FAST-START RESISTANCE OF TROUT

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SUMMARY

Rainbow trout (*Salmo gairdneri* Richardson) with a body mass of 268 ± 36 g were used to determine the acceleration resistance of a fish during fast-starts. The mass of the fish was increased by mass loads of 75, 150, 225 and 335 g. The loads were made from nesting horseshoe-shaped brass saddles which fitted snugly over the fish so that the extra mass was equally distributed in all planes about the stretched-straight body centre of mass. The weight of the saddles was taken up by a 291 cm line attached to the dorsal surface of the fish above its centre of mass. The other end of the line was attached to the ceiling. The performance of the fish with and without saddles was measured during fast-starts, initiated by a 1 v.cm^{-1} d.c. electric shock. Performance was determined in terms of the distance travelled with time, measured from high speed movie films (240 frames s^{-1}). The relationships between distance travelled and time were described by power functions for fish with and without mass loads. Exponents were not significantly different for the fish with various mass loads showing that frictional and form drag made negligible contributions to acceleration resistance in a fast-start. The resistance of the fish in a fast-start, due to fish mass and a resistance component of added water mass (apparent mass), was calculated using hydromechanical theory for representative fast-start sequences. The apparent mass was estimated at 320 g, which is $1.2 \times$ fish body mass.

INTRODUCTION

Numerous studies on fish locomotion have sought to determine drag forces during steady swimming (see recent reviews by Alexander, 1977; Wu & Yates, 1978). Few studies have considered the resistance forces for animals accelerating in water. Exceptions are Siekmann (1963), Johnson, Soden & Trueman (1972), Weihs (1972, 1973, 1977) and Webb (1975a). All these studies have emphasized theory; no experiments have been performed to determine acceleration resistance for a living animal.

The resistance to motion of a body accelerating in water is dominated by its mass plus kinetic energy dissipated in the water that can be expressed as an equivalent mass of water accelerated with the body (added mass). Frictional and form drag are expected to be small, especially as growth of the boundary layer is time dependent and does not mature until a body has moved approximately 1·5 times its length as measured in the direction of motion (see Yih, 1969; Batchelor, 1967). The major unknown resistance is usually the added mass.

The added mass is commonly expressed in coefficient form as a proportion of body volume. Most aquatic animals have a density close to unity, so that the added mass coefficient is expressed as a proportion of body mass. Added mass coefficients used for accelerating fish and cetaceans range from 0·05 (Lang, 1975) to 0·1 (Gero, 1952) and are based on values for an equivalent rigid body moving along its long axis.

However, fish accelerate in fast-starts using large amplitude lateral body movements which effect an added water mass proportional to the square of the body depth per unit length (Lighthill, 1970; Weihs, 1973). Since all parts of the body show lateral movement (see illustrations in Hertel, 1966; Weihs, 1973; Webb, 1975b, 1976; Eaton, Bombardieri & Meyer, 1977), the total added mass involved with body movements must be 2–3 times the mass of the body. As is usual in fish locomotion, thrust and resistance forces are interrelated complexly. Nevertheless, resistance components of the added mass associated with lateral motions could substantially increase the total resistance to acceleration of a fish compared to a rigid body. In addition, the boundary layer of a flexing body might stabilize earlier in each propulsive cycle than would be expected for an accelerating rigid body which could augment frictional forces.

The purpose of the experiments reported here was to determine, (a) the relative importance of mass and frictional resistance and (b) the added mass, for a fish accelerating in a fast-start.

MATERIALS AND METHODS

Fish

Experiments were performed on rainbow trout (*Salmo gairdneri* Richardson) obtained from a local hatchery. Fish were held in 200 l oval tanks, flushed continuously with water at a rate of 50 l h^{-1}. A submerged pump generated a water current against which fish swam continuously. The mean velocity experienced by the fish was approximately 20 cm s^{-1}. Fish were acclimated to the experimental temperature (15·0 ± 0·2 °C; $X \pm 2 \times$ s.e.) over 2 weeks prior to starting experiments. Dissolved oxygen levels were maintained close to air-saturation using air stones. Fish were fed daily on a maintenance ration of Purina trout chow.

The dimensions of the fish, determined after experiments using methods described in Webb (1977) were as follows: mass 268·07 ± 35·77 g, total length 29·8 ± 0·9 cm, wetted surface area 372·6 ± 30·5 cm^2 and muscle mass 148·87 ± 21·69 g ($X \pm 2 \times$ s.e.; $N = 10$).

Methods of modifying acceleration resistance

The ideal experimental method to determine the nature of resistance forces of fish during acceleration would be to vary the mass of the system. However, mass loads must be added without affecting the buoyancy of the fish. In these experiments, the increase in mass was achieved by adding mass loads, with the excess weight of the loads in water supported on a line so that the fish was not required to correct its buoyancy. The system therefore resembled a pendulum (Fig. 1).

