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An Evaluation of the Influence of Temperature on the Growth of Brook Trout in the Ford River, Dickinson County, Michigan from 1984 to 1991

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AN EVALUATION OF THE INFLUENCE OF TEMPERATURE ON THE GROWTH OF BROOK TROUT IN THE FORD RIVER, DICKINSON COUNTY, MICHIGAN FROM 1984 TO 1991

BY

MELISSA KAY TREML

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ABSTRACT

AN EVALUATION OF THE INFLUENCE OF TEMPERATURE ON THE GROWTH OF BROOK TROUT IN THE FORD RIVER, DICKINSON COUNTY, MICHIGAN FROM 1984 TO 1991

By

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The influence of late spring and summer water temperatures on brook trout growth and age structure was evaluated from 1984 to 1991 in the Ford River, Dickinson County, Michigan. Brook trout were sampled from late May through September using fyke nets and weirs at four locations within a 25.8 river km section of stream. Scale analysis was used to determine age, to estimate past length at age, and to estimate relative annual growth rates. Late spring and summer temperature patterns varied between years. Most variability occurred in May and June. Age and size structure also varied between years and was related to yearly temperature differences. Years with temperatures near 16 C in mid June were dominated by older, larger brook trout, while years already above 16 C by mid June were dominated by younger, smaller brook trout. Temperature had a significant negative affect on brook trout growth from age 2 on. Growth rates were negatively related to the number of days which had temperatures greater than 20 C and to the rate at which the water warmed. Consequently, trout stream managers must consider the thermal regime of a stream when setting management goals.

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My deepest appreciation goes to my parents (Bob and Joanne), and sister (Chris) who have always stood beside me and encouraged me to reach for my goals, regardless of what they might be.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Brook trout are highly regarded game fish and are a favorite among anglers in the eastern United States and Canada (Power 1980). Their range extends from Northern Quebec to Georgia with the northern portion of the range stretching from the Atlantic Ocean to Manitoba and the southern portion of the range confined to the Appalachian ridge (Scott and Crossman 1985, Meisner 1990). They are endemic to North America and are found under conditions which are generally described as clean, pure, and aesthetically desirable (Scott and Crossman 1985, Power 1980). Typical brook trout habitat conditions are those associated with a cold temperate climate, cool spring-fed ground waters, and moderate precipitation (Raleigh 1982).

The rate of growth and maximum size of brook trout varies significantly throughout the native range, depending on local habitat conditions (Scott and Crossman 1985). Brook trout have a greater cold water tolerance than other trout with positive growth occurring at temperatures between 5 C and 20 C (Powers 1980) and with the upper lethal temperature being 25.3 C (Fry et. al. 1946). Brook trout growth tends to be optimal between 11 C to 16 C with temperatures warmer or colder reducing growth (Raleigh 1982). Consequently, marked seasonal changes in brook trout growth rates coincide with seasonal changes in water temperature (McFadden et. al. 1967) with growth rates increasing with temperature and reaching a maximum at 16 C and then progressively decreasing at higher temperatures (Hokanson et. al. 1973).

In Michigan most brook trout growth occurs from March to June with little growth occurring from July through September with the exception of age 0 brook trout who have been noted to grow throughout their first winter (Cooper 1953). In northern Michigan, brook trout are generally slow growing (average 3 year old is approximately 201 mm long) when compared to other stream populations reported in Carlander (1969) and relatively short lived with few fish surviving past their third year (McFadden 1961, Wydoski and Cooper 1966, Cooper 1967). The short life span is most likely a function of high natural mortality and/or exploitation rates from age 2 (150 mm) on (McFadden 1961, Wydoski and Cooper 1966, Flick and Webster 1975, Cooper 1967).

Annual growth rates and the length of the growing season have been found to be positively related (Gerking 1966). The growing season of a fish is defined as the period of time where the water temperature remains within the range where positive growth can occur, for brook trout this range is between 5 C and 20 C (Powers 1980). Gerking (1966) reports that populations with rapid growth rates had longer growing seasons than those with slower growth rates. Consequently, it is important to take into account the length of the growing season when comparing annual growth rates of different fish populations (Conover 1990). In addition, since growing season is a function of temperature, temperature variations must also be considered when examining annual growth rates of a single population.

The purpose of this study was to determine the growth patterns of brook trout in the upper Ford River from 1984-1991 and to determine its relationship with growing season and summer water temperatures. This was accomplished by: (1) determining the age and size structure of brook trout in the upper Ford River, (2) determining the annual growth rate for each age class from each cohort of brook trout in the upper Ford River, (3) examining the temperature patterns of the upper Ford River during late spring and summer from 1984-1991, and (4) evaluating the relationship between late spring and summer water temperatures and the annual growth rates of brook trout in the Upper Ford River.

DESCRIPTION OF STUDY SITES

The Ford River is a fourth order stream in northern Dickinson County, Michigan. Its source is near Sagola in the northwestern corner of Dickinson County. Two Mile Creek is a tributary flowing from southern Marquette County into the Ford River from the north. The Ford River flows into northern Green Bay south of Escanaba, Michigan. The Ford River is classified as a blue ribbon trout stream because of its domination by wild brook trout, stream size and depth, diverse insect life and fly hatches, pure water conditions, and reputation for quality trout fishing (Fisheries Division, Michigan Department of Natural Resources).

Four study sites on the upper Ford River were used to collect information on brook trout age and growth from 1984-1991 (Figure 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. Site 3, the downstream site, was approximately 1.62 river km upstream of Ralph, Michigan. Site 2 was approximately 14.7 river km upstream of site 3. Site 1 was 11.1 km upstream of site 2. Site 4 was located on Two Mile Creek, approximately 11.5 km upstream of site 2. The Ford River typically has high spring discharge and low summer discharge (Figure 2). Temperatures rise during the spring and reach a high anywhere from late June to late July and remain high through August (Figure 3). The downstream region of the study section is characterized by a sandy bottom. The upstream region of the study section of river has areas with substrate ranging from pebbles to large rocks, intermitted

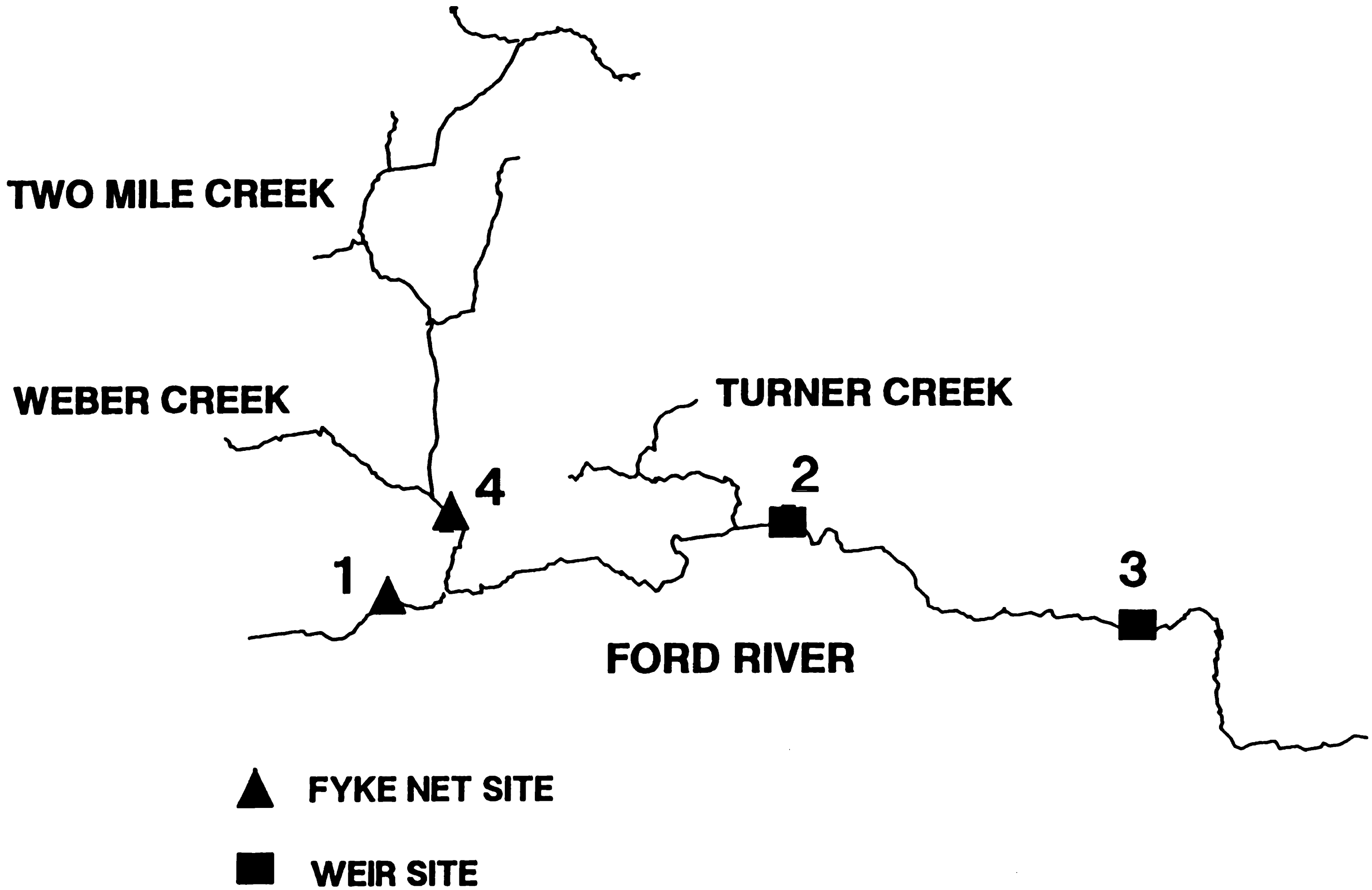

Figure 1. Location of fyke nets and weirs in the study section of the Ford River and Two Mile Creek.

