

THE SPEED OF SWIMMING OF FISH AS RELATED TO SIZE AND TO THE FREQUENCY AND AMPLITUDE OF THE TAIL BEAT

By RICHARD BAINBRIDGE

The Zoological Laboratory, Cambridge

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INTRODUCTION

A fair number of values for the speed of swimming of a representative selection of fish species now exists in the literature. Many of the figures are only estimates; some are accurate measurements, but unfortunately even amongst these the absence of the all-important values of the weight or the length of the specimens concerned renders many of them of little use.

Stringham (1924) reviews and gives references to early work and Gray (1953) summarizes some later results and also gives figures of his own. The earliest recorded experiments seem to be those of Regnard (1893) who allowed small fish to swim in an annular rotating vessel, the speed of which could be controlled by a variable resistance and an electric motor. He rotated the vessel until the swimming fish could only just keep station and then recorded this as the maximum swimming speed. He makes no reference in his account to corrections for a lag between the speed of rotation of the water and that of the container, and in this respect his results may perhaps be suspect. Figures for by far the greatest selection of species are to be found in Magnan (1930). Besides dividing 172 species up into eight great groups according to the relationship between their speed of swimming and the square root of their length, he gives a table of values for eighteen species, recording amongst other things the length of the specimens used and their maximum speed of swimming. The methods he used comprise (i) timing the animal between two fixed points a known distance apart, (ii) using a special camera to make ciné films of the animal swimming and calculating values from these, and (iii) attaching the animal to a speedometer by means of a thread, the speed at which this unrolled giving the fish's speed. He does not say which of these methods is used in any particular instance, or upon what distance of swimming any measurement is based, but regards all the figures as equally reliable. Denil (1937), in one of a series of papers, which deal exhaustively with the problem of constructing fish ladders for surmounting river obstacles, gives some measurements of the speed of various specimens swimming up passes of different design, and calculates from these figures their potential speed in open water. He also calculates the speed at which leaping fish must be moving when they leave the water. Lane (1941), in an entertaining popular article, refers to a device, made by H. E. Thompson and similar to that used in the last of

Magnan's methods, for timing the speed of running out of a line when a fish has been hooked. He gives one value obtained with this for a tuna.

More recently Fry & Hart (1948) have used an apparatus similar to Regnard's in a study of the relationship between speed and water temperature in the goldfish. They make careful allowance for the lag between water and container and give what may be considered definitive figures for a 'cruising speed' that can be sustained for, say, 15-20 min. Davidson (1949) gives figures for salmon maintaining station in a circular rearing tank in which the water was rotating, and Wales (1950) records what is probably the maximum speed of *Catostomus occidentalis*, the western sucker, swimming in a culvert containing rapidly flowing water. Radcliffe (1950) gives more figures for goldfish measured in Fry & Hart's apparatus and also records the effect of clipping off various fins. This he finds slightly increases the maximum speed, in direct contradiction to Regnard's (1893) observation that it materially decreases the speed. Gero (1952) refers to an instrument called the 'Piscatometer'. This allows both the thrust and velocity of a fish hooked during angling to be measured at sea in an open boat. The velocity is measured on a tachometer actuated as the line runs out. The tachometer dial is photographed during this process. He gives figures for two shark and a barracuda.

The results obtained by these various authors are summarized in Table 1, where all the speeds have been expressed in terms of the number of body lengths moved in 1 sec. In those cases where only the weight of the specimen was given, weight has been converted into length using the relationships given in Hecht (1916). As can be seen, the maximum speed actually recorded hitherto is that for the tuna, which Lane gives as travelling at 13.4 times its own length per second. The highest figure of all is that of Denil for a trout moving at 19.4 times its own length per second when leaving the water; but this is derived by calculation from a report of a trout of 25 cm. having leaped to a height of 1 m.

Without of course performing a great many measurements it is almost impossible to tell whether a particular fish is swimming at anything like its maximum speed. If, however, the one high figure given by Denil is taken as representing a rapid dart sustained only for a second or two, then it is seen that amongst the remainder there is a group of figures in the neighbourhood of 10 lengths per second

Bleak	10.0	Circular tank	Pike	12.7	} Photography
Trout	10.0	In fish pass	Carp	12.6	
Tuna	13.4	Line running out	Dace	9.2	
Sucker	9.8	Culvert			
Barracuda	9.4	'Piscatometer'			

These have been measured by a diversity of means, and the first five at least are based on a sustained period of swimming. It seems reasonable to assume that this speed of 10 lengths per second is the maximum that can be sustained for a period of about 1 min. The remaining figures in the table probably represent speeds sustainable for longer than this interval, or are based upon fish not exerting their maximum effort.

Table 1 *Published speeds of various fish*

Authority	Common name	Species	Speed in lengths/sec.	Data given	Remarks
Regnard, 1893	Carp	<i>Cyprinus carpio</i>	5.2	6 g., fish at 59 cm./sec. 5 g., fish at 52 cm./sec. 5 g., fish at 22 cm./sec. 1 g., fish at 50 cm./sec. 15 g., fish at 24 cm./sec.	(Carpe)
Magnan, 1930	Bleak	<i>Alburnus alburnus</i>	10.0		(Ablette)
	Chub	<i>Squalius cephalus</i>	2.0		(Chevaïne)
	Sea trout	<i>Salmo trutta</i>	2.7	34.1 g., fish at 92 cm./sec.	(Truite de mer)
	Mackerel	<i>Scomber scombrus</i>	3.2	25.2 g., fish at 81 cm./sec.	(Maquereau)
	Twaite shad	<i>Alosa finia</i>	2.5	20.7 g., fish at 75 cm./sec.	(Alose fin)
	Perch	<i>Perca perca</i>	3.6	18.4 g., fish at 66 cm./sec.	(Perche)
	Meagre	<i>Sciaenops aquila</i>	3.8	29.5 g., fish at 113 cm./sec.	(Maigre)
	Whiting	<i>Gadus merlangus</i>	1.3	17.7 g., fish at 23 cm./sec.	(Whiting)
	Bib or Pout	<i>G. luscus</i>	3.3	16.5 g., fish at 55 cm./sec.	(Tacaud)
	Grey mullet	<i>Mugil capito</i>	2.3	26.0 g., fish at 61 cm./sec.	(Mulet céphale)
	Rudd	<i>Scardinius erythrophthalmus</i>	6.0	18.8 g., fish at 114 cm./sec.	(Rotengle)
	Lesser weever	<i>Trachinus vipera</i>	1.8	22.4 g., fish at 40 cm./sec.	(Vive)
	Hake	<i>Merluccius vulgaris</i>	3.5	23.7 g., fish at 79 cm./sec.	(Merlus)
	Pike	<i>Esox lucius</i>	3.9	37.8 cm., fish at 148 cm./sec.	(Brocket)
	Red gurnard	<i>Trigla pini</i>	2.4	19.2 cm., fish at 47 cm./sec.	(Rouget)
	John Dory	<i>Zeus faber</i>	1.6	19.7 cm., fish at 30 cm./sec.	(Saint Pierre)
	Black bass	<i>Micropterus salmoides</i>	4.1	21.3 cm., fish at 88 cm./sec.	—
	Gurnard	<i>Trigla</i> sp.	5.0	26.2 cm., fish at 131 cm./sec.	(Grondin corbeau)
	Norway haddock	<i>Sebastes dactylopterus</i>	3.6	26.8 cm., fish at 98 cm./sec.	(Sébaste)
Denil, 1937	Trout	<i>Salmo fario</i>	10.0	35 cm., fish at 3.5 m./sec.	—
	Salmon	<i>S. salar</i>	6.4	75 cm., fish at 4.79 m./sec.	—
	Salmon	<i>S. salar</i>	5.8	85 cm., fish at 4.95 m./sec.	—
	Salmon	<i>S. salar</i>	8.4	80 cm., fish leaping 2 m.	Calculated from reported data
	Trout	<i>S. fario</i>	19.4	25 cm., fish leaping 1 m.	—
Lane, 1941	Salmon	<i>S. salar</i>	8.0	ca. 75 cm., fish at 6 m./sec.	—
	Tuna	<i>Thunnus thynnus</i>	13.4	60 lb. fish travelling at 44 m.p.h.	—
Fry & Hart, 1948	Goldfish	<i>Carassius auratus</i>	6.36	Fish of average wt. 4.37 gm. swimming at 100 ft./min.	Average of many measurements and sustained for 20–25 min. at 25° C.

