THE GROWTH OF BROWN TROUT (*SALMO TRUTTA* LINN.)

III. THE EFFECT OF TEMPERATURE ON THE GROWTH OF TWO-YEAR-OLD TROUT

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(With Six Text-figures)

Temperature is a limiting factor in the distribution of many animals. The ova of brown trout (*Salmo trutta*) can develop without excessive mortality at water temperatures between 3 and 15° C. (Gray, 1928), while for adult trout, mortality is high above 20 and complete above 25° C. (Gardner & Leetham, 1914; Audigé, 1921; Gardner, 1926). It is generally assumed that temperature is the most important physico-chemical factor affecting the growth of fish, especially in temperate zones, where there is an annual variation. Allen (1940) deduced from examination of salmon scales from British rivers that parr do not grow when the water temperature is less than 7° C. Pentelow (1939) and Wingfield (1940) observed the growth of yearling trout in tanks where the temperature varied with that of the external environment and was recorded once a day. They found that there was no growth at temperatures less than 6° C., and it was most rapid between 10 and 15° C. Since other environmental factors varied at the same time, the correlation between growth rate and temperature was necessarily approximate.

The present paper describes part of an investigation of the growth of trout when environmental factors were controlled as completely as possible. Observations on the early growth of trout fry and of that of two-year-old trout at a constant temperature of 11·5° C. have already been reported (Brown, 1946*a*, *b*). In the present experiments, all the environmental factors except temperature were similar to those in the constant-temperature room at 11·5° C.

APPARATUS

Two-year-old trout from the Midland Fishery, Nailsworth, Gloucestershire, were kept at different constant temperatures by using 120 l. tanks enclosed in insulating cases. Each of these consisted of two shells of wood substitute separated by a space of 4 in. stuffed with hay, and there was an air space of 4 in. between the inner shell and the glass sides of the tank. The lid was made in two halves, each consisting of a wooden frame supporting two glass plates separated by an air space of 3 in. A wooden cover above the lid carried two 40 W. electric bulbs at a height of 36 cm. above the surface of the water. The lamps were controlled by a clockwork time switch, and the fish received 12 hr. of light and 12 hr. of darkness each day.

Cambridge tap water was used throughout. The supply came from a constant-level tank set in a high window facing north, and it was distributed through a three-way junction (Fig. 1). One pipe led into a tank in which was immersed a refrigerating coil controlled by a thermostat. From this the water overflowed into a glass funnel and passed through a lagged pipe into the insulated tank *A*. The temperature of the water and its rate of flow could be controlled, and it was possible to maintain the temperature in this tank at any value between 4° C. and that of the room.

Another pipe led into a coil of metal tubing immersed in water in a dustbin lagged on the outside with felt; and from this coil, the water flowed into the insulated tank *B*. An electric immersion heater in the dustbin was controlled by a mercury-toluene thermostat in tank *B*, and the temperature of the water in this tank could be maintained at any value above that of the supply tank, which was about 14° C. in winter and rose to 17° C. in summer.

The third tank, *C*, was covered with a case of strong paper on a wooden frame, which carried two 40 W. electric bulbs. This tank could receive water either from the refrigerated tank or from the heated coil or directly from the supply tank. By combining these three sources it was possible to keep the temperature of the water at any desired value between the temperatures of the hot and cold supplies, and to alter it at any required rate. The temperature was recorded continuously by a thermograph.

All three tanks were fitted with overflow siphons which maintained constant water levels. The water in tanks *A*, *B* and *C*, in the refrigerated tank and in the dustbin, were stirred continually by compressed air.

The treatment of the fish in these tanks was exactly similar to that of the fish in the constant-temperature room at 11·5° C., as described in a previous paper (Brown, 1946*b*). They were weighed and measured generally once a fortnight, and individual records were kept for each fish. They were fed every day, except Sundays, with more meat than they would eat, and the excess food and faeces were siphoned out three times a week and dried. The dry weight was subtracted from the dry weight of food added, giving the amount of food absorbed by the fish. Trout were kept for at least 6 weeks under the experimental conditions before observations began. At the beginning of each experiment, 12 fish were placed in the tank and left to become acclimatized. At 18, 15 and 8° C., 12, 12 and 11 fish survived respectively, but at 4·5° C. only 9 survived, while at 20° C., after one unsuccessful attempt, 8 fish survived the whole period of the observations.

The environmental conditions in these tanks differed from those in experiments already described (Brown, 1946*b*) only in the temperature of the water. The fish were of the same stock and age, and the duration and intensity of illumination, the rate of flow, aeration and chemical composition of the water, the quality and quantity of food and the amount of living space were the same as those of trout in the constant-temperature room at 11·5° C.

