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The swimming of minute organisms

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Some of the processes relevant to the propulsion of small organisms are investigated using the simple mathematical model of two-dimensional waves passing through a sheet immersed in a viscous fluid. This model was first used by Taylor, who considered an inextensible sheet moving in an unbounded fluid of negligible inertia. Here the effects of fluid inertia, of straining of the wave-bearing surface, and of nearby walls are included in the study. The applicability of the results is restricted both by the unrealistic geometry of the model and by the method of analysis which gives results valid for small Reynolds numbers and for small wave amplitudes only. However, the following general results may have counterparts in nature.

The effect of fluid inertia is to increase the propulsive speed for a particular wave amplitude. Straining of the waving surface will probably reduce the propulsive velocity for a given amplitude, although there exist modes of surface straining that give augmented propulsion. If the wave celerity and the energy output in swimming remain constant in the presence of a solid wall, the amplitude of the wave is reduced as the wall is approached while the propulsive speed first rises slightly and then drops. It appears further that an organism swimming near a wall may induce a shear pattern which directs it away from the wall.

1. Introduction

In elucidating the means of propulsion of microscopic organisms Taylor (1951) considered the simple motion set up in an infinite fluid by a train of two-dimensional waves travelling across an inextensible sheet. He based his analysis on the biharmonic equation

$$\nabla^4\psi = 0 \tag{1}$$

for the stream function of a two-dimensional, viscosity-controlled flow. Taking the waving surface to be

$$y = b\sin(kx+\sigma t), \tag{2}$$

and linearizing the boundary conditions, he found the first-order solution

$$\psi = -(b\sigma/k)(1+ky)\,e^{-ky}\sin(kx+\sigma t) \quad \text{for} \quad y>0, \tag{3}$$

a solution indicating vanishingly small velocities far from the sheet, and hence suggesting that the sheet is not propelled through the fluid.

But when the boundary condition for an inextensible sheet was applied more accurately (by expanding all the relevant quantities in powers of bk) Taylor had to include in the stream function terms of the form

$$\psi = (\sigma/k)(a_1b^2k^2+a_2b^4k^4+\dots)\,y$$

(a_1, a_2, etc., are numerical constants), giving rise to a uniform velocity parallel to the waving sheet.† Alternatively, if the fluid is taken to be at rest far from the sheet, the sheet is found to be propelled in the direction opposite to that of the propagation of the distorting wave. Taking terms as high as the fourth order in the parameter bk into account, Taylor found the propulsive velocity to be

$$V/U = \tfrac{1}{2}b^2k^2(1-\tfrac{19}{16}b^2k^2), \tag{4}$$

where $U = \sigma/k$ is the wave speed.

It is proposed here to generalize Taylor's study in three respects, considering finite inertia of the perturbed fluid, extensibility of the waving sheet, and rigid walls lying parallel to the mean surface of the wave-bearing sheet.

Since Taylor's study was intended to apply to the swimming of very tiny organisms (such as bull spermatozoa, for which the Reynolds number based on wavelength is about 10^{-2} and that based on tail diameter 10^{-4}), his neglect of the inertia of the fluid was quite appropriate. At the other extreme, in the study of the swimming of large animals, inviscid flow theory can be applied to investigate the means of propulsion (although a separate calculation of friction drag is then necessary). But there will exist an intermediate range in which inertia and viscosity both influence propulsion; it is here that the first generalization of Taylor's problem may be applicable. For comparison, the influence of inertia in a closely allied forced motion will be considered also.

The most obvious way in which straining of the wave-bearing surface may arise is in maintaining the wave. But it is possible also that internal mechanisms of the swimming organism give rise to flexings of the surface, which, combined with the deflexions due to waving, produce augmented propulsion. This second class of propulsive motions has been described as 'squirming' by Lighthill (1952), who studied the motion of a sphere whose surface both pulsed and strained. In the present investigation of sheet extension the probable effect of simple waving will be considered as well as the possibility of propulsion by combined waving and squirming.

Interest in the motions of small organisms close to solid walls arises for several reasons. There is some reason to think that viscous interactions will draw a swimmer towards a nearby wall. But even if this were not the case, the natural swimming of tiny organisms will often take place in narrow passages in which close proximity of solid surfaces is a geometrical necessity. Finally, the exigencies of laboratory technique sometimes require that the organisms studied be those very near a solid wall. Thus the problem of swimming near a wall may be expected to have greater practical application than that of motion in an unbounded fluid.‡

In view of the important differences between the propulsive motions considered here and those occurring in nature (especially the restriction here to two-

† Since the propulsive velocity, if it exists, must be independent of the sign of b, it is apparent *a priori* that it can be expanded in this form. This is true only for an inextensible sheet.

‡ This paragraph owes much to discussions with Lord Rothschild concerning experimental techniques.

dimensionality), any close agreement of measured propulsive velocities with those predicted will be purely fortuitous. However, we may hope that the essential features of the physical situation have been represented well enough to provide a realistic appreciation of qualitative effects.

2. The influence of inertia of the fluid

The full Navier–Stokes equations form the basis of this investigation. In view of their complexity, we can hope to deal only with the simplest of perturbing motions. Taylor's problem of a waving sheet is chosen: it is one for which the construction of solutions is quite straightforward; also there is the opportunity for comparison with his results at each stage.

Although the results obtained here are formally valid for any Reynolds number (if the wave amplitude be small enough), their application to real swimming motions must be severely restricted. At any but the smallest Reynolds numbers, separation of the flow from the waving body must occur and the accompanying cyclic shedding of vorticity will establish circulations about the rear of the body and so give rise to forces other than those which act on an infinite wave train.

The fundamental process of the analysis is the systematic expansion of stream function, boundary conditions, and wave profile in terms of an amplitude parameter. A series of equations for the terms of the stream function is obtained, together with appropriate boundary conditions. Solutions can easily be constructed for the first few of the successive problems; only patience is required for an arbitrary degree of accuracy.

As a preliminary to the formal analysis, we should perhaps make a few remarks concerning the frames of reference to be considered, the several characteristic velocities which will subsequently be utilized, and the relationships among them. In most of the work we shall follow Taylor in adopting a frame of reference moving with the crests of the waves travelling through the sheet. As may be seen from figure 1, these crests move with respect to the fluid at infinity with velocity $u = -U+V$, so that in the frame of reference in which they are at rest, the fluid at infinity moves with velocity $u = U-V$.

Taylor noted, with characteristic insight, that the waving motion of an inextensive sheet was, in the frame of reference in which the crests are stationary, equivalent simply to the motion of each particle of the sheet tangentially along its sinusoidal path, each and every particle having the same constant speed, say Q_0. We shall later relax this requirement somewhat in order to study motions including 'squirming', although even then it is satisfied in the mean. The ratio of the sheet speed Q_0 and the wave celerity U is just the ratio of the developed length of the sine curve to the chord length measured in its mean plane, and thus depends on the amplitude parameter bk in a simple way

$$Q_0/U = 1+\tfrac{1}{4}b^2k^2+\dots.$$

For analytic convenience we shall take as the basic motion of our analysis

$$u = Q_0.$$

This differs from U only at the second order in bk, and tends to it as $bk \to 0$. We shall determine the perturbation to this basic flow as a result of the sheet's motion and finally fasten our attention on that part of the perturbation which is uniform throughout the field, neither varying sinusoidally with distance x along the sheet, nor dying out exponentially away from the plate, as do those contributions that do vary sinusoidally with x. This uniform component of the perturbation we shall denote by Δu. Then far away from the sheet

$$u = Q_0 + \Delta u,$$

where Δu depends on the amplitude parameter, and Q_0 differs from U by an amount depending on that parameter.

