

## SPEED AND STAMINA IN THREE FISH

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## INTRODUCTION

The speeds already reported (Bainbridge, 1958*a*) as attainable by various fish after measurement in the 'fish wheel' were calculated from ciné film records of swimming over a minimum distance of 1 m. Such figures give little indication of the length of time for which a particular speed can be sustained. The 29.3 cm. trout reported as travelling at 320 cm./sec., for example, had to swim at this speed for only  $\frac{1}{3}$  sec. in order to qualify for inclusion; while the lowest speeds reported, of the order of 10 cm./sec., required only 10 sec. of swimming.

A variety of reasons make it desirable to know how long particular speeds can be sustained by fish of different sizes. The most efficient design of fish-passes, for example, particularly those demanding periods of violent activity separated by periods of rest, could be dependent upon parameters of this kind. The speed at which trawls and other fishing devices should be manipulated, and the precise design of the net opening and the relative positions and lengths of headline, ground-rope and tickler-chain could also profitably be examined in the light of such information. Finally, a proper assessment of the physiological problems associated with swimming and the relationship between power output, drag and speed and a consideration of the degree of correspondence between fatigue in fish and other animals, are all dependent upon a precise knowledge of the ability of fish to sustain particular speeds of swimming.

It has already been briefly reported (Bainbridge, 1958*b*) that the duration of a burst of swimming decreases rapidly with increase in the speed attained. The lower speeds, such as can be sustained for periods of the order of hours, have commonly been termed 'cruising speeds'. Some values for such basic speeds are already available in the literature. Magnan's (1930) figures for a variety of fish should probably be counted as of this nature. The average of his measurements for seventeen different common species, mostly marine, is  $3.2L/\text{sec.}$ , where  $L$  is the body length. Fry & Hart's (1948) figures for goldfish (*Carassius auratus*) are based on periods of swimming of 20–25 min. and average at  $6.4L/\text{sec.}$  Davidson (1949) gives  $4.0L/\text{sec.}$  for salmon (*Salmo salar*) and Radcliffe (1950)  $3.4L/\text{sec.}$  for goldfish tested over 25–30 min. Similar, but slightly lower, values can be calculated from information about the long-range migrations of fish.

More recently several workers have deliberately set out to relate speed to endurance. Paulik & DeLacy (1957) give values for sockeye salmon (*Oncorhynchus nerka*), silver salmon (*O. milktschitsch*) and steelhead (*Salmo gairdneri*) tested in a

rotating tank of water. With the speed of the tank gradually increasing, individual fish were observed until they began to lose laps. The speed preceding this was then recorded as one that could be maintained for long periods. The mean value for fifteen sockeye averaging 20 in. in length was 3.0L/sec.; for nine silver salmon averaging 22 in. in length 3.4L/sec. and for ten steelhead, averaging 25 in., 3.3L/sec. These may be taken as cruising speeds. In another series of experiments silver salmon and steelhead were tested to see how long they could swim before exhaustion in water velocities ranging from 4 to 10 ft./sec. These results, on fish about 24 in. long, give accurate values for sustained swimming lasting up to about 5 min. No observations were made over periods less than about 20 sec., but the results accord well with the figures reported in this paper for periods from 1 to 20 sec. and are discussed later.

In a second paper Paulik & DeLacy (1958) make it clear that the ability of sockeye salmon to swim persistently at various velocities is greatly reduced as a result of previous exertion. They demonstrate significant changes in the length of time that fish will swim at certain selected current velocities as a result of their migrating some 350 miles up the Columbia river and climbing to a height of 1800 ft. The maximum mean time swum at the lowest velocity (6.6 ft./sec.) in a straight flume was 196.4 sec. and this figure, for fish of mean length *c.* 20 in., represents a speed of 4.0L/sec.; their highest value, 9.4 ft./sec. for 64.9 sec., converts to 5.6L/sec. and both these values seem intermediate between long sustained cruising speeds and the bursts now being measured.

Brett, Hollands & Alderice (1958) have made a study of coho salmon (*Oncorhynchus kisutch*) and sockeye in a rotating circular chamber, relating cruising speed to temperature. Defining cruising speed as the maximum speed maintained for 1 hr. under strong stimulus, their values for 5.4 cm. long coho salmon at 20° C. is 30 cm./sec. (5.5L/sec.); for similar fish at about 0° C., 6 cm./sec. (1.1L/sec.); and for 6.9 cm. sockeye, 35 cm./sec. (5.1L/sec.) and 12 cm./sec. (1.7L/sec.) at the same two temperatures. They further show that these fish, if trained and exercised, will give significantly better performances.

Finally, Blaxter & Dickson (1959) give figures for the 'average maximum speeds' of a variety of marine fish tested in flowing and still water of various kinds. Their criterion for the inclusion of results was that the fish swam at least ten times their own length. No record of the duration of these tests is given, but Mr J. H. S. Blaxter has been so kind as to inform me that the speeds reported were usually sustained for 2-5 sec. Sea trout (*Salmo trutta*) of 12 in. in length are given as travelling at *c.* 10 ft./sec. (10.0L/sec.) and herring (*Clupea harengus*) 10 in. in length at *c.* 5 ft./sec. (6.0L/sec.). 20 in. cod (*Gadus callarias*) are slower at only 2.41L/sec. but this is probably a more sustained speed. Swimming various fish to exhaustion, the authors express further results in total body lengths travelled. The maximum of these is 1121 lengths for a batch of herring from 20 to 25 cm. in length. I am further informed that the average time for this performance was 13 min., giving a mean speed of 1.5L/sec. This is necessarily somewhat low because of turning time at the ends of the trough in which the tests were made.

Messrs R. W. McCauley and J. F. Skidmore of Ontario have also kindly provided me with hitherto unpublished data, on the cruising speed of the spawning phase of the sea lamprey (*Petromyzon marinus*). For 16 in. fish at 2° C. their figures give 0.57L/sec. and at 15° C., 0.89L/sec. Each of these values derives from the mean result for ten animals tested in Fry & Hart's (1948) original chambers.

Mr W. Muir of Garve, Ross-shire, has further given me figures obtained in a most ingenious manner by timing shoals of migrating salmon over a measured distance. This was done while watching them through field glasses from a height above the water during the direction of fishing operations. The mean value for fish of 24 in. mean length, swimming over a distance of 100 yards, is 2.0L/sec. It is clear from Mr Muir's report that this speed could be maintained for long periods of time. When startled the fish would spurt up to 4.2L/sec. for 30 ft. or so.

All the figures given above are of the same order of magnitude and it would seem substantiated that most of the fish so far considered can sustain speeds of the order of three to six times their body length per second for long periods. However, none of the techniques used to produce these results permits the accurate recording of sudden bursts. The fish wheel, allowing as it does for the almost instantaneous acceleration or deceleration of the water in which the fish is swimming, lends itself particularly to a study of the more violent periods of activity below about 30 sec. duration.

#### EXPERIMENTAL METHOD

In order to facilitate the continuous recording of speeds over longer periods than hitherto the apparatus (Bainbridge & Brown, 1958) was modified by the addition of a permanent recording device and the filming of the fish itself was dispensed with. A standard Cossor double beam cathode-ray oscilloscope was linked to the electrically operated speed meter of the fish wheel, the voltage supply utilized being directly dependent upon the speed of rotation of the wheel. One spot of the oscilloscope tube was thus used as a direct indicator of the speed at which the fish was swimming and the other as a time marker. A continuously running paper-film camera attached to the oscilloscope then allowed a permanent record of speed against time to be made for any period of swimming. Such records are shown for a goldfish and a dace in Fig. 1.

In a typical experiment the wheel is filled with water at the recorded room temperature and a fish is introduced. After a period of 5-10 min. for settling down in the apparatus the fish is induced to swim and the wheel is rotated to keep him stationary at the observation point. Prolonged periods of steady swimming and shorter faster bursts can be variously induced by judicious use of a mild electric shock introduced into the wheel through a ring commutator and four diametrically placed brass plate electrodes on the floor of the Perspex tube. The shock is manually controlled through a pressure switch. Its intensity is regulated by means of a Variac; low voltages are generally used for large fish and higher voltages for smaller ones. Administration of the shock usually produces a burst of forward swimming of velocity very roughly related to the intensity of the shock. Such a burst is

followed by rotation of the wheel and is thence recorded on the oscilloscope. Occasionally a fish responds to the shock by stopping swimming or by turning round. Such specimens are not always consistent in their response and on other occasions may be more tractable. Low steady speeds are readily induced by rotating the wheel a little, so that the stationary fish is carried backwards over a striped background. The common optomotor response then results in a steady swimming to keep station and speed can be increased until the fish just starts to fall back. In contrast to the previously reported speed/frequency records, where the fish itself was photographed, the accuracy of the whole method on this occasion is entirely dependent upon keeping the fish stationary relative to the observer. At all times care has been exercised to ensure that this condition has been fulfilled.

