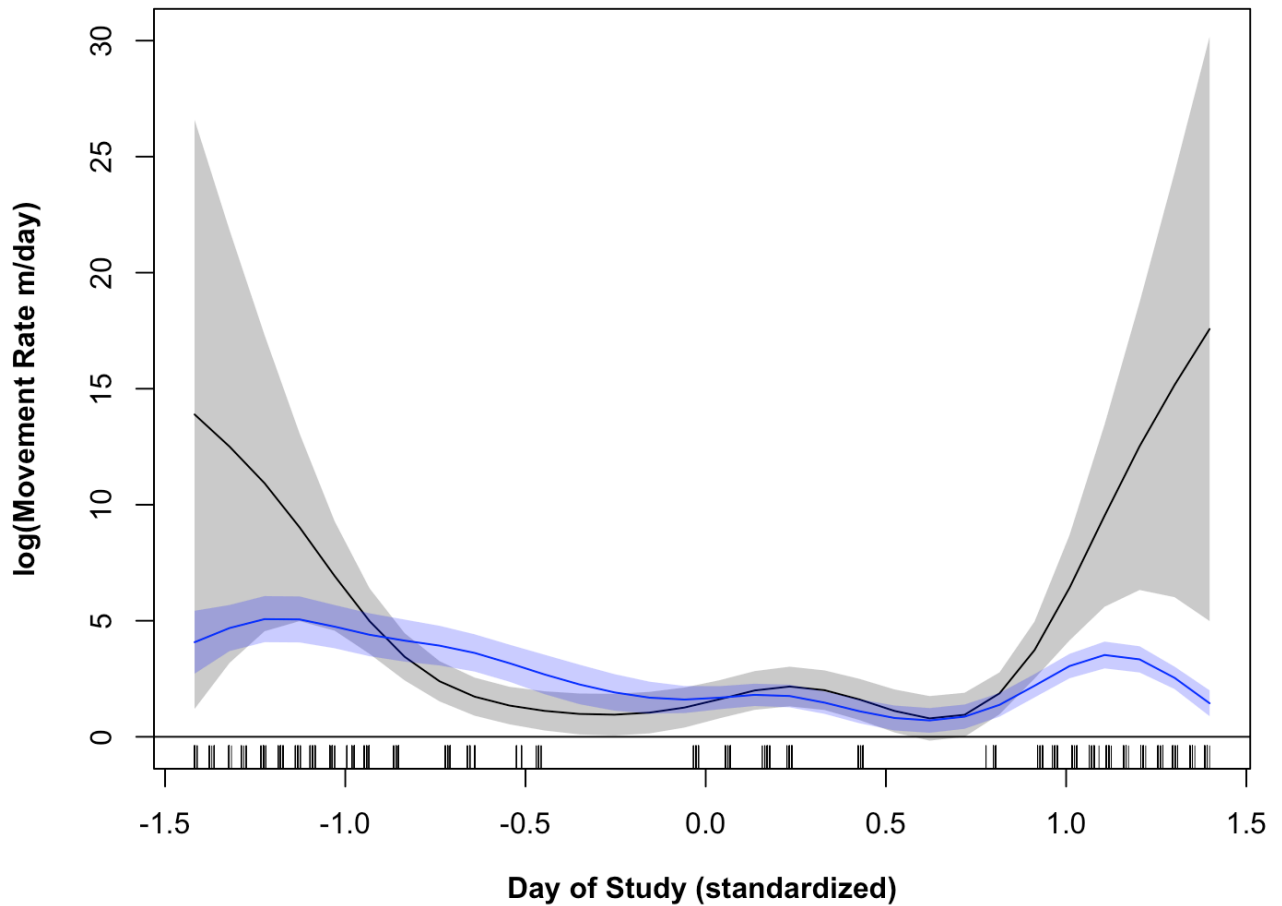


Figure 7. Summary of the interaction between fish sex and day of study (time) for radio tagged adult Shoal Bass. The black line represents the predicted relationship for females and the blue line represents the predicted relationship for males. Shaded regions indicate the 95% confidence intervals. The x-axis is the day of study (standardized) with day 1 being March 1<sup>st</sup>, 2022 and the final day of the study being May 5<sup>th</sup>, 2023. The y-axis shows the natural-log-transformed model-predicted movement rate in meters per day.

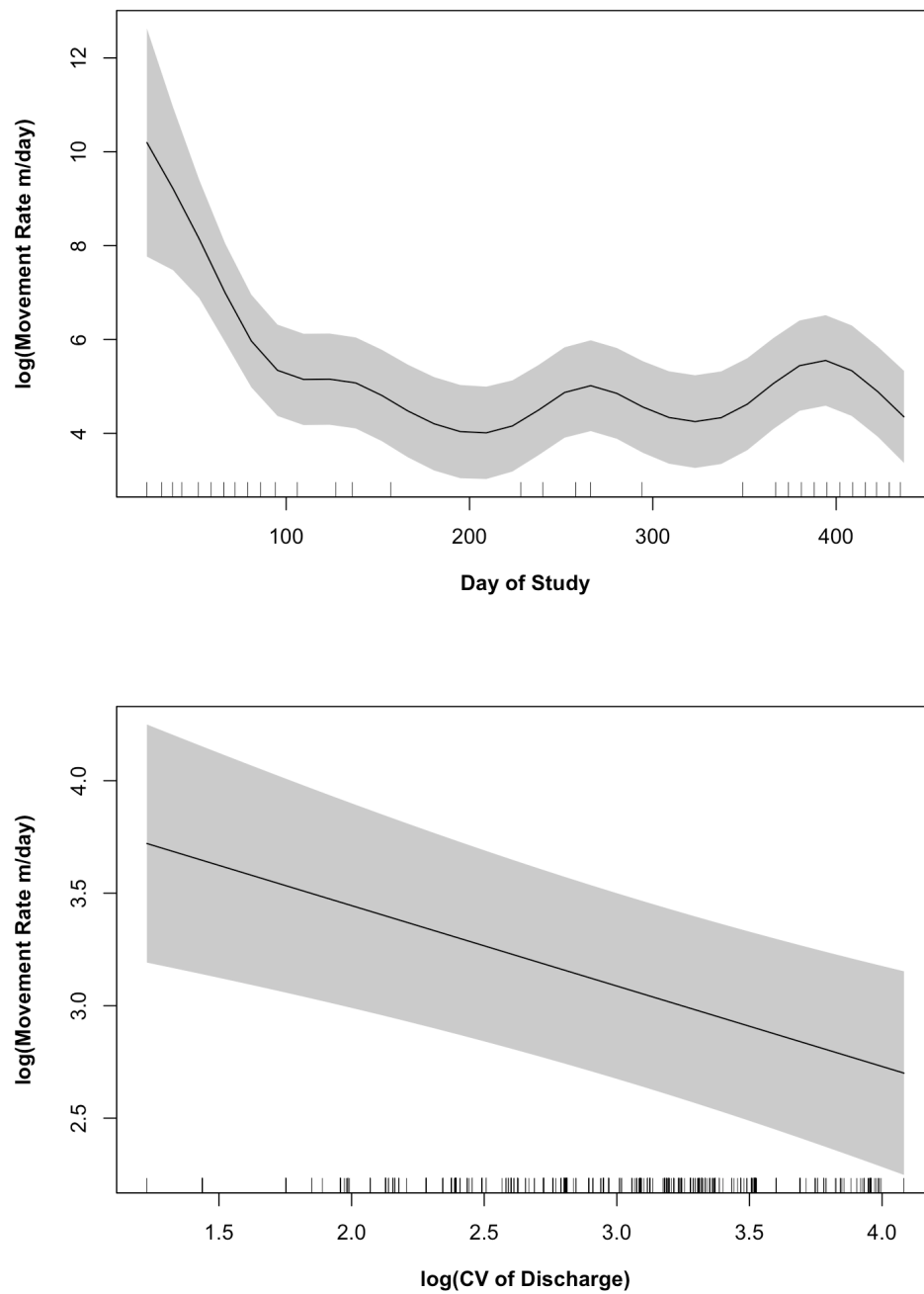


Figure 8. The non-linear relationship between movement rate and day of study (time) (top) and the negative relationship with CV of discharge ( $\text{m}^3/\text{s}$ ) (bottom) for radio-tagged Largemouth Bass from generalized additive mixed models. Shaded regions indicate the 95% confidence intervals. The y-axis on both panels shows the natural-log-transformed model-predicted movement rate (m/day). The x-axis (top) is the day of study with day 1 being March 1<sup>st</sup>, 2022 and day 400 being April 4<sup>th</sup>, 2023.

## Chapter III

### Environmental factors related to hatch timing and daily growth of age-0 Shoal Bass and Largemouth Bass

#### Introduction

Hatch timing, survival, and growth of age-0 fishes determine recruitment of stream fish into the adult population. The timing of spawning can ultimately inform survival depending on the biotic and abiotic conditions present during hatching and early life (Sabo and Orth 1995; Mion et al. 1998; Dauwalter and Fisher 2007a). Survival in the first year of life, and subsequently moving into the adult population, is known as recruitment in fisheries (Humphries et al. 2020). Adequate recruitment of age-0 fishes over time is important to population persistence (Maceina and Pereira 2007; Chambers and Trippel 2012). The majority of fish do not survive their first year of life due to predation and environmental stressors (Houde 1989; Ludsin and DeVries 1997). For example, total mortality was estimated to be 94.3% in age-0 Unspecked Hardyhead *Craterocephalus stercusmuscarum fulvus* during just the first three weeks of life (McCasker et al. 2014). Recruitment can vary spatiotemporally, resulting in variation in the abundance of year classes (Woodside et al. 2015; Houde 2016). For instance, Prairie Chub *Macrhybopsis australis* hatch success is both spatially and temporally dependent, particularly in relationship to drought versus wetter periods (Wedgeworth et al. 2022). The proper environmental conditions to promote hatch success and early-life growth may increase the probability of survival through the first year of life. Larger individuals can typically out compete, depredate, and withstand greater physiological stress than smaller individuals (Miller et al. 1988; Pereira et al. 2017; Sogard and Olla 2015). Although a stock-recruit relationship has not been demonstrated for many fishes (e.g., Largemouth Bass *Micropterus salmoides*, Allen et al. 2011), survival of some age-0 fish to age one is certainly required for population persistence. Understanding the relationship between hatch success and

environmental factors is helpful in cases where management actions may be needed to support successful reproduction.

Important relationships exist between biotic and abiotic factors and hatch success in freshwater fishes. Discharge and temperature regimes in streams have been correlated to patterns of spawn timing and recruitment by many fishes (Tyus 1990; Lobón-Cerviá 2004; Tornabene et al. 2020). In many freshwater species, interactions between high flows (Tornabene et al. 2020), warming temperatures (Fry 1971; Graham and Orth 1986), social interactions (e.g., courtship; Amorim et al. 2008; Brown et al. 2019), and chemical signals (e.g., gonadotropin hormones; Redding and Patino 1993) can cue spawning activity. Low variability in discharge after hatching is related to increased juvenile fish density and growth in several species (e.g., Atlantic Salmon *Salmo salar*, Jensen and Johnsen 1999; juvenile warmwater fishes, Craven et al. 2010). In contrast, extreme high discharge events at particular times of year can lead to larval mortality due to nest destruction and larval dislocation (e.g. centrarchids and cyprinids, Harvey 1987; salmonids, Young et al. 2011). Spawning may occur over several weeks to months; thus, individuals that hatch earlier in the year experience different physicochemical conditions than those hatched later (Bogner et al. 2016). Correspondingly, hatch phenology may confer a size and survival advantage or disadvantage to various cohorts (Phillips et al. 1995; Sammons et al. 2021; but see also Sabo and Orth 1995). In addition to cueing reproduction, thermal conditions can determine development of eggs and fry (Firkus et al. 2018). However, these important factors and cues can be disrupted by human alteration to streams, particularly via river regulation.

Flow regulation in streams can affect the phenology and successful spawning by stream fishes but can be mitigated using management strategies. A natural flow regime allows for seasonal and annual variation in discharge and temperature that stream fishes have adapted to for successful

reproduction and recruitment (Poff et al. 1997). Naturally varying discharge and temperature conditions across a watershed allow stream fishes to have among-population heterogeneity and robustness to extreme environmental events (Grossman and Sabo 2010; Miller 2019). Flow regulation disrupts the magnitude, duration, frequency, timing, and/or rate of change in discharge patterns (Poff et al. 1997). Unnatural flow regimes (e.g., hydropeaking dams) can lessen long-term variation (i.e., seasonal, interannual) in favor of short-term variation (i.e., daily; Lytle and Poff 2004). This can negatively affect stream fishes via stressors such as habitat alteration, nest-site dewatering, egg or larvae displacement (Harvey 1987; Young et al. 2011), and alter the timing of environmental cues (Tornabene et al. 2020; Cooke et al. 2022) For example, Grabowski and Isely (2007) observed that over 50% of Robust Redhorse *Moxostoma robustum* nest sites were either dewatered or exposed low flow conditions due to river regulation. Further laboratory studies on Robust Redhorse revealed that simulated hydropeaking conditions were lethal to some eggs and all hatched larvae (Fisk et al. 2013). Additionally, fish growth, physiological condition, and abundance have been negatively associated with unnatural and extreme pulsed flows (Freeman et al. 2001; Shaw and Richardson 2001). In many streams, costly mitigation strategies such as dam removal are not viable due to local reliance on energy, navigation, water supplies, and flood control (Stanley and Doyle 2003; Doyle et al. 2003). However, there are several mitigation strategies that have been used to balance the needs of fishes with the needs of humans (e.g., how and when we release water from dams Travnichek et al. 1995; Zarri et al. 2019; fish passage, Bunt et al. 2012). Understanding how warmwater stream fish reproduction and recruitment are related to human altered flows will aid managers in revisiting dam operations to approximate more appropriate flow conditions when possible.



Black basses *Micropterus* spp. are important top predators in many warmwater stream ecosystems with a dynamic reproductive strategy; however reproductive information is lacking for populations in altered riverine ecosystems. Black basses occur in all sizes of streams under varying environmental conditions. *Micropterus* spp. are assumed to build nests to spawn (but see Miller and Brewer, 2021) and typically guard their larvae for a period of 1-3 weeks post spawn (Boschung and Mayden 2004). Some species demonstrate extensive spring spawning movements, but the magnitude of movements varies by species and by stream (see Chapter 2). Black bass typically spawn in the spring and summer, but the exact timing and duration differs by latitude, species, and the physicochemical conditions during a particular year (Stroud and Clepper 1975; Graham and Orth 1986; Sabo and Orth 1995). Mortality is greatest within the first two weeks post-hatch due to higher vulnerability to predation and fungal diseases (Knotek and Orth 1998; Dauwalter and Fisher 2007a). For example, Neosho Bass *M. velox* mortality was 85% and 99% around two weeks post-hatch in Buffalo Creek and Spring Creek, Oklahoma, respectively (Brewer et al. 2019). Survival and growth of age-0 black bass can be further hindered by external stressors including disruptive flows (Reynolds and O'Bara 1991; Lukas and Orth 1995), extreme thermal conditions (Sabo and Orth 1995; Walsh et al. 2018), and density-dependence (Knotek and Orth 1998; Vøllestad et al. 2002). Besides stream populations of Smallmouth Bass *M. dolomieu* (Pflieger 1966; Simonson and Swenson 1990; Reynolds and O'Bara 1991; Sabo and Orth 1995; Lukas and Orth 1995; Pert et al. 2002; Swenson et al. 2002; Smith et al. 2005; Dauwalter and Fisher 2007a; Walsh et al. 2018) and recently, Neosho Bass (Brewer et al. 2019; Miller 2019), most research on the reproduction and early life history in black bass has been conducted in stable reservoirs and small impoundments (Goodgame and Miranda 1993; Phillips et al. 1995; Irwin et al. 1997; Ludsins and DeVries 1997; Sammons et al. 1999; Greene and Maceina 2000; Olson et al. 2003; Nohner et al. 2018).

Recruitment in lotic populations, particularly for narrow ranged endemics (Birdsong et al. 2015), is hindered due to human disturbance including the introduction of nonnative congeners (i.e., genetic hybridization; Taylor et al. 2019), flow regulation, fragmentation (Brewer and Long 2015; Sammons and Earley 2015; Cottrell 2018), and habitat degradation (Hurst et al. 1975; Birdsong et al. 2015).

Successful spawning and recruitment are of special concern in regionally endemic black bass species, such as Shoal Bass *M. cataractae* (Birdsong et al. 2015), whereas riverine Largemouth Bass *M. salmoides* are rarely studied compared to reservoir populations. Sympatric Shoal Bass and Largemouth Bass typically differ in their spawning habitats, hatch phenology, and early growth. Wheeler and Allen (2003) found that ratios of age-0 Shoal Bass to Largemouth Bass were greater in shoals relative to pools in the Chipola River, Florida. Additionally, Shoal Bass can spawn in higher velocity habitats within shoals (Bitz et al. 2014), but also other areas (Cottrell 2018), whereas Largemouth Bass commonly spawn in lower-velocity backwaters and pools (Nack et al. 1993; Gocłowski et al. 2013). Similar to other black basses (Sabo and Orth 1995; Dauwalter and Fisher 2007a; Miller 2019), successful hatches (i.e., lived to be a larger age-0 fish) in the upper Flint River, Georgia, for both Shoal Bass and Largemouth Bass are associated with steady and lower stream discharge. Largemouth Bass in upper Flint River typically successfully hatch earlier and have more protracted hatch durations than Shoal Bass (Sammons et al. 2021). However, Sammons et al. (2021) only sampled over a three-week period in late summer each year at two sites thereby possibly missing information on hatch duration and responses to variable physicochemical conditions. Additionally, interannual hatch duration is variable among years in other black basses (Sabo and Orth 1995; Phelps et al. 2008; Miller 2019) and is an important component of our understanding of early life history. Correspondingly, my study objective was

to determine the spatial and temporal variability in hatch success and growth of lotic populations of sympatric Shoal Bass and Largemouth Bass.

## **Methods**

### *Study Sites*

The study area for my second objective was the lower Flint River catchment (LFRC). The study extent included the mainstem Flint River between Lake Blackshear and Lake Chehaw (hereafter the Flint River above Albany Dam - AAD), the Flint River between Lake Chehaw and Lake Seminole (hereafter the Flint River below Albany Dam – BAD), and several of the major tributaries of the Flint River (Figure 1). This portion of the catchment contains two hydropeaking dams (Albany/Lake Chehaw and Warwick/Lake Blackshear), numerous low-head dams, and reaches and tributaries with varying levels of groundwater influence which affects both temperature and discharge patterns (Figure 1; Opsahl et al. 2007; Rugel et al. 2016). Major tributaries in this catchment begin in the Fall Line Hills physiographic district as springs and seeps that become streams with high groundwater contributions, floodplain swamps, and Ocala limestone substrates in the Dougherty Plain (Golladay and Battle 2002).

I chose 25 sites to sample for age-0 Shoal Bass and Largemouth Bass (Figure 1). I sampled 11 of these sites in 2022 and sampled all 25 in 2023 (Table 1). Sites were selected based on accessibility, USGS stream gauge locations, representation of a range of environmental conditions characteristic of the catchment, and permission to access private lands where necessary. Streamflow, drainage area, and temperature varied among sites (Tables 2 and 3). My sites included pools, run or glide habitat, shoals, and slackwater habitats (i.e., backwater, frontwater).

## *Fish Sampling*

I sampled at each site approximately once every 2 weeks in the spring and summer of 2022 and 2023 (May through August). Shoal Bass is thought to spawn in April and May at water temperatures 16-26°C (Johnson 1974; Bitz et al. 2015; Sammons et al. 2021), whereas riverine Largemouth Bass typically spawn between March and June at water temperatures 13-25°C (Nack et al. 1993; Sammons et al. 2021). If age-0 bass were not detected at a site after 3 sampling events, that site was not revisited, and efforts were focused on sites that had age-0 fish of one or both species detected. This sampling strategy is desirable to both account for sampling inefficiencies, but also ensure enough fish are sampled during the rearing period.

Daily bands on otoliths are increasingly hard to identify once fish reach >100 days old (Long and Grabowski 2017), therefore I attempted to only collect fish < 120-mm total length (TL). Sammons et al. (2021) estimated average growth rates of 0.76 and 0.67 mm per day for age-0 Shoal Bass and Largemouth Bass, respectively, in the upper Flint River. Using these estimates, I established a liberal cutoff of 120-mm TL to maintain fish younger than 100-days old.

I sampled sites via electrofishing raft or canoe during the 2022 and 2023 sampling seasons. At sites accessible by raft, I electrofished for age-0 basses using a 40-amp Midwest Lakes Electrofishing Systems shocking unit (Polo, Michigan) housed on an inflatable raft and powered by a 4000-watt generator. The raft was 4.3-m wide and 9-m long, equipped with a rowing frame, outboard motor, and boom mounted anodes that extend off the front of the netting platform on the bow. I used standard American Fisheries Society electrofishing settings based on conductivity and standardized for generator power output with initial settings placed at pulsed DC current, 60Hz, 25% duty cycle, and 500 volts and I adjusted settings based on water conductivity (Guy et al. 2009; Miranda 2009). At sites inaccessible by raft, I sampled using a DC electrofishing unit with hand-

held anode, powered by a 2000-watt Honda generator, and housed in a canoe outfitted with a steel cathode curtain (Katechis 2015). Depending on channel width and the water depth of each site, I used the raft or canoe as either a barge or boat. As a barge, I shocked in an upstream direction and as a boat I shocked in a downstream direction, alternating from left to right bank to target available habitat. Multiple passes were made where I successfully captured age-0 basses on the first pass up until I collected 50 individuals or no more age-0 bass were captured. All age-0 Shoal Bass and Largemouth Bass were placed in a live well upon capture. They were then euthanized using an overdose of tricaine methanesulphonate (MS-222) (300mg/L, Neiffer and Stamper 2009), separated by species, and stored in 1-L bottles of 70% ethanol until later laboratory processing.

