STREAM MACROINVERTEBRATE DYNAMICS ACROSS A GRADIENT OF FLOW PERMANENCE IN AN AGRICULTURAL WATERSHED

by

CHELSEA RENE SMITH

(Under the Direction of Alan P. Covich and Paul V. McCormick)

ABSTRACT

Climate shifts coupled with increasing water demand will likely decrease base flows and increase the prevalence of intermittent streams. Understanding how assemblages respond to such alterations is crucial in determining flow-ecology relationships. This study examined the affect of reduced flows during a recent drought on invertebrate assemblages across a gradient of flow permanence following an extended period of flow as well as the recovery interval of an intermittent stream following a recent drying event. Distinct assemblages were found across the gradient, with those streams that dried during the drought containing less insect and EPT richness as well as less insect relative abundance. Comparison before and after a recent drying event showed that assemblages recovered quickly (within 100 days) through a pattern from resistant to sensitive taxa. The reaches that dried maintained a similar richness to those that remained wet; however overall abundance was reduced.

INDEX WORDS: Invertebrate assemblage, flow permanence, drought, recovery, stream, environmental flows

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B.S., University of Alabama 2011

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

MASTER OF SCIENCE

ATHENS, GEORGIA

2015

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May 2015

ACKNOWLEDGEMENTS

I would like to thank my co-advisors Paul McCormick and Alan Covich for staying with me through the development of my project and reminding me to always have a back-up plan. I also want to thank Steve Golladay for his knowledge of aquatic invertebrates and help with the natural history of Ichauway. Finally I would like to thank Mary for helping me with my statistics and r code. All of you have encouraged me and helped me make it through. I am grateful to all of you for your time and effort in completing this project.

I would also like to thank the people at the Jones Center who helped make this possible. Lisa Cowart for helping me with sampling and logistics as well as hauling cinder blocks through the swamp. Nathalie Smith for her help in how to process and identify samples, along with other graduate students Nick Marzolf and David Diaz for help in the field. Above all others, JR Bolton for always being there in the field to help me sample as well as build the various contraptions I sent out into the creek. He also aided in the various cinder block adventures and was always there to chase off any snakes or alligators we came across. Thanks as well for aiding in the processing of the many samples I decided to take; I would definitely still be in the lab hovering over a microscope if it wasn’t for his help.

I would also like to thank the many people of my cohort at ecology that kept me entertained during my time in Athens (you know who you are). I would especially like to thank Katherine Adams for her invaluable help and encouragement. Sabrie Breland for always being there for me to bounce ideas off of and decipher what all the statistics mean. Finally I would like to thank the Odum School of Ecology and the Jones Center for funding me through this

endeavor. Having the opportunity to work and play at Ichauway will surely be something I will always remember fondly.

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CHAPTER 1

LITERATURE REVIEW AND SUMMARY OF OBJECTIVES

Literature Review

The southeastern USA receives abundant rainfall in most years but also experiences periodic droughts that can temporarily reduce water availability (Seager et al. 2009). Climate predictions for this region forecast a warming trend and associated increased water loss due to evapotranspiration (Hopkinson et al. 2013). While expected changes in annual rainfall are equivocal, climate models do predict an increased frequency of precipitation extremes and a shift in rainfall from the growing season to the winter and early spring (Konrad et al. 2013). These climate changes have coincided with an increase in regional human water use due to population growth in urban areas and the widespread adoption of irrigation to improve agricultural yields (Berry et al. 2014). These trends may place increasing pressure on water availability both for human and environmental needs.

Increasing water consumption for human use has resulted in decreased stream and river flows in a growing number of watersheds worldwide (Caschetto et al. 2014). The ecological effect of flow reduction is of increasing concern since flow has been recognized as a fundamental driver of stream processes (Hart and Finelli 1999, Poff et al. 2010, Warfe et al. 2014). A better understanding of how flow alterations affect fluvial processes and biota can provide a basis for establishing environmental flow requirements that minimize ecological effects from human development on water resources (Poff et al. 2010). Ideally, these requirements would be based on quantitative flow-ecology relationships (Davies et al. 2014);

however, these relationships can be difficult to develop and are not available for most rivers (Sanderson et al. 2012). Alternatives to this empirical approach have been suggested; for example, Richter et al. (2012) proposed that a set percentage of historic or natural flow volumes be allocated for instream flow needs. Approaches such as this can provide interim guidelines for resource protection, but do not replace the need for specific flow regime requirements for different stream types and species assemblages (Warfe et al. 2014).

Emergence of the environmental flows concepts

Flow has long been recognized as a crucial factor influencing the functioning of streams and rivers. An early response by ecologist and managers to flow alterations was to identify minimum allowable flows that would maintain habitat conditions to support native species, specifically fish (Tennant 1976). The derivation of this minimum flow criterion advanced with the development of the instream flow incremental methodology (IFIM), which quantified habitat condition and suitability for individual species across a broad range of flow conditions (Trihey and Stalnaker 1985). Limitations to the IFIM approach include the fact that the habitat needs of most aquatic species have not been well quantified and are likely dependent upon a range of flow conditions rather than a single level. Therefore, the recommendation to include all aspects of the natural flow regime (magnitude, frequency, duration, timing and rate of change) and its affect on water quality, energy sources, physical habitat and biota was introduced to conserve altered rivers (Poff et al. 1997). Numerous approaches have been used to assess environmental flow requirements with a recent study revealing 207 different methodologies used in 44 countries that encompass a range of the above recommendations (Tharme 2003).

Effects of Reduced Flow

Natural variation occurs within the flow regime and includes high and low flow events. More extreme variation, such as drought and flood events, can be important in structuring assemblages by regulating populations (Lytle and Poff 2004). Connection to the floodplain during high flows has been recognized as an important process that allows species with adaptations to utilize flooded areas the opportunity to reproduce and increase productivity (Junk et al. 1989). Droughts select for species that are adapted to and demonstrate resistance or resilience to low flow and drying (Hynes 1970, Resh et al. 1988, Lake 2011). These adaptations are especially important for persistence in intermittent streams, which exhibit predictable patterns of seasonal drying. Even for intermittent streams, however, alterations to the natural frequency and duration of channel drying can cause ecological impacts leading to changes in species compositions over time (Fritz and Dodds 2005). While species are adapted to natural floods and droughts, alteration of the flow regime, either through flow stabilization or increased frequency of low flow and drying, will result in a change in species composition over time.

Low flows decrease the wetted width and water depth within the channel, resulting in declines in the quantity and quality of in-stream habitat (Boulton 2003, Gordon et al. 2004, Lake 2011). Cessation of flow and disconnection of the stream channel into isolated pools leads to increases in water temperature and declines in dissolved oxygen as well as the loss of energy and nutrient inputs from the surrounding landscape (Lake 2011, Walters and Post 2011). These alterations can be physiologically stressful and alter food availability and quality through shifts in algal diversity and abundance and seston availability (Poff et al. 1990, McIntosh et al. 2002, Atkinson et al. 2009).

Macroinvertebrate responses to stream drying events are species specific and dependent on the intensity and duration of such events. Some taxa have adaptations to withstand dry conditions (i.e., are resistant) while others are able to recolonize quickly following flow resumption (i.e., are resilient; Stubbington and Datry 2013, Bogan et al. *In Press*, Datry et al. 2014). As pools form, an increase in density followed by increased mortality will occur as food resources are reduced and competition and predation increase (Stanley et al. 1997, Acuña et al. 2005). Reductions in habitat and food quality coupled with increased competition and predation all result in an altered community that tends toward resistant taxa with a loss of more sensitive, specialized taxa. Some studies have documented full recovery of streams within 100-200 days following flow resumption (Miller and Golladay 1996, Acuña et al. 2005); while others have observed distinct assemblages a year following flow resumption (Churchel and Batzer 2006). While most populations have an ability to recover from stream drying, this capacity may be diminished if the frequency of these events is too great compared with the time required for recovery.

Flow alteration in the Ichawaynochaway Creek basin

The Ichawaynochaway Creek (IC) watershed lies within the lower Flint River Basin (LFRB), which is dominated by irrigated agriculture and a smaller coverage of managed forestland and depressional wetlands. Within the IC watershed, 22% of land area is irrigated, including 20,632 ha irrigated with groundwater and 14,500 ha irrigated through surface water pumping (Couch and McDowell 2006). The consumption of water for irrigation increased rapidly during the 1970's with the introduction of center pivot irrigation. This water use is considered to be 100% consumptive (i.e., no return flows to surface waters or aquifers), and is applied at an estimated rate of 950 million gallons of water per day (3596 L/min) across the LFRB during the growing season (April-September) (Couch and McDowell 2006). While this increased water use has had little impact on average annual streamflow volumes, it has been associated with substantial reductions in summer base flows, especially during dry years (Fig 1.1) (Rugel et al. 2012). Increased water demand may have also increased the number of stream kilometers that cease flowing during droughts and the severity of channel drying events in naturally intermittent streams.

Project Objectives

The study was designed to assess the impact of reduced stream flows and stream drying on macroinvertebrate assemblages within the Ichawaynochaway Creek watershed. Variation in these assemblages across a gradient of flow permanence was examined following the end of a multi-year drought to develop relationships between the degree of stream intermittency and biotic conditions. Rates of macroinvertebrate recovery following stream drying was also documented by monitoring stream reaches before and after such an event and comparing them to other reaches that maintained flow during the same period. The goal of this work was to increase understanding of aquatic assemblages and how they respond to flow reduction to support development of flow-ecology relationships for this watershed and region.

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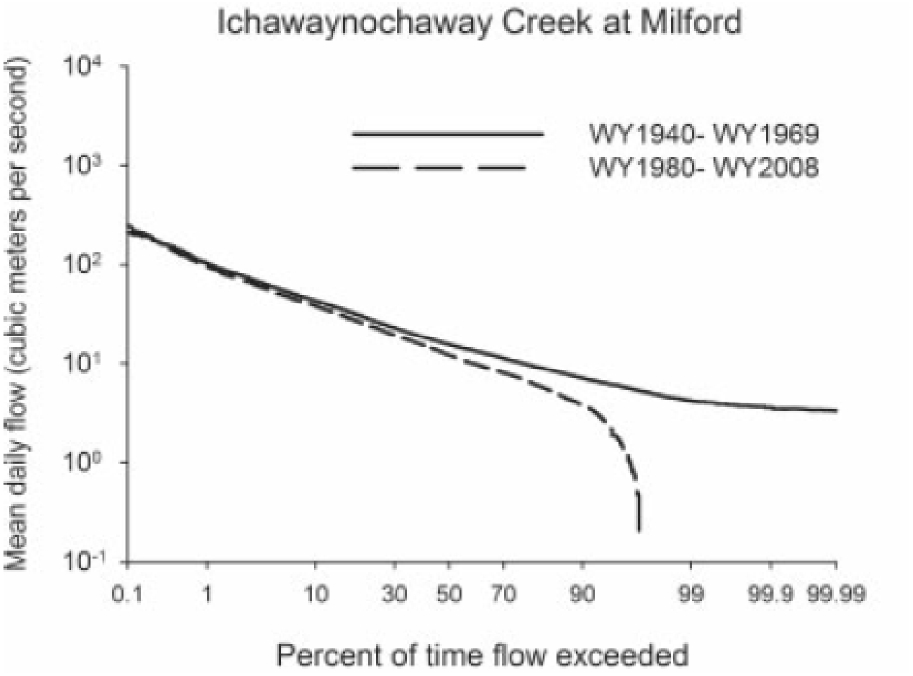

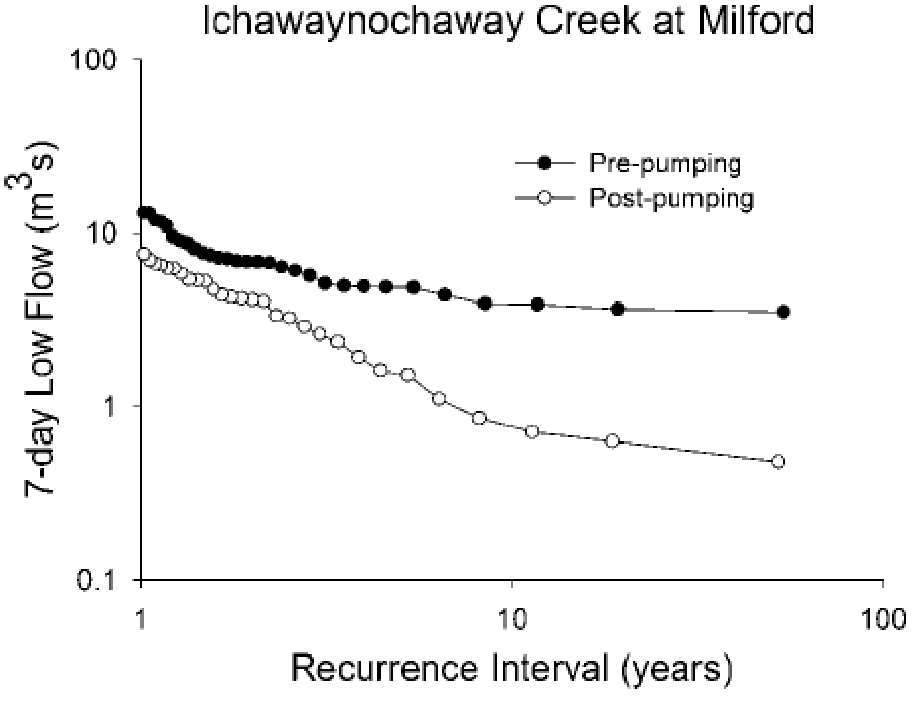

Fig 1.1: Flow duration curves and seven-day low-flow recurrence curves for pre- and post-pumping at Ichawaynochaway Creek at Milford (Rugel et al. 2012)

CHAPTER 2

COMPARISON OF MACROINVERTEBRATE ASSEMBLAGES ACROSS A GRADIENT OF FLOW-PERMANENCE IN AN AGRICULTURAL WATERSHED[1]

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[1] Smith, C.R., P.V. McCormick, A.P. Covich, and S.W. Golladay. To be submitted to *Freshwater Biology*

Abstract

Increasing water demand coupled with climate change predictions will likely result in declining streams flows and an increased prevalence of stream intermittency in many watersheds. To examine the effect of a recent multi-year drought on assemblage composition, we compared invertebrate assemblages across a gradient of flow permanence after an extended period of flow. We sampled 13 from September-December 2013 reaches within southwest Georgia, a region heavily impacted by agricultural irrigation. Reaches spanned a gradient including: perennial, intermittent-wet (ceased flowing but maintained a wetted channel during drought), intermittent-dry (seasonally dry), and intermittent-frequent (frequently dries). Assemblage composition was distinctly different across this gradient with an effect of distance to a perennial source observed. Reaches that dried during the drought had significantly less insect and EPT richness. The extent and duration of drying shaped assemblage composition through the loss of sensitive taxa (lack desiccant-resistance, univoltine). If water demand and drought conditions continue to increase in the future, an exclusion of certain taxa from reaches with increased intermittency could result in an overall change in the assemblage within the watershed.

Introduction

Increased consumptive water demand has led to declining stream flows and an increased prevalence of stream intermittency in many watersheds (Caschetto *et al.*, 2014). In some regions, this trend is being exacerbated by climate shifts that have reduced average annual precipitation and/or increased drought frequency and severity (Larned *et al.*, 2010; Hopkinson *et al.*, 2013). Recognition of these changes has resulted in an increase in the number of studies examining benthic community response to stream intermittency (Datry, Arscott & Sabater, 2011; Stubbington & Datry 2013). Benthic species possess various adaptations and life-history characteristics that affect their response to reduced stream flow and channel drying. Mobile invertebrates can disperse to avoid drying by either drifting downstream (Poff & Ward, 1991; James, Dewson & Death, 2008) or flying away (Williams, 1997). Some species can tolerate periods of drying by burrowing into wet sediment, moving into the hyporheic zone, or entering diapause (Tronstad, Tronstad & Benke, 2005; Stubbington & Datry, 2013). Once flow resumes, recolonization can occur directly through aerial dispersal and egg oviposition by flying adults and movement of desiccant-resistant taxa from the sediment or other spatial refugia (Williams & Hynes, 1976). Some taxa are less able to persist in intermittent streams either because of specific flow requirements for feeding or because of extended life cycles that reduce their dispersal ability (Robson, Chester & Austin, 2011).

Many studies of stream intermittency have been conducted in arid regions where middle or lower stream reaches are more susceptible to drying (Lake, 2011; Arscott *et al.*, 2010; Bogan, Boersma & Lytle, 2013). However, with more severe droughts, perennial sources and upstream refugia have been reduced by decreased water table levels (Bogan, Boersma & Lytle, 2014). Location within a stream network and, in particular distance from perennial reaches that may serve as propagule sources, is an important factor controlling invertebrate assemblage composition and diversity in intermittent reaches (Thompson & Townsend, 2006; Bogan & Boersma, 2012). Although drying can locally extirpate many invertebrate species within an intermittent reach, proximity to perennial sources provides opportunities for rapid recolonization upon rewetting.

Previous studies comparing invertebrate assemblages in perennial and intermittent reaches have yielded diverse results. Some have reported greater taxonomic richness in perennial streams (Fritz & Dodds, 2002; Grubbs, 2011; Bogan, Boersma & Lytle, 2013) while others have observed no difference between reach types (Feminella, 1996; Chester & Robson, 2011). Some of this apparent inconsistency may be due to differences in sampling methods and the timing of collections. For example, Churchel & Batzer (2006) documented that it required approximately five months for a stream to recover following drying (i.e. no new taxa colonizing), indicating that the time since rewetting can affect comparisons between perennial and intermittent stream assemblages. Examining hydrologic factors (annual drying duration and flow permanence) in addition to time since flow resumption could lead to a clearer picture of whether intermittent reaches maintain a less diverse assemblage or merely require an extended period of flow to achieve a composition similar to perennial stream reaches. While many taxa can persist in intermittent reaches through resistance (desiccant-resistant) or resilience (quickly recolonize following flow resumption), few are specialist (Datry et al. 2014). In streams that change from a perennial to intermittent flow regime, a greater shift in assemblage composition towards dominance by taxa with adaptation to withstand or avoid drying events could occur (Beche *et al.*, 2009; Sponseller *et al.*, 2010; Bogan & Lytle, 2011).

This study assessed the taxonomic richness and composition of invertebrate assemblages across a gradient of stream-flow permanence within a watershed where flow regimes have been altered by both surface and groundwater extraction for agricultural irrigation. We hypothesized that: (i) intermittent reaches would have lower taxonomic richness than perennial reaches due to the absence of taxa that are not adapted to survive or avoid drying; (ii) assemblages composition would converge over time if flow persisted; and (iii) proximity to a source of propagules would influence assemblage structure in intermittent reaches.

Methods

Study Site

The Ichawaynochaway Creek (IC) watershed is located within the Lower Flint River Basin in the Coastal Plain of southwest Georgia, USA (Fig. 2.1). It originates in the Fall Line Hills physiographic district as seeps and springs from the Claiborne Aquifer and then flows into the karst geology of the Dougherty Plain where the underlying Upper Floridan Aquifer is the primary water source (Hicks, Gill & Longsworth, 1987). Increases in agricultural water use since the 1970's have been associated with more frequent low-flow and no-flow periods during the growing season in historically perennial streams within this watershed (Rugel *et al.*, 2012). Drying has been most intense during recent multi-year droughts when some larger-order streams ceased flowing for several days and many smaller streams dried completely for months.

Our study was conducted in 2013 at the end of this multi-year exceptional drought in 2013 when streams within the watershed began flowing again (National Integrated Drought Information System, NIDIS; www.drought.gov). We sampled 13 stream reaches within the IC basin representing a range of flow permanence based on available hydrologic records and observations during the drought (2010-2013, Table 2.1). Four reaches were located along the perennial main stem (perennial), three on a larger tributary that ceased flowing but maintained a wetted channel during the drought (intermittent-wet), and six reaches on smaller tributaries that exhibited varying periods of channel drying during the drought (intermittent-dry) and in some cases during the subsequent sampling period (intermittent-frequent) (Fig.2.2). Intermittent-dry reaches show a seasonal pattern of drying while intermittent-frequent reaches tended to dry multiple times each year (Table 2.1). The sub-basin size of the streams varies from approximately 48 km^2 to 2,944 km^2 (Table 2.2). Intermittent reach types were located at varying distances from the perennial main stem, allowing for an examination of how distance from this propagule source might affect the rate and trajectory of invertebrate assemblage recovery.

Environmental Measurements

A 50-m reach was designated for sampling at each intermittent stream location and available substrate was quantified at eleven cross-sectional transects. Each transect was divided into five evenly spaced sampling points and the percent cover of four dominant substrates (rock, wood, sand, and organic matter (OM)) was determined within a 0.25 m^2 area at each point. Large portions of the perennial reaches were not wadeable so a visual inspection of available substrate was performed at wadeable sampling points. Water samples were collected at each site on the first sampling date to quantify total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), total suspended solids (TSS) and alkalinity, and dissolved oxygen (DO) and specific conductance were measured *in situ* at this time. Persulfate digestion followed by colorimetric analysis using the ascorbic acid method was used to process TN and TP samples (Eaton *et al.*, 2005). A Schimadzu TOC-5050 analyzer was used to analyze DOC (Schimadzu

Scientific Instruments, Kyoto, Japan). Samples for TSS were filtered through a preweighed glass fiber filter (Gelman A/E, GFF, 1-μm nominal pore size), dried (24 hr at 100 C), weighed and ashed (500 C), then reweighed (Eaton *et al.*, 2005). Alkalinity was measured within 24 hr of collection on unfiltered samples using a Mettler DL12 titrator (Mettler-Toledo Inc., Columbus, Ohio). Data loggers were deployed for a minimum of four days to measure DO and specific conductance (YSI 600XLM) at hourly intervals. Discharge was measured in each reach every other week using the cross-sectional method (Hauer & Lamberti, 2011) with a minimum of 30 measurements taken using either a Marsh-McBirney Flo-Mate^{TM} 2000 or Acoustic Doppler Current Profiler (ADCP) (RD Instruments, Poway CA) depending on stream depth. Two of the reaches had previously established U.S. Geological Survey gages that provided discharge data.

Invertebrate Sampling

Invertebrates were sampled monthly in all habitats in each reach from September through December 2013 with the exception of two reaches that were dry in November and three in December. Samples were collected by disturbing three haphazardly selected, 0.09 m^2 areas into a slack sampler (500μm mesh size), combining collected material into a single sample for each habitat within each reach, and preserved in the field in 95% ethanol (Moulton *et al.*, 2002). In the lab, samples were fractioned into coarse and fine partitions (using nested 1mm and 500μm sieves) and stained with Rose Bengal for ease of sorting. Samples with a large number of organisms were randomly subsampled volumetrically as necessary to obtain a minimum of 200 individuals per sample (Vinson & Hawkins, 1996). Individuals were identified to the lowest feasible taxonomic level. Most insects were identified to genus with the exception of Diptera, which were identified to family (Chironomidae to Tanypodinae and non-Tanypodinae). Taxa were categorized into functional feeding groups (FFG) using Merrit and Cummins (2008).

Data Analysis

Reaches were classified into four types (intermittent-frequent n=3, intermittent-dry n=3, intermittent-wet n=3 and perennial n=4). Multivariate analysis was performed using Non-metric Multi-dimensional Scaling (NMDS) with Bray-Curtis dissimilarity measures on log√x+1 transformed abundance data with rare taxa removed (those present in less than 5% of samples) to examine differences in assemblage composition among reach types over the sampling period. NMDS was performed in two to six dimensions using a random starting configuration and convergence determined through Procrustes analysis. Stress was calculated for each convergent solution and the lowest number of axes with a final stress of less than 20 was considered ecologically interpretable (Clarke, 1993). Abiotic factors were included in a secondary matrix and correlated with NMDS axes to interpret possible environmental correlations. Arcsine square-root transformed relative abundances of metrics including: FFG (functional feeding groups), insects and EPT (Ephemeroptera, Trichoptera, Plecoptera) were also included in another secondary matrix and correlated with NMDS axes to assess which metrics may be indicative of differences in reach types. Multi-Response Permutation Procedures (MRPP) were used to examine differences in *a priori* defined reach types (perennial, intermittent-wet, intermittent-dry and intermittent-frequent) followed by multiple comparisons with p-values adjusted using Bonferonni corrections. MRPP compares differences in both the mean location and distribution of a group. Indicator species analysis was then performed to identify taxa strongly associated with particular reach types. Bray-Curtis dissimilarity was also calculated between each of the intermittent reaches and the perennial reaches within habitats. Dissimilarity values were plotted against the straight line Euclidean distance to the perennial main stem (calculated in ArcGIS 10.2.2) with those sites with multiple habitats represented averaged to assess the potential influence of distance from a perennial reach on assemblage composition in intermittent reaches. All analyses were performed in R version 3.1.2 using ‘vegan’ and ‘indicspecies’ (De Caceres & Legendre, 2009; Oksanen *et al.*, 2013, R Core Development Team, 2014).

Measured water quality variables were analyzed for differences among reach types using an analysis of variance (ANOVA). Taxon richness and abundance of major invertebrate groupings (all taxa, insects, non-insects and EPT) as well as relative abundances of FFG that appeared important in the NMDS were used to compare assemblages across reach types and through time. General linear mixed models (GLMM) relating metrics to fixed effects of reach type and time were assessed with a random effect of reach to account for repeated measures. Pairwise comparisons between reach types were adjusted using Bonferonni corrections to detect significant differences for each of the metrics. Intermittent reach types were also compared with GLMM relating metrics to fixed effects of reach type and straight-line distance to the perennial mainstem with a random effect of site to assess the effect of distance to a propagule source on metrics. Richness metrics were related with a Poisson distribution and Laplace approximation, while abundances ($\log\sqrt{x+1}$ transformed) and relative abundances (expressed as proportions, arcsine square root transformed) were assessed with linear mixed models. Analysis was performed in R version 3.1.2 using ‘lme4’, ‘multcomp’, and ‘car’ (Hothorn, Bretz & Westfall, 2008; Fox & Weisberg, 2011; Bates, Maechler & Bolker, 2012, R Core Development Team, 2014).

Results

Differences in habitat availability and water quality among reach types

Substrate composition was similar between intermittent-frequent and intermittent-dry reaches, being composed mostly of sand and organic matter (Fig 2.3). These substrates were less prevalent in intermittent-wet reaches, where more than 50% of the channel bottom was rock. Substrate composition in perennial reaches varied, with upstream reaches containing mostly wood and sand, and lower reaches containing mostly rock and sand.

Environmental variables that differed significantly across reach types included TP, DOC and alkalinity. Intermittent-frequent stream reaches had significantly greater TP (df=3, F=13.8, p=.001) than all other reach types with a mean of 38 μg/L compared with a range from 23 to 25 μg/L for other reach types. Perennial reaches had DOC concentrations that were lower (6 mg/L) than intermittent-wet (11mg/L) and intermittent-frequent reaches (10 mg/L) but similar to intermittent-dry reaches (9 mg/L) (df=3,F=7.6, p=.008). Alkalinity (df=3, F=7.7, p=.008) was also lower in perennial reaches (44 ppm) than in intermittent-wet (158 mg/L) and intermittent-dry (173 mg/L) reaches, but similar in intermittent-frequent reaches (76 mg/L). Discharge in perennial reaches ranged from 3.03 to 6.81 m^3/s in the upper reaches and 11.28 to 25.77 m^3/s in the lower reaches during the sampling period, as compared to 1.14 to 6.13 m^3/s in intermittent-wet reaches and 0 to 0.81 m^3/s in intermittent-dry and intermittent-frequent reaches (Fig 2.4).

