

THE SWIMMING ENERGETICS OF TROUT

I. THRUST AND POWER OUTPUT AT CRUISING SPEEDS

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(Received 30 March 1971)

INTRODUCTION

Studies on the energetics of swimming of fish have always been restricted by the absence of data on the drag experienced by *swimming* fish. This has forced biologists and mathematicians to calculate the swimming drag on the assumption that it is the same as that experienced by an equivalent straight rigid body. The assumption is made on the basis of the observation first made by Sir George Cayley (*c.* 1809) that all fast-swimming fish have streamlined body shapes. These shapes are often similar to those of man-made vehicles designed to have a low drag (Hertel, 1966). Therefore, swimming drag has been calculated from standard hydrodynamic equations for man-made vehicles which are similar in form to fish (Gray, 1936; Bainbridge, 1961; Osborne, 1961; Smit, 1965); alternatively, the drag of fish themselves has been measured with the body stretched straight (Brett, 1963; Mearns *et al.*, personal communication).

Webb (1970) and Webb & Brett (in preparation) have shown that neither of the above methods is likely to give valid estimates of swimming drag. This conclusion is based on the published observations on the flow around swimming fish, which differs markedly from that expected for an equivalent rigid vehicle. It is expected that the drag on most swimming fish will be substantially higher than that of such vehicles.

Several studies have been made to measure the thrust and power output of swimming fish. Houssay (1912) attached fish to an ingenious balance, so that when the fish moved it was forced to lift weights of various sizes. Unfortunately, the fish were forced to swim in a tight arc, which undoubtedly reduced their performance (Bainbridge, 1958). Moreover, work was done in overcoming the resistance of the fish, and that part of the balance submerged in the water. The weights on the balance were situated a long way from the fulcrum so that the fish had to do a substantial amount of work against the inertia of the system. These fractions of the total work done were not taken into account.

Gero (1952) measured the strain on a line attached to fish swimming away from a boat. Gero points out that this method is unreliable if the fish does not swim in line with the tackle and boat. He also recognizes that the tackle must have interfered with the fish. The fish had to do work to overcome its own drag and that of the tackle submerged in the water. Hence only the thrust in excess of this was measured.

Some estimates of peak power output of fish and dolphins have been measured

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from acceleration rates and from leaps from the water (Gero, 1952; Lang & Daybell, 1963; Gray, 1968).

In practice, all the methods of measurement have been related to peak power outputs of fish, and then only a fraction of this power output has been measured. Thus it is difficult to relate the values obtained to more normal swimming behaviour, or to construct a thrust/swimming speed curve.

An alternative method of calculating the swimming thrust and power output is from one of the many mathematical models which take into account the undulating form of the body during swimming. This method has never been used, probably because most models require detailed measurements of numerous parameters of the swimming movements. However, recent papers by Lighthill (1969, 1970) contain a simple method for calculating swimming power outputs of some fish, including salmonids. It was therefore of great interest to devise a means for testing its accuracy.

This paper seeks to measure the drag on a swimming fish by adding extra drag loads to rainbow trout swimming at cruising speeds. The drag of the loads can be related to certain parameters of the propulsive wave in order to calculate the drag of an unloaded fish. This is an extension of the observations made by Bainbridge (1958), who showed that tail-beat frequency and amplitude were related to swimming speed. Since drag is proportional to swimming speed, it follows that drag will also be proportional to these characteristics of the propulsive wave.

MATERIALS AND METHODS

The Brett respirometer and the photography of swimming fish

A copy of the water-tunnel respirometer described by Brett (1964) was modified for the ciné-filming of swimming fish. The original round chamber was replaced by a square chamber constructed from $\frac{1}{4}$ in. perspex sheeting (Fig. 1). An observation section 36 cm in length was delimited within the chamber by two grids, mounted on streamlined grid frames. The upstream grid frame was orientated to improve water flow in the corners of the observation section. The downstream grid was removable and electrified, the grid being mounted on the leading edge of the grid frame so that fish could not use it as a backstop.

The corners of the chamber upstream and downstream of the observation section had fared corner strips, designed to prevent massive turbulence in the water flow in the observation section. The water flow in the observation section was found to have a good rectilinear flow profile, except in the corners. However, fish were unable to take advantage of this area of the chamber because of their size.

The water velocity in the observation section was checked against an electromagnetic flow-meter situated in the recirculation part of the respirometer. The free-stream velocity was measured independently, using (1) a standard pitot-static tube, (2) a double condenser system, and (3) by filming neutrally buoyant particles in the chamber (Webb, 1970; Webb & Brett, in preparation).

The back and bottom of the observation section were painted with black and white opto-motor stripes. These improved the station-holding ability of fish swimming in the observation section, and acted as calibration lines for the film. A mirror was mounted above the observation section at an angle of 45° in order to film dorsal and

lateral aspects of the fish synchronously. Illumination was provided by two 375 W photo-floods. Film was taken with a 16 mm Bolex camera at 64 ft/sec.

The temperature of the water was controlled at 15 ± 0.2 °C by a cold-water jacket working in conjunction with a thermistor-regulated 300 W radiant heater. Oxygen content of the water was maintained between 90 and 100% air-saturation by continuously pumping water out of the respirometer and through an aerating column before returning it to the system.

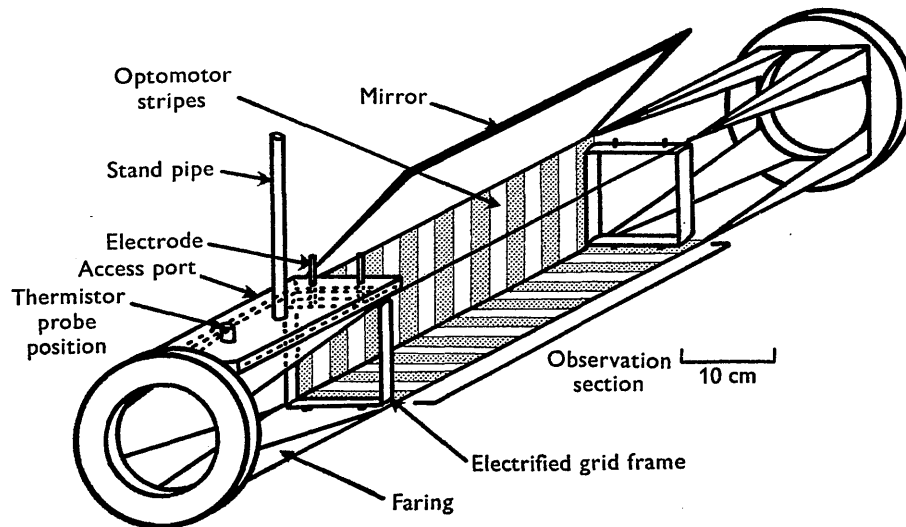


Fig. 1. The square fish chamber used in conjunction with the Brett respirometer for the photography of swimming fish.

Water-tunnel corrections

Because of the enclosed nature of the water tunnel, swimming fish experience a drag higher than that expected at any given free-stream velocity. Extra drag arises from horizontal buoyancy and solid-blocking effects (Pope & Harper, 1966). The former effect results from the growth of the boundary-layer along the chamber walls which tends to decrease the effective cross-sectional area of the tunnel through which water can flow. A pressure gradient is set up along the length of the chamber, which tends to suck the fish towards the exit and hence increase the drag. The solid-blocking effect arises from the increase in water velocity around the fish which results from the presence of that fish in an enclosed chamber. These corrections, as applicable to fish swimming in the fish chamber have been described by Webb (1970) and Webb & Brett (*loc. cit.*). The horizontal buoyancy effect could be accounted for by a correction to the free-stream velocity of about 1%. The solid-blocking effect could similarly be accounted for by a correction of 7.5 to 15% depending on the size of the fish.

In the case of swimming fish a 'propeller correction' is also necessary. This arises from pressure effects on the propeller jet, which results in an apparent thrust higher than expected. The correction applied to the free-stream velocity is about 1% and opposite in effect to the horizontal buoyancy correction (Webb, 1970; Webb & Brett, *loc. cit.*).

Since the horizontal buoyancy and propeller corrections are small and tend to

cancel out, swimming speeds reported in this paper have only been corrected for solid-blocking. The mean correction for each group of fish is included in Table 3.

Extra drag loads

Construction and attachment to fish

Drag loads of four sizes were made from grids and flat plates (Fig 2A). The load with the lowest drag was constructed from a grid of surgical thread mounted in a thin wire frame. The other three loads were constructed from $\frac{1}{16}$ in. perspex sheeting. Each load had a thin wire strut attached at its apex. The strut was free to move laterally in order that lateral movements of the fish should not be restricted. All metal parts were coated in lacquer.

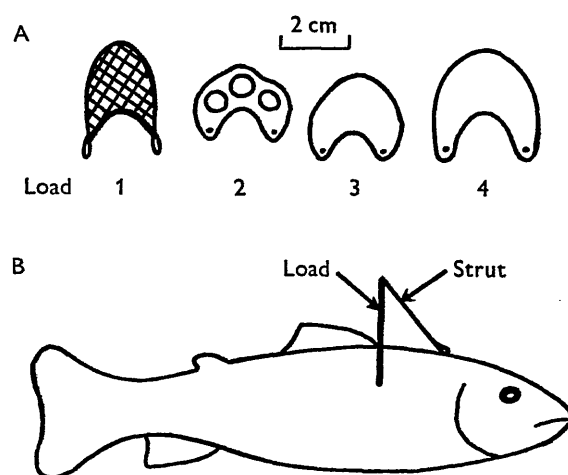


Fig. 2. The extra drag loads fitted to fish. (A) Frontal view of loads. (B) Side view of a load attached to a fish.

Loads were attached to the fish just anterior to the dorsal fin (Fig. 2B) while the fish was anaesthetized in 10 ppm MS 222. The loads were held in position by two sutures through the base of each load and the skin overlying the epaxial muscle. A third suture, through the distal end of the strut and skin, held the load vertical. This suture was well behind the brain case.

After the operation, fish were transferred to holding tanks for at least 14 h.

The drag of the loads

The drag of the loads was measured while they were attached to the freshly killed fish. This was done in the original round chamber using drag balances and methods described by Webb (1970) and Webb & Brett (*loc. cit.*), whereby the drag of a body could be measured with an accuracy of ± 0.02 g.

The drag of the loads was calculated from the difference in drag of the fish-plus-load and the drag of the fish alone. However, it was observed that the drag of freshly killed fish fell with time. This was attributed to rigor mortis stiffening the fish. Because of the decrease in fish drag with time, it was anticipated that the measurements of the load drag would be high. To check this, a model fish was constructed from wood. Lead weights were sealed in the centre to make the model neutrally buoyant.

Each load was then attached to the model, and the load drag was measured by the same method as on the dead fish.

The results for the measurement of the load drag are given in Table 1 (Fig. 3), as a function of the corrected velocity of the fish. The drag of the loads measured on the model was found to be very much lower than that measured on the dead fish.

