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Inferring Food Web Structure to Identify Seasonal and Longitudinal Patterns in Ogeechee River Invertebrate Communities

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INFERRING FOOD WEB STRUCTURE TO IDENTIFY SEASONAL AND LONGITUDINAL PATTERNS IN OGEECHEE RIVER INVERTEBRATE COMMUNITIES

by

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ABSTRACT

Understanding how the structure and function of aquatic communities vary across space and time is essential for proper management of freshwater ecosystems. Current management relies on rapid biomonitoring using metrics of community structure, but metrics that incorporate ecosystem processes and functions are only just beginning to see use in assessment and management. Food webs inferred from known species interactions have been proposed as a method of incorporating function into bioassessment without expending extra effort or sacrificing the cost-effectiveness of current monitoring schemes. To apply food webs in biomonitoring, it is first necessary to understand how communities and food webs vary across temporal and longitudinal gradients so that changes can be interpreted correctly. I conducted a study to establish such a baseline for the Ogeechee River, a large coastal plain blackwater river in the southeastern United States. Samples of invertebrate assemblages were taken quarterly for three years from 6 sites along the main course of the Ogeechee River. I then investigated the spatial and seasonal structure of communities and food webs. Food webs were inferred using a database of invertebrate diets compiled from the literature. Communities varied across sites and seasons, with lower diversity and more lentic and estuarine taxa at downstream sites, and lower diversity during the flood pulse in the winter and spring due to high numbers of certain dominant taxa. Food web structure changed little over time and space, with some diversity dependent increases in links, linkage density and connectance at upstream sites, and some diversity independent decreases in prey to predator ratios during the winter. Results suggest that community structure was both more informative and reliable than food web structure for detecting changes in river communities. Better documentation of species interactions in the literature could improve

inferred food webs so that they could work as a supplemental tool for interpreting the results of biomonitoring and for making management decisions.

INDEX WORDS: Large river ecosystems, Macroinvertebrates, Food webs, Biomonitoring, Freshwater communities, Seasonal patterns.

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DEDICATION

This page is dedicated to my parents Barry and Isabelle and my sisters Joanne and Margot for all the support they gave me during my graduate studies. Without that support I would never have been able to pursue ecology as a career.

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CHAPTER 1

INTRODUCTION

Large rivers are ecologically, economically and recreationally important landscape features, providing habitat and connectivity to a diversity of invertebrate and fish species. The importance of biodiversity to ecosystems and their function (Hooper et al. 2005) and the importance of food web connectivity to preserving diversity (Dunne et al. 2002b), means that understanding how community and food web structure varies in rivers is invaluable for effective water resource management. Benthic invertebrates are of special interest, as they form a large portion of the diet of many fish and other high trophic level consumers and are particularly vulnerable to changes in water quality. In the Southeastern Coastal Plain of the United States, rivers vary temporally due to temperature and discharge (Benke et al. 2000), with unregulated rivers undergoing seasonal floods during the winter and spring. While the seasonality of macroinvertebrate community and food web structure is well studied in low order streams, less work has been done on the impact of seasonal cycles on the variation of benthic community structure and food webs in large, lowland rivers. Understanding how these trophic networks respond to predictable seasonal variation in coastal rivers will provide insights into the stability and vulnerability of these systems to anthropogenic or environmental impacts.

Over the past 40 years, ecologists have proposed multiple models for understanding the ecology of rivers, including the river continuum concept (Vannote et al. 1980), the flood pulse concept (Junk et al. 1989), the riverine productivity model (Thorp and Delong 1994) and the riverine ecosystem synthesis (Thorp et al. 2006). All these models make predictions of how communities and food webs are structured based on longitudinal and landscape patterns. The river continuum concept predicts that large rivers are dominated by fine particulate organic matter (FPOM) and low-quality dissolved organic carbon (DOC) and that invertebrate primary consumers are mostly collectors eating detritus. This has been confirmed in coastal plain rivers such as the Ogeechee River (Benke and Wallace 2015). It also suggests that gradients

may result in longitudinal changes in community structure as the river gets larger, including a shift toward invertebrate collectors consuming FPOM. The flood pulse concept asserts that in large rivers with predictable periodic flooding, much of the particulate organic matter (POM) and DOC is produced in the floodplain and that the main channel is low in invertebrate density and diversity, except on substrate like snags or cobble. The low densities and diversity of sandy-bottomed portions of floodplain rivers and the importance of stable substrate for macroinvertebrates has been confirmed in coastal plain rivers (Benke et al. 1984, Benke and Wallace 2015). However, the extent to which floodplain resources and assemblages might contribute to the main channel is unclear. The riverine productivity model suggests that autochthonous production and riparian allochthonous inputs drive production in rivers, and suggests that outside of stable substrates, most benthic invertebrates are living on river margins. While autochthonous production doesn't contribute much to Southeastern Coastal Plain food supplies (Benke and Wallace 2015) riparian inputs may contribute to food supplies and substrate to support marginal benthic invertebrate communities. The riverine ecosystem synthesis suggests that local assemblages are the result of hierarchical hydrogeomorphic filters of a regional species pool resulting in patchy distributions of members of the benthic community. Within the main channel of Southeastern Coastal Plain rivers, this is unlikely to have a large effect, because there is little hydrogeomorphic variability in the mostly sandy-bottomed floodplain swamps. While the implications of these models have explained some of the phenomena observed in coastal plain rivers, it is still unclear how communities in these rivers vary spatially within their lower reaches.

Longitudinal differences have been observed in many streams and rivers, often during tests of the river continuum concept or riverine ecosystem synthesis. I am not aware of any longitudinal studies of Southeastern Coastal Plain river invertebrates, although Reese and Batzer (2007) did a longitudinal study of floodplain wetland invertebrates that found transitions from terrestrial invertebrates and temporary pool specialists in the upper reaches of the Altamaha to riverine taxa in mid-reaches and then finally wetland taxa in the lower coastal plain. In other ecosystems, studies have observed longitudinal changes following

the predictions of the river continuum concept in response to changes in hydrogeomorphic characteristics and food supply (Hawkins and Sedell 1981, Grubaugh et al. 1996, Jiang et al. 2011). These studies tend to confirm the predominance of collectors in large river habitats but do not indicate gradients of species composition within the large river portions of watersheds, except with respect to local hydrogeomorphology. Longitudinal gradients may also respond to anthropogenic impacts on water quality (Álvarez-Cabria et al. 2010). The impacts of gradients within the lowland portion of Southeastern Coastal Plain rivers would be a valuable addition to this body of knowledge and a useful reference for further biomonitoring.

Seasons may also impact the structure of river communities. Seasonal hydrological and physicochemical variation in conditions can impact the species that can inhabit a particular system (Dolédec 1989, Robinson and Uehlinger 2008, Boehme et al. 2016). Different taxonomic groups may occur in a stream or river at different times of year, depending on their life history (Dolédec 1989, Leunda et al. 2009). These fluctuations are often reflected in biomonitoring metrics, such as proportions of sensitive species, and may impact multi-metric indices used in decision making (Linke et al. 1999, Leunda et al. 2009, Boehme et al. 2016). However, these changes are often secondary to spatial considerations in community assembly (Principe and Corigliano 2006). Understanding how seasons impact local assemblages and how they interact with spatial and physicochemical considerations is necessary to conduct proper monitoring and management of southeastern rivers.

It is also important for river managers to understand the food webs of communities within rivers. River food webs can also change independently of community structure, and changes in structure may or may not have large impacts on food webs. Most food web research in running waters is limited in time and space, particularly in large rivers. There have been calls to expand the focus of food web research beyond summary webs of individual sites to include more temporal resolution (McMeans et al. 2015), but these studies are a relatively small portion of food web literature to date. Food web studies that employ stable isotopes often attempt to add some crude spatial discrimination of food sources (Herwig et al. 2007,

Pingram et al. 2014) and some studies have attempted to look at patterns in stable isotopes across different sites (Pingram et al. 2014, Blanchette et al. 2014). However, results are not always consistent and inferring patterns of food web structure from stable isotopes is unreliable. More methods incorporating traditional gut content analysis have been used to observed spatial and temporal trends. Much of this work in lotic environments is from streams, but a few studies have been performed in large rivers (Cross et al. 2013). Temporal patterns in food web structure are often driven by species richness (Thompson and Townsend 1999) and ontogenetic diet shifts (Tavares-Cromar and Williams 1996) or migrations (Akin and Winemiller 2006). Spatial variability has been due to several habitat related factors, often involving changes in resource availability (Thompson and Townsend 1999, 2005b, Cross et al. 2013) and predation (Cross et al. 2013). Since the Southeastern Coastal Plain is under fairly different conditions than the streams and constricted rivers where this research has been done, it would be interesting to see how food webs in coastal plain rivers vary longitudinally, and whether seasonal patterns hold.

Recently, there have been calls for improvements in biomonitoring in order to keep their basis ecologically sound and to identify and predict ecosystem processes and alterations (Friberg et al. 2011). Scientists have proposed incorporating ecological networks into monitoring programs to provide insights into ecosystem function and dynamics (Gray et al. 2014). While food webs and ecological networks have been employed to detect ecological changes in the field for monitoring purposes, these have been largely limited to intensive research projects. Food web analyses using stable isotopes have been applied in bioassessment to track energy flow (France 2015) and organic pollution (Xu and Zhang 2012). Network analysis has been used to identify anthropogenic impacts such as the impact of habitat modification on species interactions (Tylianakis et al. 2007) and the impacts of predator reintroductions (Layer et al. 2011). Despite their use in research, food webs have not been incorporated into routine monitoring. Biomonitoring of the Ogeechee River, a coastal plain river in Georgia, provides an opportunity to add food web analysis to more traditional monitoring of community composition.

Ogeechee River Study System

The Ogeechee River's headwaters rise in the Georgia Piedmont and the river flows for most of its 394 km length through the Southeastern Coastal Plain. By the time it reaches Ossabaw Sound, the Ogeechee is a 6th order river (Benke et al. 2000). The river floods during the winter months in response to increases in discharge due to lower evapotranspiration, inundating its forested floodplain (Benke et al. 2000). The lower flood plain reaches at least 50% inundation 15% of the time, at which time its relative width is approximately 19 times the width of the main channel and 100% inundation 3.6% of the time, when it's relative width is 37 times the width of the main channel (Benke et al. 2000). Habitat in the stream consists of wood snags and sandy benthos, with high diversity on the snags and high density but low biomass of midges and oligochaetes in the sand (Benke et al. 1984). Most invertebrate production in the lower river is derived from allochthonous input rather than in-stream primary production, in particular, from microbe-rich amorphous detritus (Benke and Wallace 2015). Snags harbor the majority of invertebrate production, with snag predators, including filter-feeding hydropsychid caddisflies, consuming most invertebrate production (Benke and Wallace 2015). The Ogeechee is a relatively unimpacted river with little urbanization for most of its watershed and no impoundments or obstructions of its main channel (Meyer et al. 1997). It is therefore a good reference system for the condition of coastal plain rivers. Despite some studies of invertebrate communities within the rivers, how these communities change across time and space is poorly understood, and a better understanding of this river could help river managers to accurately interpret and apply the results of biomonitoring on the river.

Objectives

The purpose of this thesis is to determine how season and associated environmental patterns drive benthic invertebrate communities and their trophic structure in the Ogeechee by indirect inference of trophic relationships using collected invertebrate assemblages and diet information from literature sources. In addition to season and any possible associated ontogenetic effects, I am interested in how

physicochemical factors impact these communities. Knowledge of these impacts would help stakeholders to understand how southeastern rivers might respond to increasing anthropogenic impacts and climate change. Additionally, I am interested in how food web structure performs detecting changes compared to traditional community-based metrics, and whether they would be worth using in conjunction with community metrics in biomonitoring. If effective, estimated food web metrics could provide a useful tool for interpreting samples from monitoring that are more informative than relying solely on simple composition-based metrics.

CHAPTER 2

OGEECHEE RIVER INVERTEBRATE COMMUNITIES

INTRODUCTION

When assessing the biological condition of ecosystems, scientists tailor their criteria to local habitats using reference sites. Understanding how community structure varies across local conditions allows scientists to identify and understand the impacts of anthropogenic disturbance. Scientists must be aware of the impacts of local habitat, as well as spatial, temporal and environmental gradients, or they will be confounded with human alterations. Seasonal cycles often influence these conditions, setting the minima and maxima of environmental variation that constrain aquatic organisms living in these habitats (Doledéc 1989) and potentially influencing their lifecycles.

Environmental Variation

Seasonality drives much of the variation in lotic systems, whether through temperature, hydrological regime or physicochemical variation. For example, in Appalachian streams, specific conductance (SPC) peaks in the late summer and early fall (Boehme et al. 2016). These seasonal trends are climate dependent; hydrological regimes can range from high discharge in the wet season and discontinuity in the dry season to perennial flow with multiple periods of high variability due to patterns of snow melt and rainfall (Puckridge et al. 1998, Habdija et al. 2003, Garcia et al. 2015). These changes are coupled with seasonal variations in food resources to drive temporal variation in community structure. Hydrologically dependent seasonal variation has been found in both algal and invertebrate production in Australia, with high productivity in the transitions between the rainy and dry seasons (Garcia et al. 2015). In alpine rivers, variation in primary productivity has been linked to seasonal environment effects such as light incidence, as well as seasonal disturbance from spates, leading to higher primary production in the summer (Uehlinger 2000, Habdija et al. 2003). Detrital resources vary with season and discharge regime, with seston availability increasing in unstable, high-discharge periods and standing FPOM and coarse

particulate organic matter (CPOM) increasing in low discharge periods (Habdija et al. 2003). Thompson and Townsend (1999) found both organic matter and algal production varied between season in their study, although which resource varied was dependent on surrounding land use.

Community Variation

Invertebrate community structure can be associated with most temporally variable environmental factors. Macroinvertebrate community metrics respond to physicochemical variation associated with water quality in ways that vary seasonally (Álvarez-Cabria et al. 2010). Responses to conductivity in particular can vary with month, altering the proportions of sensitive taxa (Boehme et al. 2016). Patterns in macroinvertebrate indices over large temporal and spatial scales have been explained by differences in discharge and hydrological variability, suggesting that hydrology is a major factor in structuring in-stream habitat (Monk et al. 2008). Certain macroinvertebrate metrics used in water-quality assessment in Spain respond to hydrological variation, although whether this effect is seasonal or not depends on the metric (Álvarez-Cabria et al. 2010). In sub-arctic streams, hydrological features contributed to the clustering of similarly structured communities, with stream width being important in the spring and current velocity being important in the fall (Tolonen et al. 2017).

Hydrological disturbance can have effects on communities independently of overall regime. Experimental flooding of a Swiss river lead to community shifts reducing species richness, biomass and standing stocks of autochthonous and allochthonous resources until the transitional community was replaced with a flood resistant community that were more resistant to flood disturbance (Robinson and Uehlinger 2008). Drought can act as a hydrological disturbance, and changes in connectivity, flow, and habitat that accompany drought can alter interspecific interactions, resource availability and community composition (Lake 2003). Disturbance from freezing had a negative effect on richness in Alaskan streams, removing fish predators (Parker and Huryn 2013). Many of these effects, such as freezing or

spates during the rainy season, are more likely in certain times of year. Therefore, hydrological events can contribute to seasonal differences in community structure even if they are unpredictable.

Biotic factors are regularly involved in observed patterns of community structure. Seasonal shifts in structure in Appalachian streams due to decreases in stream water quality were driven in part by ontogeny, as sensitive taxa whose life histories lead to higher incidence in streams at certain times of year were absent at impacted sites, distorting the seasonal patterns seen in reference streams (Boehme et al. 2016). The positive relationship between functional groups and their food resources in streams has been well documented, but seasonal patterns are not always as prominent as spatial patterns (Vannote et al. 1980, Hawkins and Sedell 1981). Seasonal variation in food availability in the Sava river contributed to the biomass and abundance of certain functional feeding groups that best exploited available resources (Habdija et al. 2003). This was driven by hydrological stability and lead to higher abundances and biomasses during the stable winter and summer periods on the river (Habdija et al. 2003). In streams where seston, FPOM standing crop and algal production are seasonally variable, they have been found to govern the proportion of filterers, collector gatherers and grazers between seasons (Thompson and Townsend 1999). CPOM has been found to help structure sub-arctic faunal communities, with the dominant behavioral habits of invertebrates being determined by CPOM in the fall but not in the spring (Tolonen et al. 2017).

Objectives

The Ogeechee River Project initiated to better understand the conditions of the river in case of future human impacts. For benthic macroinvertebrates, this means understanding the seasonal and longitudinal changes in community structure. To do this, I sampled benthic invertebrates from six sites along the river's length seasonally for three years. I anticipated seasonal patterns in chemical variables to respond to the flood pulse and seasonal temperature trends, with less oxygen in warmer weather and lower conductivity during the flood pulse, when ions are diluted in increased surface waters. I expected

invertebrate assemblages to be influenced by season, which directly influences their life cycles, available resources and the phenology of their predators. Discharge, which favors certain habits and acts as a disturbance which can remove organisms from the local species pool, should also influence macroinvertebrate composition. I anticipated species richness to be governed by disruptive effects such as discharge. Warm weather may also facilitate productivity, with influences on community structure. I did not expect temperature or dissolved oxygen to have a stronger effect than any of the above phenomenon, but it was possible that some effect would be detected as these are both involved in metabolic processes. Longitudinally, I expected certain taxa to shift over the river's length as habitat changed, causing a shift from piedmont assemblages to more lowland and estuarine species.

METHODS

Study Sites

Six sites were chosen along the course of the lower Ogeechee River in the Southeastern Plains (65) and Southern Coastal Plain (75) Level III US EPA ecoregions. Three upstream sites, at the crossing of Georgia (GA) Route 88 (R88), the crossing of GA Route 78 near Wadley (WA) and the crossing of Rocky Ford Road (RF) are in the 65 Level III ecoregion while the remaining three downstream sites, at the crossing of GA Route 24 near Oliver (OL), the crossing of GA Route 119 (R119) and the crossing of GA Route 204 at Morgan's Bridge (MO), are within the 75 Level III ecoregion (Table 2.1, Griffith et al. 2001). OL, in the 75i Level IV ecoregion, and WA in the 65l Level IV ecoregion, are very near the border of the 65p Level IV ecoregion. The Georgia Environmental Protection Division (GA EPD) uses separate multi-metric indices to assess the health of stream communities within each ecoregion, which may indicate differences in communities due to habitat that would be a source of variation among the sites. However, the EPD does not apply these indices to large rivers and does not have an index for the river-specific Floodplain and Low Terraces regions, so that variation may not apply. Distances between sites should be great enough to avoid interdependence of consecutive sites within the river (i.e. Hurlbert 1984).

The sites were chosen to capture longitudinal variation along the river course and in proximity to public boat ramps for access purposes. Invertebrate samples and physicochemical measurements were taken approximately 100 meters upstream of access points to reduce the influence of anthropogenic disturbance at the bridge crossings.

Sampling was performed as part of a larger biomonitoring project on the Ogeechee River. Samples were taken quarterly in March, June, September and December, during the middle of the month. Invertebrate samples were taken during the late morning and early afternoon, generally between 10:00 am and 2:00 pm, to keep consistent measurements of physical and chemical factors that vary on a daily basis, such as temperature and dissolved oxygen. Samples were taken between June 2014 and June 2017. The first three years of data, from June 2014 until March 2017 were used in analyses. With three years of sampling at 6 sites over 4 seasons, the final sample size was n= 72.

Physicochemical Monitoring

Physicochemical measurements were taken with a YSI multimeter before sampling invertebrates. In cases where the YSI malfunctioned, measurements were retrieved from other groups working on the biomonitoring project who were sampling during the same period. Recorded physical and chemical variables included temperature, dissolved oxygen (DO) and percent dissolved oxygen (%DO), conductivity and SPC, and pH. Discharge data were retrieved from the USGS gages located closest to each site using the readings from 10:00 am on the day of collection (Table 2.1, USGS 2019). All gages were approximately 100 meters downstream of the sample reach, except the gage closest to R119 which was several miles downstream of the site.

Invertebrate sampling

Invertebrate sampling was done using a modified version of the GA Environmental Protection Division (EPD) sampling protocol for wadeable streams (GA EPD 2007). Benthic invertebrates were collected from appropriate substrates using 1-meter jabs with d-frame nets with a mesh size of 500-µm.

20 jabs were taken per sample along a 100-meter reach of the river incorporating both banks. Jab locations were chosen in proportion to available habitat. Habitats to be sampled include snags, submerged macrophytes, root wads, leaf packs and other accumulations of organic material, and soft sediments and sandy substrate. Sandy substrate was deprioritized for sampling, because while densities within sediment may be high, biomass is low compared to snags and other habitats and species consist mostly of small oligochaetes and dipteran larvae (Benke et al. 1984). Marginal habitats were chosen because they are known to have greater richness because they provide more stability and may act as refugia during spates (Principe and Corigliano 2006). We pooled jabs into a single sample and emptied them into a 500-µm mesh sieve bucket and rinsed the material to remove fine sediments. Large debris were rinsed and removed prior to preservation.

Collected samples were placed into plastic bags and preserved with 95% alcohol and dyed with Rose Bengal. In the laboratory, technicians washed samples through a 500-µm mesh sieve, and material such as leaves and woody debris were rinsed to dislodge any organisms. Remaining materials were sorted in a large, gridded tray. Each square of the grid was assigned a number and random number generation was used to select squares to sub-sample. Material from sub-sampled grids was picked through under a dissecting microscope and invertebrates were preserved in 95% alcohol for identification. Grids were picked completely, and new grids were subsampled randomly with 200 (± 40) organisms picked. Remaining material from the grid was preserved separately for inspection for quality control purposes. Technicians conducted a search of large or rare organisms that were easily visible on the sample tray and collected and stored these separately. Subsampled organisms were then identified to lowest possible taxonomic rank, generally genus for most insects, subfamily or tribe for chironomids, genus or family for mollusks and decapod crustaceans, and order or higher for other groups (notably annelids and water mites). Identification was done with a dissecting or compound microscope using taxonomic keys (Parrish et al. 1975, Smith 2001, Merritt and Cummins 2008, Thorp and Covich 2010). Abundances of identified organisms were recorded for each sample.

Physicochemical analysis

Analyses were performed in R (R Development Core Team 2017) using the nlme (Pinheiro et al. 2018) and lme4 (Bates et al. 2015) packages. Differences in environmental variables among sites and across seasons were tested using the nlme lme function to fit linear mixed effects models including site and season as fixed effects and year as a random effect. Interactions between site and season were tested and omitted if insignificant. Year was omitted from the model and lme4's glm function was used if AIC values indicated that it did not improve the model fit, and residuals were checked visually for normality and homoskedasticity. Discharge and specific conductance were normalized using a log transformation and specific conductance was weighted using the R varPower function to remove heteroskedasticity. Principal component analysis (PCA) on correlations was performed using the R stats package prcomp function on the environmental parameters to visualize the main components of physicochemical variation. %DO and SPC were used instead of DO and conductivity to reduce the temperature dependence of those variables.

Community analyses

Community analyses were performed in R (R Development Core Team 2017) using the vegan (Oksanen et al. 2018), nlme (Pinheiro et al. 2018) and lme4 (Bates et al. 2015) packages, or in PRIMER-E v7 (Clarke and Gorley 2015) for PERMANOVA and SIMPER. I tested taxonomic richness and Shannon indices for the effect of site and season using linear mixed effects models including year as a random effect, following the same procedure as for physicochemical variables. Sample assemblages were square root transformed to reduce the impact of dominant species and compared between samples using Bray-Curtis distances. Non-metric multidimensional scaling (nMDS) was performed with the metaMDS function to ordinate assemblage data. Seasonal differences were tested using permutational multivariate analysis of variance (PERMANOVA) with season and site as fixed effects and year as a random categorical effect, as well as interactions between each pair of factors. PERMDISP was used to test

PERMANOVA's assumption of homogeneity of dispersion (Anderson and Walsh 2013). A two-way crossed SIMPER analysis (Clarke 1993) was used to quantify dissimilarity between levels of sites and seasons and to identify taxa most responsible for differences between them. Distance-based redundancy analysis (dbRDA) was performed on a model selected using the vegan ordistep method with both forward and backward stepwise searching and with year as a random effect (a condition in the dbRDA model). Permutational F (perm-F) tests were then performed on the dbRDA model and on its terms using vegan.

RESULTS

Water chemistry and hydrology

Discharge differed across both site ($F_{5,66} = 43.91$, $p < 0.001$) and season ($F_{3,63} = 26.09$, $p < 0.001$), increasing at downstream sites as well as in the winter and spring, consistent with the flood pulse (Table 2.2, Table 2.3). Temperatures differed across sites ($F_{5,61} = 2.41$, $p = 0.0463$), being about two degrees warmer at the lower three sites than at the upper three sites (Table 2.2), and across seasons, as expected ($F_{3,61} = 136.14$, $p < 0.0001$), with winter being coldest, summer being warmest, and fall being almost as warm as summer (Table 2.3). Specific conductance differed with both site ($F_{5,61} = 35.80$, $p < 0.0001$) and season ($F_{3,61} = 12.93$, $p < 0.0001$) (Table 2.2, Table 2.3). Lower conductance in the spring and winter may have been due to higher discharge levels associated with the flood pulse diluting dissolved minerals. Even after correcting for the effect of temperature using %DO, oxygen differed between sites ($F_{5,61} = 5.01$, $p = 0.0007$) and seasons ($F_{3,61} = 12.45$, $p < 0.0001$), with summer having the lowest %DO and winter having the highest. There were no significant differences in pH between sites ($F_{5,66} = 1.16$, $p = 0.3385$) or season ($F_{3,63} = 2.11$, $p = 0.1079$). There were no significant interactions between site and season, but patterns across both sites and seasons for most parameters lead to different physicochemical profiles depending on both (Table 2.4).

Plotting the environmental variables in a PCA revealed distance between samples based on season, but not as much based on sites. The first principal component, explaining about 38% of the

environmental variance among samples correlated primarily with temperature and %DO, and to a lesser extend with SPC and pH, whereas the second principal component explained about 30% of variance and correlated primarily with discharge and pH, and somewhat less with SPC (Figure 2.1). Winter samples were separated from summer and fall samples, with spring exhibiting a lot of overlap with winter but less with fall and summer, which were warmer and had lower discharge.

