CONDITION, ANNULUS FORMATION, GROWTH, AND FOOD HABITS OF BROWN AND RAINBOW TROUT FROM HABITATS WITH CONTRASTING TEMPERATURE REGIMES ON THE FIREHOLE RIVER, YELLOWSTONE NATIONAL PARK

by

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ABSTRACT

Year-round studies were made of condition, annulus formation, growth and food habits of brown trout *(Salmo trutta)* and rainbow trout *(Salmo gairdneri)* from sections of the Firehole River with contrasting temperature regimes, between July 1974 and October 1975. The study sections provided three temperature regimes, ranging from typical cold water to one resembling the warmer limits of trout distribution.

Condition of brown trout in the cold water habitat showed typical seasonal fluctuations with high values occurring during the growing season from spring through late summer and low values in fall and winter. Fluctuations in the condition of brown and rainbow trout in the warmest water habitat indicated two growth periods per year and a longer total annual growth period.

Elevated summer water temperatures restricted trout growth at the warmest water station. However, growth resumed with cooling of waters in early fall, resulting in an abnormal pattern of annulus formation with as many as three annuli being laid down per year. The presence of summer checks on scales collected at the intermediate temperature station indicated that two growth periods per year occurred in a similar manner at this station. Trout at the cold water stations did not form initial annuli until the second year of life, while those at the intermediate and warmest water stations formed annuli in their first year of life.

Brown trout showed the greatest length at age at the warmest water station and the least at the cold water station. Rainbow trout exhibited a slightly greater length at age than brown trout at the warmest water station. This advantage was attributable to more rapid early growth. Instantaneous population growth rates in weight (G_x) were estimated.

Trout at the cold water stations fed primarily on immature caddisflies, mayflies, and stoneflies. Molluscs, emerging dipterans and mayflies were the most important food in the warmest water habitat. It was speculated that molluscs, emerging insects, and general good availability of food allowed for good trout growth in the warmest water habitat.

INTRODUCTION

Responses of aquatic communities to alterations of natural temperature regimes by industrial waste discharge have received considerable attention in recent years. Heated effluents from steam-powered electric generating plants have been at the focal point of this controversy. Amounts of heat discharged can be considerably reduced by installation of "wet" cooling towers and closed cooling systems, however, the consumptive use of water by these systems itself poses a threat to the aquatic resource. Removal of water reduces river volume and typically results in increased temperatures during warm seasons. These increases are especially critical in streams whose water temperatures normally approach upper limits for growth and reproduction of certain aquatic organisms.

Temperature has been shown to be one of the most important factors influencing the growth of fishes (Brown 1957, Weatherley 1972). Much of the present knowledge concerning the growth of fishes at various temperatures has been obtained through laboratory experiments in which fish are fed a food of constant quality to satiety. However, a feeding regime of this type does not necessarily represent the natural environment where the quantity and quality of food organisms can fluctuate dramatically. Furthermore, elevated energy demands in nature resulting from competition and predation for example, cannot be duplicated in the laboratory.

Brett *et al.* (1969) recently demonstrated the interaction between temperature and food quantity and quality on the growth of sockeye salmon fingerlings *(Oncorhynchus nerka)*. Their results indicated that the optimum temperature for growth increased with an increase in ration size, however, specific growth rates were negative with certain rations at temperatures well below lethal and no growth occurred at approximately 23 C despite the presence of excess food. This suggests that the growth of fish in a stream with low macroinvertebrate productivity would be effected in a manner quite different from that of fish in a stream with good invertebrate production if both were subjected to an equal degree of thermal enrichment.

A considerable number of field studies have addressed the effects of thermal enrichment on warm water fishes and Pacific salmon, but there has been little work done on trout in the mountainous regions. The thermally enriched Firehole River of Yellowstone National Park provided a unique opportunity to compare the condition, annulus formation, growth, and food habits of brown trout *(Salmo trutta)* and rainbow trout *(Salmo gairdneri)* in habitats ranging from typical cold water to one whose elevated temperature regime may closely resemble those found at the warmer limits of trout distribution.

approximately 2319 meters (7610 ft). It was approximately 0.6 kilometer in length, with its lower reaches located approximately one kilometer above Kepler Cascades. The bottom substrate is primarily gravel and bedrock. In-stream obstructions such as logs and large rocks are common. The region is densely forested. Only a very small fraction (0.1%) of the total thermal effluent entering the Firehole River is present at this station (Allen and Day 1935).

Station 2: Below Kepler Cascades. This cold water station was approximately 0.3 kilometer in length, with its upper boundary approximately 0.4 kilometer below Kepler Cascades. It has an approximate elevation of 2300 meters (7550 ft). The bottom substrate is primarily gravel and bedrock. In-stream obstructions, especially fallen trees, are abundant. The station lies in a narrow, densely forested valley. No thermal effluent enters the Firehole River between Stations 1 and 2.

Station 3: Above Midway Geyser Basin. This intermediate temperature station was approximately 0.3 kilometer in length and is located below the Upper Geyser Basin, approximately 2.4 kilometers above the Midway Geyser Basin at an approximate elevation of 2215 meters (7270 ft). The bottom substrate is primarily bedrock with scattered areas of gravel. In-stream obstructions are abundant. Aquatic macrophytes are very common in areas of sediment deposition. The station is located in a forested region.

Station 4: Above Ojo Caliente. This warmest water station was approximately 1.6 kilometers in length and is located in the Lower Geyser Basin immediately above Ojo Caliente bridge. It has an approximate elevation of 2194 meters (7200 ft). The bottom substrate is primarily bedrock and rubble. Extrinsic in-stream obstructions are rare, however, the extremely irregular nature of the bedrock substrate provides numerous sheltered areas. Luxuriant growths of aquatic macrophytes exist in areas of sediment deposition. Grasses, sedges, and bare ground dominate the surrounding landscape but scattered conifer groves are common.

PROCEDURES

Trout in the Firehole River were sampled at various intervals between July 1974 and October 1975. Three types of electrofishing gear were used to capture fish. A Coffelt, backpack, battery-powered, D. C. unit proved to be effective at Stations 1 and 2. A Fisher D. C. rectifier used in conjunction with a 1500 watt, 110 volt A. C., gasoline-powered generator was used at Stations 1, 2, and 3, and in initial attempts at Station 4. High water temperature and conductivity at Station 4 prevented effective use of the electrofishing equipment described above. Angling was therefore the primary method used to capture fish at this station until June 1975 at which time a Coffelt VVP - 15 rectifier used in conjunction with a 3500 watt, 230 volt A. C., gasoline-powered generator was brought into operation. This electrofishing system was mounted in a flatbottom "john" boat and proved to be both maneuverable and effective.

Fish were weighed on an Ohms Model 1000 scale to the nearest gram and measured to the nearest millimeter in total length (TL). Scale samples for use in age and growth determinations were taken from the left side of the fish in the region lying between the dorsal fin and lateral line. Adipose fins were removed from fish prior to release, thus allowing for identification upon recapture and prevention of data duplication.

analyses were restricted to a given range in length. This served to keep the mean length of fish in all samples constant and eliminated potential length-related biases in comparing samples.

Impressions of scales were made on cellulose acetate slides using a heated vertical press. Scale impressions were read on a scale projector at 66X. Annuli were considered to be at the outermost border of a region of closely-spaced circuli (Tesch 1971). The time of annulus formation was considered to be the period corresponding to the formation of this outermost border. All measurements taken from scales were made along the maximum anterior radius (median axis). All scales were read twice. A third reading was performed when the two age determinations were not in agreement. Regenerate scales and scales for which no age could be determined were discarded. Length-frequency histograms were constructed and used in the verification of annuli (Hile 1941).

Fish length and anterior scale radius were found to be highly correlated ($p<.01$) at all stations. Y-axis intercepts of the regression lines were positive and of appreciable value. Although it can be given no morphological interpretation, the regression intercept of the Y-axis frequently approximates the length of fish when scales are first formed (Hile 1970). Because the straight line gave a good fit at all stations ($r = .927$ to $.971$), it is assumed that scale growth was proportional to growth in body length after the fish attained a length equal to the Y-axis intercept. The method of Fraser (1916) as described by Tesch (1971) was best suited for the back-calculation of length at time of annulus formation. The expression is:

$$L_n - C = \frac{S_n}{S} (L - C)$$

L_n = total length of fish at time of annulus 'n' formation

L = total length of fish at time scale was taken

S_n = radius of annulus 'n'

S = total anterior scale radius

C = value of Y-axis intercept

Weight at time of annulus formation was estimated using the length-weight relationship which is usually represented by the expression (Lagler 1956):

$$W = aL^b$$

with the logarithmic transformation being:

$$\log W = \log a + b(\log L)$$

where W is the weight in grams and L is the total length in millimeters. The constants a and b were determined by the method of least squares (Snedecor and Cochran 1967).

Digestive tracts for use in food habit analyses were excised in the field or in the laboratory from refrigerated specimens and preserved in 10 percent neutral buffered formalin. The portion of the digestive tract from the esophagus to the pylorus was opened and examined under a dissecting scope. Food organisms were identified and enumerated with the aid of taxonomic keys (Pennak 1953, Usinger 1956).

All statistical analyses were made according to Snedecor and Cochran (1967). The terms significant and highly significant refer to statistical significance at the $p<.05$ and $p<.01$ levels, respectively.

RESULTS

Station 1

The fish populations at Station 1 were sampled at infrequent intervals from September 1974 through May 1975. Sampling dates are given in Table 2. Brook trout and brown trout were found to be the

TABLE 2. MEAN CONDITION (K) OF BROWN TROUT ($TL \geq 100mm$, $\overline{X} = 145mm$) AT STATION 1.

Date	N	Mean K (±SD)
4 September 1974	28	1.03 ± 0.09[a]
2 October 1974	21	1.02 ± 0.09[a]
4 December 1974	33	0.95 ± 0.06
17 May 1975	17	1.12 ± 0.06

[a]Means so designated are not significantly different ($p>.05$).

only species inhabiting this station, with brook trout constituting 55.2 and 82.3 percent of comprehensive samples taken on 4 September 1974 and 17 May 1975, respectively.

No significant correlation could be demonstrated with the regression of condition on length for 99 brown trout collected throughout the study. The results of the analysis of condition are given in Table 2. Condition was found to be lowest in December ($K = .95$) and highest in May ($K = 1.12$).

The body-scale relationship for 137 brown trout was $Y = 22.31 + 2.666X$ ($r = .971$), where Y is total length of fish in millimeters and

X is the anterior scale radius (X66) in millimeters. The sample of 31 brown trout collected on 17 May 1975 consisted of 14, 15, and 2 age-group 1, 2, and 3, trout, respectively. The scales of 100, 67, and 50 percent of the members of these respective age-groups exhibited newly-formed annuli. Formation of the first annulus was completed in the second spring of life. Annuli were very distinct and readily identified.