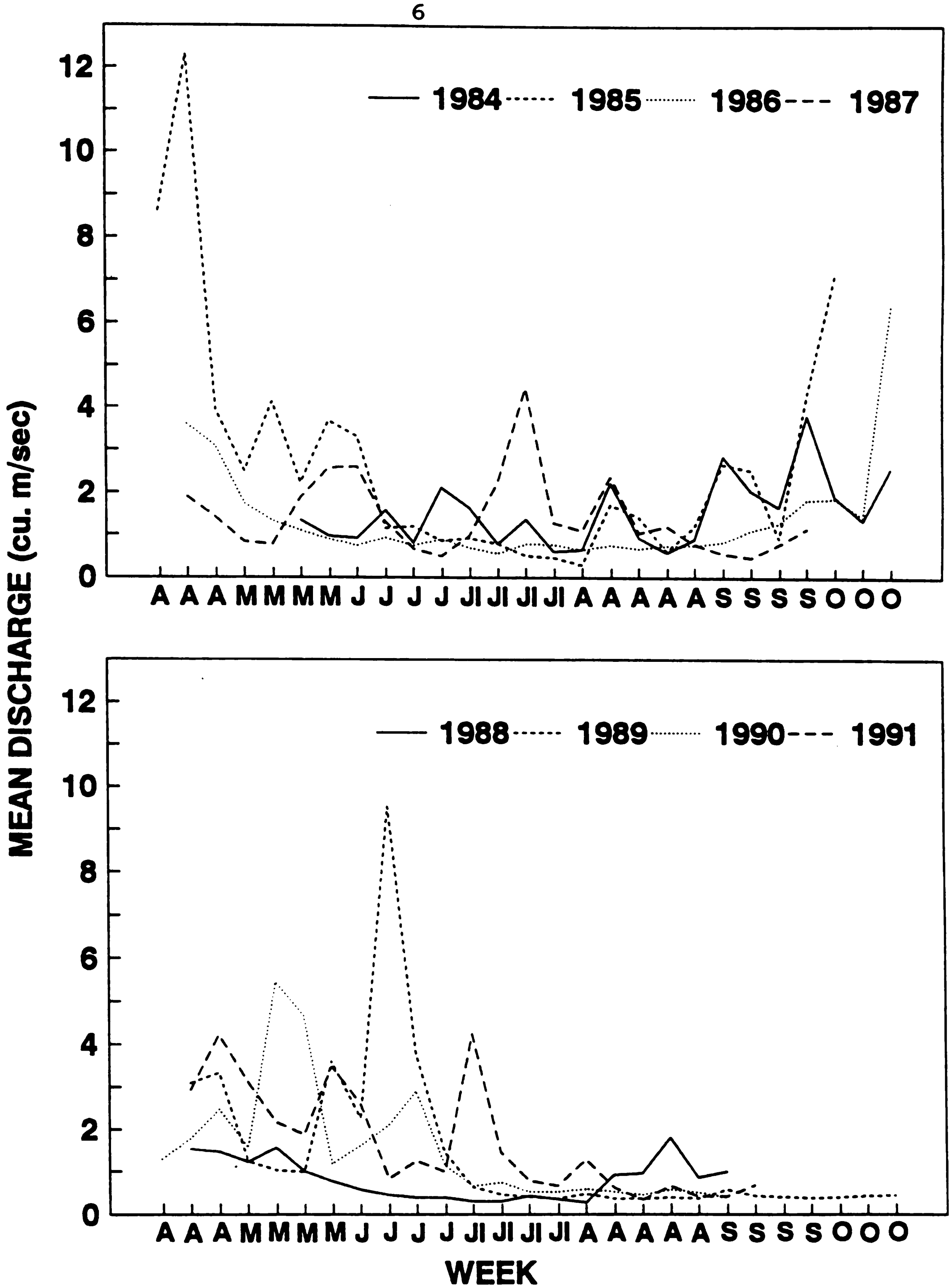

Figure 2. Mean daily discharge for late spring and summer at site 3 calculated on a weekly basis from 1984 to 1991.

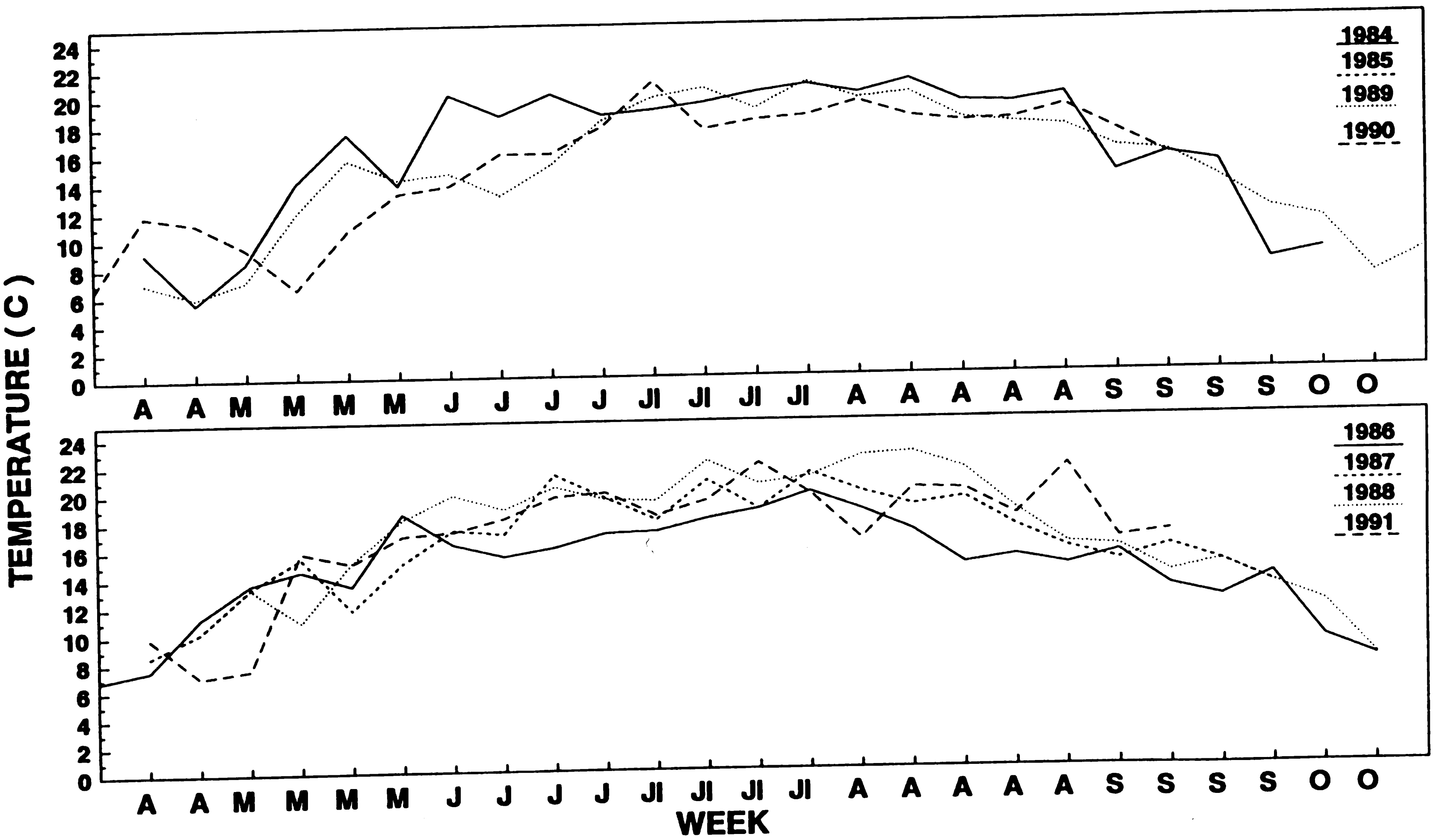

Figure 3. Mean daily temperature for late spring and summer at site 3 presented as a weekly average from 1984 to 1991.

with regions of sand.

METHODS

Fish Collection

Brook trout were generally collected with passive gear at the four study sites from at least mid-May to mid-September from 1984 to 1991. Passive gear was used to take advantage of the movement patterns of Ford River brook trout noted by other researchers (Marod and Taylor 1991). Sites 2 and 3 were fished with 1/2 inch bar mesh fyke nets arranged in tandem with one net facing upstream and one net facing downstream (Figure 4). Sites 1 and 4 were fished with 1/2 inch bar mesh hardware cloth weirs arranged in tandem. All gear was fished 7 days/week until the mean daily catch of brook trout fell below 1 fish/day, after which all gear was fished continuously from Monday morning through Friday evening. Nets were checked once daily. All wild brook trout captured were anesthetized with MS-222 at a 500 mg/l of water dosage in order to reduce handling stress (Meister and Ritizi 1958 and Schoettger and Julin 1967). Fish were then measured for total length (nearest 1 mm), weighed on a calibrated Ohaus Port-o-Gram scale (nearest 0.1 gram), and given a site specific fin clip. Additionally, in May and June a scale sample was taken above the lateral line and anterior to the dorsal fin for age and growth determination. After recovery in fresh water, all fish were released in

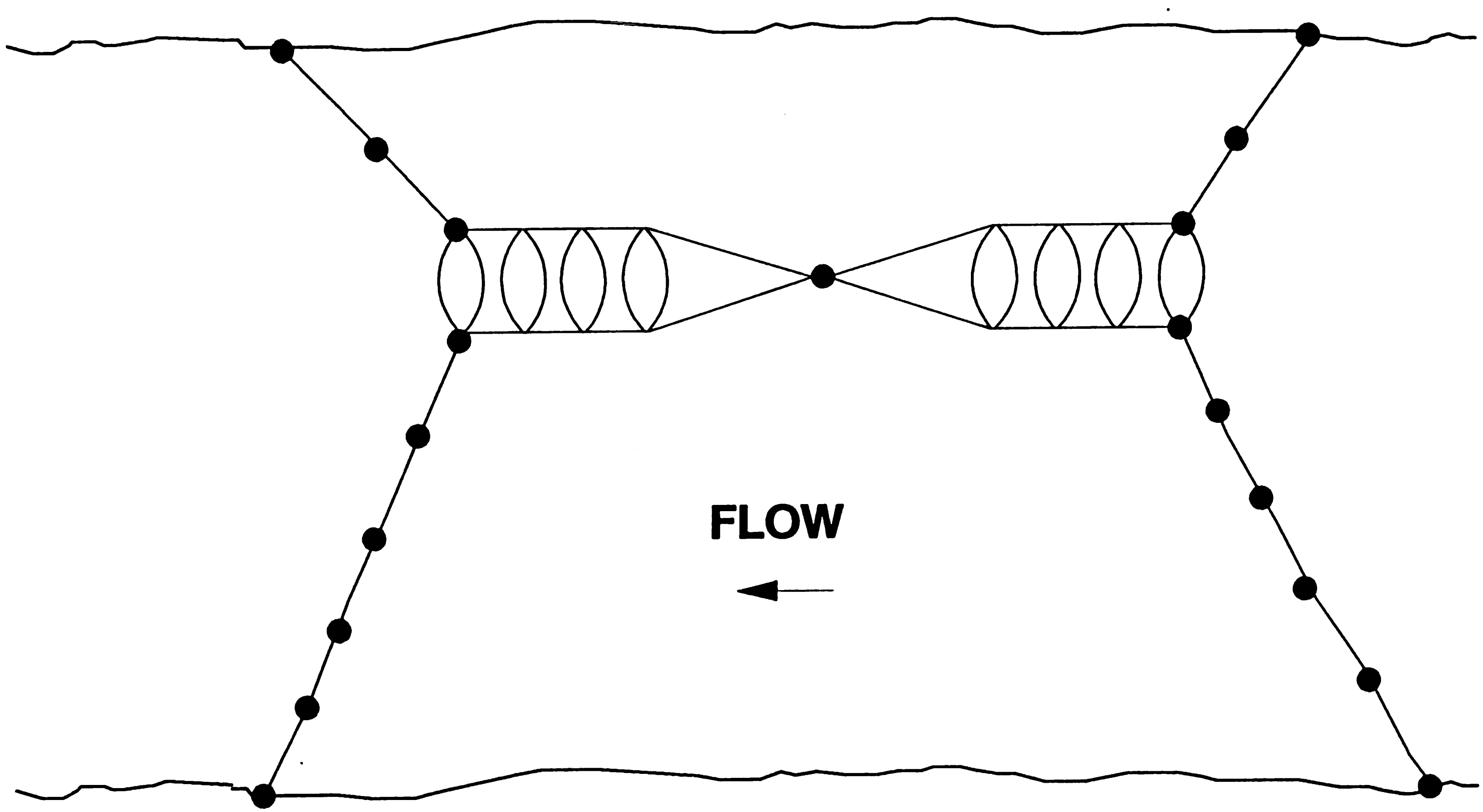

Figure 4. Fyke nets arranged in tandem across a river.

their original direction of travel. Recaptured fish were again measured, weighed, checked for a fin clip, and released.

