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Do cyanobacteria swim using traveling surface waves?

(bacteria/motility)

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ABSTRACT **Bacteria that swim without the benefit of flagella might do so by generating longitudinal or transverse surface waves. For example, swimming speeds of order 25 μm/s are expected for a spherical cell propagating longitudinal waves of 0.2 μm length, 0.02 μm amplitude, and 160 μm/s speed. This problem was solved earlier by mathematicians who were interested in the locomotion of ciliates and who considered the undulations of the envelope swept out by ciliary tips. A new solution is given for spheres propagating sinusoidal waveforms rather than Legendre polynomials. The earlier work is reviewed and possible experimental tests are suggested.**

Strains of the cyanobacterium *Synechococcus* swim in seawater at speeds of up to 25 μm/s (1). They are rod-shaped organisms measuring about 1 μm in diameter by 2 μm long. *Synechococcus* swim in the direction of their long axis, following an irregular helical track. Their means of locomotion is not known, and they have no flagella, either external or internal. As far as one can see by light microscopy, they do not change shape. Under certain growth conditions, long asymmetric cells appear, but these just roll rigidly about an axis parallel to their long axis, the direction of locomotion (T. P. Pitta, personal communication). An electrophoretic, or "ion drive," mechanism has been proposed for other bacteria (2) but has been ruled out for *Synechococcus* (3). The only propulsive mechanisms that remain possible appear to be surface flow or undulation. Here, we note that the requisite thrust might be generated by small-amplitude, high-frequency waves that travel along the outer cell membrane.

The traveling waves that we envisage are surface oscillations. They can be either normal or tangential to the surface, or a combination of the two. Even tangential waves can yield the requisite thrust. In retrospect, this propulsive mechanism for cyanobacteria could have been suggested by a number of researchers much earlier. Lighthill (4), Blake (5), Brennen (6), and Shapere and Wilczek (7) developed quantitative theories of swimming in low Reynolds number fluids by means of small surface waves. These theories were developed for ciliated organisms, the surface wave being the "envelope", or smooth approximation to, the tips of the many cilia. However, the cilia themselves were not essential for the theories.

This paper is a review of these past results with an eye toward application to cyanobacterial swimming. We have tried to put the results in a framework that will be useful to microbiologists. We have also included a technical extension of the previous theories: we can expand our surface waveforms in a Fourier basis to obtain swimming velocities, as opposed to the traditional expansions in terms of a Legendre basis.

RESULTS

Swimming Speeds. Imagine the organism as a sphere or ellipsoid with tangential waves traveling from one pole to the other, with the wave amplitudes constant along lines of latitude, as shown in Fig. 1. c denotes the speed, λ denotes the wavelength, and a denotes the amplitude of these traveling surface waves. Our model predicts that for tangential surface waves a spherical organism swims in the same direction as the surface wave at a speed V equal to

$$V = (\pi^3/2)(a/\lambda)^2 c. \quad [1]$$

This formula is based on an approximation that is only valid when a/λ is small. In particular, $16(a/\lambda)$ should be smaller than 1. The coefficient of 16 will change a bit for a rod-shaped organism, but will be the same order of magnitude. For example, take $\lambda = 0.2$ μm, $a = 0.02$ μm. To achieve a speed of 25 μm/s, we need a wave speed of 160 μm/s. The wave speed c is $\lambda\nu$, where ν is the frequency of the wave (800 s^{-1}); $1/\nu = T$ is its period (1.3 ms). The number of modes that fit into a longitudinal great circle is $n = 2\pi R/\lambda$, where R is the radius of the sphere. For $R = 1$ μm, $n \approx 31$.

In deriving this formula, we assume that the surface waves are axially symmetric, so that at any time they are constant along meridians. This implies that the organism moves in a straight line. (Since the actual organisms move in helical paths, their propulsive waves, assuming that our mechanism is the real mechanism, are not quite axially symmetric.) We also have assumed that the wave form is that of an nth Fourier mode. In other words, along any longitudinal cross-section of the sphere, the wave is given by a trigonometric polynomial. An analytic form for the waveforms we use is given below.

