Seasonal patterns in growth, diet, and prey availability of Brown Trout *Salmo Trutta* in groundwater-dominated streams in the Driftless Ecoregion of southeastern Minnesota

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sharing his passion and wisdom, and for his patience as I meandered down my own path toward a career in biology. He lived his life with virtue and intention, and I will always strive to make him proud. Pa – I love you, I miss you, and I will always be grateful that you were my dad. Always make sure that the sun keeps shining.

Dedication

This dissertation is dedicated to my father, Dr. Philip Andrew Cochran.

Abstract

Groundwater-dominated streams of southeastern Minnesota support highly productive populations of Brown Trout and aquatic macroinvertebrate fauna, but past research has shown that fish growth varies on spatial and temporal scales. As the diet of Brown Trout depends on the availability and abundance of aquatic macroinvertebrates, it is possible that spatial and temporal variations in macroinvertebrate assemblages (e.g. abundance, diversity, distribution) shape patterns in the growth, distribution, fitness, and abundance of Brown Trout populations. In particular, there is evidence that suggests spatial and seasonal variation in winter conditions (including water temperature and prey assemblages) may influence broader patterns of Brown Trout growth in this region. Although studies related to Brown Trout growth, diet, prey availability, and selectivity have been conducted in southeastern Minnesota, no research has addressed all of these factors simultaneously over multiple streams, seasons, and years. The overall goal of this dissertation was to examine seasonal and spatial patterns in Brown Trout growth, diet, and prey selection, and in the availability of macroinvertebrate prey in six streams that demonstrate a gradient in fish growth. Chapter 1 examines temporal and spatial differences in the growth and diet of Brown Trout, and identifies associations between diet and physical stream characteristics, including groundwater input, stream drainage area, and channel slope. Although stomach contents were dominated by relatively few taxa, including Chironomidae and *Brachycentrus*, there were significant differences in diet composition among streams and seasons. Overall, fish in most streams demonstrated positive growth during summer, winter, and spring; and winter growth was significantly associated with groundwater input. Chapter 2 addresses seasonal patterns in Brown Trout prey assemblages, including the abundance, diversity, and overlap of macroinvertebrate benthos and drift. Benthic and drift assemblages differed among streams and seasons, with most pronounced differences among streams. Abundances of drift and benthos varied significantly, with highest availability in spring and summer, and lowest availability during winter in most streams. Non-metric multidimensional scaling indicated associations between assemblage composition and groundwater input. The goal of the third and final chapter was to identify seasonal and spatial patterns in the availability and selection of macroinvertebrate prey by Brown Trout. Overall electivity

of benthos and drift varied spatially and temporally with a negative relationship between the total proportion of prey available and prey electivity. In general, Brown Trout consistently favored one or two taxa, including *Physella* and *Gammarus* while displaying negative selection for all other prey types. Foraging patterns suggested a preference of benthic feeding. Ultimately, the results of this dissertation will help managers take effective actions in mitigating the effects of climate change on stream communities. In addition to a better understanding of the influence of groundwater control on patterns in Brown Trout growth, foraging, and prey communities, this dissertation identifies key prey taxa associated with the growth of Brown Trout on seasonal and spatial scales. With this knowledge, managers can more accurately predict how climate-induced changes to water temperature and prey communities will alter fish productivity on a stream-by-stream basis. Considering the substantial economic and cultural importance of groundwater-dominated streams in southeastern Minnesota, conserving the integrity and health of stream communities through the development and implementation of science-based management plans should be a priority among natural resource managers, scientists, and policymakers.

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Prologue

      Brown Trout *Salmo trutta* are a popular, economically important recreational fish species with a wide global distribution. In Minnesota, Brown Trout became established shortly after being introduced to the United States in 1883, and, today, are particularly abundant in the Driftless Ecoregion of the southeastern portion of the state (Thorn et al. 1997). The Driftless Ecoregion, unaffected by the most recent Wisconsin glaciation, is characterized by a karst topography, featuring steep bluffs, deep valleys, sinkholes, and a high concentration of groundwater springs which emerge to form hundreds of kilometers of coldwater trout streams (Thorn et al. 1997; MNDNR 2003). Despite poor stream conditions associated with intensive agriculture and livestock grazing in the early 1900s, many streams have been restored (Thorn et al. 1997) to support healthy fish populations and a multi-million dollar recreational Brown Trout industry (Gartner et al. 2002; Hart and Ziegler 2008).

      Although groundwater-dominated streams of southeastern Minnesota support highly productive populations of Brown Trout and aquatic macroinvertebrate fauna (Waters 1977, 1983; Kwak and Waters 1997), past research has shown that fish growth varies on spatial (MN DNR 1997; Dieterman et al. 2004; French 2014) and temporal scales (Newman and Waters 1989). Water temperature, a principal factor regulating fish growth, was suggested as the primary limiting factor for Brown Trout productivity in southeastern Minnesota (Kwak 1993); however, results from bioenergetics modeling indicated that temperature alone did not directly account for observed differences in growth (Dieterman et al. 2004). Alternatively, this modeling suggested that variation in Brown Trout growth across southeastern Minnesota may be due to other factors, including seasonal differences in diet composition and prey availability (Dieterman et al. 2004).

      In general, groundwater-fed streams in the Driftless Ecoregion contain highly mineralized water, supporting abundant populations of aquatic macroinvertebrate fauna (Waters 1977), which are the primary prey for Brown Trout in southeastern Minnesota streams (Dieterman et al. 2004). As the diet of Brown Trout depends on the availability and abundance of aquatic macroinvertebrates, it is possible that spatial and temporal variations in macroinvertebrate assemblages (e.g. abundance, diversity, distribution)

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shape patterns in the growth, distribution, fitness, and abundance of Brown Trout populations. Research in other regions shows that the diet of stream-dwelling trout shifts on a seasonal basis, often following the availability of aquatic and terrestrial macroinvertebrates (Newman and Waters 1984; Kelly-Quinn and Bracken 1990; Forrester 1994; Nakano et al. 1999; Sweka and Hartmen 2001; Lagarrigue et al. 2002; Gíslason and Steingrímsson 2004; Kara and Alp 2005; Laudon et al. 2005; Romero et al. 2005; Romaniszyn et al. 2007). There is also evidence that seasonal growth of stream-dwelling salmonids increases when temperatures are optimal (Jensen 1990; Filbert and Hawkins 1995; Drake and Taylor 1996) and prey is more abundant (Cada et al. 1987; Filbert and Hawkins 1995); however, most research has addressed these trophic levels separately, and on limited spatiotemporal scales (Richardson 1993; Waters 1993).

Although studies examining Brown Trout growth, diet, prey availability, and selectivity have been conducted in southeastern Minnesota, no research has addressed all of these factors simultaneously over multiple streams, seasons, and years. In particular, there is evidence that suggests seasonal disparities in Brown Trout diet and growth, with studies documenting substantial winter growth (Kwak and Waters 1997; Anderson 2012; French et al. 2014), low winter mortality (Dieterman and Hoxmeier 2011), and seasonal variations in prey assemblages, including the presence of ultra-cold stenotherm insects that develop and emerge during winter (Bouchard and Ferrington 2009). Elsewhere in the literature, winter has been traditionally considered a period of dormancy for aquatic ecosystems, during which growth rates, condition, and survival of salmonids and availability of prey may decline (Quinn and Peterson 1996; Schultz and Conover 1999; Post and Parkinson 2001). In contrast, winter may be a period of critical growth of Brown Trout in southeastern Minnesota, and spatial and seasonal variation in winter conditions (including water temperature and prey assemblages) may influence broader patterns of survival and growth in this region. Particularly, groundwater inputs may create conditions that are favorable for Brown Trout and their prey, including thermal refugia during winter and cool water refuges during summer. Groundwater influence has been associated with increased winter survival of stream-dwelling salmonids in Wisconsin (Hunt 1969) and Idaho (Smith and Griffin 1994), and increased benthic

productivity and richness (Coleman and Dahn 1990; Hagerthey and Kerfoot 1998; Dent et al. 2000).

Understanding seasonal and spatial patterns in Brown Trout growth, foraging, prey availability, and prey selection may aid in the future management of groundwater-dominated streams, as climate change is expected to alter physical conditions and biological communities of streams in this region (Lyons et al. 2010; Johnson 2015). Overall, stream ecosystems in southeastern Minnesota support healthy communities of fish and aquatic invertebrates, and sustain relatively stable thermal conditions due to the constant influx of groundwater inputs. Climate change, however, is expected to alter water temperatures, and thereby impact stream biota (Pilgrim et al. 1998; Lyons et al. 2010). Coldwater fish species and cold-adapted prey inhabiting these streams may be especially vulnerable, as southeastern Minnesota already has the warmest and wettest climate of the entire state (annual average air temperature 9.4°C annual precipitation averaging 86.9 cm) (Mundahl et al. 2015). In order for managers to take effective actions in mitigating effects of climate change on stream communities, it is necessary to better understand the influence of groundwater control on patterns in Brown Trout growth, foraging, and prey communities. Also, by identifying key prey taxa associated with Brown Trout growth on seasonal and spatial scales, managers can more accurately predict how climate-induced changes to prey communities will alter fish productivity. In addition to increased stream temperatures, climate change is expected to influence other aspects of weather, including the magnitude and intensity of rainfall events, which can directly impact aquatic macroinvertebrate communities through increased discharge and physical disturbances. Coupling spatial-temporal information about macroinvertebrate assemblages with the knowledge of how changes in physical habitat or disturbances may influence the availability of specific taxa can drive more effective management decisions. Considering the substantial economic and cultural importance of groundwater-dominated streams in southeastern Minnesota, conserving the integrity and health of stream communities through the development and implementation of science-based management plans should be a priority among natural resource managers, scientists, and policymakers.

Chapter summaries

The overall goal of this dissertation was to examine seasonal and spatial patterns in Brown Trout growth, diet, and prey selection, and in the availability of macroinvertebrate prey in a six streams that demonstrate a gradient in fish growth (Dieterman et al. 2004) and groundwater influence (Krider et al. 2013).

Chapter 1 examines temporal and spatial differences in the growth of Brown Trout, and in the composition of Brown Trout diets, identifying key prey taxa among streams and seasons. Patterns in diet composition among streams were compared with non-metric multidimensional scaling to identify associations between diet and physical stream characteristics, including groundwater input, stream drainage area, and channel slope. Chapter 2 examines seasonal patterns in Brown Trout prey assemblages, including the abundance, diversity, and overlap of macroinvertebrate benthos and drift. The goal of Chapter 3 is to identify seasonal and spatial patterns in the availability and selection of macroinvertebrate prey by Brown Trout.

Format of the chapters

Each chapter was prepared as a separate manuscript for publication within the primary literature. Chapter 1 was prepared for submission to *North American Journal of Fisheries Management* (Taylor and Francis), and Chapters 2 and 3 were prepared for submission to *Freshwater Science* (BioOne). The contents of these chapters may differ from those that are published in the primary literature.

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Chapter 1

Seasonal patterns in growth and diet of Brown Trout across six groundwater-fed streams in the Driftless Ecoregion of southeastern Minnesota

(Formatted for submission to *North American Journal of Fisheries Management*)

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Summary

Despite high overall productivity, growth rates of Brown Trout *Salmo trutta* vary across streams in the Driftless Area Ecoregion of southeastern Minnesota. Although water temperature is widely considered the most important regulator of fish growth, previous research in southeastern Minnesota suggested that seasonal variation in diet composition and prey availability may play an equally important role in determining growth. We collected stomach samples from Brown Trout in six streams on a seasonal basis between November 2010 and October 2013 to investigate seasonal and spatial patterns in diet. Growth was measured directly from fish that were marked and recaptured simultaneously with diet collection. In all streams, Brown Trout fed continuously and demonstrated positive growth during most seasons of the year: winter, spring, and summer; and there was a positive relationship between winter growth and groundwater input. Overall, Brown Trout diets contained mostly aquatic macroinvertebrates and demonstrated little seasonal variation within individual streams and when diet data from all streams were aggregated. However, comparisons of winter and spring diets across all streams revealed stream-specific variation. Diet composition may be similar in streams that share thermal conditions during spring, and to a lesser extent winter. In contrast to surface-fed streams, groundwater-dominated streams are strongly controlled by thermal inputs that likely shape the community of available prey and regulate growth potential. With knowledge about what Brown Trout consume and how they grow on a seasonal basis, fisheries managers can identify key prey and predict how changes in prey communities may impact trout production.

Key words: Brown Trout, Salmonidae, trophic ecology, seasonal growth, Driftless Ecoregion

Introduction

        Historically, groundwater-dominated streams in southeastern Minnesota have supported productive populations of Brown Trout (MN DNR 1997). In this region, streams that yield faster growing fish typically produce larger bodied individuals, which are favored by many anglers (Gartner et al. 2002). Such recreational importance is especially relevant for introduced Brown Trout *Salmo trutta* in the Driftless Ecoregion of Illinois, Iowa, Minnesota, and Wisconsin (Snook and Dieterman 2006). In Minnesota, sport fishing for Brown Trout contributes more than 150 million dollars to the state's economy (Gartner et al. 2002).

        However, despite high overall productivity, previous research has indicated that growth rates of Brown Trout vary across groundwater-dominated streams in southeastern Minnesota (MN DNR 1997; Dieterman et al. 2004). Across the global range of Brown Trout, there have been several factors associated with variation in growth rates, including water temperature (Elliott 1994), social structure, population density and intraspecific competition (Fausch 1984, 1988; Alanärä et al. 2001), and patterns of movement (Lobón-Cerviá 2005; Kaspersson and Höjesjö 2009). Until recently, few studies have examined the importance of these factors on growth in the Driftless Ecoregion of the upper Midwestern United States (Dieterman 2012). Although Kwak (1993) suggested water temperature to be a limiting factor for Brown Trout growth in southeastern Minnesota, more recent bioenergetics modeling found that temperature alone did not explain differences in growth among streams in this region (Dieterman et al. 2004). These bioenergetics models predicted slower growth in streams where observed growth rates were faster during the summer. In addition, predicted weight gains from the model using constant temperature and field estimated consumption rates were associated with observed weight gains, whereas there were no associations in predicted and observed weight gains in the model run with constant consumption rates and field measured temperature regimes. This suggested that factor(s) associated with Brown Trout diets or consumption may have been larger modifiers of growth than water temperature. When temperature was held constant, hypothetical diets predicted greater weight gains for fish eating higher amounts of energy-rich prey. Overall, variation in Brown Trout growth in

southeastern Minnesota may be due to factors in addition to temperature, such as seasonal differences in diet composition and prey availability (Dieterman et al. 2004).

Accounting for variation in seasonal growth is an important, but challenging step in understanding what drives differences in growth among allopatric populations of stream-dwelling salmonids. On a temporal basis, seasonal shifts in several environmental factors, including water temperature and food availability, have been shown to result in variation in the growth of stream-dwelling salmonids (Cooper 1953; Jones et al. 2002; Letcher and Gries 2003). Typically, seasonal growth of stream-dwelling salmonids increases when food is more abundant (Cada et al. 1987; Filbert and Hawkins 1995) and temperatures are optimal (Jensen 1990; Filbert and Hawkins 1995; Drake and Taylor 1996).

Many studies examining food consumption and the mechanisms governing growth of Brown Trout have focused on a single stream or were restricted to the typical growing season (spring through autumn) (Spalding et al. 1995; Quinn and Peterson 1996; Kahler et al. 2001; Hesthagen et al. 2004; Arnekleiv et al. 2006). However, a focus on a single season or stream may not adequately explain the substantial variation in growth and yield observed in southeastern Minnesota. Kwak and Waters (1997) documented Brown Trout production in southeastern Minnesota streams during winter, but research in other regions has suggested that winter is stressful for trout, during which growth rates, condition, and survival may decline (Quinn and Peterson 1996; Schultz and Conover 1999; Post and Parkinson 2001). Slower growth rates during winter are often attributed to the effects of decreased temperature on Brown Trout metabolic function, with a minimum temperature of approximately 3.6°C required for growth (Elliott et al. 1995). In surface water-dominated streams, water temperatures fluctuate relative to air temperatures and often drop below 3.6°C during winter in temperate regions (Pilgrim et al. 1998). In contrast, the water temperature of groundwater-dominated streams, such as those in southeastern Minnesota, fluctuates less on a seasonal basis. Thermal regimes of groundwater-dominated streams are buffered by springs and seeps, which provide a continuous inflow of water at a temperature that is generally equal to mean annual air temperature (Erickson and Stefan 2000). Such thermal buffering may contribute to

winter water temperatures that remain suitable for Brown Trout growth even when air temperatures are below freezing across southeastern Minnesota (Dieterman et al. 2012; Krider et al. 2013; French 2014), as has been documented in other regions (Power et al. 1999; O'Driscoll and DeWalle 2006). Warmer winter temperatures of groundwater-dominated streams may allow Brown Trout to actively feed and to grow through efficient functioning of metabolic processes (Cunjak and Power 1987). In a study comparing growth patterns of Brown Trout among different thermal regimes, Nicola and Almodóvar (2004) found that models underestimated growth in the coldest rivers, suggesting that factors other than water temperature may regulate variation in growth, as well as the possibility of local adaptation. Although the volume of groundwater input varies among streams in southeastern Minnesota (Williams and Vondracek 2010; Krider et al. 2013), a recent study in this region positively associated variability in groundwater input with Brown Trout growth and condition during winter (French 2014).

Seasonal shifts in other environmental conditions may also influence patterns of Brown Trout growth across seasons, as mediated by foraging activity and metabolism. During summer, many populations of stream-dwelling trout may rely on terrestrial macroinvertebrates as a potentially significant food source (Kelly-Quinn and Bracken 1990; Bridcut 2000; Kawaguchi and Nakano 2001; Utz and Hartman 2007); however, Laudon et al. (2005) found that terrestrial fauna were poorly represented in Brown Trout diets in a single stream in southeastern Minnesota. Although most trout feed on aquatic macroinvertebrates during winter (Cunjak et al. 1987; Kelly-Quinn and Bracken 1990), limited production of aquatic macroinvertebrates coupled with the absence of terrestrial macroinvertebrates during winter may be significant enough to cause substantial declines in growth (Newman and Waters 1984; Gíslason 1985; Rundio and Lindley 2008). In southeastern Minnesota, winter abundances of aquatic macroinvertebrates in groundwater-dominated streams may be higher relative to surface-water dominated streams during winter, supporting the potential for overwinter growth of Brown Trout (Bouchard and Ferrington 2009; Anderson 2012).

Among the aquatic macroinvertebrate taxa available, several ultra-cold stenotherm Chironomidae species that develop and emerge during winter (Bouchard and

Ferrington 2009; Jane Mazack, personal communication) have been documented as an important winter food resource for Brown Trout across southeastern Minnesota (Newman and Waters 1984; French 2014). To date, the importance of contributions of seasonally available prey, including ultra-cold stenothermic aquatic species during winter and terrestrial invertebrates during summer, to groundwater-dominated stream food webs is poorly understood, but may be associated with seasonal variation in growth of Brown Trout.

In addition to the importance that understanding the factors driving variation in growth among Brown Trout populations may have on the management of recreational fisheries in southeastern Minnesota, this knowledge may also shed light on how the trophic web in groundwater-fed streams may shift in response to climate change. To date, most studies have focused on the impact of climate change on the survival and distribution of stream-dwelling fishes (Lyons et al. 2010). With respect to groundwater-fed streams, groundwater input and thermal refugia are primary factors that determine the response of coldwater habitat to climate change and the subsequent distribution of various fish species, including Brown Trout (Meisner et al. 1988; Chu et al. 2008). In Michigan and Wisconsin, Wehrly et al. (2007) found that upper lethal temperature limits for Brown Trout depended on the number of consecutive days of exposure to high stream temperature. Other studies have reported that low flow conditions and groundwater input during summer or fall limited salmonid survival (Chu et al. 2008; Arismendi et al. 2012; Grantham et al. 2012). Groundwater-fed streams with groundwater input are projected to be more resilient to climate change, providing a greater degree of stability to help salmonids survive the predicted extreme fluctuations in flow and temperature (Petty et al. 2012). Alternatively, land development activities such as forestry and urbanization may have the opposite effect, resulting in stream communities that are less resilient to changes in physical conditions related to climate change (Curry et al. 2002; Nelson et al. 2009). By examining the seasonal dynamics of Brown Trout in several groundwater-fed streams along a gradient of water temperature and observed growth, we may gain insight as to how the timing and availability of critical resources may alter the health of trout populations in southeastern Minnesota.

The goal of this study was to examine seasonal and spatial variation in the diet and growth of Brown Trout between November 2010 and October 2013 in six streams. Specifically, our objectives were to: 1) determine whether the proportional composition of prey types varied seasonally and spatially; 2) quantify and identify seasonally important aquatic invertebrate prey taxa in Brown Trout diets, specifically including winter; 3) examine relationships of groundwater input, stream drainage area, and channel slope with patterns of Brown Trout diet composition across seasons; and 4) quantify seasonal and spatial trends in growth rates of Brown Trout.

Methods

Study area

      This study was conducted in six groundwater-dominated streams located in the Driftless Ecoregion of southeastern Minnesota (Figure 1). This region was relatively unaffected by the most recent glaciations and is characterized by a karstic geology that supports a high density of groundwater fed streams (MNDNR 2003; Williams and Vondracek 2010). A high concentration of active springs provides these streams with a continuous supply of fertile water, supporting highly diverse and abundant assemblages of aquatic invertebrates (Waters 1977), and productive populations of Brown Trout (Thorn et al. 1997; Newman and Waters 1989; Kwak and Waters 1997).

Sample sites

      To examine spatial variation in diet and growth of Brown Trout, we selected six streams using Dieterman et al. (2004), which provided estimates of annual growth for Brown Trout in several streams across the study area. Site selection was based on stream accessibility, fish abundance, and a gradient of growth as characterized by Dieterman et al. (2004). Physical characteristics (e.g. thermal regime, drainage area) were typical of groundwater-dominated streams of southeastern Minnesota (Table 1). A reach of about 200m was selected at each stream for fish sampling. Most streams contained varying degrees of habitat alteration for trout management (Thorn et al. 1997). Study streams demonstrated a "summer-cold/winter-warm" effect and remained free of ice during winter, with the exception of Rush Creek where surface ice formed in pools and areas of low flow.

Fish and diet collection

      To examine seasonal variation in growth and diet of Brown Trout, we collected trout at each site on four to six sample dates per year from 2010-2013 using a Smith Root® (Washington, USA) LR 20B backpack electrofisher (Table 1). Although we attempted to sample equally during all seasons, logistical limitations and Brown Trout spawning resulted in some disparity among the number of sample dates within each season across all streams. Following a single pass of electrofishing, captured fish were

placed within in-stream holding pens, anesthetized with an immobilizing dose of clove bud oil, weighed (± 1g), and measured (± 1mm TL). Up to 150 trout (>100mm total body length) per stream per year were tagged in the anterior portion of the body cavity with 9mm passive integrated transponder (PIT) tags (Biomark Inc.; Idaho, USA) to measure instantaneous daily growth (mg). Random subsamples of up to 30 fish on each sampling date were selected to examine diet composition using gastric lavage. After processing, fish were placed into a separate holding pen within the stream to recover from anesthesia and then released into the study site. Stomach contents were preserved in 95% ethanol in the field and later processed in the laboratory.

Estimation of physical variation

Drainage area and 10-85% channel slope were calculated for each stream with the sample site as the downstream boundary. Linear regression models of air-water temperature relationships to estimate groundwater input in study streams were created using Microsoft Excel. Air temperatures were obtained online from NOAA's National Climatic Data Center. Daily maximum and minimum air temperatures were averaged on a weekly scale. Mean weekly water temperatures were obtained from HOBO temperature loggers placed in each stream. Y-intercepts reflect water temperature when air temperature is 0°C; slopes close to one suggest less groundwater input and a greater influence of air temperature on water temperature, whereas slopes close to 0 suggest more groundwater input and a reduced influence of air temperature on water temperature. Air-water temperature regressions were only conducted for the first two years of the study due to lost water temperature loggers during the final year of the project (Table 2).

Analysis

Aquatic macroinvertebrates in diet contents were sorted, identified to the lowest practical taxonomic group, and counted; only intact specimens or fragments greater than one-half an intact individual were included. Since direct measurements of mass were not possible due to partial digestion, dry weight of aquatic invertebrates was estimated with mean morphological measurements using equations from Benke et al. (1999) and Méthot et al. (2012). Mean morphological measurements of aquatic invertebrates (body length, shell width) were calculated for each sample date using subsamples of 20 intact

individuals per taxon randomly selected from Brown Trout diets. Dry weight was multiplied by taxa counts to obtain dry weight composition of diet for each fish. A one-way analysis of variance (ANOVA) was used to compare dry weight consumption and number of prey items per stomach among seasons and streams. In addition, frequency of occurrence (%F), and the numeric (%N) and weight (%W) contribution of each prey taxon to a given fish were calculated for each sample date. To rank the overall contribution of individual prey taxa to a sample population, we used the following formula for index of relative importance (IRI) from Pinkas et al. (1971):

$$\%IRI = \%F \ (\%N + \%W)$$

The index of relative importance (IRI) is a useful method to quantify and compare diet composition across several groups that captures the proportional contribution of prey in terms of mass, frequency, and abundance (Cortés 1997).

We evaluated pairwise and across-group differences in diet composition using multi-response permutation procedures (MRPP; Mielke et al. 1984; Mielke and Berry 2001) performed in program R (version 3.1.2). MRPP makes no distributional assumptions and calculates a distance matrix using any number of possible distance measures (Smith 1998). Probability of type I error is calculated using a randomization algorithm that allows for comparison between observed δ (weighted mean within-group distance) and the randomized δ distribution. This probability value expresses the likelihood of generating a random δ smaller than the observed value. An effect size of *A* was also calculated as

$$A = 1 - \frac{observed\ \delta}{expected\ \delta}$$

and represents observed within-group homogeneity relative to what can be expected by chance (McCune and Grace 2002). For our purposes, this is a measure of the overall dietary agreement among Brown Trout feeding within the group designated (e.g. stream, season, year). Within-group homogeneity is greater than the random observation when *A>0* and less when *A<0*. The *A*-value is useful in attaching ecological significance to observed differences among groups because it is independent of sample size (Mielke et al. 1984; McCune and Grace 2002). Prey groups with a relative importance >1% were retained for analysis, and proportions of diet contents were arcsine transformed prior to

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analysis. Small numbers of fish were collected in Rush Creek (Table 1), thus this site was omitted from the MMRP analyses.

Non-metric multidimensional scaling (NMDS) was used to examine patterns of diet composition among streams and seasons, and the influence of three stream physical characteristics: drainage area, channel slope, and groundwater input. NMDS is an ordination technique that allows qualitative assessments of diet composition patterns based on the positioning of streams and prey taxa on a multi-dimensional plot. NMDS plots were constructed to identify trends in seasonal diet composition within and among the study streams. Prey taxa closer to a stream on an NMDS plot make up a larger portion of the diet for that stream than taxa further apart. NMDS was conducted in program R (version 3.1.2) using the metaMDS function, located in the vegan library. Default settings for metaMDS were used for all analyses. Stress values lower than 0.20 are generally considered to provide a useful ordination. Diet items that made up <1% of the mean total dry weight for each stream in each season were omitted from the analyses. Groundwater input, drainage area, and channel slope were fit to NMDS plots using the envfit function from the vegan library in program R to examine their relationship with diet composition patterns. Additionally, sampling was limited due to overlap with Brown Trout spawning during fall, thus this season was omitted from the NMDS analyses.

Instantaneous daily growth (G) was calculated for all tagged fish recaptured on at least two, subsequent sampling events to estimate seasonal growth of Brown Trout, using the following equation:

$$G = \frac{lnW_2 - lnW_1}{t_2 - t_1}$$

where W represents weight (g) and t represents the number of days between resampling events. Variation in mean seasonal growth rates both within and among streams and seasons were analyzed using ANOVA followed by Tukey's HSD test.

Results

Diet composition

  Across all six streams, 2176 Brown Trout stomachs were collected and analyzed for diet contents between November 2010 and October 2013 (Table 1). Empty stomachs were rare (less than 5% in each stream). During summer Brown Trout consumed a mean of 34.5 prey by number, followed by spring ($\bar{x}$=32.5), fall ($\bar{x}$=27.0), and winter ($\bar{x}$=19.3), but there were no significant differences across seasons (Figure 2). In contrast, spatial variation in prey consumption was more pronounced (Figure 2). Brown Trout collected in Garvin Brook contained a mean of 48.9 prey items, which was significantly greater than the mean number of prey consumed in Rush Creek ($\bar{x}$=14.4; p<0.01) and Gribbon Creek ($\bar{x}$=21.9; p=0.04) (Figure 2).

Similar to number of prey consumed, total dry weight (mg) of prey in Brown Trout stomachs did not vary significantly among seasons, but followed a similar pattern. Overall, stomachs contained the highest mass of prey during summer ($\bar{x}$=70.9 mg), followed by spring ($\bar{x}$=63.1 mg), fall ($\bar{x}$=38.0 mg), and winter ($\bar{x}$=28.7 mg) (Figure 3). In contrast, spatial differences in mean dry mass consumed were more significant, and ranged from 19.1 mg in Trout Run Creek to 86.2 mg in Rush Creek (p=0.02) (Figure 3). Across all study streams, there were no significant correlations between seasonal diet consumption (mg dry mass/mm) and air-water temperature regression slopes (fall: F=0.98, p=0.41; winter: F=0.12, p=0.32; spring: F=2.7, p=0.17; summer: F=3.0, p=0.15).

  Diet composition displayed little variation among or between seasons when data from all streams were combined (excluding Rush Creek) based MRPP analyses (Table 2). Collectively, > 75% of diet composition consisted of Trichopterans (consisting mostly of encased *Brachycentrus* and Limnephilidae larvae), Chironomidae (mostly larvae and pupae), Gastropoda (dominated by *Physella*), and *Gammarus* based on relative importance values (Figure 4). Similarly, diet composition did not vary substantially on a seasonal basis within streams (see Appendix P), except for Beaver Creek (MRPP, A=0.13, p<0.01) (Table 3). In contrast, variation in diet was more pronounced when seasonal diets were compared across all streams, particularly during winter (MRPP, A=0.27, p<0.01) and spring (MRPP, A=0,12, p<0.01) (Table 3). During winter,

Trichopterans, including *Brachycentrus*, *Glossosoma*, and Limnephilidae, were the most important prey items, exceeding 40% of relative importance within all streams, except Daley Creek, where winter diets were dominated by *Gammarus* (Figure 5). Additionally, Chironomidae was an important prey item in all streams except Gribbon Creek, where Gastropoda (mostly *Physella*) contributed greater than 50% of relative importance (Figure 5). During spring, Chironomidae, *Brachycentrus*, and Limnephilidae combined to contribute >50% relative importance in Trout Run Creek, Beaver Creek, and Garvin Brook (Figure 5). In Daley Creek, *Gammarus* and Gastropoda dominated spring diets, whereas Ceratopogonidae, Chironomidae, and Gastropoda dominated spring diets in Gribbon Greek (Figure 5).

Overall diet composition among streams (excluding Rush Creek) was significantly different when diet data from all seasons were combined (MRPP, A=0.11, p<0.01) (Table 3). Likewise, all pairwise comparisons of diet composition between streams revealed significant differences, with the exception of Trout Run Creek and Garvin Brook (Table 3). Brown Trout consistently fed on Trichopteran (*Brachycentrus* and Limnephilidae) and Chironomidae, which made up the two most important prey groups by relative importance in Beaver Creek (44.5%, 24.4%, respectively), Garvin Brook (35.7%, 26.2%, respectively), and Trout Run Creek (22.2%, 38.7%, respectively) (Figure 6). In Daley Creek, *Gammarus* was the most important prey item (48.9%) and Gastropoda, mostly *Physella*, was the most important prey item in Gribbon Creek (32.2%) (Figure 6).

Fish growth

The number of recaptured Brown Trout varied among streams and sample dates, and ranged from 0 to 64 tagged fish (Table 1, Appendices A-E). When values from all seasons and years were combined, instantaneous daily growth rates (G) of Brown Trout varied significantly across all streams (F=5.8, p<0.01). Brown Trout demonstrated the highest growth rates in Daley Creek ($\bar{x}$=0.20), which were significantly greater than those observed in Garvin Brook ($\bar{x}$=0.13, p<0.01) and Trout Run Creek ($\bar{x}$=0.10, p<0.01) (Figure 7). When only measurements of annual growth rates are considered, growth by fish in Daley Creek ($\bar{x}$=0.22) was still significantly greater than growth of fish in Trout

Run Creek ($\bar{x}$=0.11, p<0.01), however, growth rates in the remaining streams followed a different pattern (Figure 8).

When growth estimates from all streams during all years were combined, growth rates also varied significantly by season (F=16.1, p<0.01). Overall, fastest growth occurred during spring ($\bar{x}$=0.22), followed by summer ($\bar{x}$=0.19), winter ($\bar{x}$ = 0.15), and fall ($\bar{x}$ =0.02) (Figure 10). Variation in instantaneous daily growth rate was highest during spring (SD=0.24) and winter (SD=0.22), and lowest during fall (SD=0.11) (Figure 9).

When growth estimates from all years were combined, seasonal growth rates varied significantly within all streams (Beaver Creek: F=4.5, p<0.01; Daley Creek: F=8.1, p<0.01; Garvin Brook: F=6.3, p<0.01; Gribbon Creek: F=5.6, p<0.01; and Trout Run Creek: F=6.3, p<0.01). Overall, growth rates were consistently lowest during fall in all streams across all study years (Figure 10). Although mean growth rates were generally positive during remaining seasons, seasons of fastest growth varied considerably within each stream and across years. For instance, in the first year of the study, the fastest and slowest growth rates were both observed during winter (Daley Creek: $\bar{x}$=0.23; Trout Run Creek: $\bar{x}$= −0.08). Likewise, although the slowest fish growth occurred during winter in Beaver Creek ($\bar{x}$=0.04) and Garvin Brook ($\bar{x}$=−0.03) during the first year (2011) of the study, this season was the period of fastest growth for fish in these streams during year two (2012) ($\bar{x}$=0.19, $\bar{x}$=0.28, respectively). With the exception of Gribbon Creek, fastest growth rates consistently occurred during spring, the season of fastest growth occurred in >1 season when all years were compared in the remaining streams (Figure 10).

When seasonal growth data were combined across all years, fastest growth rates were achieved during spring by fish in Daley Creek (43.8%) and Gribbon Creek (44%) (Figure 11). Brown Trout achieved the greatest overall growth during summer in the remaining streams, including 38.3% in Beaver Creek, 39.9% in Garvin Brook, and 51.1% in Trout Run Creek (Figure 11). Winter ranked third in seasonal growth in all streams, with the exception of Gribbon Creek, where winter growth ranked second (Figure 11). Mean winter growth rate and groundwater input (represented by the slope of the air-water

temperature regression) were significantly correlated (r^2=0.43, p=0.04) during the first two years of the study (Figure 12).

NMDS analyses

Non-metric multidimensional scaling identified patterns in seasonal Brown Trout diet composition within and among streams. Ordinations resulted in convergent solutions when seasonal diet was analyzed in all seasons and within all streams, excluding Rush Creek. Groundwater input ($r^2 = 0.85$, p=0.06), drainage area ($r^2 = 0.45$, p=0.36), and channel slope ($r^2 = 0.31$, p=0.52), were not significantly associated with diets during winter (Figure 13). In spring, groundwater input was significantly associated with diet ($r^2 = 0.94$, p=0.01), however, drainage area ($r^2 = 0.69$, p=0.16) and channel slope ($r^2 = 0.15$, p=0.78) were not significantly associated with diet (Figure 14). Likewise, groundwater input ($r^2 = 0.06$, p=0.91), drainage area ($r^2 = 0.37$, p=0.52), and channel slope ($r^2 = 0.39$, p=0.40) were not significantly associated with summer diets (Figure 15).

Discussion

       In this study, Brown Trout demonstrated active, year-round foraging based on low percentage of empty stomachs (<5% on all sample dates) and the quantity of prey consumed, ranging from a mean of 19.1 items and 27 mg during winter to 34.5 items and 70.9 mg during summer. The mean number or mass of prey consumed across seasons were not significantly different; however, spatial differences between streams were more pronounced. Interestingly, Brown Trout in Rush Creek contained the fewest prey by number (14.4), but highest overall mass (86.2 mg), with stomach contents dominated by larger bodied macroinvertebrates, including encased larval *Brachycentrus* and Limnephilidae. Brown Trout in Trout Run Creek contained the smallest mean mass of prey (19.1 mg), primarily small-bodied larval aquatic Dipterans, including Chironomidae and Simuliidae.

       Water temperature regulates Brown Trout foraging activity, with reduced feeding rates at temperatures near 3.6°C (Elliott 1975a). Maximum feeding rates, as well as the amount of food consumed by Brown Trout, are also influenced by water temperature. Elliott (1975b) found feeding rates to peak between 6.8 and 19.3°C, with marked decreases below and above this temperature range. Brown Trout obtain more energy per food item at higher temperatures because of an increased absorption efficiency, which increases with temperature up to approximately 15°C (Elliott 1976). Although there was no significant relationship between groundwater input and seasonal mean prey consumption by Brown Trout in this study, seasonal temperatures remained >5°C during winter, and low enough during summer for fish to maintain active foraging. Therefore, seasonal differences in prey consumption in these five streams were likely driven by factors other than water temperatures, such as the types and abundances of prey (Dieterman et al. 2004).

       Overall, when data from all streams were combined, only five aquatic macroinvertebrate taxa yielded > 75% of relative importance: *Brachycentrus*, Limnephilidae, Chironomidae, Gastropoda (dominated by *Physella*), and *Gammarus*. During winter, the majority of diets consisted of aquatic macroinvertebrates, which has been observed in other populations of stream-dwelling trout (Cunjak et al. 1987; Kelly-

Quinn and Bracken 1990). Although aquatic macroinvertebrate abundance can be reduced during the winter season (Newman and Waters 1984; Gíslason 1985; Rundio and Lindley 2008), recent evidence suggests that the presence of seasonally available taxa can increase the relative abundance of aquatic macroinvertebrates in groundwater-dominated streams relative to surface-water dominated streams during winter (Bouchard and Ferrington 2009). French et al. (2014) and Anderson (2012) found that the winter diets of Brown Trout in southeastern Minnesota were dominated by aquatic macroinvertebrate taxa including *Gammarus*, Trichopterans, and Dipterans, especially Chironomidae.

Although Brown Trout have demonstrated size-selective foraging in southeastern Minnesota (Newman and Waters 1984), Chironomidae, the smallest bodied of the top prey consumed, were the most important prey type during fall, winter, and spring in all streams in the present study. The consumption of Chironomidae may reflect elevated abundance and accessibility, especially during late winter and early spring when large emergences were often observed. In addition, similar to reports by French et al. (2014) and Anderson (2012), *Physella* was an important winter prey item that may be a unique contributor to diets of Brown Trout in southeastern Minnesota when compared to other geographic regions.

Although the relative importance of prey types shifted during summer, the majority of Brown Trout diets consisted of the same five aquatic macroinvertebrate taxa. In many stream systems, summer may coincide with a lower availability of aquatic insects and elevated availability of terrestrial invertebrates (Hunt and Krokhin 1975; Garman 1991; Rincón and Lobón-Cerviá 1997; Nakano et al. 1999; Nakano and Murakami 2001). Consequently, trout may consume higher amounts of terrestrial invertebrates during summer (Nilsson 1955; Nakano et al. 1999; Nakano and Murakami 2001; Mistak et al. 2003). Terrestrial invertebrates made up 10% of trout diet and only 3% of available drift in a southeastern Minnesota stream, suggesting possible selection toward terrestrial prey (Laudon et al. 2005). In the present study, we observed Brown Trout to opportunistically consume high proportions of terrestrial invertebrates on sample dates following significant rainfall events, but the overall contribution of terrestrial prey to diets was less than 5% overall. In contrast to studies such as Cada et al. (1987), where

low summer growth of Brown Trout was attributed to inadequate prey base and high metabolic demands due to warm water temperatures, the present study provides evidence that aquatic prey availability is not limited during summer in southeastern Minnesota. In addition to consuming the high quantities of prey during summer, Brown Trout in our study consistently achieved positive growth.

Although the seasonal variation in Brown Trout diet composition across all streams and within individual streams was not substantial, spatial differences in overall diet (when data from all seasons were combined) were much more pronounced. Trichopterans (mostly larval, encased forms of *Brachycentrus* and Limnephilidae) contributed at least 40% of relative importance in every stream, with the exception of Daley Creek, where *Gammarus* dominated stomach contents. Although remaining prey largely consisted of Chironomidae and *Physella*, the proportions varied significantly across streams.

Fastest mean growth ($\bar{x}$=0.22/day) occurred in spring, followed by summer ($\bar{x}$=0.19/day), winter ($\bar{x}$=0.15/day), and fall ($\bar{x}$=0.02/day) when growth rates from all streams and study years were combined. However, comparing seasonal contributions toward overall growth within each individual stream, fastest growth occurred in summer in three of five study streams [Beaver Creek (38.3%), Garvin Brook (39.9%), and Trout Run (51.1%)], whereas the highest growth occurred during spring in Daley Creek (43.8%) and Gribbon Creek (44.1%).

Other studies have reported fastest growth in spring and summer for stream-dwelling salmonids in southeastern Minnesota (Dieterman et al. 2012) and elsewhere (Carlson et al. 2007; Utz and Hartman 2009; Xu et al. 2010). Carlson et al. (2007) attributed the pattern to increased flow and food availability during the spring. Although a linear regression between mean seasonal growth rate and mean seasonal food consumption (prey number and mass) did not reveal a significant relationship, Brown Trout stomachs contained the highest mean mass/number of prey in spring and summer, suggesting that active foraging may support elevated growth during these periods. A widespread reduction in growth took place during fall in all streams, although mean consumption ($\bar{x}$=10.9 mg and 27.0 prey items), water temperature and prey availability

were likely suitable for Brown Trout growth. Elliott (1989) suggested that this trend could be related to seasonal rhythms in feeding motivation, with a loss of appetite associated with the onset of fall and reductions in water temperature. In addition, changes in photoperiod may influence growth, where the progressive increment of day length may stimulate growth in spring but diminish in fall (Boeuf and Le Bail 1999).

Interestingly, despite reports of poor winter growth in other populations of stream-dwelling Brown Trout (e.g. Cunjak and Power 1987; Kelly-Quinn and Bracken 1988; Carlson et al. 2007), Brown Trout demonstrated positive growth in 14 of 16 intervals measured during winter. Across all years of the study, winter growth accounted for at least 20% of overall growth in all streams. Likewise, Dieterman et al. (2012) observed positive winter growth in 3 streams and French (2014) in 17 of 24 groundwater-dominated southeastern Minnesota streams. However, despite documenting a consistent pattern in positive winter growth, the present study demonstrates significant spatial and interannual variation in the extent of winter growth. For example, in Beaver Creek and Garvin Brook, winter was the period of slowest growth in the first year of the study, but the season of fastest growth during the second year of the study. This spatial and temporal variation applies to other seasons as well. With the exception of Gribbon Creek, where Brown Trout grew the fastest during spring in all years of the study, no single season within the remaining streams ranked highest in growth across all years of the study. Interestingly, the two streams with the highest extent of groundwater control based on the slope of the air-water temperature regression, Gribbon Creek and Daley Creek, were the only streams to have the period of fastest growth occur in winter or spring in each year of the study. In addition, fastest growth occurred in Gribbon Creek and Daley Creek, overall, in this study. Fastest fish growth occurred during summer in at least two of the three years of the study in Trout Run Creek and Beaver Creek the streams with the highest air-water temperature regression slope. In general, the year-to-year variation in seasonal growth that we observed is consistent with interannual variation documented in other studies, which was found to be substantial in some cases (e.g. Newman and Waters 1989; Lobón-Cerviá 2005).

More isothermic thermal regimes are buffered by groundwater input, and may be linked with spring and winter water temperatures more suitable for foraging and growth. We found a positive correlation between fish growth during winter and groundwater input. This relationship is supported by other studies that documented positive winter growth of Brown Trout in streams where water temperature was significantly buffered by groundwater (Dieterman et al. 2012; French et al. 2014) or a mild local climate (Lobón-Cerviá and Rincón 1998). French et al. (2014) found that the degree to which a stream was thermally buffered by groundwater showed a significant positive relationship with trout growth and condition. Similarly, Dieterman et al. (2012) attributed continuous growth of Brown Trout in three streams in southeastern Minnesota to the influence of groundwater springs and seeps, and found that seasonal changes accounted for the most variation in growth among the smallest and youngest trout, indicating a strong influence on younger age classes. By contrast, studies where stream-dwelling salmonids experienced no or minimal winter growth and decreased survival were conducted in streams with little groundwater or climatic buffering of water temperatures (e.g. Cunjak et al. 1987; Schultz and Conover 1999; Post and Parkinson 2001; Biro et al. 2004).

Drainage area and channel slope were not significantly associated with diet composition; however a NMDS ordination revealed a significant correlation between groundwater input and diet during spring. Although the correlation between groundwater input and diet in winter was not significant, groundwater input explained 85% of variation in diet across sites. Daley Creek, the stream with the both the highest degree of groundwater control and fastest growth rates during winter and spring, was strongly associated with diets rich in *Gammarus*. In this stream, Brown Trout stomachs contained a mean of 14 Gammarids (of 23 total prey items) during spring and 22 (of 34 total prey items) during winter. Gammarids are an energy-rich and important prey item for smaller and younger Brown Trout in southeastern Minnesota, especially in streams where aquatic vegetation is abundant and temperatures remain cold (Waters 1982; Newman and Waters 1984; Bachman 1991; Grant 1999). *Gammarus* have been documented as a consistently abundant year-round source of prey for Brown Trout in southeastern Minnesota (Newman 1984), and high abundances in Daley Creek may support elevated growth

during the winter and spring. Bioenergetics models by Dieterman et al. (2004) predicted fast growth in young Brown Trout with diets rich in *Gammarus*, and *Gammarus* abundance has been positively related to trout biomass in this region (Kwak 1993).

Relatively small variation in drainage area and channel slopes across study streams may have masked associations between these variables and diet composition. Examining these physical attributes at a larger scale that include streams located in geographically disparate regions at higher latitudes and altitudes may have revealed more positive associations. Or, an examination of physical habitat features at a finer scale (e.g. water depth and velocity, riparian vegetation, substrate type, aquatic plant richness, etc.) may have revealed variation that explains differences in diet relative to abundance and availability of aquatic macroinvertebrates and terrestrial inputs (Cunjak and Power 1986; Jowett et al. 1991; Merritt and Cummins 1996; Bouchard and Ferrington 2009; Dieterman et al. 2012).

Climate change models developed by Lyons et al. (2010) predict warming scenarios that may result in a widespread loss of suitable thermal habitat based on summer water temperatures for salmonids in Wisconsin, including the southwestern portion of the state adjacent to our study area in southeastern Minnesota. However, the models assumed that all streams would experience the same increase in water temperature for a given increase in air temperature. Streams vary in the extent to which water temperatures will increase relative to air temperatures based on stream flow, relative groundwater inputs, stream channel morphology, solar radiation inputs, riparian and catchment vegetation, and land use practices (Wehrly et al. 2009). In southeastern Minnesota, groundwater springs typically act as a buffer, slowing the rate at which water temperatures increase relative to air temperatures (Krider 2013). This relationship may result in summer water temperatures that are relatively cooler than those predicted by Lyons et al. (2010), as well as relatively warmer water temperatures during winter.

This study provides evidence that streams with the highest degree of groundwater control (and, hence, relatively warmer winter and cooler summer water temperatures) also support the fastest growing populations of Brown Trout, and that winter is an important period of growth in these streams. Although the exact mechanism for faster

growth in these streams is presently unknown, the influence of groundwater input may result in conditions that are more metabolically suitable for achieving growth. This may be especially important during winter and summer, when periods of extremely high and low temperatures due to surface runoff or fluctuations in ambient air temperatures may potentially impede Brown Trout growth in streams that are not buffered by groundwater inputs. Therefore, when identifying streams with the best potential for sustaining productive, fast-growing Brown Trout populations amidst rising air temperatures due to climate change, managers should consider prioritizing streams with greatest degree of groundwater control.

Conclusion

In all streams, Brown Trout fed continuously and demonstrated positive growth during winter, spring, and summer. The overall composition of Brown Trout diets contained mostly aquatic macroinvertebrates and demonstrated little seasonal variation within streams and among streams. Spatial differences were more pronounced, with considerable variation in overall diet, winter diet, and spring diet across streams. Diet compositions may be similar in streams that share thermal conditions during spring, and to a lesser extent winter. When compared to streams influenced by surface water, the thermal regimes of groundwater-dominated streams likely shape the availability of prey and regulate growth potential. With knowledge about what Brown Trout consume and how they grow on a seasonal basis, fisheries managers can identify key prey items and predict how changes in prey communities may impact trout production. Subsequent changes in prey communities, such as the decline or increase of certain prey types, may influence how a stream is managed. Results from this study, however, stress the importance of a stream-specific approach, as both patterns in growth and diet varied much more considerably within streams than on broader spatial scales. Additionally, since the majority of prey consumed by Brown Trout was aquatic macroinvertebrates rather than terrestrial or allochthonous inputs, managers should consider in-stream management activities and habitat improvements that support the growth and life history of aquatic macroinvertebrates through suitable water quality, healthy macrophyte communities, and coarse woody structures. We provide evidence that growth rates may

be higher in streams where thermal regimes are more strongly buffered by groundwater inputs, and that winter and spring may be important seasons that contribute to high growth and productivity. In Minnesota, streams that are more heavily influenced by groundwater may also be more resilient to projected increases in air temperature due to climate change (Johnson et al. 2015). Thus, managers may choose to allocate limited resources toward management activities that protect the integrity of streams that are buffered by groundwater springs. These actions may include strategies that protect groundwater springs specifically, such as limiting withdrawals and regulating agricultural, industrial, or urban development in areas where springs are especially abundant.

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Tables

Table 1. Sample dates, number of lavage samples, size range of fish collected, number of fish tagged and number of fish recaptured, drainage area, channel slope, and site location from six southeastern Minnesota streams during 2010 – 2013. Drainage area, channel slope, and UTM coordinates were obtained from French (2014). Each stream is identified as having fast[1], average[2], slow[3], or unknown[4] fish growth rates following Dieterman et al. (2004).

Stream	Sample date	Total # fish sampled	Gastric lavage samples	Size range of fish sampled (mm)	# fish tagged/# fish recaptured	Drainage area (km^2)	Channel slope (m*km^{-1})	UTM Coordinates
Beaver[3]	19 Nov 2010	90	30	126-279	90/0	29.1	10.81	577026, 4889127
	5 Feb 2011	150	30	101-316	63/7			
	16 Mar 2011	96	30	115-309	18/0			
	24 Jun 2011	191	30	135-325	0/16			
	19 Jul 2011	65	30	136-337	0/16			
	14 Aug 2011	56	30	107-330	0/12			
	26 Jan 2012	153	30	100-340	137/16			
	29 Mar 2012	47	30	187-342	0/43			
	05 Jun 2012	83	30	115-305	0/27			
	13 Sep 2012	136	30	95-303	0/31			
	17 Jan 2013	161	30	110-354	0/22			
	22 Apr 2013	82	30	100-450	0/18			
	11 Jun 2013	62	30	112-272	0/9			
	18 Sep 2013	55	30	154-291	0/6			
Daley[4]	06 Jan 2011	150	30	103-342	150/0	15.2	22.7	605606, 4845390
	5 Feb 2011	80	30	100-280	0/40			
	26 Mar 2011	66	30	123-277	0/40			
	13 Jun 2011	99	30	123-385	0/49			
	21 Jul 2011	69	30	73-394	0/30			
	23 Sep 2011	85	30	100-365	0/19			
	22 Jan 2012	116	30	101-370	91/25			
	04 Apr 2012	74	30	116-374	10/64			
	14 Jun 2012	82	30	74-370	0/35			
	23 Sep 2012	100	30	76-335	0/41			
	12 Jan 2013	165	30	100-441	133/32			

	20 Apr 2013	96	30	102-347	0/29			
	27 Jun 2013	36	30	115-335	0/11			
	30 Sep 2013	54	30	107-405	0/13			
Garvin[1]	05 Dec 2010	95	30	101-295	95/0	19.7	15.5	595503, 4873356
	12 Jan 2011	98	30	100-379	63/29			
	03 Mar 2011	91	30	108-274	0/41			
	10 May 2011	70	30	111-400	0/0			
	18 Jun 2011	141	30	73-315	0/19			
	05 Aug 2011	91	30	115-315	0/12			
	14 Jan 2012	143	30	102-460	139/11			
	23 Mar 2012	53	30	125-402	0/52			
	04 Jun 2012	62	30	125-325	0/37			
	30 Sep 2012	100	30	80-476	0/36			
	11 Jan 2013	193	30	101-320	150/19			
	26 Apr 2013	129	30	104-336	0/24			
	07 Jun 2013	103	30	107-347	0/31			
	17 Sep 2013	89	30	102-343	0/16			
Gribbon[3]	17 Dec 2010	151	30	133-361	151/0	20.4	13.9	587631, 4839986
	3 Feb 2011	136	30	100-497	0/10			
	25 Mar 2011	109	30	134-282	0/28			
	16 Jun 2011	157	30	90-365	0/15			
	28 Jul 2011	95	30	110-424	0/13			
	28 Aug 2011	108	30	75-332	0/15			
	31 Jan 2012	150	30	100-400	137/13			
	06 Apr 2012	75	30	110-302	0/58			
	07 Jun 2012	151	30	100-335	0/29			
	22 Sep 2012	100	30	90-360	0/26			
	12 Jan 2013	166	30	100-386	150/13			
	20 Apr 2013	82	30	100-365	0/16			
	26 Jun 2013	19	19	109-266	0/3			
	30 Sep 2013	69	30	135-456	0/12			
Rush[2]	07 Jan 2011	7	7	100-239	7/0	56.5	17.1	591328, 4865564
	02 Apr 2011	6	6	105-254	0/2			
	09 Jun 2011	5	5	159-264	0/0			
	07 Jun 2011	10	10	173-320	0/2			
	15 Aug 2011	13	13	93-283	0/2			

	21 Jan 2012	3	3	119-150	3/0		
	25 Mar 2012	11	11	135-358	0/1		
	22 Jun 2012	9	9	166-370	0/2		
	27 Sep 2012	13	13	96-252	0/0		
	22 Jan 2013	10	10	129-301	10/0		
	23 Apr 2013	9	9	104-320	0/1		
	06 Jul 2013	3	3	134-272	0/0		
	13 Sep 2013	2	2	195-284	0/0		
Trout Run[3]	18 Dec 2010	73	30	105-352	73/0	43.7	17.1	575358, 4857802
	28 Jan 2011	85	30	100-422	80/7		
	02 Apr 2011	32	30	168-354	0/5		
	08 Jun 2011	39	30	117-295	0/2		
	13 Jun 2011	56	30	26-337	0/9		
	28 Aug 2011	73	30	125-440	0/11		
	15 Jan 2012	145	30	140-450	135/15		
	24 Mar 2012	57	30	155-355	0/29		
	13 Jun 2012	69	30	119-351	0/22		
	09 Sep 2012	138	30	96-349	0/37		
	16 Jan 2013	127	30	112-445	17/32		
	23 Apr 2013	31	30	117-400	0/17		
	10 Jun 2013	16	16	125-285	0/12		
	29 Sep 2013	36	30	145-350	0/17		

Table 2. Seasonal variation in diet composition across five streams (excluding Rush Creek) in southeastern Minnesota, 2010-2013, based on a MRPP test.

		Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall			0.69	0.69	0.004	0.31
Winter (N=17)		0.72				
Spring (N=26)		0.70				
Summer (N=15)		0.69				
Fall (N=11)		0.65				
Pairwise	Winter (N=17)	0.65	0.69	0.69	0.01	0.09
	Spring (N=26)	0.71				
	Winter (N=17)	0.65	0.67	0.67	0.005	0.28
	Summer (N=15)	0.69				
	Spring (N=26)	0.71	0.70	0.71	0.01	0.08
	Summer (N=15)	0.69				
	Winter (N=17)	0.65	0.68	0.66	-0.02	0.91
	Fall (N=11)	0.72				
	Spring (N=26)	0.71	0.71	0.71	-0.01	0.88
	Fall (N=11)	0.72				
	Summer (N=15)	0.69	0.70	0.69	-0.01	0.85
	Fall (N=11)	0.72				
By stream						
Beaver	Winter (N=3)	0.59	0.53	0.61	0.13	0.006
	Spring (N=4)	0.58				
	Summer (N=5)	0.45				
	Fall (N=1)	NA				
Daley	Winter (N=4)	0.58	0.50	0.52	0.03	0.26
	Spring (N=5)	0.57				
	Summer (N=2)	0.73				
	Fall (N=3)	0.25				
Garvin	Winter (N=4)	0.64	0.64	0.56	-0.15	0.97
	Spring (N=6)	0.54				
	Summer (N=2)	0.88				
	Fall (N=2)	0.76				
Gribbon	Winter (N=3)	0.53	0.64	0.65	0.02	0.32
	Spring (N=5)	0.71				
	Summer (N=3)	0.67				
	Fall (N=3)	0.62				
Trout Run	Winter (N=3)	0.44	0.46	0.45	-0.03	0.58
	Spring (N=6)	0.48				
	Summer (N=3)	0.49				
	Fall (N=2)	0.39				

[a] Distance is the mean Sorenson distance between each combination of quadrats from each site; [b] Observed delta is determined from sample data; [c] Expected delta is calculated from a null distribution; [d] A is the chance-corrected within-group agreement

[e] P-value measure of significance (at 0.05)

Table 3. Variation in diet composition across five streams (excluding Rush Creek) in southeastern Minnesota, 2010-2013 based on a MRPP test.

	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall		0.61	0.69	0.11	0.0002
Beaver (N=13)	0.68				
Daley (N=14)	0.58				
Garvin (N=14)	0.61				
Gribbon (N=14)	0.69				
Trout Run (N=14)	0.52				
Pairwise					
Beaver (N=13)	0.70	0.64	0.72	0.12	0.0002
Daley (N=14)	0.58				
Beaver (N=13)	0.70	0.66	0.68	0.03	0.03
Garvin (N=14)	0.62				
Beaver (N=13)	0.70	0.69	0.73	0.05	0.01
Gribbon (N=14)	0.69				
Beaver (N=13)	0.70	0.60	0.64	0.05	0.002
Trout Run (N=14)	0.52				
Daley (N=14)	0.58	0.60	0.66	0.09	0.0004
Garvin (N=14)	0.62				
Daley (N=14)	0.57	0.62	0.70	0.11	0.0006
Gribbon (N=14)	0.67				
Daley (N=14)	0.57	0.54	0.60	0.09	0.001
Trout Run (N=14)	0.51				
Gribbon (N=14)	0.69	0.65	0.70	0.07	0.0008
Garvin (N=14)	0.62				
Garvin (N=14)	0.62	0.57	0.58	0.02	0.09
Trout Run (N=14)	0.52				
Gribbon (N=14)	0.69	0.60	0.65	0.09	0.0004
Trout Run (N=14)	0.51				
By season					
Fall		0.67	0.72	0.07	0.21
Beaver (N=1)	NA				
Daley (N=3)	0.69				
Garvin (N=2)	0.83				
Gribbon (N=3)	0.63				
Trout Run (N=2)	0.52				
Winter		0.47	0.65	0.27	0.0006
Beaver (N=3)	0.31				
Daley (N=4)	0.24				
Garvin (N=4)	0.68				
Gribbon (N=3)	0.57				
Trout Run (N=3)	0.51				

		Distance[a]	Observed delta[b]	Expected delta[c]	A[d]	P[e]
Spring			0.62	0.71	0.12	0.0008
	Beaver (N=4)	0.67				
	Daley (N=5)	0.60				
	Garvin (N=6)	0.62				
	Gribbon (N=5)	0.72				
	Trout Run (N=6)	0.53				
Summer			0.70	0.69	-0.02	0.60
	Beaver (N=5)	0.56				
	Daley (N=2)	0.89				
	Garvin (N=2)	0.88				
	Gribbon (N=3)	0.79				
	Trout Run (N=3)	0.61				

[a] Distance is the mean Sorenson distance between each combination of quadrats from each site; [b] Observed delta is determined from sample data; [c] Expected delta is calculated from a null distribution; [d] A is the chance-corrected within-group agreement; [e] P-value measure of significance (at 0.05)

Table 4. Y-intercepts and slopes from air-water temperature regressions for six streams in southeastern Minnesota, 2011-2012.

	Year 1 (2011)		Year 2 (2012)	
	y-intercept	slope	y-intercept	slope
Beaver Creek	6.11	0.44	5.91	0.37
Daley Creek	7.17	0.20	7.66	0.16
Garvin Brook	6.10	0.35	8.33	0.25
Gribbon Creek	7.04	0.25	7.42	0.18
Rush Creek	5.93	0.51	5.45	0.45
Trout Run Creek	6.41	0.31	5.40	0.32

Figures
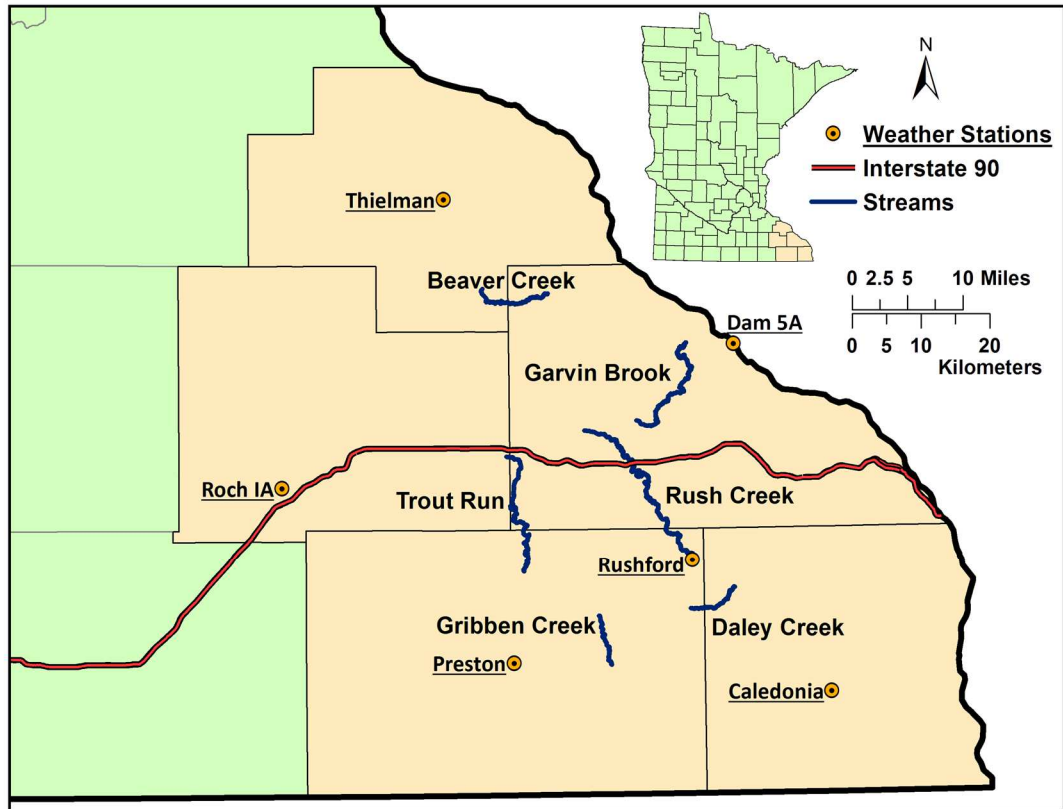
Figure 1. Map of the Driftless Ecoregion of southeastern Minnesota and six streams sampled for Brown Trout, 2010-2013. Weather stations from which air temperature data were collected are depicted.

A)
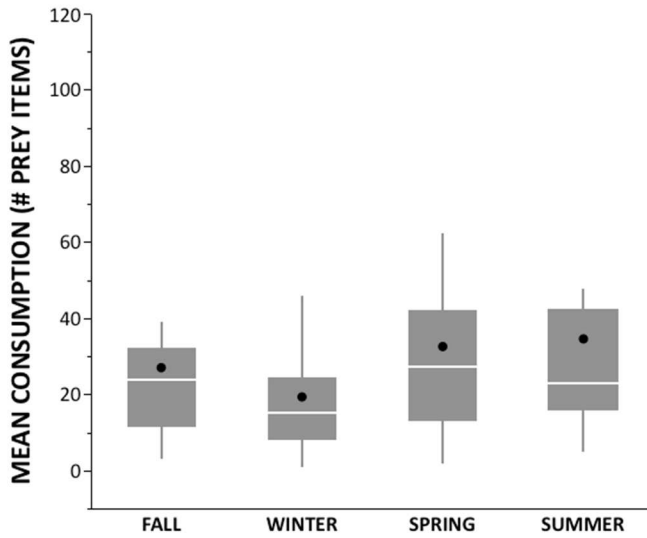
B)
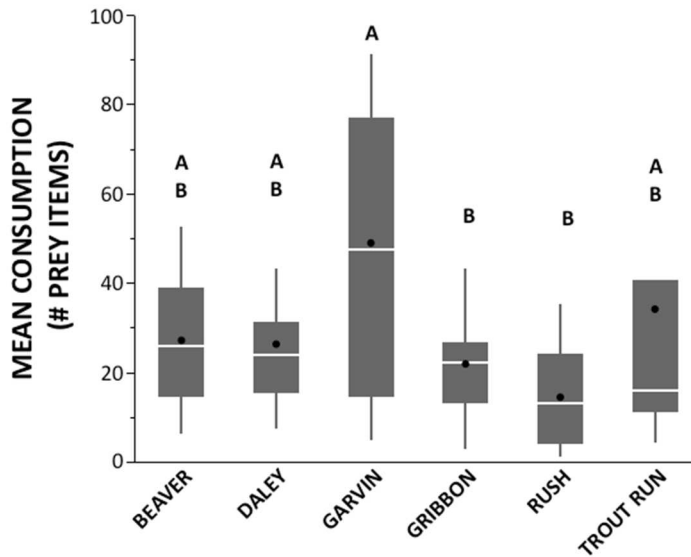
Figure 2. Mean prey consumption (number of prey items per stomach) by Brown Trout in six southeastern Minnesota streams (A) by season, and (B) by stream, 2010-2013. Histograms with the same letter are not significantly different (Tukey's HSD, p<0.05). Means are represented by "•" and medians are represented by a white bar.

A)
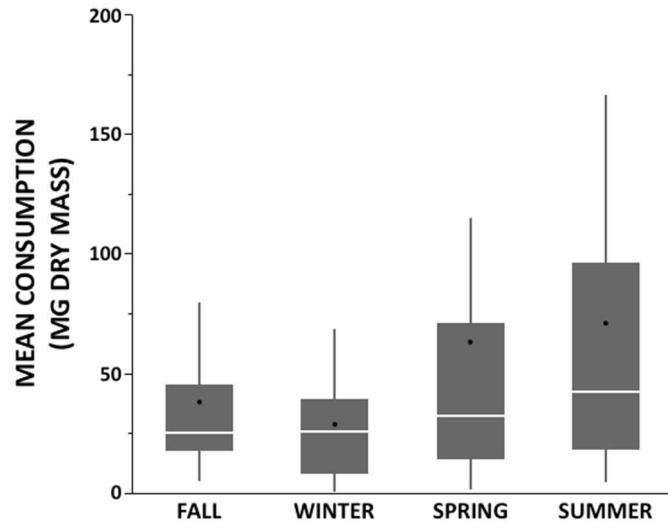
B)
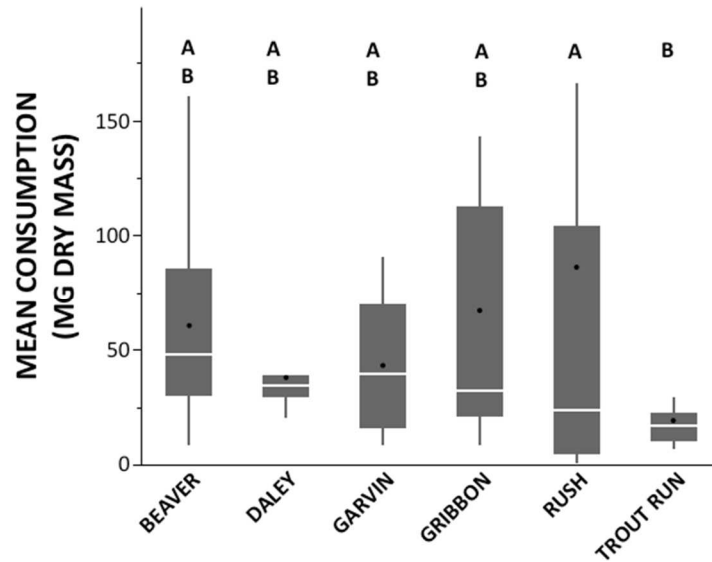
Figure 3. Mean prey consumption (total mg of dry weight consumed) by Brown Trout in six southeastern Minnesota streams (A) by season, and (B) by stream, 2010-2013. Histograms with the same letter are not significantly different (Tukey's HSD, $p < 0.05$). (Tukey's HSD, $p < 0.05$). Means are represented by "•" and medians are represented by a white bar.
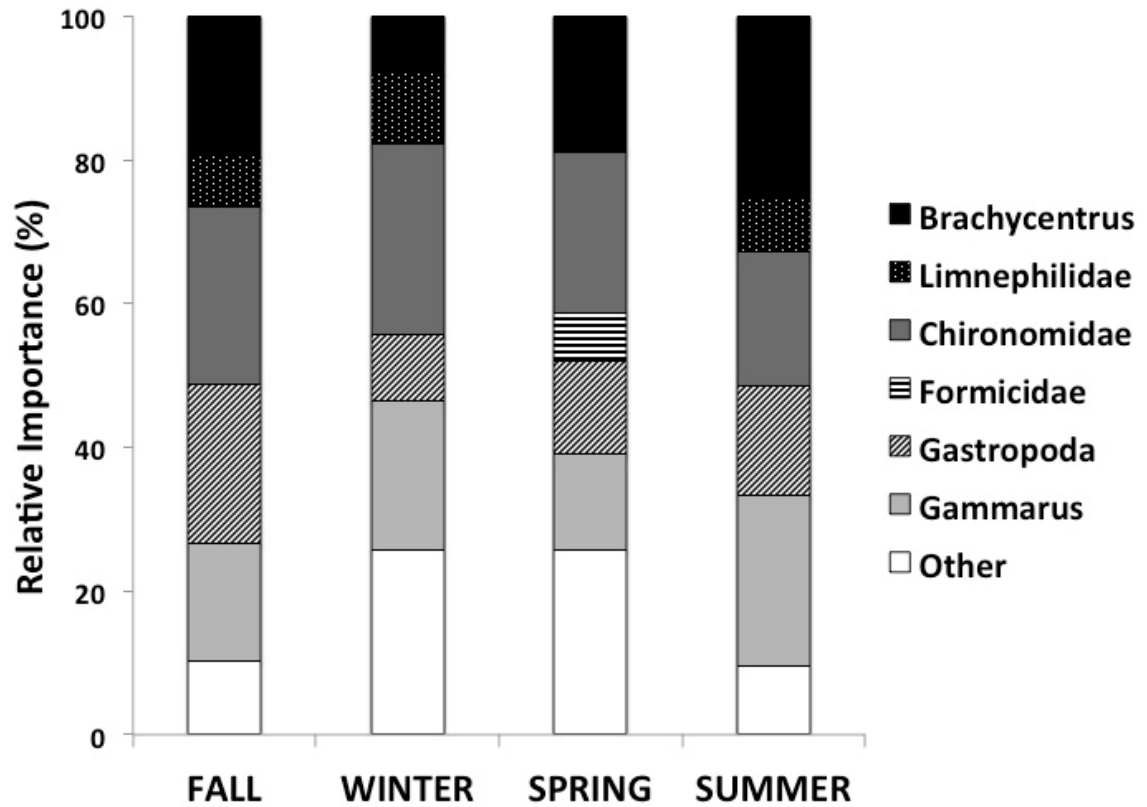
Figure 4. Relative importance (%) of prey items >5% of the total by season in the diet of Brown Trout in five streams in southeastern Minnesota, 2010-2013.
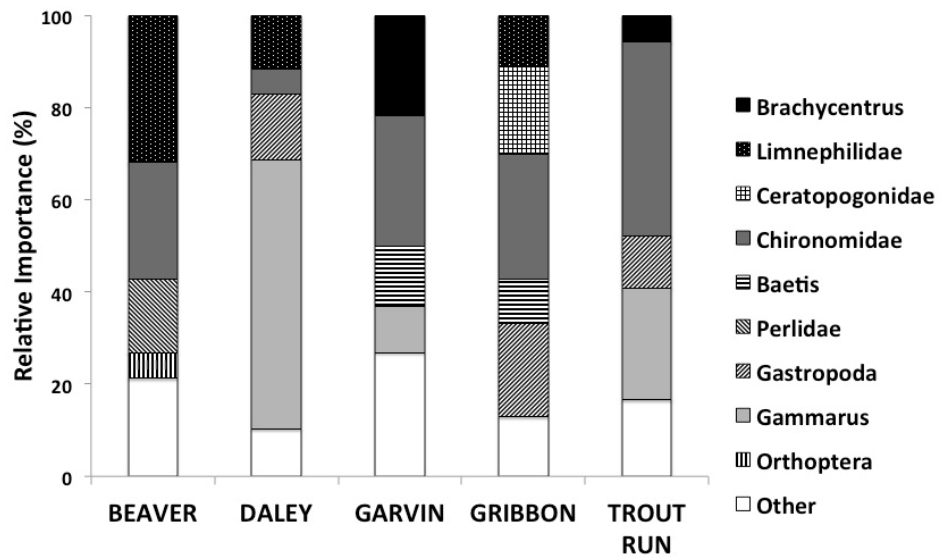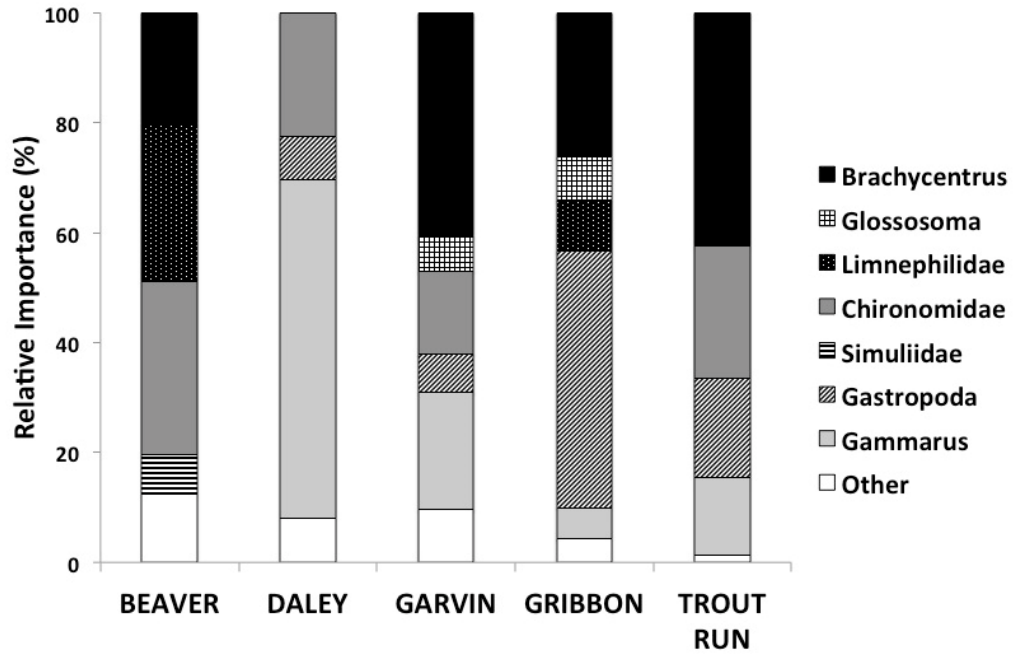
Figure 5. Relative importance (%) of prey items >5% of the total in the (A) winter, and (B) spring diet of Brown Trout in five streams in southeastern Minnesota, 2010-2013.
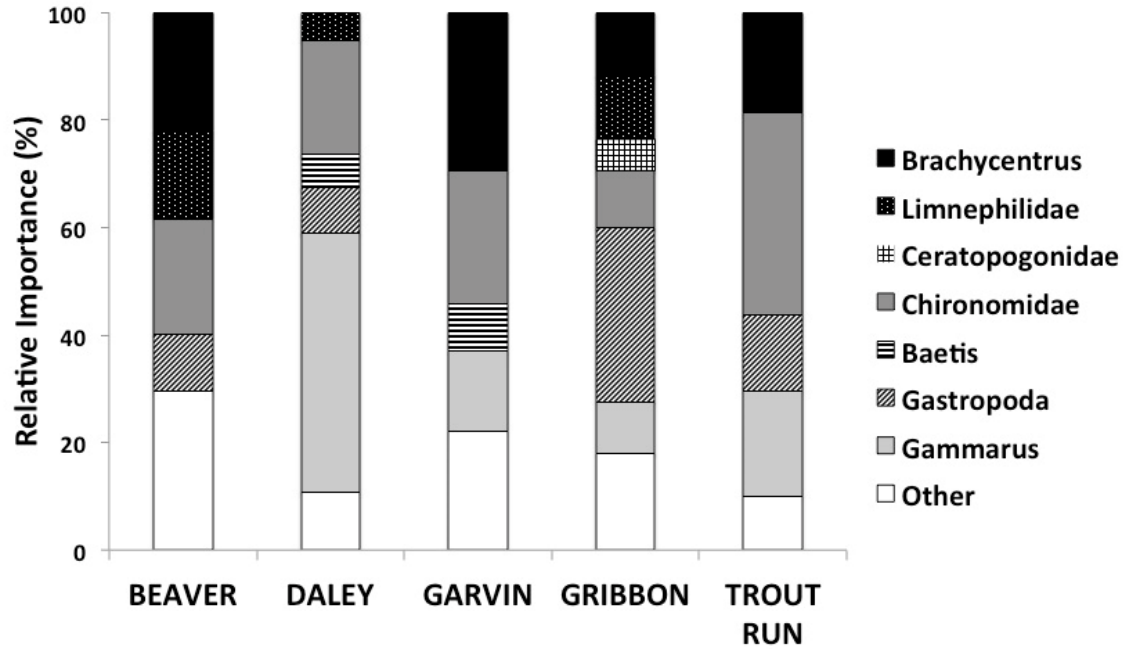
Figure 6. Relative importance (%) of prey items >5% of the total in the overall diet of Brown Trout (all seasons combined) in five streams in southeastern Minnesota, 2010-2013.
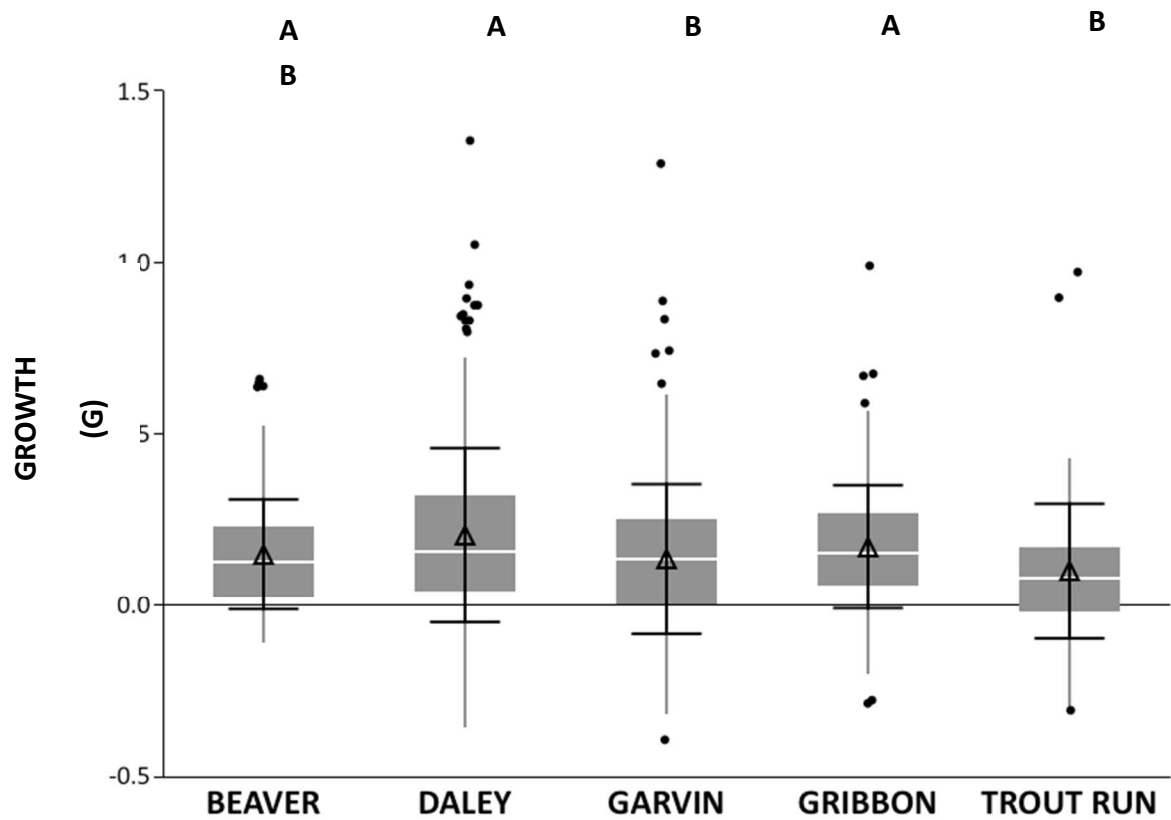
Figure 7. Instantaneous daily growth rates (G) of Brown Trout in five streams in southeastern Minnesota, 2010-2013. "Δ" represent mean growth rates; white bars represent median; error bars = 1±SD. Histograms with the same letter are not significantly different (Tukey's HSD, p<0.01).
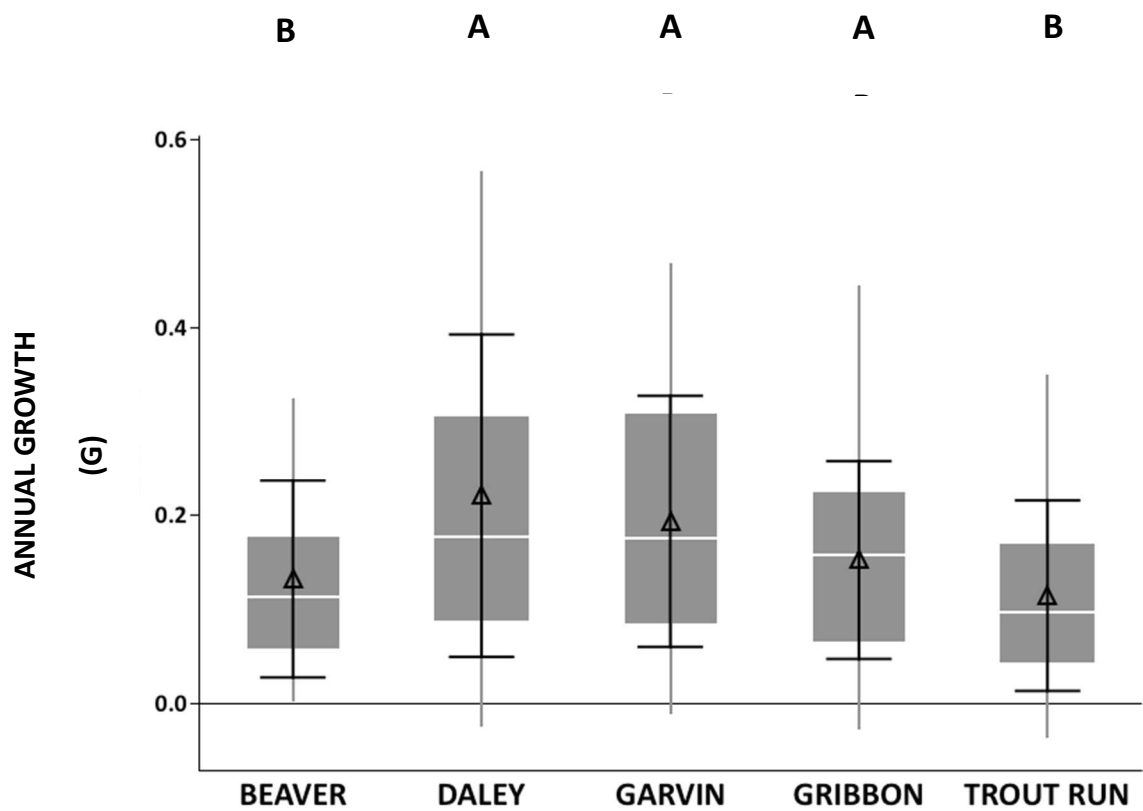
Figure 8. Annual instantaneous daily growth rates (G) of Brown Trout in five streams in southeastern Minnesota, 2010-2013. "Δ" represent mean growth rates; white bars represent median; error bars =1±SD. Histograms with the same letter are not significantly different (Tukey's HSD, p<0.01).
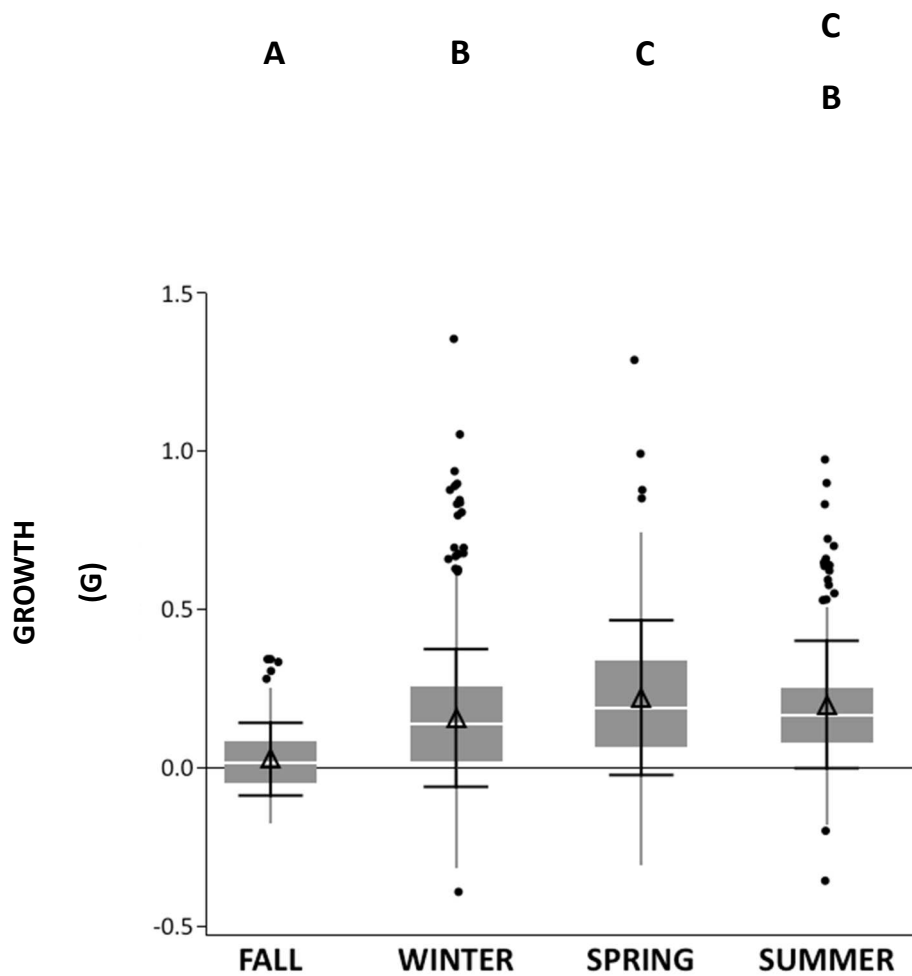
Figure 9. Instantaneous daily growth rates (G) of Brown Trout by season in five streams in southeastern Minnesota, 2010-2013. "Δ" represent mean growth rates; error bars =1±SD. Histograms with the same letter are not significantly different (Tukey's HSD, $p < 0.01$).
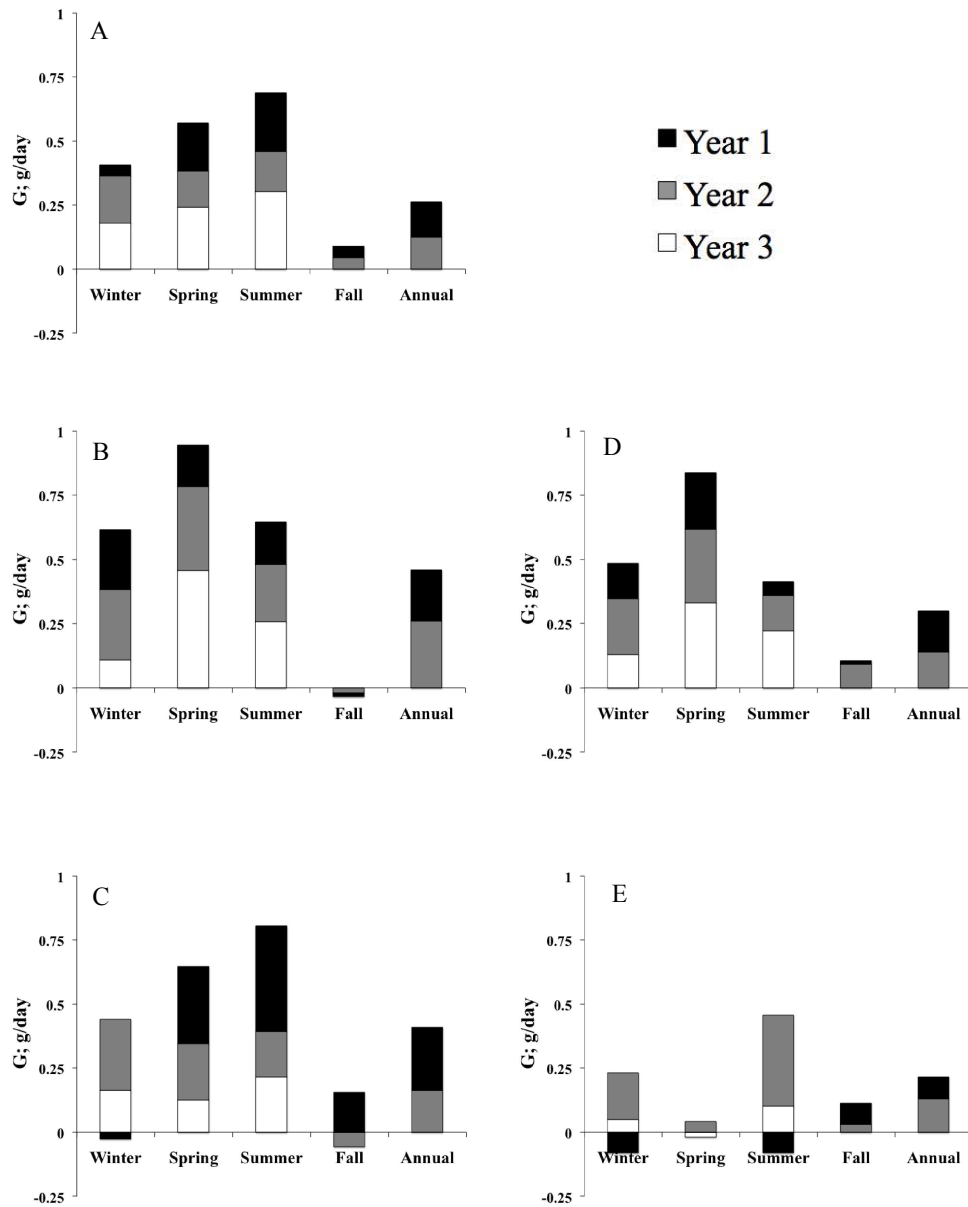
Figure 10. Mean instantaneous daily growth rates (G) of Brown Trout by season in five streams: (A) Beaver, (B) Daley, (C) Garvin, (D) Gribbon, and (E) Trout Run.
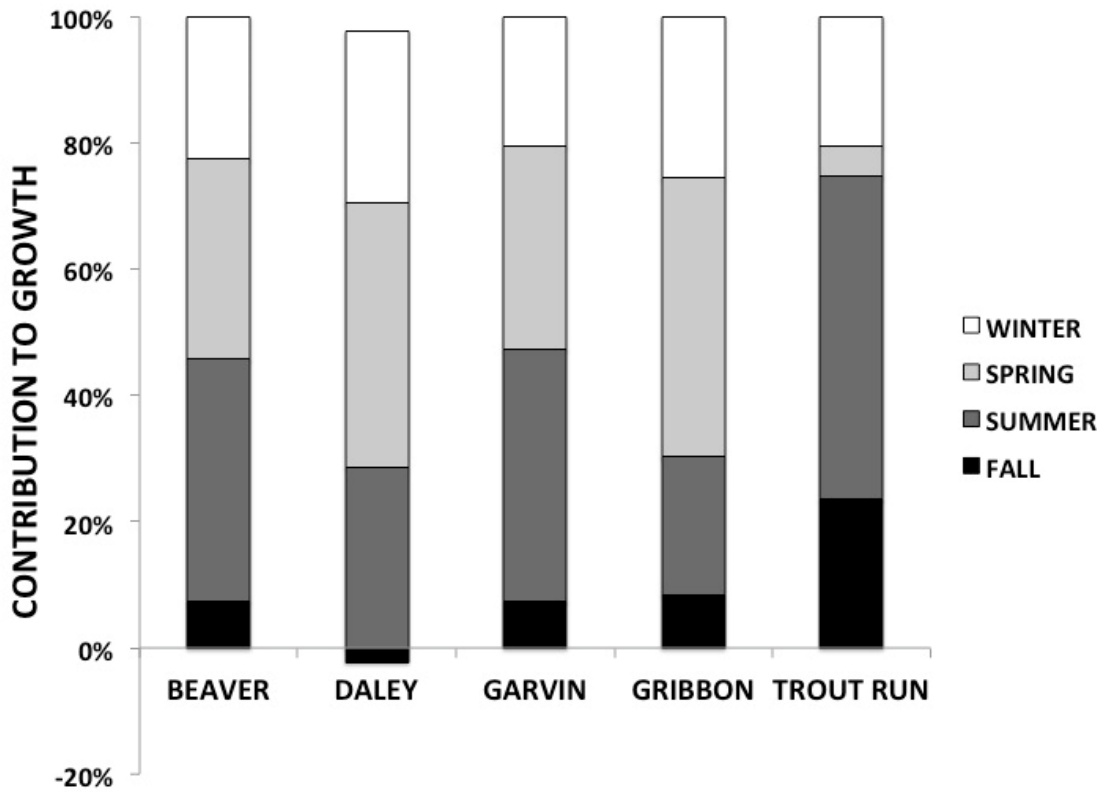
Figure 11. Seasonal contributions toward overall growth of Brown Trout in five streams in southeastern Minnesota, 2010-2013.
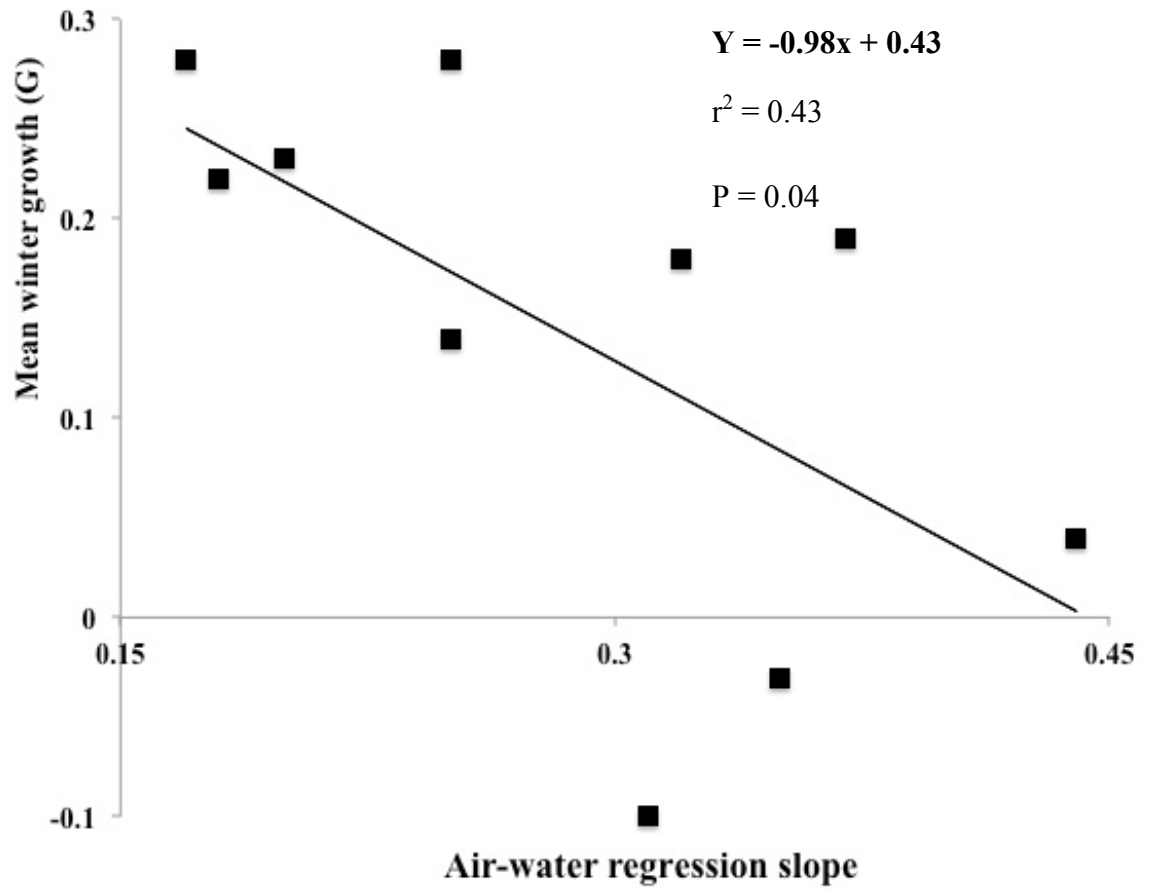
Figure 12. Relationships between mean instantaneous daily winter growth (G) and groundwater input (slope from air/water temperature regressions, 2011-2012) for all study streams (excluding Rush Creek) in southeastern Minnesota.
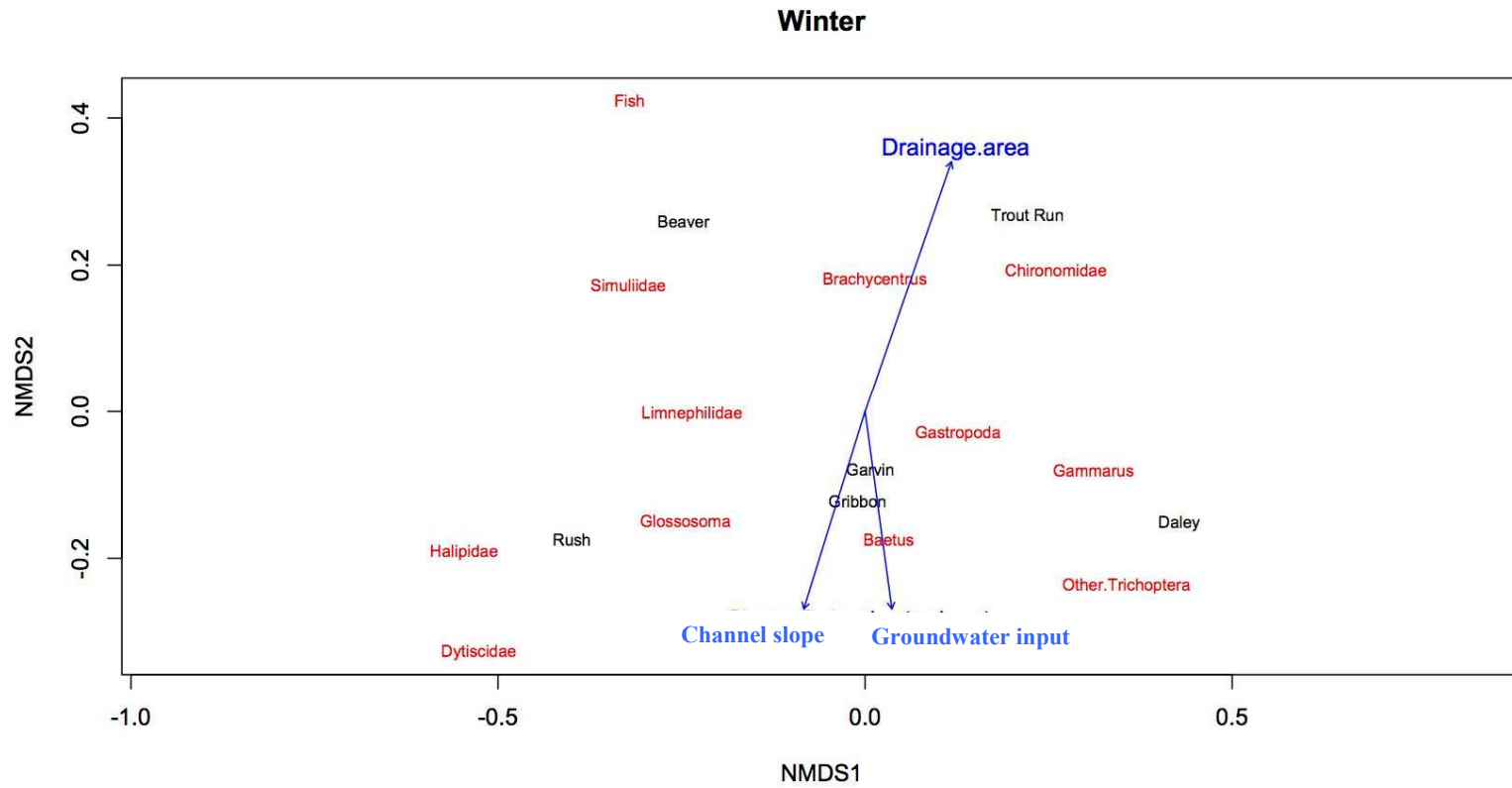
Figure 13. Brown Trout diet (proportion of total diet by dry weight) for streams in winter, 2010-2013. Streams adjacent to one another indicate a similar diet composition. Arrows indicate direction of increasing drainage area, channel slope, and groundwater input.
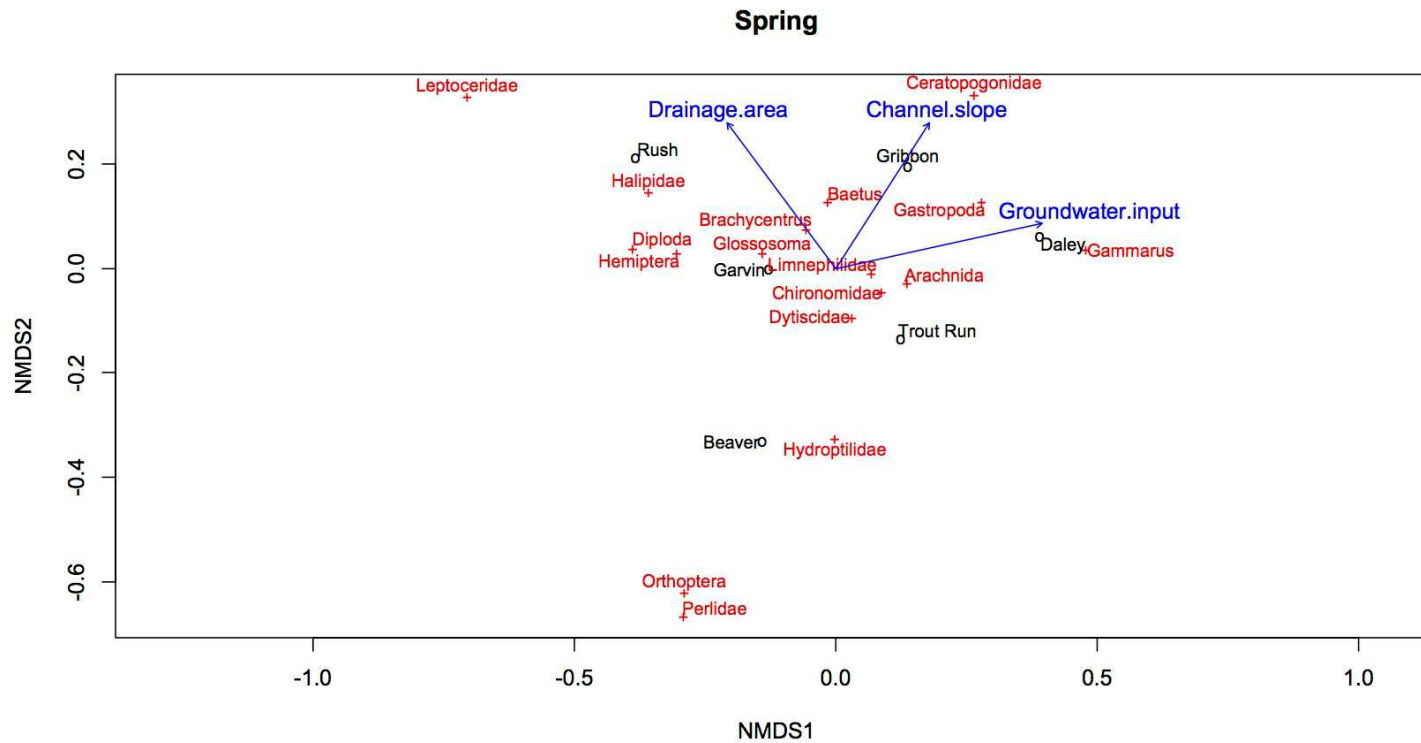
Figure 14. Brown Trout diet (proportion of total diet by dry weight) for streams in spring, 2010-2013. Streams closer to one another had more similar diet composition than streams further apart. Arrows indicate direction of increasing drainage area, channel slope, and groundwater input.
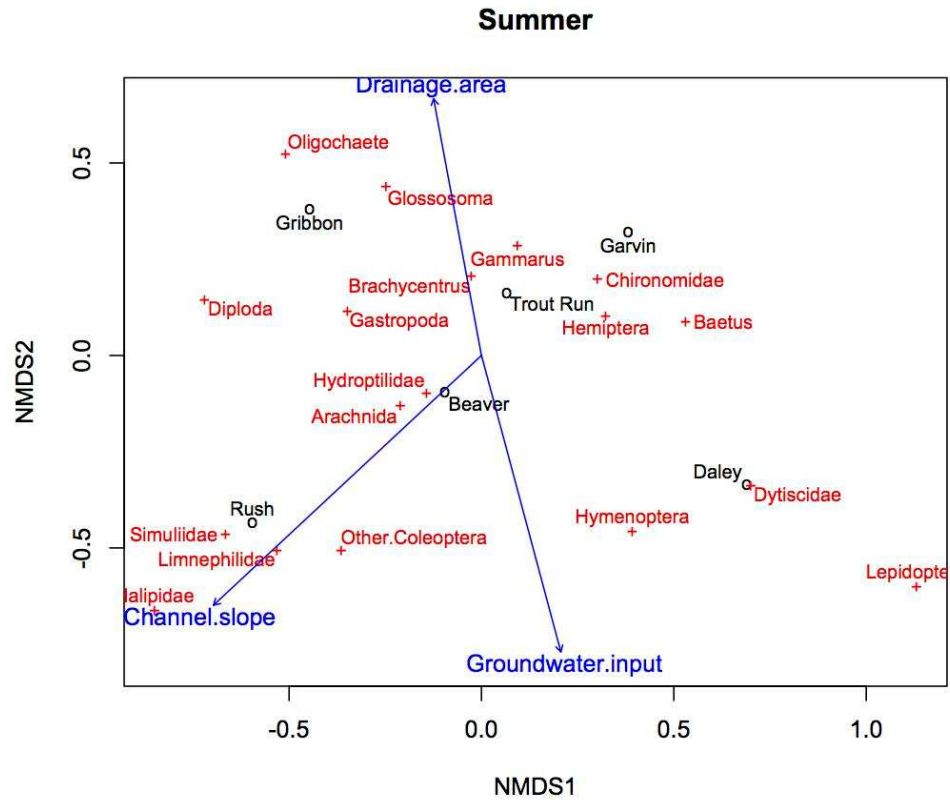
Figure 15. Brown Trout diet (proportion of total diet by dry weight) for streams in summer, 2010-2013. Streams closer to one another had more similar diet composition than streams further apart. Arrows indicate direction of increasing drainage area, channel slope, and groundwater input.

Chapter 2

Seasonal patterns in the prey assemblages of Brown Trout *Salmo trutta* in six groundwater-dominated streams in the Driftless Ecoregion of southeast Minnesota

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Running headline: Invertebrate availability in groundwater-dominated streams

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Summary

Macroinvertebrate benthos and drift are primary prey for Brown Trout (*Salmo trutta*), and seasonal differences in prey availability may explain variation in trout growth across the Driftless Ecoregion of southeast Minnesota. Seasonal abundance, diversity, and overlap of macroinvertebrate benthos and drift were investigated in six groundwater-fed streams in 2011-2013. Drift and benthos were represented by only a few taxa, including Chironomidae, *Brachycentrus*, and Simuliidae, but differed across seasons and streams. We used Morisita's Index to compare similarity and diversity, which revealed a higher degree of overlap among seasons, and less overlap among streams. Multiple response permutation procedure analysis, used to evaluate seasonal and spatial variation in assemblage structure, revealed differences in benthos and drift assemblages among streams and seasons, with the most pronounced differences among streams. Abundance of drift and benthos varied significantly, with highest availability in spring and summer, and lowest availability during winter in most streams. We found no significant associations between groundwater input, channel slope, and drainage area with measures of prey diversity and abundance based on simple linear regression. However, non-metric multi-dimensional scaling indicated associations between assemblage composition and physical variables, especially groundwater input. We suggest that management efforts to support productive populations of Brown Trout should take a stream-specific approach, and concentrate on activities that sustain healthy assemblages of aquatic macroinvertebrates, including suitable water quality and habitat complexity.

