POPULATION DYNAMICS AND DIET COMPOSITION OF INTRODUCED BLUE CATFISH IN FOUR GEORGIA RIVERS

by

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(Under the Direction of Martin J. Hamel)

ABSTRACT

Blue Catfish (*Ictalurus furcatus*) are the largest ictalurid species in North America, with the propensity to quickly expand outside of their native range. In Georgia, Blue Catfish are expanding their range over time, posing a threat to native aquatic species by competition and predation. The Altamaha, Ocmulgee, Oconee, and Satilla Rivers in Georgia contain valuable and imperiled aquatic species. The long-term ecological impacts of this opportunistic invader are not well understood or documented. Therefore, the objectives of this study were to 1) evaluate the population dynamics (i.e., age structure, growth, and mortality), and 2) characterize the feeding ecology of non-native Blue Catfish populations in four Georgia rivers.

INDEX WORDS: Invasive Species, Population Dynamics, Diet Composition

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DEDICATION

I dedicate my thesis work to my grandmothers, whose wisdom and love has shaped my life in profound ways. Your strength and grace continue to inspire me every day.

To my dear husband, my partner in this journey of life. Your encouragement, love, and shared dreams have made every moment meaningful. Thank you for everything.

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CHAPTER 1

GENERAL INTRODUCTION AND STUDY OBJECTIVES

Invasive species pose a threat to biodiversity and ecosystem services across the globe (Pysek & Richardson 2010, Ricciardi 2013). Many invasive species possess biological traits that allow them to adapt quickly in novel environments, interrupting natural ecosystem balances and food web dynamics through competition and predation of native taxa (Vander Zanden et al. 1999). Determining population dynamics is critical for evaluating management actions of invasive aquatic species. Estimating dynamic rate functions such as growth and mortality are needed for population modeling, which improves the understanding of factors that influence invasion success of an introduced species. Estimates of population parameters can vary widely depending on the introduction history of the nonnative species. Population assessments may include the quantity and description of prey in the diet (Bowen 1996). Diet composition studies allow the characterization of diet habits of fish populations, thus providing information about relative predator impacts and prey selectivity. Information derived from population

assessments are essential in fisheries management processes for improving recreational or commercial fisheries and for achieving management goals of native, endangered, and invasive species.

Blue Catfish (*Ictalurus furcatus*) are a large-bodied, generalist species endemic to North America that occupy large reservoirs, backwaters, and rivers. They are native to the Mississippi, Missouri, and Ohio River basins and have been widely introduced to both reservoir and riverine habitats in 29 states across the United States (Graham 1999). This species exhibits fast growth, non-selective feeding patterns (Bonvechio et al. 2011; Jennings et al. 2018; Schmitt et al. 2019; Belkoski et al. 2021; Evans et al. 2021), and a tolerance to various habitats, including high salinity estuaries (Nepal and Fabrizio 2019). These characteristics allow Blue Catfish to become successful invaders in novel environments.

Several studies have published estimates of population dynamics of Blue Catfish within their native and introduced ranges. For example, growth of native Blue Catfish in the Missouri and Mississippi Rivers was similar, where mark-recapture information revealed an average increase in fish TL by 39.4 mm and 39.8 mm per year (Missouri Department of Conservation 2019). A study conducted in multiple reservoirs

and tailwaters of the Coosa River, AL showed length frequency distributions that were skewed towards smaller individuals in reservoir habitats, and towards larger individuals in the tailwater habitats. Blue Catfish inhabiting the tailwater habitats had a higher mean total length when compared to fish from reservoirs. However, catfish spp. exhibited slow growth in the Coosa River, despite good body condition indicative of high prey abundance and high productivity within the system (Jolley & Irwin 2011). In Lake Wilson, AL, sex specific growth was observed, where male Blue Catfish exhibited faster growth than females beginning at age 5 (Marshall et al. 2009).

Fast growth (i.e., body size) is typically observed in non-native Blue Catfish populations. A study examining four sub-estuaries of the Chesapeake Bay showed variability in mean length at age, with faster growth (exceeding that of native populations) during the establishment phase, and a reduction in mean total length as the population aged (Hilling et al. 2021). These results are congruent with other introduced catfish studies where new populations exhibited rapid growth in novel environments. For example, Kwak et al. (2006) reported that Flathead Catfish populations introduced to the Neuse, Cape Fear, and Lumber Rivers in North Carolina exhibited faster growth than native riverine populations. Similarly, Flathead Catfish growth was compared between two

native populations in Alabama (Coosa and Tallapoosa rivers) and two introduced populations in Georgia (Ocmulgee and Satilla rivers). Results showed that the introduced populations grew rapidly when compared to native populations (Sakaris et al. 2006).

Comparatively less information is known for recruitment and mortality of Blue Catfish. In Thunderbird Reservoir, Oklahoma, variables such as hydrological factors, water quality, and air temperature were explored to assess potential impacts on recruitment. Blue Catfish year-class strength was lower in years where the air temperature in January was higher than average. In addition, total annual mortality was low (16%) in Thunderbird Reservoir when compared to several other reservoirs in Oklahoma (21-32%) (Boxrucker & Kuklinski 2006; Griffin et al. 2021). Greenlee & Lim (2011) found variable recruitment over time throughout four tidal rivers in Virginia. Trends in year-class strength was correlated amongst three out of four populations, suggesting that multiple factors may be contributing to recruitment success. Total annual mortality estimates ranged from 20.8% to 32.3% in the Mattaponi River and Pamunkey River, Virginia; however, total annual mortality was not partitioned into fishing and natural mortality. Hilling et al. (2018) used multiple empirical estimators to determine natural

mortality of Blue Catfish on four Virginia rivers. Natural mortality was similar between all rivers, but populations with earlier invasions displayed lower mortality. These studies illustrate the variability in growth among populations and environments, highlighting how factors such as hydrology, temperature, prey resources, and introduction histories can impact catfish population dynamics.

Blue Catfish are generalist omnivores that prey on abundant and readily available resources. Their wide diet breadth includes mollusks, insects, invertebrates, and fish (Graham 1999; Schmitt et al. 2017). Diet composition analyses often regard the non-native Asian clam *(Corbicula fluminea)* as a major food source for Blue Catfish (Graham 1999; Bonvechio et al. 2011; Jennings et al. 2018; Schmitt et al. 2019). In habitats where mollusks may not be abundant, Blue Catfish are known to forage heavily on gizzard shad (*Dorosoma cepedianum*) and other fishes (Edds et al. 2002; Snow et al. 2019). Blue Catfish display seasonal diet trends, with predation on shad species increasing in colder months due to similar overwintering habits in Lake Oconee (Jennings et al. 2018) and in the Chesapeake Bay (Schmitt et al. 2019), as well as increased consumption of zebra mussels in the lower Mississippi River during the summer (Eggleton & Schramm 2004). This species also demonstrates dietary ontogenetic

shifts, where the size of the predator influences prey selection. Smaller Blue Catfish often consume small aquatic invertebrates, whereas piscivory is commonly observed in mature fish belonging to larger size classes. In multiple sub-estuaries of the Chesapeake Bay, the shift to piscivory was observed at differing total lengths across systems (Schmitt et al. 2019). In Lake Ellsworth, OK, Blue Catfish were exclusively piscivorous, however this study only represented fish that were >600 mm TL (Snow et al. 2019). Because of the breadth of prey consumed throughout their life, coupled with a large gape, Blue Catfish have the potential for consuming large quantities of sportfish or imperiled native species. For example, Blue Catfish expansion into oligohaline and mesohaline habitats throughout Virginia's tidal rivers (Nepal & Fabrizio 2019), lead to increased predation on ecologically important species such as the American Shad (*Alosa sapidissima*) and the commercially valuable Blue Crab (*Callinectes sapidus*; Schloesser 2011; Schmitt et al. 2017; Hilling et al. 2023).

In Georgia, Blue Catfish are native to the Coosa River basin located in the northwestern corner of the state. Since the mid-1990's, they have gradually expanded into many waterbodies in the state, including Lake Sinclair, Lake Oconee, and the Chattahoochee, Flint, Savannah, Ocmulgee,

Oconee, Altamaha, and Satilla rivers. Intentional stocking, escape during normal reservoir releases, and periods of high flooding are viable mechanisms for the range expansion of this species in the state (Bonvechio et al. 2012). Few studies have determined the population characteristics and diet composition of Blue Catfish in Georgia. Native populations in the Coosa River exhibited slow growth and high longevity, with fish taking approximately 10 years to reach 700 mm total length (Jolley and Irwin 2011). Research on nonnative populations in Georgia include age and growth data of an established population in Lake Oconee, where maximum age was 8 years, and mean total length was 330 mm (Homer and Jennings 2011). Additionally, Bonvechio et al. (2011) reported the population metrics of a recently introduced population of Blue Catfish in the Altamaha River, where maximum age was 6 years, and annual mortality was 47%. Growth was rapid and exceeded native populations with age 6 individuals reaching 720 mm TL. Diet studies on Blue Catfish are limited, but generally align with what is known about other introduced Blue Catfish populations. The diet of Blue Catfish in Lake Oconee was composed primarily of Asian Clam, but seasonal shifts to a more variable diet including crappie and catfish occurred in the winter and spring (Jennings et al. 2018). Summer diet composition in the Altamaha River was composed

primarily of Asian Clam of all size classes, however larger Blue Catfish (<600 mm total length) preyed on American Eel and a variety of organic material (Bonvechio et al. 2011).

There is a knowledge deficit on the population dynamics and dietary habits of non-native Blue Catfish in Georgia rivers. This study will provide valuable insights into the behavior and function of Blue Catfish populations after acclimatizing to new environments. By conducting these assessments concurrently, we can examine how the primary diet of Blue Catfish influences growth in various river systems. Furthermore, we can make inferences about trophic level occupancy and identify potential consequences for native fish populations and other aquatic species.

This study will expand on current knowledge about Blue Catfish in the Altamaha River (Bonvechio et al. 2011) and provide new information about Blue Catfish in the Ocmulgee, Oconee, and Satilla Rivers, where the population status of Blue Catfish is currently unknown. Spatial (multiple rivers) and temporal (multiple years) data obtained will provide insight on how dynamic rate functions and diet of Blue Catfish vary throughout different environments and over time. The objectives of this study were to 1) evaluate the population dynamics (i.e., age structure, growth, and mortality), and 2) characterize the feeding ecology of non-native Blue Catfish

populations in four Georgia rivers with varying introduction histories to determine how these populations compare and function after becoming acclimatized to southern Atlantic Slope drainages. This research aims to provide a framework for future analyses of this species and can be utilized for future management decisions.

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CHAPTER 2

AGE, GROWTH, AND MORTALITY OF INTRODUCED BLUE CATFISH IN FOUR GEORGIA RIVERS

INTRODUCTION

Invasive species pose a threat to biodiversity and ecosystem services across the globe (Pysek & Richardson 2010, Ricciardi 2013). Many invasive species possess biological traits that allow them to adapt quickly in novel environments, interrupting natural ecosystem balances and food web dynamics through competition and predation of native taxa (Vander Zanden et al. 1999). Determining population dynamics is critical for evaluating management actions of invasive aquatic species. Estimating dynamic rate functions such as growth and mortality are needed for population modeling, which improves the understanding of factors that influence invasion success of introduced species. Estimates of population parameters vary widely depending on the introduction history of the nonnative species. Introduced fish populations grow rapidly before collapsing, a phenomenon known as 'boom and bust' (Williamson 1996). For example, invasive Flathead Catfish (*Pylodictis olivaris*) populations

in Southern Georgia underwent boom and bust cycles throughout a 22 year period, however when compared to newly introduced populations, growth and abundance was substantially lower (Kaeser et al. 2011). Recognition of phase dynamics of newly introduced populations is essential in developing effective management strategies for nonnative species.

Blue catfish (*Ictalurus furcatus*) are a large-bodied, generalist species endemic to North America that occupy large reservoirs, backwaters, and rivers. They are native to the Mississippi, Missouri, and Ohio River basins and have been widely introduced to both reservoir and riverine habitats in 29 states across the United States (Graham 1999). This species exhibits fast growth, non-selective feeding patterns (Graham 1999; Bonvechio et al. 2011b; Jennings et al. 2018; Schmitt et al. 2019; Belkoski et al. 2021; Evans et al. 2021), and a tolerance to various habitats, including high salinity estuaries (Nepal and Fabrizio 2019). These characteristics allow Blue Catfish to become successful invaders in novel environments. Several studies have published estimates of population dynamics of Blue Catfish within their native and introduced ranges. Fast growth (exceeding that of native Blue Catfish populations) was observed in recently introduced Blue Catfish (Bonvechio et al. 2011b; Greenlee and Lim 2011; Homer and Jennings 2011). Growth of invasive Blue Catfish in the

Chesapeake Bay area was variable over time, resulting in reduced growth rates as the populations became self-sustaining (Hilling et al. 2021).

Comparatively less information is known for recruitment and mortality of Blue Catfish. In Thunderbird Reservoir, Oklahoma, variables such as hydrological factors, water quality, and air temperature were explored to assess potential impacts on recruitment. Blue catfish year-class strength was lower in years where the air temperature in January was higher than average. In addition, total annual mortality was low (16%) in Thunderbird Reservoir when compared to several other reservoirs in Oklahoma (21-32%) (Boxrucker & Kuklinski 2006; Griffin et al. 2021). Greenlee & Lim (2011) found variable recruitment over time throughout four tidal rivers in Virginia. Trends in year-class strength was correlated amongst three out of four populations, suggesting that multiple factors may be contributing to recruitment success. Total annual mortality estimates ranged from 20.8% to 32.3% in the Mattaponi River and Pamunkey River, Virginia; however, total annual mortality was not partitioned into fishing and natural mortality. Hilling et al. (2018) used multiple empirical estimators to determine natural mortality of blue catfish on four Virginia rivers. Natural

mortality was similar between all rivers, but populations with earlier invasions displayed lower mortality.

In Georgia, Blue Catfish are native to the Coosa River basin located in the northwestern corner of the state. Since the mid-1990's, they have been discovered outside of their native range in Lake Sinclair and Lake Oconee, and in the Chattahoochee, Flint, Savannah, Ocmulgee, Oconee, Altamaha, and Satilla rivers. Blue Catfish were first detected in Lake Sinclair and Lake Oconee in 1996 and 1997 (Homer and Jennings 2011) during gillnet surveys performed by the Georgia Department of Natural Resources (GADNR). It is believed that regular reservoir releases were responsible for the escape of Blue Catfish into the Oconee River, resulting in fish migrating downstream to the Altamaha River where they were first discovered during creel surveys in 2005. The first Blue Catfish was captured from the Satilla River in 2011 (Bonvechio et al. 2012), during the Flathead Catfish Removal Program (FRP), which was enacted by the GA DNR in 2007 to minimize the impact of predation on native fish species through aggressive Flathead Catfish removal practices. The introduction of Blue Catfish to the Satilla River is suspected to have occurred via migration through intercoastal waterways during high water periods in 2009 (Bonvechio et al 2012).

Few studies have reported population characteristics of Blue Catfish in Georgia. Native populations in the Coosa River exhibited slow growth and high longevity (Jolley and Irwin 2011). Research on nonnative populations in Georgia include age and growth data of a recently introduced population in Lake Oconee, where maximum age was 8 years, and mean total length was 330 mm (Homer and Jennings 2011). Additionally, Bonvechio et al. (2011b) reported the population metrics of a recently introduced population of Blue Catfish in the Altamaha River, where maximum age was 6 years, and annual mortality was 47%. The objective of this study was to evaluate the population dynamics of nonnative Blue Catfish in four Georgia rivers with varying introduction histories. Specifically, we quantified population parameters including age, growth, and mortality to determine how these populations compare and function after becoming acclimatized to novel environments.

METHODS

Study Area

The study area included four major rivers located in the state of Georgia: the Ocmulgee, Oconee, Altamaha, and Satilla rivers (Figure 2-1). The Ocmulgee River begins in the Piedmont, flowing southeast through the Coastal Plain until it converges with the Oconee River to form the Altamaha River

near Lumber City, Georgia (Grabowski and Jennings 2009). The Altamaha River is the largest free-flowing river on the East Coast of the United States, flowing 220km southeastward where it empties into the Atlantic Ocean near Darien, Georgia (Bonvechio et al. 2011b). The Satilla River is a blackwater system located entirely in the coastal plain ecoregion of the state. It flows 378km eastward and empties into the Atlantic Ocean at St. Andrew Sound, which is located approximately 40km south of the Altamaha River Sound (Bonvechio et al 2009).

These rivers provide habitat to many aquatic species, including 25 species of federally and state listed freshwater mussels and several species of anadromous fish. These rivers also host angling opportunities for sportfish. The world record Largemouth Bass (*Micropterus salmoides*) was caught in Montgomery Lake on the Ocmulgee River in 1932. The Ocmulgee River is inhabited by the imperiled Robust Redhorse (*Moxostoma robustum*), which has been transplanted there from the Oconee River in attempts to establish self-sustaining populations (Grabowski & Jennings 2009). The Oconee River basin supports recreational fishing opportunities with large populations of sunfish, bass, catfish, and suckers. Both the Altamaha and Satilla rivers have large populations of centrarchids but are now dominated by non-native Flathead Catfish. There have been noticeable declines in the abundance

of highly prized Redbreast Sunfish (*Lepomis auritus*) and native Bullhead Catfish (*Ameiurus sp.)* in the Satilla River (Bonvechio et al. 2009, 2011b) resulting in extensive annual removal efforts of Flathead Catfish by the GADNR. Several anadromous species such as Atlantic Sturgeon (*Acipenser oxyrhynchus*), Shortnose Sturgeon (*Acipenser brevirostrum*), and American Shad (*Alosa sapidissima*) utilize these rivers for spawning and nursery habitats (Fox and Peterson 2019). In addition, a predation event involving a Flathead Catfish and a juvenile Atlantic Sturgeon, was documented occurring in the Satilla River, Georgia (Flowers et al. 2011).

Fish Collection

Blue Catfish were collected annually during summer standardized ictalurid sampling on the Altamaha, Ocmulgee, and Oconee rivers, and during the Satilla River FRP performed by the GADNR. Low-amperage pulsed DC electrofishing (>1 amp, 200-1,000 volt, 18 Hz) was conducted during daylight hours in a downstream direction from a 5.1-m aluminum bass tracker john boat equipped with a Smith-Root model 12B or model LR-24 backpack electrofisher (Bonvechio et al. 2011a). Blue Catfish were targeted at fixed sampling locations on each of the Altamaha, Ocmulgee, and Oconee rivers. These stations were set up in the early 1990’s by the GADNR as part of a

standardized sampling protocol (Bonvechio et al. 2011b). Blue Catfish were targeted on the Satilla River at sampling locations that were set up for the FRP. Each station was sampled where the deep, riveted, undercut banks were targeted and a chase boat was utilized to increase sampling efficiency (Daugherty and Sutton 2005). Sampling transects were of uniform length (approximately 1 rkm) and sampling duration at each site was approximately 1 hour. Fish were measured (mm; total length - TL), weighed (g), and sacrificed for age, growth, and diet analyses. During dissection, sex was determined, both lapilli otoliths (Long and Stewart 2010) were extracted, full stomachs were excised and frozen, and a subsample of fish tissue from the Altamaha and Satilla rivers were taken for stable isotope analysis.

Otolith Processing

During fish processing, both lapilli otoliths were extracted by cutting through the supraoccipital bone, approximately 3-5 mm anterior of the locked pectoral spines (Buckmeier et al. 2002). Otolith pairs were extracted using fine-tipped forceps and any remaining brain tissue was cleared. Cleaned otoliths were stored in coin envelopes that were labeled with unique fish identification numbers and additional corresponding metrics (length, weight, sex).

Otoliths were embedded in epoxy resin according to the following procedures: Silicone rubber molds (#10505 PELCO 21 Cavity EM Embedding Mold, Ted Pella Inc., Redding, California) were filled approximately 3/4 full of epoxy resin that was mixed with a slow hardener, forming the first bottom layer in each well. Otoliths were placed flat into the wells with the posterior tip of the otolith positioned toward the tapered end of the mold. Otoliths were pressed gently into the bottom of the mold to ensure the otolith remained flat. After the otolith was aligned properly with the anterior/posterior axis centered parallel inside the mold, the wells were filled with a second layer of epoxy resin to fill each well completely. Epoxy resin was cured for 24 hours to ensure that the resin was fully hardened.

Embedded otoliths were thin-sectioned using a low speed sectioning saw (#11-1280-170 IsoMet Low Speed Saw, Buhler Ltd., Lake Bluff, Illinois). Before sectioning, a graphite pencil was used to mark a straight line through the otolith core, perpendicular to the anterior/posterior axis. Embedded otoliths were placed into the vice of the saw, and the pencil markings were aligned to a 0.25 mm spacer located between two 5” diamond saw blades. The resulting thin-section revealed a transverse view of the otolith, with annuli visibly radiating from the core. The thin-sections were mounted to microscope

slides using Crystalbond adhesive. After the adhesive hardened, high grit lapping film was used to polish the surface of the thin-sections, smoothing out any striations caused by the saw blades during sectioning. Immersion oil was applied to the surface of the sections to provide enhanced visibility of the annuli. Otoliths were viewed under a stereomicroscope and imaged with transmitted light.

Age Estimation

Age was estimated based upon the number of annuli counted on each otolith. Fish were aged by two readers, who independently viewed the otolith images and assigned ages and confidence ratings (Spiegel et al. 2010, Klein et al. 2017) for each age estimation. Confidence ratings ranged between one and three, with 1 indicating low to zero confidence of the age estimate and 3 indicated high confidence. Any discrepancies in age estimates were resolved by concert readings.

Growth

The original intent to characterize growth was to construct Von Bertalanffy growth curves to estimate growth parameters (L_{inf}, K, and t_0) for each population. However, the growth models did not converge because an asymptote in growth had not occurred. Therefore, growth was modeled for ages 1-5 for each river system using linear regression and differences

in growth among rivers were assessed by analysis of covariance (ANCOVA). The slopes of the linear regressions were estimated using R-package emmeans (v.1.8.8, Lenth 2023) and a post-hoc Tukey pairwise comparison test was performed to determine variability in growth between all populations. Mean length-at-age was calculated from the observed data for ages 1-5 for each river system and compared by analysis of variance (ANOVA) of the mean lengths at ages 1-5 followed by Tukey pairwise comparisons to detect differences in mean length between populations. Ages above 5 were not used to calculate growth rates due to a lack of older fish captured and to ensure the analyses were comparable between rivers.

