INVERTEBRATE COMMUNITIES ALONG A CONTINUUM OF FLOODPLAINS IN THE ALTAMAHA RIVER WATERSHED, GEORGIA

by

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(Under the Direction of Darold P. Batzer)

ABSTRACT

Recent studies have indicated the importance of river/floodplain interactions in enhancing biological productivity and maintaining diversity in both ecosystems. However, little work has focused on floodplain invertebrate assemblages. The objective of this study was to describe invertebrate assemblages in floodplain wetlands from the headwaters to the lower reaches of a southeastern U.S. watershed, not managed for flood control. We found that floodplain invertebrate communities changed predictably along a longitudinal gradient of river discharge, with headwater floodplains being dominated by terrestrial and rapidly-developing aquatic invertebrates, with the mid-reaches characterized by an influx of invertebrates from the river, and with the lower reaches being dominated by wetland taxa with desiccation resistant stages. This variability in community structure should be taken into account when flood regimes are prescribed in more regulated watersheds.

INDEX WORDS: Invertebrates, Floodplain, Altamaha, Gradient, Watershed, Community structure, Flow requirements, NMS, Cluster Analysis, Indicator Species Analysis, PC Ord

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B. S., Mary Washington College, 1994

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

MASTER OF SCIENCE

ATHENS, GEORGIA

2004

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August 2004

ACKNOWLEDGEMENTS

I am indebted to Darold Batzer and Wyatt Cross for their guidance and support on this thesis. In addition, I would like to sincerely thank the following people for their generous help in the field and in the lab: Erica Chiao, Roy Fenoff, Ginny Lipscomb, Monica Palta and Allison Roy. I am also grateful to my committee members, Rhett Jackson and Becky Sharitz, for their helpful comments on the proposal for this study and the final draft.

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INTRODUCTION

River floodplains are areas of high biological productivity and diversity, and are vital components of riverine ecosystems (Junk *et al.* 1989, Gladden and Smock 1990, Bayley 1995, Wissinger 1999, Benke 2001, Tockner and Stanford 2002). Historically, the inundation of floodplain wetlands has been viewed as negatively impacting flora and fauna and as a hazard to humans (Resh *et al.* 1988). In fact, massive engineering efforts have been undertaken to regulate floodplain inundation. However, recent studies have revealed that inundation is an essential interaction between the river and its floodplain that enhances biological productivity and maintains diversity (Junk *et al.* 1989, Ward *et al.* 1999, Bayley 1995, Sparks 1995, Tockner *et al.* 2000, Benke 2001).

The high productivity and biodiversity characteristic of riverine wetlands is due, in large part, to the many-fold increase in aquatic area that occurs upon inundation (Junk *et al.* 1989, Bayley 1995). The lateral "pulse" of flood water carries nutrient-rich subsidies between the river and its floodplain, and has been postulated to drive productivity of fish and invertebrates in the river channel (Junk *et al.* 1989, Bayley 1995, Benke 2001). The nature of pulses into floodplains will change depending on climate and the size and position of the river in the watershed (Tockner *et al.* 2000). In the low-gradient rivers of the southeastern U.S., the pattern of flooding and drying (i.e. the hydroperiod) changes character along a longitudinal gradient of river discharge throughout a watershed, with headwater-associated floodplains flooding less predictably and for shorter durations, and with floodplains in lower reaches flooding more predictably and for longer durations (Bedinger 1981, Benke 2001) (Fig. 1, Table 1).

Aquatic invertebrates in floodplain wetlands function as important intermediaries between basal resources and higher trophic levels, and are an essential food resource for birds, amphibians, fish and terrestrial insects (Ross and Baker 1983, Batzer and Wissinger 1996, Hering and Plachter 1997, O'Connell 2003). Several studies have shown that floodplain invertebrate production can be orders of magnitude higher than invertebrate production in the associated channel (Gladden and Smock 1990, Benke 2001), indicating the importance of floodplain invertebrates to overall ecosystem processes. One of the primary factors affecting invertebrates in floodplain wetlands is hydroperiod (Gladden and Smock 1990, Smock 1999, Whiles and Goldowitz 2001). In part, the pattern of flooding and drying in floodplains determines the life history and physical adaptations of invertebrates that can inhabit them (Gladden and Smock 1990, Huryn and Gibbs 1999, Smock 1999, Wissinger 1999). Therefore, it is likely that as the character of hydroperiod changes along the gradient of river discharge in a watershed, the invertebrate assemblages will also change.

Recently, attempts to assess the ecological importance of floodplain wetlands have revealed a lack of information on their basic ecology, and have prompted a call for empirical studies at the landscape level (Bayley 1995, Johnson and Richardson 1995, Ward and Tockner 2001, Tockner and Stanford 2002). The objective of this study was to describe invertebrate assemblages in floodplain wetlands of a southeastern U.S. watershed from the headwaters to the lower reaches. Results will help to generate a theoretical framework to explain how lateral flood pulses affect invertebrate communities along a longitudinal gradient. Furthermore, since the watershed used for this study was not managed for flood control and had natural flood pulses and intact floodplain complexes, the data gathered will be useful as reference data for assessing flood regimes in regulated rivers.

METHODS

Study Region

Study sites were located in streams and river floodplains of the Altamaha watershed of Georgia (Fig.1). The headwaters of the Altamaha River Basin are located in north-central Georgia, and the river's waters flow through the Piedmont physiographic province onto the Atlantic Coastal Plain of southeast Georgia. The major rivers in the upper watershed are the Oconee and Ocmulgee Rivers, which converge to form the Altamaha in the lower reaches. Two large dams do occur along the mainstem of the Oconee River. However, these dams are not managed for flood control, and downstream floods have not been affected by dams. Therefore, flood pulses are allowed to inundate downstream floodplain wetlands in a near-natural manner. The lower Ocmulgee and the entire Altamaha flow unimpounded for a distance of about 480 km.

Floodplains of the Altamaha River alone span an area greater than 150 km in length and range between 2 and 10 km in width (TNC and USEPA 2000). They contain some of Georgia's last remaining bottomland hardwood forests and cypress swamps. As is typical in southeastern riparian systems, the floodplains associated with this watershed are low-lying and flat (gradient of about 0.2 m km^{-1}) (Mitsch and Gosselink 2000, Smock 1999), and exhibit a strong seasonal hydrology. Although monthly variability in precipitation is small (ranging from 6 – 13 cm per month), low evapotranspiration rates in winter cause floodplains to become inundated, while higher evapotranspiration rates in the summer and spring usually limit inundation. In the context of this study we considered standing water on the floodplain to constitute inundation, even when the floodplain was not completely flooded.

Study Sites

We located nine sites in backwater swamps in the Altamaha watershed, beginning in the headwaters of the Oconee River near Athens, GA, and ending near the mouth of the Altamaha River just above the upper extent of tidal influence (Fig. 1). Sites were chosen along a gradient of river discharge (Table 1) and numbered consecutively, with Site 1 being associated with the lowest river discharge, and Site 9 with the greatest. All sites were located on protected natural areas (county, state or federal preserves, or wildlife management areas).

Rainfall in the central part of Georgia averages around 122 cm per year (NOAA 30 yr data set). Average river discharge typically ranges from 35 to 137 $m^3 s^{-1}$ in the Oconee (Sites 5 and 6) and 318 to 386 $m^3 s^{-1}$ in the Altamaha (Sites 7, 8 and 9) (Table 1). Year 1 of our study (2002) was near the end of a 4 year drought, and precipitation was lower than average at 117 cm. River discharge was correspondingly low – about 65 % below average in the Oconee and 68 % below average in the Altamaha (Table 1). The second study year (2003) was wetter, with a greater than average annual rainfall of 130 cm. River discharge was also greater – about 35 % above average in the Oconee and 42 % above average in the Altamaha (Table 1).

Sampling Methods

Invertebrate Sampling. We focused our sampling efforts on backswamp habitats (low lying areas behind the natural levee) because these were the only areas that reliably retained water between major flooding events. Once floodplains became inundated, sites were sampled every 4 – 6 weeks until they dried. Samples were collected only when there was standing water, and therefore no samples were taken when floodplains were dry. We sampled from January to May of 2002 (Year 1) and from November 2002 to July 2003 (Year 2).

A Hess sampler (860 cm^2, 500 µm mesh, Wildlife Supply Co., Buffalo, NY, U.S.A.) was used to quantitatively sample invertebrates in the benthos and water column. Water and sediments were swirled inside this large corer and forced through the attached collection net. Four sub-samples were collected randomly at each site on each sampling date, and combined into single composite samples. These were preserved in 95% ethanol, and returned to the lab where they were rinsed through standard sieves (1 mm and 0.3 mm) and divided into > 1 mm and < 1 mm aliquots. All samples were sub-sampled, and invertebrates were removed from the debris under a dissecting microscope. Invertebrates were counted, measured and identified to lowest possible taxon (order, family or genus), using keys in Pennak 1989, Peckarsky *et al.* 1990, Stehr 1991, Thorp and Covich 1991, Eppler 1996, and Merritt and Cummins 1996. We measured the lengths of all invertebrates, and used published length-mass regression models (Benke *et al.* 1999, Hodar 1996, Sabo *et al.* 2002) to estimate biomass. However, length-mass regression models were not available for several taxa, and in these cases we substituted a published regression for an invertebrate with a similar morphology.

