Unsteady swimming of small organisms

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(Received 1 February 2012; revised 14 March 2012; accepted 1 April 2012)

Small planktonic organisms ubiquitously display unsteady or impulsive motion to attack a prey or escape a predator in natural environments. Despite this, the role of unsteady forces such as history and added mass forces on the low-Reynolds-number propulsion of small organisms, e.g. Paramecium, is poorly understood. In this paper, we derive the fundamental equation of motion for an organism swimming by means of the surface distortion in a non-uniform background flow field at a low-Reynolds-number regime. We show that the history and added mass forces are important as the product of Reynolds number and Strouhal number increases above unity. Our results for an unsteady squirmer show that unsteady inertial effects can lead to a non-zero mean velocity for the cases with zero streaming parameters, which have zero mean velocity in the absence of inertia.

Key words: micro-organism dynamics, propulsion, swimming

1. Introduction

Planktonic organisms play an important role in tropic dynamics, marine ecosystem and biomedical applications. They use contractile elements (cilia and flagella) and appendages to propel themselves. They undergo oscillatory motions or impulsive jumps to displace, change their swimming direction, attack a prey or escape a predator (Daniel 1984; Jiang & Kiørboe 2011). Ciliates, such as Paramecium, swim by metachronal beating of cilia on the surface. Recently, Hamel et al. (2011) showed that Paramecium uses synchronized beating of the cilia to rapidly accelerate away from an intermediate aggression, which is followed by a large oscillation in velocity. For more severe aggression, Paramecium shows jumping behaviour to escape. Other planktonic protists, such as the ciliate Balanion comatum, also escape from hydromechanical signals by jumps. During these jumps, the swimming velocity of the organism increases more than a five-fold in the period of time required to move one bodylength (Jakobsen 2001). Jumping is common among protozoan and metazoan plankton (Jiang & Kiørboe 2011). Copepods, the most abundant metazoans in the ocean, ‘swim by sequentially sticking the swimming legs posteriorly’ (Jiang & Kiørboe 2011), which results in sequences of small jumps for the purpose of ambush feeding. Since jumping organisms respond to hydromechanical signals rather than direct contact, ambient fluid motion (e.g. turbulent flows) can also trigger micro-organisms’ acceleration in addition to flow disturbances generated by a prey or a predator (Magar & Pedley 2005). Unsteady motion has also been reported for flagellated organisms. Recently, Gollub

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and coworkers (Guasto, Johnson & Gollub 2010) resolved the oscillatory velocity field, induced by synchronous and asynchronous beating flagella of a free swimming algal cell. In order to better understand these cases, it is essential to explore the physics of fluids that lies behind the motion of accelerating micro-organisms. Despite the widespread implications of unsteady swimming on micro-organisms in nature, the role of unsteady hydrodynamic forces on their propulsion has not been explored in the literature. In this manuscript, we derive the fundamental equation of motion for unsteady swimming of small organisms.

Even though unsteady swimming of micro-organisms is poorly understood, the study of unsteady motion of rigid particles has a long history (Ardekani et al. 2009). Boussinesq (1885), Basset (1888) and Oseen (1927) examined unsteady motion of a spherical particle in an unbounded stagnant flow of an incompressible Newtonian fluid. The hydrodynamic forces acting on a spherical particle consist of three terms: Stokes drag, history (Basset) force and added mass force (Basset 1888). The role of history force on the motion of particles is stronger when their density is comparable to the density of ambient fluid environments, \( \rho_p/\rho_f \sim O(1) \), where \( \rho_p \) is the particle density (van Aartrijk & Clercx 2010). This condition holds for swimming organisms and thus the history force cannot be neglected for unsteady bio-locomotion. Arminski & Weinbaum (1979) studied the Basset–Langevin equation for different unsteady excitation forces of different waveforms. The equation of motion for an isolated sphere (Maxey & Riley 1983 and, independently, Gatignol 1983) and interacting spheres (Ardekani & Rangel 2006) in an unsteady non-uniform background flow have been developed in the limit of small particle Reynolds number. The Reynolds number, \( Re = \rho_f U a/\eta \), is the ratio of convective to viscous forces, where \( U \) is the particle velocity, \( a \) the particle radius, \( \rho_f \) the fluid density and \( \eta \) is the fluid viscosity. These studies include unsteady inertia due to the fluid and particle but neglect convective inertial effects. Consequently, the Basset force’s integration kernel decays as \( t^{-1}/2 \), where \( t \) is the time. Mei & Adrian (1992) included the convective term in the limit of a small Strouhal number \( Sl \ll Re \ll 1 \) and found that the Basset force’s integration kernel decays as \( t^{-2} \) instead of \( t^{-1}/2 \). The Strouhal number, \( Sl = a/U \tau \), is a measure of the convective time scale to the time scale of unsteadiness, \( \tau \). When the vorticity generated at the particle boundary has not diffused out of the Oseen distance, the unsteady inertia dominates the hydrodynamic forces, while the correction of convective inertial effects to the hydrodynamic forces is \( O(Re) \) and can be neglected as noted by Lovalenti & Brady (1993). Unsteady hydrodynamic forces have been used to determine transport of small particles in turbulent flows, particle dispersion and deposition (Lovalenti & Brady 1993). For swimming micro-organisms, the unsteadiness arises from unsteady propulsion mechanisms (e.g. unsteady beating of flagella or cilia), turbulent velocity fluctuations of the ambient fluid and/or velocity disturbances generated by a prey or predator. In this paper, we assume unsteady inertia is large compared with convective inertia, \( Sl \gg Re \), which is the case for the examples discussed above since micro-organisms live in a low-Reynolds-number regime. For example, a swimming algal cell has Reynolds and Strouhal numbers of 0.001 and 1, respectively (Guasto et al. 2010).

