THE ROLE OF THE FINS IN THE EQUILIBRIUM
OF THE SWIMMING FISH

I. WIND-TUNNEL TESTS ON A MODEL OF
MUSTELUS CANIS (MITCHILL)

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(With Eight Text-figures)

INTRODUCTION

In spite of the many studies which now exist on the locomotion of fish, it is only recently that Gray (1933 a, b, c) has provided a satisfactory mechanical explanation of the propulsive force exerted by the fish body and tail. It is not surprising that the rather more complex problem of the stability of the fish in motion has scarcely been touched. Many experimenters have attempted to gain some knowledge of the subject by amputation of the fins of living fish. (For a recent summary of this work the reader is referred to Grenholm (1923).) But the complexity of the reflex system of which the labyrinth and other sense organs serve as the receptors has proved an almost insurmountable obstacle to the correct understanding of the results. The extent of such reflex compensating mechanisms is such that in many fish almost the whole fin area can be excised before any serious effect upon the stability can be noticed.

The movement of the fins which is necessary to produce these compensating forces is usually so slight that it is difficult if not impossible to perceive it. It seems therefore logical to attack the problem from the other end, and to work out in the first place the stability characteristics of a suitable model of the animal. This was first done by Houssay (1912) and described in his now classical monograph on the stability of fish. Houssay obtained many interesting results with the aid of geometrical models approximating to the shape of the fish body form. He suggested that the important element in the locomotion of any fish is the "nage filée", the glide without body movement following two or three powerful propulsive strokes, and he stated that this intermittent method of swimming was characteristic of all the fish he had investigated. On this basis he justified his use of a rigid mechanical model in elucidating the fundamental action of the fins in producing stability during locomotion.

Houssay's basic assumption is open to question. Observations made by the writer while diving in the tropics suggest that the "nage filée", while frequently
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employed, is by no means a usual method of locomotion. It is, however, sufficiently common to make it profitable to investigate the conditions under which such a free glide becomes a stable motion. Perhaps it would be as well before going further to explain what is meant by a "stable" motion in this sense. An aeroplane flying without the attention of the pilot is in stable motion if, when it veers slightly from its line of flight, the new wind forces produced upon its planes tend to restore the original direction of motion. This type of stability has received at the hands of the workers in aerodynamics the somewhat unfortunate name of "static" stability, to distinguish it from the "dynamic" stability studied in the oscillations of the machine when these restoring forces are acting. It is possible to use the term "stability" in yet another sense, for which it is not generally employed. Even though such an aeroplane were unstable in the sense of the word defined above, it could possibly be flown with the aid of a gyroscope mechanism as an automatic pilot, altering the controls in order to bring the machine back to its normal line of flight. It would be possible for a fish to swim in a straight line with the same sort of pseudo-stability, using its labyrinth and sense organs as a gyroscope pilot, controlling its fin movements by reflex mechanisms.

The extent to which the fish body in motion owes its rectilinear path to its static stability and to this reflex compensation can be roughly determined by working on an accurate model. Here reflex compensation is no longer possible and the "static" characteristics alone are determined. In effect, this is what Houssay did in his experiments, but he neglected one very important factor. The inertia which is producing the motion of the fish in a glide must be assumed to act as a force at the centre of gravity; a model towed by a thread attached to the anterior end does not reproduce the conditions of the same model in free gliding movement. This one factor changes the whole picture of fish equilibrium, as the present paper hopes to show.

An accurate model was cast in plaster of an average specimen of the common American dogfish, Mustelus canis, obtained from the tanks of the New York Aquarium. In order to prevent the entry of air into the gut, which would distort the shape of the animal, it was first anaesthetised with ethyl urethane while still under water, and then rapidly pithed. Immediately it became limp and motionless. Two-piece plaster moulds were prepared, the work being done by an experienced model-maker at the American Museum of Natural History under the supervision of the author. Every care was taken to support the animal during the casting so as to achieve the least possible distortion of the body form—no easy task in these sharks, as the body wall is extremely soft and plastic. When the mould had hardened, the fish was removed, the fins cut off and separate moulds made for each one. Care was taken at all times to ensure that the body and each separate fin was perfectly straight, as far as this was possible. That the process was not entirely successful in this respect will appear in the later results. The casting of the final plaster model was made by "pouring" into the two-piece mould, while the fins were cast in wax in their respective moulds. Wax fins were used, since they could be warmed and straightened if any bending had occurred during the making of the mould, and also
because they could easily be attached to or detached from the model during the experiments. In this way the completed model consisted of nine separate unit castings, viz. the two pectoral fins, two pelvics, first and second dorsal, anal and caudal fins, and the body. The plaster model was covered with two coats of shellac to give a smooth surface, and slight surface irregularities were "faired" (stream-lined into the general body contour) with "Plastolene", which was also employed to "fair" the attachment of the fins to the body.