Temperature Monitoring

Late spring and summer water temperatures were monitored (half hour intervals) with Omnidata data pods using thermistors at sites 2 and 3 from mid-April to October (Burton 1991). Temperature was monitored at site 4 using Ryan Tempmentors in 1988 (10 minute intervals), 1990 (10 minute intervals), and 1991 (30 minute intervals). Temperature was not monitored at site 4 in 1989 because of equipment failure. The 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 maximum and minimum temperature at sites 2, 3, and 4 for all net days in all years.

Age Determination and Size Structure

A stratified random subsample of brook trout were aged from each year's total catch by counting scale annuli as described by Cooper (1951), McFadden (1959), and Van Oosten (1929). The criteria for an annuli were those given by Cooper (1951); the crowding of adjacent circuli, irregularity or incompleteness in circuli form, the cutting over of circuli in the posterio-lateral areas and the sudden change in the growth pattern of the circuli. Only scale samples taken in May and June were used for age determination and annual growth determination because samples taken as close to annulus formation as possible have the least amount of variation in the body-scale relation (Carlander 1982, Weatherly and Gill 1987). The mean length at capture for age classes 1, 2, and 3 was then determined. The determined ages were used to construct an age-length key to estimate the age structure of the total brook trout catch each year. Due to small sample sizes (N < 6 for all years combined) of fish greater that 3+ years olds, only fish through age 3+ were included in my study. The size structure of each year's brook trout population was described by a length frequency distribution of the total yearly catch. For the 1988 total catch no age 3 (1985 cohort) fish were aged because no scales were collected from age 3 fish; consequently, the age-length key for the 1988 total catch only contains age 1 and 2 fish.

Annual Growth Rates

Once aged, the fish were separated into cohorts to minimize error in the body-scale relation (Carlander 1981). For example, age 1 fish caught in 1984 belonged to the 1983 cohort as did age 2 fish caught in 1985 and age 3 fish caught in 1986. This was necessary because a sample taken at one time really represents a series of year classes. As a result, a single years catch cannot be used to determine the body-scale relationship and the back-calculation equations for brook trout from different cohorts. The annual growth rates of the brook trout in the upper Ford River watershed were estimated by first back-calculating the previous lengths at age from scale analysis (Bagenal and Tesch 1978).

The Fraser-Lee method of back-calculation was used to estimate past length at age. This method assumes that body growth of the fish is related to the proportional growth of its scale (Carlander 1981). The Fraser-Lee back-calculation formula is (Carlander 1981):

$$L_i = a + [\ L_c - a\ ] * \frac{S_i}{S_c}$$

Where,

L_c = length at capture
a = Y-intercept of the body-scale regression
L_i = length at age i
S_c = scale radius at capture
S_i = scale radius at age i

The back-calculated lengths were then compared to observed lengths at capture for each age class of the same cohort to determine if the back-calculated lengths were realistic.

Relative annual growth rates were determined using the equation given by Ricker (1975):

$$G = \frac{L_i - L_{i-1}}{L_{i-1}}$$

where,

G = annual growth rate
L_{i-1} = length at age i-1
L_i = length at age i

A relative growth rate was used because the effects of temperature on growth are dependent on the size of the fish (Baldwin 1956). In addition, annual growth rates were only calculated from the last complete year of growth for each age class, i.e. age 1 growth rate was determined only from age 2 fish and age 0 growth rates were determined from only age 1 fish. This method minimizes uncertainty due to Lee's Phenomenon and reverse Lee's Phenomenon (Gutreuter 1987), which was found to occur in several cohorts. For the annual growth rate of young of the year (YOY) fish, length at time i-1 was assumed to be 22.86 mm which is the average size of brook trout in northern Wisconsin streams at swim-up and the onset of feeding (Avery 1983). The average size at swim-up for brook trout in northern Wisconsin streams was used rather than that of brook trout from streams in the Lower Peninsula of Michigan. This was because the Ford River is thermally and geologically more closely related to northern Wisconsin streams.

Temperature Patterns

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 when the weirs were checked were averaged and presented as the mean value. 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 mean daily temperatures obtained from the tempmentors (Figure 5). Similarity in water temperature between sites was tested with Pearson's Correlation. Similarity between sites allowed the use of data from only one site when evaluating the relationship between growth patterns and late spring and summer temperatures. Only temperatures between May 1 and September 30 of each year were used because temperatures were below the range for optimal growth prior to May 1 and after September 30 in all years of my study. Cumulative mean daily temperature distributions from May 1 to September 30 were used to describe the temperature patterns of each year. In addition, I measured the relative rate at which the water warmed each year by counting the number of days from May 1 that it took to reach a mean weekly temperature of 11 C (lower end of range for optimal growth), 16 C (optimal growth), and 20 C (upper bound on positive growth). I also measured the number of days the water was within the range of optimal growth, poor growth (greater than 16 C but less than 20 C), and no positive growth (greater than 20 C).

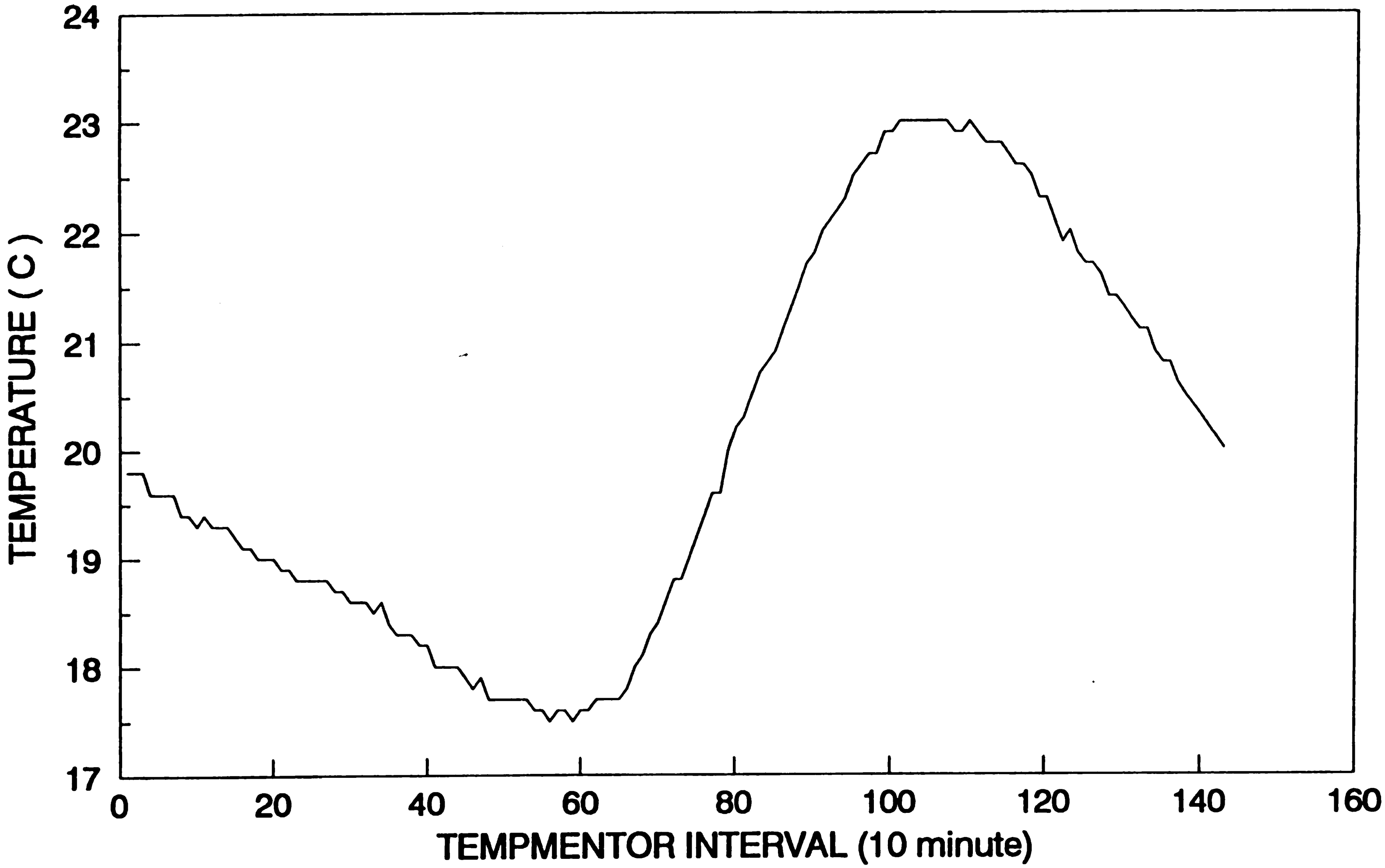

Figure 5. Twenty-four hour daily temperature pattern for Two Mile Creek determined at 10 minute intervals with a Ryan Tempmentor.

Length of Growing Season

The growing season is the time when water temperatures support positive growth (5 C to 20 C). Since the water temperatures reached 5 C prior to the onset of temperature monitoring in my study, the length of the growing seasons had to be estimated indirectly. One indirect way of comparing the effects of different growing seasons on brook trout growth was to compare the number of days during the summer that had temperatures too high for positive growth (number of days greater than 20 C) to the mean annual growth rates and lengths at age of brook trout. An alternative method was to compare the relative rate at which water temperatures reach a mean temperature that is best suited for the overall welfare of brook trout (11 C) to the lengths at age and age specific growth rates for each cohort. Since 11 C is at the lower end of the temperature range best for the overall welfare of brook trout (Raleigh 1982), the number of days from May 1 that it took to reach a weekly mean temperature of 11 C were used to evaluate the effects of the relative rate at which temperatures rise in the spring on annual growth rates and length at age.

Effect of Temperature on Growth

The effect of temperature on growth was evaluated by comparing the following temperature conditions with the mean length at age and the mean age specific growth rate for each age class for each cohort: 1) the mean daily temperature between May 1 and September 30, (2) the cumulative temperature distribution (3) the rate at which temperatures rise (4) the number of days with temperatures within the range of optimal growth (5) the number of days with temperatures greater than those for optimal growth but still with the positive growth range, and (6) the number of days with temperatures higher than the upper bound on positive growth.