Introduction

Physical habitat and food resources are the primary factors that likely influence and limit salmonid productivity in streams; however management efforts typically only emphasize physical habitat (Chapman 1966; Poff and Huryn 1998). With regard to food resources, the simplest explanation for differences in growth rate is that some streams have higher invertebrate production, which allows individuals to maintain or increase their growth with higher food availability. Establishing a correlation between the growth of salmonids and food availability has been difficult, as demonstrated by "Allen's Paradox," in which estimated production of benthic invertebrates was determined to be insufficient to support trout populations in the Horokiwi stream in New Zealand (Allen 1951). Based on a literature review, Waters (1988) concluded that production of benthic macroinvertebrates was likely not sufficient to support trout production in most streams; however, the lack of relationship may be due to trout selectively feeding on additional sources of food, such benthic macroinvertebrates in the hyporheic zone and terrestrial inputs including insects (Elliott 1970, 1973; Waters 1972; Cada et al. 1987).

Recent research has provided evidence that growth, condition, and productivity of stream-dwelling salmonids may be frequently food-limited (e.g. Hughes and Dill 1990; Richardson 1993; Filbert and Hawkins 1995). In some cases, increases in salmonid growth were correlated with increases in primary production from nutrient additions (Johnston et al. 1990; Peterson et al. 1993), or with the modification of in-stream food resources (Mason 1976). Leeseberg and Keeley (2014) speculated that higher abundances of drift explained differences in the growth rate and size of stream-dwelling salmonids in the western United States. In southeastern Minnesota, bioenergetics models suggested that variation in Brown Trout growth could be explained by seasonal differences in prey consumption and availability (Dieterman et al. 2004). Follow-up studies found that winter was a period of active growth for many Brown Trout populations, including several of the same streams investigated by Dieterman et al. (2004) (French et al. 2014; Cochran-Biederman unpublished), despite being a time when

terrestrial and benthic macroinvertebrates are absent or reduced (Newman and Waters 1984; Gíslason 1985; Rundio and Lindley 2008).

Winter conditions in north temperate zones, especially critically low temperatures, create a challenging environment for trout and their prey to thrive; however, invertebrates have developed unique morphological, ecological, behavioral, and biochemical adaptations to survive and reduce thermal stress (Danks 1991; Lencioni 2004; Danks 2007; Eggermont and Heiri 2012). Winter growth of Brown Trout in groundwater-dominated streams of southeastern Minnesota may actually be supported by high abundances of aquatic macroinvertebrates, including ultra-cold stenotherm Chironomids that develop and emerge during winter (Bouchard and Ferrington 2009). A study of a Brown Trout population in Minnesota found increases in consumption of aquatic macroinvertebrates during winter (Newman and Waters 1984), including species that are ultra-cold stenotherms (Bouchard and Ferrington 2009; Anderson 2012; French et al. 2014).

Although terrestrial insects have been the focus of many studies, the belief that cold climates seasonally restrict activity and development of most aquatic species has resulted in little ecological research of aquatic invertebrate communities during winter (Danks 2007). In addition, few studies have assessed food availability for stream-dwelling trout, regardless of season, despite the known influence of food resources on fish production (Fausch 1988; Nislow et al. 1998). This lack of research may be in part due to obstacles related to taxonomic identification (Rosenberg and Resh 1993; Merritt and Cummins 1996) and sampling requirements (Elliott 1977). However, if seasonal variation in Brown Trout growth across southeast Minnesota is a function of the proportion of potential prey that can be detected, captured, and consumed, then a first step in predicting the actual food or energy available for salmonids would be to evaluate spatial and seasonal differences in availability of benthic and drifting taxa (Rader 1997). The failure to specifically consider seasonal food availability, especially during winter, may constrain restoration and management of stream salmonids.

The goal of this study was to examine seasonal and spatial patterns in the availability and diversity of benthic and drifting macroinvertebrates from June 2011 to

October 2013 in six groundwater-dominated streams in southeast Minnesota. Measures of macroinvertebrate drift and benthic diversity, overlap, and abundance were compared among streams and among seasons. Specifically, our objectives were to: (1) describe and quantify variation in taxonomic diversity, abundance, and overlap of benthic and drifting macroinvertebrate communities on a seasonal and spatial basis, and (2) investigate correlations between physical stream variables (groundwater input, drainage area, and channel slope) and measures of macroinvertebrate diversity and abundance among six groundwater-dominated streams.

Methods

Study area

This study was conducted in six groundwater-dominated streams located in the Driftless Ecoregion of southeast Minnesota (Figure 1). The region, was relatively unaffected by the most recent glaciations. The Driftless Ecoregion is characterized by a karstic geology that supports a high density of groundwater-fed streams (Williams and Vondracek 2010). Supplied with fertile water by a high density of active springs, these streams yield productive populations of Brown Trout (Kwak and Waters 1997), and diverse and abundant assemblages of aquatic invertebrates (Waters 1977). Study streams were selected to represent a range of thermal stability and Brown Trout growth based on growth rates reported in Dieterman et al. (2004). Study streams demonstrated a "summer-cold/winter-warm" effect and remained free of ice during winter, with the exception of Rush Creek where surface ice formed in pools and areas of low flow. Drainage area and 10-85% channel slope were calculated for each stream with the sample site as the downstream boundary. Slopes from air/water temperature regression equations developed by Krider et al. (2013) were used as an estimate of groundwater input in each stream. Slopes close to one indicate less groundwater input and a greater influence of air temperature on water temperature, whereas slopes close to 0 indicate more groundwater input and a reduced influence of air temperature on water temperature. Regression equations were available for all the streams sampled in this study, and predicted water temperature at an air temperature of 0°C ranged from 5.1°C in Rush Creek to 7.1°C in Daley Creek (Krider et al. 2013) (Table 1).

Benthic invertebrate collection

We sampled benthic macroinvertebrates using a Hess stream bottom sampler (0.086 m^2) on four to six sample dates per year. Although we attempted to sample equally during all seasons, logistical limitations and Brown Trout spawning resulted in some disparity among the number of sample dates within each season across all streams. Five samples were taken from riffles randomly selected within the sampling reach by disturbing the substrate for three minutes. Each collection was passed through a 125μm

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sieve prior to preservation in 70% ethanol, and transported to the laboratory for processing, where macroinvertebrates were picked from each sample, sorted and identified to the lowest practical taxonomic group using a dissection microscope. Samples were sorted for a maximum of four hours. Nearly all benthic samples (215 of 224, or 96%) were completely sorted within four hours. However, if sorting was not completed in four hours, the percentage of the sample processed was estimated, recorded, and multiplied by counts of individuals already sorted for each taxon.

Invertebrate drift collection

Drifting macroinvertebrates were collected on the same sample dates as benthic invertebrate collections. Four drift nets (45 cm x 25 cm, with a 1 m long bag and 363 μm Nitex mesh) were placed in a contiguous line perpendicular to the shoreline in a randomly selected riffle within a 200 m reach of the stream. The mouth of each net was anchored in the center of the upstream end of the riffle. Water velocity and depth was measured in three locations across the mouth of each net using a Marsh-McBirney Flo-Mate™ Model 2000 Flowmeter. Sampling was conducted within about one hour of sunrise and one hour before sunset to represent the period when salmonids are actively foraging on invertebrate drift during summer, spring, and fall. During winter, drift nets were set about one hour before sunset and remained in the stream for a minimum of 12 hours. As for benthic samples, contents of the drift nets were passed through a 125μm sieve, preserved in 70% ethanol, and transferred immediately to the lab for processing where macroinvertebrates were picked, sorted, and identified to the lowest practical taxonomic group using a dissection microscope. Samples were sorted for a maximum of four hours. Nearly all drift samples (339 of 345, or 98%) were completely sorted within four hours; however, if sorting was not completed, the percentage of the sample processed was estimated, recorded, and multiplied by the total count of each taxa already sorted.

Analysis

Benthic density (number invertebrates/m^2) was calculated for each collection using the following equation:

$$Benthic\ density = \frac{N}{0.086m^2}$$

where N is the total number of invertebrates and 0.086 represents the total area of the Hess sampler. The mean density of all benthic collections on each sampling date was calculated and used to compare spatial and temporal variation in benthic density across streams and seasons using a one-way ANOVA followed by a Tukey's HSD test.

Drift density (number of invertebrates/100m^3) was calculated for each drift sample on a given sampling event using the following equation:

$$Drift\ density = \frac{N(100)}{(t)(W)(H)(V)(3600)}$$

where N is the total number of invertebrates, t is the duration that the net was set in hours, W is net width in meters, H is net height in meters, V is mean velocity in meters/second, and 3600 converts hours to seconds. The mean drift density on each sampling date was used to evaluate spatial and temporal variation across streams and seasons with a one-way ANOVA followed by a Tukey's HSD test.

Overlap in the diversity of invertebrates among streams and seasons were calculated using Morisita's Index of Similarity (C_λ) (Morisita 1959; Krebs 1999)

$$C_\lambda = \frac{2\ \Sigma\ X_{ij}X_{ik}}{(\lambda_1 + \lambda_2)N_j N_k}$$

where

$$\lambda_1 = \frac{\Sigma[X_{ij}(X_{ij}-1)]}{N_j(N_j)-1},$$

$$\lambda_2 = \frac{\Sigma[X_{ik}(X_{ik}-1)]}{N_k(N_k)-1},$$

and X_{ij}, X_{ik} is the number of individuals of taxon i in sample j and sample k, N_j is the total number of individuals in sample j, and N_k is the total number of individuals in sample k. Horn's (1966) modification (C_{MH}) was used to compare overlap in drift, which is appropriate when data are presented as proportions (Krebs 1999):

$$C_{MH} = \frac{2\ \Sigma\ X_{ij}X_{ik}}{[(\Sigma X_{ij}^2 IN_j^2) + (\Sigma X_{ik}^2 IN_k^2)]N_j N_k}$$

where all terms are defined as above. Both Morisita's Index of Similarity and Horn's modification are frequently used overlap indices (Linton et al. 1981) and generate overlap

values ranging form 0 to 1. Typically, values equal or greater than 0.60 are considered to represent high overlap (Zaret and Rand 1971).

Diversity of benthic samples was measured using Simpson's Diversity Index (D_s):

$$D_s = \frac{1 - (\sum n(n-1))}{N(N-1)}$$

where n represents the total number of organisms of a particular species and N represents the total number of organisms of all species. Simpson's Diversity Index incorporates the number of species present, as well as the relative abundance of each species; therefore, D_s will increase relative to species richness and evenness. The value of D_s ranges between 0 (no diversity) and 1 (infinite diversity).

A multiple response permutation procedure (MRPP) (Zimmerman et al. 1985; McCune et al. 2002) was performed in program R (version 3.1.2) to compare community composition of drift and benthos between streams and seasons. MRPP makes no distributional assumptions (Smith 1998) and a distance matrix is calculated using any number of possible distance measures. Each analysis was performed using proportions of each invertebrate taxa, determined by dividing the number of individuals from a given taxon by the total number of individuals collected on each sample date. Only taxa >1% of total invertebrates were used in the analysis. Proportions were arcsine transformed prior to analysis, and separate tests were run for drift and benthos. Probability of type I error is calculated using a randomization algorithm that allows for comparison between observed δ (weighted mean within-group distance) and the randomized δ distribution. This probability value expresses the likelihood of generating a random δ smaller than the observed value. An effect size of A was also calculated as

$$A = 1 - \frac{observed\ \delta}{expected\ \delta}$$

and represents observed within-group homogeneity relative to what can be expected by chance (McCune and Grace 2002). For the purposes of this study, A provides a measure of the overall agreement among the relative quantity and diversity of invertebrates within the group designated (e.g. stream, season, year). Within-group homogeneity is greater than the random observation when $A>0$ and less when $A<0$. The A-value is useful in

attaching ecological significance to observed differences among groups because it is independent of sample size (Mielke 1984; McCune and Grace 2002).

Relationships between physical stream variables (groundwater input, drainage area, and channel slope) and measures of invertebrate diversity and abundance (taxonomic richness of drift, taxonomic richness of benthos, drift density, benthic density, and Simpson's diversity) were investigated using simple linear regression.

Non-metric multidimensional scaling (NMDS) was used to examine patterns of macroinvertebrate assemblage composition among streams and seasons, and to evaluate the influence of three stream physical characteristics (drainage area, channel slope, and groundwater input) on assemblage structures. NMDS is an ordination technique that allows qualitative assessments of community composition patterns based on the positioning of streams and macroinvertebrate taxa on a multi-dimensional plot. Invertebrate taxa closer to a stream on an NMDS plot make up a larger portion of the availability for that stream than taxa further apart. NMDS was conducted in program R (version 3.1.2) using the metaMDS function, located in the vegan library. Default settings for metaMDS were used for all analyses. Stress values lower than 0.20 are generally considered to provide a useful ordination. Taxonomic groups that made up >1% of the relative abundance for each stream in each season were used in the analyses. Groundwater input, drainage area, and channel slope were fit to NMDS plots using the envfit function from the vegan library in program R to examine their relationship with community composition patterns.

Results

Benthos

  Richness and assemblage composition. Taxonomic richness of benthic assemblages varied among streams, and was highest in Beaver Creek (n=37) and lowest in Trout Run Creek (n=22). Across all streams, taxonomic richness of benthos was greatest during spring (n=40) and lowest during fall and winter (n=27) (Table 2).

  With the exception of Rush Creek (MRPP, A=0.10, p=0.03), the taxonomic composition of benthic assemblages within streams did not significantly change on an annual basis (Table 3). When data from all streams were combined, Chironomidae (predominately larvae and pupa) were the most common benthic macroinvertebrate taxon collected, comprising 29.6% of the total composition, followed by encased *Brachycentrus* larvae, which made up 21.8% of all benthic macroinvertebrates collected (Figure 2). Although there were significant differences in benthic macroinvertebrate assemblages among streams (MRPP, A=0.14, p<0.01) (Table 4), Chironomidae were the most common benthic taxa collected in four of the six streams, including Daley Creek (36.4%), Gribbon Creek (21.6%), Rush Creek (37.4%), and Trout Run Creek (49.8%) (Figure 2). *Brachycentrus* was the most common benthic taxon in Beaver Creek (36.1%) and Garvin Brook (29.2%), and the second most common macroinvertebrate collected in Rush Creek (16.8%) and Trout Run Creek (31.2%) (Figure 2). In addition, MRPP revealed widespread variation in the composition of benthic macroinvertebrate assemblages between streams; of 15 stream-to-stream comparisons, all comparisons were significantly different (p<0.05) except comparisons between Beaver Creek and Garvin Brook (A=0.22, p=0.08), Daley Creek and Trout Run Creek (A=0.03, p=0.09), and Rush Creek and Trout Run Creek (A=0.02, p=0.15) (Table 4).

  Seasonal assemblages of benthos were significantly different among streams during all seasons: winter (MRPP, A=0.55, p<0.01), spring (MRPP, A=0.08, p=0.02), summer (MRPP, A=0.18, p<0.01), and fall (MRPP, A=0.23, p=0.04) (Table 4). In addition, the composition of benthic assemblages from all streams combined was also significantly different among seasons (MRPP, A=0.02, p=0.05) (Table 5). Overall,

Chironomidae were the most common benthic taxa collected during fall (23.1%), spring (33.6%), and summer (36.2%). During winter, *Brachycentrus* was most abundant taxon (36.8%) followed by Chironomidae (17.5%) (Figure 2). Pairwise comparisons of benthic macroinvertebrate assemblages between seasons were only significantly different between winter and summer (MRPP, A=0.04, p=0.04) (Table 5). Within streams, benthic macroinvertebrate assemblages varied significantly from season to season in only two streams: Beaver Creek (MRPP, A=0.28, p=0.04) and Trout Run Creek (MRPP, A=0.43, p<0.01) (Table 6).

Diversity and overlap. Overall diversity (D_s) of benthic assemblages was highest in Garvin Brook (0.82) and lowest in Trout Run Creek (0.53), and there were no significant differences across all streams (F=1.3, p=0.27) (Figure 3). Likewise, no significant differences were detected in diversity across seasons when data from all streams were combined (F=1.4, p=0.26); however, benthic diversity was highest during spring ($\bar{x}$=0.80) and lowest during winter ($\bar{x}$=0.59) (Figure 3). There were no significant differences in seasonal diversity of benthic macroinvertebrate assemblages within streams (Appendix I).

Morisita's Index of Similarity (C_λ) was considered low (<0.60) in 13 of 15 stream-to-stream comparisons of benthic assemblages, with Garvin Brook and Daley Creek being least similar (C_λ=0.33), and Trout Run Creek and Rush Creek being most similar (C_λ=0.81) (Table 6). In contrast, seasonal similarities in benthic assemblages exceeded 0.60 in all season-to-season comparisons, with exception of winter and summer (C_λ=0.55) (Table 6). Benthic assemblages were most similar during winter and spring (C_λ=0.83) (Table 6). Although seasonal similarity of benthic assemblages within streams varied, mean seasonal overlap was highest at Rush Creek (0.78) and lowest at Beaver Creek (0.56).

Availability. Overall, mean density (number of individuals/m^2) of benthic macroinvertebrates varied considerably across all streams, ranging from 1654/m^2 in Gribbon Creek to 5021/m^2 in Garvin Brook (F=4.6, p<0.01) (Figure 4). Across all

streams, Chironomidae were present in the highest density ($\bar{x}$=883/m^2), followed by *Brachycentrus* ($\bar{x}$=676/m^2) (Figure 5). Chironomidae were the most abundant taxa in four of six streams, ranging in mean density from 354/m^2 in Gribbon Creek to 1338/m^2 in Trout Run Creek, and *Brachycentrus* was the dominant taxon in Beaver Creek ($\bar{x}$=744.m^2) and Garvin Brook ($\bar{x}$=1882/m^2) (Figure 5).

Mean density of benthic macroinvertebrates did not vary significantly among seasons when data from all streams were combined, ranging from 2255/m^2 in winter to 4070/m^2 during summer (F=2.2, p=0.09) (Figure 4). However, although the highest mean density occurred during summer when data from all streams were aggregated, mean benthic macroinvertebrate density was highest during spring in three streams, and highest during summer in only two streams (Figure 6). Overall, Chironomidae had the highest mean density during all seasons, ranging from 504/m^2 during winter to 1282/m^2 during summer, followed by *Brachycentrus*, which ranged from 474/m^2 during winter to 851/m^2 during summer (Figure 5). Within streams, benthic density among seasons was significantly different in Beaver Creek (F=4.7, p<0.01) and Gribbon Creek (F=4.4, p<0.01). In Beaver Creek, mean benthic density peaked during summer (4570/m^2) and was lowest during winter (239/m^2). In Gribbon Creek, mean benthic density was highest during winter (3076/m^2) and lowest during spring (1003/m^2) (Figure 6).

Drift

Richness and assemblage composition. Taxonomic richness (total number of different taxa) of drift was higher than benthos in all seasonal and spatial comparisons (Table 2). Overall, taxonomic richness of drift was lowest in Trout Run Creek and Garvin Brook (n=41), and highest in Gribbon Creek (n=51) (Table 2). Seasonal richness of benthos and drift was positively correlated (r^2=0.96, p=0.02). Similar to benthos, the richness of drifting taxa was highest during spring (n=60) and lowest during winter (n=31) (Table 2). On an annual basis, the composition of drifting macroinvertebrate assemblages did not significantly change from year to year in any of the study streams (MRPP, p>0.05) (Table 3).

Overall, Chironomidae (predominately larvae and pupa) were the most common drifting taxa collected across all streams, comprising 50.0% of total composition, followed by Simuliidae (predominately pupa and larvae of the genus *Simulium*), which made up 13.0% of all drift collected (Figure 6). Drifting macroinvertebrate assemblages were significantly different among streams (MRPP, A=0.06, p<0.01) (Table 7). Chironomidae were the most abundant drifting macroinvertebrate in all streams, ranging from 34.2% in Garvin Brook to 61.6% of all drift collected in Daley Creek (Figure 7). Simuliidae were the second most abundant macroinvertebrate in the drift in Beaver Creek (13.3%), Daley Creek (8.6%), Gribbon Creek (24.1%), and Trout Run Creek (17.0%), and *Brachycentrus* was the second most abundant drifting macroinvertebrate in Garvin Brook (21.4%) (Figure 7). Overall, terrestrial taxa were not highly represented in the drift (Figure 6). Formicidae comprised 5.5% of drift collected from all streams combined during summer and 5.6% of all drift collected in Daley Creek (Figure 6).

In contrast to benthic macroinvertebrate assemblages, we observed less spatial variation of drifting macroinvertebrate assemblages between streams. Unlike benthos, where 13 of 15 stream-to-stream comparisons of macroinvertebrate assemblages were significantly different, only eight of 15 pairwise comparisons of drifting macroinvertebrate assemblages were significantly different based on MRPP analysis (Table 7).

Within streams, drifting macroinvertebrate assemblages did not significantly vary from season to season (Table 8). In addition, unlike benthos, where spatial differences in macroinvertebrate assemblages were significant among streams within all seasons, drift assemblages only varied across streams during winter (MRPP, A=0.19, p=0.01) (Table 7). The composition of drift (when all streams were combined) was significantly different across seasons (MRPP, A=0.02, p=0.03, Table 7). Chironomidae were the most common drifting macroinvertebrates during all seasons: fall (53.4%), winter (38.5%), spring (44.5%), and summer (50.4%) (Figure 7). Simuliids were the second most common drifting taxon during winter (14.5%), spring (17.6%), and summer (9.0%); and *Brachycentrus* was the second most common drifting taxon during fall (22%) (Figure 7). Between seasons, there was greater variation in the composition of drifting assemblages

than of benthic assemblages. Drifting macroinvertebrate assemblages were significantly different between winter and summer (MRPP, A=0.03, p=0.04), winter and fall (MRPP, A=0.05, p=0.01), and between spring and fall (MRPP, A=0.02, p=0.04) (Table 8).

Overlap. Comparisons of symmetric overlap of drifting macroinvertebrate assemblages between streams yielded a greater range in overlap than comparisons of benthos, with the lowest similarity occurring between Garvin Brook and Trout Run Creek (C_{MH}=0.05), and highest similarity between Daley Creek and Rush Creek (C_{MH}=0.76) (Table 6). Similar to benthos, 10 of 15 stream-to-stream comparisons of drifting macroinvertebrates indicated low overlap (C_{MH}< 0.60). In contrast, seasonal similarities in drifting assemblages exceeded 0.60 in all comparisons (Table 9). Drifting macroinvertebrate assemblages were most similar during fall and summer (C_{MH}= 0.91) and least similar during summer and winter (C_{MH}= 0.72) (Table 9). Measures of benthic and drift overlap were not significantly related among streams (r^2=0.05, p=0.44) or seasons (r^2=0.14, p=0.47).

Availability. Mean density of macroinvertebrate drift (number of individuals/100 m^3), when all sample dates were combined, was significantly different across all streams (F=2.8, p=0.01), ranging from 6.2/100 m^3 in Gribbon Creek to 23/100 m^3 in Garvin Brook (Figure 8). Chironomidae were the most abundant macroinvertebrate taxa in all streams, with highest mean density occurring at Rush Creek (12/100 m^3) and lowest mean density occurring in Gribbon Creek (2.1/100 m^3). Overall, Chironomidae occurred in the highest density ($\bar{x}$ = 7.2/100 m^3), followed by Simuliidae ($\bar{x}$ = 1.7/100 m^3) (Figure 9a). Simuliidae had the second highest density in all streams except Rush Creek, with the highest density occurring in Garvin Brook ($\bar{x}$ =6.6/100 m^3) (Figure 9).

The mean density of drifting macroinvertebrates also varied significantly across seasons when data from all streams were combined (F=5.8, p<0.01), with highest mean drift density occurring in spring (20/100 m^3), followed by fall (8.8/100 m^3), summer (8.5/100 m^3), and winter (2.4/100 m^3) (Figure 9). Similar to benthos, Chironomidae demonstrated the highest density of all drifting taxa during every season, with highest density occurring during spring ($\bar{x}$=12/100 m^3) and lowest density in winter ($\bar{x}$=0.9/100 m^3) (Figure 9). *Baetis* had the second highest mean density during winter (0.5/100 m^3),

summer (8.4/100 m^3), and spring (3.4/100 m^3); and Simuliidae had the second highest mean density during fall (0.6/100 m^3) (Figure 8). Within streams, seasonal differences in drift density were significant in all streams except Garvin Brook (F=1.4, p=0.23) and Trout Run Creek (F=2.4, p=0.06) (Figure 10). Lowest rates of drift density occurred during winter in all streams, except Trout Run Creek, where mean drift density was lowest during fall (4.8/100 m^3) (Figure 10). Peak drift density occurred during spring in all streams, except Daley Creek, where drift density was highest during summer ($\bar{x}$=17/100 m^3), and Gribbon Creek, where drift density peaked during fall ($\bar{x}$=8.4/100 m^3) (Figure 10).

No significant correlations were detected between physical stream variables (groundwater input, drainage area, and channel slope) and measures of macroinvertebrate diversity or abundance (including taxonomic richness of drift, taxonomic richness of benthos, drift density, benthic density, and Simpson's diversity) among streams (Table 10).

NMDS results

Non-metric multidimensional scaling identified overall and seasonal patterns in the composition of drifting and benthic macroinvertebrate assemblages. Ordinations that resulted in convergent solutions for drift included: all seasons combined (2 dimensions, stress=0.006), spring (2 dimensions, stress=0.05), summer (2 dimensions, stress=0.003), and fall (2 dimensions, stress=0.007) (Figure 9). Ordinations that resulted in convergent solutions for benthic assemblages included all seasons combined (2 dimensions, stress=0.009) and spring (2 dimensions, stress=0.05) (Figure 10). Spring benthos was the only ordination without any significant associations with physical variables (groundwater input: r^2=0.71, p=0.17; drainage area: r^2=0.62, p=0.21; channel slope: r^2=0.33, p=0.55) (Figure 9). Groundwater input was significantly associated with ordinations of benthic assemblages when data from all seasons were combined (r^2=0.92, p=0.04) (Figure 10), and ordinations of drift assemblages when data from all seasons were combined (r^2=0.99, p=0.001), summer (r^2=0.84, p=0.05), spring (r^2=0.91, p=0.03), and fall (r^2=0.87, p=0.04) (Figure1 9). Most notably, Daley Creek had the highest degree of groundwater control,

and ordinations were tightly linked with the occurrence of *Gammarus*. Channel slope was significantly associated with ordinations of spring drift (r^2=0.89, p=0.03) (Figure 9) and overall benthos (r^2=0.88, p=0.04) (Figure 10); but was not significant in other ordinations. Drainage area was significantly associated with the ordination of benthos when data from all seasons were combined (r^2=0.85, p=0.05) (Figure 10).

Discussion

Most studies in temperate climates have reported seasonal dissimilarity in the structural attributes of macroinvertebrate assemblages; however, few studies have assessed these assemblages simultaneously in more than one stream across multiple seasons and years (Stoneburner and Smock 1979; Allan 1987; Shearer et al. 2002; Leung et al. 2009). We found distinct patterns in the diversity and abundance of drifting and benthic macroinvertebrates on a spatial and seasonal basis in six groundwater-fed streams across southeastern Minnesota. Overall, taxonomic richness of macroinvertebrate drift was higher than benthos across spatial and seasonal scales; however, both were dominated by only a few taxa, including Chironomidae, *Brachycentrus*, Simuliidae (predominately *Simulium*), and *Baetis*. Based on Morisita's Index of Similarity, there was a high degree of overlap in drift and benthic macroinvertebrate assemblages between seasons, but less similarity between streams.

Although the composition of prey assemblages may vary from stream to stream, most were dominated by only a few prey taxa. Such a high degree of taxonomic overlap between benthos and drift, however, would not be unexpected. Waters (1972) emphasized that there is no distinct drift fauna, but rather, that benthic macroinvertebrates enter the drift due to several abiotic and biotic factors. Overall, the collective composition of drift represents a mixture of drifting organisms with varying densities, and depends on the species present in the benthos, and their propensity to drift. To better characterize these differences, Waters (1965) proposed a classification scheme that distinguished between behavioral, constant (also known as accidental), and catastrophic drift. Behavioral drift refers to drift occurring at a consistent period of the day, resulting from behavioral patterns that vary among species. Constant drift refers to the continuous occurrence in the drift of representatives of all species, in low numbers, and at all times of day, and includes inputs of terrestrial insects from wind or rain events. Lastly, catastrophic drift occurs as the result of a physical disturbance of benthic fauna from events such as floods, extreme temperatures, or pollution. In this study, drift diversity was mostly represented by taxa that demonstrate behavioral drift, most notably

Chironomids, which are documented as an important and frequently abundant component of Dipteran drift (Waters 1969).

Our analysis revealed important distinctions among macroinvertebrate assemblages, although relatively few taxonomic groups dominated the benthic and drifting assemblages. Despite a high degree of overlap between seasons, MRPP analysis indicated significant variation in drift and benthic assemblages across all seasons and among all streams when data from all samples were combined. Benthic assemblages were also significantly different among streams within seasons (e.g. streams contained distinct assemblages of benthos during fall, winter, spring, and summer); however, macroinvertebrates in the drift were only significantly different across streams during winter. Within each individual stream, assemblages of drifting and benthic macroinvertebrates typically did not change from one season to the next, suggesting that seasonal variation in aquatic community assemblages is more likely to occur on a broader scale between streams. Pairwise comparisons of drifting and benthic assemblages between streams were also significantly different in over half of all comparisons. Although there was little overall diversity in the taxa that made up the majority of benthos and drift, variation in the proportional abundance of dominant taxa has the potential to significantly alter assemblage structure on a spatial and seasonal basis.

Understanding how the structure of aquatic macroinvertebrates changes across seasons is an important consideration in the management of Brown Trout in southeastern Minnesota. Overall, we found that the taxonomic richness and diversity of benthic assemblages was highest during spring, and that benthic density was highest during spring in three of six streams sampled. Drift followed a similar pattern, with greatest taxonomic richness observed during spring and highest drift rates and densities occurred during spring in most streams. In contrast, the lowest taxonomic richness for both benthos and drift occurred in winter, as well as lowest levels of benthic diversity, benthic density, drift density, and drift rate. Stream flows declined between summer and winter, and the lowest taxonomic richness of benthos was concurrent with low winter flow. Other studies have linked reductions in benthic richness and abundance with declines in habitat availability and complexity relative to flow recession (McIntosh et al. 2002;

Wood and Armitage 2004), and linked higher benthic diversity with forested streams buffered from extreme fluctuations in flow, temperature, and discharge (Likens and Bormann 1974; Karr and Schlosser 1977).

Substantial seasonal variation in drift density and drift rate has generally been reported by most studies (Waringer 1992; Ilg et al. 2001; Robinson et al. 2002), with changes often dependent upon fluctuations in flow (Corigliano et al. 1998). The typical pattern for drift abundance in temperate streams is characterized by a maximum in spring, which may be a function of higher flows and increased densities of benthic macroinvertebrates (Waters 1966; Hynes 1970). Relatively stable hydrological conditions over prolonged time periods of time, including winter, allows benthos to associate with specific microhabitats and thus increase their densities and presence in the drift during early spring (Poff and Ward 1991). In this study, stream discharge was generally lowest during winter, which may have provided stable conditions to allow benthic macroinvertebrate abundances to increase over time, as reflected in high rates of benthic density during spring. In addition, discharge was typically highest during early spring (associated with spring snowmelt), potentially contributing to elevations in drift abundance and density, a pattern that has been observed elsewhere in Minnesota (Waters 1966).

In addition, we found that drifting and benthic macroinvertebrate abundances were generally lowest during winter, a pattern also noted in other studies (Clifford 1972; Brittain and Eikeland 1988; Martin et al. 2001). Such declines may relate to low discharge (Waringer 1992), decreases in invertebrate activity levels (Martin et al. 2001), or perhaps a combination of these factors. Brown Trout are often characterized as drift feeding fish (Elliott 1973; Ringler 1979; Bachman 1984; Watz and Piccolo 2011), thus reductions in winter prey availability may pose additional stress for fish experiencing a lower metabolic rate with cold winter temperatures. In particular, low winter prey availability may pose energetic consequences for Brown Trout in streams that are less controlled by groundwater, and subsequently, relatively colder during the winter season. Prey capture maneuvers by Brown Trout take significantly longer at temperatures below 8°C, with a 30% decline in capture efficiency from 10°C to 5.7°C (Watz and Piccolo

2011). Furthermore, energetic costs associated with elevated risk of missing a prey item during foraging may be higher at lower temperatures. In addition, low winter discharge may restrict the ability of invertebrates to enter drift, subsequently forcing fish to expend more energy in search for other food sources.

During summer, terrestrial contributions to drift are considered an important resource for stream-dwelling fish because this peak often coincides with a seasonal reduction in aquatic invertebrate production (Needham 1928; Hynes 1970; Hunt and Krokhin 1975; Garman 1991; Sanders and Fausch 2007; Romanisyzn et al. 2007). In fact, terrestrial contributions to the drift were identified as a necessary subsidy for stream-dwelling fish when Allen (1951) noted that aquatic invertebrate production was insufficient to support Brown Trout production in a New Zealand stream. This observation, known as "Allen's paradox" (Hynes 1970), is supported by studies of production budgets (e.g., Waters 1988), including those in which terrestrial inputs comprised up to 53% of the total annual energy budget (Kawaguchi and Nakano 2001; Nakano and Murakami 2001). In contrast, we found that terrestrial macroinvertebrates contributed relatively little to overall drift over a broad spatial and seasonal scale. Collectively, terrestrial macroinvertebrates made up about 9.0% of all drift during summer, dominated by Formicidae, Aphidae, Orthoptera, and Isopoda. Of these groups, Formicidae was the only terrestrial taxon that ranked among the top five contributors of drift density ($\bar{x}$=0.4 per 100m^3) and drift rate ($\bar{x}$=0.3 per minute), and the only terrestrial taxon to contribute an excess of 5% toward all drift during summer (5.6%). However, although terrestrial contributions to drift were low, the influence of terrestrial subsidies can vary widely across landscapes, watersheds, and seasons due to differences in timing of emergence and oviposition, and the stochastic nature of their entry into the drift. Notably, we found that contributions of terrestrial macroinvertebrates occasionally spiked on sampling dates following storm events during late spring and summer. For example, although Aphidae ranked in the top five taxa contributing to drift during spring ($\bar{x}$=0.04 per minute) and summer ($\bar{x}$=0.03 per minute), the overall contribution was less than 1.5% of all drift during these seasons. In general, the occurrence of Aphidae in the drift was

very low, with spikes occurring on two particular dates in late spring and mid-summer, when drift rates reached as high as 3.6 individuals per minute.

Despite the low terrestrial subsidies observed in the present study, these inputs may provide an important food resource for Brown Trout, as suggested by evidence of trout selectively feeding on terrestrial drift in other regions (Elliott 1973; Hubert and Rhodes 1989; Garman 1991; Young et al. 1997; Nakano et al. 1999). In a recent review of the literature, Syrjänen et al. (2011) found that terrestrial prey contributed an average of 17% toward salmonid diets, being highest for large fish (>15cm). In contrast, Laudon et al. (2005) found that terrestrial macroinvertebrates contributed about 3% of the biomass to the drift and 3% of biomass to the diet of Brown Trout in a single stream in southeastern Minnesota. In addition to the neutral selection of terrestrial macroinvertebrates, Brown Trout typically avoided Formicidae, the top contributor of terrestrial drift in our study. Although we did find evidence that Brown Trout would readily exploit temporary influxes of terrestrial insects, overall, terrestrial macroinvertebrate taxa are unlikely to represent a consistent or necessary food resource for Brown Trout in southeastern Minnesota.

We found that the extent of groundwater input was significantly associated with ordinations of drifting and benthic macroinvertebrate assemblages when data from all seasons were combined, as well as ordinations of drift during spring, summer, and fall. *Gammarus* was strongly associated with Daley Creek, the stream with the highest degree of groundwater control, where it ranked among the top five drifting taxa during fall and winter. Overall, *Gammarus* was most common in the benthos, and was among the top five taxa with highest benthic densities in three of six streams, and during all seasons, except summer. As reported in other studies of aquatic macroinvertebrate communities in southeastern Minnesota, *Gammarus* is an energy-rich and important prey item for smaller and younger Brown Trout, especially in streams where aquatic vegetation is abundant and temperatures remain cold (Waters 1982; Newman and Waters 1984; Bachman 1991; Grant 1999). Kwak (1993) linked *Gammarus* abundance with trout biomass, an observation that is supported by our current research. In Daley Creek, where availability of *Gammarus* is highest among all study streams, Brown Trout also

demonstrated the fastest growth in the sampling period that coincided with the macroinvertebrate collections (Cochran-Biederman, unpublished, see Chapter 1). Furthermore, fish growth in Daley Creek was also significantly associated with a high degree of groundwater input (Cochran-Biederman, unpublished, see Chapter 1).

Identifying prey taxa that are important contributors toward fish growth and productivity is an important step when managing healthy populations of Brown Trout. Although there is limited evidence that *Gammarus* abundance may be linked with trout productivity and growth in southeastern Minnesota, this relationship should not overshadow the role that other more abundant and widespread taxa have in supporting Brown Trout communities in this region. In particular, we found that Chironomidae was consistently the most widely available and abundant prey item in both benthos and drift across all seasons and in most of our study streams. Among the most species-rich of aquatic insect families (Ferrington 2008), Chironomidae often comprises over half of the macroinvertebrates available in a stream community (Coffman and Ferrington 1996). Despite being smaller bodied and offering relatively lower caloric density than other aquatic macroinvertebrates we sampled, the abundance of Chironomidae makes them major source of protein that can promote the growth of multiple fish species, including trout (Armitage 1995). Recent research suggests that groundwater-dominated streams across southeastern Minnesota contain a high diversity of Chironomidae (Ferrington 2000, 2007; Bouchard and Ferrington 2009; Anderson et al. 2011; Anderson 2012). Of these, there are over 40 species that cold-tolerant and winter-active, potentially serving as a critical food resource during winter, when other types of aquatic macroinvertebrates may naturally decline in abundance (Anderson 2012; French et al. 2014).

Although the manner in which groundwater input shapes assemblages of aquatic macroinvertebrates, and subsequent impacts on fish growth, are not well understood (Boulton et al. 1998), higher stream temperatures may indirectly increase rates of accidental drift through increased insect activity and production during cold periods of the year (Dudgeon 1990; Williams 1990; Winterbottom et al. 1997). Furthermore, past studies have linked groundwater–surface water interactions with benthic invertebrate abundance and taxonomic richness, periphyton respiration, and increased growth of

epibenthic algae (Coleman and Dahn 1990; Hagerthey and Kerfoot 1998; Dent et al. 2000; Hunt et al. 2006). In particular, the positive relationship between algae growth and groundwater input suggests that the number and location of springs may indirectly control the abundance and diversity of grazing invertebrates, and benthic communities in general (Ward 1989; Boulton 1993; Brunke and Gonser 1997). Certain benthic taxa, including recently discovered ultra-cold stenothermic species (Bouchard and Ferrington 2009), may rely on upwelling zones for critical development stages (Pugsley and Hynes 1983) and thrive in these highly stable thermal environments (Vannote and Sweeney 1980). In southeastern Minnesota, thermally-driven dynamics that influence aquatic macroinvertebrate availability, diversity, and behavior may be an important factor in understanding patterns of Brown Trout growth on a seasonal and spatial basis.

In addition to groundwater input, we also investigated associations between drainage area and channel width, and measures of macroinvertebrate assemblage structure, including diversity, abundance, and composition. We found no significant relationships with simple linear regressions, and NMDS revealed few significant associations with the exception of groundwater input. In addition to a relatively small sample size of streams (n=6), the similarity among sites at the scale these variables were measured may have reduced our ability to identify additional associations relative to assemblage composition. The seasonal evaluation of in-stream characteristics at a finer scale, such as substrate composition, depth, flow, and seasonal macrophyte abundance, may reveal more specific associations between physical features and macroinvertebrate assemblages on a seasonal basis. Alternatively, an analysis of streams from disparate geological and geographical regions may also reveal stronger associations, as many factors that shape aquatic invertebrate assemblages may function on much broader scales. Watershed topography and land use influence several factors important to aquatic macroinvertebrates, such as temperature, discharge, flood frequency and magnitude, the delivery of sediment and nutrients (Lemly 1982; Troelstrup and Perry 1989; Lenat and Crawford 1994), and dissolved oxygen concentrations (Hilsenhoff 1982, 1987; Plafkin et al. 1989). One or more of these factors may influence variation among aquatic

macroinvertebrate assemblages; however since these measurements were beyond the scope of this study, their impact remains unknown.

Conclusion

The purpose of this study was to investigate spatial and temporal patterns in the prey assemblages of Brown Trout in selected streams where prey availability was suggested as a potential factor limiting fish growth in southeastern Minnesota. There have been few simultaneous studies of drifting and benthic macroinvertebrate assemblages within several streams across multiple years, and none that have been conducted in southeastern Minnesota. Our results provide detailed information about the prey resources of Brown Trout and will be particularly useful in helping fisheries managers identify and manage key macroinvertebrate taxa on a year-round basis.

Understanding spatial and temporal patterns of aquatic macroinvertebrates as prey resources may have important implications for managing Brown Trout. For instance, the present study identifies *Gammarus* as commonly available aquatic macroinvertebrate taxon that is particularly abundant in a stream with a high degree of groundwater control and fast growing populations of Brown Trout. Although *Gammarus* may support high productivity of Brown Trout, this taxon has been shown to recover slowly following catastrophic flooding events in southeastern Minnesota (Mundahl and Hunt 2011). As future climate projections predict stronger, more frequent rainfall events in this region due to climate change (Johnson et al. 2015), such catastrophic flood events may reduce the distribution and abundance of *Gammarus*. Although mitigating efforts to reduce the impacts of climate change may include the reintroduction of *Gammarus*, along with other taxa linked with high fish productivity, managers should also focus on sustaining healthy assemblages of flood-resistant aquatic macroinvertebrates, such as winter-emerging Chironomids (Anderson 2012). In addition to being resilient to extreme rainfall and flood events, Chironomids are highly abundant in southeastern Minnesota, providing more than half of the composition of available aquatic macroinvertebrates in many streams throughout the year.

In addition, although only a few taxonomic groups represented a majority of the

aquatic macroinvertebrates sampled in this study, we found that the structure of macroinvertebrate assemblages, including diversity and availability, varied significantly across time and space. Differences in the taxonomic composition of prey assemblages were most pronounced between streams, highlighting the inherent limitations of aquatic macroinvertebrates to disperse and recolonize new streams, with terrestrial environments serving as a primary barrier. Therefore, managers should take a stream-specific approach to management efforts that relate to aquatic macroinvertebrate communities, and attempt to mitigate the impacts that climate change, land use, and pollution may have on aquatic macroinvertebrate species that are especially critical for supporting Brown Trout growth and survival.

Lastly, in contrast to other regions, our results suggest that terrestrial macroinvertebrate taxa are unlikely to represent a consistent or abundant food resource for Brown Trout in southeastern Minnesota. Therefore, when attempting to manage food resources that support productive populations of Brown Trout, an emphasis should be placed on in-stream efforts that promote suitable water and habitat quality for benthic macroinvertebrates.

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Tables

Table 1. Slope of air-water temperature regression (groundwater input), drainage area, channel slope, and site location from six southeastern Minnesota streams during 2011 – 2013. Air-water temperature regressions are from Krider et al. (2013). Drainage area, channel slope, and UTM coordinates are from French (2014).

Stream	Air-water regression slope	Drainage area (km^2)	Channel slope (m*km^{-1})	UTM Coordinates
Beaver Creek	0.44	29.1	10.8	577026, 4889127
Daley Creek	0.20	15.2	22.7	605606, 4845390
Garvin Brook	0.35	19.7	15.5	595503, 4873356
Gribbon Creek	0.26	20.4	13.9	587631, 4839986
Rush Creek	0.51	56.5	17.1	591328, 4865564
Trout Run Creek	0.31	43.7	17.1	575358, 4857802

Table 2. Total number of taxonomic groups identified by stream and season, and results of linear regression.

Stream	Benthos	Drift	Season	Benthos	Drift
Beaver Creek	37	46	Fall	27	33
Daley Creek	25	37	Winter	27	31
Garvin Brook	27	41	Spring	40	60
Gribbon Creek	29	51	Summer	33	50
Rush Creek	24	45			
Trout Run Creek	22	41			
	$r^2=0.22$	$p=0.30$		$r^2=0.96$	$p=0.02$

Table 3. Annual variation in benthic assemblages across six streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

Benthos	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]	Drift	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Beaver Creek		0.62	0.61	-0.01	0.449	*Beaver Creek*		0.53	0.52	-0.02	0.598
2011 (n=4)	0.59					2011 (n=3)	0.41				
2012 (n=3)	0.65					2012 (n=4	0.48				
2013 (n=3)	0.62					2013 (n=4)	0.68				
Daley Creek		0.52	0.50	-0.04	0.708	*Daley Creek*		0.46	0.44	-0.03	0.743
2011 (n=3)	0.50					2011 (n=3)	0.35				
2012 (n=4)	0.48					2012 (n=4)	0.46				
2013 (n=4)	0.63					2013 (n=4)	0.53				
Garvin Brook		0.52	0.56	0.06	0.111	*Garvin Brook*		0.51	0.52	0.01	0.354
2011 (n=3)	0.56					2011 (n=3)	0.45				
2012 (n=4)	0.45					2012 (n=4)	0.53				
2013 (n=4)	0.57					2013 (n=4)	0.54				
Gribbon Creek		0.61	0.61	-0.01	0.558	*Gribbon Creek*		0.47	0.50	0.05	0.215
2011 (n=3)	0.56					2011 (n=2)	0.61				
2012 (n=4)	0.56					2012 (n=4)	0.50				
2013 (n=3)	0.74					2013 (n=4)	0.38				
Rush Creek		0.62	0.69	0.10	**0.027**	*Rush Creek*		0.49	0.50	0.02	0.269
2011 (n=3)	0.57					2011 (n=3)	0.38				
2012 (n=4)	0.56					2012 (n=4)	0.47				
2013 (n=4)	0.72					2013 (n=4)	0.59				
Trout Run Creek		0.70	0.71	0.02	0.334	*Trout Run Creek*		0.44	0.44	0.004	0.388
2011 (n=3)	0.77					2011 (n=3)	0.33				
2012 (n=4)	0.59					2012 (n=4)	0.50				
2013 (n=4)	0.72					2013 (n=4)	0.44				

Table 4. Variation in benthic assemblages across six streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall		**0.49**	**0.58**	**0.14**	**0.0002**
Beaver Creek (n=10)	0.48				
Daley Creek (n=10)	0.41				
Garvin Brook (n=11)	0.49				
Gribbon Creek (n=10)	0.47				
Rush Creek (n=11)	0.56				
Trout Run Creek (n=10)	0.55				
Pairwise					
Beaver Creek (n=10)	0.60	0.54	0.69	0.22	**0.0002**
Daley Creek (n=10)	0.48				
Beaver Creek (n=11)	0.50	0.50	0.52	0.03	0.08
Garvin Brook (n=11)	0.51				
Beaver Creek (n=10)	0.60	0.65	0.69	0.06	**0.006**
Trout Run Creek (n=10)	0.71				
Beaver Creek (n=10)	0.51	0.55	0.60	0.08	**0.005**
Rush Creek (n=11)	0.59				
Beaver Creek (n=10)	0.51	0.54	0.62	0.13	**0.002**
Trout Run Creek (n=10)	0.57				
Daley Creek (n=10)	0.49	0.52	0.62	0.15	**0.0002**
Garvin Creek (n=11)	0.55				
Daley Creek (n=10)	0.48	0.53	0.58	0.09	**0.001**
Gribbon Creek (n=10)	0.59				
Daley Creek (n=10)	0.44	0.51	0.59	0.13	**0.0002**
Rush Creek (n=11)	0.59				
Daley Creek (n=11)	0.42	0.40	0.41	0.03	0.09
Trout Run Creek (n=11)	0.39				
Gribbon Creek (n=10)	0.55	0.57	0.60	0.04	**0.01**
Garvin Brook (n=11)	0.59				
Garvin Brook (n=11)	0.54	0.56	0.60	0.06	**0.015**
Rush Creek (n=11)	0.59				
Garvin Brook (n=11)	0.55	0.63	0.65	0.03	**0.05**
Trout Run Creek (n=10)	0.71				

Gribbon Creek (n=10)	0.52	0.55	0.61	0.09	**0.0002**
Rush Creek (n=11)	0.59				
Gribbon Creek (n=10)	0.58	0.65	0.8	0.05	**0.004**
Trout Run Creek (n=10)	0.71				
Rush Creek (n=11)	0.59	0.58	0.59	0.02	0.15
Trout Run Creek (n=10)	0.57				

By season					
Fall		0.50	0.65	0.23	**0.04**
Beaver Creek (n=1)	NA				
Daley Creek (n=3)	0.36				
Garvin Brook (n=1)	NA				
Gribbon Creek (n=3)	0.36				
Rush Creek (n=2)	0.77				
Trout Run Creek (n=0)	NA				
Winter		0.31	0.69	0.55	**0.001**
Beaver Creek (n=2)	0				
Daley Creek (n=2)	0.44				
Garvin Brook (n=2)	0				
Gribbon Creek (n=2)	0.55				
Rush Creek (n=2)	0.85				
Trout Run Creek (n=2)	0				
Spring		0.57	0.62	0.08	**0.02**
Beaver Creek (n=2)	0.66				
Daley Creek (n=4)	0.44				
Garvin Brook (n=6)	0.59				
Gribbon Creek (n=4)	0.66				
Rush Creek (n=5)	0.62				
Trout Run Creek (n=5)	0.50				
Summer		0.48	0.58	0.18	**0.003**
Beaver Creek (n=5)	0.42				
Daley Creek (n=2)	0.99				
Garvin Brook (n=2)	0.80				
Gribbon Creek (n=2)	0.27				
Rush Creek (n=2)	0.33				
Trout Run Creek (n=3)	0.25				

Table 5. Seasonal variation in benthic assemblages across six streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

Overall		Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Winter (n=12)		0.65	**0.56**	**0.58**	**0.02**	**0.05**
Spring (n=25)		0.58				
Summer (n=16)		0.46				
Fall (n=9)		0.59				
Winter (n=12)		0.68	0.64	0.65	0.01	0.10
Spring (n=25)		0.61				
Winter (n=12)		0.68	0.59	0.61	0.04	**0.04**
Summer (n=16)		0.52				
Winter (n=12)		0.68	0.66	0.67	0.01	0.24
Fall (n=9)		0.64				
Spring (n=25)		0.62	0.58	0.58	0.002	0.35
Summer (n=16)		0.52				
Spring (n=25)		0.62	0.62	0.62	0.001	0.37
Fall (n=9)		0.64				
Summer (n=16)		0.51	0.56	0.57	0.01	0.17
Fall (n=9)		0.64				
Beaver Creek	Winter (n=2)	0	0.37	0.51	0.28	**0.04**
	Spring (n=2)	0.63				
	Summer (n=5)	0.41				
	Fall (n=1)	NA				
Daley Creek	Winter (n=2)	0.42	0.36	0.42	0.15	0.07
	Spring (n=4)	0.43				
	Summer (n=2)	0.30				
	Fall (n=2)	0.22				
Garvin Brook	Winter (n=2)	0	0.63	0.56	-0.14	0.98
	Spring (n=6)	0.58				
	Summer (n=2)	0.80				
	Fall (n=1)	NA				
Gribbon Creek	Winter (n=2)	0.55	0.50	0.52	0.03	0.34
	Spring (n=4)	0.65				
	Summer (n=2)	0.23				
	Fall (n=2)	0.43				
Rush Creek	Winter (n=2)	0.84	0.63	0.59	-0.07	0.78
	Spring (n=5)	0.61				
	Summer (n=2)	0.32				
	Fall (n=2)	0.77				
Trout Run Creek	Winter (n=2)	0	0.32	0.56	0.43	**0.007**
	Spring (n=5)	0.49				
	Summer (n=3)	0.24				
	Fall (n=0)	NA				

Table 6. Morisita's Index of Similarity in drifting/benthic taxonomic composition among study sites, 2011-2013. Values greater than 0.60 represent high similarity and are in bold (Zaret and Rand 1971).

