RESPONSE OF AQUATIC MICROINVERTEBRATES WITHIN ISOLATED TALLGRASS PRAIRIE STREAM POOLS TO EXPERIMENTAL DRYING

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The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science.

Thomas Luhring, Committee Chair

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Andrew Swindle, Committee Member

DEDICATION

To Dr. Donald Distler.

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ABSTRACT

Intermittent streams experience varying drying and rewetting cycles that influence the organisms that are able utilize these systems. These disturbance regimes are expected to be greatly impacted by climate change and other anthropogenic impacts. Aquatic microinvertebrates have unique abilities to resist dying in dormant states that allow for emergence once rehydrated and can aid in the re-establishment of aquatic food webs after drying disturbance. To explore the response of microinverterabtes to drying, an experimental microcosm study was conducted to test the hypotheses: (1) aquatic microinvertebrate abundance will be lower after drying compared to those that remain filled, and (2) aquatic microinvertebrate abundance will be lower after a longer drying duration when compared to a shorter drying duration. Specifically, different microinvertebrate groups with differing resistant traits and strategies to survive drying will be assessed. Ten isolated intermittent stream pools were sampled from Youngmeyer Ranch, Elk County, Kansas in August of 2020. Three microcosms per pool were collected and randomly assigned one of three treatments (control, two-week drying period, or four-week drying period). Microcosms were then sampled three times a week with individual microinvertebrates identified and counted. We found support for our hypotheses and observed the potential for most taxa groups included to emerge after drying. Our findings indicate a dynamic response to drying durations. With increased awareness of the potential impacts to this endangered ecosystem, understanding how aquatic organisms cope with changes in disturbance regimes is critical to their protection.

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CHAPTER 1

INTRODUCTION

Non-perennial streams make up 59% of watercourses within the United States (Goodrich et al. 2018, Busch et al. 2020). Tallgrass prairie streams are complex systems, with perennial and non-perennial streams, but many headwaters are classified as intermittent (Dodds et al. 2004). With approximately 5% of remnant tallgrass prairies remaining, their stream systems are considered endangered ecosystems (Larson et al. 2013). Common traits of these streams include having good water quality, heterotrophic conditions, and important habitat for maintaining populations of some sensitive species (Larson et al. 2013). These systems are subject to variable drying and rewetting cycles, and the aquatic organisms that utilize these habitats must be adapted to their harsh conditions (Bertrand et al. 2013, Leigh et al. 2015, Busch et al. 2020).

1.1 Background

Historically, stream ecologists have focused their studies on perennial systems (Larned et al. 2010, Leigh et al. 2015, Busch et al. 2020). With increased interest in understanding the role of non-perennial streams, a greater importance has been placed on correctly classifying and characterizing these stream types across disciplines to better inform policy makers (Leigh et al. 2015, Busch et al. 2020). Perennial streams have larger channels, more constant water flow and a riparian canopy cover. In general, non-perennial streams are smaller, consisting of headwaters that periodically dry producing isolated pools. Non-perennial systems are further classified as intermittent or ephemeral, differing in respect to long term flow patterns. Intermittent streams hold water during wet portions of the year, continue to gain water, and can have

considerable groundwater inputs. Ephemeral streams are greatly influenced by precipitation inputs, with their channels formed and only holding water immediately after rain events (Busch et al. 2020). These classifications can also exist along the length of an individual stream reach, with perennial headwaters draining into an intermittent middle reach, before connecting back to a more permanent perennial flow (Bertrand et al. 2013).

Aquatic invertebrates are a major contributor to the biological diversity and trophic complexity of tallgrass prairie streams (Datry et al. 2014, Hay et al. 2018). These invertebrates are commonly classified into two main groups, macroinvertebrates that are large enough to be visible to the naked eye, and microinvertebrates, or meiofauna, that are small and only identified by microscopic observation (Stubbington et al. 2020). Macroinvertebrates common to tallgrass prairie streams include molluscs, crustaceans, and the larval and adult stages of aquatic insects. Of all stream invertebrates, insects are one of the most well-studied due to their high abundance and diversity (Thorp and Covich 2010). Expected microinvertebrates include nematodes (Nematoda), microturbellarians (Platyhelminthes), oligochaetes (Annelida), rotifers (Rotifera), and microcrustaceans (Crustacea: Ostracoda, Branchiopoda, Copepoda).

Aquatic invertebrates play a central role within the trophic structure of streams. Many consume primary producers and detritus, eventually becoming prey for larger bodied taxa including aquatic insects, crayfish, and fishes (Bertrand et al. 2013). Others are filter-feeders, whose feeding strategy benefits aquatic systems through water clarification. They also provide transfer of materials between aquatic and terrestrial systems (Stubbington et al. 2020). Aquatic invertebrates have developed complex life

history strategies to survive within the variable nature of these intermittent streams and are crucial to their ecological functioning.

Within intermittent streams, physical factors have been shown to be more important in structuring invertebrate assemblages than biological factors (Bertrand et al. 2013). Generally, streams with increased channel width, water permanency, and connectivity offer increased habitat types and more predictable conditions that allows for increased invertebrate abundance and diversity. These generalizations have been shown to hold true even within an initially perennial headwater stream that shifted to an intermittent middle reach (Whiting et al. 2011). Although, this consensus is not concrete evidence that this holds true for all tallgrass prairie streams or all invertebrate taxa. Some studies have shown that intermittent reaches can have higher invertebrate abundance of certain taxa when compared to nearby perennial reaches (Flinders and Magoulick 2003, Dodds et al. 2004).

The length of the hydroperiod, the duration of surface water, of stream pools can determine the composition of aquatic invertebrate communities (Rolls et al. 2018). Hydroperiod is expected to be a function of pool volume and depth, as pool size increases, so does the potential to hold water over time. Streams with high water permanency are expected have higher invertebrate abundance and diversity (Dodds et al. 2004). A decrease in pool hydroperiod and volume would limit the amount of available space and resources, increasing interactions like predation and competition (Majdi et al. 2020). Most studies of stream invertebrates sample shallow riffles rather than pool habitats (Stagliano and Whiles 2002). Within intermittent streams, large numbers of pools, with and without flow, can become important refuge for aquatic

organisms. Studies that incorporate the collection of aquatic invertebrates within stream pools may provide a more realistic component of their distribution within intermittent streams that have limited connectivity.

Climate change and other anthropogenic impacts threaten to alter the natural disturbance regimes of all aquatic ecosystems (Hay et al. 2018). There is an expectation that the number of perennial streams reclassified as intermittent will increase in the future as they experience higher rates of drying, due to increased drought, water diversions, and impoundments (Larned et al. 2010, Datry et al. 2018, Majdi et al. 2020). Future impacts of a changing climate for Kansas grasslands include increased frequency of intense rainstorms and periods of prolonged drought that could directly influence drying and flooding regimes (Bertrand et al. 2013). An increase in intense storms could cause flash floods that increase the (longitudinal) connectivity to upper reaches of a stream, allowing for rapid colonization by larger macroinvertebrates and fishes. Once colonized, these taxa can persist in isolated pools. Longer periods of drought decrease the connectivity to permanent refuge and increase the number of isolated pools (Larned et al. 2010). For non-perennial streams that naturally experience variable drying and flooding cycles, these impacts could further limit the organisms able to utilize these systems (Datry et al. 2014, Hay et al. 2018).

Aquatic organisms within tallgrass prairie streams are more immediately impacted by consequences of human land use, including cattle ranching and alterations to natural streamflow. Much of tallgrass prairie within Kansas is utilized as pasture, with limited ability to be converted to agricultural land, lessening the impact of common anthropogenic disturbances to streams, such as pollution and increased nutrients from

agricultural runoff (Dodds et al. 2004). While cattle grazing helps to mimic natural grazing patterns, increased stocking rates and the diversion of water to sustain the number of cattle can cause significant impacts. Cattle with access to streams can degrade banks and increase nutrient inputs. The diversion of water for the creation of cattle ponds or fishing ponds can affect aquatic invertebrates by disrupting natural flow patterns and creating large, unnatural bodies of water (Dodds et al. 2004). These ponds act as permanent refuge along a stream reach that could increase the number of large predators able to colonize upstream pools. Fishing ponds that are created for recreational use can have the added negative effect of being stocked with sport fishes. Fishes are an important component of intermittent streams and can influence the distribution of other aquatic organisms. They are a major predator of aquatic invertebrates and have been shown to directly influence their distribution and abundance. It has been suggested that predatory fishes can congregate in high abundance within pools during low flow periods, resulting in decreased invertebrate biomass and production (Whiting et al. 2011).

There has been limited study into the aquatic invertebrates of tallgrass prairie streams, with most research conducted at the Konza Biological Field Station in northeastern Kansas (Kansas State University) (Stagliano and Whiles 2002, Larson et al. 2013). Of these, non-insect invertebrate groups remain understudied (Dodds et al. 2004). Expanding the number of study locations that incorporate a diverse assemblage of aquatic invertebrates will contribute to our growing knowledge of prairie streams (Larson et al. 2013). Specifically, determining how invertebrate assemblages with different dispersal strategies are distributed within pools of varying hydrology and their

ability to withstand drying in isolated pools can contribute to our understanding how invertebrates utilize these systems and how they respond to expected change in disturbance regimes (Gleason and Rooney 2017).

1.2 Resistance to Drying

Aquatic invertebrates have adapted to historical hydrology regimes through various dispersal and life history strategies (Hay et al. 2018). Macroinvertebrates rely heavily on aerial dispersal or physical movement to escape stream drying. In contrast, most microinvertebrates have developed life history strategies that make them able to withstand drying and immediately recolonize after drying events. Microinvertebrates are an often overlooked aspect of invertebrate studies, especially for freshwater habitats (Majdi et al. 2020). More studies are needed to determine if their resistant abilities facilitate recolonization and re-establishment of trophic connections after drying and refilling of isolated pools (Majdi et al. 2020).

If these pools lose all surface water for long periods of time, then once refilled resistant microinvertebrates could quickly recolonize and aid in the reestablishment of ecological processes (Gaudes et al. 2010, Majdi et al. 2020). It is also reasonable to assume, as drought increases, species that are able to cope with these extremes may have the potential to become dominant with their major predators unable to survive and recolonize due to the harsh conditions (Altermatt et al. 2009, Strachan et al. 2015). Prolonged drought may limit the survival and colonization of isolated pools by actively dispersing macroinvertebrates. Decreased lateral connectivity may decrease the number of aerial dispersals that would be potential first consumers of primary producers and microinvertebrates. Short spates of increased flow from heavy rains may not create

the conditions that would usually enable large macroconsumers to move upstream. Because of their potential to rapidly recolonize after drying disturbance, microinvertebrates may play an important role in restoring aquatic food webs and “kick-starting” ecosystem functions (Gaudes et al. 2010, Majdi et al. 2020).

