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Brook Trout Behavioral Thermoregulation and Habitat Selection in a Small Michigan Coldwater Stream: Implications for Successful Management

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Dedication

In memory of my Grandpa, Robert E. Wegner, who instilled my passion for fishing and fascination with the outdoors…

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Abstract

Global warming and conversion of forests for urbanization, agriculture and mineral extraction are increasing water temperatures throughout Brook Trout's range causing population declines; particularly in populations persisting in marginal habitats and in the southern limits of their distribution. The Brook Trout is an ectotherm that can cope with elevated water temperature by moving to coldwater refuge such as groundwater seeps, coldwater tributary confluences, and headwaters. Availability of coldwater refuge is vital for the survival of Brook Trout populations threatened by increasing water temperatures. I used radio telemetry to study the movement, habitat use, and behavioral thermoregulation of Brook Trout living in Cedar Creek, a stream in southwest Michigan impacted by the deleterious effects of agriculture and urbanization on stream temperature. I evaluated Brook Trout thermoregulatory effectiveness during the summer when ambient water temperatures often exceed the ideal range for Brook Trout. My results helped direct management efforts aimed at restoring Brook Trout habitat in Cedar Creek. Overall, Brook Trout body temperatures conformed closely to ambient water temperatures. Brook Trout in a forested section maintained body temperatures within the ideal range for growth for most of the summer and occupied habitats characterized by large woody debris and overhanging vegetation. In a section routinely clear-cut and bordered by agriculture, Brook Trout body temperatures were often above proximate ambient water temperatures, and Brook Trout occupied deep microhabitats with little cover. Several Brook Trout emigrated from the clear-cut section into a forested section; however, most Brook Trout were largely sedentary. My results illustrate the importance of a forested riparian corridor in providing

woody cover and thermal refuge in a marginal trout stream. Management efforts to restore Brook Trout habitat should prioritize evaluating target systems to identify limiting factors that provide important ecological benefits to threatened populations.

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Abbreviations

d_b : Deviation of body temperature from set point.

d_e : Deviation of operative temperature from set point.

E : Effectiveness of thermoregulation.

k : Thermal inertia.

LWD: Large woody debris.

PC : Principal components.

PCA: Principal components analysis.

T_b : Body temperature.

T_e : Operative temperature.

TL : Total length.

T_{set} : Set point.

Chapter 1

INTRODUCTION

The Brook Trout *Salvelinus fontinalis* is a fish in the family Salmonidae native to the waters of eastern Canada, the Appalachian Mountains, and parts of the Great Lakes Region (MacCrimmon and Campbell 1969). Best known for their popularity among anglers, Brook Trout is intolerant of environmental degradation and is considered an indicator of high-quality coldwater streams (Lyons et al. 1996). Today, Brook Trout distribution is limited primarily by water temperature; widespread introductions of Brook Trout have been largely successful, especially in regions where water temperature is similar to their native range (MacCrimmon and Campbell 1969; Fausch 2008).

Most populations of Brook Trout are stream dwelling; however, lacustrine and anadromous populations also exist (MacCrimmon and Campbell 1969). In their native range, Brook Trout thrive in coldwater streams within forested watersheds (Hudy et al. 2008) with stable water temperatures (Wehrly et al. 2003) that remain between 0 and 20°C annually (Power 1980). Similar to many stream-dwelling salmonids, adult Brook Trout generally select microhabitats that offer greater depth (Magoulick and Wilzbach 1997), reduced water velocity (Ecret and Mihuc 2013), and overhead cover (Power 1980). Due to their sensitivity to water temperature, Brook Trout often congregate where groundwater seepages (Power 1980; Biro 1998; Baird and Krueger 2003) or coldwater tributaries (Petty et al. 2012) offer refuge from elevated water temperature.

In parts of their introduced range, Brook Trout displace native Bull Trout *Salvelinus confluentus* along thermal gradients by outcompeting the more temperature-sensitive Bull Trout at warmer water temperatures (Rieman et al. 2006; McMahon et al. 2007; Rodka and

Volpe 2007). Conversely, in much of their native range, the Brook Trout is dominated and displaced by Brown Trout *Salmo trutta*, a widely-introduced species not native to North America that is more tolerant than Brook Trout of warm water temperature and large fluctuations in water temperature (Fausch and White 1981; Wehrly et al. 2003; McKenna et al. 2013). Competition with Brown Trout and habitat loss from anthropogenic alterations to the landscape threaten Brook Trout populations in parts of their native range (Waters 1983; Hudy et al. 2008). As a result, many management efforts aim to improve or protect stream habitat for threatened and struggling populations of Brook Trout.

Brook Trout are native in Michigan's Upper Peninsula and naturalized populations now exist in most of the Lower Peninsula (MacCrimmon and Campbell 1969). Most of the Michigan streams that now sustain Brook Trout populations also contain Brown Trout. Many Lower Michigan streams have warm headwaters that transition to coldwater systems downstream (Zorn et al. 2002) and do not exemplify the classic pattern of rivers with cold, high-gradient headwaters that transition to slow, warm water systems downstream (Vannote et al. 1980). There is high regional variability in thermal regimes among Michigan streams largely due to the influence of a stream's underlying geology and surrounding landscape (Zorn et al. 2002; Wehrly et al. 2003). Rising global temperatures and local trends of increasing residential development, surface water withdrawals, and commercial groundwater use (for fracking, agriculture, etc.) are further elevating ambient summer water temperatures by increasing runoff, decreasing summer stream flows, and altering groundwater recharge rates (AWRI 2000; Paul and Meyer 2001; Weltman-Fahs and Taylor 2013; Nuhfer et al. 2017). Groundwater input, influx of water from coldwater tributaries, and stream shading from riparian vegetation are essential for maintaining cool, stable summer water temperatures that are necessary for trout survival and growth, and in providing coldwater refugia from naturally high ambient summer water temperatures (Cross et al. 2013: Kanno et al. 2014).

Ideal water temperatures for Brook Trout are generally reported to be between 10 and 16°C (MacCrimmon and Campbell 1969; McCormick et al. 1972; Hokanson et al. 1973; Power 1980; Xu et al. 2010). A study of Michigan streams and their fish communities found that Brook Trout densities are highest in streams with summer water temperatures of 18°C or lower, and weekly summer water temperature fluctuations less than 5°C (Wehrly et al. 2003). Water temperature influences Brook Trout movement patterns, habitat preference, and feeding behavior (Magoulick and Wilzbach 1998; Baird and Krueger 2003; Petty et al. 2012); water temperatures above their ideal range reduce survival, increase metabolism, and decrease growth rates (Fry et al. 1946; McCormick et al. 1972; Tang and Boisclair 1995; Drake and Taylor 1996). Brook Trout seek refuge from high water temperatures by moving to coldwater refugia including deep pools, coldwater tributary confluences (Baird and Krueger 2003; Petty et al. 2012), groundwater seepages (Biro 1998), and headwaters (Hayes et al. 1998). One study reported a marked increase in Brook Trout movement at water temperatures above 18°C associated with dispersal to coldwater refugia (Petty et al. 2012). Brook Trout in an Adirondack Mountain river kept their body temperatures an average of 2.3°C, and as much as 17°C, colder than the ambient water temperature by moving to coldwater refugia during periods of high ambient water temperature (Baird and Krueger 2003). These findings clearly illustrate that water temperature can affect Brook Trout behavior and habitat preference. However, few studies have directly examined whether Brook Trout movements to coldwater refugia in a stream, when ambient water temperature exceeds their preferred range, translate into efficient maintenance of body temperature within a biologically relevant range (e.g., the range for growth).

PURPOSE

I studied the movement and habitat use of Brook Trout in a small coldwater stream (mean July temperature <19°C, Wehrly et al. 2003) in southwest Michigan to guide management efforts that aim to improve stream habitat specifically to protect a population of Brook Trout. My objectives were to evaluate the streams thermal suitability for Brook Trout growth and survival in the summer, evaluate the thermoregulatory efficiency of Brook Trout in the context of available thermal habitat, and characterize the physical components of habitat selected by Brook Trout.

SCOPE

Many studies have examined the movement patterns and habitat preferences of Brown Trout in Michigan (Clapp et al. 1990; Regal 1992; Diana et al. 2004); however, comparatively less is known about Brook Trout movement, habitat preference, and thermoregulatory behavior in Michigan's Lower Peninsula streams where stream temperatures may be marginal for Brook Trout. This study explores Brook Trout response to elevated ambient water temperatures in a common Michigan stream type; a low gradient stream impacted by urbanization, agriculture, and an altered riparian corridor. Anthropogenic alterations that disconnect streams from their riparian zones are a growing threat for Brook Trout populations throughout their native range (Weltman-Fahs and Taylor 2013; DeWeber and Wagner 2015). These impacts often exacerbate thermal threats for Brook Trout that persist in marginal streams where summer water temperatures approach the limits of their thermal tolerance (Cross et al. 2013; Nuhfer et al. 2017). This study contributes to scientists understanding of Brook Trout behavior in small, marginalized streams, particularly those impacted by urbanization and agriculture.

Results of this study lend insight into the behavioral responses and habitat preferences of Brook Trout in lower Michigan and similar low gradient Midwest streams but are also applicable to native populations of Brook Trout persisting in the southern extent of their distribution where increasing global temperatures and anthropogenic land use changes are reducing suitable Brook Trout habitat. These results also contribute to the understanding of introduced, naturalized populations of Brook Trout persisting in marginalized habitats outside of their native range.

I demonstrate an approach to the analysis of body temperature data (Hertz et al. 1993) from telemetered fish that has, to my knowledge, not been used in the freshwater fisheries field. This method of evaluating thermoregulatory behavior in the context of available thermal habitat and biologically important temperature ranges provides a meaningful framework for understanding efficiency of thermoregulation. This type of analysis could be used to answer questions of thermoregulatory efficiency of many fish species and may prove particularly useful for understanding the importance of coldwater refugia for supporting coldwater species in marginalized streams. In the future, identifying and protecting coldwater microhabitats may be vital for sustaining native populations threatened by habitat loss resulting from global warming and anthropogenic land alterations.

ASSUMPTIONS

I assume that the Brook Trout tracked in this study are representative of the population of Brook Trout in Cedar Creek. Radio telemetry requires transmitters to be surgically implanted inside of fish and for fish to carry the transmitters over the course of the study. Research shows Brook Trout recover quickly from anesthesia and surgery (Moore et al. 1990) and that Brook Trout survival and swimming performance is not significantly altered by transmitters less than 2% of their body weight (Smircich and Kelly 2014). I assumed that my surgical procedures minimized handling stress and did not significantly influence fish behavior, and radio transmitters and their trailing antennas did not hinder fish movement or influence their behavior over the course of the study.

For my data collection and analysis of body temperature data, I assumed that the thermal inertia of Brook Trout tagged in this study was negligible. Under this assumption I used temperatures recorded by radio transmitters as water temperature at fish focal points, and I assumed that temperature loggers provided a sufficient physical model of Brook Trout body temperature for my purposes.

HYPOTHESIS

I anticipated that ambient water temperature in Cedar Creek would exceed the ideal range for Brook Trout growth in summer, and I hypothesized that as water temperatures increased, Brook Trout would seek refuge from warm ambient water temperatures by moving to zones of coldwater discharge. Consequently, I predicted that cool water temperature would be a key component of home site selection during the summer months and that availability of thermal refugia would translate into efficient maintenance of body temperatures within a range ideal for growth.

SIGNIFICANCE

This study demonstrates that a more complete understanding of trout behavior under stream specific ecological conditions can provide meaningful direction for management efforts aimed at protecting, restoring, and improving available habitat for specific species persisting in marginal habitats. I illustrate how analysis of fish body temperature and available stream water temperature can be used to provide managers with a complete picture of fish behavior and habitat selection and assist in identifying habitat features that are important or limited in a system. My analysis contributes to the understanding of Brook Trout behavior in Lower Michigan streams and will be used to direct habitat improvement and restoration efforts for Brook Trout in Cedar Creek. I advocate for a holistic approach to management that accounts for watershed characteristics, species interactions, and biological requirements that influence fish behavior, habitat selection, and survival. The methods I employ can be used in other systems to explore the influence of water temperature on fish behavior and habitat selection, and may help to identify limiting features important for the protection of threatened fish populations in other regions.

DEFINITIONS

The following are an explanation of terms, variables, and equations used in Chapter 2:

Effectiveness of thermoregulation (*E*)

A measure of an animal's efficiency of thermoregulation given the body temperature of an animal, and the suite of temperatures available in the animal's habitat. This measure was adapted from Hertz et al. (1993). To calculate *E,* an animal's body temperature is monitored with temperature sensitive radio transmitters over a period of time. Physical models that approximate the study species thermal inertia (*k*, the instantaneous rate of change in body temperature) are placed throughout the animal's habitat to record temperatures available at the time animals are tracked. To calculate *E*, the following variables are collected or derived over the course of the study:

Body temperature (T_b)

The internal body temperature of an animal given by the temperature sensitive radio transmitter surgically implanted in its body cavity.

Operative temperature (T_e)

The thermal habitat available to an organism within its habitat measured by a physical model of the animal.

Set point range (T_{set})

An animal's preferred range of temperatures, typically determined a priori in a controlled lab setting or obtained from the literature.

Deviation of body temperature (d_b)

The deviation in an animal's body temperature from T_{set} such that for T_b greater than the upper bounds of the set point range (T_{set}):

$$d_b = T_b – T_{set}\ max$$

For T_b within the set point range (T_{set}):

$$d_b = 0$$

and for T_b less than the lower bounds of the set point range (T_{set}):

$$d_b = T_b - T_{set}\ min$$

Deviation of operative temperature (d_e)

The deviation in operative temperature measured by physical models of the study animal from T_{set} such that for T_e greater than T_{set}:

$$d_e = T_e - T_{set}\ max$$

For T_e within T_{set}:

$$d_e = 0$$

and for T_e less than T_{set}:

$$d_e = T_e - T_{set}\ min$$

Using these variables, effectiveness of thermoregulation can be calculated with the equation:

$$E = 1 - (\bar{d}_b / \bar{d}_e),$$

where $\bar{d}_b$ is the mean deviation of body temperature recorded for an individual or population and $\bar{d}_e$ is the mean deviation of operative temperatures recorded by physical models in the animal's habitat during the study. Therefore, values of E that are close to 1 indicate active thermoregulations towards the animals set point range, E values close to 0 indicate thermal conformity, and negative E values may indicate an active avoidance of temperatures within the animals set point range. If $\bar{d}_e$ is zero the thermal environment is within the set point range and E is undefined.

