

Effects of reduced summer flows on the brook trout population and temperatures of a groundwater-influenced stream

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Abstract – Withdrawal of water from streams and groundwater is increasing in Midwestern North America and is a potential threat to coldwater fishes. We examined the effects of summer water withdrawals on brook trout *Salvelinus fontinalis* populations and water warming rates by diverting 50–90% of summer baseflow from a 602-m treatment zone (TZ) in a groundwater-influenced Michigan stream during 1991–1998. We compared density of brook trout in fall, and spring-to-fall growth and survival of brook trout, between the TZ and an adjacent reference zone (RZ) whose flows were not altered. Flow reductions had no significant effects on the density of brook trout in fall or spring-to-fall survival of brook trout. However, spring-to-fall growth of brook trout in the TZ declined significantly when 75% flow reductions occurred. Cold upstream temperatures and the relatively short study reach kept thermal habitat conditions excellent for brook trout in the TZ throughout the dewatering experiments. These findings suggest that brook trout can tolerate some seasonal loss of physical habitat if temperature conditions remain suitable. In summer 1999, we experimentally assessed the influence of flow reduction on the warming rate through the TZ by diverting from 0% to 90% of flow around the TZ in 3- or 4-day trials on a randomised schedule. Average daily temperature increased exponentially as stream flows declined from normal summer levels. Our findings suggest the risk of trout habitat loss from dewatering is potentially large and proportional to the magnitude of withdrawal, especially as thermal conditions approach critical levels for trout.

Key words: trout; water temperature; streamflow; growth; density

Introduction

Withdrawal of water from streams and groundwater is increasing in the Midwestern North America. For example, the amount of land in the state of Michigan that is irrigated for agriculture increased by 18.3% (202,520 ha to 239,677 ha) between 2007 and 2012 (USDA 2014), in contrast with 39,255 ha of land under irrigation in 1974 (USDA 1999). The resulting rise in water use for agricultural, industrial and domestic purposes poses a potential threat to streams and raises concerns about the effects of reduced stream flows and increased warming of streams on coldwater fishes. Although numerous studies of the

effects of flow reduction on trout have occurred in the western United States (e.g. Poff et al. 1997; Poff & Zimmerman 2010), where irrigation withdrawals to support agricultural operations have resulted in severe flow reductions in many streams, relatively little information is available to fisheries managers in the glaciated Midwest where groundwater-driven streams are widespread.

Negative relationships observed between summer water temperatures and stream trout density (e.g. Li et al. 1994; Wang et al. 2003; Wehrly et al. 2007; Zorn et al. 2011) suggest that watershed activities that increase summer water temperatures may reduce trout growth and survival in some types of

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streams. An array of factors such as solar radiation, atmospheric radiation, evaporation, and initial flow volume and temperature affect heat flux within a river reach (Bartholow 1989). At reduced flows, such as those resulting from surface water or groundwater withdrawals, water moves more slowly through a stream reach and its temperature more quickly equilibrates to ambient air temperatures. During summer, this typically results in increased warming rates for coldwater streams. If water withdrawals increase summer warming rates, then downstream habitats that are marginally warm for trout may become unsuitable.

The need to protect aquatic habitats in the western United States from excessive withdrawals led to the development of instream flow models, such as the Instream Flow Incremental Methodology (IFIM) (Milhous et al. 1989), which typically involve field data collection and habitat modelling and are used to project impacts on fish and habitat from altered streamflow. The primary input variables for IFIM models are water depth and velocity, substrate and cover. Even though it exerts a major influence on the distribution and density of salmonids and other fish species (Eaton et al. 1995; Stoneman & Jones 2000; Wehrly et al. 2003; Zorn et al. 2004), water temperature has often received less consideration in applications of these models. In addition, others have suggested caution when applying IFIM models in cold, groundwater-dominated streams (Nuhfer & Baker 2004; Wills et al. 2006). Clearly, a need exists to quantify the relationship between reduced stream flow, warming rate and trout abundance in groundwater-influenced streams.

In this study, we examined the effects of flow diversions (that simulated summer water withdrawals) on brook trout *Salvelinus fontinalis* in a small groundwater-influenced Michigan stream. We were also interested in the effects of water withdrawal on stream temperature because water temperature exerts a prominent influence on the physiology and behaviour of brook trout (Wehrly et al. 2007). Our objectives were to 1) assess the effects of the experimental water withdrawals on the density, growth and survival of brook trout, considering the reach's thermal characteristics; and 2) estimate the effects of water withdrawals on the warming rate of a small, groundwater-fed trout stream. Our project used data collected during a 15-year study of relationships between habitat availability (measured using IFIM protocols) and brook trout population dynamics (Nuhfer & Baker 2004) to highlight the importance of temperature in assessing the effects of streamflow changes on brook trout.

Methods

Study area

Hunt Creek is a small, third-order tributary to the Thunder Bay River, which flows through the north-eastern portion of Michigan's Lower Peninsula (Fig. 1). Its 24-km² catchment drains extensive glacial sands and gravels deposited approximately 10,000 years ago (Dorr & Eschman 1970). Hunt Creek has extremely stable groundwater-dominated streamflows. For example, from 1998 through 2006, the 95% exceedence flow at the downstream end of the Hunt Creek study area was 0.60 m³·s⁻¹, and the 5% exceedence flow was 0.84 m³·s⁻¹. Riparian vegetation consists primarily of mature white cedar *Thuja occidentalis*, tamarack *Larix laricina* and balsam fir *Abies balsamea*. During the course of the study, Hunt Creek supported a self-sustaining and relatively stable brook trout population and was closed to angling. The only common fish species in the Hunt Creek reach besides brook trout were mottled sculpin *Cottus bairdi* and slimy sculpin *Cottus cognatus* (Alexander & Hansen 1986).

Flow manipulations

We divided the study area of Hunt Creek into two sections: a 602-m (0.28 ha) treatment zone (TZ) and an 806-m (0.50 ha) reference zone (RZ) immediately downstream of where diverted flow returns to the channel (Fig. 1). Our ability to manipulate flows for the study was limited to the confines of the Hunt Creek Trout Research Area, which encompasses several kilometres of the headwaters of the stream. An upstream reference reach was not feasible because two similar-sized tributaries join less than 100 m upstream of the TZ and the upstream reaches differed from the TZ in size, channel dimensions and slope. The downstream RZ was closest in size, hydrology, gradient and length to the TZ and was situated entirely within the research area property. Canopy closure is nearly complete throughout the upper 500 m of the TZ.

During 1989–1990, we excavated a diversion channel around the 602-m-long, 4.6-m-wide TZ. We installed bulkheads at the upstream and downstream ends of the TZ (hereafter referred to as the upstream and downstream bulkheads) to provide a way to control discharge through the TZ and to support traps used to monitor fish movement (Fig. 1). Diverted discharge returned to Hunt Creek at the downstream bulkhead (mixing with TZ waters at a riffle immediately downstream) and flowed through the RZ.

