ECOLOGICAL IMPACTS OF FLOW REGULATION ON RIVERS AND FLOODPLAINS: MACROINVERTEBRATE DYNAMICS OF THE CHATTAHOOCHEE, ALTAMAHA, AND SAVANNAH RIVERS

by

COURTNEY R. HOLT

(Under the Direction of Darold Batzer)

ABSTRACT

Aquatic habitats are among the world's most valuable ecosystems, including rivers and floodplains. Humans have significantly influenced these ecosystems the world over, particularly in the form of river regulation via dams. The objective of this dissertation is to document effects of river regulation in rivers and floodplains of the southeastern United States. Specifically, I focused on the effects of river regulation on macroinvertebrate dynamics in the Chattahoochee, Altamaha, and Savannah Rivers (Georgia). Direct effects of annual and daily flow variation on the macroinvertebrate communities of the Chattahoochee River below Buford Dam were investigated over an 11 year period. In addition, to assess indirect effects of river regulation, I investigated populations of predaceous diving beetles (Coleoptera: Dytiscidae: *Neoporus*) on the floodplains of the regulated Savannah River and the unregulated Altamaha River. The results from my research indicate significant effects of regulation within the river channel and across the floodplains. Shifts in macroinvertebrate community assemblages were detected between high- and low-flow years on the Chattahoochee, and changes to the overall community occurred over the length of the study area, with improved biological metric scores (H', EPT richness, and sensitive taxa richness) as distance from the dam increased. On floodplains, *Neoporus* beetles exhibited significant sympatry but were overall negatively affected regarding their distribution and propensity for flight as a result of river regulation. With little overbank flooding in the regulated system, *Neoporus* were more likely to be restricted to permanent waters on the floodplain and were less likely to disperse via flight than populations in the unregulated system. These results suggest a need for altered river management strategies where ecosystem integrity is taken into account in addition to human needs. River management strategies should be developed in the context of climate change and increasing pressures on water resources.

INDEX WORDS: Altamaha River, ANOSIM, Chattahoochee River, *Crangonyx*, dams, diversity, Dytiscidae, EPT taxa, flow regime, indicator analysis, macroinvertebrates, *Neoporus*, regulated rivers, Savannah River, sympatry

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DEDICATION

I would like to dedicate this dissertation to my parents, Dave and Carolyn Holt, who have always been my biggest supporters (despite the fact that they cannot comprehend why I enjoy being in swamps and rivers searching for bugs) and to my husband, Matthew McDaniel, who has supported me unquestioningly and been my biggest cheerleader, particularly when I needed it most.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Floodplains are among the most valuable ecosystems in the world, contributing over \$25,500 ha-^{1} yr-^{1} worth of ecosystem services to our planet (Costanza et al. 2014). They are located in every major biome of the world and contain a vast array of the earth's diversity. However, the influence humans have had on rivers and floodplains is widespread and pervasive. The most pervasive environmental change caused by dams is undoubtedly the alteration of the natural flow regime (i.e. the natural dynamism of river flows within and among years) (Poff et al. 1997). Until recently, management strategies have not taken into account the natural dynamic character of flowing systems (Poff et al. 2007). Even now with evidence exhibiting the importance of natural variation in river flows, many management agencies remain limited in their ability and/or willingness to reinstate natural flow regimes.

While many studies have now been completed regarding ecological effects of altered river flows, the direction of these responses (i.e. positive or negative) varies greatly among the studies (Poff and Zimmerman 2010). While fish respond negatively overall to either increased or decreased flow magnitudes, macroinvertebrates exhibit varying responses to altered flow magnitudes according to a literature review of 55 peer-reviewed studies (Poff and Zimmerman 2010). This indicates a need for region-specific macroinvertebrate studies in order to gain a better understanding of the specific effects of altered flow regime.

The southeastern Coastal Plain provides excellent opportunities for studying the effects of altered flow regimes on river and floodplain macroinvertebrates. There are a number of large-scale dams with which to work as well as unaltered rivers that still exhibit historical (natural) flow patterns. In this dissertation, I focus on macroinvertebrates to determine what effects such alteration of flow has had in southeastern river systems. Specifically, my research identifies distributional, behavioral, physiological, and community assembly impacts of flow regulation on riverine and floodplain macroinvertebrates.

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CHAPTER 2

MACROINVERTEBRATE COMMUNITY RESPONSES TO ANNUAL FLOW VARIATION FROM RIVER REGULATION: AN 11-YEAR STUDY[1]

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[1] Holt, C. R., D. Pfitzer, C. Scalley, B. A. Caldwell, and D. P. Batzer. 2015. River Research and Applications 31:798-807.

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Abstract

The majority of the world's large river systems are affected by dams. The influences of unnatural regimes induced by flow management are wide-ranging from both biotic and abiotic standpoints. However, many of these effects are not evident over short (1-2 year) time periods (e.g. impacts of annual flow variation). This study examines the long-term effects of annual flow variation on the macroinvertebrate community in the Chattahoochee River (GA) in the reaches below Buford Dam, the major water control structure on the river. Quarterly macroinvertebrate samples were taken from 2001-2011 using Surber and Hester-Dendy plate samplers at six locations spread across 65 river Km below the dam. Data were analyzed via ANOSIM to determine differences in community composition between high-flow (mean discharge = 58.27 m^3/s) and low-flow (mean discharge = 26.53 m^3/s) years. Taxa that contributed most to community differences were determined via SIMPER analyses and subsequent t-tests. Several insect taxa (e.g. *Cheumatopsyche* and *Ceratopsyche* caddisfly larvae, *Maccaffertium* mayfly nymps, and *Taeniopteryx* stonefly nymphs) were more prevalent under the high-flow regime. Non-insect macroinvertebrates (e.g. *Crangonyx* amphipods, Tricladida flatworms, and *Caecidotea* isopods) were more abundant under low-flow conditions. In terms of taxon richness, no significant effects of flow regime were detected. Implications of macroinvertebrate patterns for the fishery and ecological health of the river are discussed.

Introduction

More than half of the world's large river systems are impacted by dams (Nilsson et al., 2005). In the northern hemisphere alone, over three-quarters of rivers are managed for human use and are no longer free-flowing (Dynesius & Nilsson, 1994). The impacts of dams are wide-ranging and often affect the entirety of river systems—sediment transport, animal and plant dispersal, biodiversity, floodplain functions, nutrient availability, etc. (Ward and Stanford, 1983; Poff et al., 1997; Richter and Thomas, 2007). Effects of river regulation on aquatic biodiversity (from plants to invertebrates to fish) have been studied extensively (Poff et al., 1997; Bunn and Arthington, 2002).

In river ecosystems, macroinvertebrate communities are important in aquatic food webs, can be useful as bioindicators of water quality (Lenat, 1993), and are often dependent on specific flow characteristics. For these reasons, many studies on the impacts of dams have focused on macroinvertebrates (McKinney et al., 1999; Vinson, 2001; Tszydel et al., 2009; Kelly et al., 2013; Tonkin and Death, 2013). Some of these impacts include declines in taxon richness and shifts in relative abundance of major groups following dam construction (Vinson, 2001), shifts in the macroinvertebrate food resources from terrestrial inputs to algae directly below dams (Kelly et al., 2013), and decreases in macroinvertebrate production and biomass following a controlled flood (Cross et al., 2011). Poff and Zimmerman (2010) reported conflicting results after an extensive review of the effects of river flow regulation on macroinvertebrate communities, with some communities responding positively to changes in flow and others responding negatively.

Most studies are conducted over a relatively short time span, however (i.e. one to three years). While such short-term studies can yield important information on the status of a river system at a certain point in time, they may fail to paint a complete picture of the dynamics of riverine ecosystems and, as a result, are not sufficient for long-term management decisions. Long-term studies, simply by encompassing a broader time period, are more likely to incorporate fully the breadth of variation that occurs in a given system. Flow management, in particular, requires long-term assessment as alteration to the flow regime varies greatly based on precipitation. A two- or three-year study may fail to incorporate the wide variety of flows (e.g. extreme high or low flows) that a system will experience over decadal time spans. For example, recovery of macroinvertebrate populations following multiple years of chronic low-flow conditions may take more than one year. A community assessment directly following a span of low-flow years may lead to skewed conclusions.

In the southeastern U.S., the Chattahoochee River is of critical importance to water supplies, hydroelectric power generation, recreation, and regional biodiversity. Because of these multiple uses, it can serve as a model system for other managed rivers in the Southeast and elsewhere. There are several major dams on the Chattahoochee River. Buford Dam, completed in 1957, is the first major dam along the river's length and provides a major source of water and electricity to the metropolitan Atlanta area, as well as recreation in the form of the Lake Lanier reservoir and a productive fishery in the 60–70 km stretch of river below the dam. Morgan Falls dam (~50 km downstream of Buford Dam) exerts additional control in the downstream reaches of the fishery. With a rapidly increasing human population and periods of severe drought, increasing pressure is being placed on the water resources of this river system. Gibson et al. (2005) predict lower minimum and maximum flows on the Chattahoochee as a result of future demands for water and a changing climate. This scenario is not unique to the Chattahoochee River, however. Many rivers across the southeast and U.S. will be experiencing similar trends, making it all the more important to quantify changes to the ecosystem in order to gain an understanding of what may be happening at a larger scale.

For this study, we used an 11-year (2001–2011) dataset from the Chattahoochee River to assess the influence of annual flow variation on the aquatic macroinvertebrate community. The ways in which these changes in flow affect the macroinvertebrate community (both spatially and temporally) could be extremely useful in characterizing the health of the recreational fishery (from a bottom-up perspective), as well as the health of the river overall, and in helping to predict what can be expected based on future demand and climate scenarios. The results of this study can serve as a baseline with the potential for extrapolation to other river systems and fisheries around the world.

Methods

Study Site

The Chattahoochee River begins in the southern Appalachian Mountains and flows approximately 620 km southward where it eventually (after joining with the Flint River to become the Apalachicola River) flows into the Gulf of Mexico. The drainage area of this system is approximately 50,760 km^2. The Chattahoochee has been highly modified by humans through dams, channelization, and urbanization. This study focused on six locations along the 65 km stretch of river from Bowman's Island (site A) (just below Buford Dam) to Cochran Shoals (site F) (near Interstate 285) (Fig. 1). This stretch of river lies within the Piedmont physiographic province. Average rainfall at the study site is approximately 126 cm per year. Average rainfall over the study period (2001-2011) was 119 cm per year. Sites A through C are most strongly influenced by water releases from Buford Dam, whereas a secondary dam at Morgan Falls (just below site D) exerts additional control over sites E and F. Average discharge over the 11-year study period was 42.40 m^3/s at the beginning of the study reach (site A) and 60.30 m^3/s at the end (site F) (Fig. 2). Prior to dam construction, flows were typically higher in winter and spring and lower in summer and fall. That same pattern holds under the current management regime, but most months of the year exhibit either similar or increased discharge volumes compared to pre-dam flows. Increased base flows and more constant flows among rivers regulated by hydroelectric dams is a common occurrence (Graf, 2006). Summer flows have increased by approximately 28 m^3/s compared to pre-dam flows, while February and March flows have decreased (Gibson et al., 2005). On a seasonal time scale, flow variability has increased in the spring but decreased in summer and winter since Buford Dam was completed (Gibson et al., 2005). Currently, Buford Dam creates a highly variable intra-daily flow regime on this stretch of river, leading to fluctuations of up to 280 m^3/s, which may occur up to three separate times daily. Associated fluctuations in temperature accompany these hypolimnetic releases. Water temperatures at site A range from 6.2º C to 17.6º C (USGS, 2013) and alkalinity is typically within a range of 20-25 mg/L (GA DNR, unpublished data). Substrate in the study area consists of a combination of bedrock, loose gravel, and sand (O'Rouke, 2014).

Community sampling

Invertebrate community samples were collected from the six study sites along the Chattahoochee River from 2001 through 2011. Both Hester-Dendy plates (Hester & Dendy, 1962) and a Surber sampler (Surber, 1937) were used to collect samples at each site (except for Site E where only Hester-Dendy plates were used due to water depth restrictions). Each Hester-Dendy multiplate sampler consisted of nine 76 mm^2 masonite plates and was attached with wire cable to a permanent structure on or near the bank of the river and deployed into a free-flowing section of the river. Hester-Dendy plates remained in place until the next sampling date (approximately 3 months). The Surber sampler used for benthic macroinvertebrate sampling consisted of a 500 µm net (with a 22.9-cm diameter opening) and a 30.5 cm^2 open base (which enclosed the sampling area for each Surber deployment). Samples were taken at random locations in a variety of representative habitats including sand, small gravel, and bedrock covered with algae or vegetation. Three replicates were taken at each site using each sampling method on a quarterly schedule (spring, summer, fall, winter) from 2001-2011.

All macroinvertebrates were preserved in 70% isopropyl alcohol, enumerated, and identified to the lowest possible taxonomic level (genus in most cases) using keys in Klemm (1995), Wiggins (1996), Kathman and Brinkhurst (1999), Needham et al. (2000), Epler (2001), Stewart and Stark (2002), Adler et al. (2004), Dillon et al. (2003), Westfall and May (2006), Mackie (2007), Merritt et al. (2008), and Thorp and Covich (2010). The caddisfly genus *Ceratopsyche* was treated as a separate genus in this study although it is now considered a sub-group within *Hydropsyche* (Geraci et al., 2010).

Statistical Analyses

For analysis, data were grouped into two flow regime categories: low-flow (2001, 2002, 2008, and 2009) and high-flow (2003, 2005, 2010, and 2011) based on discharge from Buford Dam (Fig. 2). Mean discharge for the low-flow regime was 26.53 m^3/s; for the high-flow regime, it was 58.27 m^3/s (t-test, p=0.001). Three years (2004, 2006, and 2007) had intermediate discharge levels, but statistically, we were not able to differentiate these intermediate years from either the high- or low-flow years based on annual discharge. Thus, these three years were excluded from the analyses. Discharge patterns throughout the study site mirrored the high/low pattern at Buford Dam. Quantitative data from Hester-Dendy plates and Surber samplers were kept separate in order to account for differences in units and relative catch efficiencies between the two devices for different taxa. Due to the lack of normality, typical of benthic invertebrate samples, all count data were log(x+1) transformed prior to analyses.

Nonmetric multidimensional scaling (NMDS, Bray-Curtis similarity, Kruskal fit scheme 1, 25 restarts) was used to visualize patterns among the samples. Analysis of Similarities

(ANOSIM) was used to test the overall macroinvertebrate communities for significant differences in taxon composition between high- and low-flow years. Because preliminary analyses showed significant differences among seasons and sites, we separated data by season and/or site for all analyses reported. Seasons (with all sites included) were analyzed via two-way ANOSIM (Bray-Curtis similarity, 999 permutations, two-way crossed layout, factors = flow regime, site). Within each season, sites were also analyzed via one-way ANOSIM (one-way layout, factor = flow regime). For samples that exhibited significance, a similarity percentages (SIMPER) analysis (Bray-Curtis similarity, 999 permutations, one-way layout, factor = flow regime) was performed to identify the primary taxa contributing to the difference between high- and low-flow years. Only taxa with an average dissimilarity/standard deviation ratio $\geq$ 1 were considered for further analysis (see below) as this variable indicates how consistently (i.e. low SD) they contributed to the overall dissimilarity between flow regimes. T-tests were used to determine if the organisms indicated by SIMPER exhibited significantly different abundances in high- vs. low-flow years. Because SIMPER is a multivariate analysis, it is inherently less conservative than the t-tests. Thus, there are several instances in which SIMPER indicated a taxon contributed significantly to differences in the community, but the t-test for that taxon was nonsignificant. Each provides useful information regarding the macroinvertebrate community but from differing approaches. We also tested for differences in overall taxon richness (number of taxa per sample) between high- and low-flow years using a 2-way ANOVA (factors = flow regime, season).

All significance testing used $\alpha = 0.05$. NMDS, ANOSIM, and SIMPER analyses were performed using Primer v6 software (Primer-E Ltd, Devon, UK). All other statistical analyses were performed using SAS software (version 9.3; SAS Institute, Inc., Cary, NC, USA).

Results

For a general overview of the macroinvertebrate community, the ten most abundant taxa present in each flow regime category are listed in Table 1. An overall NMDS contrast between high-flow years (2003, 2005, 2010, and 2011) and low-flow years (2001, 2002, 2008, 2009) that included all seasons and all sites did not indicate community differences (Fig. 3A). However, that analysis was clearly confounded by variation among seasons and sampling sites. With all samples taken into account, a significant difference was detected among seasons (summer, fall, winter, spring; ANOSIM, p=0.001) and sites (A through F; ANOSIM, p=0.001). Thus, all further analyses were separated by season and/or site. When separated by season, a comparison between high- and low-flow years (2-way ANOSIM with flow regime and site as factors) exhibited significant differences for each season (Fig. 3B-E) (Table 2). The lone exception was spring samples using Hester-Dendy plates that resulted in a marginally non-significant difference between high- and low-flow years (2-way ANOSIM, spring: p=0.056).

With all sites taken into account, differences between taxa in high- and low-flow years across the seasons emerged (Table 3). In summer, fall, and spring, *Crangonyx* (amphipods) were among the strongest contributors to dissimilarity between flow regimes and were significantly more abundant in low-flow years. In fall and winter, *Cheumatopsyche* (caddisfly larvae) were a strong contributor to dissimilarity between flow regimes and were significantly more abundant in high-flow years. *Maccaffertium* (mayfly nymphs) and *Simulium* (black fly larvae) were also contributors to the dissimilarity in winter and were more abundant in high-flow years.

Because both site and season had an effect, analyses were further broken down to assess individual sites during each of the four seasons. In the summer, all but site A exhibited differences between high- and low-flow years (Table 2). These differences were primarily driven by organisms that were more abundant in low-flow years (Table 3). The only taxon that appeared to benefit from high flows in the summer was *Maccaffertium* at one site (site F). The pattern in the fall and winter, however, shifts in the other direction: the majority of taxa that contributed most strongly to the dissimilarity by site were more abundant in the high-flow years (Table 3). Another shift occurs moving into spring: all taxa that contributed significantly to the dissimilarity by site between flow regimes were more abundant in low-flow years (Table 3). Throughout all seasons, no significant differences in community composition were seen throughout the study period at site A, directly below Buford Dam (Table 2).

Taxon richness was marginally significant between flow regimes (Table 4), and clearly non-significant among seasons (2-way ANOVA, richness: flow regime, p=0.052; season, p=0.83). Even though weak, the general trend for taxon richness appears to be skewed towards low-flow regimes. The macroinvertebrate groups (Class, Order) that comprised community richness contributed equally to richness under both conditions, and unique taxa also occurred in both regimes with equal frequency (Table 4).

Discussion

Flow variation in the Chattahoochee River favored the development of different macroinvertebrate communities over the 11-yr study period. Many of the same taxa were abundant under both flow regimes but in differing proportions (Table 1). Natural variation among seasons and sampling sites was considerable, and when these variables were taken into account distinct annual patterns emerged.

One of the most striking patterns to emerge was that many aquatic insects were less abundant in low-flow years. Only one out of the five most abundant taxa during high-flow years was a non-insect (*Crangonyx*) whereas three out of the five during low-flow years were non-insects (*Crangonyx*, Tricladida, and *Lirceus*) (Table 1). In particular, EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) that are often used as water quality bioindicators (Lenat, 1993) were consistently more abundant in the high-flow years (Table 3). The only seasons in which EPT taxa appeared to benefit from lower flows were the fall and spring, and then only for three genera. For the most part, high flows were much more beneficial to these oxygen-sensitive insect taxa. Due to increased oxygen levels during turbulent high flows, oxygen-sensitive taxa (e.g. *Taeniopteryx, Cheumatopsyche,* and *Maccaffertium*) may have a better chance of survival (Lenat, 1993). In addition to oxygen demands, a recent study by Robinson (2012) also found an increase in some EPT taxa following experimental floods on a regulated river, which he attributed to their smaller overall size (as compared to an amphipod whose abundance decreased following the floods), suggesting these organisms may be more resistant to high-velocity flows. In addition, many of the taxa that benefitted from high flows are collector-filterers (e.g. *Cheumatopsyche, Simulium*), which rely on flow for food delivery. Walters & Post (2011) noted a decrease in body size of collector-filterers as result of drought conditions, suggesting low flows do indeed have negative impacts on this functional feeding group. Thus, there may be multiple benefits of high-flow regimes for these types of organisms.

Fall and winter are also the primary feeding and growth seasons for immature caddisflies in this region, and life cycle changes may contribute to an increase in *Cheumatopsyche* abundance during these seasons and may amplify differences between high- and low-flow years. In addition, oxygen levels in the winter are higher due to turnover in Lake Lanier (Xiao-Qing & Rasmussen, 1999; Wetzel, 2001) and, when paired with high flows, might strongly benefit oxygen-sensitive organisms such as *Cheumatopsyche, Maccaffertium,* and *Taeniopteryx*

(Camargo & Voelz, 1998; Thorp & Covich, 2010). The lack of positive response by aquatic insects to high flows in the spring and summer, however, might result from the fact that the most extreme discharge peaks during high-flow years typically occurred in the spring. These events of extremely high flows may stress many organisms, including those that otherwise benefit from higher than normal flows. Cross et al. (2011) also detected a decrease in invertebrate secondary production following a flood on the Colorado River. Spring might also be a low-point for immature aquatic insect abundance and biomass due to life cycle phenology (Cross et al., 2011), with continuing mortality, plus natural adult emergence, reducing numbers of immatures. Because releases from Buford Dam are hypolimnetic, summer flows have lower oxygen levels. Since the EPT taxa are typically oxygen-sensitive, and new cohorts are just beginning to become established, summer may be a seasonal low-point for their abundance.

While most aquatic insects were favored by high flows, the river is not devoid of macroinvertebrate life during low-flows. Instead of aquatic insects, non-insect macroinvertebrates such as amphipods (*Crangonyx*) and flatworms (Tricladida) dominated the macroinvertebrate community during lower flows (Table 3). During the spring, summer, and fall, the genus *Crangonyx* was the primary driver of differences between high- and low-flow years overall, and this taxon was much more abundant in low-flow years. Interestingly, *Crangonyx* was also abundant in high-flow years during the fall (only at site B). This may speak to the general hardiness of *Crangonyx,* particularly considering the more highly variable flow conditions at site B (compared to sites further downstream) (USGS, 2013). Crustaceans in general are tolerant of less oxygenated, lower quality water conditions (Lenat, 1993), which could explain why this amphipod consistently did well in low-flow conditions during this study. With decreased flow volumes, organic matter accumulation in the channel may increase as well, providing a larger food source for these collector-gatherers. Previous studies have found a similar pattern with low-flow phases of an impounded river favoring amphipods and flatworms compared to high- flow stages (McKinney et al., 1999; Robinson & Uehlinger, 2008; Robinson, 2012). Even among amphipods, MacNeil et al. (2000) found that a species of *Crangonyx* was particularly well equipped to tolerate low-oxygen waters. In the southeastern U.S., *Crangonyx* thrives in lentic, floodplain habitats (Reese & Batzer, 2007) and other wetlands (Batzer et al., 2005; Kratzer and Batzer, 2007) where oxygen levels can become very low. Haxton and Findlay (2008) performed a meta-analysis on studies concerning effects of flow alteration on fluvial specialists versus habitat generalists and found that, overall, fluvial specialists decreased in abundance in response to flow alteration while habitat generalists were not affected. Our study lends further support to that pattern.

