

## A spherical envelope approach to ciliary propulsion

By J. R. BLAKE

Department of Applied Mathematics and Theoretical Physics, University of Cambridge

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In this paper, an attempt has been made to model the dynamics of ciliary propulsion through the concept of an ‘envelope’ covering the ends of the numerous cilia of the microscopic organism. This approximation may be made in the case when the cilia are close together, as can occur in the case of the symplectic metachronal wave (i.e. the wave travels in the same direction as the effective beat). For simplicity, a spherical model has been chosen, and the analysis which follows is a correction to Lighthill’s (1952) paper on squirming motions of a nearly spherical organism. The velocity and efficiency compared to the work done in pushing an inert organism are obtained, and compared to that of a ciliated organism.

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### 1. Introduction

The ‘mechanics of ciliary propulsion’ has barely been touched upon from the mathematical point of view, and only passing comment that an approach would be desirable has been made. Gray (1928) in his book said, “little is known of the forces which surround very small elongated structures when they are moving through water at very low speeds”. Although numerous calculations have been made for the case of the single flagellum, little material has appeared for the case of high concentrations of cilia on the surface of a flat or elongated organism, so even today Gray’s comments remain remarkably true. Similar comments to this were also made by Lighthill (1969).

In 1675, the Dutch microscopist Leeuwenhoek was perhaps the first person to view and record the movements of cilia. In a letter to the Royal Society, he described the incredibly thin feet or little legs by which a small animal can propel itself through water. Muller, in 1876, appears to have been the first person to use the name ‘cilia’.

The following analysis is only concerned with the hydrodynamical interactions and nothing is said about the neuroid and/or electrical co-ordination of the ciliated organism. The main advantages of ciliation is that the body may perform work on the fluid without undergoing drastic changes in shape which in turn require impractical amounts of straining of its tissue. Ciliary propulsion is suited to small organisms which are either elongated or flat, so that the ‘rowing type’ beat will be more effective in these situations.

In this paper, the mechanics of this method of propulsion are studied with a mathematical model involving an ‘envelope’ (i.e. an instantaneous surface covering the ends of the numerous undulating cilia, see figure 1) over the surface

of the organism. Thus we are replacing the individuality of the cilia by a progressive waving envelope. The no-slip condition is applied at the surface of the waving envelope. This approach is perhaps valid for the case of the symplectic metachronal wave (i.e. when the direction of beat and wave transmission are in the same direction). In this case, any cilium is in phase in a transverse line, but at different stages of the beat in the longitudinal direction, so that an axisymmetric flow about a symmetric organism may be considered.

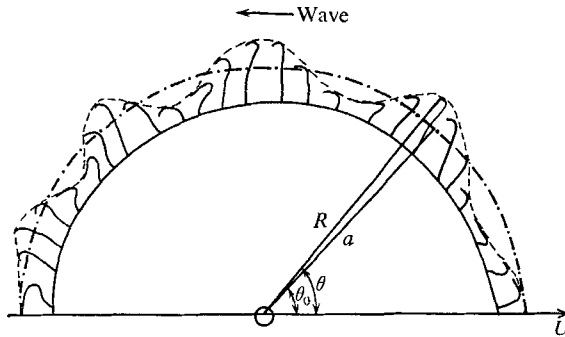


FIGURE 1(a). The arrow represents the direction of metachronal wave. - - - -, the instantaneous surface over the organism; · · · · ·, the surface  $r = a$  in analysis; —, the actual surface of the organism. The upper hemisphere has only been included as the flow is axisymmetric.

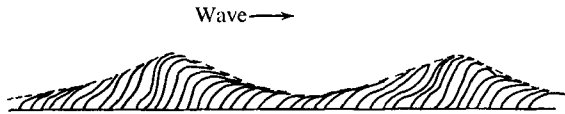


FIGURE 1(b). - - - -, envelope over metachronal wave of *Opalina*; →, direction of metachronal wave (Sleigh 1962).

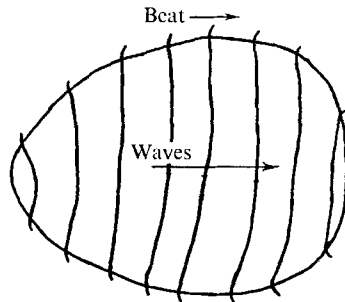


FIGURE 1(c). View from above of *Opalina* to show symplectic metachronal wave patterns (Sleigh 1962).

