

Influence of Variable Interannual Summer Water Temperatures on Brook Trout Growth, Consumption, Reproduction, and Mortality in an Unstratified Adirondack Lake

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Abstract.—Stressful water temperatures negatively affect physiological processes in fishes, yet evidence for how elevated temperatures influence population-level characteristics is rare. An 8-year field study of brook trout *Salvelinus fontinalis* in an unstratified Adirondack lake revealed that an aggregate measure of chronically stressful summer water temperatures strongly influenced brook trout population-level characteristics. We quantified chronic thermal stress using the cumulative degree-days over which bottom temperatures exceeded a range of thresholds (18–22°C) and found that the strongest relationships were with cumulative degree-days over 20°C (DD_{>20}). Across years with similar brook trout densities, warmer summer water temperatures resulted in decreased brook trout growth, but growth was not reduced in a year with high water temperatures and low density. Maximum stomach fullness was negatively related to water temperature. Reproductive activity was negatively correlated with stressful summer thermal conditions and was less dependent on female brook trout density. Periods of chronically stressful summer water temperatures resulted in the apparent mortality of age-2 and older fish during a moderately stressful summer (156 DD_{>20}) and apparent mortality of age-1 and older fish during the most stressful summer (210 DD_{>20}). In contrast, extensive mortality was not evident in any year-classes when DD_{>20} was less than 115. Anthropogenic impacts on the thermal conditions of aquatic ecosystems occur at small (hydrology) and large (climate change) spatial extents, and in situ studies at the margin of an organism's thermal range can provide important insights into changes that will occur if temperatures increase.

Temperature plays a primary role in governing most life processes in fish (Brett 1971). Thermal preferences and temperature effects on fishes have been described for many taxa and are commonly determined in controlled laboratory settings (Baldwin 1956; Hokanson et al. 1973, 1977; Selong et al. 2001) or through bioenergetics simulations (Schofield et al. 1993; Reis and Perry 1995; Johnson et al. 2006). Less common are field studies that specifically document and quantify the influence of warm water temperatures on fish populations over multiple years (Drake and Taylor 1996; Baird et al. 2006; Biro et al. 2007). The effect of water temperature on fish varies with body size and life

stage (Schmidt-Nielsen 1990; Lester et al. 2004). For a given species, larger fish are generally more sensitive to temperature increases than smaller fish due to greater metabolic demands and lower thermal preferences (Baldwin 1956; Coutant 1977; Hartman and Cox 2008). However, most studies examining the influence of temperature on fish have focused on juvenile life stages due to the ease of sampling and rearing under laboratory conditions (Elliott 1975; Dockray et al. 1996; Biro et al. 2007; Spina 2007). Long-term studies in intact lake ecosystems are needed to understand how variability in annual temperature conditions affect different life stages in fish populations. Studies at this spatial and temporal scale provide relevant insight into how potential changes in annual temperature regimes may impact population-level characteristics in the presence of environmental variation.

Anthropogenic impacts on the thermal conditions of aquatic ecosystems occur at small (e.g., land management influences on groundwater seeps) and large (climate change impacts on lake stratification) spatial

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extents (Beschta and Taylor 1988; Trombulak and Wolfson 2004; IPCC 2007). Global climate change has been implicated as a factor responsible for altering thermal regimes, precipitation patterns, groundwater inputs, and evaporation rates within aquatic ecosystems (Meisner 1990a; Schindler et al. 1996; Hayhoe et al. 2006; Burns et al. 2007). The negative effects of warm temperatures on coldwater fish species in the northern hemisphere are most pronounced at low elevations and at the southern margins of the species' ranges, especially in systems that may already be thermally stressful (Meisner 1990b; Reis and Perry 1995; Eaton and Scheller 1996; Parmesan and Yohe 2003). Predicted future warming trends may cause some waters with suitable thermal habitat to become marginal, while waters already experiencing high summer temperatures may become unsuitable for some coldwater species (Clark et al. 2001; Schindler 2001; Flebbe et al. 2006).

Populations of brook trout *Salvelinus fontinalis* have been greatly reduced in the species' native range, and changes in thermal regimes are among the largest threats to their continued persistence (Hudy et al. 2005). Water temperature changes associated with a warming climate and human modifications to watersheds have been predicted to alter brook trout growth (Reis and Perry 1995; King et al. 1999), available thermal habitat (Meisner 1990a), and distributional range (Meisner 1990b). Brook trout populations are particularly vulnerable because these fish require relatively cool water temperatures and rely on upwelling groundwater for reproduction and thermal refuge (Curry and Noakes 1995; Borwick et al. 2006). Although the impact of temperature increases on brook trout has been documented and predicted for stream populations (Meisner 1990a, 1990b; Wehrly et al. 2007), little attention has been paid to similar impacts in lentic systems. After a thorough review of the available literature, Power (1980) concluded that brook trout typically inhabit waters ranging in temperature from 0°C to 20°C. Schofield et al. (1993) demonstrated that optimal growth occurs between 11°C and 16°C. At 20°C, brook trout activity rates are lowest (Fisher and Sullivan 1958) and metabolism is maximized (Hartman and Cox 2008). The upper incipient lethal temperature for yearling brook trout was identified as 25.3°C (Fry et al. 1946), but others have suggested that published upper thermal tolerance limits may be slightly overestimated for larger brook trout (Ricker 1979; Schofield et al. 1993).

Our goal was to establish how chronically stressful summer water temperatures could influence a lentic brook trout population and to explore possible mechanisms for the observed effects. Specifically, we

hypothesized that the duration of chronically stressful summer water temperatures would be negatively correlated with brook trout growth rate, reproductive effort, and consumption. We were also interested in whether uncharacteristically severe mortality events corresponded with the most thermally stressful summers. Our results illustrate the importance of making in situ evaluations of fish populations living in well-characterized thermal environments to more fully understand the influence of changing water temperature conditions on brook trout and similar stenothermal species. We identify a range of annual thermal stress levels that affect mortality and reproductive effort, and this information should aid brook trout conservation and management in thermally stressed ecosystems. Furthermore, we illustrate population-level changes and relationships associated with variable summer thermal conditions that may be expected in other lentic systems if climate warming trends continue.

Study Site

Rock Lake is located near the southern boundary of brook trout's lentic range, and the thermal regime in this unstratified lake is at the upper margin of the species' thermal tolerance. The lake is located on private land within the Adirondack Park of New York (43°57'N, 74°52'W) and has a surface area of 78.9 ha, a maximum depth of 5.5 m, a mean summer total phosphorus level of approximately 3.1 µg/L, and a mean summer pH of approximately 5.7 (authors' unpublished data). The watershed is almost completely forested, with the exception of one cabin on the lake shoreline. The lake does not thermally stratify in the summer, resulting in bottom temperatures that regularly exceed 20°C and that approach or exceed lethal levels for brook trout in some years. The brook trout is the only fish species present in the lake. Based on a temperature-sensitive radiotelemetry effort as well as many years of observation and temperature monitoring, we have established that midsummer thermal refuge areas of nearshore upwelling groundwater are not available to yearling and older brook trout in Rock Lake (Robinson 2008). From 1978 to 2002, the lake was stocked annually with fall fingerling brook trout that received a fin clip for age verification, but stocking ceased in 2002 after successful reproduction was observed within the lake. During 1996 through 2002, the lake was stocked at a consistent annual rate of 25 fish/ha in late September (prior to trap-net surveys). Since the cessation of stocking, the brook trout population has been sustained solely by natural reproduction of fish spawning on in-lake shoals. Until 2005, a barrier was maintained at the lake's outlet to prevent fall emigration by adult brook trout. Since that

time, an outlet fish trap has been maintained and fall emigration has been assessed and found to be negligible. Almost all (~95%) angling mortality in the lake results from our sampling efforts.

