Environmental Biology of Fishes **45**: 41–51, 1996.

Influence of spring and summer water temperature on brook charr, *Salvelinus fontinalis*, growth and age structure in the Ford River, Michigan

Melissa Treml Drake[1] & William W. Taylor
Department of Fisheries and Wildlife, 13 Natural Resources Bld., Michigan State University, East Lansing, MI 48824, U.S.A.
[1] *Current address: Minnesota Department of Natural Resources, Section of Fisheries, 1200 Warner Road, St. Paul, MN 55106, U.S.A.*

Received 27.5.1994 Accepted 27.2.1995

Key words: Thermal regime, Optimal temperature, Size, Fish, Salmonid

Synopsis

The influence of late spring and summer water temperatures on brook charr, *Salvelinus fontinalis*, growth and age structure was evaluated from 1984 to 1991 in the Ford River, Michigan. Temperature was monitored and brook charr sampled for vital statistics from late May through September using fyke nets and weirs at four locations within a 25.8 km section of stream. Scale analysis was used to determine captured brook charr age, past length at age and relative annual growth rates. Late spring and summer water temperature patterns varied between years with the greatest variability occurring in May and June. Age and size structure also varied between years and was significantly related to temperature. Years with cooler late spring and summer temperature patterns were dominated by older (age 2 and 3), larger brook charr, while years with warmer spring and summer temperature patterns were dominated by younger (age 1), smaller brook charr. Spring and summer temperature did not appear to have a significant effect on the growth of age 0 or age 1 brook charr. However, temperature was negatively related to brook charr growth from age 2 on. As spring and summer water temperatures are critical to brook charr growth and survival, it is important that a streams thermal regime be considered when establishing management goals for this species.

Introduction

Brook charr, *Salvelinus fontinalis*, are a highly regarded game fish that are generally found under conditions described as clean, pure, and aesthetically desirable (Power 1980). Typical habitat conditions are associated with a cold temperate climate, cool spring-fed ground waters, and moderate precipitation. However, because of high susceptibility to angling and thermal habitat degradation from forestry and agricultural practices, industrial water use, dams, and water pollution, brook charr distribution is shrinking (Power 1980).

Water temperature appears to be the single most important factor limiting brook charr distribution and production (McCormick et al. 1972). Brook charr are coldwater stenotherms with positive growth occurring at temperatures between 5° C and 20° C (Power 1980), and an upper lethal temperature of 25.3° C (Fry et al. 1946). Optimal brook charr growth occurs between 11° C and 16° C (Raleigh 1982) with growth rates increasing with temperature up through the optimal range and then rapidly decreasing at higher temperatures (Hokanson et al. 1972). As a result, year to year changes in thermal regime can result in significant variations in brook charr growth and survival.

While conducting a long term study on brook charr in the Upper Peninsula of Michigan, fisheries researchers observed a pronounced spring movement of brook charr (Marod et al. 1991). This movement was directed upstream and appeared to be strongly associated with increasing watet temperatures. In addition, tagging studies indicated that brook charr caught at the various study sites comprised a single population. Further, it was observed that brook charr age and size structure varied between years and these differences were suggested to be a function of spring and summer water temperatures (Marod et al. 1991). The goal of this study was to determine the relationship between spring and summer water temperature and brook charr growth in the Ford River.

Study sites, materials, and methods

The Ford River is a fourth order trout stream in northern Dickinson County, Michigan (Fig. 1). The Ford River typically had relatively high spring and low summer discharge (Marod et al. 1991). Water temperatures generally began to rise in mid-April and reached a maximum between late June to late July and remained high through August (Fig. 2). Temperatures were near 0° C from November through March (Burton et al. 1991). Four study sites on the upper Ford River were used to collect information on spring and summer water temperature and its relationship to brook charr age and growth from 1984 to 1991 (Fig. 1). The first three sites were located on the mainstream of the Ford River and the fourth site was located on Two Mile Creek, a tributary.

Fish collection

Brook charr were collected with passive gear at the four study sites from May through mid-September from 1984 to 1991. Passive gear was used to take advantage of observed spring and summer movement patterns of Ford River brook charr (Marod et al. 1991). Sites 2 and 3 were fished with 12.7 mm bar mesh fyke nets arranged in tandem across the entire width of the stream, while Sites 1 and 4 were fished using 12.7 mm bar mesh hardware cloth weirs. All gear was fished 7 days week^{-1} until the mean daily catch of brook charr fell below 1 fish day^{-1}, after which all gear was fished continuously from Monday morning through Friday evening. Nets were checked once daily. All brook charr captured were anesthetized with MS-222 at 500 mg l^{-1} of water in order to reduce handling stress (Meister & Ritizi 1958) and then measured for total length (the nearest 1 mm), weighed (nearest 0.1 g) and given a site

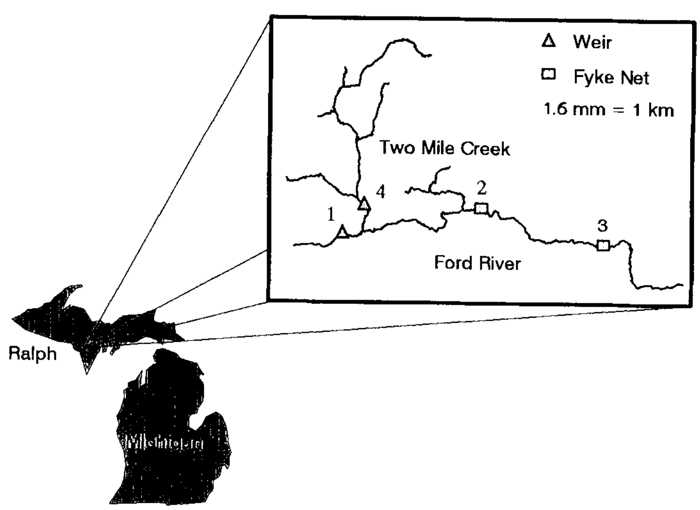

Fig. 1. Location of weir and fyke net sites in the Ford River.