Table 1 (continued)

Authority	Common name	Species	Speed in lengths/sec	Data given	Remarks
Davidson, 1949	Salmon	<i>Salmo salar</i>	4.0	$\left\{ \begin{array}{l} 5.2 \text{ cm. fish, av. speed} \\ 21.6 \text{ cm./sec.} \\ 4.3 \text{ cm. fish, av. speed} \\ 16.7 \text{ cm./sec.} \\ 3.2 \text{ cm. fish, av. speed} \\ 13.1 \text{ cm./sec.} \end{array} \right.$	Each an average of twenty fish
Wales, 1950	Western sucker	<i>Catostomus occidentalis</i>	9.8	Fish 12-14 in. swimming at 2 ft./sec. in water flowing at 8.6 ft./sec.	Sustained 5 sec.
Radcliffe, 1950	Goldfish	<i>Carassius auratus</i>	3.4	3.38 body lengths/sec.	Normal After clipping fins
Gero, 1952	Goldfish	<i>C. auratus</i>	4.9	4.90 body lengths/sec.	
	Southern ground shark	<i>Carcharias leucas</i>	3.4	60 in., fish at 17.1 ft./sec.	'Piscatometer'
	Southern ground shark	(= <i>commersonii</i>) <i>C. leucas</i> (= <i>commersonii</i>)	3.9	21 lb., fish at 13.3 ft./sec.	
	Spotted jewfish	<i>Promicrops itaiara</i>	1.8	17 lb., fish at 5.7 ft./sec.	Photography of darting fish
	Lemon shark	<i>Negaprion brevirostris</i>	1.3	72.5 in., fish at 8.0 ft./sec.	
	Barracuda	<i>Sphyræna barracuda</i>	9.4	51.0 in., fish at 40.0 ft./sec.	
	Rainbow trout	<i>Salmo irideus</i>	8.5	20 cm., fish at 1.7 m./sec.	
	Pike	<i>Esox lucius</i>	12.7	16.5 cm., fish at 2.1 m./sec.	
	Pike	<i>E. lucius</i>	7.5	20 cm., fish at 1.5 m./sec.	
	Carp	<i>Cyprinus carpio</i>	12.6	13.5 cm., fish at 1.7 m./sec.	
	Rudd	<i>Scardinius erythrophthalmus</i>	5.9	22 cm., fish at 1.3 m./sec.	
	Dace	<i>Leuciscus leuciscus</i>	9.2	18.15 cm., fish at 1.7 m./sec.	
	Salmon	<i>Salmo salar</i>	9.2	3 ft., fish assumed jumping 6 ft.	
Gray, 1953	Salmon	<i>S. salar</i>	12.2	3 ft., fish assumed jumping 10 ft.	— —

Some indication of the rate during a very prolonged period of swimming may be obtained from marking experiments on migrating fish. For instance Dahl & Sømme (1936) describe how a fish marked at Titran in Norway was recovered at Drammenfiord, 1100 km. away, after 11 days. The specimen was 85 cm. long and this represents an average rate of progression of 1.4 lengths per second. As the route would almost certainly not be straight, and the migration did not necessarily start and finish at the times of release and capture, it is probable that this figure is low.

EXPERIMENTAL METHOD

It is reasonable to suppose that the speed at which a particular specimen travels depends upon several properties—the form of the body, its surface texture, the size of the specimen and the frequency and amplitude of beating of the tail (or of undulating the body or of moving the paired fins). The form of the body is known for all the species listed, as is the approximate length. Hitherto, however, no record has been made of the relationship between the speed and the frequency or the amplitude of tail beat or body movement. If speed could be related to these variables and limits could be ascribed to them, then it should be possible to forecast with accuracy the speed attainable by any particular specimen.

With this end in view it seemed desirable to make, if possible, more accurate measurements of the speed of swimming of various fish, and to relate this clearly to at least the three factors size, frequency and amplitude. An apparatus was therefore devised in which the fish was harnessed to the end of a light arm free to rotate in the horizontal plane. The fish was allowed to swim in a circular tank of water, and the rotation of the arm was recorded electrically on a smoked drum. The fish's speed was calculated from this recorded speed of rotation and the length of the arm. Attempts were made to obtain a photographic record of the fish's body movements over an arc of the circle in order to correlate the frequency of tail beat with the speed. While the preliminary results obtained with this apparatus were of some interest, it became clear that movement of the fish was made unnatural by its having to swim in a curved path, and to some extent the arm which had to be carried round constituted a load on the fish. It was consequently decided to develop an apparatus in which a free-swimming fish could be kept under continuous observation, while at the same time being able to travel unlimited distances.

The principle adopted was that described by Hardy & Bainbridge (1954) and utilized to facilitate a study of the vertical migrations of plankton organisms. Essentially it consists in moving the animal's environment bodily in a direction opposite to, and at the speed of, any movement that the animal cares to make. The 'fish wheel', as the apparatus built became known, consisted in the first instance, as shown in Fig. 1, of a horizontal circular tube of rectangular cross-section, built up of pieces of $\frac{1}{8}$ in. transparent Perspex. The tube so formed was $2\frac{1}{2}$ by 3 in. in cross-section and the internal diameter of the wheel was 2 ft. It was supported on three $\frac{1}{2}$ by $3\frac{1}{2}$ in. diameter ball races set on edge under the centre of the tube, each with a rubber tyre, and was secured to a central bearing, about which it could rotate,

by three wooden spokes and a boss. To facilitate cleaning, the entire top of the tube could be unbolted and removed, but one sector, 6 in. long, was secured separately to provide an opening for purposes of filling the tube and introducing the fish. Relative movement between the tube and its contained water was prevented by two Perspex sliding doors, moving vertically and fitting closely into guides on each side of the tube. These were made to open and close by means of the cam and rod mechanism shown in Fig. 2. The cam was arranged to keep a door fully open over

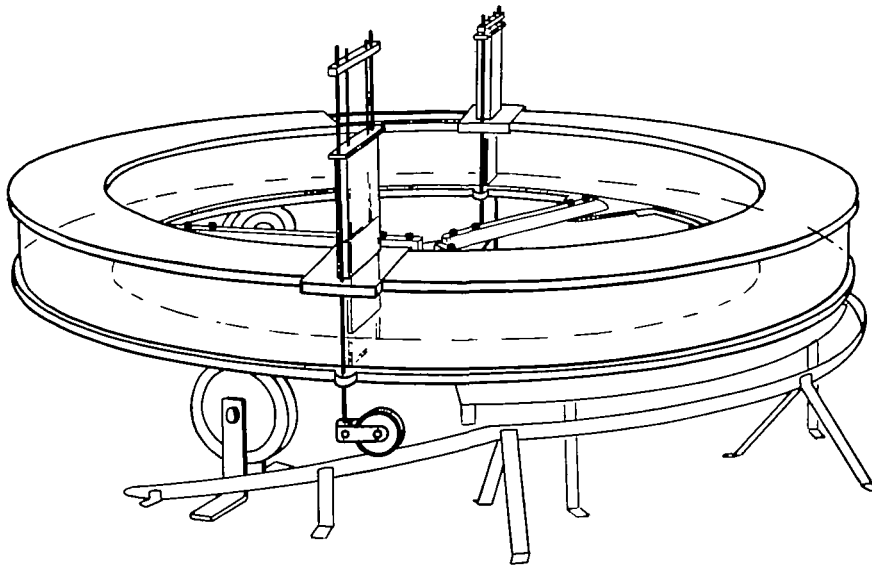


Fig. 1. Perspective view of small fish wheel. The animal swims on the extreme right where the vertical doors pass in the open position. On the left the doors close, thus locking the water to the wheel.

an arc of 90° and the opening and closing movements each occupied about 45° . The doors being diametrically opposite each other this arrangement ensured that one was always closed, while the other was open to allow for the passage of the fish. Radial black lines 10 cm. apart were drawn on the underside of the floor of the tube and showed distinctly against a white background. They were used to simplify analysis of the film records taken. A simple speedometer driven by one of the rotating ballraces was also arranged to be in the field of the camera. It was roughly calibrated by rotating the whole apparatus at various known speeds. This apparatus was used to obtain about half the records described here. The remainder, all of larger specimens, were obtained with the larger electrically operated apparatus described in the succeeding paper (Bainbridge & Brown, 1958).

For both types of apparatus records were taken with a ciné camera mounted directly above the point at which the fish swims. Illumination was by two or three Mazda no. 1 Photofloods about 24 in. from the fish, and the field of view included the fish, the speed indicator and a time marker. Generally, it was found that twenty-

four or forty-eight frames per second on 35 mm. film was sufficient to permit analysis of tail beat, etc., but occasionally 16 mm. films were taken at speeds up to sixty-four frames per second.

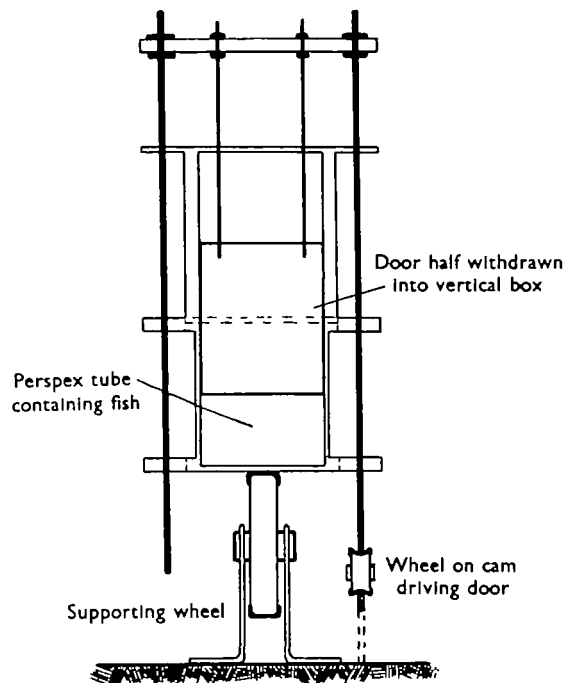


Fig. 2. Half-section of the wheel with a vertical door half-open.