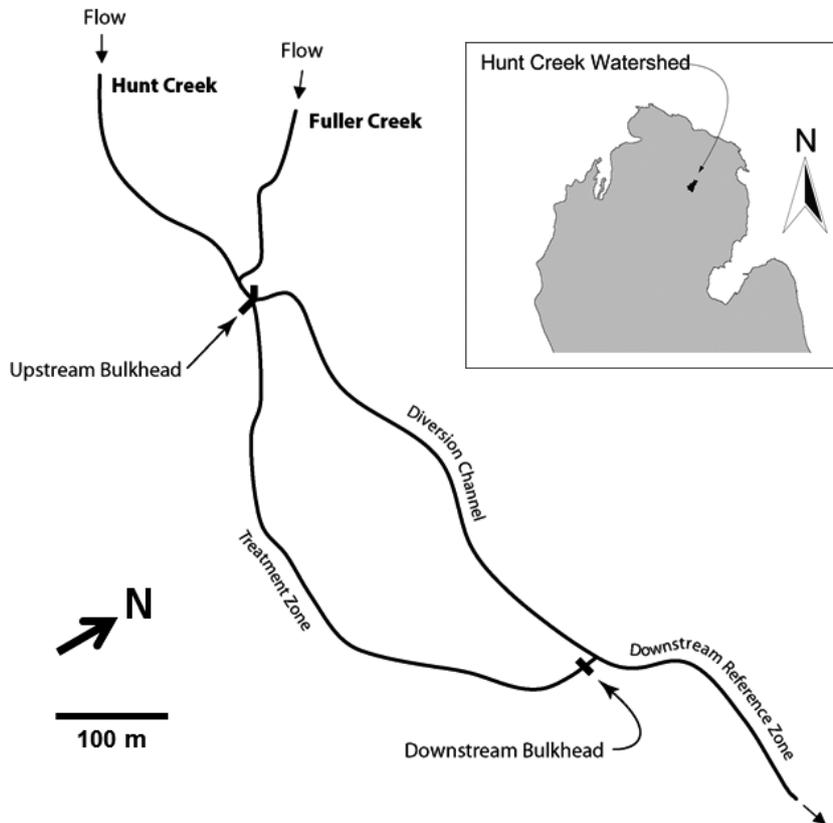


Fig. 1. Map of Hunt Creek study reach in the north-eastern portion of Michigan's Lower Peninsula showing location of flow diversion structure, treatment zone and reference zone. Temperature loggers were deployed at the upstream and downstream ends of the treatment zone.

To assess the effects of flow reduction on brook trout, we diverted water around the TZ between 1 June and 31 August each year from 1991 to 1998. Approximate diversion rates were 50% during 1991–1994, 75% during 1995–1996 and 90% in 1997–1998. These percentages were based on an average summer flow of $0.45 \text{ m}^3 \cdot \text{s}^{-1}$ in the TZ. We adjusted logs in the upstream bulkhead so that discharge was $0.23 \text{ m}^3 \cdot \text{s}^{-1}$ for 50% withdrawal simulations, $0.11 \text{ m}^3 \cdot \text{s}^{-1}$ for 75% and $0.045 \text{ m}^3 \cdot \text{s}^{-1}$ for 90%. We measured discharge at least once per month during each summer when diverting water to ensure that flow through the TZ was maintained at the desired level. Despite Hunt Creek's extremely stable, groundwater-driven hydrology, slight variation in daily flows occasionally occurred due to rainfall events. We systematically increased (as opposed to randomly selecting) flow diversion percentages during the 8 years that brook trout populations were monitored for two reasons. First, we hypothesised that if high flow reduction treatments adversely affected brook trout year classes in the TZ, these effects could carry forward to subsequent years when lower flow reduction treatments occurred, confounding study results. Second, starting with smaller diversions in early years allowed additional time for revegetation of the banks in the constructed bypass channel.

Effects on brook trout density

We estimated brook trout densities during the spring and fall (third week of April and third week of September) each year during 1984–1998 in both the TZ and the RZ, with 1984 to 1990 samples occurring under 0% withdrawal conditions. We used two-pass mark-and-recapture electrofishing with a 2-probe, 240-volt DC electrofishing unit towed behind wading electrofishers. Fish sampling began at the downstream end of the study area and proceeded upstream. We gave trout captured on the marking run a small caudal fin clip to identify them on the recapture run; clips regenerated between seasonal sampling events. Recapture collections were made 2 days after marking. We did not give different marks to fish in the TZ and the RZ because the bulkheads and fish traps (which were operated when electrofishing) blocked movement of trout between zones. The bulkheads blocked all upstream emigration from the TZ and the RZ during mark-recapture density estimate periods. Traps intercepted fish attempting to migrate downstream from the TZ, and we returned any trapped fish to the TZ. A 13-m-long culvert with high-velocity flows limited downstream movement of fish from the RZ.

We computed population estimates for 25-mm-length groups of trout using the Chapman

modification of the Petersen mark–recapture method (Hayes et al. 2007). We aged 20 or more brook trout per 25-mm-length group (if sufficient fish were available) from scales collected each spring and fall, and used the ageing results to apportion population estimates by length groups into estimates by age group for age-0 to age-4 fish. The spring and fall sampling periods and methods used provided data consistent with annual population estimate surveys for brook trout in Hunt Creek that extend back to 1949 (Grossman et al. 2012). We calculated spring-to-fall survival by dividing the fall density estimate by the spring density estimate for each age group of brook trout.

Downstream movement into or out of the TZ during water diversion experiments was determined from catches in inclined screen fish traps (Wolf 1950) located at the upstream and downstream bulkheads. The upstream and downstream bulkhead traps were operated from June 1 to August 31 during 1991–1996. All traps were not operated prior to June 1 because high flows and debris transport rapidly plugged traps, rendering them nonfunctional. Upstream traps were not operated after 1 September because they rapidly plugged with debris (especially falling leaves) at this time of year. The downstream traps were operated each year until fall population estimates had been made. During other times of the year, larger trout were able to move downstream or upstream if they jumped over the 0.5-m-high stop logs in the bulkhead. In 1997–1998 (90% flow reduction years), we made an extra effort to operate all traps during the entire period between spring and fall population estimates. When operating, the traps only caught fish moving downstream and totally prevented upstream fish movement, because the screen (trap entrance) rested on the stop logs and intercepted all water flowing over the stop logs. The traps were usually checked three times per week. All brook trout captured in the traps were counted, measured and released downstream.