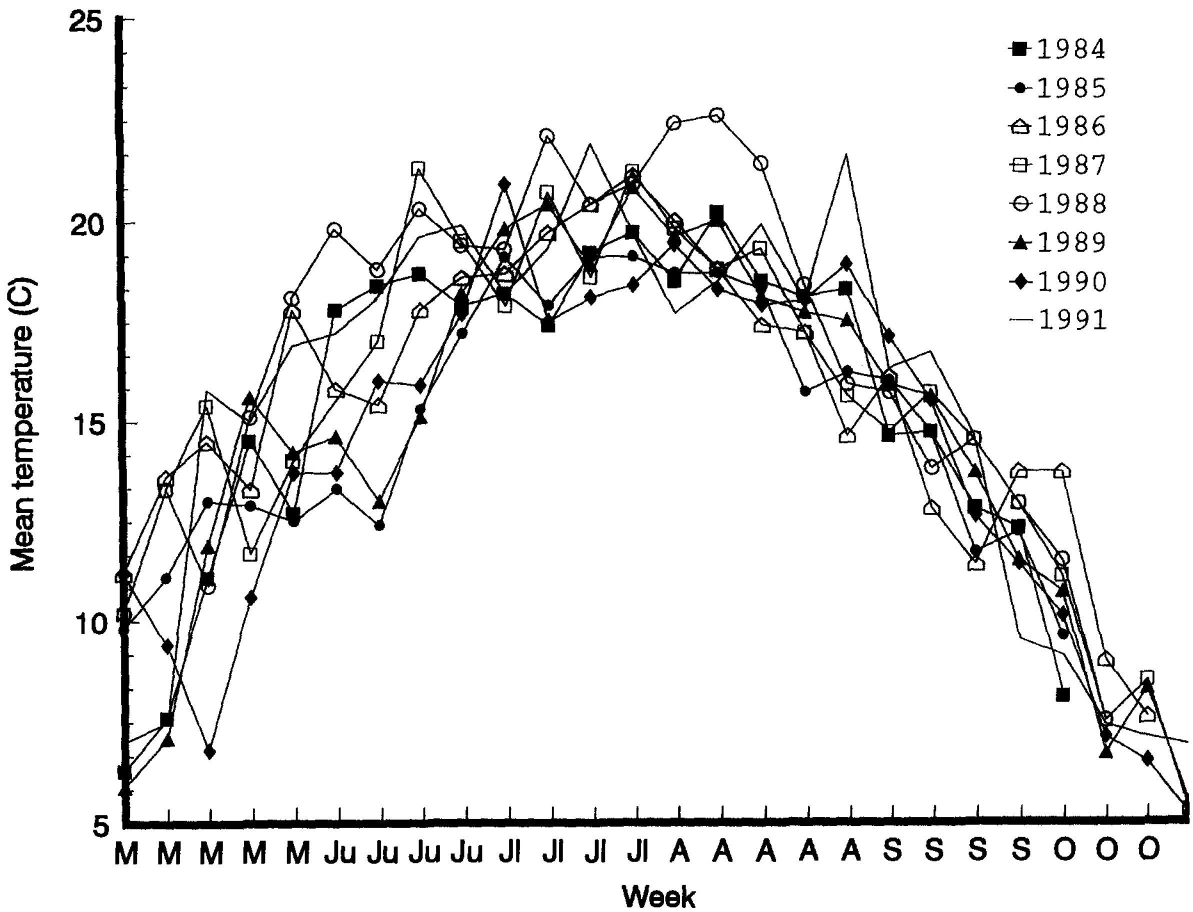

Fig. 2. Mean daily water temperature calculated on a weekly basis from 1 May to 30 September in the Ford River from 1984 to 1991.

specific fin clip. Additionally, for fish captured during May and June a scale sample was taken above the lateral line and anterior to the dorsal fin for age and growth determination. Fish were then placed in fresh water for recovery and released in their original direction of travel. Recaptured fish were again measured for length, weight, and checked for a fin clip before being released in their original direction of travel.

Age determination and growth

A random sample of brook charr was aged from each year's catch by counting annuli as described by Cooper (1951), McFadden (1959), and Van Oosten (1929). Mean lengths at capture for age classes 1, 2, and 3 were determined for each cohort. Due to small sample sizes of fish greater than age 3 ($n = 6$ for all years combined), only fish through age 3 were included in this study. Aged brook charr were used to construct an age-length key (Ricker 1975) for each year to estimate the age structure of the total annual brook charr catch.