Methods

Temperature monitoring.—Water temperature was monitored at the deepest point in the lake (5.5 m) using temperature loggers (1-h intervals) during mid-May through mid-October from 2000 to 2007, and the mean bottom temperature for each day was calculated over a 24-h period starting at 2400 hours. The relative degree of thermal stress in each year was estimated using the cumulative degree-days over which the mean bottom temperature exceeded 20°C ($DD_{>20}$). For example, if the mean bottom temperature on a given day was 19.5°C, the degree-day value for that date would be zero, whereas if the mean bottom temperature was 22.5°C, the degree-day value would be 2.5. Therefore, the $DD_{>20}$ metric accounted for both the duration and magnitude of stressful water temperatures. We assigned 20°C as the temperature above which brook trout would experience thermal stress based on published metabolic, activity, and thermal preference levels (Fisher and Sullivan 1958; Power 1980; Hartman and Cox 2008); however, for comparison, cumulative degree-days were also calculated using 18, 19, 21, and 22°C stress thresholds. The number of days during which the mean bottom temperature exceeded 20°C and the maximum bottom temperature were also calculated for each year. In addition, growing degree-days were calculated by summing the mean daily bottom temperature on each day in which bottom temperatures did not exceed 20°C between May 15 and September 15 (2000, 2001, and 2007).

Fish sampling and processing.—To sample a variety of habitat types within the lake, both gill nets and angling were used to capture brook trout from May to September during 2000, 2001, and 2007. Ten sinking, multifilament gill nets (1.2 × 50.0 m) with mesh sizes of 44.5 and 60.0 mm (five nets of each mesh size) were set for 2 h (1000–1200 hours) on each sampling date. Four anglers fished while gill nets were in the water. The majority of fish (~70%) were captured by angling. All fish captured through gillnetting and angling were euthanized and placed on ice for transport back to a laboratory, where total length and weight were measured. Gut contents were then removed and preserved in a 95% solution of ethanol. To calculate a stomach fullness index (dry weight basis), we assumed that the average percent water content for brook trout in Rock Lake was 74% (authors' unpublished data). To determine dry weight, stomach contents and the ethanol in which they were stored

were dried at 60°C until weight stabilized. Sagittal otoliths were extracted, cleaned, and dried.

Fall surveys were conducted using Oneida-style trap nets during mid-October in each year of the study (2000–2007) to evaluate relative brook trout abundance and population size structure. The number of nets set varied by year. An additional one-time gill-net survey was conducted directly after the fall 2005 trap-net survey to corroborate the absence of yearling and older fish in that year's trap-net catch. All fish captured in trap nets were measured for length and weight, visually examined for sex and maturity status, and returned to the lake.

Reproductive effort (spawning) was estimated by conducting whole-lake redd surveys in 2000–2007. Redd counts were conducted in late October or early November, depending on the timing of ice formation. Using a small boat, a two-person crew navigated the entire lake shoreline over approximately 2 m of water and, while looking toward shore, counted all visible redds. Water clarity allowed the crew to see the lake bottom in at least 3 m of water, but redds were rarely observed deeper than 2 m.

Age analysis.—Brook trout were aged using sagittal otoliths. Many of the otolith pairs contained at least one malformed (vateritic) otolith, in which case the least-deformed otolith (based on visual inspection) was selected for evaluation (Bowen et al. 1999). Otoliths were embedded in an epoxy resin (Araldite 502), and then a 0.32-mm transverse section was cut through the nucleus and perpendicular to the sulcus. The section was mounted on a glass slide and polished using successively finer lapping film, and ages were assigned based on enumeration of annuli (Casselman 1983). The ages of all known-aged fish (i.e., fin-clipped fish) were interpreted by a single reader as a means of age verification, and correspondence between ages assigned with fin clips versus otoliths was greater than 95%.

Data analysis.—No consistent differences were found in the total length or weight at age between wild and stocked fish, therefore the two groups were pooled for all analyses. Using gill-net and angling data, linear regressions of length and weight as a function of capture date were used to test for significant growth in length and weight over time for each age-class in 2000, 2001, and 2007 over the course of the growing season. Multiple-regression analysis was used to test for homogeneity of slopes associated with changes in total length (ΔL) and weight (ΔW) between 2000 and 2001. Residuals associated with these analyses were visually inspected for patterns.

Stomach fullness (SF) was determined for all fish captured in 2000 and 2001 using a method similar to

TABLE 1.—Cumulative degree-days over which mean lake bottom temperature exceeded 20°C (DD_{>20}), maximum bottom temperature, number of days exceeding 20°C, and brook trout growing degree-days in each year within Rock Lake, New York. Numbers in parentheses indicate hours at maximum temperature. Growing degree-days were calculated between May 15 and September 15 using 20°C as the maximum temperature for positive growth. “NA” means not applicable.

Year	DD _{>20}	Maximum temperature	Days > 20°C	Growing degree-days
2000	6.6	21.7 (5)	19	2,322
2001	98.1	25.2 (7)	51	1,676
2002	156.2	25.2 (8)	69	NA
2003	95.5	24.0 (5)	56	NA
2004	28.4	22.1 (36)	36	NA
2005	209.6	25.6 (5)	83	NA
2006	47.8	23.2 (9)	34	NA
2007	114.5	24.0 (25)	75	1,291

that described by Boisclair and Leggett (1988):

$$SF = (G/P) \times 100, \tag{1}$$

where *G* is the dry weight (g) of the gut contents and *P* is the estimated dry weight of the fish. To avoid extreme values, the mean of the upper quartile of SF on each sampling date was used to represent maximum SF in the regression. Given that only two fish (both with empty stomachs) were captured on August 16, 2001, a value of zero was used to represent the maximum SF for that date. Linear regression was used to determine the influence of water temperature on the maximum gut fullness. Residuals were found to be normally distributed using the Shapiro–Wilk test for normality.

Akaike’s information criterion corrected for small-sample bias (AIC_c; Burnham and Anderson 1998) was used to select the most parsimonious linear model explaining fall redd counts using the four possible parameter combinations of DD_{>20} and fall trap-net catch per unit effort (CPUE) of mature females. Among-year differences in fall trap-net CPUEs were analyzed using a one-way analysis of variance and post hoc comparisons (Tukey’s honestly significant difference [HSD] test). Length frequency histograms from trap-net catches and length-at-age data were used to follow cohorts through time to identify those years and cohorts that experienced mortality events. Trap-net catch data used in the histograms were standardized by effort for each year by dividing the number of individuals in each histogram bin by the number of trap-net nights in the corresponding fall. Apparent total mortality events were identified based on cohort absence in a given year that could not be attributed to (1) mortality of that particular cohort in a previous year or (2) year-class absence due to low spawner

abundance, lack of spawning in a previous year, or both. Because of the potential for gear selectivity or bias, instances in which cohorts were poorly represented but still present were not considered total mortality events.

