

8-2016

## Evaluating Foraging Habits, and Estimating Prey Consumption, and Growth of Brook Trout in a Coolwater Michigan Stream

Graeme R. Zaparzynski  
*Grand Valley State University*

Follow this and additional works at: <https://scholarworks.gvsu.edu/theses>



Part of the [Biology Commons](#)

---

### ScholarWorks Citation

Zaparzynski, Graeme R., "Evaluating Foraging Habits, and Estimating Prey Consumption, and Growth of Brook Trout in a Coolwater Michigan Stream" (2016). *Masters Theses*. 819.  
<https://scholarworks.gvsu.edu/theses/819>

This Thesis is brought to you for free and open access by the Graduate Research and Creative Practice at ScholarWorks@GVSU. It has been accepted for inclusion in Masters Theses by an authorized administrator of ScholarWorks@GVSU. For more information, please contact [scholarworks@gvsu.edu](mailto:scholarworks@gvsu.edu).

Evaluating Foraging Habits, and Estimating Prey Consumption, and Growth of Brook Trout in a  
Coolwater Michigan Stream

Graeme R. Zaparzynski

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

Biology Department

August 2016

## **Acknowledgements**

I would like to thank my graduate advisor, Dr. Mark Luttenton, for his continued support and advice throughout the course of this research, as well as my graduate committee members, Dr. Eric Snyder and Dr. Carl Ruetz III. I thank Justin Wegner, Travis Ellens, Emily Dean, and Zach Kuzniar for their help collecting data in the field and analyzing samples in the laboratory. Also, I would like to thank Schrems West Michigan Chapter of Trout Unlimited, Trout Unlimited National, and specifically Nichol DeMol for funding and support with the project. Additional funding was provided by a Grand Valley State University Presidential Research Grant, and an Annis Water Resources Institute Graduate Assistantship. I thank the private land owners in the Cedar Creek watershed for allowing us to access the stream to collect data. Lastly, I would like to thank my family and friends for their continued support throughout the pursuit of this degree.

## Abstract

Brook trout (*Salvelinus fontinalis*) are a cold water ectotherm whose native distribution includes most of eastern Canada, the upper Midwestern United States, and the eastern and mid-Atlantic United States as far south as Georgia. The native range of brook trout in the United States has been reduced as a result of interspecific interactions with introduced species, and anthropogenic land use changes that drive water temperature changes in many of their native watersheds. Anthropogenic land-use changes tend to increase thermal regimes of aquatic systems, affecting brook trout physiology and limiting them to colder, headwater reaches. The threat of thermal disturbance to brook trout distribution is most pertinent in systems that experience temperatures near 19°; the upper margin of the species' optimal range. Cedar Creek, located in Kent Co. Michigan, contains a self-sustaining population of introduced brook trout and experiences temperatures >19°C during the summer. Cedar Creek presents a novel system to understand brook trout growth at the upper limits of their preferred temperature range, and predict how their growth may change under further thermal disturbance. I conducted a study to examine the foraging habits and growth of brook trout in Cedar Creek between June and August, 2015, and used a bioenergetics model to predict how brook trout growth would change if water temperatures were to increase during summer. Brook trout limited their activity during summer by remaining sedentary, and consumed energy dense terrestrial invertebrates, especially late in summer. But, the growth rate of trout that were recaptured was negative on average, and the bioenergetics model predicted that brook trout would lose body mass if the thermal regime of Cedar Creek were to warm. The major takeaway from this study is that riparian canopy, to cool the stream and promote terrestrial energy subsidies to brook trout diets, should be conserved in cool and coldwater streams. Although Cedar Creek is outside the native range of brook trout, I

believe that this study has provided insight into brook trout growth, and the potential impact of increased water temperature on thermally-stressed populations.

## Table of Contents

|   |    |
|---|----|
| <b>List of Tables</b> .....   | 8  |
| <b>List of Figures</b> .....  | 9  |
| <b>Chapter I</b> .....  | 10 |
| Introduction .....  | 10 |
| Purpose .....   | 12 |
| Scope .....   | 13 |
| Assumptions .....   | 13 |
| Hypotheses .....  | 14 |
| Significance .....  | 15 |
| Definitions.....  | 16 |
| References .....  | 19 |
| <b>Chapter II</b> .....   | 24 |
| <b>Evaluating Foraging habits, and estimating prey consumption and growth of brook trout in a coolwater Michigan Stream</b> ..... | 24 |
| Abstract .....  | 24 |
| Introduction .....  | 26 |
| Methods.....  | 28 |
| <i>Study area</i> .....   | 28 |
| <i>Field sampling</i> .....   | 29 |
| <i>Evaluating foraging habits</i> .....   | 30 |
| <i>Growth, Condition, and Modeling Bioenergetics</i> .....  | 31 |
| <i>Statistical Analysis</i> .....   | 35 |
| Results.....  | 36 |
| <i>Evaluating foraging habits</i> .....   | 36 |
| <i>Growth, condition, and modeling bioenergetics</i> .....  | 39 |
| Discussion .....  | 40 |
| Acknowledgements .....  | 49 |
| Tables .....  | 50 |
| Figures.....  | 55 |
| References .....  | 61 |
| <b>Chapter III</b> .....  | 68 |
| Extended Literature Review .....  | 68 |
| <i>Introduction</i> .....   | 68 |
| <i>Brook Trout Ecology</i> .....  | 69 |
| <i>Bioenergetics Models</i> .....   | 76 |
| <i>Discussion</i> .....   | 82 |

|                                    |    |
|------------------------------------|----|
| Extended Methods.....              | 84 |
| <i>Field Procedures</i> .....      | 84 |
| <i>Laboratory Procedures</i> ..... | 89 |
| References .....                   | 93 |

## List of Tables

| Table   | Page |
|---|------|
| Table 2.1. The number of fish sampled for total length and wet weight (N), total number of gut samples taken (n), sample reach (D=downstream, U=upstream) and the interval when drift samples were collected (Time). Both reaches were electrofished on 8/25/2015, but drift samples were taken at the downstream reach.....  | 50   |
| Table 2.2. Mean Strauss' Linear Index ( $L_i$ ) value and corresponding percentage of taxa in the drift ( $p_i$ ) for the five most selected prey taxa and least selected prey taxa on each sample date. $L_i$ values were calculated for all taxa using the percentage of prey items in the diet of each trout. The mean $L_i$ value for taxa are reported.....  | 51   |
| Table 2.3. Observed growth rates and consumption estimates from the bioenergetics model for each individual trout that was recaptured throughout the study. The arbitrary number (Fish #), and the initial day (Day <sub>I</sub> ) and final day (Day <sub>F</sub> ) of capture are listed for each trout. Initial weight ( $W_I$ , g) and final weight ( $W_F$ , g) of each trout were used to calculate its instantaneous growth rate ( $G$ , d <sup>-1</sup> ). The bioenergetics model estimated the proportion of each trout's maximum consumption ( $P-C_{MAX}$ ) and its total consumption ( $C_T$ , g) over the study period. To calculate the average specific consumption rate ( $C_R$ , g·g <sup>-1</sup> ·d <sup>-1</sup> ) of each trout, its estimated $C_T$ was divided by its average weight between capture events, and subsequently divided by the number of days between capture events..... | 54   |
| Table 3.1. The two-digit tagging system used to individually mark trout with elastomer pigment.....   | 87   |
| Table 3.2. Estimates of the relationship between total length (TL, mm) and dry mass (DM, g) for invertebrate taxa based on linear regression models. Relationships are estimated using the equation $\ln(DM) = \ln(\alpha) + \beta \cdot \ln(TL)$ . I report the sample size of each taxon used in the linear regression (n), estimates of $\ln(\alpha)$ and $\beta$ with the standard error of each term (SE), the test statistics of the linear regression model (P, $R^2_{adj}$ ), and the number of times the equation was used in my analyses (N).....   | 91   |
| Table 3.3. Estimates of the relationship between (HC, mm) and (DM, g) for invertebrate taxa based on linear regression models. Relationships are estimated using the equation $\ln(DM) = \ln(\alpha) + \beta \cdot \ln(HC)$ . Symbols in this table represent the same values as those in Table 3.2.....  | 92   |



## List of Figures

| Figure   | Page |
|--|------|
| Figure 2.1. Map of Cedar Creek, Kent County, Michigan. Red star indicates the study site.....  | 55   |
| Figure 2.2. Mean ( $\pm$ SE) invertebrate drift density of drift samples collected at the downstream reach in the morning during each month (n=12). Lowercase letters indicate significant differences determined by a pairwise Wilcoxon test. For specific collection times and dates, see Table 2.1.....   | 56   |
| Figure 2.3. The number of prey items (range and quartiles) consumed by brook trout that were sampled during June (n=30), July (n=14), and August (n=15). Lowercase letters indicate significant differences in the number of prey items consumed by brook trout among months, determined by a pairwise t-test performed on square-root transformed data..... | 57   |
| Figure 2.4. Initial and final condition (range and quartiles) of trout recaptured throughout the study. Final condition was significantly lower than initial condition (T-test, P=0.001, t=-3.75, d.f.=12).....  | 58   |
| Figure 2.5. Estimated change in weight of a 66.5-g brook trout under altered thermal regime scenarios when $C_T$ is held constant (153.247 g), and when $P-C_{MAX}$ is held constant (0.421).....  | 59   |
| Figure 2.6. Percentage of energy contributed from aquatic, terrestrial, and non-obligate taxa to brook trout diets during each month.....  | 60   |

## Chapter I

### Introduction

Scientists and resource managers face the task of understanding the effects of anthropogenic disturbance to aquatic ecosystems. Long-term anthropogenic disturbance, such as carbon emissions, combined with more immediate anthropogenic threats, such as land-use changes, threaten the natural regimes of aquatic systems and their biota (Wiley et al. 2010). Combined impacts of long, and short term, anthropogenic disturbances on surface waters potentially will drive shifts in fish species distributions resulting in altered fish communities (Ficke et al. 2007; Buisson et al. 2013). Stream dwelling salmonids have already experienced shifts in distributions and the impact of thermal change on salmonid populations (distribution and abundance) has received considerable attention (McCullough et al. 2009). Model predictions suggest that stream-dwelling salmonids could continue to be impacted by disrupted aquatic regimes, particularly altered thermal and flow regimes associated with disturbance (Nakano et al. 1996; Wenger et al. 2011).

Native to cold North American rivers, the brook trout *Salvelinus fontinalis* has faced range reduction throughout the United States due to increased stream temperatures that have been linked to anthropogenic disturbance (Hudy et al. 2008; Stranko et al. 2008). As a coldwater ectotherm, brook trout physiology is driven by water temperature, which plays a substantial roll in their distribution; this is in spite of the fact that brook trout can persist in systems that range from 5-20°C (Power 1980). However, due to the relationship among temperature, metabolism, and prey consumption, brook trout growth is highest between 10 and 19°C (Hartman and Sweka 2003). Exposure to temperatures lower than 10°C reduce brook trout growth rates, but exposure to temperatures that approach, or exceed, 20°C cause brook trout to experience energetic

changes, rapidly reducing body condition (Hartman and Sweka 2003). Therefore, increases in water temperature subjecting brook trout populations to temperatures at, or above, their upper optimum threatens individual condition factors and could potentially influence species distribution.

Fish bioenergetics models allow investigators to apply the mass balance equation governing energy intake and expenditure of a species, and have become a popular tool in fisheries biology to address questions at multiple ecological scales (Chipps and Wahl 2008; Hartman and Kitchell 2008). By integrating temperature, diet, and growth data, bioenergetics models present the most effective strategy to evaluate how changes in water temperature may impact fish condition factors and ultimately distributions. For example, previous applications of bioenergetics models have predicted that increased temperatures would reduce brook trout growth and fecundity (Xu et al. 2010) as well as available summer habitat (Ries and Perry 1995). Both studies utilized growth as a key predictive metric but not diet. In an effort to refine model predictions, Hartman and Cox (2008) developed a bioenergetics model designed specifically for brook trout. The Hartman and Cox (2008) model not only provides a brook trout specific model that quantifies temperature driven changes in growth, but also incorporates diet estimates that relate energy consumption to growth, which enhances interpretation of model outputs. This modeling approach will be especially important in systems where the combination of high existing temperatures during the summer and anthropogenic thermal threats exists.

The Rogue River Watershed, located in west central Michigan, lies in close proximity to the Grand Rapids metropolitan area and provides a range of recreational opportunities. Although the Rogue River is managed for a coldwater fishery, warm headwater sources, warmed urban runoff, and water withdrawal were identified in the Rogue River Watershed Management Plan

(AWRI 2001) as threats to the Rogue River and its tributaries. In 2010, the Rogue River was recognized in the Trout Unlimited National Home Rivers Initiative, and consequent management decisions in the watershed have aimed at improving brook trout habitat. One tributary in particular, Cedar Creek, supports a self-sustaining population of brook trout and is an important source of cold water to the Rogue River. However, July water temperatures  $>20^{\circ}\text{C}$  have been recorded at several locations in Cedar Creek (MDEQ 2009). Because Cedar Creek already reaches temperatures above the upper optimum for brook trout growth, and faces thermal threats from anthropogenic disturbance, it presents an excellent opportunity to understand the effects of increased water temperature on brook trout growth.

### Purpose

This research addresses several objectives. Foremost, I quantified the potential impact increased water temperature may have on brook trout growth. To accomplish this goal, I collected length-weight data and diet samples of brook trout to quantify existing temporal trends in brook trout prey consumption, energy sources, and growth. These data were used to estimate brook trout prey consumption between June and August using a bioenergetics model, and helped determine the important dietary energy sources for brook trout in Cedar Creek during these months. The growth data and consumption estimates derived from the model then served as a baseline to compare model predictions of brook trout growth for both warmer and colder water temperature regimes in Cedar Creek. Additionally, to gain insight into specific prey selection I quantified the macroinvertebrate prey base of Cedar Creek and compared it with the diets of trout sampled throughout the study. Through collaboration with Schrems West Michigan Chapter of Trout Unlimited this data will also contribute to the broader objective of conserving brook trout, and ultimately coldwater habitat, in the Rogue River Watershed.

## Scope

The current study focused on Cedar Creek (Kent Co., MI), a small second order stream that faces urban and agricultural development in its headwaters. The mix of urban and agricultural land use is common throughout watersheds in Michigan, and is a source of thermal disturbance influencing brook trout distribution throughout their native range in the United States (Hudy et al. 2008). Urbanization increases impervious surface area resulting in increased stormwater runoff and decreased groundwater recharge, which compromises a streams ability to buffer increases in water temperature (Paul and Meyer 2001). Agricultural practices, such as center-pivot irrigation systems and clearing the riparian corridor can have similar effects on water temperature (Allan 2004). Currently, Cedar Creek approaches, and even exceeds, the upper optimal temperature limit for brook trout growth during the summer. Hartman and Sweka (2003) suggested that land-use changes in watersheds where this is the case could be particularly detrimental to brook trout populations if thermal refugia are not available. Consequently, this study, in a stream facing anthropogenic threats that reaches temperatures above the upper optimum for brook trout growth, will have implications throughout the geographic range for brook trout; particularly in systems where land-use practices present similar challenges to coldwater fisheries.

## Assumptions

Analysis and interpretations from this work relies on the assumption that length and weight data, as well as prey consumption data that I recorded on brook trout during the study is representative of the population. Several of my analyses included data taken from fish that were captured by backpack electrofishing multiple times throughout the study. This introduces the potential for injury or a behavioral shift by trout due to electroshocking and human handling that

could alter growth rates, influencing experimental error. However, several studies reported the effects of electrofishing on salmonid growth rates to be negligible (Ainslie et al. 1998; Carline 2001). Additionally, to reduce the probability of changes in fish behavior caused by handling-induced stress, fish were anesthetized using the recommended concentration of AQUI-S 20E (AQUI-S New Zealand LTD, Lower Hutt, New Zealand) while they were handled for data collection. I also assumed that other chemical and physical parameters are generally similar to previous and future conditions.

### Hypotheses

Based on my existing knowledge of Cedar Creek, several inferences regarding potential results of the study could be made. I knew that July temperatures recorded in Cedar Creek approached the upper optimal limit for brook trout growth during the summer (MDEQ 2009). Combining this baseline knowledge with information from similar studies (Ries and Perry 1995; Xu et al. 2010), I hypothesized that the bioenergetics model would predict a decrease in the condition factor of trout with increases in water temperature.

I also developed hypotheses regarding prey consumption and important energy sources based on the literature. A temporal decrease in brook trout prey consumption from spring to fall has been noted by several authors (Allan 1981; Utz and Hartman 2006). And, Sotiropoulos et al. (2006) suggested that brook trout adopt a low-risk, low-reward strategy regarding prey consumption when water temperature becomes high and prey availability becomes low. Thus, I hypothesized that brook trout would have more prey items in their diets during June than in July or August. Finally, terrestrial invertebrates contribute substantially to the diet and energy intake of brook trout during the summer (Allan 1981; Utz and Hartman 2007; Sweka and Hartman 2008; Wilson et al. 2014). However, much of this work took place in Appalachia, and although I

hypothesized that terrestrial invertebrates would contribute energy to brook trout diets I was unsure how important they would be to the overall energy intake of brook trout in Cedar Creek.

### Significance

My bioenergetics analysis will contribute to ongoing management efforts to conserve brook trout, and overall coldwater habitat, in the Rogue River Watershed; a system of local recreational value. Cedar Creek is one of five major coldwater tributaries to the Rogue River. The results from this study regarding management recommendations to preserve coldwater habitat have the potential to be applied to other coldwater tributaries in the Rogue River Watershed as well as in other cold and coolwater systems throughout the upper Midwestern United States (Lyons et al. 2009). In addition, quantifying temporal trends in brook trout prey consumption, energy sources, and growth during summer months will contribute to the broader body of literature that has been compiled on this subject. Brook trout diets have been studied in southern Appalachia (e.g. Utz and Hartman 2006; Utz and Hartman 2007; Petty et al. 2014), the northeastern United States (e.g. Forrester et al. 1994; Sotiropoulos et al. 2006), and the western United States (e.g. Allan 1981; Duffield and Nelson 1998). These studies have led to conclusions about temporal trends in prey consumption and the importance of terrestrial energy contributions to brook trout populations in these areas. However diet studies of brook trout and quantitative estimates of terrestrial energy contributions in the upper Midwestern United States appear limited in the literature (Elwood and Waters 1969; Miller 1974). This study should contribute to the understanding of brook trout ecology by quantifying brook trout diets and growth patterns in a small midwestern stream where they have been introduced and experience temperatures near the upper limit of their preferred range.

## Definitions

The variables quantified, analyzed, and interpreted in Chapter II of this manuscript are subsequently defined and explained, including mathematical formulas.

### *Strauss' Linear Index ( $L_i$ )*

I used a modified version of Strauss' Linear Index (Strauss 1979) to compare the diet of brook trout sampled throughout the study with the invertebrate prey items collected in drift samples on corresponding sample dates.  $L_i$  is calculated as:

$$L_i = r_i - p_i$$

where  $r_i$  and  $p_i$  represent the percentage of prey taxon  $i$  in the diet of brook trout and the percentage of taxon  $i$  in the drift, respectively. Based on this formula,  $L_i$  can range from -100 to 100. Positive  $L_i$  values indicate that a taxon represented a higher percentage in the diet than in the drift, and negative  $L_i$  values indicate a taxon was more highly represented in the drift than in the diet.

### *Instantaneous Growth Rate ( $G$ )*

The instantaneous growth rate of each trout recaptured during the study was calculated as:

$$G = \frac{[\ln(W_F) - \ln(W_I)]}{\Delta t}$$

Where  $W_F$  is the wet weight of the fish (g) at final capture and  $W_I$  is the wet weight of the fish when initially captured, and  $\Delta t$  represents the number of days between capture events.

Instantaneous growth rate represents the number of grams gained or lost by a fish per gram of its own body weight over a given time interval, and is reported in units per day ( $d^{-1}$ ). Brook trout display seasonal trends in instantaneous growth rate. Utz and Hartman (2009) reported highest



growth rates in June ( $> 0.001 \text{ d}^{-1}$ ), potentially negative growth rates in late summer ( $\leq 0.0 \text{ d}^{-1}$ ), and slightly positive growth throughout the winter ( $> 0.0 \text{ d}^{-1}$ ).