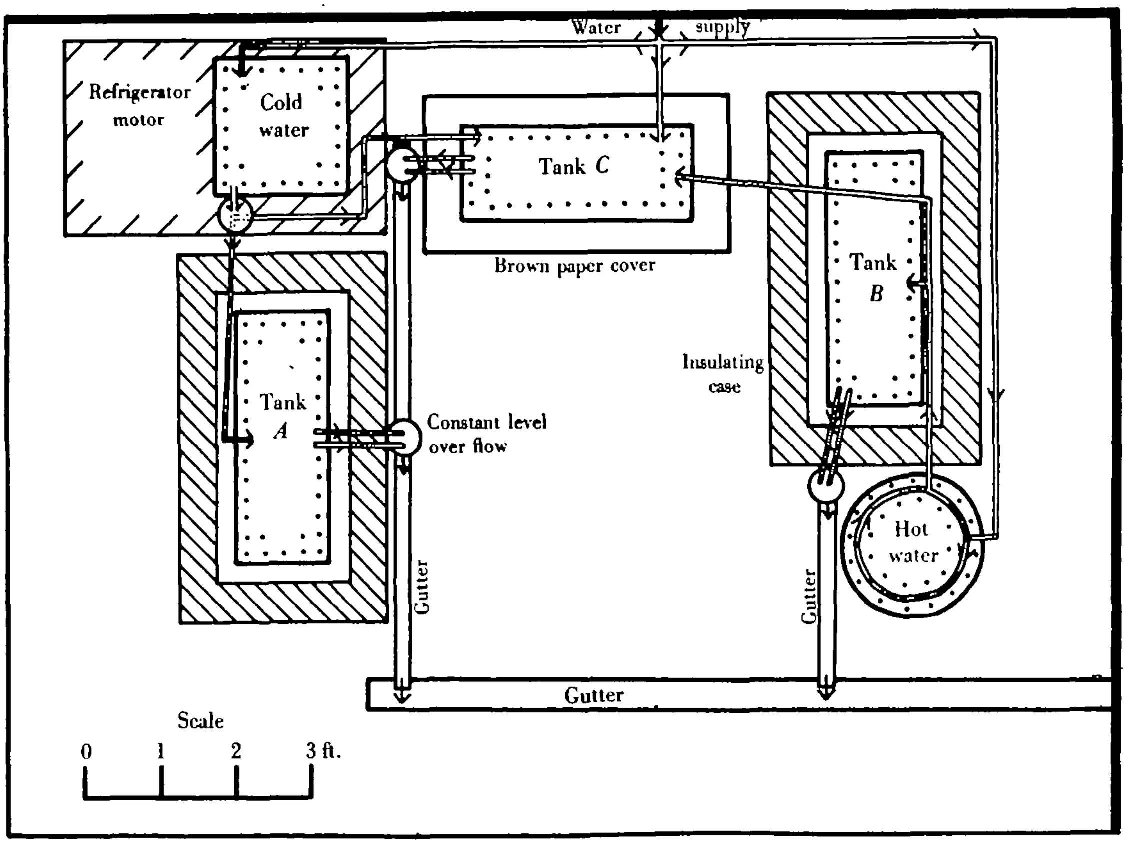

Fig. 1. Plan to show the arrangement of tanks and circulation of the water when trout were grown at different temperatures. *A*, tank with water temperature lower than that of the supply; *B*, tank with water temperature higher than that of the supply; *C*, tank with water temperature which could be adjusted to any value between that of the water in tanks *A* and *B*.

THE GROWTH OF TROUT AT DIFFERENT CONSTANT TEMPERATURES

Since there were only two insulating cases, tanks *A* and *B* were used successively to obtain the following temperatures: tank *A*, 4·5 and 8° C., and tank *B*, 15, 18 and 20° C. Fish living in water of constant temperature have an annual growth-rate cycle (Brown, 1946*b*), and consequently it was not possible to compare the growth of fish at all these temperatures directly with each other, but each must be compared with fish of the same age growing at 11·5° C. There were differences between the growth rates of the individual fish in each group; these appeared to be associated with their positions in the 'size hierarchies', and to be comparable with the differences between individuals growing at 11·5° C. It is thus possible to compare the mean specific growth rates of all the fish in each tank and also the specific growth rates of fish having the same positions in the size hierarchies of different tanks. All the fish showed fluctuations of growth rate over periods of from 4 to 6 weeks, and these appeared to be related to the condition factor, *K*, as was observed at 11·5° C.; only the specific rates calculated from weight data have therefore been considered in detail.

The significance of the difference between the growth rates of trout at 11·5° C. and at the other temperatures has been estimated by two statistical methods: first, by comparison of the means, with due allowance for the small size of the samples; and secondly, by analysis of variance, comparing the performance of fish in the same positions in the size hierarchies of different tanks. The results of these tests are given in Table 2. The mean specific growth rate of the fish at 8° C. was significantly higher and that of the fish at 4·5° C. was significantly lower than that of fish of the same age at 11·5° C. By analysis of variance, individuals at 11·5° C. grew significantly faster than those of corresponding positions in the size hierarchy of the tank at 20° C. and probably faster than those at 15° C. and more slowly than those at 18° C.

Table 1. *Comparison of the mean specific growth rates (calculated from weight data) of trout living in water of different constant temperatures*

Temp. in °C.	4·5	8	11·5	15	18	20
Mean specific growth rate (as percentage weight per week):						
Fish aged 90–102 weeks	—	4·81 ± 1·00	2·81 ± 1·30	—	3·98 ± 2·00	—
Fish aged 114–126 weeks	2·13 ± 0·63	—	4·06 ± 1·80	2·85 ± 0·78	—	2·30 ± 1·26

Table 2. *Results of statistical tests of the significance of differences between the specific growth rates of trout at* 11·5° C. *and at other temperatures*

Temp. °C.	Tested by comparison of means		Tested by analysis of variance	
	P	*t*	*P*	*t*
4·5	<0·01	2·9	—	—
8	<0·01	4·1	—	—
15	0·05	2·0	0·04	2·3
18	0·1	1·6	0·03	2·4
20	<0·05	2·2	<0·01	4·3

The average condition factors varied very little, all the means lying between 1·04 and 1·10.

