

8-2020

Competitive Interactions: Spatial and temporal niche partitioning between Brook and Brown Trout in southwest Michigan

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Competitive Interactions: Spatial and temporal niche partitioning between Brook and Brown
Trout in southwest Michigan

Frederick J. Glassen

A Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Master of Science in Biology with emphasis in Aquatic Sciences

Biology Department

August 2020

DEDICATION

This thesis is dedicated to my mother, Gretchen M. Glassen, my great aunt, Mary G. Stieglitz, my cousin, Kurt J. Stieglitz, my uncle, Tim J. Drascic and my grandparents, Jim R. and Barb A. Drascic. Thank you for supporting me on my journey through graduate school and believing in me.

ACKNOWLEDGEMENTS

I thank my major advisor, Dr. Eric Snyder, as well as my committee members, Dr. Carl Ruetz III and Nichol DeMol, for their valuable input and assistance in throughout my thesis. Sampling efforts were supported by undergraduates Grayson Kozak, Anahi Huitron, Connor O'Brian, and graduate students Josh Arnold, Tyler Harman, and Billy Mulligan. All sampling and handling of fish were carried out in accordance with guidelines for the use and care of fishes by IACUC (Permit #: 19-16-A). Funding was provided by Grand Valley State University (GVSU Presidential Grant), Trout Unlimited: Kalamazoo Chapter (George L. Disborough Research Grant), and Michigan Space Grant Consortium (NASA Grant #NNX15AJ20H).

ABSTRACT

Niche diet partitioning between Brook Trout and Brown Trout were studied in two southwestern Michigan, USA streams, one dominated by Brook Trout, the other with both Brook and Brown Trout. Brook Trout are endemic to eastern North America and have been introduced throughout the world for sport fishing. Brown Trout were first introduced to Michigan in 1883 using a genetic strain from Germany. Stomach contents were collected from a population of Brook Trout in the absence of Brown Trout in Frost Creek, while the other population was in potential competition with Brown Trout in Cedar Creek. Absent Brown Trout, Brook Trout exhibited greater niche feeding breadth compared to those in direct competition. This unique study with seasonal sampling over a one-year timeframe indicates that in Cedar Creek, niche partitioning does take place with Brook Trout focusing on benthic invertebrates in the presence of Brown Trout (Pairwise ADONIS, $P = 0.006$). Those not in competition with Brown Trout fed opportunistically between drift and benthos (Pairwise ADONIS, $P = 0.006$ drift/benthos). Ivlev's electivity Index indicated Brook Trout in Frost Creek were found to prefer Crustacea, Diptera, and Trichoptera while avoiding Plecoptera and Ephemeroptera. Brook Trout in Cedar Creek preferred Plecoptera and Ephemeroptera to a greater degree than those within Frost Creek. Stomach sampling following a flood pulse indicated that both Brook and Brown Trout were feeding almost exclusively on terrestrial annelids, washed into the stream as flood waters subsided (Ivlev's electivity: Brook Trout 0.96 and Brown Trout 0.97). The thermal regime was significantly warmer (17.8°C vs. 16.1°C mean daily summer temperature) in the stream where Brook and Brown Trout co-occurred vs. the stream with solely by Brook Trout. Frost Creek had a lower mean summer temperature below thermal stress levels for Brook Trout. Cedar Creek had a higher mean annual temperature, likely increasing the competitiveness of Brown Trout over

Brook Trout. Cold thermal regimes give Brook Trout a competitive edge and aid in slowing Brown Trout invasions into headwater streams. In addition to thermal regimes, successful recruitment as evidenced by high young-of-the-year (YOY) abundance is an important indicator of robust Brook Trout populations. In Frost Creek 45 YOY were captured vs. 4 YOY in Cedar Creek. I hypothesize that this low recruitment is potentially due to predation pressure – possibly from larger Brown Trout, although there was no evidence of this in stomach sampling. Variables likely linked to the continued persistence of Brook Trout in headwater streams include maintenance of groundwater inputs, which contribute to cooler thermal regimes, a robust food resource, and high-quality habitat that promotes successful recruitment. Isolated Brook Trout populations in small headwater streams will likely become threatened as climate change warms streams above their thermal tolerances and through increased winter precipitation, which may negatively affect YOY abundance through scouring of redds.

Table of Contents

Chapter	Page
I. INTRODUCTION	
Introduction.....	8
Purpose.....	11
Scope.....	12
Assumptions.....	12
Objectives.....	13
Significance.....	13
Definitions.....	15
II. COMPETITIVE INTERACTIONS: SPATIAL AND TEMPORAL NICHE PARTITIONG BETWEEN BROOK AND BROWN TROUT IN SOUTHWEST MICHIGAN	
Title Page.....	16
Abstract.....	17
Introduction.....	19
Methodology.....	21
Results.....	26
Discussion.....	29
Ackowledgements.....	37
References.....	38
Tables.....	55
Figures.....	58
III. EXTENDED LITERATURE REVIEW	
Extended Literature Review.....	64
APPENDICES.....	75
BIBLIOGRAPHY.....	80

Chapter I

Human have been introducing and transferring species between biogeographic regions for centuries. Currently the pace of transference between regions is faster and farther than at any other time history (Ricciardi 2007), in some cases resulting in enormous changes to recipient ecosystems (Asner and Vitousek 2005; Ehrenfeld 2011; Simberloff 2011). Despite technological advances and our understanding of how species spread, our ability to forecast when and where species will exert strong or weak ecological impacts is lacking (Ricciardi et al. 2013). In some cases, the changes are dramatic and may result in the extinction of native species or extreme changes in ecosystem functions. Relatively little is known about a vast majority of non-native species and the consequences of their introduction to new ecosystems (Kulhanek et al. 2011; Larson et al. 2013; Simberloff et al. 2013). Often times authors are not explicit about their definition of impacts by non-native species, which inhibits the ability of other scientist to use systematic reviews, comparative analyses and meta-analyses to synthesize the growing body of literature (Koricheva et al. 2013). There are many questions that must be answered to help define the impact of a non-native species including directionality (uni or bi-directionality), which describes the potential ecological niche shift that can occur as a result of direct and indirect competition; classification and measurement in which the term impact is only used if the change caused by a non-native exceeds a threshold or any change in the measurement; and the socio-economic impacts that may result from the introduction and establishment of non-native species (Jeschke et al. 2014). Socio-economic and ecological impacts may appear to be correlated, but that relationship still needs to be investigated further (Vilà et al. 2010). The scale of the impact may show a net increase in species richness at small spatial scales, while leading a decline in global species richness through the extinction of endemic or rare native species (Sax and Gaines

2003; Clavero and Garcia-Berthou 2005). Differences between short and long-term impacts by non-native species on ecosystems can vary widely (Strayer et al. 2006). Often times, the impacts by non-native species are only detected until after major impacts have already occurred on native species within the ecosystem (Vilà et al. 2011).

The impacts of non-native species on ecosystems have been largely examined using species traits, exhibited by the either/both non-native and native species (Ricciardi et al. 2013). Species traits have been linked to degree of invasiveness (Kolar and Lodge 2002; Van Kleunen et al. 2010), but less so how these traits might translate into impacts on ecosystems (Byers 2002; Pyšek et al. 2012; Lockwood et al. 2013). Elevated fecundity, for example, is a species trait that can allow non-native species to dominate a landscape (Ricciardi et al. 2013) and these traits can provide a competitive advantage to non-native species for habitat selection. The niche-based hypothesis focuses on the niche differences between native and non-native species within the community, with the assumption that the exploitation of unused resources (empty niches) or more thorough and more efficient ways of accessing resources (niche replacement) allows non-native species to integrate into a community (Ricciardi et al. 2013). Direct competitive effects can cause resource limitation, which can exclude native species, while use of novel resources may not have any direct competitive effects but may have indirect effects on the native community. Impacts from niche overlap with a superior non-native competitor would result in areas of coexistence and areas of exclusion for both species (Bryce et al. 2002). Non-native competitors that exclude a native species from a portion of their potential habitat or can affect the entire range leading to potentially catastrophic declines or extirpation of native species (Hoopes and Hall 2002). Determining the degree of overlap in ecological niches is important. Limited overlap can result in coexistence, while significant overlap can result in exclusion and local or

regional extinction (Melbourne 2007; MacDougall et al. 2009). Brown Trout is outcompeting and slowly excluding Brook Trout from habitat at small scales throughout their native range, creating a large-scale issue for the species.

One method of invasion sometimes overlooked is through intentional stocking of fish species. For example, Chinook salmon (*Oncorhynchus tshawytscha*) were first introduced to the Great Lakes to control invasive Alewife (*Alosa pseudoharengus*) populations and have since become a necessary fishery that supports the regional economy. This method of introduction has produced a direct positive effect as one species controls the other while supporting local fisheries.

Brook Trout is native to eastern North America, but have been introduced throughout the world for sport fishing (MacCrimmon 1969; Kershner et al. 2019). Brown Trout was first introduced to North America in 1883 using a genetic strain from Germany (MacCrimmon 1968). The eggs were incubated and released into the Baldwin River in Lower Peninsula of Michigan (MacCrimmon 1968). By the early 1900s, biologist began to realize that Brown Trout was a superior competitor to native salmonids and extirpating them locally (MacCrimmon 1968; Bryce et al. 2002). As native salmonids declined, non-native species expanded their range. Like Brook Trout, Brown Trout can exhibit multiple life history traits that have allowed them to occupy multiple niches from small streams to lakes (MacCrimmon 1968). Non-native species with multiple life histories; resident, lake-dwelling or anadromous life histories; increase their chances of establishing populations, as well as opening doors in new habitats to facilitate the establishment of new species or populations (Simberloff and Von Holle 1999; Kolar and Lodge 2001). Brook and Brown Trout now reside throughout the state of Michigan, with examples of both sympatric and allopatric populations. Previous studies have explored their diet, competition

for space, and behaviors (Fausch and White 1981; Bachman 1984; Dewald and Wilzbach 1992; Lovén-Wallerius et al. 2017).

Our study fills a research gap by showing how diets of Brook and Brown Trout vary throughout the year, vs. seasonal studies, when living in sympatry. Through diet analyses I determined which aquatic macroinvertebrate orders trout were selecting for or against and the amount of overlap between Brook and Brown Trout feeding. This study is unique as we compared two streams, one with a dominant Brook Trout population vs. a similar stream dominated by Brown Trout with a small Brook Trout population. We were able to compare Brook Trout diet changes throughout the year in the presence and absence of Brown Trout.

Although this study occurs outside of the native range of Brook Trout, given that our best information indicates that the native range extended only in the northern portion of Michigan's Lower Peninsula (MacCrimmon 1969), we think the results are applicable to headwater streams throughout the native range. Brown Trout are encroaching on Brook Trout populations throughout their native range and knowing how their diets are overlapping can inform management, for example by better prioritizing limited restoration, habitat enhancement and habitat protection efforts (Fausch and White 1981).

Purpose

The purpose of this study was to determine whether diet niche partitioning was occurring among wild Brook and Brown Trout in headwater streams located in southwestern Michigan. Headwater streams are intimately connected with the surrounding landscape through flooding events, with organic matter input (allochthonous detrital material), fish spawning and feeding habitat becoming available to the stream network (Ward 1989; Ward and Stanford 1995). Specifically, I determined how diets of Brook and Brown Trout shift throughout the year.

Additionally, I determined whether competition between species results in aquatic macroinvertebrate orders being selected for or against through niche partitioning.

Scope

Previous literature has focused on spring/summer diets during peak growing periods for Trout (Griffith 1974; Bridcut and Giller 1995; Laudon et al. 2005; Utz and Hartman 2007; Courtwright and May 2013) and a few studies that have focused on winter diets (Anderson et al, 2016; Cunjak & Power, 1987; French et al, 2016; Lord, 1933). There have been a few year-round studies (Cunjak et al. 1987; Needham 1929; Utz & Hartman 2006), but they have focused on a single species; not the competition between two. Niche partitioning is an aspect of competition that is important in our understanding of how species interact. The Competitive Exclusion Principle (Hardin 1960) first proposes that competition for identical resources results in three different outcomes; exclusion of the inferior competitor, bimodal or unimodal selection. In order for species to co-exist, they must occupy difference ecological niches (Hardin 1960). This study will expand upon previous research in habitat selection (Fausch and White 1981) by including an assessment of diet partitioning (focusing on aquatic macroinvertebrates within the drift and benthos) between Brook and Brown Trout.

Assumptions

1. Sampled stomachs taken from a subset of fish in the population were representative of all fish.
2. Macroinvertebrate sampling techniques (drift nets and Hess benthic samples) accurately represented the macroinvertebrate community located within streams and therefore the food resources potentially available to feeding fish.