In order to make it possible to calculate the mechanical properties of the model in reasonably simple terms, it has proved convenient to take the organism to be spherical. One organism that has been studied in detail and exhibits symplectic metachronism is *Opalina* (Sleigh 1962), which is an oval-shaped flat-disk organism. Figures 1(b) and (c) show the metachronism of *Opalina* viewed from the side and above respectively. Considering the problem of a sphere is highly idealizing the

shape of the organism, but at low Reynolds number the shape does not alter the hydrodynamical features very greatly. When the cilia are densely packed the shape will affect the metachronism, as we would expect them to co-ordinate more easily in a flattened or elongated position. Another reason for the flat or elongated shape is that the surface area to volume ratio is high, which in turn implies a large number of cilia to propel the organism (e.g. *Opalina*). An alternative model of a relatively tractable kind is an infinite waving plate such as Taylor (1951) studied, but uncertainty about how far the finiteness of the body shape may influence the mechanics induced the author to investigate the simplest body of finite extent, namely the sphere. In any case, the biological world provides much variety so the following problem may closely model some organism!

## 2. Equations of motion

The analysis in this section will closely follow that of Lighthill's (1952) paper on squirming motions of spherical organisms. This paper, however, will include corrections to his work, which result from the omission of two series terms in his solutions for the velocities. The mean shape of the organism is taken as a sphere of radius  $a$ . Incompressible axisymmetric flow around the sphere will be considered, so that equations of motion for the velocity  $\mathbf{q}$  and pressure  $p$  at low Reynolds number are

$$\nabla \cdot \mathbf{q} = 0, \quad \nabla p = \mu \nabla^2 \mathbf{q}, \tag{1}$$

where  $\mu$  is the viscosity. In spherical polar co-ordinates the solution in terms of radial and azimuthal velocities  $u$  and  $v$  is,

$$u = -U \cos \theta_0 + A_0 \frac{a^2}{r^2} P_0 + \frac{2}{3}(A_1 + B_1) \frac{a^3}{r^3} P_1 + \sum_{n=2}^{\infty} \left[ \left( \frac{1}{2}n \frac{a^n}{r^n} - \left(\frac{1}{2}n - 1\right) \frac{a^{n+2}}{r^{n+2}} \right) A_n P_n + \left( \frac{a^{n+2}}{r^{n+2}} - \frac{a^n}{r^n} \right) B_n P_n \right], \tag{2}$$

$$v = U \sin \theta_0 + \frac{1}{3}(A_1 + B_1) \frac{a^3}{r^3} V_1 + \sum_{n=2}^{\infty} \left[ \left( \frac{1}{2}n \frac{a^{n+2}}{r^{n+2}} - \left(\frac{1}{2}n - 1\right) \frac{a^n}{r^n} \right) B_n V_n + \frac{1}{2}n \left(\frac{1}{2}n - 1\right) \left( \frac{a^n}{r^n} - \frac{a^{n+2}}{r^{n+2}} \right) A_n V_n \right], \tag{3}$$

where values on the surface of the sphere  $r = a$  are

$$(u)_{r=a} = \sum_{n=0}^{\infty} A_n(t) P_n(\cos \theta_0), \quad (v)_{r=a} = \sum_{n=1}^{\infty} B_n(t) V_n(\cos \theta_0). \tag{4}$$

$V_n$  is defined as

$$V_n = \frac{2}{n(n+1)} \sin \theta_0 P'_n(\cos \theta_0) = \frac{-2}{n(n+1)} P_n^1(\cos \theta_0), \tag{5}$$

$P_n^1$  being an associated Legendre function of the first kind. In the solution for  $u$  and  $v$  we have taken an origin moving relative to the fluid with velocity

$$U = \frac{1}{3}(2B_1 - A_1) \tag{6}$$

as is necessary so that the motion has finite total energy; this condition also requires us to omit the Stokeslet term in the solution for the velocities. This solution can also be derived from the stream-function equation (see Happel & Brenner 1965, (4.23)). In the above solutions for  $u$  and  $v$  ((2) and (3) respectively), the last term in each was absent from Lighthill's solution.

From the equations of motion (1) the pressure

$$p = \mu \sum_{n=2}^{\infty} \frac{2n-1}{n+1} (nA_n - 2B_n) \frac{a^n}{r^{n+1}} P_n(\cos \theta_0) \quad (7)$$

can be obtained.