We used analysis of variance (ANOVA) to determine whether brook trout density in fall, spring-to-fall growth of brook trout or spring-to-fall survival of brook trout were significantly different between the TZ and the RZ during the four time periods of flow reduction treatments. Focusing on growth and survival between the spring and the fall surveys (as opposed to annual growth and survival) allowed us to better assess the effects of each year's flow treatment on fish, because these estimates were less influenced by prior events (e.g. earlier flow treatments or winter conditions) that could affect annual estimates of growth and survival. We looked at density for brook trout up to age-4, spring-to-fall growth for brook trout up to age-3 (mean length-at-age of age-0 fish in

fall) and spring-to-fall survival of brook trout for age-1 to age-3 fish. Spring-to-fall growth and survival analyses were limited to brook trout younger than age-4 because relatively few age-4 and older fish were captured, leading to high variation in growth and survival values for these older age groups. Zone (TZ or RZ), time period (years of 0%, 50%, 75% or 90% flow reduction) and age class of brook trout were main effects in each ANOVA model. When appropriate, we transformed the data to meet the necessary distributional assumptions of ANOVA. We focused our analyses on finding significant zone \times time period interactions that would be indicative of variability in fall density, spring-to-fall growth or spring-to-fall survival of brook trout between the TZ and the RZ during the flow reduction time periods. Once we identified significant interactions with ANOVA, we focused on comparisons among levels of each main effect involved in the interaction to assess differences between zones for each time period. We used Bonferroni-adjusted *P*-values for all multiple comparisons. We set the rejection criterion α at 0.05 for all comparisons. All analyses were conducted with PASW Statistics for Windows (version 18.0; SPSS 2009).

Effects on downstream warming rate

From 1 June to 31 August 1999, after the brook trout population evaluation phase of the study had concluded, we experimentally assessed the influence of flow reductions on the warming rate of water flowing through the TZ. We diverted 0–90% of flow from the TZ for 3- or 4-day trials (2 trials per week). Stream discharge levels used during the trials were randomly selected and ranged from $0.05 \text{ m}^3 \cdot \text{s}^{-1}$ to $0.59 \text{ m}^3 \cdot \text{s}^{-1}$. We deployed multiple Onset Stowaway XTI thermometers at both the upstream and the downstream ends of the TZ to ensure that data would be available even if some thermometers malfunctioned. We calibrated thermometers selected for deployment based on 240 measurements taken over a 10-day deployment in an enclosed tank receiving constant flow from an artesian spring with a mean temperature of $7.8 \text{ }^\circ\text{C}$. We deployed only thermometers that yielded the same mean temperature reading and same difference between maximum and minimum readings over the 10-day period. We used the same calibration methods at the end of the 1999 diversion experiments to confirm that thermometers maintained calibration through the summer, and only used data from thermometers that maintained the same calibration (relative to each other) at the beginning and end of the summer. All thermometers were set to take hourly readings throughout the summer. The downstream thermometers took temperature

readings 30 min later than the upstream thermometers to allow for transport time of water through the study reach. The 30-min value corresponded to the estimated travel time of water through the TZ based on the average current velocity estimate at a 75% flow reduction. We measured hourly air temperature during the summer with two Onset Stowaway XTI thermometers deployed inside a ventilated thermometer shelter placed 1.7 metres above the ground in a shaded location near the TZ and used daily mean, minimum and maximum air temperature data from them as potential parameters in warming rate models.

We subtracted the upstream temperature from the downstream temperature for each hourly reading taken throughout the summer. We typically completed twice-a-week adjustments to stop logs to initiate a new flow diversion treatment by 10:00 am. For these days, we deleted hourly temperature data collected at any hour that day prior to noon to assure that temperature data collected during that day applied only to the new discharge level. We deleted temperature data collected during hours when rainfall might have caused a substantial change in stream discharge. Measurements of stream stage at 15-min intervals throughout the year (from a Sutron stage height recorder located in the RZ) allowed us to determine precisely when stream stage began to rise and when it returned to normal levels. After removing hourly temperature data affected by our intentional changes to discharge and those caused by rainfall events, we calculated daily mean and daily maximum water temperatures. We determined the mean daily change in temperature in the TZ by subtracting mean daily temperature upstream from mean daily temperature downstream. We also computed the daily differences between maximum daily temperatures measured at the upstream and the downstream sites. We standardised values to heating per km of stream by dividing observed heating by the 0.602 km length of the TZ.

We used multiple linear regressions to describe the relationship between downstream warming rate and the stream discharge and air temperature variables (daily mean, daily minimum and daily maximum values). We used the resulting regression equation relating increase in mean daily water temperature to stream discharge to estimate downstream losses of thermally suitable habitat from Hunt Creek at different levels of flow reduction. To make predictions of habitat loss, we assumed that no additional downstream changes in flow occurred and designated the upstream diversion bulkhead and its mean July temperature (14.5 °C) as our starting point. Then, for the warming rate associated with each flow reduction, we calculated how many kilometres water would travel before its mean daily temperature reached 19 °C,

above which wild brook trout density would likely be reduced (Wehrly et al. 2007; Zorn et al. 2011).

Results

Effects on brook trout population

Flow reductions had little effect on fall densities of brook trout in the TZ. The Zone × Period × Age interaction result indicated no significant difference in densities of individual age groups between the TZ and the RZ among flow reduction treatment periods (ANOVA: $F = 0.54$; d.f. = 12, 110; $P = 0.887$; Table 1). We found no significant differences among flow reduction treatment periods in fall brook trout densities between the TZ and the RZ, as evidenced by the nonsignificant Zone × Period interaction (ANOVA: $F = 0.68$; d.f. = 3, 110; $P = 0.566$; Table 2; Fig. 2). Significant differences in fall densities occurred among brook trout age classes (ANOVA: $F = 908.05$; d.f. = 4, 110; $P < 0.001$) and between the TZ and the RZ for individual age classes (ANOVA: $F = 3.28$; d.f. = 4, 110; $P = 0.014$). The ANOVA model assessing effects of reach, period and age accounted for 98% of the variation in fall brook trout density estimates (Table 1).

Flow reductions in the TZ had some effects on the growth of brook trout from spring to fall. We found a

Table 1. Summary of ANOVA models used to assess the effects of treatment or reference zone (Zone), flow reduction period (Period) and brook trout age class (Age) in explaining variation in fall density, spring-to-fall growth and spring-to-fall survival of brook trout in Hunt Creek, Michigan. N = total number of samples used in analysis.