### *Laboratory Processing*

I measured size of each fish and removed their sagittal otoliths to estimate age (d). Daily ring formation in sagittal otoliths has been validated for both species (Miller and Storck 1982; Long and Porta 2019). However, varying levels of accuracy in daily ring formation of Shoal Bass were documented by Long and Porta (2019) due to unnaturally cold temperatures of hypolimnetic tailwater affecting growth rates and daily ring spacing. I assumed daily ring formation was accurate due to the temperature conditions experienced by the fish. Before otolith extraction, I measured TL (0.01 mm) of each fish using digital calipers (VWR Traceable Digital Calipers). I removed sagittal otoliths under a lighted magnifying glass using small scissors and fine-tipped forceps and then placed them in a petri dish. Otoliths were then placed on a microscope slide and mounted using thermoplastic cement (Crystalbond 509, Electron Microscopy Sciences, Hatfield, PA). I melted a very small amount of cement on the microscope slide and then placed otoliths in the pooled cement convex side up (i.e., sulcus ascusticus facing upwards; Ramsey 2023).

I sanded and polished the otoliths by hand in a circular pattern until the daily bands were visible. I began polishing with the coarsest paper and then transitioned to finer grains as daily rings became visible. For larger otoliths, I polished the otoliths using 800-3000-grit sandpaper, and then polished the otoliths using 1.0 and 3.0- $\mu\text{m}$  diamond lapping film (Diamond Lapping Film, 8" diameter, plain backing, Electron Microscopy Sciences, Hatfield, Pennsylvania). For smaller otoliths, I began polishing with a finer grit paper (e.g., 1500) rather than 800. I regularly examined each otolith under a compound microscope at 40X-100X magnification to ensure it was not over-polished. Larger otoliths had a more pronounced concavity compared to smaller ones. Therefore, after polishing the convex side so that the nucleus was clearly visible, I carefully flipped larger otoliths over, remounted them in cement, and polished the concave sides following the same methods described above (Miller and Storck 1982). Flipping the otolith was necessary to better polish the edge of the otolith without over polishing the nucleus. Polishing was complete when all daily bands were visible.

We counted the daily bands of my polished age-0 Shoal Bass and Largemouth Bass otoliths to estimate hatch dates and daily growth rates using a compound microscope at 40X-100X. Mineral oil was applied to otoliths, as needed, for clarification. Daily rings were counted by two independent readers. Readers counted opaque daily bands from the outer edge of the otolith towards the center (Figure 2). Each reader aged each otolith once in a non-consecutive, random order with no prior knowledge of fish size, species, or previous reads. If mean counts between readers were within 10% of one another, the average of both counts was used as the final age. If >10% differences existed between both readers, a consensus was attempted via a joint reading. If a consensus could not be reached, that otolith was excluded from the dataset (Miller and Storck

1982; Graham and Orth 1987). This method of blind reading and reaching a standardized consensus reduces the bias of age estimates (Buckmeier et al. 2017).

I estimated hatch date using the following equation (Sammons et al. 2021):

$$\text{Hatch date} = \text{Collection date} - \text{Age} - X$$

where collection date was the date of fish collection, age was the final mean daily ring count (days), and X was the estimated number of days between hatching and formation of the first daily ring increment (i.e., 5 days; Miller and Storck 1982; Sammons et al. 2021).

I estimated mean daily growth rates (mm/day) from hatch date to collection date using the following equation (Sammons et al. 2021):

$$\text{Daily growth rate} = \frac{TL}{\text{Age} + X}$$

where TL (0.01 mm) is measured prior to otolith extraction, age is the final mean daily ring count (days), and X is equal to 5 as the number of days between hatching and formation of the first daily ring increment.

### *Environmental Measurements*

I measured multiple environmental variables that I hypothesized would be related to successful hatch and growth of Shoal Bass and Largemouth Bass (Table 4). In lotic fishes, spawning, successful hatching, and growth rates can be dictated by changes in discharge, temperature, and photoperiod (Fry 1971; Shuter et al. 1980; Graham and Orth 1986). Multiple species of riverine black bass were documented successfully hatching during periods of receding and stable flows and after a threshold water temperature had been reached that is conducive to

early-life growth (Smallmouth Bass, Shuter et al. 1980; Bestgen 2016; Shoal Bass, Alabama Bass *M. henshalli*, Redeye Bass *M. coosae*, and Largemouth Bass, Sammons et al. 2021). Therefore, I collected mean daily discharge ( $\text{m}^3/\text{s}$ ; USGS 2023) data from the USGS stream gauges located nearest to my sites (Table 2; Figure 1). Discharge data were also provided by the Crisp County Power Commission for dam releases from Warwick Dam (site 32; Figure 1). I converted discharge data into measurements of scaled discharge (i.e., discharge divided by drainage area [ $\text{m}^2$ ] at stream gauge) to make discharge comparable across different stream sizes (Bosch and Hewlett 1982; Qi et al. 2022; Wedgeworth et al. 2022).

I also quantified thermal conditions and time of year to further describe environmental conditions related to hatch success and age-0 growth (Table 4). To measure thermal conditions, I used continuous temperature loggers (Onset Hobo MX2201, Bourne, Massachusetts) fixed within submerged cinderblocks that block direct sunlight to measure water temperature ( $0.1\text{ }^\circ\text{C}$ ). Cinderblocks were submerged 1-3 m deep in well-mixed areas at each sampling site (Figure 1). I also used temperature data collected from the NEON sensor station (NEON Station: FLNT; Precision Measurement Engineering Inc. T-Chain RS 232/485) located downstream of Newton, Georgia (site 30; Figure 1). Hobo loggers were deployed in April 2022 (11 initial sites) and March 2023 (remaining 14 sites). These dates were slightly later ( $\sim 3\text{-}5$  weeks) than I needed for appropriately modeling hatch success. Additionally, gaps of 1-2 weeks occurred in some temperature data due to battery failure or logger tampering. I estimated all temperature-data gaps using least-squares regression with temperature values from the closest upstream or downstream site, except for early-season 2022 sites which were estimated from the Flint River NEON sensor station. If gaps occurred on a stream that only had one sampling site, temperature values were estimated by comparison with another site of similar drainage area and latitude (all  $R^2 = 0.89 -$



0.99). Finally, I recorded calendar day (i.e., January 1<sup>st</sup> is 1, May 1<sup>st</sup> is 120, August 31<sup>st</sup> is 242; Wedgeworth et al. 2022) because timing of spawning, and thus hatch, can greatly affect survival and growth due to seasonally varying environmental conditions (Shuter et al. 1980; Goodgame and Miranda 1993; Miller and Brewer 2020). Additionally, calendar day is highly correlated with photoperiod which is linked to spawning initiation and termination in temperate fishes (de Vlaming 1972; Munz and Higgins 2013).

### *Hatch Analyses*

I grouped observed hatches by week (7-d) and characterized flow and temperature conditions prior to each hatch week. Hatches were grouped by week starting in February and ending in August because stream fish often respond in their spawning behavior to antecedent flow and temperature variation and conditions rather than concurrent conditions (Forsythe et al. 2012; King et al. 2016; Vine et al. 2019). Additionally, grouping hatches by weeks helps accommodate hatch-date uncertainty due to inexact estimation of the timing of the first daily increment formation in otoliths and reader error when enumerating daily rings (Buckmeier et al. 2017). Therefore, I also calculated the coefficients-of-variation (CV; mean/SD) and means of scaled discharge and water temperature for 7-d prior to each grouped hatch week to represent conditions prior to successful hatches. By examining plots of my data, it appeared that, like other populations of black bass (Sabo and Orth 1995; Dauwalter and Fisher 2007a; Miller 2019; Sammons et al. 2021), most successful hatches by both species occurred after a flood-pulse and during a period of stable and receding flows. Therefore, for each grouped hatch week, I also characterized the rate of change (ROC; Olden and Poff 2003) in scaled discharge 14-d prior and the number of days post-peak flow (Bestgen 2016) to quantify this relationship. Peak flow was determined for each site as the date that flows reached their highest value during that calendar year (i.e., highest spring flow).

Prior to analysis of successful hatch date, I made any necessary transformations and standardizations to predictor variables to meet the basic assumptions of linear regression. I log-transformed mean scaled discharge and CV of discharge due to skewness. I tested for multicollinearity among independent variables using Pearson's correlation coefficient and only retained variables in the models that had reasonable correlation ( $|r| < 0.6$ ; Roever et al. 2014). Mean temperature was highly correlated with mean scaled discharge ( $r = -0.61$ ), number of days post-peak flow ( $r = 0.73$ ), and calendar week of hatch ( $r = 0.92$ ; Table 5). Number of days post-peak and calendar week of hatch were also multicollinear ( $r = 0.86$ ), therefore I retained only mean temperature, CV of discharge, and ROC in discharge in hatch analyses. Retained continuous covariates were then standardized to a mean of 0 and a standard deviation of 1 to aid in model interpretation and convergence (McCune et al. 2002).

I used two-part hurdle models to assess environmental variables associated with Shoal Bass and Largemouth Bass spawning and hatch success (Martin et al. 2005; Hofstetter et al. 2016; Wedgeworth et al. 2022). Shoal Bass and Largemouth Bass were modelled separately. Hurdle models accommodate zero-inflation (i.e., causing a non-standard distribution) and overdispersion (i.e., the variance of the data exceeds the mean; Mullahy 1986), both of which occurred in my data due to discontinuous hatches over the spawning season (Wedgeworth et al. 2022). I was not able to discriminate between true and false zeros in my data (i.e., failure to detect hatch versus no hatch). Hurdle models cannot account incomplete detection and instead consider all zeros to be true and models non-zero counts separately from zero counts in a two-part framework (Hofstetter et al. 2016).

The two parts of my hurdle models were a zero model (e.g., the probability of hatch) and a count model (e.g., the number of hatches per day that hatches occur). The zero model was a

logistic regression model with a binary outcome (i.e., 0 = no hatches occurred, 1 = hatches occurred). If a successful hatch occurred (i.e., crossing the hurdle), the count model was then used to analyze variation in non-zero counts. The count model was a zero-truncated negative binomial model. I built my hurdle models following Wedgeworth et al. (2022) and built the zero and count models separately for each species. I built zero-models using the *lme4* package (Bates et al. 2023) and count models using the *glmmTMB* package (Brooks et al. 2023) in the statistical software R (Version 4.3.2, R Core Team 2023). In these models, I analyzed all subsets of fixed effects and included the random effect of stream in every model to account for unequal sample sizes and unexplained variation among locations (Table 6; Wagner et al. 2006; West et al. 2007). Fixed effects included environmental covariates listed above and the categorical effect of year (2022 and 2023). For count models, both linear and quadratic relationships between continuous covariates and hatch frequency were explored. I ranked candidate model sets for both zero models and count models using  $AIC_c$  as described in Chapter 2. Briefly, all models with  $\Delta AIC_c < 2$  were considered to have equal empirical support (i.e., competitor for drawing inference) if they contained the same number of or fewer parameters than the top model (Burnham and Anderson 2002; Arnold 2010). I calculated marginal and conditional  $R^2$  values using the *performance* package (Lüdecke et al. 2021) in the statistical software R (Version 4.3.2, R Core Team 2023) to determine the variance explained by my fixed and random effects (Nakagawa and Schielzeth 2013). For my top ranked zero models, I then used binned residual plots to evaluate goodness-of-fit. If ~95% of residuals fell within the bounds, I concluded adequate model fit (Gelman and Hill 2006). For my top ranked count models, I used the *DHARMA* package (Hartig 2022; Wedgeworth et al. 2022) in the statistical software R (Version 4.3.2, R Core Team 2023) to examine and compare diagnostic residual plots (QQ and scatterplots of residual and fitted values).

### *Growth Analyses*

Prior to my analysis of growth rates, I calculated environmental metrics representative of conditions during the growing season and made any necessary transformations and standardizations to predictor variables to meet the basic assumptions of linear regression. I calculated environmental covariates during the period between hatch date and capture date of each fish (i.e., conditions during fish growth). These covariates included mean scaled discharge, CV of discharge, and mean temperature. I also included the calendar date of hatch based on the hypothesis that fish hatched at different times would exhibit different growth rates (Phillips et al. 1995; Durham and Wilde 2005; Rogers and Allen 2009). I log-transformed mean scaled discharge and CV of discharge due to skewness. I retained covariates that were not multicollinear (see above). Mean temperature and hatch date were multicollinear ( $r = 0.60$ ; Table 7), therefore I only retained temperature to avoid confounding effects. Retained continuous covariates were then standardized to a mean of 0 and a standard deviation of 1 to aid in model interpretation and convergence (McCune et al. 2002).

I built a set of linear mixed models using multiple regression and model selection to assess the relationships between average daily growth of basses and measured environmental variables (Maccina 1992; Miller 2019). Shoal Bass and Largemouth Bass were analyzed separately. Fixed effects included environmental covariates listed above and the categorical effect of year (2022 and 2023). I included stream as a random effect to account for unequal sample sizes and unexplained variation among my sites (Wagner et al. 2006; West et al. 2007). I assumed random effects were normally distributed as  $N(0, \sigma^2)$ , where  $\sigma^2$  represents the variance among levels (e.g., among years). The full mixed linear model can be expressed as a modified version of that described by West et al. (2007) :

$$Y_{it} = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \dots + \beta_N X_{Ni} + v_i + \varepsilon_{it}$$

where  $Y$  is daily growth rate (mm/d) for fish  $I$  from stream  $t$ ,  $\beta_0$  is the grand intercept,  $v_i$  is the random intercept for stream,  $\varepsilon_{it}$  is the residual error term for fish  $I$  at stream  $t$ , and  $\beta_0$  through  $\beta_N$  are the coefficients of covariates  $X_1$  through  $X_N$ . I analyzed all subsets of fixed effects (Table 8), ranked and selected my models using  $AIC_c$ , calculated marginal and conditional  $R^2$  values for my top ranked models, and assessed goodness-of-fit using binned residual plots as described above for hatch analyses.

## Results

### *Fish Sampling*

I completed 136 surveys (19 in 2022 and 117 in 2023) across 25 sites during my sampling seasons (Table 1). In 2022, sampling efforts were extended across the catchment to identify sites where age-0 Shoal Bass could be located and across a range of environmental conditions. During this period, I emphasized spatial coverage rather than extensive repeated sampling at each location. In contrast, in 2023, I conducted surveys approximately once every two weeks at each site until mid-June, pausing during extensive flooding and also for boat repairs. Thereafter, I prioritized sampling at locations where Shoal Bass had been detected to capture the hatch duration at these locations. Thus, after mid-June, sampling effort was uneven among sites (Table 1).

The detection and number of age-0 bass varied across species, years, and sites. Age-0 Largemouth Bass were detected in all sampled streams but not at every site (Figure 3). Sites 20 and 31 on the lower Ichawaynochaway Creek were the only sites sampled during both years where age-0 Largemouth Bass were detected in 2022 but not 2023. In contrast, age-0 Shoal Bass were found both upstream and downstream of Albany Dam in the Flint River in both years, but only

detected in Ichawaynochaway and Muckalee creeks in 2022 (Figure 4). Age-0 Shoal Bass were not detected in Kinchafoonee, Chickasawhatchee, Cooleewahee, or Abrams creeks. I collected 114 and 415 Largemouth Bass (Table 9) and 149 and 140 Shoal Bass in 2022 and 2023, respectively. Over both years, I also collected 23 age-0 bass that were determined to be either Spotted Bass or hybrids of Spotted Bass and Shoal Bass. These fish were not aged. Overall, the most age-0 bass were found in the mainstem Flint River compared to tributaries, with the greatest number of both species collected between Warwick Dam and Lake Chehaw (sites 32 and 16) in the mainstem Flint River AAD during both sampling years. The fewest age-0 bass were collected from Abrams Creek.

### *Ageing and Growth*

Otoliths that met my reader agreement criteria were retained for both hatch and growth analyses. I processed and aged 803 otoliths from age-0 Shoal Bass and Largemouth Bass (Table 10). I retained 97% (502/514) of aged Largemouth Bass otoliths and 97% (282/289) of aged Shoal Bass otoliths for my analyses. Ages of Largemouth Bass ranged from 29 to 158 days and ages of Shoal Bass ranged from 26 to 118 days.

Largemouth Bass hatch timing was variable between years and among streams. Successful hatches began one week later in 2022 but ended later in 2023 (Figure 5). Thus, the 2023 hatch season was more protracted, lasting four weeks longer than the 2022 season (12 weeks). The earliest observed Largemouth Bass hatch date was March 15<sup>th</sup> in 2022 in Ichawaynochaway Creek and March 10<sup>th</sup> in 2023 in Chickasawhatchee Creek (Figures 7 and 8, Table 10). The latest observed hatch dates were June 1<sup>st</sup>, 2022, and June 26<sup>th</sup>, 2023 in the Flint River AAD and Cooleewahee Creek, respectively (Figures 6 and 8). The highest frequency of successful hatches across all sites was in mid-May in 2022 but shifted to late April in 2023 (Figure 5).

Successful hatch dates of Shoal Bass were less protracted than Largemouth Bass but were similarly variable among streams and years. Successful hatching occurred among streams over a seven-week period in both 2022 and 2023 (Figure 5). However, hatches began and ended one week later in 2022 than in 2023 with the highest frequency of hatches occurring during the weeks of May 10<sup>th</sup>, 2022 and April 26<sup>th</sup>, 2023 (Table 10). In 2022, hatches initiated earliest in the mainstem Flint River BAD on April 25<sup>th</sup>. However, in 2023 hatching occurred earliest in the mainstem Flint River AAD on April 16<sup>th</sup>. In 2022, successful hatches extended into early June in both Ichawaynochaway Creek and the Flint River AAD whereas in 2023, the latest Shoal Bass hatch date detected was May 26<sup>th</sup> in the Flint River BAD (Figure 9, Table 10).

Age-0 black bass size and daily growth varied between species and years. Fish lengths for Largemouth Bass and Shoal Bass ranged 23.11 – 110.81 mm and 19.1 – 116.88 mm (Table 10), respectively. Growth rates ranged from 0.65 – 1.58 mm/day for Shoal Bass and 0.45 – 1.48 mm/day for Largemouth Bass across all streams (Table 11).

### *Environmental Conditions*

Discharge and water temperatures varied between years and among sites (Table 3). Discharge patterns across both years were similar with typical spring flood pulses occurring in April across most sites (Figure 11). These pulses represented the peak spring flow for mainstem sites in both years, whereas tributary sites experienced an earlier peak flow in 2023 due to variable local precipitation patterns (Table 3; Figure 11). Summer flow conditions generally reflected typical baseflow conditions of the catchment (Schoonover et al. 2006; Golladay et al. 2007), except for a flood pulse in mid-June 2023 that affected the entire catchment (Figure 11). These flows were the highest recorded June flows on record for Ichawaynochaway, Chickasawhatchee, Kinchafoonee, and Muckalee creeks (Figure 11). Daily hydropeaking conditions were observed

below both Albany and Warwick dams after May 17<sup>th</sup> in both years, except during the mid-June 2023 flood event (Figure 10). Overall, discharge was higher in 2023 than 2022. Correspondingly, water temperatures across the study site were slightly cooler and more variable in 2023 than in 2022 (Figure 12). Between years, Flint River sites had the warmest water temperatures, whereas tributary sites had cooler average water temperatures (Table 3; Figure 12).

### *Hatch Analyses*

My top ranked hatch probability model (zero model) for Largemouth Bass included the additive fixed effects of 7-d water temperature and year, and the random effect of stream (Table 12). Successful Largemouth Bass hatches occurred at mean daily water temperatures ranging from 11.9 °C to 28.5 °C. Water temperature was negatively related to the probability of successful hatches (Table 13; Figure 13), indicating that warmer water temperatures 7 d prior to hatch resulted in lower hatch probabilities. On average, the probability of successful hatching was higher in 2023 than 2022 for Largemouth Bass. Assessment via a binned residual plot demonstrated adequate fit for this top ranked model (Gelman and Hill 2006; Appendix 2). Fixed effects explained 19% of variability in this model and the random effect of stream explained an additional 6% of variation in these data (Table 12).

In contrast, my top-ranked hatch probability model for Shoal Bass included the additive fixed effects of 7-day CV of discharge, 14-day ROC of discharge, and a random effect for stream (Table 12). Both discharge metrics were negatively related to the probability of hatching (Table 13). Higher flow variability resulted in a lower hatch probability, whereas hatch probability was higher after 14-d of declining flows (i.e., negative ROC in discharge; Figure 14). The top-ranked model demonstrated adequate fit when assessed via a binned residual plot (Appendix 2). My fixed



effects explained 30% of variability in these data and an additional 8% of variation was explained by accounting for stream as a random effect (Table 12).

My top ranked hatch frequency model (count model) for Largemouth Bass contained 7-d CV of discharge as a fixed effect and the random effect of stream (Table 14). This model predicted a negative relationship between discharge variation prior to hatch and the number of successful Largemouth Bass hatches (Table 15; Figure 15). Adequate model fit was confirmed by the uniform distribution of the QQ-plot and the absence of patterns in residual distributions in the scatterplot of the DHARMA diagnostic figures (Appendix 3).

There were two top models with similar empirical support but differing predictor variables for the frequency of Shoal Bass hatches. My top two models contained 1) the fixed effect of 14-d ROC of discharge and the random effect of stream and 2) a quadratic term for 7-d water temperature as a fixed effect and the random effect of stream (Table 14). Hatch counts increased from ~18-24°C then decreased from ~24-27°C; however, these estimates had high uncertainty (Table 15; Figure 16). Additionally, hatch counts increased with lower rates-of-change in discharge (i.e., ROC near 0). These models had adequate fit as determined by uniform distribution of the QQ-plot and lack of patterns in residual distributions in the scatterplot of the DHARMA diagnostic figures (Appendix 4). Four other models were within 2  $\Delta$ AICc of the top ranked model. However, they were not considered to have adequate support due to either being 1) more complex than the top model or 2) not displaying reasonable model fit in DHARMA residual diagnostic plots (Table 14).