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Chapter 2

Brook Trout Behavioral Thermoregulation and Habitat Selection in a Small Michigan Coldwater Stream: Implications for Successful Management

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ABSTRACT

The Brook Trout *Salvelinus fontinalis* is particularly sensitive to elevated water temperature and is reported to behaviorally thermoregulate during periods of thermal stress. As global temperatures increase, access to thermal refugia during the summer will be vital for Brook Trout to effectively regulate their body temperature towards the ideal range for growth or survival to persist in threatened and marginal systems. I evaluated Brook Trout thermoregulatory efficiency and habitat use during the summer in a Michigan stream when ambient water temperatures often exceeded the range for positive individual growth. I demonstrate a simple approach to analyzing body temperature data from telemetered fish to evaluate effectiveness of thermoregulation in the context of available thermal habitat. Overall, Brook Trout body temperature conformed closely to the ambient water temperature. Brook Trout in a stream segment with an intact riparian zone effectively regulated body temperatures towards the range for growth for most of the summer. However, Brook Trout in a degraded clear-cut section did not occupy thermally optimal habitat despite its availability and may have prioritized habitat that offered cover. Brook Trout in both sections selected habitat with greater depth and cooler water temperature than random points. Brook Trout home sites in the degraded section had greater maximum depths then home sites in the forested section which had greater percent overstory density and large woody debris surface area. My results illustrate the importance of evaluating the specific ecological requirements limiting a trout population when approaching restoration efforts with pointed goals of restoring or improving habitat to protect specific species.

INTRODUCTION

The Brook Trout *Salvelinus fontinalis* is native to the waters of eastern Canada, the Appalachian Mountains, and parts of the Great Lakes Region (MacCrimmon and Campbell 1969). And, although the Brook Trout is an environmentally sensitive species (Lyons et al. 1996), it has been introduced in 49 countries (Fausch 2008), largely due to their popularity as a sport fish. Today, in North America, naturalized populations of Brook Trout are established throughout the Rocky Mountains, and Michigan's Lower Peninsula (MacCrimmon and Campbell 1969; Fausch 2008).

Brook Trout distribution is primarily constrained by water temperatures that fall within their tolerance range between 0°C and 20°C (MacCrimmon and Campbell 1969; McCormick et al. 1972; Hokanson et al. 1973; Power 1980; Xu et al. 2010). Brook Trout distribution is also influenced by current and emerging ecological issues. For example, in many parts of their native range, Brook Trout is threatened by competition with introduced species (Waters 1983). The Brown Trout *Salmo trutta* is introduced throughout Brook Trout's native range and outgrow (Carlson et al. 2007) and outcompete Brook Trout for resources (Fausch and White 1981; DeWald and Wilzbach 1992; Hitt et al. 2017). The Brown Trout is also more tolerant of warm water (Wehrly et al. 2003) and degraded watersheds (McKenna et al. 2013) than Brook Trout. In addition, Brook Trout populations are threatened by habitat loss caused by global warming (Ries and Perry 1995), water withdrawals (Weltman-Fahs and Taylor 2013), and conversion of forested riparian zones for urbanization and agriculture (Nislow and Lowe 2003; Hudy et al. 2008; Stranko et al. 2008; Deweber and Wagner 2015). These anthropogenic factors result in warmer stream conditions that reach or exceed thermal tolerance of Brook Trout throughout much of their range, particularly at the southern extremes of their distribution.

When ambient water temperature exceeds their preferred range, Brook Trout seek relief by moving to coldwater refugia including deep pools, discharge from coldwater tributaries (Baird and Krueger 2003; Petty et al. 2012), groundwater seepages (Biro 1998), and headwaters (Hayes et al. 1998). Studies report distinct increases in Brook Trout movement, typically upstream toward higher-gradient coldwater refugia (Petty et al. 2012), and Brook Trout attempting to maintain body temperatures cooler than ambient water temperatures during periods of thermal stress (Baird and Krueger 2003). However, few studies have directly examined whether Brook Trout movements to coldwater refugia in a stream translate into efficient maintenance of body temperature within a biologically significant range (e.g., the range for growth).

The classic pattern of most rivers in the native range of Brook Trout is cold high gradient headwaters that transition to slow, warm water systems downstream (Vannote et al. 1980). Lower Michigan streams that support Brook Trout, and many low-gradient Midwest streams, do not exemplify the classic pattern of most rivers in the native range of Brook Trout. Lower Michigan streams often have warm headwaters that transition to coldwater systems downstream (Zorn et al. 2002). Water withdrawals (Weltman-Fahs and Taylor 2013), impervious surface runoff (Paul and Meyer 2001), and alterations to streams riparian corridor (Cross et al. 2013) also impact a streams thermal characteristics by altering the availability and distribution of coldwater refugia. Several studies have examined the movement patterns and habitat preferences of Brown Trout in the Midwest (Clapp et al. 1990; Meyers et al. 1992; Regal

1992; Diana et al. 2004); however, comparatively little is known about Brook Trout movement, habitat preference, and thermoregulatory behavior in Michigan's Lower Peninsula streams where stream temperatures may be marginal for Brook Trout.

I studied the movement and habitat use of Brook Trout in a small coldwater stream (mean July temperature <19°C, Wehrly et al. 2003) in southwest Michigan impacted by anthropogenic watershed alterations. My objectives were to evaluate the streams thermal suitability for Brook Trout growth and survival in the summer, evaluate the thermoregulatory efficiency of Brook Trout in the context of available thermal habitat, and characterize the physical components of habitat selected by Brook Trout. I demonstrate how the analysis of trout behavior can provide meaningful direction for restoration efforts that aim to improve stream habitat specifically for the protection of a trout population and stress the importance of a holistic approach to management.

METHODS

Study site.—This study was conducted on Cedar Creek, a low-order coldwater tributary of the Rogue River in southwest Michigan (Figure 2.1). Cedar Creek is a state-designated natural river with a drainage area of 77.5 km^2 that contains self-sustaining populations of Brook Trout and Brown Trout (AWRI 2000). The Trout Unlimited Home Rivers Initiative designates Cedar Creek as a trout stream threatened by urbanization, specifically increased sedimentation, rising summer water temperatures, and reduced groundwater inputs. Cedar Creek is now the focus of restoration efforts to improve and protect Brook Trout habitat in the Rogue River watershed.

I divided my study reach into two sections, hereafter referred to as the upstream and downstream sections (Appendix A). I designated sections based on a distinct shift in condition of the riparian zone and bordering land use. Each section was approximately 3 km in length and had a mean stream width of 6 m. In the upstream section, Cedar Creek meanders through a powerline easement that is regularly clear-cut and mowed to the ground, leaving little riparian vegetation along the stream bank. What vegetation does persist is primarily grass, and small patches of young deciduous forest where the stream meanders away from the powerlines. Additionally, much of the upstream section of the study area is bordered closely by agricultural land use and at least one agricultural operation diverts and withdraws water from Cedar Creek for irrigation immediately above the upstream study reach. In contrast, aside from a small livestock operation and several road crossings, the downstream section flows through an intact riparian corridor that is largely forested. The dense canopy shades nearly the entire downstream stream channel, and overhanging vegetation and deadfall provide woody cover. Additionally, there are at least two small coldwater tributaries that discharge to the downstream section.

Stream temperature.—Nine temperature loggers (HOBO TidbiT v2 and Pendant models, Onset Computer Corporation, Bourne, Massachusetts), hereafter referred to as loggers, evenly spaced throughout the entire study reach (n = 4 upstream, n = 5 downstream) continuously monitored hourly stream temperature from June 17 through October 2, 2015. I anchored loggers in the bottom half of the water column so that they would remain submerged for the entire summer.

Fish tracking.—I used radio telemetry to monitor the movement and body temperature of 12 Brook Trout implanted with temperature sensitive radio transmitters (Model #F1555, Advanced Telemetry Systems, Isanti, Minnesota). In early June 2015, I captured five Brook Trout in the upstream and downstream sections (total = 10 Brook Trout) using backpack electrofishing units

(Model ABP-3, ETS Electrofishing Systems LLC). Collection sites were approximately 3 km apart, and were chosen for ease of access necessary to perform surgeries. I targeted Brook Trout large enough to carry a transmitter (TL >185 mm) until I captured five individuals. To ensure tag retention, and prevent impacts on survival and swimming performance, transmitters did not exceed 2% of Brook Trout body weight (Smircich and Kelly 2014). I anesthetized Brook Trout prior to surgery with AQUI-S 20E (25 mg/L) (AQUI-S New Zealand LTD, Lower Hutt, New Zealand). Once Brook Trout were sedated, I surgically implanted transmitters using a modified shielded needle technique where an incision is made in the abdominal wall, and the transmitter's antenna is threaded through a hollow needle, under the pelvic girdle, and out a pinhole behind the pelvic fins (Ross and Kleiner 1982). Incisions were sutured and sealed with a topical glue. Following surgery, Brook Trout were revived from anesthesia in a flow-through recovery enclosure until normal motor function resumed at which point they were released at their location of capture. Over the course of the study, there was one mortality from an apparent attack by a small mammal, and one mortality from angling. Transmitters recovered from mortalities were sterilized and implanted into new Brook Trout captured in the upstream reach (Fish ID U10 and U11 in Table 2.1).

I tracked fish approximately three times a week during daylight hours from June 16 through October 2, 2015 using a three-element yagi antenna and a R410 receiver (Advanced Telemetry Systems, Isanti, Minnesota). To determine fish body temperature, I used an R4500 receiver (Advanced Telemetry Systems, Isanti, Minnesota), which calculates temperature based on transmitter pulse rate and a regression equation provided by the manufacturer that is unique to the transmitter. I tracked fish in a rotating order to ensure that each fish was located at different times of the day over the course of the study. To account for sporadic behavior following surgery, locations recorded during the 2 weeks following surgeries were excluded from data analysis (Pickering et al. 1982).

Once a fish was located, its position was monitored at maximum signal strength for at least 1 min. Fluctuations in signal strength indicated activity, and positions were only recorded when fish were inactive (Young 1999; Teixeira and Cortes 2011). I attempted to visually confirm fish locations each time fish were located. I recorded the number of successive times fish were located in the same location; if I tracked a fish to the same location four times in succession without visual confirmation, then I disturbed the fish to ensure it was still alive. If a fish was located in a new position, I measured the distance moved from the last known location using a tape measure for distances < 100 m and ArcGis version 10.0 (ESRI, Redlands, California) for distances > 100 m. I assigned positive values for upstream movements and negative values for downstream movements.

To compare the physical characteristics of fish focal points (Fausch and White 1981) to the available stream habitat, I measured physical characteristics of the stream at focal points and at a paired random point near the fish's location. I located paired random points by randomly selecting a direction (upstream or downstream) to place a transect perpendicular to the direction of flow of five evenly spaced points, one mean stream width from the fish's focal point. A randomly selected number between one and five dictated where the random point was located along the transect. I took measurements at fish focal points and random points in a random order to avoid autocorrelation. At each fish focal point and random point, I recorded the time, closest logger, and GPS coordinates in UTM (GeoExplorer 2005 series, Trimble

Navigation Inc., Sunnyvale California). I also measured depth, and water velocity at 60% column depth (hereafter, mid-column) and 2 cm from stream bottom (FH950, Hach Company, Loveland Colorado). I used the temperature given by the fishes radio transmitter for the fish focal point water temperature. At the random points, I measured water temperature at mid-column and 2 cm from the stream bottom using a digital thermometer (HH503, Omega Engineering Inc., Norwalk, Connecticut).

Habitat quantification.—In addition to measurements taken at fish focal points each tracking event, I quantified the physical characteristics of Brook Trout home sites. Similar to previous telemetry studies of trout in Michigan, I defined home sites as locations or specific structures an individual fish was tracked to five or more times (Clapp et al. 1990; Diana et al. 2004). I quantified home sites late in the summer when the river was near base flow and air temperatures had been near historic averages for three consecutive days. At the center, upstream, downstream, left and right edges of each home site structure, I measured the depth; dominant substrate; overhead cover (using a spherical densitometer); surface, mid-column, and bottom water velocity; and the interstitial (streambed surface) and mid-column water temperature. I used the average of these five point measurements for data analysis. Additionally, I measured the length, width, maximum depth, large woody debris (LWD) count, LWD surface area, and vegetation overhang at each home site. LWD is defined here as any piece of wood with a diameter $\geq$ 10 cm.

Data analysis.—To evaluate the thermal quality of Cedar Creek for Brook Trout, and the effectiveness of Brook Trout thermoregulation in Cedar Creek, I used a method commonly used in studies of thermoregulation by reptiles described in detail in Hertz et al. (1993). In this method, body temperatures are recorded from telemetered animals and compared to available thermal habitat throughout the study site. This approach provides a biologically meaningful framework to evaluate differences between Brook Trout body temperature and ambient water temperature.

Effectiveness of thermoregulation (E) is quantified by measuring departures of Brook Trout body temperature (T_b) from their preferred range of temperatures, termed set point range (T_{set}), in the context of the thermal habitat available to Brook Trout, hereafter called the operative temperature (T_e). Set point range is determined in a laboratory setting where animals are provided a gradient of temperatures and their final preferenda, or physiological performance at given temperatures, is recorded (Hertz et al. 1993). E is defined as $1 - (\bar{d}_b / \bar{d}_e)$, where $\bar{d}_b$ and $\bar{d}_e$ are the mean deviations of body temperature and operative temperature, respectively, from T_{set} such that d is the difference between T and the upper limit of T_{set} for temperatures (T_b or T_e) above T_{set}, d is zero for temperatures within T_{set}, and d is the difference between T and the lower limit of T_{set} for temperatures below T_{set} (Hertz et al. 1993). Therefore, an E near one indicates effective thermoregulation, an E of zero indicates thermal conformity, a negative E may indicate an active avoidance of optimal thermal habitat, and where E is undefined ($d_e = 0$) the available thermal habitat is ideal (Hertz et al. 1993).