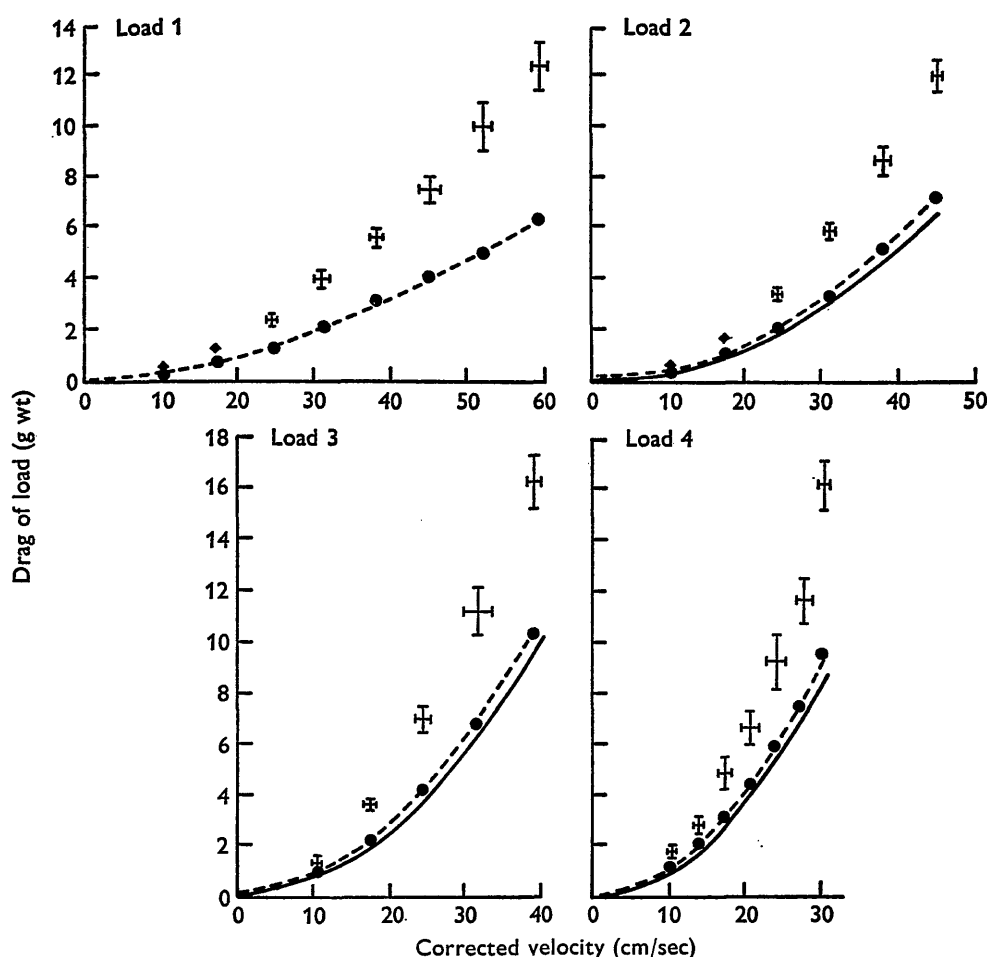


Fig. 3. The relationship between the drag of the loads attached to the fish and to a model, and the water velocity corrected for solid-blocking of the fish. Vertical horizontal bars represent the means and two standard errors of load drag and corrected velocity, respectively, for drag measured on freshly killed fish. ● — ●, Drag measured on a model fish. —, Represents the theoretical drag measured for loads 2-4.

The former drag was similar to the theoretical drag calculated from the standard hydrodynamic equations:

$$D = \frac{1}{2} \rho S (kV)^2 C, \quad (1)$$

where D = load drag (dynes), ρ = density of water (g/cm^3), S = wetted surface area of one side of the plate loads; (cm^2) (Table 2), V = corrected velocity of the fish (cm/sec), k = velocity correction for blocking of the load (Table 2), C = drag coefficient.

C was assumed to be equal to that of a circular flat plate normal to the flow; that is, 1.12 (Prandtl & Tietjens, 1934).

The drag of the loads was expected to exceed the theoretical values, because they cause premature separation of the boundary-layer of the model. This was also expected to occur on the fish with the loads, and hence is part of the total load drag. The drag of the loads measured on the model was used to calculate the drag of the loads experienced by the fish at any swimming speed.

Table 1. *The drag of the extra loads measured on dead fish and on a model fish*

(Mean and 2 standard errors are given)

Corrected velocity of fish and model		Load drag on fish		Load drag on model
cm/sec (mean)	2 S.E.	gm wt. (mean)	2 S.E.	(gm wt., mean)
Load 1				
10.3	0.3	0.46	0.09	0.20
17.4	0.6	1.19	0.11	0.70
24.7	0.6	2.32	0.19	1.21
31.1	0.8	3.94	0.07	0.19
38.0	0.9	5.60	0.32	3.10
44.7	1.4	7.47	0.37	4.11
52.0	1.26	10.00	0.91	5.97
59.3	1.06	12.38	0.93	6.35
Load 2				
10.3	0.0	0.66	0.07	0.42
17.2	0.32	1.69	0.13	1.10
24.1	0.4	3.46	0.19	2.16
30.9	0.7	5.87	0.27	3.38
37.9	0.8	8.69	0.62	5.25
44.7	0.4	12.08	0.59	7.15
Load 3				
10.4	0.5	1.34	0.17	0.90
17.3	0.8	3.64	0.18	2.10
24.2	0.8	7.03	0.55	4.21
31.2	1.7	11.25	0.92	6.81
38.5	0.8	16.32	1.04	10.32
Load 4				
10.3	0.5	1.85	0.24	1.25
13.7	0.6	2.92	0.31	2.01
17.1	0.8	5.00	0.65	3.15
20.5	0.9	6.79	0.64	4.50
23.9	1.1	9.42	1.07	6.00
27.5	0.8	11.82	0.89	7.54
30.0	0.6	16.31	1.00	9.81

Interference of the loads with the fish

Buoyancy. The weight of the loads in water (Table 2) must have initially increased the density of the fish. It was observed that fish frequently took air from the surface in the recovery tanks after the loads had been attached. Since fish were all neutrally buoyant when they were anaesthetized prior to their introduction to the fish chamber, it was assumed that the fish adjusted their buoyancy by taking air into the swim bladder.

Static equilibrium. Anaesthetized fish always assumed a belly upward position in

water, indicating that the centre of buoyancy was below the centre of gravity. The position of the loads will tend to raise the centre of gravity, and hence increase the rolling couple on the fish.

Table 2. *Characteristics of the drag loads fitted to fish*

	Load 1	Load 2	Load 3	Load 4
Total blocking correction (k)	—	1.04	1.05	1.06
Surface area of one side (cm ²)	—	5.0	1.05	1.48
Weight in air, including strut (g)	2.00	1.25	1.80	2.50
Weight in water, including strut (g)	1.00	0.35	0.45	0.60

Dynamic equilibrium. The position of the loads creates a large drag force that is some distance from the line along which thrust develops. This results in a large pitching couple, tending to raise the head. Close examination of ciné film of swimming fish and without drag loads failed to reveal any compensatory behaviour by the fish. Some compensation must have been necessary, and if this was associated with an additional induced drag force, then the final drag values calculated for non-loaded fish will tend to be low.

The position of the loads also shadows the dorsal fin. This probably decreases the stability of the fish to yawing (Harris, 1936).

Alternative positions for the loads

Any additional drag load must interfere with the fish to some extent. The position selected was considered to cause least interference. Lateral excursions of the body just anterior to the dorsal fin are small (Bainbridge, 1963), so that the drag force will remain directed along the axis of progression of the fish. In any other position the load would present a changing angle of attack to the flow. This would result in large fluctuating side forces and large yawing movements of the fish. Other positions would also have interfered with the propulsive wave.

Furthermore, the loads could not have been positioned below the fish, as the trout tended to swim near the bottom of the fish chamber. Positions of the load downstream from the fish would not interfere with the flow around the fish, nor with its stability. There is no practical method of attaching the loads in this position without seriously interfering with the freedom of movement of the body.

The fish

All experiments were performed on healthy intact rainbow trout, approximately 30 cm total length. The fish were obtained from a hatchery at Nailsworth, Gloucestershire, where they have been inbred for at least 50 years.

Fish were transported by road from the hatchery in large darkened plastic containers. On arrival, fish were transferred to aerated 550 l tanks, where they were held for at least 2 weeks prior to use. The fish were fed on chopped liver and heart.

The holding tanks were continuously supplied with recirculated water at 15 °C. The water was passed through a sterilizer and filters. The water hardness was controlled to 50 ± 5 ppm calcium carbonate. The oxygen content was maintained close to air-saturation.

Water entered the tanks from the side, causing the water to rotate slowly. Fish swam in the current in order to keep station. Swimming movements were made with the pectoral fins, or the caudal fin moving at low frequency and small amplitude. The fish should, therefore, be considered unexercised prior to any experiment.

Experimental procedure

Experiments were performed on five groups of fish – a control group, and groups 1–4 with drag loads of increasing size. The characteristics of the fish are given in Table 3. Fish were starved for a total of 3 days prior to each experiment in order to allow time for the elevated rate of metabolism following feeding to return to normal (Saunders, 1963; Beamish, 1964).

Table 3. *Characteristics (mean and 2 S.E.) of the fish in control and groups 1–4*

	Length (<i>L</i> , cm)	Depth (<i>d</i> , cm)	Width (<i>w</i> , cm)	Fine- ness ratio*	Wetted surface area (<i>S_w</i> , cm ²)	Mass (<i>M</i> , g wt.)	Muscle mass (<i>M_m</i> , g)	Speed correc- tion
Control	28.2 ± 0.2	5.5 ± 0.3	2.7 ± 0.1	6.9	311.3 ± 9.2 = 0.40 <i>L</i> ²	198.4 ± 14.2 = 0.009 <i>L</i> ³	89.2 ± 17.1 = 0.45 <i>M</i>	1.12
Group 1	30.0 ± 0.4	6.0 ± 0.4	3.1 ± 0.4	6.6	347.1 ± 28.6 = 0.39 <i>L</i> ²	260.1 ± 57.8 = 0.01 <i>L</i> ³	130.0 ± 39.8 = 0.50 <i>M</i>	1.13
Group 2	30.8 ± 1.0	6.3 ± 0.2	3.3 ± 0.2	6.2	349.1 ± 21.4 = 0.37 <i>L</i> ²	291.6 ± 21.6 = 0.01 <i>L</i> ³	143.9 ± 23.6 = 0.49 <i>M</i>	1.17
Group 3	29.1 ± 0.8	5.8 ± 0.4	3.1 ± 0.2	6.5	346.7 ± 46.0 = 0.40 <i>L</i> ²	244.1 ± 42.0 = 0.01 <i>L</i> ³	121.5 ± 20.0 = 0.50 <i>M</i>	1.11
Group 4	29.7 ± 0.4	5.9 ± 0.2	3.1 ± 0.2	5.9	357.0 ± 13.4 = 0.40 <i>L</i> ²	254.0 ± 20.6 = 0.01 <i>L</i> ³	135.1 ± 16.2 = 0.53 <i>M</i>	1.13

$$* \text{ Fineness ratio} = \frac{L}{\frac{1}{2}(d+w)}.$$

Each fish was lightly anaesthetized and introduced to the fish chamber. The water velocity was set at 0.3 ft/sec (0.3 body lengths/sec), until the fish was fully recovered. During the first 2 h of a 14- to 18-h acclimation period fish were trained to swim steadily in the observation section, using the electrified grid. The photofloods were switched on and off during this period, and the fish rapidly became accustomed to the lights and showed no excitement. The acclimation period allows sufficient time for fish to recover from excitement (Smit, 1965) and from the effects of handling (Black, 1957).