Fig. 2A shows the mean specific growth rates of fish aged 90–102 weeks at 8, 18 and 11·5° C. The average rate at the last temperature was lower than those at the other two (Table 1), while the variation in rate, as measured by the standard deviations from the means, was greatest at 18 and least at 8° C. Fig. 2B shows the mean specific growth rates of trout aged 114–126 weeks at 4·5, 15, 20 and 11·5° C. The mean rate at the last temperature was higher than those at the others, and the variation between individuals was also greater (Table 1). The six largest fish at 11·5° C. grew more rapidly than the corresponding individuals at the other temperatures, but the smaller fish grew at similar rates at 11·5, 15 and 4·5° C.

The mean growth rates of trout at all six constant temperatures are compared in Fig. 3. Growth at 4·5° C. was slow, with little difference between individuals; at 8° C. the average specific rate was much higher; above this the variation among individuals was greater, and the mean specific rate fell to a minimum at 15° C., while at 18° C. some individuals were growing very rapidly and others comparatively slowly; and at 20° C. the variation was less, and the fish grew less rapidly, on the average, than they did at 11·5° C. If trout survived at higher temperatures, the mean specific rates would probably be still lower.

It might be argued that the differences in specific growth rate at the different constant temperatures were the result of genetical differences between the individual fish used in the experiments. To test this possibility, 12 two-year-old trout were kept in the insulated tank *A* for 2 months at 5° C., then for 3 months at 12° C. and then for 4 months at 8° C. The fish were allowed as much food as they would eat, and were weighed and measured once a fortnight. The mean specific growth rates at each temperature have been expressed as a percentage of the mean rate of fish of the same age at 11·5° C. (Table 3).

In this experiment, growth was relatively more rapid at 8 than it was at 12 or at 5° C., and this confirms the deductions made from comparison of different groups of individuals growing at these constant temperatures. It is therefore probable that

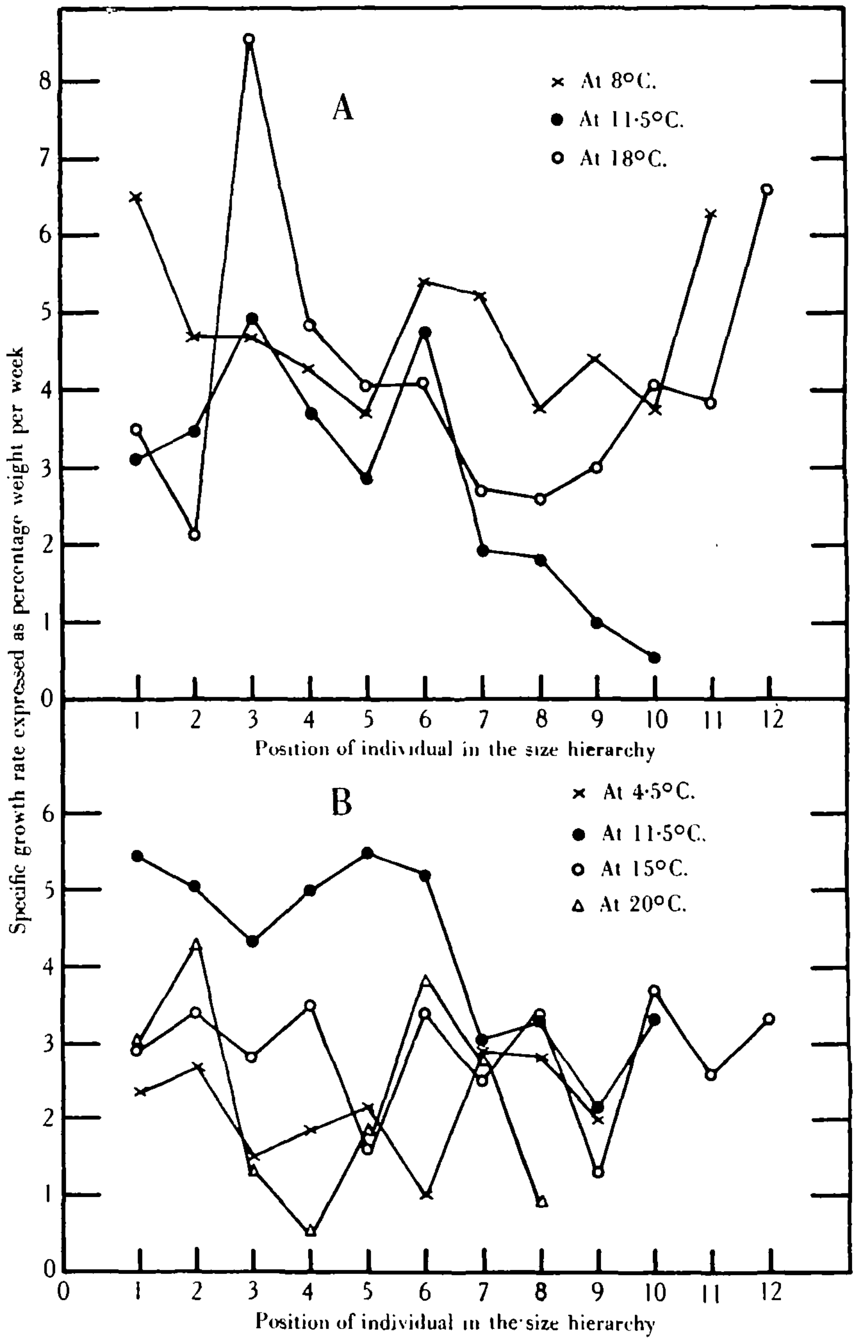

Fig. 2. Mean specific growth rates (calculated from weight data) of individual trout living at different constant temperatures. A, fish aged 90–102 weeks. Temperatures 8, 11·5 and 18° C.; B, fish aged 114–126 weeks. Temperatures 4·5, 11·5, 15 and 20° C.

