

PRESSURE DISTRIBUTION ON THE BODY SURFACE OF SWIMMING FISH

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(Received 3 August 1973)

Although there are a number of papers on how fish swim (Gray, 1957; Aleev, 1969; Lighthill, 1969), we have been unable to find any measurements of the pressure on the body surface measured while a fish is swimming. A preliminary calculation using the Pitot equation indicated that the pressure against the anterior surface of the fish, expressed in centimetres of water, would be approximately equal to the square of the speed of the fish in miles per hour. A fish one foot long, swimming at six miles per hour, would have a pressure of about 36 cm H₂O against the front of his head. Such pressures, if actually present, might be large enough to affect the body functions, particularly circulatory, and ultimately influence the body structure of aquatic animals. They are of the same order of magnitude as the hydrostatic pressures due to gravity acting on land animals of equal body size, and as the blood pressure in fish (Satchell, 1971). In addition, the determination of the pressure distribution on the body surface of swimming fish may be of help in explaining the mechanism of fish locomotion. Compared to pressure distribution on the body surface of dead fish, or casts, the difference may be responsible for the otherwise unexplained ability of some fish to sustain locomotion with relatively little energy expenditure (Gray, 1957; Schmidt-Nielsen, 1972). In this study we measured the pressure on the body surface of swimming bluefish, and we speculate as to the physiological implications of the pressures which were found.

METHODS

Several medium-size bluefish (*Pomatomus saltatrix*) were used. The fish were anaesthetized by placing them in a solution of tricaine methanesulphonate (Finquel, Ayerst Laboratories; 2 g dissolved in 10 gal of sea water) for 10-15 min. The fish were placed on a V board. Sea water containing the anaesthetic agent at half concentration was passed through the mouth and gills.

The following method was devised to measure pressure on the body surface. A hollow needle was inserted through the skin at the points to be studied, and was passed subcutaneously and then out through another point on the skin 1 or 2 in posterior to the point of entry. A fine polyethylene catheter 3 ft long (Clay-Adams PE 50 I.D. 0.58 mm O.D. 0.965 mm) was passed into the no. 17 needle, and the needle was pulled out through the skin. The catheter, whose end had been flared in a flame, was drawn through the tract under the skin until the flared end lay snugly within the

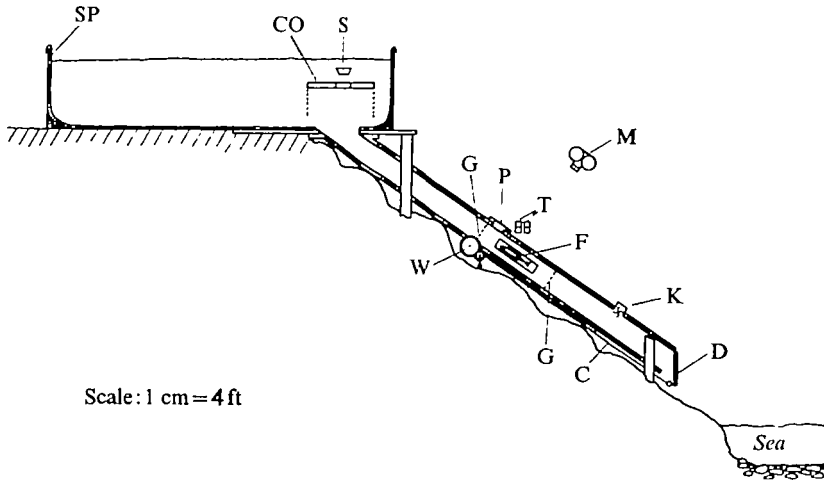


Fig. 1. Schematic diagram of apparatus. F, fish; G, wire grids; SP, swimming pool; CO, removable wooden covers; S, stopper; D, hinged door; C, wire cable; W, winch; P, handport; T, strain-gauge transducer-manometers; K, Knotmeter; M, cine camera.