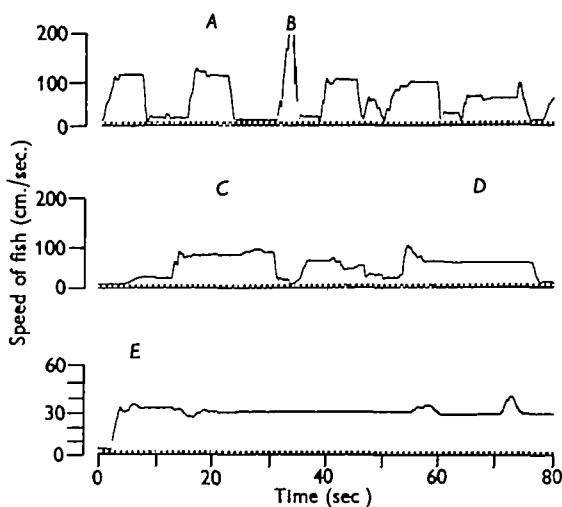


Fig. 1. Oscilloscope records of the speed of swimming of goldfish and dace showing *A*, a 5 sec. burst at 110 cm./sec., *B*, 1 sec. at 200 cm./sec., *C*, 15 sec. at 60 cm./sec. and *D*, 20 sec. at 50 cm./sec., all by a 13.5 cm. goldfish. *E* shows a 10.0 cm. dace swimming at about 30 cm./sec. for a longer period.

A particular fish is experimented with in this fashion over a period of several days, attempts being made to accumulate records of bursts of swimming of a variety of speeds and duration. The oscilloscope traces are then analysed to determine the maximum speeds that were sustained for a series of arbitrarily selected periods of 1, 2.5, 5, 10, 15 and 20 sec. These were chosen because of the relatively rapid initial fall off over the first few seconds and because by 20 sec. the low steady cruising speed seems generally to have been reached. In order to ensure that the absolute maximum speed has been recorded for any particular time period, it is necessary to repeat the observations again and again. Inspection of the records will eventually make it clear that a maximum has been reached, and such a speed can finally be attained on a good many occasions but never exceeded. Confidence in the experimental technique is further increased by considering the effect of size upon the results. From this it is clear that, while there is a general dependence upon size, individual specimens amongst a group of one size and a single species

have their own idiosyncrasies. Some will be more lethargic than others and will consistently give a poorer performance over a long series of observations to the extent of concealing somewhat the relationship with size (see below).

The oscilloscope traces are analysed using a transparent Perspex scale transferred from a calibration trace made with the wheel running at a series of convenient known steady peripheral velocities. This scale can be laid over the experimental trace and the parameters of any burst of swimming readily determined. No measure has been made of the rapidity of acceleration or deceleration. The speeds reported have been sustained at a constant level for the period of the observation. If the speed fluctuated during the period then the value accorded to that burst is the minimum reached during the period and not the average. This average would generally be only slightly higher than the figure recorded. Whenever possible absolutely steady speeds for the period involved have been selected. Typical readings, taken from the records illustrated, are given in the caption to Fig. 1.

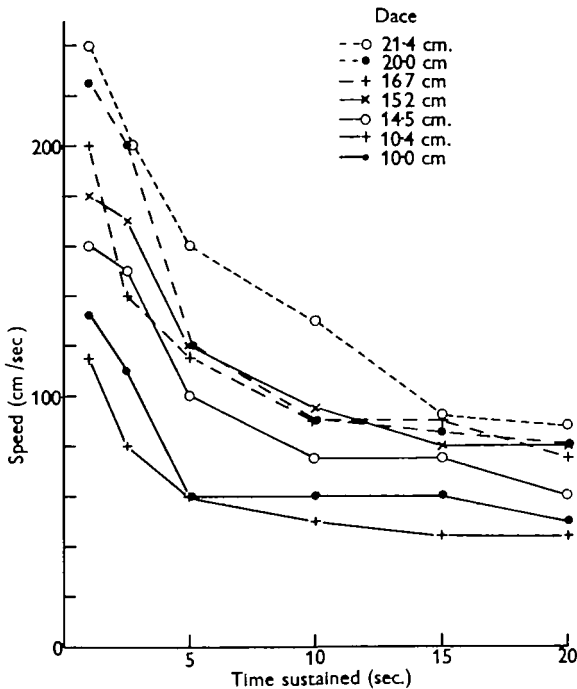


Fig. 2. Relationship between speed and the length of time it can be sustained for seven dace (*Leuciscus leuciscus*) ranging in size, as shown, from 21.4 cm. to 10.0 cm. in body length.

## EXPERIMENTAL RESULTS

### *The dace, Leuciscus leuciscus*

The first results to be examined relate to a series of seven dace ranging in length from 21.4 to 10.0 cm. Fig. 2 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.

Examination of the points for the 21.4 cm. specimen shows a rapid decline from a speed of 240 cm./sec., which is maintained for only 1 sec., down to 130 cm./sec. when the burst lasts for 10 sec. and 90 cm./sec. when it lasts for 20 sec. The flattening nature of the curve shows that a speed of 80 or 90 cm./sec. is probably one that can be maintained for some time. With the 10 cm. specimen the capacity to sustain speed declines with even greater rapidity, so that by 10 sec. of swimming the fish is already reduced to what is probably its cruising speed.

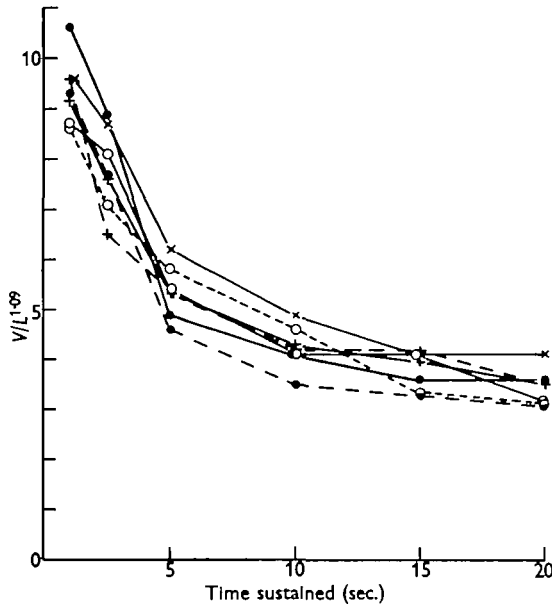


Fig. 3. Data shown in Fig. 2 with the speed in every case divided by the length of the specimen concerned raised to the power of 1.09. Symbols as in Fig. 2.

The figures for the specimens intermediate in size show the same type of relationship. Assuming that ability to maintain speed is some function of the length of these different sizes of fish, it is possible to express this relationship in the form  $V/L^\alpha = F(T, spp.)$ , or  $\log V = \alpha \log L + K_{T, spp.}$ , where  $V$  = velocity,  $L$  = length,  $F$  = a function peculiar to one species for a particular time interval. A plot of the logarithm of the velocity against the logarithm of the length, for the results for different sized fish at one particular time interval, should thus give a straight line whose slope is the value of  $\alpha$ . Repetition of this operation for the various time intervals gives six values of  $\alpha$ : 1.03, 1.15, 1.33, 1.11, 1.0 and 0.93 for the dace; the mean of these is 1.09.

Fig. 3 shows all the dace results of Fig. 2 treated on the assumption that the ability of different fish to maintain speed is dependent upon their length raised to the power of 1.09. The values of speed have in each case been divided by the size of the specimen, measured from the tip of the snout to the most posterior part of the tail, raised to the power of 1.09. These transformed values are again plotted

against time sustained and, as can be seen, give an acceptable correlation. The implications of this are considered later.