Results

Thermal Conditions

The DD_{>20} varied among years, ranging from 6.6 in 2000 to 206.9 in 2005 (Table 1; Figure 1). The number of days exceeding 20°C was greatest in 2002 (69 d), 2005 (83 d), and 2007 (75 d). Maximum bottom water temperatures exceeded the upper incipient lethal temperature for brook trout (25.6°C) on August 10 and 11, 2005, and approached lethal levels in 2001 (25.2°C) and 2002 (25.2°C; Table 1). Of the 3 years in which seasonal growth was evaluated, 2000 was the most favorable year based on growing degree-days and plots of mean bottom temperature over time, followed by 2001 and 2007 (Table 1). The warmest conditions were found from early to mid-August in all years (Figure 1).

Brook Trout Catch

Overall, 257 brook trout were captured using gill nets and angling on 10 dates in 2000, 259 brook trout were captured on seven dates in 2001, and 69 brook trout were captured on eight dates in 2007 (Table 2). Naturally spawned fish constituted 61, 54, and 100% of fish captured in 2000, 2001, and 2007, respectively (stocking ceased in 2002). The number of fish captured ranged from 16 (June 2) to 38 (August 30) in 2000; from 2 (August 16) to 54 (May 24) in 2001; and from 5 (August 17) to 16 (June 14) in 2007. The number of fish captured per day remained relatively constant in 2000, whereas in 2001 and 2007 it became increasingly difficult to capture fish as water temperature increased. The lowest catch (2 fish) occurred on the sampling date with the warmest mean bottom temperature (August 16, 2001: 23.3°C).

Trap-net CPUE ranged from 2.2 to 61.3 fish/night during the 8-year study (Table 2). Analysis of trap-net CPUE in 2000, 2001, and 2007 (years in which growth was measured) revealed a significant effect of year (*F* = 203.5, *P* < 0.0001). Tukey’s HSD test showed that the mean CPUE in 2007 (2.2 fish/night) was significantly lower than that in 2000 (61.3 fish/night) or 2001 (54.2 fish/night; *P* < 0.0001). No difference in CPUE was observed between 2000 and 2001 (*P* = 0.30); age structure and size structure were also very similar in 2000 and 2001 (Figure 2). Some of largest trap-net CPUEs ever recorded over 27 years of observations in Rock Lake occurred in 2000 and 2001, while trap-net

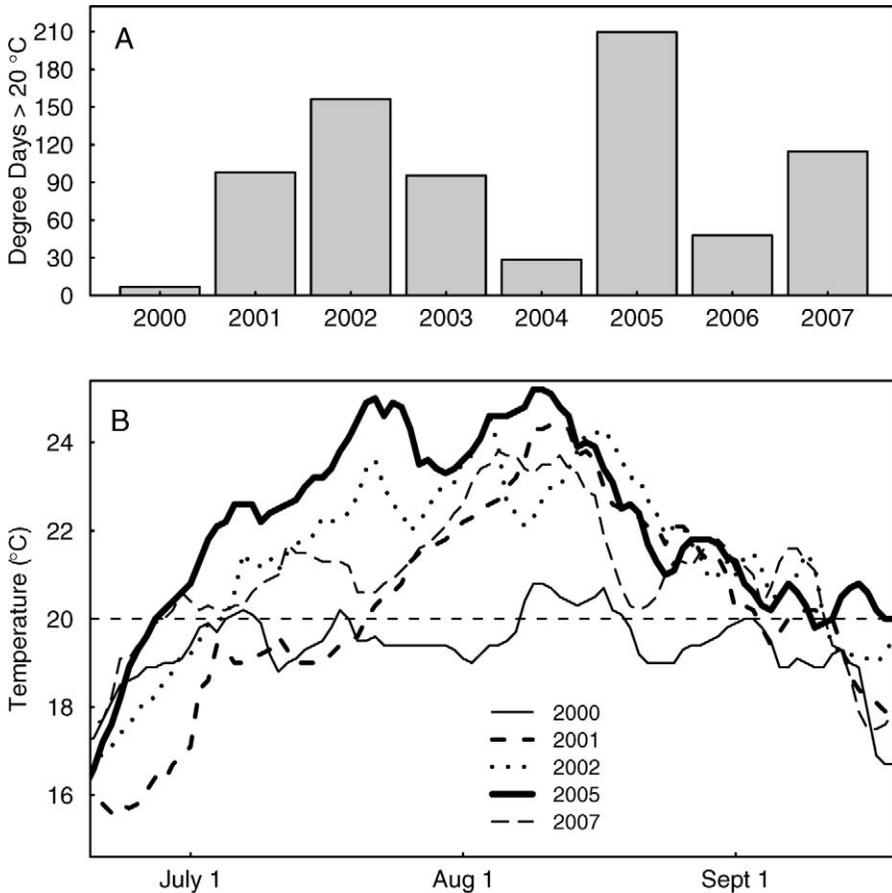


FIGURE 1.—(A) Degree-days exceeding 20°C in each year and (B) thermographs representing daily mean bottom temperature of Rock Lake, New York, in 2000, 2001, 2002, 2005, and 2007. Horizontal dashed line represents the designated thermal stress threshold for brook trout (20°C).

catch in 2007 was the lowest observed over the 8-year study.

Age and Growth

Ages were determined from otoliths for 415 fish captured in 2000 and 2001, but ages could not be determined for 101 (43 wild, 58 stocked) fish due to vateritic otoliths (Bowen et al. 1999). Age was determined for the 58 stocked fish based on fin clips, allowing these fish to be used in the growth analysis. The maximum age of both wild and stocked fish was 4 years, with the exception of a single 6-year-old wild fish.

Within-year changes in length at capture varied among years and age-classes (Figure 3). A significant increase in length over time was observed for age-1 and age-2 fish in 2000 and for age-2 fish (only age-class captured) in 2007 but not for fish of any age in 2001. Differences in slope (ΔL) between 2000 and 2001 were

significant for age 1 ($P = 0.04$) but not for the other age-classes (age 2: $P = 0.95$; age 3: $P = 0.36$; age 4: $P = 0.27$).

Within-year changes in weight at capture also varied among years and age-classes (Figure 4). A significant increase in weight over time was observed for age-1, age-2, and age-3 fish in 2000. The weight increase of age-2 fish in 2007 was moderately significant ($P = 0.06$). In 2001, there was no increase in weight over time at any age, and the age-4 fish decreased in weight over time. Differences in slope (ΔW) between 2000 and 2001 were significant for age 1 ($P = 0.03$), age 2 ($P = 0.02$), and age 3 ($P < 0.01$) but not for age 4 ($P = 0.09$).

Stomach Fullness

Patterns of SF during the growing season were similar for 2000 and 2001, with SF declining throughout the growing season, indicating an inverse

TABLE 2.—Brook trout sampling techniques used throughout the study and the timing, analysis, number of sampling events, total catch or count, and catch per unit effort (CPUE; fish/net-night) associated with each event in Rock Lake, New York (analysis codes: C = catch, G = growth, M = mortality, and R = reproduction). The number of nets associated with each sampling event is shown in parentheses. “NA” means not applicable.