The radial and tangential stresses exerted on the fluid by the cilia are given by,

$$\left. \begin{aligned} \sigma_{rr} &= p - 2\mu \partial u / \partial r, \\ \sigma_{r\theta} &= -\mu \left[ r \frac{\partial}{\partial r} \left( \frac{v}{r} \right) + \frac{1}{r} \frac{\partial u}{\partial \theta_0} \right], \end{aligned} \right\} \quad (8)$$

which can be obtained by substitution from (2), (3) and (7). The rate of working  $P$  on the surface of the sphere is obtained by the integral

$$\begin{aligned} P &= 2\pi \int_0^\pi (u\sigma_{rr} + v\sigma_{r\theta})_{r=a} a^2 \sin \theta_0 d\theta_0 \\ &= 2\pi\mu a \left( [8A_0^2 + \frac{8}{3}A_1^2 + \frac{8}{3}B_1^2 + \frac{16}{3}A_1B_1] \right. \\ &\quad \left. + \sum_{n=2}^{\infty} \left[ \frac{4n^2 + 6n + 8}{(2n+1)(n+1)} A_n^2 + \frac{8}{n(n+1)} B_n^2 + \frac{24}{(n+1)(2n+1)} A_n B_n \right] \right) \quad (9) \end{aligned}$$

and the hydrodynamical efficiency may be found by taking the well-known Stokes formula for drag of a sphere, multiplying by the mean velocity and dividing by the mean rate of working,

$$\eta = 6\pi\mu a \bar{U}^2 / \bar{P}. \quad (10)$$

### 3. Surface conditions

In the previous section the problem for a sphere with given velocity components at the surface was solved. We now apply this solution to the problem of the waving motion of a deformable spherical envelope.

As a cilium obviously has both normal and tangential movements, we define the surface of the envelope by considering an oscillating surface on a sphere in the form

$$R = a \left[ 1 + \epsilon \sum_{n=2}^N \alpha_n(t) P_n(\cos \theta_0) \right], \quad \theta = \theta_0 + \epsilon \sum_{n=1}^N \beta_n(t) V_n(\cos \theta_0), \quad (11)$$

where  $\epsilon$  is suitably small of

$$O\left(\frac{1}{N}\right) \quad \text{and} \quad \left| \sum_{n=2}^N \alpha_n P_n \right| \quad \text{and} \quad \left| \sum_{n=1}^N \beta_n V_n \right|$$

are order 1 in  $(0, \pi)$ . We have taken a finite valued  $N$  to ensure convergence on expansion in a Taylor series about  $(a, \theta_0)$ . Thus we have a small perturbation to the sphere  $r = a$  and  $\alpha_n(t)$  and  $\beta_n(t)$  are oscillatory functions of time. Here,  $\alpha_0$  is taken identically equal to zero as this represents surface swellings of the

organism (source-like), while  $\alpha_1 = 0$  since this mode represents oscillations about the centroid of the organism. It should also be pointed out that another necessary condition is that  $d\theta/d\theta_0 > 0$ , which allows a one-to-one relation between  $\theta$  and  $\theta_0$ .

We envisage being able to get each labelled co-ordinate  $(a, \theta_0)$  (a Lagrangian type of formulation for the envelope) to trace out the path of a tip of a cilium. Sleight (1968) has obtained numerous data on the movement of cilia on ciné films taken at 60–400 frames/sec. The movement of their tips may be matched onto the above problem and thus velocities of propulsion can be compared to experimental results. The velocities in the radial and azimuthal directions at the envelope surface due to the no slip condition are,

$$\left. \begin{aligned} u(R, \theta) &= \dot{R} = a\epsilon \sum_{n=2}^N \dot{\alpha}_n P_n, \\ v(R, \theta) &= R\dot{\theta} = a\epsilon \left( 1 + \epsilon \sum_{n=2}^N \dot{\alpha}_n P_n \right) \sum_{n=1}^N \dot{\beta}_n V_n. \end{aligned} \right\} \quad (12)$$

If we expand  $\mathbf{q}(R, \theta)$  in a Taylor series expansion about  $(a, \theta_0)$  and if  $\alpha_n$  and  $\beta_n$  are proportional to either  $\cos \sigma t$  or  $\sin \sigma t$ , we obtain a first-order harmonic term in time, a 'd.c.' second-order term and other second-order and higher harmonic terms.

