MACROINVERTEBRATE RESPONSES TO HYDROLOGICAL VARIATION IN EXPERIMENTAL WETLANDS

by

SERGIO A. SABAT-BONILLA

(Under the Direction of J. Checo Colon-Gaud)

ABSTRACT

Predicted increases in the frequency of intense storms and periods of severe drought due to climate change represent a threat to wetland macroinvertebrate communities through alterations to the hydrological regime. I used experimental ponds to assess the effects of water permanence (i.e., duration of flooding) on the communities of aquatic macroinvertebrates. I predicted that permanent ponds would harbor higher diversity of longer-lived taxa whereas temporary ones will favor colonization by quick turnover, short-lived taxa and support lower consumer diversity. Results show differences in macroinvertebrate communities between permanent and temporary ponds can be mostly explained by hydrology and the amount of time these were covered by water. While biomass (B) and richness (S) of macroinvertebrates were related to treatment type, their abundance (N) was not. I also found that across both treatments many individuals were generalist collector-gatherers of small body size inhabiting fine-sediments, the open limnetic zone or vascular plants having multiple generations per year (multivoltine) and emerging in a highly synchronous manner at all times of the season. The results from this study show that the length of time these ponds retain water and the time of year in which these flooding events occur have major impacts on the natural succession of resettlement within temporary wetlands. The data obtained in this study aids in further understanding what communities of aquatic macroinvertebrates are supported by different conditions (i.e., potential disturbances), as well as what ecosystem functions will be the most impacted by these changes along the wetlands of the southeastern Coastal Plain.

INDEX WORDS: Functional feeding groups, Climate change, Wetlands, Macroinvertebrates, Freshwater communities, Southeastern US.

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SERGIO A. SABAT-BONILLA

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Major Professor:	J. Checo Colón-Gaud
Committee:	John Carroll
	Ray Chandler

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DEDICATION

Dedico esta tesis a la vida y legado de mi padre (Sergio E. Sabat-Guernica) que falleció unos meses antes de comenzar este programa de maestría. Él dio su vida para que solo sea el tiempo lo único que limite a su familia de crecer y disfrutar de todas las oportunidades que trae cada amanecer. Y aunque no pueda celebrar este logro con él, me enorgullece saber que con cada meta que cumplo engrandezco su legado. ¡Así que seguiremos pa'lante, bien y mejorando!

I dedicate this thesis to the life and legacy of my father (Sergio E. Sabat-Guernica) who passed away a few months before starting this master's program. He gave his life so that only time would be the only thing limiting his family from growing and enjoying all the opportunities that each sunrise brings. And while I may not be able to celebrate this achievement with him, I am proud to know that with every goal I accomplish I continue to enhance his legacy. So, we will keep moving forward, doing good and getting better!

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CHAPTER 1

INTRODUCTION

Wetland Ecosystems

Wetlands are unique systems to study as they arise through an interplay between the biota, climate, hydrology, geomorphology, and physical nature of terrestrial environments (Mitsch & Gosselink 2007). Just as in rivers and streams (Hynes 1975; Vannote et al. 1980; Wallace et al. 1997), the surrounding environment influences, and is being influenced by the wetland (Higgins and Merritt 1999; Batzer et al. 2000; Palik et al. 2003), creating a well-connected system that can be highly impacted by any variation within each of its components. The diversity of environmental factors interplaying within a wetland make them an important habitat for both aquatic and terrestrial organisms, as well as the ecosystem functions that come to be from these interactions (e.g., nutrient recycling, carbon storing, flood mitigation) (Gopal & Junk 2000; Batzer & Sharitz 2006; Mitsch et al. 2015). Being depressional zones with highly saturated soils, wetlands are key in restoring surface water quality by storing nutrients (e.g., carbon, nitrogen, and phosphorus) and regulating their flows across upland and adjacent water systems (Reddy et al. 1999; Kayranli et al. 2010). For example, wetlands have been shown to store ~30% of global soil carbon while only covering ~8% of land cover (Nahlik & Fennessy 2016). This is outstanding when you consider that ~50% of all wetlands have been destroyed across the globe mostly due to anthropogenic influences (i.e., land use legacies) since historical governmental policies promoted their conversion to drained land (OECD 1996).

Aquatic Macroinvertebrates

Aquatic macroinvertebrates in wetlands play a key role in ecosystem processes by recycling nutrients across terrestrial and aquatic environments as they facilitate the decomposition of organic matter, contribute to secondary production and are prey sources for higher trophic levels (Wiley 1984; Hann 1991; Batzer et al. 1993). For example, aquatic insects serve as linkages between aquatic and terrestrial food-webs via the production of adults capable of emerging into the terrestrial environment where they can be consumed by predators (e.g., avian, arachnids, amphibians) and vice-versa with allochthonous inputs being consumed and transferred across the aquatic food-web by collector-gatherers and shredders (Henschel et al. 2001; Sabo & Power 2002). These aquatic-terrestrial fluxes are dependent on the size of the body of water and its distance to shoreline as it not only controls the habitable area within them, but also the amount of allochthonous resources that can be introduced (Gratton et al. 2009). Thus, any variability that could alter a component of this aquatic-terrestrial flux (e.g., hydrological variation, surrounding landscape alteration) can have the potential of limiting the viability of these interconnected systems.

Due to their apparent importance across aquatic ecosystems, aquatic macroinvertebrates are commonly used as indicators of ecological health and ecosystem functions, thus assessing these communities of ‘mid-level’ consumers can provide insight into the role of these experimental wetland ecosystems in mitigating natural wetland functions. Although assessment methods that target the physiochemical and biological components that help shape wetland communities continue to be developed, modified, or improved, these rarely incorporate manipulative studies of predicted scenarios to evaluate wetland condition. These typically only include measurements of water quality/chemistry instead of including detailed assessments of biotic communities. This is important to study because hydrological fluctuations in wetlands have been shown to influence greenhouse gas emissions and carbon sequestration (Ren et al. 2017) and consumers can be important mediators of these nutrient cycles.

Hydrological Regimes

The most influential factor governing wetlands is hydrology (Bataille & Baldassarre 1993; Wissinger & Gallagher 1999; Brooks 2000). Studies have compared ephemeral freshwater systems to permanent ones (Mitsch & Gosselink 2007; Porst & Irvine 2009), showing that water duration directly affects the diversity and richness within aquatic invertebrate communities. Furthermore, community richness in ephemeral ponds is also being influenced by the size of these ponds, with richness being positively related to area covered by water (March & Bass 1995). With the major habitat variability imposed by hydrological fluctuations due to seasonal variation (flooding and drying events) on aquatic invertebrate communities in wetlands, a wide range of evolutionary adaptations have proliferated due to the predictable pattern of these seasonal fluctuations (Batzer & Sharitz 2006). Wiggins et al. (1980) classified wetland macroinvertebrates into 4 groups based on their adaptations to maintain stable populations after drying events. While not every species within each of these groups has an equal chance of establishing a population once ideal conditions are met, the most common wetland inhabitants would be the ones with the capacity to withstand the wetting and drying and maintain a stable population (Batzer et al. 2004). Common species such as fairy shrimps (Anostraca), which maintain stable populations by laying eggs that can subsist in desiccated areas for years and hatch when conditions are favorable (Wissinger & Gallagher 1999) or some water boatmen (Hemiptera: Corixidae), that migrate from temporary and permanent ponds to reproduce (Wissinger 1997), have found ways that might allow them to still proliferate in areas most impacted by prolonged drying events. On the contrary, rarer specimens that have been shown to not withstand seasonal hydrological fluctuations, should be the ones most impacted by extreme climate and weather variations as expected by climate models developed for this region (Anandhi & Bentley 2018).

Impacts of Climate Change to Freshwater Ecosystems of the Southeastern US

The southeastern US is a biodiversity hotspot (Cartwright & Wolfe 2016) and while the region normally receives high quantities of annual precipitation (Rose 2009), it has been subjected to prolonged periods of drought (Mitra & Srivastava 2017) while also experiencing its warmest temperature recorded to date, all within the past decade (Ingram et al. 2013). During the 20th century, precipitation increased during spring and decreased in the summer months (Mearnse et al. 2003), but models predict a change in the range of dry to wet periods during drier periods and an increase in wetter months as we get closer to the end of the 21st century (Anandhi & Bentley 2018). Studies have proposed a positive feedback scenario, where precipitation will increase in wet areas and dry areas will become drier (Kirtman et al. 2013). Thus, these climate models allude to a shift in climate extremes, with an intensification of summer conditions. Meaning that summers with expected above-average precipitation will see higher quantities, while summers with below-average precipitation will be subjected to these conditions for a longer period (Dore 2005; Li & Li 2014). The expected intensification of weather patterns during summer months is of interest, but even more so are wet summers since it is expected that the frequency of intense storms will increase due to higher water holding capacity in warm air (Karl & Knight 1998; Trenberth 2011). Subsequently, aquatic ecosystems (e.g., rivers, floodplains, and wetlands) in the southeastern US are expected to experience increased periods of severe drought interspersed with large flood events. Thus, the stability of the system and the environments that depends on this balance will be tested.

Study Objectives

This study aimed to understand if wetland consumer communities differ in structure and function based on length of hydroperiods and presumed ecosystem stability. To do so, I quantified macroinvertebrate community structure and function in experimental wetlands with manipulated hydroperiods (i.e., permanent vs. temporary). The findings generated from this study provide key insight on what communities of aquatic macroinvertebrates are supported by different conditions that can be associated with disturbance frequency, as well as what ecosystem functions will be the most impacted by predicted changes in precipitation patterns along the southeastern US. Furthermore, my study provides baseline datasets for the potential use of other ‘re-furbished’ sites (e.g., fish farms, hatcheries, etc.) to mitigate wetland losses.

Predictions

I hypothesized that if length (or duration) of flooding influences macroinvertebrate communities (i.e., colonization, composition, etc.) then permanent and temporary wetland habitats should differ in their macroinvertebrate diversity and community composition due to timing and duration of inundation. If so, then permanent wetlands should harbor higher diversity of longer-lived taxa due to environmental stability and larger availability of colonizable area. Furthermore, ponds that experience flooding followed by rapid receding of water (i.e., temporary) would favor colonization by quick turnover (i.e., short-lived) taxa and support lower consumer diversity due to limited availability of space and decreasing water quality (e.g., lower dissolved oxygen concentrations and higher fluctuations in water temperatures).

CHAPTER 2

METHODS

Field Site

The study was conducted at the former US Fish and Wildlife Service (FWS) Bo Ginn National Fish Hatchery in Jenkins County GA (Fig. 2.1). These former hatchery ponds were subjected to variable hydroperiod lengths (i.e., duration of flooding), allowing for the comparison of aquatic macroinvertebrate community composition and successional patterns of colonization between temporary or intermittent (i.e., resembling drying or drought conditions) and permanent (i.e., resembling continuously flooded or stable conditions) ponds.

Experimental Design

Experimental ponds were either already filled (i.e., inundated) prior to the start of the study (n = 4; since February 2018) or at the onset of the study (n = 4; on January 1, 2019) (Fig. 2.2) and maintained with a continuous input of water to facilitate recirculation and account for any potential water losses due to evaporation and percolation through the soil (Table 2.1). After 14 days, water input was discontinued at half of the ponds (n = 4; temporary treatment) and these were allowed to recede until presumed entirely dry (~60-80d). This pattern of inundation and subsequent receding after 14 days was repeated two additional times in temporary ponds (January – March; March – July) for a total of two ‘intervals’ of flooding and drying. After the receding period for the March to July inundation of temporary ponds had concluded, all but one pond retained water in isolated pools. This allowed for that single pond to be sampled for an additional 2 months (i.e., until September).

All permanent ponds (n = 4; permanent treatment) continued to receive water input for approximately 4-5 days per week. On June 17, 2019, one of the continuously flooded ponds experienced a substantial loss of water due to percolation which potentially resulted in altered conditions and thus was removed from the permanent treatment after June 24, 2019, resulting in a total of 3 continuously flooded ponds from that day forward.

