

## CAUDAL FIN AND BODY MOVEMENT IN THE PROPULSION OF SOME FISH

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### INTRODUCTION

Some of the problems still outstanding in the field of fish locomotion have been reviewed by Bainbridge (1961). A number of these require for their further elucidation a more detailed knowledge of the precise form of movement of the body and the caudal fin during locomotion. This is particularly so in considering the relationships between power output, drag and speed; in assessing the efficiency of the undulatory movement in imparting energy to the water; and as a basis for further work on the nature of the flow pattern over the surface of the body and the caudal fin.

Two distinct ways of considering the theoretical relationships between power, drag and speed appear to be available. Either the hypothetical thrust derivable from the moving body surface may be calculated and equated to the calculated drag to give a value for velocity; or the potential muscle power may be calculated and similarly equated to the calculated drag. This second approach was adopted by Gray (1936), who made theoretical calculations comparing power output of the musculature with drag at the body surface for a dolphin and a porpoise. The discrepancies revealed by these calculations led him to postulate an ability on the part of such creatures to preserve a greater proportion of laminar flow over the surface than might be expected on ordinary hydrodynamical considerations. This type of approach has since been somewhat modified and used by Bainbridge (1961) to calculate the theoretical speeds of some smaller fish. By adopting rather different power factors than Gray these calculations have resulted in theoretical speeds not at all out of accord with those measured for the dace, trout and goldfish (Bainbridge, 1958*a*). Some of the larger fish and smaller mammals would, however, still seem to require either an even larger power factor or some abnormal hydrodynamic effect to account for their measured speeds.

Confirmation of these findings may come from the first, more purely theoretical approach of equating the calculated thrust derivable from the undulating body surface and the theoretical drag engendered by the same surface. The gamut of body movements resulting in locomotion ranges from ostraciiform, where only the extreme terminal part of the body is moved laterally, to anguilliform where the whole body is thrown into at least one complete sine wave. Breder's (1926) separation of these two categories of movement and also a third, carangiform, is perhaps a little misleading. While ostraciiform and anguilliform movements are most distinctive there is a whole range of intermediate types too continuous and varied to comprise the single class carangiform. It is within this series, including most of our common freshwater fish,

that a more precise description of the swimming movements is most required if any accurate calculations are to be based upon them. Gray (1933*a*) gave the first basic treatment of this problem for anguilliform movement and his work has been followed up with greater refinement by Gadd (1952) and Taylor (1952). At the other end of Breder's series Parry (1949) has made a satisfactory mathematical treatment of dolphin movement by considering the flukes as the only propulsive element and Gero (1952) has treated the rather ostraciiform-like swimming of the barracuda similarly. In the intermediate range, however, few calculations have yet been published. Lighthill (1960) sets out the mathematical treatment for a relatively simple type of carangiform movement but he neglects the lateral oscillations of the head and the fact that no part of the body really passes along the mean line of progression.

It is clear that for any satisfactory application of these, as yet largely theoretical approaches to the problem of carangiform swimming, it is necessary to have a much more precise knowledge of the extent and variability of the lateral movements of the body and the relationship of these to the speed of forward movement. It is the intention of this paper to provide some such description as basic information to enable a mathematician or hydrodynamicist to embark on the subsequent calculations.

#### EXPERIMENTAL METHOD

The observations reported here were made by means of the 'Fish Wheel' apparatus described in Bainbridge & Brown (1958). Visual observation of the swimming movements of various specimens over long periods proved extremely valuable. Permanent records of such movements were obtained by two electrically driven 35 mm. Vinten ciné cameras. These were linked by a flexible drive to ensure that exposures were synchronized on the two films. They were so arranged as to photograph the fish from above and from the side simultaneously. Eastman Tri-X panchromatic safety film was employed with illumination from 6 Siemens 275 W. photo flood lamps. The film was normally run at 50 frames per second with a shutter angle of  $10^\circ$ , giving an exposure time of  $1/1800$  sec. The films taken were usually analysed directly using frame-by-frame projection on to a screen. Appropriate measurements of different parts of the swimming movement could readily be made from such projected pictures, reference marks fixed to the wheel and photographed by both cameras acting as a scale. Occasionally prints were made of some sequences of pictures and some of these are reproduced in Pl. 1.

#### OBSERVATIONS

##### (1) *General description*

During steady, fairly fast, straight locomotion, forward progression is effected entirely by lateral movements of the body and the caudal fin. Dependent to a certain extent on the forward velocity, the paired pectoral and pelvic fins and the dorsal fin are usually closely pressed to the body. The median anal fin remains more or less extended during this type of swimming but its propulsive significance cannot be very great. With gradually diminishing velocity first the dorsal fin and then the paired fins can be seen to rise from the body. How far these fin movements are passive and how far active is not easy to judge. The pectoral fins, especially, are exposed to the water

flow in such a way as to be pressed by its movement on to the body. The dorsal fin in the goldfish, however, arises largely from the mid-line behind the hump on the middle of the body; in this position it is not likely that antero-posterior water currents would press it to the body, yet it is largely so positioned during swimming. Lateral water movements resulting from the undulations of the body might nevertheless do so.

The lateral propulsive movements of the body are in the form of a wave which travels, with increasing amplitude, from the front end of the body to the rear. The amplitude is at a maximum at the most posterior edge of the caudal fin. The most anterior tip of the snout does not move in the straight mean path of progression but oscillates about this with a moderate amplitude. No point on or in the fish's body seems to move forward on, or parallel to, the mean path of progression. The whole body in fact generally executes a sinuous path through the water.

A closer examination of the caudal fin while these lateral movements are taking place reveals a complexity of detailed movement not perhaps at first appreciated (Bainbridge, 1958*b*). Considered dorso-ventrally in the vertical plane the fin can be seen to bend regularly during the cycle of beating, so that, as shown, for example, in Pl. 1 for the dace (*Leuciscus leuciscus*), the upper and lower margins of the tail may lead and the centre lag behind. Sometimes, however, this state of affairs is reversed and the centre of the tail leads with the dorsal and ventral margins lagging. Imposed upon this dorso-ventral curvature is an antero-posterior curvature in the horizontal plane. This is of such a nature as to sustain a positive angle of attack relative to the path of movement of any section of the tail through the water at most points in the cycle of beating. This antero-posterior curvature is not to be confused with feathering, as it has precisely the opposite effect to this in continuously maintaining the possibilities for forward thrust. Finally, it may be observed that while these bending changes are taking place the whole area of the caudal fin presented to the water is varying. This regular increase and decrease in size is frequently distributed asymmetrically relative to the mean path of progression as the fin moves laterally relative to this. It appears associated with changes in the transverse speed of fin movement as will be discussed below.

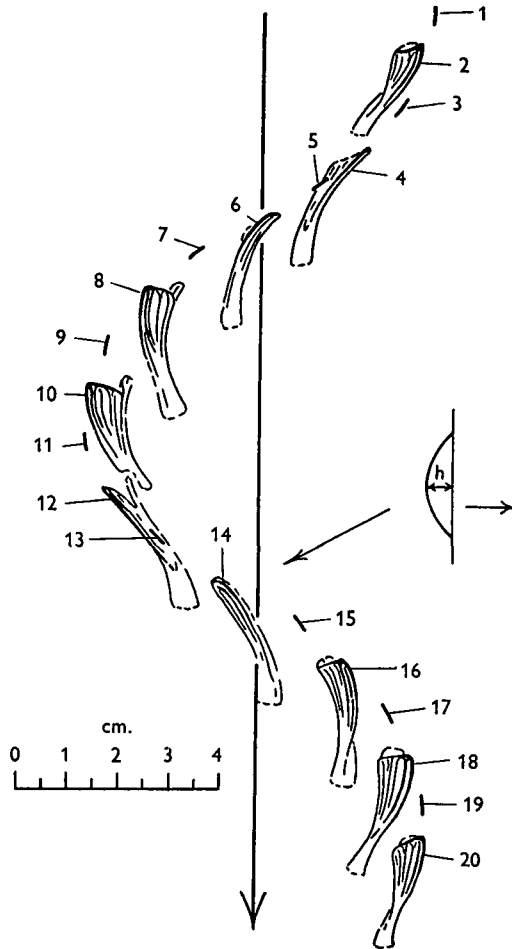
These various aspects of the body and fin movement lend themselves to separate and more detailed analysis and it is now proposed to treat each of them in turn.

### (2) *Dorso-ventral bending of the caudal fin*

Text-fig. 1 is a reconstruction of the movement of a dace caudal fin made from successive frames in a length of ciné film. It shows a series of positions of the tail as seen from above during a single cycle of tail movement. The tail is drawn in detail, at half scale, in alternate positions only. The mean path of progression of the fish is indicated by the straight central line and the direction of swimming by the arrow. The serial tail positions read from 1 to 20. The nature of the curvature of the tail is again displayed in this diagram. To first sight it is somewhat exaggerated by the fact that the amplitude of the movement of the upper edge of the tail exceeds that of the lower edge by an appreciable degree. This type of sculling motion is most common in fish swimming at only a moderate speed. The true amount of curvature is most readily assessed in this series in frames such as 6 or 14 where the upper edge of the fin is more or less directly above the lower edge. The inset shows a reconstruction to scale of the

posterior view of the edge of the tail at one of these moments and perhaps allows a readier appreciation of the degree of curvature.

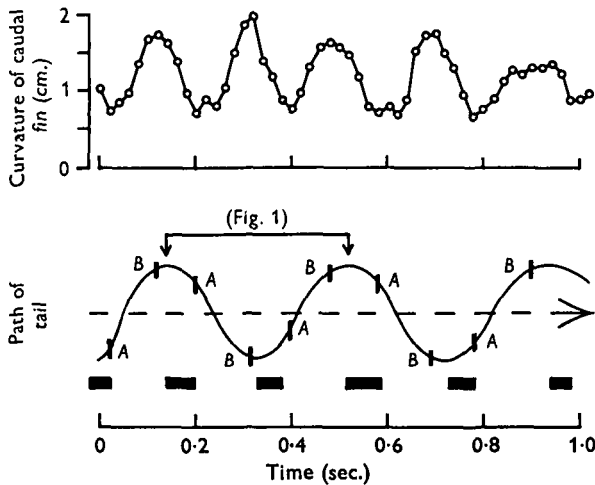
An assessment of the amount of the curvature can be made by measuring the height of the arc formed by the tail fin over the chord joining the upper and lower edges of the fin, i.e.  $h$  in the inset in Text-fig. 1. Making due allowance for the obliquity of the tail, a series of these measurements for the dace is given in Text-fig. 2. The upper line



Text-fig. 1. Reconstructed sequence of positions of the caudal fin of a dace (*Leuciscus leuciscus*) as seen from above. The fish, 30.0 cm. in length, was swimming at a forward speed of 48.0 cm./sec. in the direction of the arrow. Successive positions are at  $\frac{1}{60}$  sec. intervals. The tail is drawn in detail, at half scale, in alternate positions only. The inset shows, to scale, the amount of curvature of the tail when seen from behind.

indicates the variation in the height of the arc, the lower line the position of the tip of the tail in the cycle of beating at the time the measurement of curvature was made. The fish, as shown by the arrow, is moving from left to right in the diagram; the position of the sequence of frames illustrated in Text-fig. 1 is indicated in Text-fig. 2 by the two vertical arrows on the lower line. Text-fig. 2 shows that at no time does the tail offer a plane surface to the water. The amount of curvature is at a minimum when

the tail has moved about a quarter of the way from the extreme outward position on one side of the mean path of progress towards the extreme position on the other side. This point of minimum bending is indicated on the lower (path of tail tip) line by the letter *A*. The amount of curvature of the tail is at a maximum a little more than three-quarters of the way from the outward position of the tail on one side to the corresponding position on the other. This point of maximum bending is indicated in Text-fig. 2 by the letter *B*.



Text-fig. 2. Extent of dorso-ventral bending in the vertical plane of the caudal fin of the dace in Text-fig. 1 and its correlation with the lateral position of the tail. *Upper line*: amount of bending. *Lower line*: path of tail as seen from above. *A* indicates positions of minimum bending, *B* indicates positions of maximum bending. The fish moves from left to right in the figure. For further explanation see text.

