

## THE ANNUAL GROWTH-RATE CYCLE IN BROWN TROUT (*SALMO TRUTTA* LINN.) AND ITS CAUSE

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### INTRODUCTION

Three-year-old brown trout living in a hatchery stewpond have a growth rate which fluctuates in a regular annual cycle (Swift, 1955). The cause of these fluctuations is of interest in a study of the physiology of growth in trout. It was therefore important to establish whether these fluctuations are only found in the growth rate of fish living in a hatchery, and also whether the form of the cycle is the same in immature as in mature fish. If this form of annual growth-rate cycle is common to both mature and immature fish living both in the wild and in the hatchery, then the causes of the cycle should be ascertained.

The work undertaken is described in two parts. In the first part the growth-rate cycle of yearling trout living wild and in the hatchery is described, and its relationship with the two major variables in the external environment, water temperature and the daily length of the photoperiod, is discussed.

The second part of the work deals with the relationship between water temperature, photoperiod length and growth rate as established when the fish were grown in constant-environment aquaria.

### PART I. THE ANNUAL GROWTH-RATE CYCLE OF YEARLING TROUT GROWING IN A HATCHERY STEWPOUND AND IN THE WILD

#### *Methods*

For the examination of the growth rate under hatchery conditions a population of 100 yearling fish, selected at random from the hatchery stock, was kept in a concrete-lined stewpond holding approximately 25 kl. The fish were fed to satiation on minced liver. Each month the whole of the population was removed from the pond and the length of each fish, anaesthetized with tricaine methano-sulphonate, was recorded. From the means of these monthly measurements the average specific growth rate of the population was calculated, using the formula

$$\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100,$$

where  $\ln L_1$  and  $\ln L_2$  are the natural logarithms of the mean lengths of the populations at time  $t_1$  and  $t_2$  respectively, the time being reckoned in weeks. The temperature of the water was recorded in the morning and in the evening every day, and from these readings a monthly average was calculated. This work was first done in 1955 and was repeated during 1956 and 1957 using a fresh population of yearling fish each year.

In order to follow the growth of these fish when living wild a population of 120 was released into Scale Tarn, a small moorland tarn near Esthwaite Water, in March 1957. These fish fed naturally on the fauna of the tarn and at intervals a large sample was netted out and the lengths of the fish in the sample were measured.

Early in 1959 fifty yearling fish were released into a netted-off portion of Windermere and left there to feed naturally. Each month a large sample of these fish was netted out and the lengths of the fish were measured. Monthly growth rates were calculated as for the hatchery fish.

### Results

The results of this work are shown in Figs. 1 and 2. In these graphs the monthly specific growth rates for the various populations of fish are plotted against time. It is immediately apparent from these figures that the growth rate varies in a regular annual pattern similar to the pattern of growth displayed by the older fish (Swift, 1955). The fish always show a high growth rate in the spring and nearly always in the autumn, and a low growth rate during the winter and in mid-summer.

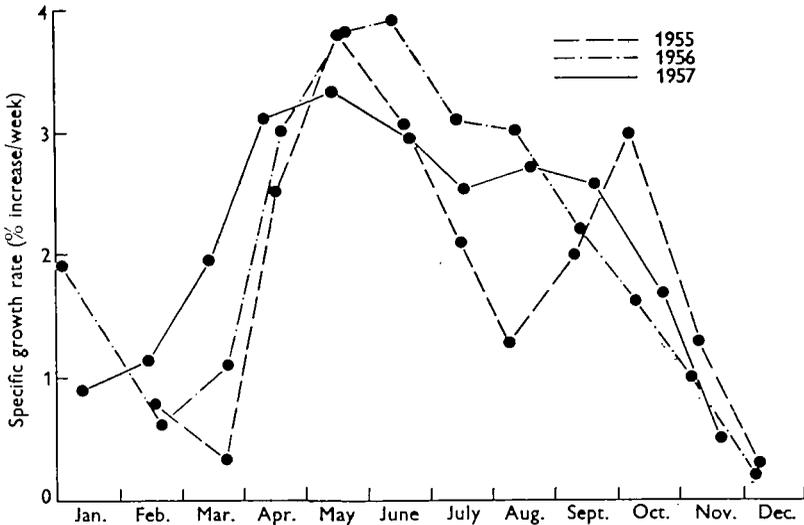


Fig. 1. The seasonal variations of specific growth rate in length of three populations of yearling trout. The growth rate is expressed as the percentage increase per week calculated from the formula

$$\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100.$$

The results were obtained by measuring the whole of the population.