Results of the back calculations of length and weight at earlier ages (annuli) are given in Table 3. Brown trout at Station 1 were estimated to be 61, 120, 186, and 245 millimeters in length and 3, 18, 64, and 142 grams in weight at the time of annulus 1, 2, 3, and 4 formation, respectively. The length-weight relationship for 151 brown trout collected throughout the study was $\log W = -4.762 + 2.894 \log L$ ($r = .994$). The increments of grand mean (increment of mean) remain similar. The mean of increments closely correspond to the increments of mean but show relatively lower values over the last two intervals. As compared to the increment of mean, the mean of increments should give a more accurate indication of the annual growth between two consecutive annuli as it is derived from only those fish which exhibit both annuli.

Length-frequency histograms were constructed and used in the verification of aging and to demonstrate the lengths of the age-groups. Figure 2 depicts the length-frequency distribution of brown

TABLE 3. CALCULATED MEAN TOTAL LENGTH (MILLIMETERS) AND WEIGHT (GRAMS) AT THE TIME OF ANNULUS FORMATION OF BROWN TROUT AT STATION 1. NUMBER OF FISH IN PARENTHESIS.

Year-Class	Annulus 1	2	3	4
1974	[b,a]60(14)			
1973	[b]62(60)	[a]117(10)		
1972	[a]56(25)	[a]118(25)	[a]179(1)	
1971	[b,a]61(10)	[a]123(10)	[a]184(10)	
1970	[b]70(4)	[a]133(4)	[a]191(4)	245(4)
Grand Mean Length	61±9.6[c](113)	120±13.6(49)	186±15.4(15)	245±11.7(4)
Increment of Mean Length	61	59	66	59
Mean of Length Increments	61	61	60	54
Calculated Weight	3	18	64	142

[a]Means so designated under a given annulus are not significantly different (p>.05).

[b]Means so designated under a given annulus are not significantly different (p>.05).

[c]Standard deviation.

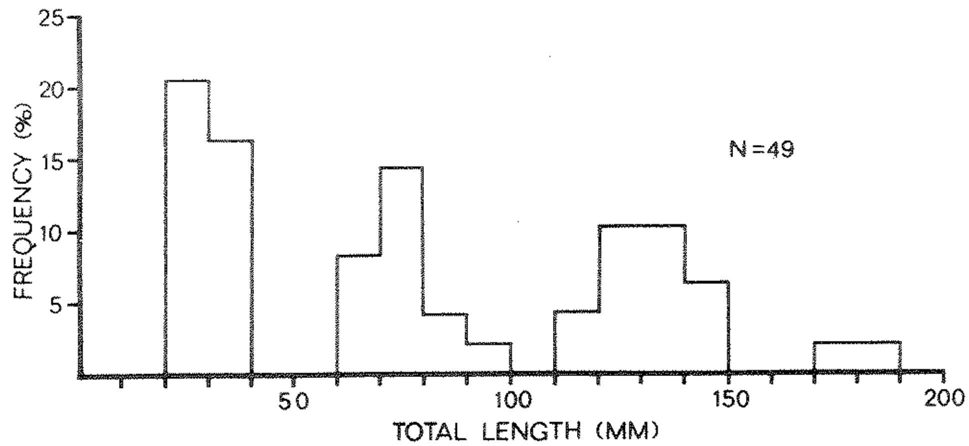

Figure 2. Length-frequency distribution of brown trout collected at Station 1 on 17 May 1975.

trout collected at Station 1 on 17 May 1975. The occurrence of distinct modal groups, each consisting of an individual age-group, is typical of distributions seen at Station 1 throughout the study. Intervals between modes agree very well with the increments of annual growth given in Table 3.

Results of the analysis of brown trout food habits at Station 1 are given in Table 4. Immature caddisflies (primarily Brachycentridae and Rhyacophilidae) were the dominant food of trout at Station 1. Stoneflies showed a dramatic upsurge in importance in December samples. Although Armitage (1961) took no sample on the Firehole during winter, Kennedy (1967) found stoneflies to be most abundant in the December benthos of Convict Creek, a stream comparable to the upper Firehole

TABLE 4. PERCENTAGE OF TOTAL AND PERCENT FREQUENCY (IN PARENTHESIS) OF VARIOUS GROUPS OF FOOD ORGANISMS FOUND IN THE STOMACHS OF 48 BROWN TROUT COLLECTED AT STATION 1. FISH RANGED FROM 76 TO 288mm IN TOTAL LENGTH WITH A MEAN OF 172±54SD. NONE OF THE STOMACHS EXAMINED WERE EMPTY.

Date	Number of Fish In Sample	Mean Number of Organisms Per Stomach	Trichoptera	Plecoptera	Ephemeroptera	Diptera	Coleoptera	Ants	Fish	Other[a]
4 September 1974	13	14.3	50.5(84.6)	9.1(53.8)	18.8(69.2)	9.1(23.1)	1.6(23.1)	10.8(46.2)	0.0(0.0)	0.0(0.0)
2 October 1974	10	14.1	66.7(90.0)	7.1(70.0)	3.5(40.0)	12.8(30.0)	2.8(40.0)	5.7(30.0)	0.0(0.0)	1.4(20.0)
4 December 1974	10	35.9	52.4(100.0)	44.6(100.0)	2.5(50.0)	0.0(0.0)	0.6(10.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
17 May 1975	15	9.5	29.4(80.0)	11.9(66.7)	44.8(86.7)	11.9(33.3)	1.4(13.3)	0.0(0.0)	0.7(6.7)	0.0(0.0)
Mean		18.5	49.8(88.7)	18.2(72.6)	17.4(61.5)	8.5(21.6)	1.6(21.6)	4.1(19.1)	0.2(1.7)	0.4(5.0)
Weighted Mean		17.3	50.4(83.3)	24.6(70.8)	13.6(64.6)	6.3(22.9)	1.3(20.8)	3.4(18.8)	0.1(2.1)	0.2(4.2)

[a]Spider, wasp

in elevation and temperature regime. Large numbers of *Ephemerella* spp. nymphs occurred with great frequency in the stomachs of trout collected in May. Armitage (1961) found *E. grandis* and *E. glacialis* to occur only in spring benthos samples. Diptera and Coleoptera were frequently encountered in stomachs but constituted only a small percentage of the food items taken. Terrestrial invertebrates such as ants occurred in fall samples only. Predation upon other fish and cannibalism were extremely rare despite the abundance of young-of-the-year trout.

Station 2

Fish at Station 2 were sampled at approximately bimonthly intervals from August 1974 through October 1975. Dates of major samples are given in Table 5. Brown trout was the dominant species, constituting 99.0 and 97.0 percent of comprehensive samples collected on 2 August 1974 and 18 May 1975, respectively, with brook trout accounting for the remainder. The only rainbow trout seen were three of approximately 285 millimeters collected on 4 December 1974 and one of similar length captured on 15 February 1975. Brown trout young-of-the-year were abundant during the May and July samplings, but no special effort was made to intensively sample this group.

There was a weak but highly significant correlation between condition (K) and length (L) for 756 brown trout which is described

TABLE 5. MEAN CONDITION (K) OF BROWN TROUT ($TL \geq 100mm$, $\overline{X} = 178mm$) AT STATION 2.

Date	N	Mean K (±SD)
2 August 1974	73	$0.98 \pm 0.06^{b,c*}$
5 September 1974	33	$0.94 \pm 0.08^{c,d}$
2 October 1974	33	$0.93 \pm 0.07^{c,d}$
23 October 1974	75	0.96 ± 0.09^{c}
4 December 1974	42	0.91 ± 0.07^{d}
15 February 1975	42	0.89 ± 0.07^{d}
18 May 1975	34	1.07 ± 0.09^{a}
2 July 1975	55	1.06 ± 0.10^{a}
18 August 1975	188	1.00 ± 0.09^{b}
12 October 1975	151	0.90 ± 0.09^{d}

*Means designated by a common letter are not significantly different ($p > .05$).

by the equation $K = .996 - .000193\ L$ ($r = -.161$). The results of the analysis of condition are given in Table 5. Condition was found to be lowest in February (K = .89) and highest in May (K = 1.07).

Large numbers of brown trout were readily collected at Station 2 throughout fall and early winter 1974. Beginning in February and continuing into July 1975, however, it became increasingly more difficult to sample the number of fish which had been present in previous months. The once-conspicuous large fish were considerably less abundant in February and were completely absent in May and July 1975. Large fish were again found in the August 1975 sample. Length-frequency distributions (Fig. 3) confirm the more casual field observations, indicating the presence of large fish at Station 2 from August through December followed by a dramatic reduction in abundance.

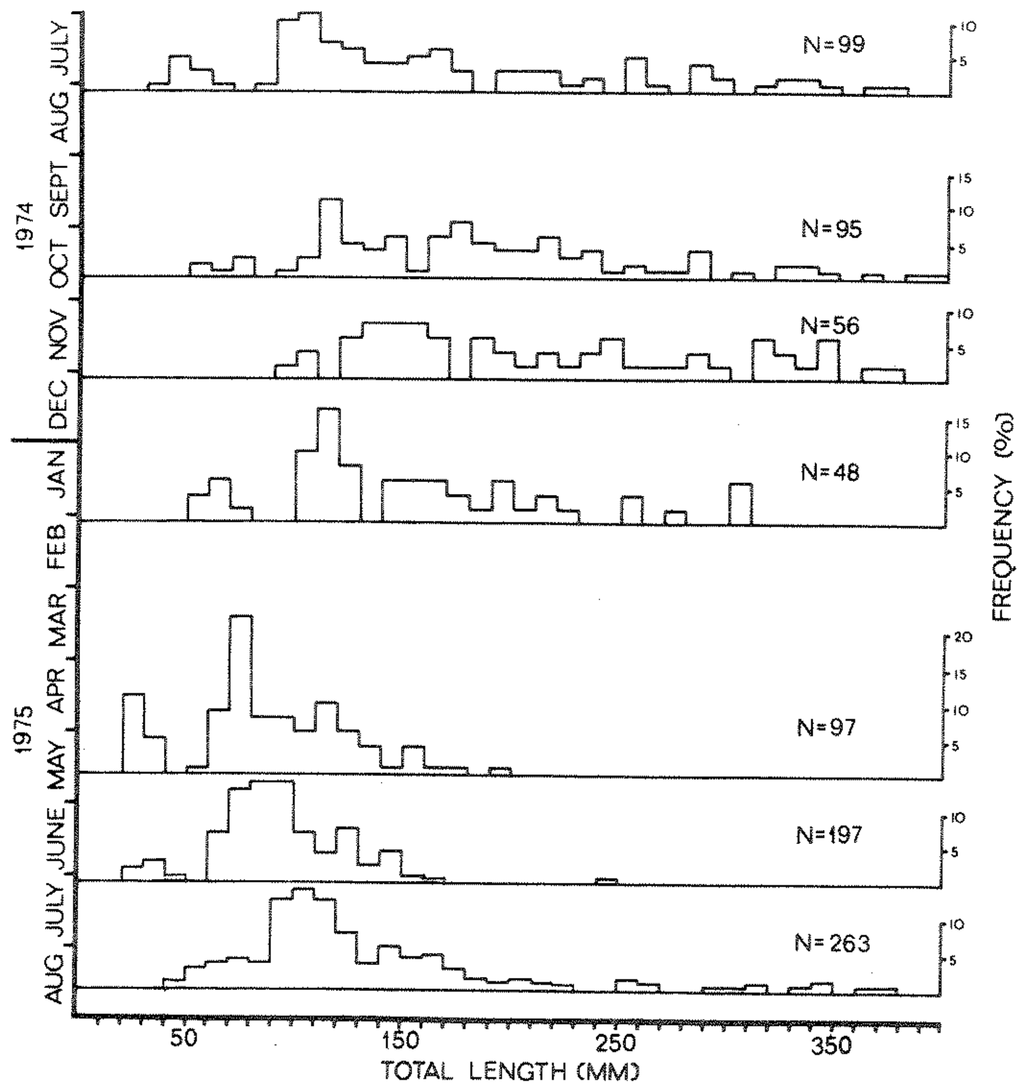

Figure 3. Length-frequency distributions of brown trout at Station 2.

