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A thermodynamic efficiency for Stokesian swimming

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Since free Stokesian swimming does no work external to fluid and body, the classical thermodynamic efficiency of this activity is zero. This paper introduces a *potential* thermodynamic efficiency by partially tethering the body so that work is done externally and instantaneously. We compare the resulting efficiency with other definitions utilized in Stokes flow, extend the instantaneous definition to encompass a full swimming stroke, and compute it for propulsion of a spherical body by a helical flagellum.

Key words: micro-organism dynamics, Stokesian dynamics, swimming/flying

1. Introduction

The concept of efficiency has often been introduced into the analysis of flying and swimming in Nature. If the effort required for locomotion is important to the organism, it is reasonable to assume that evolution will seek to minimize that effort subject to whatever constraints are appropriate. Some measure of the efficiency of this effort is therefore of interest.

It has however proved difficult to apply the classical definition of thermodynamic efficiency to problems of locomotion. In classical thermodynamics, efficiency (the thermodynamic efficiency η_T) of a mechanical system is defined in terms of the mechanical work W done by the system on the external environment, and the heat Q produced in doing this work:

$$\eta_T = \frac{W}{W+Q}. \tag{1.1}$$

The difficulty with locomotion can best be seen by fixing the problem to the swimming of a neutrally buoyant organism in a Newtonian viscous fluid governed by the Navier–Stokes equations. If the organism swims steadily in one direction, with time-averaged acceleration exactly zero, then by Newton's laws the time-averaged force exerted by the body on the fluid (and by the fluid on the body), computed through an integral of the stress tensor, must vanish. Of course the body does work on the fluid in order to locomote, but the motions introduced into the fluid decay by viscous dissipation into heat. If also the swimming speed is independent of time, a situation reasonably well approximated by a steadily swimming fish, then the

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mechanical work done by the forces aligned with the swimming direction must vanish on average. The main point is that, without some way of allowing the fluid and body to do external work, we must have $W = 0$ and $Q > 0$, so that the thermodynamic efficiency must vanish.

In the present paper we restrict our study of efficiency to *Stokesian locomotion*, i.e. swimming in a fluid at effectively zero Reynolds number. In that case, the vanishing of the average force is replaced by a stronger property, of vanishing instantaneous force. This is because the dropping of all inertial effects renders the viscous response of the fluid instantaneous. Then the time t becomes a parameter without dynamical significance. There are many advantages to focusing on the Stokesian realm, not the least of which is the possibility of defining a kind of 'instantaneous thermodynamic efficiency'.

In the context of natural locomotion, Lighthill pioneered the analysis of efficient swimming. In his discussion of the swimming of slender fish, Lighthill (1960) dealt with the problem of zero external work by adopting the *Froude efficiency*, here denoted by η_F, a concept which comes from propeller theory. Adopting an inviscid theory, Lighthill computes a thrust T developed by a fish swimming at speed U, and then sets $W = TU$. This effectively restricts the thermodynamic system to the 'propeller', i.e. those aspects of the movements of locomotion associated with the production of thrust, and the 'engine' driving the propeller. The external system on which this work is done can be thought of as that part of the body responsible for drag. Lighthill also takes the heat Q to be the rate $\mathscr{E}$ at which energy is lost into the wake (and ultimately dissipated into heat). The Froude efficiency is then

$$\eta_F = \frac{UT}{UT + \mathscr{E}}. \tag{1.2}$$

It is of course clear that for this nonlinear problem there is generally a fundamental difficulty with the division into thrust and drag. The Navier–Stokes equations provide no such distinction in steady locomotion at a finite non-zero Reynolds number. The time average of the integral of the force and moment, determined by integrating the pressure and viscous stresses over the surface of the body, vanishes, but there is no way to divide these contributions into average thrust and drag. Although the Froude efficiency is defined as an analogue of a thermodynamic efficiency, the system to which it applies is unclear. These points were the subject of a tutorial by Bill Schultz given at the 2010 IMA workshop on locomotion, and his discussion of the problem motivated the present investigation (cf. Schultz & Webb 2002).

At zero Reynolds number, however, the situation is quite different. Then the linear Stokes equations apply and it is possible to split the flow field into parts reasonably associated with thrust/torque and drag/resistance to rotation. The practice is to still introduce a Froude efficiency, which for the drag/thrust case is typically of the form kU^2/Q where k is a resistance coefficient ($6\pi a\mu$ for a sphere of radius a), and Q is taken to be the total viscous dissipation in the fluid Φ, see e.g. Lighthill (1960), Stone & Samuel (1996), Purcell (1997) and Michelin & Lauga (2010). However it turns out that this 'efficiency' is not confined to the interval $[0, 1]$, but in fact can be arbitrarily large (Leshansky *et al.* 2007), a point we develop in § 2. When Q is restricted to the flow component associated with thrust/torque, this deficiency is removed. Nonetheless this ambiguity in the definition is unsatisfying, ultimately because of the lack of any 'external work', and there remains the question of how an efficiency based upon classical thermodynamics might be defined.

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The present analysis of efficiency for Stokesian swimming will utilize fully the special features of the Stokes equations, particularly their linearity. We shall introduce below what we shall term a *potential thermodynamic efficiency*. The idea is to retain the system of body and fluid, but let the body do positive work W externally. For the thrust–drag components, for example, we can imagine a thread attached to the body, which leaves the fluid and raises an external weight as the organism swims. Once the thread is attached, the organism swims at a fraction α of its free swimming speed. An instantaneous thermodynamic efficiency $\eta_T(\alpha)$ can now be defined. Then the instantaneous *potential* thermodynamic efficiency is defined by

$$\eta_{PT} = \max_{\alpha} \eta_T(\alpha). \tag{1.3}$$

In other words, we evaluate the swimmer by finding its most efficient behaviour, in the classical thermodynamic sense, when it is allowed to do work externally. We refer to this technique below as 'partial tethering'.

Following our formulation of the problem of the Stokesian swimming problem, in § 3 we derive η_{PT} for the drag/thrust case. For the general case where both thrust and torque are created by the swimming movements, we analogously define a thermodynamic efficiency depending upon two parameters α, β and show in § 4 that the η_{PT} for the drag/thrust case is again recovered as the maximum value of $\eta_T(\alpha, \beta)$.

We shall find that η_{PT} has all the desired properties of a thermodynamic efficiency. In § 5 we shall study the specific example of a spherical body propelled by a helical flagellum. In § 6 we extend the argument developed for instantaneous efficiency to the 'global' problem of computing an efficiency over a time interval comprising a single swimming stroke.

2. Formulation

We consider for simplicity a surface S equivalent topologically to the surface of a sphere in three dimensions, enclosing a region B of fixed total mass, 'the body'. The surface deforms in time preserving the volume within. We regard all space exterior to the body to be filled with the same Newtonian viscous fluid of constant properties. As a result of the deformations of S, the body moves through the fluid. We assume that Stokes flow conditions prevail. The fluid equations are therefore

$$\nabla p - \mu \nabla^2 \boldsymbol{u} = 0, \quad \nabla \cdot \boldsymbol{u} = 0. \tag{2.1}$$

We introduce a coordinate frame, the *body frame*, attached in some way to the organism, and by the rigid body motion of the organism we shall mean the rigid body motion of the body frame. As a result of the motion of $S(t)$ at the instant t selected, the organism will have an instantaneous rigid body motion given by a velocity of translation $\boldsymbol{U}$ and an instantaneous rate of rotation $\boldsymbol{\Omega}$ of the body frame. By $S'(t)$ we mean the shape of S as determined relative to the body frame. By $S(t)$ we mean the body shape relative to the fixed (laboratory) reference frame, such that the fluid at infinity in this frame is at rest. We may choose this reference frame to coincide with the body frame at $t = 0$. The instantaneous rigid body motion of the body frame is determined by the condition that the net force and moment exerted by S on the surrounding fluid is zero.