3. By conducting random sampling, macroinvertebrate sampling was unbiased during each sampling event.
4. Bias in fish sampling was standardized between reaches, streams, and sample dates.
5. Although macroinvertebrate drift is composed of a subset of the benthic macroinvertebrate community, the difference between drift and benthos would be large enough to identify whether fish were feeding selectively from one or the other.

Objectives

The goal of my study was to determine if niche partitioning occurred between naturalized Brook and Brown Trout by using gastric lavage to compare stomach contents to macroinvertebrates available in the stream. Specifically, my objectives were to: (1) determine the aquatic macroinvertebrate and fish communities of Frost and Cedar creeks, two tributaries of the Rogue River located in south-central Michigan, (2) evaluate how diets of Brook and Brown Trout change throughout the year, (3) test whether niche partitioning occurred between Brook and Brown Trout throughout the year in Cedar Creek, and (4) quantify fish fitness via growth using PIT tags.

Significance

The limited amount of year-round, seasonal diet, and niche partitioning studies on Brook and Brown Trout have left a significant gap in our understanding of their responses to competition (Tiberti et al. 2016). This study will help fill a missing gap in our knowledge of the interaction and competition between Brook and Brown Trout in headwater streams. If evidence of direct competition for food resources is shown, then management decisions for protecting vulnerable Brook Trout populations will need to be taken in streams with both species.

Over the last few decades Brook Trout have declined in their distribution across their native and introduced range (DeWeber and Wagner 2015). This decline coincides with the expansion in the distribution of non-native Brown Trout throughout Brook Trout habitat (Davis et al. 2015; Kirk et al. 2018; Ohlund et al. 2008). Brook Trout decline within their native range has been attributed to climate change, acidification, and invasive species (Baker et al. 1996). Understanding how they interact with invasive species is important to conserving their species throughout the range.

In conclusion, this study will add to the literature of both Brook and Brown Trout diets, how they change throughout the year, and how competition influences their feeding habits. Additionally, this study will provide valuable information to conservation effects of Brook Trout populations that co-exist with Brown Trout in headwater streams.

DEFINITIONS

Sympatric – related species or populations occurring within the same geographical area; overlapping in distribution.

Allopatric – related species or populations occurring in separate non-overlapping geographical areas.

Anadromous – life history trait in which an individual or species spawns in freshwater streams and migrates to saltwater to mature into an adult before returning to freshwater for spawning.

PIT Tags – passive integrated transponders embedded with a unique code allowing for identification of individuals over time.

Gastric Lavage – stomach pumping, the process of cleaning out the contents of the stomach.

Competitive exclusion – the inevitable elimination from a habitat of one of two different species with identical needs for resources.

Ecological niche – the role and position a species has in its environment; how it meets its needs for food and shelter, how it survives, and how it reproduces.

Chapter II

Competitive Interactions: Temporal and spatial niche partitioning between naturalized Brook and
Brown Trout

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ABSTRACT

Niche diet partitioning between Brook Trout and Brown Trout were studied in two southwestern Michigan, USA streams, one dominated by Brook Trout, the other with both Brook and Brown Trout. Stomach contents were collected from a population of Brook Trout in the absence of Brown Trout in Frost Creek, while the other population was in potential competition with Brown Trout in Cedar Creek. Absent Brown Trout, Brook Trout exhibited greater niche feeding breadth compared to those in direct competition. This unique study with seasonal sampling over a one-year timeframe indicates that in Cedar Creek, niche partitioning does take place with Brook Trout focusing on benthic invertebrates in the presence of Brown Trout ($P = 0.006$). Those not in competition with Brown Trout fed opportunistically between drift and benthos (Pairwise ADONIS, $P = 0.006$ drift/benthos). Ivlev's electivity index indicated Brook Trout in Frost Creek were found to prefer Crustacea, Diptera, and Trichoptera while avoiding Plecoptera and Ephemeroptera. Brook Trout in Cedar Creek preferred Plecoptera and Ephemeroptera to a greater degree than those within Frost Creek. Stomach sampling following a flood pulse indicated that both Brook and Brown Trout were feeding almost exclusively on terrestrial annelids, washed into the stream as flood waters subsided (Ivlev's electivity: Brook Trout 0.96 and Brown Trout 0.97). The thermal regime was significantly warmer (17.8°C vs. 16.1°C mean daily summer temperature) in the stream where Brook and Brown Trout co-occurred vs. the stream dominated solely by Brook Trout. Frost Creek had a lower mean summer temperature below thermal stress levels for Brook Trout. Cedar Creek had a higher mean annual temperature, likely increasing the competitiveness of Brown Trout over Brook Trout. Cold thermal regimes give Brook Trout a competitive edge and aid in slowing Brown Trout invasions into headwater streams. In addition to thermal regimes, successful recruitment as evidenced by

high young-of-the-year (YOY) abundance is an important indicator of robust Brook Trout populations. In Frost Creek 45 YOY were captured vs. 4 YOY in Cedar Creek. We theorize that this low recruitment is potentially due to predation pressure – possibly from larger Brown Trout, although there was no evidence of this in stomach sampling. Variables likely linked to the continued persistence of Brook Trout in headwater streams include maintenance of groundwater inputs, which contribute to cooler thermal regimes, a robust food resource, and high-quality habitat that promotes successful recruitment.

Competition between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) has steadily increased throughout Brook Trout range in North America. Brook Trout habitat includes the headwaters of clean and cold flowing streams (MacCrimmon 1969; Gard and Flittner 1974). Water temperature is the single biggest factor limiting Brook Trout with tolerated temperatures ranging from 0° to 25.3°C, with thermal stress occurring above 21°C (MacCrimmon 1969; Meisner 1990; Wehrly et al. 2007). Although native to Europe, Brown Trout have been introduced throughout the world (MacCrimmon 1968). Their range within the US seems to be restricted by warmer areas where mean July temperatures can reach 27°C, unless in elevated mountain regions (MacCrimmon 1968). Brown Trout are generally considered the more aggressive or dominant salmonid compared to Brook Trout, which can prove detrimental for native populations (Fausch and White 1981; Dewald and Wilzbach 1992; Hasegawa et al. 2004; Ohlund et al. 2008). Although Brown Trout continue to expand their range upstream from midriver sections, smaller headwater streams that are dominated by Brook Trout are sometimes resistant to Brown Trout incursion (Ohlund et al. 2008). Brook Trout populations that continue to persist in a subset of these headwater refuges can serve as a template for protecting and improving these habitats (MacCrimmon 1969; Gard and Flittner 1974). In addition to clean, cold thermal regimes, Brook Trout populations require adequate food and habitat. It is suggested that competition for food has replaced the competition for space among salmonids as their territory size is linked to food availability (Chapman 1966). Less food requires larger territory. By conducting a snorkel survey to monitor positions in streams, Fausch (1981) tested Brook Trout and Brown Trout together and removed Brown Trout to see the preferred positions for Brook Trout. With the removal of Brown Trout, Brook Trout held more favorable positions for resting and similar positions for feeding (Fausch and White 1981; Hoxmeier and Dieterman 2016).

Although Brook Trout are outcompeted for preferred positions by Brown Trout, Brook Trout continue to coexist with Brown Trout throughout Michigan, at least in a subset of headwater streams. This begs the interesting question; why some streams and not others?

The niche partitioning between Brown Trout and Brook Trout within a stream system has not been studied adequately and presents a gap in our knowledge. A Brook Trout diet review by Tiberti et al. (2016) found most diet studies on salmonids are conducted during the summer with few taking place during winter, and even more rare are complete year-round diet studies. Winter diet studies have focused on energy deficiency due to slow gastric evacuation rates and how their diets change from late fall through early spring (Lord 1933; Cunjak et al. 1987; Cunjak and Power 1987; Anderson et al. 2016; French et al. 2016). Cunjak and Powers (1987) found significant overlap in diets between Brook and Brown Trout throughout the winter, feeding mostly on immature insects and crustaceans. Other studies have focused on the effects of riparian disturbances and how woody debris may impact fish diets (Utz and Hartman 2007; Courtwright and May 2013; Gustafsson et al. 2014; Kraus et al. 2016; Studinski et al. 2017). Lastly, a few studies focus on spring through early autumn seasons, which coincide with most recreational fishing seasons (Needham 1929; Benson 1951; Cochran-Bieder et al. 2017). Without a better understanding of how diets change throughout the year, including all seasons, we will not be able to accurately manage threatened Brook Trout populations. Brown Trout have become naturalized within the state of Michigan but continue to encroach on Brook Trout habitat (Fausch and White 1981; Waters 1983; Ohlund et al. 2008). There are multiple ways to mitigate invasions by non-native species, most of which are expensive. Griffith (1974) argued that using expensive fish removal or fish kill programs to remove invasive Brook Trout from Cutthroat Trout habitat was not needed as they filled different niches within the stream ecosystem. Griffith found that as

Brook Trout grew, their diets became more selective when coexisting (Griffith 1974).

Better understanding of the ecological niches filled by competing salmonid species can aid in future management decisions. Our objective was to analyze the feeding ecology and growth rates of fish in a Brook Trout vs. Brown Trout-dominated stream. We hypothesize that: (1) *Brook Trout living in absence of Brown Trout would have a broader niche breadth and feed more opportunistically*, and (2) *Brook Trout living in the absence of Brown Trout would have higher condition factor than Brook Trout that are sympatric with Brown Trout*.

METHODS

Study area.

This study was conducted in the Rogue River watershed, Kent County, Michigan which covers 678 km² (Annis Water Resource Institute 2000), specifically in Frost Creek, a 1st order tributary and Cedar Creek, a 2nd order tributary (Figure 1). The southern section of the Rogue River watershed is dominated by urban and rural areas with pastureland, upland crops, and forestland (Annis Water Resource Institute 2000). The northern section of the watershed contains mostly muckland crops (Annis Water Resource Institute 2000). Additionally, the Rogue River Watershed is part of the Home Rivers Initiative by Trout Unlimited (TU). The Home Rivers Initiative works towards removing fish barriers, reducing sources of stormwater, and engaging communities in implementing policies to help protect rivers within the watershed (De Mol 2020). Frost Creek maintains a naturally reproducing population of Brook Trout that are largely allopatric with respect to Brown Trout, although we did find an occasional Brown Trout therein. Cedar Creek contains both Brown and Brook Trout living in sympatry with one another. Both populations in Cedar Creek are naturally reproducing. The survey reaches in Frost Creek were conducted just upstream of the Algoma Avenue road-stream crossing; a culvert deemed

‘impassible’ for fish (Streamside Ecological Services 2012). The riparian zone in Frost Creek was largely intact with some riparian land owner property that was maintained as open grass (approximately 15% of the 300-m reach), while the rest of the habitat consisted of floodplain wetland forest dominated by black alder (*Alnus glutinosa*), hemlock (*Conium maculatum*), silver maple (*Acer saccharinum*), and dead/dying ash trees (*Fraxinus spp*). Similarly, in Cedar Creek, sampling was done in one of three continuous 100 m reaches. One side of the creek (the west bank) consisted of a 100-m riparian buffer followed by row-crop agriculture – specifically center-pivot irrigated corn fields, and a relatively intact riparian buffer (the east bank) that extended up on to the first Holocene flood terrace. Dominant woody vegetation consisted of black alder (*Alnus glutinosa*), silver maple (*Acer saccharinum*), dead/dying ash (*Fraxinus spp*), hophornbeam (*Ostrya*), black cherry (*Prunus serotina*), hickory (*Carya*), and the occasional white pine (*Pinus strobus*) and hemlock (*Conium maculatum*). There was one 50-m segment of stream that had no woody vegetation on the west bank and was dominated by grasses and reeds.

Field and lab protocols for fish, benthic and drifting macroinvertebrates.

