

THE GLIDING MOTION OF A BACTERIUM: *Flexibacter* STRAIN BH3

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Abstract

The flexibacters are a form of gliding bacteria which are often found on the surfaces of solid bodies in fresh and salt water. An individual organism lacks motility in the bulk aqueous phase but glides over a solid surface with its rod-like body aligned with and nearly touching the surface. It has been suggested that this gliding motion in *Flexibacter* strain BH3 may be caused by waves moving down the outer surface of the rod-shaped cell [2]. This paper is concerned with the fluid mechanical aspects of this form of propulsion.

Formulae for the velocity of the organism and for the power dissipation are obtained by using a lubrication theory analysis in the small gap between the bacterium and the wall. It is found that for any progressive waveform there is an optimum distance from the wall at which the flexibacter may maximize its speed for a given power output. Assuming that the flexibacter sits at this optimum distance and taking the waveform to be sinusoidal we calculate the power required for the flexibacter to move at the maximum observed speed. It is found that this power requirement represents only a small fraction of the power available to the cell.

1. Introduction

Although a considerable amount of research has been undertaken on the mode of motility in gliding bacteria, little is known about the mechanism of propulsion and the need for the organism to be near a surface for motility to occur. This paper examines one method of propulsion proposed for the gliding bacterium, *Flexibacter* strain BH3 [2].

The organism has a rod-like body of approximately circular cross-section with an average length of $5\mu\text{m}$ and a diameter of the order of $0.5\mu\text{m}$. The body appears from a distance to be quite rigid, and there are no flagellar or cilia on the surface, so the usual forms of low-Reynolds' number propulsion are absent.

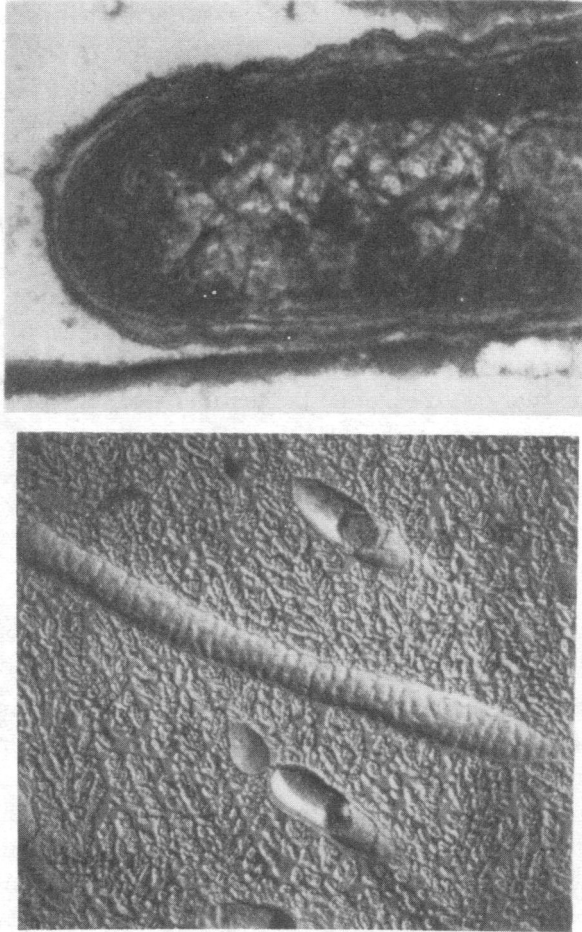


Fig. 1 Electron micrographs of the *Flexibacter* strain *BH3* showing wave-like undulations on the surface of the organisms. Fig. 1(a) is a cross-sectional view of the flexibacter near a solid boundary, and Fig. 1(b) is a top-view. The organism is of the order of $5\mu\text{m}$ long with a cross-sectional diameter of $0.5\mu\text{m}$.

