# LATERAL VARIATION IN THE COMPOSITION OF AQUATIC INVERTEBRATE COMMUNITIES ACROSS THE FLOODPLAINS OF THE ALTAMAHA AND SAVANNAH RIVERS

by

Eric G. Bright

(Under the Direction of Darold Batzer)

## ABSTRACT

Floodplain connectivity is the linkage of the main river channel to that of the alluvial floodplain, and the degree of connectivity can cause biotic differences in the floodplain. The current study examined how river-floodplain connectivity affects total invertebrate biomass and abundance, and invertebrate community structure in floodplain areas with high, mid, and low connection to the river. Conductivity varied laterally across the floodplain while pH and temperature varied only seasonally. Fish richness and abundance were greater in areas with a higher connection to the river. Invertebrate community structure and many of the individual invertebrate taxa varied between study years. Invertebrate abundance and biomass were greatest in areas with the highest connection to the river and they decreased as the connection decreased. *Caecidotea* abundance and Tanypodinae biomass were the only individual taxa responses that varied among the connection regimes. Invertebrate community composition did not vary laterally across the floodplain.

INDEX WORDS: Aquatic invertebrates, Community Structure, Connectivity, Floodplain

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# CHAPTER 1

# INTRODUCTION

Floodplain connectivity refers to the lateral linkage of the river channel to the alluvial floodplain through flooding events (Amoros and Roux 1988, Ward and Stanford 1995a, Amoros and Bornette 2002), and is an important process for river-floodplain ecological dynamics. The flood-pulse concept as proposed by Junk et al. (1989) states that this linkage of the floodplain to the river maintains both habitats as productive and diverse ecosystems. Lateral connectivity affects suspended sediments and nutrients that flow from the river to the floodplain and organic detritus and algal biomass that flow from the floodplain to the river (Kitchens et al. 1975, Brinson 1977, Mitsch et al. 1979, Mulholland 1981, Cuffney 1988, Amoros and Roux 1988, Jones and Smock 1991, Ward and Stanford 1995b, Junk 1997, Ward 1999).

The degree of river-floodplain connectivity has been shown to influence many factors of the floodplain. A study conducted along the Danube River and floodplain concluded that areas with higher connection to the river had higher concentrations of nitrate, suspended solids, and small particulate organic matter (Tockner et al. 1999). In a study along the Lower Rhine and Meuse Rivers, higher concentrations of salts, nutrients, and metals were found in floodplain lakes that had more frequent and prolonged periods of floodplain inundation (Van den Brink et al., 1993). Other studies indicate that the degree of connectivity can also influence biotic life within the floodplain with greater fish abundance and richness (Sullivan and Watzin 2009) or richer plant communities (Bornette et al. 1998, Leyer 2006) existing in areas with a greater connection to the river.

Anthropogenic modifications of river systems (e.g., dams, levees) can disconnect rivers from their floodplain. Dams affect over half of all large river systems of the world (Nilsson et al. 2005) with many of these dams used for hydroelectric power, flood control and water storage (Walker 1985, Dynesius and Nilsson 1994, Power et al. 1995). Dams influence the longitudinal connectivity of rivers and decrease downstream transport of nutrients, sediments, and organic matter (Ligon et al. 1995) and organisms (e.g, diadromous fish) (Musick et al. 2001) . Altered natural hydrology from dams and levees influence the lateral connection of the river to the floodplain. There is an estimated 40,000 km of levees, dikes, floodwalls, and embankments in the United States (Johnston Associates 1989), and these structures can limit the lateral exchange of nutrients and organic matter between the river and floodplain (Sparks 1995). Understanding how floodplain connectivity influences biota will permit a more complete assessment of how floodplain ecosystems will be altered by human modifications.

The purpose of this study was to examine invertebrate responses to differences in hydrological connectivity across floodplains. We examined the influence of river-floodplain connectivity on invertebrate biomass, abundance, and community structure. We predicted that invertebrate abundance and biomass would decrease as the connection of the river to the floodplain decreases. We also predicted that unique invertebrate community compositions would develop in areas that had different lateral connection to the river. The sites with the highest connection would be more influenced by lotic organisms while sites with the lowest connection to the river would be more influenced by non-aquatic organisms (that can tolerate some flooding). Further, interior areas of the floodplain, remote from both the river and uplands, would be dominated by lentic species, generalist aquatic organisms that can also cope with periodic drying. Studies were conducted along the Altamaha and Savannah Rivers, two major rivers of the Southeastern United States.

# CHAPTER 2

# METHODS

### *Study Rivers*

Study sites were located on the floodplains of the Altamaha and Savannah Rivers. The headwaters of the Altamaha River start in north-central Georgia and flow through the Piedmont and Atlantic Coastal Plain physiogeographic regions before emptying into the Atlantic Ocean. The major headwater tributaries of the Altamaha River are the Oconee and Ocmulgee Rivers (Figure 1). Currently, while some dams exist on these tributaries, they are not managed for flood control and flood pulses downstream in the Altamaha are natural (Figure 2). The Savannah River also flows through the Piedmont and Atlantic Coastal Plain but some of the headwaters originate in the Blue Ridge Mountains (Figure 1). Flows in the Savannah River are heavily regulated by three large dams and reservoirs, built primarily for flood control to prevent downstream flooding, and flood pulses are muted (Figure 2). Recently, the US Army Corps of Engineers has initiated releases of water from the lowest dam on the Savannah River (J. Strom Thurmond Dam) to better mimic natural flood pulses, but no pulses were released during the two study years.

### *Floodplain Locations*

We selected three locations along the floodplain of the Altamaha River and two along the floodplain of the Savannah River (Figure 2 and Table 1). The Altamaha 1 location was just downstream of the convergence of the Ocmulgee and Oconee Rivers in Bullard Creek Wildlife Management Area (WMA). The Altamaha 2 location was further downstream in the Big

Figure 1. Map indicating the five study locations along the floodplains of the Altamaha (Alt) and Savannah (Sav) Rivers. The closed circles represent USGS gauge stations where hydrological data was collected.

