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Biofluiddynamics of balistiform and gymnotiform locomotion.
Part 1. Biological background, and analysis by elongated-body theory

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Elongated-body theory has been fruitfully applied over twenty years to the biofluiddynamic analysis of modes of locomotion of elongated fishes by means of body flexure, with special emphasis on the anguilliform mode using undulatory body movements, and on the carangiform mode where oscillatory movements of only a fish's posterior end (including the caudal fin) exhibit phase lag of posterior movements behind anterior movements just as in an undulation yet not nearly as much as a whole wavelength is apparent at any one time. The extension of elongated-body theory to analyse the locomotion of elongated fishes with elongated median fins (dorsal and/or anal) in modes where the body (together with any caudal fin) remains rigid, being propelled forwards by undulations or oscillations of those median fins, has long been recognized as desirable but is here presented for the first time.

In many large groups of fishes, evolutionary adaptation to limited environments (such as coral reefs) favoured a development of defensive 'armour' at the expense of speed, to such an extent that bodies became essentially inflexible, with locomotion achieved by fin movements alone. In one principal group of such fishes, however (the sub-order Balistoidei including the trigger-fishes), a later evolutionary development restored a capacity for relatively high-speed movement even though the body remained essentially rigid. The balistiform mode of locomotion, with propulsion achieved by synchronized movements of the dorsal and anal fins, exists in two alternative forms, with either undulatory or oscillatory movements of these median fins, that are analogous to the anguilliform and carangiform modes of body flexure, respectively.

Analysis in this paper throws light on the puzzling question of why trigger-fishes are able to move so fast notwithstanding the modest extent of their fin movements. A form of the large-amplitude elongated-body theory, specially adapted to balistiform locomotion, allows a direct comparison of thrust and efficiency for different modes of propulsion. The conclusions in brief are that thrust is dominated by the mean rate of shedding of backward momentum at the posterior end of the fish's propulsive apparatus and that, for movements of median fins attached to a deep, essentially rigid body, this momentum is increased (above the momentum expected for the same movements of the fins 'on their own') by a momentum enhancement factor β of around 3 or a little more. Yet there is no such enhancement of the rate of shedding of 'unproductive' energy into the wake; accordingly, overall efficiency is improved. Also, especially for the undulatory mode of balistiform locomotion, sideforces are minimized so that the fish body avoids sideslip and yaw;

accordingly, the body drag which fin thrust must overcome is reduced by another large factor.

Alongside discussion of the Balistoidei, this paper reviews and analyses balistiform locomotion as observed in several other groups, including groups of flexible-bodied fishes that regularly use this mode as a low-energy-cost alternative to locomotion by means of body flexure. Finally, we similarly analyse gymnotiform locomotion, in which the body is again held rigid, being propelled by undulations in just a single (ventral) fin, and compare and contrast different interpretations of its advantages.

1. Introduction

The twofold challenges of *Mathematical Biofluiddynamics* as described in a book with that title (Lighthill 1975, hereinafter referred to as *MB*) are derived from the problems of mathematically analysing complicated three-dimensional unsteady flows 'energized by the working of an animal's motile external or internal surfaces, parts of which are highly flexible' (*MB*, p. 1) while recalling that 'the analyses required must be carefully defined and interpreted in a full and intricate biological context' (*MB*, p. 2). These problems are well illustrated by the study of fish locomotion, set in its biological context in *MB*, pp. 11–44 as well as in more recent monographs (Blake 1983*a*; Webb & Weihs 1983), and shown (*MB*, pp. 103–114) as demanding from the mathematician a large-amplitude analysis of the three-dimensional unsteady fluid motions.

For the quantitative study of how in a wide range of fish species body undulations of large amplitude are used for the efficient execution both of forward swimming and of fast starts and turns, there remains in the 1980s (just as there was in the 1970s) no realistic option of applying high-Reynolds-number computational fluiddynamics to calculate successive flow fields in a three-dimensional fluid region whose shape is making large changes with time. Accordingly, the analysis by 'large-amplitude elongated-body theory' (*MB*, pp. 132–137) which can be readily applied in a wide range of cases, even though it describes the motions to only a crude approximation, must be our main source of comparative information on when such body undulations can achieve good hydromechanical efficiency.†

The evident need to extend elongated-body theory to modes of swimming in which the body remains rigid and propulsion is achieved by undulations propagated along a fin alone – or a pair of fins – was noted in a list of problems requiring further study (under the heading (*a*) in *MB*, p. 42, which refers back to descriptive material on p. 37) but has not hitherto been attempted. Yet there are biologically important unsolved questions, set out in detail in §2 below, which call for just this type of analysis.

In particular, the family Balistidae of rigid-bodied fishes (popularly called triggerfishes) move unexpectedly fast by means of 'balistiform' propulsion; that is, propulsion by undulations propagated simultaneously along a posterior pair of highly flexible dorsal and anal fins. Analysis in this paper is comprehensively applied to understanding the effectiveness of balistiform propulsion in this and other families

† We should however make it clear here that we are by no means discounting the possibility that in the future an approximate treatment on somewhat different lines might be shown to be even more accurate for the description of certain types of fish locomotion, including cases of balistiform swimming.

of fishes, and is partly extended to 'gymnotiform' propulsion (where, as in the electric eel *Gymnotus*, propulsion may occur through undulations propagated along a single ventral fin). This analysis is a direct (although, as we shall see, not a completely straightforward) extension of the large-amplitude elongated-body theory used to study fish locomotion by means of body flexure, of which we now briefly recall the fundamental hydromechanical ideas.

Although this latter theory can be recognized as having developed from ideas of long standing used in 'slender-body theory', the alternative designation 'elongated-body theory' has been preferred in fish biofluiddynamics, partly because of its greater intelligibility to biologists, but mainly to highlight the special characteristics of a theory requiring careful treatment of the fluid transition between the elongated region occupied by the fish's propulsive surfaces and the posterior vortex wake. Elongated-body theory studies the rate of change of fluid momentum within a volume $\mathscr{V}$ bounded by a control surface which includes a posterior plane Π, separating the regions of attached vorticity around the body and fins from the region of shed vorticity in the wake. For a complete 'budget' of the momentum balance it is necessary to take into account momentum transfer by convection across the plane Π and also by means of the overall pressure force acting across Π.

In all other respects, the nature of the analysis is similar to that in slender-body theory. The fluid momentum per unit length of fish around each cross-section is taken to be that which would be found in two-dimensional irrotational flow generated by the instantaneous motion of that cross-section resolved at right angles to the backbone. Because, in addition to the posterior plane Π, the control surface bounding the volume $\mathscr{V}$ includes two parallel horizontal planes† above and below the plane of the fish's swimming movements (here taken as horizontal), the fluid momentum associated with that cross-sectional motion is well-defined. Indeed, when the complete cross-section moves as a whole with velocity w, that momentum takes the classical form mw, where m is the cross-sectional added mass per unit length. Furthermore, the area integral of the pressure in the fluid region between the planes (a quantity needed, as we have seen, to specify the overall pressure force acting across Π) takes the positive value $\frac{1}{2}mw^2$.

We may pause to compare this elongated-body theory with the types of slender-body theory that are much used to describe microorganism locomotion at low Reynolds numbers, with 'stokeslet' singularities distributed along the centreline of a waving flagellum. Those theories are purely linear and neglect all inertial effects; but are subject to complications resulting from the long-range character of the stokeslet velocity field, which causes substantial interactions between motions at different cross-sections. By contrast, the elongated-body theory is nonlinear and largely dominated by inertial effects (as in the form of the convective transfer of momentum across Π); but the velocity fields associated with cross-sectional motions possess the relatively short-range character associated with dipole far fields, so that interactions between motions at different cross-sections are greatly reduced.

It will be evident that, if and when elongated-body theory is to be extended to balistiform swimming (for example), the novel analyses required must include certain new two-dimensional calculations. First of all, the fluid momentum per unit length must be derived for motions of a fish cross-section where the body element is

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† The 'budget' of horizontal momentum within $\mathscr{V}$ cannot, of course, include any term due to the pressure forces acting across these horizontal planes.

stationary and only the fins are moving. Secondly, it is necessary to calculate the area integral of the fluid pressures associated with such motions in order to derive the overall pressure force acting across the posterior plane *Π*.

Out of this pair of new two-dimensional calculations, we are led by the existing elongated-body theory to expect the first to make a bigger contribution to thrust than the second. Accordingly, special attention has been given in our studies (see especially Part 3 of this paper, Lighthill 1990*b*) to calculating the fluid momentum associated with the movement of fins attached to a rigid-body cross-section.

The importance of this line of research became still clearer after preliminary calculation for a simple model of balistiform swimming, given in §4 below, showed a large enhancement of fluid momentum. Specifically, the fluid momentum produced by movements of dorsal and anal fins attached to a deep rigid-body cross-section was found to be from 3 to 4 times greater than the same fin movements would generate on their own.

By contrast, an interesting calculation of the area integral of pressure, given in Part 2 of this paper (Lighthill 1990*a*) for the same model, demonstrated that this does still make a positive contribution to thrust (as in the well established elongated-body theory), but a contribution which is in no way enhanced relative to that generated by the fin movements on their own. Accordingly, it is even less important in comparison with the contribution from fluid momentum than in the case when cross-sections move as a whole.

The striking nature of the conclusions regarding enhancement of fluid momentum made it important to check whether such enhancement occurs for accurately realistic models of balistiform swimming, in which the body cross-section is given the form of an ellipse with arbitrary axis ratio (the earlier model represents a limiting case of small axis ratio). In Part 3 appropriate conformal mappings are used to carry out this calculation, and to extend it also to gymnotiform swimming (involving motions of just a single fin). In every instance a similarly substantial enhancement of fluid momentum is found.

Nevertheless we suggest that this is just one of two important effects contributing to the 'uncannily' high-speed swimming movements observed in trigger-fishes. Certainly, the large-amplitude undulations of modest-sized dorsal and anal fins carry, as we have seen, enhanced momentum which generates an enhanced component of thrust. It is just as important, however, that the body drag, which the fin thrust must overcome, is reduced to the value associated with the uniform rigid forward motion of the body through the water; this contrasts with the value much greater (by a factor of 3 to 4) that has long been accepted (*MB*, pp. 114–116; see also Blake 1983*a*, pp. 98–101) as accompanying body undulations. The thrust enhancement and drag reduction are both by a factor of around 3 or a little more and, taken together, are sufficient to explain a similar speed enhancement for balistiform swimming.