To determine the propulsive velocity we equate the two expressions we have obtained for the velocity far from the waving sheet, obtaining

$$U - V = Q_0 + \Delta u.$$

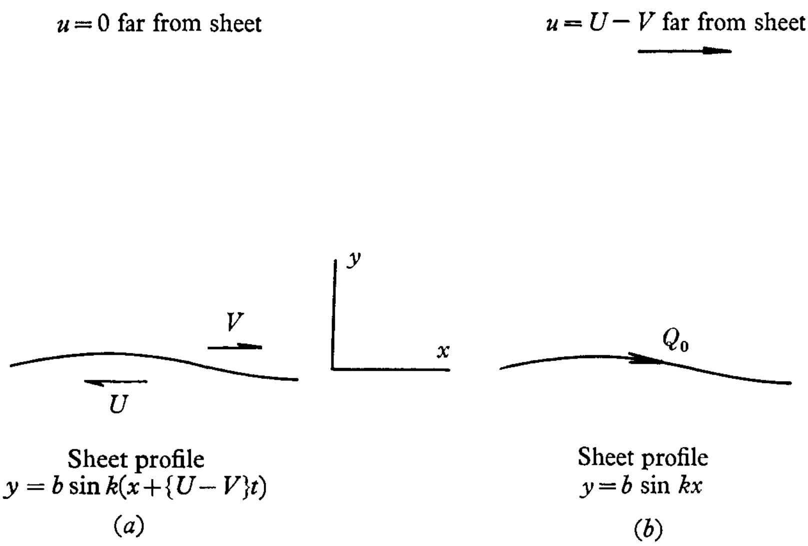

FIGURE 1. Frames of reference. (a) Frame of reference in which fluid far from the waving sheet is at rest. U, the celerity of the waves through the sheet; V, the speed at which the sheet progresses relative to the fluid far from it; $(U-V)$, the apparent speed of propagation (of wave crests to the left). (b) Frame of reference in which wave profile is at rest. Q_0, the sheet speed, the tangential velocity of the particles of the inextensible sheet as seen in this frame.

(a) *Fundamental problem*

For a two-dimensional motion we can introduce a stream function related to the velocity components by

$$u = -\partial\psi/\partial y, \quad v = \partial\psi/\partial x,$$

automatically satisfying the continuity equation for incompressible fluid and allowing the Navier–Stokes equations for steady flow to be combined to give

$$\nu \nabla^4\psi = \partial(\psi, \nabla^2\psi)/\partial(x, y). \tag{5}$$

We consider the motion set up by a sinusoidal sheet, given by

$$y = b \sin(kx)$$

moving tangentially to itself with velocity Q_0. Then on the sheet

$$u = Q_0 \cos\theta, \quad v = Q_0 \sin\theta,$$

with $\tan\theta = bk\cos(kx)$ (for $Q_0 > 0$, $-\frac{1}{2}\pi < \theta < \frac{1}{2}\pi$).

The boundary conditions for ψ are

$$\partial\psi/\partial x = Q_0 \sin[\tan^{-1}(bk\cos kx)], \tag{6a}$$

$$\partial\psi/\partial y = -Q_0 \cos[\tan^{-1}(bk\cos kx)] \tag{6b}$$

on the sheet. We require also that the flow far from the sheet be uniform and parallel to it, that is, that $\psi \propto y$ far from the sheet. Throughout we shall consider the region for which $y > 0$.

The problem thus posed is that of a wave train travelling through an inextensible sheet immersed in a fluid which is at rest except for the perturbations set up by the wave.

(*b*) *Equations for successive approximations*

We consider the stream function as $\psi(x, y; \alpha)$, with α some measure of the amplitude (later we shall take $\alpha = bk$) and expand in terms of α

$$\psi = -Q_0 y + \alpha\psi_1 + \alpha^2\psi_2 + \dots, \tag{7}$$

where $\psi_0 = -Q_0 y$ represents the undisturbed fluid in the present frame of reference (as $\alpha \to 0$, $Q_0 \to U$).

Substituting this series into equation (5), collecting the terms of each order in α, and requiring that the equation be satisfied for all small values of α, we obtain a series of equations for the terms of the expansion:

$$\left.\begin{aligned}(\nu\nabla^2 - Q_0\partial/\partial x)\nabla^2\psi_1 &= 0,\\ (\nu\nabla^2 - Q_0\partial/\partial x)\nabla^2\psi_2 &= [1, 1],\\ (\nu\nabla^2 - Q_0\partial/\partial x)\nabla^2\psi_3 &= [1, 2] + [2, 1],\end{aligned}\right\} \tag{8}$$

etc., where $$[i, j] = \partial(\psi_i, \nabla^2\psi_j)/\partial(x, y).$$

The first term is governed now by an Oseen equation in which the dominant acceleration term is included. In later equations Oseen's linear operator recurs and the non-linear acceleration terms are approximated using the contributions of lower order. However, each equation is linear in the yet-to-be-determined term of the expansion (7).

In passing, we may comment on a point of primarily mathematical interest. For the examples considered here, the non-constant contributions to the velocity perturbation vary (as do the boundary conditions) sinusoidally with x, distance measured along the waving sheet, and decrease exponentially with distance away from the sheet. Hence the Oseen approximation with which our analysis begins provides a first approximation which is uniformly valid throughout the fluid. It is then unnecessary to adopt the recently developed methods of matching inner and outer expansions to obtain approximations which are everywhere realistic.

(c) Boundary conditions for successive approximations

We can expand the boundary conditions as series in α too,

$$\left.\begin{aligned} \partial\psi/\partial x &= \alpha f_1(x)+\alpha^2 f_2(x)+\alpha^3 f_3(x)+\dots,\\ \partial\psi/\partial y &= -Q_0+\alpha h_1(x)+\alpha^2 h_2(x)+\dots \end{aligned}\right\} \tag{9}$$

to be applied on the sheet $y = \alpha g(x)$, introducing $h_0 = -Q_0$ immediately to match the first term of the condition (6*b*). These components can also be expressed using Taylor's series evaluated at $y = \alpha g$:

$$\left.\begin{aligned} \frac{\partial\psi}{\partial x} &= \left(\frac{\partial\psi}{\partial x}\right)_0+\left(\frac{\partial^2\psi}{\partial x\,\partial y}\right)_0\alpha g+\frac{1}{2}\left(\frac{\partial^3\psi}{\partial x\,\partial y^2}\right)_0\alpha^2 g^2+\dots,\\ \frac{\partial\psi}{\partial y} &= \left(\frac{\partial\psi}{\partial y}\right)_0+\left(\frac{\partial^2\psi}{\partial y^2}\right)_0\alpha g+\frac{1}{2}\left(\frac{\partial^3\psi}{\partial y^3}\right)_0\alpha^2 g^2+\dots. \end{aligned}\right\} \tag{10}$$