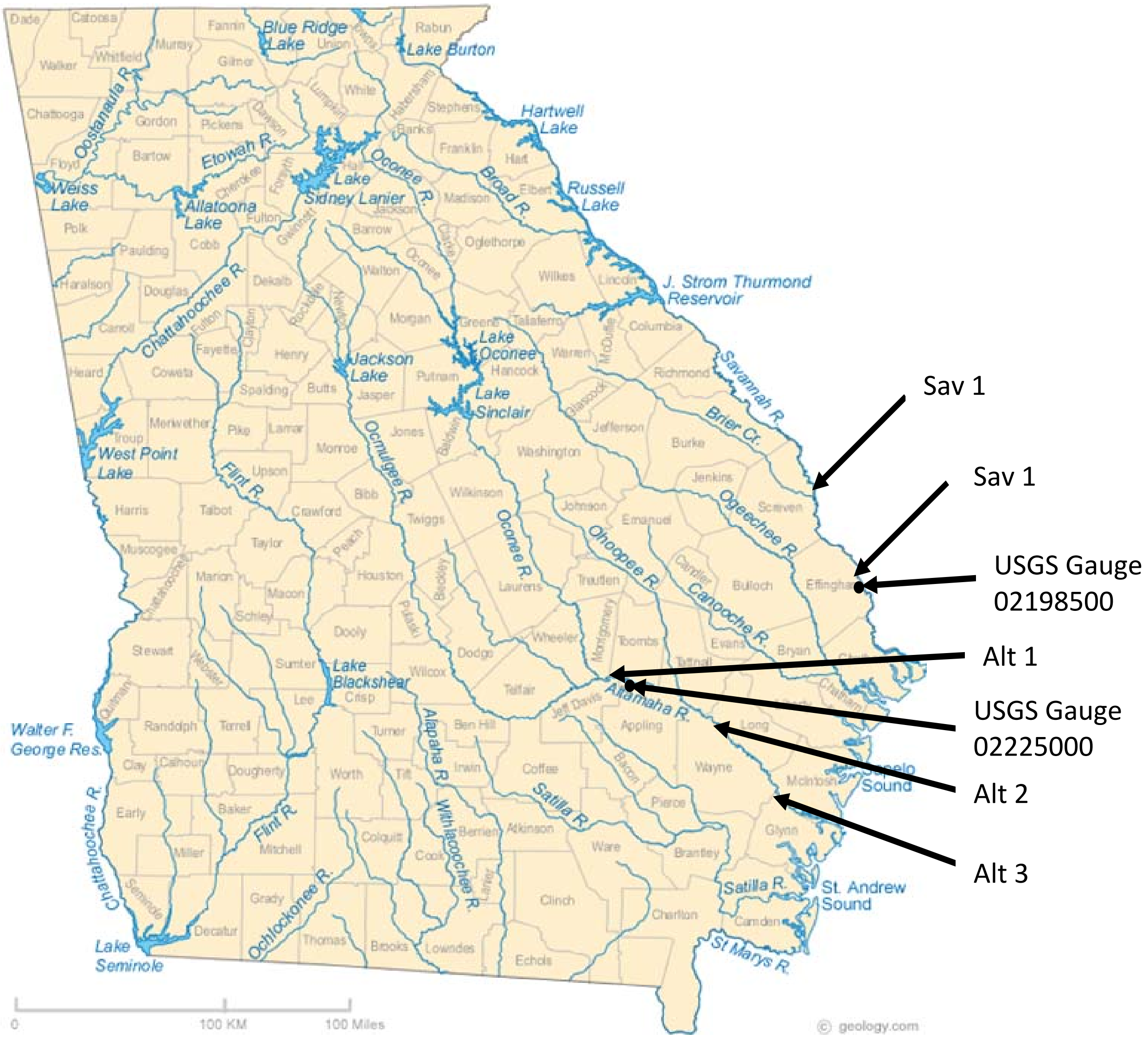

Sav 1
Sav 1
USGS Gauge 02198500
Alt 1
USGS Gauge 02225000
Alt 2
Alt 3
Blue Ridge Lake
Lake Burton
Hartwell Lake
Russell Lake
J. Strom Thurmond Reservoir
Lake Sidney Lanier
Allatoona Lake
Weiss Lake
West Point Lake
Jackson Lake
Lake Oconee
Lake Sinclair
Lake Blackshear
Walter F. George Res.
Lake Seminole
Oostanaula R.
Etowah R.
Chattahoochee R.
Oconee R.
Broad R.
Savannah R.
Brier Cr.
Ogeechee R.
Canoochee R.
Ohoopee R.
Ocmulgee R.
Flint R.
Altamaha R.
Alapaha R.
Withlacoochee R.
Ochlockonee R.
Satilla R.
St Marys R.
Sapelo Sound
St. Andrew Sound
Dade
Catoosa
Walker
Whitfield
Murray
Fannin
Union
Rabun
Gilmer
White
Chattooga
Gordon
Pickens
Dawson
Lumpkin
Habersham
Stephens
Floyd
Bartow
Cherokee
Forsyth
Hall
Banks
Franklin
Hart
Elbert
Madison
Jackson
Polk
Paulding
Cobb
Fulton
Gwinnett
Barrow
Clarke
Oglethorpe
Haralson
Douglas
Dekalb
Walton
Oconee
Wilkes
Lincoln
Carroll
Rockdale
Newton
Morgan
Greene
Taliaferro
Columbia
Fayette
Clayton
Henry
McDuffie
Warren
Richmond
Heard
Coweta
Spalding
Butts
Jasper
Putnam
Hancock
Glascock
Meriwether
Pike
Lamar
Monroe
Jones
Baldwin
Jefferson
Burke
Troup
Upson
Washington
Jenkins
Screven
Harris
Talbot
Crawford
Bibb
Wilkinson
Johnson
Emanuel
Twiggs
Taylor
Peach
Muscogee
Marion
Houston
Bleckley
Laurens
Treutlen
Candler
Bulloch
Effingham
Macon
Schley
Pulaski
Montgomery
Toombs
Evans
Bryan
Chatham
Dooly
Dodge
Wheeler
Stewart
Webster
Sumter
Wilcox
Telfair
Tattnall
Lee
Crisp
Jeff Davis
Appling
Long
Quitman
Randolph
Terrell
Turner
Ben Hill
Clay
Calhoun
Dougherty
Worth
Tift
Irwin
Coffee
Bacon
Wayne
McIntosh
Early
Baker
Berrien
Atkinson
Pierce
Glynn
Miller
Mitchell
Colquitt
Cook
Ware
Brantley
Seminole
Grady
Lanier
Clinch
Decatur
Thomas
Brooks
Lowndes
Echols
Charlton
Camden
0
100 KM
100 Miles
© geology.com

Figure 2. Hydrographs of the Altamaha River (USGS gauge 02225000 near Baxley, Georgia) and Savannah River (USGS gauge 02198500 near Cylo, Georgia) for 2007 and 2008.