Environmental Variables. Water quality measurements were collected during each invertebrate sampling visit. We used hand-held meters to measure temperature, pH, and conductivity, and HACH titration field kits (LaMotte multi-wavelength filter colorimeter, Chestertown, MD, U.S.A.) to determine nitrate and phosphate levels. River discharge for Sites 4 – 9 was obtained from United States Geological Survey water gauge records (www.water.usgs.gov), and Sites 1 - 3 were monitored using visual estimates by study personnel. In addition, floodplain inundation was recorded and converted to percent of sampling visits where inundation occurred per site per year. We visually determined whether overbank flooding had occurred by assessing water color - water entering floodplains from river channels during floods is colored by suspended clay (rust or chalk colored), while standing water from rainfall or groundwater lacks sediment staining and is either clear or darkly stained by humic compounds.

Statistical Analyses

Environmental variables were checked for normality using the Kolmogorov-Smirnov test and transformed where necessary. Patterns of environmental change across sites (1 – 9) were evaluated using a Spearman Ranks Correlation test. A Chi -square test was used to detect differences in hydroperiod among reaches, by assessing the percent of sampling visits with inundation and with overbank flooding.

Our main objective was to describe patterns of change in invertebrate assemblages along the upstream-downstream gradient. As such, we first partitioned the sites into groups based upon their similarity of invertebrate distributions, using a hierarchical, polythetic, agglomerative cluster analysis with a Sorenson (Bray-Curtis) distance measure and a flexible beta group linkage method (β = - 0.25) (McCune and Grace 2002). Both years of the study were treated separately in the cluster analyses, and sites were designated by their site number followed by a 1 or 2 to indicate study year (e.g. Site 8,2 designated floodplain Site 8 in Year 2). We then ran two-way ANOVAs to examine total abundance and biomass in each cluster, and used a pairwise multiple comparison procedure (Tukey Test) to evaluate significant results. To help assess why sites were separating into clusters, we used a non-metric multidimensional scaling (NMS) analysis that produced axis scores that were used in multiple forward regressions of invertebrate measures against environmental variables.

To characterize clusters, we first used indicator species analysis (Dufrene and Legendre 1997) to assess which taxa were useful in differentiating particular clusters. This analysis takes into account the frequency and relative abundance of each taxon in pre-defined groups (in this case our clusters) and produces indicator values for each taxon ranging from 0 (non-indicator) to 100 (perfect indicator). Indicator values were evaluated for statistical significance ($p \leq 0.05$) using a Monte Carlo permutation test with 1000 iterations, and only those taxa with significant indicator values were reported. Taxa were considered to differentiate clusters for which they had the highest indicator value (see McCune and Grace 2002 for detailed description of indicator species analysis). Next we identified taxa that occurred only in a single cluster (unique taxa), and finally, we determined which ten taxa had the greatest abundance and standing stock biomass in each cluster.

Cluster, NMS and indicator species analyses were completed using PC-ORD Version 4.1 (MJM Software Design, Glenden Beach, OR, U.S.A.). ANOVAs, Tukey Test, Spearman Rank Correlation and stepwise forward regressions were computed in SigmaStat Version 2.03 (SPSS, Inc.), and graphed in SigmaPlot 2000 Version 6.00 (SPSS, Inc.). Chi square analyses were computed using Microsoft Xcel. For parametric tests, both abundance and biomass data were $\log_{10}(x+1)$ transformed to approximate normal distribution. Rare species (those that occurred only once) were not used in analyses (final $n = 63$). All statistical analyses were considered significant at $p \leq 0.05$.

RESULTS

Hydrological and physico-chemical characterization of sites

The driest sites in the watershed were Sites 1 and 2 in the upper reaches (Table 2). Although we never detected significant inundation at Site 1, some sampling visits in the first year occurred immediately following major rain events, and we were able to collect samples in pools of standing rainwater. Return visits indicated that water persisted for only hours or days. In Year 2, visits to Site 1 did not coincide with rains and we never found standing water. In Year 1, Site 2 had significant standing water on the January sample date, but was dry thereafter, and in Year 2, this site was flooded in March but was dry by April. Neither Site 1 nor Site 2 was ever inundated by stream water flowing over the banks, and the limited flooding that occurred was from rainfall or groundwater.

Sites 3, 4 and 5 in the mid-reaches of the watershed became flooded in November of Year 1, and retained water until June. In Year 2, these sites first flooded in January and retained water until August. Site 3 received overbank flooding in the second year, but not the first, while Sites 4 and 5 received overbank flooding in both study years.

In the lower reaches, Sites 6 and 7 became inundated in January of Year 1, but Sites 8 and 9 did not flood until March. All 4 sites were dry by either May or June. In Year 2, Sites 7, 8 and 9 flooded in November, while Site 6 did not flood until January. All four sites dried by August. We did not detect overbank flow at Site 6 in either year, and rainfall on the floodplain was the only source of inundation. In Year 1, Sites 7, 8 and 9 were inundated only by rainfall and received no overbank flooding; however, in Year 2, all three of these sites were extensively flooded by river water.

Hydroperiod differences among reaches were significant in terms of both percent inundation ($\chi^2 = 21.7$, df = 4, $p < 0.001$) and overbank flooding ($\chi^2 = 7.03$, df = 2, $p < 0.05$), with Sites 1 and 2 being drier than expectation and Sites 3, 4 and 5 receiving more overbank flooding than expectation. Spearman Ranks Correlation analysis indicated that electrical conductivity (Yr 1: $r = 1.00$, $p < 0.01$; Yr 2: $r = 0.95$, $p < 0.01$), phosphate levels (Yr 1: $r = 0.65$, $p = 0.05$; Yr 2: $r = 0.67$, $p = 0.06$) and water temperature (Yr 1: $r = 0.84$, $p < 0.01$; Yr 2: $r = 0.70$, $p = 0.05$) all increased progressively from the upper to the lower reaches of the watershed (Table 2). Neither nitrate nor pH levels changed in a predictable fashion along the floodplain gradient, although nitrate levels were highly variable (Table 2). Though not significant, conductivity levels declined from Year 1 to Year 2, presumably as a result of dilution from increased rainfall.

Macroinvertebrate assemblages

We collected invertebrates from 90 taxonomic groups (Appendix). Overall density averaged 113,778 individuals m^{-2}, and standing stock biomass (dry mass, DM) averaged 6,188 mg DM m^{-2}. The most taxonomically diverse orders were Diptera (18 families and 18+ genera) and Coleoptera (15 families and 19+ genera). Cyclopoida, Chironomidae, Nematoda, and Acari were the most abundant taxa, contributing 9, 6, 6, and 5% of the total, respectively. Dytiscidae, Chironomidae, Oligochaeta, and Asellidae had the most standing stock biomass, contributing 7, 6, 5, and 5%, respectively.

Community analyses

Cluster analyses of both invertebrate abundance and standing stock biomass separated the 9 sites into 3 groups corresponding to their positions in the watershed (Figure 2). Sites 1 and 2 constituted an upper reach cluster, Sites 3, 4 and 5 constituted a mid-reach cluster, and Sites 7, 8 and 9 constituted a lower reach cluster. There were two anomalies in the groupings. In the abundance analysis, Site 8 in Year 2 clustered with the mid-reach sites; and in the biomass analysis, Site 6 in both years and Site 2 in Year 2 clustered together in their own grouping (Fig. 2). There was no significant difference in total abundance or biomass between clusters (Fig. 3).

NMS ordinations supported the results from the cluster analyses in terms of both abundance and standing stock biomass (Fig. 4). When sites were arranged in ordination space based on community similarity, the upper, mid- and lower reach clusters remained evident. For the ordination based on abundance, we chose two axes that accounted for 92% of variation among sites. The first axis explained 80% of the variation and had a significant correlation with degree of inundation (Table 3). This axis separated the drier, upper reach cluster from the wetter, mid- and lower reach clusters. The second axis, explaining 12% of variation, had a significant correlation with conductivity, and separated the lower reach cluster, with higher conductivity, from the upper and mid-reach clusters, which had lower conductivity.

In the ordination of invertebrate biomass, two axes explained 73% of variation among sites (Fig. 4). It should be noted that conductivity was correlated with both NMS Axes 1 and 2 (Table 3), suggesting that the conductivity gradient was moving from low in the bottom left corner of the ordination, to high in the upper right corner (Fig. 4). The first axis in the biomass ordination accounted for 18% of variation and was correlated to nitrate and conductivity (Table 3). This axis separated the upper and undefined clusters, which had lower conductivity and nitrate levels, from both the mid-reach cluster (with higher conductivity and higher nitrate levels) and the lower reach cluster (with higher conductivity and lower nitrate levels). The second axis explained 55% of variation and was correlated to conductivity and phosphate. It separated the upper reach cluster (with lower conductivity and phosphate levels) from the lower reach cluster (with higher conductivity and phosphate levels). The mid-reach and undefined clusters had intermediate conductivity and phosphate levels.

