

## FORCES ON THE TAIL SURFACE OF SWIMMING FISH: THRUST, DRAG AND ACCELERATION IN BLUEFISH (*POMATOMUS SALTATRIX*)

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### SUMMARY

1. Pressures on the right and left sides of the tails of swimming bluefish were measured and found to have a range of +5.9 to -5.9 cm H<sub>2</sub>O. The pressures were resolved into their forward and lateral vectorial components of force to allow calculation of forward and lateral force and power at speeds ranging from 0.26 to 0.87 m/s.

2. The peak to peak changes in force of acceleration of the body, measured with a forward accelerometer averaged 209 g or 2.05 N at 0.48 m/s, and were compared with the maximum to minimum excursions of forward tail force averaging 201 g or 1.97 N at the same speed. The mean difference was 8 g, s.d. of the mean difference  $\pm 29$ , s.e. of mean difference  $\pm 10$  g.

3. Mean tail thrust was calculated as the time average of tail force in the forward direction. It averaged 65 g, or 0.64 N, at 0.48 m/s. The mean forward power was 0.34 N m/s at 0.48 m/s. The drag of the gauges and wires accounted for 10% of this figure.

4. The mean lateral power of the tail was 1.28 N m/s at a mean speed of 0.48 m/s.

5. The propulsive efficiency of the tail, calculated as the ratio of forward power to forward plus lateral power, was found to be 0.20 s.d.  $\pm 0.04$ , s.e.  $\pm 0.01$  and was not related to speed. This suggests that 80% of the mechanical power of the tail was wasted. Turbulence in the water may have contributed to this large drag and low tail efficiency.

### INTRODUCTION

Although there have been two recent symposia on the locomotion of fish (Wu, Brokaw & Brennen, 1975; Pedley, 1977), it appears that additional measurements of tail thrust are needed to allow a more detailed analysis of the mode of swimming.

Gray (1957) described the forces acting on the body and tail and resolved them into their forward and lateral vectorial components. Some previous estimates of tail thrust have been those of Lighthill (1971), DuBois, Cavagna & Fox (1976), McCutchen (1977), and Webb (1977). The present method differs from those used by others in that it is a measure of the force of the water on the tail, and the resulting *force deduced from* acceleration of the body. The results obtained allow calculation of the power and efficiency of the tail.

## METHODS

The procedures for obtaining and anaesthetizing the fish, and the apparatus in which they were placed for swimming, were similar to those described previously (DuBois, Cavagna & Fox, 1974; DuBois *et al.* 1976). The accelerometers used were smaller, and two small flat pressure transducers were attached to the tail. A brief recapitulation of general procedures, and more detail about the newer instruments, follow.

*General procedures*

Medium sized bluefish which had been caught on a hand line were kept in a tank with running sea water. Each fish was anaesthetized by immersion for 10–15 min in a solution of tricaine methanesulphonate (2 g in 40 l). The fish was placed on a V board with sea water recirculated through the gills. This water contained the anaesthetic solution diluted to half its previous concentration. Accelerometers oriented forward and laterally were inserted to a depth of 1 cm through a small midline incision immediately in front of the anterior dorsal fin, and sewn in place. A four conductor cable was connected to the accelerometers. Pressure transducers were attached to the right and left sides of the upper fork of the caudal fin at a location between the point of bifurcation of the tail and the outer tip of the upper fork (Fig. 1). Each transducer was connected to a four conductor cable. The three cables from these gauges were attached to the anterior spine of the second dorsal fin. The fish was lowered through a handport into the observation chamber at the centre of a 30.5 cm diameter wooden tunnel 5.48 m long inclined at 33°, and through which water flowed from a pool, at a speed regulated by a hand winch which controlled the opening of a door on the outlet of the tunnel (DuBois *et al.* 1974, 1976). Grids cut from galvanized wire fencing with 1.27 cm openings between wires were located in front and back of the fish. A monofilament line was attached to the jaw to prevent the fish from turning around, but otherwise it remained slack throughout the experiment.

The forward and laterally oriented miniature accelerometers were half-bridge semiconductors (type EGBL-125-5D) manufactured by Entran Devices, Inc., Little Falls, N.J. The dimensions were 6.86 mm long and 3.56 mm square with a weight of 0.5 g. These were attached to each other at right angles, with epoxy cement, and a 1 cm guide pin was fastened along the top to maintain orientation to the skin surface. The accelerometers were connected by a single flexible four-conductor cable 1.3 mm in diameter (New England Electric Wire Corp., Lisbon, N.H.) to a 6-channel direct writing recorder (Grass Instrument Co., Quincy, Mass.).

*The pressure transducers*

Two pressure transducers were used to measure forces on the right and left sides of the tail. Each transducer consisted of a small flat pressure gauge (Flatline EPF-200-25, Entran Devices Inc., Little Falls, N.J.) 5.08 mm wide, 10.2 mm long and 1.02 mm thick. Since these are affected by rate of cooling and by bending, each was secured inside a flattened water filled balloon 9.0 mm wide, 2.0–3.0 mm deep and 3.0 cm long. The back of this balloon was attached with an adhesive (neoprene or contact cement) to a 2.7 cm × 1.6 cm × 0.4 mm piece of aluminium. The two aluminium