However, it is important to note that any apparent benefits of low-flow conditions to *Crangonyx* could be a sampling or statistical artifact. Rather than actually increasing in number during low flows, catch rates might have simply increased because *Crangonyx* populations became concentrated in residual water. Samplers were placed in similar habitats despite flow regime; thus, sampling was not biased towards *Crangonyx*-dense habitats necessarily. From a statistical standpoint, because low-flows hindered sensitive organisms such as immature insects, the relative importance of *Crangonyx* to our statistical tests evaluating differences in flow regime might have been magnified during low-flow periods.

After breaking down the data set even further to evaluate individual sites, we detected finer scale patterns within the Chattahoochee River macroinvertebrate community. First, it is interesting to note that at site A, the site closest to Buford Dam, macroinvertebrate communities never differed between high- and low-flow years. One reason that site A might have been unique is that, while the difference in discharge between high- and low-flow years was statistically significant, its magnitude was less at site A than at sites downstream (USGS, 2013). This annual flow pattern at site A could be the reason that community differences did not develop at site A among years with different flows. A second explanation centers around the fact that the environment just below the dam experiences water conditions similar to many other regulated tailwaters. Because Buford Dam is managed to generate electricity, and flows through the dam mirror daily changes in electrical demand, fluctuations of discharge within a single 24-hour period can be drastic, especially immediately below the dam. Such frequent changes in flow may prove a difficult environment for macroinvertebrates to survive. Additionally, water released is coming directly from the bottom of the dam and, therefore, is unnaturally cold and contains little oxygen (Olmstead & Bolin, 1996). Nutrient levels in dam tailwaters are also often low (Liu and Yu, 1992; Zhong and Power, 1996), potentially altering trophic conditions directly below the dam. Kelly et al. (2013) found that algal resources provided the majority of food just below a dam, while terrestrial inputs made up the base of the food web in downstream sections of the river. Finally, hydrogen sulfide concentrations (Baxter & Glaude, 1980), turbidity (Liu & Yu, 1992), and sediment loading (Baxter and Glaude, 1980; Liu and Yu, 1992; Zhong and Power, 1996) are often altered below dams.

On the other hand, at sites further downstream (C through F), daily fluctuations in flow are more muted, but longer-duration annual changes in flow level are greater. It was at these downstream sites (primarily C and F) where higher high flows appeared to benefit many insect groups, especially during the fall and winter (Table 3). Long periods of higher flow may have created a more hospitable environment year-round for a variety of long-lived insects, bolstering their survival in the downstream reaches. An increase in insect abundance at the downstream sites could also be due, in part, to increased drift from areas further upstream induced by higher water volume and velocity during high-flow years (Cross et al., 2011). Site E, just below Morgan Falls Dam, and a tributary (Fig. 1), however, did not exhibit a difference in community composition between high- and low-flow years in the fall and winter. Reasons for this are not clear, but the pattern may be attributable to Morgan Falls Dam and/or the tributary moderating flows at site E, thus muting the extreme flow variation from Buford Dam.

Regarding overall taxon richness in this system, the trend toward greater richness in low-flow years is somewhat surprising, considering the decreased oxygen levels and potential decrease in food resources due to decreased flow through the system. Other studies have found a similar decrease in macroinvertebrate richness, however, following high flows (Robinson & Uehlinger, 2008; Robinson, 2012). When this information is combined with the detailed community analysis showing a major shift in macroinvertebrate communities between flow regimes, it speaks to the importance of species identity as opposed to richness or diversity measurements alone. A major shift in community structure is not necessarily reflected in richness or diversity analyses, and, thus, these measurements may not provide a complete picture of the status of the ecosystem.

Management Implications

The overall aquatic macroinvertebrate community in the Chattahoochee appears to be distinct between high- and low-flow years. High-flow years tended to support a greater abundance of EPT taxa, which are often associated with ecologically healthy rivers. This might suggest that low flows in the Chattahoochee are ecologically stressful for some taxa. However, some taxa appeared to benefit from low flows, and low-flow years supported as many, or more total taxa than high-flows years, including rare taxa (Table 4).

With respect to the fishery on this section of the river, patterns also appear fairly equivocal. In a diet composition study on the same stretch of the Chattahoochee, O'Rouke (2014) found that four of the most commonly ingested items by rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) included Trichoptera, Plecoptera, *Simuliium,* and amphipods. Plecoptera and *Simuliium* were more abundant in high-flow years according to our study, Trichoptera were found commonly in both high- and low-flow years, and amphipods were consistently found more commonly in low-flow years. Amphipods (*Crangonyx* in particular) that dominate during low flows are a common prey of many fish species (Cross et al., 2011). Thus, it appears that fish in this system have an appropriate food source despite the flow regime and may be simply consuming the macroinvertebrates that are available at any given time. The low flows that occurred over our 11-year study period were not beyond the tolerance limits of the macroinvertebrate community as a whole, although certain groups (e.g. insects) may be negatively affected by low flows. It is important to note that these conclusions are based on solely on abundance measures, however. Macroinvertebrate biomass may differ between high- and low-flow years, which could significantly impact the productivity of the fish community. In fact, Robinson & Uehlinger (2008) and Cross et al. (2011) observed a decrease in invertebrate biomass following controlled floods. While the high-flow years analyzed in this study were not controlled floods, the same pattern may emerge if biomass were to be taken into account. In addition to potential biomass changes in the river, riparian areas may be affected by changes in the food web as a result of decreased insect emergence into the riparian zone during low-flow years.

Based on what we found in this study, changes in water management at a large scale (e.g. based on water agreements between Alabama, Florida and Georgia) could have direct impacts on the Chattahoochee River macroinvertebrate community. Water from the Chattahoochee flows from northern Georgia southward through Alabama and Florida, creating the Apalachicola-Chattahoochee-Flint (ACF) River system. During droughts, water flows from Lake Lanier have been reduced, leading to significantly lower water levels throughout the remainder of the ACF basin, including the reach below Buford dam. With reduced flows, tolerant organisms such as amphipods will be favored, while increased flows will favor the more ecologically-sensitive aquatic insect community. In terms of maintaining diverse and healthy macroinvertebrate communities, including those taxa that are important forage for fish a “one-size-fits-all” approach to flow management is probably not warranted. Instead, a variable approach, which would better mimic the natural variation inherent in most rivers, might be more appropriate.

The extensive amount of data collected in this system has been and will continue to be an extremely valuable contribution towards understanding the effects of dams on aquatic macroinvertebrate communities. Because long-term data sets are rare, this 11-year (and potentially longer) dataset will facilitate the analysis of questions that are impossible to answer over shorter time periods. With future water demand and climate scenarios suggesting that overall flows in this system will become lower (Gibson et al., 2005), continued monitoring of the macroinvertebrate community is important.

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Table 2.1 The 10 most abundant macroinvertebrates of the Chattahoochee River. Taxa are separated by flow regime. Taxa are listed in order of most- to least-abundant (within each flow regime).

Low-flow	**High-flow**
Simulium	*Simulium*
Crangonyx	*Cheumatopsyche*
Tricladida	*Ceratopsyche*
Cheumatopsyche	*Crangonyx*
Lirceus	*Maccaffertium*
Caecidotea	*Lirceus*
Ceratopsyche	Tricladida
Maccaffertium	Lumbriculidae
Lumbriculidae	*Iswaeon*
Cricotopus	*Caecidotea*

Table 2.2 Results of the analysis of similarity (ANOSIM) and similarity percentages (SIMPER) analyses. ANOSIM with all sites included ("Overall") were performed using a two-way layout (Bray-Curtis similarity, 999 permutations, factors = flow regime, site). Individual site analysis via ANOSIM was performed using a one-way layout (Bray-Curtis similarity, 999 permutations, factor = flow regime). Only those communities that exhibited significant differences via ANOSIM are included ($p \leq 0.05$). Dissimilarities between flow regimes (high vs. low) for each community are also listed (SIMPER: Bray-Curtis similarity, 999 permutations, factor = flow regime).

Season	**Site**	**Sampling Method**	**ANOSIM p-value**	**SIMPER disssimilariy (%)**
Summer	Overall	HD	0.001	80.5
		Surber	0.001	75.8
	B	HD	0.038	75.2
	C	HD	0.014	82.2
		Surber	0.004	77.6
	D	Surber	0.002	79.4
	E	HD	0.004	68.5
	F	Surber	0.028	84.1
Fall	Overall	HD	0.002	80.2
		Surber	0.001	82.4
	B	HD	0.031	86.9
	C	Surber	0.003	75.0
	D	Surber	0.001	84.6
	F	HD	0.002	70.6
		Surber	0.004	83.3
Winter	Overall	HD	0.001	79.7
		Surber	0.001	88.0
	C	HD	0.01	75.8
		Surber	0.002	77.4
	D	Surber	0.002	84.3
	F	HD	0.002	71.9
		Surber	0.003	90.1
Spring	Overall	Surber	0.012	78.8
	C	HD	0.035	71.0
	E	HD	0.044	57.4
	F	Surber	0.008	89.7

Table 2.3 Results of the similarity percentages (SIMPER) analyses. SIMPER analyses (Bray-Curtis similarity, 999 permutations, one-way layout, factor = flow regime) and subsequent t-tests for abundance differences between high- and low-flow years (separated by season) are presented. Taxa listed contributed consistently to the dissimilarity between flow regimes (average dissimilarity/SD ≥ 1) (SIMPER) and exhibited significant differences in abundance between flow regimes ($\alpha \leq 0.05$) (t-tests). Sites at which taxa exhibited significantly different abundance between flow regimes are noted. "Overall" indicates taxa abundance was significantly different between high- and low-flow years with all sites included (2-way ANOSIM).

Season	**Greater abundance in low-flow years**	**Site(s)**	**p-value**	**Greater abundance in high-flow years**	**Site(s)**	**p-value**
Summer	*Crangonyx*	Overall	0.002	*Maccaffertium*	E	0.030
		B	0.002			
		C	0.010			
		D	0.046			
	Caecidotea	B	0.006			
		E	0.003			
	Tricladida	C	<0.001			
		D	0.003			
Fall	*Crangonyx*	Overall	0.009	*Cheumatopsyche*	Overall	0.001
		D	0.001		F	<0.001
	Ceratopsyche	C	<0.001	*Ceratopsyche*	F	0.007
	Tricladida	D	<0.001	*Crangonyx*	B	0.008
				Hydropsyche	F	0.023
				Simulium	F	0.005
Winter	Tricladida	C	0.007	*Cheumatopsyche*	Overall	<0.001
		D	0.002		F	0.020
	Crangonyx	D	0.040	*Ceratopsyche*	F	0.001
				Lirceus	F	0.030
				Maccaffertium	Overall	0.002
					C	0.030
				Simulium	Overall	0.002
					C	<0.001
					F	0.010
				Taeniopteryx	C	0.008
Spring	*Crangonyx*	Overall	0.010			
	Cheumatopsyche	E	0.040			
	Caecidotea	E	0.010			
	Ceratopsyche	F	0.048			
	Dicrotendipes	E	0.020			
	Hydropsyche	F	0.010			
	Tricladida	C	0.004			

Table 2.4 Taxon richness during high- and low-flow years in the Chattahoochee River. The first two data columns include totals of all taxa found in all samples (separated by flow regime). The second two data columns include only taxa that were unique to one flow regime or the other (e.g. only found in low-flow years).

Taxa		**Total Taxa**		**Unique Taxa**	
		High-flow	**Low-flow**	**High-flow**	**Low-flow**
Mollusca		4	5	--	1
Annelida		12	17	1	5
Crustacea		6	6	1	1
Insecta	*EPT Taxa*	36	45	6	13
	Non-EPT Taxa	51	57	12	17
Other		4	4	--	--
Total		**113**	**134**	**20**	**37**

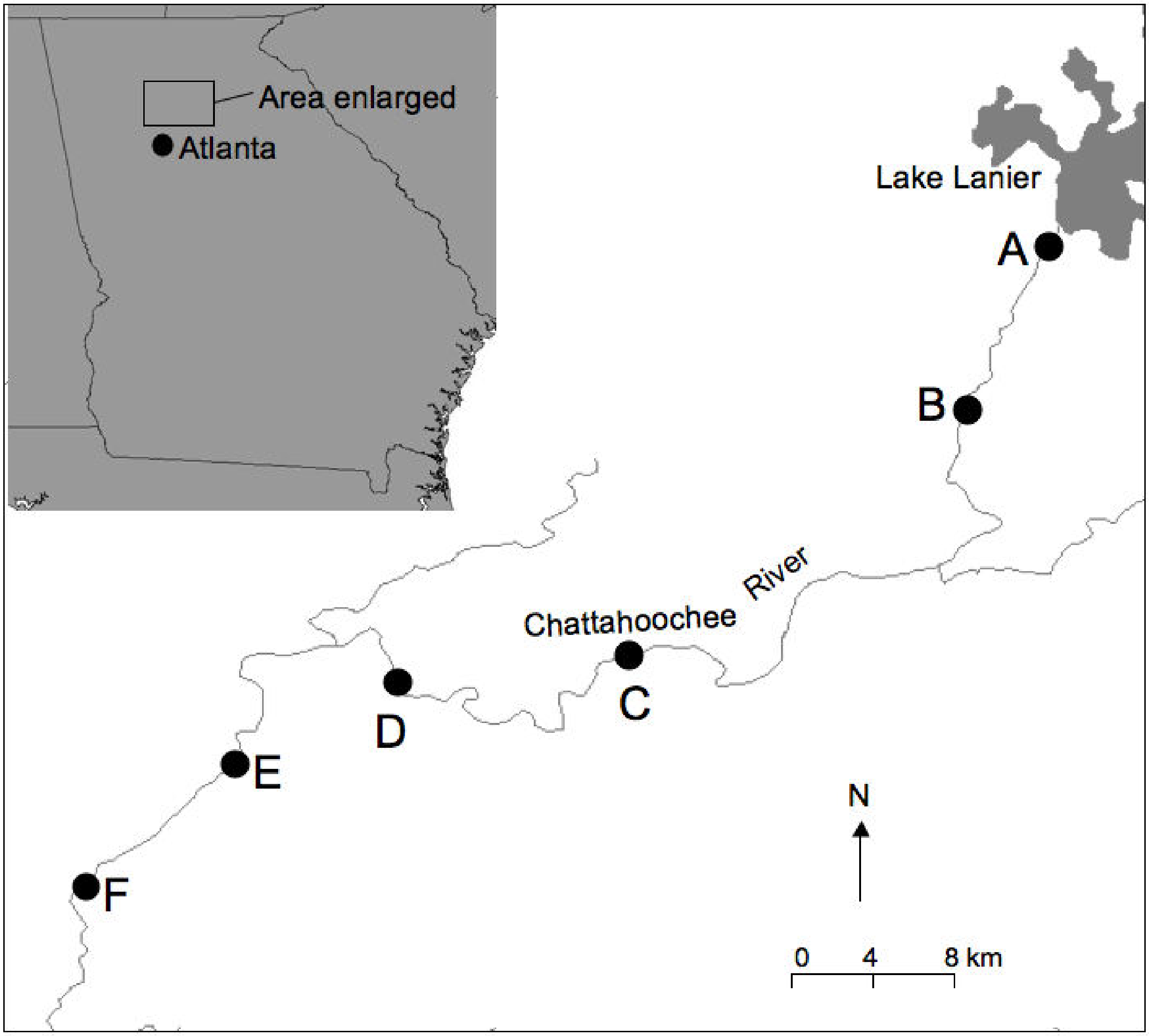

Figure 2.1 Map of the Chattahoochee River study site. Site locations are marked as following: A (Bowman's Island), B (Settles Bridge), C (Jones Bridge), D (Island Ford), E (Morgan Falls), and F (Cochran Shoals).

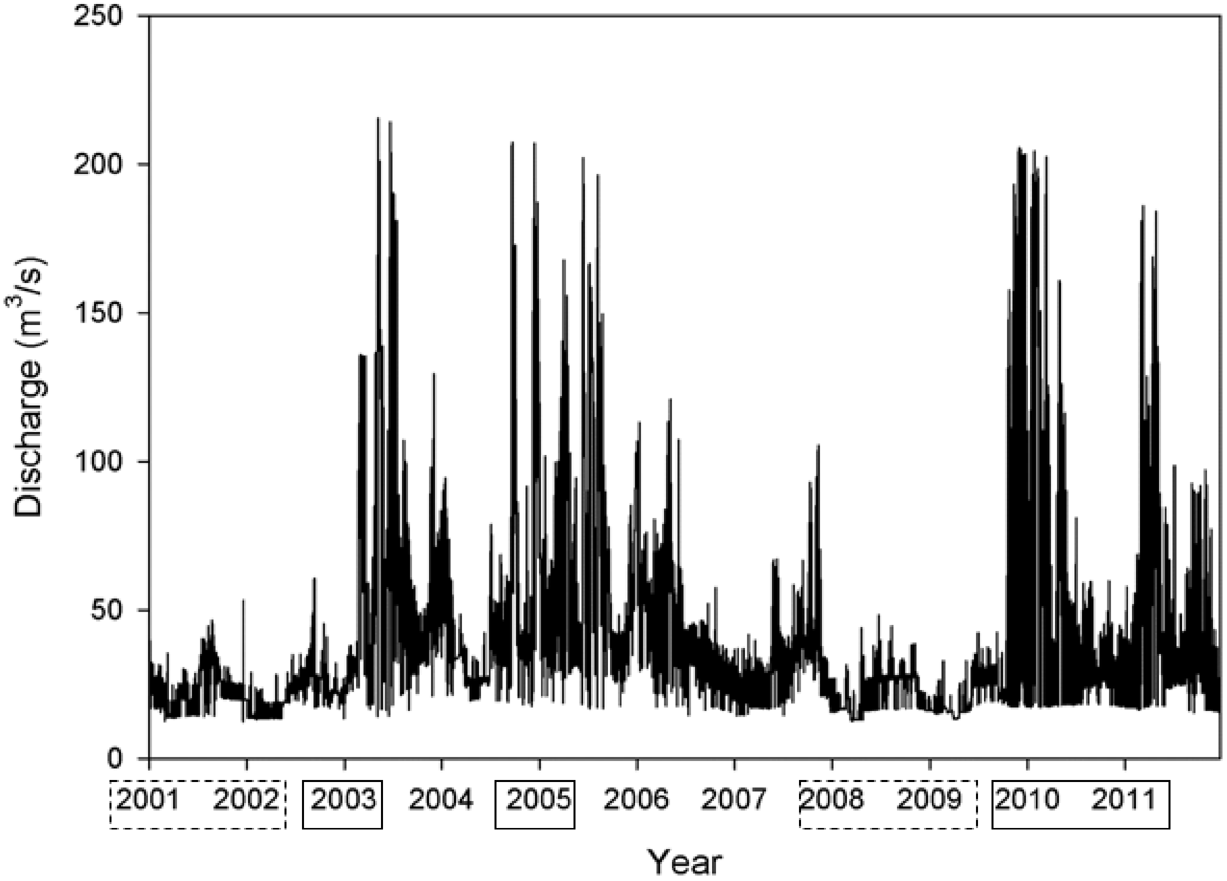

Figure 2.2 Hydrograph of the Chattahoochee River below Buford Dam. Discharge levels upstream of the first sampling location (site A) for the entire study period (2001-2011) are shown. High-flow years include 2003, 2005, 2010, and 2011 (solid boxes on x-axis) (mean discharge=58.27 m^3/s). Low-flow years include 2001, 2002, 2008, and 2009 (dashed boxes on x-axis) (mean discharge=26.53 m^3/s).

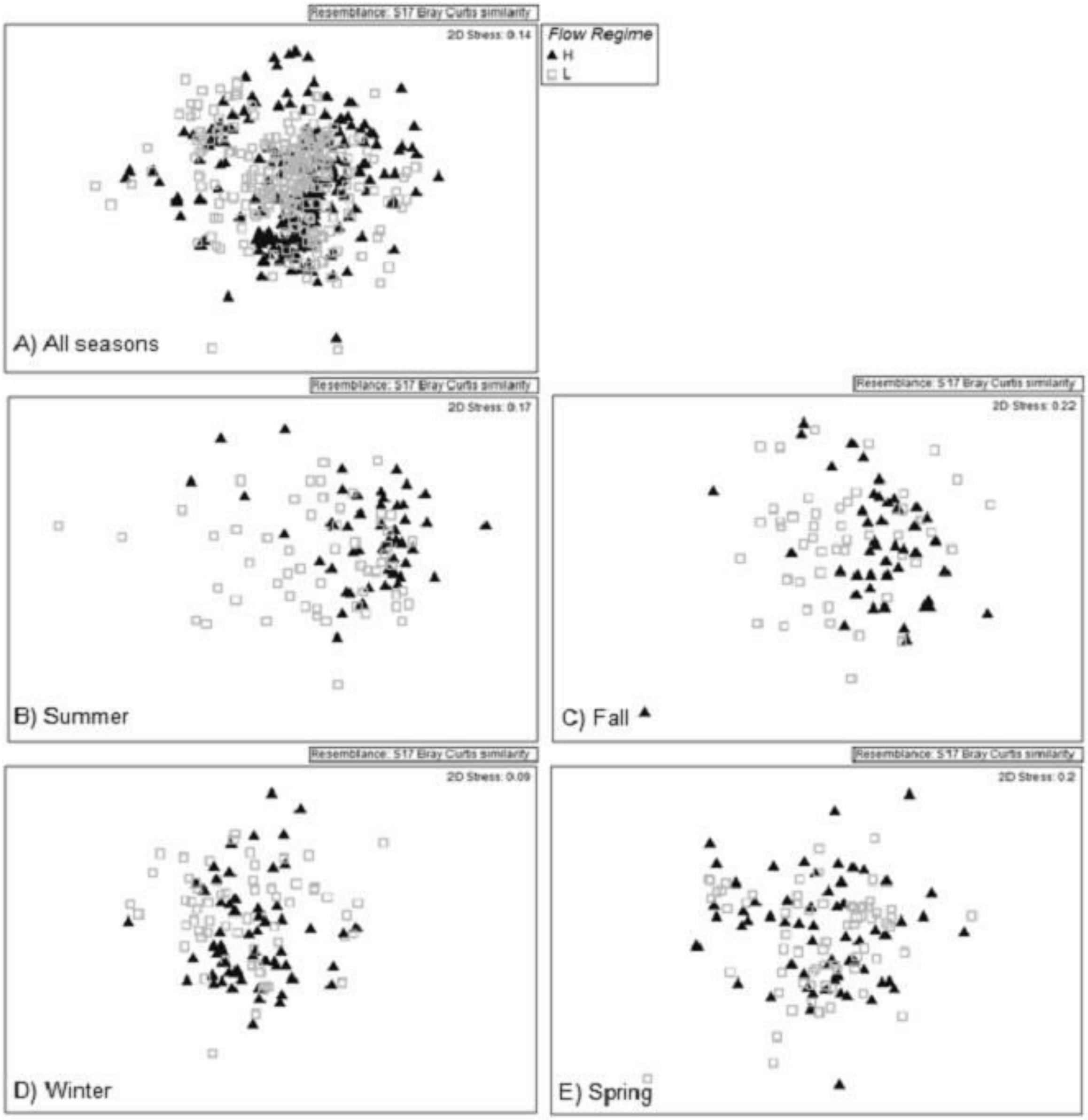

Figure 2.3 NMDS plots comparing high- versus low-flow regimes on the Chattahoochee. High-flow years are represented by filled triangles and low-flow years are represented by open squares (all 6 sites included) (Bray-Curtis similarity, Kruskal fit scheme 1, 25 restarts). A) with all seasons included, B) summer only, C) fall only, D) winter only, E) spring only.