2.1. *Splitting of the solution*

We now divide the flow field so as to identify the part associated with thrust/torque. Following Childress (1981), we split the flow field of the swimming body into the following two parts: $(\boldsymbol{u}_1, p_1)$ will denote the flow field at time t associated with the

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instantaneous rigid body motion of the instantaneous shape $S(t)$ at time t; $(\boldsymbol{u}_2, p_2)$ is the flow due to the remaining component of the instantaneous motion of $S(t)$. Let this velocity be $\boldsymbol{u}_S$. Then

$$\boldsymbol{u}(\boldsymbol{x}, t)|_{\boldsymbol{x}\in S(t)} = \boldsymbol{u}_1(\boldsymbol{x}, t)|_{\boldsymbol{x}\in S(t)} + \boldsymbol{u}_2(\boldsymbol{x}, t)|_{\boldsymbol{x}\in S(t)} \tag{2.2}$$

where

$$\boldsymbol{u}_1 = \boldsymbol{U} + \boldsymbol{\Omega}\times\boldsymbol{x}|_{\boldsymbol{x}\in S(t)}, \quad \boldsymbol{u}_2(\boldsymbol{x}, t)|_{\boldsymbol{x}\in S(t)} = \boldsymbol{u}_S. \tag{2.3}$$

Associated with this splitting we define, if V is the exterior to B and m and n are 1 or 2,

$$\Phi_{mn} = \frac{\mu}{2}\int_V \left[\frac{\partial u_{mi}}{\partial x_j} + \frac{\partial u_{mj}}{\partial x_i}\right]\left[\frac{\partial u_{ni}}{\partial x_j} + \frac{\partial u_{nj}}{\partial x_i}\right]. \tag{2.4}$$

In particular Φ_{11} and Φ_{22} are the total viscous dissipations of the two flow components. The stress tensor

$$\sigma_{mij} = -p_m\delta_{ij} + \mu\left[\frac{\partial u_{mi}}{\partial x_j} + \frac{\partial u_{mj}}{\partial x_i}\right], \quad m = 1, 2, \tag{2.5}$$

will also be used. The quantities

$$\boldsymbol{F}_m(t) = -\int_{S(t)} \boldsymbol{\sigma}_m\cdot\mathrm{d}\boldsymbol{S}, \quad \boldsymbol{M}_m(t) = -\int_{S(t)} \boldsymbol{x}\times[\boldsymbol{\sigma}_m\cdot\mathrm{d}\boldsymbol{S}], \quad m = 1, 2, \tag{2.6}$$

are the forces and moments exerted on the fluid by each component. (The normal vector on S is always outward.) By the instantaneous equilibrium in Stokes flow locomotion,

$$\boldsymbol{F}_1(t) + \boldsymbol{F}_2(t) = 0, \quad \boldsymbol{M}_1(t) + \boldsymbol{M}_2(t) = 0. \tag{2.7}$$

Now $\boldsymbol{F}_1$ is the force exerted by the fluid on the body shape $S(t)$ as a result of its rigid body motion. Customarily, when $\boldsymbol{U}$ and $\boldsymbol{F}_1$ are colinear, we refer to $-\boldsymbol{F}_1$ as the *drag* of the current shape. Since $\boldsymbol{F}_1 + \boldsymbol{F}_2 = 0$ we then identify $\boldsymbol{F}_2$ with the *thrust*, given the dictum 'drag = thrust', which here applies instantaneously. Motion at zero Reynolds number offers the only example (known to this author) where the definition of drag and thrust in fluid dynamics is transparent and precise.

2.2. *Efficiencies for Stokesian swimming*

As in Childress (1981) we may define an instantaneous *mechanical* efficiency $\eta_M(t)$ as the ratio of Φ_{11} to the total dissipation in V for $\boldsymbol{u} = \boldsymbol{u}_1 + \boldsymbol{u}_2$, $\Phi \equiv \Phi_{11} + 2\Phi_{12} + \Phi_{22}$. We first prove

THEOREM 1.

$$\Phi_{12} = -\Phi_{11} \tag{2.8}$$

and

$$\Phi_{11} \leqslant \Phi_{22}. \tag{2.9}$$

Indeed we have

$$\Phi_{11} = \int_V \frac{\partial u_{1i}}{\partial x_j}\sigma_{1ij}\,\mathrm{d}V = -\int_S \boldsymbol{u}_1\cdot\boldsymbol{\sigma}_1\cdot\mathrm{d}\boldsymbol{S} \tag{2.10}$$

$$= -\int_S (\boldsymbol{U} + \boldsymbol{\Omega}\times\boldsymbol{x})\cdot\boldsymbol{\sigma}_1\cdot\mathrm{d}\boldsymbol{S} = -[\boldsymbol{U}\cdot\boldsymbol{F}_1 + \boldsymbol{\Omega}\cdot\boldsymbol{M}_1]. \tag{2.11}$$

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But by force and moment equilibrium we have

$$\Phi_{11} = [\boldsymbol{U}\cdot\boldsymbol{F}_2 + \boldsymbol{\Omega}\cdot\boldsymbol{M}_2] = \int_S (\boldsymbol{U}+\boldsymbol{\Omega}\times\boldsymbol{x})\cdot\boldsymbol{\sigma}_2\cdot \mathrm{d}\boldsymbol{S}$$
$$= -\int_V \frac{\partial u_{1i}}{\partial x_j}\sigma_{2ij}\,\mathrm{d}V = -\Phi_{12}. \tag{2.12}$$

Thus the total dissipation is $\Phi_{22}-\Phi_{11}\geqslant 0$, establishing the theorem. The physical meaning of (2.12) is clear. The total work done by the complete flow field $\boldsymbol{u}_1+\boldsymbol{u}_2$ when subjected to rigid body motion of the boundary $S(t)$ is, by the conditions of equilibrium, zero.

Our mechanical efficiency thus becomes

$$\eta_M(t) = \frac{\Phi_{11}}{\Phi} = \frac{\Phi_{11}(t)}{\Phi_{22}(t)-\Phi_{11}(t)}. \tag{2.13}$$

The problem with this definition is that it admits arbitrarily large values, as we show in the next subsection.

2.3. *The mechanical efficiency of a squirmer*

The swimmer we consider first is a sphere of radius a whose surface S' moves exactly as the potential flow field past a rigid sphere. We use the term 'squirmer' to indicate that body motions are tangential to its surface. Here $\boldsymbol{\Omega}$ and $\boldsymbol{M}_1$ vanish, and Φ_{11} is the total dissipation in the classical Stokes flow past the sphere, $6\pi\mu a U^2$. Now $\boldsymbol{u}_1$ is the Stokes flow vanishing at infinity and equal to $\boldsymbol{U}$ on the sphere, and

$$\boldsymbol{u}_2 = -\boldsymbol{u}_1 - \nabla\phi, \quad \phi = \frac{a^3\boldsymbol{U}\cdot\boldsymbol{R}}{2R^3}. \tag{2.14}$$

Thus $\boldsymbol{u}_1+\boldsymbol{u}_2 = -\nabla\phi$ and so

$$\Phi_{22}-\Phi_{11} = 2\mu\int_V \frac{\partial^2\phi}{\partial x_i\partial x_j}\frac{\partial^2\phi}{\partial x_i\partial x_j}\,\mathrm{d}V = -\mu\int_S \nabla|\nabla\phi|^2\cdot\mathrm{d}\boldsymbol{S} = 12\pi\mu a U^2. \tag{2.15}$$

Since $\Phi_{11} = 6\pi a\mu U^2$ we obtain $\eta_M = 1/2$. An alternative derivation (see Stone & Samuel 1996) gives

$$\eta_M = \frac{3}{4}\left[\frac{\left|\int_S \boldsymbol{u}_2\,\mathrm{d}S\right|^2}{4\pi a^2\int_S |\boldsymbol{u}_2|^2\,\mathrm{d}S}\right] = \frac{3}{4}\frac{16\pi^2}{24\pi^2} = \frac{1}{2}. \tag{2.16}$$

A generalized example of this kind has been discussed in Leshansky *et al.* (2007). Here we indicate that if we imagine the sphere compressed into the disk $z=0, x^2+y^2\leqslant a^2$, translating in the direction of the positive x-axis, then the disturbance of the external flow vanishes and so $\Phi_{22}-\Phi_{11}=0$. But $\Phi_{11} = (32/3)\mu U a$ for edgewise motion of a disk, see Davis (1996). Thus in this limit $\eta\to\infty$, as in the infinitely slender squirmer of Leshansky *et al.* (2007).

2.4. *Froude efficiency*

Since we know that $\Phi_{22}\geqslant\Phi_{11}$, a Froude efficiency with values in [0, 1] is defined by

$$\eta_F(t) = \frac{\Phi_{11}(t)}{\Phi(t)+\Phi_{11}(t)} = \frac{\Phi_{11}(t)}{\Phi_{22}(t)}. \tag{2.17}$$

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Thus we have normalized by a dissipation Φ_{22} larger than the *total* dissipation $\Phi_{22} - \Phi_{11}$. The dissipation Φ_{22} associated with the 'propeller' is larger than the dissipation of the free body in steady locomotion. This is because of the rigid body motion arising to effect force and torque balance.

Adopting the Froude efficiency (2.17), the squirmer now stands out as 100 % efficient. For many Stokes flow locomoters, particularly for small deformations of the body, Φ_{22} greatly dominates Φ_{11}, $\eta_M \approx \eta_F$, and the Froude efficiency is only a few per cent.