We first derive the fundamental equation of motion for a spherical unsteady swimmer in a non-uniform flow. Then, in order to determine the effect of unsteady hydrodynamic forces on a swimming micro-organism, we use an archetypal model widely used in the literature to study low-Reynolds-number swimming called the squirmer model. The squirmer model consists of a spherical shaped body with wavelike deformations of the outer surface (Lighthill 1952) and describes the
self-propulsion of ciliates moving by synchronized metachronal beating of cilia on their surface (Blake 1971), such as cyanobacteria, colonies of flagellates such as *Volvox* (Drescher et al. 2009) and *Paramecium*. The model has been recently used to study the hydrodynamic interaction between swimmers (Ishikawa, Simmonds & Pedley 2006), mixing due to propulsion of micro-organisms (Lin, Thiffeault & Childress 2011), bio-locomotion in complex fluids (Zhu et al. 2011) and stratified fluids (Doostmohammadi, Stocker & Ardekani 2012). Unsteady squirmers have been studied by Magar & Pedley (2005) to explore the nutrient uptake of micro-organisms. Later, Giacché & Ishikawa (2010) examined interaction of two unsteady squirmers since the beating time scale is comparable to the time scale of near-field interaction. Yeomans and coworkers (Pooley, Alexander & Yeomans 2007; Alexander & Yeomans 2010) considered a different unsteady swimming model using the Stokes equations, neglecting unsteady inertia, to explore hydrodynamic interaction between three sphere swimmers of Najafi & Golestanian (2004). Even though micro-organisms in nature undergo unsteady swimming, the role of unsteady forces (history and added mass forces) on their swimming behaviour, to the best of our knowledge, has not been explored previously and is the focus of this paper.

2. Analytical description of unsteady forces

Here we consider the locomotion of an unsteady spherical swimmer that propels itself by generating tangential surface motion, $v_s$, swimming with velocity $V(t)$ in a Newtonian fluid. The swimmer’s centre of mass is instantaneously located at $Y(t)$. The undisturbed flow, in the absence of the swimmer, is described by $u(x, t)$ and the modified velocity field due to presence of the swimmer is $v(x, t)$, where $x$ is the position vector. The Navier–Stokes equations in the frame of reference translating with the velocity of the swimmer, $V(t)$, are given as

$$\rho f \frac{Dw}{Dt} = -\nabla p + \eta \nabla^2 w + \rho f \left( g - \frac{dV}{dt} \right), \quad \nabla \cdot w = 0,$$

$$w = v' + \Omega \times z \quad \text{at } |z| = a,$$

$$w = u - V \quad \text{as } |z| \rightarrow \infty,$$

where $w(z, t) = v(x, t) - V(t)$ is the velocity field in the swimmer’s frame of reference, $z = x - Y(t)$ is the position vector instantaneously measured from the centre of the swimmer, $\Omega$ is the angular velocity of the organism, $p$ is the pressure field and $g$ is the gravitational acceleration. The last term in the momentum equation (2.1) is the d’Alembert force per unit volume, which arises due to the acceleration of the frame of reference. The boundary condition, (2.2), enforces the local fluid to move with the time-dependent tangential surface velocity of the swimmer, $v'$. The last boundary condition, (2.3), indicates that the flow field approaches the background flow field at infinity. The derivative $D/Dt$ and $d/dt$ are used here to denote the time derivative following a fluid element and the swimmer, respectively. The total hydrodynamic force acting on an unsteady swimmer can be written as