Brook Trout and Brown Trout were collected starting June 2019 through May 2020. Each stream was surveyed six times over the year, in one of three continuous 100 m reaches. Reaches were rotated each month and sampled twice over 12 months (June, August, October, December, February and May). Our April sample was delayed due to COVID-19 and pushed back until May when we were able to conduct field work. Drifting macroinvertebrates were sampled using three drift nets (net area = 0.139 m², mesh 343 μm) deployed for 15 minutes, beginning approximately at civil twilight before sunrise during one of two peaks in aquatic macroinvertebrate drift, with the other peak occurring after sunset which was not sampled. Benthic samples were taken using a Hess net (area sampled = 0.86m², mesh net 343μm), and

kick net sample using a d-net for 10 minutes. Kick net sampling occurred along banks, riffles and runs throughout the reach in order to provide a comprehensive qualitative sample of the reach. All macroinvertebrates collected and preserved in 80% EtOH and returned to the laboratory for sorting and identification. We sampled for trout using backpack electrofishing (Smithroot LR-24) following standard procedures as outlined in Reynolds (1983) and Nickum (1988). All trout were anesthetized in AQUI-S-20E before total length was measured to the nearest mm and weight recorded using an electronic scale to the nearest 100th of a gram (Summerfelt et al. 1990). Trout over 120 mm had passive integrated transponder (PIT) tags (Biomark Inc, Idaho, USA) inserted directly behind the pectoral fin into the body cavity for measuring recapture rates and growth during the study. PIT tags were inserted during our first sampling event in June 2019. During each sampling effort, stomach contents of the first 10 Brook and Brown Trout each over 120mm were determined using gastric lavage (Hyslop 1980; Hartleb and Moring 1995; Kamler and Pope 2001; Hafs et al. 2011). These stomach samples were immediately preserved in 80% EtOH and returned to the laboratory for sorting and taxonomic identification. Aquatic macroinvertebrates were identified down to order due to decomposition making identification down to family or genus near impossible. Macroinvertebrates were sorted and identified using Merritt et al. (2019) under magnification (Leica MZ-8 dissecting microscope).

Water quality was measured during each sampling event using a YSI data sonde (YSI 650 MDS). We recorded temperature, specific conductivity, total dissolved solids (TDS), salinity, dissolved oxygen (DO) as both a percentage and mg/L, and pH. Stream temperatures were recorded every half hour using continuous temperature loggers (HOBO Water Temperature Pro v2) to establish thermal regime in each stream. Frost Creek had two temperature loggers, one located at the study site and one located 2 km downstream. Cedar Creek had one temperature

logger located within the middle of the 3 reaches. In addition, we monitored temperature in Duke Creek, the receiving stream for Frost Creek. Duke Creek was used as a temperature reference site with a HOBO temperature logger located just above the confluence with Frost Creek. It was used as a reference site given that no trout were sampled therein in our first Spring 2019 survey. We were curious why, and suspected an elevated thermal regime, similar to many other studies (Meisner 1990; Wehrly et al. 2007). Rainfall totals were taken from the national weather service monitoring station in Cedar Springs, MI.

Statistical methods

Fulton's condition factor was calculated using trout length and weight (Barnham and Baxter 2003) and a Wilcox test was used to determine if there was significant difference between the lengths and weights of Brook Trout in Frost vs. Cedar Creeks. Fulton's condition factor is a qualitative measure that is based on a visual assessment of a fish with values ranging from less than 0.8 (Extremely poor fish) to greater than 1.6 (excellent, trophy class fish) (Barnham and Baxter 2003). Growth was calculated using recaptured trout inserted with PIT tags. We calculated absolute growth over time as:

$$G_{absolute} = \frac{L_2 - L_1}{t_2 - t_1}$$

where $G_{absolute}$ represents growth over a given time; L_2 indicates final length; L_1 is initial length; t_2 represents final capture date; and t_1 represents the first capture date. Welch Two Sample t-test was used to determine significance between Brook and Brown Trout growth rates. No Brook Trout were recaptured in Cedar Creek.

Potential changes in feeding behavior between Frost and Cedar creek were explored using non-metric multidimensional scaling (NMDS) in RStudio software. We used pairwise

ADONIS for post hoc analyses to determine which interactions between Brook and Brown Trout and drift and benthic macroinvertebrates were significant (Rstudio Version 2.5-6, package: VEGAN, Package: pairwise comparisons). A pairwise ADONIS statistically analyzes the interactions between each fish species and the interaction or strength of association between each species and their food resources (drift vs. benthos), and interaction between drift and benthos (Appendix 1: Figure 1). Ivlev's electivity index (1961) was used to quantitatively compare the percentage of occurrence between common orders of insects in the stomachs with their frequency in the environment proceeding capture of the trout throughout the seasons. The electivity index was calculated as:

$$E = \frac{r_i - P_i}{r_i + P_i}$$

where r_i represents the proportion of an order within the stomach and P_i represents the percentage of that order in the stream environment. The index ranges from -1 with complete avoidance of a food item, to +1 with complete selection for a prey item in accordance with a prey items abundance within the environment.

Morista's overlap index (1959) was used to determine overlap in diet between Brook and Brown Trout throughout the year. The overlap index was calculated as:

$$M = \frac{2 \sum_i^n P_{ij} P_{ik}}{\sum_i^n P_{ij} \left[\frac{n_{ij} - 1}{N_j - 1} \right] + \sum_i^n P_{ik} \left[\frac{n_{ik} - 1}{N_k - 1} \right]}$$

where M represents Morista's index of niche overlap between species j and k ; p_{ij} represents proportion resource i is of the total resources used by species j ; p_{ik} represents proportion resource i is of the total resources used by species k ; n_{ij} represents number of individuals of species j that use resource category i ; n_{ik} represents number of individuals of species k that use resource category i ; and N_j , N_k represent total number of individuals of each species in the sample.

Morisita's values range from 0 to 1, with 0 representing no overlap in diet and 1 representing complete overlap.

RESULTS

Overall, 488 trout were captured (239 and 249 in Frost and Cedar creeks, respectively). Mean total length, weight and condition factor of Brook Trout in Frost creek (n = 225) and Cedar Creeks (n=43) were calculated (Table 1, Appendix 1: Figure 5). There was significant difference between total length and weight of Brook Trout between our study sites using two-sided Wilcox test (W = 5953.5, P = 0.016; W= 6047.5, P = 0.009), with larger Brook Trout in Cedar Creek. However, there were fewer trout captured in Cedar Creek, and they were larger in size (Table 1). In Frost Creek, more young-of-the-year (YOY) Brook Trout were present, suggesting strong reproduction and recruitment (Figure 2). Individuals < 100 mm in length when captured were considered YOY. We ran a second Wilcox test to confirm Brook Trout in Cedar Creek were longer and heavier than in Frost Creek (length, W=5953.5, P = 0.008; weight, W= 6047.5, P = 0.005). Wilcox test indicated no significant difference in overall condition factor between Brook Trout in Frost and Cedar creeks (W= 5372.5, P = 0.25). With greater abundance of YOY Brook trout in Frost Creek while the overall length of individuals in the population were less than Cedar Creek and health condition, assessed as length/weight relationship indicated "fair health" condition.

Mean length, weight and condition factor of Brown Trout were calculated within Cedar creek (n= 198) and Frost Creek (n=13) (Table 1, Appendix 1: Figure 5). A two-sided Wilcox test was run on Brown Trout lengths and weights in Frost and Cedar Creek and indicated no significant difference (W= 1582, P= 0.16; W= 1639, P= 0.099).

Although condition factor (as assessed with length/weight relationship) was not significantly different, growth rates for Brook Trout in Frost Creek and Brown Trout in Cedar Creek were different. Brook Trout growth from June through December was 0.13 mm/day (n = 3) and June through May was 0.07 mm/day (n = 2). In Cedar Creek, Brown Trout growth from June through December - the prime growing season for fish in temperate streams was 0.18 mm/day (n = 2), while annual growth rate (June through May) was 0.21 mm/day (n = 3). This suggests that there was increased competition for food resources during the winter months. Growth rates were not significantly different in Brook and Brown Trout from June through December ($t = -0.85$, $df = 2.3$, $P = 0.76$). Growth rates were significantly different when calculated over the entire study period (June through May) ($t = -4.45$, $df = 2.4$, $P = 0.02$). We were unable to calculate growth rates of Brook trout in Cedar Creek due to no recaptures.

We did not find significant overlap between trout diets throughout all seasons suggesting resource partitioning is occurring. The NMDS plot shows the interactions between fish stomachs and drift and benthos, and how they change through the seasons (NMDS stress: 0.20 and 0.21 in Frost and Cedar Creeks respectively) (Figures 2 and, 3). In Frost Creek, Brook Trout was significantly associated with feeding from both the drift and benthic macroinvertebrate communities (Pairwise ADONIS, Brook Trout vs. drift, $P = 0.006$; Brook Trout vs. benthic, $P = 0.006$) (Table 2), whereas in Cedar Creek Brook Trout were only associated with feeding from the benthic community (Brook Trout vs. benthic, $P = 0.006$) (Table 3). Brown Trout were significantly associated in feeding from the drift and benthos in Cedar Creek (Brown Trout vs. drift, $P = 0.006$; Brown Trout vs. benthic, $P = 0.006$) (Table 3), while Brown Trout were marginally associated with feeding from drift and benthic macroinvertebrate community in Frost Creek (Brown Trout vs drift, $P = 0.042$; Brown Trout vs. benthic, $P = 0.03$) (Table 2). This

suggests that there is some competition for benthic food resources between Brook and Brown Trout in Cedar Creek. We think this is strong evidence of competitive interference in which the niche breadth of Brook Trout has been constrained by Brown Trout (e.g. pushing them out of the drift-feeding niche). Ivlev's electivity index was used to further analyze the selection of invertebrates by Brook and Brown Trout (Figure 5). In Frost Creek, Brook Trout exhibited a greater selectivity for Crustacea (Ivlev electivity = 0.18), Diptera (Ivlev electivity = -0.32) and Trichoptera (Ivlev electivity = -0.45). Plecoptera (Ivlev electivity = -0.95) and Ephemeroptera (Ivlev electivity = -0.62) were avoided as prey items by Brook Trout in Frost Creek. Whereas in Cedar Creek, Brook Trout did not select for certain taxa as often and had a larger feeding niche breadth. Brook Trout in Cedar Creek preyed upon Plecoptera (Ivlev electivity = -0.67) and Ephemeroptera (Ivlev electivity = -0.46) and did not avoid them as much as Brook Trout in Frost Creek throughout the year. Brown Trout selected from a broad niche breadth, feeding opportunistically across multiple taxa. In May 2020, our sampling was preceded by a heavy rain (6.6 cm over 72 hours) which resulted in floodplain inundation and apparently flushed massive numbers of annelids into the stream (Appendix 1: Figure 2). Both Brook and Brown Trout stomachs were distended and were full, almost exclusively, of annelids (Ivlev electivity = 0.96, and, 0.97 for Brook and Brown Trout respectively) (Figure 4).

Morista's Overlap index, used to analyze the overlap in dietary niche's between Brook and Brown Trout in Cedar Creek, indicated low to moderate dietary overlap (mean = 0.29, range 0- 0.56) (Table 3). Morista's Index was not run on Frost Creek due to the small number of Brown Trout sampled. I was unable to sample Brook Trout in August 2019, which resulted in no overlap calculation for that month (Table 3). Food resources were relatively abundant in both streams. Macroinvertebrate mean drift densities pooled throughout the year were 177.6 +/- 120.6

and 149 +/- 118.6 individuals/100m³ in Frost and Cedar Creek, while average benthic abundance was 3265.5 +/- 1525 and 6337.2 +/- 3743.5 invertebrates/m² (Table 2). Frost Creek has a higher drift abundance when averaged over the year, while Cedar Creek had abundance within the benthic macroinvertebrate community. Aquatic macroinvertebrates had individuals from 19 orders within the stream environment (Appendix 1: Figure 6 and 7).

Temperature data was recorded every 30 minutes using HOBO loggers placed in the study sites. The yearly average temperature for Frost Creek was 9.2°C, mean daily summer temperature (5/28/2019-9/2/2019) at was 16.1°C and maximum recorded daily average of 19.8°C (Figure 5). Cedar Creek had a yearly average of 9.7°C, mean daily summer temperature (6/19/2019-9/2/2019) of 17.8°C and maximum daily average of 20.9°C (Figure 5). The mean yearly temperature of Duke Creek was 10.1°C, mean daily summer temperature (5/28/2016-9/2/2019) of 19°C with a maximum daily average of 22.9°C (Figure 5).

Discussion

We hypothesized that there would be significant niche partitioning between Brook and Brown Trout when living in sympatry, with Brook Trout having a narrow niche breadth and feeding largely from the benthos compared to Brown Trout, which we predicted would have a broad niche breadth. Our results supported this hypothesis showing niche partitioning occurring in Cedar Creek with low overlap in diets, while Brook Trout in Frost Creek were significantly associated in feeding from both macroinvertebrate drift and benthic resource pools. Our second hypothesis predicted that condition factor for Brook Trout would be higher in Frost Creek than in Cedar Creek. Our overall condition for both populations of Brook Trout were not significantly different within similar size classes. Brook Trout in Cedar Creek were larger, but abundant compared to Brook trout in Frost Creek. Stream water chemistry was similar between our two

streams, yet Frost Creek's mean temperature remained cooler throughout the year compared to Cedar Creek's mean temperature.

