EFFECTS OF SUMMER THERMAL CONDITIONS ON BROOK TROUT (*SALVELINUS FONTINALIS*) IN AN UNSTRATIFIED ADIRONDACK LAKE

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

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May 2008

ABSTRACT

Lake-dwelling populations of brook trout (*Salvelinus fontinalis*) represent a coldwater fish species potentially susceptible to climatic warming trends. Global climate change and associated warming trends may eliminate or limit temperature sensitive coldwater fish species in lake ecosystems. Important insights into the influence of summer water temperature can be gained by investigating coldwater fishes inhabiting thermally marginal lakes. This thesis examines the influence of summer water temperature conditions in an unstratified Adirondack lake, upon brook trout catch, growth, consumption, energy density, reproductive activity and mortality. The cumulative number of degree-days exceeding 20°C in each year was used as a measure of annual thermal stress. Catch, growth, size selective mortality and consumption were evaluated using data collected in two contrasting thermal years (cool: 2000, warm: 2001). Brook trout energy density and growth were also evaluated in 2007, during which ambient water temperatures were even warmer than 2001. Summer thermal conditions had a negative impact on brook trout catch and growth (e.g. both length and weight) in 2001. Evidence of size selective mortality against larger individuals was observed at all ages in 2000 and 2001. Maximum stomach fullness was negatively related to water temperature ($r^2 = 0.78$). Positive growth in 2007, a more severe thermal year than 2000 or 2001 but with a lower brook trout density, indicated that the negative impact of temperature on growth can be mediated by decreased competition for food resources. Brook trout energy density (i.e. percent water content) appeared to be negatively correlated with water temperature.

Eight continuous years of data (2000 – 2007) were used to evaluate the effect of summer thermal conditions on reproductive activity and mortality. Spawning activity (i.e., redd construction) was negatively correlated with summer thermal conditions ($r^2 = 0.85$) and was largely independent of mature female density. Summer thermal conditions caused the total mortality of all age two and older fish and all age one and older fish when the number of annual degree-days above 20°C exceeded 156 and 210, respectively. Thermal conditions below 115 degree-days above 20°C did not cause total mortality of any year class. This work highlights the importance of annual temperature monitoring, knowledge of thermal refuge habitat availability, and the use of degree-day temperature metrics when assessing the influence of temperature on brook trout populations.

BIOGRAPHICAL SKETCH

Jason Michael Robinson was born in Albany, New York on the 27th of March, 1980 to Michael and Laura Robinson. Throughout his life Jason has had a love of the outdoors, especially fishing. Jason and his family lived in Albany until the age of five at which time they moved to Rotterdam, New York where he graduated from Mohonasen High School. Jason began his collegiate academic career at the State University of New York at Morrisville. There he completed various courses in engineering before deciding on the field of Natural Resources. Jason finally decided to focus on fisheries and aquatic ecology after completing a class in ichthyology with Professor William Snyder. After graduating form Morrisville with an Associate's degree in Natural Resources in 2000, he transferred to Cornell University where he earned his Bachelor's degree in Natural Resources in 2002. After graduating Jason began working for Dr. Clifford Kraft and Daniel Josephson as a fisheries research technician at the Little Moose Field Station in the Adirondacks. His experiences working at the field station motivated him to seek a Master's degree in Natural Resources under the advisement of Dr. Kraft at Cornell University beginning in the fall of 2005. Just after beginning his graduate studies Jason was married to Elizabeth Ann Whitney on October 29th 2005.

I dedicate this thesis to my father, who instilled in me my love of the outdoors and was never too busy to take me fishing.

ACKNOWLEDGMENTS

I would like to thank Dr. Cliff Kraft, Daniel Josephson, Jesse Lepak, Brian Weidel, Dr. James Jackson, Dr. Patrick Sullivan, and Dana Warren for their guidance, advice and editorial comments. I thank Andrew Barbato, Bethany Boisvert, Michael Compton, Scott Krueger, William Rehee, Leslie Resseguie, and Theodore Treska for their field and laboratory assistance. I would also like to thank Dr. Karin Limburg for her technical advice regarding otolith processing and analysis. My family and friends, especially my wife Beth have provided endless support throughout this process. The funding and study site for this work was provided by Daniel Catlin and the Rock Lake Club.

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Introduction

This study investigates the effects of variable inter-annual temperature regimes on a brook trout population in an unstratified north temperate lake. Using data collected over an eight-year period (2000 – 2007) – including three years of intense data collection during open water months – a series of hypotheses was evaluated regarding the influence of temperature on brook trout growth, consumption, reproduction and survival. The underlying premise of this study is the long-standing recognition that temperature is a key force governing the life processes of fish (Brett 1971). This work was also conducted with the awareness of warming global climate conditions that are likely to impact fish populations in the future (Schindler 2001). We present our results as an example of the importance of making *in situ* evaluations of fish populations living in well-characterized thermal conditions as we try to more fully understand the influence of changing temperature conditions on fish populations.

Four hypotheses form the core of this study:

1) Brook trout growth will be reduced in years with warmer summers, by comparison with cooler summers;
2) Brook trout consumption will be seasonally reduced during warm water temperature conditions, by comparison with seasonal periods with cooler water temperatures;
3) Warm summer temperature conditions will result in greater brook trout mortality and reduced reproductive activity by comparison with cooler summers;
4) Larger brook trout will be more susceptible to changes in growth and mortality that occur in response to warm summer temperature conditions than smaller brook trout.

Continued warming of global climate conditions will impact fish populations both directly and indirectly (Schindler 2001). For example, growth will be impacted through changes in metabolism and consumption, and increased temperatures will lead to behavioral and physiological changes (Schmidt-Nielsen 1990) as well as changes in population structure (Walther et al. 2002). Yet the directionality of these changes will depend on the underlying physiology of each species and the magnitude of temperature change (Reis and Perry 1995; Eaton and Scheller 1996). Situations in which temperature extremes are not great enough or long enough in duration to cause mortality may result in changes in body condition (Quist et. al 2002), reproductive timing and potential (Webb & McLay 1996), and behavioral changes such as altered activity levels (Biro et al. 2007). As temperatures approach stressful or lethal levels for species over an extended period of time, a subsequent change in mortality rate will result (Biro et al. 2007). Many of the changes that may occur due to climate warming may be similar for closely related species and regions (Parmesan and Yohe 2003). As thermal conditions in lake ecosystems become more restrictive, a greater knowledge of how these changes will affect susceptible species will help us better understand the impacts and consequences associated with global climate change and may help prevent total population loss.

Global air temperatures have increased by about 0.6ºC during the 20th century (IPCC 2001). Temperature increases in the northeastern United States exceeded average global changes, increasing by about 1.1ºC, with continued temperature increases predicted even under favorable emission-reduction scenarios (Trombulak and Wolfson 2004; Hayhoe et al. 2006). Global climate change has already altered thermal regimes, precipitation patterns, groundwater properties and evaporation rates in aquatic systems (Meisner 1990a; Schindler et al. 1996; Burns et al. 2007). Continued water temperature increases will negatively affect cool-water fish species at low elevations and at the southern margins of their range, especially in systems that may already be thermally marginal (Meisner 1990b; Reis and Perry 1995; Eaton and Scheller 1996; Parmesan and Yohe 2003). Such changes may cause some systems with suitable thermal habitat to become marginal and systems already experiencing high summer water temperatures to become unsuitable for some species (Schindler 2001).

The potential impact of climate change on salmonid species is an issue of particular concern due to their cultural and economic importance. Changes in salmonid growth (Reis and Perry 1995; King et al. 1999), available thermal habitat (Meisner 1990a) and range shifts (Meisner 1990b) due to climate change have been predicted. Because salmonids require relatively cool water and some species depend on groundwater inputs for thermal refuge and reproduction (Curry and Noakes 1995; Baird and Krueger 2003), they are particularly susceptible to predicted global and regional climate change.

While many studies have documented the effects of temperature on fish, few have done so on a large scale in a natural environment (Drake and Taylor 1996; Baird et al. 2006; Biro et al. 2007). Much of the previous work regarding the effect of temperature on brook trout (*Salvelinus fontinalis)* and other fish species has been conducted in laboratory settings (Baldwin 1956; Hokanson et al. 1973, 1977; Selong et al. 2001) or through the use of bioenergetics simulations (Schofield et al. 1993; Reis and Perry 1995; McDonald et al. 1996; Johnson et al. 2006). Although it is well documented that body size and life stage influence the effect of temperature on fish and other organisms (Schmidt-Nielsen 1990; Lester et al. 2004), many field and laboratory studies that focus on the effects of temperature have been conducted on juvenile life stages, due to ease of sampling and rearing under laboratory conditions (Pentelow 1939; Baldwin 1956; Elliott 1975; Dockary et al. 1996; Biro et al. 2007).

In general, larger fish are more sensitive to high temperatures than smaller fish because larger individuals have greater metabolic demands and a lower thermal preference (Baldwin 1956; Coutant 1977; Hartman and Cox 2008). Large-scale field studies are needed to asses the effects of temperature on fish populations in natural systems and to understand how climate change may impact populations across life stages (Biro et al 2007).

Power (1980) concluded that the normal thermal range of brook trout is between 0°C and 20°C. Optimal brook trout growth occurs at temperatures between 11°C and 16°C (Schofield et al. 1993). Upper incipient lethal temperature for yearling brook trout was determined to be 25.3°C by Fry et al. (1946) in a laboratory setting at an acclimation temperature of 20°C, indicating that 50% mortality will occur after 96 hours at this temperature. Most laboratory estimates of brook trout thermal tolerance have been conducted using yearling or younger fish that tend to be more tolerant of high temperatures relative to larger fish. Therefore published upper thermal tolerance limits may be slightly high for larger, older brook trout (Ricker 1979; Schofield et al. 1993).

In this study we use natural annual variation in summer thermal conditions to evaluate the effects of temperature on a brook trout population in an unstratified lake exhibiting thermal conditions that can be stressful for this species. The broader goal of this work was to further the understanding of how variable lake thermal conditions may impact brook trout populations. In addition, we considered it particularly important to establish thermal thresholds and relationships that influence mortality and year-class recruitment in an attempt to obtain information useful for the development of management practices that can protect native brook trout populations in thermally stressful systems.

Study area

This study was conducted in Rock Lake, a 78.9 ha drainage lake in the southwestern Adirondack Mountains (New York, USA; 43°57'N, 74°52'W) (Figure 1.1). The lake's maximum depth is 5.5 m and lake productivity is low (Table 1.1). Rock Lake does not thermally stratify in the summer, resulting in bottom temperatures that regularly exceed 20ºC and approach or exceed lethal levels for brook trout (25.3°C, see Fry et al. 1946) in some years. Brook trout are the only fish species in Rock Lake. From 1978 to 2002 the lake was stocked annually with fall fingerling brook trout, and all stocked fish received a fin clip for the verification of age and origin. Stocking ceased in 2002 as a result of an increasing recognition of successful reproduction within the lake. Since that time the population has been supported by natural reproduction of fish spawning on in-lake shoals and to a limited extent in tributaries. Until 2005, a barrier was maintained to prevent fall emigration by adult brook trout. Rock Lake is an ideal setting in which to study the effects of temperatures on brook trout in a natural setting due to the lack of thermal refuge available to yearling and older fish (also see Appendix A).

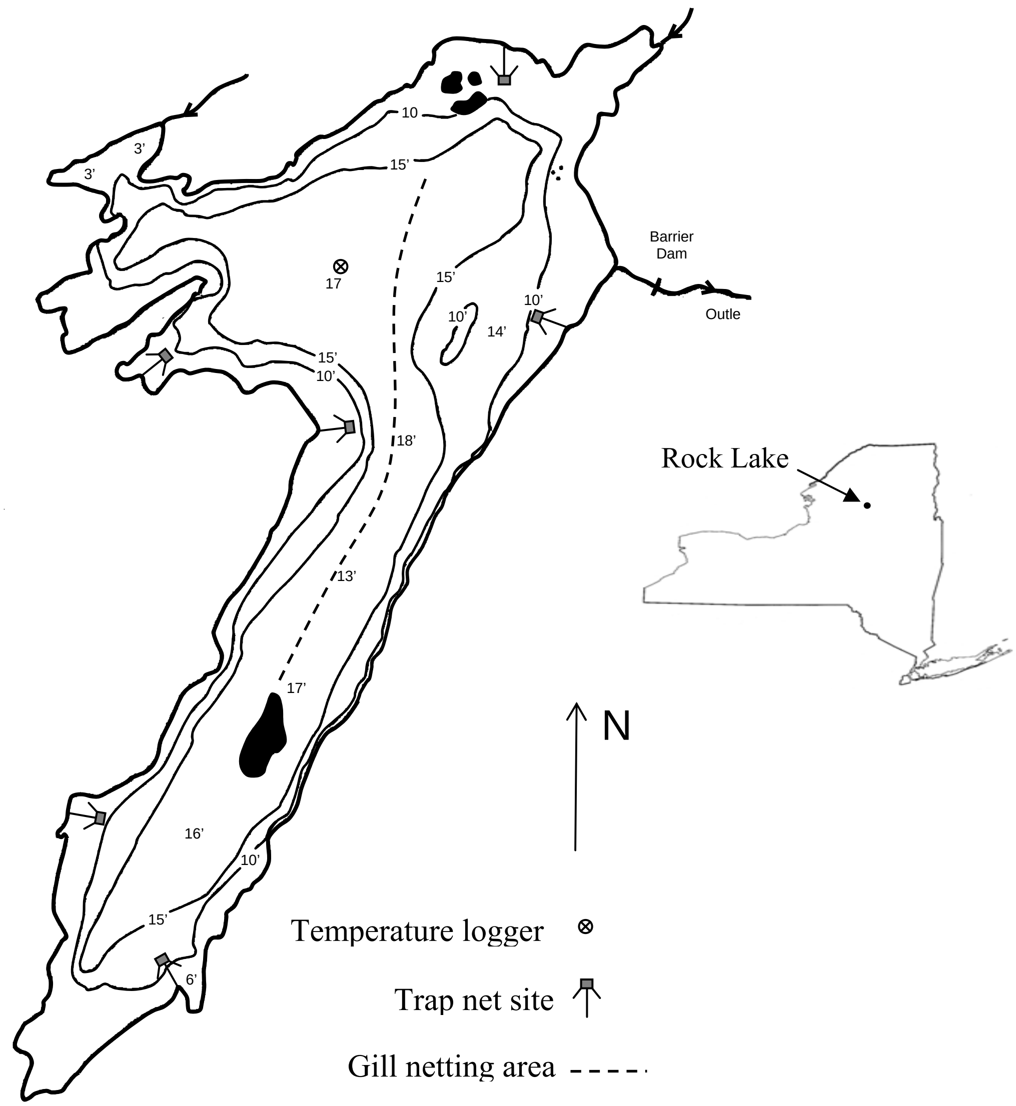

Figure 1.1. Bathymetric map of Rock Lake, New York, indicating gill net, trap net and temperature monitoring locations. Contours represent five foot depth intervals.

