

TRAINING, SPEED AND STAMINA IN TROUT

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(Received 26 May 1962)

INTRODUCTION

Considering the importance attached to training in most athletic pursuits it might be considered that the speeds measured as the maximum accomplishments of various captive fish must be less than those accomplished by similar specimens free and constantly active in nature. Gray (1953, 1957) has already suggested that experimentally measured speeds might fall short of natural ones because of some such condition factor. Brett, Hollands & Alderice (1958), in their study of the effect of temperature on the cruising speed of young sockeye and coho salmon (*Oncorhynchus nerka* and *O. kisutch*), showed incidentally that unexercised fish tended to fatigue earlier than exercised ones and that the maximum measured speed sustained for 5 min. was 33.6 cm./sec. for exercised fish (c. 6.7 cm. long) and only 25.4 cm./sec. for unexercised ones. More recently, Hochachka (1961) has looked specifically at the effect of training on oxygen debt and glycogen reserves in the rainbow trout. Fatiguing his fish before testing by chasing them about in an open trough he found a determinable difference between the time for the disappearance of a response to stimulus in fifteen trained fish (4.1 min.) and fifteen untrained ones (2.6 min.). He also demonstrated, amongst other differences, the development of an oxygen debt in the trained fish of three times that found in the untrained ones after comparable exhaustion by chasing. A further indication that wild (and presumably trained) fish might be better performers than captive laboratory-bred specimens is contained in the figures reported by Dow (1962) for the speed of swimming of the river herring or alewife, *Pomolobus pseudoharengus*. Dow recorded that 23% of a population of fish attempting to swim through a sluice or flume, down which water was flowing at 3.63 m./sec., were successful in making the passage. The mean result for these fish of 29.5 cm. length was a speed of 15.1L (body lengths) per second sustained for 3.9 sec. Other fish of a comparable size measured in the laboratory have rarely exceeded 10.0L per sec. for a period of about 1 sec. It is possible either to suppose that these laboratory figures are low because the fish were untrained or else that *P. pseudoharengus* is a better performer than the goldfish, dace and trout recorded in Bainbridge (1958). The latter explanation of the discrepancy is not unreasonable as the clupeids in general, from the form of their body and tail fin, must be expected to be good swimmers. It has not yet been possible to test such fish in the laboratory.

It has for some time been thought desirable to investigate the possible influence of training on the measured maximum speeds of laboratory fish given in Bainbridge (1958) and on the ability of these fish to sustain such speeds for various periods of time (Bainbridge, 1960). The opportunity to do this immediately for the trout, *Salmo*

irideus, has arisen through the thoughtfulness of Mr D. W. M. Herbert of the D.S.I.R. Water Pollution Laboratory at Stevenage.

EXPERIMENTAL METHOD

In a study of the effect of particulate suspended matter on their growth and survival Mr Herbert has had occasion to keep fish for long periods in constantly moving water and he has kindly supplied me with trout that have been swimming without rest for about 12 months. The fish were kept in batches of 25 in glass and slate aquaria measuring 3 ft. \times 3 ft. \times 2 ft. A central stainless steel vertical shaft carried at its lower end two paddle blades each inclined at an angle of 45°. These rotated just above the base of the aquarium and below a false floor of expanded metal coated with plastic. The fish, *Salmo irideus*, about 1 year old, were first placed in such aquaria on 4 January 1961. They were fed each day on minced bullock's heart and liver and then transferred to clean water in a similar aquarium. On 11 January the paddles were started for the first time and rotated at 13.3 r.p.m. The rate was increased to 26 r.p.m. on 17 January and to 40 r.p.m. on 1 February. This rate was maintained continuously until the end of the experiment except for two intervals, usually of less than 1 min., every weekday when the paddles were stopped for aquarium maintenance. With the paddles rotating at 40 r.p.m. the speed of the water in the part of the aquarium containing fish was about 25 cm./sec. at points half-way between the centre of the tank and the side. The paddles always rotated in an anti-clockwise direction when viewed from above and the fish swam clockwise to maintain station in the current. Most of the tanks contained various amounts of suspended matter but the control fish were kept in uncontaminated water. It was these fish that were supplied for study in the present work. Their average weight and length on 11 December 1961 were 200 g. and 24.4 cm.

The first specimens were brought to Cambridge, for testing in the 'Fish Wheel' (Bainbridge & Brown, 1958), on 10 January 1962, by which time they had been swimming continuously at a cruising speed of from 1.0 to 1.5 L/sec. for exactly one year. They were carried the 35 miles by road, two or three at a time, in enclosed circular cans of well-oxygenated water. On arrival they were given a preliminary testing in the wheel as quickly as possible and then kept, for subsequent testing, in glass tanks measuring 1 ft. \times 1 ft. \times 1 ft. 6 in. and containing well-aerated temperature-controlled water.

For this work the fish wheel was modified as in Bainbridge (1960) by using a standard Cossor double-beam cathode-ray oscilloscope with a paper film camera to obtain a continuous permanent record of speed against time for various periods of swimming. The modified apparatus was used, exactly as in Bainbridge (1960), to obtain data concerning the relationship between the speed and the length of time it can be sustained by the experimental animal.

In all cases the recordings were conducted with the fish in water at room temperature, this being about 14° C. in the present series. When not being tested the fish were kept in water at this same temperature and they also had been reared in water of more or less the same temperature.

Despite the fact that they had been swimming for 12 months in a clockwise direction they showed no preference in the wheel, swimming indiscriminately in either direction, frequently changing from one to the other and achieving equal speeds in both directions.

EXPERIMENTAL RESULTS AND DISCUSSION

The results obtained using thirteen individual trout of sizes ranging from 21.0 to 30.0 cm. are given in Fig. 1. This shows how their speed varies with the length of time for which the burst of swimming is sustained, up to a period of 20 sec. It is identical in layout and may be directly compared with fig. 4 in Bainbridge (1960). The similarity of the behaviour of the present specimens is immediately apparent even to the eye alone.