Our conclusions are important also for gymnotiform swimming, which they indicate as conferring substantial advantages through reduction of the energy cost of transport. This idea tends to reinforce an earlier suggestion (Blake 1983*b*) that evolution of gymnotiform swimming was not primarily related to the special needs of electric fishes; a suggestion consistent, indeed, with the use of gymnotiform swimming by a species, *Xenomystis nigri*, from a family Notopteridae (the knife-fishes) lacking any electrical organs.

From the general standpoint of theoretical fluid mechanics, the careful formulation in §3 of an extension of large-amplitude elongated-body theory to fish propulsion by fin undulations is of some conceptual interest; whereas the detailed calculations of fluid momentum in Part 3, although producing interesting results, involve methodologically a straightforward application of conformal-mapping techniques. Finally, the calculation of pressure in Part 2 for irrotational flows produced by motions of a flexible boundary proves (along with the deduction of its area integral) to involve more subtle analysis than might be expected, essentially because in the unsteady form of Bernoulli's equation the $\partial\phi/\partial t$ term (time-derivative of the velocity potential) is not simple to obtain when the shape of the boundary is itself varying with time.

It is a pleasure to dedicate to Professor G. K. Batchelor on his 70th birthday a paper which in its Part 2 includes material on fluid pressure distributions produced by body flexure that bears some relation to his fundamental interests in mechanics of fluids as well as to his outstanding text on the subject (Batchelor 1967), while in §3 below it provides a new application of those 'slender-body theory' ideas in which he has long taken a profound interest.

2. Biological background

Modes of propulsion of aquatic animals are of particular hydromechanical interest because about 10^9 years of animal evolution in an aqueous environment, by preferential retention of specific variations that increase ability to survive and produce fertile offspring, have inevitably produced rather refined means of generating fast movements at low energy cost, which merit study. This is mainly because at every point in the food chain, or network of predator–prey relationships, capability of movements that are fast relative to those of predator or prey, or to the distances that must be traversed before prey is found, is one out of the many important factors influencing such ability to survive.

Some of the other factors, to be sure, may in certain ecological situations be of overriding importance, so that evolution proceeds in a direction – for example, development of protective armour – that may reduce mobility although net chance of survival has improved. Defensive armour has been developed at the expense of speed within three important orders of fishes. (Tetraodontiformes, Syngnathiformes, Zeiformes†) where the resulting loss of body flexibility has been such as, in general, to preclude propulsion by body undulations. The principal alternative modes of propulsion found in such fishes are reviewed by Blake (1983*c*) as well as in Blake (1983*a*, chap. 6).

Amongst all of these modes of fish propulsion, we discuss here just one, which can perhaps be regarded as a further adaptation, in fishes that had lost body flexibility, so as to allow them nevertheless to achieve forward motion at low energy cost through a combination of good propulsive efficiency with avoidance of drag enhancement. This is the balistiform mode of swimming, associated with undulatory movements made by both of the median (dorsal and anal) fins. Here it is discussed in the first place for rigid-bodied fishes, but afterwards some cases of flexible-bodied fishes which are able under a variety of different circumstances to use either anguilliform body undulations or balistiform median-fin undulations are described and interpreted. The section is concluded by a discussion of the gymnotiform mode of swimming, which (this time normally in flexible-bodied fishes) involves undulations in just a single median fin.

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† Designated in *MB* by their older names Plectognathi, Solenichthyes, Zeomorphi.

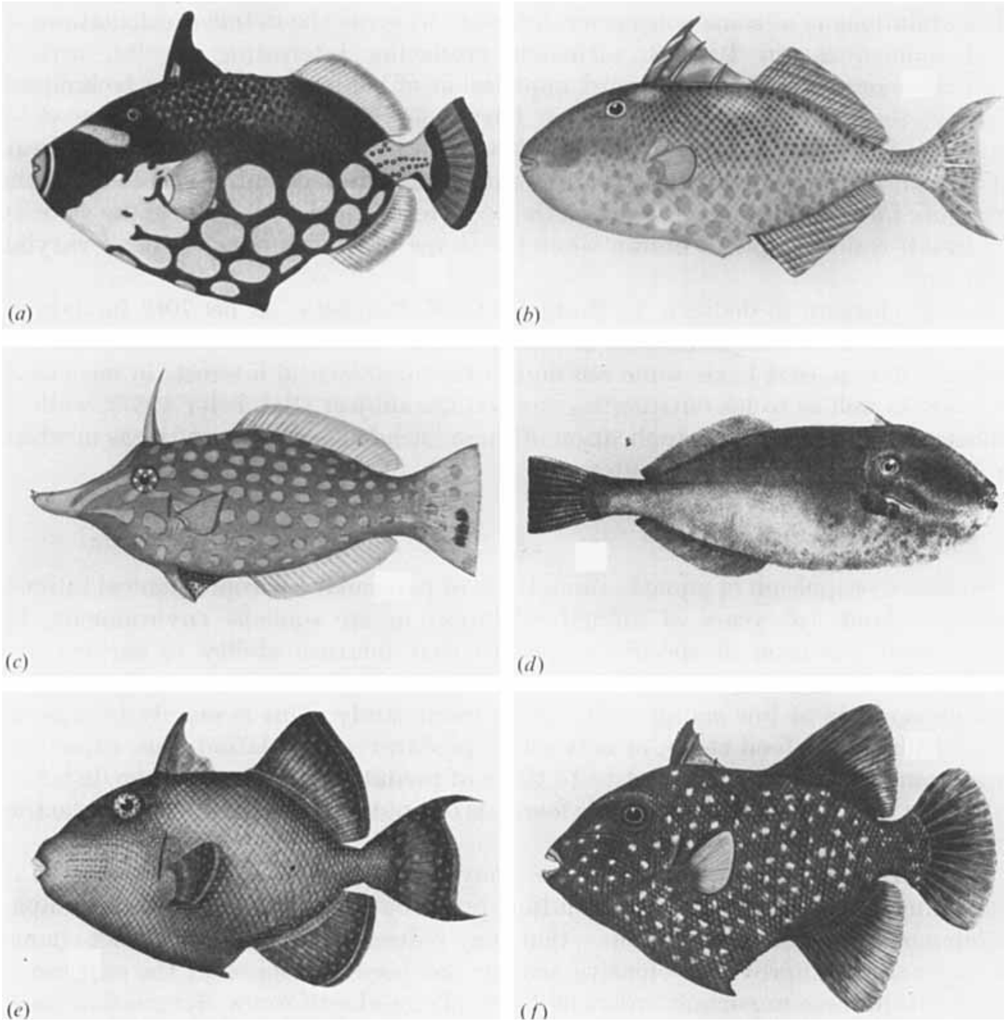

FIGURE 1. Some fish species from the sub-order Balistoidei which use balistiform locomotion, either in the undulatory mode as with (a) *Balistes conspicillum*, (b) *Abalistes stellaris*, (c) *Oxymonacanthus longirostris* and (d) *Aluterus monoceros*, or in the oscillatory mode as with (e) *Pseudobalistes fuscus* and (f) *Canthidermis rotundatus*. Photographs in figures 1 and 2 are taken from Marshall (1964), except for figure 2(b) which comes from Marshall (1965).

The balistiform mode of swimming, as a means of economically achieving more rapid locomotion than might seem compatible with a nearly rigid body, is found above all in the sub-order Balistoidei of the order Tetraodontiformes; and, particularly, in the family Balistidae (trigger-fishes, file-fishes and leather-jackets).

Figure 1 shows a range of species from the Balistoidei, all of which achieve forward locomotion primarily through simultaneous movement of posterior dorsal and anal fins. They are divided into two main groups: those in genera like *Balistes*, *Abalistes*, *Monacanthus*, *Oxymonacanthus*, and *Aluterus* where the undulation passing backwards along both fins has a wavelength considerably less than the lengths of those fins; and those in genera like *Pseudobalistes*, *Odonus*, *Canthidermis* and *Xanthichthys* where the oscillatory motion of the fins, if it were to be described as an undulation, would need to be identified as one that fails to include any entire wavelength.

Thus, any comparison between the two types of balistiform swimming must be rather similar to the comparison between body undulations in the anguilliform and carangiform modes (Gray 1968, pp. 19–38; *MB*, pp. 19–26). The second type may indeed be seen as involving not so much a wave as a lateral oscillation of each fin as a whole, with a twist at each extreme of the oscillation so that the fin's side-to-side movement includes always a backward-facing component.

For all of the fishes in figure 1 the assumptions of elongated-body theory can represent only a crude approximation, but the theory nevertheless gives us some useful guidance on the forces exerted by the fin motions. Broadly, it suggests that, although the two types of balistiform swimming exert rather similar propulsive forces, nevertheless the fully undulatory mode is a more economical way of achieving forward movement. Above all, it keeps to a minimum any fluctuating sideforce producing lateral oscillations of the body (oscillations described as 'recoil' in *MB*, p. 87), which is important because it avoids enhancement of the body drag which fin thrust has to overcome.

The theory also indicates that the relatively low ratio of fin depth to body depth characteristic of species utilizing the fully undulatory mode of balistiform swimming does not necessarily lead to reduced propulsive forces. It suggests, in fact, that the force associated with fin movements of a given magnitude is substantially enhanced when this ratio is small.

Among the other two sub-orders of the Tetraodontiformes the truly undulatory mode of balistiform swimming is not found, although several species use balistiform swimming of the oscillatory type, normally as one of a variety of different available methods of locomotion. In the sub-order Tetraodontoidei the majority of species are somewhat sluggish swimmers; on the other hand, fishes of the genus *Tetraodon* (see figure 2) are able to use oscillation of the dorsal and anal fins for reasonably fast forward locomotion. The sub-order Ostraciontoidei, on the other hand, is best known for the so-called ostraciiform mode of swimming, involving a simple rotary oscillation of the caudal fin about the base of the caudal peduncle, which is not considered to be of good hydromechanical efficiency (Blake 1981).