hole in the skin at the point of entry. The most anterior point of the bluefish is the jaw. In this case a small hole was drilled through the mandible under anaesthesia to allow passage of the plastic catheter. The tube inserted through the jaw entered the mouth and passed out through one gill aperture. The tubing was anchored in place beyond the point of exit using a stitch placed through the skin or around a spine of the anterior dorsal fin. The free end was later connected to a strain-gauge manometer to record pressure. In flaring the tube the dilated end was first made bell-shaped, then slightly flattened, and finally tilted, if necessary, so that the aperture would lie flat with the skin, and flush with the skin surface. This position was confirmed by inspection, palpation, by injection of a stream of water which issued from the flared end, and by the injection of a dye when the aperture was under water. Pressures were measured at points along the back and the side of the fish (see Fig. 4).

To let the fish swim he was placed in a compartment with two 2 ft x 5 in glass windows, one above and the other on one side. This compartment was at the centre of an hollow wooden tunnel 18 ft long, octagonal in section, with 12-inch distances between the inner surfaces (Fig. 1). The inside had been sanded and varnished. The only projections consisted of a wire grid upstream and another downstream from the fish, $3\frac{1}{2}$ ft apart, to prevent his egress. The tunnel was inclined at 33° from horizontal. A wooden flange on the upper end of the tunnel was connected to the bottom of a plastic-lined oval swimming pool 10 ft wide, 15 ft long, and 40 in deep. A 5 h.p. gasoline-powered centrifugal pump was used to fill the pool with sea water. A removable wooden cover with a 3 in stopper could be used to close the opening from the pool to the wooden tunnel. A hinged door was fitted over the outlet of the tunnel. Opening or closing of this door was controlled by a wire cable attached to a hand-operated winch to vary the rate of water flow past the fish. The pool was mounted on top of a bluff overlooking a beach, and the wooden tunnel rested on legs which were supported on boulders that protected the bluff against waves. The outlet discharged onto the beach at low tide, or into the waves at high tide.

