SEASONAL VARIATIONS IN THE GROWTH RATE, THYROID GLAND ACTIVITY AND FOOD RESERVES OF BROWN TROUT (*SALMO TRUTTA* LINN.)

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INTRODUCTION

Although it is an accepted fact that the rate of growth in salmonid fishes varies at different times of the year, the exact time and form of these fluctuations has never been precisely established. Allen (1940) and Cooper (1953) measured samples of fish from a large wild population, but under these conditions sampling errors made it difficult to assess accurately the differences in growth rate which occurred over small intervals of time, and extremely difficult to obtain information about the concurrent changes in the external environment. In the work of Pentelow (1939) and Wingfield (1940), who kept fish under laboratory conditions, the external environmental changes could be accurately assessed, but the numbers of fish used were small and the living conditions artificial.

The present work was undertaken to provide information for an investigation of the factors controlling the growth of fish. It was realized that the fundamental information which was required for this work was an accurate picture of the natural growth rate rhythm of the fish, and the time relationship between this and fluctuations in the external and internal environments. It seemed that the way to obtain this information was to work with as many fish as possible, kept under conditions as natural as they could be made without preventing accurate measurement of any fluctuations occurring in the environment.

These requirements were met by keeping a large population of fish in a stew-pond at the Freshwater Biological Association's hatchery, where the fish were subjected to all the naturally occurring fluctuations in temperature, chemical composition of the water, and day length, as were fish living in local streams. Other environmental factors, which according to previous workers, are liable to influence the growth rate, but which may vary locally, such as the kind and amount of food, the crowding and size relationships of individuals, and the varying state of sexual maturity throughout the population could, to a large extent, be controlled, and thus the possible varying effects of these factors on the growth rate of the fish eliminated. It was hoped by this means to obtain what could be regarded as a generalized growth rate curve for the trout living in this area under the conditions recorded. Trout were used for this work since (1) most previous work of this nature has been done on these fish, (2) they are readily obtainable of a known age and (3) they are easily kept in a hatchery. Fish which were 3 years old in the spring of the year of the work

were used, thus enabling information to be obtained on the maturing of the gonads.

In order to obtain a guide to the seasonal changes occurring in the internal environment, a study of the fluctuations of the food reserves of these fish, obtained by investigating the protein, water, fat and glycogen content of the muscle, liver, gut wall and gonad was undertaken.

The role played by the thyroid gland in teleost metabolism has been the subject of many workers' attention. The control of the metabolic activity by the thyroid in mammals is well known, and many workers have tried to demonstrate a similar control in fish. This work has been reviewed by Hoar (1951) and Lyn & Wachowski (1951). All workers had negative results with the exception of Smith & Matthews (1948), who, using extracts of parrot fish thyroid, induced an increase in oxygen consumption in *Bathystoma*. The work of Lieber (1936) on *Misgurnis fossilis*, Hoar (1939) on the salmon and Buchmann (1940) on the herring showed that it was reasonable to expect that the thyroid of the trout would vary seasonally in its activity. Recently, Barrington & Matty (1954) have demonstrated seasonal variations in the thyroid gland of the minnow. The methods used by previous workers to estimate the activity of the thyroid gland have either depended on histological techniques (Hoar, 1939; Buchmann, 1940), or on measurement of the amount of iodine in the blood of the fish (Fontaine & Leloup, 1952). Of these methods that of Fontaine and his co-workers is probably the better as it is felt, in agreement with Carter (1933), that 'neither the size nor the histological appearance of a gland is necessarily correlated with the amount of secretion which it is pouring into the circulation', recently Fontaine (1953) has expressed a similar opinion. It was felt that it would be useful if some estimation of the seasonal changes in the activity of the thyroid gland of the trout could be obtained and it was decided to try, if possible, to estimate the rate of turnover of iodine in the gland, by injecting radioactive iodine, Matthews (1947), La Roche (1950), Olivereau (1952) and Berg & Gorbman (1953) having shown that the teleost thyroid will concentrate the isotope. Radioactive iodine has been used by many workers to measure the activity of the thyroid, the principal technique being to kill the animal at a known time after injection and excise the thyroid gland for estimation of the amount of isotope iodine in it. The gland in teleosts is a diffuse organ closely associated with other tissue, and it is therefore impossible to dissect out a whole gland from these animals. In clinical research on cases of thyroid malfunction the iodine concentrated by the gland has been measured *in vivo* by a counter tube held against the neck. It was decided to adapt this method for estimating the thyroid activity of the fish. Since this work was started Myant (1953) has used a similar method to investigate the thyroid activity of the rabbit.