Fig. 2 is a plot of the fluid velocity field near the cell membrane. In Fig. 2, we are moving with the cell. Think of it as being one frame taken out of a movie of the cell's expansion and contraction waves and the resulting fluid motion. The successive frames would look identical, except that they would be translated in the direction of the wave motion. This plot is based on solving Stokes equations for a deforming plane as opposed to a sphere. This is a good approximation of the flow field near the sphere when a and λ are small; see Childress (8).

Spherical or ellipsoidal organisms also can swim using waveforms that are a combination of normal and tangential oscillations. If the oscillations are purely normal, then the swimmer moves in the direction opposite to that of the surface wave, as opposed to the case of tangential waves. To understand this, think of the wave as pushing the nearby fluid in its direction of motion; consequently, the whole organism moves in the opposite direction. A traveling wave of normal oscillations has troughs within which it can temporarily "trap" the fluid, whereas tangential waves have no such surface features. By using a combination of normal and tangential oscillations, an organism can achieve swimming speeds roughly double those of purely tangential waveforms, other wave parameters being held the same.

Derivation. Our results are based on an analysis of Stokes equations, the relevant equations for motion at low Reynolds number. The Reynolds number is $R_e = UL/\nu$, where U and L are a characteristic velocity and length for the problem,

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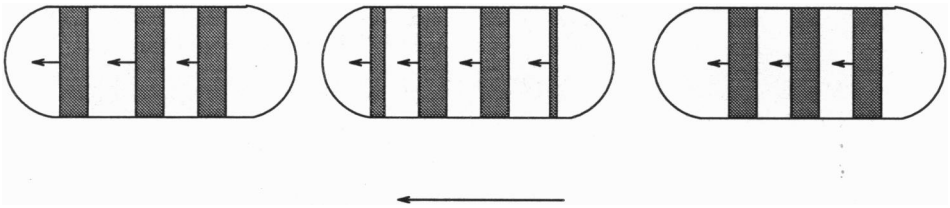

FIG. 1. It is possible to swim at low Reynolds number using traveling tangential waves. Here we depict a traveling tangential wave with wavelength about one-third of body length. The dark areas represent regions of contraction that drift to the left (short arrows). The intervening light areas are regions of expansion. Local regions of the outer cell membrane simply expand or contract: there is no net flow of membrane mass. The cell swims to the left (long arrow).

respectively, and ν is the kinematic viscosity (the viscosity of the fluid divided by its specific gravity). If R_e is much less than 1, then Stokes equations can be used with confidence. If for U and L we use the swimming speed and diameter of *Synechococcus*, we get $R_e \approx 10^{-5}$. If instead we use the wavespeed and wavelength discussed in the introduction, $R_e \approx 10^{-4}$. So Stokes equations are a valid approximation of the fluid mechanics. The cell membrane is assumed impermeable to the fluid, which means that the boundary conditions are no-slip: the fluid velocity at a point of the membrane matches the velocity of that material point. Most of what we need from this Stokesian fluid mechanics has already been worked out by Lighthill (4), Blake (5), Brennen (6), Childress (8), Shapere and Wilczek (7), and others. As noted earlier, their motivation was to understand the swimming of ciliated swimmers, using the so-called envelope model in which the cilia tips are approximated by a smooth undulating surface.

The Stokes equations are partial differential equations for the fluid velocity of the fluid outside of the cell, given the instantaneous deformation of the cell membrane. From the analytic point of view, the most important thing about these equations are that they are linear and of the "elliptic" type, like the Laplacian. Not all instantaneous deformations are possible. Only those deformations for which the net force and torque on the cell are zero are physically allowable. These last conditions together with Stokes equations determine the velocity of the organism, given a particular swimming stroke (for details, see refs. 4–12).