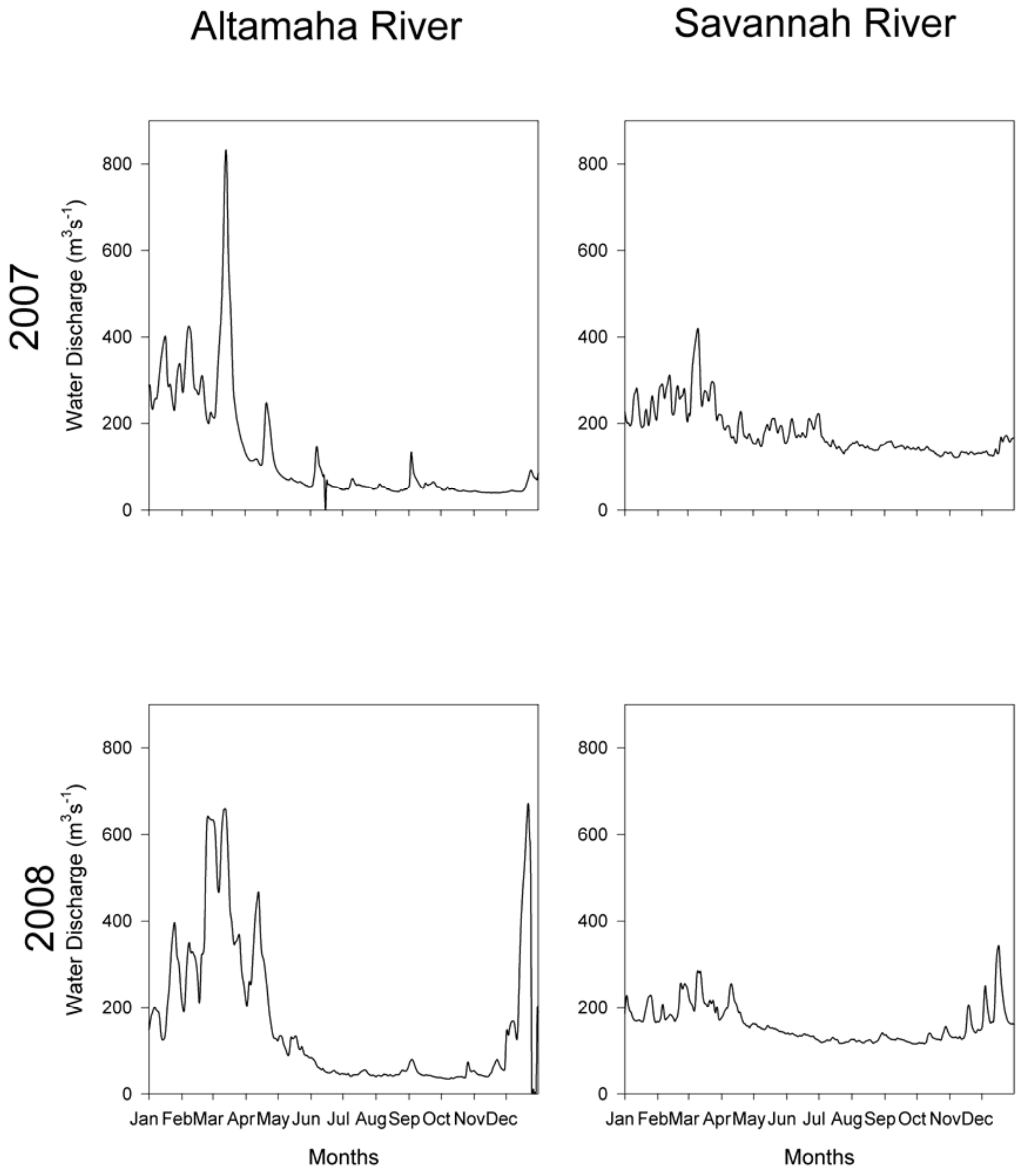

Altamaha River
Savannah River
2007
2008
Water Discharge ($m^3s^{-1}$)
0
200
400
600
800
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Months

Table 1. Locations of 15 study sites at five locations along the Savannah and Altamaha River floodplains, and relative distances (high, mid, low) to the river channels (estimated using GPS).

| Site | Connection | GPS Coordinates | Distance to River (km) |
|---|---|---|---|
| Savannah 1 | High | N 32°48.116<br>W 81°26.042 | 0.22 |
| | Mid | N 32°48.406<br>W 81°26.414 | 0.78 |
| | Low | N 32°48.444<br>W 81°26.918 | 1.54 |
| Savannah 2 | High | N 32°33.970<br>W 81°18.211 | 0.35 |
| | Mid | N 32°34.093<br>W 81°18.145 | 0.57 |
| | Low | N 32°34.270<br>W 81°18.145 | 0.90 |
| Altamaha 1 | High | N 31°57.437<br>W 82°31.603 | 0.08 |
| | Mid | N 31°57.380<br>W 82°31.479 | 0.16 |
| | Low | N 31°57.163<br>W 82°31.479 | 0.56 |
| Altamaha 2 | High | N 31°50.718<br>W 82°04.328 | 0.50 |
| | Mid | N 31°51.013<br>W 82°04.236 | 1.06 |
| | Low | N 31°52.426<br>W 82°05.717 | 1.31 |
| Altamaha 3 | High | N 31°30.597<br>W 81°39.422 | 0.09 |
| | Mid | N 31°30.641<br>W 81°39.271 | 0.34 |
| | Low | N 31°41.406<br>W 81°47.727 | 5.00 |

Hammock WMA. The Altamaha 3 location was on private lands across from the confluence with Giradi Creek, which was just above the upper extent of tidal influence. The Savannah 1 location was in Georgia's Tuckahoe WMA, and the Savannah 2 location was in South Carolina's Webb WMA, again just above the upper extent of tidal influence. Tree communities on both floodplain forests were similar, with the dominant trees being *Nyssa aquatic* (water tupelo), *Quercus laurifolia* (laurel oak), *Liquidambar styraciflua* (American sweetgum), and *Quercus lyrata* (overcup oak) (Lee 2008).

At each of the five locations, we chose three different connection regimes in relation to the river channels: high, mid, and low. High connection sites were located closest to the river, both spatially and in terms of hydrologic connection. The mid connection sites were positioned in the middle of the floodplains. The low connection sites were furthest from the river and close to the floodplain's upland edge. Direct distances from the river channel to each site were calculated using GPS and are listed in Table 1.

The 2007 and 2008 sampling years differed in water flow regimes. Rainfall in 2007 was around 40% less than the 30-year average rainfall of around 150 cm (NOAA website). While rainfall in 2008 was higher, it was still relatively low around 80% of the 30-year average. The average monthly discharge on the Altamaha River (USGS gauge near Baxley, Georgia) ranged from 41.06 $m^3/s$ to 367.24 $m^3/s$ over the two-year study (Figure 2). The 2007 and 2008 annual river discharge of the Altamaha River was around 44% and 47%, respectively, of the 38-year average annual discharge. The average monthly discharge in the Savannah River (USGS river gauge at Cylo, Georgia) was less variable and ranged from 122.78 $m^3/s$ to 266.72 $m^3/s$ (USGS website) (Figure 2). The 2007 and 2008 annual river discharge of the Savannah River was around 57% and 47%, respectively, of the 74-year average. The flood season occurred primarily from February through April (Figure 2) and the low-lying backswamp areas where sampling was conducted, first began to flood (from precipitation) in February and remained flooded at least into April or May. Flood regimes were affected by annual differences in river flow and local precipitation, with flooding being more extensive in 2008 than 2007. Despite dramatic differences in flow between the Altamaha and the Savannah Rivers (Figure 2), all of the backswamp habitats used for this study tended to hold some water over most of the winter-spring season with a few exceptions (see following).

### *Invertebrate Sampling*

We sampled for invertebrates five times over the course of the study. In 2007, we sampled in late-February/early-March and then again in April. Most sites dried soon after. In 2008, water persisted longer, and we sampled three times: late-February/early-March, April, and May. On these five dates most sites were flooded, except the low connection site at Savannah 2, which was dry all of 2007, and the middle connection site at Altamaha 3 and low connection site at Savannah 1, which were dry in May 2008.

A Hess sampler (860 $cm^2$, 500 µm mesh, Wildlife Supply Co., Buffalo, NY, U.S.A.) was used to quantitatively sample invertebrates in the water column and on the benthic substrate. This device is essentially a large core, with a collection net off to one side. Four samples were collected at randomly selected locations along a representative transect through each flooded backwater swamp. However, areas that were too deep (> 75 cm) to permit use of the Hess sampler could not be sampled, and during very high water periods sampling was restricted to shallower zones. The water column and substrate enclosed by the sampler were vigorously agitated by hand to create a slurry and a current was created through the collection net where debris, sediments, and invertebrates were trapped. Calibration studies indicated that this method efficiently collects invertebrates, and data can be expressed quantitatively (Henke 2005).

In the laboratory, samples were sieved into two different size classes; 1) > 1 mm, and 2) < 1 mm, but > 0.25 mm. Samples were sub-sampled and all invertebrates were removed manually using a stereomicroscope. Invertebrates were identified to the lowest practical taxonomic level (Pennak 1989, Peckarsky et al. 1990, Thorp and Covich 1991, Stehr 1991, Epler 1996, Merritt et al. 2008). Each invertebrate was measured to the nearest millimeter and published mass-length regressions were used to estimate biomass (Rogers et al. 1977, Pearre 1980, Sage, 1982, Hodar 1996, Benke et al. 1999, Mercer et al. 2001, Sabo et al. 2002, Baumgartner and Rothhaupt 2003, Stead et al. 2003). When a published mass-length relationship could not be found for a particular invertebrate, we substituted a regression from a similarly shaped organism.

### *Environmental Variables*

During each of the five sampling events, we measured pH (Oakton Model pH Testr 2, Vernon Hills, IL), conductivity (Oakton Model WD-35607-10, Vernon Hills, IL), and temperature (Oakton Model WD-35607-10, Vernon Hills, IL) in every flooded backswamp site using portable meters. In the initial (February/March) sample of 2008, we collected water samples from each site in plastic bottles, returned the samples to the University of Georgia where total nitrogen (TN) and total phosphorus (TP) were assessed using EPA 353.2, 4500-Norg C, and EPA 365.3 methods (EPA 1984, AMPA 1999). Previous work in regional floodplains (Reese and Batzer 2007) indicated that TN and TP levels only tended to be high early in the flood season, and subsequently became lower and more homogenized as flooding persisted. Hence, we anticipated maximum variation among sites in the February/March sample.