#### *Fulton's Condition Factor (K)*

Fulton's condition factor is:

$$K = \left( \frac{W}{L^3} \right) \cdot 1000$$

where  $W$  is the wet weight (g), and  $L$  is total length (mm), of the fish. High  $K$  values are indicative of good condition, while low values indicate poor condition

#### *Consumption ( $C_T$ , $P-C_{MAX}$ )*

Using a bioenergetics modeling package (Deslauriers and Chipps 2016) developed in Program R (R Core Team 2016), the amount of prey consumed by each recaptured trout over the study period was estimated. The model estimates prey consumption parameters using the fish's initial and final weight, the temperature experienced by the fish over the interval of interest, and the proportion of prey taxa in the diet of the fish. The basic form of the consumption function used in the model is:

$$C = C_{MAX} \cdot P-C_{MAX} \cdot f(T).$$

In this equation  $C$  represents the specific consumption rate of the fish between sample dates ( $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ ),  $C_{MAX}$  is the maximum specific consumption rate ( $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ ) of the fish based on its mass, and  $f(T)$  is the temperature dependence function of consumption for the fish species.  $C_{MAX}$  and  $f(T)$  are experimentally derived through laboratory feeding studies on brook trout. The model estimates the total mass of prey consumed ( $C_T$ , g) by the fish between capture events by adding the mass consumed on each day based on the estimated specific consumption rate. In addition, the model determines what proportion of the fish's temperature and size-driven maximum consumption rate was achieved between capture events based on the estimated  $C$  value. This is

represented in the model as  $P-C_{MAX}$  and can range from 0-1. In the field,  $P-C_{MAX}$  values reported for salmonids are typically close to 0.3 (Railsback and Rose 1999; Godby et al. 20007), and brook trout may consume food at even lower proportions of their maximum value (Hartman and Sweka 2003). Both  $C_T$  and  $P-C_{MAX}$  are reported in Chapter II, and the equations representing respiration and waste-production in the bioenergetics model, which factor into consumption estimates, are discussed in Chapter III.

*Average Specific Consumption Rate ( $C_R$ )*

After  $C_T$  was estimated using the model, I independently calculated the average specific consumption rate ( $C_R$ ,  $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) of each trout that was recaptured during the study.  $C_R$  was calculated as:

$$C_R = \frac{C_T}{\Delta t} / W_A$$

where  $\Delta t$  is the number of days between capture events and  $W_A$  is the average wet weight (g) of the fish calculated using its wet weight at initial and final capture.

## References

- Ainslie, B. J., J. R. Post, and A. J. Paul. 1998. Effects of pulsed and continuous dc electrofishing on juvenile rainbow trout. *North American Journal of Fisheries Management* 18:905-918.
- Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:184-192.
- Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257-284.
- AWRI (Annis Water Resources Institute). 2001. Rogue River Watershed Management Plan. MR-2001-1.
- Buisson, L., G. Grenouille, S. Villeger, J. Canal, and P. Laffaille. 2013. Toward a loss of functional diversity in stream fish assemblage under climate change. *Global Change Biology* 19:387-400.
- Carline, R. F. 2001. Effects of high-frequency pulsed-dc electrofishing on a wild brown trout population. *North American Journal of Fisheries Management* 21:571-579.
- Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21<sup>st</sup> century: reviewing new insights and revising old constraints. *Transactions of the American Fisheries Society* 137:298-313.
- Deslauriers, D., and S. R. Chipps. 2016. Fish bioenergetics 4.0 workshop. 76<sup>th</sup> Midwest Fish and Wildlife Conference, January 24<sup>th</sup> 2016, Grand Rapids, Michigan.
- Duffield, R. M., and C. H. Nelson. 1998. Stoneflies (Plecoptera) in the diet of brook trout (*Salvelinus fontinalis* Mitchell) in Libby Creek, Wyoming, USA. *Hydrobiologia* 380:59-65.

- Elwood, J. W., and T. F. Waters. 1969. Effects of flood on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society* 98:253-262.
- Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. *Review in Fish Biology and Fisheries* 17:581-613.
- Forrester, G. E., J. G. Chase, and W. McCarthy. 1994. Diel and density related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environmental Biology of Fishes* 39:301-311.
- Godby, N. A., E. S. Rutherford, and D. M. Mason. 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a Lake Michigan tributary. *North American Journal of Fisheries Management* 27:578-592.
- Hartman, K. J., and M. K. Cox. 2008. Refinement and testing of a brook trout bioenergetics model. *Transactions of the American Fisheries Society* 137:357-363.
- Hartman, K. J., and J. F. Kitchell. 2008. Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society* 137:216-223.
- Hartman, K. J., and J. A. Sweka. 2003. Development of a bioenergetics model for Appalachian brook trout. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 55(2001):38-51.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *North American Journal of Fisheries Management* 28:1069-1085.
- McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. S. Foott, S. L. Johnson, K. R. Marine, M. G. Mesa, J. H. Peterson, Y. Souchon,

- K. F. Tiffin, and W. A. Wurtsbaugh. 2009. Research in thermal biology: burning question for coldwater stream fishes. *Reviews in Fisheries Science* 17:90-115.
- MDEQ (Michigan Department of Environmental Quality). 2009. A biological survey of sites in the Rogue River Watershed Kent and Newaygo Counties, Michigan. MDEQ Water Bureau Staff Report 09/057, Lansing, Michigan.
- Miller, J. M. 1974. The food of brook trout *Salvelinus fontinalis* (Mitchill) fry from difference subsections of Lawrence Creek, Wisconsin. *Transactions of the American Fisheries Society* 103:130-134.
- Nakano, S., F. Kitano, and K. Maekawas. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshwater Biology* 36:711-722.
- Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333-365.
- Petty, J. T., D. Thorne, B. M. Huntsman, and P. M. Mazik. 2014. The temperature-productivity squeeze: constraints on brook trout growth along an Appalachian river continuum. *Hydrobiologia* 727:151-166.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141-203 in E. K. Balon. Charrs, salmonid fishes of the genus *Salvelinus*. The Hague; Dr. W. Junk; Kluwer Boston; Hingham, Massachusetts.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

- Ries, R. D., and S. A. Perry. 1980. Potential effects of global climate warming on brook trout growth and prey consumption in ventral Appalachian streams, USA. *Climate Research* 5:197-206.
- Sotiropoulos, J. C., K. H. Nislow, and M. R. Ross. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. *Journal of Fisheries Management and Ecology* 13:149-155.
- Stranko, S. A., R. H. Hildebrand, R. P. Morgan II, M. W. Staley, A. J. Becker, A. Rosebery-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook trout declines with land cover and temperature changes in Maryland. *North American Journal of Fisheries Management* 28:1223-1232.
- Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108:344-352.
- Sweka, J. A., and K. J. Hartman. 2008. Contributions of terrestrial invertebrates to yearly brook trout prey consumption and growth. *Transactions of the American Fisheries Society* 137:224-235.
- Utz, R. M., and K. J. Hartman. 2006. Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2675-2686.
- Utz, R. M., and K. J. Hartman. 2007. Identification of Critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms. *Hydrobiologia* 575:259-270.

- Utz, R. M., and K. J. Hartman. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66: 1072-1080.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Faush, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential decline of trout species under climate change. *Proceedings of the National Academy of Sciences* 108:14175-14180.
- Wiley, M. J., D. W. Hyndman, B. C. Pijanowski, A. D. Kendall, C. Riseng, E. S. Rutherford, S. T. Cheng, M. L. Carlson, J. A. Tyler, R. J. Stevenson, P. J. Steen, P. L. Richards, P. W. Seelbach, J. M. Koches, and R. R. Rediske. 2010. A multi-modeling approach to evaluating climate and land use change impacts in a Great Lakes River Basin. *Hydrobiologia* 657:243-262.
- Wilson, M. K., W. H. Lowe, and K. H. Nislow. 2014. What predicts the use by brook trout (*Salvelinus fontinalis*) of terrestrial invertebrate subsidies in headwater streams? *Freshwater Biology* 59:187-199.
- Xu, C., B. H. Letcher, and K. H. Nislow. 2010. Context-specific influence of water temperature on brook trout growth rates in the field. *Freshwater Biology*

## Chapter II

### **Evaluating foraging habits, and estimating prey consumption and growth of brook trout in a coolwater Michigan Stream**

#### Abstract

Land use patterns can drive changes in aquatic systems that alter biotic and abiotic characteristics. Increased stream water temperature, due to land use changes, has influenced brook trout (*Salvelinus fontinalis*) distribution throughout the United States, causing concern about the species future. Bioenergetics models present an effective method to predict how continued temperature increases may influence brook trout distribution. I conducted a diet study on brook trout during the summer of 2015 in Cedar Creek, MI, a small, coolwater stream. I quantified prey availability, evaluated brook trout foraging habits, quantified a seasonal temporal shift in energy sources, quantified growth and condition, and modeled bioenergetics parameters using diet, weight, and temperature data. I found an increase in selection for terrestrial invertebrate taxa from June to August, which translated to a shift in energy contribution, from aquatic to terrestrial, over the study period. In addition, the number of prey items per trout stomach significantly decreased from June to August; however, the availability of aquatic prey did not appear to decrease temporally. A significant decrease was observed in the condition of fish recaptured during the study, even though the bioenergetics model estimated that trout were consuming prey at a rate that is higher than typically reported in the literature. I also used the bioenergetics model to predict changes in brook trout growth that may be associated with changes in the thermal regime of the system. Model estimates indicate that brook trout in Cedar Creek would experience an 11 to 14% decrease in weight with an average temperature increase of 1°C over the course of the study. My results suggest that brook trout may lower their activity



levels in the summer by consuming fewer prey and capitalizing on conspicuous invertebrates on the water surface. I suggest that protection of riparian vegetation, to enhance stream shading and promote food-web connectivity, should be a priority to conserve brook trout populations and protect the thermal regime of Cedar Creek and other coolwater systems.

## Introduction

Research aimed at understanding the effects of increased water temperature on salmonids has become common over recent decades (McCullough et al. 2009). The Brook trout (*Salvelinus fontinalis*) has undergone range reduction throughout much of its native range in the United States as a result of increased water temperature driven by land use changes (Hudy et al. 2008; Stranko et al. 2015). Generally, brook trout persist in streams where temperatures range from 5-20°C (Power 1980). However, Hartman and Sweka (2003) suggested that the optimal water temperature range for brook trout growth is between 10 and 19°C. Understanding the relationship between temperature and growth can provide insight into a species distribution (McCullough et al. 2009). Bioenergetics models present the most effective strategy to understand that relationship, and can be used to quantitatively predict the impact of temperature changes on fish growth (Hill and Magnuson 1990). Quantifying the effects of increased temperature on brook trout growth will be critical in watersheds that already reach temperatures near their upper growth optimum in the summer (Hartman and Sweka 2003), especially if those systems face threats from land use changes. However, this will require system-specific knowledge, such as important prey sources in the diet of brook trout and their growth rates under the current thermal regime.

Brook trout forage on a diverse prey base including aquatic and terrestrial invertebrates (Allan 1981; Webster and Hartman 2005). However, several studies have identified terrestrial invertebrates as a major source of both biomass and energy in the diet of brook trout, contributing substantial portions of energy during the summer (Utz and Hartman 2006; Sweka and Hartman 2008; Wilson et al. 2014). For example, terrestrial invertebrates comprised 38-47% of annual biomass and 51-68% of annual energy intake of brook trout in several West Virginia

streams, and were particularly important in the diet between May and August (Sweka and Hartman 2008). The seasonal increase in terrestrial invertebrate consumption by brook trout during the summer may be attributable to decreased availability of aquatic prey (Wilson et al. 2014), but it may also be a result of the conspicuous nature of terrestrial invertebrates as they enter the stream (Wilzbach et al. 1986). Additionally, a number of studies have documented a decrease in the number of prey items consumed by brook trout during the summer (Allan 1981; Sotiropoulos et al. 2006). Lack of prey may limit consumption, and ultimately production, of brook trout during the summer (Ensign 1990). But, it has also been suggested that brook trout adopt a low-risk, low-reward energy strategy during the summer that could contribute to the decrease in prey consumption (Sotiropoulos et al. 2006).

The purpose of this study was to evaluate brook trout foraging habits and determine how thermal disturbance would impact their growth rates; particularly during the summer in a system that approaches temperatures above their thermal optimum. More specifically, my objectives were to 1) evaluate foraging habits of brook trout throughout the summer, including prey selection relative to temporal prey availability, and temporal energy sources; 2) quantify the growth and condition of brook trout throughout the summer under the current thermal regime, and 3) use a bioenergetics model to estimate prey consumption, as well as predict potential changes to growth associated with increased water temperatures. I focused on Cedar Creek, a small coolwater stream located in Southwest Michigan. Cedar Creek contains a self-sustaining population of brook trout and faces thermal threats in its headwaters from agriculture and warmed surface runoff (AWRI 2001). Summer temperatures  $>20^{\circ}\text{C}$  have also been recorded in Cedar Creek at several locations (MDEQ 2009).

## Methods

### *Study area*

This study was conducted during the summer of 2015 in Cedar Creek, a second order tributary of the Rogue River, Kent County, Michigan (Figure 1). As of 2001, the Cedar Creek basin consisted of 2,833 hectares of agricultural land, 809 hectares of developed land, and 4,047 hectares of undeveloped land. Soil in the Cedar Creek basin is predominantly loam and sand, and the plant community is dominated by White Pine *Pinus strobus* (AWRI 2001). In addition to brook trout, the Cedar Creek fish community includes brown trout (*Salmo trutta*), mottled sculpin (*Cotus bairdii*), central mudminnow (*Umbra limi*), creek chub (*Semotilus atromaculatus*), blacknose dace (*Rhinichthys atratulus*), white sucker (*Catostomus commersoni*), and one lamprey species (Petromyzontidae) (MDEQ 2004).

I used two reaches of Cedar Creek. For simplicity, I will refer to the two reaches as upstream and downstream. The upstream reach ran through a clear-cut powerline easement that is maintained annually, while the downstream reach was heavily forested with abundant overhanging vegetation. Average stream width of the two reaches was approximately 6 m, and average discharge at base flow was approximately 0.24 m<sup>3</sup>/s. Hourly temperature was recorded from June 19 to September 1 (ONSET Hobo temperature logger model UTBI-001). The mean water temperature in each reach from June 19 to September 1, was 17.12°C and 15.94°C for the upstream and downstream reaches respectively. Under the thermal classification scheme developed for Midwestern streams by Lyons et al. (2009), the upstream reach is considered a coolwater “cold-transition” zone with a mean July temperature of 17.68°C, and the downstream reach is considered a coldwater zone with a mean July temperature of 16.18°C.

### *Field Sampling.*

I collected brook trout on seven dates between June 19 and August 26, 2015 using backpack electrofishing equipment (model APB-3, Electrofishing Systems, LLC, Madison, Wisconsin). Each brook trout was anesthetized using AQUI-S 20E (AQUI-S New Zealand LTD, Lower Hutt, New Zealand), measured for total length ( $\pm 1$ mm) and wet weight ( $\pm 0.01$ g), and gut contents were removed using gastric lavage. An additional sample event was conducted on September 1, during which only length-weight data was collected. Gastric lavage involved flushing a constant flow of water into the stomach of the trout using a 60-cc syringe and vinyl tubing, causing gut contents to be regurgitated. All gut contents were filtered through a 250- $\mu$ m sieve and immediately transferred to 70% ethanol. Invertebrate taxa were later enumerated and identified to the lowest possible taxonomic level using Burch (1962), Borror et al. (1989), Peckarsky (1990), and Merritt et al. (2008). Although I did not estimate the efficiency of the gastric lavage procedure, it has been shown to be an effective method of flushing the stomach contents of live fish (Foster 1977), and the sampling equipment and technique were consistent among all sample dates. During all June and July sample dates, each trout was marked with a unique elastomer tag for identification during subsequent sample events. In addition, a subset of 10 brook trout, captured during the first two sample dates in June, were surgically equipped with radio-transmitters (Advanced Telemetry Systems, Isanti, Minnesota) for an ongoing telemetry study. The mean instantaneous growth rate of recaptured trout, was  $-0.0002 \text{ d}^{-1}$  and  $-0.0019 \text{ d}^{-1}$  for elastomer and radio-tagged fish respectively. These values were not statistically different (t-test,  $P=0.13$ ,  $t=-1.68$ ), so radio tagged fish were included in all of my analyses.

Gut contents were sampled on at least one morning and one evening during each month with the intent of representing brook trout prey consumption over a diel cycle. Morning and

evening samples did not occur on the same date to avoid stressing fish, but were always within one week of each other (Table 2.1). Care was taken to limit unnecessary handling of trout when air temperature was  $>21^{\circ}\text{C}$ . For this reason, total sample size, and the number of gut samples taken on each sample date were not always equal. Due to the downstream migration of several fish that were radio-tagged in the upstream reach, I elected to survey the downstream reach twice during July to increase probability of recaptures. On August 25, a deliberate attempt was made to recapture all radio-tagged trout that had been tracked throughout the duration of the study, and for this reason both reaches were electrofished on this date.

To quantify prey availability, and evaluate the selectivity of trout for available prey items, drift samples were collected for four hours leading up to electrofishing on all sample dates, except September 1. Drift samples were collected hourly for four hours using three drift nets anchored in a riffle section of the stream spanning the thalweg, so the top of the nets were above the water surface. This yielded twelve ( $n=12$ ) individual drift samples on each sample date. The water depth and velocity was recorded in front of each net so the drift density (invertebrates/ $\text{m}^3$ ) could be quantified on each date. We collected drift during the respective crepuscular period, when behavioral drift tends to increase (Elliot 1969), on all morning and evening sample dates throughout the study (Table 1). All samples were filtered through a 250- $\mu\text{m}$  sieve and immediately transferred to 70% ethanol; invertebrates were later enumerated and identified to the lowest possible taxonomic level.

### *Evaluating Foraging Habits*

A variety of indices can be used to compare the diet of a predator with the prey items that are available (Lechowicz 1982). I used a slightly modified version of Strauss' Linear Index ( $L_i$ , Strauss 1979) to compare the percentage of taxa in the drift to the percentage of taxa in the gut

contents of trout, on each sample date. I used the formula  $L_i=r_i-p_i$ , where  $r_i$  and  $p_i$  are the percentage of each taxon in the gut contents and in the drift, respectively. The percentage of each taxon in the drift ( $p_i$ ) was calculated by dividing the total number of each taxon collected by the total number of invertebrates collected over the four hour sample period and multiplying by 100. Similarly, the percentage of each taxon in the gut contents ( $r_i$ ) for each sample date was calculated by dividing the total number of invertebrates from each taxon in the gut contents of all fish by the total number of invertebrates in the gut contents of all fish and multiplying by 100. For the purpose of evaluating selectivity, all parts of invertebrates that could be identified were included in the analysis, including head parts, legs, wings, etc. However, to minimize the probability that multiple body parts from one partially digested invertebrate were interpreted as separate prey items, I matched body parts throughout the enumeration process when possible.

#### *Growth, Condition, and Modeling Bioenergetics*

I calculated the instantaneous growth rate ( $G$ ,  $d^{-1}$ ) for all recaptured trout using the formula  $G = [\ln(W_F)-\ln(W_I)]/\Delta t$ , where  $W_F$ ,  $W_I$  are the trout's final wet weight (g), initial wet weight, and  $\Delta t$  is the number of days between capture events.  $G$  standardizes for trout size and the number of days between capture events, providing a metric to evaluate growth of recaptured trout. Fulton's Condition Factor ( $K$ ) was calculated for all trout sampled throughout the study using the formula  $K = (W/L^3)*1000$ , where  $W$  and  $L$  are the wet weight (g) and total length (mm) of the trout at the time of the sample.