After the acclimation period the free-stream water velocity was increased by 0.2 ft/sec (0.2 *L*/sec) increments every 45 min until the fish was exhausted. Exhaustion was taken as the first time that the fish drifted downstream and could not flex off the electrified grid. The time to exhaustion after the last velocity increment was recorded and used in the calculation of the critical swimming speed. The procedure for group 4, with the largest load, differed from the other groups, in that 0.1 ft/sec velocity increments were used.

The critical swimming speed is a measure of the speed that the fish could just maintain for the test period, 45 min in this case (Brett, 1964). Following Brett, the

critical swimming speed, V_{crit} , was calculated by reducing the last velocity increment in proportion to the fraction of the test period for which the fish swam. Thus,

$$\Delta V_L = \Delta V(t_x/t) \quad (2)$$

and

$$V_{crit} = V_L + \Delta V_L, \quad (3)$$

where ΔV_L = last velocity increment that would give V_{crit} , ΔV = usual velocity increment, V_L = velocity preceding that at which the fish is exhausted, t_x = time to exhaustion after last velocity increment, t = test period.

After the fish became fatigued, it was removed from the respirometer and returned to the holding tanks until the round chamber could be fitted to the respirometer and the drag of the fish and load measured.

At the 15th and 30th min of each period, the time for 50 opercular beats was measured with a stop-watch. After measuring opercular rate, the photofloods were switched on and some film was exposed. At the end of an experiment the film was calibrated by means of a flashing neon light driven from the marker system of a pen recorder.

A film analyser was used that gave an image 1.5 times the size of the original object. The wavelength of the propulsive wave was measured, as well as the amplitude and frequency of the trailing edge of the caudal fin, from at least 10, usually 20, consecutive tail-beat cycles.

All the experiments were performed during winter and spring months.

RESULTS AND DISCUSSION

Observations on the swimming mode

In the control group, low swimming speeds of 0.2–0.3 L/sec (body lengths/sec) were achieved either by paddling movements of the pectoral fins or by low-amplitude waves passing vertically up or down the caudal fin. Normal propulsive movements involving a body-propagated propulsive wave were only observed when the fish increased their drag, either by angling the body so that a non-streamlined profile was presented to the water flow, or by using their pectoral fins as brakes. At speeds greater than 0.3 L/sec , and at all speeds in the loaded groups, typical propulsive waves were observed to be propagated backwards along the body as described by Gray (1933 *a, b, c*).

One complete wavelength of the propulsive wave was usually seen within the length of the body. According to Breder's (1926) classification of fish swimming types, the trout swims in the same anguilliform mode as the eel. Fish swimming in this mode are defined as showing at least one-half of a wavelength within the length of the body. Breder, however, considered that salmnoids swam in the carangiform mode, exhibiting less than half of a wavelength within the length of the body. Breder's classification should not be used too rigorously, as it represents average swimming modes in an essentially continuous range (Bainbridge, 1963). The details of the trout swimming movements can only be appreciated from observations of slow-motion films, and should probably be considered as intermediate between typical anguilliform and carangiform modes. Fierstine & Walters (1968) consider that other fish with similar body form to the trout – for example, the bream, dace and goldfish studied by Bainbridge (1963) – also swim in the anguilliform mode.

The characteristics of the propulsive wave

The propeller system of the trout can be visualized as a series of hypothetical linked segments. The amplitude of lateral movement of these segments increases towards the tail trailing edge, and hence their transverse velocity similarly increases. The thrust contributed by each segment will be proportional to the resultant of its transverse velocity, and of the backward velocity of the propulsive wave (Gray, 1933*a*, *c*; Taylor, 1952; Lighthill, 1960, 1969, 1970). The propulsive wave can then be imagined as a system which affects the adjacent water by gradually increasing its momentum to a maximum at the trailing edge. Shedding of this momentum at the trailing edge produces thrust (see particularly Lighthill, 1969).

Therefore, if the wavelength of the propulsive wave remains constant, the phase relations between the hypothetical segments will remain unchanged, and the propulsive effect can be characterized in terms of frequency and amplitude at any point. Ideally this point is the trailing edge of the body, as here the transverse movements are largest.

The important parameters of the propulsive wave are, then, the wavelength, λ , the frequency, f , and the amplitude, A .

Wavelength

The wavelength of the propulsive wave was found to be constant in all the fish studied, both with and without drag loads, and at all speeds greater than 0.3 L /sec. The mean wavelength was found to be 0.76 L (length). No node was observed as Bainbridge (1963) has pointed out.

Theory predicts (Lighthill, 1960, 1969) that at least one wavelength is to be expected. Lighthill pointed out that side forces resulting from transverse movements of the body (as described by Gray, 1933*a*, *c*) would cause angular recoils, or side-slipping of the body. For fish which are fairly constant in depth, like the trout, these forces can be reduced by the presence of a complete wavelength so that side forces tend to cancel out. Measurements of the recoil movements of the trout showed that the head tended to move through an arc of about 2° .

The body of the trout is relatively thick for its length, so morphological considerations dictate that there should be only about 1 wavelength within the body length, and that it should represent a large proportion of that length. Fish with body forms similar to that of the trout will be expected to have similar specific wavelengths, defined as λ/L .

Bainbridge's equation (1958) can be used to calculate a theoretical value for λ/L . This equation relates the swimming speed of fishes to the tail-beat frequency and body length:

$$\text{speed} = V = \frac{1}{4}[L(3f-4)]. \quad (4)$$

In order to swim, the backward speed of the propulsive wave, V_w , must exceed V (Gray, 1933*b*) and

$$V_w = f\lambda. \quad (5)$$

Assume that at the maximum sprint speed, V_s , V_w just tends to reach the value V_s . That is,

$$(V/V_w) \rightarrow 1 \quad \text{at} \quad V = V_s. \quad (6)$$

Then from equation (4):

$$f = \frac{4(V+L)}{3L}. \quad (7)$$

Substitute for f from equation (7) into equation (5); then from equation (6)

$$\frac{3LV_s}{4\lambda(V_s+L)} = 1$$

$$\frac{\lambda}{L} = \frac{3V_s}{4(V_s+L)}. \quad (8)$$

or

V_s takes values of about 10 L/sec (Bainbridge, 1958, 1960). Then

$$\lambda/L = 0.68$$

or

$$\lambda = 0.68L. \quad (9)$$

Values for λ can be calculated from data in Gray (1933*a*) and Bainbridge (1963). The data and values for λ are shown in Table 4, with values for L calculated from equation (9) for Gray's data, and values for λ calculated for Bainbridge's data. Data from Gray for extreme anguilliform swimmers has not been included in the table

Table 4. *The wavelength of the propulsive wave of some fish*

	Length	Length from eqn. (9) ($L = \lambda/0.68$)	Wave velocity (cm/sec)	Tail beat frequency (f/sec)	Wave- length (λ , cm)	Wavelength from eqn. (9) ($\lambda = 0.68L$)
From Gray (1933 <i>a</i>)						
Whiting	—	18.4	25	2	12.5	—
Mackerel	—	40	77	2.87	27.2	—
From Bainbridge (1963)						
Bream	19.0	—	—	—	11.9	12.9
Goldfish	16.0	—	—	—	11.4	10.9
Dace	25.0	—	—	—	15.1	17.0
Present paper						
Trout	30	—	—	—	22.8	20.4
Mean of Bainbridge's and present results	22.5	—	—	—	15.3	15.3

as these fish do not warrant the assumptions made in the derivation of equation (9). In these fish the body is long and thin and $\lambda \ll L$, as shown by Breder (1926). The data for a mackerel is included as this fish has a streamlined body as does the trout. However, this fish differs from the trout in that the caudal peduncle is narrow, the tail lunate, and the fish swims in the carangiform mode with $\lambda \gg L$ (Fiersteine & Walters, 1968). The value for L calculated from equation (9) is therefore expected to be high. Fish swimming in the carangiform mode apparently reduce angular recoils by narrow necking of the body where the side forces are generated (caudal peduncle). In this way recoil forces are small because the amount of water affected by the propulsive movements is small (Lighthill, 1969).

The agreement between the measured values of λ and those calculated from equation (9) is well within the range expected from variations in V_s for different fishes (see Bainbridge 1958).

Table 5. Data for the characteristics of the propulsive wave of trout at cruising swimming speeds, and opercular rates