## *Growth Analyses*

The top-ranked model for age-0 Largemouth Bass daily growth rate contained the fixed effects of mean discharge, CV of discharge, year, and the random effect of stream (Table 16). Growth rate for this species was positively related to mean discharge but negatively related to variability in discharge (Table 17; Figure 17). On average, growth rates were higher in 2022 than in 2023. Binned residual plot assessment indicated adequate fit for this top-ranked model (Appendix 5). Fixed effects explained 14% of the variability in this model, whereas the random effect of stream accounted for an additional 19% of variation (Table 16).

There were two top models with similar empirical support, but different predictor variables related to Shoal Bass growth rate. The first model included the fixed effects of mean discharge and year with the random effect of stream, whereas the second model included the fixed effects of mean water temperature and year (Table 16). Similar to Largemouth Bass, growth rates of age-0 Shoal Bass were higher in 2022 than in 2023. However, there was a negative relationship between growth rate and discharge, but a positive relationship with water temperature (Table 17; Figure 18). Both models demonstrated adequate fit when assessed via binned residual plots (Appendix 6). In the first model, fixed effects explained 40% of variability and random effects explained an additional 17% of variability (Table 16). For the second model, my fixed effects explained 49% of variation and including the random effects explained an additional 9%.

## **Discussion**

Flow variability can affect species differently and is often context dependent. In rivers with minimal hydrologic alteration, flow variability is often positively related to fish growth and abundance (Tockner et al. 2000; Arthington and Balcombe 2011). For example, Freshwater Cod *Maccullochella* spp. growth increased with higher discharge and flow variability (Tonkin et al.

2017) which conforms to common theories of the importance of flooding to riverine productivity (e.g., flood pulse concept; Junk et al. 1989). However, increased river regulation, due to its suppression of natural flow magnitude and variability, is a major contributing factor in the decline of native fish populations. River regulation typically results in altered flow variability, with reductions in the magnitude, frequency, and duration of both high flow events during winter and spring, and extreme low flow events during summer and autumn (Walker and Thoms 1993; McMahon and Finlayson 2003). Hydropeaking can depress both seasonal and interannual flow variation (Poff 1997; Bowen et al. 1998), but also create artificially high, short-term variation that is problematic for some species (Cushman 1985) including Shoal Bass (my study). In many hydropeaking rivers, the numbers of diminutive fishes that rely on shallow-water habitats decreases (Bain et al. 1988; Kinsolving and Bain 1993). However, the persistence of small-bodied fishes below dams depends on a variety of factors including how the dam is operated, but also the specific traits (e.g., reproductive mode, swimming ability) of the fishes (Craven et al. 2010).

My results indicate that successful black bass hatching below dams is interrupted by hydropeaking. Hydropeaking can dampen seasonal and interannual discharge variation in favor of short-term variation (Cushman 1985; Bowen et al. 1998; Lytle and Poff 2004). This can negatively affect stream biota (Power et al. 1996), including small-bodied fishes (Freeman et al. 2001), aquatic insects (Cushman 1985; Abernethy et al. 2021), and unionid mussels (Galbraith and Vaughn 2011; Wisniewski et al. 2019) that are unable to adapt to the artificial, rapid flow fluctuations (Lytle and Poff 2004). Given society's prevailing reliance on dams, it is important to understand the interactions between dam operations and fisheries such that successful mitigation strategies can be developed. My results show that successful Shoal Bass hatches below the dam end abruptly when hydropeaking begins but continues at other mainstem sites less affected by

dams. Hydropeaking variability may result in nests being dewatered on a daily basis or abandoned by the guarding male due to water rapidly causing mortality of eggs and/or fry (Grabowski and Isely 2007; Young et al. 2011). Short term variation in discharge negatively affects numerous age-0 stream fishes (Harvey 1987), particularly below hydropeaking facilities (Freeman et al. 2001; Halleraker et al. 2003; Korman et al. 2011). Thus, if Shoal Bass recruitment is a management priority, consideration of a longer period before the initiation of summer hydropeaking may be warranted.

My hypothesis that Shoal Bass were more likely to successfully hatch on the descending limb of the hydrograph during relatively stable flow conditions was supported by my results. Similar results were found for Shoal Bass in the upper Flint River (Sammons et al. 2021) and many populations of riverine Smallmouth Bass (Graham and Orth 1986; Reynolds and O'Bara 1991; Sabo and Orth 1995; Dauwalter and Fisher 2007a; Bestgen 2016) and Neosho Bass (Miller 2019). Shoal Bass can nest in high velocity environments within shoal complexes, but usually in areas with flow refugia (Johnston and Kennon 2007; Goclowski et al. 2013; Bitz et al. 2015). Areas of refugia may change with different discharge conditions and nest washout may explain lower hatch probabilities after flows increased (Leonard and Orth 1988; Young et al. 2011). Thus, the timing of spring flood pulses relative to when hydropeaking occurs could be especially problematic for Shoal Bass recruitment if truncation of relatively stable conditions occurs.

Interestingly, it appears that Largemouth Bass were able to successfully hatch during periods of higher discharge, however, the number of successfully hatched individuals that survived declined during these periods. Flow variability experienced by my age-0 Largemouth Bass was the greatest following spring and summer flood pulses and hydropeaking flows. Disruptions in stream fish recruitment via flood spates is well documented for some fishes (Graham and Orth

1986; Harvey 1987; Lukas and Orth 1995; Peterson and Kwak 1999; Bestgen 2016; Miller 2019). Thus, the protracted duration of successful Largemouth hatches may reflect a bet-hedging strategy to cope with natural environmental perturbations (Craven et al. 2010; McManamay and Frimpong 2015). Protracted spawning may also explain why Largemouth Bass is so resilient in areas with altered flow regimes and outside of its native range (Bain et al. 1988; Young et al. 2011; Bae et al. 2018).

Although lower, relatively stable flows appear important for Shoal Bass and other black basses, higher flows are certainly important for creating and maintaining their habitats. Flood pulses may increase the quality of spawning conditions, thereby making the receding end of the hydrograph and relatively stable flow conditions more suitable for offspring. Spring flood spates flush fine sediments, thus improving oxygenation in coarser substrates resulting in higher quality nesting habitat (Craven et al. 2010; Reiser et al. 2018). Excessive sediment deposits can be problematic for successful spawning by black basses (e.g., Smallmouth Bass, Dauwalter and Fisher 2007a; Suedel et al. 2017; Suwannee Bass *M. notius*, Strong et al. 2010). Spring flood spates may also be an important cue for spawning initiation (Taylor and Cooke 2012; Tornabene et al. 2020) and be necessary for the maintenance of important spawning and rearing habitats by promoting channel heterogeneity and transporting nutrients and sediments both longitudinally and laterally (Junk et al. 1989; Poff et al. 1997). Thus, higher flow events are indirectly important for successful spawning over the longer term.

Shoal Bass and Largemouth Bass hatch success were also associated with water temperature; however, temperature was multicollinear with other factors not included in my models. Temperature is a common cue associated with spawning phenology in black basses (Graham and Orth 1987; Warren 2009). Thermal conditions can influence spawn timing (Shuter et al. 1980;

Isely et al. 1987) and egg and fry development (Wrenn 1984) of black basses, but cues can vary spatially (Graham and Orth 1986; Dauwalter and Fisher 2007a; Rogers and Allen 2009; Miller and Brewer 2021). Temperature is among a suite of biotic (e.g., gonadotropin, Brown et al. 2019) and environmental (e.g., flow, photoperiod, presence of mates, de Vlaming 1972; Munz and Higgins 2013; Enriquez et al. 2016) factors that come together to set spawning chronologies. Water temperatures in my study area were negatively correlated with average discharge and positively correlated with calendar week of hatch and the number of days since peak spring flows. Therefore, I cannot isolate the relationship with water temperature from discharge conditions or photoperiod. Such interconnected relationships with environmental conditions may reflect the complexity of interactions between flow, temperature, and photoperiod related to spawn timing and hatch success resulting in seemingly different relationships among years (Reynolds and O'Bara 1991; Sabo and Orth 1995; Miller and Brewer 2020). My study had similar environmental conditions during the spring hatching season (apart from June 2023 flood pulse) between years, with neither being extremely wet nor dry. Monitoring recruitment in these populations over a longer period might better illuminate how environmental conditions interact to inform hatching success. Likewise, lab studies can complement field studies by isolating single factors and understanding the strength of interactions to facilitate making recruitment predictions.

The spatial and temporal variability of my hatches and hatch frequencies rely on several assumptions. One major assumption, given my models did not account for incomplete sampling detection, is that my samples reflected the true relative abundance of each site. In many cases, this may be approximated; however, sampling efficiency for juvenile black bass can be relatively low in some systems (Jackson and Noble 1995; Young 2022). Several factors can affect sampling efficiency when using electrofishing including water temperature (Borkholder and Parsons 2001),

water depth (Dauwalter and Fisher 2007b), channel width, and visibility (Price and Peterson 2010; Lyon et al. 2014). Thus, during periods of higher water when visibility was reduced, it was more likely that I could have missed some bass at various sites. However, it is unlikely that I would have missed complete hatches across the spawning season with multiple sampling attempts in Ichawaynochaway, Muckalee, and Kinchafoonee creeks in 2023. Thus, although my sampling was likely biased during some period based on physicochemical conditions, the larger spatial and temporal patterns are likely unaffected. Moreover, when discharge was low and I did not detect juvenile bass, it is most likely an artifact of failed spawning or hatching due to extreme flow events rather than related to sampling detection. Of course, lack of detection does not indicate that fish were not spawning.

Spawning may occur over a broader spatial and temporal scale, but spawning does not always relate to successful hatching. For example, I observed gravid adult females in Ichawaynochaway Creek and a male guarding a nest in Kinchafoonee Creek in May 2023 even though we did not detect juveniles. The record flood in mid-June may have been detrimental to age-0 Shoal Bass in many of the tributaries before they were at a size where they would be detected by my sampling gear. Multi-year recruitment failure of Shoal Bass in the Chipola River was similarly attributed to spring and summer high flows (Woodside et al. 2015). The relationship between spawning and successful hatches may vary over time depending on water quality and quantity (Mueller et al. 2017; Wedgeworth et al. 2022), groundwater contributions (Power et al. 1999), disease and fungus (Reynolds and O'Bara 1991), and density-dependent factors (Vandenbos et al. 2006; Allen et al. 2011).

Physical spawning and rearing habitat were not quantified in this study but can have a marked influence on the survival and growth of age-0 black bass. For instance, age-0 abundance

of riverine Smallmouth Bass and Neosho Bass were influenced by fine scale (e.g., velocity, cover type; Simonson and Swenson 1990; Pert et al. 2002; Dauwalter and Fisher 2007a; Brewer et al. 2019) and landscape-scale habitat factors (e.g., land use; Brewer and Rabeni 2011) including network position (Miller and Brewer 2020). Shoal Bass spawning and age-0 habitat has been studied in the Chipola River (Wheeler and Allen 2003; Bitz et al. 2015) but physicochemical factors (e.g., geology, drainage area, groundwater influence; Couch et al. 1996; Torak and Painter 2006) differ greatly across the range of this species. Additionally, we know very little about how habitat influences survival and growth of age-0 riverine Shoal Bass and Largemouth Bass.

My results indicate that Largemouth Bass daily growth was not as strongly associated with flow and water temperature as was Shoal Bass growth. The low  $R^2$  values associated with Largemouth Bass growth models indicate that there are other biotic and/or abiotic factors related to early life growth. Factors such as prey type and availability (Olson et al. 2003; Nohner et al. 2018), disease (Walsh et al. 2018; Schall et al. 2020), habitat availability (Lukas and Orth 1995; Irwin et al. 1997; Dutterer et al. 2013), density dependence (Deangelis et al. 1993), and interactions among them can dictate early-life growth in black bass. For example, fall weights of juvenile Largemouth Bass in five Ohio reservoirs declined with higher bass densities (Garvey et al 2000). In the upper Flint and Chipola rivers, juvenile Shoal Bass diets mainly consisted of insects, whereas Largemouth Bass were primarily piscivorous during the first summer of life (Wheeler and Allen 2003; Sammons 2012). Similarly, juveniles of each species were associated with differing channel units and substrates (Wheeler and Allen 2003). Differences in diet and habitat use between these species may explain why Shoal Bass growth variability in my data was better explained by my models than that of Largemouth Bass (i.e., high  $R^2$ ).



I found growth of age-0 Shoal Bass was negatively related to increasing discharge which may have reduced optimum velocity habitats (e.g., optimum refugia, Simonson and Swenson 1990; Swenson et al. 2002). Similar relationships were found for both young-of-year Spotted Bass (Ramsey 2023) and Neosho Bass (Miller 2019) in rivers of Oklahoma, Arkansas, and Texas. Decreased growth at higher flows may be related to several factors including greater concentrations of suspended solids diminishing invertebrate communities (i.e., main component of age-0 Shoal Bass diet; Bilotta and Brazier 2008), impairing foraging efficiency (i.e., impaired vision; Shaw and Richardson 2001), and causing physiological stress (e.g., gill abrasion; Newcombe and Jensen 1996; Young et al. 2011). Also, higher discharges may increase bioenergetic cost of swimming and associated foraging leading to lower growth rates (Shaw and Richardson 2001; Weyers et al. 2003).

Temperature and growth are strongly coupled in warmwater fish species. Thus, optimal growth occurs at species-specific optimal temperatures (Coutant 1977; Coutant and Deangelis 1983). The highest growth rates in Shoal Bass were associated with mean temperatures between 27-29 °C. Temperature was also highly correlated with hatch date revealing that earlier hatched individuals grew slower. It is often context dependent in juvenile black bass whether hatching early versus late confers an advantage to survival in the first year of life. For fish that hatch earlier, they have a longer period to grow prior to the first winter. However, the temperature when they hatch can dictate early growth and thus, the size at which juveniles switch to piscivory (Phillips et al. 1995; Ludsin and DeVries 1997). The timing of environmental perturbations can also influence both growth and survival (Sabo and Orth 1995; Bunn and Arthington 2002). Altogether, these factors may influence size advantages of juveniles as they enter their first winter (Phillips et al. 1995; Ludsin and DeVries 1997). Overall, variability in growth rates and hatch dates of a year-

class results in population heterogeneity which in turn confers resilience to environmental stochasticity.

My results add to the broader knowledge of black bass ecology and thus, are useful for developing black bass management and conservation plans. In tandem with other studies (Long and Porta 2019; Sammons et al. 2021), my results emphasize a relatively short window for successful Shoal Bass hatching. This may help inform hatcheries of more appropriate water temperatures if propagation is needed. However, determining the thermal tolerance of Shoal Bass juveniles and adults would also be useful for propagation and understanding longer-term trends in Shoal Bass populations. In conjunction with findings from my movement analyses (Chapter 2), my results highlight important locations and likely habitats in the LFRC where Shoal Bass and Largemouth Bass hatching and rearing are occurring. Finally, it appears that hydropeaking flows may be negatively related to the hatch success and growth of age-0 black basses in this system. The lower Flint River has one of the last strong populations of Shoal Bass within its native range (Sammons 2021). Stocking fingerlings was completed in previous years (T. Ingram, GADNR, personal communication), indicating successful spawning is a management concern in the lower Flint River. Spawning by the in-river population is preferred over stocking for a variety of reasons (e.g., genetic integrity, disease, cost), thus local managers might consider prioritizing conditions that lead to reproductive success of this endemic species. Extension of the time when hydropeaking conditions are not occurring could positively influence recruitment, particularly when natural spring flood cues occur later in the year. Monitoring of the juvenile year class strength of this stock can help better inform adaptive management strategies.

### Chapter III Tables

Table 1. Number of fish surveys completed at each site between May-August during 2022 and 2023. I sampled 11 sites in 2022 and 25 sites in 2023 (Figure 1). Site numbers are listed from upstream to downstream for each stream. AAD = above (upstream) Albany Dam, BAD = below (downstream) Albany Dam.

Stream	Site number	2022	2023	Total
Abrams Creek	1	-	6	6
Chickasawhatchee Creek	7	1	5	6
	15	-	3	3
Cooleewahee Creek	17	-	7	7
Ichawaynochaway Creek	18	-	3	3
	28	-	2	2
	19	-	2	2
	24	1	3	4
	20	1	4	5
	31	4	5	9
	Kinchafoonee Creek	22	-	3
Kinchafoonee Creek	21	-	3	3
	14	-	3	3
	23	2	5	7
	29	1	5	6
	Muckalee Creek	26	-	4
Muckalee Creek	5	-	4	4
	10	-	4	4
	9	2	7	9
Flint River AAD	32	-	10	10
	16	2	8	10
Flint River BAD	2	3	10	13
	6	-	2	2
	30	1	4	5
	12	1	5	6

Table 2. U.S. Geological Survey stream gauges used to obtain discharge data for age-0 hatch and growth analyses. Mean annual flow values over the period of record are provided for each gauge. Ordered by stream from most upstream gauge to most downstream. Flint River at Warwick data were provided from the Crisp County Power Commission for the year 2023. No stream gauges were present for Abrams or Cooleewahee creeks. DA = Drainage area in km<sup>2</sup>, Q<sub>mean</sub> = mean annual flow in m<sup>3</sup>/s, Q<sub>SD</sub> = standard deviation of mean annual flow in m<sup>3</sup>/s, Period = number of years of available flow data. AAD = above (upstream) Albany Dam, BAD = below (downstream) Albany Dam.

Stream	USGS stream gauge number	Location	Latitude	Longitude	DA	Q <sub>mean</sub>	Q <sub>SD</sub>	Period
Ichawaynochaway	2353265	Morgan	31.52695	-84.58278	779.59	7.99	3.48	14
Ichawaynochaway	2353500	Milford	31.38278	-84.54639	1616.16	20.84	7.56	78
Ichawaynochaway	2354800	Elmodel	31.29389	-84.49194	2590.00	25.74	13.93	20
Ichawaynochaway	2355350	Newton	31.21750	-84.47083	2693.60	21.86	16.37	11
Chickasawhatchee	2354350	Albany	31.59378	-84.45325	305.62	3.31	1.50	14
Chickasawhatchee	2354500	Elmodel	31.35056	-84.48250	841.75	8.55	5.35	30
Flint AAD	NA	Warwick	31.84938	-83.94666	9764.30	145.58	134.19	1
Flint AAD	2350512	Leesburg	31.72500	-84.01861	10196.83	118.93	42.48	57
Flint BAD	2352500	Albany	31.59417	-84.14417	13701.10	167.92	58.33	105
Flint BAD	2353000	Newton	31.30694	-84.33889	14946.89	177.26	57.48	68
Flint BAD	2355662	Hopeful	31.14056	-84.48028	17961.65	185.48	82.69	13
Kinchafoonee	2350600	Preston	32.05250	-84.54833	510.23	5.75	2.04	48
Kinchafoonee	2350900	Dawson	31.71962	-84.18546	1517.74	22.34	10.82	30
Muckalee	2351500	Americus	32.08306	-84.25806	362.60	3.77	1.33	14

Muckalee	2351890	Leesburg	31.77611	-84.13944	937.58	10.28	4.53	35
Abrams	NA	Oakfield	31.71868	-83.98866	205.90	NA	NA	NA
Cooleewahee	NA	Newton	31.33166	-84.33076	404.04	NA	NA	NA

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Table 3. Environmental covariates used for hatch and growth analyses organized by stream name and site number (Figure 1). Means and ranges (in parentheses) of mean daily temperature (Temp; °C) for 2022 and 2023 sampling seasons and date of peak flow recorded in spring of each sampling year (PF2022 and PF2023) are included. No sampling occurring at a site in 2022 is denoted by ‘-’. Streamflow data were not available for either Abrams or Cooleewahee creeks (NA). AAD = above (upstream) Albany Dam, BAD = below (downstream) Albany Dam.

Stream	Site number	Temp 2022	Temp 2023	PF2022	PF2023
Abrams Creek	1	-	21.92 (12.38-27.15)	-	NA
Chickasawhatchee Creek	15	-	22.83 (11.37-29.3)	-	2/1
	7	-	22.47 (11.49-29.32)	-	2/4
Cooleewahee Creek	17	-	22.61 (12.74-27.74)	-	NA
Ichawaynochaway Creek	18	-	21.79 (11.0-26.6)	-	1/31
	28	-	22.38 (11.71-27.92)	-	2/2
	19	-	23.02 (11.59-29.06)	-	2/2
	24	23.68 (11.32-29.61)	23.01 (11.59-29.06)	1/19	2/2
	20	23.76 (11.98 -29.87)	23.42 (12.42-28.47)	1/20	2/3
	31	23.28 (12.06-29.25)	22.76 (12.78-27.93)	1/20	2/3
Kinchafonee Creek	22	-	21.37 (10.45-26.87)	-	1/31
	21	-	21.28 (10.61-27.58)	-	1/31
	14	-	21.68 (10.77-28.01)	-	2/1

	23	22.59 (10.84-29.06)	22.20 (12.21-29.14)	4/11	2/2
	29	22.59 (10.84-29.06)	22.60 (12.66-29.67)	4/11	2/2
Muckalee Creek	26	-	22.71 (11.65-28.20)	-	1/31
	5	-	22.10 (11.70-28.13)	-	1/31
	10	-	21.76 (11.58-28.26)	-	2/2
	9	22.36 (11.05-28.90)	22.50 (11.85-29.39)	4/8	2/2
Flint River AAD	32	-	24.18 (13.64-31.29)	-	4/1
	16	24.84 (10.96-31.43)	24.23 (13.40-31.57)	4/11	4/1
Flint River BAD	2	24.83 (10.97-31.39)	24.24 (11.89-31.40)	4/11	4/2
	6	-	24.13 (12.74-30.37)	-	4/2
	30	23.67 (11.65-30.08)	23.15 (12.55-29.15)	4/13	4/3
	12	23.77 (11.92-30.15)	24.08 (13.11-30.43)	4/13	4/4

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Table 4. Environmental data collected to relate to variation in age-0 hatch timing, hatch success, and daily growth.