In a typical experiment the tube is completely filled with water at room temperature, great care being taken to exclude bubbles. The fish is introduced and the removable cover bolted on. After the fish has been allowed to settle down the apparatus is rotated until he is over the white background where the doors pass by in the open position. As soon as he starts to swim the wheel is now rotated at the same speed, but in a direction opposite to his movement, thus keeping him stationary relative to the observer. As soon as the speedometer indicates that he is swimming steadily at a speed that it is desirable to record, the ciné camera is started and a length of film lasting some 3 or 4 sec. is taken. This procedure is repeated at intervals whenever the fish obliges by swimming at a required speed. In this way a permanent record of his speed and body movement is made for subsequent analysis without any extravagant expenditure of film. If the fish declines to swim it is sometimes possible to stimulate him to do so by moving a background of vertical stripes close to the side of the tube. Often the highest speeds are obtained immediately after he has been put into the apparatus, but they may be induced by flashing lights, waving a hand or tapping on the wall of the tube.

The lengths of film so obtained are analysed by projecting frame by frame on to a paper and plotting successive positions of the fish's tail in relation to the transverse black lines on the floor of the tube. Knowing the number of frames run per second it is possible to obtain directly from such a plot (i) the exact speed of swimming through still water over any given period, (ii) the frequency, and (iii) the amplitude of beating of the tail. The length of the specimen is taken at the time of the experiment, but can also be measured from the film.

EXPERIMENTAL RESULTS

The dace, Leuciscus leuciscus

The results obtained using dace of different lengths are first examined. Fig. 3A shows the relationship between speed and frequency of tail-beat of a fish 17.5 cm. long from the tip of the snout to the most posterior part of the tail fin. Each of the thirty-two points was obtained by analysing a length of film taken when the specimen was swimming steadily at the speed indicated. Each value derives from at least 50 cm. of swimming and generally from much more. It is clear from this graph that the relationship between speed and frequency could be represented by a straight line, which would not, however, pass through the origin. The graph for a 24.0 cm. specimen (Fig. 3B) confirms this, and also shows that the larger fish travels faster at any given frequency. This same trend is shown in the opposite direction in Fig. 3C and D, representing the results for 9.0 and 5.2 cm. specimens, respectively. These two graphs further make it clear that the speed/frequency relationship is in fact linear only down to about 5 beats per second, below which it departs from linearity and presumably passes through the origin.

The direct dependence of speed upon the length of the specimen is revealed if the measured speeds are divided by the size of the fish and thus expressed as body lengths per second. These values, derived for all specimens, are plotted against frequency in Fig. 3E, which shows the observations not only for the 24.0, 17.5, 9.0 and 5.2 cm. specimens, but also those for three other fish measuring 8.5, 6.6 and 3.6 cm. In order to avoid confusion in the graph reproduced, the various sizes of fish have not been given distinguishing symbols, but when this is done and a line is drawn through the points, it can be seen (i) that for each size of fish the points are evenly distributed on either side of the line, and (ii) that it is the smaller specimens that reach the higher relative speeds and higher frequencies of tail beat, the maximum being 20 body lengths per second at 25 beats per second.

The exact form of the line describing the speed/frequency relationship is made clearer by examining the relation between frequency and distance travelled per beat. This is shown non-dimensionally in Fig. 4 for all the dace measured. The distance travelled per beat is constant above a frequency of 5 or 6 beats per second but below this value it diminishes. It follows that the speed/frequency relationship in Fig. 3E must be linear from a frequency of 5 or 6 upwards but must be curved at lower frequencies. The three very high points between frequencies 1 and 2 (Fig. 4) may be due to gliding between beats. At these low frequencies beats are often separated

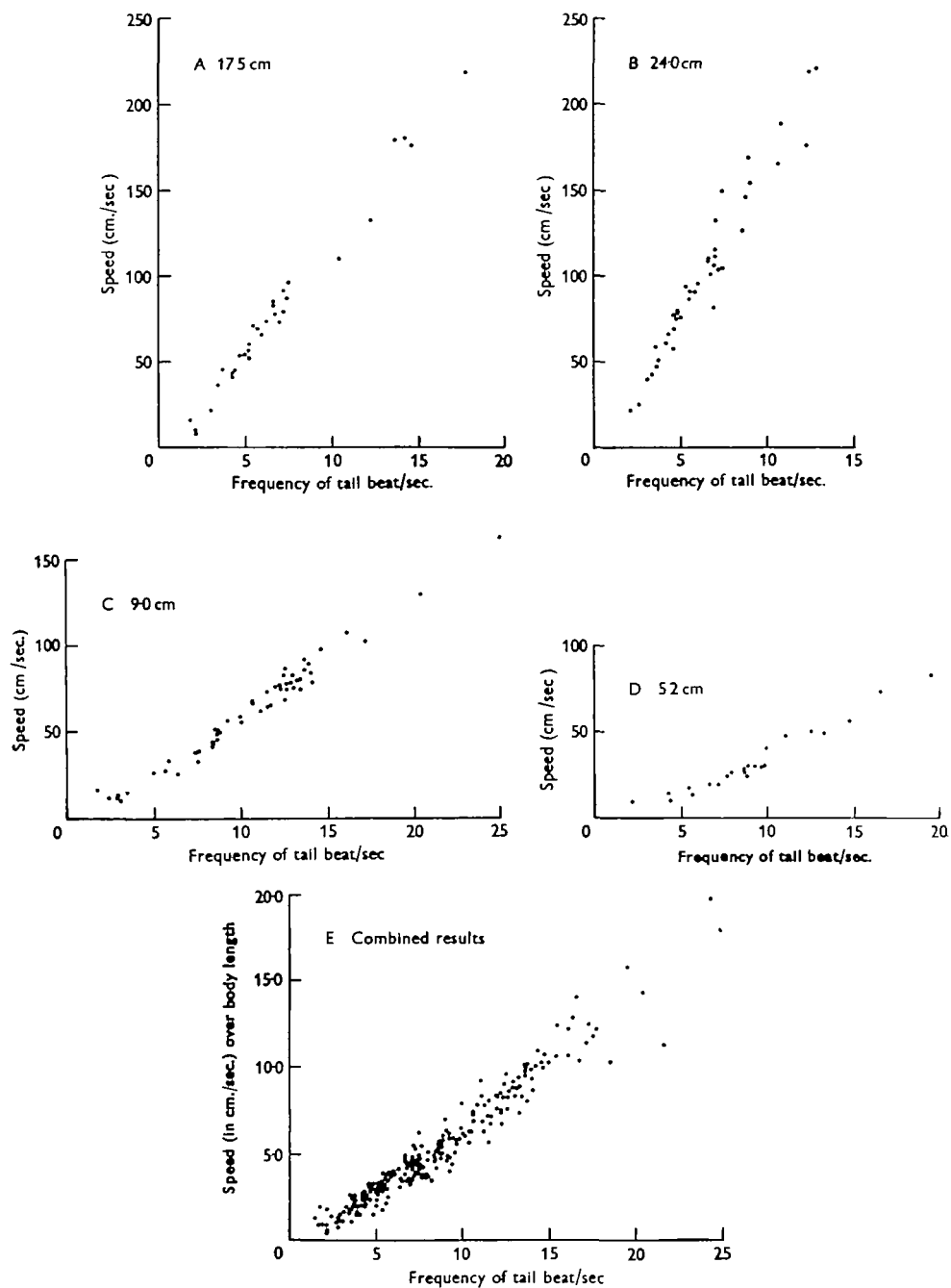


Fig. 3. Relationship between speed of swimming and frequency of beating of the tail for specimens of the dace (*Leuciscus leuciscus*). A 17.5, B 24.0, C 9.0, D 5.2 cm. long. E shows these results (and further information for specimens 8.5, 6.6 and 3.6 cm. long) with the speed expressed non-dimensionally as body lengths per second.

by periods when the fish glides without moving the tail; this possibly allows a maximum distance to be obtained from each beat but only, of course, a very low speed.

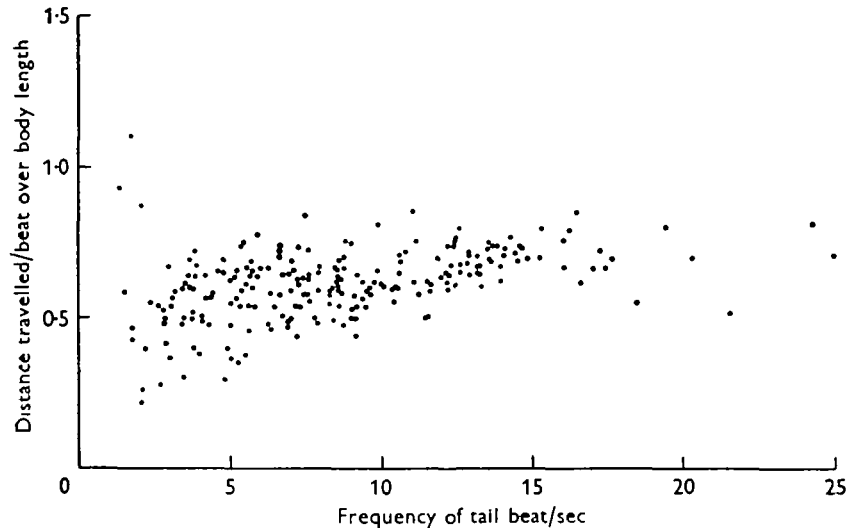


Fig. 4. Relationship between the distance travelled per beat divided by body length and frequency of beating of the tail for the 7 specimens of the dace shown in Fig. 3E.

