TAIL THRUST OF BLUEFISH
POMATOMUS SALTATRIX AT DIFFERENT BUOYANCIES, SPEEDS, AND SWIMMING ANGLES

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SUMMARY

1. The tail thrust of bluefish *Pomatomus saltatrix* was measured using a body accelerometer at different water speeds, buoyancies, and angles of water flow to determine the contribution of tail thrust in overcoming parasitic drag, induced drag, and weight directed along the track. The lengths and weights of the fish averaged 0·52 m and 1·50 kg respectively.

2. The tail thrust overcoming parasitic drag in Newtons, as measured during neutral buoyancy, was: $0·51 \times \text{speed} + 0·15$, with a standard error of estimate of 0·09 N.

3. When buoyancy was altered by the introduction or removal of air from a balloon implanted in the swim bladder, the tail thrust was altered by an amount of the same order as the value calculated for the induced drag of the pectoral fins.

4. The component of weight directed backward along the track was the weight in water multiplied by the sine of the angle of the swimming tunnel relative to horizontal. When this force was added to the calculated induced drag and tail thrust measured at neutral buoyancy, the rearward force equal to the tail thrust, at 45 ml negative buoyancy, 0·5 m s^{-1}, and 15° head up, was 0·12 N due to weight + 0·05 N due to induced drag + 0·40 N due to parasitic drag = 0·57 N total rearward force.

5. The conditions required for gliding were not achieved in our bluefish because the drag exceeded the component of the weight in water directed forward along the track at speeds above the stalling speed of the pectoral fins.

INTRODUCTION

The net force that must be overcome by thrust to enable a fish to swim would be expected to depend on the parasitic drag, buoyancy, angle of attack of the body and pectoral fins, and angle of ascent or descent relative to horizontal. Theoretical relationships among the above factors have been derived by several investigators. Breeder (1926) qualitatively described the hydrostatic elements and the methods of fin movement that different fish use to maintain equilibrium while swimming forward or remaining stationary in the water. The two main hydrostatic adjustments

a fish could make were the alteration of the amount of air in the swim bladder, and variation in the amount of fat stored. Breeder mentioned the use of the pectoral fins for propulsion, steering and lift. Harris (1936) used models to measure the lift generated by the fins of the common American dogfish *Mustelus canis*. His measurements showed that different fins help prevent roll, pitch and yaw. Bainbridge (1958) related the frequency of the tail beat to the swimming speed, and in 1963 calculated the fractional contributions of the body and tail to total thrust in a bream, dace, and goldfish. General principles of the hydrostatic and hydrodynamic forces used to compensate for negative buoyancy were outlined by Aleev (1969), and Alexander (1967, 1968). Detailed observations of a fish's pectoral fin area and buoyancy, and their relation to swimming speed, were made by Magnuson (1970, 1973, 1978), who used them to calculate the amount of lift produced by the pectoral fins. Weihs (1973) discussed the possibility of the fish saving energy by using negative buoyancy and the pectoral fins to glide. DuBois & Ogilvy (1978) showed that changes of body acceleration were closely related to changes in tail force. However, total momentum imparted to the water calculated by the method of Lighthill (1971) was greater than could be attributed to the tail alone. Ogilvy & DuBois (1981) presented data on tail thrust v. swimming speed for a negatively buoyant fish swimming upward at an angle of 33°. The fish's weight in water was resolved into a component aimed backwards along the track and another directed at right angles to this, and through the fish's abdomen.

The present objective has been to measure the contribution of each of several mechanical factors to the net drag. We estimated the drag overcome by the tail thrust by use of an accelerometer implanted in the body of fish swimming in a closed-circuit water tunnel, changed the fish's buoyancy a known amount, ran the water at various measured speeds, and altered the slope of the entire tunnel. We also estimated body angle relative to water flow. We then analysed the data obtained from these measurements to apportion the tail thrust among the factors contributing to drag.

METHODS

In this study we attempted to obtain a homogenous population of bluefish. The nine bluefish, *Pomatomus saltatrix*, used ranged from 0·49 to 0·54 m in length and 1·22 to 1·69 kg in weight. Their individual dimensions are presented in Table 1.

The fish were caught on a hook and line in waters around Woods Hole, Massachusetts, and were stored in a holding tank supplied with running sea water. For a given experiment, one fish was anaesthetized for 10–15 min in a solution of tricaine methanesulfonate (Aldrich Chemical Co., 2 g in 40 l of sea water). The fish was then placed ventral side up on a padded V-board while water containing the anaesthetic agent at half the initial concentration was circulated through the gills. An incision was made in the ventral wall of the abdomen and a latex balloon was placed in the opened swim bladder. The abdominal incision was sutured shut. A polyethylene catheter 1·0 mm in outside diameter (PE 200) ran from the balloon out through the incision to a stopcock and syringe, which allowed adjustment of the