Once aged, past lengths at age were determined by back-calculation (Carlander 1981, Bartlett et al. 1984). Due to annual temperature variability of the Ford River, a single years catch containing multiple cohorts could not be used to determine the body-scale relationship and the back-calculation equations for brook charr from different cohorts. Consequently, brook charr were separated into cohorts to minimize error in the body-scale relation. This was deemed necessary because a sample taken at one time really represents a series of year classes each of which developed under different environmental conditions (Carlander 1981). Scale data from each cohort was analyzed using methods described in Bartlett et al. (1984) and the Fraser-Lee method of back-calculation was determined valid for each cohort. The Fraser-Lee back-calculation equation is as follows:

$$l_i = a + \frac{l_c - a}{S_c} * S_i,$$

where l_i = length at age i, l_c = length at capture, s_i = scale of radius at age i, s_c = total scale radius, and a = y-intercept the regression of total length on total scale radius. Back-calculated lengths were compared to observed lengths at capture for each corresponding age class for each cohort to determine if the back-calculated lengths were reasonable. Relative growth rates were determined from the following equation (Ricker 1975):

$$\text{Growth} = \frac{l_{(t+1)} - l_{(t)}}{l_{(t)}} * 100,$$

where l_t = total length at age t, and l_{t+1} = total length at age t + 1. In addition, relative annual growth rates were only calculated from the last complete year of growth for each age class, i.e. age 1 growth was determined only from age 2 fish and age 2 growth only from age 3 fish. This method minimized uncertainty due to size selective mortality, such as Lee's phenomenon (Gutreuter 1987), which was detected in several cohorts. For determination of young of the year (YOY) relative growth rates, an average size at swim-up of 22.86 mm was assumed for all cohorts (Avery 1983). All means were tested for differences with the Kruskal-Wallis test ($p < 0.05$) and a multiple comparison test ($p < 0.05$, Miller 1981).

Temperature monitoring

Late spring and summer water temperatures were monitored (30 minute intervals) with Omnidata data pods using thermistors at sites 2 and 3 from mid-April to October (Burton et al. 1991). Temperature was monitored at site 4 using a Ryan tempmentor in 1988 (10 minute intervals), 1990 (10 minute intervals), and 1991 (30 minute intervals). Ryan tempmentors were installed from late June to mid-September in 1988 and 1991 and from early May to mid-August in 1990. In addition, Wecksler max-min thermometers calibrated daily with a laboratory thermometer were used to monitor daily maximum and minimum temperature at sites 2, 3, and 4 for all net days in all years.

The mean daily temperature was calculated for each day at sites 2, 3, and 4. At site 4, the daily maximum, minimum, and current temperature measured when the weirs were checked were averaged and presented as the mean value for years without tempmentor data. Due to the cyclic nature of the daily temperature patterns, these three points were found to adequately estimate the mean daily temperature when compared to corresponding mean daily temperatures obtained from tempmentors in 1988, 1990, and 1991. Only temperatures from 1 May through 30 September of each year were used for analyses because mean weekly temperatures were at or below the lower end of the range of optimal growth prior to 1 May and after 30 Septeber in all years of the study (Fig. 2).

Temperature and growth

Length at age and relative growth rates were compared to the following temperature conditions (Table 1): (1) the mean daily temperature between 1 May and 30 September; (2) the mean daily temperature for each month; (3) the cumulative mean daily temperature distribution; (4) the relative rate (number of days from 1 May to reach a given temperature) at which it took the water to reach a mean weekly temperature of 11° C (lower bound in range of optimal growth, Raleigh 1982), 16° C (upper bound in range of optimal growth, Raleigh 1982), and 20° C (upper bound in range of positive growth, Power 1980); (5) the number of days with a mean temperature greater than the optimal for growth (> 16° C), and the number of days with a mean temperature greater than the upper limit on positive growth (> 20° C); (6) the number of days with a mean temperature within the optimal range for growth (11° C to 16° C); (7) the number of days with a mean temperature greater than the optimal for growth but still within the positive growth range (greater than 16° C but less that 20° C); (8) the number of days with a mean temperature higher than the upper bound on positive growth (20° C). Regression analysis was used to determine the relationship between temperature and mean length at age and mean age specific relative growth rates. To enhance the power to detect differences given a low sample size we chose an alpha of 0.1 for these analyses.

The effects of temperature on growth were also analyzed using a linear model approach described by Weisberg & Frie (1987), and Weisberg (1993). This model is fit to annular scale increments similar to a two-way analysis of variance (Weisberg & Frie 1987). It divides growth in a given year into 2 major components, one due only to the age of the fish ('age effect') and the other due to environmental variation ('year effect') (Wiesberg 1993). When growth year coefficients are estimated by this model the last complete year of growth is 'aliased' and growth in all other years is assigned coefficients relative to the aliased year. For example, a positive growth year coefficient means that growth conditions in that year were more favorable relative to growth conditions in the 'aliased' year (Weisberg & Frie 1987). Temperature patterns in the Ford River were then compared to the growth year coefficients to determine if years with poor growth year coefficients corresponded to years with unfavorable temperature conditions.

Results

Temperature patterns

Two distinct temperature patterns were detected between 1984 and 1991 (Fig. 2). One pattern consisted of warm late spring temperatures followed by high temperatures throughout the summer. This pattern was seen in 1986, 1987, 1988, and 1991. The other pattern consisted of cooler late spring and early summer temperatures followed by relatively cooler temperatures throughout the remainder of the summer; 1984, 1985, 1989, and 1990 displayed this pattern.