Our basic problem is to estimate the swimming velocity of an organism whose swimming stroke consists of a small-amplitude time-periodic deformation of its surface: a traveling wave on the cell membrane. We will suppose for simplicity that this deformation can be expressed in the form:

$$\vec{x} \mapsto \vec{x} + a[\cos(\omega t)\vec{v}_1(\vec{x}) + \sin(\omega t)\vec{v}_2(\vec{x})]. \qquad [2]$$

Here $\vec{x}$ denotes a point of the surface, a is a measure of the wave amplitude, assumed to be small, t is time, and $\vec{v}_1(\vec{x})$ and $\vec{v}_2(\vec{x})$ are vector fields along (not necessarily tangent to) the cell membrane. These vector fields represent two independent deformations of the membrane. It can then be shown (7, 12) that the average swimming velocity $\vec{V}$ of the organism over one period is of the form

$$\vec{V} = \frac{1}{2} a^2 \omega \vec{F}(\vec{v}_1, \vec{v}_2) \qquad [3]$$

plus terms higher order in a^2. The key to understanding small-amplitude swimming is to understand the object $\vec{F}(\vec{v}_1, \vec{v}_2)$. It is a vector-valued functional with units of inverse length. A functional is a function of functions, which is to say, a function with inputs being functions and outputs being numbers. Our $\vec{F}$ is slightly more general. Its inputs are pairs of vector fields $\vec{v}_1 = \vec{v}_1(\vec{x})$ and $\vec{v}_2 = \vec{v}_2(\vec{x})$ (not just functions) defined along the cell surface. Its output $\vec{F}(\vec{v}_1, \vec{v}_2)$ is a fixed vector representing swimming direction. It depends parametrically on the background shape of the cell surface, which here we take to be a sphere. In addition, our $\vec{F}$ satisfies the algebraic properties of skew-symmetry $\vec{F}(\vec{v}_1, \vec{v}_2) = -\vec{F}(\vec{v}_2, \vec{v}_1)$ and bilinearity $\vec{F}(\vec{v}_1 + c\vec{v}_3, \vec{v}_2) = \vec{F}(\vec{v}_1, \vec{v}_2) + c\vec{F}(\vec{v}_3, \vec{v}_2)$, for any constant scalar c. These properties are closely related to the linearity of the Stokes equations and to the "scallop theorem" (8, 9). This theorem asserts that if the material points of the membrane retrace their path during the swimming stroke, then the net velocity is zero. [In terms of our $\vec{F}$, this becomes the assertion that if $\vec{v}_2 = 0$ or more generally that if $\vec{v}_1 = (const.)\vec{v}_2$, then $\vec{F}(\vec{v}_1, \vec{v}_2) = 0$.] Computing $\vec{F}(\vec{v}_1, \vec{v}_2)$ involves solving the Stokes equations for various deformations of the surface S.

The swimming model that we use was also used by Blake (5), Brennen (6), and others. In this model, the organism is a sphere of radius R that propels itself by oscillating its outer membrane in an axially symmetric manner. We will use spherical coordinates r_m, θ_m, and ϕ_m for the position of a material point on the deformed sphere, with θ_m being the azimuthal angle measured from the north pole. The surface waves are then described by deformations of the form:

$$r_m = r_m(\theta, t) = R(1 + f(\theta, t)), \qquad [4]$$

$$\theta_m = \theta_m(\theta, t) = \theta + g(\theta, t), \qquad [5]$$

and

$$\phi_m = \phi, \qquad [6]$$

where (θ, ϕ) are the coordinates of a material point on the undeformed sphere, and where the deformations f, g are periodic in t with a fixed period T. The particular tangential