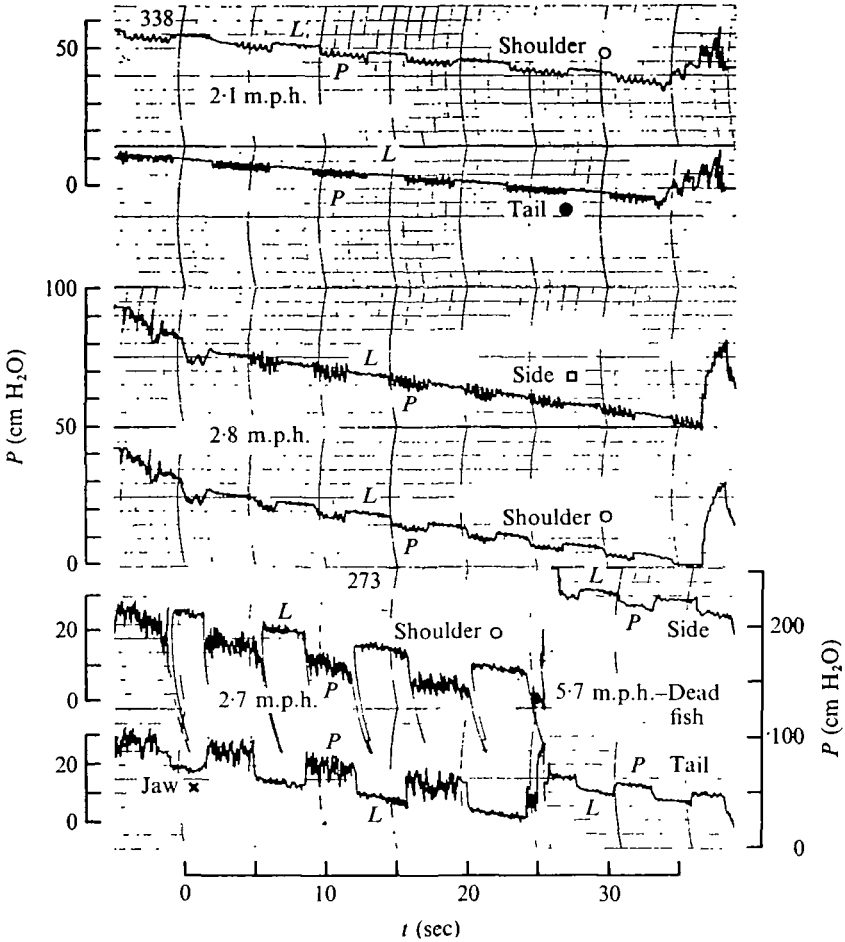


Fig. 2. Examples of pressure recordings from live and dead fish. The top pair of tracings shows pressure recordings, during one run, on the shoulder and tail of a bluefish swimming at 2.1 m.p.h. The middle records are from the side and shoulder of a bluefish swimming at 2.9 m.p.h. In the lower tracings, the records on the left are from the shoulder and jaw of a live bluefish with a water speed of 2.7 m.p.h. The bottom two records on the right are from the side and tail of a dead bluefish suspended in water with a speed of 5.7 m.p.h. The tracing from the side reflects some lateral convexity of the dead fish. Symbols in all sets of tracings of live fish are referable to the bluefish drawing in Fig. 4. One notes the oscillations in recordings from the fish, probably due to changes in the angle of attack and proximity of the fish to one or the other wall of the chamber.

At the upper section of the fish's compartment there was a handport which had a removable cover held down by wing nuts. The fish was introduced through this opening, with the compartment half-full of sea water. The plastic tubes from the fish were led out through holes in this cover. The handport was then closed, and some water allowed in through the 3 in hole in the cover of the tunnel's entrance. When the tunnel was full, the wooden cover over the entrance floated free. As the fish recovered from anaesthesia, the outlet door was opened slightly with the winch, to begin water flow and thereby keep the fish supplied with sea water and oriented upstream. Once the fish was out of anaesthesia and in position, his swimming motion was encouraged

by increasing the water speed to about a half-a-mile per hour, or more. Then, a series of recordings was made at each of several constant water speeds.

The PE 50 catheters in the fish were connected by 22-gauge needles to three-way metal stopcocks mounted on strain-gauge manometers (Statham P23 AA, P23 2D, P23 Db or P23 Dc, used two at a time on any given day). The two transducers were connected to a two-channel direct-writing recorder (Grass Instrument Co. Model 5A) located beside the pool. Readings from a water-speed indicator (Signet Knotmeter MK 12) were noted on the record. Pressure at the wall of the fish's compartment was measured from 20-gauge needles mounted in the wall and cut off flush with the water stream to register lateral or so-called static pressure, for comparison with pressure on the body of the fish. This comparison was made by turning the three-way stopcock on each of the two active strain-gauge manometers from the fish catheter to the wall tubing, back and forth, several times, each reading lasting about 3 sec (Fig. 2). One run would last about 30 sec (Fig. 2).

The pressure on one point was not always identical at each speed, but varied somewhat, probably being affected by the angle of attack of the body on the water, and sometimes by the proximity to one or another surface of the tunnel. We could not control these, and simply took an average. The variations (Fig. 2) were not great.

After two or three runs, the pool had to be refilled, and this took 10 or 15 min. During this time the fish would swim gently or rest. During one day's work, on one fish, we would obtain 5 to 10 good runs, with the fish swimming well and all gauges working properly. Even more runs had to be discarded because the fish was not swimming well or turned around, or because there was a bubble in the tubing or gauges, a leak in a stopcock, or a kinked or broken catheter. With no flow the pressure in the catheters and at the chamber wall had to be equal; otherwise there was an obstruction or a leak to be repaired.