There is a good deal of scatter amongst the points in both Figs. 3 and 4. Some of this may result from inaccuracies inherent in the experimental method: either a variable leakage of water past the doors, variations in the camera speed or errors in measuring the distances swum. Some may also be due to the inertia of the swimming fish. If the specimen was accelerating slightly some of the propulsive energy would be used in overcoming inertia and the speed measured would be less than when a steady speed was reached at that particular frequency of beating. Similarly, if the fish was decelerating then the speed measured at a particular frequency would be greater than the steady speed. While every care was taken to make records only at steady speeds, slight variations might perhaps escape detection. Most of the scatter can, however, be shown to be dependent upon variations in amplitude of the tail beat.

It did not prove possible to measure amplitude with any accuracy in the smaller specimens, but in the larger ones this was relatively easy. The average was made of ten randomly selected measurements taken from the plotted course of the fish's tail for each length of film representing a period of steady swimming. The distance measured was from one extreme lateral position of the tail to the line joining the preceding and succeeding extreme positions on the opposite side of the body. This gives the tip-to-tip amplitude which, while varying somewhat during any recorded period of steady swimming, was generally fairly constant. Fig. 5 shows the distance travelled per beat plotted against the amplitude for the 24.0, 17.5 and 9.0 cm. specimens. As would be expected, the distance travelled per beat increases with

increase in amplitude, and the relationship appears to be linear between the amplitude limits of 1 and 6 cm.

These limits are interesting. In no case does the amplitude exceed one-quarter of the body length. Amplitudes normally range between 4.5 and 5.5 cm. for the 24.0 cm. specimen, between 3.0 and 4.0 cm. for the 17.5 cm. specimen, and between 1.0 and 2.0 cm. for the 9.0 cm. one. At frequencies above 5 beats per second the ratio of mean amplitude to body length is about 1:5 (Table 2, p. 123) and the ratio of maximum amplitude to body length is about 2:9.

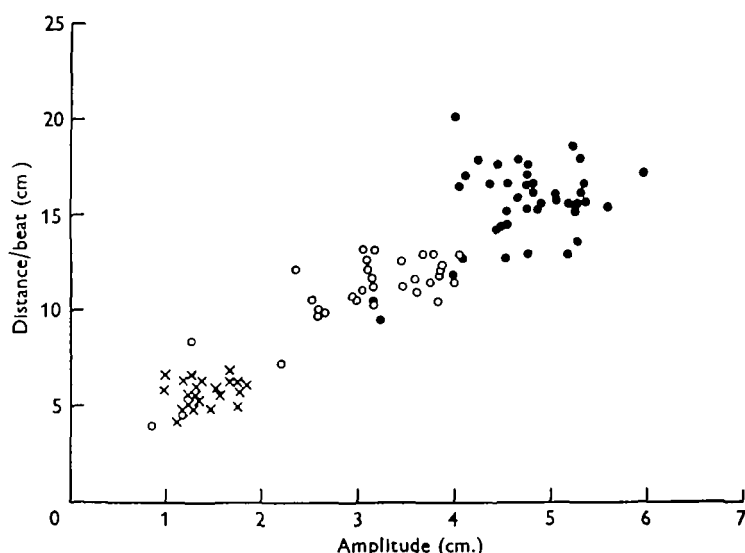


Fig. 5. Relationship between distance travelled per beat and amplitude for 3 dace measuring 24.0 cm. (black circles), 17.5 cm. (white circles) and 9.0 cm. (crosses).

As shown in Fig. 6, for the 24.0 and 17.5 cm. specimens only, amplitude increases rapidly with frequency from the lowest values recorded up to about 5 beats per second, but after this remains steady, with possibly a slight gradual decline at higher frequencies. In this may lie the explanation of the form of the speed/frequency graph shown in Fig. 3E. At frequencies below 5 beats per second the distance travelled per beat will be low by reason of the reduced amplitude; but the amplitude will increase with increasing frequency until at about 5 beats per second the amplitude reaches its maximum value and the distance travelled per beat becomes constant; thereafter the speed/frequency relationship will be linear.

If an equal degree of variability of amplitude is characteristic of all frequencies and if speed is related to amplitude multiplied by frequency, then the variability of speed at high frequencies might be expected to be greater than that at low ones. This may account for the slightly fan-like distribution of points in the speed/frequency graphs.

The final factor limiting the maximum speed attainable by any particular specimen would thus appear to be the frequency of beating of the tail. Fig. 7 shows the

maximum frequencies recorded for the various specimens studied (black circles). While there is no means of knowing that these are really the absolute maximum frequencies that may be reached by these animals there seems little reason to doubt

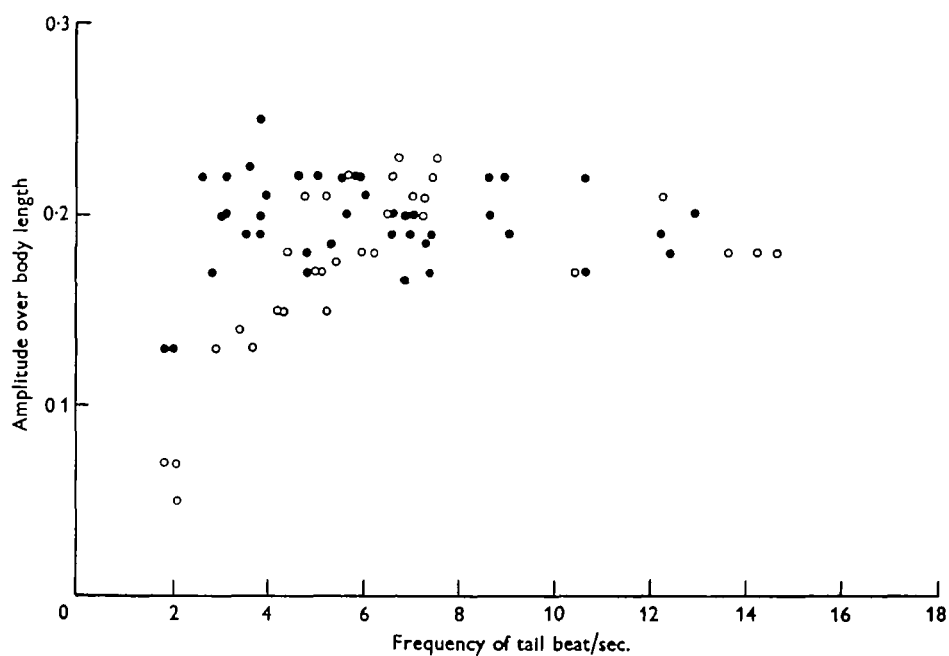


Fig. 6. Relationship between frequency and amplitude expressed non-dimensionally for two dace measuring 24.0 cm. (black circles) and 17.5 cm. (white circles).

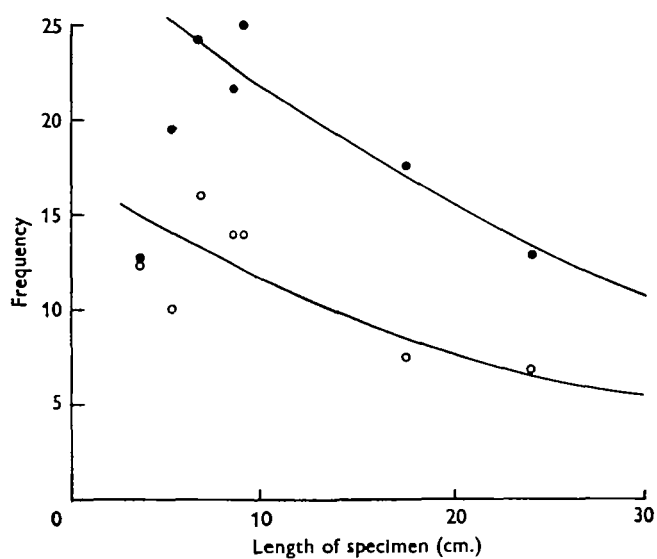


Fig. 7. Maximum recorded (black circles) and maximum sustained (white circles) frequencies for dace of different lengths. For further explanation see text.

that this is generally so, except for the smallest specimen of all. It thus appears that the larger specimens are unable to wag the tail as rapidly as the smaller ones. The implication of this in the prediction of the speed of much larger fish is considered later. The maximum frequencies recorded are rarely sustained in the wheel for any length of time. A more interesting parameter could therefore be the maximum frequency that can be sustained indefinitely. This may possibly be obtained by an examination of the distribution of recorded frequencies for each fish (i.e. as shown in Fig. 16 for a goldfish). When this is done for the 17.5 cm. dace in Fig. 3A, for example, there appears to be a discontinuity at 7.5 beats per second; while for the 9.0 cm. dace in Fig. 3C this happens at about 14.0 beats per second. It is here suggested that these discontinuities arise because of the small number of occasions upon which the maximum sustainable speed was exceeded for long enough to tempt the experimenter into taking a ciné record. Assuming that the experimenter made the same effort to obtain representative records for each size of fish it is possible tentatively to identify the discontinuity with the maximum sustainable frequency. Such values for all the specimens are also plotted in Fig. 7 (white circles) and seem to approximate to a curve at about half the maximum attainable frequency. The use of this curve in prediction is also considered later.