the differences between the growth rates of groups of different individuals at constant temperatures are not the result of genetical differences between the individuals used for the experiments.

THE RELATION BETWEEN FOOD AND GROWTH AT DIFFERENT CONSTANT TEMPERATURES

The effect of temperature on maintenance requirements

When the trout had grown for a suitable length of time at the constant temperatures with as much food as they would eat, the amount given to them was reduced until their maintenance requirements could be estimated, using the technique described in the previous paper (Brown, 1946*b*). Using the values obtained in the experiments at 11·5° C., with fish of different weights, and assuming that the relationship between body weight and maintenance requirement is the same at all temperatures, the maintenance requirements of trout of average weight 50 g. have been calculated for each temperature (Table 4, Fig. 4).

The maintenance requirement is larger at higher temperatures, but the relationship is not direct. Below about 5° C. there may be a constant level of requirement; it increases gradually up to about 9° C., then rapidly up to about 11° C., and the rate of increase falls off gradually so that the requirement becomes nearly constant at 20° C. The temperature-maintenance requirement curve is thus sigmoid, with an inflexion at about 11° C.

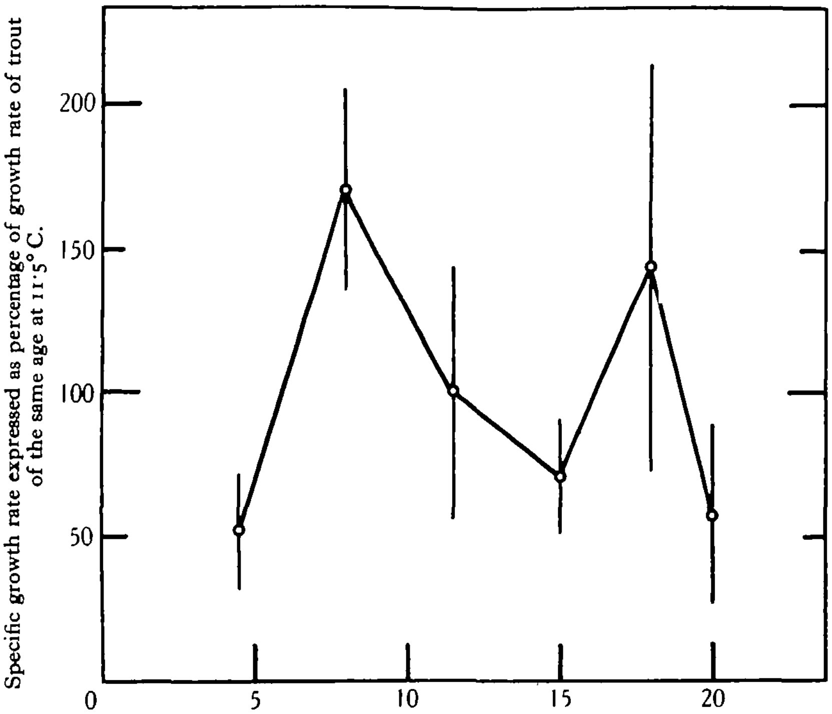

Fig. 3. Mean specific growth rates (calculated from weight data) of groups of trout living at different constant temperatures. The rates are expressed as a percentage of the growth rates of fish of the same age at 11·5° C. The height of the vertical lines = 2 × standard deviations from the means.

Table 3. *The mean specific growth rates (calculated from weight data) of a group of trout which were grown in succession at three different constant temperatures*

Age of trout weeks	Temp. ° C.	Mean growth rate expressed as a percentage of the growth rate of fish of the same age living at a constant temperature of 11·5° C.
118–126	5	42·4 ± 29
126–138	12	141 ± 55
138–154	8	192 ± 109

The effect of temperature on the amount of food eaten and the efficiency of utilization of food

The amount of food absorbed by trout when given as much meat as they would eat was determined for each fortnightly period at each temperature.

