

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

## II. THE ROLE OF THE PELVIC FINS

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(Received 18 March 1937)

(With Eight Text-figures)

### INTRODUCTION

IN a previous paper (Harris, 1936), the writer considered the equilibrium of a typical shark during gliding and swimming, particular attention being paid to the action of the fins in producing a statically stable progression. In the present and later papers of the series it is hoped to consider the part played by the different fin systems in fishes in general. The median and paired fins can be dealt with separately, since to a large extent they act independently. For example, the pitching equilibrium of the shark is largely dependent on the configuration of the paired fins, and is scarcely affected (at least during a glide) by the presence or absence of the median fins, while the yawing equilibrium is controlled almost entirely by the median fins.

The action of the paired fins in fishes offers many complex problems, and although the pectoral and pelvic fins should logically be considered together, such a discussion would be of an inordinate length. It was therefore thought better to deal with the action of each fin pair separately, even if this treatment entailed a slight overlap in the subject-matter of the separate discussions. Since the pelvic fins in most fishes are less actively motile than are the pectorals, their mode of action is more easily established, and these fins will be considered first in the series.

When one comes to study the literature on the function of the fins in fishes, it is surprising to find that very few observers have offered any opinion on the role of the pelvic fins. The explanation of this omission may be found in the fact that most of these studies have involved amputation of the various fins followed by observation of the effect on the general equilibrium. The difficulties in this method have already been referred to in the previous paper of this series; the power of the fish to compensate for such deficiencies by suitable action of the remaining fins is so great as to make the interpretation of these results very difficult. Monoyer (1866), working with *Cyprinus* spp., found little or no effect on amputation of the pelvic fins; Mayer (1866) came to the same conclusion for the shark, *Scyllium*. Duges (1905) also

obtained negative results with another cyprinodont, *Goodea*, and more recently Grenholm (1923) reported little or no disturbance of equilibrium following this operation on a number of species, including *Leuciscus*, *Cyprinus* and *Perca*.

Among those workers who obtained definite disturbances in equilibrium after removal of the pelvic fins, or who did hazard hypotheses concerning the function of these fins, Osburn (1906) gave a somewhat vague account of the role of both sets of paired fins being that of "guiding and balancing the fish when swimming, acting as brakes to stop the movement, preserving the stationary equilibrium, and producing forward and backward locomotion". No mention was made of the mode of action of the fins to produce these results. Schmalhausen (1916), basing his results on observation of intact living fish (chiefly on *Scyllium* and *Labrus*), came to the conclusion that the pelvic fins acted as vertical rudders, assisting a similar action of the pectorals. Breder (1926) suggests that these fins act in general as bilge keels and "auxiliary manœuvring instruments". He does give a rather more detailed account of their action in the stopping of the forward movement of *Esox*, but the mechanical basis of his explanation is somewhat unsatisfactory.

It is probable that many of the problems concerning the use of these and of other fins by the fishes can only be solved by a series of accurate and laborious hydrodynamical experiments. In the absence of such experiments, however, the present account is submitted as an approach to the problem from both the theoretical and experimental aspects. Only fishes approximating to the "normal" (i.e. torpedo-shaped) form will be dealt with here; specialized types which show considerable morphological changes in body and fins (rays, eels, *Pediculati*, etc.) will be omitted.

#### THE ROLE OF THE PELVIC FINN IN THE SHARKS

In almost all sharks the area of the pelvic fins is small compared with that of the pectorals. Magnan (1929) has published a large amount of data on the fin areas and positions in various fish species. From these it may be calculated that in ten species of sharks, the ratio of pelvic fin area to pectoral fin area has a mean value of 0.34. For a representative selection of bony fishes the measurements of the same author give a corresponding mean ratio of 0.70. Some measurements made by the present writer suggest that the difference may be even greater than these two ratios would indicate, since the precise proximal boundary of the shark pelvic fin is extremely difficult to define, and the effective fin area is probably less than Magnan's figures suggest. The wind tunnel experiments on a model of *Mustelus* (Harris, 1936) have revealed a further important correction factor. Fig. 1 shows the lift force on the fish model with various paired fin combinations. It is seen that the relationship between lift ( $L$ ) and angle of attack ( $\alpha$ ) is approximately linear, as in most aerofoils. It should therefore be possible from the slope of the lift curve,  $dL/d\alpha$ , to calculate the relative part played by the different fin areas in producing the lift force on the complete model. It is found that the lift contributed by the pelvic fins is only 0.092 of that of the pectoral fins. Yet the ratio of the areas of the two fins, even when

the claspers of the pelvics are excluded, is 0.20. The contribution of the pelvic fins towards the lift force is therefore less than half that which would be expected from their relative area.

This result is almost certainly due to the action of the pectoral fins in deflecting the stream of water meeting the pelvics—the “downwash effect”, as it is called in aerodynamics. Its presence can be established not only in the interaction of the two

