Protected from the Elements: Winter Ecology of Brown Trout in Groundwater Buffered Streams

A DISSERTATION SUBMITTED TO THE FACULTY OF THE UNIVERSITY OF

MINNESOTA BY

William E French

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

Bruce Vondracek and Leonard C. Ferrington Jr., advisers

September, 2014

Acknowledgements

I would like to take a moment to thank the people and organizations which have made this dissertation possible. Your continued assistance and support have been critical to the pursuit of my educational goals. First, I would like to thank my co-advisors, Bruce Vondracek and Len Ferrington Jr. Len has been a valuable asset to my dissertation research, especially during the planning and study design phases. Len’s expertise with aquatic invertebrates was a great help during the identification of trout stomach contents. His knowledge and enthusiasm regarding aquatic insects have inspired me to think more holistically about aquatic ecosystems: invertebrates are much more than simply fish food. Bruce has had an important influence on my professional development since I was an undergraduate, his door has always been open. He was always willing to review a potential publication or encourage me to attend a meeting to present my research. Bruce was always willing to pitch in and help out in the field, even in the dead of winter. He made a point to get out sampling with us on at least one trip each winter. I have always admired the passion he has for fisheries science, and hope to emulate this in my own career. Whether our discussions focused on a change in sampling protocol, a recent fishing trip, or Monday morning quarterbacking the latest Packer or Gopher Hockey game; a conversation with Bruce was always enjoyable. I am proud to say I consider him a friend as well as an advisor and mentor, and will miss the time I was able to spend with him.

Thanks also to the rest of my committee, Doug Dieterman and Jacques Finlay for their guidance and support during the past four years. Jacques was a great help with

the stable isotope component of my dissertation, and helped with planning, analyses, and discussions of results. Doug was very involved with selection of sampling sites and his knowledge of Brown Trout ecology was a great help in guiding the direction of my research. Doug and I shared many conversations regarding what I was seeing in my work and how it could relate to trout ecology and management in southeastern Minnesota.

I would like to extend a special thanks to my fellow graduate students and undergraduate volunteers who were part of our winter field work team, especially Jane Mazack and Patrick Sherman. We shared many long cold days together (and kept the Creamery and the Sawmill Inn in business through the winter) during our three winters in southeastern Minnesota, and I thoroughly enjoyed our field time. Your camaraderie played a large part in that.

I would like to thank the MN DNR staff of the Lanesboro and Lake City offices, especially John Hoxmeier and Dan Spence for their assistance, support, and advice throughout this project. Minnesota DNR provided guidance on stream trout populations and site access, loaner equipment when some had been forgotten, and often helped us out as an extra pair of hands in the field.

Thanks to the faculty and staff in the Conservation Biology Graduate Program and the US Geological Survey Cooperative Fish and Wildlife Research Unit, the Water Resources Center, and the Graduate School at the University of Minnesota for their help and assistance throughout the past four years. A special thanks to Rob Blair and Karen

Oberhauser for their efforts helping me navigate the logistical side of the Graduate School during their time as DGS. Thank you to Hattie Saloka, David Fulton and David Anderson for their support and friendship. I did my best to keep the candy on Hattie's desk fresh, and compare our latest notes on the Grouse season (or the turkey, duck, pheasant, deer, or rail season) with David Anderson and David Fulton.

I especially want to thank my friends, office mates, and fellow cohort members in the Conservation Biology program. I have thoroughly enjoyed the past four years and you all have been a big part of that. Cons Bio parties and potlucks, happy hours, random nights out on the town have all been memorable. I particularly enjoyed our unofficial ice fishing club and a special thanks to those of you who I've wet a line with over the past couple years.

Finally, I want to thank my parents, extended family, and especially my wife Jennifer for her continued support and encouragement as I have pursued my educational goals. She has constantly stood by me, waiting patiently for her husband to finally grow up, graduate and get a real job. Thank you again to you all. I would not have been able to get this far without your continued love and support.

Abstract

Winter has traditionally been considered a period of dormancy for stream dwelling trout in temperate latitudes. Seasonal changes including low water temperatures, ice formation, and reduced prey availability from aquatic and terrestrial sources often contribute to reductions in trout growth and survival. Consequentially, winter has rarely been the focus of study by fisheries scientists, and relatively little information is available regarding stream trout during winter. However, because of the potential impact on stream trout growth and survival, winter is an important season for trout populations and of particular interest to fisheries managers. The goal of this dissertation was to examine winter trophic ecology of stream dwelling trout populations, and the potential of groundwater input to buffer stream water temperatures and trout from the environmental conditions typically associated with winter. This dissertation consists of three chapters that contribute towards this goal. The first chapter examines winter diet of Brown Trout by quantifying trout consumption, identifies important winter prey taxa , and compares diet composition among a number of trout populations. The second chapter describes Brown Trout winter growth and condition, and examines the influence of groundwater buffering and trout diet composition on growth and condition. The third and final chapter uses stable isotope analyses to examine seasonal variation in Brown Trout diets, and the position of trout within winter food webs of groundwater dominated streams. My dissertation will help managers predict the potential effects of winter on important recreational stream

trout fisheries, and allow informed management decisions incorporating the best available information.

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Prologue

Winter has traditionally been thought of as a period of dormancy for aquatic ecosystems, and as a result has not often been the focus of study for fisheries scientists. This has resulted in a seasonal gap of knowledge, even for otherwise often-studied taxa. The family Salmonidae is widely distributed and contains many commercially and recreationally important species. As a consequence, a large amount of information is available describing Salmonid seasonal ecology. However, Salmonid ecology during winter has received limited study, and relatively little information describing stream Salmonids during winter is available. Recently, researchers have begun to appreciate the potential importance of winter for fish populations, and increased effort is being directed toward winter research (Brown et al. 2011; Hayden et al. 2013; Weber et al. 2013; French et al. 2014).

Stream trout diets vary throughout the year, often with significant shifts in primary prey, and ultimate energy sources (i.e., allochthonous inputs of terrestrial invertebrates during the summer months vs. autochthonous production of aquatic invertebrates available year round) throughout the year. Diets of stream trout from spring through fall have been studied in some depth, and patterns of diet shifts tend to follow seasonal availability of aquatic and terrestrial invertebrates (Newman and Waters 1984; Kelly-Quinn and Bracken 1990; Nakano et al 1999a, 1999b; Forrester 1994; Sweka and Hartmen 2001; Gislason and Steingrımsson 2004; Laudon et al. 2005; Romero et al 2005). Aquatic invertebrates in the drift are often a major component of diet for stream trout, especially during seasons where terrestrial inputs are unavailable. Invertebrate drift has been shown to vary seasonally, and at the microhabitat scale can be influenced by the foraging activities of fish (Leung et al. 2009).

In contrast to other seasons, stream trout diet during winter has been rarely studied, and limited information describing trout foraging dynamics during winter is available. Trout often continue to feed during winter, although foraging rates are typically lower than during other seasons (Cunjak and Power 1987). The overwinter period may be a stressful time for stream trout. Growth decreases during winter season, and mortality can be high (Schultz and Conover 1999; Post and Parkinson 2001). Decreases in growth are generally attributed to the effects of decreased temperature on trout physiology and energetics (Elliot et al. 1995), but reduced availability of prey (e.g., terrestrial invertebrate inputs and aquatic invertebrate emergences) may also play a role. Biro et al. (2004) found overwinter mortality of age-0 fish (60-80%) to be a primary limiting factor for rainbow trout recruitment. Depletion of lipid reserves was the primary mechanism of overwinter mortality. Kelly-Quinn and Bracken (1990) found many adult trout experienced an energy deficit and subsequent decline in condition during winter.

Cunjak and Power (1987) found winter trout diets were dominated by aquatic invertebrates, primarily ephemeropterans, trichopterans, and amphipods. Average trout stomach fullness during this study was 50%, so fish had reasonable access to potential prey. However, simply having access to prey may not be enough for trout to alleviate overwinter stress. Cunjak et al. (1987) used bioenergetic modeling to examine brook trout energy budgets over winter in four temperate Canadian streams. Although brook trout continued to feed during the winter period, fish condition declined throughout the early winter and remained low until spring. Low water temperatures limited the gastric evacuation rate, and ultimately food consumption and energy intake.

Water temperature can have a direct impact on trout foraging behavior, and subsequently growth and survival. Temperature influences energetic demands of trout, as well as their ability to capture and digest prey. Fish are generally able to more effectively capture and digest prey at higher temperatures (Elliot 1995). Consequentially, winter is often thought to be one of the most stressful times for stream trout. Near freezing temperatures reduce the ability of trout to swim, forage, and digest captured prey. Prey availability is often lower, especially with regards to inputs of terrestrial invertebrates and trout foraging activity is often reduced from summer levels. Groundwater inputs may provide local areas of thermal refugia for stream trout during winter, much as they can provide cool water refuges during the summer months. The winter-warm conditions of groundwater discharge have been associated with increased winter survival of brook trout in Wisconsin (Hunt 1969) and rainbow trout in Idaho (Smith and Griffith 1994).

The overall goal of this dissertation was to examine winter trophic ecology of stream dwelling Brown Trout. Emphasis is placed on identifying important trophic relationships, and relationships between diet and groundwater input with trout winter growth and condition. This dissertation expands on the analyses presented in French et al. (2014) by incorporating 34 additional Brown Trout populations to allow spatial comparisons among streams. Additionally, the 34 additional streams have a wide range of groundwater input, allowing the influence of groundwater on trout diet, growth, and condition to be examined. This dissertation addresses the following questions:

1. What prey taxa make up winter diet of Brown Trout in southeastern Minnesota and is diet composition similar among streams with similar physical characteristics and thermal regimes? (Chapter 1)
2. Do Brown Trout in southeastern Minnesota experience changes in growth and condition during winter? (Chapter 2)
3. Do winter diet and/or groundwater input influence Brown Trout winter growth and condition? (Chapter 2)
4. How does Brown Trout trophic position during winter compare to the annual mean, and how significant a component of the diet are rare events such as piscivory? (Chapter 3)

Chapter summaries

The goal of Chapter 1 is to identify and quantify important aquatic invertebrate prey taxa in Brown Trout winter diets with an emphasis on spatial and temporal variation. The relationship of groundwater input, stream drainage area, and channel slope with patterns of Brown Trout diet composition are also examined. Non-metric multidimensional scaling was used to compare patterns of diet composition among southeastern Minnesota streams, with groundwater input as an environmental variable. Brown Trout continued to feed during winter, often consuming 30 or more prey items per day. Aquatic invertebrates made up the majority of brown trout diet in all streams and sampling periods, with *Gammarus*, *Brachycentrus*, *Glossosoma*, Chironomidae, and *Physella* as the most common taxa. There were greater differences in diet composition among streams than between sampling periods within a stream, and measures of groundwater input were more closely correlated with diet composition during early winter sampling.

Chapter 2 examines winter growth and condition of Brown Trout in southeastern Minnesota, with an emphasis on the influence of diet and groundwater input. Growth and condition data were obtained from individually marked fish recaptured during the second sampling event in late winter. Linear mixed effects modeling was used to associate diet and environmental variables with Brown Trout winter growth and condition of trout was compared by size class and time period with 95% CI. Brown Trout had positive overwinter growth in a majority of streams sampled, and there was no significant change in condition between early and late winter. Juvenile fish grew faster than adults, and there was no significant difference in condition between adults and juveniles. Groundwater input was related to growth for both adults and juveniles, whereas diet quality only had a marginal relationship with juvenile growth.

Chapter 3 used stable isotope analyses to provide seasonal information on the relative importance of various prey taxa to Brown Trout diets, and food web structuring in groundwater-dominated streams. Two tissue types with differing turnover rates were used to allow temporal comparisons between winter and annual trout diet. Combining stable isotope data with stomach content data provided in Chapter 1 produced a more complete picture of winter Brown Trout trophic relationships than either data set alone. Brown Trout $\delta^{13}C$ and $\delta^{15}N$ were analyzed by streams and brown trout sizes with ANOVA. Brown Trout relative food web position varied both temporally and by stream. Results suggest that aquatic invertebrates were likely the predominant prey source in some streams, with piscivory being more common in others. Additionally, Brown Trout stable isotope values in most streams indicated an increased reliance on terrestrially derived resources during winter.

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 the Journal of Fish Biology (Wiley). Chapter 2 was prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences (NRC Research Press). Chapter 3 was prepared for submission to Transactions of the American Fisheries Society (Taylor and Francis). The chapters in this dissertation may differ from those published in the primary literature.

Chapter 1

Winter diet of Brown Trout *Salmo trutta* in groundwater-dominated streams of southeastern Minnesota

(Formatted for submission to the Journal of Fish Biology)

W. E. French*, University of Minnesota Conservation Biology Program,

University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

B. Vondracek, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit[1], University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

L. C. Ferrington Jr., Department of Entomology, University of Minnesota

University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

J. C. Finlay, Department of Ecology, Evolution and Behavior

University of Minnesota, 1987 Upper Buford Circle St. Paul, MN 55108, USA

D. J. Dieterman, Fisheries Research, Minnesota Department of Natural Resources, 1801 South Oak Street, Lake City, MN 55041, USA

[1] The Unit is jointly sponsored by the U. S. Geological Survey, the University of Minnesota, the Minnesota Department of Natural Resources, the U. S. Fish and Wildlife Service, and the Wildlife Management Institute

Running headline: Winter diets of Brown Trout

*Corresponding author. Hodson Hall Rm 226, 1980 Folwell Ave St. Paul, MN 55108. Email: fren0104@umn.edu. Phone:

Abstract

Fish diet is an important component of a species population dynamics, and may have greater implications for aquatic food webs. Although many studies have focused on the diet habits of trout from spring to autumn, little is known regarding trout diets during winter. Additionally, groundwater input has the potential to buffer stream water temperatures during winter, alter the thermal regime and possibly influence foraging activity and diet of trout within these systems. We examined diet composition of Brown Trout in 35 groundwater-dominated streams in the Driftless Ecoregion of southeastern Minnesota (USA) during early and late winter of 2010-2013. Aquatic invertebrates made up the majority of Brown Trout diet in all streams and sampling periods, with *Gammarus, Brachycentrus, Glossosoma,* Chironomidae, and *Physella* as the most common taxa. There were greater differences in diet composition among streams than between sampling periods within a stream, and landscape scale stream characteristics were not closely associated with trout diet. Winter was not a period of dormancy in groundwater-dominated southeastern Minnesota streams, as Brown Trout continued to forage on a variety of prey taxa, often consuming 30 or more prey items.

Keywords: Brown Trout, diet, winter, trophic ecology, Salmonidae

Introduction

Aquatic food webs are often complex and dynamic systems. Trophic interactions between species can have consequences at the species, community, and ecosystem levels (Carpenter et al. 1985, Power et al. 1985, Power et al. 1988, McIntosh and Townsend 1996). Additionally, knowledge of trophic interactions in aquatic food webs is important for understanding energy flow to consumers (Michelsen et al. 1994, Takimoto et al 2002). Perturbations (e.g. invasive species, anthropogenic disturbance, etc.) in an aquatic ecosystem often disrupt established food webs, and instigate changes in trophic interactions as community members adjust to differences in resource availability (Vander Zanden et al. 1999, Feyrer et al. 2003). A species unable to adapt to a disrupted food web may experience a decline in abundance and/or distribution, or even become locally extirpated (Guy et al. 2011).

Food webs in streams can be regulated by top down forces exerted through predation, usually by a predatory fish species (Allan 1978, Power et al. 1985, Power et al. 1988, Post et al. 1997, Ruetz et al 2002, Kishi et al. 2005). In many instances, trout (Salmonidae) are the top-level predator in groundwater-dominated streams. Accordingly, the foraging behavior of stream trout not only has a direct impact on trout population dynamics, but may have consequences for ecosystem structure and function (Huryn 1998).

An extensive amount of research has focused on variation in trout diets, foraging behavior and prey selection in cold-water streams during the spring and summer.

However, in contrast to other seasons, stream trout diet during winter has been rarely studied, and limited information is available describing trout foraging dynamics during winter. The factors influencing trout foraging behavior, and how these factors vary seasonally must be understood to identify and predict possible seasonal consequences of trout foraging dynamics.

Trout may continue to feed during winter, although foraging rates often are lower than during other seasons (Cunjak and Power 1987, Kelly-Quin and Bracken 1990). Growth may decrease during winter, and mortality can be high (Schultz and Conover 1999; Post and Parkinson 2001). Biro et al. (2004) found overwinter mortality of age-0 fish (60-80%) was the primary limiting factor for rainbow trout recruitment and was related to the depletion of lipid reserves. Decreases in growth are generally attributed to the effects of decreased temperature on trout physiology and energetics (Elliot et al. 1995), but reduced availability of prey (e.g., terrestrial invertebrate inputs and aquatic invertebrate emergences) may also play a role (Filbert and Hawkins 1995; Utz and Hartman 2007).

Summer diets of stream trout frequently include a significant proportion of terrestrial invertebrates (Kelly-Quinn and Bracken 1990; Bridcut 2000; Kawaguchi and Nakano 2001; Laudon et al. 2005; Utz and Hartman 2007), but these invertebrates are reduced or unavailable to trout during winter in northern temperate regions. Aquatic invertebrates were generally abundant in diets of stream trout during winter (Cunjak et al. 1987; Kelly-Quinn and Bracken 1990), but abundance can be reduced during winter

(Newman and Waters 1984; Gislason 1985; Rundio and Lindley 2008). Dieterman et al. (2004) suggested differences in annual growth among brown trout populations in groundwater-dominated streams in southeastern Minnesota were driven by differences in diet and prey availability. Thus, declines in prey abundance may negatively affect foraging and growth of stream trout.

Winter is often thought to be a stressful time for stream trout. Near freezing water temperatures reduce the ability of trout to swim, forage, and digest captured prey. Although continued feeding during winter appears to be fairly common (Cunjak and Power 1986, Kelly-Quinn and Bracken 1990, French et al. 2014), the effect of low water temperature on trout physiological processes (e.g. metabolism, digestion) may reduce the energetic benefits of food consumed by trout. Brocksen & Bugge (1974) found that assimilation efficiency in rainbow trout decreased from a peak of 85% at 20C° to 72% at 5C°. Cunjak et al. (1987) used bioenergetic modeling to examine Brook Trout *Salvelinus fontinalis* energy budgets over winter in four temperate Canadian streams; although Brook Trout continued to feed during winter, condition declined throughout the early winter and remained low until spring. Low water temperatures limited the gastric evacuation rate, and ultimately food consumption and energy intake. Elliot (1975) found Brown Trout feeding rates peaked and remained fairly stable between 6.8°C and 19.3°C, with marked decreases below and above this temperature range. Brown Trout are also able to obtain more energy per consumed food item at higher temperatures via increased absorption efficiency. Absorption efficiency increases with temperature up to approximately 15°C (Elliot 1976c).

Groundwater inputs may provide local areas of thermal refugia for stream trout during winter, much as they can provide cool water refuges during the summer. The winter-warm conditions of groundwater discharge have been associated with increased winter survival of brook trout in Wisconsin (Hunt 1969) and rainbow trout in Idaho (Smith and Griffith 1994). The amount of groundwater input varies between streams in southeastern Minnesota, resulting in a range of temperature regimes within a geographically small area (Krider et al. 2013). Differing temperature regimes between streams have the potential to influence aquatic invertebrate communities, Brown Trout foraging activity, and diet composition.

This study examined brown trout diet during the winters of 2010-2013 in 35 streams spanning a range of groundwater input in southeastern Minnesota. Diet composition was compared spatially among streams and temporally between early and late winter sampling events. Stream physical characteristics have the potential to affect aquatic invertebrate communities, thus trout diet composition and foraging ability, the relationship between diet composition, and stream characteristics were also examined. The objectives of this study were to: 1) Identify important aquatic invertebrate prey taxa in Brown Trout diets in winter; and 2) examine relationships of groundwater input, stream drainage area, and channel slope with patterns of Brown Trout diet composition in early and late winter.

Materials and Methods

Study area

This study was conducted in 35 groundwater-dominated streams located in the Driftless Ecoregion of southeastern Minnesota (Fig. 1). The region was bypassed by the Wisconsin and previous glaciations and is characterized by karstic geology. The area includes a large number of active groundwater springs and seeps that sustain cold-water fish assemblages and aquatic invertebrate communities in many area streams (Waters 1977; Williams and Vondracek 2010). Southeastern Minnesota streams support an exceptional recreational fishery, and Brown Trout are the primary species targeted by anglers (Thorn et al. 1997). Although average overall growth and abundance of Brown Trout populations in southeastern Minnesota are considered good, a wide range of trout growth and abundance has been observed among streams (MN DNR 1997; Dieterman et al. 2012).

Sample sites

Sample sites were selected based on accessibility during winter conditions, ability to wade under typical winter flows, to cover a range of groundwater input typically observed in southeastern Minnesota, and likelihood of capturing a sufficient number of Brown Trout for analyses. Stream size (< 2m to >15m wetted width) and thermal regime varied between sites, and encompassed the range of physical characteristics typical of streams in southeastern Minnesota (Table I). Most streams remained ice free throughout winter sampling, only East Burns Valley, Wells and Rush Creeks experienced surface ice formation in pools and areas of low water velocity.

Habitat alteration projects for trout management have a long history in the region and the majority of study sites experienced some type of alteration (Thorn et al. 1997).

Fish collection

Brown Trout were collected from 11-12 sites per year during the winters of 2010-2013 using a Smith Root® (Washington, USA) LR 20B backpack electrofisher. A towable barge electroshocker was used on two occasions (Bee Creek and West Beaver Creek in late winter) to increase catch rates. Each site was sampled during the early and late winter for a total of two sampling events per site during the study. Fish were placed within in-stream holding pens, anesthetized with an immobilizing dose of tricaine methanesulfonate (MS 222), weighed (± 1g) and measured (± 1mm TL). Gastric lavage was used on a random subsample of up to 30 fish on each sampling date to examine diet composition. Fish were allowed to recover from anesthesia in a separate holding pen and returned to the stream. Stomach contents were preserved in 95% ethanol in the field, and later processed in the laboratory.

Analyses

Aquatic invertebrates were identified to family or genus and counted; only intact specimens or fragments greater than one-half an intact individual were counted. Direct measurements of mass were not possible due to partial digestion, thus equations from Benke et al. (1999) and Méthot et al. (2012) were used to estimate dry weight of aquatic invertebrates in the diet from mean morphological measurements. Mean morphological measurements of aquatic invertebrates (body length, shell width) were calculated by stream from subsamples of 20 intact individuals per taxon randomly selected from Brown Trout diets. Dry weight was estimated for the most abundant taxa in Brown Trout diets for each stream. Dry weight estimates were multiplied by taxa counts to obtain dry weight composition of diet for each fish. Dry weight consumption was compared between early and late winter with a paired t-test.

Slopes from the air/water temperature regression equations developed by Krider et al. (2013) were used as an estimate of groundwater input. 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 23 of the 35 streams sampled in this study, and predicted water temperature at 0°C ranged from 5.9°C for Cedar Valley Creek to 8.2°C for Forestville (North Branch) Creek (Krider et al. 2013). Analyses were conducted with 22 of these streams as the Rush Creek site sampled in this study was several kilometers upstream of the site analyzed by Krider et al. (2013), and likely had a different thermal regime. The relationship between groundwater input and mean dry weight consumption by Brown Trout was examined for early and late winter with linear regression.

