REPORT

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

Joseph A. C. Humphrey^{1,2,*}, Jun Chen¹,
Tetsuya Iwasaki³ and W. Otto Friesen²

¹*Department of Mechanical and Aerospace Engineering, University of Virginia, 122 Engineer's Way, PO Box 400746, Charlottesville, VA 22904-4746, USA*

²*Department of Biology, University of Virginia, 485 McCormick Road, PO Box 400328, Charlottesville, VA 22904-4328, USA*

³*Department of Mechanical, Aerospace and Engineering, University of California at Los Angeles, 37-144 Engineering IV, Westwood Plaza, Los Angeles, CA 90095-1597, USA*

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 a snake and a leech swimming. This report identifies and corrects a mathematical error in Taylor’s paper, showing that his theory applies even better to animals of circular cross section.

Keywords: undulatory swimming; swimming diagram; optimal line; snake; leech

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 $\gg$ 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

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) $\times$ (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).

2. OVERVIEW OF TAYLOR’S (1952) WORK AND OUR CORRECTIONS

In his seminal paper, Taylor (1952) developed a formula for calculating the fluid force acting on long and narrow swimming animals at large characteristic Reynolds numbers and approximating the body by a cylinder with uniform cross section. He then considered an idealized (or approximate) case where an animal swims at velocity V , propelled by body undulation where the body takes a sinusoidal shape at each instant in time, with waves travelling down the body at a constant velocity U relative to the body. Any possible rotational motion of the body was ignored. (Although not explicitly stated, in his analysis Taylor either assumed an infinitely long body or neglected the rotational motion and possible vortex shedding due to the finite length of the body. In either case, every point on the body moves forward by the same amount after one cycle of undulation, and V can be defined as the distance travelled divided by the cycle period.) Figure 1 illustrates the body configuration and relevant variables used in this report. Based on Taylor’s theory, two important analyses were performed: (i) the development of the swimming diagram and (ii) the characterization of optimal swimming gaits.

Taylor showed that all possible swimming profiles can be characterized in terms of three parameters (r , n , α). The parameter r is defined by $r = [C_D]_p R_1^{1/2}$,

*Author for correspondence (jach@virginia.edu).

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, α) -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 α 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 α 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.

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 α 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 λ 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 $(r, n$,

α) for such steady state, which defines a curve on the (α, 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, α) 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 by N_1 and Taylor's erroneous value by N_2 . The points S_0 (star), S_1 (circle) and S_2 (triangle) in figure 2 indicate the data (A, N) , (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 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, α) . The optimal gaits were defined to be the pairs (n, α) 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 numerical error. The dash-dotted line represents the same calculation essentially devoid of numerical error.

We have also found errors in Taylor's derivation of the work rate W . The mathematical details of the errors are summarized in the next section. The optimal swimming gaits have been re-calculated using the corrected formula for W and are plotted in figure 2 as the dashed line. With both the numerical inaccuracies and the analytical error removed, the dashed line in figure 2 shows that, for conditions corresponding to the minimum work W at a given speed V or, equivalently, for conditions corresponding to the maximum speed V at a given work W , Taylor's theory predicts: (i) a larger value of B/λ for a given value of V/U in the optimal swimming, (ii) that the undulating motion of a snake (denoted by the point S_0 in the figure) is very near to the optimal line, and (iii) that the observed gait of leech swimming is further away from the corrected optimal line than from the optimal line in Taylor's original paper. These refined results, however, should be taken with the understanding that the fluid model is relatively simple and does not capture the inertial effects of added mass and vortex shedding, and that the analysis neglected potentially important factors such as non-circular animal cross sections and