Community Structure

There were more taxa on average at upstream sites ($F_{5,61} = 4.95$, $p = 0.0007$) (Table 2.7), and a slight trend toward fewer taxa in the winter and spring ($F_{3,61} = 2.71$, $p = 0.0531$) (Table 2.5). Spring had lower diversity than the other seasons ($F_{3,63} = 10.10$, $p < 0.0001$) and diversity was slightly lower at downstream sites ($F_{5,66} = 3.89$, $p = 0.0048$) (Table 2.5). Assemblages overlapped little between winter and spring, during the flood pulse, and summer and fall, during base flow (Figure 2.2). PERMANOVA corroborated seasonal differences (pseudo-$F_{3,30} = 4.47$, $p = 0.003$) as well as differences between sites (pseudo-$F_{5,30} = 3.26$, $p = 0.001$) and across years (pseudo-$F_{2,30} = 6.13$, $p = 0.001$). All interactions were also significant, including site by season interactions (pseudo-$F_{15,30} = 1.48$, $p = 0.001$), site by year interactions (pseudo-$F_{10,30} = 1.20$, $p = 0.048$), and season by year interactions (pseudo-$F_{6,30} = 2.11$, $p = 0.001$). PERMDISP revealed uneven dispersion between sites (pseudo-$F_{5,66} = 4.81$, $p = 0.002$), although PERMANOVA tends to be more robust to heterogeneity of dispersion than other similar methods such as Mantel tests and ANOSIM (Anderson and Walsh 2013). Dispersion among seasons (pseudo-$F_{3,68} = 1.89$, $p = 0.173$) and years (pseudo-$F_{2,69} = 0.45$, $p = 0.652$) were not significantly different.

SIMPER analysis revealed somewhat consistent similarities within sites and dissimilarities between sites that generally increased with distance between sites (Table 2.6). Assemblages shifted from upstream to downstream sites to include more estuarine taxa, going from predominantly chironomids and hydrobiids to assemblages dominated by isopods such as *Caecidotea* and *Lirceus* (Appendix B). Seasons also had consistent similarities within sites and winter and spring were less dissimilar to each other than to other seasons, as were summer and fall (Table 2.7). Spring and to a lesser extent winter were

dominated by isopods and mayflies such as baetids in the spring and *Baetisca* in the winter (Appendix C). Fall had greater numbers of chironomids, *Palaemonetes* shrimp, hydrobiid snails and mayflies such as *Caenis* and *Tricorythodes*. Summer was similar to fall, with higher levels of hydrobiid snails and oligochaetes and fewer mayflies (Appendix C).

Site, season, conductivity and pH were included in the dbRDA, with the model constraining 38% its inertia. A permutation test of the model was significant (perm-$F_{10,59} = 4.06$, $p = 0.001$), as were the tests for season (perm-$F_{3,59} = 7.00$, $p = 0.001$), site (perm-$F_{5,59} = 2.95$, $p = 0.001$), conductivity (perm-$F_{1,59} = 2.47$, $p = 0.008$) and pH (perm-$F_{1,59} = 2.35$, $p = 0.006$). Discharge, temperature and dissolved oxygen were not suggested by model selection, possibly due to site and seasonal dependence that rendered them redundant. The clustering of summer and fall samples, and winter and spring samples were confirmed in the ordination (Figure 2.3) along the dbRDA's first axis. Based on the centroids of each site and Figure 2.4 the second axis of the dbRDA corresponded roughly to a longitudinal gradient from upstream to downstream sites, except for MO samples.

DISCUSSION

The Ogeechee River has distinct hydrological and chemical gradients that are associated with gradients of community composition over space and time. The state of the river is driven by shifts in habitat as the river widens, by the flood pulse and by seasonal temperature changes. As the river makes its way through its watershed, tributaries contribute their water, leading to increased discharge, as one would expect. A wider river may contribute to less shading, which might drive the observed higher temperatures at downstream sites. These increases help drive lower oxygen levels, although calmer waters and differences in ecosystem metabolism, which were not measured, may have contributed to lower percent dissolved oxygen downstream. Meyer and Edwards (1990) documented declines in net daily metabolism with increasing stream order of Ogeechee river tributaries, but differences between a 4^{th} order tributary and the 6^{th} order mainstem were not negative and so the trend within tributaries may not reflect along a continuum in the large river portion of the mainstem. Conductivity changed over the course of the river,

first increasing at the middle sites, then decreasing (Table 2.2) in a manner that was not easily explained. Changes in geology or in land use may have driven increases in dissolved ions at RF and OL and warrant further investigation. Seasonal trends were as I expected, with discharge reflecting the flood pulse and temperature reflecting seasonal air temperature patterns, which in turn drove dissolved oxygen levels. Higher percent dissolved oxygen in the winter and spring may have been driven by higher discharge causing turbulence and mixing or by colder temperatures depressing ecosystem metabolism. Differences in conductivity may have been due to more dilute ion concentrations during the flood pulse. There were clear differences in physicochemical variables across seasons, and to a lesser extent sites, which lead different sites and seasons to have their own physicochemical profile. These profiles could have large impacts on invertebrate metabolism and available habitat conditions and serve as environmental filters (Power et al. 1988, Poff 1997).

Invertebrate communities also varied across time and space, probably in response to varying habitat conditions including those described above. Higher diversity in the summer and fall and at upstream sites may have reflected better conditions for native fauna. However, differences in total taxa and some of the differences in Shannon indices may been artefacts of subsampling. With a limited sample of 200 invertebrates, dominant species would lower the chance of subsampling less common species, especially if those species did not show up in the large and rare search (but see Barbour and Gerritsen 1996). This would lead to lower sampling of rare species if common species were more abundant at certain sites or at certain times of the year. If that is the case, the influence of evenness on Shannon indices is still detectable and may be exaggerated by artificially low richness. Another contributor to lower taxonomic richness and to lower evenness could be a shift in assemblages from riverine dominated to lentic or estuarine dominated fauna. Reese and Batzer (2007) documented a shift in wetland fauna along a southeastern river from riverine taxa to lentic fauna such as crangonyctids and asellids, which were common in the lower sites during our project and are numerically abundant. These less-even communities could simply suggest a shift in habitat rather than a more heavily impacted river. Available

habitat might also have shifted as the river widened, and marginal habitats, which often have the most diversity and greatest biomass in floodplain rivers due to their available substrate (Principe and Corigliano 2006), may have constituted a smaller proportion of river habitat, even with reduced sampling of sandy substrates. Seasonal differences could also be due to artefacts of using subsamples. During the winter and spring, dominant taxa such as isopods and *Baetisca* were more important, while common taxa in summer and fall were not as abundant and differences were less clear. Many invertebrates are also only present in certain seasons (e.g. Leunda et al. 2009) due to migration from other habitats (Danks 2007, Stubbington 2012) or due to ontogeny (Benke and Jacobi 1994), or may be undetected in certain life stages that are too small to be collected (Tavares-Cromar and Williams 1996, Danks 2007).

These differences were also reflected in the differences between site, season and year in community composition, which were confirmed using PERMANOVA and visible for seasons in the nMDS. Overlap in communities between fall and summer and between winter and spring suggests that the influence of the flood pulse was an important influence on community structure. Differences between years suggested possible interannual variation in environmental parameter and population dynamics but may have been due, in part, to different people identifying samples. Spatial and temporal patterns corroborated previous work in Southeastern Coastal Plain rivers. Longitudinal shifts toward more lentic crustaceans were observed in river flood plains (Reese and Batzer 2007) and seasonal differences such as summer increases in production of certain taxa such as *Baetis ephippiatus, Tricorythodes, Caenis* (Benke and Jacobi 1994) and *Chimarra moselyi* (Benke and Wallace 1997) corresponded to similar increases in relative abundances of those same genera in our current project (Appendix C). Similarities of my data to previously observed production data confirms the importance of phenology in driving at least some of the observed differences in abundance.

The DBRDA model selected to explain community differences indicated that site and season had stronger relationships with sample assemblages than highly correlated variables such as temperature and discharge, which suggests that those physical parameters had little influence on aquatic invertebrates that

was not adjusted for by habitat choice (for sites) and phenology (for seasons). It is possible that interannual variation in these parameters may have had an effect that was lost when controlling for that in the model, or that extremes of temperature or discharge might also alter community composition in ways that were not detectable using my data. Discharge, which I expected to have a large impact on composition and richness, did not, either because disturbance level discharges were not detected using sampling, or because flooding is too moderated and predictable in coastal plain rivers. Conductivity and pH did contribute to the model, and both are known to be important for certain sensitive taxa (Layer et al .2011, Hogsden and Harding 2012, Boehme et al. 2016). Nevertheless, the model appears to confirm the primary importance of spatial and temporal drivers of lotic biodiversity.

Finding spatial and temporal differences in biomonitoring is common but they are not always found in tandem. Early investigations of the river continuum concept that incorporated seasonal variation found that spatial differences were greater than seasonal ones (Hawkins and Sedell 1981). Leunda et al. (2009) found that in their Pyrenean river, despite more consistent differences in biotic indices by season, ordinations of community structure had spatial correlated axes that explained a greater proportion of variation. Other studies have found greater influence of season on biotic indices and the clustering of species assemblages (Linke et al. 1999). The Ogeechee River was also more distinctly different between seasons than across sites, but unlike most assessments of lotic invertebrate communities that examine both spatial and temporal variation, the Ogeechee is a lowland river, with no large shifts in altitude or geology to produce different habitat conditions. Consequently, seasonal differences, which are ubiquitous, had larger differences.

Samples were fairly consistent within sites or seasons, with average similarities between 43% and 50% while being quite dissimilar between sites or seasons, with average dissimilarities between 51% and 67%. Subsamples were small, which increases the level of noise in an individual sample, so getting some level of consistency in repeated samples is promising for the reliability of subsamples. Additionally, the presence of both riverine and lentic invertebrates in samples means that sampling could detect impacts on

floodplain assemblages in addition to main channel assemblages. Despite this, further work needs to be done before using jabs for large river biomonitoring. Questions remain as to whether comparisons between reference conditions and impacted conditions are possible within the Ogeechee. Currently, no biotic indices exist for the river, and biotic indices for smaller streams vary by ecoregion in ways that may not apply appropriately to larger rivers with significant flood plains. It is also unclear how this type of active sampling compares to other sampling methods such as Hess samplers, or passive sampling using leaf packs or Hester samplers. If these questions are answered, then biomonitoring using invertebrates should be possible (as assemblages were not homogenous within the river) and water resource managers could better respond to future disasters and identify proper mitigation strategies.

Table 2.1. Ogeechee River sampling sites with associated gage numbers, drainage areas, EPA Level IV ecoregions and Level IV ecoregions used for the GA EPD Multi-Metric Index (Griffith et al. 2001, USGS 2019).

Site	USGS Gage Number	Drainage Area (km^2)	Level IV US EPA Ecoregion	Ecoregion Used in Multimetric Index
Georgia Route 88	02200120	1173.19	Coastal Plain Red Uplands (65k)	Coastal Plain Red Uplands (65k)
Wadley	02201230	3470.58	Atlantic Southern Loam Plains (65l)	Atlantic Southern Loam Plains (65l)
Rocky Ford	02202040	5050.48	Southeastern Floodplains and Low Terraces (65p)	Atlantic Southern Loam Plains (65l)
Oliver	02202190	6138.27	Floodplains and Low Terraces (75i)	Sea Island Flatwoods (75f)
Georgia Route 119	02202500	6863.47	Floodplains and Low Terraces (75i)	Sea Island Flatwoods (75f)
Morgan's Bridge	02202680	7692.27	Floodplains and Low Terraces (75i)	Sea Island Flatwoods (75f)

Table 2.2. Mean (± SE) Ogeechee River hydrological and chemical parameters by site, including discharge, temperature, specific conductance, dissolved oxygen and pH.

Site	Discharge (m^3/s)	Temperature (°C)	Specific conductance (µS/cm)	Dissolved oxygen (mg/l)	pH
Georgia Route 88	3.62 (±1.03)	18.3 (±1.9)	58.36 (±2.48)	7.06 (±0.57)	6.89 (±0.13)
Wadley	15.39 (±3.36)	18.6 (±2.1)	68.02 (±2.53)	7.74 (±0.51)	6.94 (±0.10)
Rocky Ford	27.92 (±6.84)	18.7 (±1.5)	100.09 (±5.04)	6.85 (±0.44)	7.14 (±0.10)
Oliver	35.59 (±7.92)	20.8 (±1.9)	103.73 (±7.41)	6.28 (±0.43)	7.01 (±0.13)
Georgia Route 119	50.31 (±8.85)	20.2 (±1.9)	89.46 (±5.49)	6.57 (±0.52)	6.82 (±0.12)
Morgan's Bridge	51.51 (±9.29)	20.2 (±1.7)	86.78 (±5.77)	6.48 (±0.39)	6.83 (±0.12)

Table 2.3. Mean (± SE) Ogeechee River hydrological and chemical parameters by season, including discharge, temperature, specific conductance, dissolved oxygen and pH.

Season	Discharge (m^3/s)	Temperature (°C)	Specific conductance (µS/cm)	Dissolved oxygen (mg/l)	pH
Summer	19.17 (±3.56)	25.7 (±0.3)	94.20 (±4.54)	5.43 (±0.12)	7.00 (±0.07)
Fall	17.65 (±4.74)	23.4 (±0.6)	92.64 (±7.62)	5.99 (±0.22)	7.05 (±0.11)
Winter	30.65 (±5.61)	11.3 (±0.7)	79.42 (±4.31)	8.76 (±0.33)	6.74 (±0.09)
Spring	55.42 (±8.62)	17.3 (±0.8)	71.36 (±3.42)	7.15 (±0.30)	6.96 (±0.10)

Table 2.4. Mean (± SE) across three years of hydrological and chemical parameters for each site in each season, including discharge, temperature, specific conductance, dissolved oxygen and pH.

Site	Season	Discharge (m^3/s)	Temperature (°C)	Specific conductance (µS/cm)	Dissolved oxygen (mg/l)	pH
Georgia Route 88	**Summer**	1.09 (±0.14)	25.3 (±0.6)	71.20 (±0.49)	5.29 (±0.18)	6.91 (±0.29)
	Fall	0.72 (±0.24)	21.4 (±1.3)	53.95 (±3.16)	6.01 (±0.30)	7.23 (±0.12)
	Winter	3.85 (±0.94)	10.8 (±2.4)	57.31 (±2.00)	9.13 (±1.06)	6.70 (±0.34)
	Spring	8.82 (±1.24)	15.5 (±3.0)	51.00 (±1.21)	7.81 (±1.12)	6.73 (±0.25)
Wadley	**Summer**	6.45 (±0.50)	26.6 (±1.0)	75.97 (±3.03)	6.21 (±0.26)	6.99 (±0.22)
	Fall	13.43 (±9.17)	22.1 (±1.4)	71.27 (±6.48)	7.00 (±0.29)	7.13 (±0.16)
	Winter	13.57 (±3.28)	9.6 (±2.0)	65.89 (±2.25)	10.09 (±0.69)	6.81 (±0.11)
	Spring	28.10 (±5.32)	16.1 (±2.8)	58.97 (±2.07)	7.65 (±0.92)	6.80 (±0.29)
Rocky Ford	**Summer**	18.63 (±6.83)	24.7 (±0.3)	111.87 (±7.19)	5.46 (±0.38)	7.16 (±0.13)
	Fall	8.91 (±2.52)	20.6 (±1.3)	117.17 (±3.21)	6.56 (±0.68)	7.38 (±0.20)
	Winter	26.09 (±7.32)	11.5 (±1.6)	90.32 (±3.98)	8.67 (±0.90)	6.82 (±0.16)
	Spring	58.05 (±15.57)	17.8 (±1.4)	81.00 (±5.94)	6.72 (±0.43)	7.19 (±0.23)
Oliver	**Summer**	21.22 (±2.52)	26.3 (±0.3)	111.81 (±2.73)	5.26 (±0.20)	7.19 (±0.08)
	Fall	13.16 (±5.30)	26.1 (±1.5)	131.43 (±13.81)	5.34 (±0.44)	7.18 (±0.25)
	Winter	36.24 (±9.61)	12.3 (±2.0)	89.16 (±14.80)	7.94 (±1.04)	6.63 (±0.30)
	Spring	71.74 (±15.62)	18.3 (±1.5)	82.50 (±6.56)	6.60 (±0.61)	7.03 (±0.31)
Georgia Route 119	**Summer**	35.28 (±10.25)	26.3 (±0.4)	98.31 (±11.81)	5.16 (±0.06)	6.84 (±0.05)
	Fall	34.85 (±16.53)	25.0 (±0.2)	91.82 (±16.23)	5.33 (±0.59)	6.72 (±0.39)
	Winter	50.42 (±15.35)	11.5 (±1.8)	89.22 (±10.76)	8.71 (±0.71)	6.72 (±0.21)
	Spring	80.70 (±20.33)	17.8 (±2.5)	78.47 (±6.54)	7.09 (±0.90)	6.99 (±0.27)
Morgan's Bridge	**Summer**	32.36 (±4.91)	25.1 (±1.1)	96.02 (±9.62)	5.18 (±0.19)	6.88 (±0.09)
	Fall	34.85 (±16.10)	25.0 (±0.3)	90.23 (±20.26)	5.68 (±0.39)	6.64 (±0.29)
	Winter	53.71 (±14.83)	12.2 (±1.8)	84.64 (±9.19)	8.00 (±0.20)	6.79 (±0.40)
	Spring	85.14 (±22.46)	18.3 (±2.1)	76.23 (±6.22)	7.04 (±0.79)	7.00 (±0.16)

Table 2.5. Means (±SE) of total taxa and Shannon diversity index (*H'*) for all samples in the Ogeechee River, as well as by site and season.

	Total Taxa	**Shannon H'**
Ogeechee River	30.7 (±0.8)	2.57 (±0.04)
Season		
Summer	32.6 (±1.6)	2.63 (±0.07)
Fall	32.5 (±1.3)	2.78 (±0.04)
Winter	28.3 (±1.6)	2.59 (±0.09)
Spring	29.3 (±1.6)	2.28 (±0.10)
Site		
88 Crossing	35.1 (±2.3)	2.67 (±0.08)
Wadley	33.9 (±1.6)	2.79 (±0.06)
Rocky Ford	32.1 (±1.6)	2.62 (±0.10)
Oliver	29.6 (±1.5)	2.58 (±0.10)
Hwy 119	26.3 (±1.6)	2.36 (±0.14)
Morgan's Bridge	27.0 (±1.4)	2.42 (±0.11)

Table 2.6. SIMPER average % Bray-Curtis similarities within sites and dissimilarities among sites for Ogeechee river macroinvertebrate relative abundances.

	Georgia Route 88	Wadley	Rocky Ford	Oliver	Georgia Route 119	Morgan's Bridge
Average Similarities	49.77	45.47	48.94	43.97	48.46	43.73

Average Dissimilarities	Georgia Route 88	Wadley	Rocky Ford	Oliver	Georgia Route 119
Wadley	53.21				
Rocky Ford	58.75	54.61			
Oliver	62.59	59.24	51.44		
Georgia Rt 119	63.81	60.79	51.26	54.14	
Morgan's Bridge	61.20	60.69	55.75	57.91	53.85

Table 2.7. SIMPER average % Bray-Curtis similarities within seasons and dissimilarities among seasons for Ogeechee river macroinvertebrate relative abundances.

	Summer	Fall	Winter	Spring
Average Similarities	44.33	48.66	46.26	47.76

Average Dissimilarities	Summer	Fall	Winter
Fall	54.97		
Winter	65.01	62.24	
Spring	66.81	64.54	55.90

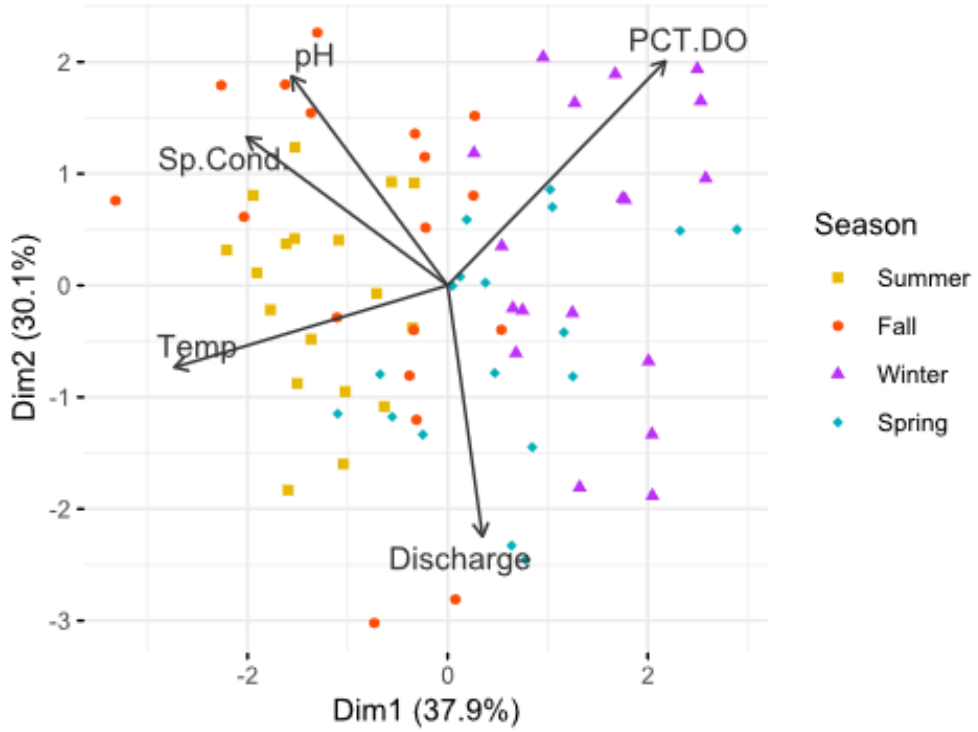

Figure 2.1. PCA on correlations biplot of discharge (m^3/s), temperature (°C), SPC (µS/cm), %DO and pH of all samples, colored by season and with factor loadings for each variable.

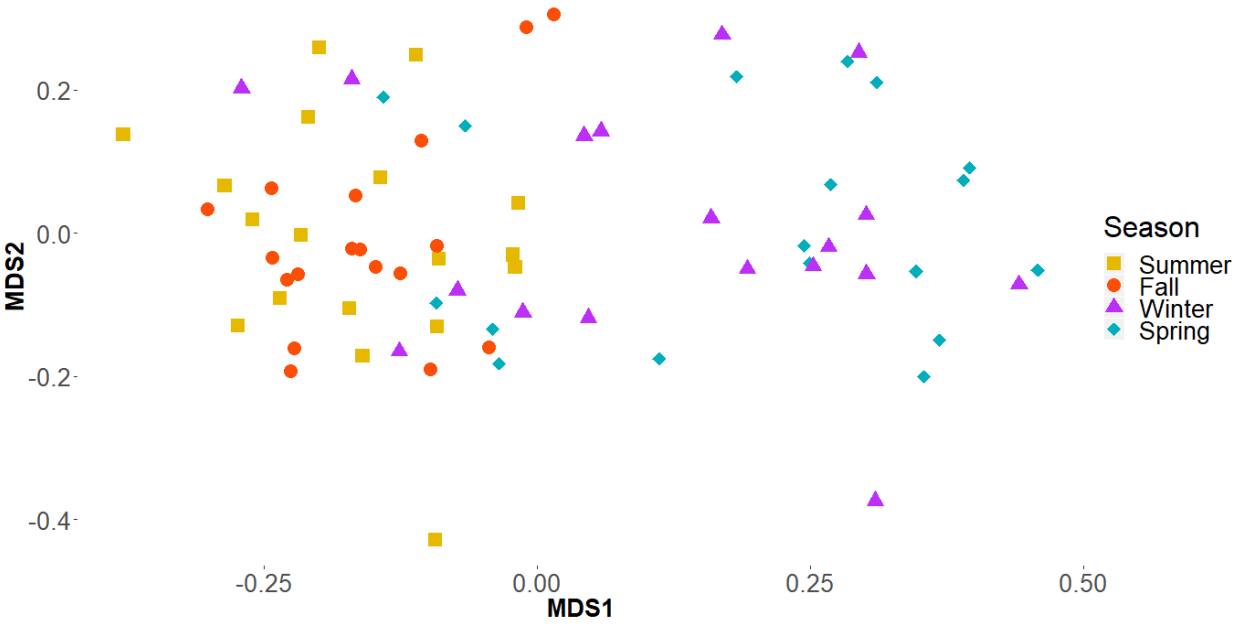

Figure 2.2. Plot of the first two dimensions of a 3D nMDS for macroinvertebrate relative abundance data demonstrating seasonal differences. Stress was 0.16.

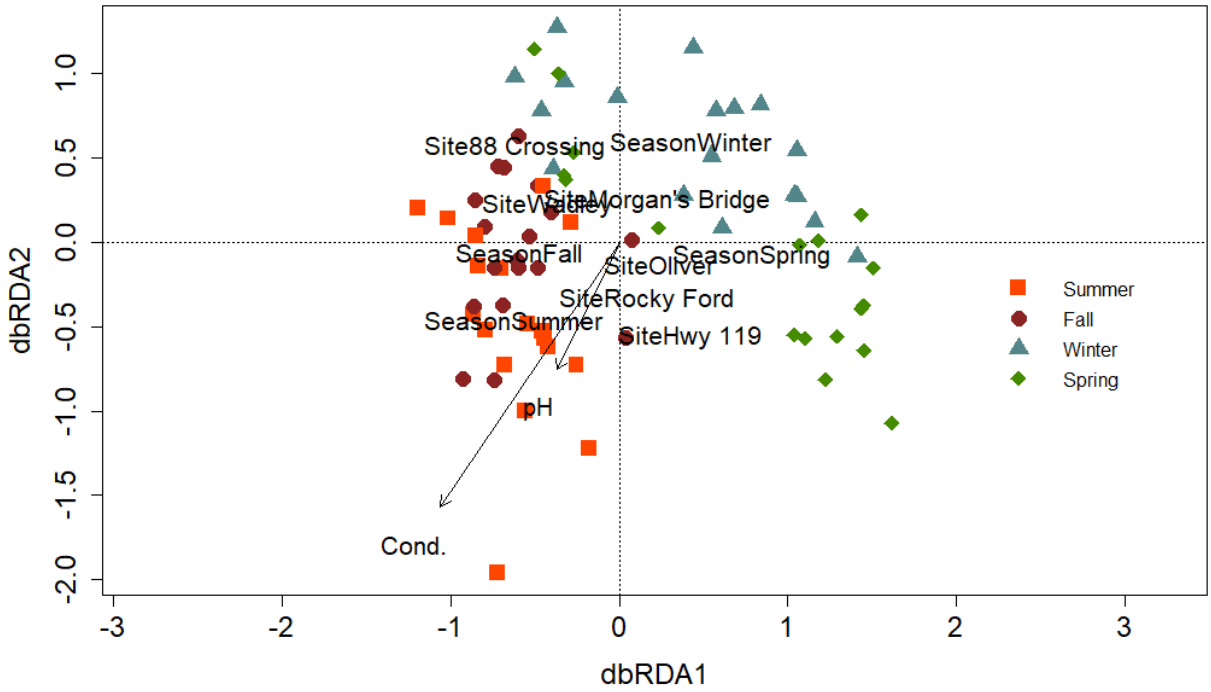

Figure 2.3. dbRDA plot for macroinvertebrate relative abundance data with samples as points colored by their season, arrows denoting the ordination of continuous constraints and labels for the centroids of sites and seasons.