Differences in assemblage composition among reach types

Sand was a dominant substrate in many of our reaches, but had low invertebrate abundance and taxon richness. Therefore, we focused our analysis on rock and wood substrates, which supported the greatest invertebrate abundance and diversity. Non-metric-multi-dimensional-scaling (NMDS) generated a convergent two-dimensional ordination (Fig. 2.5) that represented 72.8% of the variation in the original dissimilarity matrix. MRPP detected significant differences among reach types (A=0.1494, p<0.001) and pairwise comparisons with Bonferonni corrections showed that each type was significantly different from all others. The gradient of flow permanence was associated with axis 1; however, intermittent-frequent reaches were more similar to more permanent reaches than were intermittent-dry reaches. Relationships between these axes and environmental variables showed discharge and DO increased with flow permanence, while TP, DOC, specific conductance and alkalinity declined. The relative abundances of filterers, EPT and insect taxa increased with flow permanence, while that of gatherer-collectors, predators, and omnivores declined (Fig 2.6).

Indicator species analysis (Table 2.3) revealed perennial reaches had the most indicator taxa (16) including many Trichoptera, Ephemeroptera and Plecoptera as well as multiple genera of Elmidae (larval and adult). Intermittent-wet reaches contained 7 taxa including other Ephemeroptera taxa as well as *Ectopria* (larval). Taxa indicative of intermittent-dry reaches (8 taxa) consisted of all non-insect taxa (*e.g., Gammarus,* Isopoda) while those characteristic of intermittent-frequent reaches (3 taxa) included *Macromia*, Hirudinea and Physidae. Examination of the straight line distance to the perennial mainstem compared to Bray-Curtis dissimilarities of intermittent reaches to perennial reaches revealed that reaches closest to a perennial source were more similar to perennial reaches despite being more intermittent (Fig 2.7). This could be seen in the nearest intermittent-frequent site (0.28 km from the main stem) with a dissimilarity of 0.52 while the other intermittent-frequent and intermittent-dry sites ranged from 0.58 to 0.65. Those sites that remained wet during the recent drought were more similar than those that dried.

Taxonomic metrics across gradient of flow permanence

A total of 103 taxa were identified across all sites during this study. Overall taxon richness declined with decreasing flow permanence, as did the number of taxa exclusive to a particular reach type (Table 2.2). Chironomidae were the most abundant group across all reach types, comprising over 50% of the individuals encountered. Trichoptera were the next most abundant in all reach types except for intermittent-dry reaches where non-insects were more abundant (Fig 2.8). Taxa richness in each insect order was greatest within perennial reaches. Conversely, other reach types had greater non-insect richness (Fig 2.9). The number of recorded taxa of non-insects and Diptera is conservative because most specimens were not identified to genus.

Richness and abundance did not vary significantly over time (Fig 2.10); therefore time was removed from the models. Mean taxon richness per sample ranged from 18 taxa in perennial reaches to 13 taxa in intermittent-frequent reaches, but these differences were not significant (df=3, χ^2=5.98, p=0.1123) (Fig 2.11.a). Insect richness was significantly greater in perennial and intermittent-wet reaches than in intermittent-dry and intermittent-frequent reaches (df=3, χ^2=46.67, $p<0.001$) (Fig 2.11.b). EPT richness was also significantly greater in perennial and intermittent-wet reaches than in intermittent-dry and intermittent-frequent reaches (df=3, χ^2=58.83, $p<0.001$) (Fig 2.11.c). Non-insect richness was greatest in intermittent-dry reaches compared to all other reach types (df=3, χ^2=45.55, $p<0.001$) (Fig 2.11.d). Taxa and insect abundance per sample was similar across reach types (df=3, χ^2=1.50, 2.27, p=0.6815, 0.5179) (Fig 2.12.a, b). EPT abundance was significantly less in intermittent-dry reaches than all other types (df=3, χ^2=11.448, $p<0.010$)(Fig 2.12.c). Non-insect abundance was significantly greater in intermittent-dry reaches and lowest in perennial reaches (df=3, χ^2=42.592, $p<0.001$) (Fig 2.12.d).

Because intermittent-frequent sites began drying in late October, only September samples were compared for differences in distance. No significant effect of distance was seen for any of the richness or abundance metrics with distance from the perennial mainstem.

Functional Feeding Group changes with varying flow permanence

Filterer, gatherer-collector, omnivore, and predator relative abundances all differed significantly among reach types (Fig 2.14). Perennial reaches had significantly greater filterer relative abundance than intermittent-dry reaches (df=3, χ^2=14.82, p=0.001), while the relative abundance of gatherer-collectors was significantly less in perennial reaches than in intermittent-dry reaches (df=3, χ^2=10.15, p=0.017). Predators were significantly greater in intermittent-frequent reaches compared to all other reaches (df=3, χ^2=14.46, p=0.002). Omnivores were significantly greater in intermittent-dry reaches (df=3, χ^2=18.81, p<0.001).

Discussion

While many studies have compared invertebrate assemblages between intermittent and perennial streams, recently the focus has shifted to how the physical aspects of these streams and the life history characteristics of individual taxa may influence observed differences between these stream types (Feminella, 1996; Fritz & Dodds, 2005; Storey & Quinn, 2008; Bogan, Boersma & Lytle, 2013). Our sampling allowed us to assess the influence of the degree of intermittency and distance from a propagule source on assemblage recovery following historic low flows that caused many stream reaches to dewater to varying degrees. Contrary to our initial hypothesis, taxon richness and abundance were similar across this gradient of flow permanence, indicating the potential for rapid recolonization following channel rewetting. However, taxonomic and functional composition remained markedly different between intermittent and perennial reaches when our sampling ended approximately ten months after flow resumed, suggesting that full recovery of these assemblages is a protracted process. Differences between these assemblages were attributable to a lack of taxa that are unable to persist drying or that lack the ability to quickly disperse.

Taxonomic richness and abundance did not differ among reach types in our study, which is consistent with some previous studies (Feminella, 1996; Bonada, Rieradevall & Prat, 2007; Santos & Stevenson, 2011). Other studies have seen a significant difference (Arscott *et al.*, 2010; Datry, 2012; Bogan, Boersma & Lytle, 2013), which is likely the result of greater taxonomic resolution, especially within Chironomidae and Simuliidae, or the timing of sampling relative to flow resumption (Bogan, Boersma & Lytle, 2013). Our study identified Chironomidae to Tanypodinae and non-Tanypodinae, and Simuliidae to family, which may contribute to the different level of resolution. Churchel and Batzer (2006), who identified taxa to a similar resolution, noted an approximate five-month recovery time for taxon richness. However, their study also noted more unique long-term recovery patterns for assemblage composition a year following flow resumption. Our findings were similar as taxon richness did not differ across this gradient while compositional differences persisted after an extended period of flow.

The availability of propagule sources can strongly influence the rate and trajectory of stream invertebrate recovery from disturbances such as drying events (Fritz & Dodds, 2002; Arscott *et al.*, 2010). William & Hynes (1976) assessed the relative proportion of recolonization from the four main sources in a stream including drift, upstream migration, aerial recolonization and vertical migration from the sediment, and found that drift was the dominant pathway (41.4%), followed by aerial recolonization (28.2%). Recent studies examining the contribution of the invertebrate “seed bank” (i.e., those individuals that can diapause or persist in a dry stream bed) to assemblage recovery found that many taxa persist in stream sediments depending on the degree of sediment drying and the average sediment temperature (Storey & Quinn, 2013; Stubbington & Datry, 2013). The entire course of many of our intermittent streams dried completely during the recent drought, thereby limiting the importance of drift as a mode of recolonization. Furthermore, the available sediment layer in many of these streams is thin due to shallow limestone bedrock and may provide limited refugia for insects. As a result, aerial dispersal and upstream migration from the nearest wetted reach may be more important pathways for recolonization by taxa that are incapable of persisting. Under such circumstances, distance from a perennial reach can be an important factor affecting assemblage recovery in our streams. Intermittent reaches closer to a perennial source that dried completely during the recent drought showed greater similarity in assemblage composition than those more distant, independent of flow regime, though no difference was detected among richness or abundance metrics.

The resistance and resilience of an invertebrate assemblage to disturbance is better characterized by life history traits than over all diversity (Robson, Chester & Austin, 2011). Adaptations, such as a species’ likelihood to burrow and survive in sediment or their strength of flight, will increase their resistance or resilience. These adaptations are especially important as the likelihood of survival is related to the degree and timing of drying within a watershed. Because many streams within our watershed dried completely during the recent drought, rates of recovery may be dependent on the adaptations of specific taxa. This may result in an increased time needed for recolonization, especially among weak fliers and those with longer life cycles who would be required to recolonize from perennial sources. Indicator species analysis highlighted many taxa characteristic of perennial reaches including many filterers (e.g. *Hydropsyche, Isonychia*) as well as those taxa with longer life cycles (e.g. *Stenelmis, Macronychus, Baetisca*). Intermittent-wet reaches also had many Ephemeroptera and filterers (*Corbicula*). Coupled with perennial reaches, these reach types that did not dry had many more sensitive taxa (those with univoltine lifecycles or that lack a strategy to survive drying) including Elmidae (both adult and larvae) and EPT, than those reaches that dried during the previous drought. Taxa indicative of intermittent-dry reaches such as *Gammarus* and Ostracoda are highly resistant because of their capability to survive in relatively dry stream beds and to recolonize quickly (Thorp, Covich & Rogers, 2010). Other studies have highlighted the use of the hyporheic zone by *Gammarus* especially within intermittent reaches (Stubbington *et al.*, 2011). Studies within the region have noted the presence of a diverse non-insect community quickly following rewetting in seasonal isolated wetlands (Battle & Golladay, 2001). Battle & Golladay (2001) also noted the succession from a permanent non-insect community with insects colonizing over time. This succession could explain the lack of dominance of these taxa within intermittent-frequent reaches where colonization of a diverse insect community could occur more quickly from the perennial main stem as compared with intermittent-dry reaches higher in the watershed. The importance of the dragonfly larvae *Macromia* within the intermittent-frequent reaches is the product of sampling when reaches were reduced to pools. Many studies have seen an increase in predator abundance as streams dry down and organisms are crowded into smaller areas (Stanley, Fisher & Grimm, 1997; Acuña *et al.*, 2005; Lake, 2011).

Our study highlights the importance of life history characteristics in shaping the trajectory of recovery of stream invertebrate assemblages following drying. Other studies have highlighted the lack of knowledge of life history studies for those taxa that are intermittent stream specialist (Robson, Chester & Austin, 2011; Arthington, Bernardo & Ilhéu, 2014; Datry *et al.*, 2014). While taxa richness was not significantly different, the richness of more sensitive taxa (EPT and other univoltine taxa) showed that an increase in the duration and severity of drying would exclude them from some reaches. Identifying what taxa are affected by increases in low-flow and drying events will aid in the assessment of the environmental effects of water use on stream assemblages.

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Table 2.1: Summary of reach type characteristics: minimum discharge obtained from the nearest USGS gage to the reach.

Reach Type	Dried during drought	Dried during Sampling	Estimated Time Since Flow (Sep 2013, in days)	Likely drying pattern
Perennial-upper	No	No	NA	Maintains flow even during drought
Perennial-lower	No	No	NA	
Intermittent-wet	Pools	No	~665	Ceasing flowing under drought conditions
Intermittent-dry	Yes	No	~350	Seasonally dried
Intermittent-frequent	Yes	Yes	~70	Dries multiple times a year

Table 2.2: Physical characteristics and taxa within study reaches

Stream	Reach Type	Catchment Area (km^2)	Stream Order	Sites	Total Taxa Found	Unique Taxa
Ichawaynochaway	Perennial	2943.98	5	4	70	15
Chickasawhatchee	Intermittent-wet	868.16	4	3	69	7
Big Cypress	Intermittent-frequent	173.36	3	3	52	6
Kiokee	Intermittent-dry	167.08	2	1	48	4
Little Spring	Intermittent-dry	59.64	2	1		
Keel	Intermittent-dry	48.41	2	1		

Table 2.3: Indicator species analysis of reach types. A=probability that the surveyed reach belongs to the reach type given the fact that the taxa has been found (i.e. only found in this group if A=1.0), B= probability of finding the taxa in reaches belonging to the reach type (i.e. appears in all sites belonging to this group if B=1.0)

	Taxa	**A**	**B**	**P-value**
Perennial	*Hydropsyche*	0.7432	0.7895	0.005
	Simuliidae	0.5567	0.9475	0.005
	Chimarra	0.5225	0.9474	0.005
	Stenelmis	0.6636	0.6842	0.005
	Hydroptila	0.5841	0.7368	0.005
	Plauditus	0.8248	0.4737	0.005
	Microcylloepus	0.7290	0.5263	0.005
	Ancyronyx	1.0	0.3684	0.005
	Isonychia	0.8855	0.3684	0.01
	Asioplax	1.0	0.2632	0.015
	Macronychus	0.7757	0.3158	0.015
	Taeniopteryx	0.9123	0.2632	0.005
	Baetisca	1.0	0.2105	0.020
	Neoperla	0.7826	0.2632	0.03
	Crambidae	0.7483	0.2632	0.025
	Acentrella	0.8277	0.2105	0.05
Intermittent-wet	*Hemerodromia*	0.5941	0.7917	0.005
	Maccaffertium	0.5397	0.7083	0.005
	Corbicula	0.4681	0.6667	0.025
	Baetis	0.4193	0.7083	0.035
	Tricorythodes	0.6343	0.4583	0.015
	Stenacron	0.4903	0.5417	0.04
	Ectopria	0.8714	0.2917	0.01
Intermittent-dry	*Gammarus*	0.8635	0.8750	0.005
	Isopoda	0.6035	1.0	0.005
	Ancylidae	0.5704	1.0	0.005
	Ostracoda	0.7984	0.5625	0.005
	Copepoda	0.6261	0.5625	0.005
	Planorbidae	0.6597	0.5	0.005
	Lymnaidae	0.8063	0.375	0.02
	Cambaridae	0.6038	0.5	0.005
Intermittent-frequent	*Macromia*	0.95	0.5	0.005
	Hirudinea	0.5944	0.5	0.005
	Physidae	0.7484	0.3333	0.010

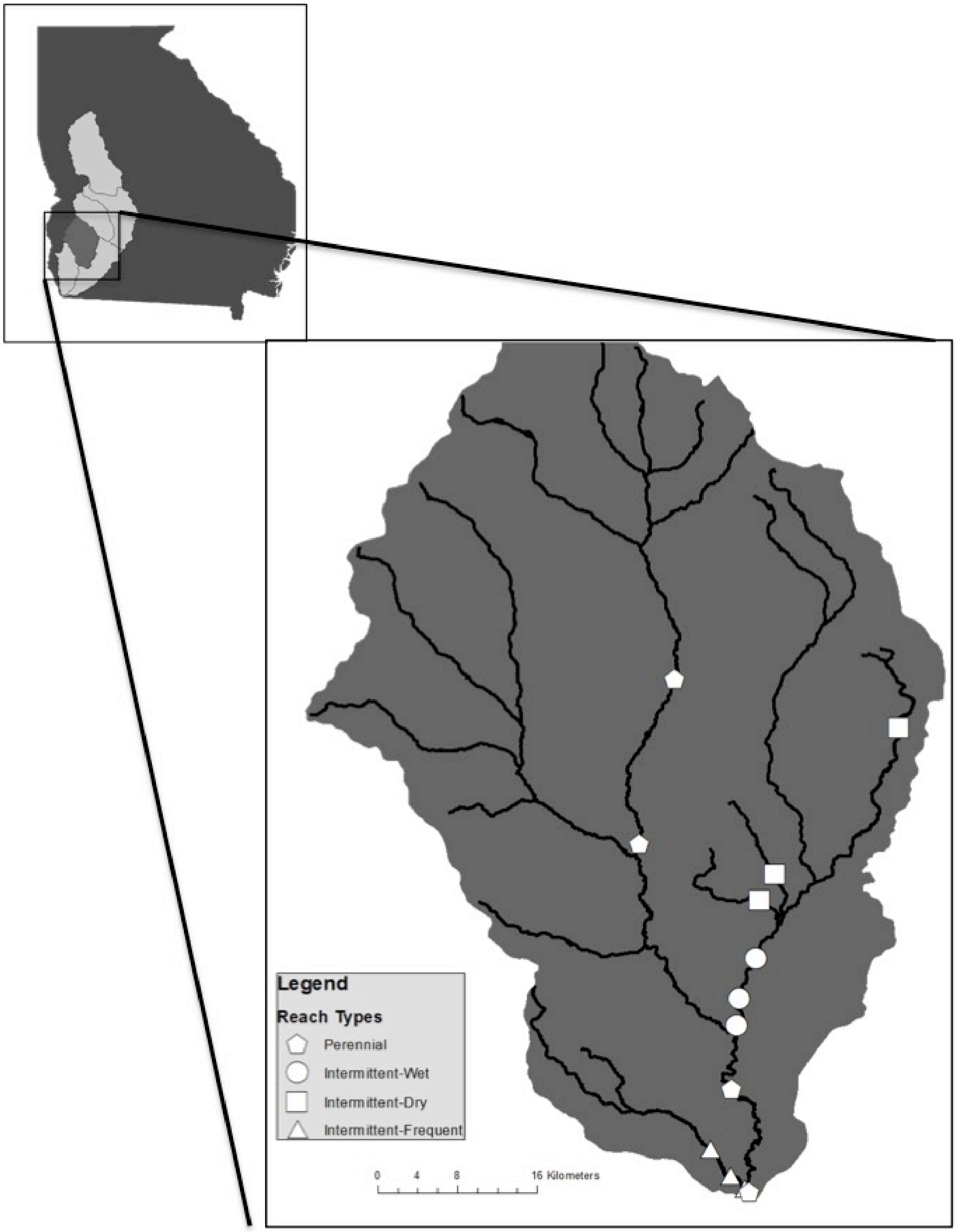

Fig 2.1: Sampling locations within the Ichawaynochaway Creek Basin

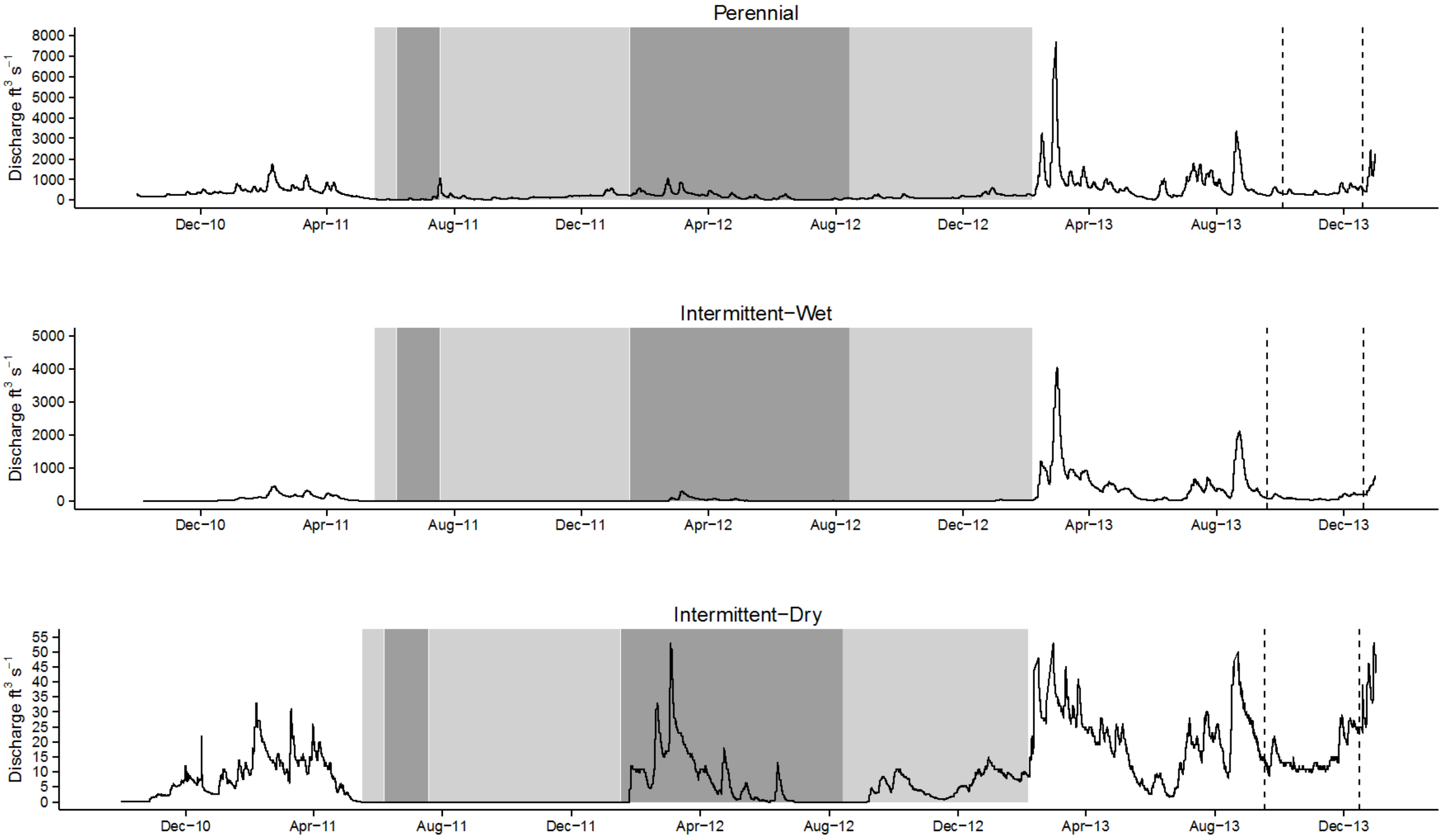

Fig 2.2: Discharge at USGS gages on perennial mainstem, intermittent-wet stream and least intermittent intermittent-dry stream. Light gray regions indicate times where the watershed had portions under extreme drought while dark gray indicate time under exceptional drought. Dashed lines indicate sampling period. (National Integrated Drought Information System, NIDIS; www.drought.gov)

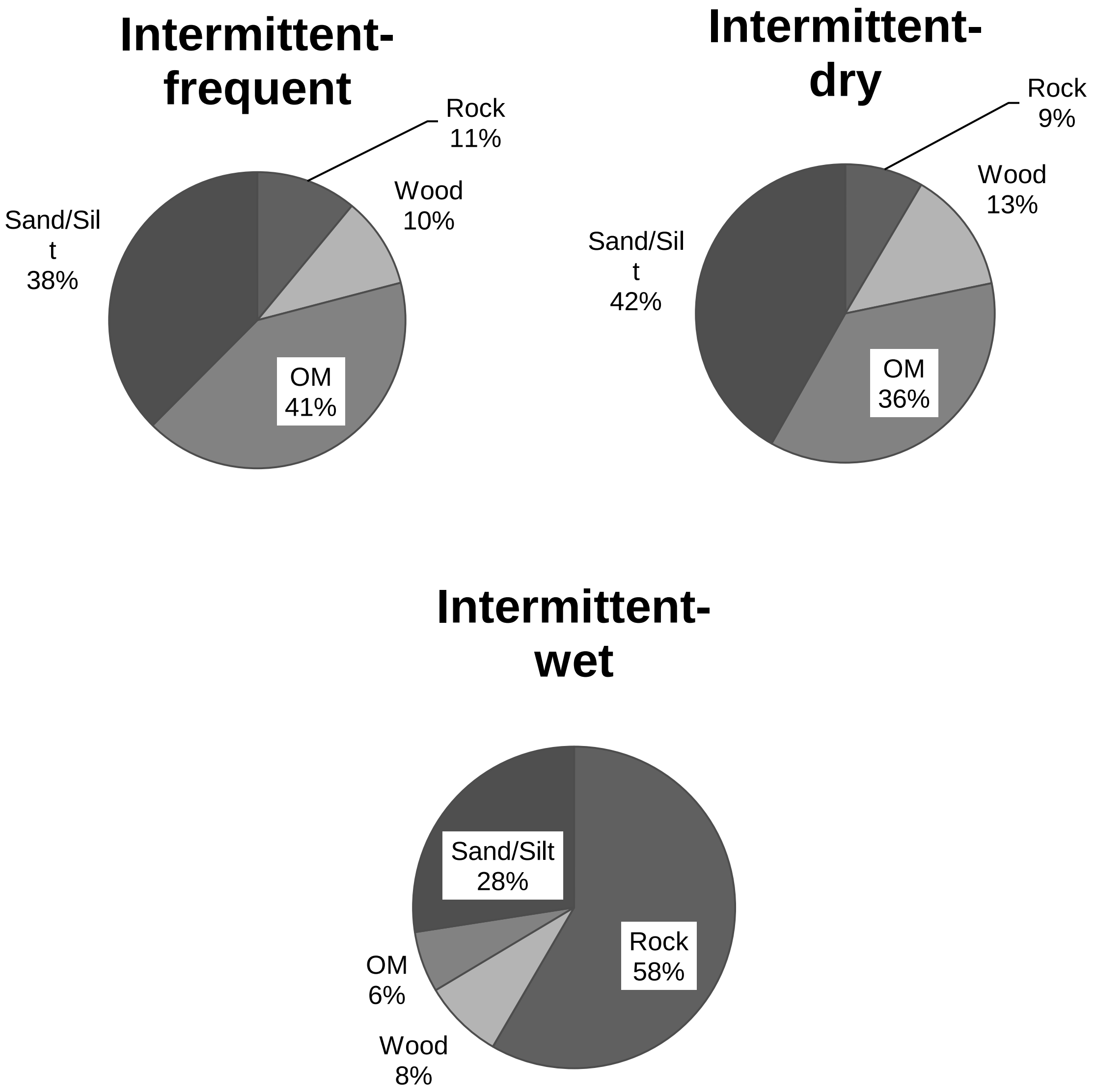

Figure 2.3: Mean percent area of each habitat found across surveyed reaches

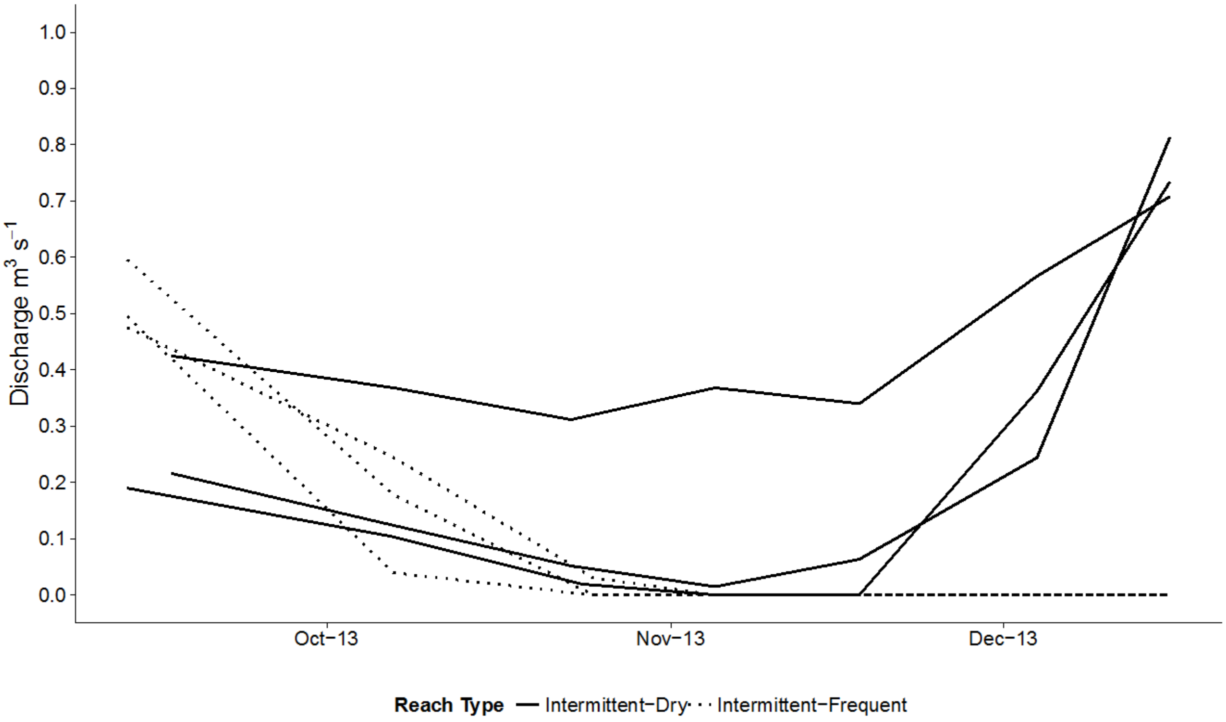

Fig. 2.4 Discharge measurements from September to December across Intermittent-dry and Intermittent-frequent reaches