Mortality

To estimate mortality, the "peak-plus" criterion was applied to the age-frequency data, which utilizes the age that is one year past the age of full recruitment into the sampling gear (Smith et al. 2012). Generalized linear models (GLM) were performed on extended age-frequency data, which added age classes up to three times the oldest age captured with zero counts. This was done to minimize the underestimation of instantaneous mortality (Millar 2015).

Generalized linear models following a Poisson distribution plus four extensions were applied to the data and the highest-ranking model in terms of Akaike weight was

chosen to estimate instantaneous mortality (Z). The age-frequency data were separated by river and by year (when applicable) to obtain accurate estimates of mortality for each population. The GLM candidates were the Poisson distribution ($GLM_{POISSON}$), and four extensions: negative binomial type 1 (GLM_{NB1}), negative binomial type 2 (GLM_{NB2}), Conway-Maxwell-Poisson (GLM_{CMP}), and generalized poisson (GLM_{GP}) which were performed by the R-package glmmTMB (v1.1.7, Brooks et al. 2017). These models were chosen because they provided more accurate estimations of mortality for over- and under-dispersed data than weighted linear regression and other common methods of estimating mortality from catch-curve data (Mainguy & Moral 2021).

Mortality estimates were compared within rivers that had multiple capture years (Altamaha 2017 and 2020; Satilla 2017-2019) to determine whether mortality varied over time. All generalized linear models described above were applied to the data, and model selection was used to calculate AIC_C (AIC corrected for small sample sizes; Burnham and Anderson 2002), ΔAIC_C, and Akaike weights to determine the top-ranking model(s). Furthermore, the best model was applied to the data, now including the interaction term "AGE*YEAR". Additionally, the same model (or model extension) was applied to the data which only included the additive effect of "AGE+YEAR". Model

selection was used to determine whether there was statistical support for the interaction between age and year. If the Akaike weight of the model including the interaction term was greater than 50%, there was sufficient support to determine that mortality between years differed (Mainguy & Moral 2021). Additionally, mortality estimates were compared between rivers to determine whether mortality was spatially variable. Following the processes described above, if the top-ranking model showed significant statistical support for a difference in mortality estimates, a post-hoc Tukey comparison test was used to determine which estimates differed using R-package emmeans (v.1.8.8, Lenth 2023). Lastly, Annual mortality (A) was calculated from instantaneous mortality (Z) estimates using the formula:

$$A = 1 - e^{-Z} \qquad \text{Eq. 1}$$

RESULTS

A total of 1,088 Blue Catfish otoliths were processed for age and growth analysis collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers between 2017-2021. The size of aged fish ranged from 106-970 mm total length and 11-11,940 g. The age-frequency distribution of Blue Catfish collected by river indicated that the age structure was skewed towards younger fish. The maximum

observed age from the entire dataset was 11 years, but maximum age varied by river (Figure 2-2). Sample sizes by river and year are provided in Table 2-1.

Growth was variable between river systems (Figure 2-3). Satilla River Blue Catfish grew approximately 109mm in length per year (Figure 2-4), which was significantly faster than growth in the other systems. Growth was also variable over time in the Satilla River (Figure 2-5), where growth rates in 2019 were significantly faster than growth in 2017 ($P < 0.001$) and 2018 ($P < 0.001$); however, growth was not temporally different between 2017 and 2020 in the Altamaha River. Observed mean length-at-age for Blue Catfish aged 1-4 varied by river, with the Oconee River population reaching significantly lower sizes (Figure 2-6). Mean total length at age 5 was similar for all populations, indicating that growth slowed in older fish.

Age-frequency data of Blue Catfish from the Altamaha, Ocmulgee, Oconee, and Satilla rivers was variable, and the age at which Blue Catfish recruited fully into the sampling gear differed according to the "peak-plus" criterion (Figure 2-7). The highest-ranking model for the Altamaha River 2017 was the GLM_{NB1} (weighted 39%) that estimated instantaneous mortality at 0.36 ±0.05 SE (A = 30.55%). For the Altamaha River 2020 dataset, the highest-ranking model was the $GLM_{POISSON}$

(weighted 28%) that estimated Z at 0.45 ± 0.05 SE (A = 36.06%). Mortality rates increased approximately 5 percent over the 3-year period. After the Altamaha River data was regrouped to assess temporal variability in mortality, the top performing model that included the interaction term 'AGE*YEAR' was the GLM_{NB2} (weighted 30%). This model was compared to a model of the same extensions that only included the additive effect of year. There was not significant statistical support for the difference in mortality rates between 2017 and 2020 (Table 2-2). For the Satilla River, instantaneous mortality was estimated at 1.73 ± 0.27 SE (A = 82.27%) in 2017 ($GLM_{POISSON}$, weighted 79%), 1.27 ± 0.28 SE (A = 71.91%) in 2018 ($GLM_{POISSON}$, weighted 58%), and 1.41 ± 0.25 SE (A = 75.58%) in 2019 (GLM_{GP}, weighted 62%). Over the 3-year period, mortality rates decreased approximately 7 percent. After regrouping the data and applying GLM models with the interaction term "AGE*YEAR", the highest performing model was the $GLM_{POSISSON}$ (weighted 61%). When compared to the additive model, the interaction was not statistically supported, indicating that the mortality estimates between years was similar (Table 2-3).

The top-ranking models used to assess spatial variability of mortality among rivers that included the interaction term "AGE*RIVER" was the GLM_{GP} (weighted 68%). When compared to the

same model including only the additive effect of river, the GLM_{GP} interaction model ranked the highest with a weight of 100%, providing strong statistical support that mortality between rivers was different (Table 2-4). Instantaneous mortality among the Altamaha (Z = 0.39 ± 0.04), Ocmulgee (Z = 0.40 ± 0.11), and Oconee Rivers (Z = 0.49 ± 0.07) was similar; however, Satilla River instantaneous mortality was significantly higher (Z = 1.03 ± 0.16, Figure 2-8). Thus, annual mortality (*A*) ranged from 32.29-38.74% in the Altamaha, Ocmulgee, and Oconee Rivers, and was 64.30% in the Satilla River.

DISCUSSION

The four introduced Blue Catfish populations described in this thesis exhibited similar growth characteristics of other introduced fish populations that are described as having rapid growth and low mortality rates during establishment. Literature suggests that once a population reaches an equilibrium state, growth rates generally slow down (Loftus and Kushlan 1987). For example, in a recent study examining growth dynamics of invasive Blue Catfish in four subestuaries of the Chesapeake Bay, growth was rapid after initial introduction, but over time slowed. Over the span of a 15 year time period, mean length-at-age decreased to a level

that has been observed in native populations (Hilling et al 2021). The expected duration of time for changes in dynamic rate functions is not well understood, but rate of change through the invasion process is likely non-linear and variable across spatiotemporal scales and environmental gradients. Furthermore, life history strategies of nonnative fish populations can shift throughout the invasion process (Feiner et al. 2012; Nepal et al. 2020; Lawson and Hill 2021). Therefore, the consideration of introduction history is important when comparing the population dynamics of nonnative species. This study was unique in that we examined dynamic rate functions at an intermediate invasion time frame where several years had passed since the initial introductions, but perhaps before the populations stabilized.

Lake Oconee is considered the parental source of these populations that gradually expanded into the Oconee, Altamaha, Ocmulgee, and Satilla rivers (Homer and Jennings 2011; Bonvechio et al. 2012). Our study showed age classes representative of these introduction timelines with the maximum ages being 10, 11, 8, and 6 years, respectively. The true maximum age of these populations is difficult to ascertain as large, older fish are rare to encounter due to sampling gear bias. It is unknown if larger fish are abundant in our study systems; however, anecdotal reports from anglers

suggest that large fish are at least present at low levels due to infrequent capture reports. The state record 110 lb, 6 oz Blue Catfish from the Chattahoochee River was aged at 23 years, and the previous state record (93 lb) from the Altamaha River was aged at 14 years using lapilli otoliths (T. Bonvechio, personal communication), suggesting that introduced Blue Catfish in the state have the ability to survive to older ages and attain large sizes.

We observed growth that exceeded native populations. Mean total lengths (mm) observed at age 5 in the Altamaha, Ocmulgee, Oconee, and Satilla rivers ranged from 520 ± 32.3 SE to 606 ± 26.5 SE. For comparison, age 5 fish from native populations in the Mississippi and Missouri rivers were 459 ± 17.6 SE and 420 ± 10.9 SE respectively, and approximately 300 mm TL in the Coosa River, Alabama (Jolley and Irwin 2011; Missouri Department of Conservation 2019). Although growth in this study exceeded rates of other native Blue Catfish populations, we detected differences in growth among our study rivers. Blue Catfish growth in the Oconee River was generally slower than the other rivers we examined, whereas the Satilla River population had the fastest growth and the highest mortality.

Variability in growth and mortality among rivers could be influenced by river-specific characteristics such as productivity and availability of prey resources (Chapter 3). During the invasion process, plentiful resources coupled with naïve predators result in fast growth rates and early onset of sexual maturity (Olden et al. 2006; Winker et al. 2011). As density increases and competition for resources becomes prevalent, growth and maturation patterns adjust. For instance, introduced Blue Catfish from the James and York rivers shifted maturity to older ages as densities reached high levels (Nepal and Fabrizio 2021). Our results suggest that Blue Catfish in our study systems are in an intermediate stage of invasion and have not yet reached an equilibrium state. As density continues to increase in these river systems, we expect a decline in growth rate, delayed sexual maturation, and extended longevity. However, additional monitoring is needed to identify how population dynamics and reproductive characteristics vary over time.

Our understanding of Blue Catfish in these systems would benefit from future research estimating relative and absolute abundance to determine how density dependence can influence changes in population dynamics of introduced species. Information on reproductive characteristics (e.g., age at maturity, fecundity, and egg size) would provide insight on

how life history traits of these introduced populations change over time. Continuous monitoring may help to facilitate shifts from the introduction phase to a more naturalized state and provide information that may help to guide strategies for managing populations of Blue Catfish that have become part of the ecosystem.

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Table 2-1. Sample sizes of Blue Catfish by river and year. Fish were captured utilizing low-frequency electrofishing.

Year	Altamaha River	Ocmulgee River	Oconee River	Satilla River
2017	188	0	0	216
2018	0	0	0	76
2019	0	0	0	234
2020	129	0	203	0
2021	0	42	0	0
Totals	317	42	203	526

Table 2-2. Comparison of GLM Poisson distributed model extensions NB2 with the interaction term "AGE*YEAR" (INT) and additive effect "AGE+YEAR" (ADD) for the Altamaha River, that includes instantaneous mortality estimates (Z) with standard error (SE), annual mortality (A), number of model parameters (K), log-likelihood (L-L), AIC_C, ΔAIC_C, and Akaike weight.

GLM Model	Z	SE	A	K	L-L	AIC_C	ΔAIC_C	Akaike Weight
NB2 (ADD)	0.47	0.05	37.41	4	-54.08	116.87	0.00	0.74
NB2 (INT)	0.44	0.06	35.80	5	-53.91	118.92	2.05	0.26

Table 2-3. Comparison of GLM Poisson distributed models with interaction term "AGE*YEAR" (INT) and additive effect "AGE+YEAR"(ADD) for the Satilla River, that includes instantaneous mortality estimates (Z) with standard error (SE), annual mortality (A), number of model parameters (K), log-likelihood (L-L), AIC_C, ΔAIC_C, and Akaike weight.

GLM Model	Z	SE	A	K	L-L	AIC_C	ΔAIC_C	Akaike Weight
POISSON (ADD)	1.49	0.17	77.50	4	-20.06	49.45	0.00	0.88
POISSON (INT)	1.73	0.27	82.26	6	-19.23	53.47	4.02	0.12

Table 2-4. Comparison of GLM Poisson distributed model extensions GP with the interaction term "AGE*RIVER" (INT) and additive effect "AGE+RIVER" (ADD) for all rivers, that includes the number of model parameters (K), log-likelihood (L-L), AIC_C, ΔAIC_C, and Akaike weight.

GLM Model	K	L-L	AIC_C	ΔAIC_C	Akaike Weight
GP (INT)	9	-116.74	252.81	0.00	1.00
GP (ADD)	6	-134.17	280.94	28.13	0.00

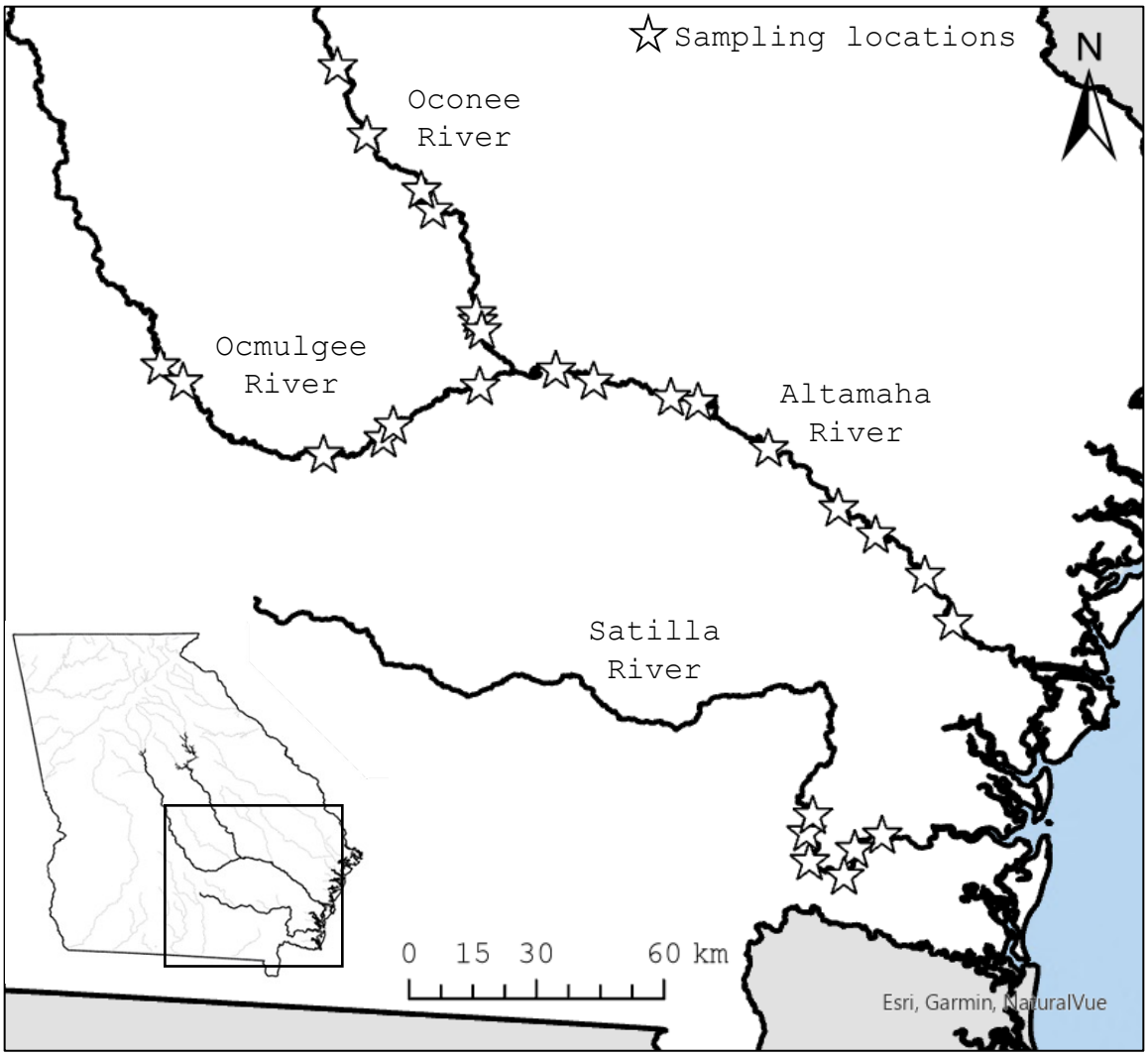

Figure 2-1. Blue Catfish (N=1,088) were collected at 28 sampling transects on the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia. Stars indicate the middle of the 1 rkm long transects that were sampled between 2017 and 2021.

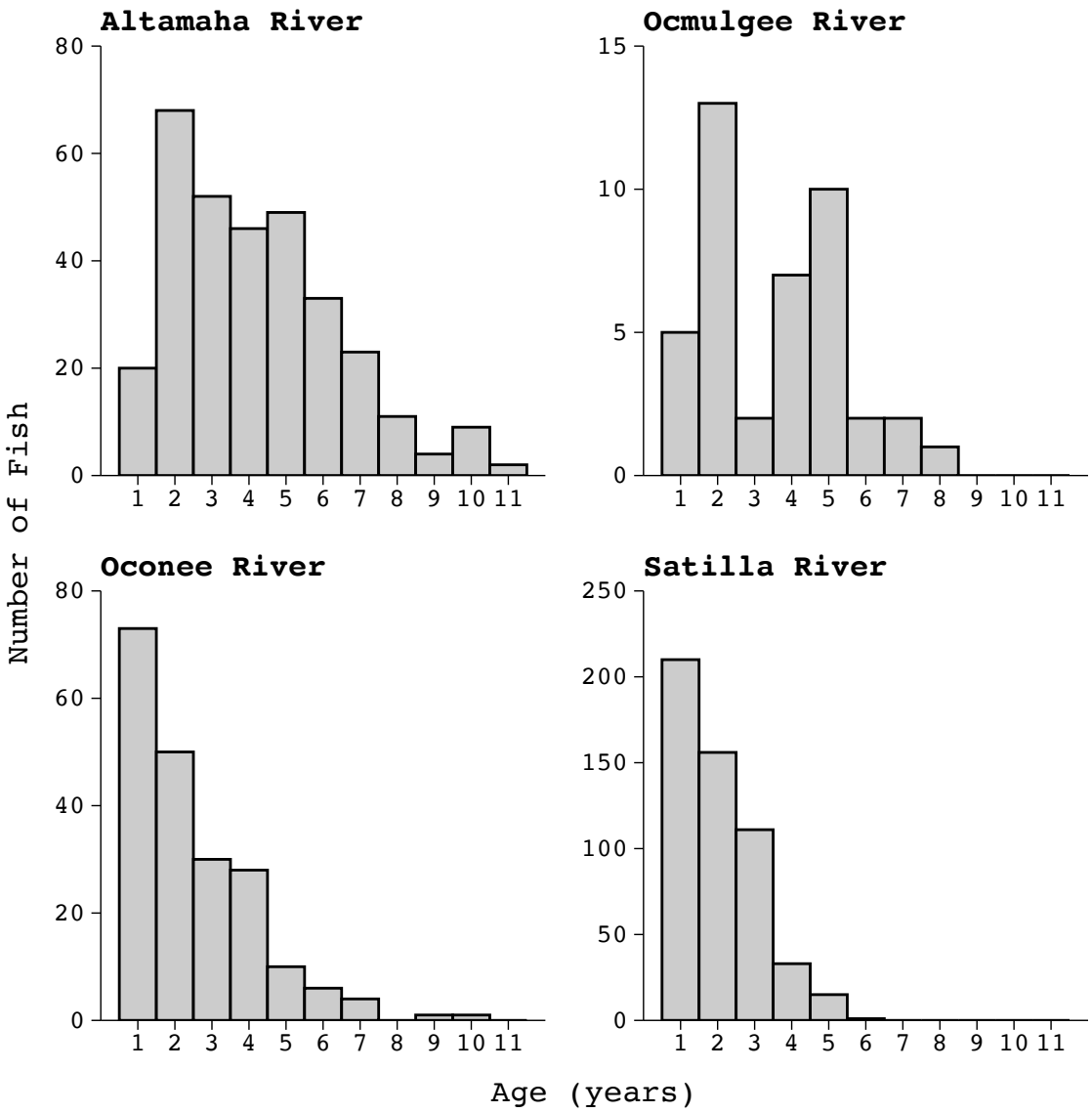

Figure 2-2. Age structure of Blue Catfish collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers between 2017-2021 via electrofishing.

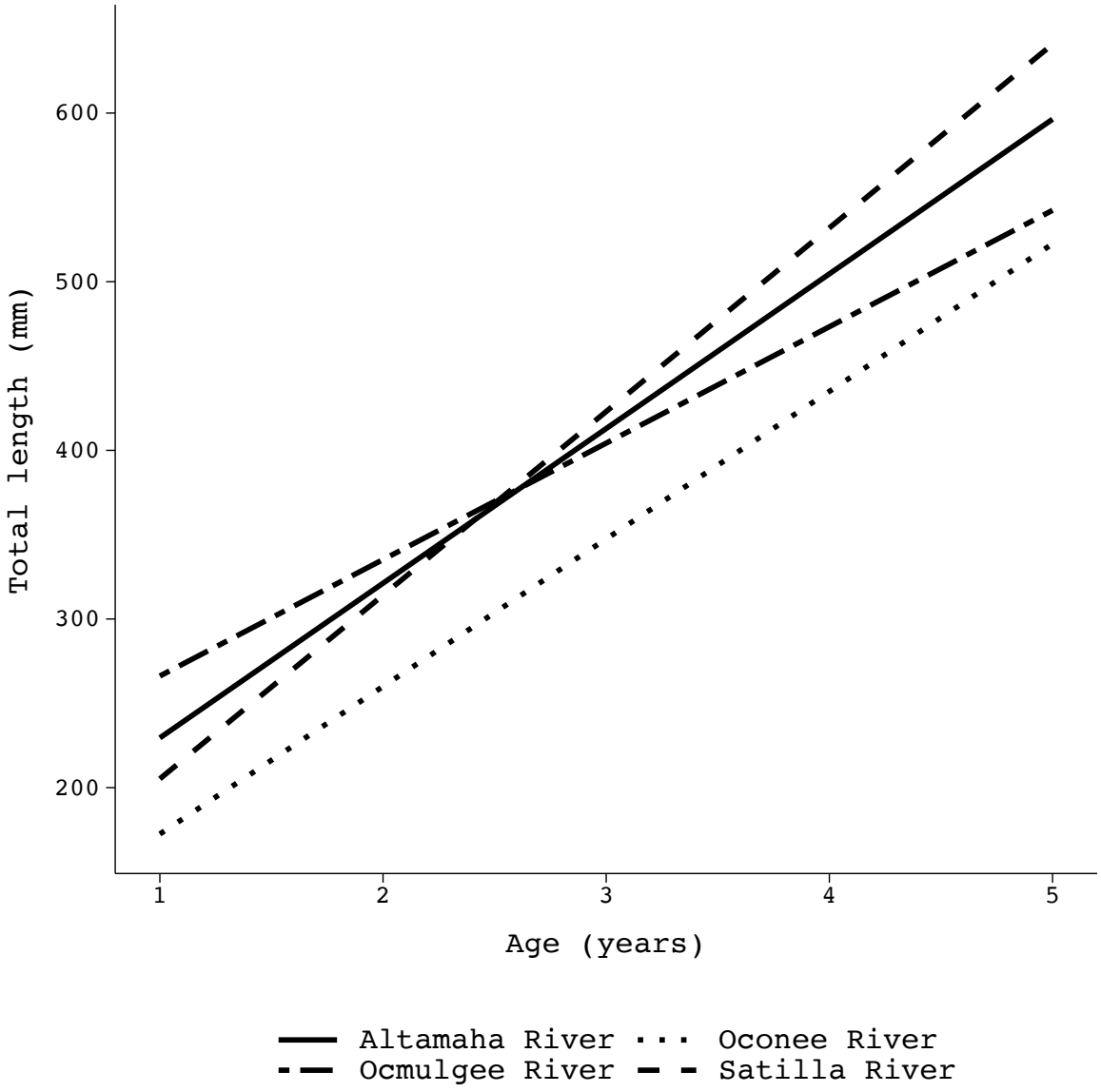

Figure 2-3. Results of analysis of covariance (ANCOVA) that examined differences in growth rates of Blue Catfish aged 1-5 years collected from the Altamaha, Ocmulgee, Oconee, and Satilla Rivers between 2017-2021.