### *Fish*

In concert with invertebrate sampling, fish communities at each site were sampled with a backpack electroshocker (Smith-Root Inc., Model 12-B POW, Vancouver, WA) on a catch-per-unit-effort basis (numbers per 750 seconds of shocking). Catch efficiency was assessed but those data are not presented in this paper. Fish were identified to species using keys in Page and Burr (1991), Etnier and Starnes (1993), and Mettee et al. (1996).

### *Statistical Analysis*

Factorial ANOVAs with the five locations, two years, three connection regimes, and sample dates as factors were used to assess variation in total abundance and biomass of invertebrates, abundance and biomass of individual invertebrate taxa, richness and abundance of fish, and water pH, conductivity, and temperature (SAS 9.0, SAS Institute Inc., Cary, NC, USA). Biomass and abundance data were both $\log_{10}(x + 1)$ transformed before ANOVAs were conducted to homogenize variance. For TN and TP levels, which were only sampled once, only locations and connection regimes were used as factors in the ANOVAs. When a significant result was determined, a Tukey HSD *post hoc* test was conducted to determine differences among levels of a factor.

Community analyses were conducted using invertebrate taxon biomass and abundance. Because fish were not present in many collections from mid and low connection sites, among connection-regime community composition analyses were not conducted. Non-metric multidimensional scaling ordinations (NMS) (PC-ORD 5, MJM Software Design, Glenden Beach, OR) were conducted using connection regime, floodplain, and temporal change (year, season) as factors, with Bray-Curtis Similarity as the distance measure for the scaling. When a resemblance matrix suggested groupings, ANOSIM tests (Primer 6, Primer-E Ltd., Plymouth, UK) were conducted to determine significance of the ordination scales. Indicator species analysis (PC-ORD 5) was conducted to identify representative taxa of the different connection regimes (Dufrene and Legebdre 1997); 5000 random permutations were used for the Monte Carlo analysis to test for significance, with only significant species being reported.

# CHAPTER 3

# RESULTS

## *Water Quality*

Annual variation was not detected for any water quality parameter measured (Table 2). Water temperatures warmed seasonally ($F_{2,61} = 21.14$, $p < 0.0001$), and as the flood season progressed, pH increased from moderately acidic (6.9) to circumneutral (7.3) ($F_{2,61} = 6.28$, $p = 0.0036$; Table 2). Temperature, pH, TN, and TP did not vary significantly among high, mid, and low connection sites (see Table 2). However, conductivity at high connection sites was significantly greater than either the mid or low connection sites ($F_{2,61} = 7.14$, $p = 0.0001$; Tukey HSD, $p < 0.05$). Variation in water quality parameters among the five different locations was negligible (data not presented).

## *Fish*

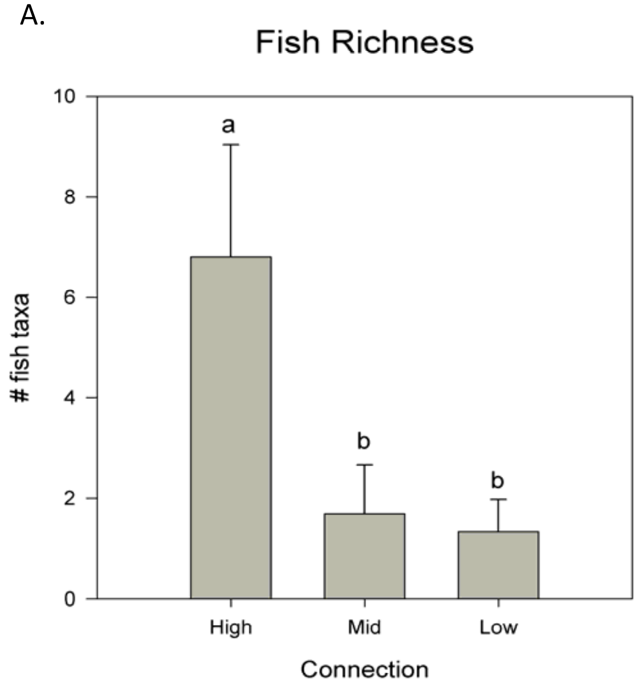
Fish species richness and abundance did not vary between 2007 and 2008, or among sampling dates. Fish species richness did vary among connection regimes ($F_{2,68} = 10.51$, $p = 0.0001$), with more species being found in high connection sites (2.88 species/sample) than either mid (0.68 species/sample) or low (0.57 species/sample) connection sites (Tukey's HSD, $p < 0.05$) (Figure 3A). Of the 413 fish collected, 78% were collected at high connection sites, 7% at mid connection sites, and 15% at low connection sites ($F_{2,68} = 9.21$, $p = 0.0003$) (Figure 3B). Modest differences in fish abundance, but not richness, existed among the five different locations (data not presented). List of fish species present in the floodplain at each connection is listed in Table 3.

Table 2. Variation in water quality parameters in floodplains of the Altamaha and Savannah Rivers. Connectivity effects reflect differences among sites with high (H), mid (M), or low (L) proximity to the river channels (see Table 1), and temporal effects reflect annual or seasonal variation. When ANOVA testing indicated significance ($P < 0.05$), *post hoc* Tukey HSD tests were conducted and results are indicate in the table. *NS = Not significant. **Dash (-) indicates effect not assessed

| Measure | Range | Connectivity effect | Temporal effect |
|---|---|---|---|
| Conductivity | 39-448 µs | H>M=L | NS* |
| Temperature | 9.5-23.5°C | NS* | Feb<April=May |
| pH | 6.20-7.8 | NS* | Feb=April<May |
| Total Phosphorus | 0.07-0.90 mg/L | NS* | -** |
| Total Nitrogen | 0.85-5.62 mg/L | NS* | -** |

Figure 3. Variation in A) fish species richness and B) fish abundance among floodplain sites with high, mid, and low connection to river channels of the Altamaha and Savannah Rivers. Different letters denote significant differences among connection regimes (Tukey HSD tests, $p < 0.05$). Error bars represent ±1 SE.

A.


Fish Richness
# fish taxa
0
2
4
6
8
10
a
b
b
High
Mid
Low
Connection

B.

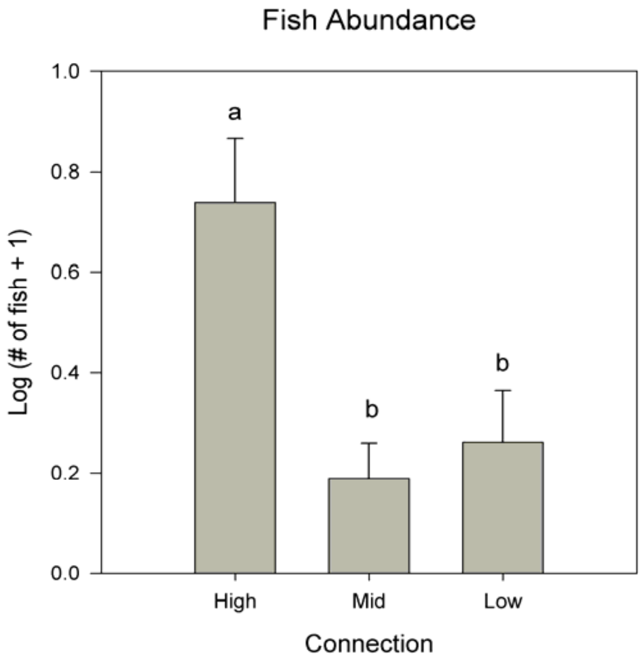

Fish Abundance
Log (# of fish + 1)
0.0
0.2
0.4
0.6
0.8
1.0
a
b
b
High
Mid
Low
Connection