The average rate of water flow (abscissae in Fig. 4) was calculated from the rate of decrease of the depth of water in the pool. Then, from the area of the pool and cross-sectional area of the tunnel the average linear speed of water in the tunnel was calculated. The velocity of the water in the centre of the tunnel was measured using a small hollow brass tube that passed from one side of the tunnel to the other, in front of the fish compartment. A small hole drilled in one side of the brass tube was turned upstream to measure the Pitot pressure at the centre of the tunnel. The water speed was calculated from the Pitot equation. It was about 10% greater than the mean flow calculated from the emptying rate of the pool. Water speed at the edge of the tunnel was measured either using the same brass tube pulled into position with the hole facing upstream about an inch from the wall, or from the reading of the Knotmeter, which was mounted on one wall between the fish compartment and the exit door. The speed near the wall was about 16% less than the mean flow velocity. Observation showed bits of seaweed streaming past the top and side windows of the observation chamber with reasonably uniform velocity from top to bottom and side to side, with some slow turning of the particles at speeds up to 1 m.p.h. and little or no turning at 3 m.p.h. Thus the fish were presented with a reasonable profile of water flow, not too unrealistic compared to the currents in which they ordinarily swim. The largest fish we studied, a 30 in long bluefish (top left tracings in Fig. 4) occupied 13% of the cross-sectional area of the tunnel, at maximum body perimeter. Although he swam

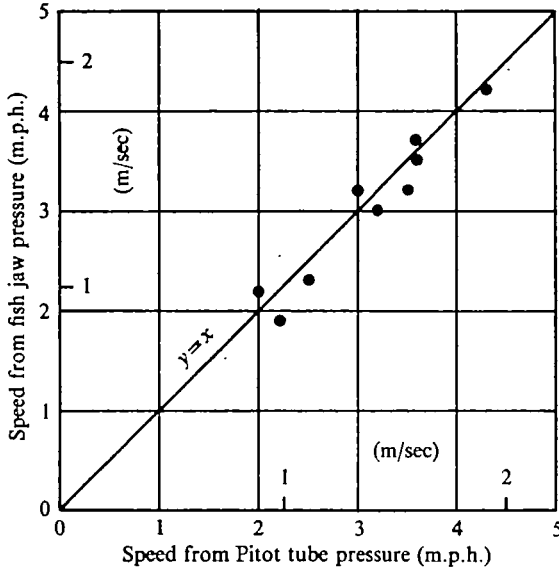


Fig. 3. Line of identity for speed calculated from Pitot pressure at the jaw of the fish and Pitot pressure from a brass tube just in front of the fish. Pressures were converted to speed using the Pitot equation (Appendix). The observed points lie closely around the line of identity ($y = x$), indicating that there is a stagnation point on the tip of the jaw.

adequately, we had the impression he had insufficient room, and consequently we sought smaller fish in order to increase room around the body for fin action. In one experiment a dead bluefish was held suspended in the swimming position by a taut cable. During this experiment pressure was recorded on the dorsum just anterior to the tail, for comparison with the pressure profile found with live fish.

RESULTS

Pressures measured on the anterior aspect of one fish were compared with pressures measured simultaneously from the hole in the brass Pitot tube in front of the fish (see Methods). Both pressures are converted to speed using the Pitot equation and are shown in Fig. 3 to cluster around the line of identity. In two other bluefish the pressure on the jaw (crosses in Fig. 4) corresponded to the theoretical pressure calculated by the Pitot equation from the emptying rate of the pool (continuous line near crosses in Fig. 4). It was concluded that the tube facing forward at the most anterior aspect of the fish can be used as a speedometer, in that the speed of the fish can be calculated from the pressure.