Table 1.1. Rock Lake water chemistry metrics. Means are based on data collected throughout the eight-year study in July and August.

Metric	Units	Mean
ANC	ueq/L	19.72
CHL. A	µg/L	1.20
DOC	mg/l	2.21
pH	pH	5.71
TDS	mg/L	15.78
TN	mg N/l	0.27
TP	µg/L	3.13

Methods

Temperature monitoring

Water temperature was monitored at the deepest point in the lake using Hobo temperature loggers (one hour intervals) from mid-May through mid-October from 2000 to 2007. The cumulative thermal stress in each year was evaluated using a measure of total degree-days in which the mean bottom temperature exceeded 20°C. Degree-days were used in order to account for both the duration and magnitude of thermal stress. For purposes of comparison, the number of days in which the mean bottom temperature exceeded 20°C and the maximum bottom temperature were calculated for each year. Growing degree-days were calculated for each year using 20°C as the maximum temperature for positive growth (Power 1980), and plots of temperature over time were constructed for all years in which growth was measured (2000, 2001 and 2007). To verify data obtained with temperature loggers, thermal profiles were taken with a YSI® temperature probe at 0.5 m intervals during every fish sampling event in 2000 and 2001 and then twice annually for the remainder of the study.

Fish sampling and processing

We attempted to capture 30 fish on each of ten sampling dates (May 10 to September 13) in 2000, 50 fish on each of seven sampling dates (May 24 to September 27) in 2001, and seven fish on each of the eight sampling dates in 2007. Brook trout were captured using both gill nets and angling in 2000, 2001 and 2007. Due to the remote location of Rock Lake and the limited time available on each collection date, two collection techniques were used concurrently to maximize effort and subsequent catch of brook trout. The majority of fish (approximately 70%) were captured by angling, which was consistently more effective in capturing fish than gill nets. Fish were angled by trolling parallel to shore using Lake Clear Wobblers™ with a trailing worm rig with a size 04 bait-hook. Anglers trolled primarily within 50 meters of the shoreline; gillnets were set in the middle of the lake. In 2000 and 2001 four anglers fished for two hours on each sampling date after setting the gillnets (ten 1.2 x 50 m sinking Swedish style multifilament gill nets with mesh sizes of 44.5 and 60 mm). Gill nets were set from the north end of the lake's large island along a line extending north to the islands at the northernmost end of the lake through the deepest portion of the lake (Figure 1.1). In 2007 a similar sampling effort was conducted with the goal of capturing approximately seven fish on each of the nine sampling dates. Age 2 brook trout were the only year class susceptible to angling in that year.

All fish captured were euthanized using MS-222 and placed on ice for transport back to the lab, where fish length and weight were measured, sagittal otoliths were extracted, and gut contents were removed and placed in 95% ethanol. In 2007, approximately 25 g of muscle tissue was also removed from the each fish for water content analysis (see below). Otoliths were subsequently cleaned and dried for age determination and growth analysis.

Oneida-style trap nets were set in mid-October from 2000 through 2007 (Figure 1.1) to provide a comparison of relative population abundance and brook trout population size structure between years. All fish captured in trap nets were returned to the lake after their length and weight were measured and sex and maturity were determined using visible traits.

Age, growth, and size-selective mortality

Otoliths were processed in a manner similar to methods described by Casselman (1983). One sagittal otolith from each fish was selected for processing. Many of the pairs contained at least one malformed otolith (vateritic), in which case the least deformed otolith (based on visual inspection) was selected for evaluation (Bowen 1999). Otoliths were placed on a hardened layer of Araldite® 502 embedding media, then covered with a second layer of resin that was allowed to harden overnight. A stereoscope with a transmitted light source was used to find the focus of each otolith, and then a line was drawn through the focus and perpendicular to the sulcus using a scalpel. A Buehler® IsoMet® low speed saw was used to take a 32µm transverse section along the line drawn through the focus. One side of each otolith section was polished using successively finer silicon carbide discs (320, 600, 800 and 1200 grit). Each section was then mounted to a slide (polished side down) using Araldite® epoxy and allowed to harden overnight, after which the remaining surface of the slide-mounted otolith sections was polished in the same manner.

Wild origin fish were often difficult to age due to the presence of a heavily pigmented area from the focus to the first annulus. In these situations the otoliths were examined under high magnification (100x), allowing the presence or absence of daily increments to be used to pinpoint the location of each annulus. Specifically, areas in which the daily increments were not visible were determined to be annuli. While this process was only necessary to determine the location of the first annulus of wild fish, daily increments were used to locate all annuli for wild and stocked fish in order to maintain consistency.

Annual otolith increments were measured for the purposes of back-calculating length. A digital image of each otolith was taken using a Kodak® scope-mounted camera and increments were measured using Image-Pro® Express Version 4.0 software. A straight line radius was drawn from the focus to the dorsal edge of each otolith. Measurements were taken along this line from the focus to the first annulus, from the first annulus to the second annulus, and so on out to the edge of the otolith.

Back-calculated lengths were obtained using the biological intercept method (Campana 1990):

$$L_{Ft} = L_{Fc} + (O_t - O_c) \cdot (L_{Fc} - L_{Fo}) \cdot (O_c - O_o)^{-1} \quad (2)$$

where L_{Ft} is the length of the fish at age *t*, L_{Fc} at capture, L_{Fo} (14.66 mm) at hatching (biological intercept), O_t is the otolith radius at time *t*, O_c at capture and O_o (66.46 µm) at the biological intercept. Brook trout size and otolith radius at hatching were taken from Theriault and Dodson (2003). The biological intercept method was used to account for the potential effects of size-selective mortality, and Lee's phenomenon, whereby back-calculated lengths of older fish are smaller than those observed in the population (Ricker 1969, 1975; Campana 1990). As an additional precaution to minimize uncertainty introduced by Lee's phenomenon, length was back-calculated to only the most recent annulus (Gutreuter 1987).

Linear regression of length (or weight) as a function of capture date was used to test for significant growth in field measured length and weight over time for each age class in 2000, 2001, and 2007. Multiple regression analysis was used to test for homogeneity of slopes associated with length (ΔL) and weight (ΔW) between 2000 and 2001.

To estimate the positive growth in length of individual fish during the year of capture, back-calculated length at the last annulus was subtracted from the total length at the time of capture. Given the expectation that growth would be impacted by high temperatures during and after the hot period of the summer (post-stress), only the back-calculations from the last two sampling events in each year were used to compare growth. For the purposes of analysis fish were separated into three groups based on age, then separate analyses were conducted for each group: age one and two fish were separated into distinct groups and age three and four fish were pooled. Multiple regression analysis was used to compare positive growth based on back-calculations between 2000 and 2001 for fish captured in the post-stress period (late August and early September) while removing variation associated with differences in length at the start of the growing season, date of capture and year of sampling. Least squares means estimates were used to compare growth rates between years within each age group.

To test for evidence of size-selective mortality in each year class, linear regression was used with the back-calculated length at the most recent annulus as the dependent variable and date of capture as the independent variable. A significant trend was considered evidence of size-selective mortality; a negative trend indicated selective pressure against larger individuals in the population while a positive trend indicated selective pressure against smaller individuals.

Stomach fullness and energy density

Brook trout diet contents were dried at 60°C until weight stabilized. Stomach fullness was determined for all fish captured in 2000 and 2001 using a method similar to that described by Hyslop (1980):

$$\text{Stomach fullness} = (\text{dry weight of stomach contents} / \text{total fish weight}) \times 100 \quad (1)$$

Linear regression was used to determine the relative influence of water temperature on the maximum gut fullness for each sampling event. To avoid extreme values the mean of the upper quartile was used to represent maximum stomach fullness in the regression. Given that only two fish were captured on August 16^{th} 2001 – both of which had empty stomachs – a value of zero was used to represent the maximum stomach fullness for that date.

Due to the potential for lipid reserves to be affected by temperature, percent water content of muscle tissue was monitored throughout the growing season in 2007 as a proxy for lipid content (Appendix C). Percent water content was measured for all fish collected in 2007. Approximately 25 g of muscle tissue was removed from each fish for water content analysis. Tissue (including skin) removed from the left side of each fish directly posterior to the head was blotted dry with a paper towel, weighed to the nearest thousandth of a gram, then placed in a 60°C drying oven until weight stabilized. Percent water content was determined as a proportion of the wet weight of the tissue sample.

Reproduction and mortality

Whole-lake redd counts were used as a relative measure of spawning activity in each year. Fall 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 and counted all visible redds. AIC_C (Akaike Information Criterion) model selection (Burnham and Anderson 1998) was used to select the most parsimonious linear model to explain fall redd counts using the four combinations of the parameters degree days exceeding 20°C and fall density of mature females.

Length-frequency histograms constructed using trap net data were used to follow cohorts through time to draw conclusions regarding the presence, absence and mortality of individual cohorts in each year. The absence of fish from a given cohort was attributed to mortality if: (1) no fish representing that cohort were captured in trap nets, (2) the absence of that cohort did not correspond to an absence of fall spawning activity in the year in which that cohort would have been produced, and (3) the absence of that cohort could not be attributed to mortality of that cohort in a previous year.

Results

Thermal conditions

Cumulative degree-days in which mean daily bottom water temperature exceeded 20°C varied greatly among years, ranging from 6.6 in 2000 to 206.9 in 2005 (Figure 1.2). Maximum bottom water temperatures exceeded the upper incipient lethal temperature in 2005 (25.6°C) on August 10th and 11th and approached lethal levels in 2001 (25.2°C) and 2002 (25.2°C) (Table 1.2). For years in which growth was measured 2000 was the most favorable based on growing degree-days (Table 1.2) and plots of temperature over time (Figure 1.3), followed by 2001 and 2007 respectively. The warmest conditions were found from early to mid-August in all three of these years.

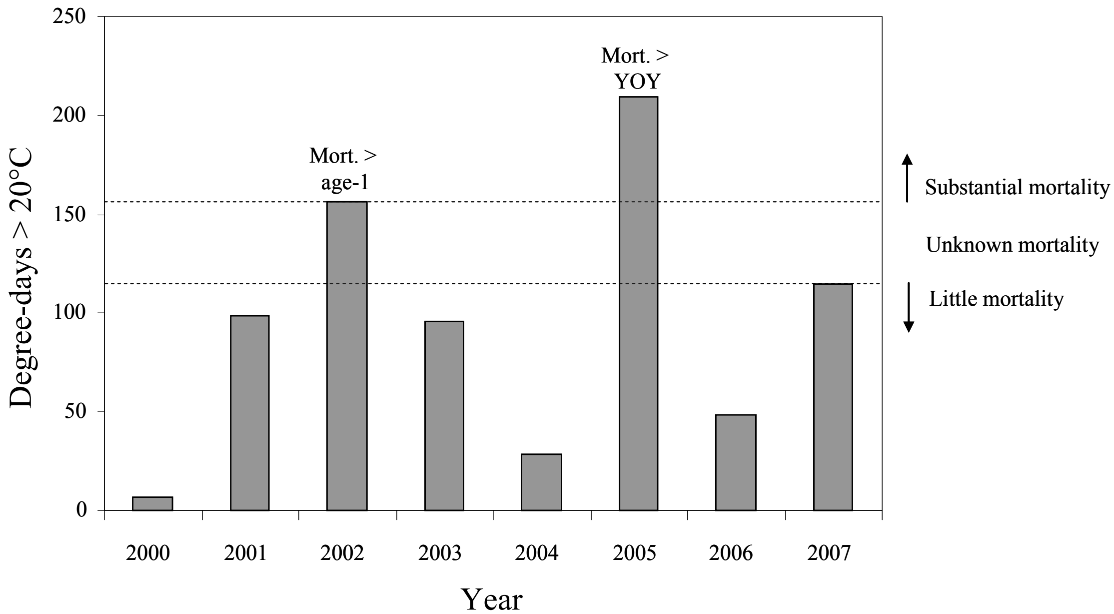

Figure 1.2. Cumulative degree-days in which the mean bottom temperature exceeded 20°C in each year. Dashed lines represent thresholds of mortality.