There are a variety of resistant traits that allow individuals to resist pool drying (Dodds et al. 2004, Strachan et al. 2015). Species can have multiple traits and strategies employed at a time or at different stages of life that allow them to better cope with variation in drying regimes (Strachan et al. 2015). Diapause and quiescence are forms of dormancy defined by a period of decreased metabolic function. They differ in the circumstances that break dormancy. Diapause ends due to biological cues, while quiescence ends when favorable conditions return. Diapause is also used to resist freezing during winter months (Strachan et al. 2015). All organisms considered for this study have the abilities to enter some state of diapause and is a process that may be used as part of their life cycle, even without any drying disturbance (Strachan et al. 2015). Only bdelloid rotifers and microcrustacean groups (ostracods, cladocerans, and copepods) undergo quiescence. Most groups considered for this study are able to produce dormant resting eggs through either diapause or quiescence that are resistant to desiccation. Anhydrobiosis is considered a form of quiescence and occurs when an organism enters a dehydrated state. While it is clear organisms utilize this strategy when faced with drying conditions, little is known about how long they can remain in this state and the costs to the organism itself (Strachan et al. 2015). For example, nematodes are unique in their ability to produce a third-stage juvenile, whose cuticle is adapted to enter anhydrobiosis (Caceres 1997, Strachan et al. 2015).

Microinvertebrates, can also enter these resistant stages at different stages of their life cycle (Strachan et al. 2015). When species can resist drying at a larval, juvenile, or adult stage, they could potentially have an advantage over other species by rapidly recolonizing when water returns (Horne 1993, Strachan et al. 2015).

These resistant abilities to survive drying has been well documented throughout the history of aquatic ecology, but were not considered of great importance to the functioning and recolonization of aquatic systems (Stanley et al. 1994, Fritz and Dodds 2004, Chester and Robson 2011, Strachan et al. 2015, Hay et al. 2018). Historically, dry sediments of intermittent aquatic habitats had mostly been deemed “biologically inactive” (Steward et al. 2012, Strachan et al. 2015). This has also been stated for aquatic invertebrates within tallgrass prairie streams (Fritz and Dodds 2002, Dodds et al. 2004), but these studies are limited to macroinvertebrates. Recent studies have contrasted with this historical view, finding dry sediments to be a significant refuge with diverse invertebrate assemblages (Hay et al. 2018).

While it is clear many microinvertebrate taxa can permit after drying, less is known about how different drying durations affect their ability to recolonize isolated pools (Robson et al. 2011, Strachan et al. 2015, Hay et al. 2018, Vargas et al. 2019). Tests of the flexibility of strategies used to survive desiccation in different environmental conditions have been limited (Strachan et al. 2015). It has been suggested that experimental manipulations, for example rehydration of sediment cores, would allow for the evaluation of the role of microinvertebrate groups (Hay et al. 2018, Majdi et al. 2020). Determining how these communities respond to drying disturbance within

intermittent tallgrass prairie streams will help aid in preserving their biodiversity (Boersma et al. 2014).

1.3 Rehydration Experiments

Many studies concerned with the recolonization of microinvertebrates after dying disturbance utilize sediment rehydration and specifically focus on the role of the resistant egg bank. Some utilize microcosms or mesocosms that consist of an enclosure placed within a greenhouse or natural setting that allows for replication and observation of aquatic communities. Most microcosm rehydration experiments are conducted on wetlands and lakes. Those that focus on streams or rivers have been conducted in dry or arid landscapes within the southwestern USA (Simovich and Hathaway 1997), Australia (Hay et al. 2018), and the Mediterranean (Majdi et al. 2020). Many of these systems have similar conditions to tallgrass prairie streams, including short hydroperiods, low connectivity, and limited riparian resources. Microcosms have been shown to be limited in their abilities to replicate the complexity of natural systems (Schindler 1998). It was therefore important to incorporate as many natural processes as possible and limit the amount of initial manipulation, to specifically focus on our questions concerning microinvertebrates and their response to drying.

Drying disturbance is difficult to study in the field setting (Jenkins and Boulton 2003, Hay et al. 2018) and most collect soil when the stream is dry for experimental rehydration (Stubbington et al. 2016, Maijdi et al. 2020). Sediments are usually collected in the field from the top layers of soil, homogenized, and divided across microcosms (Stenert et al. 2017). Few collect both water and sediment to allow for the assessment

of the invertebrate assemblage before sediments dry. Even less collect the intact sediment core for each microcosm that would represent the true sediment structure.

Experimental rehydration studies vary greatly in their design. Microcosms have been housed in the lab under 12 hour light, 12 hour dark cycles (Stenert et al. 2017), within a temperature-controlled greenhouse (Hay et al. 2018), or outside (Stubbington et al. 2016). When placed outside, many utilize a shade cloth or mesh net as a cover to avoid contamination (Diez-Brantley et al. 2002, Boersma et al. 2014). These covers limit the amount of ecological realism by limiting light penetration, dispersal or colonization, and other inputs, but ultimately allows for some control of these influencing variables (Boersma et al. 2014). Water used for rehydration includes filtered groundwater (Anderson and Smith 2004), well water (Bright and Bergey 2015). distiller water (Freiry et al. 2016), dechlorinated tap water (Stubbington et al. 2016), and deionized water (Hay et al. 2018). After rehydration treatments, the process for sampling invertebrates from microcosms have been conducted only once after a period of rehydration (Bright and Bergey 2015), a couple times a week for several weeks (Freiry et al. 2016), or on a scheme from 0, 7, 14 and 28+ days after rehydration (Ávila et al. 2015, Stubbington et al. 2016, Freiry et al. 2016, Stenert et al. 2017, Hays et al. 2018). It has been reported that after 30 days, there is an increase in algal growth and deteriorating water quality.

Collection of samples from microcosms have been completed through the use of small nets (Freiry et al. 2016, Stenert et al. 2017) to siphoning all surface water through a sieve (Hay et al. 2018). Samples have been immediately placed in ethanol or observed live. Preservation allows for a wait time before samples must be assessed, but many small invertebrates are not easily identifiable after preservation (Stubbington

et al. 2016). While live samples must be immediately analyzed, more species can be recorded and more readily identified (Stubbington et al. 2016). Some then return all collected samples back to the microcosms after identification (Boulton and Lloyd 1992, Hay et al. 2018), while others discard samples. Other manipulations of the sample populations, such as initially removing large macroinvertebrates from microcosms, is conducted in order to decrease predation of study organisms (Stubbington et al. 2016). Microcosms are considered a closed system with increased biotic interactions, that may limit their ability to mimic natural processes (Boulton and Lloyd 1992, Hay et al. 2018). The experimental design of microcosm experiments will ultimately differ based on the research questions asked, but provide a means for the assessment of experimental drying and rehydration of microinvertebrate communities (Hay et al. 2018).

1.4 Specific Aims

The aim of this project is to determine the microinvertebrate assemblages and their abilities to recolonize after pool drying within isolated pools of intermittent tallgrass prairie streams. This study addresses two main questions: (1) What microinvertebrate groups utilize isolated stream pools within the tallgrass prairie intermittent streams? (2) How do microinvertebrates respond to different drying durations? An experimental microcosm study was conducted to test the hypotheses: (1) aquatic microinvertebrate abundance will be lower after drying compared to those that remain filled, and (2) aquatic microinvertebrate abundance will be lower after a longer drying duration when compared to a shorter drying duration. Specifically, different microinvertebrate groups with differing resistant traits and strategies to survive drying will be assessed, including

nematodes, rotifers, and three microcrustacean groups, ostracods, cladocerans, and copepods.

CHAPTER 2

METHODOLOGY

2.1 Field Methods

2.1.1 Study Site

The contents of the microcosms were collected from Youngmeyer Ranch, Elk County, Kansas (37.545022, -96.489850) (Figure 1), a 1902 ha (4700 acre) Wichita State University Biological Field Station, owned and managed by the Youngmeyer Trust (Figure 2). The site is located within the Flint Hills (Ecoregion Level IV) consisting of mostly natural tallgrass prairies, with oak-hickory forests along permanent stream reaches (Chapman et al. 2001). The site includes ephemeral, intermittent, and perennial streams as well as natural springs and artificial cattle ponds, allowing for to the exploration of aquatic organisms within a variety of aquatic habitats. The mean annual temperature is 13.7ºC and mean annual precipitation is 979 mm (Houseman et al. 2016). Prescribed burning and cattle grazing have been included in the management regime for the last 20 years. The area is composed of layers of hard limestone, soft shale, and chert (flint) with silty clay loam soils (Houseman et al. 2016). The physical geology of the area lies within the western edge of the Osage Cuestas (physiographic region) (Buchanan 2010), with the west side of the property sloping to the west and the east side consisting of steeper slopes of exposed limestone (escarpments) to the east.

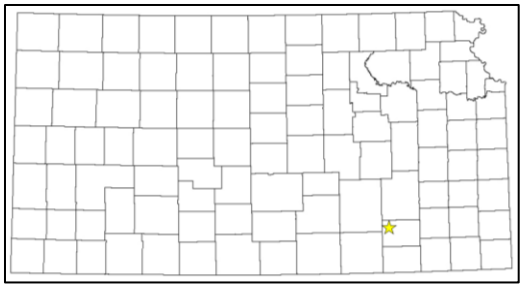

Figure 1. Map of counties within Kansas, USA. Youngmeyer Ranch (star), the field collection study site, is located within the northwestern corner of Elk County.