METHODS

Section 1. *Growth rate*

A population of 250 3-year-old hatchery-reared brown trout were kept in two stew-ponds each of 12·5 kilolitres capacity and were fed to satiation on a mixture of

minced liver and 'Dog-e-Tox' dog food. At monthly intervals a random sample of fifty fish was withdrawn from the ponds with a seine net, the fish were anaesthetized in a 2% solution of urethane, were measured to the nearest millimetre to the fork of the tail and returned to the ponds.

To overcome the possible error in these results caused by a steadily decreasing population, due to sampling for other investigations and what was afterwards considered to be an insufficient feeding level, the work was repeated in 1954, using a population of 100 3-year-old hatchery-reared fish kept in one pond. Each month all the fish were separately measured as before and also weighed to the nearest gram. For the purpose of calculating the mean length, the fish lengths were arranged in groups to the nearest centimetre and the specific growth rate calculated from the formula $\frac{\ln L_2 - \ln L_1}{T_2 - T_1} \times 100$, T being calculated in weeks. The specific growth rate in weight was calculated in a similar fashion.

Section 2. Tissue analysis

At monthly intervals a random sample of 9 fish was taken from the ponds and brought to the laboratory; each fish was separately and similarly dealt with. The fish was killed by a blow on the head, weighed and measured, the abdomen was opened and the liver, gonads and gut removed, the gut was emptied and all the organs weighed to the nearest 0·1 g. A sample of muscle was taken from a standard position in the shoulder of the fish. Each organ was separately treated, being frozen with liquid oxygen in a mortar and then ground to a fine powder with a pestle. Samples of the powdered tissue were taken for estimation of total water, protein, fat and glycogen.

Water content

About 500 mg. of tissue were heated at 100° C. in a hot-air oven to a constant weight. The difference between the initial and final weights giving the amount of water present.

Protein content

Protein was estimated by the micro-Kjeldahl method. The dried tissue from the total water estimation was dissolved in a known volume of sulphuric acid and aliquots of the solution were taken and heated in a digestion flask with a pinch of catalyst (Chibnall, Rees & Williams, 1943). The cooled digest was washed with distilled water into a Markham micro-Kjeldahl distillation apparatus, and 10 ml. of 40% sodium hydroxide solution were added. The ammonia distilled over was trapped in a 2% boric acid solution and was estimated by titration with 0·01 N hydrochloric acid, using as indicator a solution containing 0·02% methyl red and 0·1% brom cresol green. The amount of protein in the original samples was calculated from the nitrogen content using a factor of 6·25.

Fat content

About 500 mg. of tissue were placed in a 100 ml. flask with 50 ml. of 3:1 ethyl alcohol: ethyl ether mixture; the flask was refluxed for 3 hr. in a water-bath at 70° C. The tissue was then filtered off by a Whatman no. 1 filter-paper and the filtrate evaporated to dryness under reduced pressure in a water-bath at 50° C. The residue after evaporation was re-extracted with 15 ml. of petroleum ether b.p. 70–80° C. for 10 min. at 50° C., the extract being then washed through the original filter-paper with more petroleum ether into a 30 ml. beaker. Finally the petroleum ether was evaporated off in a water-bath at 50° C., and the residue, regarded as fat, was estimated by a weight difference, final traces of solvent being previously expelled in a vacuum desiccator containing calcium chloride and paraffin wax.

Glycogen content

Glycogen was seperated using the method of Good, Kramer & Somogyi (1933). Between 10 and 500 mg. of tissue were placed in a 15 ml. round-bottomed Pyrex centrifuge tube and 2 ml. of 30% potassium hydroxide added. The approximate amount of tissue taken varied with the type of tissue, so that the amounts of sugar to be estimated were kept roughly within the same limits; thus about 10 mg. of liver and about 500 mg. of muscle were used. The tubes were placed in boiling water until the tissue was dissolved, and after partial cooling the glycogen was precipitated by the addition of 2·2 ml. of 95% ethyl alcohol. The mixture, after being heated to boiling-point in a water-bath, was cooled and then centrifuged, the supernatant decanted off, and the tube inverted over filter-paper to drain. The remaining alcohol was expelled by placing the tube in a boiling-water bath. The glycogen was hydrolysed with 2 ml. of N sulphuric acid by heating in boiling water for 3 hr. The cooled solution was neutralized with N sodium carbonate and aliquots were taken for sugar estimation. The reagent described by Somogyi (1937) was used to determine the amount of sugar present, the excess iodine being titrated with 0·005N sodium thiosulphate. The glycogen content was calculated from the glucose by using the factor 1·11.