A more realistic Froude efficiency would include a quantity Q_{eff} representing the rate of heating of the system due to muscular effort associated with the deformations of the body, so that we then have

$$\eta_F(t) = \frac{\Phi_{11}(t)}{Q_{eff} + \Phi_{22}(t)}. \tag{2.18}$$

Stored elastic energy of a flagellum was included in Spagnolie & Lauga (2010) to analyse swimming efficiency. Another example of this would be to take Q_{eff} to be the viscous dissipation Φ'_{22} associated with fluid of the same viscosity as on the exterior, filling the body, with boundary velocity $\boldsymbol{u}_S$.

We note that Lighthill, Purcell, and other authors have introduced efficiencies involving approximations to the numerator Φ_{11} for η_M or η_F. We shall discuss these below in connection with the model studied in § 5.

3. Thermodynamic efficiency of a Stokesian swimmer

We have noted that one can view η_F as a thermodynamic efficiency of a restricted system. Φ_{11} represents the work done 'externally', even though in fact it is the work done in rigid body motion and is part of the swimming system we study. The effort needed to do this work is Φ. The question we face is how to eliminate this arbitrary and artificial choice of external work.

Our approach is to consider the exact hydrodynamics of the complete body, but to introduce partial tethering, wherein the body is allowing to expend a portion of its effort in doing work external to the fluid.

We consider first an axially symmetric body (S' axisymmetric), for example one passing waves down its surface, so as to swim in a straight line without any rotation about this axis. To fix ideas assume that the neutrally buoyant body moves horizontally, with gravity acting down. We assume that a line is tied to the body, passing over a pulley, so that motion of the body lifts a weight w exterior to the fluid, see figure 1. Assume that the speed of the untethered body is U. When attached to the weight, the body moves at the speed $U_1 = \alpha U$, the weight being chosen so that $0 < \alpha < 1$. If k is the resistance coefficient of the current shape ($F_1 = kU$ before being transformed), then a force $k(1-\alpha)U$ is available to lift the weight w. So $k(1-\alpha)U = w$ and the rate of working to lift the weight is $W = \alpha U w = k\alpha(1-\alpha)U^2$. The new force balance is $F_1 + F_2 + w = 0$, and if this is used in the proof of theorem 1 one finds that the dissipation in the fluid when pulling the weight is $Q \equiv \Phi_{22} - \alpha^2\Phi_{11} - 2\alpha U w$. Evaluating $Q + W$, the thermodynamic efficiency of the system of body and fluid is then obtained from (1.1).

Given that $\Phi_{11} = kU^2$ and $w = kU(1-\alpha)$ we obtain the function,

$$\eta_T(\alpha) = \frac{\alpha(1-\alpha)}{\rho + 1 - \alpha}, \quad \rho = \frac{\Phi_{22}}{\Phi_{11}} - 1. \tag{3.1}$$

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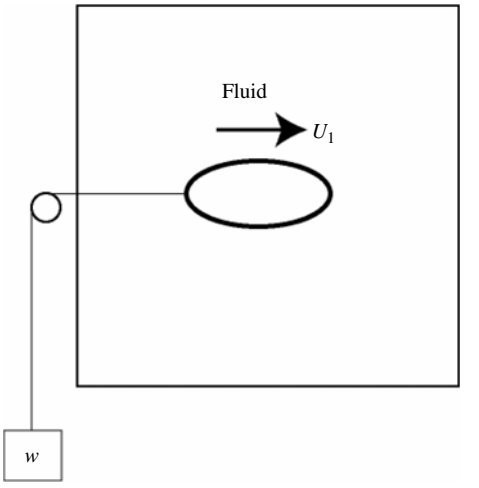


FIGURE 1. An axially symmetric Stokesian swimmer lifts a weight.

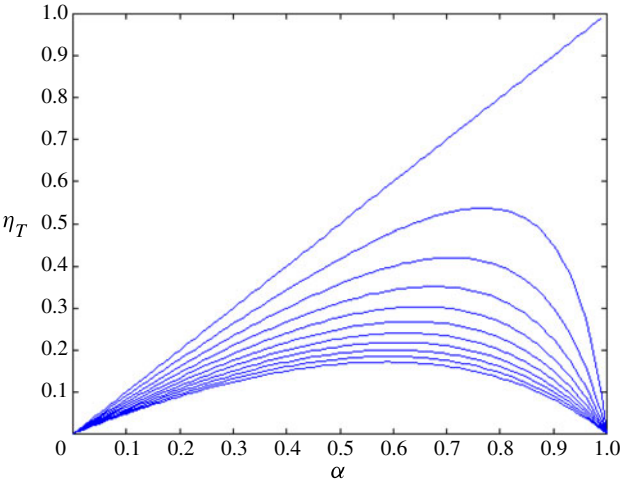


FIGURE 2. (Colour online available at journals.cambridge.org/flm) $\eta_T(\alpha)$ versus α for $\rho = 0, 0.1, 0.2, \ldots, 1$.

We show this function in figure 2. The result confirms the vanishing of thermodynamic efficiency in free swimming if $\rho > 0$, but large thermodynamic efficiency can be obtained for a near squirmer lifting a small weight.

The maximum value of $\eta_T(\alpha)$ as a function of α occurs when $\alpha = 1 + \rho - \sqrt{\rho + \rho^2}$, and is given by

$$\max_{\alpha} \eta_T(\alpha) \equiv \eta_{PT} = 1 + 2\rho - 2\sqrt{\rho + \rho^2} \equiv \eta_{PT}, \tag{3.2}$$

thus defining the potential thermodynamical efficiency for this system. η_{PT} is plotted as a function of ρ in figure 3. For large ρ the optimum efficiency is $1/4\rho$, or $1/4$ the same estimate for η_F. Since large ρ is common for micro-organisms, their potential thermodynamic efficiency is miniscule (as is their Froude and mechanical efficiencies, which are $\sim 1/\rho$).

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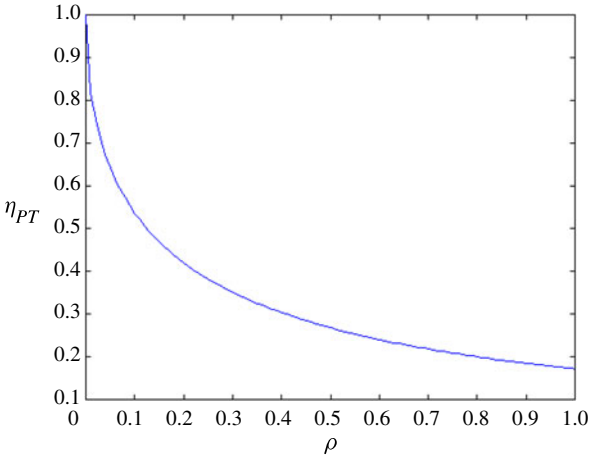


FIGURE 3. (Colour online) Potential thermodynamic efficiency as a function of $\rho = (\Phi_{22}/\Phi_{11}) - 1$.

We propose the efficiency of figure 3 as a reasonable instantaneous efficiency of an axisymmetric Stokesian swimmer, determined entirely by the instantaneous value of ρ. It is the optimal efficiency determined by a weight-lifting contest, given that the swimmer is free to choose the weight lifted. The values lie well below any of the Froude and mechanical efficiencies that have been proposed by a factor $\approx 1/4$–$1/3$.

4. The general case

We now consider an arbitrary Stokesian swimmer. We keep $\boldsymbol{u}_2, p_2$ intact but assume in $\boldsymbol{u}_1, p_1$ that $\boldsymbol{U} \to \alpha \boldsymbol{U}$ and $\boldsymbol{\Omega} \to \beta \boldsymbol{\Omega}$ where $0 \leqslant \alpha, \beta \leqslant 1$. This defines partial tethering in the general case. Keep in mind that as before all of the calculations refer to a particular time t. All quantities are functions of t but we shall omit this indication. Now in general, translation and rotation contribute to both force and moment. There exist symmetric matrices $\boldsymbol{A}$, $\boldsymbol{B}$, $\boldsymbol{C}$, $\boldsymbol{D}$ such that

$$\boldsymbol{F}_1 = \boldsymbol{A} \cdot \boldsymbol{U} + \boldsymbol{B} \cdot \boldsymbol{\Omega}, \quad \boldsymbol{M}_1 = \boldsymbol{C} \cdot \boldsymbol{U} + \boldsymbol{D} \cdot \boldsymbol{\Omega}. \tag{4.1}$$

We know from reciprocal relations that $\boldsymbol{A}$ and $\boldsymbol{D}$ are symmetric and $\boldsymbol{B} = \boldsymbol{C}^{\mathrm{T}}$ (T here denotes transpose). Also clearly $\boldsymbol{A}$ and $\boldsymbol{D}$ are positive definite. But also we have

$$A_{ij} U_i U_j + 2 B_{ij} U_i \Omega_j + D_{ij} \Omega_i \Omega_j \geqslant 0, \tag{4.2}$$

for any vectors $\boldsymbol{U}$, $\boldsymbol{\Omega}$, if we consider the dissipation with boundary data $\boldsymbol{U} + \boldsymbol{\Omega} \times \boldsymbol{x}$.