Characterization of invertebrate assemblages in clusters

Upper reach cluster (Sites 1 and 2). Mean invertebrate abundance in the upper reach cluster was 61,552 invertebrates m^{-2}, and average standing stock biomass was 1,682 mg DM m^{-2}. There were no taxa that were significant indicators of this cluster, nor were there taxa that were unique to this cluster. However, Lumbricidae, *Aedes*, Harpacticoida and terrestrial Empididae were numerically dominant only in the upper reach cluster (Fig. 5a). The rest of the abundant taxa were also common in the downstream clusters. Cantharidae, Bibionidae and Empididae comprised a major portion of the biomass in the upper reach cluster only, while the remaining taxa with high biomass also had biomass downstream (Fig. 5b). The anomalous biomass clustering of Site 2 in Year 2 with Site 6 in both years was most likely due to an unusually high biomass of Culicidae and Cambaridae occurring in both sites (Fig. 4b).

Mid-reach cluster (Sites 3, 4, and 5). The mid-reach cluster had a mean density of 176,633 invertebrates m^{-2} and a mean standing stock biomass of 4,785 mg DM/m^{-2}. Taxa that were indicators of this cluster in terms of abundance, included Chironomidae, Elateridae, Ceratopogonidae, Crangonyctidae, Leptophlebiidae and Sphaeriidae (Fig. 4, Table 4). Chironomidae and Elateridae were also indicators of this cluster in terms of biomass. Several flow-dependent families were unique to the mid-reach habitats, including 5 mayfly families, Ephemerellidae, Ephemeridae, Leptophlebiidae, Metretopodidae, and Siphlonuridae; 3 genera of elmid beetles; and an unknown Plecopteran (Appendix). Sphaeriidae were numerically dominant only in this cluster (Fig. 5c), and Leptophlebiidae, Ephemeridae, and Elateridae dominated standing stock biomass only in this cluster (Fig. 5d).

Lower reach clusters (Sites 6, 7, 8 and 9). Invertebrate density in the lower reach cluster averaged 73,393 invertebrates m^{-2} and average standing stock biomass was 8,544 mg DM m^{-2}. Indicators of this cluster were Dytiscidae and Asellidae (both abundance and biomass); Chirocephalidae, Cladocera, Cyclopoida and Ostracoda (abundance only); and Crangonyctidae (biomass only) (Table 4, Fig. 4). Taxa that were unique to this cluster included the terrestrial myriapods, Scolopendromorpha and Polydesmida; hydrophilid beetles and chirocephalid fairy shrimp (Appendix). Dytiscid beetles were dominant in terms of abundance and biomass only in this cluster (Fig. 5e,f), and Planorbidae was dominant in terms of biomass only in this cluster. As mentioned above, Site 6 clustered with Sites 7, 8 and 9 in terms of abundance, but clustered with Site 2 in Year 2 in terms of biomass, probably because of mosquitoes and crayfish. We are unsure why Site 8 in Year 2 did not cluster with the other lower reach sites in terms of abundance. However, the NMS analyses indicated that this site bordered the lower reach cluster in ordination space.

Annual variation

In general, collections from Years 1 and 2 from Sites 1 through 6 sub-clustered together, indicating that annual variation among those sites was less important than spatial variation (Fig. 2). However, for Sites 7, 8 and 9, collections from Years 1 and 2 did not form sub-clusters, indicating that temporal factors were more important there. In addition, two-way ANOVAs indicated a significant difference in biomass between Years 1 and 2 (Fig. 3, $p = 0.021$, $F = 1, 11$) which was primarily driven by higher biomass in the upper and lower clusters during Year 2.

DISCUSSION

Our hypothesis that floodplain invertebrate communities would change predictably along a longitudinal gradient of river discharge was supported by this study. We found that distinct invertebrate assemblages occurred in the upper, middle and lower reaches of the Altamaha watershed. However, we had further postulated that invertebrate communities would be primarily influenced by flood pulse characteristics which would increase in predictability and duration as they moved downstream. This study suggests that the true relationship between floodplain inundation, position in the watershed and invertebrates is more complex. We found that floodplains can become at least partially inundated even without overbank flow and that habitat flooded only by rainfall or groundwater supported vibrant invertebrate communities. Further, the predictability of overbank flow did not necessarily increase as pulses moved downstream. Nevertheless, the idea that the character of floodplain invertebrate communities varies greatly throughout watersheds has important implications to the ecology and management of floodplain habitats.

Upper reach floodplains

As expected, the floodplains associated with headwater streams were the driest. The two sites in the upper reach were dominated by terrestrial taxa, such as earthworms, orbatid mites, collembolans and assorted terrestrial fly larvae. These organisms were probably able to survive the very short periods of inundation by burrowing into the soil and remaining relatively inactive until the sites dried (Smock 1999). However, despite the very limited inundation in these floodplains, two aquatic taxa, *Aedes* mosquitoes and harpacticoid crustaceans, were abundant.

Aedes are characterized by rapid life cycles of about 10 days from egg to adult, which might enable them to complete development before drying of the floodplain occurs (Horsfall *et al.* 1975, Shaman *et al.* 2002). Harpacticoid copepods can also develop rapidly, and have also been found dominating the floodplain of a Virginia headwater stream that was inundated unpredictably during storm events (Gladden and Smock 1990). The presence of *Aedes* and harpacticoids is in concordance with Jenkins and Boulton's conclusion about dryland lakes in Australia, that weak connectivity during flooding will result in an aquatic fauna dominated by drought resistant organisms (Jenkins and Boulton 2003).

Mid-reach floodplains

Contrary to our original hypothesis, the mid-reaches, rather than the lower reaches, were the most predictably inundated. Sites 3, 4 and 5 were inundated on all sampling visits in both years, and overbank flooding occurred at Site 3 in the second year and Sites 4 and 5 in both years. There is some evidence from Pennsylvania (Cole and Brooks 2000) that groundwater dominated wetlands in floodplains flood very predictably. In our study, sites in the mid-reach were all relatively close to the toe-slope and may well have been influenced by groundwater. A combination of overbank flooding and groundwater discharge may explain the predictability and extent of inundation in the mid-reach floodplain compared with the lower reach habitats. The fauna of the middle reaches was dominated by longer-lived aquatic taxa (asellids, mayflies and aquatic oligochaetes), although some terrestrial organisms (elaterid beetles and mites) were still common. We found that families dependent on water flow, such as riffle beetles and some mayflies, were common only in these floodplains, which might suggest a strong connectivity to the river. Several mayfly families (Caenidae, Leptophlebiidae and Siphlonuridae) are known to migrate between lotic and lentic habitats (Gladden and Smock 1990, Smock 1994, Usseglio-Polatera and Tachet 1994, Huryn 2002). Mayfly occurrance has been also been linked to the predictability (Huryn 2002) and permanence (Lillie 2003) of floodplain inundation.

Lower reach floodplains

While flooded less predictably than the mid-reaches, floodplains of the lower reaches were characterized by more extensive and widespread overbank flooding, when flooding occurred. Surprisingly, even during the extensive overbank flooding of Year 2, there was little evidence of riverine invertebrates coming into the floodplains. Instead of being dominated by river-derived invertebrates as in the mid-reaches, the fauna in the lower reaches was dominated by lentic aquatic taxa (Dytiscidae, Asellidae, Crangonyctidae), most of which persist in wetlands after they dry.

A potentially important feature of the lower reach floodplains was the presence of large numbers of Dytiscidae. These predators comprised a large percentage of overall abundance in the lower reach, and dominated these habitats in terms of biomass. This was surprising because, in ponds and lakes, the presence of fish has been shown to preclude the presence of large-bodied, active invertebrate predators, such as dytiscids (Bennett and Streams 1986, Blois-Heulin *et al* 1990, Wellborn *et al.* 1996, Corti *et al.* 1997). During the extensive overbank flooding in the second year of the study, it is likely that fish were present in the floodplain at the same time we collected large numbers of dytiscid beetles. However, fish entering floodplains in the southeastern US are usually small (larval forms, diminutive taxa) (Ross and Baker 1983, O'Connell 2003), and may not consume the beetles (Corti *et al.* 1997). Alternatively, the increased turbidity during overbank flooding may protect beetles from predation. However, it seems likely that both fish and invertebrate predation are important ecological influences in the lower reach floodplains.

Environmental influence on invertebrate distribution

Based on multiple regressions between NMS axes and our environmental variables, higher conductivity seemed to be associated with higher invertebrate biomass and abundance in the lower reaches of the watershed. In rivers, this variable has been positively linked to increased urbanization (Ometo *et al.* 2000) and negatively linked to macroinvertebrate biotic integrity (Roy *et al.* 2003). However, a link between urbanization and invertebrates seems unlikely in floodplains of the Altamaha because land-use in the lower reaches tends towards lumber and agriculture, while urbanization is more common in the upper reaches. The progressive downstream increase in conductivity may simply reflect an overall increase in water-borne materials (organic and inorganic sediments, nutrients) and this change may affect invertebrates. This may partly explain the larger annual variation in invertebrate community structure in the lower reaches, since floodplains were inundated by rainwater in the first year, but by overbank flow in the second year.