There is, however, a certain inconsistency in the correlation with size. The 10.0 cm. fish, for example, is substantially better in its performance than the 10.4 cm. specimen. This difference remains despite determined efforts to extract a better performance from the slower specimen. It may be accounted for by the possession of a more phlegmatic temperament or perhaps by the one fish being in poorer condition than the other. All the dace studied were born in the wild, but had been in captivity in roomy tanks for periods of months. There is no reason to suppose that they were in different condition as a result of immediate environmental influences.

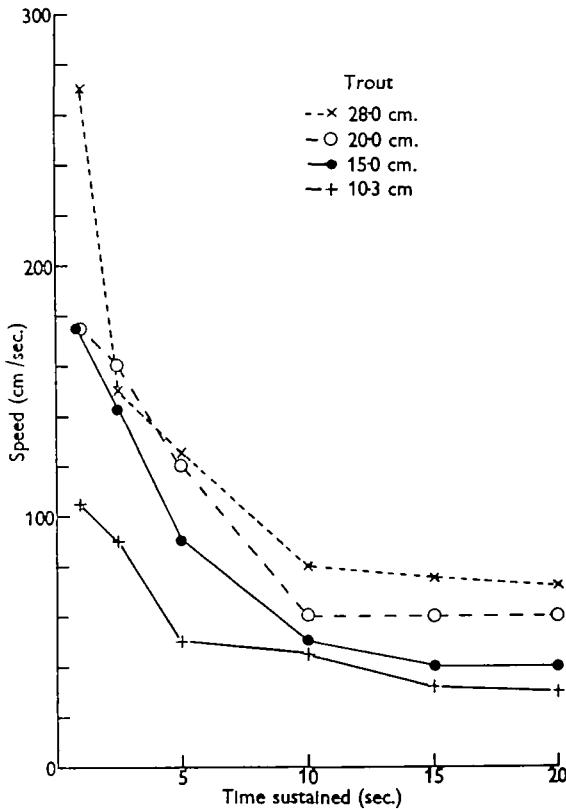


Fig. 4. Relationship between speed and the length of time it can be sustained for four trout (*Salmo irideus*) ranging in size, as shown, from 28.0 to 10.3 cm. in body length.

#### The trout, *Salmo irideus*

Fig. 4 shows comparable results for four trout ranging in size from 28.0 to 10.3 cm. The same general form of the relationship between speed and the ability to sustain it is apparent. The spread of the observations is slightly greater with the greater size of the biggest fish. This specimen sustained 270 cm./sec. for 1 sec. and 72 cm./sec.

for 20 sec. The smallest fish, 10.3 cm. in length, sustained 105 cm./sec. for 1 sec. and only 30 cm./sec. for 20 sec.

Treatment of these results in the same manner as for the dace, to determine the nature of the relationship with length, gives the following values of  $\alpha$  for the six time intervals: 0.71, 0.36, 0.70, 0.43, 0.65 and 0.65; the mean of these is 0.58. The trout records are thus shown in Fig. 5 with each value of speed divided by the length of the specimen raised to the power of 0.58. The correlation is particularly good for the lower values of speed. A direct comparison between these transformed results and those for the dace is not possible because two different powers of length have been used. Such a comparison is reserved until the goldfish figures have also been considered.

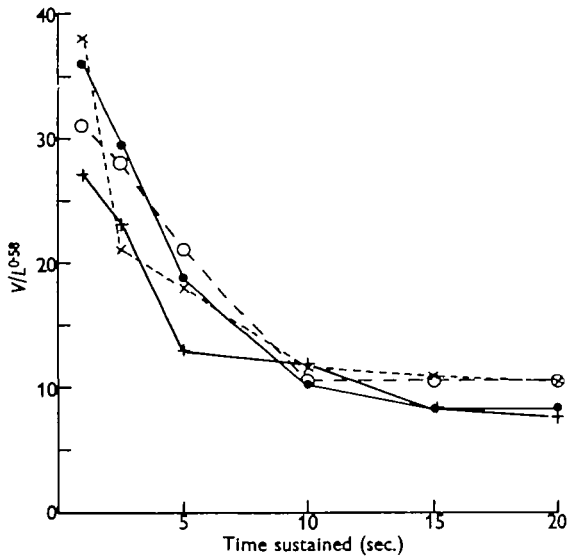


Fig. 5. Data shown in Fig. 4 with the speed in every case divided by the length of the specimen concerned raised to the power of 0.58. Symbols as in Fig. 4.

#### *The goldfish, Carassius auratus*

Fig. 6 shows values for a series of eight goldfish ranging in size from 21.3 to 6.7 cm. The general form of the relationship is as before, although the decline from the highest speeds appears to be slightly more gradual. Determination of the value of  $\alpha$  as previously gives six figures: 1.06, 0.74, 0.76, 0.70, 0.48 and 0.50; the mean of these is 0.71. Fig. 7 shows the goldfish records of Fig. 6 with the values of speed divided by the length of the specimen raised to the power of 0.71. The correlation is again seen to be good.



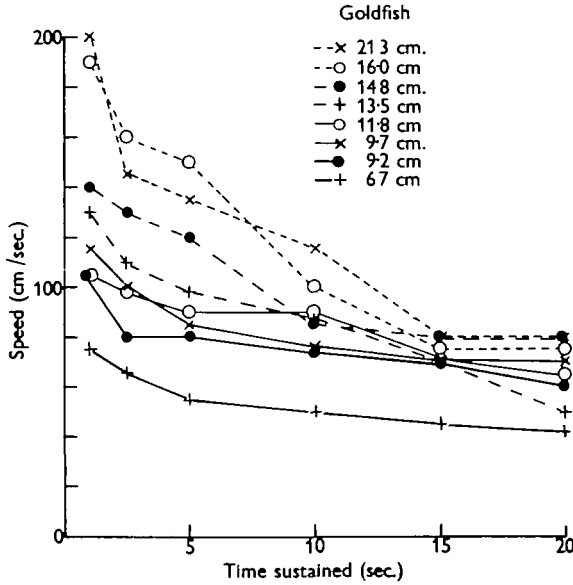


Fig. 6. Relationship between speed and the length of time it can be sustained for eight goldfish (*Carassius auratus*) ranging in size, as shown, from 21.3 to 6.7 cm. in body length.

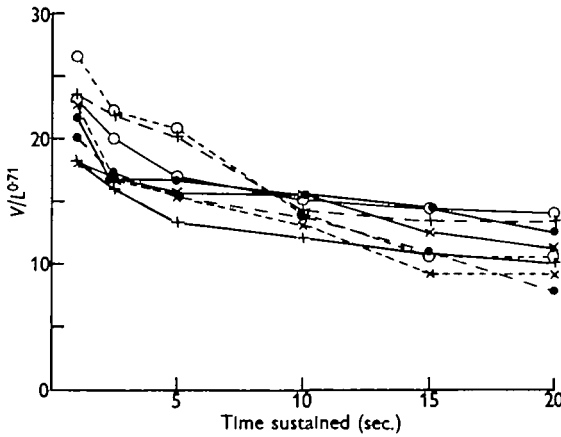


Fig. 7. Data shown in Fig. 6 with the speed in every case divided by the length of the specimen concerned raised to the power of 0.71. Symbols as in Fig. 6.

DISCUSSION

Consideration of these experimental results reveals the complex interaction of various factors. In order to lend clarity to the argument the discussion has therefore been divided into several sections in which are considered separately: first, the effect of the size range in each species of fish tested; secondly, the effect of interspecific differences; thirdly, the nature of the common relationship between time sustained and speed in all the species; fourthly, the correlation of the present results

with previous work, and lastly, some possible practical applications of the experimental observations. It becomes necessary from time to time to introduce further experimental data. This is done where the argument demands it rather than earlier, under the heading of experimental results.

(1) *The effect of size*

Neglecting for the moment the exact form of the relationship between speed and duration for the different species of fish, we shall first consider the nature of its dependence upon size in specimens of different length. The three empirically determined values for the results obtained are: dace,  $L^{1.09}$ , trout,  $L^{0.58}$  and goldfish,  $L^{0.71}$ . Of these the second two are not found to be significantly different when a  $t$  test is applied to the values and their standard errors; but the dace does differ significantly both from the goldfish and the trout. If the same relationship is assumed to hold for both the trout and the goldfish the mean value is  $L^{0.65}$ .

