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Efficiencies of self-propulsion at low Reynolds number

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We study the efficiencies of swimming motions due to small deformations of spherical and cylindrical bodies at low Reynolds number. A notion of efficiency is defined and used to determine optimal swimming strokes. These strokes are composed of propagating waves, symmetric about the axis of propulsion.

1. Introduction

Swimming micro-organisms inhabit a strange world where our ordinary Newtonian intuition does not apply, the world of low-Reynolds-number fluid mechanics. In the limit of zero Reynolds number, which is approached as the organism's radius becomes small, the importance of inertia in determining the motion of the fluid becomes negligible. The swimmer's path through the fluid then depends only on the geometry of the sequence of shapes that compose its swimming motion, and not on how rapidly the motion is made (Purcell 1977). An important consequence of the geometric nature of swimming at low Reynolds number is a gauge structure over the space of shapes, which we have described in a recent paper (Shapere & Wilczek 1989). In that paper, we exploited this structure in order to compute the net velocity of a nearly spherical organism through a fluid, due to an arbitrary cyclic swimming stroke. We also found the swimming motions of cylinders of nearly circular cross-section.

Here, we shall consider the question of efficiency of swimming at low Reynolds number. Within a restricted space of shapes, what is the best way to swim ?† We shall assume that the swimmer makes only small changes of shape. This restriction is appropriate for ciliated organisms, which swim by synchronously waving a layer of short, densely packed cilia. In an approximation known as the envelope model, the effects of individual cilia are neglected and the shape is taken to be a smooth surface covering the ciliary layer. This approximation is reasonable *a priori*, because the viscous fluid cannot follow exceedingly fine-grained motion. It is also indicated *a fortiori*, because the cilia are observed to beat collectively, in smooth waves (Childress 1978, and references therein). We shall find that the qualitative features of observed beating patterns are reproduced by our analysis.

The swimming motions of a sphere were studied in classic papers by Lighthill (1952) and Blake (1970). They considered azimuthally symmetric deformations of a sphere and computed the efficiencies of some sample motions. We extend their analyses in the first part of this paper to find maximally efficient swimming strokes.

† We should mention that there is some reason to doubt whether efficiency is the most important criterion in determining the swimming motions of micro-organisms, since the power expended for locomotion is generally a very small fraction of the organism's total power output.

Our treatment of nearly spherical swimmers does not presume a familiarity with Shapere & Wilczek (1989). Next, we do the same for cylinders of nearly circular cross-section, building on the work of Blake (1971 *a*, *b*). The qualitative similarity of our results for spheres and for cylinders and possible extrapolations to more general shapes are discussed in the concluding section.

2. Squirming spheres

In this section we shall follow the treatment of swimming motions of nearly spherical organisms given by Blake (1970). We shall restrict attention to azimuthally symmetric deformations, and assume incompressible steady flow. The equations of motion for the fluid velocity field $\boldsymbol{v}$ and the pressure p are

$$\mu\nabla^2\boldsymbol{v} = \boldsymbol{\nabla}p, \qquad \boldsymbol{\nabla}\cdot\boldsymbol{v} = 0, \tag{2.1}$$

where μ is the viscosity. A given infinitesimal change of shape leads to a net motion when we match the velocity at each point on the shape's surface to the fluid velocity field and demand that those components of $\boldsymbol{v}$ which would lead to a net force or torque on the shape vanish.

We consider cyclic swimming motions of period T composed of small deformations of a sphere of radius r_0. Such cyclic changes of shape may be expanded as series in Legendre polynomials and their derivatives:

$$\left.\begin{aligned} r'(\theta,t) &= r_0+\epsilon r_0\sum_n a_n(t)\,P_n(\cos\theta),\\ \theta'(\theta,t) &= \theta+\epsilon\sum_n b_n(t)\,V_n(\cos\theta), \end{aligned}\right\} \tag{2.2}$$

where a_n and b_n have period T and

$$V_n(\cos\theta) \equiv \frac{1}{(n+1)}\frac{\partial}{\partial\theta}P_n(\cos\theta). \tag{2.3}$$

If the radial and azimuthal velocities v_r and v_θ on the surface of the sphere $r = r_0$ are

$$v_r = \epsilon r_0\sum_{n=2}^{\infty}\dot{a}_n P_n(\cos\theta), \quad v_\theta = \epsilon r_0\sum_{n=2}^{\infty}\dot{b}_n V_n(\cos\theta) \tag{2.4}$$

then the general solution is

$$\left.\begin{aligned} v_r &= \sum_{n=2}^{\infty}\left[\tfrac{1}{2}n\frac{r_0^n}{r^n}-(\tfrac{1}{2}n-1)\frac{r_0^{n+2}}{r^{n+2}}\right]\dot{a}_n P_n+\tfrac{1}{2}n\left[\frac{r_0^{n+2}}{r^{n+2}}-\frac{r_0^n}{r^n}\right]\dot{b}_n P_n,\\ v_\theta &= \sum_{n=2}^{\infty}\left[\tfrac{1}{2}n\frac{r_0^{n+2}}{r^{n+2}}-(\tfrac{1}{2}n-1)\frac{r_0^n}{r^n}\right]\dot{b}_n V_n+(\tfrac{1}{2}n-1)\left[\frac{r_0^n}{r^n}-\frac{r_0^{n+2}}{r^{n+2}}\right]\dot{a}_n V_n. \end{aligned}\right\} \tag{2.5}$$

(Note that our series begin at $n = 2$. We are neglecting terms with $n = 1$, since these correspond to unphysical rigid self-rotations and translations.) The pressure field

$$p = \mu\sum_{n=2}^{\infty}\frac{2n^2-n}{n+1}(\dot{a}_n-\dot{b}_n)\frac{r_0^n}{r^{n+1}}P_n \tag{2.6}$$

is easily checked to satisfy (2.1).

