

SLENDER SWIMMERS IN STOKES FLOW

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Abstract

In this study, motion of slender swimmers, which propel themselves by generating travelling surface waves, is investigated. In the first approach, slender-body theory (SBT) is used to calculate the propulsion speed. The mathematical machinery used is based on the SBT by Keller & Rubinow [1]. The object considered is of arbitrary cross-section, and the surface waves considered are axisymmetric. The object is modelled using Stokeslet and source distributions along its axis. The propulsion speed is obtained by imposing the condition that the net force on the swimmer, as inertia is absent, is zero.

In the second approach, the object is assumed to be filled with a viscous incompressible fluid and its surface is assumed elastic, and the propulsion speed due to the peristaltic motion of fluid inside is calculated. Also, an improved definition of swimmer efficiency, which takes internal dissipation into account, is introduced.

1 Introduction

A swimmer is defined as “a creature or an object that moves by deforming its body in a periodic way” [2]. The way macroscopic organisms propel themselves is by using inertia of the surrounding fluid. Propulsion in the forward direction is generated due to the intermittent forces acting on the object by the surrounding fluid as a reaction to its pushing the fluid backwards [3]. The typical Reynolds number (Re), which is defined as:

$$Re \equiv \frac{F_i}{F_v} = \frac{UL}{\nu}, \quad (1)$$

where F_i and F_v are inertial and viscous forces, U is the velocity scale, L is the length scale and ν is the kinematic viscosity of the fluid, in the inertial (or Eulerian) regime is $10^2 - 10^6$ for different organisms. Swimming in the Eulerian regime can be broken into components of propulsion and drag; the former is due to some specialized organs which push the fluid backwards, thereby generating a thrust force in the opposite direction, and the latter is because of the forces encountered due to the moving object in a viscous fluid [4]. However, in the Stokes regime ($Re \approx 0$) there is no inertia, and the organisms at those small length scales have to exploit viscous stresses to generate propulsion. Typical range of Re for swimmers in this regime is $10^{-4} - 10^{-1}$.

The study of swimming microorganisms began with Taylor's study of propulsion speed induced on a transversely oscillating two-dimensional sheet in the Stokes regime [4]. Taylor showed that propulsion in a highly viscous environment is possible when an object deforms itself in a way that would generate propulsive forces in the surrounding fluid. He pointed out that separation of swimming into propulsive and drag components in the Stokes regime would lead to Stokes paradox, and that the propulsion is due to exploiting the viscous stresses due to surface deformation. Taylor's analysis has been extended by Lighthill [5] and Blake [6] to study the motion of spheres and cylinders with travelling surface waves respectively.

Stokesian swimmers (swimmers in the Stokes regime) are broadly classified into ciliates and flagellates [3]. The former set have small cilia on their surfaces, which are used for propulsion. Some of the microorganisms which fall into this category are: Paramecium (figure 1) and Opalina. The latter have flagella at the ends which rotate in a helical fashion, or oscillate in the transverse direction to generate propulsion. Spermatozoa (figure 2) and E. Coli are examples of microorganisms in this category.



Figure 1: Pictures showing paramecium. The fine cilia around the surfaces can be clearly seen. Paramecium uses these cilia to propel itself at a top speed of $500\mu\text{m}/\text{s}$.



Figure 2: Picture showing spermatozoa. Each cell has a flagellum down which the cell sends bending waves to propel itself.

2 Creeping Flow Limit ($Re \approx 0$)

The equation of motion for a viscous fluid are the Navier-Stokes equation:

$$\frac{\partial \mathbf{u}'}{\partial t'} + \mathbf{u}' \cdot \nabla' \mathbf{u}' = -\frac{1}{\rho} \nabla' P' + \nu \nabla'^2 \mathbf{u}', \quad (2)$$

$$\nabla \cdot \mathbf{u}' = 0. \quad (3)$$

Here, $\mathbf{u}' \equiv \mathbf{u}'(\mathbf{x}', t)$ is the velocity field, $P' \equiv P'(\mathbf{x}', t)$ is the pressure field, ρ is the density of the fluid, and ν is the kinematic viscosity of the fluid. Equation 3 results when the flow is assumed incompressible.

In the Stokes regime, the pressure has to be scaled with viscosity, so that the viscous term is balanced by it. To non-dimensionalize equation 2, the following scales are used: $\mathbf{u} = \mathbf{u}'/U$, $\mathbf{x} = \mathbf{x}'/L$, and $P = P'/(μU/L)$, where U and L are some velocity and length scales. Once equation 2 is scaled this way, the resulting equation is:

$$Re \left(\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla P + \nabla^2 \mathbf{u}. \quad (4)$$

Substituting $Re = 0$ gives the Stokes equations:

$$\nabla P = \nabla^2 \mathbf{u}; \quad \nabla \cdot \mathbf{u} = 0. \quad (5)$$

Equations 5 are linear, and remain unchanged if the following transformations are effected: $\mathbf{u} \rightarrow -\mathbf{u}$ and $\mathbf{x} \rightarrow -\mathbf{x}$. This implies that the equations are reversible if the velocity and displacement vectors are reversed. One more implication of the linearity is that flow depends instantaneously on the boundary conditions. If the boundary ceases to move then there would be no fluid motion at all. This is a consequence of inertia being absent from the system. This places a strong constraint on the Stokesian swimmers as to how they can deform their bodies to generate propulsive forces.

Purcell summed these effects in his famous scallop theorem, which states that an object in the $Re \approx 0$ regime cannot swim by executing strokes that are “reciprocal” in time [7]. A good example of such a creature is a scallop, which is a swimmer in the Eulerian regime, but has only one degree of freedom. It generates propulsion by quickly closing its shell, thereby pushing the fluid out through its hinge at a high speed, resulting in thrust. Re for this motion is $O(10^5)$ [3]. It then opens its shell very slowly, thereby transferring negligible momentum to the fluid. In the Stokes regime this mechanism would not work, as there is no time in the equations. The scallop’s net displacement would be zero [3].

