The efficiency of propulsion by a rotating flagellum
(bacteria/motility/hydrodynamics/low Reynolds number)

EDWARD M. PURCELL*
Department of Physics, Harvard University, Cambridge, MA 02138

ABSTRACT [At very low Reynolds number, the regime in which fluid dynamics is governed by Stokes equations, a helix that translates along its axis under an external force but without an external torque will necessarily rotate. By the linearity of the Stokes equations, the same helix that is caused to rotate due to an external torque will necessarily translate. This is the physics that underlies the mechanism of flagellar propulsion employed by many microorganisms. Here, I examine the linear relationships between forces and torques and translational and angular velocities of helical objects to understand the nature of flagellar propulsion.]

Much has been written about the fluid mechanics of the helical flagellum with which some microorganisms propel themselves [the earliest studies beginning with Ludwig (3)]. Recent theoretical studies include papers by Chwang and Wu (4), by Lighthill (5–7), by Garcia de la Torre and Bloomfield (8), and by Brennen and Winet (9). Like the classic paper by Taylor (10), these are aimed at deriving from first principles the flow around a moving helix, calculating the associated force and torque, and determining thereby the motion of the helix and a large attached body. The helical flagellum is supposed either to rotate as a whole, like a rigid corkscrew, or to deform continuously in a traveling helical wave, like a helical snake. The two motions are externally indistinguishable in the limit of vanishing thickness of the helical filament, but the latter case calls for some mechanism inside the flagellum to drive the wave. It has been shown that in the case of the bacterium Escherichia coli the flagellum simply rotates, driven by a rotary motor in or within the cell wall (11, 12). The flagellum is simply a rather gently curving helical filament of protein. Usually a cell has more than one flagellum. When the cell swims, its translational and angular velocities of helical objects to understand the nature of flagellar propulsion.]

Instead of calculating the hydrodynamic forces on a rotating flagellum of some particular shape, I want to develop some general relations by taking a different approach. Consider any propulsive device which consists of some rigid object rotating about a fixed axis. A corkscrew is only one example—the shape need not be that of a regular helix. Let us call the object, for short, a propeller. Indeed, an object shaped like a marine screw propeller could be an acceptable candidate. But whatever the shape, the rotation is to be so slow that its Reynolds number (9) is very small. [The Reynolds number of an object of...]

*Deceased March 7, 1997. The original version of this manuscript was completed by E.M.P. on April 26, 1978. It is an elaboration of thoughts presented in figures 13 and 14 of “Life at low Reynolds number” (1). A later version of the manuscript dated October 5, 1992, included an appendix in which E.M.P. worked out the propulsion efficiency of a rotating helical cylinder connected to a sphere (i.e., the power required to drag the sphere through a viscous medium, derived from Stokes law, divided by the power expended by the flagellar rotary motor). That work is not included here, because a similar calculation has been given by Childress (2), E.M.P. concluded that if the ratio of the viscous drag on a thin cylinder moving sideways at a given velocity to the viscous drag on the cylinder moving at the same velocity lengthwise were “α = 2, which it is supposed to be...” the propulsion efficiency cannot exceed 3% under any circumstances.” With more realistic values, he estimated a maximum of 1.7%. Finally, if the fluid were to slip over the surface of the filament, the efficiency would increase considerably, reaching 11% at α = 4 and 25% at α = 9. Some additions have been made to the text, in the interest of making the work more accessible to the general reader. These are set off in square brackets. The entries in Table 1, missing in both versions of the manuscript, were deduced from experiments recorded in a lab notebook dated June 23, 1978. The figures were drawn by E.M.P. as part of the original manuscript; legends have been added. The editing has been done by Aravindh D. T. Samuel, in collaboration with Howard A. Stone and Howard C. Berg. Reprint requests may be sent by mail to Howard C. Berg, Rowland Institute for Science, 100 Edwin H. Land Blvd., Cambridge, MA 02142, or by e-mail to berg@rowland.org.
Reynolds number regime [Stokes equations govern the fluid dynamics:]

\[- \nabla p + \eta \nabla^2 \mathbf{v} = 0, \quad \text{[2]}\]

where \( p \) is the pressure and there are no derivatives of time. Therefore, \( F \) and \( N \) must be linearly related to the \( v \) and \( \omega \):

\[ F = Av + B\omega \quad \text{[3a]} \]
\[ N = Cv + D\omega. \quad \text{[3b]} \]

We shall call the \( 2 \times 2 \) matrix \( \begin{pmatrix} A & B \\ C & D \end{pmatrix} \) the propulsion matrix \( P \) of this propeller. [Hydrodynamists call this object the resistance matrix (15).] The constants \( A, B, C, \) and \( D \) are proportional to the fluid viscosity \( \eta \) and depend otherwise only on the shape and size of the propeller. They scale with propeller size in this way: if every dimension of the propeller is increased by the factor \( k \), the new propulsion matrix \( P' \) has elements \( A' = kA; B' = k^2B; C' = k^3C; \) and \( D' = kD \).