<i>Covariate</i>	<i>Unit</i>	<i>Gear/Source</i>	<i>Justification and citation</i>
Temperature	°C	Hobo Pendant Logger, NEON buoy	Temperature is a highly correlated with spawning initiation and growth rate in black basses <sup>1,2,3</sup>
Scaled discharge	m/s	USGS-stream gauge, NHDPlus Flowlines	Black bass spawning and hatch success is linked to discharge and flood pulses <sup>1,4,5</sup>
Calendar day	1 d	Days since Jan. 1 <sup>st</sup>	Photoperiod is an influential cue in spawning timing in stream fishes <sup>6</sup> due to consistency across years <sup>7</sup> , and hatch timing within a spawning season may affect survival and growth <sup>8,9</sup>
Days post-peak spring flood	1 d	Days since highest recorded flow in that calendar year	Many species of black bass have been observed to successfully hatch after flood pulses and during periods of receding and stable flows <sup>4,5,8</sup>

1. (Graham and Orth 1986) 2. (Rogers and Allen 2009) 3. (Long and Porta 2019) 4. (Sammons et al. 2021) 5. (Bestgen 2016) 6. (de Vlaming 1972) 7. (O'Brien et al. 2012) 8. (Shuter et al. 1980) 9. (Goodgame and Miranda 1993)



Table 5. Pearson’s Correlation matrix (rho values) for environmental covariates used for age-0 hatch date analysis. Mean Q = mean discharge (m<sup>3</sup>/s) scaled by catchment area 7-days prior to hatch week, Mean temp = mean temperature (°C) 7-days prior to hatch week, CV Q = coefficient of variation in discharge scaled by catchment area 7-days prior to hatch week, ROC Q = rate of change scaled discharge 14-days prior to hatch week, Post peak = number of days post-peak spring flow, Week = calendar week of hatch.

	Mean Q	Mean temp	CV Q	ROC Q	Post peak	Week
Mean Q	1.00					
Mean temp	-0.61	1.00				
CV Q	0.01	0.31	1.00			
ROC Q	0.24	0.01	0.25	1.00		
Post-peak	-0.55	0.73	0.26	0.04	1.00	
Week	-0.58	0.92	0.33	0.05	0.86	1.00

Table 6. Summary of considered covariate combinations for hatch analyses (zero and count models). Temp = mean daily temperature (°C) 7-d prior to hatch week, CV Q = coefficient of variation in instantaneous (15 minute) values of discharge 7-d prior to hatch week, ROC Q = rate of change in mean daily discharge 14 d prior to hatch week, Year = the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models. Quadratic terms of each continuous variables in negative-binomial models (count models) were also considered.

Model Description
~ Temp + CV Q + ROC Q + Year
~ Temp + CV Q + Year
~ Temp + ROC Q + Year
~ Temp + CV Q + ROC Q
~ CV Q + ROC Q + Year
~ CV Q + ROC Q
~ CV Q + Year
~ Temp + CV Q
~ Temp + ROC Q
~ Temp + Year
~ ROC Q + Year
~ ROC Q
~ Temp
~ CV Q

Table 7. Pearson's Correlation matrix (rho values) for environmental covariates used for age-0 growth-rate analysis. Hatch day = calendar day of hatch. All other covariates were measured between hatch date and capture date of each fish. Mean Q = mean discharge (m<sup>3</sup>/s) scaled by catchment area, Mean temp = mean temperature (°C), CV Q = coefficient of variation in discharge scaled by catchment area.

	Mean Q	CV Q	Mean temp	Hatch Day
Mean Q	1.00			
CV Q	0.33	1.00		
Mean temp	-0.56	-0.26	1.00	
Hatch Day	-0.27	0.02	0.60	1.00

Table 8. Summary of considered covariate combinations for growth analyses. Temp = mean daily temperature (°C), CV Q = coefficient of variation of discharge, Mean Q = mean daily discharge (m<sup>3</sup>/s), Year = the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Model Description
~ Temp + CV Q + Mean Q + Year
~ Temp + Mean Q + Year
~ Temp + CV Q + Year
~ CV Q + Mean Q + Year
~ Temp + CV Q + Mean Q
~ Temp + Mean Q
~ Temp + CV Q
~ Temp + Year
~ CV Q + Year
~ CV Q + Mean Q
~ Mean Q + Year
~ Temp
~ CV Q
~ Mean Q

Table 9. The total number of age-0 Largemouth Bass and Shoal Bass collected from each of 25 sites (8 streams; Figure 1) during the summers of 2022 and 2023. Totals sum both 2022 and 2023 counts. ‘-’ indicates site was not sampled in 2022. Site numbers are listed from upstream to downstream for each stream. AAD = above (upstream) Albany Dam, BAD = below (downstream) Albany Dam.

Species	Stream	Site	2022	2023	Site Total	Stream Total
Largemouth Bass	Abrams Creek	1	-	11	11	11
		Chickasawhatchee Creek	15	-	0	0
			7	0	21	21
	Cooleewahee Creek	17	-	18	18	18
		Ichawaynochaway Creek	18	-	0	0
		28	-	39	39	
		19	-	2	2	
		24	0	2	2	
		20	1	0	1	
		31	2	0	2	46
	Kinchafoonie Creek	22	-	0	0	
		21	-	2	2	
		14	-	4	4	
		23	0	10	10	
		29	6	10	16	32
	Muckalee Creek	26	-	0	0	
		5	-	23	23	
		10	-	7	7	
		9	44	4	48	78
	Flint River AAD	32	-	178	178	
		16	30	18	48	226
	Flint River BAD	2	27	30	57	
		6	-	9	9	
		30	2	18	20	

		12	2	9	11	97
Shoal Bass	Abrams Creek	1	-	0	0	0
	Chickasawhatchee Creek	7	0	0	0	
		15	-	0	0	
	Cooleewahee Creek	17	-	0	0	0
	Ichawaynochaway Creek	18	-	0	0	
		28	-	0	0	
		19	-	0	0	
		24	0	0	0	
		20	0	0	0	
		31	12	0	12	12
	Kinchafoonee Creek	22	-	0	0	
		21	-	0	0	
		14	-	0	0	
		23	0	0	0	
		29	0	0	0	0
	Muckalee Creek	26	-	0	0	
		5	-	0	0	
		10	-	0	0	
		9	1	0	1	1
	Flint River AAD	32	-	52	52	
		16	104	14	118	170
	Flint River BAD	2	21	64	85	
		6	-	0	0	
		30	2	6	8	
		12	9	4	13	106

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Table 10. Summary of age and hatch date estimates for Largemouth Bass and Shoal Bass collected from sites in the lower Flint River catchment during summer 2022 and 2023. Abrams and Cooleewahee creeks were not sampled in 2022; ‘-’ therefore indicates either the stream was not sampled or that species was not found at that site during that year. The location of hatch (Stream), the number of otoliths aged in 2022 (R: retained otoliths meeting between reader agreement criteria in parentheses), otoliths aged in 2023 (R), the number of weeks during which a hatch occurred in 2022 (HW2022) and 2023 (HW2023), average total length (TL; mm) of each species, Age (d), and range of hatch dates in 2022 (HD2022) and 2023 (HD2023). AAD = above (upstream) Albany Dam, BAD = below (downstream) Albany Dam.

Species	Stream	2022 Aged (R)	2023 Aged (R)	HW2022	HW2023	TL	Ages	HD2022	HD2023
Largemouth Bass	Abrams Creek	-	11 (11)	-	8	29.5-84.92	40-103	-	3/20-5/17
	Chickasawhatchee Creek	-	21 (21)	-	11	29.78-77.87	33-127	-	3/10-6/23
	Cooleewahee Creek	-	18 (17)	-	10	30.37-79.65	30-111	-	3/24-6/26
	Ichawaynochaway Creek	4 (4)	43(43)	3	7	24.4-94.07	29-125	3/15-4/8	3/11-5/29
	Kinchafoonee Creek	6 (6)	26 (25)	5	10	37.01-83.89	42-131	3/20-4/28	3/27-5/24
	Muckalee Creek	44 (43)	34 (31)	6	12	23.11-80.26	36-124	3/24-5/18	3/12-6/2
	Flint River AAD	30 (30)	184 (177)	5	11	26.44-98.04	30-133	4/29-6/1	3/20-6/10
	Flint River BAD	27 (27)	66 (66)	7	15	26.86-110.81	31-158	3/23-5/18	3/11-6/23
Shoal Bass	Abrams Creek	-	-	-	-	-	-	-	-
	Chickasawhatchee Creek	-	-	-	-	-	-	-	-

Cooleewahee Creek	-	-	-	-	-	-	-	-
Ichawaynochaway Creek	12 (12)	-	5	-	19.1-84.26	26-73	5/9-6/2	-
Kinchafoonee Creek	-	-	-	-	-	-	-	-
Muckalee Creek	1 (1)	-	1	-	55.11	48	5/6	-
Flint River AAD	104 (101)	66 (64)	6	6	27.97-113.20	35-116	4/29-6/4	4/16-5/22
Flint River BAD	32(31)	74(73)	6	6	48.79-116.88	54-118	4/25-5/26	4/20-5/26

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Table 11. Summary of mean and range (in parentheses) estimates of growth rate (mm/day) for Largemouth Bass and Shoal Bass for each stream during 2022 (GR2022) and 2023 (GR2023). AAD = above (upstream) Albany dam, BAD = below (downstream) Albany Dam.

Species	Stream	GR2022	GR2023
Largemouth Bass	Abrams Creek	-	0.72 (0.58-0.86)
	Chickasawhatchee Creek	-	0.74 (0.60-1.01)
	Cooleewahee Creek	-	0.81 (0.63-1.01)
	Ichawaynochaway Creek	0.85 (0.75-1.05)	0.83 (0.55-0.97)
	Kinchafoonee Creek	0.75 (0.58-0.97)	0.73 (0.50-1.29)
	Muckalee Creek	0.69 (0.58-0.82)	0.71 (0.45-1.03)
	Flint River AAD	1.08 (0.81-1.48)	0.84 (0.57-1.40)
	Flint River BAD	0.88 (0.73-1.09)	0.76 (0.56-1.22)
Shoal Bass	Abrams Creek	-	-
	Chickasawhatchee Creek	-	-
	Cooleewahee Creek	-	-
	Ichawaynochaway Creek	0.98 (0.65-1.34)	-
	Kinchafoonee Creek	-	-
	Muckalee Creek	1.148 (1.148-1.148)	-
	Flint River AAD	1.19 (0.86-1.58)	0.88 (0.67-1.14)
	Flint River BAD	1.14 (0.80-1.51)	0.91 (0.71-1.17)

Table 12. Top ranked binomial models (zero models) describing the relationship between the probability of Largemouth Bass and Shoal Bass hatches and my covariates. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike's information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model ( $\Delta AICc$ ), model weight ( $w_i$ ), and the conditional ( $R^2_c$ ; variance explained by fixed and random effects) and the marginal ( $R^2_m$ ; variance explained by fixed effects)  $R^2$  values are also reported. Included covariates were mean temperature (Temp; °C), coefficient of variation of discharge (CV Q), rate of change of discharge (ROC Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Model	df	logLik	AICc	$\Delta AICc$	$w_i$	$R^2_c$	$R^2_m$
Largemouth Bass	Temp + Year	4	-292.39	592.84	0.00	0.33	0.25	0.19
	Temp + CV Q + Year	5	-291.92	593.92	1.09	0.19	0.25	0.19
Shoal Bass	CV Q + ROC Q	4	-109.61	227.59	0.00	0.49	0.38	0.30
	Temp + CV Q + ROC Q	5	-109.39	229.15	1.58	0.22	0.42	0.32
	CV Q + ROC Q + Year	5	-109.61	229.42	1.83	0.20	0.37	0.30

Table 13. Estimates (logit) of each covariate included in the top model related to the probability of successful hatch for Largemouth Bass and Shoal Bass. The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent mean temperature (Temp; °C), coefficient of variation of discharge (CV Q), rate of change of discharge (ROC Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Covariate	Estimate	SE	95% CI	P
Largemouth Bass	Intercept	-2.06	0.32	(-2.74, -1.37)	<0.0001
	Temp	-0.86	0.11	(-1.08, -0.64)	<0.0001
	Year	0.50	0.25	(0.02,0.99)	0.04
Shoal Bass	Intercept	-2.19	0.38	(-3.08, -1.46)	<0.0001
	CV Q	-0.89	0.25	(-1.41, -0.40)	0.0004
	ROC Q	-0.72	0.20	(-1.15, -0.35)	0.0004

Table 14. Top ranked negative binomial models (count models) for describing the relationship between the frequency of Largemouth Bass and Shoal Bass hatches and my covariates. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike’s information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model ( $\Delta AICc$ ), and model weights ( $w_i$ ) are also reported. Included covariates represent mean temperature (Temp; °C), coefficient of variation of discharge (CV Q), rate of change of discharge (ROC Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Model	df	logLik	AICc	$\Delta AICc$	$w_i$
Largemouth Bass	CV Q	4	-224.77	457.87	0.00	0.19
	CV Q + ROC Q <sup>2</sup>	6	-223.40	459.49	1.62	0.08
	CV Q + Year	5	-224.56	459.61	1.74	0.08
Shoal Bass	ROC Q	4	-115.73	240.46	0.00	0.13
	Mean T	4	-116.04	241.08	0.62	0.10
	Mean T + Year	5	-115.01	241.56	1.10	0.08
	CV Q	4	-116.32	241.63	1.18	0.07
	Meant T <sup>2</sup>	5	-115.36	242.26	1.81	0.05
	ROC Q <sup>2</sup>	5	-115.41	242.36	1.91	0.05

Table 15. Estimates (log) of each covariate included in the top model related to the frequency of successful hatches for Largemouth Bass and Shoal Bass. The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent mean temperature (Temp; °C), coefficient of variation of discharge (CV Q), rate of change of discharge (ROC Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Covariate	Estimate	SE	95% CI	P
Largemouth Bass	Intercept	-1.73	4.23	(-10.03, 6.56)	0.68
	CV Q	-0.60	0.20	(-0.98, -0.21)	0.004
Shoal Bass	Intercept	-0.2	3.4	(-6.85, -0.20)	0.95
	ROC Q	0.46	0.34	(-0.20, 1.12)	0.17
	Intercept	0.51	2.14	(-3.69, 4.72)	0.81
	Mean T (quadratic)	-0.39	0.30	(-0.97, 1.00)	0.19

Table 16. Top ranked linear regression models of daily growth rate for age-0 Largemouth Bass and Shoal Bass and their AICc scores. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike's information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model ( $\Delta AICc$ ), model weight ( $w_i$ ), and the conditional ( $R^2_c$ ; variance explained by fixed and random effects) and the marginal ( $R^2_m$ ; variance explained by fixed effects)  $R^2$  values are also reported. Included covariates represent mean temperature (Temp; °C), CV of scaled discharge (CV Q), mean scaled discharge (Mean Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Model	df	logLik	AICc	$\Delta AICc$	$w_i$	$R^2_c$	$R^2_m$
Largemouth Bass	CV Q + Mean Q + Year	6	259.53	-506.88	0.00	0.84	0.33	0.14
Shoal Bass	Mean Q + Year	5	163.79	-317.36	0.00	0.68	0.67	0.40
	Mean Temp + Year	5	162.85	-315.49	1.87	0.27	0.58	0.49

Table 17. Estimates of each covariate included in the top model related to growth of age-0 Largemouth Bass and Shoal Bass. The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent mean temperature (Temp; °C), CV of scaled discharge (CV Q), mean scaled discharge (Mean Q), and the categorical fixed effect of year where 2022 was the reference. The random effect of stream was included in all models.

Species	Covariate	Estimate	SE	95% CI	P
Largemouth Bass	Intercept	0.95	0.04	(0.88, 1.02)	<0.0001
	CV Q	-0.04	0.01	(-0.06, -0.02)	0.0001
	Mean Q	0.06	0.01	(0.03, 0.08)	<0.0001
	Year	-0.20	0.02	(-0.25, -0.15)	<0.0001
Shoal Bass	Intercept	1.04	0.07	(0.90, 1.19)	<0.0001
	Mean Q	-0.06	0.02	(-0.11, -0.01)	0.01
	Year	-0.17	0.05	(-0.26, -0.08)	0.003
	Intercept	1.12	0.04	(1.05, 1.20)	<0.0001
	Temp	0.03	0.01	(0.01, 0.05)	0.012
	Year	-0.23	0.02	(-0.28, -0.19)	<0.0001

Chapter III Figures

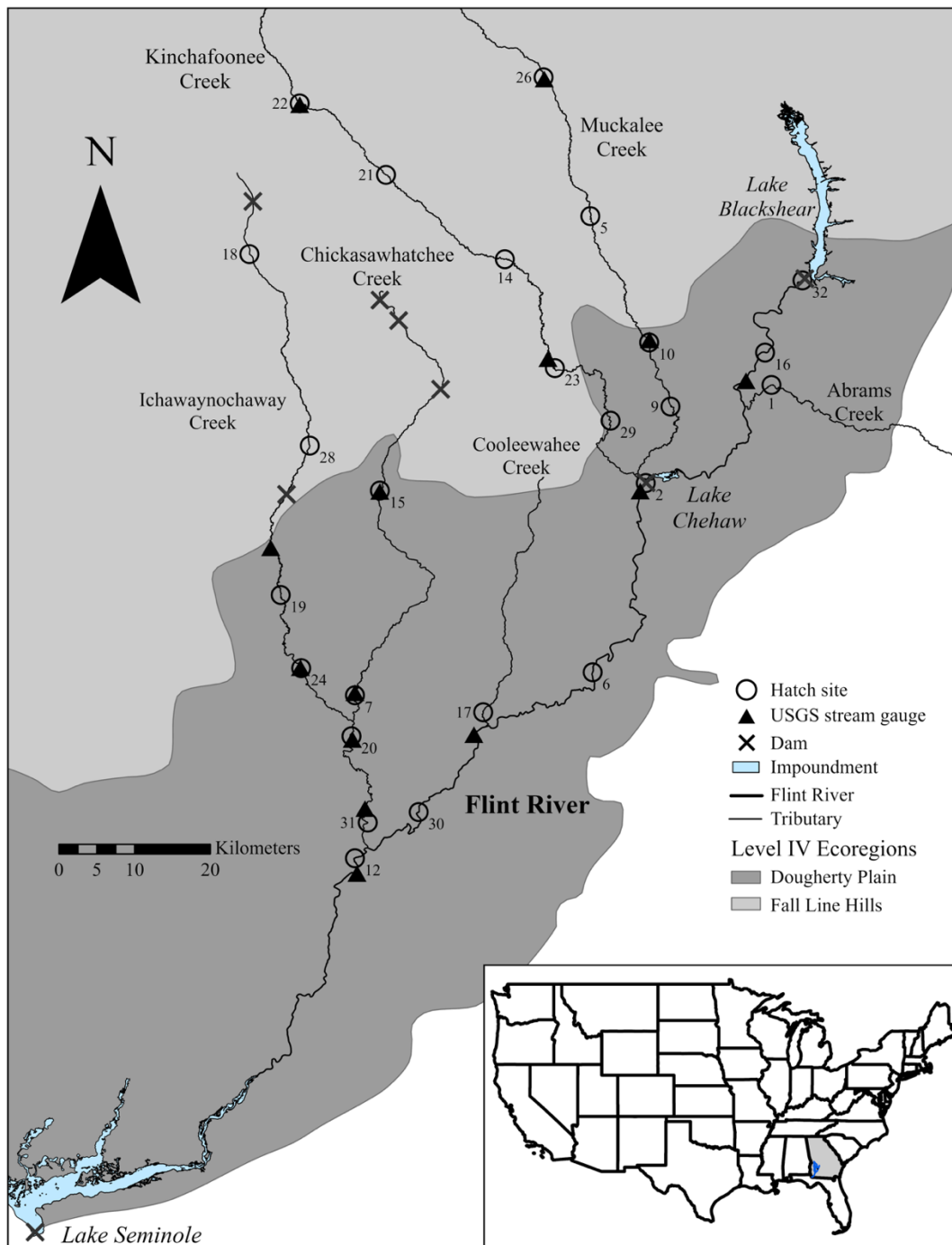


Figure 1: The lower Flint River catchment within the Dougherty Plain (dark gray) and Fall Line Hills (light gray) physiographic regions showing the study extent for age-0 hatch timing and growth analyses. Black X's represent hydropower and low-head dams, black triangles are USGS stream gauge locations, empty circles are numbered hatch (sampling) sites which are also associated with continuous temperature loggers. The thick black line is the lower Flint River, thin black lines are major tributaries, and blue polygons are impoundments.