Under partial tethering

$$\boldsymbol{F}_1 \to \alpha \boldsymbol{A} \cdot \boldsymbol{U} + \beta \boldsymbol{B} \cdot \boldsymbol{\Omega}, \quad \boldsymbol{M}_1 \to \alpha \boldsymbol{C} \cdot \boldsymbol{U} + \beta \boldsymbol{D} \cdot \boldsymbol{\Omega}. \tag{4.3}$$

Now the extra force and moment available to do external work are

$$\boldsymbol{F}_1' = (1 - \alpha) \boldsymbol{A} \cdot \boldsymbol{U} + (1 - \beta) \boldsymbol{B} \cdot \boldsymbol{\Omega}, \quad \boldsymbol{M}_1' = (1 - \alpha) \boldsymbol{C} \cdot \boldsymbol{U} + (1 - \beta) \boldsymbol{D} \cdot \boldsymbol{\Omega}. \tag{4.4}$$

We do not know the direction of these forces and moments relative to $\boldsymbol{F}_1$ and $\boldsymbol{M}_1$. However we assume that only the projection of $\boldsymbol{F}_1'$ onto $\alpha \boldsymbol{U}$ and $\boldsymbol{M}_1'$ onto $\beta \boldsymbol{\Omega}$ matter. This can be realized by pulling on a string aligned with $\boldsymbol{U}$ attached to a weight, for the force, and letting the extra moment twist up a pully in the plane orthogonal to $\boldsymbol{\Omega}$, so as to wind up a string which lifts a second weight, see figure 4.

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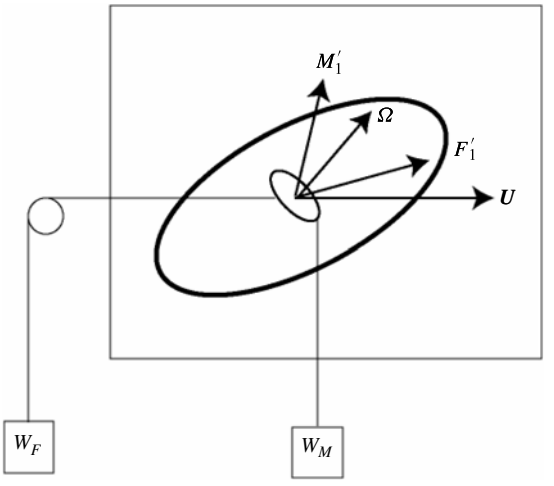


FIGURE 4. A general swimmer lifts two weights.

Proceeding as in the previous calculation for the axisymmetric swimmer we arrive at the following expression for thermodynamic efficiency under reduction of data:

$$\eta_T(\alpha, \beta) = \frac{\alpha(1-\alpha)a + (\alpha+\beta-2\alpha\beta)b + \beta(1-\beta)c}{\rho + (1-\alpha)a + (2-\alpha-\beta)b + (1-\beta)c} \equiv \frac{N}{M}, \tag{4.5}$$

where

$$a = \Delta^{-1}\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}, \quad b = \Delta^{-1}\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega}, \quad c = \Delta^{-1}\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}, \tag{4.6}$$

$$\Delta = \boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U} + 2\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega} + \boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}, \tag{4.7}$$

and again $\rho = \Phi_{22}/\Phi_{11} - 1$. We note that

$$a > 0, \quad c > 0, \quad a + 2b + c = 1, \quad ac > b^2, \tag{4.8}$$

the inequality following from (4.2).

We now need a condition ensuring that we are dealing with a physically realizable system, in the sense that non-negative external work is being done under partial tethering. It is easy to see by examining values on the boundary, in view of (4.8) and the fact that $\rho \geqslant 0$, that $M > 0$ provided that $b \geqslant 0$. For N, we observe that the unique interior extremal is at $\alpha = \beta = 1/2$, where $N = 1/4$. Also on the boundaries we obtain the values $b + (1-\beta)c$, $b + (1-\alpha)a$, $b + \beta c$, $b + \alpha a$. It follows that $N \geqslant 0$ (and hence $W \geqslant 0$) provided that $b \geqslant 0$. We now restrict consideration to systems satisfying this last inequality.

We now have the following satisfying result.

THEOREM 2. *If $b \geqslant 0$ the potential thermodynamic efficiency for the general case is again given by $\eta_{PT} = 1 + 2\rho - 2\sqrt{\rho + \rho^2}$.*

Proof. Let us first assume that $b > 0$. If we differentiate $\eta_T(\alpha, \beta)$ with respect to α and β we obtain

$$\left.\begin{aligned}[(1-2\alpha)a + (1-2\beta)b]M &= -N(a+b),\\ [(1-2\alpha)b + (1-2\beta)c]M &= -N(b+c),\end{aligned}\right\} \tag{4.9}$$

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where M, N are the terms in (A 15) in the appendix. Adding the last two equations and using (4.8),

$$[1 - 2\alpha(a + b) - 2\beta(b + c)]M = -N. \tag{4.10}$$

Using this in (4.9) and again using (4.8) we have

$$(\alpha - \beta)b = (\alpha - \beta)(a + b)(b + c), \quad Vc = (\alpha - \beta)\,(b + c)^2\,. \tag{4.11}$$

If $\alpha \neq \beta$ then, if $b + c = f$, we see that $c = f^2$, $b = f(1 - f)$, $a = (1 - f)^2$. Thus $ac = b^2$, which violates the second of (4.8). Thus we must have $\alpha = \beta$, and therefore, from (4.9), $(1 - 2\alpha)M + N = 0$, which is the condition for the extremal of η when $\alpha = \beta$ and $\eta_T = \alpha(1 - \alpha)/(\rho + 1 - \alpha) = \eta_{PT}$.

There remains the checking of points on the boundary of the domain of the function $\eta_T(\alpha, \beta)$. If $\alpha = 0$ for example, then

$$\eta_T|_{\alpha=0} = \frac{\beta(b + c) - \beta^2 c}{\rho + 1 - \beta(b + c)}. \tag{4.12}$$

Introducing $\tilde{\beta} = \beta(b + c)$, we obtain

$$\eta_T|_{\alpha=0} = \frac{\tilde{\beta} - \tilde{\beta}^2\gamma}{\rho + 1 - \tilde{\beta}}, \tag{4.13}$$

where $\gamma = c/\,(b + c)^2$. But recalling $a + 2b + c = 1$, $ac > b^2$, we see that $c = ac + 2bc + c^2 > (b + c)^2$ and so $\gamma > 1$. It follows from (4.13) that $\max_{\alpha=0, 0\leqslant\beta\leqslant1} \eta_T < \eta_{PT}$.

Similarly, when $\alpha = 1$ we have

$$\eta_T|_{\alpha=1} = \frac{(1 - \beta)(b + \beta c)}{\rho + (1 - \beta)(b + c)}. \tag{4.14}$$

Now set $\tilde{\beta} = (b + \beta c)/(b + c)$. Then

$$\eta_T|_{\alpha=1} = \frac{\tilde{\beta} - \tilde{\beta}^2}{\tilde{\rho} + 1 - \tilde{\beta}}, \tag{4.15}$$

where

$$\tilde{\rho} = \gamma\rho. \tag{4.16}$$

Now at the given value of ρ, (4.15) allows $\eta_{PT}(\tilde{\rho})$ to be obtained as the largest value. Since $\gamma > 1$ and $\eta_{PT}(\rho)$ is a decreasing function of ρ, it follows that $\eta_{PT}(\tilde{\rho}) < \eta_{PT}(\rho)$. The other two boundary segments yield similar results by the symmetry of η_T in α, β. Thus theorem 2 is established when $b > 0$.