Lighthill (1952) defines the efficiency of a swimming stroke as the ratio of the rate of drag on a sphere moving with velocity $\bar{U}$ to the average power output required to swim with average velocity $\bar{U}$

$$\eta_0 \equiv \frac{6\pi\mu r_0 \bar{U}^2}{\bar{\mathscr{P}}}. \tag{2.7}$$

As we shall discuss in the next section, this definition of efficiency is problematic. Fortunately, it leads to the same optimal swimming motions as our alternative definition,

$$\eta_1 \equiv \frac{\bar{U}/\bar{\mathscr{P}}}{(\bar{U}/\bar{\mathscr{P}})_{\max}}, \tag{2.8}$$

where the denominator is maximized over swimming strokes with period T and infinitesimal amplitude. By the latter restriction we mean that only shapes that deviate pointwise from the average shape by a maximum distance of less than ϵ are considered. To calculate either efficiency, we must know the net swimming velocity and power output for a given cyclic swimming motion.

The power output required to deform a sphere according to a given velocity field on its surface is obtained from the fluid stress tensor σ_{ij} as an integral over the surface of the sphere (Batchelor 1970)

$$\mathscr{P} = \int_S v_i \, \sigma_{ij} \, \mathrm{d}S_j. \tag{2.9}$$

For azimuthally symmetric flow, the relevant stresses exerted by the cilia on the fluid are

$$\sigma_{rr} = p - 2\mu \frac{\partial v_r}{\partial r}, \qquad \sigma_{\theta r} = \mu \left[\frac{v_\theta}{r} - \frac{\partial v_\theta}{\partial r} - \frac{1}{r}\frac{\partial v_r}{\partial \theta} \right], \tag{2.10}$$

from which Blake computes

$$\begin{aligned} \mathscr{P} &= 2\pi \int_0^\pi (v_r \sigma_{rr} + v_\theta \sigma_{\theta r})_{r=r_0} r_0^2 \sin\theta \, \mathrm{d}\theta \\ &= 2\pi\mu r_0^3 \epsilon^2 \sum_{n=2}^{\infty} \left[\frac{4n^2+6n+8}{(2n+1)(n+1)} \dot{a}_n^2 + \frac{2n^2}{n(n+1)} \dot{b}_n^2 + \frac{12n}{(n+1)(2n+1)} \dot{a}_n \dot{b}_n \right] \\ &\equiv 2\pi\mu r_0^3 \epsilon^2 \sum_{m,n} P_{mn} \dot{\alpha}_m \dot{\alpha}_n. \end{aligned} \tag{2.11}$$

In the last line, α is the vector $\{a_n, b_n\}$.

Blake also calculates the net velocity of the sphere, which points in the z-direction for azimuthally symmetric boundary conditions:

$$\begin{aligned} U = r_0 \epsilon^2 \sum_{n=2}^{\infty} \Bigg\{ & \frac{(n+1)^2 a_n \dot{a}_{n+1} - (n^2-4n-2)\, a_{n+1} \dot{a}_n}{(2n+1)(2n+3)} \\ & - \frac{(n+1)(n+2)\, a_n \dot{b}_{n+1} - n(n+1)\, b_{n+1} \dot{a}_n}{(2n+1)(2n+3)} \\ & + \frac{n(3n+2)\, a_{n+1} \dot{b}_n + n(n+2)\, b_n \dot{a}_{n+1}}{(2n+1)(2n+3)} - \frac{n(n+2)\, b_n \dot{b}_{n+1} - n^2 b_{n+1} \dot{b}_n}{(2n+1)(2n+3)} \Bigg\} + O(\epsilon^3) \\ \equiv r_0 \epsilon^2 & \sum_{m,n=2}^{\infty} F_{mn} \alpha_m \dot{\alpha}_n. \end{aligned} \tag{2.12}$$

(This expression differs from Blake's equation (18) because our normalization (2.3) of the V_n is different.) Here F_{mn} is the 'field strength' tensor defined in Shapere & Wilczek (1989). In averaging the net velocity over one cycle, we may antisymmetrize on the terms in (1.12) by integrating by parts. Then Lighthill's efficiency (2.7) becomes

$$\eta_0 = 3\epsilon^2 \frac{\left[\int_0^T \mathrm{d}t \sum F_{[mn]} \alpha_m \dot{\alpha}_n\right]^2}{T \int_0^T \mathrm{d}t \sum P_{mn} \dot{\alpha}_m \dot{\alpha}_n} \equiv 3\epsilon^2 \frac{N^2}{D}. \tag{2.13}$$

Note that η_0 is invariant under time rescaling; henceforth, we set $T = 1$.