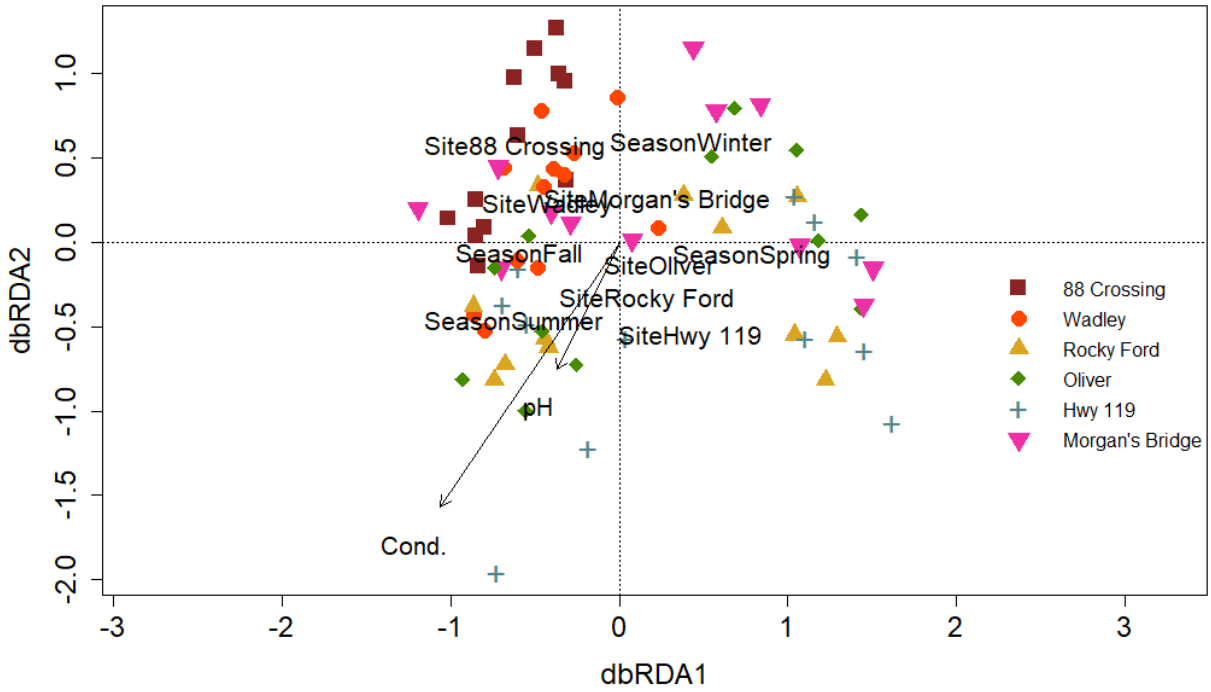

Figure 2.4. dbRDA plot for macroinvertebrate relative abundance data with samples as points colored by their site, arrows denoting the ordination of continuous constraints and labels for the centroids of sites and seasons.

CHAPTER 3

INFERRING FOOD WEBS FROM LITERATURE SOURCES TO ANALYZE SPATIAL AND TEMPORAL VARIATION IN FOOD WEB STRUCTURE

INTRODUCTION

Community composition has a long history of use in bioassessment and applied community ecology, but strides have been made to expand other measures that incorporate ecosystem processes and function (Usseglio-Polatera et al. 2000, Gessner and Chauvet 2002, Friberg et al. 2011). One new approach has been to incorporate food webs, due to their ability to detect interactions within larger systems and to tie compositional data to overall function (Gray et al. 2014). The Ogeechee River's invertebrate food web has been previously studied based on the snag habitat at a single site (Wallace et al. 1987, Benke and Wallace 2015, Benke 2018), but knowledge of the longitudinal and temporal variation in the river are limited. Greater study of the river across time and space would be useful for detecting and understanding environmental impacts. In-depth study of the river like that used by Benke and Wallace (2015) is too labor intensive for biomonitoring, but using inferred food webs based on known feeding relationships is an increasingly popular method (Schneider 1997, Gray et al. 2015, Lu et al. 2016, Thompson et al. 2018) and is more feasible for rapid monitoring.

Food Webs

Food webs have a number of topological properties that fluctuate predictably in response to external factors and can impact the stability of ecological systems (Dunne 2009). Early research into food web properties suggested that many of these properties were scale invariant (Briand and Cohen 1984), but later research suggested that scale invariance was the result of methodological issues such as low taxonomic resolution, binning of phylogenetically or functionally related taxa, ignoring age structure and

inadequate documentation of diets and interactions (Martinez 1991, Polis 1991). These results spurred further research into the patterns of variation in food web properties using larger, more detailed webs.

The qualitative network structure of a food web, often referred to as its topology, revolves around species, represented by nodes, and species trophic interactions, represented by links between nodes. The number of nodes (S) in a web represents the species richness or web size, while the number of links (L) are a basic measure of its connectivity (Dunne 2009). Complexity and connectivity of a web can be studied using multiple properties, such as the linkage distributions and clustering coefficients, but the most commonly studied are links per species and connectance. Links per species, also known as linkage density, is calculated as L/S, while connectance, the proportion of links out of all possible links, is calculated as L/S^2 (Dunne 2009). Connectance is of importance to conservation as high connectance reduces the rate of species lost to secondary extinctions when a system is subject to primary extinctions (Dunne et al. 2002b). Connectance tends to be low, with one meta-analysis finding that connectance ranged from 0.026 to 0.315 (Dunne et al. 2002a).

To understand the trophic composition of food webs, scientists often compute proportions of different taxa. Proportions of basal, intermediate and top taxa are commonly investigated, where basal taxa are defined as web members that do not consume other organisms and top taxa are defined as web members that are not consumed by other organisms (Dunne 2009). Proportions of other groups such as cannibals and omnivores (defined as animals that feed on multiple trophic levels) are sometimes measured (Dunne 2009). Most commonly the ratio of prey to predators is measured by dividing the total of all species that are prey (bottom and intermediate species) by the total of all species that are predators (intermediate and top species) (Cohen 1977). Prey to predator ratios have been widely argued to be constant (Jeffries 2002, Donald and Anderson 2003), although this is subject to debate (Raia et al. 2007, Shulman and Chase 2007) and not generally reflected in stream food webs (Thompson and Townsend 1999, Schmid-Araya et al. 2002, McHugh et al. 2015).

Food chain length is a measure of the number of links from a basal taxon to a given taxon in a food chain, generally computed as mean chain length, the average of all food chain lengths for all taxa in a web (Dunne 2009). Food chain length is often estimated using stable isotopes. Mean trophic level is a related measure that is averaged from the individual trophic levels of all organisms in a web. It can be calculated in several ways based on the trophic levels of a species' prey (Dunne 2009). Many food web attributes are highly correlated and analysis of published webs suggests food web attributes covary, with connectance correlated to mean trophic level and proportion of intermediate species, and richness correlated with linkage density and mean chain length (Vermaat et al. 2009). Meta-analysis suggests that diversity and web size drive increases in links and linkage density and decreases in connectance based on power law relationships (Riede et al. 2010)

Structural Variation in Food Webs in Rivers

Understanding of the patterns of variation in food webs in lotic ecosystems draws on general hypotheses of food web structure proposed for a wide variety of systems. With regards to food chain length, three major hypotheses have been proposed; a) the ecosystem size hypothesis, in which increases in habitat size lead to increases in species richness which in turn increase food chain lengths, b) the productivity hypothesis, in which increases in available energy allow that energy to flow through more trophic levels without being completely metabolized, and c) the productive space hypothesis which combines the two (Post et al. 2000). These hypotheses are sometimes expanded to other structural properties. For instance, the ecosystem size hypothesis has found support in pitcher plant communities, where both food chain length and linkage density increased with pitcher size, corresponding to an increase is species richness (Baiser et al. 2012). In stream mesocosms, the ecosystem size hypothesis has also been supported, with mesocosms having smaller food chains than larger natural systems (Brown et al. 2011). In drying streams, decreases in habitat size led to lower richness, smaller food chain lengths and higher prey-predator ratios as predators went missing from streams faster than prey (McHugh et al. 2015). A study of large rivers found support for the ecosystem size hypothesis for food chain lengths and not the

productivity hypothesis, although only primary productivity was tested and not availability of allochthonous organic materials for decomposers (Sabo et al. 2010). However, this study linked the effects of the ecosystem size hypothesis to increased discharge variability in smaller rivers, suggesting that disturbance may be reducing food chain length (Sabo et al. 2010). On the other hand, in New Zealand, in a study of streams in pine forests (where allochthonous material is of low quality), open pastures and tussock, mean food chain length was found to increase with higher primary productivity but not with greater detrital food resources (Townsend et al. 1998, Thompson and Townsend 1999). Food chain length has also been correlated with primary productivity in arctic streams (Parker and Huryn 2013). Research on streams in New Zealand found support for both the productivity hypothesis in autotrophic streams and for the ecosystem size hypothesis in detritally based heterotrophic streams, but no trend that corresponded to both at once, as would be required by the productive space hypothesis (Thompson and Townsend 2005a).

Disturbance in lotic systems has been previously defined as disruptive events with a frequency and intensity outside of a predictable range, such as a spate in a stream where discharge is several standard deviations above average discharge for that time of year (Resh et al. 1988). However, predictable events are sometimes considered disturbances, based on physical impacts and ecological responses (Poff 1992). Disturbance from flooding has been shown to decrease stability of post-disturbance food webs, making them more vulnerable to secondary extinctions (Calizza et al. 2015). Linkage density and connectance were negatively correlated with percent bed movement, a measure of hydrologic disturbance, in arctic streams (Parker and Huryn 2013). In New Zealand streams, links down per species (links between a species and its prey) have been found to decrease with disturbance due to reductions in species richness (Townsend et al. 1998). Opposite effects have been suggested from modeling and experimentation in California rivers, where preventing floods led to dominance of predator resistant, competitive caddisflies, reducing algal productivity and therefore potentially shrinking web size and other associated food web properties (Wootton et al. 1996).

Habitat has also been implicated in structuring benthic food webs. Heterogeneity of habitat has been found to contribute to variation in species richness and connectance of stream food webs at patch and reach scales (Thompson and Townsend 2005b). Landscape-scale variation also contributes to variation within aquatic systems. Latitude-dependent climate variables have been found to impact a wide range of food web structural variables in phytotelmata at a continental scale (Baiser et al. 2012) and large-scale longitudinal changes in species richness and connectance in rivers have been documented in response to changes in physiography (Romanuk et al. 2006).

The presence or absence of predators can often have major impact on food webs, expanding food chains and shifting the species composition and diets of other food web members. In addition to increasing mean food chain length, the arrival of a single generalist predator can cause large increases in the number of links and amount of omnivory in a web (Woodward and Hildrew 2001). Predators can also facilitate other ecological patterns, such as whether increases in productivity drive increases in food chain length (Parker and Huryn 2013). In the presence of disturbances which reduce predator resistant dominant taxa, predators can enhance productivity and available food by reducing grazing pressure on algae, although larger predators can also exclude smaller predators, negatively impacting supply of basal resources (Power et al. 2008). The dynamic effect of predation makes its impact hard to generalize, but it needs to be considered when analyzing patterns in web structure.

Food Web Variation

Food webs can be highly seasonal, with yearlong summary web structure not reflecting the webs of discrete time periods. Summary webs overestimate richness, number of links and links down per species, and average food chain length values for different seasons in autotrophic streams (Thompson and Townsend 1999), and overestimate links, linkage density, proportions of intermediate species and connectance in heterotrophic streams (Tavares-Cromar and Williams 1996). Taxa that occur in certain seasons but not others can alter species richness and number of links, and therefore connectance

(Thompson and Townsend 1999). Prey-predator ratios have been found to be higher in the summer and autumn compared to winter and spring due to increases in richness in the warmer months (Thompson and Townsend 1999, Schmid-Araya et al. 2002).

The seasonality of these webs can be based on several factors other than shifts in community composition. Thompson and Townsend (1999) found seasonal variation in most food-web properties based on availability of food resources such as gross primary production or organic matter. Ontogeny of stream invertebrates can lead to diet shifts, inactivity, immigration and emigration at certain times of year. Seasonal shifts in proportions of top, intermediate and basal species in Ontario food webs were attributable to ontogenetic diet shifts (Tavares-Cromar and Williams 1996). In a Texas saltmarsh Akin and Winemiller (2006) found seasonal shifts in diet came from a combination of growth and migration, with increases in connectance and mean trophic level as developing fish grew into the size range of larger predators. Combined with community structural shifts, these effects could severely alter trophic relationships and the vulnerabilities of these systems.

Objectives

The Ogeechee and other rivers in the Southeastern Coastal Plain could be better managed for fisheries, recreation and water resources with a more complete understanding of the natural variation of species interactions within food webs. I constructed food webs based on known interactions from the literature to understand whether consistent estimates could be garnered from biomonitoring data and whether those inferred interactions varied across sites and seasons. Number of links and linkage density are often highly correlated with food web size and as such I expect them to behave similarly. Both are reduced with disturbance and therefore higher discharge in the winter and may be higher in the summer and fall when discharge is lower, and many invertebrates are active and productive. Transitional periods like spring and autumn may support both flooding and baseflow adapted taxa, so it is possible that one or both periods support more taxa and more links. Connectance is likely to exhibit similar trends, being

higher during periods of lower discharge and disturbance, and when assemblages are more diverse and interactions are higher, likely in the summer (Thompson and Townsend 1999). However, connectance is sometimes negatively correlated with richness and therefore linkage density, so it is possible that the opposite will be found (Parker and Huryn 2013). Length of food chains has been well studied and is likely to increase with productivity and decrease with disturbance and is therefore likely to be higher in the summer and autumn. Prey-predator ratios may also decrease with diversity and therefore behave similarly to links and linkage density as found by McHugh et al. (2015) but may possibly be constant, depending on whether prey diversity drops with predator diversity or not. If prey-predator ratios vary with season but not with other effects, it may indicate ontogenetic effects which might be reflected in community composition analysis. Proportion of intermediate taxa and top taxa may depend on ontogeny and intermediate taxa are more likely to occur in seasons where top taxa are large enough to consume at higher trophic levels, so possibly in the summer or autumn (Tavares-Cromar and Williams 1996).

Potential for use of Food Web Metrics in Biomonitoring

Food web metrics, particularly from inferred data, have been proposed for bioassessment (Gray et al. 2014, Morales-Castilla et al. 2015). Due to the heavy dependence of certain food web metrics on community structure estimates such as species richness (Bengtsson 1994, Dunne et al. 2002a) and concerns about the reliability of inferred food web estimates, it remains possible that inferred food webs, at least at present, may not add anything to current monitoring schemes. Therefore, it is important to determine if food web metrics can detect changes that community-based metrics cannot detect just as well or better. I anticipate that several of the metrics, as mentioned above, will exhibit changes, but that those changes will be tied to compositional metrics such as species richness, which will outperform the food web metrics.

METHODS

Food webs were constructed from the sample assemblages collected in Chapter 2. The 500-µm sieves used in collection of those samples fail to collect meiofauna, which have been found to contribute greatly to some stream webs (Schmid-Araya et al. 2002). Therefore, the invertebrate sub-web may underrepresent both links and nodes from low-level consumers. Fish and other vertebrate consumers were also unrepresented, which would underestimate higher level consumers and food chain lengths. Food web research in New Zealand streams suggests that pooling samples from patchy habitats into one reach-wide sample may lead to overestimates of number of links and prey-predator ratios and underestimates of connectance due to pooling intermediate consumers that are highly linked but do not always occur in the same microhabitats (Thompson and Townsend 2005b). However, the study also found greater variation between reaches than between patches within reaches, suggesting that differences between samples may still be evident regardless of pooling of sub samples.

Taxonomic resolution can have a significant impact on food web metrics. Martinez (1991) found that successive aggregation of species within his food web in Little Rock Lake, Wisconsin initially overestimated and then underestimated connectance and linkage density, while prey-predator ratios exhibited an opposite trend of initial underestimation followed by over estimation as taxonomic aggregation increased. Food chain lengths were always underestimated. This was due to initially aggregating trophically redundant species, and then clustering trophically dissimilar species (Martinez 1991). Further research confirmed that reducing to trophically redundant species lead to lower percentages of top taxa, higher percentages of basal and intermediate taxa, and higher connectance, while further reduction led to decreases in linkage density, proportion of intermediate taxa and food chain length, and increases in proportions of basal and top taxa (Martinez 1993). However, these results are not always reflected in streams, where connectance may increase with less resolution but most other properties remain fairly constant (Thompson and Townsend 2000). Additionally, inconsistent resolution that bins certain species such as algae into a single group leads to lower connectance, prey-predator ratios and linkage density (Thompson and Townsend 2000). This should not interfere much with between-

sample comparisons if invertebrate species are consistently identified to the same taxonomic levels and if community composition doesn't shift toward low resolution groups such as oligochaetes. Absolute values of food web characteristics may be off, with some potential for under or overestimating connectance and underestimating linkage density.

Food Web Construction

I constructed food webs using the WebBuilder R function (Gray et al. 2015) based on presence/absence data collected from Ogeechee River samples and a custom database of known feeding interactions from the literature. The database (Figure 3.1) and associated forms were built and run in Microsoft Access (2016) so that they could easily be added to by non-experts. Following the format of Gray et al. (2015), the database tracked consumer and resource taxa, their taxonomic classification (genus, subfamily, family, order, class) as well as category (Invertebrate, Vertebrate, Algae, etc.), life stage, evidence for the link between consumers and resources (observed, inferred) and the literature source for the interaction (including authors, journal information, date of publication and the title of the article). Taxonomic information was verified using the Global Names Resolver (http://resolver.globalnames.biodinfo.org/), but contrary to Gray et al. (2015), the Integrated Taxonomic Information System (ITIS) was used as the primary dataset instead of Global Biodiversity Information Facility (GBIF), as it was more up to date for North American taxa. Wallace et al. (1987) have done previous work on the lower portion of the river near the bottom two most sites, and have dietary data for primary consumers, as well as caddisflies and predators (Benke and Wallace 1997, Benke et al. 2001). Additional literature was found using online database searches for individual taxa and their close relatives (same genus or family) found in the samples as well as large published food webs from continental North America, with emphasis on the southeastern United States. Basal resources were binned into major resource groups including filamentous algae, unicellular algae, vascular plant detritus, amorphous detritus, wood, fungi and diatoms. Basal resources such as algal species being aggregated can skew their proportion of basal to intermediate species and as such would not be reliable for further analysis

(Martinez 1991). Similar problems may occur for species whose diets are inferred by binning taxonomic or functional feeding groups, which could lead to overestimating links. Web structural properties were calculated in R using the cheddar package for food web analysis (Hudson et al. 2013, R Development Core Team 2017). Structural features generated included number of links, nodes, linkage density, directed connectance, mean chain length, prey to predator ratio, proportion of intermediate nodes and proportion of top nodes. Isolated nodes that had no links to any other nodes were excluded from prey to predator ratios and proportion of intermediate and top nodes. Directed connectance assumes basal resources can act as consumers, even though this is not always realistic. Jaarsma et al. (1998) excluded impossible basal resource links from their calculation of connectance, as did studies that followed (Thompson and Townsend 1999, 2000, 2005a, 2005b), but other food web research has not. Compared to studies where basal consumption links are excluded from connectance calculations, these results may be somewhat underestimated.

Food web analyses

Linear mixed effects models were constructed in R (R Development Core Team 2017) using the nlme (Pinheiro et al. 2018) and lme4 (Bates et al. 2015) packages, including sites and seasons as fixed effects and year as a random effect, as was done for physicochemical variables and diversity measurements in Chapter 2. Interactions between site and season were tested and omitted if insignificant. Year was omitted from the model if it did not improve the model fit, and residuals were checked for normality and homoskedasticity, as in Chapter 2. Number of links was log transformed to ensure normality. Models were used to test richness, number of links, linkage density, connectance, mean food chain length, percentage of top and intermediate taxa and prey-predator ratios. Food web metrics, especially connectance, number of links and linkage density, can be dependent on species richness. Thus, I corrected variables with significant effects using log-log regressions of each metric with number of nodes and reran linear mixed models on their residuals to see if patterns persisted (Bengtsson 1994). Regressions were performed in R using the lm function.

I performed PCA on correlations of the food web properties and diversity metrics to examine the structure of the data. Total number of taxa, Shannon's index, number of links, linkage density, directed connectance, mean chain length, prey to predator ratios and proportion of intermediate nodes were included in the PCA. Proportion of top nodes and basal nodes were excluded because they were both dependent on the proportion of intermediate nodes, since basal nodes were binned food categories. PERMANOVA (Clarke and Gorley 2015) was used to further examine differences between groups, using site, season and year as fixed effects, since there was some heterogeneity of multivariate normality. I used PERMDISP (Anderson and Walsh 2013) to check for heterogeneity of dispersion.

RESULTS

Interaction database

The final database contained 3373 recorded interactions from 74 sources (Appendix A), and 540 taxa were recorded in the database (Table 3.1). Some of these were of high taxonomic rank, up to order or class, due to binning or poor taxonomic resolution in the source literature, particularly for resource taxa. To assess the completeness of the database with respect to Ogeechee River food webs, I calculated the number of isolated nodes in each food web (Figure 3.2). A mean of 13.27% (standard deviation 2.97%, standard error 0.35%) of nodes in a food web were isolated in each food web. Some of these may have been basal resources, which were assumed to occur but were not recorded. Isolated nodes do not give information about taxa with only some of their links missing or feeding relationships that do not occur in nature but were assumed by WebBuilder, and thus do not provide us with a complete picture of how well food webs infer links.

Food web metrics

Number of links declined at downstream sites ($F_{5,61} = 4.708$, $p = 0.0011$) (Figure 3.3) but did not perceptibly change across seasons ($F_{3,61} = 1.237$, $p = 0.3042$). Linkage density was similar, with differences by site ($F_{5,66} = 2.7819$, $p = 0.0247$) but not by season ($F_{3,63} = 0.2674$, $p = 0.8486$). R119 was

especially lower than the other sites (Figure 3.3) as it was when measuring the number of links. Neither site ($F_{5,66} = 1.5193$, $p = 0.1966$) nor season ($F_{3.63} = 2.6391$, $p = 0.0571$) was significantly different for directed connectance, although seasonal changes were marginally significant in response to a 0.01 increase in connectance in the winter and spring (Figure 3.4). Low species richness drives increases in connectance (Riede et al. 2010, Parker and Huryn 2013) in small food webs because the number of potential links (S^2) is small relative to larger webs, so actual links make up a larger portion of total links. High connectance may therefore be an artifact of the small size of individual samples, and the lower diversity of winter and spring. Mean chain length also differed by site ($F_{5,61} = 3.4030$, $p = 0.0089$) but not season ($F_{3,61} = 0.98322$, $p = 0.4067$). R88 had longer food chains than all other sites and MO and especially R119 had shorter food chains (Figure 3.5), mirroring the trend in taxonomic richness across sites. Prey to predator ratios didn't change between sites ($F_{5,66} = 0.2975$, $p = 0.9125$) and were only marginally significant between seasons ($F_{3,63} = 2.6199$, $p = 0.0585$), with little difference in means, compared to the amount of variance (Figure 3.6, Table 3.2). There were no significant differences between sites for proportions of intermediate nodes ($F_{5,66} = 0.2154$, $p = 0.9547$) or top nodes ($F_{5,66} = 0.1127$, $p = 0.9892$), nor were there significant seasonal differences (intermediate $F_{3.63} = 2.1336$, $p = 0.1048$; top $F_{3,63} = 2.3193$, $p =0.0839$). Given that basal resources were fixed, proportions of top nodes and intermediate nodes had an inverse linear relationship, the slight variability between the two was due to isolated basal nodes that were excluded from calculations, slightly shifting the proportions of both.

Log-log regressions for properties that depended on significant or marginally significant factors including number of links ($R^2 = 0.7912$, $F_{1,70} = 265.3$, $p < 0.0001$), linkage density ($R^2 = 0.3896$, $F_{1,70} = 44.67$, $p < 0.0001$), directed connectance ($R^2 = 0.1086$, $F_{1,70} = 8.532$, $p < 0.0047$) and mean chain length ($R^2 = 0.3273$, $F_{1,70} = 34.06$, $p < 0.0001$) were significant, but prey to predator ratios were not ($R^2 = 0.02766$, $F_{1,70} = 1.992$, $p = 0.1626$). After rerunning models on the log-log residuals, number of links and linkage density were equivalent, having effectively removed the denominator from linkage density when regressing against nodes and were no longer different between sites ($F_{5,66} = 1.4613$, $p = 0.2152$) (Figure

3.3). Directed connectance's seasonal differences were no longer even marginally significant ($F_{3,63}$ = 1.2768, p = 0.2900). However unlike number of links and linkage density, the trend remained consistent (Figure 3.4). This suggests that either the data were inconclusive to begin with, that it lacked the power to detect differences but was not entirely dependent on richness, or that the relationship between taxonomic richness and connectance was not linear and was not corrected for properly. Mean chain length was also no longer significant ($F_{5,66}$ = 1.3002, p = 0.2753) and differences between sites both before and after correction (Figure 3.5) were similar to the behavior of number of links and linkage density (Figure 3.3). Prey to predator ratios, which are not dependent on species richness and consequently did not have a significant regression against number of nodes in the food web, still had marginally significant differences across seasons ($F_{3,63}$ = 2.6351, p = 0.0574) and the position of the data was relatively well preserved (Figure 3.6).

No real structure was observed in the PCA plot (Figure 3.7) with respect to sites or seasons, and the first component explained 56% of the variance, while the second component explained another 23%. The first principal component correlated most strongly with number of links, linkage density and mean chain length, with the latter two being strongly dependent on the former two, while the second principal component correlated most with diversity metrics, connectance and prey to predator ratios. A PERMANOVA test produced highly significant effects of site (perm-$F_{5,61}$ = 4.2321, p = 0.0010), but not season (perm-$F_{3,61}$ = 1.2273, p = 0.3067). Year was marginally significant (perm-$F_{2,61}$ = 2.5482, p = 0.0751). These differences mirrored univariate differences between sites driven by taxonomic richness. When repeated with response variables corrected via a log-log regression against number of nodes, sites were no longer significantly different (perm-$F_{5,61}$ = 1.4929, p = 0.1513) but seasons were marginally different ($F_{3,61}$ = 1.8449, p = 0.0956), perhaps reflecting the seasonal differences in metrics such as prey to predator ratios that were insensitive to food web metrics and the evenness component of the Shannon index. Year was significantly different ($F_{2,61}$ = 9.1683, p = 0.0001) suggesting interannual variation or

identifier artefacts that caused differences in community composition which drove evenness and prey to predator ratio differences.