Water Chemical Parameters

I measured water chemistry parameters weekly at each pond using a YSI ProDSS multi-parameter probe (Yellow Spring Instruments, Yellow Springs, OH) to assess for differences in water temperature (°C) and dissolved oxygen (DO; mgL^{-1}) between ponds, all of which could be contributing factors for possible differences in macroinvertebrate abundance and biomass within treatments. In addition, Hobo® temperature loggers (Onset Computer Corporation, Bourne, MA) were deployed at each pond for the duration of the study (January 2019 – January 2020) to allow for continuous and localized measurements of temperature across the different ponds. Knowing that these water chemistry parameters are highly influenced by seasonal changes, I was interested in assessing for differences in temperature between seasons and its potential influence on macroinvertebrate abundance and biomass. Since the temporary ponds went through the flooding and drying period (~3-months) on 2 different occasions (i.e., intervals), I also observed and analyzed these separately to assess for potential seasonal differences in abundance and biomass across temporary ponds, while also allowing me to assess potential preliminary patterns associated with increased frequency of disturbance. Since one of the temporary ponds retained isolated wetted areas and was sampled beyond the July date when all other temporary ponds had dried. This allowed for sampling of a single temporary pond for a longer period of time. Hence, temporary treatment intervals (January – March, March – September) were also compared to permanent ponds.

Aquatic Macroinvertebrate Sample Collection

Collections of aquatic macroinvertebrates occurred at three points within each pond by walking ~20ft to any direction within the pond’s access or entry point (i.e., bank). This sampling point selection was done in a haphazard manner due to the limitations imposed by the water depth in which our sampling equipment could function properly. Collections varied between permanent and temporary ponds, with permanent ponds being sampled monthly and temporary ponds initially sampled weekly to capture the successional stages of macroinvertebrate colonization, then every two weeks during the receding or drying period (~60-80d) to capture potential variation associated to habitat loss. Macroinvertebrate sampling of permanent ponds occurred from January 2019 – January 2020 (13 consecutive months) to assess for potential changes in community structure over the course of a year (e.g., seasonal patterns). Samples were collected using a dip net (500-µm mesh) within an enclosed area of 0.0625 m^2 with the sides of the enclosure also covered by a 500-µm mesh, creating a standardized area for every sample. The dip nets were initially used to disturb the sediment by jabbing it to the surface along the enclosed area, followed by three sweeps along the water column to collect any organisms displaced from the benthos. Once samples were obtained with the dip net, these were immediately placed in labeled plastic bags and preserved with ~95% ethanol.

Laboratory Processing of Samples

In the laboratory, samples were rinsed over stacked 500µm and 250µm sieves to separate coarse and fine contents, as well as remove excess sediment to facilitate sorting. After samples were washed, fine and coarse portions were stored in labeled jars with ~95% ethanol until further processing. Macroinvertebrates collected from samples were identified to the lowest taxonomic level possible (usually genus for most insects, and class, order, or family for non-insects) and categorized into by common functional traits describing aspects of the organism’s life history, dispersal, morphology, ecology (see Table 2.2; Twardochleb et al. 2021). Macroinvertebrates were counted to estimate abundance (ind./m^2) and measured to the nearest 1-mm to estimate biomass (mg/m^2) using published length-mass relationships (Benke et al. 1999).

Data Analyses

All statistical analysis were done in R statistical software version 3.5.2 (R Development Core Team 2015). To assess for differences in the abundance and biomass of macroinvertebrates across ponds with varying hydrology, I used permutational multivariate analysis of variance (PERMANOVA) for each community with 10,000 permutations using the adonis function of the vegan package (Oksanen et al. 2016). Data for PERMANOVA were calculated via Bray-Curtis dissimilarity matrix using the vegdist function. Non-metric multidimensional scaling (NMDS) ordination plots were generated with the metaMDS function to visualize the dissimilarities (i.e., distance) between permanent and temporary pond communities using both abundance and biomass estimates across treatments. Using the simper function from the vegan package, Similarity Percentages (SIMPER) analyses were used to determine which taxonomic groups were contributing the most to dissimilarities between treatments. Additional comparisons were conducted using PERMANOVA and NMDS to compare between temporary ponds inundated during different times of the year (i.e., intervals). Furthermore, the envfit function (also from the vegan package) was used to test the correlation between environmental factors and the abundance/biomass of macroinvertebrates. Lastly, the Pearson's product moment correlation coefficient test was done to test the association between days since last flooding event with abundance, biomass and richness follow independent normal distributions using the core.test function within the ggpubr package (Kassambara 2020).

Table 2.1. Experimental design with number of ponds receiving each treatment and date of flooding events.

Treatment	# of Ponds	Inundation Date	Description
Permanent	4	3/14/2018	Inundated in prior project (see Schaffer 2019)
Temporary	4	1/1/2019	Temporary ponds were flooded for the first time
		3/18/2019	Temporary ponds were flooded for second time

* One of the permanent ponds was unable to retain water, thus was removed from the permanent treatment on 6/17/2019. Beyond this date only three ponds were sampled as part of the permanent treatment.

Table 2.2. Macroinvertebrate functional traits describing features of the organism's life history, dispersal strategies, ecology, and morphology. Modified from Twardochleb et al. 2021.

Trait Feature	Trait Category	Trait	Description
Life history	Generations per year	Multivoltine	Multiple generations per year
		Semivoltine	Less than one generation per year
		Univoltine	One generation per year
	Emergence synchrony	Poorly	Emergence happens weeks or months apart
		Well	Emergence happens a few days apart
	Emergence season	Fall	Emerging between September and November
		Winter	Emerging between December and February
		Spring	Emerging between March and May
		Summer	Emerging between June and August
Dispersal	Female dispersal (adult flying)	High	>1 km flight before laying eggs
		Low	<1 km flight before laying eggs
Ecology	Habit	Burrower	Inhabiting the fine sediments

	Climber	Adapted to moving vertically on stem-type surfaces
	Clinger	Adapted for attaching to surfaces
	Crawler	Adapted for crawling on the surface of floating leaves of vascular hydrophytes or fine sediments on the bottom of water bodies
	Planktonic	Inhabiting the open water limnetic zone of standing waters
	Skater	Adapted for skating (gliding) on the water surface
	Sprawler	Inhabiting the surface of floating leaves of vascular hydrophytes or fine sediments
	Swimmer	Adapted for fish-like swimming in lotic or lentic habitats
FFG	Collector-filterer	Insects that collect and filter living algal cells or detritus
	Collector-gatherer	Insects that collect and consume decomposing organic matter
	Herbivore	Insects that scrape algae or that shred

			or pierce living aquatic plants
		Parasite	Parasites that consume living animal tissue
		Predator	Insects that ingest prey whole or in parts (engulfers) or that pierce prey tissues and suck fluids (piercers)
		Shredder	Insects that shred decomposing vascular plant tissue (detritivores)
Morphology	Max body size	Small	<9 mm
		Medium	9–16 mm
		Large	>16 mm
	Respiration	Gills	A thin-walled structure with trachea, used for the absorption of oxygen
		Plastron, spiracle	Oxygen is absorbed from the atmosphere, from aquatic plants or from a temporary air store, such as an air film or bubble on the surface of the body, or a permanent air store (a plastron)

Tegument	An outer covering, outer enveloping cell layer or membrane used to acquire oxygen

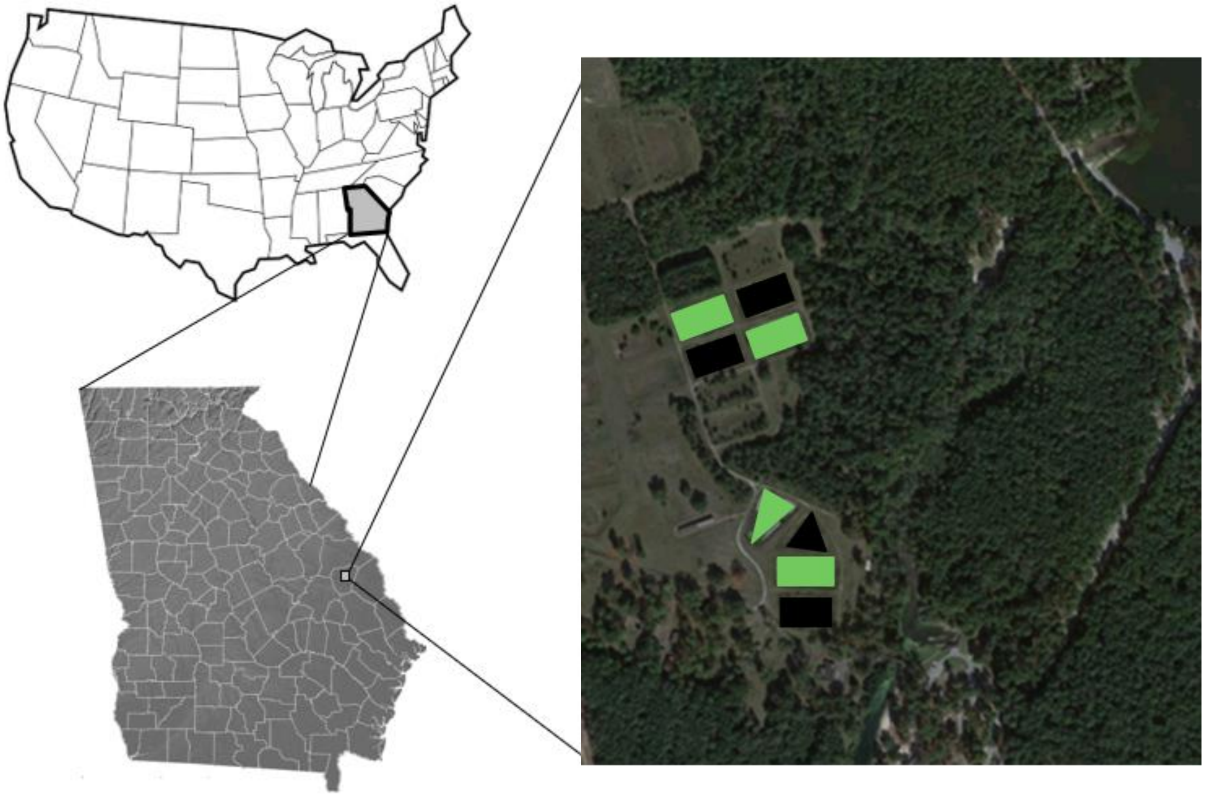

Figure 2.1. Location of the US FWS Bo Ginn National Fish Hatchery in Jenkins County. The site is adjacent to Magnolia Springs State Park near Millen, GA. Permanent ponds are represented by green squares and triangles, while temporary ones are represented by black squares and triangles.

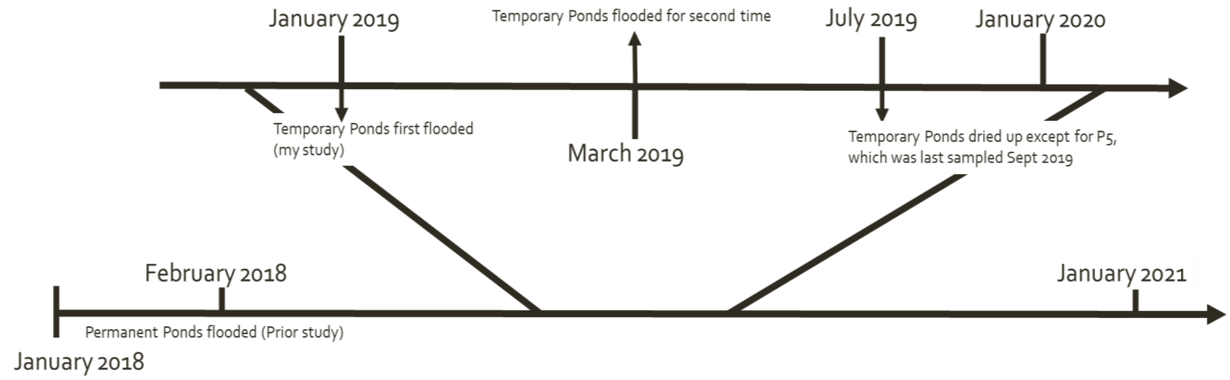

Figure 2.2. Timeline of study highlighting flooding and drying events, permanent ponds were flooded in February 2018 for a previous study and were kept filled until the end of the study (January 2020). Temporary ponds were first flooded in January 2019 and were left to dry after 4 weeks, once fully dried these temporary ponds were flooded again in March 2019.

CHAPTER 3

RESULTS

Environmental variables

I found no variation in water quality between permanent and temporary ponds for neither the weekly nor the continuously recorded data across both temperature and dissolved oxygen concentration (Table 3.1).

Macroinvertebrate Taxa Richness, Abundance, and Biomass

I collected and identified a total of 16,388 individuals, within a total of 58 distinct taxa including family, genera, or tribe (e.g., Diptera: Chironomidae) of macroinvertebrates across all ponds. However, over 81% of all individuals collected belonged to only 5 of genera or tribes: *Chironominae* (27.48%), *Caenis* (26.54%), *Daphnia* (11.25%), *Culicoides* (8.80%) and *Tanypodinae* (7.15%). A total of 30 distinct taxa (genera and tribe) were found in permanent ponds with 4 of these accounting for almost 85% of all the individuals collected: *Caenis* (38.46%), *Chironominae* (28.35%), *Culicoides* (10.63%) and *Tanypodinae* (7.30%). While in temporary ponds only 27 taxa (genera and tribe) were collected and only 2 out of the 5 dominant ones (~83% of individuals) were found in permanent ponds: *Daphnia* (33.03%), *Chironominae* (25.67%), *Gammarus* (10.31%), *Physa* (8.92 %) and *Culicoides* (5%).