A 15 lb (6·8 kg) test monofilament line was sewn to the dorsal surface of the fish above the expected location of the centre of mass, determined for a subsample as described by Webb (1978). A small slip-ring universal coupler was located on the
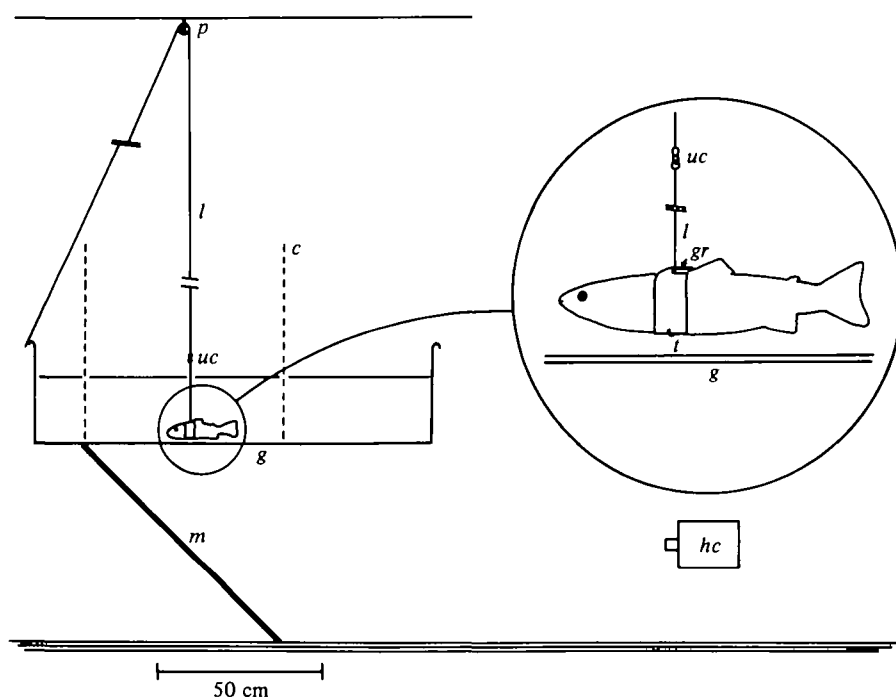
Fig. 1. Diagrammatic representation of the system used in experiments. c, Cage delineating observation chamber; g, glass bottom; gr, groove; hc, high-speed camera; l, monofilament line; m, mirror; p, pulley; s, saddle; t, saddle restraining threads; uc, universal coupler.

line 25 cm above the fish to avoid twisting and tangling. The remainder of the line above the fish ran over a pulley attached to the ceiling. The length of the line was adjusted so that the fish would rest in a normal position just above the floor of the tank. The length of the line was 291 cm.

Four nesting horseshoe-shaped saddles were made from $\frac{1}{8}$ in. (0·32 cm) brass sheet. The effective mass of these saddles (see below) was 75, 150, 225 and 335 g. A groove in the top of the saddles allowed them to fit over the pendulum line. The sides of the saddles fitted snugly about the body of the fish. The saddles were secured dorsally to the pendulum line, and ventrally to threads sewn to the belly. This prevented the saddles shifting during acceleration. Saddles could be put in place or removed in less than 2 min. The maximum dimensions of the saddles were 2·5 cm in length and 6 cm in depth, equal to the mean depth of the fish at the location of the centre of mass. The length of the saddles would have restrained body bending in the immediate vicinity of the saddles, but at that point the body bends relatively little in acceleration (see figures in Eaton *et al.* 1977). The mass of the saddle was equally distributed in all planes about the centre of mass. The use and location of the pendulum line prevented rotation of the body, thereby eliminating rotational added mass components.

Alternative methods

Other possible methods were explored, but found less satisfactory. These are briefly summarized here for completion.

(*a*) Increase the added mass by means of plates normal to the body axis, similar to those used for steady swimming drag determinations by Webb (1971*a*). This was rejected because very large plates would be required.

(*b*) Attach neutrally buoyant loads. This method was rejected because loads were too large. As a result, they were rarely accelerated without substantial rotation about the point of attachment to the fish. This problem could not be eliminated without greatly restricting the freedom of motion of the fish.

(*c*) Lifting loads. Houssay (1912) forced fish to lift loads by attaching them to a balance. However, his fish were forced to move in very tight vertical arcs and lateral movements typical of fast-starts were prevented. This arrangement was therefore rejected. In an alternative approach it was found that fish would not lift loads attached via a line running over a smooth pulley without turning towards the load. In addition, the small elasticity of such a line introduced formidable analysis problems at the high acceleration rates observed in fish.