Mean daily temperatures at sites 2, 3, and 4 were all highly correlated during the study period each year (Pearson's correlation; minimum $r = 0.758$, maximum $r = 0.999$). Because of high correlations all remaining temperature calculations were based on site 3 to avoid problems with colinearity. The mean daily temperature (Table 1) between 1 May and 30 September ranged from 15.4° C (1985 and 1990) to 17.7° C (1988). One-way analysis of variance detected significant differences between the means ($p < 0.05$). Paired t-tests (blocked by day) revealed no significant differences ($p < 0.05$) between mean daily temperature in 1984 and 1989 or between 1985 and 1990. In addition, mean daily temperature did not differ significantly between 1986, 1987, and 1991. Mean daily temperature was significantly higher in 1988 than in all other years. The Kolmogorov Smirnov test ($p < 0.05$) detected two distinct cumulative mean daily temperature distributions. Distributions for 1986, 1987, 1988, and 1991 were significantly different from 1989 and 1990 distributions; however, 1984 and 1985 distributions did not differ significantly from either group. When mean daily temperature was calculated on a monthly basis, the largest between year differences were seen in May and June (Table 2). In May the mean daily temperature ranged from 9.9° C (1990) to 14.2° C (1986) with 1984 (10.7° C), 1989 (11.6° C), and 1990 having the lowest temperatures. In June the mean daily temperature ranged from 15.3° C (1985) to 19.4° C (1988) with 1985, 1989 (15.4° C), and 1990 (16.1° C) having the lowest temperatures. During July and August the mean daily temperatures were above the optimal growth range in all years, ranging from 17.1° C (August 1986) to 21.2° C (July 1988). By September, temperatures were cooled to between 13.0° C (1984) and 14.4° C (1987) in all years.

Brook charr catch

During the sampling periods from 1984 to 1991, the total number of net days varied from 197 (1986) to 335 (1984). Average catch per net day (CPUE) was 2.44 brook charr with CPUE ranging from 1.28 (1989) to 3.54 (1984) (Table 3). The number of brook charr caught varied between sites and be-

Table 1. The mean daily temperature in the Ford River between 1 May and 30 September for each year, the relative rate at which temperatures warmed[1], and the number of days within the temperature range of optimal growth[4], poor growth[2,5], and no growth[3] for each year.

	Year							
	1984	1985	1986	1987	1988	1989	1990	1991
Mean daily temperature	15.9	15.4	16.4	16.7	17.7	15.8	15.4	16.8
Days to 11° C[1]	14	7	-5	5	2	13	-9	10
Days to 16° C[1]	32	53	27	39	27	50	42	23
Days to 20° C[1]	97	153	78	45	29	63	58	75
Days > 16° C[2]	80	55	69	67	81	66	67	90
Days > 20° C[3]	13	6	20	28	48	20	11	21
Days between 11° C & 16° C[4]	18	46	27	34	25	37	42	13
Days between 16° C & 20° C[5]	65	100	51	6	2	13	16	52

tween years. Over 90% of the brook charr caught in all years were moving in the upstream direction (Marod et al. 1991), with peak movement times coinciding with mean daily temperatures exceeding the upper end of the optimal growth range (16° C).

Age structure

Length-frequency distribution and age length key of the total annual brook charr catch for each year indicated that age-specific growth rates differed between years. In addition, percent composition by age varied between years (Table 3). One year olds comprised the majority of the annual catch in 1986, 1987, 1988, and 1990 while two year old brook charr dominated in 1984, 1985, 1989, and 1991. Three year old brook charr also comprised a major portion of the 1989 catch. A strong year class produced in 1989 dominated the 1990 and 1991 catch.

Growth

Mean annual relative growth rates (Table 4) for YOY brook charr averaged 390%, ranging from 290% (1987 cohort) to 420% (1983 cohort). The mean length of brook charr at age 1 averaged 111.5 mm and ranged from 89.2 mm (1987 cohort) to 119.2 mm (1983 cohort). Although there were significant yearly differences between the mean length at age and mean age-specific relative growth rate, none were significantly related to any of the evaluated temperature variables.

The mean annual relative growth rate (Table 4) of yearling brook charr averaged 58% and ranged from 45% (1986 cohort) to 72% (1987 cohort). No significant relationships were detected between yearling relative growth rates and temperature.

Brook charr mean length at age 2 averaged 184.2 mm and ranged from 161.2 mm (1986 cohort) to 202.4 mm (1984 cohort) (Table 4). A significant negative relationship ($p = 0.041$, $R^2 = 0.600$, d.f. =

Table 2. The mean monthly water temperatures in the Ford River from 1 May through 30 September from 1984 to 1991.

	Year								
	1984	1985	1986	1987	1988	1989	1990	1991	Mean
May	10.7	12.1	14.2	13.3	14.1	11.6	9.9	13.0	12.4
June	18.1	15.3	17.1	18.3	19.4	15.4	16.1	18.8	17.3
July	18.7	18.8	20.1	19.7	21.2	20.0	18.7	19.4	19.6
August	18.7	17.3	17.1	17.8	19.7	18.4	18.3	19.4	18.3
September	13.0	13.2	13.5	14.4	14.0	13.8	13.7	13.5	13.6

Table 3. Catch per net day (CPUE) and the percent age composition of brook charr of age classes 1, 2, and 3 in the total annual catch from 1984 to 1991 in the Ford River.