Implications

The importance of floodplain habitats is now widely accepted. However, information is still lacking on their basic ecology. Although floodplain invertebrates are an important part of riverine ecosystems, very little is known about their community structure or their contribution to ecological processes. This study was among the first to describe a pattern of change in floodplain invertebrate communities at a watershed level. Our study indicates that the character of invertebrate community structure varies greatly among floodplains, with headwater floodplains being dominated by terrestrial and rapidly-developing aquatic invertebrates, with the mid-reaches characterized by an influx of invertebrates from the river, and with the lower reaches being dominated by wetland taxa with desiccation resistant stages. Water resource policy makers should take this variability into account when determining flood regimes in regulated rivers, and should prescribe flooding that mimics the natural character for a given watershed position.

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Figure 1. Study site locations in the Altamaha watershed, Georgia. USGS hydrographs show sample river discharge from gauges associated with the upper Oconee River (A) and Altamaha River (B), and indicate the changing character of the flood pulse throughout the watershed. (USGS data from 2002)

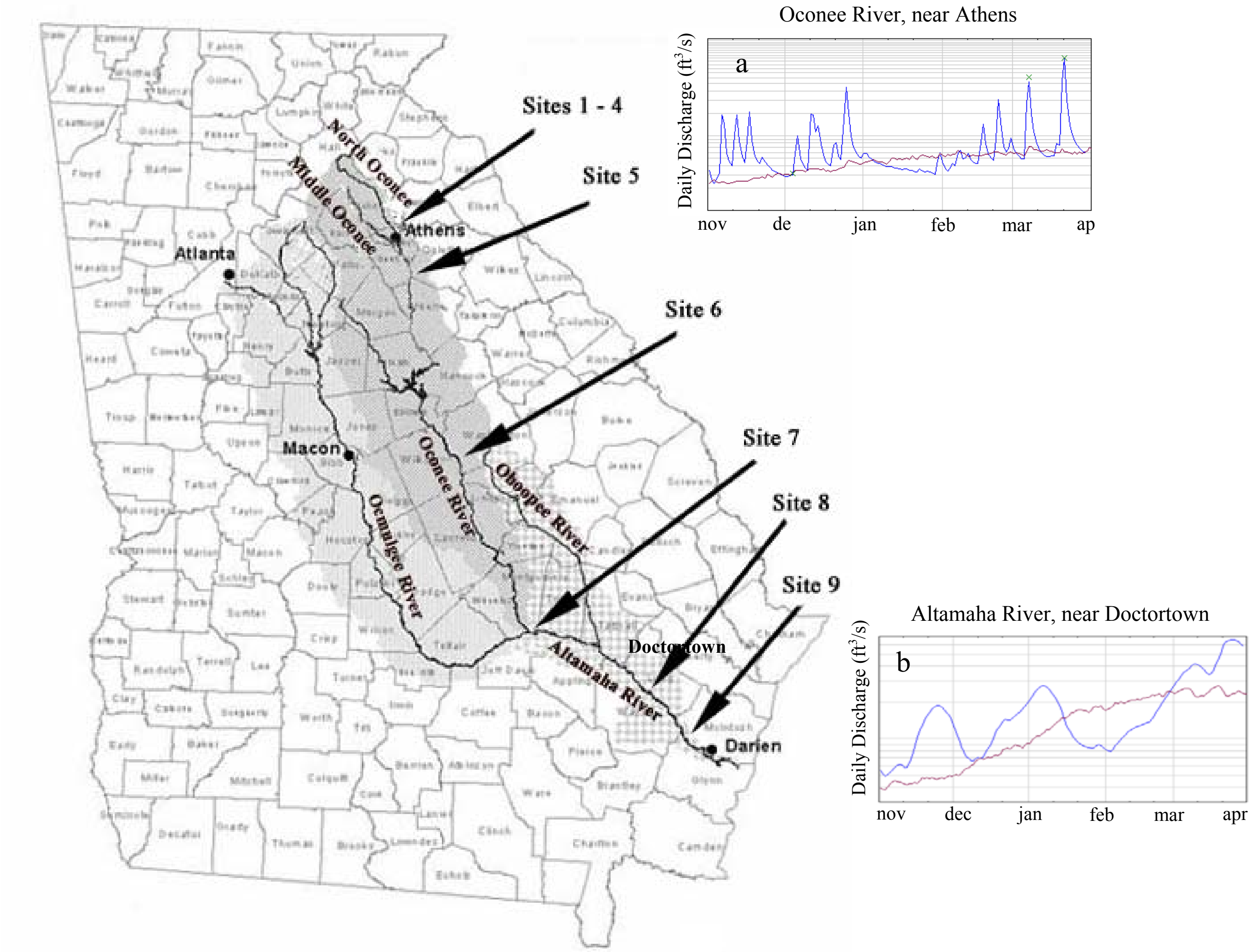
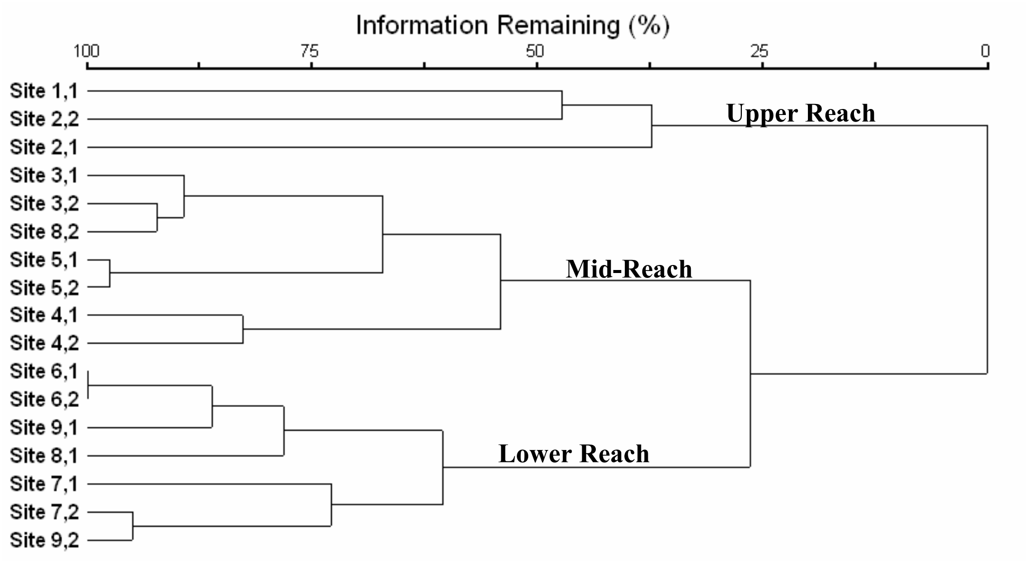

Sites 1 - 4
Site 5
Site 6
Site 7
Site 8
Site 9
Atlanta
Athens
Macon
Doctortown
Darien
North Oconee
Middle Oconee
Oconee River
Ocmulgee River
Ohoopee River
Altamaha River
Oconee River, near Athens
a
Daily Discharge (ft^3/s)
nov
de
jan
feb
mar
ap
Altamaha River, near Doctortown
b
Daily Discharge (ft^3/s)
nov
dec
jan
feb
mar
apr

Figure 2. Cluster analyses of invertebrate assemblages at 9 study sites, with each year treated separately. Dendrogram A is the result of the abundance analysis and dendrogram B is the result of the biomass analysis. Site numbers are followed by a 1 or 2, indicating study year 1 or 2.

A. Abundance



B. Biomass

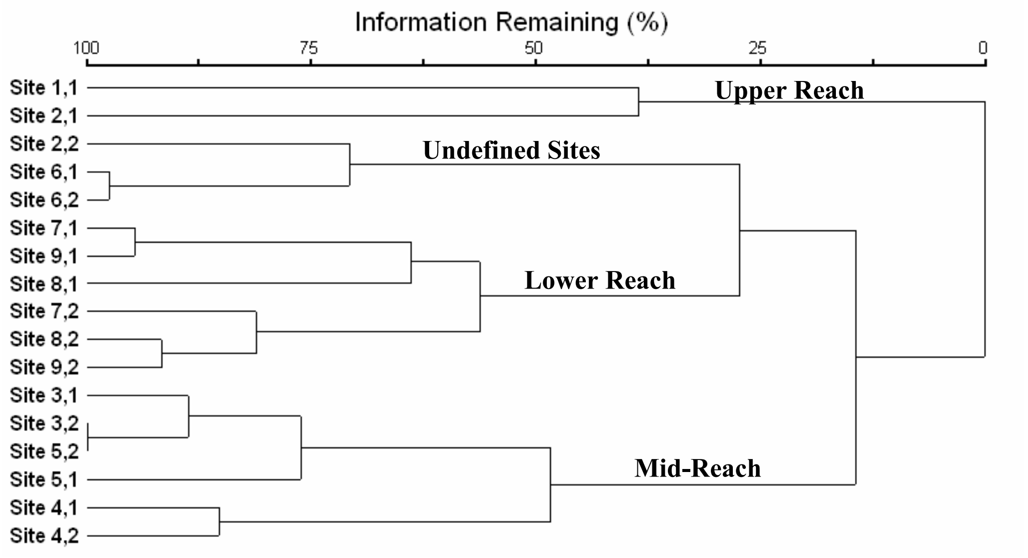


Figure 3. Total abundance (invertebrates m $^{-2}$) and biomass (mg DM m $^{-2}$) of invertebrates at 9 floodplain sites in the Altamaha watershed. Error bars indicate standard error.