3 Motivation

As mentioned in the previous section, the propulsion mechanisms of ciliates and flagellates have been well studied for the past 62 years; but there are certain organisms like *Synechococcus* (a type of Cyanobacteria) which neither possess cilia nor flagella on their surface, yet they manage to move at around $25\mu m/s$ [8]. Ehlers *et al.* [8] studied the motion of this bacterium and suspected that the motion might be due to travelling surface waves. However, the bacterium was modelled as a sphere, though it has an aspect ratio, $\epsilon = a/L$, where a is

the diameter and L is the length of the bacterium, $\epsilon < 1$. These bacteria are abundant in the oceans and are a primary source of nutrients to the organisms lying above them in the food chain [9]. Using slender-body theory to find the propulsion speed, so as to take the small aspect ratio into account, is one of the aims of this study.



Figure 3: Synechococcus, a type of Cyanobacteria. It neither has cilia nor flagella to propel itself, and is suspected to use travelling surface waves [8].

Collective motion of microorganisms has been studied in various contexts, and recently it has been speculated that these organisms might be involved in the large scale mixing of oceans – called biogenic mixing of ocean [10]. Hence, a study of the motion of individual cells, which can be used to construct a continuum model for this species, becomes important.

4 Slender-Body Theory

Slender-body theory was developed to exploit the small aspect ratio of objects in calculating the disturbance flow field set up by them in the Stokes regime ($Re \approx 0$). SBT has been able to resolve the Stokes paradox for the case of cylinder, where the governing equations in the two-dimensional form have a logarithmic singularity at infinity. The scale dependence of drag on the cylinder on the aspect ratio can be found using SBT.

In the following analysis, velocities have been scaled by the travelling surface wave speed (c), distances have been scaled with the length of the slender body (L), and time by L/c .

The following are the different regions around the slender object, where different equations are solved:

- **Inner region:** This is the region where the distance from the cylinder, ρ , is such that $\rho \ll L$. One would sense the object to be two-dimensional in this limit, so the governing equation for the fluid flow would be the two-dimensional Stokes equations. The object is assumed to move only along its axis, which is taken to be the z -axis. The velocity field set up due to this can be written down as:

$$\mathbf{u}_{inner}(\mathbf{x}) \sim \mathbf{k}\beta(z) \log\left(\frac{\rho}{a}\right) + \mathbf{e}_r \frac{1}{2\rho} \frac{\partial a^2}{\partial t}, \quad (6)$$

where $\beta(z)$ is some function of z and $a(z, t)$ is the radius of the object. $\beta(z)$ is unknown, and has to be found by matching this solution to the outer solution.

- **Outer region:** In this limit, $|\mathbf{r}| \gg a$. The flow senses the three-dimensional body. However, owing to the small aspect ratio, the object appears to be a singular line from far, and hence can be modelled using singular distributions of force and source densities. The velocity field in this region can be written as:

$$\mathbf{u}_{outer}(\mathbf{x}) = \mathbf{W} + \int_0^1 \left(\frac{\alpha \mathbf{k}}{R} + \frac{\mathbf{R} \mathbf{R} \cdot \mathbf{k} \alpha}{R^3} + \frac{\delta \mathbf{R}}{R^3} \right), \quad (7)$$

where $\alpha(z)\mathbf{k}$ is the Stokeslet distribution, and $\delta(z)$ is the source distribution along the slender body, $\mathbf{W}$ is the far-field velocity of the fluid, and $\mathbf{R} = \mathbf{R}_0 + (z - z')\mathbf{k}$ is the position vector of the point under consideration from the point z' on the centre-line of the object. $\alpha(z)$ is the singular force distribution and $\delta(z)$ is the singular source distribution. The velocity field due to these distributions automatically satisfies the far-field boundary condition of $\mathbf{u}(\mathbf{x}) \rightarrow \mathbf{W}$ as $|\mathbf{x}| \rightarrow \infty$. Both $\alpha(z)$ and $\delta(z)$ are unknown, and have to be found by matching this solution to the inner solution.

- **Matching region** In this region, both the inner and outer solutions are valid. The unknown terms in both these velocity fields are obtained by equating the two velocity fields in the following limits:

$$\lim_{\rho \rightarrow \infty} \mathbf{u}_{inner}(\mathbf{x}) = \lim_{R_0 \rightarrow 0} \mathbf{u}_{outer}(\mathbf{x}). \quad (8)$$

Both sides of equation 8 have singularities (logarithmic and algebraic), which balance each other.

4.1 Evaluation of the Outer Velocity Field

The outer velocity field is partially evaluated to separate out the singularities and to explicitly find their forms. Guided by our knowledge of the inner velocity field we should have $\log(R_0)$ and $1/R_0$ singularities hidden in the $\mathbf{u}_{outer}(\mathbf{x})$ term too. To do this we separate the right hand side (RHS) of equation 7 as in the following:

$$\begin{aligned} u_{z,outer}(\mathbf{x}) = & W + \int_0^1 \frac{\alpha(z') - \alpha(z)}{R} dz' + \int_0^1 \frac{\alpha(z') - \alpha(z)}{R^3} (z - z')^2 dz' \\ & + \int_0^1 \frac{\delta(z') - \delta(z) - \delta_z(z)(z' - z)}{R^3} (z - z') dz' + \int_0^1 \frac{\alpha(z)}{R} dz' \\ & + \int_0^1 \frac{\alpha(z)}{R^3} (z - z')^2 dz + \int_0^1 \frac{\delta(z) + \delta_z(z)(z' - z)}{R^3} (z - z') dz'. \end{aligned} \quad (9)$$

Except for the last three integrals in equation 9 the remaining integrals are well behaved. One can take the limit of $R_0 \rightarrow 0$ in the regular integrals, which on simplification give

$$\begin{aligned}
u_{z,outer}(\mathbf{x}) = & W + 2 \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} dz' + \int_0^1 \frac{\delta(z') - \delta(z) - \delta_z(z)(z' - z)}{|z - z'|(z - z')} dz' \\
& + 2 \int_0^1 \frac{\alpha(z)}{R} dz' + \int_0^1 \frac{\delta(z) + \delta_z(z)(z' - z)}{R^3} dz'.
\end{aligned} \tag{10}$$

