LONGITUDINAL VARIATION IN COMMUNITY STRUCTURE OF FLOODPLAIN FISHES OF THE ALTAMAHA AND SAVANNAH RIVER SYSTEMS

by

Jeffrey A Garnett

(Under the direction of Darold Batzer)

ABSTRACT

Many studies have examined whether longitudinal variation exists in stream fish communities. Despite the acknowledged importance of adjacent floodplains, no study has investigated longitudinal variation in fish communities in floodplain wetlands. I conducted research to determine if distinct fish communities exist between upper and lower floodplains reaches. I predicted that upper reach floodplains, where flooding is brief and intense, would be dominated by opportunistic fishes. In contrast, lower reach floodplains, which experience longer and more predictable flooding, would primarily consist of fishes specifically adapted to live and breed on the floodplain. To test this hypothesis, I examined fish populations along a gradient of discharge at floodplain sites along the lengths of the Oconee/Altamaha and Broad/Savannah river systems in eastern Georgia. Two unique communities were discovered related to stream reach, yet community utilization of reach-specific floodplains remains unclear. The results of this study should aid in wetland conservation and restoration projects.

INDEX WORDS: Community Structure, Fish, Floodplain, Longitudinal, Reach, River

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B.S., University of Georgia, 2003

A Thesis Submitted to the Graduate Faculty of the University of Georgia in Partial Fulfillment of the Requirements of the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2011

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May 2011

DEDICATION

I dedicate this work to my late and very good friend, Eli. He accompanied me for many long walks in the woods and taught me to live more in the moment. He also loved rolling around in dead fish.

ACKNOWLEDGMENTS

I could probably fill another forty pages with all of the many people who deserve thanks. In an effort to keep it brief, however, I'd like to thank my advisor, Darold Batzer, for his thoughtful guidance, willingness to help, and open-door policy. My committee has been invaluable, as well. Mary Freeman deserves many thanks for her patience as I darkened her doorway often with questions. She has also taught me much about stream ecosystems and fishes over the years. Amanda Wrona-Meadows provided a unique, on-the-ground perspective and many insightful comments, and I appreciate her constant enthusiasm and devotion to the health of Georgia's floodplains and wildlife. In addition to all the mosquitoes, alligators, and snapping turtles joining me out on the floodplains, I could not have completed any of this work without stellar field help. Sarah "Bowfin Wrangler" Beganyi, Eric "Boatermen" Bright, and Mark "Northern Aggressor" Galatowitsch were all excellent with a dip-net and not half-bad field companions either. Subomi Adeyemo, Brant Batzer, and Ross Batzer also pitched in on a couple occasions to help with sampling: thank you. I'm grateful to Rachel Katz and Brett Albanese for help with some statistical analyses. I'd also like to express my appreciation to The Nature Conservancy and the USGS Georgia Water Resources Institute, whose generous support helped to fund this research. The landowners who allowed me access to floodplain sites on their property deserve considerable thanks. I also must thank my parents for always being a good ear and an endless well of sage advice. Finally, I especially want to thank my wonderful wife, Maria, for being right beside me the whole way through the process: I could not have kept my sanity without the calming presence that you, Eli, and Jada provided for me! Thank you.

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CHAPTER ONE

INTRODUCTION

In the last few decades, several paradigms have been constructed in an attempt to explain shifts in biotic communities across river systems. The River Continuum Concept (Vannote et al. 1980) described the evolution of biotic communities longitudinally (with emphasis on macroinvertebrates). However, the River Continuum Concept was limited to in-channel variation and did not take adjacent floodplain habitats into consideration. The Flood Pulse Concept, as described by Junk et al. (1989), expressed the importance of these floodplain habitats and postulated how biotic assemblages may change laterally from the river channel out across a floodplain. Despite the inclusion of seasonally flooded habitats along a river channel, though, the Flood Pulse Concept did not explicitly address longitudinal variation in floodplains. Ward (1989) was one of the few who combined the ideas presented by both the River Continuum Concept and the Flood Pulse Concept. He took a four-dimensional approach when contemplating shifts in riverine biotic communities, looking at longitudinal, lateral, vertical (hyporheic), and temporal influences on variation. Ward (1989) stressed the importance of integrating the dimensions that make up riverine ecosystems, but his analysis was primarily in-channel focused and unspecific in regards to how lateral movement of water into a floodplain influences biotic assemblages on a longitudinal gradient of floodplains.

Regional topography and hydrology can affect longitudinal flood pulse patterns (Ward et al. 2002, Junk and Wantzen 2006). Higher gradients and natural levees in the upper reaches of river systems can restrict flooding so that it is brief and infrequent. In a river’s lower reaches, however, floodplain hydroperiod can be long in duration due to a generally flatter topography. This difference in flood pulse dynamics among reaches may cause biotic shifts to occur longitudinally within floodplains. Reese and Batzer (2007) examined the longitudinal change of invertebrate communities within the Altamaha River system and found three distinct assemblages characterizing floodplains of the upper, middle, and lower reaches. In a similar fashion, Lee (2008) documented variation of floodplain plant communities along the length of both the Altamaha and Savannah River systems. In both catchments, she found a higher percentage of upland vegetation in upper reach floodplains, while obligate wetland vegetation was much more common in the lower reaches (Lee 2008). It is likely that other groups of organisms could show similar patterns of change.

Utilization of riverine floodplains by fishes has long been studied. Fishes have been observed using floodplains for brood rearing, predator avoidance, and exploiting allochthonous food resources otherwise unattainable in the river channel (Paller 1987, Lambou 1990, Hoover and Killgore 1998). In the wake of the River Continuum Concept (Vannote et al. 1980), several studies have observed longitudinal community shifts in fish populations within the stream channel (Edds 1993, Esselman et al. 2006, McGarvey and Ward 2008). A number of studies have likewise looked into lateral variation of fish communities (Fernandes et al. 2010, Bright et al. 2010) and compared floodplain fish community structure with that of the adjacent stream community (Lyons 2005, Sullivan and Watzin 2009, Baumgartner et al. 2010). Little research, however, has been conducted examining how fish communities within floodplain habitats may change along length of a river system.

Understanding how fish and other biotic communities change within floodplains along the length of a river system is of importance in terms of conservation (McGarvey and Ward

2008), specifically wetland mitigation and restoration. Knowledge of distinct, reach-specific communities allow for the design of management strategies that take into account and protect all native biota.

Using Reese and Batzer (2007) and Lee (2008) as models, I investigated the variation that might exist longitudinally within fish communities of riverine floodplain wetlands. I hypothesized that fish communities would be distinctly different within upper reach and lower reach floodplains. I predicted that lower reach floodplains would contain more wetland obligate species of fishes that rely on the floodplains and the long duration of flooding to carrying out life processes; fishes in upper reach floodplains were expected to primarily be opportunistic and consist of species that are known otherwise not to depend on flooding for survival.

CHAPTER 2

METHODS

Study Sites

I chose the Altamaha and Savannah River systems to assess variation of fish communities along a longitudinal gradient of flood habitat (Figure 1). Primary tributaries of the Altamaha River are the Ocmulgee and Oconee Rivers. The Savannah River is primarily formed from the Seneca and Tugaloo Rivers. The headwaters of both systems drain the Piedmont physiographic region of northeast Georgia and northwest South Carolina and continue flowing through the Atlantic Coastal Plain in southeast Georgia. The mouths of the two rivers are only approximately 100km apart when they empty into the Atlantic Ocean.

My study aimed to compare fish communities within upper reach floodplains of these watersheds with those of lower reach floodplains. Thus, I divided the two catchments into two longitudinal regions. In this study, upper reach floodplains were located in the Piedmont, and consisted of sites along the Oconee River and tributaries (Altamaha basin) and Broad River and tributaries (Savannah basin). Lower reach floodplains were situated on the Coastal Plain itself and were along the main stem of each river.

Despite draining into different downstream rivers, the Oconee and Broad Rivers are adjacent to each other in northeast Georgia. Not only do they drain similar landscapes, but their watersheds are of similar size. The upper Oconee River drains 2,435km^2, while the Broad River drains a slightly larger 3,704km^2 (Gotvald et al. 2005). Annual mean discharge near the most downstream Oconee floodplain site is 34.94m^3/s; annual mean discharge near the most downstream Broad floodplain site is 50.01m^3/s (Gotvald et al. 2005).