The precedence of the upper and lower edges of the tail means that they reach the limit of their lateral movement before the centre of the tail. There is consequently a phase during the cycle when they are starting to move back towards the mid-line of the body while the centre of the tail is still moving away from it. This is not readily appreciated from Text-fig. 1. It results in a certain drop in tension in the fin itself and is especially noticeable in the goldfish. One of its effects is to put the tail into a series of rather irregular folds. These can be detected in the photographs and their position in the cycle of beating is indicated in Text-fig. 2 by the solid bars below the line indicating the path of the tip of the tail. They are thus seen immediately to precede the point of minimum curvature of the tail (indicated by *A*).

### (3) *Antero-posterior bending of the caudal fin*

As well as the dorso-ventral bending in the vertical plane that has just been considered, the caudal fin is at the same time undergoing an antero-posterior bending in the horizontal plane. This curvature is an extension into the tail of the lateral movements of the more anterior part of the body. The propulsive oscillations of the body, passing antero-posteriorly, increase in amplitude and finally impart these corresponding lateral movements to the caudal fin itself. Thus a continuous series of waves

passes into the fin and throws it into the sequence of curves shown in Pl. 1. As the waves are increasing in amplitude the posterior part of the body and successively more posterior parts of the caudal fin do not pass along the same line of motion through the water. Each part of the body and the fin is held at an angle to its line of motion through the water. This angle, the angle of attack, is of course of the utmost significance in determining the propulsive attributes of the whole system.

From tracings of successive positions of the caudal fin and the posterior part of the body it is possible to reconstruct the mean path of movement of the tail through still water. When this reconstructed mean path is then superimposed upon individual tracings or photographs of the caudal fin it becomes possible to see how the varying antero-posterior curvature of the tail is related to this movement. It further provides a convenient means for measuring the angle of attack of different parts of the caudal fin at various points in the cycle of beating.

Table 1. *Angles of attack, at successive  $\frac{1}{50}$  sec. intervals, of goldfish and dace tails during steady forward swimming*

Goldfish			Dace		
Tip of caudal fin	Centre of caudal fin	Caudal peduncle	Tip of caudal fin	Centre of caudal fin	Caudal peduncle
7	20	24	9	5	18
12	24	-27	15	17	11
12	0	7	20	20	15
-6	-9	11	-30	0	7
8	9	21	0	17	16
12	20	15	15	25	-21
12	23	-6	25	-28	12
8	-20	10	-19	0	4
0	0	7	11	9	12
Mean positive angle 14°			Mean positive angle 13°		

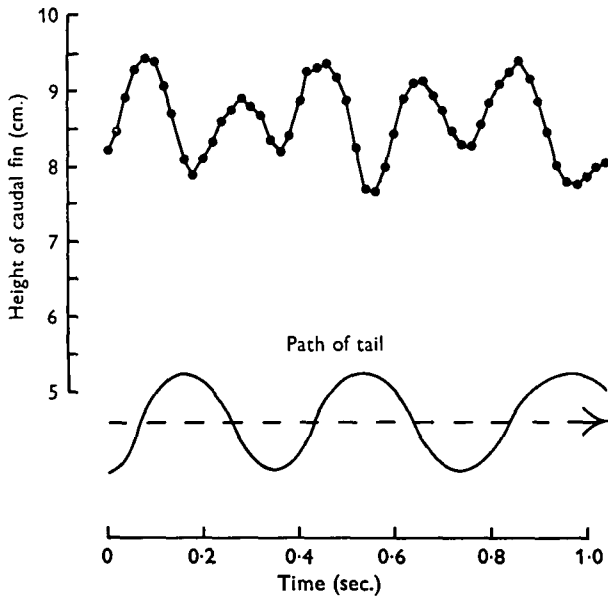
Two sets of such measured angles of attack, for a goldfish and a dace, are given in Table 1. The nine lines of figures in the table give for each fish the angle of attack at successive  $\frac{1}{50}$  sec. time intervals for three separate regions of the tail: the posterior tip of the caudal fin, the centre of the fin and the caudal peduncle. The sign of the majority of these measurements shows that a forward thrust is being developed. Those angles of attack giving a retarding force are indicated by a negative sign and are printed in heavy type. They are seen to lie diagonally in the table and occur as each successive part of the tail reaches the extreme lateral position in the cycle of beating. This sequential appearance in time ensures that there is no instant when all parts of the tail are simultaneously giving no positive forward thrust. By the time the posterior tip of the caudal fin is at the extreme lateral position and is giving no thrust, the peduncle is already well into the next phase of movement and is again generating thrust by moving in the opposite direction.

The mean of all the measured positive angles of attack for the goldfish is 14°, that for the dace is 13°. These are values which will result in the maximum possible thrust (i.e. lift) being obtained from the tail if it is considered as an inclined plate. The exact significance of these measurements is, however, further dependent upon possible movement (relative to the tail) of water displaced by the oscillatory movements of the

body. The measured angles given here have been determined by examining the recorded position of the tail relative to its reconstructed path through still water. Secondary water movements resulting from the lateral movement of the body must to some extent complicate the situation. An attempt to determine these and assess their significance is about to be made.

(4) *Area of the caudal fin*

As may be seen from the lateral views in Pl. 1, the varying curvature of the tail imparts to it distinctive outlines at different points in the cycle of movement. As well as changing in outline, however, measurement of the height of the fin (from its most



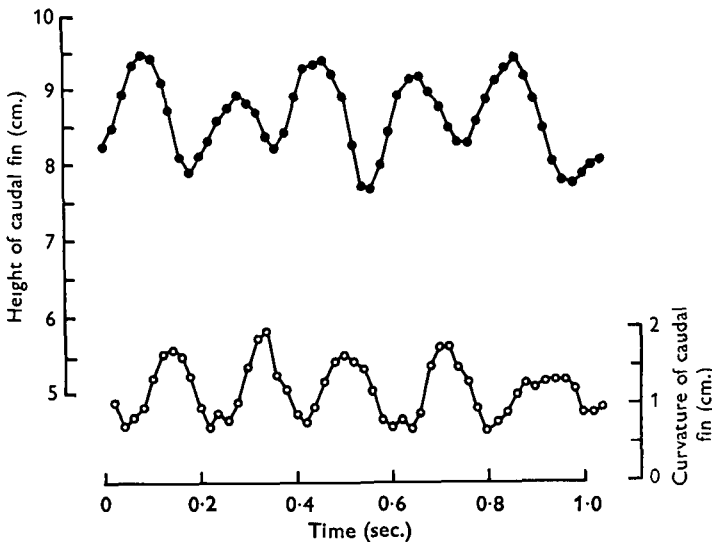
Text-fig. 3. Fluctuating apparent height of the caudal fin of the dace in Text-fig. 1 as seen from the lateral viewpoint. *Upper line*: height of the caudal fin. *Lower line*: path of tail as seen from above.

posterior ventral point to its most posterior dorsal point) indicate that it may also be varying in area at different positions in the cycle of movement. A characteristic series of measurements of this fluctuating height is shown in Text-fig. 3. These are for the dace already illustrated in Pl. 1. The upper line of Text-fig. 3 represents the height of the tail measured from successive frames of the film. In the swimming fish this height usually fluctuates symmetrically about the horizontal mid-line of the fish's body, but in the diagram it is plotted from a fixed base-line corresponding to the most ventral posterior point of the tail. The lower line in Text-fig. 3 represents the position of the tail in the cycle of beating as viewed from above. The mean axis of progression of the fish is indicated by the dotted line; its direction by the arrow. The line showing the position of the tail is diagrammatic only and its lateral extent in no way corresponds to the amplitude of the tail beat nor its wave length to the actual wave length of the movement through the water.

The rhythmical nature of the variation in the height of the tail is apparent in Text-

fig. 3 as is also some variability in the extent of this fluctuation. It is further clear that the minimum height of the tail occurs regularly at the lateral extremes of movement of the tail, that is when its transverse velocity is zero. It is not so clear from this diagram exactly where the maximum height of the tail occurs except that it is during the transverse movement of the tail and somewhat after the mean axis of progression has been passed over.

Measurements of the apparent height of the tail in this manner are not necessarily indicative of a real change in its area. The periodic curving of the tail dorso-ventrally must affect its apparent lateral height to a certain extent. Two factors, however, militate against this being the complete explanation of the observed variation in height. First, the measured curvature, as indicated by the height of the chord-to-arc measure-



Text-fig. 4. Correlation between the changes in bending and height of the dace caudal fin shown in Text-figs. 2 and 3. *Upper line*: height of caudal fin. *Lower line*: amount of bending.

ments in Text-fig. 2 and the inset in Text-fig. 1, would result in an apparent change in height of only *ca.* 15%. The changes in height indicated in Text-fig. 3 are of the order of *ca.* 30%. Secondly, there is not the exact correlation between variation in curvature and apparent height that such a causal relationship would require. Text-fig. 4 shows the height variation, already plotted in Text-fig. 3, together with the simultaneous changes in dorso-ventral curvature taken from Text-fig. 2. From this it can be seen that the two variations are out of phase in such a manner that they cannot be mutually explainable. The minimum amount of curvature occurs when the tail is about half-way through its period of increasing height. Thereafter the tail continues to increase in apparent height while at the same time increasing in curvature. During this period its actual height must therefore be even greater than that indicated by the substantial increase in its apparent height. Thereafter the tail begins to decrease in height while the curvature still increases and at the lateral extremes of the transverse movement of the tail the apparent height is at a minimum while the amount of curvature is still decreasing.



There can be little doubt about the ability of the tail to extend and contract within these limits. The tail heights of a series of trout were measured under anaesthetic. First, the natural relaxed height of the caudal fin was recorded and then the height when stretched without undue strain between the fingers. These figures are given in Table 2, together with the length of the specimens concerned. The percentage increase in height of the stretched fin over the relaxed one is given in the last column. A certain amount of variability is apparent but the mean of 36% is of the order required to cover both the directly observed apparent increase in height during swimming and also that additionally required to allow for a certain amount of curvature.

Table 2. *Natural limits of the variability in height of the caudal fin of the trout (Salmo irideus)*

Length of specimen (cm.)	Relaxed height of tail (cm.)	Stretched height of tail (cm.)	% increase on stretching
26.0	4.8	6.0	25
23.1	4.0	5.2	30
25.7	3.5	5.0	43
30.5	5.5	6.5	36
29.9	4.5	6.4	38
29.1	4.4	6.3	43
26.8	4.3	6.5	51
23.5	3.2	4.1	28
27.0	4.5	5.9	32

Mean increase on stretching 36%

These measurements have been made of increase in the *height* only of the tail fin. The chief interest from the hydrodynamical point of view must lie with the changes in *area* of the fin. These are not necessarily properly indicated by the height measurements, because the proximal part of the fin is inextensibly attached to the most distal part of the body. The proportionate increase in area corresponding to any particular increase in height is dependent upon the relationship between the height of the proximal attached base of the tail and the most distal varying height itself. Only if the attached base were zero would the proportionate increase in area be the same as the increase in distal height. In both the dace and the goldfish the distal height divided by the attached base gives the figure 2.4. An increase in distal height of 15% in such a tail gives a corresponding increase in area of about 10%. An increase in height of 30% gives an increase in area of about 21%. The actual surface area of the fin will of course be larger than that indicated by these measurements of apparent height, to an extent dependent upon the degree of curvature, but the figures given will represent the area that will be swept through the water.

Nursall (1958) in measuring the dimensions of various fins for the purpose of calculating their aspect ratio encountered the problem of deciding whether to take a relaxed or a stretched measurement of the tail. His figures show that in some fish the aspect ratio may be doubled by gently stretching the fin while in others the fin is rigid.

(5) *Speed of transverse movement of the caudal fin*

Measurements of the frequency and the amplitude of movement of the caudal fin (Bainbridge, 1958*a*) allow, by simple multiplication, the calculation of the mean velocity of transverse movement of the tail. The relationship of this figure to the resulting forward speed of the fish is of some interest. The oscillatory movement of the tail, however, results in moments at the extremes of the cycle when there is no lateral movement at all of particular parts of the fin and consequently no propulsive thrust from these. Of greater interest than the mean speed of transverse movement is therefore the variation of this speed during a typical cycle of movement.