RESULTS

Fish Collection

During the sampling periods from 1984 to 1991, the total number of net days varied from 197 in 1986 to 335 in 1984 (Table 1). The number of net days at each sampling site varied between sites and between years (Table 2). The mean annual catch was 590.6 fish and ranged from 317 in 1986 to 1186 in 1984 (Table 1). In addition, the total number of fish captured at each site varied among sites and years (Table 3). Site 4 had the highest annual catch every year except 1987 where site 2 had the highest annual catch. In 1989 site 1 and 4 had equal annual catches. Mean catch per unit effort (CPUE - mean daily catch per net per day) was 2.40 and ranged between 1.28 in 1989 and 3.54 in 1984 (Table 1). Sampling had began by the third week of May in all years except 1987 in which sampling did not begin

Table 1. The total number of net days, total catch, CPUE, and sampling time for the sampling periods from 1984 to 1991.

Year	Number of net days	Total catch	CPUE	Sampling Time
1984	335	1186	3.54	5/14 to 11/10
1985	214	616	2.88	5/22 to 9/18
1986	197	317	1.61	5/21 to 9/19
1987	201	673	3.35	6/16 to 10/10
1988	218	333	1.53	5/19 to 10/6
1989	253	324	1.28	5/23 to 10/13
1990	265	400	1.51	5/30 to 9/17
1991	253	876	3.46	5/17 to 9/11

Table 2. Total net days each year at sites 1, 2, 3, and 4 from 1984 to 1991.

	Year							
Site	1984	1985	1986	1987	1988	1989	1990	1991
1	44	53	52	48	56	52	69	69
2	78	42	42	57	55	69	69	59
3	92	58	52	59	53	61	58	52
4	121	61	51	37	54	71	69	73

Table 3. Total annual catch at sites 1, 2, 3, and 4 from 1984 to 1991.

	Year							
Site	1984	1985	1986	1987	1988	1989	1990	1991
1	180	62	34	16	28	0	139	90
2	313	147	84	148	72	94	33	123
3	170	97	77	357	47	51	89	109
4	523	310	122	152	186	179	139	554

until mid June due to the late arrival of necessary equipment (Table 1).

Temperature

The temperature at sites 2, 3, and 4 were all highly correlated during the late spring and summer each year (minimum p = .758, maximum p = 0.999). Consequently, site 3 was chosen for all remaining temperature calculations. The mean daily temperatures for each year between May 1 and September 30 are given in Table 4, along with temperature variables used to describe the relative rate at which water temperatures rise, the number of days within the range of optimal growth, poor growth, and no positive growth. The average for the late spring and summer of all years was 16.26 C and ranged from 15.35 C in 1985 to 17.67 C in 1988. One way analysis variance detected significant differences between the means ($F = 7.14$, $df = 7$, $P < 0.05$). Fisher's Least Significant Difference (LSD) multiple comparison test ($P < 0.05$) revealed that the mean temperatures during the study period in 1985 (15.4 C) and 1990 (15.4 C) were significantly lower than the mean temperatures in 1988 (17.7 C) and 1991 (16.8 C), and the means of the remaining years fell in between. The temperature patterns for the periods from May 1 to September 30 for each year are depicted by the cumulative mean daily temperature distributions in Figure 6. The Kolmogorov Smirnov test ($P < 0.05$) detected two distinct cumulative temperature distributions. The distributions for

Table 4. The mean daily temperature between May 1 and September 30 for each year, the relative rate at which temperatures warmed, and the number of days within the temperature range of optimal growth, poor growth, and no growth 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 11C[1]	14	7	0	5	2	13	0	10
Days to 16C[1]	32	53	27	39	27	50	42	23
Days to 20C[1]	97	153	78	45	29	63	58	75
Days > 16C	80	55	69	67	81	66	67	90
Days > 20C	13	6	20	28	48	20	11	21
Days Between 11C & 16C	18	46	27	34	25	37	42	13
Days Between 16C & 20C	65	100	51	6	2	13	16	52

[1] Mean weekly temperature

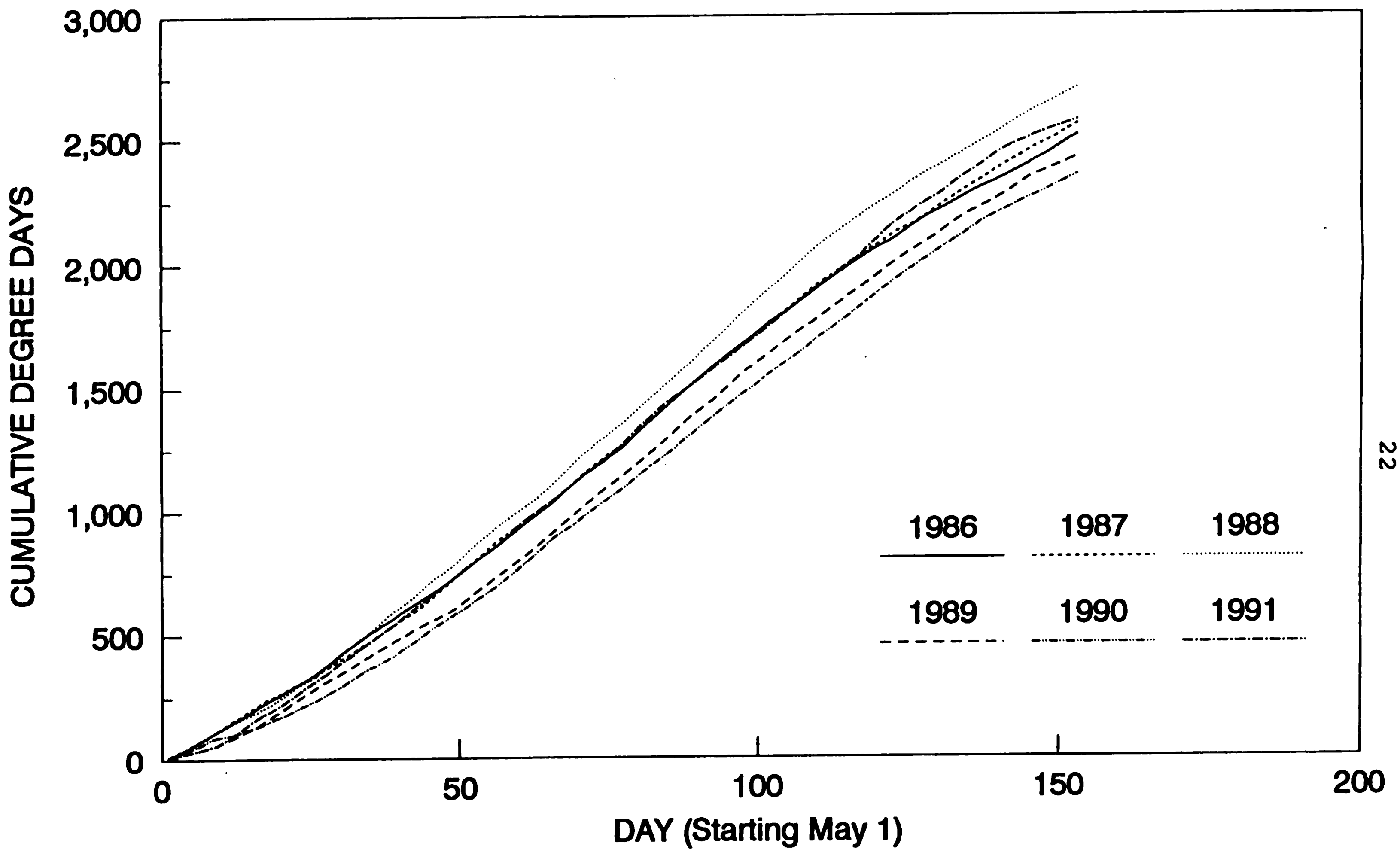

Figure 6. Cumulative mean daily temperature distribution from May 1 to September 30 from 1986 through 1991.

1986, 1987, 1988 and 1991 were significantly different from the 1989 and 1990 distributions, however the distributions of 1984 and 1985 were not significantly different from either of these groups. When the mean daily temperatures were calculated on a monthly basis, the largest between year differences were seen in May and June (Table 5).

Table 5. The mean monthly temperatures for May through September from 1984 to 1991.

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

The mean daily temperature in May of 1984, 1985, 1989, and 1990 ranged from 9.09 C to 12.01 C, where as the mean daily temperature in May of 1986, 1987, 1988, and 1991 ranged from 12.99 C to 14.22 C. In addition, the mean monthly temperature in June of 1985, 1989, and 1990 ranged from 15.31 C to 16.12 C and during all the other years the mean temperature was above the optimum (16 C) ranging from 17.07 C in 1986 to 19.45 C in 1988. During July and August the mean monthly temperature was above the optimum in all years ranging from 17.09 C in August of 1986 to 21.16 C in July of 1988. The only years with mean a monthly temperatures above 20 C were July of 1986, 1988, and 1989. By September the mean monthly temperature had fallen to between 12.97 C (1984) to 14.36 C (1987) in all years. Combining the mean monthly temperatures and the cumulative distribution information, it appears that the two distinct temperature patterns occurred during the late spring and summers from 1984 to 1991. One temperature pattern consisted of warm late spring temperatures and hot temperatures throughout the summer. Years with this hot temperature pattern were 1986, 1987, 1988, and 1991. The other temperature pattern consisted of years with cool late spring and early summer temperatures and relatively cooler summer temperatures. Years displaying this cooler temperature pattern are 1984, 1985, 1989, and 1990.

Age Determination and Size Structure

The size structure and age structure of the brook trout population in the Ford River from 1984 to 1991 (Appendix A Figures 7-10) are shown by the length-frequency distribution and the age-length key of the total annual catch. Peaks signify the mean size of each age class at the time of capture. Since the mean length at capture for each age class for each cohort (Appendix A Table 15) corresponded with the peaks in the length frequency distribution it was assumed that the determined ages were correct. In addition, the age-length keys and length frequency distributions depicted that the overlap in length between different aged fish from different cohorts varied, indicating that age specific growth rates differed between years.

The age-length key was also used to determine the percent composition by age of the total catch. As shown by the length frequency distribution and the age-length key the percent composition by age of the total catch varied between years (Table 6). One year olds comprised the majority of the total catch in 1986, 1987, 1988, and 1990. Two year olds dominated in 1984 and 1991. When the percent composition by age was compared to the temperature patterns, relationships were detected. When years were repeatedly hot such as in 1986, 1987, and 1988 the total yearly catch was dominated by 1 year olds. Also, when there was two consecutive cool years as was the case for the 1991 catch, two year olds

Table 6. The percent age composition of age classes 1, 2, and 3 in the total annual catch from 1984 to 1991.

Year	% Age 1	% Age 2	% Age 3
1984	33	59	8
1985	41	46.8	5.8
1986	67	30	3
1987	65	29	5
1988	60	26	?
1989	30	39	31
1990	77	14	8
1991	37	57	6

dominated the total catch.

Length at Age and Age Specific Growth Rates

The body-scale relationship regression for the 1983 through 1990 cohorts are given in Table 7. All relationships were linear; therefore, the Fraser-Lee back-calculation was an acceptable method. The intercepts of the regressions were used in the Fraser-Lee back-calculation equation.

