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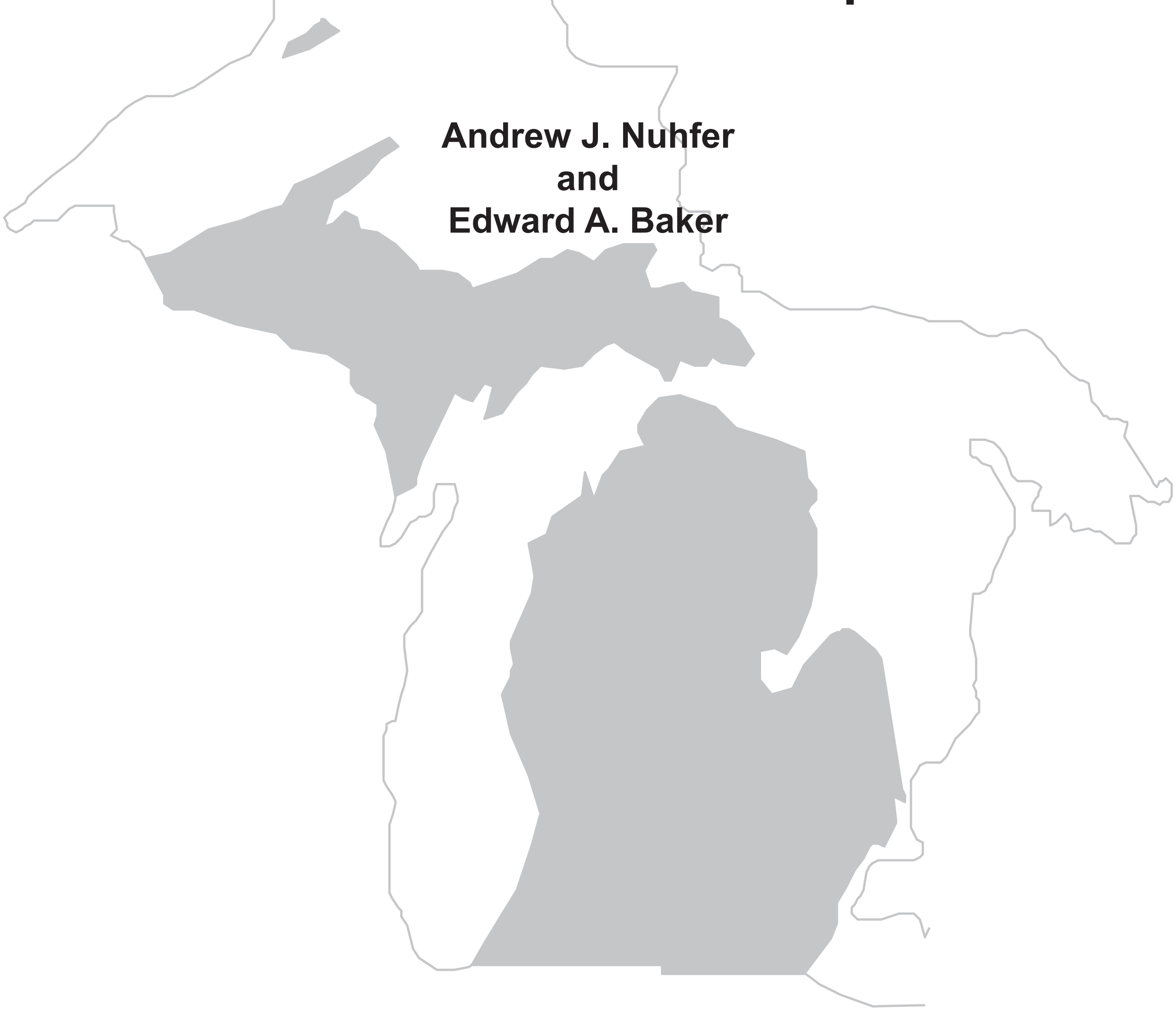

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A Long-term Field Test of Habitat Change Predicted by PHABSIM in Relation to Brook Trout Population Dynamics during Controlled Flow Reduction Experiments

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Abstract.–We assessed the utility of the Physical Habitat Simulation system (PHABSIM) in a Michigan trout stream by testing the assumption of a positive linear relation between modeled habitat (weighted usable area, WUA) and brook trout *Salvelinus fontinalis* population levels. We also determined the effects of water withdrawal on brook trout survival, growth, and movement. We simulated irrigation withdrawals by diverting water from a 0.6-km reach of Hunt Creek from 1 June through 31 August each year during 1991-98. We withdrew about 50% of normal summer discharge in 1991-94, 75% in 1995-96, and 90% in 1997-98. We compared abundance, survival, and growth of brook trout between each dewatering period and to pretreatment levels during 1984-90. Ratios of brook trout population parameters in the treatment zone to those in upstream and downstream reference zones were used to help identify temporal influences unrelated to dewatering treatments.

Overall, we found poor correlation between WUA predictions at different flows and brook trout abundance or survival rates. Fall abundance of yearling-and-older (YAO) brook trout and survival of YAO fish from spring to fall was positively related to nocturnal (resting) WUA but not with diurnal (foraging) WUA. Fall abundance of young-of-the-year (YOY) brook trout was not significantly correlated with either diurnal or nocturnal WUA. Predicted changes in WUA at reduced discharge levels, compared to normal flow, were generally small relative to natural between-year variation in trout abundance and survival, suggesting that low summer flows had less influence on the population than other factors.

Spring-to-fall survival of YAO brook trout in the dewatered zone, relative to reference zones, was significantly higher when flow was reduced by 75% than at normal flow, or when discharge was reduced by 90%. Fall abundance of YOY brook trout in the treatment section, relative to reference zones was usually highest when 75% of flow was diverted. Fall condition of brook trout in the dewatered zone was significantly lower when 50% or 90% of water was diverted, as compared to condition in reference zones. Mean fall length at age did not change in response to

reductions in summer baseflow. Fewer brook trout emigrated when 75% or 90% of water was diverted than when flow was reduced by 50%.

Water warming rate increased when ≥75% of flow was diverted. Mean summer water temperatures increased 1.6 ^{o}C/km when 75% of water was diverted and 2.4 ^{o}C/km when 90% was diverted. In contrast, mean summer water temperature cooled by an average of 0.2 ^{o}C/km during two summers when flow was normal. 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.

Our findings of generally insignificant, or inconsistent relationships between WUA and population parameters such as abundance, survival, and growth, suggest that PHABSIM was poorly suited for predicting biological impacts of water diversions from low gradient brook trout streams draining glacial outwash sand and gravel. Increases in water warming resulting from water diversion probably pose the greatest threat to coldwater fish communities.

Introduction

Seasonal water withdrawals from streams, lakes, and aquifers pose a potential threat to stream fishes. The area of land irrigated for agricultural purposes in Michigan increased from 39,255 ha in 1974 to 159,042 ha in 1997 (USDA 1999). Seasonal withdrawals for golf course and lawn irrigation are also common, and increasing in northern Michigan. Approximately 15,378 ha of golf courses in Michigan were irrigated in 1999 (Michigan Water Use Reporting Program, Unpublished data).

The need to protect aquatic habitats from excessive withdrawals was recognized in the 1970s in the Western United States and led to the development of the Instream Flow Incremental Methodology (IFIM) (Milhous et al. 1989). IFIM is a protocol for protecting instream flows that depends on field data collection, computer based habitat modeling, and negotiation over projected impacts on fish and habitat from reduced streamflow. The suite of habitat modeling programs is collectively known as the Physical HABitat SIMulation system (PHABSIM). The assumption underlying PHABSIM is that predicted habitat availability (weighted usable area, WUA) is linearly related to fish abundance or biomass (Milhous et al. 1989). PHABSIM has been widely used in the Western United States but has not been extensively used in Michigan (Gowan 1984; Reiser et al. 1989; Bovee et al. 1994; Baker and Coon 1995a).

Several critical biological assumptions underlying PHABSIM have not been extensively tested under controlled conditions. IFIM assumes that a positive relationship between WUA and fish abundance exists, but this assumption is difficult to test in natural systems because many factors can prevent fish from attaining maximum carrying capacity. Morhardt and Mesick (1988) proposed the use of behavioral carrying capacity (BCC) - the endpoint density of fish remaining in a habitat after it has been overstocked - as a short-term response variable for testing the assumption that WUA predictions at different flows accurately reflect habitat suitability. Because salmonids stocked at high densities in natural and artificial channels adjust their density through emigration (Chapman 1962; Slaney and Northcote 1974; Mesick 1988; Bugert and Bjornn 1991) one would expect accurate predictions of WUA at different flows to be positively correlated with abundance in streams that are "driven" to carrying capacity through overstocking. However, Zorn and Seelbach (1995) did not find a positive relation between WUA and smallmouth bass *Micropterus dolomieu* biomass when they used the BCC technique in a controlled-flow experiment. Although BCC experiments can address short-term movement responses to reduced flow, the carrying capacity of a natural population of fish would be the result of a more complex suite of variables such as, recruitment, survival, and growth.

In the present study we examined relationships between these variables and both summer stream discharge and projections of WUA over a 15-year period in Hunt Creek, Michigan. We are unaware of any similar long-term study designed to determine if habitat availability projected by PHABSIM is significantly related not only to fish abundance, but also to population regulation parameters such as recruitment of YOY, survival, growth, or emigration within a natural stream. To evaluate the validity and applicability of the PHABSIM system in small Michigan trout streams we first collected information on abundance, mortality rates, and growth rates of the brook trout *Salvelinus fontinalis* population in Hunt Creek for a seven-year period prior to water diversion experiments. In the following eight years, 50-90% of summer streamflow was annually diverted from a treatment section of Hunt Creek. Habitat availability was modeled with PHABSIM, and model projections of WUA were examined for correlation with fall abundance of young-of-the-year (YOY) brook trout, abundance and survival of yearling-and-older (YAO) brook trout, and growth rates. We also measured the effects of water withdrawal on stream temperature because water temperature exerts a prominent influence on the physiology and behavior of trout.

Our objectives were to: 1) evaluate the impacts of a simulated irrigation withdrawal on abundance of YOY, abundance and survival of YAO, and growth rates for the brook trout in Hunt Creek, 2) to project the effects of the simulated withdrawal on the brook trout habitat using PHABSIM, 3) to determine if brook trout abundance, survival, or growth, was correlated with PHABSIM projections of WUA at different discharge levels, and 4) to evaluate the effect of the water withdrawal on stream temperature.

Methods

Study area

Hunt Creek was chosen as the study stream for this research because the brook trout population in Hunt Creek was self-sustaining, protected from angling, and relatively stable over time. Thus, any response of the brook trout population to water withdrawal had a reasonable likelihood of being attributable to a change in the natural mortality rate, emigration rate, growth rate, or some other factor related to the treatment. The Hunt Creek watershed lays in northern Oscoda and southern Montmorency counties of Michigan's Lower Peninsula (Figure 1). Hunt Creek is a groundwater dominated stream draining extensive glacial sands and gravels deposited approximately 10,000 years ago (Dorr and Eschman 1970). Hunt Creek has extremely stable discharge: from 15-March 1999 through 15-March 2001, the 90% exceedence flow was 0.75 m^3/s and the 10% exceedence flow was 0.87 m^3/s at the downstream end of the study area.

The study area of Hunt Creek was divided into three sections: a 1,254-m (0.45 ha) upstream reference zone (RZ), a 602-m (0.28 ha) treatment zone (TZ) and a 1,534 m (0.94 ha) downstream RZ (Figure 1). Hunt Creek is a second order stream upstream of the confluence with Fuller Creek, which flows into Hunt Creek immediately upstream of the TZ. Hunt Creek is a third order stream through the remainder of the study area.

The brook trout population in Hunt Creek is composed primarily of small fish; approximately 96% of the fish in the treatment zone (TZ) are less than 17.7-cm total length (Alexander and Hansen 1986). The only common fish species in Hunt Creek are brook trout, mottled sculpin *Cottus bairdi*, and slimy sculpin *Cottus cognatus* (Alexander and Hansen 1986). White sucker *Catostomus commersoni*, creek chub *Semotilus atromaculatus,* fathead minnow *Pimephales promelas,* northern redbelly dace *Phoxinus eos,* bluntnose minnow *Pimephales notatus,* central mudminnow *Umbra limi,* brook stickleback *Culaea inconstans,* Iowa darter *Etheostoma exile,* and brown trout *Salmo trutta* are found occasionally. These uncommon species are primarily emigrants from lakes and ponds in the extreme headwaters of the watershed.

Water Diversions

During 1989-90, a diversion channel was excavated around the 602-m TZ. Bulkheads were installed at the upstream and downstream ends of the TZ to provide a way to control discharge and to support traps used to monitor fish movement (Figure 1, referred to as the upstream and downstream bulkheads respectively in remainder of text). The upstream bulkhead was used to divert water around the TZ between 1-June and 31-August each year of the study during 1991-98. During 1991-94 50% of streamflow was diverted, in 1995-96 75% was diverted, and during 1997-98 flow in the TZ was reduced by 90%.

PHABSIM modeling

Methods used to collect diurnal and nocturnal brook trout habitat use data and construct use-habitat suitability criteria were described in Baker and Coon (1997). We calculated microhabitat suitability scores by multiplying depth and velocity suitability values, as in a PHABSIM analysis (Milhouse et al. 1989). We did not use substrate and cover data to compute microhabitat suitability scores because these variables did not vary with changes in discharge.

Baker and Coon (1995) used a representative reach approach for modeling the habitat in the TZ of Hunt Creek with PHABSIM. They selected representative reaches by first measuring and marking the TZ into 50 m contiguous reaches, omitting the 130-m reach of impounded water at the downstream end of the section (reach B5 in Figure 1) as well as the 122-m reach downstream of the upstream bulkhead (reach B1 in figure 1). They then randomly selected two of the 50-m reaches to model by use of PHABSIM (reaches B2 and B4 in Figure 1). They measured habitat availability at 385 locations (cells) along 19 transects in reach B2 and 530 locations along 21 transects in reach B4. Mean distance between transects was 2.5 m in reach B2 and 2.6 m in reach B4, and the maximum distance between any two transects was 6.6 m in reach B2 and 5.2 m in reach B4. Weighted usable area (WUA) estimates for reaches B2 and B4 were expanded to provide an estimate of WUA for a 350-m middle reach of the TZ where mesohabitat was similar. WUA was estimated for the altered stream reaches near the upstream and downstream bulkheads in 1998.