$$\mathbf{q}(R, \theta) = \mathbf{q}(a, \theta_0) + (R - a) (\partial \mathbf{q} / \partial r)_{r=a} + (\theta - \theta_0) (\partial \mathbf{q} / \partial \theta_0)_{r=a} + \text{higher order terms.} \quad (13)$$

The surface coefficients  $A_n(t)$  and  $B_n(t)$  are attained from the  $\mathbf{q}(a, \theta_0)$  term on the right-hand side of (13). From (13) the first-order approximation can be obtained,  $A_n = A_n^{(1)} = a\epsilon \dot{\alpha}_n$ ;  $B_n = B_n^{(1)} = a\epsilon \dot{\beta}_n$  ( $n = 1, 2, \dots, N$ ).

For all other  $n$ ,  $A_n^{(1)} = B_n^{(1)} = 0$ . This first approximation can be substituted into all the previous equations in § 2. It is noted that if we take the mean with respect to time, the net stresses and velocity of propulsion are identically equal to zero because they are linear in  $\dot{\alpha}_n$  and  $\dot{\beta}_n$  (i.e. to the first approximation there is no motion). This is not unexpected as in results for swimming sheets (Taylor 1951) it is necessary to go to the second approximation to obtain propulsion.

If we substitute the first-order approximation into the derivatives of  $\mathbf{q}$  on the right-hand side of (13) we can then find the second-order effects in  $\mathbf{q}(a, \theta_0)$ , i.e. to the second approximation,

$$u(a, \theta_0) = a \left[ \epsilon \sum_{n=2}^N \dot{\alpha}_n P_n + \epsilon^2 \left\{ \sum_{n=2}^N \alpha_n P_n \left( 2\dot{\beta}_1 P_1 + \sum_{n=2}^N 2(\dot{\alpha}_n + \dot{\beta}_n) P_n \right) - \sum_{n=1}^N \beta_n V_n \sum_{n=2}^N \dot{\alpha}_n dP_n/d\theta_0 \right\} \right], \quad (14)$$

$$v(a, \theta_0) = a \left[ \epsilon \sum_{n=1}^N \dot{\beta}_n V_n + \epsilon^2 \left\{ \sum_{n=2}^N \alpha_n P_n \left( 2\dot{\beta}_1 V_1 + \sum_{n=2}^N ((2n+1)\dot{\beta}_n - n(\frac{1}{2}n-1)\dot{\alpha}_n) V_n \right) - \sum_{n=1}^N \beta_n V_n \sum_{n=1}^N \dot{\beta}_n dV_n/d\theta_0 \right\} \right]. \quad (15)$$

Therefore the second approximations for  $A_n$  and  $B_n$  are,

$$\left. \begin{aligned} A_n^{(2)} &= \frac{1}{2}(2n+1) \int_0^\pi u(a, \theta_0) P_n(\cos \theta_0) \sin \theta_0 d\theta_0, \\ B_n^{(2)} &= \frac{1}{8}n(n+1)(2n+1) \int_0^\pi v(a, \theta_0) V_n \sin \theta_0 d\theta_0, \end{aligned} \right\} \quad (16)$$

or on integrating by parts,

$$B_n^{(2)} = \frac{1}{4}(2n+1) \int_0^\pi (dv/d\theta_0 + \cot \theta_0 v) P_n \sin \theta_0 d\theta_0. \quad (17)$$

From this it is noticed that,

$$A_n^{(2)} = A_n^{(1)} + O(\epsilon^2 f_1), \quad B_n^{(2)} = B_n^{(1)} + O(\epsilon^2 f_2),$$

where  $f_1$  and  $f_2$  are functions of  $\alpha_n, \dot{\alpha}_n, \beta_n, \dot{\beta}_n$  and  $N$ . Lighthill evaluated both  $A_1^{(2)}$  and  $B_1^{(2)}$  to obtain the velocity of propulsion, which in corrected form is as follows,

$$\begin{aligned} U = a \left[ \frac{2}{3}\epsilon\dot{\beta}_1 - \epsilon^2 \left\{ \frac{8}{15}\alpha_2\dot{\beta}_1 + \frac{2}{5}\dot{\alpha}_2\beta_1 \right. \right. \\ - \sum_{n=2}^{N-1} \frac{(2n+4)\alpha_n\dot{\beta}_{n+1} - 2n\dot{\alpha}_n\beta_{n+1} - (6n+4)\alpha_{n+1}\dot{\beta}_n - (2n+4)\dot{\alpha}_{n+1}\beta_n}{(2n+1)(2n+3)} \\ - \sum_{n=1}^{N-1} \frac{4(n+2)\beta_n\dot{\beta}_{n+1} - 4n\dot{\beta}_n\beta_{n+1}}{(n+1)(2n+1)(2n+3)} \\ \left. \left. + \sum_{n=2}^{N-1} \frac{(n+1)^2\alpha_n\dot{\alpha}_{n+1} - (n^2-4n-2)\alpha_{n+1}\dot{\alpha}_n}{(2n+1)(2n+3)} \right\} \right]. \quad (18) \end{aligned}$$