Extremization of η_0 over paths $\{a_n(t), b_n(t)\}$ is performed by setting the variation of the expression (2.13) with respect to each of the a_n and b_n equal to zero. In our abbreviated notation, this gives

$$\frac{\delta \eta_0}{\delta \alpha_n} \propto \sum_m 2F_{[mn]} \dot{\alpha}_m - \frac{N}{D} P_{mn} \ddot{\alpha}_m = 0. \tag{2.14}$$

To make our problem finite, let us assume that only modes k to $k+p$ are excited.

First, we shall solve (2.14) in the large-k limit. In this limit, P and F simplify considerably. We obtain $2p+2$ simultaneous linear differential equations for a_n and b_n, with $k \leqslant n \leqslant k+p$:

$$\frac{\delta \eta_0}{\delta a_n} \propto \tfrac{1}{2}(\dot{a}_{n+1} - \dot{a}_{n-1} - \dot{b}_{n+1} + \dot{b}_{n-1}) - 2\frac{N}{D} \ddot{a}_n = 0, \tag{2.15}$$

$$\frac{\delta \eta_0}{\delta b_n} \propto \tfrac{1}{2}(-\dot{b}_{n+1} + \dot{b}_{n-1} - \dot{a}_{n+1} + \dot{a}_{n-1}) - 2\frac{N}{D} \ddot{b}_n = 0. \tag{2.16}$$

For large k, we may rewrite these equations as the eigenvalue equation of an antisymmetric matrix $A \sim P^{-1}F$ with imaginary eigenvalue $\mathrm{i}\lambda \equiv \mathrm{i}4N/D$ and complex eigenvector $V = (a_n, \ldots, b_n, \ldots)^{\mathrm{T}}$:

$$AV = \mathrm{i}\lambda V. \tag{2.17}$$

This equation is pivotal in solving our restricted optimization problem. If V has A-eigenvalue λ, then

$$\alpha(t) = \mathrm{Re}\,[\mathrm{e}^{-2\pi \mathrm{i} t} V] \tag{2.18}$$

is a cyclic path of extremal efficiency. Indeed, the eigenvectors of maximum $|\lambda|$ correspond to swimming motions of *maximum* efficiency. This is seen by relating $\lambda = 4N/D$ to the efficiency $\eta_0 = 3\epsilon^2 N^2/D$. N is very roughly the area in shape space enclosed by one cycle of the swimming stroke, and D is roughly its perimeter squared. N is maximized over paths of given shape-space perimeter by circular paths, and D is minimized over paths of given 'area' by the same. It should not be surprising, then, that the strokes of extremal efficiency correspond to evolution via an antisymmetric rotation matrix A. Such a matrix always leads to a circular trajectory through shape space, traversed at a uniform speed. Now for an organism whose cilia are all of length 2ϵ, all possible shape-space trajectories lie within a $(2p+2)$-dimensional sphere of radius ϵ. An extremal swimming stroke will therefore be a circle in shape space of radius ϵ, for which $D = (2\pi\epsilon)^2$. Hence,

$$\eta_0 = 3\epsilon^2 \left(\frac{N}{D}\right)^2 D = \tfrac{3}{4}\pi^2 \epsilon^2 \lambda^2. \tag{2.19}$$

The eigenvectors and eigenvalues of A are computed in the Appendix; the maximum eigenvalue is found to be $2\sqrt{2}\cos(\pi/(p+2))$. Hence, the maximum possible efficiency of a swimming stroke in which only modes $k, \ldots, k+p$ are excited is

$$\eta_0 = \tfrac{3}{4}\pi^2\epsilon^2\left(2\sqrt{2}\cos\left(\frac{\pi}{p+2}\right)\right)^2 < 6\pi^2\epsilon^2. \tag{2.20}$$

This gives the upper bound on η_0, for large p. It is approached asymptotically as both p and k go to infinity by the solutions given in the Appendix. These solutions have the qualitative appearance of those shown in the figures. In words, the optimal large-k swimming stroke is a travelling-wave-like motion, with waves emanating from the north pole of the sphere and terminating at the south pole. The detailed form of the two solutions of maximum $|\lambda|$ is

$$\left.\begin{aligned} r'(\theta,t) &= r_0+\epsilon r_0 N_\pm(1\pm\sqrt{2})\sum_{j=1}^{p+1}\mathrm{Re}\left\{\mathrm{e}^{-2\pi\mathrm{i}t}\,\mathrm{i}^{j-1}\sin\left(\frac{\pi j}{p+2}\right)\right\}P_{k+j-1}(\cos\theta),\\ \theta'(\theta,t) &= \theta+\epsilon N_\pm\sum_{j=1}^{p+1}\mathrm{Re}\left\{\mathrm{e}^{-2\pi\mathrm{i}t}\,\mathrm{i}^{j-1}\sin\left(\frac{\pi j}{p+2}\right)\right\}V_{k+j-1}(\cos\theta).\end{aligned}\right\} \tag{2.21}$$

The normalization factor $N_\pm$ should be chosen so that the maximum deformation of the sphere is ϵr_0.