Table 1.2. Degree-days in which the mean bottom temperature exceeded 20°C, maximum bottom temperature, days in which the mean bottom temperature exceeded 20°C and growing degree days for each year. Numbers in parentheses indicate hours at maximum temperature.

Year	Degree-days > 20°C	Max. temp. (°C)	Days > 20°C	Growing Degree-days
2000	6.6	21.7 (5)	19	2413
2001	98.1	25.2 (7)	51	1755
2002	156.2	25.2 (8)	69	1462
2003	95.5	24.0 (5)	56	1469
2004	28.4	22.1 (36)	36	1877
2005	209.6	25.6 (5)	83	1325
2006	47.8	23.2 (9)	34	2227
2007	114.5	24.0 (25)	75	1586

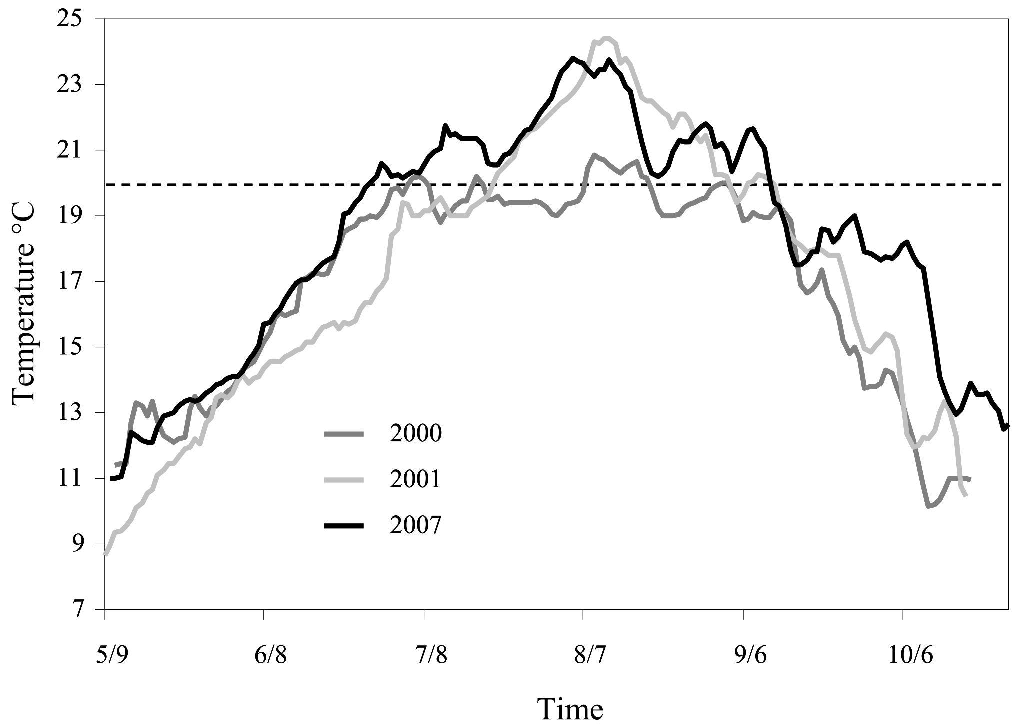

Figure 1.3. Thermographs of mean daily bottom temperature (5.5 m) in Rock Lake in 2000, 2001, and 2007. Dashed line represents the temperature above which brook trout experience thermal stress (20°C).

Brook trout catch

Two hundred fifty-seven brook trout were captured on 10 dates in 2000; 259 fish were captured on seven dates in 2001 (Table 1.3). Naturally spawned fish comprised 61% of brook trout captured in 2000, compared to 54% in 2001. In 2000 the number of fish captured ranged from 16 on June 2nd to 38 on August 30th. In 2001 the number of fish captured varied from 2 on August 16th to 54 on May 24th (Table 1.3). Increasing catches of age-1 fish in May and June of both years may indicate that the age-1 cohort is not fully recruited to the gear at the onset of sampling (Table 1.3). The overall number of fish captured remained relatively constant through time in 2000, while in 2001 it became increasingly difficult to capture the target number of fish as water temperature increased. The lowest catch occurred on the sampling date with the highest mean bottom temperature (August 16, 2001: 23.3°C).

Trap net CPUE was similar between 2000 and 2001 ($t = 4.30$, $p = 0.475$). Age and size structure were also very similar between the two years (Figure 1.4). Some of largest trap net CPUE's ever observed in Rock Lake (over 27 years of observations) occurred in 2000 and 2001, while trap net catch in 2007 was the lowest observed over the eight year study.

Age, growth, and size-selective mortality

A total of 415 otoliths were aged from 2000 and 2001. One hundred-one otoliths could not be aged due to poor formation (vateritic) (Bowen et al. 1999) or error in the mounting, sectioning or extraction processes. Forty-three of these fish were wild and 58 were stocked. Age was determined for the 58 stocked fish based on fin clips so these fish could be used in the length and weight analysis. The maximum age of

Table 1.3. Total brook trout catch including both gill net and angling captures, for each sampling date and at each age in 2000, 2001 and 2007.

Year	Date	Age-1	Age-2	Age-3	Age-4	Age-6	Unknown	Total
2000	10-May		11	10			1	22
	24-May	4	13	6	1		3	27
	2-Jun	7		6	2	1		16
	22-Jun	14	6	6	2		2	30
	5-Jul	8	6	6			2	22
	19-Jul	8	6	7	1			22
	2-Aug	15	5	5			3	28
	17-Aug	9	6	7			4	26
	30-Aug	14	10	12	1		1	38
	12-Sep	14	7	5				26
							Total:	257
2001	24-May	1	24	15	11		3	54
	14-Jun	10	21	9	6		2	48
	5-Jul	10	24	4	5		5	48
	25-Jul	13	19	6	9		5	52
	16-Aug	1			1			2
	4-Sep	9	11	4			3	27
	27-Sep	7	10	1	3		7	28
							Total:	259
2007	10-May		7					7
	23-May		10					10
	14-Jun		16					16
	4-Jul		10					10
	27-Jul		6					6
	17-Aug		5					5
	7-Sep		7					7
	26-Sep		8					8
							Total:	69

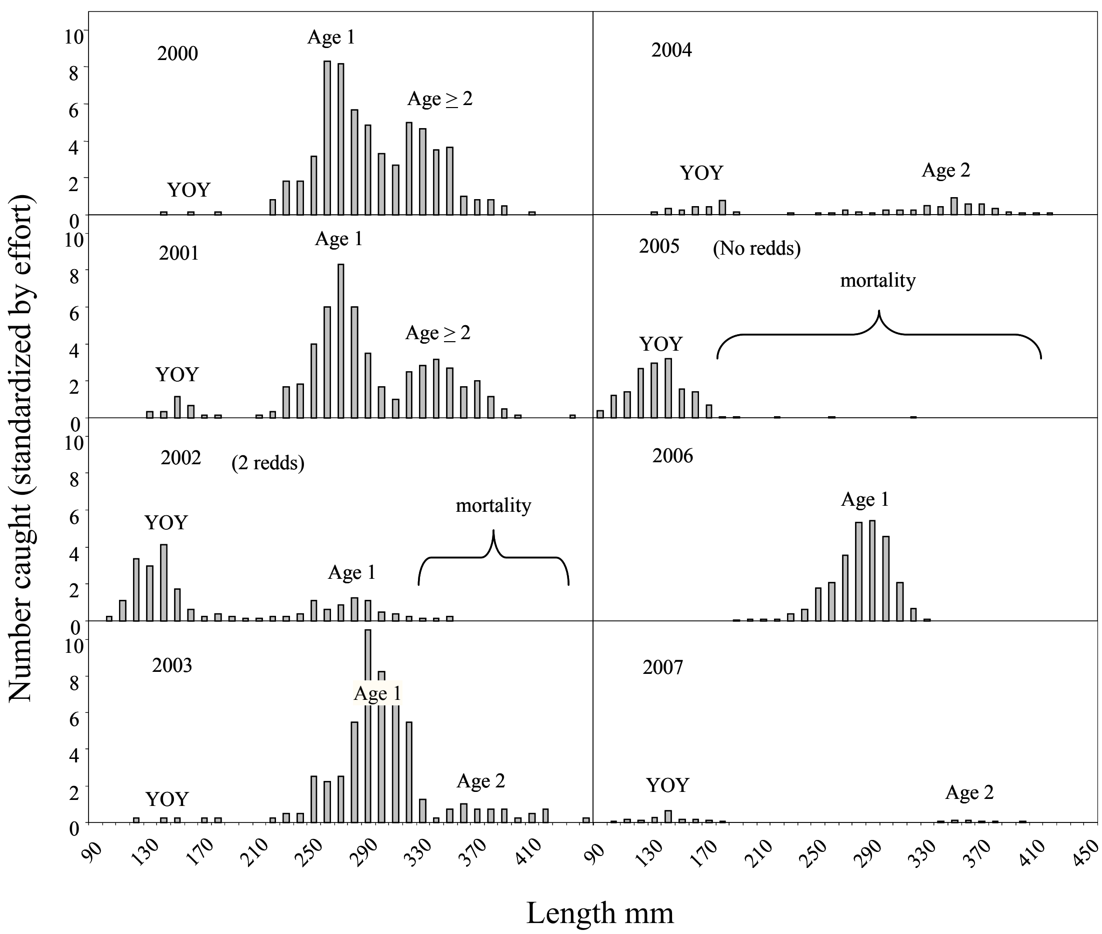

Figure 1.4. Length frequency histograms based on trap net catches in each year (standardized by effort). Mortality events and years with poor reproduction are noted.

both wild and stocked fish was four years, with the exception of a single six year old wild fish. Wild and stocked fish were pooled for analysis.

Length back-calculations based on otoliths indicated that brook trout showed positive somatic growth in both 2000 and 2001 (Figure 1.5). Based on total length at capture, the age-1 and age-2 cohorts in 2000 showed a significant overall increase in length over the duration of the sampling (age-1, $p < 0.01$; age-2, $p < 0.01$); age-3 and age-4 cohorts in 2000 showed no change in length over time (age-3, $p = 0.97$; age-4 $p = 0.77$) (Figure 1.6). None of the cohorts showed a significant increase in length in 2001 (age-1, $p = 0.11$; age-2, $p = 0.14$; age-3, $p = 0.62$; age-4, $p = 0.39$) (Figure 1.6). The slopes of the regression lines for the age-3 and age-4 cohorts were negative but not significant in 2001. The age-2 cohort showed a significant increase in length in 2007 ($p < 0.01$, Figure 1.6). Between-year differences in slope (ΔL) were significant at age-1 ($p = 0.04$) but not for the other age classes (age-2, $p = 0.95$; age-3, $p = 0.36$; age-4, $p = 0.27$).

Based on weight at capture, the age one, age two and age three cohorts showed a significant increase in body weight over the duration of the sampling in 2000 (age-1, $p < 0.01$; age-2, $p < 0.01$; age-3, $p < 0.01$) and the age-4 cohort showed no change in weight ($p = 0.64$) (Figure 1.7). One, two and three year old cohorts showed no increase in weight in 2001 (age 1, $p = 0.44$; age 2, $p = 0.48$; age 3, $p = 0.21$) (Figure 1.7). Though not significant, the slope of the regression line for the age-3 cohort in 2001 was negative. The age-4 cohort showed a significant decrease in weight in 2001 ($p = 0.04$, Figure 1.7). In 2007 the age-2 cohort showed an increase in weight ($p = 0.06$, Figure 1.7). Between-year differences in slope between 2000 and 2001 (ΔW) were significant for age-1 ($p = 0.03$), age-2 ($p = 0.02$) and age-3 ($p < 0.01$) cohorts but not for the age-4 cohort ($p = 0.09$).