In the present state of our knowledge it does not seem possible to provide a complete theoretical explanation of such a variable dependence upon length in different species. At least four factors would seem directly concerned: (a) the degree of non-isometric growth may vary between species, different sizes of fish being thus differently equipped with muscle; (b) the roughness of the surface may differ and have different proportional effects on laminar/turbulent flow at different sizes; (c) the fineness ratio and body form generally may vary with similar effects; and (d) the influence of Reynolds number must be considered. The first factor would influence the different amounts of power available to different sized fish, the remainder would influence the amount of drag encountered while moving through the water. Combined, these would necessitate different efforts at different speeds and hence result in variable staying power. They will each be considered in turn.

(a) *The effect of non-isometric growth*

Basically for a series of specimens of one species showing isometric growth, one can argue along various lines in order to determine how speed and the ability to sustain it may be related to length. In general, we may assume that the volume of the body and hence the proportionate amount of muscle increases as the cube of the length, while the surface area increases as the square of the length. From these two assumptions D'Arcy Thompson (1917) deduces that velocity must be proportional to  $L^{0.5}$ . Making the further assumption that power is limited not by volume of the muscle, but by the surface area of the lungs or gills, he reaches an alternative conclusion that maximum velocity is constant and not related to length at all. Hill (1950) develops this same idea, adding the concept of heart capacity and blood flow through vessels whose cross-sectional area increases as the square of length, and also arrives at the conclusion that maximum speed is independent of length. While respiratory factors may well be of some limiting consequence, it is clear from the present results that neither of these two simple relationships holds for the fish so far examined.

(i) *Relationship of weight and length.* The first modification of the above simple theory concerns the assumption that the mass of muscle is proportional to  $L^3$ . Le Cren (1951) makes it clear that the cube law concerning the weight of fish of different lengths is rarely obeyed, the exponent  $n$  in the formula  $W = aL^n$  usually lies between 2.5 and 4.0 and can vary during the life of the fish. There is no reason to suppose that this deviation from 3 concerns only parts of the body other than muscle; although the relative weight of the gonads does change considerably in association with the breeding cycle. All the fish used in these experiments were therefore weighed and measured and  $n$  was found to be 3.2 for the goldfish, 3.0 for the trout and about 2.8 for the dace. These values, unfortunately, in no way clarify the problem. The goldfish with the most favourable muscle/length ratio has the intermediate value for dependence of staying power upon length ( $L^{0.71}$ ); the dace, with the least favourable muscle/length ratio has the highest value for staying power ( $L^{1.08}$ ). In any case a disproportionate increase in bulk with increase in length means a corresponding increase in surface area and hence in the value for total drag. The opposing effects of these two tendencies might be to some extent mutually cancelling.

(ii) *Relative percentages of muscle.* A deviation from the principle of isometric growth that would not be self-corrective in this way would be a change, within a series of specimens of otherwise normal weight/length relationship, in the quantity of muscle relative to the remaining skeletal, digestive, nervous, etc., tissue of the fish. Information concerning such a change does not seem readily available in the literature, although Jacquot & Creac'h (1950) give references recording the *mean* proportion of muscle and its chemical constituents in many different edible fish. Reay, Cutting & Shewan (1943) give a figure for only one of the fish we are studying—trout—with 63% of muscle including skin. This accords well with the values reported below. Their figure of 33% for the perch is also interesting in comparison with our goldfish values.

All the propulsive trunk musculature was dissected from a series of dace, trout and goldfish. Some of the fish were freshly killed and lightly boiled to facilitate removal of the muscles, others had been fixed in formalin some time previously. All were weighed and measured both while fresh and after treatment. The different types of treatment had no determinable effect on the final results. The muscular and remaining components were weighed separately in a wet state after removing excess water by exposure in a standard manner to reduced pressure with a filter pump. It did not prove possible to separate the skin readily in all cases and its weight is therefore included with that of the muscle. From cases where the separation was made this would seem to introduce a consistent error of the order of 2%. From the figures the percentage wet weight of muscle, relative to the wet weight of the total fish, was calculated for each specimen. The results are summarized in Fig. 8 which demonstrates a general increasing trend in the proportion of muscle to total body weight. With increasing size, from the smallest specimens measured up to about 17.5 cm., there is an increase of about 10–15% in the relative amount of muscle in all species studied. Specimens within this size range form an

important proportion of the fish tested in the wheel. At a length of about 17.5 cm. the percentage of muscle appears to become roughly constant, although still showing some variability. The average proportions at this constant level are different for each of the three species and the significance of this is considered later.

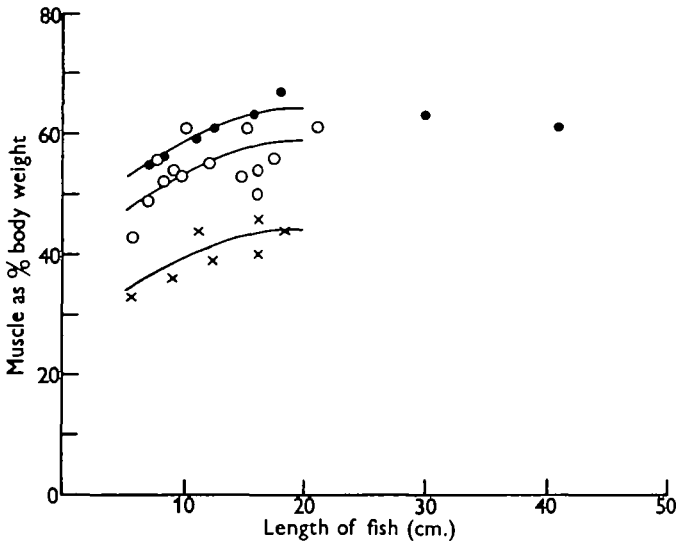


Fig. 8. Wet weight of propulsive trunk muscle as a percentage of total body weight plotted against length for various fish: dace (white circles), trout (black circles) and goldfish (crosses).

If these figures for change in muscle proportion with length are incorporated with those concerning the deviation of weight from the cube law (see above), the combined relationship between length and weight of muscle is then: dace  $L^{3.04}$ , trout  $L^{3.08}$  and goldfish  $L^{3.40}$ . There is thus in this respect little deviation from the cube law except in the goldfish, which changes advantageously with respect to power as size increases.

#### (b) *The roughness of the body surface*

There being nothing else immediately determinable in the propulsive mechanism of the fish that could account for the observed variations with length, we turn to consider the factors affecting the drag of the body. These fall under three headings, the first concerning the nature of the body surface itself. The layer presented immediately to the water would seem invariably to be one of mucus secreted by glands in the skin; beneath this is the epidermis, consisting of several layers of cells; and beneath this again, and largely determining the contours of the epidermis, is a layer of scales. The pattern of distribution of scales is more or less constant for a particular species. The full complement of scales appears early in life (in the speckled trout, *Salvelinus fontinalis*, scales have spread over practically the entire body by the time the fish is 6.0 cm. long—Elson (1939)) and thereafter the scales

increase in size by isometric growth in regular proportion to the growth of the whole body. The number of scales lying along the lateral line may be taken as some indication of the degree of roughness of the body. In the goldfish this is about 28, in the dace 52 and in the trout 126. The maximum lengths normally reported as being reached by these three fish are 40, 25 and 60 cm., respectively. This makes their maximum scale size about 1.5, 0.5 and 0.5 cm., respectively. The minimum scale size, when the pattern is first fully developed at say 6.0 cm., would be goldfish 0.2 cm., dace 0.1 cm., trout 0.05 cm., approximately.

The scales, overlapping as they do, will thus impart to the surface, though covered by epidermis and mucus, a pattern of roughness varying between these limits and changing in a uniform manner with the length of the specimen. The likelihood of this variation in roughness affecting the drag of the body in the way necessary to account for the observed variations of swimming ability with size is extremely small. Richardson (1936) has already shown that wooden models of fish respectively roughened, smoothed and varnished, and oiled were all of practically the same resistance as a dead fish. The variability in roughness of his models is greater than that within the size range of any one of the species we are considering and, if the roughness varies isometrically, its effects will in any case be covered by Reynolds number.