CHAPTER 3

LONGITUDINAL VARIATION IN MACROINVERTEBRATE ASSEMBLAGES BELOW A LARGE-SCALE HYDROELECTRIC DAM

[1] Holt, C. R., D. Pfitzer, C. Scalley, B. A. Caldwell, and D. P. Batzer. 2015. Hydrobiologia 755:13-26.

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Abstract

Worldwide, dams have had pervasive impacts on their associated river systems. In this study, we examined the effects of a large-scale dam on the downstream macroinvertebrate assemblages of a 65-km stretch of the Chattahoochee River (Georgia, USA) over an 11-year period. We quantified differences among six sites within the study reach using NMS, ANOSIM, invertebrate metrics (Shannon-Weiner diversity, number of EPT taxa, and number of sensitive taxa), and indicator analysis. We compared results from this study to the nearby unregulated Middle Oconee River. There were significant differences among all sites and increases in all macroinvertebrate metrics as distance from the dam increased (and diel flow variation decreased). Indicator analysis supported this pattern: no EPT indicator taxa existed directly below the dam, whereas 17 were indicators at the final site. Similarity between the Middle Oconee and the Chattahoochee was moderate (52%). Our results suggest that impacts of the dam are far-reaching and long-term, and that the macroinvertebrate assemblage does not return to a fully representative state even 65 km downstream. This study contributes to the small but growing field of research on effects of dams over long temporal and spatial scales.

Introduction

Dams have had a pervasive impact on the majority of the world's river systems, ranging from altered temperature regimes and sedimentation patterns (Poff et al., 1997; Vinson, 2001) to substantial changes in biological communities (Poff et al., 1997; Vinson, 2001; Haxton & Findlay, 2008; Holt et al., 2015). Many researchers consider flow regime as the most important variable shaping biotic communities and abiotic factors in lotic systems (Poff et al., 1997; Gibson et al., 2005; Kennard et al., 2007; Konrad et al., 2008; Poff & Zimmerman, 2010; Holt et al., 2015). This concept holds for dam-impacted streams as well and may in fact play an even larger role depending on the dam management regime. Large-scale hydropower dams, in particular, create highly variable stream flows based on energy demands at different times of the day (Richter & Thomas, 2007). In general, this involves a rapidly-changing hydrologic cycle, with discharge peaks that may be much higher than in a natural system followed by very low water releases aimed at recharging the reservoir (Richter & Thomas, 2007). These extreme alterations in hydrologic amplitude can occur over short periods of time (24 h) and may result in heavy scouring of the river channel, altered temperature regimes, displacement of riverine organisms, and stranding of slow-moving aquatic organisms (Andrews, 1986; McKinney et al., 1999; Topping et al., 2000; Richter & Thomas, 2007).

On the other hand, artificially cold tailwater habitat below dams has created productive coldwater fisheries that otherwise would not have been present based on geographical and ecological constraints. From a recreational standpoint, these fisheries provide excellent angling opportunities and generate a significant source of revenue for local natural resources agencies. However, while dams create these man-made habitats, they can have differing degrees of impact on the macroinvertebrate communities based on their operations, in turn impacting the primary food source for fish. Therefore, it is of primary importance to investigate the effects of dam operations on the macroinvertebrate community in order to gain a bottom-up perspective on the overall health of the ecosystem.

Recent studies have characterized macroinvertebrate communities below dams (Haxton & Findlay, 2008; Poff & Zimmerman, 2010). Overall, these studies show severe impacts on the communities with decreased species richness and abundance as well as a shift to more disturbance-tolerant assemblages (Vinson, 2001). Few studies have examined changes over large spatial scales, however (Stevens et al., 1997; Marchetti et al., 2011; Cross et al., 2013; Minshall et al., 2014). The majority of the research has focused on relatively small sections of rivers (from 150 m to 27 km) immediately below dam. Our study adds to the small but growing field of research on large-scale impacts of dams on macroinvertebrate communities.

The goal of our study was to investigate assemblage patterns along a 65-km stretch of river below a major dam over an 11-year study period. This study took place on the Chattahoochee River near Atlanta, Georgia (USA). This river is highly impacted by humans, primarily in the form of Buford Dam, a large-scale hydroelectric dam. The primary objectives of this study were to (1) characterize the macroinvertebrate assemblages within the 65-km tailwater section of the Chattahoochee below Buford Dam, (2) assess spatial variation in the macroinvertebrate assemblages along this 65-km section, and (3) compare the macroinvertebrate assemblage in this section of the Chattahoochee with a historically published assemblage from the nearby unregulated Middle Oconee River.

Materials and Methods

Study Sites

The Chattahoochee River begins in the Appalachian Mountains of north Georgia and flows south to the Gulf of Mexico after joining the Flint River in southern Georgia to form the Apalachicola River. The drainage area of this river system is approximately 50,760 km^2. The current study focuses on a 65-km stretch of the Chattahoochee River just below Buford Dam, located within the Chattahoochee River National Recreation Area in the Piedmont region of Georgia (Fig. 1). Buford Dam is a major hydroelectric dam that provides service to a large portion of the Atlanta population. The dam was completed in 1956 and has exerted exclusive control over this section of the river since its construction. Based on demand for electricity, water flow through this dam can be highly variable. Buford Dam is managed to maintain a base flow of 21.2 m^3 s^{-1} at Peachtree Creek (approximately 76 km downstream from the dam) to guarantee downstream communities receive sufficient water. However, the amount of variation that can occur within a single day can be quite extreme, with fluctuations of up to 280 m^3 s^{-1}, creating a very unnatural flow regime within the river below Buford Dam. The most extreme diel amplitude fluctuations occur in the section directly downstream of the dam (Fig. 2). Average daily amplitude just below Buford Dam is 133.53 m^3 s^{-1}. As distance from the dam increases, diel amplitude fluctuations decrease (average diel amplitude 73 km downstream from Buford Dam = 40.38 m^3 s^{-1}) (Fig. 2). Releases from the dam are hypolimnetic, creating a fluctuating temperature regime in addition to the fluctuating amplitude. Water temperatures directly below the dam range from 6.2ºC to 17.6ºC, creating (at times) an abnormally cold stretch of river for this region. As a result, a productive recreational trout fishery has developed and is managed by the Georgia Department of Natural Resources (DNR). Until recently, few biological studies have focused on this section of the river (O'Rouke, 2014; Holt et al., 2015) but the National Park Service (NPS) is interested in quantifying the ecological effects of the current dam management regime regarding spatial variation in the macroinvertebrate communities and how these communities compare to an unregulated river in the Georgia Piedmont.

In addition to Buford Dam, a second smaller hydroelectric dam (Morgan Falls Dam) 56 river km downstream from Buford Dam exerts influence over the final section of the study area (15 km). Minimum flow from this dam is maintained at 21.2 m^3 s^{-1}, and the river below this dam experiences far less diel amplitude variation (Fig. 2), which may help moderate some of the extreme differences in flow from Buford Dam.

Within the study reach, six sites were chosen for macroinvertebrate sampling ranging from just below Buford Dam (site A) to Cochran Shoals (site F) (Fig. 1). These specific sites were chosen based on their proximity to the two dams controlling water flow in the study reach: two sites just below Buford Dam (A and B), two sites part-way between Buford and Morgan Falls Dams (C and D), and two sites below Morgan Falls Dam (E and F). See Figure 1 for specific locations of sites within the study area. The substrate throughout the study area is characterized by bedrock, loose gravel, and sand. Specific substrate data is not available for each individual sampling site. Large woody debris occurs sporadically but is limited by peaks of discharge associated with power production. The two sites closest to Buford Dam (A and B) experience more severe scouring of the substrate than the remainder of the study area. Site E (below Morgan Falls Dam) is significantly deeper than the remaining sites with increased scour as well (though to a lesser degree than sites directly below Buford Dam). The land bordering the river throughout the study area is composed primarily of bottomland hardwood forest (Zomlefer et al., 2012). Regarding fish populations in the study area, the primary consumers of macroinvertebrates include stocked rainbow trout (*Oncorhynchus mykiss*) and naturally-reproducing brown trout (*Salmo trutta*). Population numbers of these species are fairly similar throughout the study reach, with the exception of site B, which tends to have slightly lower numbers of each (O'Rouke, 2014). Sites below Morgan Falls Dam were not sampled for fish by O'Rouke (2014).

In addition to the primary Chattahoochee River study area, we also incorporated a study from the nearby unregulated Middle Oconee River (Grubaugh & Wallace, 1995) as a means for comparison to the regulated Chattahoochee. The Middle Oconee study site is located approximately 68 km east of the Chattahoochee study area in the Piedmont region of Georgia

(Fig. 1). While the Chattahoochee is in a highly urbanized area, the Middle Oconee watershed remains rural. We do not consider this a "reference site," however, due to the impact of animal agriculture in the Middle Oconee watershed (see below). In addition, the Middle Oconee drainage area (at the sampling site) is smaller than the Chattahoochee drainage area (at the head of the study reach) (1030.8 km^2 vs. 2693.6 km^2, respectively). The differences between these two watersheds impose limitations on the comparison between these two systems. Unfortunately, published taxa lists from Piedmont rivers of a similar size in Georgia are lacking. Thus, this study was our only opportunity for comparison with a river of approximately similar size in the Piedmont region of Georgia. Despite these limitations, we believe a comparison between the regulated Chattahoochee and unregulated Middle Oconee can still provide useful insights into the effects of river regulation. They are both in the Piedmont physiographic region and have been influenced historically by intensive row crop agriculture prior to the early 20th century (Grubaugh & Wallace, 1995). Since then, row crop agriculture has significantly decreased in both systems. Urbanization has increased significantly in the Chattahoochee watershed whereas the Middle Oconee has experienced an increase in animal agriculture (e.g. poultry, dairy, and cattle farms).

Macroinvertebrate sampling

Both Hester-Dendy (HD) multi-plate samplers (Hester & Dendy, 1962) and a Surber sampler (Surber, 1937) were used to collect macroinvertebrates over an 11-year period (2001-2011). HD multi-plate samplers contained nine 76 mm^2 masonite plates attached to a wire cable anchored on or near the river bank to a permanent structure. The plates were deployed in a free-flowing section of the river at each of the six sites and remained in place for a period of three months during each of the sampling periods. Surber samplers consisted of a 500 µm net (with an opening of 22.9 cm in diameter) and a 30.5 cm^2 open base. Surber samples were taken at only five of the six sites (A-D and F) due to excessive depth at site E. Sampling locations at each site were determined based on accessibility and were stratified to target available habitats in which macroinvertebrates are likely to occur: sand, small gravel, bedrock covered with algae, and/or vegetation. Quarterly for 11 years, three replicate samples were collected using each sampling device.

All macroinvertebrates collected in the field were preserved in 70% isopropyl alcohol, enumerated, and identified to the lowest possible taxonomic level (genus in most cases) using keys in Klemm (1995), Wiggins (1996), Kathman and Brinkhurst (1999), Needham *et al.* (2000), Epler (2001), Stewart and Stark (2002), Adler *et al.* (2004), Dillon *et al.* (2003), Westfall and May (2006), Mackie (2007), Merritt *et al.* (2008), and Thorp and Covich (2010). The caddisfly genus *Ceratopsyche* was treated as a separate genus in this study, although it is now considered a sub-group within *Hydropsyche* (Geraci et al., 2010).

The specific sampling methodology for the Middle Oconee study can be found in Grubaugh & Wallace (1995). In summary, the authors sampled one site on the Middle Oconee River on a monthly basis over a period of one year. The authors used a modified T-sampler (Merritt et al., 2008) (similar to a Surber sampler) to collect macroinvertebrates on the substrate, which was composed of bedrock and large boulders. Macroinvertebrates were preserved in the field in 5-10% formalin and identified in the laboratory to the lowest taxonomic level possible (typically genus or species).

Assemblage analyses

Differences in overall macroinvertebrate assemblages among the six study sites (A-F) within the Chattahoochee were analyzed to determine changes along the length of the study area.

Abundance data from HD plates and Surber samplers were kept separate for all analyses due to differences in sampler catch efficiencies. Each replicate sample (each site, season, and year) was kept separate for all analyses unless otherwise noted. All abundance data were log(x+1) transformed due to lack of normality and relativized by sample. Nonmetric multidimensional scaling (NMDS, Bray-Curtis Similarity, Kruskal fit scheme 1, 25 restarts) was used to visualize patterns in assemblages among sites. Analysis of Similarities (ANOSIM, Bray-Curtis similarity, 999 permutations, one-way layout, factor = site) was used to test for statistical significance among macroinvertebrate assemblages at each site. R-values from ANOSIM indicated whether the between- or within-site dissimilarity was greater in each pairwise comparison between sites, where $0 \leq R \leq 1$. Larger R-values indicated greater dissimilarity in the macroinvertebrate assemblages between the two sites versus within each site individually. Indicator analysis (Dufrene & Legendre, 1997) was used to identify taxa that represented each site, followed by randomization (Monte Carlo) tests (4999 permutations) to determine significance. Indicator taxa are those that are both abundant and consistently found at a specific site relative to the remaining taxa. Based only on the indicator taxa for each site, average tolerance values were calculated (see following for tolerance value explanation). In addition to indicator analysis, three macroinvertebrate metrics were used to help characterize the overall assemblages at each site: Shannon-Weiner diversity (H'), mean number of EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa, and mean number of sensitive taxa. Sensitive taxa were based on tolerance values from the North Carolina Biotic Index (NCBI) (Lenat, 1993) and Grubaugh & Wallace (1995). For this study, sensitive taxa were considered those with a tolerance value ≤ 3 (GADNR, 2007). We used ANOVA (one-way, factor = site) and post-hoc Tukey tests to determine significance among these metrics. Seasons within years were pooled for these analyses (years and sites remained independent).

We investigated assemblage change over the length of the river in response to (1) distance from Buford Dam and (2) diel hydrologic amplitude using USGS flow data from gaging stations at sites A (gage 02334430), C (gage 02335000), D (02335450), E (gage 02335815), and F (gage 02336000). Average diel amplitude was calculated at each of these sites over four years (2008-2011) (USGS, 2013). Site B was not included due to absence of a nearby USGS gage. Amplitude was log(x+1) transformed due to lack of normality. To determine if a pattern existed between distance from Buford Dam and diel amplitude variation, we performed a linear regression using four years of flow data (2008-2011) from each of the gages listed above and the distance of each gage from Buford Dam. Based on this regression, we determined average diel amplitude at site B as well. Regression analysis also was used to determine difference in H', mean number of EPT taxa, and mean number of sensitive taxa over the length of the study area (km from dam) as well as over the range of diel amplitudes within the study reach. Sites and years were treated independently for these analyses; seasons within each year were combined.

The taxa list for the Chattahoochee River below Buford Dam was then compared to the macroinvertebrate data set from a comparable site on the Middle Oconee River (Grubaugh & Wallace, 1995). Sorenson's Index was calculated to determine similarity between the two river assemblages using the equation: $\beta = 2c/(S_1 + S_2)$, where c is the number of taxa in common, S_1 is the number of taxa in the Chattahoochee River, S_2 is the number of taxa in the Middle Oconee River, and $0 \leq \beta \leq 1$ ($\beta = 0$ indicates no similarity between the two rivers and $\beta = 1$ indicates 100% similarity). Because the Middle Oconee was sampled using only a modified T-sampler, only Surber data from the Chattahoochee River were used for a more direct comparison. Due to changes in taxonomy and differences in level of identification for some groups, we used a conservative approach when calculating the similarity index between these two assemblages. To determine whether the macroinvertebrate community of the Chattahoochee differed from that of the Middle Oconee, Sorenson's Index was calculated using (a) the entire Chattahoochee study area (versus the Middle Oconee) and (b) only the site furthest downstream from Buford Dam (site F) (versus the Middle Oconee). The latter was used to determine whether the macroinvertebrate assemblage 65 km from the dam returned to a more representative Piedmont river condition. Percent EPT and percent sensitive taxa were also calculated for the Chattahoochee River (overall), site F only, and the Middle Oconee River to determine whether differences were being generated by indicators of high water quality.

NMDS, ANOSIM, and H' analyses were performed using Primer v6 software (Primer-E Ltd, Devon, UK). Indicator analysis was performed using PC-ORD (version 6; MjM Software, Gleneden Beach, OR, USA). All other statistical analyses were performed using SAS software (version 9.3; SAS Institute, Inc., Cary, NC, USA). All significance testing used $\alpha = 0.05$.

Results

All taxa collected during the study along with tolerance value designations are listed in Online Resource 1. Overall, 159 taxa were collected comprising 145 genera, 60 families and 22 orders. Site-specific analysis among the six study sites (A-F) on the Chattahoochee River shows that the macroinvertebrate assemblage at each site was significantly different from all other sites (Table 1). There was also a general community progression from site A through site F (Fig. 3), indicating a successive change in assemblages from one site to the next. Sites furthest from each other exhibited the greatest difference in macroinvertebrate assemblages. A temporal effect was detected as well based on the NMDS plot. However, in this study the focus was on spatial variation. For temporal effects see Holt et al. (in press). Numerous indicator taxa were identified for each of the six study sites (Table 2). While compositions of indicator taxa differed, there was no difference among sites in average tolerance values of these indicator taxa. H’ (HD samples only) was significantly lower at site A compared to the other five sites (Table 3). Based on Surber samples, A and B had significantly lower H’ than C, D, and F (Table 3). Number of EPT taxa and sensitive taxa generally increased from site A to site F (Table 3) with sites closest to each other being most similar. However, the number of sensitive taxa in HD samples did not differ between sites A, B, and C.

Significant patterns emerged in relation to linear distance from Buford Dam as well. Average diel amplitude decreased significantly with increasing distance from Buford Dam ($R^2 = 0.39$, $p = 0.003$) (Fig. 2c). Annual amplitude variation did not change in response to distance from the dam ($R^2 = 0.04$, $p = 0.38$). There was a significant positive relationship between H’ and distance from Buford Dam for both HD and Surber samples (HD: $R^2 = 0.32$, $p < 0.001$; Surber: $R^2 = 0.52$, $p < 0.001$) (Fig. 2d). Number of EPT taxa vs. distance from the dam exhibited a similar relationship (HD: $R^2 = 0.63$, $p < 0.001$; Surber: $R^2 = 0.47$, $p < 0.001$). Although slightly weaker, the relationship between number of sensitive taxa and distance from Buford Dam was also positive (HD: $R^2 = 0.25$, $p < 0.001$; Surber: $R^2 = 0.26$, $p < 0.001$).

From a hydrological perspective, there were many similar patterns to those mentioned previously. Because of the relationship between diel amplitude and distance from Buford Dam, it is not surprising that H’ showed a significant increase as diel amplitude decreased (HD: $R^2 = 0.38$, $p < 0.001$; Surber: $R^2 = 0.58$, $p < 0.001$) (Fig. 2e). Number of EPT taxa and (to a weaker extent) number of sensitive taxa follow that same trend [EPT (HD): $R^2 = 0.55$, $p < 0.001$; EPT

(Surber): $R^2 = 0.53$, $p < 0.001$; sensitive taxa (HD): $R^2 = 0.13$, $p = 0.001$; sensitive taxa (Surber): $R^2 = 0.27$, $p < 0.001$).

Comparison between the Chattahoochee and Middle Oconee Rivers showed moderate assemblage similarity, with the Middle Oconee exhibiting a stronger tendency towards sensitive taxa (Table 4). Despite the fact that the total number of EPT taxa was greater in the Chattahoochee than in the Middle Oconee (36 vs. 26 EPT taxa, respectively), percent EPT was similar between the two rivers (Table 4). Focusing only on site F, the two rivers appear less similar with respect to EPT taxa: the Chattahoochee at site F has fewer total EPT taxa than the Middle Oconee (23 vs 26 EPT taxa, respectively) and a lower percentage of EPT to total taxa (Table 4). This dissimilarity was also apparent when comparing taxa unique to each system as well as those that are common to both (Table 5). The Middle Oconee contained a greater number of unique EPT and sensitive taxa than did the Chattahoochee. No Plecoptera were unique to the Chattahoochee while the Middle Oconee contained five unique plecopterans (all of which are sensitive taxa). On the other hand, the Chattahoochee contained four macrocrustaceans that are unique to that system (*Caecidotea, Crangonyx, Hyalella, and Lirceus*), whereas the Middle Oconee contained none.

Discussion

The distinct assemblages that developed at each of the six sites indicate considerable variation exists within tailwater systems. Many of the R-statistics from ANOSIM (Table 1) indicate strong differences among the six study sites, emphasizing significant variation in macroinvertebrate assemblages from site to site. We documented a general progression in various assemblage metrics as the distance from the dam increased and diel variation in amplitude decreased. In general, the macroinvertebrate compositions improved (i.e. H', numbers of EPT taxa, and numbers of sensitive taxa) with increasing distance from the dam. This result is logical considering the non-natural conditions directly below any large-scale hydroelectric dam (Graf, 2006; Richter & Thomas, 2007; de Oliveira Naliato et al., 2009). Linear relationships between invertebrate metrics and increasing distance from the dam were most likely in response to changes in diel hydrological amplitude. Extreme variation in amplitude over short time periods (e.g. within a single 24-hour period) creates a challenging environment for invertebrates. Water releases from hydroelectric dams increase turbidity and scour, leading to decreased nutrient levels (Baxter & Glaude, 1980; Liu & Yu, 1992; Zhong & Power, 1996). Filter-feeders that require significant water flow for food delivery can still thrive (i.e. *Simulium*) (Merritt et al., 2008), but organisms that are either inefficient at attaching to substrates or use different functional feeding strategies (e.g. grazers, predators) would have a more difficult time. As distance from the dam increases, the amplitude becomes more muted and effects on the hydrologic regime are lessened, allowing for survival of a wider variety of macroinvertebrates.