During 1997, when approximately 90% of water was diverted from the TZ, we noticed that reaches not included in the modeling were important for many fishes. Mesohabitat in the 122-m stream reach located downstream of the upstream bulkhead (reach B1 in Figure 1) was different from other sections of the TZ - narrower and deeper - because it carried only the discharge of Fuller Creek before the upstream bulkhead was constructed. Mesohabitat was also different in the 130-m stream reach upstream of the downstream bulkhead (reach B5 in Figure 1) because habitat in this reach was slightly impounded to allow operation of the fish traps.

To quantify WUA in these previously un-modeled reaches, we established additional transects and made estimates of habitat availability in the upstream and downstream ends of the TZ in 1998. Habitat availability in reach B1 was estimated from water depth and velocity data collected along 12 transects spaced 10 m apart throughout the entire reach (178 cells) at 4 discharge levels representing baseflow (0.45 m^3/s) and reductions of 50% (0.23 m^3/s), 75% (0.11 m^3/s), and 90% (0.04 m^3/s) in 1998. Habitat availability was also estimated separately for the 130-m stream reach upstream of the downstream bulkhead (reach B5 in Figure 1). Habitat in this reach was characterized along 11 equidistantly spaced transects (246 cells) at the same four discharge levels described for B1. Total WUA for the entire TZ was then estimated by PHABSIM from habitat data collected from all four reaches.

Habitat Suitability Criteria (HSC)

The HSC developed from frequency-of-use data were fully presented in Baker and Coon (1997) and are summarized here (Table 1). The diurnal use-HSC largely represents the suitability of foraging microhabitats for brook trout in Hunt Creek because 87% of observations used in constructing HSC were from actively foraging fish. In contrast, nocturnal use-HSC was mostly based on observations of inactive fish (93% of all nocturnal observations) and largely represented the suitability of resting microhabitats (Table 1). All of the inactive brook trout observed at night were in direct contact with the substrate, and some were burrowed into vegetation (primarily watercress, *Nasturtium officinale*) or wedged between sticks.

Immigration and Emigration

Movement into, or out of, the TZ during water diversion experiments was determined from catches in fish traps located at the upstream and downstream bulkheads. Inclined screen traps were constructed in spring 1990 on the downstream bulkhead and used to monitor downstream fish movement out of the TZ during summer 1990 before water diversion began (Wolf 1950). Fish traps were operated at both the upstream and downstream bulkheads between 1-June and 31-August from 1991-96. The upstream traps were not operated after 1-September from 1991-96 because they rapidly plugged with debris at this time of year and required extensive maintenance to effectively trap fish. However, the downstream traps were operated until fall population estimates were conducted in each year of the study from 1992-98. During 1997-98, extra effort was spent to operate all traps during the entire period between the time spring and fall population estimates were made—approximately from the 4th week of April through the 3rd week of September. The traps only caught fish moving downstream, and prevented upstream fish movement when they were operated. During other times of the year, adult fish were able to move downstream or upstream if they jumped over the 0.5 m-high stop logs. Younger trout incapable of this could not move upstream past bulkheads. Trout captured in the traps were counted, measured, and released downstream of the respective bulkheads.

Population estimate methods

Trout populations were estimated in spring and fall from 1984-98 by two-pass mark and recapture electrofishing with a 2-probe, 240-volt DC electrofishing unit towed behind wading electrofishers. Sampling was done during the third week of April and September each year. During 1987-90, populations were also estimated during the last week of August immediately before natural discharge levels were restored in the TZ. These estimates were discontinued after we determined that there were no significant differences between August and September estimates. Fish sampling commenced at the downstream end of the 3.4-km study area and proceeded upstream. Recapture collections were made two days after marking. Data were recorded separately for the TZ, the downstream reference zone (RZ) and the upstream RZ (Figure 1). Population estimates and variances were computed using the Bailey modification of the Peterson mark-and-recapture method (Bailey 1951). We stratified population estimates by 25-mm length groups. Age data from brook trout scales were used to apportion population estimates by length groups into estimates by age group for each section and sampling period. Approximately 4,800 trout were weighed to the nearest 0.1 g during 1993-98 to provide data for an analysis of length to weight relations in each stream section during each experimental water withdrawal period.

Effects of dewatering on water temperature

Electronic thermometers located near the upstream and downstream boundaries of the TZ were used to record water temperature once every hour from October, 1992 through 2001. These data were used to determine warming during study periods when summer flow was normal or reduced by 50%, 75%, and 90%.

In summer 1999, we assessed the effects of both discharge level and air temperature on warming within the TZ. Five calibrated thermometers were deployed in the TZ to provide replicate temperature measurements and to insure that data would be available even if some thermometers malfunctioned. An additional thermometer was used to collect air temperature data. During summer 1999 from 0-90% of flow was diverted from the TZ for three or four days a week on a random schedule. Thus, flow conditions in the TZ ranged from 0.05 to 0.51 m^3/s during summer 1999.

Statistical analyses

Population data from 1984-90 were used as a pre-treatment reference period because mesohabitat and fish populations were relatively stable during that time. We used the Bonferroni multiple t-test technique (Miller 1981) to identify significant differences in abundance and survival between experimental periods within zones. We used the same technique to test for differences in the ratios of abundance, survival, or growth in the TZ to those in the upstream and downstream RZs for each level of water diversion. Differences were judged significant for P values ≤ 0.05.

Both mean length at age and the slopes of $\log_{10}$ (length) vs. $\log_{10}$ (weight) regressions were compared to assess growth. We pooled data from the reference zones when the slopes of length-weight regressions were not significantly different. We used Bonferroni-t multiple comparison tests to make comparisons between slopes of length-weight regressions for each zone and period. Data on condition of fish collected from the TZ in 1996 were excluded from analysis because the fish were gorged with aquatic oligochaeta ingested following a period of heavy rainfall, and fish weight data were not collected in 1995 because our electronic scale malfunctioned. Thus, we could not make statistical comparisons of condition of fish collected after either summer when 75% of flow was diverted.

We used linear regression to assess relations between brook trout abundance and survival versus estimates of WUA at each level of discharge. Ratios of abundance in the TZ to that in the upstream and downstream RZs were also plotted against WUA to determine if adjustments to account for factors unrelated to the water withdrawal would change the relation between WUA and population response. Similar ratio analyses and linear regression were used to evaluate relations between survival and WUA estimates. Linear regression coefficients were judged significant for $P \leq 0.05$.

We summarized temperature data by first determining daily maximum, minimum, and average temperature–based on hourly measurements–near both the upstream and downstream boundaries of the TZ. Differences in temperature between the upstream and downstream boundaries of the TZ were compared on both a monthly and seasonal basis for different levels of summer discharge.

We used regression analysis to assess water warming in the TZ relative to discharge and air temperature in 1999. The change in temperature between the upstream and downstream ends of the TZ at different discharge levels was regressed against flow and air temperature. Water temperature data collected during periods when discharge temporarily increased due to precipitation were excluded from analysis. We also excluded water temperature data collected for approximately 4 hours after stop logs were added or removed from the upstream bulkhead.

Results

Trout abundance prior to each test of reduced discharge

We first evaluated spring densities of brook trout to determine if populations were similar at the starting point of each dewatering test period. Spring densities of yearling-and-older (YAO) brook trout varied from year to year, but with a few exceptions were reasonably similar among years in the TZ and both RZs. Density of YAO brook trout in the TZ was comparable prior to each experimental flow reduction period (Figure 2). In the TZ, spring abundance of YAO brook trout was significantly higher in 1995-96 - years when 75% of summer flow was later diverted - than during the pretreatment period from 1984-90 (Figure 2). Conversely, in the downstream RZ, spring abundance of YAO was 15% lower in 1995-96 than during the pretreatment period, and about 12% less abundant than during the 50% dewatering period. In the upstream RZ, spring abundance of YAO was dramatically lower in 1997-98 than during any of the other three study periods. This decline in abundance of YAO in the upstream RZ occurred in conjunction with declines in brook trout reproduction. Reduced reproduction in the upstream RZ occurred in conjunction with the catastrophic failure of an upstream beaver dam. Sand sediment exported from the beaver pond was trapped and removed at the upstream bulkhead before it entered the TZ or downstream RZ. Overall, the similar and high densities of YAO in the TZ over the period when water was diverted provided a reasonably uniform starting point for test of effects of each level of water diversion on brook trout population dynamics.

Effects of water withdrawal on fall YAO abundance

Mean fall abundance of YAO in the TZ was significantly lower during the pretreatment period than during all periods when summer discharge was reduced (Figure 2, Appendix 2). The highest fall abundance of YAO brook trout in the TZ over the study followed summers when flow was reduced by 75%. Yearling-and-older trout were more abundant after this 75% reduction than after summers when flow was normal or reduced by 50% or 90% (Figure 2, Appendix 2). This occurred largely because YAO survival from spring to fall was higher when 75% of water was diverted (Figure 3).

Overall, fall abundance of YAO in the downstream RZ was quite stable over the entire study, averaging approximately 1,600 per hectare during periods when flow in the TZ was normal or reduced by 50%, and about 1,420 during periods when flow was reduced by 75-90% in the TZ. Fall numbers of YAO in the upstream RZ were significantly lower during the period when flow was reduced 90% in the TZ than during any other experimental period. This decline in abundance of YAO in the upstream RZ occurred in conjunction with declines in brook trout reproduction, that in turn, were associated with increases in sand sediment released following the failure of an upstream beaver dam. This sediment was trapped and removed at the upstream bulkhead before it entered the TZ or downstream RZ.

Trends in fall density of YAO over the course of the study and various levels of flow reduction were similar in the two RZs but a different temporal pattern was evident in the TZ (Figure 2). In the TZ, density of YAO increased relative to the RZs when flow was reduced by 75%, before declining when 90% of flow was withdrawn (Figure 2).

Effects of water withdrawal on YAO survival

Water withdrawals did not reduce survival from spring to fall below the average rate observed during normal-flow years. Average survival of YAO from spring to fall was significantly higher in the TZ when 75% of water was diverted than when no water was diverted or during years when 90% of summer flow was diverted (Figure 3, Appendix 3). The average percentage of YAO surviving from spring to fall in the TZ ranged down from 80% when 75% of flow was diverted, to 61% when flow was reduced 90%, and 57% at normal flow (Figure 3). Average survival in the TZ during the four years when half the normal summer flow was diverted was not different from survival following other reduced discharge regimes.

Mean spring-to-fall survival in the upstream and downstream RZs was not different between study periods (Figure 3, Appendix 3). The ratio of survival of YAO from spring to fall in the TZ compared to RZs was significantly higher when flow was reduced by 75% compared to ratios at normal flow, or when discharge was reduced by 90% (Figure 4). For example, survival of YAO in the TZ was about 1.3 times higher relative to the upstream RZ during the period when flow was reduced by 75%, whereas they survived only about 0.93 times as well when summer flow in the TZ was normal (Figure 4).

Density dependent survival of YAO in the TZ was not evident during this study. Survival of YAO was inversely related to spring density of YAO in both RZs but not in the TZ during the period from 1984-99 (Figure 5). The best-fit relation between survival and spring density of YAO occurred in the upstream RZ where average spring density of YAO was highest ($R^2 = 0.62$). However, the coefficient of determination and slope of the analogous relationship in the downstream RZ was also significant even though mean spring density in this zone was lower than in either the TZ or upstream RZ (Figure 2).

Effects of water withdrawal on recruitment of YOY

Mean fall abundance of young-of-the-year (YOY) brook trout in the TZ was significantly higher when 75% of water was diverted than during the pretreatment period or when 50% of summer discharge was diverted (Figure 6). Mean YOY abundance in the TZ was similar between the baseflow period and periods when discharge was reduced by 50% or by 90% (Figure 6). Mean YOY abundance in TZ and both RZs was similar between the pretreatment period and the period when 50% of summer discharge was diverted from the TZ. Depressed numbers of YOY in the upstream reference zone during periods when 75% or 90% of flow was diverted were associated with increases in sand sediment released following the failure of an upstream beaver dam. Over the

15-year study, YOY total abundance was consistently highest in the upstream RZ, and lowest in the downstream RZ.

There was no clear pattern in recruitment variation between the TZ and RZs. All but one paired comparison of mean fall abundance of YOY during an experimental period were inconsistent between the TZ and the upstream and downstream RZs (Figure 6, Appendix 4). Mean abundance of YOY was similar in all zones when means for the normal flow period were compared to means for the 50% withdrawal period. Thereafter, differences in abundance between periods, within zones, were not synchronous between the TZ and the RZs (Appendix 4). For example, in the TZ, YOY were more abundant when 75% of flow was diverted compared to at normal flow, but abundance was similar between these study periods in the downstream RZ, and in the upstream RZ abundance of YOY was lower during the period when 75% of flow was diverted compared to the period when flow was normal. Immigration or emigrations were not the cause of these results.

Fall abundance of YOY in the TZ was generally higher relative to reference zones during the period when 75% of summer base flow was diverted compared to other flow regimes (Figure 7). Abundance of YOY in the TZ relative to the upstream RZ was significantly lower when summer flow was normal or reduced 50% than when flow was reduced by either 75% or 90% (Figure 8, Appendix 4). When 75% of water was diverted, fall abundance of YOY in the TZ was higher relative to the downstream RZ, than during any other period (Figure 7). For instance, when 75% of water was diverted, YOY in the TZ were 1.6 times more abundant than in the downstream RZ whereas they were about 1.2 times more abundant at other discharge levels.

Effects of water withdrawal on Growth and Condition

Reductions in summer baseflow had no discernable effect on growth rates of brook trout. The mean lengths of age-0 through age-3 brook trout in late September were not different among test periods in any zone (Table 2). Moreover, the ratios of mean length at age in the TZ to length at age in either RZ were not significantly different among the four test periods.

Fall condition of brook trout in the TZ was significantly lower when 50% or 90% of water was diverted, as compared to condition in the RZs. Fish weight data from the TZ following diversion of 75% of normal summer discharge were unavailable or excluded from analysis (see methods). Data from both RZs were combined for this analysis because Bonferroni-t multiple comparisons of the slopes of $\log_{10}$ (weight) vs. $\log_{10}$ (length) regression slopes were not significantly different between the upstream and downstream RZs within any test period. Our analysis detected no differences in condition of brook trout between RZs among test periods.