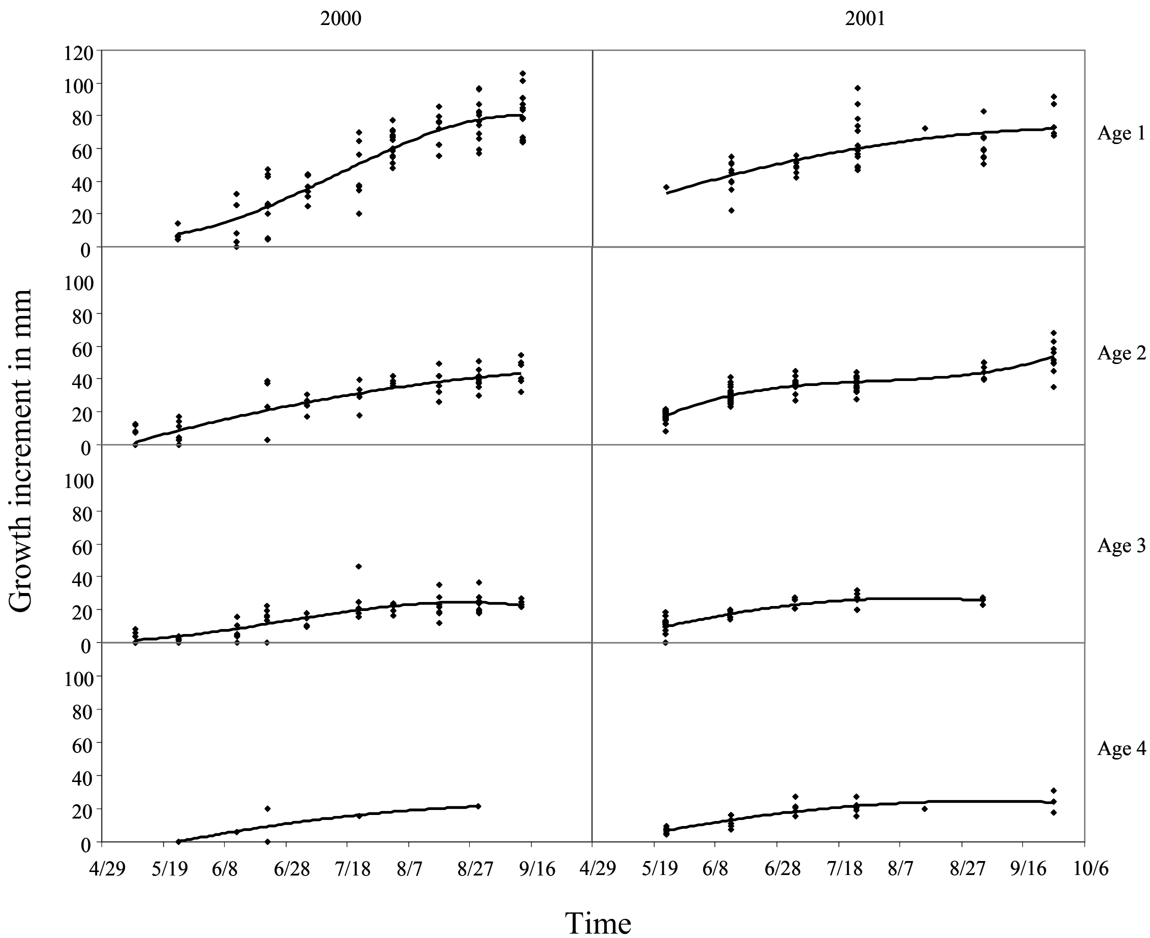

Figure 1.5. Current year's growth in length over time for each age class based on otolith back-calculations. Regressions represent best fit curves

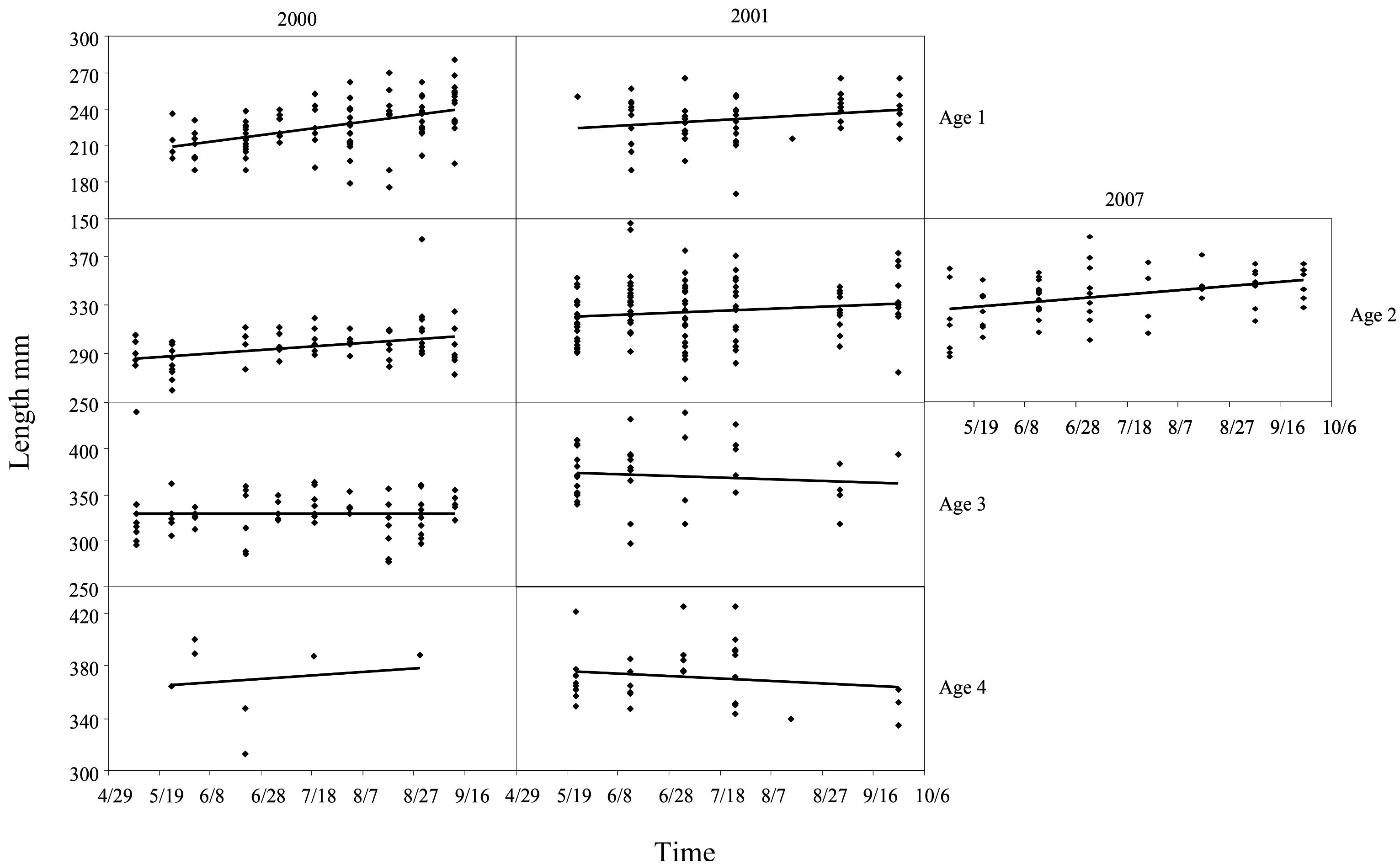

Figure 1.6. Field measured length for each age class through time in 2000, 2001 and 2007, with associated linear regressions.

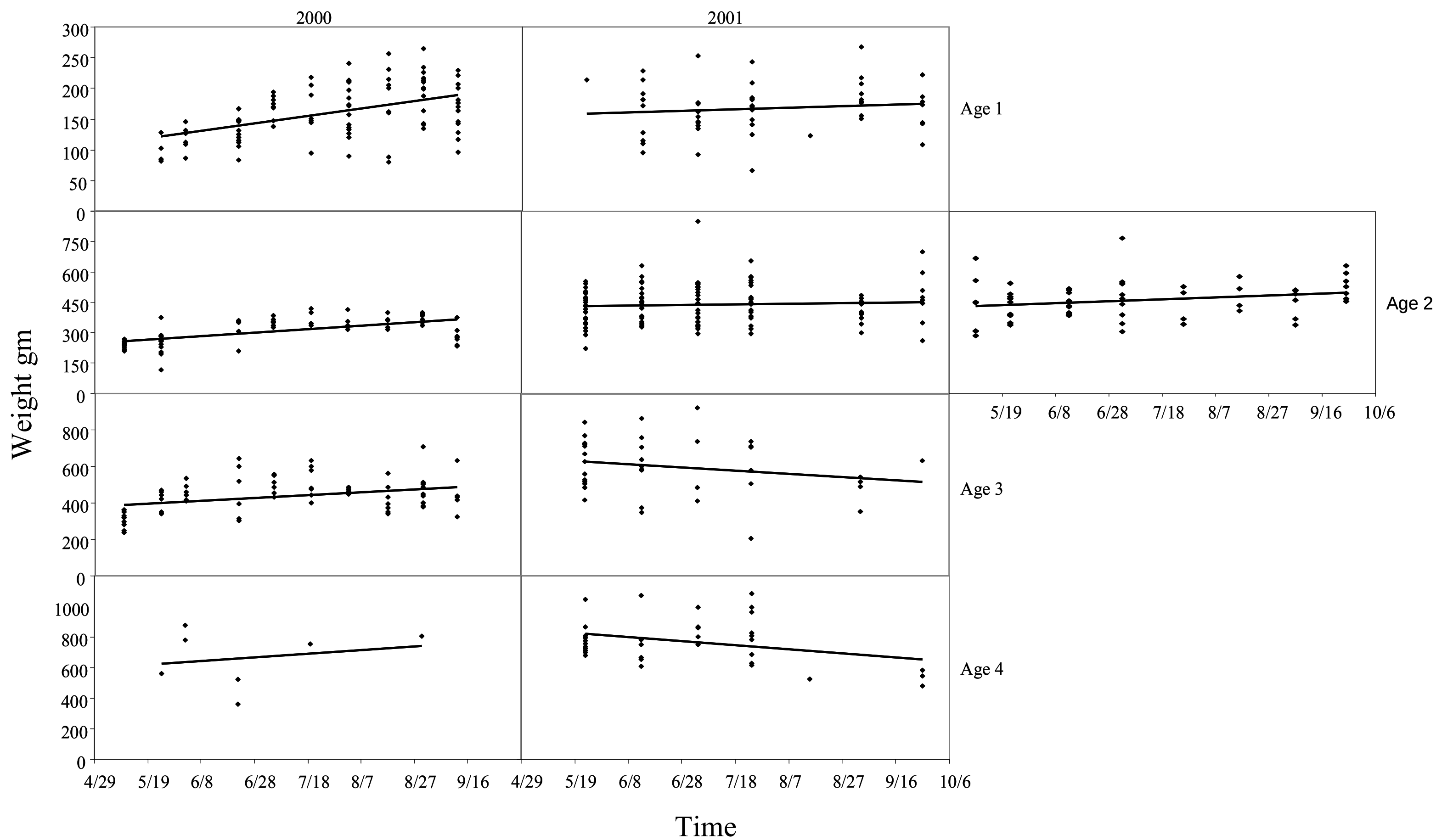

Figure 1.7. Field measured weight for each age class through time in 2000, 2001 and 2007, with associated linear regressions.

After accounting for variation associated with length at the start of the growing season and date of capture using multiple linear regression, differences in growth between years in the post-stress period (i.e. after early August) varied by age class. Age-1 fish grew significantly more during the post-stress period in 2000 (78.7mm) than in 2001 (68.4mm; $t = 2.30$, $p = 0.03$), but age-2 fish showed significantly more growth in 2001 (49.0mm) than in 2000 (41.3mm; $t = -2.60$, $p = 0.01$). No differences were found in the growth of age-3 and age-4 fish between years (2000: 23.9 mm, 2001: 25.2 mm; $t = -0.61$, $p = 0.55$) (Figure 1.8, Tables 1.4, 1.5 and 1.6 respectively). Evidence of size-selective mortality was found in nearly all age classes in both years in which otoliths were examined (Figure 1.9). For instance, a typical age-1 brook trout captured in May of 2000 was approximately 200 mm at the time of annulus formation (April), whereas a fish from the same year class captured in September of 2000 was approximately 160mm at the time of annulus formation. A significant negative relationship was found between length back-calculated to the most recent annulus and the date of collection for age-1, age-2 and age-3 cohorts (age-1: $p < 0.01$, $n = 82$; age-2: $p < .01$, $n = 60$; age-3: $p = 0.03$, $n = 69$; age-4: $p = 0.77$, $n = 6$). In 2001, all four cohorts showed a significant negative relationship at $\alpha = 0.1$ (age 1: $p = 0.02$, $n = 46$; age 2: $p = 0.07$, $n = 85$; age 3: $p = 0.06$, $n = 34$; age-4: $p < 0.01$, $n=33$).

Stomach fullness and energy density

Patterns of stomach fullness throughout the growing season were similar for 2000 and 2001, with stomach fullness declining through the growing season indicating a relationship between stomach fullness and temperature (Figure 1.10). Maximum stomach fullness on each sampling occasion was negatively correlated with mean

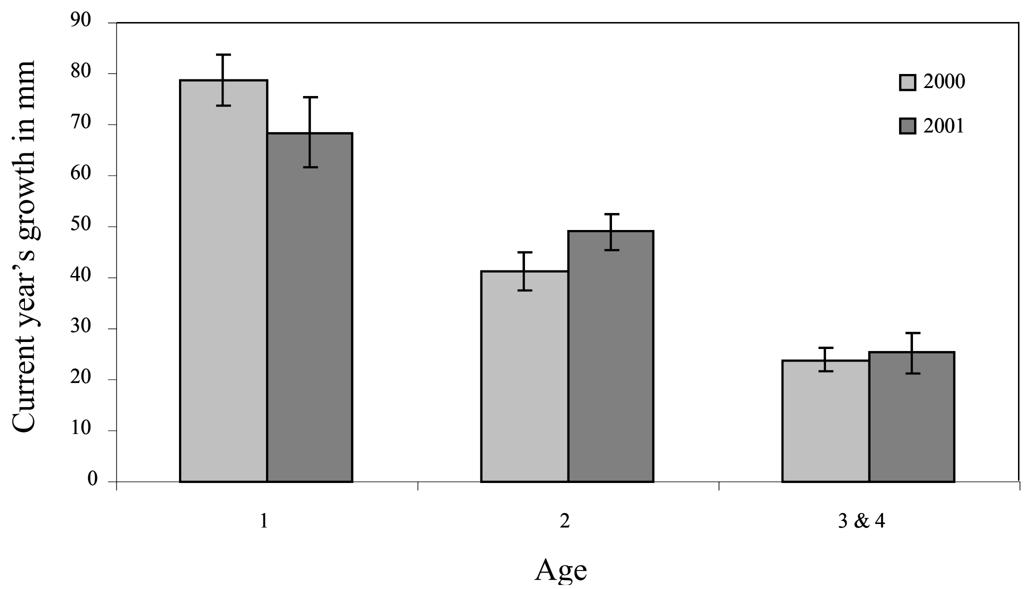

Figure 1.8. Current year length increases based on otolith back-calculations of fish captured in the post-stress period (late August – September) for each age class in 2000 and 2001. Error bars represent two standard errors from means.