Our initial hypothesis that Brook Trout living in the absence of Brown Trout will have a broad niche breadth, feeding opportunistically was supported by our results. Brook Trout within Frost Creek feed opportunistically from both the drift and benthic macroinvertebrate pools, similar to the feeding behavior of Brown Trout in Cedar Creek (Table 4). Ivlev's electivity index indicates that Brook Trout positively selected for Crustaceans in relation to their abundance within the stream environment, while actively avoiding Plecoptera and Trichoptera (Figure 4).

Our results indicated that niche partitioning does occur between Brook and Brown Trout when living in sympatry, given low overlap in diet occurring throughout the year (Table 3). With both species in Cedar Creek having a fair condition level based on the length-weight relationship, the overlap suggests that there are enough food resources available to maintain a positive energy balance (Table 1,3; Figure 4). However, in the presence of Brown Trout, we found that Brook Trout do have a narrower niche feeding breadth, with preference for the benthos, similar to results reported by Griffith (1974) (Table 5). Griffith (1974) found that Brook Trout preferred Ephemeroptera, Trichoptera and Plecoptera when in sympatry with Cutthroat Trout (*Oncorhynchus clarkii*). In Cedar Creek, Brook Trout fed primarily on Crustacea, Trichoptera, Plecoptera and Ephemeroptera. Brown Trout in Cedar Creek fed across all taxa throughout the year without a preference for specific taxa (Figure 4). During the month of May following a flooding event, both Brook and Brown Trout preyed upon annelids almost exclusively (Figure 4).

Brown Trout diet in Cedar Creek shows high preference for Crustaceans which could create competition with Brook Trout (Figure 4). Hasegawa et al. (2004) showed that smaller

bodied Brown Trout will outcompete larger individuals of a less dominant species, which may have an effect on the growth and overall condition of Brook Trout within Cedar Creek. With competing populations, Fausch and White (1981) showed that when living in sympatry, Brown Trout will outcompete Brook Trout for preferred resting and feeding positions leaving Brook Trout in less ideal positions. In mixed populations, Brown Trout often grow faster and have a negative effect on the Brook Trout population (Carlson et al. 2007; Dewald and Wilzbach 1992). Unfortunately, with no recaptured Brook Trout in Cedar Creek, we were unable to verify growth rates of Brook Trout within this stream. Cooper (1953) and Fausch and White (1986), are the only two studies to have previously looked at sympatric growth rates between Brook and Brown Trout populations. Brook Trout populations were found to increase in average size faster but had higher mortality from sport fishing compared to Brown Trout (Cooper 1953). YOY Brook and Brown Trout in contrast, were found to emerge and grow at similar rates during their first summer, but subsequent seasons were not reported (Fausch and White 1986). In both Frost and Cedar Creek, we theorize that there are at least 3 age classes in the populations (Figure 6).

Our second hypothesis was that overall health, or condition of Brook Trout populations living in the absence of Brown Trout will be greater than populations living in the presence of Brown Trout. Brook Trout condition factor between Frost and Cedar Creeks was not different. This suggests that food resources are abundant enough to support both populations, albeit with fair condition vs. great condition factor (Barnham and Baxter 2003). We surveyed fewer, but larger Brook Trout in Cedar Creek (Table 1) and theorize this is due to Brown Trout predation on YOY Brook Trout, resulting in relatively few YOY Brook Trout in Cedar Creek (Figure 6). Brown Trout have been known to feed on other fish species, especially smaller (<100 mm) in size (Hyvarinen and Huusko 2006). In Frost Creek where Brown Trout are extremely rare ($n =$

13 over one year), we see a greater abundance of YOY Brook Trout (< 100 mm) compared to Cedar Creek (45 vs. 4 YOY, respectively) (Figure 6). Other possible factors that influence fish reproduction and YOY recruitment include variation in temperature and precipitation (Kanno et al. 2016). Because our two river systems were within 10 km, and part of the same river drainage basin, these abiotic variables should be similar. Water quality parameters were nearly identical outside of specific conductivity, which was higher in Cedar Creek (Appendix 1: Figure 3 and 4). Substrate in Frost Creek is mostly small gravel with little large woody debris (LWD), while Cedar Creek is characterized by sandy substrate with numerous LWD throughout reaches 1 and 3. Reach 2 in Cedar Creek has little to no LWD, but many undercut banks and small gravel for substrate.

Thermal stress for Brook Trout starts at 21°C, and temperatures regularly at or above this will exclude Brook Trout (Meisner 1990; Taniguchi et al. 1998; Wehrly et al. 2007). Once that barrier is reached, feeding, reproduction and growth are reduced in Brook Trout (Brett 1971; Elliot 1981; Dickerson and Vinyard 1999; Selong et al. 2001; Meeuwig et al. 2004; Hartman and Cox 2008). Kanno et al. (2016) demonstrated that seasonal temperatures can affect YOY abundance, which is more important in regulating population dynamics than adult abundance. Cedar Creek is slightly warmer than Frost Creek during the summer, and, coupled with increased competition from Brown Trout may result in a fewer Brook Trout. In the context of climate change, as streams continue to warm, Brown Trout which have a higher thermal tolerance (of 24°C), will likely continue to move into these headwater streams displacing and eventually replacing Brook Trout (Waters 1983; Meisner 1990; Zorn and Nuhfer 2007). In Duke Creek, with daily temperatures ranging above Brook Trout's thermal limit and near Brown Trout's thermal limit, we theorize that this is the reason why we were unable to locate either trout species

in several reaches of Duke Creek. Climate change is continuing to work against these cold-water refuges as climates become warmer (Waters 1983; Ohlund et al. 2008). According to Hayhoe et al. (2010), climate in the Great Lakes region will continue to increase in temperature as well as have substantial increases in winter and spring precipitation. Rising air temperatures will raise stream temperatures slowly over time as well. Brown Trout slowly replace Brook Trout by excluding them from cold groundwater refuges through competition as they move upstream with watersheds (Hitt et al. 2017). Greater winter precipitation, which is expected to increase as climate change continues, can negatively affect YOY Brook Trout abundance (Hayhoe et al. 2010; Kanno et al. 2016). An increase in intensity of precipitation events will result in more frequent flooding and theoretically more pulses in terrestrial macroinvertebrate food resources. These pulses could change the composition of diets among fish species as well as changing growth rates, feed and resting positions within the stream environment.

Currently, Frost and Cedar creeks are both open to fishing for trout to private landowners and through public access points. Of highest concern is Frost Creek's population of Brook Trout, given that the stream is small (1st order) and the population robust. It needs continued protection and we recommend long-term monitoring specifically to try and track short-term changes in Brown Trout abundance, as well as the longer-term potential consequences of climate change. This is a very small population and its reproduction has not yet been studied. With this population being this small it would be easy to overfish, removing reproductive adults from the population. In addition, the watershed is currently mostly rural farmland with residential properties relying on groundwater wells. Assuming that water tables could be lowered by the withdrawal of groundwater for irrigation, the contribution of groundwater to stream-flow would decline, thus increasing stream temperatures and reducing water flow (Meisner 1990; Waco and

Taylor 2010; Snyder et al. 2015). Brook Trout is known to use groundwater upwellings for spawning and thermal refuge during winter and summer (Waco and Taylor 2010; Snyder et al. 2015). Groundwater has been directly linked to relatively stable stream flows and cold temperatures within streams (Wiley and Seelbach 1997). Determining the extent to which groundwater use is affecting Frost Creek may be important to conserve and protect this isolated population of Brook Trout. Additionally, the riparian environment should be restored where possible, allowing for increased resiliency to climate change effects on the stream (Wondzell et al. 2019). Wondzell et al. (2019) studied whether stream temperatures were more vulnerable to discharge rates, changing air temperatures, or riparian vegetation in future climate change scenarios. Wondzell et al. (2019) found that riparian vegetation was the most important factor in creating a resilient stream ecosystem. Riparian restoration can lead to cooler stream temperatures, creating a healthier stream environment for aquatic macroinvertebrates and fish species.

Cedar Creek has a healthy population of coexisting Brown Trout and Brook Trout. However, there is evidence of food partitioning and thereby the potential for competition. Also troubling is the relatively limited number of YOY Brook Trout surveyed in Cedar Creek. Cedar Creek has a much larger watershed and runs through downtown Cedar Springs, MI. This stream has already experienced anthropogenic changes such as the commercial and residential growth of Cedar Springs. Future management of this watershed would include monitoring groundwater well usage, long-term monitoring of water quality as well as active urban stream management such as the use of vegetated buffer strips, raingardens, etc. Water temperature is a critical factor affecting both Brook and Brown Trout. If groundwater withdrawal is increased, then stream temperatures can increase due to the reduction of cold groundwater influx that moderates daily

and seasonal extremes in air temperature (Waco and Taylor 2010; Snyder et al. 2015).

Restoration work should focus on areas less influenced by humans where we would be able to create a natural riparian area that would protect the stream and mitigate any ground water reduction (Waco and Taylor 2010; Wondzell et al. 2019).

Future research on Frost Creek should be conducted as a multi-faceted project with long-term water quality and trout population monitoring. Long-term projects would allow us to see how a Brook Trout population is influenced by anthropogenic changes without significant pressure from Brown Trout. Frost Creek has small watershed and is heavily influenced by groundwater infiltration and stream temperatures are sensitive to changing air temperatures, but are most affected by changing riparian vegetation (Wondzell et al. 2019). Determining how the riparian area affects the water quality and food resources (terrestrial and aquatic macroinvertebrate communities) will aid us in creating more effective management plans for small headwater populations of Brook Trout.

Within Cedar Creek, future research using a larger diet study between Brook and Brown Trout would yield greater insight to the competition for resources within the system. One aspect of diet to study within both streams is how feeding differs after heavy precipitation compared to normal feeding over the course of a year. Previous studies have shown that Brook Trout exhibit niche partitioning when living in sympatry with other species, especially as they age (Griffith 1974; Hammar 1998). Additionally, scale collection and greater PIT tagging efforts will allow us to create a length-age key within this watershed and determine growth rates within both populations. With a larger dataset containing diets, growth and age classes, we will be to create a more comprehensive management plan within the watershed. Determining how these trout partition not only aquatic food resources, but also how terrestrial invertebrates' impact seasonal

diets will help in understanding how Brook Trout use the riparian area food resources throughout the year.

Within the Rogue River watershed an aspect that warrants consideration is looking at potential barriers to fish passage throughout the headwater tributaries. On Frost Creek the culvert at Algoma Avenue is considered a barrier to fish passage and we believe it is one mechanism that has helped Brook Trout remain dominant. However, during our sampling efforts, we did not perceive it to be a barrier throughout the year. Identifying barriers to passage and the fish communities within those streams will help determine if there are any isolated populations of Brook Trout within the watershed. We are not advocating installing barriers but rather consider maintaining or modifying existing barriers such that they continue to protect isolated populations of Brook Trout, while still allowing for a more natural flow regime.

Conclusion

In conclusion, we found evidence of low to moderate competition between Brook and Brown Trout living in sympatry, leading to some niche partitioning. Creating a long-term study on trout diet interactions was necessary to determine how niche partitioning affects these populations. We found that abundant food resources likely reduced the potential negative consequences of interspecific competition. Thus maintenance, protection and enhancement of habitat attributes that promote healthy stream systems is critical. For example, riparian restoration will be key to protecting the stream environment in which Brook Trout reside by shielding it from sunlight and providing habitat, in the form of large woody debris, and food resources, in the form of allochthonous detritus, for aquatic macroinvertebrates which they prey upon. As rivers continue changing and suitable habitat shrinks, our top predators within stream systems will face increased interspecific competition. This will aid us not only in understanding

competition in headwater streams, but also expand our knowledge into their year-round life history. Headwater streams provide an important habitat refuge for cold water species throughout the United States from the effects of climate change. As humans continue to expand into these forested worlds, it is important to protect these areas and the life they sustain.

ACKNOWLEDGEMENTS

I'd like to thank Eric Snyder (Grand Valley State University) for assisting with study design and field work. Sampling efforts were supported by undergraduates Grayson Kozak, Anahi Huitron, Connor O'Brian, and graduate students Josh Arnold, Tyler Harman, and Billy Mulligan. All sampling and handling of fish were carried out in accordance with guidelines for the use and care of fishes by IACUC (Permit #: 19-16-A). Funding was provided by Grand Valley State University (GVSU Presidential Grant), Trout Unlimited: Kalamazoo chapter (George L. Disborough Research Grant), and Michigan Space Grant Consortium (NASA Grant #NNX15AJ20H).