Effects of water withdrawal on Trout Movement

Data on immigration and emigration prior to water diversion experiments were unavailable because fish traps at the upstream bulkhead were not constructed before 1991 when water diversions were initiated. During the diversion treatments fewer brook trout emigrated from the TZ when 75% or 90% of water was diverted than when 50% of summer baseflow was diverted (Table 3). More fish emigrated during years when 50% of water was diverted, but immigration into the TZ was also higher during the same period. The mean number of emigrants during the 50% withdrawal period was 70 compared to 16 and 18 emigrants when 75% or 90% of baseflow was diverted. Mean immigration into the TZ was slightly higher than mean emigration during all dewatering periods. The mean increase in trout numbers in the TZ from immigration was 21 from 1991-94, 10 trout from 1995-96, and two in 1997-98.

Effects of net immigration on trout abundance in the TZ were negligible for all years and age groups. The mean net increase in YOY from immigration (assuming that all fish lived) in the TZ during years when 50% of water was diverted was 36/ha, or 1.3% of mean fall number of YOY. Net change in YOY abundance due to immigration was -0.4% of fall YOY when 75% of water was diverted and 0.2% when 90% was diverted. Increases in YAO abundance when 50%, 75%, and 90% of water was diverted were 2.3%, 2.2%, and 0.1% of mean fall abundance, respectively. The majority of both immigrants and emigrants in all years were either YOY or yearling trout.

Effects of water withdrawal on water temperature

The rate of water warming increased substantially when 75% or more of summer baseflow was diverted from the TZ (Table 4). Increases in average daily temperature in summer months when baseflow was reduced by 90% ranged from 1.7°C/km in June 1998, to 2.8°C/km in July 1997 (Table 4). Increases in maximum daily temperature ranged from 2.7°C/km in August 1997, up to 4.4°C/km in July 1998. Average daily summer (June-August) temperature increased approximately 1.6°C/km when 75% of baseflow was diverted and 2.4°C/km when 90% of baseflow was diverted. On average, maximum daily temperature increased 1.5°C/km when flow was reduced 75% and 3.6°C/km when baseflow was reduced by 90%. The largest increases in both mean and maximum temperature occurred in July. Temperature changes in the TZ were inconsistent between the 2 years when 50% of baseflow was diverted. In 1993, water temperature appeared to be cooler at the downstream end of the TZ whereas in 1994 it was were slightly warmer (Table 4). Average summer water temperature was an average of 0.2°C/km lower during years when baseflow was normal (2000-01).

Average daily temperature increased exponentially in the TZ in 1999 as stream discharge decreased from normal summer levels of 0.45 m3/s to 0.05 m3/s (Figure 8A). Air temperature had no significant effect on the fit of the regression model relating the increase in average daily temperature to stream discharge. The regression equation for the increase in average daily temperature per km in °C was y = -0.3179*Ln (discharge in m3/s) – 0.0736. The regression equation for the increase in maximum daily temperature in the TZ in °C was y = -0.4873*Ln (discharge in m3/s) + 0.4095 (Figure 8B).

PHABSIM Model Predictions of WUA

Predicted changes in WUA for YAO brook trout were relatively small for the experimental discharge levels evaluated in this study (Figure 9). PHABSIM model output indicated that diurnal WUA for YAO brook trout would not change after summer baseflow was reduced by 50%, but would decline by 12% if 75% of baseflow was diverted and by 36% at a 90% dewatering level (Figure 9). Nocturnal WUA for YAO trout was predicted to increase approximately 20% when 50% or 75% of water was diverted (Figure 9). The predicted amount of nocturnal WUA for YAO trout at a 90% dewatering level was only 4% lower than at normal baseflow.

Model output predicted relatively larger changes in nocturnal WUA than for diurnal WUA for YOY brook (Figure 9). Nocturnal WUA for YOY was predicted to be higher at all reduced discharge levels as compared to baseflow conditions. The highest overall WUA estimate, nocturnal and diurnal combined occurred for a 75% dewatering level. Estimates of nocturnal WUA for YOY were similar for 50% and 90% dewatering rates. Diurnal WUA for YOY brook trout was predicted to increase approximately 16% when 50% or 75% of water was diverted, and decline by 13% at a 90% dewatering level.

Relation of YAO abundance to WUA

Fall abundance of YAO was significantly correlated with nocturnal, but not diurnal, estimates of WUA (Figure 10). Although fall abundance of YAO was positively related to nocturnal WUA, there was considerable scatter around the linear regression line and the coefficient of determination was not large (R^2 = 0.30). A predicted 18% increase in nocturnal WUA for YAO, compared to normal baseflow, when 50% of water was diverted was associated with a 19% increase in mean fall abundance of YAO. However, a similar predicted increase in nocturnal WUA at a 75% dewatering level was associated with a 58% higher abundance of YAO brook trout (Figure 10).

Fall abundance of YAO was not correlated with WUA estimates derived from diurnal use-habitat suitability criteria (Figure 10). The largest predicted decline of 36% in diurnal WUA for YAO (compared to baseflow) was projected for a dewatering level of 90%, but mean YAO abundance was actually 21% higher compared to mean abundance at baseflow (Figure 10). The predicted decline of 12% in diurnal WUA for YAO (compared to baseflow) when discharge was reduced by 75% was associated with a 58% increase in mean YAO abundance.

Relation of YAO survival to WUA

Survival of YAO from spring to fall was positively correlated with nocturnal WUA, but not to diurnal WUA (Figure 11). A predicted increase in nocturnal WUA of 18% when half of summer flow was diverted was associated with a 17% higher estimate of mean survival from spring to fall (Figure 11). Although YAO survival from spring to fall was positively related to nocturnal WUA ($R^2 = 0.36$), there was substantial scatter of data points around the linear regression line. Mean survival of YAO was significantly higher when half of the summer flow was diverted than during the normal-summer-discharge period although diurnal WUA projections were virtually identical for these discharge levels (Figure 11).

Our analysis of the ratio of survival in treatment and reference zones again indicated that WUA estimates were not consistently related to spring-to-fall survival of YAO. The relationship between nocturnal WUA and spring-to-fall survival in the TZ relative to survival in the upstream RZ (ratio of survival rates) was significant and the coefficient of determination was similar to that for survival of YAO and nocturnal WUA. However, ratios of survival in the TZ to the downstream RZ were not significantly correlated with nocturnal WUA. Similarly, there was no relation between diurnal WUA and spring-to-fall survival in the TZ relative to survival in reference zones.

Relation of emigration rate to WUA

Numbers of YOY and YAO brook trout emigrating from the TZ were not significantly correlated with PHABSIM projections of WUA at the four discharge levels that were modeled and tested. In fact, the slopes of regression lines for the relations between both diurnal and nocturnal WUA and numbers of YAO that emigrated were positive, albeit statistically insignificant. The average number of emigrating YAO was highest when 50% of flow was diverted even though the sum of nocturnal and diurnal WUA estimates was highest at that discharge (Figure 9, Table 3). Few YAO emigrated when 90% of flow was diverted although the sum of nocturnal and diurnal WUA estimates was projected to be lowest at that discharge level.

Relation of growth rate to WUA

WUA projections could not be related to changes in growth rates because we did not detect any change in the mean length at age for any age class of brook trout. Our data were not amenable to statistical tests of relationships between condition of trout and WUA because we had to exclude fish condition data collected when 75% of water was diverted. However, observations of fish condition in the TZ relative to the reference zones suggest that condition of fish was not obviously related to WUA. For example, condition of brook trout in the TZ was lower relative to condition in the reference zones when flow was reduced by 50% yet the diurnal (foraging) WUA estimate was highest for this discharge level (Figure 9).

Relation of YOY abundance to WUA

Fall abundance of YOY brook trout was not correlated with either diurnal or nocturnal WUA projected by PHABSIM modeling for the discharge levels tested (Figure 12). The magnitude and direction of projected changes in WUA for YOY were not consistently mirrored by changes in the magnitude and direction of changes in YOY abundance. Diurnal and nocturnal WUA for YOY in the TZ was projected to increase by 17% and 24% compared to baseflow, respectively, when discharge was cut by 50%, yet mean YOY abundance actually declined by 3% (See Figures 6 and 9). Conversely, projected increases in diurnal (15%)

and nocturnal (42%) WUA for YOY when 75% of water was diverted were associated with a 25% increase in mean YOY abundance.

YOY abundance in the TZ was higher relative to reference zones when 75% of water was diverted as compared to relative abundance at normal or 50% of normal flow (Figure 7), but WUA projections did not consistently reflect this. Abundance of YOY in the TZ relative to the upstream RZ was positively correlated with nocturnal WUA, but the analogous relationship for YOY abundance in the TZ relative to the downstream RZ was not significant.

Similarly, the lowest estimate for diurnal WUA for YOY was projected when flow was reduced by 90% and the highest occurred at 50% of normal flow. However, the mean ratio of YOY in the TZ to the upstream RZ changed in the opposite direction and was 1.7 times higher following summers when flow was reduced by 90% (Figure 7). Abundance of YOY in the TZ relative to abundance in either RZ was unrelated to diurnal WUA estimates.

Discussion

Our findings that brook trout populations suffered few adverse effects from summer water withdrawals indicates that the species is well adapted to summer drought conditions, at least in streams with morphology and temperatures like those of Hunt Creek. We are not aware of similar studies of population response to reduced flow to use as a basis of comparison. White et al. (1976) inferred that higher baseflow in Midwestern streams would increase trout abundance. However, in the streams they studied, higher winter baseflow appeared to be more important than summer baseflow. The widespread geographic distribution of brook trout across cold North American streams, some with very low natural summer flows, is further evidence of the brook trout's resilience to summer drought flows.

The assumption that PHABSIM projections of WUA and fish abundance are positively and linearly related clearly was not supported for this low gradient, high-groundwater, Michigan trout stream. Estimates of WUA were rarely correlated with brook trout abundance in Hunt Creek over a 15-year period. This finding mirrors that of Nehring (1979), who reported no relation between WUA and biomass of wild brook trout in Colorado streams. He suggested that the data used to generate probability curves might have been unreliable or inapplicable to the test streams. In our study, probability curves were developed from use-habitat suitability criteria collected in Hunt Creek so we expected WUA estimates to be applicable to our test population.

Tests of the validity of the assumed correlation between WUA and fish abundance by other investigators have produced contradictory or inconclusive results. In Wyoming, Conder and Annear (1987) reported non-significant or negative correlations between WUA and standing stocks of salmonids among different streams. By contrast, other early investigations of the relationship between WUA and brown trout standing crops found strong positive relationships (Nehring 1979; Stalnaker 1979). Similarly, Wolff et al. (1990) reported a four- to six-fold increase in brown trout standing stock associated with about a five-fold increase in estimated WUA for adult fish when minimum flows were increased in Douglas Creek, Wyoming. However, in that study, wetted stream width at low flow was doubled, whereas in Hunt Creek, differences in wetted width or WUA at the discharge levels tested generally varied less than 20%. Bourgeois et al. (1996) found 14 statistically significant ($P<0.05$) relationships between WUA and density of juvenile Atlantic salmon *Salmo salar* among the 44 regressions they reported but only 9 of these relationships were positive. Moreover, their evaluation looked for relationships between density of Atlantic salmon and WUA within short stream segments representing different habitat types such as runs, riffles, and deep flats. Hence, localized immigration and emigration could have obscured effects of different flow levels on survival or other population parameters affecting populations at a larger scale. Negative relationships between WUA and fish density are a clear indication that either IFIM assumptions have been violated or the population is limited by factors other than those measured.

Reports of significant positive relationships between WUA and standing crops are not necessarily a validation of this IFIM assumption. For example, Mathur et al. (1985) argued that significant positive relationships between WUA and standing stocks reported by Orth and Maughan (1982) for three riffle-dwelling fish species in a warmwater Oklahoma stream were associated with high variability in fish abundance at different projected levels of WUA. This should not occur if the model assumption is valid. The between-year variation in trout abundance and survival we observed during the seven years before water was diverted and during years when equal percentages of summer flow was diverted also indicates that factors other than streamflow volume were affecting population dynamics in Hunt Creek. This observation is particularly relevant to the potential utility of PHABSIM for projecting impacts of reduced flow because Hunt Creek is among the most hydrologically stable streams in Michigan or the U.S. Hence, the trout population in Hunt Creek is seldom subjected to stresses such as damaging flood events that can induce high variability in fish survival and abundance through time (Poff and Ward 1989; Strange et al. 1992; Nuhfer et al. 1994).

The poor relation between WUA and abundance in Hunt Creek may also be attributable to the relatively low gradient of the test reach. Conder and Annear (1987) reported strong positive relationships between WUA and trout standing crops predicted from a habitat quality index model for high gradient streams (Slope $\geq$ 0.8%) whereas negative relationships were often observed for low gradient streams (Slope $\leq$ 0.3%). The slope of Hunt Creek in the treatment zone was 0.27%.

One hypothesis frequently advanced to explain poor correlations of abundance and WUA is that the population is not at carrying capacity for the habitat (Morhardt and Mesick 1988). The relatively low level of emigration observed during our study indicates that natural population densities in Hunt Creek were below behavioral carrying capacity as defined by Morhardt and Mesick (1988). However, the density of YOY and YAO in the experimental stream reach of Hunt Creek was almost certainly within the top 5% of all Michigan brook trout streams (Michigan Department of Natural Resources Fisheries Division unpublished data). This was one reason that Hunt Creek was chosen for controlled flow reduction studies. If consistent significant relationships between WUA and abundance could not be found for the dense Hunt Creek population, they are even less likely to be detected in similar brook trout streams with less dense populations. Thus, our findings lead us to believe it is unlikely that a significant linear correlation of WUA and abundance of brook trout could be demonstrated in any low-gradient brook trout stream of the type typified by Hunt Creek, i.e. small, high-groundwater, hydrologically-stable streams draining glacial outwash sand and gravel.

Abundance of YAO was not correlated with diurnal WUA but was positively correlated with nocturnal WUA. This could mean that availability of resting habitat was more limiting than foraging habitat in Hunt Creek. However, the variation in YAO abundance between years at each discharge level clearly showed that factors other than physical space had the most influence on YAO abundance.

If the key assumption of PHABSIM, that WUA and fish abundance or biomass is positively related is correct, then perhaps our estimates of WUA were inaccurate. Kondolf et al. (2000) noted that the specific location of transects used in PHABSIM modeling can have a large influence on WUA predictions because of the great variations in channel form and velocities that exist within a modeled stream reach. Williams (1996) recommended that confidence limits of WUA over discharge be developed before using PHABSIM projections for decisions because of the great uncertainty resulting from the chance location of transects. Railsback (1999) pointed out that habitat will not be adequately modeled if the number of transects is too small to represent all the hydraulic conditions in a reach. In Hunt Creek, we made velocity and depth measurements at 1,339 locations (cells) distributed along 63 transects to generate estimates of WUA. We submit that if these efforts were not sufficient to characterize habitat in a 600 m stream reach, then the labor required for adequate model projections would be prohibitive for most resource agencies.

