

Large-Amplitude Elongated-Body Theory of Fish Locomotion

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Large-amplitude elongated-body theory of fish locomotion

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The elongated-body theory of the reactive forces on a fish moving in water (that is, forces resulting from the inertia of associated water movements) is extended so that a prediction of instantaneous reactive force between fish and water is obtained for fish motions of arbitrary amplitude, regular or irregular (§2). A preliminary application of the theory to the balance of reactive thrust and resistive drag in regular carangiform swimming of fishes with slender caudal fins is made (§3). Comparison with data (Bainbridge 1963) on the dace *Leuciscus* suggests that an important feature of this balance may be a substantial enhancement of drag for such fishes when swimming movements commence, an enhancement here interpreted in terms of a boundary-layer-thinning mechanism first suggested by Dr Quentin Bone.

1. INTRODUCTION

The undulatory motions that most elongated animals make to propel themselves through water have been investigated theoretically, with the aim of estimating their energy cost and the forces between the animal and the water which they generate, by two main methods. The older theory may be called ‘resistive’ in that the force between a small section of the animal and the water was regarded as a resistive force depending exclusively, though not necessarily linearly, on the instantaneous value of the velocity of that section relative to the water. An excellent feature of the more advanced papers (Taylor 1952; Hancock 1953; Gray & Hancock 1955) which expound the resistive theory is that the methods are so developed as to be applicable to undulatory motions of arbitrarily large amplitude.

A newer theory (Lighthill 1960) may be called ‘reactive’ in that it lays principal emphasis on reactive forces between a small volume of water and the parts of the animal’s surface in contact with it. These forces, due to the inertia of the water and proportional to rate of change of the relative velocity of animal surface which a given volume of water feels, are neglected on the resistive theory. They can be particularly important when the cross-section of the animal is much thinner in the direction of the bodily displacements that it makes for swimming purposes than in a perpendicular direction; then, the ‘virtual mass’ of water which acquires momentum through such displacements far exceeds the associated animal mass.

A survey of aquatic animal propulsion (Lighthill 1969) indicated that the undulatory motions associated with elongated invertebrates are best studied by the resistive theory. This is obvious in the many cases when the Reynolds number is low (meaning that water inertia is relatively unimportant), but appears probable even for several cases of swimming, with the Reynolds number around 10^3 , in those worms whose cross-sectional form is not such as to enhance virtual-mass effects.

With the vertebrates, however, posterior lateral compression of body cross-

section appears. This has the advantage that it allows significant reactive forces on body cross-sections to contribute to propulsive effort, with less energy wasted in generating a vortex wake than in the case of resistive forces. In fishes, the undulatory mode of propulsion is called anguilliform, after the eel *Anguilla*, a good example of an animal which needs a propulsive method with low energy wastage because its life-cycle requires it to traverse huge distances.

Anguilliform propulsion of elongated fishes probably uses a combination of resistive and reactive forces (Lighthill 1970). The other main type of propulsive movement capable of producing fast forward motion in fishes seems, however, to have developed so as to make a more exclusive use of reactive forces. In this movement, known as carangiform, the front half of the body has lost its flexibility and flexural movements are confined to the rear half, or even the rear one-third, of the body length.

The characteristic wavelike feature, that the phase of lateral oscillations of any posterior section lags behind that of any anterior section, is retained in carangiform motion, which probably developed from the more obviously wavy anguilliform motion. In other respects, however, carangiform motion is very different: wave amplitude (which in anguilliform motion increases gradually from head to tail) shows such a steep increase towards the tail in the last one-third of the body length that the observer of carangiform motion cannot see anything like a whole wavelength at any one time. He is much more conscious, simply, of lateral tail oscillations with the posterior end lagging behind anterior sections.

The reactive forces dominate in carangiform motion because the acceleration of water passed by the fish takes place very fast, during the time required for a short posterior portion to pass and flick it into motion through the instantaneously acting virtual-mass effect. By contrast, little time is available for build-up of resistive forces through the usual process of vortex shedding in the cross flow (typically, the water feels a total lateral displacement of fish surface against it of only half a cross-sectional depth).

Lighthill (1970), in a paper constituting a sort of mathematical appendix to his 1969 survey, showed that these features give an advantage over anguilliform motion with respect to efficiency, provided that carangiform motion is combined (as is found in practice) with certain morphological features, including especially a pronounced reduction in depth of body cross-section just anterior to the caudal fin, whose effect is to minimize 'recoil' motions of yaw and sideslip due to unbalanced oscillations of sideforce. Although Lighthill (1960) had assumed that such recoil would result in too much loss of efficiency unless the swimming motions included practically a whole wavelength at any one time, Lighthill (1970) calculated that this local depth reduction makes the oscillations of sideforce much smaller, while maintenance of substantial depth of cross-section for a lengthy extent of fish around its mass centre reduces what yaw and sideslip does result by involving a large mass of water in any such motions.