Table 3. Fish species present in the different connections of the floodplain to the river. Bolded fish species were only found in the high connection sites.

| High Connection | Mid Connection | Low Connection |
|---|---|---|
| ***Ameiurus nebulosis*** | *Cyprinella leedsi* | *Amia calva* |
| *Amia calva* | *Esox americanus* | *Centrarchus macropterus* |
| ***Aphredoderus sayanus*** | *Esox niger* | *Esox americanus* |
| *Centrarchus macropterus* | *Gambusia* spp. | *Gambusia* spp. |
| *Cyprinella leedsi* | *Labidesthes sicculus* | |
| ***Elassoma zonatum*** | *Lepomis gulosis* | |
| *Esox americanus* | *Lepomis macrochirus* | |
| *Esox niger* | | |
| *Gambusia* spp. | | |
| ***Heterandria formosa*** | | |
| *Labidesthes sicculus* | | |
| ***Lepomis auritus*** | | |
| *Lepomis gulosis* | | |
| *Lepomis macrochirus* | | |
| ***Lepomis marginatus*** | | |
| ***Notemigonus chrysloeucas*** | | |
| ***Notropis petersoni*** | | |

### *Invertebrate Responses*

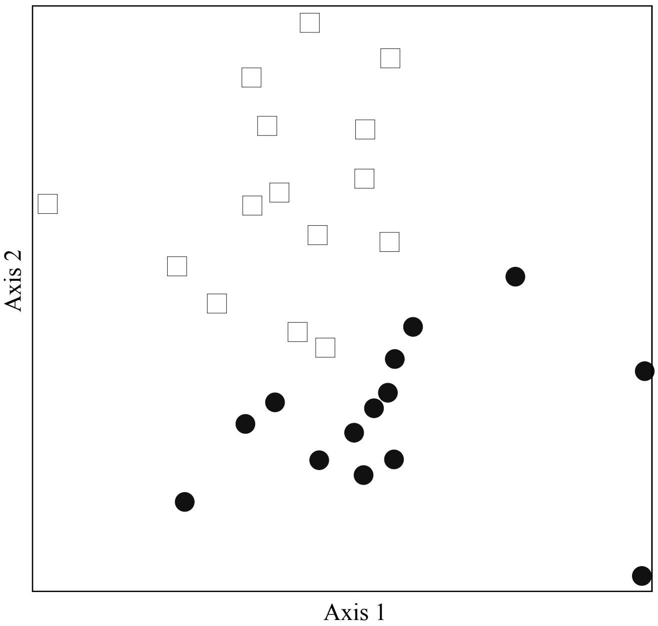
### *Temporal Variation*

Invertebrate total abundance ($F_{1,29} = 2.320$, $p = 0.146$) and total biomass ($F_{1,29} = 0.01$, $p = 0.935$) did not differ between 2007 and 2008. However, in terms of community composition, NMS ordinations for community abundance (Figure 4A) and biomass (Figure 4B) both suggested differences between years, which was confirmed by ANOSIM (abundance Global R = 0.552, $p = 0.001$; biomass Global R = 0.405 , $p = 0.001$). Many of the invertebrate taxa that contributed the most to overall abundance and biomass differed between 2007 and 2008. *Caecidotea* ($F_{1,29} = 8.77$, $p = 0.0075$), Scairidae ($F_{1,29} = 6.10$, $p = 0.0222$), Nematoda ($F_{1,29} = 14.74$, $p = 0.0010$), Oligochaeta ($F_{1,29} = 8.14$, $p = 0.0095$), Chironominae ($F_{1,29} = 18.00$, $p = 0.0004$), Collembola ($F_{1,29} = 19.90$, $p = 0.0002$) and Planorbidae ($F_{1,29} = 12.53$, $p = 0.0019$) had a greater abundance in 2008 than 2007. Cyclopodia ($F_{1,29} = 6.45$, $p = 0.0191$) was more abundant in 2007 than 2008. Biomass of cladocerans ($F_{1,29} = 4.43$, $p = 0.0475$), Chironominae ($F_{1,29} = 67.98$, $p < 0.0001$), Tanypodinae ($F_{2,29} = 1.35$, $p = 0.0058$), Dolichopodidae ($F_{2,29} = 6.34$, $p = 0.0020$), Cecidomyiidae ($F_{1,29} = 4.46$, $p = 0.0468$), and Oligochaeta ($F_{1,29} = 47.31$, $p < 0.0001$) was greater in 2008 than 2007.

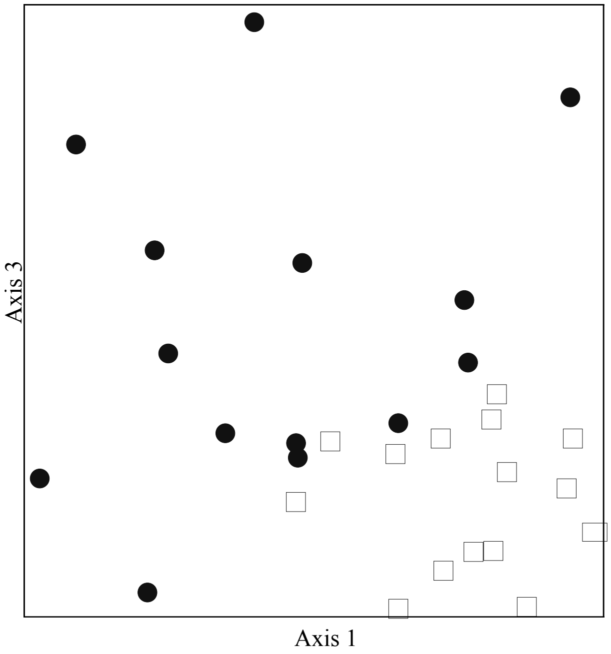
In terms of seasonality, total abundance ($F_{4,75} = 0.50$, $p = 0.6829$) and biomass ($F_{4,75} = 2.05$, $p = 0.0977$) of invertebrates did not differ among sample dates. However, community composition in terms of abundance varied among dates (Global R = 0.254, $p = 0.0001$), with February-March 2007 differing from April 2007, April 2008, and May 2008; February-March 2008 also differed from April 2007.

Figure 4. NMS ordinations in terms of A) abundance and B) biomass for 15 study sites in 2007 and 2008. In each case, samples from 2007 (solid circles) and 2008 (open squares) separated into distinct groups (ANOSIM, $p < 0.001$). NMS stress value for abundance analysis = 15.85, and for biomass analysis = 11.59.

A) Invertebrate Abundance



B) Invertebrate Biomass



### *Spatial Variation*

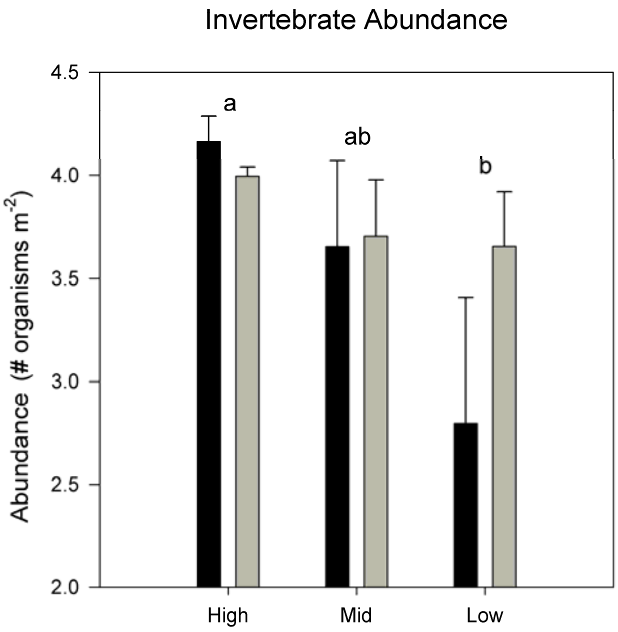
Total invertebrate abundance varied with floodplain connection to the river, with high connection sites (11,546 organisms·$m^{-2}$) differing from the low connections sites (2,050 organisms·$m^{-2}$), and mid connection sites (4,857 organisms·$m^{-2}$) being intermediate ($F_{2,75} = 3.15$ $p = 0.0494$) (Figure 5A). Total invertebrate biomass also varied with connections regime ($F_{2,75} = 3.42$, $p = 0.0388$) (Figure 5B) with high connection sites (3,489 mg DM $m^{-2}$) having greater biomass than low connection sites (586 mg DM $m^{-2}$). Mid connection sites had an intermediate biomass (1,681 mg DM $m^{-2}$).