The ranges of reductions or increases in projected quantities of WUA for YOY at the discharge levels tested were small compared to the year-to-year variation in trout populations under normal summer flow conditions. Our findings suggest that more than two years of data at each discharge level are needed to better define the range of between-year population variation. September abundance of YOY in the TZ ranged from 1549 to 4998/ha between 1949 and 1990 before water diversion experiments commenced (A. J. Nuhfer, Unpublished data). If a relation between YOY abundance and WUA existed, it was masked by natural year-to-year variation in YOY abundance. If estimates of both diurnal and nocturnal WUA were biologically meaningful, then the net change in WUA was even smaller relative to expected natural year-to-year fluctuations in YOY abundance.

The ranges of reductions or increases in projected quantities of WUA for YAO at the discharge levels tested were also small compared to the year-to-year variation in trout populations under normal summer flow conditions. September abundance of YAO ranged from 943 to 2312/ha from 1949 to 1990. By comparison, most predicted changes in WUA compared to baseflow were less than 25%. The largest predicted reduction in WUA (diurnal) was 36% for YAO when 90% of water was diverted. If estimates of both nocturnal and diurnal WUA were biologically meaningful, the inverse relationship between changes in diurnal and nocturnal WUA estimates at intermediate flow levels (50%-75% diversions), compared to WUA at baseflow, would have reduced the probability of strong biological response.

WUA and survival

Our analysis showed that estimates of WUA were poor predictors of YAO survival during low-water periods. Brook trout in the dewatered zone of Hunt Creek could have "adjusted" their population to available habitat through either emigration or changes in survival rates. Our analysis showed that there were significant differences between mean survival in the dewatered zone at different summer discharge levels but these differences were not consistently related to estimates of WUA. Nocturnal WUA was positively related to survival of YAO but our analysis of the ratio of survival in the TZ to the RZs suggested that the correlation might be spurious. If nocturnal WUA had a controlling influence on YAO survival, we would have expected to find significant differences between the TZ: RZ ratios of survival for the following pair-wise comparisons between water withdrawal levels: 50% versus normal flow, 75% versus normal flow, 50% versus 90%, and 75% versus 90%. However, the only TZ:RZ ratios of survival that were significantly different were those derived from data from the 75% dewatering period. Some unknown aspect of habitat increased survival in the TZ when 75% of water was diverted but we conclude that neither diurnal nor nocturnal WUA estimates accurately or consistently reflected it.

Brook trout may have adapted their habitat preferences to conditions prevailing in the TZ when 90% of water was diverted because their abundance, growth, and survival did not change in accordance with changes in PHABSIM projections of WUA. We did not collect habitat use data at this low discharge level because shallow water precluded snorkel diving in much of the TZ. Adult rainbow trout have been reported to prefer deeper and faster water at higher discharges (Pert and Erman 1994). Shirvell (1994) found that microhabitat selection by juvenile coho and chinook salmon changed with discharge. The low emigration rates observed in Hunt Creek at low discharge when overall depths and velocities were much reduced indicates that brook trout adapted their habitat preference to prevailing conditions rather than seeking out the "preferred" condition estimated by the habitat suitability criteria curves. Kallenberg (1958) observed that territorial behavior and habitat use by Atlantic salmon and brown trout changed as water velocity was reduced. At low water velocities territorial behavior declined and these species formed schools as the energetic costs of foraging in higher velocity waters was reduced. We frequently observed schooling behavior of brook trout in deeper pools in the TZ of Hunt Creek when discharge was reduced by 75 to 90%. At low discharges, when habitat conditions were nearly lentic, changes in feeding and territorial behavior by brook trout may preclude positive relations between abundance and WUA because HSC used to estimate habitat availability at higher discharges change.

Reduced predation related to movement of fish from shallow to deeper-water habitats may explain why survival of YAO was generally higher at reduced discharge levels. Channel-shaping discharge in the Hunt Creek TZ is about

1 m^3/s. Many of the pools and deepwater runs created at this discharge level remained even when discharge was reduced to 0.04 m^3/s. We observed rapid movement of fish into these deep-water refugia each year when flows were rapidly reduced by either 75% or 90% on 1-June. We speculate that avian and mammalian predators were less efficient at capturing fish in these deeper habitats where YAO-brook trout congregated at low discharge. 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. Juvenile Atlantic salmon also exhibit a strong tendency to move upstream in response to drops in water levels (Huntingford et al. 1999). Upstream movement out of the TZ in Hunt Creek was blocked by fish traps. However, 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.

Net movement of trout into the treatment zone is an unlikely explanation for higher survival when 75% of water was diverted. In years when immigrants outnumbered emigrants, the net change had a negligible effect on survival estimates because the population of YAO was very large. It is possible that survival estimates could be biased upward for the years from 1991 to 1996 if immigration greatly exceeded emigration during the months of May and September when fish traps were not operated. However, analysis of trap data collected during May and September of 1997 and 1998 indicates that net increases from immigration - if the fish had all lived - would have increased estimates of YAO survival from spring to fall by about 2% in 1997 and 0% in 1998.

Effects of water diversions on growth

We found little evidence of significant adverse effects of summer water diversions on brook trout growth. Although fall trout condition in the TZ relative to the RZs was significantly lower when 50% or 90% of water was diverted, mean length at age did not change. This finding was not surprising in light of the wide confidence limits for mean lengths at age. Rimmer (1985) ascribed reductions in instantaneous growth rates of underyearling rainbow trout to reduced flow rates in seminatural channels, but these changes were not evident until discharge was reduced for about two months. The reduced condition of trout we observed after three months of reduced discharge may indicate that instantaneous growth rates declined when water was diverted. If reduced discharge caused slower growth during summer in Hunt Creek, then growth during the rest of the growing season was sufficient to mask effects on mean length at age. Weisberg and Burton (1993) reported that white perch *Morone americana*, yellow perch *Perca flavescens*, and channel catfish *Ictalurus punctatus*, had better condition and growth rates downstream of a hydroelectric dam after higher minimum flows were instituted. However, the previous minimum flows in their study were much more severe, dewatering half the stream width, and of longer duration, more than 200 d/year.

Temperature analysis

The increase in water warming that we observed when 75% or more of water was diverted indicates that water diversions could have biologically significant adverse effects on coldwater stream fish communities. We are unaware of similar studies in the literature that quantified the increased rate of warming attributable to water withdrawal in groundwater-dominated streams. In Hunt Creek, the increased heating observed occurred even though the dewatered zone was relatively short — 602 m — and completely shaded throughout most of that distance. Less warming is expected in streams when they are well shaded and when width to depth ratios are low (Bartholow 1989). In addition, the net rate of warming may have been reduced by groundwater infiltration in the Hunt Creek TZ, especially at low discharge levels. If 0.01 m^3/s of 9 ^0C 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

m^3/s. We could not accurately assess this by comparing discharge estimates at the upstream and downstream ends of the TZ because field estimates of discharge were not accurate enough to detect such a small increase in flow.

Temperature is a key factor limiting the distribution and abundance of brook trout and other salmonid species (Eaton et al. 1995; Wehrly et al. 1998; Zorn et al. 1998). Wild brook trout abundance in Michigan streams rarely exceeds 10 kg/ha if mean July water temperature exceeds 19 ^{0}C. Similarly, wild populations of Michigan's other inland salmonid species, brown and rainbow trout, are rarely abundant when mean July water temperature exceeds 20 ^{0}C. Temperature did not limit brook trout in our study because the mean July temperature at the downstream end of the TZ was only 14.5 ^{0}C, well below thermal tolerance limits for brook trout. However, Figure 13 illustrates the dramatic contraction of suitable trout habitat (downstream km) for the three levels of water diversion in our study, barring continued downstream inputs of groundwater. We conservatively predict that diversion of 90% of summer baseflow would result in a loss of over 20 km of thermally suitable brook trout habitat in a small stream like Hunt Creek. Predicted losses when 75% or 50% of water is diverted were 18 and 14 km, respectively.

Management Implications

Increased rates of water warming resulting from water diversions probably poses the greatest threat to coldwater fishes in Midwestern streams. The increases in maximum daily temperatures we observed (2.7-4.4 ^{o}C/km) at high dewatering levels would make many Midwestern trout streams uninhabitable by coldwater species. 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. Effects of water withdrawal would be most apparent downstream where thermal conditions approach critical levels for trout. By increasing the rate of water warming (in summer), upstream water withdrawal activities cause critical thermal levels to be reached further upstream.

PHABSIM appears poorly suited for projecting potential adverse effects of water withdrawals on brook trout in low gradient trout streams like Hunt Creek. Our study indicated that summer low-flow habitat was not the primary factor limiting brook trout standing crops. Projections of habitat availability (WUA) were not well correlated with population regulation parameters such as survival, growth, and emigration. Moreover, PHABSIM modeling does not account for effects of water temperature, which is the dominant factor influencing trout distribution and abundance in Michigan streams (Wehrly et al. 1998; Zorn et al. 1998). Finally, the method was very labor intensive.

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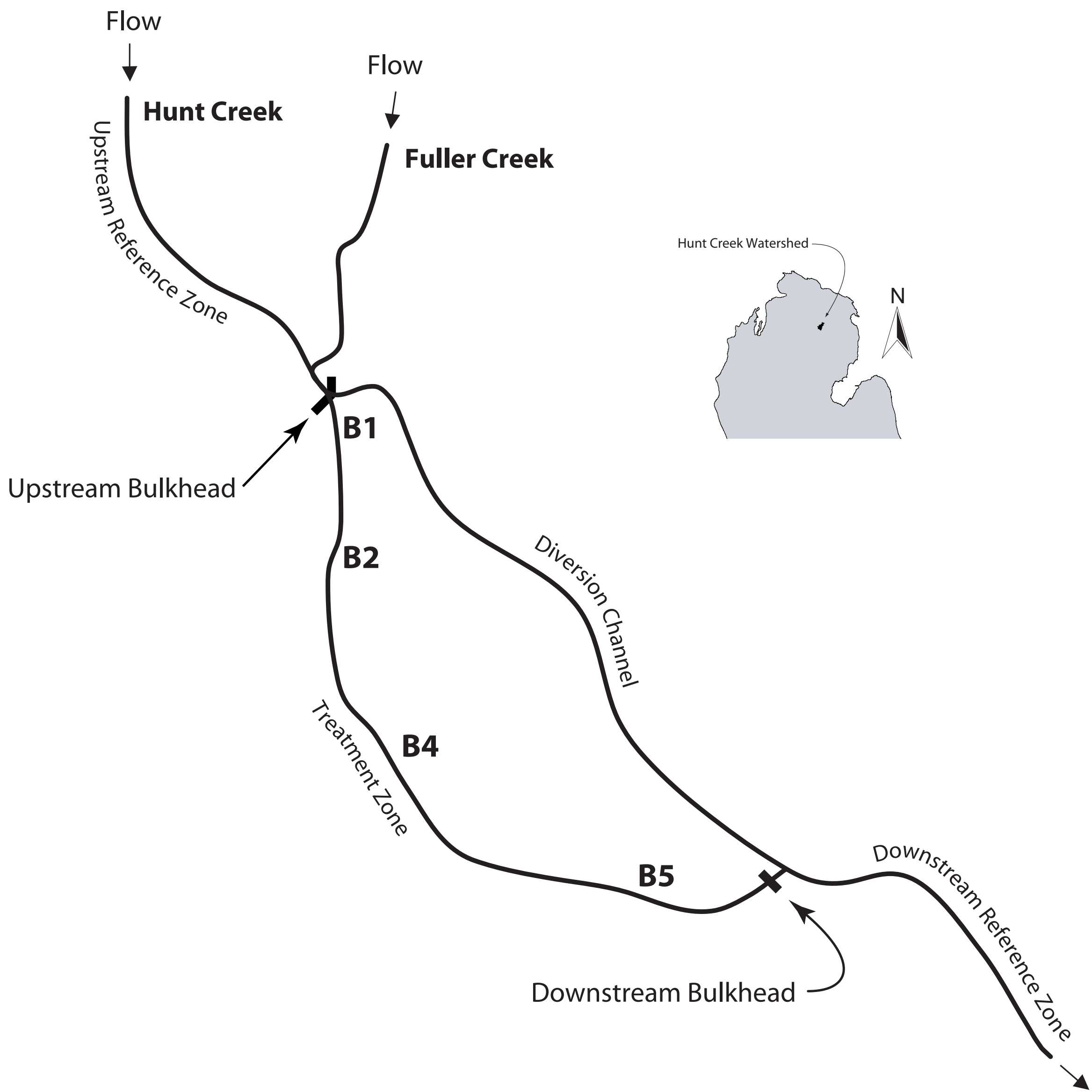

Figure 1.–Map of the Hunt Creek study area. The upstream bulkhead was the boundary between the upstream reference zone and the treatment zone. The downstream bulkhead was the boundary between the treatment zone and the downstream reference zone. The labels B1, B2, B4, and B5 denote the approximate locations of reaches within the treatment zone where physical habitat availability measurements were made for PHABSIM modeling. Inset shows the position of the Hunt Creek watershed in the northeastern portion of Michigan's Lower Peninsula.