	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Beaver Creek	0.55/0.24	0.07/0.56	0.41/0.48	0.58/0.44	**0.75**/0.42
Daley Creek		0.17/0.34	**0.66**/0.41	**0.76/0.64**	**0.73/0.77**
Garvin Brook			0.16/0.56	0.12/0.47	0.05/0.53
Gribbon Creek				0.61/0.47	0.56/0.56
Rush Creek					**0.69/0.81**

Table 7. Variation in drift assemblages across six streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall		**0.49**	**0.52**	**0.06**	**0.0004**
Beaver Creek (n=11)	0.47				
Daley Creek (n=11)	0.42				
Garvin Brook (n=11)	0.50				
Gribbon Creek (n=10)	0.47				
Rush Creek (n=11)	0.47				
Trout Run Creek (n=11)	0.39				
Pairwise					
Beaver Creek (n=11)	0.50	0.46	0.48	0.03	**0.05**
Daley Creek (n=11)	0.42				
Beaver Creek (n=11)	0.50	0.50	0.52	0.03	0.08
Garvin Brook (n=11)	0.51				
Beaver Creek (n=11)	0.51	0.49	0.50	0.01	0.17
Gribbon Creek (n=10)	0.47				
Beaver Creek (n=11)	0.50	0.49	0.49	0.002	0.37
Rush Creek (n=11)	0.47				
Beaver Creek (n=11)	0.50	0.45	0.45	0.001	0.37
Trout Run Creek (n=11)	0.40				
Daley Creek (n=11)	0.42	0.46	0.51	0.09	**0.001**
Garvin Brook (n=11)	0.51				
Daley Creek (n=11)	0.42	0.44	0.47	0.06	**0.003**
Gribbon Creek (n=10)	0.46				
Daley Creek (n=11)	0.43	0.43	0.47	0.04	**0.02**
Rush Creek (n=11)	0.47				
Daley Creek (n=11)	0.42	0.40	0.41	0.03	0.09
Trout Run Creek (n=11)	0.39				
Gribbon Creek (n=10)	0.51	0.49	0.50	0.01	0.19
Garvin Brook (n=11)	0.47				
Garvin Creek (n=11)	0.51	0.51	0.47	0.05	**0.01**
Rush Creek (n=11)	0.47				
Garvin Brook (n=11)	0.50	0.45	0.48	0.07	**0.01**

Trout Run Creek (n=11)	0.39				
Gribbon Creek (n=10)	0.47	0.47	0.50	0.06	**0.001**
Rush Creek (n=11)	0.47				
Gribbon Creek (n=10)	0.46	0.43	0.44	0.03	**0.05**
Trout Run Creek (n=11)	0.39				
Rush Creek (n=11)	0.47	0.43	0.44	0.03	0.07
Trout Run Creek (n=11)	0.39				
By season					
Fall		0.42	0.43	0.03	0.41
Beaver Creek (n=1)	NA				
Daley Creek (n=3)	0.26				
Garvin Brook (n=1)	NA				
Gribbon Creek (n=1)	NA				
Rush Creek (n=2)	0.66				
Trout Run Creek (n=0)	NA				
Winter		0.43	0.53	0.19	**0.01**
Beaver Creek (n=2)	0.68				
Daley Creek (n=2)	0.51				
Garvin Brook (n=2)	0.46				
Gribbon Creek (n=2)	0.41				
Rush Creek (n=2)	0.33				
Trout Run Creek (n=2)	0.19				
Spring		0.51	0.52	0.02	0.21
Beaver Creek (n=4)	0.55				
Daley Creek (n=4)	0.40				
Garvin Brook (n=6)	0.53				
Gribbon Creek (n=4)	0.54				
Rush Creek (n=5)	0.51				
Trout Run Creek (n=5)	0.50				
Summer		0.48	0.49	0.03	0.33
Beaver Creek (n=4)	0.39				
Daley Creek (n=2)	0.79				
Garvin Brook (n=2)	0.69				
Gribbon Creek (n=3)	0.46				
Rush Creek (n=2)	0.47				
Trout Run Creek (n=4)	0.33				

Table 8. Seasonal variation in drift assemblages across six streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

Overall		Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Winter (n=12)		0.48	**0.47**	**0.48**	**0.02**	**0.03**
Spring (n=28)		0.49				
Summer (n=17)		0.46				
Fall (n=8)		0.41				
Winter (n=12)		0.50	0.48	0.49	0.01	0.23
Spring (n=28)		0.48				
Winter (n=12)		0.51	0.47	0.49	0.03	**0.04**
Summer (n=17)		0.44				
Winter (n=12)		0.52	0.48	0.50	0.05	**0.01**
Fall (n=8)		0.42				
Spring (n=28)		0.49	0.48	0.48	0.002	0.31
Summer (n=17)		0.46				
Spring (n=28)		0.42	0.47	0.48	0.02	**0.04**
Fall (n=8)		0.48				
Summer (n=17)		0.46	0.45	0.45	0.004	0.29
Fall (n=8)		0.42				
Beaver Creek	Winter (n=2)	0.68	0.49	0.50	0.02	0.39
	Spring (n=4)	0.55				
	Summer (n=4)	0.35				
	Fall (n=1)	NA				
Daley Creek	Winter (n=2)	0.50	0.43	0.42	-0.04	0.72
	Spring (n=4)	0.38				
	Summer (n=2)	0.80				
	Fall (n=3)	0.22				
Garvin Brook	Winter (n=2)	0.45	0.54	0.57	-0.06	0.76
	Spring (n=6)	0.52				
	Summer (n=2)	0.69				
	Fall (n=1)	NA				
Gribbon Creek	Winter (n=2)	0.40	0.46	0.47	0.02	0.35
	Spring (n=4)	0.52				
	Summer (n=3)	0.42				
	Fall (n=1)	NA				
Rush Creek	Winter (n=2)	0.32	0.48	0.48	0.007	0.36
	Spring (n=5)	0.49				
	Summer (n=2)	0.45				
	Fall (n=2)	0.64				
Trout Run Creek	Winter (n=2)	0.18	0.36	0.42	0.13	0.07
	Spring (n=5)	0.48				
	Summer (n=4)	0.30				
	Fall (n=0)	NA				

Table 9. Morisita's Index of Similarity for drifting/benthic taxonomic composition among seasons, 2011-2013, in six groundwater-dominated streams in southeastern Minnesota. Values greater than 0.60 represent high similarity and are shown in bold (Zaret and Rand 1971).

	Spring	Summer	Fall
Winter	**0.83/0.65**	**0.72**/0.55	**0.76/0.83**
Spring		**0.90/0.72**	**0.86/0.65**
Summer			**0.91/0.79**

Table 10. Relationships between measures of aquatic macroinvertebrate diversity/abundance and physical variables across six groundwater-dominated streams in southeastern Minnesota using simple linear regression.

	Groundwater input			Channel slope			Drainage area		
	F	r^2	p	F	r^2	p	F	r^2	p
Benthic density (# individuals/m^2)	0.53	0.12	0.50	0.04	0.01	0.85	0.03	0.01	0.86
Drift density (#individuals/100m^3)	0.19	0.19	0.39	0.06	0.01	0.82	0.18	0.04	0.69
Simpsons diversity (D$_s$)	0.06	0.01	0.82	3.0	0.43	0.16	3.0	0.43	0.16
Taxonomic richness of drift	0.31	0.08	0.58	5.0	0.55	0.09	0.07	0.02	0.80
Taxonomic richness of benthos	0.26	0.06	0.63	5.0	0.56	0.08	0.5	0.12	0.50

Figures
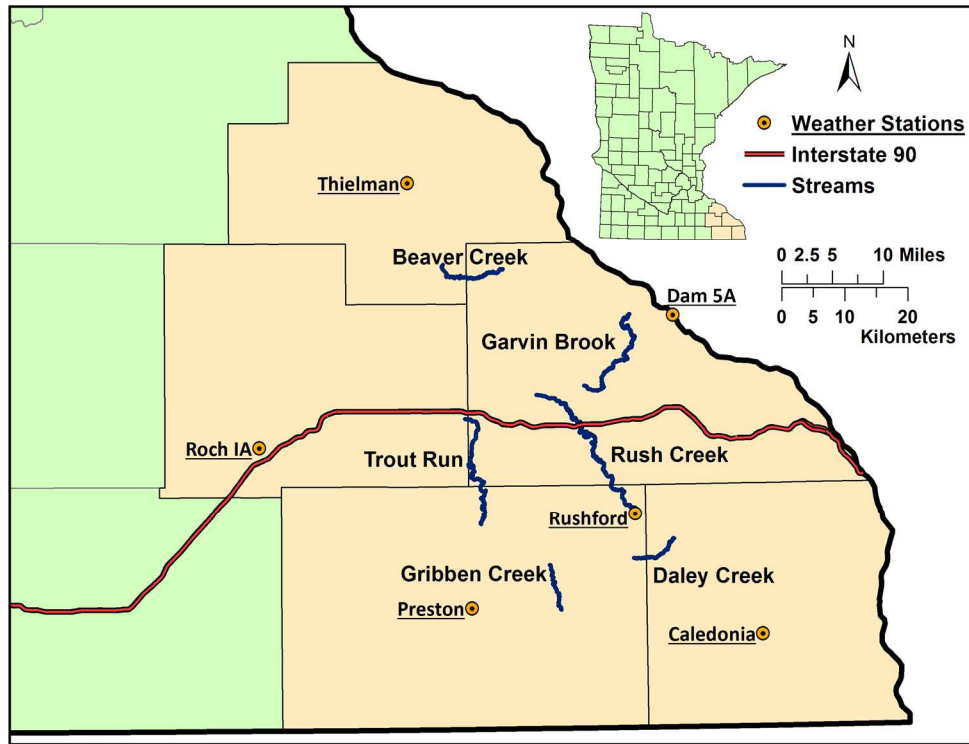
Figure 1. Map of the Driftless Ecoregion of southeastern Minnesota and six streams sampled for benthic and drifting macroinvertebrates, 2011-13. Weather stations from which air temperature data were collected are depicted.

A)
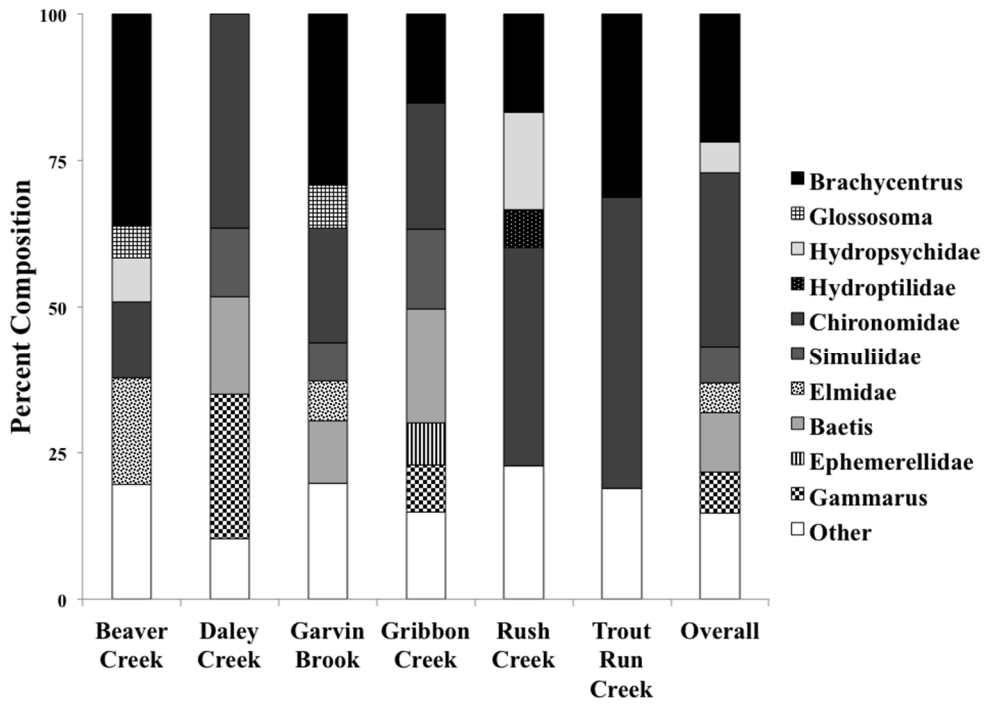
B)
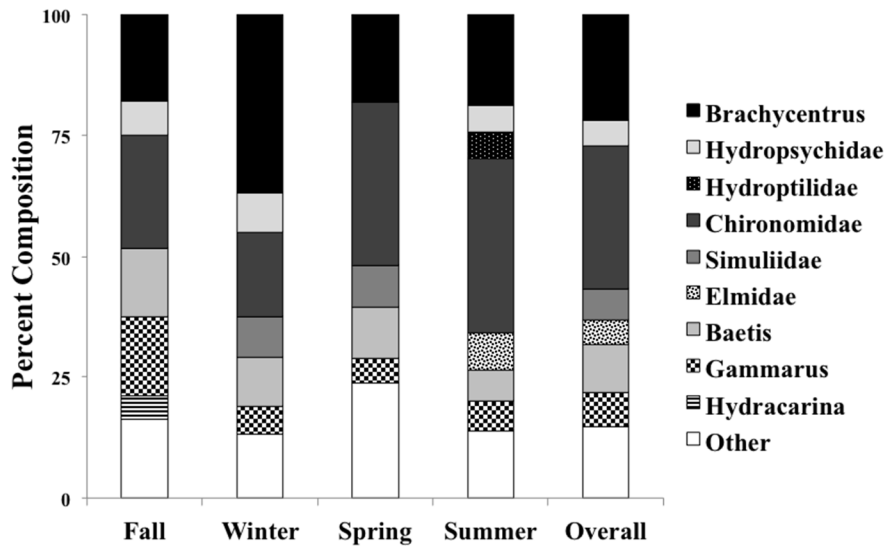
Figure 2. Percent composition of benthic macroinvertebrates >5% of the total by (A) stream and (B) season, 2011-2013.

A)

B)
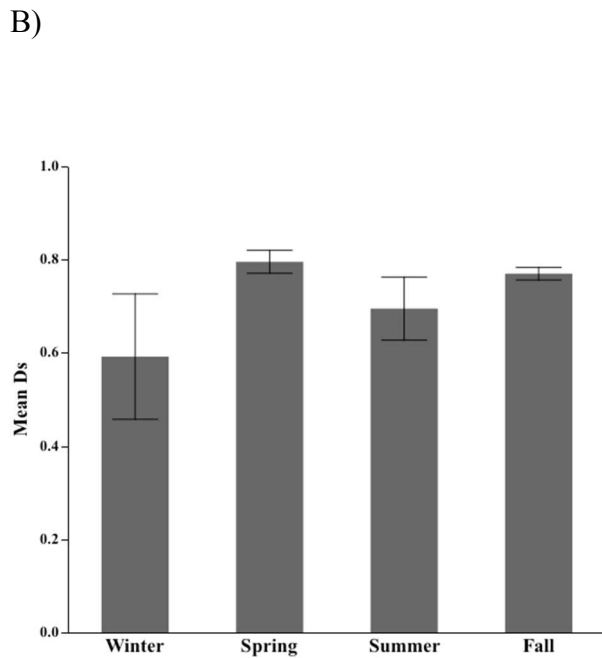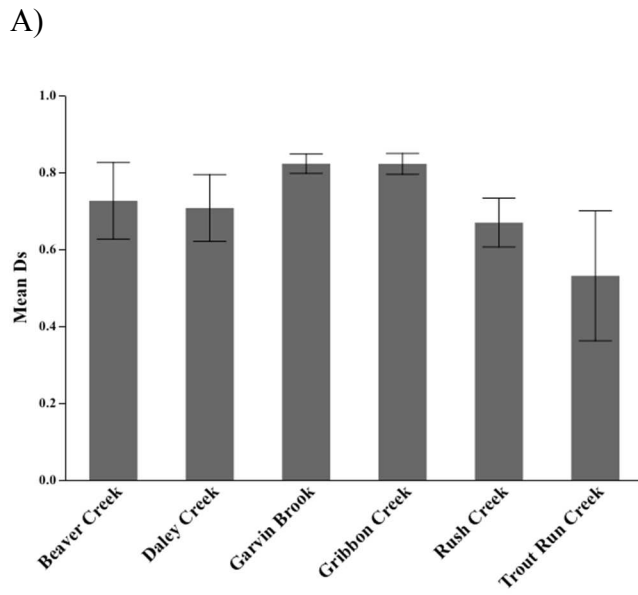
Figure 3. Simpson Diversity Index (Ds) of benthic macroinvertebrate assemblages by (A) stream and (B) season, 2011-2013. Error bars = ± 1 SE. No significant differences among sites (F=1.3, p=0.27) or seasons (F=1.4, p=0.26).

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A)

B)
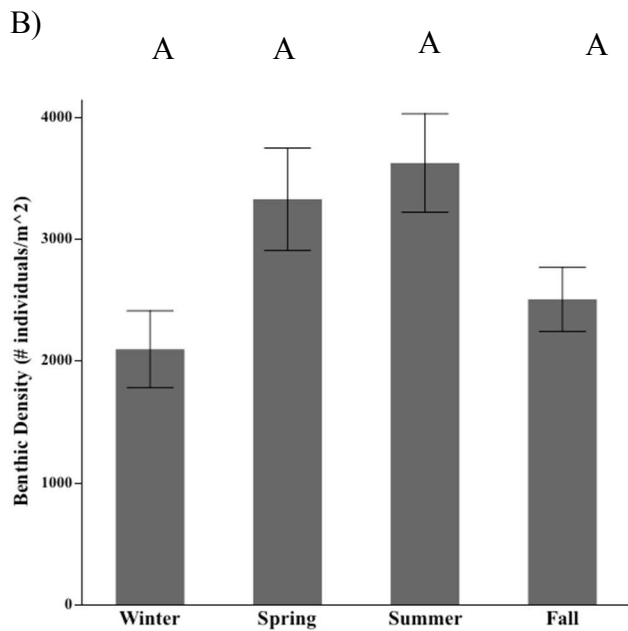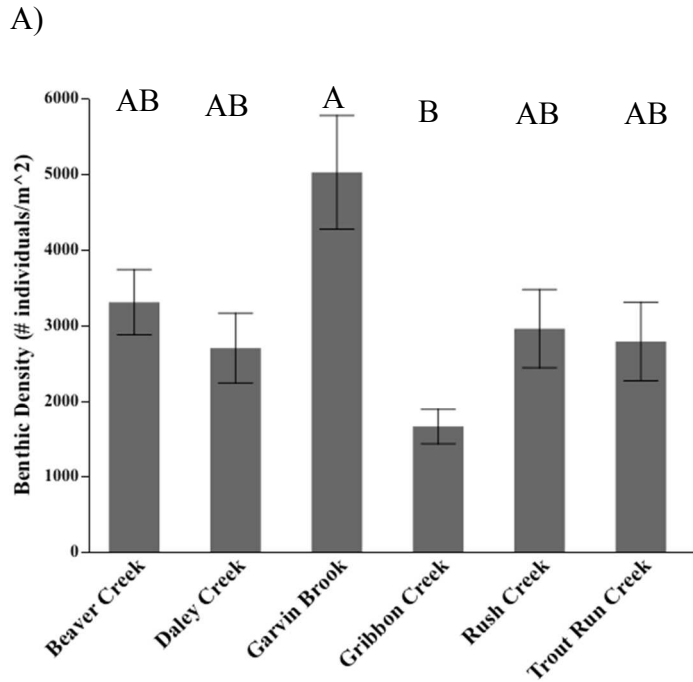
Figure 4. Mean benthic macroinvertebrate density (number of individuals per m^2) by (A) stream and (B) season, 2011-2013. Error bars = ± 1 SE. Bars with the same letter are not significantly different ($p<0.05$).

A)

B)
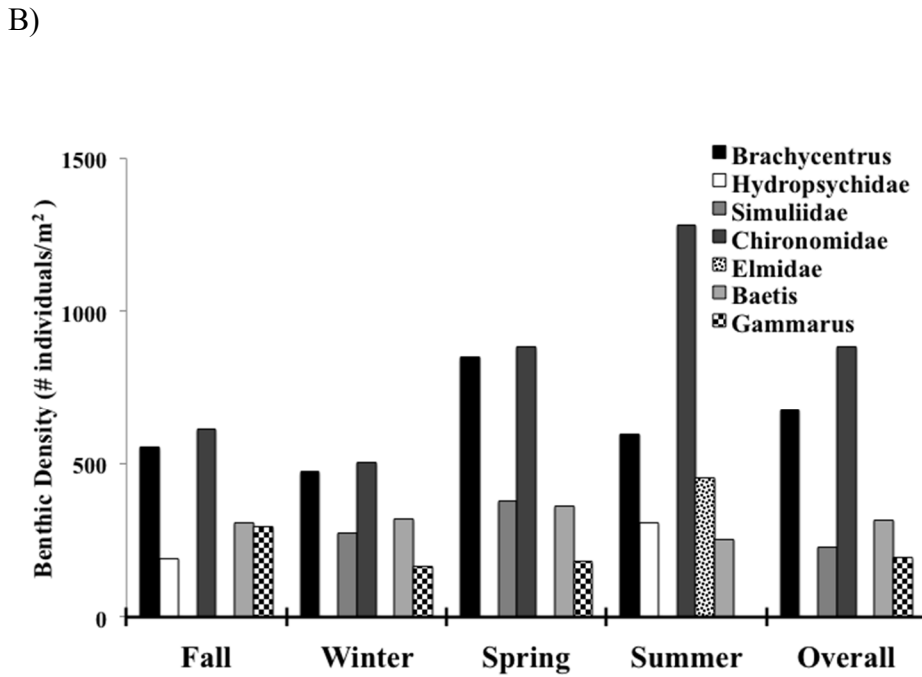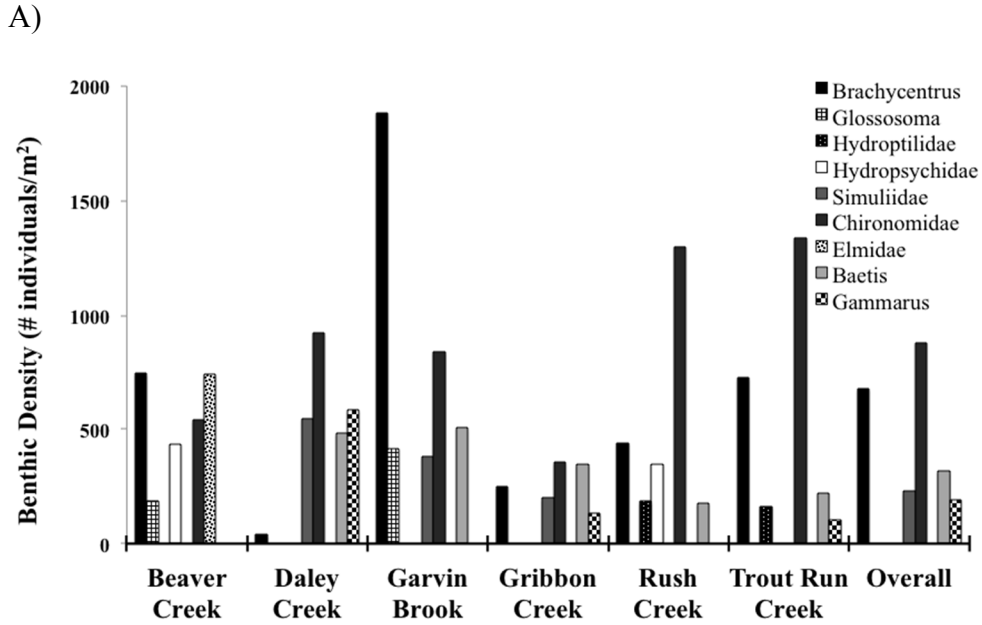
Figure 5. Mean benthic density (number of individuals per m^2) of five most abundant macroinvertebrate taxa by (A) stream and (B) season in six streams across southeastern Minnesota, 2011-2013.

A)

B)
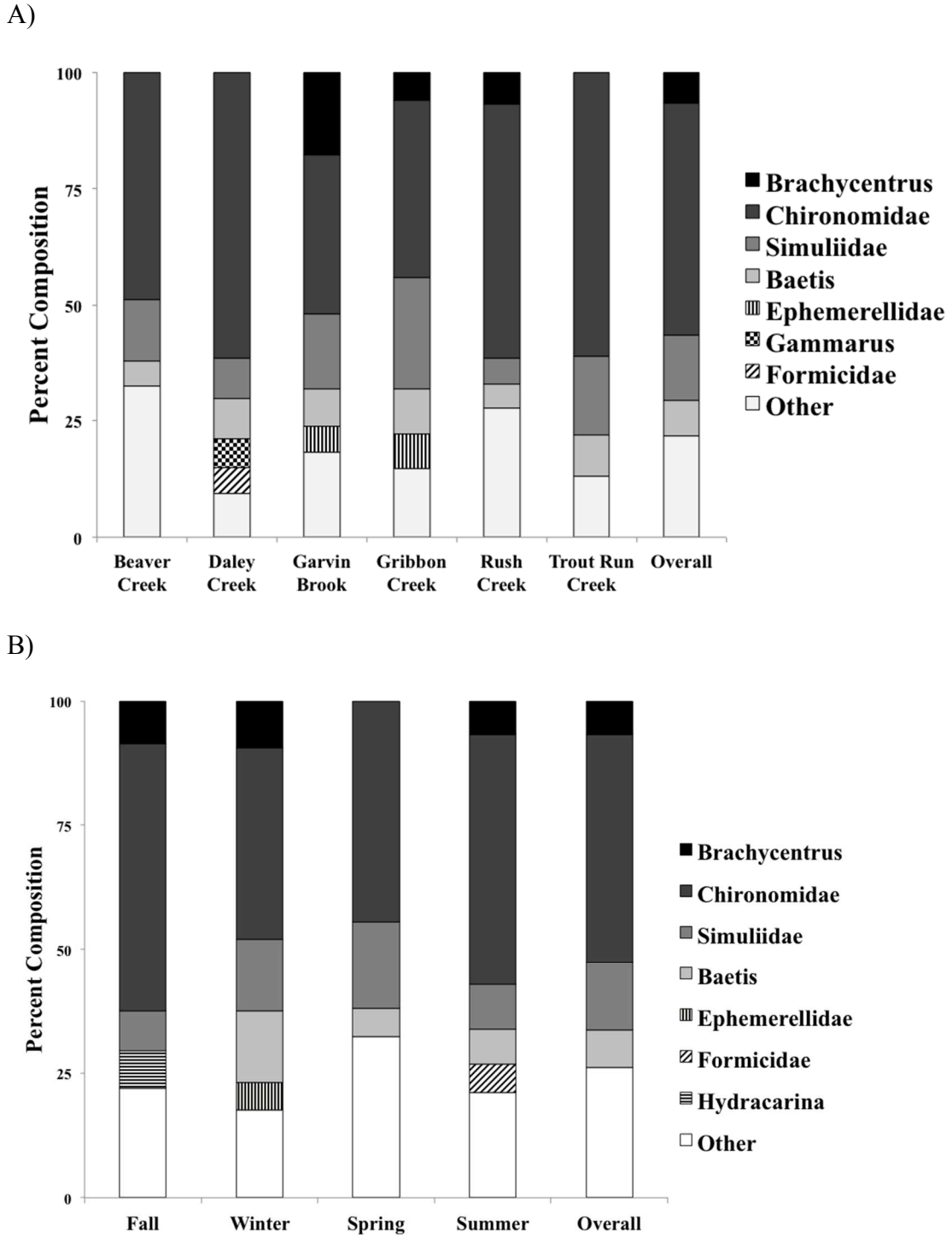
Figure 6. Percent composition of drifting macroinvertebrates >5% of the total by (A) stream and (B) season, in six streams across southeastern Minnesota, 2011-2013.
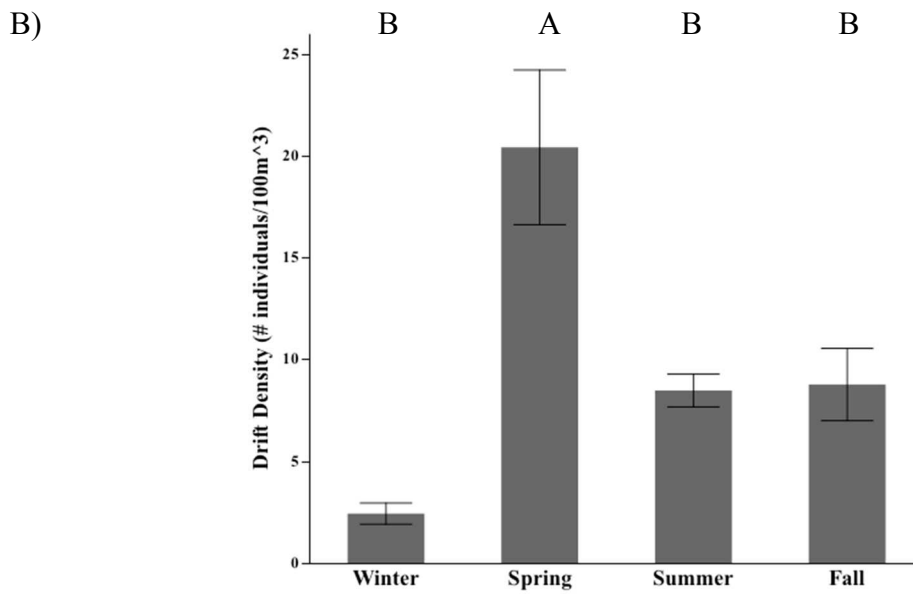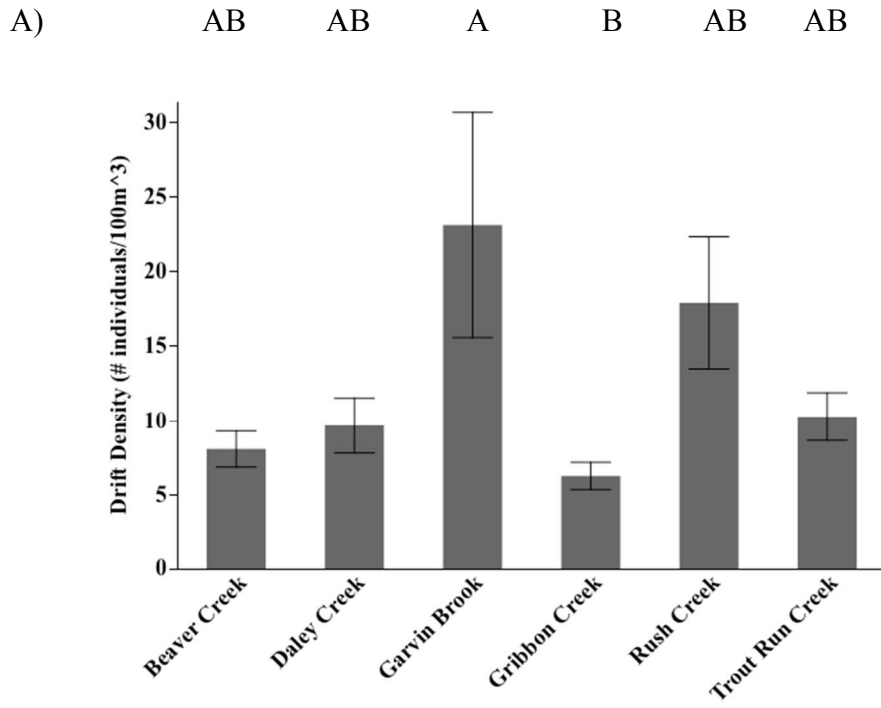
Figure 7. Mean drift density (number of individuals per 100m^3) by (A) stream and (B) season in six streams across southeastern Minnesota, 2011-2013. Error bars = ± 1 SE. Bars with the same letter are not significantly different ($p<0.05$).

A)

B)
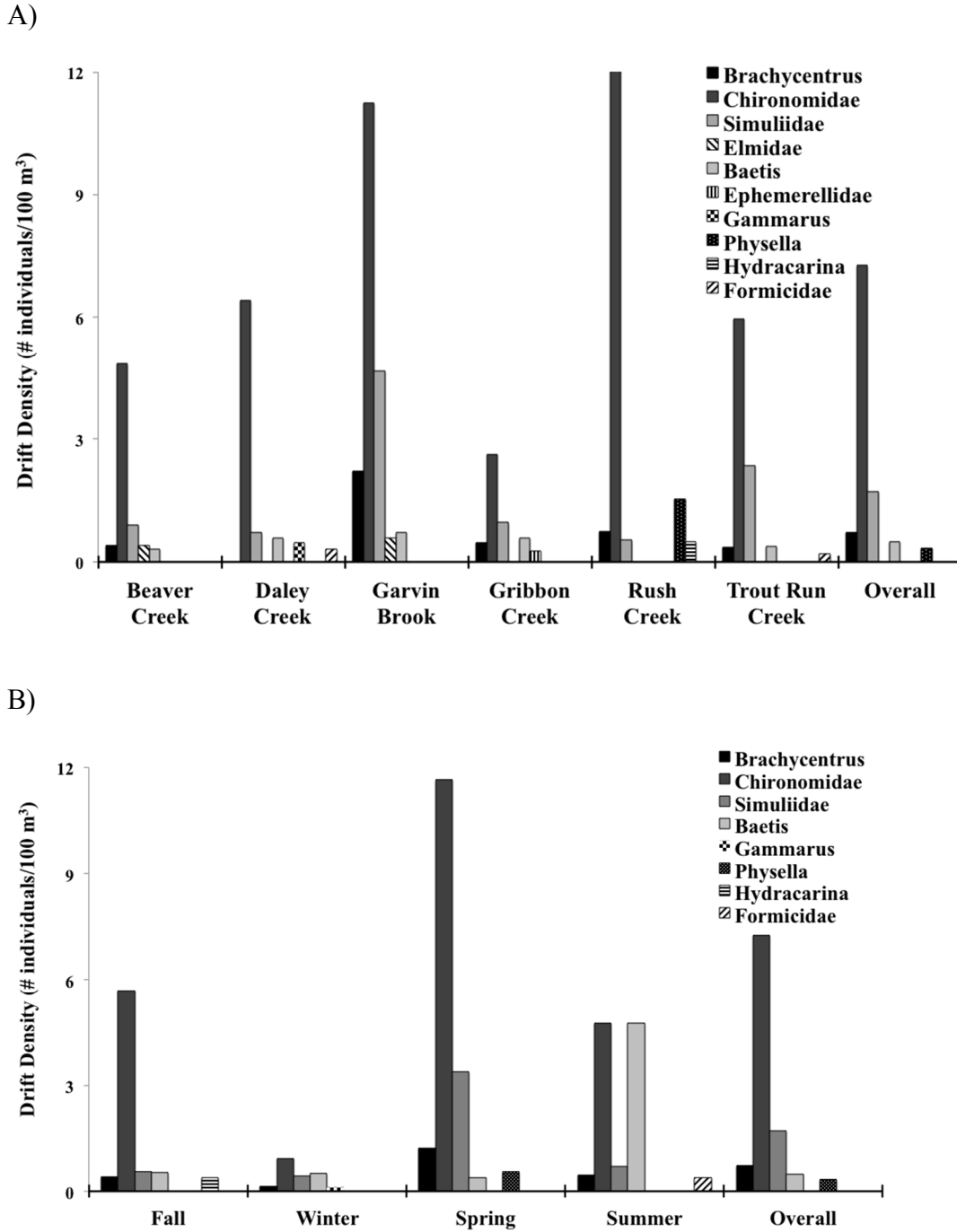
Figure 8. Mean drift density (number of individuals per 100 m^3) of five most abundant macroinvertebrate taxa by (A) stream, and (B) season in six streams across southeastern Minnesota, 2011-2013.

(A) Overall, all seasons combined
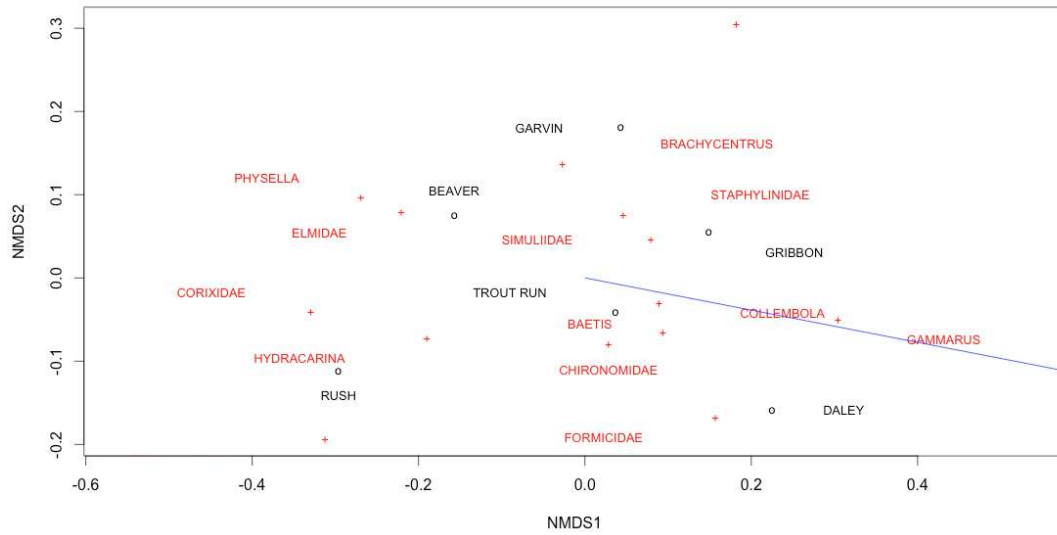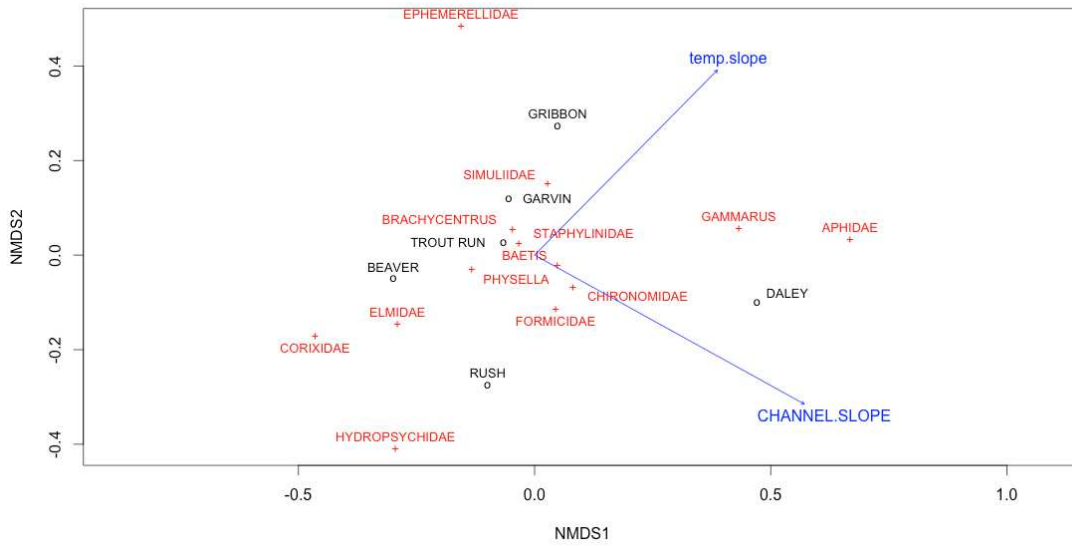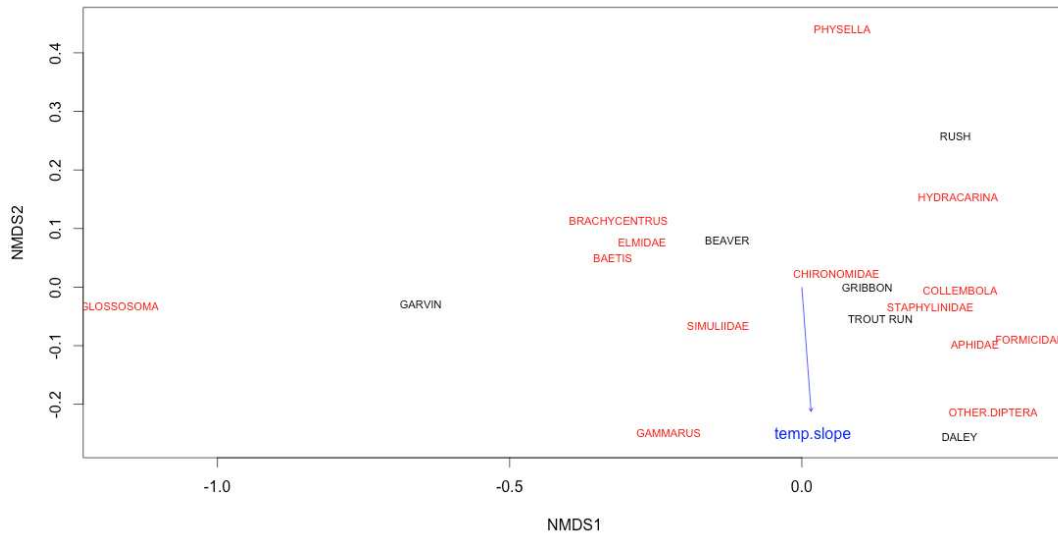
(B) Spring

(C) Summer

(D) Fall
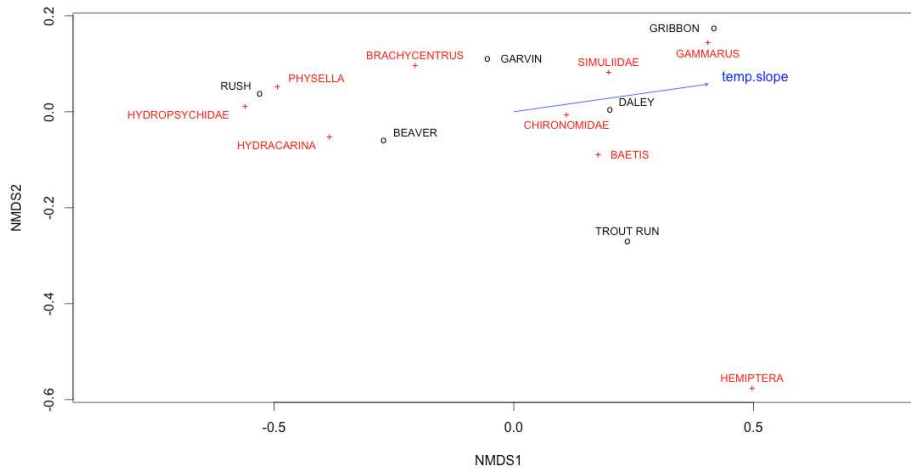
Figure 9. NMDS analysis of drifting macroinvertebrates, 2011-2013, during (A) all seasons combined, (B) spring, (C) summer, and (D) fall, using proportions of total taxa collected. Streams closer to one another had more similar community composition of drift than streams further apart. The arrow indicates the direction of increasing value for physical variables that were significantly associated with the ordination ($p < 0.05$).

(A) Overall, all seasons combined
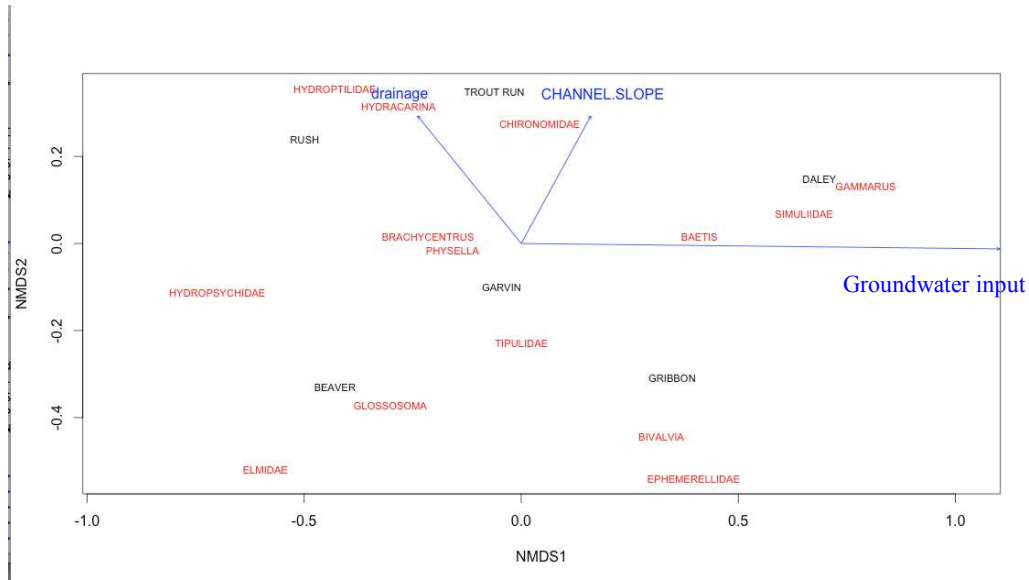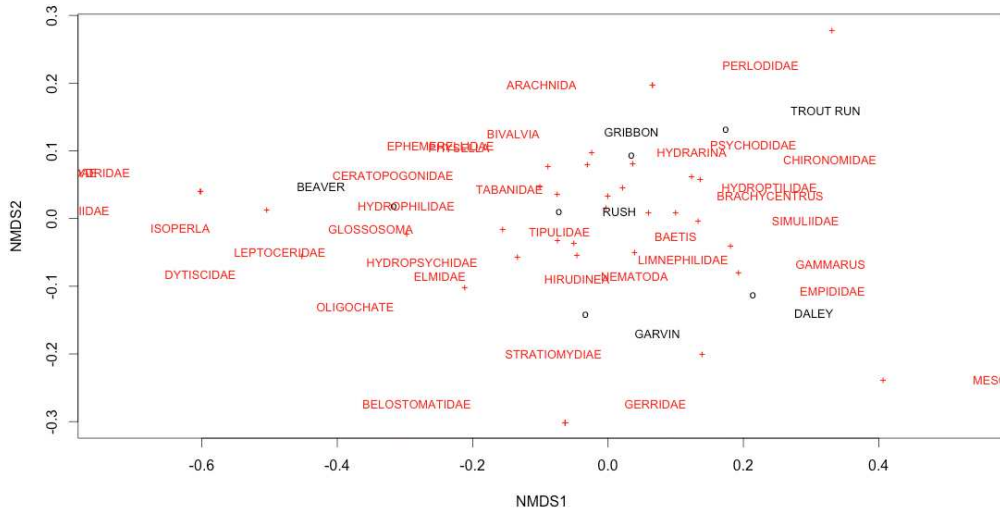
(B) Spring

Figure 10. NMDS analysis of benthic macroinvertebrates, 2011-2013, during (A) all seasons combined and (B) spring, using proportions of total taxa collected. Streams closer to one another had more similar community composition of benthos than streams further apart. The arrow indicates the direction of increasing value for physical variables that were significantly associated with the ordination (p<0.05).

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Chapter 3

Seasonal feeding selectivity of Brown Trout *Salmo Trutta* in five groundwater-dominated streams in the Driftless Ecoregion of southeastern Minnesota

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Running headline: Seasonal feeding selectivity of Brown Trout

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Summary

Availability and selection of macroinvertebrate prey may be an important factor in explaining temporal and spatial variation in growth among stream salmonids. However, few studies contain detailed information (multiple recaptures of marked individual fish, frequent samples of prey availability and selection) required to identify such relationships, particularly on a seasonal and spatial scale. The objectives of this study were to quantify drift and benthic macroinvertebrate prey availability and selection by Brown Trout on a seasonal basis in five streams across three years in southeastern Minnesota. Although there was considerable variability in drifting and benthic prey assemblages within streams and seasons, few taxa were dominant in trout diets and the environment. Brown Trout consistently selected only one or two taxa, including *Physella* and *Gammarus*, while displaying neutral or negative selection for all other taxa. Foraging patterns suggested a preference of benthic feeding. Overall electivity of benthos and drift varied spatially and temporally with a negative relationship between the total proportion of prey available and prey electivity. On a broad scale, there was no relationship between seasonal growth and prey electivity across all streams, but a positive relationship was detected within two of five streams. Understanding seasonal patterns in prey availability and selection may provide insight into why Brown Trout demonstrate variable growth across streams with seemingly similar physical characteristics.

Keywords: Brown Trout, Driftless Ecoregion, seasonal diet, prey selectivity

Introduction

Growth of stream-dwelling salmonids varies greatly among seasons, reflecting the highly seasonal nature of temperate stream environments (Letcher et al. 2002). Reductions in temperature, light, and macroinvertebrate productivity has been linked with low or negative growth in many streams (Metcalfe and Thorpe 1992); however, in southeastern Minnesota, there appears to be considerable spatial and seasonal variation with respect to maximum growth rates of Brown Trout (Dieterman et al. 2004; Dieterman et al. 2012; French et al. 2014). Groundwater-dominated streams in this region support highly productive populations of Brown Trout, but demonstrate broad variation in production and diversity of aquatic macroinvertebrates (Troelstrup and Perry 1989; Waters 2000).

Invertebrate availability and accessibility on a seasonal and temporal scale may influence corresponding patterns of Brown Trout prey selectivity, potentially altering patterns of growth in small groundwater-dominated streams where aquatic insects are the major prey items (Elliott 1970; Hunt and Krokhin 1975; Pedley and Jones 1978; Allan 1981). Trout are opportunistic generalists throughout the year (Lord 1933; Maciolek and Needham 1952; Reimers 1957; Cunjak and Power 1987; Ozvarol et al. 2011) and some studies have linked growth with the abundance of drifting invertebrate prey (Wilzbach et al. 1986; Erkinaro and Niemelä 1995). Many studies emphasize the importance of drifting prey to trout diet (e.g. Hunt and Krokhin 1975; Bachman 1984; Dahl 1998), whereas the contribution of benthos has been less studied (Tippets and Moyle 1978; Johansen et al. 2010), and little weight has been placed on the extent to which benthos are selected for by Brown Trout (Ringler and Brodowski 1983). Past research in southeastern Minnesota provides evidence for drift feeding of Brown Trout during summer (Newman 1987) with neutral selection of terrestrial drift (Laudon et al. 2005), and a switch to predominately benthic feeding during fall and winter (Newman 1987; Grant 1999; Anderson 2012; French 2014). To date, no studies have evaluated Brown Trout selectivity of benthos and drift on a seasonal scale.

Studies in temperate climates have reported seasonal dissimilarity in the composition of macroinvertebrate assemblages and in the foraging patterns of Brown

Trout; however few studies have assessed these patterns simultaneously in more than one stream across multiple seasons and years (Stoneburner and Smock 1979; Allan 1987; Gualdoni et al. 1991; Shearer et al. 2002; Leung et al. 2009). Although food resources are necessary to support growth and survival of Brown Trout, prey resources are often overlooked in habitat assessment, monitoring, and management, and poorly understood on a seasonal and spatial scale (Fausch 1988). There are many potential reasons why past research has failed to address the role of macroinvertebrates when examining the growth of salmonids. First, fish production is a complex function of multiple environmental factors, but a direct link between growth and the quality or quantity of prey can be difficult to verify (Folt et al. 1998). Additionally, populations of aquatic macroinvertebrates, the primary food resource for stream-dwelling Brown Trout and other salmonids, can vary considerably on temporal and spatial scales (Resh et al. 1988). Accurate quantification of macroinvertebrate abundances is challenging; thus, it is difficult to establish certainty in the role that such abundance plays in the growth of salmonids.

In general, studies of fish growth, prey resources, and selection in temperate climates are largely restricted to spring, summer, and fall. Few investigations have addressed winter dynamics, including the influence of macroinvertebrate assemblage composition on trout during cold periods (e.g. Lord 1933; Maciolek and Needham 1952; Cunjak et al. 1987; Cunjak and Power 1987; Heggenes et al. 1993; Fochetti et al. 2003; Utz and Hartman 2007; White and Harvey 2007; Johansen et al. 2010). Furthermore, many studies are limited to fish in a single stream (e.g. Lord 1933; Maciolek and Needham 1952; Cunjak and Power 1987; Johansen et al. 2010), milder climates (White and Harvey 2007), and examine diets without addressing prey preference or the availability of prey (Cunjak et al. 1987; Cunjak and Power 1987). Of investigations that have considered prey resources, many only examined prey as associated with drift (e.g. Heggenes et al. 1993; Simpkins and Hubert 2000) or benthos (e.g. Fochetti et al. 2003). Lastly, studies of Brown Trout growth and prey availability in groundwater-dominated streams of southeastern Minnesota are limited. Although recent work has examined winter diet and growth (French 2014; French et al. 2014), and winter prey selectivity

(Anderson 2012) in southeastern Minnesota, to date, no study has simultaneously addressed Brown Trout growth and selectivity of both benthic and drifting macroinvertebrate assemblages, and spanned multiple seasons, years, and streams. Thus, it is unknown whether variation in the diet and growth of Brown Trout in southeastern Minnesota reflects differences in prey assemblages and selectivity on a seasonal and spatial scale.

The objectives of this study were to: (1) Characterize seasonal and spatial trends in the assemblages of benthic and drifting prey; (2) Determine whether Brown Trout select prey relative to availability in the environment, and identify seasonal and spatial trends in how prey are selected; and (3) Investigate seasonal and spatial relationships between Brown Trout growth and prey selectivity. Understanding seasonal and spatial relationships among growth, foraging, prey availability, and prey selection may aid in the future management of groundwater-dominated streams, as climate change is expected to alter physical conditions and biological communities of streams in this region. Identifying the prey taxa most important to the growth of Brown Trout will provide managers with critical information for taking actions that mitigate the impacts of climate change on groundwater-dominated streams in southeastern Minnesota.

Methods

Study area

        This study was conducted in five groundwater-dominated streams located in the Driftless Ecoregion of southeastern Minnesota (Omernik and Gallant 1988) (Figure 1). This region was relatively unaffected by the most recent glaciation, and is characterized by sandstone valleys, limestone bluffs, and 181 groundwater-dominated streams that comprise 1,268 stream kilometers (MNDNR 2003). These coldwater streams are supplied with fertile water by a high number of active springs, and yield diverse and abundant assemblages of aquatic invertebrates (Waters 1977) and productive populations of Brown Trout (Thorn and Ebbers 1997). Brown Trout, which were first introduced to the region in 1888 (Thorn et al. 1997), are now the most abundant salmonid species in southeastern Minnesota (Thorn 1990).

Sample sites

        Site selection was based on stream accessibility, fish abundance, and a gradient of growth as characterized by Dieterman et al. (2004). Physical characteristics (e.g. thermal regime, discharge area) of the selected streams were typical of groundwater-dominated streams of southeastern Minnesota. Within each stream, a reach of approximately 200m was selected for fish and invertebrate sampling. Most streams contained varying degrees of habitat improvement for trout management (Thorn et al. 1997). Study streams were "summer-cold/winter-warm" and remained free of ice during winter.

Fish collection, diet and growth measurements

        Brown Trout were sampled in each stream on four to six sample dates per year in 2010-2013. Although we attempted to sample equally during all seasons, logistical limitations and Brown Trout spawning resulted in some disparity among the number of sample dates within each season across all streams. Fish were collected using a Smith Root® (Washington, USA) LR 20B backpack electrofisher. Following a single pass of electrofishing along the entire study reach, captured fish were placed within in-stream holding pens, anesthetized with an immobilizing dose of clove bud oil, weighed ($\pm$ 1g),

and measured (± 1mm TL). Up to 150 Brown Trout (>100mm TL) per stream per year were tagged in the anterior portion of the body cavity with 9mm passive integrated transponder (PIT) tags (Biomark Inc.; Idaho, USA) to measure instantaneous daily growth (G). Random subsamples of up to 30 fish on each sampling date were selected to examine diet composition using gastric lavage. When possible, the subsample contained 10 fish within each of the following size ranges to evaluate diets across a variety of available age classes: 100 and 199mm, 200 and 299mm, and >300mm. Captured fish were placed into a separate holding pen within the stream to recover from anesthesia and then released into the study site. Stomach contents were preserved in 95% ethanol in the field. In the laboratory, aquatic macroinvertebrates in stomach samples were sorted, identified to the lowest practical taxonomic group, and counted. Only intact specimens or fragments greater than one-half an intact individual were counted.

Instantaneous daily growth (G) was calculated for all tagged fish recaptured on at least two, subsequent sampling events using the following equation:

$$G = \frac{lnW_2 - lnW_1}{t_2 - t_1}$$

where W represents weight (g), and t represents the number of days between sampling events.

Invertebrate collection

Drifting macroinvertebrates were collected within 24 hours preceding or following fish collections. Four drift nets (45 cm x 25 cm, with a 1m long bag and 363um Nitex mesh) were placed in a contiguous line perpendicular to the shoreline in a randomly selected riffle within the study reach. Water velocity and depth was measured in three locations across the mouth of each net using a Marsh-McBirney Flo-Mate™ Model 2000 Flowmeter. Sampling was conducted within approximately one hour of sunrise and one hour before sunset to represent the period when salmonids are actively foraging on macroinvertebrate drift during summer, spring, and fall. During winter, drift nets were set approximately one hour before sunset and remained in the stream for a minimum of 12 hours. Contents of the nets were passed through a 125μm sieve,

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preserved in 70% ethanol, and transferred immediately to the lab for processing.

In the laboratory, macroinvertebrates were picked, sorted, and identified to the lowest practical taxonomic group that was reasonable for accuracy (typically Family or Genus) using a dissection microscope. Samples were sorted for a maximum of four hours. Nearly all drift samples (339 of 345, or 98%) were completely sorted within four hours; however, if sorting was not completed, the percentage of the sample processed was estimated, recorded, and multiplied by the total count of each taxon already sorted.

Benthic macroinvertebrate samples were collected immediately following fish collection with a Waters-Knapp modification of a Hess stream bottom sampler (0.086 m^2). Five samples were taken from riffles randomly selected within the sampling reach by disturbing the substrate for three minutes. As with drift samples, benthic collections were passed through a 125μm sieve prior to preservation in 70% ethanol. Macroinvertebrates were picked from each sample, sorted, and identified by taxa using a dissection microscope. Samples were sorted for a maximum of four hours. Nearly all benthic samples (215 of 224, or 96%) were completely sorted within four hours. However, if sorting was not completed in four hours, the percentage of the sample processed was estimated, recorded, and multiplied against counts of individuals already sorted for each taxon.