The other curves in Fig. 4 show how the average pressure on various spots along the back and side of the fish varies with the increasing average speed of the fish. Each set of tracings in Fig. 4 corresponds to data obtained on one fish. It appears that the pressure changes with the speed in a non-linear (probably quadratic) fashion. Fig. 5 shows the pressure profile at various points along the back (upper tracing) and sides (lower tracing) for a speed of 4 m.p.h. As expected, the pressure is positive (+17 cm H_2O) on the front of the fish, becomes negative (-9 cm H_2O) over its widest parts and tends to increase again towards the tail. The negative values on the back are

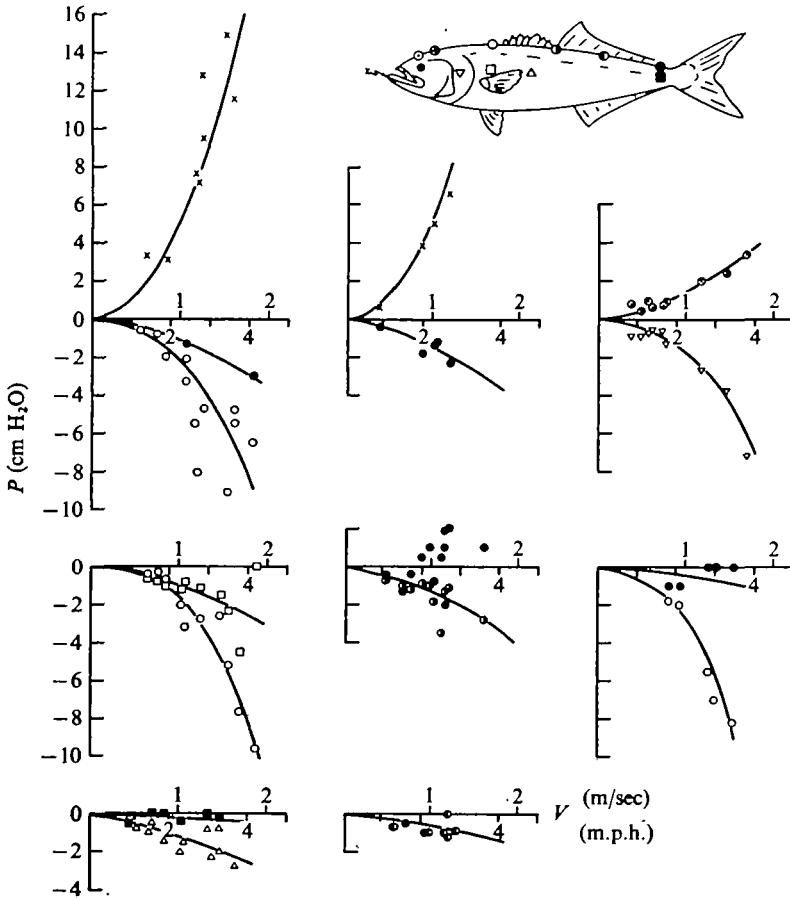


Fig. 4. This series of 8 graphs reflects the change of pressure seen on the various surface points with increasing speed. Symbols on the drawn bluefish indicate the position from which the pressure was recorded. Each of the 8 graphs contains the data obtained on an individual fish. One notes the general tendency for the positive pressure on the front of the fish to increase in a quadratic fashion with increasing speed. Pressures at the region of widest girth and the back portion become increasingly negative with speed. In the dorsal region, just behind the eye (symbol \oplus) both negative and positive values were recorded, indicating its proximity to the position where pressures switch from positive to negative.

greater than those of the side. The dynamic pressure difference from jaw to shoulder in the bluefish is +17 to -9, a difference of -26 cm H₂O over a length of 17 cm from jaw to shoulder. The ratio $-26 \div 17$ is -1.5 cm H₂O per cm length, and this is the average rate of change of pressure along the forward part of the back of the fish. The rate of change of pressure along the side of the fish was -1.9 cm H₂O per cm length, on the front part, and $+0.2$ cm H₂O per cm length on the rear part of the body.

Rhythmic fluctuations of pressure were recorded at some points on the body (see Fig. 2). Pitot pressure on the jaw sometimes fluctuated rhythmically in time with tail frequency, moving up when the tail moved to one side, and down when the tail moved to the opposite side. We did not observe any catheter whip to explain this phenomenon. The effect was greatest at a tail frequency of 2 to 3 cycles per second. These fluctuations will be discussed later.