Within the other two main orders of fishes where development of protective armour has reduced body flexibility, it is above all the Zeiformes (John Dories, boar-fishes, etc.) which have adopted the truly undulatory mode of balistiform swimming. For example, the boar-fish *Capros aper* (figure 2) is typical of fishes in this order in its use of undulations propagated along opposed soft dorsal and anal fins to propel itself forward. The qualitative conclusions of this paper may be broadly relevant to the understanding of balistiform swimming in zeiform fishes; where, however, an unusually low ratio of overall length to body depth makes the use of elongated-body theory much less appropriate than in the case of the Balistoidei.

On the other hand, within the order Syngnathiformes (the tube-mouthed fishes, from sea-horses and pipe-fishes to cornet-fishes and trumpet-fishes), it is mainly the family Aulostomidae (trumpet-fishes) that uses the truly undulatory mode of balistiform swimming. A fish like *Aulostomus chinensis*, also shown in figure 2, adopts this as its regular mode of swimming, which, however, it can supplement with caudal-fin motions when hard pressed.

Among the flexible-bodied fishes, there are several with long dorsal and anal fins which are able to use the truly undulatory mode of balistiform swimming as an

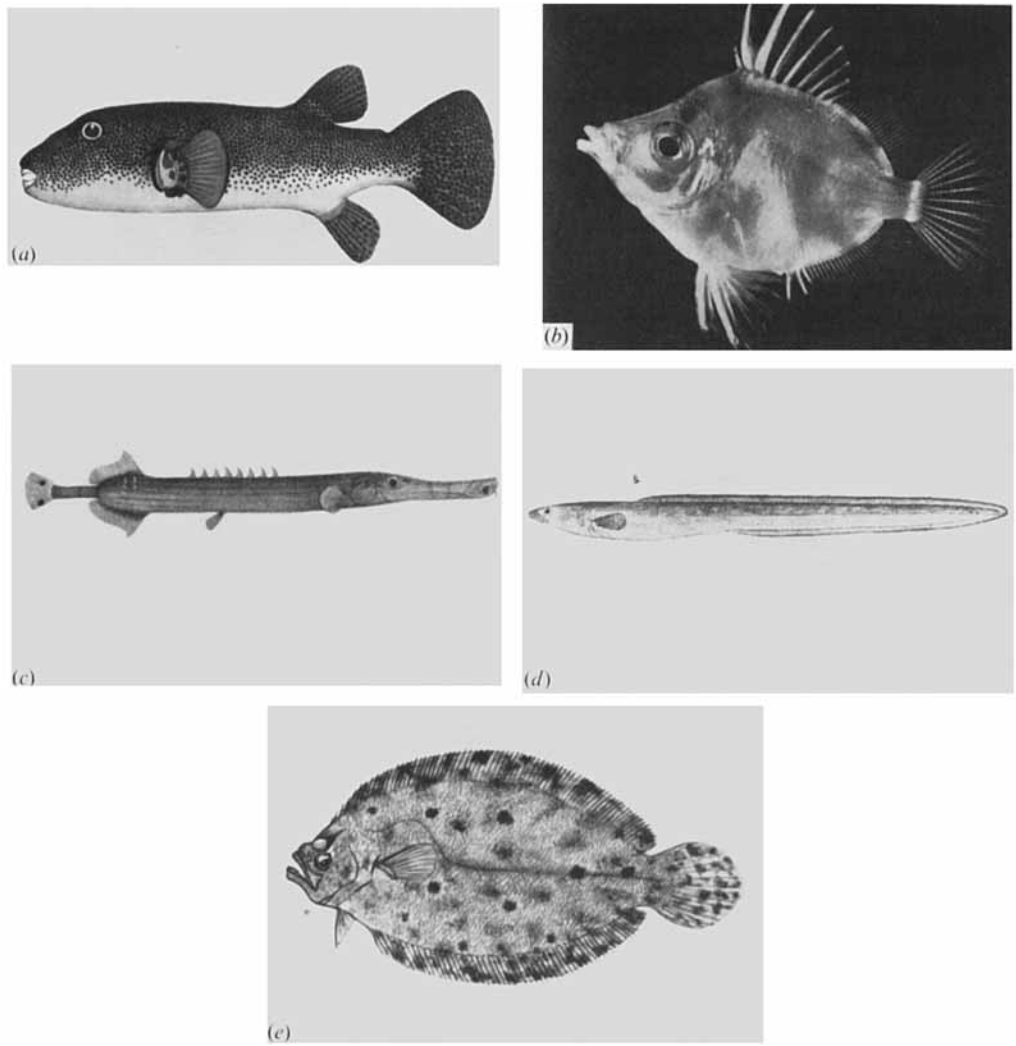

Figure 2. Some other fish species able to use balistiform locomotion: (*a*) *Tetraodon stellatus*, (*b*) *Capros aper*, (*c*) *Aulostomus chinensis*, (*d*) *Conger labiatus* and (*e*) *Pseudorhombus arsius*.

alternative low-cost means of progression when they do not need the higher speeds available with anguilliform body undulations. This is particularly characteristic of the order Anguilliformes† (the eels), as illustrated in figure 2 by the conger-eel *Conger labiatus*.

The same tendency is characteristic of the Pleuronectiformes† (flat-fishes) which, it must be emphasized, adopt the characteristically anguilliform mode of swimming in their very early stages of life, after which a flat-fish turns over onto one side while the eye on that side moves round to the other. It retains the anguilliform mode of swimming for faster movements and also, as in Anguilliformes, the undulatory mode of balistiform swimming for relatively slower movements; but the motions of body

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† The older names Apodes and Heterosomata were used in *MB* for the orders Anguilliformes and Pleuronectiformes.

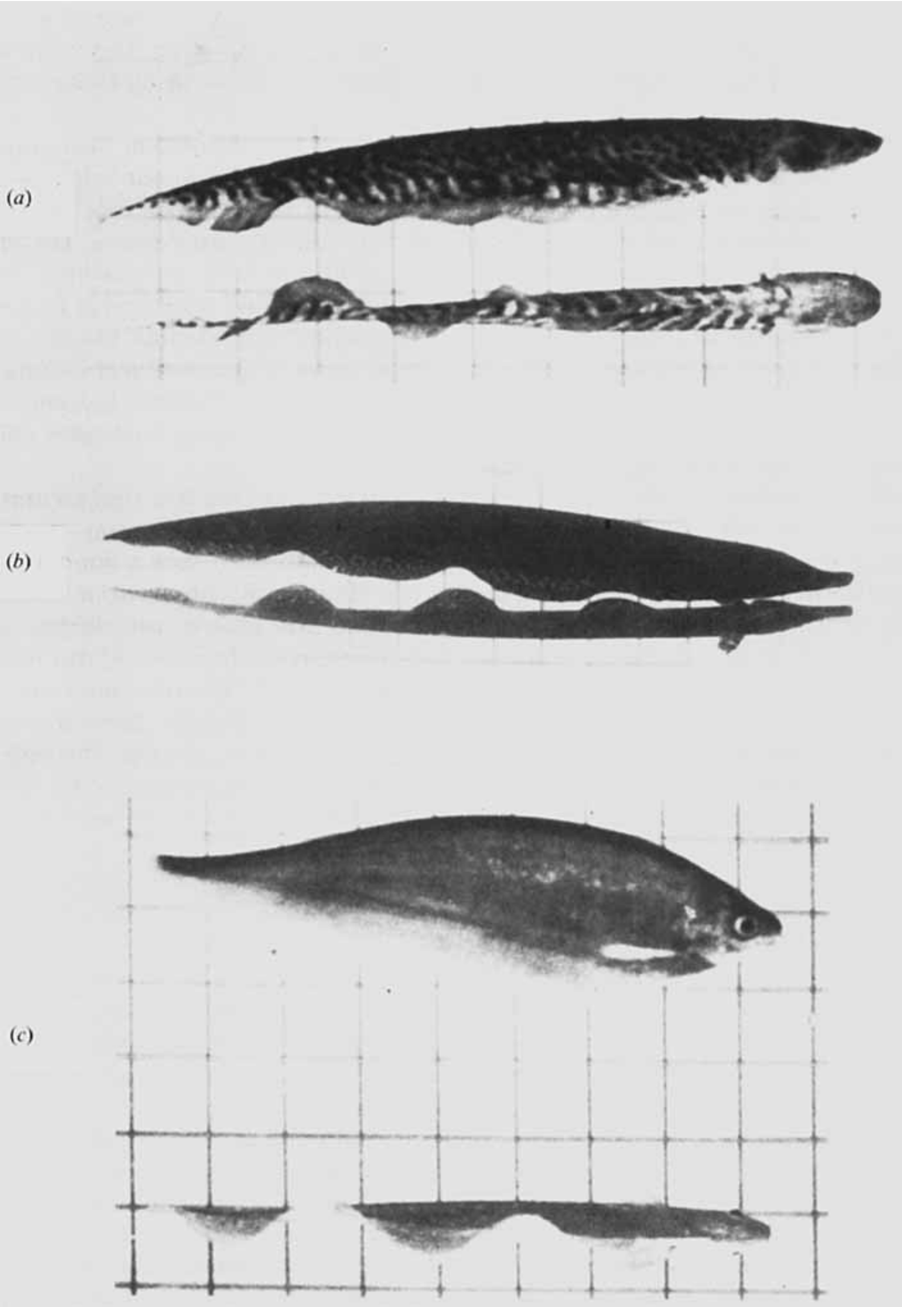

Figure 3. Synchronous side and bottom views of gymnotiform swimming in two gymnotid species: (*a*) *Gymnotus carapo* and (*b*) *Gymnorhamphichythys hypostomus*, and in one notopterid species: (*c*) *Xenomystis nigri*.

and/or fins after it has turned over are, of course, vertical. The median fins in a flatfish are usually referred to as 'marginal fins' (see figure 2 for the case of a flounder *Pseudorhombus arsius*) and, in the balistiform mode of swimming, their undulatory motions are similar to those observed in Balistoidei except for being turned through 90°.