Year	CPUE	% age 1	% age 2	% age 3
1984	3.54	33	59	8
1985	2.88	41	47	6
1986	1.61	67	30	3
1987	3.35	65	29	5
1988	1.53	60	26	[a]
1989	1.28	30	39	31
1990	1.51	77	14	8
1991	3.46	37	57	6

[a] No age 3 brook charr were found in the scale samples, the remaining 14% of the total annual catch is age 2 or greater.

1,5) existed between length at age 2 and the mean daily temperature between 1 May and 30 September during the second growing season (Fig. 3a). Years with a higher mean temperature produced smaller 2 year olds. In addition, length at age was also inversely related to the number of days with a mean temperature greater than 20° C during the second summer of life ($p = 0.073$, $R^2 = 0.510$, d.f. = 1,5). As the number of days greater than 20° C increased the mean length of brook charr at age 2 decreased. Significant negative relationships also existed between length at age 2 and mean temperature in May ($p = 0.026$, $R^2 = 0.664$, d.f. = 1,5) and mean daily temperature for May and June combined ($p = 0.036$, $R^2 = 0.617$, d.f. = 1,5).

The mean annual relative growth rate for all age 2 brook charr (Table 4) was 34% and ranged from 26% (1984 cohort) to 50% (1987 cohort). Brook charr growth rates during the third summer of life were significantly positively related ($p = 0.047$, $R^2 = 0.780$, d.f. = 1,3), to the relative number of days it took water temperatures to reach a mean weekly temperature of 11° C (Fig. 3b). The slower water temperatures rose the higher the relative annual growth rate of age 2 brook charr.

The mean back-calculated length at age 3 (Tasble 4) for Ford River brook charr averaged 246.4 mm and varied from between 217.7 mm (1984 cohort) to 288.1 mm (1988 cohort). Three year olds from the 1988 cohort were significantly larger than all other cohorts. Two significant relationships were detected between length at age 3 and temperature during the third growing season. Mean length at age 3 was negatively related to mean temperature in May ($p = 0.037$, $R^2 = 0.810$, d.f. = 1,3) (Fig. 3c) and mean temperature in May and June combined ($p = 0.045$, $R^2 = 0.787$, d.f. = 1,3). Years that averaged cooler temperatures in May and June had larger fish than years with warmer May and June temperatures.

Growth model

When age 1, 2, and 3 brook charr were analyzed together using Weisberg's linear growth models (1993), analysis of variance of the scale increment model revealed a significant age by year interaction ($p < 0.05$). This suggested that growth conditions present in a given year did not affect different aged

Table 4. Average back-calculated length at age LN (mm), average age-specific relative growth rate GR (%), and sample size N for Ford River brook charr for each cohort from 1984 to 1991 (standard deviation given in parentheses).

Cohort	Age 1			Age 2			Age 3		
	LN	GR	N	LN	GR	N	LN	GR	N
1983	119.2 (16.4)	420 (76)	9	201.1 (24.3)	65 (15)	19	239.3 (14.1)	38 (5.3)	6
1984	115.1 (15.2)	404 (68)	20	202.4 (25.5)	61 (15)	43	217.7 (27.8)	26 (8.4)	14
1985	110.5 (16.2)	383 (71)	69	169.0 (22.8)	54 (14)	83	[a]		
1986	117.0 (13.7)	412 (60)	174	161.2 (19.3)	45 (14)	8	238.5 (26.1)	29 (10.8)	50
1987	89.2 (11.8)	290 (52)	56	172.8 (29.6)	72 (18)	34	248.2 (49.4)	50 (13.8)	20
1988	115.9 (9.9)	407 (47)	7	184.7 (20.7)	55 (16)	21	288.1 (27.8)	29 (9.4)	22
1989	106.7 (13.2)	367 (58)	78	198.5 (22.6)	57 (13)	183			
1990	118.7 (16.5)	419 (72)	114						

[a] Data not available.

fish in the same manner. Evaluation of this interaction by age group revealed that age 1 brook charr were responsible for the age by year interaction. This was supported by the fact that no significant relationships were detected between temperature and first year growth, while significant negative relationships were detected between temperature and age 2 and 3 brook charr growth. Removing age 1 fish resulted in an insignificant age by year interaction ($p < 0.05$), indicating yearly growth conditions affected age 2 and 3 brook charr in a similar manner.

Comparing growth year coefficients for age 2 and 3 brook charr combined (Table 5), it appears that 1986, 1987, and 1988 had poor growth conditions ('year effects') relative to 1990 and that 1982, 1983, 1984, 1985, and 1989 had conditions similar to 1990. Furthermore, partitioning the growth year coefficients for each age separately showed that while age 2 and 3 fish were generally effected by environmental conditions ('year effects') in the same manner, they were not affected to the same degree. Growth conditions in 1990 appeared to be more favorable for 2 year olds than 3 year olds. When a temperature index (difference between mean temperature in 1990 and the other growth years) was compared to growth year coefficients an inverse relationship was detected between temperature and growth. Years with relatively poor growth conditions corresponded to years with relatively higher mean daily temperatures for both age 2 and age 3 brook charr.