Analysis

A multiple response permutation procedure (MRPP) (Zimmerman et al. 1985; McCune et al. 2002) was performed in program R (version 3.1.2) to compare Brown Trout diet and taxonomic composition of drift and benthos between streams and seasons. MRPP makes no distributional assumptions (Smith 1998) and a distance matrix is calculated using any number of possible distance measures. Each analysis was performed using proportions of each invertebrate taxon, which were determined by dividing the number of individuals from a given taxon by the total number of individuals collected on each sample date. Only taxa >1% of total invertebrates were used in the analysis. Proportions were arcsine transformed prior to analysis, and separate tests were run for drift and benthos. Probability of type I error was calculated using a

randomization algorithm that allows for comparison between observed δ (weighted mean within-group distance) and the randomized δ distribution. This probability value expresses the likelihood of generating a random δ smaller than the observed value. An effect size of *A* was also calculated as

$$A = 1 - \frac{observed\ \delta}{expected\ \delta}$$

and represents observed within-group homogeneity relative to what could be expected by chance (McCune and Grace 2002). For the purposes of this study, *A* provides a measure of the overall agreement among the relative quantity and diversity of invertebrates within the group designated (e.g. stream, season, year). Within-group homogeneity is greater than the random observation when *A*>0 and less when *A*<0. The *A*-value is useful in attaching ecological significance to observed differences among groups because it is independent of sample size (Mielke 1984; McCune and Grace 2002).

A Kruskal-Wallis test (H), which analyzes non-parametric independent samples of equal or unequal size (Sokal and Rohlf 1981), was used to determine whether there was a statistically significant difference among means of the relative proportion of taxonomic groups among seasons and streams. This test does not indicate what the difference between the means is, only whether the difference is statistically significant. For this analysis, all prey data were expressed as a proportion or percentage contribution of a particular taxon to the overall collection. Prey categories comprising less than 5% of total prey were combined into a single "Other" category.

The Manly-Chesson index (α) (Manly 1974; Chesson 1978, 1983) was used to analyze patterns in drift and benthic prey selectivity across streams and seasons using the numerical proportion of each prey category in Brown Trout diets as follows:

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{m} r_i/p_i}$$

where r_i is the proportion of food item *i* in the diet, p_i is the proportion of food item *i* in the environment, and *m* is the number of food items in the environment. Invertebrate categories that comprised less than 5% of total diet and available prey were combined into a single "Other" category.

Values of α range from 0 (complete avoidance) to 1 (complete preference). When α = 1/m, the predator feeding is random and prey are consumed in proportion to abundance in environment, whereas α > 1/m indicates preference, and α < 1/m indicates avoidance. Manley-Chesson's index allows for temporal and spatial comparisons among selectivity values even if the relative abundances of prey types in the environment change (Chesson 1983). Further, one can statistically test for differences between a mean selectivity value and the value for random feeding by testing the null hypothesis that α is equal to 1/m. Significance was evaluated using a t-test comparing mean $α_i$ with 1/m for each prey category to identify significant trends in positive and negative prey selection within seasons and streams (Chesson 1983).

Overall electivity, or preference, of each prey item (ε_i) was determined by centering the estimated values of α on zero using the following equation:

$$\varepsilon_i = \frac{m\hat{a}_i}{(m-2)\hat{a}_i + 1}$$

Electivity (ε) scales from -1 to 1; where -1 indicates total avoidance of a prey; 0 indicates that a prey is taken in proportion to its abundance; and 1 indicates total preference for a prey. Prey electivity was calculated as the mean of the absolute value of ε. A Kruskal-Wallis test was performed to identify statistical differences in Brown Trout prey electivity among streams and seasons.

The potential relationship between mean fish growth (mg/g/day) and mean prey selectivity (α) on a seasonal basis was evaluated using simple linear regression on a broad scale (data from all streams were combined) and at a stream-scale using data from each individual stream.

Results

Diet composition

When data from all streams were combined, the composition of Brown Trout diets was similar across seasons (MRPP, A<0.001, p=0.311) (Table 1). In contrast, diet composition differed across streams (MRPP, A=0.111, p<0.001) when data from all seasons were combined (Table 2).

Drift composition

Taxonomic composition of drifting invertebrate assemblages across seasons was significantly different (MRPP, A=0.040, p=0.012) when data from all streams and sample dates were combined (Table 1). Mean proportional availability of taxa also varied significantly within all seasons (Figure 2). Chironomidae (mostly larval and pupal forms) were proportionally the most abundant drifting prey overall ($\bar{x}$ =0.59, H=111, d.f.=3, p<0.01), and within each season, ranging from 0.39 during winter (H=160, d.f.=3, p<0.01) to 0.72 during fall (H=81.4, d.f.=3, p<0.01) (Figure 2).

Likewise, the mean proportional distribution of all drifting prey types varied across seasons: *Brachycentrus* (H=16.5, d.f.=3, p<0.01), Chironomidae (H=28.5, d.f.=3, p<0.01), Simuliidae (H=13.2, d.f.=3, p<0.01), and other taxa (H=22.8, d.f.=3, p<0.01) (Figure 3). The highest relative proportions of *Brachycentrus* ($\bar{x}$ =0.54), Chironomidae ($\bar{x}$ =0.44), and Simuliidae ($\bar{x}$ =0.66) were collected during spring, whereas the lowest proportions of these taxa were collected during winter ($\bar{x}$ = 0.06, 0.04, 0.05, respectively). *Baetis* was available in the highest proportion during fall ($\bar{x}$ =0.29) and in lowest proportion during spring ($\bar{x}$ = 0.16). Overall, the total proportion of drifting macroinvertebrates varied significantly across seasons (H=27.4, d.f.=4, p<0.01); the highest proportion of drift was collected during spring ($\bar{x}$ =0.47), and the lowest proportion was collected during winter ($\bar{x}$ =0.07) (Figure 3).

The distribution of drifting prey types also varied significantly across streams when data from all sample dates and seasons were combined (MRPP, A=0.04, p=0.01) (Table 2). Chironomidae were the most abundant drifting prey collected in all streams,

with the highest mean proportion in Daley Creek ($\bar{x}$=0.66, H=121, d.f.=3, p<0.01), followed by Beaver Creek ($\bar{x}$=.60, H=104, d.f.=3, p<0.01) (Figure 2).

Likewise, the mean proportional distribution of most drifting prey types varied across streams (Figure 3). The proportional distribution of Simuliidae and other taxa across sites was similar, but *Brachycentrus* (H=62.7, d.f.=4, p<0.01), Chironomidae (H=13.2, d.f.=4, p<0.01), and *Baetis* (H=9.4, d.f.=4, p=0.05) varied significantly (Figure 3). Interestingly, highest mean proportions of all drifting prey taxa were collected in Garvin Brook, ranged from 0.28 of all *Baetis* to 0.63 of all *Brachycentrus* (Figure 3). There was no variation in the mean proportion of total drift collected across streams (Figure 3).

Benthic composition

There were significant differences in the taxonomic composition of benthic assemblages (MRPP, A=0.019, p=0.050) (Table 1) across seasons, and in the relative proportion of benthic prey types within each season (Figure 4). Overall, Chironomidae comprised approximately one-quarter of all benthic prey collected ($\bar{x}$=0.26, H=121, d.f.=3, p<0.01), and was also the most abundant taxa collected during summer ($\bar{x}$=0.33, H=92.9, d.f.=3, p<0.01) and fall ($\bar{x}$=0.25, H=59.1, d.f.=3, p<0.01) (Figure 4). *Brachycentrus* was proportionally the most abundant prey type during spring ($\bar{x}$=0.28, H=84.1, d.f.=3, p<0.01) and winter ($\bar{x}$=0.26, H=23.5, d.f.=3, p<0.01), and the second most available prey type overall ($\bar{x}$=0.23) (Figure 4).

Similar to the drift, the relative proportional distributions of many benthic prey taxa varied across seasons when data from all streams and sample dates were combined (Figure 5). Distributions of *Baetis*, Elmidae, and *Gammarus* were relatively similar across seasons, whereas distributions of *Brachycentrus* (H=13.2, d.f.=3, p<0.01), Chironomidae (H=14.1, d.f.=3, p<0.01), Simuliidae (predominately represented by the *Simulium*) (H=13.1, d.f.=3, p<0.01), and other taxa (H=10.0, d.f.=3, p=0.02) were significantly different (Figure 5). Proportions of *Brachycentrus* ($\bar{x}$=0.36) and Simuliidae ($\bar{x}$ =0.48) were highest during spring and lowest during fall ($\bar{x}$ =0.17, $\bar{x}$ =0.05, respectively), whereas proportions of benthic Chironomidae ($\bar{x}$ =0.42) and other taxa

($\bar{x}$ =0.33) were highest during summer, and lowest during winter ($\bar{x}$ =0.12, $\bar{x}$ =0.16,

respectively). As for drift, relative contributions of total benthic prey varied significantly

by season, and were highest during summer ($\bar{x}$ =0.33) and lowest during winter

($\bar{x}$ =0.18) (H=7.5, d.f.=3, p=0.05) (Figure 5).

The taxonomic composition of benthic assemblages was significantly different

among streams (MRPP, A=0.133, p<0.001) (Table 2), as were the relative proportions of

prey types collected within each stream when data from all sample dates and seasons

were combined (Figure 4). Chironomidae were the most abundant benthic prey collected

in Trout Run Creek ($\bar{x}$=48.0, H=100.7, d.f.=6, p<0.01), Daley Creek ($\bar{x}$=34.3, H=121,

d.f.=6, p<0.01), and Gribbon Creek ($\bar{x}$=21.4, H=70.7, d.f.=6, p<0.01) (Figure 4).

Brachycentrus was most abundant in Garvin Brook ($\bar{x}$=22.5, H=40.8, d.f.=6, p<0.01) and

Beaver Creek ($\bar{x}$=37.4, H=116, d.f.=6, p<0.01) relative to other benthic taxa (Figure 4).

The relative proportional distributions of all benthic taxa, with the exception of

Chironomidae (H=7.2, d.f.=4, p=0.11), varied significantly across streams (Figure 5).

Garvin Brook contained the highest proportions of all *Brachycentrus* ($\bar{x}$ =0.52, H=77.5,

d.f.=4, p<0.01) and *Baetis* ($\bar{x}$ =0.29, H=12.9, d.f.=4, p=0.01) that were collected, whereas

approximately 75% of all Elmid beetles were collected in Beaver Creek (H=130.9, d.f.=4,

p<0.01) (Figure 5). Daley Creek contained the highest proportions of Simuliidae

($\bar{x}$ =0.43, H=20.3, d.f.=4, p<0.01) and *Gammarus* ($\bar{x}$ =0.53, H=48.7, d.f.=4, p<0.01).

Overall, Garvin Brook contained the highest relative proportion of all benthic prey

collected ($\bar{x}$ =0.32), followed by Beaver Creek ($\bar{x}$ =0.21), whereas Gribbon Creek

contained the least ($\bar{x}$ =0.11) (H=14.1, d.f.=4, p<0.01) (Figure 5).

Prey selection

Mean electivity ($\bar{\varepsilon}$) of Brown Trout in all streams varied significantly among prey

taxa, when benthic and drift data were combined (H=135.8, d.f.=7, p<0.01) (Figure 6).

In general, Brown Trout most selected *Physella* ($\bar{\varepsilon}$=0.32) and *Gammarus* ($\bar{\varepsilon}$=0.06), and

avoided Simuliidae ($\bar{\varepsilon}$=−0.79) and Elmidae ($\bar{\varepsilon}$=−0.69) (Figure 6).

Electivity of drifting *Physella* ($\bar{\alpha}$=0.40, d.f.=31, *Brachycentrus* ($\bar{\alpha}$=0.20, d.f.=43,

p<0.01), and *Gammarus* ($\bar{\alpha}$=0.29, d.f.=5, p<0.01) was significantly greater than neutral

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selection (1/m=0.143); however, Brown Trout avoided drifting Chironomidae ($\bar{\alpha}$=0.09, d.f.=49, p>0.05) and Simuliidae ($\bar{\alpha}$=0.02, d.f.=39, p<0.01) (Table 3). In the benthos, selection of *Physella* was significantly greater than neutral (1/m=0.125) ($\bar{\alpha}$=0.37, d.f.=40, p<0.01), whereas Brown Trout avoided *Brachycentrus* ($\bar{\alpha}$=0.08, d.f.=45, p<0.05), Elmidae ($\bar{\alpha}$=0.02, d.f.=31, p<0.01), and *Baetis* ($\bar{\alpha}$=0.07, d.f.=42, p<0.01) (Table 3).

By season

  Winter. Mean electivity ($\bar{\varepsilon}$) of Brown Trout varied among prey types during winter when data from benthos and drift in all streams were combined (H=34.5, d.f.=9, p<0.01) (Figure 7). In general, Brown Trout selected Limnephilidae ($\bar{\varepsilon}$=0.55) and *Physella* ($\bar{\varepsilon}$=0.46) during winter, and avoided Ephemerellidae ($\bar{\varepsilon}$=−0.99) and Simuliidae ($\bar{\varepsilon}$= −0.83) (Figure 7).

  Mean selection of Simuliidae ($\bar{\alpha}$=0.01, d.f.=5, p<0.01), *Baetis* ($\bar{\alpha}$=0.02, d.f.=5, p<0.01), Ephemerellidae ($\bar{\alpha}$=0.0, d.f.=2, p<0.01), and Perlidae ($\bar{\alpha}$=0.0, d.f.=1, p<0.01) in the drift was significantly lower than neutral (1/m=0.11) (Table 4). Brown Trout also avoided Simuliidae ($\bar{\alpha}$=0.02, d.f.=3, p<0.01), *Brachycentrus* ($\bar{\alpha}$=0.03, d.f.=5, p<0.01), and other taxa ($\bar{\alpha}$=0.06, d.f.=5, p=0.05) during winter from the benthos (Table 4). Although Brown Trout demonstrated selection of drifting *Physella* ($\bar{\alpha}$=0.53, d.f.=3, p=0.03) during winter, other values of prey selection in the benthos and drift were not significantly different than random feeding (Table 4).

  Among streams, Brown Trout demonstrated differences in electivity ($\bar{\varepsilon}$) of drifting and benthic prey during winter (Figure 8). *Physella* was the most selected drifting prey type in Beaver Creek ($\bar{\varepsilon}$ =0.84), Daley Creek ($\bar{\varepsilon}$ = 0.89), and Gribbon Creek ($\bar{\varepsilon}$ =0.96), whereas Brown Trout selected Chironomidae in Garvin Brook ($\bar{\varepsilon}$ =0.58) and *Brachycentrus* in Trout Run Creek ($\bar{\varepsilon}$ =0.98) (Figure 8). Drifting Simuliids were avoided during winter in all streams, with mean electivity ranging from −0.97 in Daley Creek to −0.55 in Garvin Brook (Figure 8). In addition, Brown Trout avoided *Baetis* and Chironomidae in all streams except Garvin Brook, where these drifting taxa were positively selected during winter (Figure 8).

Electivity of benthic prey varied across streams. Brown Trout selected *Gammarus* in Daley Creek ($\bar{\varepsilon}$ =0.60), Chironomidae in Garvin Brook ($\bar{\varepsilon}$ =0.48), Limnephilidae in Gribbon Creek ($\bar{\varepsilon}$ =0.63), and *Physella* in Trout Run Creek ($\bar{\varepsilon}$ =0.96) and Beaver Creek ($\bar{\varepsilon}$ =0.99) (Figure 8). Similar to drift, Brown Trout selected *Physella* in the benthos in all streams, except Daley Creek (Figure 8). In addition, Brown Trout avoided *Brachycentrus* in all streams, and Simuliidae in Daley Creek ($\bar{\varepsilon}$ =0.68), Garvin Brook ($\bar{\varepsilon}$ =0.55), and Gribbon Creek ($\bar{\varepsilon}$ =0.97) (Figure 8).

Overall, Brown Trout were most selective toward drifting prey in Beaver Creek ($\bar{\varepsilon}$ = 0.80), and least selective in Garvin Brook ($\bar{\varepsilon}$ = 0.36) during winter, but variation was not significant across streams (H=8.9, d.f.=4, p=0.06) (Figure 9). In contrast, overall selection of benthos varied significantly across streams (H=12.1, d.f.=4 p=0.02). Similar to drift, Brown Trout demonstrated the highest electivity in Beaver Creek ($\bar{\varepsilon}$ =0.82) and were least selective in Garvin Brook ($\bar{\varepsilon}$=0.36) (Figure 9).

Spring. Mean electivity ($\bar{\varepsilon}$) of Brown Trout varied among prey types during spring, when data from benthos and drift in all streams were combined (H=65.1, d.f.=7, p<0.01) (Figure 10). In general, Brown Trout selected *Physella* ($\bar{\varepsilon}$=0.32) and Limnephilidae ($\bar{\varepsilon}$=0.17), and avoided Simuliidae ($\bar{\varepsilon}$=−0.72), *Brachycentrus* ($\bar{\varepsilon}$=−0.40), and *Baetis* ($\bar{\varepsilon}$=−0.40) (Figure 10).

Among drifting taxa, selection of Simuliidae was significantly less than neutral (1/m=0.125) ($\bar{\alpha}$=0.01, d.f.=20, p<0.01), whereas Brown Trout selected *Physella* ($\bar{\alpha}$=0.37, d.f.=12, p<0.01) and *Gammarus* ($\bar{\alpha}$=0.28, d.f.=14, p=0.02) (Table 4) during spring. Brown Trout also avoided Simuliidae ($\bar{\alpha}$ =0.07, d.f.=18, p=0.03) and *Baetis* ($\bar{\alpha}$=0.05, d.f.=17, p<0.01) in the benthos during spring, but selection of benthic *Physella* was significantly greater than neutral (1/m=0.125) ($\bar{\alpha}$=0.34, d.f.=15, p<0.01) (Table 4).

Across streams, mean electivity ($\bar{\varepsilon}$) for drifting and benthic prey also varied during spring (Figure 11). Drifting *Physella* was selected by Brown Trout in all streams except Garvin Brook, and ranged from 0.12 in Beaver Creek to 0.84 in Trout Run Creek (Figure 11). Likewise, *Physella* was the most widely selected benthic prey, with positive electivity in all streams except Beaver Creek, and ranged from 0.12 in Gribbon Creek to

0.67 in Daley Creek (Figure 11). Limnephilidae was the most preferred drifting prey in Beaver Creek ($\bar{\varepsilon}$ =0.94) and most preferred benthic prey in Daley Creek ($\bar{\varepsilon}$=0.75), and *Gammarus* was the most preferred drifting prey taxon in Beaver Creek ($\bar{\varepsilon}$=0.38) and Gribbon Creek ($\bar{\varepsilon}$=0.23) during spring (Figures 11). Simuliids were avoided in the benthos and drift in all streams, with the exception of Beaver Creek, were there was slight positive selection ($\bar{\varepsilon}$=0.03) (Figure 11). Likewise, Brown Trout avoided *Brachycentrus* in the benthos of all streams, with mean electivity from −0.33 in Garvin Brook to −0.83 in Gribbon Creek, and as drift in all streams, except Trout Run Creek ($\bar{\varepsilon}$=0.06). Brown Trout avoided *Baetis* in the benthos in all streams, and in the drift of all streams, except Garvin Brook ($\bar{\varepsilon}$=0.18) (Figure 11). Chironomidae were the only prey avoided in the benthos and drift in all streams during spring (Figure 11).

Overall, mean electivity ($\bar{\varepsilon}$) of benthic prey varied significantly across streams during spring (H=19.2, d.f.=4 p<0.01), whereas electivity toward drifting prey did not (H=4.1, d.f.=4 p=0.30) (Figure 12). Brown Trout in Daley Creek demonstrated highest electivity for drift ($\bar{\varepsilon}$ =0.69) and benthos ($\bar{\varepsilon}$ =0.73), whereas fish were least selective of drift in Garvin Brook ($\bar{\varepsilon}$ =0.55) and least selective of benthos at Beaver Creek ($\bar{\varepsilon}$ =0.35) (Figure 12).

Summer. Overall, Brown Trout demonstrated significant variation in selection of prey during summer when benthic and drifting prey data from all streams were combined (H=43.6, d.f.=7, p<0.01) (Figure 13). Brown Trout selected *Gammarus* ($\bar{\varepsilon}$=0.15) and avoided Simuliidae ($\bar{\varepsilon}$=−0.80) during summer (Figure 13).

Among drift, Chironomidae ($\bar{\alpha}$=0.09, d.f.=12, p=0.02), Simuliidae ($\bar{\alpha}$=0.01, d.f.=12, p<0.01), *Baetis* ($\bar{\alpha}$=0.06, d.f.=11, p<0.01), and Formicidae ($\bar{\alpha}$=0.09, d.f.=10, p=0.04) were ingested below neutral (1/m=0.143), whereas Brown Trout selected *Brachycentrus* ($\bar{\alpha}$=0.29, d.f.=11, p<0.01) and *Gammarus* ($\bar{\alpha}$=0.37, d.f.=12, p<0.01) (Table 4). Among benthos, Brown Trout demonstrated neutral selection (1/m=0.167) during summer (Table 4).

Across streams, mean electivity ($\bar{\varepsilon}$) of drifting and benthic prey also varied during summer (Figure 14). *Gammarus* was the most widely ingested drifting prey, with

positive electivity in all streams, except Trout Run Creek ($\bar\varepsilon$=0.0) (Figure 14). Electivity of *Gammarus* in the drift was highest in Daley Creek ($\bar\varepsilon$=0.68), Garvin Brook ($\bar\varepsilon$=0.51), and Gribbon Creek ($\bar\varepsilon$=0.73), whereas Brown Trout selected *Brachycentrus* in Beaver Creek ($\bar\varepsilon$=0.49) and Trout Run Creek ($\bar\varepsilon$=0.67) during summer (Figure 14). Among benthos, *Brachycentrus* was selected in Daley Creek ($\bar\varepsilon$=0.89), whereas Brown Trout selected *Gammarus* in Garvin Brook ($\bar\varepsilon$=0.46) and Gribbon Creek ($\bar\varepsilon$=0.17), and Elmid beetles in Trout Run Creek ($\bar\varepsilon$=0.24) (Figure 14). Overall, Simuliidae was the most widely avoided drifting prey in all streams, and ranged from -0.85 in Garvin Brook to -0.98 in Daley Creek (Figure 14). In addition, Chironomidae in the drift were avoided in all streams, except Garvin Brook ($\bar\varepsilon$=0.15), drifting *Baetis* were avoided in all streams, except Daley Creek ($\bar\varepsilon$=0.15), and drifting Formicidae were avoided in all streams, except Garvin Brook, where this taxon did not occur (Table 14). With respect to benthos, Brown Trout in Beaver Creek avoided Elmidae ($\bar\varepsilon$=-0.80) during summer, whereas Brown Trout in Daley Creek and Gribbon Creek avoided Chironomidae ($\bar\varepsilon$=-0.88, -0.50, respectively), and Brown Trout in Trout Run Creek avoided *Gammarus* ($\bar\varepsilon$=0.57) (Table 14).

Mean electivity ($\bar\varepsilon$) of drift in summer differed significantly among streams, and ranged from 0.47 in Beaver Creek to 0.63 in Daley Creek (H=9.1, d.f.=4, p=0.05) (Figure 15). Mean electivity of benthos did not vary significantly among streams (H=3.5, d.f.=4, p=0.52) (Figure 15).

Fall. Overall, Brown Trout demonstrated significant variation in selection of prey during fall when benthic and drifting prey data from all streams were combined (H=19.6, d.f.=6, p<0.01) (Figure 16). Brown Trout selected *Physella* ($\bar\varepsilon$=0.22) and avoided Elmidae ($\bar\varepsilon$=-0.99) during fall (Figure 16).

Among the drift, no prey types were significantly selected during fall; however selection of Simuliidae ($\bar\alpha$=0.03, d.f.=8, p<0.01) and other taxa ($\bar\alpha$=0.08, d.f.=7, p<0.01) were significantly less than neutral ($1/m$=0.143) (Table 4). Among the benthos, selection of Elmidae ($\bar\alpha$=0.0, d.f.=4, p<0.01) was significantly lower than neutral ($1/m$=0.143)

during fall, and selection of *Physella* ($\bar{\alpha}$=0.36, d.f.=8, p=0.03) was significantly higher (Table 4).

Among streams, mean electivity ($\bar{\varepsilon}$) of benthic and drifting prey varied during fall (Figure 17). *Physella* was the most preferred drifting prey in Beaver Creek ($\bar{\varepsilon}$=0.58), Garvin Brook ($\bar{\varepsilon}$=0.33), Gribbon Creek ($\bar{\varepsilon}$=0.08), and Trout Run Creek ($\bar{\varepsilon}$=0.75), but avoided in Daley Creek ($\bar{\varepsilon}$=−1.0), where Brown Trout most selected *Gammarus* ($\bar{\varepsilon}$=0.56) during fall (Figure 17). Simuliidae in the drift were avoided in Beaver Creek ($\bar{\varepsilon}$=−0.86) and Trout Run Creek ($\bar{\varepsilon}$=−0.98), whereas Brown Trout avoided *Brachycentrus* in Garvin Brook ($\bar{\varepsilon}$=−0.70) and *Gammarus* in Gribbon Creek ($\bar{\varepsilon}$=0.83) (Figure 17). Among benthic prey, *Physella* was the most selected benthic prey in Beaver Creek ($\bar{\varepsilon}$=0.88) and Gribbon Creek ($\bar{\varepsilon}$=0.76), whereas Chironomidae were selected for in Daley Creek ($\bar{\varepsilon}$=0.23) and Trout Run Creek ($\bar{\varepsilon}$=0.66) during fall (Figure 17). *Baetis* was the most selected benthic prey in Garvin Brook ($\bar{\varepsilon}$=0.78), but avoided in Trout Run Creek ($\bar{\varepsilon}$=−0.82) and Daley Creek ($\bar{\varepsilon}$=−0.63). Of the remaining streams, Elmid beetles were avoided ($\bar{\varepsilon}$=−1.0) during fall (Figure 17).

When all taxa were combined, mean electivity ($\bar{\varepsilon}$) of drift differed significantly among streams during fall, ranging from 0.23 in Garvin Brook to 0.70 in Trout Run Creek (H=12.1, d.f.=4, p=0.02) (Figure 18). Mean electivity ($\bar{\varepsilon}$) of benthos did not vary significantly among streams (H=3.8, d.f.=4, p=0.43) (Figure 18).

By stream

Beaver Creek. Brown Trout in Beaver Creek significantly selected *Brachycentrus* ($\bar{\alpha}$=0.26, d.f.=6, p<0.01) and *Physella* ($\bar{\alpha}$=0.35, d.f.=6, p=0.03) in the drift, but avoided Chironomidae ($\bar{\alpha}$=0.03, d.f.=7, p<0.01), Simuliidae ($\bar{\alpha}$=0.01, d.f.=7, p<0.01), and *Baetis* ($\bar{\alpha}$=0.05, d.f.=7, p<0.01) (Table 5). Brown Trout in Beaver Creek also selected *Physella* ($\bar{\alpha}$=0.37, d.f.=7, p=0.03) in the benthos, but avoided Hydropsychidae ($\bar{\alpha}$=0.03, d.f.=6, p<0.01), Chironomidae ($\bar{\alpha}$=0.08, d.f.=6, p=0.05), and Elmidae ($\bar{\alpha}$=0.01, d.f.=7, p<0.01) (Table 5).

Overall, mean electivity ($\bar{\varepsilon}$) of drifting prey was similar across all seasons in Beaver Creek (H=2.5, d.f.=3, p=0.45) (Figure 19), but electivity of the benthos differed

significantly, and ranged from 0.35 during spring to 0.83 during winter (H=13.9, d.f.=3, p<0.01) (Figure 19).

Daley Creek. Brown Trout selected drifting Gammarus in Daley Creek ($\bar{\alpha}$=0.46, d.f.=9, p<0.01), but avoided Chironomidae ($\bar{\alpha}$=0.07, d.f.=0, p=0.03), Simuliidae ($\bar{\alpha}$=0.02, d.f.=0, p<0.01), Baetis ($\bar{\alpha}$=0.05, d.f.=7, p=0.05), and Formicidae ($\bar{\alpha}$=0.04, d.f.=5, p<0.01) (Table 2). Benthic prey were not selected; however, Brown Trout in Daley Creek avoided Baetis in the benthos ($\bar{\alpha}$=0.01, d.f.=9, p<0.01) (Table 5). Overall, mean electivity ($\bar{\varepsilon}$) of Brown Trout of the drift (H=3.6, d.f.=3, p=0.31) and benthos (H=3.4, d.f.=3, p=0.34), was similar across seasons in Daley Creek (Figure 20).

Garvin Brook. Brown Trout demonstrated negative selection toward drifting Simuliidae in Garvin Brook ($\bar{\alpha}$=0.03, d.f.=9, p<0.01) (Table 5). Brown Trout selected Chironomidae ($\bar{\alpha}$=0.24, d.f.=9, p=0.05) in the benthos, but selection of Glossosoma ($\bar{\alpha}$=0.04, d.f.=8, p<0.01) and Elmidae ($\bar{\alpha}$=0.02, d.f.=9, p<0.01) was significantly lower (Table 5). Overall, mean electivity ($\bar{\varepsilon}$) of drifting prey varied significantly across seasons at Garvin Brook (H=8.7, d.f.=3, p=0.03), and ranged from 0.22 during fall to 0.56 during spring, but was similar for benthos across seasons (H=5.3, d.f.=3, p=0.15) (Figure 21).

Gribbon Creek. Brown Trout in Gribbon Creek demonstrated positive selection of Physella in the drift ($\bar{\alpha}$=0.41, d.f.=7, p=0.03), but avoided Brachycentrus ($\bar{\alpha}$=0.05, d.f.=9, p<0.01), Simuliidae ($\bar{\alpha}$=0.01, d.f.=10, p<0.01), and Ephemerellidae ($\bar{\alpha}$=0.0, d.f.=5, p<0.01) (Table 5). Brown Trout in Gribbon Creek also selected Physella ($\bar{\alpha}$=0.34, d.f.=9, p<0.01) and Limnephilidae ($\bar{\alpha}$=0.44, d.f.=3, p=0.04) in the benthos, but avoided Brachycentrus ($\bar{\alpha}$=0.04, d.f.=9, p<0.01), Simuliidae ($\bar{\alpha}$=0.02, d.f.=8, p<0.01), Baetis ($\bar{\alpha}$=0.05, d.f.=8, p<0.01), and Ephemerellidae ($\bar{\alpha}$=0.0, d.f.=5, p<0.01) (Table 5). Overall, mean electivity ($\bar{\varepsilon}$) of drifting prey was similar across seasons at Gribbon Creek (H=2.6, d.f.=3, p=0.45) (Figure 22a); but differed significantly for benthic prey (H=11.0, d.f.=3, p=0.01), and ranged from 0.38 during summer to 0.79 during winter (Figure 22).

Trout Run Creek. Brown Trout in Trout Run Creek selected drifting Brachycentrus ($\bar{\alpha}$=0.34, d.f.=8, p=0.03) and Physella ($\bar{\alpha}$=0.60, d.f.=5, p<0.01), but avoided Chironomidae ($\bar{\alpha}$=0.08, d.f.=8, p=0.02), Simuliidae ($\bar{\alpha}$=0.01, d.f.=9, p<0.01),

and *Baetis* ($\bar{\alpha}$=0.03, d.f.=8, p<0.01) (Table 5). Brown Trout selected *Physella* ($\bar{\alpha}$=0.52, d.f.=7, p<0.01) in the benthos, but avoided Hydroptilidae ($\bar{\alpha}$=0.03, d.f.=4, p<0.01) and *Brachycentrus* ($\bar{\alpha}$=0.03, d.f.=8, p<0.01) (Table 5). Overall, mean electivity ($\bar{\varepsilon}$) was similar across all seasons at Trout Run Creek for drifting prey (H=4.5, d.f.=3, p=0.22) (Figure 22) and benthos (H=1.6, d.f.=3, p=0.66) (Figure 23).

Overall patterns in prey selectivity

When data from all sample dates and streams were combined by season, mean electivity ($\bar{\varepsilon}$) varied for benthos (H=8.6, d.f.=3, p=0.03) and drift (H=7.9, d.f.=3, p=0.04) among seasons (Figures 24). In general, Brown Trout demonstrated highest selectivity toward drifting ($\bar{\varepsilon}$=0.69) and benthic ($\bar{\varepsilon}$=0.63) prey during winter. Fish were least selective for drift during fall ($\bar{\varepsilon}$=0.53) and least selective of benthos during summer ($\bar{\varepsilon}$=0.49) (Figures 24).

Mean electivity ($\bar{\varepsilon}$) of benthic and drifting prey also varied significantly across streams when data from all seasons were combined (Figure 25). Electivity of drifting prey ranged from 0.51 in Garvin Brook to 0.72 in Gribbon Creek (H=12.6, d.f.=4, p=0.01). For benthos, mean electivity ranged from 0.51 in Beaver Creek to 0.67 in Gribbon Creek (H=23.5, d.f.=4, p<0.01) (Figure 25).

Overall, there was a negative correlation between mean prey electivity ($\bar{\varepsilon}$) and mean proportional abundance of prey (r^2=23.3, F=4.9, p=0.04) across all sample sites and seasons; as the mean proportion of prey increased, the mean electivity of prey decreased (Figure 26).

Seasonal prey selectivity and mean growth was only positive correlated in Daley Creek (p=0.04) and Garvin Brook (p=0.03) (Table 6).

Discussion

Broad patterns

  We found broad variation in the composition and availability of aquatic macroinvertebrates assemblages across streams in southeastern Minnesota, similar to other studies in the region (Troelstrup and Perry 1989; Waters 2000). We documented variation in both benthic and drifting macroinvertebrate assemblages, and in the foraging patterns of Brown Trout, on a seasonal basis across several streams, unlike investigations in other areas that were limited to a single stream or season (e.g. Stoneburner and Smock 1979; Allen 1987; Gualdoni et al. 1991; Shearer et al. 2002; Leung et al. 2009). Benthic and drifting macroinvertebrate assemblages were dominated by relatively few taxa (including Chironomidae, *Brachycentrus*, Simuliidae, *Baetis*, Elmidae, and *Gammarus*), which was not unexpected based on other studies (Steingrimsson and Gislason 2002; Kara and Alp 2005). However, despite the low richness of dominant taxa overall, the proportional contributions of each varied among seasons and streams.

  The present study demonstrates that Brown Trout prey selection is not proportional to the environmental density of macroinvertebrates. We found that foraging patterns did not always reflect the most abundant prey available, similar to other studies (Sagar and Glova 1995; MacNeil et al. 2000; de Crespin de Billy and Usseglio-Polatera 2002). Brown Trout are visual foragers, thus prey preference and capture probability are likely influenced by the accessibility, size, color, mobility, and degree of exposure of various prey types (Rader 1997; de Crespin de Billy and Usseglio-Polatera 2002). Across all streams, Brown Trout favored *Physella* in the benthos and avoided Elmidae and *Baetis*, whereas selectivity of all other benthic prey was either neutral or not significant. Other studies attribute the avoidance of Elmidae by Brown Trout to low energetic value and/or bad taste (Ochs 1969; Power 1992; Oscoz et al. 2000; Sanchez-Hernandez et al. 2011; Sánchez-Hernández and Cobo 2013). In addition, others have documented the avoidance of *Baetis* by Brown Trout, despite being active and abundant in many streams (Mathooko 1996; Fochelli et al. 2003; Sánchez-Hernández and Cobo 2013). Although electivity may be related to size-selective predation, prey behavior may be a factor.

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Baetis has been documented to alter behavior in response to predation risk thereby reducing vulnerability to benthic feeding fish, including Brown Trout (Kohler and McPeek 1989).

All drifting taxa were found in greatest proportion in Garvin Brook, and were most abundant during spring, except for *Baetis*. Overall, the proportion of available drift was highest during spring and lowest during winter, which mirrors the typical pattern for drift abundance in temperate streams, where a spring maximum may be a function of higher discharge and increased density of benthic macroinvertebrates (Hynes 1970). Garvin Brook also contained the highest relative proportion of all benthos collected; however, spatial distributions of prey varied widely among streams. Chironomidae, Simuliidae, and *Gammarus* were present in greatest proportion in Daley Creek, *Brachycentrus* and *Baetis* were most abundant in Garvin Brook, and approximately 75% of all Elmid beetles were collected in Beaver Creek. Seasonal distributions of benthic taxa also varied, with all taxa most abundant during spring, with the exception of Elmidae and Chironomidae. Overall, the greatest proportion of benthos was collected during summer, and similar to drift, and the least during winter.

Broad patterns in selection of drift indicated that Brown Trout selected *Physella*, *Gammarus,* and *Brachycentrus*, but avoided Chironomidae and Simuliidae. The positive selection by Brown Trout for *Gammarus* and *Physella*, and avoidance of Dipterans, is consistent with studies in other regions (Cada et al. 1986; Pender and Kwak 2002; Fochetti et al. 2003; Johnson et al. 2007; Sanchez-Hernandez et al. 2011), although Pender and Kwak (2002) identified positive selection for Chironomidae among age-0 trout. Although Brown Trout consistently favored *Physella* in the benthos and drift, this taxon did not constitute a high proportion of either prey availability or prey consumed. *Physella* are larger-bodied and more abundant than other aquatic mollusks in southeastern Minnesota, and are among the most energetically rich aquatic macroinvertebrate prey taxa available (5275 j/g; Cummins and Wuycheck 1971), making them an energetically beneficial prey item for Brown Trout in southeastern Minnesota (Dieterman et al. 2004).

Seasonal and spatial patterns

Brown Trout often display size selectivity, preferentially feeding on larger bodied prey items (Newman and Waters 1984). Our analyses of electivity within streams found that Brown Trout consistently selected *Physella* and *Gammarus*, large-bodied prey taxa that are widely distributed across southeastern Minnesota, although not consistently found in all of our study streams. In addition, although Brown Trout generally selected against encased *Brachycentrus* larvae, but demonstrated positive selection toward encased Limnephilidae larvae. This pattern may reflect size selectivity, as the mean size of Limnephilidae individuals (12.5 mm) was substantially larger than Brachycentrus (6.8 mm). In other studies, these large-bodied taxa comprised a majority of Brown Trout prey consumed by dry weight during winter (Anderson 2012; French et al. 2014), and French et al. (2014) noted that smaller bodied prey, including *Glossosoma* and Chironomidae, became increasingly abundant in stomachs during late winter.

Gammarus has been identified as a dominant taxon in the drift in southeastern Minnesota, and selectively preyed upon by Brown Trout throughout the year (Waters 1972; Newman and Waters 1984). Overall, *Gammarus* was dominant in the benthos but not in the drift across all streams; however, abundance varied among streams and seasons. Unlike other aquatic macroinvertebrate taxa, reduction in water temperature during winter does not correlate with a reduction in *Gammarus* in the drift, and Brown Trout demonstrated selection for this taxon during winter in Minnesota (Newman and Waters 1984; Anderson 2012) and in other regions (Bridcut and Giller 1995). Brown Trout ingested *Gammarus* from the benthos and drift during winter, as well as in most streams and seasons, although not significantly different from neutral selection.

Chironomidae were common in Brown Trout stomachs during all seasons and in most streams, typically among the top three prey taxa in relative importance (IRI%) (see Chapter 1). Likewise, Chironomidae were widely available in the benthos and drift, making up the largest proportion of drifting prey in all streams and overall, and among the two most dominant benthic prey taxa, and most available benthic taxon overall in every season and stream (see Chapter 2). Despite the presence in diet and the environment, Brown Trout did not select Chironomidae in the benthos and drift, with the

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exception of Garvin Brook. Relative to other aquatic macroinvertebrate taxa, Chironomidae are small-bodied, and although widely abundant, may be avoided by Brown Trout in favor of larger, more conspicuous prey. In Garvin Brook, where Brown Trout demonstrated selection of Chironomidae in the benthos, and to a lesser extent in the drift, highest electivity occurred during winter, when *Diamesa mendotae* can account for up to 75% of all Chironomidae available, and approximately 15% of all benthos (Jane Mazack, unpublished data). In addition to being the most abundant and commonly found winter-emerging Chironomid found in groundwater-dominated streams across southeastern Minnesota, *D. mendotae* is among the largest Chironomid larvae available to Brown Trout during winter (mean length≈8−12mm) (Anderson 2012). Brown Trout positively selected for *D. mendotae* in two of three streams studied, including Beaver Creek, during winter (Anderson 2012). In the present study, Brown Trout in Beaver Creek avoided Chironomidae and favored *Physella* and Limnephilidae; however, Chironomidae were still the most important prey (based on IRI%) during winter, and overall (Chapter 1). This pattern highlights the importance of considering other diet metrics (e.g. IRI %) when identifying important prey resources for stream-dwelling fish. Despite low electivity values, Chironomidae are important prey across most study streams and seasons in southeastern Minnesota. The caloric value provided to Brown Trout by *D. mendotae* and other winter-emerging Chironomids may benefit populations by providing energy during winter when abundances of other aquatic invertebrate taxa are low. Stable isotope analysis has provided evidence that Chironomids are among the most important contributors toward Brown Trout growth during winter in southeastern Minnesota (French et al. 2014), and even a marginal contribution of Chironomidae to Brown Trout diets during winter may significantly influence annual growth rates (Anderson 2012). Climate change may reduce abundances of *D. mendotae* in southeastern Minnesota during winter (Anderson 2012), thus Brown Trout may face consequences that include lower rates of growth and survival in winter, especially because other benthic macroinvertebrate taxa are generally lower during winter.

Foraging strategies: drift vs. benthic selection

Brown Trout diets across most streams and seasons in southeastern Minnesota closely reflect the composition of benthic prey assemblages, with highest preference for *Physella, Gammarus,* and larval forms of large-bodied aquatic macroinvertebrate taxa. Trout are opportunistic generalists throughout the year (Lord 1933; Maciolek and Needham 1952; Reimers 1957; Cunjak and Power 1987; Ozvarol et al. 2011) and other studies emphasize the strong importance of drifting prey to the trout diet, including a widely cited study that emphasized Brown Trout taking less than 15% of their prey from the benthos (Bachman 1984). In addition, numerous studies have identified a positive selection by Brown Trout for terrestrial insects (see review by Hunt and Krokhin 1975), but not in the present study. Terrestrial macroinvertebrates generally do not contribute a large proportion of total drift or diet of Brown Trout in southeastern Minnesota, compared to reported values in other regions, where terrestrial inputs contributed up to 53% of stream drift and 82% Brown Trout diet (Dahl 1998). Laudon et al. (2005) found that Brown Trout in Valley Creek, Minnesota neutrally selected terrestrial prey during summer, which only comprised both 3% of all available drift and diet. Similarly, we found that Brown Trout generally did not favor terrestrial drift, which typically did not constitute a high proportion of available prey.

Numerous studies of prey selection demonstrate that Brown Trout foraging strategies (drift-feeding vs. epibenthic feeding) vary seasonally and spatially. Waters (1972) emphasized that there is no distinct drift fauna, but rather, benthic invertebrates enter the drift due to several abiotic and biotic factors. Overall, drift represents a mixture of drift densities, which depends on the species present in the benthos, and their propensity to drift. Therefore, assessing diet selectivity from field data when the same prey can be selected from multiple microhabitats (e.g. water column vs. substratum) is not often feasible without direct underwater observations. However, by separately assessing the selectivity of benthos and drift, we were able to infer patterns in foraging modes. On a seasonal basis, Brown Trout demonstrated higher selectivity of drift, and were less selective when foraging among benthos in all seasons, except fall. This pattern was especially prominent during summer, when all benthic prey types were not selected,

whereas there was significant selection of all drift taxa, including *Brachycentrus* and *Gammarus*. Interestingly, this high electivity for drift occurred during summer, when availability of benthic macroinvertebrates and drift was highest (see Chapter 2). Positive electivity for *Brachycentrus* was an exception to a generally observed pattern, but coincided with documented peaks in annual pupal density (June and July), larval size (June and early July), and larval drift (August and September) (Krueger and Cook 1984).

The presence of encased, larval Trichopterans in diets, as well as the significant selectivity of *Physella* and avoidance of nocturnal drifting prey, such as *Baetis*, indicate that Brown Trout may have fed on benthos during winter. Our collections typically included smaller Brown Trout (100-300mm in TL; age-0 – 2+), which may feed epibenthically as a way to evade predation, especially during winter when drift rates are lowest and there are fewer terrestrial and emerging aquatic insects (Grant 1999). This pattern was also evident in other winter studies of Brown Trout diet in southeastern Minnesota (Anderson 2012; French 2014; French et al. 2014), and for salmonids in other regions where nocturnal benthic feeding during winter was attributed to lower capture efficiency of drift because of reduced light from ice cover, elevated turbidity, lower drift rates, and avoidance of predators (Tippets and Moyle 1978; Cunjak and Power 1986; Jørgensen and Jobling 1992; Heggenes et al. 1993; Fraser and Metcalfe 1997; Johansen et al. 2010). In general, we observed Brown Trout to select larger bodied taxa, including Limnephilidae, *Gammarus,* and *Physella,* during winter and avoid smaller bodied taxa, including Chironomidae, Simuliidae, and *Baetis*. With less light available at night, larger prey are likely more obvious and susceptible to capture by visual feeders, such as Brown Trout. Interestingly, Brown Trout were also most selective of prey (both positive and negative) during winter, when the proportion of benthos and drift were lowest. Although this contradicts other studies that report a positive correlation between prey density and electivity (Ringler 1979), we documented that all significant values for prey avoidance during winter reflected small-bodied taxa, including Chironomidae, Simuliidae, and *Baetis*. The higher selectivity during winter may be an artifact of prey accessibility, reflecting a reduced ability to see and capture smaller prey items, and not necessarily that the Brown Trout are actively avoiding these prey. Furthermore, despite negative

selection toward Chironomidae during winter, the potential importance of this taxon as a food resource for Brown Trout in southeastern Minnesota should not be overlooked. Chironomids were the most abundant benthic and drifting prey type in all streams and comprised over half of all stomach contents during much of the year, including winter. Even as Brown Trout are actively foraging for other taxa, sheer abundance of Chironomidae in the environment may result in a high occurrence of incidental or accidental consumption.

Associations of selectivity with growth and prey abundance

Mean instantaneous growth (G) of Brown Trout and mean prey selectivity were not correlated on a seasonal basis across all streams. Within streams, growth increased significantly with selectivity of drift in Daley Creek and Garvin Brook. In Daley Creek, Brown Trout consistently selected and consumed *Physella,* the most energetically-rich of all prey available, and *Gammarus*, an abundant prey item that has been positively correlated with Brown Trout biomass elsewhere in southeastern Minnesota (Kwak 1993). Similarly, in addition to containing the highest abundances of *Gammarus* and proportion of drifting Chironomids of all streams in our study, Daley Creek also contained the fastest growing Brown Trout (see Chapter 1). Overall selectivity was highest during winter and spring, a period that also accounted for approximately 70% of overall annual fish growth in Daley Creek.

Although overall electivity of drift was lowest in Garvin Brook, there was a positive relationship between selectivity of drift and fish growth across seasons. In general, Garvin Brook consistently supported the highest density and relative proportion of drift of all study streams. Fastest growth occurred during spring and summer, concurrent with highest rates of selectivity and drift density. During summer, Brown Trout most favored *Gammarus* and *Brachycentrus* among drifting taxa, but demonstrated a slight positive selection for *Baetis* and *Brachycentrus* during spring. Although these prey items are not among the most energetically valuable, high availability of these taxa in the drift may have attracted foraging Brown Trout during spring and summer, resulting

in faster growth and higher rates of electivity. A similar relationship among prey electivity, prey availability, and growth of Brown Trout was reported by Ringler (1979).

Interestingly, despite seasonal associations between the abundance of available drift and prey electivity in Garvin Brook, we found a negative correlation between the mean proportion of prey available and mean electivity of Brown Trout across all samples. This relationship is contrary to the expectation that fish will demonstrate greater electivity in response to greater availability of prey (Ringler 1979). A possible explanation is that prey selection by Brown Trout is influenced by prey size, and not prey abundance, especially in our study streams, which support highly productive assemblages of aquatic macroinvertebrates. Optimal Foraging Theory (Emlen 1966; MacArthur and Pianka 1966) predicts an increasing selectivity for larger (energetically more profitable) prey would be expected with increasing prey abundance (Werner and Hall 1974). Therefore, the relationship between electivity and prey abundance may have more to do with the size of prey selected, rather than the taxa available.

Brown Trout consistently avoided three drifting taxa (*Baetis*, Simuliidae, and Chironomidae) that were proportionally the most abundant in the study streams and considered the most vulnerable, and predictably exploited, prey taxa based on drift propensity (Rader 1997). In contrast, Brown Trout typically selected taxa that were less abundant and/or less likely to drift (*Gammarus*, *Physella*, and *Brachycentrus*). In many comparisons, we found that Brown Trout were more selective on drift than benthic prey. One explanation for the higher degree of selectivity of drift relative to benthos may be that Brown Trout are predominately feeding epibenthically, whereby our electivity analyses using drift data may not actually represent the selection of prey from the water column. Epibenthic feeding varies widely among trout populations, and seasonal or spatial differences in drift density or availability of actively drifting versus less-mobile prey may influence which feeding mode is dominant. In several studies, salmonids have been shown to feed on benthos when drift is depleted (Nislow et al. 1998; Nakano et al. 1999). In one study, Brown Trout were more likely to feed on the benthos when less-mobile prey types were abundantly available (McIntosh and Townsend 1995). Fausch et al. (1997) detected an adaptive shift from drift feeding to epibenthic feeding in Dolly

Varden (*Salvelinus malma*) as drift availability was experimentally reduced in a Japanese stream.

In southeastern Minnesota, a predictive model for Brown Trout foraging did not predict feeding mode for all samples, but provided evidence for drift feeding during summer, and predominately benthic feeding during fall and winter (Newman 1987). Similarly, our study suggests that Brown Trout are especially selective for drifting taxa during summer, and that epibenthic feeding is important in all streams, and especially in winter, as observed by other studies in our region (Anderson 2012; French 2014), and elsewhere (Cunjak and Power 1987). Additionally, the consistent preference and consumption of gastropods also supports a benthic mode of feeding, which has been observed in salmonids of subarctic rivers (Brittain and Eikeland 1988; Amundsen et al. 1999; Steingrímsson and Gíslason 2002; Johnson et al. 2007) and typical of Brown Trout in southeastern Minnesota (Anderson 2012; French 2014).

Our results suggest that Brown Trout foraging occurs in response to spatial and temporal availability of food resources, as we observed that diet, prey selectivity, and macroinvertebrate taxa varied across seasons and streams, with a reduced electivity for benthic taxa. At a broad scale, our electivity analyses found general avoidance of Dipterans; however, these prey were widely abundant, both seasonally and spatially, and diets often contained a high proportion of Chironomidae. On a smaller scale, the broad comparisons may have masked important spatial differences in prey resources and foraging. For example, when data from all streams were combined, we found that Brown Trout significantly favored *Gammarus* in the drift; however, analyses within streams revealed that *Gammarus* was only significantly favored by trout in Daley Creek, where it comprised >50% of importance based on IRI (see Chapter 1). In contrast, in Beaver Creek, where *Gammarus* were absent, Brown Trout significantly favored *Physella*, whereas nearly 60% of overall diet consisted of Trichopterans and Chironomidae based on IRI (see Chapter 1).

On a temporal basis, we observed that, on a few notable occasions, stomachs contained high proportions of prey in response to a temporary spike in availability (e.g. ants and aphids following a significant rainfall event during summer, and Chironomidae

during a large emergence in late spring) that may not have been reflected in our broad comparisons of electivity due to a low frequency of these events relative to the number of sampling events. During winter; however, stable isotope analysis of Brown Trout diets in southeastern Minnesota provided evidence that the dominant prey taxa observed in stomach contents were also those that contributed toward growth (French et al. 2014). Overall, macroinvertebrate prey resources in all streams and seasons appeared to be abundant and available. Although the majority of prey available in the environment and eaten was represented by relatively few taxa, there was substantial variation in diet, prey, and patterns of selectivity on a seasonal and spatial basis. Foraging decisions are most likely shaped by a generalist or opportunist strategy that reflects site-specific prey abundance and accessibility or size.

A potential limitation of the present study is that Brown Trout stomach samples were taken at variable times of the day between early morning and early evening, therefore, observed diets may not have accurately represented feeding over a 24-hour period. For example, fish could have selected certain prey taxa during the sampling period, but the stomach contents may have been dominated by other macroinvertebrates consumed earlier in the day, perhaps relative to diel patterns in macroinvertebrate activity. Few of the prey taxa preferred by Brown Trout in this study were of terrestrial origin, however, if sampling occurred before terrestrial drift peaked (Elliott 1970), these taxa may be under-represented in diets.

In addition, the present study did not account for variation in prey size or potential differences in selectivity among Brown Trout of varying sizes and/or ages. Although some studies report an ontogenetic shift toward larger prey among older salmonids (e.g. Steingrímsson and Gíslason 2002; Montori et al. 2006; Sánchez-Hernández and Cobo 2012; Sánchez-Hernández et al. 2013), others have not found consistent, significant correlations between prey size and fish length or age of Brown Trout (Sánchez-Hernández and Cobo 2015), and no relationship between gape size and prey ingestion (Newman 1987; Rincón and Lobón-Cerviá 1999). Sánchez-Hernández and Cobo (2015) postulated that the lack of relationship might have been due to sampling predominately Brown Trout <300-mm in total length. Similarly, we collected relatively few Brown

Trout >300-mm in total length, suggesting that size-selectivity may not have been a factor shaping patterns in prey electivity in our study.

Conclusion

The purpose of this study was to investigate spatial and temporal patterns in prey selection by Brown Trout in a collection of streams where prey availability was suggested as a potential factor limiting fish growth.

Although only a few taxa represented a majority of the aquatic macroinvertebrates selected by Brown Trout, we found that the structure of macroinvertebrate assemblages and prey preference varied significantly across time and space. In general, Brown Trout selected large-bodied, energy-rich benthic prey, including *Physella* and *Gammarus*, over other more abundant aquatic macroinvertebrate taxa, such as Chironomidae, and drifting prey. Although analyses of stomach contents revealed that Brown Trout diets typically reflected prey taxa that were most abundant in the environment, including Chironomidae, the apparent preference of energy-dense benthic prey taxa, and the possible consequences for growth, warrants future study with bioenergetics modeling.

Our results provide important information about the foraging patterns of Brown Trout, and will be particularly useful in helping fisheries managers identify and manage key macroinvertebrate taxa on a year-round basis. In addition, this detailed knowledge about the preferences of Brown Trout and composition of aquatic macroinvertebrate communities can be combined with life history data and bioenergetics modeling to predict the future consequences of climate change on trophic structures in groundwater-dominated streams in southeastern Minnesota.

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Tables

Table 1. Seasonal variation in prey assemblages and diet composition across five streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

	Distance	Observed delta	Expected delta	A	P-value
Benthos		*0.670*	*0.689*	*0.019*	*0.050*
Winter	0.675				
Spring	0.701				
Summer	0.634				
Fall	0.658				
Drift		*0.464*	*0.488*	*0.040*	*0.012*
Winter	0.530				
Spring	0.482				
Summer	0.464				
Fall	0.536				
Diet		*0.693*	*0.695*	*<0.001*	*0.311*
Winter	0.538				
Spring	0.482				
Summer	0.461				
Fall	0.531				

Table 2. Variation in prey assemblages and Brown Trout diet composition among five streams in southeastern Minnesota, 2011-2013, based on a MRPP test.