Non-metric multidimensional scaling (NMDS) was used to examine patterns of diet composition among streams 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 2 dimensional plot. 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. Drainage area and 10-85% channel slope were calculated for each stream with the sample site as the downstream boundary. Groundwater input was estimated from regression slopes provided in Krider et al. (2013). NMDS was conducted in program R (version 3.0.2) 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 acceptable. Diet items that made up >1% of the mean total dry weight for each stream in early or late winter were selected for analyses. Thirteen variables (mean proportion of dry weight of *Gammarus*, Ephemeroptera, Plecoptera, *Brachycentrus*, *Glossosoma*, Limnephilidae, Hydropsychidae, Chironomidae, Simulidae, Tipulidae, Dytiscidae, *Physella*, and Isopoda) were used in the NMDS ordination. NMDS plots were constructed for early and late winter diet composition for the 23 streams analyzed in Krider et al. (2013). The stream physical variables 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. The Rush Creek site was omitted when fitting groundwater input, but included for drainage area and channel slope.

Results

Diet composition

Aquatic invertebrates made up the majority of Brown Trout diets in all streams during both sampling periods (Tables IIa,b-IIIa,b). The most common invertebrate prey taxa by number among streams included *Gammarus, Brachycentrus, Glossosoma,* Chironomidae, and *Physella*. The dominant invertebrate prey taxa by estimated dry weight among streams included *Gammarus, Brachycentrus, Physella,* Isopoda, Ephemeroptera and Limnephilidae. Empty stomachs were rare (less than 5% in all streams) and diet composition varied by both stream and sampling period. Brown Trout consumed more prey by number during the late sampling period for the winters of 2010-11 (mean consumed early=21.4, late=29.5); 2011-12 (mean consumed early=17.9, late=33.7) and 2012-13 (mean consumed early=15.3, late=34.3). By contrast, Brown Trout consumption by dry weight was significantly greater during the late sampling period during the winter of 2011-12 (mean dry weight consumed early=46.9mg, late=73.2mg); with a smaller differential in 2012-13 (mean dry weight consumed early=96.1mg, late=125mg); and minimal difference in 2010-11 (mean dry weight consumed early=57.4mg, late=58.9mg). Specific taxa often made up the majority of trout diets in some streams, and were minor components or non-existent in other streams. For example, Brown Trout in Bee Creek consumed a mean of 483 mg dry weight *of Physella*, whereas fish in Spring Creek consumed a mean of only 1.7 mg dry weight *Physella* during the late winter sampling period. Piscivory occurred in some streams, but was typically observed in less than 10% of diet samples. Sculpin *Cottus sp.* were the most commonly observed fish prey (range: 0.03-0.40 mean per trout) in streams where piscivory did occur. Other large-bodied vertebrate prey (e.g. amphibians and small mammals) were rarely observed.

There was a significant difference in mean Brown Trout consumption by dry weight between early and late winter, with greater consumption in late winter (88.3 mg dry weight) than early winter (62.7 mg dry weight, Fig. 2). There were no significant relationships between groundwater input and mean Brown Trout consumption for early or late winter (Fig. 3).

NMDS analyses

Non-metric multidimensional scaling identified patterns of Brown Trout diet composition among streams for each winter and sampling period. Ordinations resulted in convergent solutions for both early (2 dimensions, stress=0.15, Fig 4) and late (2 dimensions, stress=0.16, Fig 5) winter. The physical variables, groundwater input (r^2=0.07, P=0.48), drainage area (r^2=0.11, P=0.33) and channel slope (r^2=0.20, P=0.10), were not significantly associated with the early winter ordination. Similarly, there was no significant association of groundwater input (r^2=0.08, P=0.48), drainage area (r^2=0.08, P=0.40) or channel slope (r^2=0.03, P=0.69) with the late winter ordination. Substantially more variation in diet composition was explained by stream physical variables in early winter (~40%) than late winter (~20%).

Discussion

Winter foraging occurred regularly for Brown Trout in all sampled streams. These results were similar to those found by Cunjak and Power (1987), where mean winter stomach fullness of Brown Trout was greater than 50% in the Credit River, Ontario. However, Kelly-Quinn and Bracken (1990), observed empty stomach rates as high as 15% during winter in the River Dodder (Ireland), suggesting that the frequency and amount of winter feeding by trout may vary considerably between populations. Localized differences in stream conditions and prey abundance likely play a role in the ability of Brown Trout to effectively forage during winter.

Dissimilar stream temperature regimes among streams in this study and previous studies of Brown Trout winter diets may explain some of the observed differences in winter foraging. Ice formation can be a significant stressor for stream dwelling trout, affecting available habitat and reducing the ability of trout to feed (Brown et al. 2011). Cunjak and Power (1987) documented surface ice cover of up to 22% in the Credit River during their study period. By contrast, significant ice formation was observed in only three (East Burns Valley Creek, Wells Creek, and Rush Creek) of the 35 streams sampled in this study, and streams were never completely ice covered, suggesting groundwater input was sufficient to prevent ice formation.

Winter diets of brown trout in the 35 southeastern Minnesota streams sampled in this study were dominated by aquatic invertebrates, although the relative importance of specific taxa varied by stream and sampling date. Important taxa included

Gammarus, Brachycentrus, Glossosoma, Limnephilidae*,* Chironomidae, Ephemeroptera, Plecoptera and *Physella.* Aquatic invertebrates also made up the majority of winter Brown Trout diet in the Credit River with Trichoptera, Ephemeroptera, Plecoptera, Pericarida, and Diptera as important taxa (Cunjak and Power 1987). Similarly, Kelly-Quinn and Bracken (1990) found aquatic invertebrates, particularly Ephemeroptera and Chironomidae, made up the bulk of winter diet for brown trout in several tributaries of the River Dodder. By contrast, terrestrial invertebrates made up 50% of winter Brown Trout diets in a southern Appalachian stream (Cada et al. 1987a). However, in this southern Appalachian stream aquatic invertebrate production in the stream was suspected to be low and prey availability was hypothesized to be a limiting factor for Brown Trout growth (Cada et al. 1987b).

Differences in groundwater inputs between streams may also have influenced prey availability. Aquatic invertebrate abundance can be greater during winter in groundwater-dominated streams than in surface-water dominated streams (Bouchard and Ferrington 2009). In addition, groundwater-dominated streams may support populations of specialized cold-adapted aquatic invertebrates designated as ultra-cold stenotherm species (UCS), which include several species of Chironomidae commonly found in southeastern Minnesota streams. These species complete their life cycle during winter, and are not present in the summer aquatic invertebrate community (Bouchard and Ferrington 2009). Groundwater input is important to UCS species as it maintains water temperatures within tolerable ranges, and prevents ice cover from interfering with winter emergence. Higher aquatic invertebrate abundance and the presence of UCS species in groundwater-dominated streams may increase prey availability for trout during winter.

Although many of the taxa observed in winter Brown Trout diets during this study were similar to those found in studies conducted in other regions, Physellid snails made up a significant proportion of winter Brown Trout diet in this study, but were absent from winter diets in the Credit River and River Dodder. Physellid snails likely consume the aquatic vegetation common in many southeastern Minnesota streams, including those in this study. Anderson (2012) also identified Physellid snails as an important winter prey taxa for Brown Trout in southeastern Minnesota streams. Additonally, Physellid snails are often present in the summer diets of Brown Trout (Zimmerman and Vondracek 2007, Holumuzki 2010, Vinson and Budy 2010). The importance of Physellid snails to winter diet of Brown Trout in southeastern Minnesota streams relative to other systems may reflect differences in aquatic invertebrate communities and prey availability when compared to streams from other regions.

Brown Trout often display size selectivity, preferentially feeding on larger prey items (Newman and Waters 1984). We found large-bodied taxa (*Gammarus*, Isopoda, *Brachycentrus*, Limnephilidae, Tipulidae and *Physella*) made up the majority of prey consumed by dry weight during both early and late winter. However, smaller-bodied prey such as *Glossosoma* and Chironomidae were often dominant by number, especially during late winter. Brown Trout sampled in this study had greater numbers of prey items in their diets during the late winter sampling period, but total estimated dry weight consumed often was similar to or even decreased from early winter. This was likely related to an increase in the proportion of small-bodied to large-bodied prey taxa in late winter Brown Trout diets. For example, Brown Trout in Winnebago Creek had a mean of 17.6 *Gammarus* and 1.1 Chironomidae per diet sample during the early winter sampling period, and a mean of 1.0 *Gammarus* and 47.4 Chironomidae per diet sample during the late winter sampling period. Although the mean number of prey items per fish almost tripled from early (22.7 mean prey) to late (61.1 mean prey) winter sampling, estimated dry weight of prey decreased from a mean of 111mg per fish in early winter, to 51mg per fish in late winter. Similar patterns occurred in other streams with Chironomidae (Badger Creek, Torkelson Creek, West Branch Money Creek, Upper Money Creek, Trout Valley Creek and Big Springs Creek) and *Glossosoma* (Forestville Creek, Badger Creek, Torkelson Creek). The late winter sampling events typically occurred when many spring seasonal invertebrate taxa were beginning their emergence cycles (Jane Mazack, unpublished data). Emergences of Chironomidae were commonly observed at sampling sites during the late winter sampling period, and trout may have taken advantage of these seasonally abundant prey taxa.

Water temperature has a significant impact on Brown Trout feeding rate, with trout showing reduced rates at temperatures near 0°C (Elliott 1975). Surprisingly, there was no significant relationship between groundwater input and consumption by Brown Trout in this study, likely because water temperatures were high enough to minimize reductions in trout feeding rates. Elliott (1975) found Brown Trout feeding rates peaked and remained stable between 6.8 and 19.3°C, and the majority of streams in this study likely maintained water temperature above 6°C throughout the winter. Thus, differences in winter trout prey consumption in these 22 streams were likely driven by other factors, such as prey availability instead of water temperature.

Although groundwater input, drainage area, and channel slope were not significantly associated with diet composition, they collectively explained 40% (early winter) and 20% (late winter) of the variation observed in NMDS ordinations. Similarity between sites at the scale stream variables were measured may have made it difficult to identify significant associations relative to trout diet composition. Although variation in groundwater input, drainage area, and channel slope was observed among the streams examined in this study, the differences may not have been sufficient to significantly influence trout diet. However, stronger associations with trout diet may have been found if streams with more disparate physical characteristics had been included in the analyses, e.g. high gradient trout streams in western North America, or surface water-dominated northeastern Minnesota trout streams. Alternatively, an examination of stream habitat characteristics at a finer scale may have allowed greater differentiation between streams and stronger associations with trout diet composition. Stream habitat characteristics such as substrate coarseness, pool depth, water velocity, and aquatic macrophyte abundance can influence aquatic invertebrate community composition and trout distribution within a stream (Cunjak and Power 1986; Jowett et al. 1991; Merritt and Cummins 1996; Bouchard and Ferrington 2009; Dieterman et al. 2012). Therefore, reach scale measurements of southeastern Minnesota stream habitat characteristics could be more closely associated with trout diet composition than the landscape-scale characteristics used in this study.

Conclusion

Brown Trout diet composition varied widely within a relatively small geographical area, but trout in streams with similar habitat and thermal conditions tended to have more similar diet compositions than those in dissimilar streams. Brown Trout in southeastern Minnesota streams fed throughout winter, and aquatic invertebrates made up the majority of the diet. Diet composition of Brown Trout was likely influenced by a variety of factors including the aquatic invertebrate community, seasonal period, site-specific habitat conditions, and thermal regime. Although there was no significant association with trout diet, groundwater input has the potential to significantly alter stream thermal regime when compared to surface water-dominated streams. Differences in thermal regime between groundwater-dominated and surface water-dominated streams can impact the aquatic invertebrate community and consequentially Brown Trout diet composition.

Knowledge of seasonal trout diet composition will allow fisheries managers to quantify the relative importance of common prey taxa for Brown Trout, and the potential consequences of changes in the aquatic invertebrate community for trout populations. If managers identify a potential prey shortage within a stream, than actions could be taken to augment the aquatic invertebrate community and increase available prey for trout. For example, habitat alteration projects could be designed to incorporate coarse woody structure or promote macrophyte growth to benefit desirable invertebrate taxa. Additionally, important prey taxa such as *Gammarus* or *Brachycentrus* could be introduced to streams where they are absent to augment existing prey taxa available to trout.

Acknowledgements

We thank: J Mazack, J McCullough, J Miller, L Krider, P Sherman, C DeGuire (University of Minnesota) J Hoxmeier and D Spence (MN DNR) for assistance in the field. All animals used in this study were handled according to animal use and care guidelines established by the University of Minnesota IACUC committee. Funding for this study was provided by Environment and Natural Resources Trust Fund administered by the Legislative Citizens Committee for Minnesota Resources. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table I. Sample dates, number of lavage samples, size range of brown trout collected, slope of the air-water temperature regression (groundwater input), drainage area, 10-85% channel slope, and site location for 35 southeastern Minnesota streams sampled during winter 2010-2013. Regressions were obtained from Krider et al. (2013).

Stream	Early sample date	Early gastric lavage samples (size range mm)	Late sample date	Late gastric lavage samples (size range mm)	Air-water regression slope	Drainage area (km^2)	Channel slope ($m*km^{-1}$)	UTM Coordinates
Beaver	11/19/2010	30 (126-279)	3/16/2011	30 (115-309)	0.443	29.1	10.81	577026, 4889127
W Indian	11/20/2010	10 (109-301)	3/4/2011	17 (112-306)	0.325	52.3	6.67	567912, 4899861
Hay	12/1/2010	30 (112-306)	3/30/2011	30 (117-304)	0.388	54.64	5.76	532802, 4925099
Garvin	12/5/2010	30 (101-295)	3/3/2011	30 (108-274)	0.354	19.7	15.5	595503, 4873356
Winnebago	12/10/2010	30 (102-346)	3/15/2011	30 (111-322)	0.342	61.6	7.6	625126, 4823555
Gribben	12/17/2010	30 (133-361)	3/25/2011	30 (134-282)	0.25	20.4	13.9	587631, 4839986
Trout Run	12/18/2010	30 (105-352)	4/2/2011	30 (168-354)	0.306	43.7	17.1	575358, 4857802
Forestville	12/19/2010	30 (109-312)	4/1/2011	30 (109-359)	0.205	41.9	3.93	561631, 4831893
SB Whitewater	12/28/2010	30 (105-378)	4/6/2011	30 (111-366)	0.499	202.1	2.9	581763, 4880221
MB Whitewater	12/29/2010	30 (101-395)	4/7/2011	13 (108-352)	0.515	78.2	4.4	572079, 4876366
Daley	1/6/2011	30 (103-342)	3/26/2011	30 (123-277)	0.204	15.2	22.7	605606, 4845390
Rush	1/7/2011	7 (100-239)	4/2/2011	6 (105-254)	NA	56.5	17.1	591328, 4865564
Torkelson	11/18/2011	30 (104-334)	2/24/2012	30 (113-298)	0.322	16.8	53.7	581924, 4847176
Badger	11/19/2011	30 (108-365)	3/15/2012	30 (123-276)	0.354	9.6	20.4	616819, 4838970
Pine	12/3/2011	30 (112-630)	2/25/2012	30 (120-550)	NA	27.2	17.1	622725, 4860877
Pickwick	12/16/2011	30 (107-325)	3/2/2012	30 (103-297)	0.611	25.4	17.1	620150, 4868856
Cedar Valley	12/17/2011	30 (103-340)	3/3/2012	30 (109-294)	0.474	18.7	18.3	615026, 4866958
NB Whitewater	1/5/2012	30 (110-332)	3/9/2012	22 (109-345)	0.557	269.4	2.1	578090, 4881941
W Br Money	1/6/2012	17 (135-347)	3/9/2012	21 (114-367)	NA	23.8	12.6	605514, 4862022
Gilmore	1/7/2012	30 (100-526)	3/10/2012	30 (108-358)	0.347	14.5	24	603836, 4875961
Cold Spring	1/12/2012	30 (118-379)	3/15/2012	30 (112-391)	0.209	116.1	3.43	545284, 4904448
Wells	1/13/2012	30 (136-402)	3/16/2012	13 (147-285)	NA	118.6	4	545099, 4926094
Long	1/19/2012	30 (104-305)	3/16/2012	30 (101-276)	NA	73.6	4.8	561002, 4897553
West Albany	12/6/2012	30 (114-306)	3/6/2013	30 (132-342)	NA	44.8	4.2	556396, 4905180
Trout Valley	12/7/2012	22 (107-328)	3/7/2013	24 (100-231)	0.245	14.5	21.2	585480, 4889958
Pleasant valley	12/7/2012	30 (102-314)	3/7/2013	30 (129-318)	NA	10.2	26.5	612249, 4870078
Spring	12/8/2012	30 (151-364)	3/8/2013	29 (148-312)	NA	161.4	4.5	559710, 4905870
Camp	12/13/2012	30 (103-308)	3/16/2013	30 (119-365)	NA	62.7	6.7	576248, 4833717
South Fork Root	12/14/2012	30 (108-365)	3/17/2013	30 (112-367)	0.398	73.6	3.2	592109, 4830366
Lost	12/14/2012	30 (108-351)	3/16/2013	30 (110-347)	NA	47.1	4.76	564533, 4851249
Bee	12/17/2012	30 (205-382)	4/3/2013	30 (211-360)	NA	47.7	5.95	615463, 4817668
W Beaver	12/18/2012	30 (109-466)	3/20/2013	30 (122-521)	NA	51.2	6.5	612030, 4832019
Big Springs	12/19/2012	22 (148-312)	3/22/2013	30 (115-365)	0.178	14.5	14.9	588263, 4849436
Upper Money	1/8/2013	30 (105-312)	3/21/2013	30 (120-306)	NA	7.82	21.2	607539, 4864328
E Burns Valley	1/9/2013	22 (145-370)	3/21/2013	22 (141-397)	0.563	36.8	14.1	610408, 4875424

Table IIa. Mean prey taxa by number per fish in early winter diets of Brown Trout sampled in 35 southeastern Minnesota streams during the winter of 2010-13. Numbers in parentheses are SEM**.**

Stream	*Gammarus*	Baetidae	Emphemerellidae	Heptageniidae	Allocapnia	Isoperla	*Micrasema*	*Brachycentrus*	*Glossosoma*	Limnephilidae	Hydropsychidae	Chironomidae
Gribben	1.1(0.6)	0.1(0.1)	0	0	0	0	0.1(0.1)	6.9(1.7)	1.8(0.5)	1.2(0.4)	0.1(0.1)	0.1(0.1)
MB Whitewater	0.3(0.1)	0.1(0.1)	0	0	0	0	0	0.6(0.2)	0.4(0.2)	0.2(0.1)	0.3(0.1)	7.9(4.1)
SB Whitewater	0.3(0.1)	0.4(0.1)	0	0.6(0.2)	0.3(0.1)	0	0	10.5(2.8)	0.1(0.1)	0	0.2(0.1)	1.6(0.9)
Winnebago	17.6(7.6)	0.2(0.1)	0	0.2(0.1)	0	0	0.1(0.1)	1.1(0.3)	0.4(0.1)	1.2(0.6)	0	1.1(0.3)
Forestville	0.2(0.1)	0.1(0.1)	0	0.1(0.1)	0	0	0.8(0.3)	11.4(2.6)	3.5(0.5)	0.1(0.1)	0.1(0.1)	0
Rush	0	1.5(0.7)	0	0	0	0	0	0	0.3(0.3)	0.3(0.3)	0	0.3(0.3)
Daley	5.5(1.4)	0.9(0.4)	0	0	0	0	0	0.3(0.1)	0.1(0.1)	0.3(0.2)	0	8.4(3.5)
Trout Run	2.8(0.6)	0.1(0.1)	0	0	0	0	0	2.5(1)	0	0	0.1(0.1)	0.9(0.3)
Beaver	0.2(0.1)	0.2(0.1)	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	7.7(1.8)	0.2(0.1)	0.3(0.3)	0.1(0.1)	4.9(1.8)
W Indian	1.1(0.5)	0.1(0.3)	0	0	0	0	0	2.5(1.3)	0	0	0	0.4(0.2)
Hay	3.9(0.7)	0	0.1(0.1)	0	0	0	0	0.7(0.3)	0.1(0.1)	0	1.1(0.3)	2.6(0.4)
Garvin	4.4(0.9)	0	0	0	0	0	0	12.5(2.8)	2.5(0.7)	1.1(0.6)	0.1(0.1)	1.7(0.4)
Pickwick	0.6(0.3)	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	0	0.7(0.2)	0	0.1(0.1)	0.1(0.1)	25.9(5.7)
Pine	0.2(0.1)	0.1(0.1)	1.1(0.3)	0.1(0.1)	0	0.1(0.1)	0	0.7(0.3)	0.6(0.2)	0	0.5(0.1)	13.6(3.2)
Cedar Valley	8.5(1.2)	0.1(0.1)	0.1(0.1)	0	0.2(0.1)	0	0	0.1(0.1)	0.1(0.1)	0	0.1(0.1)	2.4(0.6)
Badger	2.7(0.7)	0.1(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	0.1(0.1)	2.3(0.7)	0.3(0.1)	0	0.3(0.1)
Wells	6.5(1.8)	0.7(0.2)	0.2(0.1)	0.2(0.1)	0.1(0.1)	0.8(0.2)	0	0.4(0.1)	0	0	3.0(0.4)	0.7(0.2)
Cold Spring	13.3(2.1)	0.1(0.1)	0.1(0.1)	0	0	1.3(0.3)	0	0.9(0.4)	7.0(2.1)	1.1(0.2)	0	0.2(0.1)
Torkelson	8.2(1.8)	0.1(0.1)	0	0	0	0	0	2.1(0.7)	0.3(0.1)	0.8(0.2)	0.1(0.1)	6.8(2.4)
W Br Money	0	0.1(0.1)	0	0	0	0	0	6.1(2.4)	0	1.8(0.5)	0.1(0.1)	5.2(1.9)
Gilmore	2.8(0.8)	0.1(0.1)	0	0	0	0	0.1(0.1)	0.2(0.1)	0.2(0.1)	0	0	1.7(0.4)
NB Whitewater	3.3(0.9)	0	0	0	0	0.5(0.1)	0	10.1(3.3)	0.1(0.1)	0	0	5.2(1.9)
Long	1.8(0.5)	4.1(0.8)	0	0	0	0.8(0.4)	0	0.1(0.1)	0	0	0.1(0.1)	3.3(0.9)
Big Springs	3.4(0.7)	0	0.1(0.1)	0	0	0	0.6(0.2)	0.6(0.3)	0.1(0.1)	0	0	2.2(0.9)
E Burns Valley	35.0(7.9)	0	0	0	0	0	0	2.5(1.7)	0.2(0.1)	0.5(0.2)	0	0.2(0.1)
W Beaver	0.5(0.1)	0	0.4(0.1)	0	0	0	0	0.8(0.2)	1.5(0.4)	0.5(0.1)	0.1(0.1)	9.0(4.4)
Upper Money	0.1(0.1)	0	0.1(0.1)	0	0	0	0	0.1(0.1)	0	0.1(0.1)	0	1.1(0.3)
South Fork Root	0.2(0.1)	0	1.1(0.2)	0	0	0	0	0.4(0.1)	1.8(0.7)	0.1(0.1)	0.2(0.1)	0.6(0.2)
Trout Valley	20.1(6.8)	0	0	0	0	0	0	0	0	1.2(0.6)	0	0.1(0.1)
West Albany	0.4(0.1)	0	1.8(0.5)	0	0	1.1(0.3)	0	2.0(0.6)	0	0	0.4(0.1)	0
Lost	3.6(0.9)	0	0	0	0	0	0	0.3(0.1)	0	0.1(0.1)	0	11.3(2.6)
Pleasant valley	13.2(2.7)	0	0.1(0.1)	0	0	0	0	0.5(0.1)	0.5(0.1)	0.2(0.1)	0.1(0.1)	0.5(0.1)
Camp	6.3(1.4)	0	0.1(0.1)	0	0	0	0	1.6(0.7)	0	0.1(0.1)	0	1.2(0.4)
Bee	0	0	0.1(0.1)	0	0	0	0	18.4(5.1)	0	0.1(0.1)	0	1.0(0.2)
Spring	3.9(0.9)	0	0.2(0.1)	0	0	0.7(0.2)	0	0.5(0.2)	0	0	0.2(0.1)	0.4(0.1)

Table IIa cont.