The elongated-body theory that goes back to Lighthill (1960), and is based on

ideas from what aerodynamicists call 'slender-body theory', is the reactive theory appropriate to the great majority of fishes using carangiform propulsion: namely, those with caudal fins that are 'slender' in the sense that each individual bony ray of which the fin is made up makes only a moderately small angle (not more than say 30°) with the backbone. A different reactive theory is appropriate to that important minority which have acquired even greater speed by abandoning slender caudal fins in favour of the so-called 'lunate' or crescent-moon-shaped tails of high aspect-ratio. The right theory for them must be one based on wing theory: for example, that developed by Wu (1961) and others, and applied by Lighthill (1969, 1970) to the fishes with lunate tails as well as to the cetacean mammals. In this paper, however, those problems are put aside in order to concentrate upon the possible improvement of elongated-body theory.

The object is to extend reactive theory so that it can be applied to interpret observational data on animal movements of arbitrary large amplitude (as was earlier mentioned to have been achieved already with resistive theory). The existing theory is based on a perturbation expansion in powers of an amplitude parameter ϵ (Lighthill 1960, Appendix) and derives thrust and energy consumption as multiples of ϵ^2 with terms of order ϵ^4 neglected. The inadequacy of such an expansion in powers of amplitude can be seen from the fact that in carangiform motion the component of caudal fin velocity at right angles to the path may rise to twice the forward velocity of the fish. A theory which takes into account the large fish flexures and lateral velocities used in propulsion is needed. Such a theory should have the additional advantage that it could be applied to study interesting questions like the mechanism of turning in fishes of the type here investigated (although no work on this application is included in the present paper).

Clues on how to obtain a large-amplitude theory may be suggested by studying the conclusions of the rather complicated perturbation theory and finding ways of interpreting them that suggest a physical basis on which a large-amplitude theory might be founded. Lighthill (1960, Section 2) gave one physical interpretation of the perturbation-theory results, in terms of rate of working and rate of energy wastage, that was further developed by Lighthill (1969, 1970), but that interpretation is not easy to extend to large-amplitude motions.

Lighthill (1970), however, finally obtained an alternative, quite different physical interpretation of the perturbation-theory results, directly in terms of the force of propulsion (see his equations (13) to (15)). It is expressed most satisfactorily in a frame of reference in which the water far from the fish is at rest, and makes use of three principles:

(i) Water momentum near a section of fish is in a direction perpendicular to the backbone and has magnitude equal to the virtual mass, m per unit length, times the component w of fish velocity in that direction.

(ii) Thrust can be obtained by considering rate of change of momentum within a volume enclosing the fish whose boundary at each instant includes a flat surface Π perpendicular to the caudal fin through its posterior end.

(iii) In the momentum balance it is necessary to take into account transfer of momentum across Π not only by convection but also by the action of the resultant $\frac{1}{2}mw^2$ of the pressures generated by the motions within the plane Π .

Fortunately, principles (i) to (iii) are in a form suitable for direct use in making a reactive theory valid for arbitrary large amplitudes of motion. This statement is supported by detailed argument in §2, but one important aspect may be noted at the onset: even though individual sections of fish have large lateral velocity components, even in excess of the forward velocity, the velocity component w perpendicular to the backbone is usually much smaller (as, indeed, is required for good efficiency). We should note, furthermore, that the estimation of recoil, an important matter for carangiform propulsion, is facilitated by the new formalism, which, finally, is also useful for studying how far the detailed motions made in carangiform propulsion have the effect of reducing variations of the thrust with time about its mean value.

It goes without saying that it would be desirable to progress ultimately to a combined resistive-reactive theory for motions of large amplitude, which might be applied to elongated animals in general. That would be an extremely complicated task, however, and it is therefore natural to make a first effort, as here, on a purely reactive theory, and to relate it to the appropriate field of application: namely, the motion of fishes with slender caudal fins which use the carangiform mode of propulsion.

2. CALCULATION OF THE REACTIVE FORCE

The theory, as already remarked, is set out in a frame of reference in which the water far from the swimming fish is at rest. The fish is supposed to be swimming at a fixed horizontal level. The y -axis is vertical, and the x - and z -axes are horizontal axes at right angles whose directions may be chosen arbitrarily, although when there is a constant *mean* direction of swimming that might suitably be taken as that of the positive x -axis.

To describe large-amplitude motions of the fish's spinal column in a horizontal plane $y = 0$, we use a 'Lagrangian' coordinate a , which takes values from 0 to l (the length of the undistorted fish), and identifies a point on the spinal column by its distance from the posterior end of the fish (tip of the caudal fin) measured along the spinal column, whose extensibility is small and will here be neglected. The position coordinates (x, z) of that point at time t within the horizontal plane $y = 0$ are regarded as functions $x(a, t)$ and $z(a, t)$ of a and t , as the point moves due (i) to swimming actions, (ii) to the resulting forward motion of the fish, and (iii) to any lateral recoil motions that may be involuntarily produced (figure 1).