The singular integrals can be further evaluated by substituting $(z' - z) = R_0 \tan \theta$, and these, after some algebra and further simplification, give the following:

$$\int_0^1 \frac{\alpha(z)}{R} dz' = \alpha(z) \{-2 \log(R_0) + \alpha(z) \log[4z(1 - z)]\}; \tag{11}$$

$$\int_0^1 \frac{\alpha(z)}{R} (z - z')^2 dz' = \alpha(z) \{-2 \log(R_0) + \alpha(z) \log[4z(1 - z)] - 2\}; \tag{12}$$

and,

$$\int_0^1 \frac{\delta(z) + \delta_z(z)(z' - z)}{R^3} (z - z') dz' = \delta(z) \frac{2z - 1}{z(1 - z)} + \delta_z(z) \{2 \log(R_0) - \log[4z(1 - z)] + 2\}. \tag{13}$$

Combining equations 10, 11, 12 and 13 and equating it to the z-component of the inner velocity field, we get

$$\begin{aligned}
\beta(z) \log\left(\frac{\rho}{a}\right) = & W + 2 \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} dz' + \int_0^1 \frac{\delta(z') - \delta(z) - \delta_z(z)(z' - z)}{|z - z'|(z - z')} dz' \\
& - 4\alpha(z) \log(R_0) + 2\alpha(z) \log[4z(1 - z)] + \delta(z) \frac{1 - 2z}{z(1 - z)} - 2\alpha(z) \\
& + 2\delta_z(z) \log(R_0) - \delta_z(z) \log[4z(1 - z)] + 2\delta_z(z).
\end{aligned}$$

Equating the terms having the logarithmic singularity gives:

$$\beta(z) = -4\alpha(z) + 2\delta_z(z);$$

and the remaining terms give an integral equation for $\alpha(z)$:

$$\begin{aligned}
\alpha(z) = & \frac{\delta_z(z)}{2} + \frac{1}{4 \log a} \left\{ W + 2 \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} dz' + \right. \\
& \int_0^1 \frac{\delta(z') - \delta(z) - \delta_z(z)(z' - z)}{|z - z'|(z - z')} dz' + 2\alpha(z) \log[4z(1 - z)] \\
& \left. + \delta(z) \frac{2z - 1}{z(1 - z)} + \delta_z(z) \{2 - \log[4z(1 - z)]\} \right\}.
\end{aligned} \tag{14}$$

Carrying out a similar analysis for the integral in the radial direction gives:

$$\delta = \frac{1}{4} \frac{\partial a(z, t)^2}{\partial t}. \tag{15}$$

The integral equation for $\alpha(z)$ can be solved iteratively, as done by Keller & Rubinow or by using asymptotic series for α and W in powers of $1/\log(\epsilon)$, where $\epsilon = A/L$ is the aspect ratio, which according to the slender body approximation is $\epsilon \ll 1$. We choose to solve the integral equation using the latter method. From 15, $\delta \sim \epsilon^2$. So, the leading order terms for α and W are $\sim \epsilon^2$. Canceling this common factor from equation 14, and using the following asymptotic series:

$$\begin{aligned}\alpha &= \alpha_0 + \frac{\alpha_1}{\log \epsilon} + \frac{\alpha_2}{(\log \epsilon)^2} + O\left[\frac{1}{(\log \epsilon)^3}\right] \\ W &= W_0 + \frac{W_1}{\log \epsilon} + \frac{W_2}{(\log \epsilon)^2} + O\left[\frac{1}{(\log \epsilon)^3}\right]\end{aligned}$$

in the integral equation 14, and equating terms of the same order we get:

- $O(1)$

$$\alpha_0 = \frac{\Delta_z}{2},$$

where $\Delta_z = \delta_z/\epsilon^2$. Provided $a(z, t)$ vanishes at the ends, the requirement that the force on the object at this order vanishes is automatically satisfied, i.e., $\int_0^1 \alpha_0 dz = 0$.

- $O(1/\log \epsilon)$

$$\alpha_1 = \frac{W_0}{4} + \frac{\alpha_0}{2} + \frac{1}{2} \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} dz' + \frac{1}{4} \int_0^1 \frac{\Delta(z') - \Delta(z) - \Delta_z(z)(z' - z)}{|z - z'|(z - z')} dz' + \Delta(z) \frac{2z - 1}{z(1 - z)}.$$

Imposing the same condition, i.e., $\int_0^1 \alpha_1 dz = 0$, we find the swimming velocity at the leading order to be:

$$\begin{aligned}W_0 &= -2 \int_0^1 \alpha_0 dz - 2 \int_0^1 \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} dz' dz \\ &\quad - \int_0^1 \int_0^1 \frac{\Delta(z') - \Delta(z) - \Delta_z(z)(z' - z)}{|z - z'|(z - z')} dz' dz - \int_0^1 \Delta(z) \frac{2z - 1}{z(1 - z)} dz\end{aligned}$$

However, after some calculation, it turns out the speed at this order is zero. So, the speed at the next order has to be considered.

- $O(1/(\log \epsilon)^2)$

$$\begin{aligned}\alpha_2 &= -\frac{W_0}{8} \log A^2 - \frac{1}{4} \int_0^1 \frac{\alpha(z') - \alpha(z)}{|z - z'|} \log A^2 dz' \\ &\quad - \frac{1}{8} \int_0^1 \frac{(\Delta(z') - \Delta(z) - \Delta_z(z)(z' - z))}{|z - z'|(z - z')} \log A^2 dz' - \frac{1}{4} \alpha_0 \log A^2\end{aligned}$$

After imposing the condition $\int_0^1 \alpha_2 = 0$, and some algebra, we obtain the general form of the propulsion speed to be:

$$W_1 = -\frac{1}{8} \int_0^1 \frac{\partial^2 A^2}{\partial t \partial z} \log A^2 dz. \quad (16)$$

Equation 16 is the general form of the propulsion speed for a slender body with an arbitrary cross-section. Taking the time average of this equation gives:

$$W_1 = \frac{1}{8} \frac{k}{2\pi} \int_0^1 \int_0^{2\pi/k} \frac{\partial A^2}{\partial z} \frac{1}{A^2} \frac{\partial A^2}{\partial t} dt dz. \quad (17)$$

The general form of the time-averaged propulsion speed of a slender swimmer at the leading order is 17. One needs the information about the way the swimmer is deforming its surface to determine its speed, i.e., the form of the travelling surface waves. Two models are considered in the next section, which lead to propulsion speeds specific to the models of surface deformation considered.