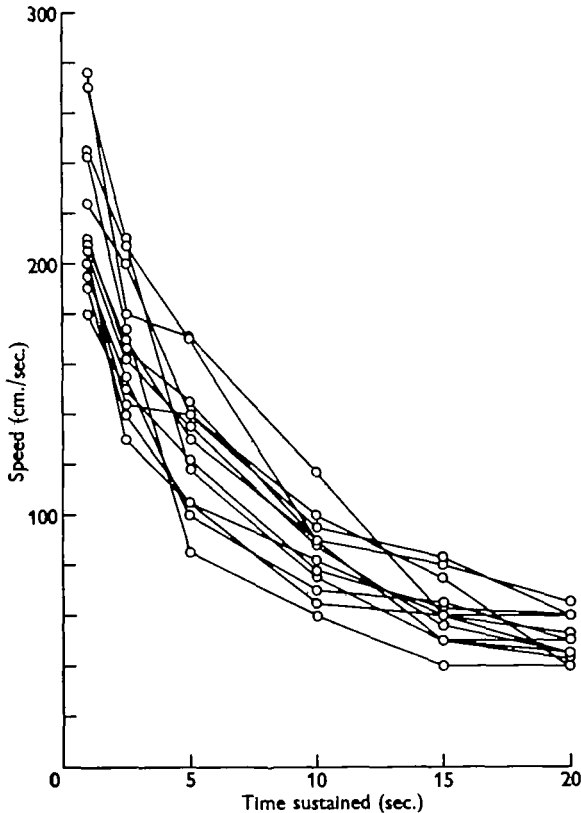


Fig. 1. Relationship between speed of swimming and the length of time it can be sustained for thirteen trout (*Salmo irideus*) that had previously been exercised for 12 months by swimming continuously at 25 cm./sec. The measurements were made by using the 'fish wheel' apparatus.

Assuming as before that the ability to maintain speed is some function of the length of the specimen, this function has again been calculated by plotting the logarithm of the speed against the logarithm of the length for the results for different sized fish at each particular time interval. The six values of α thus obtained for the six time intervals from 1 to 20 sec. are: 0.89, 0.56, 0.41, 0.33, 0.48 and 0.71. These figures show about the same degree of variability as those for the four trout previously measured in the wheel. Their mean is 0.56 compared with the figure 0.58 previously obtained. The difference between these two is so slight that the present results have been plotted in Fig. 2 with each value of speed divided by the length of the specimen raised to the

power of 0.58 rather than 0.56. Fig. 2 can thus be directly compared with fig. 5 in Bainbridge (1960), being identical with it in all respects. The amount of spread in it need cause little concern as this degree of variation might well be expected within any population of animals. Paulik & DeLacy (1958) show an equally great variability within their sample of 406 sockeye salmon tested to exhaustion in a flume of water flowing at 9.4 ft./sec. The strongest fish were able to swim for 112 sec. in such a current, but the weakest for only 22 sec. This is a range quite comparable with that found in the trout reported here.

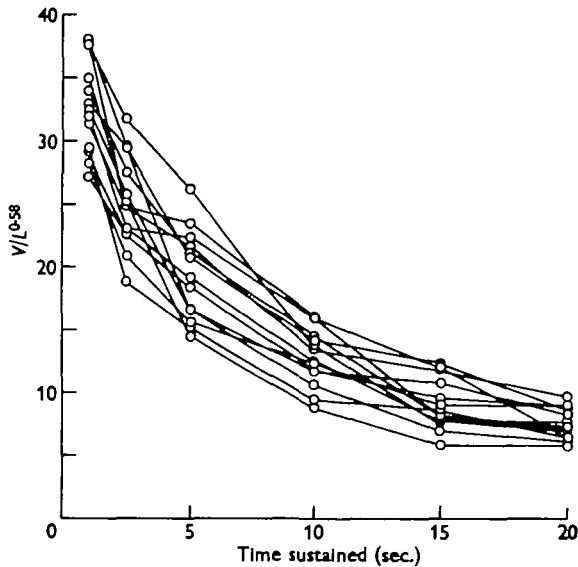


Fig. 2. Data shown in Fig. 1 with the speed in every case divided by the length of the specimen concerned raised to the power of 0.58.

(i) *The effect of exercise*

The fish studied in Bainbridge (1958, 1960) had various origins. Some, especially the smaller specimens, had been grown in tanks from eggs hatched in the laboratory; others, especially the larger specimens, had been obtained from dealers or were freshly caught in nature. During the experimental work all were kept for long periods in relatively small tanks (1 ft. × 1 ft. × 1 ft. 6 in.) without any vigorous circulation of the water. Casual observation of them during this period showed them to be at all active only on rare occasions, particularly while being fed. While apparently healthy in all respects they could not be considered to be 'in training' in the accepted athletic sense of the words.

The fish supplied by Mr Herbert, however, had been actively swimming at something like their normal cruising speed for about 12 months. At the beginning of Mr Herbert's experiments he found that, if they were made to swim against the maximum current immediately, specimens tended to lose condition somewhat and develop slightly tattered fins and other abnormalities; but if they were raised to their maximum speed gradually over a period of two or three weeks they showed no signs of distress. Their general good health and condition is amply attested to by the fact that during

the 12 months of swimming the mean length and weight of the specimens rose from 14.7 cm. and 43.4 g. to 24.5 cm. and 201 g. and none had died during the 1-year period of exercise.

It might thus be reasonably expected that any influence of prolonged exercise upon the accomplishment of these fish might show up in a comparison of the results reported in this paper with those reported previously. Fig. 3 consequently compares the mean of the values in Fig. 2 of this paper (white circles) with the mean of those depicted in fig. 5 of Bainbridge (1960) (black circles). The close correspondence of the values for

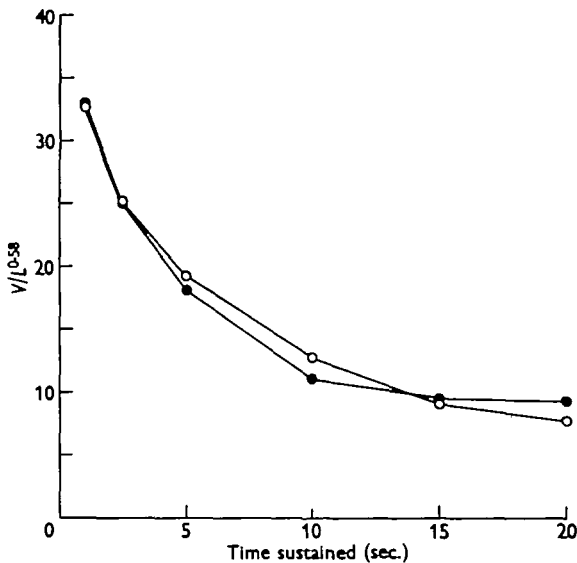


Fig. 3. Comparison between the mean of the results for the exercised fish shown in Fig. 2 (white circles) with the mean of results for unexercised fish taken from fig. 5 of Bainbridge (1960) (black circles).

all the time periods is at once apparent. For the 1.0, 2.5 and 15 sec. intervals they are almost identical and for the 5, 10 and 20 sec. intervals they are variously above and below one another. Far from showing any significant difference, the two sets of results confirm each other in a remarkable manner. It is difficult to escape the conclusion that the type of prolonged swimming that these fish have endured has in no way altered their ability to sustain bursts of swimming of different speeds.