Although the principal analysis in this paper is for balistiform swimming, we conclude this section by indicating the biological background to our briefer analysis of gymnotiform swimming. This is characteristic of the 'electric eels' of the two families Gymnotidae and Electrophoridae in the order Cypriniformes. The electric eels have flexible bodies and are capable of anguilliform body undulations. For the most part, however, they choose to keep the body rigid and to propel it forward by means of undulations propagated along their one and only median fin: the ventral fin. Figure 3 gives synchronous side and bottom views of gymnotiform swimming in two gymnotid species (*Gymnotus carapo* and *Gymnorhamphichthys hypostomus*); it has been argued (Lissmann 1958) that this mode of swimming facilitates effective utilization of the fishes' electrical organs.

On the other hand, Blake (1983*b*) has drawn attention to the fact that an unrelated species of fish without any electric organs (*Xenomystis nigri* from the family Notopteridae in the quite different order Osteoglossiformes) uses a similar type of gymnotiform swimming, also shown in figure 3. He uses this observation along with others (to the effect that certain mormyroid fishes are able to use electric organs effectively while swimming by means of body motions in the carangiform mode) to suggest that other advantages besides those specialized to electric fishes may have contributed to the evolution of gymnotiform swimming. Briefly, these include the avoidance of fluctuating sideforce and hence of any increase of drag (through body oscillations) over its rigid-body value, together with an enhancement of fin thrust as indicated by calculations in Part 3 (from which a preliminary result had been noted already by Blake 1983*b*).

3. Extension of elongated-body theory

In this section we first recall the results (*MB*, pp. 132–134) of elongated-body theory for fish swimming by body undulations in a horizontal plane where each fish cross-section is subjected only to horizontal translation and to rotation about a vertical axis. In vector notation, these results derive the horizontal force $\boldsymbol{F}$ with which water pressures act on the fish from the following principles:

(*a*) the fish acts on the water with an equal and opposite force $(-\boldsymbol{F})$;

(*b*) if we consider a region $\mathscr{V}$ of the fluid bounded internally by the fish and externally by a certain control surface, then the rate of change of horizontal water momentum in $\mathscr{V}$ can be equated to the sum of the forces acting on it (namely, $-\boldsymbol{F}$ plus the sum of the horizontal pressure forces acting across the control surface) minus the rate of transport of horizontal momentum out of $\mathscr{V}$ across the control surface;

(*c*) the control surface includes two horizontal planes at equal distance above and below the plane of the body's undulations, and this distance is taken sufficiently large so that rate of transport of momentum across the planes (a quantity of second order in the disturbances) is negligibly small; while, because the planes are horizontal, the pressure force on each – although it may not be negligibly small (since the pressure is of first order in the disturbances) – has zero horizontal component;

(*d*) the control surface includes also a vertical plane Π, attached rigidly to a posterior cross-section of the fish (and therefore undergoing the same translations and rotations as that posterior cross-section), so that it remains always perpendicular to the backbone;

(*e*) shed vorticity is found entirely behind the posterior plane Π;

(*f*) at each instant, therefore, the horizontal momentum of the fluid within $\mathscr{V}$ (that is, anterior to Π) can be related to the irrotational flows generated by the motion of body cross-sections;

(*g*) the momentum per unit length of body at every cross-section can be approximated by the value $\boldsymbol{M}$ that it would take in a two-dimensional flow associated with the motion of that cross-section;

(*h*) similarly, the pressure force acting on $\mathscr{V}$ across Π (which, as explained in (*b*) above, contributes to the expression for the propulsive force $\boldsymbol{F}$) can be approximated by the value $\boldsymbol{P}$ that it would take in a two-dimensional irrotational flow in the plane Π associated with the motion of the posterior cross-section.

To this list of principles underlying the theory, we may add the facts that (i) the momentum per unit length of body referred to in (*g*) – that is, the horizontal momentum $\boldsymbol{M}$ of the fluid between the parallel horizontal planes – is directed perpendicular to the backbone, in the plane of the cross-section; (ii) its magnitude can be expressed as mw in terms of the added mass m of the cross-section and its velocity component w perpendicular to the backbone; (iii) the magnitude of the pressure force $\boldsymbol{P}$ referred to in (*h*) can be calculated as the area integral of the pressure in the region between the two parallel planes for the two-dimensional flow produced by the cross-section's motion with velocity w, and takes the value $\frac{1}{2}mw^2$. These specific facts have relevance only to the case when cross-sections move without change of shape; results corresponding to them will need to be derived for the extension of elongated-body theory to balistiform motion, which nevertheless will continue to be founded on basic principles which are essentially those set out in (*a*)–(*h*) above.

An important check on the validity of the conclusions derived from these principles (*a*)–(*h*) – together with the specific results (i)–(iii) for the case when cross-sections move without change of shape – was given when it was shown (*MB*, p. 78) that a small-perturbation expansion for the complete three-dimensional problem gives the same results. This is an expansion in powers of a parameter ϵ characterizing the magnitude of the fluid velocities, relative to the fish's forward speed, generated in the plane of a cross-section by the fish's motion through the fluid. In cases when this parameter is small, an expansion to second order in ϵ gives the same result for the force $\boldsymbol{F}$ as is derived by the principles (*a*)–(*h*). At the same time, the soundness of the physical arguments embodied in these principles encourages us, particularly after such a check in the small-parameter case, to use them also when relatively large cross-sectional motions are involved (*MB*, pp. 105–111). Similarly, it encourages us to apply to the case of balistiform swimming a set of principles which differ from those in (*a*)–(*h*) above in only one (quite minor) respect.

This one change is made only to principle (*d*). Here, the criteria governing our choice for the orientation of the posterior plane Π no longer constrain it to remain perpendicular to the backbone.

The essential need, in fact, is for this plane Π to be the plane of the fluid motions in the neighbourhood of the posterior cross-section, so that the fluid momentum vector $\boldsymbol{M}$ lies in the plane Π. An important difference, however, between swimming by body undulations and balistiform swimming is that in the latter case the fluid momentum vector $\boldsymbol{M}$ is found (see §4) to be in a direction quite different from the direction perpendicular to the backbone specified by (i) above. Now, Π must be taken as a vertical plane through this momentum vector $\boldsymbol{M}$; and, accordingly, is directed obliquely to the backbone.

For balistiform swimming, furthermore, the correct posterior location for the plane Π is no longer the tip of the caudal fin, because the caudal fin is held rigid and plays no part in the propulsion of the fish. Instead, Π needs to be placed at the posterior end of the propulsive apparatus provided by the dorsal and anal fins.

The reasons for this relocaton are twofold. First, it does not interfere with the momentum-budget method (*b*) for finding the propulsive force $\boldsymbol{F}$ because the whole of this force is exerted within the volume $\mathscr{V}$ anterior to the plane Π; accordingly, it can be related to the rate of change of fluid momentum within $\mathscr{V}$. But the location proposed for Π is not only acceptable: it is also essential in order that the shed vorticity (see (*e*) above) is found entirely behind Π.

For balistiform swimming, in which the body and caudal fin remain rigid, the mathematical expression of the momentum budget (*b*) takes the form

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^L \boldsymbol{M}\,\mathrm{d}a = -\boldsymbol{F}+\boldsymbol{P}-U(\boldsymbol{M})_{a=0}, \tag{1}$$

where U is the forward velocity of the fish. Here, just as in the elongated-body theory for swimming by body undulations, the coordinate a signifies, for a cross-section of the fish anterior to the plane Π, its distance along the backbone† from the location of Π; that is, from the posterior end of the fish's propulsive apparatus, taken here as $a = 0$. The position $a = L$ can be taken as the anterior end of the region of undulating fin movements, since this is the only region where the momentum $\boldsymbol{M}$ per unit length defined by (*g*) above is non-zero.

Then the left-hand side of (1) represents the rate of change of the fluid momentum in $\mathscr{V}$ (which as just explained takes the value $\boldsymbol{M}$ per unit length of backbone between $a = 0$ and $a = L$). The right-hand side, as in (*b*) above, equates this rate of change to the force $(-\boldsymbol{F})$ with which the fish acts on the fluid, plus the pressure force $\boldsymbol{P}$ acting across the posterior plane Π, minus the rate of transport of momentum out of $\mathscr{V}$ across Π; since, from (*c*), there is none across the horizontal plane boundaries.

Here, the rate of transport of momentum out of $\mathscr{V}$ across Π takes the form of the product $U\boldsymbol{M}$ (the distance forward travelled by Π in unit time multiplied by the momentum per unit distance). Exactly as in the theory for swimming by body undulations it is only the translational motion of the plane Π that produces momentum transport across it. Its rotational motion about a vertical axis produces by contrast no momentum transport (compare *MB*, p. 109) because the distribution of momentum in the plane Π is an even function of distance from that vertical axis.

Analysis of how to calculate the quantities $\boldsymbol{M}$ and $\boldsymbol{P}$ which enter into (1) for the propulsive force is given in §4 (see also Parts 2 and 3). It is applied to calculate the mean propulsive force over a single cycle of the fin undulations. Just as for cases of body undulations, the expression on the left-hand side of (1) has zero mean since, when the time-derivative is integrated with respect to time over a cycle, we obtain the difference between the values of the cyclically varying quantity

$$\int_0^L \boldsymbol{M}\,\mathrm{d}a \tag{2}$$

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† Needless to say, the fact that the backbone is here straight makes the definition of a simpler than in the theory of swimming by body undulations.

at the beginning and end of the complete cycle – values which are necessarily the same. Accordingly, the mean propulsive force is

$$\bar{\boldsymbol{F}} = -\overline{U(\boldsymbol{M})}_{a=0} + \bar{\boldsymbol{P}}, \tag{3}$$

where the bars signify means and we shall find that both terms on the right-hand side make a positive contribution to the propulsive force.

This result (3) for the mean propulsive force has its direct analogy for cases of body undulations. In those cases, however, the form (1) of the equation specifying the force $\boldsymbol{F}$ also gives an important indication of the magnitude of those fluctuating sideforces which cause an overall lateral oscillation of the entire fish body (*MB*, pp. 85–92); and this in turn produces an augmentation of that body drag which the propulsive force has to overcome.

By contrast, balistiform swimming involving several wavelengths of fin undulation may be expected to produce rather little fluctuating sideforce, particularly since the integral (2) whose time-derivative appears in (1) is expected to remain small. Essentially, this is because in an integration over several wavelengths the contributions from the crests and troughs of the waves can be expected to cancel out.