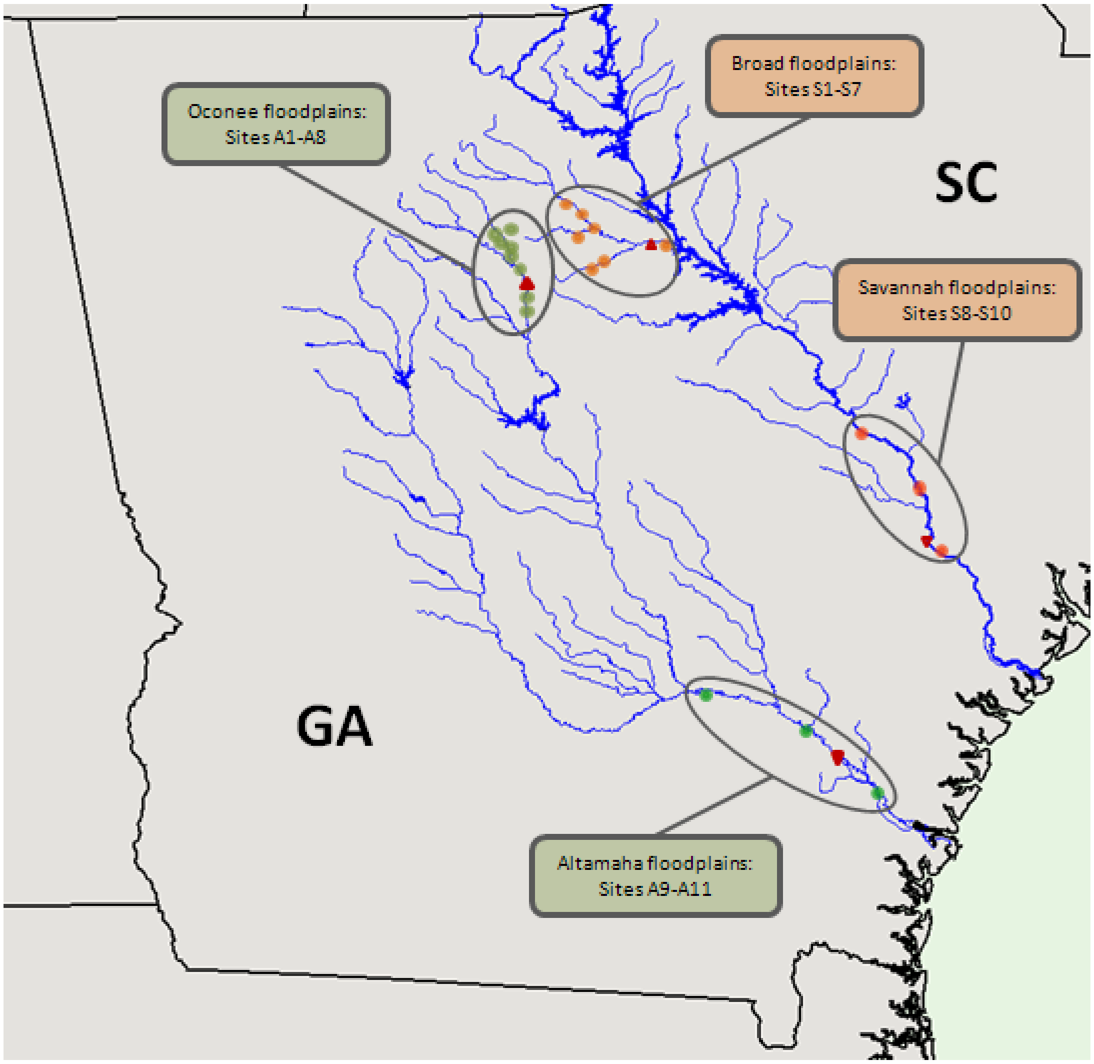

Figure 1. Map of the Altamaha and Savannah River systems showing upper reach and lower reach floodplain sampling sites. Red triangles indicate USGS stream gages at Penfield, GA (Oconee), Bell, GA (Broad), Doctortown, GA (Altamaha), and Clyo, GA (Savannah).

Much like the upper Oconee and Broad River watersheds, the Altamaha and Savannah River systems are useful for comparative study because they are of similar size and contain similar habitats. The Savannah River drains an area of roughly 25,511km^2, while the Altamaha River drains a slightly larger 35,224km^2 of land (Gotvald et al. 2005). Land use distribution of the drainages is similar: 3.30 vs. 5.42% urban, 26.40 vs. 25.02% agricultural, and 64.20 vs. 52.28% forested for the Altamaha and Savannah watersheds, respectively (Wiegner et al. 2006). Mean annual discharge of the Altamaha River is 382.84m^3/s; mean annual discharge for the Savannah River is 331.02m^3/s (Gotvald et al. 2005).

In both the Altamaha and Savannah River catchment I selected a series of floodplain sites along a gradient of discharge and numbered them consecutively in order of ascending river discharge, with site 1 having the lowest value. All sites were selected in locations where the forest was in good condition (intact and minimally disturbed), and where permission for access was granted (when possible lands protected as wildlife areas were selected, but many upper reach sites were on private property). Sites were located off of the main channel in low-lying areas behind natural levees where water would naturally flow through and collect during and after high-flow events. The last sites selected along the Altamaha and Savannah Rivers themselves were both immediately above the upper range of tidal influence.

Within the Altamaha catchment, the upper reach contained eight floodplain sites: one situated along Sandy Creek (site A1) and seven along the Oconee River (sites A2-A8), all located north of Lake Oconee in the vicinity of Athens, GA. Three floodplain sites along the Altamaha River (sites A9-A11), each in or near Bullard Creek Wildlife Management Area (WMA), Big Hammock WMA, and Sansavilla WMA, were selected as lower reach sites.

The Savannah catchment consisted of seven upper reach floodplains just east of Athens, GA along Long Creek (sites S1-S2) and the Broad River (sites S3-S7). Three floodplain sites (sites S8-S10) located in WMAs along the Savannah River (Yuchi WMA and Tuckahoe WMA in Georgia, and Webb WMA in South Carolina) comprised the lower reach sampling locations of that system.

Sites along upper reach tributaries were typical of Piedmont floodplains being generally narrow in width (approx. 50-250m) and having a relatively steep slope (Sharitz and Pennings 2006). Characteristic of higher elevation streams and associated floodplains, inundation was usually brief, yet with high amplitude (Bedinger 1981), producing "flashy" hydrographs (Figure 2 – OCO and BRO hydrographs). Canopy vegetation in these upper watershed floodplains was primarily dominated by maples (*Acer* spp.) and green ash (*Fraxinus pennsylvanica)*, while the understory was heavily populated with American hornbeam (*Carpinus caroliniana*) and in places with Chinese privet (*Ligustrum sinense*), an invasive species to North America (Lee 2008). Floodplain sites along the lower Altamaha and Savannah Rivers were expansive (approx. 2-10 km wide) and flat, characteristic of bottomland hardwood forests of the Southeastern coastal plains (Sharitz and Pennings 2006). Typical of lower elevation streams draining large areas, floodplain inundation in the lower reaches was much more prolonged and predictable (Bedinger 1981) (Figure 2 – ALT and SAV hydrographs). The forest was densely populated by water tupelo (*Nyssa aquatica*), sweetgum (*Liquidambar styraciflua*), and a variety of oaks (*Quercus* spp.) (Lee 2008). Facultative upland tree species (those that usually occur in non-wetlands) were present in significant numbers in upper reach floodplains (such as *Liriodendron tulipifera* and *Ulmus alata*); as opposed to lower reach floodplains where they were scant (Lee 2008). Wetland obligate trees (those that are almost always found in wetlands) were all but absent in the upper reach floodplains. A significant portion of plant species in lower reach floodplains of the Altamaha and Savannah were wetland obligates, such as *Fraxinus caroliniana*, *Taxodium distichum*, and *Quercus lyrata* (Lee 2008).

Across all floodplains in both the upper and lower reaches, pH was circum neutral (7.04 ± 0.42 for upper reach sites; 6.92 ± 0.37 for lower reach sites) during sample collection periods

(Figure 2). Specific conductivity of floodplain water varied somewhat among sites within reaches, however lower reach floodplains had a higher average conductivity (123.99 ± 50.38µS/cm) than upper reach floodplains (94.08 ± 34.76µS/cm). The average water temperature of lower reach floodplain sites (17.75 ± 4.45°C) was also higher than that of sites in the upper reaches (14.44 ± 6.41°C). Predictably, average temperatures steadily climbed during the course of a sampling season. Throughout late December to March, the average temperature in upper reach floodplains was 10.21 ± 3.55°C, while lower reach floodplains maintained a higher average temperature of 14.10 ± 3.69°C. During the latter part of the sampling season (April – June), average temperatures within each reach were higher (upper reach sites, 18.65 ± 5.86°C; lower reach sites, 19.84 ± 3.42°C). Dissolved oxygen levels were lower on average in lower reach floodplains (3.43 ± 2.70mg/L) than upper reach floodplains (5.58 ± 3.47mg/L). Dissolved oxygen levels in the lower reach sites, however, differed between rivers, with Savannah floodplains averaging 2.28 ± 1.19mg/L and Altamaha floodplain averaging 5.16 ± 3.18mg/L. Across all floodplain sites, dissolved oxygen levels generally declined as the sampling season progressed into summer.