Blake (1970) computes the efficiencies of some particular swimming motions with $k = 14$ and 19, $p = 3$, and $\epsilon = 0.05$. It is interesting to compare his results with our upper bound for η_0. The maximum value of η_0 that he obtains is 0.028. Equation (2.20), on the other hand, gives 0.097 as an upper bound for $p = 3$ and large k. In fact, for large p, one can do 53% better.

Thus, for optimal efficiency, one should take a stroke with large p and k and efficiency η_0 as in (2.20). There are two caveats to this conclusion. At finite minimum mode number k, we expect our bound to be modified by a term of order k^{-1}. So it is conceivable that strokes of efficiency greater than $6\pi^2\epsilon^2$ exist for some small value of k. Second, as p becomes large, the concentration of eigenvalues $2\sqrt{2}\cos(\pi j/(p+2))$ near the upper bound $2\sqrt{2}$ increases. So it is possible to form a great variety of strokes of *nearly* maximal efficiency, from superpositions of eigenvectors with eigenvalues λ near to $2\sqrt{2}$. Presumably, as p becomes large, factors due to the breakdown of the envelope model and corrections to Stokes' equation (2.1) will play a greater role in determining preferred strokes.

To close this section, we argue that only azimuthally symmetric deformations need be considered in determining optimal swimming strokes, at least for large minimum mode number k. Our argument relies on the result (equation (4.8) of Shapere & Wilczek 1989) for the translation of a sphere due to an *arbitrary* cycle of small deformations. Such deformations may be expanded in terms of vector spherical harmonics $\boldsymbol{Y}_{JLM}$; the full field strength tensor then has six indices J, L, M, J', L', and M'. Let us suppose, without loss of generality, that the translation due to one stroke is purely in the z-direction. Then, by inspection, it is seen that only the components of $F^{\mathrm{tr}}_{J,L,M,J',L',M'}$ with $M = M'$ contribute to the translational motion. Azimuthally symmetric deformations, with $M = M' = 0$, therefore decouple from non-symmetric deformations. Also, because $F_{J,L,M,J',L',M'}$ and the power matrix $P_{J,L,M,J',L',M'}$ have the same large-J behaviour as $F_{J,L,0,J',L',0}$ and $P_{J,L,0,J',L',0}$, it can do us no harm to restrict attention to the block of the matrix $P^{-1}F$ with $M = M' = 0$. This restriction has the merit of eliminating the possibility of rotational motion. A net rotation could only serve to decrease the efficiency, since the shortest distance between two points is a straight line, not a helix.

We have found the most efficient swimming strokes for a spherical organism in the limit of large wavenumber k. The question of whether more efficient strokes exist for finite k remains to be addressed. In the following section, we shall find a negative answer to the corresponding question for cylindrical swimmers.

3. Cylinders and the problem of efficiency

In a previous paper (Shapere & Wilczek 1989), we computed the net swimming velocities of a nearly circular cylinder due to an arbitrary infinitesimal deformation of its cross-section. It is natural to ask, as we did for the sphere, which swimming motions are the most efficient. However, the definition of efficiency that was used in the case of the sphere is inadequate for the cylinder. The reason for this, known as Stokes' paradox, is that it is impossible to drag an infinite cylinder rigidly through a fluid at zero Reynolds number, if we require the fluid to be stationary at infinite distances from the cylinder. To resolve the 'paradox', one may consider either a fluid with small non-zero Reynolds number Re or a cylinder of large finite length L. One then finds that the force per unit length needed to maintain a steady velocity approaches zero in either of the limits $Re \rightarrow 0$ or $L \rightarrow \infty$. (In fact (Landau & Lifshitz 1959), the required force is of order $-(\log Re)^{-1}$ or $(\log L)^{-1}$. For large L or small Re, the fluid flow is approximately uniform in a large volume around the cylinder; hence, the stresses on the cylinder, which depend on the derivatives of the flow field, become small.) In either limit, the efficiency of (2.7) always vanishes, and gives us no way of comparing different swimming motions.

A good definition of efficiency should embody the following attributes. The efficiency should be invariant under time rescalings, to ensure that it cannot be taken to infinity by, say, lengthening the period of a swimming stroke. It should also be invariant under rescaling of the radius r_0, for the same reason. Our alternative definition, given in (2.8), is indeed independent of rescalings of both T and r_0, as well as ϵ, and is furthermore automatically normalized to attain a maximum value of 1. Independence of ϵ is crucial in ensuring that the maximization over infinitesimal strokes in the denominator of (2.8) makes sense. As we shall see, the computation of η_1 is quite straightforward.

Before proceeding, we would like to compare η_1 to the efficiency defined by Blake (1971a) in the context of two-dimensional flows:

$$\eta_{\text{Blake}} = \frac{\bar{T}\bar{U}}{\bar{P}},$$

where $\bar{T}$ is an 'average characteristic thrusting force per unit area'. The problem here is that the total force exerted by the body is by assumption zero. So, in practice, one takes $\bar{T}$ to be a quantity made up of the characteristic scales appearing in the problem with appropriate dimensions, i.e. $\bar{T} \propto \mu\bar{U}/r_0$. In contrast to η_1, Blake's efficiency scales as ϵ^2 – greater efficiencies are automatically obtained for larger deformations. This discussion should serve to demonstrate that efficiency is a somewhat arbitrary concept. However, we believe that any sensible and suitably restricted notion of efficiency will lead to the same optimal strokes. This is indeed the case with η_1 and η_{Blake} (for fixed ϵ).