This conclusion is important because it suggests why balistiform swimming is able to avoid those lateral oscillations which can augment body drag. Indeed, one of the two main advantages of this mode of swimming may (as suggested in §1) be that it keeps body drag down to the value associated with rigid forward motion. The other main advantage is indicated by calculations of (3) for mean propulsive force given in the next section.

4. A simplified model of balistiform locomotion

The extension of elongated-body theory given in §3 is applied first of all to a simplified model of balistiform locomotion. This is a model in which the thickness of the fish's (essentially rigid) body is taken small compared with its depth; the body, in short, is treated simply as a flat plate. Later, however, the theoretical conclusions for this simplified model are largely generalized (see §5 and, especially, Part 3) to bodies of elliptical cross-section with arbitrary ratios of thickness to depth.

In both models – whether with an elliptical or a 'thin-plate' body cross-section – the median fins (dorsal and anal) are, we emphasize, taken as thin but capable of a specific mode of flexure. This reflects the fact that the skeleton of either fin is composed of rays, rather flexibly joined together, and each provided with muscle fibres that can cause the ray to make a lateral movement in the approximate form of a rotation about its base.

For a particular cross-section, on the present simplified model, figure 4 illustrates a sequence of four phases in the (synchronized) motion of the dorsal and anal fins. Here, the symmetrical configurations (*a*) and (*c*) represent the two phases when fin movements are at maximum velocities, so that the associated momentum $\boldsymbol{M}$ per unit length is expected to reach its peak. By contrast, in the extreme configurations (*b*) and (*d*), the fins are instantaneously at rest so that any irrotational motion around the cross-section ceases (being dependent only on the instantaneous movement of the boundary) and therefore $\boldsymbol{M} = 0$.

Our objective in this section, then, is to calculate $\boldsymbol{M}$ in configuration (*a*) and in its mirror-image configuration (*c*), configurations representing those twin peaks in the magnitude of $\boldsymbol{M}$ during a cycle that appear between the phases (*b*) and (*d*) when $\boldsymbol{M}$

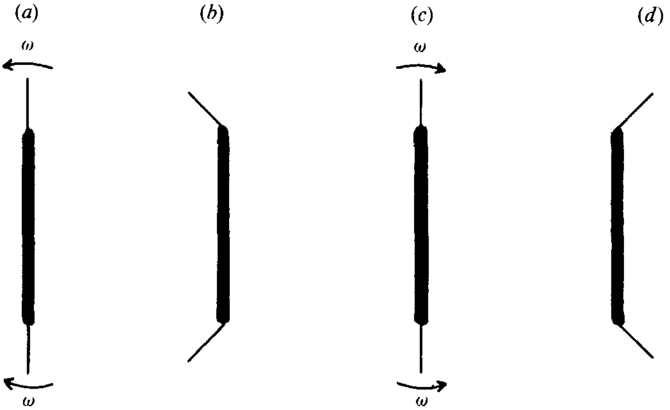

FIGURE 4. Successive configurations of a fish cross-section in the simplified model of balistiform locomotion: (*a*) symmetrical configuration with maximum angular velocity ω of fin movement; (*b*) extreme configuration with fins instantaneously stationary; (*c*) mirror-image symmetrical configuration with reversed angular velocity ω; (*d*) mirror-image extreme configuration with stationary fins.

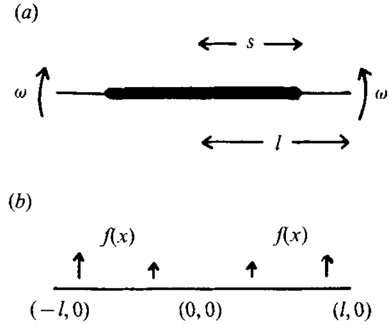

FIGURE 5. (*a*) The very precisely two-dimensional problem associated with either configuration (*a*) or configuration (*c*) of figure 4. (*b*) Generalization of the above to the case of a flexible flat plate of length $2l$ with velocity $f(x)$ normal to itself.

vanishes.† First of all we perform this calculation for a very precisely two-dimensional flow associated with configuration (*a*). This represents the seriously unrealistic case when the motions of neighbouring cross-sections are all in phase (so that each median fin flaps rigidly back and forth like a door about its hinge); later, we extend it to a truly three-dimensional type of balistiform motion (of undular form) passing along each fin, with a phase lag in the motions of posterior sections behind those of anterior sections.

The precisely two-dimensional problem of calculating the momentum M associated with either configuration (*a*) or configuration (*c*) is illustrated in figure 5 (turned through 90° in each case because this makes the fluiddynamic problem more familiar). Figure 5 also generalizes the problem to one in which the motion of a flexible flat plate $-l < x < l$ perpendicular to itself has velocity $f(x)$. The case discussed above, with the inflexible body occupying the internal region $-s < x < s$ and the fins rotating rigidly with angular velocity ω about their bases $x = \pm s$, would be represented by taking the function $f(x)$ as

$$f(x) = 0 \quad (|x| < s), \quad \omega(|x| - s) \quad (s < |x| < l). \tag{4}$$

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† Similarly, the calculations in Part 3 for bodies of elliptical cross-section are carried out for analogous symmetrical configurations of median fins.

Mathematically, the problem reduces to solving the two-dimensional Laplace equation for the velocity potential ϕ outside the plate given that

$$\partial\phi/\partial y = f(x) \quad (-l < x < l). \tag{5}$$

The required momentum $\boldsymbol{M}$ per unit length is directed along the y-axis, with magnitude

$$M = \int_{-\infty}^{\infty}\left[\int_{-\infty}^{\infty} \rho(\partial\phi/\partial y)\,\mathrm{d}y\right]\mathrm{d}x = \rho\oint\phi\,\mathrm{d}x, \tag{6}$$

where the order of integration (with respect to y first, and then to x) reflects the choice of $\boldsymbol{M}$ as the momentum between two parallel planes $|x| = X$ with X large, and where the integral on the right-hand side of (6) represents an integral around the surface of the plate in the positive (anticlockwise) sense.

The solution is well known when $f(x)$ is a simple constant, say $f(x) = 1$ (so that the entire plate moves with unit velocity). With the expression ϕ_1 used to mean the form of the potential ϕ in this classical case, its value on the surface of the plate is given as

$$\phi_1 = \mp(l^2 - x^2)^{\frac{1}{2}}; \tag{7}$$

with the $\mp$ sign standing for $-$ on the upper surface and $+$ on the lower surface of the plate. The integral (6) then gives M as $\rho\pi l^2$, the added mass for uniform motion of the plate.

This solution ϕ_1 for $f(x) = 1$ has one particular property – the fact that, by (5), $\partial\phi_1/\partial y = 1$ on the plate itself – which allows us to calculate the momentum (6) for general $f(x)$. Evidently, we can rewrite (6) as

$$M = \rho\oint\phi(\partial\phi_1/\partial y)\,\mathrm{d}x \tag{8}$$

and then use Green's theorem to rewrite it as

$$M = \rho\oint\phi_1(\partial\phi/\partial y)\,\mathrm{d}x. \tag{9}$$

This, by (5) and (7), gives M as

$$M = 2\rho\int_{-l}^{l}(l^2 - x^2)^{\frac{1}{2}}f(x)\,\mathrm{d}x, \tag{10}$$

since in the integral (6) around the plate the change in x is negative on the upper and positive on the lower surface.

The form of (10) already makes clear (for the present simplified model) the main conclusion of this paper: that a pair of moving fins, each of depth $l-s$, attached to a rigid body of depth $2s$ will generate considerably more momentum than would be derived by simply adding up the momentum that the motion of each fin on its own would produce. This is because in the integral (10) the size of the factor $(l-x)^{\frac{1}{2}}(l+x)^{\frac{1}{2}}$ on (say) the fin where $s < x < l$ is enhanced to take into account the total depth $2l$ of the body and fins combined – whereas the corresponding factor for the fin on its own would be only $(l-x)^{\frac{1}{2}}(x-s)^{\frac{1}{2}}$.

More precisely, the form (4) of the function $f(x)$ yields for the momentum (10) the expression

$$M = 2\rho\omega[\tfrac{1}{3}(l^2 - x^2)^{\frac{1}{2}}(2l^2 + s^2) - sl^2\cos^{-1}(s/l)]; \tag{11}$$

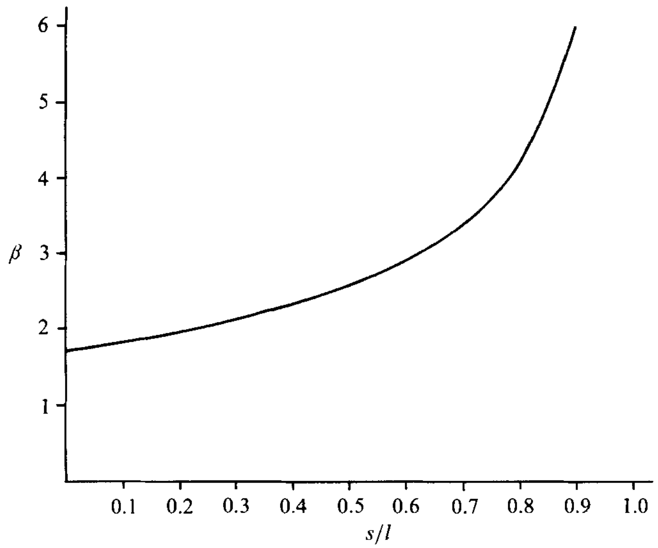

FIGURE 6. The momentum enhancement factor β, as defined in (12), is plotted as a function of s/l for the simplified model shown in figure 5.

and figure 6 plots the ratio

$$\beta = M/M_0, \quad \text{where} \quad M_0 = \tfrac{1}{4}\pi\rho\omega(l-s)^3 \tag{12}$$

stands for the combined momentum that would be produced by the motion of each of the two fins on its own. Here, β can be described as a 'momentum enhancement factor', which is seen to lie between 3 and 4 for typical values of s/l between 0.62 and 0.78. This represents a very substantial enhancement.