Table 1.4. ANOVA table, fit statistics, effects tests and least squares means estimates for the linear model accounting for the effects of starting size (size at start of growing season), year and sampling date on the annual growth (CYG) of age one brook trout in 2000 and 2001.

r^2	Coeff var	Root MSE	CYG Mean
0.32	15.94	11.96	75.1

Source	DF	Sum of squares	Mean square	F value	Pr > F
Model	3	2411.38	803.79	5.62	0.0029
Error	36	5152.77	143.13		
Total	39	7564.14			

Source	DF	Type III SS	Mean Square	F value	Pr > F
Starting size (mm)	1	601.42	601.42	4.20	0.0477
Year	1	760.61	760.61	5.31	0.0270
day	1	496.51	496.51	3.47	0.0707

Year	CYG LSMean	Pr > |t|
2000	78.7	0.0270
2001	68.4	

Table 1.5. ANOVA table, fit statistics, effects tests and least squares means estimates for the linear model accounting for the effects of starting size (size at start of growing season), year and sampling date on the annual growth (CYG) of age two brook trout in 2000 and 2001.

r^2	Coeff var	Root MSE	CYG Mean
0.47	0.47	6.54	45.2

Source	DF	Sum of squares	Mean square	F value	Pr > F
Model	3	1116.83	372.28	8.71	0.0003
Error	29	1238.87	42.72		
Total	32	2355.70			

Source	DF	Type III SS	Mean Square	F value	Pr > F
Starting size (mm)	1	147.71	147.71	3.46	0.0731
Year	1	760.61	760.61	6.76	0.0145
day	1	496.51	496.51	7.70	0.0126

Year	CYG LSMean	Pr > |t|
2000	41.3	0.0145
2001	49.0	

Table 1.6. ANOVA table, fit statistics, effects tests and least squares means estimates for the linear model accounting for the effects of starting size (size at start of growing season), year and sampling date on the annual growth (CYG) of three and four (pooled) brook trout in 2000 and 2001.

r^2	Coeff var	Root MSE	CYG Mean
0.06	17.71	4.29	24.2

Source	DF	Sum of squares	Mean square	F value	Pr > F
Model	3	24.31	8.10	0.44	0.7270
Error	21	387.08	18.43		
Total	24	411.40			

Source	DF	Type III SS	Mean Square	F value	Pr > F
Starting size (mm)	1	15.84	15.84	0.86	0.3644
Year	1	6.87	6.87	0.37	0.5480
day	1	0.25	0.25	0.01	0.9084

Year	CYG LSMean	Pr > |t|
2000	23.9	0.5480
2001	25.2	

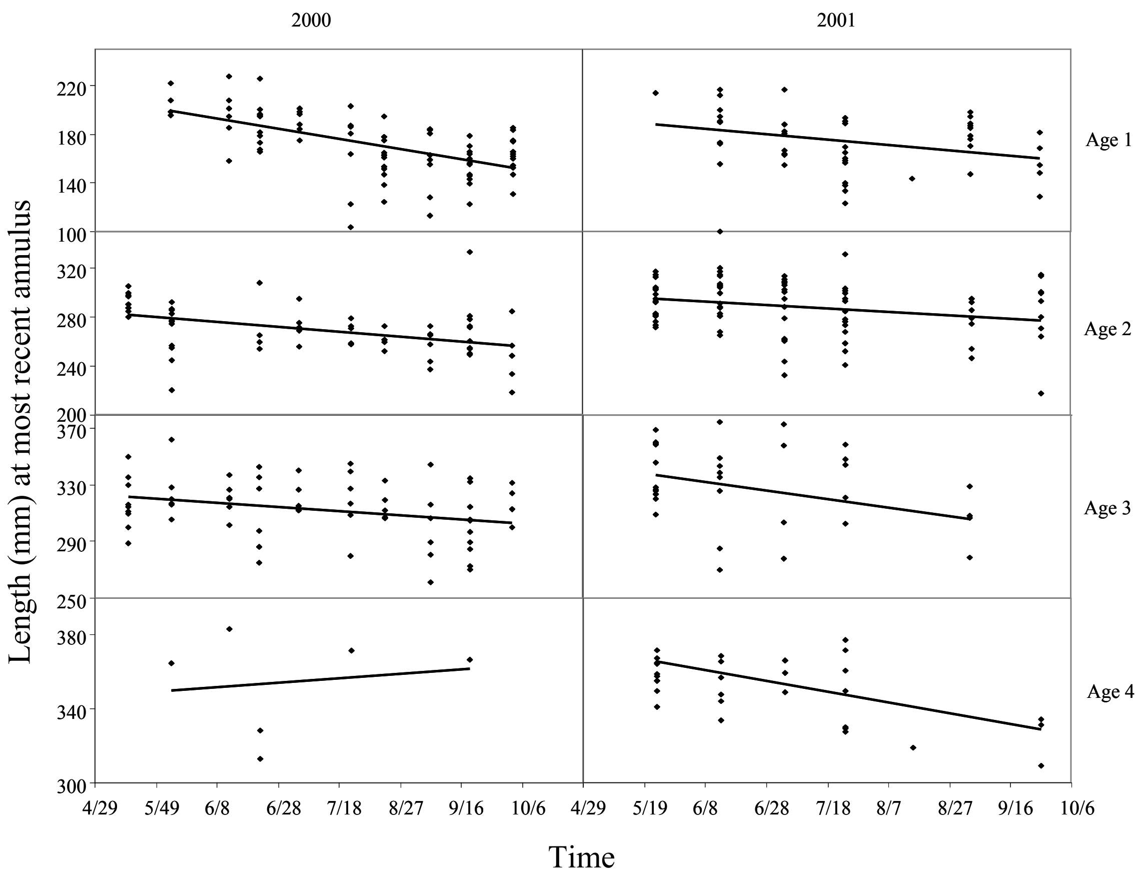

Figure 1.9. Back-calculated length at the most recent annulus through time for each age class in 2000 and 2001,with associated regression lines.

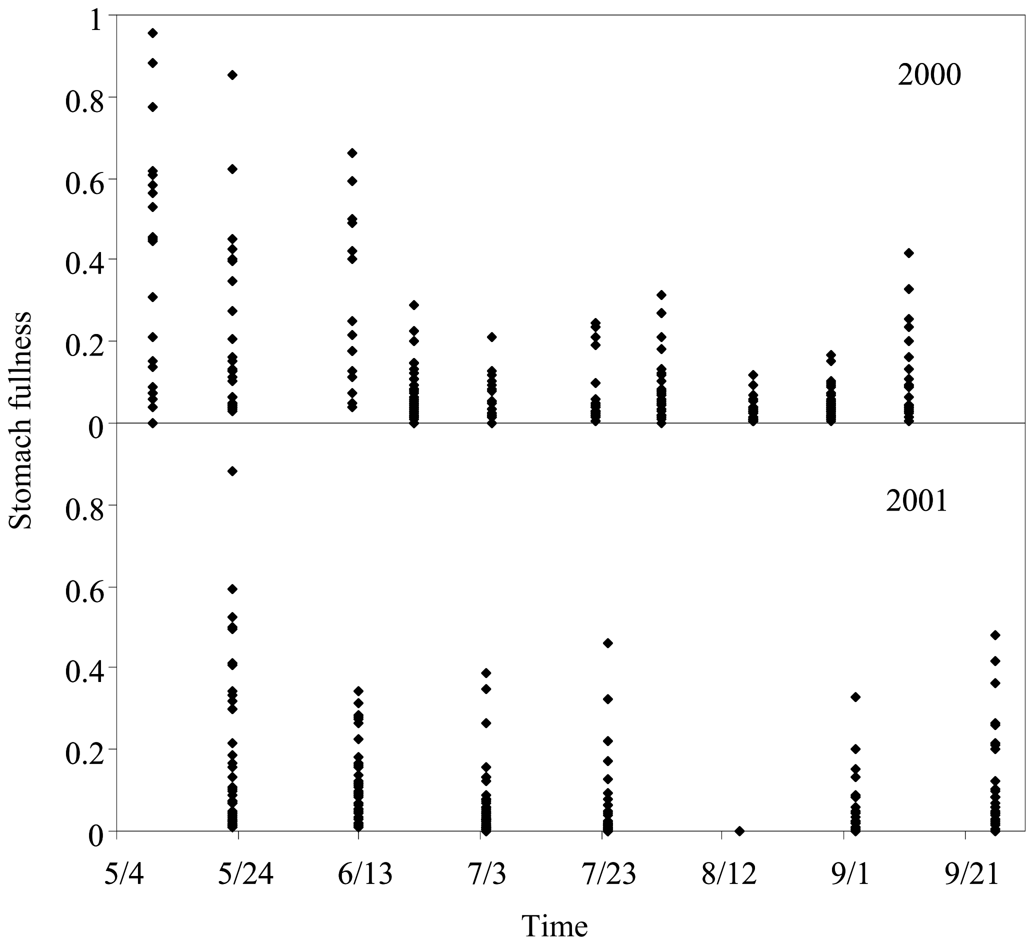

Figure 1.10. Stomach fullness of brook trout through time in 2000 and 2001.

daily bottom temperature on the corresponding date (F = 51.827, $p < 0.01$, $R^2 = 0.78$) (Figure 1.11).

Due to the potential for body condition (i.e. lipid reserves) to be affected by temperature and consumption and to subsequently impact reproduction and mortality, percent water content was monitored throughout the growing season in 2007. Percent water content showed a slight decrease from May 10 (73.5%) to July 27 (72.3%) and then increased to 75% by September 26 (Figure 1.12). Information regarding the diet composition of various brook trout size groups is provided in Appendix B.

Reproduction and mortality

Whole-lake redd counts in Rock Lake ranged from zero to 260 during the eight-year study period (Figure 1.13). The years with the lowest redd counts (2002, n = 2; and 2005, n = 0) coincided with the highest number of degree days exceeding 20°C. Based on the AIC model selection the model containing degree-days exceeding 20°C and female density was identified as the most parsimonious model for predicting redd count and accounted for 89% of the variation in annual redd construction (Table 1.7). In this model degree days had a significant effect on the construction of redds and accounted for the majority of variation (F = 20.71, p = 0.01), while the effect of fall female density was not significant (F = 2.11, p = 0.21) (Table 1.8). When regressions were run on the individual parameters, degree days exceeding 20°C were significantly and negatively related to redd count ($R^2 = 0.85$, p = 0.0011, F = 34.06; Figure 1.14). The relationship between fall female density and redd count showed a non-significant positive trend ($R^2 = 0.46$, p = 0.07, F = 5.08; Figure 1.15).

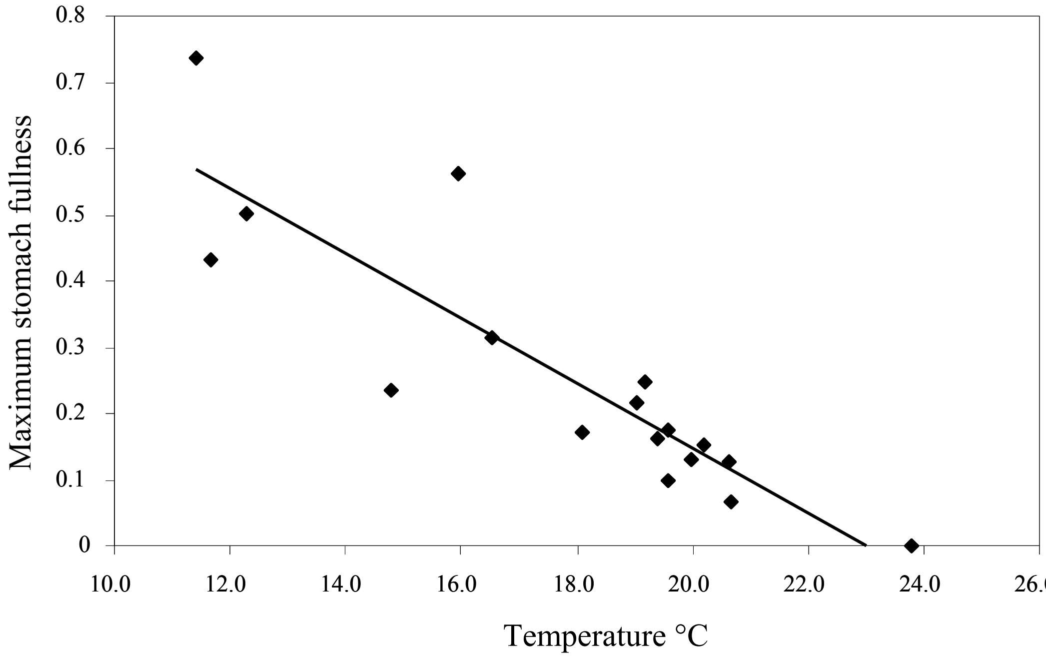

Figure 1.11. Maximum stomach fullness and mean bottom temperature in 2000 and 2001, with associated regression line. Maximum stomach fullness represents the mean of the upper quartile on each sampling date.