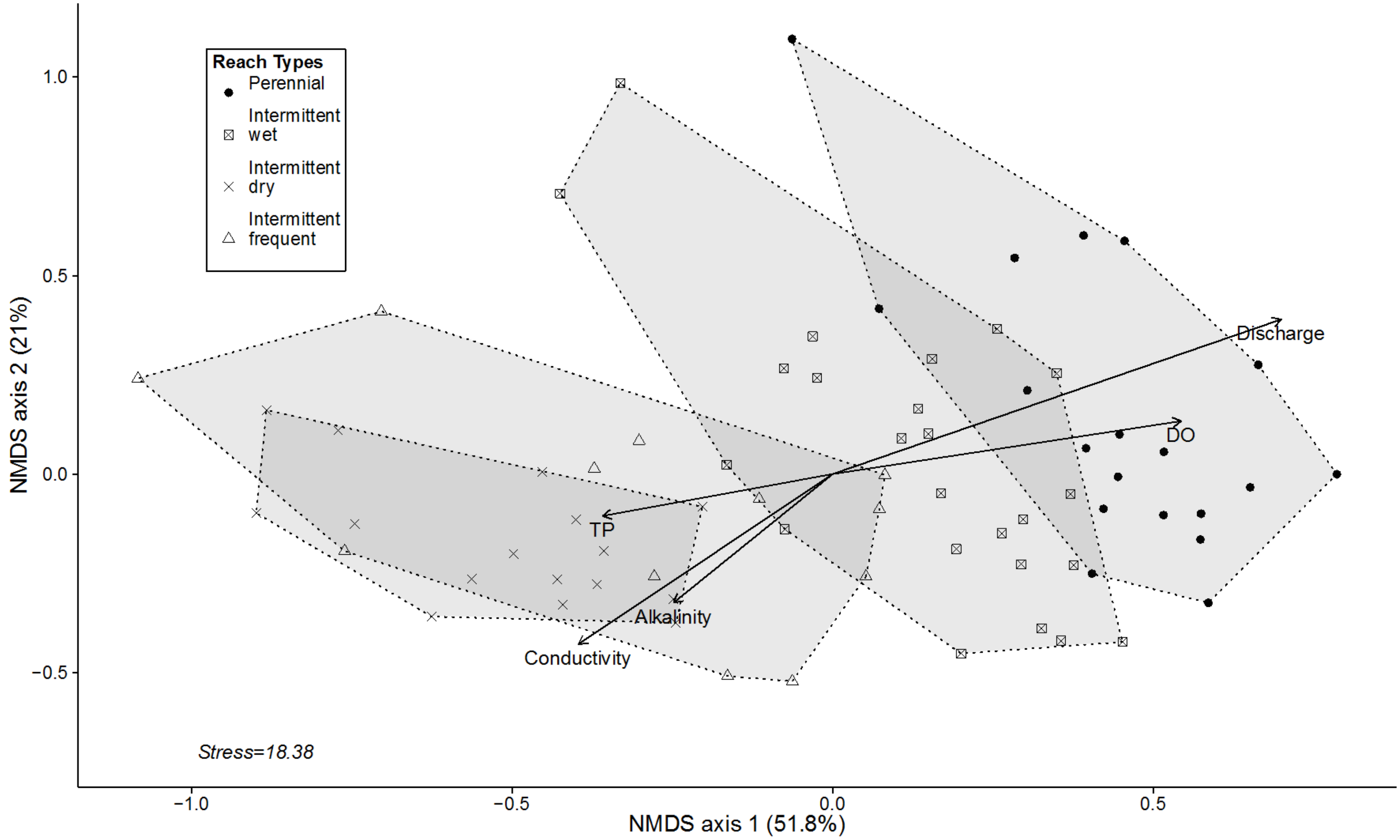

Fig. 2.5: Non-metric multi-dimensional scaling (NMDS) two-dimensional ordination of all rock and wood samples by reach based on Bray-Curtis dissimilarities. Environmental vectors show environmental measurements with significant ($p<0.05$) relationships to the axes. (TP=total phosphorus, DO=dissolved oxygen, discharge log transformed)

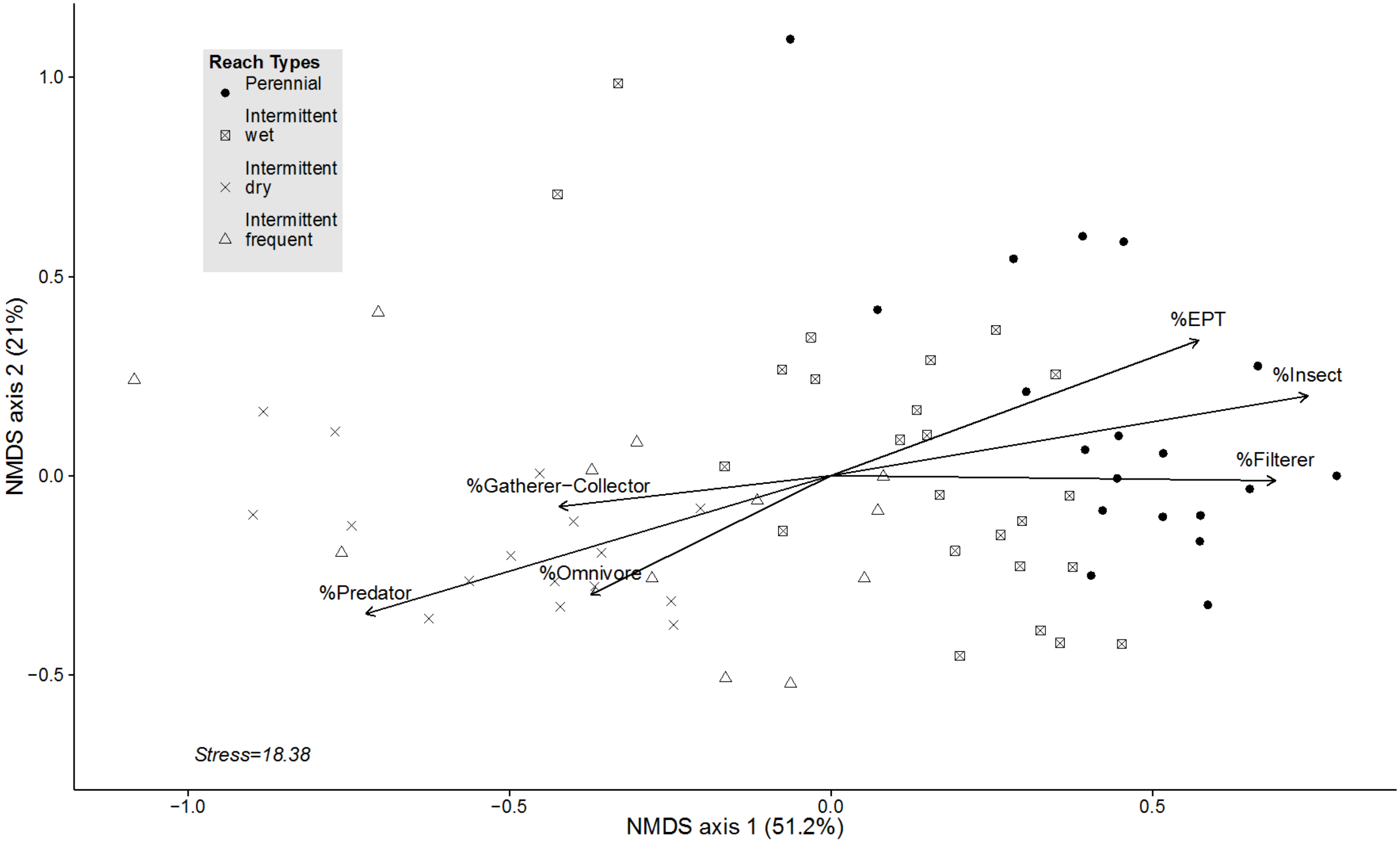

Fig 2.6: Non-metric multi-dimensional scaling (NMDS) two-dimensional ordination of all rock and wood samples by reach based on Bray-Curtis dissimilarities. Environmental vectors show relative abundances (arcsine square-root transformed) of metrics and functional feeding groups with significant ($p<0.05$) relationships to the axes.

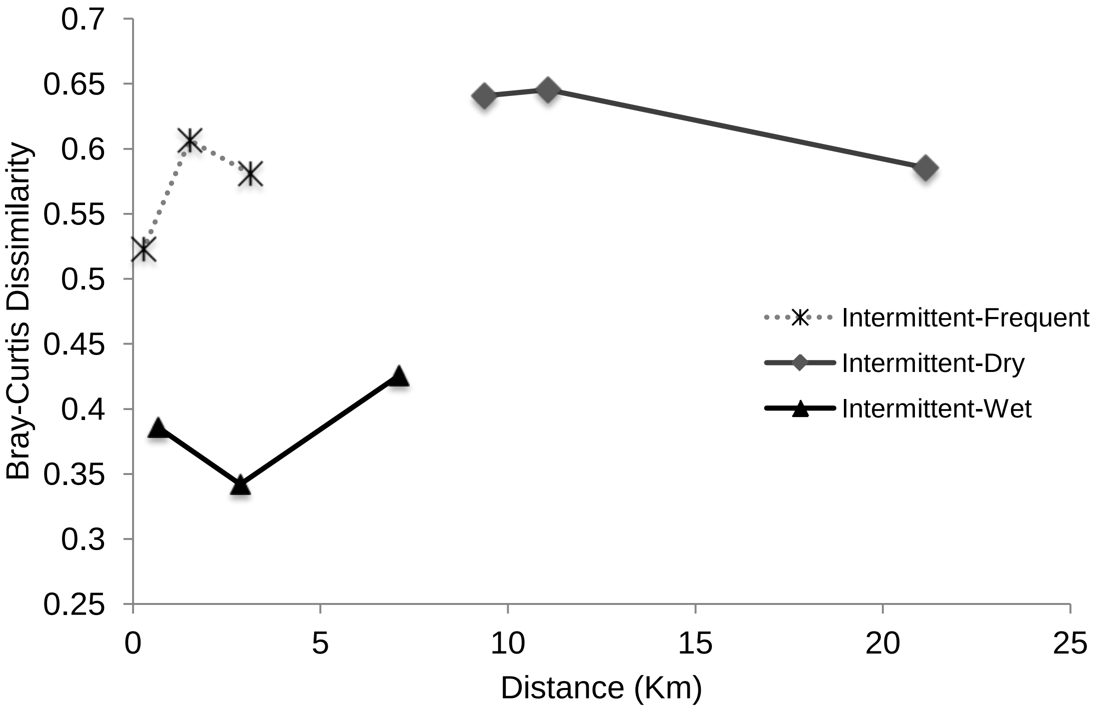

Fig 2.7: Distance from the perennial main stem compared to Bray-Curtis dissimilarity between intermittent reaches and perennial reaches.

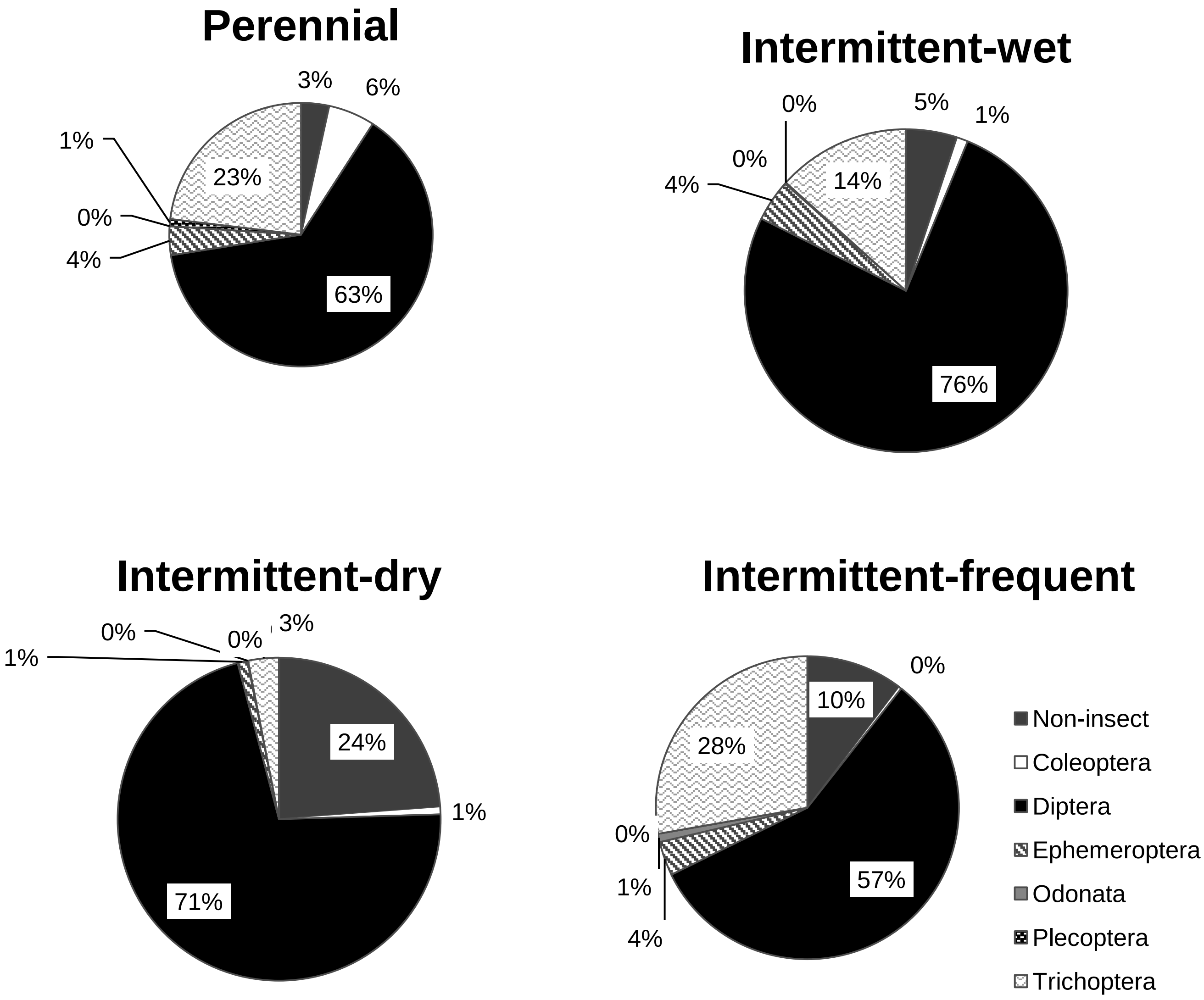

Fig 2.8. Relative Abundance of major orders across reach types grouped over the sampling period

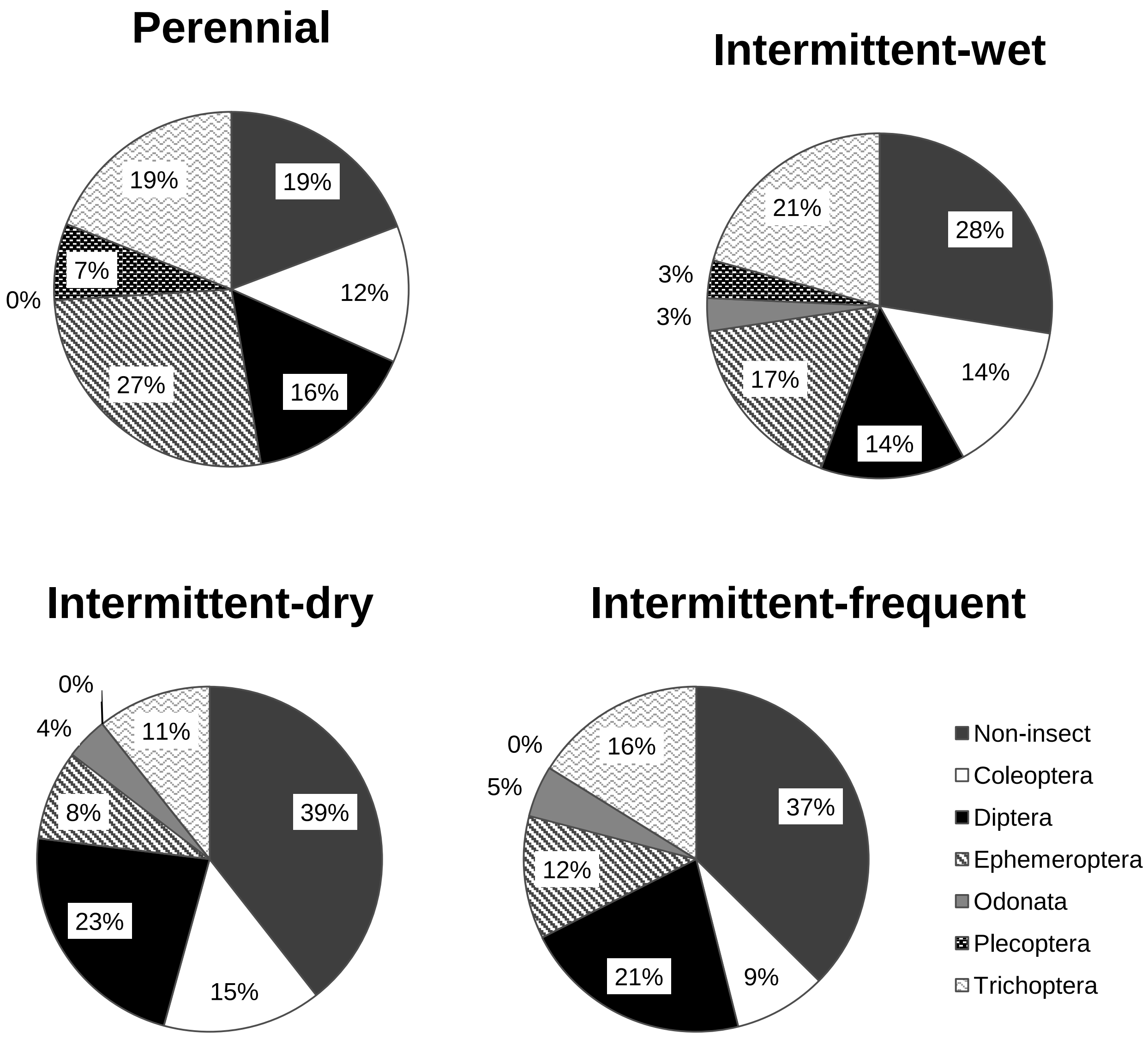

Fig 2.9. Percent of Taxa in each order contributing to total Taxa Richness over sampling period

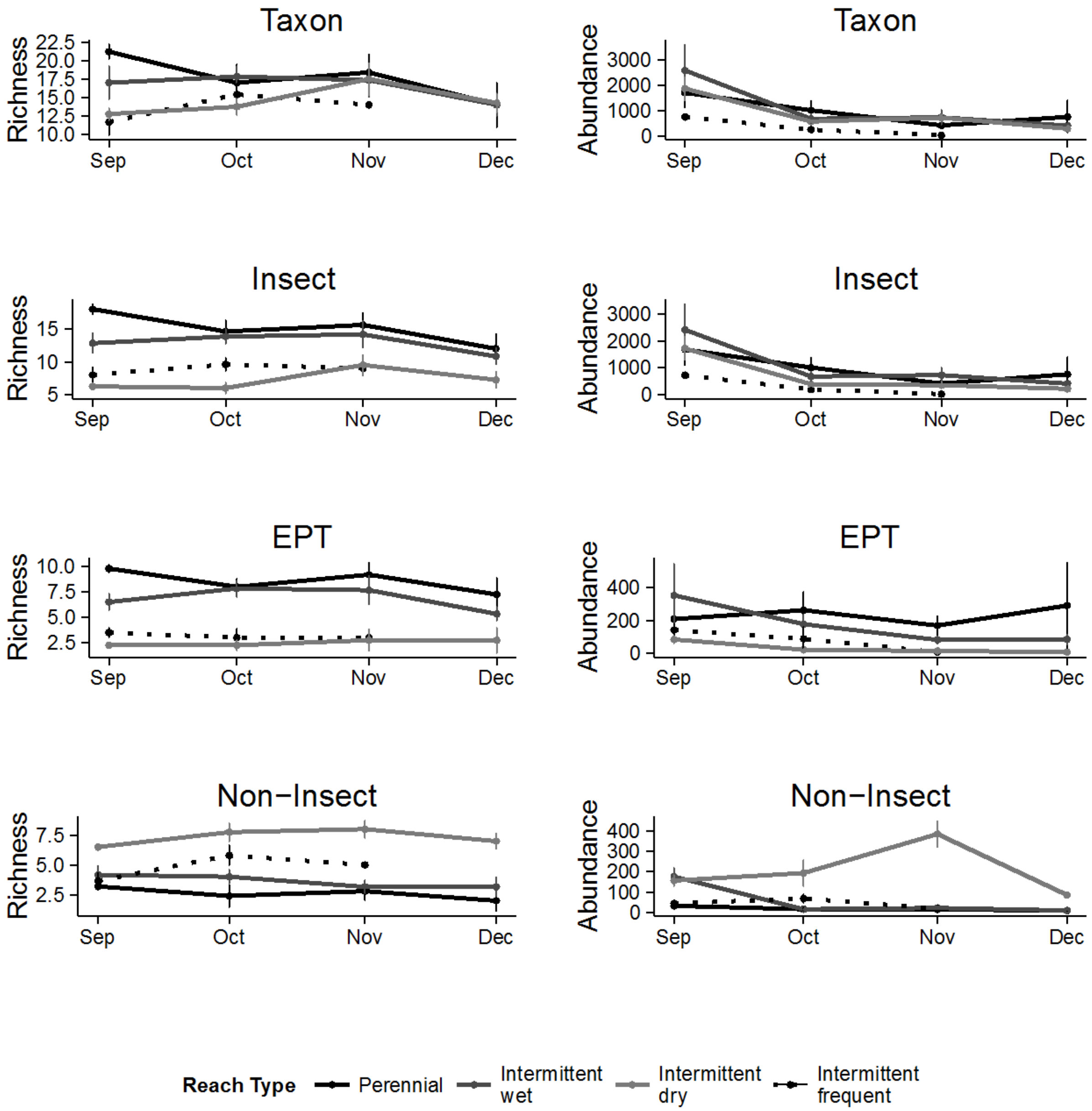

Fig 2.10: Change in taxon metrics over time.

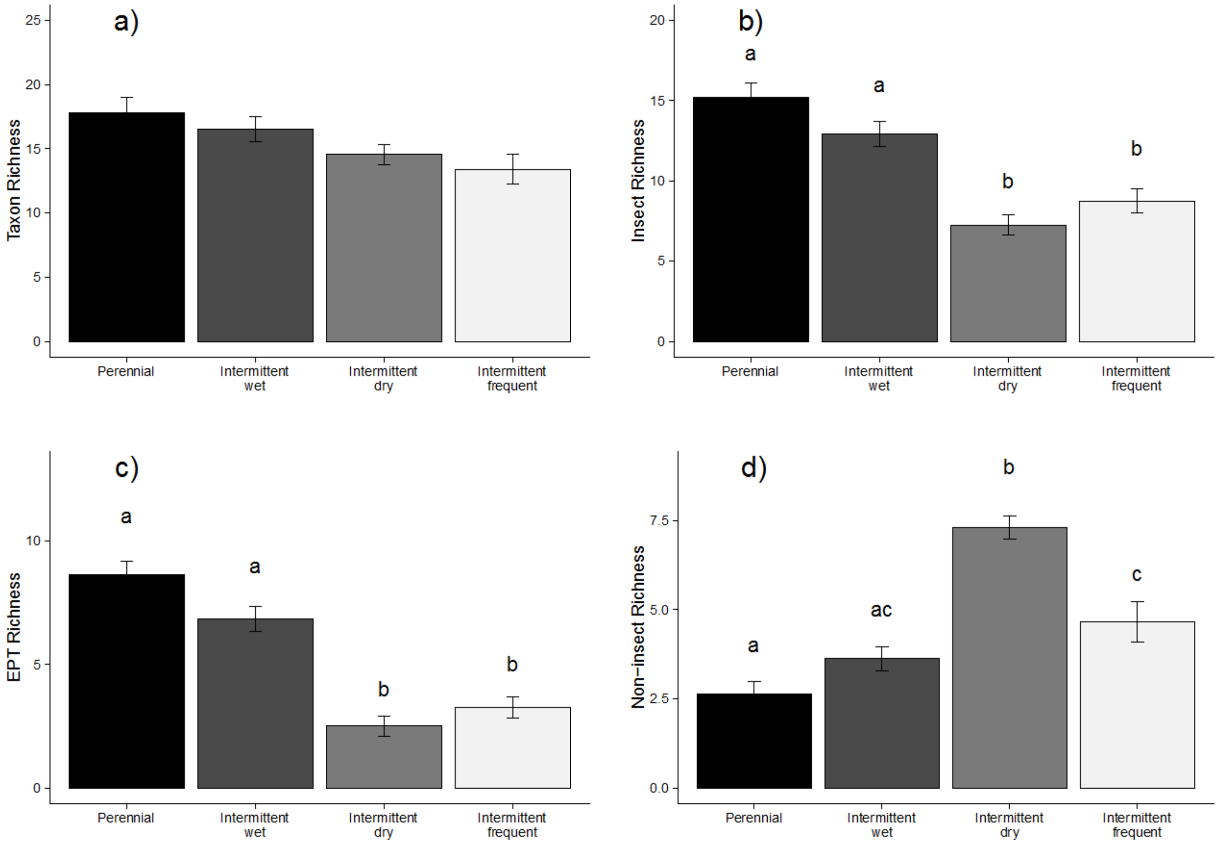

Fig 2.11: Mean±SE of richness metrics for each reach type. Letters indicate significant ($p<0.05$) differences among reach types.

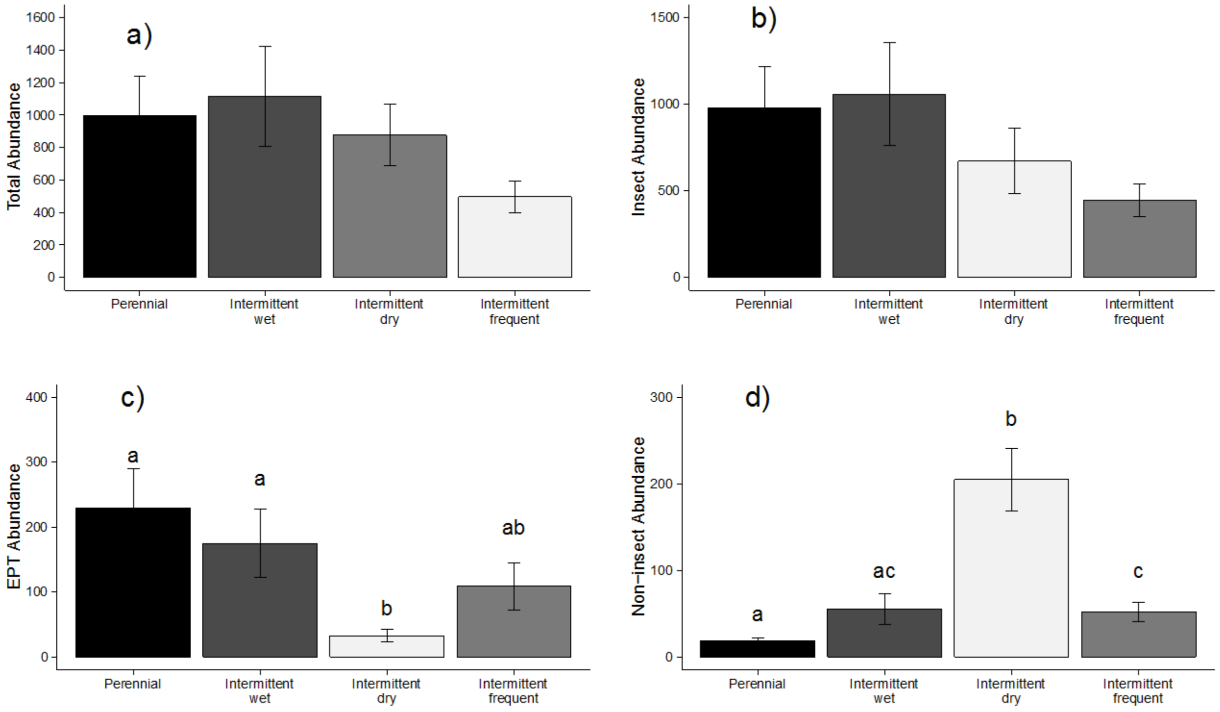

Fig 2.12: Mean±SE of abundances of significant metrics for each reach type. Letters indicate significant ($p<0.05$) differences among reach type.

