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WAYNE ALDEN WURTSBAUGH for the MASTER OF SCIENCE
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Title: EFFECTS OF TEMPERATURE, RATION, AND SIZE ON THE GROWTH OF JUVENILE STEELHEAD TROUT, SALMO GAIRDNERI

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The effects of temperature, temperature fluctuation, and fish size on the growth of juvenile steelhead trout (Salmo gairdneri) were studied in experiments which lasted 10 to 25 days. Groups of fish were fed at ration levels varying from near-starvation to repletion. Decelerating, curvilinear relationships between rates of food consumption and growth were defined in most of the experiments.

At ration levels near maintenance, temperatures elevated 3 and 6 C above the seasonal ambient temperatures decreased the growth of the trout. As feeding rate increased, the detrimental effect of temperature on growth was ameliorated. At repletion feeding levels, elevation of temperature up to approximately 17 C increased trout growth rates by increasing the maximum food consumption rates of the fish. With temperature increase from 6.9 to 22.5 C the maintenance rations of the trout increased from 2.2 to 7.4% body weight/day. Large diel temperature fluctuations of 4 and 8 C did not increase growth rates and in some cases decreased growth rates to levels below those of fish kept at constant temperatures.

Increase of fish size from 0.58 to 3.36 g decreased the maintenance rations (per gram of tissue) of the trout. This decrease was attributed to decreases in metabolic rate that are associated with increases in fish size. As a consequence of this size-dependent change in metabolic rate, large fish grew faster than small fish at low ration levels. However, at ration levels greater than 9%/day, small fish grew faster than large fish. At the highest ration levels fed (9-12%/day), gross food conversion efficiency of the large fish began to decline, while efficiencies of small fish continued to increase with increases in ration size.

Periodic sampling of steelhead trout in a small coastal stream indicated that growth rates of these wild trout ranged from -0.18 to 1.6%/day. Food consumption rates of the wild trout were estimated to range from 2.0 to 7.6%/day; considerably less than the maximum consumption rates of trout kept in the laboratory. At these food consumption rates it is estimated that increases of stream temperature above the normal seasonal temperatures would decrease the growth rates of wild steelhead trout.

Effects of Temperature, Ration, and Size on the Growth of Juvenile Steelhead Trout, *Salmo gairdneri*

by

Wayne Alden Wurtsbaugh

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Associate Professor of Fisheries
in charge of major

Redacted for Privacy

Acting Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

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INTRODUCTION

This paper deals with several factors affecting the growth of juvenile steelhead trout, Salmo gairdneri Richardson. It is important to study the growth of fish for two reasons. First, the production of fish which we use for food and recreation depends on their ability to grow. Secondly, the ultimate success or failure of a fish species depends on its ability to grow and eventually to reproduce. For anadromous salmonids, as with many fish, growth to a certain size is necessary for survival to the adult stage (Forester, 1954; Wallis, 1968).

Temperature is recognized as one of the major factors controlling the distribution and abundance of fish. With the growing problem of thermal pollution in many of our inland waters, it is important to understand how changes in temperature will affect fish and to determine temperature criteria which will protect desirable species. Many physiological responses have been used to determine temperature requirements of fish. Lethal temperatures indicate the temperature extremes within which a species might survive. The upper lethal temperature for rainbow trout (another form of S. gairdneri) is near 26 C (Bidgood and Berst, 1969). Standard and active metabolic rates

(Fry, 1947), swimming performance (Davis _et al._, 1963; Brett, 1967) and preferred temperatures (Brett, 1952; Mantleman, 1960) may be used to determine the temperature requirements of fish, but as pointed out by Brett (1971b), the temperature requirements for adequate growth may be of overriding importance to the organism.

Many people have investigated the effects of temperature on the growth of fish, particularly salmonids of economic importance. Pentelow (1939) and Brown (1946a, b) studied the growth of brown trout (_S. trutta_); Baldwin (1957) investigated the growth of brook trout (_Salvelinus fontinalis_); Banks, Fowler and Elliot (1971) studied the growth of chinook salmon (_Oncorhynchus tshawytscha_); and Olson, Tangen and Templeton (MS, no date) studied the growth of steelhead trout. These studies were concerned with the growth of fish fed unrestricted rations or at levels of food consumption just maintaining the body weight of the fish. When the fish were fed unrestricted rations, these authors found that the growth of salmonids generally improved with temperature increases up to levels ranging from 13 to 18 C. Unfortunately, studies of fish growth at high ration levels provide little information useful in understanding the distribution and abundance of wild fish when their rations may be limited to quantities well below their maximum food consumption levels.

Brody (1945), studying domestic farm animals, and Warren and Davis (1967), studying fish, emphasized the importance of feeding a range of ration levels to determine how a variable may influence the growth of an animal. Averett (MS, 1969), Brett, Shelbourn and Shoop (1969), and Everson (MS 1973) have utilized this approach to study how temperature affects the growth of two species of salmonids.

While most studies on fish growth have been conducted at constant temperatures, the temperatures of salmonid rearing streams are seldom constant, but fluctuate both dielly and seasonally. Despite its possible importance, only a few experiments have been conducted to determine what effects temperature fluctuations might have on the growth of fish (Brown, 1946b; Kelso, 1972; Everson, MS 1973).

The importance of ontogenetic changes in the growth and growth efficiencies of homeothermic animals has been stressed by Brody (1945) and these changes should not be overlooked by biologists studying fish growth. Effects of fish size on the growth of fish fed unrestricted rations have received considerable attention (Brown, 1946a; Menzel, 1959; Paloheimo and Dickie, 1966; Pandian, 1967), but at restricted ration levels, considerably less work has been done (Brown, 1946a; Gerking, 1971; Kelso, 1972).

I conducted seven experiments on the effects of water temperature, ration level and fish size on the growth of juvenile steelhead trout. In four experiments I established relationships between rates of food consumption and growth of trout kept at naturally fluctuating stream temperatures and at temperatures elevated incrementally 3 and

6 C. In one experiment I investigated the relationship between food consumption and growth of trout ranging in weight from 0.5 to over 5 g. In two experiments I compared growth rate relationships of trout kept at constant temperatures with those kept in temperature regimes which had large diel fluctuations. The experiments were conducted at the Oak Creek Laboratory, Oregon State University, between September 1971 and September 1972.

EXPERIMENTAL PROCEDURES AND RESULTS

Seasonal Growth Experiments

Methods and Materials

Apparatus. The experimental apparatus (Figure 1) used in these experiments permitted measurement of growth rates of trout kept in three fluctuating temperature treatments and fed four ration levels. The 12 tanks used in each experiment were constructed from styrofoam boxes 70 x 38 x 18 cm deep. An oval aluminum sheet was glued to the bottom of each tank with silicon rubber. The aluminum and styrofoam were painted with epoxy paint. The volume of water available to the fish in each tank was 31.7 liters. To reduce social interaction among the fish, the longitudinal axis of each tank was partially divided with a block of styrofoam 35 cm long and 5 cm wide. Each tank was covered with plastic-coated screening.

In an effort to minimize temperature-dependent spontaneous activity of the fish (Beamish, 1964), moderate current velocities were maintained in the tanks. A water jet (Figure 1A) generated water velocities varying 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. Subsequent water velocity measurements with a Neypric midget current meter allowed calculation of the

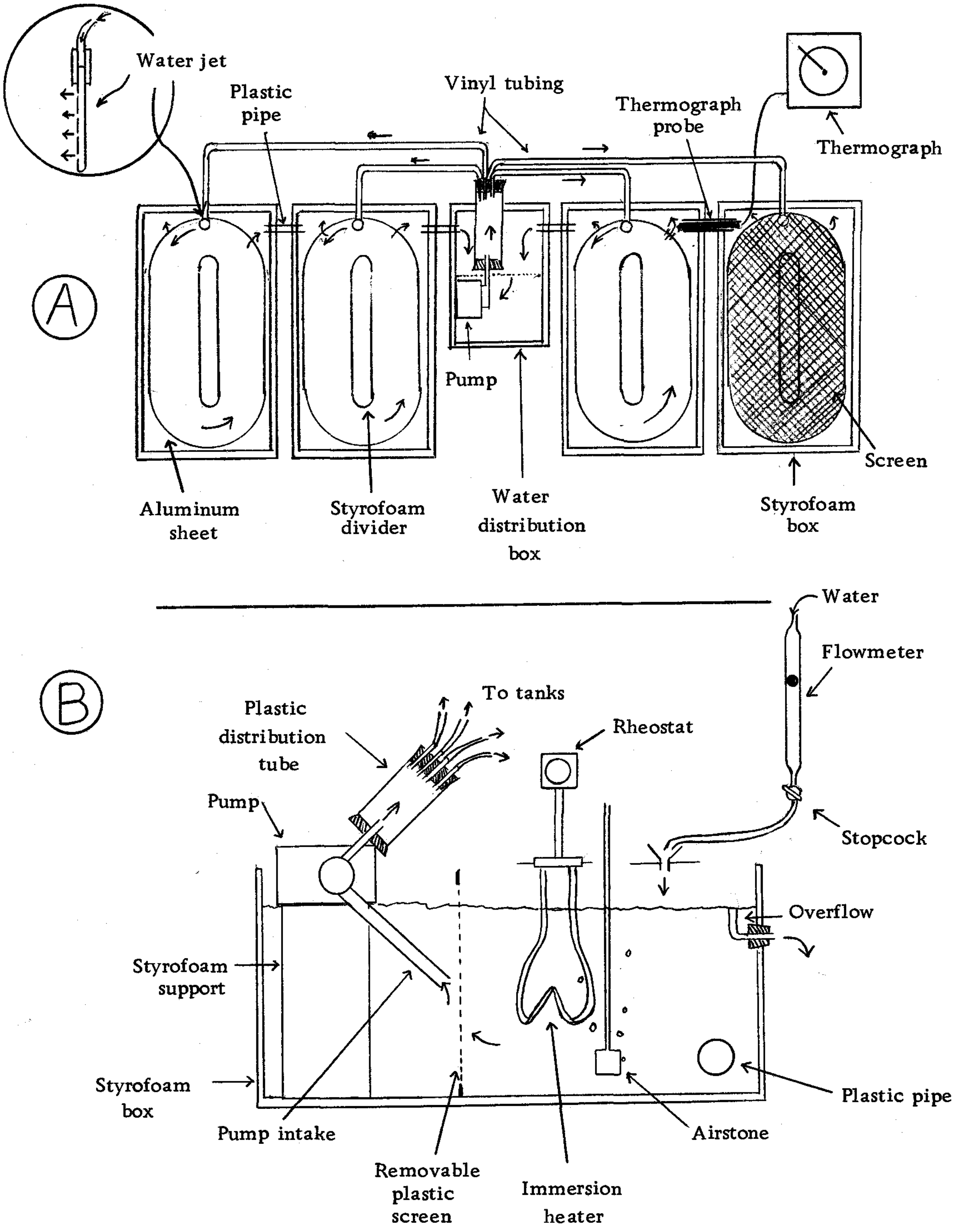

Figure 1. A: Diagram of the experimental tanks (one of the three units) used in the growth experiments.

B: Detailed side view of the water distribution box.

mean swimming velocity of the fish. The average swimming speed of the fish in all treatments was 1.2 body lengths/sec and ranged from 0.9 to 1.7 body lengths/sec (Appendix I). There was no consistent relationship between average swimming speed and either temperature or feeding rate.

The 12 experimental tanks were divided into three sets of four each. The four tanks of each set shared a common water system. Outlet water from each tank flowed through plastic pipes connecting the four tanks to a water distribution box (Figure 1B). After passing through nylon screening (12.6 mesh/cm), the water was pumped back to each tank through vinyl tubing.

Filtered creek water was exchanged in each set of tanks at a rate of 0.6 liters/min. The pH of the water varied seasonally from 7.0 to 8.1. Total alkalinity ranged from 80 to 123 mg/l as $CaCO_3$. Hardness ranged from 51 to 117 mg/l as $CaCO_3$. Aeration in each water distribution box maintained high oxygen levels. Oxygen saturation averaged 93% and ranged from 80 to 110%. Oxygen concentrations were checked a minimum of three times during each study. The diel temperature fluctuations of the creek water were dampened by storage in the laboratory water system. Diel fluctuations were restored by passing the water through a 1200 liter storage tank exposed to the sun and cool nights.

Three temperature treatments were tested in each experiment.

The control treatment followed natural temperature fluctuations of the water supply. Temperatures were elevated approximately 3 and 6 C above the control in the respective intermediate and high temperature treatments with stainless steel immersion heaters placed in the water distribution ~~boxes~~. Rheostats controlled the output of each heater. Thermographs, accurate to 0. 3 C, recorded temperature in each treatment. The mean, the average daily range, and the total range of temperature were calculated for each experiment. Temperatures recorded at each three-hour interval on the thermograph charts were used to calculate these values.

The experiments were conducted in a 15 C constant-temperature room. Fluorescent lights in the room were controlled with a timer to go on at sunrise and off at sunset. The timer was reset at weekly intervals.

Experimental Fish. Juvenile steelhead trout used in the Fall, Winter, and Spring experiments were obtained as eggs from adult fish from the North Santiam River (Marion County, Oregon). The eggs were hatched in well water at 9 C at the Oregon State University campus. Once the fry had absorbed their yolk sacs, they were transferred to the Oak Creek Laboratory and kept in creek water of ambient temperature (5-17 C). Steelhead used in the Summer growth experiment were obtained as eggs from the Oregon State Game Commission Alsea River Hatchery and hatched and reared in 12 C well water at the

Averill Fish Laboratory, Oregon State University. Both groups of fish were obtained from crossing several females and males. Stock fish were fed limited rations of Oregon moist pellet (Bioproducts, Warrenton, Oregon).

Acclimation. Trout used in the experiments were selected from the stock fish for fairly uniform, intermediate size and then distributed randomly to the experimental tanks. During the acclimation period, size differences developed among the fish. Accordingly, approximately 30% more fish were acclimated than were necessary for an experiment, so that excessively large or small fish could be rejected at the beginning of an experiment.

Fish were acclimated for 16 days to the experimental conditions. Acclimation of all fish began at the control temperature. On the second day of acclimation, temperatures of the intermediate and high temperature treatments were increased to 3 C above the control. On the third day, the temperature in the high temperature treatment was increased to 6 C above the control.