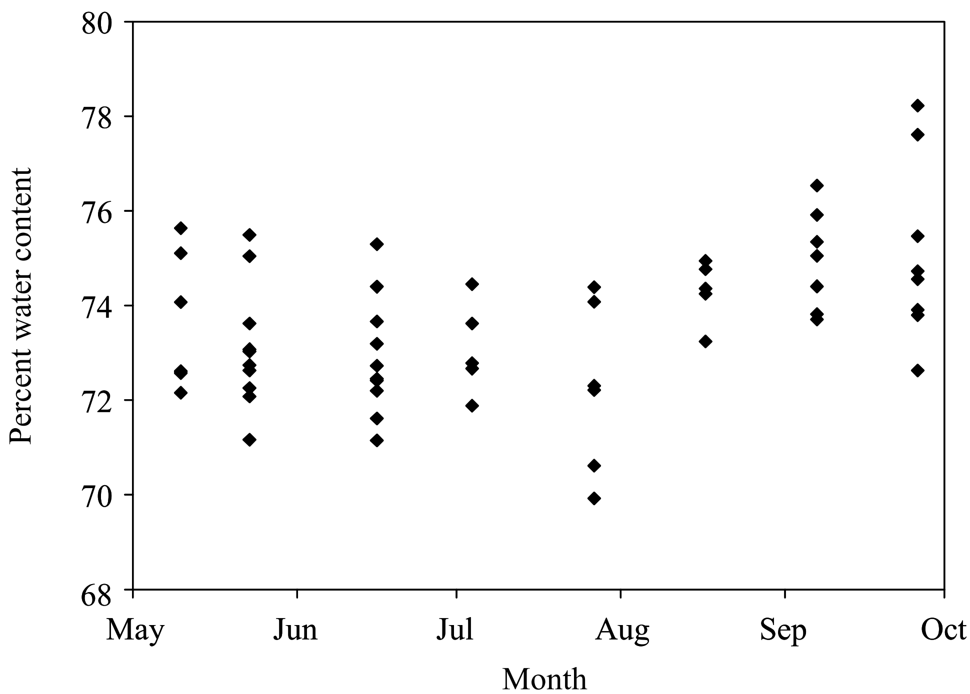

Figure 1.12. Percent water content of brook trout muscle tissue through time in 2007.

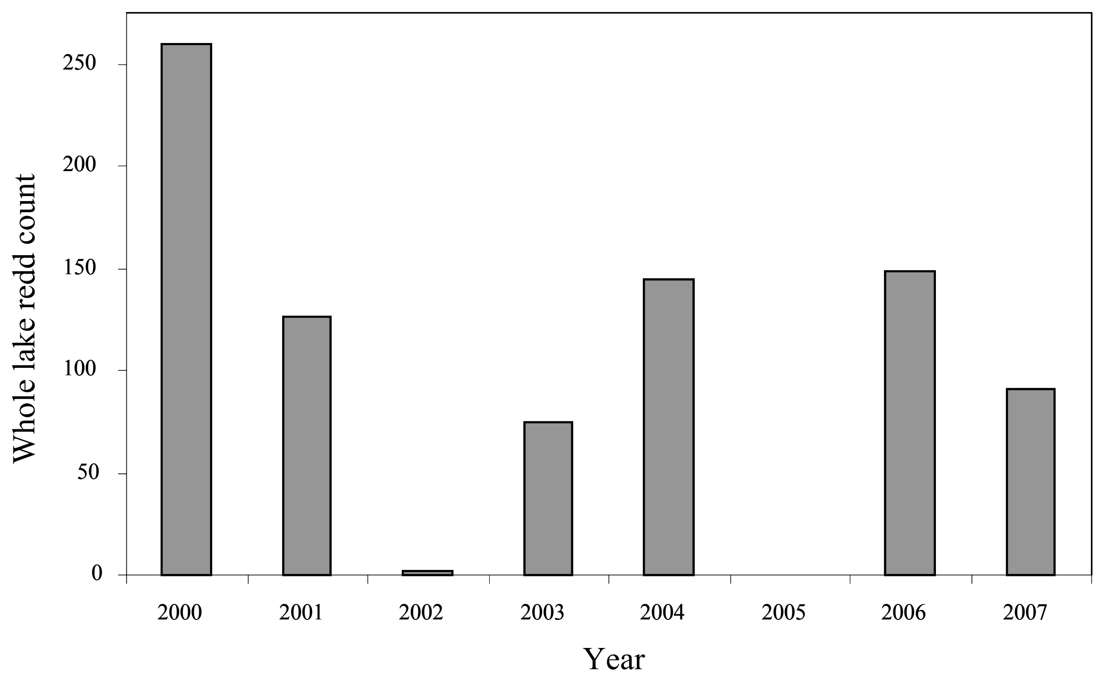

Figure 1.13. Whole-lake redd counts in Rock Lake from 2000 to 2007.

Table 1.7. Model selection for estimating redd construction. For each candidate model, the AIC, Delta AIC, AIC weight, model likelihood, and r-squared are reported. DD = degree days exceeding 20°C in each year and CPUE = fall trapnet CPUE for mature females.

Model	AIC_C	ΔAIC_C	Model Likelihood	AIC_C weight	r^2
DD + CPUE	70.9	0	1.00	0.77	0.89
DD + CPUE + DD*CPUE	74.5	3.6	0.17	0.13	0.95
DD	75.3	4.4	0.11	0.09	0.85
CPUE	79.1	8.2	0.02	0.01	0.46

Table 1.8. ANOVA table for linear model to account for the effects of mature female trapnet CPUE and degree-days exceeding 20°C on redd construction.

Source	df	MS	F	p(F)
Female density	1	2257	2.11	0.2058
Degree days > 20°C	1	22126	20.71	0.0061
Error	5	5341		

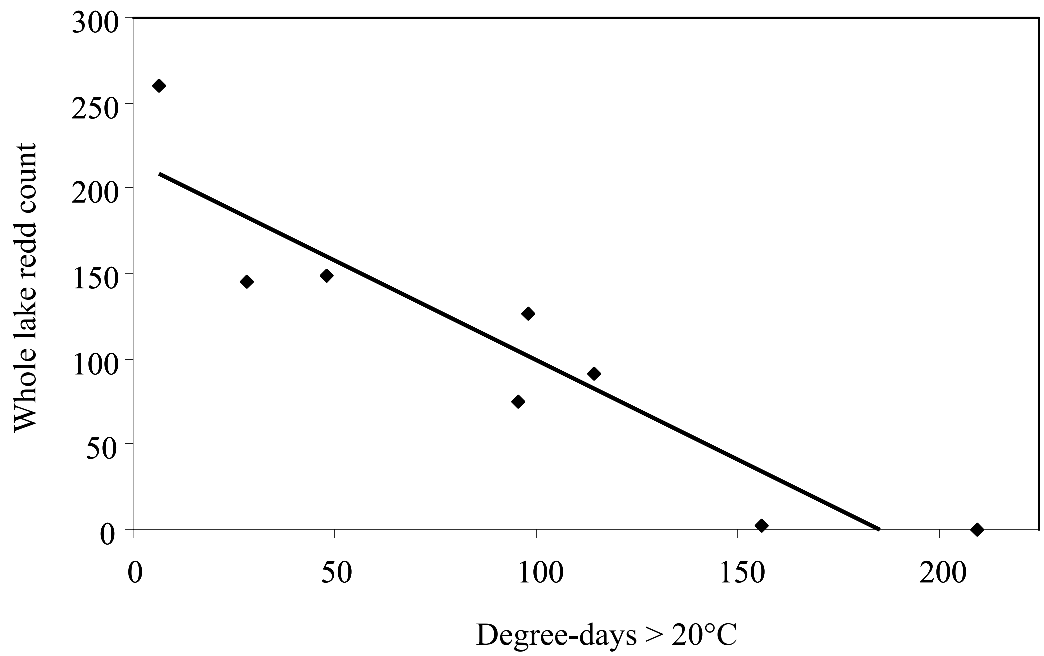

Figure 1.14. Cumulative degree-days exceeding 20°C and annual whole-lake redd count, with associated regression line.

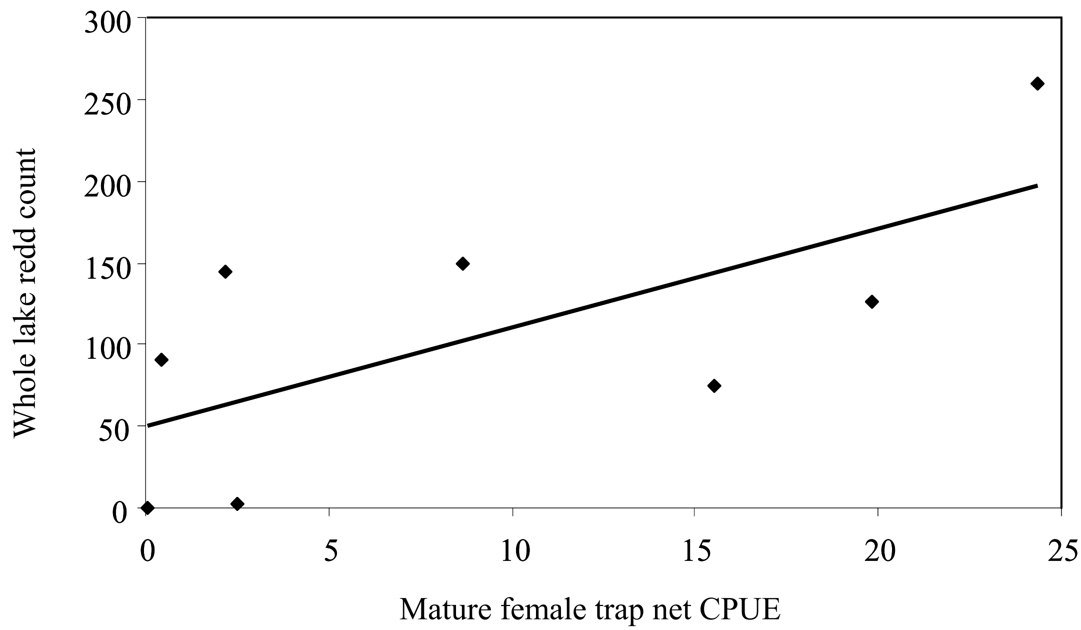

Figure 1.15. Fall trap net (CPUE) of mature female brook trout and annual whole-lake redd count, with associated regression line.

Based on length-frequency histograms derived from trap net data, substantial mortality of several year classes occurred in 2002 and 2005 (Figure 1.4). Virtually all fish age two and older were absent from the catch in 2002, and virtually all fish age one and older were absent in 2005. In all other cases in which a cohort was represented by a small catch, a low level of spawning activity was observed in a previous year corresponding to when that cohort would have been produced. The very low level of spawning in 2002 corresponded with the low catches of YOY brook trout in 2003 and yearlings in 2004; the absence of YOY brook trout in 2006 and yearlings in 2007 corresponded to the lack of spawning in 2005 (Figure 1.4). The low number of fish captured in the trap nets in 2007 was likely due to the abnormally high water temperature during the time of sampling, not a significant mortality event. This presumption is supported by the moderate level of spawning observed in 2007 (Figure 1.13).

Discussion

This study is the first to examine the effects of temperature on adult brook trout in a natural lake system by directly measuring individual and population level characteristics during periods of contrasting thermal conditions. By studying the effects of variable stressful thermal conditions on brook trout at the southern margin of their lentic range, we describe mechanisms by which brook trout populations function in thermally marginal environments. Further, this study illustrates changes and relationships that may be observed or expected in the future if warming climate trends continue. Our results suggest that available summer water temperatures in Rock Lake strongly influence brook trout growth, reproduction, consumption and survival at various life stages. In cool years (e.g., 2000), bottom temperatures reached stressful levels (>20°C), but fish were able to grow, survive and reproduce. In years with warmer summer conditions (e.g., 2005), however, only YOY brook trout survived in Rock Lake.

Brook Trout Catch

Relatively constant brook trout catches in the cool summer (2000), and declining catches in the warm summer (2001), indicate that warmer water conditions reduced our ability to capture target numbers of fish. Rock Lake contains no known thermal refuge for catchable size fish (Appendix A); therefore, temperature increases that exceed stressful levels would be expected to have a negative influence on catch. Negative effects of temperature on catch have been reported previously; however, the relationship can be confounded by the presence of thermal refuges (Baird et al. 2006). McMichael and Kaya (1991) found a negative relationship between stream temperature and angling catch of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in a Montana river. Baird et al. (2006) found no correlation between high summer water temperature and catch rate due to thermal refuges that concentrated fish, making them vulnerable to angling during hot summer conditions. Kocovisky and Carline (2001) and Quist et al. (2002) found that gillnet catch rates for walleye were lowest in mid-summer during the time of highest water temperature. These studies provide corroborating evidence that varying thermal conditions influenced the brook trout catch in Rock Lake.

Target numbers of brook trout were not obtained after temperatures decreased to non-stressful levels (<20°C) in the fall of 2001, which suggests that they had not fully recovered from stressful summer temperatures. Temperature can interact with catch rate by lowering the density of the catchable population through temperature induced mortality (Fry et al. 1946) or by changing activity and consumption levels (Dickson and Kramer 1971; Boisclair 1992; Biro et al. 2007). Fall trap net surveys in 2000 and 2001 – conducted at a time when water temperatures had cooled and at locations where fish were aggregated for spawning – did not indicate a significant difference in the overall number of fish available for capture. We conclude that the decreasing brook trout catch, as water temperatures increased in summer 2001, was due to a behavioral change associated with decreased activity and consumption rather than differing underlying mortality between the two years.