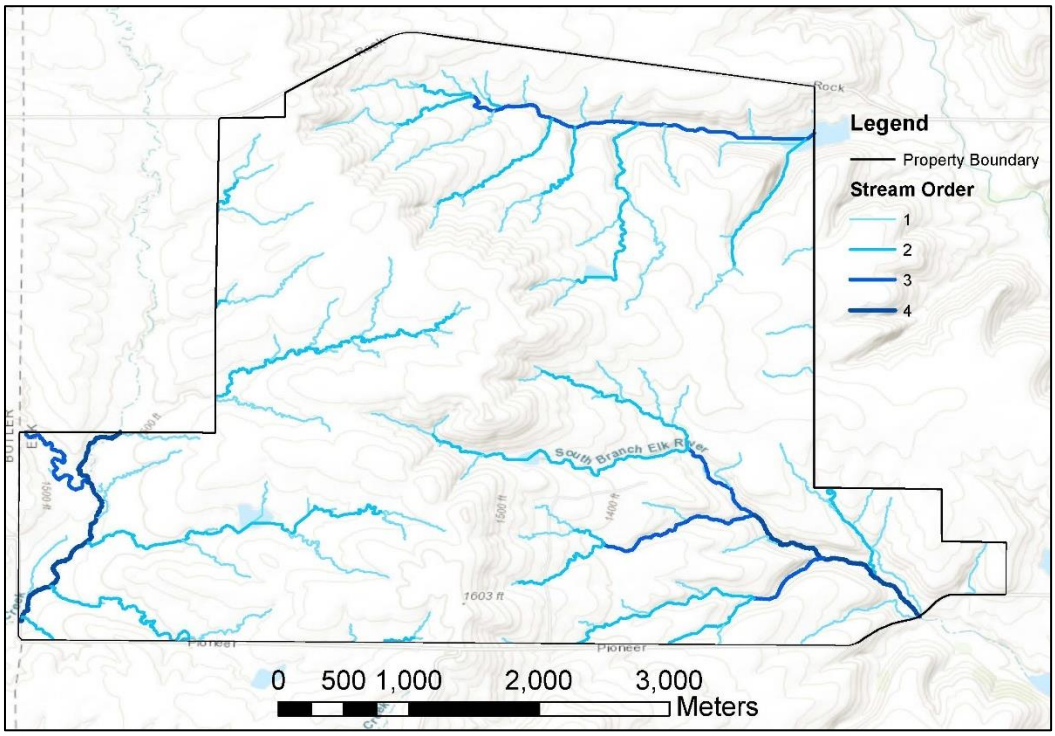

Figure 2. Map of Youngmeyer Ranch, Elk County, Kansas, showing the property boundary, streams, and elevation. Map created by Emily Ann Smith using ArcGIS software by ESRI.

2.1.2 Sample Pools Selection

An initial exploration of the streams and pools on the Youngermeyer Ranch property were initially mapped using Google Earth Pro, utilized for its accessibility. Undergraduate students within the Aquatic Ecology lab (Spring 2020) were assigned weekly tutorials to assist in mapping sample sites. Ten isolated stream pools from four

stream segments were then randomly selected from the northwest area Youngmeyer Ranch to by sampled for this study (Figure 3). This area was chosen to allow for a variety of intermittent stream systems that were managed and stocked with cattle at similar rates. Specifically, only isolated pools holding water that consisted of substrates that allowed for the collection with a sediment corer were included.

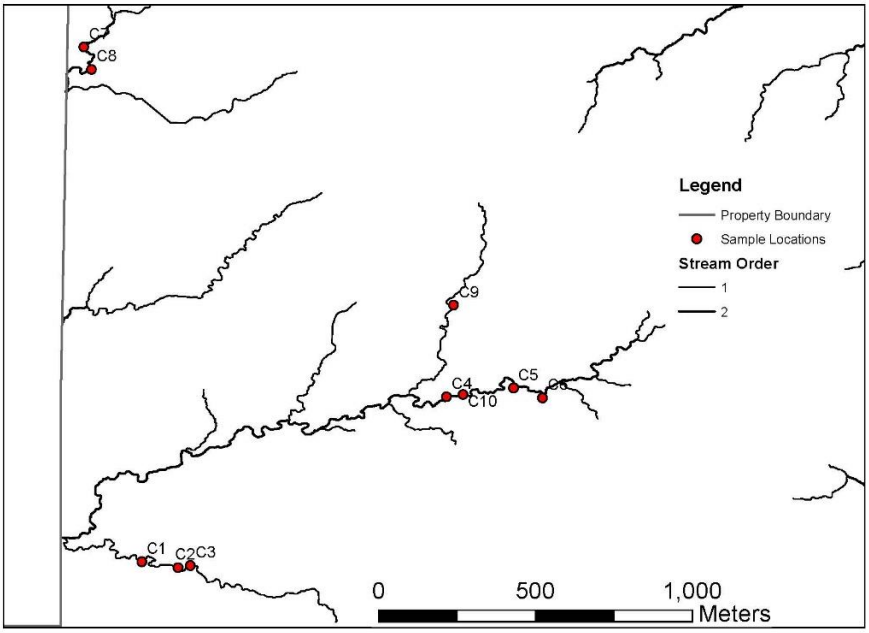

Figure 3. Map of the northwestern corner of Youngmeyer Ranch, Elk County, Kansas. Ten sample pools (red circles) are marked by their sample name. Map created by Emily Ann Smith using ArcGIS software by ESRI.

Characteristics of each pool are collected at the time of sampling. Physical characteristics of each pool included upstream to downstream length, width, and maximum depth. Biological characteristics included bank and in-stream vegetation, in-stream sediment composition, and canopy cover. Sample pools ranged from 3.5-8.8 m in upstream to downstream length, averaging 5.3 m (Table 1, Appendix). Average maximum width of sample pools was 2.2 m. Average maximum depth was 182 mm. Stream banks were dominated by grasses and sedges, with in-stream vegetation

dominated by macrophytes and exposed roots. Streambeds mainly consisted of fine material, pebble, and rock substrate.

2.1.3 Microcosm Collection

A soil sleeve (30.48 cm tall, 7.68 cm diameter), consisting of a plastic cylinder that is open on both ends, is used to collect the contents of the microcosm in the field (August 2020) (Figure 4). The sleeve is pushed through the water and sediment column, until 10 cm of sediment core is collected, or bedrock is hit. Three cores per pool are collected, each randomly selected to be collected from the middle, right of left side of the pool (Figure 4, Step 1). This provided the random selection of habitat characteristics of each pool and allowed for minimal disturbance between sample points.

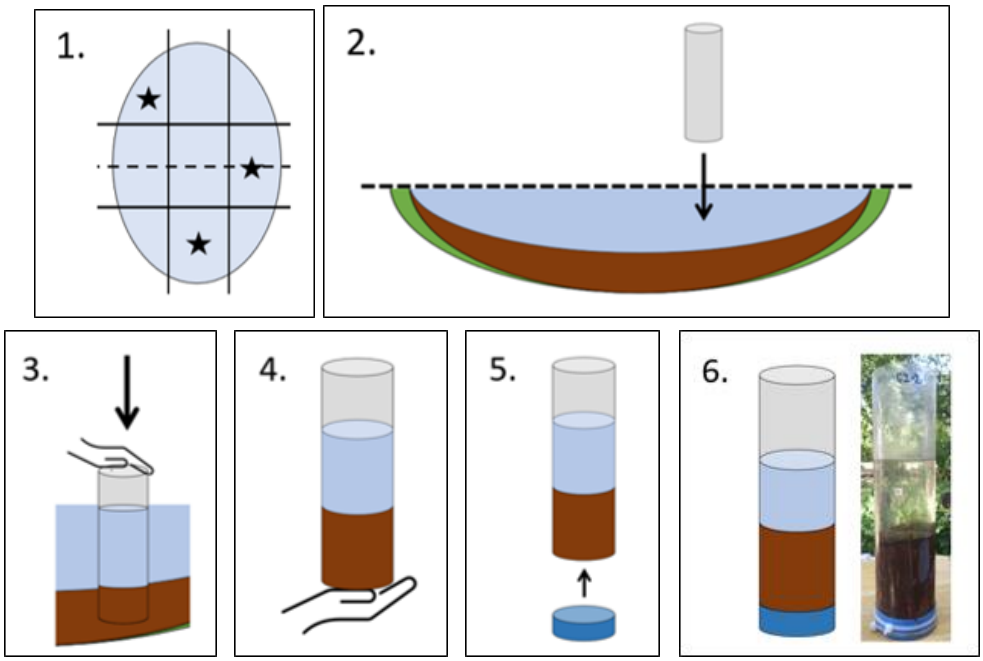

Figure 4. Microcosm field collection steps. (1) Determine sample points. Three sample points (white stars) are shown within the sample pool. (2) Hold sleeve above water, perpendicular to surface above sample point. Showing cross-section above pool. (3) Push sleeve through water and sediment column. (4) Remove sleeve. (5) Place cap on bottom of sleeve. (6) Complete microcosm. (6A) Model image of microcosm. (6B) Photo of microcosm.

2.2 Experimental Methods

2.2.1 Experimental Site

After collection, microcosms are housed outside at an off-site facility (personal home, Wichita, KS, 67203) from August 13 – October 23, 2020. Microcosms therefore experience similar seasonal temperatures and photoperiod to the study site. The microcosms are placed within aboveground crates and confined by wooden stakes to hold them in place. After each sampling period, microcosms are rotated (”snaked”) throughout the structure to help control for any variation in light penetration. Each microcosm is covered with a fine mesh net to limit any aerial contamination. The crates are covered with a tarp that does not seal the microcosms but allows for protection during precipitation events. This cover is also used every night to discourage disturbance from animals.

2.2.2 Experimental Treatments

The three microcosms collected from each pool are randomly assigned one of three treatments: (1) a fill treatment, with microcosms receiving water additions throughout the duration of the study and not allowed to dry (control), (2) allowed to naturally dry with a complete drying duration of two-weeks before refill (2-week dry treatment), and (3) allowed to naturally dry with a complete drying duration of four-weeks before refill (4-week dry treatment). The drying treatments started once all surface water naturally dried. Water used for refill consists of collected pool water from the study site that is filtered and autoclaved. This type of water source was used to retain some of the natural properties, rather than using treated water or relying on rainwater collection. Drying treatments were eventually refilled with 100 ml of water and

50 ml on subsequent days as needed. Water was added to the control microcosms throughout the study as needed.

2.2.3 Microinvertebrate Sample Collection

Water and a small amount of the surface sediment is collected from each microcosm three times a week (Monday, Wednesday, and Friday). For each sample, 10 ml of water and sediment is collected by pipette, excluding those undergoing drying treatments. 5 ml of the collected sample is then microscopically analyzed using a dissecting scope. The entire sample was separated by placing a few drops repeatedly across a petri dish to allow for specific counts and identification of all living individuals (Thorp and Covich 2010). Collected samples are not added back to the microcosms. Characteristics and changes of each microcosm is recorded during sample collection, including sediment depth, water depth, and algae/macrophyte presence. Measured water depth of each microcosms before sample collection allows for the calculation of volume sampled.