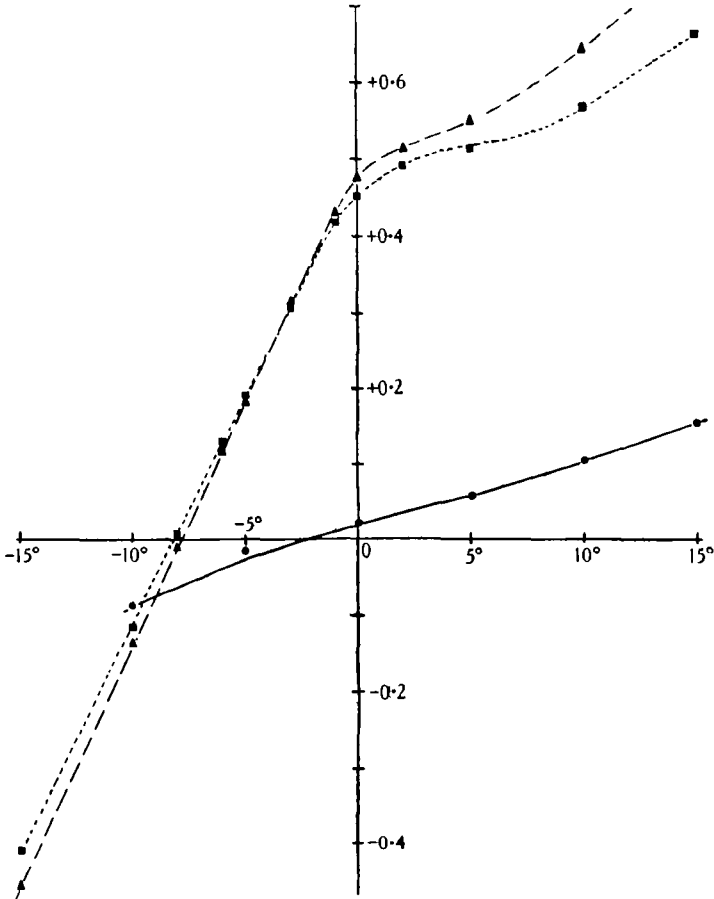


FIG. 1. Lift force on model of *Mustelus canis* in wind tunnel. Model without fins plotted as full line, with pectoral fins only as dotted line, and with pectoral and pelvic fins as dashed line. Ordinates, lift force in pounds; abscissae, angle of attack in degrees.

sets of paired fins, but also in the interaction of the anterior and posterior median fins. The stream meeting the anterior fin is deflected so that even when the two fins lie in parallel planes, the effective angle of attack of the posterior fin is not the same as that of the anterior fin. The change in effective angle of attack is expressed as a “downwash angle”, and there are various rules, theoretical and empirical, for calculating its magnitude at the tail plane of a typical aeroplane form. Unfortunately, none of them is sufficiently general to apply to an extreme case such as the present

one, where the "fuselage" (the fish body) is relatively large, and the aspect ratio of the pectoral fin (ratio of the fin breadth to its length along the body axis) is extremely low. Both Touissant's (1925) and Diehl's (1930) empirical formulae give impossibly high values for the downwash angle. Nevertheless, the magnitudes of these calculated values indicate that the downwash effect is probably a very significant factor in the action of the pelvic fins, and the relatively small part played by them is thus explained. Fig. 2 shows the (hypothetical) stream flow around the paired fin system in a dogfish, and illustrates the production of a downwash effect by the pectoral fin.

Since the size of the body is so large relative to that of the fins, it is probable that the stream of water incident upon the pectoral fins is not truly parallel to the direction of motion, i.e. there is a downwash effect of the body on the pectoral fin also to be considered. This doubtless explains the very low value obtained for the lift coefficient of these fins—about one-third of the value for a typical aerofoil.

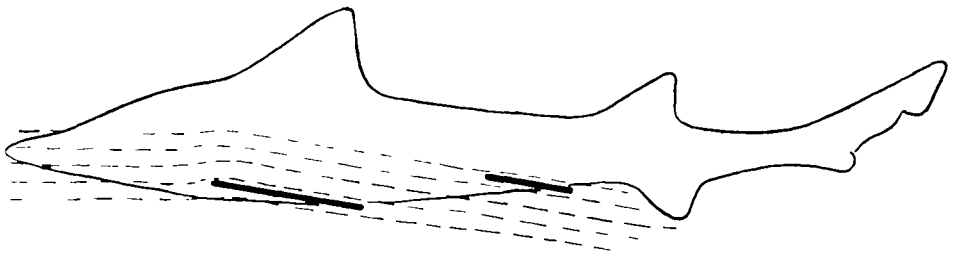


Fig. 2. A diagrammatic illustration of the "downwash effect" on the pelvic fins of *Mustelus canis*. Though the pelvic fin plane, represented as a heavy line, is parallel to that of the pectoral fin, the stream of water approaching the pectoral is deflected downwards so that the pelvic fin produces no vertical force.

The small importance of the pelvic fins in the equilibrium is entirely confirmed by the experiment of amputating these fins in a dogfish. Balance seems to be in no way disturbed; the fish is able to rise, dive and swim horizontally exactly as before the amputation. There is also no appreciable increase in rolling of the fish, so that the bilge keel action of the pelvics is apparently insignificant.

#### THE ROLE OF THE PELVIC FINS IN THE BONY FISH

In the shark it is possible with a large degree of accuracy to treat the pelvic fins as aerofoils with little power of independent movement other than that of inclination at various angles to the water stream, but this is not generally the case for the pelvic fin of the bony fish types. The actinopterygial fin is often a very mobile structure, capable of producing special types of motion (e.g. undulating movement) by virtue of the powerful muscles attached to the bases of the fin rays.

Although the palaeoniscoid fishes as a whole have paired fins which are already typically actinopterygial in form, those members on the line of evolution from

*Chondrosteus* to the modern sturgeon show a very close similarity to the selachian shark type, and a study of the fin movements and position in the living swimming sturgeons reveals an almost perfect resemblance in fin mechanism to that of the sharks. According to Magnan (1929) the density of the sturgeon is relatively high (1.05, in spite of the air bladder), and these fish stand in the same relationship to their fresh-water environment as do the sharks to their marine one.