Age, growth and size-selective mortality

The influence of temperature during the open-water season is more readily apparent when evaluating growth in weight than length. Significant between-year differences in seasonal change in length (ΔL) only occurred at age-1, with fish in 2000 showing greater increases than in 2001. Significant between-year differences in weight change (ΔW) occurred at all age classes with fish in 2000 showing greater increases than those in 2001. The larger number of year classes with between-year differences in weight change indicates that weight is more immediately influenced by warm water temperatures than is length. The effect of temperature on weight is also a more discernible characteristic because fish can diminish in weight, but not in length.

High summer water temperatures negatively impacted the growth of larger, older age classes of brook trout to a greater extent than smaller, younger age classes. 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). In Rock Lake, younger age classes (ages 1 and 2) showed increases in length in 2000, while in 2001 no increase in length was observed in any year class. Increases in weight were observed in all but the age four year class in 2000, while in 2001 no increases in weight were observed and the age four year class decreased in weight. Our results are consistent with previous field studies reporting that growth of larger, older brook trout (age ≥ 2) is negatively impacted by warm summer water temperatures (> 20°C) while the growth of younger, smaller fish is less impacted (Schofield et al. 1993; Drake and Taylor 1996; Baird et al. 2006). Drake and Taylor (1996) found that river temperature was negatively related to the growth of brook trout age 2 and older. Baird et al. (2006) observed that stocked brook, brown and rainbow trout that gained weight were usually less than 275 mm in a river system where water temperatures regularly exceeded 23°C. Schofield et al. (1993) reported that growth of YOY and yearling brook trout was not limited by summer water temperature in unstratified Adirondack lakes. The frequency and magnitude of stressful temperatures (> 20°C) reported in those studies were similar to temperatures observed in Rock Lake in 2000, which was a relatively a cool summer. However, the prevailing water temperature conditions observed during the warmer summer of 2001 frequently exceeded 20°C with greater magnitude and frequency. Contrary to other studies (Schofield et al. 1993; Drake and Taylor 1996; Baird et al. 2006), temperature extremes observed in 2001 were sufficient to impact brook trout growth at all ages measured – including yearlings.

Otolith back-calculations indicated positive growth of individuals, at all ages, throughout the growing season in 2000 and 2001; however, field collections indicated that growth only occurred within individual age classes in 2000. The lack of increase in length of age classes in field collections is most likely the result of selective mortality against larger individuals rather than a lack of individual fish growth.

Evidence of ongoing size-selective mortality of larger individuals was found in almost all age classes in 2000 and 2001.

We suggest three potential causes for the observed size-selective mortality: size-selective removals of fish collected by angling and gill nets, size-dependent physiological limitations of larger individuals, and predation upon larger fish. Although we cannot conclusively identify the extent to which each of these factors is responsible, we consider each in turn. Common loons (*Gavia immer*) are a known brook trout predator on Rock Lake, and loon predation was reported to have a large impact (50% mortality) on yearling rainbow trout in small British Columbia lakes (Beckmann et al 2006). Beckmann et al. (2006) also reported that loons rarely select YOY trout, which suggests that loons would not be selecting smaller individuals of the yearling age class in Rock Lake. Increasing catches of yearling brook trout through time suggests that smaller yearlings were not recruited to gill net or angling gear at the onset of sampling. As such, the largest yearlings were likely being selectively removed from the population as a result of our sampling. In combination with loon predation, gear induced mortality could have been the source of the size-selective pressure on the yearling age class in both years.

Larger fish are more negatively impacted at lower temperatures than younger, smaller fish (Schmidt-Nielsen 1990). Given the overlap in size of the age two, three and four year old brook trout in Rock Lake, larger individuals in each of these age classes may have experienced greater temperature-induced mortality than their smaller conspecifics. All identified potential sources of mortality would select against larger individuals in the population. Other studies have documented size-selective mortality in juvenile (Good et al. 2001; Zabel and Williams 2002) and adult (Quinn and Buck 2001) salmonids in stream environments; however, this work is the first to do so for mature lake-dwelling brook trout.

Length back-calculations obtained from otoliths indicate that fish captured at the end of the sampling period in late August and early September (post-stress) showed increases in length that were similar in both years for each age class. Differences in growth of post-stress survivors between years were significant for the age one and two cohorts, although differences were small (< 10 mm) and inconsistent. It is possible that the differences in temperature between years were not extreme enough to cause substantial differences in length of individuals captured during the post-stress period. Further, between-year differences in seasonal change in length (ΔL) of cohorts were not significant for the age two, three, or four year classes, which we expected would be most impacted by the observed high temperatures.

Additional data collections in 2007 revealed that the negative impact of temperature on growth may be mediated by decreased competition for food resources. Field measured length and weight of age two brook trout (the only age measured) increased through time even though thermal conditions within the lake were more severe and there were fewer growing degree-days in 2007 than in 2000 or 2001. Fish density in 2007 was far less than in 2000 or 2001, and only two year classes were represented in the lake (YOY and age-2). Schofield et al. (1993) demonstrated through bioenergetic analysis that brook trout in lakes with high-quality forage (e.g., fish or crayfish) would have a higher maintenance temperature than in lakes lacking large, high-energy prey items. Brook trout in systems containing high quality prey items would be able to meet the greater metabolic demands associated with high temperatures. Crayfish represented a large portion of the diet of brook trout in Rock Lake (Appendix B). Decreased competition for this food resource in 2007 may have allowed growth to occur under more severe thermal conditions compared to 2000 and 2001, when fish densities were higher.

Stomach fullness and energy density

Maximum stomach fullness was negatively correlated with water temperature at temperatures ranging from 11 - 24°C. Baldwin (1956) found that consumption and growth of yearling brook trout declined from 13 to 21°C in a laboratory setting. Pentelow (1939) showed that consumption and growth of age zero brown trout decreased at temperatures above 15.6°C. Biro et al. (2007) found that consumption by age zero rainbow trout decreased at temperatures above 17.5°C in a natural lake setting. In many species, younger fish can tolerate and grow at higher temperatures than older fish (McCauley and Huggins 1979). The observed relationship between maximum stomach fullness and temperature indicates that the amount of food consumed would be significantly reduced during periods of stressful thermal conditions. Decreased consumption in warmer years, coupled with thermal stress, supports the observed negative growth effects, poor reproductive potential, loss of energy density, and mortality in years of severe thermal stress.

Water content of fish muscle tissue provides a useful measure of lipid content and fish energy density (Hartman and Brandt 1995; Trudel et al. 2005; Peters et al. 2007), which is an important indicator of overall fish health and condition (Peters et al. 2007). During periods of favorable thermal conditions and food abundance, lipids are stored in the somatic tissues and subsequently mobilized and replaced with water during periods of thermal stress or food scarcity (Hutchings et al. 1999; Morgan et al. 2002). In 2007, the water content of brook trout muscle tissue decreased slightly during the time of optimal temperature conditions in the spring, then increased as temperatures became stressful by midsummer. Decreasing lipid content prior to spawning by brook trout may have negative effects on overall reproductive potential and overwinter survival (Hutchings 1994). Our results indicate that water content as a measure of energy density or body condition has the potential to be a useful metric in identifying the seasonal influence of varying thermal conditions upon brook trout growth and reproductive activity.

Spawning and mortality

The cumulative number of degree days exceeding 20° C was negatively correlated with fall redd count and explained a greater proportion of variation than the CPUE of mature females captured in fall trap net surveys. Although we were surprised that the density of mature females did not have a significant influence on the number of redds, female density added to the overall parsimony of a linear model after accounting for the influence of temperature. The fact that mature female density has little influence on the number of redds, by comparison with a metric accounting for the severity of summer temperature conditions, indicates that stressful summer thermal conditions can have a lasting physiological impact that precludes some (or all, under extreme conditions) mature females from spawning in the fall.

In extremely hot years (e.g., 2005) temperature-induced mortality will influence the level of spawning activity in systems without thermal refuge by reducing the number of mature individuals. Sublethal temperature conditions may influence spawning by impeding brook trout gonad development. Brook trout gonad development occurs during the summer months under favorable growth conditions, and stressful temperatures cannot be tolerated for long periods without permanent damage to gametogenesis (Hokanson 1973). For example, this suggests that the extremely warm summer conditions in 2002 prevented successful 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 poor body condition. Cooler summer 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). In 2007, the percent water content of brook trout prior to spawning (late September) was approximately 75%, and these brook trout were observed to construct redds. It is possible that in more thermally stressful years (e.g., 2002 and 2005) low brook trout energy reserves prior to spawning could have provided an indicator of an impending failure to spawn.

Extended periods of stressful 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 homogenous lake during a summer with 156 degree-days above 20°C and that in hotter years (210 degree days > 20°C) mortality of virtually all fish older than age 0 occurred. Given our 2007 observation that a similar level of mortality was not observed when the degree-day metric was 114, we believe that somewhere between 114 and 156 degree-days above 20°C is the cutoff between years in which a substantial portion of the population will survive and reproduce and when older age classes will not survive (Figure 1.3). The observed size-dependent temperature induced mortality is supported by studies that confirm the lower thermal preference of larger fish (Baldwin 1956; Coutant 1977). Future studies collecting similar data from multiple lakes and lake types will help develop degree-day thresholds relevant to spawning and mortality.

Lack of mortality of YOY brook trout in severe thermal years can be explained by the presence of thermal refuge for these smaller fish. Due to the reliance on upwelling groundwater for in-lake spawning by brook trout (Greeley 1932; Curry and Noakes 1995; Webster and Eiriksdottir 1976), lakes that support wild reproduction are likely to contain suitable summer thermal refuge for YOY brook trout. These shallow, low volume upwelling locations are used as summer thermal refuge by YOY brook trout (Biro 1998), but are unsuitable for use by larger individuals. Young-of-year can therefore survive in Rock Lake in years that are lethal to all other age classes (e.g., 2005), providing a mechanism that allows wild populations to persist in a severe thermal year in which ambient lake temperatures exceed lethal levels. However, two years of summer thermal conditions similar to those observed in 2005 could cause the total loss of this population through mortality of all fish age one and older and subsequent reproductive failure. Further, three consecutive years of thermal conditions similar to those observed in 2002 – or one year similar to 2002 followed by a year similar to 2005 – could also lead to complete population loss.

Implications

This work highlights the importance of using cumulative degree-day values rather than temperature thresholds (e.g., days exceeding 20°C) or maximum temperatures to approximate thermal stress. Previous studies have successfully relied upon temperature thresholds to assess stress in brook trout populations (Drake and Taylor 1996; Baird et al 2006; Weherly and Wang 2007). However, our results indicate that temperature thresholds and maximum temperatures can sometimes be misleading. For example, if the temperature threshold of number of days over 20°C was used, 2007 would have appeared to be a more thermally severe year than 2002 because the threshold fails to take into account the magnitude of the thermal stress in addition to the duration of stress. Additionally, the use of maximum temperatures to indicate thermal stress would indicate that 2001 and 2002 were similar thermal years. The degree-day measure takes into account both the duration and the magnitude of the thermal stress and produces a metric of thermal stress that agrees closely with observed mortality and reproductive activity. This technique may be most suitable as a metric of thermal stress in lentic systems, by comparison with streams in which daily temperature fluctuations play a large role in fish stress (Weherly and Wang 2007).

Brook trout populations are declining throughout their range as a result of many, mostly anthropogenic, factors (Huddy et al. 2005). Wild brook trout populations have inherent aesthetic, recreational and economic value to private and public stakeholders, and ideally, should support themselves with little or no interference by managers. As wild brook trout populations are lost, preserving remaining populations will become increasingly important, and management intervention may become unavoidable, especially in systems like Rock Lake that face threats to their continued persistence. Based on degree-day thresholds, adaptive stocking practices could be implemented that would mitigate the effects of temperature-induced mortality and reproductive failure on populations, helping to ensure their continued persistence.

In many cases, preservation of the population with limited anthropogenic interference may be the primary objective of stakeholders. In other instances, stakeholder groups may see angling opportunities as an important facet of the resource and may be willing to take management actions to ensure that an annual recreational fishery exists. In years during which thermal conditions cause reproductive failure through either mortality or thermal stress to reproductive individuals (e.g., 2002 and 2005), the stocking of spring or fall fingerlings (age-0) in the subsequent year would prevent the absence of a YOY year class in the population. By replacing missing year classes, it is possible to avoid a situation in which the lake lacks mature (catchable) individuals for more than one year, provided that back-to-back years of severe thermal conditions do not occur. When angling opportunities are important to stakeholders beyond simply sustaining a population, it may be necessary to stock catchable size fish in the spring following a severe thermal year to create a fishery in addition to stocking fall fingerlings or spring fry plants to replace a missing year class. Unstratified lakes such as Rock Lake can produce quality fisheries, but periods of poor performance will often follow severe thermal years. Depending on management objectives, adaptive stocking practices (e.g., stocking only when thermal conditions require such intervention) can be put into practice to prevent the total loss of this type of population while limiting the influence of management in years with suitable thermal conditions.

In Rock Lake, we observed evidence that decreased fish density may mitigate effect of high temperatures on brook trout growth by reducing competition for food resources and increasing maintenance temperature (Schofield et al. 1993). Low fish densities may also have a positive effect on the overall mortality and reproduction within the population in a hot year by increasing fish energy density going into the hot portion of the summer. Thermally marginal systems that are supported by stocking may benefit from reduced stocking densities. Further, thermally stressful systems with wild reproduction that are supplemented with stocked fish may benefit from the reduction or cessation of stocking.