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Swimming speed			Tail-beat freq./sec (<i>f</i>) mean (4)	Specific amplitude (<i>A/L</i>) mean (5)	<i>fA/L</i>		Opercular rate		% <i>V/V</i> _{crit} mean (10)	Scope (%)		Load dynes (13)	No. of fish (14)
cm/sec, mean (1)	<i>L</i> /sec, mean (2)	2 s.e. (3)			mean (6)	2 s.e. (7)	Per min, mean (8)	2 s.e. (9)		mean (11)	2 s.e. (12)		
Control group													
10.1	0.36	0.01	2.06	0.078	0.160	0.024	83.2	15.2	21	15	5	—	5
16.9	0.61	0.02	2.36	0.114	0.270	0.032	75.2	14.4	35	41	8	—	5
23.6	0.85	0.03	2.28	0.138	0.310	0.040	71.7	10.7	49	50	6	—	5
30.4	1.09	0.03	2.83	0.130	0.370	0.026	74.7	17.3	64	64	6	—	5
37.2	1.33	0.03	3.24	0.136	0.440	0.028	87.1	13.9	78	79	6	—	5
43.9	1.57	0.04	3.55	0.137	0.490	0.026	84.3	9.7	92	91	6	—	5
50.7	1.83	0.05	3.59	0.153	0.550	0.046	109.0	6.7	102	104	10	—	4
58.1	2.05	0.09	4.04	0.150	0.610	0.044	146.1	34.3	117	118	10	—	4
Group 1													
17.4	0.57	0.01	2.87	0.087	0.260	0.018	96.4	11.2	40	41	3	618	4
24.4	0.80	0.01	2.91	0.124	0.361	0.056	101.6	6.5	56	58	9	1197	4
31.4	1.03	0.02	3.14	0.138	0.433	0.046	108.9	8.9	73	69	7	2031	4
38.3	1.26	0.03	3.77	0.147	0.554	0.050	115.5	4.6	89	88	8	2914	4
45.3	1.49	0.02	4.83	0.150	0.724	0.019	125.4	2.0	105	114	3	3885	2
52.0	1.72	0.05	4.50	0.160	0.720	0.010	151.4	—	121	114	2	4944	2
Group 2													
10.7	0.35	0.05	2.05	0.089	0.182	0.014	86.6	22.7	30	25	3	441	4
17.8	0.58	0.03	2.49	0.123	0.306	0.020	97.7	20.6	50	50	4	1030	3
24.9	0.81	0.04	2.96	0.115	0.408	0.025	110.8	8.0	70	69	5	2158	4
32.0	1.04	0.05	3.22	0.138	0.489	0.066	125.1	18.1	90	88	13	3581	4
39.2	1.27	0.06	4.02	0.152	0.611	0.075	141.4	34.5	110	112	15	5297	4
Group 3													
10.3	0.35	0.02	2.63	0.102	0.268	0.074	102.2	12.2	42	45	18	785	5
17.1	0.58	0.03	2.66	0.141	0.375	0.072	107.5	20.9	71	71	18	2011	5
24.0	0.81	0.03	3.27	0.145	0.474	0.052	117.8	24.0	99	96	13	3777	5
30.9	1.04	0.08	3.87	0.158	0.611	0.083	116.0	38.3	128	130	21	6327	3
Group 4													
10.3	0.35	0.01	2.81	0.103	0.289	0.060	86.4	13.7	44	48	14	1177	5
13.8	0.46	0.01	2.65	0.132	0.350	0.072	86.9	10.3	58	61	16	1962	5
17.2	0.58	0.01	2.62	0.156	0.409	0.038	90.6	9.7	73	75	8	3139	5
20.7	0.70	0.01	2.82	0.172	0.485	0.068	109.2	14.2	88	91	15	4562	5
24.1	0.81	0.02	3.11	0.180	0.560	0.048	115.8	14.8	102	109	11	5886	5

Frequency and amplitude

Having found that λ is constant, subsequent discussion can be restricted to f and A , measured at the trailing edge of the body. Values for A have been calculated as specific amplitudes A/L , for comparison with values reported in the literature. The results of the measurement of f and A/L for the five groups of fish are given in Table 5.

Bainbridge (1958) suggested that f and A/L would be related when f took values of less than about 5/sec. which includes the cruising speed range found in the trout used here. Bainbridge found that A/L became constant in the trout at frequencies above 5/sec, and then swimming speed could be related to f by equation 1.

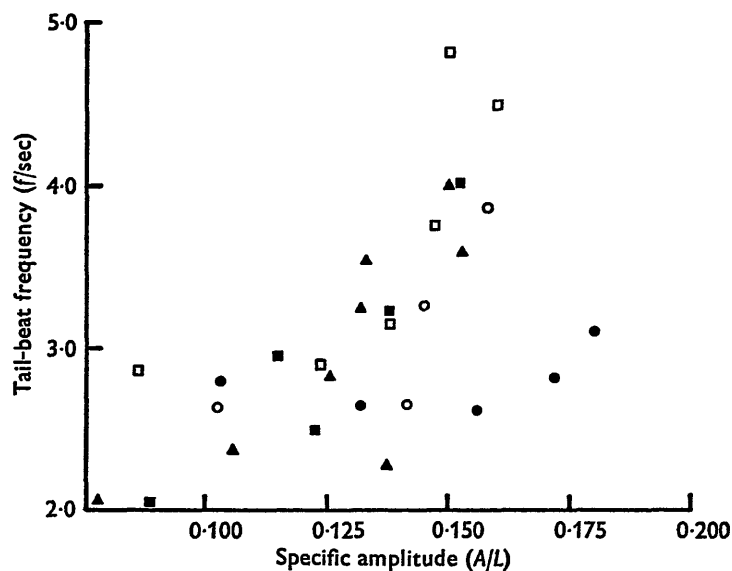


Fig. 4. The relationship between tail-beat frequency and specific amplitude of trout at cruising swimming speeds: ▲, control; □, group 1; ■, group 2; ○, group 3; ●, group 4.

A/L has been plotted against f in Fig. 4. This confirms Bainbridge's observations, although the scatter of A/L is fairly great at low values of f . A/L increases to a maximum value of about 0.175 as f approaches 5/sec. Bainbridge (1958) measured a maximum value of A/L of 0.137 for trout of similar length, although the mean value from four fish ranging from 4.0 to 29.3 cm in length was 0.174. The mean value for dace, goldfish and trout was 0.183. Hertel (1966) has reported a further value of A/L of 0.2 for goldfish. Thus the values of A/L for the trout measured here were similar to those of fish with similar body forms.

Relationship between f and A/L with swimming speed

Bainbridge (1958) has already shown that f is proportional to V when A/L is constant, and f greater than 5/sec. At lower swimming speeds it is probable that V will be proportional to the product $f \times A/L$. This will be related to the trailing-edge velocity, which is proportional to the rate at which momentum is shed to the wake, and hence to thrust (Lighthill, 1960, 1969, 1970). It was found that the product fA/L was linearly related to V in all five groups of fish (Fig. 5). Swimming speed is

shown as specific swimming speed, V/L , to maintain dimensional similarity with fA/L . Bainbridge (1958) has shown that the swimming speeds of different sizes of fish can be compared on the basis of V/L .

Linear regression equations relating V/L to fA/L are shown in Table 6, calculated by the method of least squares after Steel & Torrie (1960). The regression lines cut the abscissa when V/L is zero, except for group 1. Group 1 differs from the others

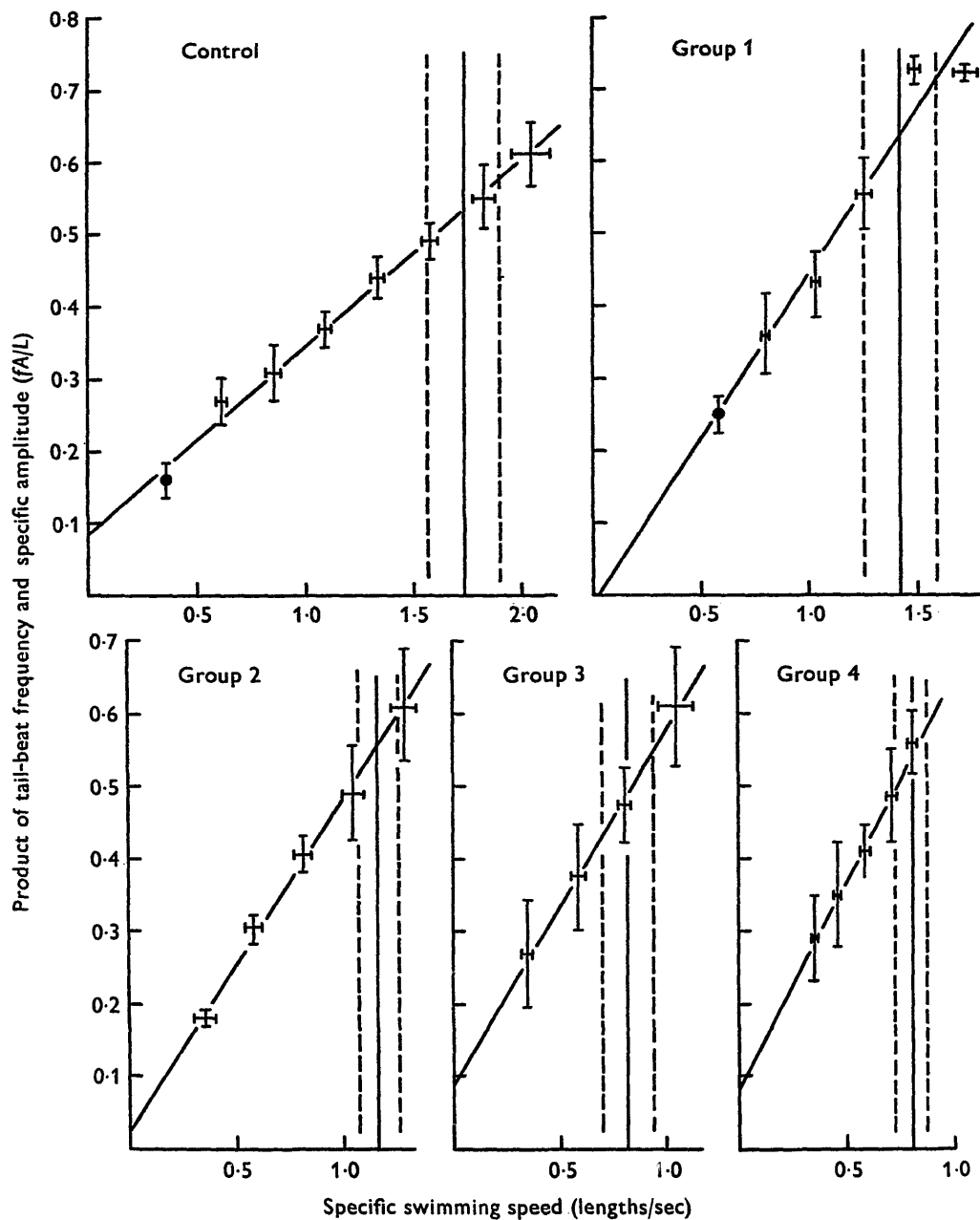


Fig. 5. The relationship between the product of frequency and specific amplitude (fA/L) and specific swimming speed in the five groups of fish. Vertical and horizontal bars represent two standard errors about the mean values of fA/L and specific swimming speed. The vertical solid line represents the critical swimming speed, and the vertical dotted lines represent two standard errors.

because of the high value for fA/L when V/L was 1.5 L/sec, and because no reliable measurement of fA/L was made at low swimming speeds. The fish in this group did not swim regularly at low speeds, and it was considered that there were insufficient consecutive tail beats for a valid measurement to be made. If this had not occurred, the regression line would have cut the abscissa within the range of the other four groups.

Table 6. *Linear regression equations relating specific swimming speed to the product fA/L calculated from the data in Table 5*

(Critical swimming speeds and maximum values of fA/L are also included.)

Group	Linear regression	Critical swimming speed			Max. fA/L
		L/sec	2 S.E.	cm/sec	
Control	$V/L = 0.391fA/L - 0.353$	1.73	0.17	48.8	0.53
Group 1	$V/L = 0.219fA/L + 0.038$	1.42	0.17	42.6	0.63
Group 2	$V/L = 0.237fA/L - 0.139$	1.16	0.10	35.7	0.55
Group 3	$V/L = 0.204fA/L - 0.182$	0.82	0.12	23.9	0.49
Group 4	$V/L = 0.172fA/L - 0.140$	0.79	0.07	23.5	0.54

It was suggested that the drag loads attached to the fishes would interfere to some extent with locomotion, and that the fish would make some compensatory behaviour. The characteristics of the propulsive wave can be compared between groups of fish, by assuming that all fish are making their maximum effort at the critical swimming speed, V_{crit} . In view of the exhausted state of the fish at the end of each experiment, this assumption is considered justified. The swimming speed in each group can then be expressed as a percentage of the critical speed, as $\% V/V_{crit}$. The values for velocity have been recalculated in this form (Table 5, column 10). The parameter f is plotted against $\% V/V_{crit}$ in Fig. 6. A theoretical line has also been calculated from Bainbridge's equation (equation 4). The data show good agreement with each other and with the theoretical line, even though A/L has not been included. The variations in A/L therefore appear to be small enough for Bainbridge's equation to be applied down to values of f of about 2.5/sec. The agreement between the data suggests that the loads did not seriously interfere with the fish.