The method used by Houssay of experimenting in water, though obviously a more satisfactory one, presents numerous technical difficulties, and the present work was actually carried out in air, in the small wind tunnel of the Guggenheim School of Aeronautics in New York. It is possible to obtain results which are accurately comparable with those which would be obtained in water, if the wind speed in the "air" test is calculated from the following equation:

$$(R.N.) = \frac{V_a l_a}{\nu_a} = \frac{V_w l_w}{\nu_w},$$

where $(R.N.)$ is the Reynold's Number, the factor which represents mathematically the conditions of such an experiment in any medium.

- $V_a$ is the velocity of the air-stream or of the model in the air test.
- $l_a$ is the length of the model used in the air test.
- $\nu_a$ is the kinematic viscosity of air.
- $V_w$, $l_w$, $\nu_w$, the corresponding values of $V$, $l$ and $\nu$ for the water test.

The kinematic viscosity, $\nu$, is equal to $\mu/\rho$, the absolute viscosity divided by the density, and is about 13 times as great for air as for water at $15^\circ$ C. Since the model used was the same size as the original fish, a speed of 3 m.p.h. in water would correspond to about 40 m.p.h. in the wind tunnel. This was actually the speed for which the small wind tunnel was designed, and was therefore used throughout the tests.

The model, a diagram of which is shown in Fig. 1, was mounted on a steel shaft, $\frac{1}{4}$ in. in diameter and about 10 in. long. Two holes, one in the side and one in the belly of the model, were threaded to fit the end of the shaft. In this way the data for rotation about a vertical and horizontal plane respectively were determined. The lower end of the shaft was held in the jaws of the chuck of a standard N.P.L. type aerodynamic balance. A description of this apparatus and the method of using it will be found in Glazebrook's *Dictionary of Applied Physics*; the following account will deal only with the forces measured and the method of calculating the results.

The components of the force on the model are always measured with respect to three primary axes as shown in Fig. 2. The $X$-axis (or longitudinal axis) is along the axis of the wind tunnel, and not along the axis of the fish. The $Y$-axis is horizontal and perpendicular to the $X$-axis, and the $Z$-axis is vertical. Turning about these three axes is known respectively as rolling, pitching and yawing, and the direction of positive roll, pitch and yaw is shown by the arrow on each quadrant. The forces along the three axes are known as the drag, lateral force, and lift, and
The rotational components about $OX$, $OY$, and $OZ$ are measured as rolling, pitching and yawing moments. In both pitching and yawing tests, the term “angle of attack” (symbol $\alpha$) is used to denote the angle between the axis of the fish and the $X$-axis, the angle being measured in the vertical plane for pitch tests, and in the horizontal plane for yaw tests. This angle of attack is not to be confused with the “angle of incidence”, which is the angle between the plane of the pectoral fins and the fish axis.
Fig. 3 is drawn to illustrate the use of these terms in a single experiment, the measurement of the lift and drag forces, and determination of the pitching moment for a certain fixed angle of attack. It shows also quite clearly a case of static instability. If we assume (as a rough approximation) that there is no lift force $L$, and therefore no pitching moment $Rh$ when the angle of attack $\alpha$ is zero, then the diagram shows that tilting the fish into the position where the angle of attack is as shown will result in a positive pitching moment $Rh$. This positive pitching moment will tend to turn the fish so as still further to increase the angle $\alpha$, and the system is therefore statically unstable. In contrast to this, a very obvious case of static stability is provided by a feathered arrow in flight. The large area of the tail feathers produces a resultant similar to that in Fig. 3, but acting behind the centre of gravity, and the moment $Rh$ is therefore a negative one, tending to return the arrow to its former direction of flight.

The amount or degree of stability or instability can be obviously measured by the magnitude of this negative or positive value of $Rh$ for a given deflection from the wind direction. It is customary to plot a curve showing the value of $Rh$ for any angle of attack, positive or negative. The slope of this curve $dM/d\alpha$ is then an accurate measure of the stability at any point.