Linear patterns were consistent despite the presence of a second smaller dam (Morgan Falls Dam) above site E (Fig. 1). Multivariate analyses of the communities at each site showed that all sites were different from each other with no clear distinction between sites above vs. below Morgan Falls Dam. In general, H', numbers of EPT taxa, and numbers of sensitive taxa (Table 3) did not change markedly between areas above and below the small dam with one exception: HD diversity decreased between sites D and E, indicating a potential effect of Morgan Falls Dam. Overall, however, a continuum developed of more tolerant, less diverse assemblages upstream to one with higher sensitivity and greater diversity downstream. This lack of distinction is likely due to the fact that daily flow amplitude below Morgan Falls Dam is less variable than that below Buford Dam (Fig. 2), providing further evidence for the impact of severe variation in daily flow amplitude on the macroinvertebrate community of the Chattahoochee.

In addition to changes in H', EPT, and sensitive taxa, assemblages of indicator taxa also illustrate a similar pattern. From a qualitative point of view, it is useful to point out the types of taxa indicative of each study site from the beginning of the study reach to the end (see Table 2). Taxonomic diversity of indicators was relatively low at site A compared to sites further downstream, and the taxa at site A directly below the dam consisted of only Diptera; no EPT or sensitive taxa were characteristic of this site. However, a greater variety of taxa became indicators at each successive site downstream, and the number of EPT indicators climbed steadily, culminating at site F with 17 EPT indicators. In contrast, Cross et al. (2011) found a complete absence of EPT taxa over a 25-km study area below Glen Canyon Dam (Colorado River) prior to and following an experimental flood release. The fact that there were numerous EPT indicator taxa in the Chattahoochee suggests that the flow management regime and water quality here support survival of these more-sensitive organisms. Average tolerance values at each of the Chattahoochee study sites based on these indicator taxa did not exhibit a significant pattern (albeit several taxa do not have a tolerance value associated with them).

The expansive impacts of Buford Dam on macroinvertebrate assemblages are made even more apparent when comparing the Chattahoochee study area to an unregulated section of the Middle Oconee River. Based on the moderate degree of assemblage similarity between the rivers (overall), the low assemblage similarity between site F and the Middle Oconee, and the lower percentages of sensitive taxa in the Chattahoochee River (overall and at site F), our study suggests that even after 65 km, macroinvertebrate assemblages did not return to a more representative Piedmont river condition.

Looking at the taxa that are unique to each system supports this idea as well, with fewer unique EPT and sensitive taxa being found at site F in the Chattahoochee versus the Middle Oconee (Table 5). The Middle Oconee contains five plecopterans (stoneflies) that were not found at site F in the Chattahoochee (which contained no unique stoneflies). In addition, the Chattahoochee seems to favor macrocrustaceans (absent from the Middle Oconee), which are typically disturbance-tolerant organisms. This provides further evidence that the Chattahoochee River 65 km from Buford Dam is still ecologically functioning differently from a comparably more naturally-flowing Piedmont river.

Several reasons may explain this discrepancy. (1) Low assemblage similarities between the rivers could be due to the 1-year versus 11-year sampling periods for each study (Middle Oconee and Chattahoochee, respectively), and the Middle Oconee study sampled only a single site. However, despite much less sampling, more total taxa were collected from the single Middle Oconee site than over 11 years at site F on the Chattahoochee. (2) Differences in flow variation could explain the patterns (Belmar et al., 2013), with the Chattahoochee experiencing unnatural alterations of flow due to Buford Dam and the Middle Oconee experiencing a more natural flow regime. Significant changes in Chattahoochee macroinvertebrate assemblages have indeed been documented between years with exceptionally high vs. low flows (Holt et al., 2015). (3) Differences in water quality as a result of differing land use in the watershed of each river may cause altered macroinvertebrate assemblages. The Chattahoochee is located in the metropolitan Atlanta area, which has a population of over six million people. The study site, however, is located in a protected corridor managed by the NPS, and the water cycles through a large reservoir (Lake Lanier) prior to release down the river. The Middle Oconee is located in a largely rural area, with Athens (whose 1995 population was approximately 88,760) being the primary center of urbanization in the area. However, as one of the primary poultry production areas of Georgia, the Middle Oconee basin is impacted via nutrient enrichment, which has been shown to significantly affect stream macroinvertebrate assemblages (Justus et al., 2010). Thus, while water qualities between the two rivers likely differ, both are anthropogenically impacted. Urbanization and agriculture have both been shown to significantly affect stream macroinvertebrates (Bruno et al., 2014). It is possible that urbanization at the scale of the metropolitan Atlanta area is having a greater impact on the macroinvertebrate fauna of the Chattahoochee River as compared to the agricultural inputs in the Middle Oconee watershed. (4) The abnormally cold temperatures in the tailwater section of the Chattahoochee could be favoring a macroinvertebrate assemblage that is more characteristic of streams further north in the Ridge and Valley and Blue Ridge regions rather than the Piedmont (Hynes, 1970; Johnson & Harp, 2005). Colonization of the Chattahoochee study area by these cold-water organisms, however, may be difficult as nearby local source populations may be lacking. Thus, many may be in low abundance or absent unless they have strong flight capabilities (e.g. Diptera) (Johnson & Harp, 2005).

Because of some of the limitations listed above (e.g. different sampling periods and land use practices), we cannot say with certainty that alteration to the flow of the Chattahoochee River is the sole driver of the differences in the macroinvertebrate assemblages between these two river systems. In addition, we cannot rule out the River Continuum Concept (RCC) (Vannote et al., 1980) as contributing to the linear change in macroinvertebrate assemblages within the Chattahoochee River. However, RCC effects are unlikely due to the fact that stream order remains the same throughout the study area, and the RCC typically applies to much longer stretches of river than the 68 km investigated here.

In conclusion, this study provides evidence for the influence of hydroelectric dams via diel amplitude alterations on riverine macroinvertebrate communities and is one of only a few studies to analyze these effects over long temporal and spatial scales. We have shown that macroinvertebrate assemblages change continuously over a 65-km tailwater section and that these changes appear to be in response to altered diel flow variation. Using several invertebrate metrics, we documented increasing diversity and presence of sensitive macroinvertebrates as distance from the dam increased (and diel variation decreased). Finally, we provided evidence that the macroinvertebrate assemblages in the Chattahoochee River are still different from a typical Piedmont assemblage even 65 km below the dam. The conclusions from our study suggest there are likely long-term, far-reaching impacts of many other large-scale dams around the world on aquatic macroinvertebrate assemblages well removed from dams, and that assemblages may vary dramatically within individual impacted areas.

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Table 3.1 ANOSIM R-statistic values for the Chattahoochee River. All R-statistics are significant ($p<0.05$), indicating significant differences in macroinvertebrate communities at each site. Only results from analysis of Hester-Dendy data are shown here; Surber data support these results.

	A	B	C	D	E
B	0.323	--	--	--	--
C	0.711	0.326	--	--	--
D	0.629	0.405	0.142	--	--
E	0.906	0.641	0.480	0.491	--
F	0.902	0.713	0.425	0.468	0.417

Table 3.2 Indicator taxa in the Chattahoochee River. Indicator taxa are organized by site within the study area (Hester-Dendy and Surber data combined). Average tolerance value (TV) for each site were calculated using data from Lenat (1993) and Grubaugh and Wallace (1995).

Site	Order	Family	Genus	Mean TV
A	Diptera	Chironomidae	*Cricotopus*	4.4
			Cricotopus/Orthocladius	
			Eukiefferiella	
			Orthocladius	
		Simuliidae	*Simulium*	
B	Lumbriculida	Lumbriculidae	*Lumbriculus*	6.34
	Gastropoda	Physidae	*Physa*	
	Amphipoda	Hyalellidae	*Hyalella*	
	Trombidiformes	Lebertiidae	*Lebertia*	
	Ephemeroptera	Ephemerellidae	*Ephemerella*	
	Plecoptera	Taeniopterygidae	*Taeniopteryx*	
	Diptera	Chironomidae	*Cricotopus*	
			Cricotopus/Orthocladius	
			Eukiefferiella	
			Parametriocnemus	
			Stictochironomus	
			Thienemannimyia group	
		Muscidae	cf. *Limnophora*	
		Simuliidae	*Simulium*	
C	Tricladida	--	--	4.63
	Lumbriculida	Lumbriculidae	--	
	Amphipoda	Crangonyctidae	*Crangonyx*	
	Isopoda	Asellidae	*Caecidotea*	
	Ephemeroptera	Baetidae	*Iswaeon*	
		Ephemerellidae	*Dannella*	
	Trichoptera	Brachycentridae	*Brachycentrus*	
		Lepidostomatidae	*Lepidostoma*	
	Diptera	Chironomidae	*Parametriocnemus*	
			Tvetenia	
D	Tricladida	--	--	5.9
	Lumbriculida	Lumbriculidae	--	
	Bivalvia	Cyrenidae	*Corbicula*	
	Amphipoda	Crangonyctidae	*Crangonyx*	
	Isopoda	Asellidae	*Lirceus*	
	Trombidiformes	Lebertiidae	*Lebertia*	
	Ephemeroptera	Baetidae	*Iswaeon*	
	Plecoptera	Capniidae	*Allocapnia*	
			Nemocapnia	
		Pternonarcyidae	*Pteronarcys*	
	Trichoptera	Brachycentridae	*Micrasema*	
		Hydropsychidae	*Ceratopsyche*	
	Diptera	Chironomidae	*Dicrotendipes*	
E	Isopoda	Asellidae	*Caecidotea*	5.91
	Ephemeroptera	Heptageniidae	*Maccaffertium*	
	Odonata	Coenagrionidae	*Argia*	
	Trichoptera	Brachycentridae	*Brachycentrus*	
		Hydropsychidae	*Cheumatopsyche*	

	Order	Family	Genus	Mean TV
		Hydroptilidae	*Hydroptila*	
		Leptoceridae	*Oecetis*	
		Polycentropodidae	*Neureclipsis*	
		Psychomyiidae	*Lype*	
	Coleoptera	Elmidae	*Macronychus*	
	Diptera	Chironomidae	*Corynoneura*	
			Nanocladius	
			Rheotanytarsus	
			Stenochironomus	
			Synorthocladius	
		Empididae	*Hemerodromia*	
		Limoniidae	*Antocha*	
F	Gastropoda	Pleuroceridae	*Pleurocera*	2.84
	Bivalvia	Cyrenidae	*Corbicula*	
	Isopoda	Asellidae	*Lirceus*	
	Ephemeroptera	Baetidae	*Acentrella*	
			Baetis	
			Heterocloeon	
		Ephemerellidae	*Serratella*	
			Teloganopsis	
		Heptageniidae	*Heptagenia*	
			Maccaffertium	
			Stenacron	
	Plecoptera	Perlidae	*Agnetina*	
			Perlesta	
	Trichoptera	Glossosomatidae	*Glossosoma*	
		Hydropsychidae	*Cheumatopsyche*	
			Hydropsyche	
		Lepidostomatidae	*Lepidostoma*	
		Philopotamidae	*Chimarra*	
	Diptera	Ceratopogonidae	*Forcipomyia*	
		Chironomidae	*Polypedilum*	

Table 3.3 Macroinvertebrate metrics by site on the Chattahoochee River. Shannon-Weiner diversity (H'); mean number of EPT[1] taxa; and mean number of sensitive taxa[2] in the Chattahoochee River study area (separated by sampling device). Significant differences are indicated by different superscript letters (Tukey post-hoc test, $p \leq 0.05$).

	Hester-Dendy			**Surber**		
Site	**H'**	**# EPT taxa**	**# sensitive taxa**	**H'**	**# EPT taxa**	**# sensitive taxa**
A	0.67^{a}	2.64^{a}	0.55^{a}	0.95^{a}	1.09^{a}	0.09^{a}
B	1.77^{b}	$5.18^{a,b}$	0.91^{a}	0.85^{a}	$4.27^{a,b}$	$0.55^{a,b}$
C	$2.22^{b,c}$	$8.18^{b,c}$	1.00^{a}	1.87^{b}	$7.09^{b,c}$	$1.45^{b,c}$
D	2.35^{c}	8.46^{c}	$1.73^{a,b}$	2.12^{b}	$6.73^{b,c}$	$1.09^{a,b,c}$
E	1.85^{b}	$10.09^{c,d}$	$1.55^{a,b}$	--	--	--
F	$2.21^{b,c}$	12.91^{d}	3.00^{b}	2.19^{b}	9.46^{c}	2.18^{c}

[1] Ephemeroptera, Plecoptera, Trichoptera

[2] Tolerance value ≤ 3 [see Lenat (1993) and Grubaugh and Wallace (1995)]

Table 3.4 Comparison between macroinvertebrate communities of the Chattahoochee and Middle Oconee study areas. The Chattahoochee (overall and site F) (Surber data only) is shown in comparison to the Middle Oconee River [from Grubaugh and Wallace (1995)]. Sorenson's Index compares the Middle Oconee to each of the respective sections of the Chattahoochee. Hester-Dendy and Surber data were used for these calculations.

	Sorenson's Index	% EPT Taxa[1]	% Sensitive Taxa[2]
Chattahoochee	0.52	52.17	15.9
Chattahoochee - Site F only	0.36	38.33	10.0
Middle Oconee	--	50.98	27.5

[1] Ephemeroptera, Plecoptera, Trichoptera

[2] Tolerance value ≤ 3 [see Lenat (1993) and Grubaugh and Wallace (1995)]

Table 3.5 List of unique taxa between the Chattahoochee and Middle Oconee study sites. List of taxa unique to the Chattahoochee River (site F only) (Surber data only), taxa unique to the Middle Oconee River (Grubaugh and Wallace 1995), and taxa in common between the two rivers.

	Chattahoochee (Site F)	**Common Taxa**	**Middle Oconee**
Non-insects			
	Prostoma	Turbellaria	Nematoda
	Physa	Oligochaeta	Hirudinea
	Lirceus	_Pleurocera_	_Ferrissia_
	Caecidotea	_Corbicula_	_Somatogyrus_
	Crangonyx	Hydracarina	Sphaeriidae
	Hyalella		Cladocera
	Collembola		
EPT			
	Acentrella	_Baetis_	_Ameletus_*
	Iswaeon	_Heterocloeon_	_Caenis_
	Dannella	_Ephemerella_	_Serratella_
	Ephemerella	_Maccaffertium/Stenonema_*[1]	_Epeorus_*
	Teloganopsis	_Agnetina_	_Isonychia_
	_Heptagenia_*	_Paragnetina_*	_Amphinemura_
	_Brachycentrus_*	_Perlesta_*	_Shipsa_*
	_Micrasema_*	_Taeniopteryx_	_Neoperla_*
	Ceratopsyche	_Hydropsyche_	_Pteronarcys_*
	Ceraclea	_Lepidostoma_*	_Strophopteryx_*
	_Chimarra_*	Glossosomatidae*	_Ochrotrichia_
		Cheumatopsyche	_Nectopsyche_
			Lype
			Rhyacophila
Miscellaneous insects			
	Argia	_Nigronia_	_Corydalus_
	Progomphus	_Optioservus_*	_Promoresia_
		Chironomidae (Tanypodinae)	_Stenelmis_
		Chironomidae (non-Tanypodinae)	_Chelifera_
		Simuliidae	_Hemerodromia_
		Antocha	
		Tipula	

*Sensitive taxa (tolerance value ≤ 3) [see Lenat (1993) and Grubaugh and Wallace (1995)]

[1] _Maccaffertium_ and _Stenonema_ are considered the same taxon for this comparison due to taxonomic changes between the two studies

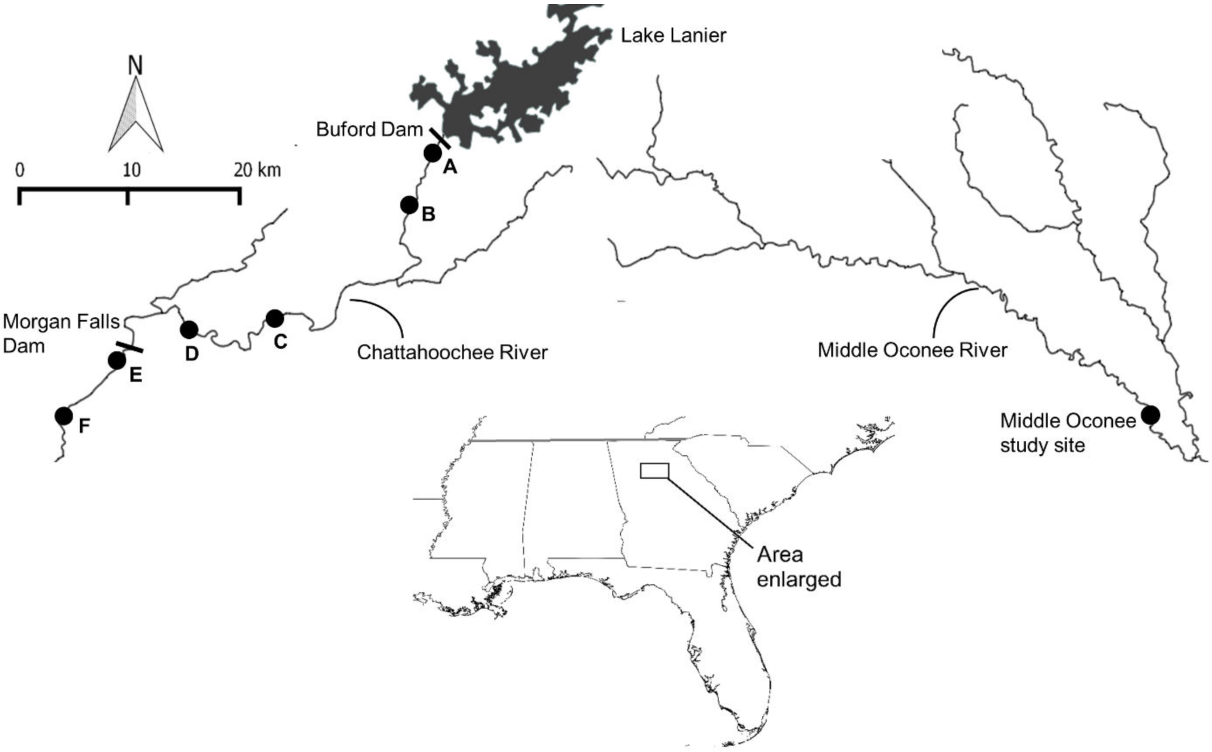

Figure 3.1 Locations of the Chattahoochee River and Middle Oconee River study areas. Study site locations within each river system are noted.

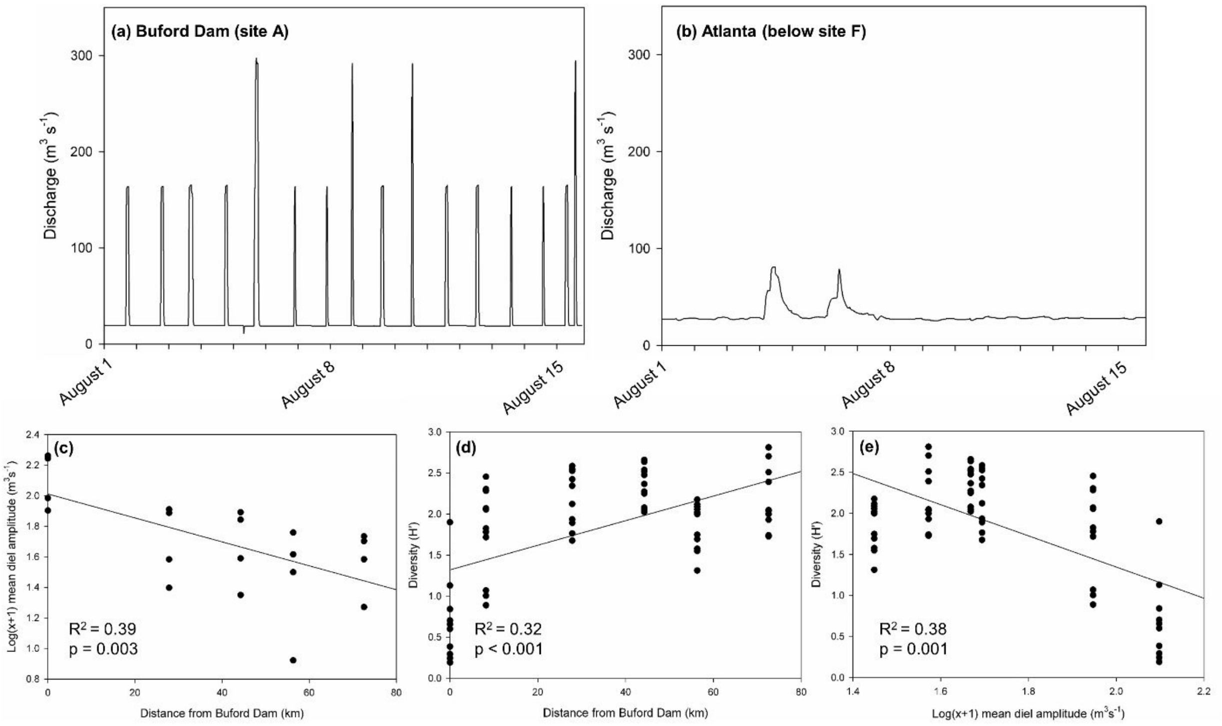

Figure 3.2 Patterns in hydrology and macroinvertebrate responses in the Chattahoochee. **(a, b)** Hydrographs depicting the difference in diel discharge over a 15-d period (2011) between **(a)** a USGS gage just below Buford Dam (site A – gage 02334430) and **(b)** a USGS gage 73 km below Buford Dam (~8 km below site F – gage 02336000). **(c)** Linear regression showing a significant negative relationship between diel amplitude and distance from Buford Dam. **(d, e)** Linear regressions (HD data only) showing significant impacts of **(d)** distance from Buford Dam and **(e)** diel amplitude variation on macroinvertebrate assemblages within the study area.