Table 1. *Dimensional data of nine bluefish*

Fish no.	Fork length (m)	Weight (kg)	Projected pectoral fin area (cm²)		
			Left fin	Right fin	Total
1	0·49	1·33	15·0	16·8	31·9
2	0·52	1·59	15·9	17·7	33·6
3	0·52	1·49	17·7	18·5	36·2
4	0·49	1·22	—	—	—
5	0·51	1·53	—	—	—
6	0·53	1·60	18·8	16·9	35·7
7	0·53	1·53	21·3	21·2	42·5
9	0·54	1·69	—	—	—
10	0·54	1·53	13·5	14·3	27·3
Mean	0·52	1·50	17·1	17·6	34·5
S.D.	0·02	0·14	2·8	2·3	5·1
S.E.	0·01	0·05	1·2	0·9	2·1

Projected fin areas were traced on to paper while the fish was on the V-board. Fin areas were only measured on the fish indicated. The mean, standard deviation (s.D.) and standard error (s.E.) of the dimensional data are shown at the bottom of each column. Fish 8 would not swim in our apparatus.

fish's weight in water. This method of altering buoyancy was used in an earlier study (Ogilvy & DuBois, 1981).

Following insertion of the balloon, the fish was turned dorsal side up on the V-board. A pair of miniature accelerometers (Entran Devices, model EGBL-125-5D) glued together at right angles was inserted into a midline incision 1 cm long made in front of the anterior dorsal fin. Proper orientation of the accelerometers was assured by a guide pin aligned with the long axis of the fish and sewn to the skin surface. A flexible four conductor cable 1·0 mm in diameter (New England Wire Co.) connected the accelerometers to a 6-channel direct writing recorder (Model 7 Polygraph, Grass Instrument Co.). Details of these accelerometers are given in an earlier publication (DuBois & Ogilvy, 1978). During the final stages of the operation, a monofilament line was attached to the fish's jaw to prevent the fish from turning around in the water tunnel. This line was kept slack when the fish was oriented properly in the swimming tunnel.

After the operation, neutral buoyancy was determined by slow inflation of the initially empty latex balloon until the fish just floated, or by reduction of the volume of a too-full balloon until the anaesthetized fish just sank in the anaesthesia tank. The volume of air needed to produce neutral buoyancy was checked periodically while the fish rested between runs in the swimming tunnel.

The water tunnel. Making the fish swim up or down hill required the design and construction of a water tunnel which could be tilted to various angles. It consisted of sections of sewer pipe made of polyvinyl chloride (Eastern Sewer Pipe Corp., Newington, CT.) with an inside diameter of 0·292 m and wall thickness of 0·91 cm, arranged in an oval which had a perimeter, on centre, of 8·4 m (Fig. 1). A large rubber O-ring surrounds the straight end of one section and lies compressed within the bell-shaped end of the next section, rendering the joints watertight.

An acrylic cylinder 1·0 m long and 0·292 m in inner diameter was installed in the
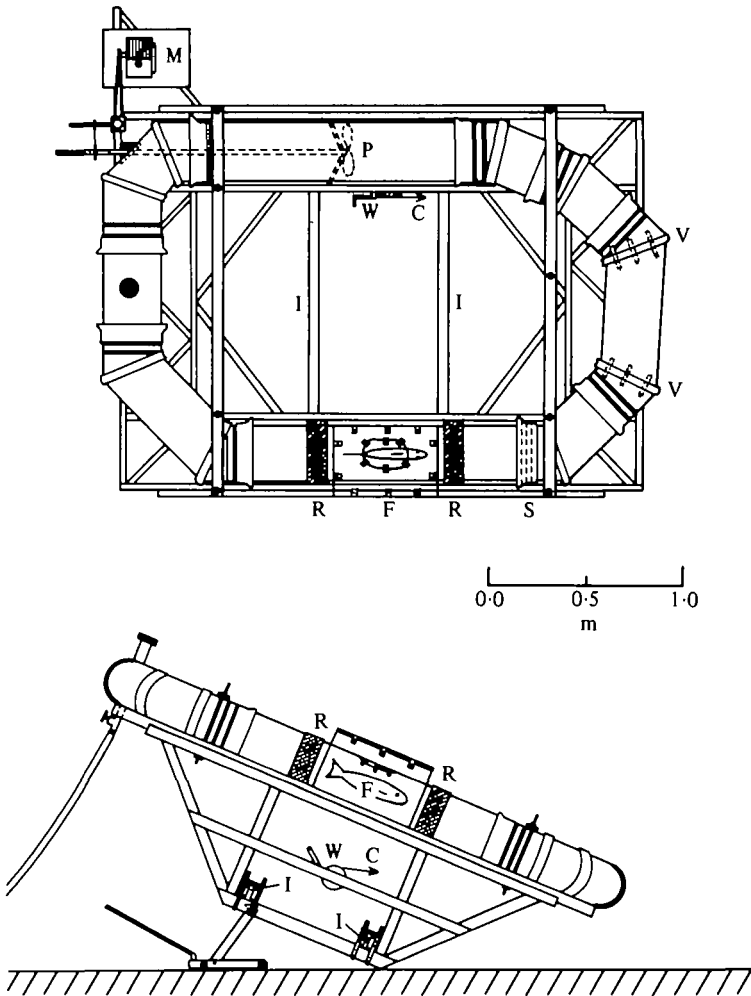
Fig. 1. A top and side view of the apparatus. The side view shows the apparatus tilted using a hydraulic jack. F = fish, R = rubber couplings, I = steel I-beams, V = wooden vanes used to help direct water, P = propeller used to drive the water around the circuit, W = winch, C = cable used to hold the tunnel onto the wooden frame during tilts, S = screens used to even out the velocity profile in the tunnel.