**RESULTS OF WIND-TUNNEL EXPERIMENTS**

(a) *The yawing equilibrium and the effect of the median fins*

Fig. 4 shows the curves obtained for the yawing (horizontal turning) forces on the model without fins or tail. For the purpose of this experiment the tail of the fish was replaced by a cone of "Plastolene" of the same taper as the actual caudal fin, so as to streamline the body correctly without adding any fin area. It will be
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seen from the curve of "lateral drag" that the model was not quite symmetrical. There is no lateral force on the model at an angle of attack of approximately $-2^\circ$, the value of $\alpha$ where the curve crosses the axis. The head and tail were perfectly in line with the axis of the wind tunnel, and it was evident that this irregularity was caused by a slight asymmetry of the body form. The positive slope of the curve for the yawing moment shows that the equilibrium in this plane is quite unstable; a slight turn off the direct course would produce a turning moment tending to increase
still further the deflection. This is a well-known property of all airship hulls, and is known as the "unstable moment" of the hull. It is corrected in the airship by the addition of suitable horizontal and vertical fin surfaces at the rear end, when the airship becomes in effect a "feathered arrow".

Fig. 5 illustrates the effect of adding to the model its caudal, anal and second dorsal fins (i.e. all its posterior vertical fins). The lateral drag forces are now large, due to the large fin area, but the moment curve has a steep negative slope, indicating great directional stability.

When the first dorsal fin is now placed in position, an interesting situation is revealed (Fig. 6). The presence of this very large median fin increases the lateral drag by about 50 per cent., but the moment curve has completely changed in character. Stable at high angles of attack in the neighbourhood of 10°, it now shows that over the whole range of smaller angles, positive and negative, the yawing moment is almost negligible. The equilibrium is neutral.
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Though in an aeroplane the wings may markedly affect the directional stability—“swept-back” wings increase this stability greatly—the corresponding effect of the pectoral fins is only very slight in the dogfish model. The magnitude of the restoring moment (stability factor) is increased by about 30 per cent, for angles of attack above 10° when these fins are added; below this limit there is little or no difference in the moment curve. This is no doubt due to the small area and length of the anterior border of the pectorals. In the flying fish, however, Breder (1930) is undoubtedly correct in suggesting that the “sweep-back” aids directional stability. The pectoral fins in these fishes are very long and narrow, and the drag force of each will possess a large yawing moment. In these forms, a slight turn to the right will oppose a longer length of the left fin to the wind pressure, thus restoring the original direction of motion. In the majority of fast-swimming teleosts the pectoral fins, when used as brakes, are strongly “swept back”, and largely contribute to the extreme steadiness of the stop. The drag force contributed to the dogfish by its pectoral fins is very small; if these experiments give a true estimate, it is not more than 15 per cent. of the total drag of the fish body.

(b) The pitching equilibrium and the effect of the paired fins

When the equilibrium of the pitching (vertical) forces is determined for the fish model, it is found that it differs considerably from that of the yawing forces. In the first place, the body of the fish is not symmetrical about a horizontal plane. Flattened on its under side, the dorsal surface is strongly curved, the general outlines of the sagittal section (see Fig. 1) bearing some resemblance to that of a modern aeroplane wing. In plan view, however, there is a very great difference. The aeroplane wing is wide relative to its length; the aspect ratio (the ratio of width to length) for the dogfish is very small. For an aerofoil, the lift force may be as much as 15 times the drag, while the maximum value of this lift/drag ratio for the dogfish is only 1.5. Nevertheless the lift of the latter is quite appreciable, and the model shows the same characteristic as the aerofoil in possessing a small lift even at zero angle of attack. The relationship between lift and angle of attack is approximately linear.

Apart from these results arising out of the asymmetry of the sagittal section, the curve for the pitching moment shows that the same instability exists in the vertical plane, as was found for turning in a horizontal plane. The moment curve in Fig. 7 has roughly the same positive gradient as that in Fig. 4.

When all the fins, both median and paired, are attached, there is seen a marked difference between the pitching and yawing equilibria. Fig. 8 illustrates the forces and moments in pitch obtained when pectoral fins are attached at an angle of incidence of 8°. The relatively large area of these fins increases the lift force about 10 times, while the new position for zero lift is at $\alpha = -7^\circ$. This angle is determined by the resultant of the negative lift of the body and the small positive lift of the inclined fin surfaces. The unstable moment is very much greater than in Fig. 7, since the pectoral fins are ahead of the centre of gravity and their contribution to the instability is only very slightly offset by that of the pelvic fins, on account of the
Fig. 7. Pitching test on model without fins. Lift force plotted as light full line, drag force as light broken line, pitching moment about centre of gravity as heavy full line. Axes and units as in Fig. 4.