(c) *The effect of the fineness ratio*

Second in the factors affecting drag, the fineness ratio (F.R.) of the body may be considered. For a three-dimensional figure this is the ratio of the length of the body to the mean of its maximum height and breadth. With isometric growth F.R. might be expected to remain constant with increasing size, but with allometric growth it should either increase or decrease according to the nature of the departure from isometry. Two components are recognized in the drag of a three-dimensional body. The *frictional resistance*, which is usually expressed in terms of a coefficient based on the total wetted surface area, and the *form drag*, usually referred to the frontal area. These two factors contribute in varying measure to the total drag of the body in proportions dependent upon Reynolds number and the shape of the body. The total drag coefficient, based on frontal area, varies with a changing F.R. For airships where a premium is placed on volume in relation to drag,  $C_d$  is at a minimum for an F.R. of 2.5 (Hoerner, 1958). It would seem likely that the case of fish is analogous, as an optimum volume for minimum drag will allow the maximum speed to be obtained. Any trend towards or away from an F.R. of 2.5 should therefore lead respectively to increasing or decreasing speed or stamina. Values for the F.R. for most of the fish used in these experiments, and some other specimens, are shown in Fig. 9. A decrease with increasing length is apparent in both the goldfish and trout, while in the dace there is a possibility of a slight increase although this is masked by the rather large variability. These changes (4.75-4.25 in the goldfish series and 6.40-5.70 in the trout) can be expected to reduce the total drag of these fish by about 4 and 5%, respectively. This is not of great significance. The marked difference in the absolute values of F.R. for the three species is, nevertheless, of

greater interest, the mean being 6.7 for the dace, 6.3 for the trout and 4.5 for the goldfish. Their significance is considered below.

(d) *The influence of Reynolds number*

The third factor which may influence the drag of the body is Reynolds number ( $R$ ). In the simple expression  $\text{Drag} \propto C_f L^2 V^2$ ,  $C_f$  is a function of  $R$ .  $R$  is expressed as  $VL/\nu$  where  $V$  is the velocity,  $L$  the length of the specimen and  $\nu$  is the kinematic viscosity of the water. The experimental values of  $V$  make it clear that  $R$  varies within each of our series of fish results. The limits of this variability are given in Table 1.

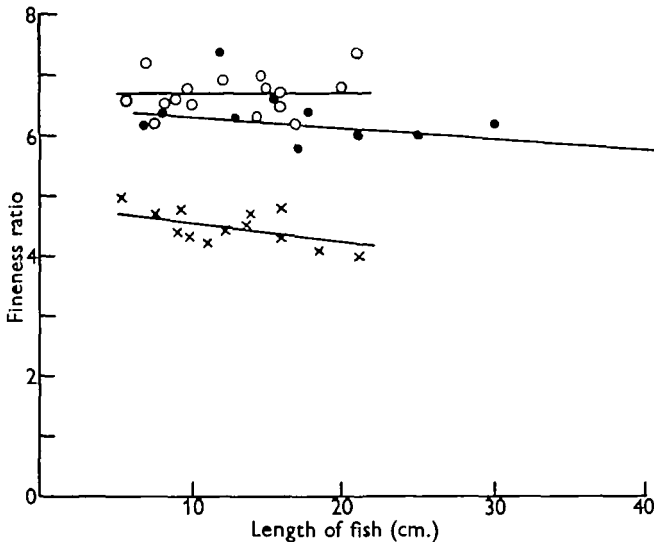


Fig. 9. Fineness ratios of various fish plotted against length for: dace (white circles), trout (black circles) and goldfish (crosses).

Table 1. *Limiting values of Reynolds number for the fish studied*

		Reynolds number	
		Minimum	Maximum
Dace	Smallest	$4.7 \times 10^4$	$1.4 \times 10^5$
	Largest	$1.8 \times 10^5$	$5.1 \times 10^5$
Trout	Smallest	$3.1 \times 10^4$	$1.1 \times 10^5$
	Largest	$2.1 \times 10^5$	$7.8 \times 10^5$
Goldfish	Smallest	$2.8 \times 10^4$	$5.0 \times 10^4$
	Largest	$1.7 \times 10^5$	$4.3 \times 10^5$

The coefficient of frictional drag relating to the wetted surface of a body moving in water varies according to the value of  $R$ , but there are unfortunately no measured values of the  $C_f$  of bodies of revolution for the low Reynolds numbers pertaining to our fish. Unless there is some unexpected influence of the roughness of the surface it seems best to assume laminar flow over most of the body at these low Reynolds numbers. The theoretical laminar  $C_f$  (based on wetted area) falls roughly

from 0.008 to 0.0015, while  $R$  goes from  $3 \times 10^4$  to  $8 \times 10^5$ . This disregards the effect of a changing F.R. With turbulent flow and a fixed F.R. of 5 the comparable change in  $C_f$  would be from 0.015 to 0.0025.

These changes are substantial and have considerable effect when incorporated in the theoretical relationship between velocity and length. D'Arcy Thompson's arguments can be used to derive the expression  $V \propto L^{\frac{1}{2}(\beta-2)}$ , where  $\beta$  is the disputed index in the formula which relates power available to length. Using modern hydrodynamical theory incorporating the effect of Reynolds number and assuming laminar flow over most of the body with  $C_f \propto R^{-\frac{1}{2}}$ , the comparable expression is  $V \propto L^{\frac{1}{8}(2\beta-3)}$ . Incorrect assumptions concerning the effect of  $R$  are undoubtedly a source of error in D'Arcy Thompson's deductions. The choice of assumptions concerning  $\beta$  are (i) that it is simply dependent upon muscle volume (broadly  $L^3$ ), or (ii) that it is entirely limited by the surface area of gills or such structures (broadly  $L^2$ ). These two values for the index would now give  $V \propto L^{0.26}$  and  $L^{0.2}$ , respectively, instead of  $L^{0.5}$  and  $V$  independent of  $L$  as in D'Arcy Thompson's analysis. Substituting our three figures for mass of muscle (dace  $L^{3.04}$ , trout  $L^{3.06}$ , goldfish  $L^{3.40}$ ) would give velocity as  $\alpha L^{0.62}$ ,  $L^{0.62}$  and  $L^{0.76}$ , respectively. Of these figures the trout and goldfish values tally well with our experimental findings but the dace is surprisingly low. Quantity of muscle is, however, probably not the limiting factor but without a careful study of relative changes in gill surface areas, circulatory systems, etc., it is not possible to say just how the power factor relates to length. Accepting the experimental results as reliable we can perhaps best at this stage only restrict our conclusions to a recognition of an empirical difference between the dace on the one hand (speed and ability  $\alpha L^{1.09}$ ) and trout and goldfish on the other ( $\alpha L^{0.65}$ ).

In the absence of so much basic information concerning limiting factors, arguments such as these must be considered as only exploratory. The basic assumption of a similar dependence upon length for all periods of swimming may even not be valid. It is possible that a burst of swimming of only 1 sec. duration might be dependent only upon the volume of muscle and hence make  $V \propto L^{0.6}$ , while more sustained swimming would begin to depend upon circulatory and respiratory transfer and hence perhaps finally make  $V \propto L^{0.2}$ . There is an indication of such a change in the goldfish results (p. 136). The series of values for  $\alpha$  with increasing time interval (1.06, 0.74, 0.76, 0.70, 0.48 and 0.50) show the required decrement. The other two species do not show this and the effect has been neglected because of the complexity of treatment it would demand. It should, nevertheless, be borne in mind as a possibility.

The discrepancy between these present experimental values and the direct dependence of speed upon length reported earlier (Bainbridge, 1958*a*) need cause no concern. The formula previously given for calculating the maximum speed incorporated both the length of the fish and the maximum frequency of beating of the tail. The latter was shown to decline differently in different species with

increasing size of the specimen. The maximum efforts for varying durations which are being studied here would not therefore be expected to be directly related to length. They should differ from this in a manner dependent upon variation in the maximum frequency of tail beat with size.

(2) *The effect of inter-specific differences*

Because of this variable dependence upon length it is not possible to make a direct comparison between the different species and thence assess their relative staying powers and the different onsets of fatigue in different species. One way in which an indirect comparison may be made, however, is by transforming the values for the mean curves in Figs. 3, 5 and 7 to values for a representative fish of arbitrarily selected length. This is done in Fig. 10 for theoretical fish of 15 cm. length, a size within the range of the experimental results for all species. The deductions which may be drawn from such a comparison are limited, because fish of such an arbitrarily selected length will not necessarily be at comparable stages in growth or development of sexual maturity.