Let us consider infinitesimal deformations of the cross-section of a cylinder in a fluid at low Reynolds number. Because the boundary conditions for Stokes' equations are

z-independent, the resulting fluid flow will also have this property. We can exploit the two-dimensionality of the problem by using the complex coordinate $z = x+\mathrm{i}y$. Then Stokes' equations (2.1) may be written

$$2\frac{\partial^2 v}{\partial z\,\partial\bar{z}} = \frac{\partial p}{\partial \bar{z}}, \qquad \frac{\partial v}{\partial z}+\frac{\partial \bar{v}}{\partial \bar{z}} = 0. \tag{3.1}$$

The general solution to these equations which does not blow up at infinity can be expressed in terms of two analytic functions

$$\phi_1(z) = \sum_{k<0} a_k\, z^{k+1} \tag{3.2}$$

and

$$\phi_2(z) = \sum_{k<-1} b_k\, z^{k+1} \tag{3.3}$$

as

$$\left.\begin{aligned} v(z) &= \phi_1(z) - z\overline{\phi_1'(z)} + \overline{\phi_2(z)},\\ p(z) &= 2(\phi_1' + \overline{\phi_1'}). \end{aligned}\right\} \tag{3.4}$$

Now consider a cyclic sequence of deformations of a circular cylinder with radius $r_0 = 1$:

$$\zeta(\sigma,t) = \sigma + \epsilon \sum_{k \neq -1} \alpha_k(t)\,\sigma^{k+1}, \tag{3.5}$$

where $\sigma \equiv \mathrm{e}^{\mathrm{i}\theta}$ parameterizes the unit circle. The velocity field on the surface of the cylinder at time t is then

$$\begin{aligned} v(\zeta(\sigma,t)) &= \epsilon \sum_{k\neq -1} \dot{\alpha}_k(t)\,\sigma^{k+1}\\ &= \phi_1(\zeta(\sigma,t)) - \zeta(\sigma,t)\,\overline{\phi_1'(\zeta(\sigma,t))} + \overline{\phi_2(\zeta(\sigma,t))}. \end{aligned} \tag{3.6}$$

In the case of a circular cylinder, with $\zeta(\sigma) = \sigma$, it is easy to solve for the resulting fluid velocity by equating Fourier coefficients on both sides of (3.6). The result is

$$\left.\begin{aligned} \phi_1(z) &= \sum_{k<0} \dot{\alpha}_k\, z^{k+1},\\ \phi_2(z) &= \sum_{k<0} \dot{\bar{\alpha}}_{-k}\, z^{k-1} + (k+1)\,\dot{\alpha}_k\, z^{k-1}, \end{aligned}\right\} \tag{3.7}$$

with $v(z)$ given as in (3.4).

The power expenditure per unit length at time t is

$$\mathscr{P} = \int_0^{2\pi} v_i\,\sigma_{ij}\,r_j\,\mathrm{d}\theta. \tag{3.8}$$

By making use of (3.1), this may be recast in complex notation as

$$\left.\begin{aligned} \mathscr{P} &= \mathrm{Re}\left[\mathrm{i}\int_0^{2\pi}\left[-pv + 2\mu\bar{v}\frac{\partial v}{\partial \bar{z}}\right]\mathrm{d}\bar{z}\right]\\ &= \mu\,\mathrm{Re}\left[\mathrm{i}\int [2v(\phi_1' + \overline{\phi_1'}) + 2\bar{v}(-z\overline{\phi_1''} + \overline{\phi_2'})]\,\mathrm{d}\bar{z}\right]. \end{aligned}\right\} \tag{3.9}$$

In computing $\mathscr{P}$, we may assume that the cylinder is circular. This is because any corrections due to the deformation of the cross-section will be smaller than the leading (undeformed) term by a factor of ϵ. Inserting the solution for a circular cylinder (3.7) into (3.9) now gives

$$\bar{\mathscr{P}} = 2\pi\mu\epsilon^2 \sum_n |n+1||\dot{\alpha}_n|^2. \tag{3.10}$$

We also need to know the average net velocity of the cylinder over one swimming cycle. This was evaluated in Shapere & Wilczek (1989), and we simply restate the result here:

$$\bar{U} = \epsilon^2 \frac{1}{T}\int_0^T \mathrm{d}t \sum_{m,n} [F_{mn}\alpha_m\dot{\alpha}_n + F_{m\bar{n}}\alpha_m\dot{\bar{\alpha}}_n + F_{\bar{m}n}\bar{\alpha}_m\dot{\alpha}_n + F_{\bar{m}\bar{n}}\bar{\alpha}_m\dot{\bar{\alpha}}_n], \tag{3.11}$$

where

$$\left.\begin{aligned} F_{mn} &= [-(n+1)\,\theta_{-n} + (m+1)\,\theta_{-m}]\,\delta_{m+n,-1}, \\ F_{m\bar{n}} &= [(n+1)\,\theta_{-n} - (m+1)\,\theta_m]\,\delta_{m-n,1}, \\ F_{\bar{m}n} &= [(n+1)\,\theta_n - (m+1)\,\theta_{-m}]\,\delta_{m-n,-1}, \\ F_{\bar{m}\bar{n}} &= [(n+1)\,\theta_{-n} - (m+1)\,\theta_{-m}]\,\delta_{m+n,1}. \end{aligned}\right\} \tag{3.12}$$

As usual, θ_n is 1 for non-negative n and zero for negative n.