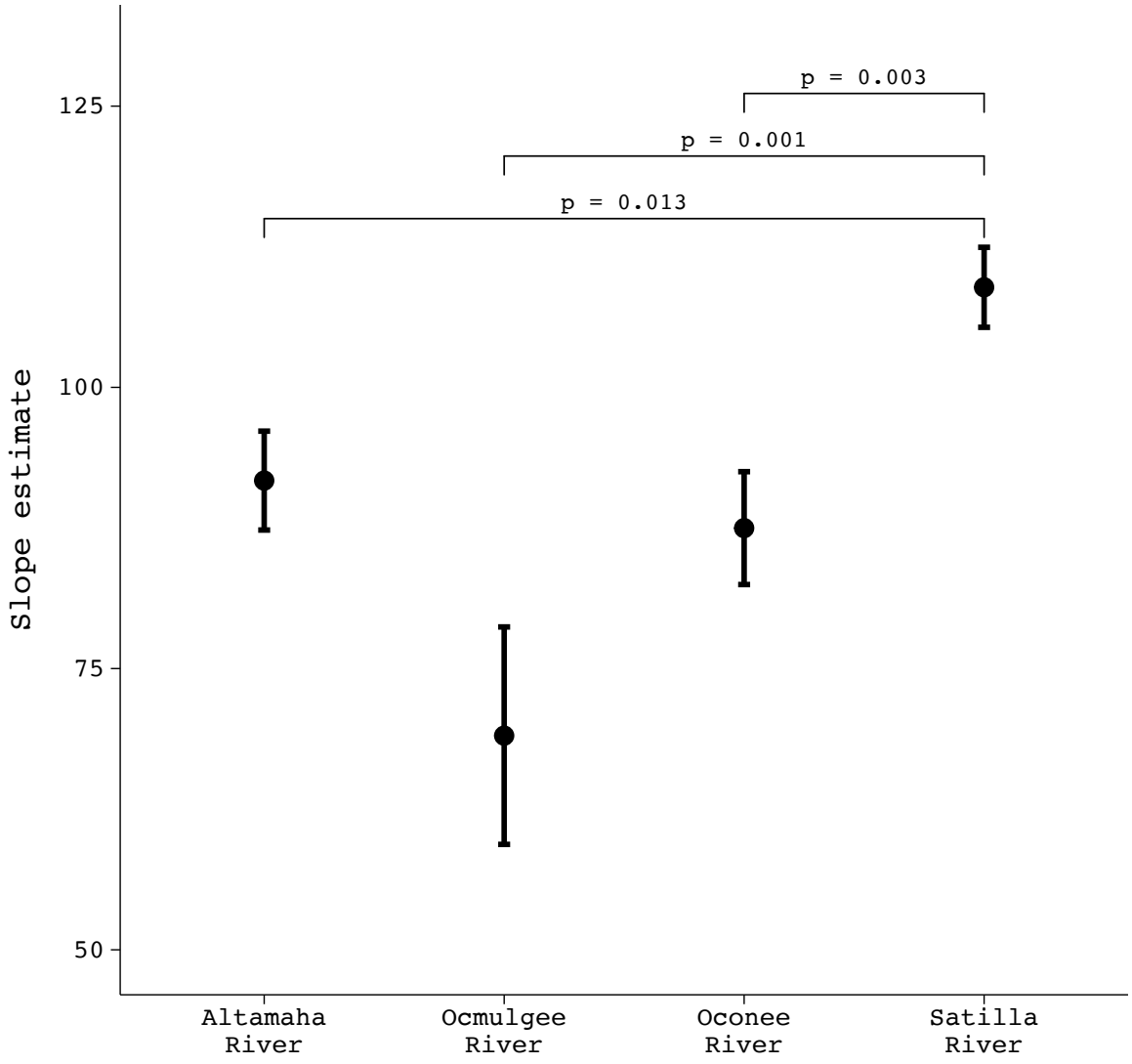

Figure 2-4. Slope estimates from analysis of covariance (ANCOVA) that examined differences in growth rates of Blue Catfish aged 1-5 years collected from the Altamaha, Ocmulgee, Oconee, and Satilla Rivers between 2017-2021, including standard error bars and significant p-values resulting from Tukey pairwise comparisons.

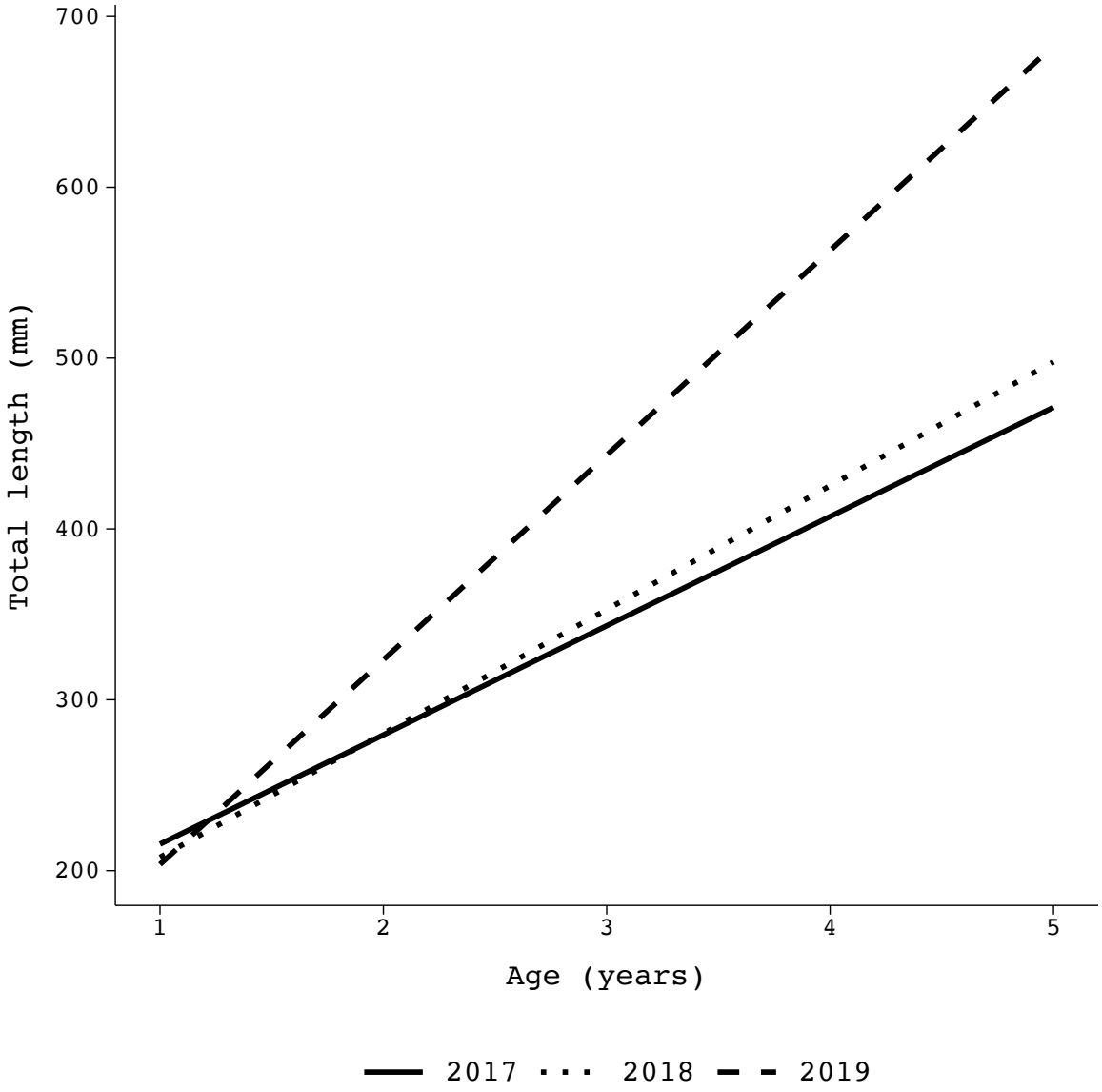

Figure 2-5. Results of analysis of covariance (ANCOVA) that examined differences in growth rates of Blue Catfish aged 1-5 years collected from the Satilla River between 2017-2019.

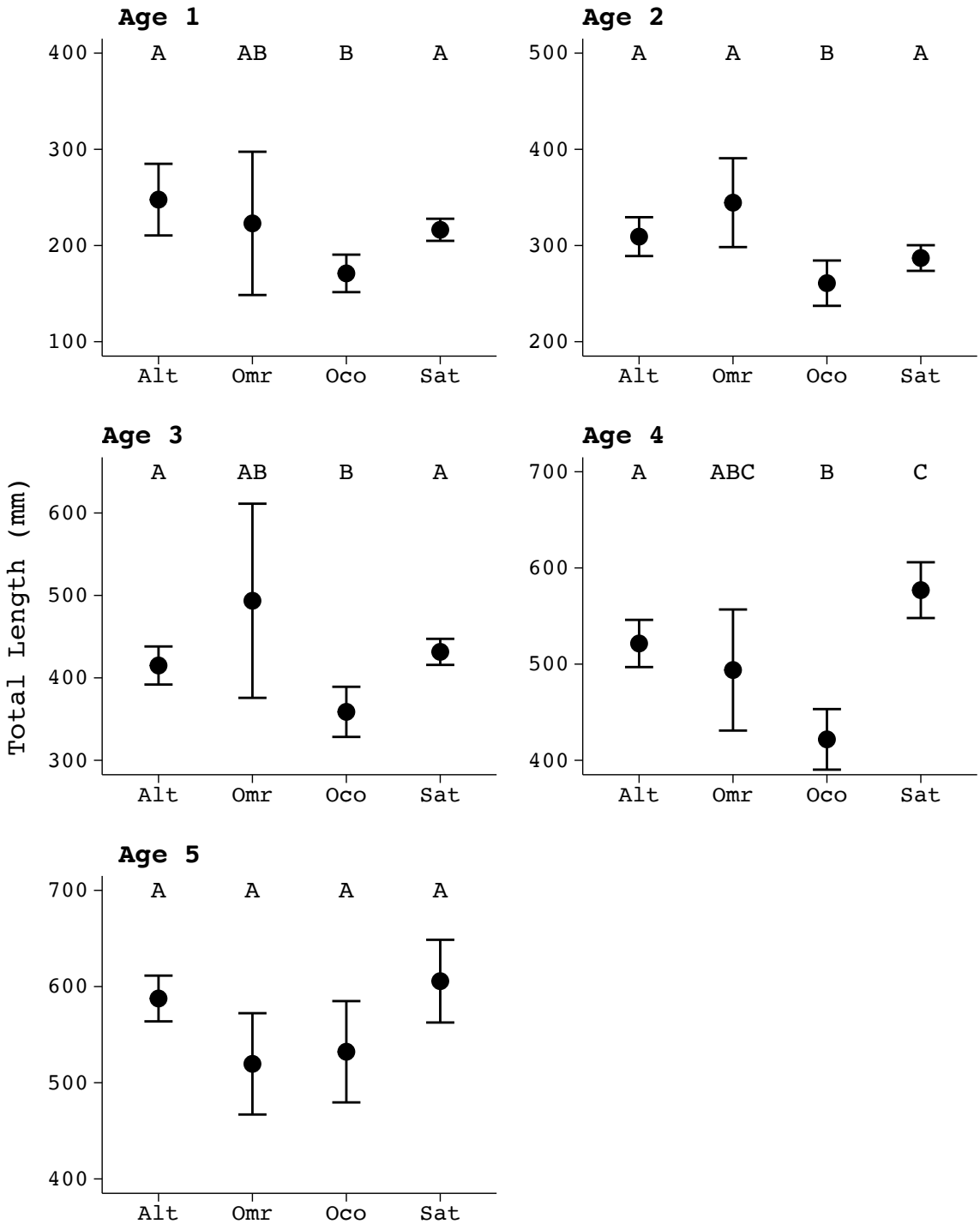

Figure 2-6. Observed mean total length with confidence intervals for Blue Catfish aged 1-5 years collected from the Altamaha (Alt), Ocmulgee (Omr), Oconee (Oco), and Satilla (Sat) rivers. Results of pairwise comparisons are indicated by letters A-C and are reported separately by age.

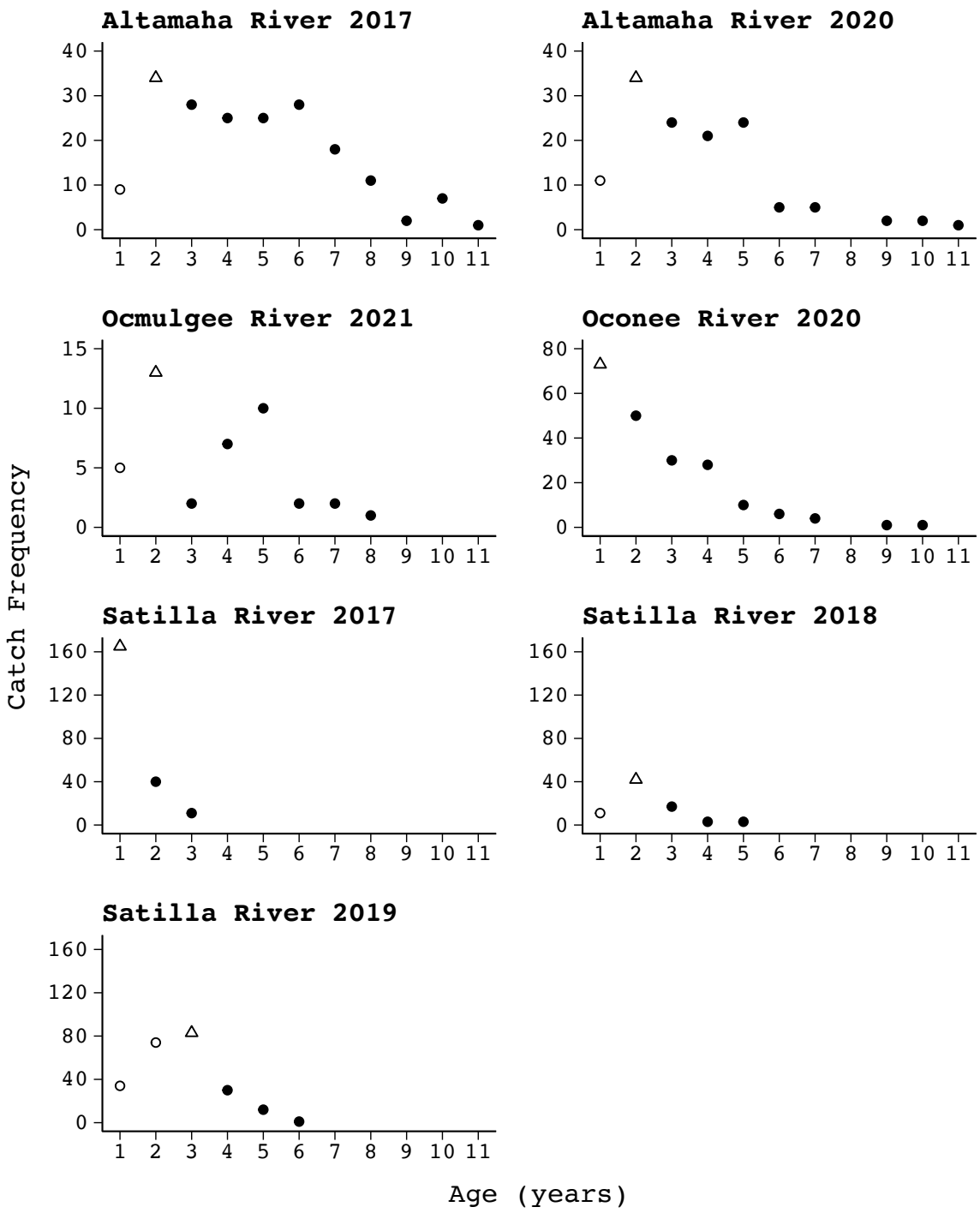

Figure 2-7. Age-frequency data of Blue Catfish collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers (separated by year when applicable) used to estimate instantaneous mortality (Z). Open circles represent ages that have not fully recruited to the sampling gear and triangles represent the "peak plus" criterion (Smith et al. 2012). Only closed circles were used in the estimation of *Z*.

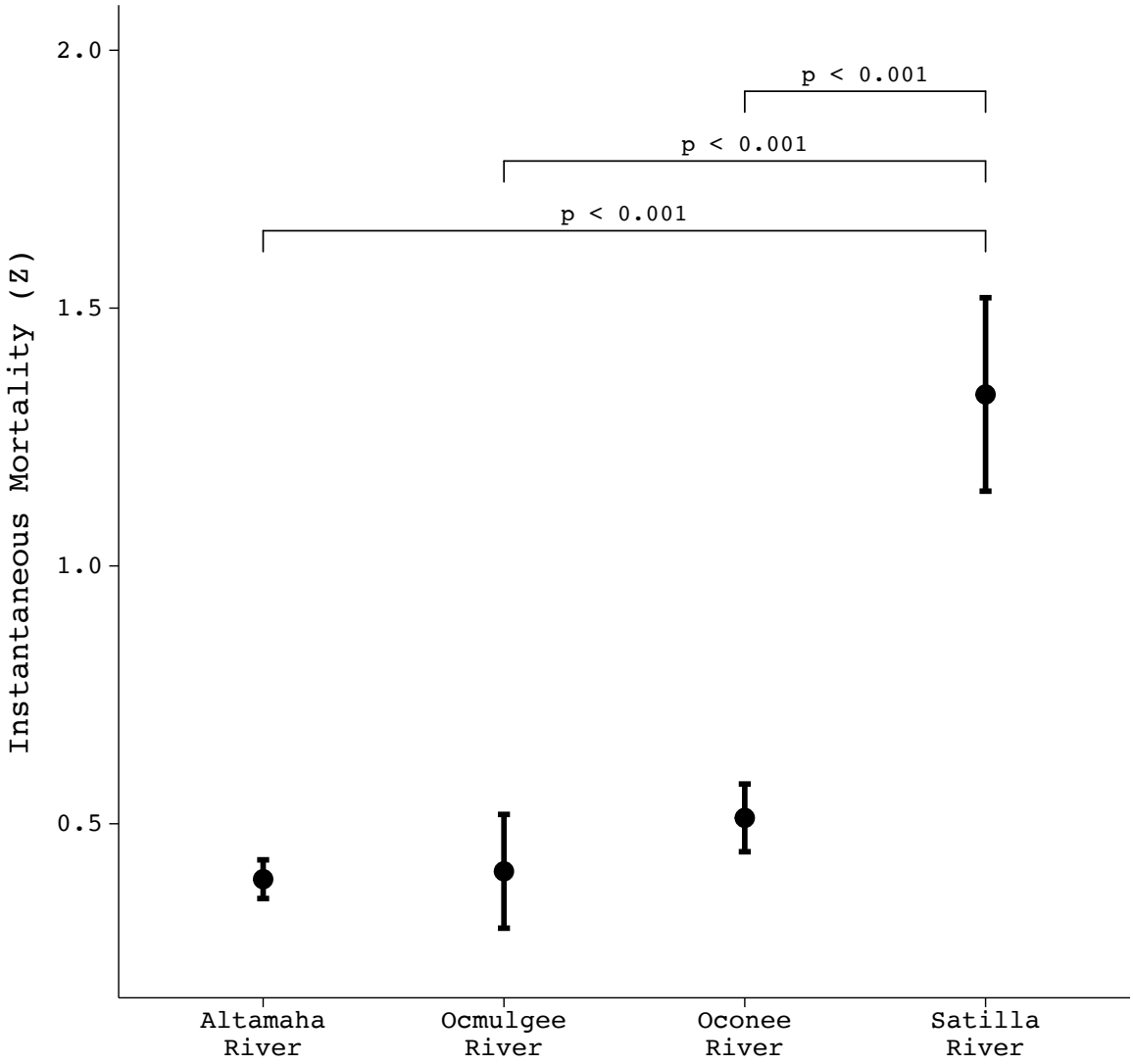

Figure 2-8. Results of generalized linear model analysis that examined differences in instantaneous mortality (Z) of Blue Catfish collected from the Altamaha, Ocmulgee, Oconee, and Satilla Rivers between 2017-2021, including standard error bars and significant p-values resulting from Tukey pairwise comparisons.

CHAPTER 3

DIET COMPOSITION OF FOUR NON-NATIVE RIVERINE BLUE CATFISH POPULATIONS IN GEORGIA

INTRODUCTION

Invasive species pose a threat to biodiversity and ecosystem services across the globe (Pysek & Richardson 2010). Many invasive species possess biological traits that allow them to adapt quickly in novel environments, interrupting natural ecosystem balances and food web dynamics through competition and predation of native taxa. Population assessments of introduced species provide pertinent information about dynamic rate functions (i.e., growth, mortality) and feeding ecology of the invader. This information heavily influences management decisions in invasive species control and the conservation of native populations.