During acclimation, the fish were fed Oregon moist pellet at levels that I predicted, from data of preliminary experiments, 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 percentage dry weight of the fish approached levels (18-22%) that I found in wild trout of sizes similar to those used in the experiments. Fish were fasted for 48 hours before an experiment was begun to allow emptying of the gastrointestinal tract.

Experimental Design. Twenty fish per tank were used in the Fall and Summer experiments. Sixteen and 15 fish per tank were used in the Winter and Spring experiments, respectively. These numbers gave approximately equal amounts of fish length in the tanks during each experiment. The duration of each experiment was 25 days. The experimental periods, mean fish weights, and other experimental conditions are summarized in Table 1.

Initial wet weights and final wet and dry weights of individual fish were measured. On the first day of an experiment, the acclimated fish from the four tanks of each temperature treatment were pooled, individually blotted on damp toweling, and weighed to the nearest 0.01 g. Fish which differed by more than 30% from the mean weight of the group were rejected. Each fish of a temperature treatment was randomly placed into one of five groups. Four of the groups were distributed to the tanks of a temperature treatment. Fish in the fifth group were sacrificed, weighed, measured, and dried for estimating the initial percentage dry weights and lengths/gram of the fish used in the experiment. On the last day of the experiment, the fish were blotted, weighed, measured, and frozen. Dry weights of the

Table 1. Experimental periods, temperatures, and the initial lengths, wet weights and numbers of fish used in the experiments.

Experiment	Dates	Initial mean wet wt. (g)	Initial mean fork lengths (mm)	Fish/ tank	Days of acclimation	Length of experiment (days)	Nominal temperatures and treatments
Seasonal growth							
Fall	October 13- November 7, 1971	1.01	50	20	16	25	Ambient, +3, +6 C
Winter	January 23- February 17, 1972	1.93	61	16	16	25	Ambient, +3, +6 C
Spring	March 21- April 15, 1972	2.29	63	15	16	25	Ambient, +3, +6 C
Summer	June 25- July 20, 1972	1.16	50	20	16	25	Ambient, +3, +6 C
Effect of Fish Size	August 11- August 26, 1972	A - 5.25	82	8	10	15	16 C
		B - 3.36	70	9			
		C - 1.10	49	13			
		D - 0.58	41	16			
Fluctuating vs. Constant Temperatures							
A	July 22- August 6, 1972	1.46	54	9	15	15	Controlled diel fluctuations and constant temperatures
B	September 14- September 29, 1972	1.45	53	8	15	15	Controlled diel fluctuations and constant temperatures
Effect of Water Velocity	May 15- May 25, 1972	2.97	70	10	6	10	Ambient

fish were determined after they were freeze-dried for 24 hours. Fish larger than 2.5 g were cut along one side to facilitate drying.

Four ration levels of the Oregon moist pellet were fed in each temperature treatment. In the Fall, Spring, and Summer experiments, the fish were fed rations varying from that amount that I predicted would just maintain the body weight of the fish (maintenance ration) to all that the fish would eat in one daily 15-minute feeding (repletion ration). In the Winter experiment, rations varied from levels near starvation to levels moderately greater than the maintenance level. Low rations were fed during the Winter experiment so that the food consumption-growth rate relationship could be defined at low feeding rates. Feeding levels were based on the initial estimated dry weight of the fish and these amounts were then fed throughout the experiment.

During each experiment, six samples of food were weighed and freeze-dried to determine the percentage dry weight of the food. Estimates of the dry weight of food consumed by the fish could then be made. The caloric content of the pooled samples from each experiment was determined with an oxygen bomb calorimeter (Parr Model 13031). Instructions given in Parr Manual 130 (1960) were followed. Two replicate determinations were made on the food from each experiment. The caloric content of the food used in each experiment and a proximate analysis of Oregon moist pellet aregiven in Appendix II.

Fish were fed starting on the second day of the experiment and feeding continued through the twenty-third day. Two days of starvation elapsed before the final weighing. At feeding levels above 3%/day, fish were fed once daily between 0900 and 1100. At lower feeding levels subordinate fish in the tanks could not get food if only a small amount was fed. To facilitate food sharing, ration levels 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 fed in the Winter experiment was fed every third day.

The pellet fed to the fish contained 3% terramycin (TM50) added as a prophylactic against bacterial disease. Additionally, the fish were treated two or three times during each experiment with 1.5 mg/l active terramycin to control disease. The antibiotic was put in the tanks and allowed to flush from the system. Despite these measures, some deaths occurred in 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 proportionally 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 are expressed, respectively, as average relative growth and average relative food consumption rates. These are calculated as follows:

$$\text{Growth rate} = \frac{W_2 - W_1}{0.5\ (W_1 + W_2)\ t}$$

$$\text{Consumption rate} = \frac{C}{0.5\ (W_1 + W_2)\ t}$$

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

C = estimated dry weight of food consumed

In those treatments where fish died, rates of food consumption and growth were estimated for the dead fish and averaged with the rates of the surviving fish. Growth and consumption rates were multiplied by 100 and expressed as percentages of body weight per day.

Food conversion efficiencies (gross efficiencies) were calculated by dividing the growth rates by the food consumption rates. Efficiency values were multiplied by 100 and expressed as percentages. Maintenance rations were determined by graphical interpolation or extrapolation to zero growth rate of the lines relating food consumption rates to growth rates.

Results and Interpretation

Decelerating, curvilinear relationships between rates of food consumption and growth were defined in most of the experiments

(Figures 2-5; Table 2). The narrow range of ration levels fed in the Winter experiment resulted in nearly linear relationships between rates of food consumption and growth.

The effects of temperature on the growth rates of the trout were dependent on the food consumption rates of the fish. At low consumption rates, increases of temperature decreased the growth rates of the fish. As consumption rates increased, curves relating rates of food consumption and growth of different temperature treatments began to converge, and at repletion feeding levels, the curves sometimes crossed (Figures 2 and 4). 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 I fed repletion rations, 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 (Figures 2, 4, and 5). However, when the mean temperature reached 22.5 C in the Summer experiment, the fish ate less than did fish kept at temperatures 3 and 6 C lower. The reduction in food consumption was possibly due to "temperature stress," as the incipient lethal temperature for the species is near 26 C (Bidgood and Berst, 1969). Temperatures in the high temperature treatment exceeded 26 C for short periods four times during the experiment. At

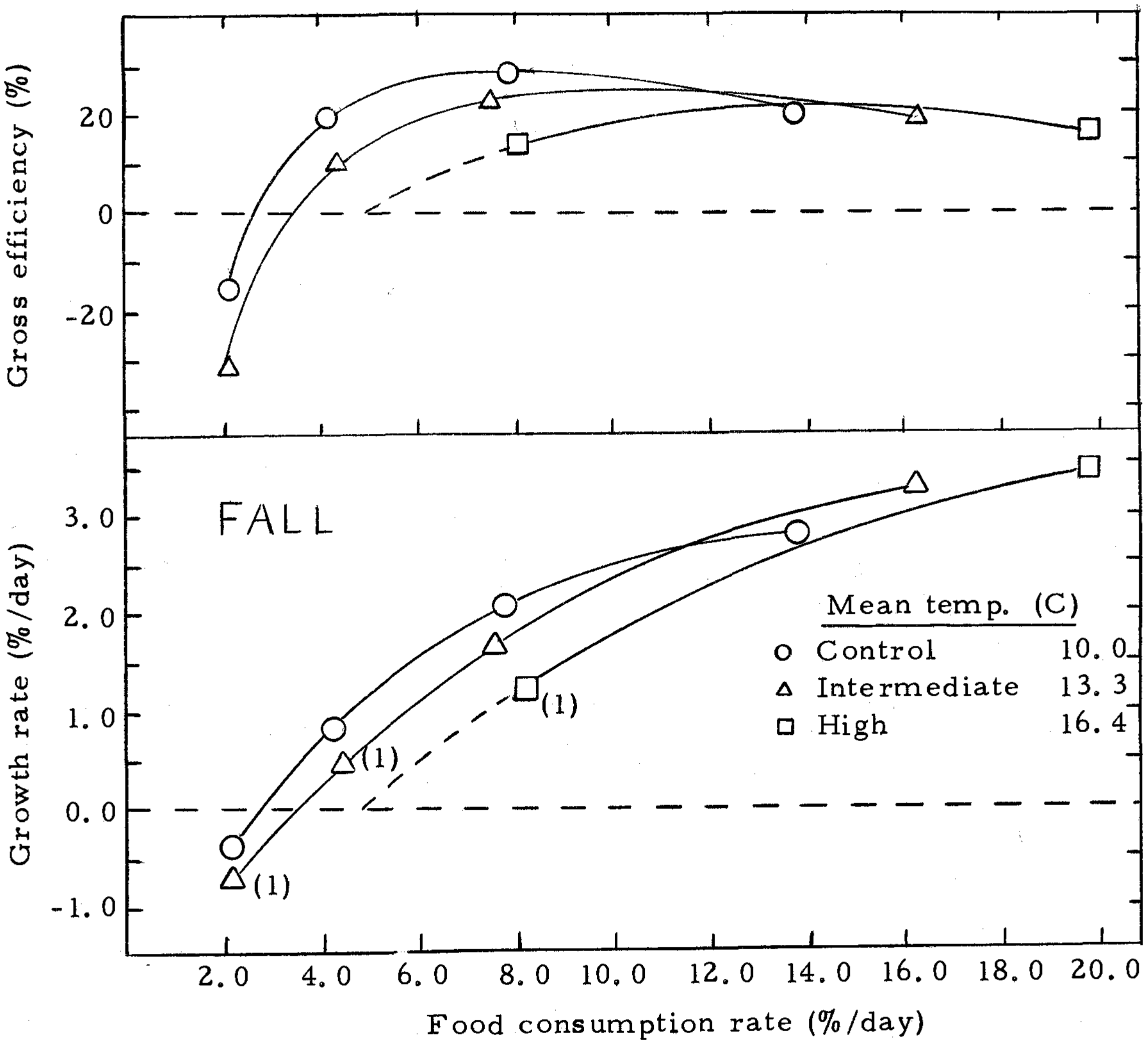

Figure 2. Relationships between rates of food consumption and the growth rates and gross efficiencies of steelhead trout kept at different temperatures in the Fall experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 1. 01 g. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

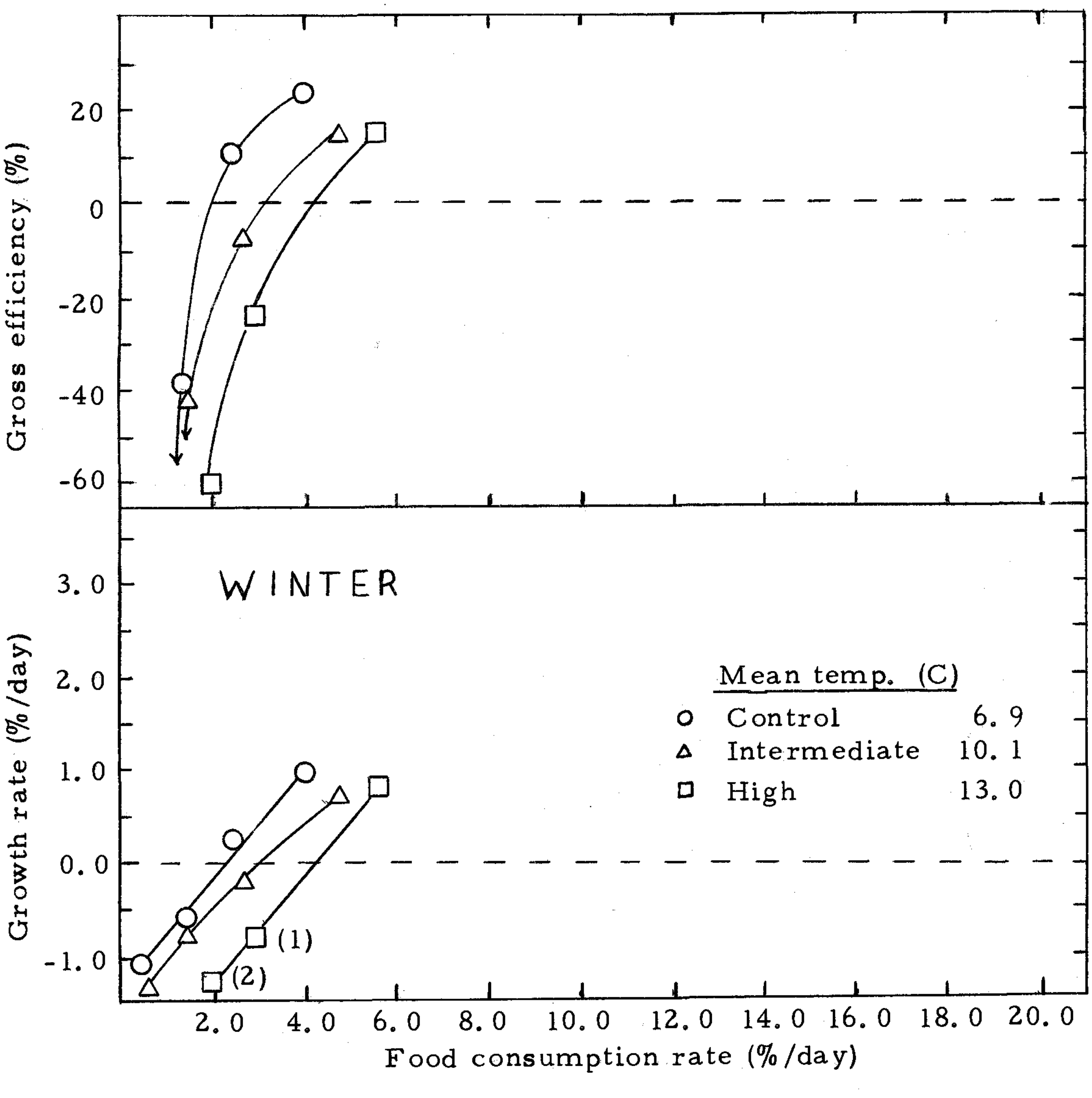

Figure 3. Relationships between rates of food consumption and the growth rates and gross efficiencies of steelhead trout kept at different temperatures in the Winter experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 1.93 g. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