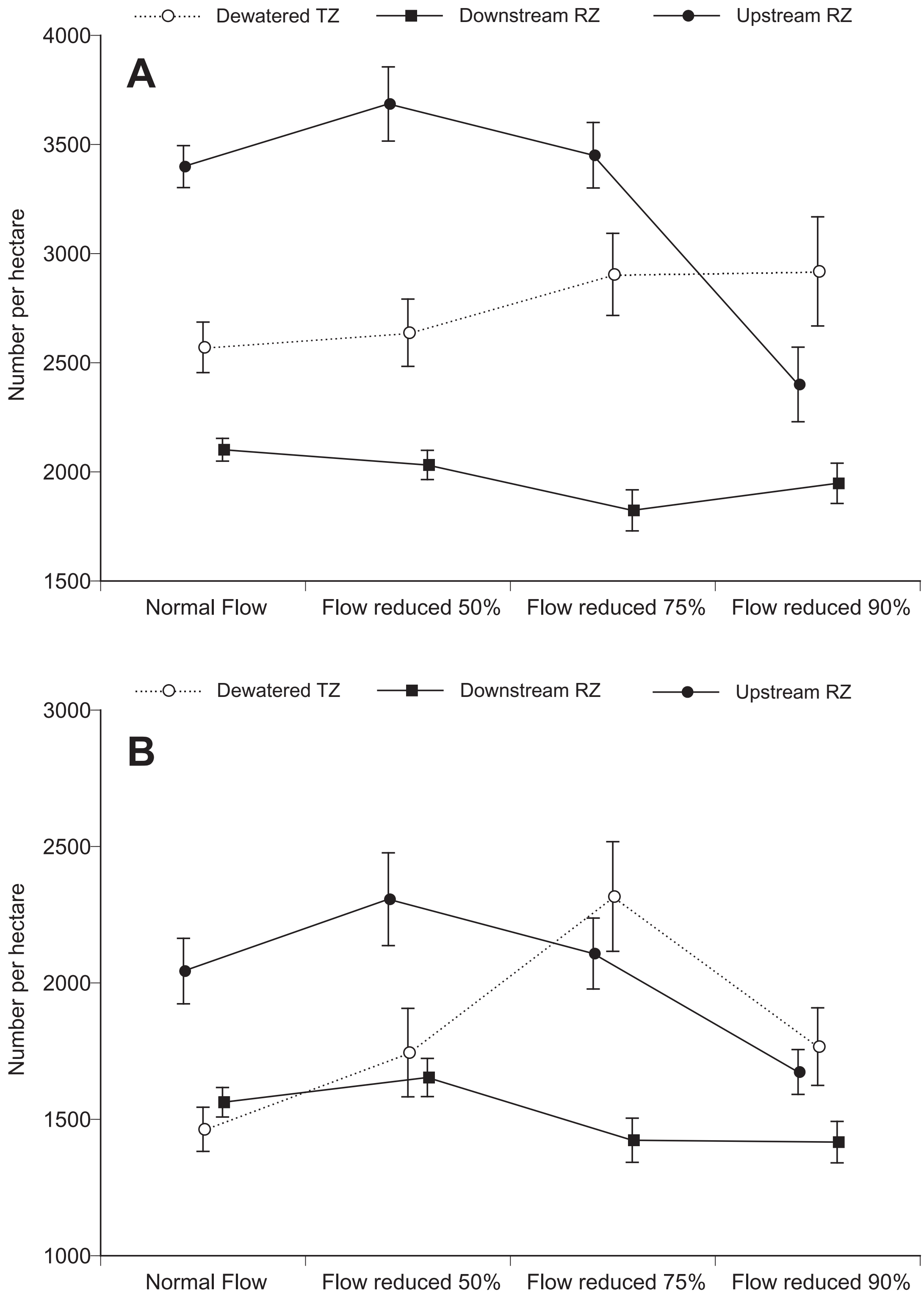

Figure 2.–Spring (A) and fall (B) number (± 2SE) of yearling-and-older (YAO) brook trout per hectare in an experimentally dewatered zone (TZ) and reference zones (RZ) in Hunt Creek. Summer discharge in the TZ was normal from 1984-90, reduced by 50% from 1991-94, reduced by 75% from 1995-96, and by 90% from 1997-98. Summer discharge in reference zones was not altered.

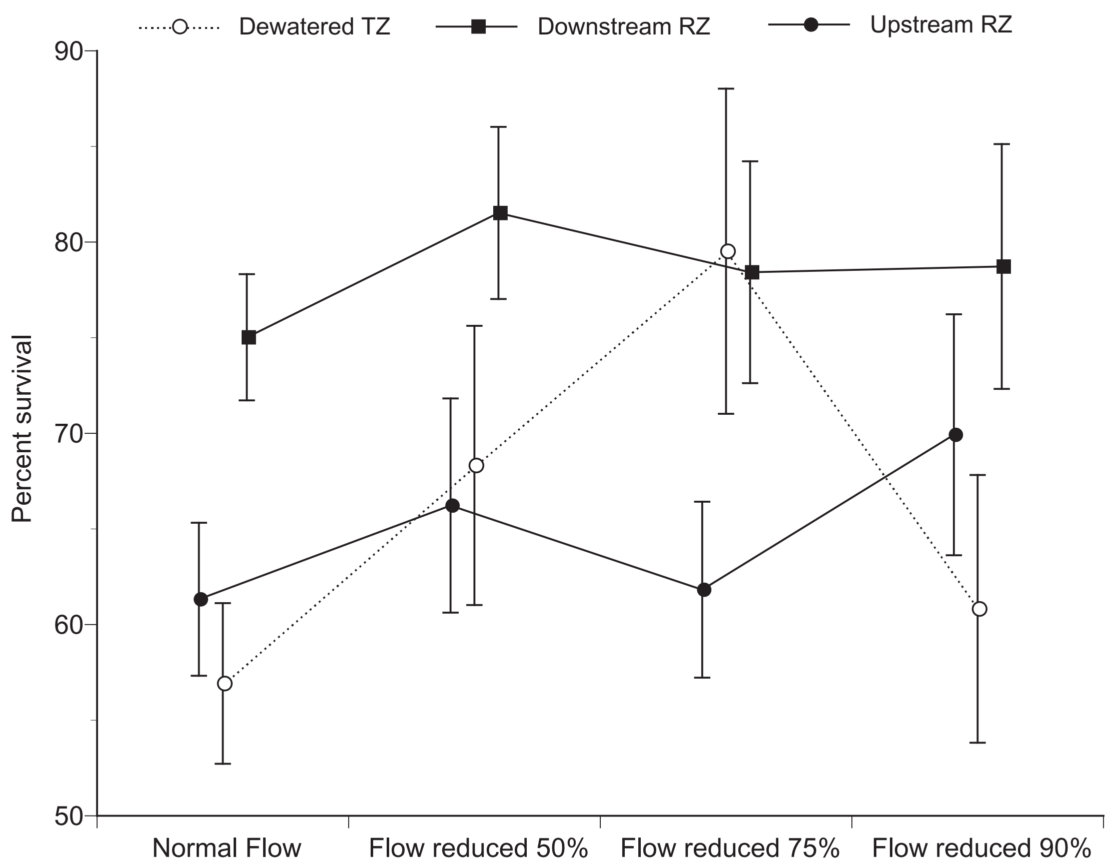

Figure 3.–Percentage (± 2 SE) of yearling-and-older (YAO) brook trout surviving from spring to fall in an experimentally dewatered zone (TZ) and reference zones (RZ) in Hunt Creek. Summer discharge in the TZ was normal from 1984-90, reduced by 50% from 1991-94, reduced by 75% from 1995-96, and by 90% from 1997-98. Summer discharge in reference zones was not altered.

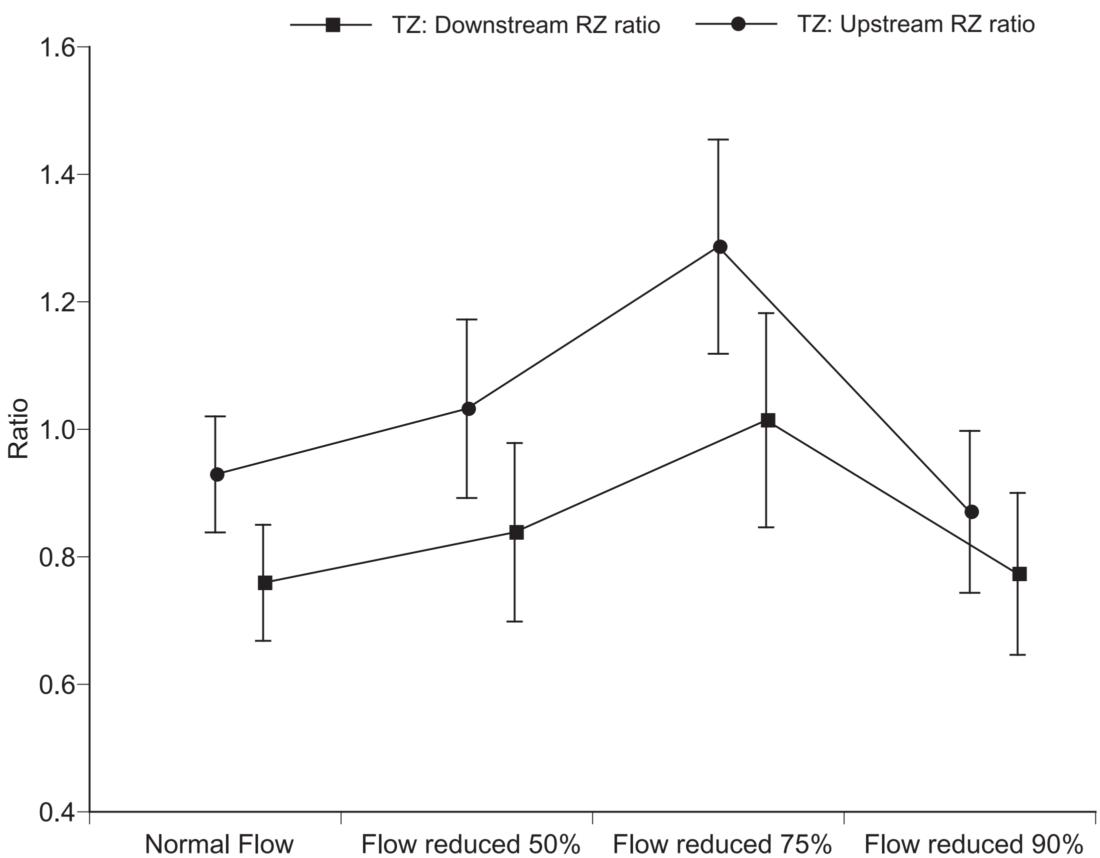

Figure 4.–Ratios of survival (± 2 SE) of yearling-and-older (YAO) brook trout in an experimentally dewatered zone (TZ) to survival in reference zones (RZ) in Hunt Creek. Summer discharge in the TZ was normal from 1984-90, reduced by 50% from 1991-94, reduced by 75% from 1995-96, and by 90% from 1997-98. Summer discharge in reference zones was not altered.

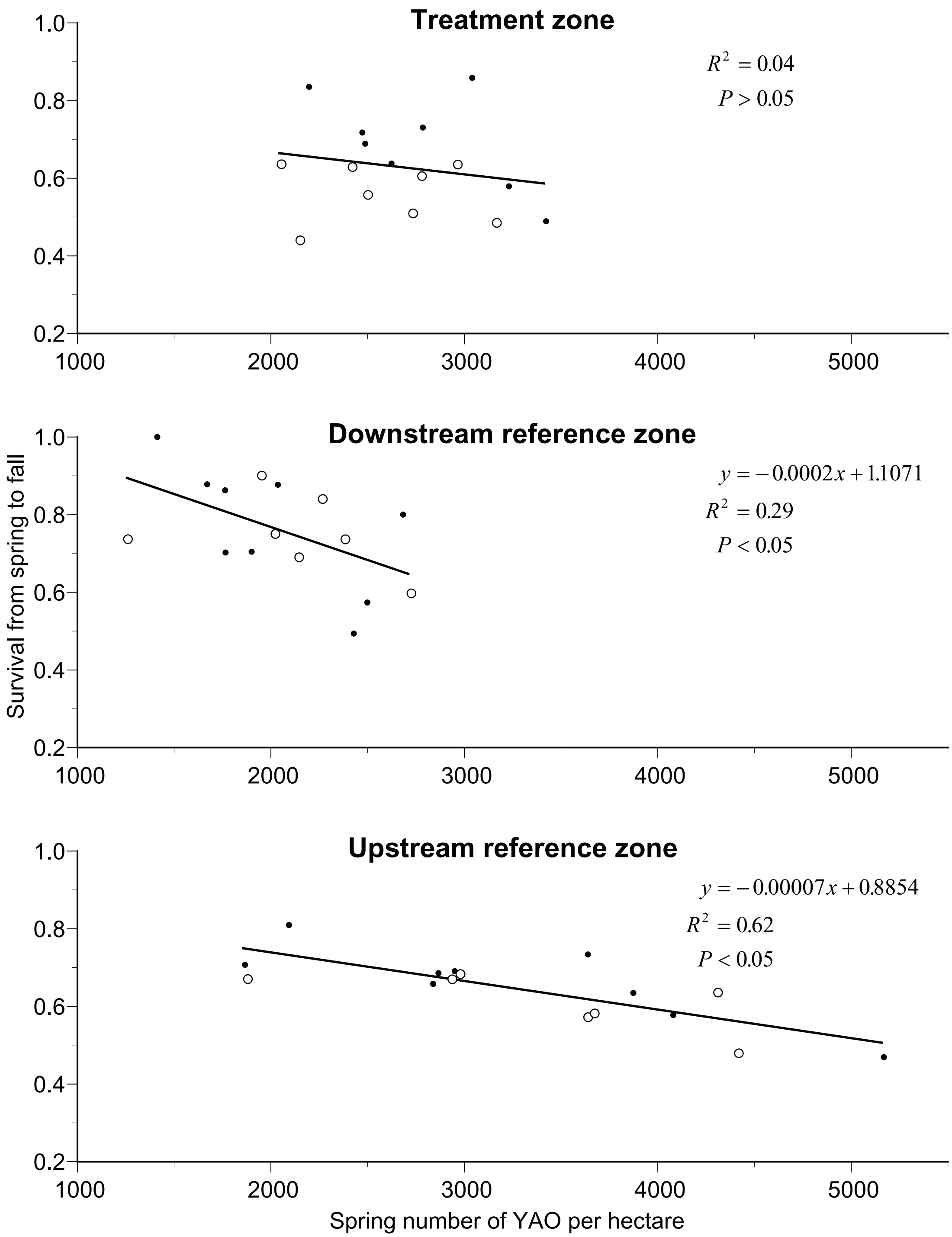

Figure 5.–Fraction of yearling-and-older (YAO) brook trout surviving from spring to fall plotted against spring density of YAO from 1984-99. Data for years when summer discharge was reduced in the treatment zone are depicted by solid circles. Open circles depict pretreatment years in the reference zones.