Summarizing, we may say that the speed of the various dace studied is dependent upon the length of the specimen and the frequency and the amplitude of the tail beat. Above about 5 beats per second the amplitude has reached a steady maximum value making the relationship between speed and frequency thereafter linear. The maximum speed attainable depends upon the maximum frequency, which decreases with increasing size of the fish.

The trout, Salmo irideus

The results obtained using four trout may now be considered. Fig. 8A-D shows the speed/frequency relationship of these specimens, measuring respectively 29.3, 23.2, 13.5 and 4.0 cm., and Fig. 8E shows speed over body length plotted against frequency for all the fish. The relationship here appears to differ slightly from that for the dace at the lowest frequencies and can most simply be represented by a straight line cutting the abscissa at a frequency of about 2 beats per second, an interpretation supported by the relationship between frequency and the distance travelled per beat over body length (graph not reproduced). This tendency for the line to cut the abscissa at a finite frequency of 2 beats per second is especially clear in the results for the 13.5 and 4.0 cm. specimens. The results for the latter, kindly provided for me by Mr T. G. Northcote, are interesting in combining two techniques. The values down to about 6 or 7 cm. per second were obtained with the small fish wheel; those below this by photographing the fish in an experimental flume through which a steady current of water was flowing. These two sets of points fall well into line and are mutually corroborative.

The dependence of speed upon amplitude is also apparent for these fish. The mean amplitude for each period of steady swimming has again been calculated, and for the 29.3, 23.2 and 13.5 cm. specimens distance travelled per beat is plotted

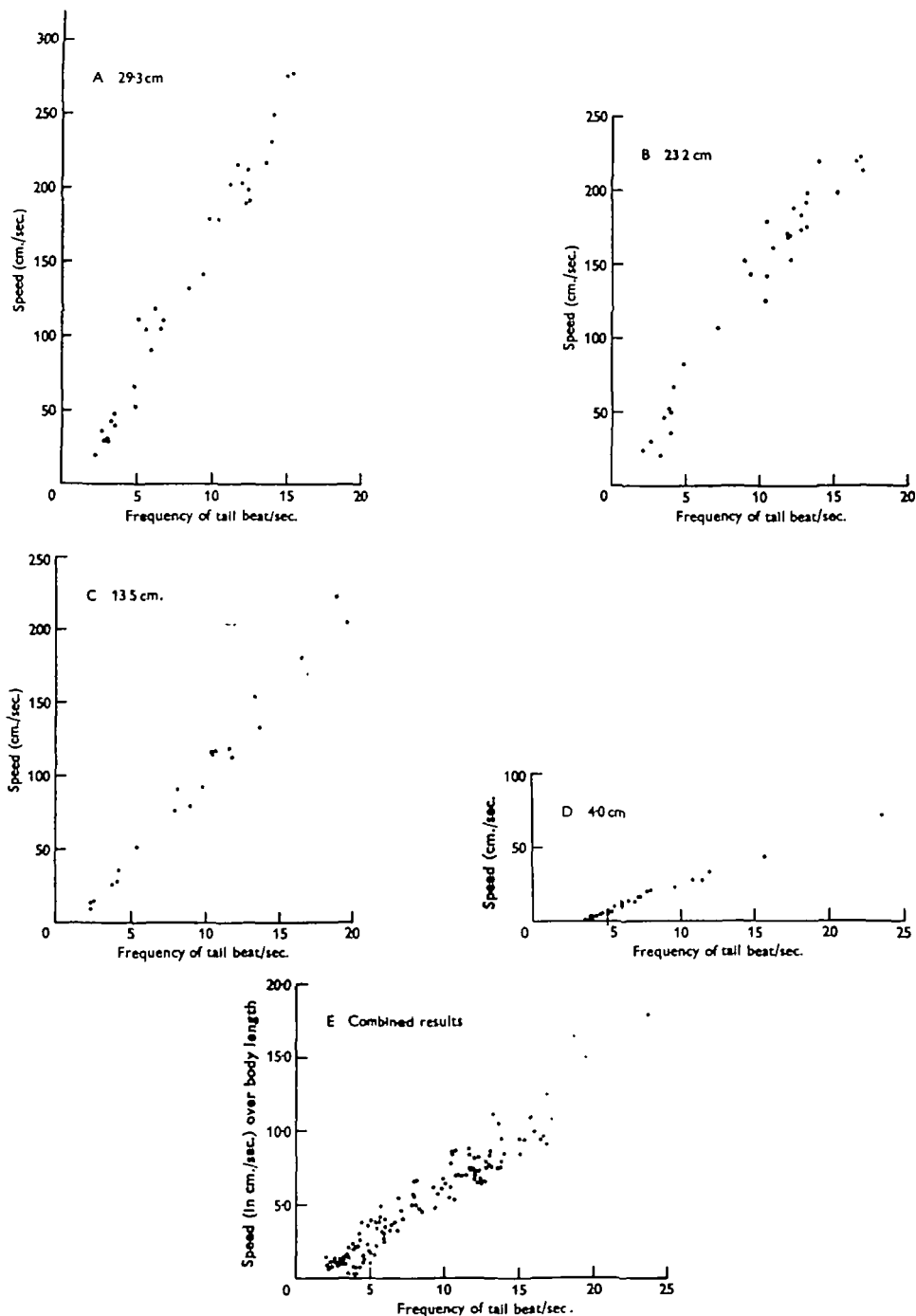


Fig. 8. Relationship between speed of swimming and frequency of beating of the tail for specimens of the trout (*Salmo irideus*). A 29.3, B 23.2, C 13.5 and D 4.0 cm. long. E shows all these results with the speed expressed non-dimensionally as body lengths per second.

against amplitude in Fig. 9. The relationship again appears linear and bears a close resemblance to that for the dace. The slope of the line is perhaps a little steeper, indicating a greater efficiency at higher amplitudes. Table 2 shows that the mean amplitude is little different, length for length, from that of the dace. The scatter in Fig. 9 shows it to be rather more variable, however, and this may be a reflexion of the greater excitability of the trout.

The relationship of amplitude over body length to frequency (Fig. 10) for the three larger fish differs from that for the dace in not showing a decrease in amplitude

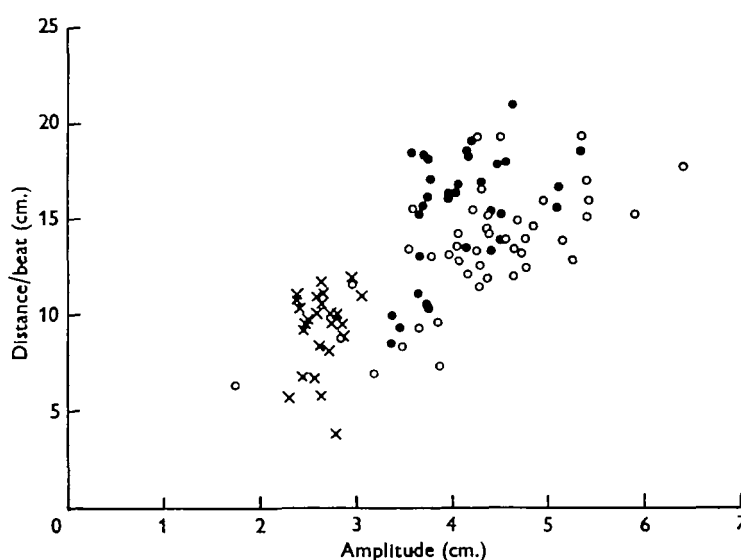


Fig. 9. Relationship between distance travelled per beat and amplitude for three trout measuring 29.3 cm. (black circles), 23.2 cm. (white circles) and 13.5 cm. (crosses).

Table 2. *Values of mean amplitude over body length at the maximum steady amplitude*

Fish	Size (cm.)	No. of observations	Mean $\frac{\text{amplitude}}{\text{body length}}$
Dace (frequencies > 5)	9.0	23	0.153
	17.5	22	0.197
	24.0	25	0.198
		Total 70	0.183
Trout (frequencies > 5)	13.5	19	0.197
	23.2	29	0.197
	29.3	32	0.137
		Total 80	0.174
Goldfish (frequencies > 3)	15.2	24	0.196
	22.5	13	0.212
		Total 37	0.202
		Grand total 187	Grand av. 0.183

at lower frequencies; and this confirms the interpretation just placed upon the speed/frequency graphs. Inspection of the points for the individual fish, however, shows a slight decrease for the 23.2 cm. specimen (open circles), which the wide scatter of the other points conceals. This raises the possibility that the speed/frequency graph is not linear at the very lowest frequencies. There is also an indication of a slight decrease in amplitude at higher frequencies, especially with the 23.2 cm. fish, and this of course would have the effect of making the speed/frequency graph sigmoid.

