

Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson

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(Accepted 12 April 1976)

The effects of temperature and ration size on the growth rate and gross efficiency of food conversion of juvenile rainbow trout *Salmo gairdneri* were evaluated during 25-day seasonal experiments. Rations ranged from near-starvation to repletion levels. Test temperatures were 3 and 6° C higher than the controls which fluctuated dielily and seasonally. At rations near maintenance, elevated temperatures decreased trout growth. As the feeding rate increased the detrimental effect of temperature on growth was ameliorated. At repletion feeding levels, elevated temperature up to 17° C improved trout growth by increasing the maximum food consumption rate. With a temperature increase from 6.9 to 22.5° C maintenance rations increased from 2.2 to 7.5% body weight per day. Gross efficiency was dependent upon ration level and temperature. As the food consumption rate increased, efficiency increased to a maximum, then generally declined at repletion levels. Elevated temperatures resulted in reduced efficiencies at low consumption rates but temperatures had little effect at high ration levels. A field study provided estimates of the food consumption relationships established in the laboratory, suggested any substantial increase of stream temperature without a concomitant increase of food abundance would result in decreased trout production.

I. INTRODUCTION

Although salmonid fishes are usually protected from lethal temperatures in streams which receive heated effluents, they may be exposed to moderate temperature increases. The effects of temperature increases to sublethal levels in streams are not understood. There may be direct physiological effects on the growth rate of the fish but, in addition, temperature-related effects on the stream community may result in changes in the quantities of benthic organisms upon which the fish subsist. Laboratory studies have defined relationships between temperature and the growth rates of several species of salmonids but, in most cases, emphasis has been placed upon repletion levels of feeding (Pentelow, 1939; Brown, 1946*b*; Baldwin, 1951; Banks *et al.*, 1971; McCormick *et al.*, 1972). In studies reported by Averett (1969) and Brett *et al.* (1969) a range of rations was provided but the fish were kept at a constant temperature. Except for studies by Everson (1973) and Elliott (1975) who measured the growth of two species of salmonids, kept at different fluctuating temperatures and fed a range of restricted rations, laboratory studies have not modeled the conditions that occur in nature,

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where fishes are exposed to temperatures that change both dielly and seasonally and rations which are usually below maximum levels.

The present study was designed to measure the inter-related effects of elevated, fluctuating temperature and ration size on the growth and food conversion efficiency of juvenile rainbow trout, *Salmo gairdneri* Richardson, and to estimate from field studies the amounts of food consumed by trout under natural feeding conditions.

II. METHODS AND MATERIALS

LABORATORY GROWTH EXPERIMENTS

Apparatus. The apparatus used (Fig. 1) permitted measurement of growth rates of trout kept at three dielly fluctuating temperatures and at four feeding levels. The 12 tanks used in each experiment were constructed from styrofoam boxes and each measured $70 \times 38 \times 18$ cm. The corners of the boxes were faired with aluminium sheets which were attached to the bottom of each tank with silicon rubber. The aluminium and styrofoam were painted with epoxy paint. The volume of water available to the fish in each tank was 32 l. To reduce social interaction among the fish, the longitudinal axis of each tank was partially divided.

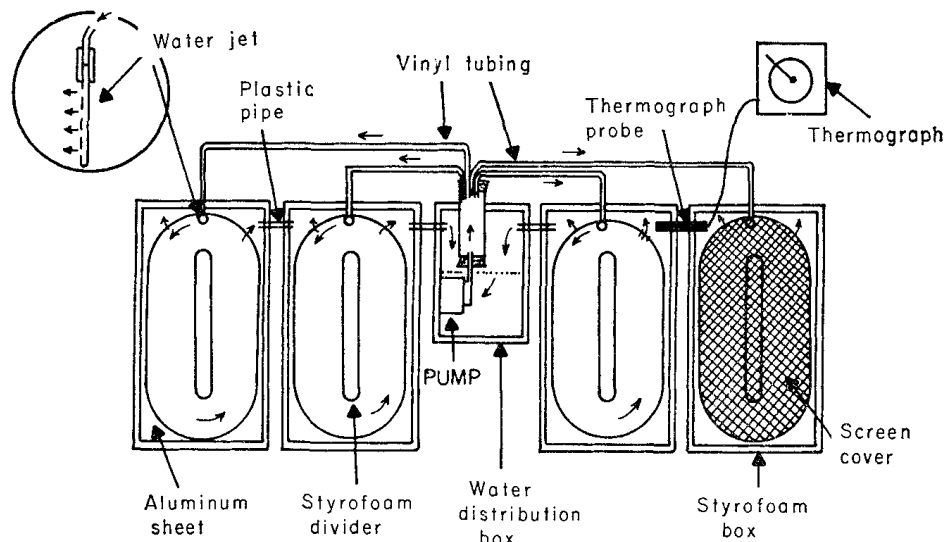


FIG. 1. Diagram of test apparatus. A standpipe in the water distribution box regulated the water level. Arrows indicate direction of flow.