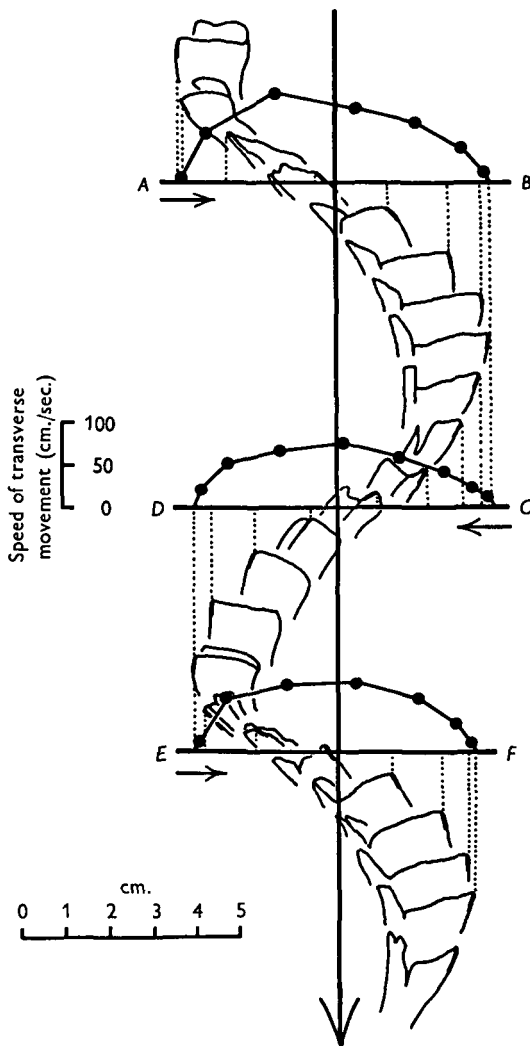
(a) *Method of analysis*

The speed of movement of any part of the swimming fish recorded by ciné-photography is most conveniently assessed by measuring the distance moved by the particular part in between successive frames of the film. As the film is moving at a steady known rate such distance measurements can readily be converted into speeds if multiplied by the appropriate factor. Text-fig. 5 shows an outline tracing of the path of movement of a caudal fin through the water (as in Text-fig. 1). Superimposed upon this are light dotted lines showing how projection of the position of the uppermost tip of the tail on to a line at right angles to the axis of progression of the fish gives a direct measure of the speed of transverse movement. These values are given by the distance between successive dotted lines. The distances are taken to represent the average speed of transverse movement during the unit time interval and are thus subsequently plotted on the transverse base-line midway between the two successive positions of the tail to which they correspond. The result of this operation is therefore, as shown at *A-B*, a graphical representation of the change in transverse velocity of the tail as it passes through a half cycle of movement from the extreme position on one side of the fish to the extreme position on the other. The next half cycle of movement is represented by the diagram *C-D* and the next by *E-F*. Despite the movement of the film at *ca.* 50 frames per second there is not a large enough number of measurements for each half cycle to obtain an exact record of the variation in transverse speed, and it is therefore desirable to combine a series of consecutive half cycles in a single diagram. If this is done by simple superposition, however, any asymmetry in the distribution of transverse speed relative to the mean axis of progression of the fish will be concealed. Such a combined diagram must therefore be constructed by reversing the measurements for each successive half cycle of movement.

(b) *Symmetrical movement of dace*

The result of such an operation is shown in Text-fig. 6. This shows the measurements for several half cycles successively reversed so that all those relating to movement from the extreme outward position up to the mean axis of progression of the fish are on the left-hand side of the diagram, while all those relating to movement away from the axis of progression up to the extreme outward position are on the right-hand side of the diagram. The central vertical line indicates the mean axis of progression of the fish and the two arrows indicate that measurements on the left relate to movements towards the mid-line and those on the right to movements away from the mid-line.

In Text-fig. 6 the upper diagram (A) shows the varying transverse velocity of the tail of a dace 21.0 cm. in length when swimming steadily forward at a speed of 32 cm./sec. A more or less symmetrical distribution of tail speed about the axis of progression is apparent. The second part of Text-fig. 6 (B) shows measurements for the same dace when

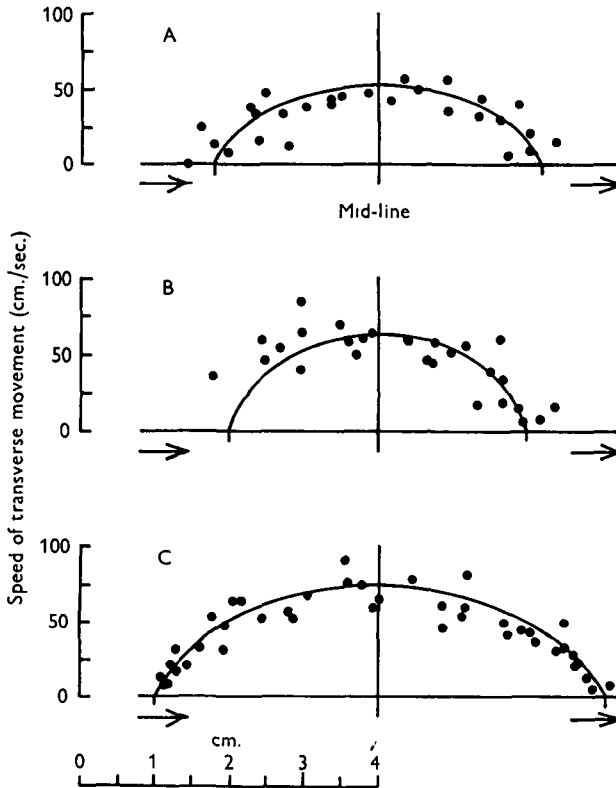


Text-fig. 5. Method of assessing the speed of transverse movement of the caudal fin. Superimposed on a sequence of positions of the fin of a dace 30.0 cm. in length swimming at 48.0 cm./sec. are construction lines showing how projection of the position of the fin on to lines at right angles to the axis of progression gives a measure of the speed of transverse movement. For further explanation see text.

swimming steadily at 61 cm./sec.; the form of the transverse speed curve is similar to that at the lower forward speed but the maximum transverse velocity is somewhat higher. The amplitude, as shown by the lateral extent of the figure, is almost exactly the same in the two cases.

Text-fig. 6 (C) gives similar results for another dace, 30.0 cm. in length. The

maximum transverse velocity of the tail is here a little greater for a forward speed of *ca.* 50 cm./sec. but the amplitude is proportionately bigger for the bigger specimen. It has already been shown (Bainbridge, 1958*a*) that the maximum amplitude of tail beat in a swimming fish is of the order of 0.2 times the body length.

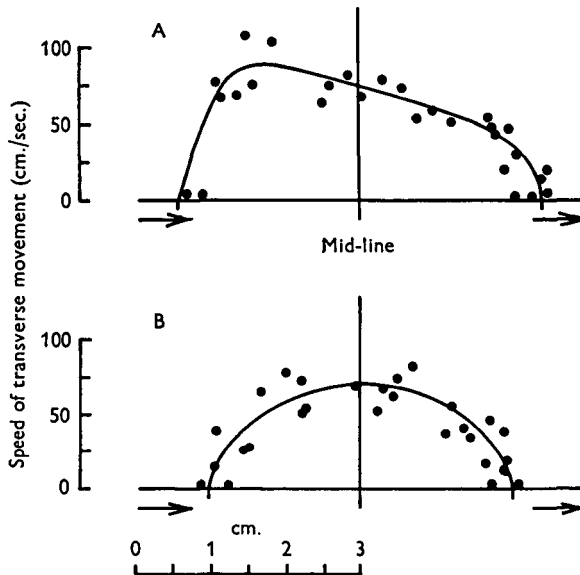


Text-fig. 6. Diagrams showing speed of transverse movement of the tail relative to the mean line of progression, measured as in Text-fig. 5. Each diagram is a combination of several half cycles of movement, the points representing individual measurements. Those for the tail moving towards the mid-line are put on the left of the figure, those for the tail moving away from the mid-line on the right. The scales indicate the extent of the lateral movement (i.e. amplitude) and the speed of the lateral movement. A, A dace 21.0 cm. long swimming steadily at 32 cm./sec.; B, the same swimming at 61 cm./sec.; C, a dace 30.0 cm. long swimming at 50 cm./sec.

### (c) *Asymmetrical movement*

In many cases the caudal fin does not move in the symmetrical manner of the three examples so far cited. Asymmetry, when it occurs, is frequently of the nature shown in Text-fig. 7. The upper part of this diagram shows the transverse velocity of the most posterior part of the caudal fin of a goldfish (*Carassius auratus*), 22.5 cm. in length, which accelerated from a forward speed of 44 cm./sec. to one of 60 cm./sec. during the period in which these observations were being made. While the fish is accelerating in this manner the tail shows a most rapid transverse acceleration at the beginning of its move from an extreme lateral position to the mid-line of the body. Its maximum speed is attained in about the first quarter of the total transverse move-

ment, to be followed by a gradual decline and a final more rapid fall in speed as the next extreme position of transverse movement is approached. The greater speed of the tail during the part of the cycle approaching the mid-line is further indicated by there being only 11 points on the left-hand side of Text-fig. 7, while there are 18 points on the right-hand side when the tail is leaving the mid-line and approaching the next

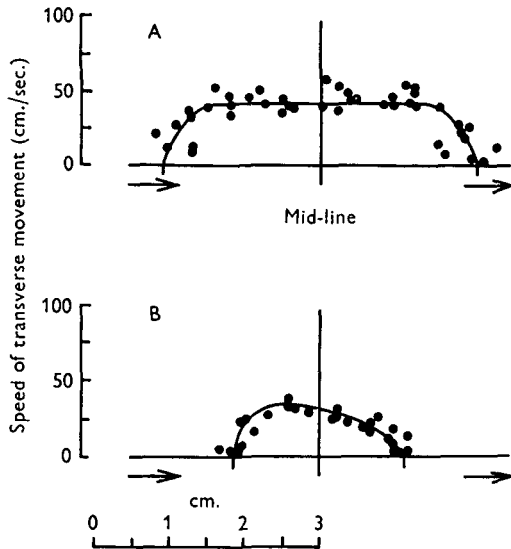


Text-fig. 7. A, Speed of transverse movement of the posterior edge of the caudal fin relative to the mean line of progression for a goldfish (*Carassius auratus*) 22.5 cm. long accelerating from 44 to 60 cm./sec. during the period of observation. B, simultaneous measurements for the caudal peduncle.

extreme position. This type of asymmetrical movement has been observed in many records of several different species of fish and appears to be normal during periods of acceleration although it may also occur during steady swimming. Its converse has been more difficult to demonstrate but there is some evidence that it may occur during slowing. The lower part of Text-fig. 7 shows the transverse speed of the caudal peduncle about 3 cm. more anterior in the fish than the fin tip shown in the upper part. These measurements are taken from the same frames as those giving the upper diagram. The movement here differs both in having a somewhat smaller amplitude but also, most markedly, in the complete absence of the asymmetry so characteristic of the tip of the tail. The light that this observation throws on the mechanism producing the more posterior asymmetrical movement is considered later.

A corresponding association of symmetrical and asymmetrical movement of the opposite kind can be seen in the bream (*Abramis brama*). Here the distribution of the transverse velocity of the tip of the tail about the mean line of progression of the fish is symmetrical, although it does not have the regular sine-like form shown previously. Text-fig. 8 (upper part) gives measurements for the tail tip of a 19.0 cm. bream swimming steadily at a forward speed of 47.5 cm./sec. and has much more the appearance of a square wave. The more flattened nature of this diagram reveals a rapid transverse acceleration followed by a steady movement across the mid-line of the

body and a subsequent rapid deceleration just before the extreme limit of lateral movement is reached. The lower part of Text-fig. 8, however, shows the transverse velocity of the caudal peduncle 4.0 cm. anterior to the tip of the caudal fin, at the same



Text-fig. 8. A, Speed of transverse movement of the posterior edge of the caudal fin relative to the mean line of progression for a bream (*Abramis brama*) 19.0 cm. long swimming steadily at a forward speed of 47.5 cm./sec. B, Simultaneous measurements for the caudal peduncle.