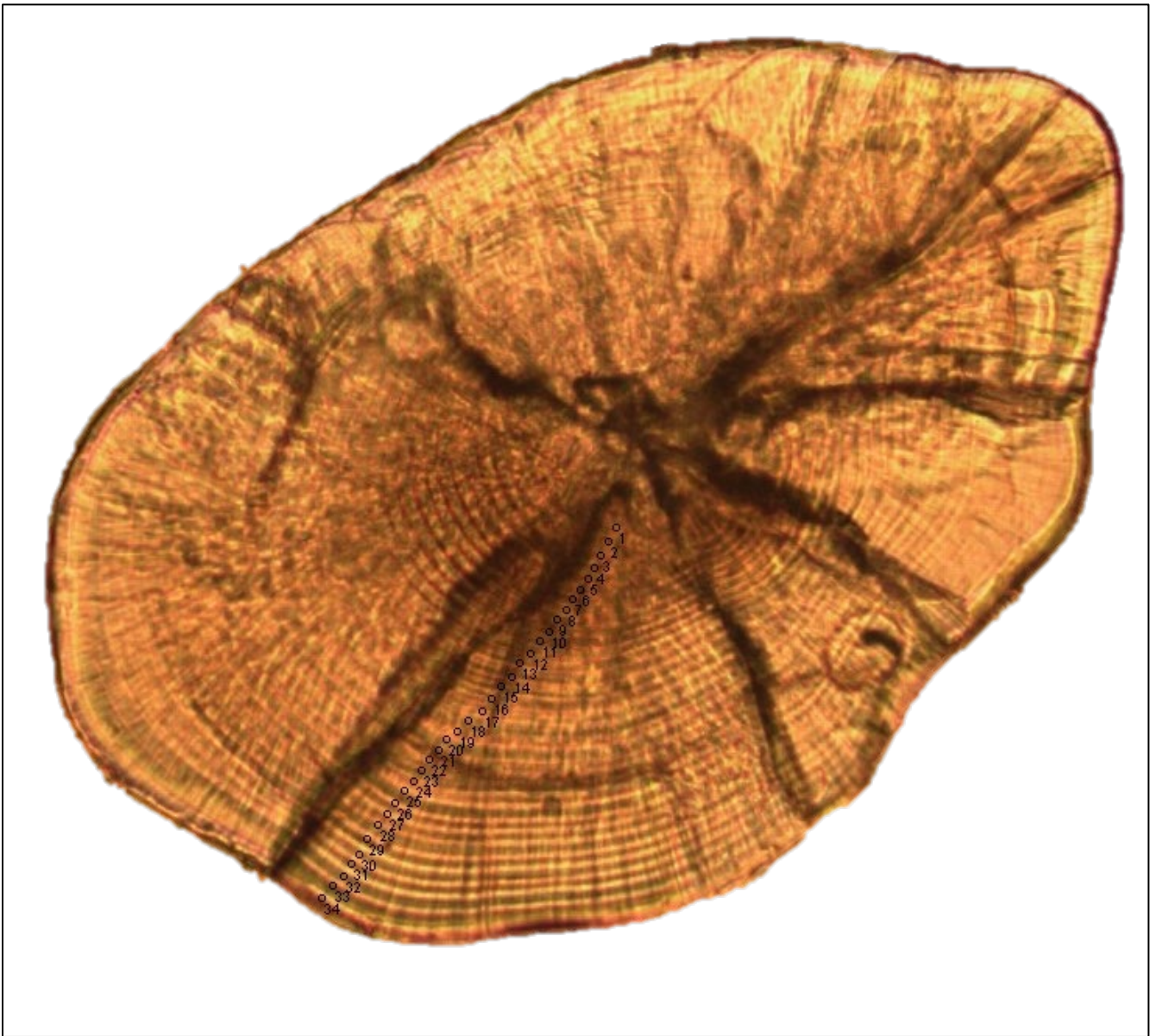


Figure 2: Example of sagittal otolith from age-0 Shoal Bass *Micropterus cataractae* viewed under a 10X magnification compound microscope (Nikon Eclipse E400 compound microscope). Each daily growth ring has an opaque and translucent unit. Opaque units were counted from the edge of the otolith towards the center. This fish had 34 daily rings, and therefore was estimated to be 39 days old (to account for 5 days swim-up time) at time of capture.

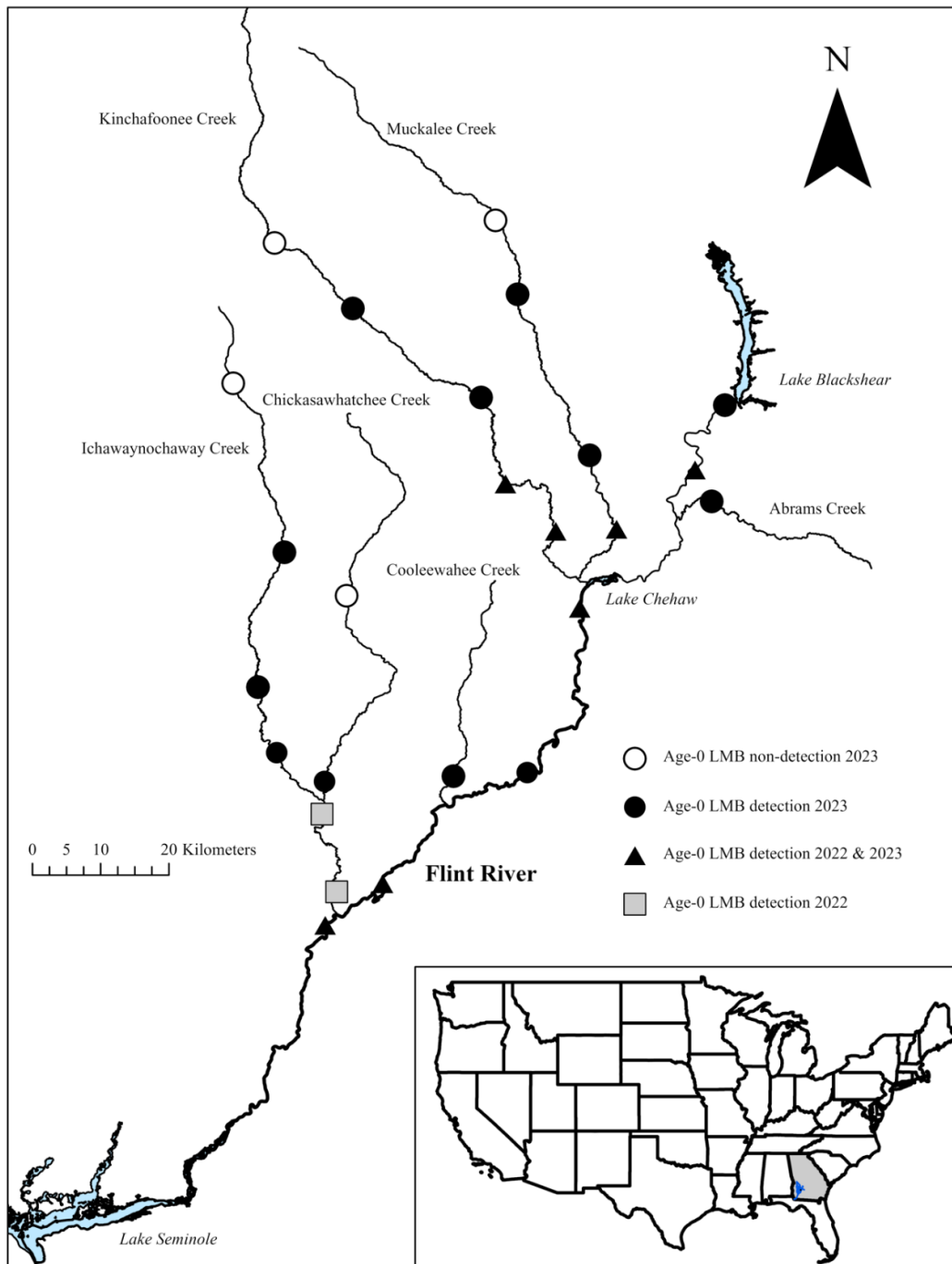


Figure 3. Sites where I detected and did not detect age-0 Largemouth Bass (LMB) during the 2022 and 2023 sampling seasons. White circles represent non-detection only in 2023, black circles represent detection only in 2023, black triangles represent detection in both years, and gray squares represent detection only in 2022. Not all sites were sampled both years. The thick black line is the lower Flint River, thin black lines are major tributaries, and blue polygons are impoundments.

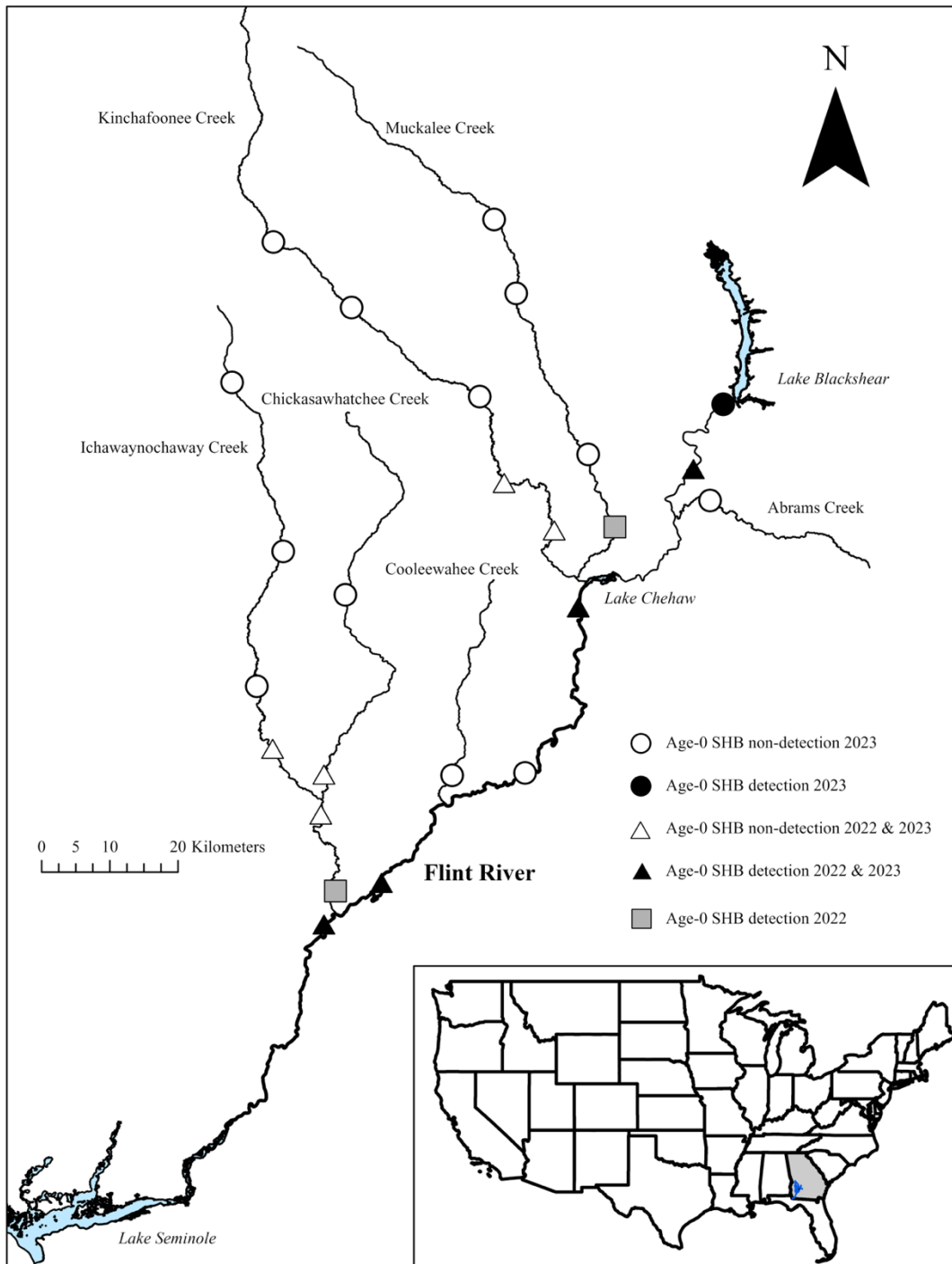


Figure 4. Sites where I detected and did not detect age-0 Shoal Bass (SHB) during the 2022 and 2023 sampling seasons. White circles represent non-detection only in 2023, black circles represent detection only in 2023, white triangles represent non-detection both years, black triangles represent detection in both years, and gray squares represent detection only in 2022. Not all sites were sampled both years. The thick black line is the lower Flint River, thin black lines are major tributaries, and blue polygons are impoundments.

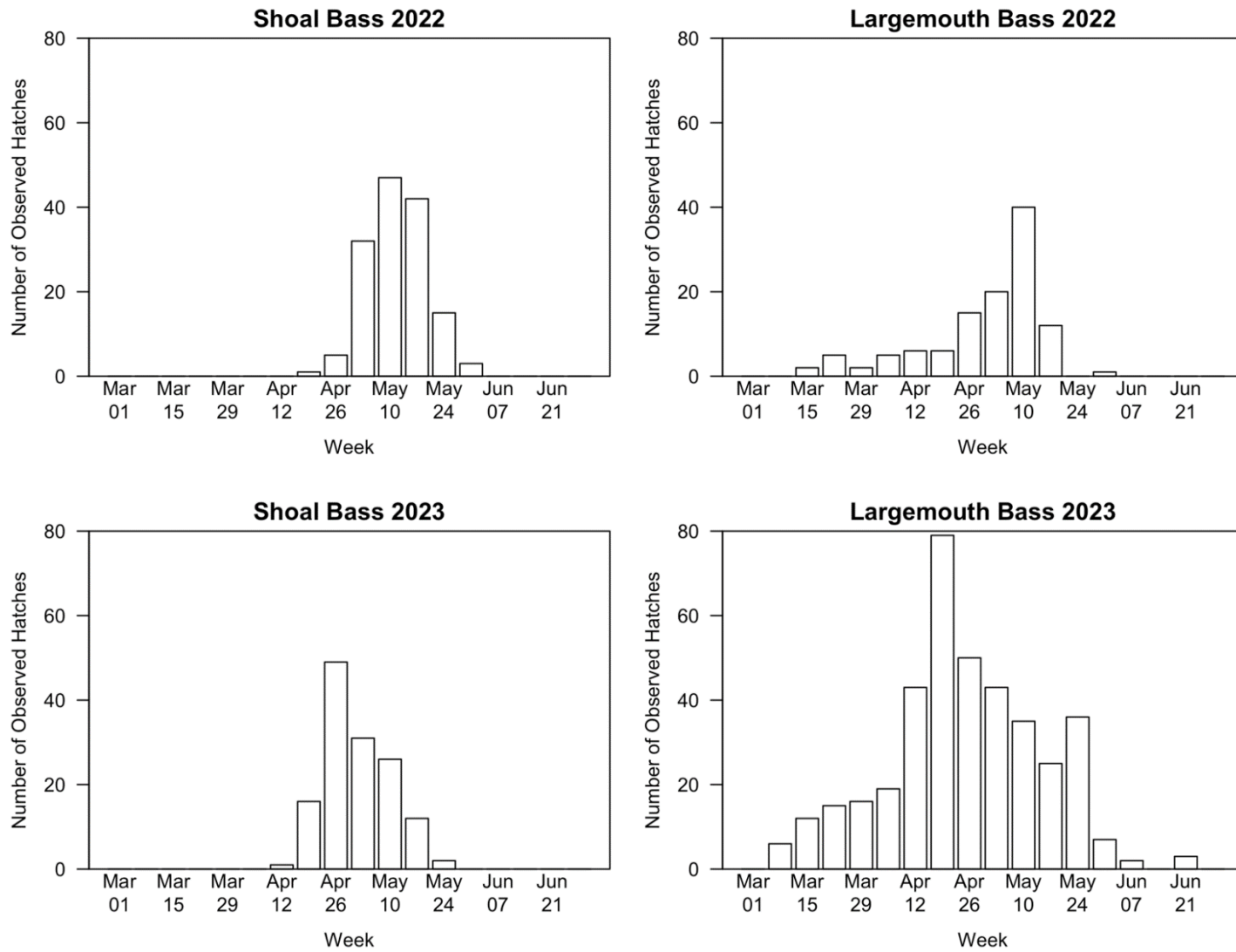


Figure 5. Frequency of age-0 bass hatch dates across all sites for the 2022 and 2023 hatching seasons. Left panels display Shoal Bass hatches, right panels display Largemouth Bass hatches, top panels display 2022 hatches, bottom panels display 2023 hatches. Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axis being the beginning of each week.

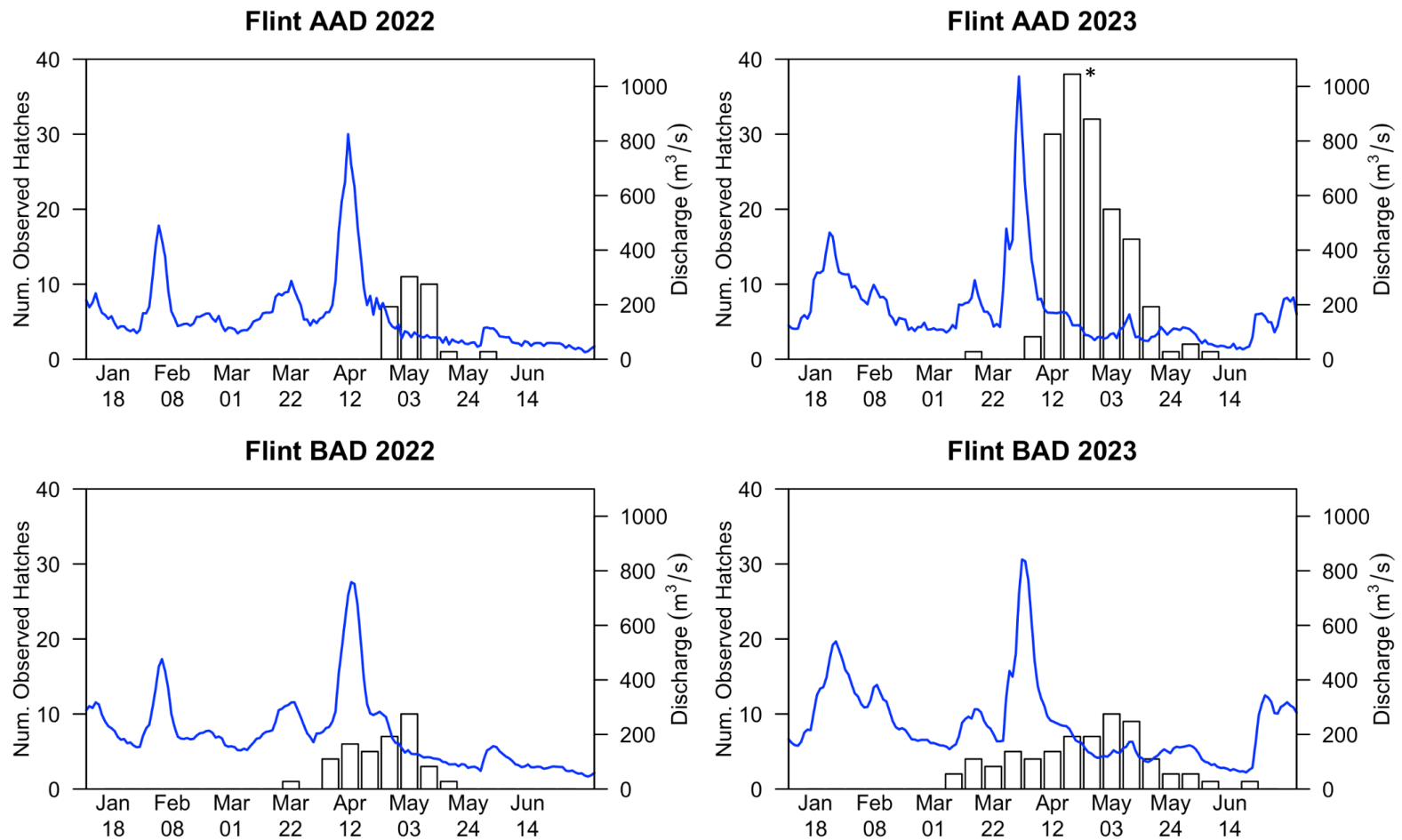


Figure 6. Largemouth Bass hatch dates across all lower Flint River sites for the 2022 and 2023 hatching seasons. Left panels display 2022 hatches, right panels display 2023 hatches, top panels display hatches for sites above Albany Dam (AAD), bottom panels display hatches for sites below Albany Dam (BAD). Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axes being the beginning of each week. Blue lines are mean daily discharge and bars represent the number of hatches per week. Weeks with over 40 hatches are indicated by “\*”: 64 hatches on the week of April 19<sup>th</sup>, 2023 in Flint AAD.

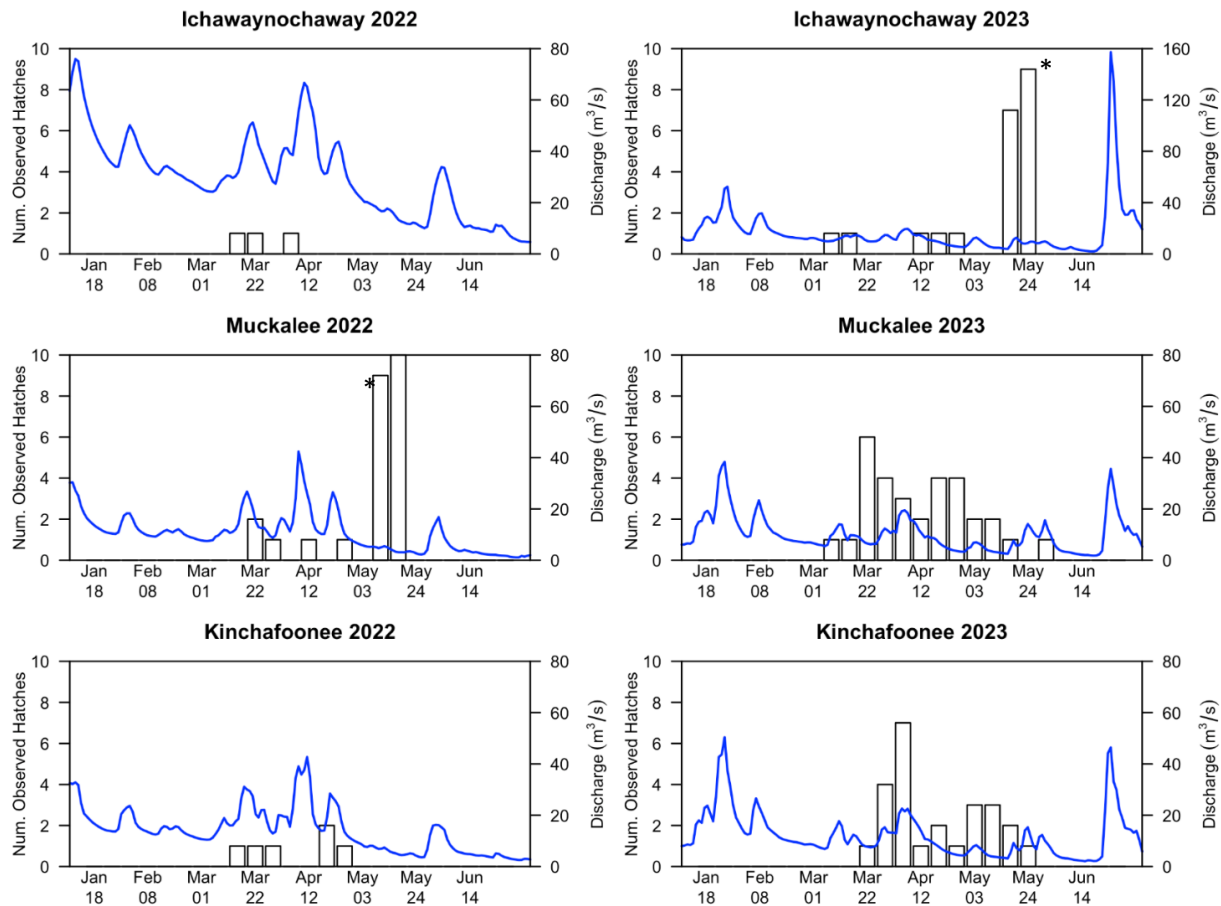


Figure 7. Largemouth Bass hatch dates across three tributaries for the 2022 and 2023 hatching seasons. Left panels display 2022 hatches, right panels display 2023 hatches, top panels display hatches for sites on Ichawaynochaway Creek, middle panels display hatches for sites on Muckalee Creek, and bottom panels display hatches for sites on Kinchafoonee Creek. Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axes being the beginning of each week. Blue lines are mean daily discharge and bars are the number of hatches per week. Weeks with over 10 hatches are indicated by “\*”: 31 hatches on the week of May 24<sup>th</sup>, 2023 in Ichawaynochaway Creek, and 28 hatches on the week of May 10<sup>th</sup>, 2022 in Muckalee Creek are not displayed.