The length-frequency distributions with respect to season suggest that spawning migrations may be producing these changes in relative abundance of larger fish. However, while spawning undoubtedly occurred at this station, the possibility of behavioral thermal regulation in a river with a thermal gradient as pronounced as that of the Firehole cannot be precluded.

The seasonal movement of larger fish into Station 2 constitutes a potential bias in growth determinations, since transient fish may exhibit a growth rate quite different from that of resident fish. Indeed, should these transient fish reside in the warmer downstream regions during winter, it is conceivable that their growth could be significantly enhanced.

In order to eliminate this potential bias, growth characteristics for Station 2 were computed for those fish in the May and July 1975 samples only. The length-frequency distributions (Fig. 3) of these samples indicate the absence of larger, transient fish.

The body-scale relationship for 261 brown trout collected in May and July 1975 was $Y = 30.08 + 2.601X$ ($r = .927$), where Y is the total length of fish in millimeters and X is the anterior scale radius (X66) in millimeters. The 18 May sample included 50, 22, and 6 trout of age-groups 1, 2, and 3, respectively. Scales of 100, 50, and zero percent of the members of these respective age-groups exhibited newly-formed annuli. Formation of the first annulus was completed in the second spring of life. Annuli were very distinct and readily identified.

The May and July 1975 samples included 262 brown trout of which 77.0, 20.7, and 2.3 percent were of age-groups 1, 2, and 3, respectively. No fish older than age-group 3 were collected.

Table 6 gives the results of the growth determinations for brown trout at Station 2. Trout were estimated to be 63, 113, and 167 millimeters in length and 3, 15, and 46 grams in weight at the time of annulus 1, 2, and 3 formation, respectively. The length-weight relationship for 244 trout was $\log W = -4.648 + 2.841 \log L$ ($r = .971$). May and July length-frequency distributions (Fig. 3) agree well with the increments of annual growth given in Table 6.

Results of the food habits analysis at Station 2 are given in Table 7. In general, the food of brown trout at Station 2 is similar to that at Station 1, with immature caddisflies of the Families Brachycentridae and Rhyacophilidae being the dominant food organisms. Stoneflies increased in importance during winter months. Mayflies (*Ephemerella* spp.) were abundant in the stomach contents of trout collected in May. Coleoptera and Diptera were frequently encountered, but constituted only a small portion of the total food. Invertebrates of terrestrial origin were found in fall samples only. Trout eggs occurred among the stomach contents in October and were extremely numerous in December. These eggs apparently became available food

TABLE 6. CALCULATED MEAN TOTAL LENGTH (MILLIMETERS) AND WEIGHT (GRAMS) AT THE TIME OF ANNULUS FORMATION OF BROWN TROUT AT STATION 2. NUMBER OF FISH IN PARENTHESIS.

Year-Class	Annulus 1	Annulus 2	Annulus 3
1974	[a]63(201)		
1973	[a]63(55)	114(55)	
1972	[a]60(6)	103(6)	167(6)
Grand Mean Length	63±9.0[b](262)	113±11.0(61)	167±16.1(6)
Increment of Mean Length	63	50	54
Mean of Length Increments	63	50	64
Calculated Weight	3	15	46

[a]Means so designated under a given annulus are not significantly different ($p>.05$).

[b]Standard deviation.

for trout as the result of being dislodged by spawning activities. Predation upon fish was rare.

Station 3

The fish populations at Station 3 were sampled on 18 September 1974, 22 July and 5 September 1975. Brown trout was found to be the dominant species, constituting 91.0, 91.6, and 91.1 percent of the samples, respectively.

There was a weak but significant correlation between condition (K) and length (L) for 170 brown trout and the relationship is described by the equation $K = 1.042 - .000240\ L$ ($r = -.190$). Table 8 gives the results of the analysis of condition at Station 3. Significant differences in condition existed among all sampling dates.

TABLE 8. MEAN CONDITION (K) OF BROWN TROUT ($TL \geq 100mm$, $\bar{X} = 160mm$) AT STATION 3.

Date	N	Mean K (±SD)
18 September 1974	41	0.95 ± 0.11
22 July 1975	39	1.06 ± 0.09
5 September 1975	85	1.01 ± 0.08

The body-scale relationship for 320 brown trout was $Y = 16.12 + 2.668X$ ($r = .951$), where Y is the fish length in millimeters and X is the anterior scale radius (X66) in millimeters. Brown trout at Station 3 were found to form two checks per year with the first being laid down in spring and the second in late summer. Newly-formed spring checks were present on scales collected on 22 July, and similar summer checks of recent formation were present on scales collected on 18 September 1974 and 5 September 1975 (Fig. 4). In order to remain consistent with standard practice, the spring check was considered the true annulus, even though the summer check was as distinct or more distinct than the former.

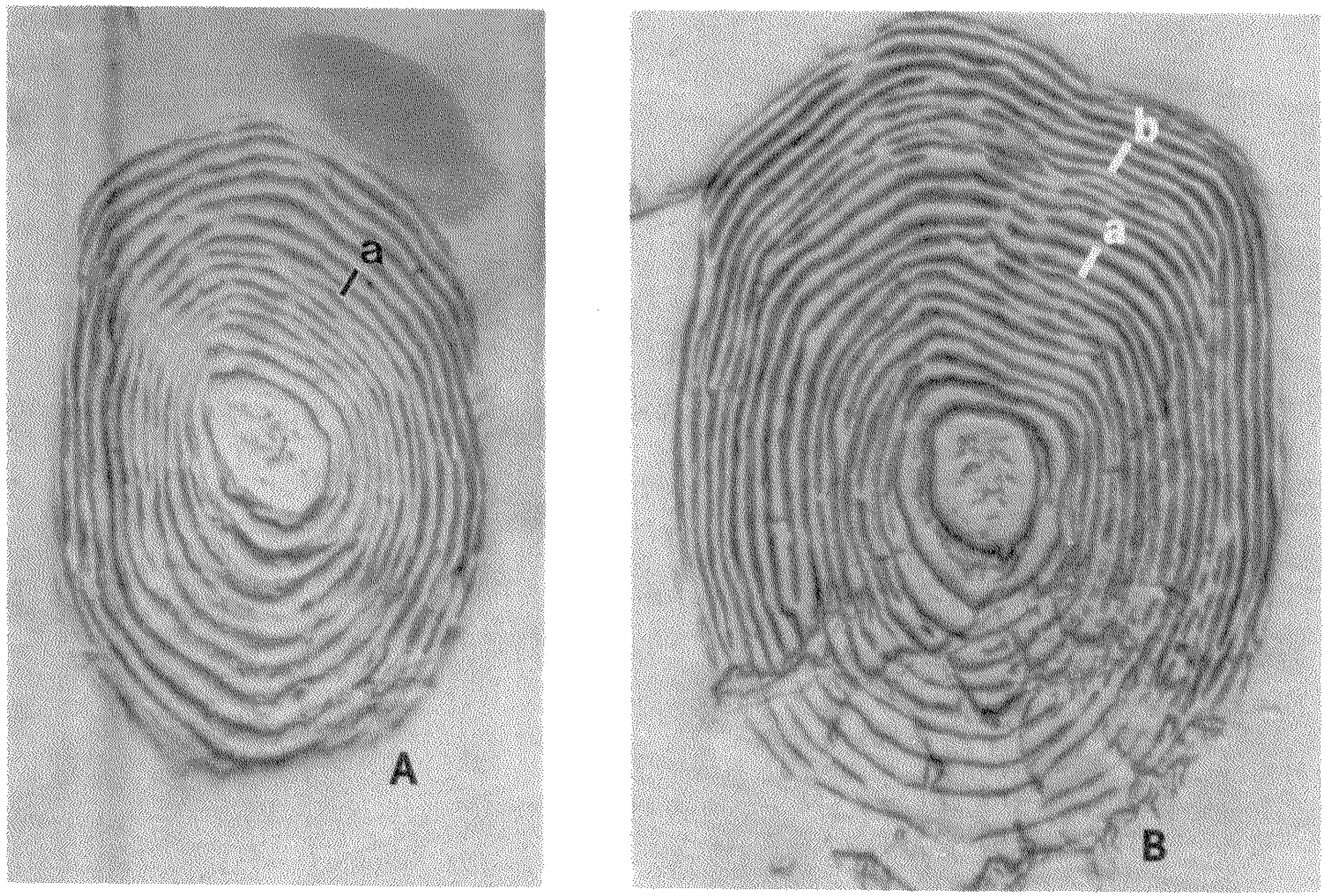

Figure 4. Scales from young-of-the-year brown trout at Station 3 taken from an 85 millimeter fish on 22 July (A) and a 105 millimeter fish on 5 September (B). Spring annuli and the summer check are indicated by the letters a and b, respectively.

The sample total of 330 brown trout included 324 fish of age-group 1 and older, with 80.2, 16.0, and 3.7 percent being of age-groups 1, 2, and 3, respectively. Six large fish could not be accurately aged because of excessive scale erosion.

The results of the back calculation of length and weight at earlier ages are given in Table 9. All calculations were made with respect to the time of spring annulus formation. Brown trout at Station 3 were estimated to be 48, 140, and 243 millimeters in length and 1, 28, and 137 grams in weight at the time of annulus 1, 2, and 3 formation, respectively. The length-weight relationship for 312 trout was $\log W = -4.800 + 2.908 \log L$ ($r = .992$).

Figure 5 depicts the length-frequency distributions of brown trout at Station 3. Three age-groups can be seen with the two youngest being most distinct. Intervals between age-groups agree well with annual growth data given in Table 9. The food habits of trout at Station 3 were not studied.

Rainbow trout of a young age-class accounted for 9.0, 8.4, and 8.9 percent of the respective samples. Mean total length of rainbow trout collected was 102 ± 6 SD, 77 ± 23 SD, and 138 ± 28 SD millimeters on the respective sampling dates. No rainbow trout larger than 181 millimeters was collected.

TABLE 9. CALCULATED MEAN TOTAL LENGTH (MILLIMETERS) AND WEIGHT (GRAMS) AT THE TIME OF SPRING ANNULUS FORMATION OF BROWN TROUT AT STATION 3. NUMBER OF FISH IN PARENTHESIS.