Mean monthly abundance of the total macroinvertebrate community was 13.20 ind/m^2 (± 2.47SE) in permanent ponds and 14.59 ind/m^2 (± 4.57SE) in temporary ponds (Figure 3.1), whereas mean monthly total community biomass was 59.03 mg/m^2 (± 6.44SE) in permanent ponds and 49.62 mg/m^2 (± 10.89SE) in temporary ponds (Figure 3.2). While mean monthly macroinvertebrate total community abundance and biomass were relatively the same between treatments, looking at these parameters along the intervals of flooding shows quite the discrepancy within temporary ponds and between permanent and temporary ones (Figures 3.3 and 3.4). There was within treatment variation in the mean monthly abundance in temporary ponds, the first interval of flooding (January – March) was 24.78 ind/m^2 (± 9.75SE) and 7.79

ind/m^2 (± 1.31SE) for the second flooding interval (March – May). This same pattern of within treatment variation was also seen when looking at the mean monthly biomass between flooding intervals in which the first interval (January – March) had 33.99 mg/m^2 (± 6.02SE), while the second interval of flooding (March – May) had 65.26 mg/m^2 (± 19.35SE). These results show that permanent ponds had a lower mean monthly abundance community than temporary ponds between January and March, but higher between March and May (Figure 3.3). The opposite trend was seen for mean monthly biomass in which permanent ponds had more biomass than temporary ponds between January – March, but less than between March and May (Figure 3.4). Furthermore, of the dominant taxa observed, most revealed patterns of higher abundance and biomass consistently throughout the year, or at least in most months, in permanent over temporary ponds. Some of the most noticeable patterns could be observed for the various tribes of the dipteran family Chironomidae (Figures 3.5 and 3.6) and for the mayfly family Caenidae (Figures 3.7 and 3.8).

By dividing the collections based on days since each pond was last flooded and attaching each collection done on that pond to see if there were any major differences in abundance, biomass and taxa richness (APPENDIX A). It is possible to see that permanent ponds have a more stable range across all 3 variables, while there is more variation between each temporary pond. The results from the Pearson's correlation test show that biomass ($t = 2.1264$, $df = 80$, $p = 0.03655$, $r = 0.23129$) and the number of taxa found ($t = 3.4812$, $df = 80$, $p < 0.001$, $r = 0.36271$) are positively correlated to the number of days since last flooding, but not abundance ($t = 1.3632$, $df = 80$, $p = 0.1767$, $r = 0.15067$) (Table 3.2).

Macroinvertebrate community structure

Nonmetric Multi-Dimensional Scaling (NMDS) plots based on abundance (N) and biomass (B) data across all ponds included twenty iterations in two-dimensional solutions resulting in stress estimates of 0.272 and 0.273, respectively (Figure 3.9-3.10). The results of the permutation test via the envfit function shows significant correlations between abundance (N) and biomass (B) by date (N, R2 = 0.3243,

$p < 0.05$; B, R2 = 0.3385, $p < 0.05$) as well as treatment type (N, R2 = 0.0242, $p = 0.05$; B, R2 = 0.0432, $p < 0.05$). I also found that that biomass had a significant correlation with the interval of flooding (January – March, March – May, Permanent) (R2 = 0. 1369, $p < 0.05$) and each pond (R2 = 0. 0995, $p < 0.05$). Similarity percentages (SIMPER) analyses (APPENDIX B-5) found that 83.95% of the differences in abundance across treatment groups were driven by 6 families: Chironomidae (24.24%), Ceratopogonidae (14.99%), Daphnidae (13.02%), Caenidae (7.92%), Physidae (6.80%) and Gammaridae (4.65%). SIMPER analyses also revealed that 83.99% of the dissimilarities in biomass across treatments were also being influenced by 6 taxa: Hydrophilidae (21.39%), Chironomidae (18.26%), Ceratopogonidae (14.63%), Caenidae (10.62%), Elmidae (4.78%) and Coenagrionidae (4.06%).

I also ran Nonmetric Multi-Dimensional Scaling (NMDS) for both abundance (N) and biomass (B) data for only temporary ponds with the same parameters as in the NMDS of all ponds, the stress estimates were of 0.251and 0.253 respectively (Figure 3.9-3.10). The results of the permutation test (envfit) showed that only date (N, R2 = 0. 3659, $p < 0.05$; B, R2 = 0. 3154, $p < 0.05$) and flooding interval (N, R2 = 0. 0645, $p = 0.05$; B, R2 = 0. 0530, $p < 0.05$) had significant correlations, while each pond only had a slight correlation with biomass (R2 = 0. 0769, $p = 0.067$) in temporary ponds. Similarity percentages (SIMPER) analyses (APPENDIX B-5) found that 82.78% of the differences in abundance across flooding intervals in temporary ponds were driven by 5 families: Daphnidae (25.05%), Chironomidae (23.62%), Physidae (10.03%), Gammaridae (8.40%) and Ceratopogonidae (5.59%). SIMPER analyses also revealed that 82.11% of the dissimilarities in biomass across flooding intervals in temporary ponds were also being influenced by 5 taxa: Hydrophilidae (28.47%), Chironomidae (24.64%), Elmidae (7.98%), Ceratopogonidae (6.21%) and Coenagrionidae (5.29%).

Since I found no variation in water quality parameters (temperature (℃) and dissolved oxygen concentration (mg/L)) across date and treatment (Table 3.1), Permutational Analysis of Variance (PERMANOVA) were performed individually to test the relations between abundance (N) and biomass

(B) to the treatments (permanent vs. temporary) in all ponds or by flooding intervals (January – March, March – May) for temporary ones, sampling dates and sampling replicates as with each pond. The PERMANOVA results for all ponds show that sampling date ($F = 11.917$, $p < 0.001$) and sampling replicates ($F = 5.808$, $p < 0.001$) were significantly related to the abundance of macroinvertebrates when tested across treatments, while the treatment type had not relation ($F = 0.8253$, $p = 0.6208$) (Table 3.3). The results of the PERMANOVA testing the relation between each pond, sampling date and sampling interval with abundance across all ponds showed a significant relation with sampling date ($F = 12.2746$, $p < 0.001$) and pond $F = 2.1836$, $p < 0.001$), but not with the sampling replicates. ($F = 0.9286$, $p = 0.5108$). Looking at only temporary ponds, the results from the PERMANOVA show that abundance is significantly related to the sampling date ($F = 4.9277$, $p < 0.001$) and flooding interval ($F = 6.0459$, $p < 0.001$), but not the pond ($F = 1.1801$, $p = 0.2132$). The PERMANOVA's for biomass across all ponds show a significant relation with each pond ($F = 1.882$, $p < 0.001$), sampling date ($F = 12.9008$, $p < 0.001$) and treatment ($F = 4.8557$, $p < 0.001$). While in temporary ones, the PERMANOVA's show that biomass is only statistically related to sampling date ($F = 8.7374$, $p < 0.001$) and flooding interval ($F = 2.2316$, $p = 0.0155$).

Community Traits

I found noticeable differences in macroinvertebrate functional traits across treatments (Table 3.4). Within the life history traits, most individuals across all ponds had multiple generations per year with a well synchronized emergence along every season. When divided by treatment types, the major differences for life history traits were in the emergence synchrony as permanent ponds were dominated by well synchronous taxa (78.25%) while temporary ones had an almost equal distribution between poor (45.06%) and well (54.94%) synchronous taxa. Across all ponds, adult dispersal had an almost equal chance of being high (44.72%) or low (55.28%). Again, the major differences were seen across treatments in which taxa in permanent ponds had lower (61.98%) dispersal while ones in temporary ponds had higher (73.65%). Around half of all collected taxa across all ponds were burrowers (28.72%), planktonic (25.24%) or sprawlers (37.91%) with most of them being gatherers (70.10%) and a small subset being either predators (18.91%) or filterers (10.59%). In permanent ponds, most individuals were either burrowers (29.55%) or sprawlers (50.11%) that gathered (79.28%) or predated (19.64%) their food, while in temporary ponds many individuals either burrowed (26.96%) or were planktonic (50.35%) in their habit as they gathered (49.70%) or filtered (32.50%) their food. Regarding morphological traits, almost all individuals were small (88.09%) in body size across both treatments, but the respiration mechanism diverged across treatments with individuals in permanent ponds utilizing gills (42.46%) or teguments (55.91%) while in temporary ponds most individuals obtained oxygen utilizing a tegument (90.06%).

Table 3.1: Seasonal (Spring, Summer, Winter) estimates for water chemistry parameters including (mean ± standard deviation) temperature (℃) and dissolved oxygen (DO) concentration (mg/L) across treatments (permanent and temporary).

Season	Treatment	Temperature	DO (mg/L)
Winter	Permanent	12.93±2.62	7.38±4.38
Winter	Temporary	12.4±2.84	7.80±3.90
Spring	Permanent	20.00±2.84	8.75±3.92
Spring	Temporary	19.25±2.47	8.35±5.76
Summer	Permanent	30.07±2.58	9.04±5.30
Summer	Temporary	30.77±2.86	8.79±5.76

Table 3.2. Pearson's correlation results based on the association between the number of days since ponds were flooded and the total macroinvertebrate community abundance (ind/m^2), biomass (mg/m^2) and richness.

	t	d.f.	*p*	*r*
Days since flooding				
Abundance	1.3632	80	0.1767	0.150666
Biomass	2.1264	80	0.03655	0.231295
Richness	3.4812	80	< 0.001	0.362708

Table 3.3. Permutational Analyses of Variance (PERMANOVA) results based on total macroinvertebrate community abundance (ind/m^2) and biomass (mg/m^2) after 10,000 permutations were performed individually for each dataset (i.e., N, B) by treatment (permanent vs. temporary) in all ponds or by flooding intervals (January – March, March – May) for only temporary ones, sampling dates and sampling replicates.

	d.f.	SS	MS	F	R2	Pseudo-P
N by Trmt. (All)						
Treatment	1	0.2680	0.2678	0.8253	0.0057	0.6208
Date	1	3.8670	3.8674	11.9170	0.0821	< 0.001
Replicates	1	1.8850	1.8849	5.8080	0.0400	< 0.001
Replicate:Date	1	0.2830	0.2833	0.8728	0.0060	0.5745
Replicate:Treatment	1	0.2480	0.2475	0.7627	0.0053	0.6971
Date:Treatment	1	0.9180	0.9178	2.8280	0.0195	0.0016
Replicate:Date:Treatment	1	0.3590	0.3587	1.1052	0.0076	0.3385
Residuals	121	39.2680	0.3245		0.8338	
Total	128	47.0960			1	
N by Pond. (All)						
Pond	7	4.7480	0.6782	2.1836	0.1008	< 0.001
Date	1	3.8130	3.8125	12.2746	0.0810	< 0.001
Replicates	1	0.2880	0.2884	0.9286	0.0061	0.5108
Replicate:Date	1	0.2720	0.2715	0.8742	0.0058	0.5748
Replicate:Pond	7	2.1770	0.3111	1.0015	0.0462	0.4693
Date:Pond	7	3.4590	0.4941	1.5907	0.0734	< 0.001

Replicate:Date:Pond	7	2.2110	0.3159	1.0171	0.0470	0.4443
Residuals	97	30.1280	0.3106		0.640	
Total	128	47.096			1.000	
N by Pond. (Temp)						
Pond	3	1.1929	0.3976	1.1801	0.0429	0.2132
Date	1	2.9977	2.9977	8.8970	0.1078	< 0.001
Replicates	1	0.2374	0.2374	0.7045	0.0085	0.7496
Replicate:Date	1	0.2522	0.2522	0.7485	0.0091	0.7051
Replicate:Pond	3	1.0439	0.3480	1.0328	0.0375	0.4081
Date:Pond	3	1.1414	0.3805	1.1292	0.0410	0.2663
Replicate:Date:Pond	3	1.0710	0.3570	1.0595	0.0385	0.3707
Residuals	59	19.8789	0.3369		0.7147	
Total	74	27.8154			1	
N by Intrvl. (Temp)						
Interval	1	2.0258	2.0258	6.0459	0.0728	< 0.001
Date	1	1.6511	1.6511	4.9277	0.0594	< 0.001
Replicates	1	0.1947	0.1947	0.5812	0.0070	0.8752
Replicate:Date	1	0.3261	0.3261	0.9732	0.0117	0.4609
Replicate: Interval	1	0.2916	0.2916	0.8702	0.0105	0.5674
Date: Interval	1	0.6977	0.6977	2.0823	0.0251	0.0216
Replicate:Date: Interval	1	0.1792	0.1792	0.5350	0.0064	0.9068
Residuals	67	22.4492	0.3351		0.8071	
Total	74	27.8154			1	
B by Trmt. (All)						