Of course, these constants will be somewhat modified by the ship or cell to which we shall eventually attach the propeller and which will be the actual source of external force and torque. But for the present we may think of the force and torque as applied by a thin, perfectly stiff, untwistable axial wire. Whether such “mathematical” wire can be found does not matter. Eventually, we shall be interested in the real flagellum’s stiffness. We may also use such a mathematical wire to connect two different propellers together to form a single propeller, as in Fig. 2. From our definition of the propulsion matrix, it follows that the propulsion matrix of the composite propeller is the sum of the individual matrices:

\[ P = P_1 + P_2. \quad \text{[4]} \]

This is true if the force of the fluid on the thin wire can be neglected, and if the two flows [elements of the propeller] are well separated. The off-diagonal elements of \( P \) are essential for propulsion; they couple rotation and translation. We shall now prove that \( B \) and \( C \) must be equal if Eq. 4 is true.

We show first that \( B \) and \( C \) must have the same sign. Consider two cases: (i) Let the propeller be pushed by an external force \( F_1 \) applied by an axial wire at speed \( v_1 \). Constrain it from rotating by a torque \( N_1 \) of precisely the strength required to make \( o_1 = 0 \). [By Eqs. 3, the] force and torque are then given by:

\[ F_1 = Av_1 \quad \text{[5a]} \]
\[ N_1 = Cv_1. \quad \text{[5b]} \]

In this case the external force \( F_1 \) must do work because the torque does none. Hence, with signs defined as in Fig. 1, \( A \) must be positive. Similarly, if the propeller were rotated by an external torque \( N_1 \) with \( v_1 \) constrained to be zero, work would be done by \( N_1 \), implying that \( D \) must be positive also. (ii) Now remove the torque \( N_1 \) and apply a force \( F_2 \) sufficient to cause the same linear speed \( v_1 \) with the propeller free from external torque. [In this case, the propeller will rotate with some rotational speed \( \omega_2 \). By Eqs. 3,]

\[ F_2 = Av_1 + B\omega_2 \quad \text{[6a]} \]
\[ 0 = Cv_1 + D\omega_2. \quad \text{[6b]} \]

Therefore,]

\[ F_2 = \left(A - \frac{BC}{AD}\right)v_1. \quad \text{[7]} \]

Comparing Eqs. 5a and 7:

\[ \frac{F_2}{F_1} = 1 - \frac{BC}{AD}. \quad \text{[8]} \]

But \( F_2 \) cannot be greater than \( F_1 \) because the change from case i to case ii amounted to the relaxation of a constraint—i.e., the removal of an external torque \( N_1 \) that was doing no work. The argument can be made by invoking the minimum dissipation theorem for inertialess flows (16). If \( F_2 \) were greater than \( F_1 \), the rotationally unconstrained system of case ii could reduce its energy dissipation by reverting spontaneously to the kinematics of case i. We conclude that \( F_2 \leq F_1 \). [In view of Eq. 8, \( BC/AD \geq 0 \). Because \( A > 0 \) and \( D > 0, AD > 0; \) therefore,]

\[ BC \geq 0. \quad \text{[9]} \]


\[ \text{FIG. 2. Two propellers with propulsion matrices } P_1 \text{ and } P_2 \text{ (Upper). The propulsion matrix of the composite propeller is } P_1 + P_2. \]

\[ \text{FIG. 3. A special propeller with a symmetrical propulsion matrix } \begin{pmatrix} B & C \\ C & B \end{pmatrix} \text{ (lower). See the text.} \]
same as the circumferential force $N/\alpha$ associated with a longitudinal speed $v$. Consequently, the propulsion matrix $P$ of this special propeller must have $B_t = C_r$. By scaling this propeller in size, we can make $B_t$ have any desired magnitude, and by reversing the propeller’s handedness, we can make $B_t$ have either sign.