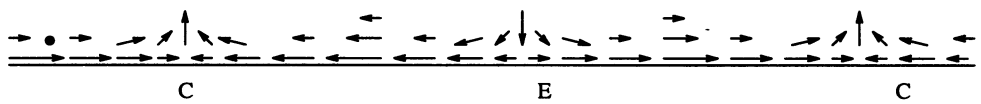

FIG. 2. How a longitudinal wave traveling on the surface of a cell affects the adjacent fluid. The arrows depict the fluid velocity profile at a frozen time t; the wave is moving to the left. Imagine a water molecule starting where indicated (●). We will describe its trajectory as the wave passes. It is initially being pushed to the right. As the region of contraction C approaches it is pushed up and to the right. As C passes, it is pushed up and to the left. Between the region of contraction C and the region of expansion E, it is pushed to the left. As E approaches, it is pushed down and to the left. Once E passes, it is pushed down and to the right, and between E and the next C it is pushed to the right. Notice that the water molecule is closer to the membrane while being pushed to the right. Because the velocity profile rapidly decays away from the membrane, the molecule is pushed farther to the right than to the left. Therefore, an organism that can move its outer membrane in this manner swims in the same direction as the wave.

waveforms of interest to us are those discussed in the introduction. For these:

$$f \equiv 0 \qquad [7]$$

and

$$g = \frac{a}{R}\cos(n\theta - \omega t)$$

$$= \frac{a}{R}[\sin(\omega t)\sin(n\theta) + \cos(\omega t)\cos(n\theta)]. \qquad [8]$$

To convert this deformation into the vector form involving $\vec{v}_1$, $\vec{v}_2$, multiply the radial deformation f by the normalized radial vector field $\vec{e}_r$, and the azimuthal deformation g by the vector field in the azimuthal direction $\vec{E}_\theta$. The latter vector field is not normalized; its length is r. Thus, $\vec{v}_1 = \sin(n\theta)\vec{E}_\theta$ and $\vec{v}_2 = \cos(n\theta)\vec{E}_\theta$. By axial symmetry, the swimming motion is in the direction of the sphere's axis. It follows that we can write F in the form $\vec{F}(\sin(n\theta)\vec{E}_\theta, \cos(n\theta)\vec{E}_\theta) = F(\sin(n\theta)\vec{E}_\theta, \cos(n\theta)\vec{E}_\theta)\vec{e}_z$, where $\vec{e}_z$ is the unit vector pointing along the sphere's axis and F is scalar valued. Our goal then, is to calculate $F(\sin(n\theta)\vec{E}_\theta, \cos(n\theta)\vec{E}_\theta)$.

The Stokes equations with boundary data on a sphere are most conveniently solved in terms of Legendre polynomials $P_n(\cos\theta)$ for the radial deformations f, and in terms of their normalized derivatives

$$V_n(\cos\theta) = \frac{2}{n(n+1)}\frac{d}{d\theta}P_n(\cos\theta) \qquad [9]$$

for the tangential oscillations g. The values of $F(V_j\vec{E}_\theta, V_k\vec{E}_\theta)$, $F(P_n\vec{e}_r, V_j\vec{E}_\theta)$, and $F(P_n\vec{e}_r, P_m\vec{e}_r)$ were calculated by Shapere and Wilczek (7) and in a different form by Blake (5). Because we are only concerned for the moment with tangential oscillations, it is convenient to drop the vector appendage "$\vec{E}_\theta$" and simply write $F(V_j, V_k)$. The results obtained by these earlier workers are $F(V_j, V_k) = 0$ unless j and k differ by 1, in which case $F(V_n, V_{n+1}) = 8/[(2n+1)(2n+3)R]$.

Now we expand our deformations in terms of the V_j:

$$\sin(n\theta) = \Sigma A_j V_j(\cos\theta) \qquad [10]$$

and

$$\cos(n\theta) = \Sigma B_l V_l(\cos\theta). \qquad [11]$$

These expansions were performed by Hobson (13) (see also equations 8.924.3 and 8.924.4 in ref. 14). By bilinearity and skew-symmetry:

$$F(\sin(n\theta), \cos(n\theta)) = \Sigma A_j B_l F(V_j, V_l). \qquad [12]$$

Hobson's expansion for $\sin(n\theta)$ only contains terms with $j \leq n$ and his expansion for $\cos(n\theta)$ only contains terms with $l \geq n - 1$. It follows that the sum for F contains only a finite number of terms, those involving $F(V_{n-2}, V_{n-1})$, $F(V_{n-1}, V_n)$, and $F(V_n, V_{n+1})$. The sum can be done explicitly, yielding the swimming velocities

$$\vec{V} = \frac{1}{2}a^2\omega F(\sin(n\theta), \cos(n\theta))\vec{e}_z, \qquad [13]$$

with $F(\sin(n\theta), \cos(n\theta)) = \pi n/4R$. This completes our derivation.