On the other hand, all of the above calculations apply only in the case of 'very precisely two-dimensional flow'. Not only is this a seriously unrealistic case as noted earlier, but we have found also that it is a case where $\boldsymbol{M}$ is directed laterally (that is, along the y-axis) and therefore reverses its direction between configurations (a) and (c) – making, accordingly, no contribution to the mean quantity $(-\overline{U\boldsymbol{M}})$ which appears in the expression (3) for propulsive force.

In the real three-dimensional balistiform motion, however, the undular character of the fin movements implies a phase lag in the motions of posterior sections behind those of anterior sections, and this twists the plane of the locally almost two-dimensional motion so that the momentum vector $\boldsymbol{M}$ is twisted always towards the posterior direction. Such a twist, as we shall see, makes the term $(-\overline{U\boldsymbol{M}})$ contribute positively to the propulsive force.

In clarifying these matters, we again focus attention, at each fish cross-section, on configuration (a) – and therefore also, by implication, on its mirror-image configuration (c). Figure 7 illustrates configuration (a) at a certain cross-section, alongside the associated configurations at posterior and anterior cross-sections with, respectively, phase lag and phase lead in their movements. An identical twist towards the posterior direction in the motions of both fins perpendicular to themselves is evident from this diagram.

We denote by κ the local twist of each fin, defined (see figure 7) as

$$\kappa = \delta\theta/\delta a. \tag{13}$$

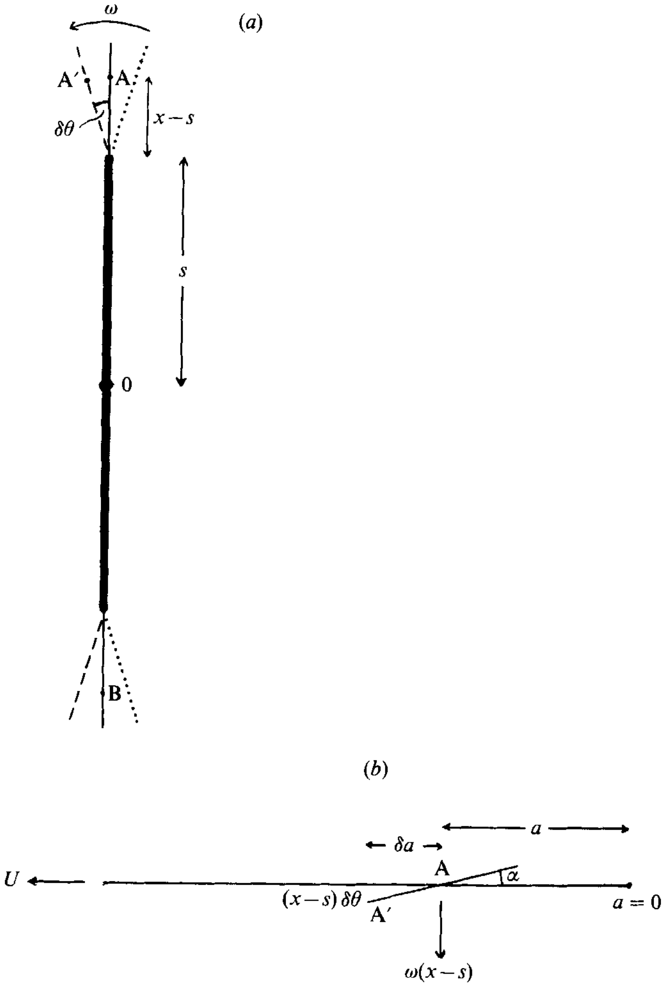

FIGURE 7. (*a*) View of fins from posterior end (drawing 'in elevation'). ——, Fin positions at a distance a from posterior end, when the fins are in configuration (*a*) (see figure 4). The points A and B are at a distance $x-s$ from the fin base. – – – – –, Fin positions with phase lead, found at a bigger distance $a+\delta a$ from the posterior end. Here the point A′ is at a distance $x-s$ from the fin base. ······, Fin positions with phase lag, found at a smaller distance $a-\delta a$ from the posterior end. (*b*) View of fin section AA′ from above (drawing 'in plan'). Since (as (*a*) shows) the point A′ is displaced by a distance $(x-s)\,\delta\theta$ from the vertical plane through the backbone, where $\delta\theta$ is the (small) angle shown, the angular displacement α of AA′ satisfies the equation $\tan\alpha = [(x-s)\,\delta\theta]/\delta a$. The motions of AA′ are lateral with velocity $\omega(x-s)$ and forward with velocity U.

Here, with a as the distance of a certain section ahead of the posterior end of the fish's propulsive apparatus and $a+\delta a$ as the same distance for an anterior section, $\delta\theta$ represents the angle between the fin positions at the two sections when projected as in figure 7 onto the same plane. (If, for example, the fin's undular motion took the form of a sinusoidal variation of θ with amplitude θ_0 and wavelength λ, then the value of κ would be

$$\kappa = 2\pi\theta_0/\lambda; \tag{14}$$

but the more general definition (13) allows for the possibility of the fin's motions not being precisely sinusoidal.)

We consider now, at a point A with coordinates $(x, 0)$ so that its distance from the fin base is $(x-s)$, the angle α of inclination of the fin (see figure 7) to the fixed vertical plane through the fish's backbone. Because, at the section anterior to A by a distance δa the fin is turned through an angle $\delta\theta$, it follows that the point corresponding to A is displaced by a distance $(x-s)\,\delta\theta$; accordingly, the tangent of the angle of inclination α is the ratio of $(x-s)\,\delta\theta$ to δa, which by (13) gives

$$\tan\alpha = \kappa(x-s). \tag{15}$$

Clearly, the direction normal (i.e. perpendicular) to the fin at A is itself inclined at the same angle α to the lateral direction (which is the direction normal to the above-mentioned vertical plane). Both at A and at the corresponding point B on the other fin – with coordinates $(-x, 0)$ – the normal instead of being in the lateral direction is twisted towards the posterior direction through this same angle α.

It follows that in configuration (*a*) the motion of each fin normal to itself at both A and B is directed not laterally but in another direction derived by angular displacement towards the posterior direction through an angle α. The magnitude of that motion (at A, for example) consists, as figure 7 shows, of two terms: the resultant $\omega(x-s)\cos\alpha$ of the fin's lateral motion with velocity $\omega(x-s)$ minus the resultant $U\sin\alpha$ of the fin's forward motion at the swimming velocity U of the fish. Equation (15) for $\tan\alpha$ allows us to express the resultant in a form

$$\omega(x-s)\cos\alpha - U\kappa(x-s)\cos\alpha = (1-V^{-1}U)\,\omega(x-s)\cos\alpha, \tag{16}$$

where we have written $V = \omega/\kappa$.

We may recall that the multiplying factor $(1-V^{-1}U)$ occurs also in classical elongated-body theory (*MB*, p. 20) with V as the velocity of propagation of the propulsive undular motion along the fish's body. This is also the interpretation of V in (16), because an undular variation in θ propagating at speed V in the posterior direction (with a decreasing) takes the form

$$\theta = f(a+Vt), \quad \text{giving} \quad \partial\theta/\partial t = V\partial\theta/\partial a \quad \text{or} \quad \omega = V\kappa. \tag{17}$$

We have found that the motion of each fin normal to itself occurs with velocity (16) and is directed not laterally but in another direction turned through an angle α towards the posterior direction. We must now ask what this implies for the approximate specification of the local fluid motion by a two-dimensional motion.

It is evident first of all that, if α were a constant instead of varying along the fin $s < x < l$ in accordance with (15), then the local approximately two-dimensional motion (produced by the motion of each fin normal to itself) would be not in the plane of the cross-section but in a plane derived from it by such a backward twist through angle α. This is because the fin movements normal to themselves would be in such a plane (while the fish's essentially rigid body does not move at all); accordingly, the consequent fluid motion and its momentum $\boldsymbol{M}$ would be in the same plane, and would therefore possess a posterior-pointing component (contributing positively, as already noted, to the term $(-\overline{UM})$ in the expression (3) for propulsive force).

Next, if we take into account the actual variation with x in the angle α through which the motions are twisted, we must ask in what plane we can then expect the momentum vector $\boldsymbol{M}$, related (as far as possible) to some approximately two-dimensional fluid motion in that plane, to lie. We note first that the motion should

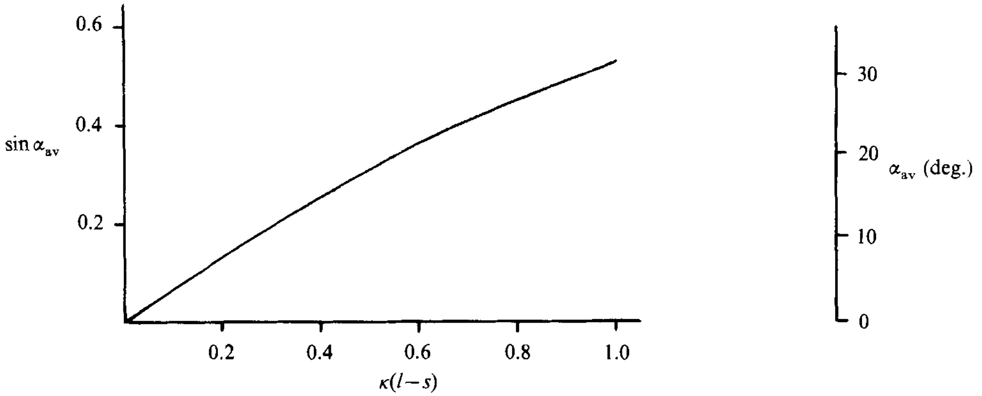

FIGURE 8. The angular displacement α_{av} calculated as a weighted average (with the velocity (16) used as a weighting function) of the angle α defined by (15). The right-hand scale gives α_{av} in degrees, while the left-hand scale gives $\sin\alpha_{av}$ (a factor appearing in the principal contribution (21) to the propulsive force).

be as nearly two-dimensional as possible if the plane is defined as one twisted backward through an angle α_{av} representing some sort of average of the angles α defined by (15). Furthermore, the momentum vector $\boldsymbol{M}$ should then be approximately the momentum per unit length associated with that two-dimensional motion, since fin movements in the region (near the fin base) with $\alpha < \alpha_{av}$ would push the fluid to one side of that plane while those in the region (near the fin tip) with $\alpha > \alpha_{av}$ would push it to the other side, and with a proper choice of α_{av} the associated components of fluid momentum normal to the plane should cancel out.