### Discussion

These results show that the growth rate of brown trout, at least in these latitudes, varies in a regular rhythmical fashion, and that this rhythm bears a definite relationship to the seasons. Furthermore, this rhythm is not affected by the state of the animals' gonads or by the type of habitat if this is not too adverse. These regular variations in growth rate must result from the response of the animal to a rhythmical change in the external environments, or from a regular endogenous rhythm in the physiology of the

animal, or from a combination of both these factors. Evidence for the existence of endogenous rhythms in animals has received renewed attention in recent years; see the reviews of Brown (1957) and Harker (1958). An endogenous rhythm in the capacity of a fish to grow could be an important factor in deciding the form of the annual growth-rate cycle in these animals. Brown (1946*b*) grew 2-year-old trout in constant-environment aquaria and obtained evidence indicating the possibility of such an endogenous rhythm in these animals. The number of fish used was small and the scatter in their growth rates during the same periods was large, making the interpretation of her results difficult. However, two interesting factors emerged from this work: first,

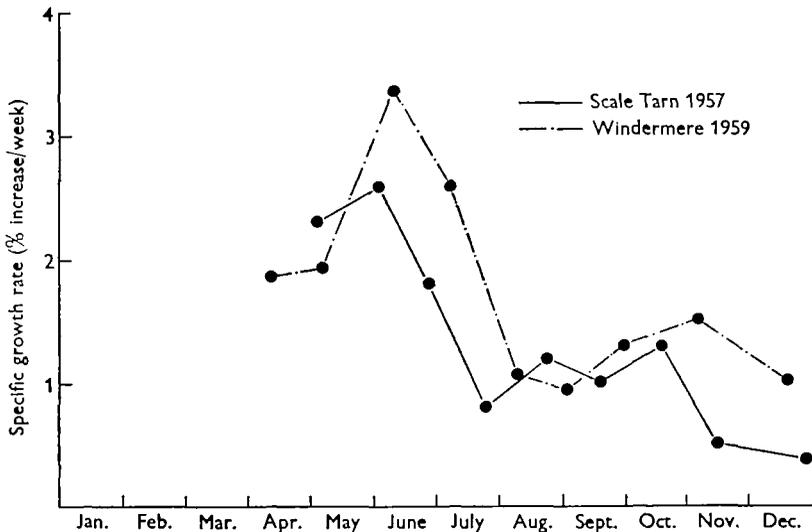


Fig. 2. The seasonal variations of the specific growth rate in length of two populations of yearling trout, one living in Windermere and the other in Scale Tarn. The growth rate is expressed as the percentage increase per week calculated from the formula

$$\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100.$$

her fish became ripe in the second autumn of their sojourn in the tanks, and secondly, they grew well during the winter when wild trout have a poor growth rate. It has been demonstrated that the trout, after reaching a certain physiological age, spawns as a result of the stimulus of the changing length of the daily light period (Hoover & Hubbard, 1937; Hazard & Eddy, 1951). The fact that the fish became ripe in the constant-environment tanks at the same time of the year as they would have done in the wild suggests that they already had a rhythm impressed on them since hatching.

Nevertheless, it does not seem clear that the changes in growth rate of Brown's fish were the result of an endogenous annual rhythm in the fish's capacity to grow—a rhythm in the production of growth hormone for example. Furthermore, there is little correspondence between the variations in growth rate in the tanks and the variations in the growth rate of the fish in the wild. If therefore an endogenous annual cycle in the capacity of these animals to grow does exist, it seems to have little

influence in deciding the actual growth rate of the fish in the wild. It was therefore decided to ignore the possibility of such an endogenous rhythm when considering the possible causes of annual growth-rate cycle described in this paper, and to consider the growth-rate cycle as being the direct result of an annual variation in the value of some component of the external environment. In these latitudes there are three