Finally consider the case $b = 0$. The derivative test proceeds as before and (4.9) immediately yields $\alpha = \beta$. But now $a + c = 1$ and we obtain again η_{PT}. On the boundaries $\alpha = 0, 1$ the argument also proceeds as before with $\tilde{\beta} = c\beta$ and $\tilde{\rho} = \rho/c$ respectively. Thus theorem 2 is established. □

The exclusion of the possibility $b < 0$ is a curious and unexpected condition, since the matrices $\boldsymbol{B}$, $\boldsymbol{C} = \boldsymbol{B}^{\mathrm{T}}$ (termed 'coupling matrices' in Happel & Brenner 1965) are not necessarily non-negative definite. However we believe that this condition is in fact necessary in Stokesian swimming. This is best motivated using an explicit example, which we introduce in the following section.

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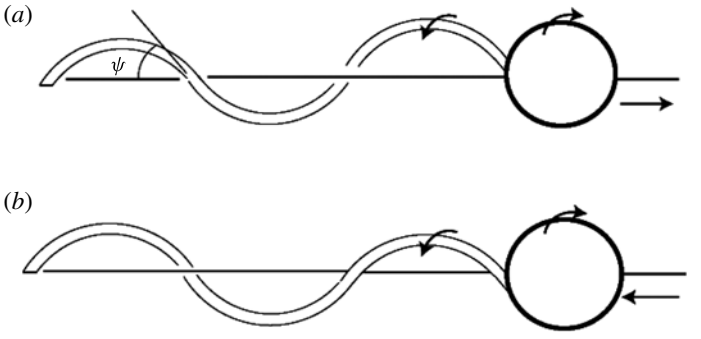


FIGURE 5. The swimmer with helical flagellum. (*a*) $\omega > 0, \Omega < 0, U > 0, B < 0, b > 0$. (*b*) $\omega > 0, \Omega < 0, U < 0, B > 0, b > 0$.

5. A body propelled by a helical flagellum

We consider the much studied example of a spherical body of radius a being propelled by a rigid helical wire, rotated relative to the body with angular velocity $\boldsymbol{\Omega}$. Our aim here is to calculate η_{PT} in this example.

We show in figure 5 both helical orientations, giving forward or reverse locomotion at positive Ω. Rigid motion consists of the translation and rotation of the head with the helix rigidly fixed to it. We assume that the helical wire is sufficiently thin and the helix sufficiently 'open' (the pitch angle ψ show in figure 5*a* sufficiently far from 90°), that resistive force theory may be applied to compute the force and moment exerted by the helical wire on the fluid. Let the radius of the helix be R. The stretched-straight length of the wire is L. The structure swims along the z-axis, and the only forces and moments we need consider are aligned with this axis. If the radius of the wire cross-section is r_0, we assume $r_0 \ll R$. In this case it is possible to neglect the torque resulting from rotation of the cross-section relative to the torque generated by the wire in tangential and normal motion according to resistive force theory.

We consider the orientation shown in figure 5(*a*). The driving velocity $\boldsymbol{u}_S$ is the rotation of the helix with prescribed angular velocity ω. The force produced (acting on the fluid) is

$$F_2 = -\omega RL \sin\psi \cos\psi (K_N - K_T), \tag{5.1}$$

where K_N, K_T are normal and tangential resistance coefficients. Typically $K_N \approx 2K_T$ so for positive ω the fluid is driven backward with a negative force. The moment acting on the fluid is positive and given by

$$M_2 = \omega R^2 L(K_N \cos^2\psi + K_T \sin^2\psi). \tag{5.2}$$

Thus

$$\Phi_{22} = \omega^2 R^2 L(K_N \cos^2\psi + K_T \sin^2\psi). \tag{5.3}$$

We now consider the rigid body motions. We have

$$F_1 = 6\pi\mu a U + UL(K_N \sin^2\psi + K_T \cos^2\psi) - \Omega RL \sin\psi \cos\psi (K_N - K_T), \tag{5.4}$$

$$M_1 = -URL \sin\psi \cos\psi (K_N - K_T) + 8\Omega\pi\mu a^2 + \Omega R^2 L(K_N \cos^2\psi + K_T \sin^2\psi). \tag{5.5}$$

We write the equations of equilibrium ($F_1 + F_2 = 0, M_1 + M_2 = 0$) in the form

$$dU + AU + B(\Omega + \omega) = 0, \quad BU + m\Omega + D(\Omega + \omega) = 0, \tag{5.6}$$

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where

$$A = L(K_N \sin^2\psi + K_T \cos^2\psi), \quad B = -RL \sin\psi \cos\psi (K_N - K_T), \tag{5.7}$$

$$D = R^2 L(K_N \cos^2\psi + K_T \sin^2\psi), \tag{5.8}$$

and $d = 6\pi\mu a$ and $m = 8\pi\mu a^3$. Solving,

$$U = -\frac{mB\omega}{F}, \quad \Omega = -\omega[(d+A)D - B^2]/F, \quad F = (d+A)(m+D) - B^2 > 0. \tag{5.9}$$

It is easily checked that $AD - B^2 > 0$ and $B < 0$, so $U > 0$ and $\Omega < 0$. Consequently $UB\Omega > 0$ and this implies that the parameter b of theorem 2 is indeed positive. Note that the coupling constant B is negative, but the angular velocity Ω is also negative since the spin of the sphere must compensate for the positive torque applied to the fluid by the helix.

Now we have

$$\Phi_{11} = (d+A)U^2 + 2B\Omega U + (m+D)\Omega^2. \tag{5.10}$$

This can be brought into the form

$$\left.\begin{aligned} &\omega^{-2}\Phi_{11} = D - [(d+A)m^2E + mE^2]/F^2 = D - mE/F, \\ &E = (d+A)D - B^2 > 0. \end{aligned}\right\} \tag{5.11}$$

Since $\Phi_{22} = \omega M_2 = \omega^2 D$ we have established that indeed $0 < \Phi_{11}/\Phi_{22} < 1$.

We note in passing, keeping in mind that for the helical swimmer the propelling velocity $\boldsymbol{u}_2$ is confined to the helical tail, that

$$\begin{aligned} \Phi_{12} &= \omega(M_1 - m\Omega) = -\omega^2[mB^2/F + ED/F] \\ &= -\omega^2[D - mE/F] = -\Phi_{11} \end{aligned} \tag{5.12}$$

as required by theorem 1. Also it is clear, from the reduction of flagellum rotation relative to the fluid at infinity, why the total dissipation in free swimming is smaller than that associated with the spin of the helical tail relative to the head. To obtain the most efficient swimmer we must maximize Φ_{11}/Φ_{22}, hence minimize

$$mE/DF = \frac{m}{D}\frac{(d+A)D - B^2}{(d+A)(m+D) - B^2}. \tag{5.13}$$

Now $AD - B^2 = R^2L^2K_TK_N$, so we need to minimize

$$\frac{m(dD + R^2L^2K_TK_N)}{D(md + mA + dD + R^2L^2K_TK_N)}. \tag{5.14}$$

We can rewrite this last expression as

$$\frac{P + rr_d}{P(1 + (1+r)r_d + rr_dr_m + (r_m - r_d)P}, \tag{5.15}$$

where

$$r = \frac{K_T}{K_N}, \quad r_d = \frac{LK_N}{d}, \quad r_m = \frac{R^2LK_N}{m}, \tag{5.16}$$

and

$$P = \cos^2\psi + r\sin^2\psi. \tag{5.17}$$

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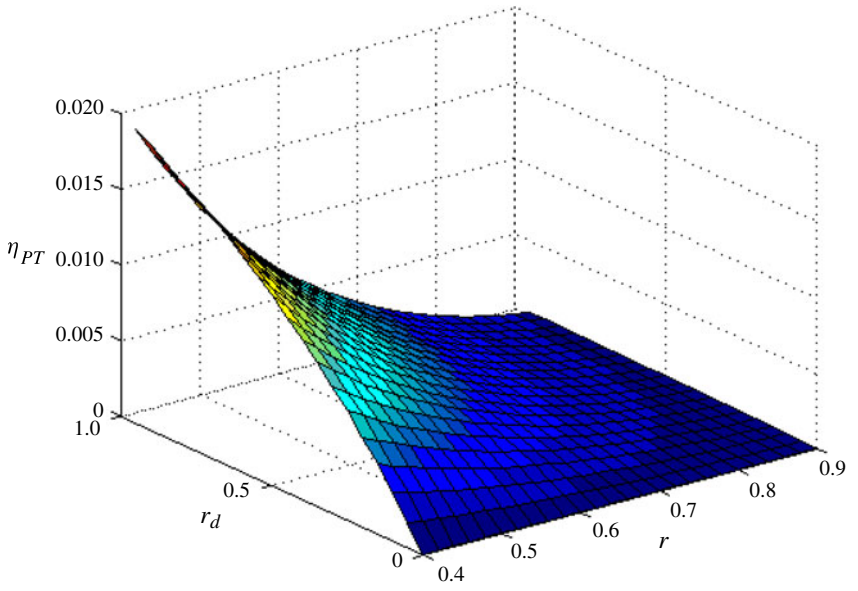


FIGURE 6. (Colour online) Optimal potential thermodynamic efficiency as a function of r and r_d, with $r_m \ll r_d$.