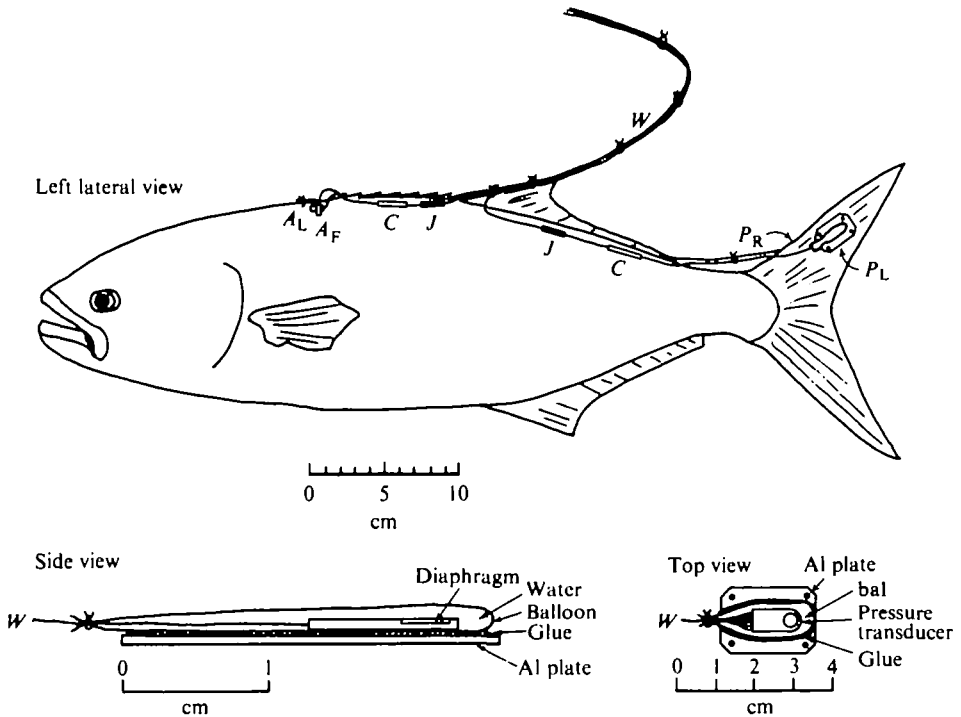


Fig. 1. Outline of a bluefish showing the size and location of the forward ( $A_F$ ) and lateral ( $A_L$ ) accelerometers, the pressure gauges on the right ( $P_R$ ) and left ( $P_L$ ) sides of the tail enclosed in water filled rubber balloons (bal) mounted on flat aluminium plates. Compensating resistors ( $C$ ) and epoxy coated junctions in heat shrink tubing ( $J$ ) connected the transducers to the three wire leads ( $W$ ).

plates were fastened on each side of the tail by a needle and thread passed through holes drilled in the four corners of the aluminium (Fig. 1). Each accelerometer and pressure transducer had a compensating resistor module 2.5 cm long and 3 mm in diameter in series with a four-conductor cable of the same type as that described above.

#### *In vitro validation*

The design of the enclosures for the pressure transducers evolved through repeated testing of several different types of enclosure. The method of testing the validity of the pressure readings was as follows. First, a thin rubber jacket was made by painting latex in layers on the surface of a fibreglass cast of a dead bluefish. When removed, this jacket had the shape of a bluefish. Then, two flaccid balloons containing some air were connected by PE 200 tubing to Statham strain gauge manometers. These balloons were attached, one on each side, to a flat stick 2 cm wide, and this was inserted between the two sides of the upper fork of the tail in the rubber model. The flat gauge assemblies to be tested were mounted on the outer surfaces of the tail of this rubber model, and the stick was moved by hand from side to side in a tank of water to move the rubber tail. These tests showed that the pressure change due to the movement of the water against the water filled balloon which enclosed the gauge outside the rubber tail was equal to the pressure change in the air filled balloon inside

the tail, and that the pressures changed reciprocally on the right and left sides as the tail was moved to one side, then to the other. After the aluminium plates, balloons, and gauges had been found to be accurate for measurement of tail surface pressures *in vitro*, they were sewn on the tail of a live, anaesthetized fish, and the peduncle of the tail was moved back and forth by hand in a tank of water at *zero forward speed*. It was found that the pressures deflected equally and opposite to each other on the right and left sides of the tail, and that the 'zero' resting pressure was the mean of the pressure fluctuation on each side. The drag of the accelerometer and pressure transducer assembly and wires was measured by drop tests in a 1 m deep tank of still water and expressed as grams of force at different speeds measured in metres per second.

#### *Additional procedures*

Movies of the swimming fish were made from above the fish using a Beaulieu 16 mm electrically driven movie camera set at 64 frames  $s^{-1}$  (nominal speed). The sequences were identified on the direct writing recorder by a hand-operated micro-switch, which appeared in the movie and activated the signal marker on the recorder. The precise speed of the film was measured by matching the movement of the time marker on the Grass recorder with the motion of the microswitch as seen on the film. The tail angles used in the calculations were measured directly from the movie. From tracings of the tail made from a movie, we calculated momentum imparted to the water by the method of Lighthill (1971). Since there was no lateral movie, we used a mean vertical height of the tail. Water speed was calculated from the rate of decrease of *side wall* pressure in the *water tunnel* as measured with a Statham strain gauge manometer. The tail outlines were traced, cut out and weighed. The mean of the areas of the spread and unspread tail was calculated.

The relationship between the force required to bend the body into a C shaped or S shaped curve and the length from the jaw to the peduncle was measured underwater in bluefish 14 which had died within the hour. The force was applied by hanging weights from the peduncle. In another bluefish, anaesthetized bluefish 17, the force required to bend the tail and the angle of the tail on the peduncle were measured in air. The force was applied at right angles to the tail surface by means of a line, which was attached to the tail, then passed over a pulley. Different weights were hung on this line.

#### *Units of measurement*

The mass of the surrounding water was neglected because it was calculated to be less than 10% of the mass of the body (Lamb, 1945). In calculation of the acceleration of the body, therefore, it was assumed that the mass, in kg, equals the weight of the fish. The forces bending the body were produced by brass weights weighed underwater. The pressure transducers were calibrated with a water manometer in cm water ( $g/cm^2$ ). In the graphs, we preserve the co-ordinates in terms of grams weight (g) but also have added a scale expressing the force in Newtons, where

$$1 \text{ N} = 1 \text{ kg m/s}^2 = 10^5 \text{ dyn. N} = \text{kg wt} \times 9.8.$$

Power was calculated as N m/s. Note that g is an abbreviation for grams weight, and not for the acceleration of gravity.

### Calculations

The peak to peak change of force, in Newtons, accelerating and decelerating the body of the fish was calculated as the peak to peak difference in forward accelerometer readings calibrated in terms of gravitational units, and then multiplied by 9.8 to convert them to  $\text{m/s}^2$ , then multiplied by the mass of the fish in kg.

The forward-backward component of tail force in Newtons, was calculated at each frame of the film as  $F = (P_R - P_L) (A) (\sin \theta)$  where  $(P_R - P_L)$  is the pressure difference between the right and left sides of the tail expressed in  $\text{N/cm}^2$ ,  $A$  is the area of the tail in  $\text{cm}^2$ , and  $\theta$  is the angle between the tail and the direction of water flow. The mean forward force was the time average of these readings. The difference between the maximum and minimum values of forward tail force (the latter were sometimes negative) was compared with the variation in the fore and aft force deduced from the peak fore and aft acceleration and deceleration of the fish.

The forward component of work of the tail on the body was calculated as the sum, or in a sense the time integral, over one body cycle, of the instantaneous forward force of the tail, resulting from its backward force on the water, multiplied by the mean velocity of the body multiplied by the time for each movie frame. The power of the tail derived from the pressure of the water against it in the forward direction in  $\text{N m/s}$  was the forward work during one body cycle divided by the duration of the body cycle.