The close correspondence shown in Fig. 3 might raise a suspicion that perhaps some physical characteristic of the apparatus is imposing an arbitrary uniformity on the results. This possibility has been most carefully considered and rejected. The generally variable behaviour of different individuals in the wheel, the nature of the records themselves, the consistency of the maximum performance of particular fish and the operator's ability to use the wheel in different gears and at different rates of acceleration all militate against this possibility.

(ii) *Variability amongst the fish tested*

As can be seen from Fig. 1 there is considerable variability amongst the recorded results from individual to individual. Even when the factor of length is removed, as in Fig. 2, there is still a considerable spread in the results. It was therefore considered worthwhile comparing the *best* performance for each separate time interval in Fig. 2 with the *best* performance for the corresponding interval in fig. 5, Bainbridge (1960). This is done in Fig. 4 where the white circles represent such results for the exercised fish reported in the present paper and the black circles represent those for the earlier

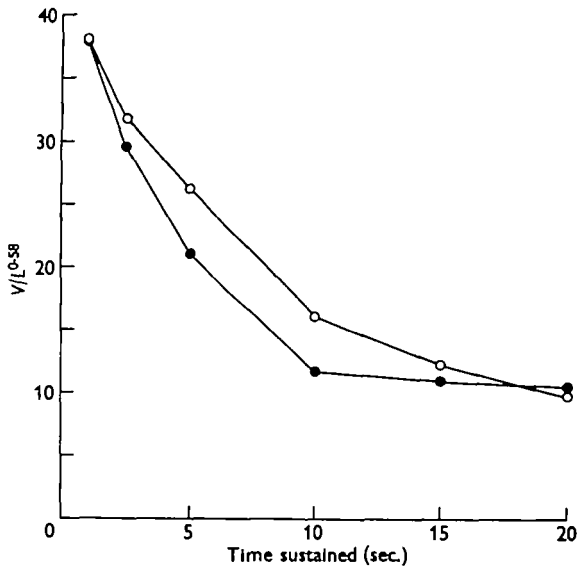


Fig. 4. Comparison between the best performance indicated in Fig. 2 for the exercised fish (white circles) and the best performance for unexercised fish (black circles) taken from fig. 5 of Bainbridge (1960).

(1960) results. It must be emphasized that the two curves shown in Fig. 4 are composite ones and do not represent two individual fish but the best recorded performance for each time interval. The points for the present experiments come from five different fish, those for the earlier ones from all the four fish tested.

It is apparent that for some of the time intervals a substantially better performance was obtained from the present exercised fish than from the earlier specimens. The biggest proportionate increase is for the 10 sec. period of swimming where the exercised fish show an improvement of 36% over the earlier ones. The mean percentage improvement in speed for all the periods is 11.0%. While this figure signifies a really better performance on the part of various of the exercised individuals above that of the earlier unexercised specimens it must be viewed in the light of the close correspondence of the two sets of mean results shown in Fig. 3. Because of the natural variability of the performance of different fish one would expect a greater spread in the results for the thirteen exercised specimens than in those for the four unexercised ones. The increased ability of the exercised fish shown in Fig. 4 must not therefore be

taken as necessarily demonstrating a significant improvement in the whole sample, but rather as more probably dependent upon the presence in it, by chance, of a few more active individuals.

The greater number of fish examined in the present work and the narrower limits of their size range further allow an investigation into the possibility of some specimens being naturally better at short distances of swimming and others better at longer distances. The likelihood of there being differences of this nature between different genera is shown in Bainbridge (1960), where the goldfish appears to be much better at sustained long-distance swimming while the trout and the dace are better at short bursts. Table 1 shows the measured speeds (expressed in terms of $L^{0.58}$) sustained

Table 1. *Detailed performances of eight individual trout (Salmo irideus) showing the differences between those fastest at 1 sec. of swimming and those slowest at this period*

(The speeds are expressed in terms of $L^{0.58}$.)

Fish	Duration of swimming burst in seconds					
	1	2.5	5	10	15	20
Fastest						
L	38.6	30.0	16.9	10.7	7.2	5.7
N	38.1	25.0	23.7	16.2	8.3	6.9
K	37.9	32.9	26.3	13.9	7.7	7.7
I	34.8	25.2	12.3	8.7	5.8	5.8
Slowest						
O	31.4	24.8	21.7	13.4	11.9	9.7
C	30.0	19.2	15.5	9.6	8.8	6.6
B	28.7	21.2	15.8	12.4	9.0	9.0
F	27.6	23.1	18.8	12.0	9.7	9.2
Fastest means	37.3	28.3	19.8	12.4	7.2	6.5
Slowest means	29.4	22.1	17.9	11.8	9.8	8.6

for the six different time intervals for: (1) the four fish with the fastest 1 sec. records (termed 'fastest' below); and (2) the four fish with the slowest 1 sec. records (termed 'slowest' below). The eight fish are arranged in the table in the descending order of their 1 sec. speeds. These data are summarized in the lower two lines of the table which give respectively the means for each period for the four 'fastest' and the four 'slowest' fish. These means show the four 'fastest' fish to be appreciably better performers not only at the 1 sec. period but also at the 2.5 and 5 sec. periods of swimming. At 10 sec. of swimming however they are only a little better than the four 'slowest' fish, and at both 15 and 20 sec. of swimming these 'slowest' fish are better than the four 'fastest' ones. The magnitude and reversal of these differences is shown more clearly in Fig. 5. The 'fastest' fish are better by about 27% than the 'slowest' fish at 1 and 2.5 sec. of swimming while the 'slowest' fish are better than the 'fastest' ones by about 25% at 15 and 20 sec. of swimming. These differences in Table 1 can readily be shown to be statistically significant. It would thus seem that amongst the fish tested some individuals are appreciably better at swimming for short distances and others at swimming for longer distances. These differences in ability account for a

certain amount of the spread apparent in Fig. 2. A parallel with the differences between sprinters and long-distance runners may be readily drawn.