	Distance	Observed delta	Expected delta	A	P-value
Benthos		*0.591*	*0.685*	*0.133*	*<0.001*
Beaver Creek	0.599				
Daley Creek	0.498				
Garvin Brook	0.551				
Gribbon Creek	0.595				
Trout Run Creek	0.713				
Drift		*0.453*	*0.483*	*0.061*	*0.002*
Beaver Creek	0.491				
Daley Creek	0.419				
Garvin Brook	0.500				
Gribbon Creek	0.477				
Trout Run Creek	0.394				
Diet		*0.619*	*0.692*	*0.111*	*<0.001*
Beaver Creek	0.682				
Daley Creek	0.586				
Garvin Brook	0.618				
Gribbon Creek	0.691				
Trout Run Creek	0.521				

Table 3. Mean prey selectivity (Manly-Chesson index, α$_i$; SD) overall for Brown Trout collected from five streams in southeastern Minnesota, 2011-2013. Values significantly different (*p< 0.05), from 1/m are indicated by "+" for positive selection and "-" for negative selection.

Overall (all sample dates combined)				
Benthos	1/m	Prey type	$\bar{\alpha}_i$	
	0.125	*Brachycentrus*	−0.081(0.135)	*
		Chironomidae	0.161(0.216)	
		Simuliidae	0.091(0.176)	
		Elmidae	−0.024(0.035)	*
		Baetis	−0.068(0.105)	*
		Physella	+0.371(0.291)	*
		Gammarus	0.154(0.180)	
		Other	0.165(0.167)	
Drift	1/m	Prey type		
	0.143	*Brachycentrus*	+0.201(0.206)	*
		Chironomidae	−0.086(0.117)	*
		Simuliidae	−0.015(0.021)	*
		Baetis	0.108(0.155)	
		Physella	+0.408(0.306)	*
		Gammarus	+0.289(0.260)	*
		Other	0.147(0.184)	

vity (Manly-Chesson index, α_i; SD) by season for Brown Trout in five streams in southeastern Minnesota, 2011-2013. Values
0.05) from 1/m are indicated by "+" for positive selection and "-" for negative selection; n is the number of independent sample dates.

Prey type	$\bar{\alpha}_i$		Drift	1/m	Prey type	$\bar{\alpha}_i$	
Brachycentrus	−0.026(0.025)	*	Winter (n=6)	0.111	*Brachycentrus*	0.286(0.430)	
Limnephilidae	0.437(0.354)				Chironomidae	0.056(0.108)	
Chironomidae	0.101(0.132)				Simuliidae	−0.008(0.010)	*
Simuliidae	−0.018(0.019)	*			*Baetis*	−0.023(0.048)	*
Baetis	0.097(0.126)				Ephemerellidae	−0.000(0.000)	*
Physella	0.412(0.408)				Perlidae	−0.001(0.001)	*
Gammarus	0.202(0.211)				*Physella*	+0.528(0.320)	*
Other	−0.064(0.073)	*			*Gammarus*	0.104(0.078)	
					Other	0.336(0.259)	
Brachycentrus	0.084(0.170)		Spring (n=21)	0.125	*Brachycentrus*	0.125(0.140)	
Limnephilidae	0.206(0.260)				Limnephilidae	0.387(0.379)	
Chironomidae	0.172(0.266)				Chironomidae	0.090(0.116)	
Simuliidae	−0.067(0.127)	*			Simuliidae	−0.011(0.011)	*
Baetis	−0.051(0.062)	*			*Baetis*	0.139(0.189)	
Physella	+0.343(0.227)	*			*Physella*	+0.372(0.311)	*
Gammarus	0.231(0.255)				*Gammarus*	+0.277(0.065)	*
Other	0.140(0.155)				Other	0.178(0.224)	
Brachycentrus	0.239(0.209)		Summer (n=12)	0.143	*Brachycentrus*	+0.293(0.190)	*
Chironomidae	0.181(0.197)				Chironomidae	−0.085(0.095)	*
Elmidae	0.099(0.154)				Simuliidae	−0.009(0.008)	*
Baetis	0.174(0.259)				*Baetis*	−0.061(0.058)	*
Gammarus	0.192(0.189)				Formicidae	−0.085(0.101)	*
Other	0.185(0.142)				*Gammarus*	+0.371(0.267)	*
					Other	0.147(0.108)	
Brachycentrus	0.103(0.197)		Fall (n=9)	0.143	*Brachycentrus*	0.226(0.192)	
Chironomidae	0.255(0.192)				Chironomidae	0.094(0.112)	

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Elmidae	−0.000(0.000)	*	Simuliidae	−0.033(0.042)	*
Baetis	0.099(0.179)		*Baetis*	0.134(0.172)	
Physella	+0.363(0.302)	*	*Physella*	0.368(0.327)	
Gammarus	0.097(0.100)		*Gammarus*	0.269(0.259)	
Other	0.094(0.076)		Other	−0.080(0.038)	*

Table 5. Mean prey type selectivity (Manly-Chesson index, α_i; SD) for Brown Trout from five streams in southeastern Minnesota, 2010-2013. Values significantly different ($p < 0.05$) from $1/m$ are indicated by "+" for positive selection and "-" for negative selection; n is the number of independent sample dates.

Benthos					Drift				
Site	$1/m$	Prey type	$\bar{\alpha}_i$		Site	$1/m$	Prey type	$\bar{\alpha}_i$	
Beaver Creek (n=8)	0.100	*Brachycentrus*	0.071(0.057)		Beaver Creek (n=8)	0.111	*Brachycentrus*	+0.263(0.213)	*
		Glossosoma	0.058(0.102)				Hydroptilidae	0.463(0.329)	
		Hydropsychidae	−0.027(0.028)	*			Limnephilidae	0.827(-)	
		Hydroptilidae	0.200(0.271)				Chironomidae	−0.030(0.031)	*
		Limnephilidae	0(0)				Simuliidae	−0.010(0.008)	*
		Chironomidae	−0.075(0.034)	*			*Baetis*	−0.051(0.036)	*
		Elmidae	−0.013(0.016)	*			Perlidae	0.006(-)	
		Baetis	0.085(0.109)				*Physella*	+0.351(0.278)	*
		Physella	+0.373(0.374)	*			Other	0.107(0.078)	
		Other	0.175(0.168)						
Daley Creek (n=10)	0.167	Chironomidae	0.132(0.210)		Daley Creek (n=10)	0.143	Chironomidae	−0.071(0.104)	*
		Simuliidae	0.100(0.256)				Simuliidae	−0.015(0.021)	*
		Baetis	−0.054(0.089)	*			*Baetis*	−0.089(0.078)	*
		Physella	0.373(0.359)				*Physella*	0.398(0.347)	
		Gammarus	0.202(0.236)				*Gammarus*	+0.458(0.294)	*
		Other	0.223(0.233)				Formicidae	−0.043(0.054)	*
							Other	0.239(0.287)	
Garvin Brook (n=10)	0.125	*Brachycentrus*	0.151(0.229)		Garvin Brook (n=10)	0.167	*Brachycentrus*	0.230(0.194)	
		Glossosoma	−0.035(0.036)	*			Chironomidae	0.169(0.123)	
		Chironomidae	+0.239(0.195)	*			Simuliidae	−0.031(0.045)	*
		Simuliidae	0.130(0.222)				*Baetis*	0.244(0.233)	
		Elmidae	−0.018(0.022)	*			*Gammarus*	0.277(0.242)	
		Baetis	0.092(0.081)				Other	0.131(0.068)	
		Gammarus	0.174(0.212)						
		Other	0.183(0.145)						

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Site		Taxon	Value		Site		Taxon	Value	
Gribbon Creek (n=11)	0.100	*Brachycentrus*	−0.041(0.061)	*	Gribbon Creek (n=11)	0.100	*Brachycentrus*	−0.046(0.043)	*
		Limnephilidae	+0.442(0.260)	*			Limnephilidae	0.174(-)	
		Ceratopogonidae	0(-)				Ceratopogonidae	0.470(0.615)	
		Chironomidae	0.142(0.231)				Chironomidae	0.068(0.132)	
		Simuliidae	−0.018(0.016)	*			Simuliidae	−0.012(0.028)	*
		Baetis	−0.049(0.049)	*			*Baetis*	0.100(0.191)	
		Ephemerellidae	−0.002(0.004)	*			Ephemerellidae	−0.001(0.002)	*
		Physella	+0.337(0.232)	*			*Physella*	+0.412(0.413)	*
		Gammarus	0.184(0.210)				*Gammarus*	0.265(0.305)	
		Other	0.091(0.066)				Other	0.138(0.208)	
Trout Run Creek (n=10)	0.143	*Brachycentrus*	−0.032(0.023)	*	Trout Run Creek (n=10)	0.143	*Brachycentrus*	+0.342(0.285)	*
		Hydroptilidae	−0.031(0.035)	*			Chironomidae	−0.082(0.081)	*
		Chironomidae	0.262(0.340)				Simuliidae	−0.008(0.008)	*
		Baetis	0.099(0.239)				*Baetis*	−0.026(0.029)	*
		Physella	+0.523(0.344)	*			*Physella*	+0.599(0.149)	*
		Gammarus	0.140(0.140)				*Gammarus*	0.182(0.201)	
		Other	0.150(0.158)				Other	0.148(0.235)	

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Table 6. Linear regressions between mean instantaneous growth (G) of Brown Trout and mean prey selectivity on a seasonal basis among streams and among seasons within each sample site; * denotes significance (<p<0.05).

	Benthos				Drift			
	β	CI	R^2	p	β	CI	R^2	p
Among streams								
Winter	-0.14	0.06/1.77	0.25	0.39	0.12	0.56/0.36	0.17	0.49
Spring	0.15	-0.01/0.86	0.02	0.80	-0.87	0.30/0.71	0.25	0.39
Summer	0.13	-0.14/0.41	0.17	0.49	0.46	-0.72/0.63	0.31	0.32
Fall	0.17	0.19/0.71	0.50	0.18	0.03	-0.05/0.96	0.04	0.75
Within streams								
Beaver Creek	-0.20	-0.79/1.39	0.16	0.60	-0.63	0.41/1.09	0.59	0.52
Daley Creek	0.62	-3.41/3.00	0.13	0.64	1.64	-3.09/3.44	0.91	0.04*
Garvin Brook	-0.04	-0.91/1.30	0.04	0.93	1.30	0.32/0.52	0.94	0.03*
Gribbon Creek	2.01	-11.8/9.29	0.14	0.63	1.32	-0.55/2.98	0.77	0.12
Trout Run Creek	-0.03	-0.82/1.00	0.01	0.90	-0.18	-0.58/0.95	0.21	0.54

Figures
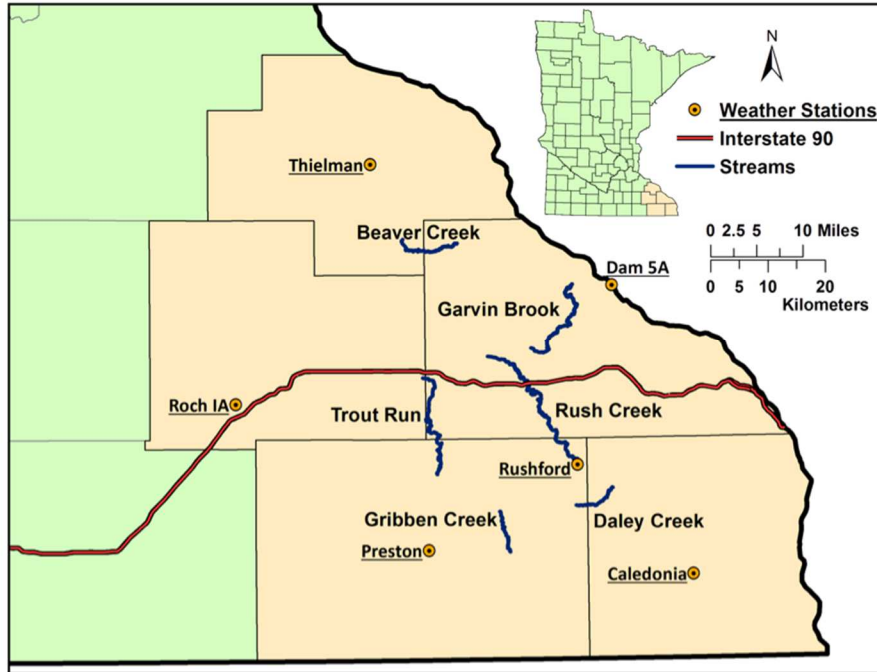
Figure 1. Map of the Driftless Ecoregion of southeastern Minnesota and five streams sampled for Brown Trout and macroinvertebrates, 2011-2013.

A)
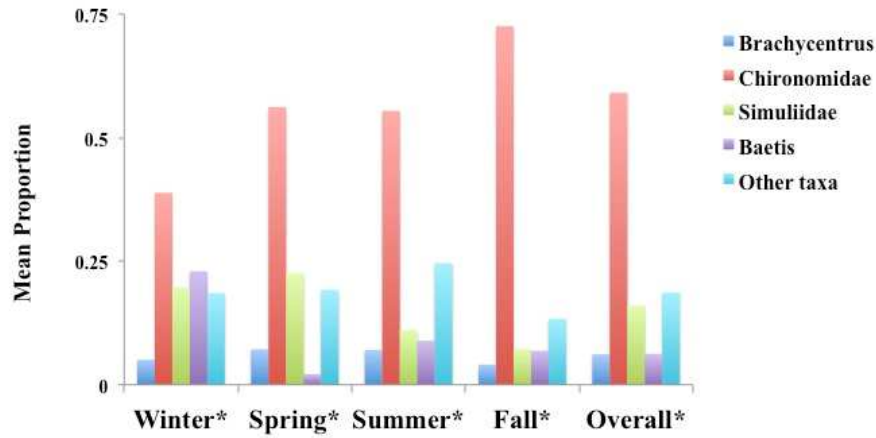
B)
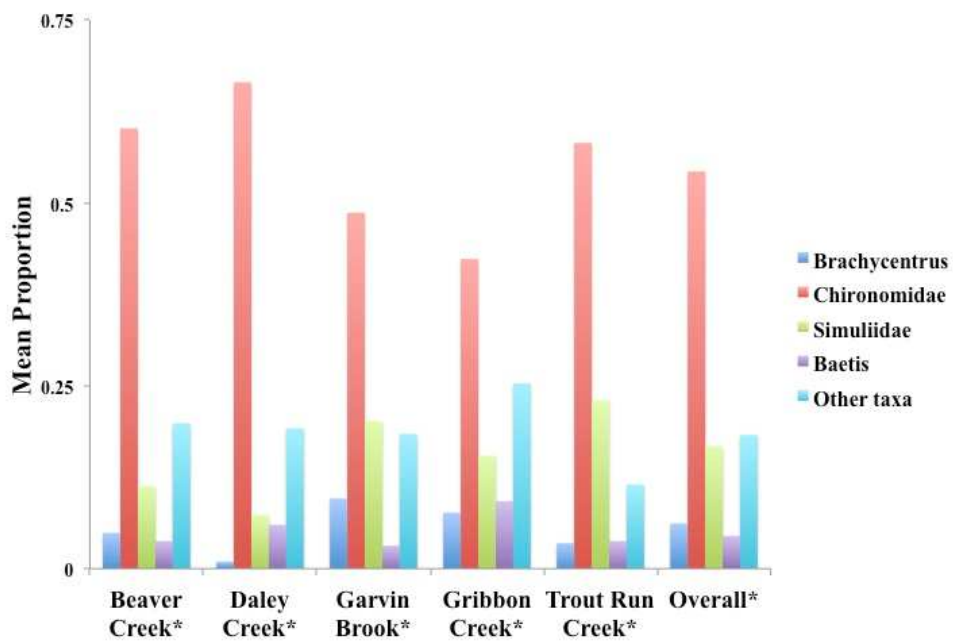
Figure 2. Mean proportions of drifting taxa (>5% of total) collected within (A) seasons and (B) streams, 2011-2013. All values within one category equal 100% and * indicates significant differences among seasons based on Kruskal-Wallis non-parametric analysis of variance (p<0.05).

A)

B)
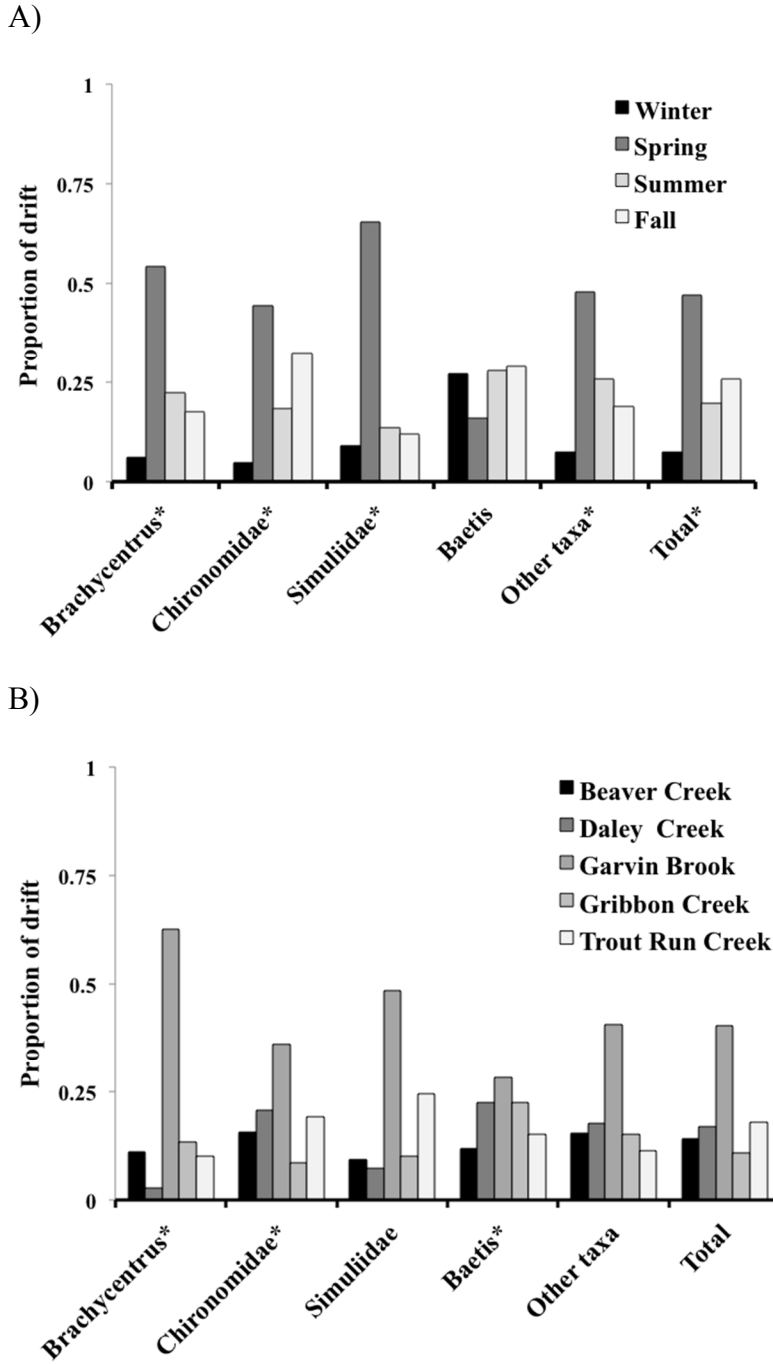
Figure 3. Proportional distribution of drifting taxa (>5% of total) across (A) seasons and (B) streams, 2011-2013. All values within one category equal 100%, and * indicates significant differences among seasons based on Kruskal-Wallis non-parametric analysis of variance ($p < 0.05$).

A)
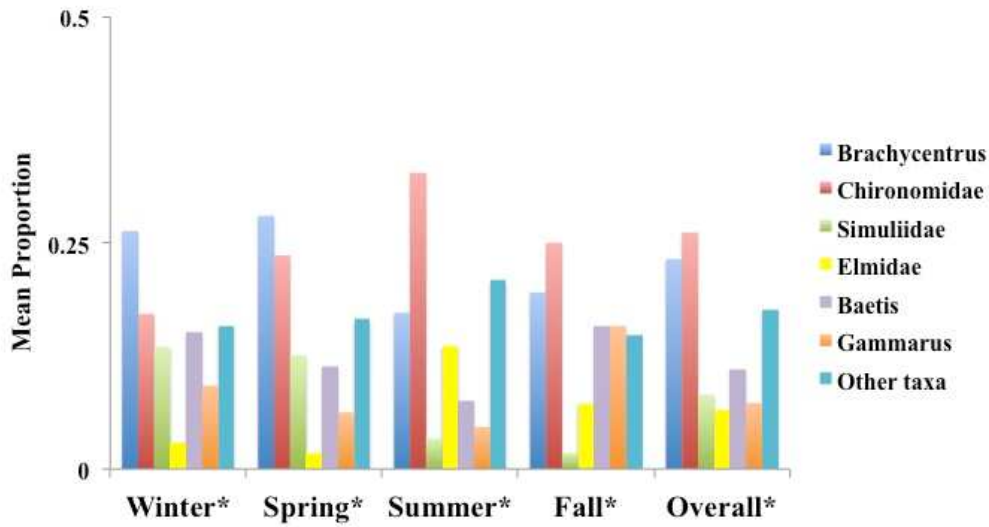
B)
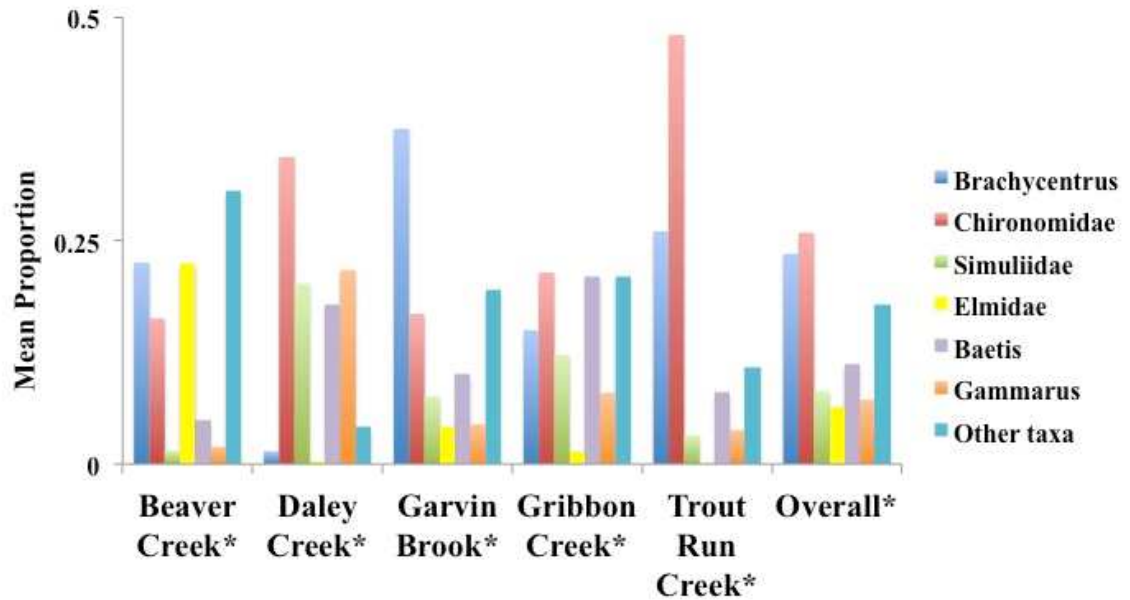
Figure 4. Mean proportions of benthic taxa (>5% of total) collected within (A) seasons and (B) streams, 2011-2013. All values within one category equal 100%, and * indicates significant differences among seasons based on Kruskal-Wallis non-parametric analysis of variance ($p < 0.05$).

A)

B)
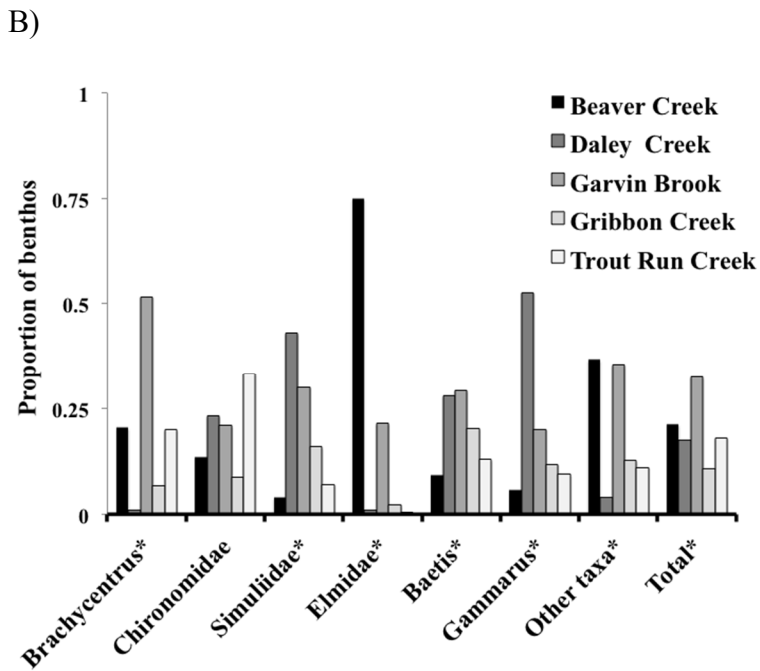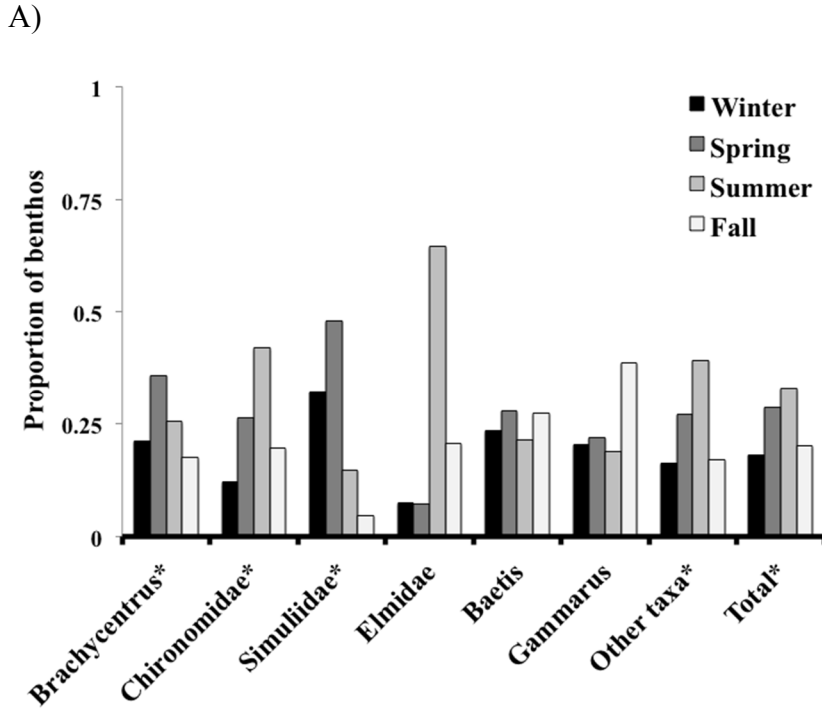
Figure 5. Proportional distribution of benthic taxa (>5% of total) across (A) seasons and (B) streams, 2011-2013. All values within one category equal 100%, and * indicates significant differences among seasons based on Kruskal-Wallis non-parametric analysis of variance ($p < 0.05$).
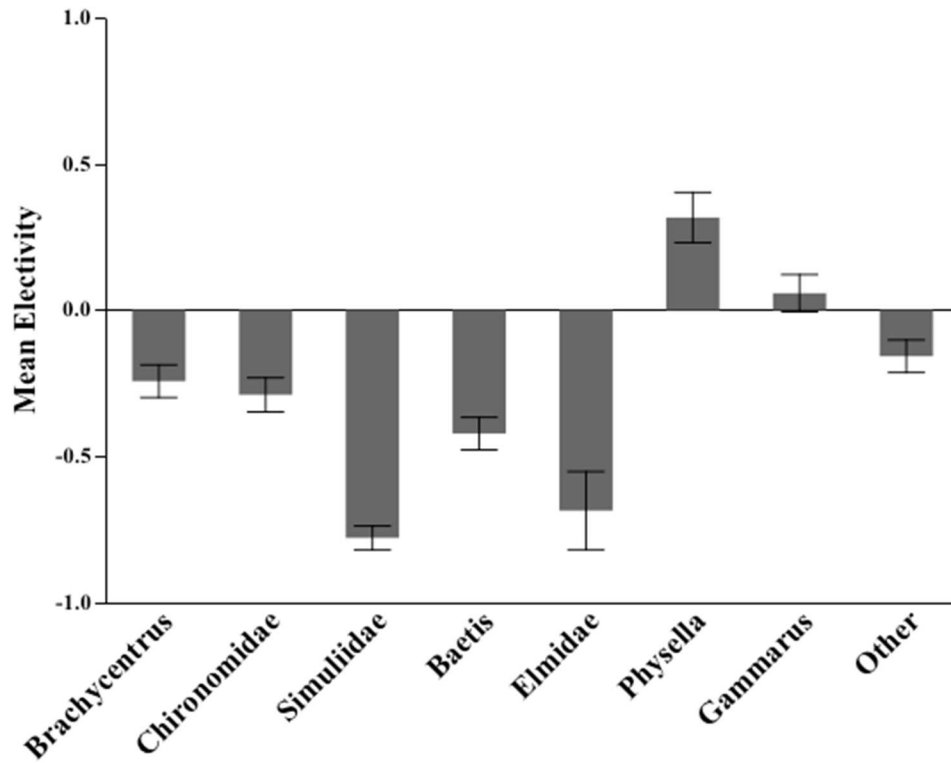
Figure 6. Mean electivity ($\bar{\varepsilon}$, ±1 s.e.) of prey taxa (benthos and drift combined) as calculated with a Manly-Chesson index, 2011-2013, in five streams across southeastern Minnesota (H=135.8, d.f.=7, p<0.01).
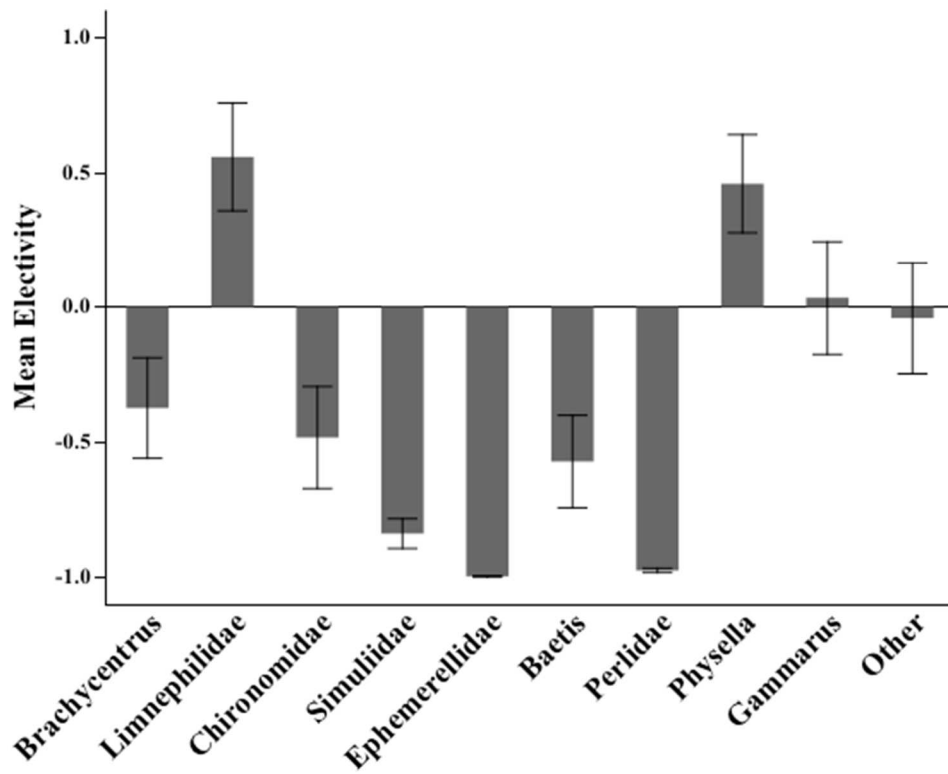
Figure 7. Mean electivity ($\bar{\varepsilon}$, ± 1 s.e.) of prey taxa (benthos and drift combined) during winter as calculated with a Manly-Chesson index, 2011-2013, in five streams across southeastern Minnesota (H=34.5, d.f.=9, p<0.01).

A)

B)
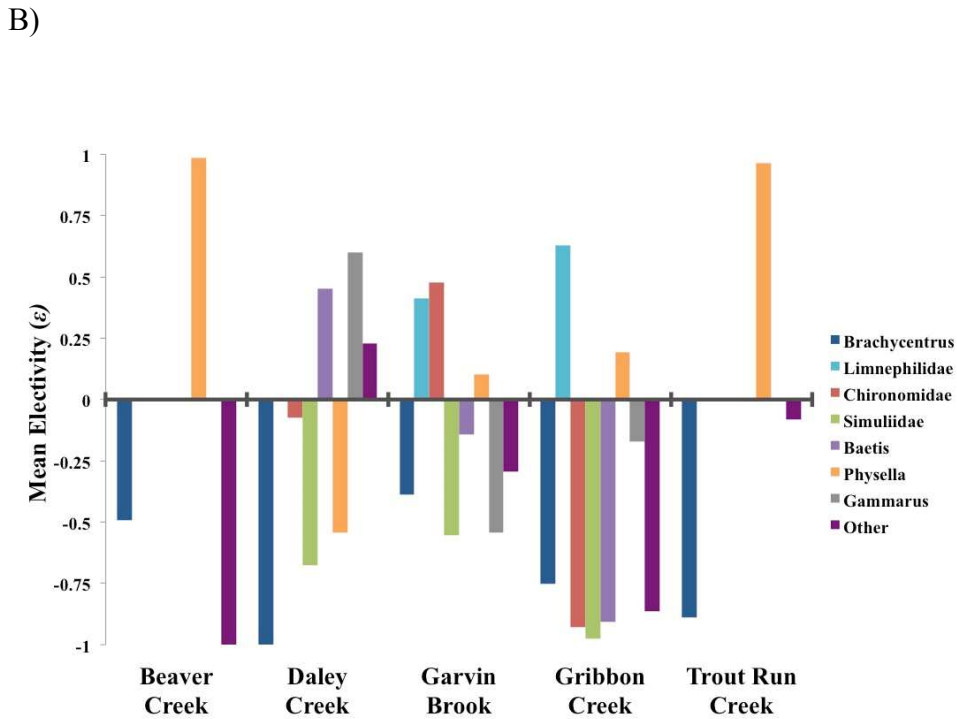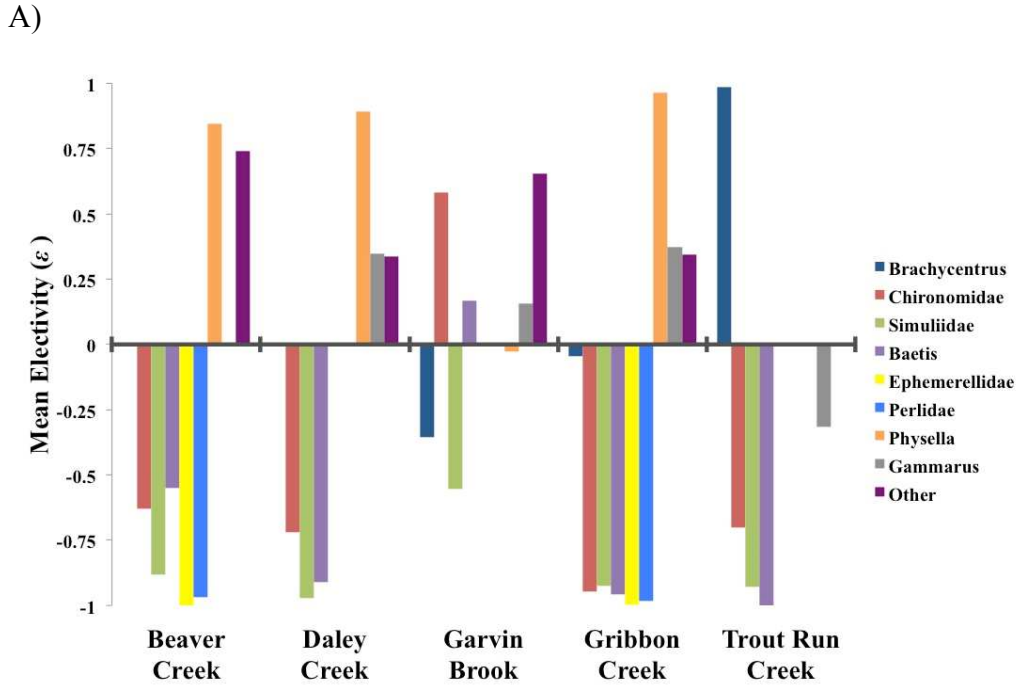
Figure 8. Electivity of Brown Trout for (A) drifting macroinvertebrates and (B) benthic macroinvertebrates at all sample sites during winter as measured by Manly-Chesson electivity index (ε).

A)

B)
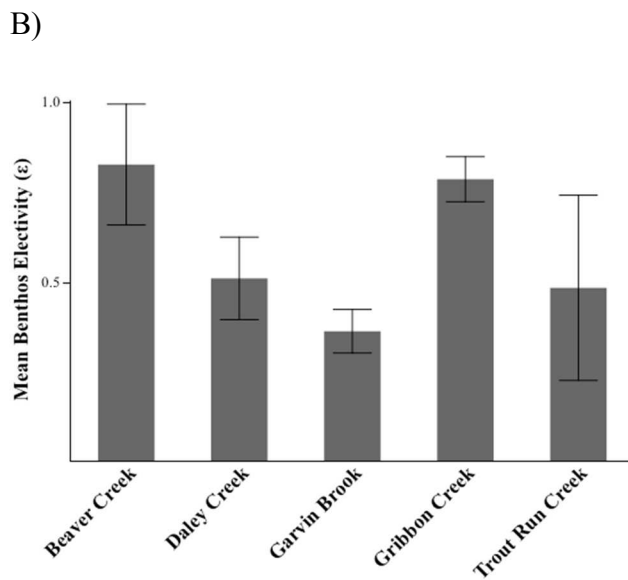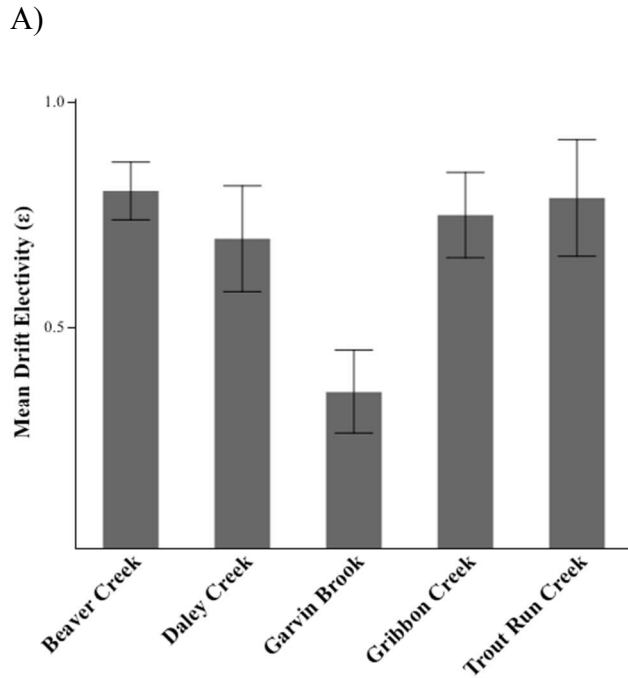
Figure 9. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of Brown Trout by stream as calculated with a Manly-Chesson index for (A) drift (H=8.9, d.f.=4, p=0.06) and (B) benthos (H=12.1, d.f.=4, p=0.02) during winter, 2011-2013.
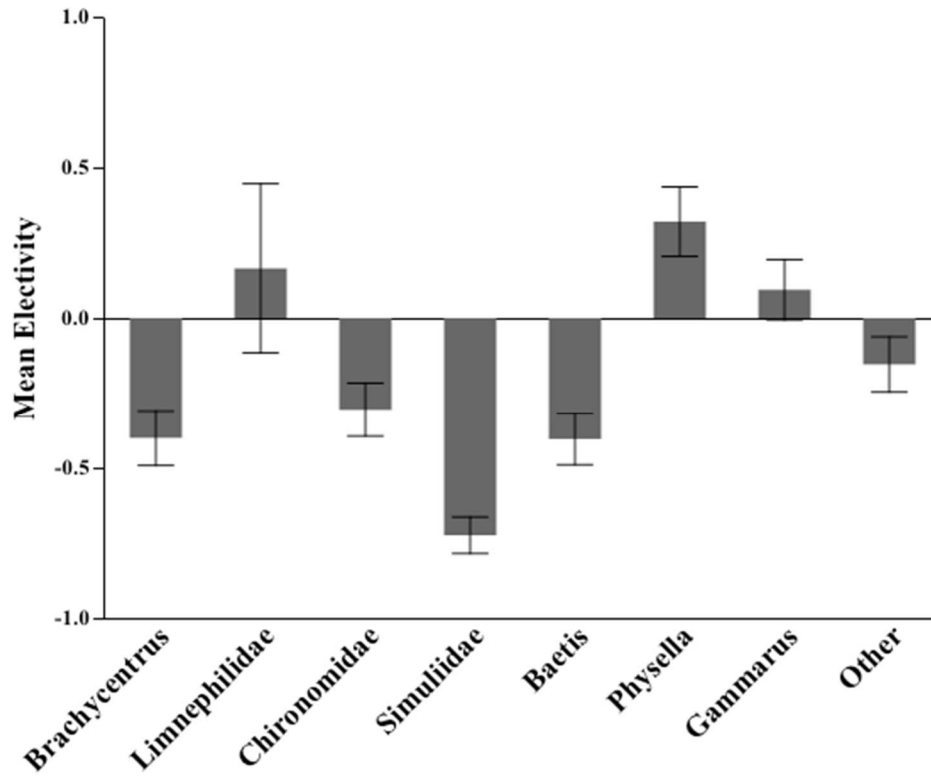
Figure 10. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of prey taxa (benthos and drift combined) during spring as calculated with a Manly-Chesson index, 2011-2013, in five streams across southeastern Minnesota (H=65.1, d.f.=7, p<0.01).

A)
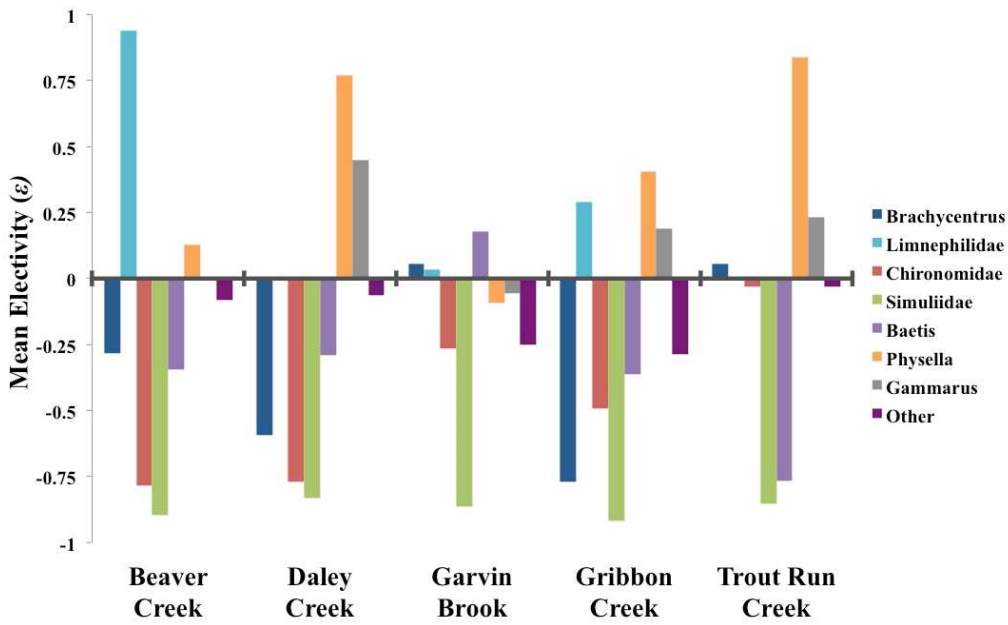
B)
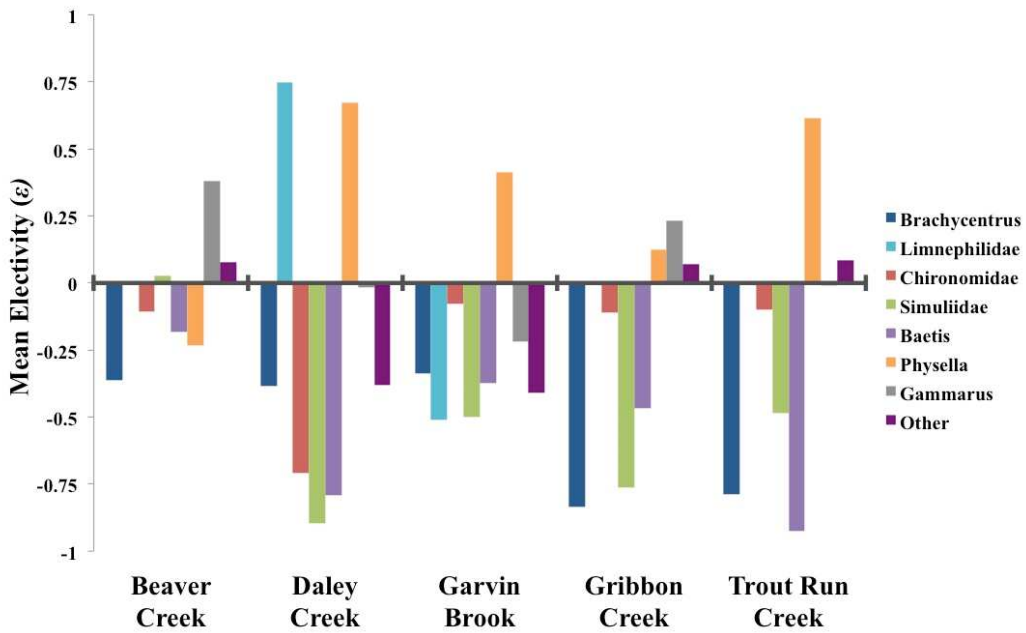
Figure 11. Electivity of Brown Trout for (A) drifting macroinvertebrates and (B) benthic macroinvertebrates at all sample sites during spring as measured by Manly-Chesson electivity index (ε).

A)
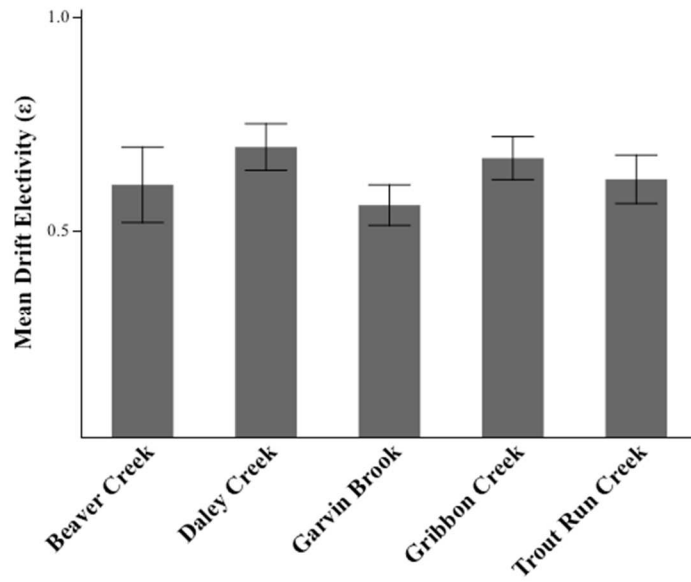
B)
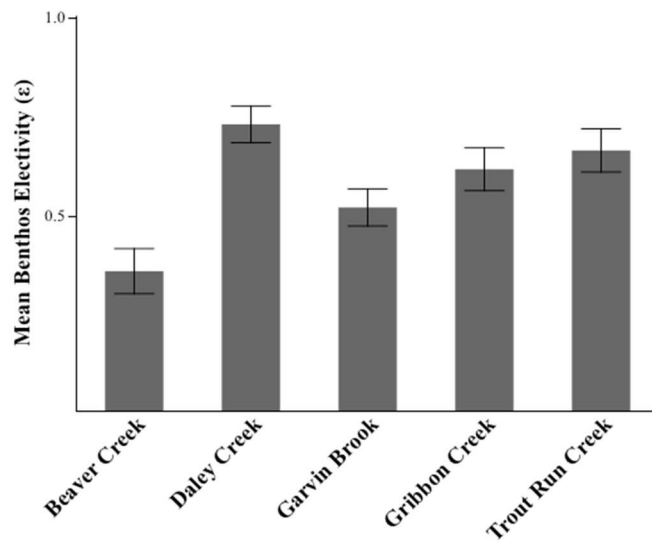
Figure 12. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of Brown Trout by stream as calculated with a Manly-Chesson index for (A) drift (H=4.1, d.f.=4, p=0.30) and (B) benthos (H=19.2, d.f.=4, p<0.01) during spring, 2011-2013.
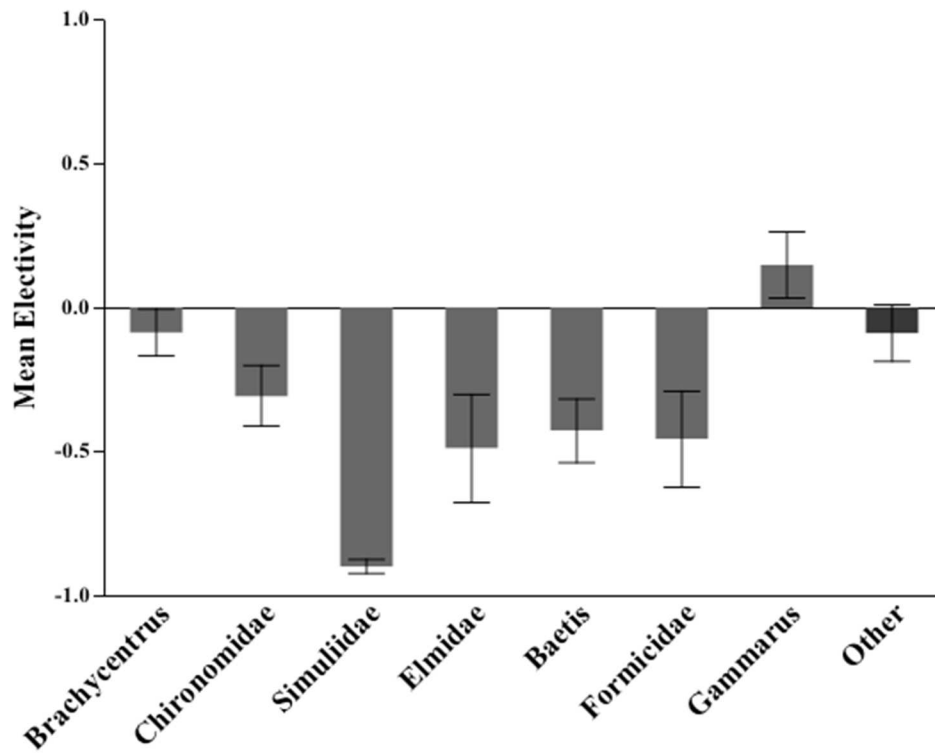
Figure 13. Mean electivity ($\bar{\varepsilon}$, ± 1 s.e.) of prey taxa (benthos and drift combined) during summer as calculated with a Manly-Chesson index, 2011-2013, in five streams across southeastern Minnesota (H=43.6, d.f.=7, p<0.01).

A)
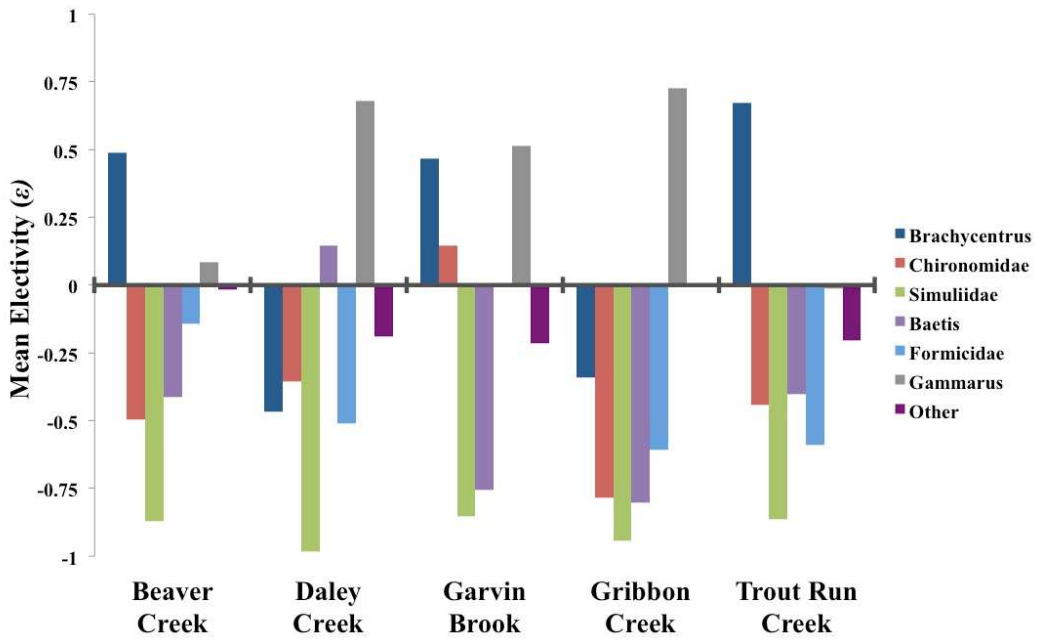
B)
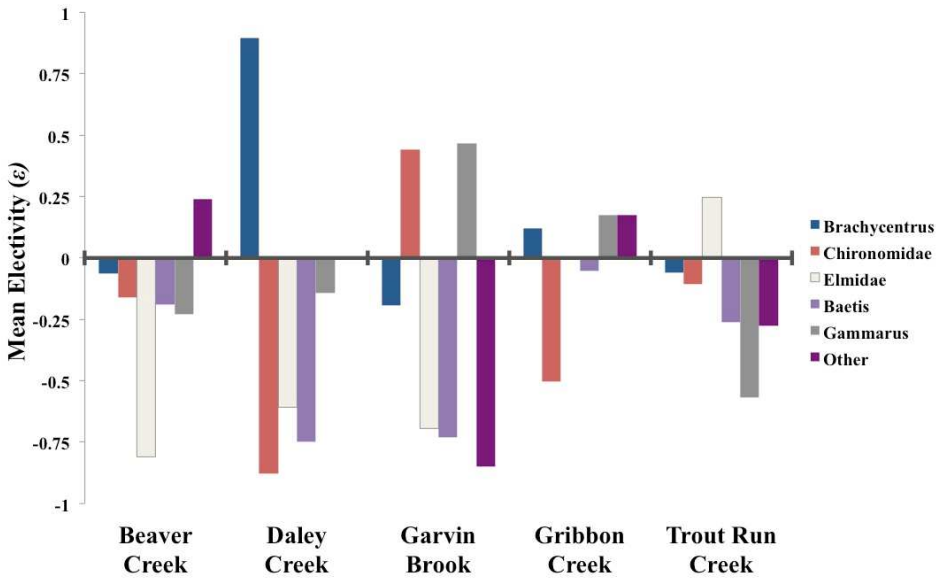
Figure 14. Electivity of Brown Trout for (A) drifting macroinvertebrates and (B) benthic macroinvertebrates at all sample sites during summer as measured by Manly-Chesson electivity index (ε).