The flexibacter is unable to propel itself through the water unless it is near a solid boundary where it moves in the direction of its axis at speeds of up to $1.5\mu\text{m}/\text{sec}$. As it glides over the surface, the flexibacter leaves a trail of sticky liquid, or “slime” in its wake. In Fig. 1(a) we show a cross-sectional view of a flexibacter, sectioned along its length[†]. From this electron micrograph it can be

[†] Fig. 1(a) is reproduced from [2] and Fig. 1(b) was kindly supplied by Dr. M. R. Dickson of the Biomedical Electron Microscope Unit, University of N.S.W.

seen that the flexibacter has an undulating surface (that is, the outer cell envelope membrane) which is separated from the wall by a thin layer of liquid. The wave-like undulations of the surface can also be seen in top-view in Fig. 1(b). The undulations are fairly irregular, having an average amplitude of about $0.03\ \mu\text{m}$ and a wavelength of $0.07\ \mu\text{m}$. The thin layer of slime between flexibacter and wall has a minimum thickness of the order of $0.01\ \mu\text{m}$.

It is observations such as these which have given rise to the theory that the flexibacter moves by sending waves down its body [2]. Unfortunately there is no means of testing this observation experimentally, for the undulations can only be seen under an electron microscope, and the organisms must be killed in order to be studied in this apparatus.

The aim of this study is to examine the feasibility of this form of propulsion from a fluid mechanical point of view.

2. The velocity and pressure fields in the thin liquid layer between the flexibacter and the wall

When two nearly-touching bodies in a liquid are in relative motion, the stresses developed in the thin liquid layer between the bodies may make a significant contribution to the force on each body. For this reason we begin our analysis by looking at the flow in the thin lubrication layer between the flexibacter and the wall. In Section 3 it will be shown that to leading order the force-balance equation for the flexibacter is dominated by the contribution from the stresses on the surface of the body in the neighbourhood of the wall. Hence we can determine the velocity of the organism and the power dissipation without the need for calculating the flow field beyond the lubrication layer.

Assuming that the flexibacter is gliding over a flat surface, we set up cartesian coordinates (x, y, z) with the x -axis lying on the surface parallel to, and directly beneath the axis of the flexibacter, and with the y -axis perpendicular to the surface, which will be referred to as "the wall". This coordinate system is illustrated in Fig. 2. As in previous studies of wave-like motions of micro-organisms [5]–[7], we let our axes move along the body with the waves, which are assumed to be regular and periodic. In this frame of reference the local surface profile and flow field does not vary with time.

We let U_w denote the speed of the wave relative to the body and U_b denote the speed of the body relative to the wall; the wave is assumed to be moving to the left in Fig. 2, relative to the body, and the speed of the body is taken to be positive if the body moves to the right, relative to the wall. In the frame of reference moving with the wave the wave is stationary, and the wall appears to be moving in the direction of increasing x with speed $U_w - U_b$.

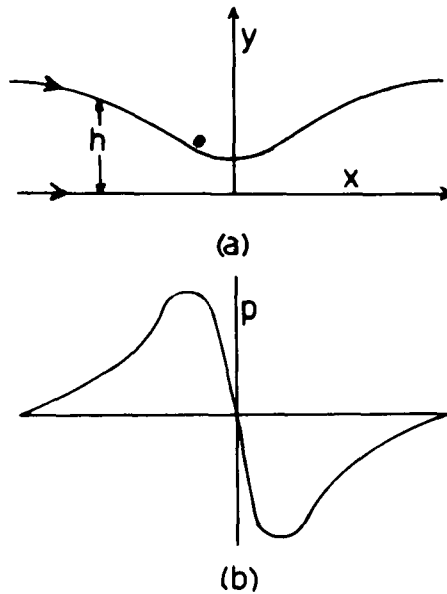


Fig. 2(a) A sketch of the thin liquid layer between the surface of the flexibacter and the wall. The (x, y) -coordinate axes are taken to be moving with the waves which travel down the surface of the organism. The arrows on the upper and lower surfaces indicate the direction of motion of the flexibacter and the wall relative to this moving coordinate system.