2.3 Statistical Analysis

Data was analyzed using generalized additive mixed models (GAMMs) to estimate smooth functional relationships between predictor variables and the response variable (microinvertebrate abundance) (Pedersen et al. 2019). The ‘gam’ function from the package mgvc (Wood 2011) was used to fit the GAMMs to the data with cubic regression splines. All analyses were conducted using R software (R Core Team 2014). The log link function ensures positive fitted values (Zuur and Ieno, 2016). The data was analyzed using a Poisson family distribution for zero-inflated count data. Assurance that the data meet the test assumptions and required transformations was performed before

analysis. Exploratory model comparisons are conducted for the determined predictor and response variables. Based on Akaike Information Criterion (AIC), model selection determined the best model for the response variable and predictor variables were consistent across all GAMMs used. The dependent (response) variable is abundance (number of individuals collected per 5 ml sample) for total macroinvertebrates and for each separate taxa group on subsequent analyses. The independent (predictor) variables are the treatment, days post refill, and from which pool each microcosm was collected from. All independent variables, besides the treatment variable, were smoother terms set to three knots within the GAMM. Treatment is a categorical variable with four levels, a two-week (2-week treatment) and four-week drying (4-week treatment) with the corresponding control (2-week control and 4-week control) that correlates to the post refill date of the control for each treatment microcosm. Day is a continuous variable that correlates to the number of days post refill. Pool is a random, categorical variable that allows for the random effect of the sample pool each microcosm was collected from to be included in the analysis.

CHAPTER 3

RESULTS

All expected taxa were collected from treatments and control microcosms (Figure 5). Nematodes, rotifers, ostracods, cladocerans, and copepods were included in the data analysis. Other taxa groups that were collected throughout the study but not found in significant numbers, and were therefore not included in the analysis, include platyhelminthes, annelids, tardigrades, and anostracons. Because microcosms were allowed to naturally lose surface water, two of the 4-week treatments that had longer drying times were not fully sampled for the entire two weeks post refill, due to unexpected freezing temperature in late October (Figure 6).

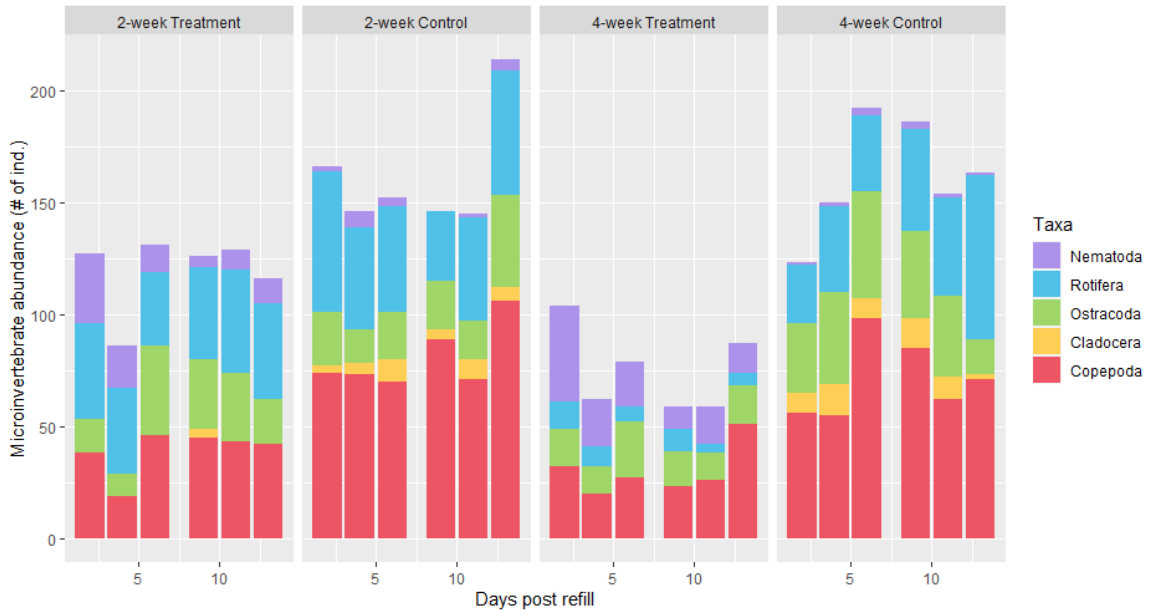

Figure 5. Stacked bar plot of total microinvertebrate abundance collected from microcosms over the two-week study for drying treatments and the corresponding days of the control.

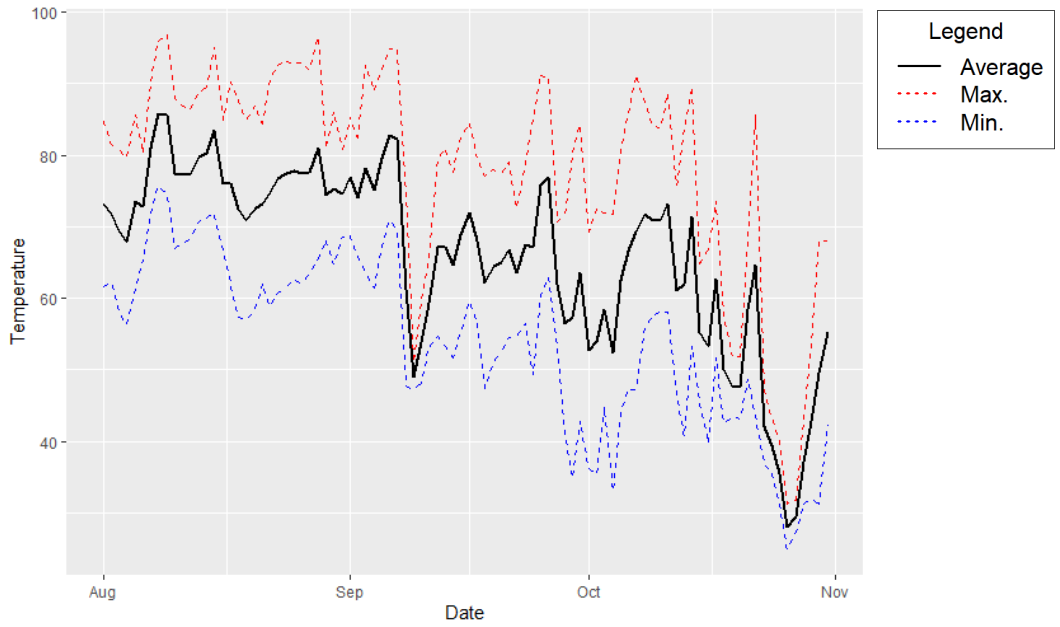

Figure 6. Change in temperature (°F) at the experimental site (Wichita, Kansas) over the course of the study (August 13 – October 23, 2020) (Kansas Mesonet 2021).

GAMMs were used to compare the change in abundance post refill (summary tables in appendix). This was conducted for abundance of total microinvertebrates and each taxa group of interest. Total microinverterbate abundance was significant for the treatment parametric term (P = <0.001) (Table 2, Appendix). For the post-refill day smooth term, the 4-week drying treatment (P = 0.001) and 2-week control treatment (P = 0.003) were also found to be significant (Table 2, Appendix). Generally, control microcosms that remained filled had higher overall microinvertebrate abundance, supporting our first hypothesis (Figure 7). Drying resulted in lowering the total microinvertebrate abundance. The longer drying treatment was lower than the shorter drying treatment, supporting our second hypothesis. Comparatively, the control had more variation in the number of microinvertebrates collected over time, and the two-week treatment showed more variation over time compared to the four-week treatment.

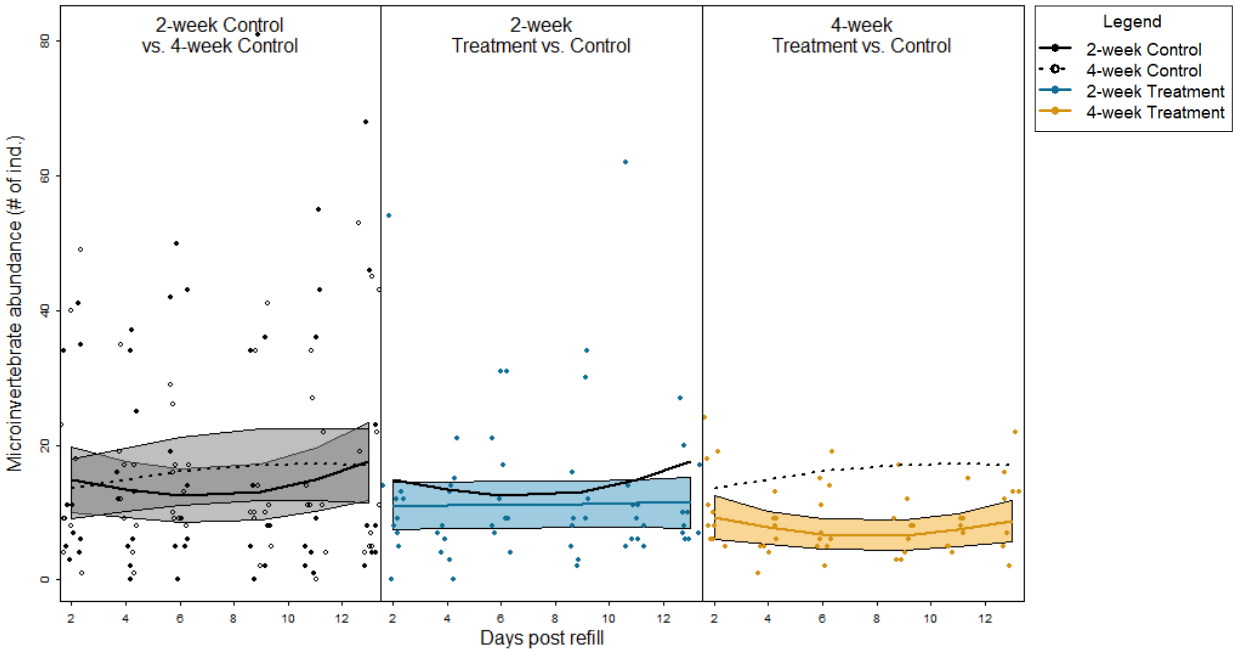

Figure 7. Generalized additive model (GAMM) plots of total microinvertebrate abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

3.1 Nematoda

Nematoda abundance was significant for the treatment parametric term (*P* = <0.001) and the post refill day smooth term (*P* = 0.002) (Table 3, Appendix). Nematodes were observed in low abundance for the control and treatments before drying treatments were initiated. Once refilled, the drying treatments showed an increase in nematode abundance when compared to the control (Figure 8). Drying resulted in increased abundance during the first days post refill and then steadily declined over time. When the two drying treatments are compared, the 4-week drying treatment had a higher number of individuals collected over the time period than the 2-week drying treatment. Both drying treatments showed similar trends, with high nematode abundance within the first days of sampling and a decrease in the number collected

over time. Over the course of the study, 87 individuals were collected from the 2-week treatment and 124 individuals were collected from the 4-week treatment. Within the control microcosm, the time frame corresponding to the 2-week treatment (2-week control) collected 20 individuals and the 4-week control collected 12 individuals.

