

## BioFluids Lecture 11: Bioconvection – what goes up must come down.

We ended last time considering how schools of fish and flocks of birds could benefit from the presence of the others. In large numbers, microorganisms also can alter their environment, whether consciously or not, by a process known as bio-convection. Essentially, they increase the density of the surrounding fluid by swimming, thus causing it to convect. The resultant large-scale fluid motion enhances mixing and can improve nutrient supply.

Bacteria and algae swim in response to a variety of stimuli. They may seek nutrients or light, processes known respectively as *chemotaxis* and *phyllotaxis*. If they have sensitive detection apparatus, they can arrange to swim up chemical gradients. However, many of them are too small to detect changes in concentration (of oxygen, say) on the length-scales of individual bacteria. Some are observed to swim for a little while in a straight line and if conditions have not improved, alter their orientation and swim off in another direction. Others arrange to swim upwards, which is usually towards the source of light and oxygen. An excellent process to achieve this is known as *gyrotaxis*, which uses gravitational torque to orientate the bacterium so that it faces upwards (essentially they are bottom-heavy.) We will suppose there are a large number of organisms all trying to swim upwards. As their density tends to be slightly higher than that of the ambient fluid, this can lead to an unstable density profile, with resultant overturning of the fluid.

We shall treat the bacteria or other organisms as a continuum, with a concentration (or number density)  $c(\mathbf{x}, t)$ . The local fluid density we suppose therefore to be  $\rho_0(1 + \alpha c)$ , where  $\rho_0$  is the density of the pure fluid and  $\alpha$  is a given positive constant. Under the Boussinesq approximation, it is consistent to treat the fluid as incompressible,

$$\nabla \cdot \mathbf{u} = 0, \quad (11.1)$$

while including in the Navier-Stokes equation a buoyancy term in the gravity direction  $\mathbf{g} = -g\hat{\mathbf{z}}$

$$\rho_0 \frac{D\mathbf{u}}{Dt} = -\nabla p + \rho_0(1 + \alpha c)\mathbf{g} + \mu \nabla^2 \mathbf{u}. \quad (11.2)$$

We require an evolution equation for  $c$ , which must reflect the fact that the bacteria are conserved. We suppose that they are advected by the local fluid velocity and swim relative to the fluid with velocity  $\mathbf{v}$ . They may also be subject to random forcing or fluctuations, we will represent these by a constant and isotropic diffusivity  $D$ , so that

$$\frac{\partial c}{\partial t} = -\nabla \cdot [c(\mathbf{v} + \mathbf{u})] + D \nabla^2 c. \quad (11.3)$$

In their seminal paper on bioconvection, Childress, Levandowsky & Spiegel (1975) allowed for differing horizontal and vertical diffusion rates, but we won't.

We assume that each organism attempts to swim vertically relative to the fluid. It is possible that fluid motion will interfere with this intent, as local shear might alter the orientation of each organism. We will consider this effect in more detail later, when we allow for *gyrotaxis*. It gives rise to a completely different instability mechanism to the one we investigate here.

Neglecting gyrotactic effects, we assume that each organism swims vertically relative to the fluid. Then there is a steady state where the concentration of bacteria is such that the vertical swimming is balanced by diffusion, with no fluid motion, so that  $\mathbf{v} = V \hat{\mathbf{z}}$

$$D \frac{dc}{dz} = cV \quad \text{or} \quad c = c_0(z) = C_0 e^{Vz/D}, \quad (11.4)$$

if  $V$  is independent of  $c$  and  $z$  and  $c \rightarrow 0$  as  $z \rightarrow -\infty$ . More realistically, we could allow  $V$  to decrease as  $c$  increases, but that complicates the algebra. If we wish to impose no flux conditions  $\frac{\partial c}{\partial z} = 0$  on lower and upper boundaries, then we cannot take  $V$  to be constant and the equilibrium concentration  $c_0(z)$  will require modification. If the bacteria suspension occupies  $0 < z < H$ , we could take, for example

$$V = V_0 z(H - z)/H^2 \quad \text{for constant } V_0 \quad (11.5)$$

which would give us the equilibrium

$$c_0(z) = C_0 \exp \left[ \frac{V_0 z^2 (3H - 2z)}{6DH^2} \right]. \quad (11.6)$$

Any equilibrium profile  $c_0(z)$  can be supported by a vertical pressure distribution,  $p_0(z)$ . We note that in an infinite layer, we can have a uniform concentration swimming upwards at constant speed, without changing the local density at all. In a container of finite depth, however, typical choices of  $V$  lead to a profile which increases with  $z$  and with the organisms concentrated into a layer of thickness  $h$ . In this last example,  $h \sim D/V_0$ . If the associated density increase exceeds some threshold, then we expect convection to occur.