Thyroid activity

Nine fish were taken at monthly intervals from the population at the hatchery and brought to the laboratory. Each fish in turn was anaesthetized in a 2% solution of urethane, marked by clipping a fin, weighed, and injected intraperitoneally via the anus, with a carrier-free solution of ^{131}I. The amount injected was such that each fish received approximately 0·1 μc./g. of fish. The fish were then returned to the hatchery.

At 6, 24, 48 and 72 hr. after injection the fish were brought to the laboratory, anaesthetized with urethane and placed over a lead shielded end-window type Geiger-Muller tube (G.E.C. type G.M.4). The fish was placed with the thyroid area over the end window (Fig. 1) and left in place for the duration of a thousand counts or 1 min., whichever was the shorter. After counting the fish were allowed

to recover in running water and then returned to the hatchery. The results, recorded as counts per minute, corrected for the background count and the natural decay of the isotope, were plotted on a logarithmic scale against the time after injection of the fish. The regression coefficient, expressing the slope of the line fitted to these points, was taken as the index of thyroid activity.

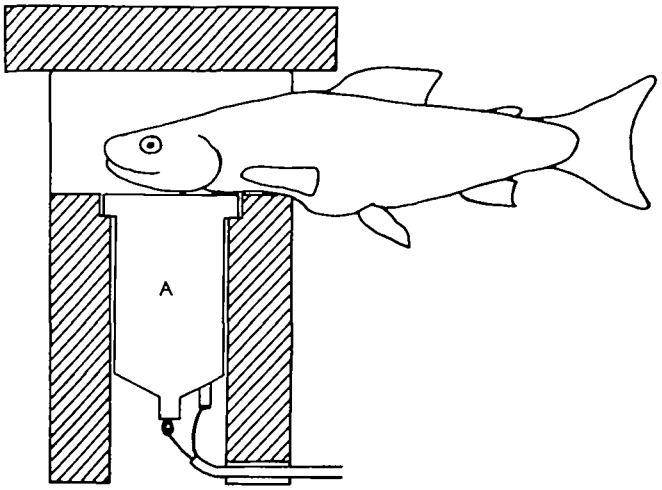

Fig. 1. Section through the lead castle showing the relative positions of the experimental fish and the Geiger–Muller tube (A).

The average monthly temperature of the hatchery water was calculated from a daily evening and morning measurement. Day length was calculated as a monthly average of the day lengths recorded by a Moll thermopile on a Cambridge recorder (threshold value 0·004 cal./cm.^{2}/min.).

RESULTS

The specific growth rate during 1954 (Fig. 2) follows the same general outline as that shown by the results for 1953 (Fig. 3). The 1954 results, however, are perhaps the more accurate ones as the 1953 curve is based on samples of fifty fish from a population which was steadily decreasing as monthly samples were taken for other work. That the fish were more intensively fed during 1954 than in 1953 is reflected in the greatly increased growth rate, but both curves are essentially the same in character. During the winter the fish grew very slowly, the specific growth rate in weight for this period (Fig. 4) reveals that the fish actually lost weight in January and February. In the spring the rate increased to reach a peak towards the end of April and then fell during May and June, increased to a new peak in August and decreased during autumn to the low winter level. A comparison of Figs. 2 and 4 shows that the specific growth rate in weight varies seasonally in a similar manner to that of length always, however, preceding it, thus the summer minimum period of growth in weight occurs during May.

The tissue analysis results are given in Table 1. The muscle and liver, apart from the liver glycogen content of the females which decreased in autumn, remained remarkably constant throughout the year. This is in marked contrast to the herring,