Source of variation	F	P	d.f.
Fall density ($N = 150$)			
Zone	1.67	0.199	1, 110
Period	3.32	0.022	3, 110
Age	908.05	<0.001	4, 110
Zone × Period	0.68	0.566	3, 110
Zone × Age	3.28	0.014	4, 110
Period × Age	1.10	0.370	12, 110
Zone × Period × Age	0.54	0.887	12, 110
Spring-to-fall growth ($N = 120$)			
Zone	12.06	0.001	1, 88
Period	1.95	0.127	3, 88
Age	89.25	<0.001	3, 88
Zone × Period	2.91	0.039	3, 88
Zone × Age	1.10	0.355	3, 88
Period × Age	1.10	0.369	9, 88
Zone × Period × Age	0.88	0.550	9, 88
Spring-to-fall survival ($N = 90$)			
Zone	4.53	0.037	1, 66
Period	3.31	0.025	3, 66
Age	82.25	<0.001	2, 66
Zone × Period	0.66	0.581	3, 66
Zone × Age	6.32	0.003	2, 66
Period × Age	1.16	0.341	6, 66
Zone × Period × Age	0.73	0.630	6, 66

Effects of flow reduction on brook trout and stream temperatures

Table 2. Mean and standard error of the mean (SE) of fall density, spring-to-fall growth (length-at-age for age-0 fish) and spring-to-fall survival of brook trout in the Treatment (T) and Reference (R) zones of Hunt Creek under four levels of flow reduction (0, 50, 75 and 90 per cent). Flow reductions occurred in the treatment zone only.

Zone	Period	Metric	Age				
			0	1	2	3	4
Fall density (number per hectare)							
T	0	Mean	2962.4	1111.6	353.6	35.7	6.8
		SE	179.4	90.8	45.3	8.1	3.5
R	0	Mean	2600.5	1019.4	435.1	72.8	6.6
		SE	124.4	123.4	59.6	19.3	1.8
T	50	Mean	2786.4	1237.9	447.2	53.2	13.8
		SE	180.7	112.2	94.3	12.6	4.4
R	50	Mean	2611.2	1187.1	482.5	55.6	17.3
		SE	179.9	108.7	163.0	10.8	4.7
T	75	Mean	3605.1	1796.2	450.2	58.2	5.8
		SE	251.9	161.8	104.9	23.7	5.8
R	75	Mean	3087.1	1134.9	391.5	48.4	24.9
		SE	641.9	86.5	15.9	5.1	11.1
T	90	Mean	3095.6	1387.7	317.6	62.0	0.0
		SE	547.3	42.9	46.1	4.0	0.0
R	90	Mean	2880.9	1027.2	343.3	62.4	13.0
		SE	9.3	59.4	68.8	3.0	0.9
Spring-to-fall growth (mm)							
T	0	Mean	80.5	36.7	43.4	55.0	14.7
		SE	1.0	1.7	2.8	5.3	9.7
R	0	Mean	83.0	36.7	39.6	53.6	50.6
		SE	1.5	2.2	3.2	4.5	7.6
T	50	Mean	79.7	32.6	36.7	43.7	17.4
		SE	1.6	3.0	8.6	13.0	16.8
R	50	Mean	85.4	38.0	49.8	40.6	39.4
		SE	1.7	4.5	6.0	5.8	13.8
T	75	Mean	75.1	32.0	25.7	36.4	41.0
		SE	1.4	1.7	0.8	5.5	
R	75	Mean	86.1	34.9	47.8	47.5	15.9
		SE	1.0	1.8	7.6	3.2	10.1
T	90	Mean	75.3	35.8	35.5	32.1	
		SE	1.9	3.3	1.5	12.4	
R	90	Mean	83.2	36.5	48.8	50.7	36.4
		SE	1.8	0.8	3.7	0.1	19.0
Per cent surviving from spring to fall							
T	0	Mean		73.4	41.5	16.1	71.3
		SE		6.6	4.9	3.2	55.7
R	0	Mean		85.1	64.8	22.6	15.5
		SE		6.3	5.9	4.7	5.4
T	50	Mean		92.8	41.8	29.2	156.1
		SE		11.9	6.6	3.0	79.0
R	50	Mean		111.2	70.0	20.2	42.6
		SE		10.2	16.8	3.2	15.3
T	75	Mean		86.7	67.0	45.0	31.4
		SE		1.2	17.7	17.9	0.0
R	75	Mean		94.1	79.6	15.2	80.9
		SE		4.7	10.3	2.4	10.9
T	90	Mean		85.4	33.2	21.6	0.0
		SE		11.0	2.3	3.6	0.0
R	90	Mean		112.5	90.2	13.2	43.7
		SE		41.0	37.2	0.9	24.7

significant Zone × Period interaction (ANOVA: $F = 2.91$; d.f. = 3, 88; $P = 0.039$; Table 1), indicating a pattern in the differences in brook trout growth between zones for flow reduction treatments. The greatest differences in growth between the TZ and the RZ occurred at higher levels of flow reduction

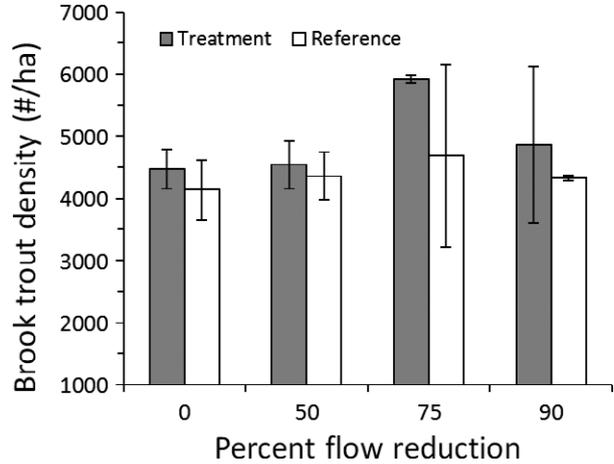


Fig. 2. Mean fall densities of brook trout in the treatment and reference zones of Hunt Creek for each flow reduction period. Flow was reduced only in the treatment zone. Error bars indicate 95% confidence intervals for estimated means.

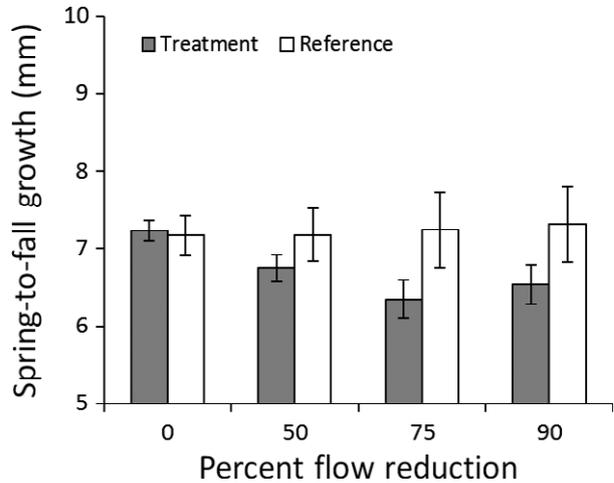


Fig. 3. Spring-to-fall growth of brook trout in the treatment and reference zones of Hunt Creek for each flow reduction period. Flow was reduced only in the treatment zone. Error bars indicate 95% confidence intervals for estimated marginal mean values.