Year-Class	Annulus 1	Annulus 2	Annulus 3
1975	[b]47(213)		
1974	[a]50(92)	[b,a]142(45)	
1973	[a]53(17)	[a]130(17)	[a]241(10)
1972	[b,a]59(2)	[b]182(2)	[a]256(2)
Grand Mean Length	48±8.6[c](324)	140±25.2(64)	243±23.6(12)
Increment of Mean Length	48	92	103
Mean of Length Increments	48	89	100
Calculated Weight	1	28	137

[a]Means so designated under a given annulus are not significantly different ($p>.05$).

[b]Means so designated under a given annulus are not significantly different ($p>.05$)

[c]Standard deviation.

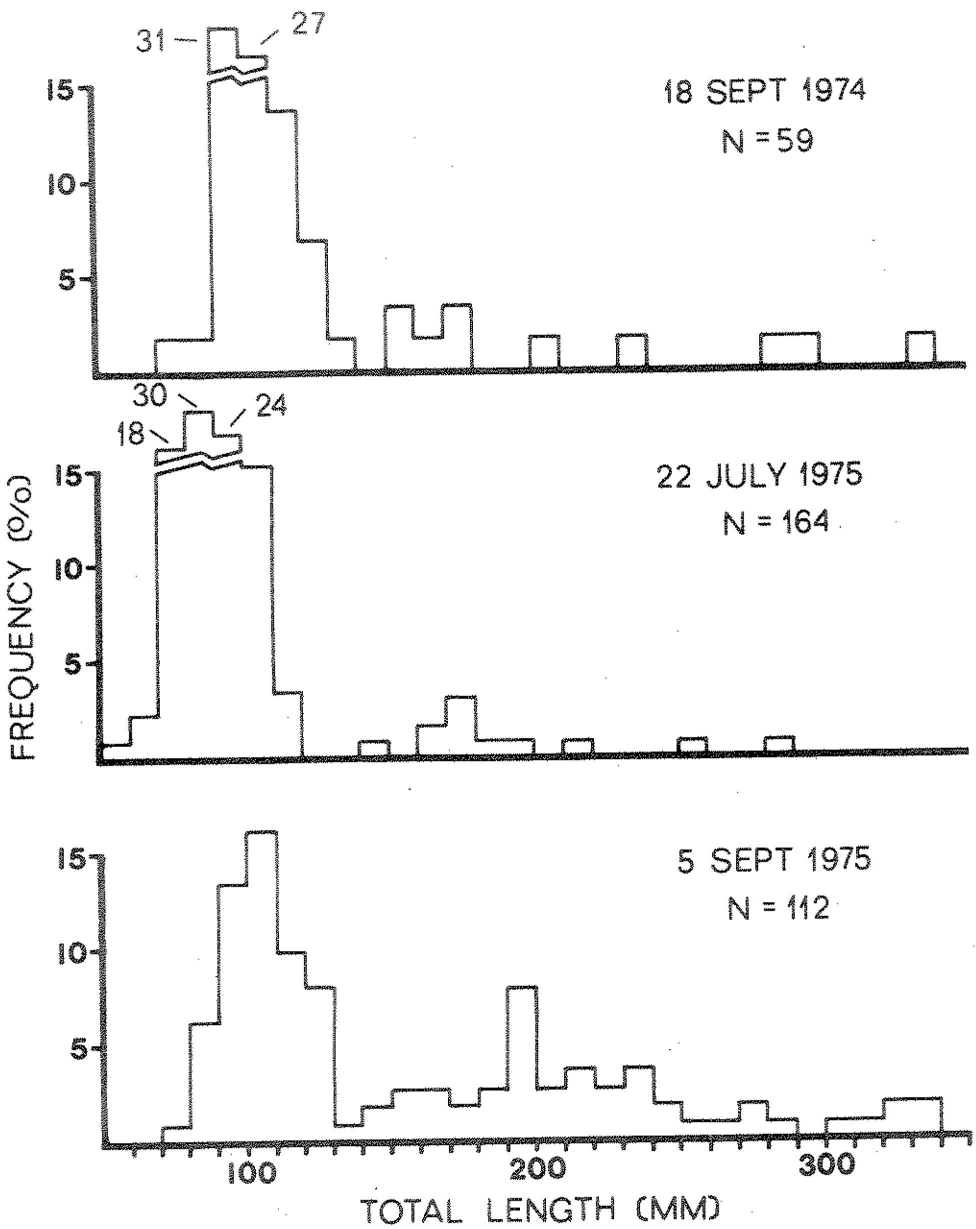

Figure 5. Length-frequency distributions of brown trout at Station 3.

Station 4

The fish populations at Station 4 were sampled at approximately monthly intervals from July 1974 through October 1975. Rainbow trout was found to be the dominant species, constituting 80.4 percent of a comprehensive sample of 526 fish collected on 24-27 June 1975. Brown trout accounted for the remainder of the sample (19.6%). Two brook trout of 155 and 170 millimeters constituted 0.5 percent of the sample in October 1975.

Brown Trout

The relationship between condition (K) and length (L) for 339 brown trout was highly correlated and described by the equation $K = 1.105 - .000591\ L$ ($r = -.522$). Results of the analysis of condition are given in Table 10. Samples collected in August and September were pooled after statistical testing failed to demonstrate significant difference in condition among the samples. Condition was low in August/September, January, and at the conclusion of the study in October.

The body-scale relationship for 202 brown trout was $Y = 24.85 + 2.895X$ ($r = .954$), where Y is the total length of fish in millimeters and X is the anterior scale radius (X66) in millimeters. Brown trout at Station 4 were found to form two distinct checks and a much weaker third check per year. Scales taken from yearling and older fish on

TABLE 10. MEAN CONDITION (K) OF BROWN TROUT ($TL \geq 100mm$, $\bar{X}$ = 265mm) AT STATION 4.

Date	N	Mean K (±SD)
17 July 1974	10	0.97 ± 0.10[a,b,c,g,h*]
August/September 1974	8	0.86 ± 0.08[c,d,h]
30 October 1974	22	0.94 ± 0.10[a,b,c,e,f,g,h]
27 November 1974	16	0.87 ± 0.04[c,d,h]
1 January 1975	12	0.80 ± 0.08[d]
16 February 1975	14	0.88 ± 0.07[c,d,f]
29 March 1975	12	0.94 ± 0.03[a,b,c,e,f]
17 May 1975	4	1.00 ± 0.10[a,b,c,e,f,g,h]
24 June 1975	41	1.00 ± 0.10[a,e,g]
5 August 1975	32	0.98 ± 0.10[a,b,e,g]
27 August 1975	48	0.97 ± 0.08[e,g,h]
16 October 1975	95	0.95 ± 0.09[e,f,g,h]

*Means designated by a common letter are not significantly different (p>.05).

16 February 1975 exhibited a strong, newly-formed check. Newly-formed checks were not detected on young-of-the-year scales, however, until June. This very faint spring check consisted of only two or three circuli and was observed on scales from a small percentage of larger trout (yearlings and older) in June. The second check is laid down in late summer and was easily detected in samples collected in October 1974.

Results of the back calculation of length and weight at annuli are given in Table 11. Calculations were made with respect to the spring check for young-of-the-year and to the winter check for older fish because of the weakness and inconsistency of the spring check in

TABLE 11. CALCULATED MEAN TOTAL LENGTH (MILLIMETERS) AND WEIGHT (GRAMS) AT THE TIME OF WINTER (SPRING IN YOUNG-OF-THE-YEAR) ANNULUS FORMATION OF BROWN TROUT AT STATION 4. NUMBER OF FISH IN PARENTHESIS.

Year-Class	Annulus 1	Annulus 2	Annulus 3	Annulus 4
1975	61(54)			
1974	[a]77(35)	[b]138(28)		
1973	[a]76(84)	[a]176(83)	[a]273(32)	
1972	[a]74(24)	[a]165(24)	[a]267(24)	[a]382(5)
1971	[a]97(2)	[b,a]185(2)	[a]304(2)	[a]356(2)
Grand Mean Length	72±14.7[c](199)	167±36.0(137)	272±31.0(58)	375±24.6(7)
Increment of Mean Length	72	95	105	103
Mean of Length Increments	72	91	106	81
Calculated Weight	4	46	187	471

[a]Means so designated under a given annulus are not significantly different (p>.05).

[b]Means so designated under a given annulus are not significantly different (p>.05).

[c]Standard deviation.

older fish. Brown trout were estimated to be 72, 167, 272, and 375 millimeters in length and 4, 46, 187, and 471 grams in weight at the time of annulus 1, 2, 3, and 4 formation, respectively. The length-weight relationship for 390 brown trout collected throughout the study was log W = -4.743 + 2.881 log L (r = .995).

Figure 6 gives the length-frequency distributions of brown trout

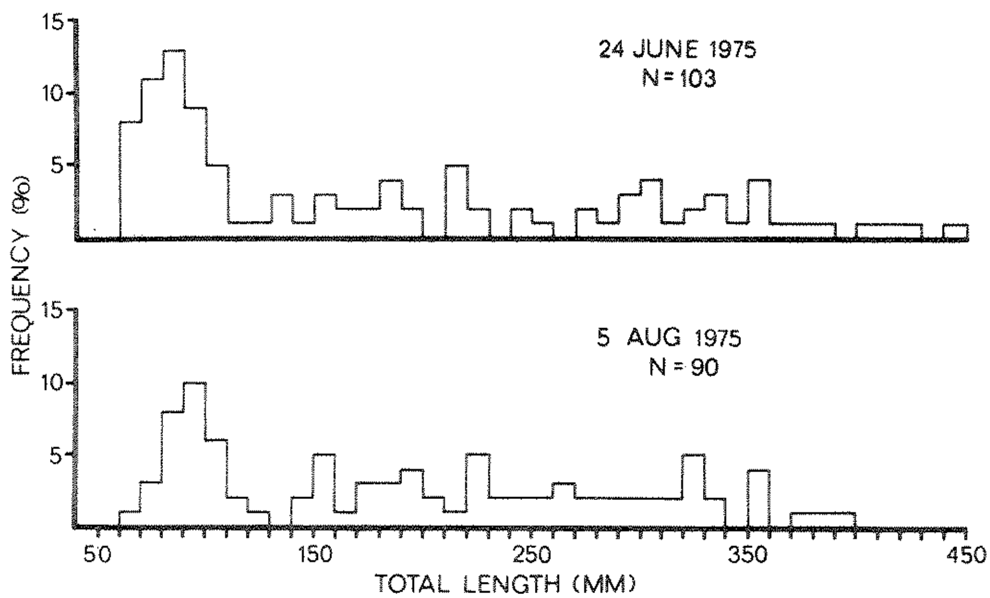

Figure 6. Length-frequency distributions of brown trout at Station 4.

collected at Station 4 on 24 June and 5 August 1975. Young-of-the-year are most clearly indicated. Two modes centering around 200 and 330 millimeters are suggested, in approximate agreement with annual growth data presented in Table 11.