The critical swimming speed

The critical swimming speeds (calculated from equations 3 and 4) which are included in Table 6, fell with each group as the size of the load increased. The mean 45 min V_{crit} for the control group was 1.73 L/sec. This speed is low in comparison with the cruising speeds of salmonids reported in the literature, some of which are included in Table 7. These values range from 1.4 L/sec to 4.1 L/sec.

Part of the reason for the low swimming speed undoubtedly involves the history of the fish. Miller (1953), Reimers (1956), Vincent (1960), Hochachka (1961) and Davies *et al.* (1963) have shown that hatchery-reared salmonids have a poor swimming ability in comparison with wild fish. Reimers (1956), Vincent (1960), Hochachka (1961) and Hammond & Hickman (1966) have suggested that this is partly a result of lack of training, which would apply to these fish reared in ponds. Brett, Holland & Alderdice (1958) also found that lack of pre-exercise in fish reduced their swimming performance, and the fish used here were not pre-exercised.

Bams (1967) found that the conditions under which eggs were incubated affected swimming performance. At Nailsworth, eggs are hatched in trays, which is apparently the worst method of incubating trout if active fish are desired.

There are also relatively large differences in the swimming performance of different stocks of fish (Brett, 1964), which may result from genetic differences. The population at Nailsworth could have been inadvertently bred to have a relatively low swimming ability.

Table 7. *The cruising speeds of some salmonid fishes*

Fish	Length (L, cm)	Cruising speed		Temperature (°C)	Duration and test	Reference
		cm/sec	L/sec			
<i>Salmo trutta</i>	34.1	92	2.7	Various	Sustained	Magnan (1930)
<i>S. salar</i>	4.2	16.8	4.0	20-25	25-30 min imposed velocity	Davidson (1949)
<i>S. gairdneri</i> and <i>S. irideus</i>	64.0	214	3.34	7.1	Critical speed in increasing velocity test	Paulik & DeLacy (1957)
Rainbow trout	28.0	72.8	2.6	c. 16	20 sec, fish wheel	Bainbridge (1960)
	24.9	46.6	1.87	c. 16	63 min; mean 8 fish swimming in fish wheel	Bainbridge (1962)
<i>Oncorhynchus nerka</i>	64	177	2.8	7.1	Critical speed in increasing velocity test	Paulik & DeLacy (1957)
	18.8	75	4.0	15	Critical speed in increasing velocity test	Brett (1964)
	30.0	96	3.2	15	Critical speed in increasing velocity test	Brett (1965)
Great Central Lake stock	17.0	73	4.3	15	Critical speed in increasing velocity test	Brett (1964)
Culthus Lake stock	18.5	54	2.9	15	Critical speed in increasing velocity test	Brett (1964)
<i>O. milkschitsch</i>	56	189	3.37	Various	Sustained, migrating fish	Ellis (1966)
Various salmon sp.	85	119	1.4	Various	From tagging experiments	Dahl & Sømme (1936)
	—	—	2.0	Various	Cruising at sea	Muir, in Bainbridge (1960)

Ventilation rate

The ventilation rates of the five groups of fish at cruising speeds are given in Table 5 (columns 8, 9) and Fig. 7. Mean ventilation rates were similar to those observed by Stevens & Randall (1967) at 10-12 °C, but are somewhat lower than those recorded by Sutterlin (1969) at 8 °C for the same species of fish. In the control group, ventilation rates decreased slightly, but not significantly at intermediate swimming speeds. In this group, ram ventilation was occasionally observed, but this lasted only for a maximum of 2 min and was not typical. The increases in ventilation rate below V_{crit} were just significant at the 5 % level in groups 2 and 4 (Student's *t* test). Changes in ventilation rate were not statistically significant in the other groups below V_{crit} . At speeds greater than V_{crit} the ventilation rate increased markedly in all groups except group 3. It was observed that the amplitude of ventilatory movements showed similar changes to the ventilatory rate.

These observations imply that there is a negligible change in the amount of ventilatory work done by the ventilatory muscles themselves. This occurs even though the oxygen consumption increases exponentially with swimming speed (Brett, 1964;

Webb, 1970). This increase in oxygen consumption could not be met by increasing the efficiency of oxygen uptake (Saunders, 1962; Randall, Holeyton & Stevens, 1967; Stevens & Randall, 1967*b*). Therefore, the work required to obtain the extra oxygen, through elevation of the ventilation volume, must be mainly performed by the propulsive muscles. This work will represent a drag force, to be added to the drag of the fish in swimming.

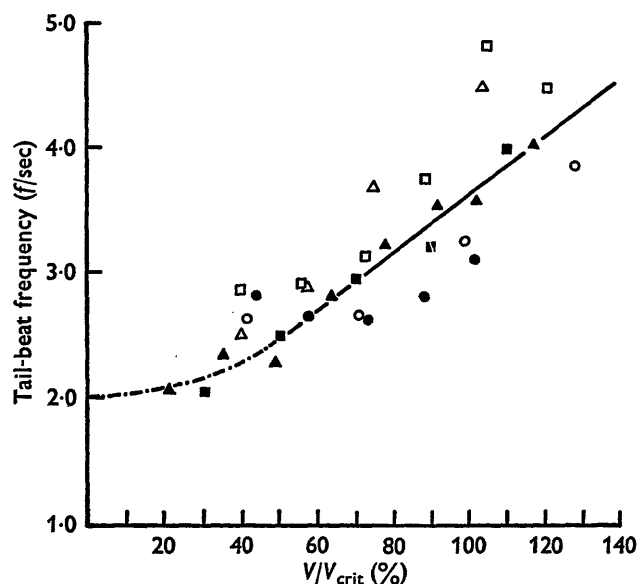


Fig. 6. The relationship between tail-beat frequency and swimming speeds, represented as a percentage of the critical swimming speed ($\% V/V_{crit}$). —, Calculated by means of Bainbridge's equation (1958). Key as for Fig. 4. Δ , Data from Sutterlin (1969).

The magnitude of this drag component is unknown. Brown & Muir (1970) have calculated that the cost of ram ventilation, in terms of a fraction of total drag, could be as low as 0.07 in skipjack tuna. However, doubling of the oxygen consumption could raise this figure to 0.27. The cost to the rainbow trout would be higher than for ram ventilation because extra costs are incurred as the fish continues to ventilate. Under these conditions energy must be supplied to accelerate water that has been slowed down in the system.

Estimation of the thrust and drag of a swimming fish

Bainbridge (1963) has shown that the locomotory movements made by fish are extremely complex. Fish continuously make small fine control movements of the propulsive surfaces, particularly of the caudal fin. However, Bainbridge's earlier work (1958) and the present results show that frequency and amplitude can be related to swimming speed, presumably as a crude expression of the mean propulsive activity of the propulsive wave.

The drag of a fish at some swimming speed, V , is related to some power of that speed, probably $v^{1.8}$ for fish in the respirometer. Since the product $f \times A/L$ used to define the propulsive wave is linearly related to V and is the source of thrust, then it

follows that thrust is proportional to some power of fA/L . Changes in fA/L should be related to the magnitude of additional drag loads, and it should therefore be possible to calculate the thrust produced by a non-loaded fish.

Standardization of the data

The results must first be standardized so that they may be compared between groups of fish, and in order to reduce the effects of variability between groups. This can be done in terms of the assumption made above that fish will make their maximum effort at the critical swimming speeds, and that the maximum effort is the same for each group. Then, intermediate levels of activity can be expressed as a percentage of the maximum level of activity.

In order to do this for the mechanical parameters of the propulsive wave, a mechanical scope for cruising activity will be defined, analagous to the metabolic scope for activity defined by Fry (1957). The mechanical scope for activity is the difference between the product $(fA/L)_{\text{zero}}$ at zero swimming speed and $(fA/L)_{\text{crit}}$ at V_{crit} . The scope for activity is then assumed to be the same for all groups of fish and represents the mechanical potential for cruising up to V_{crit} .

The value of $(fA/L)_{\text{zero}}$ was found by extrapolating the relationship between fA/L and V/L to zero swimming speed, and as such, a small error is included because fish do not normally swim at low speeds. Mechanical scope should correctly be defined in terms of the true swimming range, with $(fA/L)_{\text{zero}}$ calculated at the speed where normal swimming commences. Unfortunately, this point cannot be found in practice with any accuracy, because of the extremely variable behaviour of fish at low swimming speeds.

Intermediate levels of activity can be expressed as a percentage of the mechanical scope (% scope). If the parameters of the propulsive wave are $(fA/L)_V$ at an intermediate swimming speed, V , then

$$\% \text{ scope} = \frac{(fA/L)_V - (fA/L)_{\text{zero}}}{(fA/L)_{\text{crit}} - (fA/L)_{\text{zero}}} \times 100. \quad (10)$$

The equation calculates the percentage of the potential swimming scope required at the speed V .

Brett (1965) has used a similar analysis in conjunction with the metabolic scope for activity. He expressed intermediate levels of oxygen consumption as fractions of the metabolic scope in order to compare fish of different sizes. A similar precedent for this method of standardizing data comes from the study of muscle mechanics, where the activity of the muscle is usually expressed as a fraction of the maximum value of a particular activity (see for example Hill, 1950).

The data for speed and fA/L have therefore been recalculated in terms of percentage scope for each group of fish (Table 5, columns 11, 12). Column 13 includes drag values for the loads in Groups 1 to 4 taken from Figure 3, and converted to dynes.

The relationship between percentage scope and load drag

At any swimming speed the addition of a drag load means that a fish must perform a greater percentage of its potential swimming scope. With drag proportional to V^n and also to $(\% \text{ scope})^m$, a plot of the logarithm of the load against the logarithm of %

scope, with V constant, should be a straight line with slope m . The slope should be constant for all values of V .