(Fig. 3); pairwise comparisons showed the difference in growth of brook trout at 75% flow reduction was within rounding error of significance ($t = 2.546$; d.f. = 88; Bonferroni-adjusted $P = 0.051$). The effect was not specific to brook trout age classes, as evidenced by the lack of a significant Zone × Period × Age interaction term in the model (ANOVA: $F = 0.88$; d.f. = 9, 88; $P = 0.550$; Table 1). Spring-to-fall growth increments for age-0 to age-2 brook trout were typically higher in the RZ (ANOVA: $F = 12.06$; d.f. = 1, 88; $P = 0.001$; Tables 1 and 2). Age was also significant in the model, indicating that brook trout age class also explained significant variation in the data (ANOVA: $F = 89.25$; d.f. = 3, 88; $P < 0.001$).

We saw no significant effect of flow reductions on spring-to-fall survival of brook trout, as evidenced by

the lack of a significant Zone × Period (ANOVA: $F = 0.66$; d.f. = 3, 66; $P = 0.581$) and Zone × Period × Age (ANOVA: $F = 0.73$; d.f. = 6, 66; $P = 0.630$) interaction terms in the model (Table 1). Significant variation in annual survival was explained by Age indicating differences in survival among age classes (ANOVA: $F = 82.25$; d.f. = 2, 66; $P < 0.001$). Survival also varied among time periods, as indicated by a significant Period effect (ANOVA: $F = 3.31$; d.f. = 3, 66; $P = 0.025$).

Effects on downstream warming rate

Upstream temperatures and the relatively short study reach kept thermal habitat conditions excellent for brook trout in the TZ throughout the 1991–1998 dewatering experiments. However, we did note increased rates of downstream warming caused by the diversions. For the flow reduction treatment periods, the mean July temperature values at the upstream and downstream ends of the TZ were as follows: 50% (14.4 and 14.6 °C), 75% (14.2 and 14.6 °C) and 90% (14.2 and 14.7 °C). Across all summers when flows were diverted, mean July water temperatures at the downstream end of the TZ ranged from 13.8 to 15.0 °C. As this was the upstream end of the RZ, RZ temperatures also remained excellent throughout the study.

During the 1999 flow reduction experiments in the TZ, the difference between upstream and downstream average daily water temperatures increased exponentially as stream discharge decreased from normal

summer levels of around $0.5 \text{ m}^3 \cdot \text{s}^{-1}$ down to $0.05 \text{ m}^3 \cdot \text{s}^{-1}$ (adjusted $R^2 = 0.53$; $P < 0.001$; total d.f. = 81; Figure 4). No air temperature variables contributed significantly to the fit of the regression model relating the changes in average daily water temperature to stream discharge. Flow reductions also had significant effects on the downstream rate of change in maximum daily water temperatures in the TZ (adjusted $R^2 = 0.45$; $P < 0.001$; total d.f. = 81; Fig. 5). We estimated that withdrawal of 90% of summer baseflow from Hunt Creek could result in a downstream loss of nearly 21 km of thermally suitable brook trout habitat if no other downstream changes in flow occurred (Fig. 6). To estimate this, we used the regression equation relating increase in mean daily water temperature to flow reduction (Fig. 4) and assumed habitat becomes unsuitable for brook trout when the mean daily water temperature reaches 19 °C. Predicted losses at 75% and 50% flow reductions were 18 km and 14 km respectively (Fig. 6).

Discussion

Flow reduction effects on brook trout

The availability of suitably cold water in summer is a key factor limiting the distribution and density of brook trout in streams (Eaton et al. 1995; Zorn et al. 2002; Wehrly et al. 2003). Wild brook trout density in Michigan streams rarely exceeds $10 \text{ kg} \cdot \text{ha}^{-1}$ when mean July water temperatures are higher than 19 °C

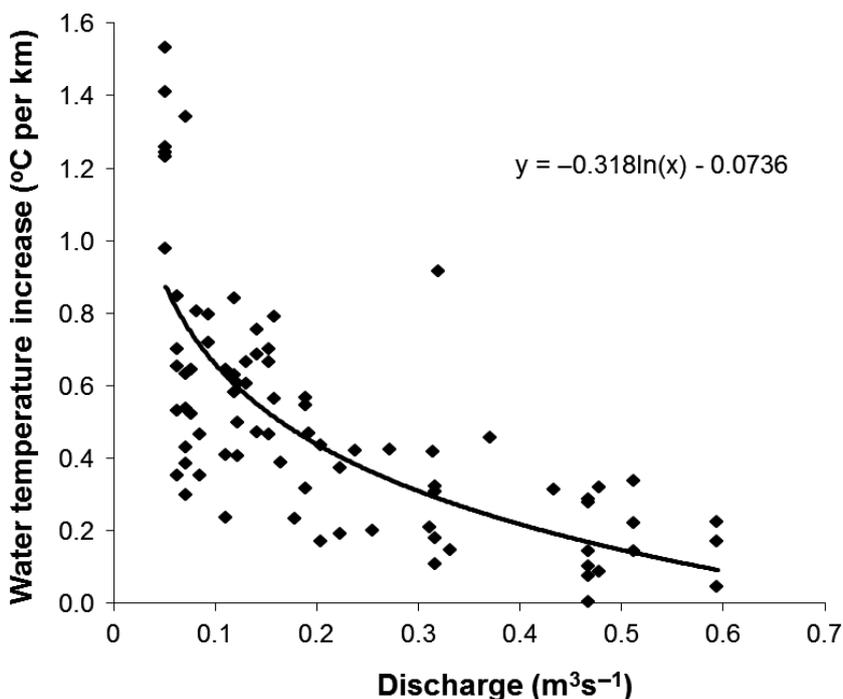


Fig. 4. Increase in mean daily water temperature ($^{\circ}\text{C} \cdot \text{km}^{-1}$) in the dewatered treatment zone of Hunt Creek as a function of discharge in June, July and August 1999 (adjusted $R^2 = 0.53$; $P < 0.001$; total d.f. = 81).