Portions of the results (3.10) and (3.12), corresponding to axially symmetric deformations, have been obtained by Blake (1971*a*).

We may now compute the efficiency η_1, by the same variational method used in §2. Again, we obtain a system of linear equations of the form

$$P^{-1}F\dot{\alpha} - \frac{N}{D}\ddot{\alpha} = 0 \tag{3.13}$$

which may be solved to yield

$$\eta_1 = \frac{N/D}{(N/D)_{\max}} \tag{3.14}$$

in terms of the eigenvalues of the matrix $P^{-1}F$. As before, if

$$V = (\alpha_{-k}, \ldots, \alpha_{-k-p}, \alpha_k, \ldots, \alpha_{k+p}) \tag{3.15}$$

is an eigenvector of $P^{-1}F$ with eigenvalue λ, then $\mathrm{Re}\,[\mathrm{e}^{-2\pi i t}V]$ is a swimming stroke of extremal efficiency.

We now restrict attention to swimming motions which are symmetric about the x-axis, i.e. for which all α_n are real. An argument similar to the one given at the end of §2 for restriction to azimuthally symmetric deformations applies. Suppose that the net translation due to one cycle is in the x-direction, i.e. that $\bar{U}$ is real. Then taking the real part of (3.11), we see that the real and imaginary parts of the α_n decouple, in both $\bar{U}$ and $\bar{\mathscr{P}}$. Hence we lose no efficiency in considering only real α_n. In this case,

$$\begin{aligned}(P^{-1}F)_{mn} &= P^{-1}_{mm}(F_{mn} + F_{m\bar{n}} + F_{\bar{m}n} + F_{\bar{m}\bar{n}}) \\ &= \left(-\frac{m+2}{m+1}\delta_{m,n-1} + \delta_{m,n+1} - \delta_{m,-n-1} + \delta_{m,-n+1}\right)\theta_{-m} \\ &\quad + \left(-\frac{m-2}{m+1}\delta_{m,-n+1} + \frac{m}{m+1}\delta_{m,-n-1} + \frac{m}{m+1}\delta_{m,n+1} - \delta_{m,n-1}\right)\theta_m. \end{aligned} \tag{3.16}$$

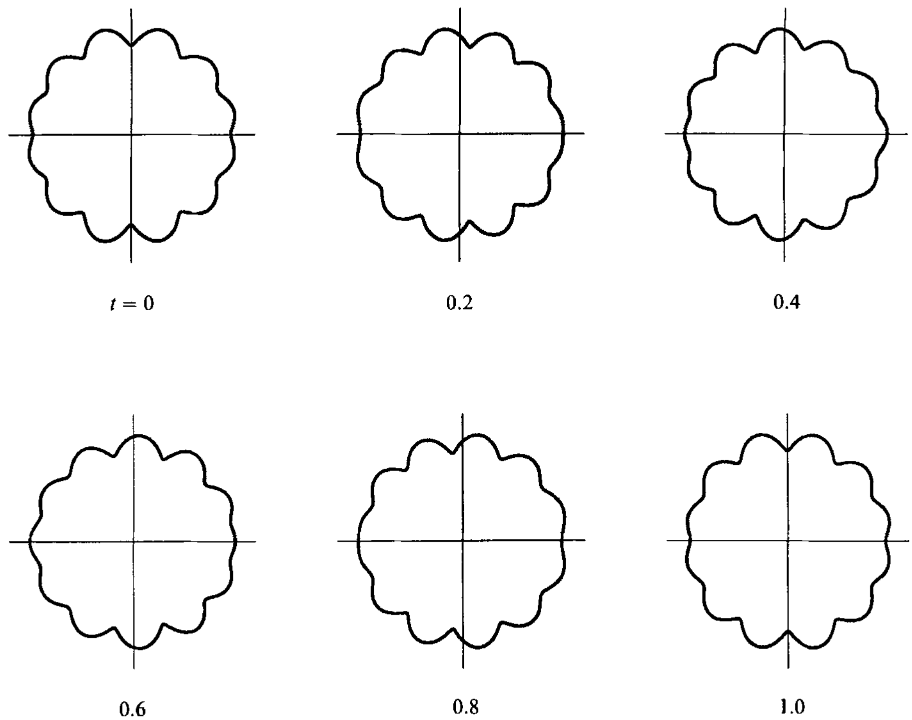

FIGURE 1. One cycle of a swimming stroke composed of small deformations of the cross-section of a circular cylinder. The stroke is a maximally efficient coupling of modes $\pm 10, \ldots, \pm 13$. Waves move from left to right along the top and bottom of the cross-section, leading to a net motion to the left of 0.009 per cycle (not shown), in units of the average radius. The efficiency is 0.81.