Results of the food habits analysis for brown trout at Station 4 are given in Table 12. Dipterans, mayflies, and molluscs were the most important food of brown trout at Station 4. Intense feeding on emerging insects resulted in large numbers of organisms per stomach. This can be seen in the November sample which was collected while trout were feeding on emerging mayfly nymphs (primarily Baetidae), and in the January and March samples which were collected during dipteran (Chironomidae) hatches. Insect emergence and subsequent feeding by trout in the warm waters of Station 4 was commonly observed throughout the study. Samples collected during insect hatches tend to bias weighted mean values to favor the emergent group and result in the divergence of mean and weighted mean values. Molluscs (mainly *Physa* sp.) constituted a large percentage of the total stomach content and were very frequent in all samples. Odonates and amphipods (*Gammarus* sp.) occurred frequently in the food, but constituted only a small percentage of the total stomach contents. Armitage (1961) found *Ophiogomphus* (Odonata) in large numbers at Station 4. Caddisflies (primarily Hydropsychidae) occurred very frequently, but were unimportant in terms of total stomach content. Stoneflies were found in one stomach. Armitage (1961) found stonefly populations to be severely depressed at Station 4. No fish were found among the stomach contents.

TABLE 12. PERCENTAGE OF TOTAL AND PERCENT FREQUENCY (IN PARENTHESIS) OF VARIOUS GROUPS OF FOOD ORGANISMS FOUND IN THE STOMACHS OF 79 BROWN TROUT COLLECTED AT STATION 4. FISH RANGED FROM 109 TO 462mm IN TOTAL LENGTH WITH A MEAN OF 291±54SD. NONE OF THE STOMACHS EXAMINED WERE EMPTY.

Date	Number of Fish In Sample	Mean Number of Organisms Per Stomach	Trichoptera	Plecoptera	Ephemeroptera	Diptera	Mollusca	Amphipoda	Odonata	Coleoptera	Other[a]
30 October 1974	19	51.8	4.0(73.7)	0.0(0.0)	51.9(89.5)	28.7(73.7)	14.3(89.5)	0.2(10.5)	0.0(0.0)	0.0(0.0)	0.9(5.3)
27 November 1974	18	135.6	0.7(27.8)	0.0(0.0)	91.1(88.9)	4.9(44.4)	3.1(83.3)	0.1(11.1)	0.2(11.1)	0.0(0.0)	0.0(0.0)
2 January 1975	12	74.8	6.0(66.7)	0.0(0.0)	2.1(58.3)	77.4(58.3)	13.6(83.3)	0.0(0.0)	0.6(16.7)	0.3(16.7)	0.0(0.0)
16 February 1975	14	20.9	14.3(85.7)	0.0(0.0)	0.3(7.1)	14.7(35.7)	61.8(85.7)	7.5(28.6)	1.0(14.3)	0.3(7.1)	0.0(0.0)
29 March 1975	12	216.2	2.8(66.7)	0.0(8.3)	16.6(91.7)	70.0(100.0)	9.9(100.0)	0.3(33.3)	0.2(16.7)	0.2(16.7)	0.0(0.0)
17 May 1975	4	18.2	5.5(75.0)	0.0(0.0)	8.5(100.0)	28.8(100.0)	54.7(75.0)	0.0(0.0)	1.3(75.0)	1.3(50.0)	0.0(0.0)
Mean		86.3	5.6(65.9)	0.0(1.4)	28.4(72.6)	37.4(68.7)	26.2(86.1)	1.4(13.9)	0.6(22.3)	0.4(15.1)	0.2(0.9)
Weighted Mean		94.2	3.2(63.3)	0.0(1.3)	43.0(70.9)	40.6(63.3)	12.2(87.3)	0.5(15.2)	0.3(13.9)	0.1(8.9)	0.1(1.3)

[a]Hemiptera

Rainbow Trout

Condition (K) and length (L) were highly correlated for 909 rainbow trout and the relationship is described by the equation $K = 1.160 - .000630\ L$ ($r = -.471$). Table 13 gives the results of the analysis of condition. Condition was low in January 1975, and August of both years.

TABLE 13. MEAN CONDITION (K) OF RAINBOW TROUT (TL≥100mm, $\bar{X}$ = 287mm) AT STATION 4.

Date	N	Mean K (±SD)
17 July 1974	13	0.95 ± 0.09[a,b,c,f,g*]
1 & 7 August 1974	19	0.89 ± 0.11[c]
4 September 1974	17	0.91 ± 0.08[c,g]
2 October 1974	7	0.92 ± 0.04[a,b,c,f,g]
30 October 1974	18	1.04 ± 0.08[a,d,f]
27 November 1974	14	0.95 ± 0.07[a,b,c,d,e]
2 January 1975	25	0.86 ± 0.05[c]
16 February 1975	17	0.92 ± 0.10[b,c,e]
29 March 1975	30	0.92 ± 0.06[b,c,e]
17 May 1975	28	1.00 ± 0.07[a,b,d,e,f]
24 June 1975	72	1.00 ± 0.08[d,f]
5 August 1975	112	1.00 ± 0.11[d,f]
27 August 1975	106	0.96 ± 0.07[d,e,f,g]
16 October 1975	140	1.01 ± 0.07[d,f]

*Means designated by a common letter are not significantly different ($p>.05$).

The body-scale relationship for 533 rainbow trout was $Y = 15.63 + 3.037\ X$ ($r = .962$), where Y is the fish length in millimeters and X is the anterior scale radius (X66) in millimeters. Rainbow trout were found to form three checks per year in a pattern similar to that of brown trout at this station. Scales taken from fish in February exhibited a distinct, newly-formed winter check which was easily seen in March (Fig. 7). Scales collected in June exhibited a newly-formed, relatively weak spring annulus (Fig. 8), similar to the weak check formed by brown trout at this time. Scales taken from fish in October exhibited a very strong summer check of recent formation (Fig. 9). The scale taken in March (Fig. 7) exhibits both the strong winter check and the weaker spring annulus of the previous year. Scales from young-of-the-year collected in June exhibited either no annuli, the spring annulus only, or both spring annulus and winter check, with 6 (1.7%), 127 (36.9%), and 211 (61.3%) individuals belonging to these categories, respectively. Generally, the strong winter check is easily distinquished from the spring annulus (Figs. 7 and 8). Annuli were distinct and identifiable to spring of the third year of life. Fish older than three years could not be accurately aged because of crowding of annuli and checks.

Table 14 gives the results of the back calculation of length and weight at the various annuli and checks. Rainbow trout were estimated to be 91, 238, and 314 millimeters in length and 8, 134, and 304 grams in weight at the time of spring annulus 1, 2, and 3 formation, respectively. The length-weight relationship for 1065 rainbow trout was $\log W = -4.935 + 2.971 \log L$ ($r = .998$).

Length-frequency distributions of rainbow trout are given in Figure 10. Young-of-the-year and three-year-old and older fish

Figure 7. Scale taken at Station 4 on 29 March 1975 from a yearling rainbow trout of 256 millimeters. The recently formed winter check (d), the check formed the previous summer (c), the spring annulus (b), and the winter check (a) are indicated.

Figure 8. Scale taken at Station 4 on 10 June 1974 from a young-of-the-year rainbow trout of 106 millimeters. The recently formed spring annulus (b) and winter check (a) are indicated.

Figure 9. Scale taken 30 October 1974 from a young-of-the-year rainbow trout of 141 millimeters at Station 4. The newly-formed summer check is indicated (a).

TABLE 14. CALCULATED MEAN TOTAL LENGTH (MILLIMETERS) AND WEIGHT (GRAMS) AT THE TIME OF ANNULUS (AND CHECK) FORMATION OF RAINBOW TROUT AT STATION 4. NUMBER OF FISH IN PARENTHESIS.

	Year of Life							
	1 Annulus			2 Annulus			3 Annulus	
Year-Class	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring
1975	[a]65(211)	[a]89(339)						
1974	[a]64(36)	106(38)	157(38)	197(38)	249(38)			
1973	[a]61(9)	[a]85(12)	127(12)	165(14)	210(14)	259(14)	289(13)	314(13)
Grand Mean	64±8.8[b](256)	91±21.2(389)	150±30.6(50)	189±33.7(52)	238±40.4(52)	259±32.1(14)	289±20.9(13)	314±10.8(13)
Increment of Grand Means	64	27	59	39	49	21	30	25
Increment of Spring Means		91			147			76
Mean of Spring Increments		91			139			101
Calculated Weight	3	8	34	67	134	172	238	304

[a]Means so designated under a given annulus are not significantly different ($p>.05$).

[b]Standard deviation.

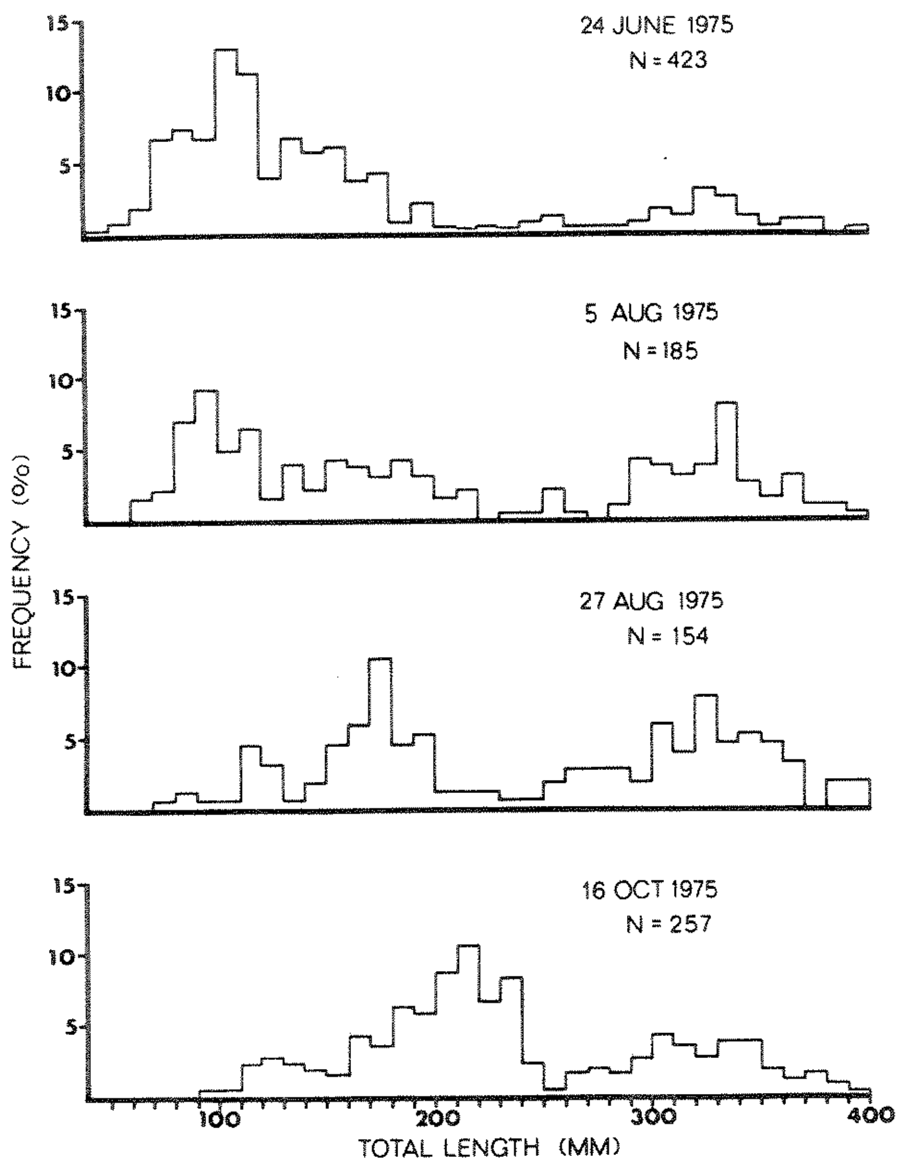

Figure 10. Length-frequency distributions of rainbow trout at Station 4.

compose the two most distinct length groups. Comparison of the June and October distributions indicates rapid young-of-the-year growth.