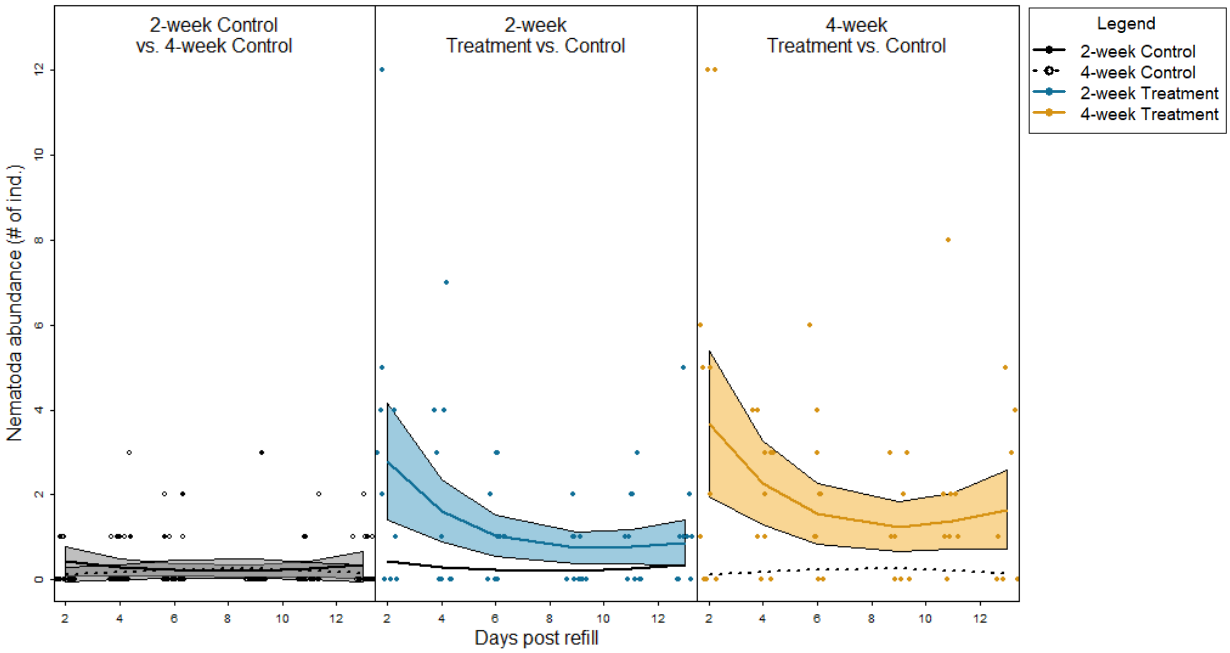

Figure 8. Generalized additive model (GAMM) plots of total Nematoda abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

3.2 Rotifera

Both subclasses of rotifers (Monogononta and Bdelloidea) were collected from the microcosms. These subclasses were grouped together for total abundance due to low numbers of bdelloids collected over the course of the study. Rotifera abundance was significant for the treatment parametric term (P = <0.001) and the post refill day smooth term (P = 0.037) (Table 4, Appendix). The 4-week drying treatment was significant for the post refill day smooth term (P = 0.002) (Table 4, Appendix). Rotifer

abundance within the 2-week drying treatment (244 total individuals collected) was similar in the number of individuals collected to the 2-week control (289 individuals) and 4-week control (269 individuals) over the sampling time period (Figure 9). Within the 2-week treatment and control a stable trend in rotifer abundance was observed. This was contrasted with the 4-week drying treatment, with 48 total individuals collected and lower abundance compared to the 4-week control. No rotifers were collected over the time period from one 4-week drying microcosm (C10-3).

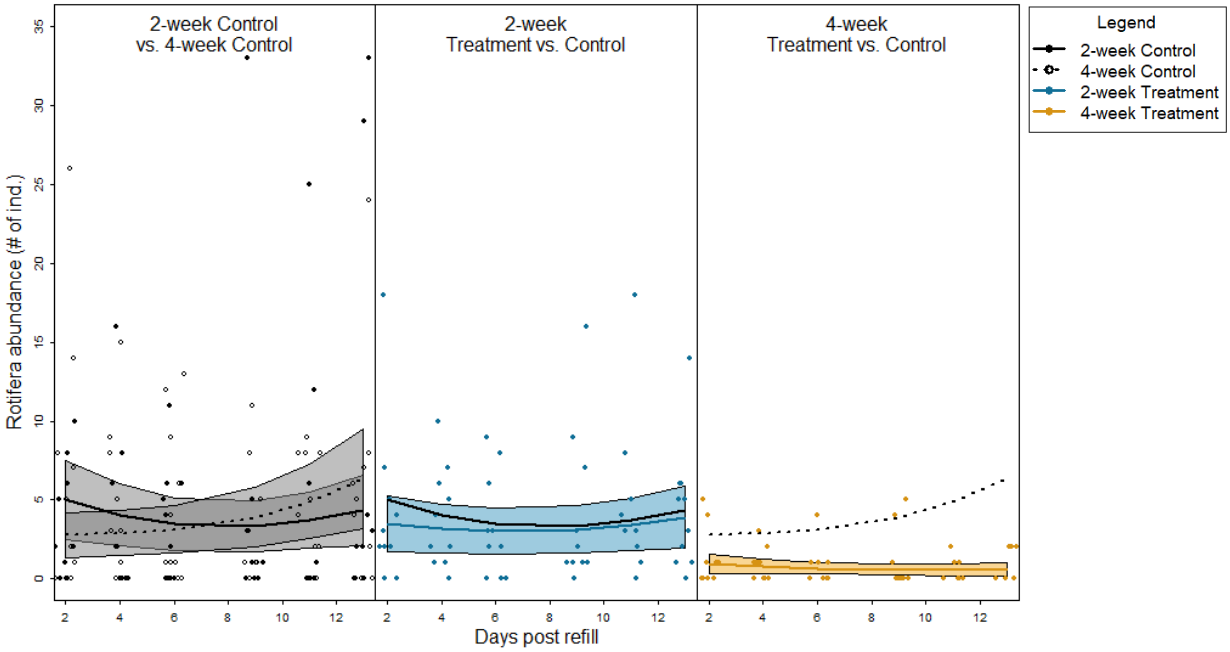

Figure 9. Generalized additive model (GAMM) plots of total Rotifera abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

3.3 Ostracoda

Ostracoda abundance was significant for the treatment parametric term (P = <0.001) and the post refill day smooth term (P = 0.041) (Table 5, Appendix). For the post-refill day smooth term, the 2-week drying treatment (P = 0.001) and 4-week control

(*P* = 0.001) were also found to be significant (Table 5, Appendix). Ostracod abundance was higher in the 4-week control (211 individuals) than the 2-week control (140 individuals) over the sampling period (Figure 10). The 2-week treatment (146 individuals) and 2-week control had a similar number of total individuals collected, although a slight increase after day six was observed within the 2-week treatment and an opposite trend was found within the 2-week control. The 4-week drying treatment had a lower total number of ostracods over time (99 individuals). When compared with the 4-week control, the 4-week treatment resulted in slightly lower abundance.

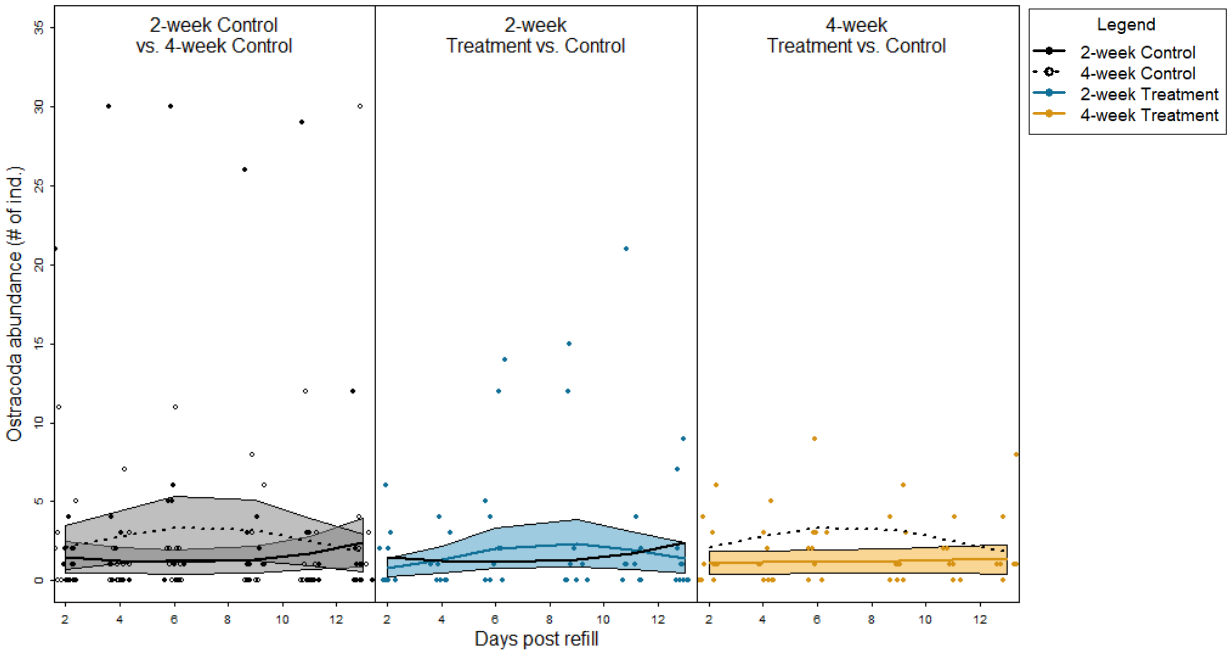

Figure 10. Generalized additive model (GAMM) plots of total Ostracoda abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

3.4 Cladocera

There were no significant results for Cladocera abundance, with few cladocerans being collected from drying treatments (Table 6, Appendix). Cladocera abundance

remained low after both drying treatments when compared to the control (Figure 11). Four individuals were collected from the 2-week drying treatment and no cladocerans were collected from the 4-week drying treatment. This contrasts with the control, with 37 individuals collected from the 2-week control and 57 individuals collected from the 4-week control.