A)

B)
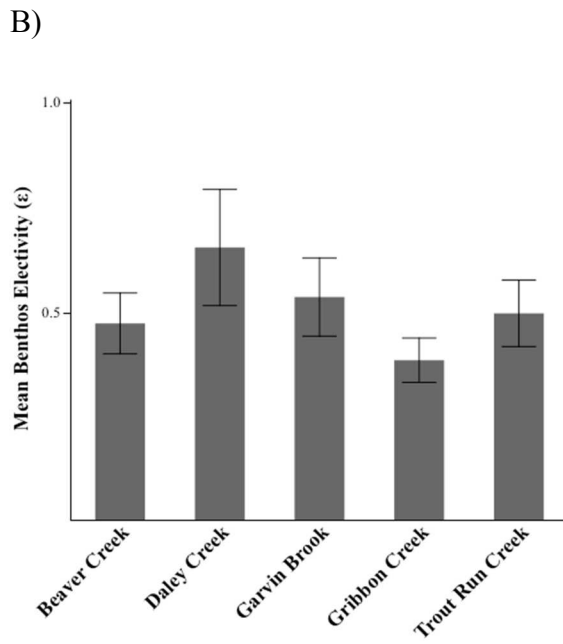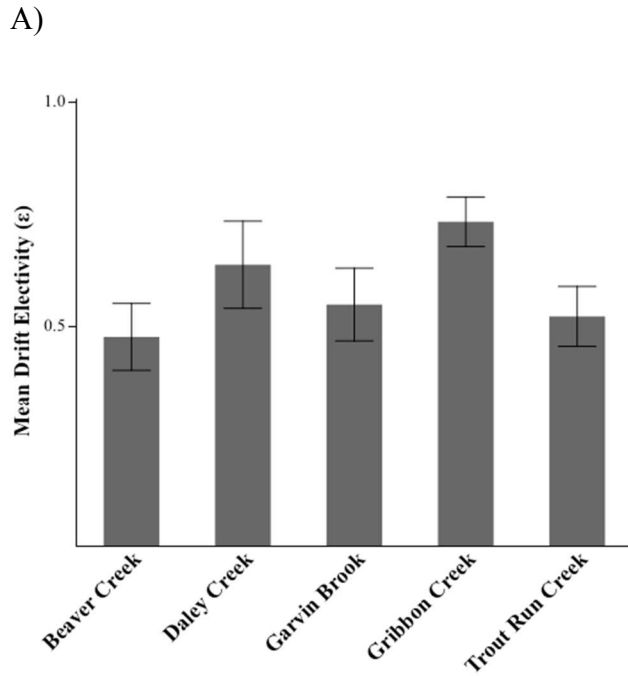
Figure 15. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of Brown Trout by stream as calculated with a Manly-Chesson index for (A) drift (H=9.1, d.f.=4, p=0.05) and (B) benthos (H=3.5, d.f.=4, p=0.52) during summer, 2011-2013.
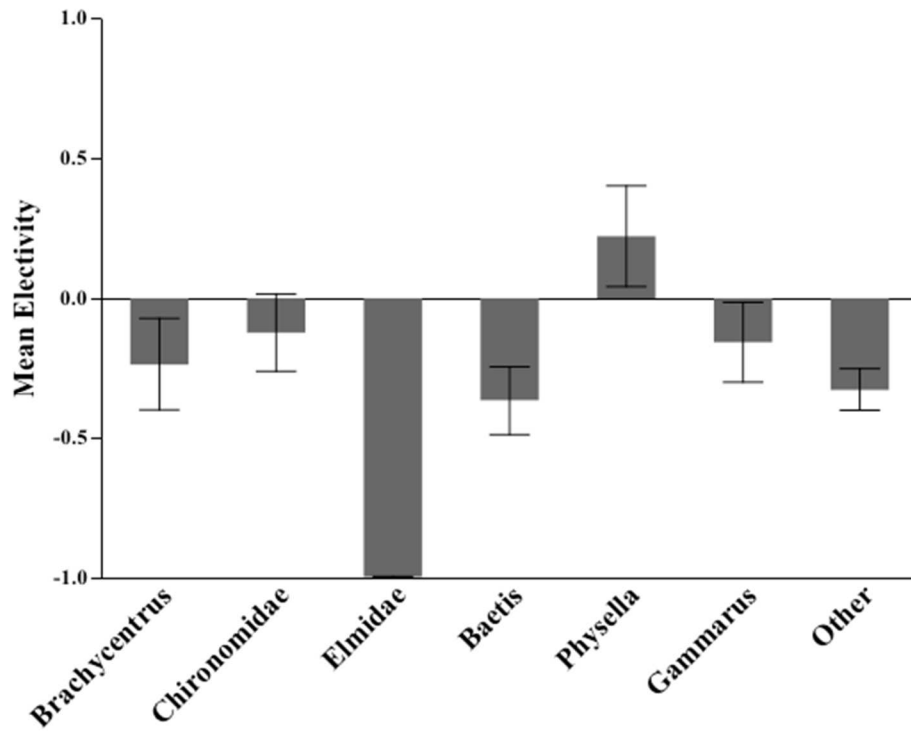
Figure 16. Mean electivity ($\bar{\varepsilon}, \pm 1$ s.e.) for prey taxa (benthos and drift combined) during fall as calculated with a Manly-Chesson index, 2011-2013, in five streams across southeastern Minnesota (H=19.6, d.f.=6, p<0.01).

A)

B)
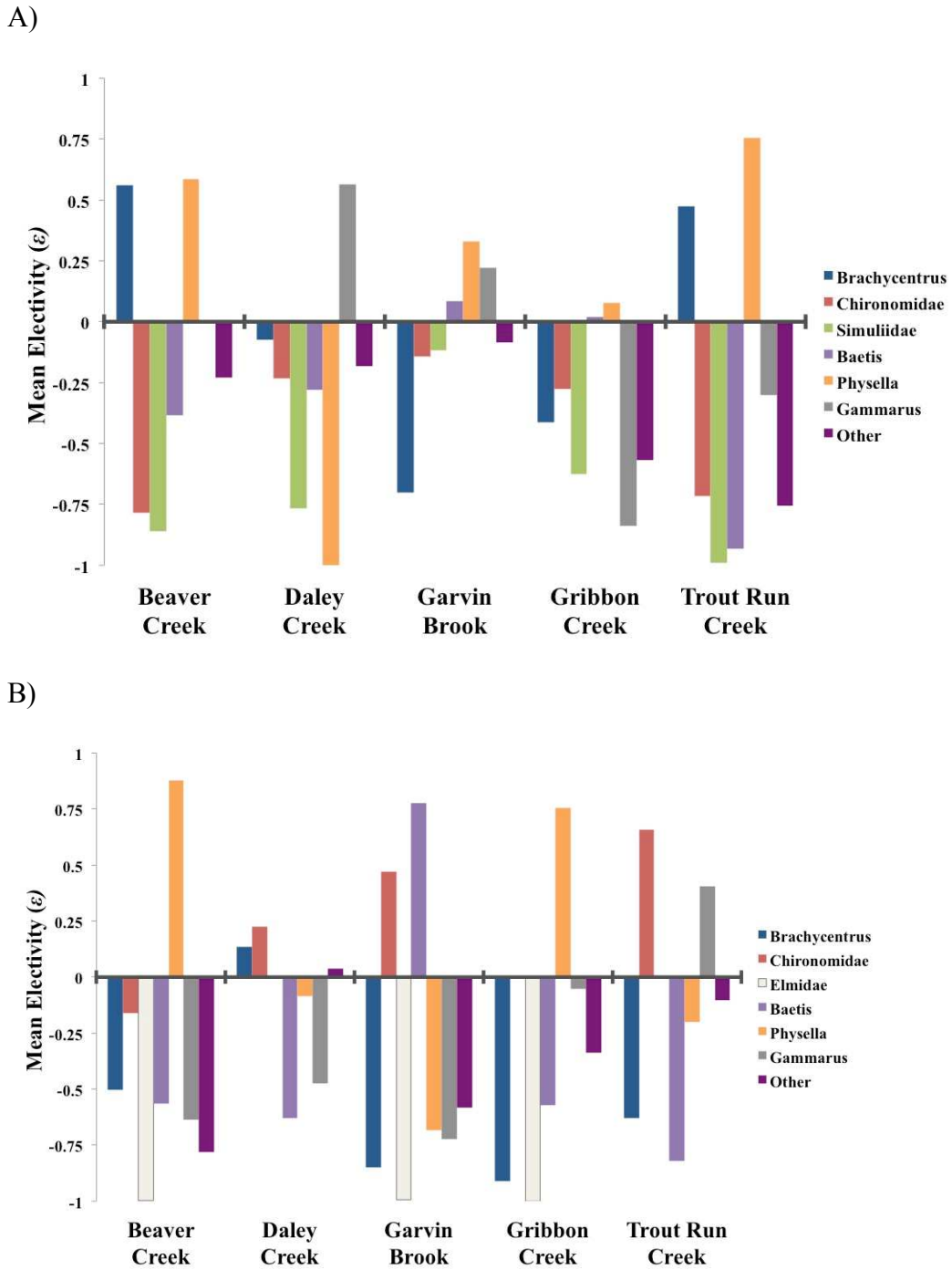
Figure 17. Electivity of Brown Trout for (A) drifting macroinvertebrates and (B) benthic macroinvertebrates at all sample sites during fall as measured by Manly-Chesson electivity index (ε).

A)

B)
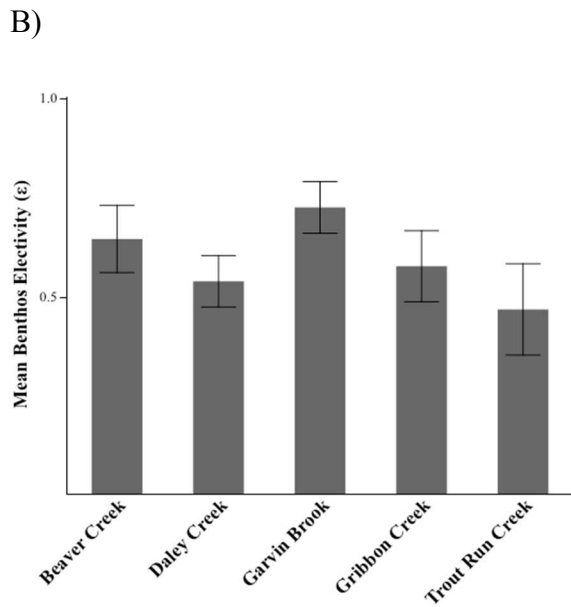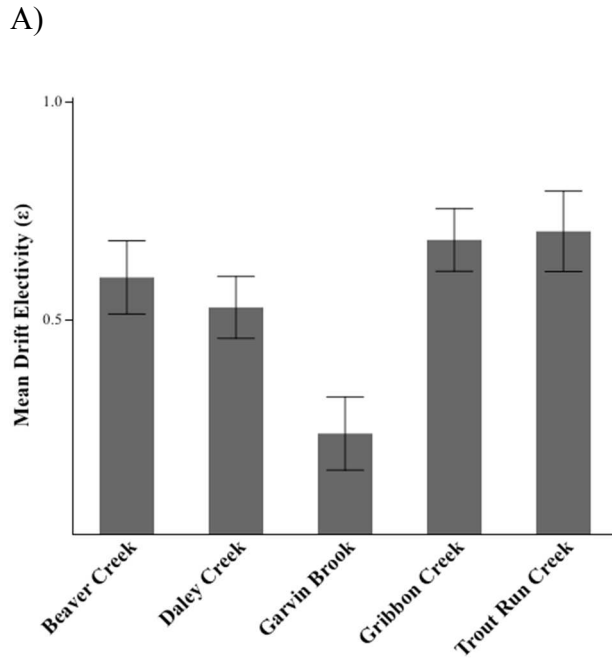
Figure 18. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of Brown Trout by stream as calculated with a Manly-Chesson index for (A) drift (H=12.1, d.f.=4, p=0.02) and (B) benthos (H=3.8, d.f.=4, p=0.43) during fall, 2011-2013.

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A)

B)
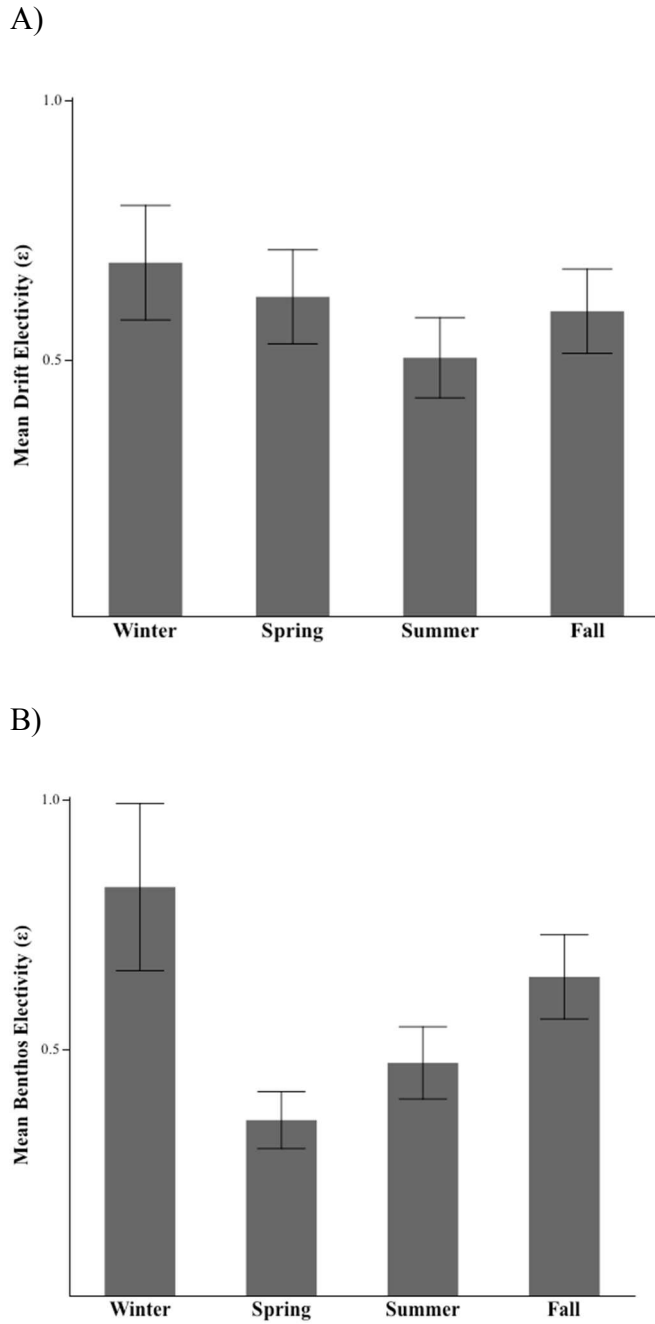
Figure 19. Mean electivity ($\bar{\varepsilon}$, ± 1 s.e.) of Brown Trout by season as calculated with a Manly-Chesson index for (A) drift (H=2.5, d.f.=3, p=0.45) and (B) benthos (H=9.1, d.f.=3, p=0.03) in Beaver Creek, 2011-2013.

A)

B)
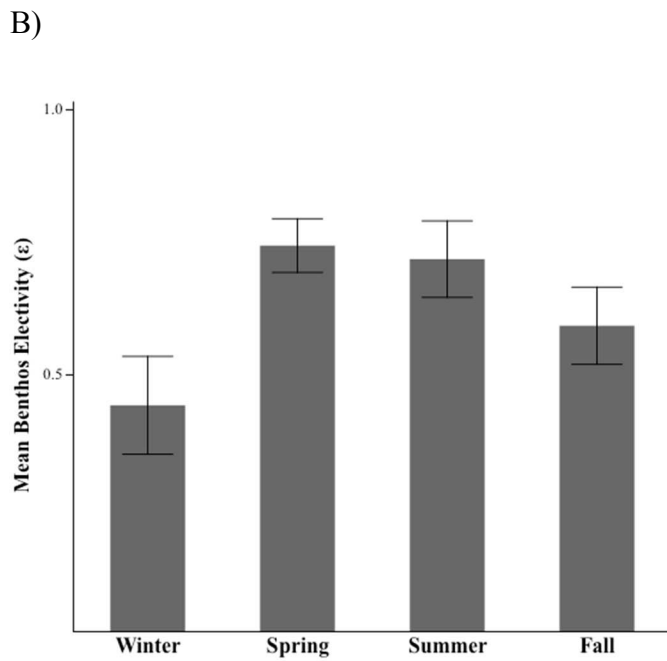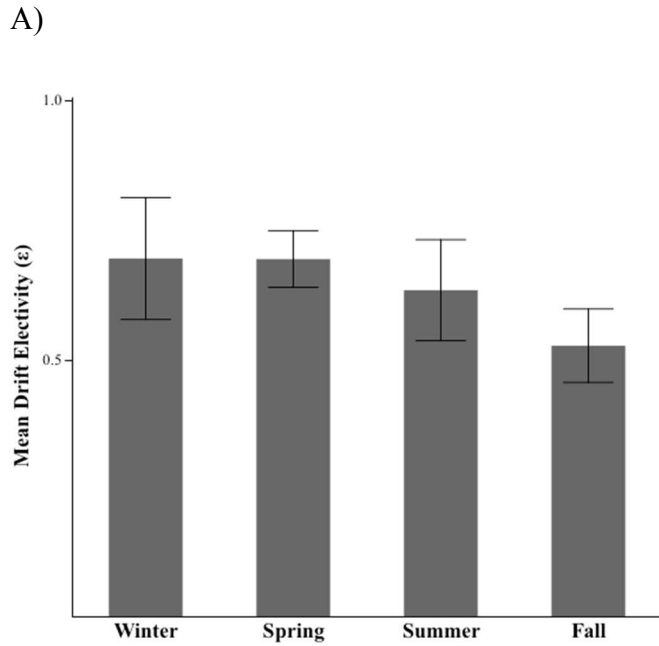
Figure 20. Mean electivity ($\bar{\varepsilon}$, ±1 s.e.) of Brown Trout by season as calculated with a Manly-Chesson index for (A) drift (H=3.6, d.f.=3, p=0.31) and (B) benthos (H=6.7, d.f.=3, p=0.08) in Daley Creek, 2011-2013.

A)
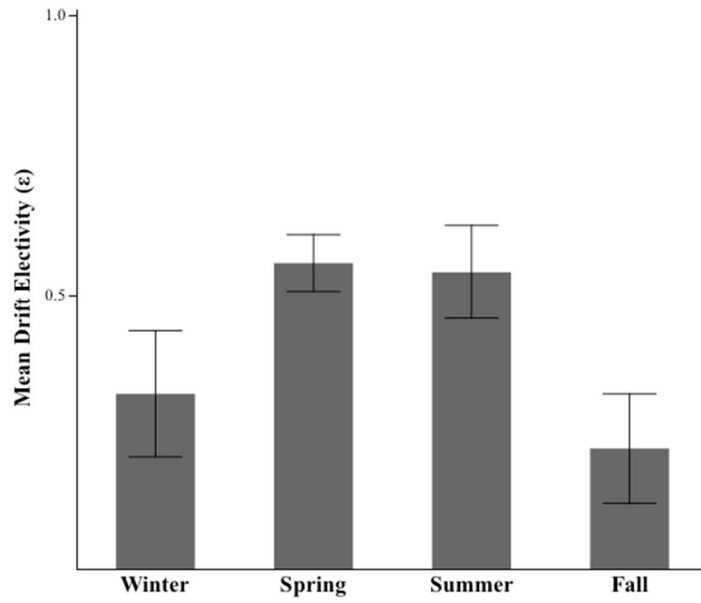
B)
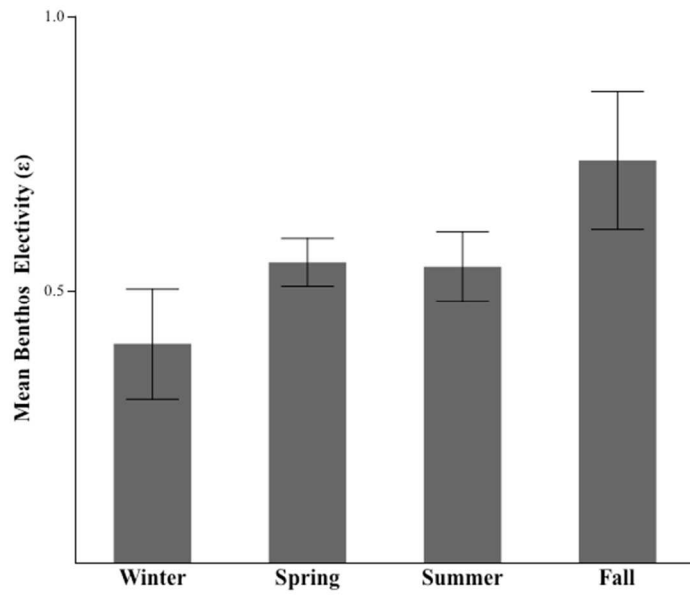
Figure 21. Mean electivity ($\bar{\varepsilon}$, ± 1 s.e.) of Brown Trout by season as calculated with a Manly-Chesson index for (A) drift (H=8.7, d.f.=3, p=0.03) and (B) benthos (H=5.3, d.f.=3, p=0.15) in Garvin Brook, 2011-2013.

A)

B)
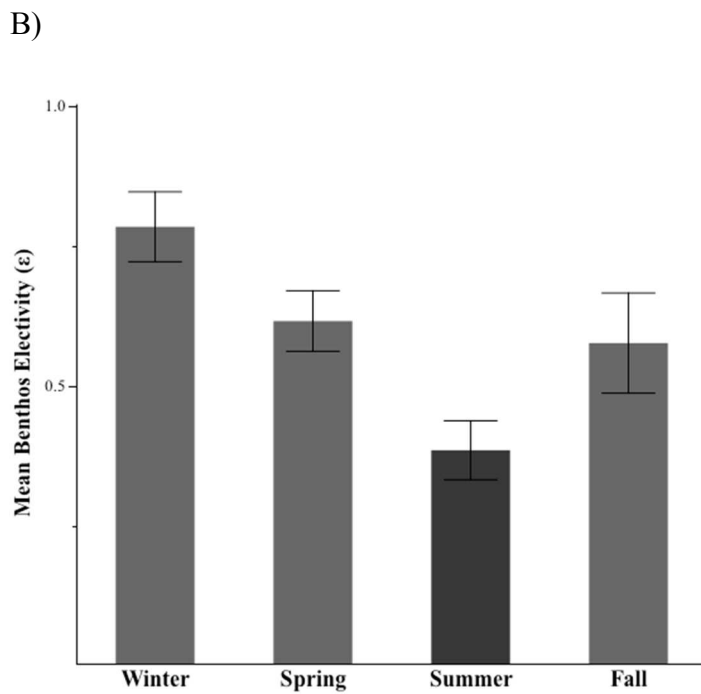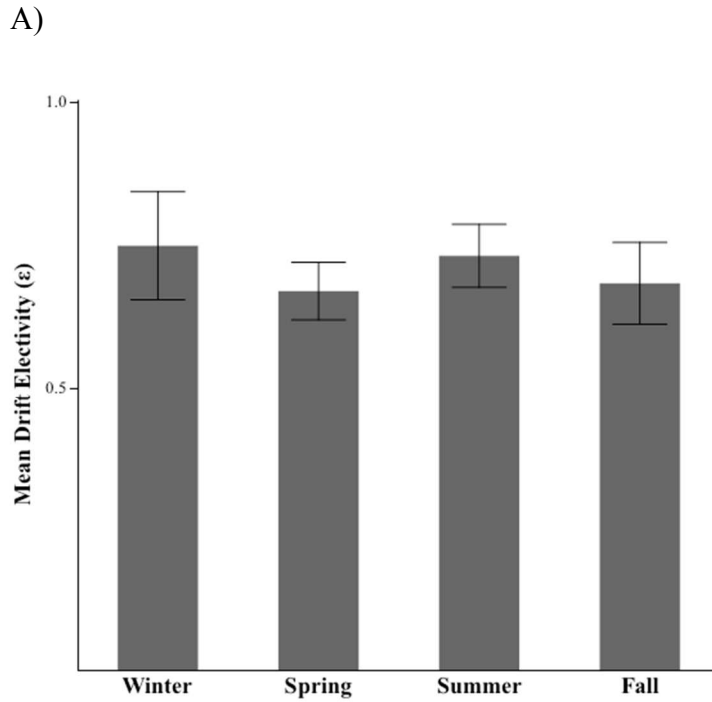
Figure 22. Mean electivity ($\bar{\varepsilon}$, $\pm$1 s.e.) of Brown Trout by season as calculated with a Manly-Chesson index for (A) drift (H=2.6, d.f.=3, p=0.45) and (B) benthos (H=11.0, d.f.=3, p=0.01) in Gribbon Creek, 2011-2013.

A)

B)
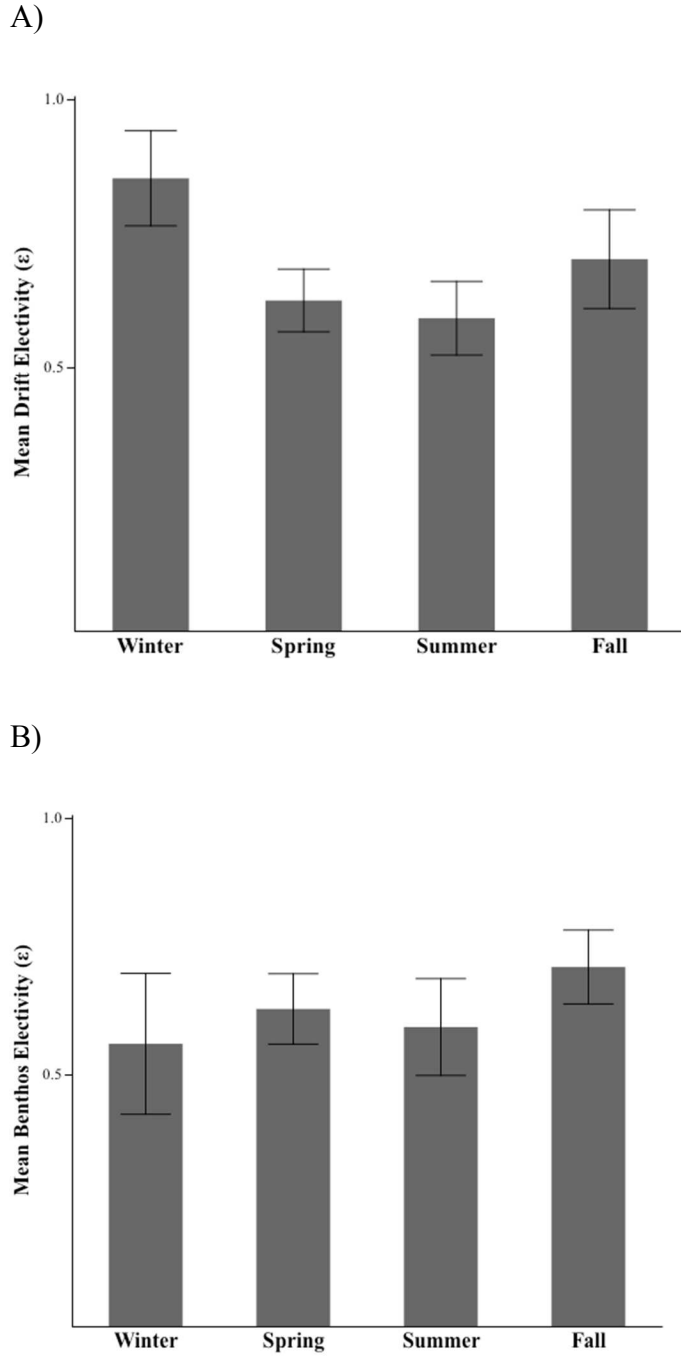
Figure 23. Mean electivity ($\bar{\varepsilon}$, ± 1 s.e.) of Brown Trout by season as calculated with a Manly-Chesson index for (A) drift (H=4.5, d.f.=3, p=0.22) and (B) benthos (H=1.6, d.f.=3, p=0.66) in Trout Run Creek, 2011-2013.
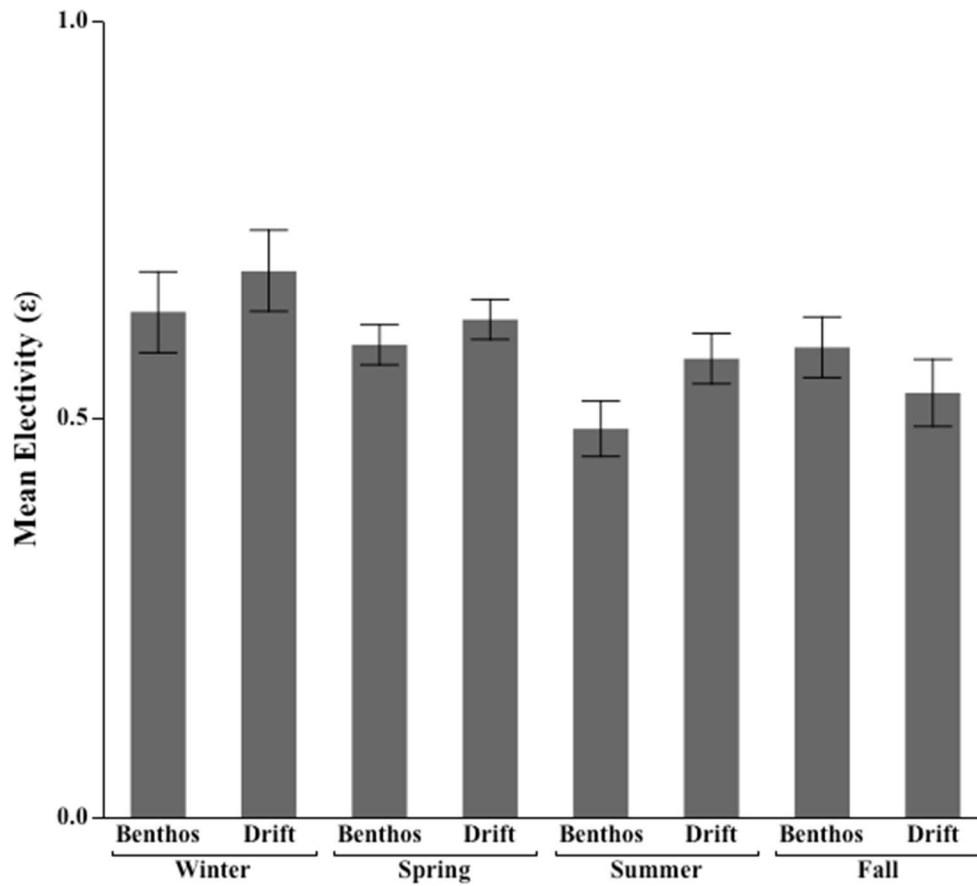
Figure 24. Mean electivity ($\bar{\varepsilon}, \pm 1$ s.e.) of Brown Trout by season as calculated with a Manly-Chesson index of selectivity for benthos (H=8.6, d.f.=3, p=0.04) and drift (H=7.9, d.f.=3, p=0.04) in 5 streams across southeastern Minnesota, 2011-2013.
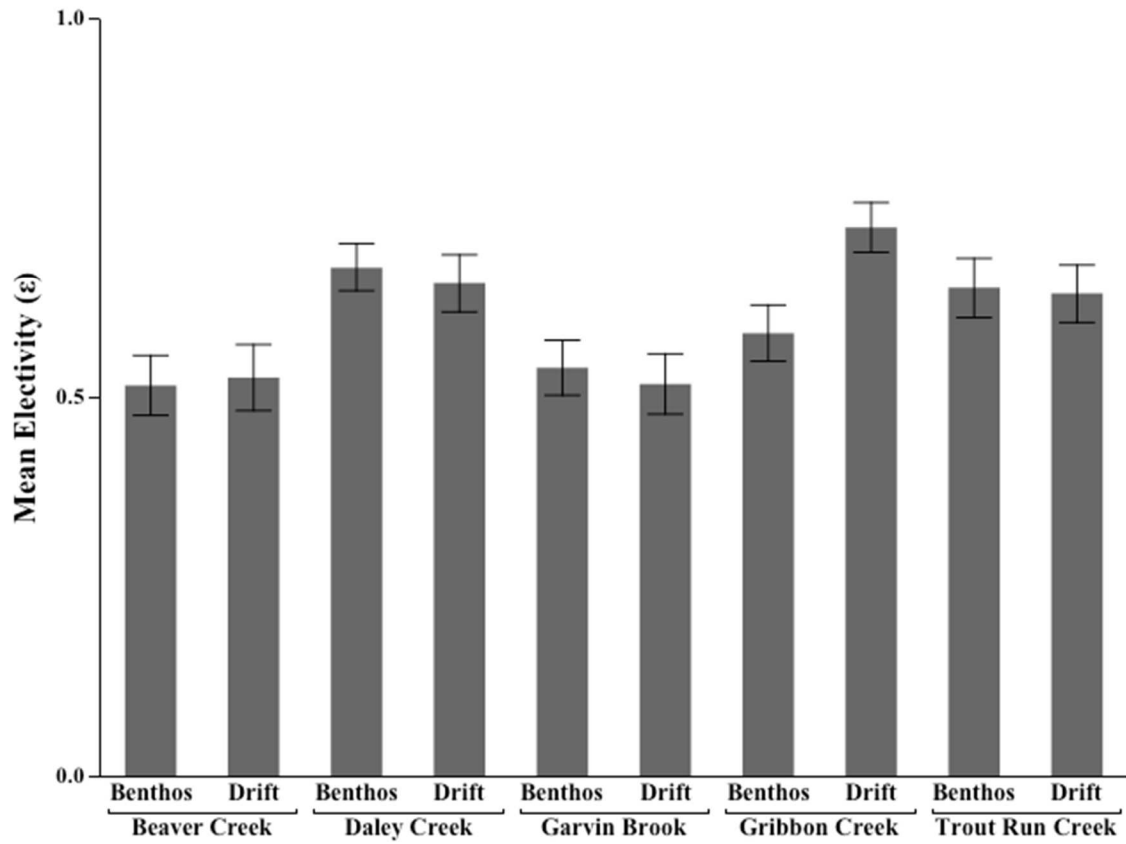
Figure 25. Mean electivity (ε, $\pm$1 s.e.) of Brown Trout as calculated with a Manly-Chesson index for benthos (H=12.6, d.f.=4, p=0.01) and drift (H=23.5, d.f.=4, p<0.01), in five streams across southeastern Minnesota, 2011-2013.
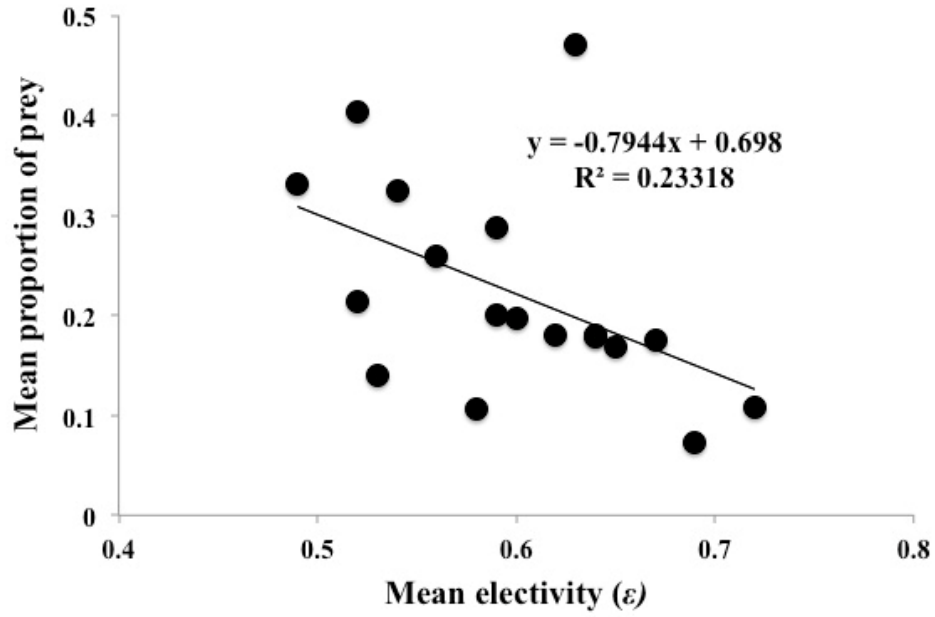
Figure 26. Simple linear regression between mean proportion of total prey available and mean prey electivity across all sample dates, 2011-2013, in five streams in southeastern Minnesota (r^2=0.23, F=4.9, p=0.04).

Epilogue

Groundwater-dominated streams of southeastern Minnesota support highly productive populations of Brown Trout and aquatic macroinvertebrate fauna, but past research has shown that fish growth varies on spatial and temporal scales. As the diet of Brown Trout depends on the availability and abundance of aquatic macroinvertebrates, it is possible that spatial and temporal variations in macroinvertebrate assemblages (e.g. abundance, diversity, distribution) shape patterns in the growth, distribution, fitness, and abundance of Brown Trout populations. In particular, there is evidence that suggests spatial and seasonal variation in winter conditions (including water temperature and prey assemblages) may influence broader patterns of Brown Trout growth in this region. Although studies related to Brown Trout growth, diet, prey availability, and selectivity have been conducted in southeastern Minnesota, no research has addressed all of these factors simultaneously over multiple streams, seasons, and years.

The overall goal of this dissertation was to examine seasonal and spatial patterns in Brown Trout growth, diet, and prey selection, and in the availability of macroinvertebrate prey in six streams that demonstrate a gradient in fish growth. Chapter 1 examined temporal and spatial differences in the growth of Brown Trout, and in the composition of Brown Trout diets, identifying key prey taxa among streams and seasons. Patterns in diet composition among streams were compared with non-metric multidimensional scaling to identify associations between diet and physical stream characteristics, including groundwater input, stream drainage area, and channel slope. In all streams, Brown Trout fed continuously and demonstrated positive growth during most seasons of the year: winter, spring, and summer; and there was a positive relationship between winter growth and groundwater input. Winter emerged as an important period for growth, accounting for at least 20 percent of overall growth in all streams. Also, fish in faster-growing streams tended to achieve more growth during spring and winter than fish in slower-growing streams. Overall, Brown Trout diets contained mostly aquatic macroinvertebrates and demonstrated little seasonal variation within individual streams and when diet data from all streams were aggregated. However, comparisons of winter

and spring diets across all streams revealed stream-specific variation. In general, diets of fish in faster-growing streams were associated with larger-bodied and energy-rich prey, including Gastropods (*Physella*), *Gammarus,* and Limnephilidae), whereas diets of fish in slower-growing streams were associated with smaller-bodied and less energetically-rich prey, including Chironomidae and *Brachycentrus*. Diet composition may be similar in streams that share thermal conditions during spring, and to a lesser extent winter. In contrast to surface-fed streams, groundwater-dominated streams are strongly controlled by thermal inputs that likely shape the community of available prey and regulate growth potential.

Chapter 2 examined seasonal patterns in Brown Trout prey assemblages, including the abundance, diversity, and overlap of macroinvertebrate benthos and drift. Overall, we found that drift and benthos were represented by only a few taxa, including Chironomidae, *Brachycentrus*, and Simuliidae, but that proportions differed across seasons and streams. We used Morisita's Index to compare similarity and diversity, which revealed a higher degree of overlap among seasons, and less overlap among streams. Multiple response permutation procedure analysis, used to evaluate seasonal and spatial variation in assemblage structure, revealed differences in benthos and drift assemblages among streams and seasons, with the most pronounced differences among streams. Abundance of drift and benthos varied significantly, with highest availability in spring and summer, and lowest availability during winter in most streams. We found no significant associations between groundwater input, channel slope, and drainage area with measures of prey diversity and abundance based on simple linear regression. However, non-metric multi-dimensional scaling indicated associations between assemblage composition and physical variables, especially groundwater input. In general, streams with a higher degree of groundwater influence were associated with the occurrence of *Gammarus*.

The goal of Chapter 3 was to identify seasonal and spatial patterns in the availability and selection of macroinvertebrate prey by Brown Trout. Although there was considerable variability in drifting and benthic prey assemblages within streams and seasons, few taxa were dominant in trout diets and the environment. Brown Trout

consistently selected only one or two taxa, including *Physella* and *Gammarus*, while displaying neutral selection or avoiding all other taxa. Foraging patterns suggested a preference toward benthic feeding. Overall electivity toward benthos and drift varied spatially and temporally with a negative relationship between the total proportion of prey available and prey electivity. On a broad scale, there was no relationship between seasonal growth and prey electivity across all streams, but a positive relationship was detected within two of five streams. In general, foraging selection was likely influenced by prey size, location, and energy density.

Our results provide important information about the foraging patterns of Brown Trout, and will be particularly useful in helping fisheries managers identify and manage key macroinvertebrate taxa on a year-round basis. With knowledge about what Brown Trout consume and how they grow on a seasonal basis, fisheries managers can identify key prey items and predict how changes in prey communities may impact trout production. Subsequent changes in prey communities, such as the decline or increase of certain prey types, may influence how a stream is managed. Results from this study, however, stress the importance of a stream-specific approach, as both patterns in growth and diet varied much more considerably within streams than on broader spatial scales. Additionally, since the majority of prey consumed by Brown Trout was aquatic macroinvertebrates rather than terrestrial or allochthonous inputs, managers should consider in-stream management activities and habitat improvements that support the growth and life history of aquatic macroinvertebrates through suitable water quality, healthy macrophyte communities, and coarse woody structures. We provide evidence that growth rates may be higher in streams where thermal regimes are more strongly buffered by groundwater inputs, and that winter and spring may be important seasons that contribute to high growth and productivity. In Minnesota, streams that are more heavily influenced by groundwater may also be more resilient to projected increases in air temperature due to climate change. Thus, managers may choose to allocate limited resources toward management activities that protect the integrity of streams that are buffered by groundwater springs. These actions may include strategies that protect groundwater springs specifically, such as limiting withdrawals and regulating

agricultural, industrial, or urban development in areas where springs are especially abundant.

In addition, our results provide detailed information about the prey resources of Brown Trout and will be particularly useful in helping fisheries managers identify and manage key macroinvertebrate taxa on a year-round basis. For instance, the present study identifies *Gammarus* as commonly available aquatic macroinvertebrate taxon that is particularly abundant in a stream with a high degree of groundwater control and fast growing populations of Brown Trout. Although *Gammarus* may support high productivity of Brown Trout, this taxon has been shown to recover slowly following catastrophic flooding events in southeastern Minnesota. As future climate projections predict stronger, more frequent rainfall events in this region due to climate change, such catastrophic flood events may reduce the distribution and abundance of *Gammarus*. Although mitigating efforts to reduce the impacts of climate change may include the reintroduction of *Gammarus*, along with other taxa linked with high fish productivity, managers should also focus on sustaining healthy assemblages of flood-resistant aquatic macroinvertebrates, such as winter-emerging Chironomids. In addition to being resilient to extreme rainfall and flood events, Chironomids are highly abundant in southeastern Minnesota, providing more than half of the composition of available aquatic macroinvertebrates in many streams throughout the year.

In addition, although only a few taxonomic groups represented a majority of the aquatic macroinvertebrates sampled in this study, we found that the structure of macroinvertebrate assemblages, including diversity and availability, varied significantly across time and space. Differences in the taxonomic composition of prey assemblages were most pronounced between streams, highlighting the inherent limitations of aquatic macroinvertebrates to disperse and recolonize new streams, with terrestrial environments serving as a primary barrier. Therefore, managers should take a stream-specific approach to management efforts that relate to aquatic macroinvertebrate communities, and attempt to mitigate the impacts that climate change, land use, and pollution may have on aquatic macroinvertebrate species that are especially critical for supporting Brown Trout growth and survival.

Lastly, in contrast to other regions, our results suggest that terrestrial macroinvertebrate taxa are unlikely to represent a consistent or abundant food resource for Brown Trout in southeastern Minnesota. Therefore, when attempting to manage food resources that support productive populations of Brown Trout, an emphasis should be placed on in-stream efforts that promote suitable water and habitat quality for benthic macroinvertebrates.

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Appendices

Appendix A. Mean instantaneous growth (G) between sample dates and sample size used to estimate growth of Brown Trout in Beaver Creek.

		1 19 Nov 2010	2 11 Jan 2011	3 16 Mar 2011	4 24 Jun 2011	5 19 Jul 2011	6 14 Aug 2011	7 26 Jan 2012	8 29 Mar 2012	9 05 Jun 2012	10 13 Sep 2012	11 17 Jan 2013	12 22 Apr 2013	13 11 Jun 2013	14 18 Sep 2013
1	19 Nov 2010	–	0.04 N=6	0.09 N=8	0.26 N=11	0.19 N=9	0.27 N=7	0.14 N=10	0.13 N=13	0.19 N=9	0.14 N=7	0.12 N=6	0.04 N=1	- N=0	- N=0
2	11 Jan 2011		–	0.06 N=13	0.20 N=6	0.20 N=10	0.25 N=5	0.13 N=8	0.16 N=8	0.21 N=6	0.14 N=6	0.08 N=5	0.03 N=1	- N=0	- N=0
3	16 Mar 2011			–	0.19 N=1	0.12 N=2	0.12 N=1	0.15 N=2	0.10 N=5	0.13 N=1	0.07 N=1	0.04 N=3	- N=0	- N=0	- N=0
4	24 Jun 2011				–	0.20 N=8	0.22 N=5	0.07 N=6	0.09 N=8	0.15 N=5	0.11 N=7	0.09 N=3	- N=0	- N=0	- N=0
5	19 Jul 2011					–	0.29 N=4	0.07 N=4	0.07 N=6	0.14 N=4	0.11 N=4	0.08 N=4	- N=0	- N=0	- N=0
6	14 Aug 2011						–	0.04 N=7	0.04 N=7	0.16 N=4	0.13 N=5	0.05 N=4	0.07 N=1	- N=0	- N=0
7	26 Jan 2012							–	0.19 N=33	0.20 N=21	0.22 N=25	0.13 N=16	0.17 N=6	0.24 N=2	0.22 N=2
8	29 Mar 2012								–	0.14 N=15	0.13 N=15	0.08 N=10	0.06 N=2	0.04 N=1	0.06 N=1
9	05 Jun 2012									–	0.16 N=13	0.02 N=6	0.06 N=2	- N=0	- N=0
10	13 Sep 2012										–	-0.01 N=12	0.11 N=2	0.10 N=2	0.08 N=1
11	17 Jan 2013											–	0.18 N=12	0.29 N=6	0.34 N=5
12	22 Apr 2013												–	0.24 N=3	0.24 N=2
13	11 Jun 2013													–	0.30 N=5
14	18 Sep 2013														–

Appendix B. Mean instantaneous growth (G) between sample dates and sample size used to estimate Brown Trout growth in Daley Creek.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		06 Jan 2011	5 Feb 2011	26 Mar 2011	13 Jun 2011	21 Jul 2011	23 Sep 2011	22 Jan 2012	04 Apr 2012	14 Jun 2012	23 Sep 2012	12 Jan 2013	20 Apr 2013	27 Jun 2013	30 Sep 2013
1	06 Jan 2011	_	0.17 N=40	0.25 N=39	0.32 N=48	0.28 N=29	0.30 N=20	0.18 N=26	0.22 N=31	0.22 N=19	0.20 N=21	0.19 N=9	0.16 N=5	0.14 N=1	0.17 N=2
2	5 Feb 2011		_	0.35 N=15	0.33 N=15	0.25 N=7	0.27 N=6	0.25 N=8	0.20 N=9	0.23 N=3	0.22 N=6	0.22 N=5	0.10 N=2	0.15 N=1	0.09 N=1
3	26 Mar 2011			_	0.16 N=11	0.21 N=8	0.18 N=5	0.19 N=10	0.20 N=9	0.21 N=6	0.15 N=7	0.18 N=3	0.12 N=1	- N=0	0.06 N=1
4	13 Jun 2011				_	0.21 N=16	0.20 N=10	0.11 N=11	0.15 N=17	0.12 N=5	0.17 N=8	0.10 N=2	0.08 N=1	- N=0	0.07 N=1
5	21 Jul 2011					_	0.10 N=15	0.03 N=11	0.14 N=13	0.09 N=9	0.12 N=11	0.07 N=4	0.11 N=3	- N=0	0.07 N=1
6	23 Sep 2011						_	-0.02 N=10	0.07 N=12	0.10 N=8	0.16 N=8	0.10 N=5	0.07 N=3	- N=0	- N=0
7	22 Jan 2012							_	0.28 N=47	0.27 N=26	0.28 N=28	0.26 N=19	0.23 N=9	0.29 N=5	0.26 N=4
8	04 Apr 2012								_	0.33 N=18	0.31 N=24	0.21 N=20	0.12 N=6	0.22 N=5	0.27 N=4
9	14 Jun 2012									_	0.22 N=13	0.11 N=8	0.08 N=3	- N=0	0.29 N=1
10	23 Sep 2012										_	-0.02 N=15	-0.01 N=5	0.13 N=5	0.11 N=4
11	12 Jan 2013											_	0.12 N=20	0.34 N=9	0.19 N=8
12	20 Apr 2013												_	0.46 N=1	0.40 N=1
13	27 Jun 2013													_	0.26 N=6
14	30 Sep 2013														_

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Appendix C. Mean instantaneous growth (G) between sample dates and sample size used to estimate growth of Brown Trout in in Garvin Brook.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		05 Dec 2010	12 Jan 11	03 Mar 2011	10 May 2011	18 Jun 2011	05 Aug 2011	14 Jan 2012	23 Mar 2012	04 Jun 2012	30 Sep 2012	11 Jan 2013	26 Apr 2013	07 Jun 2013	17 Sep 2013
1	05 Dec 2010	_	-0.14 N=29	-0.01 N=23	- N=0	0.23 N=12	0.34 N=10	0.25 N=10	0.29 N=8	0.24 N=4	0.25 N=5	- N=0	0.15 N=1	0.17 N=3	0.23 N=1
2	12 Jan 11		_	0.07 N=29	- N=0	0.29 N=15	0.32 N=8	0.24 N=8	0.25 N=3	0.17 N=3	0.21 N-5	0.01 N=1	0.12 N=3	0.14 N=2	0.13 N=1
3	03 Mar 2011			_	- N=0	0.30 N=8	0.29 N=4	0.21 N=5	0.23 N=1	0.16 N=1	0.19 N=2	- N=0	0.15 N=2	0.15 N=2	0.14 N=1
4	10 May 2011				_	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=1
5	18 Jun 2011					_	0.41 N=8	0.18 N=9	0.17 N=4	0.15 N=6	0.17 N=4	0.03 N=1	0.10 N=0	0.15 N=3	0.17 N=2
6	05 Aug 2011						_	0.16 N=5	0.09 N=1	0.20 N=3	0.16 N=3	- N=0	0.11 N=2	0.12 N=10	0.12 N=1
7	14 Jan 2012							_	0.28 N=48	0.27 N=35	0.22 N=32	0.18 N=20	0.17 N=19	0.14 N=10	0.17 N=5
8	23 Mar 2012								_	0.22 N=16	0.18 N=11	0.13 N=11	0.12 N=9	0.12 N=7	0.06 N=2
9	04 Jun 2012									_	0.18 N=15	0.09 N=10	0.09 N=8	0.09 N=4	0.10 N=3
10	30 Sep 2012										_	-0.06 N=8	0.05 N=12	0.05 N=6	0.15 N=4
11	11 Jan 2013											_	0.16 N=48	0.18 N=22	0.18 N=5
12	26 Apr 2013												_	0.13 N=11	0.11 N=5
13	07 Jun 2013													_	0.22 N=4
14	17 Sep 2013														_

Appendix D. Mean instantaneous growth (G) between sample dates and sample size used to estimate growth of Brown Trout in Gribbon Creek.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		17 Dec 2010	4 Feb 2011	25 Mar 2011	16 Jun 2011	18 Jul 2011	28 Aug 2011	31 Jan 2012	6 Apr 2012	7 Jun 2012	22 Sep 2012	12 Jan 2013	20 Apr 2013	26 Jun 2013	24 Sept 2013
1	17 Dec 2010	_	-0.04 N=10	0.15 N=28	0.20 N=15	0.15 N=12	0.22 N=12	0.17 N=13	0.18 N=9	0.13 N=9	0.10 N=5	0.13 N=4	0.06 N=1	- N=0	0.12 N=2
2	4 Feb 2011		_	0.30 N=10	0.20 N=4	0.12 N=4	0.16 N=5	0.11 N=3	0.10 N=1	0.12 N=1	- N=0	- N=0	- N=0	- N=0	- N=0
3	25 Mar 2011			_	0.22 N=8	0.14 N=7	0.20 N=4	0.13 N=6	0.14 N=5	0.14 N=5	0.25 N=1	0.16 N=3	- N=0	- N=0	0.18 N=1
4	16 Jun 2011				_	0.02 N=8	0.14 N=4	0.21 N=5	0.10 N=5	0.09 N=4	0.12 N=2	0.13 N=2	- N=0	- N=0	0.15 N=1
5	18 Jul 2011					_	0.01 N=2	0 N=4	0.02 N=3	0.06 N=5	0.05 N=1	- N=0	- N=0	- N=0	- N=0
6	28 Aug 2011						_	0.02 N=3	0.07 N=5	0.05 N=3	0.02 N=1	- N=0	- N=0	- N=0	0.04 N=1
7	31 Jan 2012							_	0.22 N=53	0.23 N=19	0.20 N=20	0.14 N=11	0.12 N=5	0.25 N=1	0.12 N=3
8	6 Apr 2012								_	0.28 N=14	0.26 N=16	0.16 N=8	0.14 N=5	0.25 N=1	0.12 N=1
9	7 Jun 2012									_	0.14 N=11	0.15 N=4	0.18 N=3	- N=0	0.10 N=3
10	22 Sep 2012										_	0.10 N=9	0.12 N=5	0.13 N=1	0.10 N=3
11	12 Jan 2013											_	0.13 N=17	- N=0	0.23 N=10
12	20 Apr 2013												_	0.33 N=3	0.20 N=3
13	26 Jun 2013													_	0.22 N=1
14	24 Sept 2013														_

Appendix E. Mean growth (G) between sample dates and sample size used to estimate growth of Brown Trout in in Trout Run Creek.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		18 Dec 2010	28 Jan 2011	02 Apr 2011	08 Jun 2011	13 Jun 2011	28 Aug 2011	15 Jan 2012	24 Mar 2012	13 Jun 2012	09 Sep 2012	16 Jan 2013	23 Apr 2013	10 Jun 2013	29 Sep 2013
1	18 Dec 2010	_	-0.14 N=8	-0.01 N=2	-0.07 N=1	0.09 N=5	0.02 N=5	0.03 N=7	-0.15 N=3	0.09 N=4	0.15 N=3	0.11 N=3	0.11 N=3	- N=0	0.11 N=1
2	28 Jan 2011		_	0.09 N=2	0.24 N=2	0.15 N=3	0.01 N=4	0.13 N=9	0.09 N=3	0.19 N=3	0.18 N=3	0.21 N=5	0.15 N=2	- N=0	0.09 N=2
3	02 Apr 2011			_	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0
4	08 Jun 2011				_	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0	- N=0
5	13 Jun 2011					_	-0.18 N=1	0.12 N=2	0.03 N=1	0.20 N=1	0.21 N=1	0.23 N=1	0.19 N=1	- N=0	- N=0
6	28 Aug 2011						_	0.08 N=2	0.07 N=3	0.12 N=3	0.25 N=1	0.15 N=2	0.08 N=1	- N=0	0.14 N=1
7	15 Jan 2012							_	0.18 N=18	0.14 N=17	0.19 N=34	0.13 N=27	0.08 N=5	- N=0	0.10 N=10
8	24 Mar 2012								_	0.04 N=5	0.19 N=6	0.12 N=9	0.05 N=2	0.08 N=1	0.06 N=3
9	13 Jun 2012									_	0.36 N=12	0.12 N=10	0.10 N=3	0.06 N=2	0.03 N=2
10	09 Sep 2012										_	0.03 N=17	04 N=4	- N=0	.012 N=5
11	16 Jan 2013											_	0.05 N=14	0.09 N=4	0.04 N=8
12	23 Apr 2013												_		0.10 N=5
13	10 Jun 2013													_	
14	29 Sep 2013														_

Appendix F. Seasonal variation in diet composition across six streams in southeastern Minnesota, 2010-2013 based on a MRPP test.

		Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall			0.71	0.72	0.009	0.12
Winter (N=21)		0.70				
Spring (N=31)		0.72				
Summer (N=18)		0.68				
Fall (N=13)		0.73				
Pairwise	Winter (N=21)	0.75	0.73	0.74	0.01	0.10
	Spring (N=31)	0.70				
	Winter (N=21)	0.70	0.69	0.70	0.01	0.15
	Summer (N=18)	0.69				
	Winter (N=21)	0.70	0.71	0.71	-0.01	0.80
	Fall (N=13)	0.74				
	Spring (N=31)	0.75	0.73	0.74	0.02	0.02
	Summer (N=18)	0.69				
	Spring (N=31)	0.75	0.74	0.74	-0.007	0.83
	Fall (N=13)	0.74				
	Summer (N=18)	0.69	0.71	0.71	0.001	0.39
	Fall (N=13)	0.73				
By stream						
Beaver	Winter (N=3)	0.55	0.59	0.70	0.15	0.01
	Spring (N=4)	0.67				
	Summer (N=5)	0.55				
	Fall (N=1)	NA				
Daley	Winter (N=4)	0.24	0.55	0.57	0.04	0.22
	Spring (N=5)	0.58				
	Summer (N=2)	0.88				
	Fall (N=3)	0.69				
Garvin	Winter (N=4)	0.68	0.71	0.62	-0.14	0.98
	Spring (N=6)	0.62				
	Summer (N=2)	0.87				
	Fall (N=2)	0.83				
Gribbon	Winter (N=3)	0.57	0.68	0.69	0.01	0.36
	Spring (N=5)	0.72				
	Summer (N=3)	0.78				
	Fall (N=3)	0.64				
Rush	Winter (N=4)	0.88	0.77	0.78	0.01	0.34
	Spring (N=5)	0.89				
	Summer (N=3)	0.69				
	Fall (N=2)	0.35				
Trout Run	Winter (N=3)	0.51	0.53	0.51	-0.05	0.69
	Spring (N=6)	0.51				
	Summer (N=3)	0.60				
	Fall (N=2)	0.54				

Appendix G. Variation in diet composition across six streams in southeastern Minnesota, 2010-2013, based on a MRPP test.

	Distance[a]	Obs Delta[b]	Exp Delta[c]	A[d]	P-value[e]
Overall		0.63	0.72	0.12	0.0002
Beaver (N=13)	0.67				
Daley (N=14)	0.57				
Garvin (N=14)	0.60				
Gribbon (N=14)	0.67				
Rush (N=14)	0.77				
Trout Run (N=14)	0.51				
Pairwise					
Beaver (N=13)	0.70	0.64	0.72	0.12	0.0002
Daley (N=14)	0.58				
Rush (N=14)	0.78	0.65	0.73	0.11	0.0002
Trout Run (14)	0.52				
Beaver (N=13)	0.70	0.66	0.68	0.03	0.03
Garvin (N=14)	0.62				
Beaver (N=13)	0.70	0.69	0.73	0.05	0.01
Gribbon (N=14)	0.69				
Beaver (N=13)	0.70	0.60	0.64	0.05	0.002
Trout Run (N=14)	0.52				
Daley (N=14)	0.58	0.60	0.66	0.09	0.0004
Garvin (N=14)	0.62				
Daley (N=14)	0.57	0.62	0.70	0.11	0.0006
Gribbon (N=14)	0.67				
Daley (N=14)	0.58	0.68	0.77	0.12	0.0002
Rush (N=14)	0.78				
Daley (N=14)	0.57	0.54	0.60	0.09	0.001
Trout Run (N=14)	0.51				
Gribbon (N=14)	0.69	0.65	0.70	0.07	0.0008
Garvin (N=14)	0.62				
Garvin (N=14)	0.62	0.70	0.76	0.08	0.0004
Rush (N=14)	0.78				
Garvin (N=14)	0.62	0.57	0.58	0.02	0.09
Trout Run (N=14)	0.52				

Gribbon (N=14)	0.69	0.74	0.75	0.02	0.04
Rush (N=14)	0.78				
Gribbon (N=14)	0.69	0.60	0.65	0.09	0.0004
Trout Run (N=14)	0.51				
By season					
Fall		**0.62**	**0.73**	**0.15**	**0.05**
Beaver (N=1)	NA				
Daley (N=3)	0.70				
Garvin (N=2)	0.84				
Gribbon (N=3)	0.64				
Rush (N=)	0.37				
Trout Run (N=2)	0.52				
Winter		0.54	0.69	0.22	0.001
Beaver (N=3)	0.31				
Daley (N=4)	0.22				
Garvin (N=4)	0.68				
Gribbon (N=3)	0.57				
Rush (N=)	0.85				
Trout Run (N=3)	0.51				
Spring		**0.66**	**0.75**	**0.11**	**0.0008**
Beaver (N=4)	0.67				
Daley (N=5)	0.59				
Garvin (N=6)	0.63				
Gribbon (N=5)	0.72				
Rush (N=)	0.89				
Trout Run (N=6)	0.53				
Summer		0.69	0.69	-0.008	0.54
Beaver (N=5)	0.55				
Daley (N=2)	0.89				
Garvin (N=2)	0.87				
Gribbon (N=3)	0.78				
Rush (N=)	0.68				
Trout Run (N=3)	0.61				

Appendix H. Mean prey taxa by number per fish in fall diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	7.7	0.3	9.3	2.7	1.6	3.0
Glossosoma	0.2	0.01	2.1	0.38	0	0.03
Hydroptilidae	0	0.02	0	0.03	0	1.5
Limnephilidae	0.3	0.13	0.73	0.94	6.9	0
Other Trichoptera	0.03	0	2.1	0.09	0.12	0.2
Trichoptera total	8.3	0.48	14	4.1	8.7	4.8
Chironomidae	0	27	15	2.9	1.8	17
Dixidae	0	0.01	0	0.06	0.42	0
Empididae	0	0.01	0.03	0.26	0	0
Simuliidae	0	0.44	2.2	0.16	0.29	0.03
Other Diptera	0.03	0.16	0.4	0.02	0.12	0.05
Diptera total	0.03	27	18	3.4	2.7	17
Dytiscidae	0.03	0.01	0	0.03	0	0.12
Elmidae	0.03	0.11	0.07	0	0	0
Coccinelidae	0	0	0	0	0	0.13
Other Coleoptera	0.03	0.04	0.05	0.04	0.15	0.07
Coleoptera total	0.10	0.17	0.12	0.08	0.15	0.32
Belostomatidae	0	0.02	0.32	0	0.08	0
Corixidae	0	0.02	0.15	0	0	0
Aphididae	0	0.17	0	0	0.08	0
Other Hemiptera	0	0.22	0.18	0.01	0.15	0.18
Hemiptera total	0	0.43	0.65	0.01	0.31	0.18
Baetis	0.10	1.8	2.3	1.2	0.04	0.63
Other Ephemeroptera	0.03	0	0	0.06	0	0
Ephemeroptera total	0.13	1.8	2.3	1.3	0.04	0.63
Lepidotera	0	0	0.13	0	0	0
Hymenoptera	0	0.24	0.25	0	0.15	0.08
Gastropoda	0.07	0.82	2.3	6.9	1.9	0.83
Gammarus	0.17	6.2	3.2	0.82	0	1.6
Arachnida	0	0.08	0.58	0.08	0.38	0.12
Eggs	0.07	0	0	0	0	0.10
Misc total	0	0.29	0.08	0.12	0.08	0.08
TOTAL	**8.97**	**37.98**	**41.27**	**16.79**	**14.38**	**25.82**

Appendix I. Mean prey taxa by number per fish in winter diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	6.1	0.17	16	4.2	0.88	4.0
Glossosoma	0.58	0.08	0.88	1.0	0.1	0.03
Hydropsychidae	0.14	0	0	0.03	0	0
Limnephilidae	0.79	0.24	0.34	0.77	1.4	0.05
Odontoceridae	0	0.21	0	0	0	0
Uenoidae	0	0.26	0	0	0	0
Phyrganeidae	0.02	0.01	0.02	0.27	0	0
Other Trichoptera	0.04	0.08	1.4	0.02	0	0.02
Trichoptera total	7.7	1.0	19	6.3	2.4	4.1
Chironomidae	12	9.0	9.5	0.58	0.26	4.7
Empididae	0.03	0.12	0.10	0.03	0	0
Simuliidae	1.8	0.05	1.6	0.2	0.26	0.08
Other Diptera	0.08	0.12	0.36	0.07	0.05	0.07
Diptera total	14	9.3	12	0.88	0.57	4.8
Halipidae	0	0	0.01	0	0.23	0.03
Other Coleoptera	0.12	0.01	0.1	0.08	0.08	0.08
Coleoptera total	0.12	0.01	0.11	0.08	0.30	0.11
Belostomatidae	0.06	0	0.21	0	0	0
Corixidae	0.01	0	0.19	0	0	0
Other Hemiptera	0	0	0.13	0	0	0
Hemiptera total	0.07	0	0.53	0	0	0
Baetis	0.32	1.7	1.7	0.47	0.3	0.08
Ephemeroptera total	0.37	1.7	1.7	0.52	0.3	0.08
Capniidae	0.22	0	0	0.06	0	0
Other Plecoptera	0.28	0	0	0.04	0	0
Plecoptera total	0.5	0	0	0.1	0	0
Gastropoda	0.24	1.9	1.6	4.8	1.4	1.5
Gammarus	0.6	9.5	2.5	0.91	0.25	0.79
Hydracarina	0.51	0	0.34	0.13	0	0
Eggs	0	0.03	0	0	0	0.10
Fish	0.14	0.01	0.02	0.04	0.05	0.15
Misc total	0.07	0.06	0.40	0.09	0	0.01
TOTAL	**24.6**	**22.3**	**42.3**	**13.8**	**5.2**	**34.4**

Appendix J. Mean prey taxa by number per fish in spring diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	0.86	0.42	16	2.9	3.9	2.7
Microsema	0.66	0	0.20	0.2	0	0.07
Glossosoma	0.51	0.11	0.97	0.61	0.2	0.02
Hydropsychidae	0.76	0.01	0.03	0.04	0.11	0.01
Hyroptilidae	1.2	0.01	0.77	0.06	0	1.9
Leptoceridae	0.09	0	0.04	0.01	0.16	0
Limnephilidae	3.6	0.74	0.14	1.9	4.3	0.42
Other Trichoptera	0.38	0.07	0.36	0.06	0.09	0
Trichoptera total	8	1.4	18	5.8	8.8	5.1
Ceratopogonidae	0.07	0	0.05	3.9	0	0.12
Chironomidae	14	3.3	17	11	2.2	20
Empididae	0.13	0.33	0.04	0.03	0	0.05
Simuliidae	0.44	0.86	0.48	0.34	0.12	1.5
Tabanidae	0.36	0.01	0.06	0	0.05	0.13
Tipulidae	0.13	0.06	0.11	0.12	0.59	0.14
Other Diptera	0.41	0.03	0.27	0.43	0.06	0.07
Diptera total	15	4.6	18	16	3.0	22
Curculionidae	0.06	0.03	0.01	0.01	0.18	0.03
Dytiscidae	0.07	0.05	0.29	0.16	0	0.19
Elmidae	0.31	0.02	0.19	0.03	0.1	0.02
Halipidae	0.08	0.01	0.04	0.01	0.08	0.18
Staphylinidae	0.10	0	0.27	0.01	0	0.03
Chrysomelidae	0.16	0.01	0.02	0.18	0	0
Other Coleoptera	0.17	0.06	0.12	0.13	0.24	0.07
Coleoptera total	0.93	0.16	0.94	0.52	0.60	0.51
Hemiptera total	0.29	0.04	0.59	0.07	0.65	0.05
Baetis	1.7	0.82	3.4	1.7	2.7	0.36
Ephemerellidae	0.28	0.05	0.29	0.24	0	0
Heptageniidae	0.13	0	0	0	0	0
Other Emphemeroptera	0.08	0.01	0	0.13	0	0
Ephemeroptera total	2.2	0.87	3.7	2.1	2.7	0.36
Perlidae	1.2	0	0.01	0	0	0
Perlodidae	0.17	0	0	0	0	0
Plecoptera total	1.3	0	0.01	0	0	0
Lepidoptera	0.12	0.01	0.01	0	0	0.01
Hymenoptera	0.17	0.01	0.16	0.08	0.09	0.08
Gastropoda	0.38	1.2	0.49	4.9	1.6	1.4
Gammarus	0.32	14	2.1	1.1	0	2.2
Other Isopoda	0.03	0.03	0.02	0.05	0.04	0.13
Hydracarina	0.57	0.48	0.70	0.18	0.61	0.86
Hirudinea	0.01	0.03	0.01	0.84	0	0.02
Diploda	0.07	0	0.09	0.01	0.45	0.03
Fish	0.04	0.02	0.05	0.02	0.17	0.06
Misc total	0.29	0.05	0.19	0.17	0.18	0.13
TOTAL	**29.98**	**23.03**	**45.62**	**31.57**	**18.69**	**33.26**

Appendix K. Mean prey taxa by number per fish in summer diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	7.1	0.3	15	3.8	2.9	10
Microsema	0.05	0	0	0.3	0	0
Glossosoma	1.1	0.03	1.1	1.7	0	0
Hydropsychidae	0.35	0	0.05	0.07	0.09	0
Hyroptilidae	2.3	0	0.20	0.09	0.17	0.78
Limnephilidae	0.14	0.23	0.03	0.41	1.23	0
Other Trichoptera	0.18	0.10	0.02	0.08	0.07	0.14
Trichoptera total	11	0.62	17	6.4	4.5	11
Chironomidae	6.4	3.8	38	1.4	1.1	49
Simuliidae	0.46	0.25	0.55	0.21	0.59	0.61
Tabanidae	0.44	0.02	0.07	0.02	0	0.02
Tipulidae	0.23	0.13	0	0.10	0.07	0.06
Other Diptera	0.09	0.1	0.15	0.10	0.10	0.19
Diptera total	7.6	4.3	39	1.9	1.9	50
Curculionidae	0.11	0.15	0	0.02	0.19	0.03
Dytiscidae	0.31	0.22	0.12	0.06	0.13	0.11
Elmidae	0.29	0.15	0.15	0.05	0.34	0.1
Halipidae	0.01	0	0.08	0	0.22	0.02
Chrysomelidae	0.08	0	0.02	0	0.19	0
Other Coleoptera	0.06	0.12	0.02	0.02	0.03	0.01
Coleoptera total	0.86	0.63	0.38	0.15	1.1	0.27
Corixidae	1.1	0.12	1.4	0.03	0.07	0.07
Other Hemiptera	0.14	0.13	0.03	0.11	0.28	0.04
Hemiptera total	1.2	0.25	1.4	0.14	0.34	0.11
Baetis	1.2	0.82	2.3	0.54	0.03	0.77
Other Ephemeroptera	0.03	0.02	0.02	0.01	0	0
Ephemeroptera total	1.3	0.85	2.3	0.56	0.03	0.77
Isoperla	0.02	0	0	0	0.13	0
Other Plecoptera	0	0	0	0.02	0	0
Plecoptera total	0.02	0	0	0.02	0.13	0
Pyralidae	0.01	0.40	0	0.02	0.03	0
Other Lepidoptera	0.01	0	0	0	0	0
Lepidoptera	0.01	0.40	0	0.02	0.03	0
Hymemoptera	1.5	1.5	0.07	0.24	0.63	0.61
Gastropoda	3.3	0.20	0.52	2.3	4.3	4.1
Gammarus	0.79	3.5	5.4	4.1	0	1.2
Arachnida	1.1	3.6	5.4	4.2	1.0	2.1
Oligochaeta	0.04	0.57	0	1.4	0	0.01
Nematoda	0.05	0.13	0	0.02	0.03	0.11
Diploda	0.05	0.03	0	0.10	0.23	0
Fish	0.09	0.02	0.08	0	0.20	0.01
Misc total	0.07	0.12	0.13	0.14	0.06	0.05
TOTAL	28.4	13.3	66.2	17.6	14.5	69.3

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Appendix L. Mean dry mass (mg) per fish of invertebrate prey taxa in fall diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	7.0	0.23	8.2	2.5	0.46	2.8
Glossosoma	0.36	0.01	2.0	0.61	0	0
Hydropsychidae	0	0.01	0	0.02	0	0.49
Limnephilidae	0	0.30	5.8	9.8	4.8	0
Trichoptera total	7.4	0.54	16	13	5.3	3.3
Chironomidae	0	2.9	1.4	0.74	0.12	0.56
Dixidae	0	0.04	0	0.18	0.97	0
Empididae	0	0	0.03	1.6	0	0
Simuliidae	0	0.11	1.0	0.17	0.11	0.02
Other Diptera	0	0.04	0.11	0	0.02	0.01
Diptera total	0	3.0	2.6	2.7	1.2	0.59
Dytiscidae	0	0	0	0.28	0	0.18
Hydrophilidae	0	0	0.06	0	0.11	0
Coccinellidae	0	0	0	0	0	0.38
Chrysomelidae	0	0.11	0	0.19	0.56	0
Other Coleoptera	0	0.11	0.09	0	0.12	0.10
Coleoptera total	0	0.23	0.15	0.47	0.78	0.66
Belostomatidae	0	2.3	18	0	4.9	0
Gerridae	0	0	0	0.10	0	0
Saldidae	0	0	0.03	0	0.65	0
Other Hemiptera	0	0.15	0.13	0	0.06	0
Hemiptera total	0	2.4	18	0.11	5.7	0
Baetis	0.23	4.6	4.6	5.7	0.02	1.3
Leptophlebiidae	0	0	0	0.21	0	0
Ephemerellidae	0.30	0	0.06	0.03	0	0
Ephemeroptera total	0.53	4.6	4.7	5.9	0.02	1.3
Lestidae	0	0.11	0	0	0	0
Odonata total	0	0.11	0	0	0	0
Pyralidae	0	0	0.65	0	0	0
Lepidopteral total	0	0	0.65	0	0	0
Formicidae	0	0.56	0.92	0	0.51	0.57
Apidae	0	4.4	2.6	0	0	0
Hymenoptera total	0	4.9	3.6	0	0.51	0.57
Gastropoda	0	2.5	8.0	42	0.78	6.0
Gammarus	0.48	9.9	10	1.2	0	6.2
Hirudinea	0	0.48	0	0.11	0	0
Oligochaeta	0	0.10	0	0	0	0
Orthoptera	0	0.50	0	0	0	0
Diploda	0	1.2	0	0	0	0
Misc total	0	0.03	0.02	0.06	0.01	0
TOTAL	**8.4**	**30.5**	**63.8**	**65.8**	**14.2**	**18.6**

Appendix M. Mean dry mass (mg) per fish of invertebrate prey taxa in winter diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	5.3	0.03	12	2.5	0.51	2.5
Molannidae	0	0	0	0.18	0	0
Glossosoma	1.1	0.11	1.9	1.5	0.17	0
Limnephilidae	16	3.7	4.2	5.6	4.0	0.49
Lepidostomatidae	0	0.12	0	0	0	0
Odontoceridae	0	2.3	0	0	0	0
Phryganeidae	0.29	0	0	2.5	0	0
Trichoptera total	23	6.3	18	12	4.6	3.0
Chironomidae	1.6	1.2	0.59	0.01	0.03	0.55
Simuliidae	0.4	0.01	0.33	0.08	0.05	0.02
Tipulidae	0.11	0.02	0.09	0.07	0.03	0.09
Diptera total	2.2	1.2	1.0	0.16	0.10	0.67
Dytiscidae	0	0	0	0.84	0.43	0
Halipidae	0	0	0	0	0.87	0.09
Hydrophilidae	0.15	0	0.03	0	0.03	0.06
Chrysomelidae	0	0	0.16	0	0	0
Coleoptera total	0.15	0	0.19	0.84	1.3	0.15
Belostomatidae	2.3	0	5.3	0	0	0
Hemiptera total	2.3	0	5.3	0	0	0
Baetis	0.62	1.9	2.5	0.28	0.43	0.14
Ephemeroptera total	0.62	1.9	2.5	0.28	0.43	0.14
Capnidae	0.16	0	0	0.04	0	0
Perlidae	0.12	0	0	0	0	0
Perlodidae	0	0	0	0.25	0	0
Plecoptera total	0.29	0	0	0.29	0	0
Hymenoptera	0	0	0.26	0	0	0
Gastropoda	0.36	2.9	10	20	8.0	3.5
Gammarus	2.0	22	6.7	2.1	0.15	1.7
Oligochaeta	0	0.12	0	0	0	0
Misc total	0.22	0.09	0.16	0.21	0	0.05
TOTAL	**30.8**	**34.4**	**44.5**	**36.1**	**14.6**	**9.3**

Appendix N. Mean dry mass (mg) per fish of invertebrate prey taxa in spring diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	0.37	0.07	11	2.2	1.6	0.51
Micrasema	0.22	0	0.1	0.04	0	0.03
Glossosoma	0.23	0.2	1.1	0.79	0.34	0.02
Hydropsychidae	1.2	0	0.08	0.04	0.06	0.01
Hydroptilidae	0.29	0	0.25	0.02	0	0.81
Limnephilidae	22	2.8	0.87	24	15	0.87
Phryganeidae	0.24	0.1	0	0.05	0.49	0
Other Trichoptera	0.14	0	0.02	0.01	0.1	0
Trichoptera total	24	3.2	13	27	18	2.2
Ceratopogonidae	0.04	0	0.04	1.9	0	0.1
Chironomidae	0.58	0.34	0.84	0.98	0.37	1.9
Empididae	0.06	0.22	0.03	0.01	0	0.05
Simuliidae	0.07	0.24	0.13	0.12	0.06	0.25
Stratiomydiae	0.05	0	0.14	0.02	0.01	0
Muscidae	0	0	0	0	0	0.12
Tabanidae	0.68	0.02	0.13	0	0.08	1.2
Tipulidae	0.76	0.07	0.21	0.03	2.2	0.33
Diptera total	2.3	0.89	1.54	3.1	2.6	3.9
Dryopidae	0.12	0.01	0.05	0.02	0	0.03
Curculionidae	0.05	0.08	0.02	0.01	0.32	0.10
Dytiscidae	0.36	0.28	8.6	0.18	0	0.77
Elmidae	0.40	0.01	0.17	0.03	0.04	0.01
Gyrinidae	0.27	0	0.04	0	0.06	0
Halipidae	0.11	0.01	0.04	0.03	0.18	0.36
Hydrophilidae	0.52	0	0.20	0.05	0.12	0.01
Staphylinidae	0.09	0	0.24	0	0	0.03
Chrysomelidae	2.0	0.17	0.33	4.7	0	0
Coleoptera total	4.0	0.55	9.7	5.0	0.73	1.3
Belostomatidae	1.3	0	2.9	0	0	0.96
Corixidae	0.07	0	0.12	0.01	0.11	0
Gerridae	0	0	0.10	0	1.7	0.05
Saldidae	0	0	0.13	0	0	0
Hemiptera total	1.4	0	3.2	0.01	1.9	1.0
Baetis	1.4	1.2	5.3	4.8	3.5	0.54
Ephemerellidae	0.46	0.06	0.46	0.07	0	0
Ephemeroptera total	1.9	1.3	5.8	4.9	3.5	0.54
Capnidae	0.14	0	0	0	0	0
Perlidae	17	0	0.04	0	0	0
Perlodidae	2.3	0	0	0	0	0

Plecoptera total	19	0	0.04	0	0	0
Pyralidae	2.8	0	0.12	0	0	0.13
Lepidopteral total	2.8	0	0.12	0	0	0.13
Megaloptera	0.14	0	0.21	0.14	0	0
Hymenoptera	1.5	0.03	1.7	0.67	0.28	0.40
Gastropoda	1.6	4.0	1.6	30	4.2	3.6
Gammarus	0.15	34	2.6	2.5	0	6.8
Terrestrial Isopoda	0.16	0	0.04	0.04	0.07	0.27
Hirudinea	0.02	0.12	0.02	0	0	0.08
Oligochaeta	0.16	0.02	0.31	0.05	0.20	0.23
Orthoptera	22	0	0.49	0	0	0
Diploda	11	0	2.9	0.62	72	5.0
Misc total	0.17	0.02	0.06	0.02	0.10	0.09
TOTAL	**93.6**	**44.5**	**43.6**	**73.7**	**103.9**	**25.7**

Appendix O. Mean dry mass (mg) per fish of invertebrate prey taxa in summer diets of Brown Trout sampled in six southeastern Minnesota streams, 2010 – 2013.

SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	3.2	0.14	2.3	0.50	1.1	1.1
Micrasema	0.01	0	0	0.15	0	0
Glossosoma	1.0	0.02	1.6	1.6	0	0
Hydropsychidae	0.29	0	0.06	0.12	0.16	0
Hydroptilidae	0.11	0	0.07	0.03	0.05	0.27
Limnephilidae	1.3	2.9	0.42	2.1	6.8	0
Trichoptera total	6.0	3.1	4.5	4.5	8.1	1.4
Chironomidae	0.64	0.77	2.2	0.16	0.14	2.9
Simuliidae	0.1	0.01	0.1	0.06	0.28	0.28
Stratiomydiae	0.06	0	0.15	0.03	0	0
Tabanidae	0.86	0	0.1	0.05	0	0.03
Tipulidae	2.8	0.58	0	0.07	1.5	0.06
Diptera total	4.4	1.4	2.6	0.37	1.9	3.3
Curculionidae	0.22	0	0	0.02	0.3	0.05
Dytiscidae	0.65	5.5	0.49	0.5	1.0	0.62
Elmidae	0.16	0.1	0.15	0.04	0.27	0.03
Halipidae	0	0	0.4	0	0.22	0.03
Carabidae	0.5	0	0	0	0	0
Hydrophilidae	0.18	0	0	0	0	0
Chrysomelidae	0.62	0	0	0	21	0
Coleoptera total	2.3	5.6	1.0	0.56	22	0.73
Belostomatidae	0.72	1.7	0	0	7.8	0
Corixidae	0.23	0.05	0.78	0.01	0.02	0.01
Gerridae	0.61	0	0	0	0	0
Notonectidae	0.17	0	0	0	0.15	0
Hemiptera total	1.7	1.7	0.82	0.05	8.0	0.02
Baetis	2.9	6.6	2.4	0.38	0.05	1.9
Ephemeroptera total	2.9	6.6	2.4	0.38	0.05	1.9
Isoperla	0.12	0	0	0	0.49	0
Perlodidae	0	0	0	0.31	0	0
Plecoptera total	0.12	0	0	0.31	0.49	0
Pyralidae	0	10	0	0.37	1.0	0
Lepidopteral total	0	10	0	0.37	1.0	0
Megaloptera	0	0	0	0.14	0	0
Hymenoptera	11	7.1	0.58	1.2	96	1.7
Gastropoda	16	0.45	3.1	4.8	14	29
Gammarus	0.78	2.4	1.9	4.3	0	3.1
Terrestrial Isopoda	0.02	0.04	0.07	0.25	0.09	0.08
Hirudinea	0.16	0	0	0.01	0.04	0.03
Oligochaeta	0.1	0	0	35	0	0
Orthoptera	0.25	0.25	0	8.8	0	0.09
Diploda	0	0	0.75	0	0	0
Misc total	16	0.06	0.14	27	23	0.09
TOTAL	**61.2**	**38.9**	**17.8**	**87.6**	**176.1**	**41.3**

Appendix P. Relative importance (%) of prey items in the diet of Brown Trout in six streams in southeastern Minnesota, 2010-2013.

| SITE	Beaver Creek	Daley Creek	Garvin Brook	Gribbon Creek	Rush Creek	Trout Run Creek
Brachycentrus	21.94	0.91	29.53	11.68	14.82	18.63
Glossosoma	2.44	0.04	3.52	3.49	1.15	0.04
Hydroptilidae	2.40	0.00	0.48	0.03	0.06	2.34
Leptoceridae	0.03	0.00	0.04	0.00	4.90	0.00
Limnephilidae	16.59	5.10	1.14	11.89	24.79	1.19
Trichoptera total	44.52	6.12	35.03	27.67	45.81	22.29
Ceratopogonidae	0.01	0.00	0.01	5.85	0.00	0.07
Chironomidae	21.05	21.32	24.69	10.67	5.39	37.58
Simuliidae	1.98	0.59	0.83	0.94	2.30	0.67
Diptera total	24.01	21.56	26.08	17.02	8.00	38.63
Dytiscidae	0.25	0.49	2.00	0.09	0.89	0.79
Halipidae	0.01	0.00	0.04	0.01	2.15	0.20
Coleoptera total	1.16	0.63	2.40	0.29	4.23	1.12
Belostomatidae	0.12	0.10	1.15	0.00	0.68	0.14
Hemiptera total	1.13	0.22	2.01	0.03	1.67	0.16
Baetis	2.37	6.15	8.85	4.96	11.01	1.89
Ephemeroptera total	2.51	6.22	9.06	5.03	11.01	1.89
Perlidae	4.98	0.00	0.02	0.00	0.00	0.00
Plecoptera total	5.62	0.00	0.02	0.01	0.02	0.01
Pyralidae	0.16	2.26	0.01	0.01	0.02	0.01
Lepidoptera total	0.16	2.26	0.01	0.01	0.02	0.01
Formicidae	3.46	3.17	0.26	0.20	2.31	0.40
Hymenoptera total	3.50	3.63	0.63	0.23	2.33	0.43
Gastropoda	10.53	8.04	4.49	32.32	13.02	14.13
Gammarus	1.92	48.18	14.00	9.64	7.14	19.05
Arachnida	0.92	0.95	2.04	0.11	0.56	0.92
Oligochaete	0.06	0.59	0.05	4.40	0.03	0.05
Orthoptera	1.68	0.02	0.06	0.00	0.00	0.00
Diploda	0.85	0.01	2.10	1.51	4.04	0.36
Miscellaneous total	1.43	1.57	2.04	1.74	2.12	0.96
	100.00	100.00	100.00	100.00	100.00	100.00

Appendix Q. Relative importance (%) of prey items in the diet of Brown Trout by season in six streams in southeastern Minnesota, 2010-2013.

|	Fall	Winter	Spring	Summer
Brachycentrus	19.44	7.91	18.85	25.26
Glossosoma	0.81	0.70	3.34	3.15
Hydroptilidae	0.54	1.75	1.48	0.00
Limnephilidae	7.18	10.00	0.86	7.42
Trichoptera total	28.30	21.11	24.84	36.93
Ceratopogonidae	0.01	3.08	0.01	0.00
Chironomidae	24.52	26.38	22.37	18.82
Simuliidae	0.81	1.07	0.38	1.48
Diptera total	25.44	31.16	23.56	20.59
Dytiscidae	0.06	1.49	0.84	0.04
Coleoptera total	0.14	2.15	1.46	0.06
Corixidae	0.02	0.23	1.19	0.01
Hemiptera total	0.84	0.49	1.49	0.32
Baetis	5.45	6.42	4.60	2.43
Ephemeroptera total	5.48	6.96	4.61	2.45
Perlidae	0.00	2.59	0.00	0.01
Plecoptera total	0.00	2.83	0.01	0.16
Pyralidae	0.01	0.09	2.27	0.00
Lepidoptera total	0.01	0.09	2.27	0.00
Formicidae	0.24	0.17	6.81	0.01
Hymenoptera total	0.86	0.36	6.83	0.01
Gastropoda	22.31	9.24	12.81	15.17
Gammarus	16.38	20.67	13.40	23.83
Arachnida	0.07	2.08	0.80	0.24
Oligochaete	0.04	0.06	5.08	0.00
Diploda	0.01	1.49	2.42	0.00
Miscellaneous total	0.12	1.31	0.43	0.24
	100.0	100.0	100.0	100.0
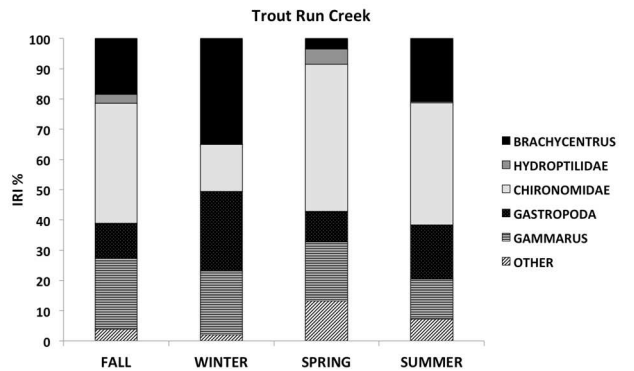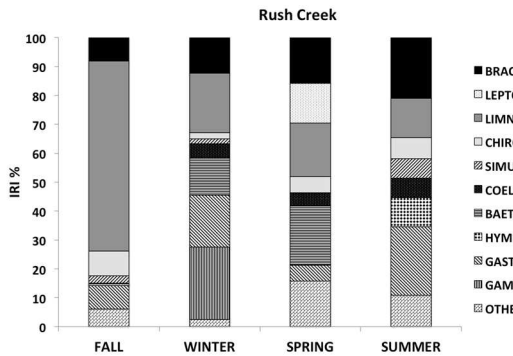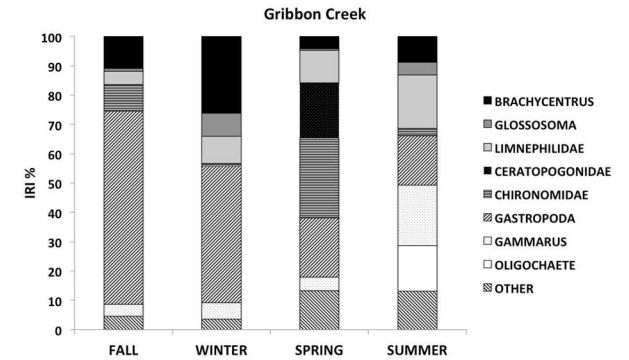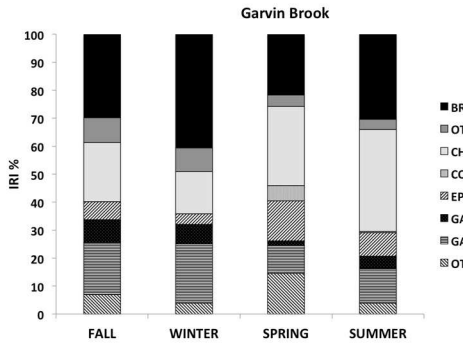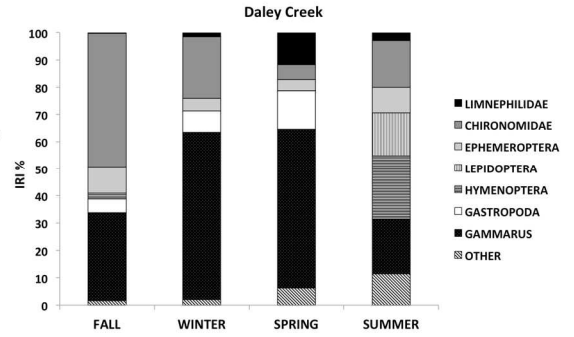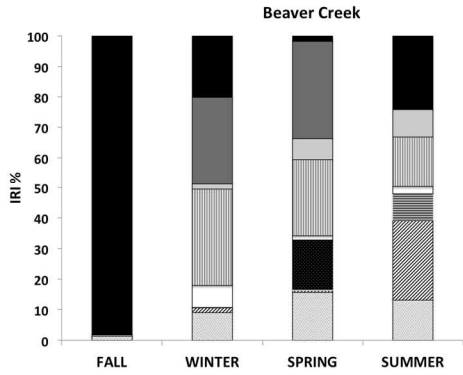
Appendix R. Relative importance (%) of invertebrates in the diet of Brown Trout in six streams by season, 2010-2013.
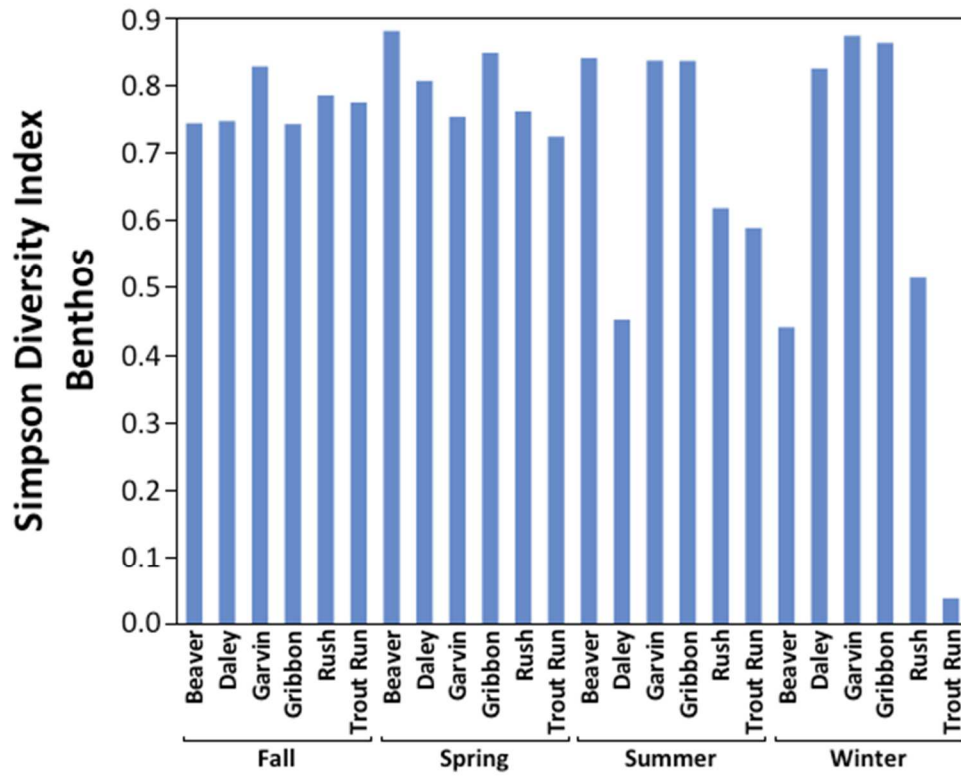
Appendix S. Simpson Diversity Index (Ds) of benthic invertebrate assemblages by season and stream, 2011-2013.
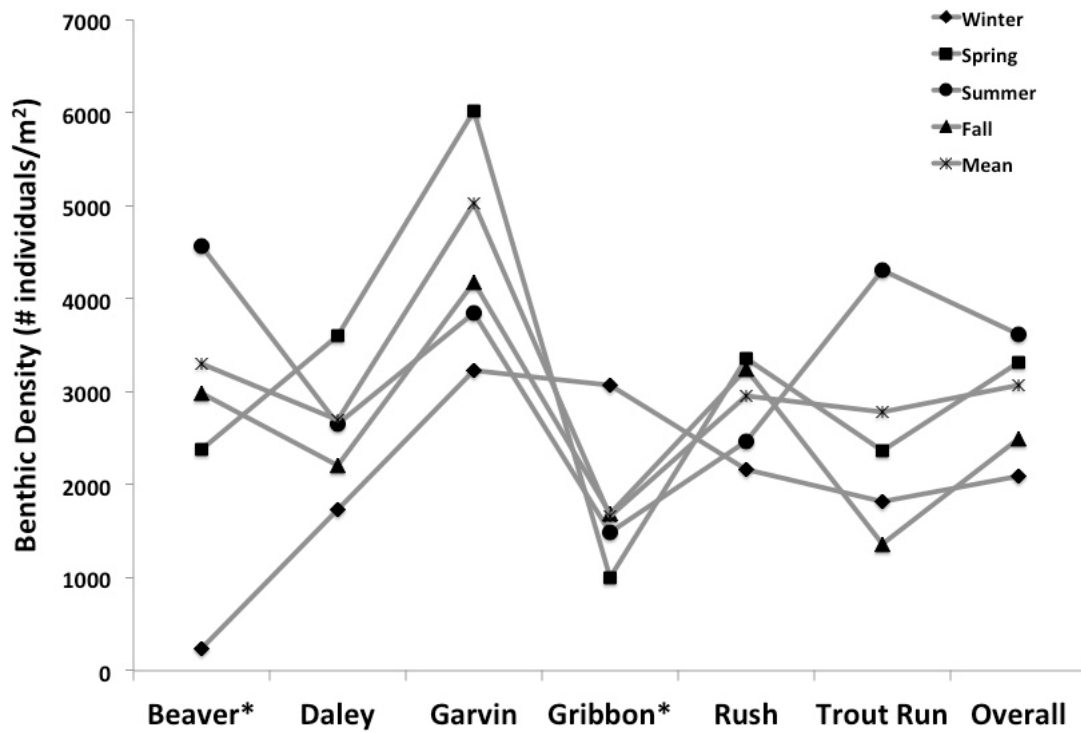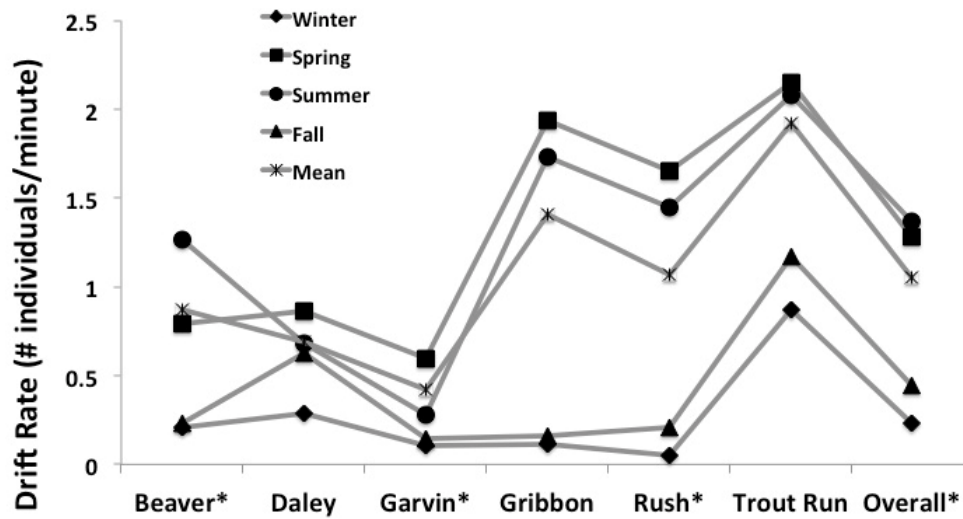
Appendix T. Mean benthic density (number of individuals per m^2) by season in six streams across southeastern Minnesota, 2011-2013. (*) indicates significant differences (p<0.05) among seasons (Beaver: F=4.6, p<0.01; Daley: F=3.9, p=0.01; Gribbon: F=4.4, p<0.01).
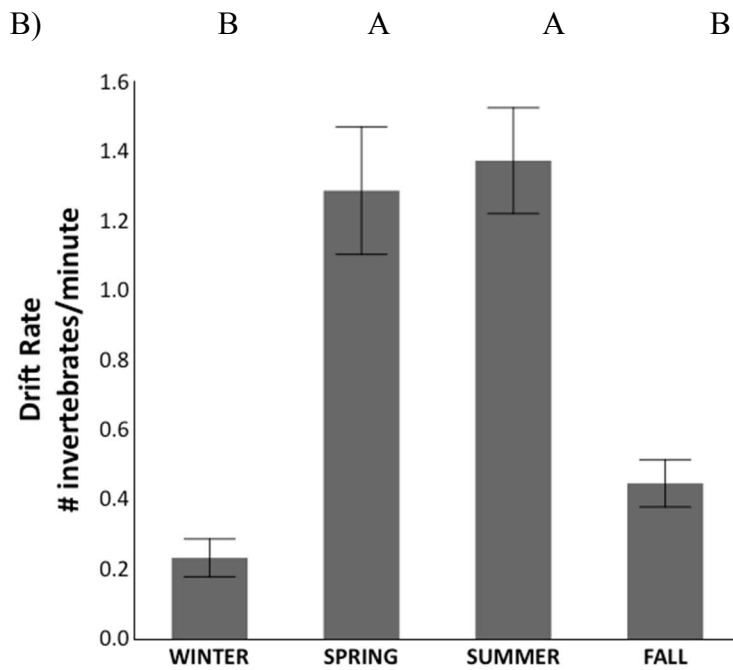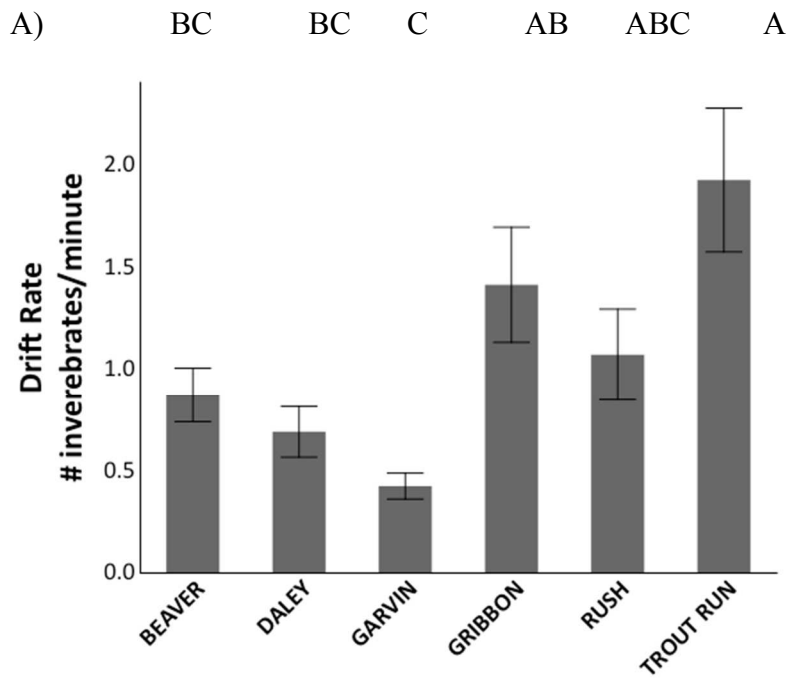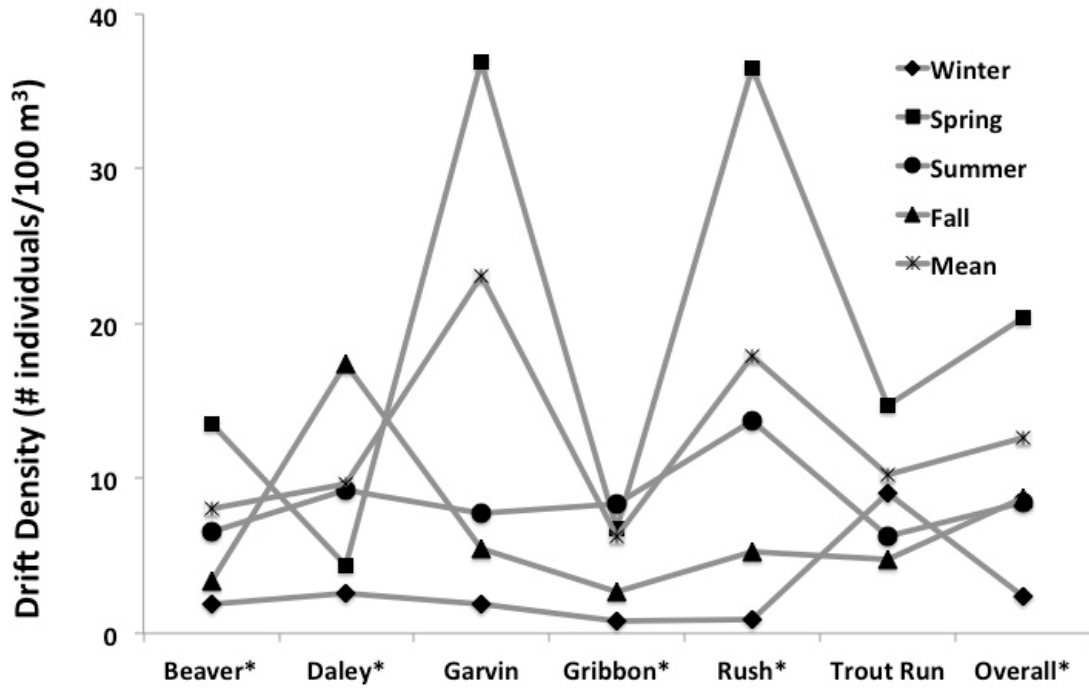
Appendix U. Mean drift rate (number individuals per minute) by (A) stream and (B) season in six streams across southeastern Minnesota, 2011-2013. Error bars = ± 1 SE. Bars with the same letter are not significantly different (p<0.05).

A)

B)
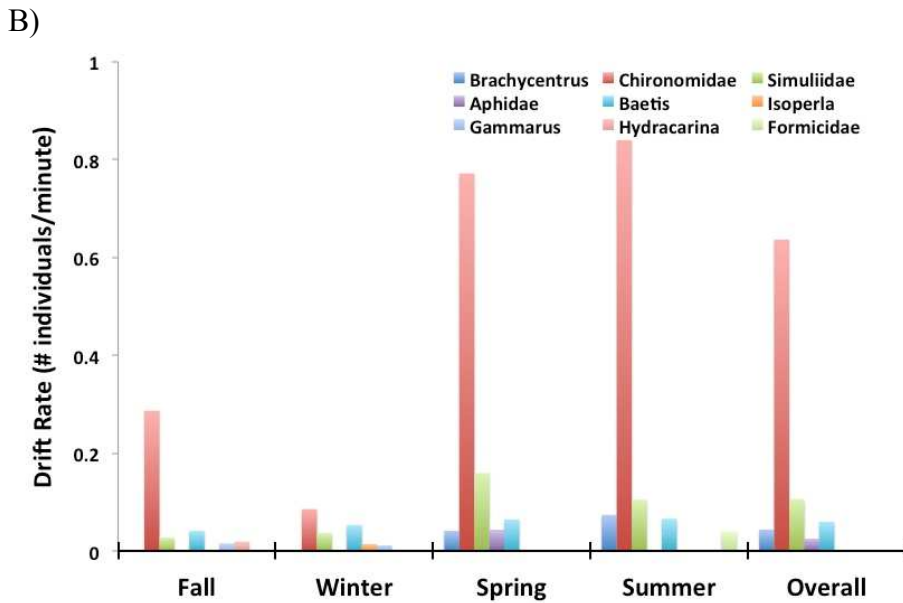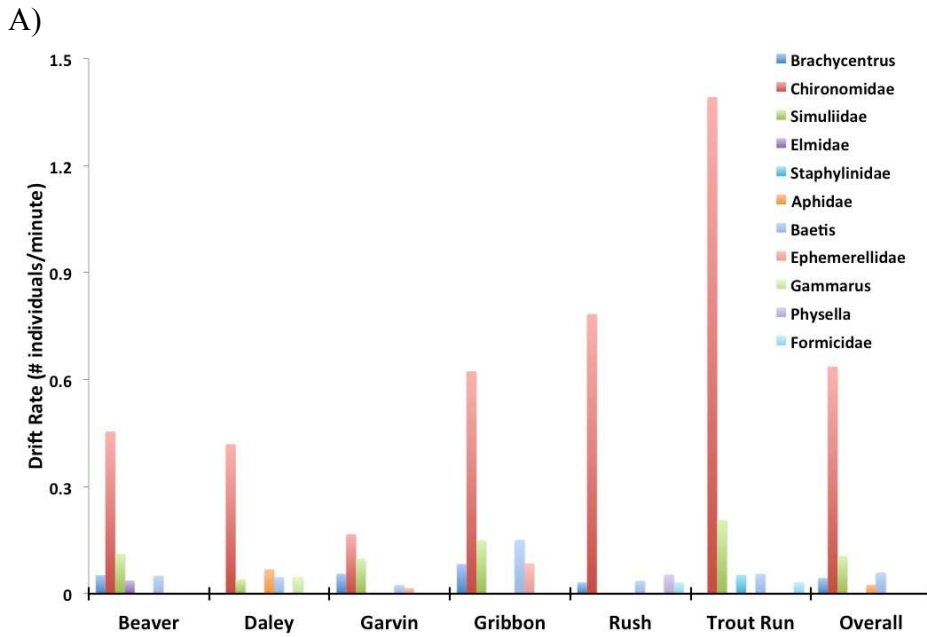
Appendix V. Mean drift rate (number of individuals per minute) of five most abundant macroinvertebrate taxa by (A) stream and (B) season in six streams across southeastern Minnesota, 2011-2013.

Appendix W. Mean drift rate (number of individuals per minute) by season in six streams across southeastern Minnesota, 2011-2013. (*) indicates significant differences ($p<0.05$) among seasons (Beaver: $F=3.5$, $p=0.02$; Garvin: $F=3.9$, $p=0.01$; Rush: $F=3.4$, $p=0.02$; overall: $F=8.0$, $p<0.01$.

Appendix X. Mean drift density (number of individuals per 100 m^3) by season in six streams across southeastern Minnesota, 2011-2013. (*) indicates significant differences ($p<0.05$) among seasons (Beaver: $F=4.6$, $p<0.01$; Daley: $F=3.9$, $p=0.01$; Gribbon: $F=3.3$, $p=0.02$; Rush: $F=3.7$, $p=0.02$; overall: $F=2.4$, $p=0.06$).