The possession of an air bladder of relatively large size has undoubtedly assisted the bony fish in an upward migration into the middle waters, instead of cruising over the substratum, as do the sturgeons and many of the sharks. Though it is true that the equilibrium of such a form possessing an air bladder is hydrostatically unstable, nevertheless very little fin movement is required to keep the fish at a constant depth. Only very small vertical forces need be exerted, and the elaborate mechanism of pectoral "aerofoils" and a lifting heterocercal tail is no longer needed for the maintenance of a constant horizontal cruising plane. Concomitant with the loss of the heterocercal tail in evolution occurs a rapid and tremendous adaptive radiation of the pectoral fin form and function. (The reader is referred to a general paper by the writer (Harris, 1937) for a more expanded treatment of this topic.)

In the primitive bony fish, where the pelvic fins retain their posterior position, it is frequently found that they become capable of oscillating and undulatory movements. In the Holostei, *Amia* and *Lepidosteus* show a considerable power of undulating the pelvics as well as the pectoral fins, and the normal hovering movement in these fishes is controlled largely by the water currents produced by these undulating fins. These forms are slow and rather clumsy swimmers, and the development of the pectoral fins as powerful brakes, so typical of the later Teleostei, is not required.

Among the cypriniform fishes, the siluroids show a secondary approach to the sharks. Their specific gravity, as in most Teleostei, approximates to that of their environment, so that in order to swim close to the bottom they have simulated the mechanical effect of the heterocercal tail by the use of a large anal fin, placed relatively far back along the body. During the swimming oscillations of the body, this fin will continuously produce an upward force which will tend to push down the head. Correlated with this specialization there is an adaptation of the pectoral fin as an aerofoil, paralleling the pectoral fin mechanics of the sharks. This will be more fully dealt with in a later paper of this series; for the present, it is sufficient to say that the resemblance between the selachian and siluroid mechanics is sufficiently close for the pelvic fins to function similarly in both. Their main function is to produce a lift force, when this is required, and for this purpose they can trail the posterior border downwards at a steep angle. A similar elevating function may be attributed to the pelvic fins in the generalized cyprinoid and clupeoid fish types though in these, as in some siluroids and in all of the more advanced teleostean fishes, the pelvic fins are extremely flexible, producing depressing as well as elevating forces. Nevertheless, the pelvic fins are never so important in these primitive groups as they are in the percoid types, and amputation experiments show that they can be removed without impairing to any appreciable extent the equi-

brum or powers of locomotion of the fish. This is doubtless the explanation of the negative results of the writers quoted in the introductory section, results which have been substantially confirmed by the experiments of the present author on *Carassius* and *Leuciscus*.

The Haplomi exhibit considerable variations within the group, but in general there is a distinct parallelism in fin mechanics with the condition already described in the Holostei—compare, for example, *Esox* with *Lepidosteus*. The smaller members of this group employ extremely rapid undulatory movements of the fins in maintaining equilibrium while hovering.

Apart from a number of specialized groups, the rest of the Teleostei all tend to be similar to the percoid type, the pectoral fins being placed high up on the side of the body. Such pectoral fins are used largely as brakes; they are thrown out almost perpendicular to the long axis of the fish, the fin plane being almost, but not quite, vertical. In this position they produce a very large drag force and a small additional lift force. The lift force, as in the shark, is accompanied by a current of water which produces a large downwash effect behind the fin. Aerodynamical results have shown that the downwash effect of such an aerofoil placed high on the body surface is very much larger than for the case of a “ventrally” situated aerofoil. In such circumstances, there is an obvious advantage in having the pelvic fins moved forwards, where the effect of the downwash is not felt. But there is another still more important reason for the forward migration of these fins.

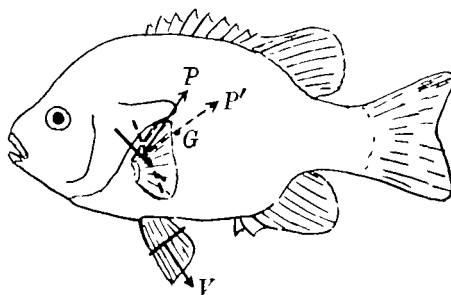


Fig. 3. Forces produced by the fins of *Lepomis auritus* during deceleration. The pectoral and pelvic fin planes are represented by the heavy lines.  $P$  and  $V$ , the resultant forces on the pectoral and pelvic fin pair respectively. Dotted line and force  $P'$ , condition during action of pectoral fins only, pelvic fins being held in “neutral” position.  $G$ , position of centre of gravity.

Fig. 3 illustrates the force on the pectoral fin of a typical percoid which is using these fins in order to stop quickly. It will be seen that the fin produces (a) a drag force, used to stop the forward motion, (b) a lift force, which tends to make the fish rise, and also (c) in some cases a pitching moment, whose magnitude and sign depend on the position of the pectoral fin centre of pressure with respect to the centre of gravity of the fish. The resultant force of the pectoral fin may be made to pass through the centre of gravity, as in Fig. 3,  $P'$ , in which case this pitching moment is zero, but there still remains the lift force which must be neutralized if the fish is to stop without rising through the water. Observation of the living fish shows that this rise does not occur on stopping, and it can be shown that the pelvic fins are largely responsible for the neutralization of this lift force.

Omitting for the moment the question of how this downward force is produced, let us consider its effect on the general equilibrium of the fish. If the pelvic fins are placed far back along the axis of the body, the downward force which they are

required to exert when the fish stops will tend to depress the tail and raise the head—i.e. to produce a positive pitching moment. This rotational effect can only be neutralized by lowering the position of insertion of the pectorals once again, or by reducing the braking effect of the pectorals, or by both methods. In both cases the braking efficiency will be considerably lowered. But if the pelvic fins are moved forward, then they will produce a much smaller positive pitching moment, and may even be made to give a negative one, if their resultant passes in front of the centre of gravity of the fish. The equilibrium of the two sets of paired fins during such a deceleration is diagrammatically represented in Fig. 3, the pelvic fins being shown in the thoracic position.