An alternative explanation of this reversal of the difference between the 'fastest' and 'slowest' fish at long time intervals ought perhaps to be borne in mind. If the fish that give the 'fastest' results for short time periods do so because of some sensitivity to stimulus or because of nervous instability of some kind then they might be expected to expend a good deal of their available energy on rapid bursts as soon as

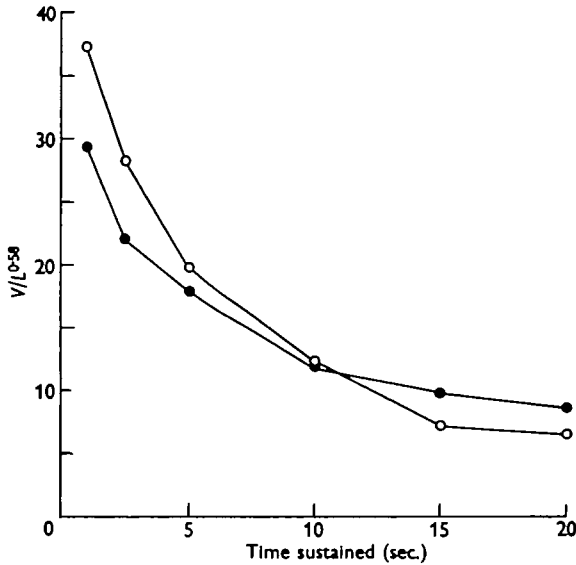


Fig. 5. Comparison between the overall behaviour of two groups of fish selected from the data in Fig. 2. White circles show the mean results for the four fish with the best performance of 1 sec. duration. Black circles show the corresponding results for the four fish with the poorest performance of 1 sec. duration. For further explanation see the text. Table 1 gives the detailed results for these eight fish.

recordings start to be made. They might then be less capable of doing well over longer periods of swimming. Conversely, if the 'slowest' fish at short intervals are less sensitive, or more phlegmatic in temperament, then they would expend less energy over the shorter bursts and consequently be able to swim rather faster over the longer periods. The results would thus be an indication of varying response to external stimuli rather than of any intrinsic difference in musculature or the rate of its power output. In this context it may be recalled that much human training for sprinting or long-distance running concerns emotional control and the acquisition of the power to regulate the rate of energy output of the musculature and apportion it according to the distance to be covered.

(iii) *Performance over longer periods*

Little attention was paid in Bainbridge (1960) to swimming performances for periods longer than 20 sec. The data there reported suggested that the trout, the dace and the goldfish had all perforce dropped to a cruising speed by the time they had been swimming for as long as 20 sec. and it was assumed that this speed could be

sustained for long periods. Figure 13 (Bainbridge, 1960) demonstrated the close correlation between results for the dace and those for the silver salmon, *Oncorhynchus milktschitsch*, reported by Paulik & DeLacy (1957) and covering periods of swimming from 20 sec. up to 200 sec.

While recording the performance of the present trout the opportunity was taken to allow some of them to swim for much longer periods in order to obtain an accurate assessment of their sustained cruising speeds. The means of these measurements are shown in Fig. 6 where speeds sustained for periods up to 5 min. of swimming are

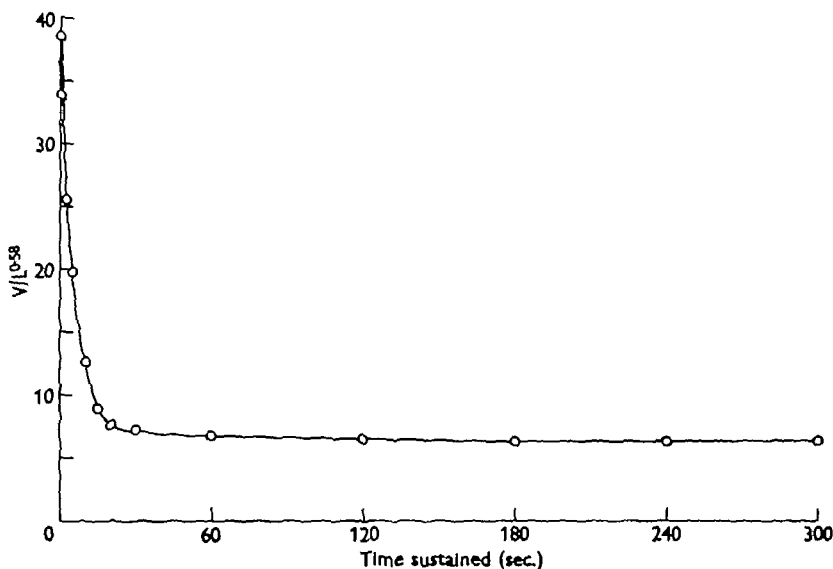


Fig. 6. Mean values for the relationship between speed and the length of time it can be sustained for periods of swimming from 0.5 sec. to 5 min. for eight trout (*Salmo irideus*) that had previously been exercised for 12 months by swimming continuously at 25 cm./sec. Speed is expressed in terms of body lengths raised to the power of 0.58. Measurements for these fish are also included in Fig. 1.

again expressed in terms of $L^{0.58}$. It was thought of interest also to include in this graph the mean of all the records for 0.5 sec. of sustained swimming. This interval was ignored in the earlier work as being of little more than academic interest. With fish of the size at present being tested however this short interval becomes of some consequence. Most of the specimens can travel about $1\frac{1}{2}$ m. in this time and such a distance must be assumed of importance in nature where it could well determine survival during a predatory attack or success in securing some particularly active prey.

The form of the graph in Fig. 6 emphasizes the extremely short duration of the most rapid bursts of swimming; it confirms that for these fish a speed of about 10 body lengths per second is the maximum that can be attained; and it shows that a cruising speed of the order of 2.0 lengths per second can be maintained by a specimen otherwise fairly fatigued, for periods up to 5 min. and probably for a matter of hours. The correspondence of the form of this Fig. 6 to that of fig. 13 of Bainbridge (1960) does not need to be discussed. It must, however, be remembered that these trout results

are expressed in terms of $L^{0.68}$ while the composite dace-silver salmon results of fig. 13 (Bainbridge, 1960) are expressed in terms of $L^{1.09}$. Only the form of the curves and not the absolute values can therefore be compared.

In order to obtain a satisfactory record for swimming sustained for even longer periods it was necessary to avoid excessive and sudden stimulation of the fish, and the ultimate cruising speed had to be approached by slow and gradual acceleration of the fish wheel over a period of 10 or 15 min. If this technique was not adopted the fish would indulge in a series of rapid bursts of swimming interspersed with periods of rest and no continuous record could be obtained. Once the fish was swimming steadily it could be made to exceed its presumably natural cruising speed by further accelerating the wheel. When this was done, however, the fish, after a few seconds of steady swimming at the higher speed, would show one or other of two responses. Either it would begin to fall back slowly and could only be kept in the standard position of observation by slowing the wheel or it would swim in short bursts much more quickly than the wheel was rotating, the bursts being separated by a few seconds of rest during which it might be carried back to about the original observation point. When this second type of behaviour occurred it was frequently necessary to accelerate and decelerate the wheel alternately and the fish often became confused, would only swim steadily at a much lower speed, and had again to be brought up to the cruising speed by slow and steady acceleration. These behavioural variations often made it possible to judge when the cruising speed had been reached.

Even with the most cautious approach to the cruising speed, however, some specimens could not be induced to swim steadily at even low speeds and a considerable degree of variability in behaviour might be found. Fig. 7A shows three attempts to bring trout E (26.8 cm. in length) up to the cruising speed.