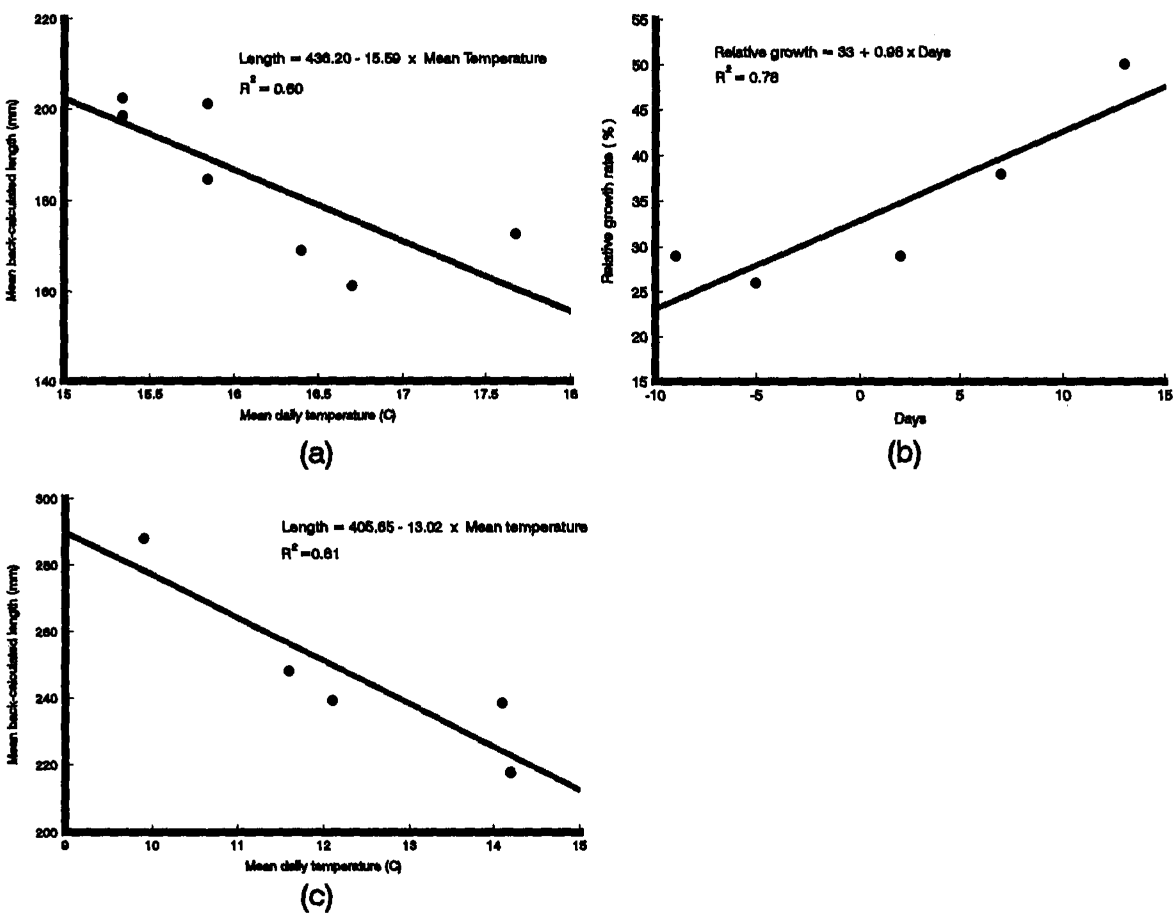

Fig. 3. Relationships between brook charr growth and temperature in the Ford River from 1984 to 1991: a – mean length at age 2 and mean daily temperature from 1 May to 30 September, b – age 2 relative growth rate and the number of days to reach a mean weekly temperature of 11° C, c – mean length at age 3 and the mean daily temperature in May.

Table 5. Growth year coefficient estimates for ages 2 and 3 combined, age 2, and age 3 Ford River brook charr sampled from 1984 to 1991, and the annual temperature index for 1 May through 30 September from 1984 to 1991.

Growth year	Age 2 and 3 combined	Age 2	Age 3	Temperature index
1982	– 0.0176	– 0.0201	[a]	[a]
1983	– 0.0024	– 0.0055	0.0278	[a]
1984	– 0.0111	– 0.0132	0.0048	0.5
1985	– 0.0171	– 0.0199	0.0055	0.0
1986	– 0.0536	– 0.0572	– 0.0278	1.0
1987	– 0.0501	– 0.0526	[a]	1.3
1988	– 0.0408	– 0.0474	– 0.0166	2.3
1989	– 0.0066	– 0.0116	0.0186	0.4
1990	aliased	aliased	aliased	aliased

[a] Data not available.

Temperature conditions for 1982 and 1983 were not available.

Discussion

The preferred temperature of brook charr is an integrated optimum of all metabolic processes (Kelch & Neill 1990). Because fish are poikilothermal the amount of energy required to maintain basal metabolism is determined by the temperature of their environment. As temperature increased more energy is required for basal metabolic processes resulting in less energy for growth (Coutant 1987, Magnuson et al. 1979, Kelch & Neill 1990, Schofield et al. 1993). However, at temperatures below optimum increased temperature can result in increased growth rates if the energy gain from increased feeding activity is greater than the increase in basal metabolism (Baldwin 1956). Furthermore, above optimum temperatures have a greater negative impact on the growth of older, larger fish which metabolize less efficiently than younger, smaller fish (Schofield et al. 1993).