Stream	*Simulidae*	*Tipulidae*	*Corixidae*	*Gyrinidae*	*Dytiscidae*	*Physella*	*Fish (no ID)*	*Brown Trout*	*Cottus sp.*	*Percidae*	*Rana sp.*	*Trout eggs*	*Isopoda*	**Total**
Gribben	0	0	0	0	0.1(0.1)	12.1(5.1)	0	0	0	0	0	0	0	23.5(5.5)
MBWhitewater	0	0.1(0.1)	0	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	1.6(1.3)	0	27.8(4.4)
SBWhitewater	0.1(0.1)	0.1(0.1)	0	0	0	0	0.2(0.1)	0	0	0.2(0.1)	0	0	0.4(0.1)	29.5(2.9)
Winnebago	0.1(0.1)	0	0	0	0.2(0.1)	0.6(0.3)	0.1(0.1)	0	0.1(0.1)	0	0	0	0.1(0.1)	22.7(8.5)
Forestville	0	0.1(0.1)	0	0	0	2.2(0.6)	0.1(0.1)	0	0	0	0	0	0	33.9(3.7)
Rush	0.1(0.1)	0	0	0	0.1(0.1)	0	0	0	0	0	0	0	0	6.3(1.5)
Daley	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0.2(0.1)	0.1(0.1)	0	0.1(0.1)	0	0	0.1(0.1)	0	16.2(3.6)
Trout Run	0	0.1(0.1)	0	0	0.1(0.1)	0.3(0.1)	0	0	0	0	0	0	0	21.7(2.1)
Beaver	0	0.1(0.1)	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	0	0	0.1(0.1)	0	14.1(2.6)
W Indian	0	0	0	0	0	0.1(0.1)	0	0	0	0	0	0	0	9.9(1.5)
Hay	0.1(0.1)	0	0.4(0.1)	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	0	0	1.0(0.6)	0	10.5(1.6)
Garvin	0	0	0	0	0	0	0.1(0.1)	0	0.1(0.1)	0	0.1(0.1)	0	0	22.5(3.2)
Pickwick	0.1(0.1)	0.1(0.1)	0	0	0	3.3(1.2)	0	0	0	0	0	0.1(0.1)	8.2(2.7)	40(7.1)
Pine	0.1(0.1)	0.2(0.1)	0	0	0	0.1(0.1)	0	0	0	0	0.1(0.1)	0	0	17.6(3.6)
Cedar Valley	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0.9(0.3)	0	0	0	0	0.1(0.1)	0.1(0.1)	0.2(0.1)	13.2(1.7)
Badger	0.1(0.1)	0.2(0.1)	0	0	0	1.1(0.4)	0	0	0	0	0	0.1(0.1)	0	7.6(1.1)
Wells	0.1(0.1)	0.7(0.2)	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0	0	0.1(0.1)	13.9(2.4)
Cold Spring	0	0	0	0	0.1(0.1)	0	0	0	0	0	0	0	0	24.4(2.8)
Torkelson	0.1(0.1)	0.5(0.2)	0	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0.1(0.1)	1.9(0.5)	21.5(3.4)
W Br Money	2.6(2.2)	0	0	0	0	0	0	0	0	0.1(0.1)	0	0	0	16.4(4.4)
Gilmore	0.10(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	0	0	0	0	0	0	1.2(0.3)	6.6(1.1)
NBWhitewater	0	0	0	0	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0.1(0.1)	5.2(1.3)	24.6(5.4)
Long	1.4(0.6)	0.1(0.1)	0	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0	0	11.8(1.9)
Big Springs	0	0	0	0.1(0.1)	0	2.7(1.7)	0	0	0	0	0	0.2(0.1)	0	10(2.3)
E Burns Valley	0	0.6(0.1)	0	0	0	2.9(0.8)	0	0	0	0	0.1(0.1)	0	5.8(1.5)	48.2(8.9)
W Beaver	0.1(0.1)	0.3(0.3)	0.1(0.1)	0	0.1(0.1)	1.6(0.4)	0.1(0.1)	0	0.1(0.1)	0	0	0	0	15.5(4.6)
Upper Money	0	0	0.1(0.1)	0	0	1.0(0.3)	0.1(0.1)	0	0	0	0	0	4.8(0.9)	7.4(1.1)
South Fork Root	0.3(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	0	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0	5.2(1.2)
Trout Valley	0	0.1(0.1)	0	0	0	6.2(2.9)	0	0	0	0	0	0	0	27.6(9.2)
West Albany	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	3.1(1.1)	0	0	0	0	0	0.1(0.1)	0.1(0.1)	9.2(1.6)
Lost	0.3(0.1)	0.2(0.1)	0	0	0.1(0.1)	0.3(0.1)	0	0	0	0	0	0	0	16.3(3.2)
Pleasant Valley	0	0.1(0.1)	0.1(0.1)	0	0.2(0.1)	0.1(0.1)	0	0	0	0	0.1(0.1)	0	4.7(1.4)	20.5(3.6)
Camp	0	0	0	0	0	0.8(0.5)	0	0	0	0	0	0.1(0.1)	2.0(0.5)	12.2(2.3)
Bee	0	0.1(0.1)	0	0	0	16.9(3.5)	0	0	0.1(0.1)	0	0	0	0	36.6(6.2)
Spring	0	0.8(0.3)	0	0	0	0.5(0.3)	0	0	0	0	0	0	0	7.4(1.4)

Table IIb. Mean prey taxa by number per fish in late winter diets of Brown Trout sampled in 35 southeastern Minnesota streams during the winter of 2010-13. Numbers in parentheses are SEM.

Stream	*Gammarus*	Baetidae	Emphemerellidae	Heptageniidae	Allocapnia	Isoperla	*Micrasema*	*Brachycentrus*	*Glossosoma*	Limnephilidae	Hydropsychidae	Chironomidae
Gribben	0.8(0.1)	3.4(1.1)	0.5(0.1)	0	0	0	0.1(0.1)	15.3(3.1)	1.9(0.4)	6.0(1.5)	0.1(0.1)	0.9(0.4)
MB Whitewater	0.8(0.4)	2.3(0.8)	0	0	0	0	0	0.3(0.1)	0.7(0.4)	0	0.3(0.1)	3.1(1.4)
SB Whitewater	0.1(0.1)	0.9(0.2)	0.1(0.1)	0.1(0.1)	0	0.1(0.1)	0.3(0.1)	2.3(0.6)	0.1(0.1)	0	0.2(0.1)	0.3(0.1)
Winnebago	1.0(0.3)	4.4(1.1)	0.4(0.1)	0.1(0.1)	0	0.1(0.1)	0.2(0.1)	5.8(2.0)	1.1(0.3)	0	0.1(0.1)	47.4(15.5)
Forestville	0.1(0.1)	3.2(1.1)	0	0	0	0.3(0.1)	0.4(0.1)	15.1(3.7)	3.9(0.9)	0.1(0.1)	0.3(0.1)	0.2(0.1)
Rush	0	7.1(1.4)	0	0	0	3.6(3.6)	0	0.5(0.5)	1.0(0.4)	0	0.1(0.1)	0
Daley	27.2(7.8)	3.7(1.2)	0	0	0	0	0	0.1(0.1)	0.3(0.1)	0.2(0.1)	0	1.3(0.4)
Trout Run	1.0(0.3)	0.5(0.2)	0	0	0	0.1(0.1)	0	0.8(0.2)	0.1(0.1)	0	0	0.9(0.3)
Beaver	0.6(0.2)	0.6(0.3)	0.1(0.1)	0	0.1(0.1)	0.2(0.1)	0.1(0.1)	17.1(4.4)	1.5(0.4)	0	0.3(0.1)	30.7(4.3)
W Indian	1.7(0.4)	4.3(1.2)	0	0	0	0	0	2.7(0.7)	0.1(0.1)	0	0	6.8(2.4)
Hay	3.8(1.1)	0	2.8(0.8)	0.1(0.1)	0	0	0	0.3(0.1)	0	0	0.6(0.2)	17.2(2.8)
Garvin	1.1(0.3)	0.5(0.1)	0	0	0	0	0	8.0(2.1)	1.8(0.9)	0.1(0.1)	0	2.2(0.6)
Pickwick	1.0(0.3)	0.4(0.2)	3.3(0.6)	0.1(0.1)	0	0	0	5.4(2.4)	0.1(0.1)	0	0.6(0.1)	12.0(4.3)
Pine	0.2(0.1)	0.2(0.1)	2.9(0.7)	0	0	1.5(0.5)	0.1(0.1)	3.9(0.9)	0.5(0.2)	0	1.2(0.3)	25.6(4.4)
Cedar Valley	6.9(1.8)	0.1(0.1)	2.0(0.3)	0.1(0.1)	0	0.1(0.1)	0	3.1(0.9)	0.2(0.1)	0	0.2(0.1)	9.3(1.6)
Badger	1.8(0.3)	1.1(0.2)	0.1(0.1)	0	0	0	0	0.8(0.6)	4.9(0.7)	0.1(0.1)	0.1(0.1)	4.3(0.9)
Wells	0.6(0.6)	2.5(1.8)	5.7(3.7)	0.3(0.2)	0.1(0.1)	0	0	0.2(0.2)	0	0	0.6(0.4)	2.0(0.8)
Cold Spring	9.7(2.3)	2.3(0.7)	0	0	0	0.1(0.1)	0	0.5(0.1)	0.2(0.2)	12.4(5.2)	0	0.2(0.1)
Torkelson	7.9(1.4)	0	0	0	0	0	0.1(0.1)	2.1(0.7)	3.8(1.1)	0.7(0.3)	0.1(0.1)	14.8(4.8)
W Br Money	0.1(0.1)	0	0.1(0.1)	0	0	0	0	18.3(6.1)	0	2.5(0.5)	0.8(0.2)	30.6(11.6)
Gilmore	3.6(1.1)	0.2(0.1)	1.3(0.3)	0	0	0	0.2(0.1)	0.7(0.3)	0.2(0.1)	0.1(0.1)	0	12.0(3.2)
NB Whitewater	1.1(0.5)	0.1(0.1)	0.3(0.2)	0.3(0.1)	0	0.1(0.1)	0	27.9(11.3)	0	0.1(0.1)	0	32.1(8.8)
Long	2.6(0.6)	2.3(0.6)	0.1(0.1)	0	0	0.1(0.1)	0	2.4(0.6)	0.1(0.1)	0	0.1(0.1)	16.9(3.4)
Big Springs	5.2(1.3)	0.2(0.1)	0.2(0.1)	0	0	0	0	5.1(2.8)	0.1(0.1)	0.1(0.1)	0.1(0.1)	1.3(0.3)
E Burns Valley	7.6(1.8)	0	0	0	0	0	0	1.1(0.3)	0	0.5(0.1)	0	0.5(0.3)
W Beaver	0.3(0.1)	0	0.9(0.2)	0	0	0.1(0.1)	0	35.9(6.5)	0.1(0.1)	1.9(0.5)	0.2(0.1)	1.0(0.2)
Upper Money	0	0	0.1(0.1)	0	0	0	0	0.5(0.2)	0	0.1(0.1)	0	23.3(3.7)
South Fork Root	0.7(0.2)	0	5.8(0.7)	0	0	0.2(0.1)	0	2.1(0.6)	1.3(0.6)	0.6(0.2)	1.7(0.4)	1.0(0.4)
Trout Valley	3.8(0.8)	0	0.2(0.2)	0	0	0	0	0	0.5(0.3)	0.1(0.1)	0	5.0(1.9)
West Albany	0.7(0.2)	0	4.7(1.1)	0	3.5(0.9)	0.3(0.1)	0	0.7(0.2)	0	0	0.1(0.1)	1.0(0.3)
Lost	9.2(5.0)	0	1.4(0.4)	0	0	0.1(0.1)	0	0.8(0.3)	0	0.9(0.7)	0.1(0.1)	85.3(17.2)
Pleasant valley	3.8(0.9)	0	0.2(0.1)	0	0	0.1(0.1)	0.2(0.2)	0.3(0.2)	1.1(0.4)	0	0.1(0.1)	1.7(0.7)
Camp	65.9(16.2)	0	0	0	0	0	0	1.8(0.4)	0.1(0.1)	0.1(0.1)	0.1(0.1)	2.8(2.1)
Bee	0	0	0.1(0.1)	0.1(0.1)	0	0	0	14.1(1.5)	0.1(0.1)	0.1(0.1)	0	0.1(0.1)
Spring	1.8(0.5)	0	0.3(0.1)	0	0	41.2(10.9)	0	0.2(0.1)	0	0	0	0.4(0.4)

Table IIb cont.

Stream	Simulidae	Tipulidae	Corixidae	Gyrinidae	Dytiscidae	*Physella*	Fish (no ID)	Brown Trout	*Cottus* Sp.	Percidae	*Rana* sp.	Trout eggs	Isopoda	Total
Gribben	0.1(0.1)	0.2(0.1)	0	0	1.3(0.3)	10.1(2.6)	0	0	0	0.2(0.1)	1.0(0.3)	0.1(0.1)	0	42.6(5.5)
MBWhitewater	0	0.1(0.1)	0	0	0.3(0.2)	0	0.1(0.1)	0.1(0.1)	0.3(0.2)	0	0.1(0.1)	0	0	16.5(2.1)
SBWhitewater	0	0	0.1(0.1)	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0.1(0.1)	0	0	0	20.4(1.7)
Winnebago	0	0.2(0.1)	0	0	0.1(0.1)	0	0.1(0.1)	0	0	0	0	0	0	61.1(16.7)
Forestville	0.2(0.1)	0.1(0.1)	0	0	0	0.2(0.1)	0	0.1(0.1)	0.1(0.1)	0	0	0	0	40.1(4.0)
Rush	0	0.3(0.3)	0	0	0	0.3(0.3)	0	0	0.3(0.2)	0	0	0	0	17.2(4.9)
Daley	0	0	0	0	0.1(0.1)	0.6(0.2)	0	0	0	0	0	0	0.1(0.1)	33.9(7.7)
Trout Run	0	0.1(0.1)	0	0	0.1(0.1)	0.3(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	0	0	3.9(1.0)
Beaver	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0	0.1(0.1)	0	0	51.9(7.9)
W Indian	0.2(0.2)	0.1(01)	0.1(0.1)	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0.4(0.2)	0	0	0	0	25.8(3.5)
Hay	0.1(0.1)	0.1(0.1)	0.2(0.1)	0	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0	25.7(3.4)
Garvin	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0.1(0.1)	0.1(0.1)	0	0	0	14.1(3.1)
Pickwick	6.7(1.5)	0.3(0.1)	0.1(0.1)	0	0.1(0.1)	3.6(1.1)	0.1(0.1)	0	0.2(0.1)	0	0	0	5.3(1.0)	40.2(7.3)
Pine	2.4(0.6)	0.3(0.1)	0	0	0	0.1(0.1)	0	0	0	0	0.1(0.1)	0	0	39.3(5.5)
Cedar Valley	0.2(0.1)	0.7(0.2)	0	0	0.1(0.1)	0.5(0.3)	0	0	0	0	0	0	0	23.8(3.9)
Badger	0.3(0.1)	0.2(0.1)	0	0	0.1(0.1)	0.5(0.2)	0	0.1(0.1)	0	0	0	0	0	14.6(1.4)
Wells	0	0	0	0	0	0	0	0	0	0	0	0	0	12.9(3.9)
Cold Spring	0	0	0.2(0.1)	0.1(0.1)	0.1(0.1)	0	0.1(0.1)	0	0	0	0	0	0	25.9(5.5)
Torkelson	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0	0	0	0	0	0	0	1.4(0.4)	30.6(5.8)
W Br Money	15.5(8.2)	0.1(0.1)	0	0	0.2(0.1)	0.1(0.1)	0.1(0.1)	0	0	0.3(0.2)	0.1(0.1)	0	0.1(0.1)	69.3(18.5)
Gilmore	0.1(0.1)	0.1(0.1)	0	0	0.1(0.1)	0	0.1(0.1)	0	0.1(0.1)	0	0	0.1(0.1)	0.6(0.2)	19.5(3.4)
NBWhitewater	0	0.2(0.1)	0	0	0	0	0.1(0.1)	0	0	0	0	0	3.4(2.1)	66.2(14.5)
Long	0	0.1(0.1)	0	0	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0	0	28.9(5.3)
Big Springs	0.1(0.1)	0.1(0.1)	0	0	0	0.6(0.5)	0	0	0	0	0	0	0.1(0.1)	12.9(3.5)
E Burns Valley	0	0.2(0.1)	0	0	0	0.9(0.2)	0	0	0	0	0	0	1.5(0.3)	12.5(2.3)
W Beaver	1.0(0.2)	0.2(0.1)	0	0	0.1(0.1)	0.6(0.5)	0.1(0.1)	0	0.2(0.1)	0	0	0	0	42.7(6.7)
Upper Money	0.1(0.1)	0	0.1(0.1)	0.1(0.1)	0	0.2(0.1)	0	0	0	0	0	0.1(0.1)	0.7(0.2)	25.2(3.7)
South Fork														17.8(2.3)
Root	2.5(0.7)	0.1(0.1)	0.1(0.1)	0	0.1(0.1)	1.0(0.4)	0	0	0.1(0.1)	0	0	0	0	
Trout Valley	0.1(0.1)	0	0	0	0	0.3(0.1)	0	0	0	0	0	0	0	10.2(2.1)
West Albany	0.1(0.1)	0.4(0.1)	0	0	0	0.2(0.1)	0.1(0.1)	0	0	0	0	0	0.1(0.1)	12.1(1.8)
Lost	3.1(0.8)	0.5(0.1)	0	0	0.3(0.1)	1.4(0.5)	0.1(0.1)	0.1(0.1)	0	0	0	0.1(0.1)	0	103.7(18.3)
Pleasant Valley	0	0.1(0.1)	0	0	0.1(0.1)	0.1(0.1)	0.1(0.1)	0	0	0	0	0	0.8(0.2)	8.9(1.3)
Camp	0	0.1(0.1)	0	0	0.1(0.1)	0.9(0.3)	0	0.1(0.1)	0.1(0.1)	0	0	0	7.0(1.4)	79.1(16.7)
Bee	0	0.4(0.1)	0.1(0.1)	0	0.1(0.1)	23.6(5.4)	0	0	0.4(0.1)	0	0	0	0	35.1(3.8)
Spring	0	4.1(1.8)	0	0	0	0.1(0.1)	0	0	0	0	0	0.7(0.7)	0	49.1(10.8)

Table IIIa. Mean dry weight (mg) per fish of aquatic invertebrate prey taxa in early winter diets of Brown Trout sampled in 35 southeastern Minnesota streams during the winter of 2010-13. Numbers in parentheses are SEM.

Stream	*Gammarus*	Ephemeroptera	Plecoptera	*Brachycentrus*	*Glossosoma*	Hydropsycidae	Limnephilidae	Chironomidae	Simulidae	Tipulidae	Isopoda	*Physella*	Total
Gribben	4.0(2.4)	NA	NA	39.2(9.3)	0.3(0.1)	NA	12.9(4.5)	NA	NA	NA	NA	100.7(42.2)	157.7(40.3)
MB Whitewater	2.4(0.4)	NA	NA	3.3(0.9)	0.1(0.1)	NA	NA	0.9(0.5)	NA	NA	NA	NA	5.7(1.4)
SB Whitewater	1.2(0.4)	1.0(0.3)	NA	57.6(16.3)	NA	NA	NA	0.2(0.1)	NA	NA	1.0(0.3)	NA	61.2(16.4)
Winnebago	71.4(30.7)	NA	NA	6.0(1.4)	NA	NA	23.7(14.1)	0.1(0.1)	NA	NA	NA	9.9(5.5)	111.3(33.9)
Forestville	NA	NA	NA	64.6(14.9)	1.1(0.5)	NA	NA	NA	NA	NA	NA	37.5(18.8)	84.3(18.8)
Rush	NA	2.6(1.2)	NA	NA	0.1(0.1)	NA	3.5(2.2)	0.1(0.1)	NA	NA	NA	NA	6.3(3.1)
Daley	22.4(5.6)	NA	NA	NA	NA	NA	3.5(1.8)	1.0(0.4)	NA	NA	NA	2.2(0.9)	30.9(6.7)
Trout Run	11.4(2.6)	NA	NA	13.9(5.8)	NA	NA	NA	0.1(0.1)	NA	NA	NA	2.8(1.3)	28.3(6.7)
Beaver	0.6(0.1)	0.3(0.1)	NA	43.9(8.0)	0.1(0.1)	NA	NA	0.6(0.1)	NA	NA	NA	NA	45.7(8.3)
W Indian	4.4(1.8)	0.1(0.1)	NA	23.4(7.4)	NA	NA	NA	0.1(0.1)	NA	NA	NA	NA	18.9(7.3)
Hay	15.5(2.9)	0.1(0.1)	NA	4.0(1.4)	NA	NA	NA	0.3(0.1)	NA	NA	NA	NA	19.9(3.4)
Garvin	18.1(3.8)	NA	NA	71.0(15.9)	0.4(0.1)	NA	12.2(6.7)	0.2(0.1)	NA	NA	NA	NA	102.1(16.8)
Pickwick	2.5(1.3)	NA	NA	NA	NA	NA	NA	3.2(0.7)	NA	NA	20.0(6.8)	27.6(10.3)	53.4(12.4)
Pine	NA	2.1(0.6)	NA	4.1(1.8)	0.1(0.1)	3.2(1.0)	NA	1.7(0.4)	NA	NA	NA	NA	11.3(2.4)
Cedar Valley	34.7(4.9)	0.1(0.1)	NA	0.7(0.4)	NA	NA	NA	0.3(0.1)	NA	NA	NA	7.7(3.2)	43.5(6.2)
Badger	5.9(1.5)	NA	NA	NA	0.2(0.1)	NA	1.5(0.5)	0.1(0.1)	NA	1.8(1.3)	NA	3.8(1.4)	13.5(2.7)
Wells	45.5(26.4)	1.7(0.4)	NA	NA	NA	33.9(16.8)	NA	0.1(0.1)	NA	6.5(2.1)	NA	NA	87.9(31.2)
Cold Spring	53.9(8.6)	NA	5.5(1.3)	(5.4(2.6)	1.1(0.3)	NA	11.5(2.5)	NA	NA	NA	NA	NA	77.5(9.2)
Torkelson	33.5(7.5)	NA	NA	12.3(4.0)	NA	NA	9.3(3.0)	0.8(0.3)	NA	7.7(2.8)	NA	NA	63.7(8.8)
W Br Money	NA	NA	NA	35.1(14.0)	NA	NA	9.5(2.9)	0.6(0.2)	1.1(0.9)	NA	NA	NA	46.5(15.5)
Gilmore	11.6(3.2)	0.2(0.1)	NA	1.3(0.6)	NA	NA	NA	0.2(0.1)	NA	NA	2.9(0.9)	NA	16.3(3.6)
NB Whitewater	13.5(3.6)	NA	NA	57.2(18.9)	NA	NA	NA	0.8(0.2)	NA	NA	12.6(3.1)	NA	84.1(22.5)
Long	7.3(2.2)	7.2(1.4)	2.7(1.4)	NA	NA	NA	NA	0.4(0.1)	0.6(0.2)	NA	NA	NA	18.2(2.9)
Big Springs	14.0(2.9)	NA	NA	2.7(1.4)	NA	NA	NA	0.2(0.1)	NA	NA	NA	22.6(14.5)	39.8(15.8)
E Burns Valley	145.0(32.8)	NA	NA	11.8(8.3)	NA	NA	2.7(1.2)	NA	NA	NA	14.2(3.8)	24.4(6.9)	198.6(36.1)
W Beaver	NA	NA	NA	4.4(1.4)	NA	NA	6.1(2.0)	1.1(0.5)	NA	5.7(5.2)	NA	13.5(3.7)	30.9(6.9)
Upper Money	NA	NA	NA	0.1(0.1)	NA	NA	0.3(0.3)	0.1(0.1)	NA	NA	NA	8.5(2.9)	20.8(3.6)
South Fork Root	NA	3.7(0.9)	NA	2.0(0.9)	0.2(0.1)	NA	NA	NA	0.2(0.1)	NA	NA	0.9(0.5)	7.1(1.6)
Trout Valley	56.8(18.5)	NA	NA	NA	NA	NA	6.2(2.9)	0.1(0.1)	NA	NA	NA	51.9(23.1)	115.1(38.7)
West Albany	NA	3.1(0.5)	NA	11.7(2.1)	NA	NA	NA	NA	NA	NA	NA	57.9(10.5)	72.9(13.3)
Lost	14.5(3.8)	NA	NA	1.7(0.8)	NA	NA	NA	2.0(0.4)	NA	5.0(2.5)	NA	4.9(1.7)	29.2(6.5)
Pleasant valley	32.0(6.6)	NA	NA	NA	0.1(0.1)	NA	NA	0.1(0.1)	NA	0.8(0.8)	11.5(3.5)	NA	44.6(8.9)
Camp	15.2(3.4)	NA	NA	9.1(4.5)	NA	NA	NA	0.2(0.1)	NA	NA	4.8(1.4)	13.6(8.8)	43.1(13.6)
Bee	NA	NA	NA	112.9(31.5)	NA	NA	NA	0.2(0.1)	NA	1.4(1.4)	NA	346.5(72.1)	461.1(76.9)
Spring	35.1(8.5)	NA	2.4(0.8)	5.5(2.2)	NA	NA	NA	NA	NA	3.1(1.2)	NA	6.6(4.5)	49.5(10.5)

Table IIIb. Mean dry weight (mg) per fish of aquatic invertebrate prey taxa in late winter diets of Brown Trout sampled in 35 southeastern Minnesota streams during winter of 2010-13. Numbers in parentheses are SEM.