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Tables

Table 1. Mean averages of length, weight, and condition values with SD for Brook and Brown Trout populations in Frost and Cedar Creek.

FROST CREEK			
	Mean length (mm)	Mean weight (g)	Mean Fulton's
BROOK TROUT	142.68 +/- 45.09	39.92 +/- 35.98	1.11 +/- 0.96
BROWN TROUT	183.85 +/- 62.99	86.38 +/- 81.31	1.03 +/- 0.16
CEDAR CREEK			
	Mean length (mm)	Mean weight (g)	Mean Fulton's
BROOK TROUT	160.09 +/- 39.42	52.46 +/- 36.49	1.07 +/- 0.2
BROWN TROUT	210.38 +/- 68.19	139.13 +/- 138.06	1.1 +/- 0.19

Table 2. Pairwise ADONIS results comparing Brook and Brown Trout to drift and benthic macroinvertebrates in Frost Creek. Significant interactions designated by (**) and marginally significant (*). Significant interactions indicate there is a strong association between the two interactions.

PAIRS	DF	F. MODEL	R ²	P. ADJUSTED SIG
BROOK TROUT VS. BROWN TROUT	1	1.47	0.032	0.972
BROOK TROUT VS. DRIFT	1	4.32	0.08	0.006**
BROOK TROUT VS. BENTHIC	1	10.44	0.18	0.006**
BROWN TROUT VS. DRIFT	1	4.35	0.35	0.042*
BROWN TROUT VS. BENTHIC	1	10.99	0.57	0.03*
DRIFT VS. BENTHIC	1	7.03	0.41	0.012*

Table 3. Pairwise ADONIS results comparing Brook and Brown Trout to drift and benthic macroinvertebrates in Cedar Creek. Significant interactions designated by (**) and marginally significant (*). Significant interactions indicate there is a strong association between the two interactions.

PAIRS	DF	F. MODEL	R ²	P. ADJUSTED SIG
BROOK TROUT VS. BROWN TROUT	1	1.26	0.26	1.00
BROOK TROUT VS. DRIFT	1	2.2	0.035	0.14
BROOK TROUT VS. BENTHIC	1	8.25	0.001	0.006**
BROWN TROUT VS. DRIFT	1	3.57	0.001	0.006**
BROWN TROUT VS. BENTHIC	1	8.31	0.001	0.006**
DRIFT VS. BENTHIC	1	7.18	0.004	0.012*

Table 4. Morista's Overlap index comparing the diet of Brook vs. Brown Trout in Cedar Creek. Scale is 0-1 with 0 representing no overlap in diet and 1 representing complete overlap.

MONTH	DIET OVERLAP	NUMBER OF TROUT
JUNE	0.57	Brook = 6, Brown = 6
AUGUST	N/A	Brook = 0, Brown = 5
OCTOBER	0.27	Brook = 3, Brown = 7
DECEMBER	0.29	Brook = 4, Brown = 10
FEBRUARY	0.36	Brook = 3, Brown = 10
MAY	0.33	Brook = 5, Brown = 8

Table 5. Number of invertebrates located within the drift per 100m³ and the benthos m² within Frost and Cedar Creeks during the months of June, August, October, December of 2019, and February and May of 2020.

FROST CREEK

	June	August	October	December	February	May
BENTHIC	3372.09	4034.88	895.35	2348.84	5383.72	3558.14
DRIFT	380.21	248.69	96.39	47.29	169.52	123.68

CEDAR CREEK

	June	August	October	December	February	May
BENTHIC	7372.09	12430.23	2930.23	1883.72	6418.61	8988.37
DRIFT	135.69	276.89	26.65	115.51	33.72	305.21

Figures

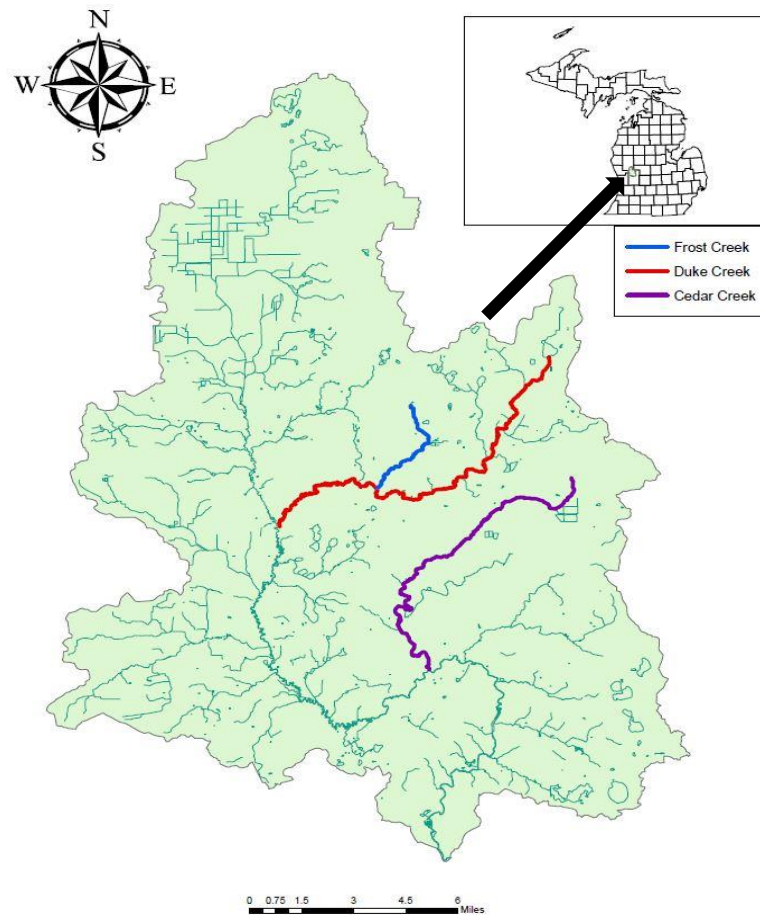


Figure 1. Stream locations within Rogue River watershed. Frost Creek (blue) and Cedar Creek (purple) were sampling sites used for gastric lavage and pit tagging. Duke Creek (red) was used as a temperature reference since Brook and Brown Trout were not found within several reaches sampled.

Brook Trout lengths in Frost and Cedar Creek

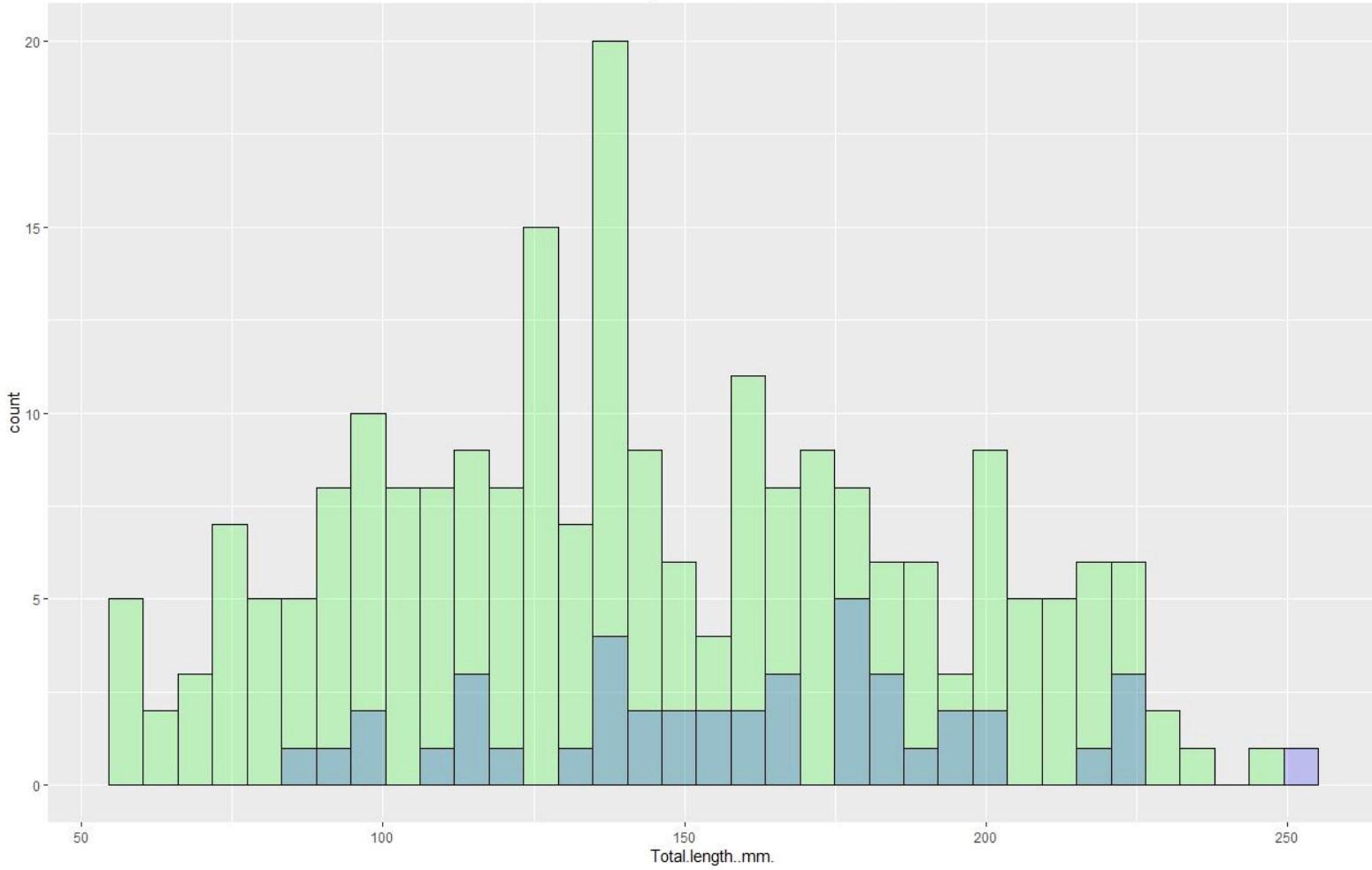


Figure 2. Length frequency histogram of Brook Trout lengths in Frost and Cedar Creek. Frost Creek is denoted by the green bars, while Cedar Creek is denoted by the blue bars.