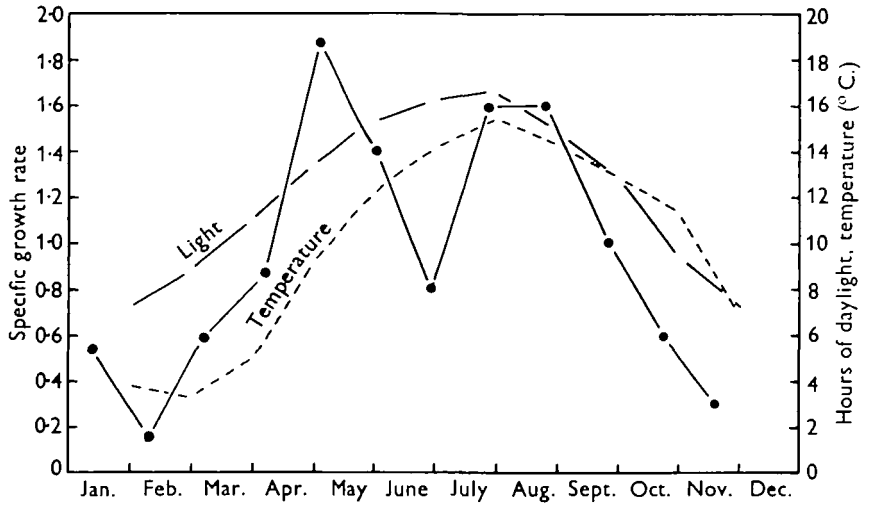

Fig. 2. The seasonal variations of specific growth rate in length during 1954. The growth rate is expressed as the percentage increase per week calculated from the formula $\frac{\ln L_2 - \ln L_1}{T_2 - T_1} \times 100$. The results were obtained by measuring the whole of the population.

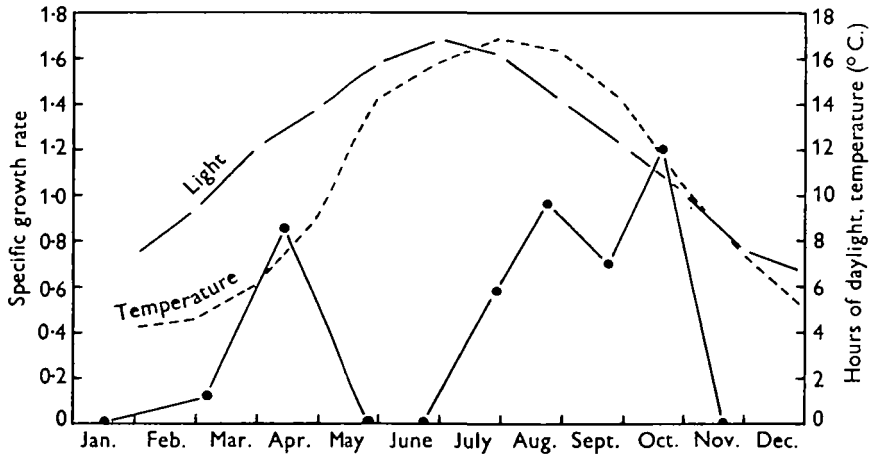

Fig. 3. The seasonal variations of specific growth rate in length during 1953. The growth rate is expressed as the percentage increase per week calculated from the formula $\frac{\ln L_2 - \ln L_1}{T_2 - T_1} \times 100$. The results were obtained by measuring random samples of 50 fish.

the muscle and liver of which, according to Channon & El Saby (1932), vary seasonally in their fat contents and would seem to act as food reserve stores. The gut wall of the trout, the fat content of which varied considerably over the year, is the

principal storage organ for fat which is the main food reserve of these fish. The immature fish in the autumn of 1951 had a fat content of about 12 % by weight (Table 1), during the winter this rose to about 20 %. This winter increase in reserves was probably due to the unnaturally abundant food in the hatchery. During the spring and early summer the fat reserves decreased to about 15 % in June, then increased very rapidly to a peak of 23 % in July. Throughout the late summer and early autumn they were heavily drawn upon so that by October they had decreased in the now ripe fish to a very low level of 5 %. Glycogen was detected in small amounts in the gut, muscle and gonad indicating that this compound is not stored there. The maturation of the gonads commenced during June in the females, and a little