Fig. 8. Pitching test on model with all fins. Angle of incidence of pectoral fins 8°. Lift, drag and pitching moment as in Fig. 7.
small size of the latter. The curves shown in Fig. 8 differ only slightly from those which are obtained without the pelvic fins.

DISCUSSION OF WIND-TUNNEL RESULTS

In assessing the value of these results in the study of the balance of the living swimming dogfish, it must first of all be admitted that the conditions which obtain for the model are rarely met with in life. It is a matter of observation that the fish spends comparatively little of its time in gliding with body rigid, the greater part being occupied in active swimming. Furthermore, the fins are by no means flat and rigid structures like their wax counterparts in the model; they may become limp or stiff at will, and are capable of bending movements. How far do these factors invalidate the conclusions already reached?

Both of the above possibilities give the fish a very much greater degree of control than the wind-tunnel experiments admit. The unstable moment created by the first dorsal fin when the fish is gliding could be almost eliminated by allowing it to become limp, and by contrast increasing the muscular tonus of the posterior median fins. Alternatively the neutral equilibrium of the model could in the living fish be altered to an unstable one by the reverse procedure, the tensing of the muscles of the first dorsal. But this argument in itself implies that the fish in neutral equilibrium is in its most "useful" state, since the stability can be changed from zero to a positive or negative value at will with a minimum of effort. When gliding in a straight line, a negative value (rigidity of the posterior fins) gives it the directional stability it requires; when a turn is to be executed, a positive value (increased tonus in the first dorsal fin muscles) will produce an increase in the turning moment. The work of Gray (1933) can be cited with advantage here. He showed that the turning of a fish is produced by a flexure of the head region, not of the tail, which merely followed the original path of the fish until the turn was almost accomplished. This turn could obviously be very effectively aided by a large dorsal fin placed anteriorly. The action is reminiscent of the "servo" principle; a small initial turn of the head produces a water pressure on the first dorsal fin which generates a greatly increased turning moment.

Apart from gliding movement, however, it must be admitted that during normal swimming the yawing forces are largely, perhaps almost exclusively determined by the motion of the body which produces the propulsive force. Any degree of asymmetry in the propulsive wave would obviously produce a turning force far larger than any of the turning moments considered in the above data. The lateral forces of the posterior median fins in particular must be very great during active swimming, and these fins must play a role which is much more active than passive.

A somewhat greater importance attaches to these results when the teleost group of fishes is considered. The author has spent a good deal of time watching marine fishes in their natural surroundings at the Tortugas Laboratory of the Carnegie Institution of Washington, using for this purpose the now familiar diving helmet in shallow depths of 10–12 ft. In marine teleosts, gliding motion is a very frequently
used method of progression, steady swimming being the exception rather than the rule. It seems logical to assume (though up to the present the writer has no experimental data of the above type to prove the contention) that the role of the median fins in these forms is the same as in the dogfish. If this be so, then the teleost shows a great advance over the dogfish in the extent of its control of directional stability. The muscles which serve to deflect the median fins to one side or the other, the so-called inclinator muscles, are usually not large in Teleostei, except in groups such as the Plectognathi, where they are used for locomotion. But the erector and depressor muscles of these fins are usually very well developed, especially in the first dorsal fin which in many forms can be completely retracted into a groove in the dorsal surface of the body (e.g. Scombroids). That this large dorsal fin may be erected in order to increase the unstable moment during turning is suggested by many of the above observations while diving. Frequently in the course of a glide many of these teleosts were seen to erect the first dorsal fin, normally depressed while swimming and gliding, and immediately to turn. This turn was usually accomplished by "braking" action of one pectoral, occasionally by action of the pelvics alone.

The dorsal fin is also of importance in acting as a keel, and preventing rolling, but its use for this purpose is outside the scope of the present paper.

In the light of this remarkably well-controlled stability for yawing (turning) movements of the fish while in a rectilinear glide, the results obtained for the pitching (rising and diving) equilibrium are of great interest. At first sight one would imagine that the same considerations would apply in both cases, that it would be of distinct advantage to the fish to be in a state of neutral equilibrium in the vertical plane, as well as in the horizontal one. This is not actually true. The fish body is laterally very flexible, and this fact, as has been already mentioned, gives it an almost unlimited power of turning by asymmetrical swimming movements. Experiments recorded later in this paper show that complete deprivation of its first dorsal fin scarcely impairs the turning powers of the dogfish. But in the vertical plane, the amount of flexure of the body is extremely limited, and the asymmetrical rising and diving force produced by such means must therefore be small. Yet it is of great importance to the fish to be able to execute these rising and diving "turns", so as to be able to control its level of swimming.