Indeed, this argument suggests what type of average should be used in calculating α_{av}; namely, a weighted average for $s < x < l$ with the velocity (16) as the weighting function. Figure 8 plots the angle α_{av} so calculated, as a function of the product $\kappa(l-s)$ of the twist (13) and the depth of a fin.

Although the three-dimensional effects discussed above suggest an angular displacement α_{av} (given by figure 8) for the direction of the momentum $\boldsymbol{M}$ per unit length of fish, they do not give rise as regards its magnitude M to any prediction very greatly modified from that (given by figure 6) emerging from the two-dimensional theory. The one important change is the incorporation of the $(1-V^{-1}U)$ factor from (16).

This equation, indeed, implies that, at a point (such as A in figure 7) with coordinates $(x, 0)$, the fin's velocity component in the plane of the approximately two-dimensional motion can be written as

$$(1-V^{-1}U)\,\omega(|x|-s)\cos\alpha_{av}. \tag{18}$$

We illustrate in figure 9 a short length δa of fish on which the lines at angle α_{av} to the backbone show how the actual fin movements are represented as closely as possible by movements (18) giving rise to a locally two-dimensional motion. These movements represent a reduction by a factor $(1-V^{-1}U)\cos\alpha_{av}$ in the fin velocities (4) assumed in the earlier, strictly two-dimensional theory. Accordingly, the momentum per unit length of the fin itself, given by (12) as βM_0, is reduced to

$$\beta M_0(1-V^{-1}U)\cos\alpha_{av}. \tag{19}$$

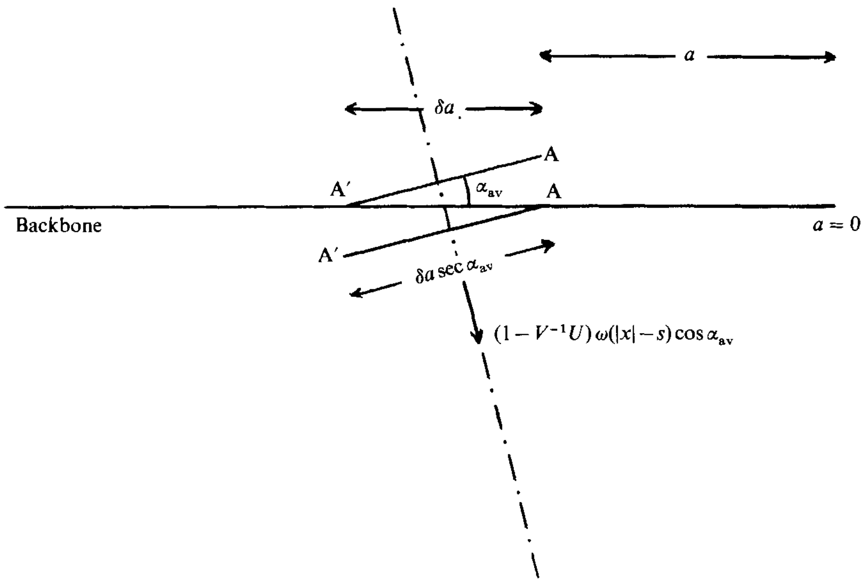

FIGURE 9. View from above (drawing 'in plan') of the motion of the fin section AA′. —·—·—, Plane of the associated approximately two-dimensional motion of fluid.

However, the fin length shown in figure 9 is $(\delta a)\sec\alpha_{av}$ and so the overall momentum is $\beta M_0(1 - V^{-1}U)\,\delta a$, giving

$$M = \beta M_0(1 - V^{-1}U) \tag{20}$$

as the magnitude of the momentum per unit length of fish.

In summary, then, the momentum $\boldsymbol{M}$ in configuration (*a*) has magnitude M and is directed at an angle α_{av} to the lateral direction. As noted earlier, its strictly lateral component $M\cos\alpha_{av}$ is reversed in the mirror-image configuration (*c*), and therefore is not expected to contribute to the mean value $\overline{U\boldsymbol{M}}$. On the other hand, the momentum component $M\sin\alpha_{av}$ in the posterior direction is unchanged in that mirror-image configuration (*c*), in between configurations (*b*) and (*d*) when both components are zero; and, for the corresponding component of $U\boldsymbol{M}$, this represents a fluctuation at twice the fundamental frequency between $UM\sin\alpha_{av}$ and zero, with a best estimate of its mean value as $\frac{1}{2}UM\sin\alpha_{av}$ (where (20) gives the approximate value of M). The corresponding term $(-\overline{U\boldsymbol{M}})$ in the propulsive force (3) is, because of the minus sign, directed forwards with the same magnitude

$$\tfrac{1}{2}U\beta M_0(1 - V^{-1}U)\sin\alpha_{av}. \tag{21}$$

This term (21) seems to be the leading contributor to propulsive force. It corresponds directly to the term $\overline{umw\,\partial z/\partial a}$ in large-amplitude elongated-body theory (*MB*, equation (5) on p. 109), with U corresponding to u and $\sin\alpha_{av}$ to $\partial z/\partial a$; but the momentum enhancement factor β, plotted in figure 6, increases considerably the importance of this term (21).

By contrast, the other term in the propulsive force (3) – namely, the mean of the pressure force $\boldsymbol{P}$ acting across the posterior plane – is recognized in large-amplitude elongated-body theory as of only minor importance. Furthermore, it contributes even less in the present theory because it turns out not to be subject to any such enhancement.

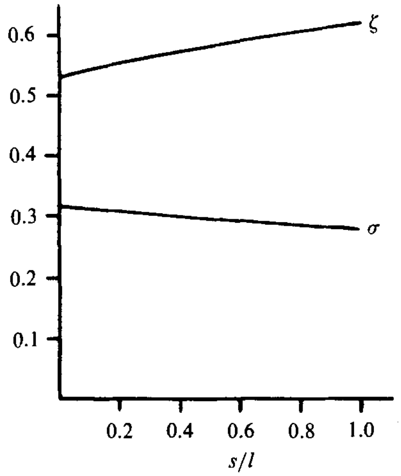

FIGURE 10. Effective absence of enhancement (as s/l increases) in the pressure force P or in the kinetic energy per unit length E. The graphs, taken from figure 1 of Part 2, show the variation of $\zeta = P/P_0$ and of $\sigma = E/P_0$ as a function of s/l for the simplified model illustrated in figure 5, where $P_0 = \rho\omega^2(l-s)^4$.

To make this clear, we note that in Part 2 the magnitude of $\boldsymbol{P}$ is calculated for a very precisely two-dimensional motion (with velocities as in (4) above) in the form

$$P = \zeta P_0, \quad \text{where} \quad P_0 = \rho\omega^2(l-s)^4 \tag{22}$$

and the coefficient ζ takes values ranging (see figure 10) from 0.53 to 0.62 instead of becoming specially enhanced as s/l approaches 1. The replacement of ω by $\omega(1-V^{-1}U)\cos\alpha_{\text{av}}$ in (18) changes (22) into

$$P = \zeta(1-V^{-1}U)^2 P_0 \cos^2\alpha_{\text{av}}, \tag{23}$$

where, just as in classical elongated-body theory, the reduction factor $(1-V^{-1}U)$ appears in a squared form that contributes to the relative insignificance of P. The vector pressure force $\boldsymbol{P}$ is directed at right angles to the plane of the motions so that its forward component is $P\cos\alpha_{\text{av}}$ in configurations (*a*) and (*c*) – compared with zero values in configurations (*b*) and (*d*) – and the best estimate of its mean value is $\frac{1}{2}P\cos\alpha_{\text{av}}$, giving

$$\tfrac{1}{2}\zeta(1-V^{-1}U)^2 P_0 \cos^3\alpha_{\text{av}} \tag{24}$$

as the contribution of $\bar{\boldsymbol{P}}$ in (3) to the propulsive force.

We can confirm the unimportance of this contribution (24) by writing out its ratio to the leading term (21) as

$$\frac{\frac{1}{2}\zeta(1-V^{-1}U)^2\rho\omega^2(l-s)^4\cos^3\alpha_{\text{av}}}{\frac{1}{2}U\beta[\frac{1}{4}\pi\rho\omega(l-s)^3](1-V^{-1}U)\sin\alpha_{\text{av}}} \tag{25}$$

(using (22) and (12) for P_0 and M_0) and substituting $\omega = V\kappa$ from (16). Then the ratio (25) becomes

$$\left(\frac{4\zeta}{\pi\beta}\right)(VU^{-1}-1)\left[\frac{\kappa(l-s)}{\sin\alpha_{\text{av}}}\right]\cos^3\alpha_{\text{av}}; \tag{26}$$

and, with ζ between 0.53 and 0.62 and β in the region of 3 to 4, the quantity in the first bracket is small; and that in the second is also expected to be small, while the product of the remaining factors (see figure 6) is close to 1 or a bit less.

To sum up, the propulsive force (3) is dominated by the term (21) representing the rate of shedding of the backward-pointing component of fluid momentum at the posterior end of the fish's propulsive apparatus. This momentum is enhanced by a substantial factor β which represents the effect of the fin movements being attached to a deep, essentially rigid, body.

Finally, the rate of shedding of kinetic energy at the posterior end of the fish's propulsive apparatus is not so enhanced; which, of course, has favourable implications for the efficiency of balistiform propulsion. In Part 2, indeed, for a very precisely two-dimensional motion (with velocities as in (4) above), the kinetic energy per unit length is calculated in the form $E = \sigma P_0$, where the coefficient σ takes values which vary only slightly (see figure 10), from 0.32 to 0.28. It follows that, in the approximately two-dimensional motion illustrated in figure 9, with ω replaced by $\omega(1-V^{-1}U)\cos\alpha_{\mathrm{av}}$, the kinetic energy in a length δa of fish becomes

$$[\sigma(1-V^{-1}U)^2 P_0 \cos^2\alpha_{\mathrm{av}}](\delta a)\sec\alpha_{\mathrm{av}}. \tag{27}$$

Accordingly, the rate at which fin movements generate 'unproductive' energy which is shed in the vortex wake is

$$U\sigma(1-V^{-1}U)^2 P_0 \cos\alpha_{\mathrm{av}} \tag{28}$$

in configurations (*a*) and (*c*); or (see (21) above) half as much on a time-averaged basis.