Results of the rainbow trout food habits analysis are given in Table 15. In general, the food habits of rainbow trout very closely resemble those of brown trout at this station. Molluscs, dipterans, mayflies, and caddisflies were found to be the most important food items.

TABLE 15. PERCENTAGE OF TOTAL AND PERCENT FREQUENCY (IN PARENTHESIS) OF VARIOUS GROUPS OF FOOD ORGANISMS FOUND IN THE STOMACHS OF 147 RAINBOW TROUT COLLECTED AT STATION 4. FISH RANGED IN TOTAL LENGTH FROM 125 TO 402mm WITH A MEAN OF 290±51SD. NONE OF THE STOMACHS EXAMINED WERE EMPTY.

Date	Number of Fish In Sample	Mean Number of Organisms Per Stomach	Trichoptera	Plecoptera	Ephemeroptera	Diptera	Mollusca	Amphipoda	Odonata	Coleoptera	Ants	Other[a]
4 September 1974	12	68.2	2.6(66.7)	0.0(0.0)	4.9(75.0)	65.0(91.7)	23.8(75.0)	0.7(41.7)	0.1(8.3)	0.6(25.0)	1.7(41.7)	0.5(25.0)
18 September 1974	5	85.6	1.2(40.0)	0.0(0.0)	12.4(40.0)	2.6(60.0)	82.2(100.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	1.2(20.0)	0.5(20.0)
2 October 1974	7	94.6	22.1(57.1)	0.0(0.0)	2.0(28.6)	2.9(71.4)	72.5(85.7)	0.2(14.3)	0.0(0.0)	0.0(0.0)	0.5(14.3)	0.0(0.0)
30 October 1974	18	69.1	5.6(88.9)	0.2(5.6)	14.1(72.2)	13.3(72.2)	66.2(100.0)	0.2(11.1)	0.1(5.6)	0.4(16.7)	0.0(0.0)	0.0(0.0)
27 November 1974	14	132.1	4.1(92.9)	0.1(7.1)	70.5(100.0)	3.8(57.1)	21.4(85.7)	0.1(7.1)	0.0(0.0)	0.1(7.1)	0.0(0.0)	0.1(14.3)
2 January 1975	25	368.7	9.2(96.0)	0.0(0.0)	7.3(72.0)	81.3(88.0)	2.1(52.0)	0.0(12.0)	0.1(24.0)	0.0(4.0)	0.0(0.4)	0.0(0.4)
16 February 1975	17	42.3	30.0(100.0)	0.3(11.8)	1.8(47.1)	44.2(41.2)	21.6(76.5)	1.1(23.5)	1.0(23.5)	0.0(0.0)	0.0(0.0)	0.0(0.0)
29 March 1975	22	334.2	7.6(90.9)	0.0(4.5)	7.7(95.5)	80.9(95.5)	3.6(86.4)	0.1(22.7)	0.1(18.2)	0.1(27.3)	0.0(0.0)	0.0(0.0)
17 May 1975	27	104.9	13.7(88.9)	0.2(18.5)	12.9(85.2)	20.4(88.9)	48.8(77.8)	1.8(63.0)	0.7(48.1)	1.3(51.9)	0.1(11.1)	0.2(18.5)
Mean		144.4	10.7(80.2)	0.1(5.3)	14.8(68.4)	34.9(74.0)	38.0(82.1)	0.5(21.7)	0.2(14.2)	0.3(14.7)	0.4(9.7)	0.1(8.7)
Weighted Mean		170.9	9.3(87.1)	0.0(6.8)	12.7(74.8)	60.2(77.6)	16.9(78.9)	0.3(25.9)	0.2(19.7)	0.2(19.0)	0.1(7.5)	0.1(7.5)

[a] Hemiptera, grasshopper, bee, wasp

DISCUSSION

Temperature has been shown to be one of the most important factors influencing the growth of fishes (Brown 1957, Weatherley 1972). Several investigators have determined optimum temperatures for brown trout growth, and their results are somewhat varied. Pentelow (1939) demonstrated optimum growth of brown trout at temperatures ranging from 10 -15 C when fed to satiety. Hewitt (1943, cited by Brown 1946b) found optimum growth from 15 -19 C and Swift (1961) found an optimum at 12 C under a similar feeding regime. Brown (1946b) found the specific growth rate of brown trout to be highest between 7 and 9 C and between 16 and 19 C when fed to satiety. She felt optimum temperatures for most rapid growth are those at which appetite is high and maintenance requirements are relatively low. Weatherley (1972), however, points out that later critical evaluation of this work by Frost and Brown (1967) resulted in the conclusion that good growth could be expected to occur between 7 and 19 C with excess food.

The availability of excess food, however, does not necessarily represent the natural environment where the quality and quantity of food organisms show dramatic temporal and spatial differences which are themselves influenced by temperature. Doudoroff (1969) stressed the importance of food quality and quantity in determining optimum temperatures for growth. Brett *et al.* (1969) found that the optimum temperature for growth of sockeye salmon fingerlings increased with an increase in ration size, however, specific growth rates were negative with certain rations at temperatures well below lethal and no growth occurred at approximately 23 C despite the presence of excess food. Brett *et al.* (1969) concluded that a general physiological optimum occurs at 15 C in freshwater when food is not limiting. Atherton and Aitken (1970) demonstrated 12 C was the optimum temperature for growth of rainbow trout fed a low fat diet, however, an optimum temperature of 16 C was demonstrated with a high fat diet.

Such observations suggest that the growth of fishes in a stream with low macroinvertebrate productivity would be affected in a manner quite different from that of fish in a stream with good invertebrate production if both were subjected to an equal degree of thermal enrichment. Furthermore, since temperature not only influences the activity and metabolic demands of fishes but also strongly influences the quality and quantity of macroinvertebrates available to fish as food, it is not possible to attribute changes in the growth rate of fishes in nature wholly to the direct influence of temperature, nor is it possible to accurately predict the effect of a given degree of thermal enrichment on fish growth.

Condition (K) has been used to indicate the relative vitality of fishes and the suitability of various environments. Fluctuations in K often reflect normal seasonal changes in nutritional balance and the pattern of maturation and subsequent release of reproductive products (Lagler 1956). Brown (1946a) found growth in length to be directly proportional to condition in brown trout under laboratory conditions and many workers have found condition and growth rate to be strongly correlated in natural environments (Allen 1941, Cooper and Benson 1951, Le Cren 1951, Cooper 1953, Beyerle and Cooper 1960). Ellis and Gowing (1957) point out that because of this relationship, condition is a useful measurement as it defines the season when growth is most rapid.

Seasonal variations in the five-day mean water temperatures and mean condition (K) at the four sampling stations are given in Figure 11. Thermograph malfunctions and inaccessibility during winter months prevented the compilation of more complete temperature records at Stations 1 and 2 (Fig. 11C). The thermograph at Station 3 was not installed until May 1975. Fluctuations in temperature, however, are similar at all stations with the notable exception of spring runoff in May and June. Runoff markedly lowered water temperatures at Stations 3 and 4 but had little effect at Stations 1 and 2. In general, water temperatures at Station 4 were approximately 5 C greater than at Station 3 and approximately 11.5 C greater than at Stations 1 and 2.

The seasonal trends in mean condition of brown trout at the cold water Stations 1 and 2 are similar (Fig. 11A). Condition at Station 2

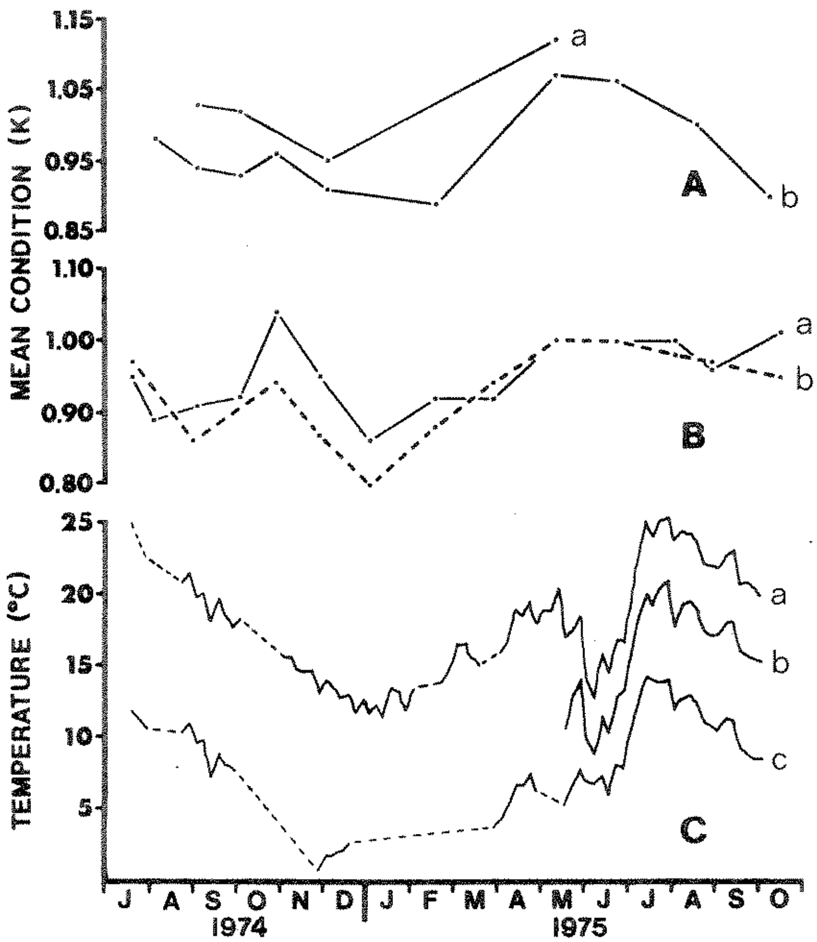

Figure 11. Mean condition (K) of brown and rainbow trout, and five-day mean water temperature, at the four sampling stations on the Firehole River, from July 1974 through October 1975.

Figure 11A. Mean condition (K) of brown trout at Station 1 (a) and Station 2 (b).

Figure 11B. Mean condition (K) of rainbow (a) and brown trout (b) at Station 4.

