Corrections to the theory and the optimal line in the swimming diagram of Taylor (1952)

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The analysis of undulatory swimming gaits requires knowledge of the fluid forces acting on the animal body during swimming. In his classical 1952 paper, Taylor analysed this problem using a ‘resistive-force’ theory. The theory was used to characterize the undulatory gaits that result in the smallest energy dissipation to the fluid for a given swim velocity. The optimal gaits thus found were compared with data recorded from movies of snake and leech swimming.

Taylor (1952) theoretical model was based on experimental measurements of fluid forces acting on an inclined cylinder in an air flow of constant velocity. The resulting model, referred to by Lighthill (1975) as a ‘resistive-force theory’, described the fluid force as a function of the cylinder’s velocity and inclination angle, containing the pressure and viscous terms. The model was used to characterize the undulatory gaits (body shape and the speed of travelling waves) that result in the smallest energy dissipation to the fluid for a given swim velocity. The optimal gaits thus found were compared with data recorded from movies of snake and leech swimming.

Lighthill (1960, 1970, 1975) considered anguilliform swimming of slender body animals. His theoretical model assumed unsteady, inviscid flow, and the fluid force was deduced from the acceleration of the fluid mass. His analysis has shown that the thrust is generated only at the tip of the tail. Optimal swimming gaits were analysed in terms of the Froude efficiency, that is, the ratio of (thrust) × (forward swimming velocity)/(the work done to produce both thrust and vortex wake). The optimal distribution of body inertia and body geometry to increase Froude efficiency was also discussed.

The theoretical analyses by Taylor and Lighthill have remained seminal even after the discipline of computational fluid dynamics (CFD) was established. Their analytical results provide insight into the mechanisms of undulatory swimming that CFD analyses cannot reveal. Simple fluid models of this type are especially useful for integrated analysis of swimming behaviour that involves muscle activation and/or neuronal control mechanisms in addition to interactions of body and fluid (Bowtell & Williams 1991; Ekeberg 1993; Jordan 1996; Ekeberg & Grillner 1999; McMillen & Holmes 2006).

1. PROBLEM BACKGROUND

The analysis of undulatory swimming gaits requires knowledge of the fluid forces acting on the animal body during swimming. Forty years ago and earlier, when current powerful computing capabilities were not available, it was impossible to estimate the fluid forces by simulating fluid motion numerically, thus motivating experimental and analytical work by Taylor (1952) and Lighthill (1960, 1970). In particular, Taylor’s high Reynolds number work (inertial forces > viscous forces) on the undulatory swimming of snakes and leeches was so foundational as to be considered ‘classical’ today.

Taylor’s (1952) theoretical model was based on experimental measurements of fluid forces acting on

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where $[C_d]_p$ is the drag coefficient for the pressure term of the fluid force, and $R_1$ is the Reynolds number, defined after equation (3.3) below. The parameter $n$, defined by $n = V/U$, is the ratio of the swim velocity to the travelling wave velocity and represents the propeller efficiency. The parameter $\alpha$ is the largest angle that the body takes over a cycle with respect to the line of swim direction. This parameter relates to the body shape of undulation through $\tan \alpha = 2\pi B/\lambda$, where $B$ is the amplitude and $\lambda$ is the wavelength.

During steady swimming at a constant velocity, the thrust and drag due to the fluid forces should cancel each other to result in zero acceleration on average over each cycle. Taylor derived the condition on $(r, n, \alpha)$. 

Figure 1. Definition of $x$–$y$ coordinate axes and variables relevant to the analysis defined in text (from fig. 3 in Taylor (1952)).

Figure 2. Corrected form of fig. 4 in Taylor (1952), showing lines of constant $r$ (solid lines) on the $(n, \alpha)$-plane, calculated using more accurate numerical integration. The dotted curve corresponds to Taylor’s original line A, as read from fig. 4 in his paper. The dash-dotted curve was calculated using Taylor’s equation for $W$ with more accurate numerical integration. The dashed curve was calculated using the corrected formula for $W$ derived in the next section. The points $S_0$ and $L_0$ (stars) correspond to the experimental measurements of $\alpha$ and $n$ from snapshots of the snake and leech swimming. The points $S_1$ and $L_1$ (circles) correspond to the calculated value of $n$ for the snake and leech by solving the equilibrium equation of fluid force on the body for the given values of $\alpha$ and $r$. The point $S_2$ (triangle) corresponds to the value of $n$ calculated by Taylor for the snake and contains numerical error. We could not generate the point $L_2$ because the necessary data for $n$ were not given in Taylor’s paper.