Annual rainfall greatly differed during the two study years. In 2008, rainfall was approximately 100cm across all of my study sites, which was 80% of normal (NOAA website). More rain fell in 2009, with 152cm of precipitation in the upper reach sites (125% of normal) and 127cm of rainfall in the lower reaches (100% of normal). Consequently, river discharges were higher in 2009 compared to 2008. Annual discharge in the Oconee River (USGS gage at Penfield, Georgia) was 12.85m^3/s in 2008 and rose to 25.96m^3/s in 2009 (USGS website). Annual discharge within the Broad River (USGS gage at Bell, Georgia) varied similarly, ranging from 17.33m^3/s in 2008 to 33.33m^3/s in 2009. Discharge also increased from 2008 to 2009 in the lower reaches. Annual discharge in the lower Altamaha River (USGS gage at Doctortown, Georgia) climbed from 192.16m^3/s in 2008 to 317.43m^3/s in 2009. In the lower Savannah River (USGS gage at Clyo, Georgia), annual discharge increases were muted (155.60m^3/s in 2008 and 177.43m^3/s in 2009). It should be noted that the Savannah River is regulated for flood control by a series of three dams in the Piedmont. The lower Savannah was the only area in this study where flows were highly regulated.

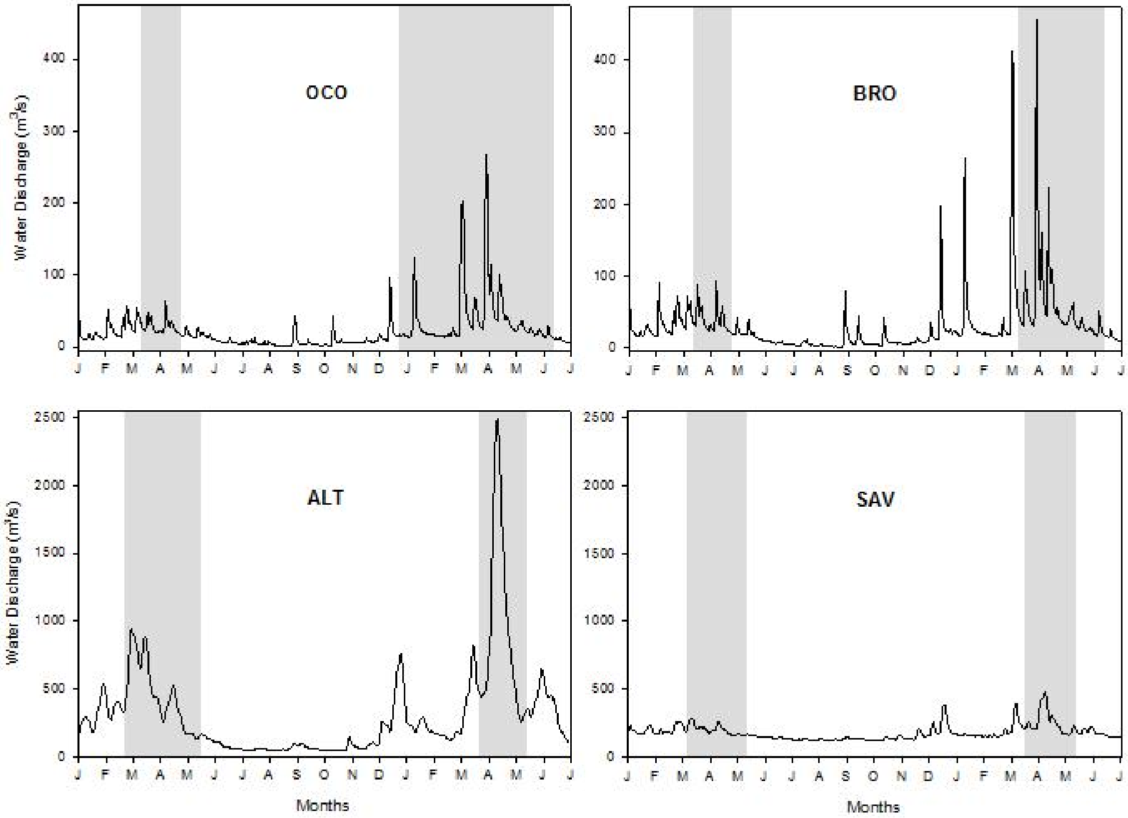

Figure 2. Hydrographs of the four watersheds studied beginning from January 1, 2008 to July 1, 2009. Gray bars indicate when sampling took place within the floodplain sites of that watershed. OCO = Oconee, BRO = Broad, ALT = Altamaha, and SAV = Savannah.

Fish Sampling

High variability of flow, turbid water, and underwater obstacles make sampling for fish difficult in floodplain wetlands. Electro-shocking is considered by some to be the single most effective sampling means for fish in these types of habitats (Knight and Bain 1996), and thus I collected fish with a backpack electro-shocker (Smith-Root Inc., Model 12-B POW, Vancouver, WA). An assistant followed behind with a dip-net to capture stunned fish. I still recognized, however, that my sampling effort might result in low detection of some fish species, which could potentially skew community structure estimates (Peterson et al. 2004). Therefore, I used modified closed-population mark-recapture methods described by MacKenzie et al. (2002) and similar to those of Albanese et al. (2007) to estimate detection. Sub-sampling was utilized to create site-specific capture histories and hierarchical models that helped to better determine detection estimates for each fish species. Sampling duration at each site was 750 seconds of shocking, split into seventy-five 10-second intervals. Upon completion of each 10-second shock, I recorded fish captured along with several covariates: capture depth (in cm), the presence or absence of flow, and the presence or absence of large woody debris (defined as woody material larger than 10cm in diameter). An effort was made to sample across all micro-habitats representative of each site (various depths, open water versus amongst large woody debris, flowing water versus stagnant water) in order to better detect all species that may have been present.

Fish sampling occurred in winter and spring months (late December – early June) during 2008 and 2009. Sampling during this period allowed me to capture the largest and most important seasonal flood pulses. Most flooding occurs during this time of year, because evapotranspiration is low (as temperatures are mild and deciduous trees have yet to fully leaf out) resulting in higher amounts of runoff (Benke 2001). Most sampling took place shortly after or between large rain events to ensure a better chance of floodplain inundation and allow fish to colonize low-lying backwater swamps. In the lower reaches, however, I avoided sampling during high flows because access was difficult and dangerous. Furthermore, previous sampling (Bright et al. 2010) indicated that capture efficiency was low during high water because fish are dispersed over a wide area. Finally, my sampling equipment was not well suited for deep water collection. I visited each site on at least three occasions during the season, provided water was present on the floodplain.

All fish captured were identified to species and standard length was measured. Most fish were identified in the field and released back into the habitat. If positive identification could not be made, fish were euthanized (MS-222 solution bath buffered with $CaCO_3$), preserved in a 10% formalin solution, and brought back to the laboratory for closer inspection and identification using descriptions, plates, and/or keys in Page and Burr (1991), Etnier and Starnes (1993), Boschung and Mayden (2004), and Marcy et al. (2005). Once tissues had been fixed by formalin (approximately two weeks), fish were transferred to a 70% ethanol solution for permanent preservation. After positive identifications were made, preserved fish were donated to the Georgia Museum of Natural History. Two species of *Gambusia* (*G. affinis* and *G. holbrooki*) were collected but were only identified to genus because an accurate and efficient identification was difficult to make in the field.

Statistical Analysis

Variation in fish community composition among upper and lower reach floodplains was assessed using total abundance data of individual species. For each species, numbers of individuals collected at a given site over the course of a sample year (multiple sampling occasions) were added together, resulting in a matrix of numbers of fish per site per year. *Gambusia holbrooki* and *G. affinis* were combined into a generic category. Fish collection data were standardized on a catch-per-unit-effort (CPUE) basis. To do so, the total number of fish caught at each site was divided by the number of visits to that site within a sample year. Abundance data (CPUE) were then $\log_{10}(x+1)$ transformed to homogenize variance and produce more normal distributions. Fishes were further divided into 10 different size classes (10mm intervals, 10–19, 20–29, ..., 90–99, 100+ mm) based upon their standard length. Size class groupings were developed for Cyprinidae, Centrarchidae, *Gambusia*, and others (i.e., all other genera and families).

I conducted non-metric multidimensional scaling (NMS) ordinations (PC-ORD 5, MJM Software Design, Glenden Beach, OR) using stream reach (upper vs. lower) as a factor and Bray-Curtis Similarity as the distance measure to determine if any differences in fish community composition were apparent between reaches. NMS plots sample values in a multidimensional space (in this case two-dimensional) to visualize groupings (here reaches) in order to gauge how groups of data varied. When the resulting resemblance matrix indicated distinct groupings, I ran an analysis of similarity (ANOSIM) test (Primer 6, Primer-E Ltd., Plymouth, UK) to generate a significance level (p-value), again using the Bray-Curtis distance measure. Additionally, I tested communities among the two reaches on a per year basis to assess annual variation. Finally, to assess lateral variation, I ran NMS ordinations and ANOSIM tests to compare the Oconee and Broad Rivers (upper vs. upper) and the Altamaha and Savannah Rivers (lower vs. lower).