Blue catfish (*Ictalurus furcatus*) are a large-bodied, generalist species endemic to North America that occupy large reservoirs, backwaters, and rivers. They are native to the Mississippi, Missouri, and Ohio River basins and have been widely introduced to both reservoir and riverine habitats in

29 states across the United States. The mechanisms of introducing this species vary, including intentional stocking to establish commercial and recreational fisheries or for biological control (Graham 1999). Blue Catfish are omnivorous predators that prey on abundant and readily available resources. Their wide diet breadth includes mollusks, insects, invertebrates, and fish (Graham 1999; Schmitt et al. 2017). Diet composition analyses often regard the non-native Asian Clam (*Corbicula fluminea*) as a major food source for Blue Catfish (Graham 1999; Bonvechio et al. 2011b; Jennings et al. 2018; Schmitt et al. 2019). Eggleton and Schramm (2004) concluded that Blue Catfish consume large amounts of Zebra Mussels (*Dreissena polymorpha*) and Asian Clam during the summer in the main channel of the Mississippi River. In habitats where mollusks are less abundant, Blue Catfish forage heavily on Gizzard Shad (*Dorosoma cepedianum*) and other fishes (Edds et al. 2002; Snow et al. 2019). Predation on shad species is elevated in colder months due to similar overwintering habits (Jennings et al. 2018; Schmitt et al. 2019).

Blue Catfish demonstrate ontogenetic dietary shifts, where the size of the predator influences prey selectivity. Small Blue Catfish consume aquatic macroinvertebrates, whereas piscivory is observed in mature fish belonging to

larger size classes. In multiple sub-estuaries of the Chesapeake Bay, VA, the shift to piscivory was observed at varying total lengths across systems, ranging between 500 mm and 900 mm total length (Schmitt et al. 2019). In Lake Ellsworth, OK, Blue Catfish were exclusively piscivorous, however this study only represented fish that were greater than 600 mm total length (Snow et al. 2019). Because of the breadth of prey consumed throughout their life, coupled with a large gape, Blue Catfish have the potential for consuming large quantities of sportfish or imperiled native species. Blue Catfish expansion into oligohaline and mesohaline habitats throughout Virginia's tidal rivers (Nepal & Fabrizio 2019), lead to increased predation on ecologically important species like the American Shad (*Alosa sapidissima*) and the commercially valuable Blue Crab (*Callinectes sapidus*; Schloesser 2011; Schmitt et al. 2019). A recent study estimated that Blue Catfish have the potential to consume approximately 401 metric tons of Blue Crab in the James River, VA (Hilling et al. 2023).

The ecological impacts of non-native Blue Catfish are not well documented or understood. However, an increase in Blue Catfish abundance has been found to negatively impact native catfish species. There was an observed decline of White Catfish (*Ameiurus catus*) abundance in the Chesapeake Bay, VA

(Schlosser 2011) and in Lake Oconee, GA (Jennings et al. 2018) that coincided with the introduction and substantial expansion of non-native Blue Catfish.

In Georgia, Blue Catfish are native to the Coosa River basin located in the northwestern corner of the state. Since the mid-1990's, they have been discovered outside of their native range in Lake Sinclair and Lake Oconee, and the Chattahoochee, Flint, Savannah, Ocmulgee, Oconee, Altamaha, and Satilla rivers. Intentional stocking, escape during normal reservoir releases, and periods of high flooding are viable mechanisms for the expansion of this species in the state (Bonvechio et al. 2012). The Flathead Catfish (*Pylodictis olivaris*) was the first invasive catfish species in Georgia and has been documented to predate on the federally endangered Atlantic Sturgeon (Flowers et al. 2011). Although the feeding strategies differ amongst these two catfish species, similar outcomes regarding the effect on native fish communities should be anticipated and mitigated if possible.

Research on the feeding ecology of introduced populations of Blue Catfish is necessary because the long-term ecological impacts of this species are yet to be documented. Although large Blue Catfish tend to primarily feed on non-native Asian Clam, there is a natural risk of predation on important aquatic species given their

opportunistic feeding strategies. The objective of this study was to characterize the feeding ecology of nonnative Blue Catfish in four Georgia rivers. Specifically, we conducted stomach content and stable isotope analyses, determined ontogenetic dietary shifts, and assessed how diet varied spatially by river and longitudinally within rivers. We expect diet composition to be similar among river systems, with Asian Clams being the dominant food source. We predict that Blue Catfish will become increasingly piscivorous at larger sizes. Additionally, we predict that stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ will be analogous to direct observations in diet. The data obtained from this study will provide insight on how the diet of Blue Catfish varies throughout different novel environments and can be used to inform management goals for this nonnative species.

METHODS

Study Area

The study area included four major rivers located in the state of Georgia: the Ocmulgee, Oconee, Altamaha, and Satilla Rivers (Figure 3-1). The Ocmulgee River begins in the Piedmont, flowing southeast through the Coastal Plain until it converges with the Oconee River to form the Altamaha River near Lumber City, Georgia (Grabowski and Jennings 2009). The Altamaha River is the largest free-flowing river on the East

Coast of the United States, flowing 220km southeastward where it empties into the Atlantic Ocean near Darien, Georgia (Bonvechio et al. 2011b). The Satilla River is a blackwater system located entirely in the coastal plain ecoregion of the state. It flows 378km eastward and empties into the Atlantic Ocean at St. Andrew Sound, which is located approximately 40km south of the Altamaha River Sound (Bonvechio et al 2009).

These rivers provide habitat to many aquatic species, including 25 species of federally and state listed freshwater mussels and several species of anadromous fish. These rivers also host angling opportunities for sportfish. The world record Largemouth Bass (*Micropterus salmoides*) was caught in Montgomery Lake on the Ocmulgee River in 1932. The Ocmulgee River is inhabited by the imperiled Robust Redhorse (*Moxostoma robustum*), which has been transplanted there from the Oconee River in attempts to establish self-sustaining populations (Grabowski & Jennings 2009). The Oconee River basin supports recreational fishing opportunities with large populations of sunfish, bass, catfish, and suckers. Both the Altamaha and Satilla rivers have large populations of centrarchids and are now dominated by non-native Flathead Catfish (*Pylodictis olivaris*). There have been noticeable declines in the abundance of highly prized Redbreast Sunfish (*Lepomis auritus*) and native Bullhead Catfish (*Ameiurus sp.)*

in the Satilla River (Bonvechio et al. 2009, 2011a) resulting in extensive removal efforts of Flathead Catfish by the GA Department of Natural Resources. Several anadromous species such as Atlantic Sturgeon (*Acipenser oxyrhynchus*), Shortnose Sturgeon (*Acipenser brevirostrum*), and American Shad (*Alosa sapidissima*) utilize these rivers for spawning and nursery habitats (Fox and Peterson 2019). In addition, a predation event involving a Flathead Catfish and a juvenile Atlantic Sturgeon, was documented occurring in the Satilla River, Georgia (Flowers et al. 2011).

Fish Collection

Blue Catfish were collected during annual summer standardized ictalurid sampling events on the Altamaha, Ocmulgee, and Oconee Rivers, and during the Flathead Removal Program performed by the Georgia Department of Natural Resources (GA DNR) on the Satilla River. Sampling occurred May-October over the course of five years (2017-2021), however not every river was sampled annually following GA DNR protocols. Low-amperage pulsed DC electrofishing (>1 amp, 200-1,000 volt, 18 Hz) was conducted during daylight hours in a downstream direction from a 5.1-m aluminum bass tracker john boat equipped with a Smith-Root model 12B or model LR-24 backpack electrofisher (Bonvechio et al. 2011a). Blue Catfish were targeted at fixed sampling locations on each of

the Altamaha, Ocmulgee, and Oconee Rivers. These stations were set up in the early 1990's by the GA DNR as part of a standardized sampling protocol (Bonvechio et al. 2011b). Blue Catfish were targeted on the Satilla River at sampling locations that were set up for the Flathead Removal Program. Each station was sampled where the deep, riveted, undercut banks were targeted and a chase boat was utilized to increase sampling efficiency (Daugherty and Sutton 2005). Sampling transects were of uniform length (approximately 1 rkm) and sampling duration at each site was approximately 1 hour. Fish were measured (mm; total length), weighed (g), and sacrificed for age, growth, and diet analyses. During dissection, sex was determined, both lapilli otoliths were extracted, full stomachs were excised and frozen, and a subsample of fish tissue was taken for stable isotope analysis.

Stomach Content Analysis

Thawed gut contents were identified to the lowest discernable taxonomic resolution, weighed (g), and enumerated. Prior to analysis, prey items were sorted into broad prey categories based upon taxonomic and biological similarities to reduce biases in the variability of prey identification (Cortés 1997). The prey category "Crustaceans" contained prey that were identified as crayfish or shrimp; "Fishes" contained identified and unidentified prey of fish

origin; "Insects" contained insects and other arthropods; "Mollusks" contained *Corbicula fluminea, Elliptio sp.,* and freshwater snails; and "Vegetation" contained aquatic vegetation, fruits, and detritus. Contents found in the gut that were excluded from analyses were anthropogenic items, rocks and sediment, unidentifiable prey, and other vertebrates (amphibians and mammals).

Diet data were used to calculate the frequency of occurrence (O_i), proportion by number (N_i), and proportion by weight (W_i) of each prey category denoted by subscript i. Diet composition was described by the relative importance index (RI_i), which combines the unique properties of the diet (frequency, number, and weight) into a single measure.

Frequency of occurrence (O_i) describes how often a particular prey type is detected in the gut contents. The number of fish containing prey i (J_i) is divided by the number of fish with food in their stomachs (P):

$$O_i = \frac{J_i}{P} \qquad \text{Eq. 1}$$

Proportion by number (N_i) describes the ratio (by count) that prey i contributes to the total number of prey items (Q) and proportion by weight (W_i) describes the ratio (weight in grams) that prey i contributes to the total weight of all prey:

$$N_i = \frac{N_i}{\sum_{i=1}^{Q} N_i} \quad \text{Eq. 2}$$

$$W_i = \frac{W_i}{\sum_{i=1}^{Q} W_i}, \quad \text{Eq. 3}$$

These three measures of fish diet were combined (AI_i) to calculate the relative importance index for each prey category (RI_i), which is a single proportional measure that describes the relative importance of all prey detected in the gut contents:

$$RI_i = 100 * \frac{AI_i}{\sum AI_i}, \qquad where\ AI_i = O_i + N_i + W_i, \quad \text{Eq. 4}$$

Sample Size Sufficiency

Prey accumulation curves (PAC) were created using the R-package vegan (v2.6-4; Oksanen et al. 2009), where the cumulative number of prey categories were plotted against the number of individual stomachs sampled. Rarefaction curves were generated with 95% confidence bands for each river system to assess whether the number of stomachs sampled were sufficient to describe the diet composition of Blue Catfish in each river system. The Weibull-logistic model was used to fit the prey accumulation curves, which proved to be more robust in estimating species richness than other models (Zou et al. 2023). When the PAC created from the extrapolated values reached an asymptote, it was determined that unique prey items were found less frequently as the number of

stomachs sampled increased (Ferry & Cailliet 1996). To quantify this measure, the slope (*B*) of each PAC was calculated. When B < 0.05, sample size sufficiency was achieved (Cook & Bundy 2010).

Feeding Strategies

Amundsen et al. (1996) adapted a graphical model from Costello (1900) that depicts feeding strategy, relative prey importance and niche variation based on the distribution of individual prey items. These important aspects of fish diet were determined by plotting prey-specific abundance (P_i) against frequency of occurrence (O_i). Prey-specific abundance was calculated as the proportion by weight that prey i contributed to the total weight of prey in only predators that consumed prey i:

$$P_i = \left(\frac{\sum S_i}{\sum S_{ij}}\right) 100, \qquad \text{Eq. 5}$$

where S_i equals the abundance of prey i in stomachs, and S_{ij} equals the total abundance of prey in the stomachs that only contain prey i.

This graphical model informed the feeding strategy (specialized or generalized), importance (dominant or rare), and niche variation (high within population or high among individuals) for prey represented on the bivariate plots.

Spatial Variation in Diet Composition

To determine spatial variation of diet composition within rivers, the mean proportion by weight (MW_i) of the pooled prey categories was calculated at each sampling location. Mean proportion by weight is defined as:

$$MW_i = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{W_{ij}}{\sum_{i=1}^{Q} W_{ij}}\right), \quad \text{Eq. 6}$$

where P equals the number of fish with food in their stomachs, subscript i equals prey item, and subscript j equals fish.

Diet variation among rivers was determined by comparing the mean proportion by weight (MW_i) of pooled prey categories that were present in all four rivers (i.e., crayfish, fishes, insects, mollusks, and vegetation). Using the R-package rstatix (v0.7.2; Kassambara 2023), a Kruskal-Wallis rank sum test was performed to test the significance of means (α = 0.05), followed by Wilcoxon pairwise tests with Bonferroni adjusted p-values (α = 0.008) to identify spatial differences in mean composition by weight of the major prey categories.

Ontogenetic Dietary Shifts

Blue Catfish prey selection varies as fish grow to larger sizes; an ecological phenomenon known as ontogenetic dietary shifts (ODS). To determine river-specific ontogeny, these analyses were performed separately by river. Diet data were split into three size classes based on total length

measurements (e.g., ≤ 300 mm, 301-599 mm, and ≥ 600 mm) which are representative of differing life stages of Blue Catfish (juvenile, subadult, and adult). Relative importance was calculated for each prey category for each size class. For each prey category, a chi-squared test of the equality of proportions was performed to determine whether a relationship existed between relative importance and size class. Pairwise comparisons of proportions were then calculated with Bonferroni corrections for multiple testing to determine the directionality of the shift (i.e., increase or decrease as the fish grows; Figure 3-2).

Stable Isotope Analysis

Direct measurements of diet composition can be biased based on feeding patterns and stomach evacuation rates. Therefore, we analyzed stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to corroborate diet observations from two of our study rivers. Whole carcasses were provided from the Altamaha and Satilla rivers, providing a means to assess isotopic signatures. Therefore, muscle tissue was biopsied from a subsample of fish collected from the Altamaha (N = 25; 171-767 mm TL) and Satilla (N = 50; 182-700 mm TL) rivers. Samples were dried by lyophilization, a process where water is removed from the tissue in the form of ice under low pressure by sublimation. Samples were placed in a lyophilizer for at least 24 hours,

and then placed in a drying oven (50°C) for at least 48 hours. Samples were then ground to a uniform fine (talc-like) texture using a Spex ball-mill and transferred into individual tin capsules. Carbon and nitrogen isotopic signatures were determined using a Thermo 253 Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific Inc. Waltham, MA). All samples were analyzed by the Stable Isotope Ecology Laboratory at the University of Georgia. Stable isotope ratios were expressed as $\delta^{13}C$ and $\delta^{15}N$, relative to international standards V-PDB (Vienna Pee-Dee Belemnite) for carbon and Air for nitrogen.

Mean stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were calculated for subsamples of Blue Catfish from the Altamaha (N = 25) and Satilla Rivers (N = 50). A Kruskal-Wallis test was performed to determine significant differences of mean stable isotope values between river systems. Additionally, mean $\delta^{13}C$ and $\delta^{15}N$ was calculated for each size class (juvenile, subadult, and adult) to identify whether isotopic signatures varied by size class within each population. Kruskal-Wallis tests were used to determine significance and a Wilcoxon pairwise test was used to identify in which size classes these differences occurred. Lastly, linear regression models were used to assess the relationship of $\delta^{13}C$ and $\delta^{15}N$ and total length. The estimated slope parameters were

compared to determine whether the relationships between $\delta^{13}C$ and $\delta^{15}N$ and length were similar between populations.

RESULTS

A total of 936 Blue Catfish stomachs were excised and processed for diet analyses, with 846 stomachs containing prey (90.38%). The size range of fish containing prey was 87-970 mm total length. Blue Catfish diets were comprised of a wide variety of taxa, including mollusks, insects, crustaceans, fishes, other vertebrates, and vegetation. Asian Clam (*Corbicula fluminea*) was the most dominant prey consumed in frequency (36.96%), number (96.76%) and weight (69.33%) in all rivers combined (Table 3-1). After pooling prey items based on taxonomic and biological similarities, the relative importance index was calculated for each major prey category. The relative importance for each population was as follows: crustaceans: 0.1-13.2, fishes: 2.2-9.5, insects: 1.6-9.0, mollusks: 56.1-81.6, and vegetation: 4.6-22.1 (Table 3-2). All prey accumulation curves generated for each river system reached asymptotes ($B < 0.05$), indicating that an adequate number of stomachs were sampled to describe diet composition of these populations (Figure 3-3; Cook & Bundy 2010).

Blue Catfish diets in the Altamaha, Ocmulgee, and Oconee Rivers were dominated by mollusks (i.e., Asian Clam), indicating that these predator populations had a narrow niche

width. Prey that was consumed occasionally (generalization) included crayfish, fish, insects, and vegetation. These prey items were considered 'rare' due to lower prey specific abundance and frequency of occurrence in the diet. In the Satilla River, mollusks were consumed by few individuals that displayed a 'specialist' feeding strategy. Blue Catfish in the Satilla River had a broad niche width, shown by the gradient of all prey types located on the left side of the diagram (Figure 3-4).

Diet variation within the Altamaha River showed a high mean proportion by weight of mollusks in the six most upstream sites, and an increase in vegetation at the remaining sites located downstream (Figure 3-5). The Ocmulgee River population consumed primarily mollusks throughout the study area, but the variation of prey types increased at the lowest site closest to the confluence of the Oconee River. The Oconee River population consumed more mollusks at the lowest sites but maintained a higher variation of prey items throughout the study area compared to the Altamaha and Ocmulgee populations. Satilla River Blue Catfish had the most variable diet, where they regularly consumed a wide variety of prey items throughout the entirety of the study area. Diet overlaps between crayfish and shrimp occurred in half of the sampling

sites but were consumed in similar amounts where they were both readily available.

The diets of Blue Catfish were spatially variable. In the Altamaha River, the mean composition by weight of vegetation was significantly higher than the other systems (Figure 3-6), and insect consumption by weight was the lowest (Figure 3-7). The Satilla River population consumed significantly more crayfish and fishes, but fewer mollusks when compared to the other populations (Figures 3-8, 3-9, & 3-10). The Ocmulgee and Oconee River populations consumed similar weights of all prey categories.

Relative importance of the five major prey categories (crustaceans, fishes, insects, mollusks, and vegetation) were variable among size classes in each river system (Table 3-3). Mollusks were the dominant prey category of every size class within each system (excluding Satilla River juveniles; RI = 11.3) with relative importance values ranging from 48.6-88.6. Relative importance values of vegetation ranged from 0-33.9. Juveniles from the Altamaha River had the highest RI value of vegetation (33.9), followed by Satilla juveniles (27.8), Altamaha adults (20.5), and Altamaha subadults (20.1). Relative importance values of insects ranged from 0.9-25.6. Juveniles from the Satilla River had the highest RI value of insects (25.6), followed by Ocmulgee juveniles

(23.4), and Oconee juveniles (14.2). Altamaha juveniles consumed less insects than juveniles from the other systems (2.7). Relative importance values of crustaceans ranged from 0-23.4. Juveniles from the Satilla River had the highest RI value of crustaceans (23.4), followed by Satilla subadults (17.8), and Satilla adults (4.9). Relative importance values of fishes ranged from 0-18.9. Adults from the Oconee River had the highest RI value of fishes (18.9), followed by Satilla subadults (12.8), Satilla juveniles (11.8), and Altamaha adults (11.3).

Ontogenetic shifts were detected in all river systems. In the Altamaha River, significant differences in the relative importance of mollusks (X^2 = 12.12, P = 0.002), vegetation (X^2 = 20.66, P < 0.001), and fishes (X^2 = 54.93, P < 0.001) were detected among size classes (Figure 3-11). There were no significant differences in RI values of insects or crustaceans. Relative importance for vegetation was significantly higher in the juvenile size class (RI = 33.9) than in subadults (RI = 20.1; P < 0.001) and adults (RI = 20.5; P < 0.001). Relative importance of mollusks was significantly higher in the subadult size class (RI = 75.8) than juveniles (RI = 36.5; P = 0.003); however, no significance was found between adults (RI = 66.7) and juveniles or subadults. Relative importance of fishes was

significantly higher in adults (RI = 11.3) than juveniles (RI = 0; $P < 0.001$) and subadults (RI = 1.8; $P < 0.001$).

In the Ocmulgee River, significant differences in the relative importance of mollusks ($X^2 = 37.78$, $P < 0.001$), insects ($X^2 = 83.39$, $P < 0.001$), fishes ($X^2 = 13.02$, $P = 0.001$), and crustaceans ($X^2 = 17.59$, $P < 0.001$) were detected among size classes (Figure 3-12). No significant differences in RI values of vegetation were found among size classes. Relative importance of insects was significantly higher in juveniles (RI = 23.4) than subadults (RI = 3.6; $P < 0.001$) and adults (RI = 4.6; $P < 0.001$). Relative importance of mollusks was significantly higher in subadults (RI = 87.5) and adults (RI = 81.6) when compared to juveniles (RI = 67.9; both $P < 0.001$). Relative importance of fishes and crustaceans was significantly higher in adults (both RI = 4.5) than in juveniles that consumed zero fishes or crustaceans (both $P = 0.002$).

In the Oconee River, significant differences in the relative importance of mollusks ($X^2 = 27.89$, $P < 0.001$), fishes ($X^2 = 73.08$, $P < 0.001$), insects ($X^2 = 38.77$, $P < 0.001$), vegetation ($X^2 = 36.68$, $P < 0.001$), and crustaceans ($X^2 = 20.39$, $P < 0.001$) were detected among size classes (Figure 3-13). Relative importance of insects was significantly higher in juveniles (RI = 14.2) than subadults (RI = 4.4; $P < 0.001$)

and adults (RI = 2.3; $P < 0.001$). Relative importance of vegetation was also highest in juveniles (RI = 9.9) compared to adults that consumed no vegetation (RI = 0; $P < 0.001$). Relative importance of mollusks was significantly higher in subadults (RI = 88.6) than in juveniles (RI = 72.8; $P < 0.001$) and adults (RI = 73.9; $P < 0.001$). Oconee River adults had significantly higher relative importance values of fishes (RI = 18.9) than juveniles (RI = 3.1; $P < 0.001$) and subadults (RI = 2.2; $P < 0.001$), and of crustaceans (RI = 4.9) than juveniles that consumed zero (RI = 0; $P = 0.001$).