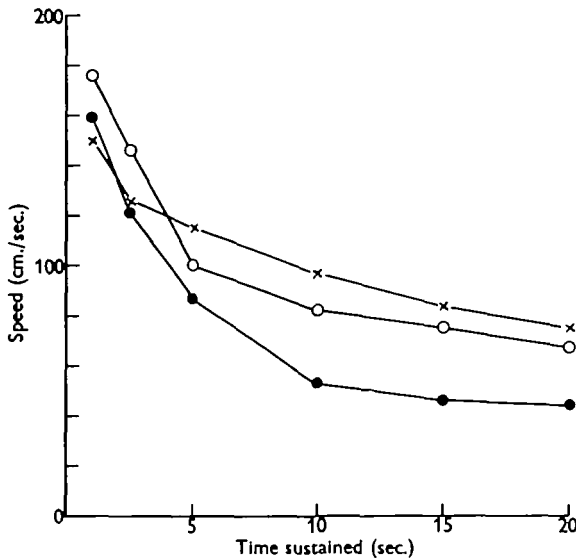


Fig. 10. Calculated relationship between speed and the length of time it can be sustained for three 15.0 cm. fish: dace (white circles), trout (black circles) and goldfish (crosses). Points derived from the means of the values in Figs. 3, 5 and 7.

Fig. 10 reveals certain differences between the three species which are perhaps somewhat unexpected. Starting with the shortest time interval of 1 sec. the dace is the best performer, the trout the next at about 15 cm./sec. or 13% slower, and the goldfish poorest at 10 cm./sec. lower still. With increase of the time interval to 2½ and 5 sec. all three species show a marked decline in speed to about 60% of their maximum. The goldfish is by now, however, slightly better than the other two species. This ascendancy is maintained with increasing time intervals, so that



for 20 sec. of swimming the goldfish maintains a speed almost double that of a trout of comparable size and almost 10 cm./sec., or 10%, greater than that of a similar dace. All species show a marked decline with time in the ability to maintain speed, the goldfish falling to 50% of its maximum value, the dace to 38% and the trout to 28%; the mean of these three figures is 40%.

Two pieces of information might correlate with this order of ability: the fineness ratios and the muscle percentages already calculated. In this context it is the differences between species that will be of consequence and not the changes with increasing length. With optimum laminar conditions, with  $R$  at  $4 \times 10^5$ , the  $C_f$  (based on frontal area) for the goldfish on the one hand at F.R. 4.5 is 0.048, while for the dace and trout on the other hand with F.R. *c.* 6.5 it is 0.065. These figures are greater than those already quoted for  $C_f$  (wetted area) as they are based on different parameters of the body. This would lead one to expect a better performance (of the order of 10–20%) on the part of the goldfish, as is indeed found over the longer time intervals. Combined with this there must be some effect of the different percentages of muscle in the three species. The magnitude of this effect is difficult to assess because of the unknown influence of area-dependent factors such as the gills. If muscle volume alone were the determining factor it can be shown that this should depend upon (% muscle)<sup>3</sup>. Treatment in this way of the mean muscle percentages for fish above 15 cm. (dace 56%, trout 63% and goldfish 45%) gives the following factors: dace 14.6, trout 15.8, goldfish 10.8. The goldfish with the most favourable  $C_f$  has thus the most unfavourable muscle factor. When these two factors are combined the relative abilities should be: dace 21, trout 22 and goldfish 20. These are virtually identical and there would thus appear not to be any immediately determinable factors accounting for the observed variations in ability to sustain different speeds. The differences appear to be real and one may be forced to invoke some hitherto undetermined hydrodynamical or physiological factor to account for them. In this context Black (1955) has already made it clear that there are a number of interspecific physiological differences of as yet undetermined effect amongst fish. In particular his results show a large difference in the increase in blood lactic-acid content after 15 min. of forced exercise between carp, with low values (mean 65 mg. %) and Kamloops trout with high values (mean 91 mg. %). These he supposes must in turn be related to capacity to survive at different temperatures and possibly also to activity.

### (3) *Nature of the time/speed relationship*

Accepting these partly unaccountable variations related to size and species we may now consider more closely the nature of the relationship between speed and the time for which it is sustained. For this purpose size and species may be ignored and Fig. 11 gives the speed/time curve for a hypothetical fish of 15 cm. length. It is derived from Fig. 10 by taking the mean of the three values for each time interval. This mean curve shows that the fish have little power to sustain any of the higher speeds. The maximum speed, as recorded previously (Bainbridge, 1958*a*), is of the order of 10*L*/sec. This is kept up only for periods of the order of 1 sec. With 2½ sec.

of swimming it has already dropped to  $7L/sec.$ , with 10 sec. to  $5L/sec.$  and with 20 sec. to  $4L/sec.$  The ability to sustain high speeds is thus much lower than that suspected previously. The form of the curve suggests that speeds of  $12L/sec.$  ( $180\text{ cm./sec.}$ ) would be attainable by such a fish as this but these would be sustained for no more than  $0.5\text{ sec.}$

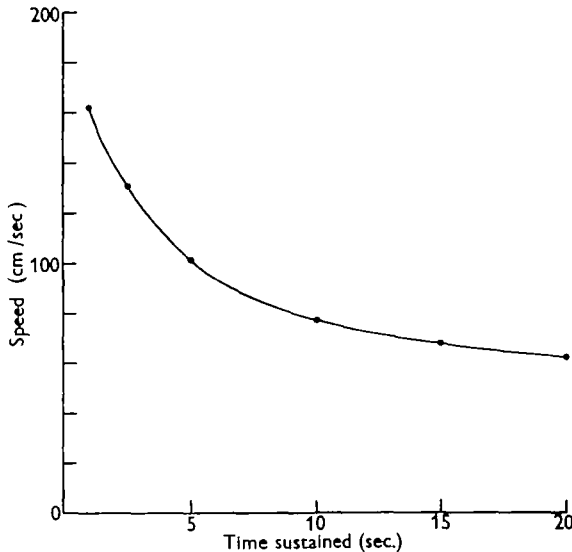


Fig. 11. Calculated relationship between speed and the length of time it can be sustained for a hypothetical  $15.0\text{ cm.}$  fish. Points derived from the means of the values in Fig. 10.

It seems reasonable to suppose that there may be two factors contributing to determine the nature of this curve. With increasing time interval it clearly approaches an asymptote of between  $3$  and  $4L/sec.$  This must represent the 'cruising speed' of the fish and physiologically it must be more or less a steady state, determined itself by the rate at which the muscles can be supplied with the raw materials for contraction and relieved of their waste products. The rest of the curve, above a base line of  $3-4L/sec.$ , represents potential available for a burst of swimming. This potential may perhaps be expressed in length-second units, of which about twenty appear to be available. These can be expended quickly or slowly according to the degree of motivation as, for example, an extra  $4L/sec.$  above the cruising speed if sustained for only  $5\text{ sec.}$ , an extra  $2L/sec.$  if sustained for  $10\text{ sec.}$  or  $1L/sec.$  for  $20\text{ sec.}$  The factors limiting the size of this potential may well concern a store of raw material available for use by the muscles (as glycogen within the cells themselves or oxygen bound in muscle haemoglobin or in close proximity to the cells), or it may perhaps depend upon the inhibitory nature of some waste product such as lactic acid. The rapid accumulation of this and its subsequent more leisurely removal would also account for the diminution in the  $20$  length-seconds potential as it is expended in shorter and shorter periods. (It is reduced to  $c. 15$  length-seconds at  $2\frac{1}{2}\text{ sec.}$  and to  $8$  at  $1\text{ sec.}$ ) The uppermost limit of all to the speed of swimming is probably

determined mechanically by the strength of connective tissue junctions within the myotomes or perhaps by internal friction and viscosity within the fibres themselves.

Anaerobic conversion of glycogen to lactic acid is certainly one of the important mechanisms providing energy for muscular contraction. The appearance of such lactic acid in the blood of the fish appears to be somewhat delayed. Black (1956, 1957) gives information on the rate at which lactic acid appears in and disappears from the blood of various fish after violent exercise. He found no regularly determinable change in blood lactic-acid content up to 240 sec. after only 1 min. or so of violent activity associated with capture and the withdrawal of blood. Production must already have taken place in the muscles, however. During 15 min. of violent activity the mean rate of appearance in the blood was 10 mg./%/min. over the first 1-5 min. Normality might not be regained for as long as 12 hr. and this relates well to Paulik, DeLacy & Stacy's (1957) work on the effect of rest on the swimming performance of fatigued adult silver salmon. They found recovery after an exhaustive effort was only 31% complete after a rest of 1 hr., 43% after 2 hr., 67% after 3 hr. but not wholly complete until 18-24 hr. had elapsed.