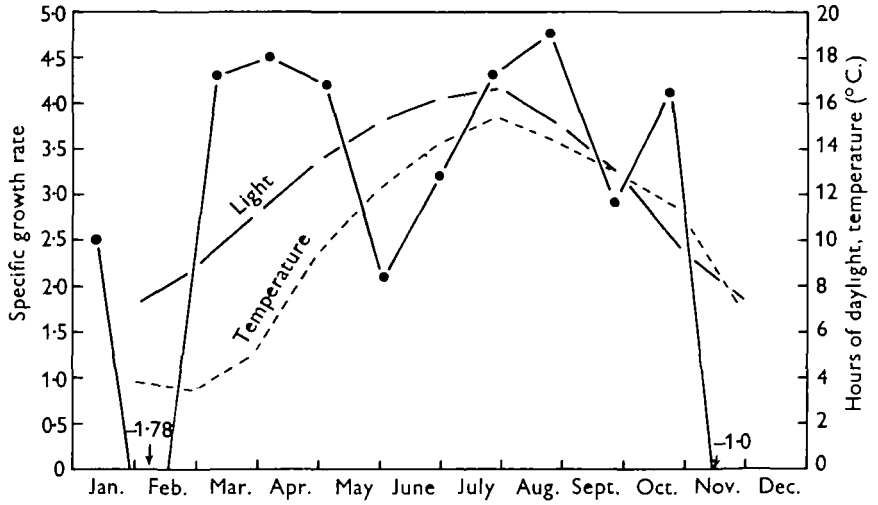

Fig. 4. The seasonal variations of specific growth rate in weight during 1954. The growth rate is expressed as the percentage increase per week calculated from the formula $\frac{\ln W_2 - \ln W_1}{T_2 - T_1} \times 100$. The results were obtained by measuring the whole of the population.

later in the males (Table 1). Ripening proceeded steadily until completion in September and October. The protein content rose 16 % in the ovary and 10 % in the testis, and the ovary fat level rose 3 %. In both the gonad and gut the water content varied inversely with the fat and protein.

When isotope iodine is injected into a fish it enters the blood stream and then it is excreted by the kidneys and gut, or else it is trapped by the thyroid. On entering the thyroid the isotope iodine is probably very quickly distributed throughout the gland, so that some of the isotope may be immediately secreted in organic combination. However, it seems certain that more isotope iodine will, at this stage, be entering than leaving the gland and so a peak concentration of isotope in the gland is reached. After this peak has been reached the isotope content of the gland falls, showing that the rate of secretion in organic combination must now exceed the rate of uptake of isotope from the blood, some isotope presumably returning to the gland in inorganic form after being split from its organic combination. Thus the

Table 1. *Percentage composition by weight of the fish tissues*

	October	November	January	February	March	April	June	July	September	October	December
Muscle											
Water	77·8 (6)*	78·8 (7)	77·8 (5)	77·8 (8)	80·0 (8)	77·7 (6)	79·1 (9)	77·2 (9)	78·4 (9)	79·2 (9)	79·1 (9)
	0·4†	0·4	0·4	0·4	1·2	0·5	0·6	0·4	0·3	0·4	0·4
Protein	18·4 (5)	18·6 (7)	17·7 (5)	18·7 (8)	17·8 (8)	19·3 (6)	18·8 (9)	19·7 (9)	19·4 (9)	18·0 (9)	17·6 (9)
	0·7	0·4	1·1	0·2	0·9	0·2	0·7	0·5	0·3	0·7	0·4
Fat	2·5 (6)	2·3 (6)	4·5 (4)	2·8 (8)	2·7 (8)	2·7 (8)	2·3 (9)	2·6 (9)	2·2 (9)	2·3 (9)	2·9 (9)
	0·3	0·3	1·4	0·2	0·3	0·3	0·2	0·2	0·1	0·2	0·4