2(b) A sketch of the pressure variation p in the liquid layer, for the waveform shown in Fig. 2(a) (see Section 3).

As the waves pass down the flexibacter they cause the surface of the cell to deform; in order to specify the velocity of the surface we must make an additional assumption about the way in which the surface deforms. Following Taylor [7], we assume that the surface is inextensible; in the frame of reference moving with the waves the material on the cell surface therefore moves tangential to the surface of the wave, with uniform speed given by [7], equation (20), to be

$$\frac{U_w}{\lambda} \times (\text{the arclength of a wave}), \quad (2.1)$$

where λ is the wavelength.

In the absence of any information to the contrary, we assume that the layer of slime between the flexibacter and the wall behaves as a Newtonian liquid. Since the inertial forces in the liquid are negligible in this case, the velocity \mathbf{u} and pressure p satisfy the Stokes' equations

$$\mu \nabla^2 \mathbf{u} = \nabla p, \quad (2.2)$$

and

$$\nabla \cdot \mathbf{u} = 0, \quad (2.3)$$

where μ is the viscosity of the liquid.

To determine the flow field in the lubrication layer we must solve these equations subject to the boundary condition that the fluid on the flexibacter surface moves with speed given by (2.1) and the fluid at the wall moves with speed $U_w - U_b$ in the direction of increasing x .

The pressure and velocity in the lubrication layer vary in the z - and x -directions on length scales of the order of the cross-section radius of the organism ($\approx 0.25\mu\text{m}$) and the wavelength ($\approx 0.07\mu\text{m}$) respectively. Since we are attempting only a very approximate analysis here, we shall assume that the gradients in the x -direction are much larger than those in the z -direction and that as a result the flow in the lubrication layer is approximately two-dimensional; that is, the local velocity and pressure depend only on x and y , and the fluid flow is parallel to the (x, y) -plane.

We are therefore faced with the problem of determining the two-dimensional flow between a wavy sheet and a wall. Two approximate solutions to this problem have appeared in the literature, both concerned with sinusoidal waves. The earlier analysis, by Reynolds [6], is not relevant here, since it is valid only if the wave amplitude is small compared with the minimum film thickness, in which case there is only a weak interaction between the wall and the sheet. The second approximate solution, obtained by Katz [5] using lubrication theory, is valid if the slope of the wave relative to the wall is small.

Although this assumption is not strictly valid for the flexibacter (see Fig. 1(a)) we shall employ lubrication theory here in the hope of obtaining rough estimates of the speed of the organism and power dissipation for a wave of arbitrary shape.

The lubrication theory approach to this problem is based on the observation that, if the slope of the wavy surface is everywhere small, the flow in the thin liquid layer is locally the same as the flow between two parallel flat plates separated by the local film thickness ([1], page 219). In this case the equation (2.2) reduces to ([5], page 40)

$$\mu \frac{\partial^2 u}{\partial y^2} = \frac{\partial p}{\partial x}$$

and

$$\frac{\partial p}{\partial y} = 0,$$

where u is the component of the liquid velocity in the x -direction. The arclength of a wave of small slope is, to leading order, equal to the wavelength, and thus

the boundary condition (2.1) reduces to

$$u = U_w$$

on the upper plate (which represents the flexibacter surface) and, on the wall ($y = 0$), to

$$u = U_w - U_b.$$

The solution to the above equations and boundary conditions is

$$u = U_w + U_b \left(\frac{y}{h} - 1 \right) + \frac{1}{2\mu} \frac{dp}{dx} (y - h)y, \quad (2.4)$$

where $h(x, z)$ is the local film thickness. The pressure gradient dp/dx is determined from the incompressibility constraint (2.3), which in this case can be written in the form

$$\int_0^h u \, dy = Q, \quad (2.5)$$

where Q is a constant representing the rate of fluid flow in the gap (relative to axes moving with the wave) per unit width in the z -direction.