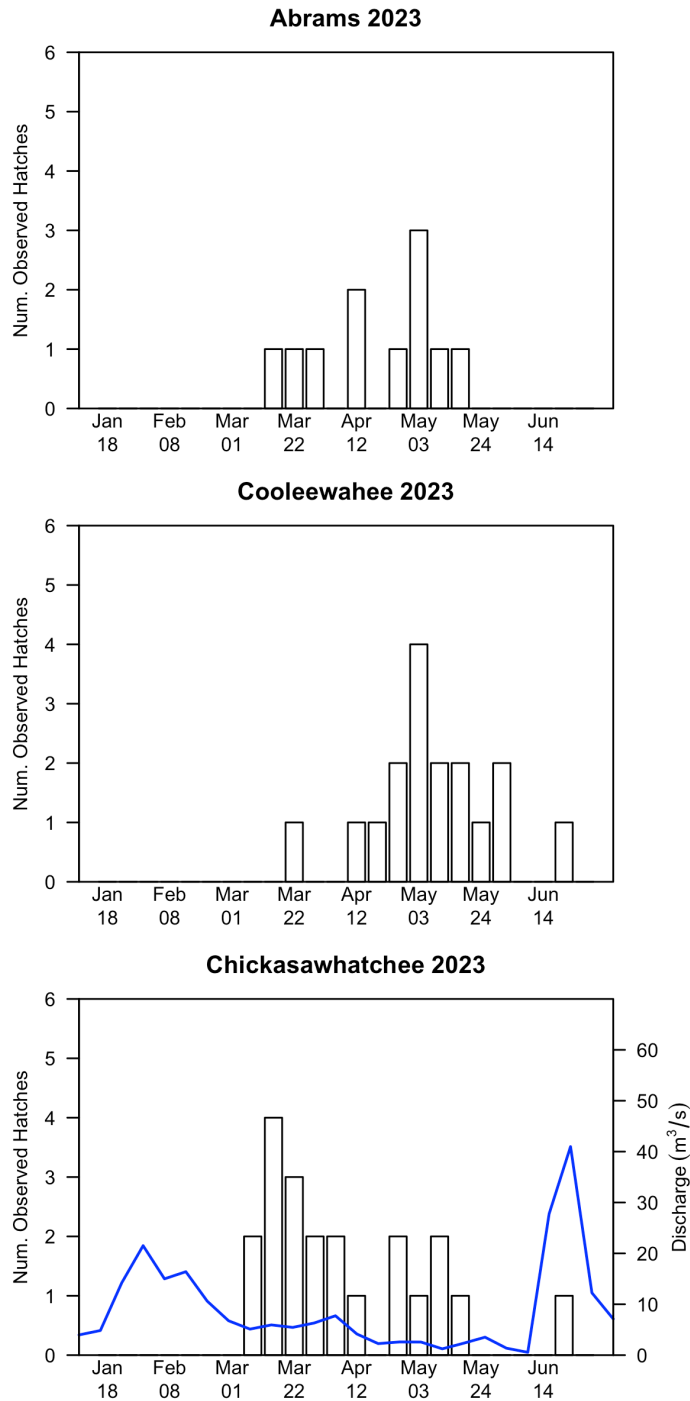


Figure 8. Largemouth Bass hatch dates across three tributaries for the 2023 hatching season. Top panel displays hatches for Abrams Creek, middle panel displays hatches for Cooleewahee Creek, and bottom panel displays hatches for Chickasawhatchee Creek. Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axes being the beginning of each week. Blue line is the mean weekly discharge and bars are the number of hatches per week. Discharge data were not available for Abrams and Cooleewahee creeks.

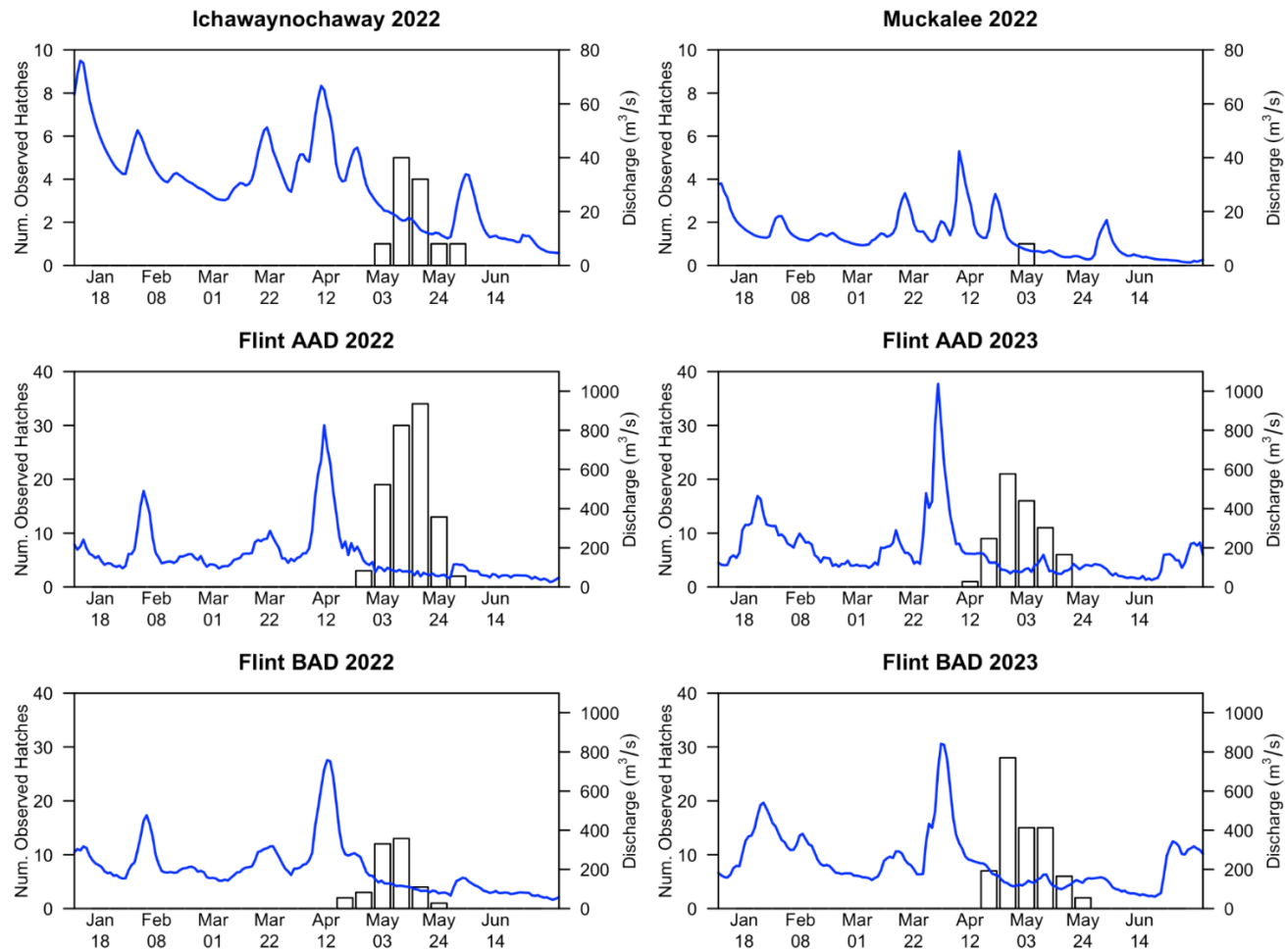


Figure 9. Shoal Bass hatch dates across all LFRC sites for the 2022 and 2023 hatching seasons. Top panels display tributary sites where age-0 SHB were detected in 2022 (left – Ichawaynochaway, right – Muckalee). Age-0 SHB were not detected at any tributary sites in 2023. Middle panels display hatches for sites above Albany Dam (AAD; left – 2022, right - 2023), bottom panels display hatches for sites below Albany Dam (BAD; left – 2022, right - 2023). Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axes being the beginning of each week. Blue lines are mean daily discharge and bars represent the number of hatches per week.



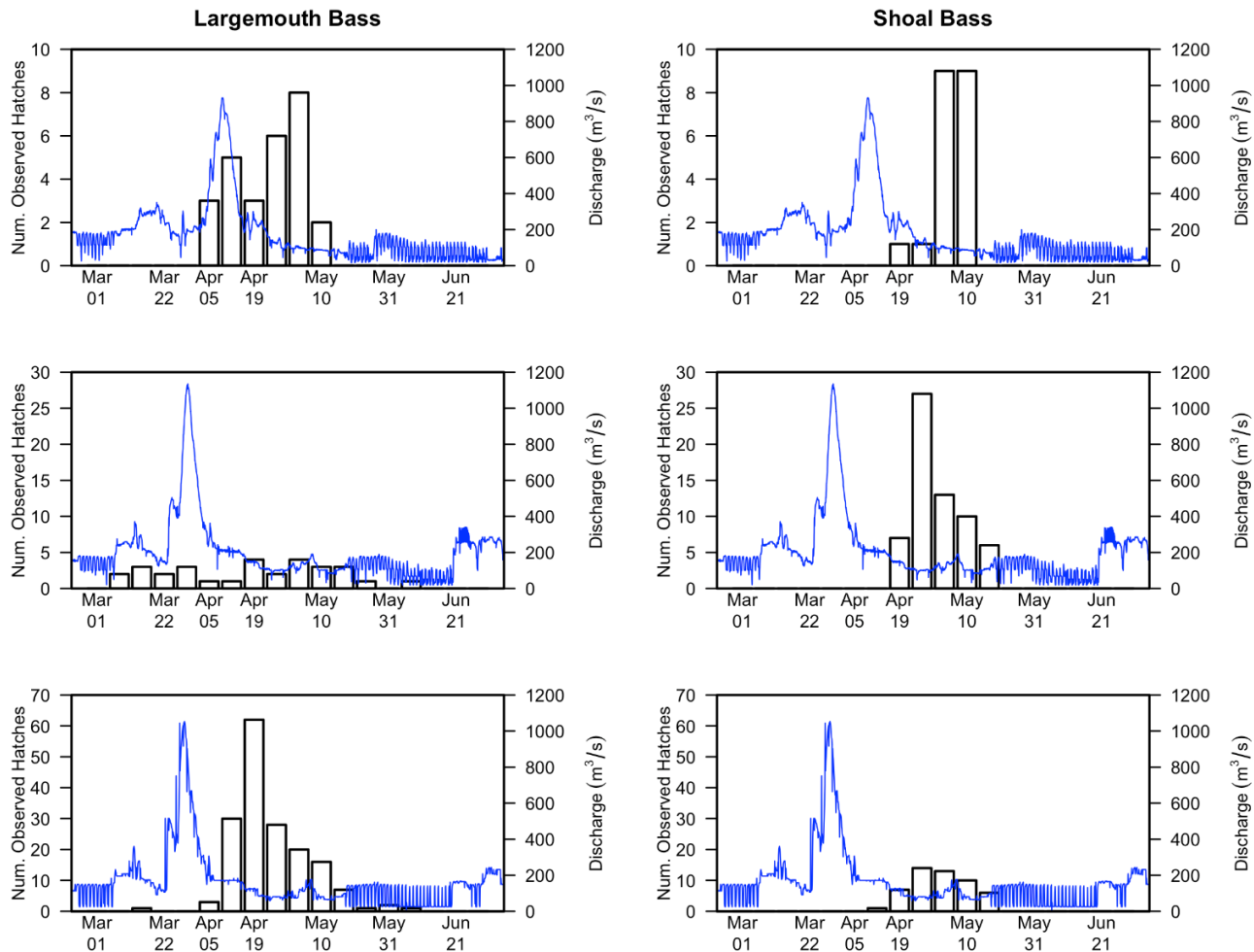


Figure 10. Largemouth Bass (left panel) and Shoal Bass (right panel) hatch dates across sites below hydropeaking dams for the 2022 and 2023 hatching seasons. Top panel and middle panels display hatches directly downstream of Albany Dam (site 2) in 2022 (top) and 2023 (middle). Bottom panel displays hatches directly downstream of Warwick Dam (site 32) in 2023. Observed hatches are grouped into week-long (7 day) bins with the dates displayed on the x-axes being the beginning of each week. Blue lines are discharge (1-h intervals), bars represent the number of hatches per week.

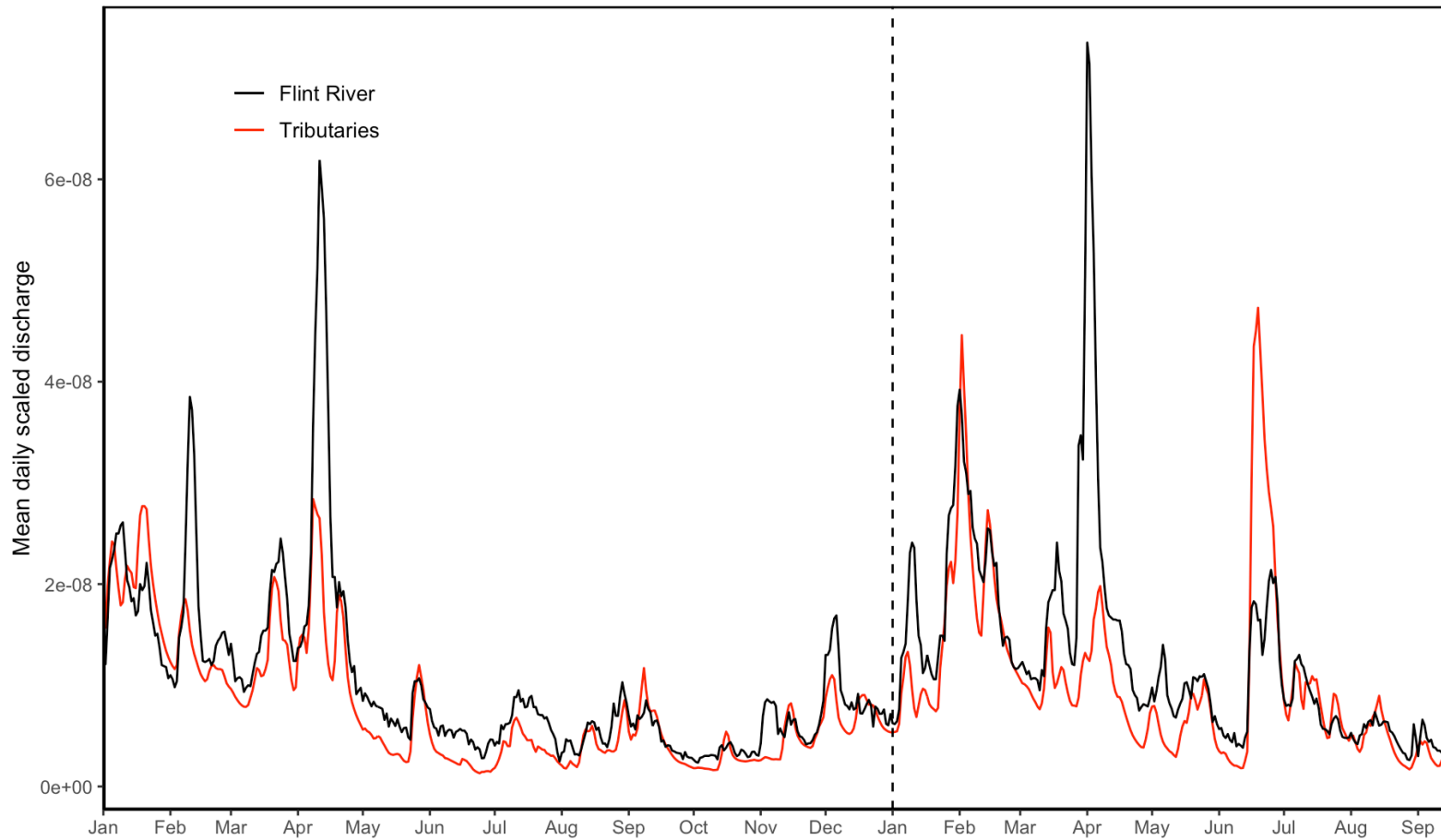


Figure 11. The difference in magnitude and timing of peak spring and summer flows between tributaries (averaged across tributaries where data were available, as they show similar patterns) and the mainstem Flint River. Mean daily scaled discharge ( $\text{m}^3/\text{s}$  divided by drainage area) averaged across all gauged tributaries (red) and all stream gauges on the Flint River (black). The x-axis ranges from January 2022 to September 2023 with a horizontal dashed line representing the beginning of 2023. Discharge data were not available for Coolewahee or Abrams creeks.

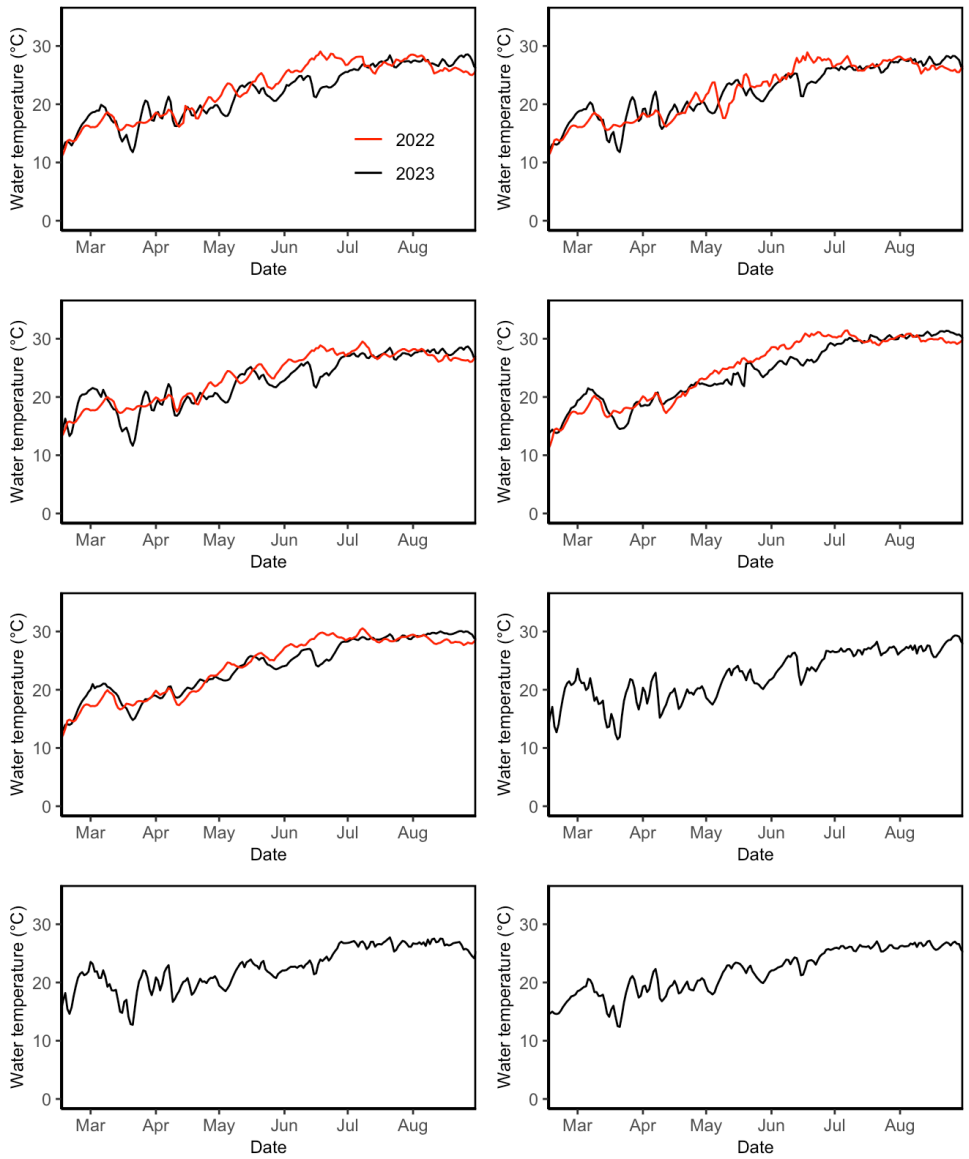


Figure 12. Mean daily water temperature (°C) across all streams for the 2022 (red) and 2023 (black) hatching seasons (February 15<sup>th</sup>-August 31<sup>st</sup>). Left to right and top to bottom: Kinchafoonee Creek, Muckalee Creek, Ichawaynochaway Creek, Flint River above Albany Dam, Flint River below Albany Dam, Chickasawhatchee Creek, Cooleewahee Creek, and Abrams Creek.