For evaluation of  $A_n^{(2)}$  ( $n > 1$ ) the integral of  $P_n P_l P_m$  and  $P_n V_l dP_m/d\theta$  and for  $B_n^{(2)}$  ( $n > 1$ ),  $V_n V_l P_m$  and  $V_n (dV_l/d\theta) V_m$  must be considered. To do this the formulae derived by Gaunt (1929) may be of some use, but the algebraic manipulation is very complicated, so no attempt will be made to continue further in this direction.

#### 4. Metachronal wave

When cilia occur all over the body it is necessary that they should be organized to beat in some regular manner. This is called the metachronal wave and appears as a wave passing over the surface of the organism. Sleight (1968) and Holwill & Sleight (1969) have analyzed the movements of various types of cilia, and have also used a model to derive the work done by a single cilium (*Sabellaria*).

Theoretically it is possible to model the metachronal wave by a travelling wave over the surface of the form  $\cos(ka\theta - \sigma t)$  and  $\sin(ka\theta - \sigma t)$ , but they both possess infinite series expansions in terms of  $P_n$  and  $V_n$ , so the possibility of predicting velocities and efficiencies would be extremely limited, as we then obtain an infinite number of terms in the series solution for velocity and rate of working. However, we can approximately model the metachronal wave by considering modes  $\alpha_n, \alpha_{n+1}, \beta_n$  and  $\beta_{n+1}$ , remembering that  $P_n, P_{n+1}, V_n$  and  $V_{n+1}$  are oscillating functions on the interval  $(0, \pi)$  and that  $P_n$  and  $P_{n+1}$  (and also  $V_n$  and  $V_{n+1}$ ) are about a quarter wavelength out of phase over most of the interior of the interval  $\theta_0 = 0$  to  $\pi$  (a necessity for a progressive wave). From the solution

for the velocity (18) we gain the erroneous impression that the propulsion for large  $n$  is dominated by the  $\alpha_n \alpha_{n+1}$  modes, but this is only a product of the analysis. As we would expect, there is an equal contribution from all four series: as  $|\Sigma \alpha_n P_n|$  and  $|\Sigma \beta_n V_n|$  are  $O(1)$ , we observe that  $|\beta_n|$  may be much larger than  $|\alpha_n|$ , due to the definition of  $V_n$  which is small in the interval  $(0, \pi)$  for large  $n$ , whereas  $|P_n|$  is 1 at  $\theta = 0$  and  $\pi$ . If we used the orthonormalized multiples of  $P_n$  and  $V_n$ , we would in fact see that each series can contribute an equal amount to the velocity of propulsion, for equivalent magnitude of  $\alpha_n^*$  and  $\beta_n^*$ , where  $\alpha_n = (\frac{1}{2}(2n+1))^{\frac{1}{2}} \alpha_n^*$  and  $\beta_n = (\frac{1}{8}n(n+1)(2n+1))^{\frac{1}{2}} \beta_n^*$ .

Let the surface of the organism, to represent the metachronal wave, be given by,

$$\left. \begin{aligned} R &= a[1 + \epsilon\{\cos \sigma t(a_{N-2}P_{N-2} + a_N P_N) + \sin \sigma t(a_{N-3}P_{N-3} + a_{N-1}P_{N-1})\}], \\ \theta &= \theta_0 + \epsilon\{\cos \sigma t(b_{N-2}V_{N-2} + b_N V_N) + \sin \sigma t(b_{N-3}V_{N-3} + b_{N-1}V_{N-1})\}. \end{aligned} \right\} \quad (19)$$

With this definition, we include two special cases; (i)  $a_{N-3} = a_N = b_{N-3} = b_N = 0$ ; (ii)  $R = a$  at  $\theta = 0, \pi$ ; all  $t$ . The distinction between the two is that in (i) the maximum radial amplitudes occur at/around the ends  $\theta = 0$  and  $\pi$ , whereas in (ii) they occur in the mid-section of the spherical organism. This second case is physically more reasonable (and mathematically also, because of the singular nature of the Legendre functions at  $\theta = 0$  and  $\pi$ ) that the maximum amplitudes should be near the 'middle' of the organism.