$$F = \oint_S \sigma \cdot n \, dS,$$

where the surface integral is over the surface of the spherical swimmer. Here $n$ is the unit outward normal to $S$, $\sigma = -pI + \eta(\nabla w + \nabla w^T)$ is the stress tensor and $I$ is the identity tensor. Following Maxey & Riley (1983), the force can be decomposed to
the hydrodynamic forces due to the undisturbed flow field, \( \mathbf{w}'' = \mathbf{u} - \mathbf{V} \), and disturbed flow field, \( \mathbf{w}^d = \mathbf{v} - \mathbf{u} \), referred to as \( \mathbf{F}'' \) and \( \mathbf{F}^d \), respectively. The force due to the undisturbed flow is identical to the one for a rigid particle of a size much smaller than the length scale of the variation of the undisturbed flow and the equation of motion can be written as

\[
m_s \frac{d\mathbf{V}}{dt} = (m_s - m_f) \mathbf{g} + m_f \frac{D\mathbf{u}}{Dt} |_{\mathbf{V}(t)} + \mathbf{F}^d, \tag{2.5}
\]

where \( m_s \) is the swimmer mass and \( m_f \) is the mass of fluid displaced by the swimmer. The detailed derivation of \( \text{(2.5)} \) is given in Maxey & Riley (1983, equations (20)–(26)) and is not repeated here. Next, we shall consider the hydrodynamic forces acting on the swimmer due to the disturbed flow, \( \mathbf{w}^d \), which is different from that corresponding to the rigid sphere due to the surface disturbances generated by the swimmer. Since the micro-organisms’ Reynolds number is small \( (Re \ll 1 \text{ and } Sl \gg Re) \), convective inertia generated by the micro-organism can be neglected. Thus, the governing equations for the disturbed flow field can be described by unsteady Stokes equations

\[
\begin{align*}
\rho_f \frac{\partial \mathbf{w}^d}{\partial t} &= -\nabla p^d + \eta \nabla^2 \mathbf{w}^d, \tag{2.6a} \\
\mathbf{w}^d &= \mathbf{V} - \mathbf{u} + \mathbf{\Omega} \times \mathbf{z} + \mathbf{v}^i \quad \text{at } |\mathbf{z}| = a, \tag{2.6b} \\
\mathbf{w}^d &\rightarrow \mathbf{0} \quad |\mathbf{z}| \rightarrow \infty, \tag{2.6c}
\end{align*}
\]

where superscript \( d \) corresponds to disturbed flow variables. Using the Lorentz reciprocal theorem, which has also been used to calculate the hydrodynamic force due to the disturbed flow of a rigid sphere (Maxey & Riley 1983), we can derive the equation of motion for a swimming micro-organism. Consider the flow field around an impulsively started sphere, \( \mathbf{V}_\text{aux} = \delta(t)\mathbf{e}^{(1)} \), generating the velocity and stress fields of \( \mathbf{v}_\text{aux} \) and \( \sigma_\text{aux} \), respectively:

\[
\int_S \mathbf{n} \cdot \hat{\sigma}^d \cdot \mathbf{v}_\text{aux} \, dS - \int_S \mathbf{n} \cdot \hat{\sigma}_\text{aux} \cdot \mathbf{w}^d \, dS = \int_V \rho_f \left[ \mathbf{w}^d(z, 0) \cdot \mathbf{v}_\text{aux}(z, s) - \mathbf{v}_\text{aux}(z, 0) \cdot \mathbf{w}^d(z, s) \right] \, dV, \tag{2.7}
\]

where \( \hat{\cdot} \) denotes the Laplace transform operator and \( s \) is the Laplace variable. The velocity and stress fields of an impulsively started sphere, the chosen auxiliary problem, is given by Burgers (1938) after solving unsteady Stokes equations