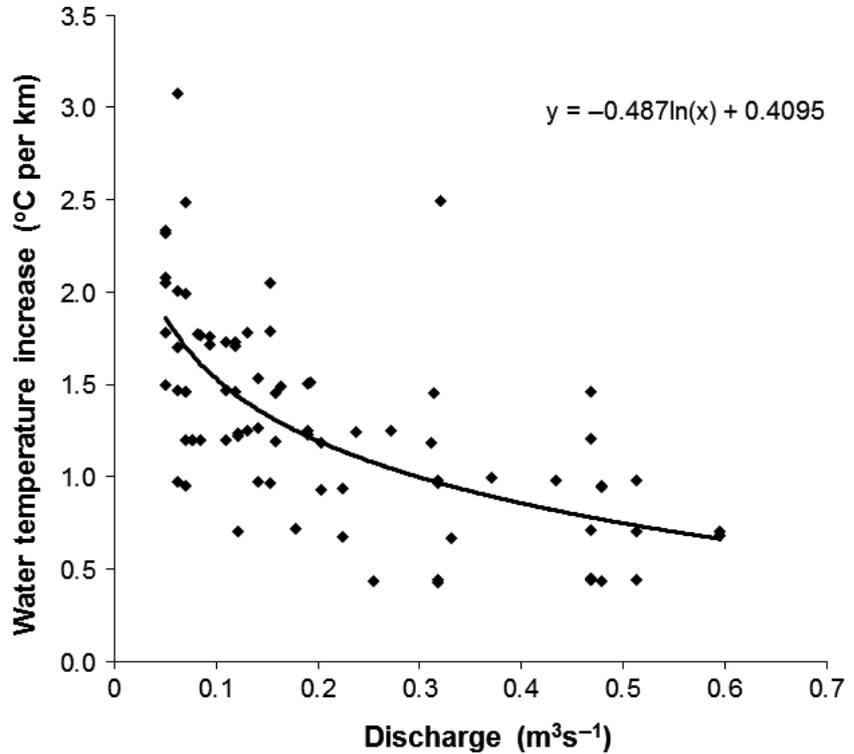


Fig. 5. Increase in maximum daily water temperature ($^{\circ}\text{C}\cdot\text{km}^{-1}$) in the dewatered treatment zone of Hunt Creek as a function of discharge in June, July and August 1999 (adjusted $R^2 = 0.45$; $P < 0.001$; total d.f. = 81).

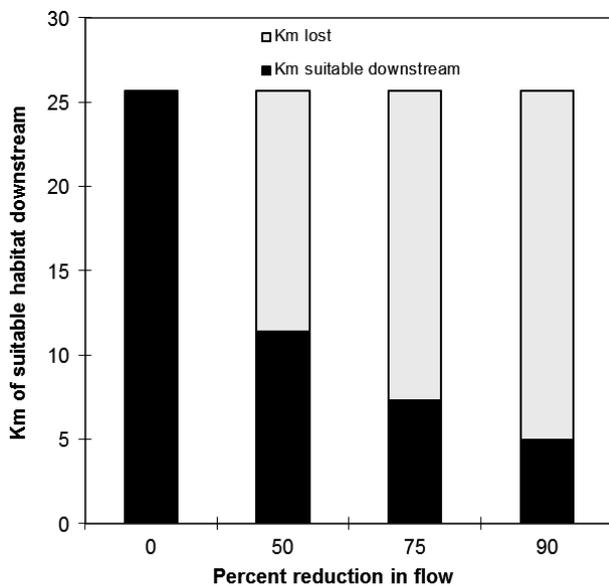


Fig. 6. Estimates of thermally suitable habitat (black bars) for brook trout and habitat lost (gray bars) downstream of the upstream end of the treatment zone of Hunt Creek at different percentages of flow reduction. Estimates used Hunt Creek's initial mean daily water temperature (14.5°C), and the warming rate (in $^{\circ}\text{C}\cdot\text{km}^{-1}$) of the stream associated with the discharge at each level of flow reduction (Fig. 4). Estimates assume no additions or losses of flow downstream. Habitat was considered unsuitable for brook trout when mean daily water temperature reached 19°C .

(Wehrly et al. 2007; Zorn et al. 2011). Our finding that the brook trout population in the Hunt Creek TZ suffered few adverse effects from summer water

withdrawals indicates that the species can tolerate some loss of physical habitat if temperature conditions remain suitable. We found little change in brook trout density in the TZ, despite flow diversions up to 90%, but noted that temperatures in the TZ or the RZ remained well below 19°C . Nuhfer & Baker (2004) found poor correlations between estimates of habitat availability (i.e. weighted usable area estimates from Physical Habitat Simulation (PHABSIM) models) for the Hunt Creek TZ at flows used in this study and brook trout density or survival over summer. White et al. (1976) inferred that higher baseflow in Midwestern streams would increase trout density, but in the streams they studied, higher winter baseflow appeared to be more important than summer baseflow. The widespread geographical distribution of brook trout across cold North American streams, some with very low natural summer flows, is further evidence of the species' tolerance to summer drought flows when coldwater habitats are accessible.

Despite suitable temperatures, we noted a significant pattern of differences in spring-to-fall growth of brook trout between the TZ and the RZ at higher levels of flow reduction. Such declines may relate to reduced food availability. For example, significantly lower densities of filter feeding and grazing insect taxa, as well as insects classified as obligate erosional zone taxa (e.g. Ephemeroptera, Plecoptera and Trichoptera), were documented in the TZ when 90% of flow was diverted (Wills et al. 2006). Hakala &

Hartman (2004) noted that brook trout condition declined in several headwater streams in West Virginia during drought conditions, despite suitable water temperatures and dissolved oxygen levels. Consistent with our findings, Railsback & Rose (1999) found that summer growth of rainbow trout *Oncorhynchus mykiss* in California streams was more affected by factors controlling food consumption than by the direct effects of temperature. Hinz & Wiley (1998) noted a significant relationship between growth rates of brook trout and macroinvertebrate densities in Michigan streams.

The lack of change in spring-to-fall survival of brook trout in Hunt Creek may relate to limited movement of brook trout from deeper pools and their tolerance for crowding under low-flow conditions. Many of the pools and deep runs created at the channel-shaping discharge in the Hunt Creek TZ continued to provide suitable habitat when discharge was reduced to 10% of baseflow levels. We observed rapid movement of fish into these deep-water refugia on 1 June in each year that we reduced flows by 75% or 90%. After that, downstream movement of brook trout into or out of the TZ during dewatering experiments was negligible, with the net change in density of age-0 and age-1 and older fish in any flow reduction treatment being less than 3% of the estimated number of fish in the TZ that year (Nuhfer & Baker 2004). Binns (1994) observed that deeper and narrower stream channels formed by stream improvement devices helped brook trout survive severe drought flows in Wyoming streams. Kraft (1972) also observed movement of tagged brook trout from runs into pools when summer flows were reduced by 90%. Clothier (1954) found that severe flow reduction in irrigation canals induced upstream movement of trout. Hayes et al. (1998) documented migration of brook trout to a headwater stream several kilometres upriver to avoid stressful summer temperatures in the mainstem of a river in Michigan's Upper Peninsula. Even though traps blocked upriver movement of fish out of the TZ, the fact that survival rates remained high (even at severe levels of dewatering) indicates that reduced living space in the TZ did not constrain survival.