middle of one straight section of the tunnel, and a propeller was located in the opposite straight section (Fig. 1). Rubber collars connected the acrylic section to the PVC sections. A rectangular chamber of acrylic sheets was built around the acrylic cylinder and filled with water to reduce image distortion caused by curvature. Retaining grids made of 0·6 mm diameter fishing wire spaced 2·6 cm apart were placed in front and back of the fish. These grids do not significantly disturb water flow in the tunnel (Ogilvy & DuBois, 1981). An oval handport was cut in the transparent section of the tunnel to permit introduction and removal of the fish through a removable cover attached by wing nuts.

To flatten the velocity profile, wooden vanes shaped like airfoils were placed in

two of the corners, and three nylon mesh screens set 3·5 cm apart were installed 6·38 m upstream from the first retaining grid. The velocity profile in the tunnel was measured using a long, thin, brass tube that passed through both walls of the rubber collar surrounding the tunnel. A hole was drilled into one side of the brass tube and faced upstream. The tube was used to traverse the inner diameter of the tunnel in front of the swimming compartment and showed a blunt, even velocity profile, as calculated using the Pitot equation from the stagnation pressure minus static pressure measured at a side-tap on the wall of the tunnel three inches forward of the thin brass tube. The hole in the brass tube was placed in the centre of the tunnel and its pressure relative to static pressure was used to determine water speeds throughout the experiments.

The water was pushed around the tunnel by a 0·29 m diameter propeller placed in the middle of the straight section of the tunnel. A one inch diameter propeller shaft was installed in the 90° corner of the water tunnel. The shaft emerged from the 90° bend and was driven by a 5 h.p. gasoline engine. A series of reduction pulleys with V-belts, and adjustments of the engine throttle, allowed control of the water speed between zero and $1·1$ m s^{-1}. Further modification of this propulsive mechanism might involve the use of larger diameter sections of tunnel before and after a larger propeller to allow higher water velocities in the fish compartment.

The water tunnel was mounted on a wooden frame made of 2×4 inch lumber. The base of the frame was built like a rocking chair, with the bottom squared off. Two three-inch-wide steel I-beams were bolted across the base. The apparatus was tilted by a hydraulic jack placed under either of the steel beams (Fig. 1). Once the tunnel and frame had been tilted to the desired angle, two automobile jack stands were set at a fixed height and placed under the I-beams. To prevent the tunnel from sliding off the frame during a tilt experiment, it was clamped by 2×4 inch timbers bolted down across each end. The corners of the tunnel were held in place by a steel cable wrapped around the frame and tunnel parallel to the long axis of the oval. Tension in the cable was maintained by a winch fastened to the frame.

Interpretation of accelerometer records. When a fish swims at a constant velocity, a rhythmically recurrent pattern of acceleration is recorded. The steps and assumptions used to calculate tail thrust and its contribution to overcoming drag are: (1) In records where the speed of the fish does not change from one cycle to the next (though, of course, it changes within each cycle) the average acceleration is zero. (2) As the peaks and the valleys in the acceleration records are mirror images, zero acceleration is at a level halfway from valley to peak. (3) We assume that instantaneous tail thrust varies from a maximum value down to zero twice each cycle, but is never negative. (4) Therefore, the peak deceleration times the effective mass of the fish gives at that instant the fraction of drag previously overcome by tail thrust, plus the component of any buoyancy force directed aft along the track of the fish. (5) Hydro-dynamic added mass is neglected; the effective mass of the fish is approximately equal to its true mass. (6) The drag overcome by tail thrust is assumed not to vary over the swimming cycle, so the peak thrust is twice this constant rearward force, and the time-average tail thrust equals the 'time-average drag' it overcomes. (7) In records where peaks and valleys were not all the same height the average heights

of the peaks and of the valleys respectively were used in the calculations (Ogilvy & DuBois, 1981). (8) The centre of mass is not altered be bending of the body. (9) The accelerometer remains well oriented throughout the body cycle.

Angle of water flow and angle of the fish's body. The angle of water flow and the fish's body angle relative to this flow were measured at different buoyancies. A protractor and plumb-line were fastened to the wooden frame. The angle of water flow was read from this inclinometer. For measurements of the fish's body angle relative to water flow, the plumb line was held parallel to the fish and the angle was read on the protractor. The angle of the fish's body relative to horizontal was the sum of these two angles.