The assumed inextensibility of the spinal column can be expressed mathematically by the equation

$$\left(\frac{\partial x}{\partial a}\right)^2 + \left(\frac{\partial z}{\partial a}\right)^2 = 1. \quad (1)$$

The horizontal velocity vector $(\partial x/\partial t, \partial z/\partial t)$ then has a component

$$u = \frac{\partial x}{\partial t} \frac{\partial x}{\partial a} + \frac{\partial z}{\partial t} \frac{\partial z}{\partial a}, \quad (2)$$

directed tangentially to the spinal column in the forward sense, and a component

$$w = \frac{\partial z}{\partial t} \frac{\partial x}{\partial a} - \frac{\partial x}{\partial t} \frac{\partial z}{\partial a}, \quad (3)$$

directed perpendicularly to the spinal column, in a sense so that (u, w) make a left-handed system of axes if (x, z) do (figure 2).

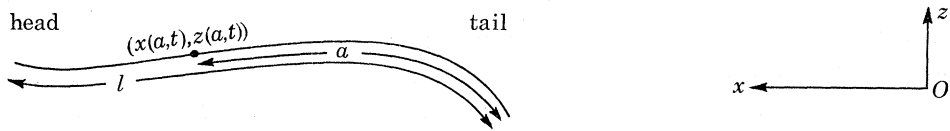


FIGURE 1. The coordinate system used to describe the spinal column's configuration in the plane $y = 0$ at time t .

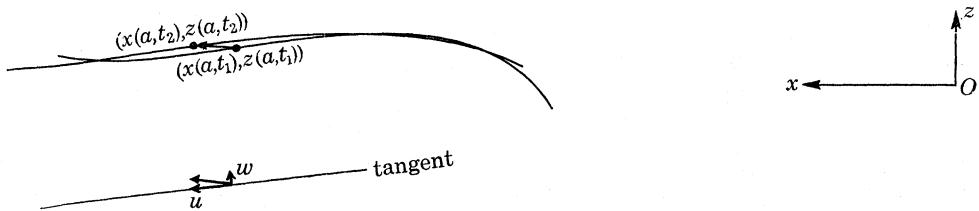


FIGURE 2. The spinal column's configuration at two successive instants t_1 and t_2 . The arrow indicating the displacement of a particular point on the spinal column between the two instants represents the velocity vector of that point multiplied by the time separation $t_2 - t_1$. The lower diagram shows this velocity vector resolved into components u tangential to the spinal column and w perpendicular to it.

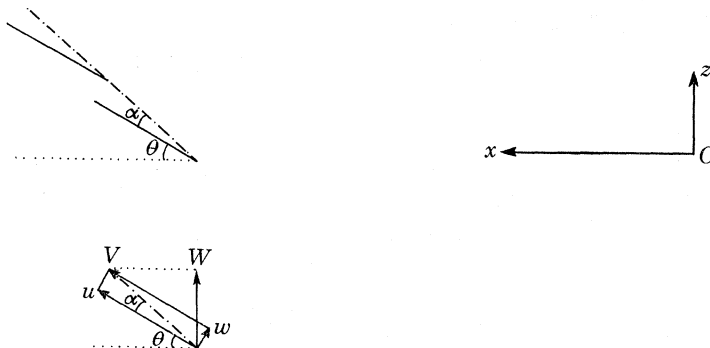


FIGURE 3. Motion of the tip of the caudal fin. The upper diagram shows its position at two successive instants and defines the angles θ and α . The lower diagram shows how the tip's velocity vector, of magnitude V , may be resolved either into components u tangential and w perpendicular to the tip, just as in figure 2, or alternatively into a component W perpendicular to the direction of mean motion (see equation (10) below).

The essential property characteristic of an 'elongated body' is that the virtual mass, m per unit length, in respect of the w motions (perpendicular to the backbone) is large, whereas the u motions (tangential to the backbone) have negligible virtual mass. Those tangential motions, to be sure, are what actually contribute the viscous resistance that will have to be considered as balanced by the reactively produced thrust; one way to put this is to say that tangential motions will be treated resistively and perpendicular motions reactively. We begin that process in this Section, however, by simply determining the reactive force associated, on purely inviscid considerations, with the momentum of the w motions.