For this model of the wave, the mean with respect to time of the velocity (18) becomes ( $N > 5$ );

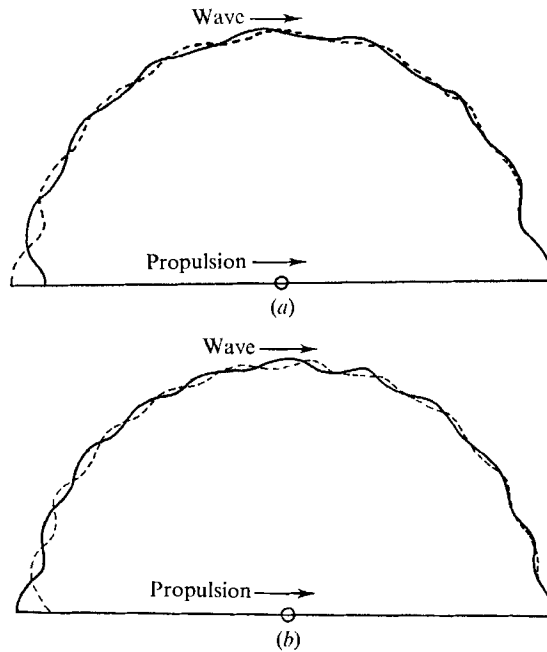
$$\begin{aligned} \bar{U} &= a\sigma\epsilon^2 \left[ \sum_{n=N-3}^{N-1} \frac{(-1)^{N-n}}{(2n+1)(2n+3)} \right. \\ &\quad \left. \times \{2(n+1)a_n b_{n+1} + 2na_{n+1}b_n + 4b_n b_{n+1} - (n^2 - n - \frac{1}{2})a_n a_{n+1}\} \right]. \end{aligned} \quad (20)$$

From (20) it is obvious that we need a careful choice of  $a_n$  and  $b_n$  to obtain the maximum velocity, especially if we are also applying constraint (ii) above. In (20) we have twelve terms contributing to the velocity, so for maximum velocity we need the dominant terms to have the same sign. In tables 1 and 2 we note the effect on the velocity of propulsion and efficiency of changing the sign of  $b_n$  with respect to  $a_n$ , as the rate of working is less for modes with the same magnitude but different sign (see (9)).

### 5. Calculations

In the calculations we have taken two examples at  $N = 17$  and  $N = 22$ , to show the shape of the organism. For this case we have taken  $\sigma = 25 \text{ sec}^{-1}$  and  $a = 100 \mu\text{m}$  as this is indicative of the angular frequency of movement of the cilium and length of the organism concerned respectively. (*Opalina* is 200–300  $\mu\text{m}$  long, wave velocity 100–400  $\mu\text{m}/\text{sec}$ , cilium length 10–15  $\mu\text{m}$ , beat frequency 1–4 per sec, velocity of propulsion 100–200  $\mu\text{m}/\text{sec}$ .) For conversion from these dimensional units we, however, note from (20) that  $\bar{U}$  is proportional to  $a\sigma$  to this order of calculation for the velocity.

	$a_{N-2}$	$a_N$	$a_{N-3}$	$a_{N-1}$	$b_{N-2}$	$b_N$	$b_{N-3}$	$b_{N-1}$	$U(\mu\text{m}/\text{sec})$	$\eta(\%)$
1.1	1.4	0	0	1.4	10	0	0	10	5.2	0.1
1.2	4	-4	4	-4	-15	15	-15	15	99.1	2.8
1.3	4	-4	4	-4	-10	10	-10	10	89.2	2.4
1.4	3.8	-4	-3.8	3.9	-15.3	20.5	14.3	-18.8	-95.2	2.4
1.5	3.9	-4	-3.8	3.9	0	0	0	0	-55.5	1.2
1.6	0	0	0	0	-15.3	20.5	14.3	-18.8	21.4	0.8
1.7	3.9	-4	3.8	-3.9	15.3	-20.5	14.3	-18.8	-27.2	0.4

TABLE 1. Velocity ( $\mu\text{m}/\text{sec}$ ) and efficiency for  $N = 17$ .  $\epsilon = 0.05$ FIGURE 2. The hemispherical surface of organism for (a)  $N = 17$  and (b)  $N = 22$ . The coefficients in (19) are given in tables 1.1 and 2.1 for these surfaces. (---) is  $t = \frac{1}{4}T$  later than (—).