The parameters r_d, rr_d, r_m are respectively measures of normal and tangential flagellum force relative to head drag, and flagellum moment relative to head torque. To optimize over ψ we set the derivative with respect to ψ equal to zero, giving

$$\sin\psi\cos\psi(1-r)\left[P^2+2rr_dP-rr_d\frac{1+r_d(1+r)+rr_dr_m}{r_d-r_m}\right]=0. \tag{5.18}$$

At $\psi=0,\pi/2$ we have $P=1,r$ and

$$mE/DF=\left[\frac{1}{1+r_m},\frac{1}{1+rr_m}\right]. \tag{5.19}$$

At this point it is helpful for comparative purposes to simplify the model. We will assume $R\ll a\ll L$, corresponding to a helical flagellum, long relative to head radius and tightly wound. In this case we are justified to assume $r_m\ll r_d$. For the moment we retain r_d but set $r_m=0$, yielding the optimum P,

$$P=-rr_d+\sqrt{r^2r_d^2+r(1+r_d(1+r))}. \tag{5.20}$$

In figures 6 and 7 we show the optimal η_{PT} and the optimal ψ as functions of r and r_d. For comparison we show in figure 8 the optimal $\eta_F=\Phi_{11}/\Phi_{22}$ under the same approximation, as a function of r, r_d.

We consider now another definition of efficiency that has been utilized in Stokesian swimming. Purcell (1997) considered the present model swimmer and utilized a simplified mechanical efficiency given (in our notation) by

$$\eta_M'=\frac{dU^2}{\Phi}=\frac{dU^2F}{mE\omega^2}=\frac{mdB^2}{EF}. \tag{5.21}$$

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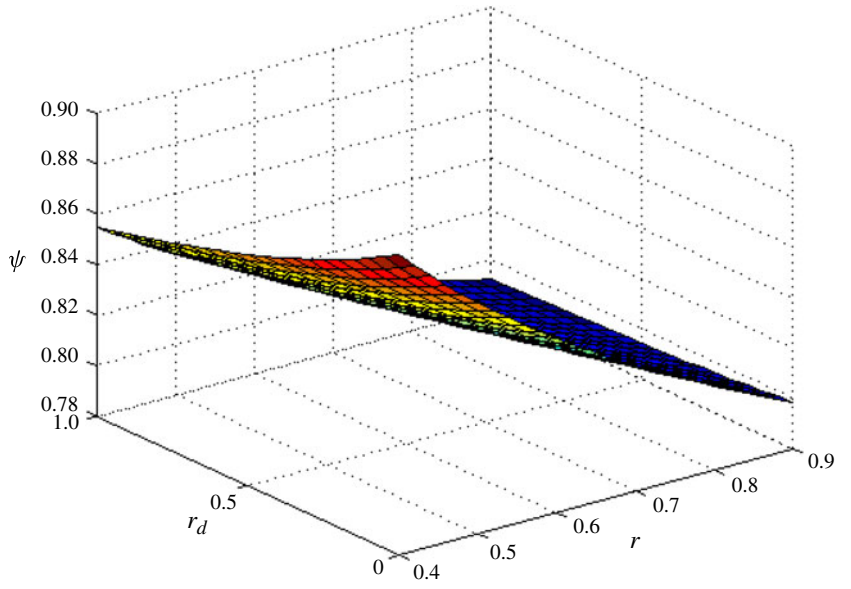


FIGURE 7. (Colour online) Optimal pitch angle ψ as a function of r and r_d, with $r_m \ll r_d$.

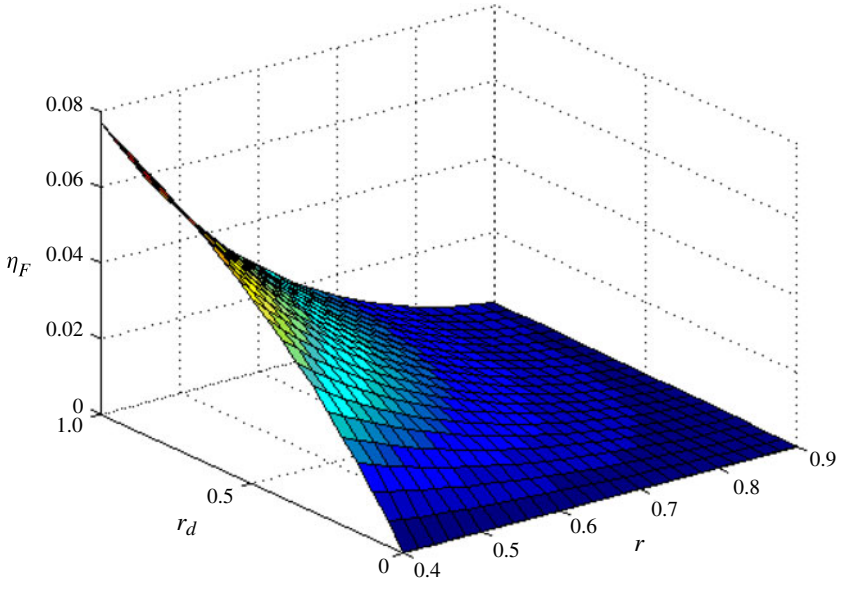


FIGURE 8. (Colour online) Optimal $\eta_F = \Phi_{11}/\Phi_{22}$ with $r_m \ll r_d$ as a function of r, r_d.

With our previous approximation $r_m \ll r_d$ we obtain

$$\eta'_M = \frac{r_d\,(1-r)^2 \sin^2\psi\cos^2\psi}{[1 + r_d(\sin^2\psi + r\cos^2\psi)][\cos^2\psi + r\sin^2\psi + r_d r]}. \tag{5.22}$$

Lighthill (1975) improves (5.21) by replacing d by $d + K_T L$ in the numerator, i.e. by including the drag of the stretched-straight flagellum in the numerator. Then (5.22)

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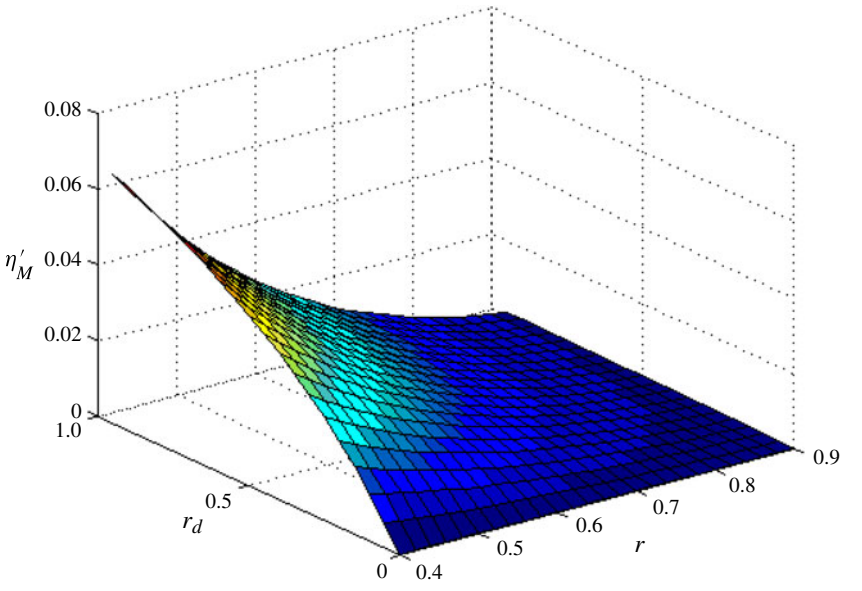


FIGURE 9. (Colour online) Lighthill's optimum η'_M (Lighthill 1975), given by (5.25).

becomes

$$\eta'_M = \frac{(r_d + rr_d^2)\,(1-r)^2 \sin^2\psi\cos^2\psi}{[1 + r_d(\sin^2\psi + r\cos^2\psi)][\cos^2\psi + r\sin^2\psi + r_d r]}. \tag{5.23}$$

Expressing the right-hand side of (5.23) as a function of $\tan^2\psi$, we optimize over ψ to obtain Lighthill's results:

$$\tan^2\psi = \frac{1 + rr_d}{(1 + r_d)r^{1/2}}, \tag{5.24}$$

$$\eta'_M = (1 - \sqrt{r})^2\,\frac{r_d}{1 + r_d}. \tag{5.25}$$

We show this result in figure 9.