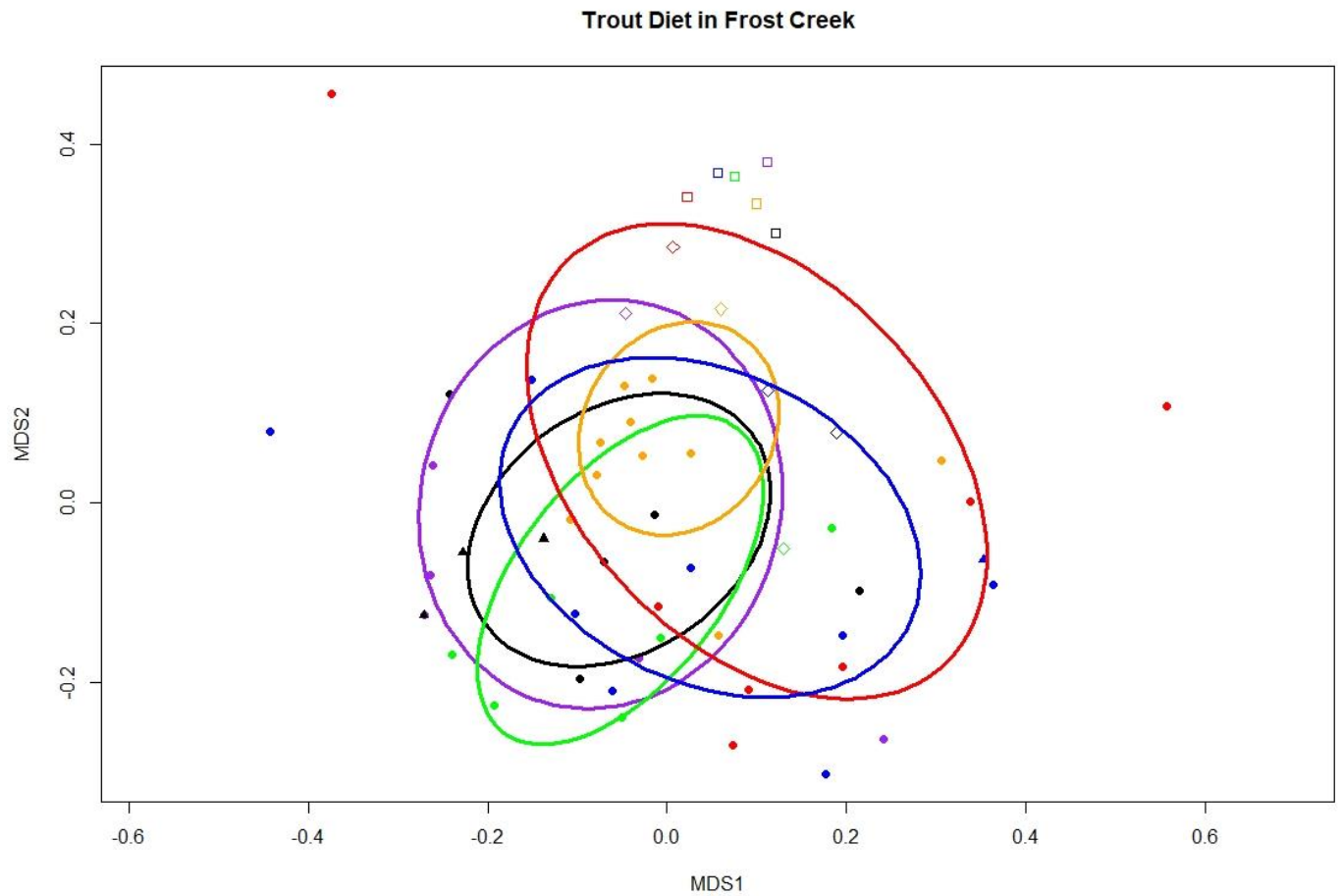


Figure 3. Nonmetric-multidimensional scaling analysis comparing macroinvertebrates located within drift and benthos vs. macroinvertebrates in trout stomachs in Frost Creek in June, August, October, December, February and May (Bray-curtis distance metric, stress = 0.20). Solid triangles represent drift samples, squares represent benthic samples, upside down triangles represent Brown Trout, and circles represent Brook Trout samples. Colors are as follows: red = June, purple = August, blue = October, black = December, green= February and orange = May.

Trout Diet in Cedar Creek

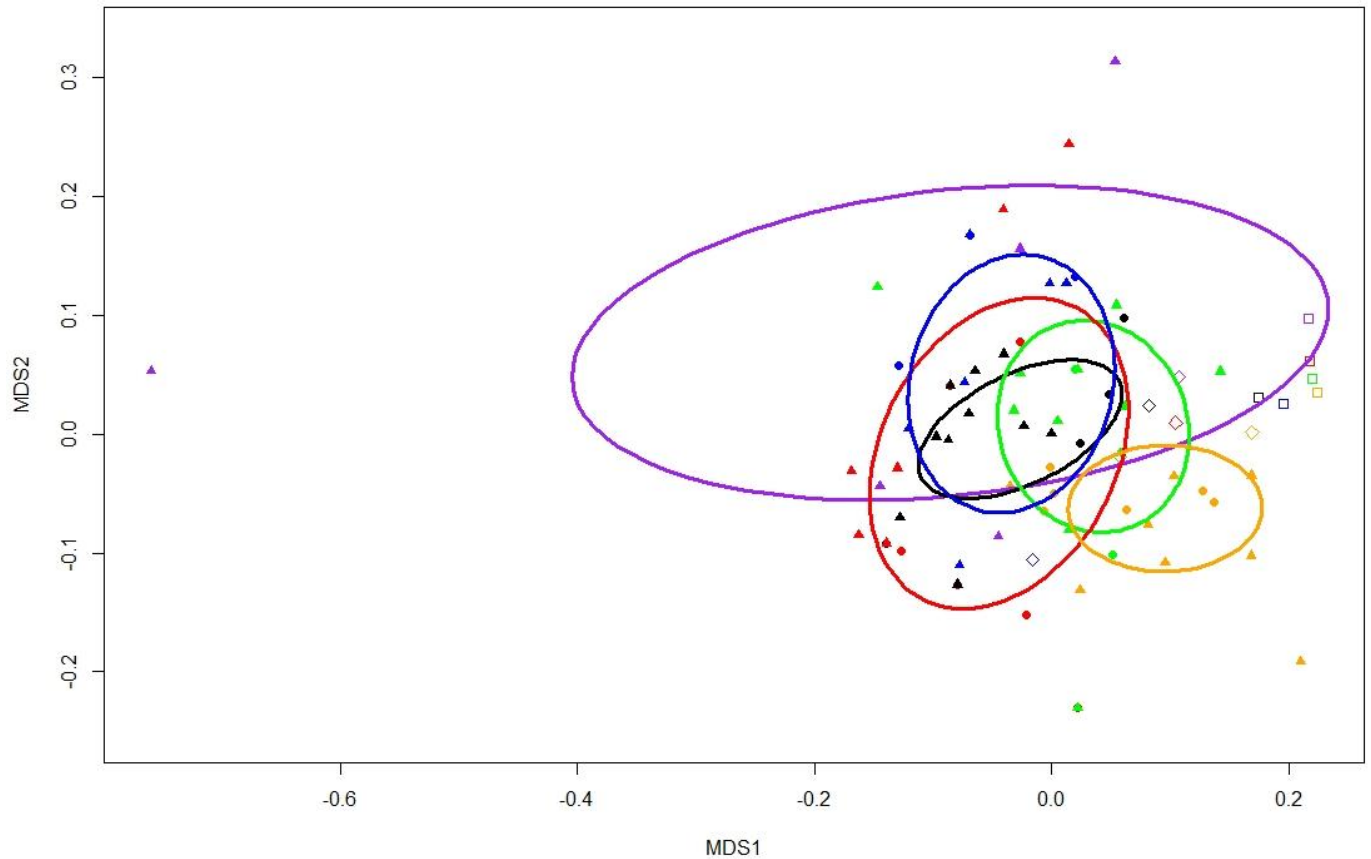


Figure 4. Nonmetric-multidimensional scaling analysis comparing macroinvertebrates located within drift and benthos vs. macroinvertebrates in trout stomachs in Cedar Creek in June, August, October, December, February and May (Bray-curtis distance metric, stress = 0.20). Solid triangles represent drift samples, squares represent benthic samples, upside down triangles represent Brown Trout, and circles represent Brook Trout samples. Colors are as follows: red = June, purple = August, blue = October, black = December, green = February and orange = May.

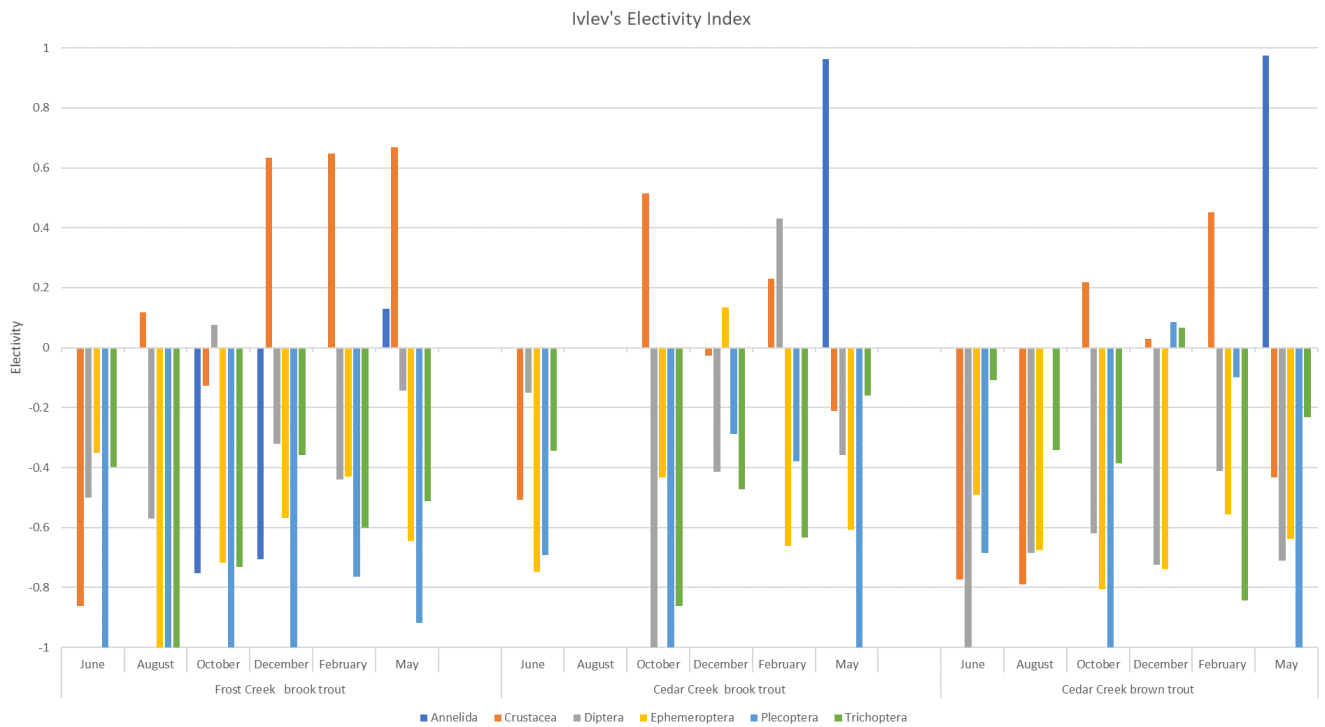


Figure 5. Ivlev's electivity index showing six common orders within the diets of Brook and Brown Trout. Frost Creek Brook Trout (left), Cedar Creek Brook Trout (Center) and Brown Trout (Right).

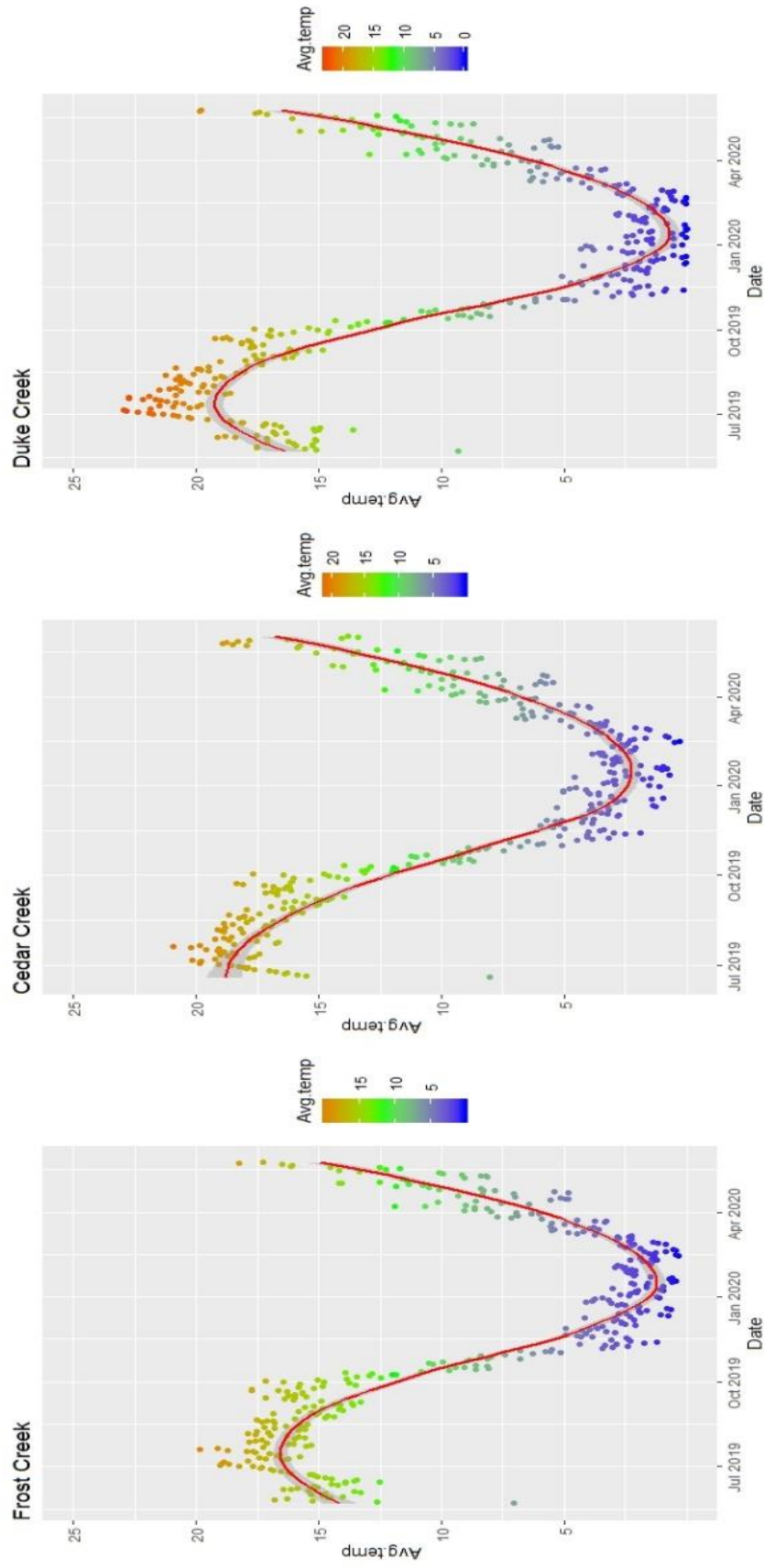


Figure 6. Temperature comparison between Frost, Cedar, and Duke creeks. Mean summer temperatures for Frost, Cedar, and Duke Creek were 16.1°C, 17.8°C, and 18.9°C.