Using the Fish Bioenergetics 4.0 application in Program R (Deslauriers and Chipps 2016) and a bioenergetics model developed for brook trout (Hartman and Cox 2008), I estimated the total consumption ( $C_T$ , g), and the proportion of maximum consumption ( $P-C_{MAX}$ ) for each recaptured brook trout between sample events.  $C_T$  represents an estimate of the entire mass (g) of

prey consumed by a trout between capture events, and  $P-C_{MAX}$  estimates what proportion of the trout's temperature and size-driven maximum consumption rate that was achieved between capture events. The combination of growth data and consumption estimates, specifically  $P-C_{MAX}$ , can provide insight into the limitations placed on fish in a particular system (e.g. is growth limited by temperature or prey availability). Bioenergetic model inputs include temperature ( $^{\circ}\text{C}$ ), energy density of brook trout (Joules/g, wet weight), proportion of prey taxa in the diet, by mass, and the energy density of prey taxa in the diet (J/g, ww). I elected to use the mean daily water temperature from the downstream reach to calibrate the model for two reasons. First, 12 of the 13 brook trout that were recaptured were found in the downstream reach. Second, using mean daily temperature recorded at the downstream reach between June 19 and September 1 yielded a model simulation period of 75 days that provided more conservative model predictions of final weight due to the cooler temperatures at the downstream reach (compared to the upstream reach). The energy density of brook trout was kept constant at  $6473.5 \text{ J/g}^{-1}$  (Hartman and Sweka 2003) throughout the simulation. Because the proportion of prey taxa in the diet is determined based on mass, only head capsules and entire prey items were used to calculate the mass of taxa in the diet. Dry mass for each taxon was calculated based on published length-mass or head-capsule width-mass equations (Smock 1980; Sage 1982; Sample et al. 1993; Benke et al. 1999; Sabo et al. 2002). For taxa with no published equations, I used invertebrates that had either been collected in drift samples for this project, or previously frozen drift samples from nearby streams to calculate my own length-mass and head-capsule width-mass equations. Several taxa present in trout diets were not found in drift samples (e.g. Oligochaeta, Arionidae, and Gastropoda), so I directly dried, and weighed each individual of these taxa found in diet samples to estimate dry mass. The total dry mass value for each taxon was then converted to wet mass, for the model,



using taxon-specific conversion factors from the literature (Brodman and Reyer 1999; Grey 2005). I determined the proportion of each prey taxon in the diet by combining the wet mass of each taxon that was consumed in the morning and evening samples in each month. This method increased the sample size with which prey taxa proportions were estimated for the model, and was more representative of consumption over a diel period. Because drift and gut samples were not collected on September 1, I assumed that the proportions of prey taxa from August 25 and 26 were representative of trout diets on the final day of the simulation period. Determining prey taxa proportions using this method yielded estimates of the proportion of each taxon in the diet for model days 1, 34, and 75. Energy densities of each prey taxon were taken from the literature (Cummins and Wuycheck 1971; Grey 2005), and assumed to be constant throughout the simulation period. I also assumed that each prey item was completely digestible, which made the estimates of  $P-C_{MAX}$  and  $C_T$  conservative. Based on the model estimates of  $C_T$  for each recaptured brook trout, average specific consumption rate ( $C_R$ ,  $g \cdot g^{-1} d^{-1}$ ) was calculated by dividing  $C_T$  by the number of days between capture events, and subsequently dividing by the average weight of the trout between capture events. Calculating  $C_R$  standardized for fish size, and number of days between capture events, providing a metric to evaluate the consumption rate of recaptured brook trout.

In addition to estimating  $P-C_{MAX}$  and  $C_T$  for the empirical data, a main objective of this study was to determine the metabolic costs to brook trout associated with a range of water temperature changes. To predict these metabolic costs I first used linear regression to estimate a power function expressing the length-weight relationship for the brook trout population in Cedar Creek, based on all of the brook trout sampled during the study ( $P < 0.05$ ,  $R^2_{Adj} = 0.988$ ). Using this relationship I estimated the mass of a 190.0 mm fish, which was the mean length of all brook

trout captured during June, to be 66.5 grams. Maintenance  $P-C_{MAX}$  and  $C_T$  values for a 66.5-g brook trout over the 75 day study period were estimated by fitting the model to an initial and final weight of 66.5 g. Subsequently, I ran a series of model simulations evaluating the change in final weight that would occur with average daily water temperature changes ( $\Delta T$ ) of  $-2^\circ$ ,  $-1^\circ$ ,  $+1^\circ$ , and  $+2^\circ\text{C}$  assuming that either the estimated maintenance  $P-C_{MAX}$  or  $C_T$  values remained constant. The model was fit to the estimated maintenance  $P-C_{MAX}$  value across the range of average water temperature changes providing 4 predictions of final weight; one for each average change in water temperature. Similarly, the model was fit to the estimated maintenance  $C_T$  value across the range of average water temperature changes resulting in 4 different predictions of final weight. The two different constant consumption scenarios have different ecological relevance. Assuming that  $P-C_{MAX}$  remains constant means that the fish will change its consumption relative to the change in water temperature during each simulation (e.g.  $C_T$  will change for each simulation at a different temperature). Alternatively, assuming  $C_T$  remains constant means that the fish will not change its consumption relative to the change in water temperature (e.g.  $P-C_{MAX}$  will change for each simulation at a different temperature). To simulate the desired change in average daily water temperature I added, or subtracted, that value from the observed water temperature on each study day. For example, to simulate an average water temperature change of  $1^\circ\text{C}$  over the 75 day study, I added 1 to the water temperature value on all 75 days in the model.

Lastly, to understand how the energy sources in brook trout diets shift temporally, I calculated the energetic contribution of each prey taxon from the diet samples taken in each month, and categorized each taxon as aquatic, terrestrial, or non-obligate. The energy density (J/g wet weight) of each taxon was multiplied by the combined wet mass (g) of that taxon that was consumed during the morning and evening sample event in each month, providing the

energy (Joules) contributed by each taxon to the diet of brook trout during each month. For each month, the energy contributed by each taxon was then divided by the total energy (Joules) consumed by brook trout during that month. This calculation provided the proportion of energy contributed by each taxon during the sample dates in each month. Taxa were then categorized based on their ecology and life-history information using Borror et al. (1989), and McCafferty and Provonsha (1998). Aquatic taxa were those that required water for the completion of a life cycle. Taxa were categorized as terrestrial if they did not require water to complete a life cycle. Non-obligate taxa were those that rely on aquatic environments for prey (e.g. Hymenopterans) or use moist or damp soil throughout their life-cycle (e.g. terrestrial Coleopterans). Additionally, partially digested prey items that could only be identified to order were categorized as non-obligate if their order contained both aquatic and terrestrial families.

### *Statistical Analyses*

All statistical computing was performed in Program R version 3.1.3 (R Core Team 2016). Data were tested for normality using Shapiro-Wilk normality test, and significance was determined at the  $\alpha=0.05$  level. I used a Kruskal-Wallis test to examine difference in invertebrate drift density among months based on the morning drift samples taken at the downstream reach. A post-hoc, pairwise Wilcoxon test was used to determine significant differences among groups when they were detected. After a square-root transformation to meet normality assumptions, a one-way ANOVA was used to test for differences in the number of prey items found in the stomachs of brook trout among months. Post-hoc comparisons were made using a pairwise t-test to determine significant differences among groups when they were detected. A paired, one-tailed t-test was used to test the hypothesis that the condition factor ( $K$ ) of brook trout that were recaptured throughout the study would decrease between their initial and final capture events.

## Results

### *Evaluating Foraging Habits*

Invertebrate drift density was significantly lower in July than in June or August ( $P=0.05$ ,  $\chi^2=12.66$ , d.f.=2, Figure 2.2). The mean ( $\pm$ SE) drift density of drift samples collected on June 22 between 04:00:00 and 07:00:00 was 1.54 ( $\pm$ 0.16) invertebrates/m<sup>3</sup>. Mean drift density on July 21 decreased to 1.03 ( $\pm$ 0.08) invertebrates/m<sup>3</sup> during the same time interval. Mean drift density was 2.16 ( $\pm$ 0.25) invertebrates/m<sup>3</sup> on August 25; samples were collected between 05:00:00 and 08:00:00 because of the later sunrise on this date. The increase in drift density in August was primarily due to the increase in the number of *Baetis* nymphs collected in each 1 hour drift sample. The mean ( $\pm$ SE) number of *Baetis* nymphs in the 12 drift samples collected in June and July was 66.16 ( $\pm$ 9.64) and 56.83 ( $\pm$ 5.59) respectively. In August, mean number of *Baetis* nymphs per sample rose to 147.25 ( $\pm$ 30.78).

A total of 90 brook trout ranging in total length from 75 to 288 mm, and ranging in wet weight from 6.30 to 261.10 g, were captured throughout the study. Of these, 59 trout ranging in total length from 121 to 288 mm, and ranging in wet weight from 19.97 to 261.10 g, were sampled for gut contents. The mean ( $\pm$ SE) number of prey items per trout stomach was 19.3 ( $\pm$ 4.7) in June, ranging from 0 to 121. In July, the mean number of prey items per stomach was 8.1 ( $\pm$ 2.2), and ranged from 1 to 29. And in August, the mean number of prey items per stomach was 6.3 ( $\pm$ 2.4), ranging from 0 to 37. An ANOVA performed on square-root transformed prey item data showed a significant difference in prey consumption among months ( $P=0.043$ ,  $F=3.34$ , Figure 2.3). The number of prey items per stomach was significantly higher in June than in August. However, there was no significant difference in the number of prey items per stomach between the months of June and July, or between July and August.

Taxa selected by brook trout rarely represented a substantial percentage of the corresponding drift ( $p_i$ ), and were often taxa that I'd expect to find on the water surface. In June, brook trout selected primarily aquatic taxa, but showed selection for adult aquatic life stages and occasionally selected some terrestrial and non-obligate prey. On June 19, adult hydropsychids were heavily selected but only comprised 0.42% of the drift, and brook trout showed selection for adult dipterans that only made up 0.98% of the drift. Additionally, a family of terrestrial gastropods (Arionidae) were the third most selected taxa on June 19, but were not collected in the drift (e.g.  $p_i=0$ ) and non-obligate, adult curculionid beetles were the second most selected taxa but made up only 0.28% of the drift. Other adult coleopterans were fourth most selected on June 19, but comprised only 0.41% of the drift. On June 22, brook trout again showed strong selection for taxa on the water surface. Adult *Baetis* and adult hydropsychids were the top two selected taxa and were 0.47 and 0.11% of the drift respectively. Adult dipterans were the fifth most selected taxa, making up 0.47% of the drift; and ants (Formicidae) were fourth most selected but were only 1.45% of the drift. On June 23, brook trout seemed to select taxa below the water surface, including *Ceratopsyche* larvae, chironomid larvae, *Cheumatopsyche* larvae, and Asellidae, but these taxa only made up 0.26, 1.27, 0.03, and 0.12% of the drift respectively. On July 21, brook trout again showed selection for taxa on the water surface. Adult hydropsychids, adult *Tricorythodes*, and adult curculionids were selected for, but only comprised 2.40, 0.04, and 0.09% of the drift respectively. On July 23, selection for non-obligate and terrestrial taxa was high, and brook trout again selected taxa that were likely on the water surface. Non-obligate adult beetles were selected for, including adult chrysomelids and adult curculionids, which weren't collected in any drift samples. Brook trout also showed a relatively high selection for ants, which were 2.04% of the drift, and selected a family of terrestrial

stinkbugs (Pentatomidae) that were not collected in drift samples. In August, brook trout selected primarily terrestrial taxa on both sample dates, and these taxa were rare in the drift. On August 25, terrestrial plant hoppers (Cicadellidae), psocids (Psocoptera), moths (Lyonetidae) and hemipterans were all selected for, but none comprised more than 1.50% of the drift. On August 26, four terrestrial taxa, Flatidae, Cercopidae, Aradidae, and Acrididae, were selected for, but none of these taxa were collected in drift samples.

Alternatively, the five least selected taxa on each sample date were often relatively abundant taxa found in drift samples. On June 22 and August 26 the five least selected taxa (Table 2.2) represent the five most abundant taxa in the drift. On June 19, June 23, July 23 and August 25, the five least selected taxa include four of the five most abundant taxa in the drift. *Baetis* nymphs were the fifth most abundant prey taxa in the drift on June 19 (7.45%) and on June 23 (4.10%), but are not represented in the five least selected taxa. On July 23, chironomid larvae are the fourth most abundant taxa in the drift (5.67%), but were not represented in the five least selected taxa. And on August 25, amphipods were the fifth most abundant taxa the in drift (2.94%), but were not represented in the five least selected taxa. The one exception to this trend was July 21, when only *Baetis* nymphs and adult chironomids, the two most abundant taxa in the drift, were represented in the five least selected taxa. On this date, chironomid larvae were third most abundant in the drift (11.52%); chironomid pupae were fourth most abundant (3.98%) and *Ceratopsyche* larvae were fifth most abundant (3.36%), but none were represented in the five least selected taxa.

Similar to the temporal shift in selectivity, terrestrial taxa became more important as an energy source from June to August (Figure 5). In June, aquatic taxa contributed 56.3% of energy to the diet of brook trout, terrestrial taxa contributed 29.3%, and non-obligate taxa contributed

14.5%. Brook trout obtained 64.7% of their energy from aquatic taxa in July as well as 21.8% from terrestrial taxa, and 13.5% from non-obligate taxa. In August, brook trout obtained 6.7% of their energy from aquatic taxa, 68.5% from terrestrial taxa, and 24.8% from non-obligate taxa.

### *Growth, Condition, and Modeling Bioenergetics*

Water temperature at the upstream reach ranged from 13.30°C to 22.30°C with an average temperature of 17.12°C over the study period. Water temperature reached daily maximum values >19°C on more than 50% of the days at this reach. At the downstream reach, water temperature ranged from 12.48°C to 19.98°C with an average temperature of 15.94°C over the study period. Temperature at the downstream reach peaked at >19°C, on 21% of study days.

A total of 13 trout were recaptured during the study (Table 2.3). Upon their initial capture, the 13 trout ranged in wet weight from 32.34 to 171.43 g, and at their final capture they ranged in weight from 32.37 to 160.02 g. Initial  $K$  of the 13 recaptured trout ranged from 0.094 to 0.126 with a mean ( $\pm$ SE) value of 0.103 ( $\pm$ 0.002). Final  $K$  ranged from 0.085 to 0.101 with a mean value of 0.094 ( $\pm$ 0.001).  $K$  of the 13 recaptured trout decreased significantly between their initial and final capture events ( $P < 0.05$ ,  $t = -3.75$ , Figure 3). Furthermore, the mean ( $\pm$  SE)  $G$  of all trout recaptured during the study was  $-0.0009 (\pm 0.0005) \text{ d}^{-1}$ , and 8 of the 13 trout that were recaptured displayed a negative  $G$ . Model estimates of  $P-C_{MAX}$  for recaptured trout ranged from 0.322 to 0.493 between capture events, with a mean ( $\pm$  SE) value of 0.410 ( $\pm 0.016$ ). Recaptured trout displayed  $C_R$  values ranging from  $0.022 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  to  $0.047 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  with a mean ( $\pm$  SE) value of  $0.031 (\pm 0.002) \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ .

Model estimates of the maintenance  $P-C_{MAX}$  and  $C_T$  values for a 66.5-g brook trout were 0.421 and 153.247 g respectively. A maintenance  $P-C_{MAX}$  value of 0.421 is only slightly higher than the mean  $P-C_{MAX}$  value observed for the 13 trout recaptured during the study (0.410).

Similarly, based on maintenance  $C_T$ , the maintenance  $C_R$  of a 66.5-g brook trout between June 19 and September 1 was approximately  $0.031 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ , which is the same as the mean  $C_R$  value of the 13 recaptured trout. Growth of a 66.5-g brook trout would increase with a decrease in water temperature over the simulation period, and growth would be negative with an increase in water temperature over the simulation period (Figure 2.5). Holding maintenance  $C_T$  constant, a 66.5-g brook trout would increase in weight by approximately 26% to 83.5 g with a decrease in average water temperature of  $2^\circ\text{C}$ , and decrease in weight by approximately 20% to 53.4 g under the opposite scenario. Final weight would increase by approximately 12% to 74.7 g with a decrease in average water temperature of  $1^\circ\text{C}$ , and final weight would decrease by 11% to 59.2 g if average water temperature increased by  $1^\circ\text{C}$  and  $C_T$  remained constant. The effect of a change in temperature on the final weight of a 66.5-g brook trout over the study period is slightly amplified when maintenance  $P-C_{MAX}$  is held constant at 0.421. Under this scenario a  $2^\circ\text{C}$  decrease in water temperature will result in a 29% increase in final weight to 85.9 g, and a  $2^\circ\text{C}$  increase in water temperature will yield a 26% decrease in final weight to 49.5 g. Average water temperature changes of  $-1^\circ\text{C}$  and  $1^\circ\text{C}$  would yield final weight values of 76.3 g and 57.2 g; a 15% increase and 14% decrease respectively when  $P-C_{MAX}$  is held constant.

## Discussion

Coldwater fisheries will continue to face changing environmental conditions due to shifts in land use, groundwater resources, and regional climates. Evaluating the impacts of these changes on populations at the margins of their native range may offer one way to develop predictions for future changes in populations of coldwater species. Alternatively, systems like Cedar Creek that support introduced populations, but are near the upper temperature limits for species such as brook trout provide a natural experiment, particularly to study the influence of



temperature change. The reduction in the condition factor of brook trout in Cedar Creek during the current study provides insights into the physiological state of thermally stressed populations and offers a partial explanation of how thermal disturbance may impact these populations.

Brook trout in Cedar Creek consumed a variety of prey items over the course of the study, including aquatic and terrestrial taxa. Substantial diversity in brook trout diets has been reported elsewhere (Allan 1981; Forrester et al. 1994). However, Allan (1981) found that taxa common in brook trout diets were often correspondingly abundant in the drift. My results show the opposite trend; on all seven dates that diet samples were collected, selected prey taxa rarely represented more than 2% of the corresponding drift. This was driven by a disproportionate selection for taxa that I'd expect to find on the water surface, but were rarely captured in drift samples. For example, adult hydropsychids, adult *Baetis*, and adult dipterans as well as several adult, non-obligate beetle families were selected by brook trout throughout the study. In addition, brook trout selected terrestrial taxa, particularly during August, including several families of homopterans, psocids, orthopterans, and hemipterans. Because my drift nets were anchored in the stream so that the top of the net was above the water surface, I would expect to capture invertebrates drifting on the water surface. One reason I may not have captured more terrestrial and non-obligate taxa is that my drift nets were always centered about the thalweg, which was often close to the center of the stream channel and not near the margin where these invertebrates fall into the water. However, the adult aquatic life stages that were selected by brook trout were also rarely captured in drift nets. I would expect adult aquatic invertebrates to be distributed across the entire surface of the stream, but be concentrated in the thalweg where the nets were placed. Several authors have reported the selection for taxa on the water surface by cutthroat trout due to the conspicuous nature of these prey items, and also noted that surface invertebrates

account for low proportions of the drift relative to their proportion in trout diets (Wilzbach et al. 1986; Young et al. 1997). This supports my observation of selection for taxa on the water surface by brook trout, despite the fact that these taxa were rare in the drift, and suggests that brook trout may target conspicuous prey items drifting on the surface during the summer.

The shift in selection, from aquatic to terrestrial, translated to brook trout in Cedar Creek deriving approximately 69% of their energy from terrestrial taxa in August. Webster and Hartman (2005) noted that brook trout consistently consumed aquatic prey, particularly Diptera larvae that remained abundant throughout the summer, but that terrestrial prey items contributed approximately 75% of biomass consumed by brook trout in September. My data suggests a similar trend; brook trout selected for chironomid pupae on August 25 and adult dipterans on August 26, but 69% of the energy consumed by brook trout came from terrestrial sources in August. Utz and Hartman (2007) also observed substantial energy contributions from terrestrial sources to the diet of brook trout in several West Virginia streams. Terrestrial energy consumption in their study was highest in May and June, and remained greater than aquatic energy consumption throughout most of the year. Sweka and Hartman (2008) modelled energy inputs of brook trout and noted terrestrial energy contributions between 51 and 63% on an annual scale, and terrestrial energy contributed almost 70% to overall brook trout energy intake during May. I observed the highest terrestrial energy contribution to brook trout diets in August, but my study was limited to three months and my sample size was small relative to Utz and Hartman (2007) and Sweka and Hartman (2008). Had I sampled over a longer temporal scale, or during multiple years, I may have seen higher energy contributions from terrestrial sources throughout the summer as well as into the fall. Nonetheless, my estimates of substantial terrestrial energy contributions to brook trout diets during the summer are comparable to those reported in the

studies listed above, and lend support to the importance of terrestrial invertebrates in brook trout diets.

