The two previous papers in this series have dealt almost exclusively with the movements of fish, such as the eel or the butterfish (Centronotus gunnellus) whose bodies are long and flexible and which exhibit very well-defined waves of muscular contraction when the fish are travelling through the water. The present paper deals primarily with pelagic fish which differ from the eel in two important respects; they possess well-developed caudal fins and the ratio of body length to body width is much smaller.

When observed visually, a whiting, and still more a mackerel, appears to swim by executing a series of transverse vibrations of the caudal fin. When recorded photographically, however (see Gray, 1933, Figs. 5 and 6), the movements of the body are found to be of the same fundamental type as those of the eel, for in both cases waves of curvature pass alternately down each side of the fish. In the whiting the amplitude of these waves remains quite small until the posterior region of the tail is reached, where it increases more abruptly than is the case in the eel. The effect of these waves is such as to maintain the leading surface of the body inclined obliquely backwards relative to the head (see Pl. I). A similar orientation is also maintained by the leading surface of the caudal fin itself, and since the area of the fin is considerable, it is of interest to know how far it plays an essential rôle as a propellant surface or how far the surfaces of the body itself are of predominating importance. It is well known that fish with badly lacerated tail fins can swim actively, and the observations of Breder (1926) show that amputation of the caudal fin of Scardineus does not markedly affect the speed of propulsion. The inference is that the body itself forms the main propulsive surface of the fish. During the present series of observations, the caudal fin has been removed from a variety of forms—e.g. rudd, whiting, perch, and in each case the results have confirmed those of Breder. For technical reasons it has not been possible to observe the effect of amputation of the caudal fin on fish moving at a high speed, but it seems fairly clear that the “cruising” speed is not appreciably reduced. At the same time amputation of the fin results in a marked modification in the fish’s movements,
and this modification throws considerable light on the fundamental functions of the caudal fin in the intact fish.

Pl. I, figs. 1–16, shows the successive forms of a normal whiting during one complete transverse stroke of the body. It can be seen that all parts of the body (posterior to the pectoral fins) including the tail fin are directed obliquely backwards during the whole of their transverse movements; these movements are essentially of the same type as those seen in the eel (see Gray, 1933). Pl. II, figs. 1–12, shows the movements of the same whiting after amputation of the tail fin.

Text-fig. 1 A. Movements of the hind end of the body of an intact whiting relative to the head. The small displacements at the base of the muscular tail are omitted.

Text-fig. 1 B. Movements of the hind end of the body of a whiting after amputation of the caudal fin—also relative to the head.

These drawings are constructed from actual photographs. The numerals indicate arbitrary but successive positions during one complete cycle and are each comparable to the corresponding number shown in Text-fig. 2, where they are enclosed in circles.

It is obvious that the two sets of figures differ markedly from each other. In Pl. II it can be seen that at no time does the body show the double flexure so typical of the intact fish, for in the absence of a tail fin, the tail and body of the fish lie along a straight line at the moment when each transverse stroke is half completed (fig. 6). As the tail moves beyond the central point of its stroke (fig. 7) its leading surface, instead of being directed obliquely backwards, is now directed obliquely forwards towards the head of the fish (figs. 7–12). If we define the movements of the tail relative to the head of the fish, the difference caused by the presence or absence of a tail fin can be seen from Text-fig. 1.
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This effect of the tail fin is clearly attributable to the force which it generates when it is set in motion from the extreme positions of its displacement. At these positions the surface of the fin is approximately at right angles to the direction in which the muscles lying at the anterior end of the muscular tail are tending to move it, and consequently it exerts a maximum resistance to movement through the water. As the tail fin moves towards the central axis of its transverse movement it is no longer at right angles to its direction of motion, but its transverse velocity is higher than that of any other parts of the fish, so that its resistance is still high. The tail thus represents a surface of high resistance lying posteriorly to the region of contraction and it causes the intervening part of the body (which is flexible) to bend into an arc with its convex surface towards the direction of motion. The nett effect of the tail fin is thus to make the region of the body posterior to the point of muscular contraction lag behind all those parts which lie between itself and the point of contraction—consequently each group of muscles as it comes into play is always operating on a region of the body which is so orientated as to cause a backward thrust when this region is set in motion. The effect is exactly parallel to that produced by attaching a flat plate to the end of a thin steel wire and oscillating the proximal end of the wire through a small angle. Without a flat plate each part of the wire moves in practically the same phase as any other part—but when the plate is present the distal end of the wire lags behind the proximal end and a series of movements is set up which is strikingly similar to the normal movements of a fish's body—whereas without the attached plate the movements of the wire are comparable to those of the fish from which the tail fin has been removed.