Calculation of stalling speed. It is given from fluid dynamic theory that the lift (F_L) of an airfoil can be calculated using the following equation: $F_L = (1/2)\,C_L S\rho V^2$, where C_L is the dimensionless lift coefficient, S is the area of the pectoral fins, ρ is the density of the fluid, sea water, and V is the velocity of the water over the fins (Salisbury's Kent, 1967). Any lift from the rest of the fish's body is ignored. Rearranging this equation we have: $V = (2F_L/(C_L S\rho))^{\frac{1}{2}}$. The pectoral fin area was taken as 0·0035 m² which is the average of the values for 6 fish (see Table 1). In cross section, the bluefish pectoral fins are similar to known airfoils with concave lower surfaces. Such airfoils begin to stall at an angle of attack of 15°. At this angle, C_L is 1·2 (Salisbury's Kent, Fig. 3, p. 15–08). The low aspect ratio of the pectoral fins may well raise the stalling angle above this value, while having little effect on the lift coefficient at stall (Abbott & Von Doenhoff, 1959). The possibility of vortex lift is discussed later in this article. The lift must equal the component of weight directed downwards through the fish's belly perpendicular to water flow. Thus $F_L = F_W \cos \theta$, where F_W equals the fish's weight in water and θ is the angle of the water tunnel with respect to horizontal. As the density of sea water is 1022 kg m⁻³ we have the stalling speed of the pectoral fins, $V_{PS} = (2\,F_W \cos \theta/(1\cdot2 \times 0\cdot0035 \times 1022))^{\frac{1}{2}}$. Because the fins are positioned at the wide section of the fish's body where the velocity of water is 1·13 times the average flow in the tunnel (Ogilvy & DuBois, 1981), the swimming speed (V_S) at which the fins stall is $V_{PS}/1\cdot13$. Values calculated for V_S appear in Fig. 4 as the lower end of each line.

Calculation of the proportionate distribution of thrust along the body. The method described by Bainbridge (1963) was used to estimate the portion of thrust contributed by the tail and by the remainder of the body of bluefish no. 8, 48 cm fork length, swimming at 0·87 m s⁻¹, as published previously (DuBois & Ogilvy, 1978). Amplitudes of lateral excursions of the body and tail were read from the film of the fish and lateral accelerometer record. Projected body areas were calculated from Fig. 1 of that paper.

RESULTS

The data are organized to show the relationships between the mechanical factors which affect the amount of tail thrust required by swimming fish. First, we present 'time-average tail thrust' (hereafter simply 'tail thrust') *v.* swimming speed at neutral buoyancy. From this, one can derive the part of parasitic (pressure plus skin) drag overcome by tail thrust. Secondly, we show how tunnel angle (surprisingly)
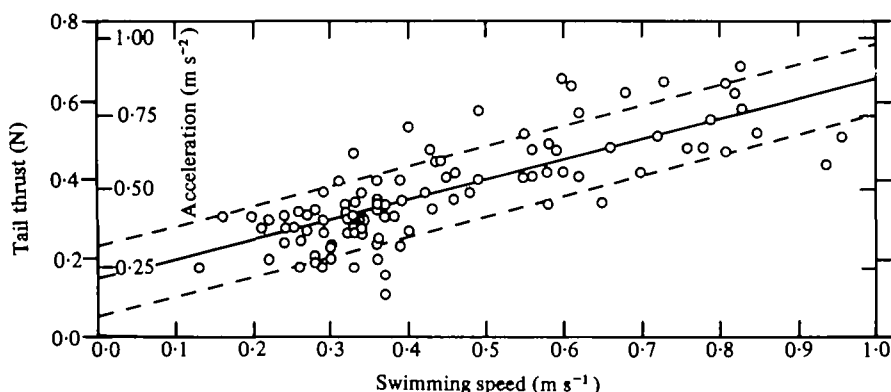
Fig. 2. Results of eight bluefish. $Y = 0.5(x) + 0.15$, $r = 0.73$. The tail thrust measured from the accelerometer records is plotted against swimming speed for eight neutrally buoyant bluefish swimming at different angles of water flow. The change in acceleration is also plotted on the Y-axis (acceleration). A regression line was calculated using the least squares regression method (solid line). The regression line ($F_D = 0.68 \times$ speed $+ 0.05$) obtained in an earlier study from data of a neutrally buoyant fish (no. 8, Fig. 6, Ogilvy & DuBois, 1981), swimming head up at $33.5°$, intersects the same point at 1.0 m s^{-1} as the regression line shown. The dashed lines represent one standard error of estimate above and below the regression line.

influences the relationship between the measured tail thrust and speed at neutral buoyancy. Third is shown the influence of tunnel angle on the relation of tail thrust to speed when various amounts of air have been added to or removed from the balloon in the swim bladder. Fourth, we show the observations of body angle relative to horizontal at different tunnel angles and at different buoyancies. Figs. 2–5 illustrate the above points. Fifth, we estimate the portion of thrust generated by the tail versus the rest of the body.