(*d*) Internal loads (metal rod or mercury in flexible tubes) could not be prevented from moving when the fish accelerated, except by more traumatic surgery than used in the experiments. Rigid loads also had to be long relative to the length of the fish, restricting bending.

Calibration of mass loads

The acceleration of the saddles is called here the effective mass, defined as sum of mass and added mass resisting acceleration. The sum of mass and added mass of entrained water is called the virtual mass, but the added mass alone is sometimes also called the virtual mass. The term effective mass is used to avoid this confusion. Thus the effective mass of the saddles accelerating in water was measured using an electrically driven catapult. The catapult consisted of a trolley driven along a track, 2 m long, above a water trough. The track was constructed from two parallel L-beams, 15 cm apart. Roller bearings on the trolley ran along the top edge to carry the weight and horizontally against the bottom lip of the L to prevent wobble. The trolley was towed along the tracks via braided steel wires wound around an axle driven by an induction motor. Acceleration rates from 0·5 to 15 g ($1 g = 9\cdot81$ m s^{-2}) were obtained by using a variable transformer to vary the voltage to the motor.

A balance was attached to the trolley. This consisted of a vertical reinforced and streamlined rod, 40 cm long, pivoted on bearings 10 cm from its upper end. The upper end was connected to a force transducer (Grass Instruments). The lower end was inserted into a model fish at a point corresponding to the centre of mass of live fish. Saddles were attached to the model. The model was carved from balsa wood so that its mass would be small.

A miniature oil-damped accelerometer (Entran Devices) was securely glued into the base of the balance rod at the location of the centre of mass of the fish. A second accelerometer was located on the trolley. Acceleration rates were compared from these

two accelerometers to check for possible elastic artifacts due to bending of the balance rod. The streamlining allowed reinforcement so that no significant effect was found.

The force transducer was calibrated using known weights. The accelerometers were calibrated in two ways. First, a $\pm 1 g$ calibration was obtained by orienting the accelerometer to the earth's gravitational field. Secondly, for acceleration rates in excess of $1 g$, simultaneous measurements of acceleration rate and distance travelled with time were obtained using the accelerometers and high speed movie films (500 frames s^{-1}) respectively. The acceleration rate data were integrated to obtain velocity and the distance-time data from film analysis were differentiated to obtain velocity. The two velocity calculations were compared. The response of the accelerometers was linear, so that the $\pm 1 g$ calibration was subsequently used in experiments.

The catapult system was constructed of materials that were as rigid as feasible. However, the instantaneous forces at high acceleration rates were sufficient to distort the drive system elastically. A variety of methods was tried to overcome the problem without success. As a result, the acceleration rate increased regularly for only the first 100–150 ms. After this period, instantaneous acceleration rates oscillated with decreasing amplitude while mean acceleration rate continued to increase until the trolley was stopped. The frequency of oscillations was 50–60 Hz suggesting that they might have been due to the normal a.c. frequency of the line voltage driving the motor. However, exactly the same pattern was found when the motor was replaced by a 200 kg bag of sand which fell under the force of gravity to drive the trolley. The major fish fast-start stages lasted about 150 ms (see below) so that the elastic recoil of the system did not constitute a problem in calibrating the instruments and saddles.

The effective mass of the saddles was measured by attaching them to the model fish and recording the resistance forces when accelerated in water. A model fish was used to minimize non-saddle mass and to eliminate the known but uncontrollable errors in using dead fish for drag measurements (Webb, 1975 a). Corrections were made for the resistance of the fish and the balance arm.

Experimental procedures

Surgery to attach the pendulum line was performed on lightly anaesthetized (MS 222) fish 24 h before an experiment. Individual fish were then placed in a glass-bottomed observation chamber 50 cm long and 50 cm wide, filled with water to a depth of 20 cm. The fish hung on the pendulum line at the centre of the chamber (Fig. 1). After the 24 h recovery period, saddles were slid onto the fish. For controls, they were immediately removed again. After a further 8 h, fish were stimulated to accelerate using a 1·0 V cm^{-1} d.c. electric shock of 10 ms duration. Fast-starts were recorded on movie film via a 45° mirror beneath the chamber. The framing rate was 240 Hz as determined using a 100 Hz calibration signal. Two fast-starts were recorded. Saddles were then removed and new ones located in place. After a further 12 h fast-starts were again recorded with new saddles. The sequence for the addition of the loads was randomized.