In passing it may be noticed that unlike the eel, the form of the body of a whiting is substantially affected by the resistance of the water—whereas in the eel this is only true for the posterior end of the body. The whole of the effective movements of the whiting's body (when the caudal fin is present) are comparable to the movements of the posterior end of the eel only, for in both cases the body is operated on anteriorly by a region of active muscular contraction and posteriorly by the pressure of the water against the body and against the tail fin.

Reference to Pl. I, fig. 2, in Gray (1933), shows that as a wave passes over the surface of an eel the mechanical conditions change as the posterior of the body is approached. The movements of the central region of the body are controlled by two muscular waves, one lying towards the head of the animal and the other lying towards the tail on the other side of the body. Soon after the wave crest has passed the tip of the tail, however, the latter region is no longer the seat of muscular activity, and consequently the region of the body lying posterior to the next wave approaching on the opposite side will be subjected to forces different from those controlling the movements of regions of the body lying further forward towards the middle of the body. In the former case, the forces acting on the hind end of the body are (1) the active muscular changes going on at its anterior end, (2) the pressure of the water against the surface of the tail. By reference to Pl. I of the present paper it can be seen that it is only under the latter conditions that the amplitude of the movements of a whiting's (or mackerel's) body are significantly large.

In view of the very pronounced mechanical effect which follows amputation of the caudal fin, it is surprising that this operation does not affect, to a greater
degree, the powers of locomotion of the fish. In the absence of a caudal fin the movements of a whiting’s body are symmetrical about the longitudinal axis of the fish and it might, therefore, be supposed that no nett propulsive force would be obtained. During the first half of any given transverse cycle the surface of the body moves with its leading surface directed backwards relative to the head (Pl. II, figs. 1–6), but during the second half of the cycle the body surface is directed forwards relative to the head (Pl. II, figs. 7–12). It might be imagined that the forward thrust exerted during the first half of the cycle would be exactly neutralised during the second half of the cycle by the backward thrust of the anteriorly directed leading surface. That such a neutralising effect does not occur, is obvious from the fact that the fish moves forward—and the reason is forthcoming from an examination of the movements of the body, not relative to each other, but to the surrounding water or a fixed point in the environment.

Text-fig. 2 A shows the track of the distal end of the caudal fin of an intact fish through the water. It will be noticed that the two halves of each half-cycle of transverse movement are symmetrical. When moving from left to right the horizontal component of the first half of the stroke is approximately identical with that of the second half of the stroke. The axis of symmetry is the line (ab) along which the head of the fish is travelling—and the tail sweeps evenly on both sides of this line—being accelerated as the line is approached, and checked in speed as the line is past.