To minimize temperature-dependent spontaneous activity of the fish (Beamish, 1964), moderate current velocities were maintained in the tanks. A water jet generated velocities ranging from 160 mm/sec at the periphery of each tank to nearly 0 mm/sec at the center. During the winter, spring, and summer experiments, observations were made periodically of the position of each fish in the tanks. Water velocity measurements with a current meter allowed calculation of the mean swimming velocity of the fish. The average swimming speed of the fish in all treatments was 1.2 body length/sec and ranged from 0.9 to 1.7 body lengths/sec. No consistent relationship between average swimming speed and temperature or feeding rates was found.

The 12 experimental tanks were divided into three sets of four. Creek water was exchanged in each set at a rate of 0.6 l/min. Before water was pumped to each tank it passed through nylon screening (12.6 mesh/cm). Aeration maintained oxygen levels between 80 and 100% of air saturation.

Three temperature conditions were tested in each experiment. The control temperatures followed natural fluctuations of the water supply. Temperatures were elevated approximately 3 and 6° C from the control in the respective intermediate and high temperature treatments with stainless steel immersion heaters placed in the water distribution boxes. Thermographs, accurate to 0.3° C, recorded temperatures for each set of tanks. The mean, the average daily range, and the total range of temperature were calculated for each experiment from values recorded at each three-hour interval on the thermograph charts. Fluorescent lights, controlled with a timer, normally illuminated the tanks from sunrise to sunset. More detailed information on this apparatus is presented by Wurtsbaugh (1973).

Experimental fish. Rainbow trout *S. gairdneri* used in the experiments were from anadromous stocks, locally known as steelhead trout. Juvenile trout used in the fall, winter, and spring experiments were obtained as fertilized eggs. The eggs were hatched at 9° C and later kept at ambient creek water temperatures (5–17° C) until the experiments began. Trout used in the summer experiment were obtained as fertilized eggs hatched and reared at 12° C. Both groups of fish were obtained from crosses of several females and males. The fish were kept in stock tanks and fed limited rations of Oregon moist pellet (Hublou, 1963).

Acclimation. Trout used in the experiments were selected from stock tanks for uniform, intermediate size and distributed randomly into the experimental tanks where they were acclimated to control and treatment conditions for 14–16 days. One day after introduction, temperatures of the intermediate and high treatments were increased 3° C. On the following day, the temperature of the high temperature treatment was increased by an additional 3° C.

During acclimation, the fish were fed Oregon moist pellet at levels that we predicted would produce a growth rate of 0.2%/day. Ration sizes that would give this growth rate were dependent upon water temperature and ranged from 2.5 to 7.5% body weight/day. By feeding small rations during acclimation, the mean dry weight percentages of the fish approached levels (18–22%) that we found for wild trout of sizes similar to those used in the experiments. Fish were fasted for 48 hours to allow emptying of the gastrointestinal tract before an experiment was begun.

Weighing and feeding. Twenty fish per tank were used in the fall and summer experiments. During the winter and spring experiments fish were larger in size and numbers were reduced to 16 and 15 fish/tank, respectively. Only fish which differed by less than 30% from the mean weight of the group were used. The duration of each experiment was 25 days.

Wet weights were determined after fish were anaesthetized with MS 222 and blotted on damp toweling. Dry weights were determined after lyophilizing fish for 24 h. Weights of individual fish were recorded to the nearest 0.01 g. The initial dry weight percentage of the fish used in the experiments was estimated by lyophilizing a subsample of fish randomly chosen from the test fish. Caloric values of fish and food were measured during the spring experiment to determine if relationships between rates of food consumption and growth at the different test temperatures differed from those based upon measurement of dry weight. Pooled samples of dry fish from each temperature treatment and from initial subsamples were homogenized in a food blender, pressed into pellets and replicate caloric determinations were made with an oxygen bomb calorimeter (Parr Model 13031). Instructions given in Parr Manual 130 (1960) were followed.