Movie film was analysed frame by frame to observe kinematics and to measure performance. Methods are described in detail by Webb (1978). Briefly, performance was measured from the distances travelled by the centre of mass of the stretched

straight body. This closely approximates the point about which propulsive forces act. The X and Y co-ordinates were recorded for the centre of mass in each frame as well as the direct distance travelled between frames (i.e. the net motion measured along the path of the centre of mass). The latter is the measure of the net performance of the fish, and is the one that is most important in terms of the normal behaviour of the fish. The measure of net movements is also the most accurate, especially at the start of acceleration when displacements are small.

The additional forces acting on the fish due to the displacement of the pendulum were calculated. At the observed acceleration rates and displacements, the additional force was $< 1\%$ of the mass load. Therefore, no corrections were applied. The mass of the pendulum line and universal couplers were also negligible compared to the mass of the fish.

<div align="center">RESULTS</div>

Fast-start movements

All fish, with or without saddles, showed similar fast-start body movements. These were the typical 3-stage movements originally described by Weihs (1973) and norm-ally seen in fish (see Eaton *et al.* 1977). There were no differences in the time to complete stages 1 and 2, the major acceleration period, for fish with or without loads. Overall mean times were 0.075 ± 0.002 s $(\bar{X} \pm 2 \times \text{S.E.})$ to complete stage 1 and 0.146 ± 0.007 s to the end of stage 2.

Fast-start performance

The measure of performance used to compare fish with various mass loads was the distance covered in a given time. This is the measure obtained directly from analysis of movie film and, in contrast to derived estimates of velocity and acceleration rate, is least subject to error. The relationships between the net distance travelled (measured along the path of the centre of mass) and elapsed time from the start of acceleration were found to be well described by power functions for each mass load (Table 1). The exponents were not significantly different from each other (Duncan's multiple-range t test; $\alpha = 0.05$) and had a mean value of 1.51. The regression coefficient declined with increasing mass load.

The distance travelled in a given elapsed time for the fish accelerating from rest also decreased with increasing mass load. Best-fit linear regression equations were obtained for log-transformed data. The non-linear relationship between distance covered in a given time and mass load is expected for two main reasons. First, the similarity of propulsive movements but variation in performance of fish with various loads would have affected the water velocity incident to the body and hence the magnitude of thrust force components and hydromechanical efficiency (see below and Webb, 1971*b*). Secondly, it is assumed that the rate of working and total work done in a given time is constant for all fish so that performance differences between groups would be proportional to the square of the distance travelled.

The addition of mass loads not only reduced net forward progression, but also lateral recoil movements of the centre of mass (Fig. 2).

Table 1. *Best-fit regression equations for the relation between distance travelled with time for rainbow trout during fast-starts with and without extra mass loads: S is distance travelled (cm) and T is time (ms)*

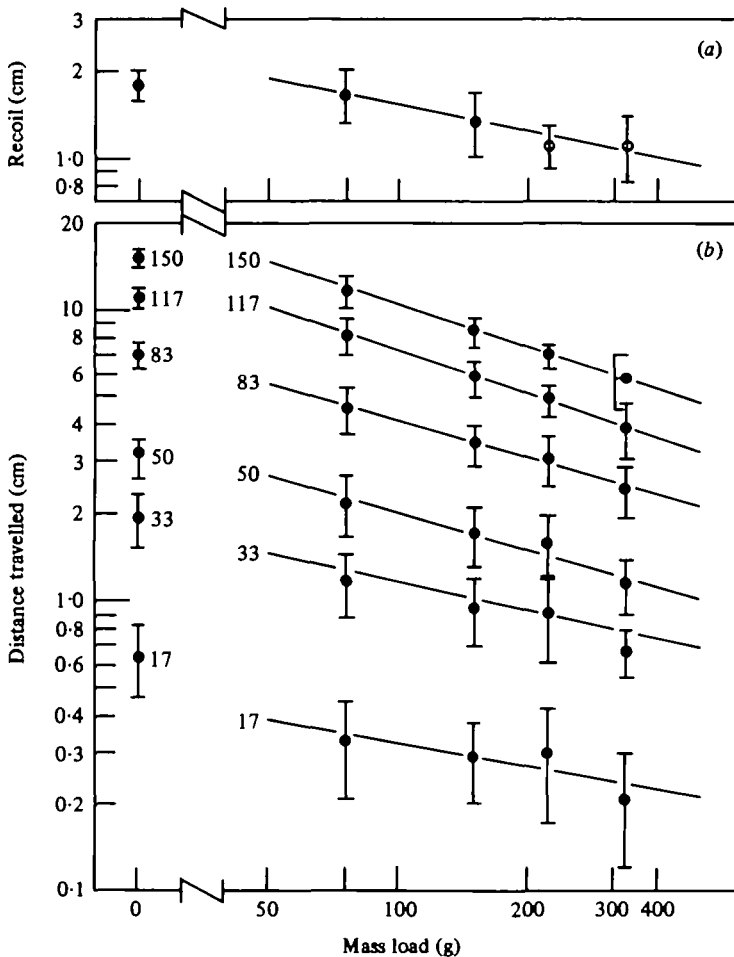| Extra mass load (g)	Equation of motion	r^2
0	$S = 259 \ T^{1\cdot49\pm0\cdot04}$	0.9836
75	$S = 206 \ T^{1\cdot55\pm0\cdot05}$	0.9586
150	$S = 168 \ T^{1\cdot50\pm0\cdot06}$	0.8641
225	$S = 125 \ T^{1\cdot62\pm0\cdot08}$	0.9377
335	$S = 92 \ T^{1\cdot49\pm0\cdot12}$	0.8970