DISCUSSION

Of all the variation in food web structure, most was marginally significant ($0.05 < p < 0.1$) or only weakly significant ($0.01 < p < 0.05$), and effect sizes were generally small, which brings in to question the reliability of these differences. Many of the stronger relationships, such as the number of links and mean chain length, were dependent on taxonomic richness. Number of links, and linkage density behaved similarly and were different across sites, but the relationship completely disappeared after controlling for the influence of number of nodes in the food web. While I had expected variation to be dependent on taxonomic richness, I had anticipated seasonal differences, but despite lower diversity in the winter and spring the only significant differences were between sites. Winter and spring do have fewer links (Table 3.2), so perhaps some of the differences were simply too noisy or weak to translate from taxonomic richness. Another possibility is that fauna that differed between sites, but not seasons, were either better or more poorly represented in the database. Connectance was stable and only exhibited marginal increases in the spring and winter, which were dependent on taxonomic richness. I had expected that connectance might increase with web size as it does in some webs (Thompson and Townsend 1999) or decrease with web size as an artefact of small web size, and it appears to have done the latter, as Parker and Huryn (2013) reported similar effects with web sizes of around ~30. My webs were only slightly larger and inferring links may have exacerbated the problem if common taxa found in most webs had overrepresented numbers of interactions or rare taxa found mostly in larger webs had underrepresented numbers of interactions. When controlling for web size, the relationship became non-significant but persisted. This may have been due to a non-linear relationship, as connectance is based partially on the square of the number of nodes in a food web, but it is unclear how to examine connectance independent of taxonomic richness without obliterating much of the meaning of the property. Relatively invariable connectance is not surprising for a single river, and connectance is more robust to aggregation than other

measurements, so might be more reliable (Martinez 1991). Mean chain length was also different between sites, with longer food chains upstream at more taxon rich sites, and not between seasons as I had expected. The relationship became non-significant when regressed against number of nodes, indicating dependence on web size. It is possible that larger mean chain lengths were indicative of more complete webs with more links between consumers, rather than just links between consumers and basal resources or totally isolated nodes of consumers that had no inferred feeding relationships. More predators represented could also increase mean chain length as it often does (Woodward and Hildrew 2001, Parker and Huryn 2013), but given the lack of similar patterns in prey to predator ratios, it is possible that the pattern is purely a case of increasing numbers of nodes adding and increasing number of links, leading to more opportunities for chains of links. The PCA (Figure 3.7) corroborates this, as mean chain length and linkage density were both very correlated to the first PCA axis.

Prey to predator ratios followed a different pattern from other food-web metrics. Prey to predator ratios were not dependent on web size, and differed between seasons, although the difference was only marginally significant, and may not have been reliable. I had predicted seasonal variation but had suggested that smaller web sizes in the winter and spring might increase prey to predator ratios. Instead prey to predator ratios were lowest in the winter and the differences were unaffected by web size. Lower ratios may have been due to fewer predators present in the winter leading to more primary or low-level consumers being interpreted as predators but not as prey in calculation. This could even be an artefact of subsampling, which could fail to detect smaller intermediate level predators when certain primary consumers were dominant in the winter. Alternatively, it could simply be a phenological effect on community composition, where certain taxa are missing from the system at different times of year due to ontogeny, either fewer predators during the winter (and to a lesser degree the summer) or more primary consumers during the spring and fall. Ontogeny and phenology have been found to affect temporal variation in food webs (Tavares-Cromar and Williams 1996, Akin and Winemiller 2006). Despite the similarities between proportions of intermediate taxa, proportions of top taxa and prey to predator ratios,

the former two structural components didn't exhibit significant trends, they were noisier metrics that inversely proportional due to basal resources being relatively fixed.

Most differences, particularly between sites, were driven by taxonomic richness, which suggests that most variation in food web structure along the Ogeechee River is not dependent on shifts in taxonomic composition between differently connected taxa. Given the reliance on a few general basal resources of many Ogeechee River taxa (Wallace et al. 1987, Benke and Wallace 2015) and the generalist diets of most invertebrate predators in the river (Benke and Wallace 1997, Benke et al. 2001), this result is not surprising. The importance of web size in driving food web structure was not just visible in the impact of log-log regressions of structural properties against number of nodes, but in the ordination of structural properties. The first axis of the ordination explained most of the variation among samples, but interestingly was more strongly related to links, linkage density and mean chain length. While these are all dependent on web size, and therefore taxonomic richness, the strength of the relationship suggests that the major spatial gradient of food web structure in the Ogeechee is complexity. PERMANOVA seemed to support this as site, but not season, had significant effects on food web structure. The same result was observed with links, linkage density, and mean chain length, which were strongly explained by the first PCA axis. Prey to predator ratios only had seasonal variation and diversity metrics had both site and seasonal variation, and both were explained less well by the first principal component and were partially explained by the second principal component. The effect of web size is commonly reported in food webs (Bengtsson 1994, Thompson and Townsend 1999, Vermaat et al. 2009, McHugh et al. 2015) although it is not always consistent between studies. Diversity dependence of food web structure is natural, but the dependence visible here may have been affected by features of the interaction database. Taxa with more recorded interactions in the database due to more available literature, or taxa that were widely eaten, especially when binned to higher taxonomic levels (e.g. chironomid subfamilies) would help drive diversity. The more taxa in a food web, the greater the likelihood these link-rich taxa would be included, and the more complexity there would be. If subsamples were larger, or all interactions were known, then

it might turn out that different taxa are driving greater numbers of links or longer food chains, and that the importance of diversity is less important. If it is assumed that the effect is real, it might still be influenced by composition. Invertebrates at lower sites, where connectivity was less, might also be less widely palatable, and less diverse or lower quality prey might support less diverse secondary consumers and smaller, simpler webs overall. Further investigation into the component organisms within food webs might help to identify if that is the case.

Prey to predator ratios varied across seasons independently of taxonomic richness. On the PCA, prey to predator ratios were similar to connectance (Figure 3.7) which also varied by season in a marginally significant way. When the influence of richness was removed from the PERMANOVA analysis, seasons became highly significant, suggesting that prey to predator ratios drove that variation, and that taxonomic richness gradients had interfered with that variation. Prey to predator ratios have been found to vary with richness in response to habitat size (McHugh et al. 2015) and seasonal variation (Thompson and Townsend 1999, Schmid-Araya et al. 2002), changes in the ratio independent of those effects are uncommon. Prey to predator ratios are likely to be governed by community structure and are likely to be influenced by community composition metrics. Understanding these patterns would be useful for determining if prey to predator ratios might complement or be redundant with common biomonitoring metrics.

Compared to many other food webs in the literature (Dunne et al. 2002a), the average food web structure of the Ogeechee was not out of place. Despite being derived from small, incomplete webs, Ogeechee River connectance had a mean of 0.119 (SE±0.002), which was very similar to the average reported by Dunne et al. (2002a) and in the middle of the range used by Riede et al. (2010) and a linkage density of 4.21 (±0.09) was on the lower end for Dunne et al. (2002a) and Riede et al. (2010) but similar to linkage densities reported by Havens (1992). Mean chain lengths were also similar (Schmid-Araya et al. 2002) or higher (Thompson and Townsend 1998, Thompson and Townsend 2005a) than numbers reported elsewhere for freshwater invertebrate focused webs, with an average of 4.96 (SE±0.17) links

long. Prey to predator ratios were quite low compared to those found in other streams (Schmid-Araya et al. 2002, Thompson and Townsend 2005a, McHugh et al 2015) with an average of 0.828 (SE±0.013) that suggests more predators than prey on average. This is likely an artefact of excluding fish and binning basal taxa. Prey to predator ratios behaved opposite of seasonal patterns in Schmid-Araya et al. (2002), which didn't bin basal taxa or exclude fish, and had much higher proportions of top taxa and fewer intermediate taxa.

Interpretation of many of the metrics was hampered by possible artefacts of the interaction database and sampling protocol. It appears that the small subsamples used in rapid biomonitoring, while cost-effective for composition-based monitoring (Barbour and Gerritsen 1996) might be inadequate if managers want to make use of food web metrics. Identifying cost effective sample sizes for use with inferred food webs would require identifying how many rare taxa could be excluded while still getting usable results and then calibrating subsample sizes accordingly. The interaction database is also still relatively small and ill equipped for other regions, gaining access to more interaction data, especially from some of the more modern food web research that does not provide clear records of individual interactions, would improve performance considerably. Some groups had spotty records of interactions, for instance, very little literature identifies mollusks or oligochaetes as prey to other invertebrates, often due to difficulty identifying remains in gut contents. Other taxa have poor records of their diets, particularly predator-piercers and crustaceans, because they grind or liquify their food and are excluded from analysis (e.g. Hall et al. 2000). Lentic floodplain taxa and riverine taxa often don't have records of interaction despite overlap in sampling; further food web research may need to be done on these ecotones. Certain literature (e.g. Benke et al. 2001) bin taxa in certain interactions at very high taxonomic ranks (e.g. Zygoptera). These may overestimate interactions considerably and being able to replace them with higher resolution data would lead to better results. With these improvements, better estimates of basic structural properties would be possible. This includes potentially sensitive ones such as prey to predator

ratios, which might misrepresent prey as top predators if too many taxa have few interactions recorded. Finally, data from fish, macrophytes and algae would also be useful for more holistic management.

For the moment, it appears that food web structure provides no advantage over analysis of community structure for biomonitoring. Analysis of community structure in Chapter 2 discerned many differences across sites and seasons and did so with more certainty and reliability than food web metrics. On top of that, differences distinguished by food web metrics were redundant to community metrics. Community analysis may also provide better understanding of ecosystem function using functional feeding groups (Cummins 1973) and functional traits (Menezes et al. 2010). Responses of food web structure to diversity also mean that most of the results of food web analysis were predictable.

In the future, better databases could be used to perform more sophisticated data analyses. With mass or abundance estimates, inferred webs can be used to estimate trivariate measures such as link angles (Cohen et al. 2009) which have been used to identify impacts of chemical spills on the transfer of energy through food webs (Thompson et al. 2016), increases in biomass flux in restored river food webs (Thompson et al. 2018) and constrained feeding relationships in experimental drought food webs (Woodward et al. 2012). Inferred food webs can also be applied to investigate web substructure, such as investigating the impact of food web "cores" to understand how webs compensate for species loss (Lu et al. 2016). Even without improvements to the database, the food webs I generated could be applied to management by examining interactions to predict responses to management. Identifying resource pathways or potential keystone species by inspecting connectance webs could be used in decision making for fisheries management or if restoration is required. If the response of taxa to a certain management action is known, food webs can be used to understand how they will propagate through the system. For instance, Cross et al. (2013) suggested using the results of a flow food web study to increase fish production based on known relationships with their primary food sources. Therefore, it would be beneficial to communicate with managers about what priorities food web monitoring could facilitate.

The importance of taxonomic richness within food webs of the Ogeechee River further confirms the importance of biodiversity. Although food webs and their properties can impart robustness and resistance to collapse on an ecological community in response to events such as species extinctions or droughts (Dunne et al. 2002b, Lu et al. 2016), the maintenance of the complexity required to do so involves maintaining diversity. Promoting biodiversity and promoting stable food webs go hand in hand and it is important to manage for both if we are to secure both for the future.

Table 3.1. Number of taxa in the database at each taxonomic rank. There were 93 subfamilies, but this number was excluded due to certain families lacking subfamilies.

Taxonomic Rank	Number of Unique Entries
Total Taxa	540
Genera	320
Families	143
Orders	49
Classes	24

Table 3.2. Means (±SE) of food web structural properties for all samples in the Ogeechee River, as well as by site and season.

	Nodes	Links	Linkage Density	Directed Connectance	Mean Chain Length	Prey to Predator Ratio	Proportion of Intermediate Nodes	Proportion of Top Nodes
Ogeechee River	35.7 (±0.7)	153 (±6)	4.21 (±0.09)	0.119 (±0.002)	4.96 (±0.17)	0.828 (±0.013)	0.620 (±0.012)	0.267 (±0.011)
88 Crossing	38.8 (±2.1)	173 (±15)	4.39 (±0.20)	0.115 (±0.005)	6.07 (±0.52)	0.817 (±0.027)	0.615 (±0.024)	0.274 (±0.022)
Wadley	39.0 (±1.6)	171 (±12)	4.34 (±0.17)	0.112 (±0.003)	4.91 (±0.29)	0.806 (±0.030)	0.616 (±0.030)	0.279 (±0.028)
Rocky Ford	37.8 (±1.4)	174 (±13)	4.57 (±0.20)	0.122 (±0.005)	5.05 (±0.35)	0.817 (±0.027)	0.632 (±0.020)	0.267 (±0.022)
Oliver	34.8 (±1.5)	156 (±12)	4.44 (±0.24)	0.129 (±0.007)	4.94 (±0.28)	0.833 (±0.033)	0.639 (±0.035)	0.255 (±0.032)
Hwy 119	32.1 (±1.5)	119 (±11)	3.65 (±0.22)	0.115 (±0.006)	4.12 (±0.39)	0.848 (±0.029)	0.617 (±0.031)	0.257 (±0.027)
Morgan's Bridge	31.6 (±1.2)	125 (±11)	3.89 (±0.23)	0.123 (±0.006)	4.70 (±0.50)	0.846 (±0.047)	0.600 (±0.039)	0.268 (±0.039)
Summer	37.8 (±1.7)	161 (±11)	4.18 (±0.16)	0.112 (±0.004)	5.12 (±0.31)	0.820 (±0.030)	0.633 (±0.028)	0.264 (±0.027)
Fall	37.2 (±1.2)	161 (±11)	4.27 (±0.17)	0.115 (±0.003)	5.27 (±0.36)	0.852 (±0.023)	0.646 (±0.018)	0.244 (±0.018)
Winter	33.7 (±1.5)	142 (±12)	4.10 (±0.21)	0.122 (±0.005)	4.65 (±0.38)	0.772 (±0.024)	0.567 (±0.027)	0.317 (±0.023)
Spring	33.9 (±1.2)	148 (±11)	4.30 (±0.21)	0.128 (±0.005)	4.81 (±0.33)	0.868 (±0.023)	0.633 (±0.020)	0.242 (±0.019)

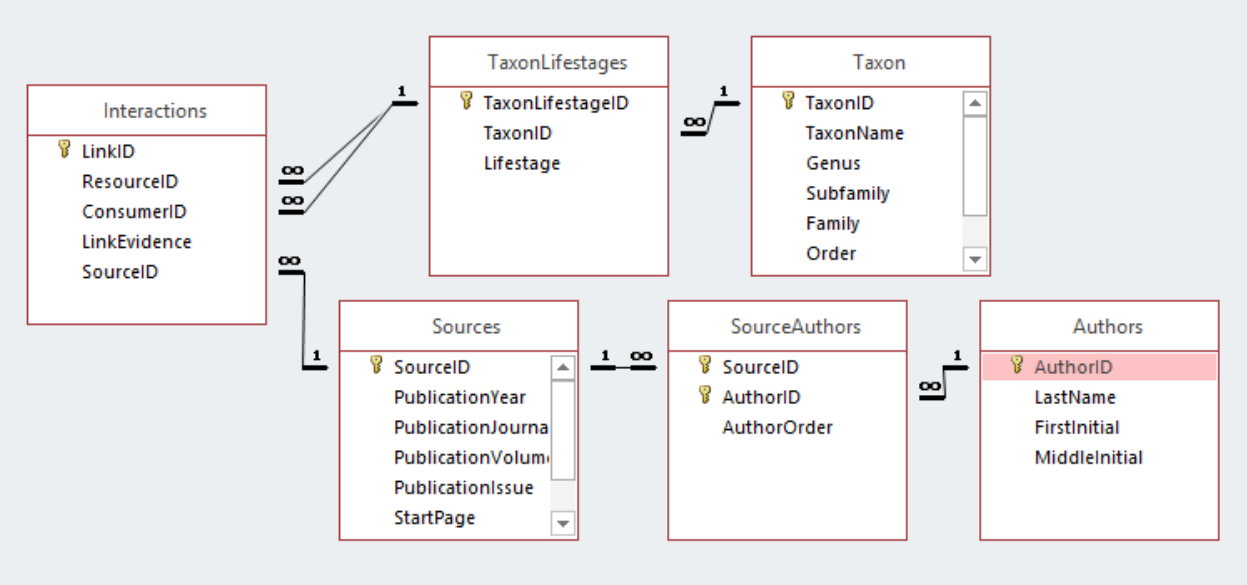

Figure 3.1. Structure of the feeding interaction database. Boxes are tables with their fields listed below the table name. Key images to the left of a field indicate primary keys. Black lines represent relations linking foreign keys to their primary keys in another table. ∞ symbols represent many and 1's represent one in a one-to-many relationship between tables. Interactions between consumers and their resources were recorded in a table along with the literature source for that record and information on whether the feeding relationship was observed or inferred. Both resource and consumer taxa had their taxonomy and life stages recorded in a pair of linked tables, with the table for each life stage linked to any interactions that life stage was recorded in. Reference sources were recorded with all their information except for authors, due to the many-to-many relationship between sources and authors, author information was stored separately and linked via an associative table.

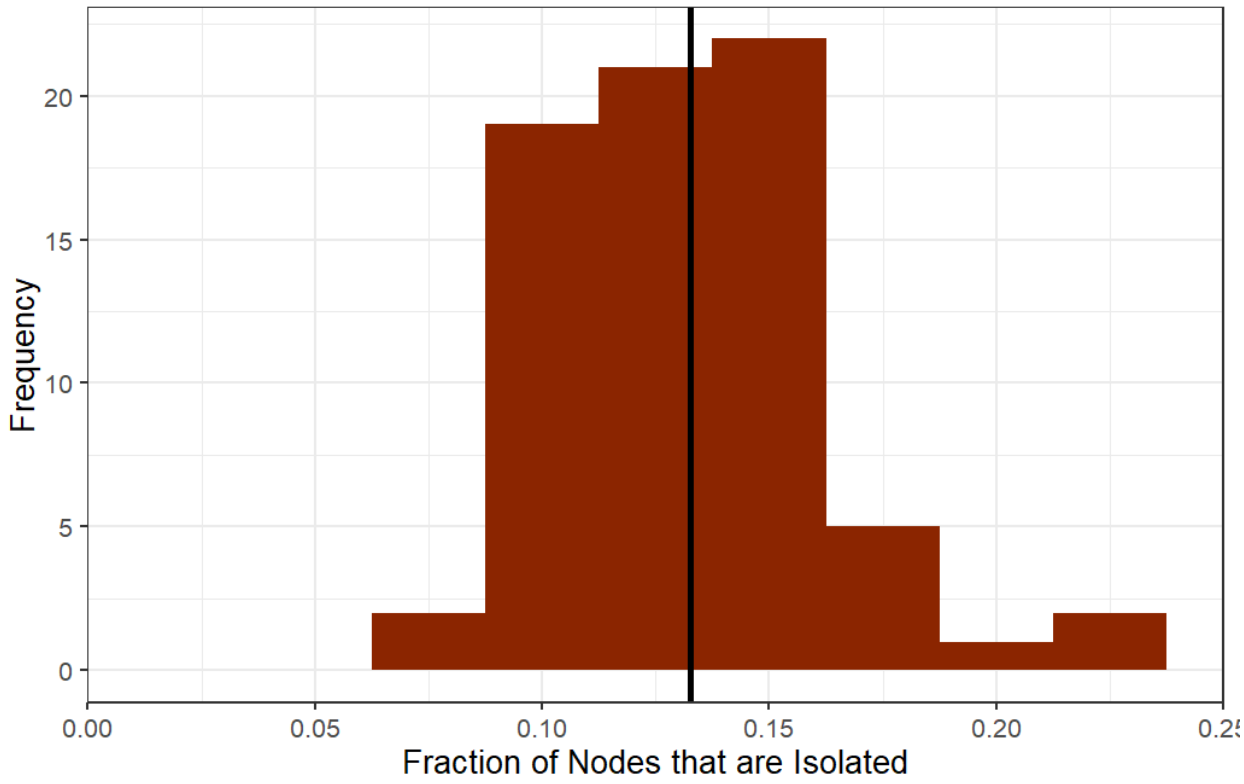

Figure 3.2. Histogram of the fraction of isolated nodes per sample food web. Bin widths are 0.025. The black line represents the mean, 0.133.

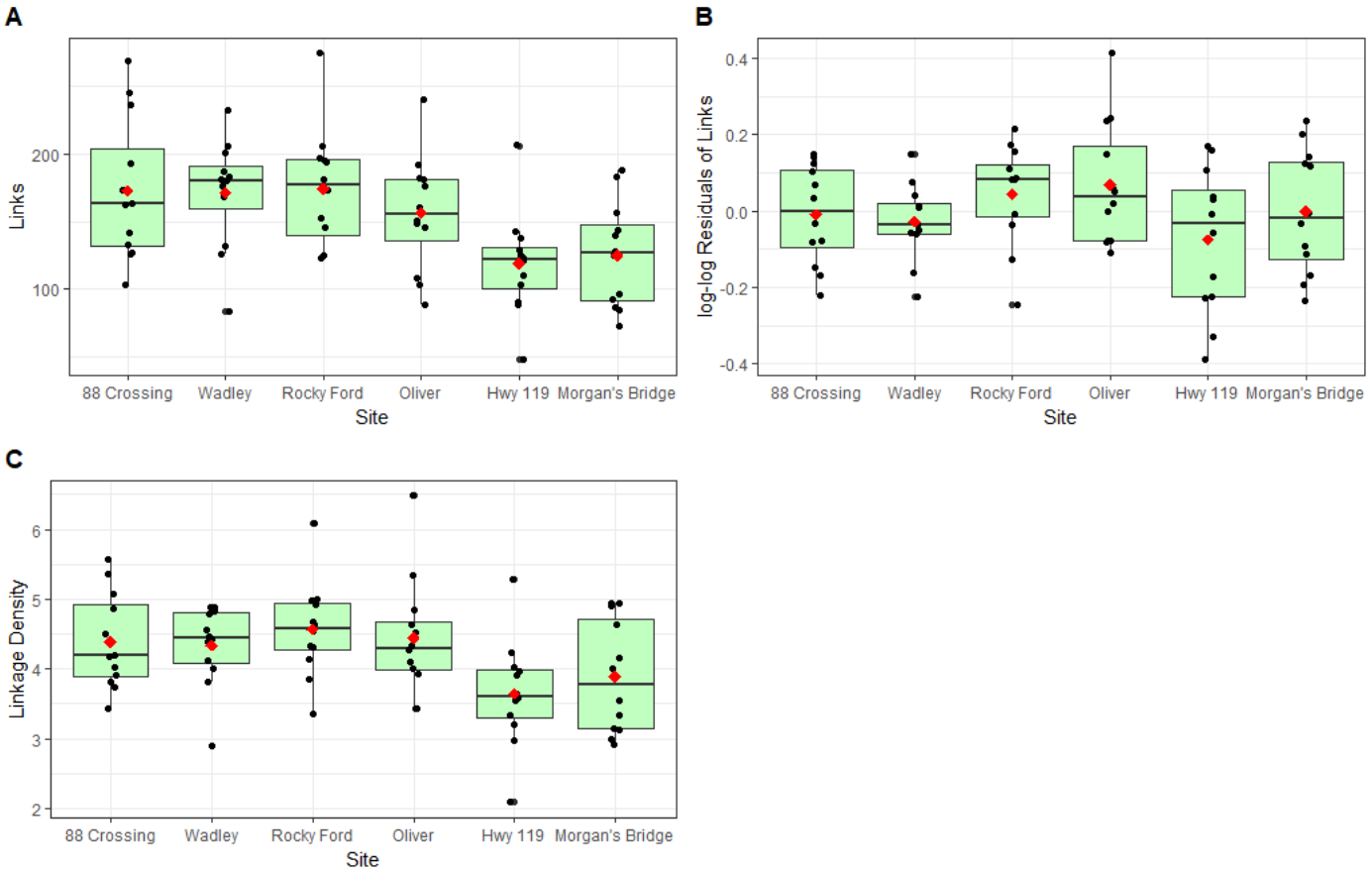

Figure 3.3. Box and whisker plots of (A) number of links, (B) residuals of links after a log-log regression against number of nodes, and (C) linkage density, grouped by site. Log-log regressions of linkage density were identical to those of links. Individual values are superimposed as black points. Red points represent group means.

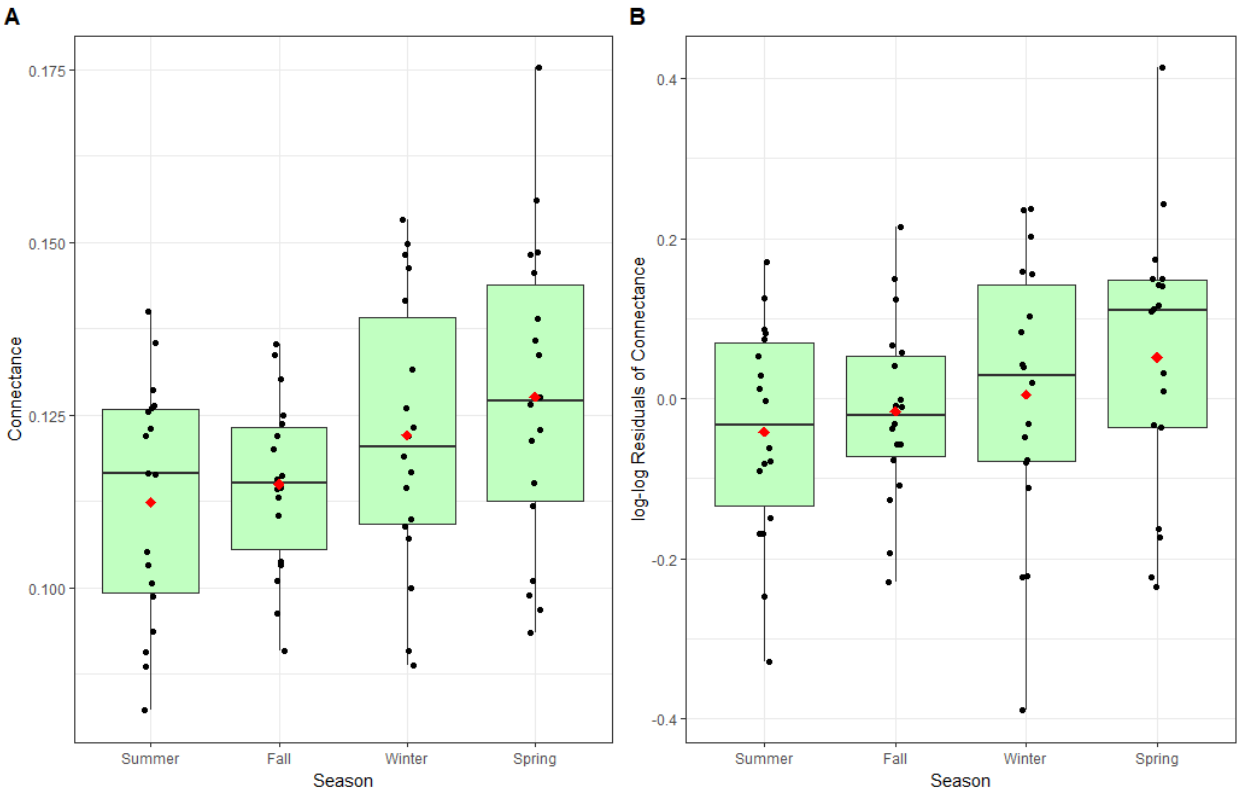

Figure 3.4. Box and whisker plots of (A) directed connectance, and (B) residuals of directed connectance after a log-log regression against number of nodes, grouped by season. Individual values are superimposed as black points. Red points represent group means.