Typically, in studies using this method, physical models are constructed that approximate the study organisms size, shape, color, and thermal inertia to measure the distribution of body temperatures an animal not actively regulating its body temperature could achieve in the study area (Bakken 1992; Hertz et al. 1993). In my study, operative temperatures were taken from the loggers placed throughout my study reach. I compared T_b to T_e measured in locations Brook Trout were likely to occupy, so I placed loggers in locations that emulated Brook Trout habitat based on descriptions reported in the literature and previous experience tracking Brook Trout in Michigan. All logger locations had some sort of in-stream or overhead cover and were sufficiently deep to conceal a large Brook Trout when the river was at base flow.

Pépino et al. (2015a) used a non-linear mixed modeling approach to estimate the instantaneous rate of change in body temperature (*k*, or thermal inertia) of Brook Trout with temperature-sensitive radio transmitters in a series of temperature step change experiments where Brook Trout were exposed to instantaneous changes in water temperature of 4°C, 9°C and 13°C. They found that the *k*-coefficient was best modeled as a function of the absolute difference in water temperature the fish experienced, and their results supported other studies (Stevens and Sutterlin 1976; Fechhelm and Neill 1982) that show the *k*-coefficient is negatively related to fish mass (Pépino et al. 2015a). This means that small Brook Trout have a high *k*-coefficient and body temperatures rapidly equilibrate to changes in ambient water temperature.

The Brook Trout in my study were much smaller than those used by Pépino et al. (2015a) and the absolute difference in water temperature recorded anywhere in my study reach over the duration of my study did not exceed 6°C. Additionally, I observed Brook Trout to have relatively high site fidelity and limited movement in my study system; consequently, it is highly unlikely that Brook Trout in my study experienced rapid fluctuations in temperature of the magnitude that may be common for lacustrine populations of Brook Trout living in thermally stratified lakes studied by Pépino et al. (2015a). Therefore, the time required for

Brook Trout body temperature to equilibrate to changes in ambient water temperature was likely negligible in my study. For these reasons, I assumed that the thermal inertia (*k*-coefficient) of the plastic-encased loggers approximated that of a small Brook Trout and thus provided an accurate physical model of Brook Trout body temperature for quantifying available operative temperatures within my study reach (Bakken 1992; Hertz et al. 1993).

I calculated E, d_b, and d_e using Brook Trout body temperatures for T_b, and temperatures recorded by loggers for T_e. To evaluate Cedar Creek's thermal quality and Brook Trout thermoregulatory effectiveness at a fine scale, the water temperature recorded at the nearest logger was used for T_e. For a section and reach scale comparison, I used the mean of all temperatures recorded by loggers in the section or reach for T_e. For all T_e values, I used the temperature or mean temperature recorded by loggers at the hour closest to the time T_b was recorded. Since Brook Trout final temperature preferenda and the effect of temperature on Brook Trout growth in laboratory and field settings is well documented (Jobling 1981; Wehrly et al. 2003; Xu et al. 2010; Petty et al. 2012; Cross et al. 2013), I used published values to define the set point range for Brook Trout. For this study, T_{set} was 14-16°C, the intersection between the ideal temperature range (13-16°C) for Brook Trout maximum growth (Hokanson et al. 1973) and the optimum suitable temperature range (14-18°C) for Brook Trout in Michigan (Wehrly et al. 2003).

As an additional metric of thermal suitability, I calculated the mean July weekly water temperature and mean July weekly fluctuation in water temperature for the entire study reach, and the upstream and downstream sections (Wehrly et al. 2003). Weekly mean July water temperatures are the average of all hourly temperature recordings from all loggers in the respective reach or section. Mean July weekly fluctuation, is the difference between maximum and minimum mean hourly temperature recorded by all loggers in the reach or section. The mean July water temperature is the average of hourly temperature readings for the three full weeks of July, and the mean July fluctuation is the average of the three July weekly fluctuations.

To assess Brook Trout habitat selection, I used the physical variables recorded at fish focal points and random points in a principal components analysis (PCA) to determine which factors explain the most variation in the data along axes I deemed interpretable by examining scree plots. I also used PCA for data reduction of home site physical variables and to examine patterns of home site selection by Brook Trout in the upstream and downstream sections.

Since water temperatures recorded at home sites were measured on different days and at different times, I standardized water temperature by using the difference between water temperature recorded at the home site and water temperature recorded by loggers on the same day at the hour closest to the time home site water temperatures were measured. For mean interstitial and mean mid-column water temperature at each home site, I calculated the difference in temperature from the logger closest to the home site, the mean hourly temperature of all loggers in the home site's section (upstream or downstream), and the mean hourly temperature of all loggers in the study reach. This produced six standardized measurements of temperature that were used with the 12 other variables measured at each home site in an initial PCA. Overstory density was arcsine square root transformed to reduce skew. Variables with the largest factor loadings in interpretable principal component (PC) axes were retained in successive PCAs to reduce the ratio of variables to descriptors and focus interpretation on variables that explained the most variation in the data.

To determine if Brook Trout select focal points with physical characteristics that are different from random points and if the focal points and random point physical characteristics varied by section, I compared PC scores using *t*-tests and Wilcoxon tests depending on normality. Similarly, depending on normality, I used *t*-tests and Wilcoxon tests to compare the PC scores of home sites to determine if their physical characteristics were different in the upstream and downstream sections. All data analysis was done in Program R version 3.3.2 (R Core Development Team 2017) and PCAs were fit using the vegan package.

RESULTS

The mean July water temperature in Cedar Creek was 16.80°C with a mean weekly July fluctuation in water temperature of 5.69°C. The upstream section was warmer and had larger fluctuations in water temperature than the downstream section, which had cooler and more stable water temperatures (Figure 2.2).

Brook Trout tagged at the upstream site primarily moved downstream (Table 2.1). Individual fish traveled between 0 m and 1,831 m. However, fish that dispersed from the upstream section remained relatively sedentary for the remainder of the study. Fish captured at the downstream site had high site fidelity and little movement.

The average T_e measured in Cedar Creek over the duration of the study (16.59 ± 0.12 °C) was above the ideal range for maximum Brook Trout growth (T_{set}) (Figure 2.3; Table 2.2). A total of 210 observations of T_b and T_e were used for thermoregulation analysis. T_b closely conformed to operative temperatures (Figure 2.3). Fish in the upstream section had an average T_b higher than the average T_e in that section. Both T_b and T_e in the upstream section were outside of T_{set}, resulting in negative *E* values for Brook Trout (Figure 2.3; Table 2.2). In contrast, average T_b in the downstream section was within T_{set}, despite an average T_e above T_{set} (Figure 2.2; Table 2.2). Collectively, Brook Trout in Cedar Creek had $\bar{d}_b$ less than $\bar{d}_e$, indicating some degree of active thermoregulation. However, in the upstream section, $\bar{d}_b$ was greater than $\bar{d}_e$, indicating fish in that section were not actively regulating T_b towards T_{set} (Table 2.2).

The physical characteristics of 185 fish focal points and 147 random points were used for focal point analysis (incomplete measurements caused by equipment failure were excluded). Water temperature, depth, and mid-column velocity were included in the PCA of physical characteristics measured at Brook Trout focal points and random points (Figure 2.4). Overstory density was highly skewed left due to inconsistencies in field measurements at fish locations, so it was excluded from the analysis. The first two axes of the PCA explained 72.3% of the variation in the data. Depth and velocity were positively correlated with the first axis (38.2% of variation), which described a gradient of low depth and slow velocity to greater depth and faster velocity. Warm water temperature was negatively related to the second axis (34.1% of variation). Comparisons of PC scores indicated fish focal points were deeper and had greater water velocity than random points (P = 0.001). Temperature at fish focal points was cooler than water temperature at random points (t = 5.27, df = 329.92, P < 0.001). Upstream fish focal points had greater depth and velocity (P < 0.001) and warmer temperatures (t = -2.19, df = 60.73, P = 0.016) than downstream fish focal points. Random points in the upstream section also had slightly greater depth and velocity than random points in the downstream section (P = 0.020), but water temperature at random points was not significantly different between sections (t = -0.83, df = 47.80, P = 0.413).

The physical characteristics of home sites for 14 Brook Trout were used in the home site PCA. Overstory density, LWD surface area, maximum depth, and temperature difference between mid-column and section average were retained in the final PCA of home site characteristics (Figure 2.5). The first axis explained the majority of variation in the data (50.2%) and reflected a gradient of high percent overstory density to deeper maximum depths. The second axis explained 26.6% of the variation in the data and was positively correlated with LWD surface area. Home sites in the downstream section were characterized by significantly higher percent overstory density and shallower maximum depths than upstream home sites, which had greater maximum depths and lower percentage overstory density (t = 4.80, df = 10.91, P < 0.001). Home sites strongly associated with LWD surface area were located in the downstream section, but overall there was no significant difference between LWD surface area (PC2 scores) at upstream and downstream sites (P = 0.504).

DISCUSSION

Maintaining coldwater fisheries for environmentally sensitive species such as Brook Trout is a growing challenge as ecological conditions that support them are increasingly altered by human activities. Loss of forested land to urbanization and agriculture as well as warming temperatures (Stranko et al. 2008) may cause declines in Brook Trout populations. Elevated water temperatures clearly influence Brook Trout movement and habitat selection, particularly their use of thermal refugia (Baird and Krueger 2003; Petty et al. 2012). In general, Brook Trout in Cedar Creek moved to thermal refuge during the warmer summer period, which may account for the persistence of the population in this degraded system. As global temperatures continue to rise, and forested land is converted for urbanization, agriculture, and mineral extraction, identifying and protecting coldwater refugia and migratory pathways that allow fish passage throughout stream systems will be essential for maintaining Brook Trout populations, particularly those in marginal habitats.

Cedar Creek's ambient summer water temperature during my study was slightly outside of the range suitable for growth. Despite this, some Brook Trout effectively maintained body temperatures within their ideal range for growth. Brook Trout in the forested downstream section regulated body temperatures more efficiently and selected different habitat than Brook Trout in the degraded upstream section. Differences in Brook Trout thermoregulatory efficiency and habitat selection between the two study sections seem to be related to the condition of the surrounding riparian zone that likely influence water temperature and available in-stream and above stream cover. Consequently, I recommend that restoration efforts to improve Brook Trout habitat in Cedar Creek and other Midwest streams impacted by land cover alterations should focus on the protection and restoration of the riparian corridor.

Overall Brook Trout movement rates and total displacement observed in my study was similar to other studies of Brook Trout movement in small tributaries of their native range (Bélanger and Rodríguez 2001; Hartman and Logan 2010; Petty et al. 2012). However, in a distinct departure from typical patterns of upstream summer migration by Brook Trout in search of coldwater refugia in headwaters and tributaries (Biro 1998; Hayes et al. 1998; Baird and Krueger 2003; Petty et al. 2012), Brook Trout in my study primarily moved downstream. The downstream movement pattern was largely driven by Brook Trout initially captured in the upstream section that emigrated to the downstream section (Table 2.1). Although increased movement and erratic behavior by Brook Trout following surgeries has been reported

(Pickering et al. 1982; Bélanger and Rodríguez 2001), only the five Brook Trout initially captured in the upstream section exhibited movement greater than 50 m from their capture location in the 2-week period following surgery; moving downstream into a small stretch of the upstream section that was noticeably deeper than where they were captured (data not shown).Trout initially captured downstream exhibited little movement and had high site fidelity. Brook Trout that remained in the upstream section for the duration of the study resided entirely within pools in this deeper stretch. Brook Trout movement may also be influenced by high flow events (Davis et al. 2015) or optimal foraging theory (Gowan and Fausch 2002). However, I think the downstream movements observed early in the study were a response to the changing thermal conditions or available habitat in the upstream section.

Overhanging vegetation in an intact riparian zone provides trout with cover above the stream and deadfall inputs for in-stream cover. Forested riparian vegetation also offers terrestrial food subsidies to stream communities during the late summer when aquatic forage availability is lower than early spring and winter (Nakano and Murakami 2000; Zaparzynski 2016). Sweka and Hartman (2008) report that reductions in terrestrial prey availability can induce negative Brook Trout growth during the summer, and that total loss of terrestrial food subsidies would require Brook Trout to increase aquatic prey consumption in excess of 100% in order to maintain positive growth. In addition to coldwater tributaries and groundwater inputs, riparian shading plays an important role in maintaining cool stream water temperatures that are within the ideal range for Brook Trout growth and survival. Cross et al. (2013) found that, in the summer, forested stream segments cooled maximum daily water temperature nearly

0.5°C/km; in contrast, water temperature increased more than 1°C/km in segments that were dominated by grass vegetation, similar to the upstream section of Cedar Creek.

Riparian vegetation, and therefore overstory density, in the upstream section of Cedar Creek is dramatically reduced by agricultural land use and routine clear-cutting. As a result, available in-stream habitat in the upstream section is largely homogeneous and devoid of woody cover. Cover in the upstream section is provided primarily by undercut grass banks and pools. Scarcity of in-stream woody cover and lack of cover from overhanging riparian vegetation in the upstream section may leave trout vulnerable to predation; over the course of my study I found multiple trout along the banks of the upstream section that had been killed by avian predators. Depth provides stream fish protection from predation, particularly where the stream channel lacks complexity (Harvey and Stewart 1991; Lonzarich and Quinn 1995; Pépino et al. 2015b).