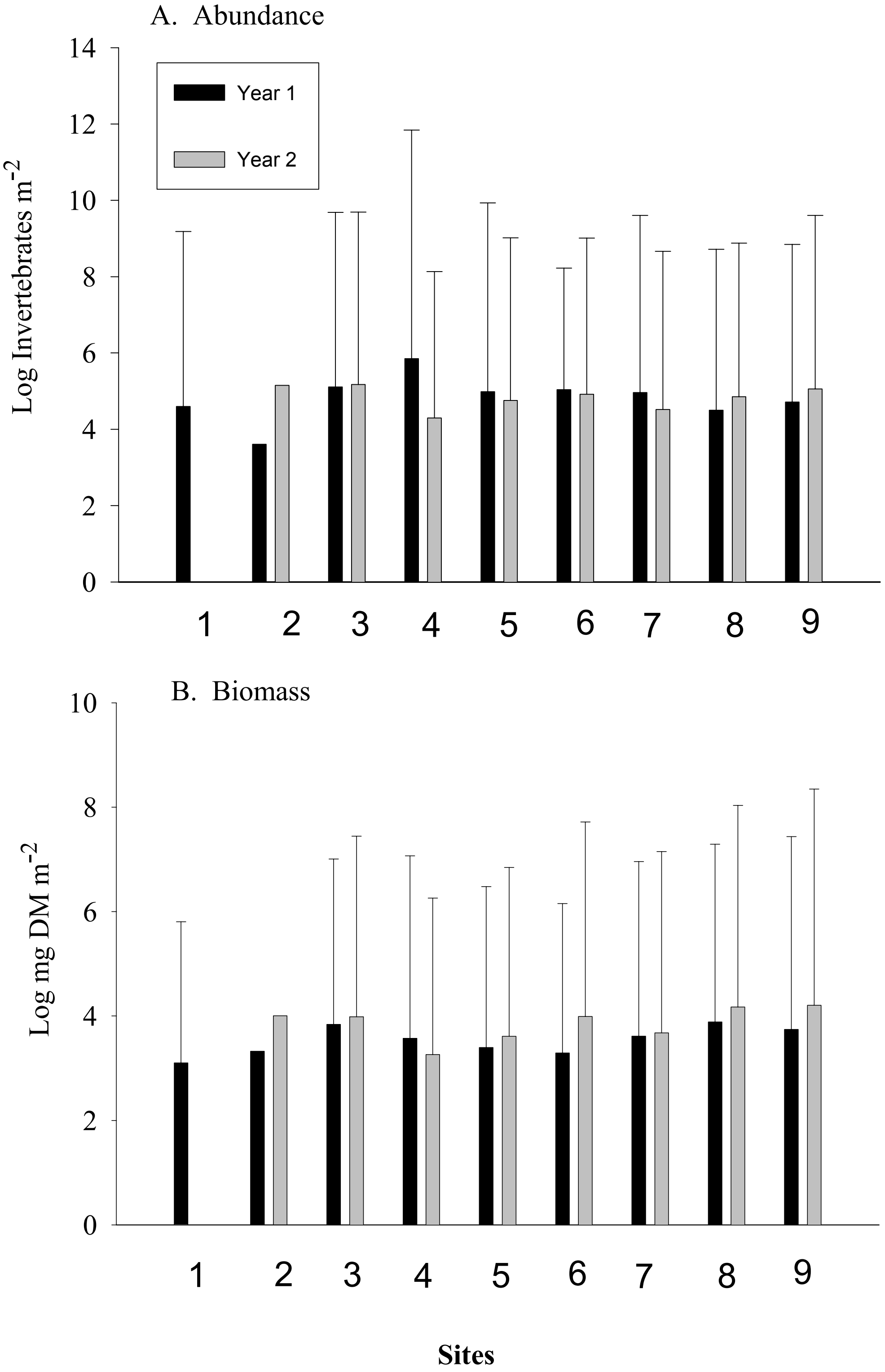
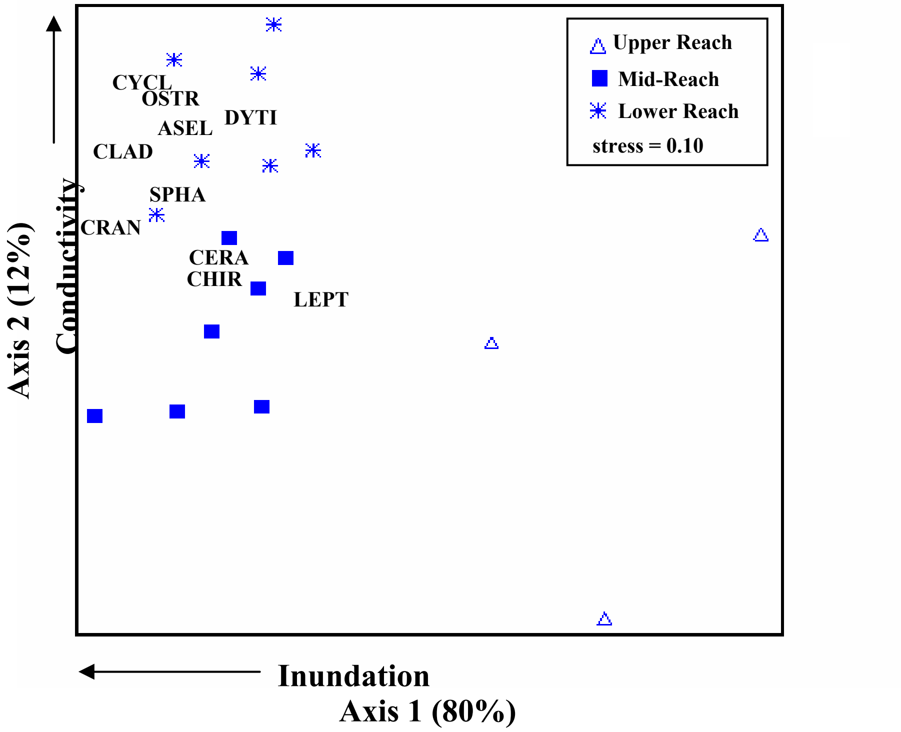

A. Abundance
Log Invertebrates m^{-2}
0
2
4
6
8
10
12
14
Year 1
Year 2
1
2
3
4
5
6
7
8
9
B. Biomass
Log mg DM m^{-2}
0
2
4
6
8
10
1
2
3
4
5
6
7
8
9
Sites

Figure 4. Non-metric multidimensional scaling ordination of sites in taxa space based on abundance (A) and biomass (B). The amount of variation explained by each axis is shown in parentheses. Physico-chemical variables are arranged along the axes to which they were significantly correlated, and correlation coefficients are listed in Table 3a. Arrows indicate direction of increasing duration (hydroperiod) or concentration (chemistry). Significant indicator taxa are plotted based on their scores for each axis. Full taxa names and indicator values are listed in Table 4.

A. Abundance



B. Biomass

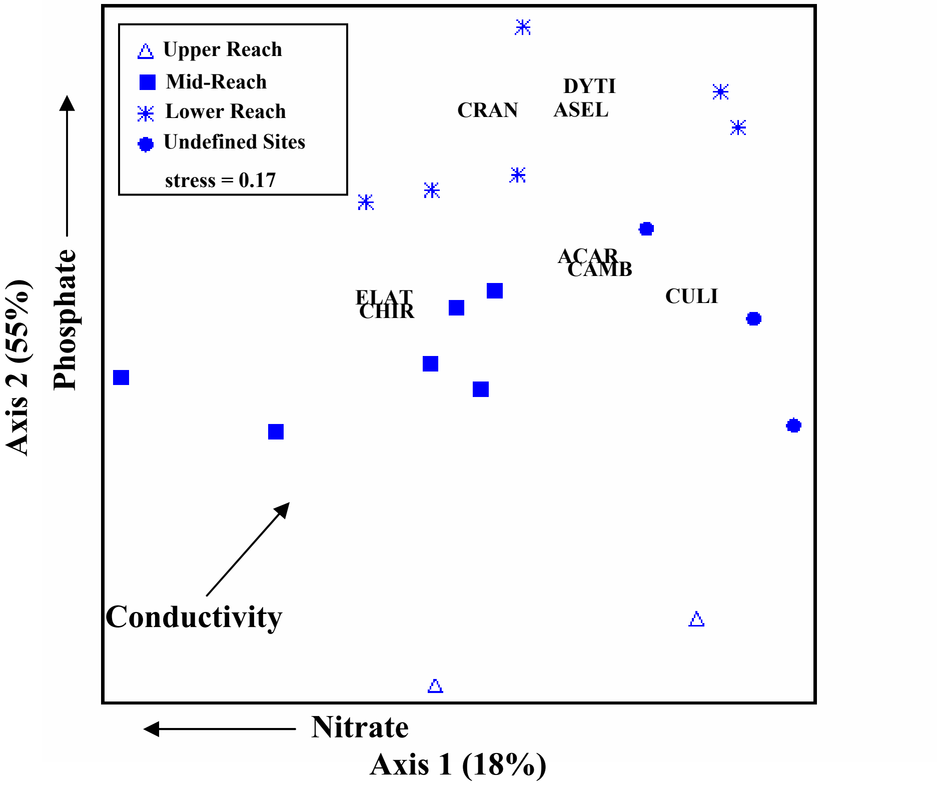


Figure 5. Ten most abundant taxa in sites clustered by abundance, and 10 taxa with greatest standing stock biomass in sites clustered by biomass. Percent dominance of each taxon is noted on column. *Indicates Lumbricidae (terrestrial earthworms).