Fig. 7A represents a continuous record of speed against time and is a plot of a series of 30 sec. readings taken from the oscilloscope record. The first attempt involving fairly rapid acceleration (from 15 cm./sec. up to 48 cm./sec. in about 4 min.) resulted in a complete disappearance of the optomotor response after about 10 min. of swimming. The second attempt, following immediately after the first one, was little more successful. The overall acceleration was more gentle (from 20 cm./sec. up to 50 cm./sec. in 6 min.) but this was again followed by a complete change in the fish's response and after 12 min. of testing no further swimming could be elicited at all. The third attempt was more successful. The fish was accelerated from 20 cm./sec. to about 60 cm./sec. in 11 min. and seemed settled to swimming at about 56 cm./sec. for a long period. However, more violent fluctuations, including a burst of 97 cm./sec. set in and finally, after 32 min. of swimming, the optomotor response vanished.

A fish with much more consistent behaviour is shown in Fig. 7B. This is trout H (22.5 cm. in length) which was accelerated to a speed of about 50 cm./sec. over a period of 30 min. It then appeared to be prepared to swim more or less indefinitely, with only minor fluctuations, about a mean of 51.5 cm./sec. It was followed for a total of 1½ hr. without showing any change in behaviour, and is more representative of the general response found in the fish at present being studied.

While a specimen was swimming steadily at its cruising speed it would often accelerate and decelerate spontaneously for a period of about 5 or so min. at intervals of about 20 min. These bursts of swimming may well correspond to the rapid dart

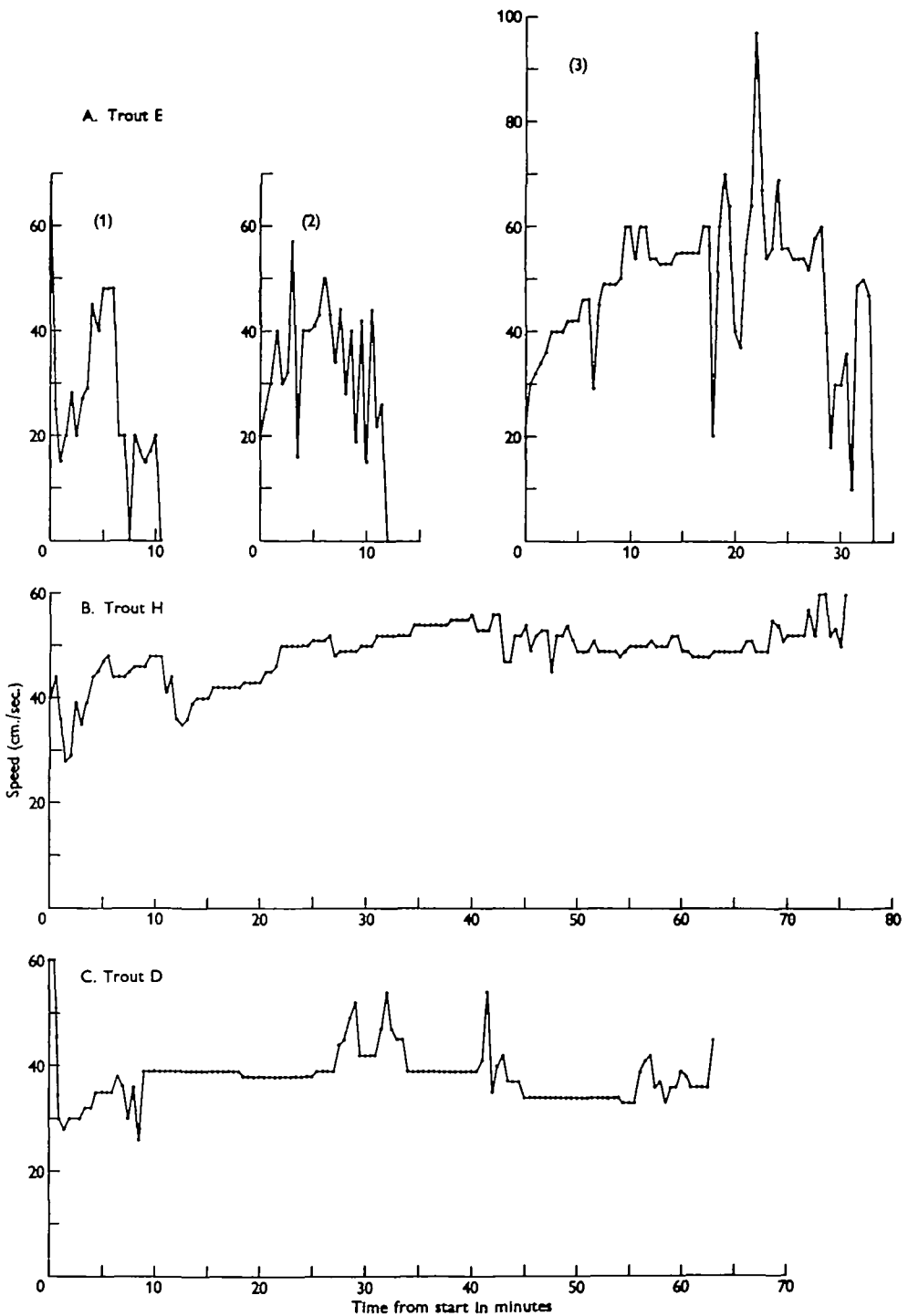


Fig. 7. Graphs showing speed of swimming plotted against time for three exercised trout (*Salmo irideus*). The half-minute values shown here are taken from continuous oscilloscope records of speed made with the 'fish wheel' apparatus, during attempts to establish cruising speed values. A, Three successive records for trout E (26.8 cm. in length), B, record for trout H (22.5 cm. in length), C, record for trout D (21.0 cm. in length). For further explanation see the text.

reported by Brett *et al.* (1958) for the sockeye and coho salmon and found by them to be characteristic of the first 20–40 min. of swimming in water of gradually increasing speed (although a 20 min. frequency in the variation of speed is also detectable in their fig. 4 throughout the entire period of swimming).