If we non-dimensionalise length with respect to  $H$ , time with respect to  $H^2/D$  and the modified pressure ( $p + \rho_0 g z$ ) with respect to  $\mu D/L^2$  we obtain

$$\left. \begin{aligned} \sigma^{-1} \frac{D\mathbf{u}}{Dt} &= -\nabla p + Rc \hat{\mathbf{z}} + \nabla^2 \mathbf{u} \\ \frac{Dc}{Dt} &= -\frac{\partial}{\partial z}(Vc) + \nabla^2 c, \end{aligned} \right\} \quad (11.7)$$

where the Schmidt number  $\sigma$  and the ‘Rayleigh number’  $R$  are defined by

$$\sigma = \frac{\nu}{D} \quad \text{and} \quad R = \frac{g\alpha C_0 H^3}{\nu D}, \quad (11.8)$$

where  $\nu = \mu/\rho_0$ . We call  $R$  the Rayleigh number to draw a parallel with Rayleigh-Bénard convection – in that context  $\sigma$  is usually called a Prandtl number. Experimental data suggest that  $\sigma > 1$  and  $R < 100$ .

We can now investigate stability of the equilibrium  $\mathbf{u} = 0$ ,  $c = c_0(z)$ , perturbing with a mode  $\propto \zeta \equiv e^{ilx + imy} e^{st}$ . The horizontal wave number,  $k = (l^2 + m^2)^{1/2}$  is real, while the growth rate  $s$  may in principle be complex. Formally, for some small  $\varepsilon$  we write

$$c = c_0(z) + \varepsilon c_1(z)\zeta, \quad p = p_0(z) + \varepsilon p_1(z)\zeta, \quad w = \varepsilon W_1(z)\zeta, \quad (11.9)$$

where  $w$  is the  $z$ -component of velocity. We can eliminate the pressure and the other velocity components by taking the curl of the curl of the Navier-Stokes equation and evaluating the  $z$ -component. After some rearrangement of the concentration equation, we obtain the coupled system

$$\left. \begin{aligned} \frac{s}{\sigma} \left( \frac{d^2}{dz^2} - k^2 \right) W_1 - \left( \frac{d^2}{dz^2} - k^2 \right)^2 W_1 &= k^2 R c_1 \\ s c_1 + W_1 c_0'(z) - \frac{d}{dz} \left[ c_0 \frac{d}{dz} \left( \frac{c_1}{c_0} \right) \right] + k^2 c_1 &= 0 \end{aligned} \right\} \quad (11.10)$$

On  $z = 0$  and  $z = 1$  we require  $c_1' = 0$  and  $W_1 = 0$ . If the walls are rigid then we must have no slip ( $W_1' = 0$ ), but if they are free we should impose  $W_1'' = 0$ , no tangential stress. Very often, say in a pond, the lower boundary is rigid but the upper is a free surface.

We now have 6 boundary conditions for the 6th order ODE-system (11.10), dependent on the two parameters,  $\sigma$  and  $R$ . The solution obviously also depends on the equilibrium concentration  $c_0(z)$  – at the very least this introduces a 3rd parameter implicitly, namely  $HV_0/D$  in the above solutions.

For given values of the parameters, we aim to find the wave-numbers  $k$  which give rise to growth rates  $s$  with a positive real part. In fact, if  $V$  is constant (or more generally if  $V/D$  does not depend explicitly on  $z$ , but possibly on  $c$ ) it can be shown that  $s$  is real. We multiply the first equation in (11.10) by  $W_1^*$  (the complex conjugate of  $W_1$ ) and the second by  $c_1^*/c_0$  and integrate over the entire domain. Integrating by parts a few times we obtain a relation between  $s$ , real integrals and boundary terms, which vanish for our boundary conditions. It follows that  $s$  must be real. Just as with Sturm-Liouville equations it follows that the eigenvalue problem can be rewritten in variational form if we so choose.

By analogy with thermal convection, we expect there to be a critical Rayleigh number, above which we have instability. Dependence on the Schmidt number is not so critical, nor the type of boundary (rigid or free).

Typical numerical results show indeed that there is a critical Rayleigh number  $R_c$ . At this critical value, instability usually occurs for all small  $k$  (long waves;  $k_c = 0$ ). However, for  $R > R_c$  the instability with greatest growth rate occurs at some finite value  $k_m$ , which increases rapidly from zero as  $R$  increases to about  $2R_c$  before levelling off at some finite value. Thus the theory predicts that for a given concentration of organisms there will be a minimum depth necessary for bioconvection to occur, and it also predicts that large wavelength patterns may be visible just above critical. The first prediction is well borne out by experiment, but very long wave patterns are not observed for slightly supercritical conditions, as predicted by the linear theory. The likely reason for this is that the bifurcation at  $R = R_c$  is *sub-critical*, which would result in the nonlinear saturated states differing substantially from the linear instability. This was shown in some unpublished work by Spiegel and Childress.

The model we've looked at so far assumes that the organisms swim upwards even in non-uniform fluid motion. This is unlikely to be true, however, because viscous torque would cause them to rotate. So we shall now include *gyrotaxis* in the picture, which we will see can render even a uniform collection of swimming organisms unstable.