Year	Events	Catch or count	CPUE
Spring–fall gill net and angling (C, G)			
2000	10	257	NA
2001	7	259	NA
2007	8	69	NA
Fall trap net (R, M)			
2000	1 (2)	368	61.3
2001	1 (2)	325	54.2
2002	1 (2)	183	22.9
2003	1 (6)	215	53.8
2004	1 (6)	93	7.8
2005	1 (6)	283	15.7
2006	1 (6)	485	26.9
2007	1 (6)	40	2.2
Late-fall redd survey (R)			
2000	1	260	NA
2001	1	126	NA
2002	1	2	NA
2003	1	75	NA
2004	1	145	NA
2005	1	0	NA
2006	1	149	NA
2007	1	91	NA

relationship between SF and water temperature. Maximum SF on each sampling occasion was negatively correlated with mean daily bottom temperature on the corresponding date ($F = 51.827$, $P < 0.01$, $r^2 = 0.78$; Figure 5A). In both years, maximum SF was greatest during the spring and lowest during midsummer and then increased again during the later summer and fall (but not to spring levels; see Figure 5B).

Reproduction and Mortality

Whole-lake redd counts in Rock Lake ranged from 0 to 260 during the 8-year study period (Table 2). Based on observation of spawning sites and sampling of mature fish, it is clear that some of the age-1 fish are spawning in this system. The years with the lowest redd counts (2002: $n = 2$; 2005: $n = 0$) were those with the greatest $DD_{>20}$, and the best model (based on AIC_c) describing variability in redd count included $DD_{>20}$ and mature female density (trap-net CPUE; Table 3). The model indicated that $DD_{>20}$ had a significant negative effect on the construction of redds, while the positive effect of fall female density was not significant (Table 3). Regressions of individual parameters showed that redd count was negatively related to $DD_{>20}$ ($r^2 = 0.85$, $P < 0.01$, $F = 34.06$) but was

unrelated to fall female density ($r^2 = 0.46$, $P = 0.07$, $F = 5.08$; Figure 6). The number of days exceeding 20°C explained a similar amount of variation ($r^2 = 0.82$, $P < 0.01$, $F = 28.07$) in redd count compared with $DD_{>20}$, and maximum bottom temperature explained less variation ($r^2 = 0.71$, $P < 0.01$, $F = 14.92$). Degree-days exceeding 18°C and 19°C also explained a similar amount of variation in redd count ($r^2 = 0.83$ and 0.85 , respectively) compared with $DD_{>20}$, and the number of degree-days exceeding 21°C and 22°C explained less ($r^2 = 0.76$ and 0.60 , respectively).

Length frequency histograms of trap-net catches suggested that substantial mortality of several year-classes occurred in 2002 and 2005 (Figure 2). Specifically, virtually all fish of age 2 and older were absent from the trap-net catch in 2002, and virtually all fish of age 1 and older were absent in 2005. All other cases in which a cohort was absent from fall trap-net catches could be explained by low levels of spawning or a mortality event in a previous year. The very low level of spawning in 2002 corresponded with low catches of young-of-the-year (age-0) brook trout in 2003 and yearlings in 2004; the lack of spawning in 2005 corresponded with the absence of age-0 brook trout in 2006 and yearlings in 2007. The apparent mortality event in 2005 corresponded with the lack of age-2 and older fish in 2006 (Figure 2). Gill-net surveys conducted directly after trap-net surveys in 2005 revealed a similar size structure, with no fish larger than 191 mm (i.e., yearling and older) being captured by either gear type. The low number of age-2 fish captured by the trap nets in 2007 was probably due to the abnormally high water temperature at the time of sampling and not to a significant mortality event; this interpretation is supported by observations of age-3 fish in surveys conducted in 2008 (Adirondack Fishery Research Program, unpublished data) and moderate levels of redd construction observed in 2007.

Discussion

We explored the effects of summer temperature conditions on lake-dwelling adult brook trout by directly measuring individual and population-level characteristics during years with contrasting water temperature patterns. By studying a brook trout population in a thermally stressful—but otherwise unimpacted—field setting, we explored the effect of stressful summer water temperatures on growth, consumption, reproductive effort, and mortality. Furthermore, we described mechanisms by which lake-dwelling brook trout populations can function in thermally stressful environments at the southern margin of the species' lentic range. This is the first study to use the number of degree-days exceeding a given thermal