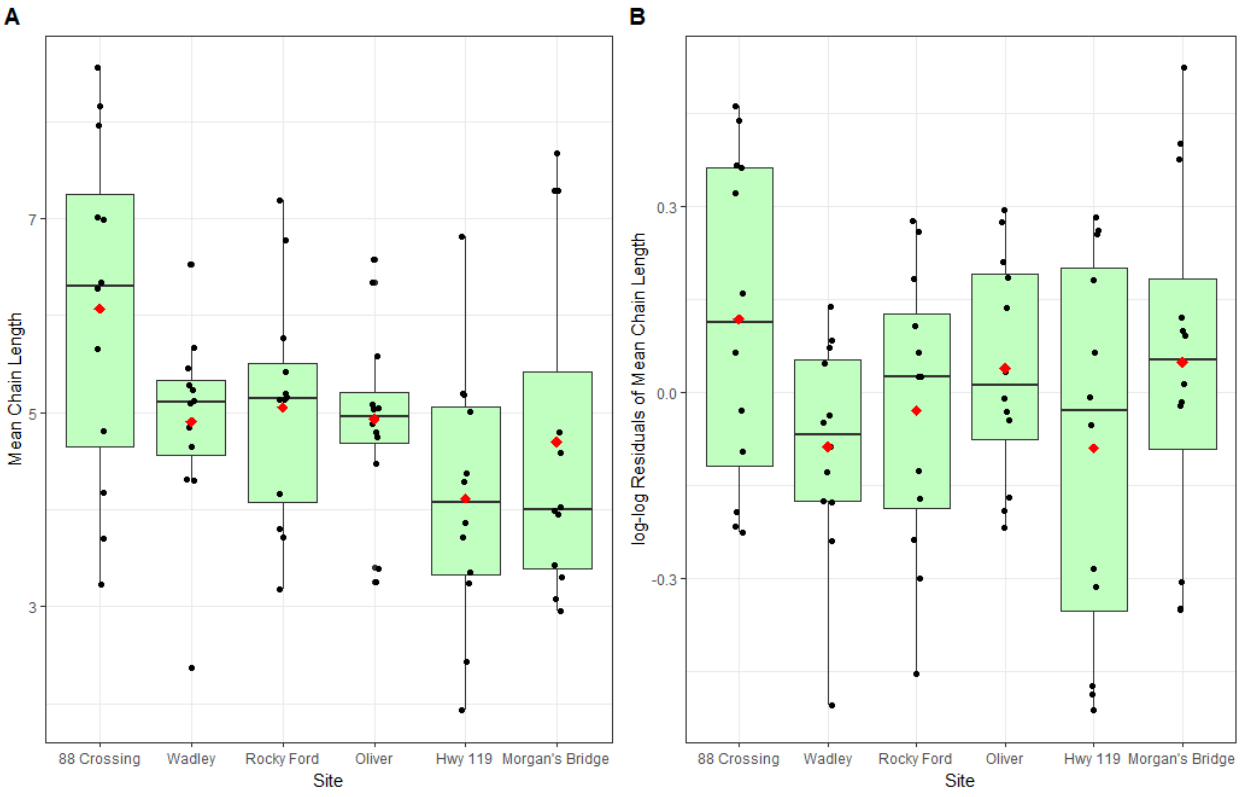

Figure 3.5. Box and whisker plots of (A) mean chain length, and (B) residuals of mean chain length after a log-log regression against number of nodes, grouped by site. Individual values are superimposed as black points. Red points represent group means.

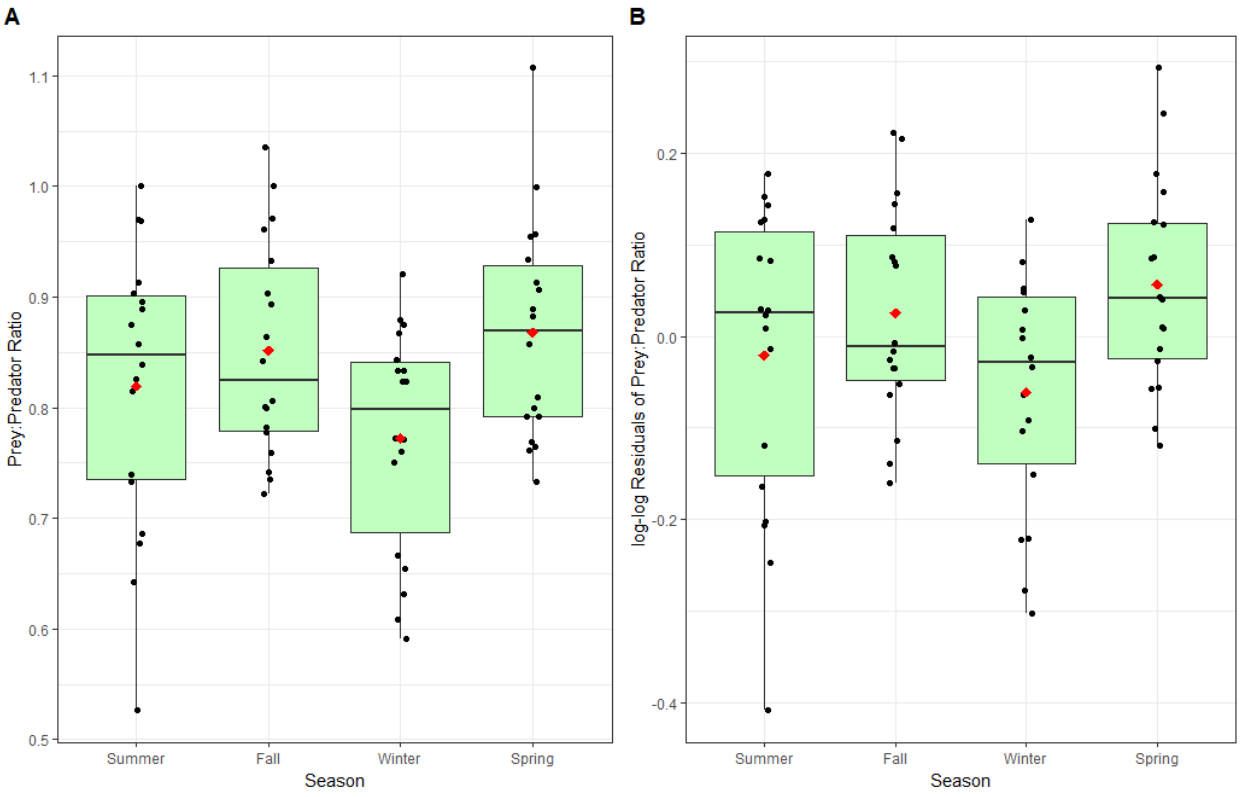

Figure 3.6. Box and whisker plots of (A) prey to predator ratios, and (B) residuals of prey to predator ratios after a log-log regression against number of nodes, grouped by season. Individual values are superimposed as black points. Red points represent group means.

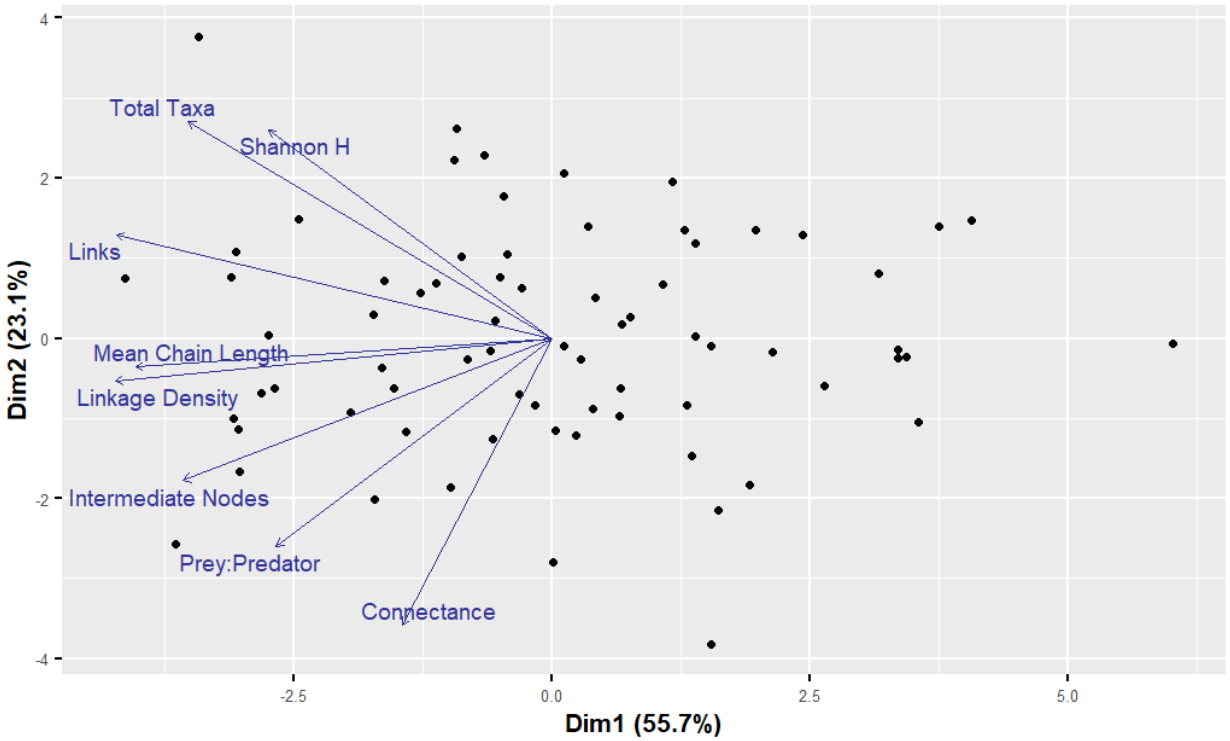

Figure 3.7. PCA on correlation biplot of total taxa, Shannon index, number of links, linkage density, directed connectance, mean chain length, prey to predator ratios and proportions of intermediate nodes, with factor loadings for each variable.

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APPENDIX A

INTERACTION DATABASE LITERATURE SOURCES

Literature used in the database, with the number interactions derived from each source and the number of taxa for which there were recorded interaction in each source. Taxa were sometimes binned into higher taxonomic groupings, especially as resources for other consumers, so there may be some double counting.

Reference	Interactions	Taxa
Armitage MJ, Young JO. The feeding biology of the triclad *Phagocata vitta* (Dugès): A laboratory study. Hydrobiologia 1991;215:63-72.	5	6
Beam BD, Wiggins GB. A comparative study of the biology of five species of *Neophylax* (Trichoptera: Limnephilidae) in southern Ontario. Canadian Journal of Zoology 1987;65(7):1741-1754.	15	8
Beck JT, Cowell BC. Life History and Ecology of the Freshwater Caridean Shrimp, *Palaemonetes paludosus* (Gibbes). The American Midland Naturalist 1976;96(1):52-65.	11	12
Beck K, Neves RJ. An Evaluation of Selective Feeding by Three Age-Groups of the Rainbow Mussel *Villosa iris*. North American Journal of Aquaculture 2003;65(3):203-209.	3	4
Beier S, Bolley M, Traunspurger W. Predator–prey interactions between *Dugesia gonocephala* and free-living nematodes. Freshwater Biology 2004;49(1):77-86.	1	2
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APPENDIX B

SITE SIMPER RESULTS

SIMPER results for within site similarities and among season dissimilarities, cutting off at a cumulative 80% similarity or dissimilarity to omit low contributing or rare taxa.

Group 88 Crossing

Average similarity: 49.77

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironominae	7.4	9.52	3.5	19.13	19.13
Tanypodinae	5.13	6.34	2.27	12.75	31.88
Hydrobiidae	3.83	4.63	2.36	9.31	41.18
Orthocladiinae	3.19	3.11	2.01	6.26	47.44
Copepoda	2.21	2.47	1.31	4.97	52.42
Hydrachnidiae	2.54	2.4	1.81	4.83	57.24
Oligochaeta	2.44	2.2	0.99	4.42	61.67
Palaemonetes	2.17	1.83	1.3	3.67	65.34
Sphaeridae	1.79	1.57	0.86	3.16	68.5
Ceratopogonidae	1.45	1.3	1.01	2.62	71.12
Hyalella	1.18	1.3	0.69	2.61	73.73
Cambaridae	1.63	1.25	0.89	2.52	76.25
Chironomidae	1.82	1.14	0.64	2.29	78.54
Hexagenia	0.8	0.91	1.11	1.83	80.37

Group Wadley

Average similarity: 45.47

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironominae	5.97	7.14	4.89	15.7	15.7
Tanypodinae	3.78	4.72	1.72	10.38	26.08
Hydrobiidae	3.96	3.82	1.88	8.4	34.49
Palaemonetes	2.57	2.84	1.13	6.25	40.74
Hydrachnidiae	2.64	2.78	1.5	6.12	46.86
Orthocladiinae	1.97	2.01	1.37	4.42	51.28
Oligochaeta	1.84	1.91	1.78	4.21	55.49
Maccaffertium	1.79	1.76	1.71	3.87	59.36
Cheumatopsyche	1.95	1.54	0.7	3.38	62.74

Caecidotea	1.33	1.28	0.94	2.81	65.55
Copepoda	1.55	1.21	0.74	2.66	68.21
Cambaridae	1.52	1.17	0.94	2.57	70.78
Baetidae	1.96	0.96	0.86	2.12	72.9
Stenelmis	1.34	0.96	0.66	2.12	75.02
Chironomidae	1.56	0.93	0.54	2.04	77.05
Ceratopogonidae	1.35	0.91	0.91	2	79.05
Planoorbidae	0.99	0.87	0.78	1.91	80.96

Group Rocky Ford

Average similarity: 48.94

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lirceus	3.74	4.31	0.97	8.81	8.81
Chironominae	3.84	4.09	2.08	8.35	17.16
Tanypodinae	3.22	3.64	2.95	7.44	24.59
Hydrobiidae	3.88	3.5	0.83	7.15	31.74
Hydrachnidiae	2.87	3.42	1.99	6.98	38.72
Caecidotea	2.97	2.93	0.74	5.99	44.72
Baetidae	2.74	2.67	1.45	5.46	50.17
Palaemonetes	2.57	2.57	1.03	5.26	55.43
Cambaridae	2.24	2.41	2.44	4.93	60.36
Tricorythodes	1.57	1.66	1.02	3.39	63.75
Maccaffertium	1.36	1.48	1.54	3.03	66.78
Baetisca	1.05	1.37	0.82	2.79	69.58
Orthocladiinae	1.48	1.24	1.16	2.54	72.12
Planoorbidae	1.38	1.23	0.85	2.51	74.63
Stenelmis	0.99	1.1	0.88	2.25	76.88
Oligochaeta	1.3	0.82	0.74	1.68	78.56
Chironomidae	1.29	0.78	0.65	1.6	80.16

Group Oliver

Average similarity: 43.97

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lirceus	3.48	4.19	0.77	9.54	9.54
Chironominae	3.55	4.02	1.78	9.14	18.67
Tanypodinae	3.04	2.95	1.41	6.71	25.39
Baetidae	3.13	2.53	0.53	5.75	31.14
Hydrobiidae	2.69	2.22	0.82	5.05	36.19
Hydrachnidiae	2.18	2.13	0.96	4.85	41.04
Orthocladiinae	1.9	1.75	1.19	3.97	45.01

Baetisca	1.39	1.6	0.56	3.65	48.66
Maccaffertium	1.69	1.52	1.26	3.47	52.12
Palaemonetes	1.7	1.42	0.73	3.22	55.35
Cambaridae	1.81	1.36	1.2	3.09	58.44
Caenis	1.7	1.33	0.82	3.02	61.46
Tricorythodes	1.93	1.32	0.63	3.01	64.46
Caecidotea	1.67	1.27	0.88	2.88	67.34
Stenelmis	1.34	1.15	0.75	2.61	69.95
Oligochaeta	1.29	1.09	0.66	2.47	72.42
Perlesta	1.13	0.84	0.55	1.91	74.34
Ceratopogonidae	1.13	0.82	0.8	1.86	76.2
Planoorbidae	1.08	0.79	0.66	1.81	78.01
Cheumatopsyche	1.47	0.72	0.74	1.64	79.65
Ephemerella	0.78	0.67	0.65	1.53	81.18

Group Hwy 119

Average similarity: 48.64

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lirceus	4.51	6.73	0.87	13.84	13.84
Caecidotea	4.25	3.89	1.34	8	21.85
Tanypodinae	3.18	3.61	1.73	7.42	29.26
Planoorbidae	3.08	3.52	1.7	7.24	36.51
Chironominae	3.16	3.34	1.24	6.87	43.38
Hydrobiidae	3.11	2.96	0.97	6.09	49.47
Baetisca	1.69	2.63	0.6	5.4	54.87
Palaemonetes	2.47	2.57	1.24	5.29	60.16
Hydrachnidiae	2.36	2.43	1.06	4.99	65.14
Copepoda	1.87	1.65	1.13	3.39	68.53
Maccaffertium	1.17	1.38	0.76	2.84	71.37
Physa	1.06	1.19	0.86	2.44	73.81
Baetidae	1.52	1.18	0.89	2.43	76.24
Cambaridae	1.24	1.14	1.08	2.33	78.58
Caenis	0.95	1.1	0.55	2.27	80.85

Group Morgan's Bridge

Average similarity: 43.73

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lirceus	3.59	5.02	0.74	11.48	11.48
Chironominae	4.21	4.63	2.53	10.6	22.08
Hyalella	3.7	3.96	1.15	9.05	31.14

Tanypodinae	2.82	3.46	3.79	7.91	39.04
Hydrachnidiae	3.13	3.33	1.47	7.61	46.66
Baetisca	1.68	2.66	0.61	6.09	52.75
Hydrobiidae	2.47	2.62	1.04	5.99	58.74
Planoorbidae	1.5	1.93	1.78	4.41	63.15
Caecidotea	1.99	1.9	0.75	4.35	67.5
Caenis	1.21	1.37	0.55	3.14	70.64
Orthocladiinae	2.2	1.33	1.32	3.05	73.69
Oligochaeta	2	1.1	0.87	2.52	76.21
Maccaffertium	1.21	1.05	0.77	2.41	78.62
Baetidae	1.44	0.98	0.69	2.23	80.85

Groups 88 Crossing & Wadley

Average dissimilarity = 53.21

Species	**Group 88 Crossing Av.Abund**	**Group Wadley Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Tanypodinae	5.13	3.78	1.77	1.61	3.33	3.33
Chironominae	7.4	5.97	1.77	1.3	3.32	6.65
Palaemonetes	2.17	2.57	1.45	1.27	2.73	9.39
Baetidae	0.94	1.96	1.38	0.99	2.59	11.98
Hydrobiidae	3.83	3.96	1.38	1.24	2.59	14.57
Orthocladiinae	3.19	1.97	1.27	0.96	2.38	16.95
Oligochaeta	2.44	1.84	1.21	1.23	2.27	19.22
Hydrachnidiae	2.54	2.64	1.19	1.45	2.23	21.46
Cheumatopsyche	0.39	1.95	1.17	0.77	2.2	23.66
Chironomidae	1.82	1.56	1.1	1.16	2.06	25.72
Sphaeridae	1.79	0.84	1.01	1.26	1.89	27.61
Copepoda	2.21	1.55	0.99	1.27	1.87	29.47
Tricorythodes	0.52	1.24	0.98	0.98	1.84	31.32
Cambaridae	1.63	1.52	0.94	1.27	1.77	33.09
Ceratopogonidae	1.45	1.35	0.87	1.11	1.64	34.73
Ferrissia	1.17	0.37	0.86	0.83	1.62	36.35
Dubiraphia	1.2	0.86	0.86	1.12	1.61	37.97
Maccaffertium	0.82	1.79	0.85	1.14	1.59	39.56
Hyalella	1.18	0.83	0.84	1.15	1.58	41.14
Hydroptilidae	0.37	1	0.82	0.95	1.54	42.68
Stenelmis	0.63	1.34	0.82	1.19	1.53	44.22
Eurylophella	0.44	1.18	0.77	0.48	1.44	45.66
Caecidotea	0.74	1.33	0.76	1.67	1.44	47.09
Caenis	0.49	0.95	0.74	0.8	1.39	48.48

Peltodytes	0.87	0.43	0.71	0.88	1.34	49.82
Chromagrion	0.86	0.47	0.67	1.05	1.26	51.07
Macromia	0.39	0.8	0.61	1	1.15	52.22
Chimarra	0.17	0.78	0.6	0.6	1.13	53.35
Corbicula	0.39	0.79	0.59	0.73	1.11	54.46
Dineutus	0.14	0.65	0.59	0.75	1.1	55.56
Planoorbidae	0.68	0.99	0.58	1.06	1.09	56.65
Hexagenia	0.8	0	0.56	1.35	1.06	57.71
Lirceus	0.34	0.57	0.56	0.74	1.05	58.76
Pleurocera	0.8	0.43	0.55	0.93	1.04	59.8
Macronychus	0.25	0.74	0.53	0.71	0.99	60.79
Pycnopsyche	0.66	0.12	0.53	0.62	0.99	61.78
Ancyronyx	0.71	0.74	0.52	1	0.98	62.76
Leptoceridae	0.3	0.53	0.48	0.82	0.91	63.67
Crangonyx	0.12	0.5	0.48	0.59	0.9	64.57
Ephemerella	0.32	0.35	0.47	0.55	0.88	65.45
Neoporus	0.53	0.48	0.46	0.88	0.86	66.31
Simulium	0.47	0.69	0.45	1.07	0.85	67.16
Hydroptila	0.27	0.54	0.45	0.92	0.85	68
Oecetis	0.39	0.6	0.44	0.83	0.83	68.83
Nectopsyche	0.08	0.69	0.44	0.77	0.83	69.65
Hirudinea	0.71	0.51	0.44	0.87	0.82	70.47
Physa	0.31	0.53	0.42	0.98	0.78	71.25
Polycentropodidae	0.45	0.33	0.37	0.84	0.69	71.94
Ormosia	0.37	0.17	0.36	0.58	0.68	72.62
Diptera	0.45	0	0.35	0.8	0.66	73.27
Rheumatobates	0.31	0.25	0.34	0.56	0.65	73.92
Leptophlebiidae	0.23	0.39	0.34	0.59	0.63	74.55
Phylocentropus	0.39	0.08	0.33	0.79	0.63	75.18
Corixidae	0.39	0.08	0.33	0.81	0.62	75.8
Argia	0	0.42	0.32	0.83	0.6	76.41
Baetisca	0.17	0.35	0.32	0.66	0.6	77.01
Boyeria	0.24	0.28	0.32	0.6	0.6	77.6
Sialis	0.4	0.08	0.31	0.62	0.59	78.19
Neureclipsis	0.4	0.12	0.31	0.56	0.58	78.77
Hydrotrupes	0.17	0.25	0.3	0.65	0.57	79.34
Polycentropus	0.25	0.23	0.3	0.75	0.56	79.9
Ceraclea	0.32	0.12	0.28	0.47	0.53	80.43

Groups 88 Crossing & Rocky Ford

Average dissimilarity = 58.75

Species	Group 88 Crossing Av.Abund	Group Rocky Ford Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironominae	7.4	3.84	2.75	1.63	4.68	4.68
Lirceus	0.34	3.74	2.67	0.96	4.55	9.23
Tanypodinae	5.13	3.22	2.05	1.45	3.49	12.72
Caecidotea	0.74	2.97	1.83	0.8	3.11	15.83
Baetidae	0.94	2.74	1.65	1.22	2.8	18.63
Hydrobiidae	3.83	3.88	1.57	1.39	2.68	21.31
Orthocladiinae	3.19	1.48	1.53	1.19	2.61	23.92
Palaemonetes	2.17	2.57	1.35	1.01	2.3	26.22
Copepoda	2.21	0.67	1.31	1.26	2.23	28.45
Oligochaeta	2.44	1.3	1.23	1.05	2.09	30.54
Tricorythodes	0.52	1.57	1.15	1.33	1.96	32.5
Hydrachnidiae	2.54	2.87	1.12	1.5	1.91	34.41
Sphaeridae	1.79	0.85	1.08	1.35	1.84	36.25
Chironomidae	1.82	1.29	1.08	1.24	1.84	38.09
Ceratopogonidae	1.45	0.71	0.98	1.32	1.66	39.75
Dubiraphia	1.2	0.73	0.96	1.14	1.64	41.39
Ferrissia	1.17	0.72	0.96	1.05	1.63	43.02
Hirudinea	0.71	1.39	0.94	0.56	1.6	44.61
Cambaridae	1.63	2.24	0.92	1.31	1.57	46.18
Crangonyx	0.12	1.26	0.92	0.85	1.56	47.74
Planoorbidae	0.68	1.38	0.82	1.23	1.4	49.15
Stenelmis	0.63	0.99	0.8	1.64	1.36	50.51
Hyalella	1.18	0.7	0.77	0.95	1.3	51.81
Baetisca	0.17	1.05	0.66	0.65	1.12	52.93
Cheumatopsyche	0.39	0.82	0.64	1.02	1.09	54.03
Peltodytes	0.87	0	0.64	0.74	1.09	55.12
Chromagrion	0.86	0.14	0.62	1.01	1.06	56.18
Simulium	0.47	0.8	0.62	0.68	1.05	57.23
Ephemerella	0.32	0.62	0.61	0.65	1.04	58.26
Gammarus	0.17	0.7	0.59	0.76	1.01	59.28
Hydroptilidae	0.37	0.67	0.59	0.84	1.01	60.29
Pleurocera	0.8	0.57	0.58	0.88	0.99	61.28
Macromia	0.39	0.65	0.57	1	0.96	62.24
Macronychus	0.25	0.8	0.56	0.88	0.95	63.19
Maccaffertium	0.82	1.36	0.55	1.08	0.94	64.13
Hexagenia	0.8	0.12	0.53	1.24	0.91	65.03
Physa	0.31	0.63	0.52	0.9	0.88	65.92
Pycnopsyche	0.66	0	0.49	0.58	0.83	66.75
Corbicula	0.39	0.56	0.47	0.7	0.79	67.54