Treatment	1	1.6730	1.6729	4.8557	0.0336	< 0.001
Date	1	4.3930	4.3928	12.7502	0.0882	< 0.001
Replicates	1	0.1050	0.1055	0.3061	0.0021	0.9950
Replicate:Date	1	0.2100	0.2096	0.6084	0.0042	0.8551
Replicate:Treatment	1	0.5700	0.5702	1.6550	0.0115	0.0743
Date:Treatment	1	0.7850	0.7849	2.2781	0.0158	0.0109
Replicate:Date:Treatment	1	0.3870	0.3869	1.1230	0.0078	0.3168
Residuals	121	41.6880	0.3445		0.8369	
Total	128	49.8110			1	
B by Pond. (All)						
Pond	7	4.4670	0.6382	1.8820	0.0896	< 0.001
Date	1	4.3750	4.3746	12.9008	0.0877	< 0.001
Replicates	1	0.1020	0.1016	0.2995	0.0020	0.9956
Replicate:Date	1	0.1950	0.1947	0.5743	0.0039	0.8855
Replicate:Pond	7	2.3840	0.3406	1.0045	0.0478	0.4680
Date:Pond	7	3.4010	0.4858	1.4328	0.0682	0.0099
Replicate:Date:Pond	7	2.0690	0.2956	0.8718	0.0415	0.8004
Residuals	97	32.8920	0.3391		0.6594	
Total	128	49.8850			1.000	
B by Pond. (Temp)						
Pond	3	1.1929	0.3976	1.1801	0.0429	0.2132
Date	1	2.9977	2.9977	8.8970	0.1078	< 0.001
Replicates	1	0.2374	0.2374	0.7045	0.0085	0.7496
Replicate:Date	1	0.2522	0.2522	0.7485	0.0091	0.7051

Replicate:Pond	3	1.0439	0.3480	1.0328	0.0375	0.4081
Date:Pond	3	1.1414	0.3805	1.1292	0.0410	0.2663
Replicate:Date:Pond	3	1.0710	0.3570	1.0595	0.0385	0.3707
Residuals	59	19.8789	0.3369		0.7147	
Total	74	27.8154			1	
B by Intrvl. (Temp)						
Interval	1	0.7742	0.7742	2.2316	0.0270	0.0155
Date	1	3.0311	3.0311	8.7374	0.1057	< 0.001
Replicates	1	0.2557	0.2557	0.7369	0.0089	0.6974
Replicate:Date	1	0.2399	0.2399	0.6914	0.0084	0.7567
Replicate: Interval	1	0.2895	0.2895	0.8346	0.0101	0.6088
Date: Interval	1	0.5076	0.5076	1.4631	0.0177	0.1281
Replicate:Date: Interval	1	0.3245	0.3245	0.9354	0.0113	0.4972
Residuals	67	23.2433	0.3469		0.8108	
Total	74	28.6657			1	

Table 3.4. Proportional distribution of macroinvertebrates by functional trait in all ponds sampled (All), permanent, and temporary ponds.

Trait Feature	Trait Category	Trait	All	Permanent	Temporary
Life History	Gen. per year	Multivoltine	83.01%	83.74%	80.06%
		Semivoltine	0.79%	0.40%	2.38%
		Univoltine	16.20%	15.87%	17.56%
	Emerge sync.	Poorly	25.04%	21.75%	45.06%
		Well	74.96%	78.25%	54.94%
	Emerge season	Fall	26.28%	26.15%	26.82%
		Winter	22.27%	22.49%	21.32%
		Spring	23.92%	23.98%	23.69%
		Summer	27.53%	27.38%	28.17%
Dispersal	Fem. dispersal	High	44.72%	38.02%	73.65%
		Low	55.28%	61.98%	26.35%
Ecology	Habit	Burrower	28.72%	29.55%	26.96%
		Climber	2.58%	1.68%	4.48%
		Clinger	3.42%	4.04%	2.13%
		Crawler	0%	0%	0%

		Planktonic	25.24%	13.32%	50.35%
		Skater	0.18%	0.24%	0.04%
		Sprawler	37.91%	50.11%	12.21%
		Swimmer	1.95%	1.06%	3.83%
	FFG	Filterer	10.59%	0.73%	32.50%
		Gatherer	70.10%	79.28%	49.70%
		Herbivore	0%	0%	0%
		Parasite	0%	0%	0%
		Predator	18.91%	19.64%	17.29%
		Shredder	0.40%	0.35%	0.51%
Morphology	Max body size	Small	88.09%	89.67%	82.04%
		Medium	9.53%	8.39%	13.91%
		Large	2.38%	1.95%	4.05%
	Respiration	Gills	34.96%	42.46%	5.26%
		Plastron, spiracle	2.25%	1.63%	4.68%
		Tegument	62.80%	55.91%	90.06%

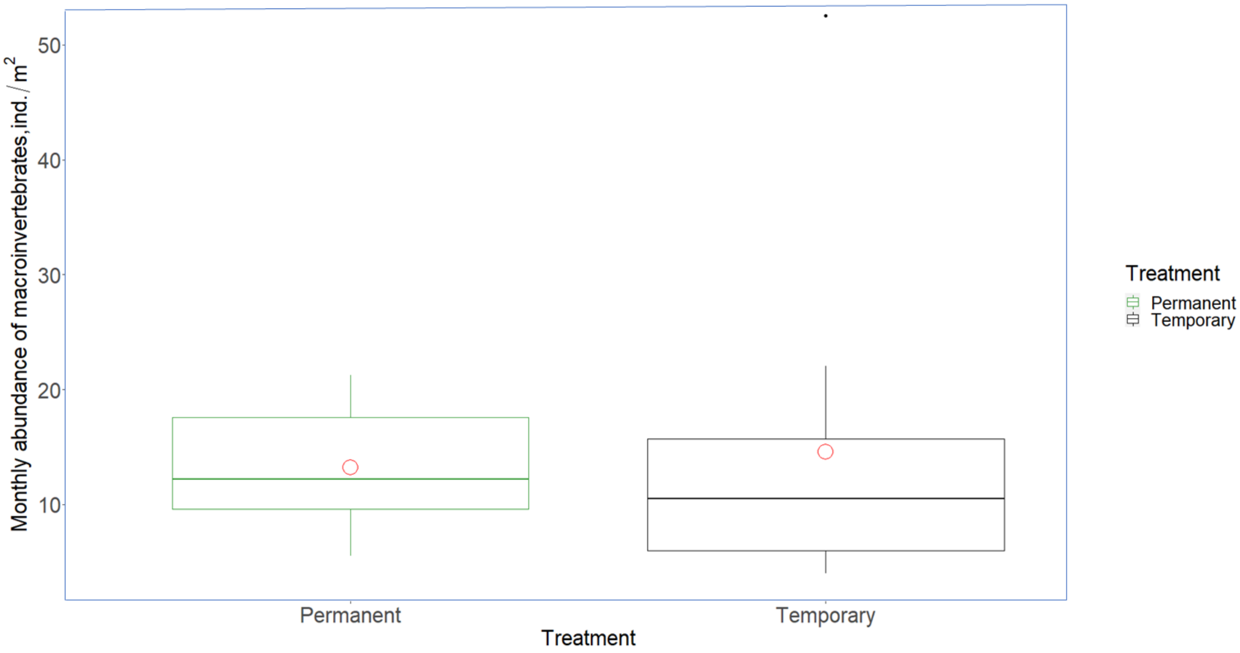

Figure 3.1. Mean-monthly abundance (ind./m^2 ± SE) of macroinvertebrates by treatments (permanent vs. temporary). The boxes represent the middle fifty percent of the data, dots outside of box plots represent outliers for each group, red circles show the mean and the line within the box represents the median.

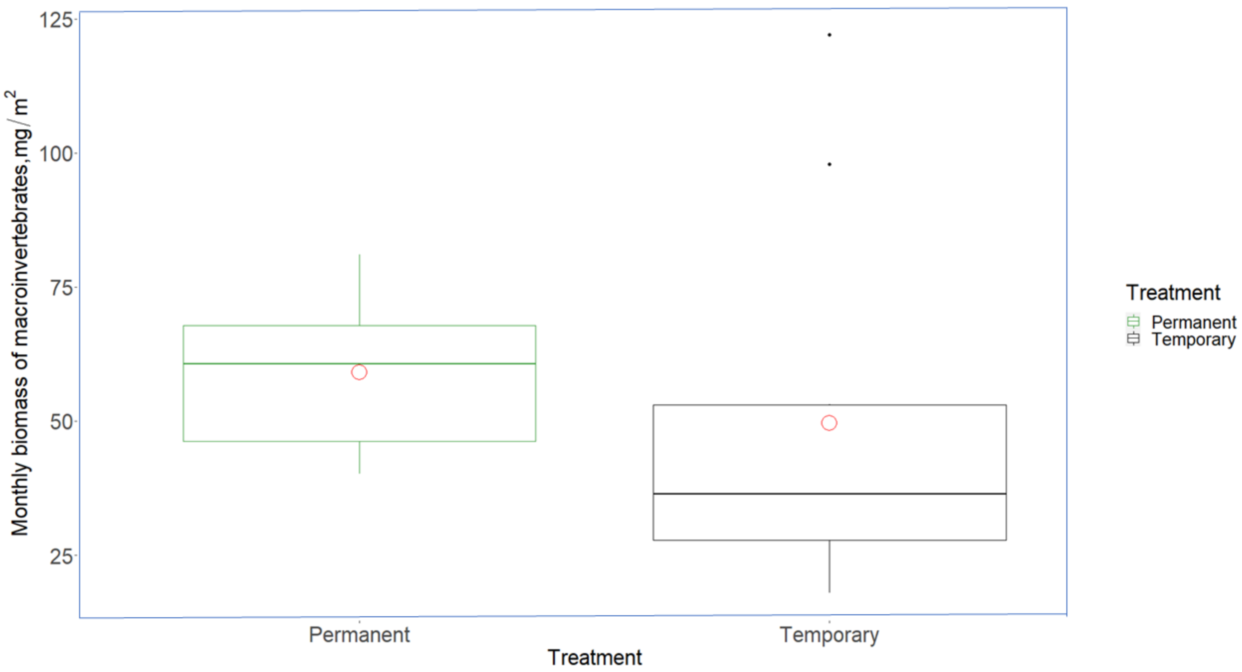

Figure 3.2: Mean-monthly biomass (mg/m^2 ± SE) of macroinvertebrates by treatments (permanent vs. temporary). The boxes represent the middle fifty percent of the data, dots outside of box plots represent outliers for each group, red circles show the mean and the line within the box represents the median.

