BioFluids Lecture $4\frac{1}{2}$: Ciliar swimming – the envelope model.

See the course Webpage: http://www.ma.ic.ac.uk/~ajm8/BioFluids

Many organisms employ large numbers of flagella (which we now call cilia) to generate forward motion. The essence of ciliar swimming is that rather than have each flagellum perform a travelling wave, a wave may be generated by suitable time lapses between cilia undergoing a simple, identical motion. We will assume each cilium moves periodically. Typically, this motion consists of a wide sweep at some distance from the boundary, which we call the swimming stroke, followed by a recovery stroke with the cilium close to the boundary. This may be likened to the technique of a child on a swing, although the mechanical processes are very different. If the swimming stroke is in the same direction as the travelling wave the motion is called *simplectic*, whereas if it is in the opposite direction it is called *antiplectic*.

Each cilium might swim by itself if its motion is irreversible (remember the scallop theorem.) However, the essence of ciliar swimming is that a large number of these motions are superposed in a travelling wave-like manner. This kind of ciliar motion is also used inside the body to transport mucus linings, for example in the lungs; there the fluid may well be non-Newtonian, however.

We consider an organism with a planar surface $y = 0$ which is coated with an array of cilia. We shall assume the cilia undergo a z-independent, sinusoidal travelling wave motion in the x-direction. Thus as they wave around, the tip of the cilium tethered at $(x_0, 0)$ is at (x_s, y_s) where

$$x_s = x_0 + a\cos(\xi - \phi), \qquad y_s = y_0 + b\sin\xi \qquad \text{where} \quad \xi = kx_0 - \omega t. \tag{4.1}$$

Here x_0 is a variable essentially labelling the cilia, whereas y_0 is an average extension which we will take to be the same for each cilium. We could easily extend the theory to include z-dependence, but that would increase the algebra.

We will assume $k > 0$ and $\omega > 0$, so that the wave travels to the right with phase speed k/ω. We have included a phase factor ϕ to allow for various swimming modes. When the cilium is fully extended ($\xi = \frac{1}{2}\pi$) the x-component of its tip velocity is $\partial x_s/\partial t = a\omega\cos\phi$, so that the motion is *simplectic* for $|\phi| < \frac{1}{2}\pi$.

Eliminating t from(4.1), we find that the orbit of the cilium at position x_0 is

$$\big[b(x_s - x_0) - a\sin\phi(y_s - y_0)\big]^2 + a^2\cos^2\phi(y_s - y_0)^2 = a^2b^2\cos^2\phi \tag{4.2}$$

so that the tip of each cilium (x_s, y_s) describes an ellipse.

Now the fluid is constrained to have the cilium velocity at each point (x_s, y_s). So if the density of cilia is high enough we expect it will be reasonable to model the array of cilia as a rigid sheet with shape (x_s, y_s). This sheet is in some sense the **envelope** of the ciliar motion. At each time instant t, the sheet shape is given parametrically in terms of x_0. Note that the sheet so defined will not in general be inextensible as we ensured for the single flagellum. However, there is no reason why it should be, as it models a discrete set of cilia.

We therefore consider the Stokes flow above the boundary given by (4.1). On this boundary, the velocity must be given by

$$\mathbf{u} = \left(\frac{\partial x_s}{\partial t},\, \frac{\partial y_s}{\partial t},\, 0 \right) = (a\omega \sin(\xi - \phi),\, -b\omega \cos \xi,\, 0) \qquad \text{on } x = x_s,\, y = y_s. \tag{4.3}$$

Note that x appears implicitly in this equation through ξ. Combining (4.1) and (4.3) will generate terms like $\sin n\xi$ for all integers n.

We seek the solution to the Stokes equations in $y > y_s$ satisfying (4.3). As we have a two-dimensional geometry, we can use a streamfunction ψ with

$$\mathbf{u} = \nabla \wedge (0,\, 0,\, \psi) = (\psi_y,\, -\psi_x,\, 0) \tag{4.4}$$

so that the Stokes equations reduce to the biharmonic equation for ψ

$$\nabla p = \mu \nabla^2 \mathbf{u} \quad \Longrightarrow \quad \nabla^2(\nabla^2 \psi) = 0. \tag{4.5}$$

We shall assume the amplitudes a and b of the wave motion are small (and of similar order) compared to the wavelength, and seek a power series solution in ka, kb. We will also need a boundary condition as $y \to \infty$. As we are using a frame fixed in the body, if the organism swims the fluid at infinity will appear to move in the opposite direction, so we expect

$$\frac{\partial \psi}{\partial y} \to U, \qquad \frac{\partial \psi}{\partial x} \to 0 \qquad \text{as } y \to \infty, \tag{4.6}$$

where positive U indicates the organism swims in the negative x-direction.

If we Fourier analyse in the x-direction, an appropriate set of separable solutions to the biharmonic equation $\nabla^4 \psi = 0$ are

$$\psi = \sum_{n=0}^{\infty} V_n \equiv \sum_{n=0}^{\infty} \left[(A_n + B_n \eta) \sin n\xi + (C_n + D_n \eta) \cos n\xi \right] e^{-n\eta} \tag{4.7}$$

where we have written

$$\eta = ky, \qquad \xi = kx - \omega t. \tag{4.8}$$