In the Satilla River, significant differences in the relative importance of mollusks ($X^2 = 272.88$, $P < 0.001$), vegetation ($X^2 = 36.33$, $P < 0.001$), insects ($X^2 = 101.65$, $P < 0.001$), crustaceans ($X^2 = 43.76$, $P < 0.001$), and fishes ($X^2 = 8.93$, $P = 0.012$) were detected among size classes (Figure 3-14). Relative importance of vegetation was significantly higher in juveniles (RI = 27.8) than subadults (RI = 12.8; $P < 0.001$) and adults (RI = 11.5; $P < 0.001$). Relative importance of insects was significantly higher in juveniles (RI = 25.6) than in subadults (RI = 7.9; $P < 0.001$) and adults (RI = 0.9; $P < 0.001$). Relative importance of crustaceans was also significantly higher in juveniles (RI = 23.4) than adults (RI = 4.9; $P < 0.001$). Relative importance for fishes was higher in juveniles (RI = 11.8) and subadults (RI = 12.8)

than adults (RI = 6.2), but significance was only detected for the comparison between subadults and adults (P = 0.006). Relative importance of mollusks was significantly higher in adults (RI = 76.5) than juveniles (RI = 11.3; P < 0.001) and subadults (RI = 48.6; P < 0.001).

Mean $\delta^{13}C$ and $\delta^{15}N$ values for the Altamaha River were -28.01‰ (±0.20) and 13.92‰ (±0.16); for the Satilla River, mean $\delta^{13}C$ was -25.91‰ (±0.23) and mean $\delta^{15}N$ was 11.81‰ (±0.11). Stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were significantly different between the Altamaha and Satilla Rivers ($\delta^{13}C$: H = 31.7, P < 0.001; $\delta^{15}N$: H = 41.1, P < 0.001; Figure 3-15). The only significant difference in stable isotope signatures amongst size classes was detected in the Satilla River comparison of mean $\delta^{15}N$ between juveniles and adults (H = 96, P = 0.005; Figure 3-16). The relationship between $\delta^{13}C$ and total length was significantly different between populations, where $\delta^{13}C$ increased with fish length in the Altamaha River, but decreased in the Satilla River. For $\delta^{15}N$, there was a positive relationship with total length in the Satilla River, and a negative relationship in the Altamaha River (Figure 3-17).

DISCUSSION

The diet composition of the four non-native riverine populations of Blue Catfish described in this thesis is

consistent with diet studies of introduced populations of Blue Catfish that are dominated by Asian Clam (Graham 1999, Bonvechio et al. 2011b, Jennings et al. 2018, Schmitt et al. 2019, Belkoski et al. 2021, Evans et al. 2021). Blue Catfish in the Altamaha, Ocmulgee, Oconee, and Satilla River systems displayed specialist feeding strategies on mollusks and consumed other prey occasionally and at low quantities.

The Satilla River population showed unique properties of diet compared to the Altamaha, Ocmulgee, and Oconee rivers. For example, the prey accumulation curve constructed to assess sample size sufficiency in the Satilla River reached an asymptote significantly faster than the other systems, indicating that Satilla River Blue Catfish consume a wider variety of prey. For example, frequency of occurrence for all major prey categories was generally around 20% in the Satilla River, whereas the diets from the Altamaha, Ocmulgee, and Oconee rivers were dominated by mollusks in both frequency and prey-specific abundance. Similarly, the mean proportion by weight of prey resulted in a wider diet breadth that was not dominated by a specific prey group in the Satilla River.

Blue Catfish exhibited a decreased consumption of insects and vegetation as fish grew to larger sizes. This ontogenetic shift was observed among all river systems. Consumption of crustaceans and fishes increased as Blue

Catfish grew in the Altamaha, Ocmulgee, and Oconee Rivers. Conversely, the Satilla River population consumed less crustaceans and fishes as Blue Catfish grew. Mollusks were consumed by all size classes in similar amounts (although highest in the subadult size class) in the Altamaha, Ocmulgee, and Oconee rivers. In the Satilla River, consumption of mollusks increased as fish grew to larger sizes. Our ontogeny results differ from recent diet studies of invasive Blue Catfish in the Pamunkey River, Virginia. Prey were identified using high-throughput DNA sequencing, which allowed a finer taxonomic resolution for prey identification. The results showed that juvenile Blue Catfish (0-300 mm TL) consumed noticeably more Asian Clam than larger size classes, and a shift occurred around 500 mm TL where Blue Catfish decreased consumption of mollusks and vegetation and increased consumption of crayfish and fish (Evans et al. 2021). In our study, although ontogenetic shifts occurred at larger sizes, Asian Clam persisted as the dominant prey consumed for all size classes and are consistent with previous research examining the initial diet metrics of Altamaha River Blue Catfish conducted prior to this study (Bonvechio et al. 2011b).

Stable isotope analyses can be used in diet studies to estimate trophic level position and to identify potential

impacts on prey resources and prey foraging patterns. In Cape Fear River, North Carolina, Blue Catfish isotopic signatures of carbon and nitrogen increased with fish size (Beloski et al. 2021). Furthermore, estimation of stable isotopic signatures of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ revealed that migrating anadromous species contribute to the diet of Blue Catfish in the Rappahannock River, Virginia (MacAvoy et al 2009). Stable isotope analyses were limited in this study as tissue samples were only available from two of the four populations. Additionally, the lack of stable isotope ratios of prey items prevented trophic level determination of the predators by calculating $\delta^{15}N$ fractionation. Despite these limitations, information gained from stable isotope analysis lends support to the conclusions drawn from stomach content analysis. Stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were significantly different between the Altamaha River and Satilla River, indicating that feeding strategies and prey selectivity are variable between populations. All size classes of Blue Catfish in the Altamaha River had similar $\delta^{13}C$ and $\delta^{15}N$ levels, evidenced by similar diet composition between size classes. In the Satilla River, $\delta^{15}N$ values differed between adults and juveniles, corroborating stomach content analyses indicating that adults consume large quantities of mollusks. Inverse relationships between $\delta^{13}C$ and total length suggest that the

sources of vegetation differ between these two river systems. Although the prey category "Vegetation" was pooled in this study, Satilla River Blue Catfish consumed large amounts of fruit, (i.e., persimmon, saw palmetto, and swamp tupelo) whereas in the Altamaha River, aquatic vegetation and algae were consumed most frequently by larger fish in the estuarine portions of the river. Future stable isotope analyses of both predator and prey populations in coastal rivers of Georgia will provide a better understanding of river-specific foraging patterns and contributions of marine resources in the diet.

Differences in diet among rivers could be attributed to a variety of factors such as prey availability, density dependence, and environmental characteristics. Studies conducted in four tributaries of the Chesapeake Bay, Virginia concluded that opportunistic feeding strategies support a broad array of diets representative of seasonal and spatial variation in estuarine habitat (i.e., freshwater, mesohaline, oligohaline; Schmitt et al. 2019). Marine contributions to Blue Catfish diet increase with migration into more saline habitats in response to increased densities of Blue Catfish during high recruitment years (Schloesser et al 2011).

While Blue Catfish diets in three of our four rivers studied were found to be dominated by *Corbicula,* we do not

have data on prey availability among our sites. Because of this, it is difficult to ascertain whether Blue Catfish are preferentially selecting *Corbicula*, or whether abundance in the diet represents abundance in the system. Furthermore, despite a lack of prey abundance data, differences in habitat among rivers could also play a role in mediating prey abundance. The Satilla River is an acidic blackwater river with a pH of 4.5–6.0, which may support slower population growth and densities of *Corbicula* (Sandow et al. 1974; Sites et al. 1995). While exact introduction dates are unknown for either river system, the USGS Nonindigenous Aquatic Species Database has first reports of Corbicula in the Altamaha and Ocmulgee rivers in the 1970's, but they were first reported as established in the early 2000's in the Satilla (United States Geological Survey 2023). Both a later introduction as well as suboptimal habitat could explain lower Corbicula densities in the Satilla, thereby resulting in lower proportions in the diet.

Additionally, diet specialization could be attributed to intraspecific competition. For example, Blue Catfish in the Rappahannock River had large population densities that coincided with wider diet breadths when compared to other Virginia tributaries (Greenlee and Lim 2011). Environmental factors such as daily flow rates have been shown to correlate

with Blue Catfish diet metrics from the Pamunkey River. Sampling days with lower flow rates provided Blue Catfish diets of higher diversity than days with higher flows (Evans et al 2021). The relative abundance of Blue Catfish, native fishes, and prey assemblages in our study systems have not yet been assessed, therefore predator-prey dynamics that occur in these systems are not well understood. Future work to quantify these metrics may explain the spatial variation of diets and help to quantify the ecological impacts these introduced fishes have on native fish communities.

Management of Blue Catfish in our study systems is minimal; however, the fish community in the Satilla River is altered annually during the Flathead Catfish Removal Program. This program was enacted in 2007 aiming to minimize the impact of Flathead Catfish predation on native fish species through annual aggressive removal practices. These large culling events of both Flathead Catfish and Blue Catfish resulted in over 100,000 Flathead Catfish being removed as of 2023, and over 2,300 Blue Catfish being removed since their introduction to the system in 2011 (Georgia Department of Natural Resources, 2023). Notable declines in the size structure of Flathead Catfish and earlier onset of maturation have been observed since the implementation of the removal program (Bonvechio et al. 2011a), and it is likely that Blue

Catfish have experienced similar shifts (Chapter 2). These ongoing efforts to reduce catfish densities are likely playing a role in structuring the fish community, including prey availability and consumption rates. Future work aimed at evaluating the impact of removal practices on population dynamics of Flathead and Blue Catfish would provide valuable information for managing other introduced populations.

Examining how diet influences dynamic rate functions is an important step to learning how these introduced populations function in a novel environment. The diet of juvenile Blue Catfish in the Satilla River was high in both crustaceans and fish, which may contribute to observed faster growth patterns (Chapter 2) due to a higher caloric intake provided by these prey sources. This hypothesis could be tested by studying the energetic benefit of the wide variety of prey that Blue Catfish consume. Prey caloric value coupled with consumption rates and population size would provide valuable information toward understanding energy transfer in these large river systems (Nisbet et al. 2012; van Poorten and Walters 2016).

These data provide new information about introduced riverine Blue Catfish populations that are gradually expanding over time and altering food web dynamics across the state of Georgia. However, additional understanding is needed

to adequately describe the feeding ecology of this successful invader and to identify potential ecological impacts this species may have on native aquatic taxa. We suggest that future research should focus on the collection of Blue Catfish during colder months to fill knowledge gaps about the seasonal diets of Blue Catfish, which tend to include larger quantities of fish in winter and spring seasons (Jennings et al. 2018, Schmitt et al. 2019). Additionally, future collection of Blue Catfish should incorporate the utilization of nets to target larger individuals. Previous studies have demonstrated a shift to a primarily piscivorous diet at sizes ranging from 500-900mm in four subestuaries of the Chesapeake Bay (Schmitt et al. 2019) and few fish of this size were captured in this study. It is unknown if larger fish are abundant in our study systems; however, anecdotal reports from anglers suggest that large fish are at least present at low levels due to infrequent capture reports. The long-term ecological impact that Blue Catfish may have on native fish assemblages via predation may not be adequately described without the inclusion of large Blue Catfish diet information. We suggest that future research and monitoring of these populations utilize more robust sampling approaches and methods for diet description to fully characterize the diet metrics of Blue Catfish.

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Table 3-1. Frequency of occurrence (%O), proportion by number (%N), proportion by weight (%W), and relative importance (RI) of all diet items found in Blue Catfish diets collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia combined (N = 846).

Prey Category	All Rivers			
	%O	%N	%W	RI
Crustaceans				
Crayfish				
Unidentified crayfish	3.95	0.14	0.69	1.68
Shrimp				
Palaemonetes sp.	7.22	0.25	0.43	2.80
Fishes				
Anguillidae				
Anguilla rostrata	0.19	0.01	0.00	0.07
Centrarchidae				
Unidentified sunfishes	0.67	0.02	0.65	0.46
Lepisosteidae				
Unidentified gars	0.19	0.01	1.84	0.66
Ictaluridae				
Unidentified catfishes	1.54	0.06	0.75	0.81
Unknown				
Unidentified fishes	7.89	0.31	4.74	4.44
Insects				
Arachnids				
Aranea	0.10	0.00	0.00	0.04
Insects				
Blattodea	0.19	0.01	0.01	0.07
Coleoptera	2.21	0.12	0.11	0.87
Diptera	0.48	0.01	0.02	0.18
Ephemera	0.10	0.00	0.00	0.04
Hemiptera	0.19	0.01	0.01	0.07
Hymenoptera	1.25	0.06	0.03	0.48
Lepidoptera	0.10	0.00	0.00	0.04
Megaloperta	1.83	0.09	0.09	0.71
Odontata	0.38	0.01	0.01	0.14
Orthoptera	1.06	0.03	0.06	0.41
Plecoptera	0.19	0.01	0.00	0.07
Trichoptera	0.29	0.04	0.01	0.12

Table 3-1 (continued)

Prey Category	All Rivers			
	%O	%N	%W	RI
Insects				
Unidentified insects	6.35	0.25	0.16	2.40
Millipedes				
Polydesmida	0.10	0.00	0.00	0.04
Mollusks				
Clams				
Corbicula fluminea	36.96	96.76	69.33	66.60
Mussels				
Elliptio downeii	0.10	<0.01	0.08	0.06
Elliptio sp.	2.02	0.24	0.10	0.83
Snails				
Unidentified snails	0.38	0.07	0.02	0.17
Vegetation				
Miscellaneous	23.68	1.47	20.78	15.60
Vertebrates				
Amphibia	0.10	0.00	0.00	0.04
Rodentia	0.29	0.01	0.07	0.13

Table 3-2. Frequency of occurrence (%O), proportion by number (%N), proportion by weight (%W), and relative importance (RI) of prey categories found in Blue Catfish diets collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia.

Prey Category	Altamaha River				Ocmulgee River			
	%O	%N	%W	RI	%O	%N	%W	RI
Crustaceans	0.34	0.80	0.02	0.13	3.39	0.03	0.06	1.33
Fishes	7.75	0.16	7.12	5.13	5.08	0.04	0.79	2.21
Insects	4.28	0.09	0.07	1.60	13.56	0.42	0.49	5.51
Mollusks	52.94	98.81	63.00	70.79	57.63	98.78	94.40	81.56
Vegetation	34.22	0.93	29.67	22.14	20.34	0.74	4.27	9.38

Table 3-2. (continued)

Prey Category	Oconee River				Satilla River			
	%O	%N	%W	RI	%O	%N	%W	RI
Crustaceans	1.83	0.09	0.67	0.86	28.08	3.94	5.91	13.23
Fishes	6.42	0.39	15.31	7.37	16.54	2.77	8.46	9.53
Insects	22.94	1.51	0.93	8.46	20.47	3.20	1.99	9.00
Mollusks	57.34	97.46	81.36	78.72	13.91	82.87	76.47	56.10
Vegetation	11.47	0.56	1.73	4.59	12.14	21.00	7.23	7.16

Table 3-3. Frequency of occurrence (%O), proportion by number (%N), proportion by weight (%W), and relative importance (RI) of prey categories found in Blue Catfish diets (by size class) collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia.

Prey Category	Altamaha River			Ocmulgee River		
	Juvenile	Subadult	Adult	Juvenile	Subadult	Adult
Crustaceans	-	0.47	0.41	-	1.20	4.48
Fishes	-	1.84	11.29	-	2.71	4.52
Insects	2.65	1.81	1.08	23.37	3.58	4.60
Mollusks	63.46	75.81	66.68	67.87	87.49	81.60
Vegetation	33.89	20.07	20.54	8.76	5.02	4.80

Table 3-3. (continued)

Prey Category	Oconee River			Satilla River		
	Juvenile	Subadult	Adult	Juvenile	Subadult	Adult
Crustaceans	-	1.10	4.86	23.42	17.84	4.91
Fishes	3.05	2.20	18.93	11.82	12.83	6.16
Insects	14.18	4.36	2.31	25.63	7.92	0.90
Mollusks	72.84	88.62	73.91	11.34	48.59	76.50
Vegetation	9.93	3.72	-	27.78	12.81	11.52

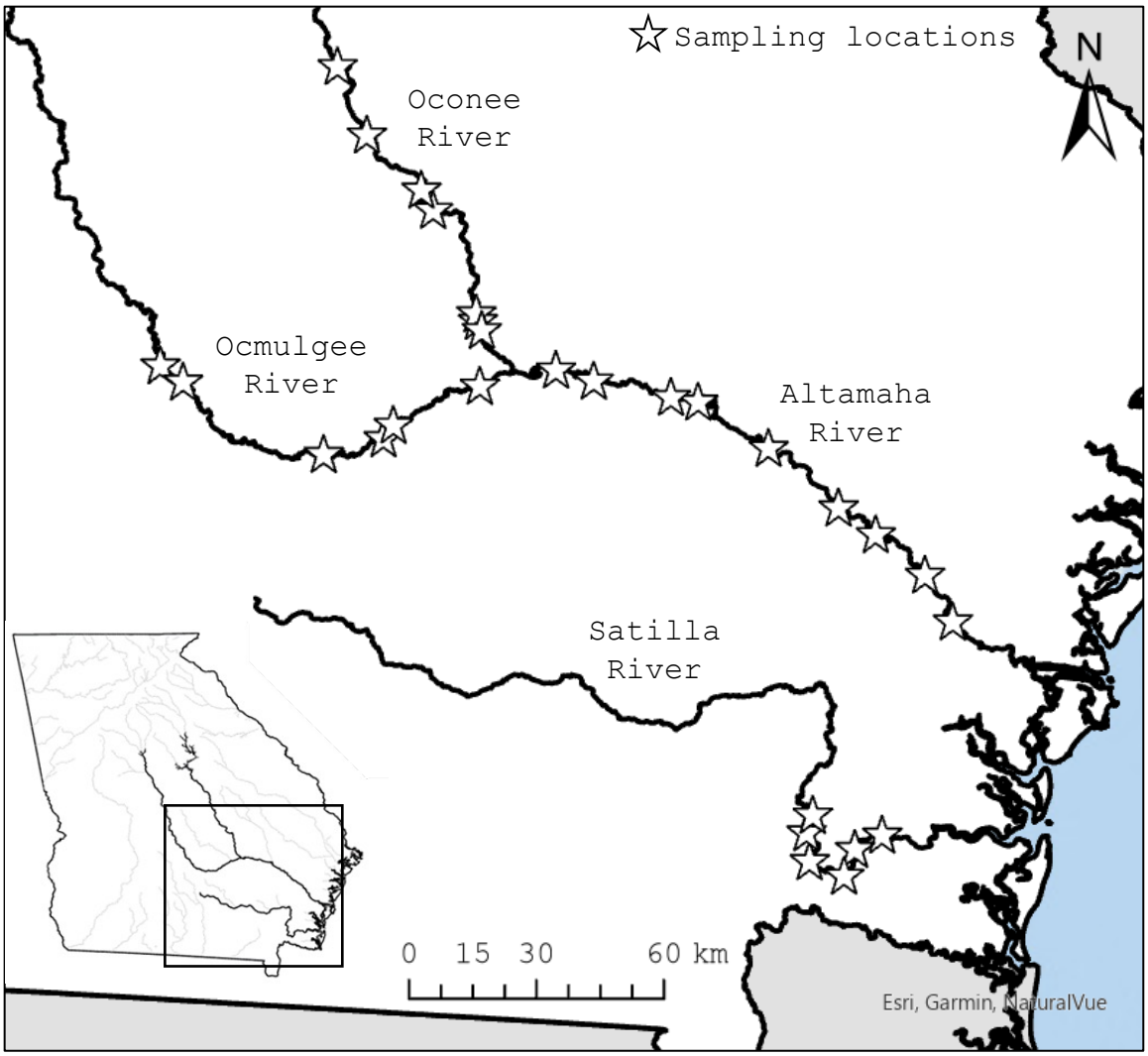

Figure 3-1. Blue Catfish (N=936) were collected at 28 sampling transects on the Altamaha, Ocmulgee, Oconee, and Satilla Rivers in Georgia. Stars indicate the middle of the 1 rkm long transects that were sampled between 2017 and 2021.

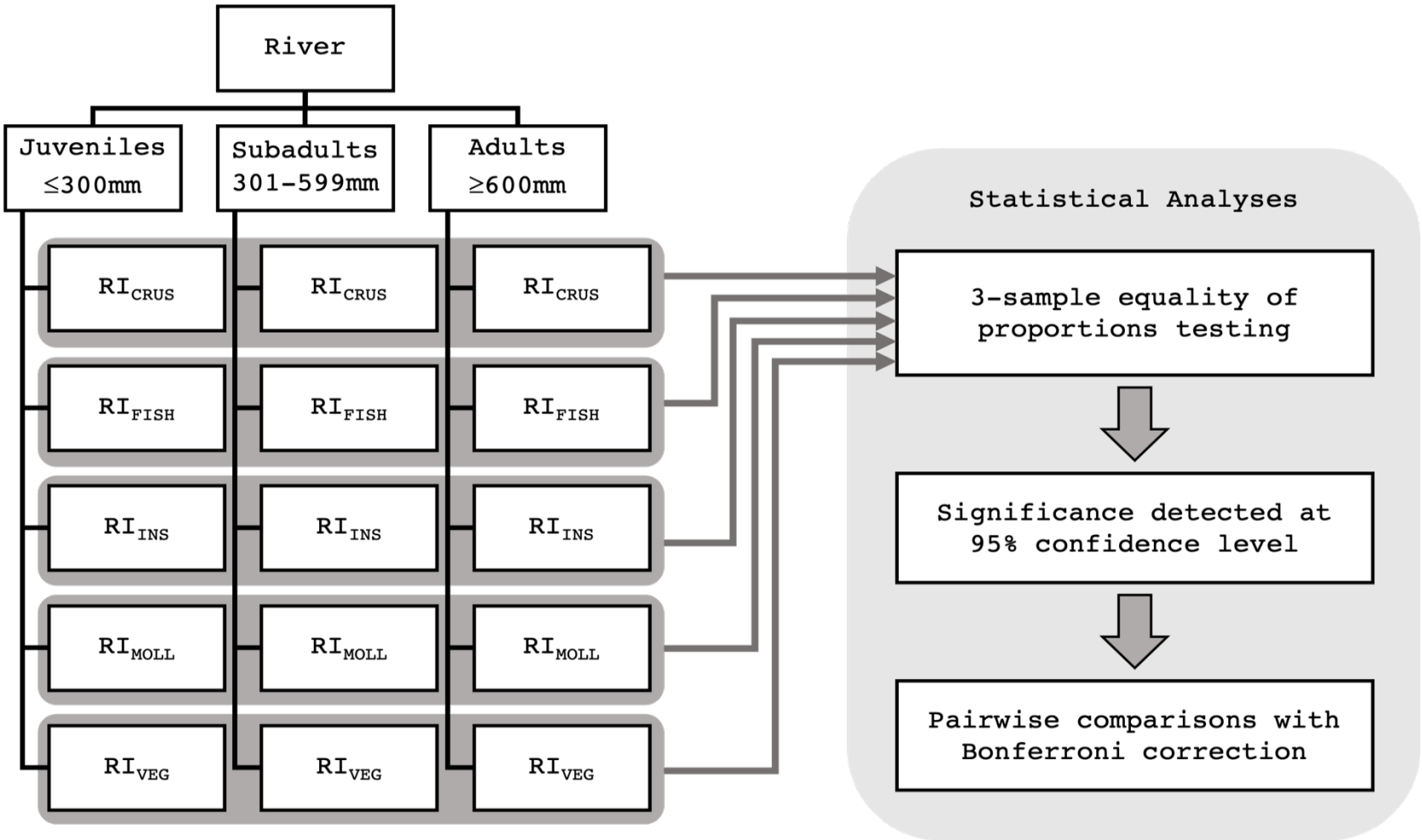

Figure 3-2. Flow chart of the process to determine ontogenetic dietary shifts. The process begins with separating diet data by river, then by size class, followed by the calculation of Relative Importance for each prey category (Eq 4; Left side of chart). The process ends with statistical analyses described in the light gray panel on the right side of the chart.