Neutral buoyancy. Before grouping the data on tail thrust *v.* speed, we inspected the relationship in individual fish. At neutral buoyancy, there was a linear trend and the line was independent of body size over this narrow range of variation in size. Therefore, we grouped the data and used linear regression analysis. In Fig. 2 the regression equation of tail thrust on speed is calculated for all data on 8 bluefish at neutral buoyancy, at all tunnel angles. The line cannot be extrapolated through the origin. The standard error of estimate, calculated as the root mean square of the *y*-deviations about the fitted curve, is shown by the dotted lines. The ordinate axis of Fig. 2 is marked with two scales. On the left is the tail thrust, calculated from half peak to peak acceleration multiplied by the mass of each individual fish. On the right is a scale of peak-to-peak acceleration applicable to fish having the mean mass of the group, 1.53 kg. Since data points in Fig. 2 are based on the tail thrust of each fish, the points are automatically normalized around the mean mass of the fish so far as the 'acceleration' scale is concerned.

Fig. 3 shows regression lines and correlation coefficients calculated for tail thrust versus speed in eight neutrally buoyant fish swimming with the water tunnel tilted head up at $15°$, horizontal, or head-down $9°$, $17°$, and $23°$. A composite graph of the regression lines at different tunnel angles is in the lower right-hand corner.
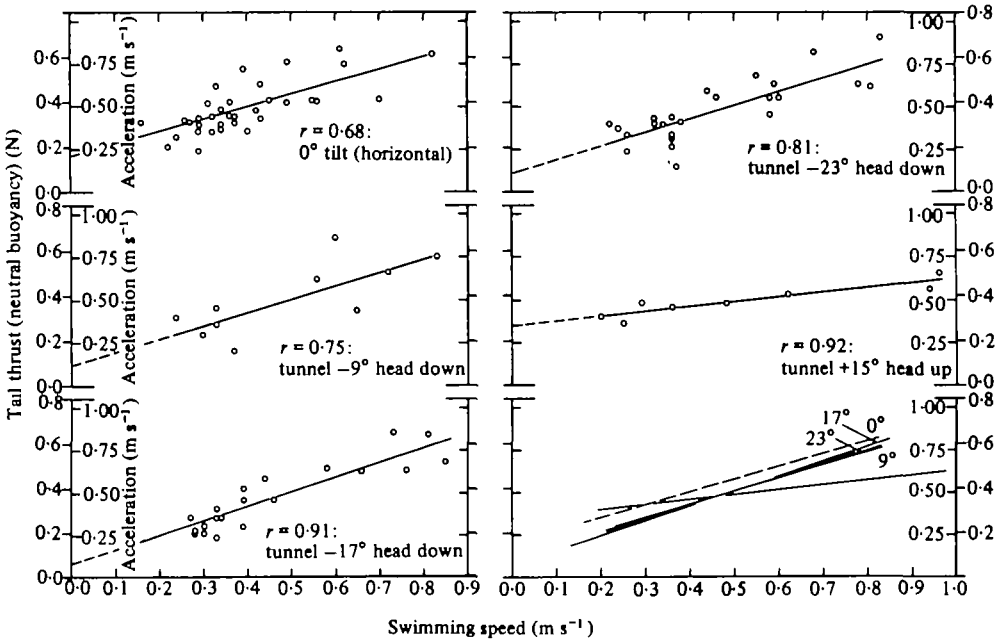
Fig. 3. Regression lines are shown for thrust as a function of speed of several different blue-fish each at neutral buoyancy. The abscissa and ordinate are similar to those in Fig. 2. The right lower panel shows all of the regression lines. The regression line calculated from the data obtained when the fish was swimming horizontally is shown as a dashed line (0°). Positive angles represent tunnel tilts with the fish head up, whereas negative angles are when the tunnel was tilted with the fish head down. Correlation coefficients (r) are shown in the lower right-hand corner of each graph.
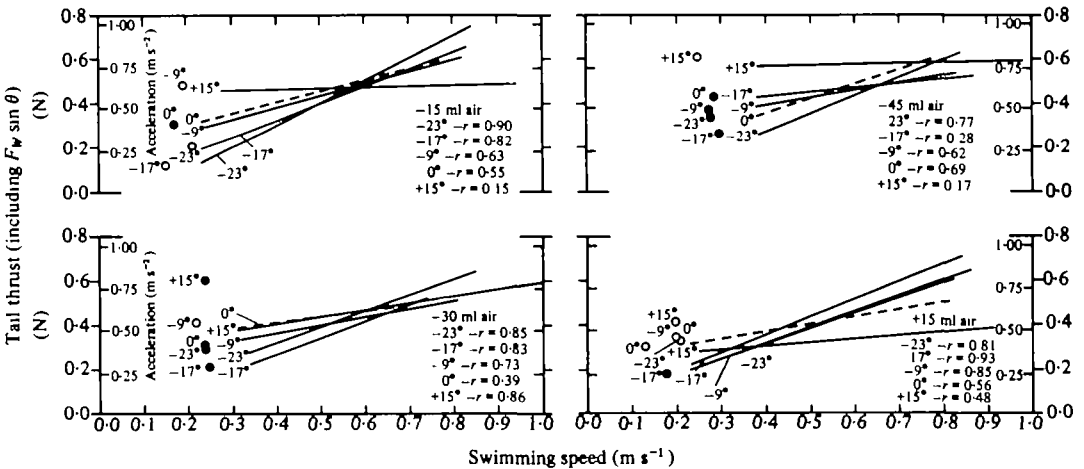