After the removal of the caudal fin, however, the track of the distal end of the fish is strikingly different (Text-fig. 2 B). In this case, the amplitude of the whole stroke of the tail is usually somewhat greater than that characteristic of the intact fish, but the two halves of the stroke are no longer symmetrical in respect to the surrounding medium although they are symmetrical in respect to the head of the fish. From Text-figs. 1 B and 2 B it can be seen that whilst the tail is moving from position 1 to position 5 in respect to the head (Text-fig. 1 B), the tip of the tail has moved from position 1 to position 5 in respect to the surrounding medium (Text-fig. 2 B); similarly, on moving from position 5 to position 8 in respect to the head, the tail has moved from position 5 to position 8 in respect to the medium. It will be noticed that the track from 1 to 5 is substantially longer than from 5 to 8, and that it is during the first and longer part of the whole transverse movement that the tail is meeting the water at such an angle as will produce a forward thrust. As far as this phase of the transverse movement is concerned, the essential difference between the movements of the intact fish and the tailless fish is the marked absence of phase difference between the base and tip of the tail in the absence of the tail fin, consequently the angular and transverse velocity of the tip of the tail is greater than in the intact fish. As described elsewhere (Gray, 1933) the thrust exerted by any region of the fish’s body depends among other things on the transverse velocity of the region and on the angle which it makes with the longitudinal axis of motion. By removing the tail fin the transverse velocity of movement is increased but the “pitch” angle of the body is increased also—so that the two effects more or less neutralise each other.
Text-fig. 2 A. Track of the posterior tip of an intact whiting. The dotted line $ab$ indicates the axis of motion along which the head of the fish is travelling. Note that the movements of the tail are symmetrical about this line. The arrows indicate the points at which the tip of the tail lies in line with the median longitudinal axis of the head (see photographs 3, 9, 15 in Pl. I, and positions 3 and 7 in Text-fig. 1 A). The numerals in circles correspond to the numerals in Text-fig. 1. The dots along the sinusoidal path of motion show the position of the tip of the tail at successive and equal intervals of time as shown by a series of photographs.

Text-fig. 2 B. Track of the posterior tip of the whiting after amputation of the caudal fin. The arrows show the positions at which the tail is in line with the longitudinal axis of the head (see photograph 6 in Pl. II, and positions 5, 11 in Text-fig. 2 B). Note the asymmetry of the two phases of the movement through the water. The numerals correspond to those shown in Text-fig. 2 B. Note also the asymmetrical path of the tail through the water.
During the second phase of the transverse movement (from position 5—position 8 in Text-fig. 1), however, the tail begins (in the absence of a caudal fin) to encounter the water which is flowing past the sides of the fish. This water is moving backwards relative to the head, whereas the tail is moving forwards relative to the head—consequently the speed of movement of the tail through the water is checked during the second phase of its stroke, and the orientation of the tail—relative to the head—is maintained by a movement of the anterior part of the tail and of the head relative to water (see Pl. II, figs. 8–12) and not—as in the normal fish—solely by a movement of the posterior part of the tail through the water. It is clear that by exerting a mechanical resistance to transverse movement through the water, the caudal fin of the whiting maintains the necessary phase difference between successive regions of the muscular body and tail and thereby enables the whole of the energy of the muscular contractions to be expended in a smooth symmetrical manner.

After amputation of the caudal fin, the movements carried out by the tail of a whiting relative to the head are those characteristic of a comparatively short flexible rod oscillating about a fixed base and are, in fact, almost indistinguishable from those which can be induced in the body of a dead fish (without caudal fin) when the body is oscillated about a point lying towards the base of the muscular tail. An examination of Pl. II and Text-fig. 1B reveals very little evidence of a transmitted wave along the muscular tail. From Pl. I, however, it is clear that a well-defined wave is present when the caudal fin is present—and a precisely similar wave is seen in the case of the dead fish when, with caudal fin, the body is oscillated about the base of the tail. These facts suggest that the transmission of the waves along the body of a normal fish are controlled by mechanical factors. It is clear that when the muscles (lying on one side of the base of the muscular tail) contract, their energy can be transmitted mechanically along the body of the fish just as such energy can be transmitted along the length of an elastic wire. The energy is transmitted in the form of tension by the stretched skin and muscles of the leading side of the body. If the muscles lying nearer to the tip of the tail are to be usefully employed they must liberate their energy in phase with that of the mechanical wave. When the mechanical wave reaches any given point it first tends to store energy at that point by bending the body into a convex curve—and then this energy is subsequently liberated as the tension is released. If, therefore, the muscles at any point are to supplement this mechanical cycle it follows that they must begin to contract at the moment when a similar shortening process is being induced by the mechanical wave. This would occur if the stimulus to contract were automatically induced by a stretching of the muscle itself. Such a proprioceptive mechanism is well defined among other vertebrate types and would account for many otherwise unrelated facts.