\[
\begin{align*}
\hat{\mathbf{v}}_\text{aux} &= \mathbf{e}^{(1)} \cdot \nabla \hat{\psi} - \mathbf{e}^{(1)} \nabla^2 \hat{\psi}, \tag{2.8a} \\
\hat{\mathbf{v}}_\text{aux} (s) &= \mathbf{e}^{(1)} \quad \text{at } r = a, \tag{2.8b} \\
\hat{\psi} &= \frac{Q_1}{r} + \frac{Q_2}{r} e^{-\lambda r}, \tag{2.8c} \\
\mathbf{n} \cdot \hat{\sigma}_\text{aux} &= -\frac{1}{2} \rho_f s \mathbf{z} \cdot \mathbf{e}^{(1)}/a - \frac{3}{2} \eta/a(1 + \lambda a)\mathbf{e}^{(1)} \quad \text{at } r = a, \tag{2.8d}
\end{align*}
\]

where \( \mathbf{e}^{(1)} \) is a unit vector along the swimming direction (without loss of generality \( \mathbf{e}^{(1)} = (1, 0, 0) \)), \( r \) is the radial distance from the centre of the sphere, \( \lambda^2 = \rho_f s/\eta \) and the coefficients are defined as \( Q_1 = 3a\eta(1 + \lambda a)/2\rho_f s + a^2/2 \) and \( Q_2 = -3a\eta \exp(\lambda a)/2\rho_f s \). For a swimmer and background flow field that are initially
zero, the force from disturbed flow can be written, in the Laplace space, as

\[
\hat{F}^d_i = \epsilon^{(1)} \cdot \int_S \mathbf{n} \cdot \hat{\sigma}^d \, dS = \int_S \mathbf{n} \cdot \hat{\sigma}_{\text{aux}} \cdot \hat{\mathbf{w}}^d \, dS. \tag{2.9}
\]

Recall that the swimmer is much smaller than the length scale corresponding to the variation of the background flow. Thus, \( \mathbf{w}^d \) in the neighbourhood of the swimmer can be approximately represented by its Taylor expansion at the origin. After satisfying the boundary condition listed in (2.6) on the surface of the spherical swimmer, the velocity \( \hat{\mathbf{w}}^d \) can be written as

\[
\hat{\mathbf{w}}^d = \hat{\mathbf{V}}_i - \hat{\mathbf{u}}_i[Y, s] + \hat{\mathbf{v}}^d(z_S, s) + \frac{1}{2} z_j z_k \hat{D}_{jk}, \tag{2.10a}
\]

\[
\hat{C}_{ij} = - \frac{\partial \hat{\mathbf{u}}_i}{\partial z_j} |_{Y(t)} - \epsilon_{ijk} \hat{\omega}_k, \quad \hat{D}_{ij} = - \frac{\partial^2 \hat{\mathbf{u}}_i}{\partial z_j \partial z_k} |_{Y(t)}, \tag{2.10b}
\]

where \( \epsilon \) is the permutation tensor and \( z_S \) corresponds to the position vector on the surface of the swimmer. After combining the results of (2.8)–(2.10), the hydrodynamic forces acting on the swimmer due to the disturbed flow can be written as

\[
\hat{F}^d_i = - (\hat{\mathbf{V}}_i - \hat{\mathbf{u}}_i) \cdot \left\{ 6\pi a \eta (1 + \lambda a) + \frac{1}{2} m_f |S| - a^2 \left[ (\hat{\mathbf{D}}_{ij} + 2 \hat{\mathbf{D}}_{ji}) \pi \eta a (1 + \lambda a) + \frac{1}{20} m_f s \hat{\mathbf{D}}_{ij} \right] \right\} \]

\[
- \frac{3}{2} \eta (1 + \lambda a) / a \int_S \hat{\mathbf{w}}^d \, dS. \tag{2.11}
\]

Finally, we can calculate the Laplace inverse of (2.11) and evaluate the fundamental equation of motion for an unsteady spherical swimmer in a non-uniform background flow field

\[
\frac{m_s}{\dot{V}} = (m_s - m_f) \mathbf{g} + m_f \frac{\mathbf{Du}}{\dot{t}} \bigg|_{Y(t)} - 6\pi a \eta \left\{ \mathbf{V}(t) - \mathbf{u}(Y(t), t) - \frac{1}{6} a^2 \nabla^2 \mathbf{u} \bigg|_{Y(t)} \right\} \]

\[
- \frac{1}{2} m_f \frac{\mathbf{Du}}{\dot{t}} \left\{ \mathbf{V}(t) - \mathbf{u}(Y(t), t) - \frac{1}{10} a^2 \nabla^2 \mathbf{u} \bigg|_{Y(t)} \right\} \]