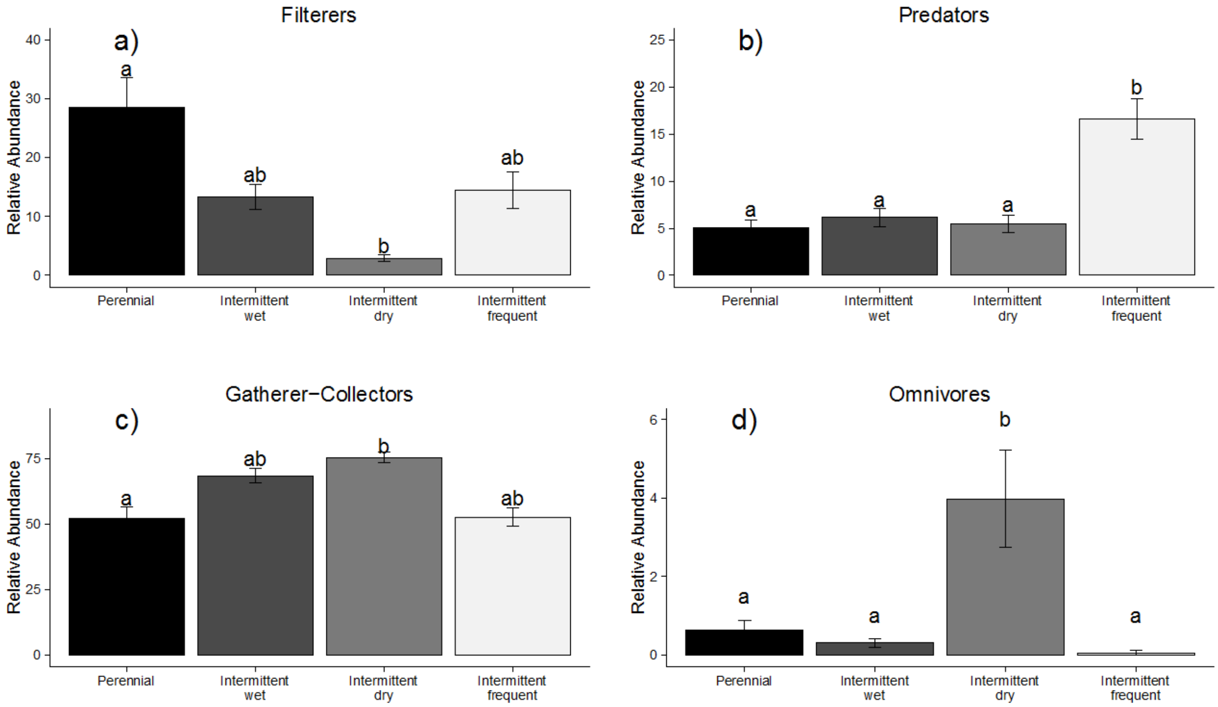

Fig 2.13: Mean±SE relative abundance of significant functional feeding groups for each reach type. Letters indicate significant (p<0.05) differences among reach types.

CHAPTER 3

RECOLONIZATION DYNAMICS WITHIN AN INTERMITTENT STREAM[2]

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[2] Smith, C.R., P.V. McCormick, A.P. Covich and S.W. Golladay, to be submitted to *Freshwater Science*

Abstract

Increasing water demand and climate change will likely increase the frequency and severity of stream drying and the prevalence of intermittent stream reaches. Examining how assemblages recover following drying will be important in understanding what affect increasing the frequency and severity of drying will have. We examined invertebrate assemblages before and after a drying event within an intermittent stream (DR) and compared assemblage recolonization to pre-drying levels and to intermittent streams that remained wet (RW). Prior to flow cessation, assemblage composition was different as a result of a greater abundance of some non-insect taxa within RW reaches and *Cheumatopsyche* within DR reaches. Following flow resumption, the emergence of resistant taxa (adapted to drying) occurred within 11 days while resilient (no desiccant resistance, multivoltine) richness took approximately 65 days. No change in sensitive taxa (no desiccant resistance, univoltine) richness was observed. Abundances of resistant taxa peaked quickly following flow resumption (~36 days), followed by more resilient taxa (~96) and finally sensitive taxa (~65-96 days). Richness comparisons to RW reaches did not differ while overall abundance was less in DR reaches. Increasing the frequency and severity of drying could ultimately result in a shift to more resistant taxa if the recurrence interval is greater than the time required for recovery.

Introduction

Intermittent streams are a significant component of drainage networks in many regions of the world and support an aquatic community dominated by species that are adapted to cycles of drying and rewetting (Arthington, Bernardo & Ilhéu, 2014; Datry *et al.*, 2014; Larned *et al.*, 2010). Increasing human water demand and climate change may increase the frequency and severity of stream drying and the prevalence of intermittent stream reaches (Hopkinson *et al.*, 2013), with consequent effects on species richness and composition (Datry *et al.*, 2014). Increased frequency and severity of drying, such as that seen in supra-seasonal droughts, have been associated with an increased recovery time for invertebrate assemblages and a shift in assemblage composition as a result of longer-lived taxa and those with poor dispersal ability being replaced by more drought tolerant taxa and those with adaptations for rapid dispersal (Lake, 2011; Gasith & Resh, 1999; Bogan, Boersma & Lytle, 2014). Because intermittent streams already contain assemblages adapted to seasonal drying, the transition from perennial to intermittent flow will cause a larger shift in assemblage composition than increased frequency and duration of drying in intermittent streams (Beche *et al.*, 2009; Sponseller *et al.*, 2010).

The rate and trajectory of assemblage recovery following drying are influenced by life history strategies of individual species as well as the availability of spatial refugia (Chester & Robson, 2011). Species inhabiting intermittent streams possess various adaptations to deal with loss of flow and channel drying. These adaptations can confer either resistance (the ability to survive) or resilience (the ability to recover quickly) in response to drying events (Bond, Lake & Arthington, 2008; Robson, Chester & Austin, 2011; Lake, 2003;2011). Some species are capable of persisting within the sediments depending on substrate type, extent of drying, and the presence of hyporheic flow (Datry, 2012; Larned, Datry & Robinson, 2007; Paltridge *et al.*, 1997). Mechanisms of recovery following flow resumption include the emergence of desiccant resistant taxa from sediments, aerial oviposition, and movement within the stream through crawling or drifting (Williams & Hynes, 1976; MacKay, 1992). Factors controlling aerial oviposition and adult colonization include species' voltinism, prevailing winds (Briers *et al.*, 2004) and distance from a perennial source (Bogan & Boersma, 2012). Drift from upstream refugia is the main source of recolonization for streams with perennial headwaters (Gore, 1982; Williams & Hynes, 1976; McKay & King, 2006). Most studies have found that streams recover from drying through these mechanisms within 100-200 days after flow resumption (Churchel & Batzer, 2006; Miller & Gollday, 1996; Malmqvist *et al.*, 1991).

Habitat fragmentation and drying within a stream can strongly influence the resident invertebrate assemblage (Verdonschot *et al.*, 2015). Some studies have found the presence of local refugia to have no effect on recolonization patterns (Churchel & Batzer, 2006), while others have documented a faster recovery of the pre-drying assemblage when perennial pools are nearby or upstream (Bogan & Lytle, 2007; Fritz & Dodds, 2004; Paltridge *et al.*, 1997). Sediments generally are not an important local propagule source, although some taxa of Coleoptera and Diptera can utilize these refugia (Stubbington & Datry, 2013; Chester & Robson, 2011). Increased severity of drying reduces the number of taxa capable of surviving due to decreased sediment moisture and increased temperature (Stubbington & Datry, 2013; Fritz & Dodds, 2005; Paltridge *et al.*, 1997). With decreased survival within a reach, perennial sources become more important to recolonization. Increasing the spatial extent of intermittency could result in a decrease in available perennial sources, resulting in greater distances to propagule sources. Increasing distance to a propagule source has been negatively related to macroinvertebrate richness and abundance in intermittent reaches (Bogan & Boersma, 2012), and therefore is an important factor determining assemblage composition within streams.

We examined the response and recovery of invertebrate assemblages in relation to stream drying across a gradient of stream intermittency in a southeastern coastal plain watershed in Georgia, USA. This gradient included both stream reaches that maintained flow for an extended period and those that ceased flowing and dried for a short period. Assemblage development was followed once flow resumed and compared to those in reaches that did not dry in order to measure the rate of recovery from drying. We hypothesized that dried reaches would recover to pre-drying richness and abundance levels within 100-200 days (as seen in previous studies) but would maintain a distinct assemblage from those that did not dry.

Methods

Study Area

This study was conducted within the Ichawaynochaway Creek watershed, a 2,944-km^2 catchment in the lower Flint River Basin of southwestern Georgia, USA (Fig 3.1). Study sites are located within the Dougherty Plain physiographic district, which is underlain by Ocala Limestone, a fractured and porous rock layer that is the principal water bearing strata for the upper Floridan Aquifer (Hicks, Gill & Longsworth, 1987). Low topographic relief and the porous nature of the limestone cause many of the smaller streams in the region to be naturally intermittent (Hicks & Golladay, 2006). Land-use in the area is predominantly irrigated agriculture and pine plantations. Increased pumping of surface and ground water for irrigation in recent decades has altered flow regimes within the lower Flint River basin, reducing minimum flows and causing some previously perennial streams to cease flowing or dry during extreme droughts (Rugel *et al.*, 2012).

Six tributary stream reaches were selected to encompass a range of flow. Three reaches were located on a very intermittent stream that ceased flowing during our study; the other three reaches were located on intermittent streams that either maintained flow or at least a wetted channel during our sampling period (Fig 3.1).

Habitat Measurements

A 50-m reach was delineated at each location and available substrate was quantified at eleven evenly spaced cross-sectional transects. Each transect was divided into five evenly spaced sampling points and the percentage of four dominant substrates (rock, wood, sand, organic matter (OM)) was determined within a 0.25 m^2 area at each point. These measurements were then averaged to estimate habitat percentages for the entire reach. Canopy cover was also measured at three points along the reach using a concave spherical densiometer (Forest Densiometers, Bartlesville, OK) and averaged for the reach. Discharge was measured in each reach every other week from September 2013 to May 2014 using the cross sectional method with a minimum of 30 measurements taken using a Marsh-McBirney Flo-Mate^{TM} 2000 (Hauer & Lamberti, 2011).

Invertebrate Sampling

Invertebrates from all habitats in each reach were sampled monthly from September 2013 through May 2014. No samples were collected during the period when certain reaches dried completely (November-December 2013) although remaining pools were sampled when available. Samples for each habitat were collected by disturbing three haphazardly selected, 0.09m^2 areas into a slack sampler (500μm mesh size), combining collected material into a single sample for each habitat within each reach, and preserving material in the field in 95% ethanol. Samples were partitioned into coarse and fine fractions in the laboratory (using nested 1mm and 500μm sieves) and stained with Rose Bengal for ease of sorting. Samples with large numbers of organisms were randomly subsampled volumetrically as necessary to obtain a minimum of 200 organisms per sample (Vinson & Hawkins, 1996). Organisms were identified to the lowest feasible taxonomic level. Most insects were identified to genus while Diptera were identified to family (Chironomidae to Tanypodinae and non-Tanypodinae. Taxa were then classified as to their sensitivity to drying based on their voltinism, and whether other studies have found them in sediments that were dry for more than a month (Stubbington & Datry, 2013; Datry, 2012; Robson, Chester & Austin, 2011; Larned, Datry & Robinson, 2007). Taxa that can persist within the stream during drying were categorized as resistant. Taxa that are not adapted to resist desiccation were then further classified based on life cycle with resilient taxa being multivoltine and sensitive univoltine.

Data Analysis

Non-metric multi-dimensional scaling (NMDS) based on abundance of taxa present in at least 5% of samples (log√x+1transformed) with Bray-Curtis distances was performed across habitats and sampling dates for all reaches to examine change in taxonomic composition over time. NMDS was performed in two to six dimensions using a random starting configuration and convergence on a stable solution was determined through Procrustes analysis. Stress was calculated for each convergent solution and the lowest number of axes with a final stress of less than 20 was considered ecologically interpretable (Clarke, 1993). Correlation with NMDS axes was then performed with a secondary matrix including time since flow and discharge. Abundances of invertebrate families were also included in a secondary matrix and correlated with NMDS axes to identify taxa associated with each axis. Taxa with a significant correlation ($p<0.01$) and an $r^2>0.15$ were considered to be associated with an axis. Permutational multivariate analysis of variance (PERMANOVA) was conducted between reach types at the start of sampling (September 2013), the first sampling date following flow resumption in dried reaches (January 2014), and in the final month of sampling (May 2014) to compare similarity between assemblages at specific time points of interest. All analysis was performed in R version 3.1.2 using 'vegan'(R Core Developement, 2014; Oksanen *et al.*, 2013).

To examine the effect of drying on richness and abundance in the DR reaches, data from the inital sampling date (September 2013) when these reaches were flowing was compared to each of the five sampling dates after flow resumed following drying (January-May 2014). Cumulative richness across all habitats was calculated within a reach for each time point, while abundance measures were calculated separately for each habitat type within the reach because of differences in habitat availability at each reach. Richness and abundance was calculated for all taxa, insects, EPT (Ephemeroptera, Plecoptera, Trichoptera), resistant taxa, resilient taxa and sensitive taxa. EPT taxa can indicate disturbance within a stream (Resh, Norris & Barbour, 1995) and have been shown to decrease with increasing intermittency (Feminella, 1996; Datry *et al.*, 2014). These comparisons were performed using general linear mixed models (GLMM) with a Poisson distribution for richness metrics using the 'lme4' package (Bates, Maechler & Bolker, 2012) and a negative binomial distribution for abundance metrics using the package 'glmmADMB' (Fournier *et al.*, 2012). The models included a fixed effect of time (pre-drying and successive post- drying) and a random effect of reach to account for repeated measures. Comparisons were then performed between the initial (pre-drying) date and successive post-drying dates using the ‘multcomp’ package (Hothorn, Bretz & Westfall, 2008).

To account for seasonality as reaches dried recovered, those that remained wet were compared with DR reaches at the start of sampling and following flow resumption. Reaches that remained wet provided a baseline for seasonal dynamics as compared to those that resulted from recovery in dried reaches. For the first sampling date, a t-test was performed among reach types on richness and abundance metrics. Richness metrics met the assumption of normality and equal variances while abundance metrics required a negative binomial distribution and were run using the ‘MASS’ package (Venables & Ripley, 2002). Comparisons following flow resumption were then performed between reach types using GLMM with a Poisson distribution for richness metrics and a negative binomial distribution for abundance metrics within the packages ‘lme4’ and ‘glmmADMB’ (Fournier *et al.*, 2012; Bates, Maechler & Bolker, 2012). Models included a fixed effect of reach type and time (post-drying date) and their interaction as well as a random effect of reach to account for repeated measures. Comparisons were then made between reach types on each date in the ‘multcomp’ package (Hothorn, Bretz & Westfall, 2008).

Results

Environmental Measurements

Composition of streambed materials in DR (stream reaches that dried) and RW (reaches that remained wet) reaches was similar with all reaches being predominantly comprised of sand and organic matter. All habitats were available in the DR reaches while only one RW reach contained rock (Fig 3.2). Canopy cover was similar across all reaches and ranged from 89-95%

in DR reaches and 93-95% in RW reaches (Table 3.1). All DR reaches ceased flowing between late October and January; while two RW reaches maintained flow and one ceased flowing in November but maintained a wetted channel (Fig 3.3).

Taxonomic Composition

Non-metric multi-dimensional scaling (NMDS) generated a three-dimensional solution with a stress of 16.5. The first two axes represented the greatest variation in the distance matrix (82%) while the third axis represented 12 % (Fig. 3.4). Samples from RW reaches were grouped more closely within the ordination space than those from DR reaches. Variation in taxonomic composition through time in RW reaches was assumed to include seasonal trends and the broader variation displayed for DR reaches was assumed to reflect the impact of drying and reflooding in addition to this seasonality. Along axis 1, the separation between reach types was the result of those samples dominated by Chironomidae, Ancylidae and Planorbidae and those with a greater abundance of Hydropsychidae, Philopotamidae, Baetidae and Trombidiformes. Axis 2 was positively correlated with Copepods, Scirtidae and Culicidae while Simuliidae was negatively correlated. When examining environmental variables, Axis 1 was correlated with time since flow while axis 2 was correlated with discharge (Fig 3.5). Comparisons of the first sampling date (September 2013) when all reaches were flowing ($F=6.173$, $df=1$, $p<0.001$), the first date following flow resumption in DR reaches (January 2014) ($F=3.2528$, $df=1$, $p=0.016$) and the final date of sampling (May 2014) ($F=19.378$, $df=1$, $p<0.001$) detected significant differences in taxonomic composition between reach types on all dates.

Recolonization of Dried Reaches

Total invertebrate and insect richness was similar to pre-drying levels ($\chi 2$=4.27,10.42, df=5, p=0.512,0.064) on the first sampling date following flow resumption (approximately 11 days after) (Fig 3.6.a, 3.6.b). Resistant taxa richness and sensitive taxa richness showed the same pattern ($\chi 2$=2.64, 7.60, df=5, p=0.76, 0.18) while EPT and resilient taxa declined significantly following drying with recovery to pre-drying levels observed approximately 65 days after flow resumed (Fig 3.6.c-f). Many of the EPT taxa observed on this date were resilient taxa such as *Cheumatopsyche*, *Hydroptila*, Baetidae (*Baetis, Acerpenna),* and *Caenis.*

Total and insect abundance was significantly reduced across all habitats as a result of drying and returned to pre-drying levels approximately 36 days following flow resumption (Table 3.2). EPT abundances recovered within approximately 96 days on wood and sand habitats but had not attained pre-drying levels on rock and OM by the time our sampling ended (~134 days following flow resumption) (Fig 3.7.c, 3.8.c). The dominant EPT taxa that returned were *Acerpenna* and *Cheumatopsyche,* which were also dominant before drying along with *Baetis.* The lack of recovery seen in rock and OM were the result of greater pre-drying abundance within these habitats compared to wood and sand. Resistant taxa recovered to pre-drying levels approximately 35 days after flow resumed for all habitat types and then declined in abundance thereafter (Fig. 3.7.d, 3.8.d). and non-tanypodinae were the dominant resistant taxa on rock and wood habitats at this time, while Isopoda and non-tanypodinae were dominant on OM and sand. Recovery of resilient taxa occurred approximately 96 days following flow resumption in wood and sand habitats but no significant increase was seen in OM or rock (3.7.e, 3.8.e). These results are again attributable to EPT taxa mentioned above. Sensitive taxa rebounded approximately 36 days following flow resumption in wood habitats, then declined and finally continued to increase through the end of sampling (3.7.f). The increase approximately 35 days after flow resumed was largely the result of Crambidae. This group was not subsequently observed during sampling, and therefore, recovery was assigned to the next non-significant sampling date. Increases in the final months of sampling were seen for rock and OM but no significant increase was seen in sand (3.8.f). The increase seen in rock and OM were the product of increased abundance of *Tricocorixia* and Ancylidae.

Comparison to reaches that remained wet

To account for any initial differences in invertebrate richness and abundances between reach types, DR and RW reaches were compared on the first sampling date (September 2013) when all reaches were flowing. There was no significant difference between reach types for any richness metrics (Fig 3.9.a). Insects comprised 66% of the total taxa found in DR reaches as compared to 51% in RW reaches. Within sand samples (Fig 3.9.b), DR reaches contained a greater abundance of EPT (χ^2=24.482, df=1, $p<0.001$) and resilient taxa (χ^2=8.287, df=1, $p=0.004$). For wood samples, RW reaches contained a greater taxon (t=-15.961, df=4, $p<0.001$), insect (t=-17.1831, df=4, $p<0.001$) and resistant taxa (t=-21.1523, df=4, $p<0.001$) abundance than DR reaches (Fig 3.9.c). No significant differences in abundance metrics were detected for OM samples (Fig 3.9.d) and rock samples were not compared because only one RW reach contained rock habitat (Fig 3.9.e). Wood and OM samples contained the greatest abundance of organisms in both reach types.

Upon flow resumption in DR reaches, no significant difference was seen in richness metrics between reach types (Fig 3.10). Because rock was not available at all RW reaches, comparisons for abundance were made only within wood and OM habitats. Taxon abundance had a marginally significant interaction effect in wood habitats (χ^2=9.315, df=4, p=0.054) and a significant effect in OM habitats (χ^2=16.805, df=4, p=0.002). DR reaches had less total abundance within approximately 11 days of flow resumption and then increased at a slower rate in the final months of sampling (Fig 3.11.a, 3.12.a). Insect abundance also had a significant interaction in both wood and OM habitats ((χ^2=12.430,29.256, df=4, p=0.014,<0.001). Insect abundance remained similar between reach types until the final month when RW reaches were greater (Fig 3.11.b). For OM, DR reaches were initially less than RW reaches followed by a peak in the second month before becoming similar (Fig 3.12.b). EPT abundance was less in DR reaches within wood samples across the sampling period (χ^2=19.66, df=1, p<0.001), with both reach types increasing over time (Fig 3.11.c, 3.12.c). Both habitats had an interaction effect for resistant taxa ((χ^2=10.780, 17.201, df=4, p=0.029, 0.002) with DR reaches containing a lower abundance at the start and end of sampling (Fig 3.11.d, 3.12.d). Resilient taxa abundance showed similar patterns to EPT, with DR reaches having less resilient taxa abundance in wood habitats (χ^2=19.25, df=1, p<0.001) and both habitats changing over time (Fig 3.11.e, 3.12.e). For sensitive taxa, wood samples had an interaction effect (χ^2=13.52, df=1, p=0.009) with DR reaches being less in January, March and April, similar to the results seen in comparison with pre-drying (Fig 3.11.f). Within OM samples (Fig 3.12.f), an effect of reach type and time were seen with DR reaches remaining lower throughout the sampling period (χ^2=19.25, df=1, p<0.001).

Discussion

This study showed that macroinvertebrate recovery from drying varied with taxa life history, and habitat. As noted in other studies, increasing the frequency and duration of drying can result in a decrease in the number of taxa capable of persisting in intermittent stream reaches (Bogan, Boersma & Lytle, *In Press*; Datry *et al.*, 2014). A better understanding of survival and recovery strategies of intermittent stream organisms during and following flow interruption is needed in order to predict the affect of increased drying frequency and duration. This is particularly important in areas with abundant annual rainfall, but seasonal dry periods or where climate projections suggest increasing drought frequency and intensity. This study examined the rate of recovery in a recently dried stream as compared with other intermittent streams. Differences in RW and DR reach trajectories showed both the effect of seasonality and drying within these reaches. Overall richness immediately after drying was similar to pre-drying levels and to levels in reaches that remained wet, but total abundance was greatly reduced. These findings highlight the recovery sequence following rewetting as resistant taxa rebound quickly followed by resilient and finally sensitive taxa. Understanding the organisms that can persist and recover following drying will aid in predicting how stream assemblages will respond in the event that their flow regime shifts from perennial to intermittent.

Reaches that remained wet exhibited some temporal variation in taxonomic composition, likely due to seasonality, but less than those reaches that dried (Fig 3.4). Similar trajectories have been noted between wet and dry years within the same intermittent stream in other regions (Acuña *et al.*, 2005). Differences in assemblage composition at the start of sampling are attributable to greater abundance of Hydropsychidae and Philopotamidae within DR reaches as compared with RW reaches, which had a greater abundance of Gammaridae. Because Trichoptera are often weak dispersers and move more readily within the stream channel, their presence and greater abundance in DR reaches is likely the result of proximity to a perennial source (Petersen *et al.*, 2004). Gammaridae have been found to be abundant in temporary pools and wetlands within the region despite their lack of desiccation resistance (Battle & Golladay, 2001). These taxa have been shown to utilize the hyporheic zone as refugia during drying events (Stubbington *et al.*, 2011). Simuliidae grouped with the initial recovery period in DR reaches and have been shown to be desiccant resistant and quickly dominate re-flooded reaches (Malmqvist *et al.*, 1991; Hammock & Bogan, 2014). As DR reaches recovered, resilient taxa (Hydropsychidae and Baetidae) became more dominant. The tolerance level and life history of the organisms determines which will persist or subsequently recolonize following stream drying.

Many studies have seen a sharp decline in survival in dry stream sediments after one month and a steady decrease in taxa survival for every subsequent week that streams remain dry (Datry, 2012; Larned, Datry & Robinson, 2007). Despite these streams having dried for approximately two months, no change in taxa or insect richness was detected within ~11 days of flow resumption in DR reaches while EPT richness recovered in ~65 days. Total and insect abundance recovered within ~36 days, although ~96 days was needed for EPT taxa. Similar results have been observed with initial recovery occurring rapidly (taxa appearing in ~4 days) through resistant taxa while the return of resilient taxa can take ~100-200 days (Churchel & Batzer, 2006; Miller & Golladay, 1996; Malmqvist *et al.*, 1991). Sensitive taxa comprised a small portion of overall richness within both RW and DR reaches as compared to resilient and resistant taxa. This result is likely the influence of the organisms of these streams being those adapted to frequent drying. Other studies have shown a shift from sensitive taxa to more resistant taxa with increased drying frequency and severity (Bogan, Boersma & Lytle, *In Press*). Resistant taxa richness was not affected by drying and abundances returned within ~36 days. The majority of the resistant taxa that quickly recovered consisted of Chironomidae and Simuliidae, which have desiccant-resistant life stages. These taxa made up 86% of the total abundance ~36 days following flow resumption as compared to 64% on the initial sampling date. The increase in tolerant taxa at three to four months following flow resumption was largely due to an increase in *Acerpenna* (Baetidae). Studies in the region have noted that Baetidae are present as adults at all times of the year and likely take less than six months to reach maturity (Berner & Pescador, 1988) which is consistent with the pattern of recolonization we observed. The observed pattern of recovery followed expectations with resistant taxa quickly rebounding, followed by resilient taxa within ~100-200 days of re-flooding.

Seasonality has an effect on community recovery as a result of differing growth rates and life histories (Miller & Golladay, 1996). By comparing DR reaches to RW reaches, we were able to examine changes in assemblage composition as a result of seasonal variation as opposed to recovery alone. While differences in EPT richness were seen as compared to pre-drying levels in DR reaches, no difference was seen between DR and RW reaches over the recovery period. The dominant EPT taxa within these streams included genera of Baetidae and *Cheumatopsyche*. Baetidae as well as *Cheumatopsyche* have been shown to be very resilient to differing levels of disturbance and are often found within intermittent streams (Miller & Golladay, 1996; Wiggins, 1996). RW reaches did have a greater abundance of EPT taxa within wood habitats during the recovery period despite having similar levels before drying. Abundance within RW reaches continued to increase from January to May while DR reaches saw fluctuation in abundance level as a result of the replacement of different dominant taxa. After the initial increase in resistant taxa within DR reaches, an overall difference in taxa abundance was observed. These results suggest that drying may not affect overall richness within intermittent streams as a result of adapted taxa but impacts the assemblage abundance. However, with more frequent drying, the time for sensitive and some resilient taxa to recover will likely be reduced resulting in a loss of those taxa.