5 Models for Surface Deformation

5.1 Model - 1

Assuming the surface deforms as: $A^2 = f(z)^2 [1 + \theta \sin(kz - kt)]$, and using this in equation 16 gives the propulsion speed as:

$$W = \frac{\epsilon^2}{\log 1/\epsilon} \frac{k^2}{8} S(\theta) \int_0^1 f(z)^2 dz, \quad (18)$$

where $S(\theta) = [1 - (1 - \theta^2)^{1/2}] \approx \theta^2 \left(\frac{1}{2} + \frac{\theta^2}{8} + \dots \right)$, and $f(z)$ represents the undeformed radius of the object. A schematic of the model for $f(z)^2 = 4z(1 - z)$ is shown in figure 4.

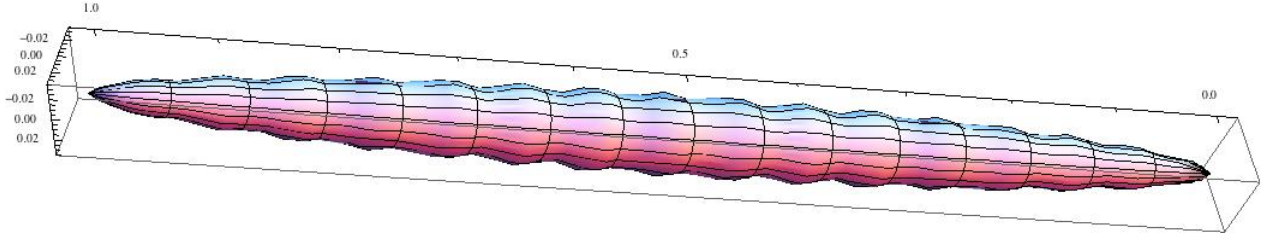


Figure 4: A schematic for model-1, which is $A^2 = f(z)^2 [1 + \theta \sin(kz - kt)]$, where $f(z)^2 = 4z(1 - z)$.

At the leading order, the solution obtained resembles one obtained by Taylor [4]. To test the correctness of the solution, we consider the solution obtained by Setter *et al.* [12] for the case of an infinite cylinder moving due to travelling surface waves. Propulsion speed in that case is:

$$W_{Setter} = -\frac{k^2 \epsilon^2 (\theta/2)^2}{2} \frac{\beta [K_0(\beta)^2 - K_1(\beta)^2]}{\beta K_1(\beta)^2 - 2K_1(\beta)K_0(\beta) - \beta K_0(\beta)^2},$$

where $\beta = ka$ is their non-dimensional radius, $K_0(\beta)$ and $K_1(\beta)$ are modified Bessel functions of second kind of order zero and one respectively. In the limit $\beta \rightarrow 0$, the above solution reduces to:

$$W_{Setter} = \frac{k^2 \epsilon^2 \theta^2}{16 \log(\beta)},$$

which is exactly what we get at the leading order when we substitute $f(z) = 1$ in equation 18.

5.2 Model-2

If one considers the peristaltic motion of fluid inside the organism, assuming that it is completely filled with a viscous incompressible fluid, then model-1 would not be suitable as it does not conserve volume. Hence, a second model for surface area, which conserves volume and vanishes at the ends, is introduced. It is given by:

$$A^2 = \frac{\partial}{\partial z} \left[2z^2 \left(1 - \frac{2z}{3} \right) + 4\theta z^2(1-z)^2 \cos(kz - kt) \right]. \quad (19)$$

The undeformed object is a prolate spheroid, which is $f(z)^2 = 4z(1-z)$ in this case. A schematic of the model is shown in 5.

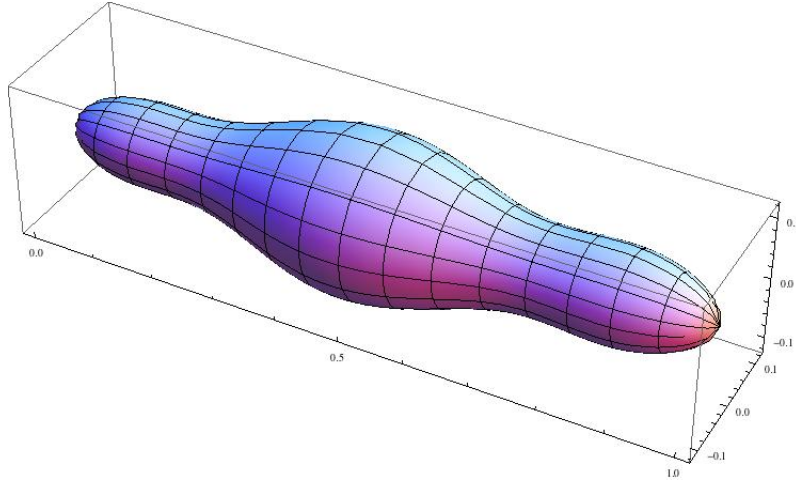


Figure 5: A schematic for model-2, which is $A^2 = \frac{\partial}{\partial z} \left[2z^2 \left(1 - \frac{2z}{3} \right) + 4\theta z^2(1-z)^2 \cos(kz - kt) \right]$.

Using equation 19 in expression 17, we get the propulsion speed as:

$$W = \frac{16k^2\theta^2\epsilon^2}{\log 1/\epsilon} \frac{1}{2\pi} \int_0^1 \int_0^{2\pi} \frac{2G'^2 \sin^2 \phi - G \cos^2 \phi (G'' - k^2 G)}{F + 4\theta (G' \cos \phi - Gk \sin \phi)} d\phi dz, \quad (20)$$

where $F = 4z(1-z)$, $G = z^2(1-z)^2$ and the primes denote the derivatives. Solving equation 20 for $\epsilon = 0.2$ and $\theta = 0.1$ for $1 \leq k \leq 20$, we get the propulsion speed as shown in figure 6. It can be shown by curve fitting that for this model $W \sim k^3$.