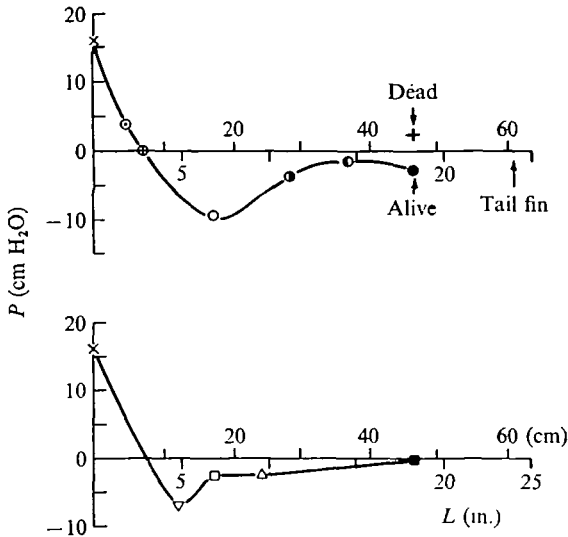


Fig. 5. Pressure profile from the back and side of the bluefish at 4 m.p.h. The distances were normalized to an average overall length of the fish of 24 in. Symbols are referable to the drawing in Fig. 4. One notes the marked contrast of the positive pressure recorded on the top of the tail of the dead bluefish with the negative pressure recorded on the same point of live fish.

DISCUSSION OF METHODS

At the outset, we had been unsure whether it would be possible to find a method by which to measure pressure at the skin surface without disturbing the flow at the surface. The device which made this possible was the plastic tube with the flared end. We soon found that such a tube cannot be used with a stationary gauge and the fish swimming freely in a tank because the resultant bending of the tube raises the pressure by reducing the volume, and a pressure artifact is seen. With the fish swimming in the water tunnel, the fish kept the same distance from the tube attachment, and the artifact was eliminated. The tubing assumed a U shape in the flowing water, but did not whip except when caught on a fin.

The second area of uncertainty had been whether fish would swim within the observation chamber in response to water flow. Preliminary observations on a tautog and a striped bass showed that these, as well as a bluefish, would swim and keep station well enough for hydrodynamic studies. The bluefish was chosen because he is an active, agile swimmer, of suitable size and well streamlined.

The third problem had been to make water flow fast enough in a large enough pipe. Calculation of equipment needed for a closed circuit showed it would be rather massive at the speeds we selected. We wanted to be able to do some tests on models at 10–15 m.p.h. if necessary. The pool and wooden tunnel were chosen as a compromise, and functioned reasonably well, though in an exposed location. Care was taken not to disturb the pattern of water flow, in that bends, constrictions, and projections were avoided in the design.

The fourth topic for discussion under Methods concerns the potential future use of the tube which measures pressure on the forward end of the fish for purposes of correlating instantaneous speed of the fish through the water with the oscillatory

motion of the body and tail. During its locomotion the fish must use the kinetic energy generated by the thrust of its body and tail to store energy while coasting and repositioning its body and tail in readiness for the next thrust. The tube which registers forward speed could be used to measure the velocity, and from this to calculate the instant-by-instant kinetic energy of the fish. Preliminary observations, both visual and by cinephotography, seem to indicate that in some cases the frequency of the cyclical change in kinetic energy corresponded to the frequency of the tail beat. If this is substantiated by further measurements, it implies that at times the fish may have an asymmetrical thrust of its body and tail, the body accelerating when the tail moves toward one side and decelerating when the tail moves toward the opposite side.