Substituting the expression (2.4) for u in (2.5) and integrating, we find that the pressure gradient is given by

$$\frac{dp}{dx} = \frac{6\mu(2U_w - U_b)}{h^2} - \frac{12\mu Q}{h^3}, \quad (2.6)$$

and hence the pressure drop over one wavelength is

$$\Delta p = 6\mu(2U_w - U_b) \int_0^\lambda \frac{dx}{h^2} - 12\mu Q \int_0^\lambda \frac{dx}{h^3}. \quad (2.7)$$

With the aid of this expression we now determine the flow rate Q .

The total pressure drop over the body is $\Delta p L / \lambda$, where L is the length of the organism; in principle, Δp must be determined by matching this inner solution to the outer solution for the flow fluid beyond the lubrication layer. This outer flow field may be regarded as the superposition of two flows:

- (i) a local flow which decays to zero at distances of order λ from the surface, caused by the wavelike motion of the surface, and
- (ii) a "long range" flow field due to the motion of the body as a whole.

The pressure field associated with the flow field (i) will, like the flow itself, be a periodic function of distance along the surface of the body, and consequently the net pressure drop along the body due to this flow is zero.

At distances of more than a few cross-sectional radii R from the ends of the body the flow field (ii) will be similar in form to the flow generated by an infinite cylinder, of cross-sectional radius R , moving along its axis, parallel to

and nearly touching the wall. This two-dimensional flow does not result in any pressure gradients, and thus the only place where significant pressure drops can occur is in the neighbourhood of the front and rear of the organism.

To estimate these pressure drops we note that, since the flow field in these regions varies on a length scale of order R , the pressure gradients required to balance the viscous force term $\mu \nabla^2 \mathbf{u}$ in the Stokes' equation (2.2) will be of order $\mu U_b / R^2$. The regions of non-uniform pressure extend a distance of $O(R)$ from the ends of the body and thus, with the aid of the above estimate for the pressure gradient in these regions, we find that the magnitude of the pressure drop over the length of the organism is $\mu U_b / R$; hence the pressure drop per wave Δp is of order $\mu U_b \lambda / RL$.

Assuming that the body speed U_b and wave speed U_w are of the same order of magnitude, we find that the first term on the right hand side of (2.7) is of order $\mu U_b \lambda / h^2$, where h is a measure of the film thickness; the ratio of this term to Δp is therefore $O(RL/h^2)$. Thus we may neglect the pressure drop term in (2.7), which yields

$$Q = \left(U_w - \frac{1}{2} U_b \right) \left\{ \int_0^\lambda \frac{dx}{h^2} / \int_0^\lambda \frac{dx}{h^3} \right\}. \quad (2.8)$$

With the aid of this result we can write the formulae (2.4) and (2.6) for the velocity and pressure gradient in the lubrication layer in terms of U_b , U_w and h .

3. Calculating the speed of the flexibacter

The speed of the flexibacter is determined from the requirement that the net horizontal force on the body is zero. From our lubrication layer analysis we can calculate the contribution to the force-balance equation from the stresses on the surface of the organism close to the wall:

The horizontal component of the stress on the flexibacter surface in this region is given by

$$-\mu \frac{\partial u}{\partial y} \Big|_{y=h} - p \frac{\partial h}{\partial x}. \quad (3.1)$$

Although the wave slope $\partial h / \partial x$ is assumed to be small, the pressure in the lubrication layer may be quite large, and consequently we cannot neglect the product $p(\partial h / \partial x)$ in (3.1).