This model will be used when we re-define efficiency based on internal dissipation.

6 Efficiency

Efficiency of swimmers can be calculated based on the power input to the swimmer by the surrounding fluid, and energy lost due to drag forces during its motion [13]. The calculations

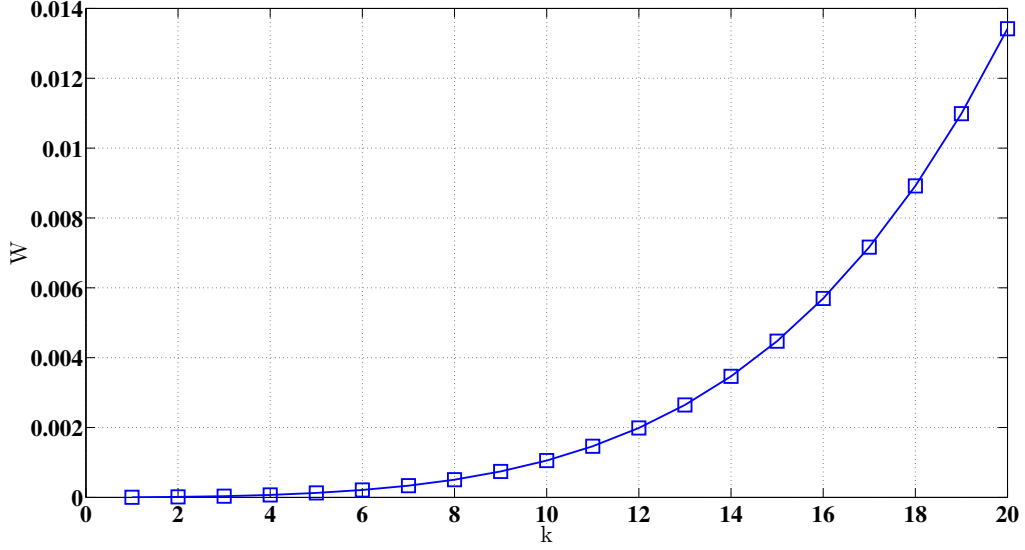


Figure 6: W vs. k for $\epsilon = 0.2$ and $\theta = 0.1$. From this model, $W \sim k^3$.

in this section are for model-1 only, and it will be shown in the next section that when one considers the flow inside the organism, the energy spent in moving the fluid inside is far greater than the energy input outside, and hence it should be taken into account – at least when considering slender swimmers.

From SBT, the velocity field in the inner region can be written as:

$$\mathbf{u} = \beta(z) \log\left(\frac{\rho}{a}\right) \mathbf{k} + \frac{1}{2\rho} \frac{\partial a^2}{\partial t} \mathbf{e}_r.$$

The deviatoric stress tensor is given by:

$$\sigma' = \begin{pmatrix} \sigma_{\rho\rho} & 0 & \sigma_{\rho z} \\ 0 & \sigma_{\theta\theta} & 0 \\ \sigma_{z\rho} & 0 & \sigma_{zz} \end{pmatrix}$$

The unit vector at any point on the deformed surface of the object is given by:

$$\mathbf{n} = \frac{1}{\sqrt{1 + \left(\frac{\partial a}{\partial z}\right)^2}} \begin{pmatrix} 1 \\ 0 \\ \frac{\partial a}{\partial z} \end{pmatrix}$$

The power input to the object is given by: $P = -\int_S (\sigma \cdot \mathbf{n}) \cdot \mathbf{u} dS$, where σ ($= -p\mathbf{I} + \sigma'$) is the stress acting on the body, p is the pressure field, and $\mathbf{I}$ is the identity tensor. p can be calculated from the momentum equation, and it turns out to be $O(\epsilon^2)$. For the calculation of the term $(\sigma \cdot \mathbf{n}) \cdot \mathbf{u}$, we have:

$$(\sigma \cdot \mathbf{n}) \cdot \mathbf{u} \approx \left(\sigma_{\rho\rho} + \frac{\partial a}{\partial z} \sigma_{\rho z} \right) u_\rho + \left(\sigma_{z\rho} + \frac{\partial a}{\partial z} \sigma_{zz} \right) u_z.$$

u_z vanishes on the surface of the object, hence the second term in the above equation does not contribute to the power input. On calculating the stresses, we get:

$$\begin{aligned}\sigma_{\rho\rho} &= -\frac{\mu}{\rho^2} \frac{\partial a^2}{\partial t} = O(1); \\ \sigma_{\rho z} &= \mu \left(\frac{\partial u_\rho}{\partial z} + \frac{\partial u_z}{\partial \rho} \right).\end{aligned}$$

The first term in $\sigma_{\rho z}$ is $O(\epsilon)$ and the second term is $O(1/\log \epsilon)$, hence $\sigma_{\rho z}$ and p can be neglected in comparison to $\sigma_{\rho\rho}$. A little algebra gives the time-averaged power to be:

$$P = -\pi\mu k^2 \epsilon^2 S(\theta) \int_0^1 f(z)^2 dz.$$

Considering the body is moving with a constant speed W , the drag force exerted on it by the viscous fluid in the slender-body limit is [1]:

$$F_d = \frac{2\pi\mu}{\log 1/\epsilon} W;$$

and the dissipation due to this is:

$$D = -\frac{2\pi\mu}{\log 1/\epsilon} W^2;$$

So, the efficiency, $\eta = D/P$, is:

$$\eta = \frac{k^2 \epsilon^2}{32 (\log 1/\epsilon)^3} S(\theta) \int_0^1 f(z)^2 dz. \quad (21)$$

As can be seen from expression 21, the efficiency of the slender swimmer is $O[\epsilon^2/(\log 1/\epsilon)^3]$. This shows that the efficiency of these swimmers, like others, is not large.

7 Tube Dynamics

In this section, we consider the Stokes flow inside of the object. The object is supposed to be made of a viscous incompressible fluid, with its wall (cell wall) being elastic. The aim of doing this is to see if the definition of efficiency could be improved by including terms which are more dominant in the denominator.