Using the same technique, one can calculate the swimming velocities due to a wave that is a combination of tangential and normal sinusoidal oscillations. In this case, material points on the sphere follow elliptical paths. Calculations of this kind were done by Blake (5) for Legendre-based waves. As mentioned earlier, the swimming speeds attained can be about twice as fast as those for the purely tangential waves, the other wave parameters being the same.

DISCUSSION

Earlier Work. The implications of low Reynolds number to problems of self-propulsion were realized as early as 1930 (15). Various authors have presented infinite models for low Reynolds number swimming. Taylor (16), Reynolds (17), Tuck (18), Blake (19), and Childress (8) treat an infinite swimming sheet; Blake (19, 20) and Shapere and Wilczek (7) treat infinite swimming cylinders. An analytical model for approximating the translational velocities of spherical organisms that swim using small amplitude oscillations was first proposed by Lighthill (4). Traveling surface waves were approximated using two spherical harmonics whose orders differed by one. He obtained an infinite sum expression for the swimming speed V, but he did not compare his predictions with observations.

In 1971, Blake (5, 19, 20) adapted Lighthill's model to explain ciliary propulsion by replacing the loci of the cilia tips with a continuous envelope. For certain organisms, *Opalina ranarum* for example, the cilia tips remain close together during the swimming stroke, and for such organisms the model provided good results. Blake found an expression for the instantaneous velocity of a sphere undergoing Legendre-polynomial deformations. Since the expansion of sinusoidal deformations as a series of Legendre polynomials contains an infinity of terms, Blake's equation for velocity seemingly contains an infinity of terms. However, inspection of this series reveals that only products of consecutive Legendre polynomials appear. Using the expansions for $\sin(n\theta)$ and $\cos(n\theta)$ described above, one can show that the average velocity of a sphere propagating longitudinal waves reduces to a single term, identical to our Eq. **1**.

In 1974, Brennen (6) proposed an oscillating boundary-layer theory to explain ciliary propulsion. In his model, the fluid surrounding the organism is divided into two regions: (*i*) an oscillating boundary-layer close to the cell and (*ii*) an external complimentary region of steady Stokes flow. The unsteady boundary-layer fluid motions, generated by the surface oscillation, attenuate like $\exp(-r/\lambda)$, where λ is the wavelength of the surface wave and r is the distance from the surface. These are matched to the exterior flow. Finally, the condition of zero net force on the self-propelling organism is used to obtain a further constraint on the flows, which is applied to obtain the propulsive velocity. Brennen (6) obtains the velocity formula $V = (4\pi^2/3)(a/\lambda)^2 c$.

In 1989, Shapere and Wilczek (7) proposed a geometrical model for propulsion at low Reynolds number. The quantity we refer to as F was introduced here, where it is called the field strength or curvature. They generalized the results of Lighthill (4) and Blake (5) by treating *arbitrary* small amplitude surface oscillations of a spherical swimmer and by obtaining expressions for the rotational as well as the translational velocities.

While all of the authors after Lighthill (4) were concerned with ciliary propulsion, their models are applicable, without modification, to organisms with oscillatory membranes. In fact, the general framework of Shapere and Wilczek (7) is applicable to any low Reynolds number swimmer. However, they only applied their framework to certain two-dimensional swimmers and to spherical swimmers.