Interestingly, terrestrial invertebrate consumption by brook trout was linked to a decrease in the availability of aquatic prey during the summer by Wilson et al. (2014), and other investigators have suggested that decreased prey consumption during the summer may also be due to decreased aquatic prey availability (Allan 1981, Ensign 1990). After observing increased terrestrial invertebrate consumption and decreased prey consumption by brook trout from June to August, Sotiropoulos et al. (2006) suggested that these trends may be due to brook trout adopting a low-risk, low-reward energy strategy under low-flow, high-temperature conditions. The low-risk, low-reward strategy involves brook trout reducing energy expenditure by remaining sedentary in deeper pools, and consuming fewer prey items when water temperature is high and drift density is low. Sotiropoulos et al. (2006) reported that drift density decreased from June to August and ranged from 0.04 to 0.84 invertebrates/m<sup>3</sup>. In Cedar Creek, drift density remained high in August (>2.0 invertebrates/m<sup>3</sup>), but brook trout may adopt a similar low-risk, low-reward energy strategy by consuming fewer prey items and targeting conspicuous surface invertebrates. There are several elements that may be driving the adoption of a low-risk, low-reward strategy by brook trout in Cedar Creek, despite relatively high drift densities. First, evidence suggests that the size-distribution of aquatic invertebrate communities decreases from May to August (Mittelbach 1981). This is driven by the completion of invertebrate life cycles as water temperatures warm throughout summer, and results in an aquatic community that is comprised of early-instar, small invertebrates when water temperature peaks late in summer. Second, terrestrial taxa are more energetically dense than aquatic taxa (Cummins and Wuycheck 1976; Grey 2005) and, in general, taxa on the water surface may be more conspicuous than those below

the surface (Wilzbach et al. 1986). Combining these two elements, it seems energetically advantageous for brook trout to lower their activity levels, when water temperatures are high, by remaining sedentary and targeting conspicuous invertebrates on the water surface, rather than actively foraging on inconspicuous aquatic invertebrates. Water temperatures throughout Cedar Creek regularly approached 19.0°C, which would cause thermal stress and drive the basic metabolic rate of brook trout up. Brook trout in Cedar Creek consumed fewer prey items and targeted conspicuous invertebrates on the water surface throughout summer, especially during August when drift density was highest. And, the increase in drift density in August was driven by increased abundance of *Baetis* nymphs, a relatively small aquatic invertebrate. Consequently, it seems like brook trout in Cedar Creek attempted to limit the negative energetic impacts of high water temperatures by consuming fewer prey items and targeting conspicuous surface invertebrates rather than consuming smaller, abundant aquatic prey (e.g. a low-risk, low-reward energy strategy).

The mean estimate of  $P-C_{MAX}$  (0.410) for all trout recaptured throughout the study is relatively high compared to commonly reported values ( $\approx 0.300$  reported by Allan 1981; Railsback and Rose 1999; Godby et al. 2007) and does not correspond to the decreased prey consumption, the negative average  $G$ , or the decrease in body condition that I observed. Sources of error that could contribute to inaccurate estimates of consumption by bioenergetics models include consumption-dependent error, changes in fish activity levels due to prey base, and physiological adaptations (Chipps and Wahl 2008). Consumption dependent error results in the overestimation of consumption for fish feeding at low rations (see Chipps and Wahl 2004) and is the result of modeling consumption dependent terms in the bioenergetics model as fixed proportions of energy consumed, rather than accounting for ration size. The bioenergetics model

I used accounts for ration size when modeling egestion and excretion using the equation produced by Elliot (1976). However, a decrease in specific dynamic action associated with low feeding rates could contribute to model inaccuracy. For example, a depression in specific dynamics action of western mosquitofish (*Gambusia affinis*) fed low rations yielded higher than expected consumption estimates using a traditional bioenergetics model like the model used here (Chipps and Wahl 2004). Brook trout in Cedar Creek seemed to consume prey at low rations throughout most of the summer, so a decrease in specific dynamic action could have contributed to the high consumption estimates produced by the model.

Changes in predator activity levels that result from prey population dynamics could also yield model inaccuracy. Predator activity levels can vary with prey size and morphology (Selch and Chipps 2007), as well as prey composition and abundance (Rennie et al. 2005). Selch and Chipps (2007) noted that largemouth bass (*Micropterus salmoides*) fed large bluegill (*Lepomis macrochirus*) had increased activity levels, associated with capturing larger prey, which contributed to underestimation of prey consumption by a bioenergetics model. Rennie et al. (2005) identified differences in the growth rate of two populations of yellow perch (*Perca flavescens*) in lakes with different prey bases. Interestingly, the lake where yellow perch grew faster they consumed fewer prey, but had much lower activity levels associated with finding prey because invertebrate density was higher. It seems that brook trout in Cedar Creek adopted a low-risk, low-reward energy strategy to lower their activity levels when water temperatures were high, and aquatic prey size distribution decreased. This explanation provides an additional source of error that may have contributed to high consumption estimates by the model.

My results emphasize the importance of terrestrial prey items in the diet of brook trout during the summer. Energetically-dense, terrestrial taxa seem to provide essential meals for

brook trout when they may adopt behavioral shifts due to high temperatures and decreased prey size-distribution. Despite consumption of energy-dense, terrestrial taxa, recaptured trout had a negative average  $G$ , suggesting energy supplementation by terrestrial invertebrates was insufficient to meet temperature-driven metabolic demands during the summer of 2015. I should note that Utz and Hartman (2009) also reported negative brook trout growth rates in August; however, my average  $G$  of  $-0.0009 \text{ d}^{-1}$  was less than the lower limit of their 95% confidence interval ( $\approx -0.0005 \text{ d}^{-1}$ ) of reported growth rate values. Although I did not evaluate the relationship between  $C_R$  and  $G$  statistically, it seemed as though recaptured brook trout with higher  $C_R$  values grew at a faster rate. Also, I observed wide variation in the foraging habits of individual brook trout that were sampled throughout the study. For example, on June 23, the average number of prey items consumed by brook trout was 20.7, which included two trout with 0 prey items in their stomachs and one trout with 121 prey items in its stomach. Similarly, Utz and Hartman (2006) observed the majority of sampled trout consuming few prey items while several trout that consumed many prey items drove up the mean value of prey items present in trout stomachs. I suspect that the variability associated with individual foraging habits resulted in values of  $G$  ranging from  $-0.00433$  to  $+0.00239 \text{ /d}$ . These data suggest that although mean values indicate negative trends in growth, some fish in the population may consume prey at high rates, and exhibit positive growth.

A main objective of this study was to evaluate the potential consequences of altered thermal regimes on the growth of brook trout to aid watershed management efforts. When maintenance consumption values were held constant and temperature was increased by only  $1^\circ\text{C}$ , the model predicted a decrease in weight between 11 and 14% for a 66.5-g brook trout over the course of the study. Because prey consumption is partially, temperature-driven, I'd expect brook

trout to consume prey at a similar  $P-C_{MAX}$ , and change their  $C_T$ , if water temperatures were altered. But, I saw that brook trout seemed to limit their energy expenditure by consuming fewer prey items when water temperature was high; a strategy that would be exacerbated under an increased thermal regime (e.g. they would achieve a lower  $P-C_{MAX}$  at higher temperatures but  $C_T$  would remain similar). Thus, the hypothetical scenario that held  $C_T$  constant may provide a more realistic expectation of how brook trout growth would respond to increased water temperature in the summer. Other studies have also suggested that warmer stream temperatures will negatively impact brook trout growth (Ries and Perry 1995, Xu et al. 2010) and fecundity (Xu et al. 2010). However, Ries and Perry (1995) point out that the true advantages and disadvantages that brook trout may experience as a result of thermal disturbance are highly dependent on the existing thermal regime of the system. My predictions suggest that growth during the summer would be negatively impacted if water temperatures were to rise, particularly in streams that may already approach temperatures near the upper optimal limit for brook trout. Increased water temperature could potentially increase growth rates during winter and spring, but Xu et al. (2010) suggested that these gains would likely be negated by the decreases in growth rate that would occur during summer and autumn.

A disadvantage of the bioenergetics model employed here is that it does not allow for error associated with its outputs to be easily quantified. Maintenance  $P-C_{MAX}$  and  $C_R$  values for a 66.5-g brook trout over the study period were similar to the observed values for all recaptured trout. However, brook trout seemed to lower their activity levels by consuming fewer prey items, which may have caused the consumption estimates to be slightly high. The bioenergetics model was calibrated under several assumptions, including the assumption that all prey were digestible, and that all fish experienced the cooler thermal regime of the downstream reach. Although 12 of

the 13 recaptured trout were recaptured in the downstream reach, I confirmed that brook trout remained in the upstream reach throughout summer, based on August electrofishing samples. It is likely that brook trout throughout the system experience a broader thermal regime which would translate to greater variation in estimated parameters, especially predicted growth. My assumptions and model parameters probably provide the most conservative predictions of the impacts of thermal disturbance on brook trout growth in Cedar Creek.

Though it is difficult to accurately predict how potential changes in climate may impact the temperature of Cedar Creek, the data presented here suggests protecting Cedar Creek's thermal regime from increases in temperature associated with land-use should be a priority. Empirical growth rate data and hypothetical model predictions suggest that the current thermal regime in Cedar Creek may be sub-optimal for brook trout during the summer, and any increase in the thermal regime would be detrimental to brook trout growth. Additional incentive to protect Cedar Creek's thermal regime should come from the fact that Cedar Creek is a valuable coldwater source to the Rogue River; a popular coldwater fishery that faces anthropogenic disturbance. In addition, the importance of terrestrial invertebrates in the diet of brook trout demonstrated here, and in the literature, deserves consideration when managing for brook trout. Conservation and enhancement of riparian vegetation and groundwater should be treated as an important management action to conserve brook trout habitat at the watershed scale, particularly in coldwater and cold-transition streams (Lyons et al. 2009). The important role riparian vegetation plays in stream shading, to enhance thermal habitat, has been demonstrated in other Midwestern streams (Cross et al. 2013). Additionally, riparian vegetation provides habitat for terrestrial invertebrates that contribute substantial amounts of energy to brook trout diets, particularly during thermally-stressful, summer months.



## Acknowledgements

I thank Schrems West Michigan Chapter of Trout Unlimited, and specifically Nichol DeMol for their contributions to this research. I also thank Justin Wegner for the time he spent assisting with the project. In addition, Travis Ellens, Emily Dean, and Zach Kuzniar deserve acknowledgement for their roles in the collection of field data and laboratory assistance. Lastly, I thank the private land-owners who graciously allowed us access to Cedar Creek. Without those mentioned above, this study would not have been possible. Fish handling procedures followed the methods approved by Grand Valley State University's Institutional Animal Care and Use Committee protocol 15-09-A.

## Tables

Table 2.1. The number of fish sampled for total length and wet weight (N), total number of gut samples taken (n), sample reach (D=downstream, U=upstream) and the interval when drift samples were collected (Time). Both reaches were electrofished on 8/25/2015, but drift samples were collected at the downstream reach.

| Date      | Reach | Time              | N  | n  |
|-----------|-------|-------------------|----|----|
| 6/19/2015 | U     | 04:00:00-07:00:00 | 14 | 14 |
| 6/22/2015 | D     | 04:00:00-07:00:00 | 6  | 6  |
| 6/23/2015 | D     | 19:00:00-22:00:00 | 11 | 10 |
| 7/21/2015 | D     | 04:00:00-07:00:00 | 8  | 8  |
| 7/23/2015 | D     | 18:00:00-21:00:00 | 7  | 6  |
| 8/25/2015 | Both  | 05:00:00-08:00:00 | 11 | 11 |
| 8/26/2015 | U     | 15:00:00-18:00:00 | 4  | 4  |
| 9/1/2015  | D     | NA                | 29 | 0  |

Table 2.2. Mean Strauss' Linear Index ( $L_i$ ) value and corresponding percentage of taxa in the drift ( $p_i$ ) for the five most selected prey taxa and least selected prey taxa on each sample date.  $L_i$  values were calculated for all taxa using the percentage of prey items in the diet of each trout.

The mean  $L_i$  value for taxa are reported.

| Date                                      | Taxa   | Mean Strauss ( $L_i$ ) | Total Drift Percentage ( $p_i$ ) |
|---|--|------------------------|----------------------------------|
| 6/19/2015<br>(n=14)                       | Adult Hydropsychidae <sup>A</sup>                        | 33.96                  | 0.42                             |
|   | Adult Curculionidae <sup>N</sup>                         | 12.38                  | 0.28                             |
|   | Arionidae <sup>T</sup>                                   | 9.05                   | 0.00                             |
|   | Adult Coleoptera <sup>N</sup>                            | 5.29                   | 0.14                             |
|   | Adult Diptera <sup>A</sup>                               | 1.73                   | 0.98                             |
|   | Chironomidae larvae <sup>A</sup>                         | -6.95                  | 10.13                            |
|   | Chironomidae pupae <sup>A</sup>                          | -7.03                  | 7.03                             |
|   | Adult Chironomidae <sup>A</sup>                          | -7.53                  | 8.44                             |
|   | Perlidae <i>Perlesta</i> nymph <sup>A</sup>              | -10.6                  | 16.03                            |
|   | Pleidae Neoplea <sup>A</sup>                             | -18.14                 | 18.14                            |
| 6/22/2015<br>(n=6)                        | Adult Baetidae <i>Baetis</i> <sup>A</sup>                | 13.34                  | 0.47                             |
|   | Adult Hydropsychidae <sup>A</sup>                        | 11.07                  | 0.11                             |
|   | Lepidostomatidae <i>Lepidostoma</i> <sup>A</sup>         | 8.37                   | 0.18                             |
|   | Formicidae <sup>T</sup>                                  | 7.76                   | 1.45                             |
|   | Adult Diptera <sup>A</sup>                               | 6.11                   | 0.47                             |
|   | Leptohiphidae <i>Tricorythodes</i> nymph <sup>A</sup>    | -2.97                  | 3.26                             |
|   | Pleidae Neoplea <sup>A</sup>                             | -3.47                  | 3.47                             |
|   | Chironomidae pupae <sup>A</sup>                          | -4.28                  | 4.94                             |
| 6/23/2015<br>(n=10)                       | Baetidae <i>Baetis</i> nymph <sup>A</sup>                | -25.53                 | 28.82                            |
|   | Adult Chironomidae <sup>A</sup>                          | -37.89                 | 37.89                            |
|   | Hydropsychidae <i>Ceratopsyche</i> larvae <sup>A</sup>   | 15.20                  | 0.26                             |
|   | Chironomidae larvae <sup>A</sup>                         | 12.74                  | 1.27                             |
|   | Hydropsychidae <i>Cheumatopsyche</i> larvae <sup>A</sup> | 11.08                  | 0.03                             |
|   | Adult Curculionidae <sup>N</sup>                         | 3.40                   | 0.46                             |
|   | Asellidae <sup>A</sup>                                   | 2.78                   | 0.12                             |
|   | Sciaridae <sup>N</sup>                                   | -2.19                  | 2.19                             |
|   | Chironomidae pupae <sup>A</sup>                          | -2.89                  | 4.82                             |
|   | Adult Empididae <sup>A</sup>                             | -3.60                  | 4.56                             |
| Adult Baetidae <i>Baetis</i> <sup>A</sup> | 8.63   | 15.88                  |                                  |
| Adult Chironomidae <sup>A</sup>           | -43.48   | 43.48                  |                                  |

<sup>A</sup> Denotes aquatic taxa

<sup>T</sup> Denotes terrestrial taxa

<sup>N</sup> Denotes non-obligate taxa

Table 2.2 Continued.

| Date                                      | Taxa   | Mean Strauss<br>( $L_i$ ) | Total Drift<br>Percentage ( $p_i$ ) |
|---|--|---------------------------|-------------------------------------|
| 7/21/2015<br>(n=8)                        | Adult Hydropsychidae <sup>A</sup>                      | 12.81                     | 2.4                                 |
|   | Adult Leptohyphidae <i>Tricorythodes</i> <sup>A</sup>  | 8.65                      | 0.04                                |
|   | Asellidae <sup>A</sup>                                 | 7.88                      | 0.82                                |
|   | Hydropsychidae <i>Ceratopsyche</i> larvae <sup>A</sup> | 5.34                      | 3.36                                |
|   | Adult Curculionidae <sup>N</sup>                       | 4.26                      | 0.09                                |
|   | Elmidae larvae <sup>A</sup>                            | -2.04                     | 2.04                                |
|   | Simuliidae larvae <sup>A</sup>                         | 2.31                      | 2.31                                |
|   | Leptohyphidae <i>Tricorychodes</i> nymph <sup>A</sup>  | -3.22                     | 3.22                                |
|   | Baetidae <i>Baetis</i> nymph <sup>A</sup>              | -22.23                    | 30.93                               |
| Adult Chironomidae <sup>A</sup>           | -22.5  | 29.02                     |                                     |
| 7/23/2015<br>(n=6)                        | Adult Diptera <sup>A</sup>                             | 7.94                      | 0.88                                |
|   | Formicidae <sup>T</sup>                                | 6.77                      | 2.05                                |
|   | Adult Coleoptera <sup>N</sup>                          | 5.49                      | 0.39                                |
|   | Hydropsychidae larvae <sup>A</sup>                     | 4.71                      | 1.17                                |
|   | Adult Chrysomelidae <sup>N</sup>                       | 4.41                      | 0                                   |
|   | Adult Curculionidae <sup>N</sup>                       | 4.41                      | 0                                   |
|   | Pentatomidae <sup>T</sup>                              | 4.41                      | 0                                   |
|   | Sciaridae <sup>N</sup>                                 | -3.71                     | 3.71                                |
|   | Collembola <sup>A</sup>                                | -4.5                      | 4.5                                 |
|   | Adult Baetidae <i>Baetis</i> <sup>A</sup>              | -12.2                     | 18.08                               |
| Adult Chironomidae <sup>A</sup>           | -14.27   | 14.27                     |                                     |
| Baetidae <i>Baetis</i> nymph <sup>A</sup> | -16.72   | 16.72                     |                                     |
| 8/25/2015<br>(n=11)                       | Cicadellidae <sup>T</sup>                              | 7.56                      | 0.28                                |
|   | Psocoptera <sup>T</sup>                                | 6.34                      | 1.5                                 |
|   | Chironomidae pupae <sup>A</sup>                        | 5.07                      | 2.77                                |
|   | Adult Leptohyphidae <i>Tricorythodes</i> <sup>A</sup>  | 3.92                      | 0                                   |
|   | Adult Lyonetidae <sup>T</sup>                          | 3.92                      | 0                                   |
|   | Adult Hydropsychidae <sup>A</sup>                      | 3.89                      | 0.03                                |
|   | Aquatic Gastropoda <sup>A</sup>                        | 3.89                      | 0.03                                |
|   | Terrestrial Hemiptera <sup>T</sup>                     | 3.89                      | 0.03                                |
|   | Trichoptera larvae <sup>A</sup>                        | 3.89                      | 0.03                                |
|   | Hydropsychidae <i>Ceratopsyche</i> larvae <sup>A</sup> | -1.73                     | 1.73                                |
|   | Simuliidae larvae <sup>A</sup>                         | -1.95                     | 3.91                                |
|   | Chironomidae larvae <sup>A</sup>                       | -2.03                     | 3.99                                |
|   | Adult Chironomidae <sup>A</sup>                        | -18.08                    | 22                                  |
| Baetidae <i>Baetis</i> nymph <sup>A</sup> | -42.19   | 50.03                     |                                     |

<sup>A</sup> Denotes aquatic taxa<sup>T</sup> Denotes terrestrial taxa<sup>N</sup> Denotes non-obligate taxa

Table 2.2. Continued

| Date      | Taxa                                      | Mean Strauss<br>( $L_i$ ) | Total Drift<br>Percentage ( $p_i$ ) |
|-----------|---|---------------------------|-------------------------------------|
|           | Flatidae <sup>T</sup>                     | 18.18                     | 0                                   |
|           | Cercopidae <sup>T</sup>                   | 15.91                     | 0                                   |
|           | Aradidae <sup>T</sup>                     | 11.36                     | 0                                   |
|           | Adult Diptera <sup>A</sup>                | 10.61                     | 0.75                                |
| 8/26/2015 | Acrididae <sup>T</sup>                    | 4.55                      | 0                                   |
| (n=4)     | Baetidae <i>Baetis</i> nymph <sup>A</sup> | -6.02                     | 6.02                                |
|           | Sciaridae <sup>N</sup>                    | -6.02                     | 6.02                                |
|           | Chironomidae pupae <sup>A</sup>           | -6.48                     | 6.48                                |
|           | Adult Chironomidae <sup>A</sup>           | -7.68                     | 7.68                                |
|           | Collembola <sup>A</sup>                   | -18.37                    | 18.37                               |
|           | Chironomidae larvae <sup>A</sup>          | -18.98                    | 18.98                               |