Figure 11C. Five-day mean water temperature at Stations 1 and 2 (c), Station 3 (b), and Station 4 (a). Broken line represents no data.

was low in February and rose rapidly with increasing water temperature to a high in May. A midwinter sample was not obtained at Station 1 because of its inaccessibility at this time. Scales collected at Stations 1 and 2 in May exhibited newly-formed annuli. The rapid rise in condition and coincident formation of annuli demonstrate a dramatic increase in growth rate at this time. Condition remained high in June at Station 2 and declined to the end of the study in October, indicating that the most favorable conditions for growth of brown trout at Stations 1 and 2 are present during spring and early summer. These findings are consistent with those of other workers who have studied trout in typical stream environments (Cooper and Benson 1951, Cooper 1953, Ellis and Gowing 1957, Beyerle and Cooper 1960). Le Cren (1951) found sexual maturation and subsequent release of reproductive products to significantly affect the condition of the perch *(Perca fluviatalis)*. Brown trout at Station 2 showed a slight though not statistically significant increase in condition during the spawning season in October 1974.

Brown and rainbow trout at the warmest water Station 4 show similar seasonal fluctuations in condition (Fig. 11B). Two periods of growth are indicated; one commencing prior to mid-February and continuing to the period of highest water temperature, the other, a more brief period in fall following high water temperatures. Trout in the October sample exhibited developing gonads, however, this degree of development persisted with later samples (Dr. Calvin M. Kaya, personal communication) when condition values were decreasing. Newly-formed checks were present when condition was rising at both times of the year, further supporting the contention that these rises in condition are associated with increased growth. While continuous data on condition are not available at the intermediate temperature Station 3, the formation of two distinct checks per year by brown trout indicates that two periods of growth occur in fish at this station as in fish at Station 4. Condition data for Station 4 (Fig. 11B) and the occurrence of summer checks on scales collected at Stations 3 and 4 indicate that the temperatures of July and August with means of approximately 21 C and extremes of 24 C at Station 3 and 25 C with extremes of 29 C at Station 4 are too great to allow for trout growth.

An additional late spring check was formed by rainbow and to a lesser degree by brown trout at Station 4 when water temperatures dropped dramatically during spring runoff. With cooler temperatures, maintenance requirements are reduced, energy conversion is more efficient, and growth rates may be enhanced. Spring checks were often faint, probably because they represent good growth followed by better growth rather than the sequence of poor growth followed by good growth which typically results in very distinct annuli. Trout at Station 4 therefore form three discernable checks per year. Benson *et al.* (1959) did not mention such abnormalities in annulus formation by trout in this stream.

The onset of growth at the cold water Station 2 appears to be correlated with an elevation in water temperature above 5 C at a time when benthic insect standing crops are high (Armitage 1958). Loss of condition and retardation of growth in August could be attributable to elevated metabolic demands resulting from higher water temperature at a time when food availability in this stream is low according to Armitage (1958). Ellis and Gowing (1957) attributed a similar late summer to early fall drop in condition of brown trout in a Michigan stream to low standing crops of food organisms, however, they did not also consider the compounding effect of elevated maintenance requirements of trout during this period.

The onset of trout growth at the warmest water Station 4 was noted in mid-February, prior to which water temperature had not changed significantly for several months (Fig. 11C). This growth therefore seems not attributable to a change in temperature, but rather, possibly, to an increased availability of food. Armitage (1958, 1961) took no winter benthic samples and the status of the winter invertebrate community in these waters is not known. It is possible, however, to speculate that the cycle of seasonal invertebrate growth in these warm, fertile waters may be well in advance of those in "normal" waters which are limited by low temperatures during winter.

Heaton (1966) found dipterans emerging year-round and mayflies emerging in all months except January on the Madison River of Yellowstone National Park, which is formed by the confluence of the Gibbon and Firehole Rivers. He reported maximum summer temperatures of 25.6 C.

A resumption of growth accompanied the return of more favorable temperatures in September and October at Stations 3 and 4, but not at Station 2. Since temperatures at this time were comparable to those during the spring period, a resumption of growth would be expected if food were not limiting. Several factors may contribute toward this apparently more favorable availability of food at Stations 3 and 4. Armitage (1958) found Firehole River insect standing crops to follow the typical pattern of high in spring and low in fall, however, fall standing crops in lower, warm water regions were several times greater than those in cold water areas. Further, there is a strong possibility that annual life cycles and therefore seasonal production dynamics of stream insects may be altered by the elevated temperature regime. Our casual observations of insects commonly emerging at all times of the year, including winter, support this possibility. In addition, the food habits of trout at Station 4 (Tables 12 and 15) indicate a greater variety of macroinvertebrates present and utilized as food when compared to the cold water stations, including molluscs and amphipod crustaceans in addition to insects.

Trout at the cold water Station 2 appeared to grow best in the approximate mean temperature range of 5 -10 C. Trout at the warmest water Station 4, however, were in best condition in an approximate mean temperature range of 15 -20 C and were growing in winter at mean temperatures of approximately 13 C. Armitage (1958) found the biomass of insects at Station 4 to be approximately seven times that of Station 2. From the results of Brett *et al.* (1969), we might expect trout growth to be best at higher temperatures, within the limits of excessive temperatures, when food is more available. The elevated temperature regime and apparent good availability of food in the lower Firehole appear to lengthen the annual growing season of trout.

Length-frequency distributions of brown trout (Figs. 2, 3, 5, 6) corroborate the estimates of annual growth at the various stations (Tables 3, 6, 9, 11). Young-of-the-year form distinct modal groups in all cases. Yearlings and two-year-olds were quite distinct at Stations 1 and 2 and somewhat less distinct at Stations 3 and 4. Inherent variation in the growth potential of fishes logically yields a greater range of lengths at later age in more productive habitats and thereby limits the usefulness of length-frequency distributions.

Young-of-the-year rainbow trout at Station 4 show a much wider distribution (Fig. 10) in length than brown trout of the same age-class. This dramatic amount of variation at early age would not be expected unless recruitment into the fishery extended over a relatively long period, perhaps because of variation in the times of hatching.

Recruitment of rainbow trout young-of-the-year into the fishery over an extended period resulted in variation in the number of annuli formed. Early recruits (61.3% of young-of-the-year in 10 June sample) were large enough to form winter checks and later formed spring annuli. Later recruits (36.9%) were too small or were not present at the time of winter check formation, however, they did form spring annuli. The latest entrants (1.7%) were too small or were not present at the time of spring annulus formation. These data indicate that the majority of rainbow young-of-the-year are large enough to form winter checks, which were exhibited by yearlings and older individuals in mid-February 1975.

Brown trout at the cold water Stations 1 and 2 did not form an annulus until the second spring of life, but virtually all trout at the warm water Stations 3 and 4 formed annuli in the initial spring. Because of this difference in age at formation of first annulus and apparent temporal differences in the formation of later annuli, simple comparison of estimated mean lengths at annuli among the stations has no meaning. Growth comparisons must be made on fish of the same age. Figure 12 describes the absolute growth of trout at the four sampling stations. For this comparison, all fish were assigned a 1 January hatching date. The lengths and apparent growth rates of young-of-the-year collected in early spring at Station 4 and early summer at Station 3, and the discovery of redds containing sac fry and advanced eyed

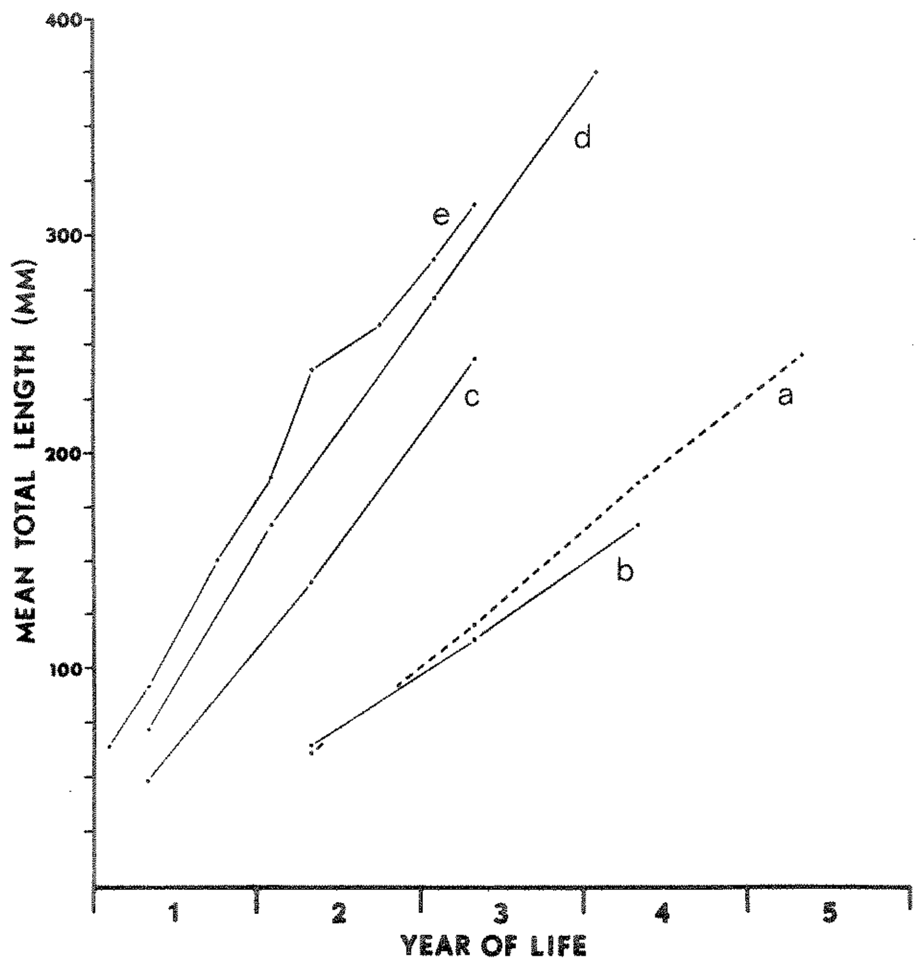

Figure 12. Estimated length at age of brown trout at Station 1 (a), Station 2 (b), Station 3 (c), Station 4 (d), and rainbow trout at Station 4 (e).

eggs during a recent collection at Station 4 in mid-December, indicate that this assigned date is reasonable for fish from these stations. The occurrence of young-of-the-year brown trout at Stations 1 and 2 indicated that hatching occurred at a much later date at these stations, however, only an insignificant amount of growth would be expected to occur between 1 January and their actual hatching dates at the very low winter temperatures of these stations. Winter checks were considered to form on 1 February, spring annuli on 1 May, and summer checks on 1 October.

Rainbow trout length at age was slightly greater than brown trout at Station 4 and there was a progressive decrease in brown trout length at age from Station 4 to Stations 1 and 2 (Fig. 12). The slopes of the growth curves at Stations 3 and 4 indicate approximately equal increments of absolute growth, suggesting that trout at Station 4 gain advantage in length at age by more rapid initial growth. This apparent rapid growth may be partly due to the assignment of the 1 January hatching date when actual hatching occurred earlier, however, rapid growth of fry would be expected at Station 4 at this time as water temperatures are near optimal and food is available as suggested by the growth of older fish. Brown trout at the physically similar Stations 1 and 2 were of approximately equal length at age.