This momentum per unit length of fish is represented by the vector

$$mw(-\partial z/\partial a, \partial x/\partial a), \quad (4)$$

where the factor in parentheses is a unit vector in the w -direction (expressed in terms of its x - and z -components). Lighthill (1970) gives a full discussion† of the appropriateness of regarding m for a given cross-section of fish as a constant close to $\frac{1}{4}\pi\rho s^2$, where ρ is the water density, and s the depth of the cross-section; in the present notation this would normally make m a fixed, known function $m(a)$ of the distance a from the posterior end of the fish. However, in cases like those described by Bainbridge (1963) where fishes with flexible caudal fins cause their depth to vary with time t during the swimming cycle, m needs to be written as $m(a, t)$, and we shall for generality's sake assume this in what follows.

It might be thought straightforward to use the momentum distribution (4) to infer the reactive force between fish and water. For this purpose, however, Lighthill (1970) showed that any method based on the rate of change of momentum of the whole water mass encounters a serious difficulty: that of calculating the rate of change of one element of that momentum, namely, the momentum in the wake (that consists of vorticity shed from the caudal fin's trailing edge). The approximate method for doing this given in equation (18) of that paper would be hard to extend to large-amplitude motions.

A much more satisfactory approach is based on a study of the rate of change of momentum in a certain part only of the fluid; a part V , that excludes the wake. To give a definition of V , at each moment of time, in a manner satisfactory for large-amplitude motions, we first imagine a vertical plane Π intersecting the tip of the caudal fin at right angles to the tip of the spinal column; this plane has to be thought of as swinging around as the fin moves. Then at each instant the part V of water whose momentum is considered is that half-space, bounded by the plane Π , which includes the fish and excludes the wake.

† Note that this includes discussion of the influence of cross-section non-uniformity. When that non-uniformity can be analysed into sine-wave components, the error is less than 25% for all components with wavelengths greater than $5s$. It may also be noted from aerodynamic slender-wing theory that the overall forces at small angle of incidence on a 'delta' shape (an isosceles triangle with apex forwards, such as one might indeed use to represent a caudal fin) are given to within 25% by using the above value of m if the total included angle at the apex is less than 60° .

The momentum† in V can be written as the integral of expression (4) from 0 to l with respect to a , and its rate of change can be written as the sum of three terms: (i) rate of change due to convection of momentum out of V across the plane Π ; (ii) rate of change due to the pressure force acting across Π ; (iii) minus the reactive force (P, Q) with which the fluid acts on the fish.

To estimate (i), we note that convection across Π is produced to only a negligible extent by any motion of fluid in the u -direction perpendicular to Π , since only the w -motion of the fin produces significant fluid motion. Convection arises, however, from the motion of Π itself; this consists of a forward translation at the u -velocity (2) and a rotation; however, since fish cross-sections are laterally symmetric the water-momentum distribution has lateral symmetry and therefore no net rate of change of momentum within V results from the rotation of Π .

Lighthill (1970, equations (14) and (15)) gave a simple argument, directly applicable also to large-amplitude motions, proving that the pressure force in (ii), that is, the resultant over Π of the pressures associated with the w -motion of a laterally symmetric section with virtual mass m per unit length, is $\frac{1}{2}mw^2$. It acts in the tangential direction represented by the unit vector $(\partial x/\partial a, \partial z/\partial a)$. Using this with the results of the last two paragraphs, we obtain

$$\frac{d}{dt} \int_0^l mw \left(-\frac{\partial z}{\partial a}, \frac{\partial x}{\partial a} \right) da = \left[-umw \left(-\frac{\partial z}{\partial a}, \frac{\partial x}{\partial a} \right) + \frac{1}{2}mw^2 \left(\frac{\partial x}{\partial a}, \frac{\partial z}{\partial a} \right) \right]_{a=0} - (P, Q), \quad (5)$$

where the terms on the right-hand side are written down in order as in (i), (ii) and (iii) above.

Inspection of the square bracket in (5) shows that it can be usefully simplified. In fact, if the $\frac{1}{2}$ were absent, then equations (1) to (3) show that it would reduce to $mw(\partial z/\partial t, -\partial x/\partial t)$, as can easily be verified if mw is taken out as a factor. It follows that we can rewrite the actual equation (5) as

$$(P, Q) = \left[mw \left(\frac{\partial z}{\partial t}, -\frac{\partial x}{\partial t} \right) - \frac{1}{2}mw^2 \left(\frac{\partial x}{\partial a}, \frac{\partial z}{\partial a} \right) \right]_{a=0} - \frac{d}{dt} \int_0^l mw \left(-\frac{\partial z}{\partial a}, \frac{\partial x}{\partial a} \right) da. \quad (6)$$

Equation (5) and this simpler form of it (6) are, respectively, generalizations of equations (13) and (11) of Lighthill (1970), that extend them so as to give the force in vector form for the case of large-amplitude motions.