The lateral component of work of the tail on the water in  $\text{N m}$  was calculated frame by frame to obtain the time integral, throughout one body cycle, of the pressure difference between the right and left sides of the tail multiplied by the cosine of the angle between the tail and direction of the water flow multiplied by the tail area multiplied by the lateral distance moved by the tail, measured as the displacement, from left to right, of the fork of the tail relative to the centre of the body of the fish. This yields lateral work of the tail with respect to the body divided by the duration of the body cycle. Total power of the tail was the sum of the forward and lateral components of power, and propulsive efficiency of the tail was the ratio between forward power of the tail and total power of the tail.

### RESULTS

Of the 17 bluefish used in this study, complete data were obtained from six. Table 1 lists the data obtained from the six fish on which measurements were made. Fish 8, 9, 14 and 17 swam at constant speed, and therefore the measurements are considered valid. Fish 10 and 11 drifted backward during the movie, and it appears that they did not have sufficient forward thrust to maintain a forward velocity equal to that of the water flow even at slow water flow. This implies that drag exceeded thrust. The remaining 11 fish were unable to swim, or broke the gauges, or else equipment failure terminated the experiment before measurements could be made.

The maximum and minimum pressures measured on either side of the tail are shown in Table 1. The mean of peak negative pressures is  $4.0 \text{ cmH}_2\text{O}$ , and of positive pressures  $3.1 \text{ cmH}_2\text{O}$ , at a mean speed of  $0.48 \text{ m/s}$ . The standard error of the mean difference between each positive and negative pressure is  $0.11 \text{ cmH}_2\text{O}$ , indicating a significant difference. The greatest values obtained were  $\pm 5.9 \text{ cmH}_2\text{O}$ . An approxi-

TABLE I. Summary of data and derived values

Fish no.	Length (cm)	Weight (kg)	Tail area (cm <sup>2</sup> )	Swim- ming speed (m/s)	Body fre- quency (Hz)	Max. tail press. (cmH <sub>2</sub> O)	Min. tail press. (cmH <sub>2</sub> O)	Δ fwd accel. force (g)	Δ fwd tail force (g)	Mean fwd tail force (g)	Tail pwr fwd (kg m/s)	Tail pwr lat. (kg m/s)	Tail pwr fwd and lat. (kg m/s)	Tail eff. ratio
10	58	2.15	83	0.53	1.8	2.7	-3.9	140	113	-3	—	—	—	—
11	56	2.07	93	0.53	1.9	2.4	-3.6	190	118	-51	—	—	—	—
8	48	2.22	77	0.29	1.7	2.4	-2.7	210	157	51	0.0148	0.071	0.086	0.17
9	54	1.84	72	0.68	2.2	5.2	-5.9	370	366	87	0.0592	0.255	0.314	0.19
14	51	1.36	63	0.87	3.0	3.9	-5.2	280	295	101	0.0879	0.257	0.345	0.25
17	48	1.27	63	0.47	2.3	2.0	-3.4	180	137	46	0.0216	0.109	0.131	0.16
				0.26	1.8	1.5	-1.5	110	78	28	0.0073	0.033	0.040	0.18
				0.44	2.4	3.4	-5.0	180	227	74	0.0326	0.154	0.187	0.17
				0.53	2.4	3.2	-5.7	200	298	105	0.0557	0.174	0.230	0.24
				0.29	1.8	1.6	-2.6	160	107	44	0.0128	0.036	0.049	0.26
				0.45	2.5	3.5	-3.3	190	148	48	0.0216	0.090	0.112	0.19
Mean	50	1.67		0.48		3.1	-4.0	209	201	65	0.0348	0.131	0.166	0.20
S.D.				0.52		1.4	1.4	75	99	28	0.0270	0.085	0.111	0.04
S.E.				0.17		0.4	0.4	25	33	9	0.0090	0.028	0.037	0.01

The body frequency is listed in the table as one full cycle which includes an excursion of the tail to each side. Δ Fwd accel. force is the peak force calculated from body mass x peak to peak change in acceleration.

Δ Fwd tail force is the peak to peak force calculated from differential pressure of right and left sides of the tail x tail area x sin tail angle. The difference between paired values of Δ fwd accelerating and tail force was 8, s.d. of mean difference 29, s.e. of mean difference 10 g.

Tail pwr fwd is the work of the tail in the forward direction, per second.

Tail pwr lat. is the work of the tail on the body, in the lateral direction, per second.

Tail pwr fwd and lat. is the sum of power in the forward and lateral directions.

Tail efficiency is the ratio between the tail power in the forward direction and the sum of the power in the forward and lateral directions.

Max. and min. tail pressures refer to greatest positive or negative readings on either side of the tail at each speed.

The mean, s.d., and s.e. pertain to fish 8, 9, 14 and 17.