Equating alternative expressions (9) and (10), substituting the expansion for the stream function (7), and again collecting terms of like order in α, we obtain the following series of boundary conditions to be applied in the plane $y = 0$

$$\left.\begin{aligned} &\frac{\partial\psi_1}{\partial x}=f_1(x),\quad \frac{\partial\psi_1}{\partial y}=h_1(x);\\ &\frac{\partial\psi_2}{\partial x}=f_2-\left(\frac{\partial^2\psi_1}{\partial x\,\partial y}\right)_0 g,\quad \frac{\partial\psi_2}{\partial y}=h_2-\left(\frac{\partial^2\psi_1}{\partial y^2}\right)_0 g;\\ &\frac{\partial\psi_3}{\partial x}=f_3-\left(\frac{\partial^2\psi_2}{\partial x\,\partial y}\right)_0 g-\frac{1}{2}\left(\frac{\partial^3\psi_1}{\partial x\,\partial y^2}\right)_0 g^2, \end{aligned}\right\} \tag{11}$$

etc. This treatment of the boundary conditions is equivalent to Taylor's, although here their application has been separated into distinct stages.

The functions $f_i(x)$, $h_i(x)$ introduced in (9) are obtained simply by expanding the exact conditions (6*a*, *b*):

$$\partial\psi/\partial x = Q_0[\alpha\cos(kx)-\tfrac{1}{3}\alpha^3\cos^3(kx)+\tfrac{9}{24}\alpha^5\cos^5(kx)+\dots], \tag{6c}$$

$$\partial\psi/\partial y = -Q_0[1-\tfrac{1}{2}\alpha^2\cos^2(kx)+\tfrac{3}{8}\alpha^4\cos^4(kx)+\dots], \tag{6d}$$

where we have now taken $\alpha = bk$ as the amplitude parameter.

The simplicity of these results provides the justification for adopting $\psi = -Q_0 y$ ($Q_0 =$ const., $U = U(\alpha)$) as the basic flow, rather than $\psi = -Uy$ ($U =$ const., $Q_0 = Q_0(\alpha)$). Neither of the two correctly represents the uniform flow at infinity, $u = U - V$, both differing from it by a term $\sim O(\alpha^2)$. However, the second choice, $\psi = -Uy$, would result in more complicated forms for the coefficients of α in 6(*c*, *d*).

(d) First-order solution

The boundary conditions for ψ_1 are

$$\partial\psi_1/\partial x = Q_0\cos(kx),\quad \partial\psi_1/\partial y = 0\quad \text{on}\quad y = 0.$$

The form of these conditions and of the equation (8) for ψ_1 suggests that a solution of the form

$$\psi_1 = f(y)\,e^{ikx}$$

be sought. Elementary solutions bounded as $y \to +\infty$ are

$$f(y) = e^{-ky}, \quad \exp[-\beta k y e^{i\phi}],$$

with $\beta = (1+s^2)^{\frac{1}{4}}$, where $s = Q_0/\nu k$ is a Reynolds number based on sheet velocity, and $\tan 2\phi = s$, $0 \leqslant \phi \leqslant \frac{1}{4}\pi$.

The solution satisfying the boundary conditions is

$$\psi_1 = [Q_0/k(1+\beta^2-2\beta\cos\phi)]\,[-\beta e^{-ky}\{\sin(kx+\phi)-\beta\sin(kx)\} + e^{-\beta ky\cos\phi}\{\sin(kx-k\beta y\sin\phi)-\beta\sin(kx-\beta ky-\phi)\}]. \qquad (12)$$

A. Limiting case of small viscosity, $s \to \infty$.

$\psi_1 \to \psi_A = (Q_0/k)\,e^{-ky}\sin(kx)$, except for very small y. Save in a thin layer near the surface, the solution degenerates to the irrotational motion prescribed by the normal velocity of the sheet.

B. Limiting case of large viscosity, $s \to 0$.

$$\psi_1 \to \psi_B = (Q_0/k)\,(1+ky)\,e^{-ky}\sin(kx) \quad \text{if} \quad y \ll \nu/Q_0.$$

This is equivalent to the solution (3) found by Taylor on neglecting all acceleration terms. Once again the perturbations diminish quickly away from the sheet. But note that

$$\psi_B/\psi_A \simeq k\nu/Q_0 \quad \text{as} \quad y \to \nu/Q_0 \gg 1.$$

Taylor's limit is approached only for $y \ll \nu/Q_0$. It is within this region that the inertia terms he neglected are in fact small compared to the viscous forces.

The motion given by equation (12) for finite Reynolds number may be thought of as a superposition of the potential motion of limit A (dominant far from the sheet) and an unsteady boundary layer (like that sketched by Schlichting 1955, p. 68) decaying exponentially away from the surface, but satisfying the no-slip condition at the sheet.

(*e*) *Second-order propulsive velocity*

The boundary conditions for ψ_2 are found to be $\partial\psi_2/\partial x = 0$,

$$\partial\psi_2/\partial y = \tfrac{1}{2}Q_0[\tfrac{1}{2}-(1+\beta^2)(1-\beta\cos\phi)/(1+\beta^2-2\beta\cos\phi)]\,[1+\cos(2kx)] - \tfrac{1}{2}Q_0\beta\sin\phi\sin(2kx) \quad \text{on} \quad y = 0.$$

It is no longer sufficient to construct a solution purely from sinusoidal terms. They cannot give rise to the constant term in $\partial\psi_2/\partial y$ required to satisfy the boundary conditions. The uniform velocity which must be introduced to satisfy the second-order boundary conditions is

$$\Delta u = -\alpha^2\tfrac{1}{2}Q_0[\tfrac{1}{2}-(1+\beta^2)(1-\beta\cos\phi)/(1+\beta^2-2\beta\cos\phi)].$$

As was explained earlier, the sheet velocity Q_0, wave velocity U, propulsive speed V, and the perturbation contribution to the velocity far from the sheet Δu are related by

$$U - V = Q_0 + \Delta u,$$

while the wave speed and sheet velocity are related by

$$\frac{Q_0}{U} = \frac{\text{arc length of wave}}{\text{chord length of wave}} = 1 + \tfrac{1}{4}b^2k^2 - \tfrac{3}{64}b^4k^4 + \ldots.$$

Then, to the second order in α,

$$\frac{V}{U} = -\frac{\Delta u}{Q_0} - \frac{\alpha^2}{4}, \tag{13}$$

and the first term in the series for the propulsive velocity can be written

$$\frac{V}{U} = \frac{\alpha^2}{4}\left[\frac{\beta - \cos\phi}{\cos\phi - 1/\beta} - 1\right] \quad \text{with} \quad \cos\phi = [(1+\beta^2)/2\beta]^{\frac{1}{2}}.$$

Considering again the limiting cases:

A. Small viscosity, $s \to \infty$.

$$V/U \to \tfrac{1}{4}\alpha^2(2Q_0/\nu k)^{\frac{1}{2}}.$$

B. Large viscosity, $s \to 0$.

$$V/U \to \tfrac{1}{2}\alpha^2.$$

This is just Taylor's second-order result (cf. equation (4)).