Four ration levels of the Oregon moist pellet* were fed at each test temperature. In the fall, spring, and summer experiments, the fish were fed rations ranging from the amount required to maintain constant body weights (maintenance ration) to all the food the fish would consume in one daily 15-minute feeding (repletion ration). In the winter experiment, rations varied from levels near starvation to those moderately greater than the maintenance level to better define the food consumption-growth rate relationship at low feeding rates. Feeding levels were based on the initial estimated dry weight of the fish; these amounts were then fed throughout the experiment. The dry weight percentages and caloric content of the food were determined by lyophilization and calorimetric measurement of random samples of food.

*Proximate analysis (dry basis): fat, 10.1%; protein, 59.7% carbohydrate, 18.7% (Phillips, 1972). Percent dry weight: \bar{X} = 74.3%. Caloric content (cal/g d. wt.) in each experiment \pm s.d.: Fall, 4910 \pm 70; Winter, 5018 \pm 55; Spring, 4909 \pm 70; Summer, 4839 \pm 37. The pellet contained 3% terramycin (TM 50) added as a prophylactic against bacterial disease.

Fish were fed beginning on the second day of the experiment and the feeding continued to the twenty-third day. Two days of starvation elapsed before the final weighing. At feeding levels greater than 3% body weight/day, fish were fed once daily between 09.00 and 11.00. At lower feeding levels subordinate fish in the tanks could not get food if only a small amount was fed. To facilitate food sharing, rations between 1.0 and 3.0%/day were fed every two days (i.e., 2.0 or 6.0%/feeding) and the 0.5%/day ration for the winter experiment was given every third day.

Some deaths occurred during each experiment, usually at the higher temperatures and smaller ration levels. Dead or dying fish were weighed and their dry weights determined. Rations were reduced in proportion to the number of fish removed from a tank. If more than three fish in a tank died, the results from that tank were not used in the analysis.

Calculations and definitions. Growth and food consumption rates were expressed as average relative growth and average relative food consumption rates, respectively, (Warren, 1971) and were calculated as follows:

$$\text{growth rate (\%/day)} = \frac{W_2 - W_1}{0.5 (W_1 + W_2)t} \times 100$$

$$\text{consumption rate (\%/day)} = \frac{C}{0.5 (W_1 + W_2)t} \times 100$$

where:

W_1 = initial estimated dry weight of a group of fish,

W_2 = final dry weight of the group of fish,

t = duration of the experiment in days (25 days),

C = estimated dry weight of food consumed.

Gross efficiencies of food conversion were calculated by dividing total growth by total food consumption (dry weights). Efficiency values were multiplied by 100 and expressed as percentages. Maintenance rations were determined by graphical interpolation or extrapolation to zero growth rates of the curves relating food consumption rates to growth rates.

FOOD CONSUMPTION AND GROWTH OF WILD TROUT

Samples of steelhead trout were collected on seven occasions between 9 September 1971 and 14 August 1972, from a local creek to estimate growth rates of the trout and from this their food consumption rates. In the small coastal stream used, minimum summer flows were near 10 l/s and maximum winter flows may reach several thousand litres per second. The fish were collected in the central 3 km section of the creek with a d.c. electric shocker. The trout were kept at the laboratory overnight to allow emptying of the gastrointestinal tract. The following day the fish were blotted on damp toweling and weighed to the nearest 0.01 g. Only fish of the 1971 year class were used. When necessary, ages were checked by scale analysis. Dry weights were determined by methods described previously.

Growth of wild trout was assumed to be exponential and growth rates were consequently calculated as daily instantaneous growth rates (Brody, 1945). The mean dry weight of the fish in each of the samples was used to calculate growth rates during the sampling intervals. Growth rates were expressed as percent per day, and were roughly comparable to the average relative growth rates calculated for fish studied in the laboratory.

A thermograph kept a nearly continuous record of the creek temperatures between 12 October 1971 and 14 August 1972. For each period between fish collections, the mean water temperature was calculated by averaging the daily high and low temperatures.

