BioFluids Lecture 2:   Introduction to animal locomotion

We begin with external biofluidmechanics, and consider fluid motion outside the body, in particular how animals move through fluids. Let's begin with some basic questions:

(a) What is locomotion? Typically, it is deliberate motion from A to B. We exclude passive effects like Brownian motion or being blown by the wind. Marine animals which alter their buoyancy do not technically swim. But a hovering bird or insect is flying.

(b) What is the difference between swimming and flying? Clearly, flight requires support of the body against gravity. Swimming we will define to be self-driven motion of a neutrally buoyant body through a fluid. Some sharks are denser than water, and would naturally sink if they stopped moving they are really flying not swimming.

(c) What is the difference between fish and birds and ships and planes? Obviously the fuel sources are different, but there is a more fundamental fluid mechanical difference. Man-made devices are usually almost rigid, whereas animals generate their forward thrust by moving their bodies around. Moving boundary problems are generally hard, and we anticipate the need for some approximations in analysing the associated flows. A further point is that the study of ships and planes is partly motivated by the desire to improve design. The animal kingdom has evolved to the stage where it is very good at efficient locomotion in its natural environment. We do not always know what it is trying to optimise, but we can learn from it.

A basic summary of forces due to rigid motion through fluids.

When a (rigid) body moves relative to the surrounding fluid it does work for two reasons. Firstly, it must move the fluid out of its way, imparting kinetic energy to the fluid. Secondly, it must overcome the internal fluid friction, as measured by the **viscous** term. The relative importance of these two effects can be estimated by looking at the Reynolds number

$$\frac{|\rho \mathbf{u} \cdot \nabla \mathbf{u}|}{|\mu \nabla^2 \mathbf{u}|} \simeq \frac{\rho U_0^2 / L}{\mu U_0 / L^2} = \frac{\rho U_0 L}{\mu} = R \ . \tag{2.1}$$

Where we have estimated the size of the terms rather crudely, letting U_0 be a typical magnitude of $|\mathbf{u}|$ and L be a typical length-scale of variation. The whole nature of the motion depends crucially on the size of this number. Flows which are small-scale, slow and sticky have **Low Reynolds Number**, whereas motions which are large, fast and momentum dominated have a **High Reynolds Number.** For swimming in water, $R \sim 10^{-5}$ for a bacterium, $R \sim 0.1$ for a protozoan, $R \sim 3 \times 10^5$ for a medium sized fish and $R \sim 2 \times 10^6$ for a human. The idea of **dynamic similarity** comes from this: for the fluid dynamics, only the value of R is important. A protozoan swimming in water is just like a human swimming through syrup at 0.1m/s, apart from shape differences. Our fluid dynamical knowledge leads us to expect vastly different propulsion mechanisms at high and low Reynolds numbers.

Note that although we are interested in a body moving in stationary fluid, it is mathematically equivalent to consider the body at rest and the fluid moving past it. This is because the Navier-Stokes equations are Galilean invariant. Note also that if the body translates at some average velocity, then the average force it exerts on the fluid must be zero. Of course, this doesn't mean the body does no work. Overcoming viscous drag (at low R) or imparting kinetic energy to the fluid (at high R) may involve considerable effort.

Drag at Low Reynolds Number:

When the inertial term is much smaller than the viscous term, the nonlinear term can be neglected. This linear problem is relatively easy to solve. A body moving with speed $\mathbf{U}_0$ through a fluid when $R \ll 1$ experiences a **drag** force

$$\mathbf{D} = 6\pi L\mu\, M\mathbf{U}_0 \qquad \text{where } M \text{ is a dimensionless geometrical tensor.} \qquad (2.2)$$

If the direction of $\mathbf{U}_0$ is along a principle axis of M, then $M\mathbf{U}_0 = \alpha\mathbf{U}_0$, and the drag acts in the opposite direction to the velocity. For a sphere of radius L, it is found that $\alpha = 1$. α does not vary too much for other shapes. Neither does it matter very much in which orientation the body lies; the drag force tends to be governed by the greatest linear dimension of the body. This is in marked contrast to flows at higher R, where a streamlined shape is very important. (Try pushing a boat sideways!) Despite this, we will see that low Reynolds number swimming exploits the difference in resistance coefficients for motion parallel and normal to flagella.

The crucial point is that the drag force varies **linearly** with the velocity. Note also that the entire flow is reversible: if we replace $\mathbf{u}$ by $-\mathbf{u}$, then $\mathbf{D}$ goes to $-\mathbf{D}$. Note also a general body will rotate in response to a net torque.