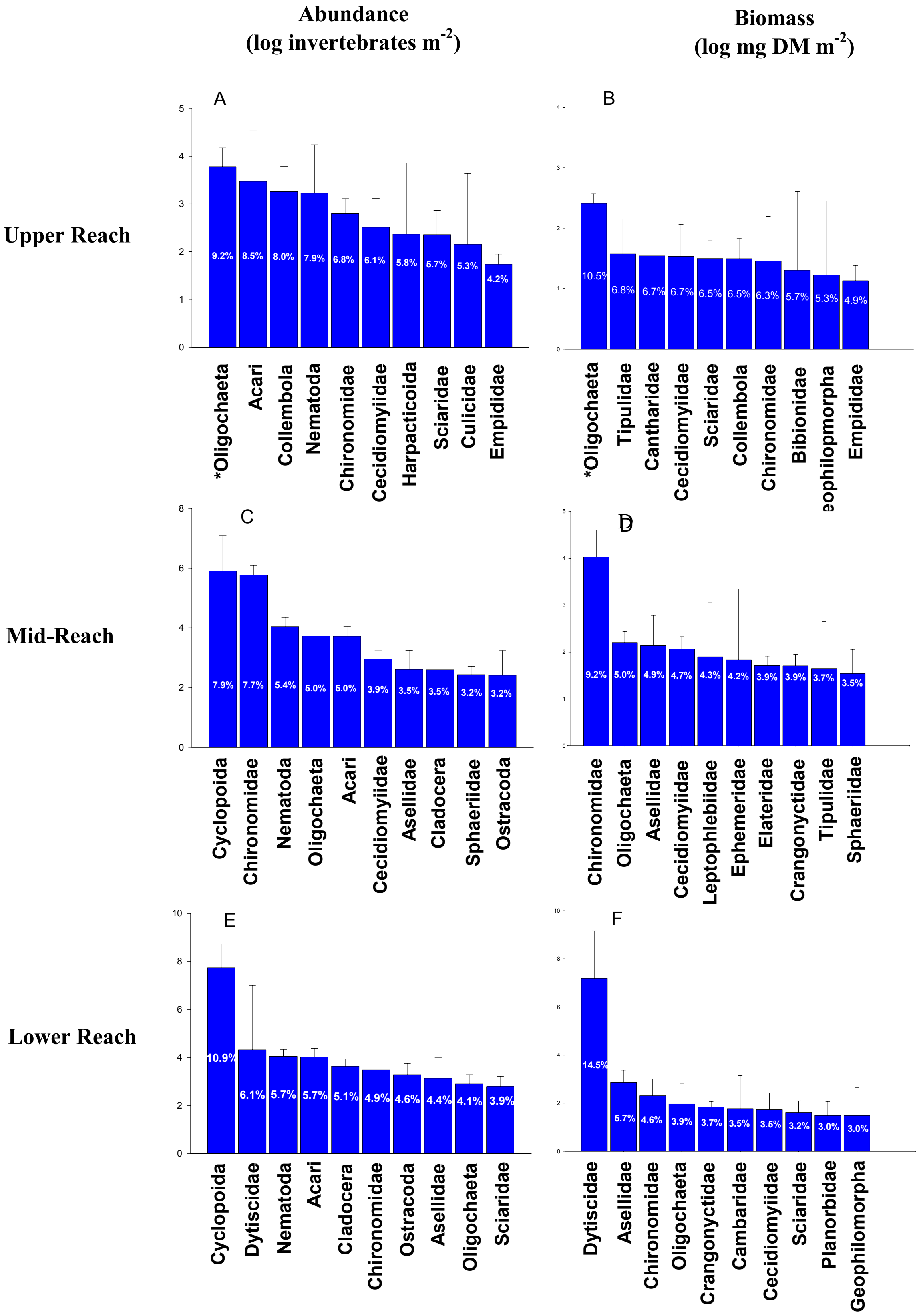

Abundance
(log invertebrates m-2)
Biomass
(log mg DM m-2)
Upper Reach
Mid-Reach
Lower Reach
A
0
1
2
3
4
5
9.2%
8.5%
8.0%
7.9%
6.8%
6.1%
5.8%
5.7%
5.3%
4.2%
*Oligochaeta
Acari
Collembola
Nematoda
Chironomidae
Cecidiomyiidae
Harpacticoida
Sciaridae
Culicidae
Empididae
B
0
1
2
3
4
10.5%
6.8%
6.7%
6.7%
6.5%
6.5%
6.3%
5.7%
5.3%
4.9%
*Oligochaeta
Tipulidae
Cantharidae
Cecidiomyiidae
Sciaridae
Collembola
Chironomidae
Bibionidae
eophilopmorpha
Empididae
C
0
2
4
6
8
7.9%
7.7%
5.4%
5.0%
5.0%
3.9%
3.5%
3.5%
3.2%
3.2%
Cyclopoida
Chironomidae
Nematoda
Oligochaeta
Acari
Cecidiomyiidae
Asellidae
Cladocera
Sphaeriidae
Ostracoda
D
0
1
2
3
4
5
9.2%
5.0%
4.9%
4.7%
4.3%
4.2%
3.9%
3.9%
3.7%
3.5%
Chironomidae
Oligochaeta
Asellidae
Cecidiomyiidae
Leptophlebiidae
Ephemeridae
Elateridae
Crangonyctidae
Tipulidae
Sphaeriidae
E
0
2
4
6
8
10
10.9%
6.1%
5.7%
5.7%
5.1%
4.9%
4.6%
4.4%
4.1%
3.9%
Cyclopoida
Dytiscidae
Nematoda
Acari
Cladocera
Chironomidae
Ostracoda
Asellidae
Oligochaeta
Sciaridae
F
0
2
4
6
8
10
14.5%
5.7%
4.6%
3.9%
3.7%
3.5%
3.5%
3.2%
3.0%
3.0%
Dytiscidae
Asellidae
Chironomidae
Oligochaeta
Crangonyctidae
Cambaridae
Cecidiomyiidae
Sciaridae
Planorbidae
Geophilomorpha

Table 1. Hydrological characterization of the Altamaha watershed based on United States Geological Survey (USGS) river gauges associated with study sites.

Study Site	**Associated USGS Gauge Location**	**Contributing Drainage Area (km^2)**	**Annual Discharge (m^3/s)**		
			Average	**2002**	**2003**
4	North Oconee River, at Athens	683	no data*	no data*	14
5	Oconee River near Penfield	2,435	35	16	54
6	Oconee River near Dublin	11,396	137	44	178
7, 8	Altamaha River near Baxley	30,044	318	107	452
8, 9	Altamaha River near Doctortown	35,224	384	117	542

*North Oconee River gauge established in 2003.

Table 2. Mean annual values (± SE) for environmental data at 9 floodplain sites, with each sampling year treated separately. (Number following site number indicates study year 1 or 2)

	Inundation (% of visits*)	**Overbank flooding**	**Conductivity (µS/cm)**	**pH**	**NO3 (ppm)**	**PO4 (ppm)**	**Temp (°C)**
Site 1,1	0	No	25 ± 5.0	6.4 ± 0.05	0.00 ± 0.00	0.16 ± 0.04	10.0 ± 1.0
Site 1,2	0	No					
Site 2,1	25	No	30	5.3	0.00	0.05	14.0
Site 2,2	20	No	20	6.6	0.00	0.10	
Site 3,1	100	No	33 ± 6.8	6.6 ± 0.33	0.12 ± 0.17	0.32 ± 0.08	15.3 ± 3.0
Site 3,2	100	Yes	30 ± 5.0	6.9 ± 0.09	0.61 ± 0.43	0.39 ± 0.33	12.0 ± 4.0
Site 4,1	100	Yes	40 ± 5.8	6.9 ± 0.24	1.20 ± 1.65	0.16 ± 0.15	14.5 ± 2.7
Site 4,2	100	Yes	34 ± 3.9	7.2 ± 0.17	1.01 ± 0.86	0.20 ± 0.06	15.0 ± 4.0
Site 5,1	100	Yes	63 ± 12.1	6.9 ± 0.17	0.70 ± 1.00	0.27 ± 0.22	17.1 ± 3.9
Site 5,2	100	Yes	44 ± 8.1	6.9 ± 0.11	0.48 ± 0.60	0.26 ± 0.07	16.5 ± 1.5
Site 6,1	50	No	70 ± 10.0	6.5 ± 0.75	0.00 ± 0.00	0.37 ± 0.03	14.5 ± 0.5
Site 6,2	80	No	35 ± 5.0	6.7 ± 0.35	0.16 ± 0.10	0.83 ± 0.52	12.5 ± 6.5
Site 7,1	100	No	83 ± 27.3	6.1 ± 0.37	0.02 ± 0.03	0.28 ± 0.06	18.5 ± 3.4
Site 7,2	100	Yes	50 ± 11.2	6.8 ± 0.22	0.47 ± 0.45	0.34 ± 0.18	14.3 ± 3.6
Site 8,1	50	No	85 ± 25.0	6.1 ± 0.75	1.67 ± 1.67	0.37 ± 0.13	16.5 ± 1.5
Site 8,2	100	Yes	45 ± 7.1	7.1 ± 0.16	1.03 ± 0.75	0.55 ± 0.22	19.0 ± 5.0
Site 9,1	75	No	123 ± 17.8	6.2 ± 0.55	0.29 ± 0.36	0.31 ± 0.24	18.8 ± 4.1
Site 9,2	100	Yes	63 ± 19.9	6.9 ± 0.25	3.08 ± 3.82	0.49 ± 0.22	19.0 ± 5.0

*Sampling occurred 4 times from January 2002 to June 2002, and 5 times from November 2002 to June 2003.