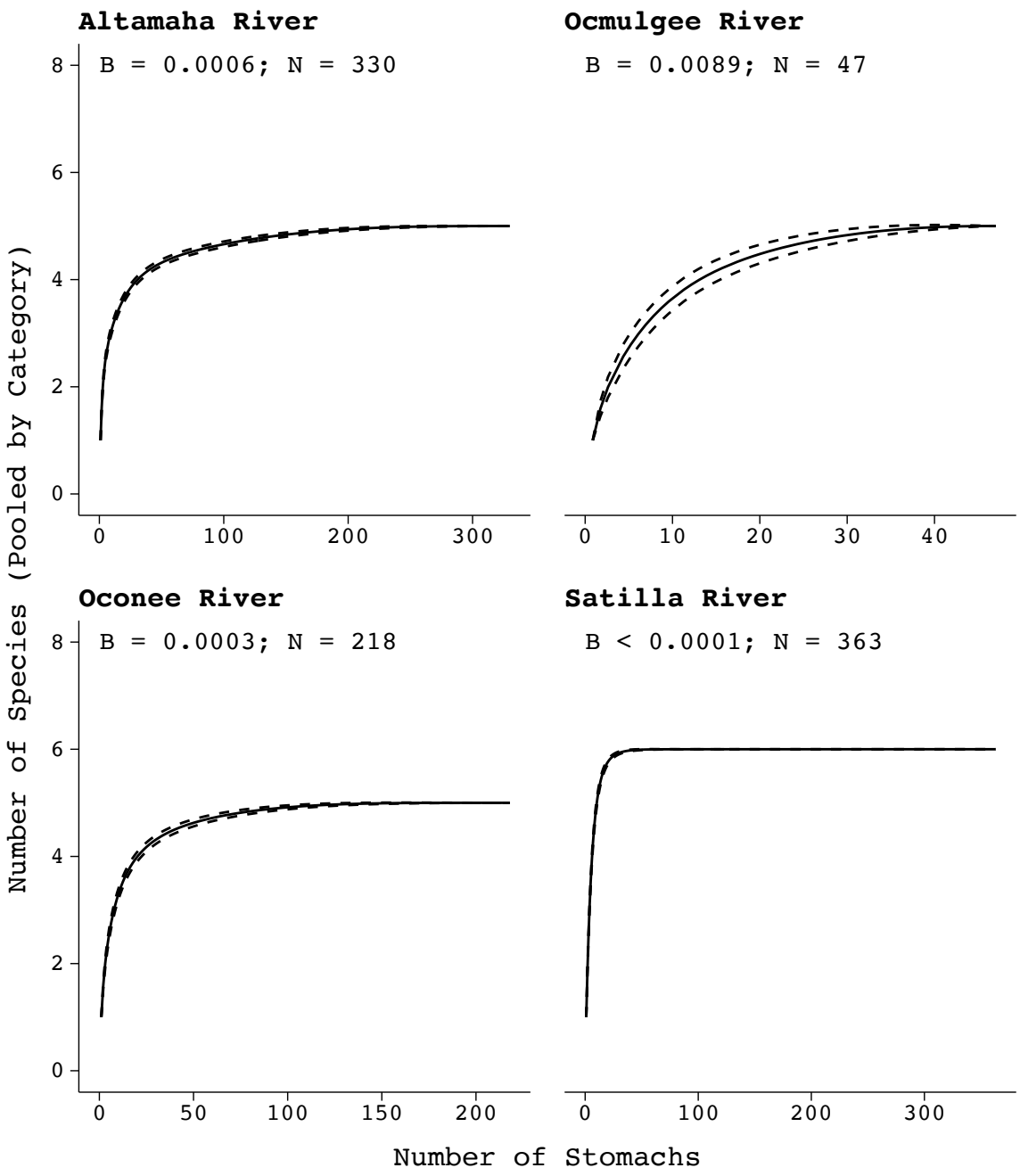

Figure 3-3. Prey accumulation curves (solid lines) with 95% confidence intervals (dashed lines) generated from stomach content data from Blue Catfish collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers. All prey accumulation curves reached asymptotes, indicating that the number of stomachs sampled was sufficient to describe diet (B < 0.05), where B represents the slope of the curve.

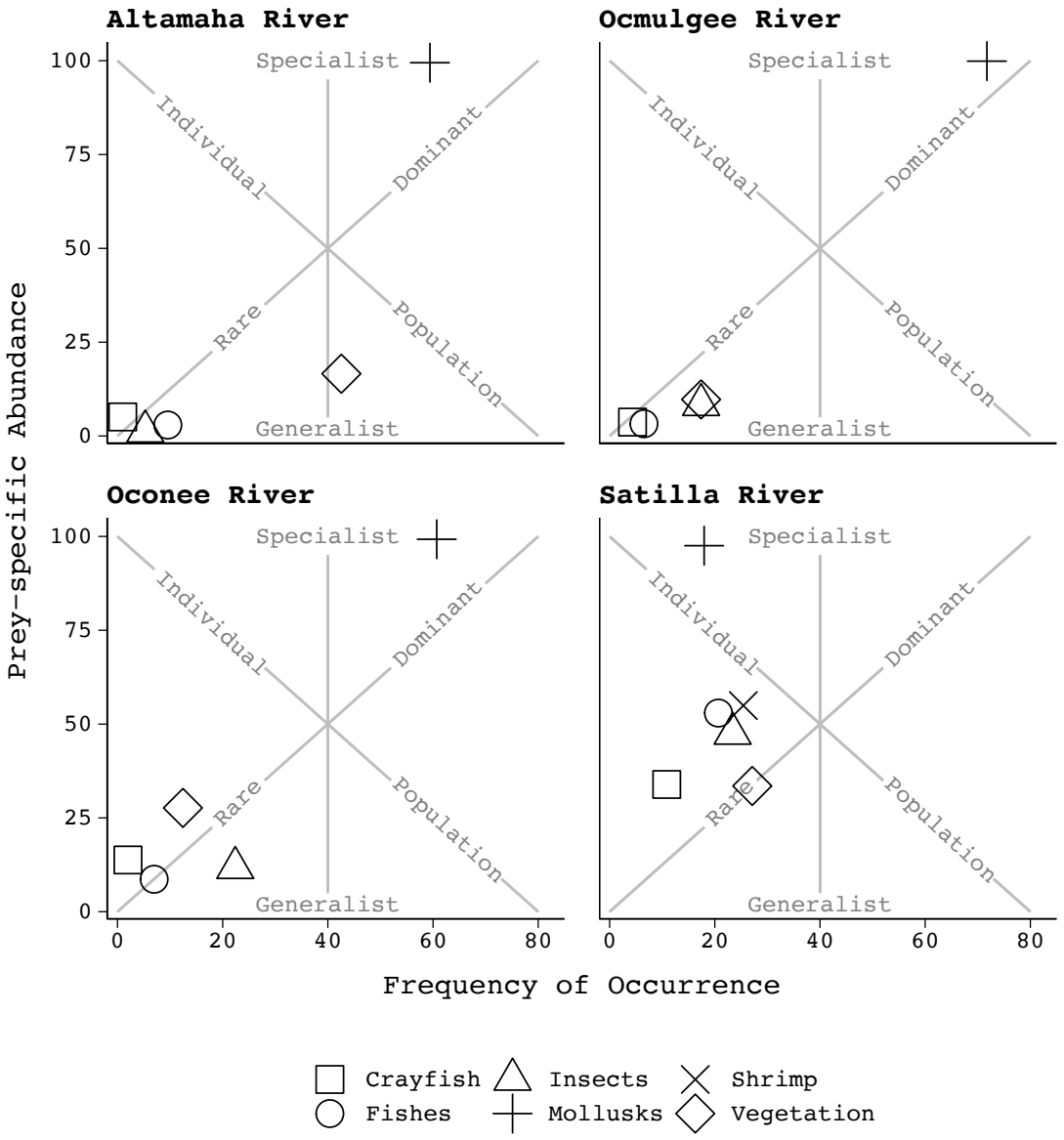

Figure 3-4. Predator feeding diagrams (Amundsen et al. 1996) for Blue Catfish collected from the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia. Prey-specific abundance is defined as the proportion by weight that prey *i* contributed to the total weight of prey in only predators that consumed prey *i* (Eq 6). The vertical line represents feeding strategy (specialist vs generalist), the negative vertical line represents niche variation (high among individuals vs high within population), and the positive vertical line represents prey importance (dominant vs rare).

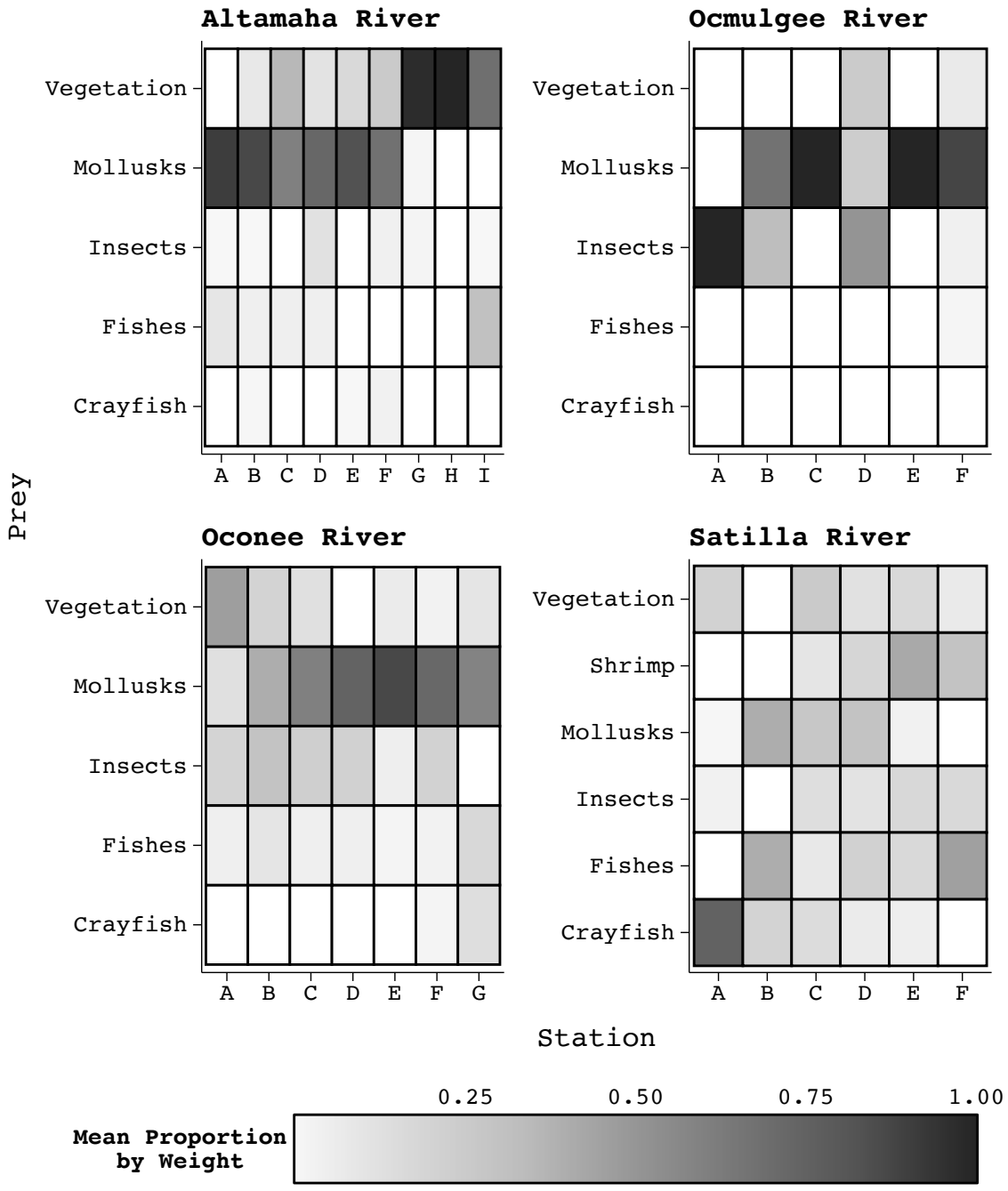

Figure 3-5. Diet variation of the major prey categories consumed by Blue Catfish represented by mean proportion by weight within each river system. Stations are lettered, where A is the uppermost site in each system.

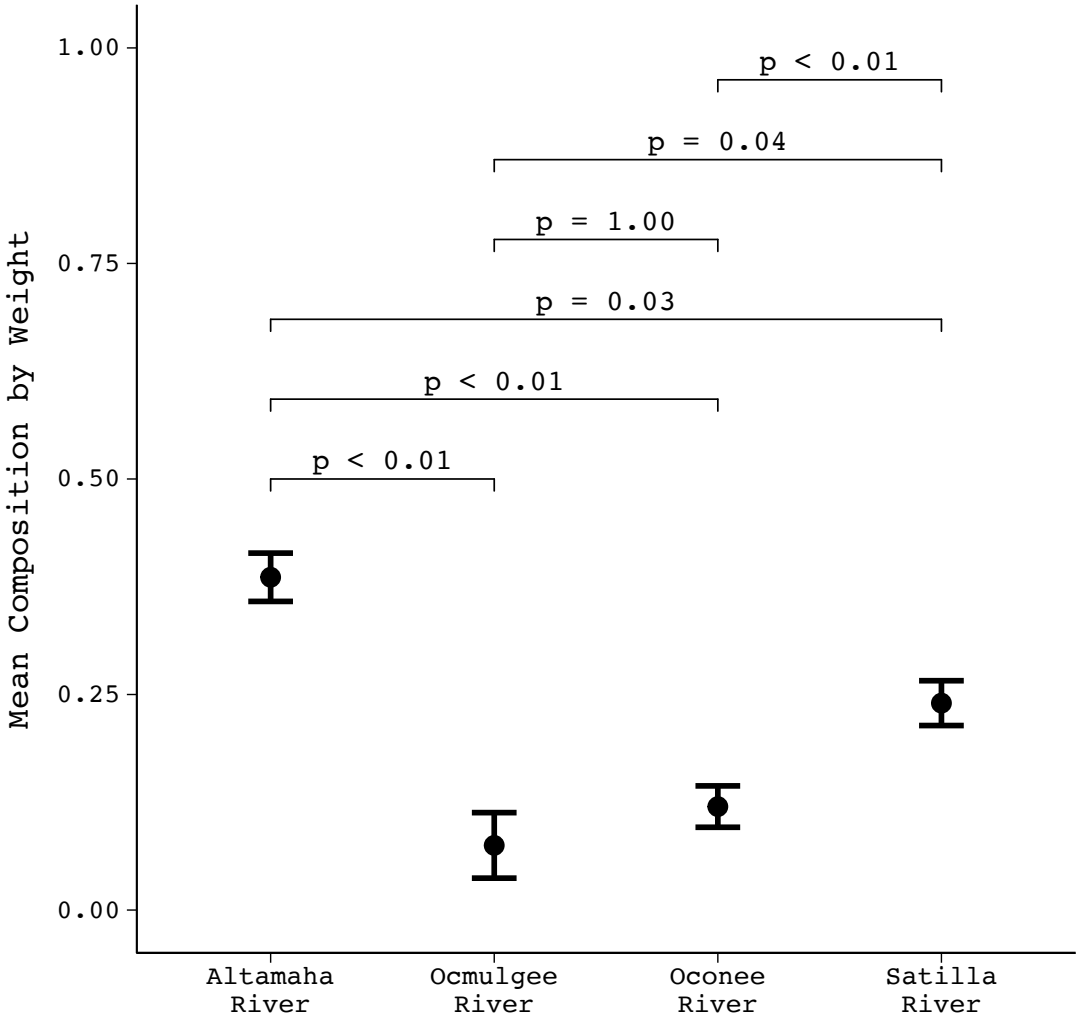

Figure 3-6. Mean composition by weight of the prey category "Vegetation" represented with standard error bars. P-values are shown as the result of the six pairwise comparisons using a Wilcoxon rank sum test.

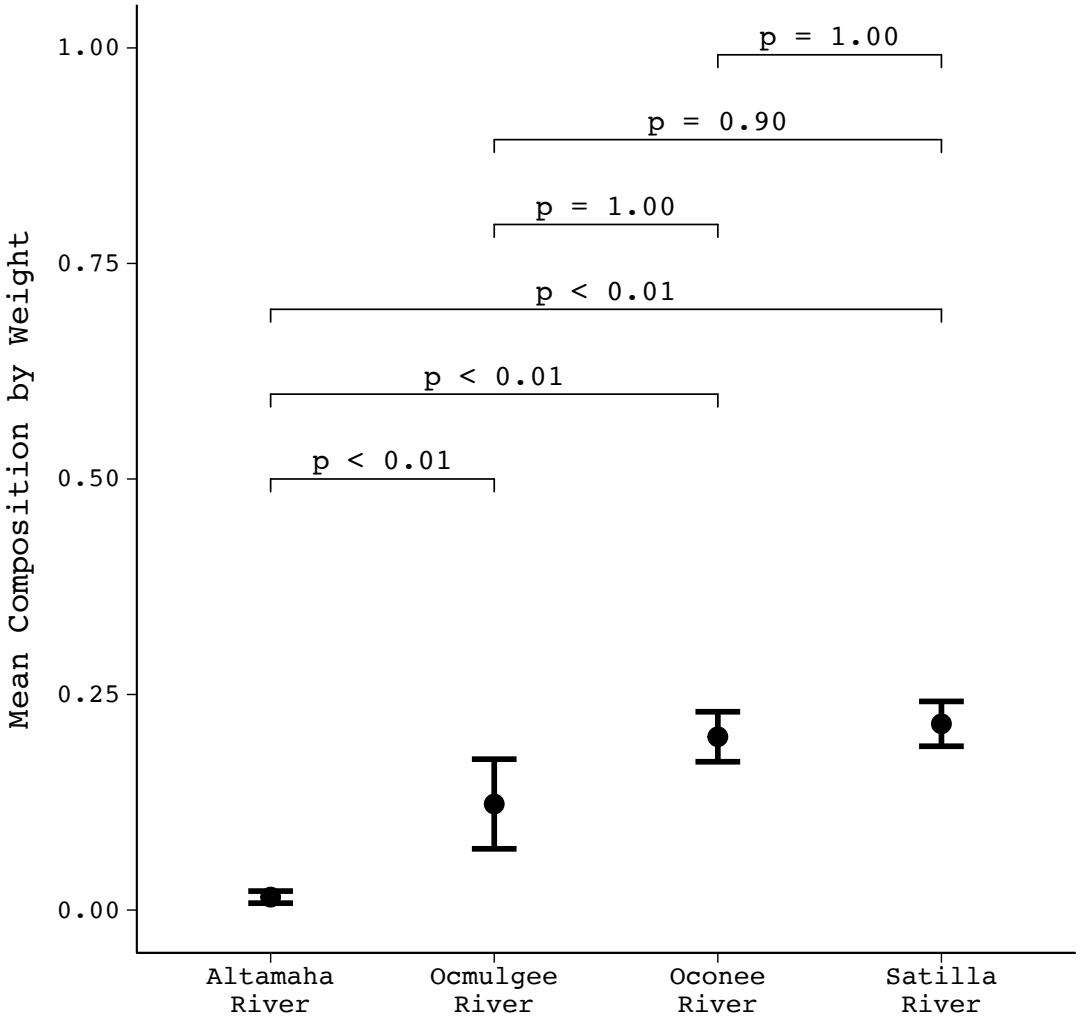

Figure 3-7. Mean composition by weight of the prey category "Insects" represented with standard error bars. P-values are shown as the result of the six pairwise comparisons using a Wilcoxon rank sum test.