Food consumption rates for trout in the creek were estimated by comparing the fishes' calculated growth rates with growth rates of trout kept in the laboratory and fed known rations. Values of the food consumption rate for each sampling interval were taken from consumption-growth curves established in the laboratory at temperatures which closely approximated the mean temperatures of the stream. This method of estimating food consumption rates of wild fish was discussed by Davis & Warren (1968) and its validity was supported by experiments by Brocksen *et al.* (1968), Carline & Hall (1973) and Elliott (1975) which demonstrated that consumption-growth relationships of salmonids kept in aquaria do not differ greatly from those of fish kept in model streams.

III. RESULTS

LABORATORY GROWTH EXPERIMENTS

Decelerating, curvilinear relationships between rates of food consumption and growth were defined for most of the experiments (Fig. 2; Table I). The narrow range of ration levels fed in the winter experiments resulted in nearly linear relationships between rates of food consumption and growth. Since individual fish could not be identified and facilities were not adequate to replicate the different treatments, appropriate statistical analyses were precluded. However, in a similarly designed

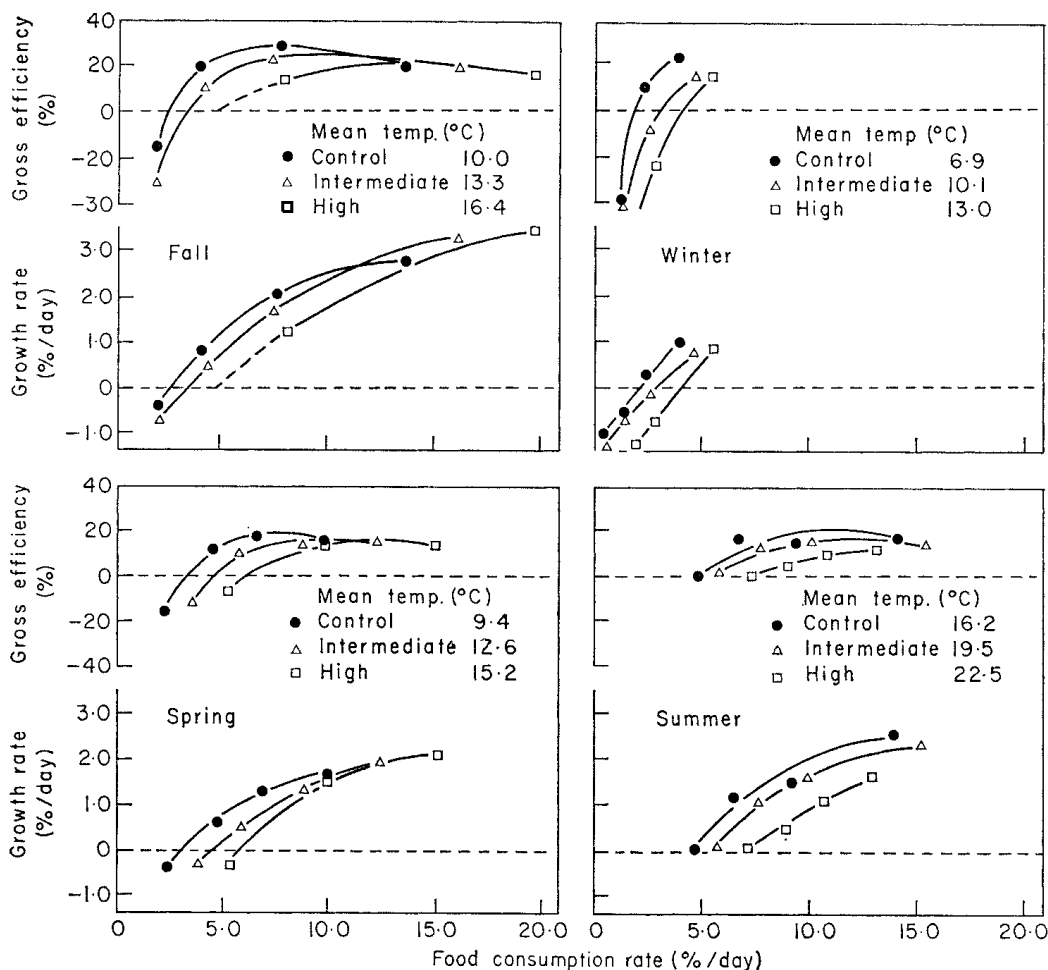


FIG. 2. Relationships for each seasonal experiment between food consumption rate and growth rate and gross efficiency of *S. gairdneri* kept at different fluctuating temperatures. Rates are based upon dry weights. Efficiency values are not plotted for very low rates of food consumption during the winter. Lines fitted by inspection.

study of the effects of temperature increase on the growth of juvenile chinook salmon, *Oncorhynchus tshawytscha*, we found the coefficient of variation in growth rates to be 3%.