The analysis can be simplified because the drag of the fish and the loads tends to increase in a similar fashion with V . Under these conditions, a plot of the logarithm

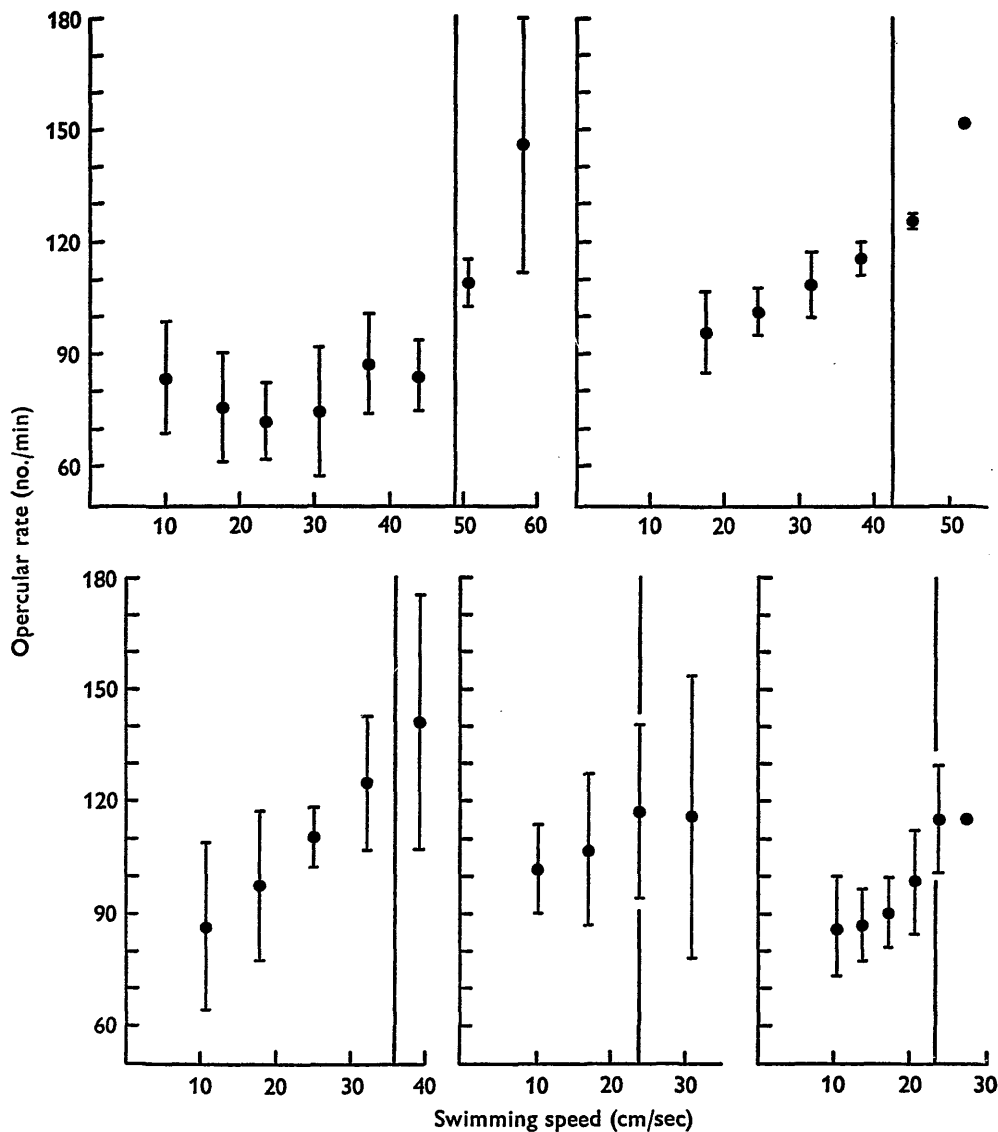


Fig. 7. The opercular rate of trout at cruising swimming speeds in the five groups of fish. Vertical bars represent two standard errors about the mean opercular rate. The vertical line represents the critical swimming speed.

of load against the logarithm of % scope can be drawn that is independent of the swimming-speed parameter as shown in Fig. 8. This gives a single line with a slope of 1.81, which can be described by the equation:

$$\text{load (dynes)} = 76 + 0.96 (\% \text{ scope})^{1.81}. \quad (11)$$

The relationship between load and $(\% \text{ scope})^{1.81}$ should now be a straight line (Fig. 9), and can be used to calculate the thrust developed by an unloaded fish. This is

done by calculating the load that must be added to a fish to double its drag at a particular swimming speed. This extra load drag will be equal to the drag of the fish at that speed, and is the load required to double the $(\% \text{ scope})^{1.81}$. For example, consider

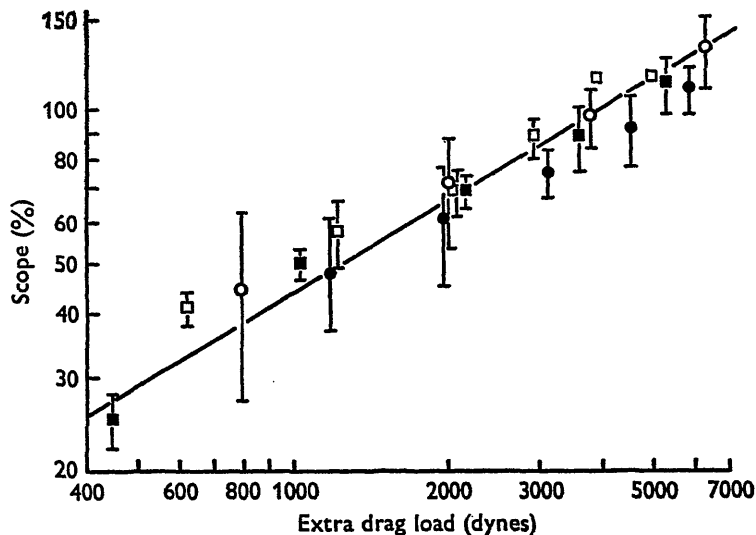


Fig. 8. The relationship between the percentage of scope for mechanical activity and the drag of the loads attached to the fish. Vertical bars represent 2 standard errors about the mean % scope. Key as for Fig. 4.

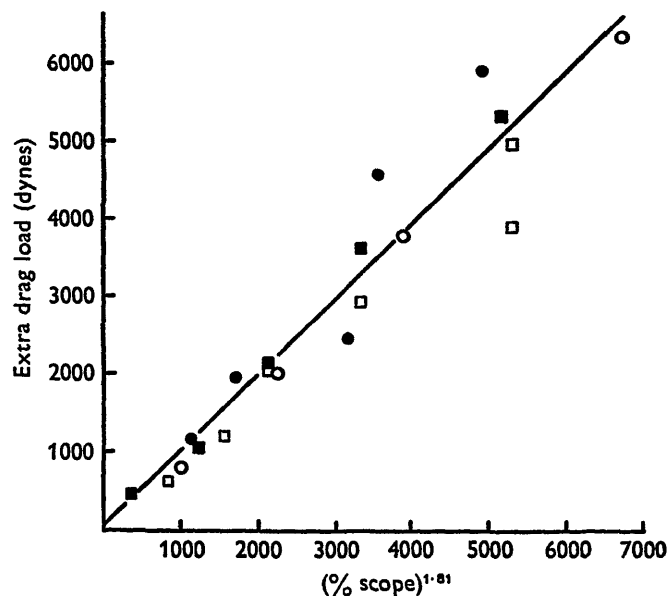


Fig. 9. Relationship between the extra drag loads and percentage scope raised to the power 1.81. Key as for Fig. 4.

a control fish swimming at a speed of 24.4 cm/sec when 50 % of the potential scope is performed. The $(\% \text{ scope})^{1.81}$ is then 1189. If a load is applied which requires 60 % of the scope to be performed at that speed, then $(\% \text{ scope})^{1.81}$ is 1653 and the load 1.7×10^3 dynes from Fig. 9. If a load is added which doubles the fishes' performance -

that is, increases the (% scope)^{1.81} from 1189 to 2378 – this load is equal to the drag on the swimming fish and is equal to 2.4×10^3 dynes.

The required load to double the fishes' drag in the control group has been calculated for each level of (% scope)^{1.81}. The swimming speed representing each level has also been calculated, and the drag plotted against swimming speed in Fig. 10 (Table 8). This represents the thrust/swimming speed relationship for the trout at cruising swimming speeds. The linear regression equation was calculated:

$$\text{thrust} = 7.9V^{1.79}. \quad (12)$$

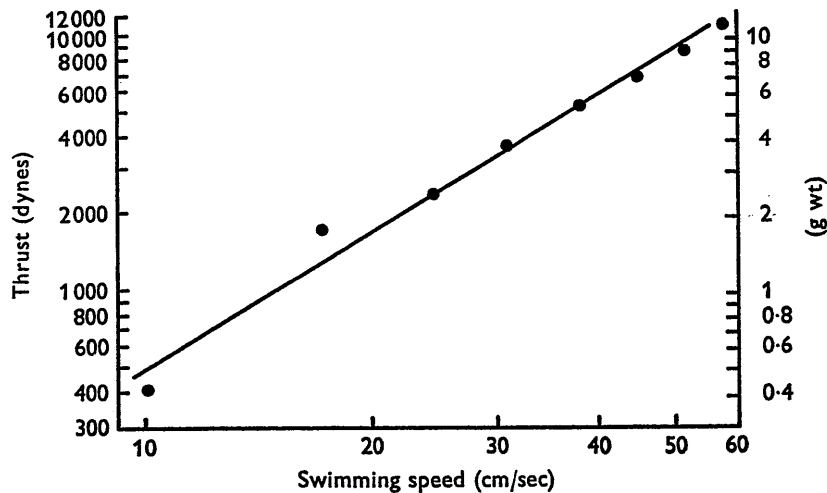


Fig. 10. Thrust/swimming speed relationship for trout at cruising swimming speeds.

Table 8. The thrust and power output developed by trout at cruising swimming speeds

Swimming speed (cm/sec)	Thrust		Power output (ergs/sec)
	Dynes	g. wt.	
10.1	411	0.42	0.04×10^5
16.9	1746	1.78	0.30×10^5
23.6	2435	2.48	0.58×10^5
30.4	3721	3.79	1.14×10^5
37.2	5374	5.48	2.02×10^5
43.9	6899	7.03	3.06×10^5
50.7	8742	8.91	4.51×10^5
58.1	10950	11.16	6.33×10^5

DISCUSSION

Thrust

It is important to clarify the meaning of the thrust measured. The friction drag of the fish is assumed to be unchanged by the loads, and only the pressure drag component altered. This is probably not strictly correct, as it is likely that the loads caused premature separation of the boundary-layer. However, any change in the friction drag will be small in comparison with the load drag, and was probably included in the measured load drag as this was measured on a fish model.

The characteristics of the propulsive wave have been related to one of the

components of the drag usually experienced by the body of the fish. The measured thrust represents the drag experienced by the body, but does not include induced drag components.

The thrust measured exceeds that expected for a flat plate of the same wetted surface area by a mean factor of 3.03, and exceeds the drag on an equivalent rigid straight streamline body by 2.78. This implies that the pressure drag of the swimming fish is high, undoubtedly associated with the boundary-layer separation observed by Allan (1961). Lighthill (1971) calculated that the drag of a swimming dace was about four times the theoretical value for a rigid straight fish, but under laminar flow conditions.

It must be remembered that the drag of a swimming fish at cruising speeds also includes some of the work done in ventilating the gills.