\[
- 6\pi a^2 \eta \int_0^t d\tau \frac{\mathbf{V}(\tau) - \mathbf{u}(Y(\tau), \tau) - \frac{1}{6} a^2 \nabla^2 \mathbf{u} \bigg|_{Y(\tau)} \right\} / \mathbf{v} \right\} \bigg|_{Y(t)} 
\]

\[
- \frac{3}{2} \eta / a \int_S \mathbf{v} \, dS - \frac{3}{2} \eta \int_S \int_0^t \frac{d\mathbf{v} / d\tau}{[\mathbf{v}(t - \tau)]^{1/2}} \, d\tau \, dS. \tag{2.12}
\]

where \( \mathbf{v} \) is the kinematic viscosity of fluid. Here, we have derived the unsteady Faxen equation for a self-propelled particle in a non-uniform flow. The first and second terms on the right-hand side of (2.12) are the gravity force and pressure gradient of the undisturbed flow, respectively. The next three terms correspond to the Stokes drag contribution, the added or virtual mass forces and the Basset force or history term due to the translation of the swimmer in a non-uniform background flow; the last two terms correspond to the Stokes drag contribution and the Basset forces due to the surface distortion of the swimmer. The acceleration of the organism imposes an acceleration of the flow field which leads to inertial forces acting on the organism, referred to as added mass force. It should be noted that the added mass force of a spherical swimmer that propels by surface oscillation tangential to its surface is
identical to that for a rigid sphere. Equation (2.12) can be used for an accelerating swimmer moving in an unsteady non-uniform background flow.

3. Unsteady squirmer

In this section, we apply the fundamental equation of motion to a specific swimming model called a ‘squirmer’. The unsteady squirmer is first introduced by Blake (1971). The metachronal beating of cilia on the surface of micro-organisms can be modelled with a tangential surface velocity on the surface of the organisms. Here we neglect small radial displacements of cilia (Giacch ´e & Ishikawa 2010). The tangential surface velocity on the surface of the squirmer can be described as

\[ v^s_\theta = \sum_{n=1}^{\infty} B_n(t)V_n(\mu), \]  

(3.1)

where \( V_n \) is defined as

\[ V_n = \frac{2\sqrt{1-\mu^2}}{n(n+1)}P'_n(\mu), \]  

(3.2)

where \( \mu = \cos \theta \) and \( P_n \) is the Legendre polynomial of the first kind of degree \( n \). Here \( r, \theta \) and \( \phi \) denote spherical polar coordinates, where \( \theta = 0 \) is along the swimming direction. The surface tangential velocity is axisymmetric and independent of \( \phi \).

Following Magar & Pedley (2005), we retain the first three terms of the tangential surface velocity whose coefficients can be defined as a function of three modal amplitudes \( b_1, b_2 \) and \( b_3 \) (Blake 1971; Magar & Pedley 2005; Giacch ´e & Ishikawa 2010)

\[ B_1 = B_{10} + B_{11} \cos \omega t + B_{12} \cos 2\omega t, \]  

(3.3a)

\[ B_2 = B_{21} \sin \omega t + B_{22} \sin 2\omega t, \]  

(3.3b)

\[ B_3 = B_{30} + B_{31} \cos \omega t + B_{32} \cos 2\omega t. \]  

(3.3c)

where \( \omega \) is the frequency of surface disturbances and is equal to cilia beating frequency for ciliates (Blake 1971); \( B_1, B_2 \) and \( B_3 \) are functions of time and represent wave of tangential displacements of cilia on the surface of the micro-organism:

\[ B_{10} = a\omega \epsilon^2 \frac{2b_2}{5} \left( \frac{3b_3}{7} - b_1 \right), \quad B_{11} = a\omega \epsilon b_1, \quad B_{12} = a\omega \epsilon^2 \frac{b_2}{5} \left( b_1 + \frac{2b_3}{7} \right), \]  

(3.4a)

\[ B_{21} = -a\omega \epsilon b_2, \quad B_{22} = -a\omega \epsilon^2 \left( \frac{b_1^2}{2} - \frac{3b_1b_3}{7} + \frac{b_2^2}{14} - \frac{b_3^2}{28} \right), \]  

(3.4b)

\[ B_{30} = a\omega \epsilon^2 \frac{b_2}{5} \left( 2b_1 + \frac{b_3}{3} \right), \quad B_{31} = a\omega \epsilon b_3, \quad B_{32} = a\omega \epsilon^2 \frac{2b_2}{5} \left( \frac{b_3}{3} - 3b_1 \right). \]  