Note that, for periodic swimming movements, producing a mean motion in (say) the positive x -direction, there is no contribution to the mean thrust, that is, to \bar{P} (where the bar denotes a mean), from the integral term in (6), because its value fluctuates periodically between fixed limits, so that the time mean of its rate of change is zero. The mean thrust can therefore be written

$$\bar{P} = \overline{[mw(\partial z/\partial t - \frac{1}{2}w \partial x/\partial a)]_{a=0}}. \quad (7)$$

This suggests the same conclusion as was obtained in the small-amplitude case, that good thrust can be obtained if w and $\partial z/\partial t$ have high positive correlation but

† More strictly, the momentum as calculated from the point of view of a reactive theory, and neglecting therefore any influence of the viscous boundary layer at the fish surface.

the latter has a substantially larger amplitude of oscillation. The requirement for w to have relatively smaller amplitude is reduced however if fluctuations of w^2 are negatively correlated with those of $\partial x/\partial a$ at $a = 0$, as characteristically occurs in carangiform motion, since $\partial x/\partial a$ is the cosine of the angle between caudal fin and mean swimming direction, an angle which tends to be greatest when w is large.

It is noteworthy, moreover, that the x -component of equation (6) gives not only the mean thrust \bar{P} but also instantaneous values of P . Although the term in square brackets may have a substantial positive mean value, it falls to zero twice in each swimming cycle (when w passes through zero), so that the associated thrust is distinctly intermittent. Fortunately, the carangiform type of movement is such that fluctuations of the second term

$$\frac{d}{dt} \int_0^l mw \frac{\partial z}{\partial a} da \quad (8)$$

in P are often nearly opposite in phase, and help to smooth out very considerably the fluctuations of P .

To see this, note first that carangiform motion involves a rapid falling away in the amplitude of oscillation of $z(a, t)$ as well as of mw as a increases from its tip value $a = 0$. The integral (8) might be approximated, crudely, therefore, as a product of the amount $[-z]_{a=0}$, by which z changes between the tip $a = 0$ and an anterior section, and of a crude estimate $[\frac{1}{2}mw]_{a=0}$ of an average of mw in that region. This admittedly rough approximation to the amplitude, and underestimate of the phase of the latter average, produces exact cancelling of the fluctuations of thrust if sinusoidal variations of z and mw at $a = 0$, say

$$z = z_0 \sin \omega t, \quad mw = m_0 w_0 \cos \omega t, \quad (9)$$

are assumed. For then (6) would give

$$P = m_0 w_0 z_0 \omega \cos^2 \omega t + \frac{d}{dt} (-\frac{1}{2} m_0 w_0 z_0 \sin \omega t \cos \omega t) = \frac{1}{2} m_0 w_0 z_0 \omega. \quad (10)$$

It is probable that even in practice some such smoothing of the fluctuations, although not so complete, does occur.

In addition, (6) is important as giving the fluctuations in the sideforce ($-Q$) acting on the fish, which are needed for estimating recoil. Actually, the change in conclusions from those of small-amplitude theory is still more moderate in the case of the sideforce, which (6) gives as

$$-Q = \left[mw \frac{\partial x}{\partial t} + \frac{1}{2} mw^2 \frac{\partial z}{\partial a} \right]_{a=0} + \frac{d}{dt} \int_0^l mw \frac{\partial x}{\partial a} da. \quad (11)$$

The differences from the expression (49) in Lighthill (1970) are (i) the mean forward velocity U is replaced by the fluctuating forward velocity $\partial x/\partial t$ of the tip of the caudal fin; (ii) a third-order term $\frac{1}{2} mw^2 \partial z/\partial a$ of very modest magnitude is included; (iii) the integral is modified by the factor $\partial x/\partial a$.

None of these differences is large, and the general conclusions of Lighthill (1970), that recoil is minimized by a shape which maintains a good depth of cross-section in the anterior portion of the fish and exhibits a substantial reduction in depth immediately anterior to the caudal fin, can be drawn as before. To see in the present frame of reference that the latter feature is needed to minimize sideforce, note that where the amplitude of oscillation of $z(a, t)$ is rapidly changing with a , the second term in (3) must have a large value not offset by a correspondingly large value for the first term. Fluctuations in the integral in (11) would therefore be large unless m were greatly reduced in the same region.

Finally, we may note how the method used for calculation of the reactive force can be adapted to determine the rate at which the swimming movements which produce that force generate waste energy in the wake. On inviscid theory the kinetic energy associated with w -motions is $\frac{1}{2}mw^2$ per unit length, and the volume V loses such energy only through convection across the plane Π due to its forward translation at the u -velocity (2). (Rotation of Π again produces no net rate of change because the kinetic-energy distribution has lateral symmetry, and the pressure distribution over Π conveys negligible energy across it because velocity components perpendicular to Π are negligible.) The mean rate of energy wastage, therefore, is

$$\overline{\left[\frac{1}{2}mw^2u\right]_{a=0}}. \quad (8)$$

This predicted rate of energy wastage is greater than the value given by the small-amplitude approximation, on which u is replaced by the mean swimming speed

$$U = \overline{[u\partial x/\partial a]_{a=0}}, \quad (9)$$

with a resulting reduction in (8) since $\partial x/\partial a < 1$.