Glycogen	—	—	0·4 (5)	0·2 (5)	0·6 (8)	0·2 (9)	0·1 (7)	0·2 (9)	0·2 (9)	0·2 (9)	0·5 (9)
	—	—	0·08	0·06	0·09	0·03	0·002	0·04	0·04	0·04	0·08
Gut											
Water	70·7 (6)	71·1 (7)	66·4 (5)	64·4 (8)	68·1 (7)	68·2 (6)	68·6 (9)	61·8 (9)	72·3 (9)	75·8 (9)	77·9 (8)
	2·5	2·1	1·4	2·2	2·4	3·0	2·1	2·6	0·9	1·9	0·9
Protein	16·2 (6)	13·8 (7)	12·0 (5)	11·8 (8)	13·6 (7)	13·7 (6)	14·3 (9)	13·2 (9)	15·0 (9)	14·6 (9)	14·2 (8)
	2·0	0·5	0·7	0·4	0·05	1·0	1·1	0·6	0·5	0·6	1·1
Fat	11·3 (6)	11·0 (5)	19·9 (5)	20·5 (8)	16·1 (8)	14·4 (9)	14·6 (9)	21·4 (9)	10·7 (9)	5·2 (9)	6·1 (9)
	0·9	0·8	2·4	1·9	2·6	2·3	2·0	2·7	0·8	0·9	0·6
Glycogen	—	—	0 (5)	0 (5)	0 (9)	0·04 (9)	0·02 (9)	0·03 (9)	0·02 (8)	0 (9)	0 (9)
Liver											
Water	75·5 (6)	74·7 (7)	77·2 (5)	75·9 (8)	76·1 (8)	76·5 (6)	79·1 (9)	75·4 (9)	77·2 (9)	76·8 (9)	76·8 (9)
	0·7	0·7	2·5	0·5	0·4	0·5	0·6	0·4	0·6	0·7	0·6
Protein	15·8 (4)	15·7 (7)	14·4 (4)	15·4 (8)	17·3 (8)	17·7 (6)	16·7 (9)	15·7 (9)	14·4 (9)	13·5 (9)	14·9 (8)
	1·2	0·5	0·3	0·4	1·1	1·2	1·4	0·7	0·9	0·7	0·3
Fat	4·8 (5)	3·9 (7)	4·3 (5)	5·1 (8)	5·0 (8)	4·9 (9)	4·6 (8)	5·2 (9)	4·8 (9)	3·9 (9)	5·1 (9)
	0·8	0·3	0·9	0·2	0·1	0·2	0·3	0·6	♀ 0·2 ♂	♀ 0·1 ♂	0·4
Glycogen	—	2·6 (7)	2·6 (5)	2·2 (5)	4·0 (8)	2·5 (9)	2·7 (9)	5·5 (9)	0·8	1·0	3·5 (9)
	—	0·6	1·2	1·0	0·8	0·6	0·6	1·4	1·2 5·5 (6)	1·1 7·9 (6)	0·5
									2·2 0·6	— 1·5	
Gonad								♀ ♂			♀ ♂
Water	82·0 (5)	84·2 (7)	86·0 (3)	83·6 (5)	86·2 (8)	82·4 (5)	84·3 (7)	76·1 (6) 81·7	61·9 83·6 (6)	64·2 78·3 (6)	65·0 78·5 (6)
	2·1	0·7	1·5	0·8	1·0	1·9	0·8	2·7 84·4	61·9 1·8	63·5 1·5	65·5 1·0
								86·8	63·6	64·3	
Protein	13·0 (5)	12·7 (6)	11·4	11·8 (5)	10·9 (8)	15·0 (5)	12·7 (7)	16·7 (6) 8·2	25·4 17·4 (6)	26·2 20·5 (6)	22·9 (8)
	2·2	1·1	10·7	0·9	1·1	1·1	1·8	1·5 12·3	26·7 1·0	26·4 1·5	0·8
			12·4						28·0	26·8	
Fat	4·7 (4)	—	2·5	2·0	2·4 (5)	3·8 (6)	4·0 (6)	5·1 (6) 2·1	8·0 3·1 (6)	4·9 2·7 (4)	7·4 3·0 (6)
	1·5			3·6	0·4	1·4	0·7	1·3 2·1	8·4 0·7	7·6 0·4	7·6 0·7
								2·6	9·4	7·7	
Glycogen	—	—	0	0	0·08 (8)	0·04 (9)	0·01 (8)	0·06 (9)	0·03 (9)	0·06 (5)	0·04 (8)
			0	0							
			0·15								