Most of the taxa that comprised > 1% of the total abundance or biomass did not differ among high, mid, and low connection sites (Figure 6, Table 4). *Caecidotea* and Tanypodinae were the only individual taxa that varied among connection regimes. *Caecidotea* abundance was greater in high connection than low connection sites ($F_{2,29}$=3.52, $p = 0.0481$ Tukey's HSD, $p < 0.05$), although *Caecidotea* biomass did not differ with connection regime ($F_{2,29} = 2.07$, $p = 0.1509$). Tanypodinae abundance did not differ with connection regime ($F_{2,29} = 1.77$, $p = 0.1942$), but their biomass was greater in low connection sites than high and mid connection sites ($F_{2,29} = 9.18$, $p = 0.0014$).

Since community structure varied between years, we assessed differences in community composition among connection regimes separately for 2007 and 2008. Whether in terms of abundance or biomass, community compositions in both 2007 and 2008 were similar among connection regimes (2007 abundance, Global R = 0.082 $p = 0.1840$; 2008 abundance, Global R = -0.012, $p = 0.5580$; 2007 biomass, Global R = 0.025, $p = 0.3160$; 2008 biomass Global R = 0.01, $p = 0.3930$) (Figure 7). However, indicator species analysis showed that *Caecidotea* abundance

Figure 5. The total A) invertebrate abundance and B) invertebrate biomass among floodplain sites with high, mid, and low connection to river channels of the Altamaha and Savannah Rivers. The site with a high connection had the highest abundance and biomass, low connection had the lowest and mid connected site had an intermediate abundance. Black bars represent 2007 and grey bars represent 2008, with analyses including both years. Different letters denote significant differences among connection regimes (Tukey HSD tests, $p < 0.05$). Error bars represent ± 1 SE.

A.


Invertebrate Abundance
Abundance (# organisms m$^{-2}$)
4.5
4.0
3.5
3.0
2.5
2.0
a
ab
b
High
Mid
Low

B.

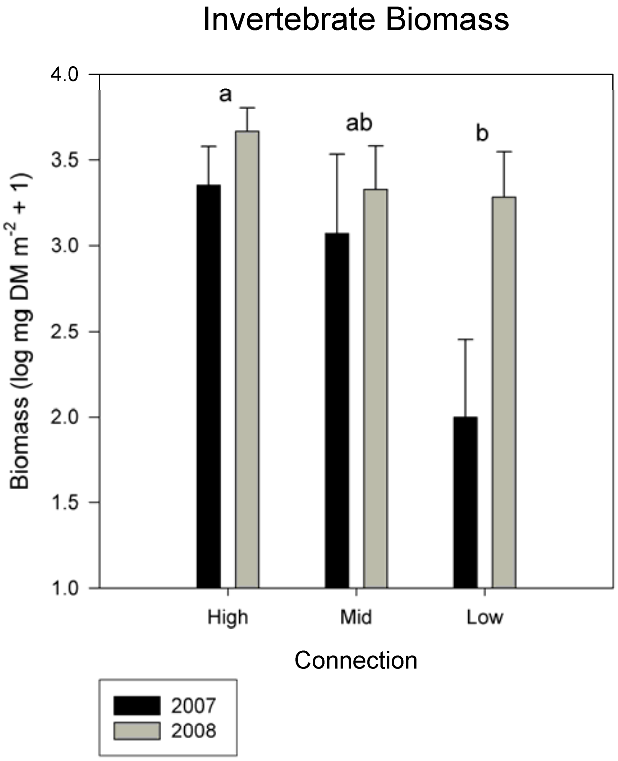

Invertebrate Biomass
Biomass (log mg DM m$^{-2}$ + 1)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
a
ab
b
High
Mid
Low
Connection
■ 2007
▨ 2008

Figure 6. The organisms that accounted for > 1% of the total biomass (left) and abundance (right) in high, mid, and low connection sites. With the exception of *Caecidotea* abundance and Tanypodinae biomass (see text) organisms did not vary among connection regimes. Error bars represent ± 1 SE.