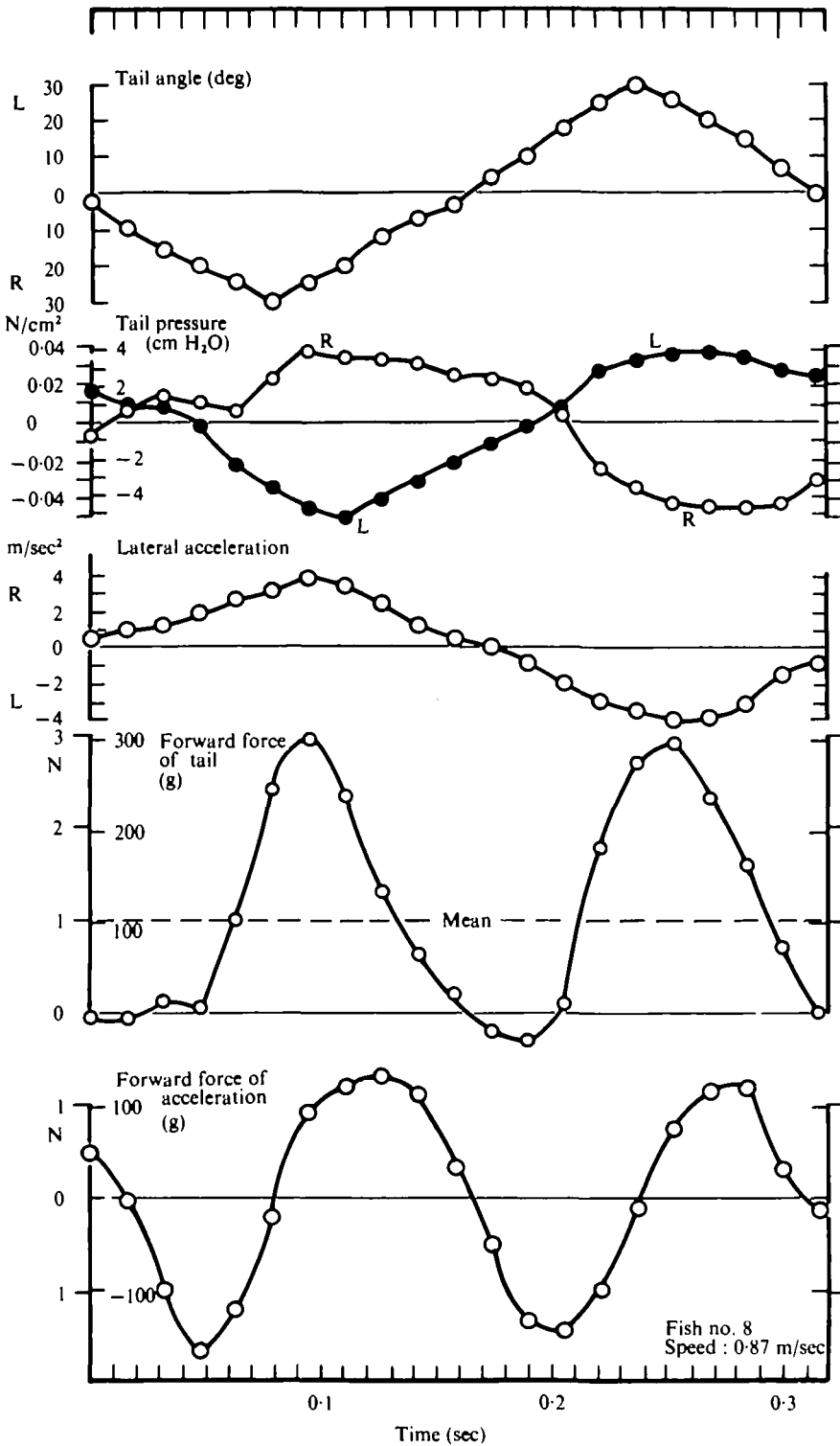


Fig. 2. Tail angle read from each frame of the movie of one body cycle of fish 8 swimming at a speed of 0.87 m/s. From simultaneous measurements of pressure on the right and left sides of the tail, the forward component of tail force was calculated as described in the text. Force of acceleration of the body in the forward direction was calculated from the forward acceleration and body weight. A lateral accelerometer was used to record transverse accelerations of the body in m/s<sup>2</sup>.

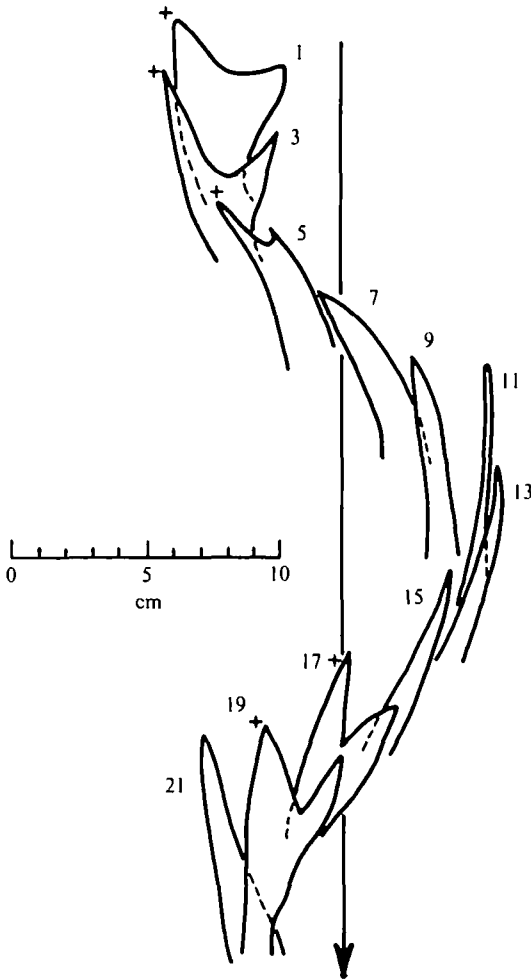


Fig. 3. Tracings of the tail of fish 8 at 0.87 m/s water speed, every other frame, corresponding to every other data point in Fig. 2, starting with 1. The upper tip of the forked tail is marked with a plus (+). In frames 7 through 15, the upper fork is directly above the lower fork. The peduncle is clearly shown as the narrowest portion in frames 1, 3 and 19. The vertical span of the tail (height) was 15.0 cm maximum and 11.5 cm minimum (mean 13.3 cm).

mately proportional relation of pressure to speed of 3.7 (2.2–5.6) cmH<sub>2</sub>O at 0.5 m/s was found. The absolute value of pressure increased with speed with a slope of approximately 7.4 cmH<sub>2</sub>O per m/s. The points ranged from 51% above to 41% below this mean.

Fig. 2 is a graph of the data obtained at 0.87 m/s on bluefish 8. It shows the angle of the tail with respect to the free water flow, the accompanying change of pressure on the right and left sides of the tail, the lateral acceleration of the body in m/s<sup>2</sup>, the force of the tail in the forward direction, and the force of acceleration of the body calculated from the forward acceleration and mass of the fish. Similar graphs were made for each speed of each of the six fish in Table 1. The information in these graphs is summarized in Table 1. The deceleration which occurs between thrusts is due to



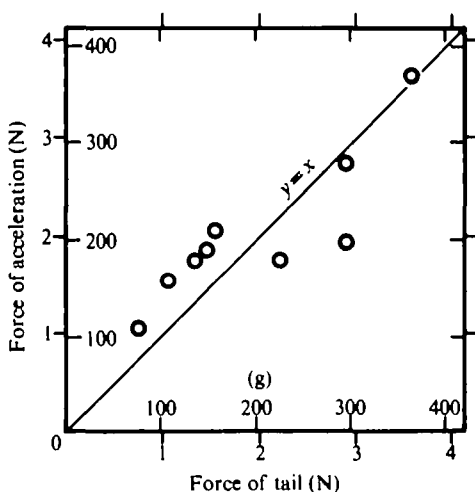


Fig. 4. Relationship between the peak to peak excursion of force of the tail in the forward direction and the amplitude of the peak to peak changes of the force of acceleration and deceleration of the body calculated from the equation: force = mass  $\times$  acceleration, in bluefish 8, 9, 14 and 17.