Brook charr age and size structure in the Ford River appeared to be related to late spring and summer water temperatures from 1984 to 1991. High temperature could affect age and size structure through increased mortality of older and larger brook charr due to limited thermal refuges (Meisner 1990, Power 1980). High late summer temperatures (> 19° C) could also affect population structure and abundance by impairing sexual maturation and reducing reproductive success (Hokanson et al. 1973). In addition, even though most brook charr are mature by the end of their second year, changes in the abundance of older/larger brook charr could decrease total reproductive success due to lower fecundity of smaller brook charr (McFadden et al. 1967).

However, even in years that were considered cool very few fish survived past age 2. Consequently, some other factor must be affecting mortality of older age fish. Fishing is a likely source of mortality as almost all age 2 Ford River brook charr are of legal size (178 mm) and many anglers fish for brook charr in the Ford River (Marod et al. 1991). High exploitation rates have long been known to alter the size and age structure of brook charr populations (Cooper 1952, Clark et al. 1981) with unexploited streams containing more older (> 3 years old) brook charr than exploited streams (Cooper 1967). Furthermore, selective removal of larger/faster growing brook charr by fishing could dampen the observed effects of temperature on growth. For example, a portion of a brook charr cohort will grow faster and larger than other members of the same cohort. However, these same fish will probably be removed from the population at a higher rate than slower growing fish of the same cohort. As a result, in years with favorable growth conditions the magnitude of the effect of temperature on growth might not be realized if only the slower growing members of a cohort remain to estimate growth.

No relationships were found between temperature and YOY and yearling growth rates or length at age 1. This agrees with Schofield et al. (1993) who found that YOY brook charr were not limited by high summer temperatures. However, according to McCormick et al. (1972) juvenile brook charr (YOY) under laboratory conditions were more thermally sensitive than older charr. Perhaps high summer temperatures do not have a strong influence on YOY and yearling brook charr growth under field conditions because they are able to find suitable microhabitats to shelter themselves from otherwise unsuitable temperature conditions (Power 1980, Elliot 1990). Some microhabitats such as groundwater fed springs were known to exist in the Ford River. Alternatively, YOY and yearling brook charr might be able to compensate for increased basal energy needs through increased foraging, whereas larger metabolically less efficient brook charr might not be able to compensate as well (Baldwin 1956, Schofield et al. 1993). However, the effects of temperature on YOY could have been masked by size selective overwinter mortality resulting in survival of only the larger YOY (Hunt 1969).

By age 2, high summer water temperatures appeared to have a detrimental effect on brook charr growth. Our results suggest that for age 2 and older brook charr to prosper, temperatures must remain relatively cool throughout the late spring and early summer. This agrees with the late spring and early summer temperature patterns of Michigan streams that are considered 'good' brook charr streams (Cooper 1953). In addition, brook charr in these 'good' streams experienced tremendous increases in growth in the late spring and early summer, which were believed to be related to the seasonal availability of aquatic and terrestrial invertebrates in the drift due to spring run-off and increased flow (Whitworth & Strange 1983, Power 1980, Cooper 1953).

The relationship between late spring and early summer temperatures and seasonal food supply could be a critical factor controlling brook charr growth. Brook charr feed heavily on aquatic and terrestrial invertebrates during spring run-off with stomach volumes being the greatest in early summer and then declining throughout the rest of the summer (Power 1980). Aquatic insect studies in the Ford River from 1984 to 1991 revealed that the amount of drift (aquatic insects) in the water was highest and most variable in the spring (April and May), with insect mass in 1986 and 1987 significantly higher than other study years (Stout 1991). Insect mass in the summer (June, July, and August) in the Ford River did not differ significantly between years or sites (Stout 1991). Consequently, it is unlikely that the observed differences in brook charr annual growth were caused by differences in food availability. Furthermore, it is probable that the differences in growth were due to the effects of temperature on brook charr basal metabolism resulting in higher maintenance costs and less available energy for growth in warmer years.

From a management point of view, this study stresses the influence of natural temperature variation on brook charr growth. This is especially true of marginal brook charr streams such as the Ford River, where thermal refugia are limited. Consequently, when considering management goals and evaluating management practices it is important to consider the thermal regime of a stream and how changes in thermal regime could impact study results. Furthermore, the influence of temperature on growth highlights the need to protect the thermal integrity of streams. Careful consideration should be given to any proposed actions that could change the thermal regime of a stream because even minor changes could significantly impact brook charr prosperity.

Acknowledgements

We thank all of those who helped collect the data used in this study, especially Steven Marod. This research was supported by IIT Research Institute, under its prime contract with the Space and Naval Warfare Systems Command (SPAWAR) of the U.S. Navy.

References cited

Avery, E.L. 1983. Population dynamics of wild trout and associated sports fisheries in two northern Wisconsin streams. Wisconsin Department of Natural Resources, Tech. Bull. 141. 31 pp.

Baldwin, N.S. 1956. Food consumption and growth of brook trout at different temperatures. Trans Amer. Fish. Soc. 86: 323–328.

Bartlett, J.R., P.F. Randerson, R. Williams & D.M. Ellis. 1984. The use of analysis of covariance in the back-calculation of growth in fish. J. Fish Biol. 24: 201–213.

Burton, T.M., D. Repert & S. Eggert. 1991. Element 1: ambient monitoring program. pp. 20–71. *In:* ELF Communications System Ecological Monitoring Program Annual Report for Aquatic Ecosystems: Tasks 5.8, 5.9, 5.10, National Technical Information Service, U.S. Department of Commerce, Springfield.

Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6(1): 2–4.