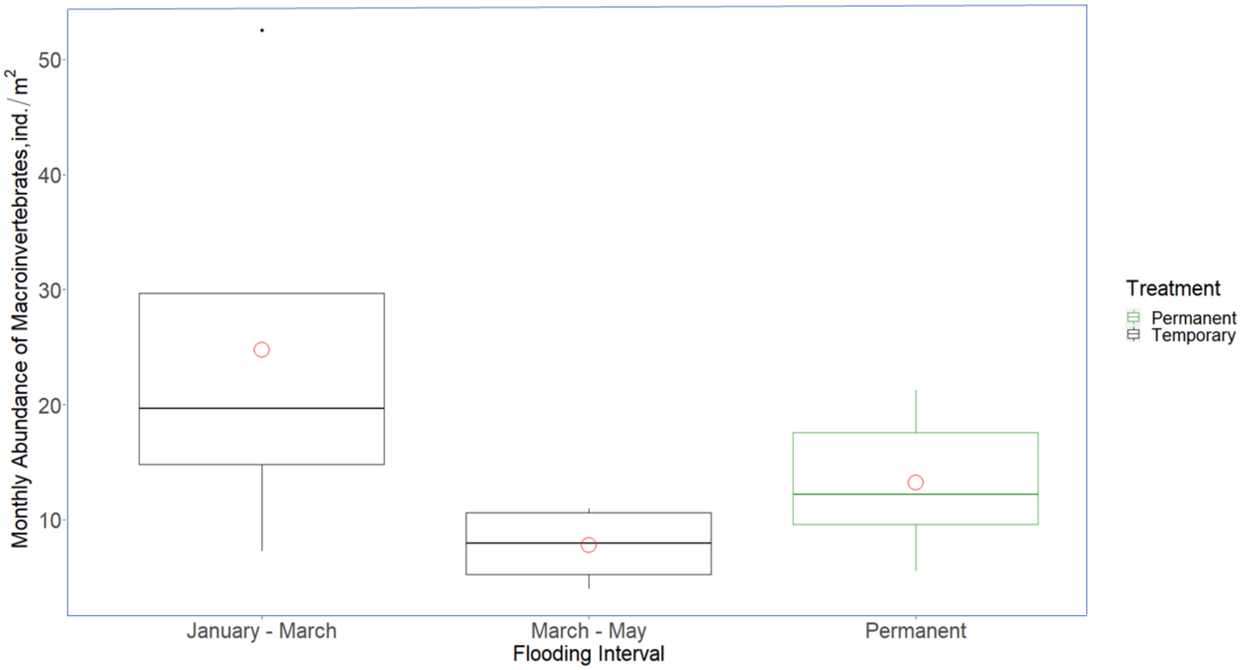

Figure 3.3: Mean-monthly abundance (ind/m^2 ± SE) of macroinvertebrates by flooding interval, including the two intervals of flooding and drying of temporary ponds (January – March 2019, March – May 2019). The boxes represent the middle fifty percent of the data, dots outside of box plots represent outliers for each group, red circles show the mean and the line within the box represents the median.

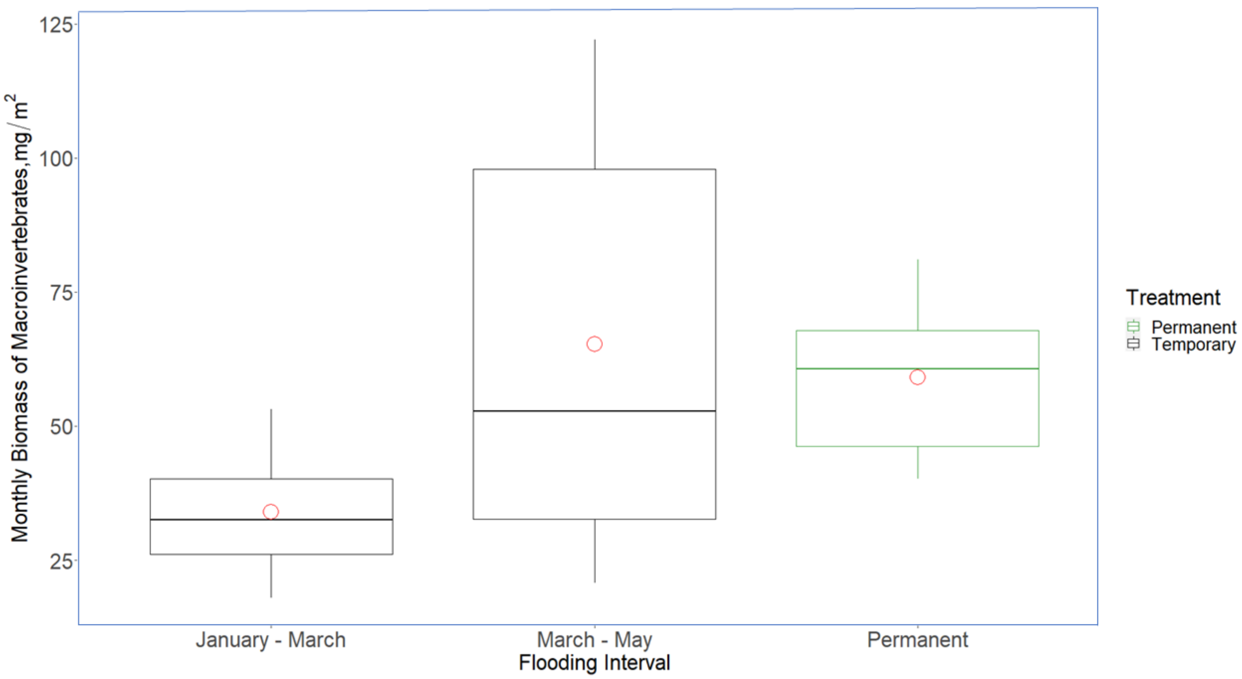

Figure 3.4: Mean-monthly biomass (mg/m^2 ± SE) of macroinvertebrates by flooding interval, including the two intervals of flooding and drying of temporary ponds (January – March 2019, March – May 2019). The boxes represent the middle fifty percent of the data, dots outside of box plots represent outliers for each group, red circles show the mean and the line within the box represents the median.

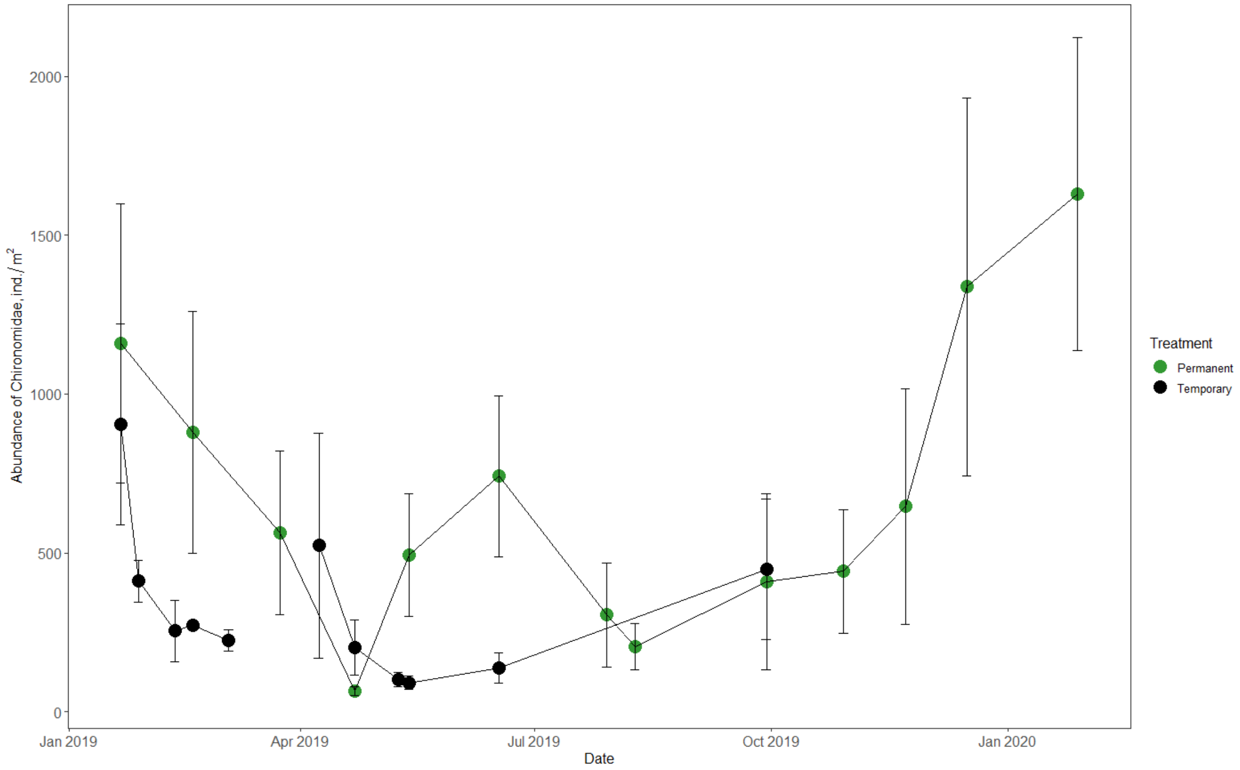

Figure 3.5: Mean-monthly abundance (ind/m^2 ± SE) of Chironomidae by treatments. *Only one temporary pond retained water beyond July and until September 2019.

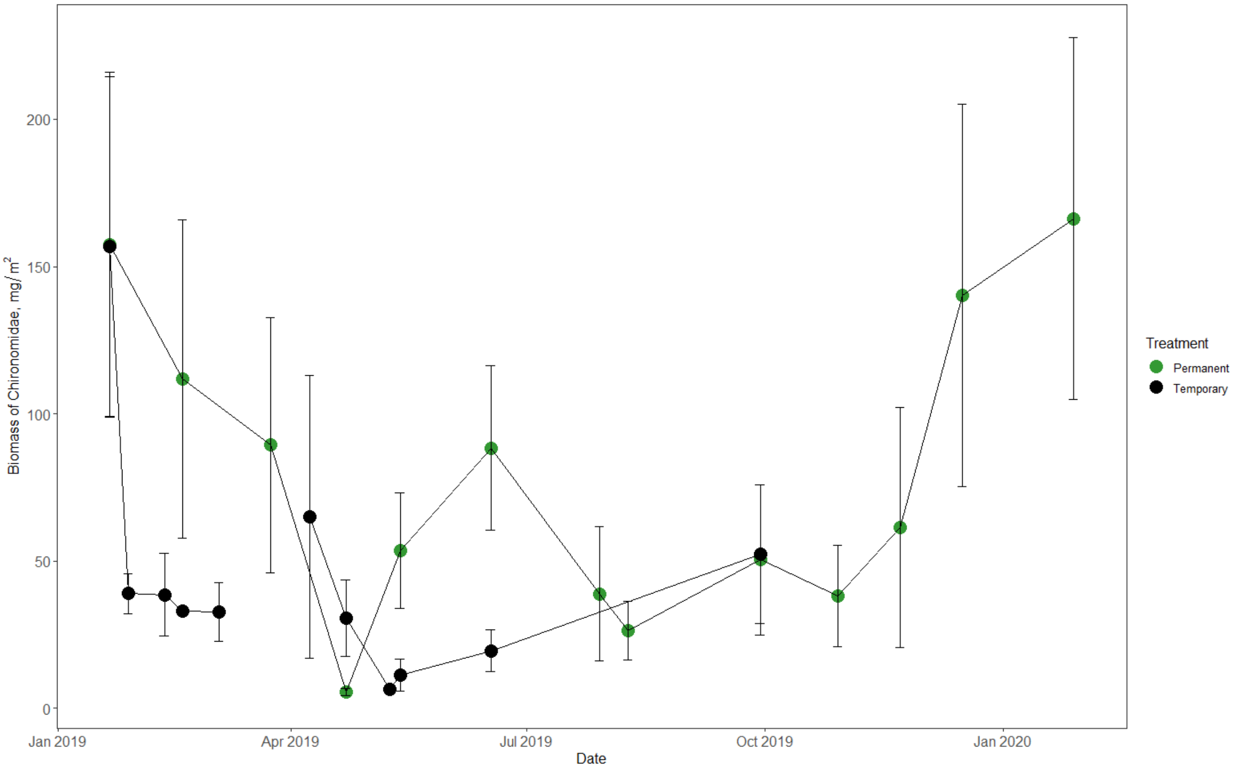

Figure 3.6: Mean-monthly biomass (mg/m2 ± SE) of Chironomidae by treatments. *Only one temporary pond retained water beyond July and until September 2019.