The net force per wavelength acting on the surface of the flexibacter close to the wall is given by

$$-\int_z \left[\int_0^\lambda \left(\mu \frac{\partial u}{\partial y} \Big|_{y=h} + p \frac{\partial h}{\partial x} \right) dx \right] dz \quad (3.2)$$

where the integral extends in the z -direction over the portion of the surface in the vicinity of the wall. Integrating the term involving $p(\partial h/\partial x)$ in (3.2) by parts, and substituting the expressions (2.4), (2.6) and (2.8) for u , dp/dx and Q , we find that the square-bracketed term in (3.2) becomes

$$6\mu U_w \left[I_1(z) - \frac{I_2^2(z)}{I_3(z)} \right] - \mu U_b \left[4I_1(z) - \frac{3I_2^2(z)}{I_3(z)} \right], \quad (3.3)$$

where

$$I_n(z) = \int_0^\lambda \frac{dx}{h^n}. \quad (3.4)$$

We shall assume that the flexibacter surface is locally parabolic in the z -direction; that is,

$$h(x, z) = h_0(x) + \frac{z^2}{2R}, \quad (3.5)$$

in the neighbourhood of the wall. In this case, the expression (3.3) decays like z^{-2} at large z and hence, if the thickness of the lubrication layer is much smaller than the cross-sectional radius R , the integral expression (3.2) for the force will be dominated by the contribution from the portion of the surface in the neighbourhood of $z = 0$. Assuming that this is the case we extend the limits of integration in (3.2) to $z = \pm \infty$. Substitution of the formula (3.3) for the square bracketed term in the integral (3.2) then yields

$$\mu(6U_w[K_1 - K_2] - U_b[4K_1 - 3K_2]), \quad (3.6)$$

where

$$K_1 = \int_{-\infty}^{\infty} I_1(z) dz \quad \text{and} \quad K_2 = \int_{-\infty}^{\infty} \frac{I_2^2(z)}{I_3(z)} dz. \quad (3.7)$$

The formula (3.6) gives the force per wavelength acting on the flexibacter surface in the neighbourhood of the wall. By the usual order of magnitude arguments it can be shown that the force per wavelength due to stresses over the remainder of the flexibacter surface is of order $\mu\lambda U_b$. From calculations of the asymptotic forms of $I_n(z)$ for small and large z we find K_1 and K_2 are of order $\lambda(R/h)^{1/2}$, where h is a typical film thickness. Thus the terms in the formula (3.6) for the force from the lubrication layer are of order $\mu\lambda U_w(R/h)^{1/2}$ and $\mu\lambda U_b(R/h)^{1/2}$, and therefore the contribution to the force balance from the stresses on the surface of the flexibacter beyond the lubrication layer is negligible provided $(R/h)^{1/2} \gg 1$. We shall assume here that this constraint is satisfied. In this case, the expression (3.6) gives the total force per unit wavelength acting

on the flexibacter. In order for this quantity to be zero the body must move with speed U_b given by

$$U_b = \frac{6(K_1 - K_2)U_w}{(4K_1 - 3K_2)}. \quad (3.8)$$

It can be shown that the coefficient of U_w in this expression is positive for an arbitrary waveform; hence the body moves in the opposite direction to the waves with a speed which, for a given U_w , does not depend on the viscosity of the slime or the length of the body.

In order to understand this mechanism of propulsion, it is useful to consider the contribution to the force on the organism from the shear stresses and pressure stresses separately. Since U_b and U_w are both positive the flexibacter surface in Fig. 2 moves to the right at a greater rate than the wall. Hence the shear stresses give rise to a retarding force in the negative x -direction.

The driving force for the motion arises from the pressure stresses. In Fig. 2(b) we sketch the distribution of pressure over a wavelength of the flexibacter surface. The pressure is found to be positive on the upstream side of the wave and negative on the downstream side. The horizontal component of these stresses give rise to a driving force in the direction of increasing x . Both the driving force and the retarding force are proportional to the viscosity of the slime, and thus the expression for the body speed U_b , obtained by equating these two forces is independent of slime viscosity.

For the symmetrical waveform shown in Fig. 2, the vertical components of the pressure on the upstream and downstream portions cancel and there is no vertical force. For other waveforms this may not be the case, and thus in general the hydrodynamic stresses will give rise to a vertical force. In addition to this hydrodynamic force there will be electrical repulsive and van der Waal's attractive forces acting on the surface of the body; by slightly adjusting its distance from the wall and its orientation relative to the wall the flexibacter should be able to balance any vertical hydrodynamic force or torque against these other forces. Hence there is no reason to expect that the net vertical force or torque due to hydrodynamic stresses will be zero.