3. DISCUSSION OF THE THRUST-DRAG BALANCE IN RELATION TO OBSERVATIONS

In this paper we make only a first attempt to use the theory of §2 in the analysis of experimental data: an attempt confined to the problem of mean thrust and its balance against mean drag in motions with constant mean speed. Within the limitations of the reactive theory of thrust production, this requires us to study, for actual carangiform movements of fishes with slender caudal fins, the balance between the mean thrust, produced reactively by their w motions (perpendicular to the spinal column), and the mean drag, produced resistively by their u motions (tangential to the spinal column).

We shall see that not nearly enough data exist to make any accurate balance possible, but that even an approximate balance suggests conclusions perhaps interesting enough to stimulate experiments aimed at obtaining more complete data. Ideally one would like, for horizontal swimming in water known to be still, pictures taken by a vertical cine camera, at not less than 16 frames per swimming

cycle, of the complete cycle of swimming movements associated with each of a range of forward speeds in the same fish. To compare with the drag estimated from its measured u motions, it would be desirable to be able to infer also the drag incurred by the same fish when not making swimming movements, e.g. from motion pictures of its gliding deceleration under such conditions.

Available data are not nearly so complete for any single fish. Bainbridge (1958, 1960, 1963) obtained controlled water conditions in his 'fish wheel' (annular fish tank with antiscrolling gate), and we analyse below his excellent motion pictures of a dace *Leuciscus* of 0.3 m length swimming at 0.48 m/s. Unfortunately this was only a small fraction of the animal's maximum speed and comparable records at higher speed were not obtained; also, no drag measurements on the animal are available. Excellent motion pictures obtained much earlier from various species by Gray (1933) are subject to the same reservations. Conversely, a few experimenters have determined the drag of a fish moving rigidly and symmetrically; for example, Sundnes (1963) in towing experiments found values for salmon and herring, C_D being around 0.01 in each case† for Reynolds number around 10^6 ; a drag value somewhat, but not excessively, above the expected smooth-body value (see below and also Hoerner 1965, chapter 6), the towing attachment being the probable cause of drag enhancement. Records of swimming movement for the same fish do not, however, exist.

Among such records of swimming movements as do exist, those involving carangiform motion with slender caudal fin represent only a small proportion, within which the clearest record seems to be that of Bainbridge (1963) on *Leuciscus*. He shows in his figure 1 the position and attitude of the caudal fin, seen from above, at successive instants 0.02 s apart, for a mean forward velocity of 0.48 m/s achieved by swimming movements at a frequency of about 2.5 Hz. From these data and from the variations in depth of the caudal fin depicted in his figure 3, it is possible to estimate the mean thrust \bar{P} as given on the reactive theory by equation (7).

Table 1 shows measured values of several parameters relating to the motion of the tip of the caudal fin at various times t in the swimming cycle. Here, V means its absolute speed relative to the water, the angle θ is its inclination to the direction of mean motion, and the angle $\alpha + \theta$ is the inclination of the path, travelled by the tip of the caudal fin, to that direction, these angles being taken positive to the right. Thus, α is an angle of incidence which is positive when the sideforce on the caudal fin is directed to the left. In these terms we have (see figure 3)

$$w = V \sin \alpha, \quad W = \partial z / \partial t = V \sin (\alpha + \theta), \quad \partial x / \partial a = \cos \theta, \quad (10)$$

quantities whose values are also shown in table 1, together with the variations in the tip value of $m = \frac{1}{4}\pi\rho s^2$ obtained from Bainbridge's measurements of the tip depth s .

† Here and elsewhere, C_D is drag divided by $\frac{1}{2}\rho U^2$ and by the total 'wetted area' of the fish.

TABLE 1. MEASURED VALUES OF SWIMMING PARAMETERS FOR *LEUCISCUS* OBSERVED BY BAINBRIDGE (1963, TEXT-FIGURES 1 AND 3)(Note: 1 N = 1 kg ms⁻² = 10⁵ dyne.)