<sup>A</sup> Denotes aquatic taxa

<sup>T</sup> Denotes terrestrial taxa

<sup>N</sup> Denotes non-obligate taxa

Table 2.3. Observed growth rates and consumption estimates from the bioenergetics model for each individual trout that was recaptured throughout the study. The arbitrary number (Fish #), and the initial day (Day <sub>I</sub>) and final day (Day <sub>F</sub>) of capture are listed for each trout. Initial weight ( $W_I$ , g) and final weight ( $W_F$ , g) of each trout were used to calculate its instantaneous growth rate ( $G$ ,  $d^{-1}$ ). The bioenergetics model estimated the proportion of each trout's maximum consumption ( $P-C_{MAX}$ ) and its total consumption ( $C_T$ , g) over the study period. To calculate the average specific consumption rate ( $C_R$ ,  $g \cdot g^{-1} \cdot d^{-1}$ ) of each trout, its estimated  $C_T$  was divided by its average weight between capture events, and subsequently divided by the number of days between capture events.

| Fish # | Day <sub>I</sub> | Day <sub>F</sub> | $W_I$ (g) | $W_F$ (g) | $G$ ( $d^{-1}$ ) | $P-C_{MAX}$ | $C_T$ (g) | $C_R$<br>( $g \cdot g^{-1} \cdot d^{-1}$ ) |
|--------|------------------|------------------|-----------|-----------|------------------|-------------|-----------|--|
| 42     | 5                | 75               | 50.67     | 60.03     | 0.00239          | 0.466       | 140.25    | 0.036                                      |
| 44     | 5                | 35               | 32.34     | 32.37     | 0.00003          | 0.493       | 47.561    | 0.047                                      |
| 41     | 5                | 35               | 52.26     | 48.56     | -0.0024          | 0.439       | 57.59     | 0.037                                      |
| 5*     | 4                | 68               | 66.19     | 68.66     | 0.00056          | 0.458       | 149.026   | 0.034                                      |
| 6*     | 4                | 68               | 171.43    | 160.02    | -0.0011          | 0.427       | 262.516   | 0.024                                      |
| 9*     | 4                | 68               | 98.8      | 82.05     | -0.0029          | 0.374       | 150.681   | 0.026                                      |
| 8*     | 4                | 68               | 90.04     | 77.82     | -0.0022          | 0.39        | 149.007   | 0.027                                      |
| 3*     | 1                | 68               | 80.99     | 60.35     | -0.0043          | 0.341       | 120.778   | 0.025                                      |
| 22     | 1                | 68               | 64.25     | 71.59     | 0.00159          | 0.486       | 165.478   | 0.036                                      |
| 45     | 33               | 75               | 103.2     | 97.76     | -0.0013          | 0.348       | 95.002    | 0.022                                      |
| 31     | 5                | 75               | 71.2      | 67.99     | -0.0007          | 0.403       | 144.039   | 0.029                                      |
| 55     | 33               | 75               | 50.88     | 52.58     | 0.00076          | 0.383       | 69.269    | 0.031                                      |
| 54     | 33               | 75               | 77.82     | 70.2      | -0.0024          | 0.322       | 70.86     | 0.022                                      |

\* Indicate fish with a surgically implanted telemetry tags

Figures

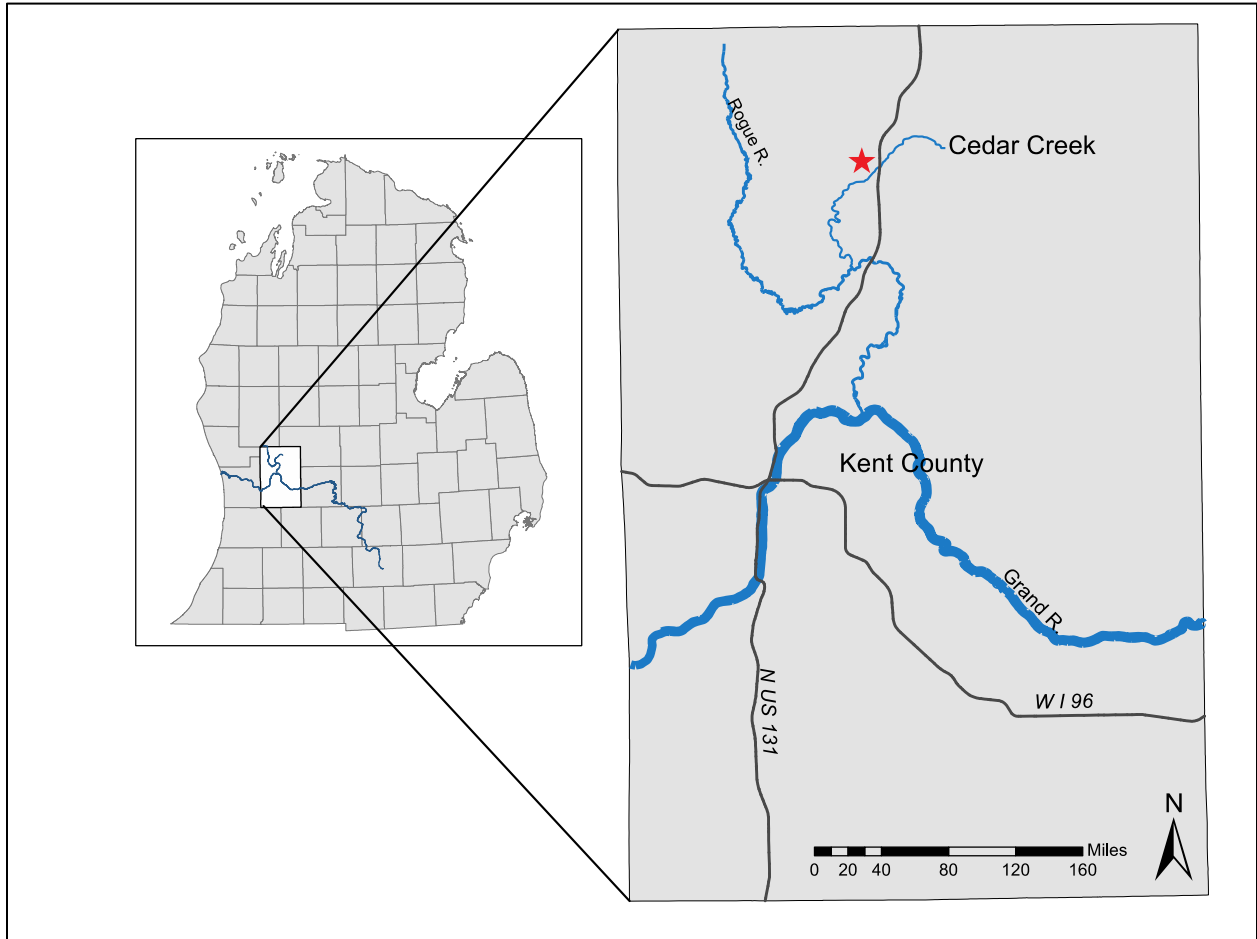


Figure 2.1. Map of Cedar Creek, Kent County, Michigan. Red star indicates the study site.

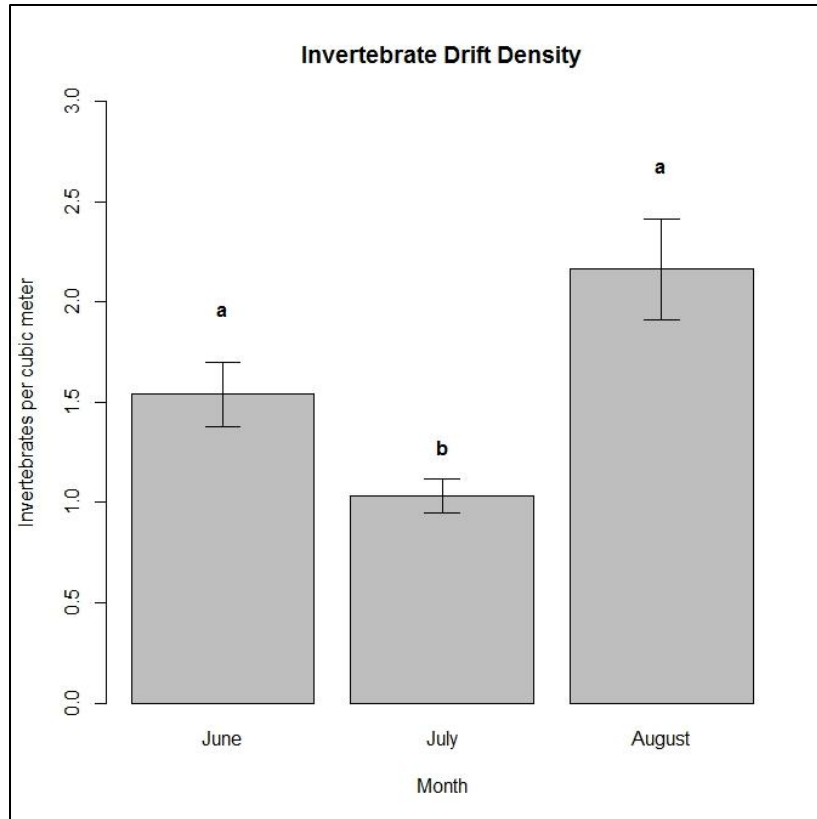


Figure 2.2. Mean ( $\pm$ SE) invertebrate drift density of drift samples collected at the downstream reach in the morning during each month (n=12). Lowercase letters indicate significant differences determined by a pairwise Wilcoxon test. For specific collection times and dates, see Table 2.1.



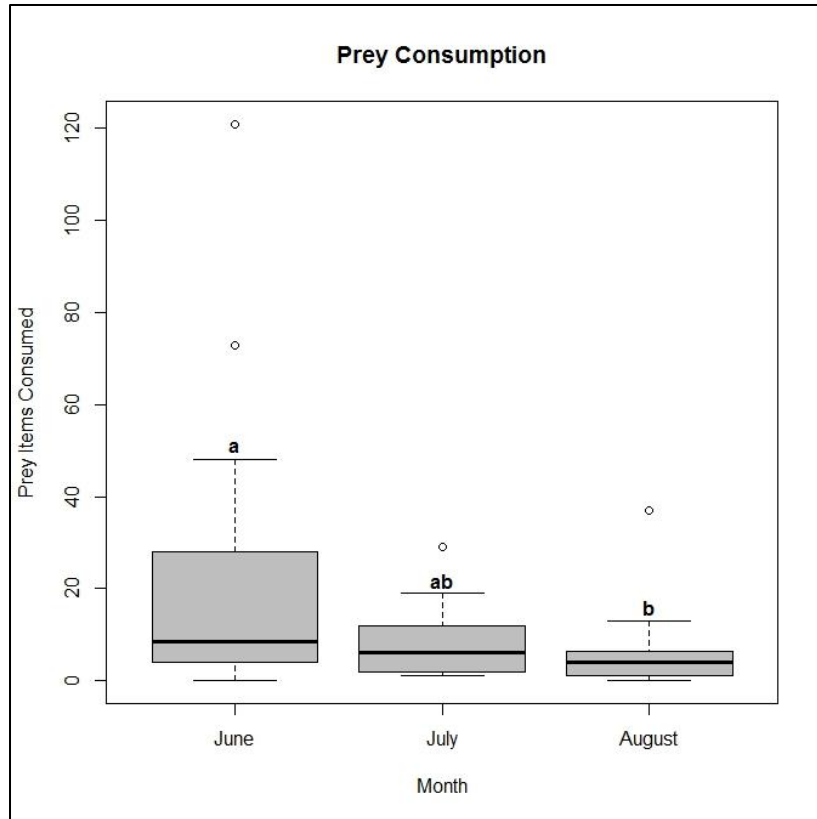


Figure 2.3. The number of prey items (range and quartiles) consumed by brook trout that were sampled during June (n=30), July (n=14), and August (n=15). Lowercase letters indicate significant differences in the number of prey items consumed by brook trout among months, determined by a pairwise t-test performed on square-root transformed data.

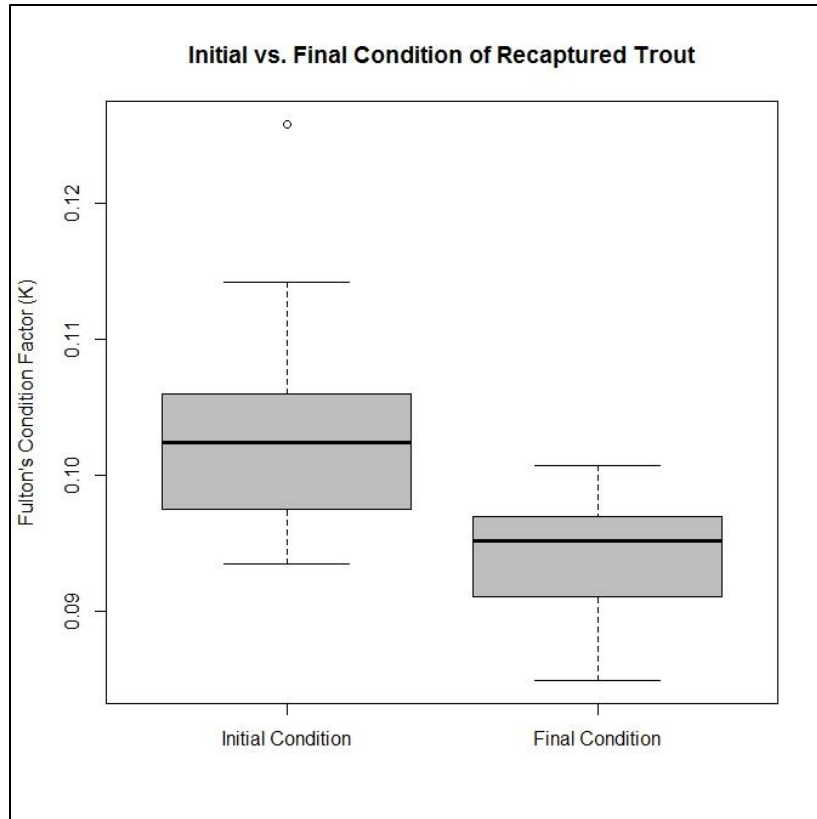


Figure 2.4. Initial and final condition (range and quartiles) of trout recaptured throughout the study. Final condition was significantly lower than initial condition (T-test,  $P=0.001$ ,  $t=-3.75$ ,  $d.f.=12$ ).

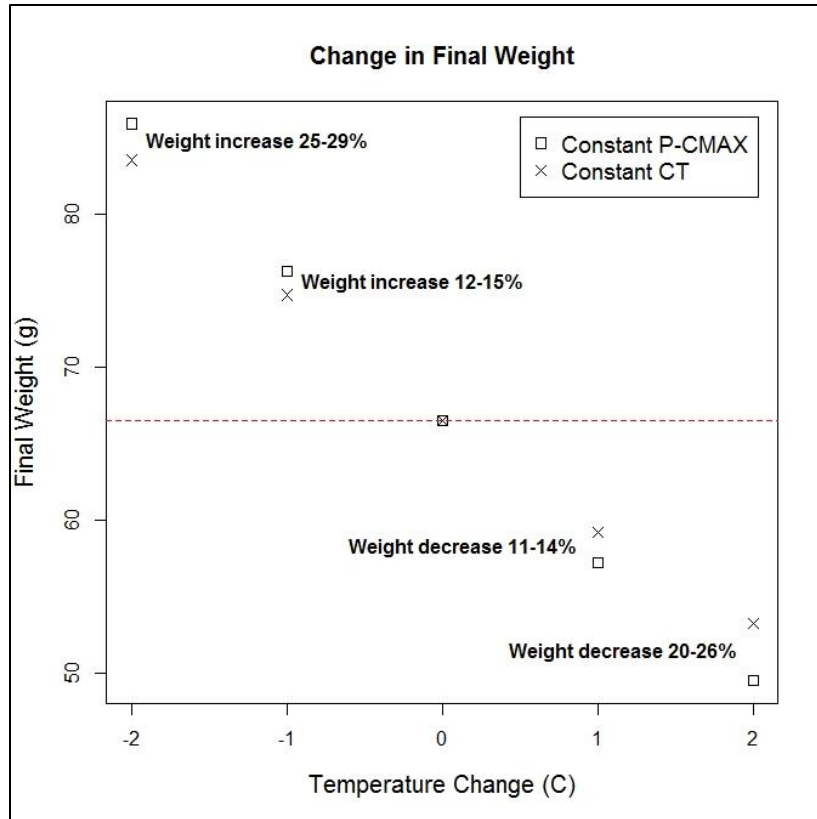


Figure 2.5. Estimated change in weight of a 66.5-g brook trout under altered thermal regime scenarios when  $C_T$  is held constant (153.247 g), and when  $P-C_{MAX}$  is held constant (0.421).

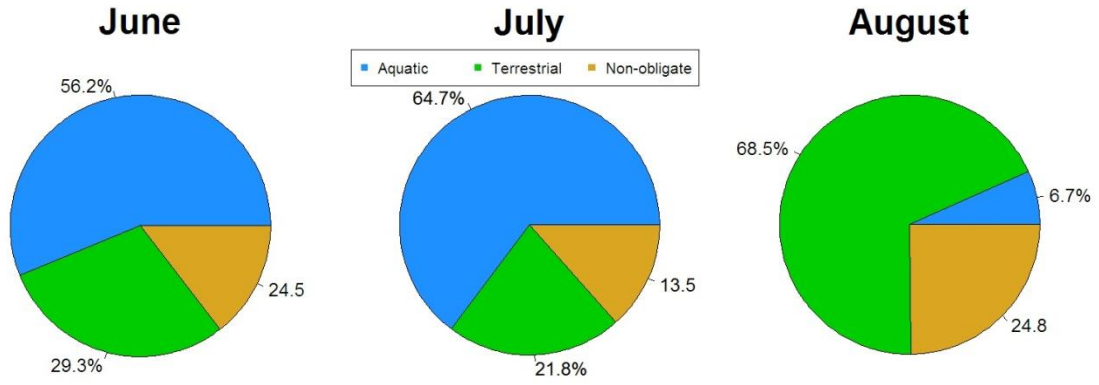


Figure 2.6. Percentage of energy contributed from aquatic, terrestrial, and non-obligate taxa to brook trout diets during each month.

## References

- Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:184-192.
- AWRI (Annis Water Resources Institute). 2001. Rogue River Watershed Management Plan.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of North American Benthological Society* 18: 308:343.
- Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects, 6<sup>th</sup> edition. Saunders College Publishers, Ft. Worth, TX.
- Brodman, P. A., and H.-U. Reyer. 1999. Nestling provisioning in water pipits (*Anthus spinoletta*): do parents do for specific nutrients or profitable prey? *Oecologia* 120:506-514.
- Chipps, S. R., and D. H. Wahl. 2004. Development and evaluation of a Western Mosquitofish bioenergetics model. *Transactions of the American Fisheries Society* 133:1150-1162.
- Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21<sup>st</sup> century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society* 137:298-313.
- Cross, B. K., M. A. Bozek, and M. G. Mitro. 2013. Influences of riparian vegetation on trout stream temperature in Central Wisconsin. *North American Journal of Fisheries Management* 33: 682-692.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *International Association of Theoretical and Applied Limnology* 18: 1-158.
- Deslauriers, D., and S. R. Chipps. 2016. Fish bioenergetics 4.0 workshop. 76<sup>th</sup> Midwest Fish and Wildlife Conference, January 24<sup>th</sup> 2016, Grand Rapids, Michigan.

- Elliot, J. M. 1969. Diel periodicity in invertebrate drift and the effect of different sampling periods. *Oikos* 20: 524-528.
- Elliot, J. M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). *Journal of Animal Ecology* 45:561-580.
- Ensign, W. E. 1990. Summer food limitation reduces brook and rainbow trout biomass in a southern Appalachian stream. *Transactions of the American Fisheries Society* 119: 894-901.
- Forrester, G. E., J. G. Chase, and W. McCarthy. 1994. Diel and density related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environmental Biology of Fishes* 39:301-311.
- Foster, J. R. 1977. Pulsed gastric lavage: an efficient method of removing stomach contents of live fish. *The progressive Fish Culturist* 30:166-169.
- Godby, N. A., E. S. Rutherford, and D. M. Mason. 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a Lake Michigan tributary. *North American Journal of Fisheries Management* 27:578-592.
- Grey, A. 2005. The Salmon River estuary: restoring tidal inundation and tracking ecosystem response. Doctoral dissertation. University of Washington, Seattle.
- Hartman, K. J., and M. K. Cox. 2008. Refinement and testing of a brook trout bioenergetics model. *Transactions of the American Fisheries Society* 137: 357-363.
- Hartman, K. J., and J. A. Sweka. 2003. Development of a bioenergetics model for Appalachian brook trout. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 55(2001):38-51.