At this point it is necessary to state an important principle of aerodynamics. This is the well-known fact that "stability" and "controllability" are inversely related. Controllability is a measure of the ease with which a body may have its line of motion artificially altered; stability is measured by the restoring force called into play automatically by any deviation from the line of motion. Obviously a very stable motion will require a large controlling force to alter its direction, and vice versa. For motions of the fish involving turning in a horizontal plane, the flexibility of the body provides an effective compromise between the two requirements of controllability and stability; with the body held rigid, the stabilising forces of the posterior fins can predominate; with the body actively flexed, large lateral steering forces can be brought into play. Such a compromise is not possible for rising and
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diving movements in the vertical plane, owing to the lack of vertical flexibility of the body. And since controllability is all-important, stability has to be completely sacrificed.

This lack of stability would seem to be a very serious drawback. But, though it is true that any deviation from the normal rectilinear path will bring about vertical disturbing forces (as opposed to restoring forces), it is equally true that with a great degree of controllability, only a small deflecting force will be required to restore the original direction of motion. This new deflecting force is provided by the muscles acting on the pectoral fins. Situated well anterior to the centre of gravity, a very slight change in the angle of incidence of these fins will produce large vertical turning forces. Such a change, of course, brings about very rapidly an over-correction, and the reflex control of the fin muscles must be continuously at work making imperceptible changes in the angle of incidence in order to maintain a rectilinear motion. But this is not at all unlikely, and will readily be admitted possible by all students of fin amputation experiments, where the most delicate compensatory movements are rapidly acquired.

The part played by the pelvic fins in this pitching equilibrium remains to be considered. The lift, drag and pitching moment curves for the dogfish model with and without pelvic fins are practically superposable, and it seems highly probable that these fins play no part in determining the stability of the fish. The relatively enormous area and forward position of the pectoral fins makes any contribution of the pelvics insignificant in comparison. For this particular specimen, the ratio of pectoral/pelvic fin area is 5.22, while for the vertical median fins the ratio anterior/posterior fin area is only 0.41, clearly illustrating the differences between the horizontal and vertical fin systems in this respect.

To be strictly accurate, the slope of the lift curve, $dL/d\alpha$, is increased in the presence of the pelvic fins by about 7 per cent., and the slope of the pitching moment curve, $dM/d\alpha$, is decreased by about 10 per cent. The increase of lift and decrease of pitching moment is of course explained by the fact that the pelvic and pectoral fins are on opposite sides of the centre of gravity, while the greater effect on the moment curve is due to the fact that pelvics are farther from the centre of gravity than are the pectorals.

During normal swimming in a straight line the pectoral fins of the dogfish are "trailed" slightly, i.e. inclined to the body axis at an angle of incidence estimated from photographs and visual observations to be about 8-10°. A reference to the graph in Fig. 8 will show that with the body horizontal ($\alpha=0^o$) there is a considerable positive lift force, and also a fairly large positive pitching moment. This by itself suggests that the fish would not be able to continue its horizontal path, but that the nose would be forced upwards. That this effect does not occur is an indication of the presence of an equal and opposite negative pitching moment, produced by some mechanism which the wind-tunnel experiments cannot imitate. Such a mechanism has been known for a considerable time and has been discussed by Ahlborn (1896) and many others; it is brought into action by the lateral movements during swimming of the heterocercal tail. The suggestion that there is a vertical lift component in the
water current produced by the tail has been affirmed by some and denied by others, the most recent contribution to the subject being a paper by Grove and Newell (1936). These authors confirmed the existence of this force by a series of mechanical models. The origin of the vertical component is obvious; the denial of its existence has been largely due to an inability to appreciate the part played by the more flexible lower lobe of the tail. The present author had an opportunity of verifying the fact while working with a mechanical device for producing lateral oscillations in the body of a dead fish. (The apparatus in question was designed and used by Gray (1933 a, b, c, d) for his studies on fish locomotion.)