Maintenance requirements, calculated for fish of that average weight at that temperature, have been subtracted from these values, giving the amounts of food available for growth during each period. These values varied from week to week for each group, but showed no correlation with the average weight. Fish

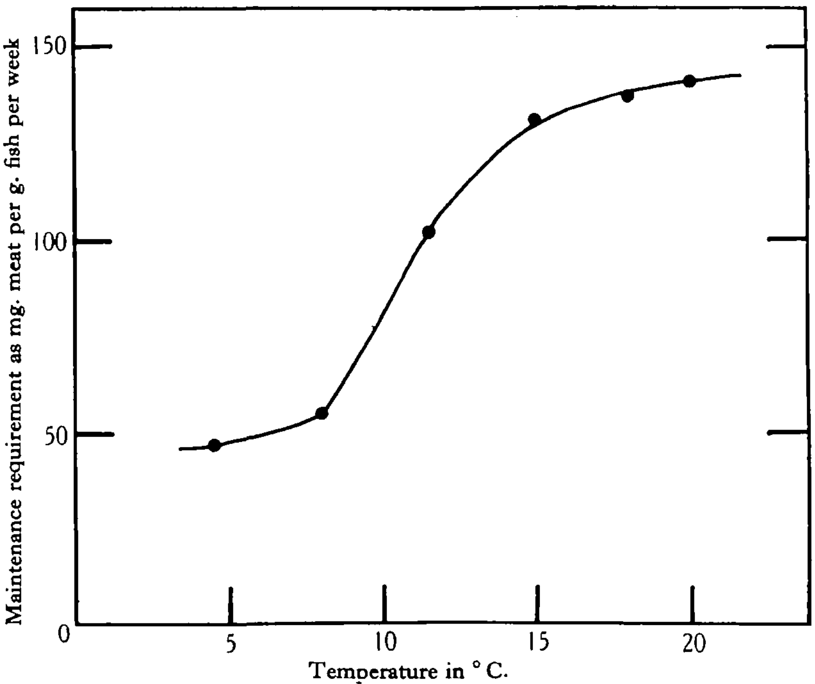

Fig. 4. To show the relation between the maintenance requirements calculated for fish of average weight 50 g. and temperature.

Table 4. *Maintenance requirements (expressed as mg. per g. fish per week) of trout living at different constant temperatures*

Temp. *t*° C.	Average weight *W* g.	Maintenance requirement	Maintenance requirement of fish of weight *W* at 11·5° C.	Maintenance requirement of fish of weight 50 g. at *t*° C.
4·5	57·8	41	89	47
8	46·9	59	109	55·5
11·5	50	102	—	102
15	73·5	91	71	131
18	32·8	188	141	137
20	70·8	100	73	141

at 8° C. ate the greatest amount of food in excess of their calculated maintenance requirements, and the variation in amount was greatest at 8 and 18° C. and was very low at 20° C. (Table 5). There was markedly less food eaten in excess of the maintenance requirements at 5 and at 20° C. than at the intermediate temperatures.

The average total amount of food absorbed by trout of average weight 50 g. at each temperature has been calculated by adding the maintenance requirement calculated for such a fish to the mean amounts of food eaten in excess of the maintenance requirements (Table 5). This amount is greatest at about 19° C. and decreases sharply above and gradually below this temperature. The change in total amount absorbed with rise in temperature is greatest below 8 and above 19° C., increasing at the former and decreasing at the latter temperature.

The efficiency of utilization of the food (that is, the change in average weight, expressed as mg. per g.

fish per week, divided by the amount of food eaten in excess of the maintenance requirement, also expressed as mg. meat per g. fish per week) was not constant from week to week at any temperature, but was correlated directly with the amount of increase in weight. The average efficiency was greatest at 8 and least at 4·5° C., and there was a minimum between 8 and 18° C. (Table 5). At 20° C., the average efficiency was high, although the specific growth rate was low.

Thus, efficiency and amount of food eaten were low below 8 and high at 8° C.; the growth rate minimum between 10 and 16° C. was associated with lower efficiency and a greater amount of food eaten; at 18° C. the efficiency was greater and relatively more food was eaten in excess of the maintenance requirements; while at 20° C. growth was limited by the small amount of food eaten, since the efficiency was high.

rates of fish of the same age living at a constant temperature of 11·5° C. The mean temperature has been calculated for each month. The range of temperature is 2° C. for each month for fish aged 90–150 weeks, and 4° C. for each month for fish aged over 158 weeks, so the correlation between mean growth rate and average temperature is necessarily an approximation. This correlation is shown in Fig. 7.

There is a growth rate maximum at a temperature above 14° C. in all records except that for fish aged 170–194 weeks, when the temperature was rising at the rate of 1° C. per week; there is a maximum at a temperature between 7 and 9° C. in all the records except that for fish aged 90–120 weeks, when the temperature was falling at the rate of ½° C. per week. The mean specific rates were the same as those of fish of the same age living at a constant temperature of 11·5° C. at a temperature between 9 and 12° C. in all the records. Fish living in a tank with the water temperature changing gradually at a constant rate thus showed approximately the same relationship between temperature and growth rate as fish living at different constant temperatures. The growth rate maximum below 10° C. was generally not so great as that above 15° C. in the changing temperature, and there was no indication that rising and falling temperatures had different effects on growth.

Table 5. *The amount of food eaten and the efficiency of utilization of food of trout at different constant temperatures*

Temp. ° C.	Amount of food eaten in excess of maintenance requirements (mg. meat per g. fish per week)	Total amount eaten by fish of average weight 50 g. (mg. meat per g. fish per week)	Efficiency of utilization
4·5	115 ± 31	160	0·12
8	174 ± 67	225	0·28
11·5	159 ± 44	260	0·22
15	146 ± 38	275	0·20
18	147 ± 54	280	0·24
20	102 ± 14	240	0·24

THE FEEDING AND GROWTH OF TROUT IN A CHANGING TEMPERATURE

The specific growth rate of trout in water with a changing temperature

Twelve fish were grown in tank C (Fig. 1), which could be supplied with either warm or cold water so that its temperature could be controlled between the limits of 4 and 20° C. The fish were given as much food as they would eat, and they were weighed and measured once a fortnight. The temperature was first reduced from 18 to 4° C., at the rate of ½° C. per week; it was then raised to 18° C. at the same rate; after 8 weeks at this temperature, it was reduced to 4° C. again, but at the rate of 1° C. per week, and then increased to 20° C. at the same rate. All the fish survived for 1 year in this tank, but seven fish died when aged 150–158 weeks, when the temperature was 18° C., and they were found on dissection to have enlarged gonads. The surviving fish, all males, lived until the end of the observations.