In order to understand the effect of drying, a better understanding of the recovery patterns following flow resumption is needed. This will allow predictions about how future droughts will impact these systems. An assemblage’s ability to respond to drying is dependent on the seasonal patterns normally experienced within that ecosystem (Datry *et al.*, 2014). While taxon richness and abundance in this study recovered within a few weeks of flow resumption, recovery of pre-drying composition took longer depending on the life cycle and adaptation to drying of individual taxa (Robson, Chester & Austin, 2011; Datry *et al.*, 2014). Intermittent stream assemblages are adapted to seasonal drying, however, increasing the frequency and degree of drying could result in the loss of some taxa that require longer periods for recovery (Fritz & Dodds, 2005; Bogan, Boersma & Lytle, *In Press*).

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Table 3.1: Physical Characteristics of reaches at the start of sampling

Reach	Stream	Type	Order	% Canopy Cover	Approximate time since flow resume
Dr 1	Big Cypress	Dried	3	95	82
Dr 2	Big Cypress	Dried	3	93	82
Dr 3	Big Cypress	Dried	3	89	82
RW 1	Kioke	Remained Wet	2	95	377
RW 2	Little Spring	Remained Wet	2	93	377
RW 3	Keel	Remained Wet	2	94	377

Table 3.2: Approximate time (days) until post drying abundances were not significantly different from pre-drying conditions in each habitat in DR reaches

	Habitat			
	Organic Matter	Sand	Rock	Wood
Total Abundance	36	36	36	36
Insect	36	36	36	36
EPT	--	96	--	96
Sensitive Taxa	96	--	65	65
Resilient Taxa	--	96	--	96
Resistant Taxa	36	36	36	36

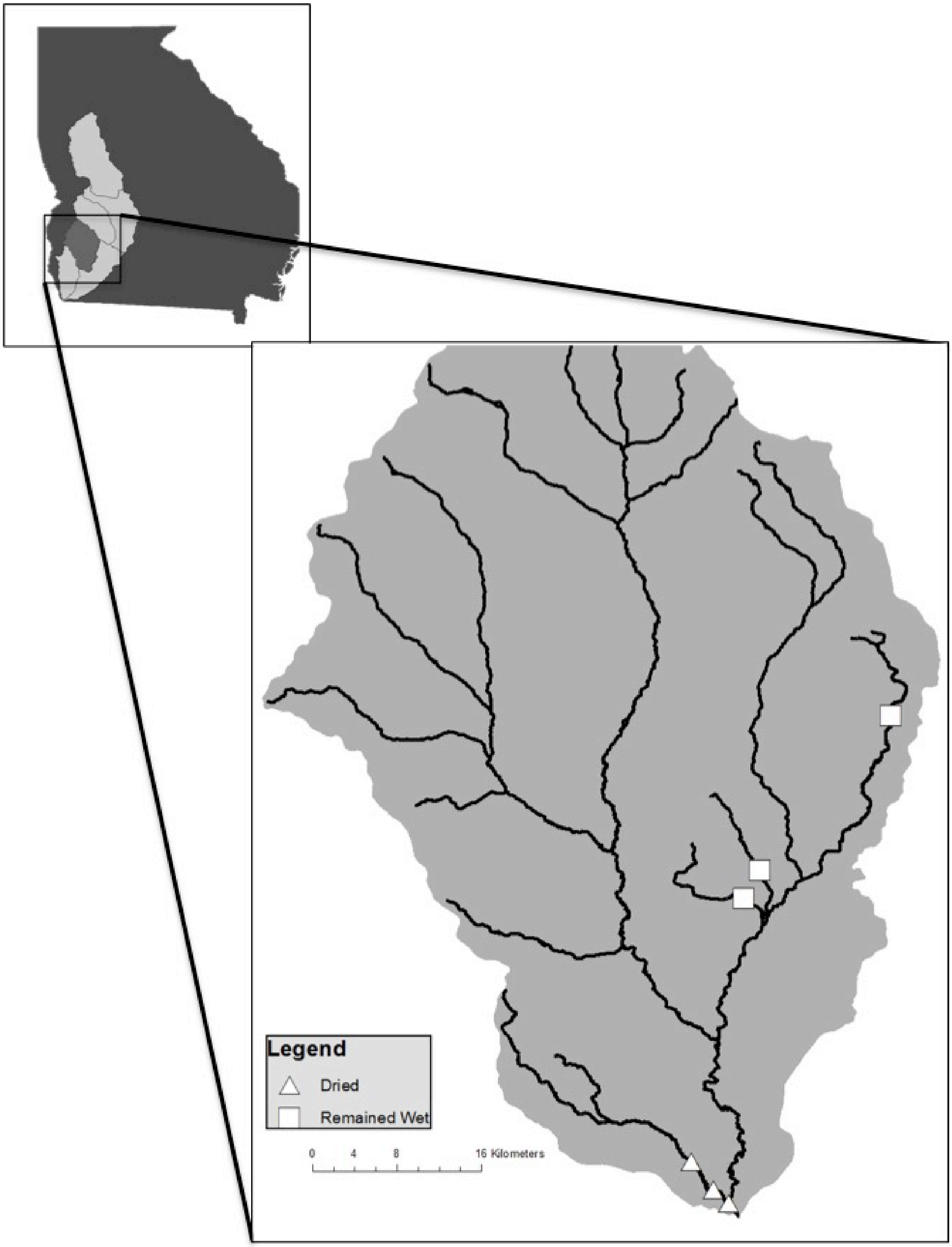

Fig 3.1: Map of study locations within the watershed

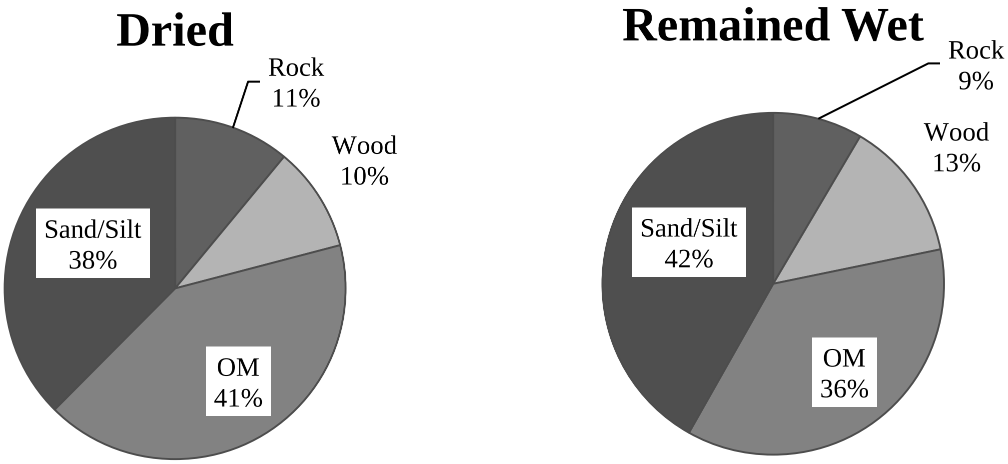

Fig 3.2: Mean percentage of habitat within each reach type on the initial sampling date

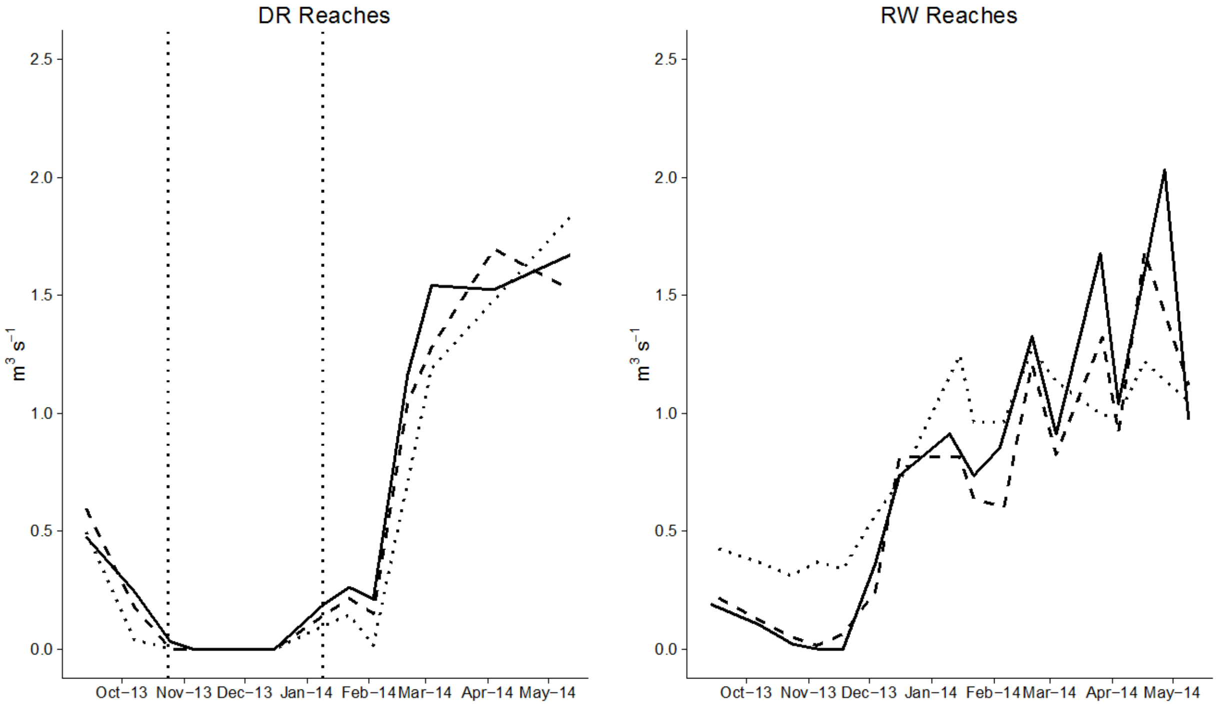

Fig 3.3: Discharge of DR and RW reaches from September 2013 to May 2014. Vertical dotted lines in DR reaches indicate cessation and resumption of flow.

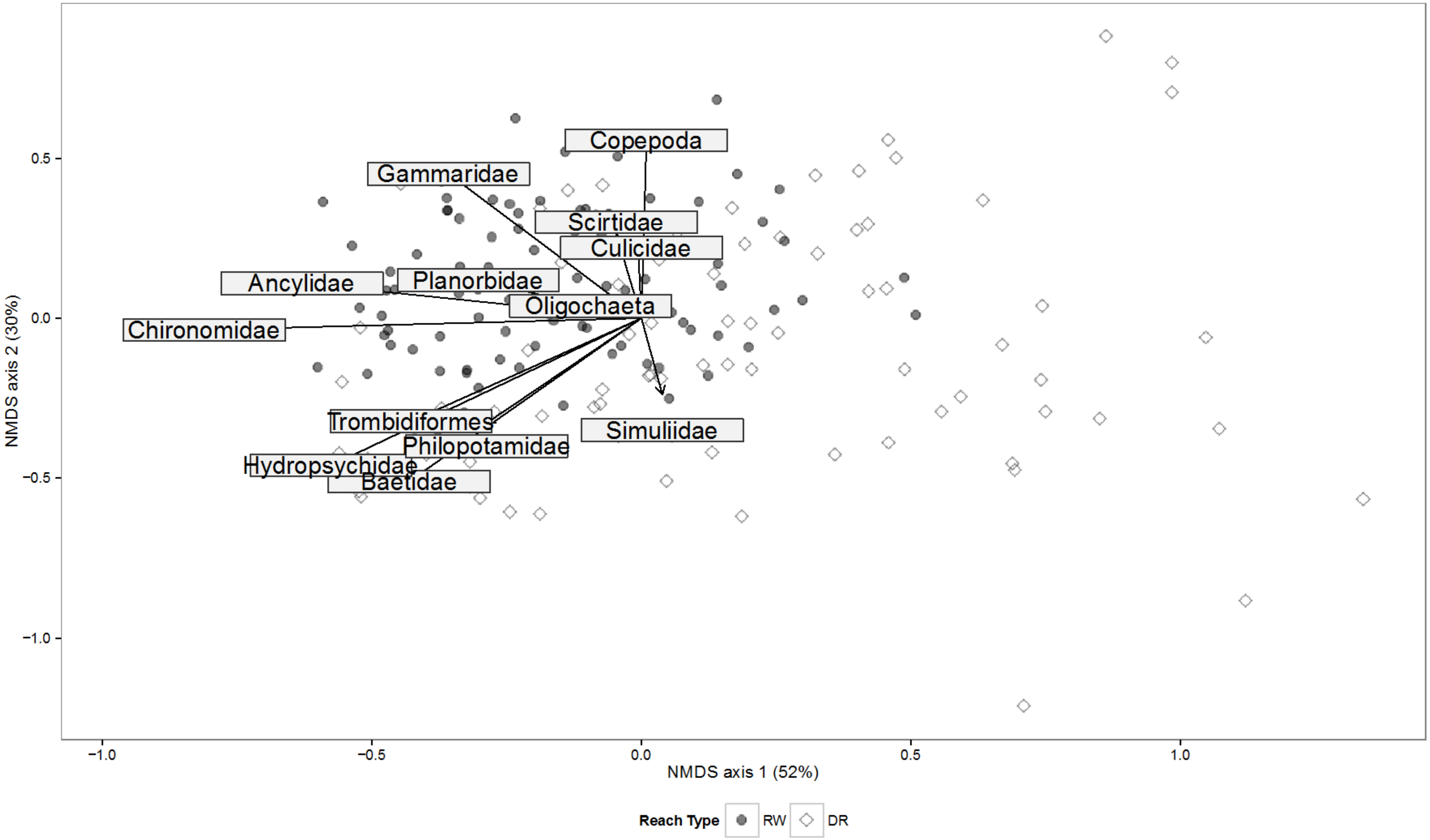

Fig 3.4: Three-dimensional non-metric multidimensional scaling (NMDS) with first two axes shown with all habitat and reaches plotted. Taxa were grouped by family and those with a significant correlation and an r^2>0.15 shown.

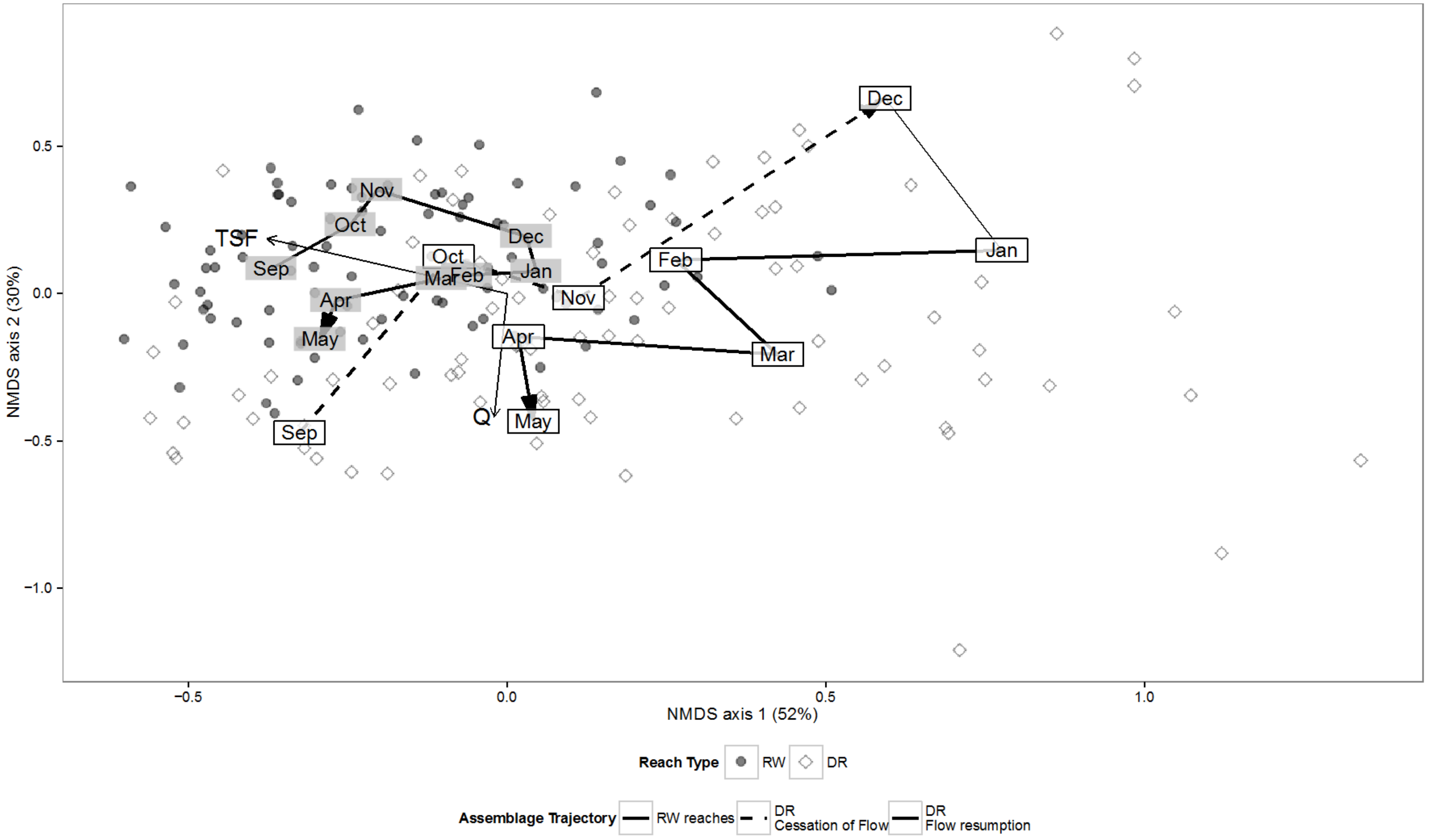

Fig 3.5:Three-dimensional non-metric multidimensional scaling (NMDS) with first two axes. Points represent habitat samples in each reach. Centroids of each date are shown and connected to trace trajectory of assemblages over time. Dr reaches ceased flowing prior to sampling in October and resumed flow following sampling in December. TSF=time since flow resumed at time of sampling, Q= discharge at time of sampling

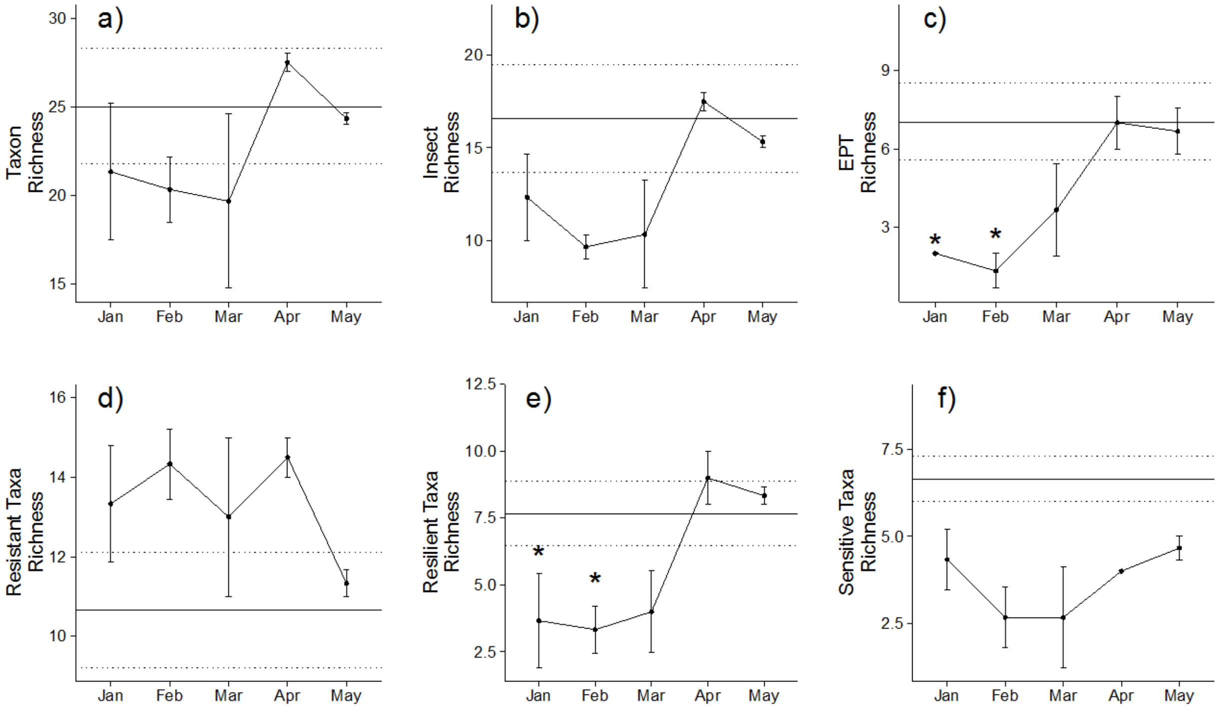

Fig 3.6: Richness metrics in DR reaches following flow resumption in late December with horizontal lines indicating pre-drying (September) mean±SE and points representing richness mean±SE of each sampling date following flow resumption. a) Taxa richness b) insect richness c) EPT richness d) resistant taxa richness e) resilient taxa richness f) sensitive taxa richness. Asterisks indicate significant differences from pre-drying levels ($p<0.05$).

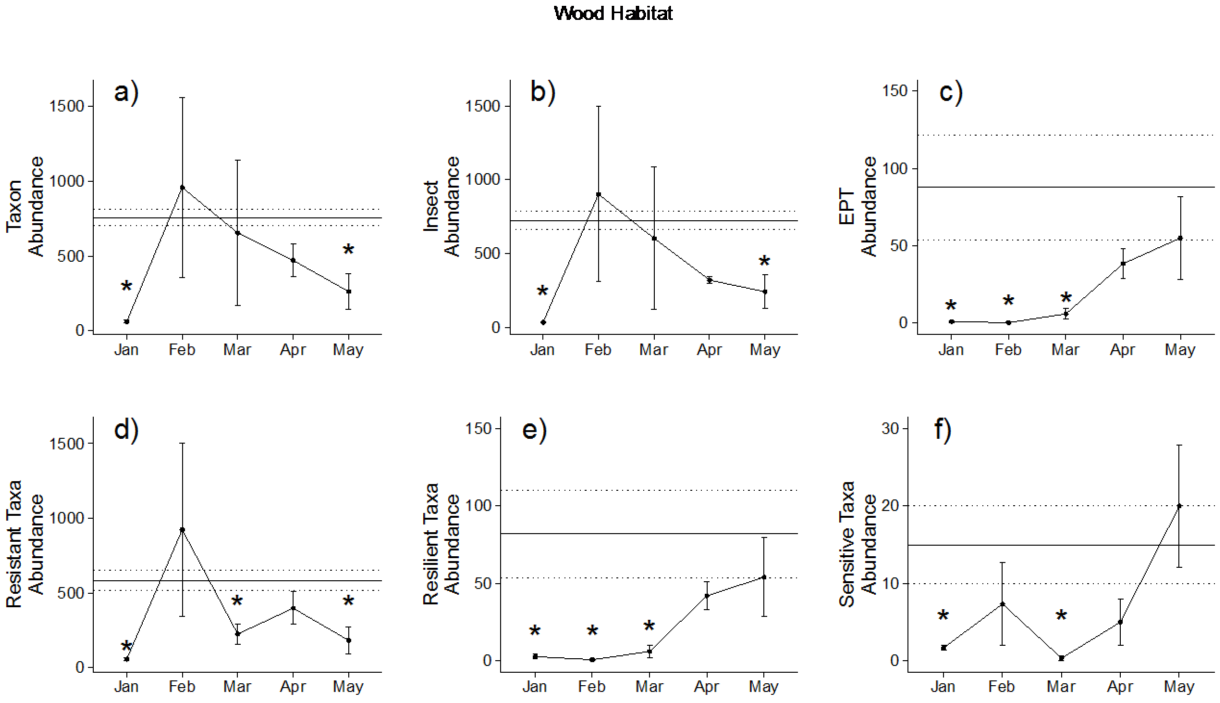

Fig 3.7. Abundance of taxa on wood in DR reaches following flow resumption in late December with horizontal lines indicating pre-drying (September) mean±SE and points representing richness mean±SE of each sampling date following flow resumption. a) Taxa richness b) insect richness c) EPT richness d) resistant taxa richness e) resilient taxa richness f) sensitive taxa richness. Asterisks indicate significant differences from pre-drying levels (p<0.05).

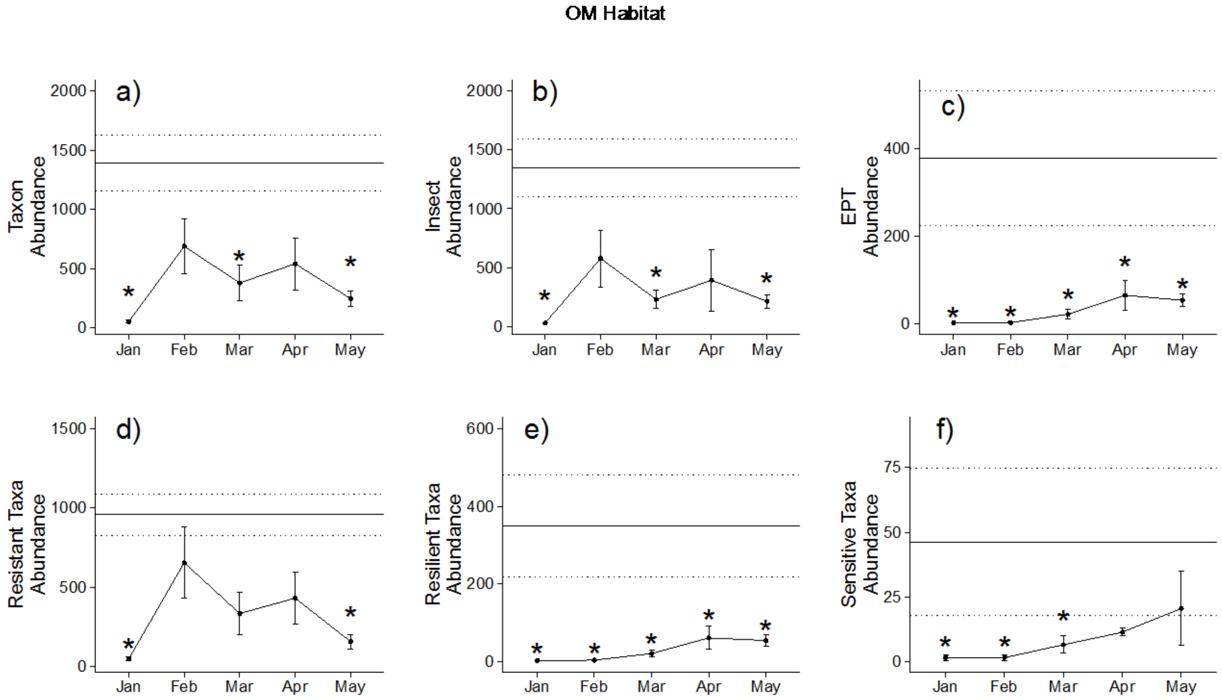

Fig 3.8: Taxa abundance in OM in DR reaches following flow resumption in late December with horizontal lines indicating pre-drying (September) mean±SE and points representing richness mean±SE of each sampling date following flow resumption. a) Taxa richness b) insect richness c) EPT richness d) resistant taxa richness e) resilient taxa richness f) sensitive taxa richness. Asterisks indicate significant differences from pre-drying levels ($p<0.05$).