This vertical lift force at the posterior end produces a negative pitching moment which neutralises the positive moment of the trailing pectoral fins. Since the forces producing these moments are both lift forces, there is a resultant force vertically upwards acting on the whole animal. This force is, during normal swimming, equal in magnitude to the weight of the fish, acting downwards through the centre of gravity. The specific gravity of the sharks is appreciably heavier than that of sea water; Mustelus canis sinks when not swimming, finally coming to rest at the bottom of the aquarium tank.

AMPUTATION EXPERIMENTS ON THE LIVING DOGFISH

The verification of some of the above results has been obtained by a series of experiments involving the amputation of various fin combinations of the living fish. But the possibility of compensating movements introduces complications into the picture of the equilibrium; as mentioned in the introduction, many such operations produce little or no effect.

(1) Amputation of the anal fin and the hypocaudal lobe of the tail. The fish swims along the bottom of the tank, unable to progress in a horizontal plane in the open water above this level. Cinematograph films of this condition show clearly the mechanism of the disturbance of movement. There is no longer any vertical (upward) component of the tail force, and therefore no negative pitching moment. The fish would therefore sink at the tail end and rise at the nose if the pectoral fins were held in their normal trailing position. If this positive pitching moment is to be avoided, the pectoral fins are held horizontally or even inclined at a slight negative angle of incidence to the body axis. In such a position there is no resultant lifting force to counteract the weight of the fish, which is thus driven to the bottom.

(2) Amputation of the second dorsal fin and of the epicaudal lobe of the tail. This operation produces comparatively little effect. The area of these fin regions is small, and the increased lift at the tail end (negative pitching moment) can easily be counteracted by a slight increase in the normal angle of incidence of the pectoral fins. The converse effect to that shown in (1), the fish tending to swim near the surface, is slight, but appreciable.

(3) Amputation of the first dorsal fin. There is a slight but noticeable increase in the rolling of the fish while swimming, but no other effect is visible.

(4) Amputation of the pelvic fins. As would be expected from the wind-tunnel
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results, this operation produces no effect on the swimming. The very slight lack of lifting force at the hind end when these fins are absent can be easily compensated by quite imperceptible changes in the inclination of the pectoral fins.

(5) Amputation of the pectoral fins. This produces the most marked effect of all such fin operations, but the actual phenomena observed require some explanation. The anterior region of the shark body is somewhat flexible in a vertical plane as well as in the horizontal one. As a consequence of the dorso-ventral compression of the body in this anterior region, the whole of the head end can act in a similar manner to the pectoral fins, if necessary. In the absence of these fins, an attempt is therefore made to compensate for the negative pitching moment produced by the tail by raising the head. But as Fig. 7 has already shown, the equilibrium without the pectoral fins is still an unstable one, and a continuous correction of the angle of inclination of the head is required. The muscles (and nerve supply) of this region are not fitted for making such continuous readjustments, and there results an irregular path with vertical undulations. Sooner or later, in every experiment made by the author, the head seems to "over-correct" in the upward direction, and an enormous positive pitching moment is produced, far more than both the tail motion and the downward flexing of the head can correct. The anterior region of the body is in consequence tilted upward to such an extent that the head soon comes quite out of the water, and the fish swims in this curious position at about 45° to the horizontal, frantically endeavouring to drive its head below the surface. So long as it still goes on swimming this is impossible; ultimately the fish tires, and on stopping swimming naturally sinks below the surface once more. When swimming is resumed, however, the same phenomenon is repeated, and it requires a very long time for the fish to gain even an approximate control over its motion in a vertical plane. After a day or two, however, the muscles of the head-neck region are able to keep the fish on a slightly wavy horizontal path, though even then if the fish is disturbed the extra swimming impulse which results usually brings on the phenomenon once more.

That the pitching moment produced under such circumstances is adequate to explain the facts observed can be demonstrated from the wind-tunnel experiments as follows. If it is assumed that the negative pitching moment produced by the tail in normal swimming is equal to the positive moment produced by the pectoral fins at an angle of incidence of 8°, the graph (Fig. 8) shows that the value of this moment is about 0.01 in.-lb. Though it is impossible without an experiment to predict the moment which can be exerted by flexing the head in the vertical plane, the moment curve in Fig. 7 suggests that the change in value of this moment for an inclination of 10° is of about the same order of magnitude. But results not shown on Fig. 7 due to the large scale of the diagram, showed that at 35° inclination (positive angle of attack) the positive moment on the finless body was at least three times this amount, and that the gradient was rapidly increasing with increase in this angle of attack. At 45° the value of the positive moment would be more than four times that at 10°, and in order to counteract this the head would have to be flexed by an amount far more than that of which it is structurally capable.
Apart from a negative result on amputation of the first dorsal fin, the above experiments are in close agreement with the predictions from wind-tunnel observations on the model. The one negative result is doubtless due to the extreme flexibility of the body of the dogfish, and the difficulty of obtaining any accurate measure of the turning efficiency of the animal. It is for this reason impossible to obtain any true estimate of the relative parts played by the head movement and the dorsal-fin resistance in determining the turn. Some teleost fishes offer better objects for study in this respect, and amputations of the anterior erectile portion of the dorsal fin of the sunfish, *Lepomis auritus*, have amply confirmed the above deductions as far as this is possible for two such different forms. Removal of this portion of the fin also produces an increased rolling movement while swimming, but also reduces considerably the efficiency of a turn. There is here much less flexibility of the anterior region of the body, and the contribution of the dorsal fin to the turning forces is relatively much greater.