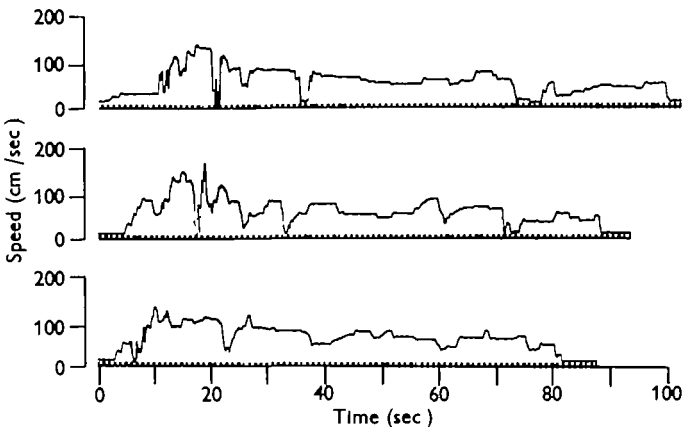


Fig. 12. Oscilloscope records of the speed of swimming of a 14.4 cm. goldfish showing three successive series of bursts of swimming lasting 80 or 90 sec. with an initial peak and a gradual decline indicative of fatigue.

The onset of fatigue must therefore be regulated by a critical balance between several variables including the ability of the contractile system to withstand high concentrations of lactic acid within itself or in its immediate vicinity, the speed with which this acid is removed from the muscles or is buffered, the speed with which it is transformed or removed from the body by the circulatory system and finally the intensity of the motivation influencing the fish at the time. The complexity of such a system of limiting factors could certainly account for both the form of the relationship shown in Fig. 11 and the interspecific differences already referred to. Another effect, not studied in detail, is illustrated by the record in Fig. 12. Here, over a period of about 1 min., a gradual decline can be seen in the speed attained during a series of successive bursts of swimming. This could presumably be determined

either by change in the rate of lactic acid removal as successive stages in the system become fully charged or perhaps by a nervous adaptation to the more or less uniform stimulus being received.

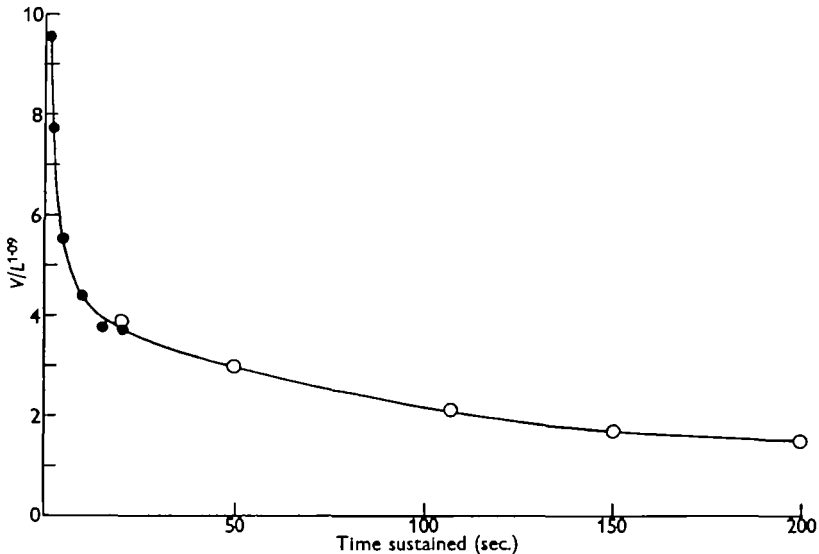


Fig. 13. Comparison between the present results for the dace (black circles) and results for the silver salmon, *Oncorhynchus milktschitsch* (white circles), from Paulik & DeLacy (1957). Both species with speed plotted as  $V/L^{1.09}$ .

#### (4) Correlation with other results

The figures described in this paper relate satisfactorily to those already published for longer time intervals. The tendency to approach a cruising speed of 3 to 4L/sec. is evident in both the values in the introduction and in Fig. 12. Fry & Hart's (1948) high figure for the goldfish correlates well with the placing of the present goldfish results in Fig. 10. The mean cruising speed derived from Fry & Hart's figure and Radcliffe's (1950) figure is 4.88L/sec. That in our Fig. 10 for a 15 cm. fish represents 5.0L/sec.

Paulik & DeLacy (1957) show a gradual decline in the swimming ability of adult silver salmon over periods up to 200 sec. The shortest mean period of swimming they record is 24 sec. Their figures, the mean of nine fish, are reproduced in Fig. 13 on a scale of  $V/L^{1.09}$ . Our dace figures are shown in the same notation. The complementary nature of these two sets of information is at once apparent. Although one might expect the correspondence of silver salmon to be greater with our trout this is not so, nor is it with the goldfish.

There is not of course such correspondence with observations on other animals. Hill (1950) gives the maximum recorded performances for man running races of different durations, man swimming and horses running. While the form of the relationship between speed and duration is precisely that found for fish in the

present work, the scales are of a different order, involving minutes in the mammal and only seconds in the fish. It is improbable that this striking difference derives from any essentially different type of muscular activity. A more likely explanation could lie in the relatively poor circulatory system of the fish. Ritchie (1928) makes it clear that the buffering capacity is very poor in fish muscle and rapid fatigue might be due to a change in pH because of an inability to remove lactic acid with sufficient speed. He further suggests that the glycogen reserve in fish muscle is extremely low and this would be a contributory factor. Black (1957) shows that after violent exercise the level of lactic acid in fish blood continues to increase for 2-3 hr., whereas in man this process continues for only 10 min. at the most. The low body temperature of fish may determine this slow rate of diffusion from the muscles. In mammals, correspondingly, the high body temperature will favour rapid transport of such diffusible substances.

Temperature of the ambient water is known to have a marked effect on the cruising ability of goldfish (Fry & Hart, 1948) and coho and sockeye salmon (Brett *et al.* 1958). No attempt has been made to study the influence of temperature in the present work. All the observations were made at room temperature and in every case this was recorded. The fish were held in tanks at the same room temperature and were therefore always acclimatized to the temperature of the water in which they were studied. For the purposes of comparison all the records may be taken as relating to 15° C., but on occasion observations were made as much as 3° C. on either side of this figure. Because of the limited number of these no consistent influence of temperature could be detected in the speeds recorded but this factor may account for some of the variability that was encountered.

#### (5) *Practical applications*

Besides raising these various physiological problems the figures reported here may be of some practical significance. Two such possible applications are now considered. For this purpose it would seem best to neglect possible variation between species and refer to a hypothetical average fish derived from the mean of all the results so far obtained. The swimming abilities of the members of a series of such animals of varying sizes should be related to each other according to their length raised to the power of 0.8; this being the mean of the three indices already calculated. Using this power and the values in Fig. 11 it is possible to construct a graph relating the speed of such hypothetical fish to the maximum distance they could swim. Such a relationship is shown in Fig. 14 for four representative lengths of fish (15, 30, 45 and 60 cm.). 60 cm. (about 24 in.) has been chosen as the upper reliable limit for extrapolation of the results, which derive from fish whose maximum length is 30 cm.; and 24 in. is also a reasonable size for a spawning salmon.

