UNSTEADY SWIMMING OF SMALL ORGANISMS

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Summary Planktonic organisms ubiquitously show unsteady, impulsive, or erratic behaviour 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 their swimming motion is poorly understood. In this paper, we derive the fundamental equation of motion for a spherical organism swimming in a nonuniform flow at low Reynolds number regime. We show that history and added mass forces are important for finite $Sl{\cdot}Re$ where Reynolds number, Re, is the ratio of inertial to viscous forces and Strouhal number, Sl, is the ratio of the time scale of unsteadiness to the convective time scale. This is particularly important since many organisms such as Paramecium and copepod live in this range.

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 [1]. Ciliates, such as *Paramecium*, swim by metachronal beating of cilia on their surface. Recently, Hamel *et al.* [2] showed that *Paramecium* uses synchronized beating of their cilia to generate rapid accelerations away from an intermediate aggression which is followed by a large oscillation in velocity before it reaches to steady value. For more severe aggressions, *Paramecium* shows jumping behavior to escape. Other planktonic protists, such as *Balanion comatum*, also escape from hydromechanical signals by jumps leading to more than five-fold increase of their swimming velocity within the time required to move one bodylength [3]. Jumping is common among protozoan and metazoan plankton [1]. Copepods, the most abundant metazoans in the ocean, "swim by sequentially sticking the swimming legs posteriorly" which results in sequences of small jumps for the purpose of ambush feeding [1]. Since jumping organisms respond to hydromechanical signals rather than direct contact, ambient fluid motion can also trigger microorganism's acceleration in addition to flow disturbances generated by a prey or a predator. Hence, microorganisms jump more frequently in turbulent flows compared to calm environments [4]. Unsteady motion has also been reported for flagellated organisms. Recently, Gollub and coworkers [5] 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 microorganisms. Despite the widespread implications of unsteady swimming in nature, the role of unsteady hydrodynamic forces on their propulsion has not been explored in the literature. In this paper, we derive the fundamental equation of motion for unsteady swimming of small organisms.

Even though, unsteady swimming of microorganisms is poorly understood, the study of unsteady motion of rigid particles has a long history. Boussinesq (1885) [6], Basset (1888) [7], and Oseen (1927) [8] 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 [7]. Maxey & Riley (1983) [9] developed the equation of motion for a sphere in an unsteady nonuniform background flow in the limit of small particle Reynolds number. The Reynolds number, $Re = \rho_f U a/\mu$, is the ratio of convective to viscous forces, where U is the particle velocity, a the particle radius, ρ_f the fluid density, and μ is the fluid viscosity. These studies include unsteady inertia due to the fluid and particle but neglect convective inertial effects and thus Basset force decays as $t^{-1/2}$, where t is the time. Unsteady hydrodynamic forces have been used to determine transport of small particles in turbulent flows, particle dispersion, and deposition [10]. For swimming microorganisms the unsteadiness arise 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 pray or predator. In this paper, we assume

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unsteady inertia is large compared to convective inertia, $Sl \gg Re$, which is the case for the examples discussed above since microorganisms live in a low-Reynolds number regime. The Strouhal number, $sl = a/U\tau$, is a measure of the time scale of unsteadiness, τ, to the convective time scale. For example, a swimming algal cell has a Reynolds and Strouhal numbers of 0.01 and 1, respectively [5].

We derive the fundamental equation of motion for a spherical unsteady swimmer in a nonuniform flow. Then in order to determine the effect of unsteady hydrodynamic forces on a swimming microorganism, we use an archetypal model wieldy used in the literature to study low-Reynolds number swimming called squirmer model. The squirmer model consists of a spherical shaped body with wavelike deformations of the outer surface [11] and describes the self-propulsion of ciliates moving by synchronized metachronal beating of cilia on their surface [12], such as cyanobacteria, colonies of flagellates like *Volvox*, and *Paramecium*. The model has been recently used to study the hydrodynamic interaction between swimmers, mixing due to propulsion of microorganisms, bio-locomotion in complex fluids, and stratified fluids [13]. Unsteady squirmers have been studied by Magar & Pedley [4] to explore the nutrient uptake of microorganisms. Even though microorganisms in nature undergo unsteady swimming, the role of unsteady forces (history and added mass forces) on their swimming behavior, to the best of our knowledge, has not been previously explored and is the focus of this paper. Our results show that unsteady hydrodynamic forces are significant for finite values of *Sl·Re* (see figure 1).

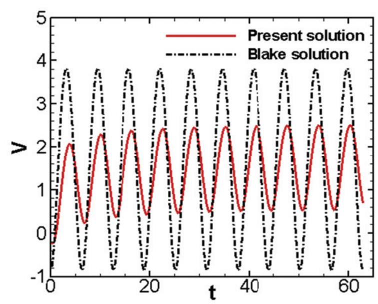

Figure 1. Dimensionless swimming velocity of an unsteady squirmer at *Sl·Re=10*: (——) unsteady hydrodynamic forces are included, (-·-·-) unsteady forces are neglected (Blake solution [12]).

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