A still more continuous variation of the cruising speed could also be detected. This consisted of a more or less rhythmical acceleration and deceleration with a period of 10 or 20 sec. In extent this was about sufficient to move the fish ahead one body length and then draw it back by the same amount. Sometimes it was possible to observe that the cause was a rhythmical variation in the frequency of the tail beat but its magnitude was not usually sufficient for this to be detectable by the eye. This minor continuous modulation of the otherwise steady cruising speed has been observed in several other fish. In particular in the goldfish it results from a periodical cessation of beating of the tail. Here a burst of 7 or 8 beats of the tail is followed by a complete pause of a few seconds while the fish falls back more or less to the point at which it was first swimming. Fig. 7C shows a continuous record of speed against time for trout D (21.0 cm. in length). It illustrates the major periods of acceleration and deceleration but not the minor ones. At the end of this hour of steady swimming the fish was stimulated to give a burst of faster swimming. Within 30 sec. three bursts, one of 120 cm./sec. lasting 1 sec., one of 130 cm./sec. lasting 2 sec. and one of 70 cm./sec. lasting 3 sec. had been recorded. This retained ability to give fast bursts after so long a period at the cruising speed was found common to all the fish tested and perhaps confirms the suggestion in Bainbridge (1960, 1961) of a 'burst potential' determined in magnitude by one kind of physiological restraint and a cruising speed determined by a steady-state physiological restraint of another kind.

(iv) *Muscle content of the specimens*

Bainbridge (1960) shows how the proportion of propulsive trunk musculature relative to the total weight of the fish differs from genus to genus and also to a certain extent during the growth of a particular fish. The possibility of similar differences between exercised and unexercised fish was therefore also considered. Phillips, Brockway, Lovelace & Podoliak (1957) show a marked difference in the protein content of hatchery-reared and natural, wild fish; the percentage proportions of the body weights being 13.7 and 21.2 respectively. They assume, however, that these differences are dietary in origin and not the result of exercise, as many of their wild fish came from lakes where they would not necessarily receive more exercise than those fish reared in ponds.

After being fully recorded in the wheel, therefore, all the trout used in the current work were treated as previously (Bainbridge, 1960) in order to assess the propulsive trunk musculature as a proportion of total body weight. This involved weighing and measuring the fish and lightly boiling them to facilitate removal of the muscle. The muscle was dissected off and weighed in the wet state separate from the wet remains of the fish. Although it was possible with these larger specimens to separate the skin from the musculature, the skin was again included in the total weight of muscle in order to make the results exactly comparable with the previous ones.

The values for muscle, expressed as a percentage of total body weight, are depicted

in Fig. 8. They are shown (white circles) together with the values for the unexercised trout (black circles) used previously and taken from fig. 8 of Bainbridge (1960). It is at once apparent that there is no appreciable change in the amount of propulsive muscle as a result of the year of continuous swimming that the present specimens have undergone, a result one might have predicted from a consideration of the similarity of the swimming performances of all the fish concerned. These figures are, however, only gross weight of musculature, and no attempt was made to assess the protein and fat content in order to demonstrate differences of the sort reported by Phillips *et al.* (1957).

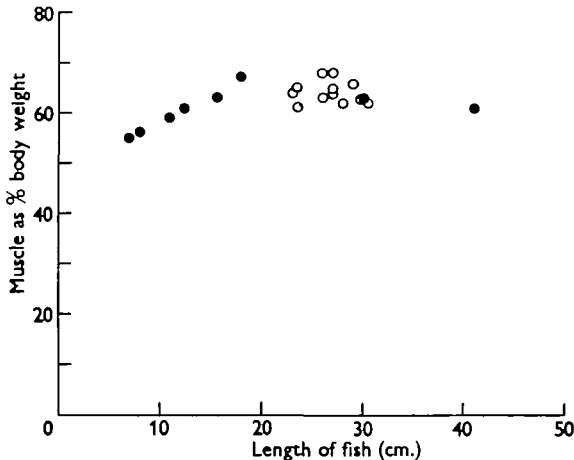


Fig. 8. Wet weight of propulsive trunk muscle as a percentage of total body weight plotted against length for various trout (*Salmo irideus*). White circles indicate the present exercised specimens; black circles indicate data for unexercised specimens taken from fig. 8 of Bainbridge (1960).

GENERAL DISCUSSION

Fig. 3 demonstrates unequivocally that the present experimental method does not reveal any significant difference between the mean behaviour of the exercised trout reported in this paper and that of the unexercised fish reported in Bainbridge (1960), when swimming for periods of up to 20 sec. in duration. There is, however, considerable variability amongst the specimens available and the best of the present fish are appreciably better than the best of the previous ones. These differences are shown in Fig. 4 and are greatest for periods of 2.5, 5 and 10 sec. of swimming. A closer analysis of the variability further reveals that some specimens are better at swimming for short periods and others at swimming for longer. These differences are seen in Fig. 5.

In view of some of the suggested differences between exercised and unexercised fish that are reported in the literature the initial identity of the means of these present measurements and of the earlier ones is perhaps puzzling. It may be doubted whether the sort of exercise the fish obtained in Mr Herbert's experimental tanks corresponded in any way to training in the athletic sense. Of the two sets of fish reported in the literature as being specifically exercised for experimental testing, Brett *et al.* (1958) had theirs swimming in water with a maximum relative speed of $3.6L$ or $7.9L^{0.68}$ at the periphery of a circular rearing tank, with an implication that the fish need not

spend all their time in the water of highest speed; and Hochachka (1961) had his exercised fish in water whose relative speed changed from $4.8L$ to $2.3L$ ($10.4L^{0.58}$ to $6.7L^{0.58}$) as the fish grew during the course of the experiment. Mr Herbert's fish, on the other hand, were only in water moving at from 1.5 to $1L$ (or $3.9L^{0.58}$ to $4.7L^{0.58}$) relative to the fish, again as they grew. Such a speed may be inadequate in effecting any change in the swimming ability of the fish concerned. It must be remembered however that the fish had to be raised gradually to this speed if they were not to go out of condition or become damaged; that most of the results suggest that a natural cruising speed of about $2L$ or $7L^{0.58}$ may be a normal one; and that the rearing or training conditions in all three cases allow a free slipping back of the fish relative to the water should it incline to swim more slowly. Under these circumstances the amount of activity Mr Herbert's fish underwent ought to be adequate to bring them into some sort of training.

The variability evident within the sample tested calls attention to the selective nature of some of the reported observations. Dow (1962), for example, found that only 23% of the fish attempting to swim up his flume were successful at the higher speeds that he measured. In any comparison it might therefore be more valuable to consider the differences between the extremes shown in Fig. 4 rather than the similarities between the means shown in Fig. 3.