Taeniopteryx	0.2	0.68	0.46	0.54	0.78	68.32
Ancyronyx	0.71	0.38	0.42	0.75	0.72	69.04
Nectopsyche	0.08	0.54	0.41	0.74	0.7	69.74
Hydroptila	0.27	0.41	0.39	0.69	0.66	70.4
Neureclipsis	0.4	0.2	0.38	0.66	0.65	71.05
Neoporus	0.53	0.39	0.38	0.58	0.64	71.69
Boyeria	0.24	0.28	0.36	0.62	0.61	72.3
Leptoceridae	0.3	0.28	0.35	0.63	0.6	72.9
Eurylophella	0.44	0	0.35	0.54	0.59	73.49
Bivalvia	0.26	0.35	0.35	0.47	0.59	74.08
Diptera	0.45	0	0.34	0.8	0.58	74.66
Ephemeroptera	0.31	0.25	0.34	0.64	0.58	75.24
Dineutus	0.14	0.32	0.34	0.68	0.58	75.82
Leptophlebiidae	0.23	0.35	0.34	0.66	0.58	76.4
Elmidae	0.08	0.53	0.33	0.45	0.56	76.96
Isonychia	0.08	0.33	0.33	0.53	0.56	77.52
Caenis	0.49	0.55	0.33	0.63	0.56	78.08
Ceraclea	0.32	0.08	0.33	0.48	0.56	78.63
Oecetis	0.39	0.31	0.32	0.78	0.55	79.18
Sialis	0.4	0	0.3	0.56	0.51	79.69
Epitheca	0.37	0.14	0.28	0.68	0.48	80.17

Groups Wadley & Rocky Ford

Average dissimilarity = 54.61

Species	**Group Wadley Av.Abund**	**Group Rocky Ford Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.57	3.74	2.63	1.02	4.82	4.82
Chironominae	5.97	3.84	1.99	1.22	3.64	8.46
Hydrobiidae	3.96	3.88	1.81	1.1	3.32	11.77
Caecidotea	1.33	2.97	1.68	0.86	3.07	14.84
Baetidae	1.96	2.74	1.45	1.16	2.66	17.5
Cheumatopsyche	1.95	0.82	1.19	0.96	2.18	19.68
Tanypodinae	3.78	3.22	1.19	1.29	2.17	21.86
Tricorythodes	1.24	1.57	1.1	1.12	2.01	23.87
Palaemonetes	2.57	2.57	1.05	1.36	1.92	25.79
Chironomidae	1.56	1.29	1.05	1.42	1.91	27.7
Crangonyx	0.5	1.26	1.03	1.06	1.89	29.6
Cambaridae	1.52	2.24	1.03	1.47	1.88	31.47
Copepoda	1.55	0.67	1	0.96	1.84	33.31
Hydrachnidiae	2.64	2.87	1	1.5	1.83	35.14

Orthocladiinae	1.97	1.48	0.97	1.14	1.78	36.92
Eurylophella	1.18	0	0.96	0.46	1.75	38.67
Simulium	0.69	0.8	0.87	0.97	1.59	40.26
Hirudinea	0.51	1.39	0.85	0.52	1.56	41.82
Hydroptilidae	1	0.67	0.85	0.95	1.55	43.38
Ceratopogonidae	1.35	0.71	0.84	1.13	1.54	44.91
Baetisca	0.35	1.05	0.84	0.72	1.53	46.45
Oligochaeta	1.84	1.3	0.84	1.33	1.53	47.98
Planoorbidae	0.99	1.38	0.83	1.34	1.52	49.5
Sphaeridae	0.84	0.85	0.82	0.91	1.5	51
Hyalella	0.83	0.7	0.81	0.93	1.48	52.48
Dubiraphia	0.86	0.73	0.76	1.11	1.39	53.87
Stenelmis	1.34	0.99	0.75	1.16	1.37	55.23
Caenis	0.95	0.55	0.71	0.92	1.3	56.53
Maccaffertium	1.79	1.36	0.65	1.07	1.19	57.73
Macromia	0.8	0.65	0.6	1	1.1	58.82
Gammarus	0.08	0.7	0.58	0.72	1.06	59.88
Corbicula	0.79	0.56	0.57	0.81	1.05	60.93
Nectopsyche	0.69	0.54	0.55	0.99	1	61.93
Ferrissia	0.37	0.72	0.54	0.88	0.99	62.92
Physa	0.53	0.63	0.54	1.14	0.98	63.9
Chimarra	0.78	0	0.52	0.51	0.95	64.85
Macronychus	0.74	0.8	0.52	0.77	0.95	65.8
Hydroptila	0.54	0.41	0.51	0.98	0.94	66.74
Ephemerella	0.35	0.62	0.5	0.8	0.92	67.67
Taeniopteryx	0.2	0.68	0.49	0.53	0.89	68.56
Pleurocera	0.43	0.57	0.48	0.77	0.88	69.44
Neoporus	0.48	0.39	0.46	0.94	0.85	70.29
Hydropsyche	0.32	0.28	0.45	0.56	0.83	71.12
Leptoceridae	0.53	0.28	0.45	0.77	0.83	71.95
Ancyronyx	0.74	0.38	0.45	0.8	0.82	72.77
Dineutus	0.65	0.32	0.44	0.72	0.81	73.58
Argia	0.42	0.36	0.44	0.91	0.81	74.39
Leptophlebiidae	0.39	0.35	0.38	0.6	0.7	75.09
Oecetis	0.6	0.31	0.38	0.74	0.69	75.78
Chromagrion	0.47	0.14	0.36	0.6	0.65	76.43
Peltodytes	0.43	0	0.34	0.52	0.62	77.05
Acroneuria	0.17	0.33	0.34	0.87	0.62	77.67
Elmidae	0	0.53	0.33	0.44	0.6	78.27
Hesperocorixa	0.25	0.14	0.31	0.55	0.56	78.83
Polycentropus	0.23	0.23	0.3	0.6	0.54	79.37
Ostracoda	0.08	0.3	0.29	0.53	0.53	79.91

Perlesta	0.19	0.35	0.28	0.56	0.52	80.42

Groups 88 Crossing & Oliver

Average dissimilarity = 62.59

Species	Group 88 Crossing Av.Abund	Group Oliver Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironominae	7.4	3.55	3.01	1.74	4.8	4.8
Lirceus	0.34	3.48	2.61	0.82	4.17	8.97
Tanypodinae	5.13	3.04	2.34	1.44	3.74	12.71
Baetidae	0.94	3.13	2.17	0.9	3.46	16.17
Copepoda	2.21	0.82	1.86	1.38	2.98	19.15
Hydrachnidiae	2.54	2.18	1.61	1.37	2.58	21.72
Hydrobiidae	3.83	2.69	1.58	1.49	2.53	24.25
Tricorythodes	0.52	1.93	1.56	0.9	2.48	26.74
Orthocladiinae	3.19	1.9	1.39	0.97	2.22	28.95
Palaemonetes	2.17	1.7	1.31	1.32	2.09	31.04
Oligochaeta	2.44	1.29	1.21	1.23	1.94	32.98
Chironomidae	1.82	1.2	1.16	1.26	1.86	34.84
Cheumatopsyche	0.39	1.47	1.08	1.04	1.73	36.57
Gammarus	0.17	1.37	1.02	0.74	1.62	38.19
Baetisca	0.17	1.39	1	0.69	1.61	39.8
Sphaeridae	1.79	0.43	1	1.25	1.59	41.39
Caecidotea	0.74	1.67	0.99	0.93	1.59	42.98
Crangonyx	0.12	1.32	0.97	0.72	1.56	44.53
Ferrissia	1.17	0.64	0.95	0.93	1.52	46.05
Cambaridae	1.63	1.81	0.95	1.34	1.52	47.57
Hyalella	1.18	0.77	0.95	1.21	1.51	49.08
Ceratopogonidae	1.45	1.13	0.93	1.17	1.48	50.56
Caenis	0.49	1.7	0.91	0.58	1.45	52.02
Maccaffertium	0.82	1.69	0.88	1.13	1.41	53.43
Simulium	0.47	1.18	0.88	0.8	1.41	54.83
Stenelmis	0.63	1.34	0.87	1.14	1.39	56.23
Perlesta	0	1.13	0.87	0.64	1.39	57.62
Dubiraphia	1.2	0.69	0.82	1.01	1.31	58.92
Planoorbidae	0.68	1.08	0.7	0.94	1.11	60.03
Ephemerella	0.32	0.78	0.68	0.71	1.08	61.11
Isonychia	0.08	0.86	0.67	0.61	1.07	62.18
Chromagrion	0.86	0	0.67	1	1.06	63.25
Ancyronyx	0.71	0.6	0.64	0.68	1.02	64.26
Peltodytes	0.87	0.14	0.61	0.79	0.98	65.24

Pleurocera	0.8	0.12	0.57	0.9	0.91	66.16
Nectopsyche	0.08	0.86	0.57	0.97	0.9	67.06
Hydroptila	0.27	0.59	0.56	0.66	0.89	67.95
Hirudinea	0.71	0.85	0.56	1.13	0.89	68.85
Taeniopteryx	0.2	0.76	0.55	0.43	0.88	69.73
Hydroptilidae	0.37	0.5	0.55	0.63	0.88	70.6
Hexagenia	0.8	0.12	0.53	1.25	0.85	71.45
Hydropsyche	0	0.67	0.52	0.76	0.83	72.28
Pycnopsyche	0.66	0	0.51	0.58	0.81	73.1
Macromia	0.39	0.53	0.5	0.92	0.8	73.9
Macronychus	0.25	0.63	0.48	0.81	0.77	74.67
Neoporus	0.53	0.51	0.48	0.75	0.77	75.44
Oecetis	0.39	0.28	0.41	0.95	0.66	76.1
Eurylophella	0.44	0	0.37	0.54	0.59	76.68
Corbicula	0.39	0.2	0.36	0.75	0.57	77.26
Argia	0	0.46	0.35	0.41	0.57	77.82
Diptera	0.45	0	0.35	0.79	0.56	78.38
Neureclipsis	0.4	0.12	0.32	0.55	0.51	78.9
Leptophlebiidae	0.23	0.37	0.31	0.6	0.49	79.39
Polycentropodidae	0.45	0.08	0.31	0.78	0.49	79.88
Sialis	0.4	0	0.3	0.56	0.48	80.36

Groups Wadley & Oliver

Average dissimilarity = 59.24

Species	**Group Wadley Av.Abund**	**Group Oliver Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.57	3.48	2.58	0.87	4.36	4.36
Hydrobiidae	3.96	2.69	2.17	1.49	3.67	8.03
Chironominae	5.97	3.55	2.14	1.36	3.61	11.64
Baetidae	1.96	3.13	2.1	0.95	3.55	15.18
Tanypodinae	3.78	3.04	1.72	1.56	2.91	18.09
Cheumatopsyche	1.95	1.47	1.61	1.07	2.72	20.82
Tricorythodes	1.24	1.93	1.52	1	2.57	23.39
Hydrachnidiae	2.64	2.18	1.4	1.28	2.36	25.75
Copepoda	1.55	0.82	1.36	0.94	2.29	28.04
Palaemonetes	2.57	1.7	1.24	1.3	2.1	30.13
Baetisca	0.35	1.39	1.17	0.7	1.98	32.11
Chironomidae	1.56	1.2	1.11	1.38	1.88	33.99
Oligochaeta	1.84	1.29	1.09	1.35	1.85	35.84
Simulium	0.69	1.18	1.03	1.01	1.74	37.57

Eurylophella	1.18	0	1.01	0.45	1.71	39.28
Crangonyx	0.5	1.32	1.01	0.8	1.7	40.99
Hyalella	0.83	0.77	1	1.14	1.7	42.68
Gammarus	0.08	1.37	0.98	0.74	1.65	44.33
Caenis	0.95	1.7	0.97	0.8	1.63	45.96
Orthocladiinae	1.97	1.9	0.96	1.18	1.63	47.59
Cambaridae	1.52	1.81	0.96	1.2	1.61	49.2
Hydroptilidae	1	0.5	0.9	0.86	1.52	50.72
Caecidotea	1.33	1.67	0.9	1.01	1.52	52.24
Ceratopogonidae	1.35	1.13	0.81	1.13	1.37	53.62
Maccaffertium	1.79	1.69	0.78	1	1.32	54.94
Ephemerella	0.35	0.78	0.77	1.01	1.31	56.25
Perlesta	0.19	1.13	0.76	0.58	1.29	57.53
Hydropsyche	0.32	0.67	0.76	0.84	1.28	58.81
Dubiraphia	0.86	0.69	0.71	1.44	1.2	60.01
Chimarra	0.78	0.28	0.71	0.71	1.2	61.21
Stenelmis	1.34	1.34	0.68	1.07	1.14	62.35
Ancyronyx	0.74	0.6	0.66	0.7	1.12	63.47
Isonychia	0.08	0.86	0.64	0.59	1.08	64.55
Planoorbidae	0.99	1.08	0.64	1.11	1.08	65.63
Hydroptila	0.54	0.59	0.62	0.84	1.05	66.68
Taeniopteryx	0.2	0.76	0.59	0.43	1	67.68
Sphaeridae	0.84	0.43	0.59	0.7	1	68.68
Ferrissia	0.37	0.64	0.59	0.74	1	69.68
Dineutus	0.65	0.25	0.59	0.89	0.99	70.67
Macromia	0.8	0.53	0.57	0.98	0.96	71.63
Corbicula	0.79	0.2	0.56	0.71	0.94	72.57
Argia	0.42	0.46	0.49	0.73	0.82	73.39
Nectopsyche	0.69	0.86	0.49	1.06	0.82	74.22
Macronychus	0.74	0.63	0.48	0.79	0.82	75.03
Neoporus	0.48	0.51	0.47	0.98	0.8	75.83
Oecetis	0.6	0.28	0.45	0.77	0.76	76.59
Hirudinea	0.51	0.85	0.44	0.84	0.74	77.33
Physa	0.53	0.49	0.44	0.98	0.74	78.07
Leptoceridae	0.53	0.12	0.41	0.71	0.7	78.77
Leptophlebiidae	0.39	0.37	0.39	0.66	0.66	79.43
Peltodytes	0.43	0.14	0.39	0.56	0.66	80.08

Groups Rocky Ford & Oliver

Average dissimilarity = 51.44

	Group Rocky Ford	**Group Oliver**

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hydrobiidae	3.88	2.69	1.9	1.48	3.69	3.69
Baetidae	2.74	3.13	1.84	1.1	3.59	7.28
Caecidotea	2.97	1.67	1.7	0.87	3.31	10.59
Chironominae	3.84	3.55	1.5	1.29	2.92	13.51
Hydrachnidiae	2.87	2.18	1.43	1.53	2.77	16.28
Lirceus	3.74	3.48	1.42	0.95	2.75	19.04
Crangonyx	1.26	1.32	1.25	1.1	2.43	21.47
Tanypodinae	3.22	3.04	1.24	1.19	2.41	23.88
Cheumatopsyche	0.82	1.47	1.15	1.09	2.24	26.12
Orthocladiinae	1.48	1.9	1.09	1.34	2.12	28.23
Gammarus	0.7	1.37	1.08	0.79	2.1	30.33
Palaemonetes	2.57	1.7	1.07	1.39	2.07	32.41
Tricorythodes	1.57	1.93	1.06	0.9	2.06	34.47
Hirudinea	1.39	0.85	1.01	0.62	1.96	36.43
Oligochaeta	1.3	1.29	1	1.19	1.94	38.37
Cambaridae	2.24	1.81	0.92	1.13	1.78	40.15
Chironomidae	1.29	1.2	0.9	1.3	1.75	41.9
Simulium	0.8	1.18	0.89	0.72	1.72	43.62
Copepoda	0.67	0.82	0.88	0.67	1.71	45.32
Caenis	0.55	1.7	0.86	0.64	1.67	46.99
Hyalella	0.7	0.77	0.85	1.03	1.65	48.65
Planoorbidae	1.38	1.08	0.85	1.23	1.65	50.3
Stenelmis	0.99	1.34	0.82	1.59	1.6	51.9
Sphaeridae	0.85	0.43	0.78	1.37	1.52	53.42
Maccaffertium	1.36	1.69	0.74	1.02	1.44	54.86
Hydroptilidae	0.67	0.5	0.72	0.75	1.39	56.25
Perlesta	0.35	1.13	0.7	0.59	1.37	57.62
Ephemerella	0.62	0.78	0.68	0.82	1.32	58.95
Ferrissia	0.72	0.64	0.64	0.81	1.24	60.18
Nectopsyche	0.54	0.86	0.63	1.12	1.23	61.41
Isonychia	0.33	0.86	0.63	0.62	1.22	62.63
Taeniopteryx	0.68	0.76	0.62	0.49	1.21	63.85
Physa	0.63	0.49	0.58	0.96	1.12	64.97
Ceratopogonidae	0.71	1.13	0.57	0.79	1.11	66.08
Hydroptila	0.41	0.59	0.55	0.68	1.06	67.14
Baetisca	1.05	1.39	0.54	0.68	1.04	68.19
Ancyronyx	0.38	0.6	0.51	0.52	0.98	69.17
Corbicula	0.56	0.2	0.5	0.83	0.98	70.15
Hydropsyche	0.28	0.67	0.46	0.79	0.89	71.04
Dubiraphia	0.73	0.69	0.43	0.96	0.84	71.88
Macromia	0.65	0.53	0.43	0.83	0.84	72.72

Pleurocera	0.57	0.12	0.42	0.68	0.81	73.52
Argia	0.36	0.46	0.4	0.53	0.79	74.31
Leptophlebiidae	0.35	0.37	0.39	0.7	0.75	75.06
Macronychus	0.8	0.63	0.38	0.75	0.75	75.81
Neoporus	0.39	0.51	0.35	0.74	0.68	76.49
Dineutus	0.32	0.25	0.35	0.81	0.67	77.16
Neoperla	0.17	0.39	0.34	0.6	0.65	77.81
Elmidae	0.53	0	0.34	0.44	0.65	78.47
Acroneuria	0.33	0.19	0.32	0.7	0.62	79.09
Ostracoda	0.3	0.08	0.3	0.51	0.58	79.67
Corixidae	0.32	0.37	0.28	0.51	0.55	80.21

Groups 88 Crossing & Hwy 119

Average dissimilarity = 63.81

Species	**Group 88 Crossing Av.Abund**	**Group Hwy 119 Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.34	4.51	3.61	0.89	5.66	5.66
Chironominae	7.4	3.16	3.51	1.4	5.5	11.16
Caecidotea	0.74	4.25	2.86	1.34	4.48	15.64
Tanypodinae	5.13	3.18	2.4	1.37	3.76	19.4
Orthocladiinae	3.19	0.25	2.34	1.56	3.66	23.06
Planoorbidae	0.68	3.08	1.91	1.51	2.99	26.05
Hydrachnidiae	2.54	2.36	1.55	1.53	2.43	28.48
Oligochaeta	2.44	1.48	1.52	1.23	2.38	30.85
Hydrobiidae	3.83	3.11	1.43	1.46	2.24	33.09
Palaemonetes	2.17	2.47	1.34	1.13	2.1	35.19
Copepoda	2.21	1.87	1.32	1.21	2.07	37.26
Baetisca	0.17	1.69	1.27	0.71	1.99	39.25
Crangonyx	0.12	1.54	1.21	0.69	1.9	41.15
Chironomidae	1.82	1.15	1.21	1.35	1.9	43.05
Ceratopogonidae	1.45	1.04	1.19	1.27	1.86	44.91
Baetidae	0.94	1.52	1.15	1.03	1.81	46.72
Sphaeridae	1.79	0.75	1.05	1.1	1.64	48.36
Hyalella	1.18	1.14	1.03	1.08	1.61	49.97
Ferrissia	1.17	0.81	1.02	1.07	1.6	51.57
Tricorythodes	0.52	1.01	0.99	1	1.54	53.12
Gammarus	0.17	1.28	0.98	0.8	1.53	54.65
Physa	0.31	1.06	0.97	1.24	1.53	56.18
Dubiraphia	1.2	0.12	0.95	1.02	1.49	57.67
Cambaridae	1.63	1.24	0.91	1.21	1.42	59.09

Simulium	0.47	0.82	0.77	0.68	1.2	60.3
Peltodytes	0.87	0.17	0.72	0.79	1.13	61.43
Chromagrion	0.86	0	0.71	0.99	1.11	62.53
Ephemerella	0.32	0.57	0.68	0.73	1.07	63.6
Hirudinea	0.71	1.11	0.66	0.89	1.03	64.64
Maccaffertium	0.82	1.17	0.65	1.02	1.02	65.65
Cheumatopsyche	0.39	0.74	0.64	1.04	1.01	66.66
Caenis	0.49	0.95	0.61	0.66	0.95	67.62
Pleurocera	0.8	0	0.6	0.89	0.93	68.55
Stenelmis	0.63	0.28	0.57	1.11	0.89	69.44
Ancyronyx	0.71	0	0.55	0.87	0.87	70.3
Pycnopsyche	0.66	0	0.54	0.56	0.84	71.15
Hexagenia	0.8	0.12	0.53	1.16	0.84	71.98
Nectopsyche	0.08	0.66	0.48	0.74	0.75	72.73
Corixidae	0.39	0.28	0.45	0.62	0.71	73.44
Hydroptila	0.27	0.33	0.44	0.59	0.69	74.13
Perlesta	0	0.53	0.43	0.43	0.68	74.81
Liodessus	0.31	0.31	0.43	0.52	0.67	75.48
Macromia	0.39	0.2	0.4	0.69	0.63	76.11
Eurylophella	0.44	0	0.38	0.54	0.6	76.72
Corbicula	0.39	0.31	0.38	0.7	0.6	77.31
Diptera	0.45	0	0.38	0.79	0.59	77.91
Collembola	0.25	0.33	0.37	0.91	0.59	78.49
Neoporus	0.53	0.44	0.37	0.59	0.57	79.07
Tabanidae	0.37	0.2	0.36	0.76	0.56	79.63
Ceraclea	0.32	0.17	0.34	0.45	0.53	80.16

Groups Wadley & Hwy 119

Average dissimilarity = 60.79

Species	**Group Wadley Av.Abund**	**Group Hwy 119 Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.57	4.51	3.67	0.95	6.03	6.03
Chironominae	5.97	3.16	2.9	1.39	4.78	10.81
Caecidotea	1.33	4.25	2.45	1.21	4.02	14.84
Hydrobiidae	3.96	3.11	1.9	1.28	3.12	17.96
Tanypodinae	3.78	3.18	1.72	1.47	2.83	20.79
Planoorbidae	0.99	3.08	1.69	1.31	2.79	23.57
Palaemonetes	2.57	2.47	1.55	1.77	2.55	26.13
Orthocladiinae	1.97	0.25	1.51	1.39	2.49	28.61
Baetisca	0.35	1.69	1.48	0.73	2.44	31.05

Baetidae	1.96	1.52	1.4	1.04	2.31	33.36
Crangonyx	0.5	1.54	1.36	0.88	2.24	35.59
Copepoda	1.55	1.87	1.19	1.37	1.96	37.56
Cheumatopsyche	1.95	0.74	1.15	0.92	1.89	39.45
Hydrachnidiae	2.64	2.36	1.15	1.17	1.89	41.34
Oligochaeta	1.84	1.48	1.14	1.13	1.87	43.21
Chironomidae	1.56	1.15	1.11	1.41	1.83	45.04
Eurylophella	1.18	0	1.06	0.46	1.74	46.77
Tricorythodes	1.24	1.01	1.05	0.85	1.72	48.5
Stenelmis	1.34	0.28	0.99	1.15	1.62	50.12
Hyalella	0.83	1.14	0.98	0.91	1.62	51.73
Maccaffertium	1.79	1.17	0.93	1.09	1.53	53.27
Simulium	0.69	0.82	0.93	0.84	1.53	54.8
Gammarus	0.08	1.28	0.89	0.75	1.47	56.26
Ceratopogonidae	1.35	1.04	0.87	1.04	1.42	57.69
Cambaridae	1.52	1.24	0.84	1.31	1.38	59.07
Hydroptilidae	1	0.2	0.81	0.85	1.34	60.4
Physa	0.53	1.06	0.75	1.12	1.23	61.64
Ferrissia	0.37	0.81	0.71	0.92	1.16	62.8
Sphaeridae	0.84	0.75	0.66	0.69	1.09	63.89
Dubiraphia	0.86	0.12	0.66	0.99	1.09	64.98
Macromia	0.8	0.2	0.62	0.92	1.03	66.01
Ephemerella	0.35	0.57	0.62	1.01	1.02	67.03
Corbicula	0.79	0.31	0.61	0.82	1	68.03
Dineutus	0.65	0.25	0.61	0.76	1	69.02
Chimarra	0.78	0.08	0.59	0.59	0.98	70
Caenis	0.95	0.95	0.58	0.78	0.95	70.96
Hirudinea	0.51	1.11	0.55	0.7	0.91	71.86
Hydroptila	0.54	0.33	0.54	0.76	0.9	72.76
Ancyronyx	0.74	0	0.52	0.78	0.85	73.61
Perlesta	0.19	0.53	0.5	0.5	0.83	74.44
Nectopsyche	0.69	0.66	0.5	0.89	0.83	75.27
Peltodytes	0.43	0.17	0.46	0.64	0.76	76.03
Neoporus	0.48	0.44	0.45	0.91	0.74	76.76
Argia	0.42	0.39	0.41	0.88	0.68	77.44
Oecetis	0.6	0.17	0.41	0.71	0.68	78.12
Leptoceridae	0.53	0	0.4	0.67	0.65	78.77
Macronychus	0.74	0.17	0.38	0.57	0.63	79.4
Chromagrion	0.47	0	0.34	0.54	0.56	79.96
Leptophlebiidae	0.39	0	0.33	0.48	0.55	80.51