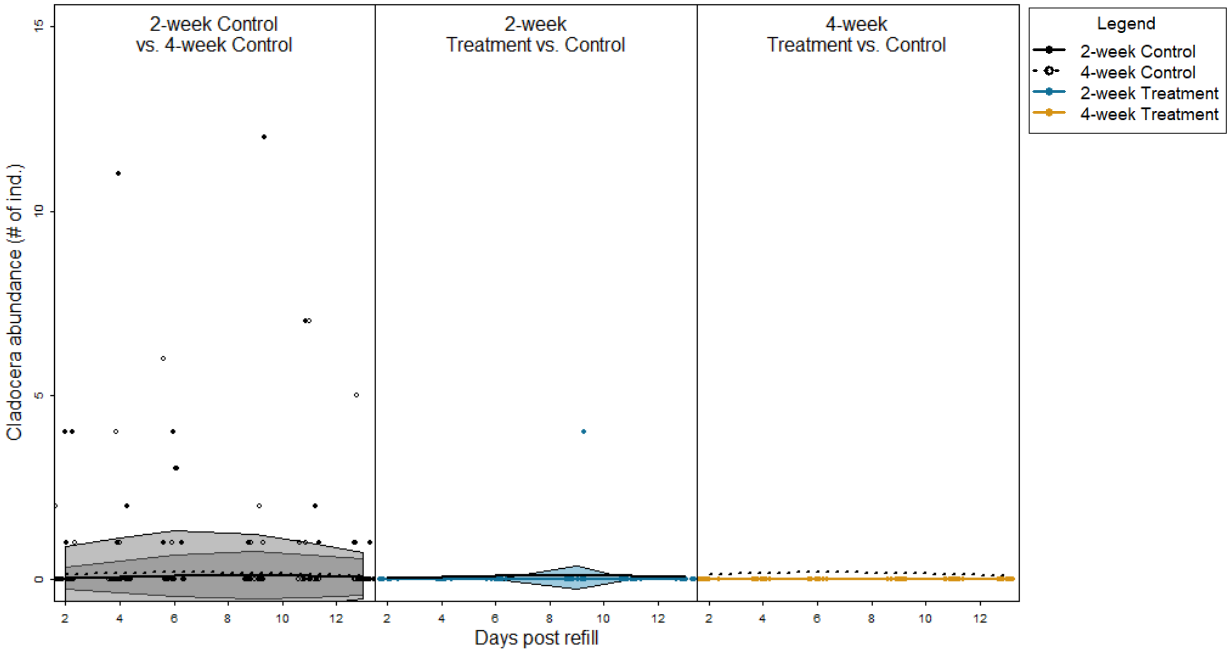

Figure 11. Generalized additive model (GAMM) plots of total Cladocera abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

3.5 Copepoda

The copepod order Cyclopoida dominated within the microcosms, although a few from the order Calanoida were observed. Due to the low number of calanoids collected, these orders were grouped together for analysis. Because larval copepods (nauplii) are morphologically different than adults, unlike other taxa groups, both larval and adult copepod stages were analyzed. Total copepod abundance includes nauplii and adult

stages (Figure 12). Total copepoda abundance was significant for the treatment parametric term (*P* = <0.001) (Table 7, Appendix). The 4-week drying treatment was significant for the post-refill day smooth term (*P* = 0.006) (Table 7, Appendix). Total copepod abundance was lower in drying treatments when compared to the control. After drying, there was a slow increase in total copepod abundance collected over time. Both drying treatments were similar in the number of copepods collected after drying. Adult copepod abundance was significant for the treatment parametric term (*P* = 0.012) (Table 8, Appendix). For the post-refill day smooth term, the 2-week drying treatment (*P* = 0.008) and the 4-week drying treatment (*P* = 0.004) were found to be significant (Table 8, Appendix). Adult copepods were observed in similar numbers and trends across all microcosms (Figure 13). 115 copepod adults were collected within the 2-week treatment and 118 adults were collected within the 2-week control. The 4-week treatment was similar to the 2-week treatment and control with 112 adults collected. Adult copepods made up a smaller percentage of the total copepod abundance when compared to larval stages. Copepod nauplii abundance was significant for the treatment parametric term (*P* = <0.001) and the post refill day smooth term (*P* = <0.001) (Table 9, Appendix). For the post-refill smooth term, the 2-week drying treatment (*P* = 0.007), 2-week control (*P* = 0.001), and 4-week control (*P* = <0.001) were found to be significant (Table 9, Appendix). Nauplii were more variable across time compared to adults within the control (Figure 14). Both drying treatments showed similar trends in having low abundance in the first days of refill, but steadily increased over time. Drying treatments for nauplii were also lower in total abundance compared to the control, with the control

treatments showing high numbers of nauplii observed over the time period (364 individuals within the 2-week control and 303 within the 4-week control).

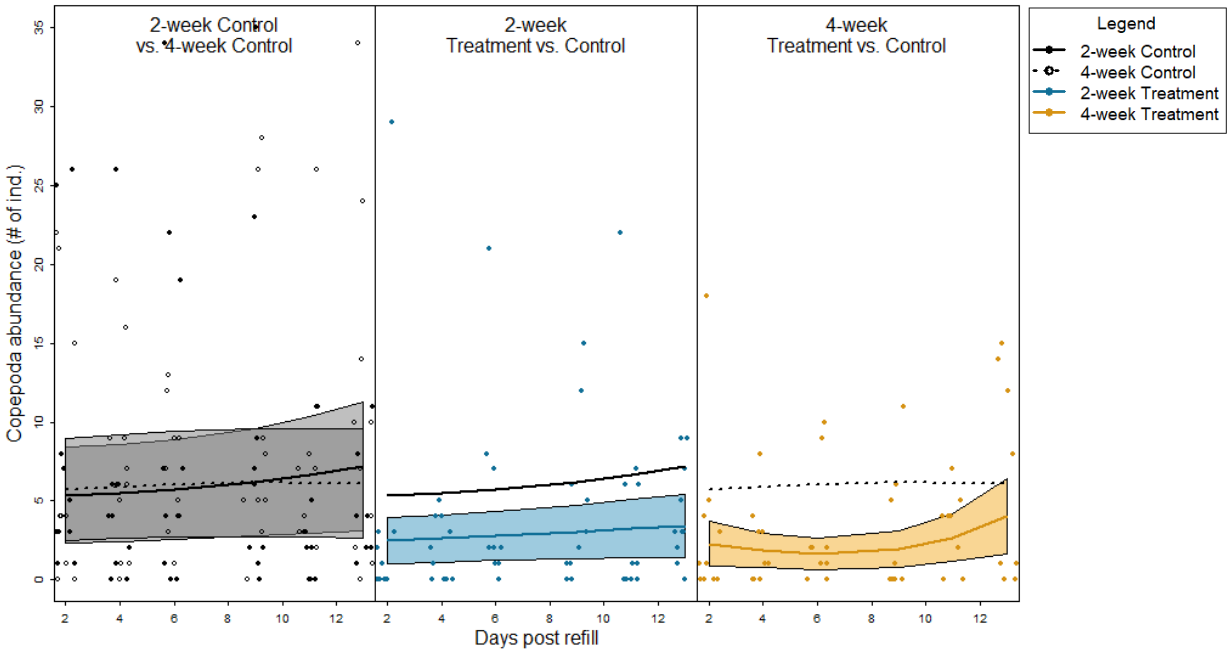

Figure 12. Generalized additive model (GAMM) plots of total Copepoda abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

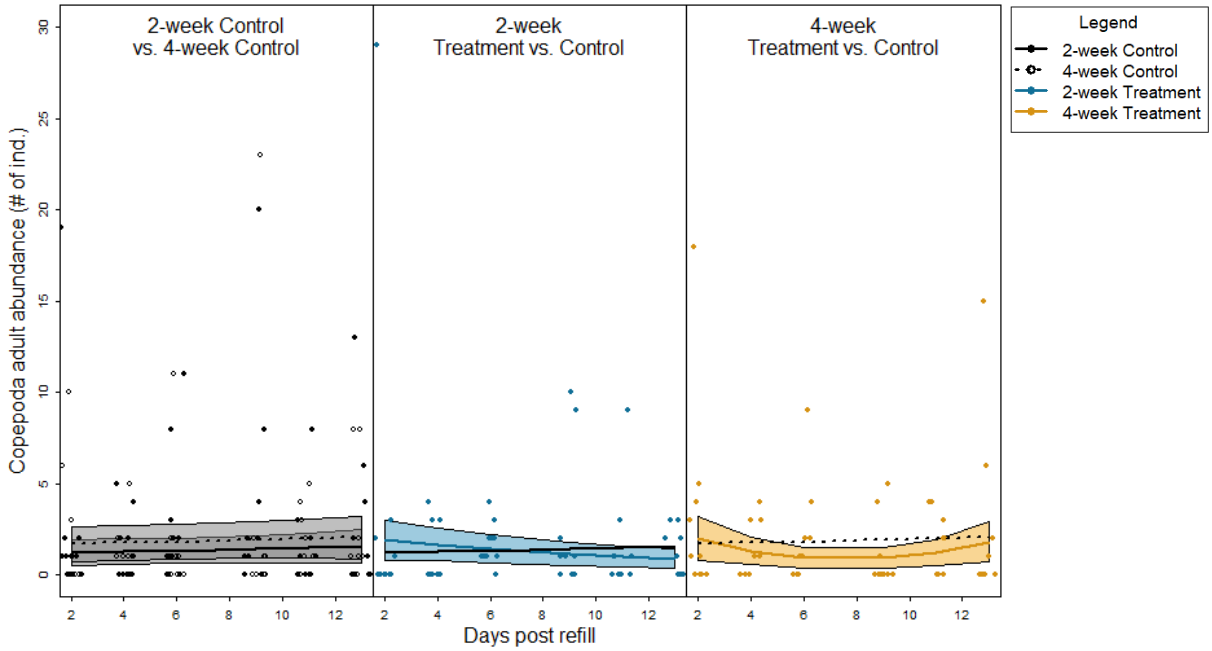

Figure 13. Generalized additive model (GAMM) plots of total adult Copepoda abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