Mean monthly specific growth rates have been calculated for this group of fish, and these rates have been expressed as a percentage of the mean specific rates of fish of the same age living at a constant temperature of 11·5° C.

The amount of food eaten and efficiency of utilization of fish in a changing temperature

The amounts of food eaten in each period by the two-year-old trout have been calculated, the estimated maintenance requirements have been subtracted, and the amounts eaten in excess of the maintenance requirements have been correlated with the average temperature (Table 6). These amounts are smaller, and decrease more markedly above the optimum temperature, than those eaten by fish at corresponding constant temperatures. The average efficiency of utilization of the food is also comparable with that of fish at different constant temperatures (Table 6), but the value for 7–10° C. is lower and that for 16–19° is higher.

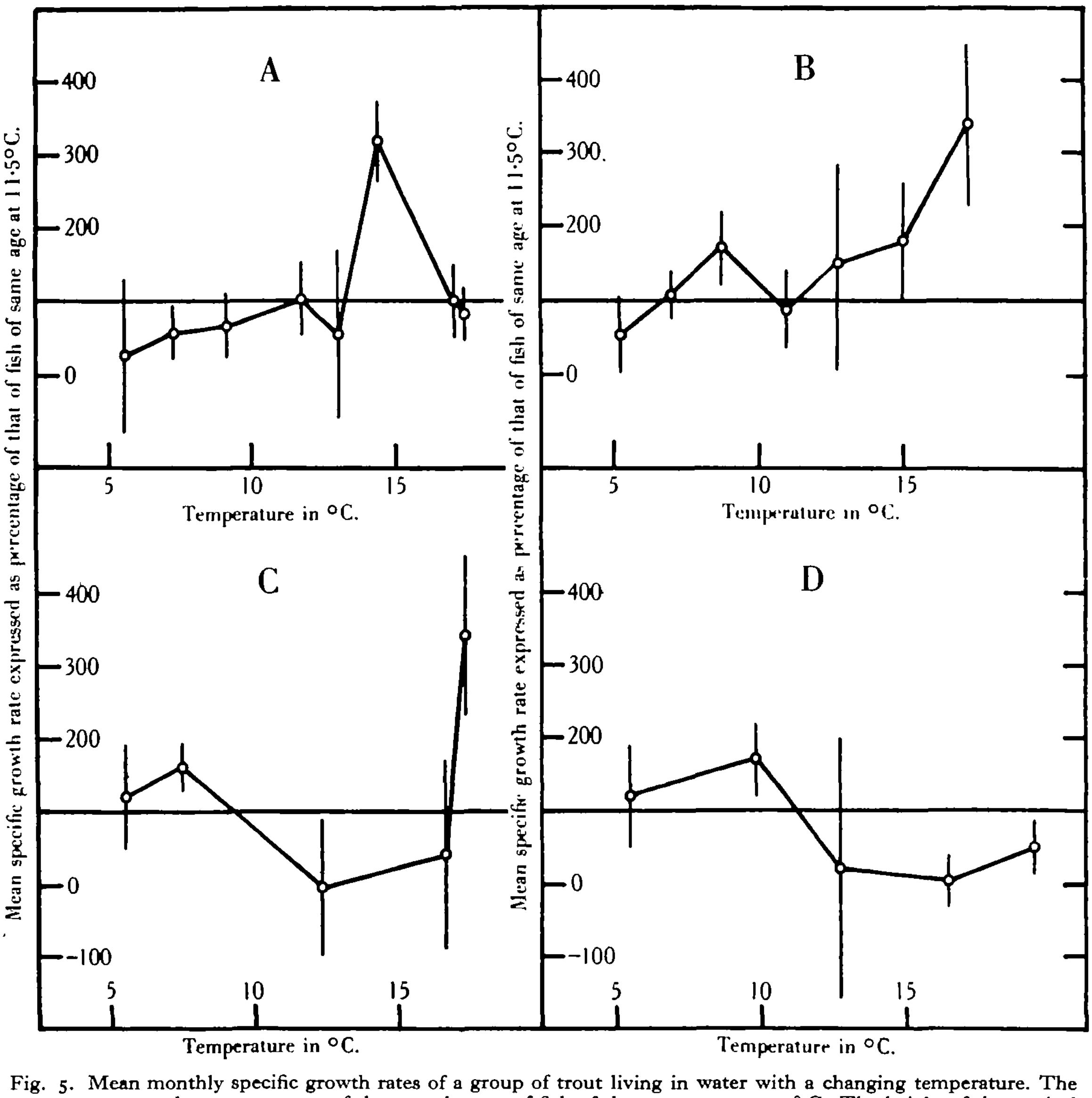

Fig. 5. Mean monthly specific growth rates of a group of trout living in water with a changing temperature. The rates are expressed as a percentage of the growth rates of fish of the same age at 11·5° C. The height of the vertical lines = twice the standard deviations from the means. A and B, with the water temperature changing at the rate of ½°C. per week: A, temperature falling, fish aged 90–120 weeks; B, temperature rising, fish aged 120–158 weeks. C and D, with the water temperature changing at the rate of 1°C. per week: C, temperature falling, fish aged 150–174 weeks; D, temperature rising, fish aged 170–194 weeks.

in a changing temperature thus show a similar relationship between food, growth and temperature to that shown by fish living at different constant temperatures, except that under the former conditions the amount of food eaten was relatively smaller and a given change in weight occurred with greater efficiency than at the corresponding constant temperatures.