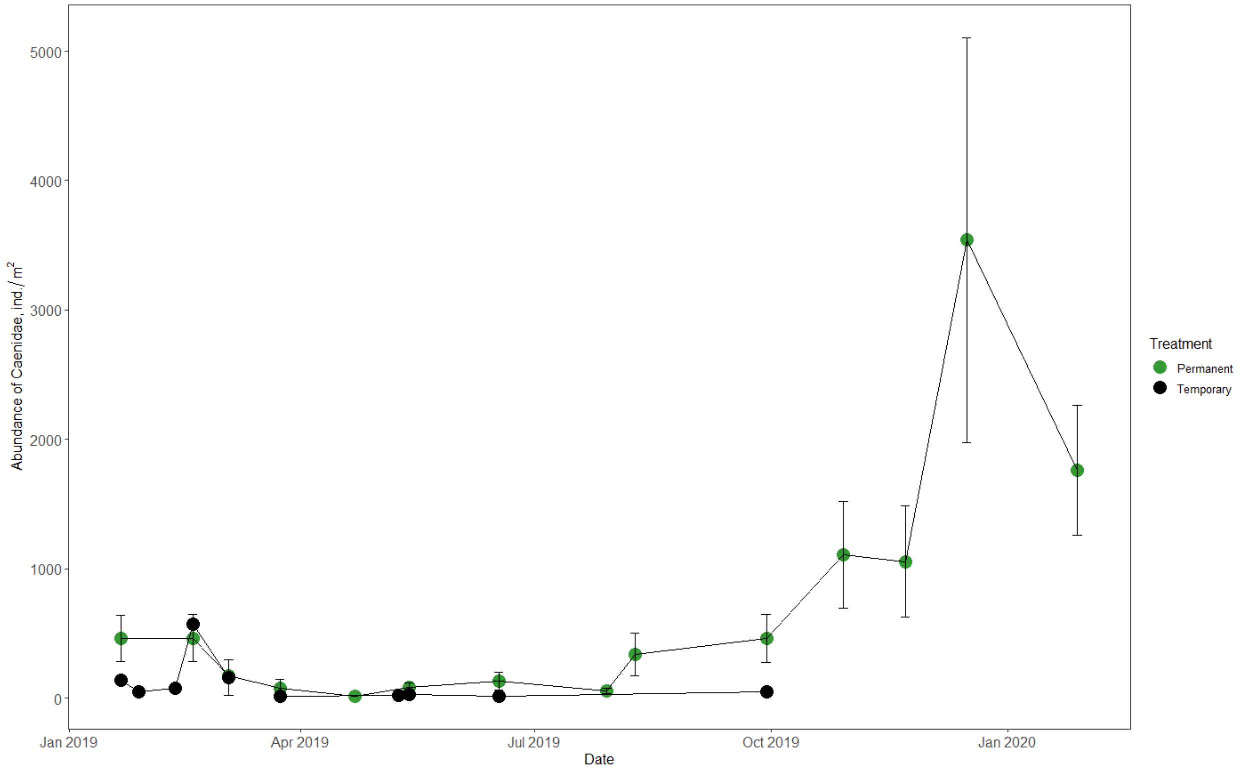

Figure 3.7: Mean-monthly abundance (ind/m^2 ± SE) of Caenidae by treatments. *Only one temporary pond retained water beyond July and until September 2019.

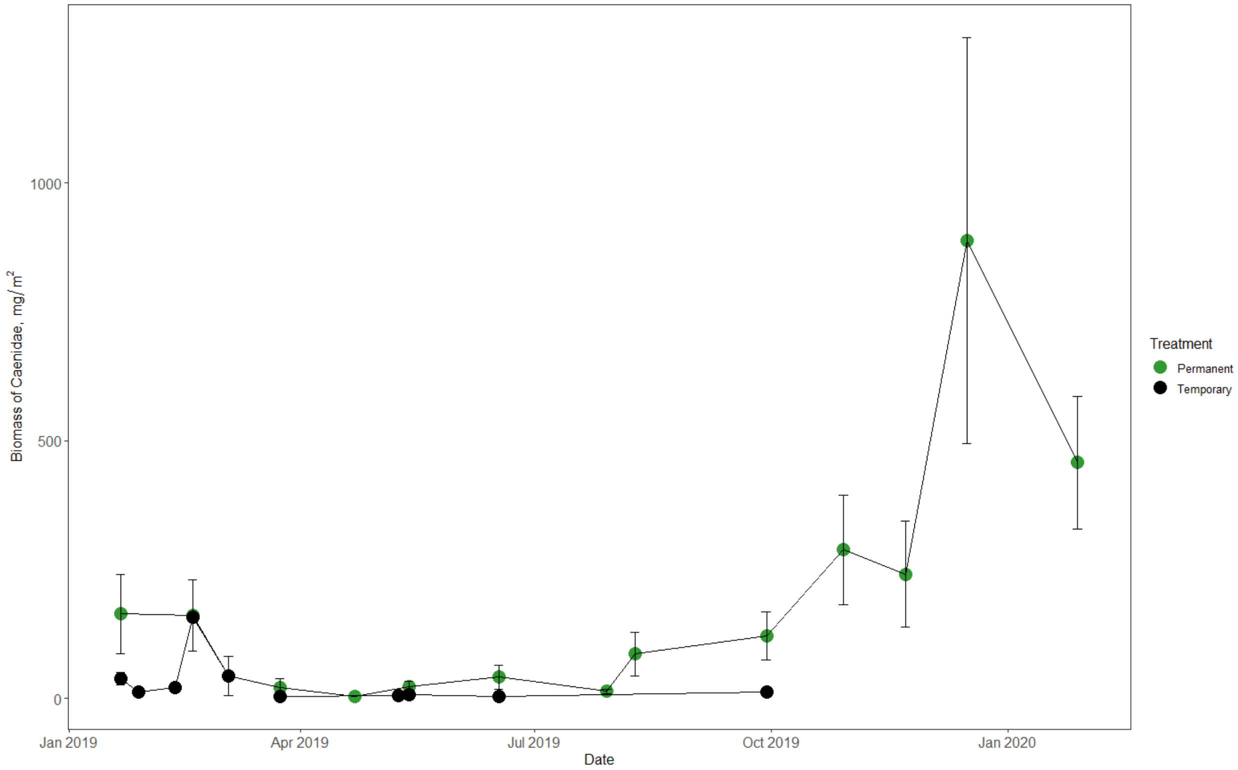

Figure 3.8: Mean-monthly biomass (mg/m^2 ± SE) of Caenidae by treatments (circles are permanent ponds and triangles are temporary ponds). *Only one temporary pond retained water beyond July and until September 2019.

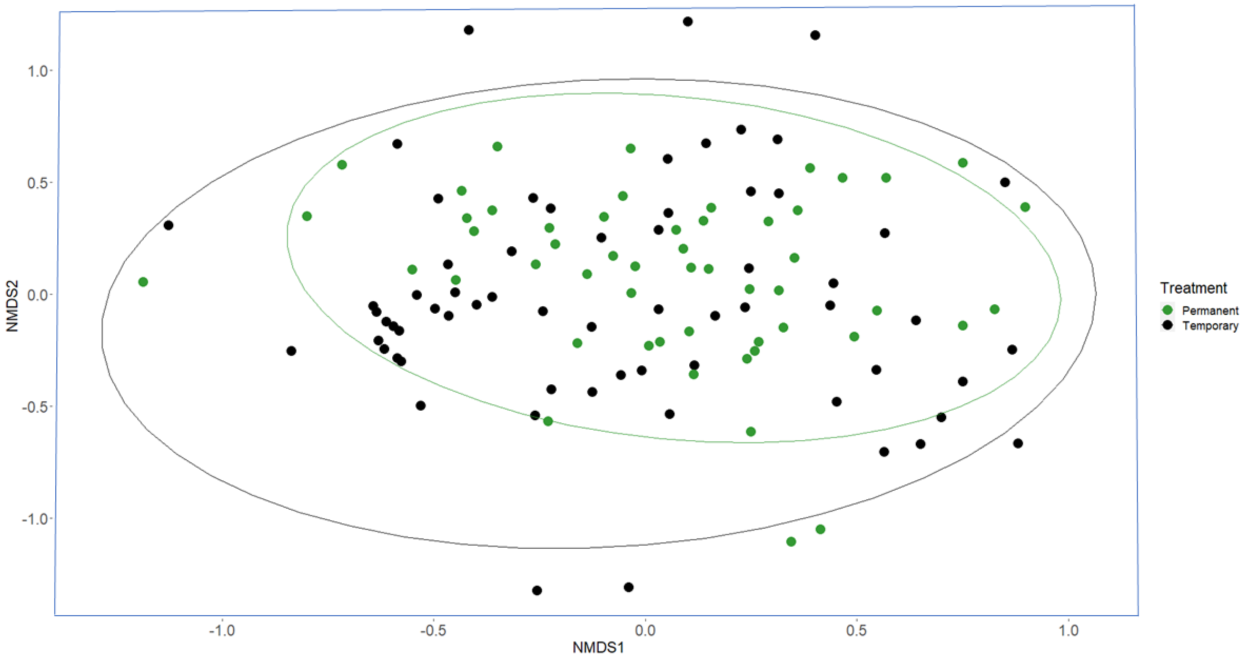

Figure 3.9: Two-dimensional NMDS ordination plot based on macroinvertebrate abundance (ind/m^2) by treatment (permanent vs. temporary). Different colored ellipses and symbols depict the macroinvertebrate composition clusters on different hydrological treatments. Stress = 0. 272.

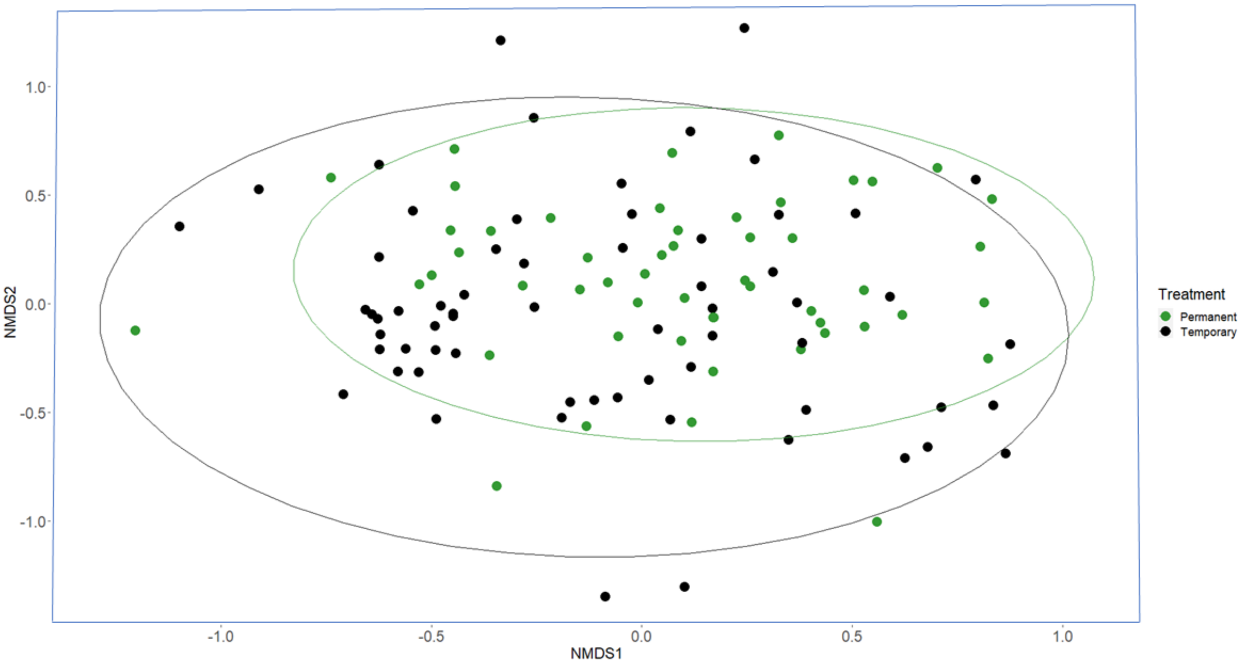

Figure 3.10: Two-dimensional NMDS ordination plot based on macroinvertebrate biomass (mg/m^2) by treatment (permanent vs. temporary). Different colored ellipses and symbols depict the macroinvertebrate composition clusters on different hydrological treatments. Stress = 0.273.

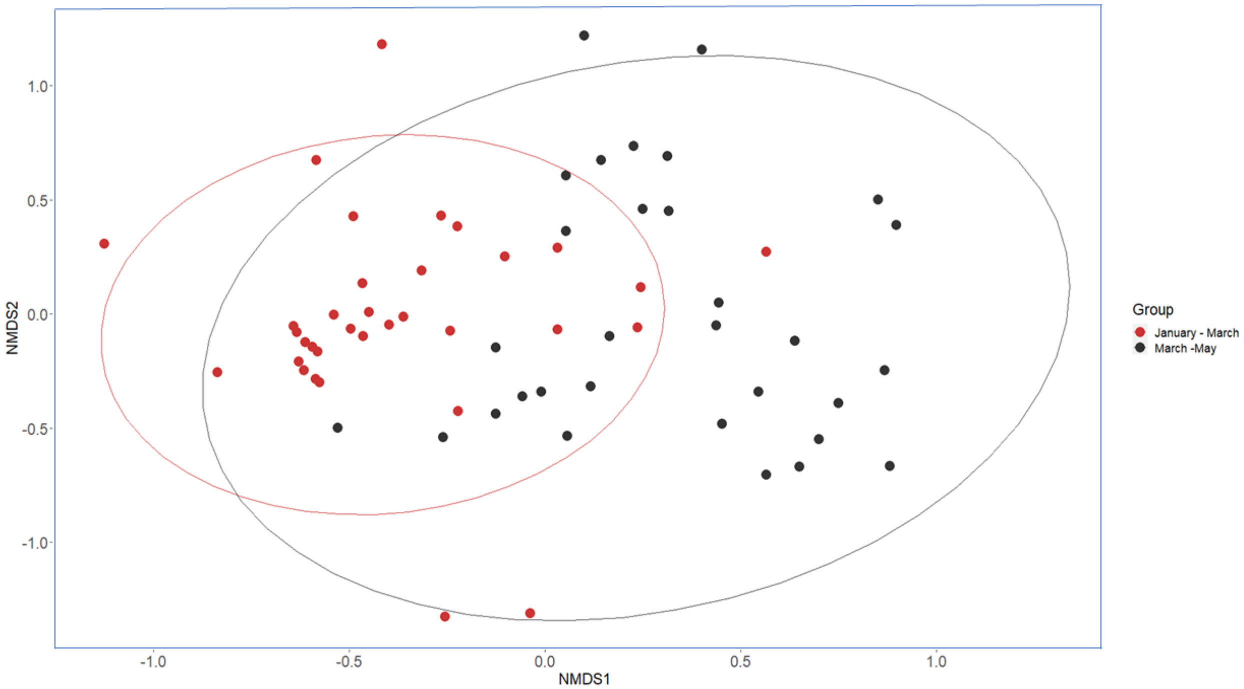

Figure 3.11: Two-dimensional NMDS ordination plot based on macroinvertebrate abundance (ind/m^2) within temporary by flooding interval, including the two intervals of flooding and drying of temporary ponds (January – March 2019, March – May 2019). Different colored ellipses and symbols depict the macroinvertebrate composition clusters on different hydrological treatments. Stress = 0.251.