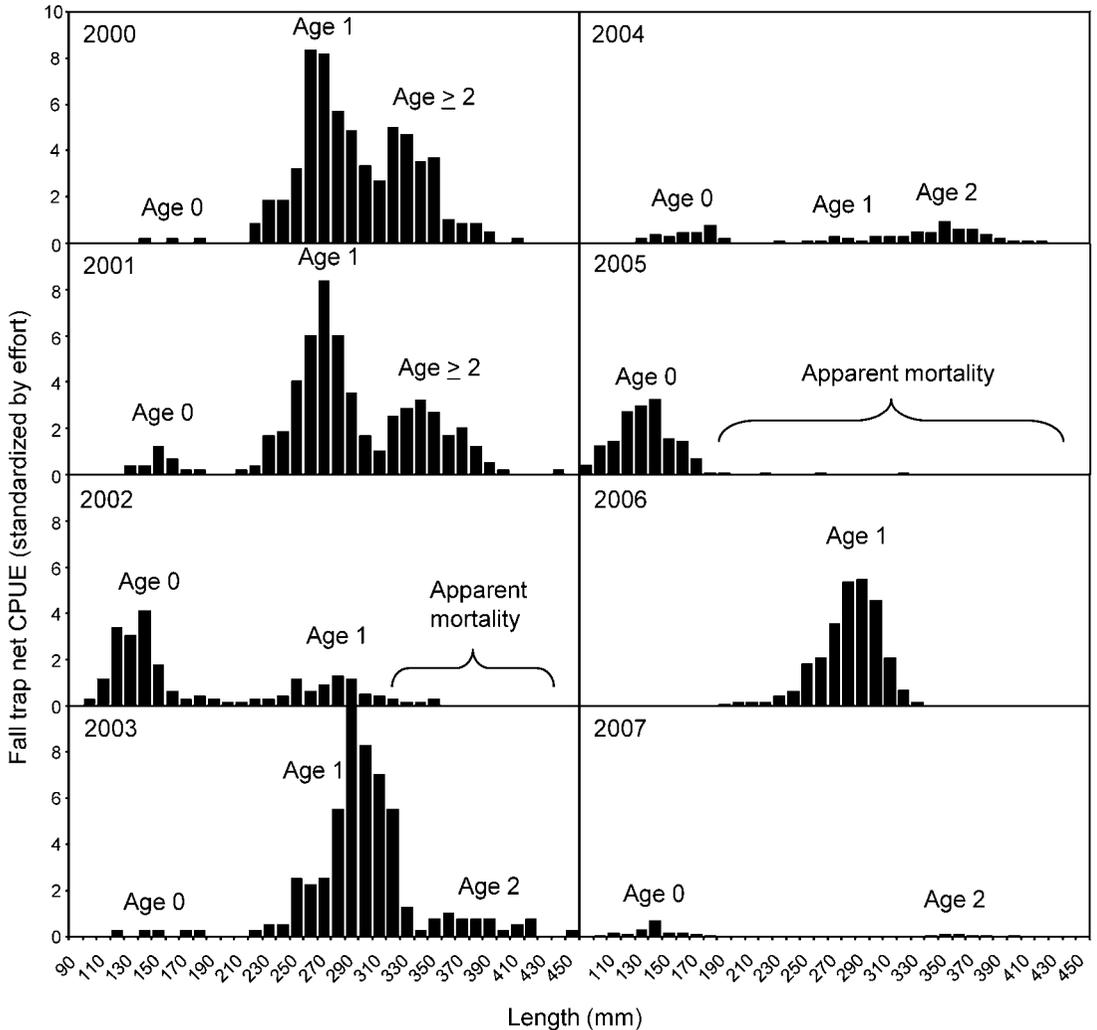


FIGURE 2.—Brook trout length frequency histograms (total length, mm) based on fall trap-net catch per unit effort (CPUE; standardized by effort) in each year within Rock Lake, New York. Apparent total mortality events were defined as year-class absence that could not be explained by a lack of spawning in a previous year. “Age ≥ 2 ” indicates that the mode contains fish from all ages including age 2; “age 2” indicates that only age-2 fish were present.

stress level as an index of cumulative annual thermal stress. We provide empirical evidence that (1) summer water temperatures strongly influence brook trout growth, consumption, reproduction, and mortality and (2) the $DD_{>20}$ is a good predictor of brook trout reproductive effort and mortality in a lake lacking summer thermal refuge.

Warm summer water temperatures negatively impacted the observed growth trend of larger, older age-classes of brook trout to a greater extent than smaller, younger age-classes. Although it appears that growth in length decreased and fish lost weight during warmer periods, it is possible that the observed changes could

have occurred due to size-selective mortality or gear avoidance by older, larger fish during late summer. However, laboratory studies support the observation that warm ambient water temperatures have a greater impact on larger fish because larger individuals have greater metabolic demands and lower thermal preference than smaller individuals (Baldwin 1956; Coutant 1977). Our results are consistent with those of previous field studies showing that the growth of older, larger brook trout (age ≥ 2) is negatively impacted by warm summer water temperatures ($>20^{\circ}\text{C}$), whereas impacts on the growth of younger, smaller fish are less evident (Schofield et al. 1993; Drake and Taylor 1996; Baird et

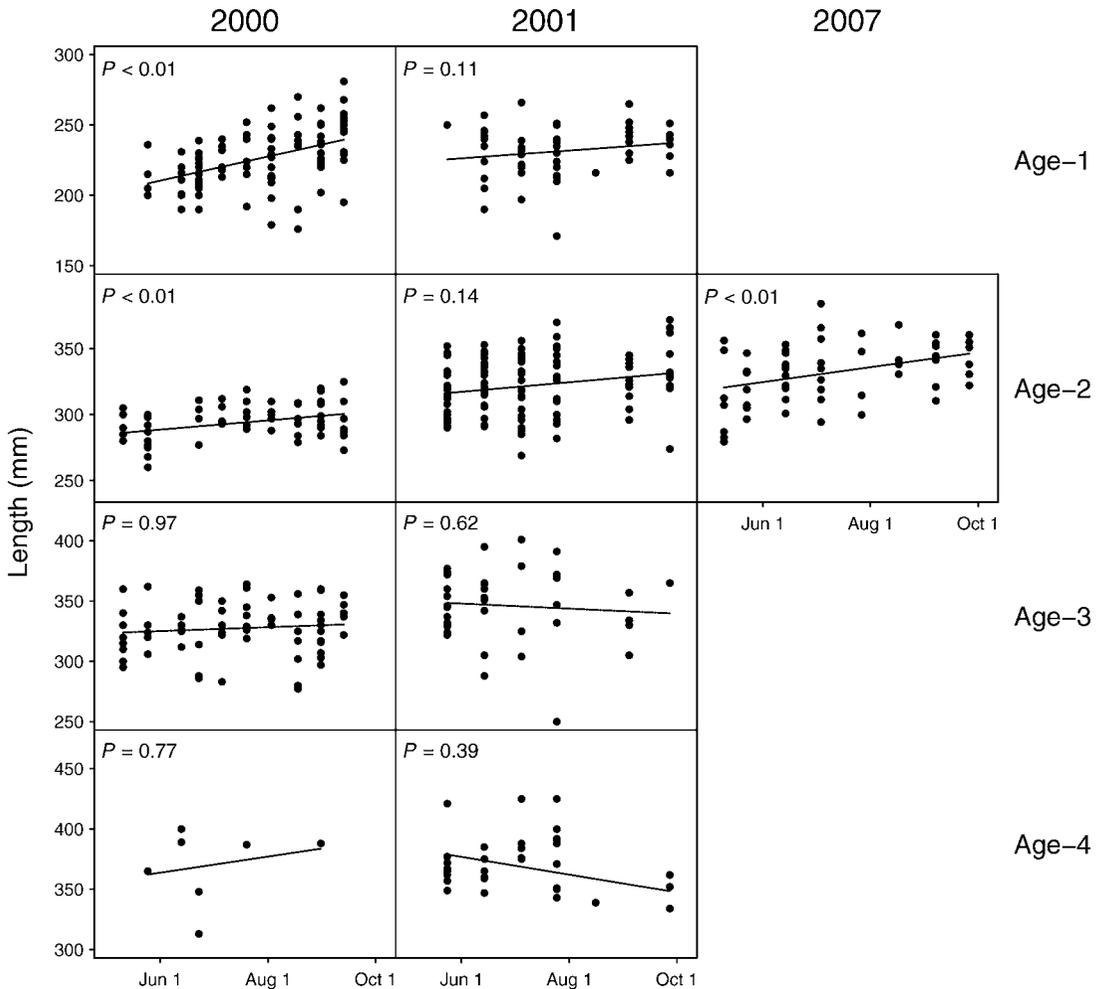


FIGURE 3.—Field-measured total length for brook trout age-classes through time in 2000, 2001, and 2007, with associated linear regressions, based on gill-net and angling data for Rock Lake, New York. Note the different scales on the y-axes.

al. 2006). Drake and Taylor (1996) found that river temperature was negatively related to the growth of brook trout of age 2 and older, while Baird et al. (2006) observed that stocked brook trout, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* that gained weight were usually smaller than 275 mm in a river where water temperatures regularly exceeded 23°C. Schofield et al. (1993) reported that growth of age-0 and yearling brook trout was not limited by summer water temperature in unstratified Adirondack lakes. The duration and magnitude of stressful temperatures (>20°C) reported in previous studies were similar to those observed in Rock Lake during the relatively cool summer of 2000. However, the prevailing water temperatures observed during the warm summer of 2001 exceeded 20°C with greater

magnitude and duration compared with the aforementioned studies. Though other field studies have documented temperature extremes sufficient to affect the growth of older brook trout (Schofield et al. 1993; Drake and Taylor 1996; Baird et al. 2006), temperature extremes observed in Rock Lake in 2001 were sufficient to impact brook trout growth at all ages measured. The effect of temperature on weight was more readily apparent than the effect on length, indicating that weight was a more sensitive measure of growth in response to stressful summer water temperatures. This is further supported by the larger number of year-classes with between-year (2000 versus 2001) differences in weight change relative to length. The fact that fish in each cohort during 2000 were generally smaller than the same age-class at the start of