These differences from the dace are, however, trivial compared with the close resemblances. Not only are the mean *amplitudes* almost identical but also, in

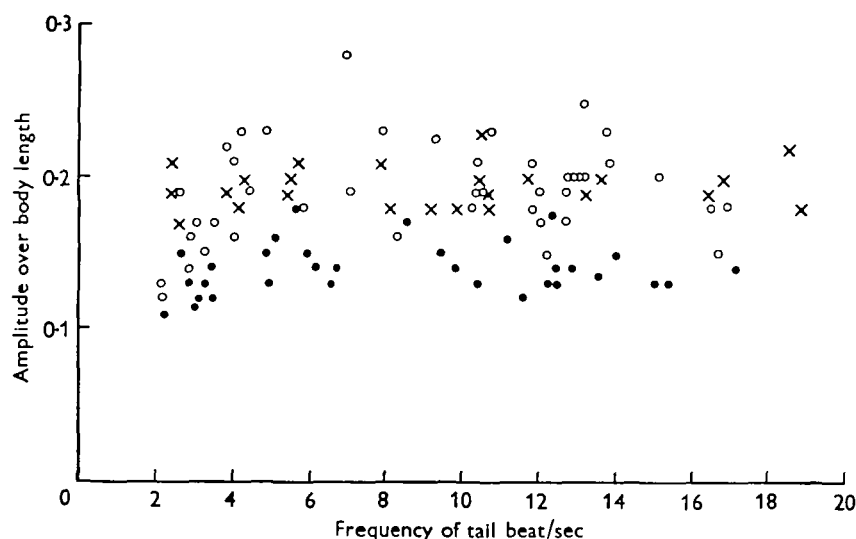


Fig. 10. Amplitude expressed non-dimensionally and plotted against frequency for the three trout shown in Fig. 9.

consequence, the mean *distances travelled per beat over body length* (Table 3). This means that, disregarding frequencies below 5 beats per second, both dace and trout have speed/frequency relationships that are virtually identical. In view of their similarity in body form some such finding might be expected, but the almost exact identity revealed is surprising.

Finally, the maximum frequencies attained by the various specimens studied are shown in Fig. 11. As with the dace a decrease in maximum frequency with increasing length is apparent; but this decrease is by no means as marked, reflecting the fact that the larger trout can reach relatively greater maximum speeds than the larger dace. The uniform distribution of recorded frequencies throughout the measured ranges in the speed/frequency graphs precludes any estimate of a maximum sustained frequency. (The disproportionate number of low measurements for the 4.0 cm. specimen derives from a deliberate attempt to record speeds as low as possible, and this graph differs in this respect from all the other records.) Indeed,

during the measurements all the trout seemed capable of sustaining even the highest frequencies and speeds for much greater periods than the dace and were consequently much easier to work with.

Table 3. *Values of mean distance travelled per beat over body length at the maximum steady amplitude*

Fish	Size (cm.)	No. of observations	Mean $\frac{\text{distance/beat}}{\text{body length}}$
Dace (frequencies > 5)	3.6	5	0.52
	5.2	21	0.63
	6.6	40	0.60
	8.5	18	0.56
	9.0	48	0.64
	17.5	22	0.67
	24.0	25	0.68
	Total	179	0.63
Trout (frequencies > 5)	4.0	18	0.52
	13.5	19	0.76
	23.2	29	0.62
	29.3	25	0.58
	Total	91	0.62
Goldfish (frequencies > 3)	4.6	8	0.57
	7.0	21	0.59
	9.5	30	0.54
	15.2	24	0.68
	22.5	13	0.68
	Total	96	0.61
		Grand total	366
		Grand av. 0.62	

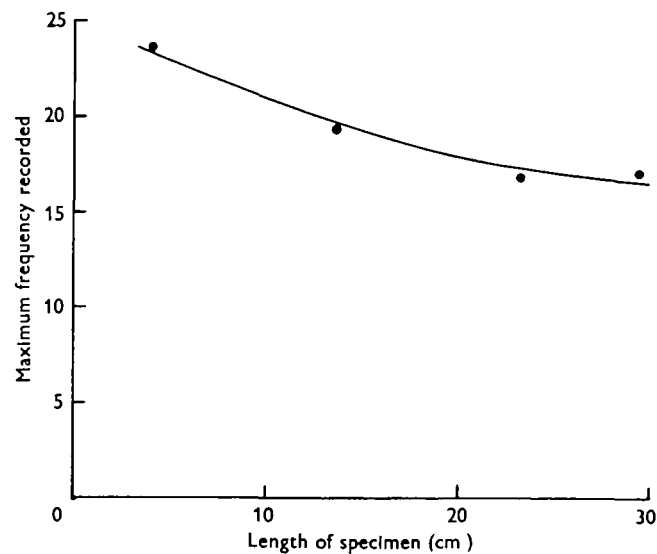


Fig. 11. Maximum recorded frequencies for the four trout shown in Fig. 8.

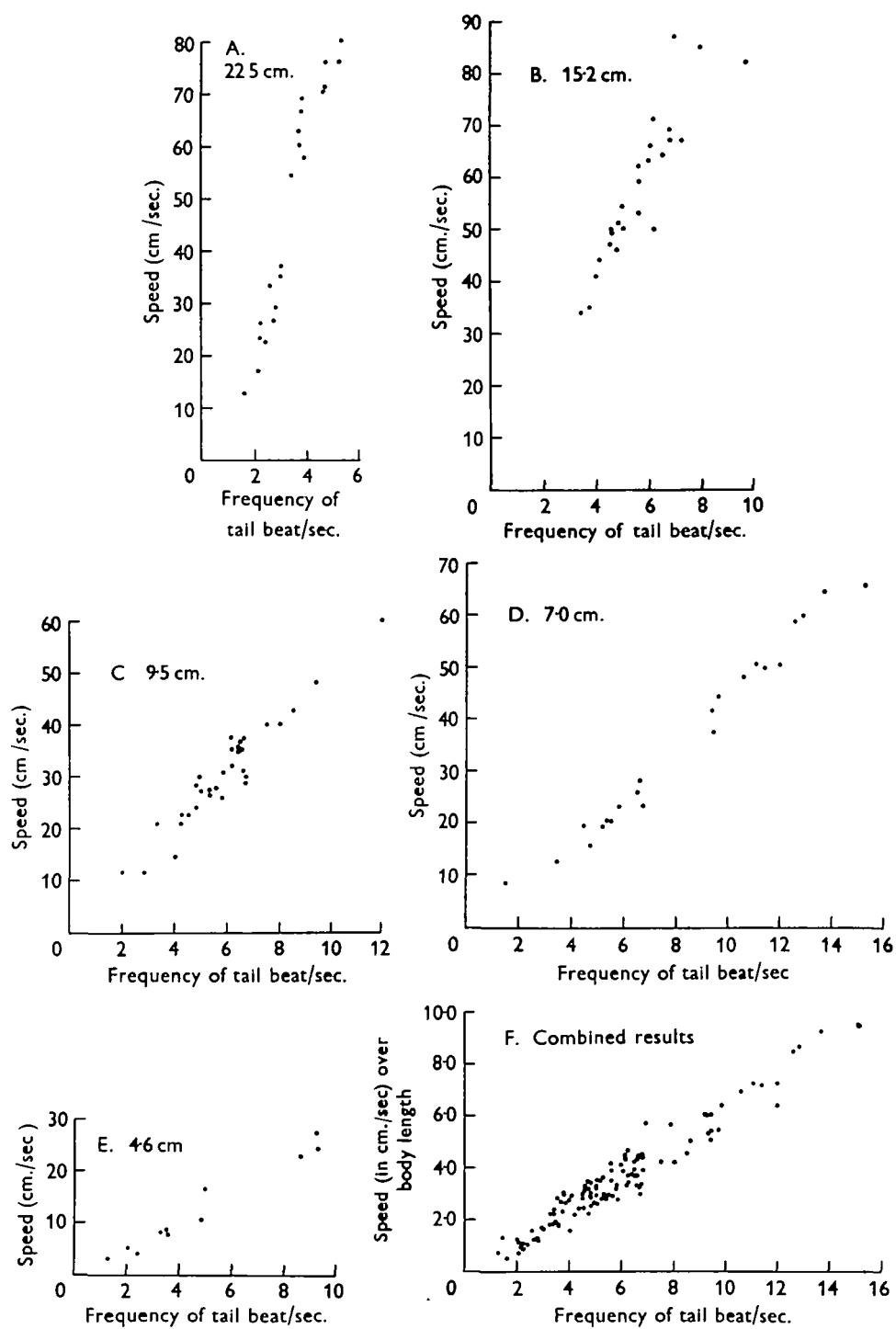


Fig. 12. Relationship between speed of swimming and frequency of beating of the tail for specimens of the goldfish (*Carassius auratus*). A 22.5, B 15.2, C 9.5, D 7.0 and E 4.6 cm. long. F shows all these results with the speed expressed non-dimensionally as body lengths per second.

Summarizing we may say that for the trout as for the dace speed is again dependent upon length, frequency and amplitude. There is little recognizable variation of amplitude with frequency, the speed/frequency relationship is entirely linear and is identical in form with that for the dace above 5 beats per second. Length for length, greater maximum frequencies and hence greater maximum speeds are attainable by the trout.