quantity	...	<i>t</i>	<i>V</i>	$\alpha + \theta$	α	<i>W</i>	<i>w</i>	$\partial x / \partial a$	<i>s</i>	<i>m</i>	<i>mwW</i>	$\frac{1}{2}mw^2$ $\partial x / \partial a$	$\frac{mwW}{\frac{1}{2}mw^2}$ $\partial x / \partial a$
unit	...	s	ms ⁻¹	deg	deg	ms ⁻¹	ms ⁻¹	1	m	kg m ⁻¹	N	N	N
		0.04	0.50	17	3	0.15	0.03	0.97	0.094	6.9	0.03	0.00	0.03
		0.08	0.60	45	3	0.42	0.03	0.74	0.087	5.9	0.07	0.00	0.07
		0.12	0.74	60	5	0.64	0.06	0.57	0.079	4.9	0.19	0.01	0.18
		0.16	0.68	48	16	0.50	0.19	0.85	0.083	5.4	0.51	0.08	0.43
		0.20	0.52	13	10	0.12	0.09	1.00	0.087	5.9	0.06	0.02	0.04
		0.24	0.62	-36	-8	-0.36	-0.09	0.88	0.088	6.1	0.20	0.02	0.18
		0.28	0.87	-60	-16	-0.75	-0.24	0.72	0.083	5.4	0.97	0.11	0.86
		0.32	0.67	-46	-10	-0.48	-0.12	0.81	0.084	5.5	0.32	0.03	0.29
		0.36	0.52	-25	-6	-0.22	-0.05	0.95	0.092	6.6	0.07	0.01	0.06
		0.40	0.48	-3	0	-0.02	0.00	1.00	0.093	6.8	0.00	0.00	0.00

From these results are obtained the values of mwW and of $\frac{1}{2}mw^2 \partial x / \partial a$ and of their difference, as given in the last three columns of table 1. The second term (physically due to the pressure force acting across the plane II) is found to make only a small negative contribution to this difference, a difference whose mean over the cycle is equal to the predicted mean thrust. This mean comes to 0.2 N, where the computation is not accurate enough to justify giving more than one significant figure.

This conclusion is interesting, however, because it implies a corresponding value for the mean resistance associated with the tangential motions of the surface, and this value is several times greater than would be expected for the gliding motion of a streamlined shape such as *Leuciscus* of length 0.3 m and velocity 0.48 m/s. The wetted surface area S of the fish can be inferred from Bainbridge's photographs to be about 0.04 m² so that the value of $\frac{1}{2}\rho U^2 S$ is about 5 N. A drag of about 0.2 N implies therefore a drag coefficient based on wetted area of about $C_D = 0.04$, something like four times greater than would be expected at a Reynolds number based on length of $R = 10^5$.

This discrepancy is big enough to be insensitive to the many inaccuracies in the thrust calculation, as well as to uncertainties in the C_D value for gliding motion. Under the circumstances, it is sufficiently accurate to estimate this C_D value from known results for streamlined bodies of revolution. The maximum cross-section of the fish (see Bainbridge's Plate I) is an oval of major and minor axes 0.07 and 0.04 m, which from a viscous-resistance standpoint may be roughly equivalent to a circle of diameter 0.06 m (which would have a perimeter of approximately equal length). The fineness ratio of the equivalent body of revolution is thus 5 based on the complete length of fish, or 4 based on the length taken to the caudal peduncle (where the cross-sectional area first becomes very small). Results summarized by Hoerner (1965, chapter 6, figure 22) suggest that C_D is normally around 0.01 for

fineness ratios between 4 and 5 when $R = 10^5$. (It might be imagined that the turbulence which was probably present in Bainbridge's 'fish wheel' would have increased the appropriate value of C_D , but data in figure 23 of Hoerner's chapter 6 indicate that drag is negligibly increased by turbulence stimulation around $R = 10^5$.)

Evidently it may be rather important to investigate the discrepancy here apparent, by something like a factor of 4, between the simplest estimates of reactive thrust and resistive drag, even though the degree of importance of the discrepancy will not be clear until similar comparisons have been made for many other fishes. In the meantime a few comments must be made about various factors that may or may not be contributing to the discrepancy.

To begin with possible sources of error in the thrust estimate, the most obvious source of error is neglect of the resistive component, but probably this can be eliminated as an explanation of the discrepancy, which it would tend to increase if anything rather than decrease (Lighthill 1970). At the same time, error in the estimate of reactive thrust itself might arise because the estimate does essentially assume some small contribution from suction force at the leading edge of the caudal fin. Although this is a small part of the whole (of order w^2 rather than wW) it may be difficult to realize because of flow separation associated with the relative sharpness of the caudal fin's leading edge. It is on the other hand, possible, in view of the caudal fin's marked degree of flexibility, that the leading edge flexes sufficiently so that flow separation is significantly postponed. The flexing observed by Bainbridge (1963) is in the right direction for this, but even if the postponement does not occur the error is much too small to explain the discrepancy.

In Bainbridge's experiments the fish swam close to the bottom of the tank. It is not certain what the effect of this on the thrust-drag discrepancy would be, but the most obvious possibility is one of substantial thrust augmentation from ground effect. Estimation of the ground effect by regarding the ground as a reflexion plane suggests that the effective depth of the tip of the caudal fin and its reflexion taken together might be doubled, leading to a quadrupled virtual mass for the two taken together. That part of the associated momentum which attaches to water above the ground plane would on this argument be half the quadrupled water momentum associated with the pair of fins. There might accordingly be a doubling of lateral momentum associated with the caudal fin when it is near the ground, and a concomitant doubling of the thrust produced by given swimming movements.