4. The asymptotic forms of U_b/U_w

When the body is extremely close to the wall the integrals K_1 and K_2 are dominated by the contribution from small portions of the surface surrounding the points of minimum separation between the body and wall. Assuming that

the thickness of the lubrication film in the (x, y) -plane, h_0 , has the parabolic form

$$h_0(x) = h_m + \frac{x^2}{b}, \tag{4.1}$$

in the neighbourhood of the points of minimum separation, we find, by the usual asymptotic methods, that

$$K_1 = 2\pi\sqrt{(Rb)}\ln\left(\frac{R}{h_m}\right) + O(1),$$

and

$$K_2 = \frac{4\pi}{3}\sqrt{(Rb)}\ln\left(\frac{R}{h_m}\right) + O(1),$$

as the minimum separation $h_m \rightarrow 0$. With the aid of these asymptotic forms we find that the expression (3.8) for the flexibacter velocity reduces to

$$U_b = \left(1 + O\left(1/\ln\left(\frac{R}{h_m}\right)\right)\right)U_w \text{ as } \frac{h_m}{R} \rightarrow 0. \tag{4.2}$$

Thus when the body is extremely close to the wall it moves in such a way that the wave appears to be stationary relative to the wall.

At distances from the wall which are large compared to the wave amplitude, we find

$$K_1 = \frac{\pi\lambda\sqrt{(2R)}}{\sqrt{\bar{h}}}\left\{1 + O\left((\bar{a}/\bar{h})^2\right)\right\}, \tag{4.3}$$

and

$$K_2 = \frac{\pi\lambda\sqrt{(2R)}}{\sqrt{\bar{h}}}\left\{1 - 3(\bar{a}/\bar{h}) + O\left((\bar{a}/\bar{h})^2\right)\right\}, \tag{4.4}$$

where \bar{h} is the mean thickness of the lubrication layer in the (x, y) -plane and \bar{a} is the mean wave amplitude. From the expression (3.8) for the speed of the flexibacter we find that

$$U_b = 18(\bar{a}/\bar{h})U_w(1 + O(\bar{a}/\bar{h})) \text{ as } (\bar{a}/\bar{h}) \rightarrow 0. \tag{4.5}$$

In Fig. 3 we show the form of U_b/U_w for the sinusoidal waveform

$$h_0(x) = h_m + a\left(1 - \cos \frac{2\pi x}{\lambda}\right). \tag{4.6}$$

In this case it is possible to obtain analytic expressions for K_1 , I_2 and I_3 . The integral (3.7) for K_2 was evaluated numerically for a number of h_m/a values. This curve is similar in form to the curve obtained by Katz ([5], equation 54) for the velocity of a wavy sheet midway between two parallel walls; in both cases

U_b/U_w decays monotonically with increasing separation from the wall, having a maximum value of unity when the wave touches the wall.