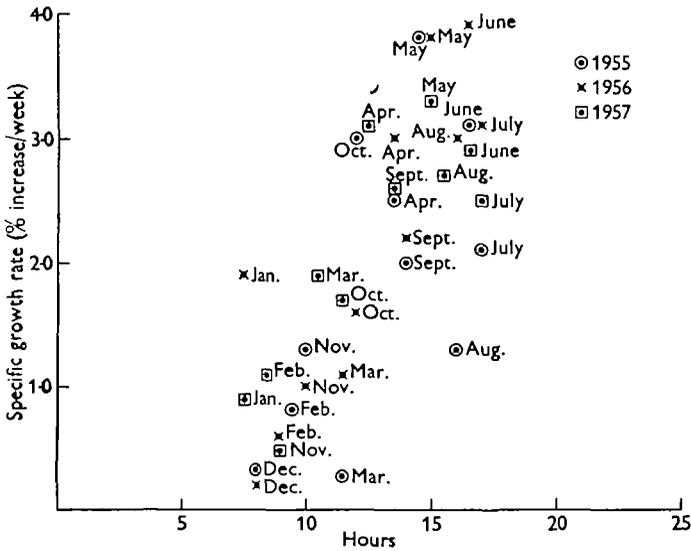


Fig. 3. The average monthly values of the specific growth rates in length plotted against the average length of the daily photoperiod over the same period of time.

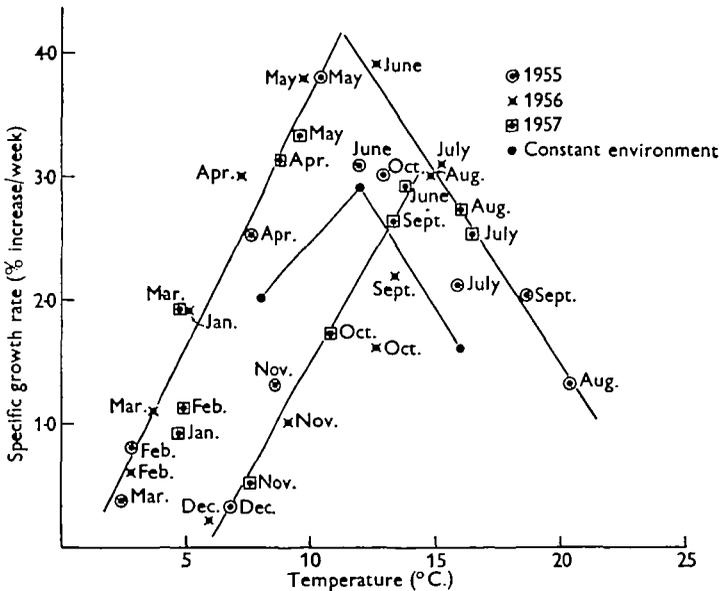


Fig. 4. The average monthly values of the specific growth rate in length plotted against the average water temperature over the same period. Also shown is the average specific growth rate in length of the fish living at different temperatures in a constant environment.

External environmental factors which vary with a frequency of 12 months: these are water temperature, photoperiod length, and concentration of solutes in the water. Changes in the solute concentration do not seem to affect the growth rate, for the order of magnitude of these changes is (for most elements) much greater in small bodies of water than in large (F. J. H. Mackereth, private communication), and it has been shown (Fig. 2) that the growth-rate cycle was the same in a large body of water (Windermere) as in a small body of water (Scale Tarn). It is a possibility that in some habitats some minor element may become limiting at some time of the year, but with our present knowledge one can do no more than note this possibility. It seems likely therefore that the growth rate is responding to change in either water temperature or photoperiod length. The average monthly values of water temperature and photoperiod length were plotted against the corresponding growth rate of the fish. There is little indication of a relationship between growth rate and photoperiod length; the slight correlation between the two (Fig. 3) is more probably the result of the contemporaneous increase in photoperiod length and in water temperature which occurs in these latitudes. Fig 4 shows the graph of growth rate plotted against water temperature. During the spring when the water temperature is rising the growth rate increases proportionally, until the water temperature reaches the 10–12° C. level; above this point the growth rate of the fish becomes inversely proportional to the temperature, so that during the summer months, as the water warms up to its maximum annual temperature and then cools, the growth rate of the fish falls and then rises. The change in the relationship between the growth rate and the water temperature which occurs between 10 and 12° C. in the spring, takes place at a higher temperature in the autumn, when the growth rate of the fish becomes proportional to the water temperature at about 14° C. This is further evidence that the photoperiod length does not, under natural conditions, influence the growth rate, for in 1955 the fall in the growth rate of the fish occurred in October whereas in 1956 and 1957 it occurred in September. The change always took place at the same water temperature but not at the same photoperiod length. If the average water temperature during the summer does not rise much above 14° C. then it follows from this relationship that the growth rate of the fish will not rise during the autumn, but will continue to fall for the rest of the year; this was the case in 1956.