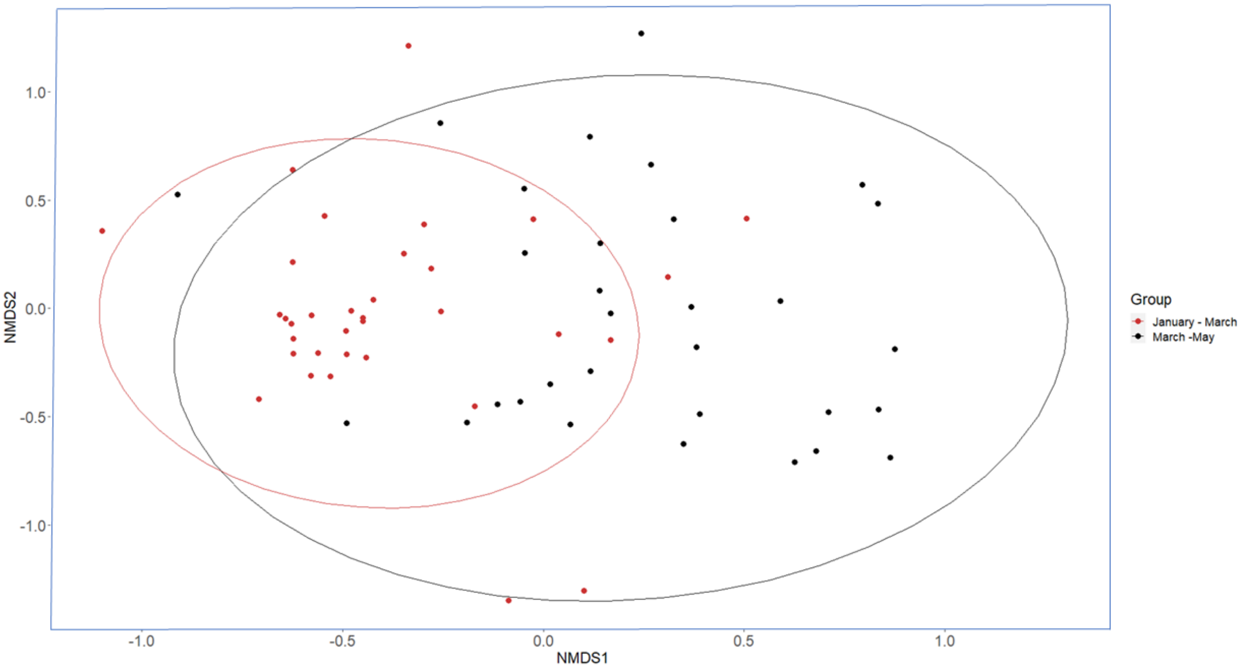

Figure 3.12: Two-dimensional NMDS ordination plot based on macroinvertebrate biomass (mg/m^2) within temporary by flooding interval, including the two intervals of flooding and drying of temporary ponds (January – March 2019, March – May 2019). Different colored ellipses and symbols depict the macroinvertebrate composition clusters on different hydrological treatments. Stress = 0.253.

CHAPTER 4

DISCUSSION

This study was conducted to assess the responses of aquatic macroinvertebrate communities to habitat instability through hydrological variation and how these potential changes might influence key ecosystem functions in wetlands of the southeastern US. Because the experimental design used a set of pre-established ponds (~10 months full prior to starting the experiment) and another group of fully dried ones with the capacity to experience flooding and drying, I was able to manipulate wetland conditions in a replicable study. This scenario allowed me to conduct an ecosystem-level study with replicable, controllable, and repeatable conditions without many of the pitfalls that come with conducting a study in a natural system (e.g., loss in ecological complexity due to scale limitations) (Ahn & Mitsch 2002).

The main findings of this study were that differences in macroinvertebrate communities between permanent and temporary ponds can be mostly explained by hydrology and the amount of time these were covered by water. I found differences in dominant taxa, species diversity as well as in behavioral and physiological traits between the two treatment groups. Since other studies had shown that permanent sites seem to have more taxa due to habitat stability, allowing poorly adapted taxa that would otherwise not have been able to survive in a more demanding environment to persist (Batzer et al. 2005). I expected to find more biomass and diversity of taxa within in ponds that retained water for a longer period of time, but I was surprised to see that the abundance of these macroinvertebrates did not show the same pattern was not significantly related to treatments.

Cañedo-Argüelles & Rieradevall (2011) conducted a study analyzing the successional patterns of aquatic macroinvertebrate within a newly created lake in Barcelona, Spain and saw a positive correlation between colonization sequence and dispersal capacity of taxa, while also seeing a successional pattern in which fast colonizing generalist taxons (e.g., Chironomidae and Physidae) were being replaced by more specialist ones as new habitats arose. This same scenario of early colonization by highly productive generalist (*r*-selected) which are replaced by longer lived and more competitive specialist (*K*-selected) taxa as the environment becomes more stable has been seen across a myriad of environments (Pianka 1970; Reznick et al. 2002; Chiu & Kuo 2012). I found that across both treatments many individuals were generalist collector-gatherers of small body size inhabiting fine-sediments, the open limnetic zone or vascular plants having multiple generations per year (multivoltine) and emerging in a highly synchronous manner at all times of the season.

When looking at divergent traits between treatments, it was interesting to find higher quantities of medium-larger sized individuals in temporary ponds than in permanent ones even though I expected that the more stable habitat would favor higher densities of larger taxa. While my study did not record non-invertebrate predators (i.e., amphibians, birds, fishes), anecdotal data of the ponds showed that permanent ponds had more complex food-webs that might be acting as a negative selection pressure on larger macroinvertebrates which was not seen in the more unstable environment of temporary ponds. Another interesting scenario was seen in respiration traits across treatments. I did not find any major differences in temperature or dissolved oxygen concentrations across treatments, seeing that almost all the individuals in temporary ponds depend on obtaining atmospheric oxygen via their teguments compared to an almost equal likelihood of respiration occurring via gills or tegument in permanent ones, seems to suggest that in fact there are differences in water quality between these treatments that I was not able to show.

By dividing up the temporary treatment into the into the two intervals of flooding and drying, I saw how the communities of these temporary ponds shifted and adapted to the disturbance pressures imposed by hydrological and temporal changes (Lake 2000). The repeated manipulations (i.e., flooding and drying) also demonstrate that even with habitat variation and disturbance frequency, macroinvertebrate assemblages in these wetlands are subset groups deriving from a larger source population in a higher quality environment (Pulliam 1988). This was interesting to see because it suggests that the amount of days these ponds retain water and the time of year in which these flooding events occur can have major impacts on the natural succession of resettlement that temporary wetlands might take once conditions are met for the migration of “cyclic colonizers” from the local source population into the sink habitat dominated by egg-laying “fugitive” taxa (e.g., *Daphnia* and *Gammarus*) (Wissinger 1997). With wetlands battling a constant flux of disturbances derived by hydrological and temporal stages shaping ecological and physiochemical variables, predicted intensification of drier and wetter summer months within this century (Anandhi & Bentley 2018) could prove detrimental to the intricate balance in wetlands sustaining source populations.

Recognizing that this work might not fully explain the variations seen across treatments, this study does provide supplemental data necessary to further understand what communities of aquatic macroinvertebrates are supported by different conditions (i.e., potential disturbances), as well as what ecosystem functions will be the most impacted by these changes along the wetlands of the southeastern Coastal Plain. Furthermore, these baseline datasets prove that ‘re-furbished’ sites (e.g., fish farms, hatcheries, etc.) could help mitigate wetland losses. Finally, the continuation of this study will prove beneficial as a long-term repository of knowledge in assessing the macroinvertebrate communities and associated functions necessary to understand the ecosystem responses to disturbances brought by a changing climate.

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APPENDIX A

MACROINVERTEBRATES BY TREATMENT

Macroinvertebrate richness (S), abundance (N; ind./m^2), and biomass (B; mg/m^2) by pond (P#), treatment (P =Permanent, T =Temporary) and days since each pond was last inundated (Flooded).

Pond	Treatment	Date	Flooded	S	N	B
P1	T	1/21/2019	20	6	46.50	32.57
	T	1/28/2019	27	4	27.00	9.11
	T	2/11/2019	41	5	26.89	23.29
	T	3/24/2019	6	2	6.00	32.58
	T	4/1/2019	14	1	22.00	43.95
	T	4/8/2019	21	1	1.00	1.94
	T	4/22/2019	35	1	1.00	35.78
	T	5/9/2019	52	6	4.70	47.85
	T	5/13/2019	56	6	3.38	18.14
P2	P	1/21/2019	313	4	18.25	33.21
	P	2/18/2019	341	10	19.07	62.23
	P	3/24/2019	375	7	3.00	30.90

	P	4/22/2019	404	9	6.00	53.64
	P	5/13/2019	426	9	4.19	36.05
	P	6/17/2019	461	14	10.77	23.20
	P	7/29/2019	503	12	8.23	37.25
	P	8/9/2019	514	10	1.94	26.93
	P	9/29/2019	565	5	4.36	57.05
	P	10/29/2019	595	9	17.75	67.98
	P	11/22/2019	619	9	21.18	53.04
	P	12/16/2019	643	6	9.22	17.69
	P	1/28/2020	686	8	34.42	98.15
P3	T	1/21/2019	20	6	116.18	105.37
	T	1/28/2019	27	8	35.18	32.97
	T	2/11/2019	41	4	24.25	7.22
	T	4/1/2019	14	1	12.33	21.14
	T	4/22/2019	35	1	7.00	32.54
	T	5/9/2019	52	8	5.27	110.97
	T	5/13/2019	56	5	2.83	51.22
P4	P	1/21/2019	313	6	14.91	53.51

	P	2/18/2019	341	5	14.60	85.87
	P	3/24/2019	375	9	2.75	7.35
	P	4/22/2019	404	4	7.22	85.30
	P	5/13/2019	426	6	9.63	66.26
	P	6/17/2019	461	5	3.64	16.80
P5	T	1/21/2019	20	11	27.00	53.00
	T	1/28/2019	27	5	8.00	75.09
	T	2/11/2019	41	9	9.91	26.99
	T	3/24/2019	6	4	1.00	21.28
	T	4/1/2019	14	5	6.00	16.90
	T	4/8/2019	21	3	2.33	10.69
	T	4/22/2019	35	5	4.67	8.01
	T	5/9/2019	52	4	4.20	165.04
	T	5/13/2019	56	7	10.06	54.58
	T	9/29/2019	188	13	12.75	171.34
P7	P	1/21/2019	313	11	14.37	64.79
	P	2/18/2019	341	8	27.00	77.44
	P	3/4/2019	355	4	12.25	68.23

	P	3/24/2019	375	10	8.53	54.96
	P	4/22/2019	404	5	5.33	13.07
	P	5/13/2019	426	9	26.00	84.84
	P	6/17/2019	461	7	24.23	55.97
	P	7/29/2019	503	7	5.77	15.42
	P	8/9/2019	514	11	11.10	116.33
	P	9/29/2019	565	8	18.80	58.07
	P	10/29/2019	595	5	17.43	70.40
	P	11/22/2019	619	5	13.44	39.37
	P	12/16/2019	643	8	116.71	419.20
	P	1/28/2020	686	6	77.33	217.82
P10	P	1/21/2019	313	11	29.84	115.72
	P	2/18/2019	341	5	24.38	98.42
	P	3/24/2019	375	8	20.70	67.60
	P	4/22/2019	404	5	3.50	22.15
	P	5/13/2019	426	7	8.64	30.55
	P	6/17/2019	461	6	15.50	39.74
	P	7/29/2019	503	6	4.00	8.46

	P	8/9/2019	514	10	8.88	38.71
	P	9/29/2019	565	6	12.91	74.82
	P	10/29/2019	595	8	34.46	243.85
	P	11/22/2019	619	7	25.09	98.69
	P	12/16/2019	643	4	25.22	51.73
	P	1/28/2020	686	7	23.46	129.25
P11	T	1/21/2019	20	3	20.50	21.53
	T	1/28/2019	27	4	18.00	13.13
	T	2/11/2019	41	7	8.09	46.95
	T	3/4/2019	62	8	7.26	40.19
	T	3/24/2019	6	1	5.00	0.02
	T	4/1/2019	14	1	1.00	1.23
	T	4/8/2019	21	7	29.63	145.72
	T	4/22/2019	35	8	9.50	54.38
	T	5/9/2019	52	11	6.40	67.83
	T	5/13/2019	56	8	26.67	364.41

APPENDIX B

SIMPER RESULTS FOR ABUNDANCES BY TREATMENT

SIMPER results for abundance by treatment showing average dissimilarities by taxa with an 80% cumulative contribution cutoff. Mean individuals per meter^2 by taxa included for each flooding interval.