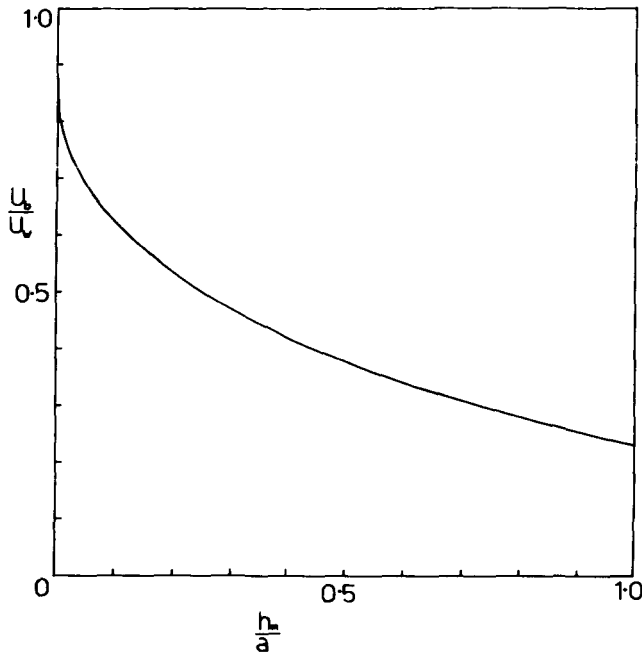


Fig. 3 The variation of (body speed/wave speed) for the sinusoidal waveform given by Equation (4.6). Here a denotes the amplitude of the wave and h_w the minimum separation between the organism and the wall.

5. The power required for this form of motion

The rate at which the organism does work on the surrounding fluid is given by

$$-\int_A \mathbf{u} \cdot \mathbf{f} \, dA, \quad (5.1)$$

where A denotes the surface of the flexibacter and \mathbf{f} is the stress exerted by the fluid on the surface. For the evaluation of this integral it is convenient to use a frame of reference which moves with the body. In this frame of reference the motion of small amplitude waves down the body causes the surface of the organism to move up and down in a direction perpendicular to the x -axis. Thus the horizontal component of \mathbf{f} does not enter into the calculation of the expression (5.1).

In the neighbourhood of the wall the surface of the organism moves in the vertical direction with speed $U_w(\partial h/\partial x)$. The vertical component of the stress is

simply equal to p , and thus the contribution to the power dissipation expression (5.1) from the portion of the flexibacter surface close to the wall is given by

$$-U_w \int p \frac{\partial h}{\partial x} dA. \tag{5.2}$$

The power transmitted to the liquid through the remainder of the surface as a result of the wave motion will be proportional to the wave slope squared[†], a quantity which in this analysis is assumed to be negligible.

Thus the power required for this form of propulsion is approximately given by the expression (5.2). Combining this expression with the formulae (2.6) and (2.8) for the pressure gradient and flow rate in the lubrication layer, we find that the power required by the organism per wavelength is

$$P = 6\mu U_w (2U_w - U_b)(K_1 - K_2), \tag{5.3}$$

or, using the expression (3.8) for U_b ,

$$P = 2\mu \left(\frac{U_w}{U_b} \right) K_1 U_b^2. \tag{5.4}$$

With the aid of the asymptotic forms for K_1 and U_b/U_w given in the previous section we find that

$$P \sim 4\pi\mu \sqrt{(Rb)} \ln \left(\frac{R}{h_m} \right) U_b^2 \tag{5.5}$$

as the minimum distance between the body and the wall $h_m \rightarrow 0$, and

$$P \sim \frac{\pi\mu\lambda \sqrt{(2Rh_m)} U_b^2}{9\bar{a}} \text{ as } \frac{h_m}{\bar{a}} \rightarrow \infty, \tag{5.6}$$

where, as before, \bar{a} is the mean wave amplitude. For fixed U_b , the power diverges as the body approaches the wall and as it moves away from the wall. This is quite different to the result obtained by Katz [5] for the two-dimensional wavy sheet; in this case it was found that the power ([5], equation (5.3)) decreases monotonically with increasing distance from the wall.

For the three-dimensional case considered here, the power diverges for small and large distances and thus there will be an optimum distance from the wall at which power dissipation is minimized for a given body speed. The location of this minimum will depend on the form of the wave. In Fig. 4 we have plotted the non-dimensional power $P/(\mu\lambda \sqrt{(R/a)} U_b^2)$ as a function of distance from the wall for the sinusoidal waveform (4.6). In this case the power curve is relatively flat in the neighbourhood of the minimum, with the power varying by less than 5 percent as h_m/a ranges from .05 to 0.3.

[†] This follows from Taylor's [7] equation (14) for power dissipation by a wavy sheet with small amplitude waves.