Fig. 2. Examples of the relationships obtained between (A) lateral recoil movements of the centre of mass and (B) distance covered with elapsed time during fast-starts by trout with various extra mass loads. Exemplary relations at 17 ms (4 frame) intervals are shown for distance travelled in various elapsed times from 17 to 150 ms, spanning the duration of a fast-start. Vertical bars show $\pm 2 \times$ s.e. about mean distances. Solid lines for each time were obtained from best-fit linear regression equations relating distance travelled and mass load.

DISCUSSION

The equation of motion for fish accelerating in water at constant depth can be written after Johnson et al. (1972):

$$F = f(M_b + M_a + M_l) + \tfrac{1}{2}\rho A U^2 C_D, \tag{1}$$

where F = thrust force, f = acceleration rate, M_b = body mass, M_a = resistance added mass, M_l = load mass, ρ = density of water, A = wetted surface area, U = swimming velocity, C_D = frictional drag coefficient.

Forces due to changes in depth in the present experiment (pendulum effects) are neglected because they were $\ll 1\%$ of the total resistance forces.

The first term on the right of equation (1) is the resistance due to mass, and the second term is that due to viscosity.

The term $M_b + M_a$ will be called the apparent mass. It is the mass component for a fish without a load that comprises the mass resistance during acceleration. The use of terms such as virtual mass for this sum, or added mass for M_a do not seem appropriate, because they should include the total mass of water involved in propulsive movements. M_a in equation (1) is a *partial* value for the *resistance* added mass only, representing the component of total added mass resisting forward acceleration of the fish. It should also be recognized that added mass itself is not real. It is in reality a simplified factor taking into account energy dissipated in the fluid by an accelerating body that can be expressed as an apparent mass increment to the body (see Batchelor, 1967; Yih, 1969). Therefore, the apparent mass, defined here as $M_b + M_a$, is the factor in the equation of motion that serves to explain the observed acceleration of a fish when a given (maximum) force is applied, as in a fast-start.

The results for the relationships between distance covered and time for fish with the various mass loads show that the frictional drag component is small. If frictional drag was significant, the exponents would vary with mass load. This is because velocities achieved in a given time decreased with increasing load, so that differences in U^2, and hence frictional drag, would be large between the fish with various mass loads. Then, for a given maximum force, as induced by an electrically stimulated fast-start, performance would fall off at a greater rate for fish with smaller loads as they achieved greater velocities more quickly. Since this effect on performance was not observed it can be concluded that frictional drag in a fast-start is small enough to neglect. Then from equation (1), the resistance to acceleration must be due to the apparent mass plus that of the load where appropriate.

It is difficult to determine the magnitude of the apparent mass. The apparent mass cannot be simply determined by proportional effects of mass loads on performance because both thrust and propulsive efficiency will be affected by the loads. This can be seen from the hydromechanical theory formulated by Weihs (1972, 1973) for unsteady large-amplitude propulsion. From Weihs (1973, his equation (7)), the thrust force at any instant is;