For a discussion of the physical processes near the sheet which give rise to propulsion, the reader is referred to the lucid analysis of Taylor (1951).

In table 1 the variation of the second-order propulsive velocity is indicated for a range of small values of s.

s	0	1	2	3	4
$\frac{1}{2}\left(\frac{\beta - \cos\phi}{\cos\phi - 1/\beta} - 1\right)$	1·00	1·10	1·26	1·44	1·60

TABLE 1. Variation of propulsive velocity with Reynolds number

The labour of carrying these calculations to the fourth order is very much greater than it is for the limiting case treated by Taylor and will not be undertaken. From Taylor's result (4) we find that the fourth-order contribution is equal to 25% of the second order when $\alpha = bk \simeq 0{\cdot}46$ for $s = 0$. For $s \neq 0$, the second-order term in the propulsive velocity will be a useful approximation for an even small range of amplitude, since the higher-order terms include progressively higher powers of s.

3. An allied case of forced motion

A motion which is closely related to that set up by a waving sheet is that due to the pulsing surface given by

$$y = b\sin(\sigma t)\cos(kx),$$

whose every point moves in a straight line so that the surface velocity is given by

$$u = 0, \quad v = b\sigma\cos(\sigma t)\cos(kx).$$

The motion excited is a simple case of what is termed 'acoustic streaming'.

Once again we expand the stream function in an amplitude parameter α

$$\psi(x,y,t;\,\alpha) = \alpha\psi_1+\alpha^2\psi_2+\alpha^3\psi_3+\dots.$$

The equations for the successive terms are now obtained from the Navier–Stokes equations written in the form

$$\left(\nu\nabla^2-\frac{\partial}{\partial t}\right)\nabla^2\psi = \frac{\partial(\psi,\nabla^2\psi)}{\partial(x,y)},$$

and are

$$(\nu\nabla^2-\partial/\partial t)\,\nabla^2\psi_1 = 0,$$

$$(\nu\nabla^2-\partial/\partial t)\,\nabla^2\psi_2 = [1,1],$$

etc. In the basic operator account is again taken of the dominant acceleration term, now a time derivative.

Generalizing the boundary conditions as

$$\partial\psi/\partial x = \alpha f(x,t), \quad \partial\psi/\partial y = 0 \quad \text{on} \quad y = \alpha g(x,t),$$

we obtain the conditions

$$(\partial\psi_1/\partial x)_0 = f(x,t), \quad (\partial\psi_1/\partial y)_0 = 0,$$

$$\left(\frac{\partial\psi_2}{\partial x}\right)_0 = -\left(\frac{\partial^2\psi_1}{\partial x\,\partial y}\right)_0 g(x,t), \quad \left(\frac{\partial\psi_2}{\partial x}\right)_0 = -\left(\frac{\partial^2\psi_1}{\partial y^2}\right)_0 g(x,t),$$

etc. We shall take $\alpha = b$ simply, so that

$$f = \sigma\cos(\sigma t)\cos(kx), \quad g = \sin(\sigma t)\cos(kx).$$

(*a*) *First-order solution*

$$\partial\psi_1/\partial x = \sigma\cos(\sigma t)\cos(kx), \quad \partial\psi_1/\partial y = 0 \quad \text{on} \quad y = 0.$$

The appropriate solution is found to be

$$\psi_1 = [\sigma/k(1+\beta^2-2\beta\cos\phi)]\,[-\beta e^{-ky}\{\cos(\sigma t+\phi)-\beta\cos(\sigma t)\} + e^{-\beta ky\cos\phi}\{\cos(\sigma t-\beta ky\sin\phi)-\beta\cos(\sigma t-\beta ky\sin\phi-\phi)\}]\sin kx, \quad (14)$$

with

$$\beta = (1+s'^2)^{\frac{1}{4}}, \quad s' = \sigma/\nu k^2, \quad \tan 2\phi = s'.$$

This solution differs only trivially from the first approximation (12) to the flow established by a wave travelling through an inextensible sheet: simple superpositions of one kind of solution give the other. In the viscous limit ($s'\to 0$) we have

$$\psi_1 \to (\sigma/k)\,(1+ky)\,e^{-ky}\sin(kx)\cos(\sigma t) \quad \text{for} \quad y \ll \nu k/\sigma.$$

This first-order motion may be thought of as a superposition of those sketched by Lamb (1932, p. 366) and Schlichting (1955, p. 68).

(*b*) *Second-order steady motion*

The boundary conditions for ψ_2 are found to be

$$\partial\psi_2/\partial x = 0, \quad \partial\psi_2/\partial y = c\sin(2kx)-c\cos(2\sigma t)\sin(2kx)+d\sin(2\sigma t)\sin(2kx) \quad \text{on} \quad y = 0,$$

with

$$d = -\tfrac{1}{4}\sigma k(1+\beta^2)\,[(1-\beta\cos\phi)/(1+\beta^2-2\beta\cos\phi)], \quad c = -\tfrac{1}{4}\sigma k\beta\sin\phi.$$

To satisfy them we must include a steady term in the second-order contribution to ψ,

$$\psi_2 = cy\,e^{-2ky}\sin(2kx).$$

The corresponding stream-function is in fact

$$\psi_s = \alpha^2\psi_2 = -\tfrac{1}{4}b^2\sigma k\,[\tfrac{1}{2}(\beta^2-1)]^{\frac{1}{2}}\,y\,e^{-2ky}\sin(2kx).$$

Even though the first-order solutions (12) and (4) are essentially equivalent, the steady secondary motions arising from them are very different. This flow is composed of cells in which there is steady flow towards the sheet at 'loops'

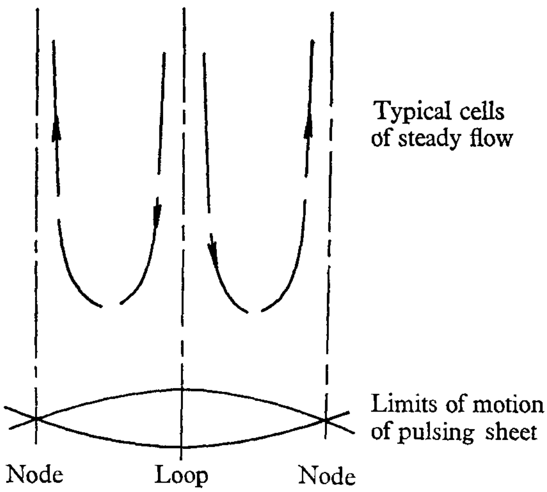

FIGURE 2. Second-order flow established by a pulsing surface.

of the primary motion and away from the sheet at its 'nodes'. The pattern is sketched in figure 2. It is quite possible that higher-order terms will reverse these relationships at large amplitudes and Reynolds numbers.