Stream	***Gammarus***	**Ephemeroptera**	**Plecoptera**	***Brachycentrus***	***Glossosoma***	**Hydropsycidae**	**Limnephilidae**	**Chironomidae**	**Simulidae**	**Tipulidae**	**Isopoda**	***Physella***	***Total***
Gribben	3.3(0.7)	NA	NA	87.2(17.7)	0.3(0.1)	NA	65.0(17.1)	NA	NA	NA	NA	11.3(2.7)	167.2(29.1)
MB Whitewater	4.4(1.8)	NA	NA	1.7(0.9)	0.1(0.1)	NA	NA	0.4(0.2)	NA	NA	NA	NA	5.7(2.6)
SB Whitewater	0.4(0.2)	1.6(0.4)	NA	13.2(3.8)	NA	NA	NA	0.1(0.1)	NA	NA	NA	NA	15.3(3.9)
Winnebago	4.3(1.3)	7.8(2.0)	NA	32.9(11.8)	NA	NA	NA	5.9(1.9)	NA	NA	NA	NA	51.1(12.6)
Forestville	NA	5.7(1.9)	NA	86.2(21.3)	0.6(0.1)	NA	NA	0.1(0.1)	NA	NA	NA	NA	92.6(20.9)
Rush	NA	12.5(2.5)	14.5(14.5)	NA	0.1(0.1)	NA	NA	NA	NA	NA	NA	NA	27.2(16.5)
Daley	110.3(31.7)	6.5(2.2)	NA	NA	NA	NA	2.1(1.1)	0.3(0.1)	NA	NA	NA	4.9(1.7)	124.3(31.4)
Trout Run	4.1(1.4)	0.8(0.3)	NA	4.5(1.3)	NA	NA	NA	0.1(0.1)	NA	NA	NA	NA	12.6(2.9)
Beaver	2.5(0.9)	1.1(0.5)	NA	97.2(25.1)	0.2(0.1)	NA	NA	3.8(0.5)	NA	NA	NA	3.1(1.1)	105.1(26.0)
W Indian	6.9(1.9)	7.6(2.2)	NA	15.7(4.2)	NA	NA	NA	0.8(0.3)	NA	NA	NA	NA	31.1(6.3)
Hay	15.7(4.3)	5.0(1.4)	NA	1.5(0.9)	NA	NA	NA	2.1(0.3)	NA	NA	NA	NA	24.5(4.9)
Garvin	4.3(1.2)	NA	NA	45.6(12.3)	0.3(0.1)	NA	1.0(0.7)	0.3(0.1)	NA	NA	NA	NA	52.7(13.3)
Pickwick	NA	5.8(1.0)	NA	30.9(13.8)	NA	NA	NA	1.5(0.5)	2.9(0.6)	NA	13.1(2.5)	30.3(9.4)	84.7(18.8)
Pine	NA	5.4(1.2)	5.2(1.9)	22.5(5.3)	NA	NA	NA	3.2(0.5)	NA	3.1(1.2)	NA	NA	39.7(6.3)
Cedar Valley	28.1(7.3)	3.4(0.6)	NA	18.0(5.4)	NA	NA	NA	1.1(0.2)	NA	NA	NA	4.4(2.5)	55.2(10.9)
Badger	3.8(0.8)	NA	NA	NA	0.5(0.1)	NA	NA	0.3(0.1)	NA	2.5(1.1)	NA	1.9(0.7)	9.6(1.9)
Wells	2.8(2.4)	14.5(6.8)	NA	NA	NA	3.4(2.6)	NA	0.2(0.1)	NA	NA	NA	NA	21.1(7.4)
Cold Spring	39.5(9.5)	4.1(1.2)	0.2(0.2)	3.0(0.9)	NA	NA	133.6(56.9)	NA	NA	NA	NA	NA	180.7(56.4)
Torkelson	32.0(6.0)	NA	NA	12.3(4.0)	0.6(0.2)	NA	7.5(3.4)	1.8(0.6)	NA	NA	NA	NA	54.4(9.8)
W Br Money	NA	NA	NA	104.5(34.4)	NA	NA	13.1(2.8)	3.8(1.4)	6.6(3.5)	NA	NA	NA	128.2(36.4)
Gilmore	14.7(4.2)	2.2(0.6)	NA	4.3(2.2)	NA	NA	NA	1.5(0.4)	NA	NA	1.6(0.5)	NA	24.5(5.4)
NB Whitewater	4.7(2.2)	NA	NA	158.9(64.3)	NA	NA	NA	4.0(1.1)	NA	NA	8.4(5.2)	NA	176.3(64.7)
Long	10.6(1.9)	4.0(0.7)	NA	14.0(2.5)	NA	NA	NA	2.1(0.3)	1.1(0.2)	NA	NA	NA	32.1(5.8)
Big Springs	14.0(2.9)	NA	NA	2.7(0.1)	NA	NA	NA	0.3(0.1)	NA	NA	NA	22.6(14.5)	50.9(16.2)
E Burns Valley	31.6(7.5)	NA	NA	5.2(1.7)	NA	NA	2.5(0.8)	NA	NA	NA	3.7(0.7)	7.5(2.2)	50.8(9.1)
W Beaver	NA	NA	NA	191.3(34.9)	NA	NA	21.2(3.9)	NA	NA	4.1(0.7)	NA	5.2(0.9)	222.1(36.4)
Upper Money	NA	NA	NA	2.3(0.9)	NA	NA	0.3(0.3)	NA	NA	NA	1.7(0.6)	2.1(0.3)	8.5(1.7)
South Fork Root	NA	19.8(2.5)	NA	11.1(3.2)	0.2(0.1)	NA	NA	NA	1.0(0.3)	NA	NA	9.1(3.7)	41.3(6.1)
Trout Valley	10.8(2.4)	NA	NA	NA	0.1(0.1)	NA	0.6(0.4)	0.7(0.3)	NA	NA	NA	2.7(1.5)	15.2(2.6)
West Albany	NA	8.2(1.9)	13.8(3.6)	4.1(1.4)	NA	NA	NA	0.2(0.1)	NA	NA	NA	4.9(1.7)	31.5(5.8)
Lost	37.5(20.3)	NA	NA	NA	NA	NA	10.0(7.5)	15.5(3.1)	NA	10.8(2.8)	NA	22.9(9.8)	103.2(29.2)
Pleasant valley	9.2(2.1)	NA	NA	NA	0.2(0.1)	NA	NA	0.3(0.1)	NA	1.7(1.7)	2.1(0.5)	NA	13.6(2.9)
Camp	159.5(39.2)	NA	NA	10.6(2.6)	NA	NA	NA	0.5(0.3)	NA	NA	17.2(3.6)	15.3(4.9)	203.2(41.4)
Bee	NA	NA	NA	86.7(9.4)	NA	NA	NA	0.3(0.1)	NA	19.0(5.4)	NA	483.0(112.4)	588.9(116)
Spring	16.1(4.7)	NA	139.5(36.9)	2.0(1.0)	NA	NA	NA	NA	NA	15.5(7.0)	NA	1.6(0.9)	175.1(36.1)

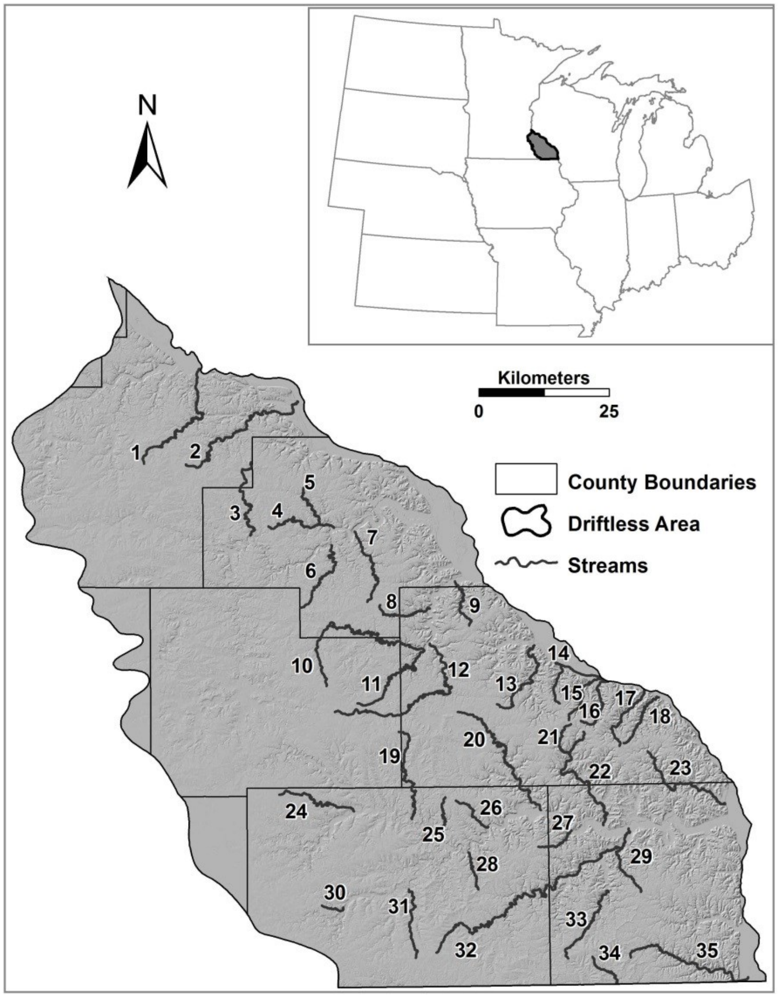

Figure 1. Map of the Driftless Ecoregion of southeastern Minnesota and 35 streams sampled for Brown Trout during winter of 2010-13. (1) Hay Creek; (2) Wells Creek; (3) Cold Spring Brook; (4) West Albany Creek; (5) Spring Creek; (6) Long Creek; (7) West Indian Creek; (8) Beaver Creek; (9) Trout Valley Creek; (10) North Branch Whitewater River; (11) Middle Branch Whitewater River; (12) South Branch Whitewater River; (13) Garvin Brook; (14) Gilmore Creek; (15) East Burns Valley Creek; (16) Pleasant Valley Creek; (17) Pickwick Creek; (18) Cedar Valley Creek; (19) Trout Run Creek; (20) Rush Creek; (21) West Branch Money Creek; (22) Upper Money Creek; (23) Pine Creek; (24) Lost Creek; (25) Torkelson Creek; (26) Big Springs Creek; (27) Daley Creek; (28) Gribben Creek; (29) Badger Creek; (30) Forestville Creek; (31) Camp Creek; (32) South Fork Root River; (33) West Beaver Creek; (34) Bee Creek; (35) Winnebago Creek.

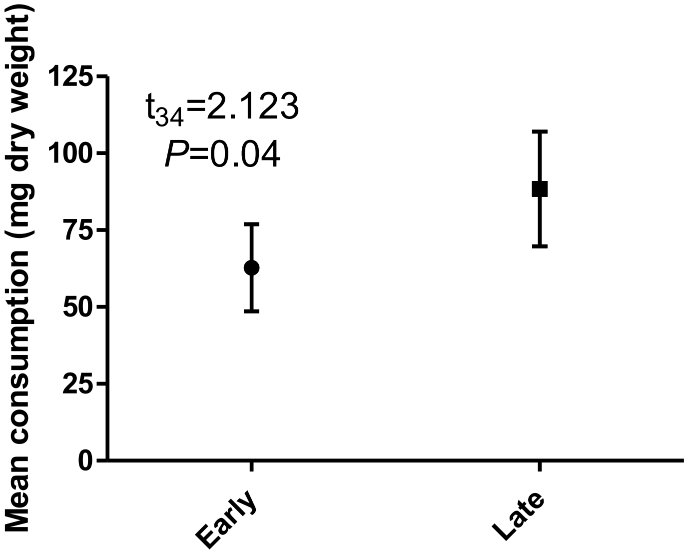

Figure 2. Comparison of mean prey consumption (total mg dry weight prey consumed) by Brown Trout in 35 southeastern Minnesota streams during early (late Nov – early Jan) and late (late Jan-early April) winter 2010-13. Error bars = 1SEM.

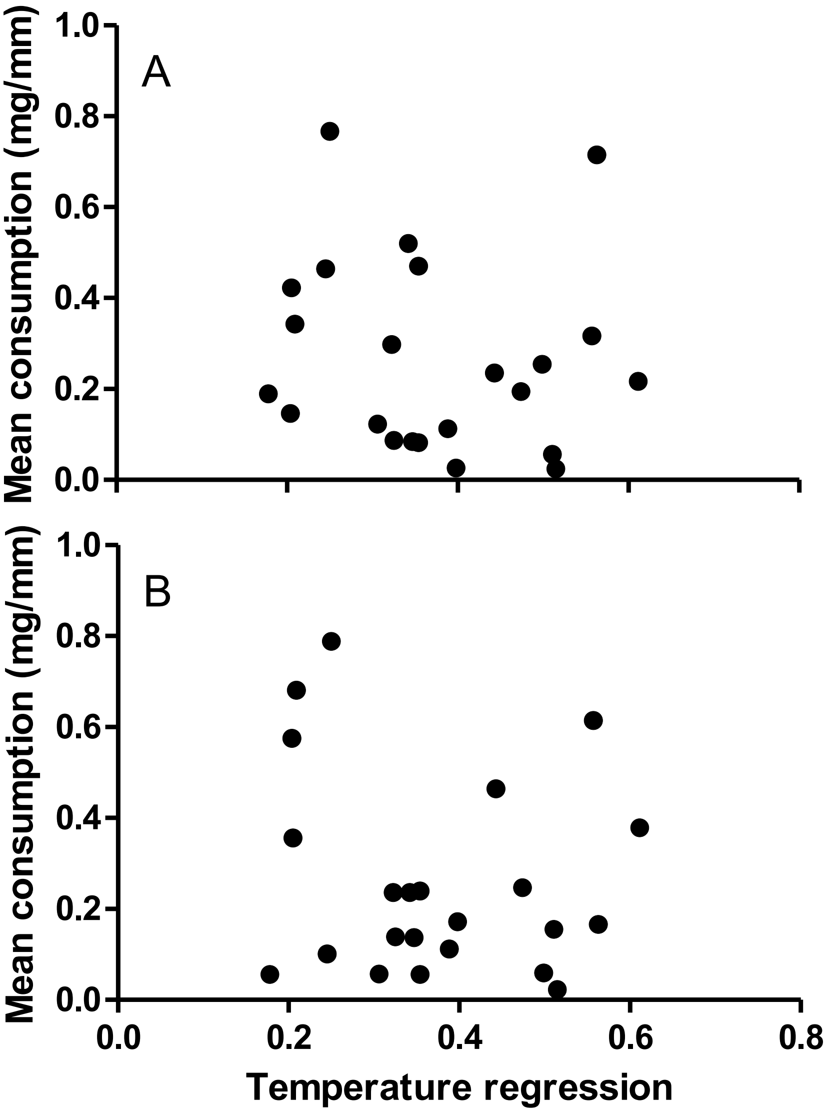

Figure 3. Relationships between mean Brown Trout consumption (total mg dry weight prey *mm total length of trout^{-1}) and groundwater input (slope from air/water temperature regressions from Krider et al. 2013) for 23 streams in southeastern Minnesota. Slopes closer to 0 reflect more groundwater input while slopes closer to 1 reflect less groundwater input.

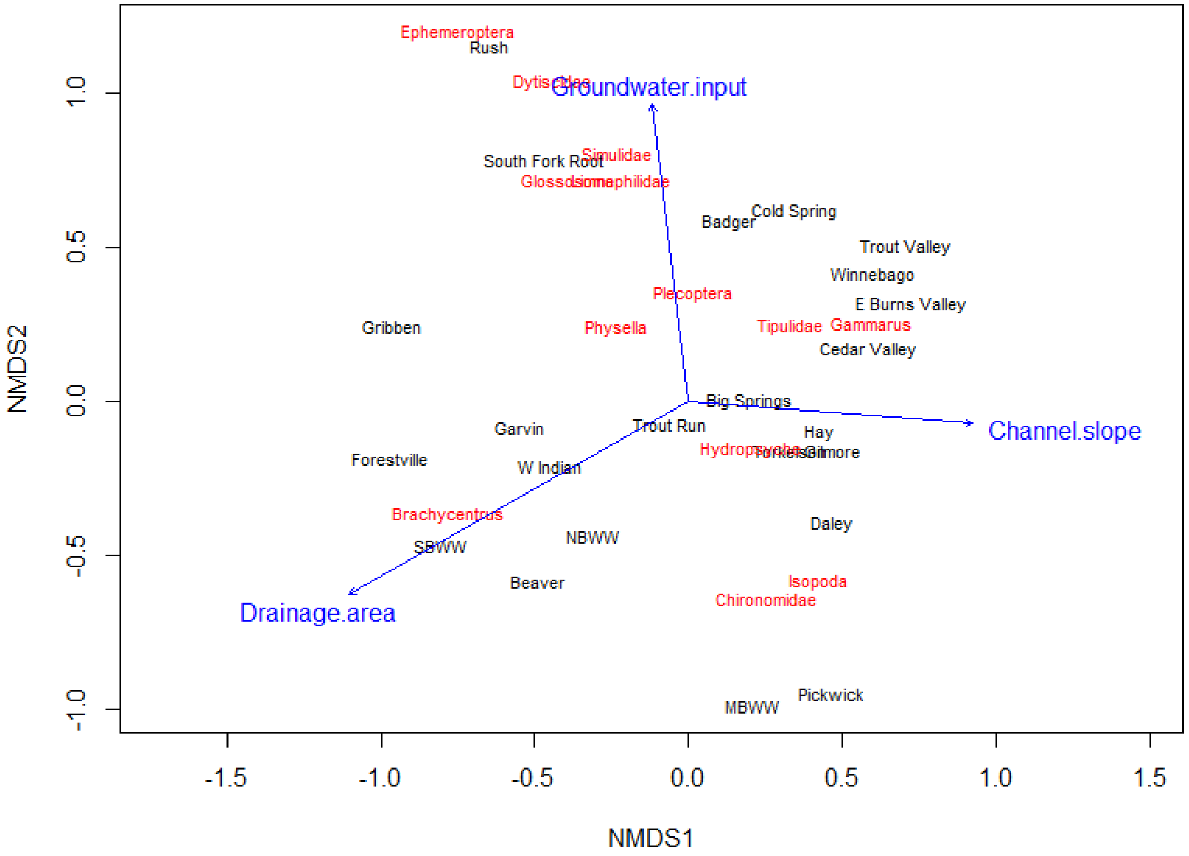

Figure 4. NMDS analyses of Brown Trout diet for streams sampled during early winter 2010-13 using taxa proportion of total diet by dry weight. Streams closer to one another had more similar diet composition than streams further apart. Arrows indicate direction of increasing drainage area, channel slope, and groundwater input.

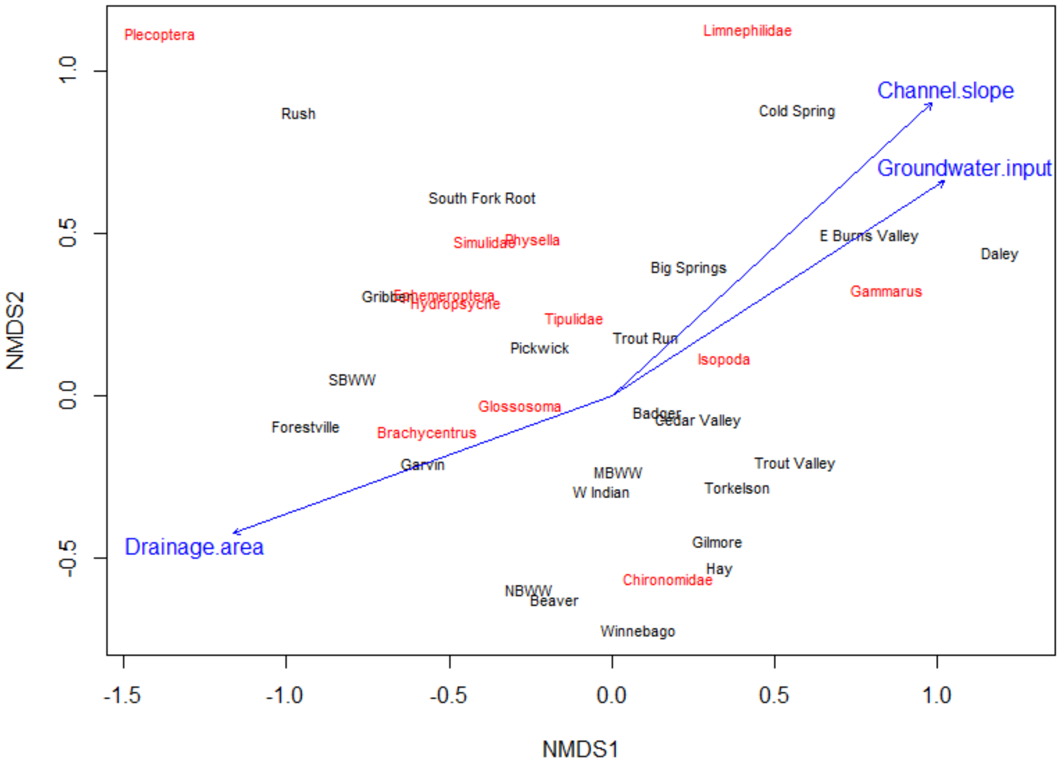

Figure 5. NMDS analyses of Brown Trout diet for streams sampled during late winter 2010-13 using taxa proportion of total diet by dry weight. Streams closer to one another had more similar diet composition than streams further apart. Arrows indicate direction of increasing drainage area, channel slope, and groundwater input.