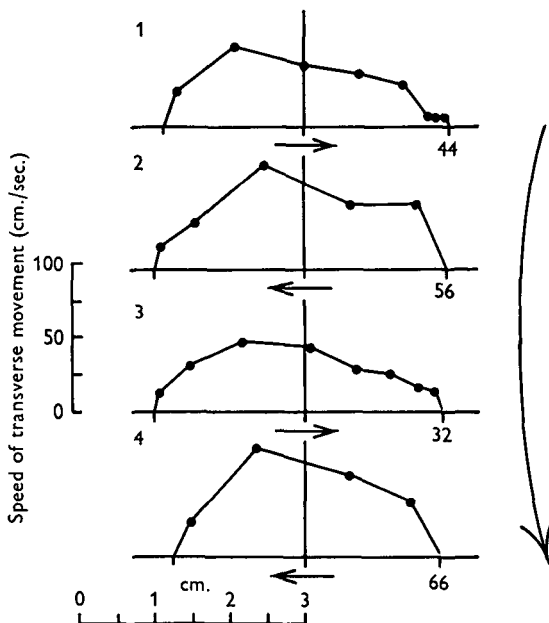
time. Here, in contradistinction to the peduncle of the goldfish shown in Text-fig. 7, the movement is now asymmetrical with the rapid acceleration and subsequent steady deceleration characteristic of the goldfish tail tip during accelerating forward movement. It would seem that the symmetrical movement of the goldfish peduncle is transformed into an asymmetrical movement in the caudal fin while in the bream an asymmetrical movement of the peduncle is transformed into a symmetrical movement more posteriorly. The amplitude of the transverse movement is again much reduced in the peduncle (about half that of the tail tip) and the transverse velocity is correspondingly low.

#### (d) *Asymmetrical movement in turning*

A further type of asymmetrical movement of the tail appears to be associated with turning from the direct line of progression during steady swimming. If a violent turn is to be made then one or other of the pectoral or even the pelvic fins is extended and the whole body may further be twisted to facilitate the move. More gentle turning can be effected, however, by asymmetrical tail movement, the pectoral fins remaining pressed to the body. Two aspects of this movement can be recognized. First, the rapid acceleration on approaching the mid-line that is shown in Text-fig. 7 (upper part) occurs here only in alternate half cycles; the other half cycle having the tail reaching its maximum transverse speed *after* passing the mid-line and while approaching the extreme limit of movement on the other side of the body. The maxima of transverse speed are arranged to be on the outside of the turn and all thus combine to provide an extra thrust moving the body in the required direction. Text-fig. 9 shows

the distribution of the transverse speed of movement of the tail in four successive half cycles of beating on the part of a goldfish turning to its left. As in the other diagrams the tail is as viewed from the fish's head. None of the half cycles has been reversed so the maximum velocity of transverse movement might be expected to be alternately on the left- and the right-hand side of the successive diagrams. As can be seen the maxima all occur on the left as viewed here, that is on the fish's right, and will consequently combine to turn him to the left.

The second aspect of this asymmetrical beating can be seen in the mean velocity of transverse movement for each successive half cycle. These values are given below



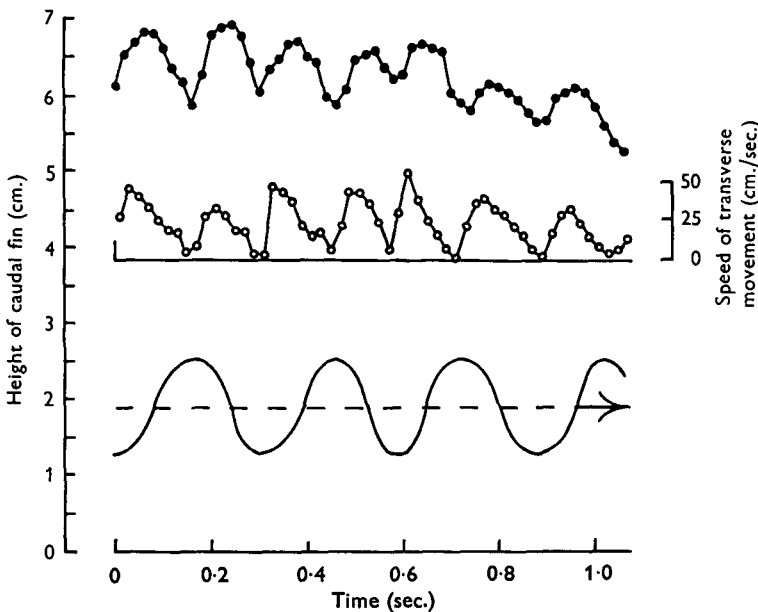
Text-fig. 9. Speed of transverse movement of the caudal fin during four successive half cycles of lateral movement by a goldfish 18.0 cm. long turning to the left. The speed is plotted relative to the mean line of progression as viewed from the fish's head. The arrows beneath each plot indicate the direction of movement of the tail. The long arrow on the right indicates the direction of turning. Note that the maxima of transverse speed are all found on the outside of the turn. The figures give the mean velocity of transverse movement for each half cycle.

each part of the figure and alternate ones are seen to be almost double the remainder. Should the thrust be dependent solely on the velocity of the tail these observations would present something of a problem as it is the wrong alternate half cycle that has the maximum speed to effect the required turn. During this part of the movement, however, the tail is much more feathered than it is during the alternate half cycles and this must remove some or possibly all the thrust deriving from the more rapid transverse movement. Perhaps still more important than this in facilitating the turn, however, is the fact that the most anterior part of the head always moves laterally in the same phase as the tail. The inclination of the head to the mean axis of progression must greatly influence the turning effect of forward movement on the body. The shorter the time it is inclined outward on the turn and the greater the time it is inclined inward, therefore, the easier will be the desired turning of the body. The rapid movement of

the tail during the half cycles in which it is travelling outwards relative to the turn may perhaps, therefore, be necessitated by the head having to point into the turn as long as possible. Hydrodynamically the turning effect of an inclination of the front end of the body would be much more effective than an increased laterally displacing force developed at the posterior end of the body.

(6) *Correlation of area changes and speed of transverse movement*

A synchronization of the variation in apparent height of the tail with the cycle of lateral movement has already been pointed out (Text-fig. 3). A more exact appreciation of this correlation can be obtained by comparing the apparent tail height (assumed

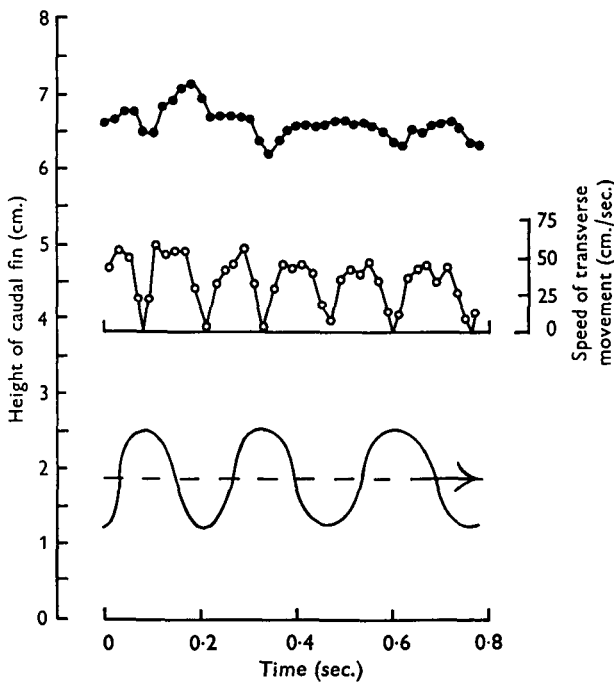


Text-fig. 10. Correlation between apparent height of the caudal fin when viewed laterally and its transverse speed of movement, for a goldfish 18.0 cm. long swimming steadily at 35.6 cm./sec. The upper line shows fin height plotted from the base-line, the second shows its transverse speed plotted from its own base-line, the third shows, diagrammatically, the position of the tail in the cycle of oscillation at the time of the measurement. The fish moves from left to right in the figure.

indicative of area) with the transverse speed of movement of the tail. This is done in Text-fig. 10 for a goldfish 18.0 cm. in length swimming steadily at a speed of 35.6 cm./sec. In this diagram, as before, the uppermost line represents the fluctuating height of the tail as recorded by the horizontally directed camera. This height is plotted from the base-line at the foot of the figure. The central line represents the lateral speed of movement of the tail as given by the distance moved between successive frames of film taken by the vertically directed camera. This speed is plotted over its own base-line and is drawn near to the height curve in order to assist in detecting correlations. The third and lower line represents diagrammatically the position of the tail in the cycle of beating at the time the upper observations were being made. The amplitude and wave length of this line are arbitrarily fixed.



It can be seen from Text-fig. 10 that the height of the tail is at a minimum either when, or immediately after the speed of lateral movement is at a minimum; i.e. when the tail is in its extreme lateral positions. The times of maximum height occur more or less symmetrically between the minima or a little later than the half-way point between minima. They therefore fall when the velocity of transverse movement is diminishing appreciably. This broad correlation is immediately apparent, but a closer inspection shows there to be no exact correlation between the absolute vertical height of the tail and its lateral speed. The maxima attained by the speed in Text-fig. 10, for example, increase from the second half cycle to the fifth half cycle while they decrease from the



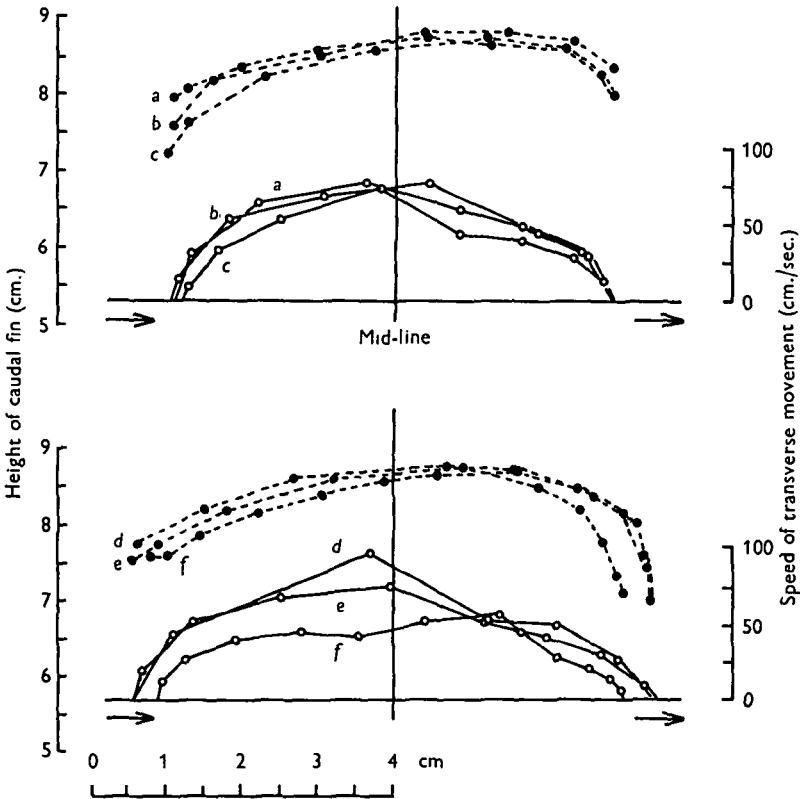
Text-fig. 11. Correlation between apparent height and transverse speed of movement of the caudal fin of a bream 19.0 cm. long swimming steadily at 47.5 cm./sec. Conventions as in Text-fig. 10.

fifth to the seventh or last half cycle; yet during the whole of this time the maxima in height of the tail are more or less steadily decreasing from the second to the seventh half cycles.

Sometimes, as with the bream shown in Text-fig. 11, there is an even more marked absence of exact correlation. This diagram is constructed exactly as is Text-fig. 10 and is for a bream, 19.0 cm. in length, swimming steadily at 47.5 cm./sec. The regular variation in lateral tail speed is most clearly shown and even the detailed square wave form of this is apparent. The tail height, however, is most irregular in its variation. In particular there is no indication of any fall in height whatsoever during the fourth minimum in lateral speed and the height remains constant despite quite a marked increase in lateral speed during the third half cycle. It should perhaps be emphasized that this example is selected specifically as an exception and the bream tail usually

shows regular fluctuations in height although these are not quite so extensive as those of the dace and goldfish.