Taxon	Av. Dissimilarity	Contribution %	Cumulative %	Mean Permanent	Mean Temporary
Chironomidae	24.24%	19.68%	28.41%	27.56	19.81
Ceratopogonidae	14.99%	18.76%	45.98%	14.98	2.73
Daphnidae	13.02%	19.82%	61.24%	3.28	26.73
Caenidae	7.92%	13.52%	70.53%	9.78	0.75
Physidae	6.80%	14.92%	78.50%	1.57	6.19
Gammaridae	4.65%	9.15%	83.95%	1.39	7.71

APPENDIX C

SIMPER RESULTS FOR BIOMASS BY TREATMENT

SIMPER results for biomass by treatment showing average dissimilarities by taxa with an 80% cumulative contribution cutoff. Mean grams per meter^2 by taxa included for each treatment.

Taxon	Av. Dissimilarity	Contribution %	Cumulative %	Mean Permanent	Mean Temporary
Hydrophilidae	21.39%	28.79%	24.36%	52.03	93.34
Chironomidae	18.26%	20.23%	45.16%	58.27	47.29
Ceratopogonidae	14.63%	20.28%	61.83%	52.73	9.28
Caenidae	10.62%	18.76%	73.92%	50.63	2.92
Elmidae	4.78%	12.86%	79.37%	11.38	19.54
Coenagrionidae	4.06%	12.22%	83.99%	9.94	8.00

APPENDIX D

SIMPER RESULTS FOR ABUNDANCES BY FLOODING INTERVAL

SIMPER results for abundance by flooding interval showing average dissimilarities by taxa with an 80% cumulative contribution cutoff. Mean individuals per meter^2 by taxa included for each flooding interval.

Taxon	Av. Dissimilarity	Contribution %	Cumulative %	Mean January - March	Mean March - September
Daphnidae	25.05%	24.40%	28.53%	52.78	1.37
Chironomidae	23.62%	19.37%	55.44%	30.08	9.82
Physidae	10.03%	18.38%	66.86%	2.81	9.47
Gammaridae	8.40%	12.70%	76.42%	15.43	0.18
Ceratopogonidae	5.59%	10.76%	82.78%	1.30	4.13

APPENDIX E

SIMPER RESULTS FOR BIOMASS BY FLOODING INTERVAL

SIMPER results for biomass by flooding interval showing average dissimilarities by taxa with an 80% cumulative contribution cutoff. Mean grams per meter^2 by taxa included for each flooding interval.

Taxon	Av. Dissimilarity	Contribution %	Cumulative %	Mean January - March	Mean March - September
Hydrophilidae	28.47%	32.83%	32.21%	9.61	174.90
Chironomidae	24.64%	26.38%	60.08%	75.01	20.31
Elmidae	7.98%	18.80%	69.10%	10.73	28.11
Ceratopogonidae	6.21%	13.86%	76.12%	3.42	14.99
Coenagrionidae	5.29%	13.47%	82.11%	12.48	3.63

APPENDIX F

FUNCTIONAL TRAIT BY TAXONS

Mean monthly total macroinvertebrate abundance (N; ind./m^2), and biomass (B; mg/m^2) from permanent (Perm) and temporary (Temp) by taxon and functional trait.

Family	Taxa	Habit	FFG	Generations per year	Max body size	Female dispersal/adult flying
Belotomastidae	Belostoma	Climbers, Swimmer	Predator	Univoltine	Large	High
Caenidae	Caenis	Sprawler	Collector/Gatherer	Multivoltine	Small	Low
Ceratopogonidae	Atrichopogon	Sprawler, Clinger	Predator, Collector/Gatherer	Multivoltine	Small	Low
	Culicoides	Burrower, Planktonic	Predator, Collector/Gatherer	Univoltine	Small	Low
Chironomidae	Chironominae	Burrower	Collector/Gatherer	Multivoltine	Small, Medium	High
	Tanypodinae	Sprawler	Predator, Collector/Gatherer	Multivoltine	Small	
Coenagrionidae	Argia	Clinger, Sprawler	Predator	Univoltine	Large	Low
	Enallagma	Climber, Swimmer	Predator	Univoltine	Large	Low
Corduliidae	Epitheca	Clinger, Sprawler	Predator	Semivoltine	Large	High
Corixidae	Hesperocorixa	Climber, Swimmer	Piercer	Multivoltine	Small, Medium	High
Crambidae	Parapoynx	Climber	Shredder	Univoltine	Large	Low
Culicidae	Psorophora	Swimmer	Filterer	Multivoltine	Small	High
Daphnidae	Daphnia	Planktonic	Filterer			
Elmidae	Microcylloepus	Climber, Clinger	Collector/Gatherer	Semivoltine	Small	High
Empididae	Hemerodromia	Sprawler, Burrower	Predator, Collector/Gatherer	Multivoltine	Medium	Low
Gammaridae	Gammarus	Planktonic	Gatherer			
Gerridae	Gerridae	Skater	Predator	Multivoltine	Large	Low
Haliplidae	Peltodytes	Climber, Swimmer	Piercer, Shredder	Multivoltine	Small	Low
Hydrachnidiae	Hydrachnidiae					
Hydrophilidae	Berosus	Climber, Swimmer	Piercer	Univoltine	Small	Low
	Tropisternus	Climber, Swimmer	Piercer	Multivoltine	Medium	High
Hydroptilidae	Neotrichia	Clinger	Scraper	Univoltine	Small	High
Hydropsychidae	Hydropsyche	Clinger, Sprawler	Filterer	Univoltine	Medium	High
Isonychiidae	Isonychia	Clinger, Sprawler	Filterer	Multivoltine	Medium	Low
Leptoceridae	Triaenodes	Swimmer	Shredder	Univoltine	Medium	High
Macromiidae	Macromia	Sprawler	Predator	Semivoltine	Large	High
Naucoridae	Pelocoris	Climber, Crawler	Predator	Univoltine	Small, Medium	Low
Notonectidae	Notonecta	Climber, Swimmer	Predator	Multivoltine	Medium	High
Physidae	Physa		Scraper			
Tabanidae	Tabanus	Sprawler	Predator	Univoltine	Large	High
Tipulidae	Tipula	Burrower	Shredder	Univoltine	Medium, Large	Low
Veliidae	Microvelia	Skater	Predator	Multivoltine	Small	Low

Family	Taxa	Emergence synchrony	Thermal Preference	Emerge Season	Respiration	Perm-B	Temp-B	Perm-N	Temp-N
Belotomastidae	Belostoma	Well	Warm eurythermal (15-30 C)	Spring, Summer, Fall	Plastron-spiracle	158.64	0	46.15	0
Caenidae	Caenis	Well	Cool-warm eurythermal (5-30 C)	Fall, Winter, Spring, Summer	Gills	18421.57	560.62	65461.54	1446.15
Ceratopogonidae	Atrichopogon	Poorly	Warm eurythermal (15-30 C)	Spring, Summer	Tegument	26.32	13.35	2061.54	984.62
	Culicoides	Poorly	Warm eurythermal (15-30 C)	Summer, Fall	Tegument	302.8	81.16	18092.31	4092.31
Chironomidae	Chironominae		Cool-warm eurythermal (5-30 C)	Fall, Winter, Spring, Summer	Tegument	380.94	166.05	48246.15	21030.77
	Tanypodinae	Well	Cool-warm eurythermal (5-30 C)	Fall, Winter, Spring, Summer	Tegument	158.16	71.25	12430.77	5600
Coenagrionidae	Argia	Well	Warm eurythermal (15-30 C)	Fall/Spring	Tegument, Gills	25.05	5.01	230.77	46.15
	Enallagma	Well	Hot euthermal (>30 C)	Spring, Summer, Fall	Tegument	50.1	26.72	461.54	246.15
Corduliidae	Epitheca	Well	Cool-warm eurythermal (5-30 C)	Spring, Summer, Fall	Gills	4440.06	3114.8	230.77	276.92
Corixidae	Hesperocorixa	Well	Warm eurythermal (15-30 C)	Summer, Fall	Plastron-spiracle	142.89	105.64	46.15	15.38
Crambidae	Parapoynx	Well	Warm eurythermal (15-30 C)			35.15	0	0	15.38
Culicidae	Psorophora	Well	Warm eurythermal (15-30 C)	Spring, Fall	Plastron-spiracle	1.82	1.67	46.15	523.08
Daphnidae	Daphnia					10.28	12.11	1292.31	27061.54
Elmidae	Microcylloepus	Poorly	Warm eurythermal (15-30 C)	Summer	Tegument	2199.32	1531.35	307.69	584.62
Empididae	Hemerodromia	Well	Warm eurythermal (15-30 C)		Tegument	35.68	0	323.08	0
Gammaridae	Gammarus					195.43	176.14	2707.69	8446.15
Gerridae	Gerridae	Well	Warm eurythermal (15-30 C)	Spring, Summer, Fall	Plastron-spiracle	264.64	17.55	323.08	30.77
Haliplidae	Peltodytes	Well	Warm eurythermal (15-30 C)	Spring, Summer	Tegument	55.85	38.43	138.46	246.15
Hydrachnidiae	Hydrachnidiae					0.49	0.02	7200	292.31
Hydrophilidae	Berosus	Well	Cool-warm eurythermal (5-30 C)	Summer, Fall	Tegument	1541.38	2433.36	415.38	1046.15
	Tropisternus	Poorly	Cool-warm eurythermal (5-30 C)	Summer, Fall	Tegument	1883.91	2111.3	507.69	907.69
Hydroptilidae	Neotrichia	Well	Cool-warm eurythermal (5-30 C)	Spring, Summer	Tegument	40.75	1.23	3384.62	107.69
Hydropsychidae	Hydropsyche	Well	Cool-warm eurythermal (5-30 C)	Spring, Summer, Fall	Gills	0.22	0	46.15	0
Isonychiidae	Isonychia	Poorly	Cool-warm eurythermal (5-30 C)	Spring, Summer	Gills	1694.16	456.11	738.46	261.54
Leptoceridae	Triaenodes	Well	Cool-warm eurythermal (5-30 C)	Summer	Gills	6.44	0	92.31	0
Macromiidae	Macromia	Well	Cool-warm eurythermal (5-30 C)	Spring, Summer, Fall	Gills	157.63	63.55	76.92	61.54
Naucoridae	Pelocoris	Poorly	Warm eurythermal (15-30 C)	Spring	Plastron-spiracle	1.53	0.96	123.08	169.23
Notonectidae	Notonecta		Warm eurythermal (15-30 C)		Plastron-spiracle	9.04	9.04	0	30.77
Physidae	Physa					890.25	538.9	3184.62	7307.69
Tabanidae	Tabanus	Poorly	Warm eurythermal (15-30 C)		Plastron-spiracle, Tegument	12.32	4.8	1476.92	923.08
Tipulidae	Tipula	Poorly	Cool-warm eurythermal (5-30 C)	Spring, Summer	Plastron-spiracle	759.41	237.77	430.77	169.23
Veliidae	Microvelia								