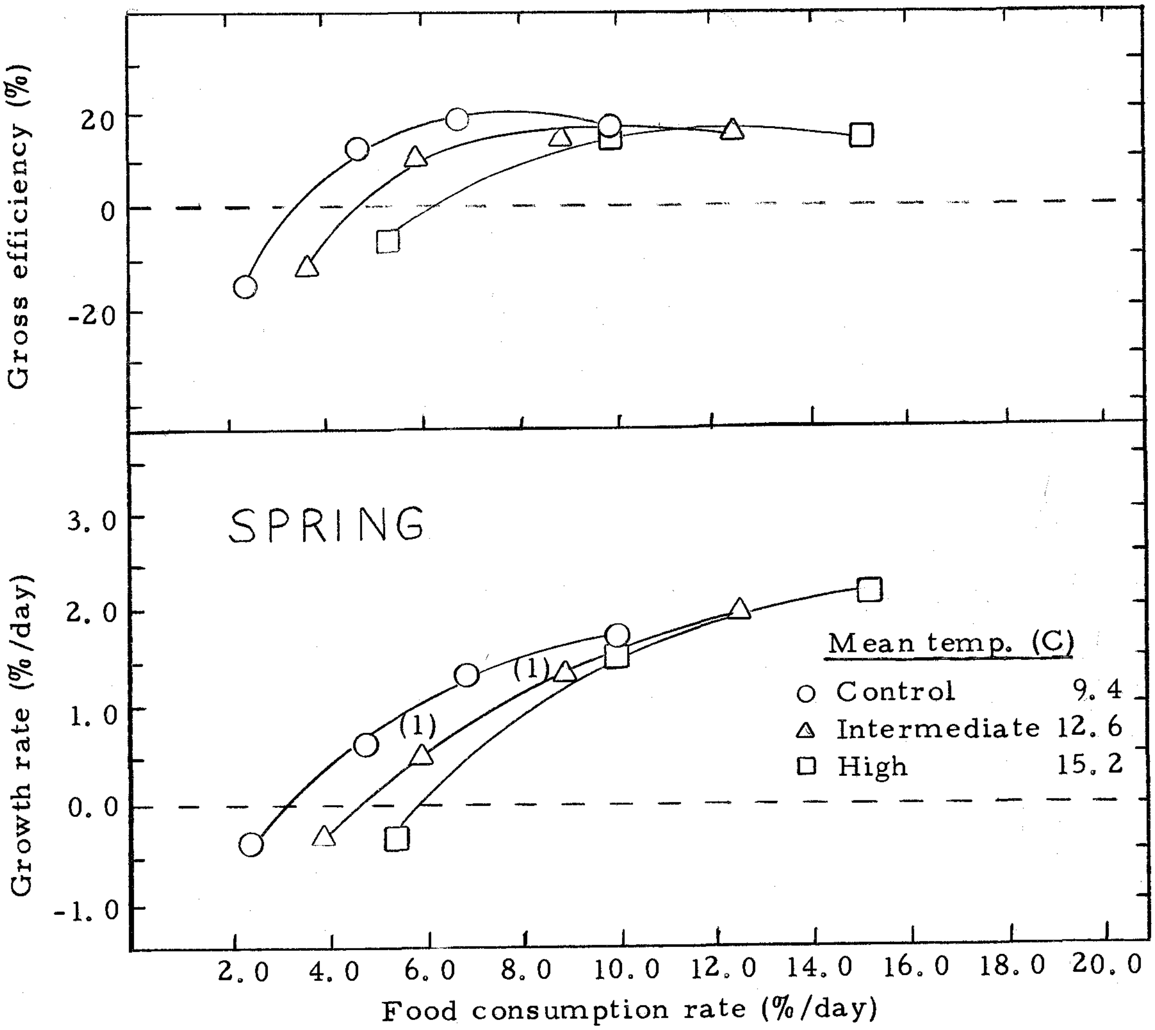

Figure 4. Relationships between rates of food consumption and the growth rates and gross efficiencies of steelhead trout kept at different temperatures in the Spring experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 2. 29 g. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

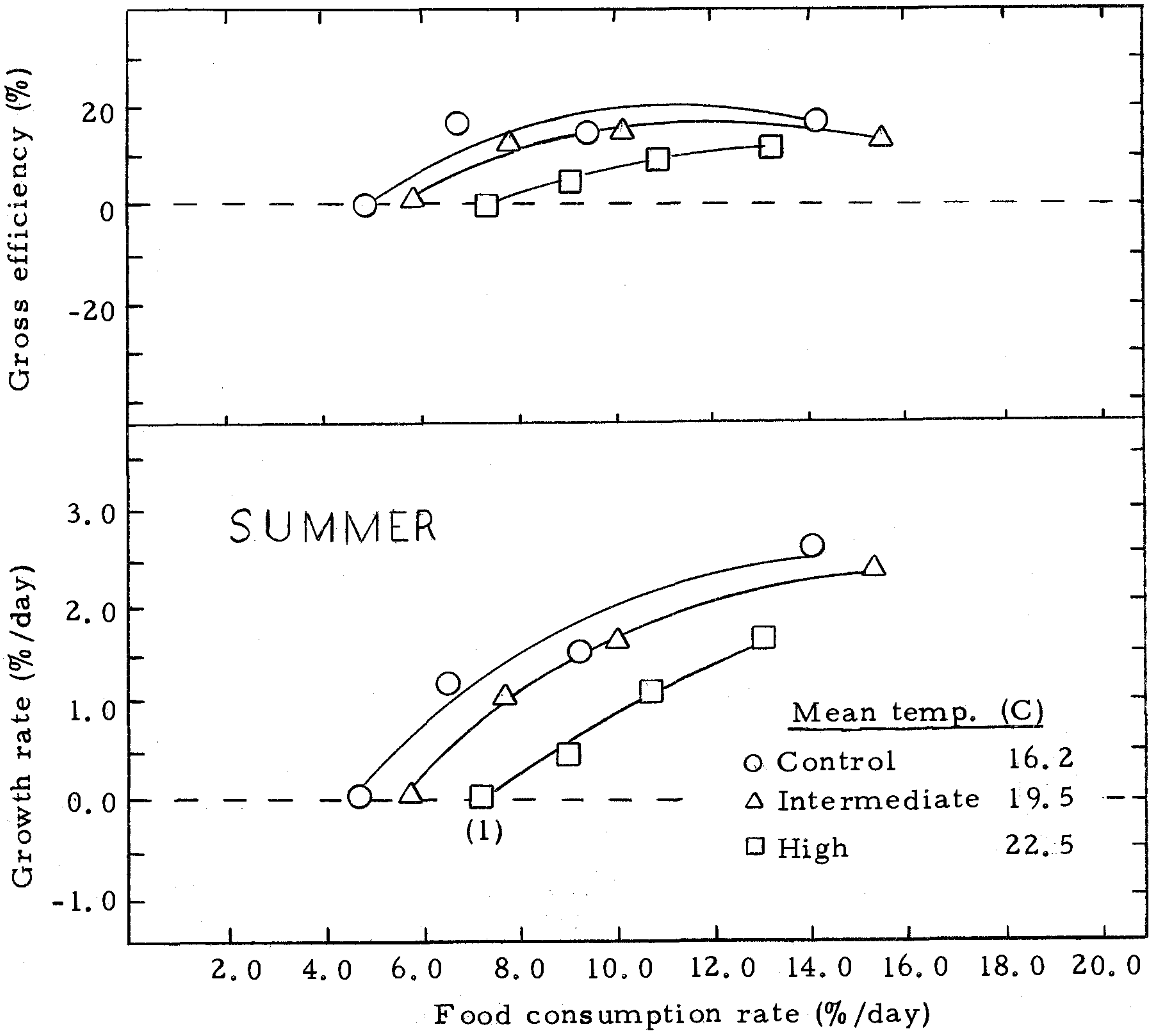

Figure 5. Relationships between rates of food consumption and the growth rates and gross efficiencies of steelhead trout kept at different temperatures in the Summer experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 1.16 g. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

[a] Coefficient of Variation (CV) is the standard deviation expressed as a percentage of the mean.

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

[c] One fish died 11-4-71; weight 0.79 g (0.09 g dry).

[d] One fish died 10-22-71; weight 1.00 g (0.11 g dry).

[e] One fish died 10-22-71; weight 0.92 g (0.15 g dry).

[f] One fish died 2-8-72; weight 1.47 g (0.24 g dry). Another died 2-16-72; weight 1.38 g (0.15 g dry).

[g] One fish died 2-16-72; weight 1.66 g (0.26 g dry).

[h] One fish died 4-7-72; weight 2.54 g (0.41 g dry).

[i] One fish died 4-12-72; weight 2.60 g (0.48 g dry).

[j] One fish died 4-1-72; weight 3.13 g (0.44 g dry). Another died 4-12-72; weight 2.50 g (0.40 g dry).

[k] One fish died 6-29-72; weight 1.22 g (0.17 g dry).

Table 2. Temperatures, and the consumption rates, initial and final wet weights, and percentage dry weights, and growth rates of steelhead trout in each of the seasonal growth experiments. Rates of food consumption and growth are based upon dry weights of food and fish.

Temperatures (C)			Consumption rate (%/day)	Total dry wt. of food consumed (g)	Initial mean wet wt.		Initial mean percentage dry wt.	Final mean wet wt.		Final mean percentage dry wt.	Mean growth rate (%/day)
Mean	Ave. daily change	Total range			(g)	(CV)[a]		(g)	(CV)		
						Fall					
10.0	2.7	6.2-13.0	2.2	2.02	0.98	(9.2)	19.4	0.96	(19.0)	18.4	-0.3
			4.3	4.88	1.04	(9.6)		1.31	(14.5)	19.9	0.9
			7.9	10.66	1.02	(12.7)		1.64	(17.1)	20.8	2.1
			14.0	21.19	1.00	(12.0)		1.89	(14.5)	21.8	2.9
13.3	3.1	9.2-16.8	2.2	2.01	1.00	(10.0)	19.9	0.93[c]	(17.2)	18.2	-0.7
			4.6	4.62	0.98	(12.2)		1.17[d]	(17.1)	19.4	0.5
			7.7	9.93	1.02	(11.8)		1.55	(16.8)	20.3	1.7
			16.5	27.41	0.97	(12.4)		2.11	(13.7)	22.4	3.4
16.4	2.8	12.3-19.9	8.3	8.95	0.94	(10.6)	19.7	1.29[e]	(22.4)	20.0	1.3
			20.1	32.80	0.92	(12.0)		2.04	(17.6)	23.0	3.5
						Winter					
6.9	1.1	3.9-10.1	0.5	0.82	2.03	(6.9)	21.8	1.82	(8.2)	18.5	-1.1
			1.5	2.37	2.01	(9.4)		1.96	(10.7)	19.4	-0.6
			2.5	4.41	1.95	(8.7)		2.10	(11.9)	21.7	0.3
			4.2	7.94	1.91	(10.5)		2.30	(12.2)	23.2	1.0
10.1	1.7	7.2-24.2[b]	0.6	0.97	1.96	(9.7)	21.1	1.66	(12.0)	18.1	-1.3
			1.5	2.31	1.96	(9.2)		1.82	(10.4)	19.3	-0.6
			2.7	4.45	1.97	(7.1)		2.02	(11.0)	19.6	-0.2
			4.9	8.82	1.94	(6.2)		2.35	(10.2)	21.1	0.8
13.0	1.2	9.6-17.8	2.0	2.71	1.92	(6.5)	20.5	1.70[f]	(8.8)	17.4	-1.3
			3.0	4.17	1.84	(10.0)		1.72[g]	(13.3)	18.4	-0.8
			5.7	9.80	1.86	(8.6)		2.21	(13.1)	21.6	0.9
						Spring					
9.4	1.5	7.2-12.1	2.5	4.23	2.35	(7.0)	20.0	2.35	(12.8)	18.3	-0.4
			4.9	8.90	2.25	(5.8)		2.71	(9.6)	19.4	0.6

(Continued on next page)

Table 2. (Continued)

Temperatures (C) Mean	Ave. daily change	Total range	Consumption rate (%/day)	Total dry wt. of food consumed (g)	Initial mean wet wt. (g)	(CV)	Initial mean percentage dry wt.	Final mean wet wt. (g)	(CV)	Final mean percentage dry wt.	Mean growth rate (%/day)
					Spring (continued)						
			7.0	14.89	2.36	(11.2)		3.19	(11.3)	20.6	1.3
			10.2	21.73	2.23	(9.9)		3.38	(14.5)	20.4	1.7
12.6	1.8	9.9-16.4	3.8	6.51	2.29	(8.1)	20.2	2.29	(13.5)	18.7	-0.3
			6.1	11.29	2.33	(8.2)		2.82[h]	(17.7)	19.2	0.5
			9.1	18.46	2.24	(10.3)		3.17[i]	(14.2)	20.5	1.4
			12.7	30.31	2.28	(10.1)		3.75	(13.1)	21.6	2.0
15.2	1.6	12.4-18.4	5.5	8.60	2.28	(6.6)	20.0	2.33[j]	(13.7)	18.0	-0.4
			10.2	21.48	2.25	(8.0)		3.17	(16.4)	21.1	1.6
			15.4	35.90	2.25	(8.4)		3.73	(20.9)	21.2	2.2
					Summer						
16.2	3.1	12.7-20.8	4.9	5.91	1.14	(10.9)	21.0	1.21	(18.0)	19.9	0.0
			6.8	10.28	1.23	(9.1)		1.57	(15.9)	22.0	1.2
			9.5	14.54	1.18	(12.0)		1.64	(16.7)	22.2	1.5
			14.3	26.75	1.20	(10.0)		2.13	(19.7)	23.2	2.6
19.5	3.4	16.0-23.9	6.0	7.76	1.19	(9.0)	21.7	1.28	(15.0)	21.4	0.1
			7.9	11.92	1.21	(10.0)		1.53	(17.0)	22.3	1.1
			10.3	16.31	1.16	(11.0)		1.63	(18.6)	23.3	1.6
			15.7	28.68	1.18	(14.2)		2.02	(19.8)	23.5	2.4
22.5	3.5	17.8-26.8	7.4	8.88	1.10	(8.2)	22.1	1.21[k]	(12.4)	21.3	0.0
			9.2	11.90	1.10	(8.0)		1.25	(11.8)	21.8	0.5
			11.0	15.71	1.11	(10.0)		1.41	(19.0)	23.1	1.1
			13.4	21.64	1.16	(8.6)		1.61	(15.3)	24.2	1.7

these high temperatures, the reduction in appetite may also have been related to elevated oxygen demands of the fish, under conditions of reduced oxygen concentration in the water. Oxygen concentration has been shown to limit maximum food consumption of both coho salmon and largemouth bass at moderately high temperatures (Doudoroff and Shumway, 1970).