Study limitations

Our study's strength lies in the eight summers of flow reduction treatment data that were collected and that we studied a relatively large, wild brook trout population in an extensive reach of a natural stream. However, our findings are somewhat limited by the methods employed in this study. For example, the TZ was located upstream of the RZ because the upstream end of the TZ provided the only feasible place to

install a diversion channel. Here, an approximately 100 m of excavated channel enabled TZ water to be diverted to a nearby natural tributary that entered Hunt Creek at the downstream end of the TZ. We could not have put the diversion at another location because the drainage topography of the Hunt Creek basin and ownership issues prevented it. As downstream thermal changes in the TZ were minor (relative to the thermal tolerances of brook trout), the flow reduction effects we observed were more likely associated with changes in physical habitat conditions than water quality conditions. The slight change in downstream temperatures (no more than 0.5 °C increase) is indicative of a lack of substantial downstream effects of the TZ on water quality conditions in the RZ. As we were studying wild populations over the course of several years, prior flow reduction treatments could potentially affect brook trout density in subsequent years (because the population structure could not be 'reset' each season). However, the relatively constant densities of brook trout we observed in the TZ, despite flow reductions that grew progressively more severe over the course of the study, clearly indicate that summer flow reduction did not induce a density response in the TZ (Table 2; Fig. 2). In addition, carry-over effects were not an issue in the growth or survival analyses because we looked at differences between spring and fall measurements (rather than year-to-year differences) and explicitly accounted for Period and Age in ANOVA analyses.

We collected brook trout spring and fall population estimate data several weeks before and after each seasonal flow reduction event occurred. We observed significant reductions in growth of brook trout at the 75% flow reduction level, but growth changes due to flow reduction may have been more severe (and potentially significant at 90% flow reduction) if field sampling had occurred immediately before and after each flow reduction treatment. Our density estimates may have differed if there was substantial movement of brook trout into or out of the TZ during these short time windows, but brook trout movement data collected for the TZ in 1997 and 1998 (when we operated traps for the entire period between spring and fall estimates) suggest this scenario is unlikely. The net change in the number of brook trout in the TZ due to downstream immigration and emigration was three fish in 1997 and 1 fish in 1998. The average change in brook trout numbers in the TZ due to immigration or emigration between 1 June and 31 August was no more than 22 fish for any flow reduction treatment (Nuhfer & Baker 2004). As the estimated number of fish in the TZ averaged more than 1250 fish for each flow reduction treatment, these numbers are comparatively small (Table 2). As movement during these time windows was limited,

our spring-to-fall survival estimates are probably robust.

Use of scale ages for brook trout could introduce a bias, but is probably not a major concern for this study. Hunt Creek has one of the longest population data sets for stream brook trout in the world, and studies here have provided the basis for understanding stream dynamics of trout populations in Midwestern North America (e.g. McFadden et al. 1976; Alexander & Hansen 1986; Grossman et al. 2012). Brook trout in Hunt Creek have been aged using scales for many decades for these and other studies, and growth patterns here are well understood. Nevertheless, in some years, we clipped adipose fins on age-0 brook trout to have known age fish in the population for subsequent recapture and age verification. The scale reader used these samples to ensure their techniques produced accurate ages. In addition, we worked with young-aged brook trout, which show relatively little bias between scale and otolith-based ages (Stolarksi & Hartman 2008). While we documented negative effects of flow reductions on brook trout growth (Fig. 3), future efforts should uniquely mark individual brook trout to enable further clarification of effects of flow reduction on growth rates.

Effects on downstream warming rate

The increase in water warming we observed when we reduced flow by 75% or more indicated a potential for biologically significant adverse effects on fish communities in coldwater streams. We are unaware of studies in the literature that quantify the increased rates of warming attributable to water withdrawal in groundwater-dominated streams. In Hunt Creek, increased heating occurred even though the TZ was relatively short (0.602 km) and completely shaded throughout most of its length. Slower warming is expected when streams are well shaded and when width-to-depth ratios are low (Bartholow 1989). The net rate of warming we observed (especially at low discharge levels) may have been reduced by groundwater infiltration in the Hunt Creek TZ. For example, if $0.01 \text{ m}^3 \cdot \text{s}^{-1}$ of $9 \text{ }^\circ\text{C}$ groundwater flowed into the TZ, it would have substantially reduced the rate of warming, especially when discharge at the upstream end of the zone was set at $0.04 \text{ m}^3 \cdot \text{s}^{-1}$. Unfortunately, our estimates of discharge at the upstream and downstream ends of the TZ were not precise enough to detect such slight differences in flow.

Temperature elevation due to flow reductions may have had little effect on the brook trout population in the TZ during our study as mean July temperature at the downstream end of the TZ averaged $14.6 \text{ }^\circ\text{C}$, well below the thermal tolerance limits for brook trout (Wehrly et al. 2007). However, the three levels of

water diversion in our study could lead to substantial losses of suitable trout habitat downstream if additional inputs of groundwater do not occur (Fig. 6). Under these conditions, we estimate that diversion of 90% of summer baseflow would result in a loss of over 80% (20 km) of thermally suitable brook trout habitat in Hunt Creek (Fig. 6).

Management implications

Our findings and the previous assessment of PHABSIM-based habitat predictions in Hunt Creek (Nuhfer & Baker 2004) suggest that depth, velocity and cover are inadequate predictors of brook trout population response to reduced summer flows and that water temperature should be considered a key aspect of summer low-flow habitat. Furthermore, increased rates of water warming resulting from water diversions may pose the greatest threat to coldwater fishes in Midwestern streams. The increased warming rate for maximum daily temperature we observed ($2.7\text{--}4.4 \text{ }^\circ\text{C} \cdot \text{km}^{-1}$) at high dewatering levels would quickly make downstream reaches of many Midwestern trout streams uninhabitable for coldwater species, unless additional groundwater enters. Our analysis of warming relative to percentage of water withdrawn showed that the risk of trout habitat loss from dewatering is very large and proportional to the magnitude of withdrawal.

Negative effects of water withdrawal on brook trout would be most apparent in streams receiving few downstream inputs of groundwater, or reaches where baseline summer temperatures under normal flow conditions approach levels stressful for brook trout. Modelled responses of fish communities in Michigan streams to flow reduction by Zorn et al. (2012) highlighted the difference in response between cold, highly groundwater-fed streams and streams that receive less groundwater and are somewhat warmer, but still suitable for trout. In the former (cold streams), they estimated that nearly half of the flow could be removed before substantial declines in populations of species characteristic of this stream type occurred. In the latter type (i.e. cold-transitional streams), declines in trout abundance typically occurred at around 10% flow reduction, because these streams had baseline summer temperatures that were closer to the edge of thermal tolerance levels for trout (Zorn et al. 2012). In acknowledgement of the importance of water temperature to fish communities, and the effects of water withdrawal on warming rates, models developed by the state of Michigan to assess the effects of water withdrawal on stream fish communities included both summer water temperature and downstream warming components (Zorn et al. 2008).