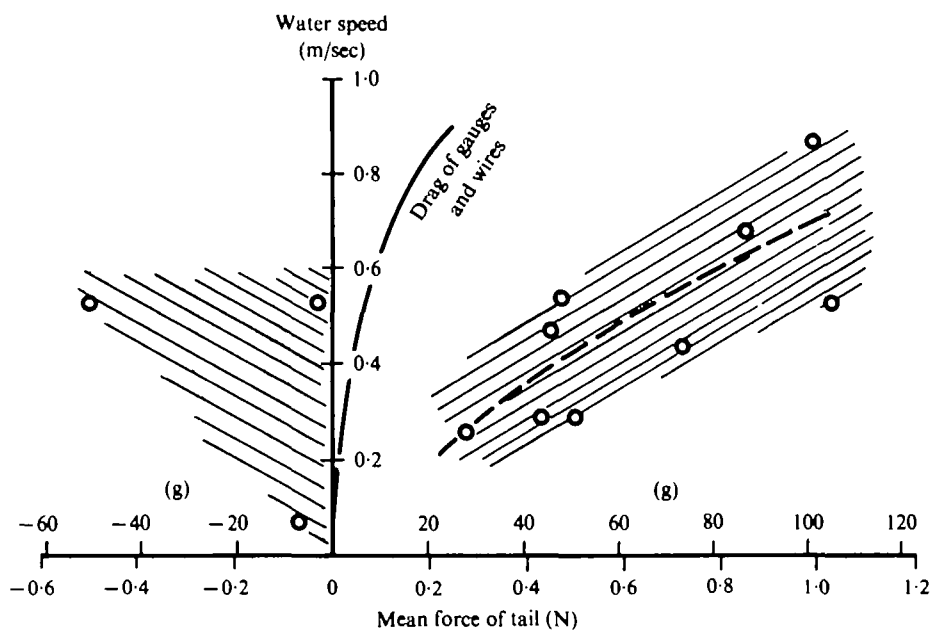


Fig. 5. Mean force of the tail calculated as the time average of the force in the forward direction derived from the pressure on each side of the tail, tail area, and sine of the angle between the tail and direction of water flow. Bluefish 8, 9, 14 and 17 on the right side. Bluefish 10 and 11, drifting backward, on the left side. The dashed line represents a visual estimate of the average, and the shaded area indicates the range of observations. The force overcoming drag of the gauges and wires at different water speeds is drawn for comparison with the mean force of the tail.

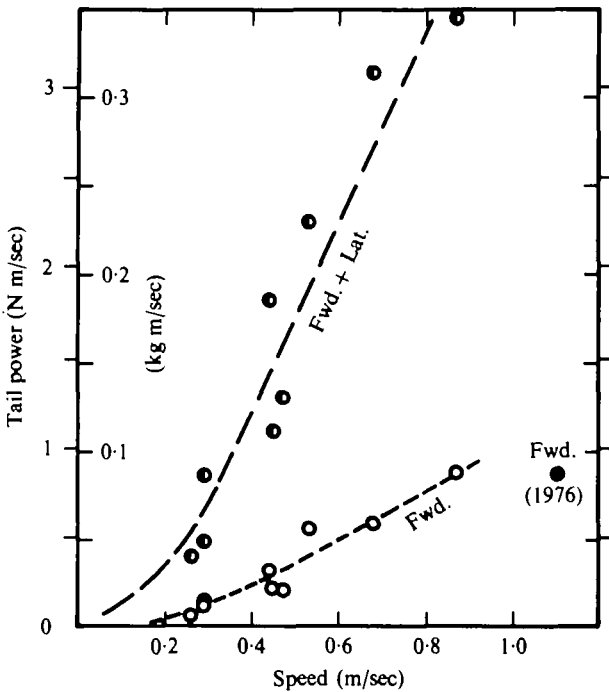


Fig. 6. The forward component of tail power compared to the sum of lateral and forward components of tail power measured at different swimming speeds in bluefish 8, 9, 14 and 17. The dashed lines represent visual estimates of the average. Point ● is the power calculated from data of DuBois *et al.* (1976).

drag which is primarily on the body with little drag on the tail. The force of acceleration and deceleration corresponds closely to the forward component of force delivered by the tail. Similar results were obtained on all 12 graphs of the data on all six fish.

Fig. 3 is a series of tracings of the tail obtained from every other movie frame at 0.87 m/s on fish 8, corresponding exactly to data presented in Fig. 2. The tracing labelled 1 is the first data point, and 21 starts the next cycle. A scale in cm is provided. This drawing is comparable to that of Bainbridge used by Lighthill (1971) to calculate impulse delivered by the tail to the water.

Fig. 4 demonstrates the relationship between the excursion of the forward component of tail force in grams force, and in Newtons, calculated from the maximum to minimum excursions of forward force (of which one example is shown in Fig. 2) and the excursions of acceleration and deceleration measured from maximum to minimum (also as shown in Fig. 2). The points appear to be scattered around the line of identity, labelled ' $y = x$ '.

Fig. 5 relates the speed of the fish through the water to the mean (time average throughout a body cycle) of the forward component of tail force. The data obtained from the four fish which swam well are on the right side of the graph. The speed increased with the mean force. The two fish which did not maintain speed through the water had negative values of mean tail thrust (left side of graph), implying that the tail drag was greater than the tail thrust. This would account for the backward drift in the movie.

The force required to overcome the drag of the wires and gauges is plotted as a function of speed in Fig. 5, and was not subtracted from the values shown for the fish. It was 7 g at 0.5 m/s and 26 g at 0.9 m/s, or 10 and 13% (by extrapolation of the dashed line) of the drag of the fish, respectively.

The total mechanical power of the tail against the water, and the forward component of this power, are plotted as a function of speed of the water in Fig. 6. The values shown also are listed in Table 1. The ratio between forward and total tail power is the propulsive efficiency of the tail. The mean value for this tail efficiency was 0.20, S.D.  $\pm 0.04$ , S.E.  $\pm 0.01$ .

The change in length of the body from jaw to peduncle (initial length 41 cm) from adding weights (corrected for displacement) to the peduncle to bend the body of dead bluefish 14 head down in water into a C shape was 6 cm for 50 g, 12 cm for 100 g, 19 cm for 200 g, and 20 cm for 400 g. The secant slope of this curve was 0.095 cm/g over the range 0–200 g force. When this body was held in an S shape, the decrease in length was a linear function of force until it was 5 cm for 200 g. Then, it was 6 cm for 400 g. The slope was 0.025 cm/g over the range 0–200 g. The body, therefore, did not act like a stiff spring, but could be characterized as 'limp' when the muscles were not contracting.