The goldfish, Carassius auratus

Graphs of speed plotted against frequency for the five goldfish studied are shown in Fig. 12 A-E. The specimens range in size from 22.5 to 4.6 cm. As with the trout the relationship again appears to be linear and this is made clearer, together with a confirmation of the essential dependence upon length, in Fig. 12 F, which shows speed over body length plotted against frequency. The plot of distance travelled per

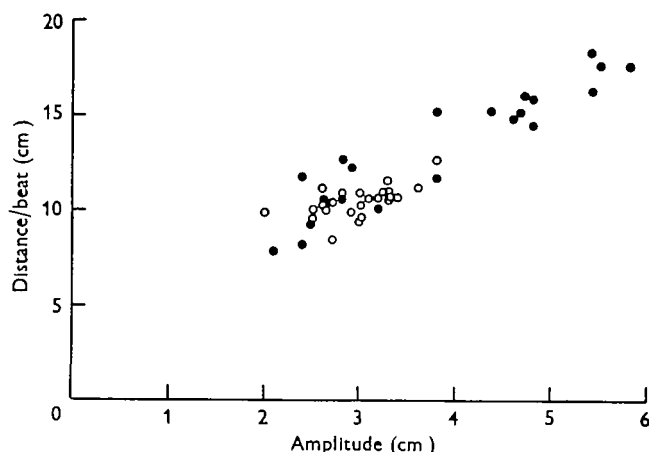


Fig. 13. Relationship between distance travelled per beat and amplitude for two goldfish measuring 22.5 cm. (black circles) and 15.2 cm. (white circles).

beat against frequency (graph not reproduced), which is more sensitive as an indicator of non-linearity at lower frequencies, suggests that there may be a very slight bend below about 3 beats per second, but this is not very clear.

The variability of amplitude and the dependence of speed upon this are even more clearly seen in the two largest goldfish. Fig. 13 shows the relationship between amplitude and distance travelled per beat for these two fish. With the 22.5 cm. specimen the relationship is linear over a range of amplitude from 2 to 6 cm. The slope of this line is almost identical with that for the dace. The range of amplitude variation for these two fish appears greater than that in most of the others, but the correlation with distance travelled per beat is much better. Calculated for frequencies greater than 3 beats per second, the mean amplitude over body length (Table 2) is a little higher than that for the dace and trout, but the distance travelled per beat over body length (Table 3) is identical.

The plot in Fig. 14 of amplitude over body length against frequency for the two fish measured reveals, especially with the 22.5 cm. specimen, what may be a slight

decrease in amplitude at low frequencies. From this it could be deduced that the speed/frequency relationship is not linear at low frequencies but resembles that for the dace. If this is so, the deviation from linearity is so slight as not to be apparent with the small number of points involved.

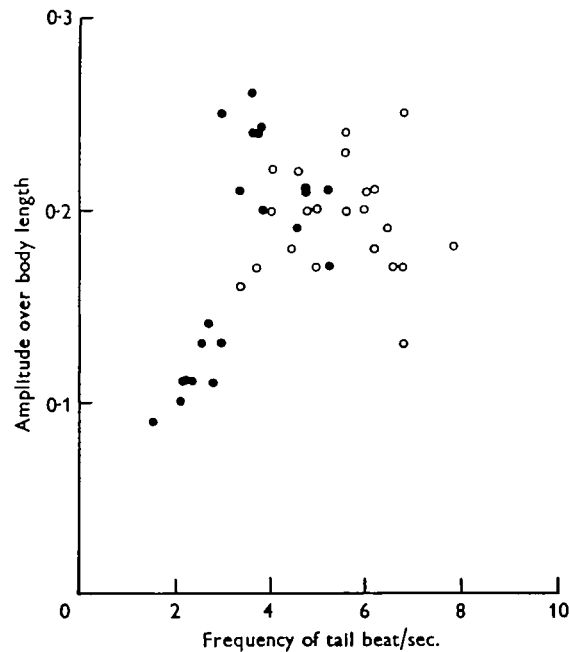


Fig. 14. Amplitude expressed non-dimensionally and plotted against frequency for the two goldfish shown in Fig. 13.

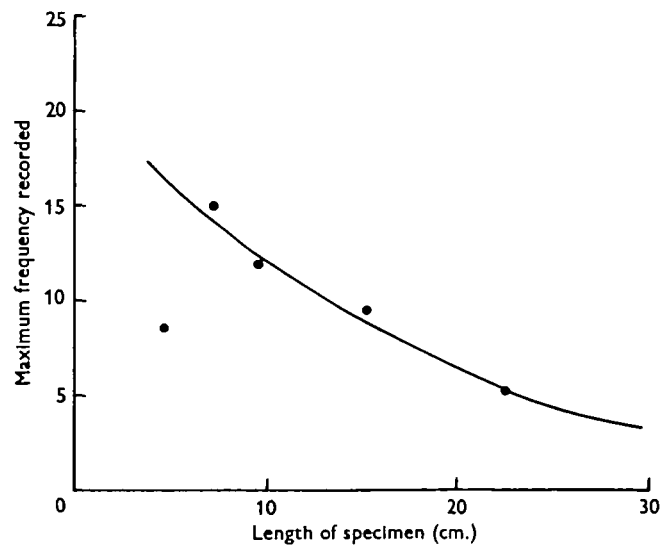


Fig. 15. Maximum recorded frequencies for the five goldfish shown in Fig. 12.

Since for the goldfish distance travelled per beat over body length is the same as for the other two genera, it follows that the linear portion of the speed/frequency graph is also the same for all. In view of the markedly different form of the goldfish body this must occasion more surprise than the resemblance between the dace and the trout. The goldfish differs from the others most obviously in the much lower maximum speed of which it appears capable, of the order of one-third of the maxima for the other two species, length for length. The identity of the speed/frequency graphs makes it clear that this limitation is imposed upon the goldfish by an inability to beat the tail more rapidly rather than, say, by inefficiency of the tail mechanism or higher resistance of the body.

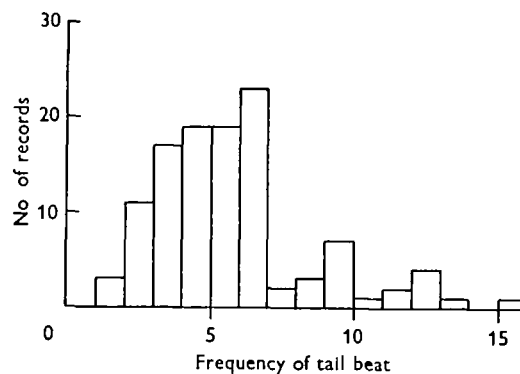


Fig. 16. Number of records at different frequencies for the five goldfish shown in Fig. 12. For further explanation see text.

The maximum frequencies recorded for the various goldfish are shown plotted against length in Fig. 15. Except for the smallest specimen, which we may presume was not at its limit, the points fall on a curve of the same general form as for the dace and the trout, but differing in that (i) the highest figure for the smallest specimens is 15 beats per second compared with about 25 for the other two species, and (ii) the lowest figure is 5 beats per second compared with 14 for the dace and 17 for the trout. These differences are reflected in the much poorer all-round performance of the goldfish. Except for the 9.5 cm. specimen the records are again fairly uniformly distributed throughout the frequency range, and it is not possible to recognize a maximum sustainable speed. Nevertheless, the impression from the experimentation remains that there probably is one and that it is fairly low, possibly corresponding to about 6 beats per second. This is supported by the histogram in Fig. 16 which shows the frequency distribution of all the records of frequency of tail beat made for the five goldfish. A limit below 7 is very clear and this would correspond to a speed of about 3.5 body lengths per second.

Summarizing, we may say that for the goldfish speed is related to length, frequency and amplitude in a manner identical with that found for both the trout and the dace. The maximum frequencies attained by the goldfish are about three-fifths of those for the trout and the dace, and the maximum speeds are correspondingly lower.

DISCUSSION

The three sets of results described have certain features in common. In all cases the direct dependence of speed at any particular frequency upon length and also upon amplitude is substantiated. Above about 5 beats per second for the dace and trout and above 3 beats per second for the goldfish the amplitude, and hence the distance moved per beat, are at a maximum. Above these frequencies the speed/frequency relationship must therefore be linear, as indeed the speed/frequency graphs show.

When distance moved per beat is plotted against amplitude for the three species studied, not only are the relationships similar but so are the absolute values. Figs. 6, 9 and 13 may all be superimposed, and the dace and goldfish points lie well within the scatter of the trout ones. This similarity is at once striking and puzzling. If the form of the body had a marked influence on the speed attained it is in these graphs that differences would be most apparent; but there is little indication of any dependence of speed upon the shape of the body. The hydrodynamical implications of this fact are yet to be considered.

If speed over body length (Figs. 3E, 8E and 12F) is plotted against frequency (discarding frequencies of less than 5 beats per second) the points, as expected, are found to lie well on a single line. This line has a slope of 1 in $1\frac{1}{3}$ and it cuts the abscissa at a frequency of $1\frac{1}{3}$. It can, therefore, be expressed conveniently by the equation $V = \frac{3}{4}\{L(f - 1\frac{1}{3})\}$ or $V = \frac{1}{4}\{L(3f - 4)\}$ where V is the speed in cm. per second, f the frequency in beats per second and L the length of the specimen in cm. This gives a single simple equation by means of which the speed of any specimen of the three species considered may be calculated from its length and the frequency of beating of the tail. While theoretically the equation applies only to frequencies greater than 5 beats per second, the deviation below this value is so slight as to make no material difference to the calculated speed except in the case of the smallest specimens.