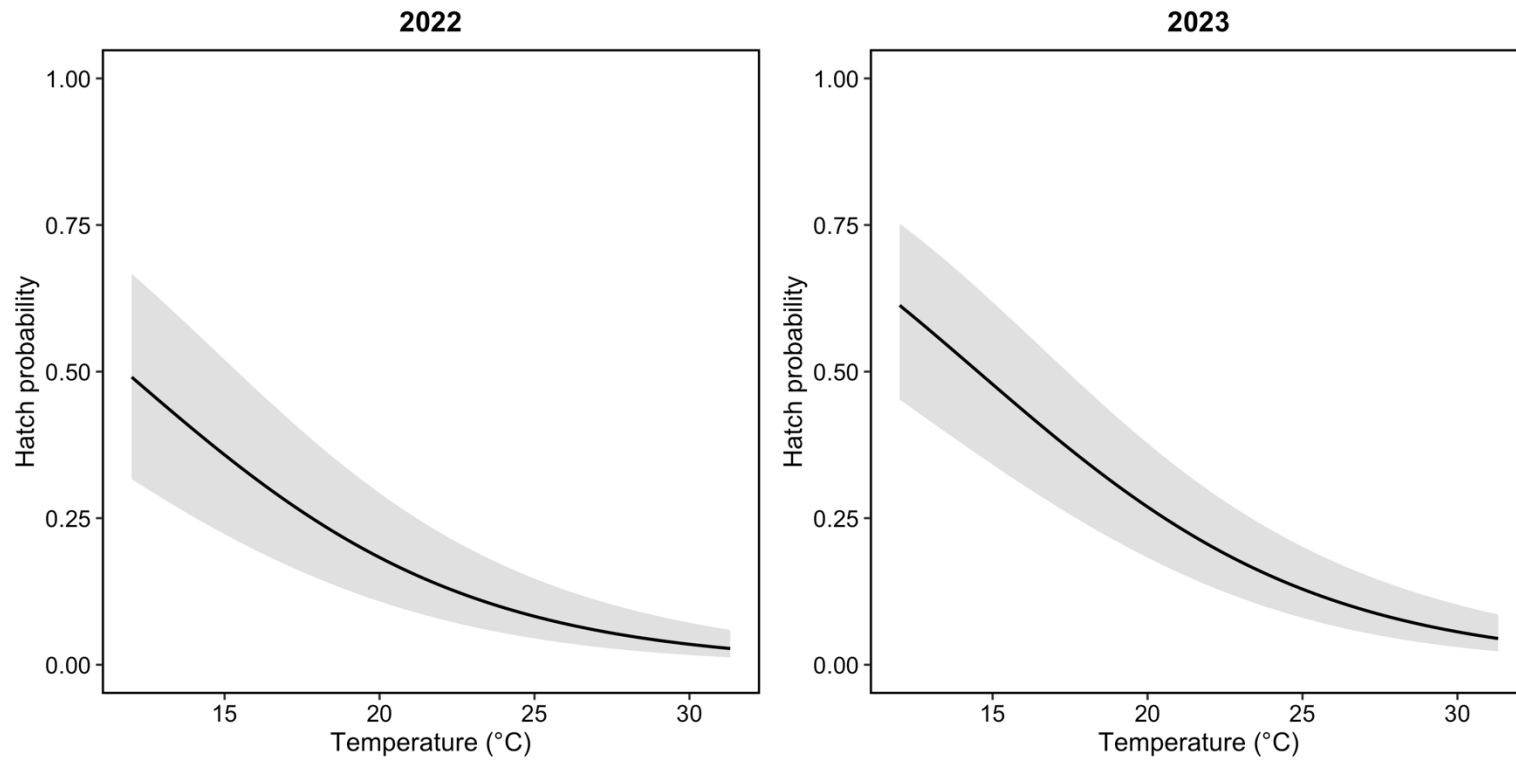


Figure 13. Negative relationship between Largemouth Bass hatch probability and water temperature (°C) during the 2022 (left panel) and 2023 (right panel) spawning seasons. The shaded areas represent the 95% confidence intervals.

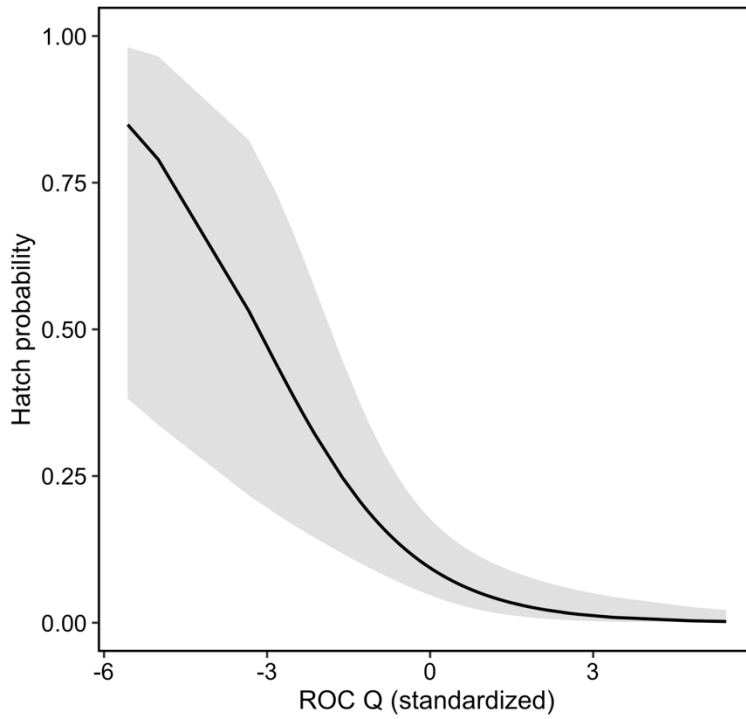
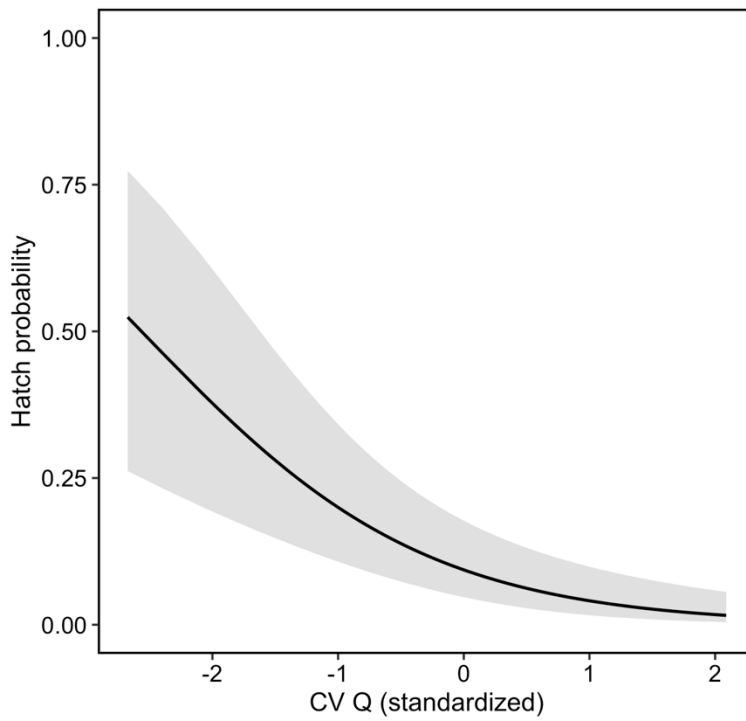


Figure 14. Negative relationships between Shoal Bass hatch probability and standardized CV of discharge (CV Q; top), and standardized rate of change in discharge (ROC Q; bottom). The shaded areas represent the 95% confidence intervals.

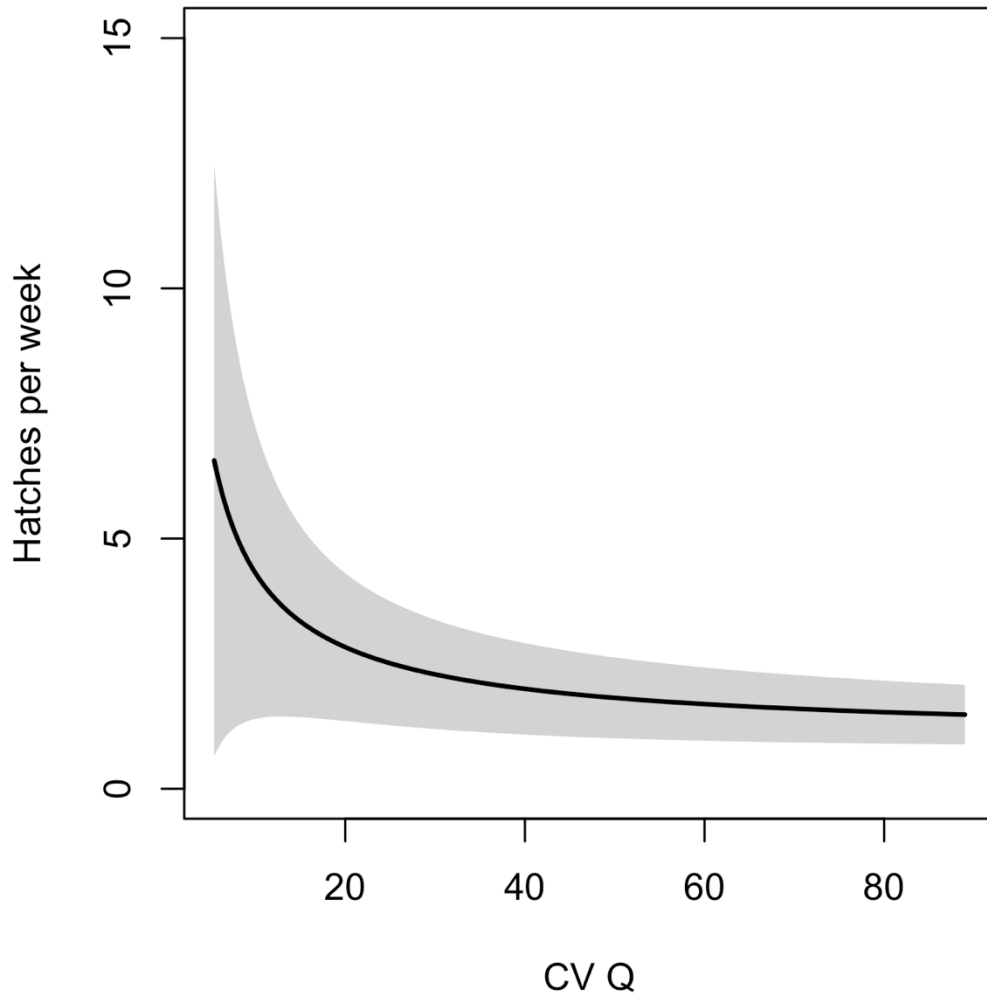


Figure 15. Negative relationship between Largemouth Bass hatch frequency (negative binomial) and CV of discharge (CV Q). The shaded area represents the 95% confidence interval.

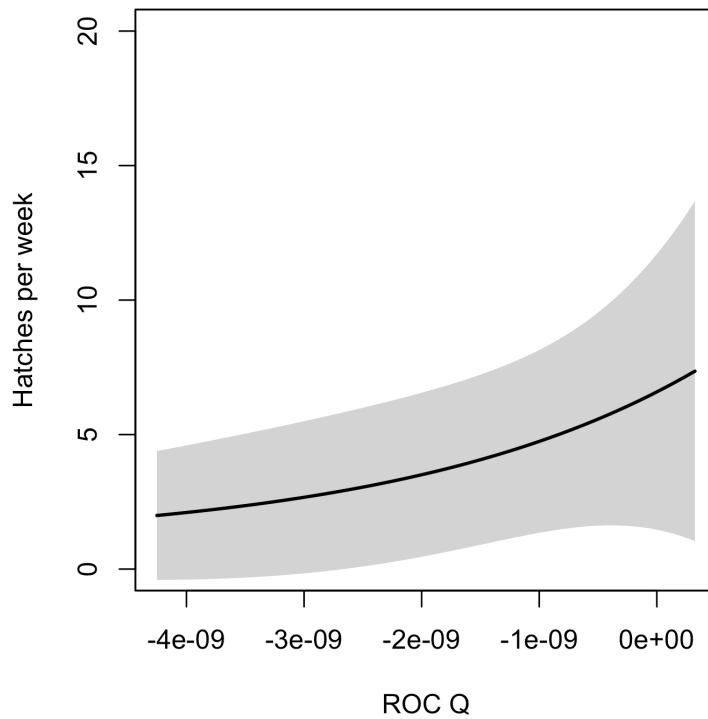
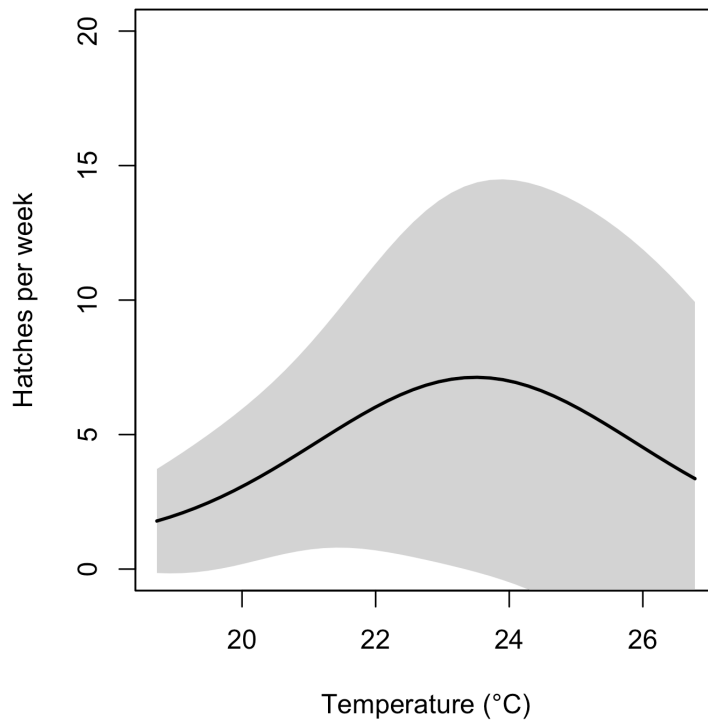


Figure 16. Relationships between Shoal Bass hatch frequency (negative binomial) and water temperature (°C; top) and rate-of-change of scaled discharge (ROC Q; bottom). The shaded area represents the 95% confidence intervals.

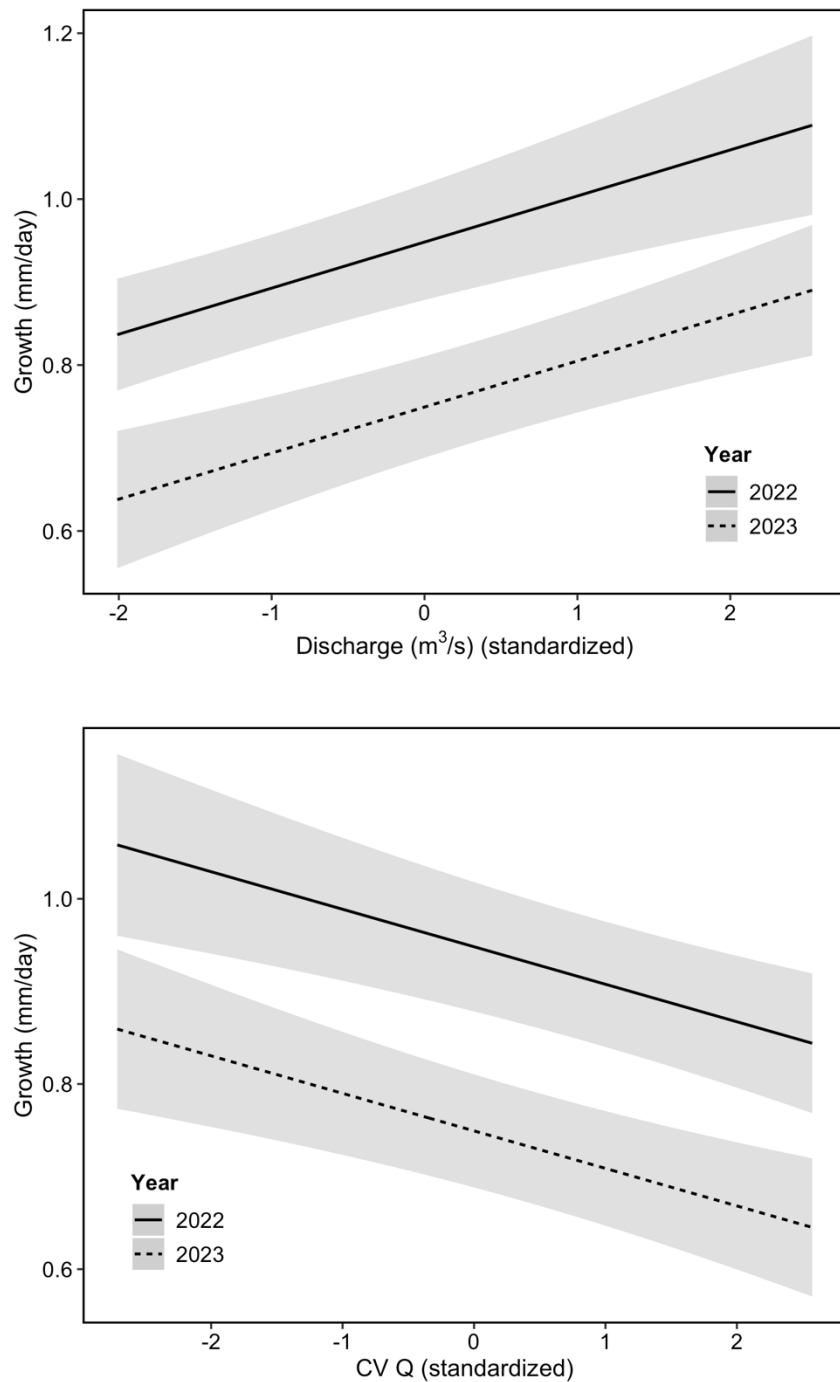


Figure 17. Positive relationship between age-0 Largemouth Bass daily growth and mean discharge (m<sup>3</sup>/s; top) and the negative relationship between growth and the CV of discharge (CV Q; bottom). Solid lines represent relationships for the year 2022 and dashed lines represent relationships for the year 2023. The shaded areas represent the 95% confidence intervals.



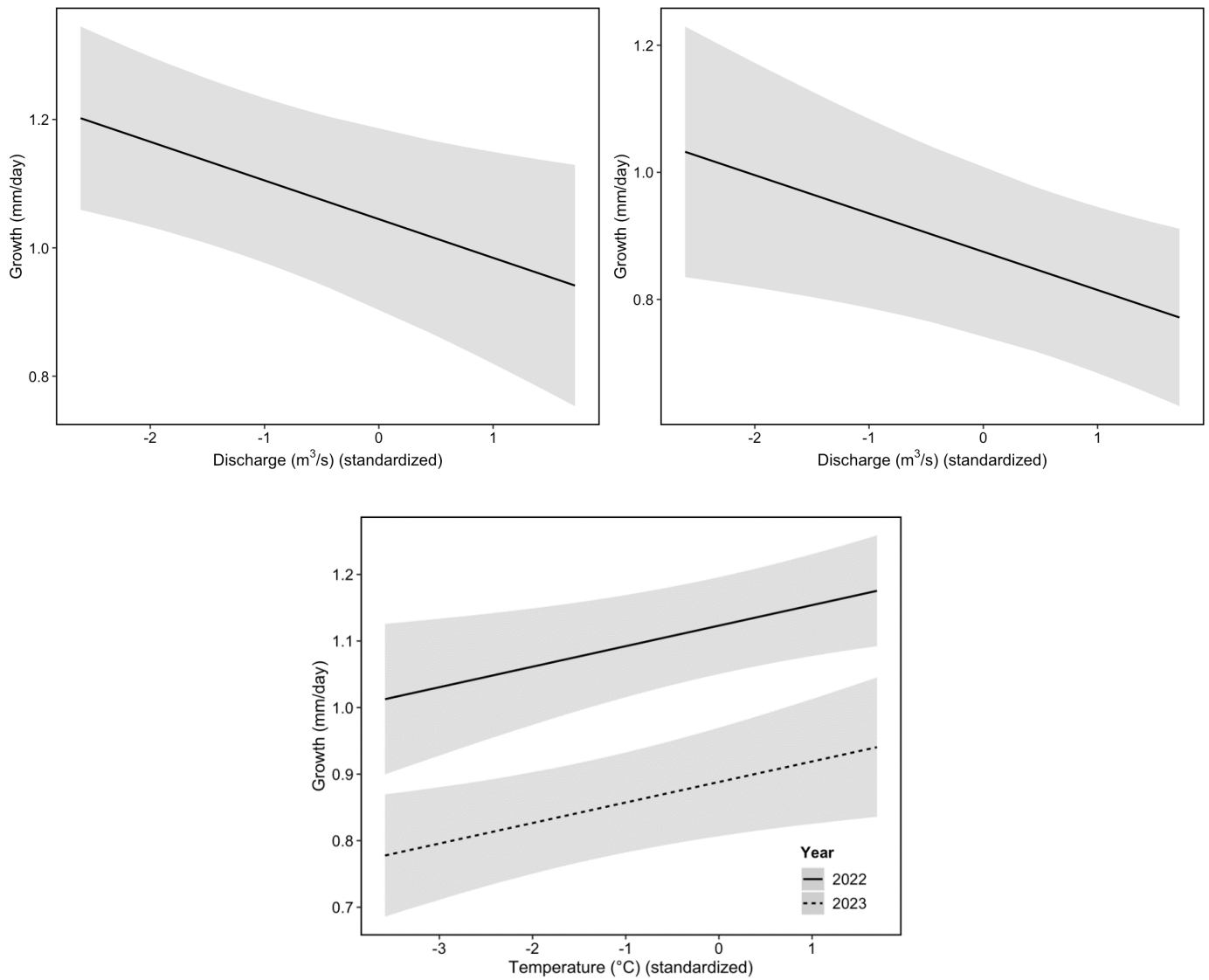


Figure 18. Negative relationship between age-0 Shoal Bass daily growth and mean discharge ( $\text{m}^3/\text{s}$ ; top) in 2022 (left) and 2023 (right) and the positive relationship between growth and mean temperature ( $^{\circ}\text{C}$ ; bottom). On the bottom panel, solid lines represent relationships for the year 2022 and dashed lines represent relationships for the year 2023. The shaded areas represent the 95% confidence intervals.