A. Case of small viscosity, $s' \to \infty$.

$$\psi_s \to -\tfrac{1}{4}b^2\sigma k\,(\sigma/2\nu k^2)^{\frac{1}{2}}\,y\,e^{-2ky}\sin(2kx).$$

B. Case of large viscosity, $s' \to 0$.

$$\psi_s \to -\tfrac{1}{4}b^2\sigma k\,(\sigma/2\nu k^2)\,y\,e^{-2ky}\sin(2kx)$$
$$\to 0 \quad \text{for all} \quad y > 0.$$

In this limit no steady second-order motion is found.

4. The extensible sheet

For simplicity we shall henceforth neglect the inertia of the fluid, the appropriate field equation then becoming the biharmonic equation (1). Again we consider waves travelling in a sheet, using the frame of reference in which the wave profile is at rest and given by

$$y = b\sin(kx).$$

But now we treat the more general case of a sheet whose surface strains as it waves, and to do so represent the velocity of the sheet along the stationary wave profile by

$$Q = Q_0[1+\delta\sin(nkx+\gamma)], \tag{15}$$

so that $u = Q\cos\phi$, $v = Q\sin\phi$ on the sheet, with $\tan\phi = bk\sin(kx) = dy/dx$.

The two cases $n = 1$ and $n = 2$ will be treated in detail. These are the modes most likely to be of significance in natural motions; also they will serve as exemplars of odd and even harmonics. For the moment we leave the phase angle γ arbitrary, later finding those values giving maximum propulsion for $n = 1$ and $n = 2$, and considering what value might be expected to arise naturally from the passage of a wave through the sheet.

To save the extra labour of expanding in the two parameters α and δ we take as basic a solution valid for all δ. The expansions (7) and (9) are generalized to

$$\begin{aligned}\psi &= \psi_0+\alpha\psi_1+\alpha^2\psi_2+\dots,\\ \partial\psi/\partial x &= f_0+\alpha f_1+\alpha^2 f_2+\dots,\\ \partial\psi/\partial y &= h_0+\alpha h_1+\alpha^2 h_2+\dots,\end{aligned}$$

and give rise to the boundary conditions:

$$\begin{aligned}&\partial\psi_0/\partial x = f_0, \qquad \partial\psi_0/\partial y = h_0,\\ &\frac{\partial\psi_1}{\partial x} = f_1-\frac{\partial^2\psi_0}{\partial x\,\partial y}g, \quad \frac{\partial\psi_1}{\partial y} = h_1-\frac{\partial^2\psi_0}{\partial y^2}g,\\ &\frac{\partial\psi_2}{\partial x} = f_2-\frac{\partial^2\psi_1}{\partial x\,\partial y}g-\frac{1}{2}\frac{\partial^3\psi_0}{\partial x\,\partial y^2}g^2,\end{aligned}$$

etc. As before we take $\alpha = bk$, $g = (1/k)\sin(kx)$.

(a) Basic solution

From the expansion (6*c*, *d*) we find

$$\partial\psi_0/\partial x = 0, \quad \partial\psi_0/\partial y = -Q_0[1+\delta\sin(nkx+\gamma)] \quad \text{on} \quad y = 0.$$

The appropriate solution of equation (1) is

$$\psi_0 = -Q_0 y[1+\delta e^{-nky}\sin(nkx+\gamma)],$$

degenerating to give a uniform stream as $\delta\to 0$.

The boundary conditions for ψ_1 are then

$$\begin{aligned}\partial\psi_1/\partial x &= Q_0\cos(kx)+Q_0\delta[\sin(nkx+\gamma)\cos(kx)+n\cos(nkx+\gamma)\sin(kx)], \qquad (16)\\ \partial\psi_1/\partial y &= -Q_0\delta n\sin(nkx+\gamma)\sin(kx),\end{aligned}$$

on $y = 0$.

(b) Propulsive velocity for $n = 1$

The solution of equation (1) satisfying the conditions (16) for $n = 1$ is

$$\psi_1 = (Q_0/k)(1+ky)e^{-ky}\sin(kx)-Q_0\delta y\cos\gamma-(Q_0\delta/2k)e^{-2ky}\cos(2kx+\gamma).$$

Note that there is a propulsive contribution of the first order in α.

The boundary conditions for ψ_2 give

$$\partial\psi_2/\partial x = \text{sinusoidal terms only,}$$

and
$$\partial\psi_2/\partial y = \tfrac{3}{4}Q_0 + \text{sinusoidal terms.}$$

To the second order in α the propulsive velocity for the case $n = 1$ is found to be, using the result (13),

$$V/U = \tfrac{1}{2}\alpha^2 - \alpha\delta\cos\gamma. \tag{17}$$

As $\delta \to 0$, this result becomes equivalent (at the second order) to Taylor's (4). The maximum propulsive effect would be achieved for the phase angle $\gamma = 180°$.

These results for $n = 1$ typify those for odd values of n: the contributions to the propulsive velocity are unchanged for even powers of α; but further terms arise containing odd powers of α coupled with powers of δ, the strain parameter.

(c) *Propulsive velocity for n = 2*

For $n = 2$ the solution of equation (1) satisfying the conditions (16) is

$$\begin{aligned}\psi_1 = {} & (Q_0/k)(1+ky)\,e^{-ky}\sin(kx) + (Q_0\delta/2k)(1+ky)\,e^{-ky}\cos(kx+\gamma)\\ & - (Q_0\delta/2k)(1+3ky)\,e^{-3ky}\cos(3kx+\gamma)\\ & - 2Q_0\delta[y\,e^{-ky}\cos(kx+\gamma) - y\,e^{-3ky}\cos(3kx+\gamma)].\end{aligned}$$

There is no propulsive velocity to the first order in α here.

The boundary conditions for ψ_2 give

$$\partial\psi_2/\partial x = \text{sinusoidal terms only,}$$
$$\partial\psi_2/\partial y = \tfrac{3}{4}Q_0 + \tfrac{3}{8}Q_0\delta\sin\gamma + \text{sinusoidal terms.}$$

Then the second-order propulsive velocity for $n = 2$ is given by

$$V/U = \tfrac{1}{2}\alpha^2(1 + \tfrac{3}{4}\delta\sin\gamma). \tag{18}$$

The maximum propulsive effect corresponds to $\gamma = 90°$; again we recover (4) as $\delta \to 0$.

For other even values of n we may expect similar results, modified contributions for even powers of α.

(d) *Probable effect of surface strain*

It has been seen that straining of the surface of a waving sheet can alter the propelling effect of the waves. Now we try to see what kind of straining is associated with the waving, assuming that the simplest pattern of strain consistent with the waving is established, and rejecting the possibility that there are complex internal mechanisms producing just those surface strains that lead to maximum propulsion. This is an attempt to study the 'involuntary' straining associated with wave propagation, rather than the 'planned' squirming capable of moving the organism most rapidly through the medium.