We may therefore conclude that if the insertion of the pectoral fin moves up the side of the body towards the dorsal surface, the pelvic fins will tend to move forwards. If the pectoral fins remain in their primitive ventral situation, the pelvic fins will always be found far back along the body.

One of the most striking exceptions to the above generalization is to be found in the exocoetid flying fish. Here, in spite of the extremely high position of the pectoral fins, the pelvics are still placed very far back along the body. In this group, however, all the forms are surface swimmers, and the problem of avoiding a rise during the stop does not exist. In point of fact, the spreading of the pectoral fins in the flying fish is the immediate preliminary to flight, and the posteriorly placed pelvics assist in producing a lift force. Many of these flying fishes with greatly expanded pelvic fins glide during their flight near to the surface of the sea, never rising to a great height above it. It is an interesting feature of this fin combination, that where the elevating structures are situated behind as well as in front of the centre of gravity, the static pitching stability may be very great.<sup>1</sup> As there is evidence that the air near the sea surface is frequently “bumpy” in the aeronautical sense (see Breder, 1930) this adaptation is of considerable value to the fish.

Among the extinct crossopterygian order of the Coelacanthini, a Triassic genus, *Laugia groenlandica*, has been described by Stensio (1932). This fish is of great interest, since, although its fins were of the archipterygial form characteristic of the group, the pectoral fins had moved high up on the side of the body. In this respect it is peculiar among the Coelacanthini. It is significant, therefore, to find that it is also peculiar among the group in being the only one to have moved forward the pelvic fins until they are anchored on to the pectoral girdle in the same manner as they are in the modern percoids. These forms undoubtedly possessed an air bladder—indeed, its ossified outline is clearly shown in the fossils of this particular species—and the conditions of equilibrium of the fish were therefore exactly similar to those governing the modern bony fish equilibrium. In other genera, where the pectoral fins are still low down on the side of the body, the pelvic fins are in their primitive posterior position.

If we assume that the pelvic fins in these fishes are used to produce a downward force, neutralizing the upward lift of the pectorals during a stop, the theoretical considerations above provide an explanation for the position changes in the pelvic

<sup>1</sup> I am indebted to Prof. Klemm for this suggestion

fins during evolution. It is, however, necessary to show that the pelvic fins are capable of producing this downward force, and also to demonstrate that the fins are actually used in the manner suggested.

The method by which the pectoral or pelvic fins of a shark can be made to exert a downward force is so obvious as scarcely to need description; it is illustrated in Fig. 4*a*, *b* and *c*. If the anterior fin rays are depressed or the posterior ones are

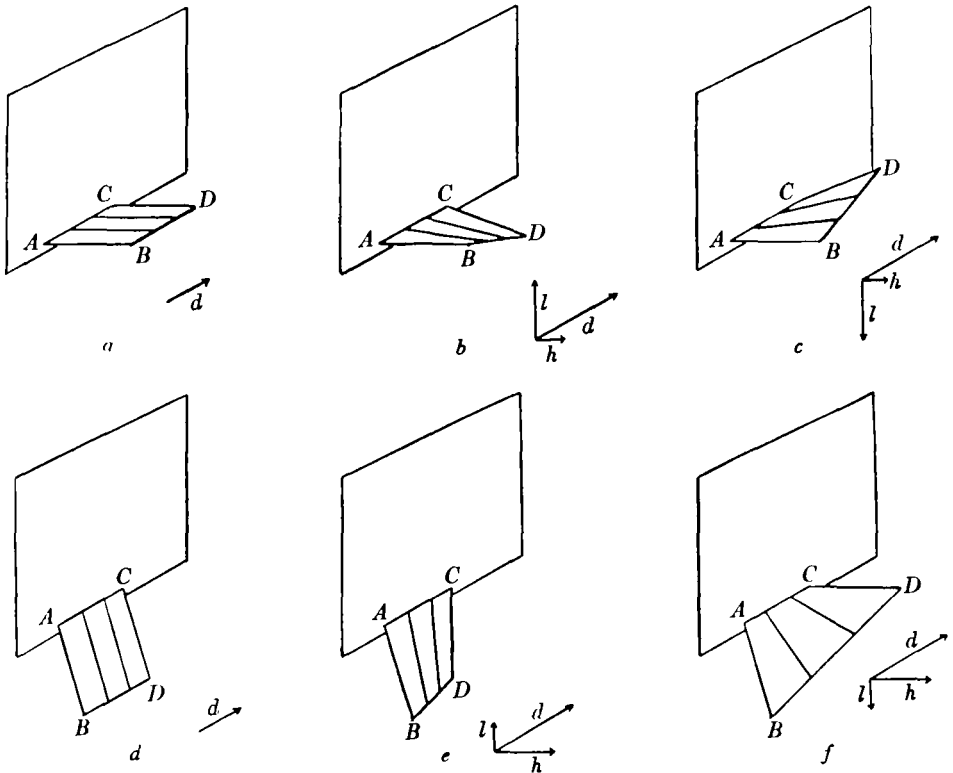


Fig. 4. Diagrammatic representation of the method of producing lift and downward forces by means of the pelvic fins *a*, *b*, *c*, shark type of fin; *d*, *e*, *f*, percoid type. *AB*, direction of anterior fin ray; *CD*, that of posterior fin ray of the pelvic fin. The vertical plane represents the plane of symmetry of the fish; *l*, *d*, *h*, lift, drag and horizontal (lateral) force produced by each position of the fin when the fish is gliding forwards. Figs 4*a*, 4*d* with fin in neutral position; 4*b* and 4*e*, fin producing an upward force; 4*c* and 4*f*, producing a downward force. Perspective representation.

elevated, the effect produced will be that of a plane surface, inclined downwards at its anterior border (Fig. 4*c*). This will exert a downward force component, and in addition will increase slightly the drag of the fin. It will also be appreciated from the diagram that, since the anterior and posterior fin rays of the fin are not parallel, but skew, that there will be a lateral force component. This lateral component is very small in the case of the horizontal fin of the shark, but is of considerable importance in the inclined fins of most bony fishes, in which it may be used to produce a rolling moment about the longitudinal axis.