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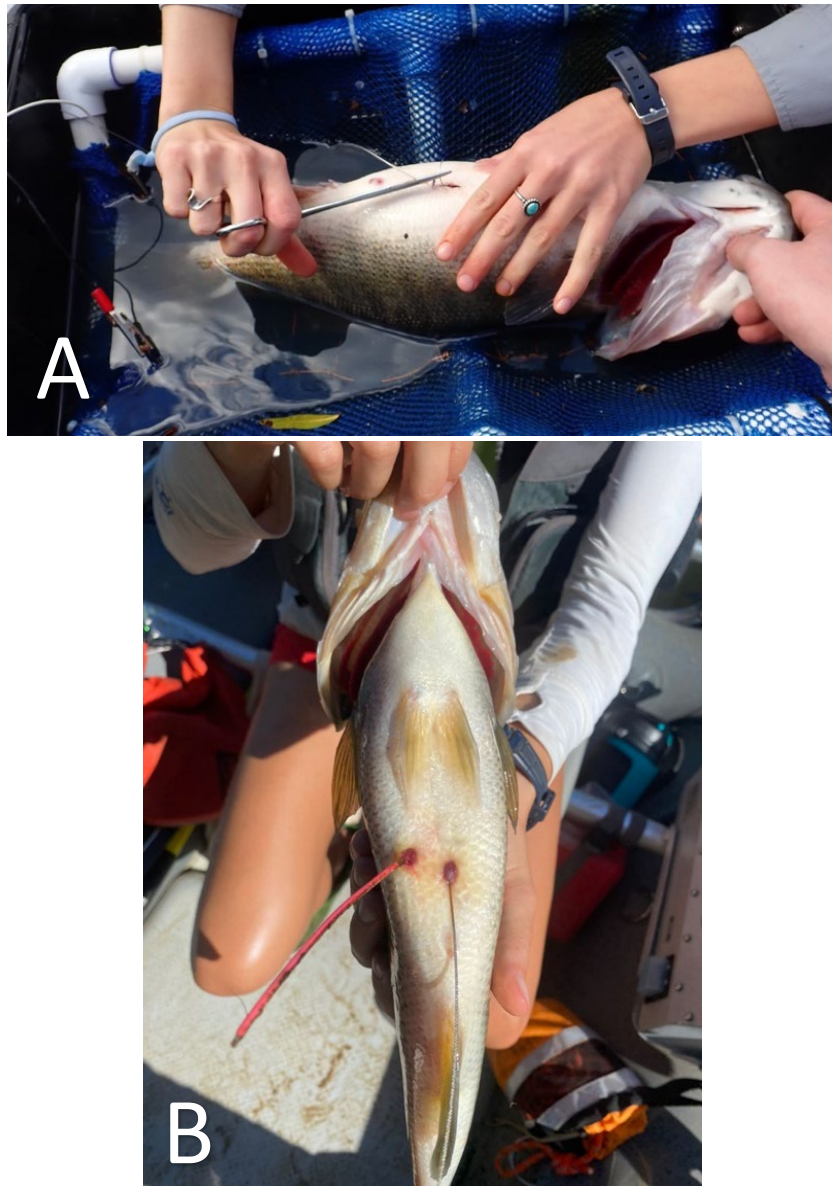
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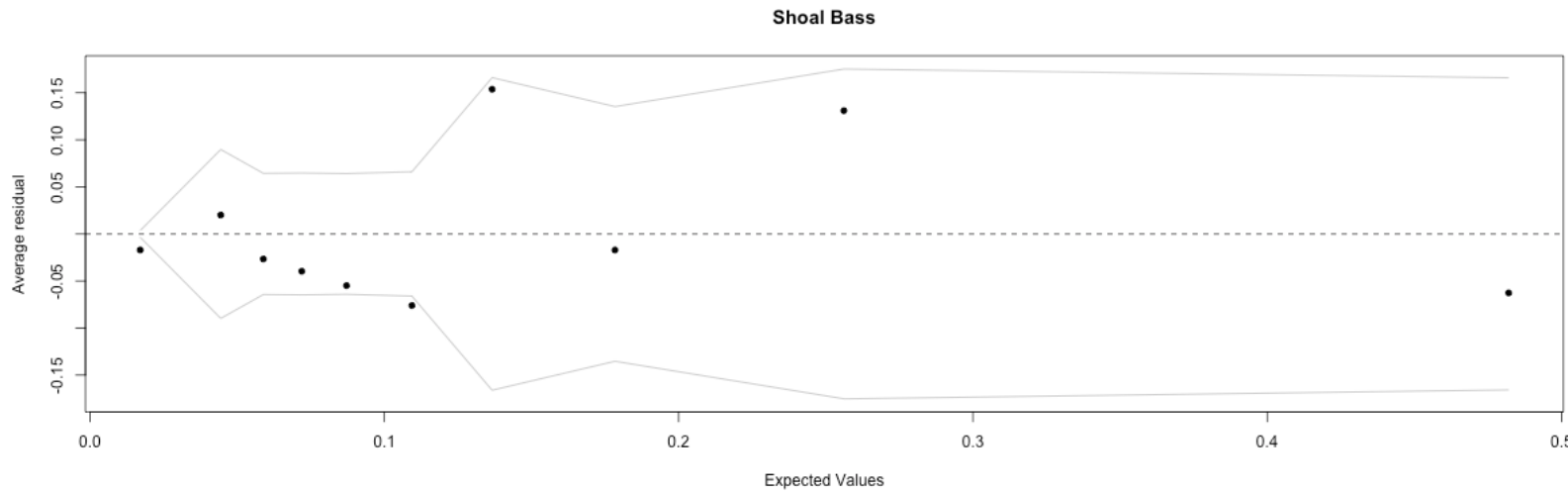
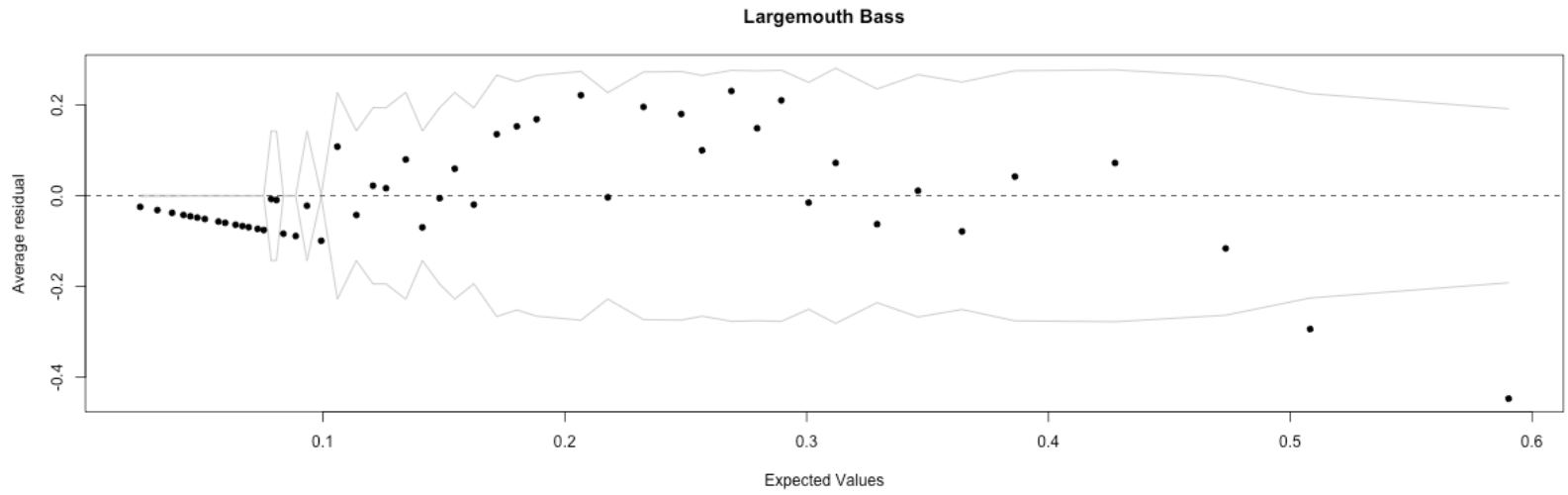
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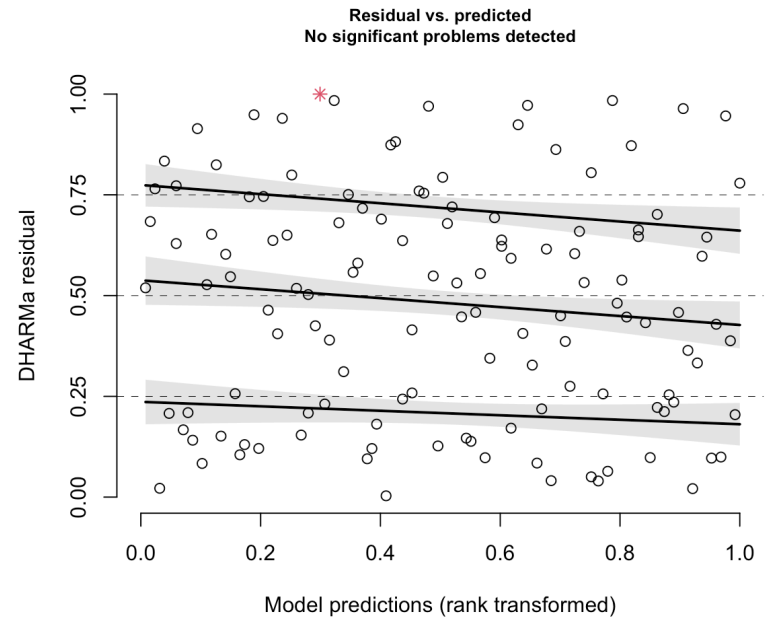
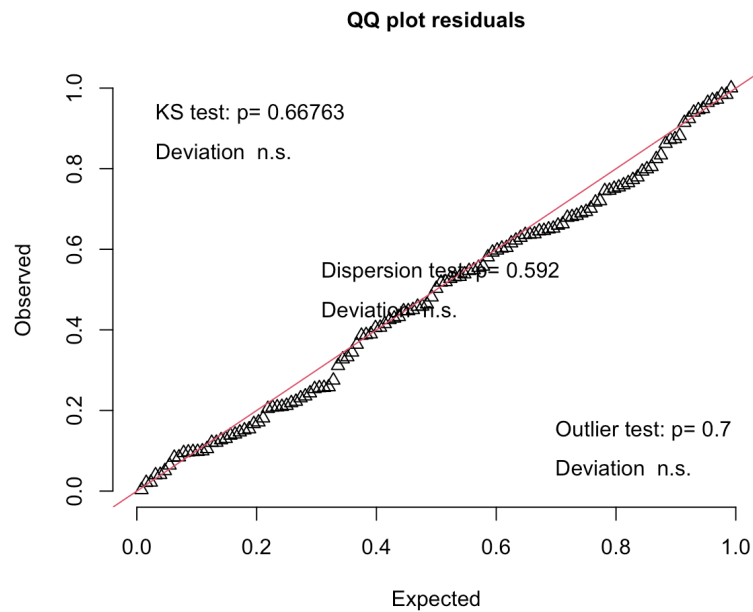
## Appendices



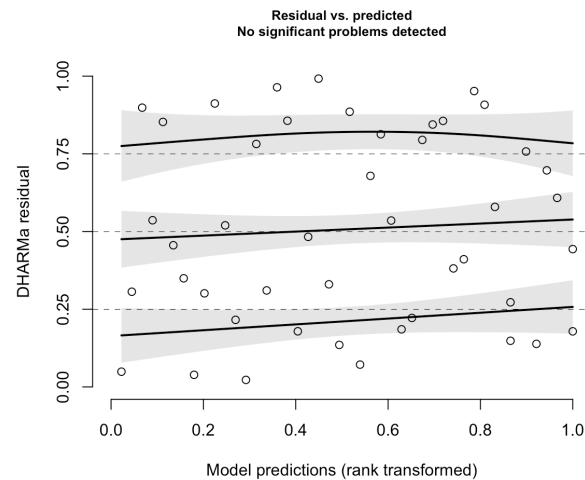
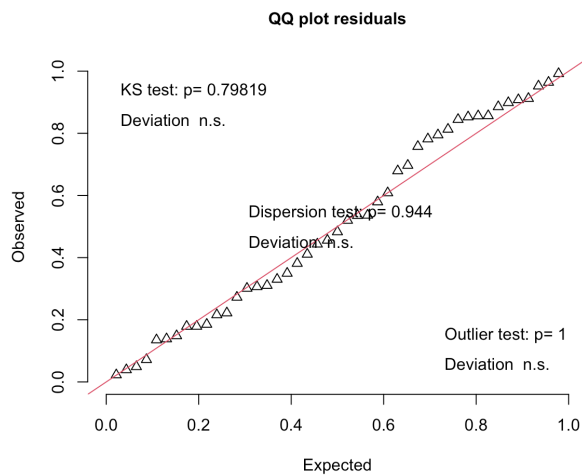
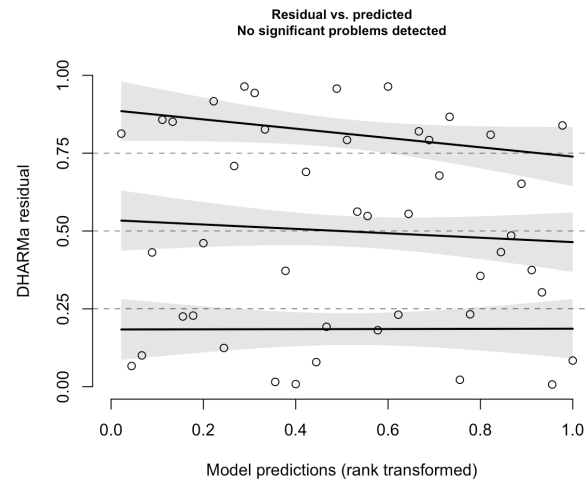
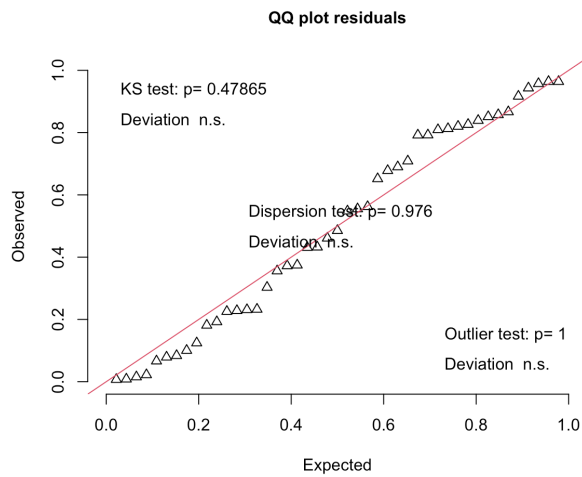
Appendix 1. Radio transmitter and anchor tag surgery on Shoal Bass and Largemouth Bass for movement analysis. Panel A shows a transmitter incision being sutured, with antenna trailing posteriorly out of the incision, while fish is immersed in water and anesthetized on electroanesthesia table. Panel B shows a fish recaptured approximately 7 months post-operation with incision wounds healed and tag placement displayed.



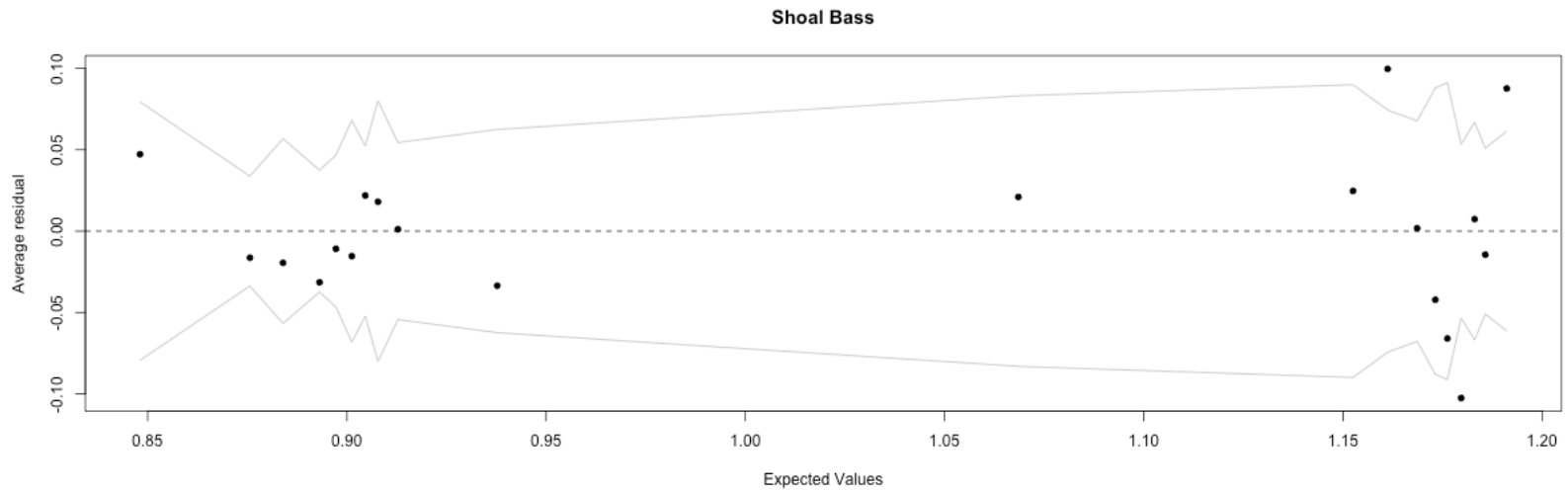
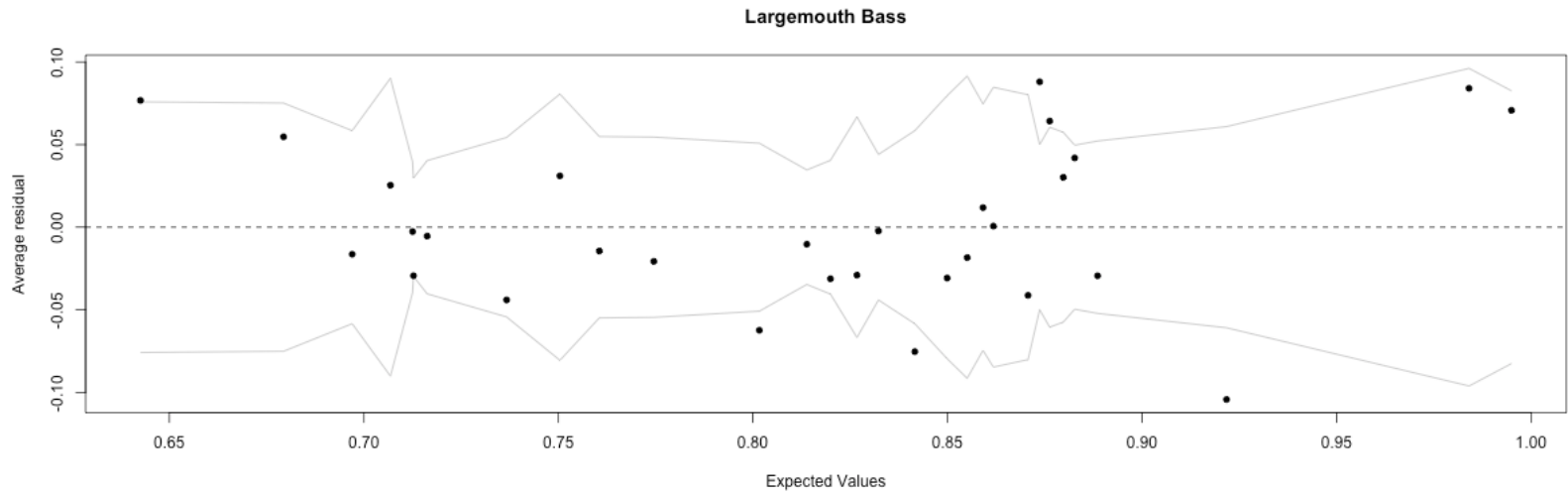
Appendix 2. Binned residual plots for the binomial logistic probability of hatch models (zero models). Black dots are the plotted residuals, and the gray lines indicate the theoretical error bounds of the model.



Appendix 3. DHARMA residual diagnostic plots of the top-ranked negative binomial model of the frequency of Largemouth Bass hatches (count model). Plots indicate reasonable model fit. The red star is an outlier that was retained after the datum was checked for accuracy.



Appendix 4. DHARMA residual diagnostic plots of the top-ranked negative binomial models of the frequency of Shoal Bass hatches (count models). Plots indicate reasonable model fit. Top panel is the model containing the linear term of rate-of-change in discharge (ROC Q). Bottom panel is the model containing the quadratic term of mean temperature.



Appendix 5. Binned residual plots for growth models (linear mixed effects models) for each species. Black dots are the plots residuals, and the gray lines indicate the theoretical error bounds of the model.