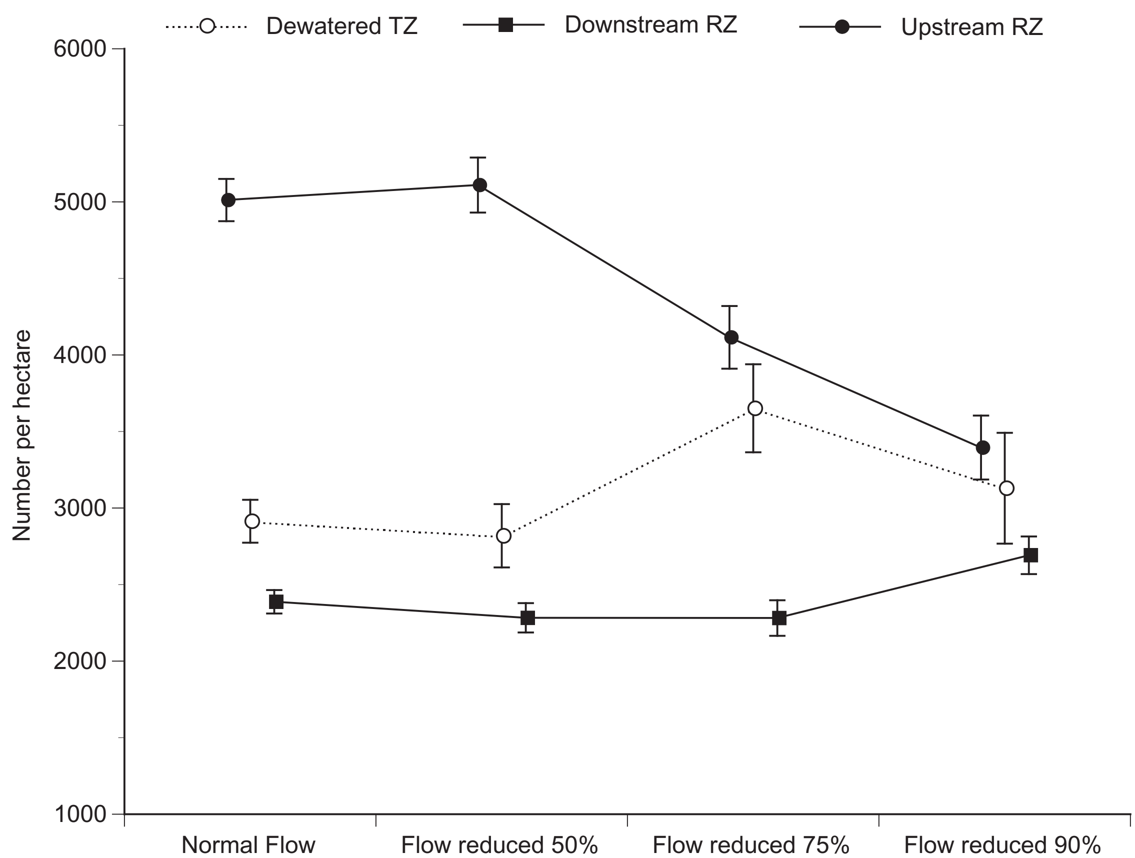

Figure 6.–Fall number (± 2 SE) of young-of-the-year brook trout per hectare in an experimentally dewatered zone (TZ) and reference zones (RZ) in Hunt Creek. Summer discharge in the TZ was normal from 1984-90, reduced by 50% from 1991-94, reduced by 75% from 1995-96, and by 90% from 1997-98. Summer discharge in reference zones was not altered.

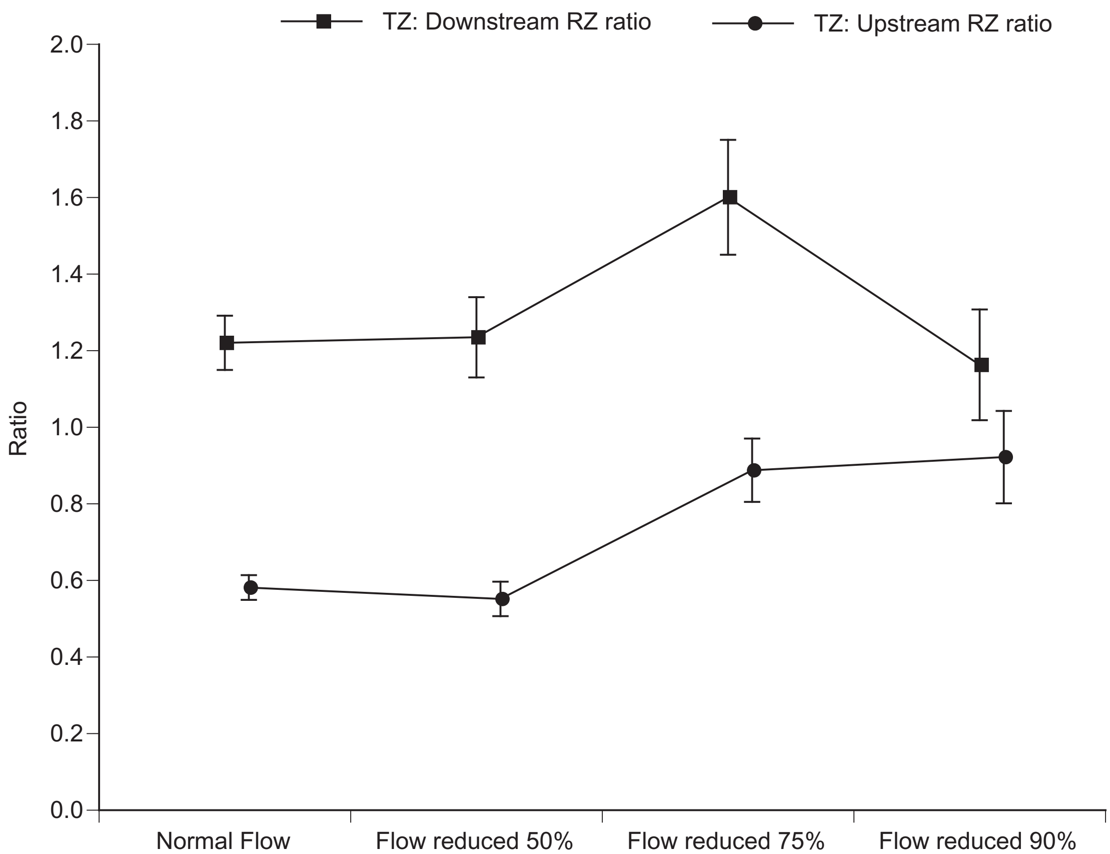

Figure 7.–Ratios of mean abundance (± 2SE) of young-of-the-year (YOY) brook trout in an experimentally dewatered zone (TZ) to abundance in reference zones (RZ) in Hunt Creek. Summer discharge in the TZ was normal from 1984-90, reduced by 50% from 1991-94, reduced by 75% from 1995-96, and by 90% from 1997-98. Summer discharge in reference zones was not altered.

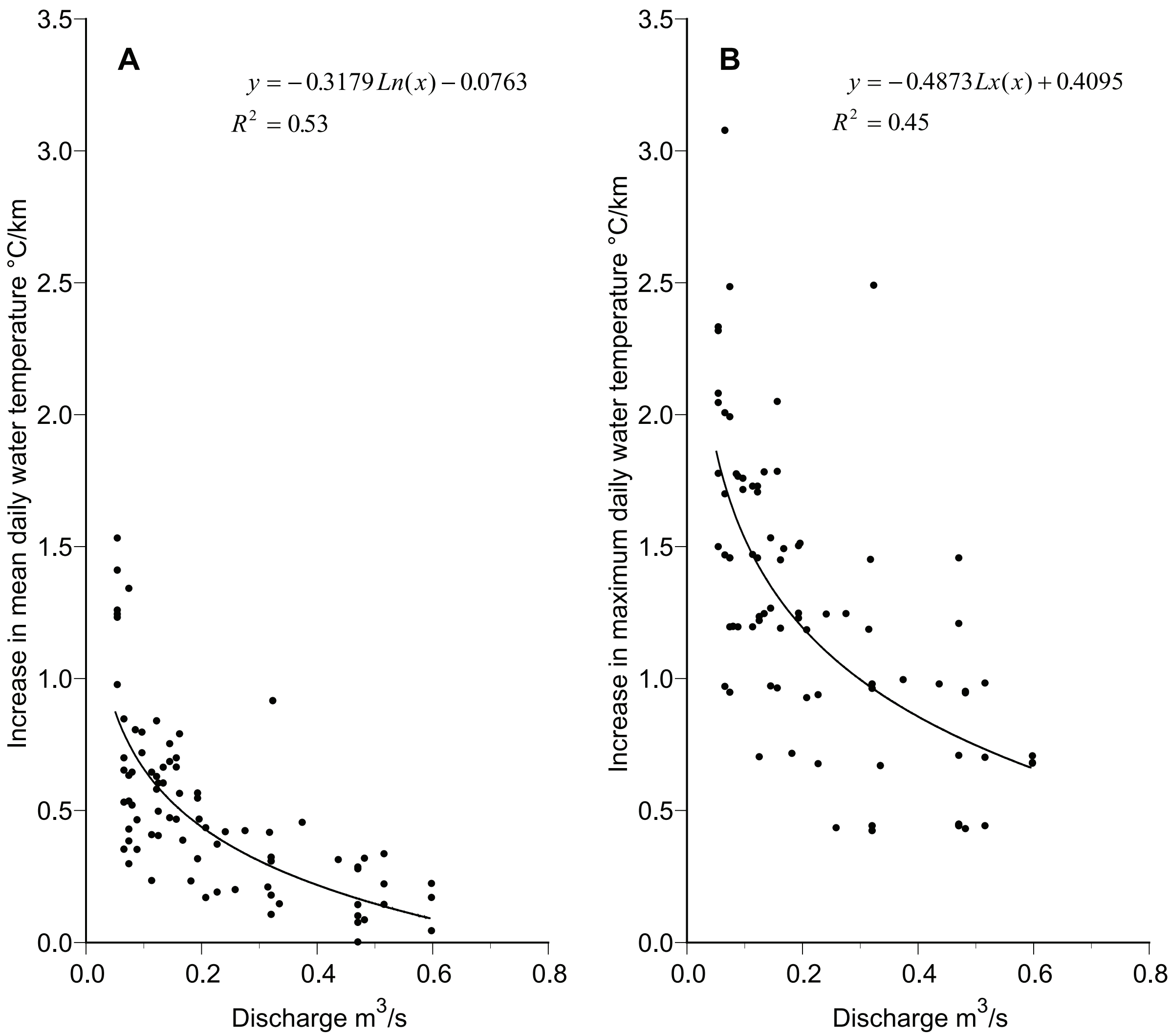

Figure 8.–Increase in daily water temperature (°C/km) in the treatment zone of Hunt Creek as a function of discharge in 1999 (A) increase in mean daily water temperature and (B) increase in maximum daily water temperature.

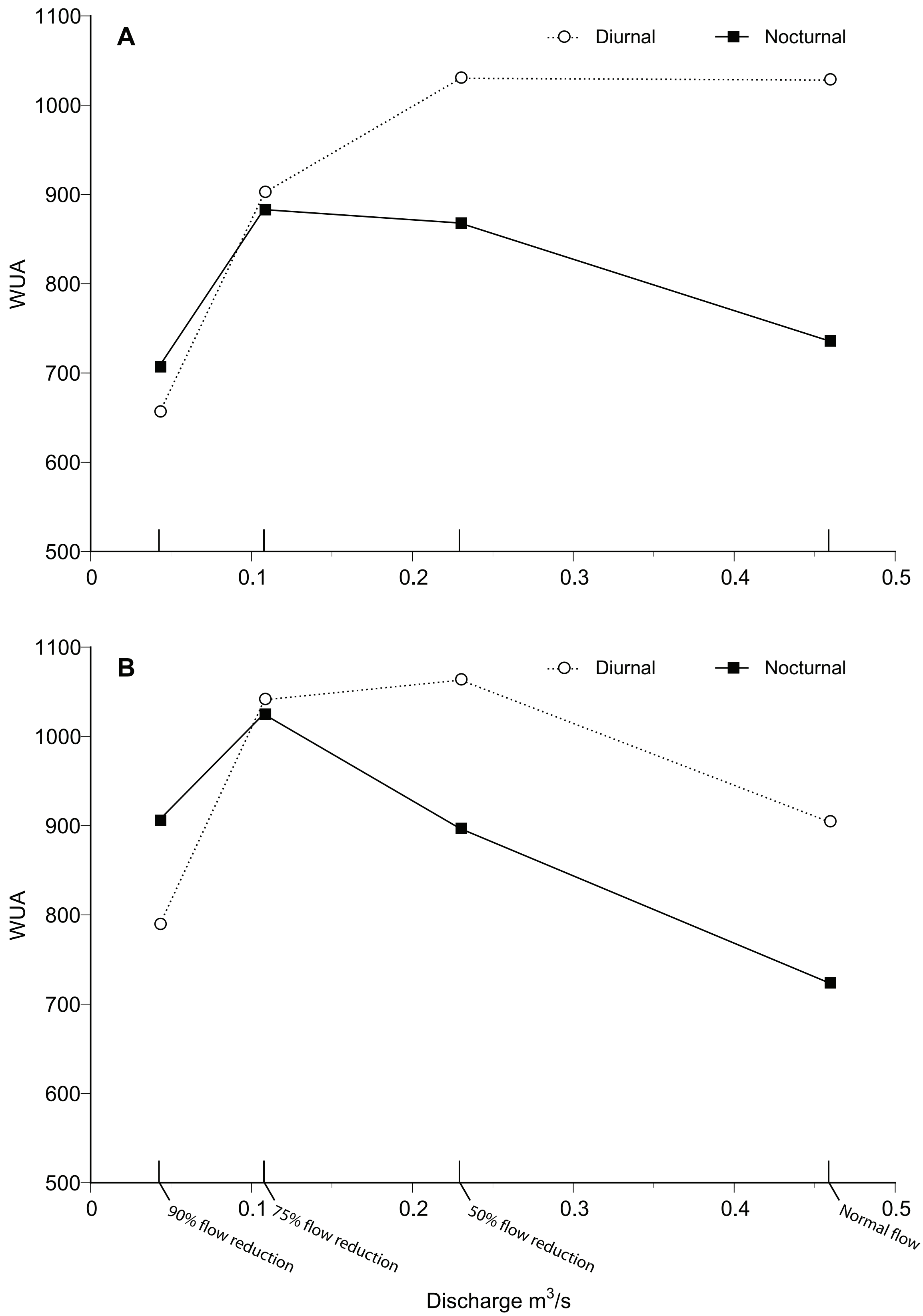

Figure 9.–Diurnal (foraging) and nocturnal (resting) estimates of WUA (m^2) for brook trout derived from use-HSC (A) YAO brook trout and (B) YOY brook trout.