$$F = \left[mw\frac{\partial z}{\partial t} - \tfrac{1}{2} mw^2 \frac{\partial x}{\partial a} \right]_{a=0} + \frac{d}{dt}\int_0^1 mw\frac{\partial z}{\partial a}\, da. \tag{2}$$
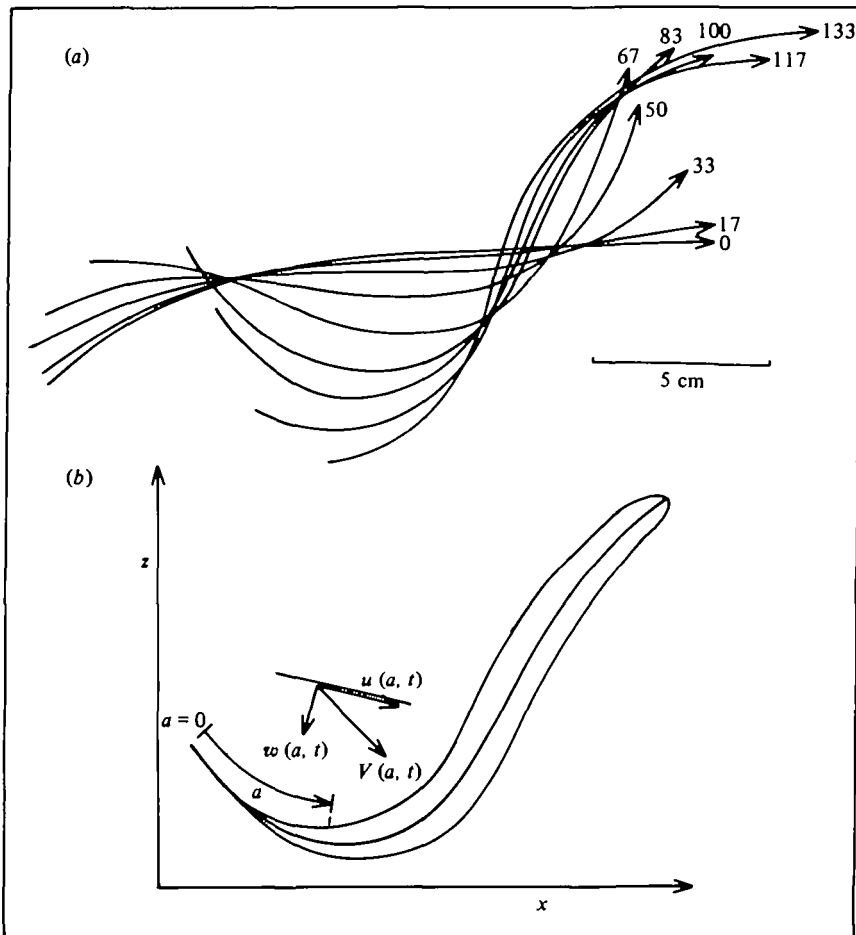
Fig. 3. (A) Tracings from movie film of the centre-line of a rainbow trout during a fast-start to show typical body movements. Tracings are shown for every 4th frame for clarity. (B) Co-ordinate system and symbols used in analysing thrust forces during a fast-start, based on Weihs (1972, 1973).

Co-ordinate systems and symbols are defined in Fig. 3. m is the added mass per unit length. Small lift forces due to the fins are not included.

In Fig. 3, V is the incident velocity, which depends on the forward speed of the fish and the lateral speed of each point along the body. At each point along the body, V is resolved into a tangential component u, the source of frictional drag, and a normal component w generating the normal force contributing to thrust.

From equation (2), it can be seen that the total force depends on w, the effective velocity given to the water by propulsive movements, but that losses depend on w^2. w depends on both the speed of lateral movements and the speed of forward progression (Lighthill, 1971; Weihs, 1973). In the present experiments, propulsive movements were similar with or without loads so that lateral velocities at various points along the body will be the same. However, distances travelled in a given time

declined so that forward velocities were not the same. Therefore, w would increase with extra mass load, but not directly proportional to the mass load, so that differences in w would affect thrust and efficiency. As a result, apparent mass cannot be obtained by simple comparison of performance of fish with and without mass loads.

Therefore, the apparent mass of the fish during a fast-start was determined by calculating F for representative acceleration sequences, one sequence being selected for each mass load. A typical fast-start sequence for zero mass load is included in Fig. 3A. Although care was taken to select representative sequences, unrecognized bias could be included that would not give typical results. To check for this possibility, average values of F were also calculated based on the five selected fast-starts and the mean performance for all fish. First, the various body motions were superimposed and average movements calculated. These were then used with the equations in Table 1, relating distance travelled and time, to place the average movements into the appropriate average time sequence. These motions were then used to calculate an average value for F. Apparent mass was obtained by dividing F by g, the acceleration due to gravity.

Analysis followed the method described in detail by Weihs (1973), who also provides an example, and used by Webb (1977) to evaluate theoretical effects of body form on fast-start performance. Thus, F was calculated using equation (2) for body movements through a fast-start and then the mean thrust value was obtained. Overall mean values of the various input parameters for the fast-start are shown in Fig. 4. This figure clearly shows changes in w increasing with mass load necessitating an analysis of the type employed.

Results of the calculations are shown in Fig. 5. The total resistance mass (apparent mass $+ M_1$) increased with increasing mass load, but results were somewhat variable for the five sequences originally selected. Calculations using averaged data showed a similar, less variable increase in total mass resistance with increasing mass load. The best fit linear regression equation was calculated by the method of least squares for all the mass resistance estimates:

$$(M_b + M_a + M_1) = 320 + 0 \cdot 97 M_1, \quad r^2 = 0 \cdot 887. \tag{3}$$

The mass resistance should be directly proportional to M_1, but the observed value of $0 \cdot 97$ is clearly not significantly different from unity.