Fig. 4. Composite graphs of tail thrust constructed as described for Fig. 3 are shown for all other buoyancies used in this study. Regression coefficients (r) are shown in the lower right-hand corner of each graph for the different angles of tunnel tilt. The force of weight directed backward along the track ($F_W \sin \theta$) is not subtracted from the force calculated from the recorded changes in acceleration. Data collected below stalling speed are shown as average points and depicted with a solid circle, ●, located to the left of the regression lines. The theoretical stalling speed is the left end of each line.
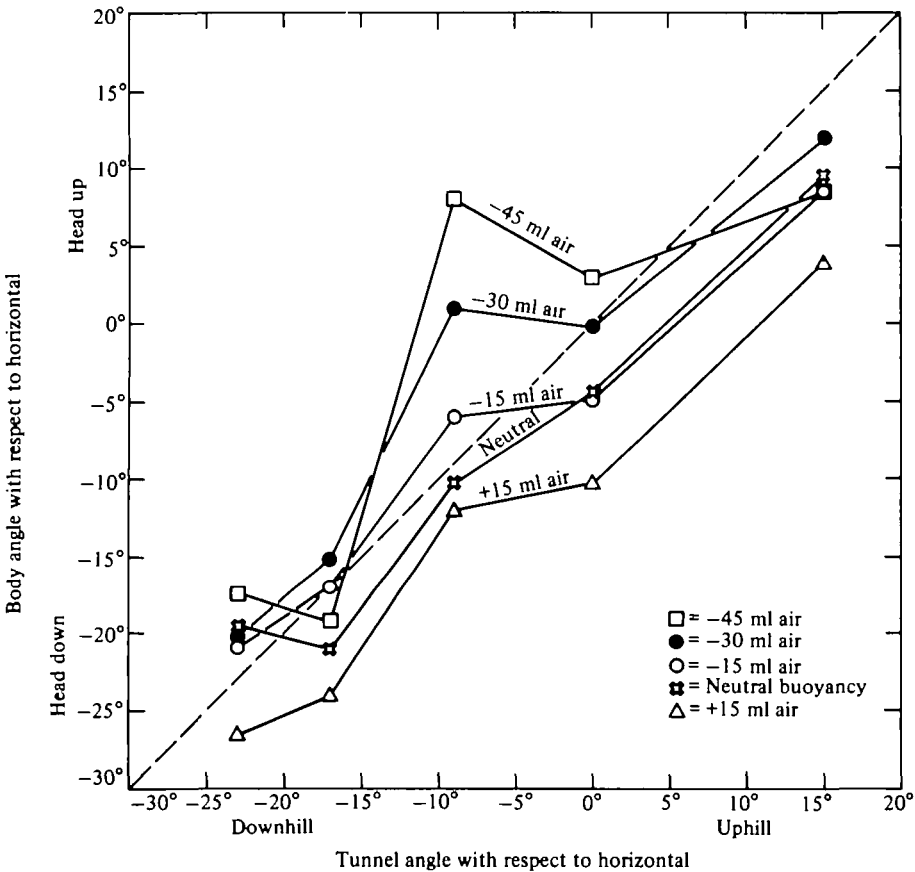
Fig. 5. Body angle varies with tunnel angle, both relative to horizontal, but each line represents a particular degree of buoyancy, from +15 to −45 ml of air relative to the amount required to produce neutral buoyancy Each point represents the average obtained at different swimming speeds. The body angle would equal the tunnel angle (dashed line, $Y = X$) if the fish pointed directly into the water flow.

The lines in Fig. 4 represent the regression of tail thrust on speed, where tail thrust is equal to rearward force, which includes both the portion of drag overcome by tail thrust and the component of weight, $F_W \sin \theta$, directed along the track (see discussion for further explanation). Each graph shows the results of changing the tunnel angle with a particular fixed buoyancy. Regression lines are calculated as they were for Fig. 2. The correlation coefficients for the regression lines are shown in the lower right-hand corner of each graph. Stalling speeds (V_S) were calculated as described earlier under 'Methods'. If more than one measurement was made below stalling speed at a given angle, the average point is plotted (solid circle).