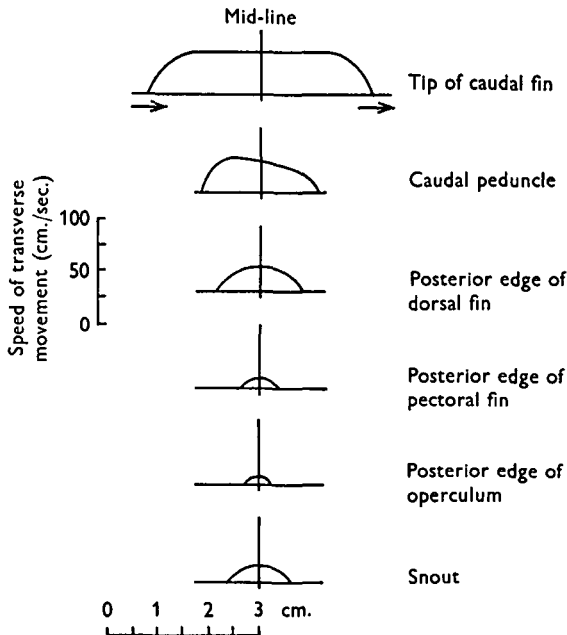
Another way of showing the nature of the correlation between height and transverse speed is illustrated in Text-fig. 12. In each of the two parts of this figure measurements for three half cycles of movement have been plotted. The speed of transverse movement of the tail is shown by the full lines connecting points which



Text-fig. 12. Correlation between apparent height and transverse speed of movement of the caudal fin of a dace 30.0 cm. long swimming at 48.0 cm./sec. In each half of the figure are shown corresponding height (upper dotted line) and speed (lower full line) measurements for three consecutive half cycles of tail movement. Values for the tail moving towards the mid-line are on the left of the figure, those for movement away from the mid-line are on the right. Corresponding height and speed lines have the same initial letters. The upper half of the figure shows the normal correlation, the lower half an exceptional lack of correlation.

represent the individual measurements of speed at different positions in the three successive half cycles of movement. As in Text-fig. 6 those relating to movement towards the mean axis of progression are put on the left of the figure, while those relating to movement away from the axis are on the right. The dashed lines represent the simultaneous measurements of the height of the tail alternately reversed in the same way, corresponding half cycles being indicated by letters. The upper part of Text-fig. 12 shows the normal state of affairs to be found in the dace. The distribution of transverse speed is somewhat asymmetrical, there being a fairly rapid increase

followed by a more gradual decline, but not by any means as markedly so as that shown for the goldfish in Text-fig. 7. The simultaneous changes in height of the tail show very clearly a reversed asymmetry. The height is at a minimum when the lateral speed is at a minimum, but it increases steadily as the tail moves from the lateral position across the mid-line to something like three-quarters of the way across the whole half cycle, when it falls quickly to its minimum value. The lower half of Text-fig. 12 shows a similar but even more marked fluctuation in height correlated in the same broad way with the asymmetrical lateral speed of the tail. The three successive half cycles here,



Text-fig. 13. Speed and amplitude of transverse movement at six positions along the length of the body of a bream 19.0 cm. in length swimming steadily at 45.0 cm./sec. Individual measurements are not shown but the conventions are otherwise as in Text-fig. 6.

however, show a marked diminution in the maximum speed of transverse movement attained. In half cycle *f* the tail crosses the mid-line at about half the speed that it does in half cycle *d*. Despite this marked difference in speed the apparent height of the tail when crossing the mid-line is identical in all three cases.

(7) *Movement of the body*

Because of the relative complexity of its movement it has seemed best to treat the caudal fin separately from the rest of the body, which it is now proposed to examine. This separation is purely a matter of convenience and it must be remembered that the source of the movement of the caudal fin is the lateral movement of the more anterior parts of the body. The most noticeable variable in the lateral movement of the body is the increase in amplitude of this movement as one passes from anterior to posterior. It has proved possible to measure both this amplitude and the velocity of transverse movement in the way in which similar measurements were made for the

extreme tip of the tail fin (see Text-fig. 5). Values for a bream 19.0 cm. in length travelling steadily at a forward speed of 45 cm./sec. are shown in Text-fig. 13. From the top of the figure downwards the sections show the amplitude and speed of transverse movement of successively: (1) the most posterior tip of the caudal fin, (2) the posterior part of the caudal peduncle (just where the fin originates), (3) the mid-line of the body at the posterior edge of the dorsal fin, (4) the mid-line of the body at the posterior edge of the pectoral fins, (5) the mid-line of the body at the posterior edge of the opercula, and (6) the tip of the snout. The horizontal and vertical scales show respectively the extent of the amplitude in cm. and the speed of the transverse movement in cm./sec. In every case values recording movement of the body from the extreme lateral position towards the mean line of progression are put on the left of the diagram and those for movement from the mean line of progression out to the lateral position are put on the right.

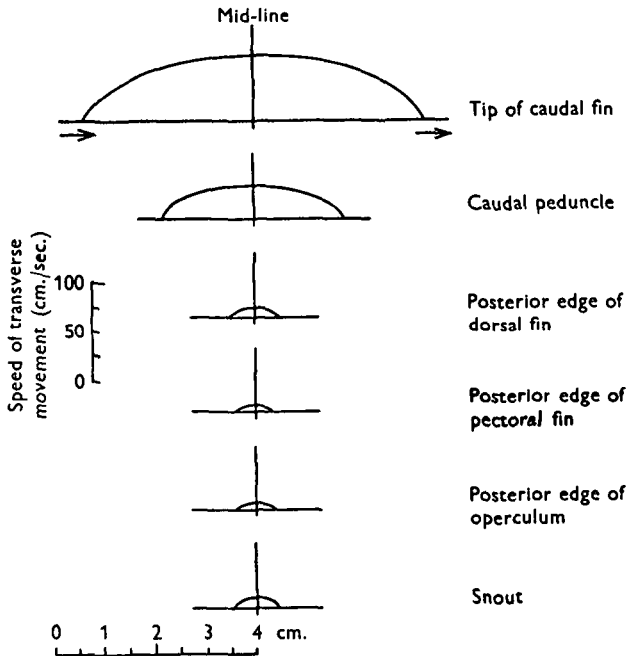
A fairly gradual decline in amplitude, in maximum and in mean transverse speed, can be seen as one passes anteriorly along the body as far as the operculum. Anterior to this all these values increase somewhat until the snout is moving laterally with the same amplitude and speed as a point more or less midway along the body. This increase in amplitude at the front of the body indicates the possibility of a node, without any lateral movement, somewhere posterior to the operculum. The observed gradual nature of the changes in amplitude makes this rather unlikely, however. The matter is further considered in the discussion. The characteristic flattened appearance of the diagram representing movement of the bream tail tip is again apparent, as is a rather asymmetrical movement of the peduncle. Neither of these variations is reflected in the more anterior lateral movement which appears symmetrical and regular.

Examination of the reconstructed paths of movement of each of the six points recorded in Text-fig. 13 gives six independent values for the wave length of the movement under consideration. From posterior to anterior these are 11.5, 12.0, 11.5, 11.6, 12.5 and 12.5 cm., giving a mean of 11.9 cm. with a very slight indication of an increase in wave length as one passes from posterior to anterior in the animal. The relationship of this value to the body length of the fish (in this case 19.0 cm.) is of some interest and indicates that at any time there are about 1.6 wave lengths down the length of the body.

A further parameter to be obtained from the analysis is the rate at which the propulsive wave travels backwards down the body. This can be measured quite accurately by comparing the phase differences of the lateral oscillations at the successive positions along the body. For the bream under consideration the wave is found to move at a speed of 59 cm./sec. This compares with the measured forward velocity of the fish of 45 cm./sec. to give a ratio of backward speed of wave/forward speed of fish of 0.76. Lighthill (1960) reaches the conclusion mathematically that for maximum propulsive efficiency this ratio should be 0.8. Gray (1933*a*) gives rather lower values for a series of six marine fish. They range from 0.67 for the butterfly and the whiting to 0.50 for *Ammodytes*, with a mean for the whole six of 0.60.

The movements of two other fish—the dace and the goldfish—have also been analysed in a similar fashion. Text-fig. 14 shows the amplitude and speed of transverse movement at six positions along the body of a dace, 25.0 cm. in length, swimming steadily at a forward speed of 42 cm./sec. Apart from the perfectly symmetrical lateral

movement at all points down the body the most noticeable way in which the dace differs from the bream is in the more rapid decline in the amplitude of the movement as one passes from the tail tip forwards along the body. There is little evidence for there being a node at any point and the anterior four positions have almost identical amplitudes and speeds of movement. The possible significance of this type of movement in determining the proportion of the total thrust coming from the tail fin is considered later. The difference between the two fish in the absolute amplitude of movement of the extreme tip of the tail can be almost entirely accounted for by the



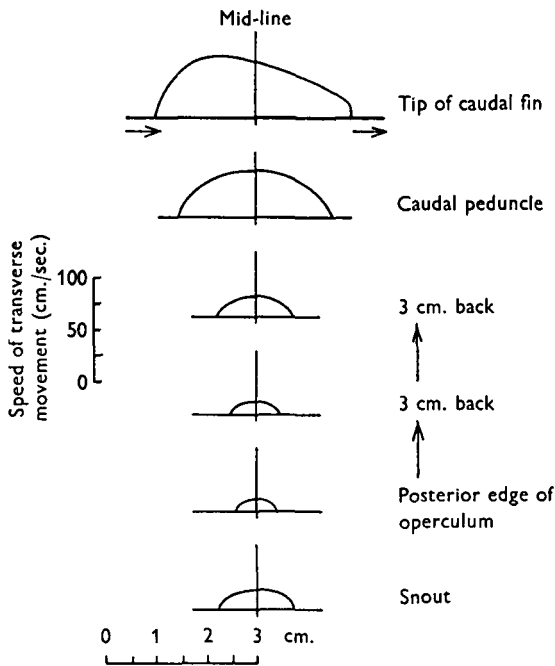
Text-fig. 14. Speed and amplitude of transverse movement at six positions along the length of the body of a dace 25.0 cm. in length swimming steadily at 42.0 cm./sec. Conventions as in Text-fig. 6.

difference in size of the two specimens. The bream amplitude measures 4.4 cm. or 0.23 times the body length, that of the dace 6.7 cm. or 0.27 times the body length.

The six values for the wave length of the dace body movement are 15.5, 15.5, 15.0, 16.0, 14.7 and 14.1 cm., passing from the most posterior to the most anterior position. There is thus no indication of an increase in wave length towards the front of the animal. The mean of these six values is 15.1 and divided into the body length this shows that at any time there are about 1.7 wave lengths down the length of the body. The speed of movement of the wave along the body has also been calculated. It passes in an antero-posterior direction at a speed of 57 cm./sec. The ratio of backward speed of wave/forward speed of fish is thus 0.74, a figure very close to that calculated for the bream.

Text-fig. 15 shows similar amplitude and speed measurements for a goldfish,

16.0 cm. long, swimming steadily at a forward speed of 46 cm./sec. Here, because of difficulty in recording on the film the positions of the posterior edge of the pectoral and the dorsal fins, the six selected positions of measurement (from anterior to posterior) are: (1) the tip of the snout, (2) the mid-line of the body at the posterior edge of the opercula, (3) a point 3 cm. behind this, (4) a point 3 cm. further behind this, (5) the caudal peduncle, and (6) the tip of the caudal fin. The form of movement of the tip of the tail is the asymmetrical one already shown to be characteristic of the goldfish, while the peduncle shows a symmetrical movement. The general decline in amplitude in passing forwards along the body is much more reminiscent of the bream than of the



Text-fig. 15. Speed and amplitude of transverse movement at six positions along the length of the body of a goldfish 16.0 cm. in length swimming steadily at 46.0 cm./sec. Conventions as in Text-fig. 6.

dace. As in the bream, too, there is a considerable increase in the amplitude at the snout. The absolute amplitude of the tail tip is 3.9 cm. or 0.24 times the body length. The six measured values for the wave length of this propulsive movement are, from posterior to anterior, 11.5, 11.3, 11.0, 11.6, 11.5 and 11.5 cm. There is again no indication of a change in wave length along the body. The mean of these six values is 11.4 cm. and divided into the body length this shows there to be 1.4 wave lengths along the body. The bream and the goldfish thus further resemble each other in having a propulsive movement of short relative wave length while the dace has one that is longer. The propulsive wave passes down the goldfish body at 65 cm./sec., giving a ratio for backward speed of wave/forward speed of fish of 0.71, a little less than the values for the bream and dace.