The intercept, 320 g is the best estimate for the apparent mass, $M_b + M_a$. This represents an apparent mass coefficient (functionally equivalent to the added mass coefficient for rigid bodies) of $0 \cdot 2$ for the fish with a mean mass of 268 g. Weihs (1973) calculated acceleration rates of trout using his hydromechanical theory which were 20–30 % greater than observed. It appears that resistance added mass was not included, when a difference of the order observed would be expected. The apparent mass calculated for lateral (recoil) movements was 400 g showing the effect of the large body and fin depth at the centre of mass assisting in reducing lateral recoil (Lighthill, 1970).

The added mass coefficient for a well designed streamline body is $0 \cdot 05$–$0 \cdot 01$ (Gero, 1952; Lang, 1975) giving mass resisting acceleration equivalent to 281–295 g. The total mass of water, also enclosing the trout body, is the integral of $\pi \times \rho \times \text{depth}^2/4$
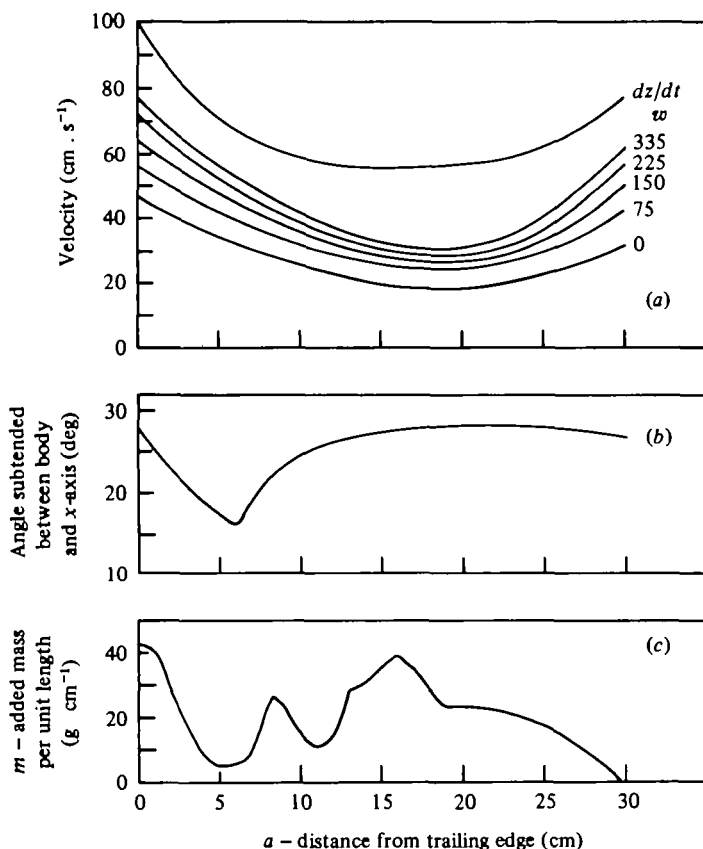
Fig. 4. Mean values of various parameters used in the calculation of the thrust (equation 2) developed during fast-starts by rainbow trout with and without extra mass loads. (A) Values of w and dz/dt for fish with various loads. (B) The angle subtended between the body and the axis of motion, dz/da. (C) The added mass per unit length, m. Note that dz/dt, dz/da and m are the same for all fish because body movements were similar.

along the body length, which from Fig. 4 C is 630 g for the fish used in these experiments. The best estimate of the apparent mass in these experiments was 320 g. It therefore appears that the apparent resistance mass of an accelerating fish is somewhat larger than would be expected for an equivalent rigid body but very much less than expected from the total mass of the system. Therefore, acceleration kinematics are effective in preventing the large added mass associated with lateral body movements from contributing to resistance. This is because the bulk of the added mass is accelerated laterally and posteriorly, normal or opposite to the resistance vector, i.e. the bulk of the added mass is associated with the generation of thrust.