Chapter III

EXTENDED REVIEW OF LITERATURE

Brook trout (*Salvelinus fontinalis*) is native to eastern North America, but have been introduced to other parts of North America, Europe, South America, Asia, and Africa for sport fishing (Kershner et al 2019b; MacCrimmon 1969). Early immigrants from Europe erroneously named it a trout rather than a char, due to its similarity to Brown Trout (*Salmo trutta*) which is native to Europe (MacCrimmon 1968, 1969). Brook Trout was first described in 1814 by Mitchell through captured specimens near New York City (MacCrimmon 1969). In the United States, their native range extended from the northern Great Lakes region through to the Northeast and through the southern end of the Appalachian Mountains (MacCrimmon 1969). Since the arrival of Europeans, Brook Trout have been extended to several states west of the Mississippi River and have become naturalized (MacCrimmon 1969). Brook Trout require clean and cold flowing streams to survive.

Brown Trout is native throughout Europe, in North Africa, and in Asia eastwards towards Afghanistan and is one of the best studied species of salmonid (Kershner et al. 2019a). The plasticity of Brown Trout has resulted in them being introduced to most places in world capable of supporting them (Bror Jonsson and Jonsson 2011b).

Brown Trout was first introduced into North America in 1883 and incubated at the Northville Hatchery, Michigan and later released into the Baldwin River in Michigan's Lower Peninsula (MacCrimmon 1968). By 1887, Brown Trout was found throughout the United States from the East Coast to the West Coast (MacCrimmon 1968). By early 1900's, biologists began to realize that Brown Trout was outcompeting and were more tolerant of environmental conditions than native salmonids (MacCrimmon 1968).

Brook Trout life history and habitat

As stated in the beginning, Brook Trout inhabit a vast range of habitats ranging from small headwaters in the Midwest, coastal tributaries, the Canadian shield in Québec and high-altitude headwaters of the Appalachian range (Kershner et al. 2019b; MacCrimmon 1969). This diversity of habitats has led to a wide array of life-histories. These life histories include resident stream dwelling populations, migratory fluvial populations, anadromous populations (salters), which occur along the Atlantic coast; and lake-dwelling and adfluvial populations (coasters), which typically occupy northern regions of the native range (Kershner et al. 2019b; MacCrimmon 1969). Brook Trout typically take two years to mature at which time they begin spawning during the fall. Brook Trout require small gravel to make their redd (spawning nest) and lay their eggs. Stream flow and temperature during winter egg incubation have been shown to be important drivers in survival and Brook Trout population dynamics (Kershner et al. 2019b).

Brook Trout typically spawn near areas with thermally moderating effects from strong groundwater upwellings (Webster and Eiriksdottir 1976). The range at which eggs are able to develop is 4.5°C to 11.5°C and will hatch within 7-13 weeks (MacCrimmon 1969). Redd scouring events due to high stream flow can severely damage redds, decreasing the survival of YOY individuals. It has been shown that overwinter survival increases with age-0 size (Hunt 1969) and since Brook Trout exhibit density dependence (Grossman et al. 2010), these events can be compensated for by increased per capita survival. Due to their short life span, Brook Trout populations are strongly sensitive to juvenile survival rates (Letcher et al. 2007). In small headwater streams where populations may be isolated from a larger source population (Aunins et al. 2014), multiple scouring events can lead to the extirpations of local populations with

recolonization events not likely to restore extirpated populations in most cases (Kanno et al. 2015).

In addition to the importance of temperature and groundwater, Brook Trout is sensitive to low pH (Kershner et al. 2019b). Low pH has been found to decrease the condition of Brook Trout (pH approx. 5.6; Wesner et al. 2011) and decrease survival (pH < 4; Robinson et al. 1976). Stream pH acidification due to acid mine drainage (AMD) (Herlihy et al. 1990) and atmospheric deposition (Baker et al. 1996). In addition to AMD and deposition, habitat degradation and introduction of non-native trout have led to reduction in Brook Trout populations throughout their range.

Water temperature is an important factor limiting distribution range of Brook Trout throughout their native range. Temperature is typically more predictive of Brook Trout occurring within a stream than geomorphological features (Rashleigh et al. 2005). Brook Trout temperature tolerance ranges from 0° to 25.3°C with thermal stress occurring above 21°C (MacCrimmon 1969; Meisner 1990; Wehrly et al. 2007). In streams where daily mean stream temperatures can exceed 23°C, Brook Trout is typically absent (MacCrimmon 1969; Meisner 1990; Wehrly et al. 2007). Groundwater provides a moderating effect, by giving thermal refugia to Brook Trout as summer heatwaves become more common (Hitt et al. 2017; Petty et al. 2012).

Throughout all of this, there is some hope as climate change continues to warm air and water temperatures around the world. There has been local adaptations for heat tolerance in Brook Trout across a small set of streams in Newfoundland, Canada (Wells et al. 2016). The spatial scale of this adaptation is currently unknown and further research will be needed across the entire range of Brook Trout to determine if more populations are capable of adapting.

Brown Trout life history and habitat

Life history traits can be influenced by the habitat environment in which the species resides (Jonsson et al. 2001). Brown Trout often exhibit three life histories, stream residents that spend their entire life cycle within a river, lacustrine-adfluvial which spawn in rivers and spend their adult life in lakes and anadromous individuals spawn in freshwater rivers and spend their juvenile and adult stages at sea (Jonsson et al. 2001; Jonsson 1989; Kershner et al. 2019c). Environmental and genetic factors play an important role between choosing freshwater residency and anadromy (Cucherousset et al. 2005).

Brown Trout typically mature between two and three years of age, although there is a north to south gradient (Jonsson and Jonsson 2011c; Letcher and Terrick 1998; Utrilla and Lobón-Cerviá 1999). As latitude increases, so does smolt size, perhaps due to the effects of decreasing water temperatures (Jonsson et al. 2001; Lund et al. 1989). Alm (1959) showed that the faster they grow, the younger they will mature. Spawning will occur between September and December in areas at the end of pool as it turns into a riffle (Stuart 1953) or in shallow swift water (Ottaway et al. 1981). Timing of the spawn varies along a latitudinal gradient as well, with northern populations spawning earlier in the year than southern (Jonsson and Jonsson 2011c). The preferred substrate for spawning is similar to that of Brook Trout in small gravel and pebbles.

Temperature is one factor that is currently threatening Brown Trout populations throughout the world. Brown Trout have similar temperature requirements of Brook Trout but are able to tolerate slightly higher water temperature with thermal stress and death beginning at 25°C (MacCrimmon 1968). Their preferred temperature ranges from 12.8°C to 19°C (Ferguson 1958; Swift 1961). These temperatures are ideal for adults, while incubating eggs require colder

temperatures between 2°C and 9°C (MacCrimmon 1968). As the earth's climate continues to warm, stream temperatures will continue to rise. Already there has been increases of 1°C and 3°C in parts of Europe and northern latitudes (Daufresne et al. 2003; Hari et al. 2006; Webb and Nobilis 2007).

With this change in climate temperature also comes a change in precipitation. Lower latitudes and altitudes will see less rainfall, while alpine areas and higher latitudes will see increased (Jonsson and Jonsson 2011a). Floods will become larger; droughts will become longer, and the plasticity of Brown Trout will be tested in the near future. The variability of Brown Trout and their ability to quickly colonize new areas will benefit them, but perhaps at the cost of native species in the systems they will colonize.

Brook Trout Diet

Brook Trout are opportunistic feeders who prey primarily on aquatic macroinvertebrates, terrestrial invertebrates, and occasionally other fish species (Allan 1981; Tiberti et al. 2016). Ingested prey diversity was not significantly correlated with the size of the trout, but was positively correlated with date of sampling (Tiberti et al. 2016). The abundance of prey type was dependent upon the type of habitat being sampled and what season you are sampling in. Trout diets show considerable variation with more prey ingested in the early summer months compared to less prey ingested in the later summer months (Sotiropoulos et al. 2006). In early summer, a majority of prey items consumed are aquatic macroinvertebrates (Diptera & Chironomidae) and adult blackflies (Sotiropoulos et al. 2006). During late summer, terrestrial derived invertebrates composed nearly 60% of prey items consumed, while 61-70% stomachs were empty from June through August (Sotiropoulos et al. 2006). Throughout the course of the year, terrestrial invertebrates can make up 38-47% of yearly biomass consumed and constitute 51-63% of the

yearly energy consumed by Brook Trout (Sweka and Hartman 2008). One aspect that can affect early summer diets in age-0 Brook Trout are riparian disturbances. Like adult Brook Trout, age-0 fish also rely heavily on terrestrial invertebrates during the summer months (Sotiropoulos et al. 2006; Sweka and Hartman 2008; Courtwright and May 2013; Studinski et al. 2017). Because of this, disturbances in the riparian have been shown to alter the composition of terrestrial invertebrates entering the stream (Studinski et al. 2017). In these areas, age-0 trout shifted their diet towards aquatic prey suggesting that in-stream invertebrate availability affects prey choice (Studinski et al. 2017). Courtwright and May (2013) designed an experimental study to test if Brook Trout select for terrestrial invertebrates during the summer months even when reduced. Even with terrestrial invertebrates only making up 7% of the abundance in the stream, Brook Trout continued to select for terrestrial invertebrates during this time period (Courtwright and May 2013). Drift is the major source of terrestrial invertebrates in streams during the summer months and during times of low flow, this reduces this critical resource for Brook Trout (Courtwright and May 2013). In intermittent streams, the inability of Brook Trout to change to benthos (bottom-dwelling) invertebrates shows that during the summer months these populations are heavily reliant on terrestrial invertebrates (Courtwright and May 2013). In the fall months, Brook Trout enter their spawning period. This period is marked by high energy expenditures related to spawning that can not be offset by calorific intake (Cunjak et al. 1987). Cunjak et al. (1987) believed that although low stomach fullness values are found during the summer months, that this is deceiving since higher water temperatures ($>15^{\circ}\text{C}$) during those collections cause the filling and evacuation of stomachs can occur 2-3 times/day. During winter months, low water temperatures limit Brook Trout to a single filling and evacuation per day of their stomachs per day (Cunjak et al. 1987). Despite continued feeding, Brook Trout continue to lose weight into the

early winter months since their calorific intake is not high enough to offset their energy expenditures, which leads to an energy deficit (Cunjak et al. 1987). After spawning the condition of fish is expected to decline, but immature trout showed the same responses as those that did spawn (Cunjak et al. 1987). One explanation is that the prey available in the winter months contain a lower energetic value compared to those available throughout the rest of the year (Cunjak et al. 1987). During the winter months, Trichoptera larvae were the most important prey item by volume and number, with Hydropsychidae and Limnephilidae the most commonly consumed families (Cunjak et al. 1987).

Brown Trout Diet

Brown Trout diets shift throughout the year between aquatic, terrestrial and other fish species. In natural streams and laboratory settings, Brown Trout populations follow a hierarchal social rank when feeding with dominant fish feeding during low light hours (Dawn/Dusk) and sub-dominant fish forced to feeding during complete darkness or diurnal (daytime) hours (Alanära et al. 2001). During spring and summer months their diet is composed of macroinvertebrates in the drift as well as terrestrial invertebrates (Ellis and Gowing 1957; Newman 1987; Laudon et al. 2005; Arzu et al. 2011; Cochran-Biederman and Vondracek 2017). Beginning with terrestrial invertebrates there has been a great deal of studies conducted with support for high and low inputs in trout diets (Laudon et al. 2005). This is influenced by the riparian environment surround the stream. The biomass of terrestrial invertebrates is lowest along agricultural land but is significantly higher along forests and grasslands (Edwards and Huryn 1996). The importance of terrestrial invertebrates within Brown Trout is therefore varied by watersheds and seasons as a result of seasons and time of emergence.