Average measurements of the fish's body angle and water flow relative to horizontal with different amounts of buoyancy are shown in Fig. 5. If the fish headed directly into the water flow the points would fall along the line of identity $(Y = X)$. But, there is a tendency for the fish to be head up relative to water flow when negatively buoyant, or head down when positively buoyant, and this is seen as a statistically

significant difference between $+15$ ml (average body angle relative to water flow equals $-8\cdot0°$, S.E. $1\cdot7$) and -45 ml (average body angle equals $3\cdot3°$, S.E. $7\cdot0$). In addition, the fish tend to be slightly more horizontal than the tunnel angle. At all buoyancies the fish held itself several degrees more head up at a tunnel angle of $-9°$ than would have been predicted by interpolating linearly between the values at $0°$ and $-17°$. The points on the graph of Fig. 5 are averages of data obtained over a range of swimming speeds. Deviations from the line of identity tend to disappear at higher swimming speeds showing that the fish tend to head directly into fast water flow.

Contribution of the tail thrust to total body thrust. The laterally directed velocity of the body, measured at the accelerometer, the dorsal fin, the peduncle, tail fork, and tip of the tail of fish 8 (DuBois & Ogilvy, 1978), swimming at $0\cdot87$ m s^{-1}, were squared, and plotted at their relative distances from the tail tip, as in the graphs published by Bainbridge (1963). Projected profile areas of the body, every 2 cm, were plotted on the same graph, and multiplied by corresponding values for velocity squared, and summed up for the tail area, and divided by the sum over the whole body including the tail. From this it was concluded that the tail thrust contributed approximately 65% of the total body thrust, assuming that hydrodynamic efficiencies of the body and tail were comparable to each other.

Additional data available on fish 8 and three other fish, at other speeds, though less complete, were analysed for lateral body and tail fork velocity, and these calculations showed that tail thrust ranged from 48 to 65% of total thrust.

DISCUSSION

The relationship between tail thrust and drag will be discussed in the following order: (1) Tail thrust as a fraction of total body thrust. (2) Parasitic drag at neutral buoyancy. (3) Parasitic drag plus the induced drag caused by the weight during negative buoyancy, swimming horizontally, and stalling speed during negative buoyancy. (4) The influence of negative or positive buoyancy during climbing or gliding. (5) The angle of attack of the pectoral fins and body relative to water flow.

Bainbridge (1963) estimated that the tail contributed between 45 and 84% of the total thrust in three different species of fish. The estimate we made using Bainbridge's method of analysis on one bluefish was 65%, a value within the same range. One problem is that it is not known whether the hydrodynamic efficiency of the body is equal to that of the tail. Bainbridge (1963) cites Lighthill (1960) as indicating that the hydrodynamic efficiency of the body varies with the ratio between water speed and body wave speed, being maximum when the ratio is $0\cdot8$. Since our measurements do not include body-wave speed, we are unable to estimate hydrodynamic efficiency of the body.

We believe that the accelerometer method measures body acceleration due to tail thrust, and body deceleration due to the portion of drag overcome by tail thrust. The evidence for this lies in the close correlation between forward force of the water on the tail and the resulting acceleration of the body produced by this tail thrust (DuBois & Ogilvy, 1978). But changes of acceleration do not reflect steady thrust and drag such as that which would be present in anguilliform locomotion. Such

▌hrust could come from the body and amount to 35% or even more of the total ▌hrust. This might explain part of the discrepancy between thrust given to the water, and appearing aft of the tail, which is 3·57 N as calculated in Table 2 of DuBois & Ogilvy (1978) by the method of Lighthill (1971), and the tail thrust (or drag), which is 1·0 N measured using pressure transducers on the tail.

At neutral buoyancy, there is no induced drag, and therefore parasitic drag can be derived from the total thrust *v.* speed relationship. We expected that at neutral buoyancy the tail thrust measured by the accelerometer method would be independent of the angle of the swimming tunnel. Instead a pattern emerged which was also found in the data of negatively or positively buoyant fish shown in Fig. 4. The tail thrust of fish swimming uphill was nearly independent of speed, whereas that required to descend was strongly dependent on speed. If tail thrust were a constant and known fraction of total body thrust, then parasitic drag could be derived at neutral buoyancy. But since tail thrust was found to vary with tunnel angle, as well as water speed, the fraction of body thrust may be variable.

During negative buoyancy and horizontal swimming, the amount of induced drag produced by the pectoral fins can be calculated using the equation: $F_{Di} = (1/2)C_{Di}S\rho V^2$. The induced drag coefficient, C_{Di}, is defined as: $C_{Di} = C_L^2/\pi A$, where C_L is the lift coefficient as defined earlier under 'Methods' and A is the aspect ratio (the wing span squared divided by the wing area), approximately 3. The average value of 34·5 cm² is used for the pectoral fin area. This formula for C_{Di} is almost exact only if the distribution of lift across the span is elliptical. For other distributions, the induced drag is somewhat higher (Abbott & Von Doenhoff, 1959). At the greatest negative buoyancy used in these experiments, the weight of the fish in water was 45 g (45 ml of air removed from the swim bladder). This would give an induced drag of only 0·047 N (4·8 g) at 0·5 m s⁻¹ or 0·012 N (1·2 g) at 1·0 m s⁻¹. For 30 g negative buoyancy at 0·5 m s⁻¹, induced drag would be 0·021 N and at 0·35 m s⁻¹ it would be 0·043 N. This is small compared to the tail thrust.