**DISCUSSION**

The fish body in the water, so long as it is at rest or moving in a straight line, must be subjected to a system of forces which are in stable equilibrium. The term “stable” used in this sense may refer to a system of statically stable forces, or simply to a set of forces which may be unstable over any very short interval of time, but continuously varied under the reflex control of the fish so as to produce over a longer period of time a sort of “steady state”. The stability for turning movements possessed by the dogfish deprived of its first dorsal fin (see Fig. 5) is of the first type, while the “hovering” of the labrid teleosts by the aid of the pectoral fins is really a “steady state”, since deprivation of its fins causes the fish to turn over on its back—the centre of gravity is above the centre of pressure when the fish is at rest. With a normal range of accomplishments in swimming, a fish may exist in at least three states of equilibrium. The experimental work in this paper has been largely concerned with the rectilinear glide, no swimming effort being produced. The state of active swimming demands a different relationship of the equilibrating forces, dealt with in the last section in considering the mechanics of the heterocercal tail. Finally, in a number of fishes, though not in the Selachii, there is a well-developed power of “hovering”—maintenance of a stationary position for long periods of time, which necessitates yet another system of forces in equilibrium.

The conditions of equilibrium in a glide and in active swimming are in themselves not constant, since the forces acting and their lines of action are not fixed, but vary with variation in the speed of the animal. The lift force and the pitching moment exerted by the pectoral fins varies approximately with the square of the speed; unless the moment produced by the heterocercal tail follows a similar law, increase or decrease of swimming speed must involve a change in the angle of incidence of the pectoral fins. The equilibrium of the living fish cannot be stated in terms of a constant system of forces.

Consider the equilibrium of the dogfish during a glide without active swimming. The heterocercal tail can only exert its negative pitching moment by virtue of its
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The fish may remain more or less horizontal in position, the normal opposing positive pitching moment produced by the pectoral fins must be reduced to zero. It is approximately true to say that if the pectoral fins are to exert no pitching moment they must produce no lift force. Since the lift of the tail and the fins must be zero, the weight of the body acting through the centre of gravity will cause the fish to glide in a downward direction. Actually, this downward glide produces the same effect as a small positive angle of attack, and it will be necessary for the pectoral fins to be inclined at a small negative angle of incidence.

It is possible that in a glide the pelvic fins may be flexed to produce a lift posterior to the centre of gravity and thus a negative pitching moment, but it is doubtful whether these fins are ever flexed sufficiently to enable the fish to glide horizontally. Inevitably, as the speed drops, the lifting forces decrease, and the fish sinks more rapidly.

Evidently the fins of the dogfish are adapted principally for continuous swimming. Only under these circumstances can the excess weight of the body be neutralised by the lift of the pectoral fins and the heterocercal tail; in addition the pitching moments exerted by these two members must balance.

It is interesting to speculate on the application of this problem of equilibrium to the primitive swimming chordate. The heterocercal tail seems to be almost a necessity to any form with a body only slightly flexible in the vertical plane, and having a specific gravity in excess of its surrounding medium. Doubtless it is for this reason that almost all the primitive swimming chordates we know have this characteristic asymmetry of the tail. The presence of pectoral fins to neutralise the negative pitching moment so produced is not essential. If the anterior region of the body is to some extent expanded laterally and capable of limited flexure in a vertical plane, it may be used as a source of lifting force, similar in every way to the use of the head region by a dogfish deprived of its pectoral fins. It is significant that most of the primitive forms possess such a lateral expansion. There is another point to be considered. A large head region, whether it be the concomitant of great development attendant upon specialisation for sensory and feeding purposes, or simply a development of "streamlining", is always accompanied by static instability, so that the continuous use of the head and anterior body muscles is needed to ensure rectilinear swimming. Probably the early chordates were very deficient in that respect; their swimming would be as irregular in its direction as the finless dogfish, or indeed the modern lamprey. With the evolution of paired lateral fin folds the first great step towards an efficient control would be accomplished; the foundation for the subsequent mastery of their liquid environment by the later fishes would be laid.