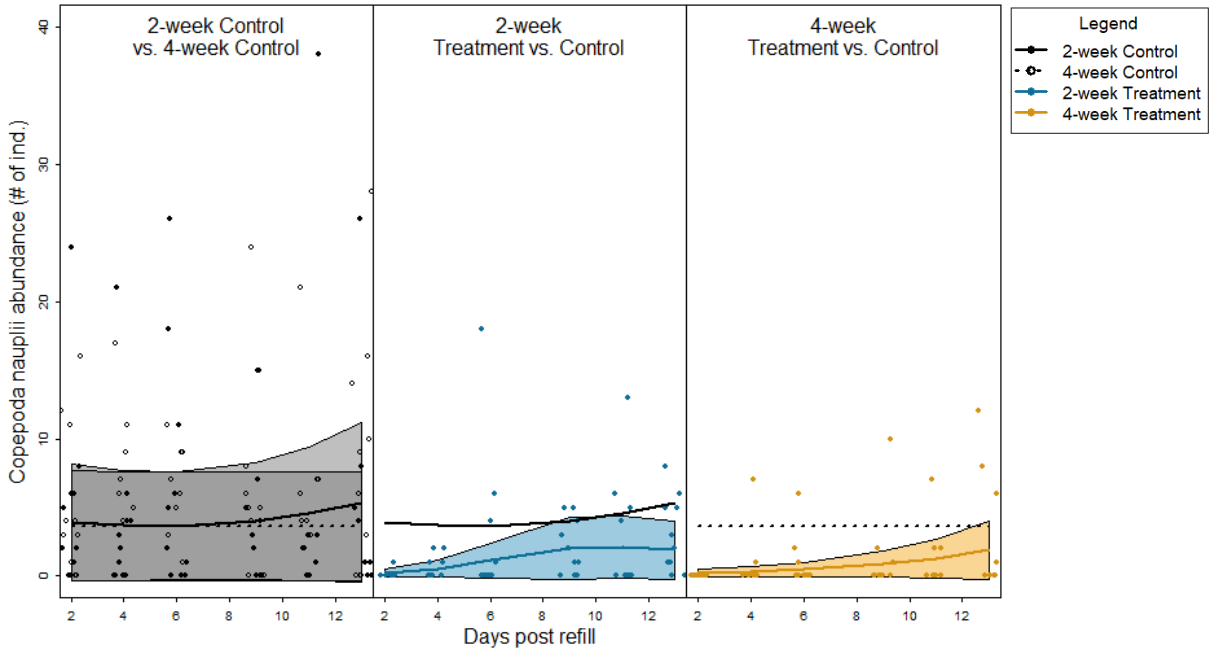

Figure 14. Generalized additive model (GAMM) plots of total larval Copepoda (nauplii) abundance (total number of individuals collected per 5 ml sample). Tick marks on the x-axis are days post refill for the 2-week and 4-week treatments with the corresponding days of the control. Shaded areas are the 95% confidence intervals.

CHAPTER 4

DISCUSSION

This study explored microinvertebrates that utilize tallgrass prairie streams and how they respond to different drying durations. The results of our study support our hypothesis that microinvertebrate abundance is lower in microcosms after drying when compared to those that remained filled. We also found evidence to support our second hypothesis that longer drying durations result in lower abundance when compared to shorter drying durations. We found that of the five major taxa groups analyzed, all but cladocerans had the resistant capabilities to quickly recolonize after differing drying regimes. While this trend was true for total microinvertebrate abundance, different taxa groups were found to vary in their response during the post refill time period. Nematodes were found in higher abundance after drying treatments compared to the control with a trend of a higher number of individuals collected within the first days of refill. Rotifers and ostracods were similar within the control and 2-week drying treatment, but lower within the 4-week drying treatment. Few cladocerans were found after drying treatments, while were still readily collected from the control. Adult copepods were found in similar numbers to the control and larval copepods were lower than the control but their abundance increased over time. The results of this study show that microinvertebrates have the potential to quickly recolonize and contribute to the productivity of intermittent stream pools after experiencing drying disturbance.

4.1 Interpretations and Implications

Although nematode numbers were low throughout the study, a trend of higher abundance following drying shows their abilities to quickly recolonize after stream pool drying. Of the few studies that included nematodes within rehydration experiments, similar findings have been reported of high abundance after the first few days of rehydration (Boulton and Llyod 1992, Majdi et al. 2020). Nematodes within intermittent streams have been found in high densities after frequent drying and rewetting cycles, which has been suggested to be due to their short generation times, the multitude of traits to withstand drying, and their body shape that allows for easy burrow into interstices (Boulton and Llyod 1992, Majdi et al. 2020, Rebecchi et al. 2020).

Free-living nematodes can be found within the streambed as well as in upland habitats (Majdi et al. 2020). Field studies that found high nematode abundance after drying, commonly equate this increase to a potential colonization of nematodes from terrestrial sites into the streambed (Boulton and Llyod 1992). When habitats experience dry conditions, it is thought that terrestrial nematodes, and potentially other invertebrates, will find refuge in adjacent, saturated streambeds (Acuña et al. 2005, Boulton and Llyod 1992, Majdi et al. 2020). Because this study did not collect dry soils, which could have upland soil incorporated into the collected sample, and no outside sediment inputs were incorporated into our microcosms over the course of the experiment, we can expect that nematodes collected during our study were freshwater nematodes (Corti and Datry 2016, Majdi et al. 2020). This gives insight that aquatic nematodes can withstand drying within the streambed and themselves recolonize quickly after inundation.

Similar to the results of our 2-week drying treatment, it has been reported that rotifers can quickly recolonize after drying (Boulton and Llyod 1992, Jenkins and Boulton 2003, Majdi et al. 2020). Rotifers of the subclass Monogononta were dominant in our study, which utilize resting eggs to reestablish after drying. Because adults can not readily undergo a dormant state or resist freezing, an assurance that eggs hatch during the right conditions are important for a population's survival (Ricci 2001). Unlike adult rotifers, their resting eggs are able to resist drying and freezing conditions (Gilbert and Schröder 2004). Although it is noted that rotifer resting eggs can deteriorate over time causing a loss in viability (Schröder 2005, Radzikowski et al. 2018, Vargas et al. 2019). The low number of rotifers found after the 4-week drying treatment may be due to the deterioration of resting eggs, although it is more likely a result of decreased air and water temperatures that did not provide the correct conditions for the hatching of resting eggs.

Microcrustacean groups differed in their emergence after drying. It has been noted that ostracods and cladocerans rely more on seasonal, environmental cues to enter and emerge from diapause or hatch from eggs, while copepods are more variable in their emergence. This may explain why our findings, with our study conducted in the fall, was unlikely to find high emergence of these taxa after drying (Brendonck and Meester 2003).

Within our study, the short drying duration may have allowed adult ostracods with the abilities to enter a short diapause stage by sealing their carapace and reemerge once rewetting, but the longer drying duration may have been too severe for them to utilize this resistant strategy (Horne 1993). Diapause via this method of dormancy is

unique among microcrustaceans (Horne 1993). Although, Majdi et al. 2020 found no pattern when comparing drying duration on the recolonization of ostracods in intermittent streams (Majdi et al. 2020).

Many studies that rehydrate dry sediments are conducted in spring and summer and report cladocerans emerge within the first days of rehydration (Boulton and Llyod 1992). The lack of cladocerans collected after drying treatments is expected to be due to the timing in which the study was conducted and the short amount of time microcosms were sampled after rewetting (Dietz-Brantley et al. 2002, Stenert et al. 2017). While cladocerans with resting eggs were observed throughout the study, they are known to need specific environmental cues to break resting egg dormancy. The hatching time of cladocerans has also been found to be species specific with hatching ranging from one to 30 days after rehydration (Boulton and Lloyd 1992, Jenkins and Boulton 1998, Nielsen et al .2000, Stenert et al. 2017). Therefore, the response of cladocerans within our microcosms indicates low recolonization after pool drying in the fall, most likely due lack to the absence of environmental cues to break dormancy and should not been seen as a complete decline of the population.

It has also been shown that when comparing reemergence of microcrustacean taxa, copepods were the only group that hatched at variable times during the year (Frisch 2002, Brendonck and Meester 2003). Bertrand et al. 2013, in a post flood study conducted after stream drying at Konza Prairie, found that cyclopoid copepods increased in density following drying within an intermittent middle reach which they associated with their short generation times (Bertrand et al. 2013). Compared to other microcrustaceans, copepods are unique in their abilities to undergo diapause as an

adult without morphological adaptions as they lack a protective cover. While it is still undetermined the exact method of diapause, it has been suggested that mucus or crystalline secretions may be involved in the process. These protective structures may contribute to copepods ease of emergence and recolonization once rehydrated (Frisch 2002).

4.2 Limitations and Future Research

Few microcosm rehydration studies focus on microinvertebrates compared to macroinvertebrates. Of those that study rehydration of microinvertebrates, most collect dry soils in order to focus of the role of the resting egg bank. Others solely focus on one taxa group or are limited to exploration of one species. There are clear limitations concerning the interpretation and comparison of our results to other studies. Due to a lack of knowledge of microinvertebrates within intermittent tallgrass prairie streams, comparisons to similar aquatic habitats within temperate regions are made, but do not exactly match expected conditions within prairies. Although our findings contribute to our understanding of these systems, due the heterogeny of streams within the tallgrass prairie, it is important to consider the limitations of stream selection within our own study (Biggs et al. 2017). Rock bottom streams with increased groundwater inputs were not included in this study, and they contribute greatly to the diversity of headwater streams within these systems.

As expected in ecological experiments, there are trade-offs between design and feasibility (Boulton and Llyod 1992). Microcosms have been commonly used for rehydration experiments and are reported to reasonably approximate the functioning of inundated riverbeds (Jenkins and Boulton 2003, Jenkins and Boulton 2007, Hay et al.