Chapter 2

Winter growth and condition of Brown Trout *Salmo trutta* in groundwater-dominated streams.

(Formatted for Canadian Journal of Fisheries and Aquatic Sciences)

W. E. French*, University of Minnesota Conservation Biology Program,
University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

B. Vondracek, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit[1], University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

L. C. Ferrington Jr., Department of Entomology, University of Minnesota
University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

J. C. Finlay, Department of Ecology, Evolution and Behavior
University of Minnesota, 1987 Upper Buford Circle St. Paul, MN 55108, USA

D. J. Dieterman, Fisheries Research, Minnesota Department of Natural Resources, 1801 South Oak Street, Lake City, MN 55041, USA

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[1] The Unit is jointly sponsored by the U. S. Geological Survey, the University of Minnesota, the Minnesota Department of Natural Resources, the U. S. Fish and Wildlife Service, and the Wildlife Management Institute

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Running headline: Winter trout growth

*Corresponding author. Hodson Hall Rm 226, 1980 Folwell Ave St. Paul, MN 55108. Email: fren0104@umn.edu. Phone:

Abstract

Although winter is typically considered a stressful or dormant period for stream dwelling fish populations, localized habitat characteristics may mitigate the effect of winter and benefit fish populations. Specifically, groundwater input may buffer water temperature, reduce or eliminate ice formation, and allow fish to maintain higher activity rates and more efficient functioning of metabolic processes. This study examined the growth and condition of Brown Trout in 24 groundwater-dominated streams. Overwinter growth and condition were examined from uniquely marked individuals in relation to the effects of groundwater input and diet quality (amount and caloric density of prey). Mean Brown Trout overwinter growth was positive in 17 of 24 streams examined in this study, and there was no significant change in condition between early and late winter. Juvenile fish grew faster than adults, and there was no significant difference in condition between adults and juveniles. Groundwater input positively influenced growth for both adults and juveniles, likely mediated through buffering of winter water temperature. Winter water temperature buffered by groundwater appeared to benefit growth and condition of Brown Trout in southeastern Minnesota streams.

Keywords: winter, Brown Trout, growth, condition, ground water

Introduction

Winter has traditionally been thought of as a period of dormancy for aquatic ecosystems, and as a result has often not been the focus of study for fisheries scientists. This mindset has resulted in a seasonal gap of knowledge, even for otherwise often-studied taxa. For example, in contrast to other seasons, Salmonid ecology during winter has received limited study, and relatively little information describing stream Salmonids during winter is available. Recently, researchers have begun to appreciate the potential importance of winter for fish populations, and increased effort is being directed towards winter research (Brown et al. 2011; Hayden et al. 2013; Weber et al. 2013; French et al. 2014).

The overwinter period may be a stressful time for fish. Growth decreases during the winter season, and mortality can be high (Schultz and Conover 1999; Post and Parkinson 2001). Decreases in growth are generally attributed to the effects of decreased temperature on trout physiology and energetics (Elliott et al. 1995), but reduced availability of prey (e.g., terrestrial invertebrate inputs and aquatic invertebrate emergences) may also play a role. Biro et al. (2004) found overwinter mortality of age-0 fish (60-80%) because of depletion of lipid reserves to be a primary limiting factor for rainbow trout *Oncorhynchus mykiss* recruitment. Similarly, Kelly-Quinn and Bracken (1990) found many adult trout experienced an energy deficit and subsequent decline in condition during winter. Formation of subsurface ice significantly reduced survival of Atlantic Salmon *Salmo salar* in a Canadian stream by reducing available habitat (Linnansaari et al. 2010). Similarly, winter was identified as the season of slowest growth for Brook Trout *Salvelinus fontinalis* in West Brook Massachusetts, USA due to low water temperatures combined with increased flows (Xu et al. 2010). Juvenile Brown Trout *Salmo trutta* experienced a loss in body mass and reduction in condition in experimental streams with water temperatures maintained at 1-2^{o}C from November through March (Koljonen et al. 2012).

Temperature influences energetic demands of trout, as well as their ability to capture and digest prey. Therefore, water temperature can have a direct impact on trout foraging behavior, and subsequently growth and survival. A significant amount of research has been directed toward the effects of temperature on energy budgets and growth in Brown Trout. Trout are generally able to more effectively capture and digest prey at higher temperatures (Elliott 1972). However, as temperatures increase, fish must consume a greater amount of food to balance the demands of their rising metabolic rate (Railsback and Rose 1999). Additionally, as fish near the upper limits of their thermal tolerance the amount of food they can consume decreases, increasing a possible energy deficit. Elliott (1976a) calculated energy budgets for Brown Trout over a range of temperatures from 3.8-21°C, and improved these models with further experiments (Elliott et al. 1995). Elliott (1975a, 1976a) found Brown Trout achieved their maximum growth efficiency in a narrow temperature range between 8-11°C at maximum rations, although the temperature for optimum growth decreased as rations decreased. The temperature for optimum growth is closely tied with ration size; for example, optimum growth occurs at 4°C with rations just above maintenance levels (Elliott 1975a). Maximum feeding rates, as well as the amount of food consumed by

Brown Trout, is also influenced by 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 1976c).

Temperature also has an effect on the rates of change (both positive and negative) in percent body fat, protein and energy levels (Elliott 1976b). Rates of change were generally low at low temperatures but increased as temperature increased, although greater rations allowed trout to maintain stable levels of body composition at temperatures up to 21°C. Fluctuating temperatures, even within an acceptable range for growth can have negative impacts on trout. Brown Trout exposed to fluctuating temperature regimes at low flow levels experienced reduced growth rates (Flodmark et al. 2004). However, the effect of temperature was reduced at higher flow levels. Temperature can also affect foraging behavior of stream dwelling salmonids. As temperatures drop, the ability of fish to swim and avoid predators becomes reduced (Brown et al. 2011). Temperature was the driving factor underlying the switch from a diurnal to a nocturnal feeding strategy in Atlantic salmon *Salmo salar* (Fraser et al. 1993). This change in strategy allowed the salmon to hide during the day, and forage at night when predation risk was minimal.

Near freezing temperatures reduce the ability of trout to swim, forage, and digest prey. Prey availability is often lower, especially with regard to terrestrial invertebrates and trout foraging activity is often reduced from summer levels. Although continued feeding during the winter appears to be fairly common (Cunjak and Power 1987; Kelly-Quinn and Bracken 1990; French et al. 2014), the energy density of ingested prey may be important, because the ability of trout to efficiently process ingested food is reduced at lower temperatures (Elliott et al. 1995). Brocksen & Bugge (1974) found that assimilation efficiency in rainbow trout decreased from a peak of 84.8% at 20C to 71.8% at 5C.

Winter water temperatures and habitat conditions are often harsh in the majority of temperate, surface water dominated streams. Near freezing water temperatures, ice formation (surface, anchor, and frazzle), and reductions in available habitat from ice blockage and reduced flows are some of the primary mechanisms governing winter severity for stream dwelling Salmonids (Brown et al. 2011). However, streams whose thermal regimes are dominated by direct groundwater input may have significantly different winter thermal regimes than surface water-dominated streams, and often support unique aquatic communities. Groundwater inputs may provide thermal refugia for stream trout during winter, much as they can provide cool water refuges during summer. The winter-warm conditions of groundwater discharge have been associated with increased winter survival of brook trout in Wisconsin (Hunt 1969) and rainbow trout in Idaho (Smith and Griffith 1994). Groundwater input buffers water temperatures, reduces or prevents ice formation, and can maintain higher base flows in winter. Therefore, winter may be less severe for trout in groundwater-dominated streams than surface-water dominated streams.

In this study, growth and condition of brown trout were examined in 24 groundwater-dominated streams in winter; significantly broader in scope than previous studies, which typically examined a single population of trout within a single stream. This study examines potential mechanisms governing winter growth of stream trout. Finally, this study provides an in-depth examination of trout populations in groundwater-dominated streams during winter, an underrepresented area of research for these systems. The objectives were to: (1) quantify and compare patterns of Brown Trout growth and condition during winter; and (2) examine the relationship of groundwater input and diet composition with Brown Trout winter growth. Linear mixed effects models were used to evaluate temperature and diet variables to identify relationships with Brown Trout winter growth.

Methods

Study area

Study sites were located within Southeastern Minnesota, in part of the Driftless Ecoregion. The region is characterized by karstic geology, with a large number of groundwater dominated streams that support cold-water fishes and invertebrates. These streams support an important recreational fishery, primarily for Brown Trout, although Rainbow Trout and Brook Trout are also present in significant numbers (Thorn et al. 1997; Gartner et al. 2002). Sampling sites consisted of a 150m reach of stream containing multiple pools, riffles, and runs. Sites were selected to be wadeable and effectively sampled by a backpack electrofisher, and stream wetted width was typically between 2m and 10m. Mean depth was generally < 1m, although deeper pools were present at some sites. Groundwater input from springs and seeps maintained stream water temperatures above freezing and prevented ice formation at most sites (Krider et al. 2013).

Fish collection, growth, and condition

Brown trout were collected from 24 groundwater-dominated streams in Southeastern Minnesota during the winters of 2010-13 using backpack electrofishing gear (Smith Root; Washington, USA; LR 20B) (Table 1). Each stream was sampled during early (November-December) and late (February-March) winter for a total of two sampling events per stream. After collection fish were placed in in-stream holding pens, anesthetized with an immobilizing dose of tricaine methanesulfonate (MS 222), weighed ± 1g and measured ± 1mm. Up to 150 trout per stream collected during early winter were tagged in the anterior portion of the body cavity with 9mm passive integrated transponder (PIT) tags (Biomark Inc.; Idaho, USA) to track growth (mg/g/day) and condition between sampling events. Relative weight (Wr) was used as an index of fish condition. Wr compares the weight-at-length of a fish to a regionalized standard for that species, values between 80 and 100 are generally considered acceptable for healthy populations (Anderson & Neumann 1996). Condition was only analyzed for fish $\geq$140mm TL; the smallest fish used to develop the standard weight equations for lotic Brown Trout established by Milewski & Brown (1994).

Analyses

Growth and condition were compared for two size categories: juvenile (≤240 mm TL) and adult (> 240mm TL) Brown Trout. Brown Trout in the region typically reach maturity by 240 mm TL (Douglas Dieterman, Minnesota Department of Natural Resources; personal communication 2013). Mean early winter, late winter, and the change in Wr of juvenile and adult Brown Trout were compared with 95% confidence intervals. Additionally, relationships between Brown Trout relative weight (Wr) and estimated groundwater input were examined using linear regression. Slopes from the air-water temperature regression equations developed by Krider et al. (2013) were used as an estimate of groundwater input. Slopes closer to one indicate a greater influence of air temperature on water temperature and less groundwater input, whereas slopes closer to 0 indicate a lesser influence of air temperature on water temperature, and more groundwater input. Predicted water temperature at 0°C ranged from 5.9°C for Cedar Valley Creek to 7.5°C for Big Springs Creek (Krider et al. 2013).

Linear mixed effects models fit by maximum likelihood were used to examine relationships between groundwater input, consumption, and diet quality on Brown Trout growth. Fixed effects examined included: groundwater input, trout prey consumption, diet quality (prey energy density) and year was modeled as a random effect (Table 2). Juvenile and adult growth was modeled separately to reduce bias from gamete production and spawning of adults in late autumn. Diet composition (Chapter 1) was incorporated into regression models to examine the effect of prey quantity and quality on winter growth. Prey taxa were assigned to either high energy (>4000 J/g) or low energy (<3000 J/g) categories based on energy densities reported by Cummins and Wuycheck (1971). These values accommodated the six most important prey taxa while establishing a substantial difference in energy density (1000 J/g) between categories. AICc was used to compare models to reduce the chance of over fitting due to small sample size and low K values (Burnham and Anderson 2002). Models with ΔAICc values of >2.0 were considered significantly different from one another. Mixed effects modeling was conducted using the lme function in the lme4 package in Program R (version 3.0.2)

Results

Growth and condition

Mean Brown Trout winter growth was positive in 17 of the 24 streams (Figure 1). Mean growth rates ranged from 2.75 mg/g/day in Daley Creek, to -1.22 mg/g/day in Pickwick Creek. There was significant individual variation within a stream; for example, several fish in Pickwick Creek that had positive winter growth. Juvenile fish typically had faster growth rates than adults from the same stream

Mean condition of Brown Trout was similar for adult and juvenile fish during early and late winter, and there was no significant change in condition between early and late winter (Figure 2). Relative weight calculations indicated fish were in generally good condition during winter, with mean Wr of 88.9 for all fish in early winter and 87.9 in late winter. Mean Wr values ranged from a high of 104.1 in early winter for Cold

Spring Brook to 72.1 in late winter from Pickwick Creek. There was a significant inverse relationship between the slope of the air-water regressions and late winter mean Brown Trout condition (Figure 3). Trout in streams with smaller slopes, indicative of increased groundwater input, generally had greater Wr values than fish from streams with larger slopes. There was a similar significant relationship between slope and overwinter change in Wr.

Mixed effects modeling

Groundwater input (slope of temperature regressions) was a coefficient in the top three growth models for juvenile and adult trout (Table 3). Growth was inversely related with slope, suggesting groundwater input had a positive effect on trout growth. Brown Trout in streams with smaller slopes for air-water regressions, indicative of increased groundwater input, had increased growth compared to fish from streams with larger slopes for air-water regressions. Addition of a prey quality variable did not improve model performance for juvenile (ΔAICc = 2.38, AICc weight=0.2), or adult growth (ΔAICc = 4.47, AICc weight = 0.09).

Discussion

The relationship between groundwater input and Brown Trout growth observed in this study suggests that water temperature buffered by groundwater input is an important factor governing winter growth. The majority of juvenile and adult Brown Trout in groundwater-dominated streams in this study experienced positive growth during winter. Similarly, Lobón-Cerviá and Rincón (1998), Dieterman et al. (2012), and

French et al. (2014) observed significant positive growth of Brown Trout during winter. Other studies have documented minimal or no growth of Brown Trout during winter in several systems including the Credit River, a Canadian tributary to Lake Ontario (Cunjak and Power 1987), the River Dodder, Ireland (Kelly-Quinn and Bracken 1988), West Brook Massachusetts, USA (Carlson et al. 2007), and in artificial stream experiments (Koljonen et al. 2012). Dissimilar stream temperature regimes likely contribute to the differences in growth observed across these studies (Table 4). Winter water temperatures where Brown Trout experienced positive growth during the winter were either significantly buffered by groundwater input (Dieterman et al. 2012, French et al. 2014), or mild local climate (Lobón-Cerviá and Rincón (1998). By contrast, studies where trout experienced no or minimal winter growth were conducted in streams with little groundwater or climatic buffering of water temperatures. For example, water temperatures were often just above freezing in the Credit River (minimum temperature 0.1 °C), West Brook (minimum temperature < 0.0°C), and the experimental stream (winter temperature range 1-2^{o}C) used by Koljonen et al. (2012).

Ice formation can be a significant stressor for stream dwelling trout, affecting available habitat and reducing the ability of trout to feed (Brown et al. 2011, Linnansaari and Cunjak 2010). Cunjak and Power (1987) documented surface ice cover of up to 22% in the Credit River during their study period. By contrast, most streams in this study had less than 10% ice cover and on no occasion did ice cover exceed 33%, suggesting groundwater input was sufficient to maintain water temperatures above freezing and prevent surface ice formation. Anchor and frazzle ice can negatively impact trout during winter by reducing access to habitat and causing stress to overwintering fish (Brown et al. 2011). Anchor and frazzle ice formation was not observed on any of the streams sampled in this study, likely because of the buffering effect of groundwater.

The differences in growth rates between juvenile and adult Brown Trout in this study support similar patterns observed by Dieterman et al. (2012). Juvenile brown trout typically exhibit faster growth rates than adult fish. This increased growth in age-0 fish can be influenced by a number of factors including habitat suitability, prey availability and sexual maturation (Dieterman et al. 2004; Harvey et al. 2006; Fowler et al. 2009).

In this study, prey quality was not a significant component when modeling winter growth of juvenile or adult Brown Trout. By contrast, Diterman et al. (2004) found variation in diet and energy richness of available prey were related to annual growth of Brown Trout in southeastern Minnesota streams, as manipulation of diet composition resulted in more accurate predictions of growth by bioenergetics modeling than manipulation of temperature. Differences in methodology may have contributed to these differing results, for example, Dieterman et al. (2004) used mean annual cohort growth rate, while we used winter growth measured for an individual trout in our analyses. Seasonal and individual variability in trout growth may have differentially impacted trout growth; however, it is difficult to directly compare our results to those of Dieterman et al (2004) due to the differences in methodology. Future research using a bioenergetics approach to investigate the consequences of specific diet composition on winter growth of Brown Trout would bridge the gaps between our study and Dieterman et al. (2004)

Several studies have found significant decreases in Brown Trout condition during winter. For example, Brown Trout experienced reduced condition during the winter in the Credit River, despite actively foraging (Cunjak et al. 1987). Kelly-Quinn and Bracken (1990) also noted a decrease in fish condition by the end of winter, particularly in mature (age-1+) brown trout. Cunjak et al. (1987) found that although brook trout continued to feed during the winter, fish condition declined throughout the early winter and remained low until spring. Low water temperatures limited the gastric evacuation rate, and ultimately food consumption and energy absorption. By contrast, in this study Brown Trout condition remained stable for juvenile and adult fish from early to late winter, and groundwater input had a significant positive effect on condition. The significant relationship between late winter fish condition, change in overwinter condition and the slopes of temperature regressions suggests that groundwater input can buffer water temperatures sufficiently to allow Brown Trout to maintain or increase their condition during the winter.

Conclusions

Winter has traditionally been considered a period of dormancy and inactivity for stream dwelling Salmonids. Groundwater input can effectively buffer water temperatures in winter, creating thermal conditions that benefit trout by increasing prey availability, foraging, growth, and metabolic efficiency. There was a positive relationship between groundwater input and Brown Trout winter growth and condition in this study. Fisheries managers may need to reconsider the importance of winter when considering management actions on stream trout populations, if trout in groundwater-dominated streams are able to grow and increase condition during winter. Specific management action to protect groundwater resources would likely benefit trout populations in groundwater-dominated streams. Expanding urban areas and changing land use practices will likely place greater demands on current aquifers. Reduced infiltration time for water on the landscape combined with greater human demands from the aquifer may result in lower groundwater flow to streams and lower quality habitat for trout.

Climate change has the potential to further impact these thermally sensitive ecosystems. Direct impacts of increasing air temperature and changes in precipitation, and indirect effects such as changes in groundwater temperature or aquifer recharge rates may have important consequences for trout populations. Changing climate may alter seasonal growth patterns of trout in southeastern Minnesota, causing seasons with cooler water temperatures, such as winter and early spring to account for a greater proportion of annual growth. Further research into the indirect effects of buffering groundwater on stream communities, current impacts of winter growth on trout population dynamics, and the potential for increased winter growth to compensate for reductions in summer growth rates as a result of climate change would allow managers to better address future challenges to groundwater-dominated streams in the Driftless Ecoregion .

Acknowledgements

We thank the following for assistance in the field: J Mazack, J McCullough, J Miller, L Krider, P Sherman, C DeGuire (University of Minnesota) J Hoxmeier and D Spence (Minnesota Department of Natural Resources). All animals used in this study were handled according to animal use and care guidelines established by the University of Minnesota IACUC committee. Funding for this study was provided by Environment and Natural Resources Trust Fund administered by the Legislative Citizens Committee for Minnesota Resources. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government

Table 1. Sample dates, the number of recaptured Brown Trout used for growth and condition analyses, slopes of air-water temperature regressions from Krider et al. (2013) where available, and locations of sampling sites for 24 southeastern Minnesota streams sampled for Brown Trout during the winter of 2010-13.

Stream	Early sample date	Late sample date	Fish recaptured	Regression slope	UTM coordinates
Big Springs Creek	12/19/2012	3/22/2013	15	0.178	588263, 4849436
Daley Creek	1/6/2011	3/26/2011	38	0.204	605606, 4845390
Cold Spring Brook	1/12/2011	3/15/2012	21	0.209	545284, 4904448
Trout Valley Creek	12/7/2012	3/7/2013	8	0.245	585480, 4889958
Gribben Creek	12/17/2010	3/25/2011	28	0.25	587631, 4839986
Torkelson Creek	11/18/2011	2/24/2012	21	0.322	581924, 4847176
Winnebago Creek	12/10/2010	3/15/2011	10	0.342	625126, 4823555
Garvin Brook	12/5/2010	3/3/2011	22	0.345	595503, 4873356
Gilmore Creek	1/7/2012	3/10/2012	28	0.347	603836, 4875961
Badger Creek	11/19/2011	3/15/2012	19	0.354	616819, 4838970
Hay Creek	12/1/2010	3/30/2011	11	0.388	532797, 4925080
South Fork Root River	12/14/2012	3/17/2013	12	0.398	592109, 4830366
Beaver Creek	11/19/2010	3/16/2011	8	0.443	577026, 4889127
Cedar Valley Creek	12/17/2011	3/3/2012	22	0.474	615026, 4866958
East Burns Valley	1/9/2013	3/21/2013	5	0.563	610408, 4875424
Pickwick Creek	12/16/2011	3/2/2012	24	0.611	620150, 4868856
Upper Money Creek	1/8/2013	3/21/2013	43	NA	607539, 4864328
Lost Creek	12/14/2012	3/16/2013	17	NA	564533, 4851249
Camp Creek	12/13/2012	3/16/2013	15	NA	576248, 4833717
West Beaver Creek	12/18/2012	3/20/2013	15	NA	612030, 4832019
Bee Creek	12/17/2012	4/3/2013	52	NA	615463, 4817668
West Albany Creek	12/6/2012	3/6/2013	21	NA	556396, 4905180
Pleasant Valley Creek	12/7/2012	3/7/2013	27	NA	559710, 4905870
Spring Creek	12/8/2012	3/8/2013	10	NA	612249, 4870078

Table 2. Fixed effects used for linear mixed effects modeling of winter growth of Brown Trout . Growth of juvenile (< 240mm TL) and adult (>240mm TL) trout were modeled separately. Slopes of air-water temperature regressions were obtained from Krider et al. (2013), and prey taxa energy densities from Cummins and Wuycheck (1971).

Variable	**Description**
Temperature regression	Slope from the temperature regression equation presented in Krider et al. (2013)
Dry weight early	Mean total dry weight of prey consumed in early winter sample
Dry weight late	Mean total dry weight of prey consumed in late winter sample
High energy early	Mean proportion of total dry weight of prey with an energy density >4000 J/g (*Gammarus,* Ephemeroptera, Plecoptera, *Physella*) during the early winter sample.
Low energy early	Mean proportion of total dry weight of prey consumed with an energy density <3000 J/g (Diptera, Trichoptera) during the early winter sample.
High energy late	Mean proportion of total dry weight of prey consumed with an energy density >4000 J/g (*Gammarus,* Ephemeroptera, Plecoptera, *Physella*) during the late winter sample.
Low energy late	Mean proportion of total dry weight of prey consumed with an energy density <3000 j/g (Diptera, Trichoptera) during the late winter sample.