DISCUSSION OF RESULTS

Fig. 5 shows the pressure distribution on the dorsal and left lateral aspect of the bluefish swimming at 4 m.p.h. The result which showed that pressure on the front of the fish was equal to the pressure calculated from the Pitot equation confirmed the initial assumption that physiologically significant pressures would arise when a fish swims. Top speeds, in feet per second, are generally taken to be about 8 to 10 times body length in feet (Bainbridge, 1958). For convenience, one can remember that 88 feet per second equals 60 m.p.h. A 1 ft fish could swim at 6 m.p.h., a 2 ft fish at 12 m.p.h., and a large fish, such as a barracuda, tuna, or swordfish at 20 or 30 m.p.h. in short bursts. Since Pitot pressure in cm H₂O happens to be about equal to the square of the speed in m.p.h., the pressures on these fish would be 36 cm H₂O at 6 m.p.h., 144 at 12 m.p.h. and 400–900 cm H₂O at 20–30 m.p.h.

The negative pressure at the point of maximum diameter or girth can be explained from the Bernoulli principle, namely, that when water accelerates, as it must to pass around the fish, the lateral pressure decreases (Shapiro, 1961). At 4 m.p.h. the negative pressure in the mid-dorsal point between the pectoral fins was about -9 cm H₂O. This would correspond to an increment of water speed of the square root of 9, or 3 m.p.h. This, added to the speed of the fish through the water, would yield 7 m.p.h. over the back of the fish. In this estimate, we neglect laminar and turbulent pressure losses.

The negative pressure along the side of the fish was not so great as it was over the back, presumably because the width of the fish is not as great as the height. Water flowing through the gills would also lessen this pressure.

The slight negative pressures back along the dorsum and sides of the body indicate that the water flow slows down as the body diameter lessens, and perhaps some viscous and turbulent energy loss occurs at the same time. We did not find positive pressures which would exist if there were complete conservation of the energy as the water diverged and converged around the shape of the fish. On the other hand, we did not measure the pressure at or behind the rear edge of the tail fin. This could be done on a dead fish or body cast.

The physiological significance of negative pressures over the back, under the front, and along the sides of the fish was not tested, but presumably such pressures would help to draw water through the gills, and if transmitted by the body structures to the outside of the heart would aid the return of the blood to the cardiac chambers. It is

suggested that the bony structure of the anterior end of the fish serves the purpose of withstanding the high pressure there. Pressures more negative on the back and less negative on the sides would seem to tend to exaggerate the height still more, if the fish were deformable in that direction. The hardness of the body would resist this tendency.

The one dead fish that was studied while suspended on a wire showed positive pressures just anterior to the tail, as seen in Fig. 5, whereas live fish had shown zero or negative pressure in the same region. This suggests that convergence of water streams in front of the tail fin of the dead fish causes a positive pressure, and this could induce boundary-layer separation and a large wake. In live fish the negative pressure in this region may be due to the action of the body and tail propelling water away from this region of the body. This could prevent boundary-layer stall, and cause narrowing of the wake. This would decrease the drag of the body. If this finding is confirmed, it could help to explain why live fish move more easily through the water than one would predict from drag tests conducted on dead fish or casts of fish.

It is interesting to compare the hydrodynamic pressure gradient from head to tail in the swimming fish with the hydrostatic pressure gradient from head to foot in a man standing. The dynamic pressure difference from jaw to shoulder in the bluefish was -1.5 cm H_2O per cm length. For comparison, the hydrostatic pressure gradient from head to foot in a man standing is 1.0 cm H_2O per cm length, assuming a blood density of 1.0 . The reason for the difference in sign is that in the case of the fish, pressure around the body is decreasing from head to shoulder, whereas in a man it is increasing inside the body. 'Transmural pressure' (pressure difference between the inside and the outside) is therefore increasing caudad in both cases. The implication of this comparison is that parts of the surface of the fish swimming in water are subjected to as great a pressure gradient as one would find inside a land animal subjected to gravity. Considering the similarity in the order of magnitude, it is tempting to speculate that the structural and functional adaptations that protect fish against hydrodynamic pressures also may have been useful to land animals when they encountered the force of gravity for the first time. The details of pressure distribution along the body are not the same. However, the skull, useful to protect against Pitot pressure, serves in land animals to prevent changes in brain volume when the head is raised or lowered. The heart, instead of having a negative pressure around it due to the Bernoulli effect, has a negative pressure around it due to the outward pull of the chest wall. The vertebral column, useful in transmitting the thrust of the tail to the anterior end to drive the head forward against hydrodynamic resistance, on land serves to support the head and body structures against the pull of gravity. This line of reasoning opens up the question of the role of hydrodynamic pressure and gravitational force in the evolution of body structure and function. All we can say at this point is that the pressures are there, the pressures are large, and they may be highly relevant.