Table 2. *Performances of six different trout (Salmo irideus) swimming continuously for a minimum period of 30 min.*

Fish	Length (cm.)	Speed (cm./sec.)	Duration (min.)	Speed in terms of	
				L /sec.	$L^{0.58}$ /sec.
N	30.0	48.9	77	1.6	6.7
F	25.3	41.6	104	1.64	6.4
F	25.3	46.3	47	1.8	7.1
H	22.5	48.6	76	2.16	7.9
H	22.5	51.5	46	2.28	8.4
D	21.0	38.1	63	1.8	6.5
B	26.2	43.5	60	1.8	6.6
E	26.8	48.8	32	1.9	7.3

Turning to consider the longer-term cruising speeds measured for the present exercised fish there are no comparable records for the trout in Bainbridge (1960) as those fish were not followed in the wheel for sufficiently long periods. The values for the present fish are summarized in Table 2 where all the results for periods of swimming of over 30 min. are given. The measured speeds are further expressed in terms of body length and (presumably a more accurate comparative figure but one not so immediately within the imaginative grasp) in terms of length raised to the power of 0.58. There is quite an amount of variability in these figures but the means are $1.9L$ /sec. or $7.1L^{0.58}$ /sec. In the absence of similar measurements for previous, unexercised trout these figures may be compared with other cruising speed measurements in the literature, although this must be done with circumspection in view of possible differences between species. Some such figures are summarized in Bainbridge (1960) where the general conclusion is reached that speeds of from three to six body-lengths per second can be sustained for long periods; but five records relating to either wild or

specifically exercised fish will be considered here in more detail. Dahl & Sømme (1936) have recorded an 11-day migration of a marked salmon that must have necessitated a continuous cruising speed for this period of at least $1.4L$ ($0.0L^{0.58}$). Harden Jones (1962) reports underwater echo-sounding records of free-swimming midwater herring in the North Sea indicating them as holding their own in tidal currents of 90 cm./sec. Sample fish were about 25 cm. in length so this figure corresponds to a speed of $3.6L$ or $13.9L^{0.58}$. The salmon record is of the same order of magnitude as the trout results reported in this paper; as a calculation it is, however, probably low as it assumes the fish swam from the point of release to that of capture in a more or less straight line. The herring record is about twice the present trout results.

Brett *et al.* (1958) report their 6.7 cm. exercised 'under yearling' (less than 1 year old) coho salmon as swimming at $5.0L$ ($11.2L^{0.58}$) but this is only for a period of 5 min. Although the fish were tested for 30-40 min. of swimming the mean speed for this period is not reported, but the exercised fish are said to have shown greater endurance at the higher speeds. In the exercising trough, as quoted above, the water moved peripherally at $3.6L$ or $7.9L^{0.58}$ and the fish may be assumed capable of swimming for long periods at this speed although they need not necessarily have remained in this region of highest speed.

More striking speeds are reported as recorded by Reimers (1956). Observing hatchery and 'stream conditioned' rainbow trout and wild brown trout of 6-8 in. in length swimming in a flume down which water was flowing at about 3 ft./sec. he found the first exhausted in 5-10 min., the second in 30 min. and the third in 60 min. Taking a mean fish length of 18 cm. and a velocity of 90 cm./sec. this gives a relative speed of $5.0L$ or $16.8L^{0.58}$, values slightly more than double those recorded in the present work.

Another figure of more or less the same order is contained in Kerr (1953). This is for wild king salmon (*Oncorhynchus tshawytscha*) of lengths from 1.25 to 1.89 in. taken from a nearby river. 112 such fish were all able to swim for 10 min. in water flowing at 1 ft./sec. but none was able to last for this length of time in water of 1.5 ft./sec. The first figure corresponds to $6.0L$ or $11.8L^{0.58}$.

Although these five sets of fish have been tested or observed under very different circumstances they were all natural and presumably healthy exercised specimens. Disregarding the varying periods of observation and the different species involved we may calculate a mean figure for their swimming performance as $4.2L$ or $12.5L^{0.58}$. The nature of the dependence of performance on length is almost certainly different in different species (Bainbridge, 1960), but whatever it is exactly it probably lies somewhere between L and $L^{0.5}$ so some sort of reliance can be placed on figures of this kind. They are to be compared with the present figures of $1.9L$ and $7.1L^{0.58}$. If the dependence is on length directly then the exercised wild fish appear about twice as capable of sustained speed as the present, presumably exercised, captive fish; if the dependence is on length to the power of 0.58 then the discrepancy is less and the wild fish are about 3/4 as capable again as the captive fish. The extent of these discrepancies is sufficiently great to demand some explanation other than the assumption that *Salmo irideus* is a much poorer swimmer than most fish.

In view of these differences it is consequently worth conjecturing how far one might expect captive unexercised and captive exercised or wild, presumably exercised fish

to differ. They might presumably differ physically and thus be capable of different absolute maximum swimming speeds or they might only differ behaviourally and, although physically capable of the same speeds, might normally not manifest this basic identity. Phillips *et al.* (1956) show chemical differences between hatchery and wild brook trout, particularly that wild trout contain less water and fat and more protein than hatchery-reared fish. These differences they attribute to diet, however, and not to exercise. There is no evidence that the differences derive from an increased proportion of musculature or muscle that differs in any way between the two types of fish. Hochachka (1961) showed that his exercised rainbow trout (*Salmo gairdneri*) had higher levels of blood haemoglobin and relatively larger hearts than unexercised fish. It was not possible to compare the present fish with those in Bainbridge (1960) in this respect, but as far as the proportion of total body weight comprising propulsive musculature is concerned both sets of fish were identical. It is possible on these grounds to suppose that unexercised and exercised fish might have identical performances for the shortest bursts of swimming, dependent only on gross mass of muscle, while the performances for larger periods, dependent upon respiratory rate and circulation, etc., might be different. Such an explanation could account both for the identity of the two sets of data in Fig. 3 and for the differences between the cruising speeds shown in Figs. 6 and 7 and those reported in the literature for wild fish.

This interpretation need not conflict with Hochachka's (1961) conclusion that greater buffering and oxygen-carrying capacity are the obvious advantages of the high haemoglobin concentrations in his trained fish. Although his initial observation was that trained trout took 4.1 min. to fatigue when being chased while untrained ones took 2.6 min., the striking differences he shows in oxygen consumption and muscle glycogen only became apparent after 1½–2 hr. Indeed the immediate rate of fall in muscle glycogen with exercise seems almost identical in his two sets of fish. It is only during recovery that the marked changes become apparent. Even the 25–30% greater utilization of glycogen in his trained fish is not measured until after 5 min. of activity, yet the real maximum bursts of swimming may be over in 5 sec. or so. Such observations would lead one to expect a similarity between trained and untrained fish in the shortest bursts of swimming but marked differences in long-term cruising. Black, Robertson & Parker (1961), summarizing present knowledge concerning carbohydrate metabolism in fish, re-emphasize the rapid depletion of muscle glycogen during severe activity. Such stores are reduced to one-half by the end of 2 min. of severe activity. One might easily expect so rapid an initial reduction to be identical in exercised and unexercised fish.