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References

- Alexander, G.R. & Hansen, E.A. 1986. Sand bed load in a brook trout stream. *North American Journal of Fisheries Management* 6: 9–23.
- Bartholow, J.M. 1989. Stream temperature investigations: field and analytic methods. Instream flow information paper 13, U.S. Fish and Wildlife Service, Biological Report 89(17). Washington, DC.
- Binns, N.A. 1994. Long-term responses of trout and macrohabitats to habitat management in a Wyoming headwater stream. *North American Journal of Fisheries Management* 14: 87–98.
- Clothier, W.D. 1954. Effect of water reductions on fish movement in irrigation diversions. *Journal of Wildlife Management* 18: 150–160.
- Dorr, J.A. Jr & Eschman, D.F. 1970. *Geology of Michigan*. Ann Arbor: The University of Michigan Press.
- Eaton, J.G., McCormick, J.H., Goodno, B.E., O'Brien, D.G., Stefany, H.G., Hondzo, M. & Scheller, R.M. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* 20: 10–18.
- Grossman, G.D., Nuhfer, A., Zorn, T., Sundin, G. & Alexander, G. 2012. Population regulation of brook trout (*Salvelinus fontinalis*) in Hunt Creek Michigan: a 50-year study. *Freshwater Biology* 57: 1434–1448.
- Hakala, J.P. & Hartman, K.J. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia* 515: 203–213.
- Hayes, D.B., Taylor, W.W., Drake, M.T., Marod, S.M. & Whelan, G.E. 1998. The value of headwaters to brook trout (*Salvelinus fontinalis*) in the Ford River, Michigan, USA. In: Haigh, M.J., Kreecek, J., Rajwar, G.S. & Kilmartin, M.P., eds. *Headwaters: water resources and soil conservation*. New Delhi: Oxford and IBH Publishing Co., pp. 175–185.
- Hayes, D.B., Bence, J.R., Kwak, T.J. & Thompson, B.E. 2007. Abundance, biomass and production. In: Guy, C., Brown, M., eds. *Analysis and interpretation of freshwater fisheries data*. Bethesda: American Fisheries Society, pp. 327–374.
- Hinz, L.C. Jr & Wiley, M.J. 1998. Growth and production of juvenile trout in Michigan streams: influence of potential ration and temperature. Ann Arbor: Michigan Department of Natural Resources, Fisheries Research Report 2042.
- Kraft, M.E. 1972. Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada* 19: 1405–1411.
- Li, H.W., Lamberti, G.A., Pearsons, T.N., Tait, C.K., Li, J.L. & Buckhouse, J.C. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. *Transactions of the American Fisheries Society* 123: 627–640.
- McFadden, J.T., Alexander, G.R. & Shetter, D.S. 1976. Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 24: 1425–1459.
- Milhous, R.T., Updike, M.A. & Schneider, D.M. 1989. Physical habitat simulation system reference manual: version 2. Instream flow information paper 26. Biological Report 89(16), Washington, DC: U.S. Fish and Wildlife Service.
- Nuhfer, A.J. & Baker, E.A. 2004. A long-term field test of habitat change predicted by PHABSIM in relation to brook trout population dynamics during controlled flow reduction experiments. Fisheries Research Report 2068. Ann Arbor: Michigan Department of Natural Resources.
- Poff, N.L. & Zimmerman, J.K.H. 2010. Ecological responses to altered flow regimes: a literature review to inform environmental flows science and management. *Freshwater Biology* 55: 194–20.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B., Sparks, R. & Stromberg, J. 1997. The natural flow regime: a new paradigm for riverine conservation and restoration. *BioScience* 47: 769–784.
- Railsback, S.F. & Rose, K.A. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. *Transactions of the American Fisheries Society* 128: 241–256.
- SPSS. 2009. PASW Statistics for Windows, version 18.0. Chicago, IL: SPSS, Inc.
- Stolarski, J.T. & Hartman, K.J. 2008. An evaluation of the precision of fin ray, otoliths, and scale age determinations for brook trout. *North American Journal of Fisheries Management* 28: 1790–1795.
- Stoneman, C.L. & Jones, M.L. 2000. The influence habitat features on the biomass and distribution of three species of southern Ontario stream salmonids. *Transactions of the American Fisheries Society* 129: 639–657.
- United States Department of Agriculture (USDA), 1999. 1997 Census of Agriculture, Michigan State and County Data, Volume 1, Geographic Area Series Part 22. Document AC97A-22, Washington, DC: USDA.
- USDA. 2014. 2012 Census of agriculture, Volume 1, Chapter 1, State level data: Michigan. Washington, DC. Available at: http://www.agcensus.usda.gov/Publications/2012/Full_Report/Volume_1,_Chapter_1_State_Level/Michigan/st26_1_009_010.pdf
- Wang, L., Lyons, J. & Kanehl, P. 2003. Impacts of urban land cover on trout streams in Wisconsin and Minnesota. *Transactions of the American Fisheries Society* 132: 825–839.
- Wehrly, K.E., Wiley, M.J. & Seelbach, P.W. 2003. Classifying regional variation in thermal regime based on stream fish

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- community patterns. *Transactions of the American Fisheries Society*. *Transactions of the American Fisheries Society* 132: 18–38.
- Wehrly, K.E., Wang, L. & Mitro, M. 2007. Field-based estimates of thermal tolerance limits for trout: incorporating exposure time and temperature fluctuation. *Transactions of the American Fisheries Society* 136: 365–374.
- White, R.J., Hansen, E.A. & Alexander, G.R. 1976. Relationship of trout abundance to stream flow in Midwestern streams. In: Osborn, J.F., Allman, C.H., eds. *Instream flow needs*, Vol. 2. Bethesda, MD: American Fisheries Society, pp. 597–615.
- Wills, T.C., Baker, E.A., Nuhfer, A.J. & Zorn, T.G. 2006. Response of the benthic macroinvertebrate community in a northern Michigan stream to reduced summer streamflows. *River Research and Applications* 22: 819–836.
- Wolf, P. 1950. A trap for the capture of fish and other organisms moving downstream. *Transactions of the American Fisheries Society* 80: 41–45.
- Zorn, T.G., Seelbach, P.W. & Wiley, M.J. 2002. Distributions of stream fishes and their relationship to stream size and hydrology in Michigan's Lower Peninsula. *Transactions of the American Fisheries Society* 131: 70–85.
- Zorn, T.G., Seelbach, P.W. & Wiley, M.J. 2004. Utility of species-specific, multiple linear regression models for prediction of fish assemblages in rivers of Michigan's Lower Peninsula. Research Report 2072, Ann Arbor: Michigan Department of Natural Resources, Fisheries Division.
- Zorn, T.G., Seelbach, P.W., Rutherford, E.S., Wills, T.C., Cheng, S. & Wiley, M.J. 2008. A landscape-scale habitat suitability model to evaluate effects of flow reduction on fish assemblages in Michigan streams. Research Report 2089. Ann Arbor: Michigan Department of Natural Resources, Fisheries Division.
- Zorn, T.G., Seelbach, P.W. & Wiley, M.J. 2011. Developing user-friendly habitat suitability tools from regional stream fish survey data. *North American Journal of Fisheries Management* 31: 41–55.
- Zorn, T.G., Seelbach, P.W. & Rutherford, E.S. 2012. A regional-scale habitat suitability model to assess the effects of flow reduction on fish assemblages in Michigan streams. *Journal of the American Water Resources Association* 48: 871–895.