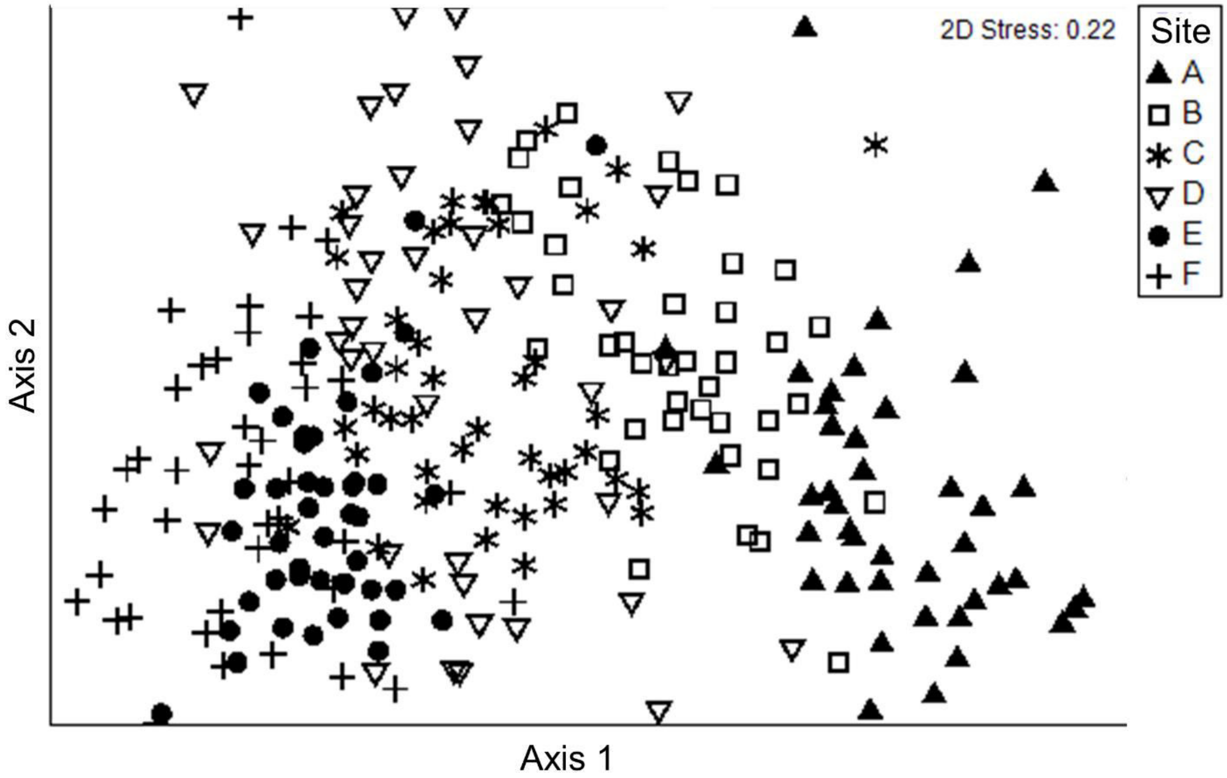

Figure 3.3 Nonmetric multidimensional scaling (NMDS) among sites. NMDS (Bray-Curtis similarity) exhibits differences in macroinvertebrate communities among the six study sites in the Chattahoochee River study area. Only Hester-Dendy samples are shown here; Surber data support this same pattern.

CHAPTER 4

SPECIES OVERLAP WITHIN A SINGLE GENUS OF PREDACEOUS DIVING BEETLES (COLEOPTERA: DYSTISCIDAE) IN AN ALLUVIAL FLOODPLAIN SYSTEM[1]

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[1] Holt, C. R., J. V. McHugh, and D. P. Batzer. To be submitted to Oecologia.

Abstract

Multiple ecological theories have been developed to suggest that the coexistence of related species should not occur in nature. However, sympatry has been documented quite commonly within the family Dytiscidae (predaceous diving beetles). This study aims to quantify the degree of overlap among species of *Neoporus*, a common genus of dytiscid in the southeastern United States. The study took place in the Altamaha River floodplains (Big Hammock Wildlife Management Area) over a three year period (2012-2014). The two primary aquatic habitats on the floodplain (permanent and temporary water bodies) were sampled seasonally for *Neoporus* adults. Abundance differences among species were analyzed between seasons, habitats, and years using ANOVA. Pearson's *r* was calculated for each species pair to determine the degree to which each species was correlated to all others. Six species of *Neoporus* were found during this study, and they did not segregate spatially or temporally. Correlation matrices show significant overlap between the majority of species, with slightly weaker correlations in temporary aquatic habitats (as compared to permanent habitats). This genus-level sympatry has rarely been documented, much less quantified, among dysticids, making this study particularly unique.

Introduction

Ecologists strive to explain patterns of species distributions over space and time. The coexistence of multiple related species, in particular, has long driven ecologists to debate about the mechanisms by which communities assemble. Multiple (often competing) theories have been developed to explain the coexistence of species in space and time, one of the first being Grinnell (1904) who postulated that species in competition for the same resource(s) could not coexist at constant populations levels, assuming other ecological factors remained constant. Grinnell's "niche theory" has been refined and built upon over time by Hutchinson & MacArthur (1959) who proposed niche differentiation occurred in response to body size ratio, and Diamond (1975) who developed assembly rules based on interspecific competition. Debate over the validity that niche differentiation and competition alone are responsible for community assemblage patterns has driven scientists to develop alternative hypotheses. A number of competing theories have developed in response to this debate, including the Unified Neutral Theory of Biodiversity (Hubbell, 2001), a null hypothesis to the niche theory which states that ecological differences among species in a community are irrelevant to their persistence. In addition, Paine (1966) and Connell (1975) proposed predation as a significant force affecting species interactions and coexistence. There is currently no consensus on which force, if any, is the overriding predictor of species coexistence.

Systems in which closely related species (e.g. organisms in the same family or genus) live in sympatry create a particularly unique situation in the debate over coexistence. Being closely related, it would be expected that organisms in the same genus or family would fill very similar niches in their shared environment. In many cases, this is true, leading to separation of their respective populations in time and/or space (see Schoener 1983). However, there are examples where species in the same family or even genus live in sympatry.

The family Dytiscidae (predaceous diving beetles) is a particular case in which sympatry occurs more often than would be expected based on niche theory. The family is extremely diverse, with nearly 4000 described species (160 genera) worldwide (Nilsson, 2001), some of which oftentimes coexist in close proximity to each other. For instance, Larson et al. (2000) found nearly 50 species of dytiscids in a single boreal pond in Canada while Alarie & Leclair

(1988) found 58 species across six ponds in Quebec. In the U.K., Juliano & Lawton (1990) found up to 11 species of dytiscids coexisting in a single canal, 10 of which were in the same genus, *Hydroporus*. However, whether these species partitioned this habitat either spatially (e.g. unique sub-habitats) or temporally (e.g. unique seasonal patterns) is unknown.

Within the family Dytiscidae, *Neoporus* (Guignot) is a common and often abundant genus in the southeastern United States. The genus, comprised of 39 species, is restricted to North America, with its highest species diversity occurring in the southeastern U.S. (Wolfe, 1984). Twenty-two species have been recorded from Georgia (Wolfe, 1984). The genus is most commonly found in lentic water bodies, both permanent and temporary, of the Piedmont and Coastal Plain physiographic regions (Scott et al., 2004). Little is known about the ecology of *Neoporus* and, according to Epler (2010), the genus is in serious need of revision. Previous research by Lee et al. (2016) documented high concentrations of dytiscids, particularly in the genus *Neoporus*, in floodplains of the Altamaha River, Georgia. Thus the objective of our study was to determine the specific characteristics of this sympatry among *Neoporus* species in Altamaha River floodplains. Because of the potential for moderate to strong interspecific competition among *Neoporus* species, we hypothesize that different species will partition this floodplain through (1) spatial and/or (2) temporal segregation of species.

Methods

Study Sites

The Altamaha River flows unimpounded through the Coastal Plain of Georgia. It begins at the confluence of the Oconee and Ocmulgee Rivers and flows southeast for 220 km where it empties into the Atlantic Ocean near Brunswick, GA. The Altamaha River is the longest free-flowing river on the east coast of the U.S. At nearly 36,000 km^2, the Altamaha watershed is one of the largest on the Atlantic Coast (USGS, 2013). The floodplain of the river is extensive, reaching up to 10 km in width at certain points. While there are no impoundments on the mainstem of the Altamaha River, the Oconee and Ocmulgee Rivers both have small, run-of-the-river dams that are not managed for flood control. Thus, flood pulses downstream have been minimally affected. The Altamaha River is one of the few large rivers in the Southeastern US that remains unimpounded, and The Nature Conservancy has designated the river a Bioreserve and listed it as one of the 75 “Last Great Places” on Earth.

Our study focused on a section of Altamaha River floodplain located in the Big Hammock Wildlife Management Area in Tatnall County, GA (Fig. 1). Average precipitation at the study site is 123.9 cm/yr and average temperature is 18.7°C. Precipitation during each year of study was as follows: 104.14 cm (2012), 148.36 (2013), and 133.86 (2014) (NOAA National Centers for Environmental information: www.ncdc.noaa.gov). Sandy soils predominate and land use in the area is dominated by pine silviculture. The floodplain along the river is low-lying and relatively flat. Bottomland hardwood forests dominate the floodplain and consist primarily of bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), sweetgum (*Liquidambar styraciflua*), and various oak species (*Quercus* spp.) (Lee, 2008).

Overbank flooding from the river typically occurs on a yearly basis, with late winter and spring experiencing the greatest flood frequencies (Fig. 2). During unusually dry years, restricted flooding occurs only in low-lying areas of the floodplain via direct precipitation. The official flood stage of the river according to the USGS river gage at Baxley, GA (gage 02225000) is 4.4 m (gage height) (Fig. 2). However, water begins entering the floodplain through breaks in the natural levees before this official flood stage is achieved. Flooding (whether overbank or precipitation-driven) creates temporary aquatic habitats on the floodplain that typically dry down by late summer or fall. In addition to these temporary aquatic habitats, the Altamaha River floodplain contains numerous permanent aquatic habitats, primarily oxbow lakes. Once part of the river channel itself, these features have become cut off from the course of the river due to natural alterations in the meander pattern of the channel. These oxbows vary greatly in size (from about 1 km^2 to nearly 6 km^2) and contain a diverse community of aquatic organisms including an abundance of fishes (D. Batzer, unpublished data). In contrast, the temporary habitats on the floodplain are either fishless or have low fish densities (compared to oxbow lakes) depending on the length of time and the degree to which the floodplain is inundated (Garnett and Batzer 2014; D. Batzer, unpublished data). Average pH and electrical conductivity (EC) in permanent water bodies was 5.73 +/- 0.93 and 82.41 +/- 11.38 µS, respectively. In temporary water bodies, average pH was 5.24 +/- 0.70 and average EC was 59.46 +/- 17.59 µS.

Sampling procedures

Sampling for *Neoporus* adults and larvae was conducted in the two habitat types described above: permanent oxbow lakes and temporarily flooded portions of the floodplain. Four permanent and four temporary sites were sampled (as available) for *Neoporus* using a D-frame net (Wildlife Supply Company Turtox Dip Net, 500 micron mesh, mouth dimensions 305 mm width x 254 mm height). Twelve 0.5-m sweeps along the shallow edge of the water were conducted at each of the sampling sites. Calibration sampling in deeper water (50 cm depths) confirmed that *Neoporus* were very uncommon away from shallow edges, likely due to their need to avoid fish predators and for frequent access to the water's surface for oxygen (both larvae and adults). Fairchild et al. (2003) confirmed this preference for shallow water among aquatic beetles is widespread. During extensive floodplain inundation, deep oxbow lakes were not accessible for sampling, and only temporary habitats were sampled. During deep flooding, the oxbows no longer contained shallow edges; thus, *Neoporus* were likely not present there due to their strong preference for shallow water. Therefore, when the floodplain was extensively inundated (and the oxbow lakes no longer had edges), we considered *Neoporus* to be absent from permanent habitats. If temporarily flooded portions of the floodplain were all dry during a sampling event, those sites were eliminated from our sampling regime for that date only.

Sampling occurred over a three-year period from January 2012 – December 2014. Samples were collected seasonally, with increased frequency during the spring flood season each year (January – May) (see Fig. 3 for specific months in which sampling occurred). All field samples were preserved on site in 95% ethanol and returned to the lab for analysis.

In the lab, field samples were rinsed over a 300 µm mesh sieve in order to retain all larval and adult *Neoporus*. When adults or larvae were very abundant, we subsampled ensuring that a minimum of 100 individuals were included in the subsample (larvae and adults were considered separately). All *Neoporus* were identified to species (adults only) using Epler (2010) and enumerated (adults and larvae). For the most abundant species, *N. clypealis*, we determined the sex of each individual as well. In samples with >100 *N. clypealis,* we subsampled 100 individuals to determine the sex ratio. All individuals were retained and preserved in 95% ethanol. Voucher specimens were deposited in the University of Georgia Collection of Arthropods (UGCA) at the Georgia Museum of Natural (Athens, GA).

Statistical analysis

To examine spatial and temporal overlap among the different *Neoporus* species, we first used analysis of variance (ANOVA) to compare abundances of all species to each other over the three year sampling period. Each individual species' abundance was compared between habitat types (permanent vs. temporary) to investigate spatial patterns of individual species. Two-way ANOVA was used initially to factor in both habitat and season, followed by subsequent t-tests if significant interaction terms existed. Temporally, patterns for each species were analyzed on an annual and seasonal basis via ANOVA. To determine differences in habitat preference and seasonal abundance of larvae we also used a two-way ANOVA (factors = habitat, season). If a significant interaction between factors resulted, subsequent one-way ANOVAs were employed to test for spatial and temporal differences independently.

Sex ratios between males and females of *N. clypealis* were calculated, and abundances across habitat types were compared via t-tests. Additionally, seasonal differences among abundance of *N. clypealis* males and females were calculated via ANOVA.

Pearson correlation matrices were calculated to determine overall degree of species spatial and temporal overlap in permanent and temporary habitats combined, in permanent habitats alone, and in temporary habitats alone. Significance testing for the correlation matrix was accomplished through the ‘rcorr’ function in the Hmisc package in R (Harrell, 2015). All statistical tests were performed in R (R Core Team 2015).

Results

In total, six species of *Neoporus* were identified from the Altamaha River floodplain in Big Hammock WMA. The most abundant species over the three years of sampling was *N. clypealis*, followed by *N. hybridus* (Table 1). One specimen of a rare species, *N. aulicus*, was found during the study.

From a spatial standpoint, none of the species (individually) exhibited a preference toward one habitat type or the other (permanent or temporary) over the three year period. *N.*

clypealis and *N. hybridus* appear to have accessed the temporary habitats more readily throughout the year, whereas the remaining less abundant species primarily accessed the temporary habitats only in late winter and spring (Fig. 3), when temporary habitats were more abundant due to overbank flooding.

From a temporal standpoint, three (*N. hybridus, N. venustus,* and *N. lobatus*) of the five common species exhibited no significant pattern among the three study years. *N. clypealis* was significantly more abundant in 2012 than 2013 ($p = 0.001$) or 2014 ($p < 0.001$). *N. vittatipennis* was significantly more abundant in 2014 than 2013 ($p = 0.046$). Among seasons, the results were somewhat varied, but most species were more common in the fall than the spring and/or summer (see Table 1). Abundances in spring and summer tended to be fairly similar except for *N. hybridus*, which was more abundant in the spring than summer. Abundances of the five common species over the entire three-year sampling period varied in a similar pattern (Fig. 3).

Among the 5 common species, most exhibited significant positive correlations with each other (7 of 10 combinations in the Table 2 correlation matrix). Correlations among the less common species were weaker. In no instance was a significant negative correlation detected. When separated by habitat (permanent and temporary), significant correlations among species in temporary habitats were less common (2 of 10 combinations) and weaker (r ranged from 0.254 to 0.456) than those in permanent habitats (9 of 10 combinations; r ranged from 0.261 to 0.743) (Table 2). Correlations between the two numerically dominant species (*N. clypealis* and *N. hybridus*) were especially strong, regardless of habitat (Table 2).

Focusing only on *N. clypealis*, the most abundant species, we did not see any significant patterns regarding distributions of males versus females. Males were equally as likely as females to be present in both habitat types, and both sexes exhibited similar abundance patterns: greater abundance in fall and winter than in spring and summer (Table 1). *Neoporus* larvae, however, were more abundant in temporary water bodies than permanent ($p_{habitat} = 0.006$) and were found exclusively in the spring (primarily March and April).

Discussion

Our hypothesis that *Neoporus* species would segregate themselves spatially and/or temporally on the floodplains of the Altamaha River was not supported. All of the species tended to occur not only in the same habitat, but also during the same periods and in the same microhabitat within the larger aquatic habitats of the floodplain. Species assemblages here appeared to exhibit a very high degree of sympatry.

Neoporus beetles appear to be habitat generalists, exploiting permanent and temporary aquatic habitats as available. During the driest of the three study years (2012), both permanent and temporary aquatic habitats were still present on the floodplain. However, the temporary habitats during this dry period resulted from direct precipitation rather than overbank flooding and, therefore, were physically isolated from the permanent habitats. Thus, *Neoporus* individuals present in these temporary waters accessed these habitats via active dispersal (i.e. flight). Blacklight sampling confirmed active flight by *Neoporus* adults in the Altamaha River floodplains (C. Holt, unpublished data). The following two years (2013 & 2014) experienced significant overbank flooding, which forced *Neoporus* to occupy the edges of the flood front. During such overbank flooding, much of the aquatic habitat on the floodplain coalesces. Thus, during wet years, *Neoporus* most likely dispersed via swimming, following the flood front as it advanced further into the floodplain.

Within the genus *Neoporus* there was a large amount of overlap in species distributions within floodplains of the Altamaha River, with minimal evidence of partitioning either spatially (within or among habitats or subhabitats) or temporally (among seasons or years). All six species were found along the same narrow margins of aquatic habitats on the floodplain (within 0.5 m from the pond edge), and all six species used the permanent and temporary habitats to an equal extent. Seasonal patterns among species were very similar to each other, although annual patterns differed slightly for two of the species. *N. clypealis* was most abundant in the dry year (2012), while *N. vittatipennis* was most abundant during the second wet year (2014). This may suggest some degree of partitioning between these two species. *N. clypealis* exhibiting greater abundance in the dry year seems somewhat counterintuitive but may be due to differential dispersal abilities. Being the smallest of the six species, *N. vittatipennis* may benefit from decreased competition or predation pressure from larger *N. clypealis* individuals. Wet years may disperse *N. clypealis* over a broader area of the floodplain, decreasing density dependent interactions, and providing more opportunities for competitively inferior species.

The degree of species overlap documented in this study (especially within a single genus) is uncommon among insects, or other groups. Likely explanations for this sympatry include two scenarios (or a combination thereof): (1) Dytiscidae as a family of insects may be unique in that many genera or species often co-exist; and/or (2) the floodplain habitats that this group inhabits are exceptionally variable, and this natural heterogeneity in space and time permits the co-existence of multiple, closely-related species.

While sympatry is typically uncommon, species distributions in the overall family Dytiscidae more commonly exhibit overlap (Alarie & Leclair, 1988; Juliano & Lawton, 1990; Larson et al., 2000; Davy-Bowker, 2002). However, sympatry within a single genus of dytiscids is still rare (Juliano & Lawton, 1990). Most generic-level sympatry involves fewer than three genera (Cuppen, 1983; Davy-Bowker, 2002; Pitcher & Yee, 2014), compared to the six species of *Neoporus* reported from this study. However, Juliano & Lawton (1990) documented 10 sympatric *Hydroporus* species in a single ditch in the U.K.; *Hydroporus* and *Neoporus* are very closely related, with *Neoporus* only recently being split from *Hydroporus* (Miller & Bergsten, 2014). Competition among sympatric dytiscids tends to be weak. Pitcher & Yee (2014) found no evidence for competition for food among two co-existing *Laccophilus* species. Juliano & Lawton (1990) reported a similar lack of interspecific competition among 10 co-existing *Hydroporus* species. Perhaps as generalist predators, multiple dytiscid species are capable of living in close proximity to each other and (under natural densities) avoiding significant competition.

Alternatively, the dynamism of floodplain habitat may be the driver of sympatry among *Neoporus* species. Floodplains are constantly-changing mosaics of aquatic and terrestrial habitat where survival requires an ability to cope with extremely variable conditions. This relative lack of stability may permit greater co-existence among species via increased niche diversity (Naiman et al., 1993). A meta-analysis by Batzer & Ruhi (2013) revealed that the family Dytiscidae (along with Chironomidae, midges) are the most commonly encountered macroinvertebrates in wetland habitats worldwide. This supports the idea that dytiscids are well-adapted to habitats that undergo regular hydrologic fluxes such as floodplains. Competition may also be reduced by frequent disturbance (Naiman & Decamps, 1997). The other example of apparent high sympatry, the 10 *Hydroporus* species reported by Juliano and Lawton (1990), also occurred in a highly variable wetland (in this case a man-made ditch). For other floodplain groups, co-existence of con-generic species has also been observed, for example among *Leptophlebia* mayflies (Galatowitsch & Batzer, 2011), *Lepomis* sunfishes (Garnett & Batzer, 2014), and *Quercus* oak trees (Jones et al., 1994). Perhaps floodplains (and other wetlands) are unique in their ability to support assemblages of sympatric species. Gallardo et al. (2008) concluded that greater diversity of water body types in a river-floodplain system in Spain contributed to a greater diversity of aquatic macroinvertebrates. Turic et al. (2015) reported an increase in Coleoptera abundance and species richness on floodplains of the Danube River as a result of frequent, large flood pulses. In addition to near-constant states of change in floodplain environmental conditions, some of which is predictable, some of which is not, each flooding-drying cycle essentially re-sets the stage for organisms to utilize the habitat, likely over-riding many previous impacts of biotic interaction (e.g. competition).

It seems likely that a combination of these two factors (characteristics of the organism and characteristics of the habitat) interact to produce the degree of species sympatry seen in this study. Not only does the family Dysticidae exhibit sympatry in a number of habitats (both disturbance-mediated and not), these beetles are also habitat generalists and are particularly well-adapted for life in frequently-changing environments. The more traditional niche theories developed within the past century do not appear to be upheld in the case of *Neoporus* species. Similar body sizes and trophic interactions do not produce segregation among species as would be expected based on niche theory. This study suggests that biology and environment can interact to produce significant sympatry, both spatially and temporally. Competition, predation, and environmental variability could all interact to promote the coexistence of these six species of *Neoporus* on the Altamaha floodplain. Further investigations into each of these components could help explain in greater detail the driving force(s) behind sympatry in this system and could shed light on why Dytiscidae often exhibits significant degrees of sympatry. Understanding the roles that biology, ecology, and environment play in species distributions can provide important insight into how species deal with competition, spatial limitations, and environmental alterations.

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Table 4.1 Mean abundance of *Neoporus* species in the Altamaha River floodplains. Sampled area covered 1.8 m^2 per sample. Standard deviation is given in parentheses. Differences in seasonal abundances for each species are included as well, along with their associated p-values (via 1-way ANOVA).

Species	**Abundance**	**Percent of population**	**Seasonal Patterns**	
			Difference	**p-value**
N. clypealis	33.570 +/- 61.769	61.11	f > sp	<0.001
			f > su	<0.001
			w > sp	0.003
			w > su	0.006
Female			f > sp	<0.001
			f > su	<0.001
			w > sp	0.003
			w > su	0.008
Male			f > sp	<0.001
			f > su	<0.001
			w > sp	0.011
			w > su	0.004
N. hybridus	17.308 +/- 36.150	25.92	f > su	0.001
			sp > su	0.044
			w > su	0.020
N. vittatipennis	13.220 +/- 38.053	12.49	NS	n/a
N. venustus	0.500 +/- 0.802	0.25	f > sp	<0.001
			f > su	<0.001
			f > w	<0.001
N. lobatus	0.391 +/- 0.499	0.21	f > su	0.030
N. aulicus	0.067 (+/- 0.258)	0.02	NS	n/a

Table 4.2 Species correlations for *Neoporus* species in the Altamaha River floodplain. Correlations for all permanent and temporary habitats combined (A) as well as permanent (B) and temporary (C) habitats separately are shown. *N. aulicus* is not included due to its rarity (only one individual was collected).