A useful comparison can be made when $r_d = \infty$, corresponding to a drag dominated by the flagellum. Then

$$\eta_{PT} = 1 + \frac{8r - 4(1+r)\sqrt{(r)}}{(1-r)^2}, \quad \eta'_M = (1 - \sqrt{(r)})^2, \quad \eta_F = \left(\frac{1-r}{1+r}\right)^2. \tag{5.26}$$

We show ratios of these quantities in figure 10.

6. Thermodynamic efficiency of a full swimming stroke

Our restriction to the efficiency at a given instant of time leaves untouched several subtle and important points connected with the extension of this concept to an efficiency of a full swimming stroke or trajectory. In fact 'locomotion' as such has been missing from our discussion, since that is something accomplished over a finite time interval. There appear to be two questions in particular which need to be addressed. First, what sort of trajectories are reasonable for defining a time-dependent

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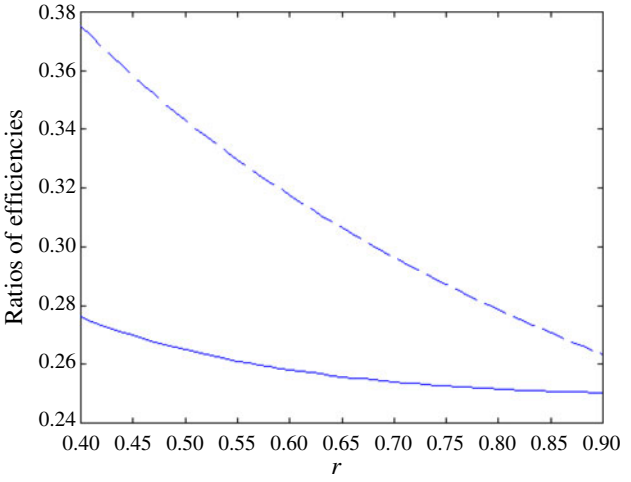


FIGURE 10. (Colour online) η_{PT}/η_F (solid line) and η_{PT}/η'_M (dashed line) as a function of r, $r_d = \infty$, see (5.26).

potential thermodynamic efficiency? Second, how can the time-dependent efficiency be use to compute an overall efficiency of a stroke?

With regard to the first question our use of partial tethering suggests that rapid adjustment of the tethers should not be allowed, despite our qualifying adjective 'potential'. We therefore stipulate that both the direction of swimming and the axis of rotation should have small angular changes over the time scale of the swimming stroke. If this condition is met we can refer to the locomotion as 'straight line', although it still allows 'swimming in circles' as a form of locomotion.

Consider then straight-line swimming by an organism executing a periodic swimming stroke with period T. Let us first assume that the velocity of swimming is nowhere zero, and restrict our argument to the axially symmetric case of § 3, where $\Phi_{11} = kU^2$. At each instant of the stroke, we have previously considered a certain value of α which, given the instantaneous stroke parameters, determined a weight w to be lifted. Let us examine the consequences of making the same assumption over a swimming cycle. That is, suppose that α is now a smooth function of t, with the weight correspondingly adjusted, so that the resulting work $W(t)$ and $Q(t)$ can be determined as before. We may then compute a stroke thermodynamic efficiency by dividing $\int_0^T W(t)\,\mathrm{d}t$ by $\int_0^T W(t)\,\mathrm{d}t + \int_0^T Q(t)\,\mathrm{d}t$. The potential thermodynamic efficiency is then

$$\eta_T^S = \sup_{\alpha(t),0\leqslant t\leqslant T} \frac{\displaystyle\int_0^T \alpha(1-\alpha)\Phi_{11}\,\mathrm{d}t}{\displaystyle\int_0^T (\Phi_{22} - \alpha\Phi_{11})\,\mathrm{d}t}. \tag{6.1}$$

Carrying out the variation of α we have

$$\Phi_{11}\left[(1-2\alpha)\int_0^T (\Phi_{22} - \alpha\Phi_{11})\,\mathrm{d}t + \int_0^T \alpha(1-\alpha)\Phi_{11}\,\mathrm{d}t\right] = 0, \tag{6.2}$$

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showing that in fact α is independent of time at the extremum. Thus (3.2) again applies for η^S_{PT} provided that ρ is replaced by

$$\rho_S = \frac{I_2}{I_1} - 1, \quad I_m = \int_0^T \Phi_{mm}\,\mathrm{d}t, \quad m = 1, 2. \tag{6.3}$$

There is however a difficulty with this definition of η^S_{PT} which occurs in straight-line swimming if $U(t)$ changes sign, as in a 'two steps forward, one step back' stroke. For example *Chlamydomonas* propels its cell body using two flagella in a 'breast stroke' involving a stroke pattern similar to the in-plane stroke of a cilium (see e.g. Bayly *et al.* 2011). According to our construction, the backward motion would still contribute to work, with the position of the tether switched from back to front. One way to remove this difficulty is to restrict the integrals in (6.3) to intervals where the motion is forward. However this results in a positive thermodynamic efficiency for a non-swimming, 'one step forward, one step back' stroke, as for a scallop, even though for a fixed tether and weight no external work is done.

We are thus led to consider fixing the weight and the position of the tether once and for all, rather than fixing the α, but to allow only weights which result in a non-negative work over the stroke. This is intuitively appealing as the logical extension of the instantaneous calculation. It seems reasonable to fix the weight to the tether, compute whatever efficiency seems appropriate, then optimize over the weight. Since the tether is not changed during backward motion, the velocity is increased by the weight, so $\alpha > 1$ and negative work is done. For example, in the case of a scallop, it is easily seen that the only way to achieve non-negative work under this scheme is to set $w = 0$ so that $\eta^S_{PT} = 0$.

To effect this change we need to now eliminate α in favour of w, calculate

$$\int_0^T W(t)\,\mathrm{d}t \Big/ \left(\int_0^T W(t)\,\mathrm{d}t + \int_0^T Q(t)\,\mathrm{d}t \right) \tag{6.4}$$

in terms of w, then optimize over w. In the notation of § 3, $w = k(1-\alpha)U$ so that $\alpha = 1 - (w/kU)$. Then $W(t) = \alpha U w = Uw - k^{-1}w^2$. We thus require w to be consistent in that $I_k w/I_U \leqslant 1$ where

$$I_U = \int_0^T U(t)\,\mathrm{d}t, \quad I_k = \int_0^T k^{-1}(t)\,\mathrm{d}t. \tag{6.5}$$

In particular, necessarily $I_U \geqslant 0$. Then

$$\eta^S_{PT} = \max_w \left[\frac{I_U w - I_k w^2}{I_2 - I_1 + w I_U} \right]. \tag{6.6}$$

The optimum w may be seen to be consistent, and we obtain

$$\eta^S_{PT} = 1 + 2\rho_S - 2\sqrt{\rho_S + \rho_S^2}, \tag{6.7}$$

provided that we define

$$\rho_S = \frac{(I_2 - I_1)I_k}{I_U^2}. \tag{6.8}$$

We propose that the definition (6.8) for (6.7) provides the natural potential thermodynamic efficiency for a swimming stroke based on the idea of partial tethering, in the restricted case considered.

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Let us see now how this idea works out in the general case. A hint as to the proper procedure is suggested by rewriting (6.6) in terms of α_S defined by $w \equiv (I_U/I_k)(1-\alpha_S)$:

$$\eta_{PT}^{S} = \max_{\alpha_S} \frac{\alpha_S(1-\alpha_S)}{\rho_S + 1 - \alpha_S}. \tag{6.9}$$

Thus the stroke efficiency takes the form of instantaneous efficiency using appropriate global variables. Can we approach the general problem in a similar way? It turns out that this is the case, although the form taken by ρ_S is considerably more complicated. It will suffice to indicate here that (6.7) still applies, with

$$\rho_S = \frac{\displaystyle\int_0^T (\Phi_{22}(t) - \Phi_{11}(t))\,\mathrm{d}t}{\mathscr{F}}, \tag{6.10}$$

where $\mathscr{F}$ is a number determined entirely by integrals over a stroke period, involving combinations of the given functions $\boldsymbol{U}(t)$, $\boldsymbol{\Omega}(t)$, $\boldsymbol{A}(t)$, $\boldsymbol{B}(t)$, $\boldsymbol{D}(t)$. We outline the computation and give these results in the Appendix.