Table 3(a). Significant multiple linear regression models using stepwise regression for the NMS ordination axes (n = 6 environmental variables, forward selection, $p \leq 0.05$).

	Adjusted R^2	**Partial R^2**	**P**	**Independent variables**
Abundance				
NMS Axis 1	0.669	0.669	<0.001	inundation
NMS Axis 2	0.437	0.437	0.004	conductivity
Biomass				
NMS Axis 1	0.544	0.373	0.002	nitrate
		0.171	0.038	conductivity
NMS Axis 2	0.683	0.443	0.002	conductivity
		0.240	0.006	phosphate

Table 4. Significant indicator taxa ($p \leq 0.05$, Monte Carlo test, 1000 randomizations) and their indicator values (% of perfect indication) in bold, for sites clustered by abundance and biomass. Code names refer to NMS ordination (Fig.3).

		Abundance Clusters			**Biomass Clusters**			
Taxon	**Code Name**	**Upper Reach**	**Mid-Reach**	**Lower Reach**	**Upper Reach**	**Mid-Reach**	**Lower Reach**	**Undefined Sites**
Acari	ACAR	---	---	---	12	22	26	**40**
Asellidae	ASEL	11	38	**45**	4	30	**40**	22
Cambaridae	CAMB	---	---	---	0	10	15	**51**
Ceratopogonidae	CERA	0	**70**	13	---	---	---	---
Chirocephalidae	CHCE	0	0	**57**	---	---	---	---
Chironomidae	CHIR	23	**48**	29	14	**39**	23	24
Cladocera	CLAD	0	36	**58**	---	---	---	---
Crangonyctidae	CRAN	0	**55**	45	0	40	**43**	11
Culicidae	CULI	---	---	---	8	3	5	**64**
Cyclopoida	CYCL	2	40	**53**	---	---	---	---
Dytiscidae	DYTI	0	7	**72**	0	1	**86**	3
Elateridae	ELAT	0	**74**	11	0	**57**	10	9
Leptophlebiidae	LEPT	0	**57**	0	---	---	---	---
Ostracoda	OSTR	0	36	**58**	---	---	---	---
Sphaeriidae	SPHA	0	**55**	39	---	---	---	---

Appendix. Taxa list with mean abundance (invertebrates m^{-2}) and biomass (mg DM m^{-2}) for all taxa collected from 9 floodplain sites. Means are the average of two years, therefore standard error is not indicated. Rare taxa (occurring in a single sample) are indicated by an asterix (*), and were not included in statistical analyses. Sites 6-9 are continued on p. 40.

	Sites									
	1		**2**		**3**		**4**		**5**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
NON-ARTHROPODS										
Nematoda	13920	20.94	4626	6.88	29324	47.88	3102	4.65	13423	17.61
Oligochaeta	4962	177.49	12798	1465.57	3949	62.56	3995	300.00	31220	219.94
Bivalvia										
Corbiculidae*										
Sphaeriidae	---	---	12	4.20	1498	182.14	290	3.88	791	48.98
Musculium										
Gastropoda										
Planorbidae	---	---	36	86.77	334	45.86	59	4.68	545	137.14
Unknowns	96	3.18	---	---	2	41.74	70	2.30	1	0.01
ARTHROPODS										
Crustacea										
Branchiopoda										
Chirocephalidae	---	---	---	---	---	---	---	---	---	---
Eubranchipus										
Cladocera	---	---	---	---	998	2.33	1008	2.40	1651	3.85
Ostracoda	---	---	---	---	2201	2.99	311	0.45	845	1.15
Branchiura										
Argulidae*										
Argulus										
Copepoda										
Calanoida	---	---	---	---	96	0.10	444	0.44	1940	2.25
Cyclopoida	---	---	768	0.77	15525	15.52	343931	343.93	8234	10.16
Harpacticoida	11040	11.04	576	0.58	12826	12.83	91	0.09	173	0.17

	Sites									
	1		**2**		**3**		**4**		**5**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Malacostraca										
Isopoda										
Asellidae	---	---	84	51.16	700	579.95	63	13.40	4195	748.84
Caecidotea										
Lirceus										
Amphipoda										
Crangonyctidae	---	---	---	---	666	68.87	50	25.03	248	101.96
Crangonyx										
Gammaridae*										
Gammarus										
Hyallelidae	---	---	---	---	---	---	2	0.77	1	0.04
Hyallela										
Unknowns	---	---	---	---	77	0.96	---	---	---	---
Decapoda										
Cambaridae	---	---	12	633.75	---	---	4	293.25	5	303.06
Palaemonidae*										
Palaemonetes										
Arachnida										
Acari	4752	12.64	38292	101.86	18238	48.51	2158	5.74	3294	8.76
Pseudoscorpiones*										
Myriopoda										
Chilopoda										
Geophilomorpha	36	281.50	---	---	8	21.25	2	161.16	3	28.10
Scolopendromorpha*										
Diplopoda										
Polydesmida	---	---	---	---	---	---	---	---	---	---

	Sites									
	1		**2**		**3**		**4**		**5**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Hexapoda										
Collembola	1728	66.27	5352	180.12	272	4.86	383	7.72	165	4.78
Ephemeroptera										
Caenidae*										
Caenis										
Ephemerellidae	---	---	---	---	---	---	270	38.17	2	0.86
Eurylophella										
Serratella										
Ephemeridae	---	---	---	---	---	---	7	17.00	---	---
Ephemera										
Hexagenia										
Leptophlebiidae	---	---	---	---	---	---	112	72.87	111	342.55
Leptophlebia										
Paraleptophlebia										
Metretopodidae	---	---	---	---	---	---	74	408.99	---	---
Siphloplecton										
Siphlonuridae	---	---	---	---	---	---	15	25.65	2	1.32
Siphlonurus										
Odonata										
Aeshnidae	---	---	---	---	---	---	---	---	3	28.44
Aeshna										
Coenagrionidae	---	---	---	---	---	---	6	0.13	---	---
Enallagma										
Ischnura										
Gomphidae*										
Plecoptera										
Nemouridae*										
Ostrocerca										
Unknowns	---	---	---	---	3	0.27	13	0.15	---	---

	Sites									
	1		2		3		4		5	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Hemiptera										
Corixidae	---	---	---	---	28	29.61	44	1.70	---	---
Hesperocorixa										
Trichocorixa										
Gerridae	---	---	---	---	3	5.98	2	2.48	---	---
Rheumatobates										
Notonectidae	---	---	---	---	3	0.27	---	---	---	---
Notonecta										
Megaloptera										
Corydalidae*										
Nigronia										
Sialidae*										
Sialis										
Trichoptera										
Hydropsychidae*										
Cheumatopsyche										
Limnephilidae	---	---	---	---	---	---	5	12.30	---	---
Hesperophylax										
Ironoquia										
Unknowns	---	---	---	---	---	---	3	0.73	---	---
Lepidoptera	---	---	12	4.24	3	0.08	7	1.56	5	2.15
Coleoptera										
Cantharidae	---	---	60	602.19	---	---	5	23.08	---	---
Curculionidae	---	---	---	---	3	0.02	3	1.11	---	---

	Sites									
	1		2		3		4		5	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Dytiscidae	---	---	---	---	3	27.07	11	0.02	---	---
Acilius										
Agabetes										
Coptotomus										
Desmopachria										
Hydrovatus										
Hygrotus										
Rhantus										
Thermonectus										
Tropisternus										
Elateridae	---	---	---	---	43	87.65	15	31.37	16	52.97
Areopidius										
Conoderus										
Dalopius										
Melanotus										
Elmidae	---	---	---	---	---	---	45	30.08	27	11.06
Dubiraphia										
Macronychus										
Stenelmis										
Gyrinidae	---	---	---	---	---	---	1	0.33	---	---
Dineutus										
Haliplidae*										
Peltodytes										
Hydrophilidae	---	---	---	---	---	---	---	---	---	---
Hydrochara										
Lampyridae	18	23.78	---	---	2	26.97	---	---	6	56.78
Phalacridae*										