The PCA of fish focal point and random point variables illustrated Brook Trout focal points in both sections were significantly deeper than random points. However, in contrast to Brook Trout in the downstream section, which had home sites strongly associated with high overstory density or LWD, Brook Trout in the upstream section occupied significantly deeper focal points (Figure 2.4), and their home sites had greater maximum depths (Figure 2.5). An affinity for depth is commonly reported for Brook Trout (Johnson 2008; Curry et al. 2002; Hartman and Logan 2010; Anglin and Grossman 2013; Ecret and Mihuc 2013), however the deep homes sites of Brook Trout in Cedar Creek are not typical of the deep plunge pools of high gradient streams in parts of Brook Trout's native range, or of large pools associated with tributary confluences in larger order streams which offer refuge from elevated ambient water temperatures (Curry et al. 2002; Baird and Krueger 2003; Petty et al. 2012). Like many small Midwest tributary streams, Cedar Creek is relatively shallow and does not have large variations in depth. Home sites in the upstream section with greater depth may have offered cover for Brook Trout where woody structure was limited, but they did not offer refuge from elevated ambient water temperatures (Table 2.2; Figure 2.3).

Inability of Brook Trout to effectively regulate body temperature during periods of thermal stress has direct implications for growth and survival. The effect of elevated summer water temperature on Brook Trout is associated with increased respiration and metabolic demands as well as decreased or negative growth rates (Elliot 1975; Drake and Taylor 1996; Sweka et al. 2004; Xu et al. 2010). Zaparzynski (2016) estimated that a 1°C increase in annual water temperature could reduce Brook Trout body weight up to 14% over the course of the summer. However, sufficient access to coldwater refugia and foraging opportunities may allow trout to moderate their bioenergetic demands and maintain or improve their condition despite warm summer water temperatures (Elliot 1975; Hartman and Sweka 2001; Sweka et al. 2004; Sweka and Hartman 2008; Xu et al. 2010).

Some Brook Trout, particularly those in the forested downstream section, effectively used thermal refugia to maintain body temperatures within T_{set} (Figure 2.3). Brook Trout in the upstream section may have selected home sites with greater depth that offered protection from predation over areas with cooler water. Negative E values observed for fish that remained in the upstream section may simply indicate selection for habitat that offers benefits other than optimal temperature, such as foraging opportunities or physical cover, but also may result from active avoidance of thermally optimal habitat due to predation threats or competition (Hertz et al. 1993).

Trout population surveys conducted in the spring and summer of 2016 indicated that Brown Trout greatly outnumber Brook Trout in Cedar Creek (Appendix B). Brown Trout often achieve higher densities (Waters 1983; Wehrly et al. 2003; Mckenna et al. 2013; DeWeber and Wagner 2015) and grow at a faster rate and to a larger size than Brook Trout (Carlson et al. 2007) in streams like Cedar Creek that are degraded by anthropogenic land uses and have water temperatures near the upper range of Brook Trout tolerance. Brown Trout outcompete Brook Trout for food resources (DeWald and Wilzbach 1992), exclude Brook Trout from optimal resting positions (Fausch and White 1981), and influence Brook Trout's use of foraging locations and thermal refugia (Hitt et al. 2017). Indeed, Brook Trout home sites in this and other Michigan streams are less complex and seemingly suboptimal compared to home sites typically occupied by Brown Trout in Michigan streams (Clapp et al. 1990; Regal 1992; Diana et al. 2004; M. Luttenton, B. Giordano, J. Wegner, and N. Akey, unpublished data).

I did not directly investigate Brook Trout and Brown Trout interactions in this study, but Hitt et al. (2017) found that, in the presence of Brown Trout, Brook Trout habitat selection shifted to positions that were less optimal for thermoregulation and foraging. I suspect that Brown Trout in Cedar Creek likely influence Brook Trout habitat selection by excluding Brook Trout from home sites with complex LWD cover that provide optimal thermal habitat, given the thermoregulation and habitat selection results of this study and observations from extensive electroshocking in Cedar Creek for this and other studies.

Brook Trout in the downstream section of Cedar Creek likely regulated their body temperature more effectively due to a combination of shade provided by riparian vegetation and the confluences of at least two small coldwater tributaries in that section. The riparian vegetation in the downstream section likely also provides cover in and above the stream that may protect Brook Trout from predation, allowing them to occupy positions that are more profitable for thermoregulation and foraging. Additionally, riparian vegetation in the downstream section likely provides important terrestrial food subsidies to Brook Trout during the summer (Zaparzynski 2016). The characteristics of the downstream section's intact, forested riparian corridor seem to provide biologically relevant advantages to Brook Trout growth and survival that may allow the population to persist despite the deleterious effects of urbanization and agriculture throughout the watershed. Therefore, riparian condition should be carefully evaluated before approaching restoration of Brook Trout stream habitat.

Although the scope of my study may be limited, I am aware of no field studies of behavioral thermoregulation in freshwater fisheries research that have employed an approach to analyzing body temperature data as presented herein; which was adapted from Hertz et al. (1993). By evaluating thermoregulatory behavior in the context of available thermal habitat and a physiologically important temperature range, scientists can glean meaningful insights into fish behavior that have implications for their ability to survive and grow during periods of thermal stress. This approach can be combined with telemetry data to identify and protect zones of thermal refuge that allow threatened species to persist in systems degraded or threatened by land use changes and increasing global temperatures.

MANAGEMENT RECOMMENDATIONS

My study suggests that alterations to riparian corridors inhibit the ability for Brook Trout in marginal systems to regulate body temperature and select microhabitats that maximize metabolic efficiency during periods of thermal stress. Brook Trout management efforts should prioritize restoration of riparian corridors to reconnect aquatic and terrestrial ecosystems and mitigate the impacts of rising summer water temperatures. At a minimum, maintaining a corridor of shrub vegetation would provide shade to potentially moderate fluctuations in water temperature and keep water cooler than segments bordered by grass vegetation alone (Cross et al. 2013).

I demonstrated how radio telemetry can be used to distinguish patterns of habitat use that may be helpful in identifying habitat features that enhance the survival and growth of trout. Additionally, the approach to analyzing body temperature data from telemetered fish adapted from Hertz et al. (1993) presented here could be easily adapted by fisheries managers to provide meaningful insights about the consequences of fish behavioral thermoregulation on growth, reproduction, or population density, especially in larger order streams with greater thermal heterogeneity.

Stream restoration efforts to improve trout habitat or increase trout density often involve the addition or manipulation of in-stream woody structures as their primary, and in many cases, only means to meet the objective. Although Brook Trout and other trout species have an affinity for deep pools and LWD (Neuman and Wildman 2002; Morris et al. 2012; Davis and Wagner 2016) and trout density is often related to abundance of LWD (Flebbe and Dolloff 1995; Zorn and Nuhfer 2007), simply adding LWD habitat to a stream may not increase Brook

Trout density (Sweka and Hartman 2006). Immediate increases in trout density at the site of habitat additions are typically caused by immigration of large trout from other parts of a stream into the structures (Riley et al. 1992; Gowan and Fausch 1996), giving the illusion that in-stream habitat manipulations have increased overall trout density. However, surveys used to quantify the increase in trout density after the installation of LWD structures, or similar in-stream habitat, can be misleading if the inherent bias against detecting simple movement into the structures from neighboring reaches is not explicitly accounted for (Gowan et al. 1994).

Failure to evaluate the physical in-stream features that are inhibiting the survival and growth of trout precludes successful habitat manipulations. Gowan and Fausch (1996) assessed the long-term efficacy of in-stream habitat additions at increasing trout density and improving trout habitat. They found that juvenile trout did not respond to habitat additions and the habitat additions had no significant effect on the growth, recruitment, or survival of trout in the 6 years after installment (Gowan and Fausch 1996). This study was re-visited 23 years later by White et al. (2011) who determined that the trout population had ultimately increased where habitat had been modified; however, the authors emphasize an important caveat: increased trout density was attributed to log drop structures that provided a specific habitat type that was limiting in the system and remained intact due to the stream’s stable banks and years of routine maintenance.

In general, I think that effective protection of specific threatened trout species, and successful restoration or improvement of their habitat, necessitates a holistic approach involving a careful evaluation of the condition of the watershed, the riparian zone, and the ecological interactions occurring within the stream and its terrestrial corridor. If the focus of restoration is to improve habitat specifically for one species (e.g., Brook Trout in this study or Bull Trout *Salvelinus confluentus* in the western United States), managers must consider how competition may inhibit the intended benefit of restoration efforts to the target species. Ultimately, restoration efforts that evaluate and explicitly address physical (water temperature, depth, cover, etc.) and biological (competition, predation, foraging, etc.) factors limiting trout survival and growth in a system are likely to provide greater benefits to trout populations than woody habitat additions alone, that occur at the scale of a fishes home site.

CONCLUSION

I have demonstrated an approach to analyzing fish body temperature data that has not been commonly used in field studies of freshwater fishes. My results illustrate how this type of analysis can be used to understand thermoregulatory effectiveness in the context of a streams thermal regime, and may help to explain habitat selection and dispersal patterns. I found Brook Trout body temperatures generally conformed to ambient water temperatures, although Brook Trout maintained body temperatures close to their ideal range throughout the summer in the forested, downstream section. Additionally, Brook Trout habitat selection differed between sections and may be related to the availability of cover and thermal refugia. The relationships revealed in this study emphasize the value of investigating biological factors limiting trout survival and growth as well as accounting for reach-scale differences in aquatic and terrestrial stream condition when attempting to protect trout populations and restore or improve habitat.

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TABLES

TABLE 2.1. Summary of the number of tracks (*N*), Brook Trout body size at capture, and movement over the course of the study between July 7 and October 2, 2015 in Cedar Creek, Michigan. Movement totals are the sum of the distances between locations for individual fish. Net movement accounts for direction upstream (+) or downstream (-), absolute movement is irrespective of direction. U (upstream) and D (downstream) in Fish ID indicate section of initial capture.

				Absolute movement		Net movement	
Fish ID	*N*	Length (mm)	Weight (g)	Total (m)	Mean rate (m/d)	Total (m)	Mean rate (m/d)
U0	20	229	115.00	144	3.6	0	0
U1	5	200	82.40	69	9.2	-9	-4.5
U2	5	201	81.54	0	0	0	0
U3	25	186	80.99	1,306	6.5	-1,306	-6.5
U4	11	219	114.23	1,831	44.8	-1,831	-44.8
D5	26	192	66.19	128	2.1	38	0.8
D6	29	260	171.43	40	0.7	0	0.1
D7	8	229	116.66	14	0.9	-14	-0.9
D8	29	199	90.04	204	1.3	188	0.7
D9	23	217	98.80	123	2.9	-3	-0.4
U10	11	190	71.68	19	0.4	19	0.4
U11	16	280	261.10	123	3.8	-91	-2.6
Mean ± SE	17 ± 3	217 ± 8	112.51 ± 15.80	333 ± 171	6.3 ± 3.6	-251 ± 182	-4.8 ± 3.7

TABLE 2.2. Summary of Cedar Creek water temperature and Brook Trout body temperature indices in Cedar Creek, Michigan during the summer of 2015. Values in the upstream and downstream rows are for the pooled observations recorded in those sections. $\overline{T}_b$ and $\overline{T}_e$ are the mean body and operating temperatures ± SE, respectively. The $\overline{d}_b$ and $\overline{d}_e$ columns are the mean deviations of body and operative temperatures ± SE, respectively, from the set point range (T_{set}). In cells with two values, top values are temperatures recorded at the logger closest to the fish location, and bottom values are the mean temperature recorded by all loggers in the entire study reach or designated section. The effectiveness of thermoregulation E is 1 – ($\overline{d}_b$/ $\overline{d}_e$). An E near one indicates effective thermoregulation, an E of zero indicates thermal conformity, a negative E may indicate an active avoidance of optimal thermal habitat.

Variable	$\overline{T}_b$	$\overline{T}_e$	$\overline{d}_b$	$\overline{d}_e$	E
Minimum	15.20 ± 0.36	15.40 ± 0.58 15.33 ± 0.58	0.21 ± 0.21	0.30 ± 0.21 0.27 ± 0.37	- 0.48 - 1.82
Mean	16.02 ± 0.15	16.21 ± 0.12 16.59 ± 0.12	0.76 ± 0.10	0.81 ± 0.08 1.04 ± 0.09	0.05 0.26
Max	17.72 ± 0.47	17.29 ± 0.42 17.35 ± 0.49	1.96 ± 0.40	1.56 ± 0.34 1.53 ± 0.37	0.73 0.83
Upstream	16.82 ± 0.35	16.67 ± 0.29 16.55 ± 0.28	1.42 ± 0.27	1.18 ± 0.21 1.08 ± 0.20	- 0.21 - 0.32
Downstream	15.74 ± 0.15	16.05 ± 0.13 16.35 ± 0.13	0.54 ± 0.09	0.68 ± 0.08 0.84 ± 0.09	0.21 0.36