Groups Rocky Ford & Hwy 119

Average dissimilarity = 51.26

Species	Group Rocky Ford Av.Abund	Group Hwy 119 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Caecidotea	2.97	4.25	2.73	1.26	5.34	5.34
Hydrobiidae	3.88	3.11	1.84	1.45	3.59	8.92
Lirceus	3.74	4.51	1.62	0.84	3.16	12.09
Chironominae	3.84	3.16	1.47	1.23	2.87	14.96
Baetidae	2.74	1.52	1.47	1.18	2.87	17.83
Planoorbidae	1.38	3.08	1.44	1.42	2.81	20.64
Crangonyx	1.26	1.54	1.37	0.89	2.67	23.31
Palaemonetes	2.57	2.47	1.28	1.56	2.5	25.82
Copepoda	0.67	1.87	1.26	1.34	2.45	28.27
Tanypodinae	3.22	3.18	1.26	1.28	2.45	30.72
Hydrachnidiae	2.87	2.36	1.17	1.59	2.28	33
Oligochaeta	1.3	1.48	1.12	1.04	2.18	35.18
Gammarus	0.7	1.28	1.1	0.95	2.14	37.33
Cambaridae	2.24	1.24	1.08	1.29	2.11	39.43
Orthocladiinae	1.48	0.25	1.06	1.19	2.06	41.49
Hyalella	0.7	1.14	0.96	1.02	1.88	43.37
Hirudinea	1.39	1.11	0.91	0.61	1.77	45.14
Chironomidae	1.29	1.15	0.89	1.41	1.74	46.88
Physa	0.63	1.06	0.85	1.28	1.66	48.54
Simulium	0.8	0.82	0.77	0.7	1.51	50.04
Sphaeridae	0.85	0.75	0.76	1.26	1.49	51.53
Cheumatopsyche	0.82	0.74	0.74	1.14	1.45	52.98
Tricorythodes	1.57	1.01	0.69	1	1.35	54.33
Stenelmis	0.99	0.28	0.69	1.06	1.34	55.67
Maccaffertium	1.36	1.17	0.69	1.3	1.34	57
Baetisca	1.05	1.69	0.68	0.69	1.33	58.33
Ephemerella	0.62	0.57	0.64	0.95	1.25	59.58
Ferrissia	0.72	0.81	0.64	0.87	1.24	60.82
Taeniopteryx	0.68	0.08	0.59	0.49	1.15	61.97
Hydroptilidae	0.67	0.2	0.58	0.73	1.12	63.09
Nectopsyche	0.54	0.66	0.56	0.88	1.1	64.19
Perlesta	0.35	0.53	0.56	0.64	1.09	65.28
Caenis	0.55	0.95	0.53	0.7	1.03	66.32
Ceratopogonidae	0.71	1.04	0.51	0.64	0.99	67.31
Macromia	0.65	0.2	0.5	0.89	0.98	68.29
Hydroptila	0.41	0.33	0.46	0.66	0.9	69.19
Corixidae	0.32	0.28	0.44	0.6	0.86	70.04

Dubiraphia	0.73	0.12	0.43	0.61	0.85	70.89
Macronychus	0.8	0.17	0.43	0.67	0.84	71.73
Corbicula	0.56	0.31	0.42	0.62	0.81	72.54
Pleurocera	0.57	0	0.39	0.6	0.77	73.31
Argia	0.36	0.39	0.36	0.61	0.7	74.01
Dineutus	0.32	0.25	0.35	0.62	0.69	74.7
Elmidae	0.53	0	0.34	0.44	0.66	75.36
Basiaeschna	0.25	0.26	0.33	0.75	0.64	76
Neoporus	0.39	0.44	0.32	0.66	0.62	76.62
Isonychia	0.33	0.25	0.31	0.58	0.61	77.23
Collembola	0	0.33	0.3	0.7	0.59	77.82
Hydropsyche	0.28	0.2	0.3	0.66	0.58	78.4
Polycentropodidae	0.33	0.12	0.3	0.73	0.58	78.98
Leptophlebiidae	0.35	0	0.29	0.48	0.56	79.54
Boyeria	0.28	0.08	0.28	0.68	0.55	80.1

Groups Oliver & Hwy 119

Average dissimilarity = 54.14

Species	**Group Oliver Av.Abund**	**Group Hwy 119 Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Caecidotea	1.67	4.25	2.59	1.36	4.79	4.79
Baetidae	3.13	1.52	2.28	0.94	4.21	9
Chironominae	3.55	3.16	2.16	1.55	4	13
Planoorbidae	1.08	3.08	1.79	1.46	3.31	16.3
Lirceus	3.48	4.51	1.79	0.76	3.31	19.61
Crangonyx	1.32	1.54	1.49	0.94	2.75	22.36
Orthocladiinae	1.9	0.25	1.48	1.37	2.72	25.08
Copepoda	0.82	1.87	1.47	1.42	2.71	27.8
Hydrobiidae	2.69	3.11	1.44	1.17	2.67	30.46
Gammarus	1.37	1.28	1.22	0.9	2.26	32.72
Cheumatopsyche	1.47	0.74	1.21	0.98	2.24	34.96
Simulium	1.18	0.82	1.17	0.78	2.17	37.13
Tanypodinae	3.04	3.18	1.16	1.2	2.14	39.26
Palaemonetes	1.7	2.47	1.15	1.21	2.13	41.39
Hydrachnidiae	2.18	2.36	1.12	1.04	2.07	43.46
Oligochaeta	1.29	1.48	1.08	1.29	1.99	45.45
Hyalella	0.77	1.14	1.06	1.2	1.95	47.4
Stenelmis	1.34	0.28	1	1.13	1.85	49.25
Cambaridae	1.81	1.24	0.97	1.29	1.79	51.04
Maccaffertium	1.69	1.17	0.97	1.06	1.79	52.83

Perlesta	1.13	0.53	0.97	0.68	1.78	54.61
Tricorythodes	1.93	1.01	0.93	0.61	1.71	56.33
Chironomidae	1.2	1.15	0.92	1.38	1.7	58.03
Physa	0.49	1.06	0.86	1.09	1.58	59.61
Taeniopteryx	0.76	0.08	0.71	0.4	1.31	60.92
Isonychia	0.86	0.25	0.7	0.62	1.3	62.22
Ceratopogonidae	1.13	1.04	0.7	0.87	1.29	63.51
Hirudinea	0.85	1.11	0.68	0.97	1.26	64.78
Caenis	1.7	0.95	0.68	0.63	1.25	66.03
Hydroptila	0.59	0.33	0.64	0.64	1.19	67.22
Ferrissia	0.64	0.81	0.63	0.85	1.16	68.38
Hydropsyche	0.67	0.2	0.62	0.85	1.15	69.53
Baetisca	1.39	1.69	0.62	0.73	1.14	70.67
Nectopsyche	0.86	0.66	0.52	1.01	0.97	71.64
Sphaeridae	0.43	0.75	0.51	0.75	0.95	72.59
Ephemerella	0.78	0.57	0.51	0.67	0.94	73.53
Hydroptilidae	0.5	0.2	0.5	0.5	0.92	74.45
Dubiraphia	0.69	0.12	0.47	0.99	0.86	75.31
Corixidae	0.37	0.28	0.46	0.52	0.85	76.16
Macromia	0.53	0.2	0.45	0.85	0.83	76.99
Ancyronyx	0.6	0	0.43	0.4	0.8	77.79
Neoporus	0.51	0.44	0.43	0.79	0.79	78.58
Corbicula	0.2	0.31	0.41	0.8	0.76	79.33
Macronychus	0.63	0.17	0.41	0.74	0.75	80.09

Groups 88 Crossing & Morgan's Bridge

Average dissimilarity = 61.20

	Group 88 Crossing	**Group Morgan's Bridge**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Chironominae	7.4	4.21	2.97	1.4	4.85	4.85
Lirceus	0.34	3.59	2.82	0.8	4.61	9.45
Tanypodinae	5.13	2.82	2.44	1.63	3.98	13.44
Hyalella	1.18	3.7	2.37	1.19	3.87	17.31
Orthocladiinae	3.19	2.2	1.97	1.32	3.22	20.53
Hydrobiidae	3.83	2.47	1.86	1.6	3.04	23.57
Hydrachnidiae	2.54	3.13	1.79	1.37	2.92	26.49
Oligochaeta	2.44	2	1.68	0.93	2.74	29.23
Ceratopogonidae	1.45	1.47	1.52	1.09	2.49	31.71
Palaemonetes	2.17	1.26	1.38	1.45	2.25	33.97
Copepoda	2.21	1.5	1.37	1.39	2.24	36.21

Caecidotea	0.74	1.99	1.31	1.06	2.13	38.34
Baetisca	0.17	1.68	1.22	0.7	1.99	40.34
Sphaeridae	1.79	1.07	1.21	1.3	1.97	42.31
Chironomidae	1.82	1.22	1.19	1.22	1.94	44.25
Cambaridae	1.63	0.6	1.18	1.5	1.93	46.18
Baetidae	0.94	1.44	1.11	0.77	1.82	47.99
Planoorbidae	0.68	1.5	1.01	1.39	1.66	49.65
Dubiraphia	1.2	0.28	0.95	1.03	1.56	51.2
Ferrissia	1.17	0.47	0.94	0.86	1.54	52.74
Caenis	0.49	1.21	0.83	0.85	1.35	54.09
Ephemeroptera	0.31	0.95	0.78	0.73	1.27	55.36
Tricorythodes	0.52	0.88	0.76	0.86	1.25	56.61
Chromagrion	0.86	0.51	0.71	1.13	1.16	57.77
Peltodytes	0.87	0.17	0.7	0.82	1.15	58.92
Maccaffertium	0.82	1.21	0.68	1.08	1.11	60.03
Physa	0.31	0.65	0.65	0.96	1.06	61.09
Simulium	0.47	0.39	0.63	0.77	1.04	62.13
Pleurocera	0.8	0	0.61	0.9	1	63.13
Hirudinea	0.71	0.39	0.6	0.95	0.99	64.12
Leptophlebiidae	0.23	0.82	0.59	0.67	0.97	65.09
Ancyronyx	0.71	0	0.58	0.87	0.95	66.04
Gyrinus	0	0.65	0.56	0.41	0.92	66.96
Pycnopsyche	0.66	0	0.52	0.57	0.85	67.8
Hexagenia	0.8	0.38	0.51	1.07	0.83	68.63
Crangonyx	0.12	0.46	0.48	0.59	0.79	69.42
Neoporus	0.53	0.61	0.47	0.76	0.77	70.19
Ephemerella	0.32	0.22	0.46	0.43	0.76	70.95
Polycentropus	0.25	0.42	0.46	0.8	0.76	71.7
Hydroptilidae	0.37	0.35	0.42	0.73	0.68	72.38
Polycentropodidae	0.45	0.08	0.41	0.95	0.68	73.06
Oecetis	0.39	0.44	0.41	0.85	0.68	73.73
Diptera	0.45	0.08	0.4	0.84	0.65	74.38
Eurylophella	0.44	0.35	0.4	0.6	0.65	75.03
Macromia	0.39	0.17	0.38	0.71	0.62	75.65
Bivalvia	0.26	0.26	0.36	0.62	0.59	76.23
Leptoceridae	0.3	0.17	0.36	0.64	0.58	76.81
Stenelmis	0.63	0.31	0.35	0.75	0.57	77.38
Chimarra	0.17	0.32	0.34	0.72	0.56	77.95
Rheumatobates	0.31	0.17	0.34	0.47	0.55	78.5
Cheumatopsyche	0.39	0.08	0.33	0.74	0.54	79.04
Sialis	0.4	0	0.33	0.56	0.54	79.58
Corixidae	0.39	0.23	0.32	0.61	0.52	80.1

Groups Wadley & Morgan's Bridge

Average dissimilarity = 60.69

Species	Group Wadley Av.Abund	Group Morgan's Bridge Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lirceus	0.57	3.59	2.73	0.83	4.5	4.5
Hyalella	0.83	3.7	2.54	1.35	4.19	8.69
Chironominae	5.97	4.21	2.32	1.58	3.83	12.51
Hydrobiidae	3.96	2.47	1.98	1.22	3.26	15.78
Baetidae	1.96	1.44	1.63	1.1	2.68	18.46
Tanypodinae	3.78	2.82	1.58	1.59	2.6	21.06
Palaemonetes	2.57	1.26	1.57	1.37	2.58	23.64
Hydrachnidiae	2.64	3.13	1.55	1.24	2.56	26.2
Orthocladiinae	1.97	2.2	1.48	1.14	2.43	28.63
Oligochaeta	1.84	2	1.47	0.77	2.43	31.05
Baetisca	0.35	1.68	1.44	0.73	2.37	33.42
Cheumatopsyche	1.95	0.08	1.42	0.87	2.34	35.77
Caecidotea	1.33	1.99	1.22	1.44	2.01	37.78
Ceratopogonidae	1.35	1.47	1.14	0.95	1.87	39.65
Copepoda	1.55	1.5	1.12	1.07	1.85	41.5
Chironomidae	1.56	1.22	1.09	1.28	1.8	43.3
Tricorythodes	1.24	0.88	0.98	0.92	1.61	44.91
Cambaridae	1.52	0.6	0.95	1.27	1.56	46.47
Stenelmis	1.34	0.31	0.92	1.06	1.52	48
Sphaeridae	0.84	1.07	0.92	0.83	1.51	49.51
Eurylophella	1.18	0.35	0.9	0.45	1.49	50.99
Maccaffertium	1.79	1.21	0.89	1.01	1.47	52.46
Hydroptilidae	1	0.35	0.86	0.96	1.41	53.88
Simulium	0.69	0.39	0.8	1.19	1.32	55.2
Planoorbidae	0.99	1.5	0.78	1.24	1.29	56.49
Ephemeroptera	0	0.95	0.78	0.65	1.28	57.77
Caenis	0.95	1.21	0.7	0.88	1.16	58.93
Chimarra	0.78	0.32	0.68	0.72	1.12	60.05
Dubiraphia	0.86	0.28	0.67	0.95	1.11	61.15
Macromia	0.8	0.17	0.65	0.95	1.07	62.22
Oecetis	0.6	0.44	0.62	0.96	1.03	63.25
Corbicula	0.79	0	0.6	0.64	0.99	64.24
Leptophlebiidae	0.39	0.82	0.6	0.62	0.99	65.23
Ancyronyx	0.74	0	0.55	0.77	0.9	66.13
Crangonyx	0.5	0.46	0.53	0.63	0.88	67.01

Gyrinus	0	0.65	0.53	0.41	0.88	67.89
Neoporus	0.48	0.61	0.53	1.01	0.87	68.76
Hydropsyche	0.32	0.35	0.53	0.59	0.87	69.63
Physa	0.53	0.65	0.52	0.89	0.86	70.5
Dineutus	0.65	0	0.51	0.62	0.83	71.33
Chromagrion	0.47	0.51	0.5	0.76	0.83	72.16
Ephemerella	0.35	0.22	0.47	0.64	0.77	72.93
Ferrissia	0.37	0.47	0.45	0.68	0.75	73.68
Hirudinea	0.51	0.39	0.45	0.8	0.75	74.42
Hydroptila	0.54	0.25	0.45	0.85	0.74	75.17
Leptoceridae	0.53	0.17	0.44	0.74	0.73	75.9
Peltodytes	0.43	0.17	0.44	0.66	0.73	76.63
Macronychus	0.74	0.12	0.43	0.56	0.71	77.34
Nectopsyche	0.69	0.17	0.42	0.7	0.69	78.03
Polycentropus	0.23	0.42	0.39	0.68	0.64	78.67
Epitheca	0	0.43	0.35	0.67	0.57	79.24
Argia	0.42	0	0.34	0.83	0.57	79.81
Pleurocera	0.43	0	0.33	0.56	0.54	80.35

Groups Rocky Ford & Morgan's Bridge

Average dissimilarity = 55.75

Species	Group Rocky Ford Av.Abund	Group Morgan's Bridge Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hyalella	0.7	3.7	2.63	1.24	4.72	4.72
Hydrobiidae	3.88	2.47	2.08	1.18	3.73	8.45
Baetidae	2.74	1.44	1.63	1.26	2.93	11.38
Caecidotea	2.97	1.99	1.6	0.88	2.87	14.25
Chironominae	3.84	4.21	1.58	1.38	2.84	17.09
Palaemonetes	2.57	1.26	1.5	1.15	2.69	19.78
Lirceus	3.74	3.59	1.43	0.98	2.56	22.34
Hydrachnidiae	2.87	3.13	1.34	1.29	2.4	24.73
Oligochaeta	1.3	2	1.3	0.61	2.33	27.07
Cambaridae	2.24	0.6	1.3	1.46	2.33	29.4
Orthocladiinae	1.48	2.2	1.28	0.89	2.3	31.7
Tricorythodes	1.57	0.88	1.16	1.19	2.08	33.78
Tanypodinae	3.22	2.82	1.1	1.41	1.98	35.75
Crangonyx	1.26	0.46	1.09	0.97	1.96	37.72
Copepoda	0.67	1.5	1.07	0.98	1.92	39.64
Ceratopogonidae	0.71	1.47	1.05	0.73	1.88	41.52
Sphaeridae	0.85	1.07	1.03	1.06	1.85	43.37

Hirudinea	1.39	0.39	1	0.5	1.79	45.16
Stenelmis	0.99	0.31	0.92	1.43	1.66	46.82
Ephemeroptera	0.25	0.95	0.92	0.75	1.64	48.46
Chironomidae	1.29	1.22	0.87	1.16	1.57	50.03
Planoorbidae	1.38	1.5	0.82	1.24	1.47	51.49
Gammarus	0.7	0.3	0.79	0.87	1.42	52.91
Caenis	0.55	1.21	0.73	0.82	1.31	54.23
Maccaffertium	1.36	1.21	0.72	1.21	1.29	55.52
Simulium	0.8	0.39	0.69	0.67	1.24	56.76
Leptophlebiidae	0.35	0.82	0.67	0.68	1.21	57.97
Gyrinus	0.2	0.65	0.67	0.51	1.2	59.17
Cheumatopsyche	0.82	0.08	0.67	0.84	1.2	60.37
Baetisca	1.05	1.68	0.65	0.7	1.17	61.54
Physa	0.63	0.65	0.63	1.04	1.14	62.68
Hydroptilidae	0.67	0.35	0.62	0.86	1.12	63.8
Ephemerella	0.62	0.22	0.59	0.7	1.06	64.86
Dubiraphia	0.73	0.28	0.54	0.68	0.96	65.82
Taeniopteryx	0.68	0.19	0.53	0.49	0.94	66.77
Macronychus	0.8	0.12	0.51	0.72	0.91	67.68
Macromia	0.65	0.17	0.5	0.84	0.9	68.58
Polycentropus	0.23	0.42	0.5	0.77	0.89	69.47
Oecetis	0.31	0.44	0.49	0.92	0.88	70.35
Ferrissia	0.72	0.47	0.48	0.7	0.87	71.22
Nectopsyche	0.54	0.17	0.47	0.81	0.83	72.05
Corbicula	0.56	0	0.45	0.6	0.8	72.85
Neoporus	0.39	0.61	0.43	0.73	0.77	73.63
Pleurocera	0.57	0	0.42	0.59	0.75	74.37
Chromagrion	0.14	0.51	0.41	0.67	0.73	75.1
Bivalvia	0.35	0.26	0.4	0.49	0.71	75.81
Hydroptila	0.41	0.25	0.4	0.74	0.71	76.52
Corixidae	0.32	0.23	0.36	0.66	0.64	77.16
Elmidae	0.53	0.08	0.35	0.44	0.63	77.79
Polycentropodidae	0.33	0.08	0.32	0.81	0.58	78.36
Ostracoda	0.3	0.08	0.31	0.53	0.56	78.93
Eurylophella	0	0.35	0.3	0.38	0.54	79.47
Leptoceridae	0.28	0.17	0.3	0.61	0.54	80

Groups Oliver & Morgan's Bridge

Average dissimilarity = 57.91

	Group Oliver	**Group Morgan's Bridge**

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hyalella	0.77	3.7	2.75	1.17	4.75	4.75
Baetidae	3.13	1.44	2.13	0.99	3.69	8.44
Chironominae	3.55	4.21	1.79	1.34	3.09	11.53
Hydrobiidae	2.69	2.47	1.77	1.12	3.05	14.59
Tricorythodes	1.93	0.88	1.7	1.09	2.93	17.52
Hydrachnidiae	2.18	3.13	1.52	0.87	2.63	20.15
Orthocladiinae	1.9	2.2	1.46	1.13	2.52	22.67
Tanypodinae	3.04	2.82	1.43	1.44	2.47	25.14
Copepoda	0.82	1.5	1.39	1.01	2.4	27.54
Lirceus	3.48	3.59	1.38	0.75	2.39	29.93
Caecidotea	1.67	1.99	1.3	1.08	2.25	32.18
Oligochaeta	1.29	2	1.25	0.7	2.16	34.34
Crangonyx	1.32	0.46	1.2	0.83	2.07	36.41
Cambaridae	1.81	0.6	1.19	1.27	2.06	38.47
Cheumatopsyche	1.47	0.08	1.18	0.91	2.04	40.51
Palaemonetes	1.7	1.26	1.18	1.22	2.04	42.55
Gammarus	1.37	0.3	1.13	0.83	1.95	44.5
Planoorbidae	1.08	1.5	1.09	1.72	1.88	46.38
Ceratopogonidae	1.13	1.47	1.05	0.87	1.81	48.19
Simulium	1.18	0.39	1.03	0.74	1.78	49.97
Chironomidae	1.2	1.22	1	1.29	1.72	51.7
Caenis	1.7	1.21	0.93	0.75	1.61	53.31
Maccaffertium	1.69	1.21	0.93	1	1.61	54.93
Stenelmis	1.34	0.31	0.91	0.95	1.57	56.49
Ephemeroptera	0.12	0.95	0.88	0.69	1.51	58.01
Perlesta	1.13	0.25	0.75	0.56	1.29	59.3
Isonychia	0.86	0.22	0.71	0.61	1.22	60.51
Leptophlebiidae	0.37	0.82	0.69	0.69	1.2	61.71
Sphaeridae	0.43	1.07	0.68	0.69	1.18	62.89
Taeniopteryx	0.76	0.19	0.64	0.41	1.11	64
Hirudinea	0.85	0.39	0.63	0.91	1.09	65.09
Ephemerella	0.78	0.22	0.63	0.7	1.09	66.18
Gyrinus	0.17	0.65	0.63	0.5	1.08	67.26
Physa	0.49	0.65	0.58	0.87	1	68.27
Baetisca	1.39	1.68	0.56	0.69	0.96	69.23
Hydroptilidae	0.5	0.35	0.55	0.61	0.95	70.18
Nectopsyche	0.86	0.17	0.55	0.91	0.94	71.12
Hydroptila	0.59	0.25	0.54	0.61	0.93	72.06
Ferrissia	0.64	0.47	0.53	0.61	0.92	72.98
Oecetis	0.28	0.44	0.52	1.03	0.9	73.88
Dubiraphia	0.69	0.28	0.52	1.01	0.9	74.78

Hydropsyche	0.67	0.35	0.51	0.81	0.89	75.67
Neoporus	0.51	0.61	0.48	0.8	0.83	76.5
Ancyronyx	0.6	0	0.47	0.4	0.8	77.31
Macronychus	0.63	0.12	0.45	0.7	0.78	78.08
Macromia	0.53	0.17	0.44	0.79	0.76	78.84
Chromagrion	0	0.51	0.41	0.66	0.7	79.54
Corixidae	0.37	0.23	0.39	0.54	0.67	80.22

Groups Hwy 119 & Morgan's Bridge

Average dissimilarity = 53.85

Species	Group Hwy 119 Av.Abund	Group Morgan's Bridge Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Caecidotea	4.25	1.99	2.85	1.44	5.29	5.29
Hyalella	1.14	3.7	2.59	1.1	4.8	10.09
Chironominae	3.16	4.21	1.97	1.5	3.66	13.75
Lirceus	4.51	3.59	1.79	0.75	3.32	17.07
Hydrobiidae	3.11	2.47	1.61	1.34	2.99	20.06
Planoorbidae	3.08	1.5	1.58	1.45	2.94	23.01
Orthocladiinae	0.25	2.2	1.52	1.01	2.82	25.83
Palaemonetes	2.47	1.26	1.52	1.11	2.82	28.65
Hydrachnidiae	2.36	3.13	1.52	1.08	2.81	31.46
Crangonyx	1.54	0.46	1.49	0.84	2.77	34.24
Oligochaeta	1.48	2	1.46	0.74	2.71	36.94
Tanypodinae	3.18	2.82	1.39	1.26	2.59	39.53
Baetidae	1.52	1.44	1.38	0.96	2.56	42.09
Copepoda	1.87	1.5	1.27	1.3	2.36	44.45
Tricorythodes	1.01	0.88	1.13	1.1	2.11	46.56
Chironomidae	1.15	1.22	0.99	1.41	1.84	48.4
Ceratopogonidae	1.04	1.47	0.96	0.73	1.78	50.17
Gammarus	1.28	0.3	0.95	0.76	1.77	51.94
Sphaeridae	0.75	1.07	0.89	0.86	1.64	53.59
Cambaridae	1.24	0.6	0.88	1.51	1.64	55.23
Ephemeroptera	0	0.95	0.85	0.65	1.58	56.8
Hirudinea	1.11	0.39	0.81	0.78	1.5	58.31
Simulium	0.82	0.39	0.8	0.64	1.48	59.79
Leptophlebiidae	0	0.82	0.73	0.64	1.35	61.14
Maccaffertium	1.17	1.21	0.68	0.88	1.26	62.4
Physa	1.06	0.65	0.65	0.99	1.21	63.61
Cheumatopsyche	0.74	0.08	0.65	0.97	1.21	64.83
Ferrissia	0.81	0.47	0.64	0.77	1.19	66.02

Gyrinus	0	0.65	0.56	0.42	1.04	67.06
Perlesta	0.53	0.25	0.56	0.56	1.04	68.1
Ephemerella	0.57	0.22	0.54	0.79	1	69.1
Nectopsyche	0.66	0.17	0.49	0.74	0.92	70.02
Stenelmis	0.28	0.31	0.48	0.83	0.89	70.91
Neoporus	0.44	0.61	0.48	0.78	0.89	71.79
Caenis	0.95	1.21	0.47	0.63	0.87	72.66
Chromagrion	0	0.51	0.43	0.66	0.79	73.45
Oecetis	0.17	0.44	0.42	0.81	0.79	74.24
Baetisca	1.69	1.68	0.41	0.84	0.75	74.99
Hydroptila	0.33	0.25	0.4	0.58	0.74	75.73
Hydropsyche	0.2	0.35	0.37	0.65	0.69	76.43
Corixidae	0.28	0.23	0.35	0.47	0.65	77.07
Epitheca	0.19	0.43	0.34	0.66	0.63	77.7
Eurylophella	0	0.35	0.34	0.38	0.62	78.33
Isonychia	0.25	0.22	0.33	0.55	0.62	78.95
Argia	0.39	0	0.32	0.52	0.6	79.55
Hydroptilidae	0.2	0.35	0.32	0.65	0.6	80.15

APPENDIX C

SEASONAL SIMPER RESULTS

SIMPER results for within season similarities and among season dissimilarities, cutting off at a cumulative 80% similarity or dissimilarity to omit low contributing or rare taxa.