During these observations on the lateral movements of the body during swimming a certain amount of rolling about the antero-posterior axis has been observed. Usually

this is most apparent over the posterior part of the trunk and is associated with the sort of sculling movement, using only the upper or lower part of the caudal fin, that has already been mentioned. It seems most apparent during slower swimming but is both intermittent and rather rarely observed and so has not been subjected to closer study.

#### DISCUSSION

While the primary object of this paper is to provide sufficiently detailed observations on the swimming movements of some fish to allow a full mathematical analysis of these external aspects of their propulsion there are, nevertheless, one or two topics which may profitably be discussed here in a general way. The first of these concerns the extent to which the fish has active control over some of the variables that have been described.

##### (1) *Active control over tail movements*

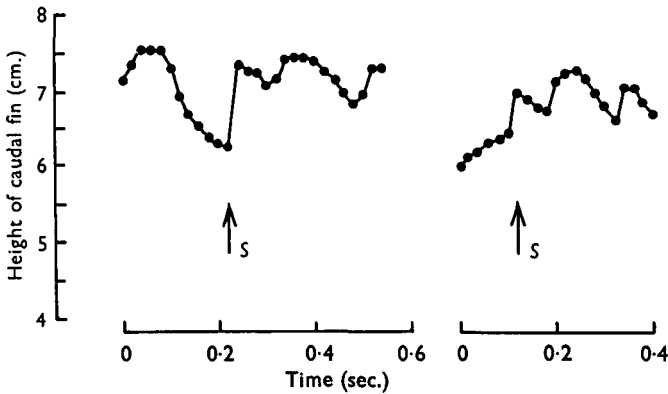
The dorso-ventral and the antero-posterior bending of the caudal fin in the vertical plane, the variation in area at different points in the cycle and the irregularly varying speed of transverse movement of the fin all demand some consideration of the degree of active control exercisable by the fish over these variables. All of them could be causally interrelated in such a way as to be mutually explicable in terms of the degree of flexibility of the tail, the position of specially stiffened fin rays, and the amount of emargination of the tail. For example, the most dorsal and ventral fin rays are usually thickened and, if connected by a fairly elastic membrane, would automatically lead as the tail moves across transversely. The gradual attenuation of these and the rest of the fin rays towards their distal ends would allow antero-posterior bending which would vary according to the speed of transverse movement. Partial emargination of the fin could affect this amount of bending in the middle region of the tail by reducing the pressure there. The transverse movement of the tail, while basically symmetrical, could have in it a sort of whiplash component which could account for some of the asymmetry in transverse movement.

The essential facts militating against such a mechanical explanation of the observations are the lack of really precise correlations and also the variability already emphasized. In particular the preservation of the same tail area at very different speeds of transverse movement (Text-fig. 12*b*) and the way the amount of bending and the tail area are just out of phase (Text-fig. 4) should both again be mentioned. While there is a general and satisfactory correlation between the several variables, these and many similar exceptions lead to the conclusion that the fish can have a good deal of control over them.

Whether or not such active control is continuously exercised there is considerable evidence that it is within the fish's power to produce the basic movements necessary. v. Holst (1934) describes a so-called 'Propeller reflex' in spinally transected goldfish stimulated on the caudal peduncle. It consists of independent lateral movements of either the more dorsal or the more ventral fin rays. Simple observation of a fish like the goldfish pottering about in an aquarium shows it to rely under these circumstances on an independent movement of different parts of the caudal fin without any observable lateral movement of the trunk. Either the top, bottom or centre of the fin may be moved in a sculling motion to propel the fish either forwards or backwards, up or

down, as required. The musculature and innervations permitting these movements have not yet been examined, but there would seem to be little doubt that they could both alter the position and stiffness of the tail and also increase or decrease its area.

v. Holst & Le Mare (1936) and v. Holst (1937) demonstrate an ability on the part of various species to erect fins and increase the caudal fin area when spinally transected specimens are stimulated mechanically on the body. The same capacity is demonstrated here in a normal unoperated fish. Text-fig. 16 shows the laterally viewed apparent height of a bream tail measured from a film record taken with the horizontal camera. At the two points marked *S* a moderate electric shock was applied through the water contained in the wheel. An immediate and marked increase in tail area occurs as a result of contraction of the fin ray muscles, other fins on the body also standing up simultaneously. During this tail movement the vertically directed camera



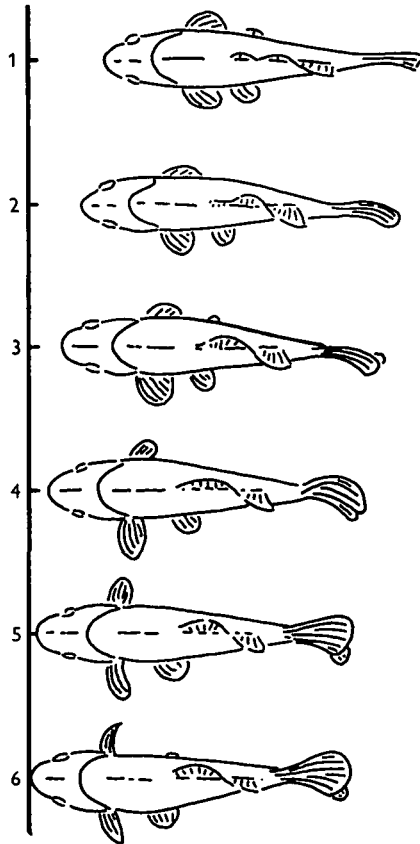
Text-fig. 16. Laterally viewed apparent height of the caudal fin of a stationary bream. Successive measurements made at intervals of  $\frac{1}{80}$  sec. *S* indicates discharge of a mild electric shock through the water. It is followed by an increase in height.

showed no determinable lateral movement of the body and the moments of stimulation were selected when the fish was quite motionless. A similar but natural increase in height of the tail has been observed occasionally immediately before a burst of swimming; the fish appearing to enlarge the tail area preparatory to lateral movement.

Evidence that the caudal fin-ray musculature can be used to effect the antero-posterior bending of the fin as well as its dorso-ventral form comes from photographs of a goldfish using its caudal fin as a brake. Text-fig. 17 gives a series of diagrams of a 23.0 cm. goldfish coming to rest quickly because of something it had observed ahead. The pectoral and pelvic fins are raised from the body and the dorsal fin is thrown into a curve against the water. Most interesting, however, is the caudal fin, which, without lateral movement of the trunk, is turned in such a way as to present a maximum surface area more or less transversely to the direction of movement. Frames 4 and 5 even show a concave surface presented forwards. This positioning of the tail fin could only be effected by active use of muscular elements able to alter the lateral bending of the fin in a horizontal plane. On another occasion this same fish has been photographed coming to rest while splaying out the caudal fin symmetrically into a sort of cone or drogue. This fin movement was again in the absence of any lateral movement of the body and in opposition to the water flow resulting from the forward movement of the fish.



It would therefore seem certain that the fish has active control over muscular elements within the caudal fin that will allow it to vary the area of the fin and also determine its amount of bending both vertically and horizontally. Whether such control is exercised during normal steady swimming is yet to be determined. Section or chemical blocking of the nervous supply of the fin, followed by detailed observation of the effects of this on the fin movements would give some indication as to whether



Text-fig. 17. Sequence of tracings, at  $\frac{1}{30}$  sec. intervals, from a film of a 22.5 cm. goldfish coming quickly to rest by the erection of various fins. The caudal fin is actively bent forwards.

constant control is effected. At the present, however, it may be fairly assumed that the considerable variability in fin bending and in area is the result of active participation on the part of the fish.

(2) *Significance of area|speed correlations in the caudal fin*

Despite the informative exceptions already emphasized there is generally a satisfactory correlation between the area of the caudal fin, as indicated by its height, and the speed of its transverse movement. The height is normally at a minimum when the tail is in the extreme lateral positions and is not therefore moving transversely. It is at a maximum some time after the mean line of progression has been passed and the transverse speed of movement is falling. The thrust generated by the moving tail

acting as an inclined plate is dependent, amongst other variables, upon its surface area and upon the square of its speed of transverse movement. The effect upon thrust of the observed variations in area and speed will therefore be (a) to allow a rapid initial acceleration of the tail by virtue of its smaller area; (b) to maintain a high and uniform thrust when the transverse speed of movement is falling by increasing the area of the tail at that time; (c) to facilitate the slowing of the tail by this increased area; (d) to add a minimum of drag to the moving body by presenting a minimum area to the water when at the extreme lateral positions in the cycle of movement. The net result of these changes will therefore be to smooth out what might otherwise be a much more intermittent thrust from the caudal fin.

Nursall (1958) distinguishes amongst four categories of fish: (a) 'typical' ones with a highly flexible caudal fin of low aspect ratio, and (b) fish such as the tuna, using a propulsive wave of low amplitude but high frequency, which have a rigid caudal fin of high aspect ratio. The propulsive efficiency of such fins of high aspect ratio must be high, but the necessary structure can clearly only be achieved at the expense of mechanical rigidity. The disadvantages of such rigidity are a great reduction in manoeuvrability at low speeds and a loss of the smoothing function of the fin. The loss of manoeuvrability is offset by high speeds and perhaps the lack of smoothing is offset by high-frequency and low-amplitude movements, both coupled with a long narrow peduncle which adds an effective lever system to the more anteriorly placed muscles. In the present work the bream was specifically chosen as a convenient freshwater fish with a tail of relatively high aspect ratio that might show characters comparable to those of the oceanic scombroids. Unfortunately the analysis of its lateral body movements shows it to have much more in common with anguilliform fish than with the scombroids.

### (3) *Significance of the bending of the caudal fin*

The dorso-ventral bending of the fin in the vertical plane causes its upper and lower parts, when they are leading, to reach the extremes of lateral movement before its centre part. As there can be no forward component of thrust at the moment when there is no lateral movement this bending thus ensures that the upper and lower parts of the tail pass this critical position while some thrust is still coming from the still moving centre part of the fin. By the time this central portion is in its turn stationary the upper and lower parts are already moving back towards the mid-line and generating thrust once more. The effect therefore of bending the fin dorso-ventrally is again to smooth out what might otherwise be a more intermittent thrust.

The antero-posterior bending of the fin in the horizontal plane has a similar effect. It can be seen from the observations on the angles of attack that while the more distal portion of the tail is still moving laterally and generating thrust the more proximal part has already passed the point of no lateral movement and is again generating thrust by moving back towards the mid-line.

The effect of both types of bending is therefore to smooth out the thrust deriving from the caudal fin. It is perhaps worth recognizing some distinction between this type of spatial smoothing, dependent upon bending, from the chroral type of smoothing dependent upon the relationship between area and speed of movement of the fin mentioned in the preceding section.