FIGURES

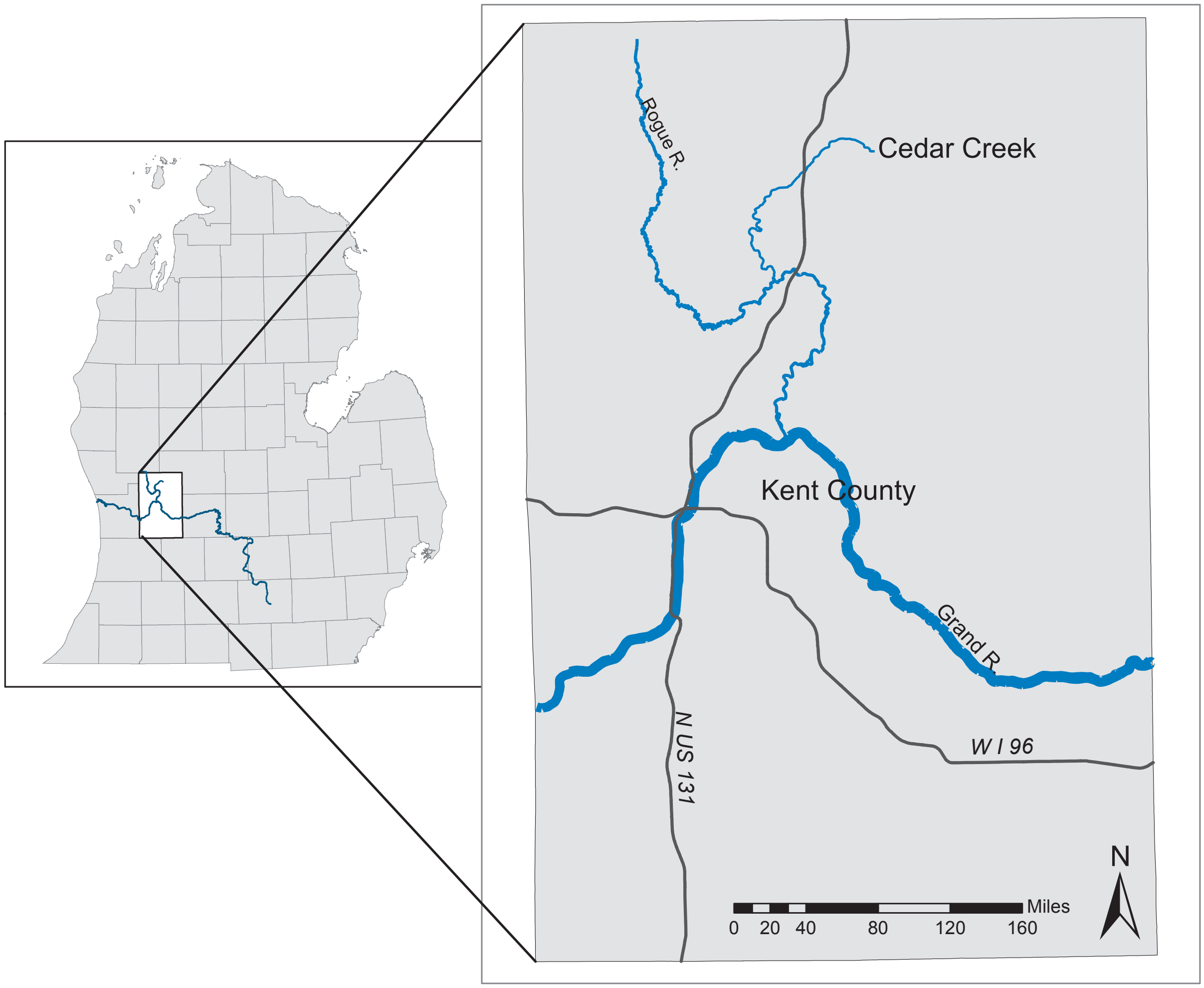

FIGURE 2.1. Map of the study stream, Cedar Creek, a small coldwater tributary of the Rogue River in southwest Michigan.

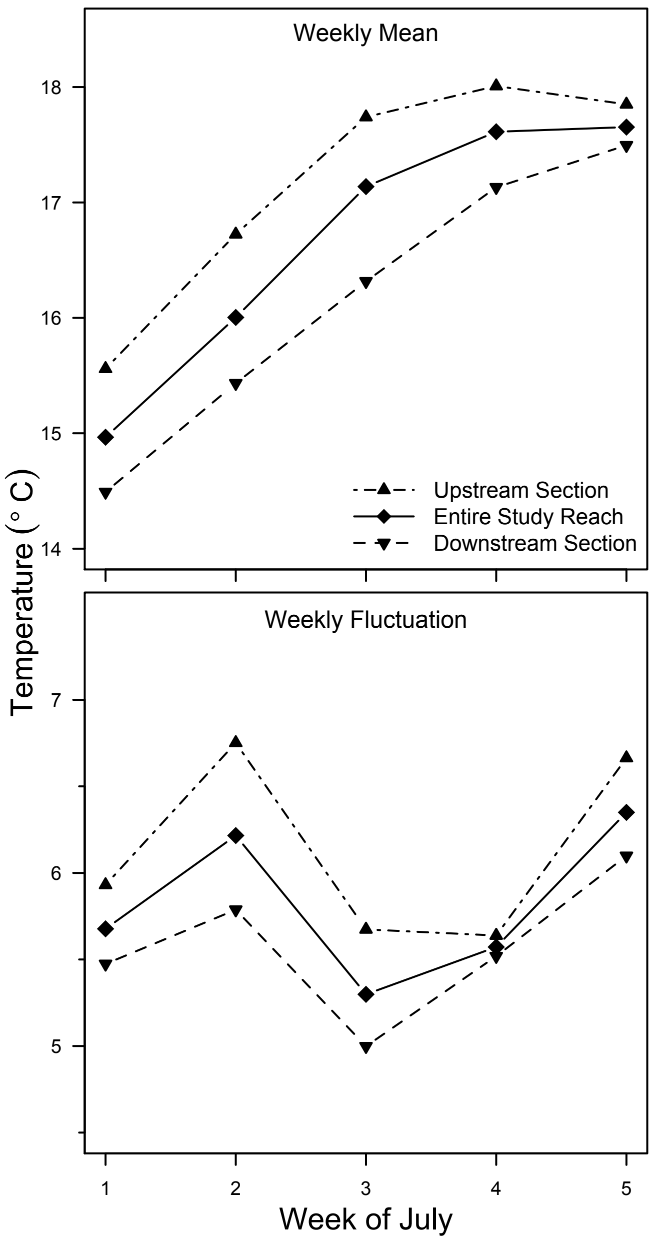

FIGURE 2.2. July weekly mean water temperature and fluctuations in water temperature recorded in Cedar Creek, Michigan in 2015. Week 1 begins June 28, 2015 and week 5 ends August 8, 2015. See text for calculation details.

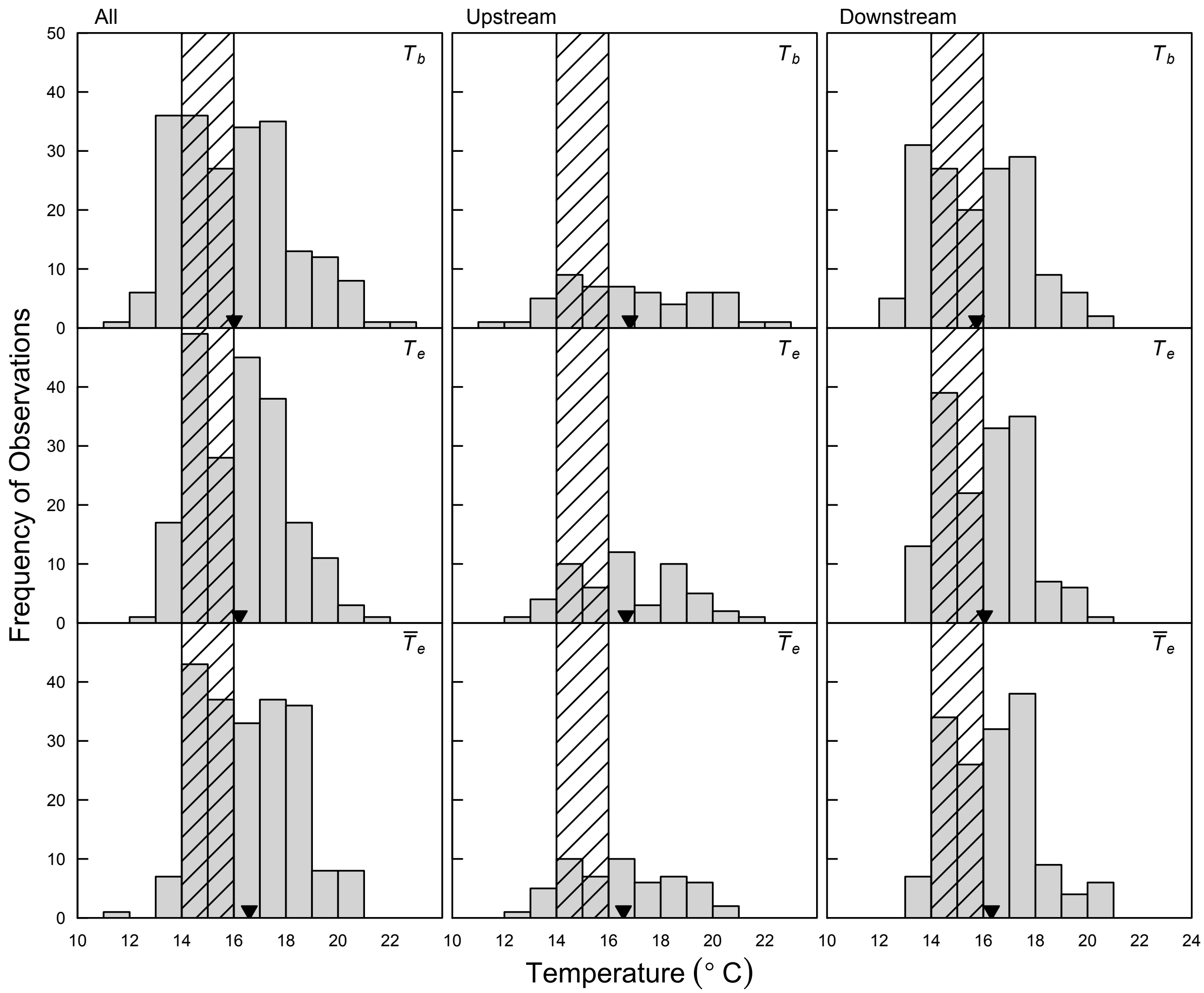

FIGURE 2.3. Frequency distributions of Brook Trout body temperatures (T_b) and operative temperatures (T_e) in Cedar Creek, Michigan in summer 2015. The All column represents the pooled observations from the entire study reach over the duration of the study. Upstream and Downstream panels represent observations recorded in those sections. Cells labeled T_e represent T_e recorded at the nearest logger. Cells labeled $\overline{T}_e$ represent the mean T_e recorded by all loggers in the study reach and in the upstream and downstream sections, respectively. Triangles indicate the mean T_b, T_e, or $\overline{T}_e$. Crosshatched bars indicate the ideal range for maximum Brook Trout growth (T_{set} range).

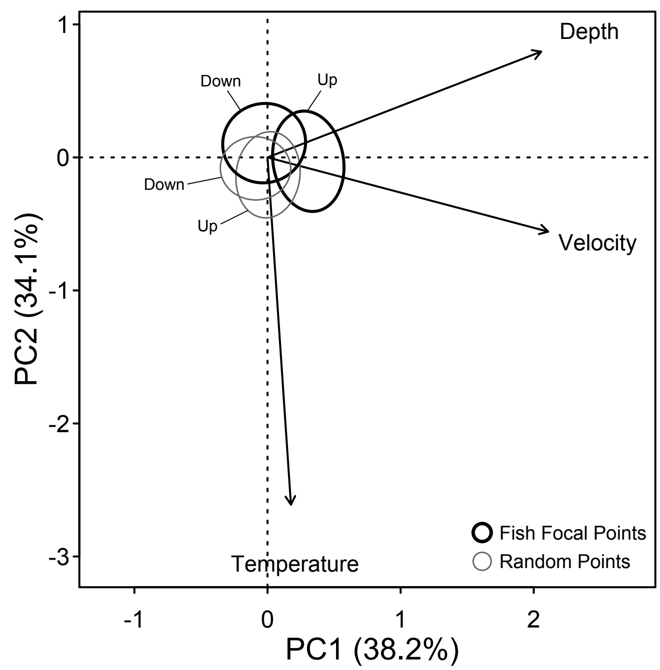

FIGURE 2.4. Biplot of the first two axes from principal components analysis of physical variables measured at random points and Brook Trout focal points in Cedar Creek, Michigan in summer 2015. Vectors indicate the direction of a variables gradient along the axes. Ellipses represent the standard deviation of site scores for the indicated groups and therefore do not contain all data points from the ordination.

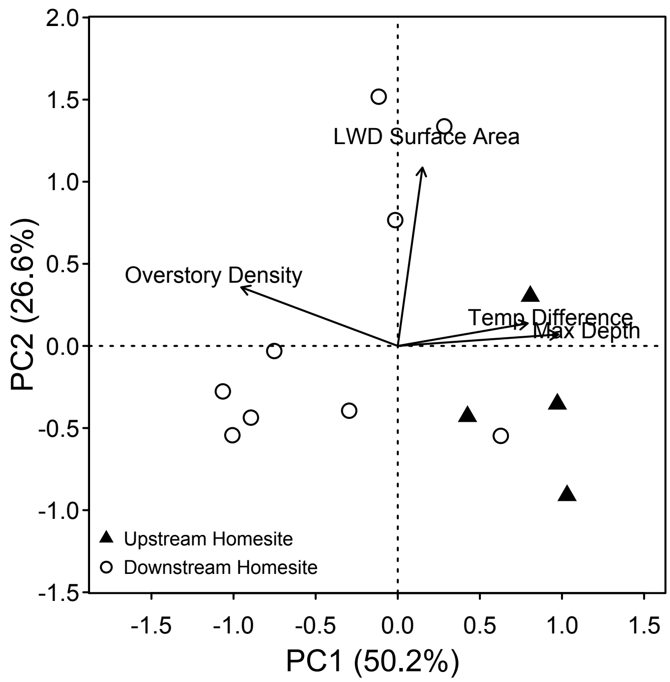

FIGURE 2.5. Axes 1 and 2 of the principal components analysis of habitat variables measured at Brook Trout home sites in Cedar Creek, Michigan in summer 2015. Vectors indicate the direction of a variables gradient along the axes, symbols represent home sites.

Chapter 3

Extended Literature Review

OVERVIEW

The Brook Trout (*Salvelinus fontinalis* family Salmonidae) is native to north eastern North America where they thrive in high elevation lakes, rivers and streams with cold, clean water (MacCrimmon and Campbell 1969). Anthropogenic alterations to ecosystems (Weltman-Fahs and Taylor 2013; Nuhfer et al. 2017), competition with introduced species (Hoxmeier and Dieterman 2013; McKenna et al. 2013), and trends of global warming (Jonsson and Jonsson 2009; Ries and Perry 1995) threaten many populations of native Brook Trout. Water temperature and access to refuge from extreme temperatures are among the most influential factors of Brook Trout survival, growth, and behavior. In much of their native and introduced range, Brook Trout survival, growth and behavior is also influenced by competition with other salmonid species (Nyman 1970; Carlson et al. 2007, Fausch 2008; Hitt et al. 2017).