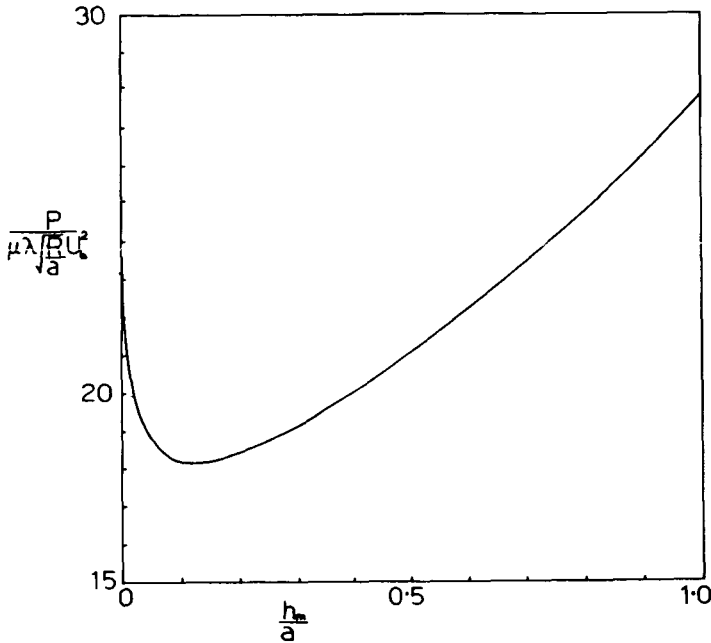


Fig. 4 The power dissipated by the organism P as a function of distance from the wall h_m , for a sinusoidal waveform. Here a is the amplitude of the wave, λ the wavelength, μ the viscosity of the slime, R the cross-sectional radius of the organism and U_b is the speed of the organism.

Assuming that h_m/a lies in this range, we find from Fig. 4 that the power per unit length required for this form of motion is approximately given by

$$18\mu\sqrt{(R/a)}U_b^2. \quad (5.7)$$

This quantity is independent of the length of the organism; thus if the power output increases in proportion to the length of the organism—and this appears to be a reasonable assumption [4]—the flexibacter speed will be independent of length. This is in accordance with the recent observations of Humphries *et al.* [3].

Using the estimate of .3 gm/cm.sec for the slime viscosity given in [2], we find from (5.7) that the power required for an organism of length $5\mu\text{m}$ to move with the maximum observed speed of $1.5\mu\text{m}/\text{sec}$ is 2×10^{-10} ergs/sec, where we have used the values of R and a given in the introduction. From measurements of the rate at which the flexibacters consume oxygen it is found that the power available to a flexibacter is of the order of [4] 5×10^{-7} ergs/sec. Clearly the above estimate of power requirement is well within the organism's capability.

The curve in Fig. 4 may also be used to determine the speed of the organism U_b for a given power output as a function of separation from the wall. From this curve it can be seen that the organism is virtually incapable of propulsion at very small and very large distances from the wall and, in the optimum range, $.05 < h_m/a < .3$, the velocity attains a maximum value of approximately $\{P/(18\mu\lambda\sqrt{(R/a)})\}^{1/2}$. This maximum decreases as the viscosity of the liquid between the flexibacter and the wall is increased. Thus the sticky slime inhibits motility; in return for this loss of motility the slime provides the flexibacter with an adhesive which prevents the organism from being swept off the surface, where it obtains its food, by the currents in the surrounding liquid [2].

The results which have been derived in this paper should be regarded as rough estimates only, for the analysis is based on a number of assumptions which are either not strictly valid—such as the assumption that the slope of the flexibacter surface relative to the wall is small; or assumptions which were made in the absence of any experimental observation—such as the assumption that the slime is a Newtonian liquid. It seems unlikely, however, that a more exact analysis would significantly alter those results which are in accordance with the few experimental observations, namely, that the power required for this form of propulsion is well within the cell's capability, that the cell is only motile in the neighbourhood of the wall, and that the cell speed is independent of the length of the cell. Thus, from a hydrodynamic point of view, this form of propulsion appears to be feasible.

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