7. Concluding remarks

In this paper we have introduced an efficiency for Stokesian locomotion, based upon the concept of partial tethering, as an approach allowing the swimmer to do work external to the system of body and fluid. In the Stokesian setting the efficiency is defined instantaneously by the current value of $\Phi_{11}(t)/\Phi_{22}(t)$. Our results show that the efficiencies commonly derived from the Froude model significantly overestimate the thermodynamic value. We also find that there is a natural extension of the instantaneous efficiency to the finite time interval of a swimming stroke.

Our analysis depends fundamentally upon the linearity of the Stokes equations, to effect the separation discussed in § 2. However the general idea could in principle be applied to swimming at any Reynolds number. For example, for a non-rotating, steady swimmer the velocity could be computed with a tether at weight w, and simultaneously Q calculated; η_{PT} would then be determined by calculations over many choices of w. However partial tethering may not be the best way to evaluate the swimming of fish, for example. Schultz & Webb (2002) have argued that speed and total power consumption in free swimming provide the best measures.

Swimming may serve other purposes than simple locomotion from A to B. We mention in particular the diverse mechanisms used by micro-organisms for feeding, all of which involve either swimming through or stirring of the fluid. The stirring of the fluid by the passage of swimming bodies has recently received attention as a possible addition to mixing in the world's oceans, see Thiffeault & Childress (2010) and Lin, Thiffeault & Childress (2011). A measure of efficiency of a feeding strategy involving the effort needed to carry out the strategy would be useful but probably have little to do with the efficiencies discussed in this paper. However Michelin & Lauga (2011) relate optimal feeding to optimal swimming in a particular case, suggesting perhaps a closer link than we have implied above.

We mention two contributions related to the present work that came to the attention of the author only recently. Chattopadhyay *et al.* (2006) carried out an elegant experiment using an optical trap to determine the force needed to hold a bacterium in place against its swimming effort. This in effect achieves total tethering with $\alpha = \beta = 0$ and allows a direct measurement of force and torque for the tethered organism. The efficiency η_M' was thereby determined to be 0.017. Raz & Leshansky

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(2008) considered the towing of a 'cargo', a passive body attached to the swimmer, and calculated efficiencies using a Stokesian Froude efficiency kU^2/Q where k is the resistance coefficient of the load, and Q now includes the dissipation of the cargo as well as the added effort exerted by the organism to tow it. From the point of view of the present paper, the towing cell and the cargo comprise a single swimmer with its own thermodynamic efficiency. However a given system of this kind is equivalent (in steady locomotion) to a partially tethered organism lifting a weight determined by the force coefficient of the cargo and the swimming speed. Examples are treated showing that there is a size ratio between cell body and cargo which maximizes efficiency, yielding a number analogous to our potential thermodynamic efficiency.

We close with a few caveats concerning the relevance of η_{PT} to the assessment of locomotion in Nature. The efficiency calculated here omits the metabolic contribution, the internal 'engine' of the organism, to the heat. We also leave untouched the question of the importance of efficiency to the organism. If the cost of the swimming effort is negligible, propulsive mechanisms may be largely independent of the issues considered here. A related point concerns the sensitivity of optimization to the parameters of locomotion. For example, for the model of § 5 the optimal $\eta_{PT}(r, r_d)$ increases from $\sim$0.0060 to 0.0076 when $r = 0.7$, as r_d is increased from 5 to 30. Given this modest gain over a large variation of the parameter, constraints other than efficiency are likely to be determining. Finally, we remark that for comparative purposes it should be emphasized that all of the efficiencies considered here are increasing functions of Φ_{11}/Φ_{22} and so would lead to the same relative ordering of swimming behaviours.

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Appendix. Stroke efficiency in the general case

Keeping the notation of § 4 we eliminate α, β in terms of w, m using

$$\left.\begin{aligned} wU &= (1-\alpha)\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U} + (1-\beta)\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega}, \\ m\Omega &= (1-\alpha)\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega} + (1-\beta)\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}. \end{aligned}\right\} \tag{A 1}$$

Thus

$$\alpha = 1 + D^{-1}[m\Omega\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega} - wU\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}], \tag{A 2}$$

$$\beta = 1 + D^{-1}[wU\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega} - m\Omega\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}], \tag{A 3}$$

where

$$D = \boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}\,\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega} - (\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega})^2\,. \tag{A 4}$$

The work done over one stroke is

$$W = \int_0^T [\alpha(1-\alpha)\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U} + (\alpha+\beta-2\alpha\beta)\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega} + \beta(1-\beta)\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}]\,\mathrm{d}t, \tag{A 5}$$

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and we must evaluate

$$\eta_T^S(\alpha,\beta)=\frac{W}{I_2-\displaystyle\int_0^T[\alpha^2\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}+2\alpha\beta\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega}+\beta^2\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}]\,\mathrm{d}t-W} \tag{A 6}$$

as a function of the constants w, m. Inserting the expressions for $\alpha(w,m)$, $\beta(w,m)$ into (A 6) we obtain after some reduction

$$\eta_T^S(w,m)=\frac{wI_U+mI_\Omega-I_{ww}w^2+2I_{wm}wm-I_{mm}m^2}{I_2-I_1+wI_U+mI_\Omega}, \tag{A 7}$$

where

$$I_\Omega=\int_0^T\Omega(t)\,\mathrm{d}t,\quad I_{ww}=\int_0^T D^{-1}\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}U^2\,\mathrm{d}t, \tag{A 8}$$

$$I_{wm}=\int_0^T D^{-1}\boldsymbol{U}\cdot\boldsymbol{B}\cdot\boldsymbol{\Omega}U\Omega\,\mathrm{d}t,\quad I_{mm}=\int_0^T D^{-1}\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}\Omega^2\,\mathrm{d}t. \tag{A 9}$$

Differentiating $\eta_T^S(w,m)$ we obtain the relation

$$m=\frac{I_UI_{wm}+I_\Omega I_{ww}}{I_\Omega I_{wm}+I_UI_{mm}}w. \tag{A 10}$$

Rather than proceeding to maximize w, m, we now define, on the basis of (A 2), (A 3), the constants

$$\alpha_S=1+m\frac{I_{wm}}{I_U}-w\frac{I_{ww}}{I_U},\quad \beta_S=1+w\frac{I_{wm}}{I_\Omega}-m\frac{I_{mm}}{I_\Omega}. \tag{A 11}$$

Thus

$$w=D_I^{-1}[I_{mm}I_U(1-\alpha_S)+I_{wm}I_\Omega(1-\beta_S)], \tag{A 12}$$

$$m=D_I^{-1}[I_{wm}I_U(1-\alpha_S)+I_{ww}I_\Omega(1-\beta_S)], \tag{A 13}$$

where

$$D_I=I_{ww}I_{mm}-I_{wm}^2. \tag{A 14}$$

Inserting (A 12), (A 13) into (A 7), the result may be written

$$\eta_T^S(\alpha_S,\beta_S)=\frac{\alpha_S(1-\alpha_S)a_S+(\alpha_S+\beta_S-2\alpha_S\beta_S)b_S+\beta_S(1-\beta_S)c_S}{\rho_S+(1-\alpha_S)a_S+(2-\alpha_S-\beta_S)b_S+(1-\beta_S)c_S}. \tag{A 15}$$

Here

$$(a_S,b_S,c_S)=\frac{(c_{mm},c_{wm},c_{ww})}{c_{mm}+2c_{wm}+c_{ww}}, \tag{A 16}$$

where

$$c_{ww}=D_I^{-1}I_{ww}I_\Omega^2,\quad c_{wm}=D_I^{-1}I_{wm}I_UI_\Omega,\quad c_{mm}=D_I^{-1}I_{mm}I_U^2, \tag{A 17}$$

and

$$\rho_S=\frac{I_2-I_1}{c_{mm}+2c_{wm}+c_{ww}}. \tag{A 18}$$

It follows that

$$\eta_{PT}^S=1+2\rho_S-\sqrt{\rho_S^2+\rho_S} \tag{A 19}$$

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as stated at the end of § 6. Note that the optimizing equation $\alpha_S = \beta_S$ is equivalent to (A 10). Also the properties of the stroke parameters given in § 4, together with the assumption $b \geqslant 0$, ensure that $c_{mm} + 2c_{wm} + c_{ww} > 0$ provided that $D_I \geqslant 0$. But this follows from

$$I_{wm} \leqslant \int_0^T D^{-1}\sqrt{\boldsymbol{U}\cdot\boldsymbol{A}\cdot\boldsymbol{U}}\sqrt{\boldsymbol{\Omega}\cdot\boldsymbol{D}\cdot\boldsymbol{\Omega}}U\Omega \,\mathrm{d}t \leqslant I_{ww}^{1/2} I_{mm}^{1/2} \tag{A 20}$$

using the Cauchy–Schwarz inequality.

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