* The figure in brackets indicates the number of samples taken; where this is less than three all the results are given.

† Standard error of the mean

curve of uptake and loss of isotope by the gland is a composite one formed by the difference at any time between the secretion and uptake of the isotope. The rate of fall of this curve is used as a comparative index of the activity of the gland. The more active the gland, the more rapidly the peak isotope concentration is reached, and the steeper the slope of the curve for the loss of isotope, as the isotope is secreted in organic combination at a greater rate. The results of the investigation into the thyroid activity are shown in Fig. 5, the regression coefficient for the iodine loss/time curve for each fish examined is given, together with the monthly mean, from which it is apparent that the peak thyroid activity in these fish occurred in mid-summer.

DISCUSSION

The rate at which an animal grows is the direct result of the interplay of many internal factors, and perhaps the simplest form of control imaginable would be for the growth rate to be directly governed by the amount of metabolites surplus to the animal's maintenance requirements. These requirements vary seasonally in a poikilothermic animal such as a fish, increasing with the rising temperature of the water in summer and decreasing in winter. The observed growth rate for brown trout (Fig. 2) belies this hypothesis at three periods of the year. Growth commences in spring while the water is still cold, the rate falls in summer and again in autumn when the water is warm.

Brown (1946) found that brown trout growing under constant environmental conditions had two temperature optima for growth, one between 7 and 9° C. and the other between 16 and 19° C. She suggests that, as the observed relationship between temperature and maintenance requirements follow a sigmoid curve, the activity of the fish rose to a maximum between 10 and 12° C., and decreased at higher temperatures; this decrease being enough to compensate for the increased basal metabolism at high temperatures, leading, with increasing temperature, to a depression followed by an increase in the growth rate. The results obtained in this work (Fig. 2) show two temperature optima for growth. In 1954 the maximum growth rate occurred between 8 and 12° C. and between 15 and 16° C., showing a remarkable agreement with those of Brown in spite of the difference in experimental conditions. During June and early July the fish were most active, difficult to handle and showed a higher mortality as a result of handling than at any other time of the year. This observation supports Brown's hypothesis that the activity of the fish rises to a maximum between the two growth rate maxima, and her explanation of the causes of the depression she observed in the growth rate will also account for that shown in this work. This increased activity presumably leads to an increase in the amount of metabolites needed for maintenance, and thus reduces the quantity available for growth, the rate of which falls in consequence. As this activity cannot be solely a temperature effect the cause must be sought elsewhere. Two other factors which could be responsible are exerting their maximum influence at this time of the year; the thyroid gland, which has reached its peak activity, and day-length which is at its maximum.

The thyroid function in teleosts has been investigated by many workers (Root & Etkin, 1937; Etkin, Root & Mofshin, 1940; Hasler & Meyer, 1942; Smith & Everett, 1943; Matthews & Smith, 1947. They have sought in vain to influence the rate of oxygen consumption in fish by the use of known mammalian thyroid stimulants and depressants, and thus to show that the function of the gland in fish is the same as that in mammals, namely to control the basic metabolic rate. A suggested reason for these negative results is that a specificity has evolved, rendering the fish insensitive to these preparations. Supporting evidence of this explanation is provided by the work of Smith & Matthews (1948) who obtained an increase in the oxygen consumption of *Bathystoma* when injected with parrot fish thyroid extract. On the other hand, Matty (1954), working with thyroidectomized dogfish, noted no decrease in the oxygen consumption of the experimental animals. This would have been fairly conclusive evidence that the thyroid, at least in elasmobranchs, does not influence the basic metabolism, if Matty had not detected protein bound iodine in the plasma of an experimental animal 6 weeks after thryoidectomy. Rats, injected with thyroid gland extracts of teleosts (Smith & Brown, 1952), and of elasmobranchs (Matty, 1954), show a positive increase in oxygen consumption, indicating that the fish gland secretes a hormone which can exert a similar effect to that of the mammalian gland.

Another approach to the problem of thyroid gland function, which has been made here and by other workers, is to survey the seasonal variations in the activity of the gland. The results of the present work show that the peak activity occurs during midsummer, but D. C. W. Smith informs me that he has found, according to histological criteria, that the thyroid gland of 1-year-old trout reaches a maximum activity in spring. There would seem to be two possible explanations for the discrepancy between these results; either that the thyroid gland in immature and maturing fish reaches its maximum activity at different times of the year or that, as has been suggested, a histological examination does not reveal the true biochemical state of the gland. Further work must be done to determine biochemically precisely what activity states of the gland are represented by the histological criteria used by previous workers.

Lieber (1936) found two peaks of activity in the gland of *Misgurnis fossilis*, one in May and the other in August, these periods preceding and following spawning in these fish. Hoar (1939) working with salmon parr found evidence of maximum activity in May. Buchmann (1940) found a seasonal activity in the gland of the herring which coincided with spawning. Barrington & Matty (1954) showed the peak thyroid activity in the minnow to occur in spring just previous to spawning. All these results suggest that the thyroid is most active immediately prior to gonad maturation. This fact has led Barrington & Matty to suggest that the thyroid function in fish is concerned with gonad activity. This hypothesis is supported by the results of their experiment (1952), which showed that minnows suffered a retardation in their gonad maturation when immersed in an 0·1 % solution of thiourea. However, even if such a relationship was shown to exist it may not be the complete thyroid function as Hoar (1939), Buchmann (1940) and von Hagen (1936), working

with the salmon, herring and eel respectively, have shown that a marked thyroid activity occurs at metamorphosis. Fontaine & Callemand (1942) have also reported two periods of marked thyroid activity in the eel which correspond to changes in the environment, and the results reported here show that peak thyroid activity in the brown trout correspond to a period of great physical activity in the fish. Thus all the fish observed with a highly active thyroid have exhibited a common factor of great physical activity, from this fact it is postulated that the thyroid hormone in fish exerts a tonic effect on the whole nervous system of the animal, rendering the animal more responsive to external environmental stimuli. These observations would