(3.4c)

Equations (3.3) and (3.4) are obtained under the assumption that a material point that is initially at \( \theta_0 \), at time \( t \) will move to the location (Blake 1971)

\[ \theta = \theta_0 + \epsilon \{ (b_1V_1 + b_2V_2) \sin \omega t + b_3V_3 \cos \omega t \}, \]  

(3.5)

where \( \epsilon \) is the amplitude of oscillation of cilia wave which is a small parameter. For micro-organisms usually \( \epsilon \sim 1/20-1/10 \), swimming speeds are about 10 body lengths per second and surface motion frequency \( \omega \sim 20-1000 \text{ s}^{-1} \) (Blake 1971; Stone & Samuel 1996). We consider a squirmer that is stationary for \( t < 0 \) while it accelerates...
for \( t \geq 0 \) due to surface disturbance as described in (3.1). Equations (2.5) and (2.11) can be simplified for a squirmer in a stagnant background flow as

\[
m_s \dot{V} = -6\pi \eta a \left[ \dot{V} - \frac{2}{3} \dot{B}_1 \right] - 6\pi \eta \lambda a^2 \left[ \dot{V} - \frac{2}{3} \dot{B}_1 \right] - \frac{1}{2} m_f s \dot{V}.
\]

(3.6)

Here, we neglect the contribution of the gravitational force compared with hydrodynamic forces due to self-propulsion of the swimmer. The first, second and third terms correspond to the quasi-steady hydrodynamic force, Basset force and added mass force, respectively. The swimming velocity of the squirmer can be expressed in Laplace space as

\[
\hat{V}(s) = \frac{2}{3} \hat{B}_1 - \frac{2}{3} \hat{B}_1 \left( \frac{1}{2} m_f + m_s \right) s \left( \frac{6\pi \eta a}{1 + \lambda a} + \left( \frac{1}{2} m_f + m_s \right) s \right).
\]

(3.7)

Only the first term of the tangential surface velocity, (3.1) (parameter \( B_1 \)), contributes to the propulsion of the organisms, while other terms affect the flow field and nutrient uptake but not propulsion. If one solves quasi-steady Stokes equations (Blake 1971), instead of the unsteady Stokes equation as done here, the swimming velocity is simply \( V = (2/3)B_1 \) and its time average can be described as \( \langle V \rangle = (2/3)\langle B_1 \rangle = (2/3)B_{10} \), which is referred to as a streaming parameter in the literature (Magar & Pedley 2005). For a non-zero streaming parameter, the micro-organism swims around with a non-zero mean velocity. When the streaming parameter is zero but \( b_1 b_2 \), referred to as a hovering parameter, is non-zero, the organism stirs the fluid around it but its mean velocity is zero. In order to include the effect of unsteady forces, we need to calculate the inverse Laplace transform of (3.7) using the contour integration technique. Let us define

\[
\hat{V}_B(s) = \hat{V} - \frac{2}{3} \hat{B}_1
\]

\[
= -\frac{2}{3} \left( \frac{1}{2} m_f + m_s \right) B_{10} + B_{11} s^2 / (s^2 + \omega^2) + B_{12} s^2 / (s^2 + 4\omega^2) \left( 6\pi \eta a \left( 1 + \sqrt{\frac{a^2 s}{\nu}} \right) \right) \left( \frac{1}{2} m_f + m_s \right) s.
\]

(3.8)

The inverse Laplace transform of the function \( \hat{V}_B(s) \) can be written as

\[
V_B(t) = \frac{1}{2\pi i} \int_\gamma e^{st} \hat{V}_B(s) \, ds,
\]

(3.9)

where \( i = \sqrt{-1} \). Since the function \( \hat{V}_B \) is analytic in the complex domain except for a finite number of isolated singularities inside the contour shown on figure 1, its inverse Laplace transform can be calculated using the residue theorem. The function \( \hat{V}(s) \) has four poles at \( \pm i\omega \) and \( \pm 2i\omega \), a branch point at \( s = 0 \) and a branch cut from \( s = 0 \) to infinity along the negative real axis as shown in figure 1. The inverse Laplace transform can be calculated after deforming the inversion contour into a keyhole contour in the complex \( s \)-plane, cut along the negative real axis and summing the
residues at the poles ±iω and ±2iω:

\[ V_B(t) = -\frac{1}{2\pi i} \left[ \int_{BC,FA} + \int_{CD,EF} + \int_{DE} \right] \times e^{\gamma x} \hat{V}_B(s) ds + \sum_{k=1}^{2} \text{res}(\pm i k \omega). \] (3.10)