Power output

The power required to produce the thrust has been calculated from the product of thrust \times swimming speed (Table 8). The power output at the critical swimming speed was 4.1×10^5 ergs/sec and the maximum value at the highest swimming speed was 6.6×10^5 ergs/sec.

Bainbridge (1961) considered that the problem in the swimming of small fish was why they swam no faster than observed. This conclusion was based on the estimated power output of the whole muscle, doing work against a swimming drag equal to that of an equivalent rigid vehicle as calculated from standard hydrodynamic equations. Thus Bainbridge's problem is at least partly answered by the higher power outputs measured here than would be expected for such a rigid body.

Bainbridge (1961) also had to estimate values for the power output of red and white muscle systems. Of the former system he said, 'It is only possible to make some intuitive guess concerning values of a sustained output and the following have been arbitrarily chosen.' For fish in cold water, the value chosen was 2×10^5 ergs/sec/g red muscle. Assuming that the efficiency of the propulsive wave is 75 %, then the power output of the muscle would have to be 5.1 and 8.2×10^5 ergs/sec at the critical and maximum observed speeds to meet the power requirements. This represents 2.6 and 4.1 g red muscle working at any instant. As only half the muscle will in fact be operating at any instant, the total amount of red muscle required will be 5.1 and 8.2 g.

Webb (1970) found that the lateral-line red muscle represented about 4 % of the myotome – that is about 5 g for the fish used here – and apparently sufficient to meet the fishes' power requirements at the critical swimming speed. However, it was found that the trout had a further 16.5 g of red muscle representing the fibres scattered amongst the white muscle, described by Green & Greene (1914), Boddeke, Slijper & van der Stelt (1959) and Wittenberger *et al.* (1969). The trout had a total of about 21.5 g red muscle (Webb, 1970) which implies that the power output was between 0.48 and 0.77 ergs/sec/g.

Since Bainbridge estimated the red muscle power output, more data has been published on the power outputs of various animals, particularly man. Some of these values have been used to calculate the expected muscle power output of man during various activities (Table 9). The muscle power outputs have been calculated on the

assumption that active muscle represents 0.2 of the body mass (M) in walking and 0.4 M for other activities (Wilkie, 1960; Bainbridge, 1961). Of this muscle mass, it was further assumed that 75 % of the muscle was effective in doing work, while the remaining 25 % was required to move the limbs back to their original positions.

Table 9 shows that the muscles produce about 2×10^5 ergs/sec/g at high levels of cruising activity. The power developed is expected to increase two to three times for each 10°C temperature rise (Hill, 1956). Therefore the equivalent muscle power output at 15°C , based on the values for man, is about 0.35×10^5 ergs/sec/g, which is not too dissimilar to the value calculated here for the trout. Thus, it appears that the value for sustained muscle power output for fish estimated by Bainbridge is high, and that a value of about 0.5×10^5 ergs/sec/g would be more appropriate.

Table 9. *Some values for human muscle power output*

Power output (ergs/sec/g muscle)	Duration	Type of activity	Reference
17.3×10^5	1 sec	Standing jump	Davies & Rennie (1968)
16.6×10^5	1 sec	Estimated peak	Wilkie (1960)
9.5×10^5	About 5 sec	Running upstairs	Margaria <i>et al.</i> (1966)
2.0×10^5	22 min	Olympic rowing crew	Hendersen & Haggard (1925)
1.7×10^5	30 min	Champion athletes	Wilkie (1960)
1.4×10^5	Sustained	Walking 250 cm/sec	Dean (1965)
0.38×10^5	Sustained	Walking 150 cm/sec	—
0.11×10^5	Sustained	Walking 50 cm/sec	—

The power output of trout calculated from mathematical models of swimming

Several mathematical, and a few mechanical, models have been formulated which make it possible to calculate the expected power output from idealized fish. A summary of the important characteristics and assumptions (from a biologist's point of view) made in formulating these models is given in Table 10.

The major problem in the formulation of all the models is the difficulty in representing the exact movements of a fish's body in concise mathematical form. Thus, the models do not accurately fulfil the condition stipulated by Breder (1926) that in the study of fish locomotion fish must be observed to perform in the specified manner. Taylor (1952) in recognizing this problem said that 'to measure the velocity and direction of motion of each element of the body of a swimming animal... would be very laborious, and it still might be impossible to measure sufficiently accurate realistic values'. This is particularly so for fish swimming in or near the anguilliform mode where fish show very variable locomotor activity at different times and between individuals (Nursall, 1958; Bainbridge, 1963). However, in view of the rather crude measurements made on the propulsive wave by Bainbridge (1958) and in this paper, which have been shown to be related to swimming performance, this criticism should not be too rigorously applied to the hydrodynamic models.

The models can be divided into two groups on the basis of the assumption that flow around the swimming fish can be considered as either quasi-static or inviscid (frictionless).

Quasi-static

The body of the fish is divided into hypothetical segments. It is assumed that the forces generated by each segment at any instant in the propulsive cycle are the same as those generated by an equivalent segment moving steadily at the same velocity and angle of attack to the flow. The mean thrust developed by each fish segment is the sum of the individual steady-state (static) thrusts for all the velocities and angles of attack represented by the fish segment in the propulsive cycle. The total thrust developed by the fish is the sum of the mean thrusts developed by each segment.

Table 10. *The characteristics of some hydrodynamic models of swimming in aquatic animals*

Type of model	Flow		Swimming mode	Amplitude of wave	Reference
	Restrictions	Separation			
Quasi-static	2 dimensions	Yes	Hydrofoil – ostra-ciform or carangiform	Small	von Holst & Kucheman (1942)
	2 dimensions	Yes	Carangiform	Large	Parry (1949)
	2 dimensions	Yes	Carangiform	Large	Gero (1952)
	3 dimensions	Yes	Anguilliform	Large constant	Taylor (1952)
Inviscid	2 dimensions	No	Anguilliform	Small increasing	Gadd (1952, 1963)
	2 dimensions	No, but discussed	Anguilliform	Small increasing	Lighthill (1960)
	2 dimensions	No	Anguilliform	Small increasing	Smith & Stone (1961)
	2 dimensions	No, but high values of R_L	Rajiiform (like skate)	Small increasing	Wu (1961)
	2 dimensions	No	Rajiiform	Small increasing	Kelly (after Wu, 1961) 1961. Also mechanical model based on the hydrodynamic model. Good fit between the two
	2 dimensions	No	Three hinged segments; probably carangiform	Small increasing	Bonthron & Fejer (1963)

The model proposed by Taylor (1952) is most similar to the swimming trout, but lays greater stress on the three-dimensional flow than other models. The mode differs from the trout in assuming that the body is long and cylindrical, and that simple harmonic waves of constant amplitude are passed backwards along the body. The model also applies to smooth fish and laminar flow conditions. The trout is smooth over most of its body, but is rough at the trailing edges of the fins.

Values for the power output of the trout from Taylor's model are derived in the appendix. Two sets have been calculated: one set on the assumption that only that length of the body within one wavelength of the propulsive wave generates thrust, and a second set assuming that the whole body generates thrust. The former condition

is more probable in the trout because the anterior portion of the body will tend to generate negative thrust, or drag (Alexander, 1967).

The power outputs from Taylor's model are low in comparison with values calculated here (Fig. 11). This is undoubtedly because the trout propulsive system does not fit the assumptions made by Taylor. Taylor's model was, however, designed for a fish like an eel which fits more closely with these assumptions.

Power outputs are high at low swimming speeds. This occurs because thrust coefficients predicted for the fish are high, and the efficiency higher than expected. Fish reach a steady thrust coefficient at higher speeds, which the model predicts should be associated with a high mechanical efficiency.

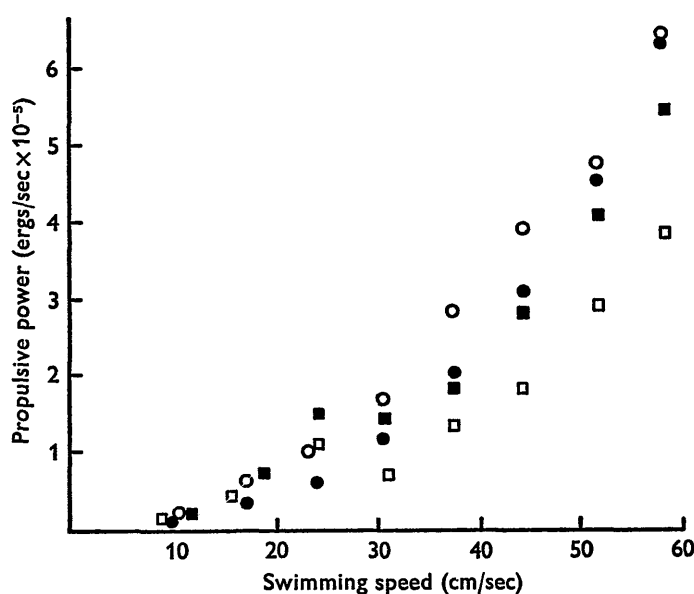


Fig. 11. Comparison between the power output measured for trout, and that calculated from models by Taylor (1952) and Lighthill (1969, 1970). ●, Values measured for trout. □, Values calculated from Taylor assuming that only that portion of the body included in one propulsive wave-length generates thrust. ■, Values calculated from the same model assuming that the whole body generates thrust. ○, Calculated from Lighthill's model.

Inviscid models

The inviscid models consider the reaction forces on the body of the fish in a perfect (frictionless) fluid. These are inertial forces, and are proportional to the rate of change of velocity of the water affected by the propulsive movements.

The model proposed by Lighthill (1960) is most similar to the swimming trout. The model is based on a long narrow fish, passing waves of increasing amplitude backwards over the body. Lighthill (1969, 1970) has proposed a simpler method for calculating the power output of the propulsive wave, which gives the same values as the earlier model. This has been used to calculate the thrust power output of the swimming trout (see Appendix).

The values from Lighthill's model show fair agreement with the measured values, particularly at higher swimming speeds (Fig. 11). The values tend to be higher than the measured values because the model assumes that the ratio between the forward

speed of the fish and the backward velocity of the propulsive wave V/V_w will tend towards 0.8 when propulsive efficiency will be high. Values for the trout (Table 11 in Appendix) show that the fish does not have high values of V/V_w , but tends towards high values at higher swimming speeds. The assumption that V/V_w is reasonably high results in the model giving high propulsive efficiency and higher thrust power outputs than those observed.

The tendency to meet the assumptions of the model at high swimming speeds suggests that the model would be a valuable tool for calculating power outputs in sprints.

Sprint speeds

The relationship between thrust and swimming speed can be extended into the sprint-speed range in order to calculate the expected maximum sprint speed. The assumption must be made that there is no change in the thrust/swimming-speed relationship.