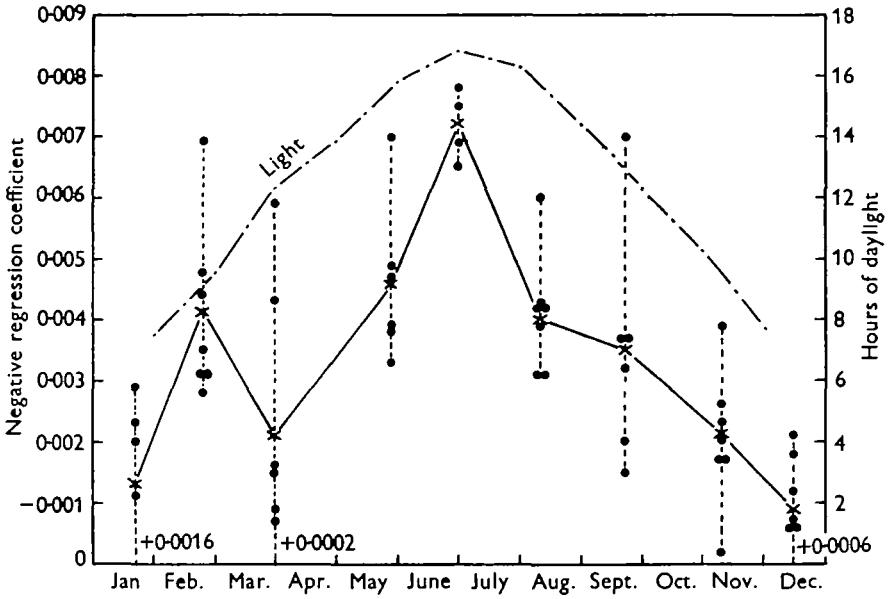

Fig. 5. Seasonal variations in the thyroid gland activity. The glandular activity is expressed by the regression coefficient for the iodine loss/time curve. The curve for the seasonal variation is drawn to the monthly means (×) of these regression coefficients.

also be in accord with a raising of the basic metabolic rate at times of great thyroid activity, but such an influence of the thyroid hormone remains to be demonstrated. The external environmental factor or factors responsible for the seasonal variation in the activity of the thyroid is unknown, the results shown here (Fig. 5) suggest that day-length may play a part in determining this activity.

At the beginning of this discussion it was pointed out that the observed growth rate of the fish differed from a proposed elementary relationship between temperature and growth at three periods, in spring, in summer and in autumn. The summer anomaly is caused, in all probability, by the increase in activity of the fish. The autumn anomaly is without doubt caused by the ripening of the gonads, which occurs during July, August and September (Table 1). During late summer when the rate of supply of metabolites from the gut, if dependent on water temperature,

must be virtually at its maximum, the fish is able to maintain a high growth rate, ripen its gonads and lay down food reserves (Fig. 2, Table 1). By August it seems that this supply of metabolites is insufficient to maintain both growth and gonad maturation. This is inferred from the fact that by October the fat stores around the gut have dropped from the July figure of 22 to 5% of the gut wall. During this period the females also draw on their liver glycogen stores. By the end of August the water temperature, and thus presumably the rate of supply of metabolites from the gut, begins to fall. The gonads are still ripening and their increased demand for metabolites from the decreasing supply available, is reflected by a fall in the growth rate. This interpretation is supported by a comparison of the growth rate curves for 1953 and 1954 (Figs. 2 and 3). In 1953 a very low percentage of the population ripened, and the fish maintained their growth rate until October, whereas in 1954 the growth rate of the fish, nearly all of which were ripe, decreased from the end of August.

That growth hormone occurs in fish (Pickford, 1954), suggests a possible cause of the commencement of growth in early spring, when this occurs the water temperature is still very low but day-length is increasing, suggesting that here again it is day-length which is the important external environmental factor.

SUMMARY

1. Seasonal variations in the growth rate, food reserves and activity of the thyroid gland of hatchery-reared brown trout have been investigated.

2. Two peaks of maximum growth rate were found, in spring and autumn. A marked depression of rate occurred during midsummer and winter.

3. Fat which was laid down along the mesenteries and pyloric caecae was found to be the main food reserve. Glycogen was found in small quantities in the liver and muscle. The composition of the muscle and liver was constant except for an autumnal fall in the female liver glycogen level. The fat reserves reached a peak of 23% by weight of the gut wall during July then fell to 5% in autumn.

4. Maturation of the gonads commenced in females in June and in males in July and was completed during October. The protein content of the ovary increased by 16%, and of the testis by 10%.The fat content of the ovary increased by 3%.

5. A new method is described for the determination of thyroid activity in fish using radioactive iodine. Peak thyroid activity was found to occur in midsummer.

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