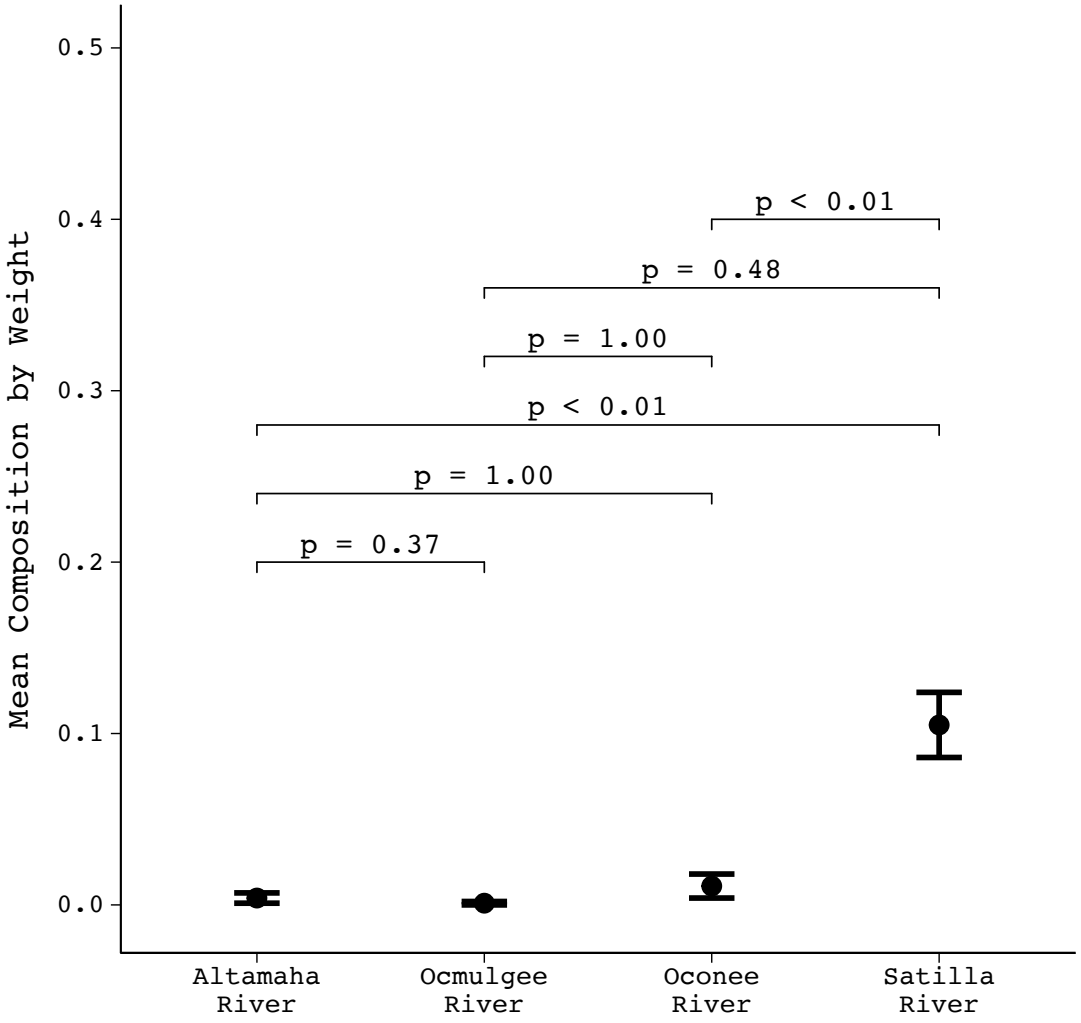

Figure 3-8. Mean composition by weight of the prey category "Crustaceans" (excluding shrimp) represented with standard error bars. P-values are shown as the result of the six pairwise comparisons using a Wilcoxon rank sum test.

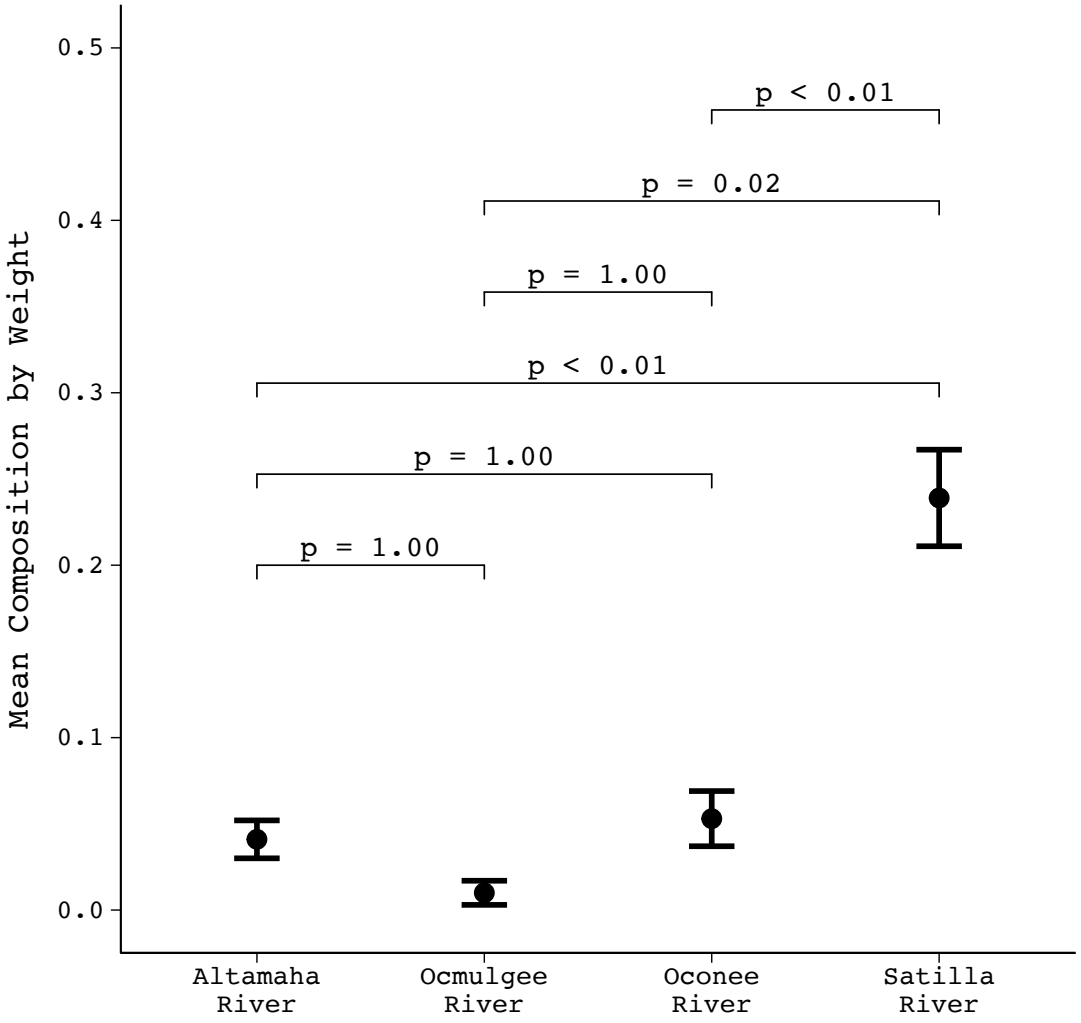

Figure 3-9. Mean composition by weight of the prey category "Fishes" represented with standard error bars. P-values are shown as the result of the six pairwise comparisons using a Wilcoxon rank sum test.

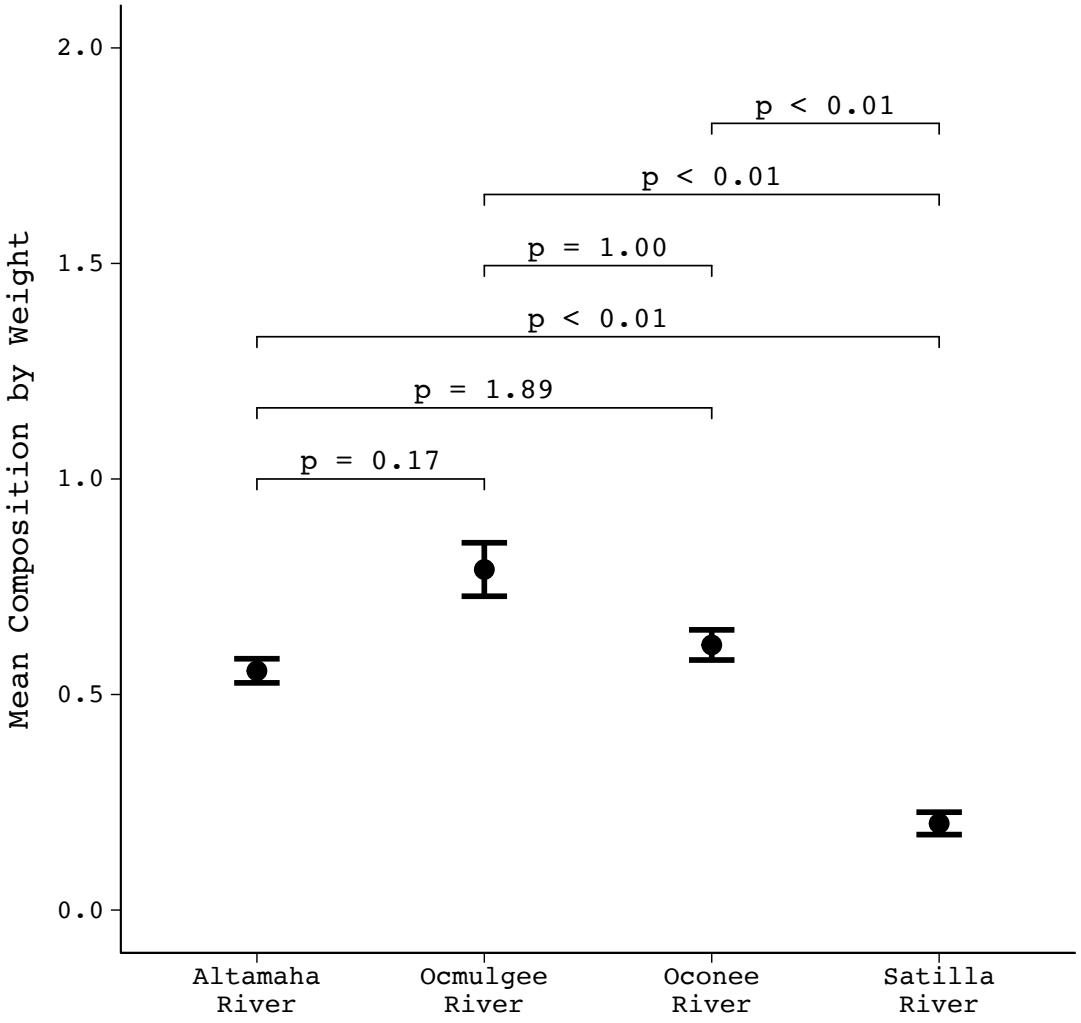

Figure 3-10. Mean composition by weight of the prey category "Mollusks" represented with standard error bars. P-values are shown as the result of six pairwise comparisons using a Wilcoxon rank sum test with Bonferroni adjusted p-values.

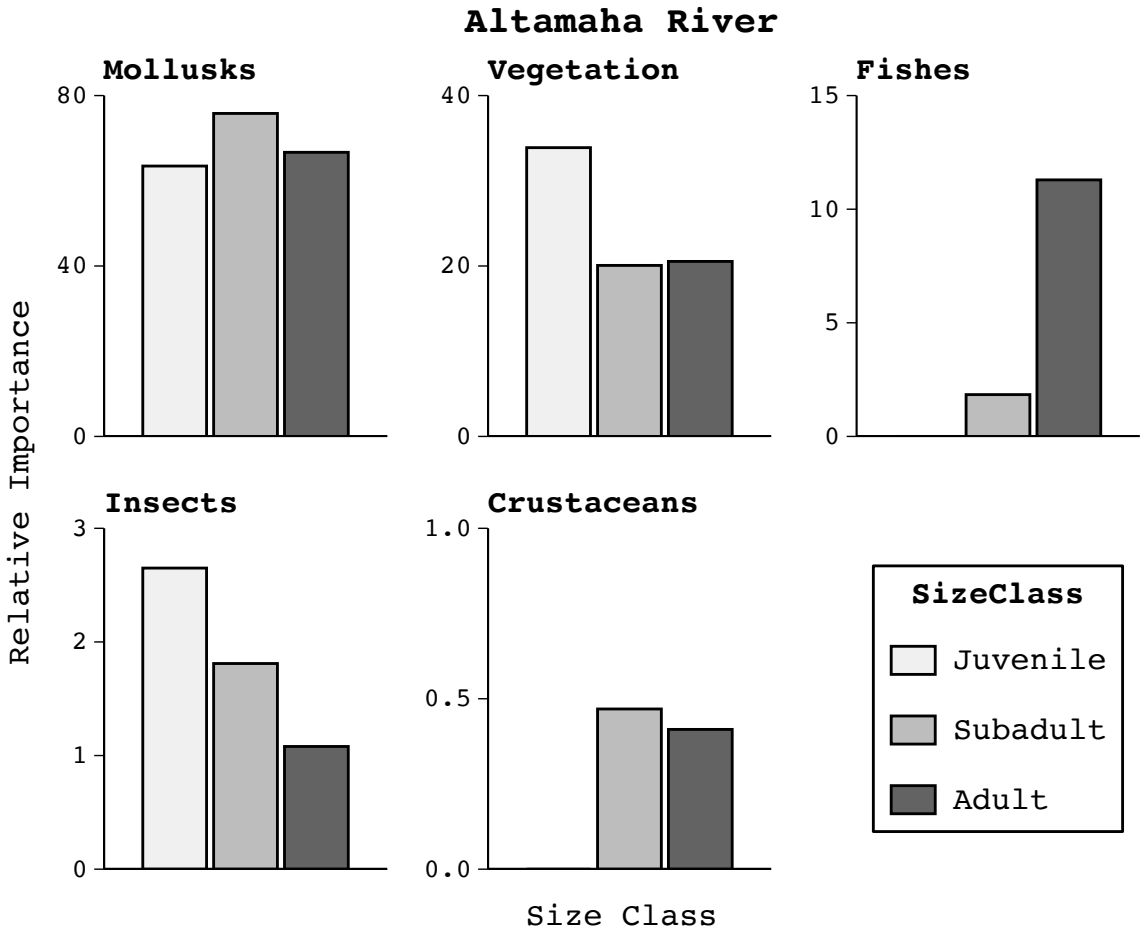

Figure 3-11. Relative importance of the five major prey categories (ranked from most important to least important from left to right) across three size classes of Blue Catfish collected from the Altamaha River in Georgia. Juveniles are individuals that are less than or equal to 300 mm total length, subadults are individuals that are 301-599 mm total length, and adults are individuals that are larger than 600 mm total length.

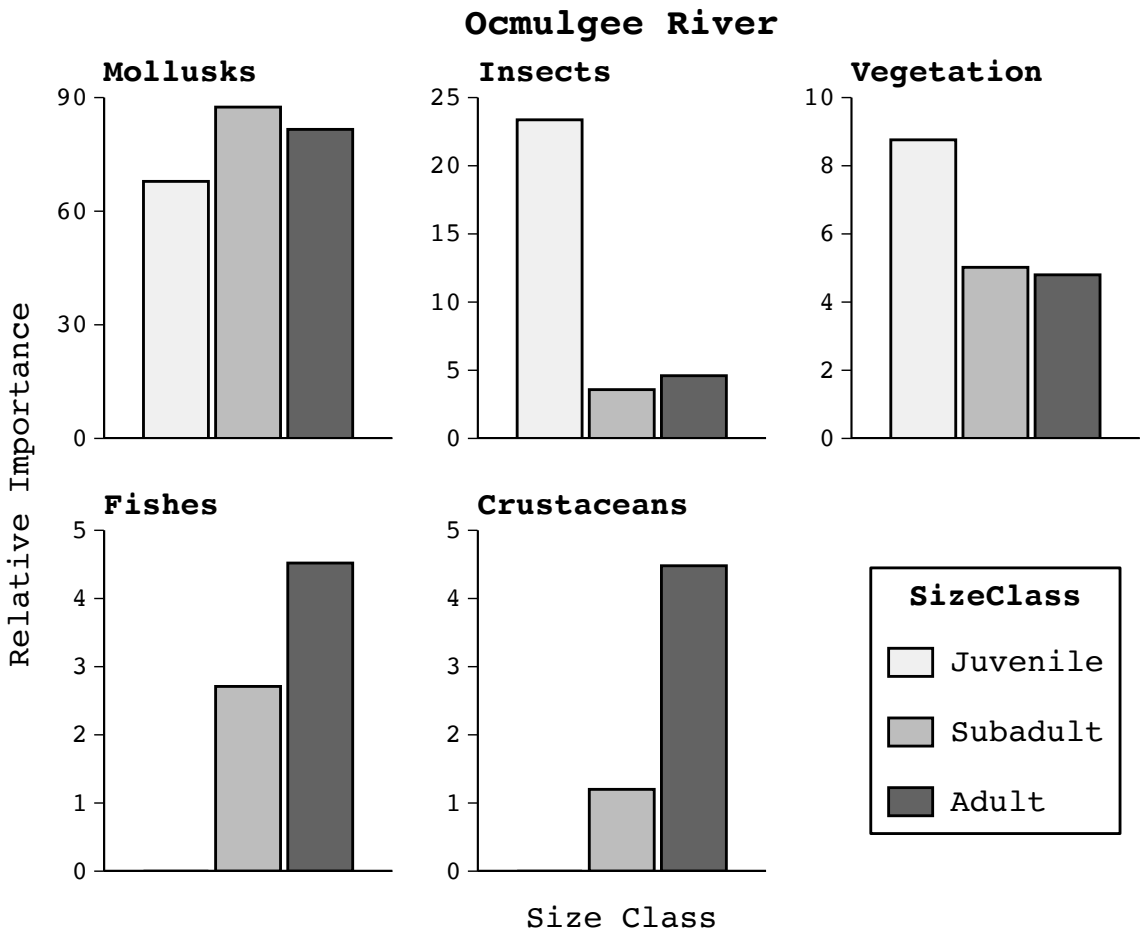

Figure 3-12. Relative importance of the five major prey categories (ranked from most important to least important from left to right) across three size classes of Blue Catfish collected from the Ocmulgee River in Georgia. Juveniles are individuals that are less than or equal to 300 mm total length, subadults are individuals that are 301-599 mm total length, and adults are individuals that are larger than 600 mm total length.

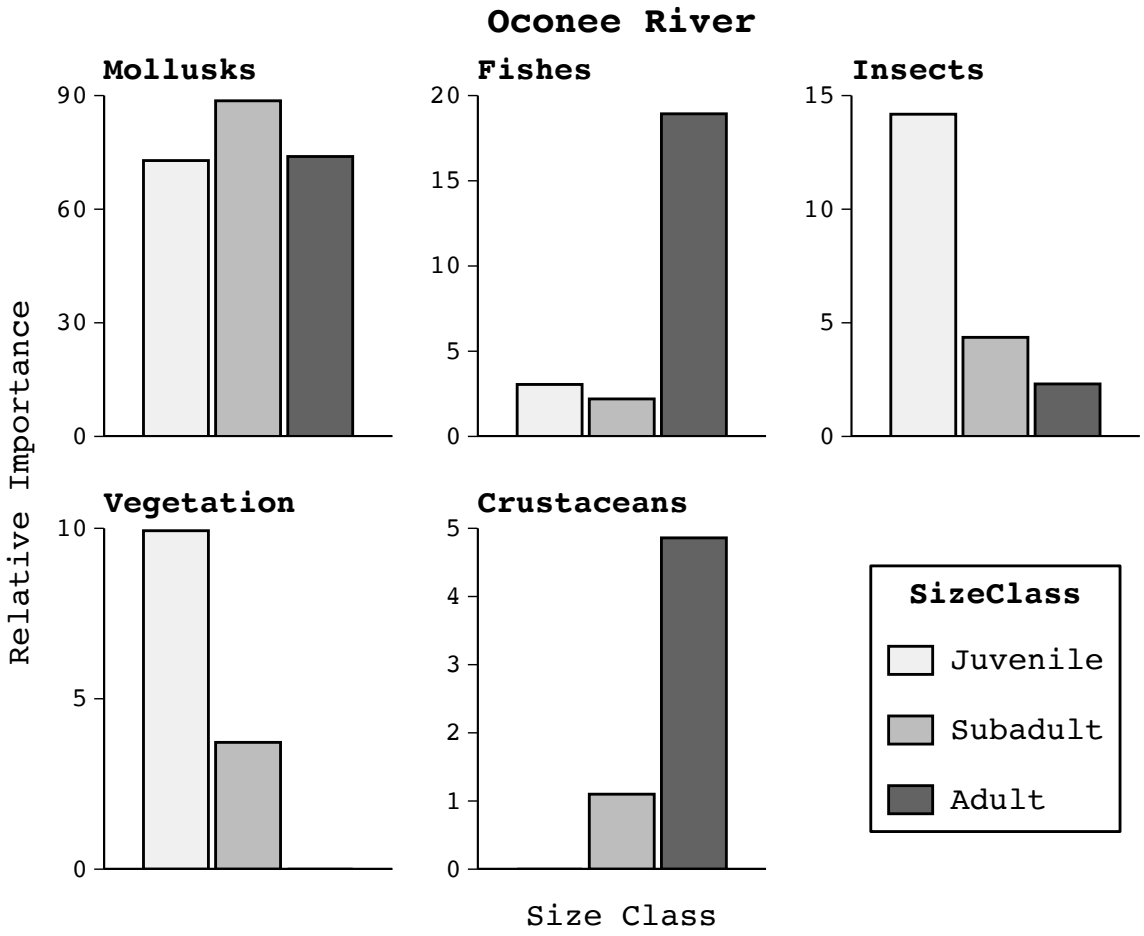

Figure 3-13. Relative importance of the five major prey categories (ranked from most important to least important from left to right) across three size classes of Blue Catfish collected from the Oconee River in Georgia. Juveniles are individuals that are less than or equal to 300 mm total length, subadults are individuals that are 301-599 mm total length, and adults are individuals that are larger than 600 mm total length.