Drag at high Reynolds number:

The situation is much more complicated when $R \gg 1$. We would like then to ignore the viscous term totally; however, it is important very close to solid boundaries in **boundary layers.** Sometimes these thin layers **separate** leading to a marked increase in drag (when flying, this is called **stall**). It is also possible for vortices to be shed, for the force to be time-dependent and for the flow to be turbulent. At high Reynolds numbers, the drag on a body moving with speed U_0 is approximately quadratic in U_0, and may be summarised

$$D = \tfrac{1}{2}C_D\,\rho S U_0^2 \qquad \text{where } S \text{ is the cross-sectional area normal to } \mathbf{u}\,. \qquad (2.3)$$

C_D is a dimensionless number known as the **drag coefficient.**, which varies with both shape and Reynolds number. In this case, for the drag to be small it is very important for the shape to be **streamlined** and to present a small cross-section to the oncoming flow. (Think of a sail, where **large** drag is desirable.)

Lift forces:

At high R also the total force may not be aligned with the velocity. (Imagine carrying a large sheet of wood slightly inclined to a strong wind.) A large force normal to the velocity can be generated, due to an asymmetric pressure distribution. This **lift** force, G, is usually

$$G = \tfrac{1}{2}C_L\,\rho U_0^2 W \qquad \text{where } W \text{ is the wing area} \qquad (2.4)$$

and C_L is the dimensionless **lift coefficient**. It is proportional to $\sin\beta$ where β is the angle between wing and oncoming flow. This lift can balance gravity and enable flight. It does however increase the drag force, by an amount known as the **induced drag**, D_I. The reasons for the induced drag are complex, and to do with the trailing vortices at the wing tips. The total drag acting in the presence of lift is given by the sum of D and D_I.

Flows with moving boundaries: parameters and general comments

The above relations are useful background, but we are interested in non-rigid motion. Let us assume the animal adopts a strategy for moving its surface which results in average motion in a given direction. We will further assume that it repeats this strategy, so that the flow is time-periodic, with frequency ω. We can then define another parameter, the Strouhal number, $St = \omega L/U_0$, which gives an indication of how the boundary motion relates to the net swimming speed. If the amplitude of boundary displacement is small compared to the body size this would introduce an amplitude parameter also. For flows where gravity is important, we may want to consider the Froude number, $F = U_0^2/(gL)$.

The Reynolds number can vary by many orders of magnitude. At low Reynolds number, the Strouhal number is usually in the 10-100, range, but for forward flight of insects and birds $St \simeq 0.3 \pm 0.1$ fairly uniformly. This suggests that the flapping rate during flight has been optimised in some manner.

What kind of simple swimming motions are possible? Consider simple tail-wagging. At high Reynolds number this simple motion drives fluid backwards, with a consequent forward force on the body. (This is like oscillating the rudder on a yacht.) At low Reynolds number however, no net forward motion occurs (see video), which is a consequence of

The Scallop Theorem: *No time reversible sequence of boundary configurations can swim at low R.* This is more general than saying no time-reversible motion can swim, because the rate at which the 'forward' stroke occurs can be different from the 'return' stroke. A scallop is a rigid bivalve, which opens and closes by rotating its two halves about an axis. Suppose the opening is slow and the closing is rapid. At $R \geqslant O(1)$ this will drive a jet of water backwards during the closing stroke, but while it opens, fluid is sucked in from all directions. Nevertheless if $R \ll 1$ no net motion can occur. Time appears as a parameter in the Stokes problem

$$\nabla p = \mu \nabla^2 \mathbf{u}, \qquad \mathbf{u} = \mathbf{U}_b(\mathbf{x}, t) \qquad \text{on the boundary,} \tag{2.5}$$

the speed of motion does not affect the argument. If we run the film backwards, we still end up where we started, even if we run the camera slowly. The scallop theorem is poorly named, as scallops **do** in fact swim with reversible motions, albeit at high R. Furthermore, unlike jellyfish, which propel themselves in the expected direction, opposite to that of an emitted water jet, the scallop actually swims in the direction of its open end, due to geometric effects. The theorem merely states that scallop must open or close quickly enough if they are to transport themselves.

It is important to note that a travelling wave is not time-reversible. This is a very common method of propulsion over a wide range of Reynolds numbers. Over the next few lectures we shall consider the cases of low and high R separately. There is a fairly clear distinction between bacteria, spermatazoa and ciliates which swim at low R, the Stokesian regime, and birds and fishes which live in the Eulerian regime at high R. Relatively few creatures, small fishes, molluscs and insects, have to cope with both inertia and viscosity.