APPENDIX

The Pitot equation is:

$$v = \sqrt{\frac{2(P_1 - P_2)}{D}},$$

where v is velocity in cm sec^{-1} , P_1 is dynamic pressure in dyn cm^{-2} , P_2 is the lateral or 'static' pressure in dyn cm^{-2} , and D is density of the medium in g cm^{-3} .

To apply this equation in fresh water, and to convert speed to m.p.h., we find:

$$\text{m.p.h.} = \sqrt{\left(\frac{2(P_1 - P_2) 980}{1.000}\right)} \times 0.02237,$$

where 980 is the acceleration of gravity in cm sec^{-2} , 0.02237 is m.p.h. per cm sec^{-1} , and P_1 and P_2 are now in $\text{cm H}_2\text{O}$. This becomes:

$$\text{m.p.h.} = 0.99 \sqrt{(P_1 - P_2)}.$$

In salt water, it is:

$$\text{m.p.h.} = \sqrt{\left(\frac{2(P_1 - P_2) 980}{1.025}\right)} \times 0.02237,$$

where 1.025 is the density of sea water in g cm^{-3} . This is:

$$\text{m.p.h.} = 0.98 \sqrt{(P_1 - P_2)}.$$

As an approximation:

$$\text{m.p.h.} \approx \sqrt{(P_1 - P_2)},$$

or

$$P_1 - P_2 \approx (\text{m.p.h.})^2.$$

SUMMARY

1. Pressures on the body surface of bluefish, swimming at 0-6 m.p.h., compared to lateral pressure, were recorded using strain-gauge manometers.

2. While in motion, the front of the fish is subject to a head-on pressure exactly equal to that calculated using the Pitot equation. In salt water, this pressure, in $\text{cm H}_2\text{O}$, is equal to the speed, in m.p.h., divided by 0.98, all squared.

3. On the widest diameter the pressure is negative while swimming. This is attributable to the Bernoulli effect.

4. Pressure on the base of the tail is still negative, but not so negative as on the shoulder, in live swimming fish. The body and tail motion seem to draw water away from the peduncle of the tail, thereby diminishing turbulence.

5. In a dead fish the pressure at the base of the tail is positive, suggesting the possibility of boundary-layer separation and increased drag in dead fish towed through water.

6. The hydrodynamic pressures in fish swimming are often as great as the hydrostatic pressures encountered in animals of equal length subjected to gravity. We conclude that body defences against hydrodynamic pressure would also be useful against gravitational hydrostatic pressure.

7. Body structures which appear to resist hydrodynamic pressures in water and hydrostatic pressures on land are the skull, the vertebral column, and the circulatory system.

8. Transition from aquatic to terrestrial life may have been facilitated by adaptation to the pressures encountered on the body surface while swimming.

We are grateful to Dr James W. Mavor, Jr., of the Woods Hole Oceanographic Institution for consultation concerning some aspects of hydrodynamics. Mr Perry E. Hall kindly donated some live bluefish to our project and Mr Charles Wheeler and Mr Harold Ruschky of the Bureau of Fisheries Aquarium kindly maintained the fish in excellent condition. Mr Manuel P. Dutra, M.B.L. carpenter, built the wooden sluice used in this study.

The authors gratefully acknowledge support of a contract NOOO 14-67-A-0216-0017 from the Office of Naval Research. Dr DuBois is recipient of a Research Career Award from the National Heart and Lung Institute of the National Institutes of Health.

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