This review focuses on the life history, habitat, thermoregulation, and movement of riverine Brook Trout within their native and introduced ranges. It explores how these aspects of Brook Trout behavior are influenced by physiological demands, physical habitat conditions, seasons, habitat alterations, and allopatric and sympatric competition. This review aims to provide context for the current study and highlights directions for future studies of Brook Trout behavior, habitat use, and biological interactions.

LIFE HISTORY

The Brook Trout life cycle can be broken into four basic stages: egg, alevin, parr, and adult. Spawning is generally initiated by autumns reduced photoperiod (Power 1980), although elevated water temperature can postpone the initiation and reduce the intensity of spawning behavior (Warren et al. 2012). Brook Trout lay their eggs in gravel beds called redds that are dug in swift running water (Power 1980) and are often associated with areas of groundwater seepage (Witzel and Maccrimmon 1983; Curry and Noakes 1995). Once fertilized, eggs develop through the winter in the protection of their gravel beds where flowing water and groundwater seepage provide stable temperatures and dissolved oxygen necessary for survival (Power 1980; Curry and Noakes 1995). Optimal temperature for Brook Trout egg survival and development is about 6°C (Hokanson et al. 1973; Power 1980), with a maximum tolerance of 13°C (Hokanson et al. 1973). Incubation period is variable and may last between 28 and 160 days depending on water temperature and dissolved oxygen levels (Power 1980).

Following incubation, Brook Trout hatch as alevins, or “sac fry”, beginning their larval life stage. Brook Trout alevin have empty swim bladders and depend on nutrients from their yolk sack (Power 1980). Alevin remain in the gravel where they continue to develop until the yolk sack has been completely consumed at which point they emerge from the gravel and fill their air bladders, a process called “swim up” (Power 1980). After swim up, neutrally buoyant juveniles disperse to river edges where they begin to feed primarily on benthic invertebrates (Power 1980). Juvenile Brook Trout are called parr.

Brook Trout age at sexual maturity varies by region and with environmental factors (Power 1980). In general, males reach sexual maturity at a younger age and smaller size than females (Witzel and Maccrimmon 1983; McCormick and Naiman 1984). The Brook Trout is a short-lived species of salmonid, rarely living longer than 4 years (Power 1980). In high elevation regions and northern latitudes where water temperatures are cooler and productivity is lower, Brook Trout growth rates are slower and they may take longer to reach sexual maturity and live up to 6 years (Power 1980; McCormick and Naiman 1984; Kennedy et al. 2003). In contrast, Brook Trout may reach sexual maturity faster and live shorter lives in lower elevation streams and southern regions, where water temperature is warmer and productivity is higher (Power 1980; McCormick and Naiman 1984; Kennedy et al. 2003).

HABITAT

Watershed.—Water temperature is considered the most important factor influencing Brook Trout occurrence, abundance, and habitat use throughout their native and introduced range. Brook Trout require water temperatures between 10° and 16° C (MacCrimmon and Campbell 1969; McCormick et al. 1972; Hokanson et al. 1973; Power 1980; Xu et al. 2010a) and grow fastest at temperatures between 12° and 16°C (McCormick et al. 1972; Hokanson et al. 1973; Cross et al. 2013). A study of Michigan streams found that Brook Trout occur in highest densities where average summer water temperature is less than 18°C with weekly fluctuations less than 5°C (Wehrly et al. 2007). As ambient water temperature exceeds 18°C and approaches the limits of Brook Trout tolerance, around 23°C (Fry et al. 1946; McCormick et al. 1972; Wehrly et al. 2007), Brook Trout respiration and metabolic demands increase (Tang and Boisclair 1995; Hartman and Sweka 2001), consequently reducing growth rates (Magoulick and Wilzbach 1998) and increasing mortality (McCormick et al. 1972). Given their sensitivity to water temperature, Brook Trout often inhabit streams where coldwater tributaries and groundwater input provide refuge from extreme water temperatures.

After water temperature, many studies report forested land cover among the most important factors in predicting Brook Trout occurrence and abundance (Hudy et al. 2008; McKenna and Johnson 2011; McKenna et al. 2013; Kanno et al. 2015). In the eastern United

States, the majority of self-sustaining native Brook Trout populations occur where forest is the dominant land cover (Hudy et al. 2008). Many Brook Trout populations have been heavily impacted by logging legacies that alter invertebrate communities (Nislow and Lowe 2006), increase water temperatures (Brown and Krygier 1970), reduce in-stream woody cover (Zorn and Sendek 2001), and ultimately cause declines in Brook Trout density (Nislow and Lowe 2003). Urbanization and conversion of forested land for agriculture also has degraded Brook Trout habitat throughout their distribution. Stranko et al. (2008) modeled Brook Trout occurrence in Maryland and found Brook Trout were not present where watersheds had more than 4% impervious surfaces. Another study found Brook Trout in their native range were less likely to occur where watersheds were dominated by agriculture or developed land (DeWeber and Wagner 2015).

Land cover characteristics, anthropogenic alterations and resource extractions directly influence stream water temperature. Forested stream segments are typically cooler and have more stable water temperatures than streams bordered by agriculture or urban centers (Cross et al. 2013). Consequently, Brook Trout are less likely to occur in stream segments dominated by or proximate to rural development or agricultural land uses (McKenna et al. 2013; DeWeber and Wagner 2015). Groundwater withdrawals and diversions increase summer water temperatures by altering groundwater recharge rates (Weltman-Fahs and Taylor 2013), and reducing available physical habitat (Nuhfer et al. 2017) and may alter community structure resulting in a reduction of fluvial invertivores such as Brook Trout (Kanno and Vokun 2010)

High-volume water withdrawals and other alterations associated with hydraulic fracturing, or “fracking”, for natural gas are a new and expanding threat to Brook Trout populations in the United States. Few studies have directly addressed the impact of fracking on Brook Trout populations, although Weltman-Fahs and Taylor (2013) identify three specific threats to Brook Trout from fracking: hydrological alterations from water withdrawals, physical alterations to stream substrates and connectivity, and chemical alterations from wastewater discharge. Identifying and mitigating threats to Brook Trout populations from fracking will be an important research topic in the future.

In-stream habitat.— Brook Trout generally select deep microhabitats (Magoulick and Wilzbach 1997) with slower water velocity (Sotiropoulus et al. 2006; Ecret and Mihuc 2013) and in-stream or overhead cover in streams (Butler and Hawthorne 1968; Curry et al. 2002; Johnson 2008; Hartman and Logan 2010; Morris et al. 2012). Lower stream velocity reduces the energy demand required for holding stream position and is characteristic of pools for which Brook Trout show a particular affinity (Fausch and White 1981; Cunjak and Green 1983; Flebbe and Dolloff 1995; Magoulick and Wilzbach 1997; Johnson 2008; Hartman and Logan 2010). Deep water found in pools also provides cover from predation (Harvey and Stewart 1991; Lonzarich and Quinn 1995; Pépino et al. 2015b) and may offer thermal refuge during periods of extreme temperatures (Baird and Krueger 2003; Sotiropoulos et al. 2006). Although these habitat preferences are common for many Brook Trout populations, microhabitat selection and preference varies by season and age and can be influenced by stream condition, competition, and predation.

In autumn during the spawning season, Brook Trout use microhabitats that are shallower (Mollenhauer et al. 2013) and offer more cover than sites occupied in the summer (Johnson 2008). Brook Trout select redd sites with gravel substrate and swift running water

(Power 1980) often at locations of groundwater input (Witzel and Maccrimmon 1983). Brook Trout egg survival is optimal at 6°C and has a maximum tolerance of about 13°C (Hokanson et al. 1973; Power 1980). Groundwater seeps provide stable water temperatures and dissolved oxygen levels necessary for embryo development throughout the winter (Power 1980; Curry et al. 1995). During the winter, mature Brook Trout also select sites where groundwater input moderates water temperature, gathering in pools and beneath submerged cover (Cunjak and Power 1986, 1987).

Older, larger Brook Trout typically occupy deeper sites with greater water velocity and woody cover than age-0 fish (Cunjak and Power 1986; Baker and Coon 1997; Johnson 2008; Morris et al. 2012; Davis and Wagner 2016). A number of factors may influence the difference in microhabitat preference between age 0 and yearling or older Brook Trout. Large fish are more vulnerable to predation, therefore greater depth and woody cover may afford protection from predators (Harvey and Stewart 1991; Lonzarich and Quinn 1995; Pépino et al. 2015b).

Foraging preferences and behavior also contribute to differences in habitat preference. Brook Trout move to foraging locations that have higher velocities than resting positions, likely due to the greater availability of drifting prey (Fausch and White 1981; Hartman and Logan 2010). Larger fish are stronger swimmers, allowing them to occupy and defend sites with greater velocity that may be more energetically profitable (Fausch and White 1981, 1986; Baker and Coon 1997). Small Brook Trout feed in riffles and are more likely to feed during the daytime, while larger Brook Trout are more reluctant to feed during the day and prefer pools for foraging (Fausch and White 1981; Hartman and Logan 2010; Ecret and Mihuc 2013).

MOVEMENT

Most studies report that the Brook Trout is relatively sedentary; however, their movement varies by system and with age, season, and stream physical conditions. Hartman and Logan (2010) report an average home range of about 500 m for Brook Trout in an Appalachian stream. Many studies report little movement for most Brook Trout, and large movements up to 6 km by some individuals (Petty et al. 2012; Davis et al. 2015). Brook Trout in larger order streams are more mobile than those in small tributaries (Hansbarger et al. 2010; Petty et al. 2012). Brook Trout in the main stem of an Appalachian stream moved an average 50 m/d, while Brook Trout in one of its second order tributaries moved 2 m/d (Petty et al. 2012). Brook Trout activity is closely related to foraging (Boisclair 1992). Brook Trout are most active at dusk and dawn (Power 1980; Allan 1981; Fausch and White 1981; Hartman and Logan 2010).

Seasonal patterns of Brook Trout movement are widely reported in the literature. Brook Trout activity generally increases in the spring time after runoff (Gowan and Fausch 1996; Curry et al. 2002; Ecret and Mihuc 2013). During the summer, Brook Trout move upstream (Gowan and Fausch 1996, Peterson and Fausch 2003; Hansbarger et al. 2010), often into colder headwaters and tributaries (Hayes et al. 1998; Curry et al. 2002; Baird and Krueger 2003; Petty et al. 2012). During autumn, the daily movement and home range of Brook Trout increases dramatically in association with upstream migration for spawning (Power 1980; Gowan and Fausch 1996; Curry et al. 2002; Mollenhauer et al. 2013). Fewer studies have explored the winter time movement of Brook Trout, and those that have reported downstream movement and a reduction in activity (Cunjak and Power 1986; Curry et al. 2002; Mollenhauer et al. 2013).

In addition to seasonal patterns, Brook Trout movement varies by size, age, and condition. Juvenile trout exhibit higher dispersal (Petty et al. 2005) and are most mobile in the spring (Ecret and Mihuc 2013). Mature Brook Trout are most mobile in the late summer and autumn during the spawning season (Power 1980; Mollenhauer et al. 2013; Gowan and Fausch 1996). Many studies report that Brook Trout movement is positively related to fish size (Riley et al. 1992; Adams et al. 2000; Bélanger and Rodríguez 2001; Mollenhauer et al. 2013). Fish that travel upstream are often larger (Riley et al. 1992) and more capable of travelling through heavy flows and high gradients (Adams et al. 2000). Gowan and Fausch (1996) found that mobile Brook Trout in a Colorado stream were large, but in poor condition, suggesting these mobile trout may be searching for optimal foraging positions (Gowan and Fausch 2002).

Brook Trout swimming speeds, foraging activity, and movement increase with increasing water temperatures up to about 18°C, at which point there is a marked decrease in activity as water temperature approaches the lethal limit of 23°C (Tang and Boisclair 1995; Magoulick and Wilzbach 1998; Petty et al. 2012). Reduction of movement and foraging activity at temperatures above 18°C may be a strategy to conserve energy during periods of thermal stress (Tang and Boisclair 1995; Sotiropolous et al. 2006). Brook Trout movement rates are also closely related to stream flow and water temperature. Movement rates are positively related to stream flow (Mollenhauer et al 2013): Brook Trout in a Pennsylvania stream increased movement during high flow events (Davis et al. 2015). Conversely, low flow events may restrict Brook Trout movement and isolate fish in pools to avoid stranding (Sotiropolous et al. 2006).

Brook Trout dispersal in many systems is limited by natural and anthropogenic barriers. In their native range, culverts and forest road crossings inhibit upstream migration, isolating populations and restricting gene flow (Fausch et al. 2006; Letcher et al. 2007; Poplar-Jeffers et al. 2009; Kanno et al. 2011). In the western United States, natural dispersal barriers such as waterfalls and high-gradient sections may prevent or limit the extent of upstream invasion of Brook Trout into Cutthroat and Bull Trout habitat (Adams et al. 2000; Fausch et al. 2009). Some research suggests that man-made dispersal barriers may be an effective strategy in controlling and preventing upstream invasion of Brook Trout and prioritizing conservation efforts of native fish (Peterson et al. 2008).

THERMOREGULATION

As ectotherms, Brook Trout body temperature is approximately the same as the water they inhabit (Stevens and Sutterlin 1976; Fechhelm and Neill 1982; Pépino et al. 2015a). Like other ectotherms, Brook Trout cope with thermal stress by occupying habitats that offer refuge from ambient water temperatures that approach or exceed their tolerance. Thermoregulation is an important strategy for Brook Trout survival and growth that influences habitat selection, behavior, and patterns of seasonal movement (Magoulick and Wilzbach 1998; Baird and Krueger 2003; Petty et al. 2012).