The effects of temperature on the growth rates of the trout were dependent on the food consumption rates of the fish. At low ration levels, increases of temperature decreased the growth rates of the fish. As consumption rates increased, curves relating rates of food consumption and growth at different temperatures began to converge,

and at repletion feeding levels, the curves sometimes crossed (Fig. 2). In the summer experiment, the growth rate curves for the different temperature treatments tended to converge, but did not meet or cross even at the highest consumption levels.

During experiments in which repletion rations were fed, elevated temperatures often led to an increase in the maximum consumption rate of the fish, and consequently to an increase in the maximum growth rate (Fig. 2; fall, spring and summer). However, when the temperature reached 22.5° C in the summer experiment, the fish ate less than fish kept at temperatures 3 and 6° C lower. The reduction in food

TABLE I. Test temperatures and mean values of food consumption rate, initial and final wet weight and percentage dry weight, final caloric content, and growth rate of *S. gairdneri* for each experiment. Caloric equivalents of food consumption and growth rates (in parentheses) are shown for the spring experiment

Temperatures (°C)			Consumption (%/day)	Initial w. wt. (g)	Initial d. wt. (%)	Final w. wt. (g)	Final d. wt. (%)	Caloric content (cal/g d. wt.)	Growth rate (%/day)
Mean	Average	Range							
<i>Fall (13/10/71-7/11/71)</i>									
10.0	2.7	6.2-	2.2	0.98	19.4	0.96	18.4		-0.3
		13.0	4.3	1.04		1.31	19.9		0.9
			7.9	1.02		1.64	20.8		2.1
			14.0	1.00		1.89	21.8		2.9
13.3	3.1	9.2-	2.2	1.00	19.9	0.93	18.2		-0.7
		16.8	4.6	0.98		1.17	19.4		0.5
			7.7	1.02		1.55	20.3		1.7
			16.5	0.97		2.11	22.4		3.4
16.4	2.8	12.3-	8.3	0.94	19.7	1.29	20.0		1.3
		19.9	20.1	0.92		2.04	23.0		3.5
<i>Winter (23/1/72-17/2/72)</i>									
6.9	1.1	3.9-	0.5	2.03	21.8	1.82	18.5		-1.1
		10.1	1.5	2.01		1.96	19.4		-0.6
			2.5	1.95		2.10	21.7		0.3
			4.2	1.91		2.30	23.2		1.0
10.1	1.7	7.2-	0.6	1.96	21.1	1.66	18.1		-1.3
		24.2*	1.5	1.96		1.82	19.3		-0.6
			2.7	1.97		2.02	19.6		-0.2
			4.9	1.94		2.35	21.1		0.8
13.0	1.2	9.6-	2.0	1.92	20.5	1.70	17.4		-1.3
		17.8	3.0	1.84		1.72	18.4		-0.8
			5.7	1.86		2.21	21.6		0.9
<i>Spring (21/3/72-15/4/72)</i>									
9.4	1.5	7.2-	2.5 (2.6)	2.35	20.0	2.35	18.3	4713	-0.4 (-0.5)
		12.1	4.9 (4.9)	2.25		2.71	19.4	4822	0.6 (0.6)
			7.0 (6.9)	2.36		3.19	20.6	5088	1.3 (1.5)
			10.2 (9.9)	2.23		3.38	20.4	5157	1.7 (1.9)
12.6	1.8	9.9-	3.8 (4.0)	2.29	20.2	2.29	18.7	4619	-0.3 (-0.6)
		16.4	6.1 (6.1)	2.33		2.82	19.2	4932	0.5 (0.6)
			9.1 (9.0)	2.24		3.17	20.5	5031	1.4 (1.5)
			12.7 (12.4)	2.28		3.75	21.6	5163	2.0 (2.3)
15.2	1.6	12.4-	5.5 (5.7)	2.28	20.0	2.33	18.0	4615	-0.4 (-0.5)
		18.4	10.2 (10.0)	2.25		3.17	21.1	5113	1.6 (1.8)
			15.4 (14.9)	2.25		3.73	21.2	5152	2.2 (2.4)