Experimental Tests. It seems unlikely that one can test models of this kind on a cell the size of *Synechococcus* by marking the flow of the external medium, e.g., by tracking displacements of fluid along the arrows of Fig. 2. The effects of Brownian motion on small test particles are too severe. However, it should be possible to fasten such particles to the outer surface of a cell. If the attachment is to an element that participates in contraction or expansion, as in C or E in Fig. 2, then a particle will move back and forth. It will vibrate at the

frequency of the wave, $\nu = 1/T$ (800 s^{-1} in the examples given in the introduction). The motion will be in a direction parallel to the surface of the cell if the wave is longitudinal or normal to this surface if the wave is transverse. In principle, motion of this kind can be demonstrated by power spectral analysis of the output of a suitable edge detector.

If, on the other hand, the surface of the cell flows in bulk, then the particle will move from one end of the cell to the other. In fact, this happens when latex particles are added to certain gliding bacteria (bacteria that fail to swim but that glide along solid substrates), e.g., *Cytophaga johnsonæ* (21) or *Cytophaga* sp. strain U67 (22). In the latter case, something quite remarkable happens: the particles move to and fro along the surface of the cell in a direction roughly parallel to its long axis, passing each other in opposite directions, even when in close proximity. Thus, the surface of the cell does not move in bulk like the tread of a tank or as it would were a layer of slime swept backwards by traveling waves of the sort envisioned here.

It was argued earlier (3) that propulsion of swimming *Synechococcus* must be due to mechanical deformation or flow of the cell surface. However, it was not appreciated at the time that longitudinal waves, which might not generate any detectable change in cell shape, could provide a viable propulsive mechanism.

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1. Waterbury, J. B., Willey, J. M., Franks, D. G., Valois, F. W. & Watson, S. W. (1985) *Science* **230,** 74–76.
2. Mitchell, P. (1972) *FEBS Lett.* **28,** 1–4.
3. Pitta, T. P. & Berg, H. C. (1995) *J. Bacteriol.* **177,** 5701–5703.
4. Lighthill, J. (1952) *Commun. Pure. Appl. Math.* **5,** 109–118.
5. Blake, J. R. (1971) *J. Fluid Mech.* **46,** 199–208.
6. Brennen, C. (1974) *J. Fluid Mech.* **65,** 799–824.
7. Shapere, A. & Wilczek, F. (1989) *J. Fluid Mech.* **198,** 557–585.
8. Childress, S. (1981) *Mechanics of Swimming and Flying* (Cambridge Univ. Press, Cambridge, U.K.).
9. Purcell, E. M. (1977) *Am. J. Phys.* **45,** 3–11.
10. Shapere, A. (1989) Ph. D. thesis (Univ. of California, Santa Barbara).
11. Ehlers, K. M. (1995) Ph. D. thesis (Univ. of California, Santa Cruz).
12. Ehlers, K., Koiller, J. & Montgomery, R. (1996) *J. Nonlin. Sci.*, in press.
13. Hobson, E. W. (1931) *The Theory of Spherical and Ellipsoidal Harmonics.* (Cambridge Univ. Press, Cambridge, U.K.).
14. Gradshteyn, I. S. & Ryzhik, I. M. (1965) *Table of Integrals, Series, and Products*, ed. Jeffrey, A. (Academic, New York), 4th Ed.
15. Ludwig, W. (1930) *Zeit. F. Vergl. Physiolog.* **13,** 397–504.
16. Taylor, G. I. (1951) *Proc. Roy. Soc. London A,* **209,** 447–461.
17. Reynolds, A. J. (1965) *J. Fluid. Mech.* **23,** 241–260.
18. Tuck, E. O. (1968) *J. Fluid. Mech.* **31,** 305–308.
19. Blake, J. R. (1971) *J. Fluid Mech.* **49,** 209–222.
20. Blake, J. R. (1971) *Bull. Austral. Math. Soc.* **3,** 255–264.
21. Pate, J. L. & Chang, L.-Y. E. (1979) *Curr. Microbiol.* **2,** 59–64.
22. Lapidus, I. R. & Berg, H. C. (1982) *J. Bacteriol.* **151,** 384–398.