(A)	*N. clypealis*	*N. hybridus*	*N. vittatipennis*	*N. lobatus*
N. clypealis				
N. hybridus	0.606*			
N. vittatipennis	0.280*	0.371*		
N. lobatus	0.318*	0.244*	0.040	
N. venustus	0.304*	0.322*	0.131	0.133
(B)				
N. clypealis				
N. hybridus	0.743*			
N. vittatipennis	0.489*	0.619*		
N. lobatus	0.509*	0.386*	0.155	
N. venustus	0.420*	0.402*	0.334*	0.261*
(C)				
N. clypealis				
N. hybridus	0.456*			
N. vittatipennis	0.024	0.143		
N. lobatus	-0.049	0.089	-0.104	
N. venustus	0.147	0.254*	-0.063	-0.049

* $p < 0.05$

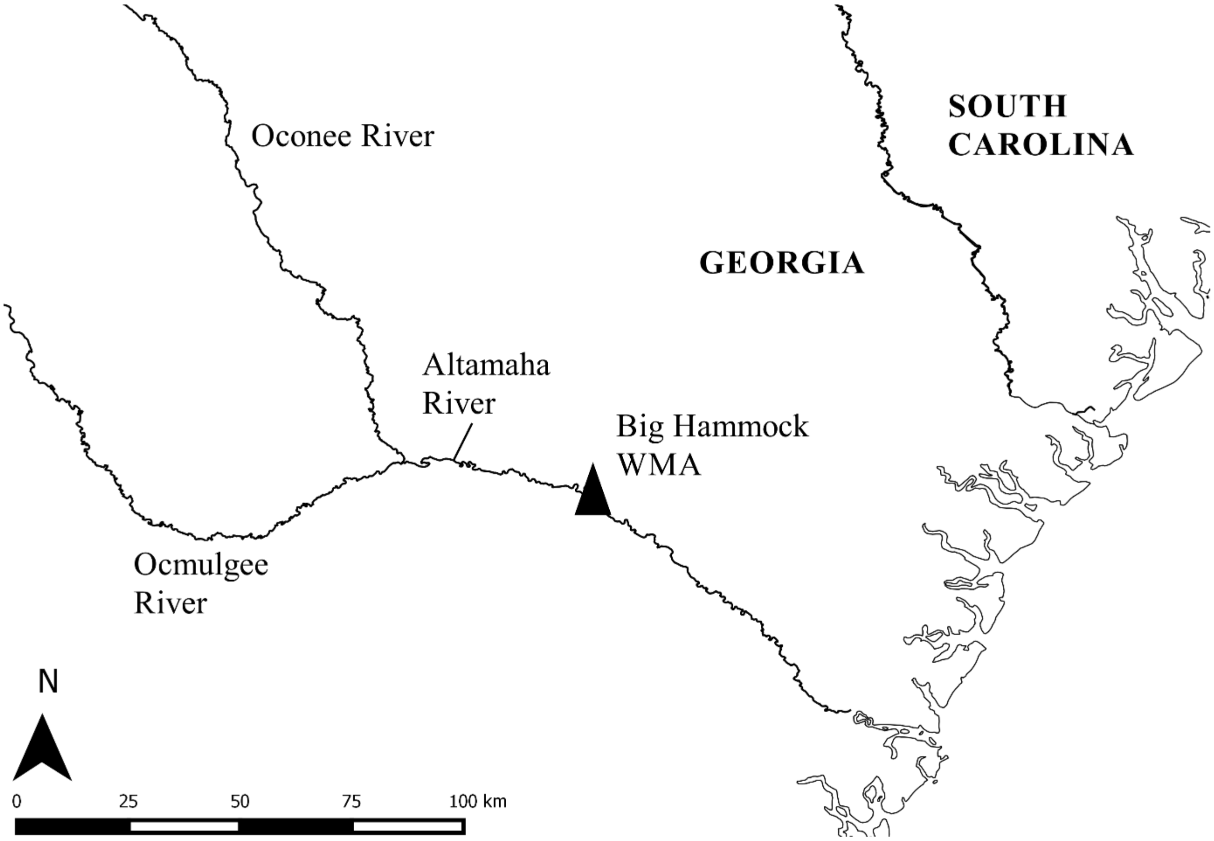

Figure 4.1 Location of Altamaha River study area. This study took place in Big Hammock Wildlife Management Area) in Tatnall County, GA.

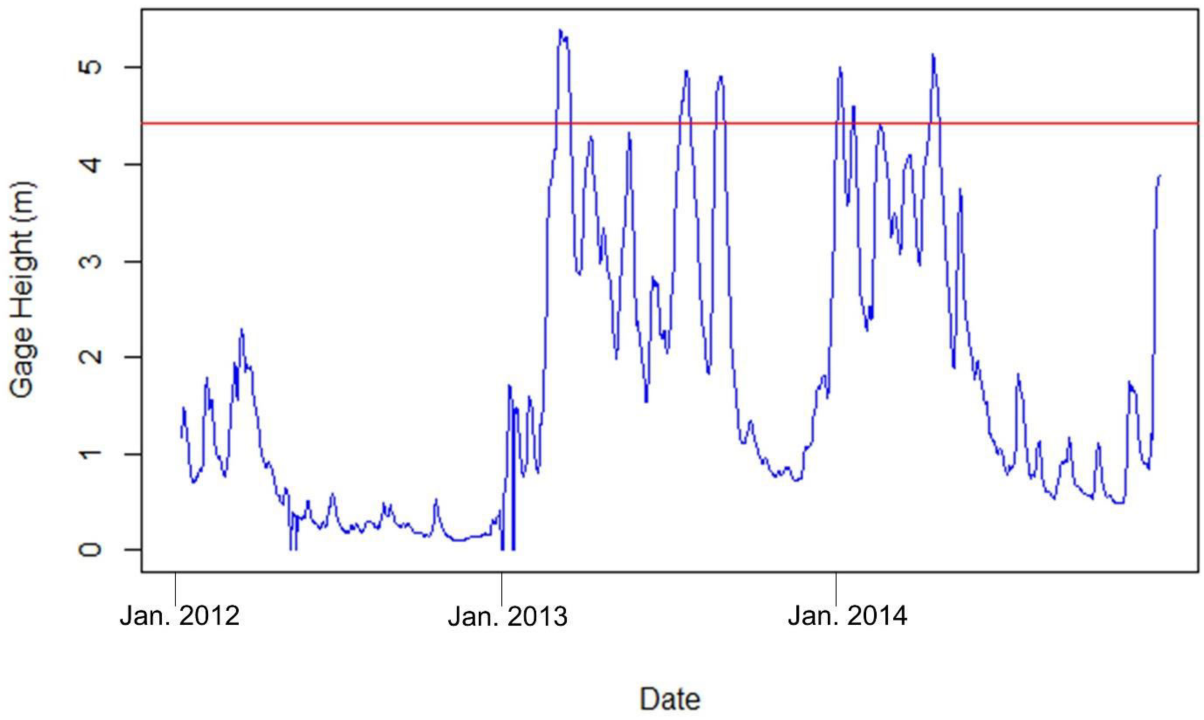

Figure 4.2 Hydrograph of the Altamaha River. Data were obtained from the Baxley USGS gage (gage # 02225000) during the study period (January 2012 – December 2014). The solid horizontal line indicates the level at which overbank flooding occurs at the study site.

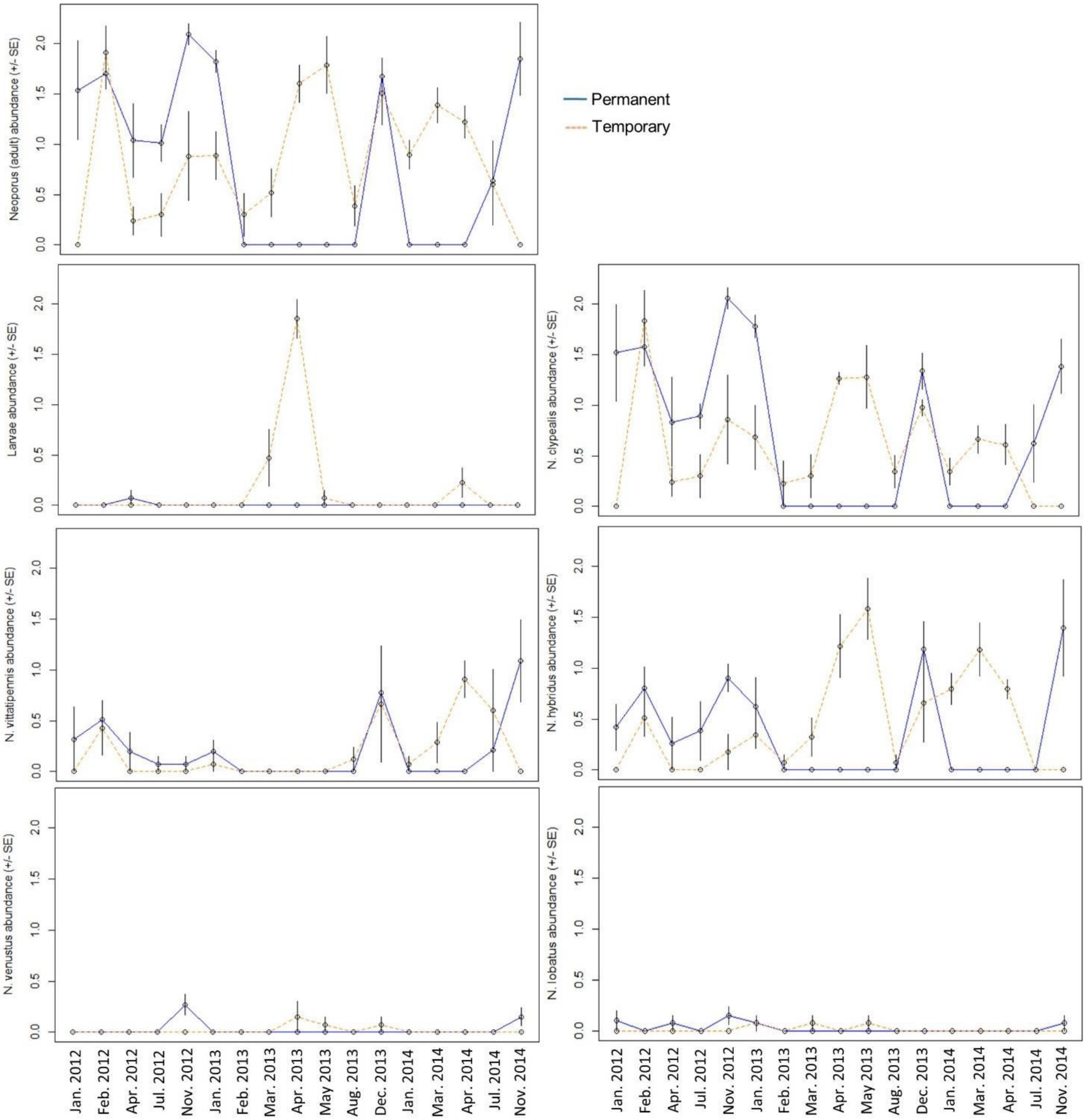

Figure 4.3 Species abundance graphs for all *Neoporus* species. Abundances are separated by habitat (permanent = solid lines and temporary = dashed lines). Sampling dates are listed on the x-axis. All data are log (x+1) transformed.

CHAPTER 5

EFFECTS OF FLOW REGULATION BEYOND THE CHANNEL: DISTRIBUTIONAL, BEHAVIORAL, AND PHYSIOLOGICAL ALTERATIONS WITHIN FLOODPLAIN POPULATIONS OF *NEOPORUS* SP. (COLEOPTERA: DYTISCIDAE)[1]

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[1] Holt, C. R. and D. P. Batzer. To be submitted to Ecological Applications.

Abstract

Lack of regular flood events on regulated rivers can have wide-ranging effects on the distribution of floodplain inhabitants. This study aims to determine the effects of flow regulation on the predaceous diving beetle *Neoporus* sp., a widespread southeastern U.S. floodplain inhabitant. Floodplains of a regulated (Savannah River) and unregulated (Altamaha River) river system were investigated over a 3.5 year period to determine differences among the systems regarding *Neoporus* (1) distribution across the floodplains, (2) propensity for flight (dispersal), and (3) lipid and protein stores. The first two objectives were investigated in relation to a series of experimental flood pulses on the regulated river. The data show distinct differences between the rivers: *Neoporus* populations were restricted to permanent waters on the regulated floodplains, while on the unregulated floodplains they regularly accessed temporary waters. Experimental flooding on the Savannah River negated these differences between rivers. Behaviorally, populations in regulated systems were significantly less likely to disperse via flight prior to the experimental flood pulses, whereas no difference was detected post-pulse. However, this change was due to a decrease in dispersal in the Altamaha population rather than an increase in the Savannah population. Physiologically, lipid concentrations within the Savannah River floodplains differed between habitat types (temporary > permanent) and protein concentration differed between river systems (Savannah > Altamaha). These results suggest that a lack of regular flood events has significantly affected multiple aspects of *Neoporus* populations in regulated systems. Thus, *Neoporus* may be a useful indicator of overall floodplain connectivity. The results of this study also suggest that river management strategies should take floodplain function and dynamics into account.

Introduction

Floodplains are among the most valuable ecosystems in the world and, according to Costanza et al. (2014), provide over \$25,500 ha^{-1} yr^{-1} in ecosystem services. While often overlooked in the study of river ecology, more emphasis has been directed towards the ecological roles of these critically important ecosystems in recent years (Junk et al., 1989; Poff et al., 1997; Mitsch & Gosselink, 2000; Benke, 2001). Benefits of floodplains to the overall river system are numerous and include nutrient and sediment removal; input of allochthonous carbon sources; and provision of habitat for an array of plants, fish, and invertebrates (Mitsch & Gosselink, 2000). However, many of these benefits rely on a direct hydrologic connection between the river channel and adjacent floodplain. This connection is accomplished via overbank flooding. The Flood Pulse Concept (Junk et al., 1989) explains the importance of this connection between river and floodplain, positing that the productivity, biotic interactions, and mere existence of floodplains are due to flood pulses.

However, river regulation has significantly reduced the frequency and duration of these pulses that are critical to maintaining the ecology of the floodplain system creating far-reaching impacts on nutrient cycling, sediment dynamics, and biotic diversity (Junk et al., 1989; Poff et al., 1997; Kennedy & Turner, 2011). Documenting and understanding the specific impacts of dam construction are critical to developing the most effective flow restoration techniques (Bunn & Arthington, 2002). A number of studies have been completed with the aim of determining flow alteration impacts on various taxonomic groups, but the results have been somewhat mixed, with macroinvertebrates exhibiting a particularly wide variety of responses (positive, negative, and neutral) to flow regulation (Poff & Zimmerman, 2010). Much of this research, however, has been focused on the river channels; little effort has been invested in determining flow alteration consequences in river floodplains.

Floodplains are dynamic systems where resident organisms are adapted to cycles of flooding and drying at predictable time intervals (Tronstad et al., 2007; Watkins et al., 2011; King et al., 2012). These floods create shifting mosaics of habitat which may include (relatively) permanent oxbow lakes; temporarily flooded pools, sloughs, and backswamps; and areas of dry land (Mitsch & Gosselink, 2000). The extent of each of these habitats depends on the magnitude of the flood pulse from the river channel. Organisms within the floodplain differentially use these various habitats based on their physiological needs, life cycles, etc. (Batzer & Wissinger, 1996; Tronstad et al., 2005; Merritt et al., 2008). Lack of floodplain connectivity (via river regulation) can lead to restricted habitat use by floodplain residents (Tronstad et al., 2005; Gallardo et al., 2008).

Predaceous diving beetles (Coleoptera: Dytiscidae) are one such floodplain resident that appears to be negatively affected by river regulation. A commonly found inhabitant of floodplains, dytiscids play a significant ecological role as both predator and prey (Batzer & Wissinger, 1996), and while they are generalist organisms, previous research has shown that dytiscids (particularly those in the genus *Neoporus*) are negatively affected by a lack of flood pulses in large river floodplains of the southeastern U.S. (Lee et al., 2016). The specific causes and consequences of this pattern, however, are unclear. In order to determine the ways in which flow alteration has affected *Neoporus* populations in the southeastern U.S., we used the regulated Savannah River (GA) floodplains to test alterations to the following biological aspects of *Neoporus*: (1) distribution, (2) behavior, and (2) physiology as compared to the unregulated Altamaha River (GA) floodplains. The southeastern Coastal Plain contains the greatest extent of large floodplains in North America (Hunt, 1967), making it an ideal focal area in which to study effects of flood pulses (or lack thereof) on floodplain inhabitants. Specifically, our hypotheses were:

(H1a) *Neoporus* populations in the regulated system less frequently access temporarily flooded portions of the floodplain compared to populations in the unregulated system,

(H1b) river regulation has had a particularly negative effect on populations of the rarer species of *Neoporus*,

(H1c) flood pulses in the regulated system will create a distribution of *Neoporus* populations that mirrors that of the unregulated system,

(H2a) dispersal via flight has been negatively impacted as a result of long-term (> 60 years) river regulation,

(H2b) reintroduction of flood pulses in the regulated system will increase flight propensity to levels found in the unregulated system,

(H3a) *Neoporus* present in novel/temporary aquatic habitats on floodplains (outside of permanent refugia) will contain greater lipid and protein reserves, and

(H3b) lipid and protein reserves in *Neoporus* from the regulated system will be significantly lower than those in the unregulated system due to the latter's greater access to temporary habitats.

Methods

Study sites

This study focused on two river floodplain systems in the Coastal Plain physiographic region of Georgia, USA: the Savannah River and the Altamaha River. The Savannah River is a highly regulated system on the Georgia-South Carolina border. Its headwaters are located in the Blue Ridge region; from there it flows through the Piedmont and into the Coastal Plain. The entire Savannah watershed encompasses nearly 27,400 km^2, making it one of the largest watersheds in the southeastern U.S. There are three major dams on the mainstem of the river, the furthest downstream of which is Clarks Hill Dam (also known as J. Strom Thurmond Dam), located just upstream of Augusta, GA. Construction of this was completed in 1954, but dam construction and diversion of the river began as early as 1947. The dam is used primarily for flood abatement but also produces hydroelectric energy and stores drinking water for Augusta and surrounding areas. The operation of this dam regulates river flows from Augusta to the mouth of the river in Savannah, GA. It is within this section of the river where the study site for this project was located. Specifically, our study took place within the Tuckahoe Wildlife Management Area (operated by the Georgia Department of Natural Resources) in Screven County, GA (Fig. 1). The study site is located approximately 120 km upstream of the mouth of the river; the approximate watershed area of the Savannah River at this location is 22,400 km^2. Over the past decade, there has been increased interest in restoring ecological flows to the lower Savannah River (Wrona et al., 2007). Two experimental flood pulses were released through Clarks Hill Dam in 2005 and 2006. However, precipitation levels were not sufficient to allow USACE to release any further experimental flood pulses until July 2013 (see below).

The Altamaha River watershed is of similar size (with a total watershed area of approximately 36,000 km^2), but, unlike the Savannah River, the mainstem of the Altamaha River contains no dams. The two rivers that form the Altamaha River (the Ocmulgee and Oconee Rivers) do contain dams but are significantly smaller than those on the Savannah River and are operated as pumped storage facilities, which pass most of high pulse flows downstream, so flow patterns on the Altamaha approximate natural hydrologic conditions. The Altamaha River is listed as one of the few large rivers in the southeastern U.S. that remains largely unimpounded, and thus it has been designated as a Bioreserve by The Nature Conservancy. Our study site on the Altamaha River was located within the Big Hammock Wildlife Management Area in Tatnall County, GA (Fig. 1). Watershed size at this location is approximately 30,000 km^2, and distance to the river mouth is 110 km.

Both rivers have large, relatively flat floodplain systems that consist of two primary categories of aquatic habitats on which we focused for this study: permanent aquatic habitats; and low-lying depressions that temporarily fill with water. The majority of the permanent water bodies on these floodplains are oxbow lakes. Formerly part of the river channel itself, oxbow lakes have been cut off from the course of the river due to changes in the meander pattern of the river over time. They vary in size, from approximately 1 km^2 to 6 km^2 (within these two WMAs) and contain a diversity of aquatic organisms, including an abundance of fish (D. Batzer, unpublished data). The temporary water bodies, on the other hand, are either fishless or contain fish at very low densities compared to oxbow lakes (Garnett & Batzer, 2014). These temporary water bodies fill via direct precipitation, groundwater discharge, and/or overbank flooding from the river. During relatively dry years with little to no overbank flooding, temporary habitats remain disconnected from the river channel or from permanent water floodplain lakes. In years where overbank flooding occurs, water first begins to enter the floodplains through breaks in the natural levees, creating channels of flow through the floodplains. As water levels continue to rise, floodwaters will overtop the levees and inundate the floodplains further. The typical flood season occurs during late winter and spring. Vegetation communities at both sites are very similar and consist of bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), sweetgum (*Liquidambar styraciflua*), and various oak species (*Quercus* spp.) (Lee, 2008).

Due to the effects of river regulation, flood patterns in the Savannah River floodplains differ greatly from those in the unregulated Altamaha River floodplains. A comparison between the hydrographs of each river (Fig. 2) illustrates this distinct difference. From January 2012 through May 2015, the Altamaha River at Baxley (USGS Gage 02225000) experienced 101 days over flood stage (4.423 m) whereas the Savannah River at Burton's Ferry (USGS Gage 02197500) experienced 59 days over flood stage (4.572 m) (Fig.2a, 2c). Because Clarks Hill Dam has been very effective in controlling floods on the Savannah for the past 60 years, very little overbank flooding occurs there compared to the Altamaha. Thus, most of the temporary habitats on the Savannah River floodplains exist solely due to precipitation and are disconnected from each other. This typical hydrology was in place during the majority of our study period (January 2012 – June 2013 and April 2014 through May 2015). During a portion of our study (July 2013 – January 2014), however, a significant increase in precipitation (Table 1) throughout the Southeast created a surplus of water in reservoirs on the Savannah River. As a result, USACE released three flood pulses (July 2013, August 2013, and January 2013); these induced pulses were responsible for all 59 of the days when flood stage was exceeded on the Savannah over our study period (Fig. 2b). This change in management essentially created a natural experiment that allowed us to empirically evaluate the potential effects of restoring flood pulses to the Savannah floodplains.

Distributional studies

Systematic sampling allowed us to compare relative abundances of *Neoporus* populations [(the genus as a whole (H1a) and individual species (H1b)] between floodplain systems over a period of 3.5 years, and it allowed for comparison between periods of average flow and periods of induced pulses (H1c). Sampling for *Neoporus* adults and larvae was conducted in the two habitat types described above: permanent oxbow lakes and temporarily flooded portions of the floodplains. In each floodplain system, four permanent and four temporary sites were sampled (as available) for *Neoporus*.