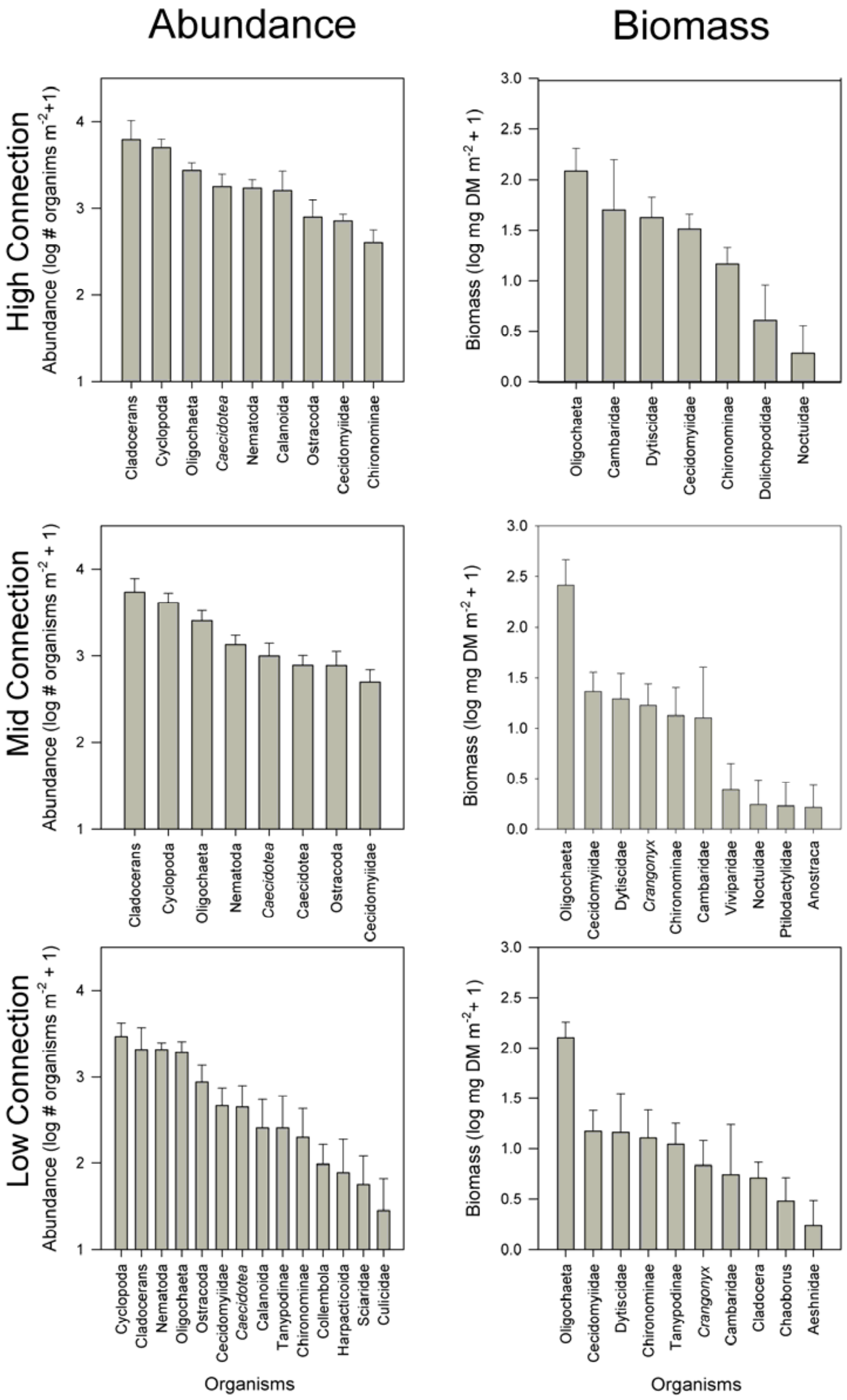
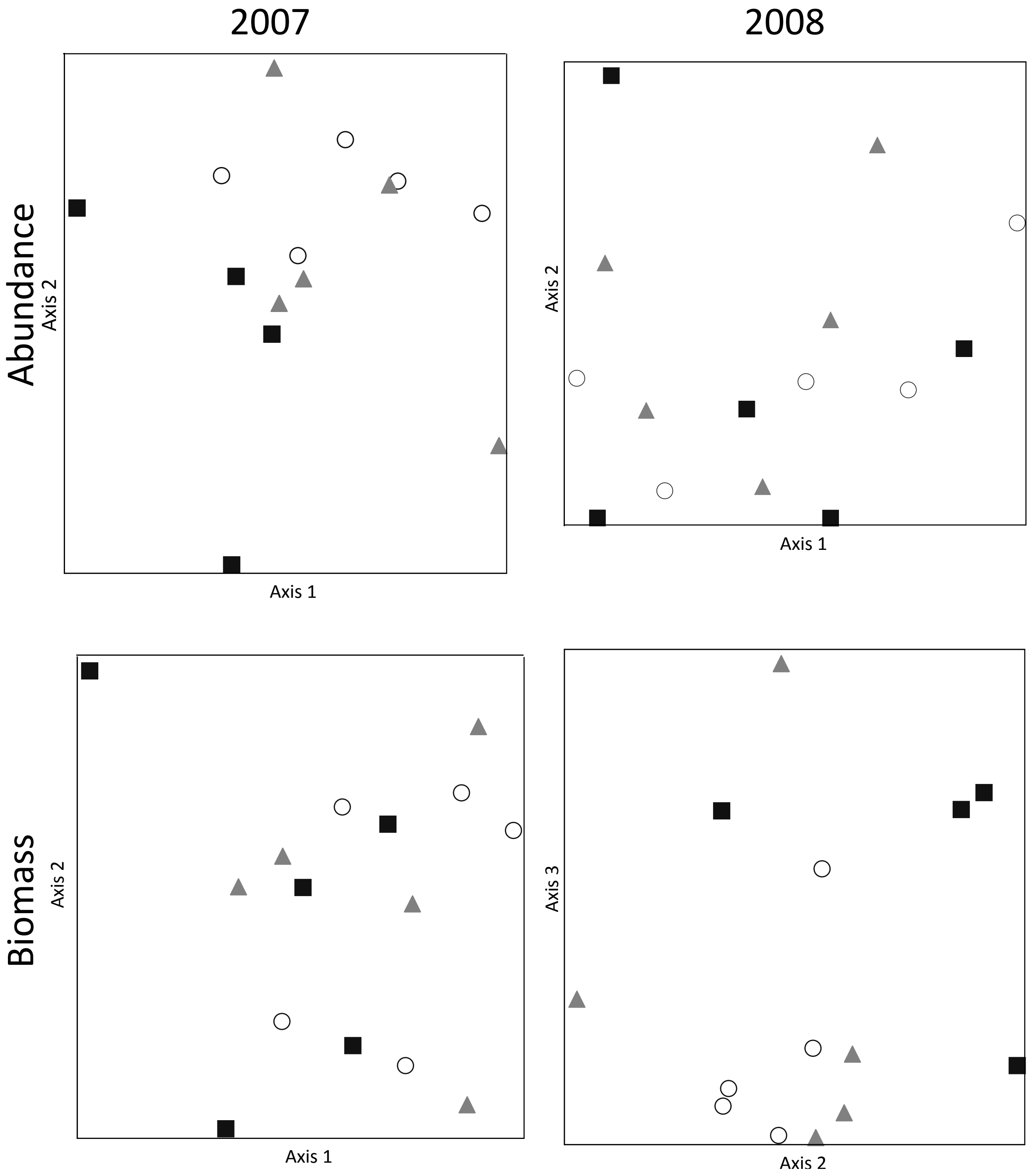

Abundance
Biomass
High Connection
Abundance (log # organims m$^{-2}$+1)
1
2
3
4
Cladocerans
Cyclopoda
Oligochaeta
*Caecidotea*
Nematoda
Calanoida
Ostracoda
Cecidomyiidae
Chironominae
Biomass (log mg DM m$^{-2}$ + 1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Oligochaeta
Cambaridae
Dytiscidae
Cecidomyiidae
Chironominae
Dolichopodidae
Noctuidae
Mid Connection
Abundance (log # organisms m$^{-2}$ + 1)
1
2
3
4
Cladocerans
Cyclopoda
Oligochaeta
Nematoda
*Caecidotea*
Caecidotea
Ostracoda
Cecidomyiidae
Biomass (log mg DM m$^{-2}$ + 1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Oligochaeta
Cecidomyiidae
Dytiscidae
*Crangonyx*
Chironominae
Cambaridae
Viviparidae
Noctuidae
Ptilodactylidae
Anostraca
Low Connection
Abundance (log # organisms m$^{-2}$ + 1)
1
2
3
4
Cyclopoda
Cladocerans
Nematoda
Oligochaeta
Ostracoda
Cecidomyiidae
*Caecidotea*
Calanoida
Tanypodinae
Chironominae
Collembola
Harpacticoida
Sciaridae
Culicidae
Organisms
Biomass (log mg DM m$^{-2}$+ 1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Oligochaeta
Cecidomyiidae
Dytiscidae
Chironominae
Tanypodinae
*Crangonyx*
Cambaridae
Cladocera
Chaoborus
Aeshnidae
Organisms

Table 4. Partial ANOVA table of non-significant organisms that comprised at least 1% of total biomass and abundance at each connection. For each organism df=2; n=29.

| Abundance | | | Biomass | | |
|---|---|---|---|---|---|
| Organism | F-value | p-value | Organism | F-value | p-value |
| Calanoida | 2.42 | 0.11 | Aeshnidae | 1.06 | 0.37 |
| Cecidomyiidae | 0.72 | 0.50 | Anostraca | 0.98 | 0.39 |
| Chironominae | 0.52 | 0.60 | Cambaridae | 0.75 | 0.48 |
| cladocerans | 1.30 | 0.29 | Cecidomyiidae | 1.11 | 0.35 |
| Collembola | 1.35 | 0.28 | Chironominae | 0.02 | 0.98 |
| Culicidae | 2.53 | 0.10 | *Crangonyx* | 1.33 | 0.29 |
| Cyclopoda | 1.19 | 0.32 | Dolichopodidae | 2.00 | 0.16 |
| Harpacticoida | 1.12 | 0.35 | Dytiscidae | 0.75 | 0.49 |
| Nematoda | 1.36 | 0.28 | Noctuidae | 0.03 | 0.69 |
| Oligochaeta | 0.61 | 0.55 | Oligochaeta | 2.37 | 0.12 |
| Ostracoda | 0.06 | 0.95 | Ptilodactylidae | 0.38 | 0.69 |
| Sciaridae | 0.97 | 0.39 | Viviparidae | 1.10 | 0.35 |

Figure 7. NMS ordinations of the invertebrate community structure in terms of abundance (top) and biomass (bottom) in 2007 (left) and 2008 (right) of high (open circles), mid (gray triangles) and low (black squares) connection.