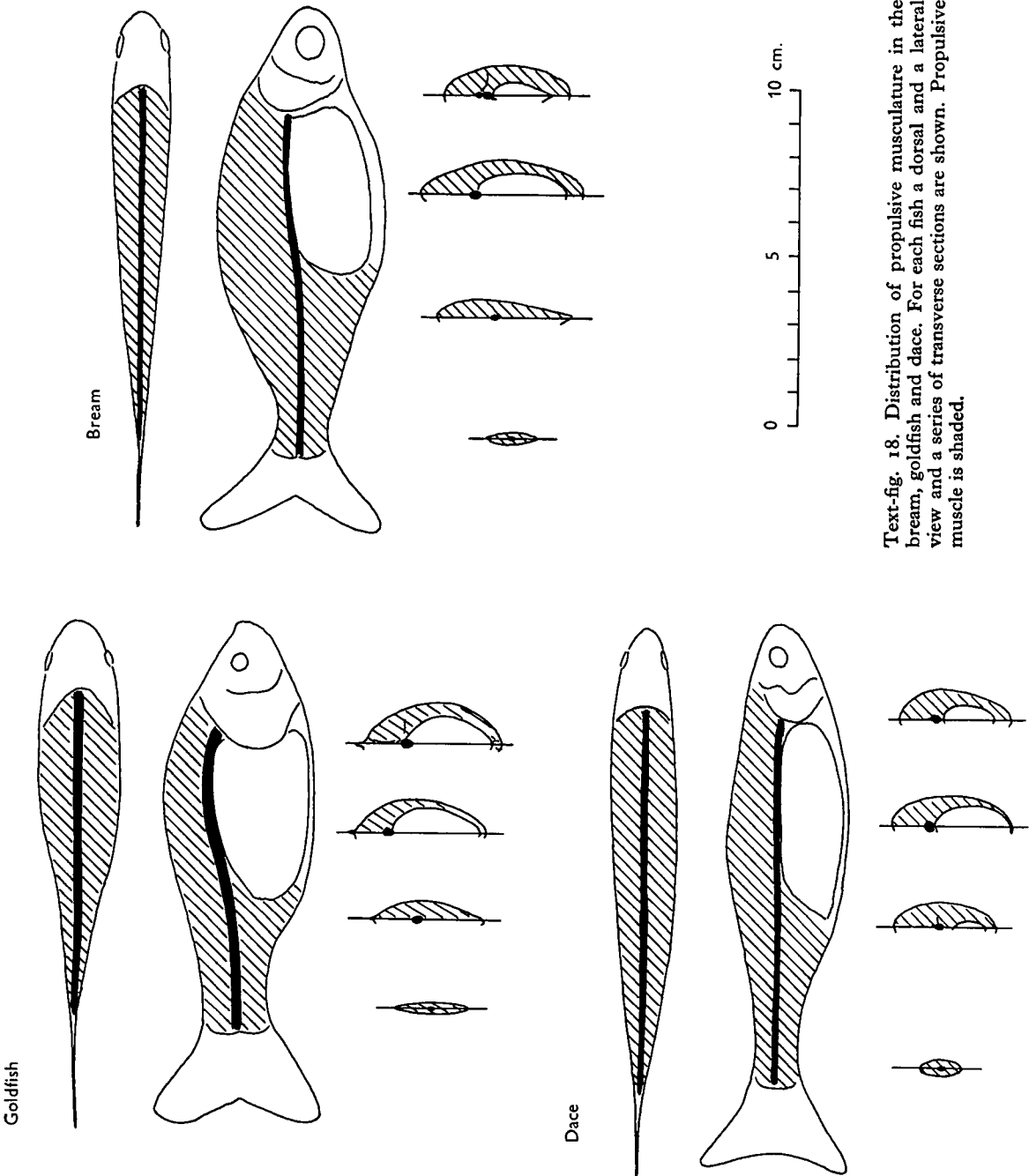
#### (4) Factors affecting body movement

Whatever the extent and significance of the part played by the caudal fin musculature in determining the exact form of its movement through the water the prime mover of the fish remains the trunk musculature. Much consideration has been given in the past both to its myotomal arrangement and to the functional significance of this relative to the propagation of propulsive waves (Nursall, 1956). One of the interests of the present observations on the different types of body movement detected lies in the factors determining the characteristics of these movements. The structural features that might influence body movement would seem to include the size and flexibility of the vertebral column, the gross distribution of musculature along the length of the body, and the insertion and detailed subdivision of this musculature. Gray (1933*b*) considers the differences in the form of the body movement between, for example, the eel (*Anguilla vulgaris*) and the whiting (*Gadus merlangus*) to be largely dependent upon the mechanical effect of the caudal fin possessed by the latter. It seems unlikely that this argument could be used to account fully for the detailed differences observed here between the bream, goldfish and dace although the damping action of the tail must have some—and probably an important—effect on the form of the body movement.

The proportion of the total body weight that is propulsive muscle can be very different in different species. A 20 cm. goldfish has only *ca.* 42% of its weight as muscle while a similar dace has of the order of 60% (Bainbridge, 1960), although the absolute weight of muscle is slightly greater in the goldfish; and a 20 cm. trout may have up to 65% (Bainbridge, 1962). In the present context, however, it is the spatial distribution of this muscle that might most affect the form of movement of the body. A preliminary examination of this shows it to be markedly different in the fish considered.

Text-fig. 18 shows the gross distribution of propulsive musculature in typical 15.0 cm. specimens of the goldfish, dace and bream. For each fish a horizontal section at the level of the vertebral column is given together with a median vertical section and four transverse vertical sections at similar points along the body. Comparison of the horizontal sections shows the bream to be the slenderest and most laterally compressed, the dace to have a fairly uniform width of muscle along the whole length of the body and the goldfish to be most stout anteriorly with a more slender region posterior to the abdominal cavity. Comparison of the median vertical sections shows various other differences. The vertebral column is fairly straight in the dace and the bream; it is much arched in the goldfish. The bream has the greater body depth and consequently much more muscle above the vertebral column. The goldfish is almost as deep as the bream but because of the arched column and large abdominal cavity it has a smaller depth of muscle above the column and the muscle there appears instead to spread more laterally, as seen in the horizontal section. Comparison of the transverse vertical sections confirms these points and also emphasizes the more cylindrical proportions of the dace body and its relatively smaller abdominal cavity.

Typical vertebrae were taken from the abdominal region of these fish and, after cleaning, the centra were measured with a micrometer eye-piece. The dace centra were found to be the smallest, being 1.6 mm. in diameter; the bream were next at 2.0 mm. and the goldfish the largest at 2.3 mm. No attempt was made to assess the flexibility of the vertebral column but freshly killed whole specimens show the dace to be



Text-fig. 18. Distribution of propulsive musculature in the bream, goldfish and dace. For each fish a dorsal and a lateral view and a series of transverse sections are shown. Propulsive muscle is shaded.

relatively stiff, the goldfish to be stiff anteriorly and the bream to be a little more flexible along its whole length. It would seem that these differences, corresponding as they do to the observed types of body oscillation, are largely dependent on the gross disposition of muscle. Simple mechanical considerations suggest that the wider the lateral distribution of muscle the less flexible the body. The bream would therefore be expected to show the most marked lateral movements of the whole body, the dace would be expected to show the least and the goldfish to show a marked movement of the posterior half of the body but not of the anterior part, where the muscle is widest and the vertebral column excessively stout. These deductions correspond well with the observed movements of the three fish but it is perhaps surprising that the dace centra are relatively so slight. A more detailed study of the exact disposition of the muscle and its subdivision into myotomes, together with the size and flexibility of the vertebrae, would probably be rewarding.

A further component influencing the path of movement of the posterior tip of the body derives in a secondary manner from the lateral movements of the body itself. Gray (1933*a*) has already shown that, when viewed from above, the tip of the tail in the glass eel traces out a figure of eight relative to the head during its lateral oscillations. The form of this figure is determined by the lateral movements of the whole body because it results from the successive lengthening and shortening of the projection of the body on to the mean line of progression of the fish, the cause of this lengthening and shortening being the lateral bending of the body. The different patterns of lateral movement already described result in a variety of figures-of-eight each peculiar in pattern to the species concerned. The path of movement of the tail through the water depends therefore on three factors: (*a*) the steady movement of the body forwards; (*b*) the lateral oscillations of the tail, which may be asymmetrical in the manner already indicated (p. 35); and (*c*) the effect of superimposing the figure-of-eight on these. The form of the figure-of-eight is such that there is a backward component in it as the tail moves towards the mid-line (and as the body projection lengthens) and a forward one as it moves away to the lateral extreme (and the body projection shortens). The first component must therefore be *subtracted* from the steady forward speed of the tail for half a cycle of beating, the second one *added* for the next half cycle. The result of these alternate additions and subtractions is to make the forward propulsive component of the tail thrust more effective during that half of the cycle when the tail approaches the mid-line and less effective when it moves away. In the fish studied here the figure-of-eight component is at a maximum at the extreme posterior end of the body and diminishes as one passes forwards. This diminution is most rapid in a fish like the dace where the amplitude of the lateral movement diminishes rapidly as one passes forwards. It is less rapid in the goldfish where the amplitude itself diminishes less rapidly. In magnitude it also depends upon how far the body is ever in a more or less straight line at some particular point in the cycle of lateral movement.

Sometimes the form of the figure-of-eight is asymmetrical in a way which reproduces in the intact animal a tail movement that resembles that demonstrated by Gray (1933*b*) for the whiting with an amputated tail. This arises from a dumbbell-shaped figure and traces of its effect are often to be seen, as, for example, in the tail shown in Text-fig. 5. The significance of such movements from the propulsive point of view is that they materially affect the propulsive efficiency at any particular time by partly

determining the path and hence the effective angle of attack of the tail. They must therefore be taken into account in any mathematical assessment of the thrust generated by the moving body.

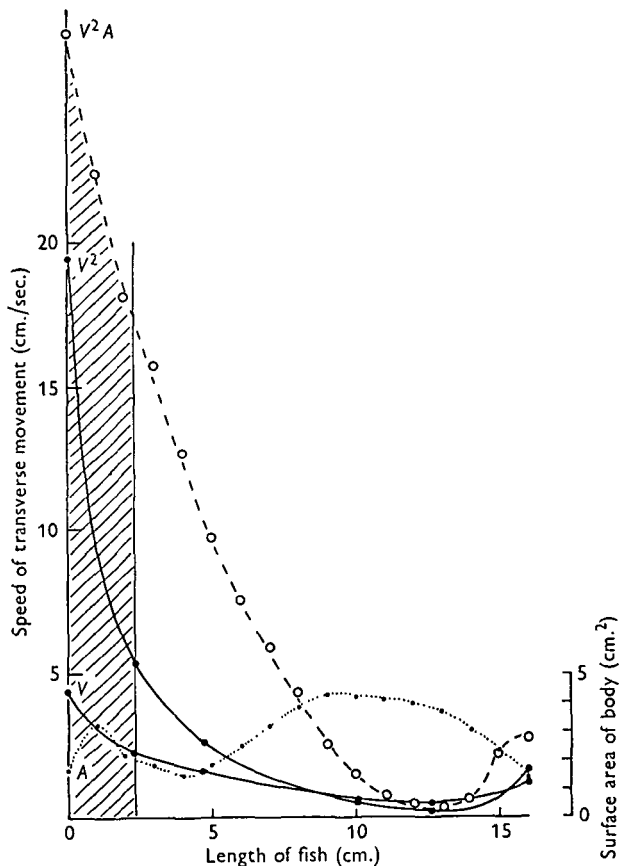
The possible occurrence of a node, or point in the body without lateral movement, has already been briefly mentioned. Breder (1926) describes such as general in fish and names it the 'orthokinetic' element, locating it in the neighbourhood of the axis vertebra. Lighthill (1960), in his mathematical treatment, supposes the front half of the body to have no lateral motion at all. This is certainly untrue in all the fish we have examined but the possibility of a node somewhere just posterior to the opercula, where the trunk musculature has its origin, remains. Such a point would be of some consequence in a mathematical analysis. However, an examination of the distribution of the speed of lateral movement down the length of the body as shown in Text-figs. 13-15 or in the lines marked  $V$  in Text-figs. 19-21 makes the occurrence of a node unlikely. The  $V$  line in the latter figures would have to fall to the axis at a node. It could not do this without distorting the otherwise smooth nature of the line and the evidence therefore suggests that no point in the fish's body moves continuously along the mean line of progression but all oscillate about this with a greater or smaller amplitude.

(5) *Proportionate contribution of thrust by the caudal fin*

Gray (1933*b*), as a result of his studies of the whiting and of a propulsive model, came to the conclusion that while a fish after amputation of the tail could swim as quickly as a whole specimen, the tail in the intact fish contributes of the order of 40% of the total thrust. While the results in the present paper will need complex mathematical treatment if some value is to be obtained for the absolute thrust produced by the moving body, it is possible immediately to make some estimate of the proportion of the total thrust contributed by the caudal fin. It has already been mentioned that surface area, the speed of movement and the angle of attack are the essential factors determining the magnitude of the thrust. For the purpose of this argument it is proposed to neglect possible variations in value of the latter and to assume that there is a positive angle of attack along the entire length of the body.