\( \alpha \) for such steady state, which defines a curve on the \((\alpha, n)\)-plane for a given value of \( r \). The swimming diagram is a collection of such curves parameterized by various values of \( r \). The diagram is reproduced here in figure 2 with the solid curves. An arbitrary undulatory (sinusoidal) gait corresponds to a point on the diagram, and the resulting swim velocity at steady state is found by identifying the curve on which the point lies. Taylor obtained experimental measurements of \((r, n, \alpha)\) from snapshots of a snake swimming, provided by Gray. Let us denote the measured values by \((R, N, A)\). The value of \( n \) can be calculated by solving the equilibrium equation for the given values of \((A, R)\), Taylor obtained a value of \( n \) in this way, but with calculation error. We denote the correct value calculated by us \( N_1 \) and Taylor’s erroneous value by \( N_0 \). The points \( S_0 \) (star), \( S_1 \) (circle) and \( S_2 \) (triangle) in figure 2 indicate the data \((A, N_0), (A, N_1)\) and \((A, N_2)\), respectively. The points \( L_0 \) (star) and \( L_1 \) (circle) are similarly generated from experimental data of leech swimming provided in Taylor’s paper. However, we could not generate the point \( L_2 \) because the necessary data for \( n \) were not given in Taylor’s paper. The results of the swimming diagram show that the predicted propeller efficiency \( (n = V/U, 0.56 \text{ at } S_1) \) is smaller than the observed value for the snake swimming (0.7 for \( S_0 \)). For the leech swimming, the calculated steady-state swimming condition (point \( L_1 \)) is close to the observed value (point \( L_0 \)).

Taylor calculated the rate at which the animal does work on the surrounding fluid per unit length of the body, denoted as \( W \). This rate of energy dissipation \( W \) was shown to be a function of \((r, n, \alpha)\). The optimal gaits were defined to be the pairs \((n, \alpha)\) that yield a given swim velocity \( V \) with the minimum \( W \). The dotted line in figure 2 indicates the optimal gaits obtained by Taylor and it contains deviations from the assumed sinusoidal shape of the body undulation. It should also be noted that optimality with respect to other criteria, such as the maximum swim speed under a fixed speed of travelling waves along the curved body (McMillen & Holmes 2006), could result in gaits similar to those characterized by the optimal line for energy efficiency discussed here. This means that a swimming animal could simultaneously optimize multiple criteria, implying, for instance, that the energetic cost may not be the only one that snakes minimize.

### 3. CORRECTION OF THE WORK RATE FORMULA DERIVED IN TAYLOR’S PAPER

With reference to figure 1, at each location along the body, the line tangent to the body forms an angle \( \theta \) with the line indicating the swimming direction. The velocity of the body segment is given by the normal component \( (U - V) \sin \theta \) and the longitudinal component \( q - (U - V) \cos \theta \), where \( q \) is the speed of the body segment observed from the reference frame that moves at velocity \( U - V \) in the direction opposite to the swimming direction. Figure 1 shows the sinusoidal curve, fixed to this moving frame of reference, along which every point on the body is assumed to move at speed \( q \). Assuming that the body is inextensible, the speed \( q \) is constant along the body and is determined by the body shape \( \alpha \) and the backward velocity of travelling waves relative to the body \( U \).

The rate, \( W \), at which the animal does work on the surrounding fluid per unit length of its body is the mean value of

\[
N(U - V) \sin \theta + L(q - (U - V) \cos \theta)
\]

or, equivalently,

\[
U(1 - n)(N \sin \theta - L \cos \theta) + qL.
\]  \( \text{(3.1)} \)

which is the power dissipated from the body to the fluid, where \( N \) and \( L \) are the normal and longitudinal components of the fluid force per unit length at the body segment, respectively.