In the limit of large k, we find a surprise: the limiting matrix is identical to the matrix A found for the swimming sphere, so our work is already done. Thus, the efficiency of an optimal stroke is, for large k,

$$\eta_1 = \cos \frac{\pi}{p+2}. \tag{3.17}$$

Furthermore, it can be shown that the eigenvalues of the *exact* matrix are always less than the bound of (3.17), for any finite value of k. The proof is sketched at the end of the Appendix.

The two solutions with maximum λ are

$$\zeta_{\pm}(\sigma, t) = \sigma + \epsilon N_{\pm}(1 \pm \surd 2) \sum_{j=1}^{p+1} \mathrm{Re}\left\{ \mathrm{e}^{\mp 2\pi \mathrm{i} t} (\pm \mathrm{i})^{j-1} \sin\left(\frac{\pi j}{p+2}\right)\right\} \mathrm{e}^{\mathrm{i}(j+k)\theta}$$

$$+ \epsilon N_{\pm} \sum_{j=1}^{p+1} \mathrm{Re}\left\{ \mathrm{e}^{\mp 2\pi \mathrm{i} t} \sum_{j=1}^{p+1} (\pm i)^{j-1} \sin\left(\frac{\pi j}{p+2}\right)\right\} \mathrm{e}^{-\mathrm{i}(j+k-2)\theta}. \tag{3.18}$$

The solution ζ_- is self-intersecting, for any finite value of ϵ and large enough p. Peculiarly, the waves described by ζ_- (in the regime where the solution is not self-intersecting) propagate in the same direction as the body. Pictures of the swimming motions ζ_+ with $k = 10$, $\epsilon = 0.1$, and $p = 3$, 9, and 15 are given in figures 1 and 2. Figure 1, for $p = 3$, should be read from left to right, top to bottom. The efficiencies of the three strokes, according to (3.17), are approximately 0.81 ($p = 3$), 0.94

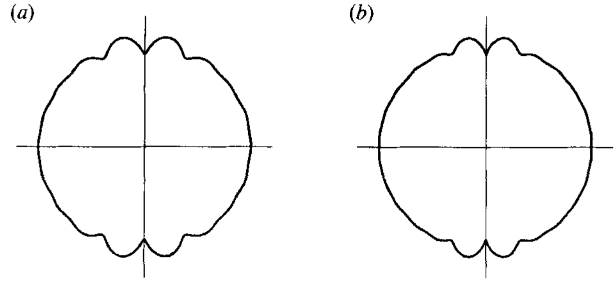

FIGURE 2. One frame of each of two maximally efficient strokes, coupling modes $\pm 10, \ldots, \pm 19$ (a) and $\pm 10, \ldots, \pm 25$ (b). The net translations per cycle are 0.0051 and 0.0039 units, and the efficiencies are 0.94 and 0.98, respectively. As the number of coupled modes increases, the wave becomes more and more localized at the midpoint.

($p = 9$), and 0.98 ($p = 15$), and the net translations per cycle are respectively $0.90\epsilon^2$, $0.51\epsilon^2$, and $0.39\epsilon^2$ units to the left. Note that, as the number of coupled modes $p+1$ (and thus the efficiency) increases, the waveform becomes more and more localized near the middle $\theta = \pm\frac{1}{2}\pi$ of the swimming shape. In all cases, the waveforms progress to the right, and the net translation is to the left. The waves begin at the front end of the body (relative to the direction of motion) and disappear at the rear, attaining a maximum amplitude near the middle. These characteristics are consistent with the observed metachronal beating patterns of ciliated organisms such as *Paramecia* (Childress 1978).

4. Conclusions

We have found maximally efficient swimming motions for spheres (in the short-wavelength limit) and for circular cylinders (in general), at Reynolds number zero. In both cases, the efficiencies were maximized by short-wavelength swimming strokes symmetric about the axis of propulsion. The waves propagate between the front and rear of the body (relative to the direction of motion), achieving a maximum amplitude near the middle.

Remarkably, in the limit of large mode number k, our calculations for the sphere and the cylinder were identical. We believe that this represents more than an artifact of our choices of mode expansions, and points to a more general property of low-Reynolds-number swimming motions. The fact that the fluid flow due to the kth mode of oscillation dies off like r^{-k} suggests that, as the wavelength of a swimming motion becomes short relative to the scale of curvature of the average shape, all effects due to the average shape of the swimmer disappear. If this conjecture is true, a reasonable approximation might be to treat the surface of the organism locally like an infinite plane sheet (see, for example, Childress 1978). Of course, the validity of this approximation for envelope-model calculations will break down as the wavelength becomes comparable with the spacing of individual cilia. But at least for wavelengths of several ciliary spacings, this approximation may be useful in determining optimal infinitesimal swimming motions of arbitrary shapes. As we have seen, this is the relevant limit for maximally efficient swimming of spheres and cylinders.