The integrals on paths BC, FA and DE are zero. The sum of residues leads to

\[ I_1(t, \omega) = \sum_{k=1}^{2} -\frac{2}{3} B_{1k} \text{SLRe} \frac{A_2 \cos k \omega t - A_1 \sin k \omega t}{A_1^2 + A_2^2}, \] (3.11)

where

\[ A_1 = 1 + \sqrt{\frac{3k \text{SLRe}}{2C}}, \quad A_2 = \sqrt{\frac{3k \text{SLRe}}{2C} + k \text{SLRe}}, \] (3.12a)

\[ \text{SLRe} = \left( \frac{1}{2} m_f + m_s \right) \omega / 6 \pi \eta a, \quad C = \left( \frac{1}{2} m_f + m_s \right) \frac{3}{2} m_f, \] (3.12b)

where C is unity for a neutrally buoyant swimmer. The integral on paths CD and EF can be written as

\[ I_2(t, \omega) = \frac{1}{2\pi i} \int_{0}^{\infty} e^{-\gamma x} [\hat{V}_B(x e^{-i\pi}) - \hat{V}_B(x e^{i\pi})] dx \]

\[ = \sum_{k=0}^{2} -\frac{2}{3\pi} B_{1k} \text{SLRe} \int_{0}^{\infty} \sqrt{\frac{3 \text{SLRe}}{C}} e^{-x^2/A_3} \frac{x^2}{k^2 + x^2} dx, \] (3.13)

where

\[ A_3(x) = (1 - \text{SLRe})^2 + \frac{3 \text{SLRe}}{C}. \] (3.14)
Organism | Size $\text{m}$ | Speed $\text{m} \text{s}^{-1}$ | $\omega/2\pi$ $\text{Hz}$ | $Re$ | $Sl$ | $Sl-Re$ | Reference
---|---|---|---|---|---|---|---
Algal cell | 2 | 0.3 | 33 | 0.0015 | 3.5 | 0.005 | Guasto et al. (2010)
Opalina | 350 | 0.1 | 4 | 0.02 | 44 | 0.8 | Brennen (1974)
Paramecium | 250 | 1 | 30 | 0.13 | 24 | 3 | Brennen (1974)

Table 1. Physical parameters for representative organisms

Consequently, the squirmer velocity can be calculated as

$$V = \frac{2}{3}B_1(t, \omega) + I_1(t, \omega) + I_2(t, \omega).$$

(3.15)

Here $I_1$ is a harmonic function of time while $I_2$ decays to zero with time. The transient behaviour of the micro-organism cannot be captured using quasi-steady Stokes equations unless $SlRe \ll 1$. Moreover, the long time unsteady swimming velocity of the micro-organism would be incorrectly predicted, and one needs to use the unsteady Stokes equation instead, as done in this manuscript. Figure 2(a) shows the dimensionless velocity of the swimmer, $V^* = V/a\epsilon\omega$, as a function of dimensionless time, $t^* = \omega t$, and it is compared with that predicted by quasi-steady Stokes equations (Blake 1971). The mean velocity of the squirmer deviates from the prediction of quasi-steady Stokes equations at early times (e.g. first three periods of oscillation). This deviation is due to the function $I_2$. The long time behaviour of the swimmer is also modified due to the history and added mass forces (due to the function $I_1$). The Basset and added mass forces are larger than the hydrodynamic forces predicted by quasi-steady solution as shown in figure 2(b), where the dimensionless force is defined as $f^* = F/6\pi\eta a^2\omega$. The long time behaviour of (3.15) can be simplified for two different limits, $SlRe \ll 1$ and $SlRe \gg 1$. In the limit of $SlRe \ll 1$, the long time velocity can be written as

$$V \sim \frac{2}{3}B_1 + \sum_{k=1}^2 B_{ik}kSlRe \sin k\omega t.$$ 

Thus, the contribution of the history and added mass forces to the swimming velocity compared with one due to the quasi-steady Stokes force scales with $SlRe$. In this limit, the Basset and added mass forces can be neglected since $SlRe$ is small. On the other hand, in the limit of $SlRe \gg 1$, the long time velocity can be written as

$$V \sim \frac{2}{3}B_1 - \sum_{k=1}^2 B_{ik} \cos k\omega t \sim \frac{2}{3}B_{10}.$$ 