By definition, the mean value of equation (3.1) is given by

\[
W = \frac{1}{l} \int_0^l qL \, ds.
\]  \( \text{(3.2)} \)

where \( s \) is the arc length along the body, \( l \) is the body length for one sinusoidal wave and the mean value of the first term in equation (3.1) vanishes owing to the force equilibrium in the horizontal direction. The expression for \( L \) is given by (Taylor 1952)

\[
L = \frac{1}{2} \rho \frac{dU}{dp} \frac{dU}{ds} \times \left( 5.4(1 - n)^{1/2} R_1^{-1/2} \sin \theta/2 \sin \gamma (1 - n) \cos \theta \right).
\]  \( \text{(3.3)} \)

where \( R_1 = U dp/\mu, \; \gamma = q/U, \; d \) is the diameter of the body cross section, and \( \rho \) and \( \mu \) are the fluid density.
and viscosity, respectively. Substituting equations (3.3) into (3.2) and integrating over the body yields

\[
W = \gamma t \frac{1}{\gamma} \int_{0}^{1} \frac{1}{2} \rho \, dU^{2} \left(5.4(1-n)^{1/2}R_{1}^{-1/2} \sin \theta^{1/2}ight) \cdot \left(\gamma - (1-n) \cos \theta\right) \, ds
\]

\[
= \gamma U \frac{1}{\gamma} \frac{1}{2} \rho \, dU^{2} \left(5.4(1-n)^{1/2}R_{1}^{-1/2}\right) \times 4 \int_{0}^{\pi/4} \sin \theta^{1/2} \left(\gamma - (1-n) \cos \theta\right) \, ds
\]

\[
= \frac{4}{\pi} \frac{1}{2} \rho \, dU^{3} \left(5.4(1-n)^{1/2}R_{1}^{-1/2}\right) \times \int_{0}^{\pi/4} \sin \theta^{1/2} \left(\gamma - (1-n) \cos \theta\right) \, ds
\]

\[
= \frac{1}{2} \rho \, dU^{3} \left(5.4(1-n)^{1/2}R_{1}^{-1/2}\right) \times \frac{2}{\pi} \int_{0}^{\pi/2} \sin \theta^{1/2} \left(\gamma - (1-n) \cos \theta\right) \, sec \theta \, dz.
\]

(3.4)

where (i) the second equality uses the fact that the integrand \(\sin^{1/2}(\gamma - (1-n) \cos \theta)\) is the same for every quarter of the sine body wave (figure 1), (ii) in the third equality, the integration variable \(s\) aligned along the centreline of the cylinder, is replaced with \(z\), aligned with the direction of motion, and (iii) the definition \(z := (2\pi/\lambda)(x+(U-V)t)\) given by eqn (3.4) in Taylor’s paper is used in the fourth equality. The final equality in equation (3.4) differs by a factor \(\gamma\) from Taylor’s corresponding result, eqn (6.2) in his paper. Eqn (6.2) also contains a typographical error in that the term written as \((1-n)^{-1/2}\) should, in fact, be \((1-n)^{1/2}\). Replacing \(U\) by \(V/n\) in the last expression of equation (3.4), we have

\[
W = \frac{5.4}{2} \rho \, dV^{3} \left(\frac{\mu}{\rho \, dV}\right)^{1/2} G(n, \alpha),
\]

(3.5)

with

\[
I_{1} = \frac{2}{\pi} \int_{0}^{\pi/2} \sqrt{\sin \theta} \, dz \quad \text{and} \quad I_{4} = \frac{2}{\pi} \int_{0}^{\pi/2} \sqrt{\sin \theta} \, \sec \theta \, dz.
\]

In contrast, Taylor’s derivation yielded the following expression for \(G(n, \alpha)\):

\[
G(n, \alpha) = (1-n)^{1/2} n^{-5/2} (\gamma I_{4} + (n-1) I_{1})
\]

which appears as eqn (6.4) in his paper. This equation is incorrect. Equation (3.6), above, is the corrected form of eqn (6.4).

REFERENCES