Table 3. Mixed effects models and selected variables for juvenile and adult Brown Trout growth (mg*g^{-1}*day^{-1}) during the winters of 2010-13. The top three models and the global model are shown. Variables: (a) groundwater input; (b) high energy early winter; (c) low energy early winter; (d) dry weight early winter; (e) high energy late winter; (f) low energy late winter; (g) dry weight late winter.

Model	AICc	ΔAICc	AICc Weight
Juvenile			
1. Growth= 3.93 - 7.50(a)	57.98	0.00	0.67
2. Growth= 2.32 - 6.46(a) + 0.02(b)	60.37	2.38	0.20
3. Growth= 3.14 - 7.29(a) + 0.01(e)	61.77	3.79	0.10
4. Growth= 32.56 – 8.88(a) + 0.10(b) + 0.06(c) – 2.14(d) – 0.38(e) -0.35(f) + 1.31(g)	102.71	44.73	0.00
Adult			
1. Growth= 1.34 - 3.72(a)	36.22	0.00	0.82
2. Growth= 1.57 – 3.58(a) – 0.004(b)	40.69	4.47	0.09
3. Growth= 0.87 – 3.36(a) + 0.008(e)	41.02	4.80	0.07
4. Growth= 0.36 – 2.97(a) – 0.001(b) + 0.001(c) – 0.55(d) + 0.008(e) + 0.53(g)	82.43	46.21	0.00

Table 4. Summary information from previous studies examining Brown Trout winter growth.

Study	Location	Primary thermal regulation	Minimum winter temperature	Mean winter growth rate/change in condition
Dieterman et al. (2012)	Southeastern Minnesota, USA	Groundwater	NA	Growth: 0-0.1 mm/day
French et al. (2014)	Southeastern Minnesota, USA	Groundwater	6.0°C	Growth: 2.55 mg/g/day
Lobón-Cerviá and Rincón (1998)	Galicia, Spain	Air temperature	3.0°C	Growth: 1.4g / Month
Cunjak and Power (1987)	Ontario, Canada	Air temperature	0.1°C	Condition: -0.15 to -0.35
Kelly-Quinn and Bracken (1990)	Leinster, Ireland	Air temperature	mean Jan air temp ~3°C	Negative between Oct and Jan
Carlson et al. (2007)	Massachusetts, USA	Air temperature	0.0°C	Minimal or negative
Koljonen et al. (2012)	Laboratory	NA	1.2°C	Growth: -0.02 to 0.04 g/day

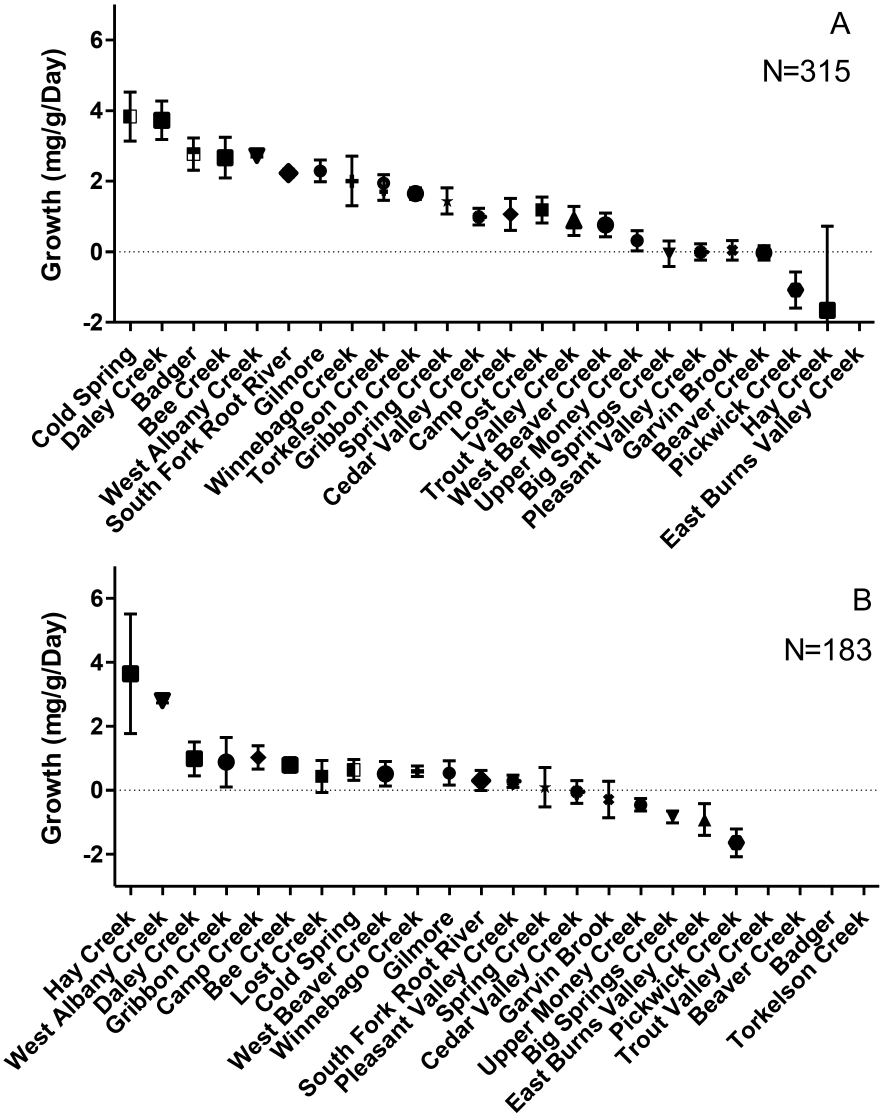


Figure 1. Mean growth (mg/g/day) of juvenile (≤240 mm, A) and adult (>240mm, B) Brown Trout recaptured from streams sampled during the winters of 2010-2013. Error bars = 1 SEM.

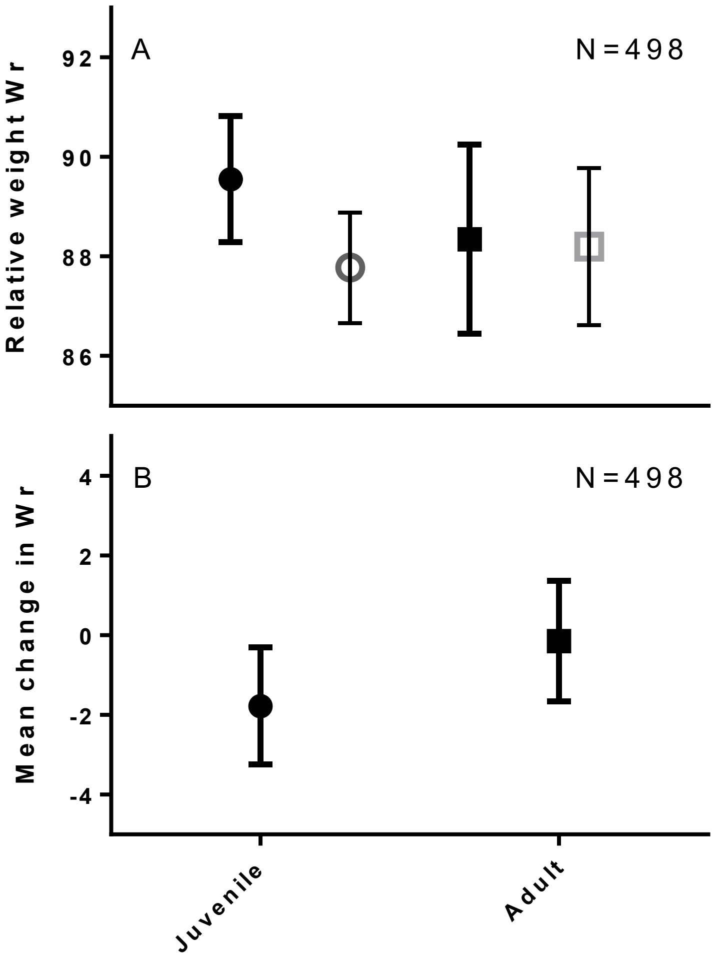


Figure 2. Mean relative weight (Wr) of juvenile (< 240 mm) and adult (>240 mm) Brown Trout recaptured from streams sampled during the winters of 2010-2013. (A) Mean relative weight during early (filled symbols) and late (open symbols) for juvenile (circle) and adult (square) trout. (B) Mean change in relative weight between early and late winter. Error bars = 95% CI.

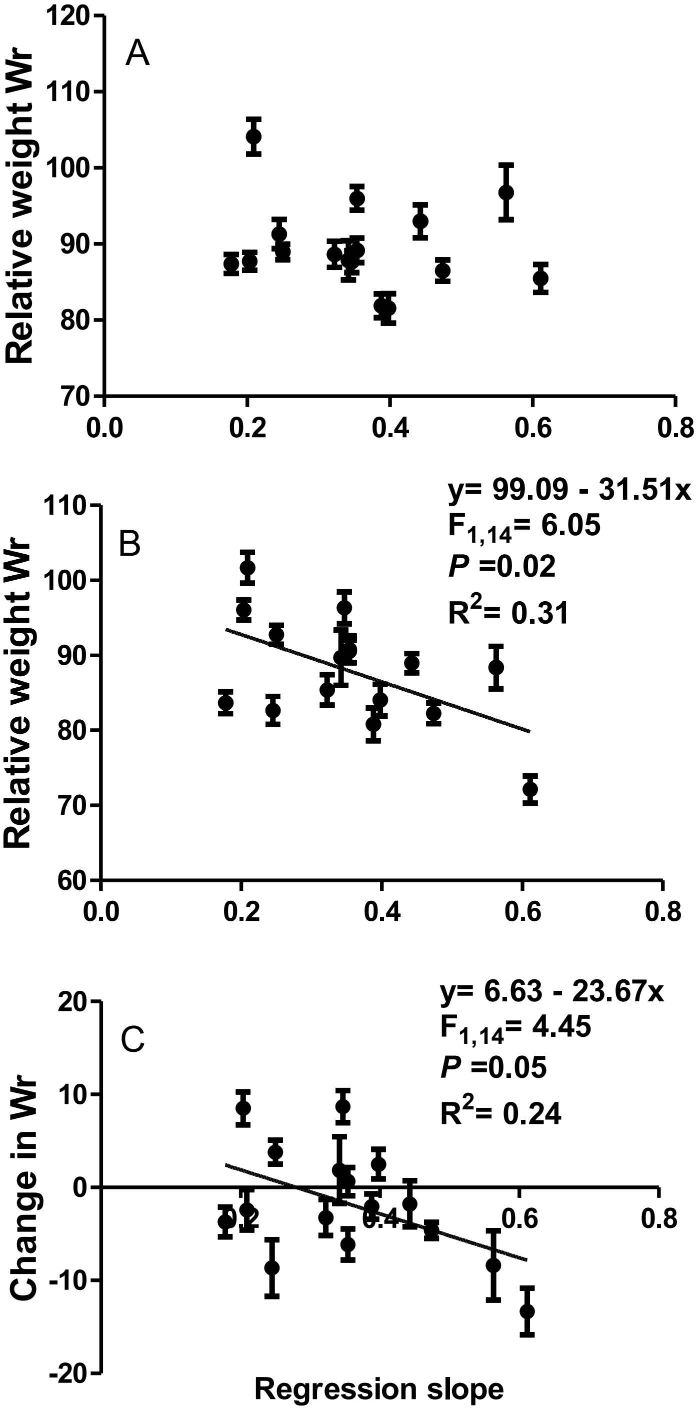


Figure 3. Regressions of mean stream early winter (A), late winter (B), and change overwinter (C) relative weight (Wr) of Brown Trout from 16 southeastern Minnesota streams during the winters of 2010-2013. Regression slope is from air/water temperature regressions from Krider et al. (2013). Error bars = 1 SEM.

Chapter 3

Seasonal Trophic Position of Brown Trout in Groundwater Dominated Streams.

(Formatted for submission to Transactions of the American Fisheries Society)

W. E. French*, University of Minnesota Conservation Biology Program,

University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

B. Vondracek, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit[1], University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

L. C. Ferrington Jr., Department of Entomology, University of Minnesota

University of Minnesota, 1980 Folwell Ave St Paul, MN 55108, USA

J. C. Finlay, Department of Ecology, Evolution and Behavior

University of Minnesota, 1987 Upper Buford Circle St. Paul, MN 55108, USA

D. J. Dieterman, Fisheries Research, Minnesota Department of Natural Resources, 1801 South Oak Street, Lake City, MN 55041, USA

[1] The Unit is jointly sponsored by the U. S. Geological Survey, the University of Minnesota, the Minnesota Department of Natural Resources, the U. S. Fish and Wildlife Service, and the Wildlife Management Institute

Running headline: Winter trout trophic position

*Corresponding author. Hodson Hall Rm 226, 1980 Folwell Ave St. Paul, MN 55108. Email: fren0104@umn.edu. Phone:

Abstract

Summer interactions of stream-dwelling Salmonidae within food webs have been frequently studied; however, relatively little is known regarding winter food webs. Groundwater may increase the availability of potential prey and create more favorable foraging conditions for trout by maintaining relatively warm winter temperatures. We used stable isotope analysis to examine the trophic position and food sources of Brown Trout *Salmo trutta* in the aquatic food webs of 12 streams across the Driftless Ecoregion of southeastern Minnesota. Two tissue types with differing turnover rates (fin and mucus) were used to examine temporal and spatial variation in relative food web position of brown trout. Although relative food web position varied both temporally and by stream, Brown Trout showed an increased reliance on terrestrially derived resources during the winter and there was a positive relationship between stream drainage area and Brown Trout trophic level. Our results suggest that allochthonous inputs may be of greater importance to stream food webs during periods of reduced autochthonous production, and ecosystem size has the potential to impact food webs in groundwater buffered streams.

Introduction

Winter is generally thought of as a period of stress and low productivity for temperate rivers and streams. Cooler water temperatures combined with reductions in terrestrial allochthonous inputs, algal productivity and potential ice cover, may cause fish species to experience reductions in growth, condition, and survival. In some cases, winter can have a negative effect on populations of stream dwelling fish communities, particularly stream trout (Salmonidae) (Cunjak and Power 1987, Kelly-Quinn and Bracken 1990, Harvey et al. 2006). Stream trout often support important recreational fisheries, and consequently, population dynamics of stream trout are of interest to fisheries managers (Dalton et al.1998; Peirson et al. 2001; Hart 2008). Relatively few studies have focused on the winter season, despite its importance for stream trout populations. Additionally, most previous studies have involved trout populations in lacustrine or surface-water dominated lotic systems.

Although temperate trout populations are faced with reduced growth and survival during winter, trout in streams with significant thermal buffering by groundwater may be less affected by winter conditions. Groundwater input can substantially increase water temperatures in streams when air temperatures are near or below freezing (Erickson et al. 2000, Krider et al. 2013). The temperature of groundwater is approximately equal to mean annual air temperature, and remains constant at 9.2 °C in southeastern Minnesota. As such, groundwater inflow buffers stream water temperature, moderating the influence of air temperature (Drake et al. 2010). During winter, groundwater input can maintain water temperatures above freezing and prevent the formation of ice cover, potentially increasing the availability of invertebrate prey while allowing trout to sustain higher activity levels and more efficient functioning of metabolic processes (Bouchard and Ferrington 2009; Anderson 2012).

Minnesota has 689 designated trout streams that represent a valuable natural resource with high economic, sport and aesthetic importance. Although Brook Trout *Salvelinus fontinalis* and Rainbow Trout *Oncorhynchus mykis* are present, Brown Trout *Salmo trutta* make up the majority of the recreational fishery. Recent reports found a wide range in growth rates and total Brown Trout yield across southeastern Minnesota streams based on studies during warmer months of the year (Dieterman et al. 2004, Dieterman et al. 2006). Season and individual variation explained a significant amount of variation in growth for Brown Trout collected in three southeastern Minnesota streams (Dieterman et al. 2012). Differences in prey availability and diet explained some of the variation observed in growth of individual Brown Trout in these studies. Although summer conditions are relatively well-understood, processes and patterns during warmer months do not adequately explain variability in annual growth and yield of trout (Dovciak and Perry 2002). Potential differences in thermal regimes and availability of food resources in winter may constrain trout productivity, resulting in differential growth rates and yields at annual scales.

Stomach content analysis has traditionally been used to construct food webs, and allows for a high degree of taxonomic precision. However, stomach contents may provide an incomplete picture of trophic structure, as it offers only a snapshot of the diet. Conversely, stable isotope analysis (SIA) offers a time-integrated method of examining trophic relationships between consumers and their prey (Peterson and Fry 1987, Vander Zanden et al. 1997). Stable isotope analysis provides information regarding trophic position of a consumer by examining ratios of C^{13} and N^{15} isotopes incorporated into tissue. Tissue $\delta^{13}C$ is commonly used to determine energy sources in fishes (Peterson and Fry 1987), and can be used to infer the relative importance of various prey to fish growth. Additionally, $\delta^{13}C$ tends to be relatively enriched in C3 terrestrial primary production when compared to aquatic primary production in small streams and can be used to examine the relative importance of autochthonous vs. allochthonous C inputs in a lotic food web (Finlay 2001; Ishikawa et al. 2012).

Trophic level can be inferred using the stable $\delta^{15}N$ ratio with approximately a 3.4 ‰ increase in $\delta^{15}N$ observed between predators and prey (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Foraging at higher trophic levels can be advantageous for trout as prey items generally increase in size and energy density as trophic level increases (e.g. fish vs. aquatic invertebrate prey), allowing trout to consume greater amounts of more energy rich food. Brown Trout often shift to a piscivorous diet as relative prey size and availability allow (Garman and Nielson 1982; L'Abée-Lund et al 1992; Jonnson et al. 1999). Trophic level and food chain length can be affected by ecosystem size, with larger ecosystems having longer food chains and predators feeding at higher trophic levels (Sabo et al. 2009; Sabo et al. 2010). Therefore, stream size may have a significant effect on Brown Trout diet, and consequentially growth and abundance in southeastern Minnesota streams.

The ability of SIA to integrate the diet history of consumers over a broad time interval facilitates the examination of stream food web structure. Additional benefits of SIA include the ability to identify which resources are incorporated into the tissue of a consumer, as well as the diet of all fish sampled (Chipps and Garvey 2002). Empty stomachs significantly reduce sample size in traditional diet studies but do not affect SIA, as non-lethal tissue samples can be taken from all fish captured. Non-lethal tissue samples for SIA can be collected quickly with a minimal amount of stress to the fish and effort in the field (Church et al. 2009; Andvik et al. 2010).

Tissue type and fish growth can influence assimilation and turnover rates of stable isotope signatures (Hesslein et al. 1993), and the specific tissue to use for SIA must be carefully considered. Use of SIA when slow growth is expected (e.g. winter) has been rare, because of low tissue turnover rates. However, a recent study has found that fish mucus is an effective non-lethal tissue for SIA, and is especially suited for slow growth conditions because of a rapid turnover rate (~30 day half-life) and continual regeneration, whereas muscle and fin tissue have turnover rates >140 day half-life (Church et al. 2009; Hanisch et al. 2010). Additionally, by choosing tissues with different turnover rates temporal changes in diet can be tracked. The faster turnover rate of mucus reflects recent seasonal consumption, whereas the slower turnover rate of fin tissue is more reflective of annual consumption.

Our goal was to examine the seasonal importance of various food sources for Brown Trout diets and food web structure in groundwater fed streams. Two tissue types (mucus and fin) with differing turnover rates for C and N were used for temporal comparisons of Brown Trout diet. The objectives were to: (1) Identify primary food sources of Brown Trout in 12 groundwater-fed streams in southeastern Minnesota during winter; (2) estimate the trophic level of Brown Trout in 12 southeastern Minnesota streams; and (3) examine relationships of Brown Trout trophic level with trout size and stream drainage area.

Methods

Study sites

This study focused on 12 streams in the Driftless Ecoregion of southeastern Minnesota (Table 1). The region is characterized by karstic geology, including a large number of groundwater-dominated streams that support cold water fish assemblages and populations of Ultra-Cold Stenothermic aquatic invertebrates. Brown Trout were the most abundant fish species in most streams, but other species such as Brook Trout *Salvenlinus fontinalis*, White Sucker *Catostomus commersonii* and Slimy Sculpin *Cottus cognatus* were also present in some streams. The sampling sites were ~150m long containing multiple pools, riffles, and runs.

Sample collection

Fish were collected with a backpack electro shocker (Smith Root; Washington, USA; LR 20B) from late February through March 2013 from 12 streams in southeastern Minnesota. Mucus and pectoral fin tissue were collected from up to 37 fish/stream for SIA using the methods described in Church et al. (2009). The most common invertebrate and fish prey taxa for trout were determined from stomach content data for each stream (Chapter 1). Slimy Sculpin, Brook Trout, and White Sucker ranging from 50-120mm were collected as potential fish prey. A sample of 15-30 of each prey item were collected, homogenized, and analyzed for stable carbon and nitrogen isotopes. Whole bodies were used for invertebrate samples, whereas fin tissue was used for fish prey. Invertebrates were kept alive for 24 hr post collection to purge their digestive systems, and then frozen. Up to four samples of autochthonous and allochthonous primary producers were collected from each stream. Samples were sent to the University of California Davis Stable Isotope Facility (http://stableisotopefacility.ucdavis.edu/index.html) where they were analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Analyses

Prior to analyses fish were split into two size groups: juvenile (< 240mm), and adult (> 240mm). As most Brown Trout in southeastern Minnesota streams reach maturity by 240mm (Douglas Dieterman, MN DNR personal communication), these size categories allowed comparisons of isotopic signatures between mature and immature fish. Brown Trout fin tissue has similar $\delta^{15}N$ and $\delta^{13}C$ to white muscle tissue (McCarthy and Waldron 2000). Therefore, the $\delta^{15}N$ and $\delta^{13}C$ values of mucus samples were adjusted by the equilibrium tissue difference for white muscle found in Church et al.

(2009) to reduce potential error between tissue types. $\delta^{15}N$ and $\delta^{13}C$ for juvenile and adult Brown Trout were analyzed separately by tissue (mucus and fin) and compared with an ANOVA (model: N or C = size class), and a Tukey's Honest Significant Difference post hoc test for multiple comparisons. Fin and mucus samples from Trout Valley Creek were compared with a t-test, as no fish greater than 240mm were collected.

Trophic level of sampled fish was estimated from $\delta^{15}N$ signatures using the method outlined in Vander Zanden et al. (1997). Trophic level of Brown Trout was calculated as:

$$((\delta^{15}\text{N Brown Trout} - \delta^{15}\text{N baseline}) * 3.4^{-1}) + 2$$

Available primary consumers varied among streams, thus mean primary consumer $\delta^{15}N$ was calculated for each stream and used as an estimate of $\delta^{15}N$ baseline. Brown Trout trophic level was estimated using $\delta^{15}N$ from fin (annual) and mucus (winter) tissues to allow seasonal comparisons within a stream. Linear regression was used to examine relationships between Brown Trout trophic level and total length, as well as mean Brown Trout trophic level and stream drainage area.

Results

Food sources

Significant differences in adult and juvenile Brown Trout fin tissue and mucus $\delta^{13}C$ were found in 10 of the 12 study streams (Table 2). In general, Brown Trout $\delta^{13}C$ signatures are consistent with diets from autochthonous and allochthonous food sources (Figure 1a,b). Although there was variation between streams, $\delta^{13}C$ of mucus tended to be enriched compared to fin tissue (Figure 2). A notable exception was Upper Money Creek, where mucus $\delta^{13}C$ was depleted relative to fin tissue. There were no significant differences for $\delta^{13}C$ between adult and juvenile Brown Trout in the majority of streams for fin tissue (3 of 11 significant) or mucus (2 of 11 significant). There was no consistent pattern of $\delta^{13}C$ enrichment between adult and juvenile Brown Trout across streams.