The summer season is when aquatic and terrestrial production peaks. When terrestrial inputs are low, trout feed from aquatic invertebrates with a focus on the drift (Newman 1987). During summer, Brown Trout have been shown to demonstrate neutral selection towards the benthos, while selecting for drifting *Brachycentrus* and *Gammarus* (Cochran-Biederman and Vondracek 2017). In July, there is a peak in terrestrial invertebrate production due to large hatches. During this time, large dominant Brown Trout will feed extensively on terrestrial and flying insects when they enter the drift (Gustafsson et al. 2014). This increase in feeding on terrestrials, reduces the competition for aquatic invertebrates allowing younger, smaller trout to feed in this niche (Gustafsson et al. 2014). Larger terrestrial invertebrates led to fewer organisms per stomach in trout during the summer months among Brown Trout (Neill 1938; Frost 1939). Even with no shortage of aquatic invertebrates, trout still selected for terrestrial invertebrates (Surber 1933). As the summer came to an end, we begin seeing a switch from terrestrial invertebrates back towards the drift and benthos niches within the stream.

Winter is a critical period for any salmonid for survival. Aquatic invertebrates located within the benthos represent an important part of the diet for Brown Trout (Anderson et al. 2016; Cochran-Biederman and Vondracek 2017). During the fall and winter months, they switch to benthic invertebrate feeding as drift species decline (Cochran-Biederman and Vondracek 2017). Smaller trout preyed on large Chironomidae more often than larger individuals (Anderson et al. 2016). Larger bodied Brown Trout preyed heavily upon Trichoptera or *Physella* (Anderson et al. 2016). Depending on the stream invertebrate composition, *Gammarus*, Limnephilidae, *Brachycentrus*, and large Chironomidae larvae can be significant components of the diets of larger Brown Trout in winter (Anderson et al. 2016). Smaller Brown Trout diets consist of *Ephemera*, *Isoperla*, *Gammarus*, and large Chironomidae larvae (Anderson et al. 2016).

Both large and small Brown Trout consume Limnephilidae; however, small trout consume primarily on *Limnephilus*, and *Pycnopsyche* and *Hesperophylax* accounted for larger portions of large trout (Anderson et al. 2016). Having a reliable and abundant food supply during the winter months is required to have stable trout populations; therefore, aquatic invertebrate communities within streams have a major impact on trout diet and growth (Anderson et al. 2016). This data lends support that Brown Trout shift their focus during the winter months from terrestrial and drift towards a more focused diet from the benthos. Due to the reduction of drift and terrestrial invertebrates in winter the increased focus on benthos leads to greater inter and intra competition. This competition can lead to deficits in energy for multiple species, including young trout (Cunjak et al. 1987).

Brook and Brown Trout Interactions

In Michigan, Brook Trout and Brown Trout occur in sympatric, or coexisting, populations. Brown Trout occur here through natural reproduction and hatchery stocking. Hatchery Brown Trout can play a large role in interactions with wild populations of Brook Trout. They can compete for habitat and feeding positions, as well as for food resources (Fausch and White 1981; Dewald and Wilzbach 1992). Brown Trout's competitive dominance has been correlated to the decline of native Brook Trout populations through its native range (Fausch and White 1981; Dewald and Wilzbach 1992; Ohlund et al. 2008). Hatchery fish tend to pose a higher threat to wild populations due to the fact that they are selectively bred for high feeding and growth rates, which may have greater aggression and competitive ability traits that accompany them (Dewald and Wilzbach 1992). Hatchery Brown Trout have been observed engaging in more agonistic encounters than wild Brown Trout and they won more contents than the wild fish (Bachman 1984; Dewald and Wilzbach 1992). If these species had evolved in

sympatry, then they may have developed mechanisms for partitioning resources (Dewald and Wilzbach 1992). Since the native distribution of Brown Trout are the northern latitudes of Europe and Eurasia and Brook Trout to Eastern Canada and Great lakes region and south to southern end of Appalachians, these species would not have developed those mechanisms (Dewald and Wilzbach 1992; MacCrimmon 1968, 1969). Öhlund et al. (2008) looked to understand the mechanisms that control species distribution through life histories and their effects on species replacement. Brown and Brook Trout that follow the stream resident life history share many features with one another, although higher growth rates and early sexual maturity have been cited as a couple of differences between the two species (Ohlund et al. 2008). It was hypothesized that when living in sympatry, there is an adaptive breakdown between species through interspecific interactions (Lovén-Wallerius et al. 2017; Závorka et al. 2017). In the case of Brown Trout and Brook Trout, two competing salmonid species living in sympatry, the competitive exclusion principle states that one of them will eventually become extinct or will experience an evolutionary shift in ecological niche, thus reducing competition (Hardin 1960). Brown Trout have gone against this principle, and several studies have shown that they shift to a diet niche closer to that of Brook Trout when living in sympatry vs. allopatric populations (Lovén-Wallerius et al. 2017). Lovén-Wallerius et al. (2017) studied the social behavior and interactions of age-0 Brown and Brook Trout to find out the underlying mechanisms as to why they were going against the competitive exclusion principle (Lovén-Wallerius et al. 2017). They found that Brown Trout showed no discrimination towards Brook Trout at an early life stage (Lovén-Wallerius et al. 2017). Early social association between heterospecifics can influence social learning, which may alter the feeding niche of Brown Trout when living in sympatry with Brook Trout (Lovén-Wallerius et al. 2017). As the trout grow, they become more territorial and

compete for resources more aggressively. In Michigan, Fausch and White (1981) looked at how they interacted and competed for positions within a stream. Although Brook Trout are found mostly in the headwaters and Brown Trout downstream, they still overlap in distribution in the middle reaches. Chapman (1966) believed that competition between species for space has been substituted for competition for food, which may be another limiting resource. He hypothesized that the size of territory is linked to the food supply, which in turn will regulate population density (Chapman 1966; Fausch and White 1981). In 1974, this hypothesis was tested and found that both aggression and territory size increased as abundance of drifting prey was reduced (Slaney and Northcote 1974). Through those investigations, space was indicated as a critical resource for stream salmonids (Fausch and White 1981).

Appendices

APPENDIX 1: Statistical modeling schematic, precipitation data, and water chemistry summary.

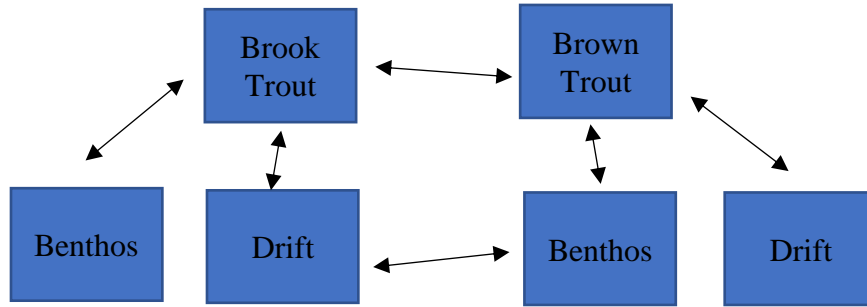


Figure 1. Pairwise comparison chart. Each interaction is tested against one another within the stream environment. Drift vs. Benthos; Brook Trout vs. Brown Trout; Brook Trout vs. Drift; Brook Trout vs. Benthos; Brown Trout vs. Drift; Brown Trout vs. Benthos

Month	Rainfall totals
June	6.6
August	0.99
October	0.43
December	1.3
February	0
May	0

Figure 2. Rainfall totals (cm) in the proceeding 3 days prior to sampling events.

Frost Creek	Average	SD	Cedar Creek	Average	SD
Conductivity ($\mu\text{S}/\text{cm}^2$)	415.5	66.3	Conductivity ($\mu\text{S}/\text{cm}^2$)	537.3	50.9
Total Dissolved Solids (g/L)	0.3	0.06	Total Dissolved Solids (g/L)	0.4	0.04
Salinity	0.2	0.04	Salinity	0.3	0.03
DO%	92.2	7.7	DO%	92	8.4
DO (mg/L)	11.3	2.6	DO (mg/L)	10.9	2.3
pH	8.7	0.1	pH	8.6	0.3

Figure 3. Water Quality data from Frost and Cedar creeks. Data is pooled over all sampling events.

	FROST CREEK DISCHARGE (CMS)	CEDAR CREEK DISCHARGE (CMS)
JUNE	0.08	N/A
AUGUST	0.04	0.1
OCTOBER	0.5	0.16
DECEMBER	1.6	0.34
FEBRUARY	0.06	0.16

Figure 4. Stream discharge in cubic meters per second (cms) during each sampling event.

	Frost Creek			Cedar Creek				
	Brook Trout	Brown Trout		Brook Trout	Brown Trout			
	Length	Weight	Length	Weight	Length	Weight		
<i>June</i>	150.3 +/- 48	45.1 +/- 34.8	206.5 +/- 63.3	101.3 +/- 87.2	174.1 +/- 24.8	60.3 +/- 19	204.6 +/- 66.7	127.7 +/- 135.7
<i>August</i>	147.2 +/- 49.3	40 +/- 32.5	178	49.2	134.3 +/- 44.4	32.1 +/- 23.1	195.6 +/- 62.3	93.9 +/- 92.9
<i>October</i>	161.4 +/- 45.5	50.8 +/- 39.1	243	144.4	148.4 +/- 45.2	39.6 +/- 28.1	185 +/- 69.9	84.1 +/- 77.8
<i>December</i>	120.8 +/- 48.7	36.9 +/- 61.6	173.5 +/- 59.6	65.3 +/- 61.7	150.1 +/- 51.5	37.6 +/- 39.9	162.8 +/- 54.8	55 +/- 54.9
<i>February</i>	119.7 +/- 36.9	20.4 +/- 18.2	N/A	N/A	154 +/- 33.1	38 +/- 24.8	264.2 +/- 65.5	219.5 +/- 155
<i>May</i>	136 +/- 32.3	35.8 +/- 30.7	156.7 +/- 73	78.1 +/- 113.8	171.9 +/- 35.4	71.9 +/- 43.1	222.5 +/- 59.9	182.7 +/- 155.5

Figure 5. Fish summary data from each sampling event with SD for total length and weight.

	JUNE	AUGUST	OCTOBER	DECEMBER	FEBRUARY	MAY
ACARIFORMES	0	0	0	0	2	0
ANNELIDA	0	0	2	4	0	2
ARACHNIDS	0	0	4	2	0	0
BIVALVIA	0	0	0	0	0	0
COLEOPTERA	52	168	169	64	112	30
COTTUS	0	1	0	0	0	0
CRUSTACEA	94	299	33	2	9	10
DIPTERA	180	242	78	27	83	126
EPHEMEROPTERA	40	44	57	46	85	36
GASTROPODA	0	0	0	0	0	0
HEMIPTERA	0	2	0	0	0	0
HYMENOPTERA	1	0	0	0	0	0
LEPIDOPTERA	0	0	1	0	0	0
MEGALOPTERA	5	3	0	0	2	1
ODONATA	0	4	1	0	1	0
PETROMYZONTIFORMES	0	0	0	0	0	0
PLATYHELMINTHES	0	0	0	0	0	0
PLECOPTERA	3	3	9	5	30	23
TRICHOPTERA	68	128	190	75	148	150

Figure 6. Aquatic macroinvertebrate abundances by month in Frost Creek.

	JUNE	AUGUST	OCTOBER	DECEMBER	FEBRUARY	MAY
ACARIFORMES	0	4	1	0	1	0
ANNELIDA	0	0	0	0	0	5
ARACHNIDS	0	1	0	0	0	0
BIVALVIA	1	0	0	0	0	0
COLEOPTERA	49	53	50	55	43	32
COTTUS	0	0	1	0	1	0
CRUSTACEA	155	673	21	34	26	135
DIPTERA	175	153	45	43	328	451
EPHEMEROPTERA	69	129	31	14	58	56
GASTROPODA	1	2	0	1	0	0
HEMIPTERA	2	1	3	0	0	0
HYMENOPTERA	1	6	0	0	0	0
LEPIDOPTERA	0	0	0	0	0	0
MEGALOPTERA	1	4	0	0	1	1
ODONATA	0	0	0	0	1	0
PETROMYZONTIFORMES	0	0	0	0	0	0
PLATYHELMINTHES	0	0	1	0	0	0
PLECOPTERA	18	0	7	7	10	6
TRICHOPTERA	183	98	101	54	114	62

Figure 7. Aquatic macroinvertebrate abundances by month in Cedar Creek.

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