Exploiting the small aspect ratio, one could write the equations of motion for the inside fluid to be (lubrication theory):

$$\begin{aligned}\frac{1}{r} \frac{\partial(ur)}{\partial r} + \frac{\partial w}{\partial z} &= 0; \\ \frac{\partial p}{\partial r} &= 0, \\ \frac{\partial p}{\partial z} &= \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial w}{\partial r} \right)\end{aligned} \quad (22)$$

[11] & [14]. It can be seen that pressure is only a function of the axial co-ordinate. The last equation can be integrated to give:

$$w(r) = \frac{1}{4} \frac{\partial p}{\partial z} (r^2 - a^2).$$

Now, the flux of mass across a cross-section is given by: $F = \int_0^a w 2\pi r dr$, which turns out to be

$$F = -\frac{\pi}{8} \frac{\partial p}{\partial z} a^4. \quad (23)$$

Assuming $a(z, t)$ is known, one can solve for the pressure by integrating the continuity equation, giving

$$\frac{\partial p}{\partial z} = \frac{8}{a^4} \int \frac{\partial a^2}{\partial t} dz = O\left(\frac{1}{\epsilon^2}\right). \quad (24)$$

The above result tells us that the pressure inside the body is far higher than the stresses outside. As has been seen earlier, the viscous normal stress and the pressure outside are $O(1)$ and $O(\epsilon)$ respectively, which are much smaller than the internal pressure which is $O(1/\epsilon^2)$. Calculating the power input from the inside, we get

$$P_{inside} = \int_0^1 \int_0^a r \left(\frac{\partial w}{\partial r} \right)^2 dr dz = \frac{1}{16} \int_0^1 \left(\frac{\partial p}{\partial z} \right)^2 a^4 dz = O(1). \quad (25)$$

The above expression shows that the power spent in moving the inside fluid is far greater than the power being imparted by the outside fluid for a small ϵ . Hence, the efficiency is re-defined as $\eta = D/P_{inside}$, and the input from the outside fluid is neglected.

To include the dissipation term from the inside of the organism, model-1 for the radius cannot be used as it does not conserve volume. A naive substitution of model-1 in to 24 leads to blowing up of pressure at the ends. For this reason model-2 is suitable as it both conserves volume and vanishes at the ends. As has been calculated previously, the propulsion speed generated using model-2 is given by expression 20. Hence, carrying out a similar calculation as has been done for model-1, one finds that the efficiency for model-2 would be $O\left[(\epsilon^2/\log 1/\epsilon)^2\right]$, which is much smaller than the model-1 efficiency.

From this, it can be concluded that if one considers the internal flow, the dissipation is much higher than the dissipation outside, and that the internal dissipation would have to be taken into account in the expression for the efficiency, which would lead to a much smaller value than obtained from just considering the outside dissipation.

8 Solving for the propulsion speed by considering peristaltic motion of the inside fluid

The analysis considered in this section is done by taking a completely different approach from what has been done in the previous sections. The organism is considered to be made up of a viscous incompressible fluid, and its surface is assumed elastic. One could think of the organism using some kind of actuators to exert a force in the radial direction in a particular sequence along its body. This would be responsible for the movement of fluid, as it would generate additional pressure inside. There would be two sources of resistance to this force:

pressure of the fluid and hoop stress. This is schematically shown in figure 7. The resistance due to the wall is modelled as a spring force, and the ‘actuator’ force is modelled as sinusoidal travelling wave down the body. As the pressure inside is $O(1/\epsilon^2)$ times larger than the viscous normal stress from the outside fluid, one can neglect the outside stresses and write the force balance on the surface as:

$$\underbrace{P}_{\text{Pressure}} = \underbrace{D[A(z,t) - f(z)]}_{\text{Spring-like}} + \underbrace{\Theta f(z) \sin(kz - kt)}_{\text{Muscles}}, \quad (26)$$

where D is the ‘spring constant’, Θ is the amplitude of actuator force, $A(z,t)$ is the deformed radius and $f(z)$ is the undeformed radius.

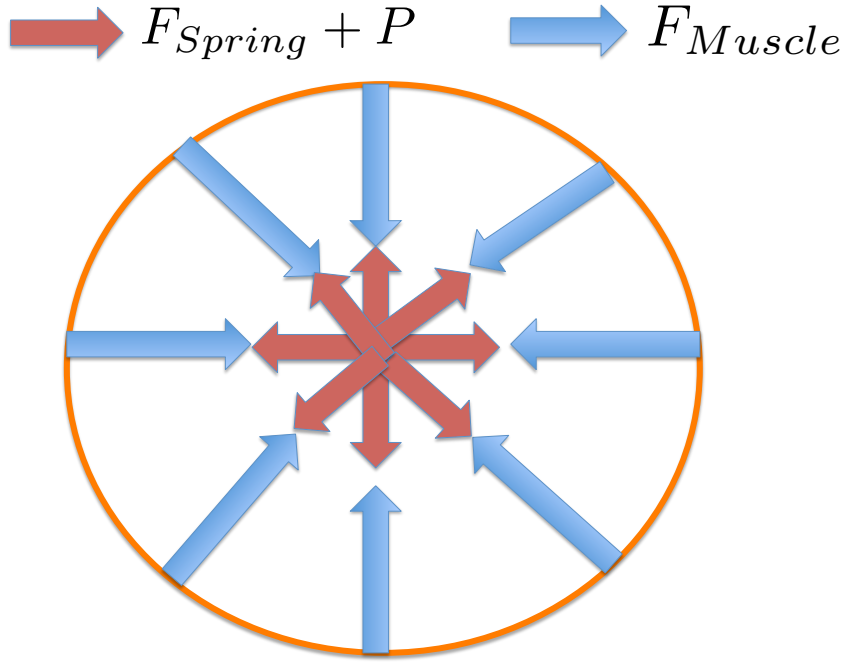


Figure 7: Force balance in the radial direction at a cross-section.

One can solve equation 26 for P , use this to determine $A(z,t)$ and use it in expression 17 to calculate the propulsion speed. The important point to note is that the flow inside is de-coupled from the flow outside, as the pressure is much larger in the inside, and outside stresses do not appreciably affect the flow inside. For this reason, one can make use of the result (equation 17) from slender-body analysis.