The small apparent mass compared to total added mass does not mean that the efficiency of the propulsive system is high because large energy losses could still be associated with water displaced laterally and posteriorly. In fact, Webb (1979) used comparative observations on rainbow trout and crayfish, *Orconectes virilis* to argue that the trout would only be about 20 % efficient in converting muscle work into useful
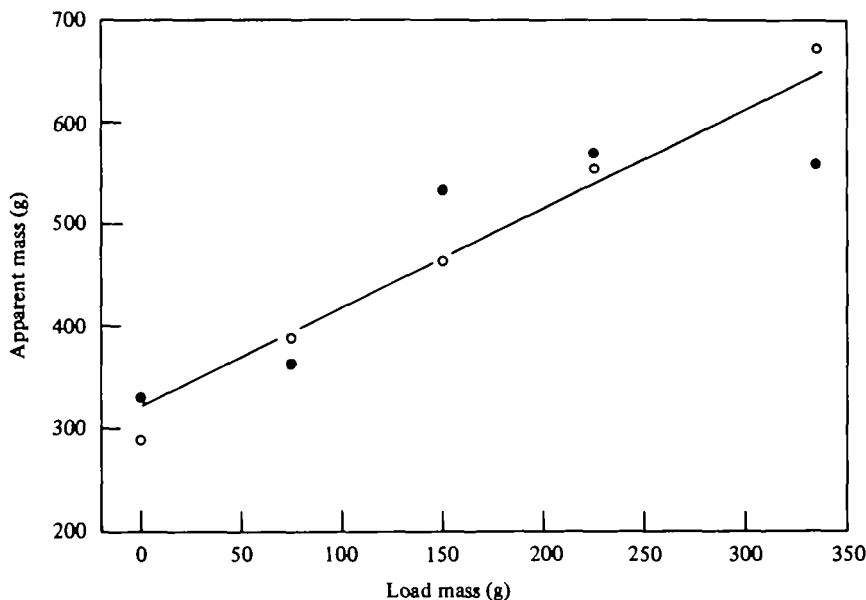
Fig. 5. The relationship between apparent mass and mass load for rainbow trout during fast-starts. ●, Values calculated from one fast-start sequence selected for each mass load. ○, Apparent mass values calculated from combined data to eliminate bias in selecting sequences. The solid line is the best-fit linear regression calculated by the method of least squares for all data points.

acceleration. For example, in the present experiments, it follows that the mean rate of working of the trout was $3\cdot4$ W in accelerating $0\cdot32$ kg to a speed of $1\cdot5$ m.s^{-1} over $0\cdot15$ cm in $0\cdot146$ s (based on the equation for control fish displacement in Table 1 and Fig. 5). The muscles of cold water can generate about 100 W.kg^{-1}, which for the present trout gives a maximum muscle power output of 15 W. Then the efficiency of the propulsion system in converting muscle power to useful work in acceleration is about 23%. This low efficiency seems related to a low Froude efficiency and energy wastage in lateral recoil (see Webb, 1979).

Webb (1971, 1975b) also found that the work performed and rate of working during acceleration was low compared to equivalent steady swimming. This suggestion was based on the limited data then available on acceleration and assumed a sustained acceleration of $4g$ for a relatively long period of time and an efficiency comparable to steady swimming. He also found that the apparent energetic advantages of acceleration declined at lower acceleration rates. These ideas need re-evaluation in the light of new observations on acceleration and the apparent mass resisting that acceleration.

A fast-start is a high-power short-duration largely stereotyped behaviour (Eaton et al. 1977; Webb, 1978). For the control fish in the present experiments, the mean speed in a fast-start was $1\cdot0$ m.s^{-1} and the maximum speed was $1\cdot5$ m.s^{-1}, both calculated up to the end of stage 2. Webb (1971) estimated the thrust required to swim at steady cruising speeds to be $0\cdot31$ (speed)$^{1\cdot79}$ N for rainbow trout of roughly similar size to the fish used in the present experiments. Therefore, the rate of energy expenditure by the caudal propeller would be about $0\cdot3$ W to swim steadily at the

mean fast-start speed, and 0·94 W at the maximum speed. It can also be readily shown that the mean thrust, work performed in travelling the same distance as in the fast-starts or in working for the same period of time are lower for steady swimming compared to fast-starts. Clearly the mechanical performance in a fast-start is more costly than that of steady swimming.

In addition, the hydromechanical efficiency of the caudal propeller in steady swimming is believed to be high, values of 0·9 being reasonable (Webb, 1975 a). Thus fish can achieve very high sprint steady speeds for the same muscle power output indicated for acceleration. Therefore, if the muscle can generate 15 W, then the maximum steady speed would be 3·9 m.s⁻¹. Using data in Wardle (1975) the maximum sprint speed of fish of the size used here would be 3·3–3·8 m.s⁻¹, based on crude estimates of the minimum twitch time of excised muscle blocks and stride length. This is of the same order as the maximum speed based on the present comparative estimates of muscle power.

These various calculations, using the most recent comprehensive studies on acceleration performance and resistance, now show that the energetic cost of acceleration is high compared to many estimates of equivalent steady swimming performance. However, fast-starts perform a different function, where the high energy costs are likely to be of secondary importance. Thus fast-starts are essential to the avoidance of predators.

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