TABLE I. *cont.*

Temperatures (°C)			Consumption rate (%/day)	Initial w. wt. (g)	Initial d. wt. (%)	Final w. wt. (g)	Final d. wt. (%)	Caloric content (cal/g d. wt.)	Growth rate (%/day)
Mean	Average	Range							
daily change									
<i>Summer (25/6/62-20/7/72)</i>									
16.2	3.1	12.7-	4.9	1.14	21.0	1.21	19.9		0.0
		20.8	6.8	1.23		1.57	22.0		1.2
			9.5	1.18		1.64	22.2		1.5
			14.3	1.20		2.13	23.2		2.6
19.5	3.4	16.0-	6.0	1.19	21.7	1.28	21.4		0.1
		23.9	7.9	1.21		1.53	22.3		1.1
			10.3	1.16		1.63	23.3		1.6
			15.7	1.18		2.02	23.5		2.4
22.5	3.5	17.8-	7.4	1.10	22.1	1.21	21.3		0.0
		26.8	9.2	1.10		1.25	21.8		0.5
			11.0	1.11		1.41	23.1		1.1
			13.4	1.16		1.61	24.2		1.7

*During a water supply failure, temperatures increased from 14.0 to 24.2° C over a 12-h period. When discovered, the temperature was reduced rapidly to the previous level. The fish showed no obvious ill effects of the high temperature.

consumption probably resulted from temperature stress, since the incipient lethal temperature for the trout is near 26° C (Bidgood & Berst, 1969). Temperatures in the high temperature treatment exceeded 26° C for short periods four times during the experiment.

Gross efficiency was dependent on both ration level and temperature (Fig. 2). As the food consumption rate increased, efficiency increased. In most cases, efficiency reached a maximum level and then declined slightly at repletion ration levels. However, where ration levels were intentionally restricted (winter experiment) or where high temperatures apparently inhibited consumption (high temperature treatment of the summer experiment) gross efficiencies continued to increase up to the highest food consumption levels.

At low consumption rates, elevated temperatures resulted in reduced gross efficiencies, but at high ration levels, temperature had little or no effect on efficiency (Fig. 2). Figure 3 shows that at a low ration level (4%/day) values of efficiency declined markedly with temperature increase. At an intermediate ration level of 8%/day, temperature increase had considerably less effect on efficiency and at a high ration level (13%/day) increased temperature reduced efficiencies only slightly.

During each season, temperature elevation led to an increase in the amounts of food required for the maintenance of the trout (Fig. 4). Maintenance requirements of the fish increased more than three-fold (2.2-7.4%/day) over the temperature range of 6.9 to 22.5° C. The relationship of maintenance ration (*M*) to temperature (*T*) in the pooled data of all the experiments was $\text{Log } M = 0.032T + 1.184$; $r^2 = 0.85$. However, in the different seasons, temperature-maintenance ration relationships were different. Maintenance rations at a given temperature were particularly high in the spring experiment.

Caloric values of the fish increased with increases of ration at each of the test temperatures during the spring experiment (Table I). Rates of food consumption and growth expressed in caloric units (Table I) defined curves that were somewhat

steeper than those presented in Figure 1 which were based upon dry weights. The increased caloric density probably resulted from increased fat deposition at high ration levels.

FOOD CONSUMPTION AND GROWTH OF WILD FISH

The growth rates of wild steelhead trout in the creek ranged from -0.2 to 1.6% /day, with a mean rate of 0.8% /day (Table II). The high variation in trout growth rates during the different periods was not necessarily the result of seasonal differences, since both the small sample sizes and the method used to assess growth could have caused considerable variation in the estimates. Estimated consumption rates of the wild trout ranged from 2.0 to 7.6% /day (Table II).

TABLE II. Sampling dates, sample sizes, mean wet weights, dry weight percentages, mean temperatures, instantaneous growth rates, and estimated consumption rates of the 1971 year class of wild *S. gairdneri*

Sampling date	Sample size	Mean w. wt. (g) and S.D.	Mean % d. wt	Mean temp. (°C)	Growth rate (%/day)	Estimated consumption (%/day)
9-9-71	88	1.42 ± 0.86	18.6		0.4	
8-10-71	68	1.43 ± 0.86	21.0	6.4	1.6	6.8
9-11-71	54	2.32 ± 0.99	21.6	6.1	-0.2	2.0
7-1-72	14	2.17 ± 1.39	21.1	3.7	1.2	4.8
4-2-72	19	2.95 ± 1.11	21.4	6.8	0.5	2.8
27-4-72	12	4.22 ± 1.47	22.0	12.8	0.9	7.6
14-8-72	17	10.34 ± 2.40	25.0			