Relationship between Temperature, Length, and Growth

The mean back-calculated length at age and mean age specific growth rate for each age class in each cohort are shown in Tables 8 through 13. All means were tested for differences using the Kruskal-Wallis test ($P < 0.05$) and a multiple comparison test ($P < 0.05$, Miller 1981). One way analysis of variance (ANOVA) was used to determine the relationship between temperature and mean length at age and mean age specific growth rates. Due to the low number of degree's of freedom ($df \leq 5$) a probability level of 0.1 was chosen as the level of significance (Winterstein Michigan State University pers. comm.). Appendix B Tables 16 to 21 provide the results from each ANOVA test for relationships between growth and temperature and between length at age and temperature.

One Year Olds

The mean length at age for 1 year olds averaged 111.5 mm and ranged from 89.23 mm for the 1987 cohort to 119.2 mm

Table 7. The regression equations describing the body-scale relationship for the 1983 through 1990 cohorts (L = length at age i, S = scale radius at age i).

Cohort	Equation	Slope	Intercept[1]
1983	L = 55.39 + 420.50 * S	a	a,b,d
1984	L = 57.31 + 403.21 * S	a	a,b,d
1985	L = 50.29 + 419.64 * S	a	a,b
1986	L = 58.56 + 397.84 * S	a	a,b,d
1987	L = 22.54 + 489.18 * S	a	c
1988	L = 65.81 + 414.21 * S	a	a,b,d
1989	L = 63.21 + 364.67 * S	a	a,d
1990[2]	L = 62.16 + 296.20 * S		

[1] Slopes and intercepts with the same letter combinations are not significantly different from each other.
[2] 1990 cohort was not compared to the other cohorts because it only contained 1 age class.

for 1983 cohort (Table 8). Mean annual growth rates of the young of the year (YOY) averaged 3.879, ranging from 2.904 for the 1987 to 4.215 for the 1983 cohort (Table 9). Although there were significant differences between the mean length at age and mean annual growth rate, none of them were significantly related to temperature. For example, the highest R^2 was between length and the number of days it took to reach a mean daily temperature of 16 C (R^2 = .091). However, the smallest and slowest growing cohort, the 1987 cohort, did grow during the middle of 3 consecutively hot years.

Two Year Olds

The mean length at age 2 averaged 184.2 mm and ranged from 161.2 mm for the 1986 cohort to 202.4 mm for the 1984 cohort (Table 10). A negative relationship (R^2 = 0.600, F = 7.51, df = 5) existed between length at age 2 and the mean daily temperature between May 1 and September 30 during the second summer of life, with years having a higher mean temperatures producing smaller brook trout. In addition, cohorts that had more days with a mean daily temperature above 20 C during the second summer of life were smaller at age 2 (R^2 = 0.505, F = 5.10, df = 5). These relationships are supported by comparing the overall temperature pattern of late spring and summer to the mean length at age. When the second year of life of a cohort coincided with the hot temperature

Table 8. Mean back-calculated length (mm) at age 1 for brook trout from the 1983-1990 cohorts.

Cohort	Mean (mm)	Standard Deviation	Confidence Interval (95%)	Number
1983	119.2	17.4	105.8-132.6	9
1984	115.1	15.6	107.9-122.4	20
1985	110.5	16.3	106.5-114.4	69
1986	117.0	13.8	114.9-119.0	174
1987	89.23	11.93	86.0-92.43	56
1988	115.9	10.72	106.0-125.9	7
1989	106.7	13.32	103.7-109.7	78
1990	118.7	16.53	115.6-121.8	114

Table 9. Mean annual growth rates of young of the year brook trout from the 1983-1990 cohorts.

Cohort	Mean	Standard Deviation	Confidence Interval (95%)	Number
1983	4.215	0.7620	3.630-4.801	9
1984	4.037	0.6806	3.718-4.356	20
1985	3.832	0.7132	3.661-4.004	69
1986	4.117	0.6014	4.027-4.207	174
1987	2.904	0.5217	2.764-3.043	56
1988	4.072	0.4691	3.638-4.505	7
1989	3.668	0.5825	3.536-3.799	78
1990	4.192	0.7230	4.058-4.326	114

Table 10. Mean back-calculated length (mm) at age 2 for brook trout from the 1983-1989 cohorts.

Cohort	Mean (mm)	Standard Deviation	Confidence Interval (95%)	Number
1983	201.1	25.0	189.1-213.1	19
1984	202.4	25.8	194.4-201.3	43
1985	169.0	23.0	163.9-174.0	83
1986	161.2	20.7	143.9-178.5	8
1987	172.8	30.0	162.3-183.3	34
1988	184.7	21.23	175.0-194.3	21
1989	198.5	22.69	195.1-201.8	183

patterns, length at age 2 was significantly smaller than cohorts whose second year of life corresponded with the cool temperature patterns. Consequently, high temperatures start to have a constraining effect on the growth and length of brook trout by age 2. In addition, brook trout that had cool summers during both years of their life were larger than brook trout that only had cool summers during their second year of life.

The mean annual growth rate of age 1 fish averaged 0.581 and varied between 0.522 for the 1988 cohort and 0.719 for the 1987 cohort (Table 11). No significant relationship was found between the growth rate of yearling brook trout and temperature, with the highest R^2 being 0.259 for the number of days with a mean temperature greater than or equal to 16 C. However, the growth rate of the 1986 cohort was slowest, and this cohort experienced the same temperature patterns as the 1987 cohort which also had the slowest YOY growth rates. But, the 1987 cohort had the fastest annual growth rate, during its second year of growth.

Three Year Olds

The mean back-calculated length at age 3 for brook trout averaged 246.4 mm and varied from between 217.7 mm for the 1984 cohort to 288.1 mm for the 1988 cohort (Table 12). Age 3 fish from the 1988 cohort were significantly larger than 3 year olds from all other cohorts. No significant relationships were found between length at age 3 and

Table 11. The mean annual growth rates of yearling brook trout from the 1983-1989 cohorts..

Cohort	Mean	Standard Deviation	Confidence Interval (95%)	Number
1983	0.653	0.152	0.579-0.579	19
1984	0.614	0.148	0.569-0.660	43
1985	0.542	0.137	0.512-0.572	83
1986	0.446	0.138	0.332-0.561	8
1987	0.719	0.184	0.655-0.783	34
1988	0.522	0.160	0.450-0.595	21
1989	0.569	0.135	0.549-0.588	183

Table 12. Mean back-calculated length (mm) at age 3 for brook trout from the 1983, 1984, 1986, 1987, and 1988 cohorts.

Cohort	Mean (mm)	Standard Deviation	Confidence Interval (95%)	Number
1983	239.3	15.4	223.1-255.5	6
1984	217.7	28.8	201.0-234.3	14
1986	238.5	26.38	231.0-246.0	50
1987	248.2	50.72	224.4-271.9	20
1988	288.1	28.43	275.5-300.7	22

temperatures during the third summer of life. The highest R^2 occurred for the number of days greater than 11 C but less than or equal to 16 C ($R^2 = 0.306$). However, a relation between mean length at age 3 and temperature pattern can be seen. Years with a cooler May and June (cool temperature patterns) had larger fish than years with warmer springs and early summers (hot temperature patterns).

The mean annual growth rate for all 2 year olds was 0.343 and ranged from 0.260 for the 1984 cohort to 0.504 for the 1987 cohort (Table 13).Brook trout growth rates during the third summer of life were positively related ($R^2 = 0.885$, $F = 23.02$, $df = 3$) to the number of days it takes to reach 11 C. The slower water temperatures had risen in late spring and early summer the faster age 2 brook trout grew. The relationship between annual growth rate and temperature can also be seen by comparing the overall temperature patterns of the different years to the mean annual growth rates. The 1983, 1987, and 1988 cohorts whose third year of growth occurred in cool years grew faster than the 1984 and 1986 cohorts whose third year of growth occurred in hot years.

The past thermal history of brook trout was also related to length at age 3. Brook trout from the 1988 cohort which had cool temperature patterns for the last 2 years of their life were the largest and also experienced reverse Lee's Phenomenon (Table 14) between their second and

Table 13. The mean annual growth rates of 2 year old brook trout from the 1983, 1984, 1986, 1987, and 1988 cohorts.

Cohort	Mean	Standard Deviation	Confidence Interval (95%)	Number
1983	0.375	0.053	0.319-0.430	6
1984	0.260	0.084	0.211-0.309	14
1986	0.287	0.108	0.257-0.318	50
1987	0.504	0.138	0.440-0.569	20
1988	0.288	0.094	0.246-0.330	22

Table 14. Occurrence of Lee's Phenomenon and Reverse Lee's Phenomenon during the second and third year of life for the 1983-1989 cohorts.

Cohort	Age 1	Age 2
1983	none	positive
1984	none	positive
1985	none	
1986	none	reverse
1987	reverse	none
1988	none	reverse
1989	reverse	

third year of life. The 1983 cohort also had cool years for their last two years of growth, but were not as large. This could have been due to size selective mortality of the larger fish, because Lee's Phenomenon was detected during their second year. The 1986 cohort which had hot temperature patterns for all years of its life and exhibited reverse Lee's Phenomenon occur during its second year was still below the mean size of three year olds for all years combined. The 1984 cohort which had cool temperature patterns for its first two years of life and a hot temperature pattern for its last had the smallest 3 year olds. However, Lee's Phenomenon was detected during its second year of life. Brook trout that had hot temperature patterns during their first two years and a cool temperature pattern during their last reached a length approximately equal to the overall mean length at age 3.

DISCUSSION

Assuming brook trout in the Ford River belong to one population and if the environment was constant then the mean length at age and mean age specific growth rates would be constant between all cohorts. However, if the environment was not constant and the limiting factor varied between years then the mean length at age and mean age specific growth rate should vary between cohorts. Temperature is the best characteristic used to describe brook trout habitat (Power 1980). Consequently, if high water temperatures are the most limiting factor in the niche of Ford River brook trout, then differences in the late spring and early summer temperature patterns should be revealed by differences in mean length at age and mean age specific growth rate of cohorts which experienced different temperature conditions.

The preferred temperature of brook trout is an integrated optimum of all metabolic processes (Kelch and 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 increases more energy is required for basal metabolic processes and less energy is available for growth (Coutant 1987, Magnuson et.al. 1979, Kelch and Neill 1990, Schofield et.al. in press). However, at temperatures below the optimum, increasing temperature results in increasing growth rates because the gain in energy from increased feeding activity is greater than the increase in basal metabolism (Baldwin 1956). The effects of high temperatures are greatest for older, larger fish that metabolize less efficiently (Schofield et. al. in press).