Gross efficiency was dependent on both ration level and temperature (Figures 2-5). Gross efficiencies at ration levels below maintenance were negative, and at the maintenance level they were zero. As food consumption rate increased, gross efficiency increased. In most cases, efficiency reached a maximum level and then declined slightly at very high consumption rates. In the Winter experiment, where I restricted maximum ration levels, and in the high temperature treatment of the Summer experiment, where maximum food consumption appeared to be inhibited by the high temperatures, gross efficiency 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. Figure 6 shows that at a low ration level (4%/day), gross efficiencies declined markedly with temperature increase. At an intermediate ration level (8%/day) temperature increase had considerably less effect on efficiency and at a high ration level (13%/day), increased temperature lowered gross efficiency only slightly.

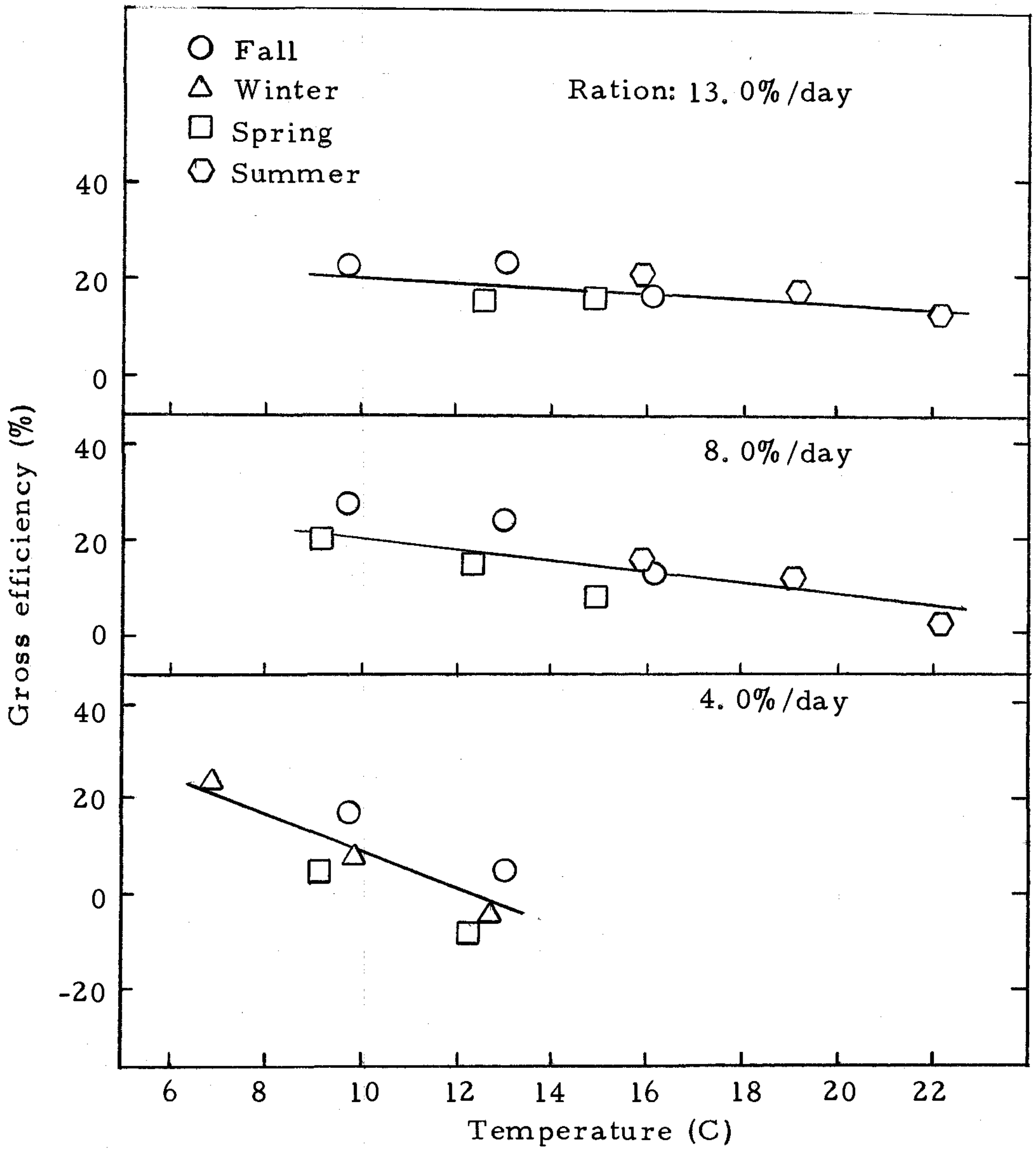

Figure 6. Relationships between temperature and gross efficiency of steelhead trout at three different ration levels. Plotted values were taken from the curves in Figures 2-5. Lines fitted by method of least squares.

During each season, temperature elevation led to an increase in the maintenance rations of the trout (Figure 7). Maintenance requirements of the fish increased over three-fold (2.2 to 7.4%/day) as temperature increased from 6.9 to 22.5 C. The relationship of maintenance ration (M) to temperature (T) in the pooled data of all the experiments was: $\log M = 0.032 \cdot T + 1.184$; $r^2 = 0.85$. However, in the different seasons, temperature-maintenance ration relationships were different. Maintenance rations at a given temperature were particularly high in the Spring experiment. The effects of season on the relationships between temperature, ration, and growth will be discussed later.

Both ration level and temperature affected the body composition of the trout. Within each temperature treatment, fish at high feeding levels had higher percentages of dry weight than fish at low feeding levels. At a given ration level, temperature increase usually reduced the final percentage dry weight of the fish (Table 2). The positive influence of ration level and the negative influence of temperature on the final dry weight percentage of the fish suggested that percentage dry weight might be strongly dependent upon the growth rate of the fish. The final percentages of dry weight and growth rates of the fish were positively correlated, but there was considerable variance in the data ($r^2 = 0.62$). However, the positive relationship between growth rate and <u>change</u> in the dry weight percentage of the fish was very good

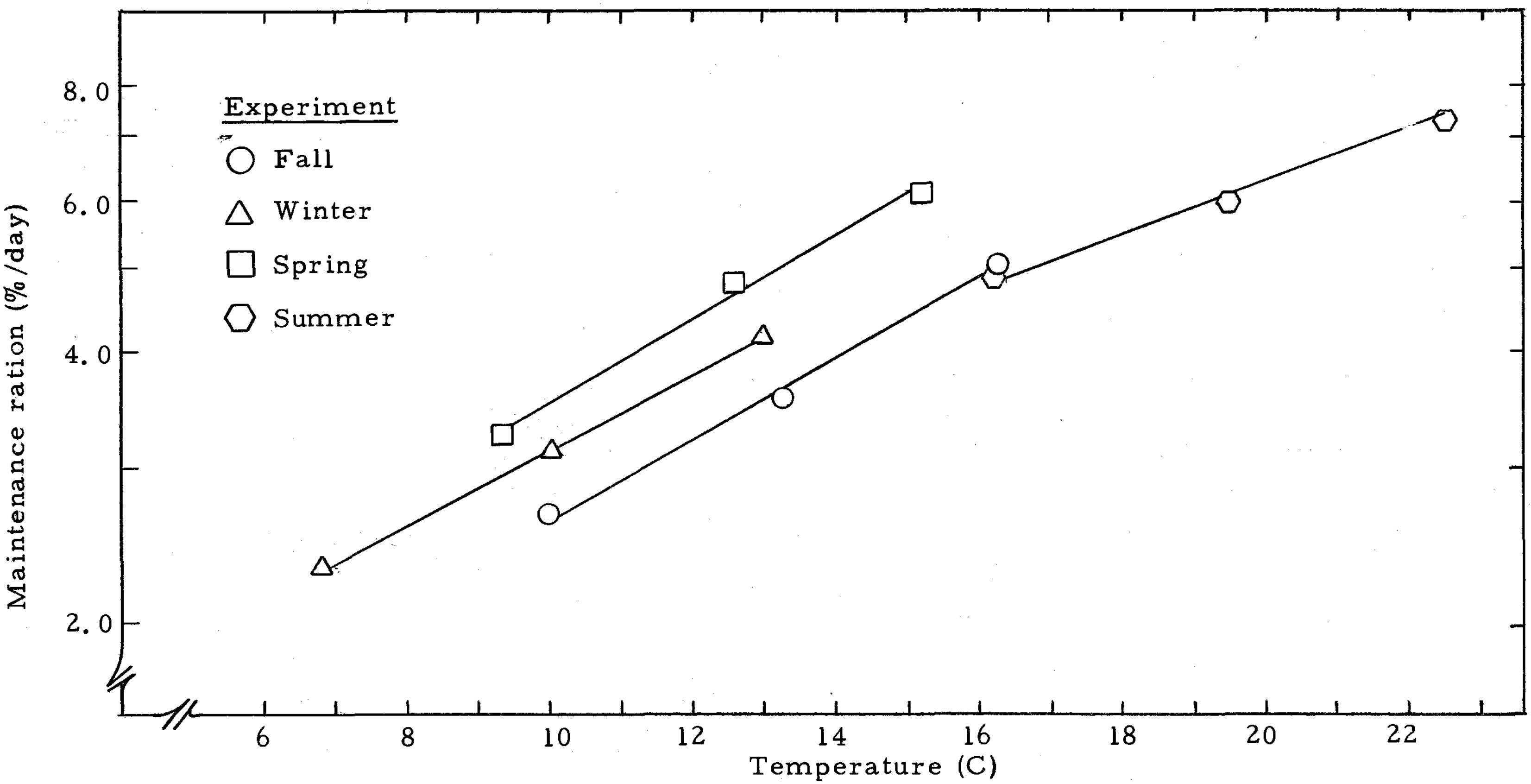

Figure 7. Relationships between temperature and maintenance rations (dry weight) of steelhead trout in each of the seasonal growth experiments. Lines fitted by method of least squares. Note log scale.

(Figure 8), suggesting that the initial dry weight percentage of the fish used in the experiments influenced their final percentage dry weight.

Change in the percentage dry weight of the trout is indicative of a change in the percentage of fat in the fish (Phillips, MS 1972) and consequently, a change in their caloric content. Caloric expressions of food consumption and growth are more meaningful than expressions in units of dry weight. To determine if the relationships between rates of food consumption and growth, at different temperatures, were different if expressed in caloric units, dried samples of fish and food of the Spring experiment were analyzed for caloric content. The pooled, dried fish from each treatment and the initial fish subsamples were homogenized in a Waring blender, pressed into pellets, and replicate caloric determinations were made.

Both caloric and gravimetric measurements resulted in approximately the same relationships between rates of food consumption and growth at different temperatures (Appendix III). Caloric measurements defined somewhat steeper food consumption-growth rate curves than those based on dry weight, indicating that increased food consumption resulted in increased fat deposition of the fish.

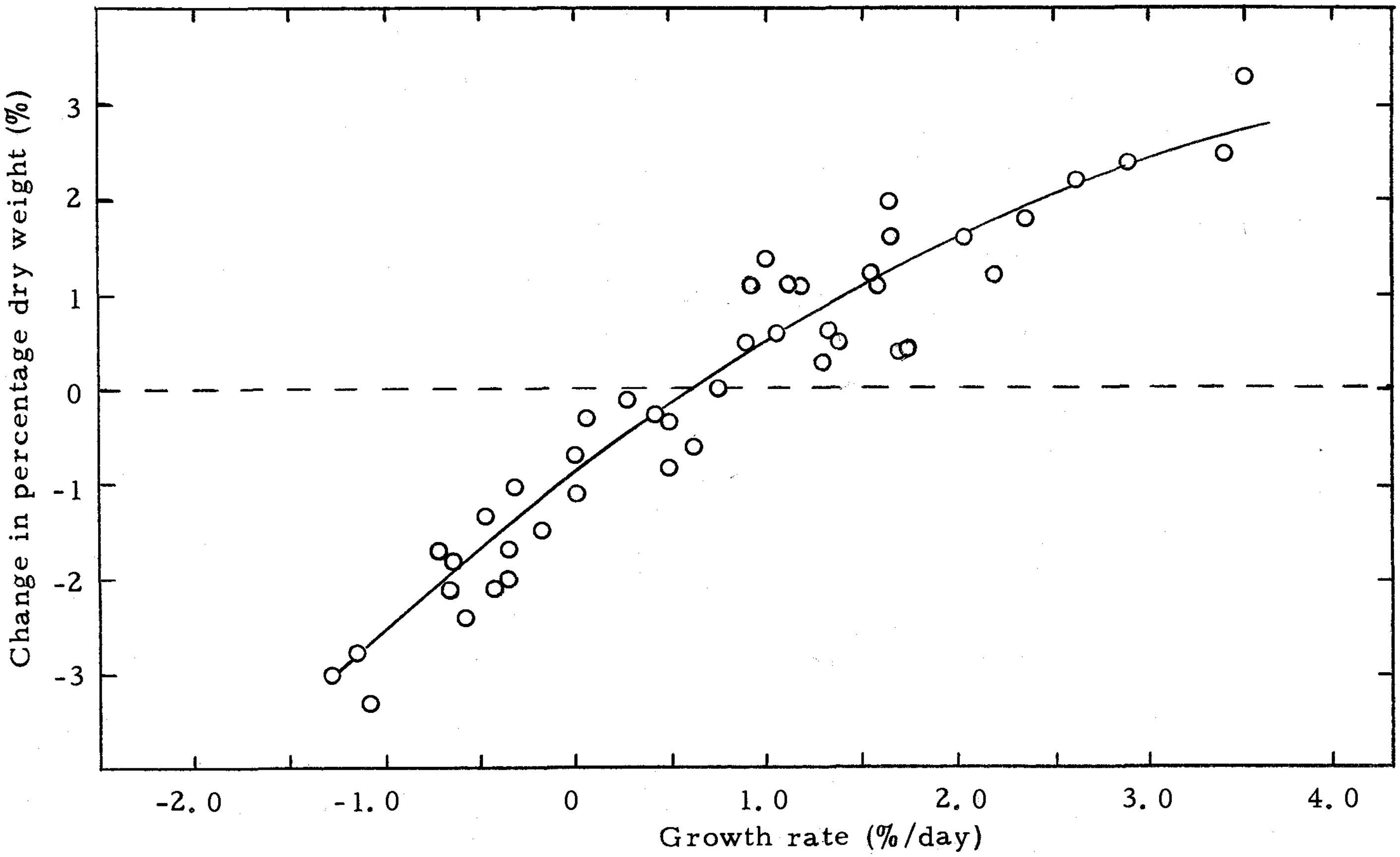

Figure 8. The relationship between the growth rate of steelhead trout and the change in percentage dry weight of the fish during the seasonal growth experiments. Line fitted by inspection.