IV. DISCUSSION

In each seasonal experiment, gross efficiency of the trout increased from zero at the maintenance ration level and was highest at intermediate consumption rates. In some cases efficiency declined slightly at repletion feeding levels. The decline in efficiency at high ration levels can be attributed to: (1) an increase in specific dynamic action, principally from increased deamination of amino acids (Iwata, 1970); (2) decreased assimilation efficiency (Averett, 1969); (3) increased activity of the fish (Kerr, 1971). Although we found no differences in the activity of fish fed different rations, our measurements were relatively insensitive and small differences in swimming activity may have existed.

The analysis of Paloheimo & Dickie (1966) which suggested that the logarithm of gross efficiency declined with increasing ration, from a maximum at low feeding levels (the *K*-line), is now generally realized to be in error. As pointed out by Warren (1971), the curve relating consumption and efficiency must be zero at the maintenance level, increases as consumption increases and sometimes declines at high ration levels. Kerr (1971), while acknowledging the occurrence of a positively sloped phase of the consumption-efficiency curve, emphasized the importance of the descending portion

of the curve. However, our results support the observations of Iwata (1970), Warren (1971) and Carline & Hall (1973), that the ascending portion of the curve is of more ecological interest than the descending limb, since fish in nature most often exist at low ration levels. Consumption rates calculated for wild trout in the creek always fell in the range of the ascending portions of the efficiency curves. Growth rates of *S. gairdneri* in other systems also suggest that all but the very young trout usually feed at rates well below maximum. Growth rates of wild trout larger than one gram are usually less than 1% per day (Everest & Chapman, 1972; Alexander & MacCrimmon, 1974), while trout in our laboratory growth experiments always exceeded this growth rate when fed repletion rations.

Trout used in the spring experiment were larger than those tested during other seasons but were unaccountably less efficient in utilizing low rations for maintenance and growth (Figs 3 and 4). On the basis of fish size alone, the highest values of

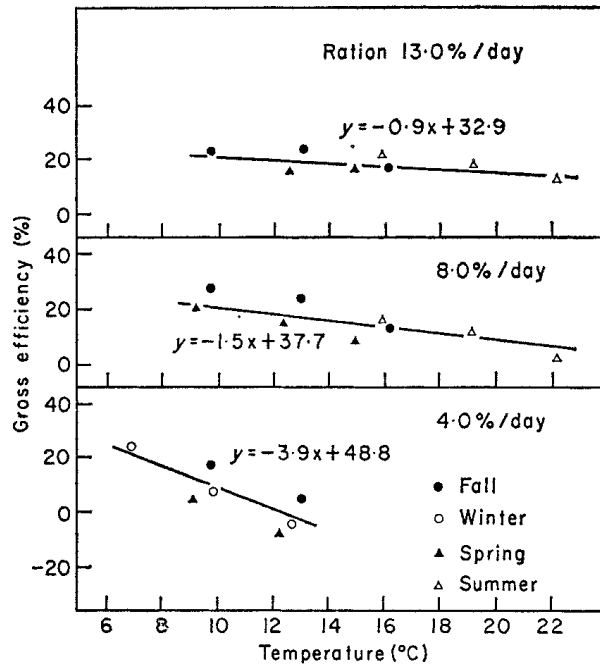


FIG. 3. Relationships between temperature and gross efficiency of *S. gairdneri* at three different ration levels. Plotted values were taken from curves presented in Fig. 2. Lines fitted by method of least squares.

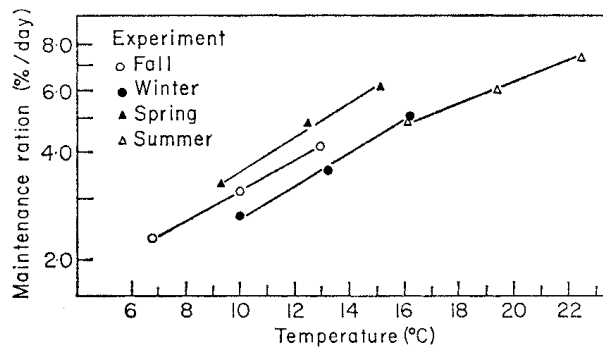


FIG. 4. Relationships between temperature and maintenance rations (dry weight) of *S. gairdneri* in each of the seasonal growth experiments. Lines fitted by method of least squares. Note log scale.