- Hill, D. K., and J. J. Magnuson. 1990. Potential impacts of global climate warming on the growth and prey consumption of great lakes fishes. *Transaction of the American Fisheries Society* 119:265-275.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *North American Journal of Fisheries Management* 28:1069-1085.
- Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia* 52:22-30.
- Lyons, J., T. Zorn, J. Stewart, P. Seelbach, K. Wehrly, and L. Wang. 2009. Defining and characterizing coolwater streams and their fish assemblages in Michigan and Wisconsin, USA. *North American Journal of Fisheries Management* 29:1130-1151.
- McCafferty, W.P., and A.V. Provonsha. 1998. *Aquatic entomology: the fisherman's and ecologist's guide illustrated guide to insects and their relatives*. Jones and Bartlett, Boston, MA.
- McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. S. Foott, S. L. Johnson, K. R. Marine, M. G. Mesa, J. H. Peterson, Y. Souchon, K. F. Tiffin, and W. A. Wurtsbaugh. 2009. Research in thermal biology: burning question for coldwater stream fishes. *Reviews in Fisheries Science* 17:90-115.
- Merritt, R.W., K.W. Cummins, and M. B. Berg. 2008. *An introduction to the aquatic insects of North America*. Kendall and Hunt, Dubuque, IA.
- MDEQ (Michigan Department of Environmental Quality). 2004. *A biological survey of the Rogue River Watershed Kent and Newaygo counties, Michigan*. MDEQ Water Division Staff Report 03/129, Lansing, Michigan.

- MDEQ (Michigan Department of Environmental Quality). 2009. A biological survey of sites in the Rogue River Watershed Kent and Newaygo Counties, Michigan. MDEQ Water Bureau Staff Report 09/057, Lansing, Michigan.
- Mittelbach, G. G. 1981. Patterns of invertebrate size and abundance in aquatic habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 38:896-904.
- Peckarsky, B.L., P.R. Fraissinet, M.A. Penton, and D.J. Conklin. 1990. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithica, NY.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141-203 in E. K. Balon. Charrs, salmonid fishes of the genus *Salvelinus*. The Hague; Dr. W. Junk; Kluwer Boston; Hingham, Massachusetts.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Railsback, S. F., and L. A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. *Transaction of the American Fisheries Society* 128:241-256.
- Ries, R. D., and S. A. Perry. 1995. Potential effects of global climate warming on brook trout growth and prey consumption in central Appalachian streams, USA. *Climate Research* 5:197-206.
- Rennie, M. D., N. C. Collins, B. J. Shuter, J. W. Rajotte, and P. Couture. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Canadian Journal of Fisheries and Aquatic Sciences* 62:767-780.



- Selch, T. M., and S. R. Chipps. 2007. The cost of capturing prey: measuring largemouth bass (*Micropterus salmoides*) foraging activity using glycolytic enzymes (lactate dehydrogenase). *Canadian Journal of Fisheries and Aquatic Sciences* 64:1761-1769.
- Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of North American Benthological Society* 21:336-343.
- Sage, R. D. 1982. Dry-weight estimates of insects and spiders based on length. *The American Midland Naturalist* 108:407-411.
- Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129: 234-240.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10: 375-383.
- Sotiropoulos, J. C., K. H. Nislow, and M. R. Ross. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. *Fisheries Management and Ecology* 13:149-155.
- Stranko, S. A., R. H. Hildebrand, R. P. Morgan, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook trout declines with land cover and temperature changes in Maryland. *North American Journal of Fisheries Management* 28:1223-1232.
- Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108:344-352.

- Sweka, J. A., and K. J. Hartman. 2008. Contribution of terrestrial invertebrates to yearly brook trout prey consumption and growth. *Transactions of the American Fisheries Society* 137:224-235.
- Utz, R. M., and K. J. Hartman. 2006. Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2675-2686.
- Utz, R. M., and K. J. Hartman. 2007. Identification of Critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms. *Hydrobiologia* 575:259-270.
- Utz, R. M., and K. J. Hartman. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66: 1072-1080.
- Webster, J. J., and K. J. Hartman. 2005. The role of terrestrial invertebrates in allopatric brook trout headwater streams in the Central Appalachian Mountains. *Journal of Freshwater Ecology* 20:101-107.
- Wilson, M. K., W. H. Lowe, and K. H. Nislow. 2014. What predicts the use by brook trout (*Salvelinus fontinalis*) of terrestrial invertebrate subsidies in headwater streams? *Freshwater Biology* 59:187-199.
- Wilzbach, M. A., K. W. Cummins, and J. D. Hall. 1986. Influence of habitat manipulations on interactions between between cutthroat trout and invertebrate drift. *Ecology* 67:898-911.
- Xu, C., B. H. Letcher, and K. H. Nislow. 2010. Context-specific influence of water temperature on brook trout growth rates in the field. *Freshwater Biology*

Young, M. K., R. B. Rader, and T. A. Belish. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. *Transactions of the American Fisheries Society* 126:428-437.

## Chapter III

### Extended Literature Review

#### *Introduction*

The brook trout (*Salvelinus fontinalis*) is a coldwater fish species that thrives in streams draining pristine, heavily-forested watersheds (Kanno et al. 2015). As a result of anthropogenic disturbance, brook trout have undergone range reduction throughout much of their native range in the United States (Hudy et al. 2008), and projections under future disturbance scenarios suggest continued habitat loss for the species (Flebbe et al. 2006; Wiley et al. 2010). The observed habitat loss has been primarily attributed to deforestation, causing increases in stream-water temperature (Stranko et al. 2008). Because brook trout are ectotherms, with limited ability to moderate body temperature, increases in stream-water temperature drive changes in their physiological rates at the individual level that effect populations (McCullough et al. 2009). For example, brook trout metabolism, food consumption, and waste production, all physiological processes that contribute to growth rate, are temperature-dependent. The relationship among temperature and the three physiological processes listed above limits the species' optimal growth range to temperatures between 10° and 19°C (Hartman and Sweka 2003). Using bioenergetics models, the relationship among temperature and the physiological processes controlling growth can be examined quantitatively. Given a fish's thermal history, prey base, and mass, specific questions about energy consumption or growth over a given timeframe can be answered (Hartman and Kitchell 2008). This method has the potential to provide insight into individual growth rates that may help explain species distribution (McCullough et al. 2009). However, effectively transferring knowledge gained through bioenergetic modeling to management decisions requires a broad understanding of the species' ecology and the utility of such models.

Herein, the general ecology of brook trout, as well as the development and utility of fish bioenergetics models will be reviewed to provide context for the use of bioenergetics modeling techniques as a tool to aid brook trout population management.

### *Brook Trout Ecology*

Brook trout were naturally distributed throughout eastern Canada, the upper portions of the Midwestern United States, and in the Mid-Atlantic states as far south as Georgia. However, the species has been transplanted and is now naturalized in many watersheds in the Western United States and Canada (MacCrimmon and Campbell 1969).

Brook trout display several life history strategies (Power 1980). In southern streams, brook trout are typically short lived and remain sedentary. Trout in these populations rarely live past age 4+, typically spawn only once, and the population's egg production comes primarily from two year old females. In mountain and northern streams, brook trout have a longer life cycle and grow slower. In these populations, females dominate older age classes, but it is common for a few males to live long and reach larger size. A third, migratory life history strategy can also be found among brook trout populations throughout their native range. Migrations may take place from streams to lakes or the sea, and back to streams, allowing trout to utilize resources outside their lotic habitat. Access to additional resources yield lower mortality, larger fish, and higher fecundity. An additional life history strategy, termed lacustrine, is described by Huckins et al. (2008). Lacustrine populations spend their entire lives in lakes, including spawning, rather than returning to the stream.

Age at maturity can vary based on sex and among life history strategies. Becker (1983) noted stream-resident, male brook trout in Wisconsin reaching sexual maturity by the end of their first summer, while females typically reached maturity as yearlings. Maturity likely occurs

somewhat later in resident populations of alpine systems that experience longer life cycles (Power 1980). Sexual maturity in migratory populations is often reached at age 3+ (Power 1980; Castonguay et al. 1982).

Brook trout spawn during the fall in gravelly riffles of streams, or on lake shoals (Power 1980; Becker 1983). Spawning takes place almost exclusively in areas of high groundwater seepage in both lentic and lotic environments (Witzel and MacCrimmon 1983; Blanchfield and Ridgway 1996). In migratory populations, spawning typically occurs annually, but if trout experience a low growth year they may skip spawning; this is more commonly observed in northern populations (White 1940, cited by Power 1980). After spawning occurs, between October and November, brook trout alevin emerge from gravel between January and May (Becker 1983).

Brook trout thrive in pristine, relatively undeveloped watersheds (Kanno et al. 2015). At the watershed scale, extensively forested land cover increases the likelihood of brook trout occurrence (Hudy et al. 2008; Stranko et al. 2008). Forested land cover and brook trout occurrence are linked because decreases in forested land cover yield increases in surface-water runoff that translate to higher stream-water temperatures (Stranko et al. 2008). A low percentage of agricultural land inside a watershed also increases the likelihood of brook trout occurrence, but a basin's ability to support brook trout is likely dependent upon the interaction between these major, watershed-scale variables and smaller, system-specific attributes (Hudy et al. 2008).

In general, McKenna and Johnson (2011) identified high elevation, steep slope, and small stream size, variables common to headwater streams, as characteristics of good brook trout habitat. At the reach scale, brook trout are influenced by abiotic factors, including watershed position, temperature, pH, and sediment regime. The upper lethal temperature for the species is

approximately 25°C (Fry et al. 1946). More specifically, Wherly et al. (2007) noted that exposure time must be taken into consideration when evaluating thermal tolerance limits. Based on data from 285 streams in the upper Midwestern United States, they estimated that seven days of exposure to maximum mean daily water temperatures of 23.3°C, and seven days of exposure to maximum daily water temperature of 25.4°C are the tolerable limits for brook trout in the field. Elsewhere in their native range, brook trout occurrence has been negatively correlated with the number of stream temperature readings >20°C (Stranko et al. 2008). Additionally, pH plays an important role at the reach scale. The lethal pH limits for the species are approximately 3.5 and 9.0 (Daye and Garside 1975, cited by Power 1980), but brook trout have been found at low pH values in the field, relative to other coldwater species (Carline et al. 1994; Baldigo and Lawrence 2000). Lastly, significant amounts of fine sediment can decrease brook trout survival by embedding gravelly substrate and choking early life stages of oxygen (Argent and Flebbe 1999).

Sympatric relationships with other salmonids also influence brook trout distribution. Brown trout *Salmo trutta* have been heavily stocked in streams throughout the native range of brook trout, and often dominate when the two species co-occur. Fausch and White (1981) observed a shift in the resting location of brook trout after brown trout were removed from a reach of the East Branch of the Au Sable River, Michigan. This shift resulted in more profitable resting positions for brook trout, indicating an ecological release with brown trout removal; a symbol of interspecific competition. The release points to the dominance by brown trout over brook trout when the two species coexist. Yet, the authors appropriately point out that additional elements including angling mortality, predation, and environmental factors interact with competition to control sympatric populations of the two species. The combination of these

factors has led to an inverse relationship between the abundance of brook and brown trout throughout a substantial portion of the brook trout's historic range (Wagner et al. 2013).

The threat to brook trout populations from rainbow trout *Oncorhynchus mykiss* is less straightforward. In a laboratory study, young-of-year rainbow trout outgrew young-of-year brook trout over an eight week period when the two species were co-stocked (Isley and Kempton 2000). The faster growth rate of co-stocked rainbow trout held true at low, medium, and high ration levels even though raceway temperatures were maintained at 12°C; a temperature that should favor brook trout. In the field, rainbow trout have been observed outgrowing brook trout once they reach age 1+, translating to higher production by rainbow trout than by brook trout in sympatric populations (Whitworth and Strange 1983). But interestingly, Strange and Habera (1998) observed no net loss in the amount of stream distance occupied by brook trout in a sympatric population with rainbow trout over a five year period in several Tennessee streams. They suggest that the replacement of brook trout by rainbow trout in the field may be a dynamic process that requires additional environmental factors such as natural catastrophe.

When stocked outside their native range, brook trout pose significant threats to native salmonids. In Finland, Korsu et al. (2007) documented the replacement of brown trout by brook trout in the headwaters of the Upper Kemijoki River. The replacement yielded species distribution patterns similar to those observed in the Northeastern United States where brown trout have been introduced. In the Western United States, introduced brook trout threaten native cutthroat trout (*Oncorhynchus clarki*) and bull trout (*Salvelinus confluentus*). Brook trout dominance over cutthroat trout stems from their adverse effects on early cutthroat trout life stages (Peterson et al. 2004; McGrath and Lewis 2007). The ability of brook trout to outcompete cutthroat trout can lead to abundance and production values higher than those displayed by



cutthroat trout. For instance, Benjamin and Baxter (2010) recorded brook trout densities 2.4 times greater, biomass 1.7 times greater, and production 2.5 times greater than cutthroat trout when brook trout invaded areas where cutthroat trout had previously been dominant. Brook trout also interact asymmetrically with bull trout, reducing their feeding and growth as well as forcing them into colder, headwater streams (McMahon et al. 2007).

Brook trout display common habitat use trends that vary over multiple temporal scales, and across age classes. Generally, they prefer locations with reduced water velocity, maximum available depth, and physical cover (Johnson 2008; Ecret and Mihuc 2013; Mollenhauer et al. 2013). However, on a diel scale, brook trout have been observed using areas with significantly less cover at night than during the day, and deeper, slower habitat is typically occupied by older age classes (Johnson et al. 2011). Habitat use may also vary on a seasonal scale. For example, Mollenhauer et al. (2013) observed the selection for deep pools during early fall (September), selection for shallow pools in late fall (October and November) by larger brook trout during spawning, and a shift back to selection for deep pools in winter. And during the summer, when ambient water temperature is higher than preferred, brook trout use tributary confluences, groundwater seeps, and deep pools to thermoregulate (Baird and Krueger 2003; Petty et al. 2012). Thermoregulation during the summer helps brook trout maintain body temperatures cooler than ambient water temperature, reducing temperature-driven metabolic expenses.

Similar to habitat use, brook trout foraging trends vary over multiple temporal scales. Allan (1981) detailed both diel and seasonal trends in prey consumption and selection. During the summer, diel peaks in prey consumption were observed during crepuscular periods, corresponding with peaks in invertebrate drift. Peaks in prey consumption were much less defined during the fall, and brook trout displayed a seasonal decrease in the amount of prey items

consumed, which correlated with the seasonal decrease in invertebrate drift density. In general, prey taxa were selected relative to their abundance in the drift, and a positive relationship existed between a prey taxon's dry weight and selection for that taxon. Subsequent diet studies on brook trout have supported Allan (1981). For instance, Forrester et al. (1994) reported considerable variation in brook trout prey consumption over a diel cycle, with the majority of foraging occurring during the evening and early morning. Brook trout also selected for larger prey items. The seasonal decrease in prey consumption observed by Allan (1981) also was reported by Utz and Hartman (2006) who documented a decrease in the number of prey items consumed by brook trout from spring to winter.

The diet of brook trout during thermally-stressful, summer months is influenced by prey availability, temperature, and population density. Ensign (1990) listed availability of food sources as a factor potentially limiting prey consumption during the summer, which could help explain the consistent observation of decreased prey consumption throughout summer that was discussed previously in this chapter. However, Sotiropoulos et al. (2006) used diet analysis combined with microhabitat data to suggest that brook trout adopt a low-risk, low-reward energy strategy with respect to prey consumption during summer, when prey availability becomes low. Their data suggests that brook trout use locations where prey is not abundant if these locations allow them to reduce energy expenditure driven by warm water temperatures. But, population density also factors into the summer foraging strategy of brook trout. Based on an inverse relationship between trout density and mean prey consumption during the summer, Utz and Hartman (2006) suggested larger reaches, with low trout density, are important areas for feeding. This concept was expanded by Petty et al. (2014) who proposed the temperature-productivity squeeze as a theory describing the constraints placed on brook trout during summer. The

temperature-productivity squeeze can be described as a continuum between productive main stem habitats where appropriate thermal habitat is limiting, and non-productive small tributaries where thermal habitat is abundant. Brook trout able to compete for appropriate thermal habitat in the main stem of the river profit from high food availability, increasing their production. Conversely, in tributary streams, where thermal habitat is more readily available, food availability is low. The habitat continuum results in high densities of trout in cool, less-productive tributaries where consumption is low, and low densities of trout in the warm, productive main stem where consumption is high.

Lastly, terrestrial prey items contribute heavily to the diet of brook trout during summer. Utz and Hartman (2007) collected gut content samples over 2 years and estimated that terrestrial energy contributions to brook trout diets were higher than aquatic contributions between April and September. Terrestrial invertebrates contributed as much as four times the amount of energy as aquatic invertebrates in May and June, and terrestrial energy inputs remained twice as high as aquatic inputs from July to September. These authors also used a bioenergetics model to show that trout feeding above maintenance rations during the summer fed on significantly higher proportions of terrestrial Coleopterans and Lepidopterans than trout feeding below maintenance rations. Similarly, Sweka and Hartman (2008) modeled energy inputs and documented brook trout receiving >50% of their annual energy from terrestrial sources. The model showed that if terrestrial invertebrates were removed from their diet, brook trout would have to increase consumption of aquatic invertebrates by approximately 130% to maintain the same growth. Both of these studies were conducted in West Virginia watersheds, but high inputs of terrestrial invertebrates to brook diets have been observed elsewhere. Terrestrial invertebrates contributed >50% of the biomass in brook trout diets in 8 of 12 streams sampled in New Hampshire during

July and August (Wilson et al. 2014). And, in Colorado the proportion of terrestrial invertebrates in brook trout diets ranked second among 25 prey taxa during sample dates in August and September (Allan 1981). Wilson et al. (2014) suggested two reasons for increased consumption of terrestrial invertebrates during the summer: the availability of aquatic prey decreases, and terrestrial invertebrates are probably conspicuous when entering the stream from above.

### *Bioenergetics Models*

Bioenergetics is defined as the way in which animals dispose of the energy they acquire (Ney 1993). That said, a bioenergetics model can be thought of as an energy budget relating energy gained with energy spent using mathematical equations, and Winberg (1956, cited by Ney 1993) was one of the first to produce a budget for fish. In its simplest form, the equation representing the energy budget of a fish can be written as

$$Consumption = Respiration + Waste Losses + Growth. \quad (1)$$

However, the respiration term can be broken into subcomponents including standard metabolism ( $R_S$ ), activity ( $R_A$ ), and digestion of food ( $R_D$ ) while the waste losses term includes egestion ( $F$ ), and excretion ( $U$ ). Including these terms in the original equation with consumption ( $C$ ) and growth ( $G$ ), yields a slightly more detailed energy budget equation

$$C = R_S + R_A + R_D + F + U + G. \quad (2)$$

Kitchell et al. (1974, 1977) expanded on the early bioenergetics model, producing a version referred to as the Wisconsin Model, which allows investigators to estimate consumption as a proportion of a temperature and size driven maximum. This model served as the template for bioenergetics software packages produced by Hewett and Johnson (1987, 1992, cited by Ney 1993), as well as a more recent version of the software package titled Fish Bioenergetics 3.0

(Hanson et al. 1997). The nuts and bolts of the energy budget used in Fish Bioenergetics 3.0 remains relatively unchanged from equation 2 and can be written

$$C = (R+A+S) + (F+U) + (\Delta B+G). \quad (3)$$

Here, consumption ( $C$ ) is equal to the sum of respiration ( $R$ ), active metabolism ( $A$ ), and specific dynamic action ( $S$ ), plus the sum of egestion ( $F$ ) and excretion ( $U$ ), plus the sum of somatic growth ( $\Delta B$ ) and gonad production ( $G$ ). Consumption and respiration of fish species are both temperature and size dependent, while waste losses can be thought of as either a constant proportion of consumption, or temperature, size, and ration dependent (Hanson et al. 1997). The major advantage of Fish Bioenergetics 3.0 is that it allows investigators the possibility to choose from specific equations produced in the primary literature (Elliot 1976; Kitchell et al. 1977; Thornton and Lessem 1978; Stewart et al. 1983) to represent the major model terms (consumption, respiration, and waste losses). Consumption can be represented in the model by one of three equations including an exponential equation (Stewart et al. 1983); a temperature dependent equation for warmwater species (Kitchell et al. 1977), or a temperature dependent equation for cool and coldwater species (Thornton and Lessem 1978). Similarly, investigators can choose to represent respiration with an exponential equation that accounts for swimming speed (Stewart et al. 1983), or a temperature dependent equation that includes an activity multiplier (Kitchell et al. 1977). The waste losses term can be represented by an equation that is proportionate to consumption (Kitchell et al. 1977); an equation that is dependent on mass, temperature, and ration size (Elliot 1976), or an equation that accounts for mass, temperature, ration size, and the amount of indigestible prey in the diet (Stewart et al. 1983). Fish Bioenergetics 3.0 provides investigators with 33 bioenergetics models representing 26 species. Bioenergetics models have become popular in fisheries literature, and are commonly used to

estimate food consumption or growth of a fish over a given timeframe based on a combination of biotic and abiotic variables (Chipps and Wahl 2008; Hartman and Kitchell 2008). The compilation of over 100 species-specific models from recent publications, and the development of a modeling application in Program R (R Core Team 2016) by Deslauriers and Chipps (2016) has the potential to further increase the use of bioenergetics models in fisheries literature.