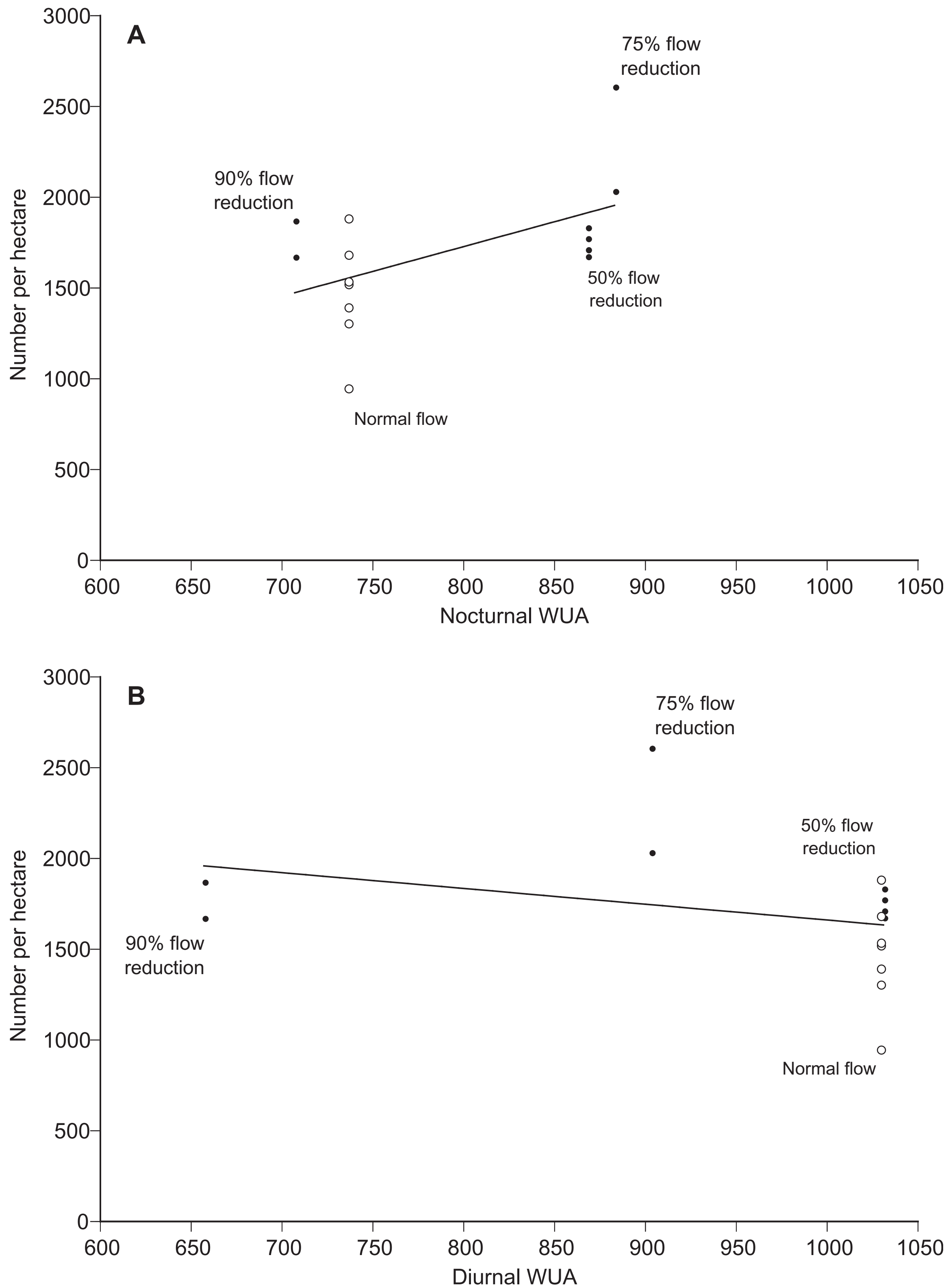

Figure 10.–Relation between fall abundance of YAO brook trout and WUA (m^2) derived from use-HSC. (A) nocturnal WUA, $R^2 = 0.30$, $P < 0.05$ and (B) diurnal WUA, $R^2 = 0.10$, $P > 0.05$. Open circles depict abundance when summer flow was normal and solid circles show abundance during years when flow was diverted.

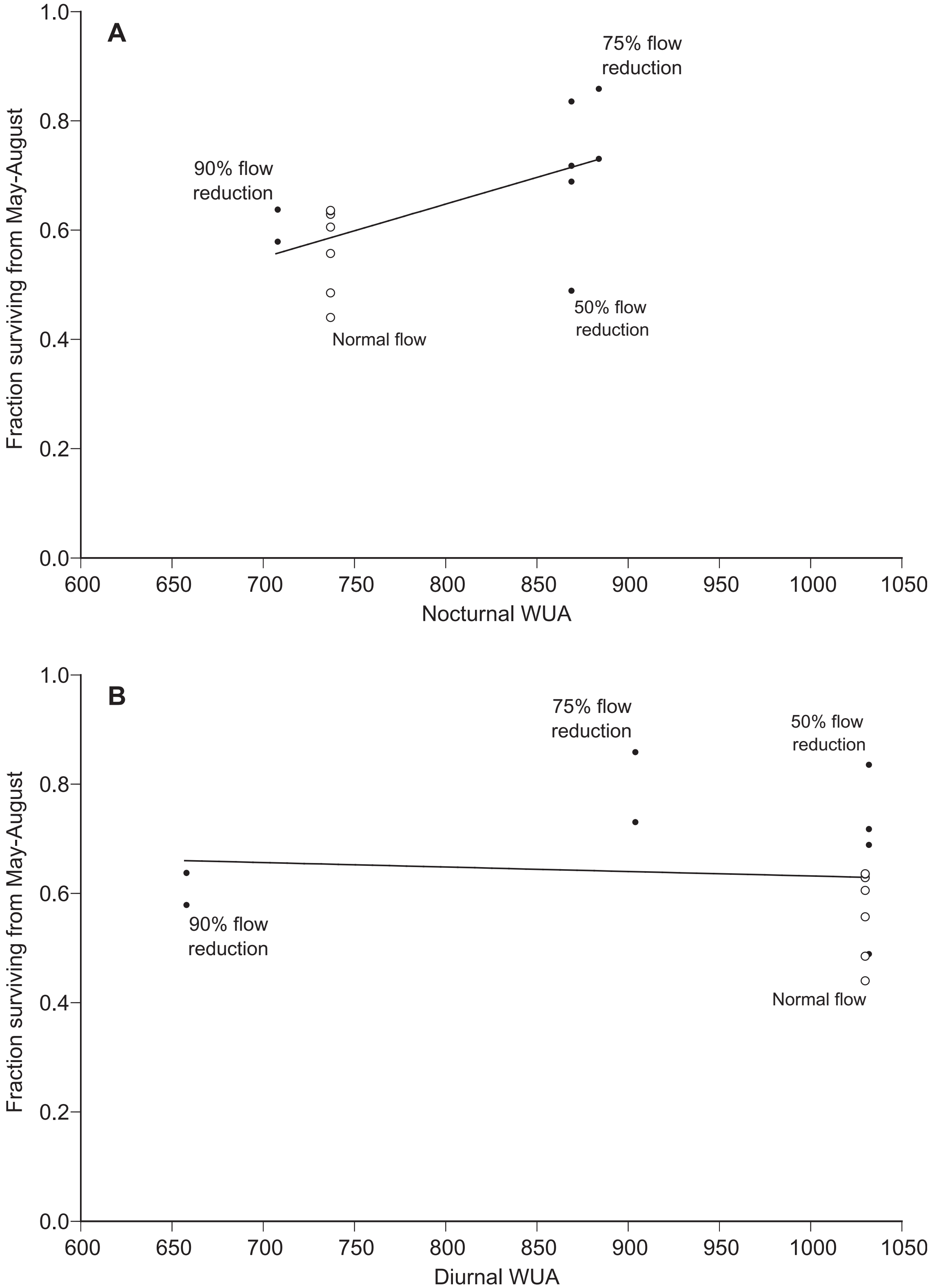

Figure 11.–Relation of spring-to-fall survival of YAO brook trout (1984-98) and WUA (m^2) in an experimentally dewatered section of Hunt Creek. (A) nocturnal WUA, $R^2 = 0.36$, $P < 0.05$ and (B) diurnal WUA, $R^2 = 0.008$, $P > 0.05$. Open circles depict abundance when summer flow was normal and solid circles show abundance during years when flow was diverted.

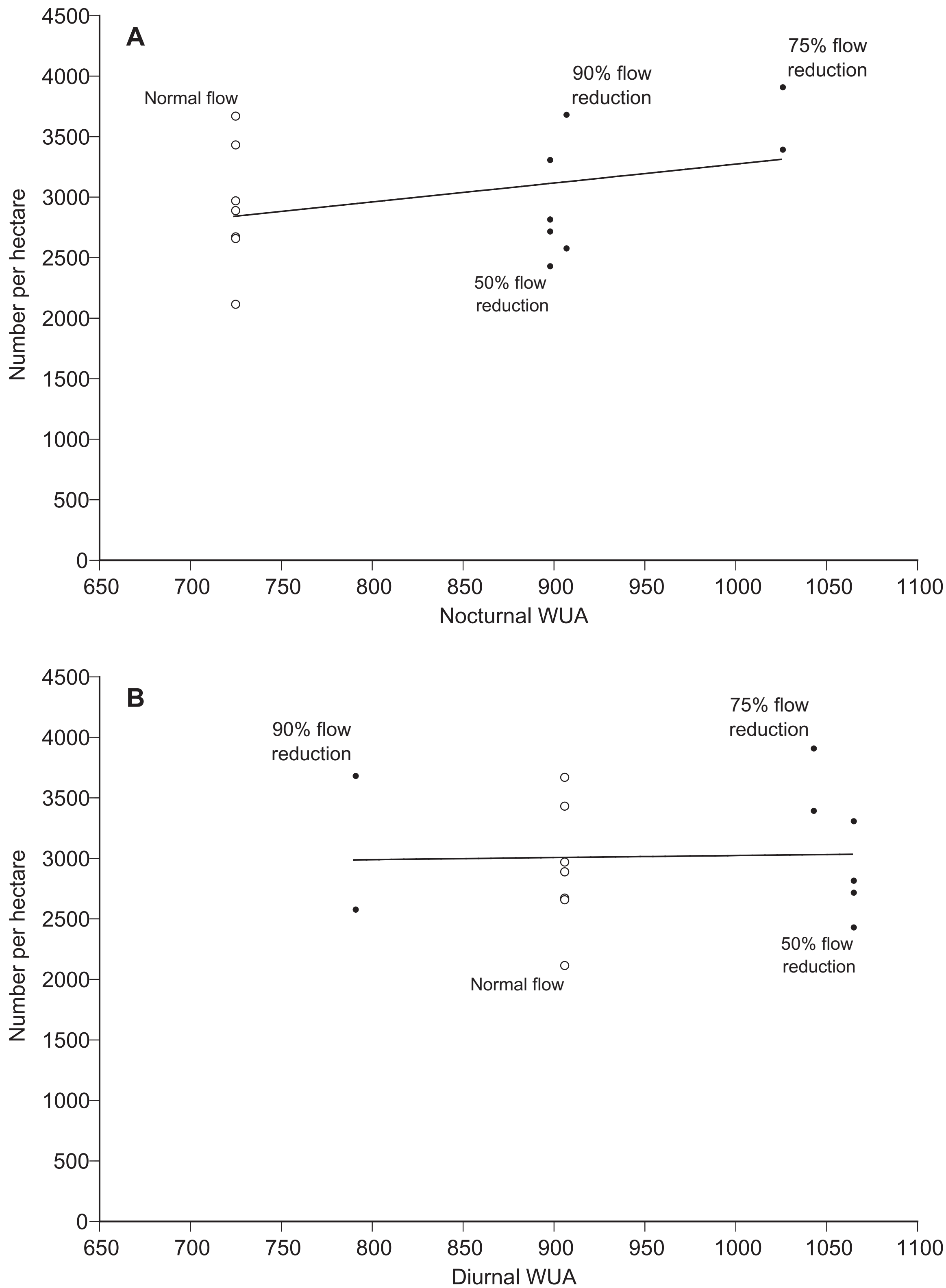

Figure 12.–Relation between fall abundance of YOY brook trout (1984-98) and WUA (m^2) in an experimentally dewatered section of Hunt Creek. (a) nocturnal WUA, $R^2 = 0.12$, $P > 0.05$ and (b) diurnal WUA, $R^2 = 0.0009$, $P > 0.05$. Open circles depict abundance when summer flow was normal and solid circles show abundance during years when flow was diverted.

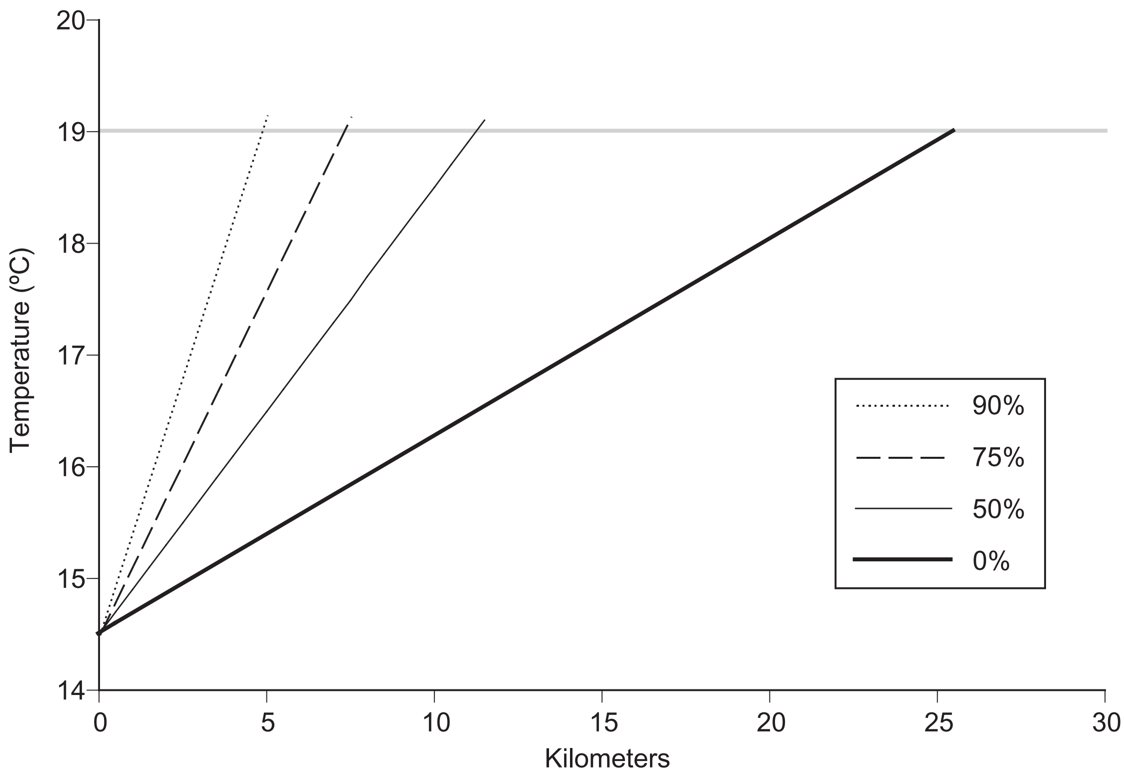

Figure 13.–Increase in mean daily water temperature as a function of percentage of summer baseflow diverted and distance downstream from the point of diversion. The y-intercept value (14.5°C) was based on mean July water temperature in Hunt Creek at the upstream bulkhead during the present study. The horizontal line represents the temperature, above which wild brook abundance is very likely to be reduced.