I found that both the age structure and size structure of brook trout in the Ford River were related to late spring and summer temperature patterns from 1984 to 1991. Temperature could effect age structure either directly by influencing the mortality of current ages (Power 1980 and McCormick et.al. 1972) or indirectly by altering reproductive success (Hokanson et.al. 1973). In years that were repeatedly hot, age one brook trout dominated. In the first of the three hot years age structure was probably effected through increased mortality of age 2 and older fish since the effects of temperature are size dependent (Power 1980). During the next two years a combination of increased mortality on age 2 and older fish and reproductive failure could have lead to the domination by age 1 brook trout and lower population levels in following years. Reproductive failure could occur either because of the lack of older and larger brook trout or because of impaired sexual maturation by the brook trout due to high temperatures (Hokanson et.al. 1973). When temperature patterns were cool for two consecutive summers the brook trout catch was again dominated by 2 year olds, such as it was in previous cool years before the period of consecutively hot years. Consequently, in order to have a brook trout population with larger and older brook trout, late spring and summer water temperatures must not be hot for consecutive years.

However, even in years that were considered cool very few fish survived past age 2. Fishing mortality could be part of the cause since almost all age 2 brook trout in the Ford River are legal size (178 mm). In addition, Marod and Taylor (1991) have noted that many anglers fish for brook trout in the Ford River. High exploitation rates have long been known to alter the size and age structure of brook trout populations (Cooper 1952, Clark et.al. 1981) with unexploited streams containing older brook trout (Cooper 1967) . In addition, predation by fish eating birds could is also known to be a significant source of mortality for brook trout of all ages, but especially smaller brook trout (A. J. Nuhfer, Michigan Department of Natural Resources pers. comm., White 1957, Alexander 1977, and Matkowski 1989). Mergansers, kingfishers, and great blue herons were seen in and around all study sites. Overwinter mortality could also be contributing to the decrease of brook trout over age 2. Whitworth and Strange (1983) observed high winter mortality of age 2 and 3 brook trout, due to a shortage of suitable winter habitat.

Length at age and age specific growth rates were found to be related to temperature patterns, especially from age 2 on. Few relationships between high temperature and young of the year growth or length at age one were found. My results agree with a study by Schofield et.al. (in press) who found that young of the year brook trout were not limited by high summer water temperatures. However, according to McCormick et.al. (1972) juvenile brook trout are thermally more sensitive than older brook trout. Perhaps high summer temperatures do not have a strong influence on YOY brook trout growth because, they are able to find suitable microhabits to shelter themselves from unsuitable temperature conditions since YOY require only small territories (Power 1980).

By age 2, high summer water temperatures were having detrimental effects on brook trout growth and length at age. It appears that by the end of their second growing season Ford River brook trout have reached a size were the increase in basal metabolism due to increasing temperatures can not be completely offset by the increase in activity (Baldwin 1956, Power 1980, Schofield et.al. in press). The results of my study suggest that for age 2 and older brook trout to prosper temperatures must be cool in the late spring and early summer. This agrees with the late spring and early summer water patterns of Michigan streams that are considered good brook trout streams (Cooper 1953). In addition, streams with similar late spring and early summer water patterns experienced tremendous increases in growth, which are believed to be related to seasonal availability of food (Whitworth and Strange 1983, Cooper 1953). If this is true, in years with high spring temperatures, even though within the range of positive growth, the abundant food supply associated with spring was not being used as efficiently, because digestive efficiency decreases with increasing temperature. Thus, in years where temperatures increase rapidly, brook trout were not able to take full advantage of the abundant spring food supply, and as a result had slower annual growth rates and smaller sizes.

It should be noted that all cohorts that passed through the summer of 1987 had the slowest growth rates of their age class. This could have been caused by temperatures exceeding 21 C in mid-June and then cycling between 18 C and over 20 C through July. The highest mean weekly temperature in June occurred in 1987 (Figure 3). Consequently, brook trout in 1987 had little time during the period of abundant spring food where temperatures were within a range suitable for efficient digestion or positive growth. This supports my idea that the speed at which water temperatures rise in the Ford River strongly influences the annual growth rate, with cooler years supporting better brook trout growth.

High summer water temperatures have long been known to be the limiting factor in brook trout distribution (Power 1980). From its late spring and summer temperature patterns, it is evident that the Ford River is not a blue ribbon trout stream from a thermal standpoint. However, as several field studies indicate brook trout populations depend on the ability to survive at the extreme of their upper thermal limit and have prospered within a relatively narrow limit where temperatures were suitable for their growth but still cool enough to limit competitors (McCormick et. al. 1972). If competitors were limited by some factor other than temperature and food was not limiting, brook trout prospered at temperatures more closely approaching their upper thermal limits (McCormick et. al. 1972). This appears to be the case with brook trout in the Ford River. Brook trout were the only salmonid species in the Ford River and they appeared to grow relatively fast when compared to trout populations reported in Carlander (1969), despite temperature conditions that were far from optimal.

From a management point of view, this stresses the importance of thermal refugia and behavioral responses to increasing temperatures. Brook trout can free themselves from the extremes of their environment by moving to more suitable environments if they exist (Power 1980). Stream brook trout are known to migrate to deeper holes in the stream or to lakes when water temperatures in the stream begin to rise (Scott and Crossman 1985) or to congregate around cold water seepages (Powers 1980). Many brook trout in the Ford River were found to migrate upstream in the late spring and early summer towards Two Mile Creek. Two Mile Creek is thought to be a thermal refugia. However, movement upstream may have been impeded by beaver dams and low summer discharge in some years. In addition, the thermal and substrate conditions in Two Mile Creek have changed over the course of this study due to increased logging in the area. Both water temperature and siltation have increased due to the removal of stream edge vegetation.

In conclusion, age structure and size structure of brook trout in the Ford River were related to late spring and summer water temperatures beginning during their second growing season. Length at age 2 was inversely related to the number of days with a mean temperature greater than 20 C. After age 2, the rate at which water warmed had a strong negative effect on annual growth rates of brook trout. Fastest growth occurred in years in which water temperatures remained cooler for a longer period of time. Additionally, years that had cooler temperatures in May and June were dominated by older, larger brook trout, while years with warmer temperature patterns were dominated by younger, smaller brook trout. Consequently, brook trout stream managers must consider the thermal regime of a stream prior to establishing management goals and implementing management practices.

APPENDICES

Appendix A

Table 15. The average length (mm) at capture for age classes 1, 2, and 3 for each cohort.

Cohort	Age 1	N	Age 2	N	Age 3	N
1983	146.1	9	265.2	19	278	6
1984	155.1	20	245.2	43	270.2	14
1985	148.1	69	232.1	83		
1986	167.0	174	197.0	8	284.9	50
1987	132.2	56	244.0	34	306.1	20
1988	148.7	7	229.3	21	318.6	22
1989	134.2	78	240.1	174		
1990	151.7	114				

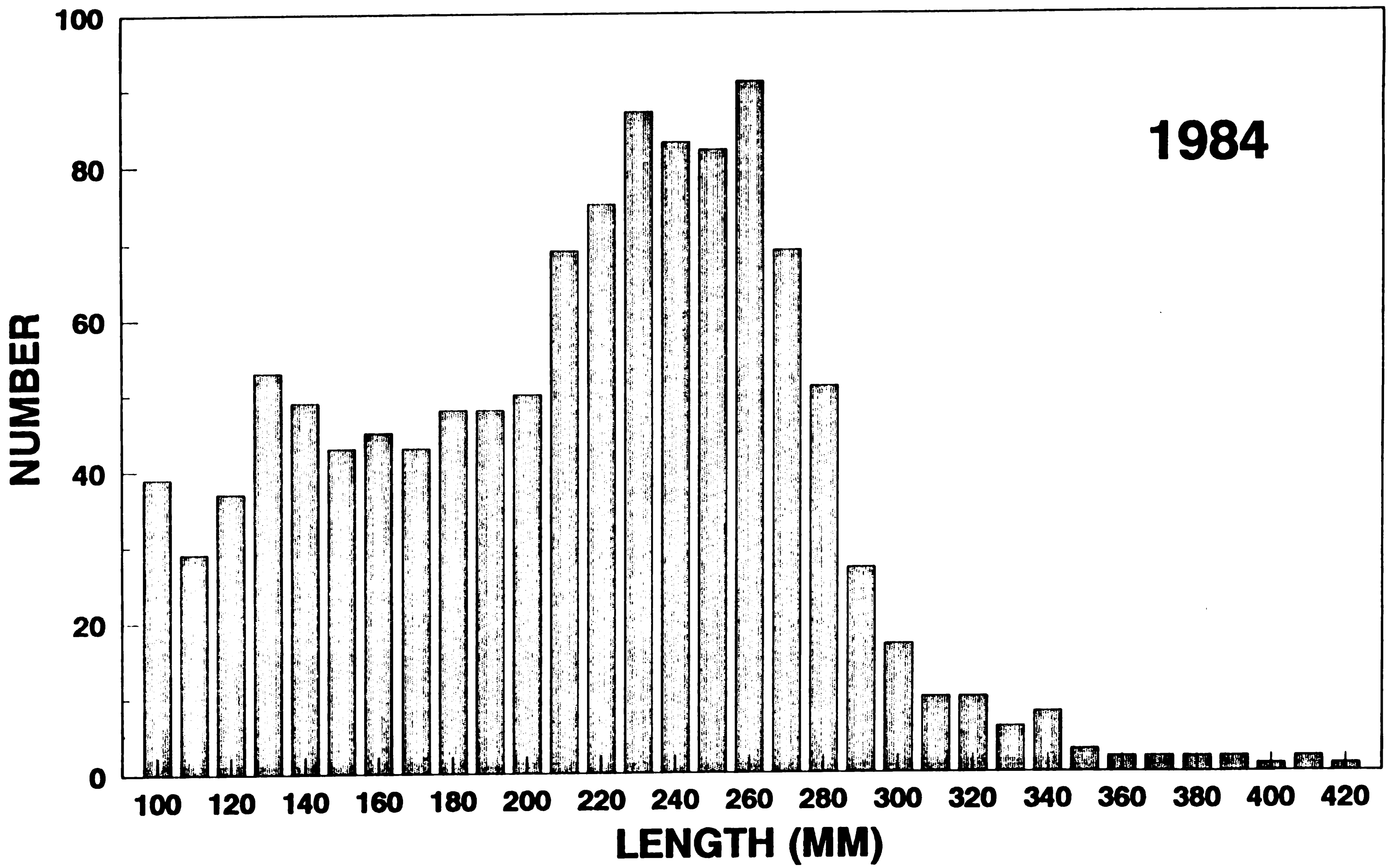

Figure 7. Length frequency distribution of the total annual catch in 1984.

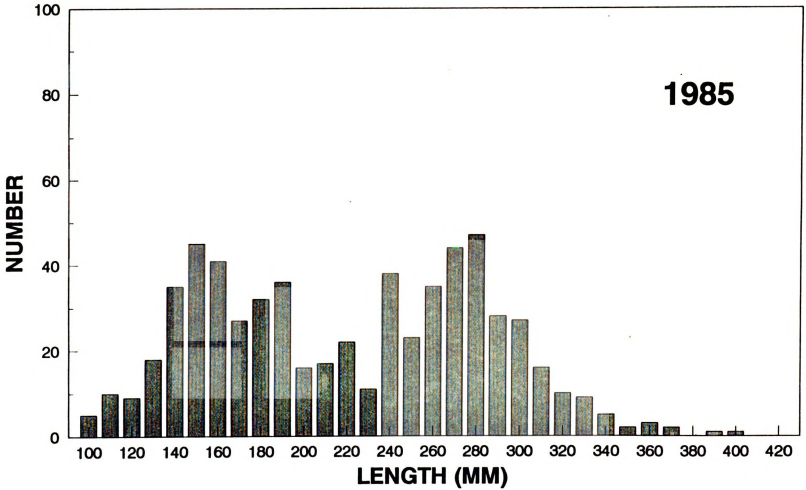

Figure 8. Length frequency distribution of the total annual catch in 1985.