Observing different incidence of fatigue mortality in salt-water and fresh-water specimens of coho salmon, Parker, Black & Larkin (1959) have proposed the interesting theory that cessation of feeding in the adult fish migrating up into fresh water is of adaptive significance in reducing the likelihood of lethally dangerous fatigue. In the non-feeding freshwater fish the absence of much immediately available carbohydrate makes energy available only relatively slowly from stored fat and non-essential protein; activity and consequent lactic acid production is therefore limited and the dangerous effects of excess lactic acid accumulation are avoided. The feeding behaviour of experimental fish might thus have a marked influence on their swimming abilities.

While being tested in Cambridge many of the present fish were certainly not taking food as well and as frequently as they had been in Stevenage, probably as a result of the shock of travel and changed environment. Such temporary under-nutrition might well materially affect their cruising abilities rather than their shorter more rapid bursts of swimming. Black, Robertson, Hanslip & Chiu (1960) demonstrate a marked depletion in liver glycogen in 1½-year-old Kamloops trout starved for 7 days while the muscle glycogen and blood glucose, etc., remain high. Further, the food reserves utilized in long-distance migrations are probably fat and protein while the more 'labile' stores such as glycogen and other carbohydrates are used in times of stress (Drummond & Black, 1960).

The possibility of behavioural differences between captive and wild fish must, however, also be considered. Reimers (1956) comments on the 'sagacity' of the brown compared with the rainbow trout, pointing out that the former seek out dead or slack water in the experimental flume and rest there, while the rainbow trout exhaust themselves by remaining in the current. Vincent (1960) reports several pertinent behavioural differences between domestic and wild strains of brook trout, and further shows these differences to be hereditary. Throughout rearing the domestic strain was tamer and exhibited less fright than the wild stock; they had a surface response, moving up to the top of the rearing trough or a tall aquarium, and lacked a desire to conceal themselves. The wild stock on the other hand could stand greater concentrations of accumulated metabolites and a higher water temperature. Such behavioural differences could well influence the extent of the response of particular fish to the more or less uniform conditions of stimulus in the wheel. The two lots of fish tested in 1960 and at present, despite their different origins and history of exercise, were both from normally captive stocks. Perhaps truly wild fish would behave differently. Vincent (1960), testing 1522 fish by swimming them to exhaustion in currents from 0.3 to 3.0 ft./sec., was able to show significant differences in stamina between domestic and wild strains of the brook trout (*Salvelinus fontinalis*) despite the fact that they were reared from eggs under identical circumstances. The wild-strain fish were able to swim for about half as long again as the domestic ones for periods of swimming ranging from 50 to 200 sec. depending upon the size and age of the fish.

If a stationary fish in the wheel responded to a slight rotation by exhibiting an optomotor response then no further stimulus was given. If a satisfactory response was not forthcoming then a mild electric shock was administered and would usually elicit swimming followed by suitable optomotor behaviour. Continued use of a shock brought on fairly quick habituation and even with an increasing voltage no further satisfactory swimming would be induced. In contrast to this normally mild motivation experienced in the wheel, the type of stimulus used in most of the tests by others on exercised fish has been relatively violent, involving either touching the fish or even nipping it, or bringing it into violent physical contact with a gauze or other barrier below it in the test flume. In contrast to this violently increasing stimulus associated with diminishing activity, the fish in the wheel experience a diminishing optical stimulus as soon as they slacken speed because the wheel itself has to be slowed at once in order to keep them at the locus of observation and away from the closing doors. The rates of continuous swimming measured in the wheel may therefore be thought of as much more natural and dependent upon the fish's normal response to mild

motivation in contrast to the rather forced response under other experimental conditions. Even in the rotating open trough technique of Fry & Hart (1948), also used by Brett *et al.* (1958), the optical stimulus automatically increases when the fish begins to lose station although the latter can, in the absence of an electric barrier, fall back indefinitely without any more violent stimulation. Such considerations therefore incline me to the opinion that the cruising speeds measured in the wheel and reported in this paper are natural ones that can be elicited with moderate motivations while speeds of possibly double their value may be maintained for long periods under more violent stimulus or by fish that are, because of their heredity or wild upbringing, more responsive to moderate stimuli.

In this context the observation is relevant that fish cruising in the wheel are still capable of quite rapid bursts of swimming even after, say, an hour at the cruising speed. Such bursts could clearly be of selective significance in nature were a fish keeping station in a river. Under these circumstances the burst might be either exploratory or evasive of predators that could otherwise more easily catch the relatively stationary fish.

The eliciting of the maximum possible response from a fish under any particular circumstances is thus a matter of both the degree and nature of the motivation and also of the responsive state of the fish. There is no ground for supposing that the simple optomotor reaction will elicit the maximum possible cruising speed but it might well do so in a fish sufficiently responsive. The meaning in behavioural terms of the necessity for gradual and prolonged acceleration in inducing an optomotor response will be examined at some future time, as will the eventual breakdown of this response if the particular natural cruising speed of the moment is exceeded. Some further work must also be done on the influence of exercise on uniform stocks of fish both from the behavioural and from the physical point of view. In such work sufficiently rigorous exercise must be imposed and a more natural form of this would probably involve steady swimming coupled with intermittent very high forced speeds.

SUMMARY

1. A number of trout (*Salmo irideus*) were kept continuously swimming for a period of 12 months in experimental tanks in which the water was made to rotate at a mean speed of 25 cm./sec.
2. These fish become available for study in the 'Fish Wheel' and measurements were made of the maximum speed they sustained for periods of swimming of different duration.
3. For bursts of swimming of up to 20 sec. duration the mean accomplishments of these fish were identical with those of the unexercised trout studied previously.
4. Considerable variability was found amongst the specimens tested and the best of the present exercised fish were appreciably better than the best of the previous unexercised ones. The biggest improvement was 36% at the 10 sec. period of swimming; the mean percentage improvement for all periods was 11%.
5. Some specimens were found better at swimming for short periods and others at swimming for longer.
6. In the absence of comparable figures for the earlier fish, the measurements of

cruising speeds sustained for periods up to $1\frac{1}{2}$ hr. were compared with other figures in the literature and found to be about half some of these for wild fish.

7. The implications of the results are considered and two interpretations stressed. First, it is assumed that there is a real identity of accomplishment for short periods of swimming, values being determined perhaps solely by gross mass of muscle; while for longer periods of swimming differences dependent upon respiratory rate etc. may well occur. Secondly, for such longer periods the discrepancies reported here may well be accounted for by differing degrees of stimulus and behavioural response under varied experimental conditions.

I am much indebted to Mr D. W. M. Herbert for initially offering me his control stock of exercised fish and for keeping them in an exercised condition during the progress of the experiments; and to Sir James Gray, F.R.S., for his sustained concern with my work.

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