There is one group of forms which do not fit into this scheme, and apparently exist in defiance of these mechanical requirements. The agnathous Anaspida have a reversed heterocercal tail, as Kiaer's (1924) work has firmly established, and this fact seems to contradict all that has been said on the necessity for the more normal type of tail form. No pectoral fins are evolved in the Anaspida; the pectoral spines
which are present are quite insufficient to produce appreciable forces, and the general appearance of the body with its armour of vertically elongated scales is suggestive of inflexibility in the vertical plane. It seems inconceivable that these types alone among primitive “fishes” could have possessed an air bladder, or could be lighter than the water in which they lived. One suggestion is that these animals were surface swimmers, and not bottom living, as were almost all of their relatives. If this were so, and the front end of the body were to be just “awash” when swimming, the extra weight of this region out of water might compensate by a negative pitching moment for the positive moment produced by the reversed heterocercal tail. For what it is worth, the terminal position of the mouth in many of these forms offers a slight piece of additional evidence in favour of this hypothesis, while the absence of any trace of a dorsal fin is significant. Whatever reason one may suggest to account for these rather abnormal features, it is some consolation to the student of fish equilibrium to see that the group never attained any great success, and rapidly died out!

One point has only lightly been touched upon in this discussion. It is the problem of the “uselessness” of the pelvic fins, at least in these shark-like forms. These fins are never found in the most primitive chordates, though structures resembling, but not necessarily homologous with, the pectoral fins are frequently encountered. In part modified as claspers in chondrichthyan types, the fin area of the pelvic is never large, their general appearance suggesting that they are small posterior rudiments of the row of paired lateral fins represented in the Acanthodii. One possible function has been alluded to—that of producing a small negative pitching moment during a glide.

The evidence of amputation experiments, as well as that from the above wind-tunnel measurements, suggests that in most forms where the pelvic fins are small and placed posteriorly, their function is negligible. This remark, however, does not apply to the teleostean pelvic fin which gained a new and increasing importance in the course of the evolution of these forms. This study will be dealt with in a future paper.

If it is assumed that the pectoral and pelvic fins of modern forms arose as an originally continuous paired fin fold, it seems reasonable to assume on the basis of the above experiments that the original function of this structure was to control the pitching movements of the body. The useful portions of the fold for this purpose are the parts situated anterior to and posterior to the centre of gravity. Hence there is at least good functional reason for supposing that the areas in these two regions would persist while the intermediate portion would be lost. And, though dermal fin folds whose inclination is regulated by the vertical flexure of the body could be used for this control of pitching movement, it is when these fin folds develop their own more or less independent musculature that they become most useful. This musculature, thanks to the controllability of the system, need only be relatively little developed to increase the efficiency of vertical steering to an enormous extent. Later, in the Teleostei, an increasingly powerful pectoral musculature is developed for quite different, but no less important, reasons.
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SUMMARY

1. An attempt was made to determine the relationship of the fins to the equilibrium of the swimming dogfish.

2. Two factors at least are involved in this equilibrium; passive mechanical forces and reflex motions of the fins themselves. The part played by the automatic (passive) components was estimated by experimenting on a model of Mustelus canis mounted in a wind tunnel tested at a suitable air speed.

3. The equilibrium in the horizontal plane (yawing equilibrium—for turning movements) is unstable without fins, completely stable only in the absence of the first dorsal fin, and is neutral when all fins are present.

4. In the vertical plane (pitching equilibrium—for rising and diving turns) the equilibrium is unstable without fins, and this instability is greatly increased by the presence of the pectorals. The pelvics have little or no effect.

5. Stability and controllability are inversely related. The fish is comparatively stable in the horizontal plane, extremely controllable in the vertical plane. This fact is closely related to the flexibility of the body for lateral movements.

6. The results obtained in the wind tunnel were confirmed by amputation of the fins of the living dogfish.

7. The normal equilibrium of the swimming dogfish in the vertical plane is determined largely by the pectoral fins and the heterocercal tail.

8. The relationship of these facts to the problem of the evolution of the swimming chordates is considered.

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