When force was directed perpendicularly to the tail to bend it on the peduncle in anaesthetized fish 17, the angles obtained were 0° for 0 g, 35° for 31.3 g, 48° for 63.1 g, and 60° for 95.7 g force. In the absence of voluntary muscular contraction, the tail was easily bent at the peduncle.

In the measurement of lateral excursions of the fork of the tail, it was found that the peduncle moved laterally leading the fork, but that the amplitude of excursion of the peduncle from side to side relative to the body's centre was approximately equal to the lateral excursion of the fork of the tail relative to the centre. For example, in fish 8 at 0.87 m/s, the peduncle's excursion was 10.1 cm and the fork of the tail's excursion was 10.1 cm, relative to the centre of mass. By comparison the tail's excursion relative to the sides of the sluice was 8.3 cm.

#### DISCUSSION

Pressure gauges placed on the tail record the force of the water. This coupled with the measurement of tail angle permitted calculation of the force vectors in Gray's diagram (p. 230, Gray, 1957), supplementing what has been deduced from water movements near the body and tail.

Finding the zero baseline of pressure is a problem. It is reasonable to assume that when swimming is regular and symmetrical, the mean pressure on the right side of the tail equals that on the left. But without an absolute reference pressure in the free stream, it is impossible to locate an absolute zero. In fact, it seems probable that mean pressure in front of the tail was negative (DuBois *et al.* 1974), the tail acting as a pump. Suppose, for example, the tail were angled to the left, and the pressure on its left side  $-3$  and right side  $+1$  cmH<sub>2</sub>O. The pressure difference, 4 cmH<sub>2</sub>O, would be indistinguishable from the same value generated by  $-2$  on the left and  $+2$  on the right. The difference,  $\Delta P$ , would be similar, and the value calculated for forward force equal in both cases. Table 1 lists peak negative pressures. Their mean is

-4.0 cmH<sub>2</sub>O. Peak positive pressures average significantly less, only 3.1 cmH<sub>2</sub>O. This difference may be explained by the negative pressure near the peduncle. Inability to locate an exact zero is a handicap, but does not appear to affect the values for  $\Delta P$ , or those calculated therefrom.

The results of this study show that during steady swimming the forward thrust of the tail is intermittent and produces an intermittent acceleration of the body which is almost synchronous with or lags  $\frac{1}{80}$  s with respect to the thrust of the tail. The force of acceleration of the body calculated from Newton's law is approximately equal to the forward component of force delivered by the water to the tail minus the force of body drag. Between thrusts, the momentum of the body sustains the forward motion, but a deceleration whose time integral is equal to the time integral of acceleration occurs due to the drag which acts on the body throughout the body cycle.

It is tempting to try to calculate the drag, corresponding in time to each frame of the movie, throughout the body cycle. Two of the basic elements are there. They are the forward force of the tail, and the reactive force required to accelerate the body. The difference should be the force of drag, and drag of the flexing body is one of the major unknowns. However, this calculation cannot be made accurately from the data such as those in Fig. 2 because one can see a lag of acceleration with respect to tail force of one or two movie frames. An error in timing, or phase difference, of only 0.01 s between the curves of forward tail force and accelerating force of the body would produce major apparent fluctuations of body drag. The timing between our movie and pressure recordings was no better than one frame, or  $\frac{1}{80}$  s, and the time required for a wave of force to pass along the body is unknown. Therefore, the calculation of drag throughout the body cycle had to be deferred.

The longitudinal mode of oscillation of the body may be thought of as a mass on a spring. McCutchen (1977) characterized the body of a much smaller fish as 'limp'. Measurements of the elasticity of the tail on the peduncle, and of the body curved in a C or S shape, show that bluefish also are limp, when the muscles are not contracting. The resonant frequency ( $F_R$ ) of a mass on a spring is  $F_R = (\frac{1}{2} \pi) \sqrt{(1/IC)}$ , where  $F_R$  is in Hertz,  $I$  is the inertance of the body in g force per cm/s<sup>2</sup>, and  $C$  is compliance of the body in cm/g force. Fish 14, used in another experiment had lost weight. It weighed 1.25 kg. Divided by 980 cm/s<sup>2</sup>, ' $I$ ' would be 1.28 g cm/s<sup>2</sup>. When the body is C shaped,  $F_R = (1/6.28) \sqrt{[1/(1.28 \times 0.095)]} = 0.46$  Hz. When S shaped,

$$F_R = (1/6.28) \sqrt{[1/(1.28 \times 0.025)]} = 0.89 \text{ Hz.}$$

Since the tail frequencies (twice the body frequency) in this study were 3.4-6.0 Hz, the body considered as a passive system would be limp, and not a resonating mass on a spring. Since the muscles bridge the elastic part of the body, this limp mode of resonance has little to do with the coupling between tail force and body acceleration. We did not attempt to measure the elastic coefficient of the body when the muscles were tense. A lag of  $\frac{1}{80}$  s between tail force and body acceleration as seen in Fig. 2 could possibly result from the time required to transmit a wave of force along the body, although we did not otherwise measure the transmission time in this study.

In two fish (10 and 11) although the changes of acceleration were in keeping with the changes of tail thrust, the mean forward component of tail force was zero or even negative, indicating that mean tail drag exceeded mean tail thrust. These fish may have

been steering with the tail or trying to slow down. They swam poorly, and drifted backwards in the movie.

In the four fish which swam well, the mean speed was related to the mean forward tail force calculated as the time average of forward force throughout the body cycle. There were several possible sources of variation between individual fish. First, the fish were not all the same size. Secondly, the wires and gauges created some drag (10–13% of the force), which may not have been equal in all fish. Thirdly, the pressure was measured at one position on the tail surface. Fourthly, the tail angle was measured as an average whereas the curvature of the tail created a range of angles at any given moment.

In one fish, two gauges were placed on the same side of the tail as far apart as possible. One was near the upper tip, and the other near the peduncle. The pressure fluctuations during swimming were not distinguishable from each other. However, the size of the gauge assemblies prevented properly detailed mapping of the tail surface, particularly near the edges.

As the tail reverses direction at the end of its stroke, it is flat. As it moves toward the opposite side, it curves laterally, but since it is stiffened by rays and by tension in the web, the angle of curvature is not so great as to preclude use of an average angle of the tail with respect to the direction of the water flow. For example, in fish 8 at medium speed, at a peak pressure difference, right–left, of 7.9 cmH<sub>2</sub>O, the mean angle was 21°, peduncle 17°, tip 26°. Thus, averaging tail pressures by using a single set of right and left pressure transducers and averaging tail angles by use of single readings did not introduce much of an error in the calculation of the forward component of tail force.