	$a_{N-2}$	$a_N$	$a_{N-3}$	$a_{N-1}$	$b_{N-2}$	$b_N$	$b_{N-3}$	$b_{N-1}$	$U(\mu\text{m}/\text{sec})$	$\eta(\%)$
2.1	1.4	0	0	1.4	10	0	0	10	2.8	0.03
2.2	2	0	0	2	-5	0	0	-5	-7.9	0.2
2.3	4	-4	4	-4	-10	10	-10	10	87.3	2.2
2.4	-4.5	4.5	-4.4	4.4	9.3	-11.7	8.6	-11	104.8	2.6
2.5	-4.5	4.5	4.4	-4.4	-9.3	11.7	8.6	-11	-40.7	0.4
2.6	-4.5	4.5	4.4	-4.4	0	0	0	0	-77.1	1.4
2.7	0	0	0	0	-9.3	11.7	8.6	-11	4.3	0.1
2.8	2.3	-2.3	2.2	-2.2	-9.3	11.7	8.6	-11	20.0	0.3
2.9	2.3	-2.3	-2.2	2.2	-9.3	11.7	8.6	-11	-31.6	0.8

TABLE 2. Velocity ( $\mu\text{m}/\text{sec}$ ) and efficiency for  $N = 22$ .  $\epsilon = 0.05$



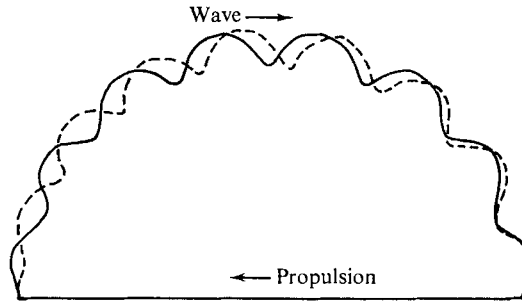


FIGURE 3. Hemispherical surface of organism at  $N = 17$ , with coefficients given in table 1.7. (---) is  $t = \frac{1}{4}T$  later than (—).

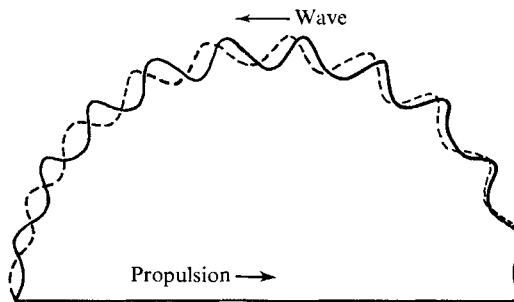


FIGURE 4. Hemispherical surface at  $N = 22$ , with coefficients given in table 2.4. (---) is  $t = \frac{1}{4}T$  later than (—).

The velocities and efficiencies are shown in tables 1 and 2, having chosen  $\epsilon = 0.05$  in both cases. The  $a_n$  and  $b_n$  are taken such that the series are of order 1. We may take the  $a_n$  to be  $O(n^{\frac{1}{2}})$  and the  $b_n$  to be  $O(n^{\frac{1}{2}})$ , provided the restriction  $d\theta/d\theta_0 > 0$  is not violated. The velocity of the organism can have both positive and negative sign, this being due to either of two things: (i) the direction in which the wave is progressing or (ii) the effect of longitudinal and transverse oscillations tending to propel the sphere in opposite directions. This second case (ii) corresponds with the observations of Tuck (1968) that longitudinal and transverse oscillations tend to propel an infinite sheet in opposite directions, so that on combination we may have either a positive or negative velocity. Large velocities occur, relatively speaking, when each  $b_n$  has opposite sign to the corresponding  $a_n$ . These larger velocities of the order of  $100 \mu\text{m}/\text{sec}$  are comparable with those observed for *Opalina*. The efficiency allows us to compare the work done in the ciliary movements to the work done by an external force pushing an inert organism at the same velocity, and as well enables us to compare the efficiency of various modes. In conclusion, this model for ciliary propulsion of a sphere compares favourably to the velocities experienced in nature and is therefore a quite amenable approach to the problem.

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