efficiency would have been expected for the largest fish since relative maintenance ration decreases with increase of fish size (Wurtsbaugh & Davis, 1977). Brown (1946a), Anderson (1959) and Averett (1969) have reported seasonal changes in the gross efficiencies of fish, and Gross *et al.* (1965) found that photoperiod affected fish growth. However, Lee (1969) found no seasonal differences in the growth of black bass (*Micropterus salmoides*) and Elliott (1975) found season did not affect the growth rates of *Salmo trutta*. Although our results suggest trout are less efficient in utilizing food for growth during the spring, we should emphasize that in experiments designed to delineate seasonal differences, any other unmeasured variable such as fish health or food quality can easily produce spurious results.

While it appears that the overall efficiency response of the trout may change with season, their response to temperature change was approximately the same, regardless of season (Figs 3 and 4). Our data, and the data obtained by Everson (1973) indicate that irrespective of season, any increase of temperature above normal seasonal levels will decrease the growth of trout and salmon fed low to moderate rations.

Increasing temperature markedly increased the maintenance requirements of the trout. This increase was expected since: (1) standard metabolism increases rapidly as temperature rises (Winberg, 1960) and; (2) most of the energy of the maintenance ration is accounted for by energy expended in standard metabolism (Averett, 1969; Niimi & Beamish, 1974). Brett *et al.* (1969), Everson (1973), Kelso (1972) and Elliott (1975) have recorded comparable increases of maintenance ration with temperature increase for other species.

The increase of maintenance ration with temperature markedly affected values of gross efficiency for trout receiving small rations. However, the efficiency values for fish fed rations near repletion were little affected by elevated temperatures (Fig. 3). Similarly, it was found by Brett *et al.* (1969) for sockeye salmon *Oncorhynchus nerka*, by Everson (1973) for coho salmon *Oncorhynchus kisutch*, and by Lee (1969) for largemouth bass *Micropterus salmoides* that the efficiency of fish fed at low ration levels was depressed by elevated temperatures. However, when consumption rates were high, temperature increase had no detrimental effect, or in some cases, increased efficiency. In contrast to these results and ours, the regression equations reported by Niimi & Beamish (1974) indicate that the gross efficiencies of largemouth bass are decreased nearly equally by temperature over the entire range of ration sizes tested. Similarly, work by Elliott (1975a, b) on brown trout showed that in most cases, temperature increases depressed gross efficiencies at all ration levels. These results are not easily reconciled with our results. However, Niimi & Beamish (1974) pooled the efficiency values of fishes of greatly differing sizes to obtain the regressions and Elliott's results are reported in units of wet weight. These procedural differences may account for the described differences. This result might be attributed to the pooling of efficiency values of fishes of greatly differing sizes to obtain the regressions. Except for the results of Niimi & Beamish and those of Elliott, the available data indicate that temperature effects, over a broad range of temperatures, are fully dependent upon the food consumption rates of the fish being considered.

The results presented here suggest that if food is abundant trout growth would be enhanced by temperature increase to approximately 16.5° C, because repletion rations increase with temperature increase up to this level. But, if the food of wild trout is limited, as indicated by estimates of food consumption rate for wild trout, then any substantial temperature increase would result in decreased growth. Trout

production would increase with temperature increase only if there was a concomitant increase in the production of stream invertebrates. Beauchamp *et al.* (1970) indicate that production of macrobenthic organisms may be increased by thermal additions to lakes and rivers. Quite different results were reported by Iverson (1972) who showed that a temperature elevation of 3.5–5° C reduced insect production by one-half in model streams which simulated natural salmonid streams. The effects of temperature increase on the growth and food conversion efficiency of trout appear to be dependent on ration size but the role that temperature plays in determining the abundance of food in a stream is less clear.

The research was supported by the U.S. Environmental Protection Agency (Training Grant Number T900117) and the Office of Water Research and Technology. Drs G. L. Larson and C. B. Schreck reviewed the manuscript. Mr Jim Golden of the Oregon Department of Fish and Wildlife assisted in culturing fish used in the study. Tim Joyce, Steve Ross and Linda Wurtsbaugh assisted with many aspects of the study.

Technical Paper No. 4128, Oregon Agricultural Experiment Station, Corvallis, Oregon 97331, U.S.A.

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