The strain pattern which first comes to mind on considering a waving sheet of finite thickness with fluid on both sides is shown in figure 3. This is the pattern set up in a uniform elastic beam to which is applied a moment distribution

$$M \propto \sin(kx).$$

However, as Taylor (1951) has shown, the moment distribution in a sheet waving in a viscous fluid is $M \propto \cos(kx)$, the maximum occurring near the section at which the curvature is zero. The crux of this mild paradox is that the applied loads and strains are not directly linked here as they are in an inanimate solid beam. For consistency with the present model we must assume that some internal mechanism adapts the sheet to its wave form, all the while independently resisting the forces so generated.

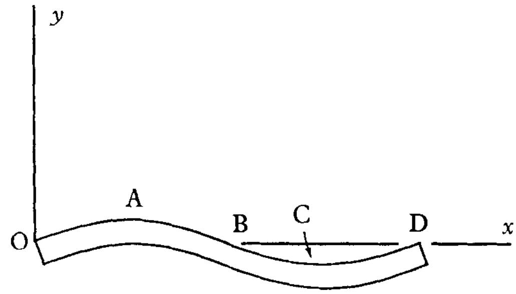

FIGURE 3. Straining of a uniform, elastic beam. O, Zero strain, maximum gradient of extension; A, maximum extension, zero strain gradient; B, zero strain, maximum gradient of compression; C, maximum compression, zero strain gradient.

In practice the elemental mechanisms operating in tiny organisms could hardly be expected to maintain this balance. Some interaction between wave form and viscous forces must be anticipated. Nevertheless, it seems likely that the mode isolated above will be an important one in the description of the straining of the surface of a waving tail.

In terms of the assumed surface velocity distribution (15) the local rate of straining is proportional to

$$dQ/dx \propto \cos(nkx+\gamma).$$

Clearly, to represent the pattern given above we must take $n = 1$. Also, for a maximum rate of straining $\cos\gamma = 1$, whence $\gamma = 0°$. Then for this mode of surface distortion the propulsive speed is given by equation (17) as

$$V/U = \tfrac{1}{2}\alpha^2 - \delta\alpha.$$

We conclude that surface straining, although it could give increased propulsion under certain circumstances, is more likely to reduce the speed of propulsion to a value below that associated with the waving of an inextensible surface.

5. Swimming near a solid wall

As in §2 we consider a sheet given by $y = b\sin(kx)$, moving along itself with velocity Q_0, a constant. But now we take the fluid to be bounded by a rigid wall at $y = h$ ($h > b$, necessarily)†. The boundary conditions to be applied at the wall are

$$u = \text{const.}, \quad v = 0 \quad \text{on} \quad y = h.$$

† We shall make no reference to the other side of the sheet at this stage. Consideration will be given later to superpositions of solutions describing a sheet surrounded by fluid.

The conditions to be applied in the mean plane of the waving sheet ($y = 0$) are once again those given by equations (6), (9) and (11). The analysis will be based entirely on the biharmonic equation (1).

The basic flow is taken, as in § 2, to be

$$u = Q_0 \quad \text{or} \quad \psi_0 = -Q_0 y,$$

the fluid at rest in contact with the wall and sheet, the whole viewed in a frame of reference translating with velocity $u = -Q_0$. It will be realized that the velocity of the frame of reference relative to the fixed wall will vary with the wave amplitude; in this formulation Q_0 is held fixed while the wave speed varies with amplitude.

(a) First-order solution

The boundary conditions are

$$\partial\psi_1/\partial x = Q_0 \cos(kx), \quad \partial\psi_1/\partial y = 0 \quad \text{on} \quad y = 0,$$
$$\partial\psi_1/\partial x = 0, \quad \partial\psi_1/\partial y = F, \text{ a constant} \quad \text{on} \quad y = h.$$

Seeking a solution of equation (1) in the form

$$\psi_1 = [(A + By)\cosh(ky) + (C + Dy)\sinh(ky)]\sin(kx) + Ey,$$

we find that it is necessary to set $E = F = 0$ to satisfy these conditions, so that the first-order propulsive velocity is zero, as might have been anticipated since $V(\alpha)$ is again an even function. The solution is

$$\psi_1 = (Q_0/k)[\cosh(ky) + c\{\sinh(ky) - ky\cosh(ky)\} + dky\sinh(ky)]\sin(kx), \quad (19)$$

with
$$c = -[\cosh(kh)\sinh(kh) + kh]/[\sinh^2(kh) - k^2h^2],$$
$$d = -\sinh^2(kh)/[\sinh^2(kh) - k^2h^2].$$

(b) Second-order propulsive velocity

The boundary conditions for ψ_2 are

$$\partial\psi_2/\partial x = 0,$$
$$\partial\psi_2/\partial y = -\tfrac{1}{4}Q_0(1 + 4d) - \tfrac{1}{4}Q_0(3 + 4d)\cos(2kx) \quad \text{on} \quad y = 0,$$
$$\partial\psi_2/\partial x = 0, \quad \partial\psi_2/\partial y = \text{const.} \quad \text{on} \quad y = h.$$

Once again, by including a uniform-flow term in the second-order solution we are able to match the boundary conditions. Using the result (13) we obtain an estimate of the propulsive speed:

$$\frac{V}{U} = -\alpha^2(d + \tfrac{1}{2}) = \frac{\alpha^2}{2}\left[\frac{\sinh^2(kh) + k^2h^2}{\sinh^2(kh) - k^2h^2}\right]. \quad (20)$$

Note that $V/U > \tfrac{1}{2}\alpha^2$, the value for an unbounded fluid, for all finite values of kh.

A. Limiting case of sheet far from wall, $kh \to \infty$.

$$V/U \to \tfrac{1}{2}\alpha^2. \quad \text{(cf. equation (4))}.$$

B. Limiting case of sheet close to wall, $kh \to \alpha = kb$.

$$\frac{V}{U} \to \left(\frac{V}{U}\right)_L = \tfrac{1}{2}\alpha^2\left[\frac{\sinh^2\alpha + \alpha^2}{\sinh^2\alpha - \alpha^2}\right].$$

In table 2 are given the values of this limiting ratio for a range of α in which the second-order estimate might be useful. It appears that the propulsive speed does not rise beyond three times the wave speed. This high limiting ratio can be justified by noting that a large relative speed is necessary to carry fluid through the narrow gaps between the wall and the crests of the wave profile.

We shall see presently that the apparent suggestion of greatly augmented propulsion near a wall is quite unrealistic.

$\alpha = kb$	0	0·1	0·2	0·3	0·4	0·5
$(V/U)_L$	3·00	3·00	3·00	3·01	3·01	3·02

TABLE 2. Propulsion near a wall

(c) *The problem of uniqueness*

None of the mathematical problems that have been studied here has been uniquely determined. But in the present case this difficulty is made more glaring by the ease with which alternative solutions satisfying the given restrictions can be constructed. Terms of the forms.

$$\psi \propto y^2,\ y^3$$

could have been included in the stream-function for the second-order problem. Their only contribution to the boundary conditions is to $\partial\psi/\partial y$ at $y = h$, where they add a constant velocity and thus alter the propulsive speed. A justification for rejecting such contributions is that away from the waving sheet the flow must tend ever closer to an undisturbed stream. This argument is convincing for large values of h/b but loses some of its force when $h/b \sim O(1)$.