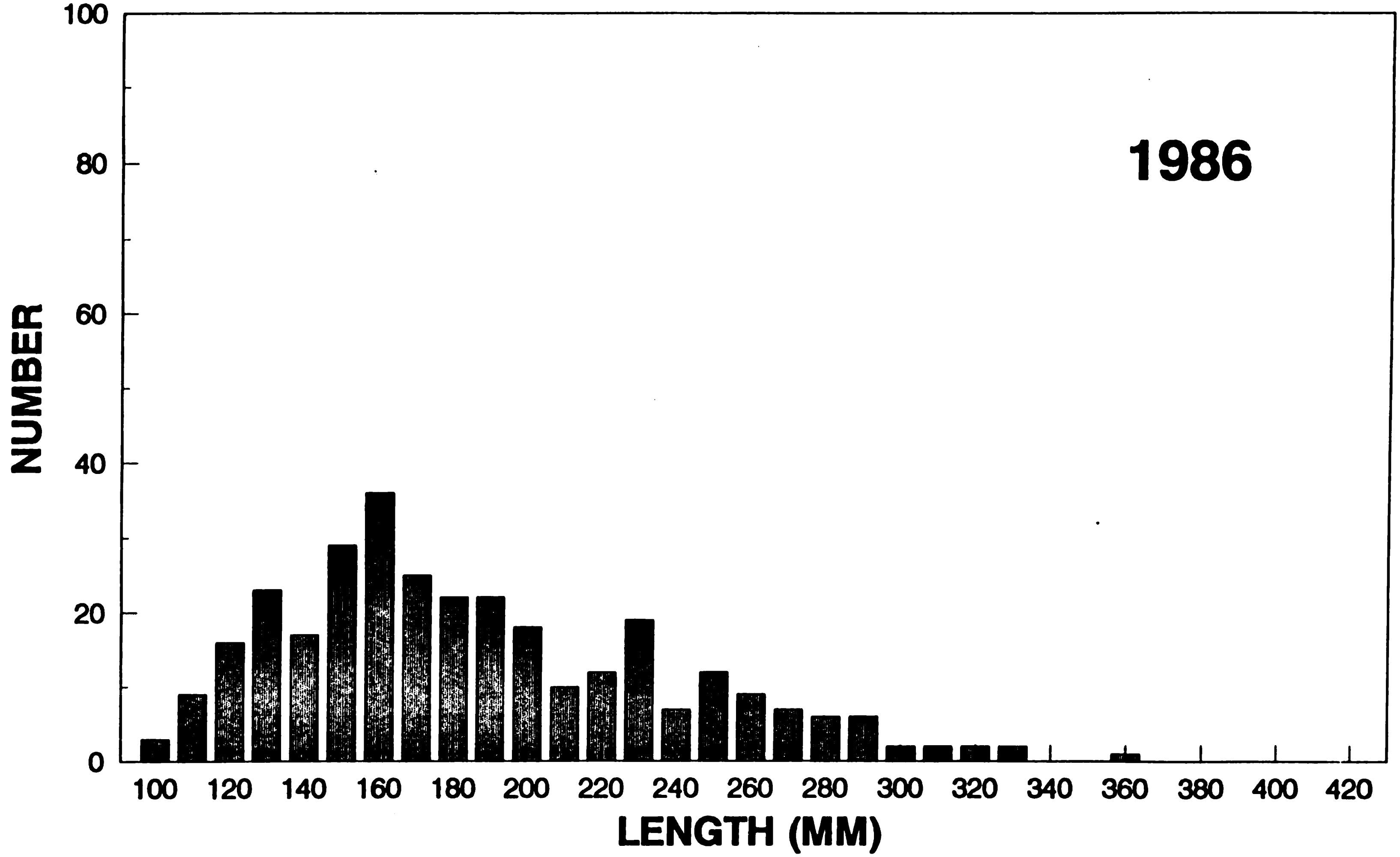

Figure 9. Length frequency distribution of the total annual catch in 1986.

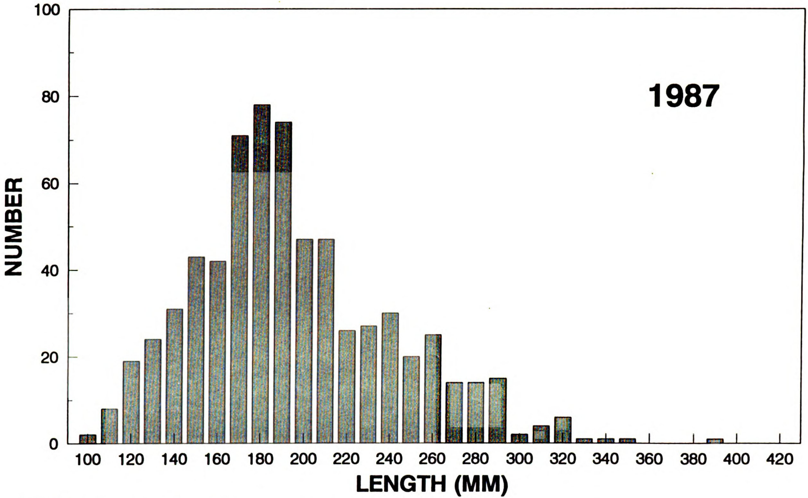

Figure 10. Length frequency distribution of the total annual catch in 1987.

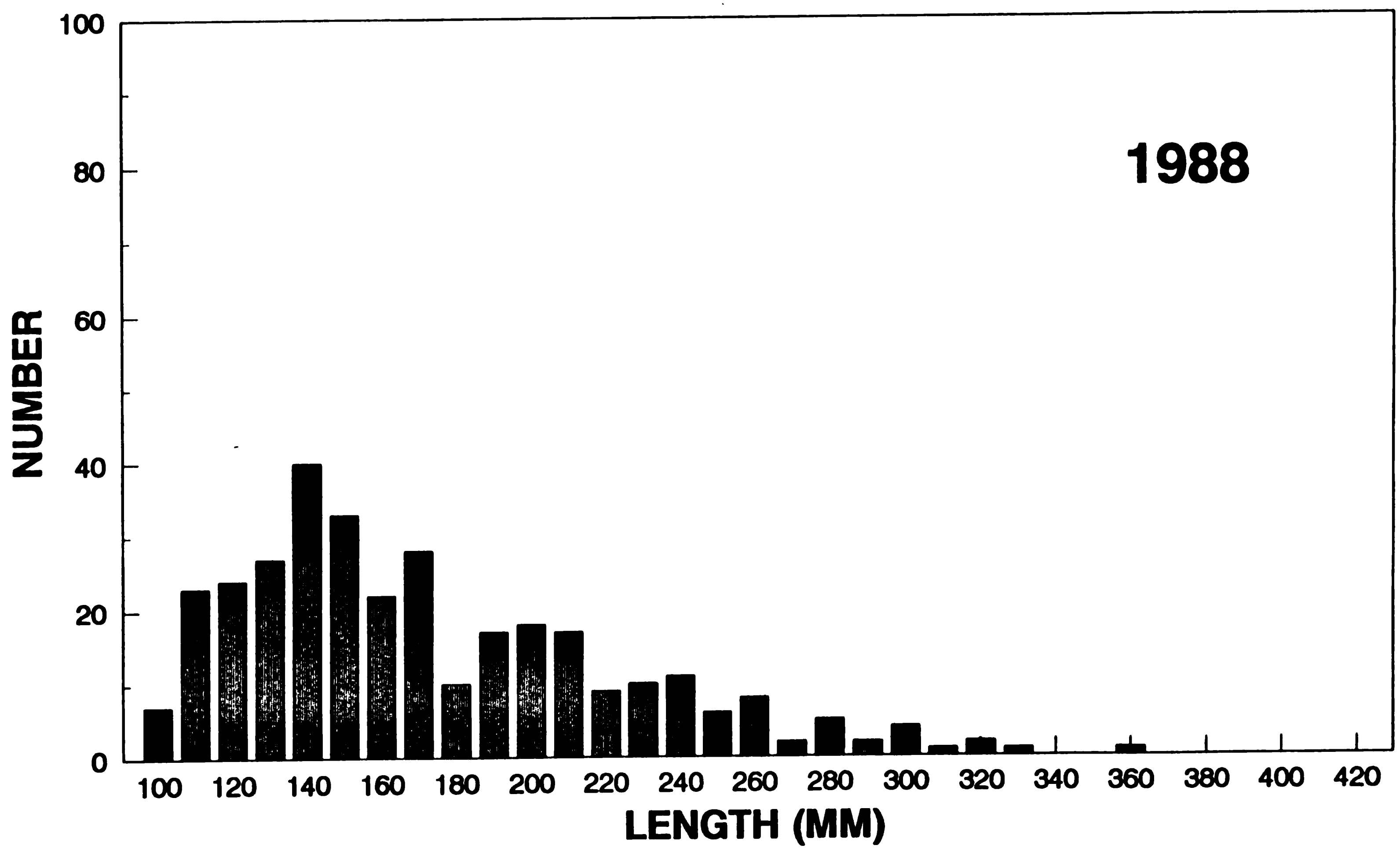

Figure 11. Length frequency distribution of the total annual catch in 1988.