## PART 2. THE GROWTH RATE OF YEARLING BROWN TROUT KEPT IN A CONSTANT ENVIRONMENT

### *Introduction*

In order to confirm the relationship between temperature and growth rate reported in the previous section a set of eight constant-environment aquaria was constructed at the Ferry House. The results of experiments in these aquaria are reported in this section.

### *Method*

Eight light-tight aquaria, each holding approximately 100 l., were constructed of wood, lined with asphalt and insulated with granulated cork. The water supply to the tanks is pumped from Windermere through a plankton net, over an ultra-violet

sterilizer and into a header tank. Here it is cooled to  $1^{\circ}\text{C}$ . below the operating temperature of the tanks. The water enters the tank at 500 ml./min. and is stirred and aerated by compressed air entering through porous ceramic blocks. The tanks are trimmed to the operating temperature by heaters and in this way the tanks are held to within  $\pm 0.1^{\circ}\text{C}$ . of the operating temperature. Each tank is illuminated by a 2 ft. 'daylight' fluorescent light, controlled by a mechanical time switch.

For these experiments each tank was stocked with ten yearling brown trout. The fish were individually identified by fin clips. They were fed to satiation daily with minced liver set in gelatine (Swift, 1960). Every 2 weeks they were anaesthetized with tricaine methano-sulphonate, weighed and measured.

During the course of these experiments which lasted from April to October some of the fish died; when this happened the dead fish was replaced by one from a stock tank. The stock tank was kept under the same environmental conditions as the experimental tank. Four populations of ten fish were used in this work. If a fish died during the course of the experiment its growth during the fortnight preceding its death was not used in the final assessment of its growth rate. The growth rate of a replacement fish which had not been living in the tank for more than 4 weeks was also omitted from the final calculations.

### Results

All the fish were kept for 3 months at each of three temperatures,  $8^{\circ}$ ,  $12^{\circ}$  and  $16^{\circ}\text{C}$ ., and at each temperature were subject to 4, 8 or 12 hr. of light per day; each different photoperiod length lasted for 4 weeks thus allowing the fish to be measured twice during this time. The growth rates showed no consistent response to changes in photoperiod length. It was decided to ignore the different photoperiods used during these experiments, and to consider the change in the lengths and weights of the fish over the 12-week period for each temperature. The first and last measurements made on each fish were used to calculate the growth rate.

The histograms in Fig. 5 show the frequency distribution of the various values of the specific growth rates of the fish, when growing at the various temperatures of the experiment. The growth rate in both length and weight was larger at  $12^{\circ}\text{C}$ . than at  $8^{\circ}$  or  $16^{\circ}\text{C}$ . This supports the relationship between temperature and growth rate discussed in the previous section. The three values for the means of the specific growth rate in length obtained at the three experimental temperatures are shown on Fig. 5. These values are also plotted on Fig. 4, and it will be seen that the slopes of the lines joining these three points correspond very closely with the slopes of the lines indicating the relationship between growth rate and water temperature as deduced from the results of the experiment with the hatchery fish. These results indicate that it is the water temperature which plays the decisive role in the control of the growth rate of trout living under natural conditions, the fish achieving their maximum growth rate at  $12^{\circ}\text{C}$ .

The second point to note in these results is the very wide scatter of rates of growth of individual fish at the different temperatures of the experiment. These rates range from 0.5 to 4.0% at  $8^{\circ}\text{C}$ ., from 1.5 to 4.5% at  $12^{\circ}\text{C}$ ., from 0.5 to 3.0% at  $16^{\circ}\text{C}$ . It was at first suspected that this wide variation in the growth rates of individual fish at any temperature was probably the result of an order of hierarchy, such as Brown (1946*a, b*) demonstrated in her brown trout populations. However, an examination of

The results showed that this was in fact not the case; within a population the growth rate of the fish was found to be independent of size, some fish growing better than others for some internal rather than external reason.