When we compare this rate of generation of 'unproductive' energy with the rate of generation of 'useful' work by only the main term (21) in the propulsive force, we obtain once more a ratio as in (25), but with ζ replaced by the somewhat smaller coefficient σ and (in partial compensation for this reduction) $\cos^3\alpha_{\mathrm{av}}$ replaced by $\cos\alpha_{\mathrm{av}}$. The resulting ratio is again small (a bit smaller than before) and for two main reasons:

(i) as in classical elongated-body theory, the factor $(1-V^{-1}U)$ appears to the first power in the rate of generation of useful work but squared in the rate of generation of unproductive energy; while

(ii) the ratio is still further reduced by the presence in the denominator of the momentum enhancement factor β.

That factor represents additionally, then, an enhancement of propulsive efficiency.

5. Generalizations and conclusions

Analysis of balistiform swimming in §4 by means of a simplified model led to some clear conclusions: that propulsive force is dominated by the rate of shedding of backward momentum, and that a substantial momentum enhancement factor β both magnifies this force and improves propulsive efficiency. We must now ask whether the model's principal geometrical simplification (characterization of the lateral thickness of the body as negligibly small) may have exaggerated the momentum enhancement effect.

The answer to this question is obtained in Part 3, §3, where fish bodies with realistically elliptical cross-sections of axis ratio t/s (ratio of the body thickness $2t$ to the body depth $2s$) are analysed and the corresponding momentum enhancement factor β derived as a function of t/s and of the solidity ratio s/l (ratio of the body depth $2s$ to the total cross-sectional depth $2l$ including fins as well as body). Part 3 illustrates the sectional geometry at the top of its figure 6 and sets out the results in its figures 7 and 8. We see from figure 7 of Part 3 that calculations for the simplified model (with t/s essentially zero) do exaggerate the momentum enhancement effect but only to a modest extent. Figure 8 of Part 3 shows indeed that, as t/s increases from 0 to as high a value as 1 (case of a circular body cross-section), the momentum enhancement factor drops from 2.9 to 2.6 when $s/l = 0.6$, from 3.4 to 2.8 when $s/l = 0.7$ and from 4.2 to 3.0 when $s/l = 0.8$. We recall that balistiform locomotion is exhibited mainly in fishes with values of t/s somewhat intermediate† between 0 and 1. The above calculations caused us to comment in §1 above that momentum enhancement for balistiform locomotion is by a factor of 'around 3 or a little more'.

The propulsive force in balistiform swimming should be dominated, then, by the momentum-shedding term

$$\tfrac{1}{2}U\beta M_0(1-V^{-1}U)\sin\alpha_{\text{av}} \tag{29}$$

(see (21)) with the above revised values of β. We have not considered it worthwhile to try to recalculate the additional term $\bar{\boldsymbol{P}}$ which, from being insubstantial in classical elongated-body theory, is made negligible (§4) as a result of momentum enhancement.

We emphasize that our conclusions apply equally to both of the two main modes of balistiform locomotion, designated in figure 1 as the undulatory and oscillatory modes. The force depends on the value of (29) at the posterior section $a = 0$ of the fish's propulsive apparatus; and this value is well defined in terms of ω, the angular velocity of fin-ray movement and κ, the twist (13) of each fin, as that section passes through the symmetrical configuration (*a*). For a truly undulatory motion, the ratio $V = \omega/\kappa$ can be interpreted (see (17)) as the propagation speed of the wave; but the ratio remains well-defined also in the oscillatory mode, where its interpretation is really only as a sort of 'equivalent wave speed'. (A similar distinction exists for modes of locomotion by body flexure (*MB*, p. 20), where a certain quantity V represents a true wave speed in the anguilliform mode but only an equivalent wave speed in the carangiform mode.)

Momentum enhancement is present, then, to much the same extent for both modes of balistiform locomotion; and we are forced to ask, therefore, what advantages, if any, may have accompanied the evolution of those more complicated neuromuscular control mechanisms that are required for the undulatory mode. The main benefit, already noted towards the end of §1 and at the end of §3, stems from the virtual elimination of fluctuating sideforces – allowing the essentially rigid body to move forward without those oscillating motions of sideslip or yaw which are known (Blake 1983*a*, pp. 98–101) to increase body drag by a factor of 3 to 4. Provisionally, then, we may expect the above-noted enhancement of thrust by a factor of about 3 or a bit more to coexist with reduction in body drag by a comparable factor, which, with body drag proportional to U^2, might enhance the swimming velocity U by (again) a similar factor.

Here we should pause and consider whether any other serious inaccuracies in our

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† At the same time, because the plane in which the fluid motions are most closely two-dimensional is inclined (see figure 9) at an angle α_{av} to the fish cross-section, the effective value of t/s for the body's elliptical section by such a plane is increased by a factor $\sec\alpha_{\text{av}}$, and it is for this increased value of t/s that the appropriate value of β needs to be read off from the curves in Part 3.

model (besides the geometrical one which has been comprehensively addressed in Part 3) may limit the value of the above conclusions. In this context their most obvious source of inaccuracy lies in the approach to determining $\boldsymbol{M}$ through its calculation for a locally two-dimensional flow that approximates as well as possible the real three-dimensional flow.[†] It is in the undulatory case, particularly if the wavelength λ of undulations is not very large, that the approximate representation of solutions of the three-dimensional Laplace equation by solutions of the two-dimensional equation

$$\partial^2\phi/\partial x^2 + \partial^2\phi/\partial y^2 = 0 \tag{30}$$

may involve substantial errors. These indeed are cases where a different two-dimensional equation

$$\partial^2\phi/\partial x^2 + \partial^2\phi/\partial y^2 - k^2\phi = 0 \quad (\text{where } k = 2\pi/\lambda) \tag{31}$$

might be thought to represent the three-dimensional Laplace equation more accurately.

Although we have not embarked on any calculations using (31), preferring at present to estimate momentum enhancement by a direct comparison of the results of applying elongated-body theory to different cases, we can see from a knowledge of the fundamental solution $K_0(kr)$ of (31) in Bessel-function form (where $(x^2+y^2)^{\frac{1}{2}} = r$) how that equation's use might affect the calculation of momentum. Basically, this solution behaves like the corresponding solution of (30) at short range but falls off far more rapidly when kr is large. Accordingly, the momentum produced by given fin movements will be spread over a gradually reduced area as k increases. Momentum enhancement, in short, may be expected to be reduced as the wavelength of an undulatory motion is itself reduced. This consideration, particularly in relation to studies of the evolution of the undulatory form of balistiform locomotion, may impose a countervailing disadvantage on any further reductions in wavelength after the initial advantage of drag limitation through reductions in body oscillations has been reaped.[‡]

We should not leave the subject of balistiform locomotion without referring to its use by certain groups of flexible-bodied fishes as an alternative low-cost means of progression when they do not need the higher speeds available with anguilliform body undulations. The thin bodies of the flat-fishes (Heterosomata) make the model of §4 rather accurate (even though the whole geometry is turned through 90°), and the conclusions in that section regarding efficiency confirm the low energy cost of propulsion of such fishes by simple undulations of the marginal fins. Analogous advantages are reaped by many eels (Apodes) which are able to hold their body straight while wave motions pass along their median fins either in the posterior or (for backward motion) in the anterior direction; although in their case, of course, the model of Part 3 is appropriate with t/s around 1.

Finally, we touch briefly on the biofluiddynamics of gymnotiform locomotion in fishes possessing a long ventral fin but no corresponding dorsal fin; that is, a mode of locomotion in which the fish's body is held rigid and undulations pass along the

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[†] By contrast, the neglect of any vorticity shed at fin tips is likely to reduce only slightly the accuracy of the irrotational-flow calculation of $\boldsymbol{M}$ for an unsteady fluid motion like this, where the rather small amplitude of oscillation of fins relative to the water limits greatly the displacement of any shed vorticity.

[‡] As Part 1 goes to press we add this footnote confirming that calculations based on equation (31), which have now been made, do indeed demonstrate such a 'countervailing disadvantage'. These calculations and their biological implications are to be set out in Part 4 of the present series (Lighthill 1990*c*).

ventral fin in the posterior direction. Our analysis follows the same form as in §4, with the omission of any dorsal-fin effects; but, needless to say, a new determination of the momentum enhancement factor is needed.

Part 3 gives this in its §2 for fish bodies with elliptical cross-sections of axis ratio t/s, and obtains the momentum enhancement factor β as a function of t/s and of the solidity ratio $2s/(l+s)$, where the latter is now the ratio of the body depth $2s$ to a total cross-sectional depth $l+s$ including the depth $l-s$ of just a single fin. Part 3 illustrates the sectional geometry in its figure 2 and sets out the results in its figures 4 and 5. The momentum enhancement is factor is here defined as

$$\beta = M/M_1, \quad \text{where}\, M_1 = \tfrac{1}{8}\pi\rho\omega(l-s)^3 \tag{32}$$

is the momentum that would be associated with the motion of just the single fin on its own (thus, comparison with (12) gives $M_1 = \frac{1}{2}M_0$). The value of β for typical solidity ratios around 0.7 is in the region of 2.4, representing a considerable momentum enhancement but not quite so much as in the balistiform mode. The estimate (21) of propulsive force in the balistiform mode has to be replaced by

$$\tfrac{1}{2}U\beta M_1(1-V^{-1}U)\sin\alpha_{av} \tag{33}$$

in the gymnotiform mode.

Very much as before, we see the advantages of gymnotiform locomotion as residing partly in an enhancement of thrust (without a corresponding enhancement of 'unproductive' energy generation) and partly in a reduction of drag, the latter reduction being evident once again from the argument given at the end of §3. These are substantial advantages, leading to a reduced energy cost of transport, and are available, of course, whether or not a fish possesses electric organs whose use may be facilitated in a mode of locomotion with the body held rigid.

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