The implications of these findings are that the changes of acceleration, as measured by an accelerometer implanted near the centre of gravity, are a reasonable representation of the tail thrust and the body drag. We show that tail thrust and tail drag can be measured if one needs to know the force generated at each moment. However, the measurement of tail pressures is not easy, and often is accompanied by electronic failure.

An approximate experimental value obtained previously from accelerometer records (DuBois *et al.* 1976) for mean drag was 0.08 kg force (0.78 N) at a speed of 1.1 m/s. The corresponding forward power 0.86 N m/s is plotted in Fig. 5 for comparison with the present results and is not appreciably different.

The size and speed of our fish are different from those used in previous studies. The relationship between drag and speed depends on whether flow is laminar or turbulent, and this information was not obtained in this study. From the tracings of the tail in Fig. 3, the speed and direction of the tip of the upper fork relative to the side of the sluice, and the angle of the tail relative to the forward axis, were calculated by the method of Lighthill (1971). The results, Table 2, are in units similar to those in Lighthill's Table 1. From his Table it can be calculated that for a dace 0.3 m long swimming at 0.48 m/s the mean momental force on the water was 0.24 N, mean force wasted as kinetic energy was 0.03 N, and force remaining to overcome mean drag was 0.2 N. For comparison, in our bluefish 8, which was 0.48 m long and swimming at 0.87 m/s, the mean momental force imparted to the water calculated in our Table 2 was 5.35 N, of which kinetic energy wasted was 1.78 N, the remainder,

Table 2. *Analysis of movement of the tip of the upper fork of the tail in bluefish 8, measured from Fig. 3*

Quantity No.	$t$ (s)	$V$ (m s <sup>-1</sup> )	$\alpha + \theta$ (deg)	$\alpha$ (deg)	$W_{tip}$ (m s <sup>-1</sup> )	$\omega$ (m s <sup>-1</sup> )	$\partial x / \partial a$ (l)	$s$ (m)	$m$ (kg m <sup>-1</sup> )	$m\omega W$ (N)	$m\omega W$	
											$\frac{1}{2} m\omega^2$ $\partial x / \partial a$ (N)	$\frac{1}{2} m\omega^2$ $\partial x / \partial a$ (N)
1	0	0.60	18	20	0.19	0.21	1.00	0.133	14.2	0.57	0.31	0.26
3	0.032	1.56	-22	-16	-0.58	-0.43	0.99	0.133	14.2	3.54	0.41	3.13
5	0.064	1.38	-49	-14	-1.04	-0.33	0.82	0.133	14.2	4.87	0.63	4.24
7	0.096	1.24	-54	-24	-1.00	-0.50	0.87	0.133	14.2	7.10	1.54	5.56
9	0.128	0.83	-82	-74	-0.82	-0.80	0.99	0.133	14.2	9.32	4.50	4.82
11	0.160	1.10	-7	-8	-0.13	-0.15	1.00	0.133	14.2	0.28	0.16	0.12
13	0.192	1.20	25	28	0.51	0.56	1.00	0.133	14.2	4.06	2.23	1.83
15	0.224	1.43	52	32	1.13	0.76	0.94	0.133	14.2	12.19	3.85	8.34
17	0.256	1.20	51	30	0.93	0.60	0.93	0.133	14.2	7.92	2.38	5.54
19	0.288	0.51	90	79	0.51	0.50	0.98	0.133	14.2	3.62	1.74	1.88

$t$  is time,  $V$  is speed of tip of tail relative to the water,  $\alpha + \theta$  is angle between displacement  $V$  and direction of the fish,  $\alpha$  is the angle between the tail and the path of the tip,  $W$  is lateral velocity of the tail relative to the wall ( $V \sin(\alpha + \theta)$ ),  $\omega$  is velocity of the tail perpendicular to its surface ( $V \sin \alpha$ )  $\partial x / \partial a$  is change in forward distance relative to distance along the curve of the tail,  $s$  is span or tip depth of the tail,  $m$  is vertical mass ( $\frac{1}{2} \pi \rho s^2$ ) per unit length. For a more detailed explanation of these terms, see Lighthill, 1971.

3.57 N, being available to overcome drag. However, from our Table 1 it can be seen that mean drag was 101 g or 1.0 N, rather than 3.57 N. The remaining movies should be analysed to determine whether differences of this magnitude are found on other fish in this series. If so, it would suggest that the momentum imparted to the water may be partly sideways as well as aft, or that energy lost in the water may be greater than that calculated from the term  $\frac{1}{2} m \omega^2 \partial x / \partial a$ . Since the drag in our experiments is large compared to that which would be calculated for a slender body in streamlined flow, it is suspected that water flow around the fish may have been turbulent. The wire grid in front of the fish may have created turbulence in the water before it reached the fish. To examine this possibility, we calculated (from Dryden *et al.* 1936) the scale and intensity of turbulence 1, 2 and 3 ft behind a  $\frac{1}{2}$  in mesh, distances which coincide with the position of the jaw, mid-body and caudal fin of our fish. If the grid wires had been 0.1 in in diameter, then the scale of turbulence would have been 0.12, 0.14 and 0.18 in respectively, and the intensity of turbulence 3.1, 2.1 and 1.4% of the mean velocity, at those respective distances behind the screen. Actually, our wires were only 40% of 0.1 in, and therefore the intensity and scale of turbulence would have been less than the values calculated from Drydens' tables. A 5 in diameter sphere placed behind a grid will have its drag coefficient modified by the turbulence. Dryden used the pressure difference between the front and back of the sphere as a criterion for the effect of a  $\frac{1}{2}$  in grid on the critical Reynolds number of the sphere. In turbulent free air,  $R_{crit}$  would be 385000 (Platt, cited by Dryden). One foot behind a  $\frac{1}{2}$  in mesh screen, the measured value was 129000, calculated value 110000. Three feet behind the screen, the  $R_{crit}$  would be 171000, measured or calculated. Briefly, the turbulence diminishes the vacuum behind the sphere so that the pressure coefficient of 1.4 at low Reynolds numbers changes to about 0.9 at a high Reynolds number. Our calculations assume that turbulence in water can be compared to turbulence in air at the same Reynolds number.