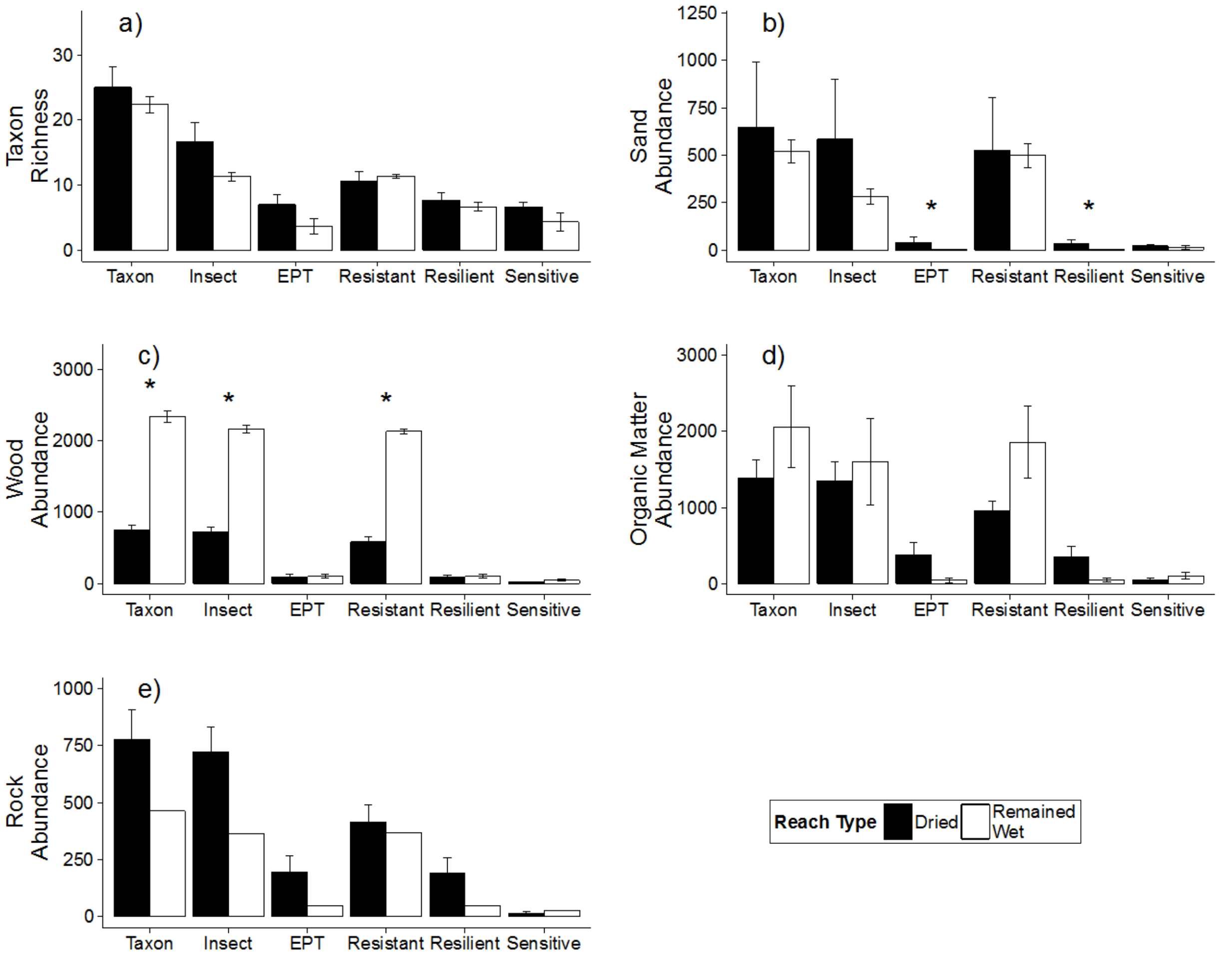

Fig 3.9: Mean±SE between DR and RW reaches at the start of sampling (September 2013) when all streams were flowing. Asterisks indicate significant ($p<0.05$) differences between reach types. Rock was not compared because of a single sample available for RW reaches. a) Richness, b) Sand habitat abundance, c) Wood habitat abundance, d) Organic matter habitat abundance, e) Rock habitat abundance

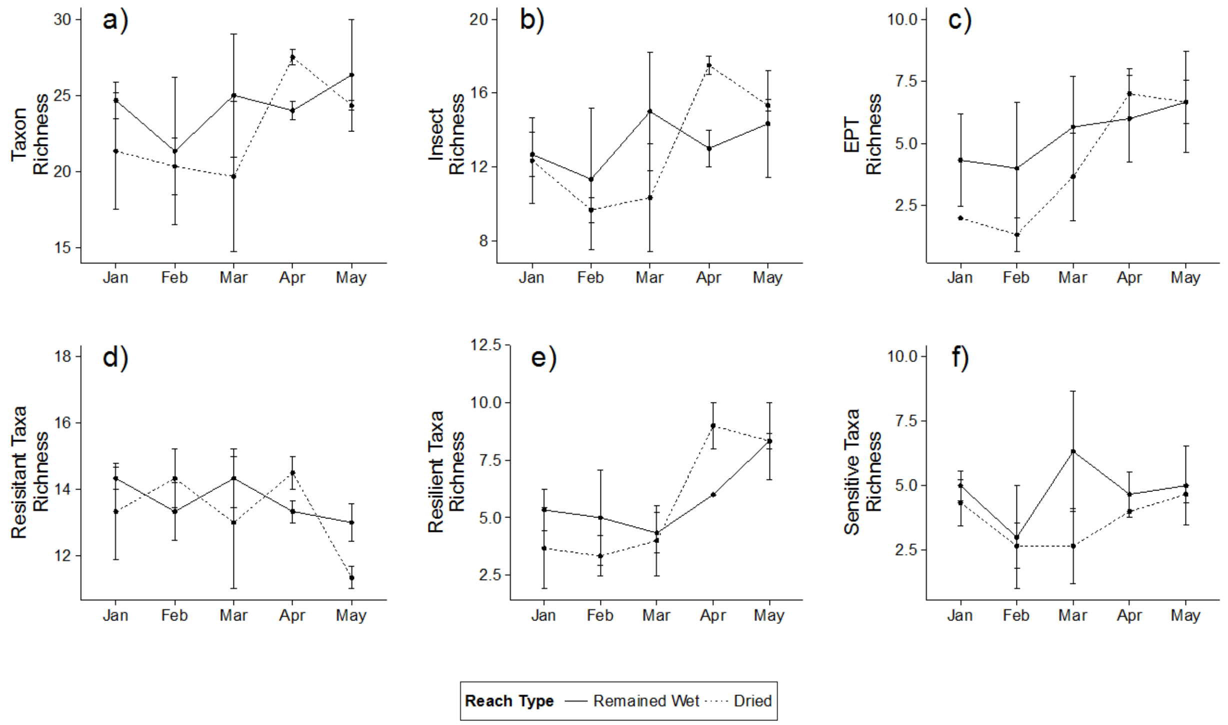

Fig 3.10: Richness comparisons across metrics between RW and DR reaches following flow resumption. a) Taxon richness b) insect richness, c) EPT richness, d) resistant taxa richness, e) resilient taxa richness and f) sensitive taxa richness

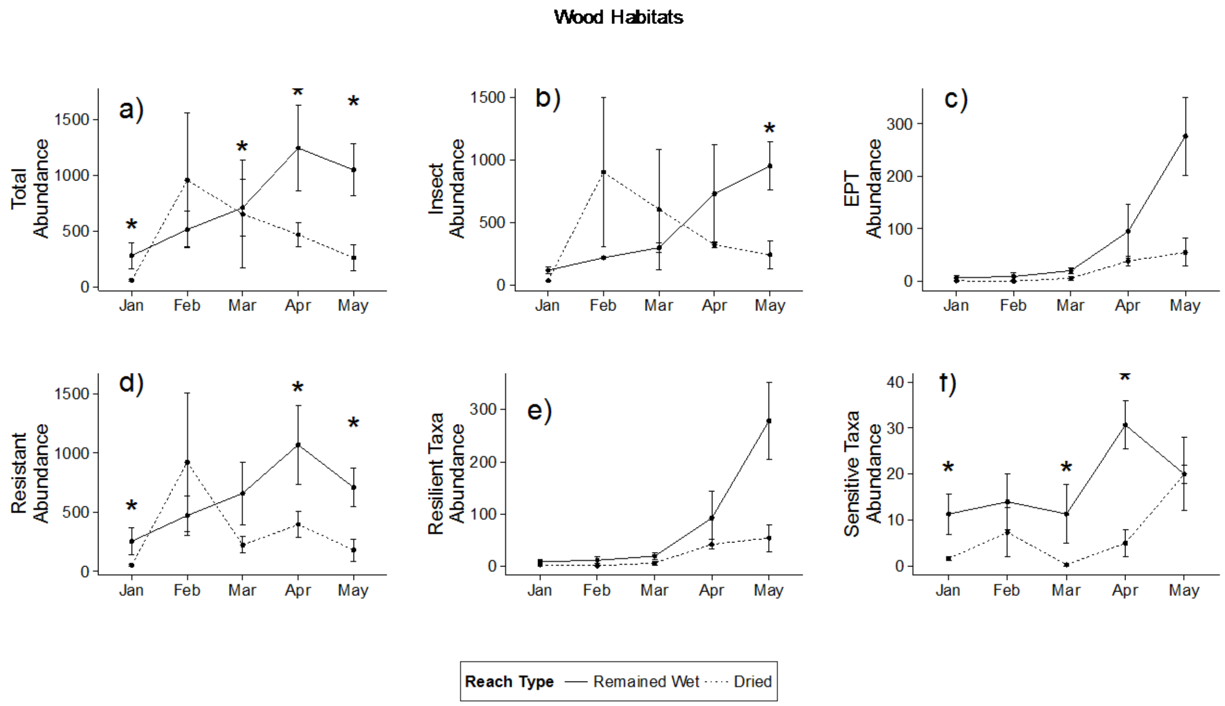

Fig 3.11: Abundance comparisons within wood habitats across metrics between RW and DR reaches following flow resumption. a) Taxon richness b) insect richness, c) EPT richness, d) resistant taxa richness, e) resilient taxa richness and f) sensitive taxa richness.

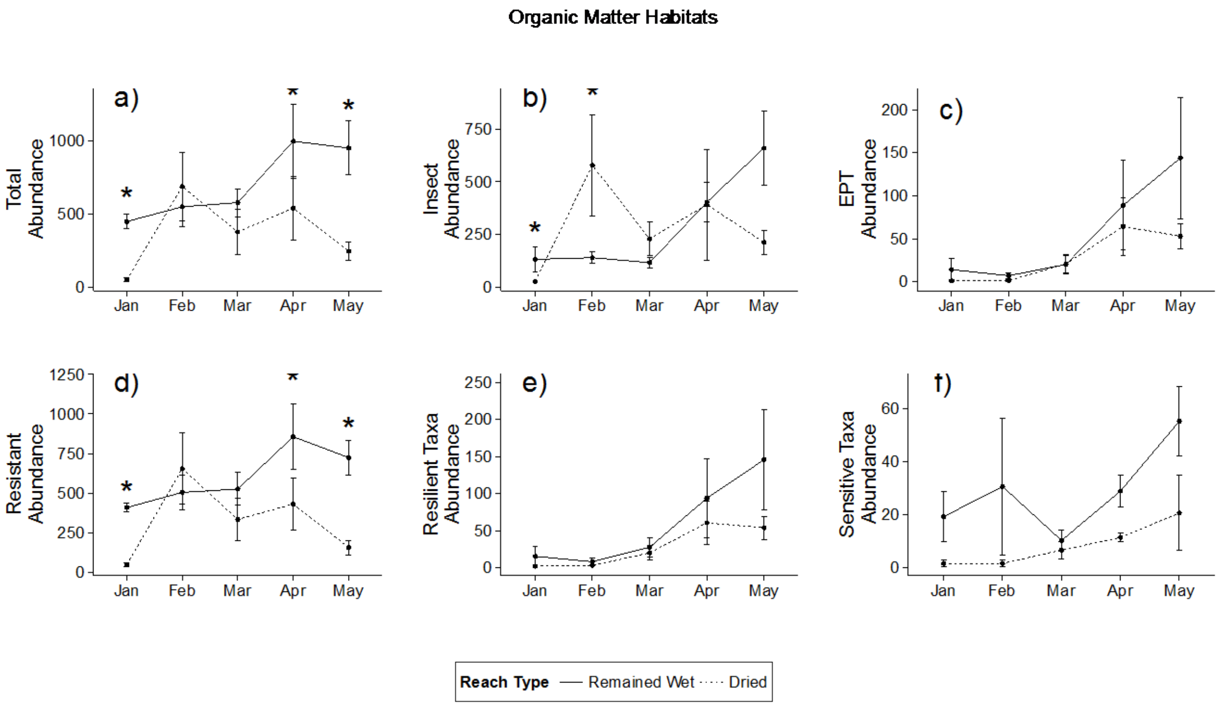

Fig 3.12: Abundance comparisons within organic matter habitat across metrics between RW and DR reaches following flow resumption. a) Taxon richness b) insect richness, c) EPT richness, d) resistant taxa richness, e) resilient taxa richness and f) sensitive taxa richness

CHAPTER 4

CONCLUSIONS

Summary

Climatic variability and water use has increased the importance of understanding the ecological relationships between aquatic organisms and environmental flows. Many studies have sought to apply the framework set within 'ELOHA' (Ecological Limits of Hydrologic Alteration) to better understand how their system is being affected (Poff et al. 2010). Recent multi-year droughts within southwest Georgia have highlighted the need to apply this framework within the lower Flint River basin because irrigation withdrawal coupled with droughts has resulted in many previously perennial streams ceasing to flow (Rugel et al. 2012). In order to understand the effect of reduced flows on biota within a tributary watershed of the lower Flint River, Ichawaynochaway Creek, we examined macroinvertebrate assemblages across a gradient of flow permanence approximately six months after the end of a multi-year drought. Smaller intermittent streams were monitored for an extended period of time to better understand the recovery process following drying in some reaches as compared to similar streams that maintained flow.

Assemblages differed among reach types across the gradient of flow permanence. While total richness and abundance did not differ among reach types, differences were seen in certain taxa. Taxa belonging to some functional feeding groups (*e.g.* filterers) and more sensitive taxa (those with longer lifecycles) were less abundant in more intermittent streams. Analysis suggested that distance from a perennial source also played a role in how these assemblages recovered with a highly intermittent stream with close proximity to the perennial mainstem having more EPT taxa than more stable reaches further removed. These observations suggest that the increasing frequency of extreme low flows within the system could ultimately exclude certain taxa from extensive areas of stream. With summer low flows now resulting in previously perennial streams ceasing to flow, the harshness of the dry period of intermittent streams will also increase.

Because many of our smaller streams within the watershed are intermittent, we investigated the rate of recovery following drying within a highly intermittent stream (DR) and compared the assemblage trajectory to that seen in other intermittent streams that remained wet (RW). Within DR reaches, recovery of resilient taxa richness (those with desiccant resistance and multi-voltine lifecycles) occurred within ~11 days of flow resumption while abundances recovered in ~36 days. A large portion of the total abundance at this time consisted of Chironimidae and , which have desiccation resistant eggs and can quickly mature. No difference was seen in resilient taxa richness (multi-voltine taxa without desiccant resistance), however recover of abundance took ~96 days. Sensitive taxa richness was not reduced as a result of drying, though this was likely the result of few of these taxa persisting within intermittent streams. Other studies have also shown that initial colonization by resistant taxa is rapid but recovery of the previous assemblage can take anywhere from 100 to 200 days with more sensitive taxa arriving up to a year after flow resumes (Miller and Golladay 1996, Acuña et al. 2005, Churchel and Batzer 2006). Richness during recovery in DR reaches did not differ from RW reaches, however, RW reaches tended to have a greater abundance. These differences suggest that assemblages within these streams are adapted to drying, resulting in a quick recovery of richness but not abundance. Overall, these results suggest that increasing the dry period, and as a result reducing recovery times, will create a shift in assemblages towards more resistant and tolerant taxa. This shift could ultimately alter the overall functionality of a watershed over time.

Recent studies have indicated a need to quantify biotic response to changing flow conditions through quantitative modeling (Arthington et al. 2006, Kennen et al. 2014). In order for this to occur, however, a greater understanding of life histories is needed within regions and especially within smaller headwater or intermittent streams (Robson et al. 2011). Within the lower Flint, increasing pressure during low-flow periods will result in increased periods of flow cessation in previously perennial streams and increased dry periods in intermittent streams. Headwater and low-order streams are often highly diverse systems and in some cases biodiversity hotspots (Meyer et al. 2007, Clarke et al. 2008, Datry et al. 2014, Mazor et al. 2014). Reduction of diversity within these smaller streams and alteration of flow within larger perennial streams in this ecosystem over time may result in the loss of sensitive taxa and an increase in tolerant taxa abundance.

Future Research

While this study explored the effect of a multi-year drought on recovery across a gradient of flow permanence, a better understanding of the natural assemblages within these streams is needed. Variation in stream order across this gradient could explain some differences seen as well as the seasonality of certain organisms. Monitoring the response of macroinvertebrates across all streams before, during and soon after a low flow event could aid in better understanding how assemblages within this system are affected. In addition, a better understanding of the importance of refuges within intermittent streams is needed to help explain some observed variation. Because the duration of dry periods will likely increase in these streams, monitoring which organisms are capable of surviving in dry sediments and the physical parameters that control survival could be key. Increasing water demand and droughts in this area will result in more extreme low flow events with a more frequent return interval. Understanding the time needed for assemblages to recover following such events will be crucial in determining at what limit any irreversible losses can occur.

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APPENDICES

APPENDIX A: Abundances of taxa found by reach in Chapter 2: OM=organic matter, R=rock, S=sand, W=wood

Sampling Date 1		Intermittent-Frequent			Intermittent-Dry			Intermittent-Wet			Perennial			
		1	2	3	1	2	3	1	2	3	1	2	3	4
	Habitats Sampled:	R,W	R,W	R,W	W	W	R,W	R,W	R,W	R,W	R	R,W	W	W
Annelida Clitellata	**Hirudinea**		10			4					1	4		
	Oligochaeta		2	22		4	20	88	48			28	4	
Arthropoda		1362	1507	1547	2219	2225	2816	2246	2402	10353	3322	4298	385	500
Arachnida	**Tombidiformes**	27	6	2	10		39	80	12	432	3	32	32	36
Insecta		1334	1500	1503	2100	2128	2646	2166	2384	9918	3319	4266	353	464
	Coleoptera		4	4	1	4	20	45	15	4	372	324	17	52
	Elmidae		2				19	45	14		372	324	15	52
	Ancyronyx (larval)											4	1	10
	Dubiraphia		2					8	1				2	
	Adult		2						1					
	larval							8					2	
	Macronychus							8				16	4	10
	Adult												2	8
	larval							8				16	2	2
	Microcylloepus (larval)							12	1		320	232		24
	Oulimnius (larval)							8						
	Stenelmis						19	9	12		52	72	8	6
	Adult							1			32	24		4
	larval						19	8	12		20	48	8	2
	Unknown (larval)													2
	Psephenidae								1				2	
	Ectopria (larval)								1				2	
	Gyrinidae		2	4	1	4	1			4				
	Dineutus (larval)		2	4	1	4	1			4				
	Collembola		1		2						4			
	Entomobryidae		1		2						4			
	Cyphoderus		1		2						4			
	Diptera	834	966	1090	1960	2076	2377	1785	1983	7832	2684	3035	264	279
	Ceratopogonidae		17					12				17	2	
	Atrichopogon		16									17		
	Bezzia		1					12					2	
	Chironomidae	824	949	1071	1960	2072	2376	1752	1618	7412	396	2928	226	244
	Non-tanypodinae	562	650	891	1848	1984	2069	1644	1470	6356	332	2616	219	223
	Tanypodinae	228	246	144	112	48	228	92	108	860	16	160	2	15
	pupa	34	53	36		40	79	16	40	196	48	152	5	6
	Empididae	1						21	80	40		2	14	4
	Hemerodromia	1						21	80	40		2	14	4
	larval	1						20	80	32		2		2
	pupa							1		8			14	2
		9		19			1		285	380	2288	88	22	31
	pupa	4		1					1	32	176	4	2	
	Tipulidae					4								
	Ephemeroptera	6	8	42	16	8	59	97	140	293	42	108	19	11
	Baetidae	6	8	42	16		59		58	256	19	32	8	

Acentrella		2								17	28		
Acerpenna	2	2				11			16				
Baetis	4		42			32		56	240				
Plauditus										2		4	
Procleon		4				16							
Pseudocentroptiloides												4	
Pseudocleon				16							4		
Unknown								2					
Baetiscidae											4	3	7
Baetisca											4	3	7
Ephemerellidae							1	14		16	32		
Seratella							1	14		16	32		
Heptageniidae					8		44	54	37	5	4	6	4
Maccaffertium							36	42	33	5	4	4	4
Stenacron					8			12					
Unknown							8		4			2	
Isonychiidae												2	
Isonychia												2	
Leptohyphidae							52	14		2	36		
Asioplax										1	12		
Tricorythodes							52	14		1	24		
Hemiptera	2	2					4						
Gerridae	2	2					4						
Limnoporus		2											
Trepobates	2						4						
Lepidoptera	2										2		
Crambidae	2										2		
Petophila											2		
Unknown	2												
Megaloptera							1	1		1	4		
Corydalidae							1	1		1	4		
Corydalus							1	1		1	4		
Odonata	2	6	4			1		16					
Coenagrionidae	2							16					
Amphiagrion								16					
Unknown	2												
Gomphidae			4										
Dromogomphus			4										
Macromidae		6				1							
Macromia		6				1							
Plecoptera													2
Perlidae													2
Paragnetina													2
Trichoptera	488	513	363	121	40	189	234	229	1789	216	793	53	120
Hydropsychidae	458	484	354	121	40	189	196	162	1561	179	536	18	40
Cheumatopsyche	191	370	180	81	40	133	76	150	1037	32	320	8	14
Hydropsyche			4							118	4	10	9
Macrostemum													2
Unknown	267	114	170	40		56	120	12	524	29	212		15
larval	267	114	170	40		56	120	12	524	28	212		15

	pupa										1			
	Hydroptilidae		1					17	26	4	32	117	6	
	Hydroptila							17	8		16	64	6	
	Neotrichia								16			1		
	Oxyethira		1						2	4		4		
	Unknown										16	48		
	larval											16		
	pupa										16	32		
	Leptoceridae		16	1				4	1	4		32	6	3
	Nectopsyche							4					2	
	Oecetis		16	1					1	4		32	4	3
	Philopotamidae	20	8	4				8	40	219	5	108	23	77
	Chimarra	20	8	4				8	40	219	5	108	23	75
	Wormaldia													2
	Unknown (pupa)			4										
	Psychomyiidae							8						
	Lype							8						
	Pupa	10	4	4				1		1				
Malacostraca	**Amphipoda**	1			43	40	6							
	Gammaridae	1			43	40	6							
	Gammarus	1			43	40	6							
	Decapoda				1	1	1		6	1				
	Atyidae								1					
	Cambaridae				1	1	1		5	1				
	Procambarus				1	1	1		5	1				
	Isopoda		1	41	49	48	124			2				
Maxillopoda	**Copepoda**			1	16	8								
Mollusca	**Bivalvia**							204	83				2	8
	Veneroida							204	83				2	8
	Corbiculidae							204	83				2	8
	Corbicula							204	83				2	8
	Gastropoda	4	124	21	56	16	138	8	15	64		9		2
	Ancylidae		6	20	56	16	72		2	64		4		2
	Physidae	4	103	1			7							
	Planorbidae		15				59		1					
	Pleuroceridae								4					
	Valvatidae											1		
	Viviparidae							8	8			4		
Platyhelminthes	**Tricladida**							4	6					
	Planariidae							4	6					
	Planaria							4	6					

Sampling Date 2		Intermittent-Frequent			Intermittent-Dry			Intermittent-Wet			Perennial			
		1	2	3	1	2	3	1	2	3	1	2	3	4
	Habitats Sampled:	R	R,W	R,W	W	W	R,W	R,W	R,W	R,W	R	R,W	W	W
Annelida Clitellata		38	4		4		56	2	2	6	2	7		
	Hirudinea	4	2		4						2			
	Oligochaeta	34	2				56	2	2	6		7		
Arthropoda Arachnida	**Tombidiformes**	6	3	1			7	3		3		7		16
Insecta		529	291	159	333	492	*746*	1393	1559	1121	2488	1245	135	1174
	Coleoptera	2	3	2		3	2	73	42	5	154	199	1	78
	Dytiscidae			1										
	Neoporus			1										
	Elmidae					1	2	73	30	5	154	199	1	78
	Ancyronyx (larval)											1		12
	Dubiraphia												1	34
	Adult													32
	larval												1	2
	Macronychus (larval)							8				11		
	Microcylloepus (larval)					1		60	4	5	122	103		
	Stenelmis						*2*	5	26		32	84		32
	Adult							2			16	25		24
	larval						2	3	26		16	59		8
	Psephenidae								12					
	Ectopria (larval)								12					
	Scirtidae	2	3			2								
	Cyphon (larval)	2	2			2								
	Scirtes (Adult)		1											
	Gyrinidae			1										
	Dineutus (Adult)			1										
	Collembola	6	2	3				2			4			
	Entomobryidae	6	2	3							4			
	Cyphoderus	6	2	3							4			
	Sminthuridae							2						
	Diptera	150	210	114	315	475	*681*	1072	1126	662	1940	731	107	456
	Ceratopogonidae					7	2							
	Atrichopogon					6								
	Bezzia					1	2							
	Chironomidae	146	204	107	311	468	*679*	1064	1116	606	516	714	85	294
	Non-tanypodinae	108	142	59	275	417	592	1021	1082	544	510	667	80	270
	Tanypodinae	10	37	27	32	39	*62*	21	14	46		8	2	14
	pupa	28	25	21	4	12	25	22	20	16	6	39	3	10
	Culicidae		1	7	4									
	Anopholes		1	4	4									
	Culex			3										
	Empididae		1					3	9	6		4		16
	Hemerodromia		1					3	9	6		4		16
	larval							3	9	6		4		16
	pupa		1											
		4	4					5	1	50	1424	13	22	146
	larval	4	4					5	1	50	1392	9	22	138
	pupa										32	4		8

Ephemeroptera	138	10	9			29	72	47	148	60	100	6	40
Baetidae	138	9	9			*9*	12	7	86	54	66	6	24
Acentrella							3			54	28		
Acerpenna						*9*		1			1		
Baetis	138	9	9				1	6	86			4	24
Plauditus							8				37	2	
Caenidae		1											
Caenis		1											
Heptageniidae						20	15	30	62	6	24		12
Maccaffertium							3	28	10	6	24		
Stenacron						*20*	12	2	52				12
Isonychiidae											2		
Isonychia											2		
Leptohyphidae							45	10			8		4
Asioplax													4
Tricorythodes							45	10			8		
Hemiptera			1				2						
Notonectidae			1										
Notonecta			1										
Unknown							2						
Nepidae			1										
Ranatra			1										
Lepidoptera					4						9		
Crambidae											9		
Petrophila											5		
Unknown											4		
Geometridae					4								
Megaloptera											2		2
Corydalidae											2		2
Corydalus											2		2
Odonata		41	2				1						
Coenagrionidae							1						
Chromagrion							1						
Gomphidae		2											
Hagenius		2											
Macromidae		39	2										
Macromia		39	2										
Plecoptera							1					2	23
Perlidae							1					2	23
Attaneuria													13
Neoperla							1					2	10
Trichoptera	233	25	27	18	10	34	170	344	306	330	204	19	575
Brachycentridae								1					3
Brachycentrus								1					3
Hydropsychidae	224	12	19	18	9	14	155	263	185	283	147	10	56
Cheumatopsyche	224	11	19	18	9	14	125	255	105	28	89		18
Hydropsyche		1					8	8	80	255	28	10	22
Unknown							22				30		16
Hydroptilidae					1		8	9	11	16	39	1	
Hydroptila					1		6	4		16	39	1	