An additional line of argument can be advanced against the form $\psi \propto y^2$. It represents a constant-shear flow exerting a second-order shear force on the sheet. Computing the pressure distribution corresponding to the first-order solution (19), we have

$$p = -2\alpha Q_0 k\mu[c\cosh(ky) - d\sinh(ky)]\cos(kx),$$

which can be seen to give Taylor's (1951) result as $h \to \infty$. Following the procedure he outlined, we compute (to the second-order) the mean pressure drag on the waving sheet,

$$F_1 = \overline{p(dy_0/dx)} = -b^2k^3Q_0\mu c, \quad \text{with} \quad y_0 = b\sin(kx),$$

and the mean second-order viscous drag,

$$F_2 = \mu\overline{(\partial u/\partial y)_0} = b^2k^3Q_0\mu c, \quad \text{with} \quad u = -\alpha(\partial\psi_1/\partial y).$$

(Here the overbars denote averaging over a wavelength.) Since $F_1 + F_2 = 0$, we have self-propulsion without introducing a further second-order force on the sheet.

The addition of a contribution $\psi \propto y^3$ implies that a pressure gradient acts in the fluid between the sheet and the wall; a second-order shear stress acts on the wall, but not on the sheet. For a sheet symmetrically placed in a channel we rule out such contributions on the grounds that they would give rise to a net force on the channel.

(d) Swimming in the centre of a channel

These results may be interpreted as describing the motion of an organism along the centre line of a two-dimensional channel containing fluid at rest save for the disturbance of the swimming. They indicate that the propagation of waves along an organism in a channel will propel it more rapidly than would the same waves in an unbounded fluid.

A somewhat more realistic view of the efficiency of propulsion through a channel may be obtained by requiring that the energy output of the waving sheet be constant no matter what the width of the channel. We shall consider the case in which the wave amplitude adjusts itself to the channel width so as to maintain constant dissipation, the other parameters (Q_0, k, μ)† being fixed.

The mean energy output from the sheet is

$$W = \alpha Q_0 \, \mu\overline{(\partial^2\psi_1/\partial y^2)_0} = -\alpha^2 Q_0^2 k\mu c,$$

to the second order. Then using equation (20) we have

$$V/U = W(d+\tfrac{1}{2})/Q_0^2 k\mu c,$$

giving the propulsive speed as an explicit function of $c(kh)$ and $d(kh)$, if W, Q_0, k, and μ are fixed. More conveniently,

$$\frac{V}{V_0} = \frac{2}{c}(d+\tfrac{1}{2}) = \frac{\sinh^2(kh)+k^2h^2}{\cosh(kh)\sinh(kh)+kh},$$

and
$$\frac{\alpha}{\alpha_0} = (-c)^{-\frac{1}{2}} = \left[\frac{\sinh^2(kh)-k^2h^2}{\cosh(kh)\sinh(kh)+kh}\right]^{\frac{1}{2}},$$

whence
$$\frac{b}{h} = \frac{\alpha_0}{kh}\left[\frac{\sinh^2(kh)-k^2h^2}{\cosh(kh)\sinh(kh)+kh}\right]^{\frac{1}{2}},$$

where V_0 and α_0 are the propulsive speed and wave amplitude in an unbounded fluid. Note that $\alpha/\alpha_0 < 1$ for all finite kh. For small kh,

$$b/h \simeq \alpha_0(\tfrac{1}{6}kh)^{\frac{1}{2}}, \quad V/V_0 \simeq kh,$$

showing that the wave crests do not approach the wall in this limit and, further, that propulsion is ultimately impossible.

In table 3 these characteristics of the propulsive motion are shown as functions of kh and h/λ $(\lambda = 2\pi/k)$. We see that the ratio of amplitude to channel width attains a maximum between $kh = 1$ and $kh = 2$. Only a small increase in propulsive speed occurs as the channel width is reduced; in very small channels propulsion is less efficient than in an unbounded fluid. The wave amplitude drops off more quickly than the propulsive speed.

The present analysis has not taken account of the possibility that an organism might be stimulated to a greater or reduced effort when the amplitude of its tail waving is restricted by the presence of a wall. Further, an organism swimming

† These restrictions are made for heuristic purposes only. There is no precise observational justification for holding constant the wavelength and (very nearly) the wave celerity, as we do here.

near a plane wall, or in a narrow cell, is still able in actuality to move its tail with relative freedom in a plane parallel to the wall. Nevertheless, the analysis does suggest that large increases in propulsive speed will not be possible unless the energy output is increased significantly. On the other hand, the necessity of swimming near a wall seems unlikely to reduce the velocity of an organism's progress, even though the vigour of the propelling motion may appear to be reduced if judged directly by observations of amplitude.

kh	h/λ	α/α_0	$b/\alpha_0 h$	V/V_0
0	0	0	0	0
1	0·159	0·368	0·368	0·846
2	0·318	0·765	0·383	1·096
3	0·478	0·939	0·312	1·053
4	0·638	0·986	0·246	1·017
5	0·796	0·998	0·200	1·002
∞	∞	1·000	0	1·000

TABLE 3. Propulsion in a channel

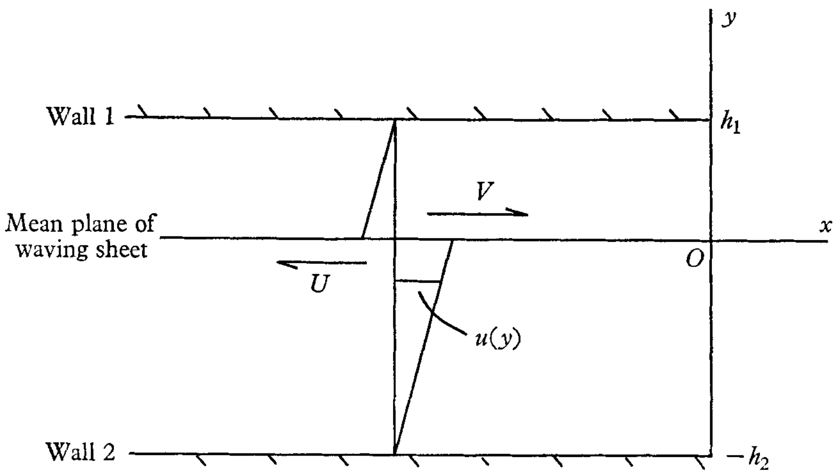

FIGURE 4. Waving sheet asymmetrically located in a channel. The variation of the steady second-order component of the velocity, $u(y)$, is shown. U and V are the wave velocity and sheet propagation speed, respectively.

(e) *Swimming not along channel centre line*

We consider now a waving sheet which is asymmetrically located in a two-dimensional channel, as illustrated in figure 4.

The first-order solution can be written down immediately from the result (19): For the region above the sheet

$$\psi_1 = (Q_0/k)\,[\cosh(ky) + c_1\{\sinh(ky) - ky\cosh(ky)\} + d_1 ky\sinh(ky)]\sin(kx),$$

where $c_1 = c$ with $h = h_1$, $d_1 = d$ with $h = h_1$.