Trophic level

Significant differences in adult and juvenile Brown Trout fin and mucus $\delta^{15}N$ were found in all 12 study streams (Table 3). Mucus $\delta^{15}N$ was relatively depleted in comparison to fin $\delta^{15}N$ in all streams (Figure 3). $\delta^{15}N$ in adult Brown Trout was significantly enriched compared to juvenile Brown Trout for fin tissue (3 of 11 significant) and mucus (4 of 11 significant). Significant positive relationships between estimated trophic level and trout size were found in 7 of 12 streams sampled (Figure 4a, b, c). Four of the seven streams had significant relationships for both mucus and fin tissue derived trophic estimates. Two streams (Lost Creek and West Albany Creek) had significant relationships between TL and fin tissue estimates only, whereas Upper Money Creek had only a significant relationship with TL and mucus estimates.

There was a significant positive relationship between mean Brown Trout trophic level, and stream drainage area (Figure 5). Stream drainage area ranged from 7.8 km^2

for Upper Money Creek to 161 km^2 for Spring Creek. Mean estimated Brown Trout trophic level ranged from 3.25 in Upper Money Creek to 3.80 in Spring Creek.

Discussion

Food source

The $\delta^{13}C$ of tissues from invertebrate prey and Brown Trout suggest that the food webs of most of the 12 streams examined in this study may be derived from a combination of allochthonous (leaf litter, riparian grasses) and autochthonous (*Spyrogyra* and aquatic macrophytes) carbon sources. East Burns Valley Creek and Pleasant Valley Creek were exceptions, in that Brown Trout $\delta^{13}C$ was primarily from allochthonous C sources. In all but three streams (Lost Creek, Bee Creek, and the South Fork of the Root River), autochthonous production $\delta^{13}C$ was depleted compared to allochthonous production, a pattern consistent with small streams. In Lost Creek, Bee Creek, and the South Fork of the Root River, *Spirogyra* had depleted $\delta^{13}C$ compared to leaf litter or riparian grasses. Hadwen et al. (2010) found variation in filamentous algae $\delta^{13}C$ up to 8‰ between sampling dates at sites in 5 Australian streams. Variation in algal $\delta^{13}C$ can be caused by a wide variety of factors including temperature, stream flow, and depletion of the inorganic C pool by increasing algal and macrophyte biomass (Finlay et al. 1999; Finlay 2004; Hill and Middleton 2006). A combination of several of these factors may be responsible for the unexpectedly enriched $\delta^{13}C$ observed in Lost Creek, Bee Creek, and the South Fork of the Root River.

High primary productivity in streams can have a significant effect on $\delta^{13}C$ of in-stream algae growth. Algal and primary consumer $\delta^{13}C$ was enriched in more productive downstream sections (-31‰ to -23‰) of streams when compared to less productive headwater (-44‰ to -30‰) reaches, and dissolved CO_2 concentrations were identified as the leading cause of $\delta^{13}C$ variation (Finlay 2004). In our study, Bee Creek and Lost Creek contained substantial areas of dense algal and macrophyte growth, and $\delta^{13}C$ of algal growth in these two streams was enriched compared to terrestrially derived leaf litter. The high levels of primary productivity observed in these two streams may have sufficiently reduced dissolved CO_2 concentrations to enrich algal $\delta^{13}C$.

Brown Trout mucus $\delta^{13}C$ was significantly enriched relative to fin tissue for 9 of 12 streams sampled, which indicates Brown Trout within these streams may be shifting towards more allochthonously derived food sources during the winter, as autochthonous production decreases. Similarly, French et al. (2013) found shifts in the winter diet of Brown Trout toward allochthonously derived food sources in a groundwater-dominated stream in southeastern Minnesota. Mucus $\delta^{13}C$ was depleted relative to fin tissue in Upper Money Creek, suggesting a shift towards autochthonously derived food sources. The site on Upper Money Creek was in an area with little riparian tree cover, which may have limited the potential for allochthonous inputs of leaf litter while increasing the amount of light available for autochthonous production. Large amounts of filamentous algae (*Spirogyra*) were observed within the Upper Money Creek site during sampling events, and the $\delta^{13}C$ of potential Brown Trout prey

(Hydropsychidae*,* Chironomidae*,* and *Brachycentrus*) suggest that aquatic invertebrates fed on algal biomass.

Trophic Level

Significant differences among size classes for $\delta^{15}N$ were found for both fin tissue (Bee Creek, West Beaver Creek, South Fork Root River) and mucus (Bee Creek, West Beaver Creek, South Fork Root River, Upper Money Creek). In all cases, $\delta^{15}N$ was enriched in adult fish compared to juvenile fish, suggesting adult fish were feeding on enriched $\delta^{15}N$ prey and/or at a higher trophic level than juvenile fish. The largest Brown Trout were found in Bee Creek, West Beaver Creek, and South Fork Root River and potential fish prey species (Slimy Sculpin and White Sucker *Catostomus commersonii*) were also present. Upper Money Creek was the only stream with a significant difference in $\delta^{15}N$ between Brown Trout size classes for mucus. Adult fish in Upper Money Creek may have used a more enriched $\delta^{15}N$ food source than juvenile fish, possibly by cannibalizing age-0 Brown Trout.

Mucus and fin tissue $\delta^{15}N$ for Brown Trout in Bee Creek and Upper Money Creek was not significantly different. Fish sampled from Bee Creek had one of the largest size structures of the 12 streams included in this study, with 20 of 37 individuals greater than 300mm TL. An abundance of Slimy Sculpin were observed in Bee Creek during sampling, possibly allowing Brown Trout to maintain a comparable amount of piscivory in winter as during summer and autumn, which resulted in similar $\delta^{15}N$ between tissue types. Conversely, Upper Money Creek had one of the smallest size structures, with only 2 of 30 fish greater than 300mm TL, and Brown Trout were the only fish species observed during sampling. Thus, most of these fish were likely too small to cannibalize age-0 Brown Trout, and the diets were dominated by aquatic invertebrates, resulting in similar $\delta^{15}N$ values for fin tissue and mucus. A similar pattern was reported in a southeastern Minnesota stream by French et al. (2013) where diets were dominated by aquatic invertebrates and no significant differences in $\delta^{15}N$ were found between Brown Trout size classes.

The significance of the relationship between estimated trophic level and trout size observed in some streams suggests fish prey may be an important component of Brown Trout diet in some streams but not in others. In South Fork Root River, Bee Creek, Big Springs Creek, and West Beaver Creek significant relationships were observed for both fin and mucus tissues with estimated trophic levels exceeding 3.5 (i.e. a primarily tertiary consumer) at ~300mm TL. Previous studies have documented substantial variation in the size at which brown trout shift to piscivory. A number of studies that have identified ontogenetic diet shifts to piscivory in Brown Trout analyzed stomach contents. Garman and Nielson (1982) reported piscivory in ~280mm TL Brown Trout, whereas L'Abée-Lund et al (1992) found Brown Trout as small as 130mm TL were piscivorous. Jonnson et al. (1999) reported the onset of piscivory for Brown Trout in a Norwegian lake and stream system occurred between 175-360mm and between 3yr and 8yr of age.

Trophic level of Brown Trout in southeastern Minnesota is likely influenced by food chain length (FCL) within a stream reach. A considerable amount of research has focused on factors influencing FCL and the mechanisms behind them (Post 2002; Post 2007; Sabo et al 2009; Sabo et al. 2010). In lotic systems, FCL is positively related to ecosystem size, with larger streams supporting longer food chains (Sabo et al. 2010). Our data are consistent with the relationship between ecosystem size and FCL, as we found a significant relationship between trout trophic level and stream drainage area. Streams with piscivorous trout generally were larger streams with larger trout size structure, and more potential prey species. Streams with few piscivorous trout, had smaller trout size structures, and few, if any potential prey species were observed during sampling. The longer FCLs of larger streams may have allowed Brown Trout to function as higher order consumers, resulting in higher trout trophic levels in larger streams.

Hydrologic variability has been proposed as an underlying mechanism governing the effects of ecosystem size on FCL, streams with greater variation in flow generally have shorter FCL (Sabo et al. 2010). Groundwater input can reduce the hydrologic variability of a stream by maintaining higher levels of base flow, potentially resulting in increased FCL independent of ecosystem size in groundwater-dominated streams (Hayashi and Rosenberry 2002). Further research examining the possible impact of varying groundwater input on trout trophic levels may allow ecologists to more accurately predict changes in hydrologic stability on stream food webs.

Mucus $\delta^{15}N$ was significantly depleted relative to fin tissue $\delta^{15}N$ in 10 of the 12 study streams. The difference in $\delta^{15}N$ between tissue types suggests that Brown Trout in these streams exhibited seasonal shifts in diet, as depletion of consumer $\delta^{15}N$ can indicate a reduction in trophic level (Vander Zanden et al. 1997). Although information regarding winter diets of Brown Trout is limited, several studies have documented seasonal shifts in trophic level of adult brown trout, generally by a reduction in piscivory during early and mid-winter (Cunjak and Power 1987; Lehane et al. 2001). The observed depletion in mucus $\delta^{15}N$ could be explained if Brown Trout in the 10 streams with depleted $\delta^{15}N$ experienced a similar reduction in piscivory during winter. Significant relationships between estimated trophic level and Brown Trout size in 2 streams (Lost Creek, and West Albany Creek) were found for fin tissue but not for mucus. This difference may indicate that adult brown trout within these streams are piscivorous during the summer and autumn, but revert to an invertebrate-dominated diet during the winter. Perhaps the lower energy expenditure required to capture invertebrate prey is preferable for Brown Trout during winter in these streams, or fish may no longer be available as prey for some reason. A unique pattern was observed in Upper Money Creek, where no significant relationship between estimated trophic level and Brown Trout TL was observed for fin tissue estimates, but mucus estimates were significant. Brown Trout were the only fish species observed during winter sampling in Upper Money Creek, possibly limiting the number of potential fish prey available to adult Brown Trout. Additionally, heavy aquatic macrophyte growth was observed during early winter sampling on Upper Money Creek. However, by late winter much of the macrophyte growth had died back, and age-0 Brown Trout had reached a size of 75-100mm. The increased size of age-0 Brown Trout and the reduction of possible refugia provided by aquatic macrophytes relative to summer and autumn may have allowed some adult Brown trout to cannibalize age-0 Brown Trout during winter.

Stable isotope signatures suggest minimal overlap in diet between Slimy Sculpin and Brown Trout in both Bee Creek and South Fork Root River where both species were collected. Slimy sculpin were depleted in $\delta^{13}C$ compared to Brown Trout fin $\delta^{13}C$ in both streams, suggesting that Slimy Sculpin used more allochthonously derived prey resources than Brown Trout. By contrast, Brown Trout and White Sucker $\delta^{13}C$ signatures in Spring Creek were quite similar, indicating that Brown Trout and White Sucker in Spring Creek may be relying upon similar prey resources.

Finally, $\delta^{13}C$ and $\delta^{15}N$ of fin tissue collected from Brown Trout and Brook Trout in Trout Valley Creek were almost indistinguishable from one another. All trout collected were similar in size (100-230mm TL) and both species appear to be using similar prey resources, potentially leading to competition between the two species. Competition between Brown Trout and Brook Trout has been documented in other systems, and may be of interest to managers, especially in Trout Valley Creek, which is specifically managed for Brook Trout.

Conclusions

Winter diets of trout are poorly understood and rarely studied, but winter is an important period in the life cycle of stream resident trout. Stable isotope analysis allowed the evaluation of patterns of seasonal diet and trophic level of Brown Trout in 12 southeastern Minnesota streams. Brown trout in most streams displayed a reduced trophic level and shifted towards more allochthonously derived resources during winter. Significant amounts of piscivory likely occurred year-round in four streams, and seasonally in three additional streams. SIA suggested that aquatic invertebrates dominated Brown Trout diets from summer through winter in the five remaining streams.

The use of SIA to investigate aquatic food webs during the winter is relatively novel, and may lead to further use of the technique. A better understanding of winter foraging and trout energy intake may help explain the range of trout growth and annual survival observed in southeastern Minnesota streams. Winter diet shifts by Brown Trout towards more allochthonously derived resources may be of interest to managers when selecting sites for habitat protection and restoration efforts. Leaf litter from forested riparian areas may be important inputs for the winter food webs of stream reaches downstream as well as within forested areas. By strategically locating riparian areas for restoration efforts managers may be able to more efficiently distribute sources of nutrient inputs for stream food webs. Additionally, piscivory appears to be an important component of the diet of Brown Trout in some southeastern Minnesota streams. As piscivorous trout often benefit by increased growth and condition, managers may be interested in establishing populations of potential native prey fishes (e.g. Sculpin) through reintroduction efforts. This study will aid managers in selecting stream reaches that have the potential to support piscivorous Brown Trout. Care should be taken to avoid reaches with small drainage areas, as these are not likely to support food chains of sufficient length to allow trout to act as higher order consumers. Our data suggest stream reaches must have a drainage area of approximately 50 km^2 or greater for mean Brown Trout trophic level to reach 3.5.

Table 1. Stream drainage area, number and size range (mm) of Brown Trout collected, number of fish per size class (adult >240mm, juvenile < 240mm) used for SIA, and the number of viable fin and mucus samples used in the analyses of SIA data from 12 southeastern Minnesota streams.

Stream	Drainage area (km^2)	Trout collected	Trout size range (mm)	Juvenile trout SIA	Adult trout SIA	Fin samples SIA	Mucus samples SIA
Upper Money Creek	7.82	45	120-306	17	13	30	29
Pleasant Valley Creek	10.2	61	129-318	21	7	28	26
Trout Valley Creek	14.5	24	100-231	24	0	24	19
Big Springs Creek	16.1	40	116-365	19	11	30	28
East Burns Valley	36.8	22	141-397	2	20	22	22
West Albany Creek	44.8	30	132-342	23	7	30	27
Lost Creek	47.1	54	110-347	21	9	30	26
Bee Creek	47.7	58	101-390	9	28	37	29
West Beaver Creek	51.2	54	122-521	15	15	30	29
Camp Creek	62.7	78	119-365	15	15	30	30
South Fork Root River	73.6	73	111-367	17	13	30	30
Spring Creek	161.4	22	148-312	12	10	22	22

Table 2. Comparisons of $\delta^{13}C$ using ANOVA (F) and Tukey's HSD (q) between adult (>240mm TL) and juvenile (<240mm TL) Brown Trout fin and mucus tissues collected from 12 southeastern Minnesota streams in March 2013. A t-test was used to compare juvenile Brown Trout fin tissue and mucus $\delta^{13}C$ from Trout Valley Creek, as no adult Brown Trout were sampled. Numbers in parentheses are mean difference.

Stream	ANOVA	Adult BNT mucus vs. fin (mean difference)	Juvenile BNT mucus vs. fin (mean difference)	Adult BNT vs. juvenile BNT fin (mean difference)	Adult BNT vs. juvenile BNT mucus (mean difference)
Pleasant Valley Creek	NS	NS	NS	NS	NS
Big Springs Creek	$F_{3,57}=17.14$, $P<0.001$	(1.36), q=4.06, $P<0.05$	(2.23), q=9.21, $P<0.001$	NS	NS
Bee Creek	$F_{3,65}=14.1$, $P<0.001$	(0.92), q=5.3, $P<0.01$	(2.08), q=7.14, $P<0.001$	NS	(-0.97), q=3.91, $P<0.05$
Trout Valley Creek	NA	NA	(1.67), $T_{41}=5.45$ $P<0.001$	NA	NA
East Burns Valley	NS	NS	NS	NS	NS
Upper Money Creek	$F_{3,55}=5.34$, $P<0.05$	NS	NS	(1.70), q=4.61, $P<0.05$	NS
Lost Creek	$F_{3,55}=8.862$, $P<0.001$	NS	(1.78), q=5.146, $P<0.01$	(-1.86), q=4.31, $P<0.05$	NS
Camp Creek	$F_{3,59}=14.37$, $P <0.001$	(1.86), q=5.43, $P<0.01$	(2.60), q=7.55, $P<0.001$	NS	NS
Spring Creek	$F_{3,43}=11.47$, $P<0.001$	(3.363), q=6.79, $P<0.001$	(2.15), q=4.76, $P<0.01$	NS	NS
West Beaver Creek	$F_{3,58}=18.96$, $P<0.001$	(1.03), q=4.36, $P<0.05$	(2.31), q=9.60, $P<0.001$	NS	NS
West Albany Creek	$F_{3,53}=24.88$, $P<0.001$	(3.53), q=6.74, $P<0.001$	(1.99), q=6.64, $P<0.001$	NS	(3.03), q=7.05, $P<0.001$
South Fork Root River	$F_{3,56}=26.09$, $P<0.001$	(2.92), q=6.27, $P<0.001$	(3.84), q=9.43, $P<0.001$	(2.10), q=4.81, $P<0.01$	NS

Table 3. Comparisons of δ^{15}N using ANOVA (F) and Tukey's HSD (q) between adult (>240mm TL) and juvenile (<240mm TL) Brown Trout fin and mucus tissues collected from 12 southeastern Minnesota streams in March 2013. A t-test was used to compare juvenile Brown Trout fin tissue and mucus δ^{15}N from Trout Valley Creek, as no adult Brown Trout were sampled. Numbers in parentheses are mean difference.

Stream	ANOVA	Adult BNT mucus vs. fin (mean difference)	Juvenile BNT mucus vs. fin (mean difference)	Adult BNT vs. juvenile BNT fin (mean difference)	Adult BNT vs. juvenile BNT mucus (mean difference)
Pleasant Valley Creek	$F_{3,53}=25.27$, $P<0.001$	(-1.91), q=7.67, $P< 0.001$	(-1.42), q=9.59, $P< 0.001$	NS	NS
Big Springs Creek	$F_{3,57}=42.1$, $P<0.001$	(-1.37), q=6.63, $P<0.001$	(-1.93), q=12.93, $P<0.001$	NS	(1.03), q=5.53, $P<0.01$
Bee Creek	$F_{3,65}=16.34$, $P<0.001$	NS	NS	(0.86), q=4.87, $P<0.01$	(1.62), q=8.431, $P<0.001$
Trout Valley Creek	NA	NA	(-1.71), $t_{41}=10.81$, $P< 0.001$	NA	NA
East Burns Valley	$F_{3,43}=77.22$, $P<0.001$	(-2.07), q=21.12, $P<0.001$	(-1.28), q=4.5, $P<0.05$	NS	NS
Upper Money Creek	$F_{3,58}=6.41$, $P<0.001$	NS	NS	NS	(1.16), q=5.10, $P<0.01$
Lost Creek	$F_{3,55}=58.52$, $P<0.001$	(-2.16), q=10.35, $P< 0.001$	(-2.25), q=15.52, $P<0.001$	NS	NS
Camp Creek	$F_{3,56}=27.32$, $P<0.001$	(-1.47), q=9.36, $P<0.001$	(-1.33), q=8.48, $P<0.001$	NS	NS
Spring Creek	$F_{3,43}=7.18$, $P<0.001$	(-1.13), q=3.90, $P<0.05$	(-1.40), q=5.27, $P<0.01$	NS	NS
West Beaver Creek	$F_{3,58}=19.48$, $P<0.001$	(-1.55), q=6.88, $P<0.001$	(-1.40), q=6.11, $P<0.001$	(1.01), q=4.48, $P<0.05$	(0.86), q=3.76, $P<0.05$
West Albany Creek	$F_{3,53}=57.2$, $P>0.001$	(-2.17), q=10.33, $P<0.001$	(-1.83), q=15.19, $P<0.001$	NS	NS
South Fork Root River	$F_{3,56}=49$, $P<0.001$	(-2.49), q=11.87, $P<0.001$	(-1.98), q=10.81, $P<0.001$	(1.09), q=5.54, $P<0.01$	NS

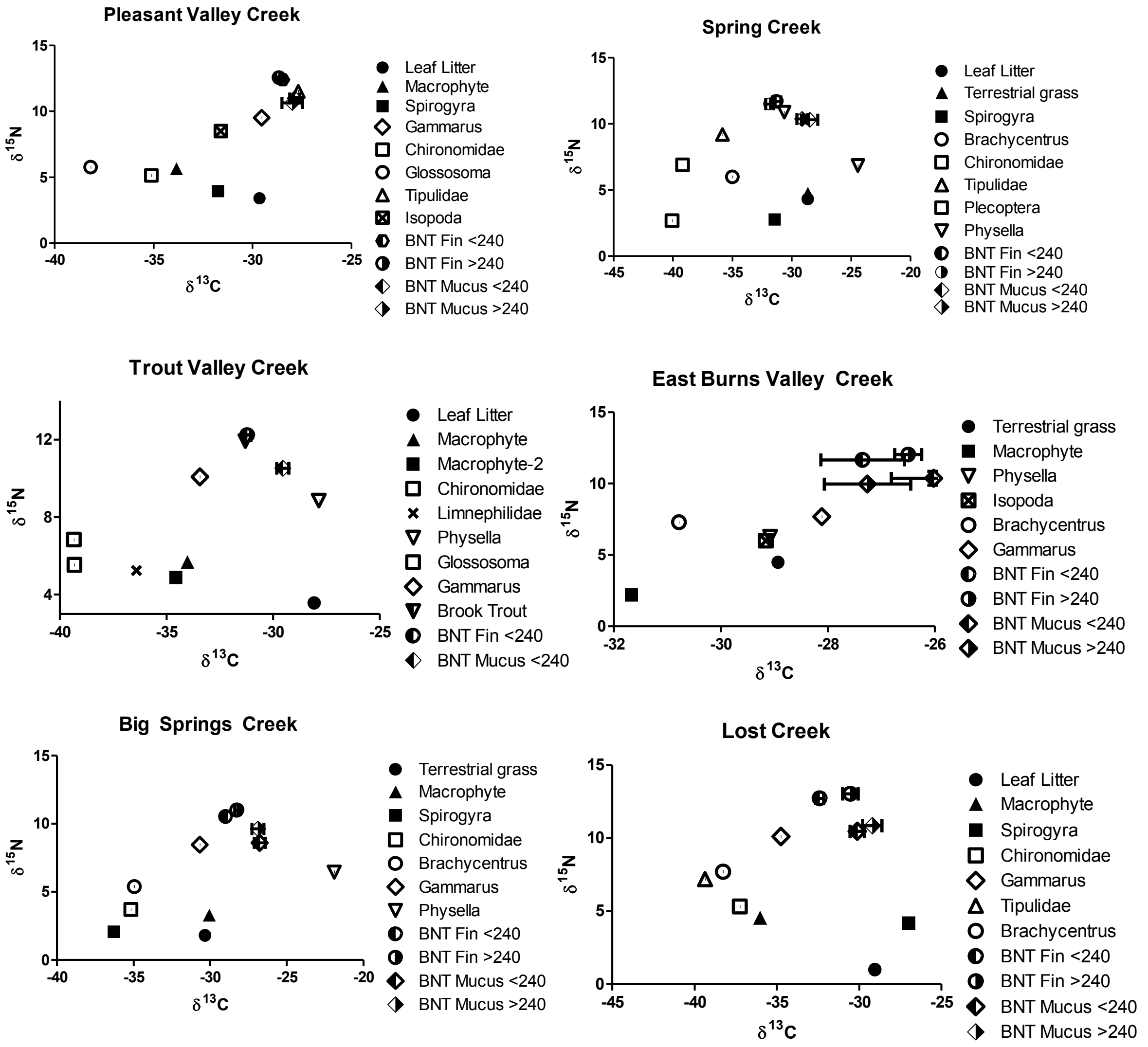


Figure 1a. Carbon-Nitrogen bi-plots of mean values for adult and juvenile Brown Trout fin and mucus tissues, potential prey species, and primary producers collected from 6 southeastern Minnesota streams in March 2013. Error bars represent 1 SEM.