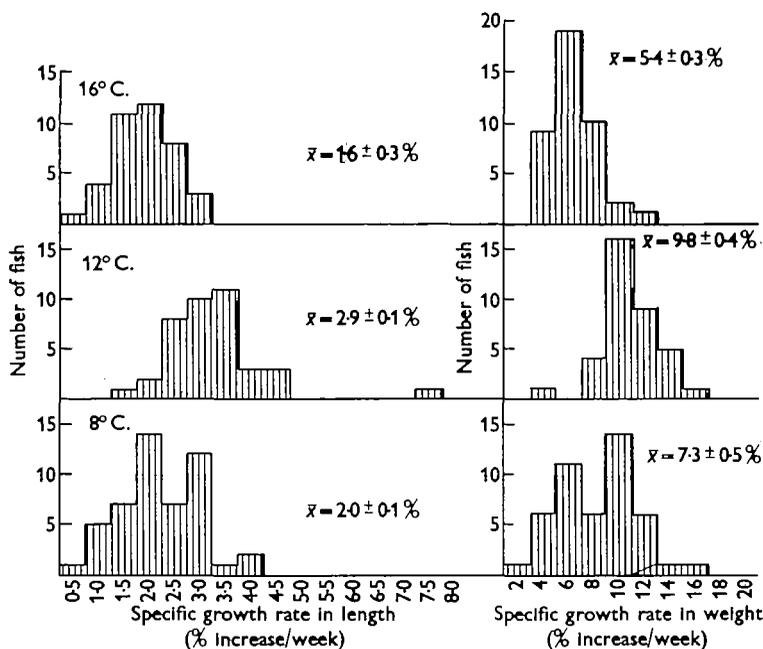


Fig. 5. The frequency distribution of the various values of specific growth rate in length and weight of the fish growing at various temperatures in constant environments. The means and the standard error of the means are shown.

### Discussion

There can be no doubt that the photoperiod length does influence the physiology of fish (Hoover & Hubbard, 1937; Brown, 1946*b*; Hazard & Eddy, 1951; Hoar, 1955; Eisler, 1957).

Eisler and Brown both demonstrated a direct effect on the growth rate by the photoperiod length, but this response took some time to become apparent, 6 weeks for Eisler's fish and 2 and 5 months for Brown's; my fish showed no effect after 1 month.

It is important to try to distinguish between the effect of day-to-day changes in photoperiod length and the effect of the length of the photoperiod when this is constant from day to day. The work on the ripening of fish gonads (Hoover & Hubbard, 1937; Hazard & Eddy, 1951) has shown that for this it is the changing length of the daily photoperiod that is important. The apparent lack of any relationship between photoperiod length and growth rate of wild fish (Fig. 3) suggests that the growth rate is not affected by the natural day-to-day change in photoperiod length.

Pentelow (1939) working with brown trout found that the growth was roughly proportional to food, and that food consumption fell above 15°C., suggesting an optimum temperature above 10°C. and below 15°C. Baldwin (1956) found that *Salvelinus fontinalis* consumed most food and made their best growth at 13°C. The

optimum temperature for growth of the fish found by both these workers agrees well with the optimum temperature reported in this paper.

The only previous investigation of the growth of trout in constant environments is that of Brown (1946*b, c*). Brown found that her fish grew best between 7° and 9° C. and between 16° and 19° C., compared to the optimum temperature of 12° C. reported here. As has been shown in Fig. 5, at any given temperature there is a large scatter in the growth rates of individual fish. This fact coupled with the small numbers of fish used by Brown makes the interpretation of her results a little difficult, for an inspection of her Figs. 2 and 3 (Brown, 1946*c*, pp. 148, 149) shows that as the standard deviations are large it is difficult to establish with any degree of certainty the optimum temperature for growth; the high growth rate recorded at 18° C. results from the very high growth of one fish out of the population of ten. It is apparent from Table 1 that in one experiment the fish actually made their best growth at 11.5° C. This being so there is perhaps less discrepancy than might appear at first sight between Brown's results and those reported in this paper.