Now suppose we have [a test] propeller for which $B_t \neq C_r$. We could construct a special propeller with $B_t = C_r = -(B_t + C_r)/2$ and attach it in series with our [test] propeller by one of our thin, rigid axial wires. [The propulsion matrix of the composite propeller would be $P = P_s + P_t$ for which

$$B_t C_r = \left( B_t - \frac{(B_t + C_r)}{2} \right) \left( C_r - \frac{(B_t + C_r)}{2} \right) = -\frac{(B_t - C_r)^2}{4}. \quad [10]$$

[But if $B_t \neq C_r, B_t C_r$ is negative,] in violation of Eq. 9. Hence, a propeller with $B_t \neq C_r$ cannot exist. Every propulsion matrix must be symmetrical. We have here a reciprocity theorem typical of a linear system. Note that it implies that a structure like our “special” propeller will have $B_t = C_r$ even with the rods set at some other angle. It should perhaps be emphasized that the extremely idealized nature of our hypothetical special propeller and connecting hardware does not, in itself, compromise the rigor of the proof.

We turn now to the question of propulsion of the bacterial cell by a rigidly rotating flagellum or flagellar bundle, assured by some factor $k$ that the proximity of the cell does not seriously affect the action and reaction of both forces and torques at the propeller shaft requires

$$A_{p}v = -A v - B \omega \quad [11a]$$

$$D_{p} \Omega = -B v - D \omega. \quad [11b]$$

The rotation speed of the motor itself, that is, the speed of the “rotor” attached to the flagellum relative to the “stator” attached to the cell wall, is $\omega - \Omega$, which is greater in magnitude than $\omega$. Let us call the motor speed $\Omega_m$ and derive from Eqs. 11 the relation between $v$ and $\Omega_m$:

$$v = -\frac{BD_0}{(A_0 + A)(D_0 + D) - B^2} \Omega_m. \quad [12]$$

As expected, the swimming speed is proportional to $\Omega_m$. The torque $N$ exerted by the motor on the propeller is

$$N = \frac{B^2 - D(A_0 + A)}{B} v. \quad [13]$$

Let us compare the power output of the motor, which is $N \Omega_m$, with the least power that would be required to move the cell at speed $v$ by any means of propulsion whatever, namely $A_{p}^{\beta \omega^2}$. The ratio of $A_{p}^{\beta \omega^2}$ to $N \Omega_m$ provides a definition of the propulsive efficiency $\epsilon$. Using the relations above, we find

$$\epsilon = \frac{A_{p}^{\beta \omega^2}}{N \Omega_m} = \frac{A_0 D_0 B^2}{[(A_0 + A)(D_0 + D) - B^2]} \quad [14]$$

It will be a good approximation to drop the $B^2$ terms in the denominator, for it will turn out that $B^2$ is considerably smaller than $A_0$ in practical cases. [For $B^2 \ll AD$, Eqs. 12 and 14 may be well approximated by

$$v = -\frac{BD_0}{(A_0 + A)(D_0 + D)} \Omega_m, \quad [15a]$$

and]

$$\epsilon = \frac{A_0 D_0 B^2}{(A_0 + A)^2 (D_0 + D)} \quad [15b]$$

To the same approximation, the factor $D_0/(D_0 + D)$ is just the ratio $\omega/\Omega_m$, which, to anticipate again, will be fairly close to unity in cases of interest. That is, the counter-rotation of the large cell is relatively slow compared with the rotational speed of the flagellum (17). [Therefore, Eqs. 15 can further be approximated by

$$v = -\frac{B}{A_0 + A} \Omega_m, \quad [16a]$$

and]

$$\epsilon = \frac{A_0 B^2}{(A_0 + A)^2 D} \quad [16b]$$

Consider now a flagellar propeller of some particular specified shape. Suppose we are free to scale it up or down in size by some factor $k$. The resulting propulsion matrix will have elements $kA_p, k^2B_p$, and $k^3D_p$, where $A_p$, $B_p$, and $D_p$ refer to

![Fig. 4](image-url)
some prototype of a particular size. Is there a size of propeller that maximizes $\epsilon$ for the propulsion of a cell of given $A_0$? There is, as we find by substituting into Eq. 16b:

$$e = \frac{A_0 B_p^2}{D_p} \frac{k}{(A_0 + kA_p)^2}. \quad [17]$$

The maximum efficiency, $\epsilon_{\text{max}}$, is attained when $k = A_0/A_p$ and has the value

$$\epsilon_{\text{max}} = \frac{B_p^2}{4A_p D_p}. \quad [18]$$

$\epsilon_{\text{max}}$ depends only on the shape of the propeller itself, and the unknown error arising from interference of the flow fields around cell and propeller. It seems unlikely that such an effect would increase the efficiency, so we are probably safe in regarding Eq. 18 as an upper bound on the propulsion efficiency attainable with a flagellum of a given shape. For any given shape of propeller, the elements of the propulsion matrix $A$, $B$, and $D$ can be determined by very simple experiments with a model. Consider the propeller of Fig. 5a realized in the form of a steel wire. Let this object sink under its own weight, with its axis vertical, in a fluid of viscosity $\eta$. The results are given in Table 1.