Effects of Fish Size on Growth

Methods and Materials

Experimental Fish. For this experiment, it was desirable to have trout that differed greatly in size, but which had similar ages and treatment histories. Accordingly, steelhead trout eggs of a single cross, obtained at the Oregon State Game Commission Alsea River Hatchery, were given the following treatment: The trout eggs were divided evenly into four groups (termed A, B, C, and D), and each was incubated at a different temperature to induce differential rates of development. Incubation temperatures were obtained by introducing water at 6 C at the top of a Heath vertical flow incubator and adding 12 C water at increasing rates to successively lower trays. This arrangement provided incubation temperatures of 11.8, 9.2, 6.9, and 5.7 (± 0.5) C for groups A, B, C, and D, respectively. The mean times to absorption of the yolk sacs at these temperatures were 57, 83, 111, and 132 days, respectively. Gas supersaturation in the well water used for incubation caused mortalities varying from approximately 50% in Group A to approximately 5% in Group D. All fish noticeably effected were removed. Immediately after individuals of each group absorbed their yolk sacs they were transferred to 12 C water. The fish were fed Oregon moist pellet ten times daily to insure rapid growth rates. Group A fish were fed for 116 days while

Group D fish were fed for only 41 days. The different feeding periods resulted in nearly a 10-fold size difference between groups A and D by the start of the experiment (Table 1). The eggs were incubated and hatched at the Oregon State Game Commission Research Laboratory. The fish were fed at the Averill Fish Laboratory, Oregon State University.

Apparatus and Methods. This experiment was designed to measure the growth rates of steelhead trout of four different sizes at three feeding levels. The apparatus and methods used in the study were similar to those used in the seasonal growth experiments, except that: (1) water temperatures were kept at 16 ± 0.3 C; (2) the fish were acclimated for 10 days before the experiment began; and (3) the duration of the experiment was 15 days. Size groups A, B, C, and D had, respectively, 8, 9, 13, and 16 fish per tank. These numbers of fish provided equal amounts of fish length in each tank. Mean swimming velocities for the different size groups ranged from 1.0 to 1.2 body lengths/sec (Appendix I). The dates, mean fish weights, and other experimental conditions are summarized in Table 1.

The three ration levels fed to each size group were 5.0, 9.0, and 14.0%/day of the estimated initial dry weights of the fish. The 5.0%/day ration was predicted to be near the maintenance requirements of the fish, and the 14.0%/day ration was the maximum amount that Group A fish would eat at the start of the experiment. The Oregon moist pellet (containing 3% TM50) fed in this experiment was from a single lot which was ground and sieved to obtain pellet sizes appropriate for the different sizes of fish.

Five fish died during the experiment. Their growth and consumption rates were estimated and averaged with the rates of the other fish.

Results and Interpretation

The effect of fish size on growth rate was dependent on the consumption rates of the trout (Figure 9B; Table 3). As fish size increased from 0.58 to 3.36 g, the maintenance requirement (per gram of fish tissue) declined. The relative maintenance requirements of fish weighing 5.25 and 3.36 g appeared to be similar. However, the value estimated as the maintenance level of the largest fish (5.25 g) is only tentative, as two deaths occurred in the group fed rations near the maintenance level.

As ration sizes increased from maintenance levels, the difference in growth rates between large and small fish decreased (Figure 9B). At the highest comparable ration levels, large fish (3.36 and 5.25 g) grew at the same rates or slower than small fish (0.58 and 1.10 g). The growth rates of the large fish failed to remain greater than those of the small fish because the gross efficiencies of the large

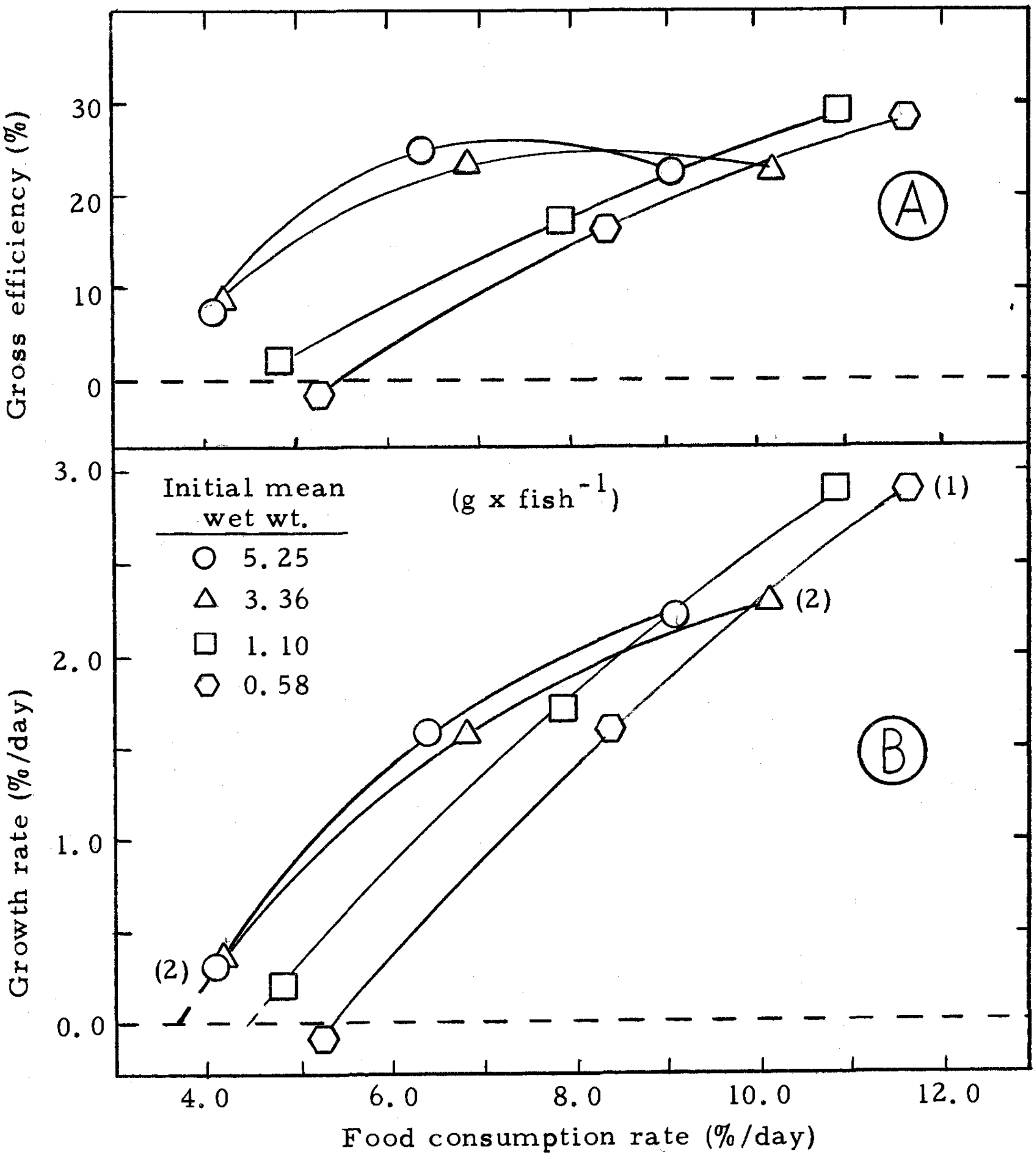

Figure 9. Relationships between rates of food consumption and the growth rates and gross efficiencies of steelhead trout of different sizes. Rates of food consumption and growth are expressed in dry weights. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

Table 3. Consumption rates, initial and final wet weights and percentage dry weights, and growth rates of steelhead trout in the experiment on the effects of fish size. Rates of food consumption and growth are based upon dry weights of food and fish.

Size group	Consumption rate (%/day)	Total dry wt. of food consumed (g)	Initial mean wet wt. (g)	(CV)	Initial mean percentage dry wt.	Final mean wet wt. (g)	(CV)	Final mean percentage dry wt.	Mean growth rate (%/day)
A (5.25 g)	4.1	5.86	5.33	(2.7)	23.4	5.63[a]	(11.0)	23.4	0.3
	6.4	10.63	5.19	(4.4)	23.4	6.40	(8.8)	24.2	1.6
	9.1	16.10	5.22	(4.2)	23.4	7.07	(11.9)	24.3	2.3
B (3.36 g)	4.2	4.22	3.39	(6.3)	22.1	3.55	(6.0)	21.5	0.4
	6.9	7.73	3.33	(6.1)	22.1	4.17	(7.9)	22.4	1.6
	10.2	11.90	3.46	(5.0)	22.1	8.04[b]	(15.0)	22.6	2.3
C (1.10 g)	4.8	1.92	1.05	(7.3)	19.2	1.10	(15.0)	18.8	0.2
	7.9	3.83	1.12	(7.9)	19.2	1.39	(8.0)	20.1	1.7
	10.9	5.85	1.12	(7.7)	19.2	1.61	(12.0)	20.8	2.9
D (0.58 g)	5.2	1.32	0.58	(6.4)	18.2	0.58	(15.5)	17.9	-0.7
	8.4	2.43	0.58	(5.8)	18.2	0.72	(16.6)	18.7	1.6
	11.6	3.60	0.58	(6.2)	18.2	0.85[c]	(12.9)	19.2	2.9

[a] One fish died 8-20-72; weight 5.61 g (1.19 g dry). Another died 8-24-72; weight 5.67 g (1.24 g dry).

[b] One fish died 8-19-72; weight 4.06 g (0.78 g dry). Another died 8-23-72; weight 3.88 g (0.78 g dry).

[c] One fish died 8-16-72; weight 0.67 g (0.10 g dry).

fish declined at the high ration levels, while the efficiencies of the small fish continued to increase with ration increases to the highest levels offered (Figure 9A).

Effects of Water Velocity on Growth

Methods and Materials

To determine what effect the water velocity in the test tanks had on the growth of the trout, an experiment was designed to measure growth rates of fish kept at the normal current velocities in the tanks, and in still water. The source and culture methods of the trout used in this experiment were identical to those used in the Winter seasonal growth experiment. Except as noted, the apparatus and methods used in this study were similar to those used in the seasonal growth experiments.

Six tanks were used in the experiment, allowing three ration levels to be fed in both the normal velocity treatment and in the still water treatment. Still water was obtained in three tanks by facing the water jets directly at the sides of the tanks. Water temperatures during the experiment fluctuated from 10.8 to 16.3 C ($\overline{x}$ = 12.8 C). The fish were acclimated to the experimental conditions of temperature, feeding conditions, and the respective velocity treatments for six days. The duration of the experiment was 10 days. The swimming speeds of the fish in the normal velocity treatment were estimated at 0900 and 1900 daily by methods previously described. Experimental conditions of the experiment are summarized in Table 1.

Results and Interpretation

Fish reared in water with a current grew at approximately the same rates as fish reared in still water (Figure 10, Appendix IV). Trout reared in the tanks with a water current had mean swimming velocities ranging from 1. 1 to 1. 3 body lengths per second (Appendix IV). Since the differences in growth rates between the two velocity treatments were small, it appears that the energy costs expended by trout in still water are similar to those of fish swimming at velocities near one body length per second. These results were expected. Brocksen, Davis and Warren (1968), and Carline (MS 1968) found that both cutthroat trout (Salmo clarki) and coho salmon grew at similar rates whether they were fed in aquaria or while swimming in model streams.

Growth in Fluctuating and Constant Temperatures

Methods and Materials

Apparatus. Growth rate measurements were made of trout kept at two "constant" temperatures (16 and 18 C) and at temperatures

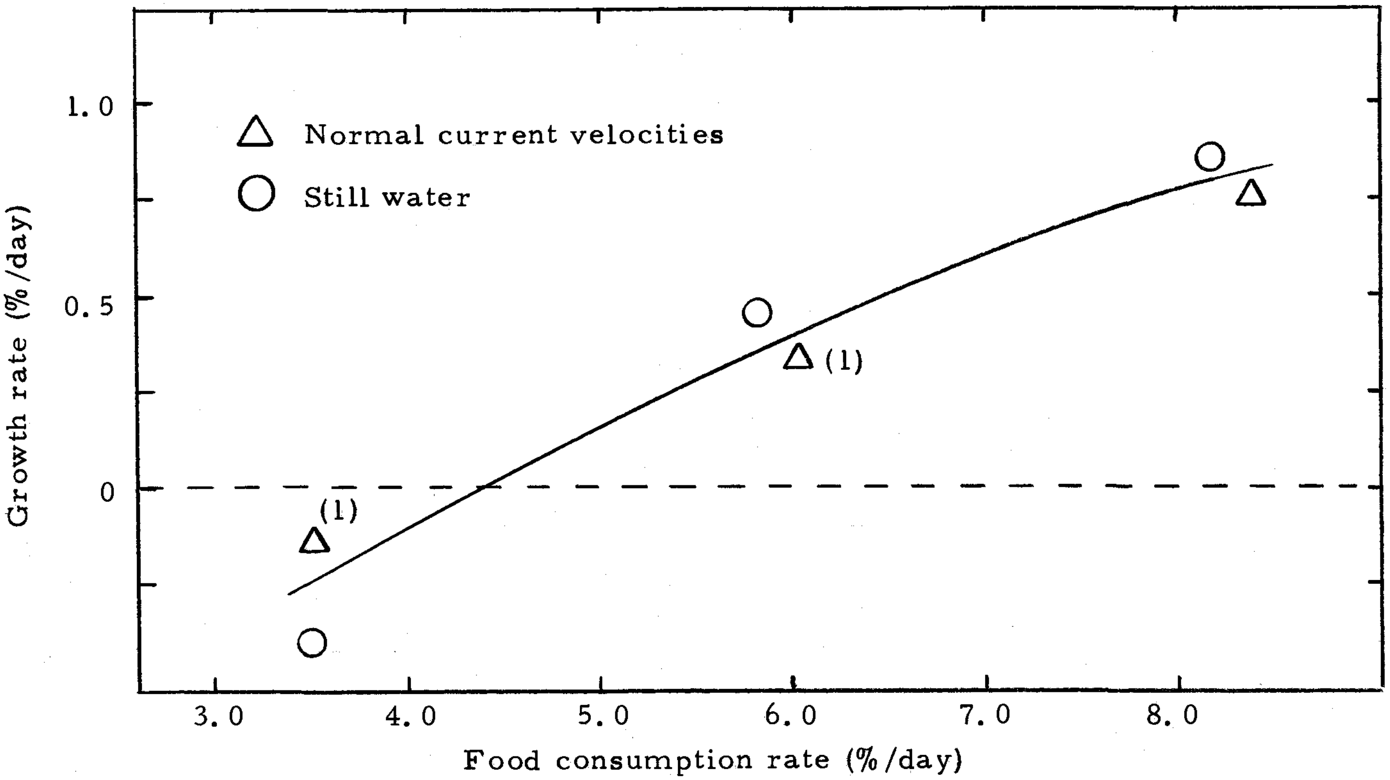

Figure 10. Comparison of growth rates of groups of steelhead trout kept in still water with those kept in tanks which had a gradient of water velocity from 0 to 160 mm/sec. Numbers in parentheses indicate the number of fish which died in a treatment. Line fitted by inspection.