At frequencies below 3–5 beats per second the exact form of the speed/frequency graph is not clear and one may be tempted to distinguish fundamental differences between the three species. However, in all cases at low frequencies the amplitude varies with frequency. This fact is especially clear with the 24.0 and 17.5 cm. dace, with the 23.2 and 13.5 cm. trout and with the 22.5 cm. goldfish. It implies that all the fish are responding similarly, although in some cases the small number of points at low frequencies and the smallness of the differences prevent this being apparent. Thus, at these low frequencies the amplitude itself is apparently related to the frequency and the speed is therefore related to the square of the frequency. This dual dependence upon frequency produces a curve which may or may not go through the origin. In the dace it probably does so, in the trout not. In the goldfish it probably goes through the origin, but becomes linear earlier than in the others, since the amplitude reaches its maximum sooner.

Preoccupation with these small differences at low frequencies must not divert our attention from the striking identity of the relationship at higher frequencies; and in considering the prediction of the maximum speeds attainable by larger fish it is

legitimate to ignore such differences. Making the assumption that the equation $V = \frac{1}{4}\{L(3f - 4)\}$ is applicable to fish of any size and species we may consider how calculated values of speeds for larger fish compare with such as have already been reported in the literature. In calculating possible maximum speeds the upper limit of f remains as the controlling factor. Unfortunately, a certain amount of conjecture is involved in estimating its maximum value for bigger fish, our only evidence being the trends in Figs. 7, 11 and 15. Taking first the values for the trout in Fig. 11 it appears by extrapolation that a 100 cm. specimen (*ca.* 3 ft.) might have a maximum frequency of *ca.* 14 beats per second. Substituting in the equation above, this would give a top speed of $9.5L$ or 950 cm. per second, that is about 20 m.p.h. This figure compares favourably with the first of Gray's (1953) calculations of $9.2L$ and $12.2L$ for a 3 ft. salmon assumed jumping 6 and 10 ft. out of the water. On the other hand, his photographic record giving $8.5L$ for a 20 cm. rainbow trout is probably low, as such a specimen could easily attain a maximum frequency of 18 and a consequent speed of $12.5L$.

Gero's (1952) value of $9.4L$ for a 51.0 in. barracuda (130 cm.) also seems reasonable if this fish is thought to be as efficient as the trout. Its maximum frequency might be down to 13, which would give a velocity of $8.8L$. The value given by Lane (1941) for a 60 lb. tuna of $13.4L$ per second does however seem surprisingly high. This fish, weighing 60 lb., may be calculated as 147 cm. long and its maximum frequency on the trout scale could hardly be over 12, giving a speed of $8.0L$. Assuming the accuracy of the estimate of speed the tuna must then be thought of as being highly efficient compared with the trout. The last very high figure is that of Denil (1937) for a 25 cm. trout reported as leaping 1 m. It would seem very unlikely that such a specimen could exceed a speed of $12.0L$ and his value of 19.4 must be counted as exaggerated. Such reasonable confirmation of speeds of the order of 10 or $12L$ per second for larger fish emphasizes again the physiological problems involved in driving the tail sufficiently rapidly to produce such speeds for any length of time. These problems, that of drag at the body surface and the functioning of the tail as an organ of propulsion, may be considered at some later time.

These calculations have all been based on the assumption of a diminution in frequency with length, similar to that seen in the trout. The maximum frequency curve for the dace shows a much more rapid decline and any extrapolation based on it would give values substantially less. Such figures might be comparable with the low speeds given by Gero (1952) for some of the sharks.

While the dace and trout may be looked upon as fairly similar in their general behaviour, the goldfish differs fundamentally in having its maximum speed so markedly limited by the frequency of beating of the tail. Its mean maximum amplitude of beating is $0.202L$ compared with $0.174L$ for the trout and $0.183L$ for the dace (Table 2). Despite this slightly higher amplitude the goldfish travels a slightly shorter distance for each beat of the tail at its maximum amplitude: the mean values for distance travelled per beat being: goldfish $0.61L$, trout $0.62L$ and dace $0.63L$. These values are all well within the limits of variability for each series of fish (Table 2), and it must be assumed that the mean maximum amplitude and

hence the distance travelled per beat is the same for all three species. In the case of the goldfish this is surprising as its body shape is such as to present a greater resistance to passage through the water than in the case of the dace and the trout, which resemble each other closely. The explanation may lie in its greater tail area and the laterally flattened peduncle which may also provide greater thrust. The greater power needed to propel it the same distance per beat with a bigger tail would also impose a lower maximum frequency upon a fish of any given length.

Since the calculated values correspond reasonably well with such recorded values as exist for the speed of larger fish, we may draw the following conclusions. The speed of any fish may be calculated from the formula $V = \frac{1}{4}\{L(3f-4)\}$. The maximum values of f attainable vary according to the species; for 30 cm. specimens of dace, trout and goldfish they may be taken as 11, 17 and 3, respectively. Above this size prediction depends upon the relation between maximum frequency and length. For a trout type the decline of frequency with length seems to be gradual and values may be as high as 15 for a 60 cm. fish and 14 for a 100 cm. one. For a dace and a goldfish type corresponding values might be down to 1 or 2, and in any case with these fish the maximum frequency may not be sustained for any length of time. A maximum sustainable frequency for these fish would perhaps be about half the maximum attainable one.

There seems every likelihood that the linear relation between speed and frequency should apply to much bigger fish. It may, therefore, be possible to assess the speed of large fish not by timing, which in nature is very difficult, but simply by listening to and recording the sound of their tail beat. The development of a hydrophonic device for picking up and recording the frequency of these sounds should not be insuperably difficult and would open up the possibility of rewarding field work.

SUMMARY

1. An apparatus is described in which it is possible to study and record the continuous swimming of fish at speeds up to 20 m.p.h.
2. Records made of the swimming at different speeds of dace, trout and goldfish measuring up to 30 cm. in length are reproduced.
3. Speed at any particular frequency of tail beat is shown to be directly related to the length of the specimen, measured from the tip of the snout to the most posterior extremity of the tail.
4. Above a frequency of 5 tail beats per second speed is directly dependent upon frequency up to the maximum values recorded. The results for all sizes and species recorded may be adequately expressed by the formula $V = \frac{1}{4}\{L(3f-4)\}$, where V is the speed in cm. per sec., f is the frequency in beats per sec. and L is the body length in cm.
5. The distance travelled per beat (and hence the speed) is directly dependent upon the amplitude of the tail beat.
6. The amplitude increases with increasing frequency up to a maximum reached at about 5 beats per second. This maximum amplitude is the same for all fish tested and is about one-fifth of the body length.

7. The maximum frequency attainable decreases with increasing size of the specimen. This decrease is slight in the trout and more pronounced in the dace and goldfish. Estimation of the possible maximum frequencies of much bigger fish allows for prediction of the maximum speeds they may be able to attain. Such predicted speeds are in accord with the few measurements that have been made and are of the order of 10 body lengths per second up to a size of 1 m.

I am indebted to Professor Sir James Gray, F.R.S., for his continued helpful interest in this work; to Dr R. H. J. Brown who shared in the construction of the large wheel; and to Messrs Watts, Watts and Company Ltd., the British Steamship Company Ltd. and the British Thomson-Houston Company Ltd. for their generous gifts which made possible the building of the large apparatus.

REFERENCES

- BAINBRIDGE, R. & BROWN, R. H. J. (1958). An apparatus for the study of the locomotion of fish. *J. Exp. Biol.* **35**, 134-7.
- DAHL, K. & SØMME, S. (1936). Experiments in salmon marking in Norway, 1935. *Skr. norske Vidensk. Akad. I. Matem. Naturvid Klasse* 1935. No. 12, 1-27.
- DAVIDSON, M. VIOLA (1949). Salmon and eel movement in constant circular current. *J. Fish. Res. Bd. Can.* **7**, 432-48.
- DENIL, G. (1937). La mécanique du poisson de rivière. Chapitre X. Les capacités mécaniques de la truite et du saumon. *Ann. Trav. publ. Belg.* **38**, 412-33.
- FRY, F. E. J. & HART, J. S. (1948). Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Bd. Can.* **8**, 169-75.
- GERO, D. R. (1952). The hydrodynamic aspects of fish propulsion. *Amer. Mus. Novit.* no. 1601, 1-32.
- GRAY, J. (1953). The locomotion of fishes. In *Essays in Marine Biology*, 1-16. Edinburgh: Oliver and Boyd.
- HARDY, A. C. & BAINBRIDGE, R. (1954). Experimental observations on the vertical migrations of plankton animals. *J. Mar. Biol. Ass. U.K.* **33**, 409-48.
- HECHT, S. (1916). Form and growth in fishes. *J. Morph.* **27**, 379-400.
- LANE, F. W. (1941). How fast do fish swim? *Ctry Life, Lond.*, 534-5.
- MAGNAN, A. (1930). Les caractéristiques géométriques et physiques des poissons. *Ann. Sci. nat.* **13**, 355.
- RADCLIFFE, R. W. (1950). The effect of fin clipping on the cruising speed of goldfish and coho salmon fry. *J. Fish. Res. Bd. Can.* **8** (2), 67-72.
- REGNARD, P. (1893). Sur un dispositif qui permet de mesurer la vitesse de translation d'un poisson se mouvant dans l'eau. *C.R. Soc. Biol., Paris*, Ser. 9, **5**, 81-3.
- STRINGHAM, E. (1924). The maximum speed of fresh water fishes. *Amer. Nat.* **58**, 156-61.
- WALES, J. H. (1950). Swimming speed of the western sucker *Catostomus occidentalis* Ayres. *Calif. Fish Game*, **36**, 433-4.