To identify representative species for either stream reach, indicator species analysis (PC-ORD 5) was conducted (Dufrene and Legendre 1997). Indicator species analysis highlights species of fish that heavily influence distinct community groupings and are integral in making a community unique. Species were assessed by the frequency and relative abundance with which they occurred in each reach, and then were given an appropriate indicator value from 0 (non-indicator) to 100 (absolute indicator). A Monte Carlo test of these species indicator values with

5000 random permutations revealed significant species associated with each stream reach. Strong indicators displayed a p-value of less than 0.05, while weak indicator species were defined as those whose p-value was between 0.05 and 0.10.

The analysis described above did not consider differences among sites, reaches, or years that could have been caused by variation in capture efficiency. To examine potential bias in those results caused by differences in the ability to capture different species, in differing habitat settings, I also analyzed the data to account for variation in species-specific detection probabilities. To calculate species detection (p), defined as the probability of capture assuming the species is present, I used the occupancy estimator in Program MARK (White and Burnham 1999). The occupancy estimation procedure in Program MARK allows for the calculation of detection estimates without marking individuals since the analysis is focused on taxon (and not individual) presence/absence. This procedure also estimates site occupancy rates (Ψ) of species based upon the frequency of detection during sampling occasions and over multiple visits to a site. Occupancy is defined here as the probability that a species is present at a site at any one time. Sites were assumed to be open to gains and losses between visits (yet closed during sampling visits), and there was an assumption of independence between shocking intervals. Several models were constructed for each species that estimated detection and occupancy on all geographic levels (reach, watershed, and site) and for each year of the study. Models were assessed for best fit using Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c; Burnham and Anderson 1998). The model with the largest AIC_c weight was used to provide estimates of Ψ and p for each species. Covariates (capture depth, presence of flow, presence of large woody debris) were not included in the analysis, primarily because their greatest value is in identifying microhabitats that a species may readily occupy. This was not a major objective of our study, however the collection of covariates make future occupancy analyses of species of concern possible. Furthermore, I excluded covariates because I wished to determine detection across a wide range of microhabitats (Albanese et al. 2007).

Estimates of Ψ were inserted into a site/species matrix and a NMS ordination was run to detect any differences in occupancy of site-specific fish assemblages. Similar to the abundance ordinations without any estimates of detection/occupancy, Bray-Curtis Similarity was used as the distance measure and stream reach was used as a factor. Additionally, an ANOSIM test was conducted to quantify significance of groupings. Indicator species analysis was also run for the occupancy ordination. Carrying out these complementary analyses using occupancy estimates (in addition to analyses of abundance data), allowed me to determine if the quantity of species collected were in relative proportion to best estimates of overall community composition. Because estimates of Ψ are calculated via detection during surveys and across site visits and since levels of detection are closely related to species abundance, occupancy measures can be used as a surrogate to test relative abundances of species and community structure (Gaston 1996).

Detection estimates provided by Program MARK indicated p for one shocking set (p_{set}; i.e. the probability of capture during one 10-second shock interval). Therefore, I calculated cumulative detection for each species by using the following equation: $1\text{-}(1\text{-}p)^{75}$, which compounded the detection rate over the duration of the 75 shocking sets. This allowed me to assess the cumulative probability of capture for a species (provided it was present) throughout the duration of a site survey, which I refer to as p_{survey}. Detection estimates were used independent of NMS ordinations as a cautionary measure to further evaluate the accuracy of those community structure ordinations and to assess the relative importance of indicator species.

CHAPTER 3

RESULTS

Fish Collection Analysis

Over the two year study 1,697 fish were captured. A majority of these fish (910) were caught in the floodplains of the Oconee River (70 in 2008; 840 in 2009). I collected 275 fish from Broad River floodplains (92 in 2008; 183 in 2009), 331 from Altamaha River floodplains (191 in 2008; 140 in 2009), and 181 from Savannah River floodplains (90 in 2008; 91 in 2009). A total of 443 fish were caught in 2008 versus 1,254 fish in 2009. Spanning both years and across all rivers, 42 species of fish, representing 14 families, were captured (Table 1). Cyprinidae and Centrarchidae were the most speciose families, accounting for over half of the species captured (14 and 10 species, respectively). The next most speciose family was Catastomidae with three species represented. *Gambusia* spp. (Poeciliidae) was the most ubiquitous fish with 391 individuals collected. The most widespread fishes were *Gambusia* spp. and centrarchids *Centrarchus macropterus*, *Lepomis gulosus*, and *Lepomis macrochirus*. These four fishes were present within all four individual floodplain watersheds. Fish were collected from all but three of the 21 floodplain sites. Those three sites were all located along the Broad River and were either sampled but yielded no fish (site S4) or not sampled due to a lack of water on the floodplain (sites S5 and S7).

Oconee River system floodplains

Twenty-five species were collected from sites along the Oconee River and Sandy Creek, with the numerically dominant taxa being *Cyprinella callisema* (Cyprinidae), *Pomoxis* *nigromaculatus* (Centrarchidae), *Micropterus salmoides* (Centrarchidae), and *Gambusia* spp. Centrarchids *Lepomis macrochirus* and *Lepomis auritus* were also abundant. Centrarchids consisted of over half all of all fish collected (479 out of 910 individuals), represented by eight species. Most centrarchids were small; approximately 75% were <40 mm in length. Cyprinids (295 individuals) totaled nearly a third of all fish from these floodplains, consisting of nine species. Cyprinids were also small: 83% were <40mm. Of the 98 *Gambusia* spp. collected, 65 were in the 20–29mm size class. Seven "other" species (see Table 1) spanned the spectrum of standard length.

Of the 25 species collected, 13 were captured only in Oconee basin floodplains. Of note were the fairly ubiquitous *C. callisema* and *Notropis hudsonius* (Cyprinidae) (of which 17 individuals were collected), and the only two species of darters caught over the course of the study: *Etheostoma hopkinsi* and *Percina nigrofasciata* (both Percidae). A school of *Dorosoma petenense* (Clupeidae), presumably introduced, was also captured along the Oconee: the only clupeid collected during the study.

Over 90% of fishes caught in the Oconee floodplains were captured in the higher water year of 2009. A multitude of juvenile fishes including *Notemigonus crysoleucas* (Cyprinidae), *P. nigromaculatus*, *M. salmoides*, and *Centrarchus macropterus* (Centrarchidae) greatly increased the number of individuals collected that year.

Broad River system floodplains

Floodplains of the Broad River and Long Creek were dominated by *Gambusia* spp. and six species of centrarchids. *Gambusia* spp. comprised approximately 53% of all fishes collected, with most (57%) in the 20–29mm size class. Centrarchids were primarily represented by *L. macrochirus*, *L. auritus*, and *C. macropterus*. I captured five species of Cyprinidae, but they only accounted for 18 of the 275 fishes collected (with *N. crysoleucas* being most common). Both cyprinid and centrarchid collections were evenly distributed across size classes, although centrarchid size distribution followed more of a bell-shaped curve, peaking in size class 50–59mm. Four other species (*Erimyzon oblongus*: Catastomatidae; *Ameiurus natalis*: Ictaluridae; *Ameiurus nebulosus*: Ictaluridae; *Esox niger*: Esocidae) were collected, but all were rare. Three species of fishes were captured only in the Broad River floodplains (the cyprinids *Notropis cummingsae* and *Pimephales promelas*, and the ictalurid *A. natalis*), but each was collected in very small numbers.

In 2008, I collected 92 individuals, and in 2009, I collected 183 individuals. This increase was largely due to centrarchids such as *L. macrochirus*, *L. auritus*, and *Lepomis gulosus*.

Altamaha River floodplains

I collected 17 species of fish in Altamaha River floodplains over the two-year study including three Cyprinidae, five Centrarchidae, *Gambusia*, and seven other species. The most abundant taxa captured in Altamaha floodplains were *Amia calva* (Amiidae) (102 individuals), *Gambusia* spp. (54), *Cyprinella leedsi* (Cyprinidae) (33), *L. gulosus* (29), and two species of *Esox* (Esocidae): *E. americanus* (20) and *E. niger* (20). Ninety-nine of the 102 *A. calva* collected consisted of schooling juveniles (50–59mm in length) captured during one sampling visit. Almost two-thirds (65%) of cyprinids were 30–49mm in length, with the rest of the individuals collected being of smaller class sizes. Most centrarchids were of medium size, with 72% ranging in size from 50–79mm. *Gambusia* spp. collected ranged from 10–49mm in length, but most were in the 20–29mm (43%) and 30–39mm (22%) size classes.