	Sites									
	1		2		3		4		5	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Phengodidae*										
Ptilodactylidae	---	---	---	---	---	---	27	39.88	---	---
Staphylinidae	12	0.85	---	---	---	---	348	57.88	---	---
Scarabaeidae	---	---	---	---	---	---	---	---	---	---
Unknowns	---	---	26	57.67	2	9.25	4	6.46	5	14.85
Diptera										
Asilidae*										
Bibionidae	180	403.77	---	---	---	---	10	2.42	---	---
Cecidiomyiidae	564	114.24	843	247.59	1934	281.08	290	61.39	888	112.03
Ceratopogonidae	---	---	---	---	130	1.14	398	4.65	6	0.12
Chaoboridae	---	---	---	---	7	22.41	---	---	31	49.96
Chaoborus										
Chironomidae	192	4.16	1134	148.98	50639	6539.09	8521	588.55	9119	854.96
Non-Tanypodinae										
Tanypodinae										
Culicidae	192	21.45	7596	2348.07	154	4.18	5	0.54	2	0.16
Dolichopodidae	---	---	---	---	12	4.73	---	---	2	0.25
Raphium										
Empididae	66	6.55	72	16.74	---	---	39	4.14	13	5.67
Hemerodromia										
Ephydridae	42	18.79	---	---	---	---	---	---	3	0.14
Phoridae*										
Psychodidae	---	---	---	---	6	3.12	---	---	---	---
Pericoma										
Sciaridae	1326	60.66	114	8.67	388	19.36	60	4.36	98	5.16
Stratiomyidae	96	0.49	---	---	---	---	2	2.89	---	---
Nemotelus										
Syrphidae	---	---	12	0.51	---	---	3	12.45	---	---

	Sites									
	1		**2**		**3**		**4**		**5**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Tabanidae	---	---	12	17.81	---	---	3	0.94	4	1.90
Chrysops										
Haematopota										
Tabanus										
Tipulidae	30	35.24	6	4.46	12	15.77	44	52.07	13	17.82
Helius										
Hexatoma										
Limnophila										
Limonia										
Molophilus										
Paradelphomyia										
Rhabdomastix										
Tipula										
Unknowns	---	---	210	18.33	79	3.59	194	20.07	3	2.34

	Site							
	6		**7**		**8**		**9**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
NON-ARTHROPODS								
Nematoda	18348	27.38	6110	5.43	11328	18.75	28852	57.94
Oligochaeta	2718	114.09	1345	299.66	13434	4048.83	479	17.01
Bivalvia								
Corbiculidae*								
Sphaeridae	1068	64.07	223	4.80	2148	128.94	294	10.31
Musculium								
Gastropoda								
Planorbidae	1350	47.48	311	56.69	351	128.61	29	13.20
Unknowns	6	189.06	79	10.35	21	34.24	26	75.40
ARTHROPODS								
Crustacea								
Branchiopoda								
Chirocephalidae	546	2391.20	10	63.36	6	26.48	---	---
Eubranchipus								
Cladocera	8502	23.27	7512	17.52	726	1.69	4434	10.93
Ostracoda	3558	4.84	14095	19.17	294	0.40	1280	1.74
Copepoda								
Argulidae*								
Argulus								
Calanoida	1824	1.82	1382	1.38	---	---	1435	1.44
Cyclopoida	21420	21.42	20026	20.03	8016	8.02	15117	15.18
Harpacticoida	---	---	---	---	---	---	---	---

	Site							
	6		7		8		9	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Malacostraca								
Amphipoda								
Crangonyctidae	24	12.46	136	166.54	302	44.49	172	62.00
Crangonyx								
Gammaridae*								
Gammarus								
Hyallelidae	9	2.46	2	0.28	---	---	---	---
Hyallela								
Unknowns	---	---	---	---	96	9.70	---	---
Decapoda								
Cambaridae	21	1168.69	12	698.97	---	---	35	6007.21
Palaemonidae*								
Palaemonetes								
Isopoda								
Asellidae	204	201.74	2097	777.97	1732	642.99	1289	396.19
Caecidotea								
Lirceus								
Arachnida								
Acari	30396	80.85	5241	13.94	8330	22.16	19978	53.14
Pseudoscorpiones*								
Myriopoda								
Chilopoda								
Geophilomorpha	---	---	19	442.09	14	1003.16	12	240.98
Scolopendromorpha*								
Diplopoda								
Polydesmida	---	---	158	0.57	1	0.57	463	2.02

	Site							
	6		7		8		9	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Hexapoda								
Collembola	294	5.31	276	5.89	1776	86.66	2998	54.42
Ephemeroptera								
Caenidae*								
Caenis								
Ephemerellidae	---	---	---	---	---	---	---	---
Eurylophella								
Seratella								
Ephemeridae	---	---	---	---	---	---	---	---
Ephemera								
Hexagenia								
Leptophlebiidae	---	---	---	---	---	---	---	---
Leptophlebia								
Paraleptophlebia								
Metretopodidae	---	---	---	---	---	---	---	---
Siphloplectron								
Siphlonuridae	---	---	---	---	---	---	---	---
Siphlonuris								
Odonata								
Aeschnidae	---	---	---	---	6	191.07	---	---
Aeschna								
Coenagrionidae	---	---	7	39.51	---	---	---	---
Enallagma								
Ischnura								
Gomphidae*								
Plecoptera								
Nemouridae*								
Ostrocerca								
Unknowns	---	---	---	---	---	---	---	---

	Site							
	6		**7**		**8**		**9**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Hemiptera								
Corixidae	---	---	15	17.41	15	1.87	2	0.68
Hesperocorixa								
Trichocorixa								
Gerridae	---	---	---	---	---	---	2	1.12
Rheumatobates								
Notonectidae	3	0.49	7	20.74	---	---	16	19.54
Notonecta								
Megaloptera								
Corydalidae*								
Nigronia								
Sialidae*								
Sialis								
Trichoptera								
Hydropsychidae*								
Cheumatopsyche								
Limnephilidae	---	---	3	4.54	---	---	---	---
Hesperophylax								
Ironoquia								
Unknowns	---	---	---	---	6	25.84	---	---
Lepidoptera	---	---	5	6.42	24	42.95	7	4.56
Coleoptera								
Cantharidae	---	---	5	15.38	---	---	---	---
Curculionidae	---	---	---	---	3	0.48	5	0.50

	Site							
	6		**7**		**8**		**9**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Dytiscidae	3	162.27	572	1201.94	297	2324.07	146	681.86
Acilius								
Agabetes								
Coptotomus								
Desmopachria								
Hygrotus								
Hydrovatus								
Rhantus								
Thermonectus								
Tropisternus								
Elateridae	18	2.91	---	---	9	42.58	5	48.42
Areopidius								
Conoderus								
Dalopius								
Melanotus								
Elmidae	---	---	---	---	---	---	---	---
Dubiraphia								
Macronychus								
Stenelmis								
Gyrinidae	---	---	9	33.81	---	---	2	41.76
Dineutus								
Haliplidae*								
Peltodytes								
Hydrophilidae	---	---	---	---	6	882.10	2	0.11
Hydrochara								
Lampyridae	---	---	---	---	---	---	---	---
Phalacridae*								
Phengodidae*								

	Site							
	6		7		8		9	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Ptilodactylidae	---	---	---	---	---	---	34	26.32
Staphylinidae	---	---	---	---	5	4.88	36	17.54
Scarabaeidae	---	---	---	---	2	404.73	2	9.25
Unknowns	---	---	4	0.87	3	7.44	7	67.11
Diptera								
Asilidae*								
Bibionidae	---	---	---	---	233	298.54	355	842.49
Cecidiomyiidae	941	230.78	391	49.26	1662	438.70	740	109.69
Ceratopogonidae	192	0.26			141	7.65	52	1.17
Chaoboridae	336	490.11	109	153.86	---	---	---	---
Chaoborus								
Chironomidae	3672	481.96	1203	92.73	1223	114.26	1675	199.17
Non-Tanypodinae								
Tanypodinae								
Culicidae	408	117.43	---	---	---	---	193	196.19
Dolichopodidae	---	---	---	---	57	22.58	---	---
Raphium								
Empididae	9	2.55	11	1.87	3	0.49	125	38.45
Hemerodromia								
Ephydridae	---	---	2	0.06	---	---	---	---
Phoridae*								
Psychodidae	---	---	3	2.07	---	---	---	---
Pericoma								
Sciaridae	720	18.68	608	27.43	162	21.38	2555	130.71
Stratiomyidae	---	---	---	---	---	---	---	---
Nemotelus								
Syrphidae	---	---	---	---	---	---	---	---

	Site							
	6		**7**		**8**		**9**	
	Abun	Mass	Abun	Mass	Abun	Mass	Abun	Mass
Tabanidae	---	---	10	10.64	15	6.06	2	0.66
Chrysops								
Haematopota								
Tabanus								
Tipulidae	---	---	16	128.73	---	---	34	72.60
Helius								
Hexatoma								
Limnophila								
Limonia								
Molophilus								
Paradelphomyia								
Rhabdomastix								
Tipula								
Unknowns	---	---	13	11.63	48	7.82	150	43.28