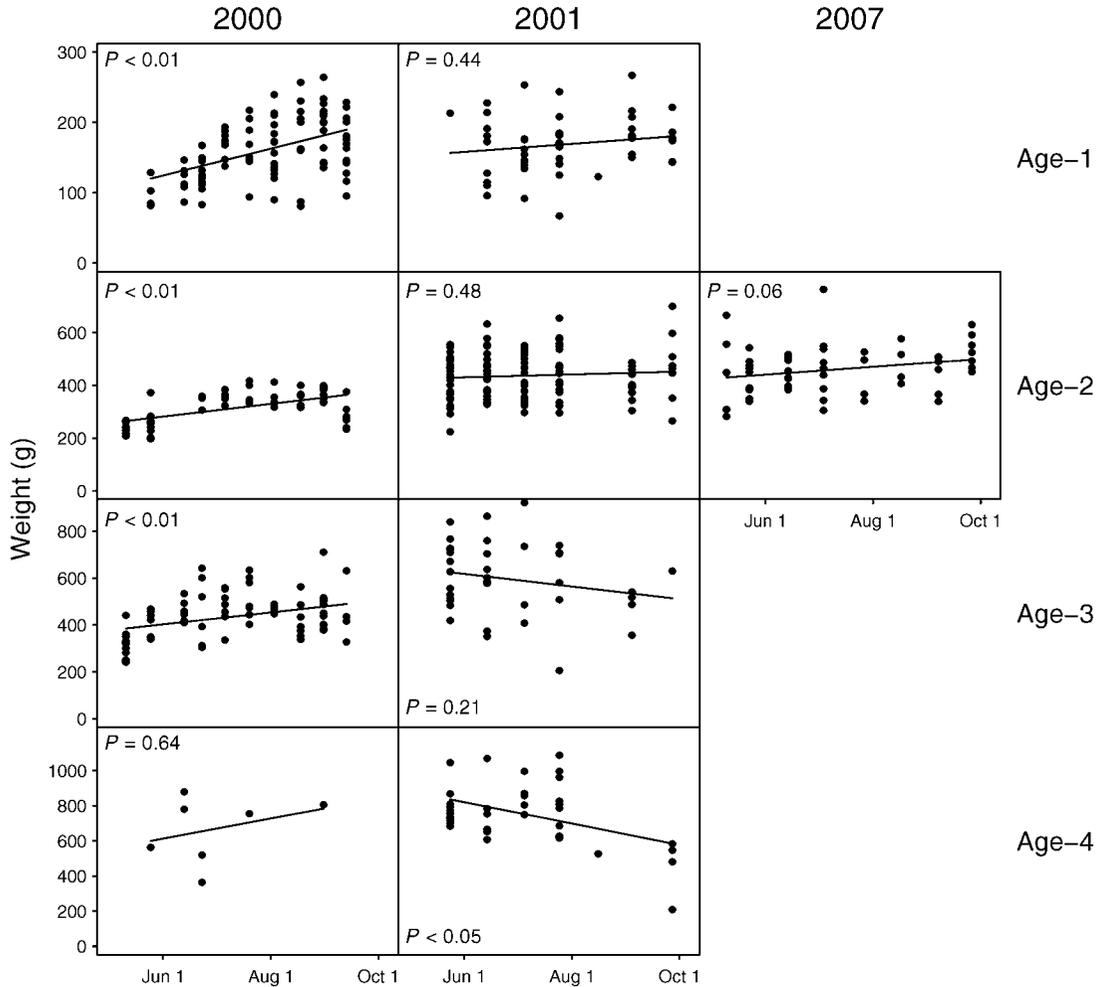


FIGURE 4.—Field-measured weight for brook trout age-classes through time in 2000, 2001 and 2007, with associated linear regressions, based on gill-net and angling data for Rock Lake, New York. Note the different scales on the y-axes.

2001 could have resulted from (1) size-selective mortality of smaller fish during winter 2000–2001 or (2) growth occurring from October through April, outside the sampling period.

Schofield et al. (1993) demonstrated that brook trout in lakes with high-quality forage (e.g., fish or crayfish) could maintain a positive energy balance at a higher temperature than those in lakes lacking large, high-energy prey items. Post et al. (1999) suggested that limited food resources could negatively impact fish growth, particularly at larger size-classes (i.e., age-2 brook trout in 2007). Big water crayfish *Cambarus robustus* represented a large proportion (~50% dry weight) of the diet of age-2 brook trout in our study lake in 2000 and 2001 (Robinson 2008). We expect that decreased competition for this food resource in

2007 may have allowed growth to occur under more stressful thermal conditions compared with 2000 and 2001, when fish densities were greater. The observed positive growth in this thermally stressful year suggests that low fish densities could have a positive effect on the overall mortality and reproduction within the population in a warm year by increasing fish energy density at the start of the warmest portion of the summer. Evidence that reduced fish density in 2007 mitigated the impact of high temperatures on brook trout growth indicates that thermally stressful systems with limited harvest and supported by stocking could benefit from reduced stocking densities. Additionally, thermally stressful systems that host wild reproduction and that are supplemented with stocked fish may benefit from the reduction or cessation of stocking.

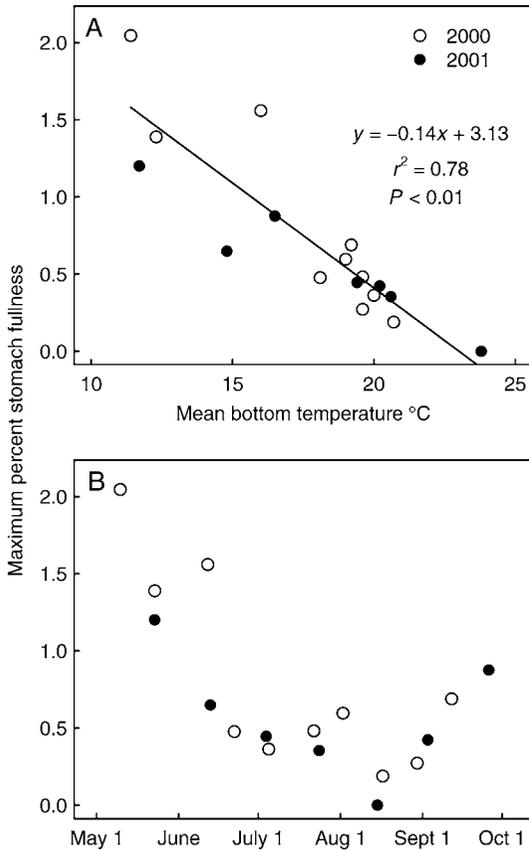


FIGURE 5.—Linear regression of maximum percent stomach fullness in brook trout versus (A) mean bottom temperature or (B) date based on gill-net and angling data for Rock Lake, New York (open circles = 2000 data; closed circles = 2001 data). Maximum percent stomach fullness represents the mean of the upper quartile of percent stomach fullness data on each sampling date. The regression line is based on pooled data. Mean bottom temperatures represent 24-h means on each sampling date.