For the region below the sheet

$$\psi_1 = (Q_0/k)[\cosh(ky) - c_2\{\sinh(ky) - ky\cosh(ky)\} + d_2 ky\sinh(ky)]\sin(kx),$$

where $c_2 = c$ with $h = h_2$, $d_2 = d$ with $h = h_2$.

In attempting to determine the second-order motion we encounter a difficulty —the velocity differences between the sheet and the two walls predicted by the second-order solution (20) are not the same. To remove this inequality we add terms $\psi \propto y^2$ to the second-order stream functions for the regions above and below the sheet. It has been shown that the net second-order drag on the sheet for motions given by equation (19) is zero. The added terms $\psi \propto y^2$ will give rise to additional second-order drag forces. If the sheet is to be self-propelling these must be equal and opposite. Then the added terms must represent a simple shear flow with a velocity gradient which is constant across the channel, that gradient being chosen to make the two relative wall velocities equal.

Repeating this argument in symbolic form, we take

$$\psi_2 = a_1 y + b_1 y^2 + \text{sinusoidal terms} \quad \text{(above the sheet)},$$
$$\psi_2 = a_2 y + b_2 y^2 + \text{sinusoidal terms} \quad \text{(below the sheet)}.$$

To satisfy the boundary conditions on the sheet we must have

$$a_1 = -\tfrac{1}{4}Q_0(1+4d_1), \quad a_2 = -\tfrac{1}{4}Q_0(1+4d_2). \tag{21a}$$

Now

$$\partial\psi_2/\partial y = a_1 + 2b_1 y + \text{sinusoidal terms} \quad \text{(above)},$$
$$\partial\psi_2/\partial y = a_2 + 2b_2 y + \text{sinusoidal terms} \quad \text{(below)}.$$

Requiring the constant terms at the boundaries to be equal, we have

$$\Delta u = a_1 + 2b_1 h_1 = a_2 - 2b_2 h_2. \tag{21b}$$

Further

$$\partial^2\psi_2/\partial y^2 = 2b_1 + \text{sinusoidal terms} \quad \text{(above)},$$
$$\partial^2\psi_2/\partial y^2 = 2b_2 + \text{sinusoidal terms} \quad \text{(below)}.$$

If the second-order shear is to be continuous across the sheet we must take

$$b_1 = b_2. \tag{21c}$$

The equations (21) are sufficient to determine the steady component of the second-order motion. Solving, and using the result (13), we have for the propulsive velocity

$$V/U = \tfrac{1}{2}\alpha^2[-(1+d_1+d_2) + (d_1-d_2)(h_1-h_2)/(h_1+h_2)],$$

and for the basic velocity gradient

$$\partial u/\partial y = -2b_1\alpha^2 = -\alpha^2 Q_0(d_1-d_2)/(h_1+h_2).$$

For the case in which $h_1 < h_2$, as shown in figure 4,

$$d_1 - d_2 < 0 \quad \text{and} \quad \partial u/\partial y > 0.$$

The steady component of the second-order flow is sketched in figure 4. According to the description we have evolved, there is a jump across the sheet of $\alpha^2 Q_0(d_1-d_2)$ in the second-order mean velocity, and a net mass flux in the direction of propulsion. This flux could be removed by introducing terms of the form $\psi \propto y^3$ into the stream function. However, it is not obvious that this 'refinement' would give more insight into the three-dimensional motions (those about flagella of finite length) that are of ultimate interest.

The shear stresses in the fluid tend to drag the far wall after the sheet (that is, in the direction of propulsion) and to push the near wall backwards in the direction of wave propagation. The net drag on the channel is, of course, still zero. If a basically similar system of shears were set up around an organism swimming near a solid surface, it would be subjected to the shear stresses indicated in figure 5. This system would tend to rotate the organism's head away from the wall and thus to direct its swimming away from the surface.

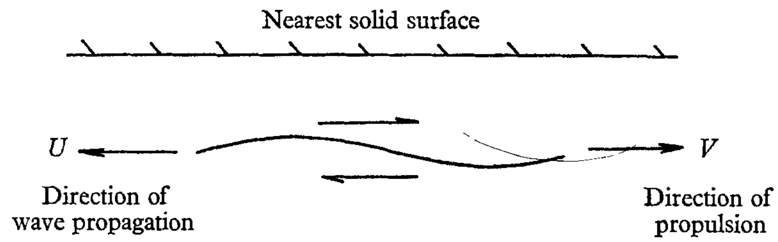

FIGURE 5. Organism of finite length swimming near a wall. The arrows on either side of the sheet indicate the directions of the postulated mean shear stresses.

It seems likely that this mechanism would lower the concentration of swimming organisms near the walls of a container below that in the body of the fluid. This conclusion is not in accord with the opinions of observers of the swimming of spermatozoa, although no systematic observations have been made to decide the question, so far as is known.

Perhaps some further justification is necessary for adding terms $\psi \propto y^2$ in this case, while rejecting them in the previous analysis. So far as the fluid on one side is concerned, the sheet is no longer self-propelled in this asymmetric case. By virtue of its off-centre position it exerts a net force on the fluid on each side; this force must be transmitted to the channel wall. Then the requirement that the flow approach a uniform stream far from the sheet is here quite unrealistic and must be replaced by the requirement of a uniform shear flow far from the sheet. All the relevant earlier results are recovered as special cases of the results obtained on this basis.

6. Summary of results

Here are gathered together the several expressions for the propulsive speed of a waving sheet.

The wave profile is $y = b\sin k(x+Ut) = b\sin(kx+\sigma t)$.

Effect of fluid inertia.

$$\frac{V}{U} = \tfrac{1}{4}\alpha^2\left[\frac{\beta-\cos\phi}{\cos\phi-1/\beta}-1\right],$$

with $\alpha = bk$, $s = U/\nu k$, $\beta = (1+s^2)^{\frac{1}{2}}$, $\cos\phi = [(1+\beta^2)/2\beta^2]^{\frac{1}{2}}$.

Effect of straining of waving sheet.

For surface velocity,

$$Q = Q_0[1+\delta\sin(nkx+\gamma)].$$

For $n = 1$, $\qquad V/U = \tfrac{1}{2}\alpha^2-\alpha\delta\cos\gamma.$

For $n = 2$, $\qquad V/U = \tfrac{1}{2}\alpha^2(1+\tfrac{3}{4}\delta\sin\gamma).$

Effect of nearby walls.

Waving sheet in centre of channel of width $2h$,

$$\frac{V}{U} = \tfrac{1}{2}\alpha^2 \left[\frac{\sinh^2(kh) + k^2h^2}{\sinh^2(kh) - k^2h^2}\right].$$

Waving sheet in a channel, distance h_1 from one wall and h_2 from other,

$$V/U = \tfrac{1}{2}\alpha^2[-(1+d_1+d_2) + (h_1-h_2)(d_1-d_2)/(h_1+h_2)],$$

with

$$d = -\sinh^2(kh)/[\sinh^2(kh) - k^2h^2].$$

I should like to thank Lord Rothschild for introducing me to this subject and to acknowledge profitable discussions with both him and Sir Geoffrey Taylor.

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