The plane of the pelvic fins of most advanced teleosts is not horizontal, but is inclined in the manner shown in Fig. 4*d*. The fin rays are normally coplanar, the plane containing them being parallel to the long axis of direction of motion of the fish, so that there is no force exerted by these fins even when extended, except for an extremely small drag force. From this "neutral" position of the fin, vertical and lateral forces are produced by altering the inclination of the *posterior* fin rays. The first fin ray is normally held in a fixed position by the action of its powerful arrector muscles, which are used mainly to erect the fin membrane, and not to incline it. If the posterior fin rays are now inclined downwards towards the vertical position, there will be a lift force on the fin, as well as a lateral (outwardly directed) component (Fig. 4*e*). Conversely, if the posterior fin rays are elevated towards the horizontal plane, a downward force (together with a lateral inwardly directed component) will be produced, as in Fig. 4*f*. Careful observation of any species of percid fish, in which these movements are readily seen, will show that the latter type of fin movement is far more frequently encountered, suggesting that the main use of these fins is to produce a downward force. The existence of the neutral position of the fin explains the curious fact that the fish in many cases swims with its pelvic fins closed or erected indifferently.

The above description of the motion of the pelvic fins is in all essential respects similar to that of Schmalhausen (1916), who suggested that these fins act as "vertical rudders". He did not, however, appreciate the fact that they were usually employed to produce the downward force, and consequently regarded them as accessory structures which merely assisted the pectoral fins to produce the same type of result. He therefore missed the fact that the two pairs of fins are normally employed to produce opposing vertical forces, and not to reinforce each other.

One of the species of North American sunfish, *Lepomis auritus*, is a very suitable subject for the experimental study of the role of the pelvic fins in the percid. Normally, the fish swims either with the pelvic fins closed against the surface of the body, or extended in the "neutral" position described above. In backing movements, the pelvic fins are always closed, as, if this were not so, the bending of the flexible posterior border of the fin would result in a considerable resistance to the backing motion.

The role of the pelvic fins is well shown in one of these fishes in which the pectoral fins have been amputated. When swimming with the pelvic fins extended, such a fish tends to swim with the head tilted slightly downwards, as a result of the combined downward and drag force of the pelvic fin pair. Should it roll over to one side while swimming, the pelvic fin on the opposite side is immediately extended in the manner illustrated in Fig. 5. The resultant of the downward and lateral forces rapidly rights the tilting of the body, as shown. Normally, when swimming on an even keel, both pelvics will be always extended simultaneously. If one pelvic fin is

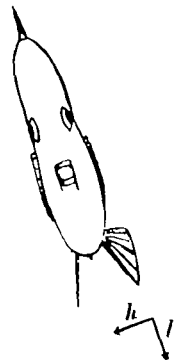


Fig. 5. Front view of *Lepomis auritus* producing a rolling moment by the action of one pelvic fin. *l*, *h* as in Fig. 4.

amputated, the fish rolls to the uninjured side when the remaining fin is extended.

If both pelvic fins of a *Lepomis* are amputated, whenever the fish is brought to a stop by extending the pectoral fins, it rises vertically upwards during the deceleration, and there is a noticeable lack of steadiness in the motion. (Breder (1926), has also remarked on the slow and uncertain nature of the stop under these conditions.) These results can be explained by the fact that the pitching moment produced by the pectoral fins can be varied by changing their angle of attack, and that this moment may be zero if the resultant force on the fin passes through the centre of gravity. This condition has been illustrated in Fig. 3. Such an adjustment, however, will be difficult to keep constant during the stop, since the lift/drag ratio, and therefore the slope of the resultant, probably varies with the speed. In any case, the lift force exerted by the pectoral fins will cause the rising upwards of the fish while stopping. Fig. 6 shows the motion of such a fish during a stop produced by extending the pectoral fins. Though the body remains horizontal throughout, the stop is more

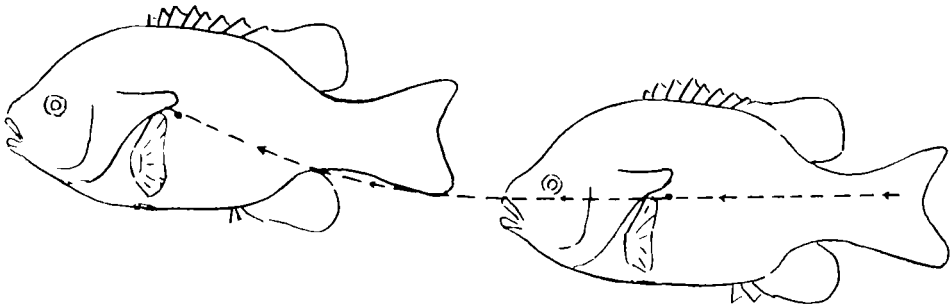


Fig. 6. *Lepomis auritus*, stopping by extending pectorals. Pelvic fins amputated, and although body remains horizontal, fish rises during the stop.

slowly accomplished, more uncertain, and is accompanied by the rise which has already been described.

A further example of the use of the pelvic fins in the normal fish has been observed when the fish is gliding in a slightly upward direction. The pelvic fins are then extended without any other fin action, and the nose becomes tilted downwards so that the direction of the glide is now horizontal.