Quantitative sampling was carried out using a D-frame net (Wildlife Supply Company Turtox Dip Net, 500 micron mesh, mouth dimensions 305 mm width x 254 mm height) and performed 12 0.5-m sweeps along the shallow edge of the water were conducted at each of the sampling sites. Sampling in deeper water (50 cm depths) confirmed that *Neoporus* were very uncommon away from shallow edges (C. Holt, unpublished data), likely due to their need to avoid fish predators and for frequent access to the water's surface for oxygen (both larvae and adults). Fairchild et al. (2003) confirmed that a preference for shallow water among aquatic beetles is widespread. During extensive floodplain inundation, deep oxbow lakes were not accessible for sampling, and only temporary habitats were sampled. During deep flooding, the oxbows no longer contained shallow edges; thus, *Neoporus* were likely not present there due to their strong preference for tracking shallow water. Therefore, when the floodplain was extensively inundated (and the oxbow lakes no longer contained shallow edges), we considered *Neoporus* to be absent from permanent habitats. If temporary habitats were completely absent from the floodplain during sampling (e.g. during drought periods), the sites were eliminated from our sampling regime for that date only.

Sampling occurred from January 2012 – April 2015. Samples were collected seasonally, with increased frequency over the spring flood season each year (January – May) (see horizontal axis of Fig. 3 for specific months in which sampling occurred). All field samples were preserved on site in 95% ethanol and returned to the lab for analysis.

In the lab, field samples were rinsed over a 300 µm mesh sieve in order to retain all larval and adult *Neoporus*. We subsampled when numbers of individuals exceeded 100 (larvae and adults were considered separately). All *Neoporus* were identified to species (adults only) using Epler (2010) and enumerated (adults and larvae). Voucher specimens were deposited in the University of Georgia Collection of Arthropods (UGCA) at the Georgia Museum of Natural History (Athens, GA).

Dispersal microcosm experiment

Beetles from aquatic habitats (primarily permanent habitats as available) in each system were collected via grab sample to test for differences in flight propensity between the two river systesm using a microcosm experiment (H1a and H1b). Prior to the induced pulses on the Savannah River, we conducted the experiment monthly between January 2013 and May 2013. To test for effects of the induced pulses, we repeated the experiment once in April 2015. Live beetles for the microcosms were collected from temporary or permanent water bodies (as available) in each system and returned to Athens, GA. Beetles were acclimated for two days upon their arrival in Athens. Experimental tubs (38 cm x 20 cm x 20 cm) were filled 1/3 full with water and a thin layer of leaf litter and placed outside in partial shade. During each of the monthly 2013 (pre-pulse) trials, 15 *Neoporus* individuals were placed in each of six experimental tubs (three with only Altamaha beetles and three with only Savannah beetles), which were left uncovered. Positive control tubs (n=3 for Altamaha and n=3 for Savannah per trial) were also placed in the same location as experimental tubs but were covered with 1 mm mesh in order to account for mortality/cannibalism of individuals (n=10 beetles/tub). In addition to the positive control and experimental tubs, four uncovered tubs with only leaf litter and water (i.e. negative controls with no beetles) were interspersed throughout the experimental and control tubs to determine whether beetles might disperse between tubs. In 2015 (post-pulse), we set up seven experimental tubs per system (due to the fact that we completed only one round of the microcosm experiment during 2015) with 10 *Neoporus* individuals in each. Positive and negative control tub set up for the 2015 experiment was the same as in the 2013 experiment. All tubs were arranged in a random fashion. Each experiment ran for 16 days, at the end of which the final number of beetles remaining in each tub was determined. For both the experimental and control tubs, we did not distinguish among *Neoporus* species prior to introducing them to tubs as identifying them while live would have required significantly greater handling time and identification under a microscope, which could have potentially injured or stressed the beetles further. However, the two most common species (*N. clypealis* and *N. hybridus*) were among the larger individuals, and we were able to target them.

Physiology measures

To investigate differences in *Neoporus* nutrient stores between temporary and permanent aquatic floodplains habitats (H3a) as well as between the Savannah and Altamaha floodplain systems overall (H3b), we analyzed lipid and protein concentrations over a one-year period (2012). *Neoporus* individuals were collected via grab sample (in January, February, April, July, and November) from each of the permanent and temporary sites (as available) on the Altamaha and Savannah River floodplains, returned to the lab on ice, and frozen at -20°C. *Neoporus clypealis* females from each site at each date (n=3 beetles per site-date combination) were analyzed to determine their lipid and protein content via vanillin (Van Handel, 1985) and Bradford (Bradford, 1976) assays, respectively.

Statistical analyses

Due to non-normality, all *Neoporus* abundance data were log (x+1) transformed. To test for overall differences in *Neoporus* distribution between habitats on the Savannah and Altamaha floodplains (H1a), we used a linear model and three-way ANOVA (factors = habitat type, river, and date). Adults and larvae were analyzed separately. All factors were considered fixed effects. Subsequent one-way ANOVAs were used if a significant interaction term resulted from the three-way ANOVA.

To determine whether flood pulses on the Savannah River floodplains created a more "natural" *Neoporus* distribution (i.e. similar to that of the Altamaha River floodplains) (H1b), we used a linear model and ANOVA, using the following groups: Altamaha pre-flood, Altamaha post-flood, Savannah pre-flood, and Savannah post-flood. Post-hoc Tukey tests were used to determine differences among groups. Only temporary habitats were used in this analysis in an effort to determine whether the pulses created greater access for *Neoporus* to the larger floodplain area (beyond the permanent habitats), and all four temporary samples collected per date were pooled for analyses.

Differences in species distributions between rivers (H1c) were analyzed via a Chi-square test. To investigate differences among individual species' abundances, we used t-tests.

In order to determine effects of long-term flow regulation on dispersal propensity in *Neoporus* (H2a), we used a linear model and a two-way ANOVA (factors = river, date) for the five monthly repetitions completed in 2013 (pre-pulse period) (dispersal percentages were arcsine square root transformed prior to analysis). All factors were considered fixed effects. If the interaction term was significant, subsequent one-way ANOVAs were used to discern differences within factors. To assess whether the induced flood pulses on the Savannah led to an increase in dispersal (H2b), we used a t-test to analyze differences in dispersal percentages within rivers (April only) and between rivers (post-pulse iteration only).

Differences in lipid and protein concentrations between habitats (H3a) and river systems (H3b) were analyzed via a linear model and three-way ANOVAs (factors = habitat, river, and date). All factors were considered fixed effects. Lipid concentrations were non-normal and, thus, log (x+1) transformed. Protein concentration exhibited a normal distribution. If significant interaction terms resulted, subsequent one-factor ANOVAs were carried out. To determine if density-dependent relationships existed between *Neoporus* abundance and lipid and protein concentrations, we calculated correlation coefficients (Pearson's *r*).

All statistical tests were performed in R (R Core Team 2015) using a significance level of $\alpha = 0.05$.

Results

Distribution among habitats and river systems (H1a)

In total, nearly 9000 *Neoporus* individuals were collected during the three and a half year study, 4094 (3991 adults and 103 larvae) of which were found in the Savannah River floodplains and 4828 (4340 adults and 488 larvae) of which were found in the Altamaha River floodplains.

With the entire genus taken into account, adult *Neoporus* exhibited significant distributional differences based on habitat, river, and date. A significant interaction existed between habitat and river ($p < 0.001$) and habitat and date ($p < 0.001$). Within the permanent habitats, abundance of *Neoporus* was greater in the Savannah floodplains compared to the Altamaha ($p = 0.023$) (Fig. 3a). In the temporary habitats, abundance in the Altamaha was greater than in the Savannah ($p < 0.001$) (Fig. 3b). Within each river, the Savannah River exhibited greater *Neoporus* abundance in permanent habitats compared to temporary habitats ($p < 0.001$) (Fig. 4b), whereas the Altamaha River exhibited greater *Neoporus* abundance in temporary habitats ($p = 0.003$) (Fig 4a).

Neoporus larvae displayed distributional differences based on habitat and river, many of which were similar to the patterns described above for adults. As with adults, a significant interaction existed between habitat and river for the larvae ($p < 0.001$). Overall, there was no significant difference in larval abundance between the two floodplains. However, within permanent habitats only, larval abundance was greater in the Savannah floodplains compared to the Altamaha ($p = 0.009$). Temporary habitats exhibited the opposite pattern – larval abundance was greater in Altamaha temporary habitats compared to Savannah temporaries ($p = 0.009$). Overall, larvae were found more frequently in temporary water bodies compared to permanent ones ($p = 0.020$). Within the Altamaha system, larvae were more common in the temporary water bodies ($p < 0.001$). No pattern emerged among habitats in the Savannah River floodplains. While no significant pattern was found among dates regarding larval abundance, all larvae were found either in late winter or spring.

Species compositions among river systems (H1b)

Six species of *Neoporus* were found between the two systems (*N. aulicus*, *N. clypealis, N. hybridus, N. lobatus, N. venustus,* and *N. vittatipennis*). All six species were found in the Altamaha system; all except *N. venustus* were found in the Savannah system. *N. clypealis* and *N. hybridus* were by far the most dominant species among the six and occurred in equal proportions between the two systems. Distributions of the rarer species, however, differed significantly between the two rivers (X^2, $p < 0.001$); *N. vittatipennis* drove this difference and was significantly more abundant in the Altamaha floodplains ($p < 0.001$).

Effects of flood pulses on Neoporus *distribution (H1c)*

The large 2013-2014 flood pulses had significant effects on the distribution of *Neoporus* in each system. In the pre-pulse period, greater numbers of *Neoporus* were present in the temporary habitats of the Altamaha floodplains compared to those of the Savannah floodplains ($p = 0.026$) (Fig. 3b). In the post-pulse period, there was no difference in abundance of *Neoporus* between temporary habitats in each system.

Dispersal differences between river systems (H2a & H2b)

Results from the dispersal microcosm study indicate the existence of significant differences in flight propensity of *Neoporus* between the two river systems. In the first iteration of the experiment (2013: pre-pulse), differences in dispersal percentages were detected among dates ($p < 0.001$) and between rivers ($p < 0.001$). Dispersal increased in beetles from both systems as time progressed (and temperatures warmed), and beetles from the Altamaha River floodplains were significantly more likely to disperse overall. In 2015 (post-pulse), however, results differed: river was no longer a significant factor in explaining dispersal rates among *Neoporus*. Comparisons within each river between the two time periods revealed a significant decline in dispersal among Altamaha beetles from 2013 to 2015 ($p = 0.002$) and no change in dispersal among Savannah beetles between the two time periods.

Lipid and protein concentrations among habitats and river systems (H3a & H3b)

Regarding lipid concentrations (see Table 2), river and habitat exhibited a significant interaction ($p = 0.042$). River alone did not affect lipid concentrations, but habitat did have a significant effect. Within the Savannah floodplains, lipid concentrations were greater in temporary habitats compared to permanents ($p = 0.021$). The Altamaha exhibited no significant pattern. There was a strong negative correlation between lipid concentration and abundance (R = -0.42, p = 0.003) with both rivers and habitats included.

Protein concentrations (see Table 2) exhibited significant differences between rivers and dates (no interactions were significant). *Neoporus* populations in the Savannah River floodplains contained greater concentrations of proteins than did beetles in the Altamaha River floodplains (p = 0.015). Temporally, beetles contained greater protein concentrations in November than in February (p = 0.019) or March (p = 0.007). The correlation between protein concentration and abundance was strong and negative (R = -0.46, p = 0.001).

Discussion

Our study suggests river regulation has significantly affected *Neoporus* species in the Savannah River floodplains by limiting their access to temporary habitats, and perhaps even decreasing their propensity for aerial dispersal.

Distribution among habitats and river systems (H1)

Neoporus populations in the Altamaha River floodplains more readily accessed temporary aquatic habitats than those in the Savannah River, as predicted in H1a. However, following large flood pulses, distributions between the two systems became similar, supporting H1b. Overall, species composition differed between the two systems, with rarer species (particularly *N. vittatipennis*) being more negatively impacted in the Savannah, supporting H1c.

The extreme, long-term flow management of the Savannah River has significantly impacted the genus *Neoporus* by creating a static system rather than a dynamic one as we see in the Altamaha River. The lack of significant, regular overbank flooding in the Savannah River has greatly reduced the amount of aquatic habitat on the floodplain. Permanent oxbow lakes are the only significant aquatic habitats present on a regular basis. Obligate aquatic organisms such as dytiscids are unlikely to find suitable habitat outside of these oxbows. Thus, we see a distribution pattern that appears static, with beetles limited to permanent water bodies in the Savannah system (Fig. 4b). When we examine a river with natural flood pulses such as the Altamaha, we see a very different picture. Overbank flooding occurs nearly every year on the Altamaha River, creating a dynamic floodplain system with a frequently-changing aquatic-terrestrial transition zone (ATTZ *sensu* Junk et al. 1989). This ATTZ advances and retreats with the floodwaters. During dry portions of the year, the majority of the floodplain consists of terrestrial habitat. As river levels rise during the flood season, water begins to inundate portions of the floodplain, increasing the aquatic habitat availability. The ATTZ along the edge of this flood front is a shallow area with low flow velocities and is a preferred habitat of *Neoporus*. Thus, as flood waters advance, *Neoporus* will track this shallow ATTZ (via swimming or flight) as it advances into the floodplain. As the flood waters begin to recede, *Neoporus* will again track the ATTZ, eventually returning to permanent water bodies on the floodplain. This creates the distribution pattern we see in the Altamaha (Fig. 4a), which is one of dynamism and change based on the natural flooding-drying cycle in the system. In the Savannah floodplains, the ATTZ is essentially non-existent, consisting of a disconnected mosaic of only occasionally rain-filled pools and permanent-water oxbow lakes. There are rarely alterations to this pattern due to flow management in the Savannah system, creating a static environment in which *Neoporus* remain primarily in permanent water bodies (see Fig. 4b).

Dispersal propensity (H2)

Our second set of hypotheses regarding dispersal rates in each system were partially supported: prior to significant flooding on the Savannah River, *Neoporus* individuals from the

Savannah floodplains were less likely to disperse via flight compared to those from the Altamaha floodplains, which supports H2a. However, the second component of that hypothesis (H2b) was rejected: flood pulses on the Savannah River did not increase dispersal via flight as we had predicted. Although dispersal became similar between systems post-pulse, that difference was due to a decrease in Altamaha dispersal, rather than an increase in Savannah dispersal.

Different interconnections between reliable permanent aquatic habitat (oxbows) and interspersed temporary aquatic habitat on the Altamaha and Savannah floodplains may result in different dispersal strategies being efficacious in each system. Dispersal is a high-risk activity that is, ideally, accompanied with high rewards such as decreased competition, decreased predation, and/or increased access to food resources. Dytiscids are well-known for their dispersal abilities, both the distance they are able to disperse as well as their propensity for dispersal (Jackson, 1952; Davy-Bowker, 2002; Lundkvist et al., 2002; Yee et al., 2009; Pitcher & Yee, 2014). In the case of the Altamaha system, the risk of dispersal is mitigated by the fact that ample aquatic habitat exists outside of the permanent water refugia. Thus, we see *Neoporus* departing from oxbows and accessing temporary water bodies on a regular basis. In contrast, because temporary water bodies are few and far between on the Savannah floodplains, the risk associated with dispersal from permanent water refugia is greatly increased, destabilizing the balance between risk and reward in this system. Our flight dispersal microcosm prior to the flood pulses confirms this concept (Altamaha beetles were more likely to disperse via flight than were Savannah beetles).

The introduction of significant overbank flooding on the Savannah River was expected to increase the likelihood of dispersal by decreasing the risk associated with leaving the refugia via flight, thus creating a dispersal rate similar to that of the Altamaha population. While dispersal percentages did not differ between the two rivers post-pulse, the dispersal percentage did not change in the Savannah River due to the pulse. The similarity between the two rivers was, instead, due to a significant decrease in dispersal among the Altamaha population. This was an unexpected outcome, but it can be explained by examining the two modes of dispersal used by *Neoporus* – flying and swimming. During the pre-pulse period (2012) on the Altamaha River, there were numerous temporary water bodies on the floodplain, but they were disconnected from each other and the permanent water bodies due to below-average precipitation. Therefore, *Neoporus* could have only accessed them via flight (which they did). However, during the following two years of high precipitation, many of the temporary habitats were directly connected to each other and the flooded oxbow lakes, allowing *Neoporus* to disperse along the edge of the ATTZ via swimming (flight was not required). This behavioral plasticity may help explain why the post-pulse dispersal microcosm (2015) resulted in a decrease in dispersal in the Altamaha system as we were only accounting for dispersal via flight, and during that high water water year, most beetles likely dispersed via swimming. Regarding the Savannah River population, their likelihood of flight did not change (pre- vs. post-pulse), indicating the Savannah population may have lost this behavioral plasticity (i.e. they almost exclusively swim). Perhaps if more large flood-pulses were introduced to the Savannah, regularly creating extensive temporary waters on the floodplain, resident beetle populations may develop more behavioral plasticity to efficaciously exploit both permeant and temporary habitats.

Lipid and protein concentrations among habitats and river systems (H3)

Most of our hypotheses regarding greater lipid and protein concentrations in temporary habitats (versus permanent habitats) and the Altamaha floodplains (versus the Savannah floodplains) were rejected. Overall, beetles in temporary aquatic habitats did not contain greater lipid and protein concentrations than those in permanent habitats (does not support H3a). Within the Savannah floodplains alone, however, lipid concentrations were significantly greater in beetles found in temporary habitats. Also, Altamaha beetles did not exhibit greater lipid and protein concentrations than Savannah beetles (does not support H3b); in fact, the Savannah River populations contained greater protein (but not lipid) concentrations. However, the strong negative correlations between *Neoporus* abundances and lipid and protein concentrations suggest that intra-specific competition is affecting beetle physiological condition.

Neoporus densities in temporary water bodies of the Savannah floodplains were much lower than densities in the permanent oxbow lakes. In addition, the temporary habitats on the Altamaha floodplain had significantly greater beetle abundances, which may explain the lack of difference between permanent and temporary habitats in that system. So, while our hypothesis was rejected, it appears there may be a physiological benefit to accessing areas with lower beetle densities; whether those are permanent or temporary habitats may depend on the dynamics of the system in question.

Management considerations

River regulation has been shown to affect taxa other than *Neoporus* as well. Lee et al. (2016) documented greater abundances of three fish – *Esox* spp. (pickerels), *Lepomis marginatus* (dollar sunfish), and *Notropis petersoni* (coastal shiner) – in Altamaha River floodplains compared to Savannah River floodplains. In addition, Garnett & Batzer (2014) investigated differences between fish communities in upper- vs. lower-river floodplains in the Altamaha and Savannah systems and identified three indicator species in the lower Altamaha floodplains (where our study took place) – *Esox americanus, Aphredoderus calva,* and *A. sayanus* – all of which time their spawning with flood pulses (Marcy et al., 2005). These fish were rare on the

Savannah floodplains. Like *Neoporus*, these fish species use permanent water bodies on the floodplain, such as oxbow lakes, as refugia between floods. Lee et al. (2016) also showed that seedling recruitment of bottomland trees was reduced in the Savannah compared to the Altamaha floodplains. An experimental flood pulse during their study increased seedling numbers on the Savannah floodplains, indicating bottomland trees (seedlings) are sensitive to flood cycles.

This suite of organisms, ranging from plants to invertebrates to vertebrates, that is affected negatively by lack of regular overbank flooding speaks to the wide-reaching effects of river management. Belmar et al. (2013) documented changes in physical habitat of riparian forests due to flow regime alteration. Valett et al. (2005) found evidence for alterations to biogeochemical cycling in a disconnected floodplain. Kennedy & Turner (2011) found lower macroinvertebrate richness and density in the riparian zone of the Rio Grande River as a result of channelization due to river regulation. Timing of inundation in the Murray-Darling Basin in Australia greatly affected zooplankton via alterations to the riparian vegetation in the floodplains as well (Watkins et al., 2011). These widespread effects of river regulation on floodplain ecosystems are well-documented and ubiquitous. Our findings further this knowledge by providing evidence that regulation can affect both species distributions on the floodplain and behavior of floodplain resident organisms. Our results suggest incorporation of flood pulses into regulated rivers may re-distribute *Neoporus* (and other floodplain specialists) in a pattern similar to unregulated systems. Further, more frequent large floods may create reliable, predictable access to habitat outside of permanent water bodies on the floodplain, eventually inducing behaviors conducive to exploiting the full range of available habitat. By reconnecting sub-habitats within the floodplain, and the river channel and floodplain, a suite of organisms from plants to invertebrates to fish to waterfowl will undoubtedly benefit, creating a more natural and highly utilized floodplain ecosystem.

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Table 5.1 Mean pH and electrical conductivity. Values are presented by river system and habitat. In addition, total precipitation and mean discharge by year for each of the study sites are presented.

River	**Habitat**	**Mean pH (+/- SE)**	**Mean EC (+/- SE)**	**Total Precipitation (cm)**[a]				**Mean Discharge (m^3s^{-1})**[b]			
				2012	**2013**	**2014**	**2015***	**2012**	**2013**	**2014**	**2015***
Altamaha	**Permanent**	5.73 +/- 0.93	82.41 +/- 11.38	104.14	148.36	133.86	45.85	75.16	379.04	319.77	448.96
	Temporary	5.24 +/- 0.70	59.46 +/- 17.59								
Savannah	**Permanent**	5.75 +/- 0.45	97.58 +/- 21.81	104.75	157.05	125.22	47.98	130.79	264.07	265.72	207.66
	Temporary	5.58 +/- 0.36	98.13 +/- 45.80								

[a] Precipitation data from NOAA (http://www.ncdc.noaa.gov/)

[b] Discharge data from USGS (http://www.usgs.gov/water/)

*2015 only includes data through May (the end of the study period)

Table 5.2 Lipid and protein concentrations in *Neoporus clypealis* females. Data are separated by river system and habitat (with SE in parentheses).