All these considerations of possible refinements in the thrust calculation lead one with increasing conviction to the view, first expressed to the author by Dr Bone, that the viscous drag on the fish while it is swimming (that is, the drag needed to balance this reactive thrust) must for some reason be many times greater than that which would be associated with gliding motion. This conclusion is in the opposite sense to the famous 'Gray's paradox', but we must emphasize that it is being drawn here for a quite different group of animals.

In phrasing this conclusion, the term 'viscous drag' has been used to emphasize

that the resistance associated with tangential movements (u -movements) is involved. The wave-like character of the fish's movements ensures, by contrast, that the vortex-force associated with any perpendicular movements (w -movements) would be in the thrust direction. This is why, as already mentioned, any such force must make a positive resistive contribution to the total thrust.

Some other studies have shown how, when a fish is passively towed through the water, but lateral flutter of its body and fins is permitted, resistance similarly exceeds (and by a comparable factor) the value associated with rigid gliding motion. Webb (1970, p. 98) found this for freshly killed trout in a water tunnel, and obtained a resistance increasing with the degree of flutter permitted. His values of C_D with flutter practically restricted to the fins are about 0.015, agreeing well with values obtained for live trout in a measurement of gliding deceleration by Gray (1957). When the posterior portion of the dead trout, though stiffened by wires, was able to flutter significantly, Webb obtained values clustered about 0.03. It is uncertain whether these are primarily augmentations of viscous resistance, such as we postulate for drag augmentation by swimming movements, but the arguments that follow suggest this as a possibility.

Some independent evidence of viscous drag augmentation by swimming movements is provided by Smit (1965). He estimates the power output of the swimming muscles in goldfish (*Carassius auratus*) from their oxygen consumption when swimming in a fish wheel, and calculates (assuming 80% propulsion efficiency) that it exceeds by a factor 3.6 that needed to overcome viscous resistance in a rigid gliding motion (estimated approximately as above). This factor 3.6 obtained in a fish wheel, where relative velocity of fish and water is known rather accurately, is to be preferred to the factor that Smit obtained in water-channel experiments because fishes commonly use the slower flow in a channel boundary layer to reduce their required power output.

Dr Bone has suggested to the author one explanation of the augmentation of viscous drag through swimming movements, which seems quite the most promising at the present time. It is based on the idea that skin-friction over a large part of the surface is probably much greater than would be expected at a body length corresponding to a Reynolds number of 10^5 , because lateral movements prevent boundary layers from growing to anything like the thickness associated with such a body length.

The possibility that large drag augmentation may result from this is suggested by calculations of boundary-layer thicknesses on highly simplified assumptions. For example, a Blasius boundary layer (with uniform external stream velocity U) has a 'frictional boundary-layer thickness' δ (defined so that skin friction is $\mu U/\delta$) equal to $3\sqrt{(\nu x/U)}$ at a distance x from the leading edge. We may compare with this value a frictional boundary-layer thickness δ for a flat section of depth s moving perpendicularly to itself with velocity w , which is $0.6\sqrt{(\nu s/w)}$ on the side towards which the section is moving.

Evidently, the two thicknesses differ by a factor of around 5, since the two square

roots would be close to each other in value for typical fish-swimming conditions. In practice, recoil causes there to be some significant w -velocity all along the swimming fish, for which therefore the effective boundary-layer thicknesses may be very substantially reduced below those associated with gliding motion.

On this view it would be the balance, existing between viscous diffusion of vorticity away from the fish's surface and convection of vorticity towards the surface by relative lateral motion between it and the water, that would determine the boundary-layer thickness, and hence also the skin-friction drag associated with the tangential u -motion. On parts of the surface that have a component of movement towards the undisturbed water, the skin friction might be increased over that for gliding flow by a large factor, around 5. This is the sort of difference that is needed to explain the thrust-drag discrepancy.

On this explanation, the relatively large amplitudes of tail motion exhibited by most swimming fishes must be interpreted in terms of the need to produce reactive thrusts sufficient to balance the greatly enhanced viscous drag that appears once any lateral movements commence. Steady swimming with small amplitudes of tail motion would on this hypothesis be rather futile, and indeed less efficient as a means of achieving a moderate rate of progress than production of thrust by those large-amplitude movements, interspersed with periods of gliding, such as are commonly observed among fishes in tanks.

In conclusion, it is necessary to emphasize the tentative nature of these suggestions about a probable thrust-drag discrepancy and its possible explanation. More data to reach greater clarity on the subject are urgently needed.

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