Table 6. *The amount of food eaten and the efficiency of utilization of food of trout living in water of changing temperature*

Mean temp. ° C.	Amount of food eaten in excess of maintenance requirements (mg. meat per g. fish per week)	Efficiency of utilization
4–7	67	0·17
7–10	120	0·24
10–13	102	0·18
13–16	77	0·24
16–19	58	0·33

DISCUSSION

Temperature affects the growth rates of animals by altering the rates of various metabolic processes, and its effects are likely to be more marked if the animals are poikilothermic than if they are homoiothermic. Increase in temperature increases the respiratory metabolism of fish (Gardner & Leetham, 1914; Gardner, 1926; Wells, 1935; Clausen, 1936; Sumner *et al.* 1938, 1942), and there is an increase in the maintenance requirements (Dawes, 1930; Pentelow, 1939), and more rapid loss of weight during starvation (Pentelow, 1939; Lawrence, 1940). Increase in temperature also increases the activity of fish, leading to increased food intake (Hathaway, 1927), and there is increase in the rate of digestion (Scheuring, 1928; Hewitt, 1943) and the efficiency of conversion of food into fish may be altered (Hayes & Pelluet, 1945).

The effect of increase in temperature is thus to increase the amount of food required for maintenance and also to increase the amount eaten by the fish. The rate of growth will vary with the ability of the fish to digest more food than is required for maintenance at that temperature, and it is probable that, with increase in temperature, the growth rate will increase to a maximum and then decrease, becoming negative at high temperatures. This relationship between temperature and growth rate was found by Audigé (1921) for *Cyprinus*, *Carassius* and *Scardinius*, with an optimum at 25° C.; by Pentelow (1939) for *Salmo trutta*, with an optimum between 10 and 15° C.; by Donaldson & Foster (1940) for *Onchorhyncus*, also with an optimum between 10 and 15° C.; and by Hewitt (1943) for *Salmo trutta*, with an optimum between 15 and 19° C. Wingfield (1940) suggested that rising and falling temperatures have different effects on the growth rate of yearling trout.

The effect of temperature on the embryonic growth of *Salmo fario* illustrates the same principles (Gray, 1928; Wood, 1932). The time required for complete development of the embryo was less at higher temperatures, but between 7 and 12° C. the total amount of oxygen consumed during development was the same at all temperatures, and the resulting fry were of equal size. Above and below these temperatures, the total amount of oxygen consumed was greater and the fry were smaller.

The experiments described in the present paper indicated two temperature optima for rapid growth of two-year-old brown trout, one between 7 and 9° C. and the other between 16 and 19° C., and these optima occurred when fish were grown in a changing temperature as well as at different constant temperatures. The maintenance requirements increased, relatively, with increase in temperature, but the curve was sigmoid. The requirement as estimated included not only the amount of food required for basal metabolism (i.e. to replace tissues broken down and to provide energy for the fish to live while at rest) but also the amount required to provide energy for locomotion. The basal metabolic rates of animals increase with rise in temperature, the rate of increase generally rising with the temperature. Since the observed relation between temperature and maintenance requirement followed a sigmoid curve, it is suggested that the activity of the fish rose to a maximum at 10–12° C. and decreased above this temperature; the reduction of activity at the higher temperatures was sufficiently great to compensate partially for the increase in basal metabolism.

The amount of food eaten was at a maximum between approximately 10 and 19° C., so that the upper optimum temperature (18° C.) coincided with a large amount of food eaten and low activity, and the slower growth above 19° C. may be explained by the smaller amount of food eaten and increased basal metabolic rate (Fig. 6). At 5° C. both activity and amount of food eaten were small, while at 8° C. both were higher, but the basal metabolic rate was still low. Between 10 and 15° C. the amount of food eaten and activity were both maximal, and the basal metabolic rate had increased. Thus, the lower optimum temperature coincided with a maximum in the amount of food eaten in excess of the maintenance requirement. Thus it is possible to explain the existence of two optimum temperatures for trout growth by postulating a differential effect of temperature on the amount of food eaten and the activity of the fish (Fig. 6).

The efficiency of utilization of the food also varied with the temperature, being low at 5, high at 8 and above 17° C. and low between these two temperatures. Thus, the efficiency was low when the temperature was low and also when the activity was high (Fig. 6). This would exaggerate the growth rate maxima and minima.