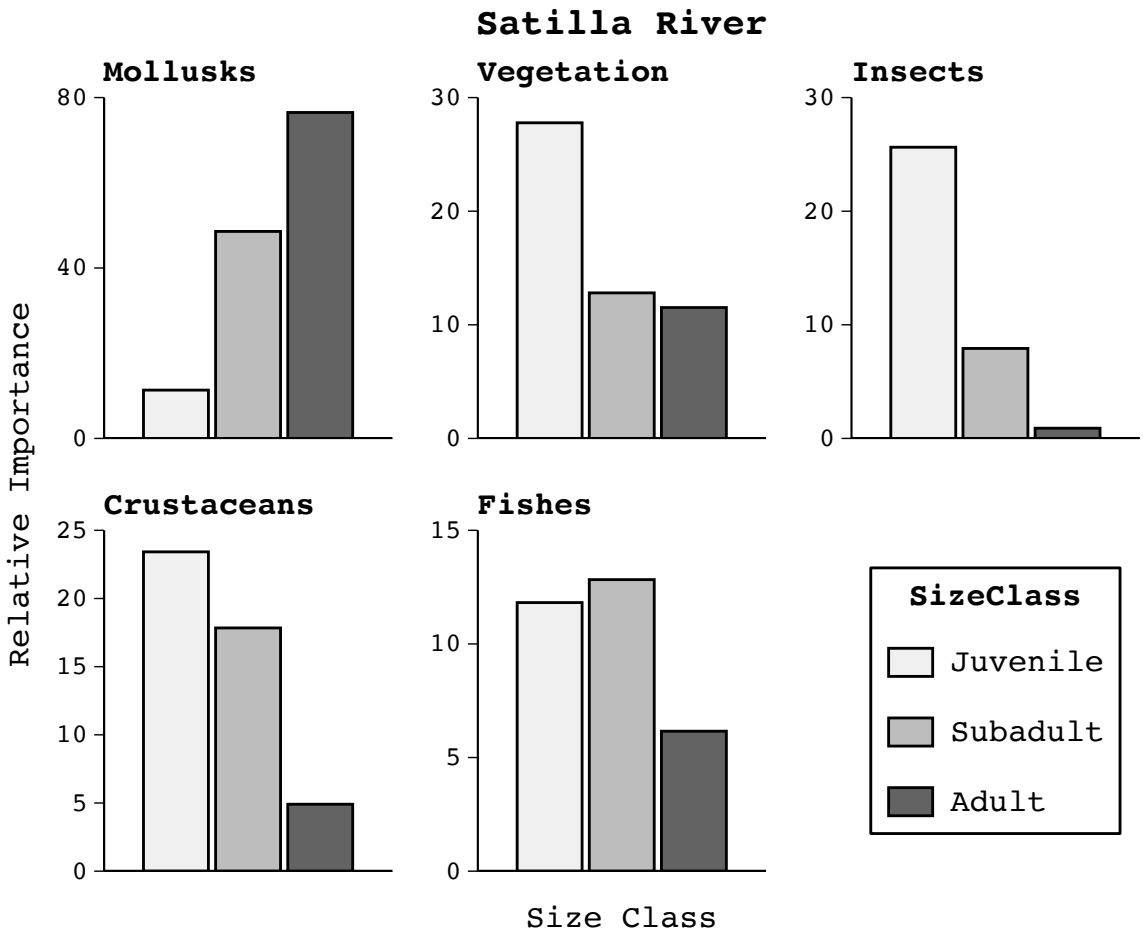

Figure 3-14. Relative importance of the five major prey categories (ranked from most important to least important from left to right) across three size classes of Blue Catfish collected from the Satilla River in Georgia. Juveniles are individuals that are less than or equal to 300 mm total length, subadults are individuals that are 301-599 mm total length, and adults are individuals that are larger than 600 mm total length.

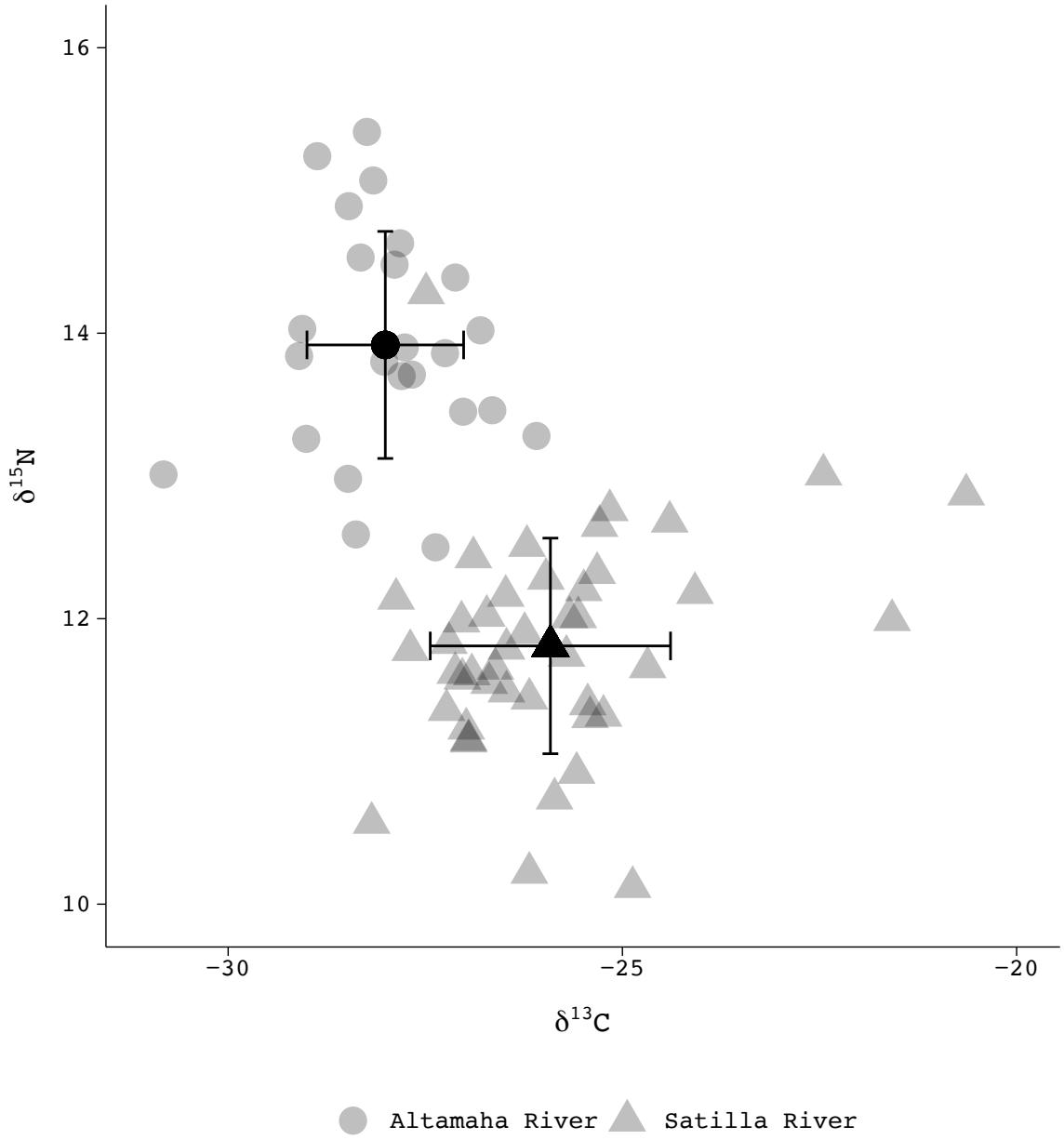

Figure 3-15. Stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ from subsamples (N = 75) of Blue Catfish tissue collected from the Altamaha (circles) and Satilla (triangles) rivers in Georgia. The bold shapes represent the mean SIR in each river with vertical and horizontal standard error bars.

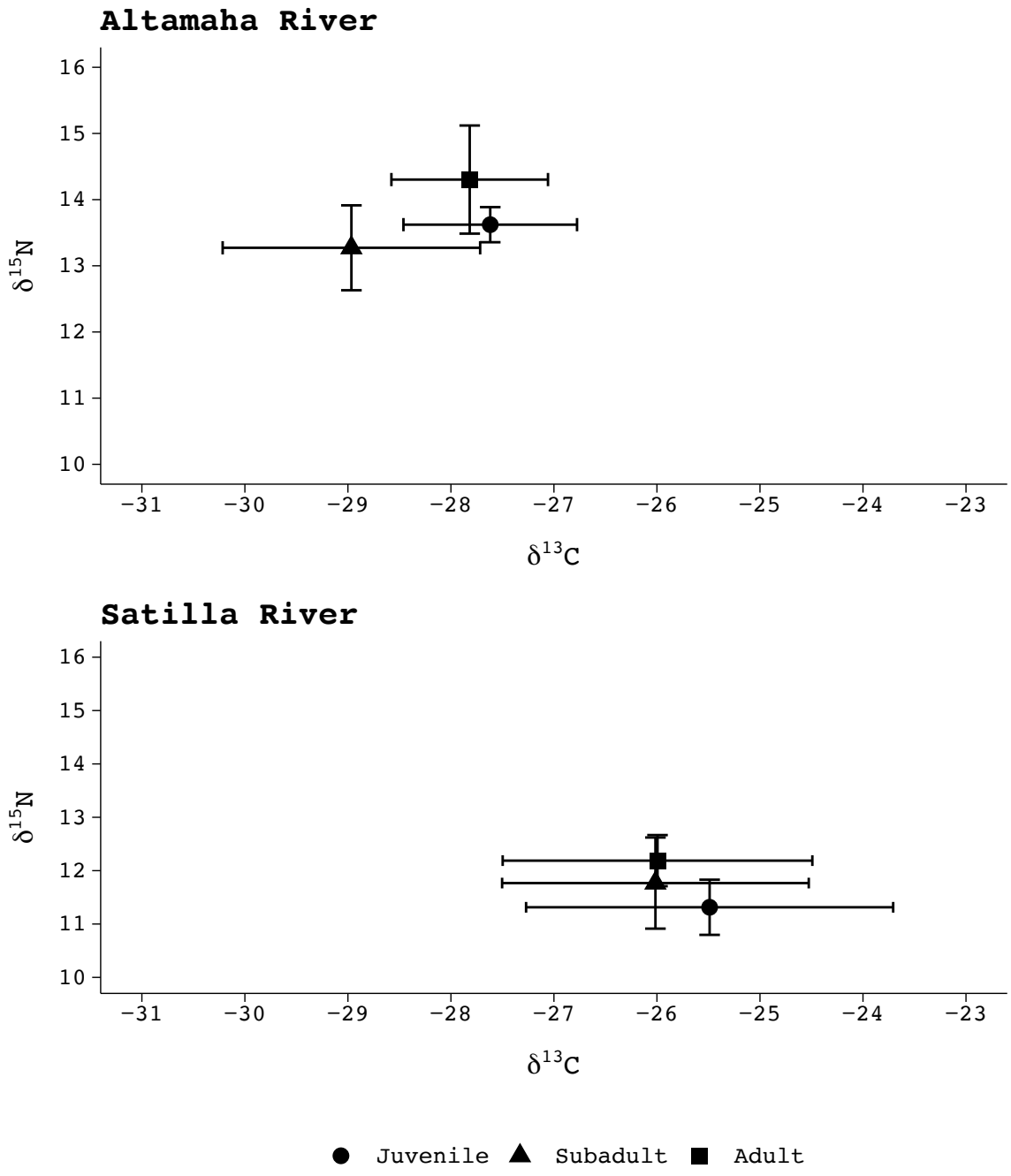

Figure 3-16. Mean stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ for juvenile, subadult, and adult Blue Catfish (N = 75) collected from the Altamaha and Satilla rivers in Georgia, represented with vertical and horizontal standard error bars.

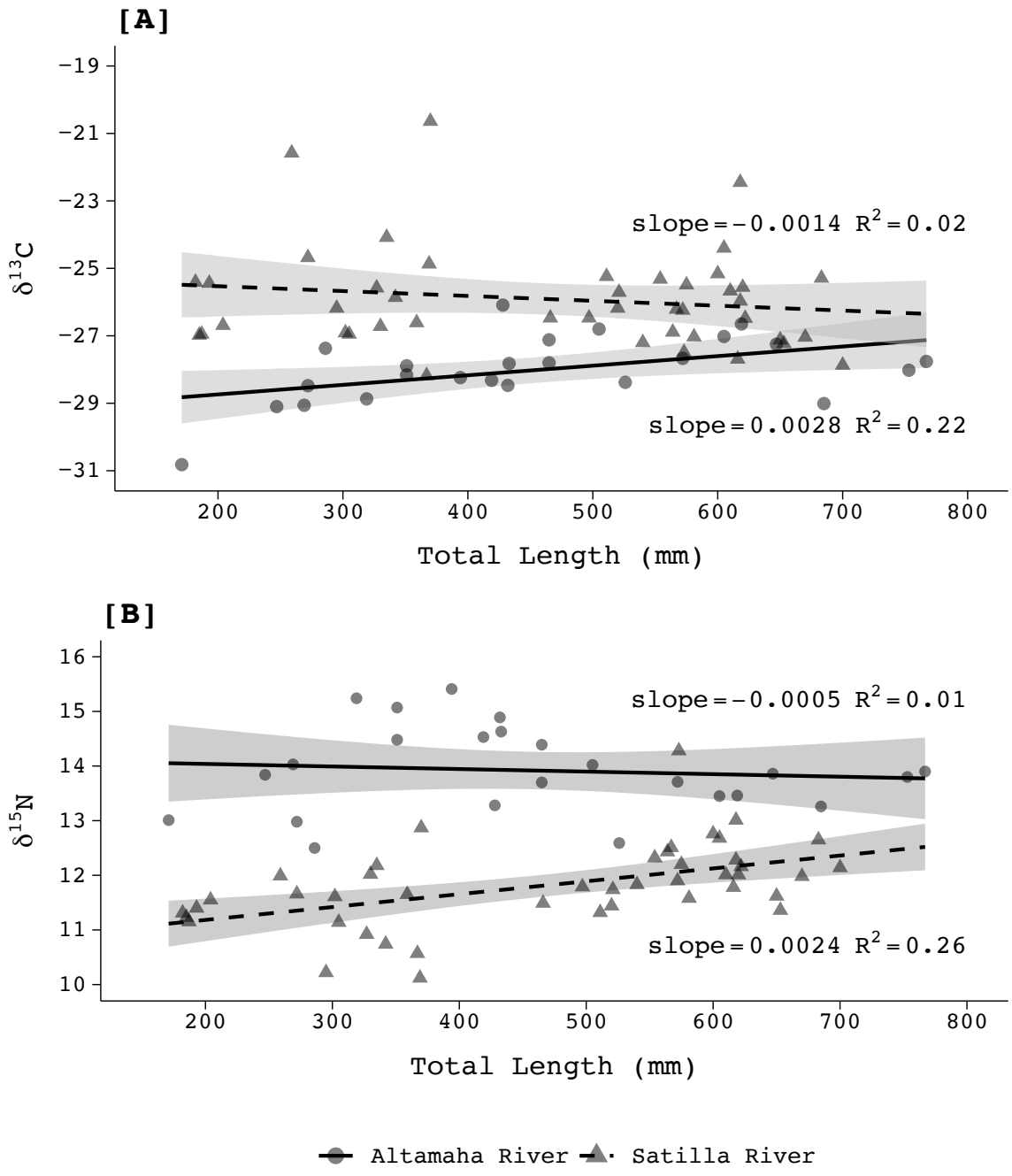

Figure 3-17. Relationship between $\delta^{13}C$ [A] and $\delta^{15}N$ [B] and total length (mm) of Blue Catfish (N = 75) collected from the Altamaha (circles; solid line) and Satilla (triangles; dashed line) rivers in Georgia, with 95% confidence interval bands. Slope and R^2 are included for each linear regression.

CHAPTER 4

CONCLUSIONS, FUTURE RESEARCH, AND MANAGEMENT IMPLICATIONS

CHAPTER 2 CONCLUSIONS

This study examined age, growth, and mortality characteristics of Blue Catfish populations with varying introduction timelines in the Altamaha, Ocmulgee, Oconee, and Satilla rivers in Georgia. We observed age structures that were representative of known introduction timelines, however large, older fish were captured less frequently. Growth characteristics were variable among rivers, with the Satilla River population exhibiting higher mean length-at-age and the highest average increase in total length per year. Additionally, the Satilla River population had the highest mortality rates among the rivers examined. Our findings suggest that Blue Catfish in the Satilla River, which is the most recently introduced population, are in the early stages of the invasion process and are likely undergoing life history shifts in response to many factors, including large annual culling events of both Flathead and Blue Catfish.

Blue Catfish in the Oconee River are the earliest introduced population examined in this study, with the

parental source originating from regular reservoir releases of Lake Oconee and Lake Sinclair (Homer and Jennings 2011). Blue Catfish are highly mobile and are believed to have migrated downstream into the Altamaha River before dispersing into the lower reaches of the Ocmulgee River at the confluence. It is unknown whether Blue Catfish establish residency and remain in a specific river for life, or if they migrate through connected river systems freely, depending on resource availability and habitat use requirements. Utilization of telemetry and otolith chemistry would be valuable in determining how Blue Catfish movement and dispersal occur throughout connected systems and would provide insight to how colonization may take place in novel environments.

This study is the first to report the population characteristics of Blue Catfish in the Ocmulgee, Oconee, and Satilla rivers, that provides a baseline for nonnative, riverine Blue Catfish research in the state. Additionally, this research adds to the current literature published about introduced Blue Catfish populations in the Altamaha River, where the population was examined in the early stages of invasion and had not yet reached an equilibrium state (Bonvechio et al 2011). Our results showed that Blue Catfish in the Altamaha River are self-sustaining, with older age

classes observed than the initial study and an observed reduction in annual mortality. Growth rates in the Altamaha River remained fast, and it is likely that equilibrium has not yet been reached. More information is necessary to evaluate the status of Blue Catfish in the Oconee and Ocmulgee rivers. Although growth in these systems were generally slower than the other rivers we examined, these populations exhibited growth that is faster than their native conspecifics.

Information about how introduced Blue Catfish populations function after acclimating to novel environments is limited. Although this study provides baseline diagnostics for introduced riverine populations of Blue Catfish in Georgia, more information is required to fully understand the broad array of factors that influence dynamic rate functions over spatiotemporal scales. Blue Catfish are exceptionally plastic and have the ability to adapt quickly to changes in their environment. Density-dependent factors can impact growth rates, shift life history traits, influence movement into new habitats, and guide population-wide and individual feeding strategies.

We recommend that future research should obtain abundance estimates for existing introduced populations, as it would be valuable in understanding the variation in growth

and mortality rates among these populations. Sexual dimorphism observed in Blue Catfish should be taken into consideration to identify sex-specific growth characteristics and how reproductive traits vary over time. The incorporation of environmental parameters into population modeling can help detect potential abiotic impacts on population characteristics. For instance, average air temperatures influence recruitment and year-class strength in Thunderbird Reservoir, Oklahoma (Griffin et al. 2021). Additionally, we suggest assessing the effectiveness of management practices through an evaluation of removal efforts, to lend a better understanding of how native and nonnative species respond to these efforts and whether the implementation of similar practices will be beneficial in other systems experiencing new invasions of nonnative species.

CHAPTER 3 CONCLUSIONS

Blue Catfish diets in the Altamaha, Ocmulgee, Oconee, and Satilla rivers correlated with current information known about Blue Catfish diets. Stomach content analysis described diet compositions that were high in the nonnative Asian Clam, and additional prey sources including insects, vegetation, crustaceans, and fish. This study documented the wide diet breadth of Blue Catfish, however feeding strategies differed among the rivers we examined. Density-dependent factors can

drive feeding strategies on both the population and individual levels. Individual Blue Catfish in the Satilla River demonstrated a specialized feeding strategy on mollusks, but overall had the broadest niche width compared to the other study rivers.

Habitat and river characteristics could explain variations in diet; for example, both the Altamaha and Satilla rivers flow into the Atlantic Ocean and contain many intercoastal waterways. Blue Catfish tolerance of high salinity (Nepal and Fabrizio 2019) may contribute to range expansion into estuarine habitat where a variety of marine prey sources are available. Colonization of these habitats will increase predation probability on anadromous species; however, the seasonality of sampling events should be well thought out and timed accordingly to determine the threat level on species of recreational or commercial importance and of conservation concern.

Few studies have investigated the bioenergetics of Blue Catfish. For example, Eggleton and Schramm (2004) determined that energetic benefits were highly variable between habitats of the Lower Mississippi River (i.e., floodplain lakes, secondary river channels, mainstem channel) and that periods of flooding and high-water levels influence the caloric densities of prey consumed. In Virginia's tidal rivers, daily

ration, maximum daily ration, and consumption per unit of biomass varied depending on temperature, prey type, fish size, and river system (Schmitt et al. 2021). Hilling et al. (2023) estimated the annual predatory impact of Blue Catfish by incorporating abundance estimates, diet information, and consumption rates, concluding that Blue Catfish consume over 100 metric tons of species of interest and 400.7 metric tons of Blue Crab in the James River. Prey caloric value coupled with consumption rates and population size would provide valuable information toward understanding energy transfer in these large river systems (Nisbet et al. 2012; van Poorten and Walters 2016).

GENERAL MANAGEMENT IMPLICATIONS

Identifying whether Blue Catfish are negatively impacting native species of interest and conservation concern is paramount to guiding management decisions of this nonnative species. Observed declines in native White Catfish have coincided with increased abundance of Blue Catfish (Schloesser et al. 2011; Jennings et al. 2018). There is evidence of Blue Catfish predation on at-risk sturgeon species in the Pamunkey River, VA (Evans et al. 2021). In Georgia, Atlantic and Shortnose Sturgeon are state and federally listed as endangered, that utilize the Altamaha and Satilla rivers for spawning and nursery habitat (Fox and

Peterson 2019). Sturgeon species have also been observed in the Ocmulgee and Oconee rivers (T. Bonvechio, personal communication), where potential spawning migrations may be occurring. The opportunistic feeding strategies demonstrated by Blue Catfish suggest that it is possible that Blue Catfish may increase predation pressure on sturgeon species as Blue Catfish expand into estuarine habitats.

The current management approaches towards Blue Catfish are minimal and the species is regarded as an aquatic nuisance species. No fishing regulations are in effect for this species; however, Channel and Flathead Catfish are considered game species with no daily bag limits. The state record for Blue Catfish is a 110 lb, 6 oz individual captured from the Chattahoochee River in October of 2020, by a Florida man during a fishing tournament. Noodling, bow fishing and spear fishing are all permissible fishing methods for this species. Creel surveys could provide invaluable information from the public to gauge angler attitude towards Blue Catfish and help inform fisheries managers on future management and regulations for the species.

We should expect continued invasion success and range expansion in Georgia waters over time. Blue Catfish presence occurs in 11 of 14 river basins in the state. Species eradication is likely unobtainable, and aggressive removal

efforts are not feasible on a large, multi-river scale due to high economic and laborious demands of such a program. We suggest that effort should be redirected in quantifying the threat level of Blue Catfish on native taxa, and targeted efforts be focused on specific habitats and watersheds to help alleviate predation pressure. An alternative approach is to manage Blue Catfish as a sportfish and implement fishing regulations, where slot limits could align with size-classes that are most likely to contribute to invasion success. For example, in populations that are exhibiting rapid growth and early maturation, maximum length limits could be implemented to specifically target young mature fish to achieve management goals.

We suggest that long-term monitoring continue, and management strategies be evaluated regularly. Specifically focusing on how introduction timelines contribute to differing population characteristics. It is likely that management should be implemented on a river by river basis, depending on the current status of the population (e.g., which phase of invasion the population is in).

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