Another potential management approach for ameliorating conditions in thermally stressfully systems that has proven successful in some situations is the construction of artificial thermal refugia. One potential method for accomplishing this is to use a stratified body of water in the watershed, located above the thermally stressful system in the watershed, to deliver (via a pipe) a quantity of cool water to the stressful lake during the hottest portion of the summer. This can be accomplished by means of hydrostatic pressure without the use of pumps and has proven successful in some situations (AFRP unpublished data). Hydraulic dredging has also been employed in small lake systems (< 20 ha) for a variety of management goals including increasing lake volumes for recreation (swimming, boating), increasing fish production and spawning habitat, reducing macrophytes, increasing benthic production and decreasing nutrient concentrations in the water column (Carline and Brynildson 1977; Peterson 1982). Evaluation of this technique for creating summer thermal refuge in systems such as Rock Lake could be beneficial for the management of populations in thermally stressful lakes.

In systems that are thermally marginal, it is essential to monitor summer water temperatures and to establish the extent and quality of thermal refuge habitat present in the system. Thermal data should be considered for a number of years in order to establish the range of thermal conditions that can occur within a lake. It is critical to consider the annual variation in thermal characteristics of lakes before allocating resources to management actions such as stocking programs or restoration efforts such as reclamations.

Clear evidence indicates that air temperatures are increasing both globally and regionally (Hayhoe et al. 2006, IPCC 2001). This will translate into more years in which summer thermal conditions are stressful to brook trout and other cool-water fish species. By studying ecosystems at the margins of species thermal tolerances, we can identify specific changes that can be expected to occur as global temperatures increase as well as actions that may be taken to ameliorate these changes. While not ideal, it is likely that increasingly heavy-handed management actions may be required if we desire to preserve currently intact populations of species that may be negatively affected by increasing global temperatures. Knowledge gained from studies such as this will be crucial to the conservation and management of wild brook trout populations and other species likely to be negatively impacted as global temperatures rise.

APPENDIX A

ASSESSING SUMMER THERMAL REFUGIA IN ROCK LAKE USING RADIO TELEMETRY

Brook trout research and management requires knowledge of the extent and location of available thermal refugia, especially in lakes characterized by mid-summer water temperatures that exceed those suitable for growth and survival. When summer water temperatures reach stressful levels (>20°C), adult brook trout seek out and occupy thermal refugia in deep cool water, springs, or ground-water fed tributaries to regulate their body (Schofield et al. 1993; Baird and Krueger 2003). Rock Lake is unstratified during the summer months, and no springs or tributary habitats suitable for adult fish (fish > 200mm) were known to exist. To verify this assumption, temperature-sensitive radio telemetry tags were deployed in adult brook trout in an attempt to identify the presence of thermal refugia in Rock Lake.

Methods

Five brook trout ranging in size from 301 to 385 mm were angled and tagged with Advanced Telemetry Systems® temperature- and mortality-sensitive radio transmitters (model# F1820T) on July 4, 2007. Tags were surgically implanted using apparatus and surgical methods described by Ross and Kleiner (1982) and Winter (1996). The tagged fish were tracked twice during the hottest portion of the summer on July 27 and August 17. Relative location was determined for each fish using the ATS Model: R2100 receiver and methods described by Winter (1996). Ten incoming pulses were timed five separate times to calculate the mean period (in milliseconds), which was converted to fish body temperature using regression coefficients provided for each tag by ATS (ATS Inc. Temperature Calibration Manual). Total depth and ambient bottom temperature were measured by lowering a YSI® temperature probe to the lake bottom at each tag location.

Results

Four of the five tags placed in individual brook trout were audible on the first sampling date (24 days after tagging). One of the four tags was emitting a mortality signal indicating that the fish had died. Only two tags were audible on the second sampling date (45 days after tagging), one of which transmitted a mortality signal. Based on these observations each of the located fish had moved a distance of at least 500 m from where they were returned to the lake after tagging in early July. All observed fish were found in areas with depths of approximately 5 m. Calculated fish body temperatures ranged from 21.7-22.6°C, which corresponds to ambient lake bottom temperatures at these locations that ranged from 21.6 to 21.9°C. Observed differences between tag and probe temperatures ranged from 0.0 to 1.0°C with the probe temperature always being less than or equal to tag temperatures (Table A.1).

Discussion

These results indicated that no summer thermal refugia for adult brook trout were present in the lake. All fish were located in areas with temperatures considered stressful to brook trout (Power 1980). If thermal refuges were present in the lake, it seems unlikely that brook trout would remain at locations with the temperature conditions observed. By comparison with continuous thermal monitoring records from 2007 and the measured temperature probe measurements, it appears that the radiotagged fish were located in the deepest, coolest water available in the lake. This radio-telemetry assessment provides additional evidence that no suitable summer thermal refugia for yearling and older brook trout is available in Rock Lake.

Table A.1. Summary data for brook trout radio telemetry experiment.

		7/27/2007			8/17/2007		
Tag number	Fish length(mm)	Body temp.(°C)	Bottom temp.(°C)	Depth(m)	Body temp.(°C)	Bottom temp.(°C)	Depth(m)
272	301	mortality			mortality		
724	385	22.0	21.6	5.00	22.6	21.6	5.00
914	324	no signal			no signal		
1404	317	21.7	21.7	5.00	no signal		
1654	343	22.1	21.9	4.75	no signal		

APPENDIX B

DIET COMPOSITION OF BROOK TROUT IN ROCK LAKE

Methods

All macro invertebrate diet items were counted and identified to order with the exception of *Hexegenia*, which made up 97% percent of the Ephemeroptera in the diets by number. Life stage was also noted in all cases. Zooplankton were counted and identified to the species level. When zooplankton were too numerous to count, numbers were estimated by counting all individuals in a 1 ml aliquot taken from a known volume of water containing all zooplankton in the sample and extrapolating to the entire volume. Diet items from each fish were separated into three groups: zooplankton, crayfish, and other macroinvertebrates. Each group was dried separately at 60°C until weight stabilized. Using the three diet item groups, percent composition of the diet was calculated across six fish length categories (150-200, 201-250, 251-300, 351-400, 401-450 and 451-500) on a dry weight basis. Fish outside these length categories were not included in the percent composition analysis. Percent composition was calculated for 2000, 2001 and for both years combined.

Results

Percent diet composition varied based on fish size class (Figure A.1). As fish size increases the proportion of the diet composed of zooplankton and macroinvertebrates decreases and the proportion comprised of crayfish increases. Macroinvertebrates make up a significant portion of the diet at all size classes sampled (never less than 24%), but decreased as fish size increased. Crayfish made up a small percentage of the diets of the smaller size classes (150-200: 0.0% and 201-250: 3.4%). Conversely, few zooplankton were consumed by the largest size classes of fish (301-350: 2.9%, 351-400: 0.9, 401-450: 0.0%).

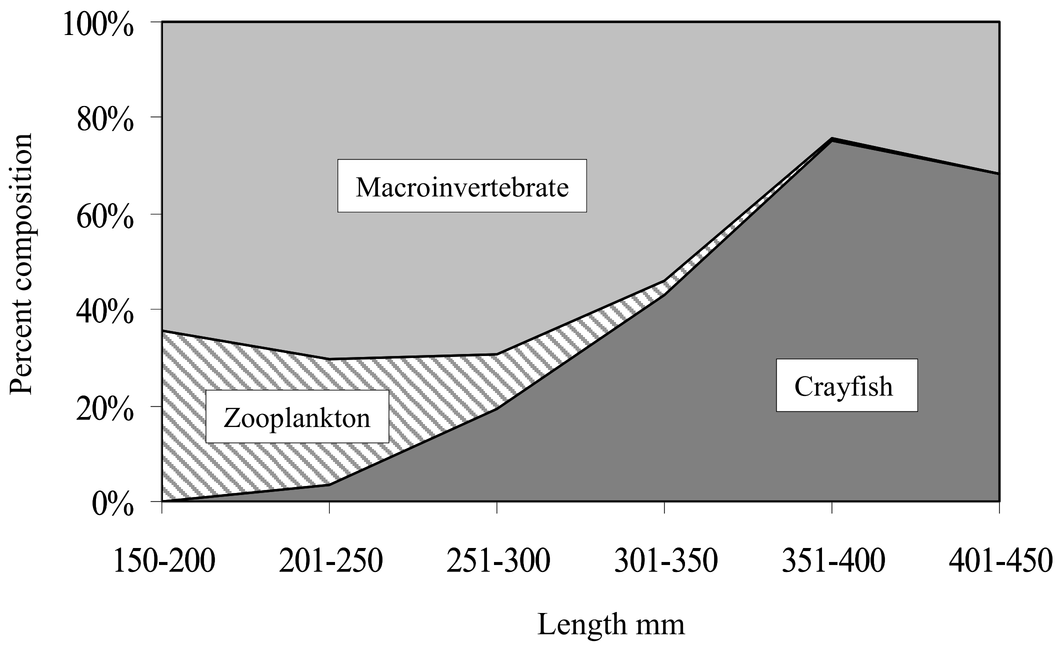

Figure A.1. Percent composition of brook trout diet items on a dry-weight basis by fish size class.

APPENDIX C

A COMPARISON OF CONDITION METRICS FOR BROOK TROUT IN ROCK LAKE

Lipids are important indicators of overall fish health and condition, but measuring lipid levels is time-consuming and expensive (Peters et al. 2007). During periods of favorable thermal conditions and food abundance lipids are stored in the somatic tissues and subsequently mobilized and replaced with water during periods of stress (e.g., unfavorable thermal conditions) or food scarcity (Hutchings et al. 1999; Morgan et al. 2002). Historically, body metrics such as Fulton's condition factor (*K*) and relative weight (W_r) have been used as relative measures of fish health and condition (Anderson and Neumann 1996). Both statistical and mechanical issues have been raised regarding the use of these traditional condition indices (Cone 1989). Furthermore, these measures of body condition have been found to have little correlation to whole fish lipid content, while water content of fish muscle tissue has been found to be strongly negatively correlated with lipid content (Trudel et al. 2005; Peters et al. 2007). To examine the relationship between water temperatures and fish condition in Rock Lake, as well as the utility of using historic length-weight data to draw conclusions regarding brook trout condition in past years, percent water content of muscle tissue was measured throughout the growing season in 2007. Additionally Fulton's K was calculated for qualitative comparison of the two methods.

Methods

See chapter one methods for description of percent water processing and calculation. Fulton's K was calculated using the equation:

$$K = \frac{W \cdot c}{L^3} \quad \text{(A1)}$$

Where *W* is weight (g), *L* is length (mm), and *c* is a constant (10^5).

Results and Discussion

Percent water content showed a slight decrease from May 10 to July 27 and then increased from July 27 to September 26 (Figure 1.12). Fulton's K showed a decreasing trend from May 10 to September 7 and then increased from September 7 to September 26 (Figure A.2). The results of condition analyses using these two metrics do not correspond. While the percent water analysis indicates that condition is increasing during the spring period, Fulton's K indicates the opposite trend. Further, Fulton's K indicates an increase in body condition during the later portion of the summer, while percent water indicates a decrease in condition during the same time period. Based on the literature (Cone 1989) and the disparate results of these two metrics and the thermal conditions observed in the lake during the study, percent water content appears to be the more appropriate measure of condition for this system and this species. In the future, percent water content should be used instead of body metrics when considering brook trout condition, and caution should be used with regards to historic condition data based on Fulton's K, since this metric may not reflect actual condition of the fish with regard to energy reserves.

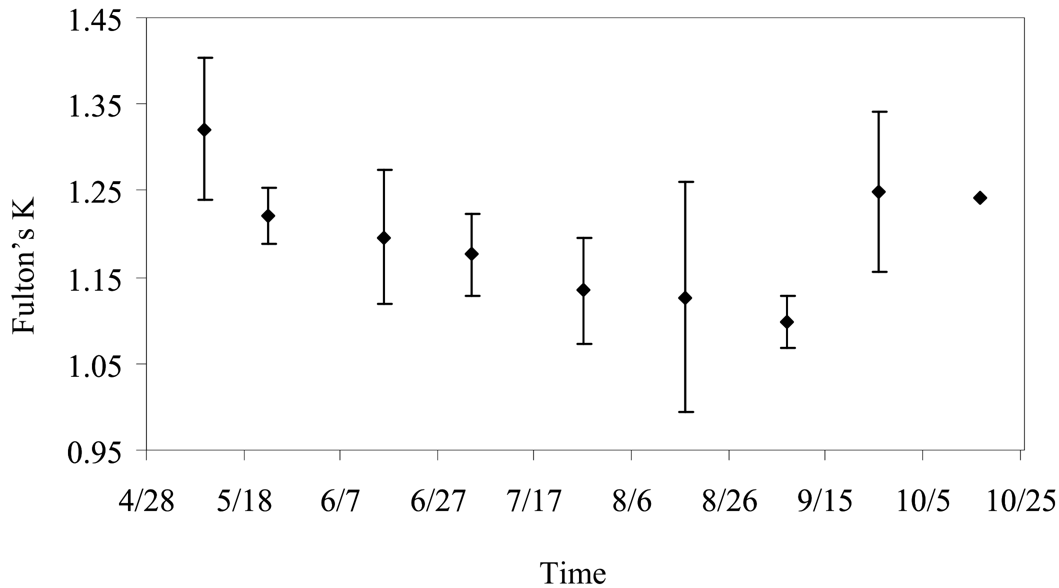

Figure A.2. Fulton's condition factor (K) through time in 2007.

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