Text-fig. 19 shows, in the full line marked  $V$ , the mean speed of transverse movement of the body of a bream at six different positions along its body length. These values are simply taken from Text-fig. 13 and plotted along an axis representing the length of the fish. The upper full line, marked  $V^2$ , represents the square of these values, and the thrust generated along the body length must be directly dependent upon this. The lower dotted line marked  $A$  represents the surface area of the body as viewed laterally, the values being obtained by counting the squares covered by an image of the fish projected on to graph paper and plotted here on the axis representing the length of the fish. The uppermost heavy dashed line is the multiple of the area and velocity squared values and is thus an indication of the proportionate distribution of thrust along the length of the body. It can be seen that this is at a maximum at the most posterior end and that it falls fairly steadily to a point about at the opercula, finally rising a little towards the snout. The position of the posterior edge of the caudal peduncle, i.e. the site of origin of the caudal fin, is marked on the diagram by a vertical line. The area to the left of this line may be taken as indicative of the thrust deriving from the caudal fin, that to the right of the line as deriving from the peduncle and the

rest of the trunk. The proportionate contribution of the caudal fin in these terms is 45 %, a figure not far removed from Gray's estimate of 40 % for the whiting. The two chief errors that may affect this assessment are that resulting from the propulsive surface being dorso-ventrally curved rather than flat and that from the angle of attack possibly diminishing as one moves forward along the body and being affected func-

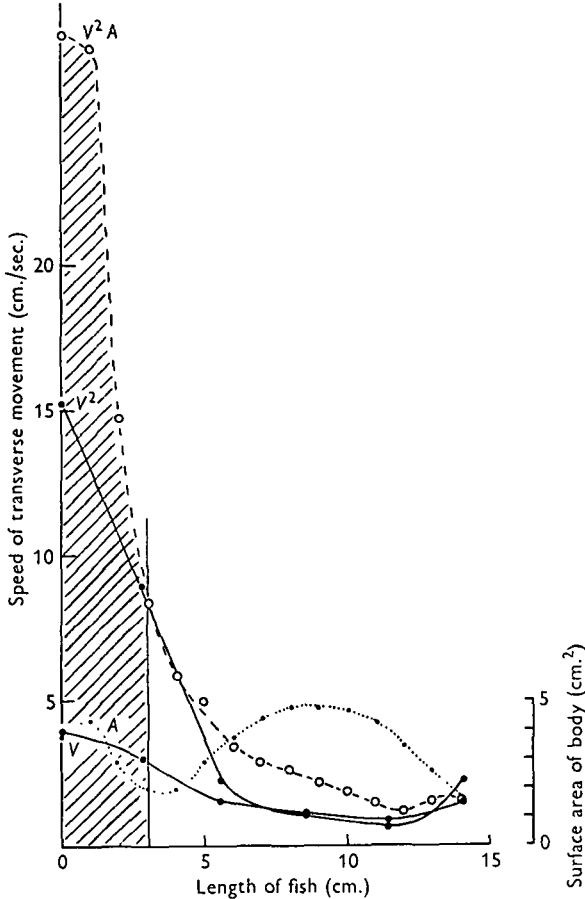


Text-fig. 19. Proportionate distribution of propulsive thrust along the length of the body of a bream. Axis: length of the fish in cm. with the head to the right. Abscissa:  $V$  (full line), speed of transverse movement of body;  $V^2$  (upper full line), the same squared;  $A$  (dotted line), surface area of the body;  $V^2A$  (dashed line), product of speed squared and area, indicating the propulsive thrust. The vertical line shows the anterior boundary of the caudal fin; the shaded area represents its contribution to the total thrust.

tionally by movement of water over the body surface. It is, nevertheless, of interest as a first approximation.

A similar treatment of values for the goldfish is shown in Text-fig. 20. Some striking differences are immediately apparent. The value for the speed of transverse movement falls much more gradually than in the bream so that the caudal peduncle (as already shown in Text-fig. 15) is moving only a little more slowly than the tip of the tail. By the time the tip of the dorsal fin is reached, however, the transverse speed has fallen to about that of the bream and it resembles this further by having a marked rise at the snout. The body outline of the goldfish is very different from that of the

bream in having a relatively much larger caudal fin and a deeper but rather shorter peduncle; the trunk is also rather deeper. The combined effect of these factors is to produce a proportionate thrust curve of quite different form. The base of the tail is here providing as much thrust as its posterior tip but further anteriorly there is a



Text-fig. 20. Proportionate distribution of propulsive thrust along the length of the body of a goldfish. Conventions as in Text-fig. 19.

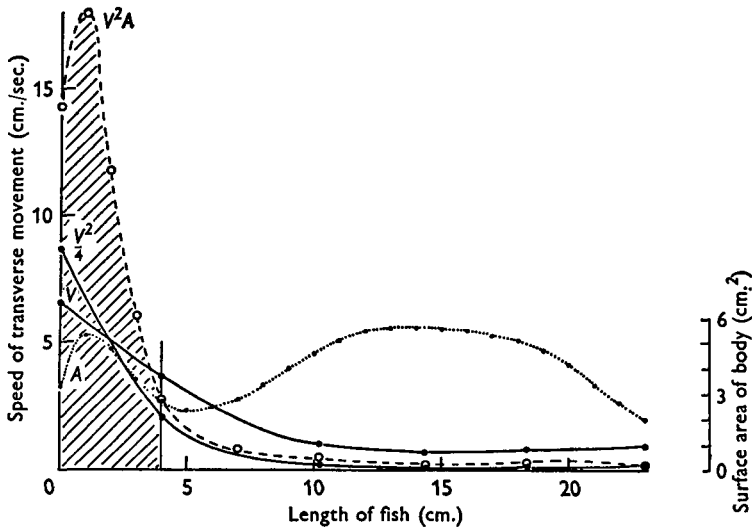
much more rapid fall than in the bream. This increases the relative contribution of the caudal fin and comparison of the two areas to the left and right of the vertical line on the graph shows 65% of the total thrust to come from the fin.

Text-fig. 21 shows a similar treatment of values for the large dace already analysed in Text-fig. 14. Here there is a much more rapid fall in transverse speed as one passes forward along the body and the parts of the trunk anterior to the caudal peduncle could almost be neglected because of their low values. The caudal fin is proportionately large and the flanks are long and deep but the multiple curve of area and velocity squared shows the thrust to be distributed very differently as compared with either the bream or the goldfish. The maximum thrust no longer comes from the tail tip but instead somewhat farther forward, at about the middle of the fin. There is after this an even more rapid and dramatic fall than in the goldfish and the body an-



terior to the peduncle contributes a negligible amount to the total thrust. Comparison of the appropriate areas shows that in the dace 84 % of the total thrust comes from the caudal fin.

It thus seems probable that in different fish the caudal fin contributes very differently to the total thrust developed by the body surface. These differences may in turn be largely dependent on the differences in shape, skeletal structure and musculature of the body which determine the form of the body movement. In those fish transmitting the greater part of the total thrust to the water through the caudal fin the



Text-fig. 21. Proportionate distribution of propulsive thrust along the length of the body of a dace. Conventions as in Text-fig. 20.

importance of the variable modifications of area and shape of the fin in smoothing out the thrust might be expected to be greater than in those fish using most of the body surface for propulsion. These variations are, for example, as would be expected, more noticeable and regular in the dace than in the bream.

SUMMARY

1. Observations made on bream, goldfish and dace swimming in the 'Fish Wheel' apparatus are described. These include:
2. An account of the complex changes in curvature of the caudal fin during different phases of the normal locomotory cycle. Measurements of this curvature and of the angles of attack associated with it are given.
3. An account of changes in area of the caudal fin during the cycle of lateral oscillation. Detailed measurements of these changes, which may involve a 30% increase in height or a 20% increase in area, are given.
4. An account of the varying speed of transverse movement of the caudal fin under various conditions and the relationship of this to the changes in area and amount of bending. Details of the way this transverse speed may be asymmetrically distributed relative to the axis of progression of the fish are given.

5. An account of the extent of the lateral propulsive movements in other parts of the body. These are markedly different in the different species studied. Measurements of the wave length of this movement and of the rate of progression of the wave down the body are given.

6. It is concluded that the fish has active control over the speed, the amount of bending and the area of the caudal fin during transverse movement.

7. The bending of the fin and its changes in area are considered to be directed to the end of smoothing out and making more uniform what would otherwise be an intermittent thrust from the oscillating tail region.

8. Some assessment is made of the proportion of the total thrust contributed by the caudal fin. This is found to vary considerably, according to the form of the lateral propulsive movements of the whole body, from a value of 45% for the bream to 84% for the dace.

I am much indebted to Sir James Gray, F.R.S., for his interest in this work and for his continued support.

#### REFERENCES

- BAINBRIDGE, R. (1958*a*). The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. Exp. Biol.* **35**, 109-33.
- BAINBRIDGE, R. (1958*b*). The locomotion of fish. *The New Scientist*, **4**, 476-8.
- BAINBRIDGE, R. (1960). Speed and stamina in three fish. *J. Exp. Biol.* **37**, 129-53.
- BAINBRIDGE, R. (1961). Problems of fish locomotion. *Symp. Zool. Soc. Lond.*, no. **5**, 13-32.
- BAINBRIDGE, R. (1962). Training, speed and stamina in trout. *J. Exp. Biol.* **39**, 537-55.
- BAINBRIDGE, R. & BROWN, R. H. J. (1958). An apparatus for the study of the locomotion of fish. *J. Exp. Biol.* **35**, 134-7.
- BREDER, C. M. (1926). The locomotion of fishes. *Zoologica, N.Y.*, **4**, 159-297.
- GADD, G. E. (1952). Some hydrodynamical aspects of the swimming of snakes and eels. *Phil. Mag.* **43**, 663-70.
- GERO, D. R. (1952). The hydrodynamic aspects of fish propulsion. *Amer. Mus. Novit.* no. **1601**, 1-32.
- GRAY, J. (1933*a*). Studies in animal locomotion. I. The movement of fish with special reference to the eel. *J. Exp. Biol.* **10**, 88-104.
- GRAY, J. (1933*b*). Studies in animal locomotion. III. The propulsive mechanism of the whiting (*Gadus merlangus*). *J. Exp. Biol.* **10**, 391-400.
- GRAY, J. (1936). Studies in animal locomotion. VI. The propulsive powers of the dolphin. *J. Exp. Biol.* **13**, 192-9.
- v. HOLST, E. (1934). Studien über Reflexe und Rhythmen beim Goldfisch (*Carassius auratus*). *Z. vergl. Physiol.* **20**, 582-99.
- v. HOLST, E. (1937). Bausteine zu einer vergleichenden Physiologie der lokomotorischen Reflexe bei Fischen. II. Mitteilung. *Hippocampus, Scorpaena, Corvina, Heliastes, Apogon, Trigla*. *Z. vergl. Physiol.* **24**, 532-62.
- v. HOLST, E. & LE MARE, D. W. (1936). Bausteine zu einer vergleichenden Physiologie der lokomotorischen Reflexe bei Fischen. I. Mitteilung. *Crenilabrus-Labrus, Sargus, Uranoscopus*. *Z. vergl. Physiol.* **23**, 223-36.
- LIGHTHILL, M. J. (1960). Note on the swimming of slender fish. *J. Fluid Mech.* **9**, 305-17.
- NURSALL, J. R. (1956). The lateral musculature and the swimming of fish. *Proc. Zool. Soc. Lond.* **126**, 127-43.
- NURSALL, J. R. (1958). The caudal fin as a hydrofoil. *Evolution*, **12**, 116-20.
- PARRY, D. A. (1949). The swimming of whales and a discussion of Gray's paradox. *J. Exp. Biol.* **26**, 24-34.
- TAYLOR, G. (1952). Analysis of the swimming of long and narrow animals. *Proc. Roy. Soc. A*, **214**, 158-83.

#### EXPLANATION OF PLATE

Sequence of photographs of a 30.0 cm. dace (*Leuciscus leuciscus*) swimming steadily at 45.5 cm./sec.

The upper two pictures show the complete fish; the lower two rows show simultaneous dorsal and lateral views of the tail during one half cycle of lateral oscillation. The sequence reads from left to right in each row; the interval between successive pictures is  $\frac{1}{16}$  sec.