		Oxyethira							2	5	11				
	Leptoceridae		1	13	7			20		1	2		7		
		Oecetis	1	13	7			20		1	2		7		
	Philopotamidae		8		1				7	70	108	31	11	8	516
		Chimarra	8		1				7	70	108	31	11	8	516
Malacostraca			12	93	15	289	167	67	2	14	6		1		5
	Amphipoda					62	51	5		6					
	Gammaridae					62	51	5		6					
		Gammarus				62	51	5		6					
	Decapoda					1	1			3					1
	Cambaridae					1	1			3					1
		Procambarus				1	1			3					1
	Isopoda		12	93	15	226	115	62	2	5	6		1		4
Maxillopoda				11	12	32	1		8						
	Copepoda			11	12	32	1		8						
	Ostracoda			35		5	16	2							
Mollusca			72	26	14	30	6	92	15	24	7		16		22
	Bivalvia		2		1	25	2	6	15	14	5		1		22
	Veneroida		2		1	25	2	6	15	14	5		1		22
	Corbiculidae		2		1	25	2	6	15	14	5		1		22
		Corbicula	2		1	25	2	6	15	14	5		1		22
	Gastropoda		70	26	13	5	4	86		10	2		15		
	Amnicolidae									10			14		
	Ancylidae		70	17	11	4	4	36			2		1		
	Lymnaeidae			3		1		7							
	Planorbidae			6	2			43							
Platyelminthes	**Tricladida**												4		
	Planariidae												4		
		Planaria											4		

Sampling Date 3		Intermittent-Frequent	Intermittent -Dry			Intermittent-Wet			Perennial			
		1	1	2	3	1	2	3	1	2	3	4
	Habitats Sampled:	R	W	W	R,W	R,W	R,W	R,W	R	R,W	W	W
Annelida Clitellata	**Hirudinea**	1										
	Oligochaeta	6	4		14		12			5		
Arthropoda Arachnida	**Tombidiformes**	2				2	8	5	12	28	1	9
Arthropoda Insecta		24	241	164	1015	1999	1890	475	574	1128	102	292
	Coleoptera		25		4	5	40	16	7	26		6
	Curculionidae							1				
	Tyloderma (Adult)							1				
	Dryopidae		2									
	Pelonomus (larval)		2									
	Dytiscidae				1			6				
	Acilius (Adult)				1							
	Neoporus (Adult)							6				
	Elmidae					5	34		7	26		6
	Ancyronyx (larval)									1		4
	Dubiraphia (larval)						7					
	Macronychus (larval)									4		2
	Microcylloepus (larval)					1	3		4	6		
	Stenelmis					4	24		3	15		
	Adult						8			4		
	larval					4	16		3	11		
	Hydrophilidae				1							
	Berosus (Adult)				1							
	Psephenidae						4					
	Ectopria (larval)						4					
	Scirtidae		23		2		2	9				
	Cyphon (larval)		16		2		2	7				
	Sacodes		7									
	Scirtes (larval)							2				
	Collembola	8			4	14	2	4	2	1		
	Entomobryidae	7			2	14	2	4		1		
	Cyphoderus	7			2	14	2	4		1		
	Sminthuridae	1			2				2			
	Diptera	5	212	153	946	1830	1612	328	280	634	57	188
	Ceratopogonidae			1								3
	Atrichopogon			1								
	Bezzia											3
	Chironomidae	5	208	152	932	1819	1600	317	106	608	53	154
	Non-tanypodinae	4	203	148	820	1702	1550	236	92	555	52	139
	Tanypodinae	1	4	2	92	36	6	71	8	6	1	3
	pupa		1	2	20	81	44	10	6	47		12
	Culicidae				8							
	Anopholes				8							
	Empididae				2	8	12	5		2		3
	Hemerodromia				2	8	12	5		2		3
	Psychodidae				2							
						3		6	174	24	4	28
	larval					3		6	166	20	4	28

pupa								8	4		
Tabanidae		2									
Tipulidae		2									
Ephemeroptera	2		7	24	43	71	108	26	33	8	19
Baetidae					5	2	25	12	6	7	2
Baetis					2	2	25	6		7	2
Plauditus					3			6	6		
Caenidae						4					1
Caenis						4					1
Ephemerellidae						14		10	2		7
Dannella						8		10			
Eurylophella											7
Seratella						6			2		
Heptageniidae	2		7	24	33	42	83	4	10	1	7
Maccaffertium			1	2	29	31	46	4	10		7
Stenacron	2		6	22	4	11	37				
Unknown										1	
Isonychiidae					1	1			4		2
Isonychia					1	1			4		2
Leptohyphidae					4	8			11		
Asioplax									1		
Tricorythodes					4	8			10		
Hemiptera	1			1		1	4				
Notonectidae				1							
Notonecta				1							
Pleidae						1					
Neoplea						1					
Veliidae	1						2				
Rhagovelia	1						2				
Unknown							2				
Lepidoptera								8	1		
Crambidae								4	1		
Petrophila									1		
Unknown								4			
Megaloptera	1	2						1			
Corydalidae	1	2						1			
Corydalus	1	2						1			
Odonata			4	6		4			4		
Calopterygidae				2							
Hetaerina				2							
Coenagrionidae			4	4		4			4		
Chromagrion				4		4					
Unknown			4						4		
Plecoptera							1	2	6	1	12
Perlidae									2	1	4
Neoperla											2
Unknown									2	1	2
Perlodidae							1				2
Clioperla							1				1
Isoperla											1

	Taeniopterygidae								2	4		6
	Taeniopteryx								2	4		6
	Trichoptera	7	2		30	107	160	14	248	423	36	67
	Hydropsychidae	5	2		8	71	59	10	134	179	5	12
	Cheumatopsyche	5	2		8	55	58	10		123	3	11
	Hydropsyche					16			134	56	2	1
	Unknown						1					
	Hydroptilidae				2	21	70		88	188	1	
	Hydroptila				2	20	54		84	163	1	
	Oxyethira					1	8					
	Pupa						8		4	25		
	Leptoceridae	2			18	5	24	4		14		
	Ceraclea									6		
	Nectopsyche					2						
	Oecetis	2			18	3	24	4		8		
	Philopotamidae				2	10	2		26	42	30	55
	Chimarra				2	10	2		26	42	30	55
	Polycentropidae						5					
	Cyrnellus						5					
Malacostraca	**Amphipoda**		92	95	24		2	5				
	Gammaridae		92	95	24		2	5				
	Gammarus		92	95	24		2	5				
	Decapoda		2	1								
	Cambaridae		2	1								
	Procambarus		2	1								
	Isopoda	8	179	128	216		6	24				3
Maxillopoda	**Copepoda**		42	52	8							1
	Ostracoda		7	236	36							
Mollusca	**Bivalvia**		1		58	22	33			1		5
	Veneroida		1		58	22	33			1		5
	Corbiculidae		1		58	22	33			1		5
	Corbicula		1		58	22	33			1		5
	Gastropoda	2	4	24	314	2	5	3	6	5		
	Amnicolidae					2	5		6			
	Ancylidae	2	2	24	122			1		1		
	Lymnaeidae		2		44			2				
	Planorbidae				148					3		
	Pleuroceridae									1		

Sampled Date 4		Intermittent-Dry			Intermittent-Wet			Perennial			
		1	2	3	1	3	4	1	2	3	4
	Habitats Sampled:	W	W	R,W	R,W	R,W	R,W	R	R	W	W
Annelida Clitellata	**Oligochaeta**	1		14	2			4			2
Arthropoda		241	99	756	1278	854	389	2673	222	77	100
Arachnida	**Tombidiformes**	1		16	18	3	3	8			9
Insecta		153	54	675	1248	851	383	2657	220	77	89
	Coleoptera	30		2	2	6	3	7	1		2
	Elmidae			2				7	1		2
	Dubiraphia (larval)			1					1		
	Microcylloepus (larval)							7			
	Stenelmis (larval)			1							2
	Psephenidae					6					
	Ectopria (larval)					6					
	Scirtidae	30					3				
	Cyphon (larval)	30					3				
	Gyrinidae				2						
	Gyrinus (Adult)				2						
	Collembola	14		3	20	6	1			2	
	Entomobryidae	14		3	20	6					
	Cyphoderus	14		3	20	6					
	Sminthuridae						1			2	
	Diptera	107	51	636	1122	490	311	1571	167	68	63
	Ceratopogonidae					2	1	18			
	Atrichopogon					2	1	18			
	Chironomidae	106	50	628	1106	347	239	992	159	67	44
	Non-tanypodinae	103	48	564	1046	332	213	890	148	64	37
	Tanypodinae	1		37	16	5	19	10	5		1
	pupa	2		27	44	10	7	92	6	3	6
	Empididae			6	14	1	2			1	1
	Hemerodromia			6	14	1	2			1	1
		1	1	2		140	68	558	4		17
	larval	1	1	2		140	67	526	4		17
	pupa						1	32			
	Tabanidae						1		4		
	Tipulidae							3			
	Unknown				2						1
	Ephemeroptera		1	22	29	46	52	34	6	3	8
	Baetidae			11	2	7	41	8	1	2	1
	Acerpenna			5			1				
	Baetis			6	2	7	40	8		2	1
	Plauditus								1		
	Baetiscidae										1
	Baetisca										1
	Ephemerellidae					4		4	2		2
	Dannella										2
	Eurylophella							4			
	Seratella					4			2		
	Heptageniidae		1	11	27	35	11	18			4
	Maccaffertium			4		35	5	18			4

	Stenacron		1	7	27		6				
	Isonychiidae							4	3		
	Isonychia							4	3		
	Leptophlebidae									1	
	Halorophlebia									1	
	Lepidoptera						1				
	Crambidae						1				
	Megaloptera	2									
	Corydalidae	2									
	Corydalus	2									
	Odonata		1			1					
	Coenagrionidae		1								
	Argia		1								
	Gomphidae					1					
	Dromogomphus					1					
	Plecoptera				4		1	16		4	10
	Perlidae				2		1	8		4	2
	Neoperla				2		1			3	2
	Perlesta							8			
	Unknown									1	
	Taeniopterygidae				2			8			8
	Taeniopteryx				2			8			8
	Trichoptera		1	12	71	302	14	1029	46		6
	Hydropsychidae			8	25	41	7	81	4		
	Cheumatopsyche			8	25	41	2	76	4		
	Hydropsyche						5	5			
	Hydroptilidae			3	40	250	5	930	40		
	Hydroptila			2	40	248	5	904	40		
	Oxyethira			1				26			
	pupa					2					
	Leptoceridae				6				1		
	Oecetis				6				1		
	Limnephilidae			1			2				
	Ironoquia			1			2				
	Philopotamidae		1			6		18	1		5
	Chimarra		1			6		18	1		5
	Psychomyiidae					5					1
	Lype					5					1
Malacostraca		75	13	65	6		1	8	2		
	Amphipoda	13	3	1	4						
	Gammaridae	13	3	1	4						
	Gammarus	13	3	1	4						
	Decapoda			3	2						
	Cambaridae			3	2						
	Procambarus			3	2						
	Isopoda	62	10	61			1	8	2		
Maxillopoda		11	4		6		2				1
	Copepoda	11	4		6		2				1
	Ostracoda	1	28								1
Mollusca		5	18	89	10	7	1				

Bivalvia	2	1	5	8	2	
Veneroida	2	1	5	8	2	
Corbiculidae	2	1	5	8	2	
Corbicula	2	1	5	8	2	
Gastropoda	3	17	84	2	5	1
Amnicolidae					2	1
Ancylidae	2	17	51	2	1	
Physidae	1		1			
Planorbidae			32			
Pleuroceridae					2	

APPENDIX B: Abundances found by reach in Chapter 3: DR= Dried reaches, RW= Remained wet reaches. OM=organic matter, R=rock, S=sand, W=wood

		Sampling Date 1:						**Sampling Date 2**					
		DR			RW			DR			RW		
		1	2	3	1	2	3	1	2	3	1	2	3
	Habitats Sampled:	OM,R,S,W	OM,R,S,W	OM,R,S,W	OM,S,W	OM,S,W	OM,R,S,W	OM,R,S,W	OM,R,S,W	OM,R,S,W	OM,S,W	OM,S,W	OM,R,S,W
Annelida													
Clitellata		10	76	112	119	303	77	132	9	10	135	122	86
	Hirudinea	9	14	0	0	13	0	9	7	8	4	0	0
	Oligochaeta	1	62	112	119	290	77	123	2	2	131	122	86
Arthropoda		3202	3893	3183	5478	3877	4493	1668	2313	442	2359	2491	1900
Arachnida		43	14	14	26	4	73	25	3	1	1	0	25
	Tombidiformes	43	14	14	26	4	73	25	3	1	1	0	25
Insecta		3158	3876	3098	5121	3207	4198	1391	1290	331	1373	1592	1665
	Coleoptera	0	8	12	4	4	20	4	109	33	10	3	5
	Curculionidae	0	2	0	0	0	0	0	0	0	0	0	0
	Tyloderma (Adulta)	0	2	0	0	0	0	0	0	0	0	0	0
	Dryopidae	0	0	0	2	0	0	0	0	0	0	0	0
	Pelonomus (larval)	0	0	0	2	0	0	0	0	0	0	0	0
	Dytiscidae	0	0	0	0	0	0	2	8	2	0	0	2
	Neoporus	0	0	0	0	0	0	2	8	2	0	0	2
	Adult	0	0	0	0	0	0	2	8	2	0	0	0
	larval	0	0	0	0	0	0	0	0	0	0	0	2
	Elmidae	0	2	0	0	0	19	0	0	0	10	1	3
	Dubiraphia	0	2	0	0	0	0	0	0	0	10	0	0
	Adult	0	2	0	0	0	0	0	0	0	0	0	0
	larval	0	0	0	0	0	0	0	0	0	10	0	0
	Microcylloepus (larval)	0	0	0	0	0	0	0	0	0	0	1	1
	Stenelmis (larval)	0	0	0	0	0	19	0	0	0	0	0	2
	Gyrinidae	0	2	4	2	4	1	0	0	5	0	0	0
	Dineutus	0	2	4	2	4	1	0	0	5	0	0	0
	Adult	0	0	0	0	0	0	0	0	5	0	0	0
	larval	0	2	4	2	4	1	0	0	0	0	0	0
	Hydrophilidae	0	0	8	0	0	0	0	0	0	0	0	0
	Berosus (larval)	0	0	8	0	0	0	0	0	0	0	0	0
	Scirtidae	0	2	0	0	0	0	2	101	26	0	2	0
	Cyphon (larval)	0	2	0	0	0	0	2	100	26	0	2	0
	Scirtes (Adult)	0	0	0	0	0	0	0	1	0	0	0	0
	Collembola	0	3	0	3	0	0	7	4	9	0	0	1
	Entomobryiidae	0	1	0	2	0	0	7	4	8	0	0	1
	Cyphoderus	0	1	0	2	0	0	7	4	8	0	0	1
	Sminthuridae	0	2	0	0	0	0	0	0	1	0	0	0
	Diptera	1971	3094	2326	4868	3129	3913	674	884	220	1327	1569	1540
	Ceratopogonidae	0	17	0	0	4	0	2	16	0	0	13	2
	Atrichopogon	0	16	0	0	0	0	0	0	0	0	6	0
	Bezzia	0	1	0	0	4	0	2	16	0	0	7	2
	Chironomidae	1944	3075	2307	4867	3121	3912	668	836	197	1323	1556	1538

Non-tanypodinae	1496	2218	1684	4561	2923	3322	430	611	89	1255	1439	1265
Tanypodinae	388	588	515	196	126	473	160	178	87	61	71	190
pupa	60	269	108	110	72	117	78	47	21	7	46	83
Culicidae	0	0	0	1	0	0	0	26	23	4	0	0
Aedes	0	0	0	0	0	0	0	9	0	0	0	0
Anopholes	0	0	0	1	0	0	0	9	13	4	0	0
Culex	0	0	0	0	0	0	0	4	10	0	0	0
pupa	0	0	0	0	0	0	0	4	0	0	0	0
Empididae	1	0	0	0	0	0	0	1	0	0	0	0
Hemerodromia	1	0	0	0	0	0	0	1	0	0	0	0
larval	1	0	0	0	0	0	0	0	0	0	0	0
pupa	0	0	0	0	0	0	0	1	0	0	0	0
	26	2	19	0	0	1	4	4	0	0	0	0
larval	22	2	18	0	0	1	4	4	0	0	0	0
pupa	4	0	1	0	0	0	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	0	0	1	0	0	0	0
Tipulidae	0	0	0	0	4	0	0	0	0	0	0	0
Ephemeroptera	12	29	63	72	8	69	329	25	9	0	0	38
Baetidae	12	29	62	72	0	69	319	21	9	0	0	18
Acentrella	0	2	0	0	0	0	0	0	0	0	0	0
Acerpenna	4	21	0	56	0	21	24	0	0	0	0	17
Baetis	8	2	54	0	0	32	293	21	9	0	0	0
Plauditus	0	0	0	0	0	0	2	0	0	0	0	0
Procleon	0	4	0	0	0	16	0	0	0	0	0	0
Pseudocentroptiloides	0	0	0	0	0	0	0	0	0	0	0	1
Pseudocleon	0	0	8	16	0	0	0	0	0	0	0	0
Caenidae	0	0	1	0	0	0	6	4	0	0	0	0
Caenis	0	0	1	0	0	0	6	4	0	0	0	0
Heptageniidae	0	0	0	0	8	0	4	0	0	0	0	20
Stenacron	0	0	0	0	8	0	0	0	0	0	0	20
Unknown	0	0	0	0	0	0	4	0	0	0	0	0
Hemiptera	2	2	0	0	3	0	0	4	7	0	0	4
Corixidae	0	0	0	0	0	0	0	3	0	0	0	2
Tricocorixia	0	0	0	0	0	0	0	1	0	0	0	0
Unknown	0	0	0	0	0	0	0	2	0	0	0	2
Gerridae	2	2	0	0	2	0	0	0	0	0	0	0
Limnoporus	0	2	0	0	1	0	0	0	0	0	0	0
Rheumatobates	0	0	0	0	1	0	0	0	0	0	0	0
Trepobates	2	0	0	0	0	0	0	0	0	0	0	0
Nepidae	0	0	0	0	0	0	0	0	1	0	0	0
Ranatra	0	0	0	0	0	0	0	0	1	0	0	0
Notonectidae	0	0	0	0	0	0	0	0	2	0	0	0
Notonecta	0	0	0	0	0	0	0	0	2	0	0	0
Velidae	0	0	0	0	1	0	0	1	4	0	0	0
Microveilia	0	0	0	0	1	0	0	0	2	0	0	0
Rhagovelia	0	0	0	0	0	0	0	0	2	0	0	0
Unknown	0	0	0	0	0	0	0	1	0	0	0	0
Unknown	0	0	0	0	0	0	0	0	0	0	0	2
Lepidoptera	2	0	0	0	0	0	0	0	0	0	4	0

	Crambidae	2	0	0	0	0	0	0	0	0	0	0	0
	Geometridae	0	0	0	0	0	0	0	0	0	0	4	0
	Odonata	15	8	7	1	11	1	6	144	12	0	4	3
	Aeshnidae	0	0	0	1	1	0	0	0	0	0	0	0
	Nasiaschna	0	0	0	1	1	0	0	0	0	0	0	0
	Calopterygidae	0	0	0	0	0	0	0	0	0	0	0	2
	Hetaerina	0	0	0	0	0	0	0	0	0	0	0	2
	Coenagrionidae	10	0	0	0	0	0	4	0	6	0	0	0
	Amphiagrion	8	0	0	0	0	0	0	0	0	0	0	0
	Chromagrion	0	0	0	0	0	0	4	0	6	0	0	0
	Unknown	2	0	0	0	0	0	0	0	0	0	0	0
	Cordulidae	0	0	0	0	0	0	0	1	1	0	0	0
	Neurocordulia	0	0	0	0	0	0	0	1	1	0	0	0
	Gomphidae	0	0	4	0	0	0	0	23	0	0	0	0
	Dromogomphis	0	0	4	0	0	0	0	1	0	0	0	0
	Hagenius	0	0	0	0	0	0	0	6	0	0	0	0
	Stylurus	0	0	0	0	0	0	0	16	0	0	0	0
	Libellulidae	0	0	2	0	10	0	0	0	0	0	0	0
	Libellula	0	0	2	0	10	0	0	0	0	0	0	0
	Macromiidae	5	8	1	0	0	1	2	120	5	0	4	1
	Macromia	5	8	1	0	0	1	2	120	5	0	4	1
	Trichoptera	1156	732	690	173	52	195	371	120	41	36	12	74
	Hydropsychidae	1043	674	660	173	52	189	318	14	20	20	11	14
	Cheumatopsyche	776	560	486	133	52	133	318	13	20	20	11	14
	Hydropsyche	0	0	4	0	0	0	0	1	0	0	0	0
	Unknown	267	114	170	40	0	56	0	0	0	0	0	0
	Hydroptilidae	0	3	1	0	0	0	2	0	0	0	1	0
	Hydroptila	0	0	0	0	0	0	0	0	0	0	1	0
	Oxyethira	0	3	1	0	0	0	2	0	0	0	0	0
	Leptoceridae	0	37	13	0	0	4	43	106	20	16	0	60
	Nectopsyche	0	12	0	0	0	0	0	0	0	0	0	0
	Oecetis	0	25	13	0	0	4	39	33	10	16	0	60
	Trianodes	0	0	0	0	0	0	4	73	10	0	0	0
	Philopotamidae	103	12	12	0	0	2	8	0	1	0	0	0
	Chimarra	103	12	12	0	0	2	8	0	1	0	0	0
	larval	103	12	8	0	0	2	8	0	1	0	0	0
	pupa	0	0	4	0	0	0	0	0	0	0	0	0
	pupa	10	6	4	0	0	0	0	0	0	0	0	0
Malacostraca		1	1	70	300	640	220	225	890	51	825	850	197
	Amphipoda	1	0	0	156	290	7	0	0	0	270	223	13
	Gammaridae	1	0	0	156	290	7	0	0	0	270	223	13
	Gammarus	1	0	0	156	290	7	0	0	0	270	223	13
	Decapoda	0	0	0	2	4	1	5	0	8	4	2	0
	Cambaridae	0	0	0	2	4	1	5	0	8	4	2	0
	Procambarus	0	0	0	2	1	1	5	0	8	4	2	0
	Unknown	0	0	0	0	3	0	0	0	0	0	0	0
	Isopoda	0	1	70	142	346	212	220	890	43	551	625	184
Maxillopoda		0	0	1	27	20	2	2	35	54	58	1	0
	Copepoda	0	0	1	27	20	2	2	35	54	58	1	0
	Ostracoda	0	2	0	4	6	0	25	95	5	102	48	13

Mollusca		17	172	49	254	87	550	115	50	29	203	361	508
	Bivalvia	0	0	2	50	54	56	18	0	1	190	190	44
	Veneroida	0	0	2	50	54	56	15	0	1	64	78	16
	Cobiculidae	0	0	2	50	54	56	15	0	1	64	78	16
	Corbicula	0	0	2	50	54	56	15	0	1	64	78	16
	Gastropoda	17	172	47	204	33	494	97	50	28	13	171	464
	Ancylidae	2	16	45	180	30	234	79	29	19	10	72	232
	Hydrobiidae	0	0	0	0	0	8	0	0	0	0	0	0
	Lymnaeidae	9	12	0	0	0	12	0	3	0	1	0	7
	Physidae	4	123	1	0	3	21	11	12	5	0	6	25
	Planorbidae	2	21	1	24	0	219	7	6	4	2	92	200
	Viviparidae	0	0	0	0	0	0	0	0	0	0	1	0
Nematoda		0	0	0	0	0	0	0	0	1	4	0	4

		Sampling Date 3:				Sampling Date 4				
		DR	RW			DR		RW		
		3	1	2	3	1	3	1	2	3
	Habitats Sampled:	OM,R	OM,S,W	OM,S,W	OM,R,S,W	OM	OM	OM,S,W	OM,S,W	OM,R,S,W
Annelida Clitellata		19	22	122	27	0	6	37	70	48
	Hirudinea	3	0	0	0	0	0	0	0	0
	Oligochaeta	16	22	122	27	0	6	37	70	48
Arthropoda		357	1602	1815	2570	42	200	579	653	1174
Arachnida		2	4	4	12	0	1	3	0	22
	Tombidiformes	2	4	4	12	0	1	3	0	22
Insecta		189	776	667	2100	27	112	309	296	1037
	Coleoptera	6	35	1	26	3	1	33	1	5
	Dryopidae	0	2	0	0	0	0	0	1	0
	Pelonomus (larval)	0	2	0	0	0	0	0	1	0
	Dytiscidae	2	4	0	1	1	1	1	0	0
	Acilius (Adult)	0	0	0	1	0	0	0	0	0
	Coptotomus (Adult)	0	1	0	0	0	0	0	0	0
	Neoporus	2	3	0	0	1	1	1	0	0
	Adult	0	3	0	0	1	0	0	0	0
	larval	2	0	0	0	0	1	1	0	0
	Elmidae	0	0	0	8	0	0	1	0	3
	Dubiraphia (larval)	0	0	0	8	0	0	1	0	1
	Stenelmis (larval)	0	0	0	0	0	0	0	0	2
	Gyrinidae	3	6	0	0	0	0	1	0	0
	Dineutus	3	5	0	0	0	0	1	0	0
	Adult	0	5	0	0	0	0	0	0	0
	larval	3	0	0	0	0	0	1	0	0
	Gyrinus (Adult)	0	1	0	0	0	0	0	0	0
	Hydrophilidae	0	0	0	1	0	0	0	0	0
	Berosus (Adult)	0	0	0	1	0	0	0	0	0
	Scirtidae	1	23	0	14	2	0	30	0	2
	Cyphon (larval)	1	16	0	14	2	0	30	0	2
	Sacodes (larval)	0	7	0	0	0	0	0	0	0
	Staphylinidae (Adult)	0	0	0	2	0	0	0	0	0
	Collembola	17	0	0	7	17	92	14	1	9
	Entomobryiidae	16	0	0	4	13	91	14	1	8
	Cyphoderus	16	0	0	4	13	91	14	1	8
	Sminthuridae	1	0	0	3	4	1	0	0	1
	Diptera	118	732	655	1977	7	18	258	291	973
	Ceratopogonidae	1	0	11	8	0	1	0	2	10
	Atrichopogon	0	0	1	0	0	0	0	0	0
	Bezzia	1	0	10	8	0	1	0	2	10
	Chironomidae	117	728	644	1951	4	17	256	288	955
	Non-tanypodinae	81	715	619	1644	4	16	250	280	855
	Tanypodinae	30	9	23	257	0	1	3	4	71
	pupa	6	4	2	50	0	0	3	2	29
	Culicidae	0	0	0	8	2	0	1	0	0
	Anopholes	0	0	0	8	2	0	1	0	0
	Empididae	0	0	0	2	0	0	0	0	6
	Hemerodromia	0	0	0	2	0	0	0	0	6