2007
2008
Abundance
Axis 2
Axis 1
Axis 2
Axis 1
Biomass
Axis 2
Axis 1
Axis 3
Axis 2

(Monte Carlo Test, $p = 0.0452$) and biomass (Monte Carlo Test, $p = 0.0488$) was marginally linked to high connection sites.

# CHAPTER 4

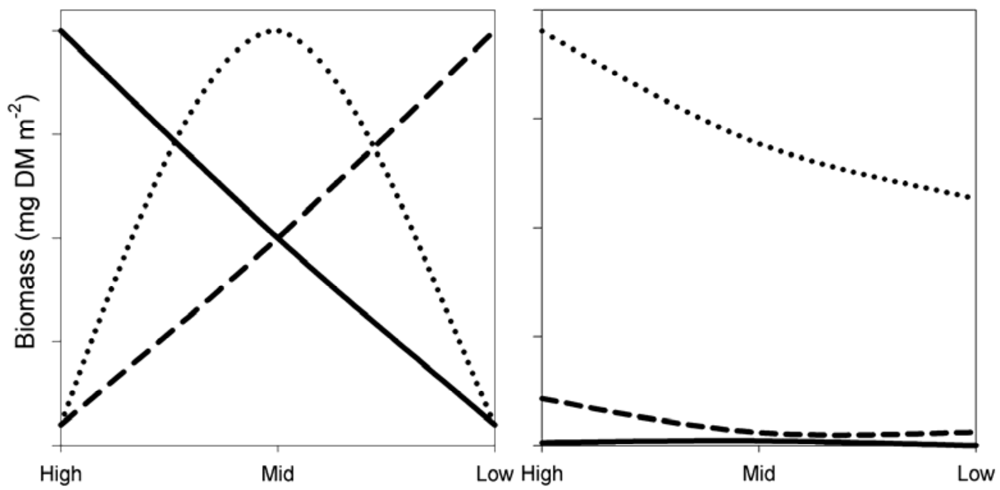
# DISCUSSION

Findings support our first hypothesis that floodplain invertebrate abundance and biomass should decrease as the connection to the river decreases. In this study, invertebrate abundance and biomass differences across the floodplain could be the result of a productivity gradient. Although we did not test productivity directly, we measured conductivity, which has been positively correlated with productivity (Rawson 1961, Russell-Hunter 1970). Conductivity decreased in the floodplain backwater swamps as connection to the river decreased. In addition, other studies have found that floodplain areas with higher connections to the river supported higher primary production than areas with lower connections (Forsberg et al. 1988, Van den Brink 1993, Hein et al. 1999). We did not detect any significant differences in nutrients levels (TP or TN) across the floodplain but those few samples containing high nutrient levels were mid-connection sites rather than high-connection sites. In other floodplain systems, floodplain areas with a higher connection to the river have also been shown to support greater invertebrate abundance and biomass (Gladden and Smock 1990, Gallardo et al. 2008).

Fish could have influenced invertebrate biomass and abundance response across the floodplain. As in other studies (Sullivan and Watzin 2009), the majority of the fish in this study occurred in sites with a high connection to the river, and fewer in the other sites. The presence of fish often reduces invertebrate abundance and biomass (Riera et al. 1991, Batzer and Wissinger 1996), and thus fish predation may have dampened differences between high and low connection sites, making our estimates of invertebrate variation conservative. Fish can also influence the size structure of invertebrates by preferentially choosing the larger organisms (Flecker and Allan 1984, Luecke 1990, Macchiusi and Baker 1991, Wellborn 1994). In our study, *Caecidotea* had a higher abundance in sites with a high connection to the river but biomass did not differ across the floodplain. This suggests a lower proportion of large *Caecidotea* individuals in floodplain areas with a high connection to the river, which may have resulted from size-selective predation. Variation of invertebrate biomass and abundance within the floodplain could influence the food supplies for fish that use the floodplain as nursery or foraging habitat.

Data did not support our second hypothesis that there would be a shift of invertebrate community structure across the floodplain. Overall, invertebrate community composition did not vary with connection regime (Figure 8). High connection sites did not have a high abundance or biomass of any lotic organisms (Ephemeroptera, Plecoptera, Trichoptera). In fact, we collected only three mayfly nymphs (Ephemeridae, Ephemerellidae), two caddisfly larvae (Polycentropodidae, Rhyacophilidae), and no stonefly nymphs over the entire duration of the study. Other studies in the Southeastern US (Gladden and Smock 1990, Smock 1994, Reese and Batzer 2007) have documented significant migrations of lotic invertebrates into floodplains, but the rivers associated with those events were much smaller than the Altamaha and Savannah Rivers. In larger rivers, movements of invertebrates from the river into the floodplain may not be pronounced (Reese and Batzer 2007). Lentic organisms (e.g., dytiscids, *Caecidotea,* cladocerans, ostracods, sphaerids) that we predicted would be most abundant in the interior of the floodplain were found throughout the entire floodplain, and they dominated the abundance and biomass at every site. Flood tolerant non-aquatic organisms (e.g., springtails, mites, centipedes; see Braccia and Batzer 2001, Adis and Junk 2002) were more common than the

Figure 8. The graph on the right is an idealized depiction of our hypothesis that the invertebrate community structure should differ across the floodplain; lotic organisms (solid line) should dominate areas with a high connection, non-aquatic organisms (dashed line) should dominate areas with the lowest connection and lentic organisms (dotted line) should dominate areas with a mid connection to the river.   The left graph represents a depiction of the outcome of the study using actual biomass data from the study; lentic organisms (dotted line) dominated all areas, non-aquatic organisms (dashed line) were prevalent across the entire floodplain, and lotic organisms (solid line) were rare across the floodplain.


Biomass (mg DM m$^{-2}$)
High
Mid
Low
High
Mid
Low

lotic organisms, but they occurred in similar abundance and biomass across the whole floodplain, and were not more prevalent in sites associated with the floodplain-upland ecotone (Figure 8). The lack of unique invertebrate community assemblages across the floodplain could perhaps be a response of the temporary nature of backwater swamp hydroperiods. Temporary habitats usually support greater abundance and biomass of habitat generalists than specialists (Scarsbrook and Townsend 1993, Poff et al. 1997, McCauley 2007).

The lack of unique invertebrate community compositions across the floodplains of along the Savannah and Altamaha River is contrary to the findings of other studies. Gallardo et al. (2008), who studied the floodplain of the Middle Ebro River in Spain, concluded that hydrological connectivity to the river accounted for 28% of invertebrate variability. A study in the Danube River-floodplain (Tockner et al. 1999) concluded that floodplain water undergoes dramatic changes in water chemistry, and biotic communities are directly linked to water levels, which are reflected by hydrological connectivity. Perhaps our results differed from these studies because unlike those researchers, we did not sample in permanent water sites (which were uncommon), but instead focused on seasonally flooded habitat.

River-floodplain connectivity affects invertebrate abundance and biomass in the Altamaha and Savannah River floodplains. The influences of river-floodplain connectivity on invertebrates may be particularly important for river-floodplain ecology because it affects the availability of floodplain invertebrates to higher consumers. The floodplain sites with the highest connection to the river shared both the greatest invertebrate abundance and biomass and the greatest fish abundance. Should river-floodplain connectivity be inhibited, invertebrates that use the floodplain might decrease and become less available to predatory fish. Invertebrates also provide other ecosystem services such as contributing to litter breakdown (Short and Holomuzki

1992), which may also be impaired by reduced connectivity. Although we did not see a dramatic difference between the regulated Savannah River and the unregulated Altamaha River in terms of connectivity, water resource managers should endeavor to maintain a high degree of river-floodplain connection to allow fish access to the invertebrate resources and preserve other ecological functions on floodplains.

# CHAPTER 5

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