Group Summer

Average similarity: 44.33

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironominae	5.14	5.6	1.93	12.62	12.62
Hydrobiidae	5.88	5.51	1.49	12.44	25.07
Tanypodinae	3.78	3.67	1.69	8.27	33.34
Hydrachnidiae	2.83	2.4	1.48	5.42	38.76
Oligochaeta	3.34	2.22	1.46	5	43.77
Planoorbidae	2.12	1.83	1.29	4.13	47.9
Palaemonetes	1.87	1.6	0.89	3.62	51.51
Cambaridae	1.89	1.6	1.38	3.6	55.11
Caecidotea	1.9	1.41	0.57	3.17	58.29
Tricorythodes	1.34	1.41	0.97	3.17	61.46
Sphaeridae	2.11	1.29	0.75	2.91	64.37
Orthocladiinae	1.76	1.24	1.09	2.79	67.16
Hirudinea	2.07	1.2	1.08	2.7	69.86
Hyalella	1.52	1.16	0.48	2.63	72.49
Chironomidae	1.59	1.01	0.66	2.28	74.77
Maccaffertium	1.29	0.96	1.03	2.17	76.94
Macronychus	1.22	0.89	0.8	2.01	78.95
Cheumatopsyche	1.35	0.78	0.4	1.76	80.71

Group Fall

Average similarity: 48.66

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironominae	5.47	6.83	2.26	14.03	14.03
Tanypodinae	4	4.79	2.86	9.84	23.88
Hydrobiidae	3.88	4.35	2.68	8.94	32.82
Hydrachnidiae	3.37	3.93	3.06	8.07	40.89
Palaemonetes	3.54	3.68	1.46	7.56	48.45

Caenis	2.73	2.94	1.37	6.04	54.49
Oligochaeta	1.96	2.02	1.24	4.16	58.65
Ceratopogonidae	1.65	1.84	2.43	3.78	62.43
Tricorythodes	2.29	1.69	0.96	3.48	65.91
Stenelmis	1.54	1.6	1.03	3.29	69.2
Cambaridae	1.66	1.46	1.25	3	72.2
Caecidotea	1.46	1.18	0.8	2.42	74.62
Orthocladiinae	1.31	1.14	1.08	2.35	76.97
Baetidae	1.51	1.12	1.05	2.3	79.27
Planoorbidae	1.13	0.93	0.78	1.92	81.18

Group Winter

Average similarity: 46.26

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Chironominae	4.33	5.3	1.84	11.46	11.46
Lirceus	4.14	5.28	1.17	11.42	22.88
Baetisca	3.18	4.84	1.12	10.46	33.34
Hydrachnidiae	3.11	3.69	1.85	7.97	41.31
Tanypodinae	3.07	3.31	1.42	7.16	48.47
Copepoda	2.11	2.26	1.1	4.87	53.34
Hydrobiidae	2.31	2.18	1.17	4.7	58.05
Orthocladiinae	2.35	2.01	1.03	4.35	62.39
Maccaffertium	1.98	1.85	1.54	3.99	66.39
Palaemonetes	1.76	1.55	1.05	3.36	69.75
Caecidotea	1.48	1.54	0.73	3.33	73.07
Baetidae	1.86	1.31	0.67	2.83	75.9
Hyalella	1.52	1.28	0.47	2.78	78.67
Cambaridae	1.22	1	1.04	2.15	80.83

Group Spring

Average similarity: 47.76

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Lirceus	5.9	8.15	1.09	17.07	17.07
Tanypodinae	3.27	4.71	1.7	9.86	26.93
Chironominae	3.83	4.1	1.36	8.58	35.51
Caecidotea	3.79	3.87	1.2	8.1	43.61
Baetidae	3.52	2.97	0.79	6.22	49.83
Maccaffertium	1.59	2.21	1.92	4.64	54.47
Orthocladiinae	1.9	2	1.31	4.19	58.66
Planoorbidae	1.58	1.92	0.82	4.03	62.69

Copepoda	1.48	1.35	0.95	2.82	65.51
Hyalella	1.58	1.15	0.56	2.4	67.92
Cambaridae	1.25	1.14	0.73	2.39	70.3
Hydrobiidae	1.24	1.13	0.91	2.37	72.67
Palaemonetes	1.33	1.13	0.75	2.36	75.03
Chironomidae	1.58	1.05	0.62	2.2	77.23
Physa	0.99	1.05	0.81	2.2	79.43
Hydrachnidiae	1.17	0.97	0.67	2.03	81.46

Groups Summer & Fall

Average dissimilarity = 54.97

Species	Group Summer Av.Abund	Group Fall Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hydrobiidae	5.88	3.88	2.46	1.28	4.47	4.47
Palaemonetes	1.87	3.54	1.77	1.59	3.23	7.69
Oligochaeta	3.34	1.96	1.72	0.91	3.13	10.82
Caenis	0.88	2.73	1.6	1.32	2.91	13.74
Tanypodinae	3.78	4	1.55	1.45	2.81	16.55
Chironominae	5.14	5.47	1.47	1.23	2.67	19.21
Ceratopogonidae	1.86	1.65	1.41	1.17	2.57	21.78
Sphaeridae	2.11	0.87	1.37	1.19	2.5	24.28
Hydrachnidiae	2.83	3.37	1.33	1.42	2.41	26.69
Tricorythodes	1.34	2.29	1.22	1.13	2.23	28.92
Hirudinea	2.07	0.82	1.18	0.76	2.14	31.06
Caecidotea	1.9	1.46	1.11	0.93	2.02	33.08
Ferrissia	0.58	1.57	1.11	1.12	2.02	35.09
Copepoda	1.21	0.95	1.1	0.84	1.99	37.09
Planoorbidae	2.12	1.13	1.09	1.45	1.97	39.06
Chironomidae	1.59	1.4	1.02	1.27	1.85	40.91
Hyalella	1.52	0.93	1.01	0.87	1.84	42.75
Orthocladiinae	1.76	1.31	0.96	0.72	1.74	44.49
Baetidae	0.93	1.51	0.94	1.33	1.72	46.21
Crangonyx	1.23	0.27	0.93	0.75	1.7	47.9
Cambaridae	1.89	1.66	0.92	1.42	1.68	49.58
Cheumatopsyche	1.35	0.64	0.91	0.72	1.66	51.24
Gammarus	1.1	0.59	0.9	0.73	1.63	52.87
Stenelmis	0.93	1.54	0.88	1.16	1.6	54.47
Dubiraphia	0.73	1.16	0.82	1.13	1.48	55.95
Macronychus	1.22	0.47	0.77	1.1	1.41	57.36
Maccaffertium	1.29	0.5	0.73	1.16	1.32	58.68

Physa	0.83	0.36	0.69	1.36	1.26	59.94
Corixidae	0.67	0.34	0.64	0.82	1.16	61.1
Corbicula	0.64	0.64	0.59	0.9	1.08	62.18
Hydroptilidae	0.69	0.41	0.59	0.86	1.08	63.26
Ancyronyx	0.69	0.79	0.58	0.67	1.06	64.32
Nectopsyche	1	0.6	0.57	1.01	1.04	65.36
Hydroptila	0.51	0.43	0.56	0.83	1.02	66.39
Oecetis	0.78	0.25	0.55	0.98	1	67.39
Argia	0.21	0.76	0.53	0.7	0.97	68.36
Chimarra	0.54	0.22	0.51	0.56	0.93	69.29
Macromia	0.17	0.7	0.49	0.86	0.89	70.18
Chromagrion	0.21	0.66	0.48	0.74	0.87	71.06
Peltodytes	0.26	0.56	0.48	0.66	0.87	71.92
Pleurocera	0.57	0.36	0.43	0.73	0.78	72.7
Gyrinus	0.43	0.06	0.4	0.33	0.72	73.43
Lirceus	0.45	0.34	0.4	0.86	0.72	74.15
Simulium	0.13	0.46	0.4	0.54	0.72	74.87
Epitheca	0.25	0.56	0.39	0.74	0.72	75.59
Rheumatobates	0.37	0.28	0.38	0.61	0.68	76.27
Polycentropodidae	0.44	0.06	0.35	0.84	0.64	76.91
Dineutus	0.47	0.24	0.32	0.63	0.58	77.5
Hexagenia	0.37	0.5	0.31	0.66	0.57	78.06
Bivalvia	0.41	0.08	0.31	0.44	0.56	78.63
Leptoceridae	0.26	0.2	0.27	0.54	0.49	79.12
Ephemerella	0	0.39	0.26	0.46	0.48	79.6
Ephemeroptera	0.18	0.17	0.26	0.38	0.47	80.08

Groups Summer & Winter

Average dissimilarity = 65.01

Species	**Group Summer Av.Abund**	**Group Winter Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Hydrobiidae	5.88	2.31	3.31	1.61	5.09	5.09
Lirceus	0.45	4.14	2.96	1.17	4.55	9.64
Baetisca	0	3.18	2.58	1.22	3.97	13.61
Oligochaeta	3.34	0.55	2.08	0.95	3.2	16.81
Tanypodinae	3.78	3.07	1.71	1.39	2.63	19.44
Hydrachnidiae	2.83	3.11	1.62	1.22	2.49	21.93
Chironominae	5.14	4.33	1.62	1.31	2.48	24.42
Copepoda	1.21	2.11	1.58	1.19	2.43	26.85
Hirudinea	2.07	0.13	1.42	0.82	2.19	29.03

Ceratopogonidae	1.86	0.49	1.39	0.94	2.14	31.17
Orthocladiinae	1.76	2.35	1.37	1.03	2.11	33.28
Sphaeridae	2.11	0.57	1.36	1.11	2.09	35.37
Caecidotea	1.9	1.48	1.27	1.01	1.95	37.32
Tricorythodes	1.34	0.62	1.19	1.32	1.83	39.15
Baetidae	0.93	1.86	1.15	1.02	1.78	40.93
Simulium	0.13	1.45	1.15	0.91	1.77	42.7
Cheumatopsyche	1.35	0.9	1.15	0.82	1.77	44.47
Planoorbidae	2.12	0.97	1.13	1.43	1.74	46.21
Hyalella	1.52	1.52	1.12	0.89	1.72	47.92
Taeniopteryx	0	1.35	1.07	0.74	1.65	49.57
Crangonyx	1.23	0.62	1.01	0.79	1.56	51.13
Chironomidae	1.59	0.92	1.01	1.3	1.56	52.68
Palaemonetes	1.87	1.76	1.01	1.26	1.55	54.23
Cambaridae	1.89	1.22	0.98	1.16	1.51	55.74
Maccaffertium	1.29	1.98	0.95	1.18	1.46	57.2
Gammarus	1.1	0.25	0.91	0.7	1.39	58.59
Macronychus	1.22	0	0.91	1.14	1.39	59.99
Eurylophella	0	1.08	0.82	0.49	1.26	61.25
Stenelmis	0.93	0.34	0.77	1.18	1.18	62.43
Caenis	0.88	0.29	0.76	0.93	1.18	63.61
Hydroptilidae	0.69	0.66	0.71	0.8	1.08	64.69
Nectopsyche	1	0.34	0.7	1.15	1.08	65.77
Neoporus	0.06	0.91	0.68	1.01	1.04	66.82
Hydroptila	0.51	0.6	0.66	0.94	1.01	67.83
Hydropsyche	0.27	0.59	0.64	0.78	0.98	68.81
Physa	0.83	0.26	0.64	1.03	0.98	69.79
Ephemerella	0	0.79	0.6	0.65	0.92	70.71
Oecetis	0.78	0.25	0.57	0.98	0.88	71.59
Ferrissia	0.58	0.25	0.54	0.69	0.83	72.42
Leptophlebiidae	0.11	0.71	0.51	0.62	0.79	73.21
Corixidae	0.67	0	0.51	0.74	0.79	74
Chimarra	0.54	0.21	0.51	0.55	0.78	74.77
Dineutus	0.47	0.32	0.49	0.85	0.76	75.53
Macromia	0.17	0.66	0.48	0.88	0.73	76.27
Corbicula	0.64	0.06	0.47	0.64	0.73	77
Ancyronyx	0.69	0	0.47	0.8	0.73	77.73
Dubiraphia	0.73	0.32	0.44	0.78	0.68	78.41
Gyrinus	0.43	0.13	0.43	0.34	0.66	79.07
Pleurocera	0.57	0.34	0.43	0.66	0.66	79.73
Polycentropodidae	0.44	0.32	0.37	0.81	0.57	80.29

Groups Fall & Winter

Average dissimilarity = 62.24

Species	Group Fall Av.Abund	Group Winter Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lirceus	0.34	4.14	3.13	1.21	5.03	5.03
Baetisca	0.19	3.18	2.64	1.28	4.24	9.27
Caenis	2.73	0.29	2.02	1.37	3.24	12.51
Palaemonetes	3.54	1.76	1.92	1.68	3.09	15.6
Chironominae	5.47	4.33	1.76	1.22	2.83	18.43
Tanypodinae	4	3.07	1.74	1.4	2.8	21.23
Hydrobiidae	3.88	2.31	1.71	1.1	2.75	23.98
Tricorythodes	2.29	0.62	1.7	1	2.73	26.71
Baetidae	1.51	1.86	1.35	1.35	2.18	28.88
Orthocladiinae	1.31	2.35	1.3	1.12	2.09	30.97
Hydrachnidiae	3.37	3.11	1.27	1.11	2.05	33.02
Copepoda	0.95	2.11	1.27	1.23	2.04	35.06
Maccaffertium	0.5	1.98	1.25	1.32	2.01	37.07
Hyalella	0.93	1.52	1.25	0.77	2	39.08
Oligochaeta	1.96	0.55	1.23	1.26	1.98	41.05
Ferrissia	1.57	0.25	1.2	1.14	1.93	42.98
Simulium	0.46	1.45	1.17	0.98	1.88	44.86
Taeniopteryx	0	1.35	1.08	0.76	1.74	46.6
Ceratopogonidae	1.65	0.49	1.06	1.74	1.7	48.31
Chironomidae	1.4	0.92	1.01	1.43	1.63	49.94
Caecidotea	1.46	1.48	1.01	1.23	1.62	51.55
Stenelmis	1.54	0.34	0.98	1.15	1.58	53.14
Eurylophella	0	1.08	0.89	0.49	1.43	54.57
Cambaridae	1.66	1.22	0.87	1.36	1.39	55.96
Dubiraphia	1.16	0.32	0.8	1.01	1.29	57.25
Ephemerella	0.39	0.79	0.75	0.77	1.2	58.45
Neoporus	0.23	0.91	0.73	1.05	1.17	59.63
Cheumatopsyche	0.64	0.9	0.7	0.91	1.13	60.75
Hydroptilidae	0.41	0.66	0.68	0.79	1.09	61.84
Planoorbidae	1.13	0.97	0.67	0.99	1.08	62.92
Sphaeridae	0.87	0.57	0.63	0.83	1.02	63.94
Hirudinea	0.82	0.13	0.62	0.99	1	64.94
Ancyronyx	0.79	0	0.6	0.58	0.97	65.91
Macromia	0.7	0.66	0.6	1.04	0.96	66.87
Hydroptila	0.43	0.6	0.6	0.74	0.96	67.82
Argia	0.76	0.06	0.59	0.66	0.95	68.77

Crangonyx	0.27	0.62	0.58	0.68	0.94	69.71
Leptophlebiidae	0	0.71	0.56	0.64	0.9	70.61
Gammarus	0.59	0.25	0.54	0.5	0.87	71.49
Corbicula	0.64	0.06	0.53	0.73	0.86	72.34
Nectopsyche	0.6	0.34	0.5	0.83	0.8	73.14
Chromagrion	0.66	0.34	0.49	0.76	0.79	73.93
Epitheca	0.56	0	0.46	0.73	0.74	74.67
Physa	0.36	0.26	0.46	0.88	0.74	75.41
Peltodytes	0.56	0.31	0.46	0.65	0.74	76.14
Hydropsyche	0.06	0.59	0.46	0.75	0.73	76.87
Dineutus	0.24	0.32	0.44	0.63	0.7	77.58
Ephemeroptera	0.17	0.44	0.43	0.45	0.69	78.26
Perlesta	0	0.49	0.36	0.39	0.58	78.84
Oecetis	0.25	0.25	0.36	0.8	0.58	79.43
Macronychus	0.47	0	0.34	0.58	0.55	79.98
Leptoceridae	0.2	0.36	0.34	0.61	0.54	80.51

Groups Summer & Spring

Average dissimilarity = 66.81

Species	**Group Summer Av.Abund**	**Group Spring Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.45	5.9	4.48	1.18	6.71	6.71
Hydrobiidae	5.88	1.24	3.84	1.76	5.74	12.45
Caecidotea	1.9	3.79	2.35	1.02	3.51	15.96
Baetidae	0.93	3.52	2.27	1.07	3.39	19.35
Chironominae	5.14	3.83	2.1	1.44	3.15	22.5
Oligochaeta	3.34	1.06	2	0.91	3	25.5
Hydrachnidiae	2.83	1.17	1.79	1.36	2.69	28.18
Tanypodinae	3.78	3.27	1.56	1.35	2.34	30.52
Sphaeridae	2.11	0.26	1.5	1.19	2.25	32.77
Ceratopogonidae	1.86	0.77	1.47	1.03	2.2	34.98
Hirudinea	2.07	0.28	1.39	0.85	2.08	37.05
Crangonyx	1.23	1.36	1.37	1.03	2.05	39.1
Hyalella	1.52	1.58	1.36	1.11	2.03	41.13
Copepoda	1.21	1.48	1.34	1.08	2.01	43.14
Tricorythodes	1.34	0.5	1.28	1.33	1.91	45.05
Palaemonetes	1.87	1.33	1.27	1.44	1.9	46.95
Orthocladiinae	1.76	1.9	1.13	0.89	1.69	48.64
Chironomidae	1.59	1.58	1.08	1.24	1.61	50.25
Cheumatopsyche	1.35	0.75	1.05	0.79	1.58	51.82

Planoorbidae	2.12	1.58	1.04	1.48	1.56	53.38
Gammarus	1.1	0.66	1.03	0.87	1.54	54.93
Cambaridae	1.89	1.25	1.01	1.36	1.51	56.44
Macronychus	1.22	0.11	0.89	1.17	1.33	57.77
Perlesta	0	1.13	0.87	0.84	1.31	59.08
Physa	0.83	0.99	0.86	1.21	1.28	60.36
Stenelmis	0.93	0.44	0.84	1.28	1.26	61.62
Maccaffertium	1.29	1.59	0.81	1.29	1.21	62.82
Nectopsyche	1	0.06	0.72	1.04	1.07	63.9
Baetisca	0	0.84	0.67	1.26	1	64.9
Caenis	0.88	0	0.66	0.85	0.98	65.88
Isonychia	0	0.82	0.64	0.74	0.95	66.83
Neoporus	0.06	0.78	0.62	1.31	0.93	67.76
Oecetis	0.78	0.19	0.61	0.96	0.91	68.67
Ferrissia	0.58	0.4	0.6	0.8	0.9	69.57
Ephemerella	0	0.72	0.57	0.8	0.85	70.43
Simulium	0.13	0.85	0.55	0.61	0.82	71.25
Hydroptilidae	0.69	0.3	0.55	0.78	0.82	72.07
Corixidae	0.67	0.11	0.54	0.82	0.81	72.89
Corbicula	0.64	0.17	0.54	0.76	0.81	73.7
Dubiraphia	0.73	0.37	0.51	0.8	0.76	74.46
Leptophlebiidae	0.11	0.62	0.5	0.71	0.74	75.21
Hydropsyche	0.27	0.3	0.44	0.58	0.66	75.87
Ancyronyx	0.69	0.13	0.44	0.79	0.66	76.52
Chimarra	0.54	0.11	0.42	0.48	0.63	77.15
Hydroptila	0.51	0.06	0.41	0.71	0.61	77.76
Gyrinus	0.43	0.06	0.4	0.33	0.6	78.36
Isoperla	0	0.53	0.4	0.84	0.6	78.96
Pleurocera	0.57	0	0.39	0.56	0.59	79.55
Ephemeroptera	0.18	0.3	0.36	0.48	0.54	80.09

Groups Fall & Spring

Average dissimilarity = 64.54

Species	**Group Fall Av.Abund**	**Group Spring Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Lirceus	0.34	5.9	4.69	1.22	7.27	7.27
Chironominae	5.47	3.83	2.29	1.31	3.55	10.82
Caecidotea	1.46	3.79	2.27	1.1	3.52	14.34
Caenis	2.73	0	2.22	1.52	3.43	17.77
Baetidae	1.51	3.52	2.19	1.06	3.4	21.17

Hydrobiidae	3.88	1.24	2.15	1.29	3.33	24.5
Palaemonetes	3.54	1.33	2.12	1.57	3.28	27.78
Hydrachnidiae	3.37	1.17	2.11	1.77	3.26	31.05
Tricorythodes	2.29	0.5	1.8	1.14	2.79	33.84
Tanypodinae	4	3.27	1.61	1.34	2.49	36.33
Hyalella	0.93	1.58	1.24	1.27	1.92	38.25
Ferrissia	1.57	0.4	1.2	1.1	1.86	40.11
Oligochaeta	1.96	1.06	1.18	1.29	1.83	41.94
Chironomidae	1.4	1.58	1.16	1.31	1.79	43.74
Crangonyx	0.27	1.36	1.15	0.74	1.78	45.51
Copepoda	0.95	1.48	1.1	1.27	1.7	47.21
Orthocladiinae	1.31	1.9	1.02	1.12	1.57	48.79
Stenelmis	1.54	0.44	1.01	1.12	1.57	50.35
Ceratopogonidae	1.65	0.77	0.98	1.74	1.51	51.87
Dubiraphia	1.16	0.37	0.97	1.24	1.51	53.38
Maccaffertium	0.5	1.59	0.97	1.3	1.5	54.88
Planoorbidae	1.13	1.58	0.95	1.13	1.48	56.35
Perlesta	0	1.13	0.89	0.85	1.38	57.74
Simulium	0.46	0.85	0.84	0.89	1.31	59.04
Cambaridae	1.66	1.25	0.82	1.15	1.27	60.31
Ephemerella	0.39	0.72	0.74	0.97	1.15	61.46
Sphaeridae	0.87	0.26	0.7	0.93	1.08	62.54
Gammarus	0.59	0.66	0.68	0.67	1.06	63.6
Hirudinea	0.82	0.28	0.67	1.09	1.04	64.64
Isonychia	0.17	0.82	0.66	0.81	1.03	65.67
Baetisca	0.19	0.84	0.65	1.23	1.01	66.68
Neoporus	0.23	0.78	0.64	1.32	0.99	67.67
Physa	0.36	0.99	0.63	0.93	0.98	68.64
Argia	0.76	0.06	0.59	0.66	0.92	69.56
Cheumatopsyche	0.64	0.75	0.58	0.99	0.91	70.47
Ancyronyx	0.79	0.13	0.58	0.57	0.89	71.36
Macromia	0.7	0.3	0.56	0.99	0.86	72.22
Leptophlebiidae	0	0.62	0.49	0.64	0.75	72.98
Corbicula	0.64	0.17	0.49	0.67	0.75	73.73
Chromagrion	0.66	0.11	0.49	0.71	0.75	74.48
Epitheca	0.56	0	0.48	0.73	0.74	75.22
Peltodytes	0.56	0.06	0.48	0.58	0.74	75.96
Nectopsyche	0.6	0.06	0.47	0.74	0.73	76.68
Hydroptilidae	0.41	0.3	0.46	0.69	0.71	77.39
Isoperla	0	0.53	0.43	0.84	0.66	78.06
Macronychus	0.47	0.11	0.4	0.68	0.62	78.68
Hexagenia	0.5	0	0.4	0.76	0.62	79.29

Corixidae	0.34	0.11	0.39	0.49	0.61	79.9
Hydroptila	0.43	0.06	0.36	0.53	0.56	80.46

Groups Winter & Spring

Average dissimilarity = 55.90

Species	Group Winter Av.Abund	Group Spring Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lirceus	4.14	5.9	2.62	1.11	4.7	4.7
Baetisca	3.18	0.84	2.48	1.28	4.43	9.13
Caecidotea	1.48	3.79	2.37	1.09	4.23	13.36
Baetidae	1.86	3.52	2.3	1.09	4.12	17.48
Hydrachnidiae	3.11	1.17	2.02	1.24	3.62	21.1
Chironominae	4.33	3.83	1.68	1.52	3.01	24.11
Hyalella	1.52	1.58	1.65	1.12	2.95	27.06
Crangonyx	0.62	1.36	1.36	0.88	2.43	29.49
Simulium	1.45	0.85	1.33	1.01	2.39	31.87
Orthocladiinae	2.35	1.9	1.27	1.19	2.27	34.14
Tanypodinae	3.07	3.27	1.2	1.37	2.15	36.29
Hydrobiidae	2.31	1.24	1.19	1.08	2.13	38.42
Palaemonetes	1.76	1.33	1.16	1.28	2.08	40.5
Taeniopteryx	1.35	0.06	1.16	0.75	2.08	42.58
Copepoda	2.11	1.48	1.11	1.37	1.99	44.57
Chironomidae	0.92	1.58	1.1	1.28	1.96	46.53
Perlesta	0.49	1.13	0.98	0.84	1.76	48.29
Maccaffertium	1.98	1.59	0.96	1.09	1.71	50
Cambaridae	1.22	1.25	0.9	1.24	1.61	51.62
Physa	0.26	0.99	0.88	0.98	1.58	53.19
Planoorbidae	0.97	1.58	0.87	0.99	1.56	54.76
Eurylophella	1.08	0.22	0.87	0.51	1.55	56.31
Ephemerella	0.79	0.72	0.86	0.94	1.54	57.85
Oligochaeta	0.55	1.06	0.85	1.03	1.52	59.36
Cheumatopsyche	0.9	0.75	0.78	0.86	1.39	60.76
Leptophlebiidae	0.71	0.62	0.75	0.9	1.35	62.1
Isonychia	0.23	0.82	0.74	0.75	1.32	63.42
Neoporus	0.91	0.78	0.73	1.22	1.3	64.72
Tricorythodes	0.62	0.5	0.69	0.71	1.23	65.96
Hydroptilidae	0.66	0.3	0.61	0.64	1.1	67.06
Gammarus	0.25	0.66	0.58	0.7	1.03	68.09
Ceratopogonidae	0.49	0.77	0.55	0.9	0.99	69.08
Macromia	0.66	0.3	0.54	0.91	0.97	70.05

Ephemeroptera	0.44	0.3	0.54	0.55	0.96	71.01
Hydroptila	0.6	0.06	0.51	0.61	0.92	71.93
Stenelmis	0.34	0.44	0.49	0.95	0.87	72.8
Isoperla	0.08	0.53	0.46	0.88	0.83	73.63
Hydropsyche	0.59	0.3	0.46	0.75	0.82	74.45
Ferrissia	0.25	0.4	0.43	0.82	0.77	75.22
Sphaeridae	0.57	0.26	0.42	0.79	0.76	75.98
Ceraclea	0.24	0.22	0.36	0.6	0.65	76.62
Dubiraphia	0.32	0.37	0.35	0.61	0.62	77.24
Attaneuria	0	0.4	0.34	0.59	0.6	77.85
Leptoceridae	0.36	0.11	0.33	0.64	0.6	78.45
Dineutus	0.32	0.06	0.33	0.57	0.59	79.04
Hirudinea	0.13	0.28	0.31	0.74	0.56	79.59
Lepidostoma	0.44	0	0.31	0.44	0.56	80.15