Bioenergetics models, however, do have their critiques. Chipps and Wahl (2008) summarized comparisons of growth and food consumption estimates derived from bioenergetics models with experimentally derived estimates of growth and food consumption. Based on 17 studies, they reported that the percent disagreement between bioenergetics and experimental estimates for these two model outputs ranged from -110 to 770% in laboratory and field studies. They also concluded that uncertainty can vary considerably both among and within species, and that model error increases when trying to account for variation across seasons and at different consumption rates. The authors summarize three potential sources of error in bioenergetics estimates: consumption-dependent error, physiological adaptations and additional abiotic effects, and the influence of prey dynamics.

Consumption-dependent error was coined by Bajer et al. (2004) and refers to error in model estimates attributed to variation in ration-size. Consumption-dependent error results in the overestimation of consumption for fish feeding at low rations, and the underestimation of consumption for fish feeding at high rations. This error also occurs when predicting growth rate. Growth rate is underestimated for fish growing quickly, and overestimated for fish growing slowly. Several explanations for this error have been proposed. Madenjian and O'Connor (1999) suggested that underestimation of consumption for lake trout (*Salvelinus namaycush*) fed ad-libitum was due to increases in standard metabolic rate, when ad-libitum feeding occurs, that are

not accounted for in the model. Similarly, Chipps and Wahl (2004) described metabolic compensation; a decrease in the standard metabolism of western mosquitofish (*Gambusia affinis*) feeding at low levels, that they postulated caused the overestimation of prey consumption by the bioenergetics model. This error is a result of modeling consumption dependent parameters, such as egestion, excretion and specific dynamic action, as constant proportions of energy consumed (see the Kitchell et al. (1977) equation for waste losses in Hanson et al. (1997)). Instead, the parameters listed above should be modeled as functions of ration-size, but only 8 of the 33 models available in Fish Bioenergetics 3.0 appropriately do so (Chipps and Wahl 2008). These models use equations from Elliot (1976) or Stewart et al. (1983) to represent waste losses as functions of ration-size, rather than as a constant proportion of the energy that a fish consumes.

Chipps and Wahl (2008) discuss several cases where localized physiological adaptations, as well as physiological variation associated with variables other than temperature and size, influence the accuracy of bioenergetics model estimates. For example, two separate groups of white sturgeon (*Acipenser transmontanus*) in the Upper Columbia River, British Columbia displayed differential mass-specific metabolic rates, temperature-dependent feeding rates, and seasonal growth patterns that resulted in different age at maturity between the two groups (van Poorten and McAdam 2010). Because the thermal regime of the two sites was similar, the authors attributed these differences to variation in prey availability between locations occupied by the two groups. Munch and Conover (2002) calculated bioenergetics parameters for Atlantic silverside (*Menidia menidia*) from localized populations in Nova Scotia, Canada and South Carolina, United States. These authors reported that the dissimilarity between all bioenergetics parameters was at least 10% and that, on average, parameters differed by approximately 28%. As was the case in van Poorten and McAdam (2010), the mass-dependent parameter of consumption

differed substantially (167%) between the two groups of silverside, yielding faster growth rates at higher latitudes. Again, localized differences in physiological response were attributed to food availability; however, Munch and Conover (2002) could not rule out that temperature also played a role in the differences they observed. Additionally, Bioenergetics models may fail to account for all abiotic variables that influence fish physiology by only taking into consideration temperature and size. Cech et al. (1985) observed a significant increase in the respiration rate of mosquitofish at 25°C when dissolved oxygen levels were increased from 150 torr  $P_{O_2}$  to 300 torr  $P_{O_2}$ . Sweka and Hartman (2001) showed that turbidity had a significant effect on the activity level of brook trout held in flow-through chambers. Brook trout experienced increased activity levels while searching for food at high turbidity, significantly decreasing their specific growth rate. As a result, bioenergetics model predictions of the fishes' final weight, based on how much food they consumed, were consistently higher than observed values. These examples illustrate the influence that localized physiological adaptations and abiotic variable other than water temperature and fish size can have on the accuracy of bioenergetics model estimates.

Lastly, Chipps and Wahl (2008) review the impact that prey dynamics can have a predator's physiology, potentially contributing to model inaccuracy. For instance, Selch and Chipps (2007) used lactate dehydrogenase to quantify the foraging activity levels of largemouth bass (*Micropterus salmoides*) fed four different sizes of bluegill (*Lepomis macrochirus*) (35, 50, 65, and 80 mm, TL). Capture efficiency of largemouth bass decreased when fed 80-mm bluegill, and lactate dehydrogenase levels indicated that foraging activity levels increased in this group as well. The authors subsequently compared observed growth of the largemouth bass to growth predicted by a bioenergetics model, based on observed prey consumption. For largemouth bass fed 65 and 80-mm bluegill, the bioenergetics model consistently underestimated consumption.



To account for increased activity in the model, Selch and Chipps (2007) increased the activity rate multiplier for respiration from 1 to 2 and 2.5 for largemouth bass fed 65 and 80-mm bluegill, respectively. In this case the larger bluegill presented an energetic disadvantage to largemouth bass due to increased activity associated with capturing the larger prey. However, Kaufmann et al. (2006) used a similar technique to quantify activity levels of walleye (*Sander vitreus*) in two lakes with and without cisco (*Coregonus artedii*), finding the opposite effect. Walleye eating diets of smaller prey had higher activity levels. It is likely that prey morphology, behavior, and abundance all contribute to variation in predator activity levels (Chipps and Wahl 2008).

Interestingly, short-term temporal variation in activity level is difficult to account for using bioenergetics models. The activity rate multiplier is a constant in the respiration equation of bioenergetics models. Evidence summarized by Chipps and Wahl (2008), and presented above, suggests that quantifying a species activity levels over a broad range of prey densities may increase the accuracy of bioenergetics model estimates.

The first bioenergetics model parameterized specifically for brook trout was produced by Hartman and Sweka (2003). Using laboratory studies, these investigators determined which of the equations commonly used in the Fish Bioenergetics 3.0 program accurately represented consumption and respiration for brook trout. Egestion and excretion parameters were assumed to be similar to those of brown trout, and the Elliot (1976) equation for waste losses was used in the model. Specific consumption rate of brook trout decreased with increasing size. The maximum amount a brook trout could consume increased rapidly with temperature until approximately 21°C before sharply decreasing. Consumption data were best described by the temperature dependent equation for coldwater species (Thornton and Lessem 1987). Specific metabolic rate of brook trout also decreased with increasing size; however, specific metabolic rate peaked at

12.6°C, unexpectedly decreased at 16.5°C, and reached another peak at 21°C. Ultimately, the temperature-dependent equation including an activity term (Kitchell et al. 1977) provided the best fit for brook trout respiration. In addition to calculating specific parameters for consumption and respiration, Hartman and Sweka (2003) attempted to validate their estimates using laboratory experiments. The bioenergetics model using their parameters underestimated final weight of brook trout by 1.0%, growth rate by 1.4%, and consumption by 19.7% on average. Lastly, based on their model they determined that low growth was possible between 4 and 20°C, but that growth is highest between 10 and 19°C in the field. However, due to the unexpected decrease in specific metabolic rate at 16.5°C noted by Hartman and Sweka (2003), Hartman and Cox (2008) re-evaluated brook trout metabolism over a range of temperatures. Their goal was to improve the metabolic parameters of the model by estimating a new activity rate multiplier for the respiration equation (Kitchell et al. 1977), which they hypothesized yielded the low consumption estimates noted by Hartman and Sweka (2003). Hartman and Cox (2008) replicated metabolic studies on brook trout in the laboratory and found a consistent increase in specific metabolic rate until it peaked at approximately 21°C, rather than the depression at 16.5°C that was observed by Hartman and Sweka (2003). They subsequently changed the activity rate multiplier from 1 to 2.89 and developed new estimates for the rest of the parameters in the respiration equation of the model. The new parameter estimates improved model accuracy to predict final weight, growth, and consumption all within 2.3%.

### *Discussion*

Future management of brook trout populations will include solving a number of problems related to their general ecology, for which bioenergetics models may help provide answers. Because they thrive in pristine, cold streams, the distribution and abundance of brook trout is

influenced by anthropogenic disturbance to the landscape throughout much of their range in the United States. In addition, asymmetric interactions with other salmonid species can influence brook trout populations. The most up to date fish bioenergetics modeling technology could be employed to evaluate system-specific problems in streams where conserving brook trout is a priority, as well as those where brook trout threaten native species. However, users of bioenergetics models should be aware of the shortcomings associated with this method. Bioenergetics estimates tend to poorly agree with experimentally derived estimates when used to predict growth and consumption over long periods, particularly when ration levels are variable. The sources of error can be numerous, making it imperative that users be conscientious of the specific equations used to represent consumption, respiration and waste losses in the model. The bioenergetics model produced by Hartman and Cox (2008) models waste losses as a function of ration size (Elliot 1976), ideally cutting down on the likelihood of consumption-dependent error. In addition, the activity rate multiplier of the model has been experimentally tested and altered to minimize disagreement between model estimates and observations. However, this does not eliminate the chance that local physiological adaptations, changes in activity levels, and additional variables could contribute to model inaccuracy if applied inappropriately. If included in the study by Chipps and Wahl (2008), then the <2.3% disagreement between model estimates and observed values reported by Hartman and Cox (2008) would be the second most accurate model behind only the lake trout (*Salvelinus namaycush*) model (Madenjian et al. 2000). Thus, relative to many species, bioenergetics modeling techniques to aid brook trout management strategies can be fruitful when used and interpreted properly.

## Extended Methods

### *Field Procedures*

To quantify prey availability in the form of drifting invertebrates, drift samples were collected on all sample dates, except September 1. I collected hourly drift samples for four hours before I began the electrofishing process using three drift nets, each 440 mm wide and 280 mm tall. The three drift nets were placed in a riffle section of the stream adjacent to one another so that the middle net was centered about the thalweg. The drift nets were held in place using metal rods driven into the streambed with a hammer. Directly in front of each net, I recorded the water depth using a meter stick and water velocity using an OTT MF Pro – Water Flow Meter (OTT Hydromet, Loveland, Colorado). The water depth and velocity were used to calculate the discharge passing through each net

Drift nets were placed in the stream exactly 1 hour before the first collection time. For example, on June 19 the drift nets were placed in the stream at 03:00:00 so that they had collected drift for one hour when I collected the samples at 04:00:00. The dolphin bucket consisted of a piece of PVC tubing fashioned onto the rear of the net, and was removable from the net without removing the entire net from the stream. Individually, the collection tray from each net was emptied into a 250- $\mu$ m sieve and stream water was used to rinse excess sediment and organic matter from the sample. After the sample had been sieved, it was transferred to a 250-ml wide-mouth sample bottle (Thermo Fisher Scientific Inc., Rochester, New York) that was filled with 70% ethanol. Each sample bottle was marked with the date, site, and net number then stored for laboratory processing. This process yielded 12 drift samples on each sample date, one sample for each drift net (3) at each collection interval (4). I always approached the drift

nets from the rear during collection to ensure the benthos remained undisturbed upstream of the collection nets.

In addition to drift samples, I sampled the benthic community using a 0.086 m<sup>2</sup> Hess sampler. Three Hess samples were taken on each sample date, except September 1. The Hess samples were collected from a separate riffle section than the drift samples. The Hess sampler was placed in the streambed with the dolphin bucket trailing downstream, and the benthos inside the sampler was thoroughly disturbed to dislodge invertebrates into the trailing container. After the benthos had been disturbed, without removing the Hess sampler from the streambed, any invertebrates that had become fixed on the trailing net were rinsed into the dolphin bucket using stream water. The bucket was then emptied into a 250- $\mu$ m sieve and stream water was used to filter fine sediment out of the sample. The sample was transferred to a 250-ml wide-mouth sample bottle, filled with 70% ethanol, marked with the date, site and sample number, and then stored for laboratory processing.

Brook trout for this project were captured with two APB-3 backpack electrofishing units (ETS Electrofishing Systems, LLC, Madison, Wisconsin) using direct current. Each electrofisher had a net to capture fish stunned in the electrical field and an additional person carrying a net was always in position to capture fish that could not be netted by those electrofishing. Upon capture, brook trout were placed into a cooler filled with stream water until electrofishing was completed. During periods of extended electrofishing, the water in the cooler was regularly replaced with fresh stream water, or electrofishing was stopped and brook trout were returned to a dark, in-stream cage.

Once electrofishing was completed, data collection was performed at a streamside station using a foldup table. Trout were transferred from the in-stream cage to a cooler containing

approximately 25 L of water and 3.5 mL of AQUI-S 20E aquatic anaesthetic (AQUI-S New Zealand Ltd, Lower Hutt, New Zealand). This concentration falls within the range recommended for fish handling (75-150 ml/1000 l of water). Trout in the anaesthetic solution were monitored closely and removed for handling when they were unable to maintain equilibrium. No trout remained in the anaesthetic solution for more than five minutes. Trout were immediately measured to the nearest millimeter using a Wildco measuring board, model #118-E40 (Wildco®, Yulee, Florida), then weighed to the nearest  $\pm 0.01$  gram using an Adventurer Pro AV812 scale (Ohaus Corporation, Pin Brook, New Jersey). After length-weight data was recorded, the trout was placed into a wooden holding trough coated with moist surgical gauze and gastric lavage was performed to expel stomach contents. Approximately 20 cm of polyethylene tubing with an 8-mm outer-diameter were connected to a 60-cc syringe filled with stream water used to flush the stomach contents of the trout into an aluminum pan. Water was forced into the gut of the trout until prey were no long being expelled or, for trout that appeared to contain no prey items, the 60-cc syringe was emptied at least three times into the gut of the trout. The stomach contents and water that accumulated in the aluminum pan were rinsed through a funnel into a specimen cup with two holes cut out of the sides that had been covered with 250- $\mu$ m mesh. Using a wash bottle filled with 70% ethanol, the stomach contents were rinsed out of the specimen cup and into a 250-ml, wide-mouth sample bottle. Each sample bottle was marked with the trout's individual number, date, and site, then stored for laboratory processing.

During all sample dates between June 19 and July 23, trout were marked with an individual elastomer tag (Northwest Marine Technology, Inc., Shaw Island, Washington) for identification during subsequent sample events. The elastomer tagging procedure was performed immediately after gastric lavage, and at this point, I filled the wooden trough with fresh stream

water until the head and gills of the trout were submerged to start the recovery process. The elastomer pigment is a mixture of colored die and curing agent in a 10:1 ratio. Prior to data collection on each sample date, the plunger was removed from a 0.3-cc injection syringe and 0.1 mL of the curing agent was injected into the syringe followed by 1 mL of the colored die. The materials were mixed using a toothpick for approximately 1 minute, the toothpick was removed, the plunger replaced, and the syringe was stored on ice until it was needed in the field. This process follows the recommended procedure provided by Northwest Marine Technology, Inc., for mixing small quantities of elastomer solution. Each trout was given an individual, two-digit number based on the color and location of their elastomer tag. The first digit represented the color and number of marks applied. I used two colors, red and yellow. The second digit represented the location of the tag. I tagged trout at the base of one of six fins: the left or right pectoral, left or right pelvic, anal, or caudal fins. The system for determining a trout's individual number based on its tag is outlined in Table 3.2.

Table 3.1. The two-digit tagging system used to individually mark trout with elastomer pigment.

| First digit                        | Second digit           |
|------------------------------------|------------------------|
| 1 = One red mark                   | 1 = Left pectoral fin  |
| 2 = One yellow mark                | 2 = Left pelvic fin    |
| 3 = Two red marks                  | 3 = Anal fin           |
| 4 = Two yellow marks               | 4 = Caudal fin         |
| 5 = One red mark + one yellow mark | 5 = Right pectoral fin |
| 6 = Three red marks                | 6 = Right pelvic fin   |

For example, a trout given a single yellow mark at the base of its left pelvic fin would be #22 in this system. To apply the elastomer tag, the 0.3-cc syringe containing the pigment was inserted into the tagging location at an angle approximately parallel to the surface of the skin so that the tip of the needle was only slightly below the skin's surface. A small mark of pigment was

injected underneath the skin, the needle was removed and a dry piece of gauze was used to dab the area dry.

In addition, a subset of 10 brook trout in the study had temperature-sensitive radio-transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota) sutured into their peritoneal cavity as part of a concurrent study to examine behavioral thermal regulation. Because data from the 10 radio-tagged trout is included in this study, I detail the surgical procedure here. For these 10 trout, the process of data collection and gastric lavage followed that specified above. However, after gastric lavage was completed, a tagging method similar to the one outlined by Ross and Kliner (1982) was used to implant radio-transmitters. An incision, approximately 2 cm long, was made in front of the pelvic girdle using a surgical scalpel. A small piece of tubing was inserted through the incision, past the pelvic girdle, and held firmly against the peritoneal wall. A 17 gauge needle (Hamilton Company, Reno, Nevada) was then inserted through the peritoneal wall, passed through the tubing and out the incision in front of the pelvic girdle. The tag's antenna was fed through the needle and out the pin-hole posterior to the pelvic girdle. The tag was placed inside the peritoneal cavity and the original incision was sewn using 6-0 synthetic absorbable suture (Ethicon, Inc., Somerville, New Jersey). All surgical equipment was kept in a solution of water and Chlorhexidine Gluconate Antiseptic Disinfectant (Aurora Pharmaceuticals, LLC, Northfield, Minnesota) throughout the surgery procedure to prevent contamination. A wash bottle filled with fresh stream water was used to keep the head and gills of trout moist during the data collection and tagging procedure. Between data collection, gastric lavage, and tagging, trout never remained fully out of the water for more than 5 minutes. When the tagging process was completed, trout were returned to the in-stream cage for recovery and monitored closely by one of the investigators until they were able to maintain self-equilibrium. For trout that had



undergone the surgical procedure, a 60-cc syringe was used to force aerated water over their gills. Additional recovery time was provided in the in-stream while I collected data on the remaining trout. On average, I estimate that after trout were handled they were allowed approximately 20-30 minutes to recover in the in-stream cage before being released into the stream. If I observed that a trout was unable to maintain self-equilibrium, I used the 60-cc syringe to force aerated water over its gills until it was able to maintain equilibrium on its own.

### *Laboratory Procedures*

Drift and benthic samples were processed in the laboratory using a Nikon SMZ645 dissecting scope (Nikon Instruments Inc., Melville, New York). First, the invertebrates, organic matter, and sediment were removed from their 250-ml bottle. All invertebrates were separated from the sample and placed into a 60-ml wide-mouth sample bottle in 70% ethanol for preservation. Each 60-ml sample bottle was labeled exactly the same as the 250-ml sample bottle that the invertebrates were separated from. Once the invertebrates from all samples had been sorted and excess material had been disposed of, most invertebrates were keyed to the family level; however, several of the more prevalent taxa were identified to genus. Invertebrates were identified using dichotomous keys in Burch (1962), Borror et al. (1989), Peckarsky (1990), and Merritt et al. (2008).