2018), but they lack the complexity of natural systems, and their small scale is an evident issue in their use (Sparks et al. 1990, Boulton and Llyod 1992, Hay et al. 2018). Enclosure effects have the potential increase predation and competition between species (Boulton and Llyod 1992, Hay et al. 2018). While coving microcosms with a fine mesh limited any outside colonization and contamination, these covers have been assumed to decrease the amount of natural light penetration that could influence temperature and primary productivity (Boersma et al. 2014). This cover also did not allow for natural allochthonous inputs and limited the amount of natural water mixing caused by wind. Further incorporation of abiotic variables, such as the collection of dissolved oxygen and soil moisture content, would allow more interpretation to the conditions influencing changes in microinvertebrate assemblage and abundance. The timing of this study limits interpretations due to many microinvertebrates requiring seasonal cues in order to emerge from diapause (Hay et al. 2018). Although, studies conducted in the fall provide insight of the microinvertebrates still utilizing these isolated pools and those which, if the organisms or resting eggs are able to remain dormant and viable over winter temperatures, would be the first to repopulate during spring rains. Regardless of scale, frequent sampling is needed to observe the rapid changes of invertebrate response to drying (Boulton and Llyod 1992). Despite the limitations of experimental microcosms, our use of soil core sleeves provided a useful methodology for the collection of the existing water and sediment column in order to test the response of microinvertebrates to different drying durations.

A larger amount of water compared to sediment was collected during our sampling regime. This allowed for more rapid sorting procedure and an attempt to not

cause great disturbance to the existing sediment structure. Only surface sediment was collected, which did not allow for the collection of subsurface organisms. This may lead to a smaller amount of benthic species collected over the course of the study. Although many benthic species were collected, including platyhelminths and annelids that would be similar to nematodes in their abilities to utilize interstitial spaces, they were not collected in high enough numbers to be incorporated into the analysis (Hay et al. 2018). Although nematodes were included and resulted in clear trends, they still may have been under sampled over the course of the study.

Long term studies are needed to determine the temporal changes within these systems to fully understand their complexity and biodiversity (Biggs et al. 2017). Microcosms collected throughout the year could expand on the observations found in this study. This is especially true for groups that need specific cues to break diapause before a population reestablishes. If historic or recent data is available on known hydroperiods and drying times associated with the pools sampled it could provide more realistic conditions experienced by microinvertebrates within tallgrass prairies. This could also aid in modeling future predictions expected in a changing climate to more accurately be simulated within experimental settings. Field observations coupled with a similar experimental approach to this study could help with the lack of realism associated with microcosm experiments by allowing for comparisons between simultaneous field and microcosm observations. This would allow for natural inputs of organic matter, predators, and competition found within isolated stream pools to be compared to those with experimental manipulations.

Knowledge on the functioning of intermittent streams is needed to clearly communicate to land managers and policy makers the importance and need for protection of tallgrasses prairie streams (Biggs et al. 2017). This is especially important considering the number of headwater streams within the remaining tallgrass prairies and their lack of regulation. Incorporating other features associated with these systems, like the role of cattle use and their influence on sediment structure, would provide insight and better inform land managers and ranchers interested in aquatic conservation efforts. Because many properties with intermittent headwater streams also are routinely burned, the effects of fire on aquatic communities would also be an important consideration for future studies. In addition to increasing awareness of intermittent streams, it has been suggested that water resource and land managers could potentially incorporate small aquatic refuge along stream channels during extreme drought to avoid biodiversity loss (Boersma et al. 2013).

4.3 Conclusion

Within the tallgrass prairie, determining the types of streams, number of streams, and which parts of watersheds are essential to sustain natural assemblages of aquatic organisms is important to understanding their function (Dodds et al. 2004). This study adds to the growing knowledge of microinvertebrates within these systems. Even when streams are dry, microinvertebrates add to the biodiversity of tallgrass prairies. Their abilities to cope with drying disturbance allows for rapid recolonization once water returns helping to reestablish the function of these systems. Our findings exhibit that the diversity of microinvertebrates differ in the response to different drying durations. Climate change may disrupt the natural disturbance regime of these systems, leading to

longer periods of drought that could influence the invertebrate assemblage and recolonization. Manipulation of the natural stream flow, for example creating impoundments within headwaters, may increase water holding capacity and not allow natural drying disturbance needed for microinvertebrate dormant stages (Hedden et al. 2018). These factors are particularly important for those taxa that rely on drying to initiate the production of resting eggs that are critical to ensuring population survival (Brock et al. 2003, Nielsen et al. 2000, Stenert et al. 2017). With limited understanding of these systems, and their multiple potential impacts, exploration of the requirements needed for a variety of aquatic organism to utilize these systems is necessary for their ultimate preservation.

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APPENDIX

APPENDIX

TABLE 1

CHARACTERISTICS OF SAMPLE POOLS USED FOR MICROCOSM COLLECTION
(YOUNGMEYER RANCH, ELK COUNTY, KANSAS)

Pool name	Collection date	Latitude	Longitude	Water temperature (°C)	Pool size		
					Length (m)	Max. width (m)	Max. depth (mm)
C1	13-08-2020	37°32'37.4"N	96°30'35.5"W	29	3.8	2.1	115.0
C2	13-08-2020	37°32'36.8"N	96°30'31.8"W	30	8.0	1.2	270.0
C3	13-08-2020	37°32'37.0"N	96°30'30.5"W	35	5.4	1.9	210.0
C4	13-08-2020	37°32'54.4"N	96°30'04.1"W	32	8.8	5.3	290.0
C5	15-08-2020	37°32'55.3"N	96°29'57.2"W	27	3.5	1.8	150.0
C6	15-08-2020	37°32'54.3"N	96°29'54.2"W	27	6.1	1.7	205.0
C7	15-08-2020	37°33'30.4"N	96°30'41.5"W	29	5.5	2.4	140.0
C8	15-08-2020	37°33'28.1"N	96°30'40.7"W	35	3.6	1.7	170.0
C9	15-08-2020	37°33'3.82"N	96°30'3.37"W	38	4.3	1.6	120.0
C10	15-08-2020	37°32'54.6"N	96°30'02.4"W	37	3.7	1.8	150.0

TABLE 2

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR MICROINVERTERBATE ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Microinvertebrate abundance	Treatment	**3**	**236.20**	**<0.001**	Day	1.0	0.00	0.977
					Pool	**9.0**	**759.93**	**<0.001**
					Day:Two-week Drying Treatment	1.0	0.29	0.593
					Day:Four-week Drying Treatment	**1.0**	**11.74**	**0.001**
					Day:Two-week Control	**2.0**	**11.25**	**0.003**
					Day:Four-week Control	1.9	4.33	0.177

Notes: Significant terms ($P < 0.05$) are bolded.

APPENDIX (continued)

TABLE 3

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR NEMATODA ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Nematoda abundance	Treatment	**3**	**99.10**	**<0.001**	Day	**2.0**	**12.93**	**0.002**
					Pool	**9.0**	**45.73**	**<0.001**
					Day:Two-week Drying Treatment	1.0	2.07	0.150
					Day:Four-week Drying Treatment	1.0	0.82	0.366
					Day:Two-week Control	0.0	0.00	0.998
					Day:Four-week Control	2.0	3.60	0.182

Notes: Significant terms ($P < 0.05$) are bolded.

TABLE 4

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR ROTIFERA ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Rotifera abundance	Treatment	**3**	**127.30**	**<0.001**	Day	**1.9**	**7.77**	**0.037**
					Pool	**9.0**	**304.99**	**<0.001**
					Day:Two-week Drying Treatment	1.0	2.02	0.155
					Day:Four-week Drying Treatment	0.0	0.00	0.996
					Day:Two-week Control	1.7	1.00	0.399
					Day:Four-week Control	**1.0**	**9.18**	**0.002**

Notes: Significant terms ($P < 0.05$) are bolded.

TABLE 5

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR OSTRACODA ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Ostracoda abundance	Treatment	**3**	**44.62**	**<0.001**	Day	**1.0**	**4.17**	**0.041**
					Pool	**9.0**	**483.71**	**<0.001**
					Day:Two-week Drying Treatment	**1.0**	**12.01**	**0.001**
					Day:Four-week Drying Treatment	1.0	0.86	0.353
					Day:Two-week Control	2.0	4.41	0.106
					Day:Four-week Control	**2.0**	**12.50**	**0.001**

Notes: Significant terms ($P < 0.05$) are bolded.

APPENDIX (continued)

TABLE 6

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR CLADOCERA ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Cladocera abundance	Treatment	1	0.00	1.000	Day	2.0	4.53	0.120
					Pool	**9.0**	**80.18**	**<0.001**
					Day:Two-week Drying Treatment	1.0	0.90	0.343
					Day:Four-week Drying Treatment	1.0	0.00	1.000
					Day:Two-week Control	1.0	0.35	0.557
					Day:Four-week Control	1.0	0.37	0.544

Notes: Significant terms ($P < 0.05$) are bolded.

TABLE 7

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR COPEPODA ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Copepoda abundance	Treatment	**3**	**196.80**	**<0.001**	Day	1.0	3.13	0.077
					Pool	**9.0**	**632.36**	**<0.001**
					Day:Two-week Drying Treatment	0.0	0.00	0.989
					Day:Four-week Drying Treatment	**2.0**	**9.79**	**0.006**
					Day:Two-week Control	1.6	0.35	0.806
					Day:Four-week Control	1.5	1.07	0.332

Notes: Significant terms ($P < 0.05$) are bolded.

APPENDIX (continued)

TABLE 8

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR COPEPODA ADULT ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Copepoda adult abundance	Treatment	**3**	**10.89**	**0.012**	Day	1.0	0.95	0.329
					Pool	**9.0**	**304.77**	**<0.001**
					Day:Two-week Drying Treatment	**1.0**	**7.03**	**0.008**
					Day:Four-week Drying Treatment	**2.0**	**11.74**	**0.004**
					Day:Two-week Control	0.0	0.00	0.997
					Day:Four-week Control	1.0	0.04	0.834

Notes: Significant terms ($P < 0.05$) are bolded.

‘

APPENDIX (continued)

TABLE 9

SUMMARY TABLE OF PARAMETRIC AND SMOOTH TERM STATISTICAL ANALYSIS OF EACH TREATMENT FOR COPEPODA NAUPLII ABUNDANCE

Response	Parametric terms	*df*	χ^2	*p*	Smooth terms	*Ref. df*	χ^2	*p*
Copepoda nauplii abundance	Treatment	**3**	**214.50**	**<0.001**	Day	**1.0**	**22.96**	**<0.001**
					Pool	**9.0**	**455.92**	**<0.001**
					Day:Two-week Drying Treatment	**1.0**	**7.33**	**0.007**
					Day:Four-week Drying Treatment	1.0	0.22	0.639
					Day:Two-week Control	**1.9**	**18.53**	**0.001**
					Day:Four-week Control	**1.0**	**19.71**	**<0.001**

Notes: Significant terms ($P < 0.05$) are bolded.