Growth rate is best described in terms of change in weight rather than length per unit time. This is especially important when making inter- or intraspecific comparisons of the growth rates of fish from different populations, which may have unique length-weight relationships. Figure 13 describes the instantaneous population growth rate in weight (G_x) which was calculated by subtracting the logarithms of weight calculated from the lengths in the uppermost complete diagonal in the growth Tables 3, 6, 9, 11, 14 (Ricker 1975). These values are normally less than the true mean instantaneous growth rate (G) because of differential mortality as a result of, for example, intensive size-selective removal (fishing mortality) or size-dependent natural mortality (Dickie 1971). Creel census data indicate that fishing probably does not contribute significantly to the total fish mortality in the Firehole River (Dean *et al.* 1975) and growth estimates (Tables 3, 6, 9, 11, 14), though limited in terms of year-class representation, do not suggest strong size-dependent natural mortality. While considerable bias probably does exist in estimates of G_x, these data do allow for general comparisons of trout growth at the various stations.

Brown trout at Station 3 and rainbow trout at Station 4 show similar G_x-values over the one year interval from first to second spring of life (Fig. 13). Brown trout at Station 4 show a relatively low G_x-value because the interval is less than one year, having been derived from the increment between formation of the initial spring annulus and that of the following winter check, a period of approximately nine months. Trout at Stations 1 and 2 are not represented in this interval

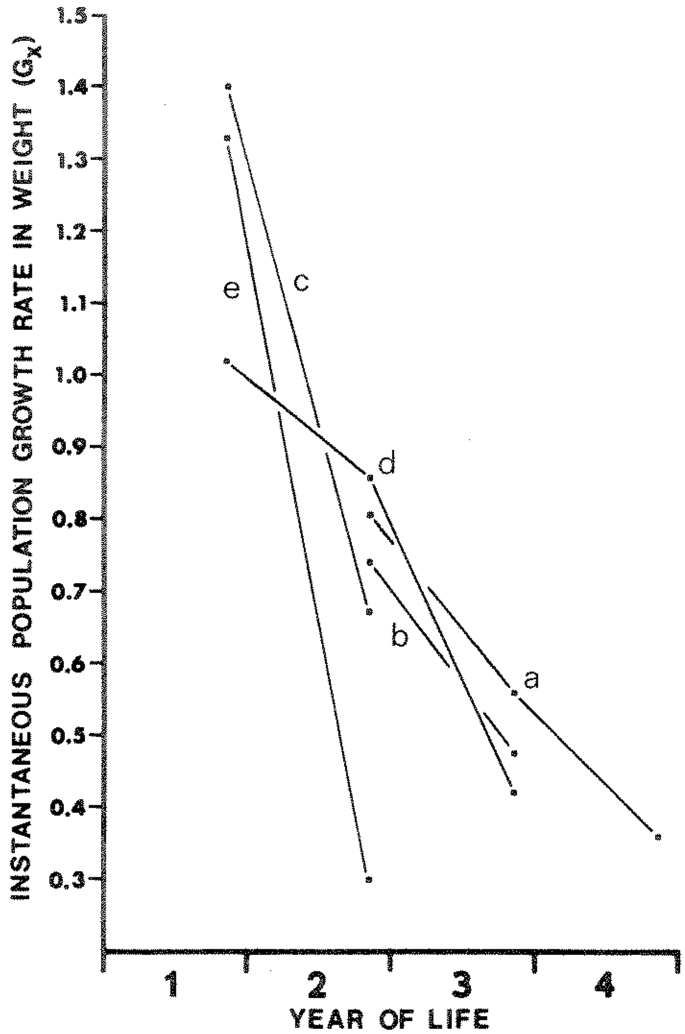

Figure 13. Instantaneous population growth rate in weight (G_x) of brown trout at Station 1 (a), Station 2 (b), Station 3 (c), Station 4 (d), and rainbow trout at Station 4 (e).

as they did not form initial annuli until the second spring of life. Brown trout at all stations show similar instantaneous rates over the intervals where complete data are available. Rainbow trout showed a sharp decline in G_x to a level well below that of brown trout over the second interval.

Absolute growth (Fig. 12) and instantaneous growth (Fig. 13) demonstrate that trout in the warm water stations are growing well, with trout at Station 4 showing the greatest length at age. Rainbow trout do not maintain a high instantaneous growth rate (Fig. 13) and therefore, overall rainbow trout advantage in length at age (Fig. 12) appears to be due to rapid early growth. Sympatry with brook trout at Station 1 does not appear to affect brown trout growth.

Many problems confront the investigator of the food habits of fishes. Diet typically changes with size and age and it is therefore best, though often not possible, to make comparisons within a given length or age-group. Daily changes occur in the diet, but it is often not possible to collect all samples at approximately the same time. Individual food preferences frequently produce greater variation within samples than between samples and such data are difficult to analyze statistically. Since the intent of this aspect of the study was only to get a very generalized indication of feeding habits, no special effort was made to collect fish of a specific length or age for use in food habits analyses, and collections were made at various times throughout the daylight period. Because of the potential biases inherent with such a nonregimented sampling scheme, a detailed analysis of the results was not attempted. A general comparison of the major groups of food organisms taken by trout at the major sampling stations is presented in Figure 14.

In general, the occurrence of insects in the diet reflect the spatial and temporal distributions described by Armitage (1961). The food habits of brown trout at Stations 1 and 2 are similar, as are those of brown and rainbow trout at Station 4. Stoneflies were frequent and seasonally abundant in the food of trout at Stations 1 and 2, but were very rare at Station 4. Caddisflies were the dominant food at Stations 1 and 2 but were of far less importance at Station 4. Mayflies were of approximately equal importance at all stations, however, trout at Station 4 were found to feed primarily on emerging mayflies while trout at Stations 1 and 2 fed on immature forms. Dipterans were of considerably more importance as food at Station 4 than at Stations 1 and 2 and were represented almost entirely by emerging forms. Emerging insects appear to be of far greater importance in the feeding of trout at Station 4 than at Stations 1 and 2. The importance of stoneflies, caddisflies, mayflies and dipterans in the diet of trout in streams has long been recognized (Needham 1938).

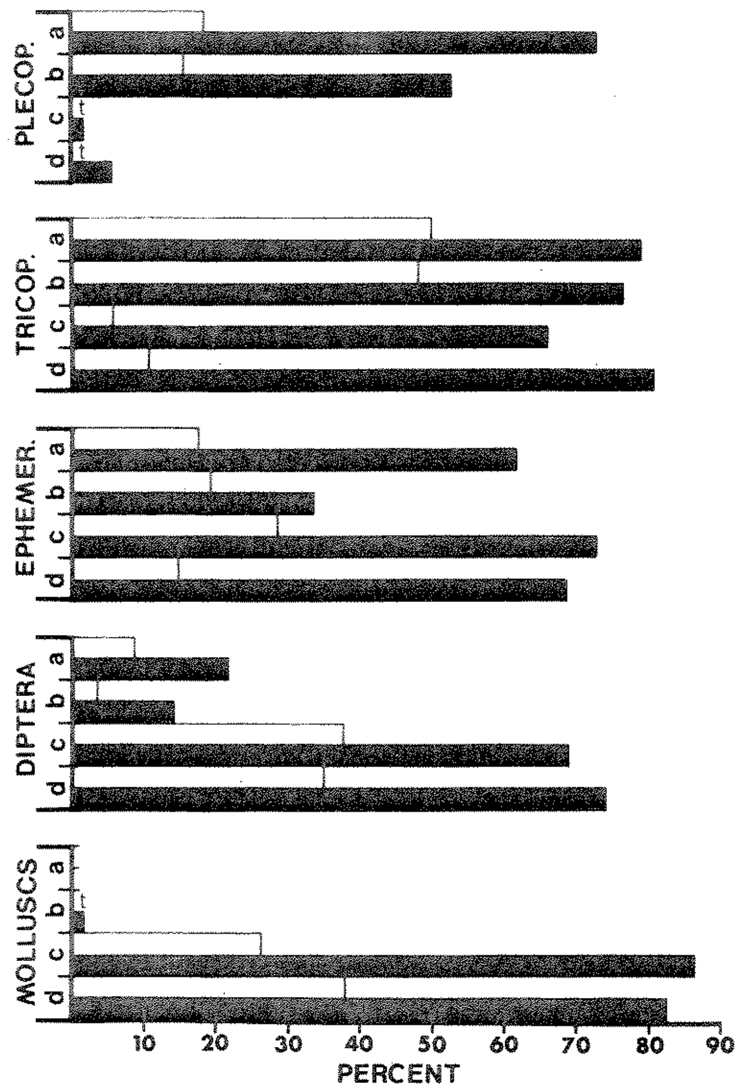

Figure 14. Mean percentage of total (open bars) and mean percent frequency (solid bars) of major groups of food organisms found in the stomachs of brown trout collected at Station 1 (a), Station 2 (b), Station 4 (c), and rainbow trout Station 4 (d). t = 0.1 or less.

Snails *(Physa* sp.*)* were the organism most frequently found in the stomachs of fish at Station 4, while molluscs were virtually absent from the food of fish collected at Stations 1 and 2. Armitage (1958, 1961) did not study the molluscs of the Firehole, however, casual field observations indicate thriving populations of *Physa* in lower, warm water regions. Heaton (1966) found *Physa gyrina* and *Gyraulus deflectus* to constitute 0.4 percent of the benthos numbers and 0.1 percent of the drift numbers on the Madison River. Van der Schalie and Berry (1973) demonstrated that *Physa gyrina* was the most thermally tolerant of six common snails assayed, existing in waters warmer than 30 C. Gillespie (1966) felt that predation was the primary agent of mortality in molluscs on the Madison River, Yellowstone National Park. He noted molluscs among the stomach contents of fish, however, no detailed stomach analyses were made. Snails may play a major role in the maintenance of good trout growth in the thermally enriched waters of the lower Firehole River. Predation upon fish and/or cannibalism is rare despite abundant young-of-the-year fish.

SUMMARY

1. Year-round studies were made of condition, annulus formation, growth, and food habits of brown and rainbow trout in habitats with contrasting temperature regimes on the Firehole River.

2. Condition of brown trout in the cold water habitat showed typical seasonal fluctuations with high values occurring during the growing season from spring to late summer and low values in fall and winter. Fluctuations in the condition of brown and rainbow trout in the warmest water habitat indicated two growth periods per year and a longer total annual growth period.

3. Elevated summer water temperatures restricted trout growth at the intermediate and warmest water stations. However, growth resumed with cooling of waters in early fall, resulting in an abnormal pattern of annulus formation with as many as three annuli being laid down per year. Trout at the cold water stations did not form initial annuli until the second year of life, while those at the intermediate and warmest water stations formed annuli in their first year of life.

4. Brown trout showed the greatest length at age at the warmest water station and the least at the cold water station. Rainbow trout exhibited a slightly greater length at age than brown trout at the warmest water station. This advantage was attributable to more rapid early growth.

5. Trout at cold water stations fed primarily on immature caddisflies, mayflies, and stoneflies. Molluscs, emerging dipterans and mayflies were the most important food in the warmest water area.

6. It was speculated that molluscs, emerging insects, and general good availability of food allowed for good trout growth in the warmest water habitat. The combination of thermal and mineral enrichment contributed by the geysers and hot springs therefore result in better growth of trout in the altered stream sections, as compared to those in the relatively unaltered upstream sections.

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