In the fast-swimming percoiid types where the pectoral fins are used almost entirely as brakes, as in the Carangidae and Scombridae, the pelvic fins are employed to a very great extent in securing the equilibrium of the fish during swimming. During periods of observation of fishes at Tortugas, using the diving helmet, the writer has frequently observed schools of *Caranx crysos* swimming past, controlling their vertical movements entirely by the use of the pelvic fins, the pectorals being held closely pressed to the side of the body during the whole period of observation. These fish seem to use their pelvic fins also for steering, though it is difficult to be certain that gross body movements are not involved, as the carangids rarely glide. Certainly rising, diving and tilting movements can be completely controlled by the

pelvic fins, the pectorals in this group being largely used for sudden stops, and occasionally for sharp turns. (It is rare for the scombroid species found at Tortugas to live for any length of time after being caught, and amputation experiments on them were therefore out of the question.)

If, as the above experiments suggest, the function of the pelvic fins in these percoid types is largely that of producing a downward force, it might be expected that the muscular anatomy of the pelvic fin would show some correlation with this specialization. To move in the manner illustrated in Fig. 4, it is essential that the anterior border of the fin should be held as rigid as possible; the magnitude and direction of the force is then controlled by the action of the abductor and adductor muscles of the posterior fin rays. If the downward force is more commonly needed and more important, then the adductor muscles of these fin rays should show a corresponding enlargement and specialization.

Fig. 7 is a diagram, redrawn from Grenholm (1923), of the pelvic fin adductor musculature in *Perca*. It will be seen that attached to the upper side of the sixth fin ray is a very powerful adductor muscle, quite distinct from all the remaining adductor fibres—the so-called *Musculus extensor proprius*. From its origin, direction and insertion, this muscle can have only one function, that of raising the posterior fin border. On the lower (abductor) side of the fin the musculature is more normally arranged, and there is no differentiation of any such specialised muscle bundle to the posterior fin rays. The *M. extensor proprius* is well developed in all percoid fishes, but is only occasionally encountered in more primitive types. There is no trace of it in the *Percesoces*, which confirms the suggestions made above of the pelvic fin function in flying fishes, that of assisting, instead of neutralizing, the lift of the pectorals.

Powerful adductor musculature to the pelvic fin is occasionally found even among the more primitive groups. Grenholm (1923) reports such a case in the scopelid, *Synodus*, where the adductor and abductor musculature to the pelvic fins is very strongly developed, though there is no definite *M. extensor proprius*. It seems probable from the form of the members of this group that there is a pronounced tendency to use these fins for much of the manœuvring. The writer, however, can only speak from experience of one species, *Synodus foetens*. Here the greatly enlarged pelvic fins play a large part in controlling the swimming movements, and amputation of these fins results in disorganizing all the normal steering, rolling and pitching movements. The pectoral fins in these fish are rarely extended, except for the purpose of stopping the forward movement.

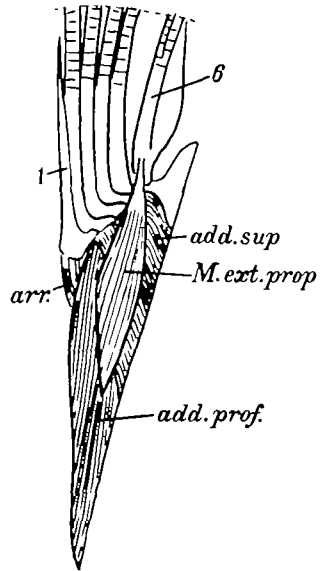


Fig 7. Diagram (after Grenholm, 1923) of the adductor musculature of the pelvic fin of *Perca* 1, 6; first and sixth fin rays. *arr.* arrector muscle to first fin ray; *add. sup.* and *add. prof.* adductor superficialis and profundus muscles; *M. ext. prop.* the extensor proprius muscle.

According to Grenholm, there is no trace of a *M. extensor proprius* in *Gadus*. Though less closely related to the Percoidei, the position of the pelvic fins suggests a similar function in both groups, and it is perhaps a little surprising to find no suggestion of this specialized muscle. The general musculature of the pelvic fin is, however, quite strongly developed, and is probably capable of fulfilling all the necessary functions of fin movement.

#### THE PELVIC FINS AS BILGE KEELS

It has been suggested by many students of fish equilibrium that the pelvic fins function as bilge keels (see for example Breder, 1926). Such bilge keels are used in ships to lessen the extent of the rolling motion, and the somewhat similar position of the pelvic fins has been largely responsible for the supposition that they function similarly. Bryan (1900) has published an excellent account of the action of the bilge keel in preventing or reducing rolling. It must be realized that the midship section of most modern vessels is approximately square, the bottom of the hull being only slightly convex. It has been found that a pair of long narrow keels, placed at the lower "corners" of this square section, and projecting perpendicularly from the side of the ship at this point, reduces the rolling by several degrees. At any other position on the side or bottom of the hull the keels are apparently less effective in producing this result. Since the geometrical position and the direction of projection of the pelvic fins corresponds rather closely with these requirements, the analogy between the two was reasonable. But, as Bryan showed, the reason for placing the bilge keels at those two positions is that by virtue of the square sectional shape of the hull, these positions have the maximum tangential velocity during a roll.

The cross-section of the fish at the region of the pelvic fins is, however, elliptical. The corresponding positions of maximum tangential velocity during rolling movement are not at the sides of the fish, but at the ends of the long axes of the ellipse—in other words, at the top and bottom of the body section, along the mid-dorsal and mid-ventral lines. The dorsal and anal fins of the fish must therefore be regarded as the main anti-rolling devices, and their favourable position and large size is such that the contribution of the pelvic fins to this purpose must be quite negligible in comparison.