In a previous paper (Swift, 1955) it was postulated that 3-year-old trout living in a hatchery stewpond showed two distinct temperature optima for growth, 11° and 14° C. An examination of Fig. 3 shows clearly that these yearling trout also display maximum growth at two different temperatures. When the fish are subject to an increasing temperature their growth rate decreases above 12° C., as in the early summer of each year; when the fish are subject to a decreasing temperature, as happens in the autumn of each year, the growth rate decreases at the higher temperature of 14° C. Thus the optimum temperature for growth would seem to depend on the previous thermal history of the fish. That the thermal history of a fish affects its metabolism is well known, see for instance the reviews by Fisher (1958) and by Fry (1951). Hoar & Cottle (1952) have shown that the water and lipid content of goldfish, together with the cholesterol/fatty acid and cholesterol/phospholipid ratios, vary with the acclimatization temperature. Kanungo & Prosser (1959) found for goldfish that the oxygen consumption, measured at 20° C., was greater for fish acclimatized to 10° C. than for fish acclimatized to 30° C. and this observation is supported by the results of Fry & Hart (1948). If the water temperature can influence the physiology of the fish in this way it is perhaps not unreasonable to suggest that the previous thermal history of the fish may determine the point at which the relationship between water temperature and growth rate changes when fish are subject to a changing water temperature.

During any given period of time the growth rate of a fish must depend basically on the supply of metabolites and oxygen to the growing tissue. Ignoring food reserves in the animal, the supply of metabolites depends on the rate of digestion, and the supply of oxygen on the rate of respiration. It is possible that either or both of these two factors may decide the growth rate of the fish, and an increasing deficiency of either of them could account for a falling growth rate.

There is little evidence of the effect of temperature on the rate of digestion of fish. Maltzan (1935) working with carp, and Swift (unpublished) working with trout, found that the rate of passage of food through the gut increased with the temperature.

The respiration of fish has received the attention of many workers and the subject has recently been reviewed by Fry (1957). The oxygen content of water falls, and the oxygen requirements of a fish rise, with increasing temperature, causing the fish's

ventilation rate to rise faster than its respiration rate. The utilization of dissolved oxygen falls with increasing ventilation rates, thus greatly increasing the cost of respiration, in terms of resting metabolism, at higher ventilation rates (van Dam, 1938). These facts support the idea that the respiratory mechanism of a fish may reach the limit of its capacity at higher temperatures. Job (1955) has found that the active respiration of 45 g. *Salvelinus fontinalis* is limited by the oxygen content of water warmer than 15° C. Fry (1957) has pointed out that in fish the greatest increase in the active over the standard respiratory rate is of the order of fourfold, while in man (Krogh, 1941) the increase is 20-fold; Fry suggested that it may be the respiratory rather than the digestive system which limits the growth rate in fish. It is suggested that the fall in the growth rate demonstrated to occur in brown trout above 12° C. is the result of the increasing cost of respiration at these higher temperatures, and the increasing incapability of the fish's respiratory capacity to meet its respiratory needs. If this is so then it would seem probable that fish given a 'choice' in a temperature gradient would 'prefer' to be in a temperature near to 12° C. Fisher & Elson (1950) found that yearling trout preferred water at 10° C., at which temperature the fish made their maximum movement in response to an electrical stimulus. Brett (1952) found that young salmon of the genus (*Oncorhynchus* preferred water at 12–14° C. Garside & Tait (1958) found that *Salmo gairdneri* preferred water at 11–16° C.

It must be pointed out that there is no direct evidence to support this suggestion as to the cause of the fall in the growth rate about 12° C.; experimental evidence is needed to prove or disprove it.

#### SUMMARY

1. A regular annual growth-rate cycle is demonstrated in wild and hatchery yearling brown trout; the fish have a high growth rate in the spring and autumn and a low growth rate during the summer and winter of each year.
2. Experimental work with constant-environment aquaria, together with the results of the field work, indicate that the water temperature is the main external environmental factor influencing the growth rate. Maximum growth rate is achieved at 12° C.
3. The reason for the fall in growth rate above 12° C. is discussed and it is suggested that inadequacy of the respiratory system of the fish is the prime cause.

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