The form of the body of a dead whiting which is subjected to artificial oscillation at the base of the tail is in striking contrast to that exhibited by the body of an eel. The body of an eel when subjected to transverse oscillations is readily thrown into a series of curves comparable to those seen in the living fish, except for the fact
that the amplitude of the waves shows a decrease instead of an increase as the waves approach the posterior end of the body. This difference is clearly due to the long and flexible body which is unable to transmit energy mechanically for any considerable distance. As far as can be inferred from the present investigation, the differences seen in the form of the body during normal motion in the eel and in the whiting are due chiefly, if not entirely, to mechanical causes. In both cases a contraction is initiated towards the anterior end of the body and on one side; some of the energy is transmitted mechanically towards the hind end of the body by the stretching of the muscles which lie between the active region and the caudal fin. As each successive region is mechanically stretched, so it begins to liberate energy by contraction of its muscles and the energy so released supplements that travelling down the fish mechanically from parts lying nearer towards the head. The

![Diagram](image)

Text-fig. 3. Diagram showing that if two constant forces are generated at the surface of a fin—one normal to the surface (OP) and the other tangential to the surface (OD), then with decreasing angle of inclination (θ) between the surface and the axis at right angles to the direction of motion of the fish (ab), the propulsive component (OT) of the normal force increases, whereas the transverse resistant component (OQ) decreases; on the other hand, as the value of θ decreases, the transverse resistant component (OR) of the tangential force increases, whilst its backward component (OS) decreases. Probably at the extreme positions of its displacement the dominating rôle of the caudal fin is due to the resistant components, whereas at the centre of the swing the propulsive components are much more important. At present it is impossible to measure the forces OP and OD—they probably vary in absolute and relative magnitude at different phases of the stroke.

differences seen in the two types of fish are due to (1) the greater flexibility of the eel’s body, (2) the relative shortness of the body of the whiting.

From the point of view of general efficiency the body of the whiting exhibits certain advantages over that of the eel. Firstly, the anterior end of the body undergoes transverse movements of very small amplitude only, so that the track of the head through the water is very nearly straight. The anterior end of the body represents therefore a stream-lined surface travelling forward with very slight resistance. Secondly, the powerful muscles lying at the base of the muscular tail are contracting almost isometrically and their energy is being expended well towards the distal end of the body where the angle of inclination of the body to the path of motion is considerably less than is the case further forwards—it may be remembered that it is only the forward component of the pressure exerted by the body against the water which propels the fish forwards (see Text-fig. 3).
THE CAUDAL FIN AS A PROPELLER.

So far the whole of the effects produced by the caudal fin are attributable to the resistance which it offers to transverse movement through the water, but it is impossible to consider these effects without reference to the role of the fin as a propeller. It is true that a fish deprived of its caudal fin can move with relatively undiminished speed, but this does not indicate that the fin has no propellant effect in the normal fish. Like every other part of the posterior end of the body, the caudal fin is moving transversely to and fro through the water and at the same time is being rotated towards and away from the axis of motion. As shown elsewhere (Gray, 1933) for the body surface of the eel, the essential condition under which the caudal fin can act as a propulsive surface is that its surface should be inclined at an acute angle to its own path of motion. If this condition is fulfilled the fin will generate both a propulsive force and a resisting force just as in the case with every other part of the fish's body (see Gray, 1933, Fig. 21). At present it is impossible to give even relative values to these forces, but if it be assumed that (when a fin is travelling at a constant angle to its own surface and at a constant velocity) a given ratio exists between (1) the pressure of the fin against the water, and (2) the viscous drag along the surface of the fin, then it can be shown that both these forces affect the efficiency of the fin both as a propeller and as a means of controlling the position of the tail relative to the head (Text-fig. 3). The precise effect of each will depend on the angle between the fin surface and the forward axis of movement of the fish. Thus in Text-fig. 3 it is clear that the smaller is this angle $(90° - \theta)$ the greater is the extent to which the resisting force of the fin is derived from the pressure exerted by the water normal to the surface of the fin—and to a less extent to the viscous drag of the water along the surface of the fin.

The only circumstances under which the fin could exert no propulsive force would be when its surface is travelling at right angles to or parallel to its own direction of motion. The former condition is probably fulfilled when the fin lies towards the extreme position of transverse displacement, whilst the second condition can only be obtained when the fin is highly flexible and can set itself parallel to its own direction of motion; in all other cases there must exist a propulsive thrust.