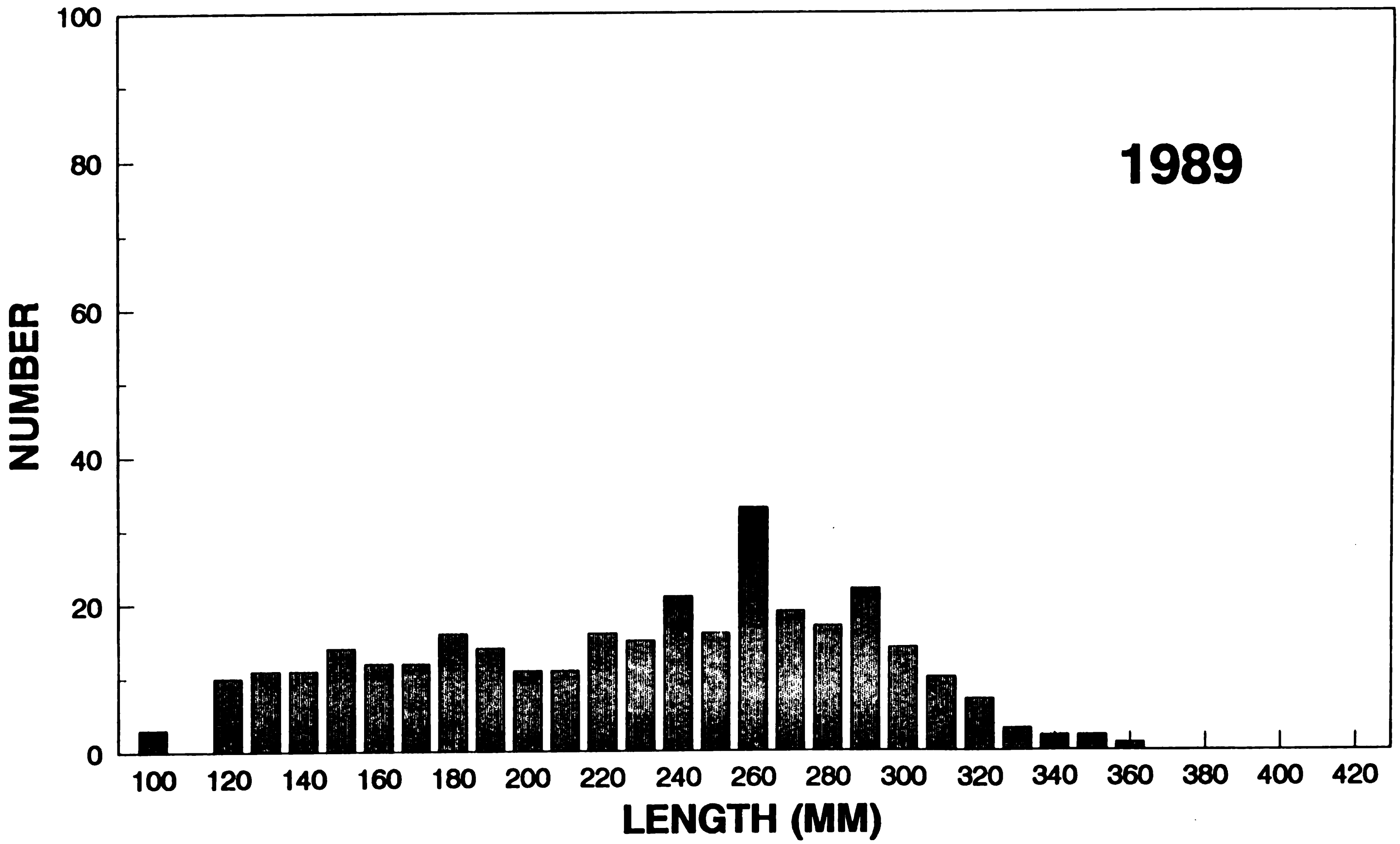

Figure 12. Length frequency distribution of the total annual catch in 1989.

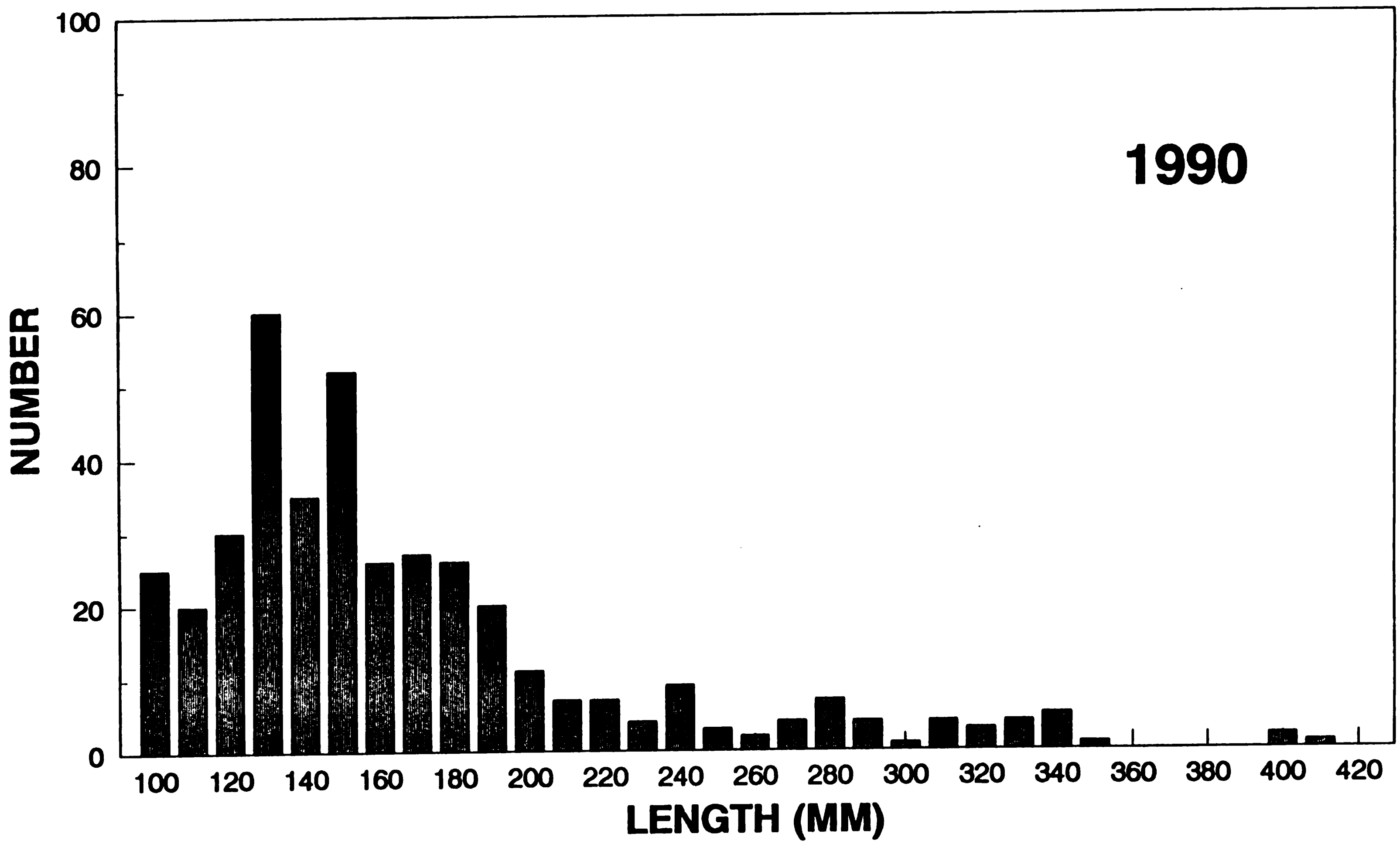

Figure 13. Length frequency distribution of the total annual catch in 1990.

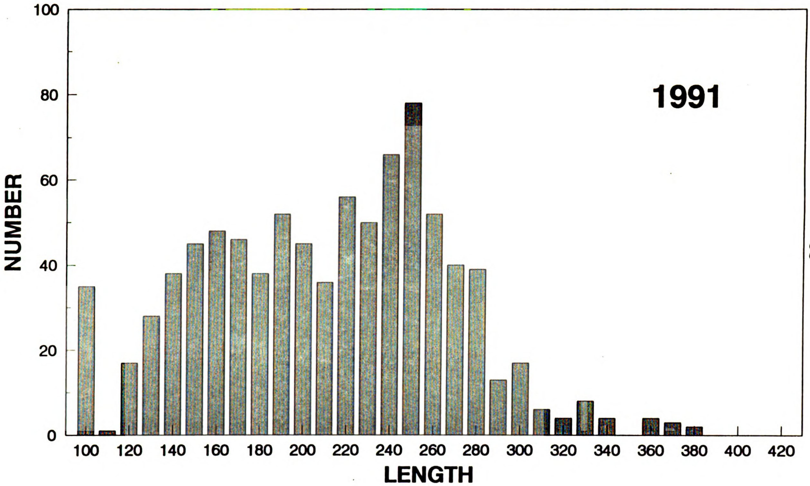

Figure 14. Length frequency distribution of the total annual catch in 1991.

Appendix B

Table 16. Results of the analysis of variance between mean annual growth rate of young of the year brook trout and temperature.

	R^2	Probability
Mean Daily Temperature	0.0273	0.7232
Days to 11C[1]	0.0481	0.6365
Days to 16C[1]	0.0891	0.5156
Days to 20C[1]	0.0277	0.7214
Days > 16C	0.0782	0.5435
Days > 20C	0.0212	0.7553
Days Between 11C & 16C	0.0350	0.6878
Days Between 16C & 20C	0.0727	0.5586

[1] Mean weekly temperature

Appendix B

Table 17. Results of the analysis of variance between mean annual growth of 1 year old brook trout and temperature.

	R^2	Probability
Mean Daily Temperature	0.1268	0.5564
Days to 11C[1]	0.0007	0.9547
Days to 16C[1]	0.1137	0.4595
Days to 20C[1]	0.0144	0.7976
Days > 16C	0.2593	0.4431
Days > 20C	0.0658	0.5786
Days Between 11C & 16C	0.1386	0.4108
Days Between 16C & 20C	0.0526	0.6208

[1] Mean weekly temperature

Appendix B

Table 18. Results of the analysis of variance between mean annual growth rate of 2 year old brook trout and temperature.

	R^2	Probability
Mean Daily Temperature	0.1268	0.5564
Days to 11C[1]	0.8847	0.0172
Days to 16C[1]	0.5547	0.1487
Days to 20C[1]	0.0285	0.7861
Days > 16C	0.1604	0.5041
Days > 20C	0.0533	0.7086
Days Between 11C & 16C	0.1175	0.5723
Days Between 16C & 20C	0.0001	0.9872

[1] Mean weekly temperature

Appendix B

Table 19. Results of the analysis of variance between mean length of brook trout at age 1 and temperature.

	R^2	Probability
Mean Daily Temperature	0.0278	0.7209
Days to 11C[1]	0.0452	0.6473
Days to 16C[1]	0.0907	0.5117
Days to 20C[1]	0.0284	0.7181
Days > 16C	0.0812	0.5355
Days > 20C	0.0219	0.7514
Days Between 11C & 16C	0.0376	0.6768
Days Between 16C & 20C	0.0744	0.5541

[1] Mean weekly temperature

Appendix B

Table 20. Results of the analysis of variance between mean length of brook trout at age 2 and temperature.

	R^2	Probability
Mean Daily Temperature	0.6004	0.0408
Days to 11C[1]	0.1536	0.3845
Days to 16C[1]	0.2245	0.2823
Days to 20C[1]	0.4284	0.1107
Days > 16C	0.0441	0.6512
Days > 20C	0.5051	0.0734
Days Between 11C & 16C	0.0738	0.5557
Days Between 16C & 20C	0.3493	0.1623

[1] Mean weekly temperature

Appendix B

Table 21. Results of the analysis of variance between mean length of brook trout at age 3 and temperature.

	R^2	Probability
Mean Daily Temperature	0.2259	0.4184
Days to 11C[1]	0.0051	0.9094
Days to 16C[1]	0.1437	0.5292
Days to 20C[1]	0.0438	0.7354
Days > 16C	0.0078	0.8880
Days > 20C	0.0873	0.6294
Days Between 11C & 16C	0.3064	0.3331
Days Between 16C & 20C	0.1297	0.5516

[1] Mean weekly temperature

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