Thus, in this limit, the contribution of the history and added mass forces leads to a steady swimming velocity even though cilia motion generates an oscillatory surface disturbance. Based on the value of $SlRe$, the contribution of unsteady forces is important for Paramecium and Pleurobrachia and it should be taken into account. Figure 2(c) shows the amplitude of oscillation of the organism’s velocity, normalized by that predicted by quasi-steady Stokes equations for the two different squirmers described in the legend of figure 2 with an identical mean velocity. It approaches unity as $SlRe$ approaches zero, but it can be reduced to 10% of the prediction of quasi-steady solution as $SlRe$ increases to $O(100)$ and reduces as $SlRe^{-1/2}$ at large values of $SlRe$. For a neutrally buoyant micro-organism, $SlRe^{-1/2} = a\sqrt{\omega/3v}$, which represents the ratio of organism size to the distance over which the vorticity generated at the organism surface diffuses during the time scale of unsteadiness. The amplitude of oscillation of Basset, added mass and Stokes forces are plotted in figure 2(d). At $SlRe \sim O(1)$, these forces are comparable, while the Basset force is much larger than the quasi-steady Stokes force as $SlRe$ increases.
Unsteady hydrodynamic forces (i.e. Basset and added mass forces) affect the swimming velocity of small organisms. (a) The dimensionless swimming velocity of the organism calculated in this manuscript is compared with the Blake solution where unsteady hydrodynamic forces are neglected. (b) The Basset and added mass forces acting on the organism are larger than the hydrodynamic forces predicted by quasi-steady Stokes equations. The data in (a) and (b) are shown for a squirmer with $B_{10} = 2.39, B_{11} = 3.5, B_{12} = 0.16$. (c) The ratio of velocity amplitude predicted by the present analysis normalized by that predicted by the Blake solution is plotted for two different squirmers with an identical mean velocity. The solid line corresponds to $B_{10} = 2.39, B_{11} = 3.5, B_{12} = 0.16$ and square symbols correspond to $B_{10} = 2.39, B_{11} = -1, B_{12} = 3.13$. (d) The amplitude of oscillation of Basset, added mass and Stokes forces are plotted for the two organisms explained in (c). (e) The velocity of a jumping copepod experimentally measured by Jiang & Kørboe (2011) is compared with the present results. The plot corresponds to $B_1 = 2.82 \text{ mm s}^{-1}, C = 1, a = 300 \mu \text{m}$ and $\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$. 

**Figure 2.** (Colour online available at journals.cambridge.org/flm)
In order to mathematically model jumping behaviour, we calculate the time-dependent swimming velocity for a spherical organism with a surface velocity of $v_s = B_1 \delta(\nu t/a^2) \sin \theta$ where $B_1$ is constant. Accordingly, the swimming velocity decays as

$$V = \frac{2}{3\pi} B_1 \int_0^\infty \frac{C_x^{3/2} e^{-\frac{\nu xt}{a^2}}}{3\{1 - Cx/3\}^2 + x} \, dx.$$  \hfill (3.16)

Figure 2(e) shows the velocity of the swimmer as a function of time. The velocity decay of a jumping organism calculated in (3.16) shows good agreement with the experimental measurements of Jiang & Kjørboe (2011) for a jumping copepod.

4. Conclusions

In this paper, we have derived the fundamental equation of motion for an unsteady micro-organism swimming in a non-uniform flow field. We showed that the unsteady inertial effects, the history and added mass forces, are not negligible for finite $SlRe$. The mean velocity of the squirmer deviates from the prediction of quasi-steady Stokes equations due to the contribution of history and added mass forces (function $I_1$). Consequently, our results show that unsteady inertial effects can lead to propulsion of an unsteady squirmer even for the cases with zero streaming parameters. These results are compatible with the recent experimental results by Hamel et al. (2011) where they showed that a Paramecium escapes an aggression by generating time-reversible effective and recovery strokes. This type of stroke does not generate any effective propulsion if all of the inertial effects are neglected (Lauga 2011) as predicted by the Purcell theorem (Purcell 1977). However, the unsteady inertial effects discussed in this paper explain the propulsion observed in the experiment.

Acknowledgement

This work is supported by NSF grant CBET-1066545.

REFERENCES