The integral form of equation 22 can be shown to be:

$$\frac{\partial (\pi a^2)}{\partial t} + \frac{\partial F}{\partial z} = 0, \quad (27)$$

where F is given by the expression 23. Equations 26 and 27 have to be solved in a time loop. To solve for $a(z,t)$, the initial condition chosen is the undeformed surface, which is $f(z)$. The following steps will lead to the mean propulsion speed:

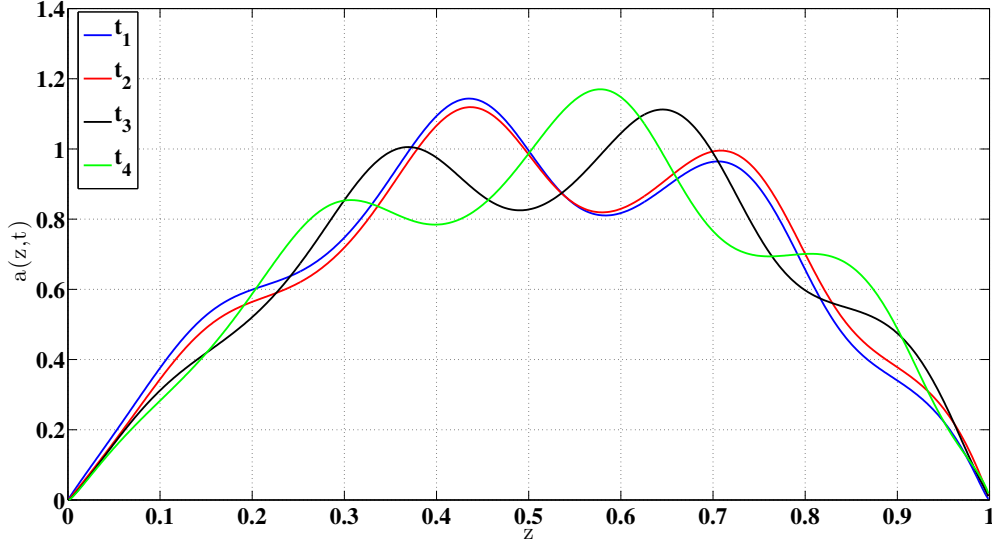


Figure 8: The radius of the organism at different time instances. The vertical axis has been magnified. Here, $t_1 < t_2 < t_3 < t_4$.

1. Solve for P using equation 26, and then calculate $\frac{\partial P}{\partial z}$.
2. Solve equation 27 numerically to obtain $a(z, t)$.
3. Compute $\frac{\partial^2 a(z, t)}{\partial t \partial z}$ and use it in expression 17 to calculate the propulsion speed.

The time evolution of the radius is shown in figure 8. This solution can now be used to compute the propulsion velocity and its mean. The solution for $D = 0.5$, $\Theta = 0.05$, $k = 20$ and $\epsilon = 0.05$ is shown in figure 9. It can be seen that W quickly settles into a periodic state due to the travelling surface waves shown in figure 8. From this the mean propulsion speed can be calculated. The same procedure can be used to compute for different ϵ , with the remaining parameters fixed to the values used in the plot 9. This is shown in figure 10. By curve fitting it can be shown that $W \sim \epsilon^2 / \log(1/\epsilon)$.

Carrying out a similar set of calculations with ϵ , D and Θ fixed to 0.02, 0.5 and 0.05 respectively, and varying k from 5 – 25, we find a quadratic trend in the propulsion speed, viz., $W \sim k^2$. This is shown in figure 11.

From the above results it is seen that the propulsion speed scales as $W \sim k^2 \epsilon^2 / \log(1/\epsilon)$, as was found for model-1. Hence, model-1 and force-balance approach differ from model-2, which was constructed to re-define the efficiency of the swimmer.

9 Summary and conclusions

In this study we have found the propulsion speed for a slender body with arbitrary cross-section, with the only condition that its radius vanishes at both ends. This study was partly motivated by the possible propulsion mechanism of cyanobacterium *Synechococcus* and by

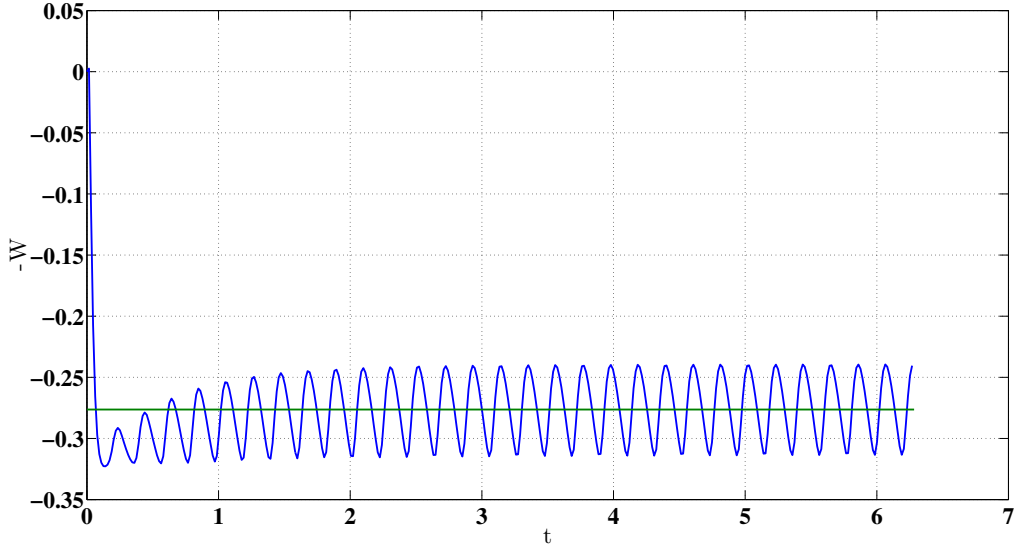


Figure 9: Time evolution of propulsion velocity for $D = 0.5$, $\Theta = 0.05$, $\epsilon = 0.05$ and $k = 20$. The green line indicates the mean value.