Table 1. Average number and standard error of fishes collected across floodplain sites within each watershed per year. Numbers were CPUE-standardized before averaging. Dark gray bars highlight indicator species for the upper reach floodplains; light gray bars highlight indicator species for lower reach floodplains.

	Oconee River		**Broad River**		**Altamaha River**		**Savannah River**	
	2008	**2009**	**2008**	**2009**	**2008**	**2009**	**2008**	**2009**
Amiidae								
Amia calva	0	0	0	0	0.22±0.22	16.67±16.67	0	0.11±0.11
Clupeidae								
Dorosoma petenense	0	0.50±0.50	0	0	0	0	0	0
Cyprinidae								
Campostoma pauciradii	0.50±0.50	0	0	0	0	0	0	0
Cyprinella callisema	1.83±1.83	5.36±2.56	0	0	0	0	0	0
Cyprinella leedsi	0	0	0	0	3.22±1.98	0.67±0.66	0	0
Cyprinella xaenura	0	0.06±0.04	0	0	0	0	0	0
Hybognathus regius	0.67±0.66	0.14±0.07	0	0	0	0	0	0
Hybopsis rubrifrons	0	0.03±0.03	0	0.17±0.17	0	0	0	0
Nocomis leptocephalus	0	0.04±0.04	0	0.11±0.11	0	0	0	0
Notemigonus crysoleucas	0	1.46±1.39	0	1.28±1.04	0.88±0.88	0	0.17±0.16	0
Notropis chalybaeus	0	0	0	0	0	0.17±0.17	0	0
Notropis cummingsae	0	0	0	0.33±0.33	0	0	0	0
Notropis hudsonius	0.67±0.44	0.39±0.16	0	0	0	0	0	0
Notropis lutipinnis	0.17±0.17	0	0	0	0	0	0	0
Notropis petersoni	0	0	0	0	0.56±0.40	0	0	0
Pimephales promelas	0	0	0	0.33±0.33	0	0	0	0
Catastomidae								
Erimyzon oblongus	0	0.03±0.03	0	0.61±0.39	0	0	0	0
Hypentelium nigricans	0.33±0.33	0.13±0.04	0	0	0	0	0	0
Moxostoma collapsum	0.50±0.50	0	0	0	0	0	0	0
Ictaluridae								
Ameiurus natalis	0	0	0	0.11±0.11	0	0	0	0
Ameiurus nebulosus	0	0	0	0.11±0.11	0	0	0.17±0.16	0
Esocidae								
Esox americanus	0	0	0	0	2.11±0.73	0.17±0.17	0.67±0.33	0.11±0.11
Esox niger	0.17±0.17	0.06±0.04	0	0.39±0.20	2.00±1.67	0.33±0.17	0	0.22±0.21

Table 1. (continued) Average number and standard error of fishes collected across floodplain sites within each watershed per year. Numbers were CPUE-standardized before averaging. Dark gray bars highlight indicator species for the upper reach floodplains; light gray bars highlight indicator species for lower reach floodplains.

	Oconee River		Broad River		Altamaha River		Savannah River	
	2008	**2009**	**2008**	**2009**	**2008**	**2009**	**2008**	**2009**
Aphredoderidae								
Aphredoderus sayanus	0	0	0	0	0.44±0.44	0.33±0.33	0.17±0.16	0
Mugilidae								
Mugil cephalus	0	0	0	0	0	0.33±0.33	0	0
Atherinopsidae								
Labidesthes sicculus	0	0	0	0	0.11±0.11	0.33±0.33	0	0
Fundulidae								
Fundulus chrysotus	0	0	0	0	0	0	0	0.33±0.33
Poeciliidae								
Gambusia spp.	7.67±6.68	2.30±0.83	16.33±5.74	9.33±1.77	4.34±2.03	2.50±2.26	9.67±9.36	3.78±2.32
Heterandria formosa	0	0	0	0	0	0	0.17±0.16	0.11±0.11
Centrarchidae								
Centrarchus macropterus	0	0.95±0.65	1.50±1.50	1.17±0.93	1.00±0.58	0	2.17±2.17	3.67±3.50
Enneacanthus obesus	0	0	0	0	0	0	0	0.11±0.11
Lepomis auritus	1.67±1.66	1.63±0.63	1.50±0.76	2.78±1.35	0	0.67±0.66	0	0
Lepomis cyanellus	0	0.03±0.02	0	0	0	0	0	0
Lepomis gulosus	0.67±0.17	0.49±0.15	0.33±0.33	1.28±0.68	3.00±2.04	0.33±0.33	0.17±0.16	0.44±0.12
Lepomis macrochirus	0.50±0.29	2.28±1.07	0	4.78±2.39	0.67±0.51	0.33±0.33	1.67±1.67	1.11±0.59
Lepomis marginatus	0	0	0	0.17±0.17	1.22±1.22	0.50±0.50	0	0
Lepomis microlophus	0	0.05±0.05	0	0	0	0	0	0
Micropterus salmoides	0	2.68±1.75	0	0	0	0	0	0.11±0.11
Pomoxis nigromaculatus	0	4.31±3.32	0	0.22±0.22	0	0	0	0
Percidae								
Etheostoma hopkinsi	0.17±0.17	0.16±0.11	0	0	0	0	0	0
Percina nigrofasciata	0	0.13±0.12	0	0	0	0	0	0
Elassomatidae								
Elassoma zonatum	0	0	0	0	1.44±1.44	0	0	0

Six of the 16 species collected were captured only in the floodplains of the Altamaha. Most of these were caught in small numbers with the exception of *C. leedsi* and *Elassoma zonatum* (Elassomatidae) (13 individuals). Two striped mullets (*Mugil cephalus*: Mugilidae) were captured in the most downstream floodplain of the Altamaha (site A11).

Fewer fish were caught in 2009 than in 2008 along Altamaha floodplains. Species richness remained constant between the two years, but collection numbers dropped for most species from 2008 to 2009. This probably does not represent reduced use of Altamaha floodplains by fish in 2009, but rather a reduced capture efficiency due to higher water levels (fish were spread across a larger area).

Savannah River floodplains

Of the four areas, the fewest fish were collected from the Savannah River floodplains. Of 181 fish collected, 92 were *Gambusia* spp. (with 66% in the 20–29mm size class). I collected five species of Centrarchidae, with *C. macropterus* (46 individuals) and *L. macrochirus* (20 individuals) being the most abundant. Centrarchids were generally small (68% were <40mm in length). Only a single cyprinid individual (*N. crysoleucas,* 100mm) was captured in the Savannah floodplains over the course of two years of sampling. Seven other species were collected, with most being represented by only one or two individuals; we collected five *E. americanus*. Three species collected in the Savannah floodplains were unique to those sites, although each was rare (*Fundulus chrysotus*: Fundulidae; *Heterandria formosa*: Poeciliidae; *Enneacanthus obesus*: Centrarchidae).

Minimal annual variation was observed between 2008 and 2009. In 2008, nine species totaling 90 individuals were collected, and in 2009, 11 species totaling 91 individuals were collected.

Contrasts among Floodplains

NMS ordinations for abundance data showed distinct fish communities existing between upper reach floodplains (Oconee and Broad Rivers) and lower reach (Altamaha and Savannah Rivers) floodplains for 2008 and 2009 combined (Figure 3). ANOSIM confirmed the significance of the groupings (Global R = 0.245, p = 0.005). Community structure was also distinct between the two reaches for the individual years of 2008 (Global R = 0.309, p = 0.022) and 2009 (Global R = 0.230, p = 0.042). Indicator analysis identified the redbreast sunfish, *Lepomis auritus*, as a strong indicator species for the upper reach floodplains (Monte Carlo Test, p = 0.0016) and the cyprinids *Cyprinella callisema* (p = 0.0564) and *Notropis hudsonius* (p = 0.0586) as weak indicator species. *Esox americanus* (p = 0.0004), *Cyprinella leedsi* (p = 0.0138), and *Amia calva* (p = 0.0480) were strong indicator species representative of the lower reach floodplains, while *Aphredoderus sayanus* (p = 0.0506) was recognized as a weak indicator. Floodplain community structure did not differ between the Oconee and Broad Rivers (Global R = -0.022, p = 0.541) or the lower Altamaha and Savannah Rivers (Global R = -0.036, p = 0.645).