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 θ 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 α 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,

$$U(1 - n)(N \sin \theta - L \cos \theta) + qL, \quad (3.1)$$

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

$$W = \frac{1}{l} \int_0^l qL \, ds, \quad (3.2)$$

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)

$$L = \frac{1}{2} \rho d U^2 \times \left(5.4(1 - n)^{1/2} R_1^{-1/2} \sin \theta^{1/2} (\gamma - (1 - n) \cos \theta) \right), \quad (3.3)$$

where $R_1 = U d \rho / \mu$, $\gamma = q/U$, d is the diameter of the body cross section, and ρ and μ are the fluid density

and viscosity, respectively. Substituting equations (3.3) into (3.2) and integrating over the body yields

$$\begin{aligned}
 W &= \gamma U \frac{1}{l} \int_0^l \frac{1}{2} \rho \, dU^2 \left(5.4(1-n)^{1/2} R_1^{-1/2} \sin \theta^{1/2} \right. \\
 &\quad \left. \times (\gamma - (1-n) \cos \theta) \right) ds \\
 &= \gamma U \frac{1}{\gamma \lambda} \frac{1}{2} \rho \, dU^2 \left(5.4(1-n)^{1/2} R_1^{-1/2} \right) \\
 &\quad \times 4 \int_0^{l/4} \sin \theta^{1/2} (\gamma - (1-n) \cos \theta) \, ds \\
 &= \frac{4}{\lambda} \frac{1}{2} \rho \, dU^3 \left(5.4(1-n)^{1/2} R_1^{-1/2} \right) \\
 &\quad \times \int_0^{\lambda/4} \sin \theta^{1/2} (\gamma - (1-n) \cos \theta) \sec \theta \, dx \\
 &= \frac{1}{2} \rho \, dU^3 \left(5.4(1-n)^{1/2} R_1^{-1/2} \right) \\
 &\quad \times \frac{2}{\pi} \int_0^{\pi/2} \sin \theta^{1/2} (\gamma - (1-n) \cos \theta) \sec \theta \, dz,
 \end{aligned} \tag{3.4}$$

where (i) the second equality uses the fact that the integrand $\sin \theta^{1/2} (\gamma - (1-n) \cos \theta)$ 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 x , 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 γ 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

$$W = \frac{5.4}{2} \rho \, dV^3 \left(\frac{\mu}{\rho \, dV} \right)^{1/2} G(n, \alpha), \tag{3.5}$$

where

$$G(n, \alpha) = (1-n)^{1/2} n^{-5/2} (\gamma I_4 + (n-1)I_1) \tag{3.6}$$

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 $G(n, \alpha)$:

$$G(n, \alpha) = (1-n)^{1/2} n^{-5/2} ((\gamma^2 - \gamma)I_4 + n\gamma I_1),$$

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

- Bowtell, G. & Williams, T. L. 1991 Anguilliform body dynamics: modeling the interaction between muscle activation and body curvature. *Phil. Trans. R. Soc. Lond. B* **334**, 385–390. (doi:10.1098/rstb.1991.0123)
- Ekeberg, O. 1993 A combined neuronal and mechanical model of fish swimming. *Biol. Cybernetics* **69**, 363–374. (doi:10.1007/BF00199436)
- Ekeberg, O. & Grillner, S. 1999 Simulations of neuromuscular control in lamprey swimming. *Phil. Trans. R. Soc. Lond. B* **354**, 895–902. (doi:10.1098/rstb.1999.0441)
- Jordan, C. E. 1996 Coupling internal and external mechanics to predict swimming behavior: a general approach? *Am. Zool.* **37**, 710–722.
- Lighthill, M. J. 1960 Note on the swimming of slender fish. *J. Fluid Mech.* **9**, 305–317. (doi:10.1017/S0022112060001110)
- Lighthill, M. J. 1970 Aquatic animal propulsion of high hydrodynamic efficiency. *J. Fluid Mech.* **44**, 265–301. (doi:10.1017/S0022112070001830)
- Lighthill, M. J. 1975 *Mathematical biofluidynamics*, pp. 117–149. Regional Conference Series in Applied Mathematics, vol. 17. Philadelphia, PA: Society for Industrial and Applied Mathematics.
- McMillen, T. & Holmes, P. 2006 An elastic rod model for anguilliform swimming. *J. Math. Biol.* **53**, 843–886. (doi:10.1007/s00285-006-0036-8)
- Taylor, G. 1952 Analysis of the swimming of long and narrow animals. *Proc. R. Soc. Lond. A* **214**, 158–183. (doi:10.1098/rspa.1952.0159)