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Appendix

To compute the eigenvectors and eigenvalues of the matrix A, defined in (2.17) as the large-k limit of $P^{-1}F$, we consider first a simpler matrix with $p+1$ rows and columns

$$B = \begin{pmatrix} 0 & 1 & & & & \\ -1 & 0 & 1 & & & \\ & -1 & & & & \\ & & & \ddots & & \\ & & & & & 1 \\ & & & & -1 & 0 \end{pmatrix}, \tag{A 1}$$

in terms of which

$$A = \begin{pmatrix} B & B \\ B & -B \end{pmatrix}. \tag{A 2}$$

As an ansatz for an eigenvector of B, take

$$V = (z, z^2, \ldots, z^{p+1})^{\mathrm{T}}. \tag{A 3}$$

Substitution of this V into the eigenvalue equation $BV = \lambda V$ leads to the equations (for $1 \leqslant j \leqslant p-1$)

$$-z^{j-1} + z^{j+1} = \mathrm{i}\lambda z^j, \tag{A 4}$$

from which we deduce

$$z_{\pm} = \frac{\mathrm{i}\lambda \pm (4-\lambda^2)^{\frac{1}{2}}}{2} = \mathrm{i}e^{\mp i\theta}, \tag{A 5}$$

where $\lambda \equiv 2\cos\theta$. So we must consider a solution of the form

$$V_B = c_- V(z_-) + c_+ V(z_+). \tag{A 6}$$

The coefficients are fixed by the first and last components of the eigenvalue equation (which we ignored in (A 4)), namely

$$\left.\begin{aligned} c_- z_-^2 + c_+ z_+^2 &= \mathrm{i}\lambda(c_- z_- + c_+ z_+) \\ -c_- z_-^p - c_+ z_+^p &= \mathrm{i}\lambda(c_- z_-^{p+1} + c_+ z_+^{p+1}). \end{aligned}\right\} \tag{A 7}$$

The first equation implies that $c_- + c_+ = 0$, and the second gives

$$\left(\frac{z_-}{z_+}\right)^{p+2} = \mathrm{e}^{2(p+2)\mathrm{i}\theta} = 1. \tag{A 8}$$

Choosing

$$\theta = \frac{\pi j}{p+2} \tag{A 9}$$

we find

$$V_B = (\sin\theta, \mathrm{i}\sin 2\theta, \ldots, \mathrm{i}^p \sin(p+1)\theta)^{\mathrm{T}} \tag{A 10}$$

with corresponding eigenvalue

$$\lambda_B = 2\cos\left(\frac{\pi j}{p+2}\right) \quad \text{for } j = 1, \ldots, p+1. \tag{A 11}$$

For a given p, the maximum possible value of $|\lambda_B|$ is $2\cos(\pi/p+2)$, which approaches 2 as p grows large.

Now we return to the diagonalization of the big matrix A. It is easy to see that the $2p+2$ eigenvectors of A may be written in terms of the $p+1$ eigenvectors of B:

$$V_A = \begin{pmatrix} (1 \pm \surd 2)\, V_B \\ V_B \end{pmatrix} \tag{A 12}$$

with eigenvalues

$$\lambda_A = \pm 2\surd 2 \cos\left(\frac{\pi j}{p+2}\right). \tag{A 13}$$

The solutions of (2.14) and (3.13) for large minimum mode number k are now obtained by inserting V_A into (2.18).

Thus far, we have been considering solutions of (3.13) in the large-k limit. We would like to know if there exists, for some finite k, a solution with greater efficiency, that is, an eigenvector V of the *exact* matrix $P^{-1}F$ (as opposed to the limiting matrix A) with eigenvalue of modulus greater than $2\surd 2$. Here we shall sketch a proof that, at least for the circular cylinder, no such solution exists. Our principal tool will be a theorem, due to Gershgorin (Goult *et al.* 1974), which puts bounds on the eigenvalues of a complex matrix.

THEOREM *For each eigenvalue λ of the matrix $A = (a_{ij})$, there is an i such that*

$$|\lambda - a_{ii}| \leqslant \sum_{j \neq i} |a_{ij}| \tag{A 14}$$

and

$$|\lambda - a_{ii}| \leqslant \sum_{j \neq i} |a_{ji}| \tag{A 15}$$

Proof Let x_i be the component of the eigenvector x with the greatest modulus. The ith component of the eigenvalue equation is

$$\sum_{j=1}^{n} a_{ij} x_j = \lambda x_i. \tag{A 16}$$

Reordering and taking absolute values gives

$$|(\lambda - a_{ii})\, x_i| = |\sum_{j \neq i} a_{ij} x_j| \leqslant \sum_{j \neq i} |a_{ij}|\,|x_j| \tag{A 17}$$

and hence

$$|\lambda - a_{ii}| \leqslant \sum_{j \neq i} \frac{|x_j|}{|x_i|} |a_{ij}| \leqslant \sum_{j \neq i} |a_{ij}|. \tag{A 18}$$

The second inequality (A 15) is proved similarly.

Note that Gershgorin's theorem gives a good bound of 2 on the absolute values of the eigenvalues of the matrix B. For the matrix $P^{-1}F$ of (2.14), we get a bound of about 4, which is greater than the desired upper bound of $2\surd 2$. However, a better bound can be obtained by applying the same similarity transformation used to bring

A into skew-diagonal form, to $P^{-1}F$. Applying the inequalities (A 17) and (A 18) to the first $p+1$ rows and the last $p+1$ columns of the transformed matrix shows that all eigenvalues of $P^{-1}F$ are less than $2\sqrt{2}$.

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