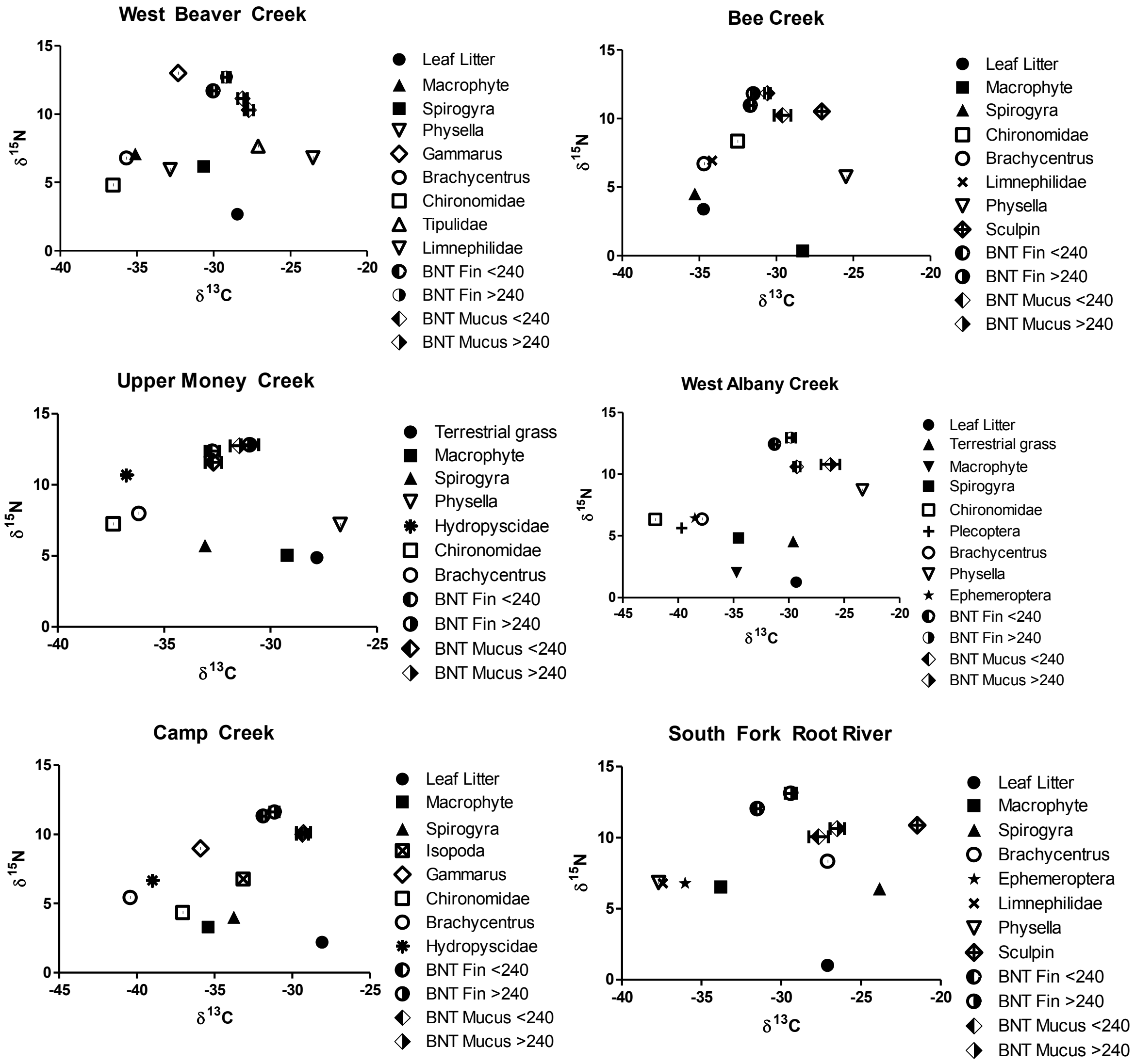


Figure 1b. Carbon-Nitrogen bi-plots showing mean values for adult and juvenile Brown Trout fin and mucus tissues, potential prey species, and primary producers collected from 6 southeastern Minnesota streams in March 2013. Error bars represent 1 SEM.

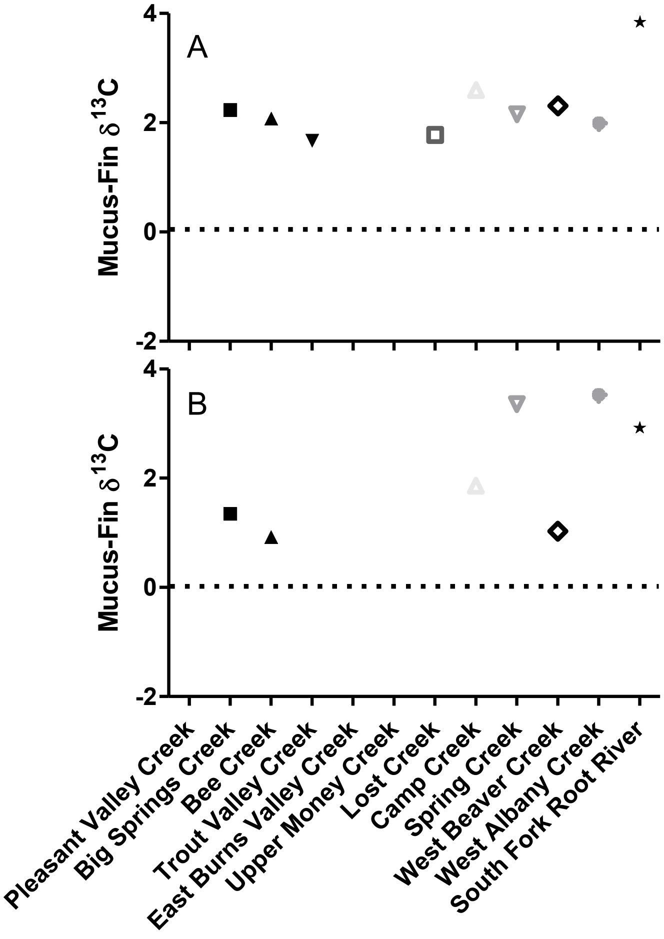


Figure 2. Difference in juvenile (A) and adult (B) Brown Trout mucus (winter) and fin (annual) tissue $\delta^{13}C$ for trout collected from 12 southeastern Minnesota streams in March of 2013. Data shown for all streams where significant differences were found with ANOVA.

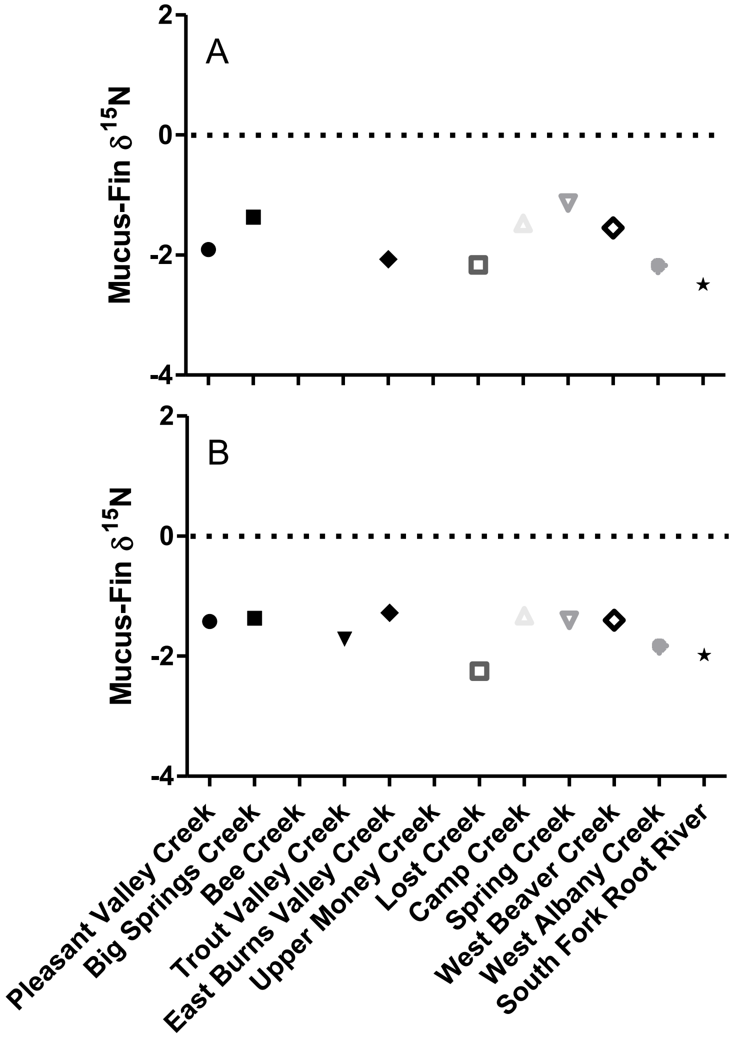
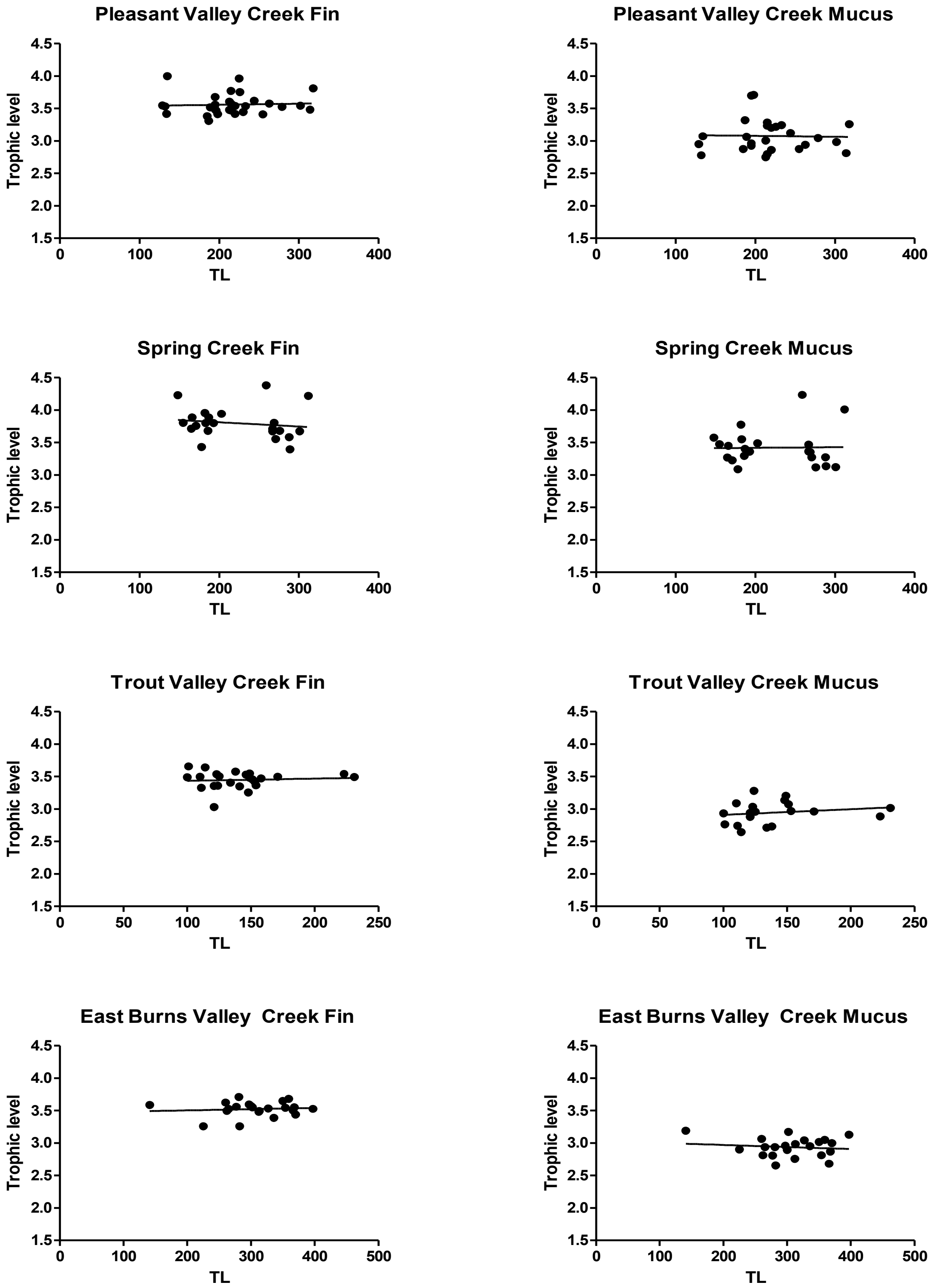


Figure 3. Difference in juvenile (A) and adult (B) Brown Trout mucus (winter) and fin (annual) tissue $\delta^{15}N$ for trout collected from 12 southeastern Minnesota streams in March of 2013. Data shown for all streams where significant differences were found with ANOVA.



Pleasant Valley Creek Fin

Pleasant Valley Creek Mucus

Spring Creek Fin

Spring Creek Mucus

Trout Valley Creek Fin

Trout Valley Creek Mucus

East Burns Valley Creek Fin

East Burns Valley Creek Mucus

Figure 4a. Regressions of fin and mucus derived estimated trophic level vs. TL (mm) of Brown Trout collected from 4 southeastern Minnesota streams in March 2013.

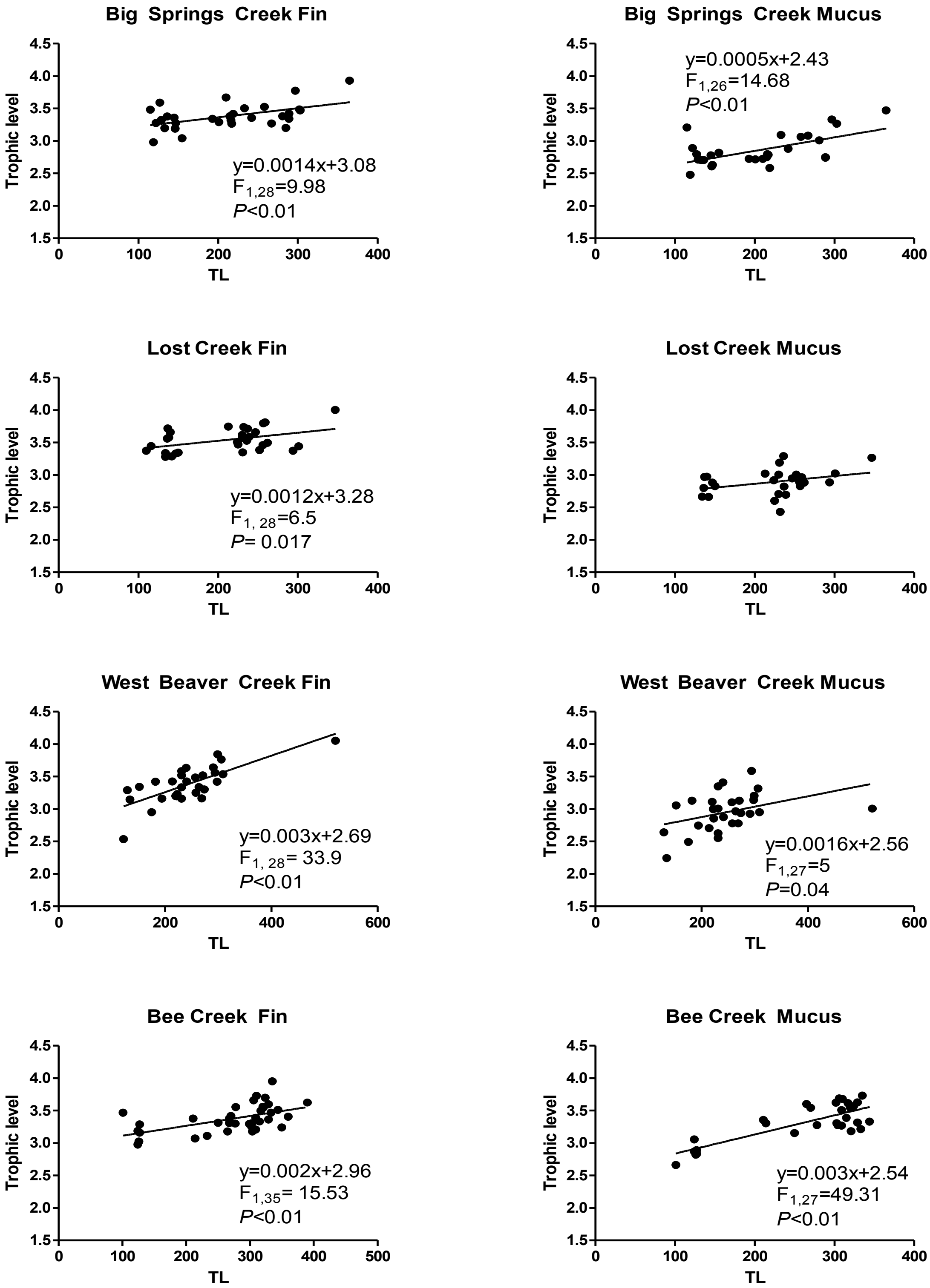
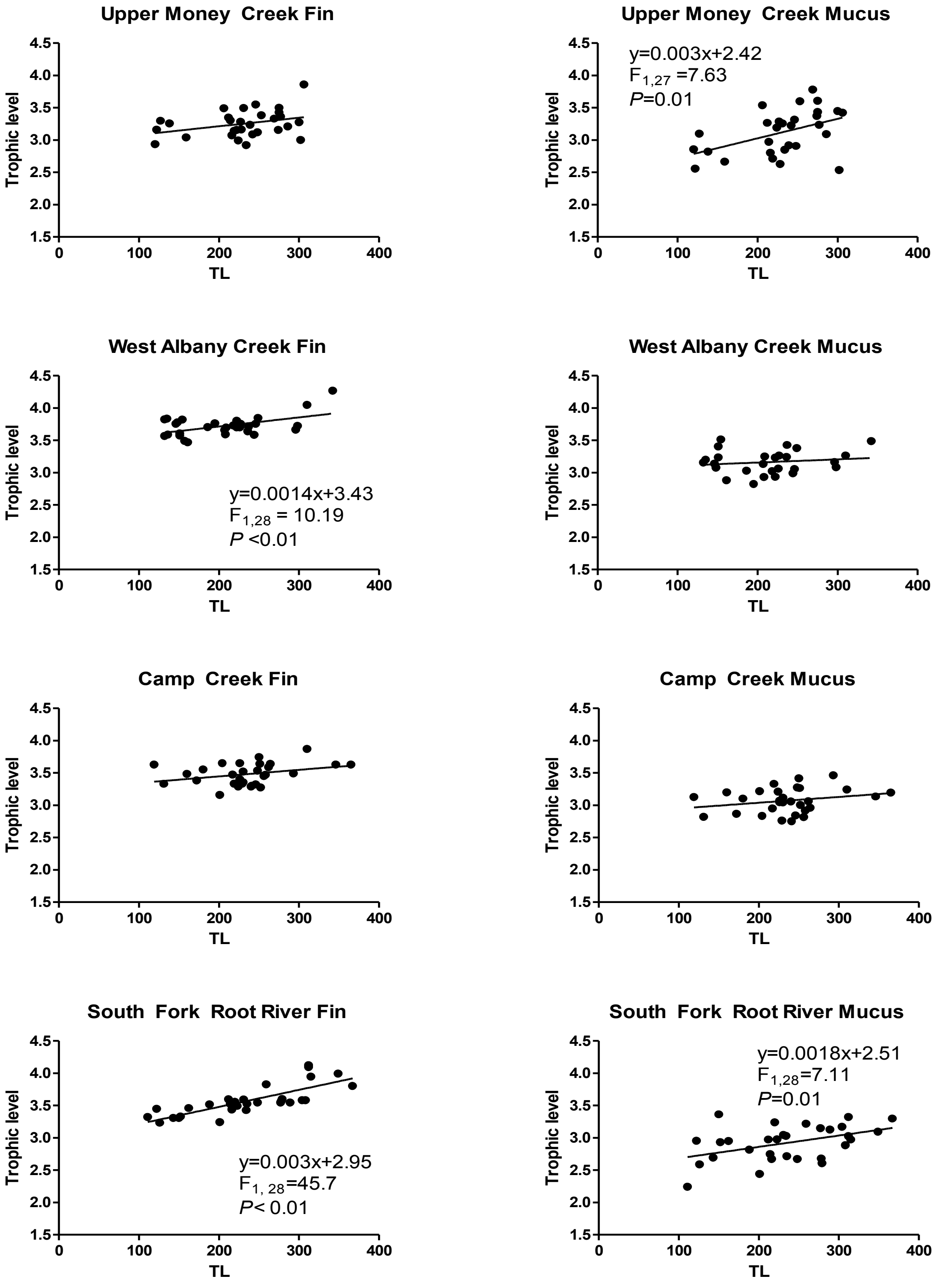


Figure 4b. Regressions of fin and mucus derived estimated trophic level vs. TL (mm) of Brown Trout collected from 4 southeastern Minnesota streams in March 2013.


Upper Money Creek Fin

Upper Money Creek Mucus

West Albany Creek Fin

West Albany Creek Mucus

Camp Creek Fin

Camp Creek Mucus

South Fork Root River Fin

South Fork Root River Mucus

Figure 4c. Regressions of fin and mucus derived estimated trophic level vs. TL (mm) of Brown Trout collected from 4 southeastern Minnesota streams in March 2013.

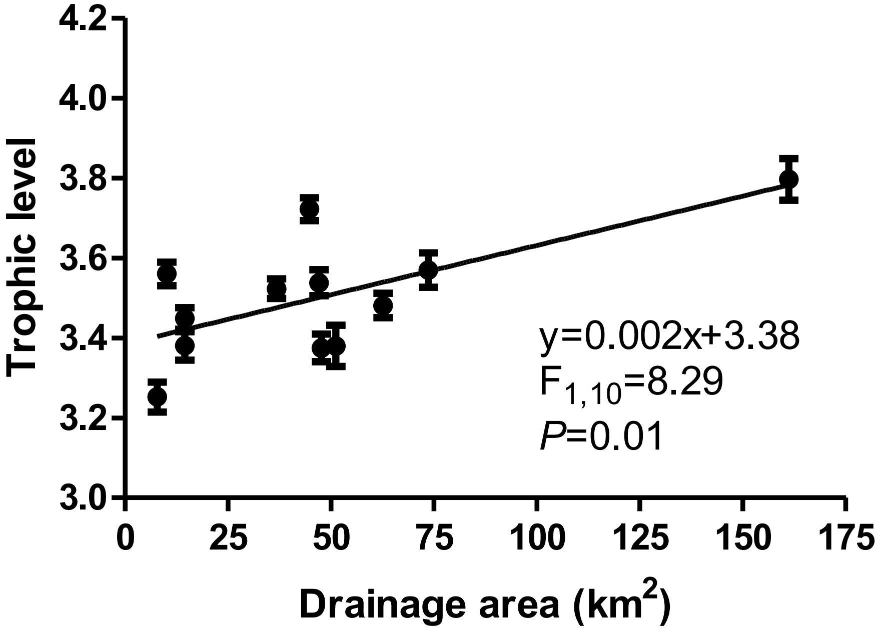


Figure 5. Relationship between mean estimated trophic level of Brown Trout and stream drainage area from 12 southeastern Minnesota streams collected in March of 2013. Trophic level was calculated from $\delta^{15}N$ of trout pectoral fin tissue. Error bars = 1 SEM.

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