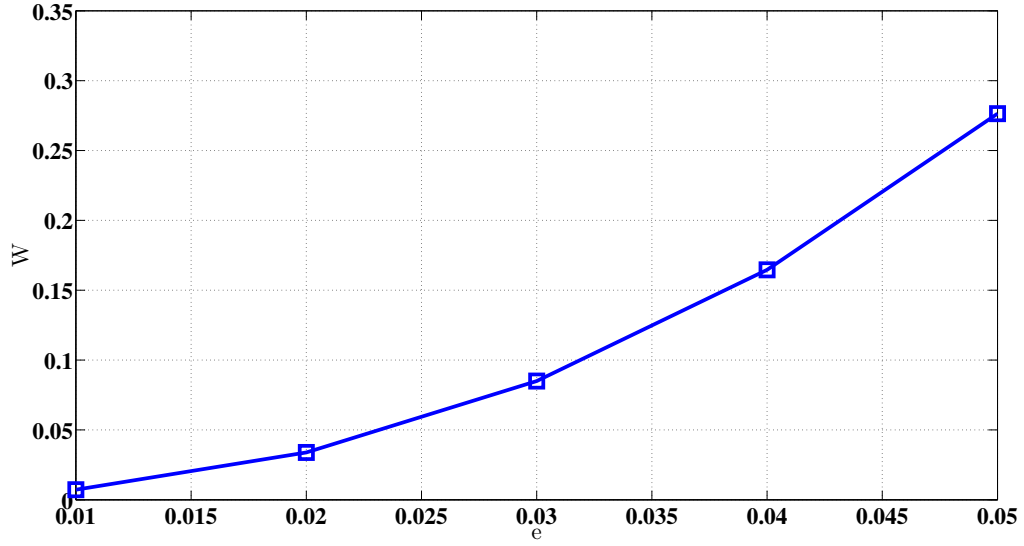


Figure 10: W vs. ϵ for $D = 0.5$, $\Theta = 0.05$ and $k = 20$. It can be shown that $W \sim \epsilon^2 / \log(1/\epsilon)$. Here, C is the speed of the travelling surface wave.

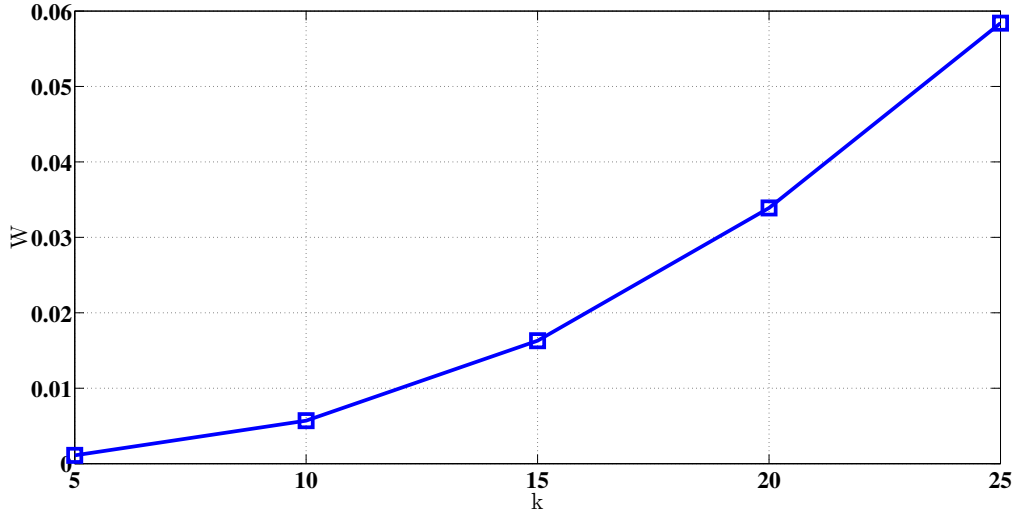


Figure 11: W vs. k for $D = 0.5$, $\Theta = 0.05$, $\epsilon = 0.02$. It is easily seen that $W \sim k^2$.

the study of propulsion of an infinite cylinder using travelling surface waves by Setter *et al.* [12]. The present study is a generalization of their problem, but restricted to slender geometries. This model can also be used to study the motion of other microorganisms like Paramecium, which moves by using the cilia on its surface, which again can be modelled as axisymmetric travelling surface waves.

From this study, it was found that the swimming speed of a slender object scales as $W \sim k^2 \epsilon^2 \theta^2 / \log(1/\epsilon)$ at the leading order. In the vanishing limit of the cylinder radius, the propulsion speed of Setter *et al.* [12] was shown to be the same as obtained by us using the SBT. When one considered the internal flow, the internal dissipation was shown to be much larger than the external dissipation, and was used to re-define the efficiency of the swimmer using an improved model (model-2) for the deformation of surface area. The resulting efficiency was found to be much smaller than the efficiency found for a previous model (model-1). Considering the pressure in the internal and external flows, it was shown that the former is much higher than the latter, and as a result the two flows could be considered to be de-coupled.

Finally, we studied the problem by considering the forces acting at a cross-section, to determine the pressure which is responsible for the fluid motion along the organism's axis, which in turn leads to the generation of travelling surface waves. The fact that the fluid motions are decoupled was used to calculate the propulsion speed using the expression from SBT once the surface deformation was determined. The resulting propulsion speed was found to scale like the propulsion speed from model-1.

10 Future work

An immediate extension of the present slender-body analysis will be to study the interaction of two slender swimmers, and to look for possibilities for generalization to more than

two swimmers. This would help in the construction of models, which would require the disturbance velocity fields as input, to study the large scale motion of these organisms.

In this study the internal fluid was considered to be Newtonian, which is generally not true, as the internal fluid in cells, the cytoplasm, is a suspension, and the stress-strain-rate relationship is not linear. An extension of this study would be to consider a non-Newtonian model for cytoplasm and solve for the resulting flow-field and then integrate it with the SBT.

The mathematical machinery used in this problem will be applied to the study of erosion from a cylindrical body placed in Stokes flow. Geometry of the body corresponding to times $t = 0$ and $t \rightarrow \infty$ serves as two limits of the SBT, however these two limits are separated in time, not space. To investigate this problem, one would have to consider the temporal evolution of the SBT analysis.

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