Elson (1942) measured the activity of *Salvelinus fontinalis* in response to an electric shock at different temperatures, and found that it was greatest at 10° C, and decreased above and below this temperature. Wells (1935), using *Fundulus parvipinnis*, noted that increase in temperature was accompanied by increase in oxygen consumption, but the temperature-respiration curve contained sudden breaks at definite temperatures, and he suggested that these were correlated with changes in the degree of activity of the fish. Gardner & Leetham (1914) and Gardner (1926) found that the oxygen consumption of brown trout was doubled for the 10° rise between 8 and 18° C., but their curves are not sufficiently detailed to show whether sudden changes in consumption occurred. Thus, it is not incompatible with other work that trout should have a maximum degree of activity between 10 and 12° C.

Pentelow (1939) and Wingfield (1940) correlated the growth of their trout with the average monthly temperatures of their tanks. In neither series of experiments was the temperature controlled, and in some months there were probably large fluctuations, so the temperature-growth correlations were necessarily approximate. Both authors deduced that the rate of growth was maximum between 10 and 15° C. There were few records for temperatures higher than 15° C., and half their observations for the temperature range 7–9° C. were made in the autumn. At this season, trout living in environments of constant temperature showed a decrease in their specific growth rates (Brown, 1946*b*), and Pentelow's table correlating temperature and growth (1939, p. 458) contains almost equal numbers of records of large and small changes in weight for temperatures between 46 and 50° F. Wingfield found that when the temperature was falling (i.e. during late summer and autumn) the growth rate for any given temperature was less than when it was rising (i.e. spring), and his fish showed increase in their growth rate in February, although there was no increase in water temperature. These aberrations can be explained by the existence of an annual growth-rate cycle.

Pentelow (1939) measured the maintenance requirements of trout and found that they increased with increase in temperature. The majority of his

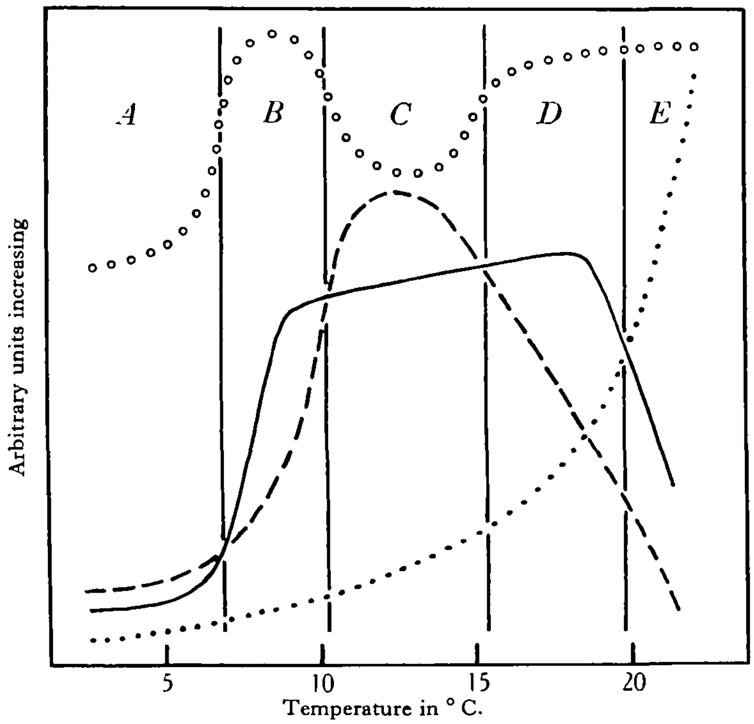

Fig. 6. Diagram to illustrate how growth rate maxima at two different temperatures could result from a differential effect of temperature on the amount of food eaten (full line), the activity (broken line) and the basal metabolic rate (dotted line) of trout. The vertical lines divide the whole temperature range into five regions. Within regions *A*, *C* and *E*, the specific growth rates would be low; within regions *B* and *D*, the rates would be high. The change in efficiency (circles) with change in temperature would exaggerate these growth rate minima and maxima.

determinations were performed at temperatures between 46 and 50° F., when the majority of values were between 70 and 102 mg. *Gammarus* per g. fish per week, the average weight of the fish being about 20 g. The requirement estimated during the experiments described in the present paper was 55 mg. meat per g. fish per week for fish of average weight 50 g. at 8° C. Since the requirements decrease, relatively, with increase in weight, the agreement between these two estimates is good.

Pentelow (1939) found that yearling trout required 3·0 g. of *Gammarus* more than the maintenance requirement for an increase in weight of 1·0 g. In the experiments described in this paper, two-year-old fish with maximum rations at 8° C. required 3·6 g. of meat more than the maintenance requirement for an increase of 1·0 g. in weight. If the difference between these two estimates is significant, either *Gammarus* is used more efficiently than meat during trout growth, or the fish use food less efficiently as they grow older.

SUMMARY

1. Two-year-old trout were grown in controlled environmental conditions in water of different temperatures.

2. The specific growth rates of trout living at different constant temperatures and of those living in water of changing temperature were high between 7 and 9° C. and between 16 and 19° C., and were low above, between and below these temperatures. The existence of these two growth rate maxima may be explained by a differential effect of temperature on the amount of food eaten and the activity of the fish, the former being maximal between 10 and 19° C. and the latter between 10 and 12° C. The efficiency of utilization of the food was low when the temperature was low and also when the activity was high.

3. The maintenance requirements of trout of equal weight increased with increase in temperature. The relation followed a sigmoid curve, which may be explained by a differential effect of temperature on the basal metabolism and on the activity of the trout.

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