which fluctuated dielly from each constant temperature within a range of 4 C (14-18 and 16-20 C) and 8 C (12-20 and 14-22 C). The apparatus used in the experiment is shown in Figure 11. Six headboxes were located above the experimental tanks. Water temperatures in the headboxes were maintained within ± 0.2 C of the desired temperatures with stainless steel immersion heaters controlled by thermoregulators. Water for the constant temperature treatments flowed directly from the appropriate headbox to a water distribution manifold located above the experimental tanks. Solenoid valves (Asco Valve model 8260), controlled by timers, regulated the water flow from two headboxes to the tanks of each fluctuating temperature treatment. Beginning at 0700 each day, "warm" water flowed to the tanks for periods of 18 hours. "Cool" water flowed to the tanks for periods of 18 hours, beginning at 1900 each day. Water was distributed to the four tanks of a temperature treatment by a water manifold. Glass faucets in the manifold regulated the water flow into each tank at a rate of 0.14 ± 0.01 liters/min. The tanks were polyethylene buckets, each containing 10 liters. The water system described provided a diel temperature cycle which approximated a sigmoid pattern, taking 11 hours to change from one extreme to the other. Temperatures in each temperature treatment were recorded by thermographs and analyzed in the same manner as described for the seasonal growth experiments.

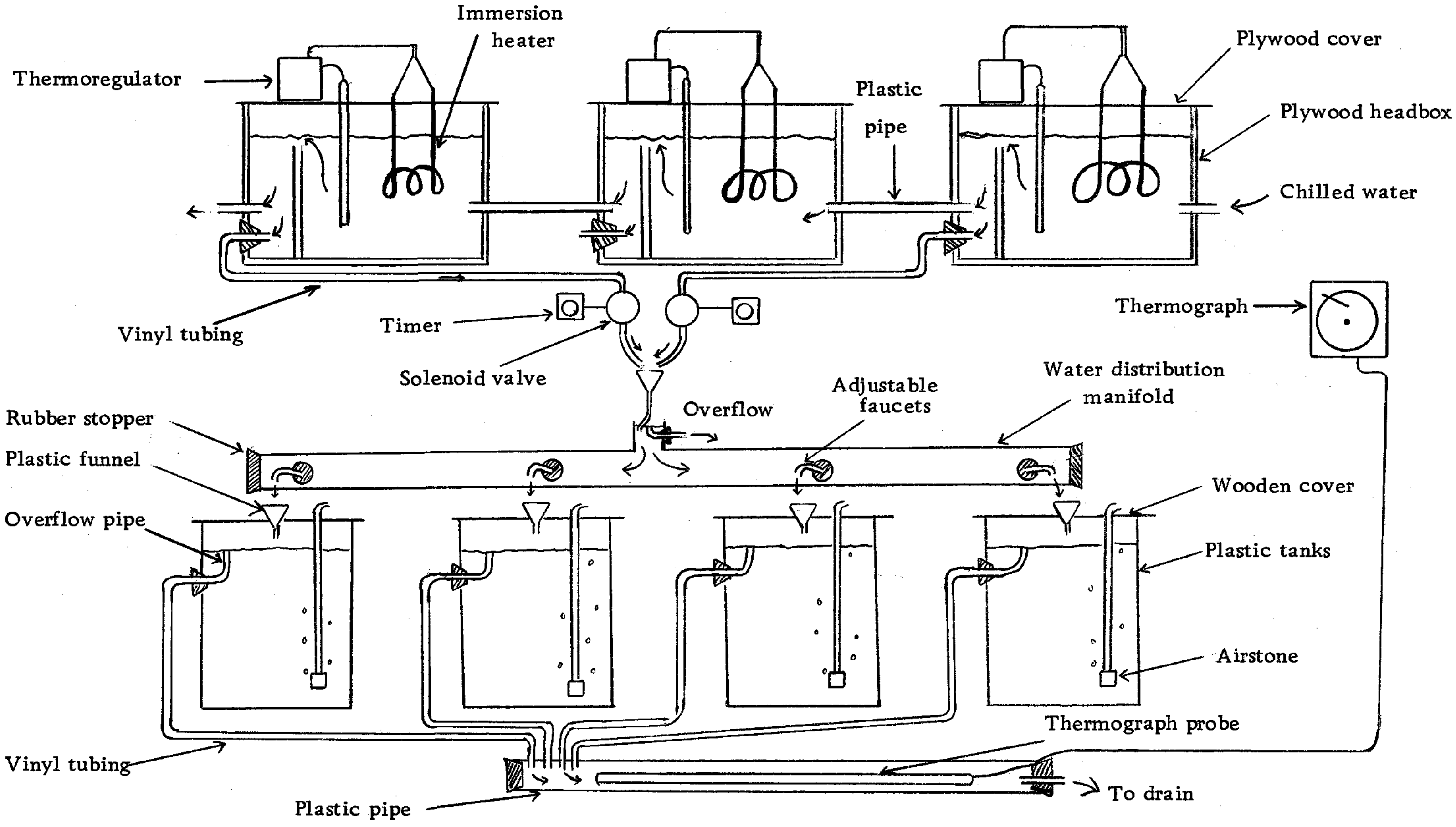

Figure 11. Diagram of the apparatus used in the experiments on the effects of fluctuating temperatures on the growth of fish. Shown are three of the six headboxes and one of the six sets of tanks.

Experimental Fish. The source and culture methods of the steelhead trout tested in this experiment were identical to those of the fish used in the Summer seasonal growth experiment. The fish were hatched and reared in 12 C well water.

Methods. Except as noted, the methods used in these experiments were similar to those used in the seasonal growth experiments. Fish were placed in the tanks at 13 C. The following morning, the temperature treatments were initiated and acclimation continued for 15 days. The duration of each experiment was 15 days. The trout in each temperature treatment were fed at levels of 5.0, 7.5, 11.0, and 16.5%/day, based on their estimated initial dry weights. These levels ranged from near maintenance to slightly below the repletion ration. The fish were fed daily at 0900 and 2000 ± 1 hr. Nine fish per tank were used in the first experiment (A). Because of a shortage of fish, only eight fish per tank were used in the replicate experiment (B). The dates, mean fish weights, and other experimental conditions are summarized in Table 1.

Six fish died of unknown causes during the first experiment. Three of the fish were in one tank, and the data from this tank were not utilized in the analysis. In the replicate experiment, fish in many of the treatments died because of an infection with myxobacteria and the results from five of the tanks had to be discarded. Errors in weighing at the start of the experiment forced me to discard the results from four other tanks.

Results and Interpretation

The first experiment comparing trout growth rates in fluctuating and constant temperatures indicated that, at most ration levels, the fish grew faster at constant temperatures than at temperatures that fluctuated 4 or 8 C daily (Figure 12; Table 4). Fish in tanks receiving the two lowest ration levels and kept at a constant 18 C had growth rates similar to those of fish in the fluctuating temperatures. However, fish in these two constant temperature tanks were diseased, and this may have reduced their growth rates. Relationships between rates of food consumption and growth in treatments with 4 and 8 C diel temperature fluctuations were similar.

Results from the replicate experiment (B) indicated that fish grew equally well in constant and fluctuating temperatures (Figure 13; Table 4). However, comparison between the different temperature treatments was difficult, because of the large number of ration level treatments which had to be discarded.

Only recently have the effects of fluctuating temperatures on fish growth been studied, and the results are variable. Kelso (1972) found that walleye (Stizostedion vitreum vitreum), fed moderate rations and kept in temperatures which fluctuated from 8 to 16 C, had lower gross efficiencies than fish kept in 12 C water. Maintenance rations were slightly higher for walleye kept in the fluctuating temperatures than in

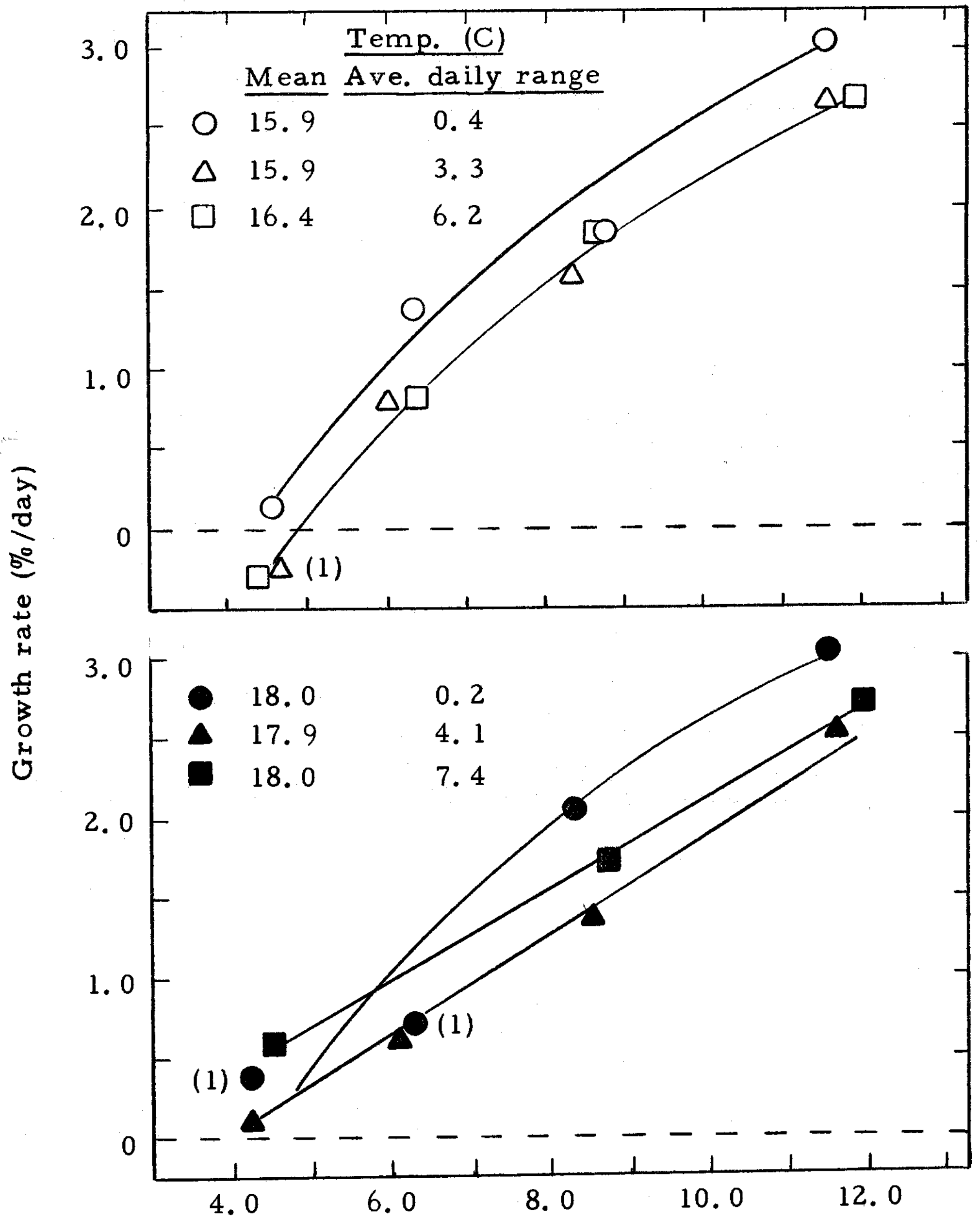

Figure 12. Relationships in experiment A between rates of food consumption and growth of juvenile steelhead trout kept at constant and at fluctuating temperatures. Rates of food consumption and growth are expressed in dry weights. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