Experiments on *Lepomis* have shown that amputation of the pelvic fins does not increase the rolling by an appreciable amount, whereas amputation of the dorsal and anal fins results in a very considerable degree of rolling during swimming and gliding movements. The pelvic fins under such circumstances are frequently fully extended, but are quite unable to reduce the rolling by any very large amount. It may therefore be stated definitely that the pelvic fins are of no importance in reducing rolling movements in the normal percoid fish. Experiments on sharks (see page 35) and also on cyprinodont fishes have led to precisely the same conclusion.

The above statements are not intended to be a denial of an *active*, as opposed to a *passive*, action of these fins on rolling. It will be seen from Fig. 5 that a pelvic

fin extended in the manner shown will produce a rolling moment which can be used to restore the equilibrium of the fish. The rolling moment so produced can only exist during the forward motion of the fish, and is the result of active flexing of the surface of the fin membrane. This use of the pelvic fins is very commonly met with, especially in deep bodied forms where the arm of the rolling couple is long, and the rolling moment thus exerted is fairly large. In the chaetodont fishes, which frequent rocky areas on the shallow regions of the sea floor, the pelvic fins are used to a considerable extent for tilting the fish to one side when passing through narrow inclined rock crevices. The angel fish, *Pomacanthus arcuatus*, has frequently been observed by the writer cruising around these rocky boulders, tilting its body from one side to the other solely by the differential action of the two pelvic fins.

## APPENDIX

An approximate mathematical treatment of the equilibrium of a fish during deceleration is given below. The forces concerned in the equilibrium are the same

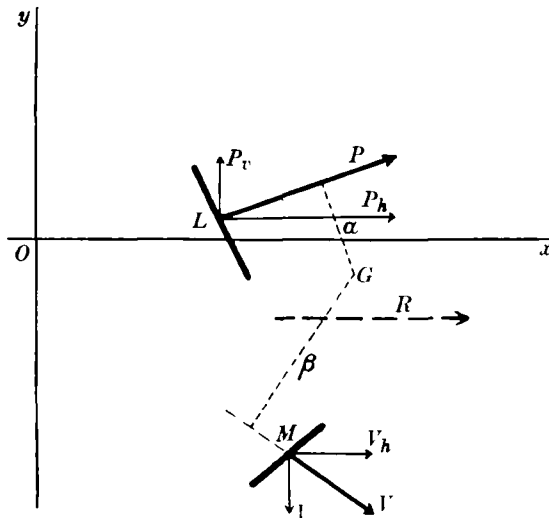


Fig 8 Equilibrium of the pectoral and pelvic fin forces during a stop with fins extended. The planes of the fins are represented by heavy lines.  $L$ ,  $M$  the centres of pressure of the pectoral and pelvic fin respectively,  $G$  the centre of gravity. For detailed description, see text.

as those shown in Fig. 3, but for the sake of clearness, Fig. 8 has been drawn to show only the system of forces, the fish body and fins being omitted.

Let  $Ox$ ,  $Oy$  be co-ordinate axes, where  $O$  is any point on the longitudinal axis of the fish,  $Ox$  is parallel to the direction of motion of the fish, and  $Oy$  perpendicular to this axis, and lying in the plane of bilateral symmetry of the body. Let  $L$ ,  $M$ , the positions of the centres of pressure of the pectoral and pelvic fins respectively, be represented by the co-ordinates  $(p, q)$  and  $(v, w)$ , and let the co-ordinates of the centre of gravity of the fish be  $(a, b)$ . The forces  $\mathbf{P}$  and  $\mathbf{V}$  represent in magnitude and direction the resultant forces on the two sets of fins at any instant during the

stop,  $\mathbf{P}_v$ ,  $\mathbf{V}_v$  being the vertical (lift) components of these two forces, and  $\mathbf{P}_h$ ,  $\mathbf{V}_h$  the horizontal (drag) components. We shall assume that the fins on either side of the fish are equally extended, and therefore that  $\mathbf{P}$  and  $\mathbf{V}$  are the total forces exerted by each fin pair. The lateral components of the fin forces (perpendicular to the plane of the diagram) will be equal and opposite, and we need only consider the equilibrium of the forces which lie in the plane of the diagram. If the fish continues during deceleration to move in a horizontal plane, the following equations represent the conditions for equilibrium.

The equilibrium of the vertical forces gives

$$\mathbf{P}_v = -\mathbf{V}_v \quad \dots\dots(1)$$

(forces acting upwards are considered positive).

For the horizontal forces, we have

$$\mathbf{P}_h + \mathbf{V}_h = \mathbf{M}f. \quad \dots\dots(2)$$

( $\mathbf{M}$  here is the mass of the fish, subject to a correction factor for the apparent additional mass contributed by the moving water around the fish body, and  $f$  is the deceleration of the fish at the instant considered. The drag of the fish body,  $\mathbf{R}$ , will be assumed as a first approximation to pass through the centre of gravity of the fish. The term in  $\mathbf{R}$  will therefore not appear in the moment equilibrium equations (3) to (6) below.)

The equilibrium of the pitching moments about the centre of gravity gives

$$\mathbf{P}_v(a-p) + \mathbf{V}_v(a-v) = \mathbf{P}_h(b-q) + \mathbf{V}_h(b-w), \quad \dots\dots(3)$$

or, from (1) and (3) above, we have

$$\mathbf{P}_v(v-p) = \mathbf{P}_h(b-q) + \mathbf{V}_h(b-w). \quad \dots\dots(4)$$

Now if the pectoral fins are ventrally placed, as in most primitive bony fishes, we may assume that, approximately,  $q=w$ , and equation (4) becomes

$$\mathbf{P}_v(v-p) = (\mathbf{P}_h + \mathbf{V}_h)(b-w). \quad \dots\dots(5)$$

It can be seen that the terms  $\mathbf{P}_v$ ,  $(\mathbf{P}_h + \mathbf{V}_h)$ , and  $(b-w)$  in equation (5) are all positive in sign, and therefore the remaining term,  $(v-p)$ , must also have a positive value. This implies that the pelvic fins must be situated behind the pectorals. Also, since  $\mathbf{P}_v$  is small compared with  $(\mathbf{P}_h + \mathbf{V}_h)$ ,  $(v-p)$  must be large compared with  $(b-w)$ , and the horizontal distance from the pectoral to the pelvic fins will be large. This is the condition found in the trout and pike.