The power required, P , to swim at a sprint speed, V_s , maintained for one second is given by:

$$P = 7.9 V_s^{1.8} V_s \text{ ergs from equation (12).} \quad (13)$$

The power output of the white muscle system is expected to be of the order of 8×10^5 ergs/sec/g muscle (Bainbridge, 1961). The trout used here had about 108 g white muscle, and hence the maximum power output maintained for 1 sec will be about 4.3×10^7 ergs, assuming that only half the muscle works at any instant. Assuming further that the efficiency of the caudal propeller is 75 %, then the power available for thrust is about 3.2×10^7 ergs. This is equal to P_s .

Therefore

$$\begin{aligned} V_s &= \sqrt[2.8]{\frac{3.2 \times 10^7}{7.9}} \\ &= 229 \text{ cm/sec or } 7.6 \text{ L/sec.} \end{aligned} \quad (14)$$

This is substantially lower than the values of 8.5 L/sec reported by Gray (1953) and of 9.5–10.5 L/sec reported by Bainbridge (1958, 1960, 1962). Bainbridge's fish had more muscle than the fish used here, the total muscle mass representing 63 % of the body mass. Correction of this value for the red muscle portion of the myotome, and calculation of V_s only gives a value of about 8.3 L/sec.

It would therefore appear necessary for the fish to reduce their drag by about half in order to swim at 10 L/sec. It might be possible to do this by not ventilating the gills.

An alternative explanation is that a 1 sec V_s should not be considered as a steady state, as assumed by the use of equation (13). The power required to swim at these sprint speeds is more likely to be related to the power required to accelerate the fish to these speeds. Acceleration rates for fish of different species suggests that they generally accelerate at rates of about 40 M/sec (Gero, 1952; Gray, 1953; Fierstiene & Walters, 1968). Thus, for a trout weighing 250 g, with an added mass of water entrained by the body representing 0.2 body mass, the acceleration power required to reach 10 L/sec from rest is of the order of 1.1×10^7 for about 1 sec. The fish would have adequate power to meet this requirement.

SUMMARY

1. The wavelength, tail-beat frequency and trailing-edge amplitude have been measured for five groups of rainbow trout at various subfatigue cruising speeds. Four groups of fish were fitted with extra drag loads. The swimming mode was anguilliform by definition, but is probably best considered as intermediate between this and the carangiform mode.

2. The wavelength of the propulsive wave represented 0.76 of the body length. The specific amplitude (amplitude/length) tended to reach a maximum value of 0.175 at tail-beat frequencies approaching 5/sec.

3. The product of frequency and specific amplitude was found to be linearly related to swimming speed in all five groups of fish.

4. The critical swimming speed for the non-loaded control group was 1.73 body length/sec, and fell in groups 1-4 as the magnitude of the extra drag loads increased. The critical swimming speed for the control group is low for salmonids, probably as a result of the unfavourable history of the fish.

5. A method is described for calculating the drag of a swimming fish from the effects of the extra loads on the characteristics of the propulsive wave. It was found that thrust, $T = 7.9$ (swimming speed)^{1.79}. The thrust was approximately 2.8 times greater than that required for an equivalent straight rigid vehicle.

6. It was calculated that the power output of the red muscle system would need to be about 0.48-0.77 ergs/sec/g muscle to overcome the drag of the fish at cruising speeds.

7. The power output of the fish was compared with values calculated by means of mathematical models proposed by Taylor and Lighthill. It was found that the fish did not fit the assumptions made in Taylor's model, and so power output calculations were not comparable with those calculated in the present paper. Lighthill's model was found to give values which were within 5 % of the values calculated here at higher swimming speeds. At lower swimming speeds the values were up to about 50 % lower than expected because again the fish did not fit the assumptions involved.

8. The relationship between thrust and swimming speed was extended into the sprint-speed range. It was calculated that fish could reach a maximum sprint speed maintained for 1 sec, provided that drag was reduced by about a half, or that the power required was that to accelerate the fish to that speed.

This work was presented in part towards the degree of Ph.D. in the Department of Zoology, University of Bristol. I wish to thank my supervisor, Dr Q. Bone, for his advice and encouragement during the course of the work, and Professor G. M. Hughes and Dr G. M. Jarman for many useful discussions.

The work was supported by a Scientific Research Council Studentship.

I also wish to thank Dr J. R. Brett for reading the manuscript for this paper, and for his valuable criticism.

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APPENDIX

Taylor's quasi-static model of fish propulsion

In this model the body was assumed to be long and cylindrical, and to pass a simple harmonic wave of constant amplitude backwards along the body. Each hypothetical segment was compared with an equivalent segment of a long straight cylinder moving at the same velocity and angle of attack. Instantaneous forces on the cylinder were calculated from empirical observations. From this data, and the equations of motion of each segment, the power output was calculated for unit segment length:

$$P_s = 2.7\rho dV^3R_d^{-\frac{1}{2}}G_{(na)}, \quad (15)$$

where P_s = power output/unit segment (ergs/sec),

ρ = density of water (g/cm³),

d = diameter of the cylinder, assumed to be equal to the mean depth of the fish, approximately 5 cm.

V = swimming speed (cm/sec),

R_d = Reynolds number based on d

$R_d = dV/\nu$, where

ν = kinematic viscosity of water (cm²/sec).

$G_{(na)}$ may be considered to be the thrust coefficient, which is dependent on parameters n and a , where

$$n = V/V_w \quad \text{and} \quad a = \alpha A_s/2\lambda,$$

where V_w = backward velocity of the propulsive wave (cm/sec),

λ = wavelength of the propulsive wave (cm),

A_s = amplitude of transverse motion of the segment (cm).

From equation (9) $\lambda = 0.68L$ where L = length (taken as 30 cm) and $V_w = f\lambda$.

Values for V and f have been taken from Table 5. Since the trout does not swim in the proposed manner, values for A_s have been calculated from the data in Table 5, and weighted with respect to the mean square amplitude. This assumes that the thrust produced is proportional to the square of the transverse velocity of each segment.

The total power, P , developed by the fish was given by

$$P = P_s l, \quad (16)$$

where l = the length of the fish developing thrust.

P was calculated for two values of l , equal to the length of the body included in one wavelength of the propulsive wave, and equal to the whole length of the body. These values are P_A and P_B respectively.

The values for V , V_w , n , a , A_s , $A_s/2\lambda$ and R_d are given in Table 11. Values for $G_{(na)}$ were taken from Table 4 in Taylor (1952). Values for P_A and P_B are shown in Fig. 11 and Table 11.

Table 11. Data and results for the calculation of the power output generating thrust from the models proposed by Taylor (1952) and Lighthill (1960, 1969, 1970)

(Further explanation is given in the text. P_A and P_B are values calculated from Taylor assuming thrust is developed by a length of the fish equal to 1 wavelength and equal to the length of the body respectively. P_G is the thrust power output of the propulsive wave, after Lighthill, and P_K is the energy of motion of the water shed into the wake.)

V (cm/ sec)	V_w (cm/ sec)	n	A (cm)	$A/2\lambda$	G_{na}	R ($\times 10^3$)	W (cm/ sec)	P_A	P_B (ergs/ sec)	P_G ($\times 10^5$)	P_K
10.1	44.1	0.23	2.4	0.05	2.5	5.1	10.1	0.10	0.14	0.14	0.09
17.2	50.5	0.34	5.3	0.10	3.2	8.6	16.8	0.50	0.70	0.61	0.30
23.9	48.8	0.49	7.6	0.16	3.0	12.0	19.8	1.07	1.50	1.01	0.35
30.7	60.6	0.51	6.8	0.11	1.5	15.4	23.3	0.69	1.39	1.76	0.57
37.5	69.3	0.54	7.2	0.10	1.3	18.8	27.4	1.31	1.83	2.82	0.84
44.3	76.0	0.58	7.6	0.10	1.2	22.1	30.8	1.98	2.77	3.90	1.04
51.6	76.8	0.67	9.2	0.12	1.2	25.8	34.4	2.90	4.06	4.75	0.93
58.1	86.5	0.67	8.8	0.10	1.2	28.9	37.8	3.86	5.40	6.42	1.28

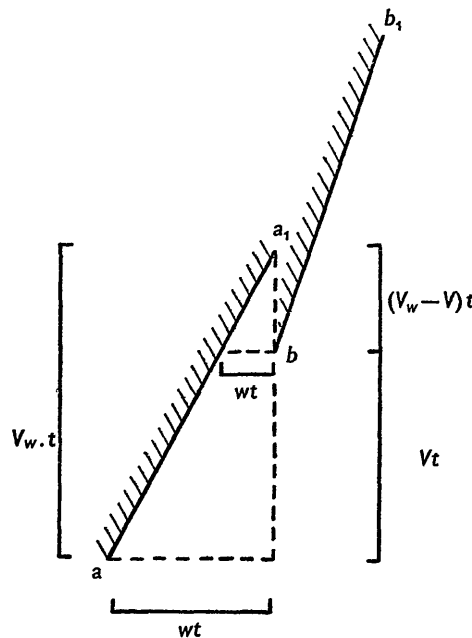


Fig. 12. Diagram illustrating the model proposed by Lighthill (1969). Further explanation is given in the text.

Lighthill's model of fish propulsion

Lighthill's model (1969, 1970) considers the momentum given to a slice water, with mass m_w , which is just left behind by a segment of the body immediately anterior to the trailing edge (Fig. 12). The momentum given to the water is $m_w w$, where w is the velocity given to the water, and is proportional to the trailing-edge transverse velocity, W , of the segment.

The length of the segment is such that the propulsive wave just overtakes the water in time t . The length is therefore $V_w t$. When $t = 0$, the water will be a distance Vt from the trailing edge, with the segment in position aa in Fig. 12. At time t , the segment will have moved to bb . The distance moved transversely by the trailing edge will be Wt , and the distance moved by the water slice, wt . Then, from similar triangles,

$$\frac{wt}{Wt} = \frac{(V_w - V)t}{V_w t} \quad (17)$$

and

$$w = \frac{W(V_w - V)}{V_w}. \quad (18)$$

The momentum gained is $m_v w$, and the rate of change of momentum is $m_v w V$. The rate of working is given by

$$P_w = m_v w V W \text{ ergs/sec.} \quad (19)$$

m_v is the virtual mass of water affected by the trailing edge, and is numerically equal to

$$m_v = \rho \Pi \frac{1}{2} (d_T)^2 \text{ g/cm}^2,$$

where d_T = trailing-edge depth which was found to be 6 cm for the trout used here.

P_w represents the total rate of working of the propulsive wave and includes the energy required to accelerate the water up to the velocity w . The fraction of the energy required for this, P_k , is given by

$$P_k = \frac{1}{2} m_v w^2 V \text{ ergs/sec} \quad (20)$$

and the power producing thrust, P_c ,

$$P_c = P_w - P_k. \quad (21)$$

W , the trailing-edge velocity, was calculated on the assumption that the tail executed simple harmonic movements. W is therefore the root-mean-square velocity, calculated from values for f and A in Table 5.

Values for V , V_w and W are given in Table 11, with values for P_c and P_k . The power output producing thrust is compared with values measured here in Fig. 11.