For brook trout diet samples, there was no need to separate any excess material from the samples. Diet samples were emptied out of their 250-ml bottles, invertebrates were identified to the lowest possible taxonomic level, and samples were subsequently transferred to 60-ml sample bottles with 70% ethanol for further storage. Because of the digestion process, invertebrates in the diet samples were often only identified to family, and sometimes could only be identified to order.

After invertebrates in the diet samples were identified, I needed to quantify the mass of each prey taxon consumed on all sample dates. To do so, the head-capsule width (HC) and total length (TL) of the invertebrates in each diet sample were measured to the nearest 0.01  $\mu\text{m}$  using a Nikon SMZ1500 microscope with a digital site attached to NIS-Elements 3.0 software, then converted to mm. For many invertebrate taxa, published TL vs. dry mass (DM) or HC vs. DM equations already exist (Smock 1980; Sage 1982; Sample et al. 1993; Benke et al. 1999; Sabo et al. 2002). However, for several taxa that were present in brook trout diets, there were no published equations available. For these taxa, I used invertebrates that had been collected in my drift samples, or invertebrates collected in drift samples from nearby streams, to develop my own TL vs. DM and HC vs. DM relationships. First, I measured the TL and HC, to the nearest 0.01  $\mu\text{m}$ , of invertebrates from each taxon that was not quantified in the literature and converted those values to mm. Then, a small piece of aluminum foil, approximately 4  $\text{cm}^2$ , was weighed to the nearest  $\pm 0.001$  mg using a Mettler Toledo microbalance model xs3 DU (Mettler Toledo, LLC, Columbus, Ohio) and folded into the shape of a tray. Each individual invertebrate was then placed in its own small, aluminum tray and dried for at least 24 hours at 50°C in a Heratherm OMH750 drying oven (Thermo Fisher Scientific Inc, Rochester, New York). After drying, the invertebrates were removed from the oven and each invertebrate, with the aluminum foil, was weighed to the nearest  $\pm 0.001$  mg and converted to g. The weight of the aluminum foil by itself was then subtracted from the weight of the invertebrate and the aluminum foil to determine the DM of the invertebrate.

I used the power function  $\text{DM} = \alpha L^\beta$  to relate TL (mm) to DM (g) and HC (mm) to DM. I performed a natural logarithm transformation on the DM, TL, and HC data for each taxon, and used linear regression to develop a model estimating the relationship between TL and DM, as

well as the relationship between HC and DM. This procedure closely follows the methods of other studies that have developed length-mass relationships of macroinvertebrates (Smock 1980; Sample et al. 1993; Benke et al. 1999; Sabo et al. 2002). Linear regression was performed in Program R version 3.1.3 (R Core Team 2016). The equations for the linear models can be written:

$$\ln(DM) = \ln(\alpha) + \beta \cdot \ln(TL)$$

$$\ln(DM) = \ln(\alpha) + \beta \cdot \ln(HC)$$

The linear model provides estimates of  $\ln(\alpha)$  and  $\beta$ . Thus, by measuring the TL, or HC, of an invertebrate its DM can be estimated using the equation. The specific taxa, and model estimates are listed in Table 3.2 and Table 3.3. I have included the estimates for each taxon that yielded a linear model with a statistically significant P-value, whether that model was used to quantify invertebrate mass in this study or not. The linear model developed for the relationship between HC and DM of Lepidoptera larvae was not statistically significant, but was used to quantify the mass of 1 invertebrate in this study, so it is included in the table.

Table 3.2. Estimates of the relationship between total length (TL, mm) and dry mass (DM, g) for invertebrate taxa based on linear regression models. Relationships are estimated using the equation  $\ln(DM) = \ln(\alpha) + \beta \cdot \ln(TL)$ . I report the sample size of each taxon used in the linear regression (n), estimates of  $\ln(\alpha)$  and  $\beta$  with the standard error of each term (SE), the test statistics of the linear regression model (P,  $R^2_{adj}$ ), and the number of times the equation was used in my analyses (N)

| Taxon              | n  | $\ln(\alpha)$ (SE) | $\beta$ (SE) | P     | $R^2_{adj}$ | N |
|--------------------|----|--------------------|--------------|-------|-------------|---|
| Araena             | 8  | -10.74 (0.27)      | 2.69 (0.21)  | <0.05 | 0.96        | 0 |
| Coleopteran adults | 15 | -10.39 (0.53)      | 2.43 (0.34)  | <0.05 | 0.78        | 0 |
| Dipteran adults    | 31 | -10.33 (0.35)      | 1.53 (0.26)  | <0.05 | 0.54        | 0 |

Table 3.2. Continued

| Taxon               | n  | $\ln(\alpha)$ (SE) | $\beta$ (SE) | P     | $R^2_{adj}$ | N |
|---------------------|----|--------------------|--------------|-------|-------------|---|
| Homoptera           | 11 | -11.45 (0.73)      | 2.82 (0.51)  | <0.05 | 0.75        | 0 |
| Hymenopteran adults | 10 | -11.90 (0.54)      | 2.85 (0.50)  | <0.05 | 0.78        | 0 |
| Hymenopteran larvae | 6  | -16.10 (1.27)      | 3.62 (0.59)  | 0.004 | 0.88        | 0 |
| Trichopteran adults | 44 | -12.59 (0.26)      | 3.13 (0.15)  | <0.05 | 0.91        | 0 |

Table 3.3. Estimates of the relationship between (HC, mm) and (DM, g) for invertebrate taxa based on linear regression models. Relationships are estimated using the equation  $\ln(DM) = \ln(\alpha) + \beta \cdot \ln(HC)$ . Symbols in this table represent the same values as those in Table 3.2.

| Taxon               | n  | $\ln(\alpha)$ (SE) | $\beta$ (SE) | P     | $R^2_{adj}$ | N  |
|---------------------|----|--------------------|--------------|-------|-------------|----|
| Araena              | 8  | -7.76 (0.18)       | 3.60 (0.42)  | <0.05 | 0.91        | 1  |
| Coleopteran adults  | 15 | -6.43 (0.23)       | 2.56 (0.45)  | <0.05 | 0.69        | 4  |
| Dipteran adults     | 31 | -7.38 (0.31)       | 1.94 (0.63)  | 0.005 | 0.22        | 4  |
| Homoptera           | 11 | -7.61 (0.11)       | 1.97 (0.20)  | <0.05 | 0.90        | 7  |
| Hymenopteran adults | 10 | -8.05 (0.24)       | 2.26(0.38)   | <0.05 | 0.80        | 1  |
| Hymenopteran larvae | 6  | -8.07 (0.15)       | 4.42 (0.34)  | <0.05 | 0.97        | 0  |
| Lepidopteran larvae | 4  | -7.83 (0.48)       | 1.75 (1.04)  | 0.234 | 0.39        | 1  |
| Trichopteran adults | 44 | -7.48 (0.06)       | 3.91 (0.26)  | <0.05 | 0.84        | 76 |

Several taxa present in the diet of trout were not found in drift samples, so I directly dried, and weighed each individual invertebrate of these taxa to estimate DM. Similar to the procedure listed above, a small piece of aluminum foil was weighed and the invertebrate was placed on the aluminum foil and dried for at least 24 hours at 50°C. The foil, and the invertebrate were then weighed together, and the mass of the aluminum foil was subtracted from the mass of the foil and the invertebrate to determine DM.

## References

- Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:184-192.
- Argent, D. G., and P. A. Flebbe. 1999. Fine sediment effects on brook trout eggs in laboratory streams. *Fisheries Research* 39:253-262.
- Baird, O. E., and Krueger, C. C. 2003. Behavioral Thermoregulation of Brook and Rainbow Trout: Comparison of Summer Habitat Use in an Adirondack River, New York. *Transactions of the American Fisheries Society* 132:1194-1206.
- Bajer, P. G., G. W. Whitley, and R. S. Hayward. 2004. Widespread consumption-dependent systematic error in fish bioenergetics model and its implications. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2158-2167.
- Baldigo, B. P., and G. B. Lawrence. 2000. Composition of fish communities in relation to stream acidification and habitat in the Neversink River, New York. *Transactions of the American Fisheries Society* 129:60-76.
- Becker, G. C. 1983. *Fishes of Wisconsin*. The University of Wisconsin Press, Madison, Wisconsin.
- Benke, A. C, A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of North American Benthological Society* 18: 308:343.
- Benjamin, J. R., and C. V. Baxter. 2010. Do nonnative salmonines exhibit greater density and production than the natives they replace? A comparison of nonnative brook trout with native cutthroat trout. *Transactions of the American Fisheries Society* 139:641-651.

- Blanchfield, P. J., and M. S. Ridgway. 1996. Use of seepage meters to measure groundwater flow at brook trout redds. *Transactions of the American Fisheries Society* 125:813-815.
- Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects, 6<sup>th</sup> edition. Saunders College Publishers, Ft. Worth, TX.
- Burch, J. B. 1962. How to know the eastern land snails. William C. Brown Co., Dubuque, I
- Carline, R. F., C. J. Sharpe, and W. E. Sharpe. 1994. Brook trout (*Salvelinus fontinalis*) population dynamics and mottled sculpin (*Cottus bairdi*) occurrence in relation to acidic episodes in streams. *Ecology of Freshwater Fish* 3:107-115.
- Castonguay M., G. J. FitzGerald, and Yvon Cote. 1982. Life history and movement of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Quebec. *Canadian Journal of Zoology* 60:3084-3091.
- Cech, J. J., M. J. Massingill, B. Vondracek, and A. L. Linden. 1985. Respiratory metabolism of mosquitofish, *Gambusia affinis*: effects of temperature, dissolved oxygen, and sex differences. *Canadian Journal of Fisheries and Aquatic Sciences* 13:296-307.
- Chipps, S. R., and D. H. Wahl. 2004. Development and evaluation of a Western Mosquitofish bioenergetics model. *Transactions of the American Fisheries Society* 133:1150-1162.
- Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21<sup>st</sup> century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society* 137:298-313.
- Daye, P. G., and E. T. Garside. 1975. Lethal levels of pH for brook trout, *Salvelinus fontinalis* (Mitchill). *Canadian Journal of Zoology* 53:639-641.
- Deslauriers, D., and S. R. Chipps. 2016. Fish bioenergetics 4.0 workshop. 76<sup>th</sup> Midwest Fish and Wildlife Conference, January 24<sup>th</sup> 2016, Grand Rapids, Michigan.

- Ecret, J., and T. B. Mihuc. 2013. Brook trout (*Salvelinus fontinalis*) habitat use and dispersal patterns in New York Adirondack Mountain headwater streams. *Northeastern Naturalist* 20:19-36.
- Elliot, J. M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). *Journal of Animal Ecology* 45:561-580.
- Ensign, W. E. 1990. Summer food limitation reduces brook and rainbow trout biomass in a Southern Appalachian stream. *Transactions of the American Fisheries Society* 119:849-901.
- Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for position in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Science* 38, 1220-1227.
- Flebbe, P. A., L. A. Roghair, and J. L. Bruggink. 2006. Spatial modelling to project southern Appalachian trout distribution in a warmer climate, *Transactions of the American Fisheries Society* 135:1371-1382.
- Forrester, G. E., J. G. Chace, and W. McCarthy. 1994. Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environmental Biology of Fishes* 39:301-311.
- Fry, F. E. J., J. S. Hart, and K. F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. *Publication of the Ontario Fisheries Research Laboratory* 54:9-35.
- Hanson, P. C., T. B. Johnson, D. E., Schindler, and J. F. Kitchell. 1997. *Fish Bioenergetics 3.0*. University of Wisconsin, Sea Grant Institute, WISCU-T-97-001, Madison.
- Hartman, K. J., and M. K., Cox 2008. Refinement and testing of a brook trout bioenergetics model. *Transactions of the American Fisheries Society* 137:357-363.

- Hartman, K. J., J. F. Kitchell. 2008. Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society* 137:216-223.
- Hartman, K. J., and J. A. Sweka. 2003. Development of a bioenergetics model for Appalachian brook trout. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 55(2001):38-51.
- Hewett, S. J., and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-87-245, Madison.
- Hewett, S. J., and B. L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-92\_250, Madison.
- Huckins, C. J., E. A. Baker, K. D. Fausch, and J. B. K. Leonard. 2008. Ecology and life history of coaster brook trout and potential bottlenecks in their rehabilitation. *North American Journal of Fisheries Management* 28:1321-1342.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *North American Journal of Fisheries Management* 28:1069-1085.
- Isley, J. J., and C. Kempton. 2000. Influence of costocking on growth of young-of-year brook trout and rainbow trout. *Transactions of the American Fisheries Society* 129:613-617.
- Johnson, J. H. 2008. Seasonal habitat use of brook trout and juvenile atlantic salmon in a tributary of Lake Ontario. *Northeastern Naturalist* 15:363-374.
- Johnson, J. H., R. M. Ross, D. S. Dropkin, and L. A. Redell. 2011. Ontogenetic and diel variation in stream habitat use by brook trout (*Salvelinus fontinalis*) in a headwater stream. *Journal of Freshwater Ecology* 26:143-152.



- Kanno, Y., B. H. Letcher, A. L. Rosner, and K. P. O'Neil, and K. H. Nislow. 2015. Environmental factors affecting brook trout occurrence in headwater stream segments. *Transactions of the American Fisheries Society* 144:373-382.
- Kaufman, S. D., J. M. Gunn, G. E. Morgan, and P. Couture. 2006. Muscle enzymes reveal walleye (*Sander vitreus*) are less active when larger prey (cisco, *Coregonus artedii*) are present. *Canadian Journal of Fisheries and Aquatic Sciences* 63:970-979.
- Kitchell, J. F., J. F. Koonce, R. V. O'Neill, H. H. Shugart, J. J. Magnuson, and R. S. Booth. 1974. Model of Fish biomass dynamics. *Transactions of the American Fisheries Society* 103:786-798.
- Kitchell, J. F., Sweart, D. J., and Weininger, D. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34:1922-1935.
- Korsu, K., A. Huusko, and T. Muotka. 2007. Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. *Proceedings of the National Academy of Sciences of the United States of America* 104:9725-9729.
- MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 26:1699-1725.
- Madenjian, C. P., and D. V. O'Connor. 1999. Laboratory evaluation of lake trout bioenergetics model. *Transactions of the American Fisheries Society* 128:802-814.
- Madenjian, C. P., D. V. O'Connor, and D. A. Nortrup. 2000. A new approach toward evaluation of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1025-1032.

- McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. S. Foott, S. L. Johnson, K. R. Marine, M. G. Mesa, J. H. Peterson, Y. Souchon, K. F. Tiffin, and W. A. Wurtsbaugh. 2009. Research in thermal biology: burning question for coldwater stream fishes. *Reviews in Fisheries Science* 17:90-115.
- McGrath, C. C., and W. M. Lewis. 2007. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. *Transactions of the American Fisheries Society* 136:1381-1392.
- McKenna, J. E., and J. H. Johnson. 2011. Landscape models of brook trout abundance and distribution in lotic habitat with field validation. *North American Journal of Fisheries Management* 31:742-756.
- McMahon, T. E., A. V. Zale, F. T. Barrows, J. H. Selong, and R. J. Danehy. 2007. Temperature and competition between bull trout and brook trout: a test of the elevation refuge hypothesis. *Transactions of the American Fisheries Society* 136:1313-1326.
- Merritt, R.W., K.W. Cummins, and M. B. Berg. 2008. *An introduction to the aquatic insects of North America*. Kendall and Hunt, Dubuque, IA.
- Mollenhauer, R., T. Wagner, M. V. Kepler, and J. A. Sweka. 2013. Fall and early winter movement and habitat use of wild brook trout. *Transactions of the American Fisheries society* 142:1167-1178.
- Munch, S. B., and D. O. Conover. 2002. Accounting for local physiological adaptations in bioenergetic models: testing hypotheses for growth rate evolution by virtual transplant experiments. *Canadian journal of Fisheries and Aquatic Sciences* 59:393-403.
- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* 122:736-748.

- Peckarsky, B.L., P.R. Fraissinet, M.A. Penton, and D.J. Conklin. 1990. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithica, NY.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: Effects of brook trout on native cutthroat trout. *Ecological Applications* 14:754-772.
- Petty, J. T., J. L. Hansberger, B. M. Huntsman, and P. M. Mazik, 2012. Brook trout movement in response to temperature, flow, and thermal refugia in a complex Appalachian riverscape. *Transactions of the American Fisheries Society* 141:1060-1073.
- Petty, J. T., D. Thorne, B. M. Huntsman, and P. M. Mazik. 2014. The temperature-productivity squeeze: constraints on brook trout growth along an Appalachian river continuum. *Hydrobiologia* 727:151-166.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Charrs, Salmonid fishes of the genus *Salvelinus* 1:141-203.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ross, M. J., and C.F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio frequency transmitters in fish. *The Progressive Fish-Culturist* 44: 41-43.
- Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of North American Benthological Society* 21:336-343.
- Sage, R. D. 1982. Dry-weight estimates of insects and spiders based on length. *The American Midland Naturalist* 108:407-411.
- Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129: 234-240.

- Selch, T. M., and S. R. Chipps. 2007. The cost of capturing prey: measuring largemouth bass (*Micropterus salmoides*) foraging activity using glycolytic enzymes (lactate dehydrogenase). *Canadian Journal of Fisheries and Aquatic Sciences* 64:1761-1769.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10: 375-383.
- Sotiropoulos, J. C., K. H. Nislow, and M. R. Ross. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. *Journal of Fisheries Management and Ecology* 13:149-155.
- Strange, R. J. and J. W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. *Transactions of the American Fisheries Society* 127:434-440.
- Stranko, S. A., R. H. Hildebrand, R. P. Morgan II, M. W. Staley, A. J. Becker, A. Rosebery-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook trout declines with land cover and temperature changes in Maryland. *North American Journal of Fisheries Management* 28:1223-1232.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681-698.
- Sweka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 58:386-393.

- Sweka, J. A., and K. J. Hartman. 2008. Contributions of terrestrial invertebrates to yearly brook trout prey consumption and growth. *Transactions of the American Fisheries Society* 137:224-235.
- Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107:284-287.
- Utz, R. M., and K. J. Hartman. 2006. Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. *Canadian Journal of Fisheries and Aquatic Science* 63:2675-2686.
- Utz, R. M., and K. J. Hartman. 2007. Identification of Critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms. *Hydrobiologia* 575:259-270.
- van Poorten, B. T., and S. O. McAdam. 2010. Estimating differences in growth and metabolism in two spatially segregated groups of Columbia River white sturgeon using a field-based bioenergetics model. *The Open Fish Science Journal* 3:132-141.
- Wagner, T., J. T. Deweber, J. Detar, and J. A. Sweka. 2013. Landscape-scale evaluation of asymmetric interactions between brown trout and brook trout using two-species occupancy models. *Transactions of the American Fisheries Society* 142:353-361.
- Wherly, K. E., L. Wang, and M. Mitro. 2007. Field-based estimates of thermal tolerance limits for trout: incorporating exposure time and temperature fluctuation. *Transactions of the American Fisheries Society* 136:365-374.
- White, H. C. 1940. Life history of sea-running brook trout (*Salvelinus fontinalis*) of Moser River, NS. *Journal of the Fisheries Board of Canada* 5:176-186.

- Whitworth, W. E., and R. J. Strange. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. *Transactions of the American Fisheries Society* 112:469-475.
- Wiley, M. J., D. W. Hyndman, B. C. Pijanowski, A. D. Kendall, C. Riseng, E. S. Rutherford, S. T. Cheng, M. L. Carlson, J. A. Tyler, R. J. Stevenson, P. J. Steen, P. L. Richards, P. W. Seelbach, J. M. Koches, and R. R. Rediske. 2010. A multi-modeling approach to evaluating climate and land use change impacts in a Great Lakes River Basin. *Hydrobiologia* 657:243-262.
- Wilson, M. K., W. H. Lowe, and K. H. Nislow. 2014. What predicts the use by brook trout (*Salvelinus fontinalis*) of terrestrial invertebrate subsidies in headwater streams? *Freshwater Biology* 59:187-199.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian University, Minsk. Translated from Russian, 1960: Fisheries Research Board of Canada Translation Series 194, Ottawa.
- Witzel, L. D., and H. R. MacCrimmon. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. *Transactions of the American Fisheries Society* 112:760-771.