Although the removal of the caudal fin does not substantially reduce the forward rate of movement, it is illegitimate to assume that the propulsive thrust from the fin is negligible in the intact animal, for it has been shown that amputation of the fin induces far-reaching changes in the movements of the remainder of the body relative to the surrounding water. A preliminary attempt to estimate the propulsive effect of the tail fin of the whiting was carried out as follows. A series of vertical rods was so mounted in a metal frame that each rod moved harmonically with the amplitude characteristic of different levels of a whiting's body; the ends of the rods were then inserted into the body of a dead whiting. By rotating a handle, the body of the fish was forced to transmit a series of waves identical with those seen in the normal living fish, and for a given frequency of waves the current produced

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1 For these observations I am indebted to Mr G. Varley.
in a tank of water was determined. The caudal fin was then removed and the current again measured. Although the method of measuring the current was not free from criticism, the results suggest that approximately 40 per cent. of the propulsive thrust from a whiting is derived from the caudal fin.

It is of interest to note that just as the propulsive thrust represents the forward component of the pressure of the fin against the water, so the transverse component of this pressure plays its part in adding to the resistance offered by the fin to transverse movements, so that the biological functions of the fin are very clearly linked together, just as is the case with the surface of the body itself. If the area of the body surface is large in comparison to that of the fin, the rôle of the fin may be relatively insignificant as in the eel, but in the pelagic type of fish the posterior region of the muscular tail is comparatively narrow and tends to present a convex surface to the water, whereas the tail fin is relatively large and presents a flat surface to the water. In the latter case the fin probably plays an increasingly important rôle as a propeller just as it plays an increasingly important rôle by virtue of its resistance. Until a very accurate method is devised for measuring the currents produced by various types of tail fin it is dangerous to speculate on the effect produced by variations in the shape of the caudal fin.

**SUMMARY.**

1. Amputation of the caudal fin of a whiting does not substantially reduce the cruising speed of the fish, but it alters the type of movements of the hind end of the body relative to the head of the fish and to the surrounding medium. These changes result in an unsteady type of movement through the water.

2. The caudal fin maintains the normal phase difference between the movements of successive regions of the fish's body and operates mechanically by virtue of its high resistance to transverse movements. The presence of the fin enables the whiting to keep the leading surface of its body directed obliquely backwards during both phases of its transverse movements and thereby to exert a steady pressure on the water.

3. The difference in the form of the muscular waves which pass over the bodies of an eel and of a whiting is due to mechanical differences in the length and flexibility of the bodies.

4. In the absence of a caudal fin, no muscular waves pass down the tail of a whiting, and it is probable that in all fish the transmission of a muscular wave is dependent on a simultaneous transmission of a mechanical wave. As each muscle is stretched mechanically, it is automatically excited to muscular contraction.

5. Probably about 40 per cent. of the thrust produced by a whiting is produced by the surface of the caudal fin, but when the fin is removed most of this loss is made good by the changes automatically induced in the movements of other parts of the body.
REFERENCES.


EXPLANATION OF PLATES.

PLATE I.
Successive photographs of a normal whiting (*Gadus merlangus*). Note that the leading surfaces of the body and of the tail fin are directed obliquely backwards. Note also the well-defined region of curvature passing backwards towards the tail of the fish. In figs. 1–7 the tail is moving to the right, in figs. 8–12 it is moving to the left.

PLATE II.
Successive photographs of the same fish as is shown in Plate I after amputation of the caudal fin. In photograph 1 the stump of the tail is deflected to the right to its maximum extent. Note that the anterior region of the fish is only slightly displaced transversely in photographs 1–6, but as soon as the leading surface of the tail begins to be directed obliquely forwards (photograph 7), the base of the muscular tail is displaced to the right whilst the tip of the tail moves to a markedly less extent than in the first half of the stroke (photographs 1–6).
GRAY—STUDIES IN ANIMAL LOCOMOTION (pp. 386—400).
GRAY—STUDIES IN ANIMAL LOCOMOTION (pp. 386—400).