Clark, R.D., G.R. Alexander & H. Gowing. 1981. A history and evaluation of regulations for brook trout and brown trout in Michigan streams. N. Amer. J. Fish. Manage. 1: 1–14.

Cooper, E.L. 1951. Validation of the use of scales of brook trout, (*Salvelinus fontinalis*), for age determination. Copeia 1951: 141–148.

Cooper, E.L. 1952. Rate of exploitation of wild eastern brook trout and brown trout populations in the Pigeon River, Otsego County, Michigan. Trans. Amer. Fish. Soc. 81: 224–234.

Cooper, E.L. 1953. Periodicity of growth and change in condition of brook trout, *Salvelinus fontinalis,* in three Michigan trout streams. Copeia 1953: 107–114.

Cooper, E.L. 1967. Growth and longevity of brook trout (*Salvelinus fontinalis*) in populations subjected to light exploitation. Trans. Amer. Fish. Soc. 96: 383–386.

Coutant, C.C. 1987. Thermal preference: when does an asset become a liability? Env. Biol. Fish. 18: 161–172.

Elliot, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta.* III. the role of territorial behavior. J. Anim. Ecol. 59: 803–818.

Fry, F.E.J., J.S. Hart & K.F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis.* Publ. Ont. Fish. Res. Lab. 54: 9–35.

Gutreuter, S. 1987. Considerations for estimation and interpretation of annual growth rates. pp. 115–126. *In:* R.C. Summerfelt & G.E. Hall (ed.) The Age and Growth of Fish, Iowa State University Press, Ames.

Hokanson, K.E.F., J.H. McCormick, B.R. Jones & J.H. Tucker. 1973. Thermal requirements for maturation, spawning, and embryo survival of brook trout, *Salvelinus fontinalis.* J. Fish. Res. Board Can. 30: 975–984.

Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. J. Fish. Res. Board Can. 26: 1473–1483.

Kelch, S.W. & W.H. Neill. 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optimum. Trans. Amer. Fish. Soc. 119: 601–610.

Marod, S., M. Treml, S. Winterstein, B. Kelley & W.W. Taylor. 1991. Element 8: brook trout movement. pp. 286–334. *In:* ELF Communications System Ecological Monitoring Program Annual Report for Aquatic Ecosystems: Tasks 5.8, 5.9, 5.10, National Technical Information Service, U.S. Department of Commerce, Springfield.

Magnuson, J.J., L.B. Crowder & P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19: 331–343.

McCormick, J.M., K.E.F. Hokanson & B.R. Jones. 1972. Effects of temperature on growth and survival of young brook trout, *Salvelinus fontinalis.* J. Fish. Res. Board Can. 29: 1107–1112.

McFadden, J.T., G.R. Alexander & D.S. Shetter. 1967. Numerical changes and population regulation in brook trout *Salvelinus fontinalis.* J. Fish. Res. Board Can. 24: 1425–1459.

McFadden, J.T. 1959. Relationship of size and age to time of annulus formation in brook trout. Trans. Amer. Fish. Soc. 88: 176–177.

Meisner, D.J. 1990. Potential loss of thermal habitat for brook trout due to climatic warming, in two southern Ontario streams. Trans. Amer. Fish. Soc. 119: 282–291.

Meister, A.L. & C.F. Ritizi. 1958. Effects of chloretone and M.S. 222 on eastern brook trout. Prog. Fish Cult. 20: 104–110.

Miller, R.G. Jr. 1981. Simultaneous statistical inference, 2nd edition. Springer-Verlag, Heidelberg. 299 pp.

Power, G. 1980. The brook charr, *Salvelinus fontinalis.* pp. 141–203. *In:* E.K. Balon (ed.) Charrs: Salmonid Fishes of the Genus *Salvelinus,* Dr W. Junk Publishers, The Hague.

Raleigh, R.F. 1982. Habitat suitability index models: brook trout. U.S. Dept. Int., Fish, Wildl. Serv. FWS/OBS-82/10.24. 42 pp.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. J. Fish. Res. Board Can. Bull. No. 191. 382 pp.

Schofield, C.L., D. Josephson, C. Keleher & S.P. Gloss. 1993. Thermal stratification of dilute lakes – an evaluation of regulatory processes and biological effects before and after base addition: effects on brook trout habitat and growth. U.S. Fish and Wildlife Service, Biological Report NEC-93/9. 36 pp.

Stout, R.J. 1991. Element 4: insect species richness and biomass studies. pp. 141–205. *In:* ELF Communications System Ecological Monitoring Program Annual Report for Aquatic Ecosystems: Tasks 5.8, 5.9, 5.10, National Technical Information Service, U.S. Department of Commerce, Springfield.

Van Oosten, J. 1929. Life history of the lake herring of Lake Huron as revealed by its scales with a critique of the scale method. U.S. Bureau Fish. Bull. 44: 265–428.

Weisberg, S. 1993. Using hard-part data to estimate age and environmental effects. Can. J. Fish. Aquat. Sci. 50: 1229–1237.

Weisberg, S. & R. Frie. 1987. Linear models for the growth of fish. pp. 127–144. *In:* R.C. Summerfelt & G.E. Hall (ed.) The Age and Growth of Fish, Iowa State University Press, Ames.

Whitworth, W.E. & R.J. Strange. 1983. Growth and production of sympatric brook trout and rainbow trout in an Appalachian stream. Trans. Amer. Fish. Soc. 112: 469–475.