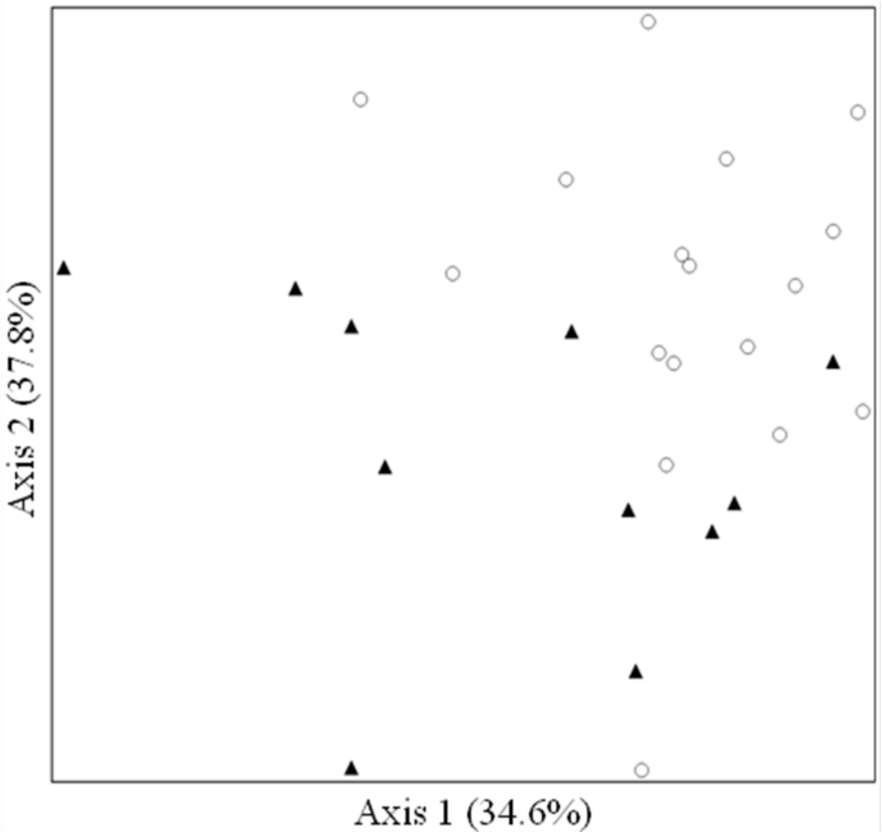

Figure 3. NMS ordination of fish community structure in terms of abundance of collected fish (CPUE standardized and $\log_{10}[x+1]$ transformed) between upper reach (open circles) and lower reach (black triangles) floodplain habitats.

Much like the ordination of standardized captured abundances, a NMS ordination of species occupancy (Ψ) estimates across sites over the two year study exhibited two distinct groupings based upon floodplain reach (Figure 4). Significance of the community distinctness was validated by ANOSIM (Global R = 0.226, p = 0.001). Indicator analysis of the occupancy ordination identified the same species as significant as did the abundance ordination. For the upper reaches, *Lepomis auritus* was identified as a strong indicator (p = 0.0030), while *Notropis hudsonius* (p = 0.0540) and *Cyprinella callisema* (p = 0.0548) were weak indicators. *Esox americanus* (p = 0.0002), *Cyprinella leedsi* (p = 0.0142), *Aphredoderus sayanus* (p = 0.0484), and *Amia calva* (p = 0.0500) all showed support for being strong indicators of lower reach floodplain community distinctness.

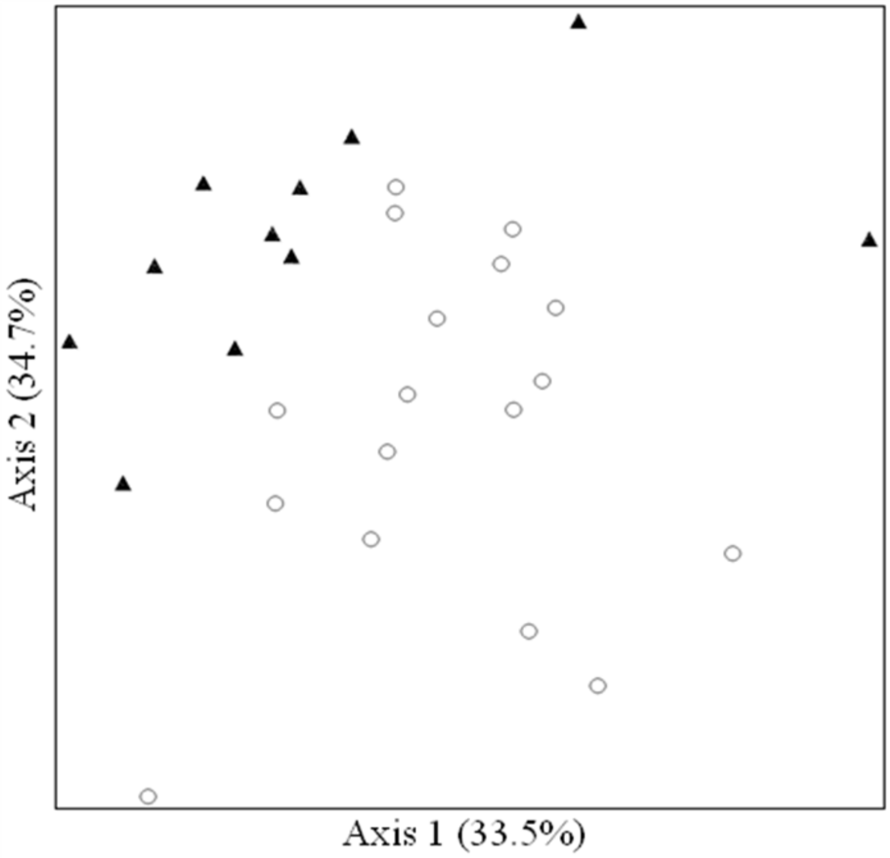

Figure 4. NMS ordination of fish community structure in terms of occupancy estimates of collected fish (as calculated from presence/absence data in Program MARK) between upper reach (open circles) and lower reach (black triangles) floodplain habitats.

Detection (*p*) was generally low for all species during the study (Table 2). Shocking set-level detection estimates (p_{set}) ranged from 0.003 – 0.267. Set-level detection rates < 0.01 were indicative of sites within a year where a species was detected on only one occasion. Species with the highest detection rates were centrarchids *Pomoxis nigromaculatus* (p_{set} = 0.267), *Centrarchus macropterus* (p_{set} = 0.267), and *Micropterus salmoides* (p_{set} = 0.173). Large abundances of juveniles in isolated, drying wetlands were responsible for relatively high detection for these species.

Cumulative detection estimates (p_{survey}) incorporated multiple capture attempts, distributed across a range of microhabitats, and thus were higher than set-level detection. Species with a $p_{\text{set}} \geq 0.100$, for example, had a near 100% probability of capture ($p_{\text{survey}} = 1.000$) over the course of a 75 set survey. Species with a p_{set} as low as 0.020 still had a 78% chance of capture during a site visit, emphasizing the power of numerous sub-samples.

Indicator species detection rates were variable. In the upper reaches, *Cyprinella callisema*, captured only in the Oconee, exhibited the highest set detection with p_{set} upwards of 0.100 at most sites ($p_{\text{set}} = 0.005 – 0.113$). Set-level detection of *Lepomis auritus* varied across sites within watersheds ($p_{\text{set}} = 0.007 – 0.080$), but was relatively high and usually indicative of nearly 100% detection during a survey. *Notropis hudsonius*, also only found in the Oconee floodplains, was the least detectable of the upper reach indicator species ($p_{\text{set}} = 0.007 – 0.024$). Of the indicator species in the lower reach floodplains, *Esox americanus* was the most detectable, though set-level detection was highly variable depending on the site ($p_{\text{set}} = 0.004 – 0.093$). Set-level detection of *Cyprinella leedsi* was relatively high in the Altamaha floodplains ($p_{\text{set}} = 0.004 – 0.060$). *Amia calva* ($p_{\text{set}} = 0.004 – 0.038$), and *Aphredoderus sayanus* ($p_{\text{set}} = 0.004 – 0.023$) were slightly less detectable indicator species of the lower reaches.

Table 2. Range of site detection estimates per shocking set (p_{set}) and cumulative detection estimates per sampling survey (p_{survey}) for fishes collected across floodplain sites within each watershed during the two year study. A sampling survey consisted of 75 10-second shocking sets at one site. Per set detection estimates were computed in Program MARK. Cumulative detection estimates were calculated with the following equation: $1-(1-p_{set})^{75}$. Ranges exclude occasions when species were not detected. Zero indicates the species was never captured in the watershed. Dark gray bars highlight indicator species for the upper reach floodplains; light gray bars highlight indicator species for lower reach floodplains.