	Psychodidae	0	0	0	2	0	0	0	0	0
		0	0	0	6	0	0	1	1	2
	Tabanidae	0	2	0	0	0	0	0	0	0
	Tipulidae	0	2	0	0	0	0	0	0	0
	Ephemeroptera	3	0	7	39	0	0	0	1	32
	Baetidae	0	0	0	3	0	0	0	0	19
	Acerpenna	0	0	0	3	0	0	0	0	12
	Baetis	0	0	0	0	0	0	0	0	7
	Heptageniidae	3	0	7	36	0	0	0	1	13
	Maccaffertium	0	0	1	2	0	0	0	0	6
	Stenacron	3	0	6	34	0	0	0	1	7
	Hemiptera	3	0	0	1	0	1	0	0	0
	Notonectidae	0	0	0	1	0	0	0	0	0
	Notonecta	0	0	0	1	0	0	0	0	0
	Velidae	3	0	0	0	0	1	0	0	0
	Microvelia	2	0	0	0	0	0	0	0	0
	Microvellia	0	0	0	0	0	1	0	0	0
	Rhagoveilla	1	0	0	0	0	0	0	0	0
	Megaloptera	1	2	0	0	0	0	2	0	0
	Corydalidae	1	2	0	0	0	0	2	0	0
	Corydalus	1	2	0	0	0	0	2	0	0
	Odonata	1	0	4	6	0	0	1	1	0
	Calopterygidae	0	0	0	2	0	0	0	0	0
	Hetaerina	0	0	0	2	0	0	0	0	0
	Coenagrionidae	0	0	4	4	0	0	0	1	0
	Argia	0	0	0	0	0	0	0	1	0
	Chromagrion	0	0	0	4	0	0	0	0	0
	Unknown	0	0	4	0	0	0	0	0	0
	Cordulidae	1	0	0	0	0	0	0	0	0
	Neurocordulia	1	0	0	0	0	0	0	0	0
	Macromiidae	0	0	0	0	0	0	1	0	0
	Macromia	0	0	0	0	0	0	1	0	0
	Trichoptera	40	7	0	44	0	0	1	1	18
	Hydropsychidae	5	6	0	8	0	0	0	0	8
	Cheumatopsyche	5	6	0	8	0	0	0	0	8
	Hydroptilidae	0	0	0	2	0	0	0	0	3
	Hydroptila	0	0	0	2	0	0	0	0	2
	Oxyethira	0	0	0	0	0	0	0	0	1
	Leptoceridae	35	1	0	32	0	0	1	0	5
	Oecetis	35	1	0	32	0	0	1	0	5
	Limnephilidae	0	0	0	0	0	0	0	0	2
	Ironoquia	0	0	0	0	0	0	0	0	2
	Philopotamidae	0	0	0	2	0	0	0	1	0
	Chimarra	0	0	0	2	0	0	0	1	0
Malacostraca		144	592	501	364	1	52	223	162	95
	Amphipoda	2	158	170	36	0	0	56	37	2
	Gammaridae	2	158	170	36	0	0	56	37	2
	Gammarus	2	158	170	36	0	0	56	37	2
	Decapoda	0	5	1	0	1	2	2	2	5
	Cambaridae	0	5	1	0	1	2	2	2	5

		Procambarus	0	5	1	0	1	2	2	2	5
	Isopoda		142	429	330	328	0	50	165	123	88
Maxillopoda			8	161	145	8	14	33	20	16	0
	Copepoda		8	161	145	8	14	33	20	16	0
	Ostracoda		14	69	498	86	0	2	24	179	20
Mollusca			108	46	220	1088	1	9	38	112	141
	Bivalvia		3	29	161	84	0	5	28	68	28
	Veneroida		0	1	0	58	0	0	2	1	5
	Cobiculidae		0	1	0	58	0	0	2	1	5
		Corbicula	0	1	0	58	0	0	2	1	5
		Unknown	3	28	161	26	0	5	26	67	23
	Gastropoda		105	17	59	1004	1	4	10	44	113
	Ancylidae		70	11	40	424	1	2	2	27	63
	Lymnaeidae		0	2	0	44	0	0	0	0	0
	Physidae		1	0	1	25	0	1	2	0	1
	Planorbidae		34	4	17	511	0	1	6	16	49
	Viviparidae		0	0	1	0	0	0	0	1	0
Nematoda			0	4	1	1	0	0	0	1	2

		Sampling Date 5						Sampling Date 6					
		DR			RW			DR			RW		
		1	2	3	1	2	3	1	2	3	1	2	3
	Habitats Sampled:	OM,R,S, W	OM,R,S, W	OM,R,S, W	OM,S, W	OM,S, W	OM,R,S, W	OM,R,S, W	OM,R,S, W	OM,R,S, W	OM,S, W	OM,S, W	OM,R,S, W
Annelida													
Clitellata		5	58	130	12	39	57	7	73	70	29	40	62
	Hirudinea	0	0	6	0	2	0	0	5	2	0	0	4
	Oligochaeta	5	58	124	12	37	57	7	68	68	29	40	58
Arthropoda		118	133	393	480	855	1607	1020	1848	5192	1071	1115	1814
Arachnida		1	15	3	0	0	23	5	5	2	0	0	39
	Tombidiformes	1	15	3	0	0	23	5	5	2	0	0	39
Insecta		110	110	261	186	187	1238	828	1785	4940	515	370	1075
	Coleoptera	0	6	5	1	4	8	9	1	4	1	0	35
	Dryopidae	0	0	0	0	2	0	0	1	0	0	0	0
	Pelonomus (larval)	0	0	0	0	2	0	0	1	0	0	0	0
	Dytiscidae	0	0	1	0	2	0	7	0	4	0	0	2
	Laccophilus (Adult)	0	0	0	0	2	0	0	0	0	0	0	0
	Neoporus (larval)	0	0	1	0	0	0	7	0	4	0	0	2
	Elmidae	0	0	1	0	0	8	0	0	0	0	0	33
	Stenelmis (larval)	0	0	1	0	0	8	0	0	0	0	0	33
	Gyrinidae	0	2	1	0	0	0	1	0	0	1	0	0
	Dineutus	0	0	1	0	0	0	1	0	0	1	0	0
	Adult	0	0	1	0	0	0	0	0	0	1	0	0
	larval	0	0	0	0	0	0	1	0	0	0	0	0
	Gyrinus (larval)	0	2	0	0	0	0	0	0	0	0	0	0
	Helophoridae	0	2	0	0	0	0	0	0	0	0	0	0
	Helophorus (larval)	0	2	0	0	0	0	0	0	0	0	0	0
	Scirtidae	0	2	2	1	0	0	0	0	0	0	0	0
	Cyphon	0	2	2	1	0	0	0	0	0	0	0	0
	Adult	0	0	1	0	0	0	0	0	0	0	0	0
	larval	0	2	1	1	0	0	0	0	0	0	0	0
	Staphylinidae (Adult)	0	0	0	0	0	0	1	0	0	0	0	0
	Collembola	3	61	50	2	2	13	3	9	35	0	0	1
	Entomobryiidae	3	56	48	1	0	13	3	9	35	0	0	0
	Cyphoderus	3	56	48	1	0	13	3	9	35	0	0	0
	Sminthuridae	0	5	2	1	2	0	0	0	0	0	0	1
	Diptera	100	41	198	179	172	920	815	1769	4868	495	369	891
	Ceratopogonidae	3	0	23	0	2	3	3	1	9	1	20	2
	Atrichopogon	0	0	10	0	0	0	3	1	0	1	17	0
	Bezzia	1	0	13	0	2	3	0	0	9	0	3	2
	pupa	2	0	0	0	0	0	0	0	0	0	0	0
	Chironomidae	83	36	168	157	159	865	809	1767	1638	453	289	817
	Non-tanypodinae	78	30	168	125	138	773	436	1682	1440	378	255	735
	Tanypodinae	3	5	0	21	15	68	322	15	82	29	24	46
	pupa	2	1	0	11	6	24	51	70	116	46	10	36
	Culicidae	0	0	0	0	1	1	0	0	0	0	0	0
	Anopholes	0	0	0	0	1	0	0	0	0	0	0	0
	Unknown	0	0	0	0	0	1	0	0	0	0	0	0

Empididae	0	0	0	0	0	11	0	0	0	0	4	4
Hemerodromia	0	0	0	0	0	11	0	0	0	0	4	4
Psychodidae	1	0	0	0	0	0	0	0	0	0	0	0
	0	0	4	20	10	40	2	1	3218	41	56	61
larval	0	0	4	20	10	40	2	1	3154	40	52	61
pupa	0	0	0	0	0	0	0	0	64	1	4	0
Stratiomyiidae	0	0	0	2	0	0	0	0	0	0	0	0
Tabanidae	1	0	1	0	0	0	0	0	1	0	0	3
Thaumaelidae	0	0	0	0	0	0	0	0	0	0	0	4
Tipulidae	11	1	1	0	0	0	1	0	2	0	0	0
Ephemeroptera	1	0	0	1	5	79	0	0	0	14	0	53
Baetidae	0	0	0	1	2	62	0	0	0	14	0	46
Acerpenna	0	0	0	0	2	24	0	0	0	14	0	24
Baetis	0	0	0	0	0	38	0	0	0	0	0	22
Pseudocleon	0	0	0	1	0	0	0	0	0	0	0	0
Heptageniidae	0	0	0	0	3	17	0	0	0	0	0	3
Maccaffertium	0	0	0	0	0	17	0	0	0	0	0	1
Stenacron	0	0	0	0	3	0	0	0	0	0	0	2
Leptophlebidae	0	0	0	0	0	0	0	0	0	0	0	4
Paraleptophlebia	0	0	0	0	0	0	0	0	0	0	0	2
Unknown	0	0	0	0	0	0	0	0	0	0	0	2
Metrotopodidae	1	0	0	0	0	0	0	0	0	0	0	0
Siphloplectin	1	0	0	0	0	0	0	0	0	0	0	0
Hemiptera	0	0	1	2	0	0	1	0	0	0	1	0
Notonectidae	0	0	1	0	0	0	0	0	0	0	1	0
Notonecta	0	0	1	0	0	0	0	0	0	0	1	0
Velidae	0	0	0	2	0	0	1	0	0	0	0	0
Microveilia	0	0	0	0	0	0	1	0	0	0	0	0
Microvelia	0	0	0	1	0	0	0	0	0	0	0	0
Rhagoveillia	0	0	0	1	0	0	0	0	0	0	0	0
Lepidoptera	1	0	1	0	0	0	0	1	16	0	0	0
Crambidae	1	0	1	0	0	0	0	1	16	0	0	0
Odonata	0	0	1	0	2	0	0	0	0	0	0	0
Libellulidae	0	0	0	0	2	0	0	0	0	0	0	0
Libellula	0	0	0	0	2	0	0	0	0	0	0	0
Macromiidae	0	0	1	0	0	0	0	0	0	0	0	0
Macromia	0	0	1	0	0	0	0	0	0	0	0	0
Plecoptera	0	0	0	0	0	2	0	0	0	0	0	3
Perlidae	0	0	0	0	0	2	0	0	0	0	0	3
Neoperla	0	0	0	0	0	2	0	0	0	0	0	3
Trichoptera	5	2	5	1	2	216	0	5	17	5	0	92
Hydropsychidae	0	0	2	0	0	202	0	0	16	1	0	78
Cheumatopsyche	0	0	2	0	0	202	0	0	16	1	0	78
Hydroptilidae	5	0	0	0	0	0	0	0	0	0	0	0
Hydroptila	5	0	0	0	0	0	0	0	0	0	0	0
Leptoceridae	0	2	3	0	0	6	0	5	1	0	0	3
Oecetis	0	1	3	0	0	6	0	1	1	0	0	3
Trianodes	0	1	0	0	0	0	0	4	0	0	0	0
Limnephilidae	0	0	0	1	0	0	0	0	0	4	0	0
Ironoquia	0	0	0	1	0	0	0	0	0	4	0	0

	Molannidae	0	0	0	0	0	1	0	0	0	0	0	0
	Molanna	0	0	0	0	0	1	0	0	0	0	0	0
	Philopotamidae	0	0	0	0	0	7	0	0	0	0	0	11
	Chimarra	0	0	0	0	0	7	0	0	0	0	0	11
	Phryganaeidae	0	0	0	0	2	0	0	0	0	0	0	0
	Agrypnia	0	0	0	0	2	0	0	0	0	0	0	0
Malacostraca		4	4	76	283	633	329	9	12	179	546	707	681
	Amphipoda	0	0	0	40	72	2	1	2	8	42	53	39
	Gammaridae	0	0	0	40	72	2	1	2	8	42	53	39
	Gammarus	0	0	0	40	72	2	1	2	8	42	53	39
	Decapoda	0	0	1	1	2	15	1	0	4	0	0	10
	Cambaridae	0	0	1	1	2	15	1	0	4	0	0	10
	Cambarus	0	0	0	0	0	0	0	0	0	0	0	1
	Procambarus	0	0	1	1	2	15	1	0	4	0	0	9
	Isopoda	4	4	75	242	559	312	7	10	167	504	654	632
Maxillopoda		1	3	24	8	12	5	135	43	45	9	14	6
	Copepoda	1	3	24	8	12	5	135	43	45	9	14	6
	Ostracoda	2	1	29	3	23	12	43	3	26	1	24	13
Mollusca		3	14	27	44	85	202	3	24	64	47	74	201
	Bivalvia	0	0	9	23	52	21	0	0	22	30	28	26
	Veneroida	0	0	0	1	6	0	0	0	0	0	0	0
	Cobiculidae	0	0	0	1	6	0	0	0	0	0	0	0
	Corbicula	0	0	0	1	6	0	0	0	0	0	0	0
	Gastropoda	3	14	18	21	33	181	3	24	42	17	46	175
	Ancylidae	0	1	7	2	19	155	2	0	10	8	28	133
	Physidae	3	2	5	3	0	4	0	6	7	0	1	7
	Planorbidae	0	11	6	8	13	22	1	18	25	9	17	35
	Valvatidae	0	0	0	8	0	0	0	0	0	0	0	0
	Viviparidae	0	0	0	0	1	0	0	0	0	0	0	0
Nematoda		1	0	1	0	0	1	0	2	2	1	0	0

	Sampling Date 7:						Sampling Date 8:				
	DR			RW			DR		RW		
	1	2	3	1	2	3	2	3	1	2	3
Habitats Sampled:	OM,R,S, W	OM,R,S, W	OM,R,S, W	OM,S, W	OM,S, W	OM,R,S, W	OM,R,S, W	OM,R,S, W	OM,S, W	OM,S, W	OM,R,S, W
Annelida											
Clitellata	5	65	104	51	31	32	45	89	43	17	43
Hirudinea	0	8	0	0	0	4	10	0	1	0	0
Oligochaeta	5	57	104	51	31	28	35	89	42	17	43
Arthropoda	388	1720	2518	828	1865	2573	1936	1060	3307	2449	2490
Arachnida	1	5	3	1	8	24	1	3	0	4	33
Tombidiformes	1	5	3	1	8	24	1	3	0	4	33
Insecta	368	1300	2197	507	375	1523	1491	809	2169	755	1715
Coleoptera	1	20	4	3	0	7	18	4	19	4	4
Curculionidae (Adult)	0	0	0	0	0	0	0	1	0	0	0
Dryopidae	0	0	0	1	0	1	3	0	0	0	0
Pelonomus	0	0	0	1	0	1	3	0	0	0	0
Adult	0	0	0	0	0	0	1	0	0	0	0
larval	0	0	0	1	0	1	2	0	0	0	0
Dytiscidae	0	20	2	0	0	0	12	0	0	0	0
Neoporus	0	20	2	0	0	0	12	0	0	0	0
Adult	0	0	0	0	0	0	2	0	0	0	0
larval	0	20	2	0	0	0	10	0	0	0	0
Elmidae	0	0	0	0	0	6	0	0	0	4	4
Stenelmis (Stenelmis)	0	0	0	0	0	6	0	0	0	4	4
Gyrinidae	0	0	2	0	0	0	0	3	0	0	0
Dineutus	0	0	2	0	0	0	0	1	0	0	0
Adult	0	0	2	0	0	0	0	0	0	0	0
larval	0	0	0	0	0	0	0	1	0	0	0
Gyretes (larval)	0	0	0	0	0	0	0	1	0	0	0
Gyrinus (larval)	0	0	0	0	0	0	0	1	0	0	0
Helophoridae	0	0	0	0	0	0	1	0	0	0	0
Helophorus (larval)	0	0	0	0	0	0	1	0	0	0	0
Hydrophilidae	0	0	0	0	0	0	0	0	1	0	0
Hydrobiomorpha (larval)	0	0	0	0	0	0	0	0	1	0	0
Scirtidae	0	0	0	2	0	0	0	0	18	0	0
Cyphon (larval)	0	0	0	2	0	0	0	0	18	0	0
Collembola	0	0	0	1	1	39	2	0	0	2	27
Entomobryiidae	0	0	0	1	1	39	0	0	0	2	27
Cyphoderus	0	0	0	1	1	39	0	0	0	2	27
Sminthuridae	0	0	0	0	0	0	2	0	0	0	0
Diptera	362	1226	2137	458	355	1151	1279	632	1748	663	1283
Ceratopogonidae	1	6	12	17	5	7	22	7	1	1	0
Atrichopogon	1	1	8	10	5	2	10	6	1	0	0
Bezzia	0	5	4	5	0	5	12	1	0	1	0
pupa	0	0	0	2	0	0	0	0	0	0	0
Chironomidae	95	425	1681	377	278	1077	1186	422	1689	646	1265
Non-tanypodinae	64	303	354	284	208	1055	979	352	1530	548	1082
Tanypodinae	5	37	48	23	43	13	52	25	49	26	53

pupa	26	85	1279	70	27	9	155	45	110	72	130
Empididae	0	0	0	0	0	39	2	11	0	0	0
Hemerodromia	0	0	0	0	0	39	2	11	0	0	0
	257	785	439	61	52	22	61	189	49	9	2
larval	257	785	408	59	40	14	55	173	49	9	1
pupa	0	0	31	2	12	8	6	16	0	0	1
Sisyrphidae	0	0	0	2	20	0	0	0	8	6	0
Sisyrpha	0	0	0	2	20	0	0	0	8	6	0
Stratiomyiidae	0	0	0	0	0	1	0	0	1	0	0
Tabanidae	0	0	0	0	0	0	0	1	0	0	0
Tipulidae	0	4	5	0	0	4	0	0	0	0	0
Ephemeroptera	3	31	43	43	12	75	160	146	164	60	124
Baetidae	3	30	43	41	12	69	158	145	164	60	120
Acerpenna	3	29	43	23	12	60	156	123	155	27	36
Baetis	0	1	0	4	0	9	2	22	9	33	84
Pseudocleon	0	0	0	14	0	0	0	0	0	0	0
Caenidae	0	1	0	0	0	0	2	1	0	0	0
Caenis	0	1	0	0	0	0	2	1	0	0	0
Ephemerellidae	0	0	0	0	0	0	0	0	0	0	2
Seratella	0	0	0	0	0	0	0	0	0	0	2
Heptageniidae	0	0	0	0	0	0	0	0	0	0	2
Maccaffertium	0	0	0	0	0	0	0	0	0	0	2
Leptophlebidae	0	0	0	2	0	6	0	0	0	0	0
Habrophlebia	0	0	0	2	0	0	0	0	0	0	0
Unknown	0	0	0	0	0	6	0	0	0	0	0
Hemiptera	1	1	0	0	4	0	4	0	0	1	1
Corixidae	1	1	0	0	0	0	3	0	0	0	1
Tricocorixia	0	0	0	0	0	0	1	0	0	0	0
Unknown	1	1	0	0	0	0	2	0	0	0	1
Notonectidae	0	0	0	0	4	0	0	0	0	0	0
Notonecta	0	0	0	0	4	0	0	0	0	0	0
Velidae	0	0	0	0	0	0	1	0	0	1	0
Microveilia	0	0	0	0	0	0	0	0	0	1	0
Unknown	0	0	0	0	0	0	1	0	0	0	0
Odonata	0	1	0	1	0	0	0	0	0	0	0
Aeshnidae	0	1	0	0	0	0	0	0	0	0	0
Gynacantha	0	1	0	0	0	0	0	0	0	0	0
Cordulegastridae	0	0	0	1	0	0	0	0	0	0	0
Cordulegaster	0	0	0	1	0	0	0	0	0	0	0
Plecoptera	0	1	1	1	2	78	2	4	3	0	4
Perlidae	0	1	1	1	2	75	2	4	3	0	4
Acroneuria	0	0	0	0	0	8	0	0	0	0	0
Neoperla	0	0	0	1	0	6	0	0	0	0	0
Perlesta	0	0	0	0	2	61	2	3	3	0	4
Unknown	0	1	1	0	0	0	0	1	0	0	0
Perlodidae	0	0	0	0	0	3	0	0	0	0	0
Isoperla	0	0	0	0	0	3	0	0	0	0	0
Thysanoptera	1	0	0	0	0	0	0	0	0	1	0
Trichoptera	0	20	12	0	0	173	26	23	235	24	272
Hydropsychidae	0	0	0	0	0	132	0	19	225	24	207

	Cheumatopsyche	0	0	0	0	0	132	0	19	225	24	207
	Hydroptilidae	0	0	0	0	0	0	12	1	1	0	48
	Hydroptila	0	0	0	0	0	0	12	1	1	0	48
	Leptoceridae	0	11	10	0	0	15	14	3	8	0	17
	Oecetis	0	3	8	0	0	15	0	2	0	0	16
	Trianodes	0	8	2	0	0	0	14	1	0	0	1
	Unknown	0	0	0	0	0	0	0	0	8	0	0
	Limnephilidae	0	1	0	0	0	0	0	0	1	0	0
	Ironoquia	0	1	0	0	0	0	0	0	1	0	0
	Philopotamidae	0	0	0	0	0	16	0	0	0	0	0
	Chimarra	0	0	0	0	0	16	0	0	0	0	0
	Ryacophilidae	0	8	0	0	0	0	0	0	0	0	0
	Ryacophila	0	8	0	0	0	0	0	0	0	0	0
	Pupa	0	0	2	0	0	10	0	0	0	0	0
Malacostraca		3	321	300	318	1453	1017	424	234	1134	1646	738
	Amphipoda	0	0	0	10	198	75	0	1	54	68	61
	Gammaridae	0	0	0	10	198	75	0	1	54	68	61
	Gammarus	0	0	0	10	198	75	0	1	54	68	61
	Decapoda	0	5	2	0	0	14	1	0	0	0	5
	Cambaridae	0	5	2	0	0	14	1	0	0	0	5
	Cambarus	0	0	0	0	0	12	0	0	0	0	0
	Procambarus	0	5	2	0	0	2	1	0	0	0	5
	Isopoda	3	316	298	308	1255	928	423	233	1080	1578	672
Maxillopoda		11	44	14	2	10	5	19	12	4	42	2
	Copepoda	11	44	14	2	10	5	19	12	4	42	2
	Ostracoda	5	50	4	0	19	4	1	2	0	2	2
Mollusca		0	31	20	95	143	67	65	56	160	149	166
	Bivalvia	0	0	10	69	124	19	0	8	95	74	26
	Gastropoda	0	31	10	26	19	48	65	48	65	75	140
	Ancylidae	0	1	1	9	5	31	0	27	51	53	93
	Hydrobiidae	0	0	0	0	0	0	0	0	1	0	0
	Physidae	0	8	4	2	0	2	10	5	2	8	14
	Planorbidae	0	22	5	15	14	15	55	16	11	13	33
	Viviparidae	0	0	0	0	0	0	0	0	0	1	0
Nematoda		0	1	1	0	0	0	4	0	0	0	0
Platyhelminthes	**Tricladida**	0	0	1	0	0	0	0	0	0	3	0
	Planarridae	0	0	1	0	0	0	0	0	0	3	0
	Planaria	0	0	1	0	0	0	0	0	0	3	0

		Sampling Date 9:					
			DR			**RW**	
		1	2	3	1	2	3
	Habitats Sampled:	OM,R,S,W	OM,R,S,W	OM,R,S,W	OM,S,W	OM,S,W	OM,R,S,W
Annelida Clitellata		12	21	21	121	76	49
	Hirudinea	3	4	0	0	4	0
	Oligochaeta	9	17	21	121	72	49
Arthropoda		424	790	1206	1908	2118	2734
Arachnida		7	13	57	20	14	66
	Tombidiformes	7	13	57	20	14	66
Insecta		388	738	1133	1737	1794	2467
	Coleoptera	1	2	5	1	5	12
	Dryopidae	0	0	0	0	4	2
	Pelonomus (larval)	0	0	0	0	4	2
	Dytiscidae	0	1	0	0	0	0
	Neoporus (larval)	0	1	0	0	0	0
	Elmidae	0	0	0	0	0	9
	Stenelmis (larval)	0	0	0	0	0	9
	Gyrinidae	0	0	5	1	0	1
	Dineutus (larval)	0	0	3	1	0	1
	Gyrinus (larval)	0	0	2	0	0	0
	Helophoridae	1	1	0	0	1	0
	Helophorus (larval)	1	1	0	0	1	0
	Collembola	0	0	0	0	0	4
	Entomobryiidae	0	0	0	0	0	4
	Cyphoderus	0	0	0	0	0	4
	Diptera	286	514	880	1432	1373	1366
	Ceratopogonidae	1	1	5	1	89	4
	Atrichopogon	1	1	1	1	88	0
	Bezzia	0	0	0	0	1	0
	pupa	0	0	4	0	0	4
	Chironomidae	256	493	651	1415	1284	1328
	Non-tanypodinae	209	404	588	1288	1125	1226
	Tanypodinae	20	39	38	40	66	73
	pupa	27	50	25	87	93	29
	Empididae	0	1	1	4	0	19
	Hemerodromia	0	1	1	4	0	19
		25	16	223	12	0	14
	larval	23	15	190	10	0	14
	pupa	2	1	33	2	0	0
	Tabanidae	0	0	0	0	0	1
	Ephemeroptera	79	99	115	132	128	420
	Baetidae	79	99	111	132	119	416
	Acentrella	0	7	0	0	0	0
	Acerpenna	30	64	47	86	13	246
	Baetis	44	27	64	46	106	170
	Plauditus	5	1	0	0	0	0
	Ephemerellidae	0	0	4	0	0	0
	Seratella	0	0	2	0	0	0
	Unknown	0	0	2	0	0	0

	Heptageniidae	0	0	0	0	9	4
	Maccaffertium	0	0	0	0	3	0
	Stenacron	0	0	0	0	6	4
	Hemiptera	2	75	3	0	2	0
	Belostomatidae	0	0	0	0	2	0
	Lethocerus	0	0	0	0	2	0
	Corixidae	2	73	2	0	0	0
	Tricocorixia	2	73	2	0	0	0
	Velidae	0	2	1	0	0	0
	Microveilia	0	2	1	0	0	0
	Megaloptera	0	0	0	0	1	0
	Corydalidae	0	0	0	0	1	0
	Corydalus	0	0	0	0	1	0
	Odonata	1	0	1	0	0	0
	Aeshnidae	1	0	0	0	0	0
	Coryphaeschna	1	0	0	0	0	0
	Macromiidae	0	0	1	0	0	0
	Macromia	0	0	1	0	0	0
	Plecoptera	0	1	0	0	0	7
	Perlidae	0	1	0	0	0	7
	Perlesta	0	1	0	0	0	7
	Trichoptera	19	47	129	172	285	658
	Hydropsychidae	6	38	123	172	280	610
	Cheumatopsyche	6	38	123	172	280	610
	Hydroptilidae	5	0	0	0	4	23
	Hydroptila	2	0	0	0	4	22
	Neotrichia	0	0	0	0	0	1
	Oxyethira	3	0	0	0	0	0
	Leptoceridae	8	9	6	0	1	1
	Oecetis	6	0	6	0	1	1
	Trianodes	2	9	0	0	0	0
	Limnephilidae	0	0	0	0	0	4
	Ironoquia	0	0	0	0	0	4
	Philopotamidae	0	0	0	0	0	8
	Chimarra	0	0	0	0	0	8
	Pupa	0	0	0	0	0	12
Malacostraca		27	30	14	149	294	173
	Amphipoda	0	0	0	18	105	50
	Gammaridae	0	0	0	18	105	50
	Gammarus	0	0	0	18	105	50
	Decapoda	0	0	0	0	0	1
	Cambaridae	0	0	0	0	0	1
	Procambarus	0	0	0	0	0	1
	Isopoda	27	30	14	131	189	122
Maxillopoda		2	4	2	2	12	28
	Copepoda	2	4	2	2	12	28
	Ostracoda	0	5	0	0	4	0
Mollusca		10	23	96	262	177	159
	Bivalvia	0	0	3	120	76	48
	Gastropoda	10	23	93	142	101	111

	Amnicolidae	1	0	0	0	0	0
	Ancylidae	0	9	88	99	53	72
	Hydrobiidae	0	0	0	0	0	1
	Physidae	4	0	2	12	4	10
	Planorbidae	5	14	3	30	38	28
	Pleuroceridae	0	0	0	0	2	0
	Viviparidae	0	0	0	1	4	0
Nematoda		1	5	1	0	1	0
Platyhelminthes	**Turbellaria**	0	0	0	0	2	0
	Tricladida	0	0	0	0	2	0
	Planariidae	0	0	0	0	2	0
	Planaria	0	0	0	0	2	0