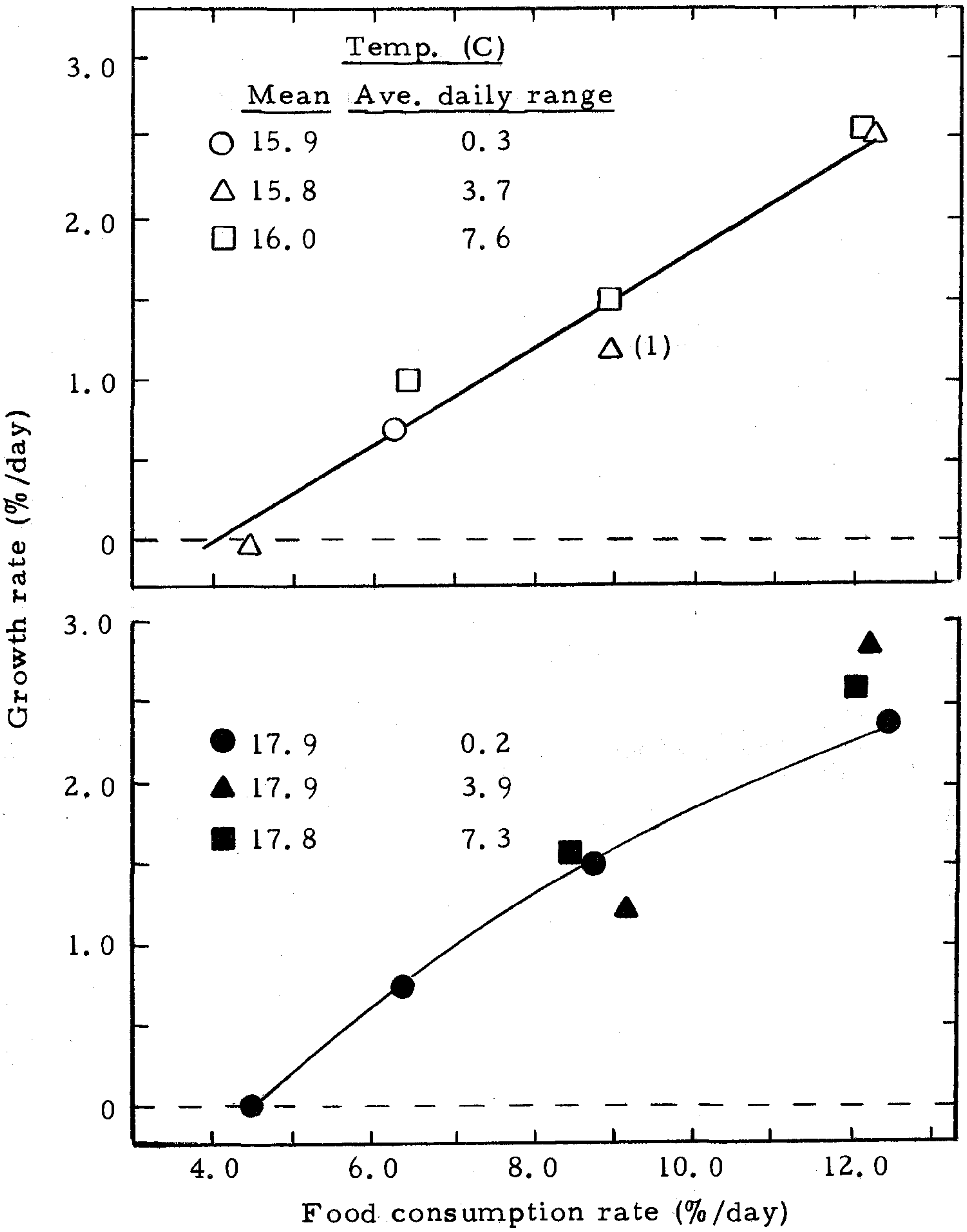

Figure 13. Relationships in experiment B between rates of food consumption and growth of juvenile steelhead trout kept at constant and at fluctuating temperatures. Rates of food consumption and growth are expressed in dry weights. Numbers in parentheses indicate the number of fish which died in a treatment. Lines fitted by inspection.

Table 4. Experimental temperatures, and the consumption rates, initial and final wet weights and percentage dry weights, and growth rates of steelhead trout in experiments A and B on the effects of fluctuating and constant temperatures. Rates of food consumption and growth are based upon dry weights of food and fish.

Temperatures (C)				Consumption rate (%/day)	Total dry wt. of food consumed (g)	Initial mean wet wt.		Initial mean percentage dry wt.	Final mean wet wt.		Final mean percentage dry wt.	Mean growth rate (%/day)
Nominal	Mean	Ave. daily change	Total range			(g)	(CV)		(g)	(CV)		
						Experiment A						
16	15.9	0.4	15.4-17.0	4.6	1.75	1.40	(8.6)	20.2	1.44	(9.8)	20.0	0.1
				6.3	2.76	1.42	(9.2)	20.2	1.65	(9.9)	21.4	1.4
				8.7	4.09	1.48	(6.8)	20.2	1.83	(6.6)	21.6	1.9
				11.5	5.84	1.43	(8.4)	20.2	2.02	(6.8)	22.8	3.0
14-18	15.9	3.3	13.9-17.8	4.6	1.97	1.51[a]	(7.3)	21.3	1.55	(9.0)	20.1	-0.3
				6.0	2.53	1.38	(9.3)	21.3	1.57	(9.9)	21.1	0.8
				8.4	3.89	1.43	(9.1)	21.3	1.76	(15.3)	22.0	1.6
				11.5	6.23	1.51	(5.5)	21.3	2.13	(6.5)	22.5	2.7
12-20	16.4	6.2	12.1-20.1	4.4	1.75	1.46	(7.5)	20.8	1.48	(8.9)	19.5	-0.3
				6.3	2.73	1.44	(7.6)	20.8	1.60	(10.7)	21.2	0.8
				8.6	4.09	1.45	(6.9)	20.8	1.81	(8.7)	22.0	1.8
				11.9	6.04	1.44	(10.4)	20.8	2.04	(11.0)	22.1	2.7
18	18.0	0.2	17.4-18.7	4.3	1.67	1.44[b]	(8.3)	20.6	1.44	(9.2)	21.5	0.4
				6.3	2.37	1.37[c]	(5.1)	20.6	1.49	(8.9)	21.5	0.7
				8.3	4.09	1.49	(10.7)	20.6	1.86	(13.2)	22.4	2.1
				11.5	6.23	1.50	(8.7)	20.6	2.09	(13.5)	23.1	3.0
16-20	17.9	4.1	15.6-20.3	4.3	1.75	1.42	(13.4)	21.3	1.42	(15.8)	21.4	0.1
				6.1	2.73	1.48	(6.0)	21.3	1.63	(11.4)	21.3	0.6
				8.6	3.70	1.35	(9.0)	21.3	1.62	(17.2)	21.7	1.4
				11.7	6.04	1.46	(12.3)	21.3	1.98	(16.6)	23.1	2.5
14-22	18.0	7.4	13.8-22.5	4.5	1.95	1.49	(10.6)	20.5	1.54	(9.2)	21.7	0.6
				8.7	4.06	1.47	(14.3)	20.5	1.75	(20.0)	22.3	1.7
				12.0	6.43	1.54	(6.4)	20.5	2.17	(9.3)	22.0	2.7

(Continued on next page)

Table 4. (Continued)

Temperatures (C)				Consumption rate (%/day)	Total dry wt. of food consumed (g)	Initial mean wet wt.		Initial mean percentage dry wt.	Final mean wet wt.		Final mean percentage dry wt.	Mean growth rate (%/day)
Nominal	Mean	Ave. daily change	Total range			(g)	(CV)		(g)	(CV)		
						Experiment B						
16	15.9	0.3	15.3-16.4	6.3	2.32	1.45	(8.0)	20.1	1.54	(10.0)	21.1	0.7
14-18	15.8	3.7	13.4-17.9	4.5	1.55	1.44	(7.0)	20.1	1.47	(10.0)	19.6	0.0
				9.0	3.49	1.46	(7.5)	20.1	1.76[d]	(12.5)	20.9	1.2
				12.3	5.42	1.49	(6.7)	20.1	2.06	(11.1)	21.2	2.5
12-20	16.0	7.6	11.6-19.9	6.5	2.52	1.49	(14.1)	20.1	1.67	(15.0)	21.0	1.0
				9.0	3.49	1.43	(8.4)	20.1	1.69	(14.2)	21.3	1.5
				12.1	5.42	1.50	(10.7)	20.1	2.04	(10.3)	21.7	2.5
18	17.9	0.2	17.4-18.3	4.5	1.55	1.42	(8.5)	20.2	1.40	(9.3)	20.4	0.0
				6.7	2.52	1.47	(6.1)	20.2	1.58	(7.6)	21.1	0.8
				8.8	3.29	1.37	(8.7)	20.2	1.47	(9.5)	23.7	1.5
				12.5	5.42	1.47	(6.8)	20.2	1.91	(9.4)	22.4	2.4
16-20	17.9	3.9	15.3-20.0	9.2	3.30	1.38	(9.4)	19.7	1.55	(12.3)	21.1	1.2
				12.2	5.23	1.43	(5.6)	19.7	1.98	(11.2)	21.9	2.3
14-22	17.8	7.3	13.6-22.3	8.5	3.49	1.45	(9.7)	20.8	1.74	(10.3)	22.0	1.6
				12.0	5.42	1.46	(6.5)	20.8	2.01	(9.4)	22.3	2.6

[a] One fish died 8-4-72; weight 1.62 g (0.22 g dry).

[b] One fish died 7-30-72; weight 1.49 g (0.32 g dry).

[c] One fish died 7-27-72; weight 1.53 g (0.25 g dry).

[d] One fish died 9-29-72; dry weight 0.24 g.

the constant temperature. Brett (1971b), after analyzing both field and laboratory data on the growth and behavioral relationships of sockeye salmon, concluded that these fish profited bioenergetically by voluntarily subjecting themselves to widely fluctuating temperatures.

My data suggest that trout may utilize food less efficiently in fluctuating temperatures than in constant temperatures. However, because of the variability within and between my experiments, I can only say with certainty that within the temperature ranges studied, large diel temperature fluctuations are not beneficial to the growth of steelhead trout fed restricted rations. Different results might have been obtained if other temperature ranges had been studied or if fish had been fed repletion rations.

Food Consumption and Growth of Wild Trout

Methods and Materials

Steelhead trout were collected seven times between September 9, 1971 and August 14, 1972, in Tobe Creek (Benton County, Oregon) to estimate their growth, and from this, their food consumption rates. Minimum flow of this small coastal stream is near 0.3 cfs (Averett, MS 1969). The fish were collected in a two-mile section of the creek with a d-c electric shocker. The trout were transported to the laboratory and held 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. The fish were freeze-dried and dry weights determined by methods described previously.

The growth rates of the steelhead trout in Tobe Creek were calculated as daily instantaneous growth rates rather than average relative growth rates, because in some cases considerable time periods elapsed between sampling days. If growth is exponential and if samples are taken infrequently, average relative growth rates may underestimate the true growth rates of the fish. The mean dry weight of the fish in each of the samples was used to calculate growth rates during the sampling intervals. Growth rates are expressed as percent per day, and are roughly comparable to the average relative growth rates.

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

Food consumption rates of the fish in Tobe Creek were estimated by comparing the fishes' calculated growth rates with growth rates of fish kept in the laboratory and fed known ration levels. This method is discussed by Davis and Warren (1968), and its validity is supported by the experiments of Brocksen, Davis and Warren (1968) and Carline (MS 1968) which demonstrated that the food consumption-growth rate relationships of salmonids kept in aquaria do not differ greatly from those kept in model streams. Values of food consumption rate for fish in Tobe Creek were taken from curves defined during the seasonal growth experiments. In each case I used a relationship that was established at the temperature which most nearly approximated the mean temperature in Tobe Creek during a given sampling interval. In some cases I had to use a growth rate curve derived at temperatures somewhat warmer than those in Tobe Creek. In these cases the food consumption rates of the Tobe Creek fish were probably overestimated.

Results and Interpretation

The growth rates of the steelhead trout from Tobe Creek varied from -0.2 to 1.6%/day, with a mean rate of 0.8%/day (Table 5). 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 methods used to assess growth could have caused considerable variation in my estimates. Despite these difficulties, I believe these growth rates provide reasonable estimates of the range of growth rates of fingerling trout in Tobe Creek.

Table 5. Sampling dates, mean temperatures and the sample sizes, mean wet weights, percentage dry weights, instantaneous growth rates, and estimated consumption rates of the 1971 year class of steelhead trout in Tobe Creek.

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

Other published growth rates of steelhead trout show reasonable agreement with my results. Fraser (1968) found that steelhead trout stocked in various densities with coho salmon in experimental stream channels had growth rates ranging from 0. 17 to 5. 70% /day. The mean growth rate of fish over 0. 78 g was 0. 40% /day and ranged from 0. 17 to 0. 74% /day. The growth in length of steelhead trout in two Idaho streams was reported by Everest and Chapman (1972). I calculated wet growth rates of the fish from their data using length-weight relationships of Tobe Creek trout. Growth rates of age 0 and age 1 trout in the two streams varied from 0. 6 to 1. 1% /day during the summer growing period. Stream temperatures ranged from approximately 9 to 18 C during this period. The growth rates of steelhead trout reported by these authors, and those I found for trout in Tobe Creek, indicate that growth rates of all but the very small wild steelhead trout are much lower than the maximum growth rates of the fish in my laboratory studies.

Estimated consumption rates of the trout in Tobe Creek ranged from 2. 0 to 7. 6% /day (Table 5). Because of the methods used, these consumption rates are only approximations of the true consumption rates of wild steelhead trout. They do indicate, however, that consumption rates of wild fish are considerably less than the maximum consumption rates of fish in the laboratory growth experiments.

DISCUSSION

The efficiency with which steelhead trout in my experiments utilized food for maintenance and growth was considerably less than that reported for other salmonids. Phillips (MS 1972) found maintenance rations of rainbow trout kept at 15 C and fed Oregon moist pellet to be 2.1%/day, while I estimated maintenance rations to range from 4.0 to 6.2%/day at a mean temperature of 15 C. Everson (MS 1973) found maintenance rations for coho salmon fed Oregon moist pellet were usually between 2.0 and 2.4%/day for fish kept in fluctuating temperatures averaging 15 C. Estimated maintenance rations of sockeye (Brett et al., 1969) and coho salmon (Averett, MS 1969) were below 3.0%/day at temperatures of 15 C, but in these experiments Oregon moist pellet was not fed, so comparison with my experiments is tenuous. Gross efficiency values of fish in my experiments were also less than those reported for other salmonids at comparable temperatures and ration levels.

Several factors in my experimental design might account for the poor food utilization by the steelhead trout. First, if food is not shared equally among fish fed in a group, and if the relationship between food consumption and growth rate is curvilinear, the mean growth rate determined for the group will be below that of fish receiving equal amounts of food. Food was undoubtedly shared unequally among the trout in my experiments, as indicated by the increase in variation of fish weights from the beginning of an experiment to the end (Tables 2, 3, and 4). The general conclusions regarding the relationships between temperature, food consumption, and growth are probably little affected by the unequal feeding, as neither temperature nor feeding level had any apparent effect on the change-in-weight variability within a group of fish. A second factor that may have affected food utilization was the use of terramycin in the food. Wagner (1954) found that rainbow trout fed repletion rations which contained terramycin grew slower than controls fed normal diets. However, Herman (1969) decided that terramycin depressed fish growth rates by influencing food palatability and consequently maximum food consumption. As the effects of terramycin on fish fed restricted rations have not been studied, I can only suggest that the antibiotic might have had a detrimental effect on food utilization. A third factor that may have depressed food utilization was disease which occurred during the experiments. Although the effects of disease on fish growth have not been studied, it is likely that food is utilized less efficiently in diseased than healthy fish. Both temperature and ration level affected mortality attributable to disease. In the seasonal growth experiments, mortality was generally highest in the high temperatures and low ration levels (Appendix V). While salmonid diseases are generally recognized to be more virulent at high temperatures (Ordal and Pacha, 1963), the effect of ration level on disease resistance of fish apparently has not received much attention.