Let us consider now the other extreme, where the pectoral fins have risen until they are as high as the position of the centre of gravity. We may now substitute in (4)  $b=q$ , and the equation becomes

$$\mathbf{P}_v(v-p) = \mathbf{V}_h(b-w). \quad \dots\dots(6)$$

The expression on the right-hand side of equation (6) has only  $\frac{\mathbf{V}_h}{\mathbf{P}_h + \mathbf{V}_h}$  of its value in equation (5). Since  $\mathbf{V}_h$  is always small compared with  $\mathbf{P}_h$  (the drag force being chiefly contributed by the pectoral fins),  $\frac{\mathbf{V}_h}{\mathbf{P}_h + \mathbf{V}_h}$  is also small, and  $(v-p)$  must be

much less than in equation (5). The value of  $v$  must therefore be decreased, and the pelvics approach the pectorals in position.

If the pectoral fins are raised above the ordinate of the centre of gravity, then  $(b-q)$  is negative, and not zero, as assumed in deriving (6). It will be seen that under these circumstances the pelvics may move forward until  $(v-p)$  is negative, i.e. may be jugular in position.

It is frequently found that the pelvic fins may be jugular in position even when the pectorals are situated below the level of the centre of gravity of the fish. This can be explained if we assume that the resistance,  $\mathbf{R}$ , of the fish body acts along a line which does not pass through the centre of gravity. If its line of action is along the ordinate  $x=r$ , and the magnitude of the resistance is  $\mathbf{R}$ , it can be seen that the effect on the pitching equilibrium is to add to the right-hand side of equation (4) an amount  $\mathbf{R}(b-r)$ . This term may be positive or negative, the former if the line of action of the resistance passes below the centre of gravity, the latter if it passes above. In the new form of equation (4), if

$$\mathbf{P}_v(v-p) = \mathbf{P}_h(b-q) + \mathbf{V}_h(b-w) + \mathbf{R}(b-r), \quad \dots\dots(7)$$

and  $(b-r)$  is negative, then it can be seen that  $(v-p)$  may be negative even if  $(b-q)$  is positive. The pelvic fins may be jugular even where the pectorals are not above the centre of gravity. A further complication which may produce the same result can occur if the resistance force possesses a vertical as well as a horizontal component. This frequently happens if the body is not symmetrical about a horizontal plane.

#### SUMMARY

1. The paired fins of fishes are largely concerned with the production of vertical forces, and thus principally affect the pitching (rising and diving) equilibrium.
2. In the sharks the pelvic fins increase to a small extent the static stability for pitching movements. Nevertheless, the relatively large area and forward position of the pectoral fins preponderates over the influence of the pelvics on the pitching stability, so that the contribution of the latter is very small. This is borne out by amputation experiments.
3. In the bony fishes, the development of the actinopterygian fin leads to a much greater mobility of the fins. In consequence, the pelvic fins of the bony fishes exhibit a considerable adaptive radiation.
4. In the percoid fishes the use of the pectoral fins as brakes produces a lift as well as a drag force. It is shown that the neutralization of this lift force by a downward force produced by the pelvic fins necessitates the forward migration of the latter. If this migration did not take place, the fish would either tilt upwards or rise bodily during the stop.
5. The dynamical basis for this migration of the paired fins is considered in an approximate mathematical treatment of the equilibrium during the stop.
6. This hypothesis is confirmed by amputation experiments, and also by the occurrence of a convergent fin migration in the Coelacanthidae. The absence of the forward pelvic fin migration in flying fishes also affords indirect support.

7. There is no evidence to suggest that the pelvic fins can function as bilge keels, though they may be used actively to produce a rolling moment.

In addition to the sources of assistance acknowledged in the previous paper of the series, the author is indebted to the Carnegie Institution of Washington for the opportunity of a visit to their laboratory at Dry Tortugas, which made possible the observation of a number of forms in their natural environment.

#### REFERENCES

- BREDER, C. M. Jr. (1926) *Zoologica*, N.Y., **4**, 159.  
— (1930). *Copeia*, p. 114.  
BRYAN, G. H. (1900). *Trans. Instn nav. Archt.*, Lond., **42**, 198.  
DIEHL, W. S. (1930). *Rep. U.S. Nat. Adv. Comm Aer* p. 293.  
DUGES, A. (1905). *Science*, N.S., **22**, 798.  
GRENHOLM, A. (1923). Uppsala Univ. Årsskr. 1923.  
HARRIS, J. E. (1936). *J. exp. Biol.* **13**, 476.  
— (1937) *Publ. Carneg. Instn*, Papers from Tortugas 1937, **31** (in the Press).  
MAGNAN, A. (1929). *Ann. Sci. nat* **12**, 5.  
MAYER, P. (1866). *Mitt. zool. stat. Neapel*, **6**, 217.  
MONOYER, F. (1866). *Ann. Sci. nat.* (5), **6**, 5.  
OSBURN, R. C. (1906). *Science*, N.S., **23**, 585.  
SCHMALHAUSEN, J. J. (1916). *Russk. zool Zh.* **1**, 185.  
STENSIO, E. A. SON (1932). *Medd. Grønland*, **83**, no. 3.  
TOUSSANT. Quoted from MONTEITH, C. N. (1925). *Simple Aerodynamics*. U.S. Air Service.