At a given buoyancy, there is a relationship between tail thrust and swimming speed observed when the water flow is horizontal. However, it was anticipated that when the tunnel was tilted head up the total thrust would be increased by a quantity $F_W \sin \theta$, and F_{Di} would be less due to a factor $(\cos \theta)^2$, provided the fish's weight in water was positive. Conversely, the active thrust required would be decreased if the tunnel was tilted head down, or the fish's weight in water was negative. Fig. 4 shows that this expected result is obtained for tail thrust at speeds below 0·6 m s⁻¹ for fish heavy in water. But above this speed, where the lines cross, the contrary effect occurs. For fish that were buoyant in water, the expected result is observed at speeds above 0·35 m s⁻¹, in other words over the major speed range. But below this, and over a lesser range, the opposite, unexpected, result was found.

The observed crossing of the regression lines of tail thrust on speed, though occurring over limited ranges of speed, was unexpected, and we have no explanation for it. This fish performs differently than would be expected if tail thrust were the only contributor. But the proportion contributed by tail thrust measured from the accelerometer record to the total body thrust may be altered by an amount dependent on the swimming angle, buoyancy, or speed.

▌ail-beat frequency varied with water speed in a manner predictable from

previously published values (Bainbridge, 1958), with the possible exception of values obtained swimming head up at 15°. These had too low a tail-beat frequency. Consequently, the water speed may have been overestimated when the tunnel was tilted in the 15° head-up position.

Stalling speeds were calculated (see 'Methods') and are shown as the lower end of the regression lines in Fig. 4. During horizontal swimming, they are 0.23 m s^{-1} for -15 ml, 0.31 m s^{-1} for -30 ml, and 0.40 m s^{-1} for -45 ml. The fact that fish swim successfully at speeds below stalling speed may be accounted for by body lift caused by nose-up or nose-down trim of the body relative to the water flow or to flapping of the pectoral fins. In addition, the maximum lift coefficient of a fin may be raised if the leading edge is swept back, and sharp. Then fluid from below the surface can separate as it flows up and around the edge to form a conical vortex sheet above each fin. The pressure in these vortices is low, so they exert a lift force on the fins (Polhamus, 1966). However, this effect does not raise the lift coefficient much above unity, so is little help in resolving the discrepancy.

One purpose of this study was to determine whether bluefish, by maintaining negative buoyancy, could glide and maintain station effortlessly on an updraft of water. The conditions required for gliding would be that $F_W \sin \theta = F_{Di} + F_D$ (where F_D is parasitic drag), and $F_W \cos \theta = F_L$. In our fish, at 45 ml negative buoyancy and 23° head down, $F_W \sin \theta$ is $0.46 \times \sin 23° = 0.18$ N. The stalling speed calculated for -45 ml, head down 23°, is 0.38 m s^{-1}. The portion of parasitic drag (F_D at neutral buoyancy) overcome by tail thrust at 0.38 m s^{-1} is 0.34 N (Fig. 2). Since F_D is greater than $F_W \sin \theta$, the fish theoretically would have been unable to glide during our experimental conditions, and indeed we never observed complete gliding. In aeroplanes the minimum drag usually occurs above the stalling speed, because going faster reduces the induced drag more than it raises the parasitic drag. The fish's body is so large relative to the pectoral fins that its large parasitic drag shifts the drag minimum to the stalling speed (or to a lower value still, if for some reason the fins did not stall).

Fig. 5 shows a definite pattern in the way in which average body angle changed when the tunnel was tilted. As the fish became heavier in water the changes in body angle relative to water flow (i.e. above or below the line $Y = X$ in Fig. 5) became more pronounced, and the results when 45 ml of air were removed from the swim bladder show the most dramatic fluctuation, from $-6.5°$ to $+17°$ to $+5.5°$ as the tunnel was tilted down. When neutrally buoyant, the body angle relative to water flow only changed from -5.5 to $+3.5°$. One might expect that as the tunnel was tilted the body angle would change in a predictable linear fashion. This occurred fairly consistently at all angles except $-9°$. At $-9°$ the fish held its head higher than expected, by an amount that increased with buoyancy, either positive or negative. This anomalous behaviour is interesting but we cannot explain it. This might be an indication that a tunnel angle of 9° head down cannot be tolerated well by the fish and, by swimming head up, lift is obtained from the body, but why it occurs with $+15$ ml of air is then a puzzle. Fish which were neutrally buoyant swam somewhat more directly into the water flow whether the tunnel was head up, hori-

zontal, or head down, but showed some degree of preference to be horizontal, in other words their balance mechanism was slightly affecting the body angle.

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