Seasonal differences in the relationship between temperature, food consumption, and growth were difficult to resolve, as fish of different sizes were used during the different seasons. It is obvious, though, that fish in the Spring experiment were less efficient in utilizing food for maintenance and growth than were fish tested during other seasons (Figures 7 and 8). On the basis of size alone, the fish tested in the Spring experiment would have been expected to have the highest gross efficiencies (at low consumption rates) because they were the largest fish used in any of the seasonal experiments. Trout reared during the Winter experiment had greater maintenance requirements than fish reared in the Fall experiment, again the reverse of what would be expected on the basis of fish size. However, at most consumption rates, the gross efficiencies of trout reared in the Fall, Winter, and Summer experiments were similar at comparable temperatures.

While season changed the efficiency of food utilization of trout, the fishes' response to temperature change was approximately the same, regardless of season (Figure 7). Averett (MS 1969) reported seasonal shifts in the optimal temperatures for growth of coho salmon fed restricted rations. However, my data, and the data on coho salmon derived by Everson (MS 1963) indicate that regardless of season, any increase of temperature above normal seasonal levels will decrease the growth of trout and coho salmon fed low or moderate rations.

The effect of trout size on food conversion efficiency was different at different ration levels. I believe that two factors which change with changes in fish size are primarily responsible for the interdependence of gross efficiency on both fish size and ration level. First, standard metabolic rate generally decreases with increase in fish size (Winberg, 1956). Because most of the energy of rations near maintenance is accounted for by energy expended in standard metabolism (Averett, MS 1969) (other fractions are accounted for by specific dynamic action, activity, and waste products), the relative maintenance rations of large fish are less than small fish. Brown (1946a) found that maintenance rations of brown trout declined with increasing fish size. Secondly, the maximum ration (as a percentage of body weight) that fish will eat decreases with increasing fish size (Brown, 1946a; Pandian, 1967; Brett, 1971a; Gerking, 1971). As consumption rates approach maximum levels, increasing portions of food energy may be lost in the feces (Kinne, 1960; Averett, MS 1969; Lee and Shumway, MS 1973), and respiratory losses will increase due to increases in specific dynamic action and perhaps increased activity (Averett, MS 1969). Consequently, the efficiency of food utilization is partly dependent on whether a fish is feeding near its maximum capacity. Although I did not feed the trout to repletion in my experiment, it was obvious from their feeding behavior that the large fish were fed nearly to capacity, but that the small fish could have eaten larger rations.

Because the highest ration levels fed were near capacity for the large fish, their efficiencies began to decline at the highest consumption rates (Figure 9). The efficiencies of the small fish would not have been expected to decline unless they had consumed rations near their maximum capacity (approximately 20 or 25%/day at 16 C).

The gross efficiency of nitrogen conversion in bluegill sunfish (Lepomis macrochirus) is also dependent on both fish size and ration level (Gerking, 1971). If Gerking's data are expressed in relative units (i. e., %/day), maintenance rations of the fish generally decreased with increase in fish size. Furthermore, a decrease in bluegill size generally led to steeper slopes of the linear regression lines relating rates of nitrogen retention and nitrogen consumption. At intermediate consumption rates the regression lines for fish of different sizes crossed. Consequently, at low ration levels, large fish were generally more efficient than small fish, but at high ration levels, small fish were more efficient than large fish.

Lee and Shumway (MS 1973) found that in largemouth bass (Micropterus salmoides), the effect of fish size on the relation between rates of food consumption and growth was somewhat different. While maintenance rations of large bass were less than those of small fish, the food consumption-growth rate curves for the two size groups did not cross, so that at equal consumption rates, the gross efficiencies of large bass were greater than those of small bass. However, small fish ate much larger repletion rations than did the large fish, and consequently, the small fish had higher maximum gross efficiencies than those of large fish.

Several authors have found that gross efficiencies of fish feeding to repletion declined with increasing fish size (for review see Paloheimo and Dickie, 1966). The decline in efficiency with increasing fish size may be due to: (1) a decreasing capacity to digest and convert large rations into tissue, as shown by my results and those of Gerking (1971); and/or (2) a decrease in capacity to consume rations in excess of the maintenance ration. Paloheimo and Dickie (1966) expressed the latter view by saying, "that not only does the rate of rations intake decrease with increase in [fish] size, but that it apparently decreases at a faster rate than does the respiratory metabolism" (p. 1223).

I have assumed that fish size is a causal factor affecting the food consumption-growth rate relationships. We should be cautioned that "physiological age" (Brody, 1945) or some other factor associated with size increase could be the actual factor changing the relationship. We should also not assume that changes in the food consumption-growth rate relationships follow smooth trends with change in fish size. For instance, Pandian (1967) found that the decline in maximum food consumption rate with increasing fish size was not a smooth function, but could be divided into a phase with a rapid initial decline, followed by a phase with a much more gradual decline.

Rapidly growing fish in my experiments had higher percentage dry weights than slow growing fish. Reanalysis of the data of Brett _et al._ (1969) shows a significant positive linear relationship between the growth rate and final percentage dry weight of sockeye salmon reared at various ration levels and temperatures.[1] My data and those of Brett _et al._ suggest that a simple measure of the percentage dry weight of a wild fish may indicate its approximate growth rate, high dry weight percentages indicating rapid growth. The percentage dry weight of fish may also change in response to variables such as size and diet (Parker and Vanstone, 1966), so this relationship must be exercised with caution.

In all of my experiments, gross efficiency of the trout increased from near zero at consumption rates near maintenance, peaked at intermediate consumption rates and in some cases declined at repletion feeding levels. Paloheimo and Dickie (1966), after an extensive

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[1] Fitted by the method of least squares, their data resulted in the following relationship: $\%DW = 6.50\ k + 20.80$; where %DW is the percentage dry weight and k is the daily percent growth rate of the fish; $r^2 = 0.84$; $t = 11.05$, 23 d. f., $p < .001$.

analysis of earlier growth experiments, concluded that the logarithm of gross efficiency declined with increasing food consumption from a maximum at low feeding levels. Warren and Doudoroff (1971) explained that this cannot happen. Paloheimo and Dickie's analysis was in error because they failed to calculate ration levels relative to the body weight of the fish. Large fish, which ate the largest total rations, had the lowest gross efficiencies, but this was because their relative rations were less than the rations of smaller fish.

Gross efficiency of steelhead trout receiving low ration levels was markedly affected by temperature increases. However, at consumption rates near repletion, temperature increase had minimal detrimental effect on gross efficiency (Figure 8). Brett *et al.* (1969), studying sockeye salmon, Everson (MS 1973), studying coho salmon, and Lee and Shumway (MS 1973), studying largemouth bass found that the gross 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 gross efficiency. My results and those of Everson, Brett *et al.*, and Lee and Shumway indicate that over a broad range of temperature, the effects of temperature on the growth of fish is fully dependent on the food consumption rates of the fish being considered.

If trout are reared in a hatchery, food may be considered unlimited, or nearly so. Under this condition my data indicate that the growth of juvenile steelhead trout will be improved by temperature increases up to approximately 16.2 C, although factors such as disease may limit successful hatchery production of trout to cooler water.

The effects of environmental variables, such as temperature, on the growth of fish should not be determined by studies in which fish are fed to repletion unless the wild fish are known to feed at high ration levels. The question of food availability to wild fish is of critical importance.

The growth rates of trout in Tobe Creek and elsewhere (Fraser, 1968; Everest and Chapman, 1972) indicate the consumption rates of wild steelhead trout are considerably below the maximum possible consumption levels of the fish. Moreover, the growth rates of salmonids are generally believed by fishery biologists to be food limited during most of the freshwater rearing period.

If steelhead trout are food limited, my experiments have shown that increases in water temperature above normal seasonal temperatures will decrease growth rates of the trout in their natural environment, provided that food availability remains unchanged. If temperature increase of a stream should lead to increased production of invertebrate food organisms, elevated temperatures might increase salmon production. Different studies on the effects of heated water on macrobenthic food organisms have shown quite different results. A study by Iverson (MS 1972) showed that temperature elevations of 3.5 to 5 C reduced insect production by one-half in model streams which simulated natural salmonid streams. Results of field studies in Great Britain (Beauchamp, Ross and Whitehouse, 1970) indicate that production of macrobenthic organisms may be increased by thermal additions to lakes and rivers. It is evident that more studies on the effects of temperature on natural communities must be made before the effects of temperature on natural populations of steelhead can be reliably predicted.

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APPENDICES

APPENDIX I

Estimated swimming speeds, in body lengths/sec, of steelhead trout in several experiments. Each value shown is the mean swimming speed for a group of fish averaged over the number of observational periods. The response of individual fish varied greatly, usually ranging from 0 to 2 or more body lengths/sec.

No. observation periods	Ration levels (lowest to highest)	Estimated swimming speeds		
		Control temp.	Intermediate temp.	High temp.
	Seasonal growth experiments			
Winter				
3	1	1.2	1.2	
	2	1.5	1.0	1.2
	3	1.0	1.0	1.2
	4	1.7	1.6	1.2
Spring				
25	1	0.9	1.1	1.2
	2	1.3	1.0	
	3	1.1	1.0	1.2
	4	1.1	0.9	1.0
Summer				
7	1	1.2	1.3	1.3
	2	1.2	1.3	1.3
	3	1.1	1.0	1.3
	4	0.9	1.0	1.3

(Continued on next page)

Appendix I. (Continued)

No. observation periods	Ration levels (lowest to highest)	Estimated swimming speeds			
		Size group A	Size group B	Size group C	Size group D
		Effects of fish size experiment			
4	1	1.4	1.2	0.9	1.1
	2	1.0	1.1	1.0	1.0
	3	1.4	1.2	1.0	1.4
		Effects of water velocity experiment			
18	1	1.3			
	2	1.1			
	3	1.1			

APPENDIX II

Caloric content and percentage dry weights of the Oregon moist pellet used in the seasonal growth experiments, and the proximate analysis of the pellet determined by Phillips (MS 1972).

	Percentage dry wt.	Analysis (dry wt. basis)				
		Cal/g (± S. D.)	Fat (%)	Ash (%)	Protein (%)	Carbohydrate (%)
Estimates[1]	77. 1	4586	10. 1	12. 3	59. 7	18. 7
Fall experiment	73. 9	4910 ± 70				
Winter	77. 7	5018 ± 55				
Spring	71. 6	4909 ± 70				
Summer	74. 1	4839 ± 37				

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[1] Based on data of Phillips (MS 1972).

APPENDIX III

Consumption rates; initial and final wet weights, percentage dry weights, and caloric equivalents; and growth rates of steelhead trout kept at different fluctuating temperatures in the Summer seasonal growth experiment. Additional information pertaining to this experiment is in Table 2.

Mean temp. (C)	Consumption rate (%/day)	Initial mean wet wt. (g)	Initial mean percentage dry wt.	Initial mean caloric content (cal/g)	Final mean wet wt. (g)	Final mean percentage dry wt.	Final mean caloric content (cal/g)	Caloric growth rate (%/day)
9.4	2.6	2.35	20.0	4895	2.35	18.3	4713	-0.5
	4.9	2.25	20.0	4895	2.71	19.4	4822	0.6
	6.9	2.36	20.0	4895	3.19	20.6	5088	1.5
	9.9	2.23	20.0	4895	3.38	20.4	5157	1.9
12.6	4.0	2.29	20.2	4842	2.29	18.7	4619	-0.6
	6.1	2.33	20.2	4842	2.82	19.2	4932	0.6
	9.0	2.24	20.2	4842	3.17	20.5	5031	1.5
	12.4	2.28	20.2	4842	3.75	21.6	5163	2.3
15.2	5.7	2.28	21.0	4835	2.33	18.0	4615	-0.5
	10.0	2.23	21.0	4835	3.17	21.1	5113	1.8
	14.9	2.25	21.0	4835	3.73	21.2	5152	2.4

APPENDIX IV

Swimming speeds, consumption rates, initial and final wet weights and percentages dry weight, and growth rates of steelhead trout kept in tanks with still water and in tanks where velocities ranged from 0 to 160 mm/sec. Rates of food consumption and growth are based upon dry weights of food and fish.

Test condition	Estimated mean swimming speed (body lengths/ sec)	Consumption rate (%/day)	Initial dry wt. of food consumed (g)	Initial mean wet wt. (g)	Initial mean wet wt. (CV)	Initial mean percentage dry wt.	Final mean wet wt. (g)	Final mean wet wt. (CV)	Final mean percentage dry wt.	Mean growth rate (%/day)
Normal velocities (0-160 mm/sec)	1.33	3.5	1.99	2.91	(8.9)	20.5	2.91[a]	(9.3)	20.6	-0.1
	1.10	6.0	3.38	2.88	(4.9)	20.5	3.01[b]	(7.0)	20.4	0.3
	1.10	8.4	5.26	2.95	(6.1)	20.5	3.16	(8.2)	20.7	0.8
Still water		3.5	2.18	3.05	(8.5)	20.9	3.04	(11.8)	20.1	-0.4
		5.8	3.69	2.96	(6.8)	20.9	3.03	(10.6)	21.4	0.5
		8.2	5.46	3.07	(8.1)	20.9	3.31	(13.3)	21.1	0.9

[a] One fish died 5-20-72; weight 2.90 g (0.51 g dry).

[b] One fish died 5-18-72; weight 2.95 g (0.56 g dry).

APPENDIX V

Percentage mortality of steelhead trout at different temperatures and ration levels during the seasonal growth experiments. The actual temperatures and ration levels for each experiment are given in Table 2.

Ration level	Percentage mortality											
	Control temp.				Intermediate temp.				High temp.			
	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su
Low	0	0	0	0	5	0	0	0	25	31	14	5
Medium	0	0	0	0	5	0	7	0	20	13	40[a]	0
High	0	0	0	0	0	0	7	0	5	6	0	0
Highest	0	0	0	0	0	0	0	0	0	0	0	0

[a] Mortality might have been higher, but this treatment was terminated 11 days before the end of the experiment because of excessive mortality.

F = Fall experiment; W = Winter experiment; Sp = Spring experiment; Su = Summer experiment