	Oconee River		**Broad River**		**Altamaha River**		**Savannah River**	
	p_{set}	p_{survey}	p_{set}	p_{survey}	p_{set}	p_{survey}	p_{set}	p_{survey}
Amiidae								
Amia calva	0	0	0	0	0.020-0.038	0.780-0.945	0.004	0.260
Clupeidae								
Dorosoma petenense	0.038	0.945	0	0	0	0	0	0
Cyprinidae								
Campostoma pauciradii	0.038	0.945	0	0	0	0	0	0
Cyprinella callisema	0.005-0.113	0.313-1.000	0	0	0	0	0	0
Cyprinella leedsi	0	0	0	0	0.004-0.060	0.260-0.990	0	0
Cyprinella xaenura	0.003	0.202	0	0	0	0	0	0
Hybognathus regius	0.003-0.020	0.202-0.780	0	0	0	0	0	0
Hybopsis rubrifrons	0.003	0.202	0.007	0.410	0	0	0	0
Nocomis leptocephalus	0.004	0.260	0.004	0.260	0	0	0	0
Notemigonus crysoleucas	0.021-0.066	0.796-0.994	0.007-0.052	0.410-0.982	0.052	0.982	0.005	0.313
Notropis chalybaeus	0	0	0	0	0.007	0.410	0	0
Notropis cummingsae	0	0	0.013	0.625	0	0	0	0
Notropis hudsonius	0.007-0.024	0.410-0.838	0	0	0	0	0	0
Notropis lutipinnis	0.007	0.410	0	0	0	0	0	0
Notropis petersoni	0	0	0	0	0.004	0.260	0	0
Pimephales promelas	0	0	0.038	0.945	0	0	0	0
Catastomidae								
Erimyzon oblongus	0.003	0.202	0.007-0.052	0.410-0.982	0	0	0	0
Hypentelium nigricans	0.013	0.625	0	0	0	0	0	0
Moxostoma collapsum	0.038	0.945	0	0	0	0	0	0
Ictaluridae								
Ameiurus natalis	0	0	0.004	0.260	0	0	0	0
Ameiurus nebulosus	0	0	0.004	0.260	0	0	0.004	0.260
Esocidae								
Esox americanus	0	0	0	0	0.007-0.093	0.410-0.999	0.004-0.032	0.260-0.913
Esox niger	0.003-0.007	0.202-0.410	0.004-0.009	0.260-0.492	0.006-0.107	0.363-1.000	0.009	0.492

Table 2. (continued) Range of site detection estimates per shocking set (p_{set}) and cumulative detection estimates per sampling survey (p_{survey}) for fishes collected across floodplain sites within each watershed during the two year study. A sampling survey consisted of 75 10-second shocking sets at one site. Per set detection estimates were computed in Program MARK. Cumulative detection estimates were calculated with the following equation: $1-(1-p_{\text{set}})^{75}$. Ranges exclude occasions when species were not detected. Zero indicates the species was never captured in the watershed. Dark gray bars highlight indicator species for the upper reach floodplains; light gray bars highlight indicator species for lower reach floodplains.

	Oconee River		**Broad River**		**Altamaha River**		**Savannah River**	
	p_{set}	p_{survey}	p_{set}	p_{survey}	p_{set}	p_{survey}	p_{set}	p_{survey}
Aphredoderidae								
Aphredoderus sayanus	0	0	0	0	0.019-0.023	0.763-0.825	0.004	0.260
Mugilidae								
Mugil cephalus	0	0	0	0	0.007	0.410	0	0
Atherinopsidae								
Labidesthes sicculus	0	0	0	0	0.004-0.007	0.260-0.410	0	0
Fundulidae								
Fundulus chrysotus	0	0	0	0	0	0	0.004	0.260
Poeciliidae								
Gambusia spp.	0.008-0.120	0.453-1.000	0.066-0.180	0.994-1.000	0.007-0.062	0.410-0.992	0.005-0.062	0.313-0.992
Heterandria formosa	0	0	0	0	0	0	0.004	0.260
Centrarchidae								
Centrarchus macropterus	0.073-0.087	0.997-0.999	0.007-0.047	0.410-0.973	0.038-0.066	0.945-0.994	0.004-0.267	0.260-1.000
Enneacanthus obesus	0	0	0	0	0	0	0.004	0.260
Lepomis auritus	0.013-0.080	0.625-0.998	0.007-0.080	0.410-0.998	0.052	0.982	0	0
Lepomis cyanellus	0.003	0.202	0	0	0	0	0	0
Lepomis gulosus	0.004-0.017	0.260-0.724	0.020-0.044	0.780-0.966	0.005-0.107	0.313-1.000	0.005-0.012	0.313-0.596
Lepomis macrochirus	0.003-0.080	0.202-0.998	0.080	0.998	0.009-0.052	0.492-0.982	0.030-0.059	0.898-0.990
Lepomis marginatus	0	0	0.007	0.410	0.020-0.093	0.780-0.999	0	0
Lepomis microlophus	0.021	0.796	0	0	0	0	0	0
Micropterus salmoides	0.106-0.173	1.000	0	0	0	0	0.004	0.260
Pomoxis nigromaculatus	0.006-0.267	0.363-1.000	0.019	0.763	0	0	0	0
Percidae								
Etheostoma hopkinsi	0.007-0.021	0.410-0.796	0	0	0	0	0	0
Percina nigrofasciata	0.021	0.796	0	0	0	0	0	0
Elassomatidae								
Elassoma zonatum	0	0	0	0	0.080	0.998	0	0

CHAPTER 4

DISCUSSION

The hypothesis that variation in fish communities existed along a longitudinal gradient of riverine floodplains was supported by the analysis of data collected in this study. Upper reach floodplain fish communities within the study's river systems were distinct from fish communities in lower reach floodplains.

In the upper reach floodplains of the Oconee and Broad River watersheds, cyprinids were much more abundant and diverse. Upper reach floodplains contained 11 species of cyprinids, while the lower reach floodplains of the Altamaha and Savannah supported only four species. Approximately 87% of all cyprinids were collected in the Oconee and Broad River floodplains (although this was mostly driven by high numbers of *Cyprinella callisema* in the Oconee system). Centrarchids were also numerous; combined with Cyprinidae, the two families comprised over half of the species collected in each of the upper reach floodplains. Darters (*Etheostoma hopkinsi* and *Percina nigrofasciata*) and catastomids were collected only in the Oconee and Broad River floodplains. Indicator species for the upper reaches did not have life history traits designed to take advantage of flood pulse patterns or floodplain geomorphology, suggesting opportunistic utilization of the floodplain. *Lepomis auritus* and *Notropis hudsonius* spawn from late May to July (Marcy et al. 2005) long after most major spring flood pulses occur. *Lepomis auritus* constructs pit nests of gravel (Marcy et al. 2005) in flowing portions of streams, typically in eddies behind obstructions (Etnier and Starnes 1993), and *N. hudsonius* broadcasts their eggs over sand and gravel patches in riffles (Marcy et al. 2005). The most numerous indicator species, *C. callisema* is a crevice spawner that prefers sandy and rocky runs (Page and Burr 1991). The floodplain sites I sampled had a predominately silt substrate and substantial flow occurred at only one site. Despite their opportunistic use of the floodplain, Ross and Baker (1983) postulated that non-breeding fish that exploit floodplains may be taking advantage of highly nutritious food resources to aid in subsequent gonadal development.

In the lower reach floodplains, species other than cyprinids and centrarchids, such as Gambusia spp., *Amia calva*, and *Esox* spp., made up half (Altamaha) or more than half of the individuals (Savannah) captured, and three of the four indicator species were from families other than Cyprinidae or Centrarchidae. Three of these species, *Amia calva*, *Esox americanus*, and *Aphredoderus sayanus*, time their spawn with the seasonal flood pulses (late winter to early spring) (Marcy et al. 2005). *Esox americanus* and *A. sayanus* scatter their eggs in dense vegetation and *A. calva* deposits eggs in constructed nests, and all prefer still, quiescent backwaters to spawn (Marcy et al. 2005). Timing of reproduction and habitat preferences suggests close relationships between these species and floodplain inundation. The fourth indicator species, *Cyprinella leedsi*, differed in that it is a crevice spawner that is reproductively active from May to September (Rabito and Heins 1985), after major flood pulses occur. This species prefers sandy runs (Page and Burr 1991) and usually is found schooling in eddies of swift currents (Marcy et al. 2005) (which I also observed). Being invertivores (Marcy et al. 2005), I suspect that, much like upper reach indicator species, *C. leedsi* may be opportunistically making use of the floodplains to feed and initiate gonadal development.

Moderate annual variation in water level was observed over the two year study, but response of fish community structure was varied. The total number of individuals and species increased in the upper reach floodplains during the higher water year of 2009, but not in the lower reaches. Higher stream discharge in the upper reaches resulted in more overbanking of the high natural levees, providing more opportunities for colonization. The increase in the number of cyprinid species in the upper reach floodplains in 2009 supports of the idea that upper reach floodplains are generally populated by opportunistic riverine species. Ross and Baker (1983) also observed increased abundance of weed shiners (*Notropis texanus*), a flood exploitive cyprinid, during high water years in a small Mississippi stream.