Table 3. *Movements of the fork of the tail measured for calculation of  $C_n$* 

Frame no.	$t$ (s)	$y_{\text{fork}}$ (cm)	$\Delta x_{\text{fork}}$ (cm)	$W_{\text{fork}}$ (m s <sup>-1</sup> )	$\Delta x/\Delta t$ (m s <sup>-1</sup> )	$\frac{1}{2}\rho V^2$ (N/m <sup>2</sup> )	$\Delta P$ (N/m <sup>2</sup> )
3	0.032	0.4	1.5	0.11	0.47	118	-59
5	0.064	-2.9	5.9	0.90	1.38	1391	-294
7	0.096	-2.2	9.0	0.68	0.96	700	-843
9	0.128	-2.9	12.0	0.90	0.94	864	-745
11	0.160	-1.8	12.4	0.56	0.14	172	-471
13	0.192	0.0	16.1	0.00	1.09	607	-206
15	0.224	1.8	19.1	0.56	1.14	824	529
17	0.256	2.5	23.3	0.79	1.12	959	794
19	0.288	1.8	26.3	0.56	0.95	618	804
21	0.320	0.7	25.8	0.23	0.17	40	559
Mean						629	530

$t$  is time, in seconds.

$y_{\text{fork}}$  is lateral displacement of tail fork relative to wall, cm, measured from movie. Zero displacement is at mean of swimming path of fish.

$\Delta x_{\text{fork}}$  is forward displacement of tail fork relative to tail in frame 1 of Fig. 3, cm, corrected for scale and parallax.

$V$  is calculated as  $\sqrt{(W_{\text{fork}}^2 + \Delta x^2)}$ , and is the velocity of the fork perpendicular to the tail surface.

We calculated  $C_n$  (Prandtl, 1952) or coefficient of pressure normal to the surface of the tail at the fork of the tail, for bluefish 8 at 0.87 m/s, from the movie and tracings of the tail (Fig. 3). Table 3 shows that  $C_n$  calculated as  $\Delta P/(\frac{1}{2}\rho V^2)$  is 530 N/m<sup>2</sup>/629 N/m<sup>2</sup> which equals 0.84. The tail is somewhat analogous to a sphere in turbulent flow.

The tail efficiency which we calculate to be 0.2 is lower than that which was previously determined by others. Our figure is based on measurements of the force and direction of force on the tail, whereas previous investigators have considered the energy lost in the wake. The forward component of tail thrust in our study is so closely related to the forward accelerating force on the body that we conclude that it is a reasonable figure. However, if the drag of the wires and of the possibly turbulent water were less, the tail might be more efficient.

The calculations of lateral power of the tail listed in Table 1 and Fig. 6 were made from the tail's lateral displacement relative to the centre of the body, rather than relative to the wall of the swimming compartment or average track of the fish as used by others (Lighthill, 1971; McCutchen, 1977). By using the displacement and force of the tail relative to the body we derived work and power of the tail on the body in the lateral direction, rather than power resulting from lateral displacement of the water by the tail alone or water by the body alone. In bluefish 8, the lateral power of the tail was calculated from the pressure on the right side minus left side times the change in distance of the fork of the tail from the sluice wall times the cosine of the angle between the tail and direction of water flow times the tail area, for each frame of the body cycle, at a speed of 0.87 m/s. The sum for all frames divided by the duration of the body cycle was 2.17 N m/s or 86% of the lateral tail power calculated from the displacement of the tail relative to the body. We assumed that the lateral power expended against the water is not just by the motion of the tail against the water, as calculated by others, but also includes lateral work done by the body against the water.

There is a question as to whether all the work of the body on the tail is used in producing force directed laterally. We calculated the forward and lateral components of power from corresponding force of water on the tail, and believe that these components are transmitted to the body. But the lateral force of the body on the tail should be equal and opposite to the lateral force of the tail on the body. Theoretically, the forward component of force of the tail on the body is opposed by an equal and opposite backward component of force of the body on the tail. Drag creates a backward force on the body, and thrust a forward force. These forces tend to compress the body. Indeed, a force of 100 g or 1.0 N would shorten a relaxed fish, in a C shape, by 0.12 m. But, the body muscles oppose this by straightening the fish and pushing longitudinally as well as laterally on the tail. For example, the mean drag on fish 8 at 0.87 m/s was 101 g or 1.0 N. At a body frequency of 3 Hz, this force if unopposed would shorten the fish by 0.12 m, six times per s, expending 0.72 N m/s of power. This figure is not greatly different from the forward component of tail power of 0.86 N m/s, as found in Table 1. Therefore, part of the energy delivered by the body to the tail is expended in overcoming force in the lateral direction, but part is used in overcoming force in the backward and forward direction. Fig. 3 and the tail fork positions which have been read from it and listed in Table 3 show fore and aft changes of velocity ( $\Delta X/\Delta T$ ) and position ( $\Delta X$ ) which contribute significantly to the reactive force of the water normal to the tail surface ( $\frac{1}{2} \rho V^2$ ).

McCutchen (1977) speculated that some of the kinetic energy of the tail and water might be recovered as the tail reversed direction. At the same time, he recognized that the body was limp, and that the muscles required to stiffen it could not absorb and return mechanical work as could a spring. The angle of the tail of bluefish 8 as it was changing direction of travel was about 10°. A force of 5–10 g would bend the tail 10° according to our measurements of the tail elasticity in which 31 g bent the tail 35° at the peduncle. The forward component would be 5–10 g  $\times$  sin 10°, or 0.9–1.7 g force. Even if the tail had been bent by the kinetic energy of the tail and water to 35°, the force required to do this, 31 g by our own measurements, would create a forward force of only 16 g, which would be small compared to the 275 g of forward force actually found when the tail was bent 29° during muscular contraction. We conclude that the kinetic energy of the tail and water is not conserved by elastic recoil of the body from elastic displacement of the tail angle. McCutchen's general suggestion that the fish saves some of the tail's energy 'by using hydrodynamic lift to reverse the tail's motion', seems true, for the following reason. Our data show that the reversal of the tail's angle at the end of its stroke appears to come from this kinetic energy, and this appears to prevent the tail drag which would occur if the fish had to use his body muscles to extend the tail into the water stream to prepare for the next stroke. Our studies show that the amount of tail drag is small. Alternatively, if the reversal of angle had depended upon the peduncle swinging toward the centre, leading the tail's trailing edge, our data in bluefish 8 show that this would have occupied about 43% of the peduncle's travel, and that this displacement toward the centre would have been wasted as if in taking up slack while reversing the tail's angle of attack, instead of providing propulsive thrust. We conclude that the laterally directed kinetic energy of the tail and water reverses the angle of attack in preparation for the next thrust transmitted through the peduncle.



At high speeds, some records showed that large accelerations accompanied by large pressures on the tail occurred periodically. This method would allow further study of these transient accelerations.

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