Table 1. [Elements of propulsion matrices and propulsion efficiencies for flagellar models dropped in silicon oil]

<table>
<thead>
<tr>
<th>$L$, cm</th>
<th>$L/\lambda$</th>
<th>Pitch angle, °</th>
<th>$A$, cm</th>
<th>$B$, cm$^2$</th>
<th>$D$, cm$^3$</th>
<th>$\epsilon_{\text{max}}$, %</th>
<th>$f$, sec$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.2</td>
<td>5</td>
<td>55</td>
<td>0.07</td>
<td>0.032</td>
<td>0.076</td>
<td>0.48</td>
<td>89</td>
</tr>
<tr>
<td>7.8</td>
<td>3</td>
<td>39</td>
<td>0.71</td>
<td>0.038</td>
<td>0.06</td>
<td>0.78</td>
<td>85</td>
</tr>
<tr>
<td>9.4</td>
<td>5</td>
<td>20</td>
<td>0.74</td>
<td>0.018</td>
<td>0.031</td>
<td>0.34</td>
<td>188</td>
</tr>
<tr>
<td>3.1</td>
<td>5</td>
<td>55</td>
<td>0.48</td>
<td>0.023</td>
<td>0.053</td>
<td>0.46</td>
<td>62</td>
</tr>
<tr>
<td>7.5</td>
<td>7</td>
<td>56</td>
<td>0.91</td>
<td>0.053</td>
<td>0.13</td>
<td>0.54</td>
<td>100</td>
</tr>
</tbody>
</table>

[Test helices (Fig. 5) of length $L$, wavelength $\lambda$, and specified pitch angle were allowed to sink under their own weight in silicon oil ($\eta \approx 1,000$ g cm$^{-1}$sec$^{-1}$). The sinking speeds and speeds of rotation were measured, and $A$, $B$, and $D$ were determined through Eqs. 20 and 21; their values have been divided by $\rho g \eta$, so that their dimensions are cm, cm$^2$, and cm$^3$, respectively. $\epsilon_{\text{max}}$ is the maximal propulsion efficiency expected when the test helix is connected to a sphere of radius $A$ (Eq. 22). $f$ is the motor speed required to drive that sphere 20/sec$^{-1}$ (Eq. 19).]

It should sink without rotating. The three measurements suffice to determine $A$, $B$, and $D$, through Eqs. 20 and 21. The maximal efficiency attainable with a propeller of the given shape, as expressed by the approximate Eq. 18, is determined by only two measurements, those of $v_1$ and $v_2$:

$$\epsilon_{\text{max}} = \frac{B_p^2}{4AD} \frac{v_1 - v_2}{4v_1}. \quad [22]$$

The values of $A$, $B$, and $D$ determined from Eqs. 20 and 21 contain the viscosity of the fluid. Dividing them by $\rho g$ will normalize them so that the dimensions of $A$, $B$, and $D$ are cm, cm$^2$, and cm$^3$, respectively, and the radius of the spherical cell to which the propeller would be matched for maximal efficiency is equal to $A$. In other words, the radius of spherical cell for which the model propeller is [most efficient] is that of a sphere that would sink at speed $v_2$ if its weight in the fluid were $W$.

Fig. 5. Two propellers made of steel wire allowed to sink under their own weight, with axes vertical, $b$ is a composite propeller consisting of propeller $a$ joined rigidly to its mirror image.

The sinking speeds and speeds of rotation were measured, and $A$, $B$, and $D$ were determined through Eqs. 20 and 21; their values have been divided by $\rho g \eta$, so that their dimensions are cm, cm$^2$, and cm$^3$, respectively. $\epsilon_{\text{max}}$ is the maximal propulsion efficiency expected when the test helix is connected to a sphere of radius $A$ (Eq. 22). $f$ is the motor speed required to drive that sphere 20/sec$^{-1}$ (Eq. 19).]