The negative relationship between maximum SF and temperature indicates that brook trout consumption was significantly reduced during periods of stressful thermal conditions. Gastric evacuation rates in fish are often temperature dependent, and this may have accounted for some portion of the observed negative relationship between brook trout SF and mean lake bottom temperature. Sweka et al. (2004) investigated brook trout evacuation rates over a range of temperatures (4.3–17°C) and found that temperature had only a slight negative effect on the proportion of diet remaining after a constant postfeeding interval. Extrapolating their results over our observed temperature range indicates that at 12°C and 24 h postfeeding, brook trout would contain approximately 64% of their

consumed diet and that at 22°C they would contain about 51% of the consumed diet. This small decrease in SF is not sufficient to explain the steep negative relationship that we observed between brook trout maximum SF and temperature, providing additional evidence that warmer water temperatures led to a reduction in brook trout feeding. Availability of prey items such as zooplankton, macroinvertebrates, and crayfish is known to vary seasonally (Somers and Green 1993; Boersma et al. 1996). Although we cannot totally rule out prey availability as a potential driver of the observed trend, others have described decreased consumption by salmonids as temperatures increase above optima in laboratory studies with constant rations (Pentelov 1939; Baldwin 1956; Myrick and Cech 2000). The rebound of maximum SF in the late summer and early fall further supports the claim that temperature rather than prey availability was driving the trend in SF. The observed decrease in consumption during warmer periods, coupled with thermal stress, supports our other observations of reduced or negative growth, reduced reproduction, and increased mortality in years of severe thermal stress.

The negative correlation between consumption and temperature may result from a behavioral change. Brook trout may reduce metabolic costs associated with activity and digestion in order to temporarily compensate for temperature-induced increases in metabolic costs. This is supported by relatively constant brook trout catches in the cool summer of 2000 and declining catches in the warmer summers of 2001 and 2007, as well as the negative influence of temperature on catch (i.e., gill net and angling) reported for other coldwater species (McMichael and Kaya 1991; Kocovsky and Carline 2001; Quist et al. 2002). Water temperatures have the potential to influence catch rates by lowering the density of the catchable population through temperature-induced mortality (Fry et al. 1946) or by decreasing activity and consumption levels (Dickson and Kramer 1971; Boisclair 1992; Biro et al. 2007). Fall trap-net CPUE in 2000 and 2001 did not indicate a significant difference in the overall number of fish available for capture between the 2 years. This suggests that the observed brook trout catch rate decreases that corresponded with increasing temperature in 2001 resulted from behavioral changes associated with decreased activity and consumption rather than temperature-induced mortality. This conclusion is supported by a similar decreasing pattern in catch rates during the thermally stressful summer of 2007.

The $DD_{>20}$ was negatively correlated with fall redd counts and explained a greater proportion of variation in redd count than did the CPUE of mature females

TABLE 3.—Selection of the best model for estimating brook trout redd construction in Rock Lake, New York. For each candidate model, the Akaike's information criterion (AIC_c ; bias corrected) weight, r^2 , and F -statistic are reported. Parameter estimates and effects test are also reported (DD = cumulative degree-days over which mean bottom temperature exceeded 20°C in each year; CPUE = fall trap-net catch per unit effort for mature females in each year).

Model	AIC_c weight	r^2	F	Parameter	Estimate	P
DD + CPUE	0.77	0.89	21.24	Intercept	179.38	<0.01
				DD	-0.99	<0.01
				CPUE	2.24	0.21
DD + CPUE + (DD × CPUE)	0.13	0.95	23.38	Intercept	162.46	<0.01
				DD	-0.82	0.01
				CPUE	4.53	0.06
				DD × CPUE	-0.04	0.12
DD	0.09	0.85	34.06	Intercept	216.24	<0.0001
				DD	-1.17	<0.01
CPUE	0.01	0.46	5.08	Intercept	50.47	0.19
				CPUE	6.04	0.07

captured in fall trap-net surveys. Although it is surprising that the density of mature females did not have a significant influence on the number of redds relative to summer thermal conditions, mature female CPUE was included in the best model based on AIC_c . The observation that mature female density had little influence on the number of redds, in contrast with the effect of $DD_{>20}$, indicates that stressful summer thermal conditions can have a lasting physiological impact that precludes some (or potentially all, under extreme conditions) mature females from spawning in the fall. Although it is possible that the stocked brook trout behave differently than the wild fish, stocked brook trout were regularly observed and captured in the vicinity of spawning shoals and were observed constructing redds and actively spawning with wild fish. However, these observations only address the construction of redds and not the viability or survival of eggs produced by stocked brook trout.

In extremely warm years (e.g., 2005), temperature-induced mortality will directly influence the level of spawning in waters without thermal refuge by reducing the number of mature individuals. Sublethal temperature conditions may also influence spawning by impeding brook trout gonad development, which occurs during the summer months under favorable growth conditions (Hokanson et al. 1973). This suggests that the extremely warm conditions in the summer of 2002 could have inhibited gonad development, thereby causing mature females to be unable to spawn. During years of stressful summer thermal conditions in Rock Lake, a combination of decreased consumption and increased metabolism caused by stressful temperatures may lead to impaired gametogenesis and lower energy density. Cooler summer

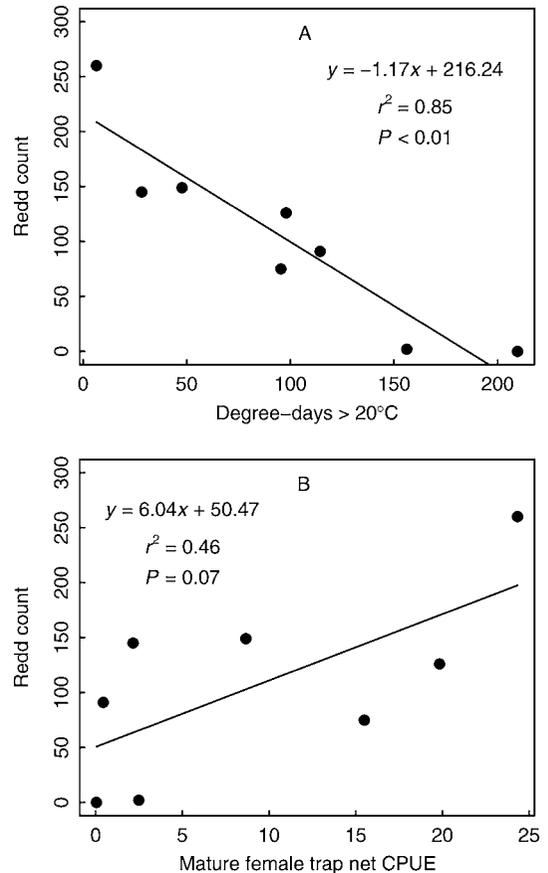


FIGURE 6.—Linear regression of annual whole-lake brook trout redd count versus (A) cumulative number of degree-days over which mean bottom temperature exceeded 20°C or (B) fall trap-net catch per unit effort (CPUE) of mature female brook trout in Rock Lake, New York.

temperatures may have the opposite effect by increasing condition, thereby allowing more females to spawn and even construct multiple redds. Spawning and gonad development reduce energy density (i.e., stored lipids) and decrease overwinter survival of brook trout and other fishes (Jonsson et al. 1991; Hutchings 1994; Hutchings et al. 1999). Energy saved by not spawning in thermally stressful years would increase the probability of overwinter survival (Rideout et al. 2005).