River	**Habitat**	**Mean lipid concentration (+/- SE) (µg/beetle)**	**Mean protein concentration (+/- SE) (µg/beetle)**
Altamaha	**Permanent**	101.78 +/- 32.98	265.88 +/- 25.11
	Temporary	47.83 +/- 12.49	286.69 +/- 45.50
Savannah	**Permanent**	40.11 +/- 9.46	354.45 +/- 21.63
	Temporary	137.44 +/-23.90	313.72 +/- 66.96

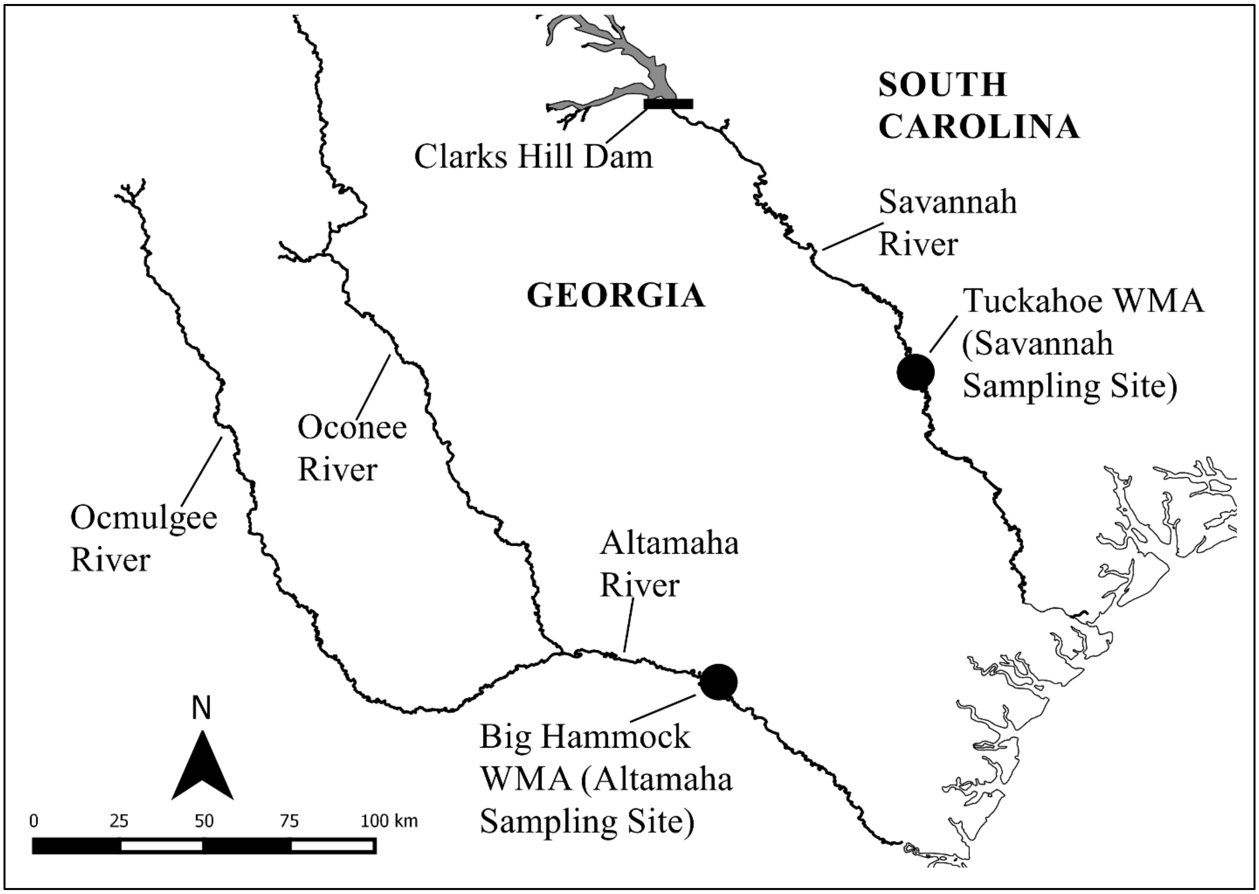

Figure 5.1 Map of the study sites on the Altamaha and Savannah Rivers. Sampling occurred in two Wildlife Management Areas (WMA) in Georgia, USA – Big Hammock WMA (Altamaha study site) and Tuckahoe WMA (Savannah study site).

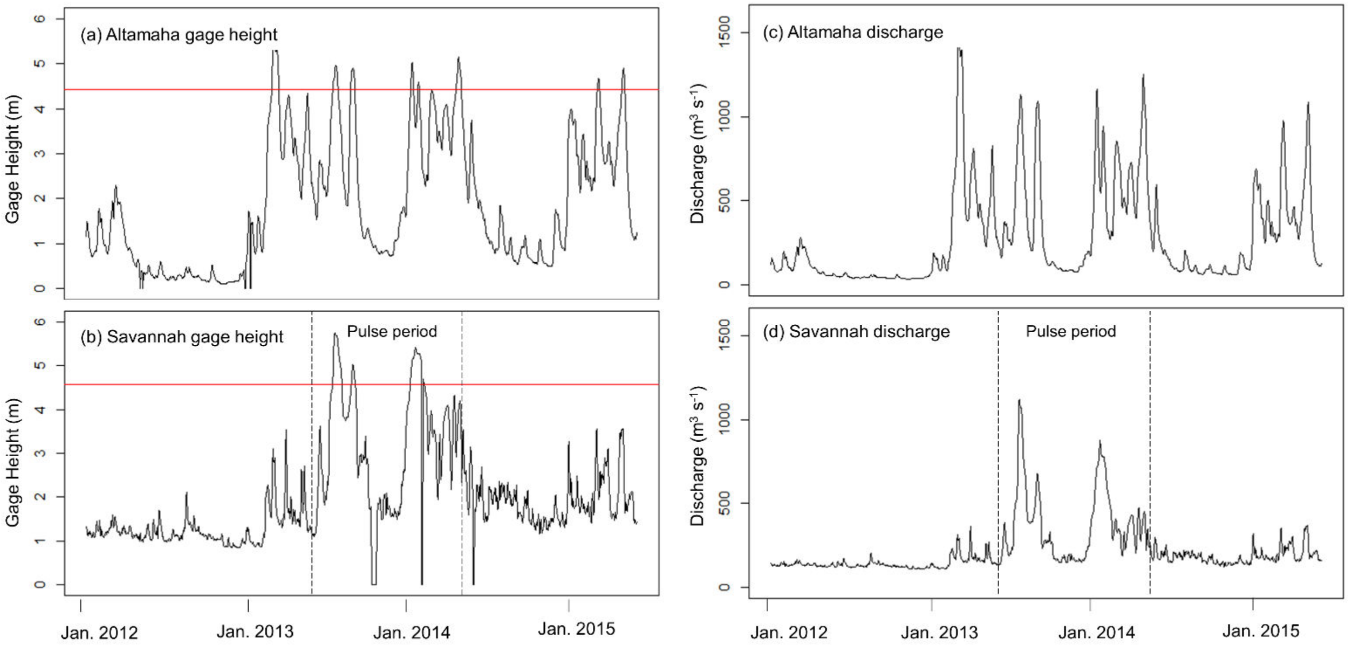

Figure 5.2 Gage height and discharge volumes of the Altamaha and Savannah Rivers. USGS gages were used to obtain this data (Altamaha gage #02225000 and Savannah gage #02197500). The horizontal lines on the gage height graphs (a & b) delineate the flood stages in each system. The area in between the vertical dashed lines on the Savannah hydrographs (b & d) represents the duration of the experimental flood pulses released by USACE from Clarks Hill Dam.

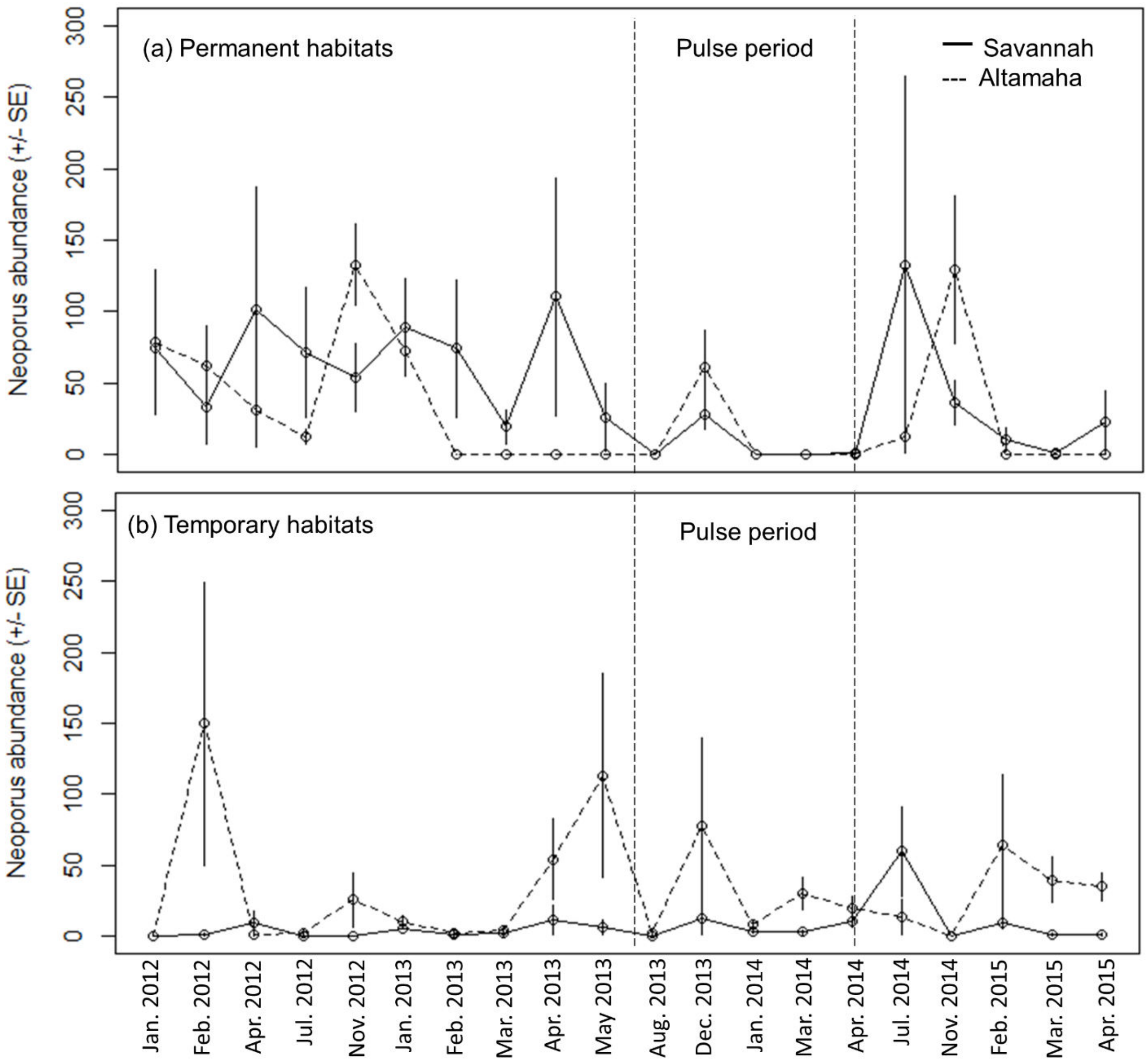

Figure 5.3 *Neoporus* abundance by habitat. Sampling dates are shown on the x-axis. Abundances in permanent (a) and temporary (b) habitats on the Savannah (solid lines) and Altamaha (dashed lines) floodplains are shown. Only adult *Neoporus* abundance is shown. The experimental pulse period is indicated by the vertical dashed lines.

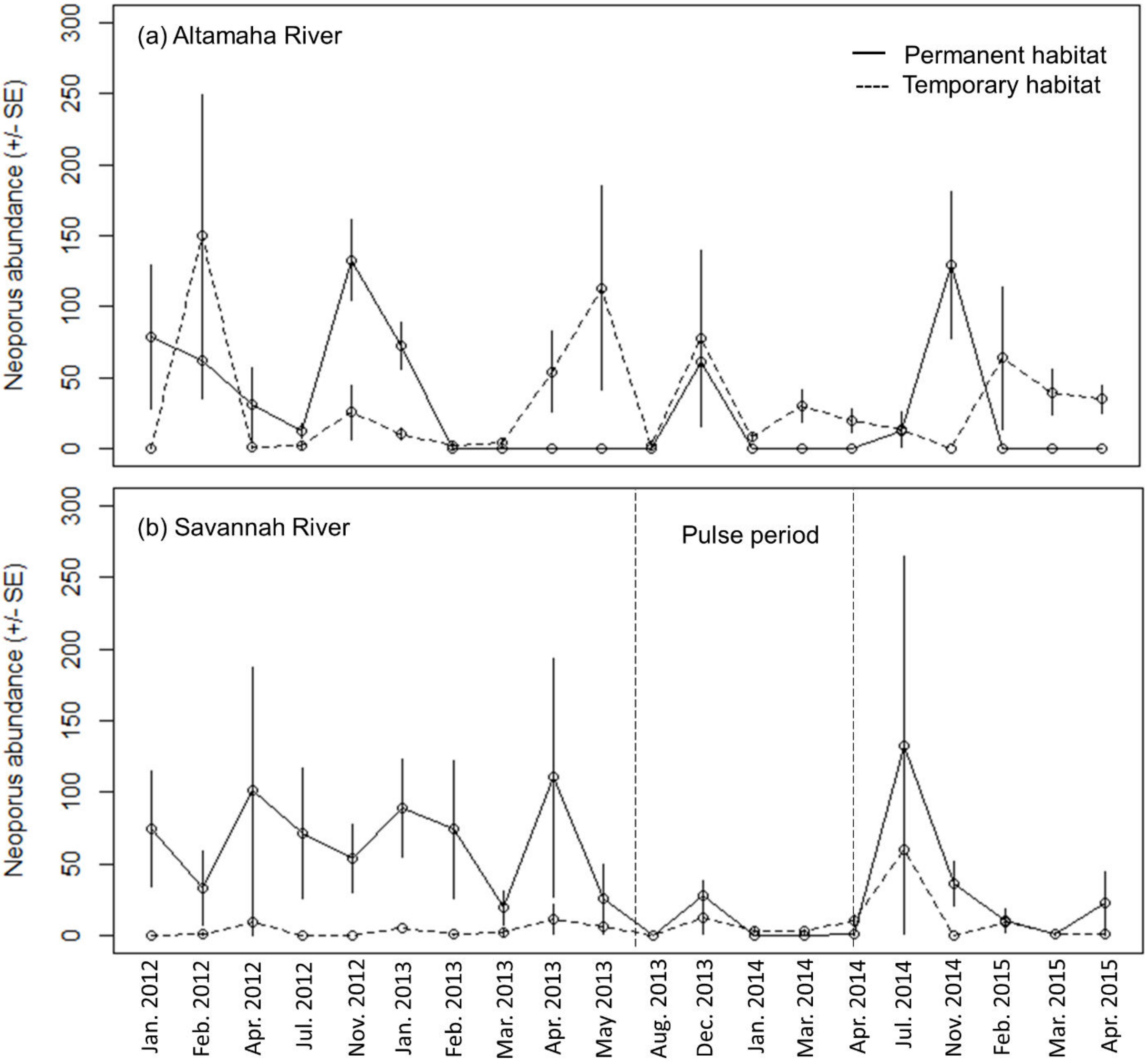

Figure 5.4 *Neoporus* abundance by river. Adult *Neoporus* abundance is shown from the Altamaha (a) and Savannah (b) River floodplains during the 3.5 year study period (sampling dates are indicated on the x-axis). Permanent habitat abundance in each graph are indicated by solid lines, and temporary habitat abundance is indicated by dashed lines. The experimental pulse period in the Savannah River is delineated by vertical dashed lines.

CHAPTER 6

CONCLUSIONS

Human civilization has centered around water resources for millions of years due to multiple factors, including food resources found in aquatic ecosystems, transportation afforded by water, and the simple fact that we (along with every other living organism) require water for survival. It is no surprise then, that we have greatly altered these ecosystems as a result of our use of them. The most intensive alterations have occurred since the beginning of the industrial revolution (McCully 1996). Damming of rivers has arguably caused the most impact on flowing aquatic ecosystems over the past century (Ward and Stanford 1983, Poff et al. 1997, Vinson 2001, Richter and Thomas 2007, Konrad et al. 2008). For this reason, it is imperative that we as scientists and citizens understand the specifics of how these alterations to natural systems are affecting them, from nutrient cycling to biodiversity.

The results from my research suggest significant, long-term changes to macroinvertebrate communities of regulated rivers and their associated floodplains. Within the Chattahoochee River, annual variation in precipitation caused a shift in the macroinvertebrate community below Buford Dam. In addition, the macroinvertebrate community changed significantly as distance from Buford Dam increased (and diel variation in flow decreased). This longitudinal change was directional in the sense that the macroinvertebrate community improved based on three metrics (H’, EPT richness, and sensitive taxa richness) as distance from the dam increased. These results reflect the severely altered state of the Chattahoochee River, particularly directly below Buford Dam where diel variation in flow can reach up to 280 m^3/s.

In addition, my research indicates flow regulation can affect not only organisms within the river channel but on the floodplains as well. A particularly diverse genus of dytiscids (*Neoporus*) found on floodplains of Coastal Plain rivers in the southeastern U.S. appears to be affected by lack of overbank flooding (due to river regulation). I documented significant sympatry among species of *Neoporus* on floodplains of the Altamaha River and found significant effects on their distribution and behavior as a result of long-term flow regulation. In a regulated system, *Neoporus* are significantly less likely to access temporary aquatic habitats on the floodplain compared to an unregulated system. However, a large experimental flood in the regulated system created significant overbank flooding and caused an increase in the number of beetles accessing the larger floodplain. Flight propensity was significantly lower in the regulated system as well and was not affected by the experimental flood.

Overall, this research indicates a need for dam management strategies that incorporate aspects of ecosystem functioning at multiple levels. Altered management strategies are particularly important in light of increasing pressure on water resources (i.e. increasing human populations), changing water uses and management at a large scale (i.e. water disputes between states), and climate change.

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APPENDICES

Appendix A – Chapter 3 Appendix

Table S1 List of taxa from the 65-km study area of the Chattahoochee River below Buford Dam (Hester-Dendy and Surber data). Tolerance values (TV) are included based on Lenat (1993) and Grubaugh and Wallace (1995).

Phylum, Order, Family	**Genus/Final ID**	**TV**
PLATYHELMINTHES		
Tricladida		-
NEMATODA		8.2
NEMERTEA		
Hoplonemertea		
Tetrastemmatidae	*Prostoma*	-
ANNELIDA		
Haplotaxida		
Enchytraeidae		10
Haplotaxidae	*Haplotaxis*	-
Tubificidae	*Ilyodrilus*	-
	Limnodrilus	9.6
	Nais	9.1
	Pristina	9.9
	Ripistes	-
	Stylaria	-
	Tubificinae w/o hair cheatae	-
	Tubificinae w/ hair chaetae	-
	Vejdovskyella	-
Opisthopora		-
Lumbricidae	*Eiseniella*	-
Lumbriculida		
Lumbriculidae	*Lumbriculus*	7.3
Arhynchobellida		
Erpobdellidae	*Erpobdella*	-
Rhychobdellida		
Glossophoniidae	*Helobdella*	-
	Placobdella	-
MOLLUSCA		
Gastropoda		

Phylum, Order, Family	**Genus/Final ID**	**TV**
Hydrobiidae	*Somatogyrus*	6.5
Physidae	*Physa*	-
Planorbidae	*Menetus*	-
Pleuroceridae	*Pleurocera*	-
Bivalvia		
Cyrenidae	*Corbicula*	-
Sphaeriidae	*Pisidium*	6.8
	Sphaerium	7.7
ARTHROPODA		
Isopoda		
Asellidae	*Lirceus*	7.7
	Caecidotea	-
Amphipoda		
Crangonyctidae	*Crangonyx*	8
Dogielinotidae	*Hyalella*	7.9
Gammaridae	*Gammarus*	-
Decapoda		
Cambaridae	*Procambarus*	9.5
Trombidiformes		
Lebertiidae	*Lebertia*	-
Collembola		-
Ephemeroptera		
Baetidae	*Acentrella*	-
	Baetis	-
	Heterocloeon	3.6
	Iswaeon	-
	Plauditus	-
Ephemerellidae		2.7
	Attenella	-
	Dannella	-
	Ephemerella	-
	Eurylophella	-
	Serratella	-
	Teloganopsis	-
Ephemeridae	*Hexagenia*	4.7
Heptageniidae	*Heptagenia*	2.8
	Maccaffertium	-
	Stenacron	-
	Stenonema	7.1
Isonychiidae	*Isonychia*	3.8
Leptophlebiidae	*Leptophlebia*	6.4
Odonata		

Phylum, Order, Family	Genus/Final ID	TV
Aeschnidae	*Boyeria*	-
Calopterygidae	*Calopteryx*	8.3
Coenagrionidae	*Argia*	8.7
	Enallagma	9
Gomphidae	*Progomphus*	-
Plecoptera		
Capniidae	*Allocapnia*	2.8
	Nemocapnia	-
Chloroperlidae	*Haploperla*	-
Leuctridae	*Leuctra*	0.7
Perlidae	*Agnetina*	-
	Eccoptura	-
	Paragnetina	1.7
	Perlesta	0
Perlodidae	*Helopicus*	-
	Remenus	-
Pteronarcyidae	*Pteronarcys*	1.7
Taeniopterygidae	*Taeniopteryx*	6.3
Hemiptera		
Corixidae	*Trichocorixa*	9
Veliidae	*Rhagovelia*	-
Neuroptera		
Corydalidae	*Chauliodes*	-
	Nigronia	-
Sialidae	*Sialis*	7.5
Trichoptera		
Brachycentridae	*Brachycentrus*	2.2
	Micrasema	-
Glossosomatidae	*Glossosoma*	1.5
Hydropsychidae		5.3
	Ceratopsyche	-
	Cheumatopsyche	6.6
	Diplectrona	-
	Hydropsyche	-
Hydroptilidae	*Hydroptila*	6.2
Lepidostomatidae	*Lepidostoma*	1
Leptoceridae	*Ceraclea*	-
	Oecetis	5.7
Limnephilidae	*Pycnopsyche*	2.3
Philopotamidae	*Chimarra*	2.8
Polycentropodidae	*Neureclipsis*	4.4
Psychomyiidae	*Lype*	-

Phylum, Order, Family	**Genus/Final ID**	**TV**
Coleoptera		
Dytiscidae	*Neoporus*	-
Elmidae	*Ancyronyx*	-
	Macronychus	-
	Optioservus	2.7
	Promoresia	-
	Stenelmis	5.4
Staphylinidae		-
Diptera		
Ceratopogonidae	*Forcipomyia*	6.8
Chironomidae	*Ablabesmyia*	-
	Brillia	5.2
	Cardiocladius	6.2
	Chironomus	9.8
	Conchapelopia	8.7
	Corynoneura	6.2
	Cricotopus	-
	Cricotopus/Orthocladius	-
	Cryptochironomus	-
	Demicryptochironomus	2.1
	Diamesa	7.7
	Dicrotendipes	7.9
	Endochironomus	-
	Eukiefferiella	-
	Glyptotendipes	8.5
	Limnophyes	-
	Micropsectra	1.4
	Microtendipes	6.2
	Nanocladius	7.2
	Nilotanypus	4
	Odontomesa	-
	Orthocladius	-
	Parakiefferiella	5.9
	Parametriocnemus	-
	Paratanytarsus	7.7
	Paratendipes	5.3
	Pentaneura	4.6
	Phaenopsectra	6.8
	Polypedilum	-
	Potthastia	-
	Prodiamesa	-
	Psectrocladius	3.8

Phylum, Order, Family	Genus/Final ID	TV
	Rheocricotopus	-
	Rheotanytarsus	6.4
	Smittia	-
	Stenochironomus	6.4
	Stictochironomus	6.7
	Synorthocladius	4.7
	Sublettea	-
	Tanytarsus	6.7
	Thienemanniella	6
	Thienemannimyia group	-
	Tribelos	6.6
	Tvetenia	-
	Xylotopus	-
Empididae	*Hemerodromia*	8.1
	Neoplasta	8.1
Muscidae	cf. *Limnophora*	7
Simuliidae	*Simulium*	4.4
Tipulidae	*Antocha*	4.6
	Erioptera	-
	Hexatoma	4.7
	Limnophila	-
	Limonia	10
	Ormosia	-
	Tipula	7.7