Most research of Brook Trout thermoregulation focuses on the response to warm summertime water temperatures. Brook Trout seek refuge from high water temperatures by moving to zones of coldwater refugia, including pools, coldwater tributary confluences, groundwater seepages, and headwaters (Biro 1998; Hayes et al. 1998; Curry et al. 2002; Baird and Krueger 2003; Petty et al. 2012). During the summer, movement to coldwater refuge often translates to upstream dispersal. Petty et al. (2012) reported a distinct increase in Brook Trout movement in a West Virginia river at water temperatures above 18°C associated with dispersal to tributaries and other zones of coldwater refuge. Similarly, Brook Trout in a Michigan stream moved to a coldwater headwater tributary when mainstream water temperature increased and exceeded 20°C for much of the summer (Hayes et al. 1998). Brook Trout in a large Adirondack river kept body temperatures on average 2.3°C, and up to 17°C colder than ambient water temperature by occupying cold water refuges during the summer (Baird and Krueger 2003). By occupying cold microhabitats during the summer, Brook Trout can maximize their growth efficiency (Larrsson 2005) and survival (Drake and Taylor 1996; Xu et al. 2010a, 2010b).

Brook Trout exhibit similar thermoregulatory behavior during periods of cold water temperature. Following the upstream movement and increased activity associated with spawning in the autumn, Brook Trout move downstream to areas of warm water refuge, including pools, spring fed tributaries, and groundwater seepages, where they remain relatively stationary throughout the winter (Cunjak and Power 1986; Curry et al. 2002; Mollenhauer et al. 2013). Groundwater, which remains just above the average air temperature year-round (Meisner 1990a), also provides warm water refuge in the winter by promoting overwinter survival and growth of adults and developing embryos (Hunt 1969; Curry et al. 1995; Xu et al. 2010b).

Increasing water temperature as a result of global warming threatens to exacerbate Brook Trout thermal habitat loss and consequently survival. Under some climate change scenarios, doubling pre-industrial atmospheric carbon dioxide concentrations may increase average stream, and groundwater temperatures up to 5°C (Meisner 1990b; Eaton and Scheller 1996; Clark et al. 2001; Kurylyk et al. 2014). Some bioenergetic models project increased water temperature could benefit Brook Trout growth, provided a proportional increase in prey availability and consumption to meet increased metabolic demands (Hill and Magnuson 1990; Ries and Perry 1995). Some local scale distribution models predict increased abundance (Clark et al. 2001) or small changes in suitable habitat (Trumbo et al. 2014) when accounting for changes in temperature alone. However, when coupled with other risk factors, such as floods (Clark et al. 2001) and land cover alterations (Trumbo et al. 2014), many models predict more deleterious effects. Larger scale models predict elevated water temperatures may reduce thermally suitable Brook Trout habitat by as much as 50% (Meisner 1990a, 1990b; Eaton and Scheller 1996).

Flood frequency and severity will likely increase under climate change scenarios (Milly et al. 2002), potentially resulting in drastic declines in Brook Trout populations (Wenger et al. 2011). Climate change also compounds threats of extirpation of native fish by non-native species (Roberts et al. 2017). As global air and water temperatures continue to increase, sufficient access to thermal refugia will become vital for the survival of Brook Trout, particularly populations at the southern extent of their distribution (Meisner 1990a).

COMPETITION

In many parts of their current distribution, Brook Trout compete with other salmonid species for habitat and resources. Sympatric interactions between salmonid species are principally related to competition for food resources. Dominant fish occupy and defend optimal feeding positions (Grant et al. 1989; Nakano 1995; Nakano et al. 1998) where they grow faster than fish relegated to suboptimal feeding positions (Fausch and White 1986; Grant 1990). Active competition for stream positions increases metabolic rates, in turn negatively impacting growth of both the dominant and subdominant species (Elliot 1975; Elliot 1976; Fausch and White 1986).

In their native range, Brook Trout compete with Brown and Rainbow Trout. These interactions typically do not favor Brook Trout and induce shifts in their habitat selection and behavior. Brook Trout in the presence of Brown Trout are reported to shift to suboptimal positions, lose weight, and contract the fungus *Saprologenia* in laboratory experiments (DeWald and Wilzbach 1992; Hitt et al. 2017). Where they occur in sympatry, Brown Trout exclude Brook Trout from favorable resting positions (Fausch and White 1981), foraging locations (DeWald and Wilzbach 1992; Hitt et al. 2017) and over time may alter the distribution and population of Brook Trout in streams (Waters 1983; Fausch 2008). When released from competition with Brown Trout, Brook Trout occupy more favorable resting locations, foraging locations, and thermal refugia (Fausch and White 1981; Hitt et al. 2017).

Native Brook Trout are also dominated and outcompeted by Rainbow Trout, although these interactions are more closely related to population dynamics and reproductive success than to direct species interactions for resources and habitat (Larson and Moore 1985; Clark and Rose 1997; Magoulick and Wilzbach 1998). Rainbow Trout occupy different microhabitats, often with greater water velocity, and warmer water than Brook Trout (Cunjak and Green 1983, 1984; Magoulick and Wilzbach 1997; Baird and Krueger 2003; Wehrly et al. 2003). Moore et al. (1983) reported that removal of non-native Rainbow Trout from streams in Great Smokey Mountains National Park resulted in increased populations of native Brook Trout; however, there is some disagreement on these findings. Strange and Habera (1998) report no change in the downstream distribution of Brook Trout in the same stream and argue each species distribution simply varies annually.

The Brook Trout is not always the subdominant species in sympatric interactions. Just as Brown Trout dominate Brook Trout at warmer water temperatures (Hitt et al. 2017), Brook Trout dominate Bull Trout and Cutthroat Trout in the southern ends of their distributions where water temperatures favor Brook Trout (Nakano et al. 1998; Rieman et al. 2006; McMahon et al. 2007). In some instances, Brook Trout have been reported to dominate Brown Trout. Fausch and White (1986) found juvenile Brook Trout to outcompete Brown Trout of the same size for optimal positions in an artificial stream. Brook Trout also dominate Brown Trout in the high-altitude lakes of Sweden (Spens et al. 2007) and may pose a threat to native Brown Trout in European headwater streams where Brook Trout are better adapted (Korsu et al. 2009). Fausch (2008) calls this phenomenon the "invasion paradox", arguing non-native invaders that are better adapted to local conditions dominate native species living in conditions near the limits of their tolerance. Brook Trout in the western United States have displaced populations of Cutthroat Trout and Bull Trout upstream from lower reaches (Dunham et al. 2002; Peterson and Fausch 2003; Rieman et al. 2006) and threaten to extirpate some populations (Rieman et al. 2006), especially when combined with the threats of climate change (Roberts et al. 2017).

SUMMARY

As global temperatures rise and Brook Trout habitat is altered by anthropogenic land uses, access to thermal refuge and other habitat requirements will be vital for the survival of Brook Trout, particularly those in the extremes of their distribution. Future management should focus on protecting areas yet untouched or impacted by human activities and restoring areas negatively impacted by past alterations. Before initiating local restoration projects, managers must identify habitat features necessary for Brook Trout success that are limited in the system and carefully account for interspecific interactions that may be limiting local Brook Trout populations.

More research is needed on effective approaches to mitigating the impacts of anthropogenic alterations to Brook Trout habitat. The need for effective mitigation strategies is particularly apparent in the eastern United States where fracking for natural gas is rapidly expanding, posing several threats to native Brook Trout populations, the potential consequences of which are largely unknown (Weltman-Fahs and Taylor 2013).

Beyond behavioral studies of Brook Trout, future research should focus on human dimensions impacting management and conservation of Brook Trout populations and stream ecosystems in general. Studies of effective approaches to citizen and stakeholder education and engagement would be particularly useful in fostering public support and advocacy for environmental protection and restoration.

Brook Trout are the topic of a great deal of scientific research, both of the species itself, and of ecological interactions with their environment and other species. In order to protect, conserve, and enhance native Brook Trout populations in the future, it is important to understand the ecology of Brook Trout as their environment continues to change, largely from anthropogenic alterations. Understanding the behavioral mechanisms Brook Trout use to cope with stressful conditions and the physical factors that allow them to do so will help identify and protect habitat necessary for Brook Trout persistence. Understanding the human dimensions influencing management decisions will help managers effectively educate stakeholders and approach mitigation and restoration efforts with public support and engagement.

Extended Methodology

STUDY SITE

To continuously monitor water temperature during this study, I installed 10 temperature loggers (HOBO TidbiT v2 and Pendant models, Onset Computer Corporation, Bourne, Massachusetts) evenly spaced throughout the study reach. Temperature loggers were placed in likely Brook Trout habitats that had sufficient depth to remain submerged throughout the study. I secured loggers with cables to large woody structure or garden stakes driven into the stream bed, recorded their GPS coordinates (GeoExplorer 2005 series, Trimble Navigation Inc., Sunnyvale California), and flagged the location along the bank with the logger's serial number. One water temperature logger failed during the study and its data were excluded from analysis. One pendant logger anchored to a tree in the upstream section continuously monitored air temperature during the study.

FIELD PROCEDURES

Fish capture and tagging.—I collected Brook Trout using two backpack electrofishing units. I worked in an upstream direction with a crew of four, shocking likely Brook Trout habitat structures. Operators positioned anodes at opposing ends of a structure before engaging the electrofisher and moving the anodes towards each other. This method proved to be effective for targeting Brook Trout.

Upon capture, Brook Trout 185 mm or larger were held in a 5-gallon bucket filled with stream water for transport to a flow-through enclosure anchored to the stream near my work station. Prior to surgery, Brook Trout were anesthetized using AQUI-S 20E (25 mg/L) in a large cooler filled with stream water kept cool with ice. Brook Trout were held in anesthetic until they lost equilibrium and became unresponsive to physical stimulation.

Once fish were anesthetized, I held them belly-up in a cradle lined with moist gauze and flushed their gills with fresh stream water as I performed surgery. Prior to surgery, all surgical equipment was sterilized in a water and chlorhexidine gluconate antiseptic disinfectant solution (Aurora Pharmaceuticals LLC, Northfield, Minnesota). I first made a small incision in the fish's abdominal wall in front of the pelvic fins, and then inserted a 17-gauge hollow needle (Hamilton Company, Reno, Nevada) behind the pelvic girdle and out the abdominal incision. The tail of a transmitter (Advanced Telemetry Systems, Isanti, Minnesota) was threaded through the hollow needle, and the body of the transmitter inserted into the abdominal cavity. I removed the hollow needle, leaving the transmitters tail hanging outside of the fish from a pinhole behind the pelvic fins. I sutured the incision with 6-0 synthetic absorbable suture material (Ethicon, Inc., Somerville, New Jersey) and sealed the sutures with a topical glue.

Following surgery, fish were revived in the flow-through container by holding the fish upright in the current and pumping water through its gills. Once fish regained equilibrium and were able to hold their position in the flow-through tank on their own, they were left in the enclosure for an additional 10-15 min to ensure they had not suffered complications from surgery. Once I was confident that fish had recovered, I released them in their initial capture locations.

Surgeries were performed on six occasions over the course of the study. Initially, four fish were tagged in the upstream section on June 19, 2015, and five fish were tagged on June 22, 2015 in the downstream section. A fifth fish was tagged in the upstream section on June 23, 2015 during a demonstration of the surgery procedure to Schrems West Michigan Chapter of Trout Unlimited. I also performed surgeries on July 7, August 6, and August 25, 2015 to implant dropped tags, or tags recovered from mortalities into new fish. I followed the same procedures for all surgeries, and recorded no mortalities that could be directly related to my surgery protocol. Radio transmitters recovered from deceased fish were sterilized in a water and chlorhexidine gluconate antiseptic disinfectant solution before being implanted in new fish using the procedure described above.

As part of a separate study, gastric lavage was performed on most fish prior to surgery and on one other occasion over the course of the study. Details of the gastric lavage procedure can be found in Zaparzynski (2016).

Fish tracking and data collection.—I tracked fish approximately three times a week from June 16 through October 2, 2015. Each day I located fish in a rotating order and attempted to begin each day of tracking at different times to ensure each fish had locations recorded in the morning, afternoon, and evening. The order of data collection at each fish location and its paired random point was determined randomly prior to tracking events.

Fish were initially located using a three-element yagi antenna and a R410 receiver (Advanced Telemetry Systems, Isanti, Minnesota). Once located, I monitored fish locations for at least 1 min to ensure they were inactive. I then recorded fish body temperatures given by a R4500 receiver (Advanced Telemetry Systems, Isanti, Minnesota) and proceeded with data collection.

Random points were located by measuring one stream width up or downstream of the fish location and randomly selecting a point along an imaginary transect of five evenly spaced points across the river. I measured the stream width using a tape measure, and divided the width by six to yield five evenly spaced points within the stream channel. A predetermined randomly chosen number between one and five dictated which point along the transect was used for the random point.

I used flags labeled with fish ID numbers to mark where I located tagged fish. Flags were also labeled with the date fish were first located at that location. Each time a fish was tracked to a previously flagged location, a hash mark was added to the flag. I used the flags to easily locate previous used locations for physical measurements when fish had moved to new locations and to identify home sites.

Trout population survey.—I conducted shocking surveys of the Brook and Brown Trout populations in my up and downstream study sections in June and August of 2016. I sampled a 100 m stretch of each section characteristic of the entire section. Block nets were secured at the upstream and downstream ends of the section, and multiple passes were made until capture efficiency was less than 30% between passes. Two individuals used backpack electroshockers with a third person assisting with netting fish and a fourth holding fish for removal. The crew worked in an upstream direction, methodically shocking the entire stretch. At the end of each pass, all fish captured were weighed and measured and held in a flow-through enclosure during successive passes. Upon completion of the survey, all fish were released back into the study reach.

Thermal gradient mapping.—In June and August of 2016, I recorded detailed measurements of stream temperature and depth in the 100 m stretches of the upstream and downstream sections where I conducted abundance surveys. I took measurements at three points evenly spaced across transects spaced 5 m apart throughout the 100 m section. At each point, I measured interstitial, mid column, and surface water temperature using a digital thermometer (HH503, Omega Engineering Inc., Norwalk, Connecticut) and depth using a meter stick resulting in a total of 180 temperature measurements and 60 depth measurements in each stretch.

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Appendixes

A. STUDY SITE AERIAL IMAGERY

FIGURE A.1. Aerial imagery of the upstream study section of Cedar Creek, Michigan taken April 2011 (top panel) and August 2013 (bottom panel).

FIGURE A.2. Aerial imagery of the downstream study section of Cedar Creek, Michigan taken April 2011 (top panel) and August 2013 (bottom panel).