Sampling fishes on floodplains is challenging, and detection was low for many species. Despite large numbers of shocking sets, one-third of species were captured so infrequently that cumulative survey detection (p_{survey}) was < 50%, indicating that they were either rare or evasive. When assigning occupancy (Ψ) estimates to species, Program MARK made the conservative assumption that very low detection (< 0.010) was indicative of species always being present but difficult to capture. These species were assigned a Ψ value of one, effectively inflating their influence in community analyses (as opposed to the low weight they exert in abundance analyses). However, occupancy and abundance ordinations were very similar, suggesting that conclusions about reach differences were robust.

Distributions of fish size collections (Figure 5) in upper vs. lower reaches were not strongly supportive of differential floodplain use. I anticipated collecting numerous juvenile fish in the lower reaches that were using the floodplains as nurseries, and collecting mostly larger individuals in the upper reaches that were opportunistically exploiting food resources. My expectation was largely met in the Broad and Savannah floodplains. Relatively large centrarchids were observed in Broad River floodplains, and a large abundance of juveniles were collected in Savannah River floodplains. Expectations were not met, however, in the Oconee and Altamaha floodplains. Despite observation of large schools of juvenile *A. calva*, there was an even distribution of size classes in the Altamaha floodplains. Larger, non-juvenile *C. leedsi* (which I suggest were using the floodplain opportunistically) and centrarchids also populated floodplains of the Altamaha. In contrast, juveniles numerically dominated floodplains of the Oconee basin. These juveniles were mostly *Pomoxis nigromaculatus*, *Micropterus salmoides*, and, to a lesser extent, *Centrarchus macropterus* and *Notemigonus crysoleucas*, species that prefer slower backwater habitats (Marcy et al. 2005). Killgore and Baker (1996) also observed numerous larval *P. nigromaculatus* and *C. macropterus* in an Arkansas bottomland hardwood wetland. *Notemigonus crysoleucas* has been reported to exploitatively broadcast eggs on *M. salmoides* nests (Kramer and Smith 1960; Chew 1974).

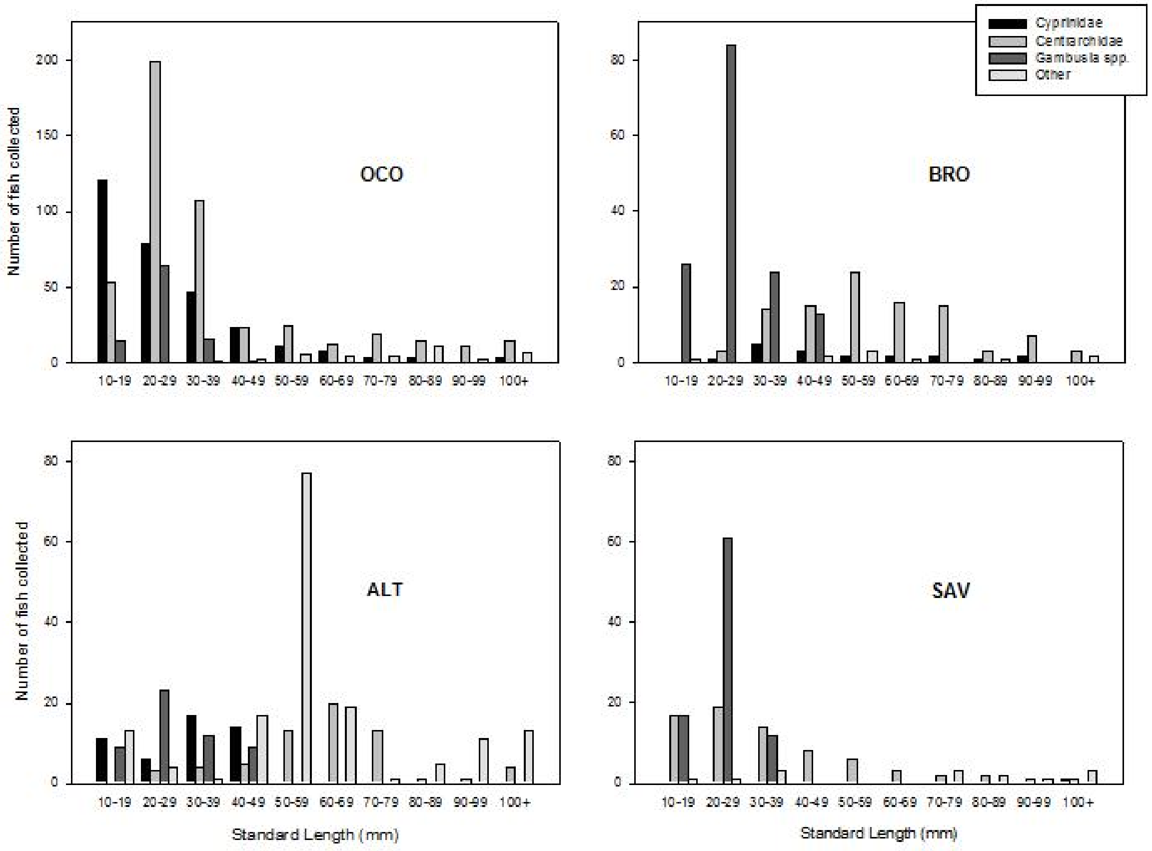

Figure 5. Size class distribution of major groups of fish collected in each of the four watersheds studied. OCO = Oconee, BRO = Broad, ALT = Altamaha, and SAV = Savannah.

While upper reach floodplains may provide spawning and nursery habitat for some species, recruitment of offspring in these hydrologically variable environments is risky (Cucherousset et al. 2007). At the two Oconee sites where most juveniles were collected, the populations became stranded on the floodplain and perished when the habitats dried.

While this study focused on longitudinal variation of fish communities in floodplains, most studies have assessed longitudinal zonation of fish assemblages within stream channels proper (Edds 1993; Esselman et al. 2006; Ibanez et al. 2007; Virbickas and Kesminas 2007; McGarvey and Ward 2008). It seems intuitive that if distinct fish communities exist longitudinally within the main channel, floodplain communities might reflect this, as a significant portion of floodplain recruits may emigrate from the channel. Among these studies, however, there is no commonality in what factors might be causing longitudinal community variation. Welcomme (2001) stated that stream gradient is a major factor influencing the distribution of fish fauna in rivers, which is echoed by Virbickas and Kesminas (2007). Edds (1993), Esselman et al. (2006), and McGarvey and Ward (2008) argued that river discharge was the most relevant factor, while Ibanez et al. (2007) found a correlation between conductivity and longitudinal species assemblages. Distribution of fish fauna, however, is rarely a result of one factor (Angermeier et al. 2002), and all of these factors are plausible causes for variation in floodplain fish community structure.

Flood pulse character is determined by regional topography (gradient) and stream hydraulics (discharge) (Ward et al. 2002, Junk and Wantzen 2006). Based on previous longitudinal studies of invertebrate (Reese and Batzer 2007) and plant (Lee 2008) communities, I suggest that flood pulse dynamics might be an important driver of floodplain fish community structure. In a comparison of temporary and permanent wetlands, Escalera-Vázquez and

Zambrano (2010) asserted that abiotic factors associated with hydroperiod (temperature, depth, dissolved oxygen, macrophyte coverage) play a more integral role in structuring fish assemblages in floodplains than those factors that typically dictate in-stream fish communities (discharge, pH, area drained, water velocity).

I do not believe that variation observed was not simply an artifact of species' natural home ranges. Using the Fishes of Georgia website (Straight et al. 2009), I determined the ranges of all species collected. Of 42 total species, 27 occur in both upper and lower reaches of at least one of the major river systems. Ten are restricted to the lower reaches, and only five are restricted to the upper reaches. Four of the seven indicator species (*Notropis hudsonius*, *Esox americanus*, *Aphredoderus sayanus*, and *Lepomis auritus*) have ranges spanning both upper and lower reaches. While *Amia calva, Cyprinella callisema, Cyprinella leedsi* have restrictive home ranges, environmental conditions related to either upper or lower river habitat probably limit distributions of these species.

To my knowledge, this is the first study to quantify longitudinal variation of fish communities in floodplain wetlands. Findings should help to inform decisions about water resource policy and management. Wetland mitigation and restoration projects should recognize that floodplain position is important to native communities of fish. Managers of regulated rivers should design flow regimes that simulate natural flooding patterns for river reaches in an effort to support natural communities. Distinct communities of fishes are comprised of species that share similar life histories and habitat requirements (Hawkes 1975; Schlosser 1987; Aarts and Nienhuis 2003). Therefore, focusing conservation efforts towards reach-specific communities may provide an efficient and holistic means of natural resource management and preservation (Angermeier and Winston 1999; McGarvey and Ward 2008).

CHAPTER 5

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