Table 1.–Optimal and suitable habitat suitability criteria values for diurnal and nocturnal periods. Data for all HSC are from Baker and Coon (1997).

		Depth (cm)	Mean column velocity (cm/s)	Substrate[a]	Cover[b]
Diurnal use-HSC					
young of the year	Optimal range	15-34	6-30	1-5.4	3
	Suitable range	3-67	0-66	1-5.4	2 & 3
yearling and older	Optimal range	27-55	6-27	1-5.4	3
	Suitable range	12-85	0-98	1-5.4	2 & 3
Nocturnal use-HSC					
young of the year	Optimal range	12-29	5-23	1-5.4	3
	Suitable range	1-73	0-39	1-5.4	2 & 3
yearling and older	Optimal range	20-46	4-22	1-5.4	3
	Suitable range	7-73	0-52	1-5.4	2 & 3

[a] Substrate codes ranged from 1 (fines composed of sand and silt), up to 5 (large gravel > 2.5 cm). The numeral beyond the decimal point is an estimate of gravel embeddedness ranging from 1 (up to 25%) to 4 (76-100%)

[b] Cover code 2 denotes a velocity shelter protruding out of the substrate but not providing visual isolation. Cover code 3 denotes a combination cover providing both visual isolation and velocity shelter.

Table 2.–Fall mean length at age in mm (± 2SE) of brook trout in a dewatered zone and two reference zones of Hunt Creek. Summer baseflow discharge (m^3/s) in the treatment zone was approximately 0.45 from 1984-90, 0.23 from 1991-94, 0.11 in 1995-96 and 0.04 in 1997-98.

	Treatment zone flow reduction	Treatment zone	Reference zones: Downstream	Reference zones: Upstream
		Age 0		
1984-90	None	79 ± 5	86 ± 4	77 ± 3
1991-94	50%	80 ± 7	87 ± 5	78 ± 4
1995-96	75%	75 ± 8	87 ± 6	77 ± 5
1997-98	90%	75 ± 11	83 ± 5	76 ± 6
		Age 1		
1984-90	None	128 ± 10	138 ± 7	131 ± 10
1991-94	50%	126 ± 17	139 ± 9	129 ± 13
1995-96	75%	125 ± 14	138 ± 11	126 ± 9
1997-98	90%	126 ± 15	138 ± 11	129 ± 8
		Age 2		
1984-90	None	180 ± 21	189 ± 15	178 ± 26
1991-94	50%	174 ± 32	193 ± 20	171 ± 28
1995-96	75%	169 ± 45	193 ± 24	174 ± 30
1997-98	90%	175 ± 40	197 ± 23	183 ± 30
		Age 3		
1984-90	None	241 ± 49	241 ± 40	224 ± 45
1991-94	50%	220 ± 61	230 ± 53	225 ± 48
1995-96	75%	218 ± 102	231 ± 68	231 ± 85
1997-98	90%	210 ± 102	231 ± 72	227 ± 73

Table 3.–Number of yearling and older (YAO) and young of the year (YOY) brook trout immigrating into, or emigrating out of, the treatment zone from 1-June to 31-August during the summer prior to water withdrawal (1990), the summers when 50% of baseflow was diverted (1991-94), the summers when 75% of baseflow was diverted (1995-96), and during 1997-98 when 90% of baseflow was diverted. Trout attempting to immigrate into the TZ that died in the fish traps are not included.

	Immigrants		Emigrants		Net change	
Year	YOY	YAO	YOY	YAO	YOY	YAO
			Normal flow			
1990	Traps not constructed		25	44	unknown	Unknown
			50% of flow diverted			
1991	20	15	19	24	1	-9
1992	9	19	29	24	-20	-5
1993	21	139	14	118	7	21
1994	83	57	32	18	51	39
Average	33	57	23	46	10	11
			75% of flow diverted			
1995	10	29	6	8	4	21
1996	2	10	15	2	-13	8
Average	6	19.5	10.5	5	-4.5	14.5
			90% of flow diverted			
1997	7	9	5	8	2	1
1998	9	15	8	15	1	0
Average	8	12	6.5	11.5	1.5	0.5

Table 4.–Change in average and maximum daily temperature (^{o}C/km) between the upstream and downstream boundaries in the TZ of Hunt Creek during dewatering experiments conducted between 1993 and 1998 and during normal flow years (2000-01).

	Percentage of summer discharge diverted							
	0%		50%		75%		90%	
Period	2000	2001	1993	1994	1995	1996	1997	1998
	Change in average daily temperature							
June	-0.6	0.0	-0.5	0.2	1.6	1.4	2.7	1.7
July	-0.2	-0.1	-0.3	0.3	1.6	1.6	2.8	2.5
August	-0.2	-0.1	-0.2	0.3	1.8	1.5	2.3	2.2
June-August	-0.3	-0.1	-0.3	0.3	1.7	1.5	2.6	2.1
	Change in maximum daily temperature							
June	-1.4	0.3	-0.9	0.6	1.9	1.4	3.4	3.6
July	0.0	0.3	-0.7	0.5	1.8	1.3	3.6	4.4
August	-0.1	0.2	-0.4	0.3	1.9	0.6	2.7	3.5
June-August	-0.5	0.3	-0.7	0.5	1.9	1.1	3.2	3.9

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Appendix 1.–Spring number (± 2SE) of yearling-and-older brook trout per hectare in an experimentally dewatered zone and reference zones of Hunt Creek.

			Reference zones			
Year	Dewatered zone		Downstream		Upstream	
	Period A – Normal Flow					
1984	2,773	±320	1,945	±95	4,303	±262
1985	2,414	±210	2,718	±128	3,632	±211
1986	2,959	±296	2,260	±149	3,666	±355
1987	3,160	±383	2,377	±175	4,411	±264
1988	2,144	±281	2,138	±116	2,930	±227
1989	2,494	±335	2,015	±138	2,972	±236
1990	2,047	±298	1,253	±150	1,873	±187
Average	2,570	±116	2,101	±52	3,398	±96
	Period B – Flow reduced 50%					
1991	2,189	±268	1,757	±127	3,865	±266
1992	2,479	±291	2,028	±142	3,630	±291
1993	3,414	±415	2,675	±143	5,160	±536
1994	2,464	±224	1,662	±124	2,085	±147
Average	2,637	±154	2,031	±67	3,685	±170
	Period C – Flow reduced 75%					
1995	2,777	±257	1,755	±92	4,071	±232
1996	3,032	±274	1,892	±163	2,830	±188
Average	2,904	±188	1,823	±94	3,450	±150
	Period D – Flow reduced 90%					
1997	3,222	±425	1,404	±130	1,858	±228
1998	2,615	±262	2,490	±129	2,942	±254
Average	2,918	±250	1,947	±92	2,400	±171
	Within zone results of Bonferroni multiple comparison tests between periods A-D					
	A=B		A=B		A<B	
	A<C		A>C		A=C	
	A=D		A>D		A>D	
	B=C		B>C		B=C	
	B=D		B=D		B>D	
	C=D		C=D		C>D	

Appendix 2.–Fall number (± 2SE) of yearling-and-older brook trout per hectare in an experimentally dewatered zone and reference zones of Hunt Creek.

Year	Dewatered zone		Reference zones: Downstream		Reference zones: Upstream	
			Period A – Normal Flow			
1984	1,679	± 242	1,751	± 119	2,734	± 299
1985	1,517	± 253	1,623	± 145	2,077	± 266
1986	1,879	± 156	1,898	± 145	2,133	± 439
1987	1,532	± 205	1,750	± 188	2,113	± 445
1988	943	± 173	1,476	± 151	1,962	± 268
1989	1,389	± 180	1,512	± 137	2,030	± 198
1990	1,301	± 268	923	± 103	1,255	± 214
Average	1,463	± 81	1,562	± 54	2,043	± 120
			Period B – Flow reduced 50%			
1991	1,829	± 283	1,235	± 120	2,452	± 338
1992	1,708	± 233	1,779	± 145	2,664	± 280
1993	1,670	± 406	2,141	± 158	2,421	± 438
1994	1,769	± 349	1,459	± 133	1,688	± 282
Average	1,744	± 162	1,653	± 70	2,306	± 170
			Period C – Flow reduced 75%			
1995	2,029	± 213	1,514	± 117	2,352	± 213
1996	2,604	± 342	1,333	± 112	1,861	± 150
Average	2,316	± 201	1,423	± 81	2,107	± 130
			Period D – Flow reduced 90%			
1997	1,866	± 213	1,404	± 98	1,314	± 105
1998	1,667	± 188	1,429	± 116	2,032	± 126
Average	1,766	± 142	1,416	± 76	1,673	± 82
			Within zone results of Bonferroni multiple comparison tests between periods A-D			
	A<B		A=B		A=B	
	A<C		A>C		A=C	
	A<D		A>D		A>D	
	B<C		B>C		B=C	
	B=D		B>D		B>D	
	C>D		C=D		C>D	

Appendix 3.–Percentage (± 2SE) of yearling-and-older brook (YAO) trout surviving from spring to fall in an experimentally dewatered zone and reference zones of Hunt Creek.

Year	Dewatered zone		Reference zones: Downstream		Reference zones: Upstream	
	Period A – Normal Flow					
1984	60.5	± 11.2	90.0	± 7.5	63.5	± 07.9
1985	62.9	± 11.8	59.7	± 6.0	57.2	± 08.1
1986	63.5	± 8.2	84.0	± 8.5	58.2	± 13.2
1987	48.5	± 8.8	73.6	± 9.6	47.9	± 10.5
1988	44.0	± 9.9	69.0	± 8.0	67.0	± 10.5
1989	55.7	± 10.4	75.0	± 8.5	68.3	± 8.6
1990	63.6	± 16.0	73.7	± 12.1	67.0	± 13.2
Average	56.9	± 4.2	75.0	± 3.3	61.3	± 4.0
	Period B – Flow reduced 50%					
1991	83.6	± 16.5	70.3	± 8.5	63.5	± 9.8
1992	68.9	± 12.4	87.7	± 9.4	73.4	± 9.7
1993	48.9	± 13.3	80.0	± 7.3	46.9	± 9.8
1994	71.8	± 15.6	87.8	± 10.3	80.9	± 14.7
Average	68.3	± 7.3	81.5	± 4.5	66.2	± 5.6
	Period C – Flow reduced 75%					
1995	73.1	± 10.2	86.3	± 8.0	57.8	± 6.2
1996	85.9	± 13.7	70.5	± 8.5	65.8	± 6.9
Average	79.5	± 8.5	78.4	± 5.8	61.8	± 4.6
	Period D – Flow reduced 90%					
1997	57.9	± 10.1	100.0	± 11.6	70.7	± 10.3
1998	63.8	± 9.6	57.4	± 5.5	69.1	± 7.3
Average	60.8	± 7.0	78.7	± 6.4	69.9	± 6.3
	Within zone results of Bonferroni multiple comparison tests between periods A-D					
	A<B		A=B		A=B	
	A<C		A=C		A=C	
	A=D		A=D		A=D	
	B=C		B=C		B=C	
	B=D		B=D		B=D	
	C>D		C=D		C=D	

Appendix 4.–Fall number (± 2SE) of young-of-the-year brook trout per hectare in an experimentally dewatered zone and two reference zones of Hunt Creek.

		Reference zones	
Year	Dewatered zone	Downstream	Upstream
	Period A – Normal Flow		
1984	3,430 ± 466	2,963 ± 197	4,755 ± 295
1985	2,968 ± 343	2,329 ± 190	4,914 ± 246
1986	2,887 ± 315	2,643 ± 210	6,085 ± 476
1987	2,113 ± 276	2,225 ± 243	4,221 ± 500
1988	3,668 ± 402	2,259 ± 187	4,916 ± 275
1989	2,670 ± 316	2,225 ± 200	4,458 ± 296
1990	2,656 ± 440	2,068 ± 191	5,727 ± 375
Average	2,913 ± 140	2,387 ± 77	5,011 ± 138
	Period B – Flow reduced 50%		
1991	2,717 ± 309	2,061 ± 169	5,601 ± 336
1992	2,816 ± 384	2,293 ± 185	4,998 ± 363
1993	2,430 ± 372	2,030 ± 161	2,952 ± 331
1994	3,307 ± 553	2,744 ± 245	6,887 ± 403
Average	2,818 ± 207	2,282 ± 96	5,109 ± 180
	Period C – Flow reduced 75%		
1995	3,908 ± 384	2,284 ± 149	4,006 ± 254
1996	3,393 ± 427	2,278 ± 178	4,221 ± 323
Average	3,651 ± 287	2,281 ± 116	4,114 ± 205
	Period D – Flow reduced 90%		
1997	3,681 ± 645	2,819 ± 176	3,699 ± 317
1998	2,577 ± 326	2,563 ± 173	3,088 ± 272
Average	3,129 ± 362	2,691 ± 123	3,394 ± 209
	Within zone results of Bonferroni multiple comparison tests between periods A-D		
	A=B	A=B	A=B
	A<C	A=C	A>C
	A=D	A<D	A>D
	B<C	B=C	B>C
	B=D	B<D	B>D
	C=D	C<D	C>D