B. TROUT POPULATION SURVEY

TABLE B.1. Summary of the number and size of Brown Trout and Brook Trout collected during multiple pass population surveys conducted in 100-m stretches of the upstream and downstream study section of Cedar Creek, Michigan in June and August 2016.

Collection Date	Section	Species	Total	Mean length ± SE (mm)
6/20/16	Upstream	Brown Trout	68	213 ± 7
		Brook Trout	11	192 ± 11
6/21/16	Downstream	Brown Trout	85	167 ± 9
		Brook Trout	37	122 ± 10
8/3/16	Upstream	Brown Trout	34	192 ±12
		Brook Trout	0	
8/4/16	Downstream	Brown Trout	64	101 ± 6
		Brook Trout	16	117 ± 13

C. THERMAL GRADIENT MAPPING

TABLE C.1. Summary of the water temperature measurements taken at three points evenly spaced along 20 transects spaced 5 m apart through 100-m stretches of the upstream and downstream study sections of Cedar Creek, Michigan in June and August 2016. Values are the difference between water temperature measured in Cedar Creek and air temperature recorded at Gerald R. Ford International Airport, Grand Rapids, Michigan at the time water temperature was recorded.

	Difference between water and air temperature (C) ± standard deviation		
	Left	Center	Right
Upstream			
June 2016			
Surface	-7.1 ± 0.1	-7.0 ± 0.1	-7.0 ± 0.1
Mid-column	-7.1 ± 0.1	-7.0 ± 0.1	-7.0 ± 0.1
Bottom	-7.1 ± 0.1	-7.0 ± 0.1	-7.1 ± 0.2
August 2016			
Surface	-8.8 ± 0.3	-8.9 ± 0.1	-9.0 ± 0.2
Mid-column	-8.8 ± 0.3	-8.9 ± 0.1	-9.0 ± 0.2
Bottom	-8.9 ± 0.4	-8.9 ± 0.1	-9.1 ± 0.3
Downstream			
June 2016			
Surface	-8.9 ± 0.1	-8.9 ± 0.1	-8.9 ± 0.1
Mid-column	-8.9 ± 0.1	-8.9 ± 0.1	-8.9 ± 0.1
Bottom	-8.9 ± 0.1	-8.9 ± 0.1	-8.9 ± 0.1
August 2016			
Surface	-12.8 ± 0.1	-12.9 ± 0.2	-12.9 ± 0.2
Mid-column	-12.8 ± 0.1	-12.9 ± 0.2	-13.0 ± 0.2
Bottom	-12.8 ± 0.1	-12.9 ± 0.2	-13.0 ± 0.2

TABLE C.2. Depth and water temperature measurements taken at three points evenly spaced along 20 transects spaced 5 m apart through 100-m stretches of the upstream and downstream study sections of Cedar Creek, Michigan in June and August 2016.

Section				Water Temperature (°C)		
Month	Transect	Point	Depth (cm)	Bottom	Mid-column	Surface
Upstream		Left	29	21.5	21.5	21.5
June	1	Middle	30	21.4	21.4	21.4
		Right	13	21.4	21.4	21.4
		Left	20	21.4	21.4	21.4
	2	Middle	29	21.4	21.4	21.4
		Right	13	21.3	21.3	21.3
		Left	19	21.4	21.4	21.4
	3	Middle	23	21.3	21.3	21.3
		Right	29	21.3	21.3	21.3
		Left	26	21.3	21.3	21.3
	4	Middle	48	21.3	21.3	21.3
		Right	51	21.3	21.3	21.3
		Left	26	21.2	21.3	21.3
	5	Middle	35	21.3	21.3	21.3
		Right	30	20.3	21.3	21.4
		Left	43	21.3	21.3	21.3
	6	Middle	46	21.3	21.3	21.3
		Left	43	21.2	21.3	21.3
		Middle	18	21.2	21.2	21.2
	7	Right	15	21.2	21.2	21.2
		Left	13	21.2	21.2	21.2
		Middle	27	21.2	21.2	21.2
	8	Right	30	21.2	21.2	21.2
		Left	17	21.1	21.2	21.2
		Middle	29	21.2	21.2	21.2
	9	Right	22	21.2	21.2	21.2
		Left	13	21.3	21.3	21.3
		Middle	30	21.2	21.2	21.2
	10	Right	24	21.2	21.2	21.2
		Left	16	21.2	21.2	21.2
	11	Middle	12	21.2	21.2	21.2

		Right	28	21.3	21.3	21.3
		Left	30	21.2	21.2	21.2
		Middle	14	21.2	21.2	21.2
	12	Left	18	21.3	21.3	21.3
		Middle	17	21.3	21.3	21.3
		Right	26	21.1	21.2	21.2
	13	Left	36	21.3	21.3	21.3
		Middle	31	21.1	21.2	21.3
		Right	17	21.2	21.2	21.2
	14	Left	24	21.2	21.2	21.2
		Middle	26	21.2	21.2	21.2
		Right	22	21.2	21.2	21.2
	15	Left	10	21.2	21.2	21.2
		Middle	22	21.2	21.2	21.2
		Right	12	21.2	21.2	21.2
	16	Left	14	21.2	21.2	21.2
		Middle	16	21.3	21.3	21.3
		Right	23	21.2	21.2	21.2
	17	Left	11	21.3	21.3	21.3
		Middle	10	21.4	21.4	21.4
		Left	25	21.2	21.2	21.2
	18	Middle	17	21.3	21.3	21.3
		Right	5	21.3	21.3	21.3
		Left	17	21.1	21.2	21.2
	19	Middle	18	21.3	21.3	21.3
		Right	6	21.2	21.2	21.2
		Left	20	21.1	21.2	21.1
	20	Middle	24	21.3	21.3	21.3
		Right	14	21.2	21.2	21.2
Downstream		Left	26	17.9	17.9	17.9
June	1	Middle	21	17.9	17.9	17.9
		Right	6	18.0	18.0	18.0
		Left	15	17.9	17.9	17.9
	2	Middle	21	17.9	17.9	17.9
		Right	15	17.9	17.9	17.9
		Left	11	17.9	17.9	17.9
	3	Middle	12	17.9	17.9	17.9
		Right	17	17.8	17.8	17.8

	Left	17	17.9	17.9	17.9
4	Middle	25	17.9	17.9	17.9
	Right	22	17.8	17.8	17.8
	Left	14	17.9	17.9	17.9
5	Middle	14	17.8	17.8	17.8
	Right	5	17.8	17.8	17.8
	Left	26	17.9	17.9	17.9
6	Middle	14	17.8	17.8	17.8
	Left	7	17.8	17.8	17.8
	Middle	25	17.9	17.9	17.9
7	Right	25	17.8	17.8	17.8
	Left	24	17.8	17.8	17.8
	Middle	23	17.9	17.9	17.9
8	Right	32	17.8	17.8	17.8
	Left	31	17.8	17.8	17.8
	Middle	28	17.8	17.8	17.8
9	Right	24	17.8	17.8	17.8
	Left	17	17.8	17.8	17.8
	Middle	17	17.8	17.8	17.8
10	Right	16	17.8	17.8	17.8
	Left	18	17.8	17.8	17.8
	Middle	11	17.8	17.8	17.8
11	Right	18	17.8	17.8	17.8
	Left	21	17.8	17.8	17.8
	Middle	14	17.8	17.8	17.8
12	Left	24	17.7	17.7	17.7
	Middle	18	17.8	17.8	17.8
	Right	13	17.7	17.7	17.7
13	Left	13	17.7	17.7	17.7
	Middle	12	17.7	17.7	17.7
	Right	20	17.7	17.7	17.7
14	Left	34	17.7	17.7	17.7
	Middle	18	17.7	17.7	17.7
	Right	13	17.7	17.7	17.7
15	Left	48	17.7	17.7	17.7
	Middle	31	17.7	17.7	17.7
16	Right	21	17.7	17.7	17.7
	Left	43	17.7	17.7	17.7

		Middle	44	17.7	17.7	17.7
		Right	32	17.6	17.6	17.6
	17	Left	48	17.7	17.7	17.7
		Middle	32	17.7	17.7	17.7
		Left	25	17.6	17.6	17.6
	18	Middle	35	17.6	17.6	17.6
		Right	34	17.6	17.6	17.6
		Left	30	17.6	17.6	17.6
	19	Middle	45	17.6	17.6	17.6
		Right	21	17.6	17.6	17.6
		Left	47	17.5	17.5	17.5
	20	Middle	55	17.6	17.6	17.6
		Right	37	17.6	17.6	17.6
Upstream		Left	17	21.0	21.0	21.0
August	1	Middle	24	20.9	20.9	20.9
		Right	8	20.8	20.8	20.8
		Left	13	20.9	21.0	21.0
	2	Middle	24	20.9	20.9	20.9
		Right	11	20.2	20.3	20.7
		Left	7	21.3	21.3	21.3
	3	Middle	19	20.9	20.9	20.9
		Right	10	20.8	20.8	20.8
		Left	15	21.1	21.1	21.1
	4	Middle	36	20.9	20.9	20.9
		Right	32	20.6	20.8	20.9
		Left	17	21.0	21.1	21.1
	5	Middle	47	21.0	21.0	21.0
		Right	35	20.4	20.8	20.9
		Left	29	20.9	21.0	21.1
	6	Middle	43	21.0	21.0	21.0
		Left	33	21.0	21.0	21.0
		Middle	13	21.0	21.0	21.0
	7	Right	7	21.1	21.1	21.1
		Left	2	21.2	21.2	21.2
		Middle	20	20.2	20.9	20.9
	8	Right	20	21.1	21.1	21.1
		Left	15	21.0	21.1	21.2
	9	Middle	16	21.0	21.0	21.0

		Right	14	21.1	21.1	21.1
		Left	7	21.0	21.0	21.0
		Middle	16	20.6	20.9	21.0
	10	Right	19	21.1	21.1	21.1
		Left	7	21.0	21.0	21.0
		Middle	12	21.2	21.2	21.2
	11	Right	19	21.0	21.0	21.0
		Left	20	21.0	21.0	21.0
		Middle	9	22.2	22.2	22.2
	12	Left	11	21.2	21.2	21.2
		Middle	22	21.1	21.1	21.1
		Right	13	21.1	21.1	21.1
	13	Left	12	21.1	21.1	21.1
		Middle	23	21.1	21.1	21.1
		Right	17	20.9	21.1	21.2
	14	Left	20	21.2	21.2	21.2
		Middle	17	21.2	21.2	21.2
		Right	6	21.2	21.2	21.2
	15	Left	9	21.2	21.2	21.2
		Middle	11	21.2	21.2	21.2
		Right	12	21.2	21.2	21.2
	16	Left	8	21.2	21.2	21.2
		Middle	13	21.1	21.1	21.1
		Right	8	21.2	21.2	21.2
	17	Left	18	21.2	21.2	21.2
		Middle	7	21.3	21.3	21.3
		Left	11	21.1	21.1	21.1
	18	Middle	10	21.1	21.1	21.1
		Right	10	21.1	21.1	21.1
		Left	17	21.2	21.2	21.2
	19	Middle	22	21.0	21.0	21.0
		Right	10	20.6	20.6	20.6
		Left	9	21.3	21.3	21.3
	20	Middle	10	21.2	21.2	21.2
		Right	9	21.1	21.1	21.2
Downstream		Left	13	17.6	17.6	17.6
August	1	Middle	26	17.4	17.4	17.4
		Right	13	17.4	17.4	17.4

	Left	15	17.7	17.7	17.7
2	Middle	20	17.5	17.5	17.5
	Right	11	17.4	17.4	17.4
	Left	7	17.8	17.8	17.8
3	Middle	18	17.5	17.5	17.5
	Right	14	17.5	17.5	17.5
	Left	8	17.8	17.8	17.8
4	Middle	25	17.6	17.6	17.6
	Right	18	17.5	17.5	17.5
	Left	9	17.7	17.7	17.7
5	Middle	21	17.5	17.5	17.5
	Right	14	17.5	17.5	17.5
	Left	17	17.8	17.8	17.8
6	Middle	25	17.6	17.6	17.6
	Left	7	17.5	17.5	17.5
	Middle	14	17.7	17.7	17.7
7	Right	28	17.6	17.6	17.6
	Left	19	17.5	17.5	17.5
	Middle	20	17.7	17.7	17.7
8	Right	39	17.6	17.7	17.7
	Left	29	17.6	17.6	17.6
	Middle	21	17.8	17.8	17.8
9	Right	29	17.7	17.7	17.7
	Left	17	17.6	17.6	17.6
	Middle	16	17.8	17.8	17.8
10	Right	24	17.7	17.7	17.7
	Left	20	17.6	17.6	17.6
	Middle	16	17.8	17.8	17.8
11	Right	20	17.7	17.7	17.7
	Left	18	17.7	17.7	17.7
	Middle	8	17.9	17.9	17.9
12	Left	26	17.7	17.7	17.7
	Middle	25	17.7	17.7	17.7
	Right	9	17.8	17.8	17.8
13	Left	30	17.8	17.8	17.8
	Middle	20	17.7	17.7	17.7
14	Right	12	17.8	17.8	17.8
	Left	15	17.8	17.8	17.8

	Middle	13	17.7	17.7	17.7
	Right	20	17.8	17.8	17.8
15	Left	35	17.8	17.8	17.8
	Middle	24	17.8	17.8	17.8
	Right	15	17.9	17.9	17.9
16	Left	41	17.9	17.9	17.9
	Middle	30	17.8	17.8	17.8
	Right	4	18.0	18.0	18.0
17	Left	29	17.9	17.9	17.9
	Middle	18	17.8	17.8	17.9
	Left	13	18.0	18.0	18.0
18	Middle	67	17.9	17.9	17.9
	Right	30	17.8	17.8	17.9
	Left	28	18.0	18.0	18.0
19	Middle	60	17.9	17.9	17.9
	Right	33	17.9	17.9	17.9
	Left	35	18.0	18.0	18.0
20	Middle	45	18.0	18.0	18.0
	Right	31	18.0	18.0	18.0