Extended periods of stressful summer temperatures caused substantial size-dependent, temperature-induced mortality of brook trout in Rock Lake. Our results indicate that mortality of older fish (age > 1) occurred in this thermally homogeneous lake during a summer (2002) with 156 $DD_{>20}$; mortality of virtually all fish older than age 0 occurred in a warmer year (2005) with 210 $DD_{>20}$. Given our 2007 observation that a similar level of mortality was not observed when the $DD_{>20}$ metric was 114, our data suggest that somewhere between 114 and 156 $DD_{>20}$ there is a cutoff below which a substantial portion of the population will survive and reproduce and above which older age-classes will not survive in this type of lake (Figure 6). The size-dependent nature of the apparent mortality events is supported by studies demonstrating that larger fish are less able to tolerate high water temperatures than their smaller conspecifics (Baldwin 1956; Coutant 1977). Ongoing evaluations of this and other Adirondack brook trout populations will allow further refinement of the $DD_{>20}$ metric as a predictor of mortality events.

Densities of brook trout in Rock Lake decreased after the cessation of stocking. However, speculation that the thermal tolerances of stocked brook trout, especially nondomestic strains, was different from that of wild fish in this system is not supported by the observed mortality event that occurred in 2002, when entire year-classes containing both wild and stocked fish were lost. Assessing the effect of stocking on the overall density of the population was confounded by the occurrence of a major mortality event during the same year in which stocking ceased, which effectively reset the population in 2002; this mortality event was followed by another in 2005. The proximity of these two events and the disruption they caused to spawning prevented even the possibility of the population returning to the densities observed under stocking in this population. If enough years of thermally favorable temperature conditions occur in the future, a comparison of the pre- and poststocking densities may be possible.

Factors other than thermal stress, such as low pH or gear selectivity, could have influenced mortality or the perception of mortality in this system. Rock Lake is located in a region where low acid-neutralizing

capacity in the watershed and low pH precipitation can reduce lake pH, especially during spring runoff events. Age-0 brook trout are most susceptible to spring acid runoff due to their spring habitat preferences (Van Offelen et al. 1994; Biro 1998). Age-0 mortality due to pH depression would be most apparent as a missing age-1 year-class in the subsequent year. The absence of an age-1 year-class occurred in 2005 and 2007, but there is strong evidence to suggest that the absence was not caused by low pH conditions. In 2004, age-0 brook trout were present in trap-net catches; the absence of age-0 brook trout in 2006 can be attributed to a complete lack of spawning in 2005. Mortality due to winterkill—in the form of starvation, low-oxygen conditions, disease, predation, or a combination thereof—could also be acting on the population (Biro et al. 2004; Beckmann et al. 2006). However, like pH, there is little evidence that these sources of mortality are driving the major mortality events that were observed in this study. Trap-net selectivity based on temperature could create the perception of severe mortality events (Hubert 1996). However, year-classes that were absent from the trap-net catches were never detected in the population during subsequent years, indicating that gear bias was not responsible for their observed absence. Even so, it is because of the potential for gear bias that partial mortality events were not considered.

Survival of age-0 brook trout in years when elevated water temperatures caused mortality of larger individuals is probably attributable to the presence of shallow thermal refuges in the form of upwelling groundwater, which is available only to these smaller fish. Due to the brook trout's reliance on upwelling groundwater for in-lake spawning (Greeley 1932; Webster and Eriksdottir 1976; Curry and Noakes 1995), lakes that support self-sustaining populations are likely to contain suitable summer thermal refuge for age-0 brook trout. These shallow, low-volume upwelling locations are used as summer thermal refuges by age-0 brook trout (Biro 1998), but telemetry results in our study lake confirmed that larger brook trout do not use these refuge areas during periods of elevated water temperatures (Robinson 2008). Therefore, age-0 brook trout are able to survive in Rock Lake during years when temperatures are lethal to individuals in other age-classes (e.g., 2005), providing a mechanism that has allowed this wild population to persist in a severely stressful thermal year in which ambient lake temperatures exceed lethal levels. Even so, several scenarios could lead to total extinction of this population. For example, two consecutive years of summer thermal conditions similar to those observed in 2005 could cause the total loss of this population through mortality of all age-1

and older fish, leading to subsequent reproductive failure. Furthermore, three consecutive years of thermal conditions similar to those observed in 2002, or 1 year similar to 2002 followed by a year similar to 2005, could also lead to extirpation of this population.

Our work highlights the utility of using cumulative degree-day values exceeding a given thermal stress level to approximate annual thermal stress in addition to long-term (e.g., annual) thermal metrics based on temperature thresholds, such as days exceeding 20°C or maximum temperatures. Previous studies have successfully relied upon “noncumulative” (i.e., one-time) temperature thresholds to assess stress in systems containing brook trout (Drake and Taylor 1996; Baird et al. 2006; Wehrly et al. 2007). Although $DD_{>20}$ and the number of days exceeding 20°C both explained reproductive effort to a similar extent, our results indicate that the use of one-time temperature thresholds and maximum temperatures to determine stressful conditions can sometimes be misleading. For instance, the temperature threshold of days exceeding 20°C would have mistakenly identified 2007 as a more thermally stressful year than 2002. Additionally, the use of maximum annual temperatures to approximate thermal stress would indicate that 2001 and 2002 were similar thermal years. Using either of these metrics for thermal stress would lead to incorrect conclusions regarding major mortality events and spawning failure in this unstratified lake. These metrics fail to take into account both important facets of thermal stress: magnitude and duration. The $DD_{>20}$ accounts for both the duration and the magnitude of thermal stress and provides a metric of thermal stress that agrees closely with our field observations of mortality and reproductive effort. This technique may be most suitable as a metric for approximating thermal stress in lentic systems relative to streams, where daily temperature fluctuation can play a large role in fish stress (Wehrly et al. 2007).

The decline of brook trout populations throughout their native range as a result of mostly anthropogenic factors (Hudy et al. 2005) and the recent observations of increasing air temperatures (Hayhoe et al. 2006; IPCC 2007) make it important to understand how summer thermal regimes can lead to stressful conditions for brook trout and other coldwater fishes. By studying ecosystems at the margins of species’ thermal tolerances, we can identify what specific changes can be expected if global temperatures increase and whether actions may be taken to mitigate these changes. Future studies collecting similar data from multiple lakes and lake types (stratified and unstratified) will help in further developing thermal metrics and thresholds that are relevant to brook trout spawning

and mortality. Knowledge gained from studies such as this will be useful to the conservation and management of wild brook trout populations and other species that are likely to be negatively affected if global and local temperatures continue to rise.

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