If one of these animals, e.g. the 60 cm. specimen, is swimming head into a current of water the distance he can travel forward relative to the ground is given by the simple relationship  $D = T(V_f - V_w)$ , where  $T$  is the duration of the burst of swimming,  $V_f$  the velocity of the fish and  $V_w$  that of the water. If this formula is applied to the data in Fig. 14 it is possible to derive the relationship shown in

Fig. 15. This gives the headway that a 60 cm. fish can make against various speeds of flowing water according to the speed at which he swims. It is at once apparent that for each water speed there is an optimum speed of swimming which will carry the fish a maximum distance. In water at 200 cm./sec., for example, for a 60 cm. fish, this is 325 cm./sec. At this speed he will make a headway of 545 cm. If he swims faster than this he fatigues before having travelled so far; if he swims slower he is

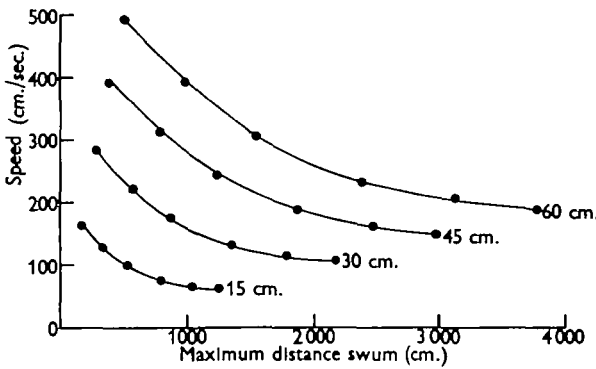


Fig. 14

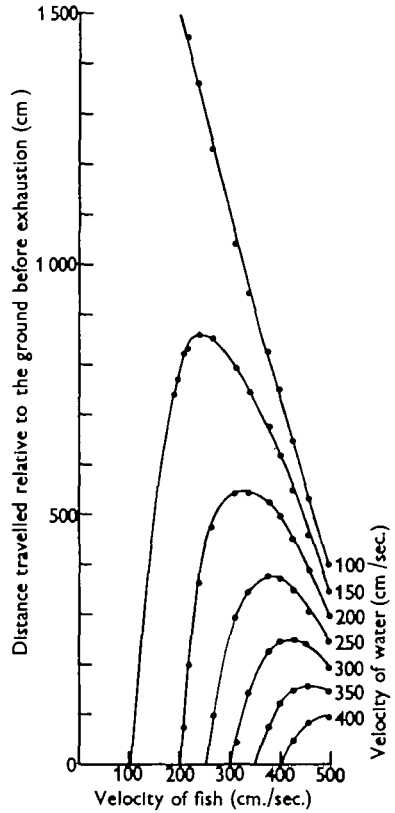


Fig. 15

Fig. 14. Relationship between speed and the maximum distance swum before exhaustion for four hypothetical fish of 15, 30, 45 and 60 cm. in length.

Fig. 15. Headway, relative to the ground, made by a hypothetical 60 cm. fish swimming at various speeds in currents of various velocities. The separate curves relate to the different current velocities; the black circles indicate distance travelled for particular speeds of swimming. For further explanation see text.

carried back too far to make as much headway. A more convenient way of presenting this information is by plotting the maximum distance that can be travelled against water velocity. This is done in Fig. 16 for the four sizes of fish; the data being derived in each case as in Fig. 15. This diagram, with scales in both cm., ft. and miles per hour, provides at once, for each of the sizes of fish listed, the absolute

maximum distance that such a specimen might be expected to traverse through water flowing at a particular speed. For example, in a current of about 3 m.p.h. (say 150 cm./sec.), 6 in. fish will have no chance of even stemming such water, 12 in. fish could traverse a maximum length of 6 ft. of it, 1 ft. 6 in. fish could traverse about 14 ft. and 24 in. fish about 26 ft. After such lengths of swimming a period of rest would be required before another effort. A somewhat reduced effort could be indulged in within seconds, an equally strenuous one possibly not for much longer.

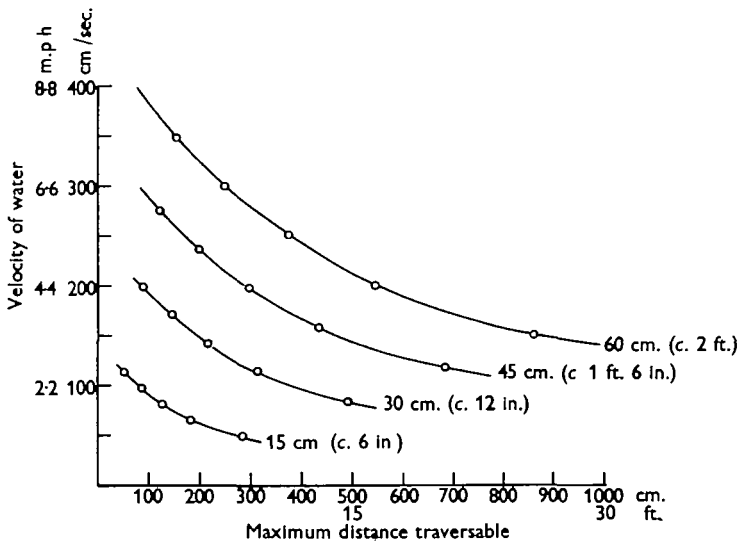


Fig. 16. Maximum distance traversable relative to the ground by four hypothetical fish swimming in water of various velocities. Data derived from Figs. 14 and 15.

The above argument assumes movement through water of constant velocity. Sir James Gray has shown (unpublished) that a fish entering water of increasing velocity could make use of the speed developed in a lower velocity region by travelling on his momentum quite a long way into the water of increasing velocity. Such an effect would tend to increase the distance that could be traversed. It is also important to stress that Fig. 16 represents an optimum effort on the part of the fish. If he swims either too fast or too slow he will not accomplish so much. Fig. 15 indicates the latitude he has, without seriously reducing his distance. In a 200 cm. current the 60 cm. fish will still cover over 500 cm. distance for speeds of swimming between 275 and 400 cm./sec. It is interesting to contemplate whether the fish has a means of judging his optimum by reference to, say, the bottom. It is certainly important that under conditions requiring a maximum accomplishment he should not be scared into trying to swim his fastest.

The application of such information as this to the passage of fish through ladders is at once evident. Maximum efficiency of a ladder is often related to the velocity of the outflow, as the faster this is the more fish it attracts. Adjustment to

an appropriate velocity could ensure entry of the maximum number of fish and also exclusion, if desirable, of those of smaller size. A second application might concern the dimensions of the openings of trawls and other nets. The modern otter trawl has a headline of the order of 100 ft. in width, which, during working, may be 10 or 15 ft. above the sea bed. It is towed along at a speed of 3 to 4 knots. Fig. 16 suggests that most fish below 12 in. would be likely to be caught by such gear. A fish of 24 in. would manage a dart of about 20 ft. at this speed. If he is within that distance of the edge of the net and moves laterally he will escape. Within the central 60 ft. of the line of towing he cannot escape except by swimming upwards, where he is easily capable of getting over the top of the net. This, however, generally overhangs the foot-rope by perhaps 10 ft.; its tendency will therefore be to make him swim downwards and along the sea bed, to be caught eventually after tiring. Laterally the Vigneron Dahl gear will increase the effective spread of the net and, preceding it somewhat will tend to scare laterally placed fish inwards where, after one of their sudden darts they will be more readily caught. Even much bigger fish will by this means be brought into the catching power of the net. It seems unlikely that the trawl, developed by long years of experience, can be improved upon by information of this kind but the results do perhaps serve to emphasize how deadly a device it already is and also show, partly, why this is so.

#### SUMMARY

1. Measurements of the maximum speed sustained during bursts of swimming of up to 20 sec. duration by dace, trout and goldfish of various lengths are reported.
2. The ability to sustain periods of swimming appears to be related differently to length in different species. In the dace it is proportional to  $L^{1.09}$ , in the trout and goldfish to  $L^{0.65}$ .
3. The dependence of this relationship upon various factors is considered. It is concluded that allometric increase of muscle and the influence of an increasing Reynolds number, possibly combined with other, physiological, factors could adequately account for the variation observed.
4. The precise form of the speed/duration relationship differs in different species. These variations are also probably accountable for by a combination of different muscle percentages and fineness ratios together with other, physiological, factors.
5. The ability to maintain speed diminishes rapidly with increasing time interval in all the species measured. The maintained speed falls from about  $10L/\text{sec.}$ , maintainable for only 1 sec. of swimming, down to  $5L/\text{sec.}$  for 10 sec. and further to a cruising speed of about  $4L/\text{sec.}$  by 20 sec. The nature of this time/speed relationship is considered to be determined by the ability of the muscle to utilize stores of raw material and by the rates at which these can be supplied to, and waste products removed from, the muscle.
6. A diagram showing the relationship between velocity of water flow and the maximum distance which various hypothetical fish could traverse in such currents is constructed; and possible applications of this information are briefly considered.



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