

Bioconvection

I. BACKGROUND

Many microorganisms have the ability to swim, enabling them to reach a more desirable location and outcompete their neighbors. Some of these motile organisms can also direct their movement in response to environmental conditions. For example, some microorganisms can respond to chemical cues (chemotaxis), oxygen levels (aerotaxis), and/or light (phototaxis). Experiments with a suspension of *Tetrahymena pyriformis*, a protozoan capable of moving by waving cilia (Fig. 1a), found spontaneous pattern formation, visible as alternating patches of high and low population density (Fig. 1b). This is an example of *bioconvection*, which can occur when relatively heavy organisms swim upward and accumulate near the surface of the fluid. Eventually, the near-surface concentration and density can become large enough that the suspension becomes unstable to convective overturning. In this project, your team will analyze bioconvection using linear stability analysis and nonlinear numerical simulations.

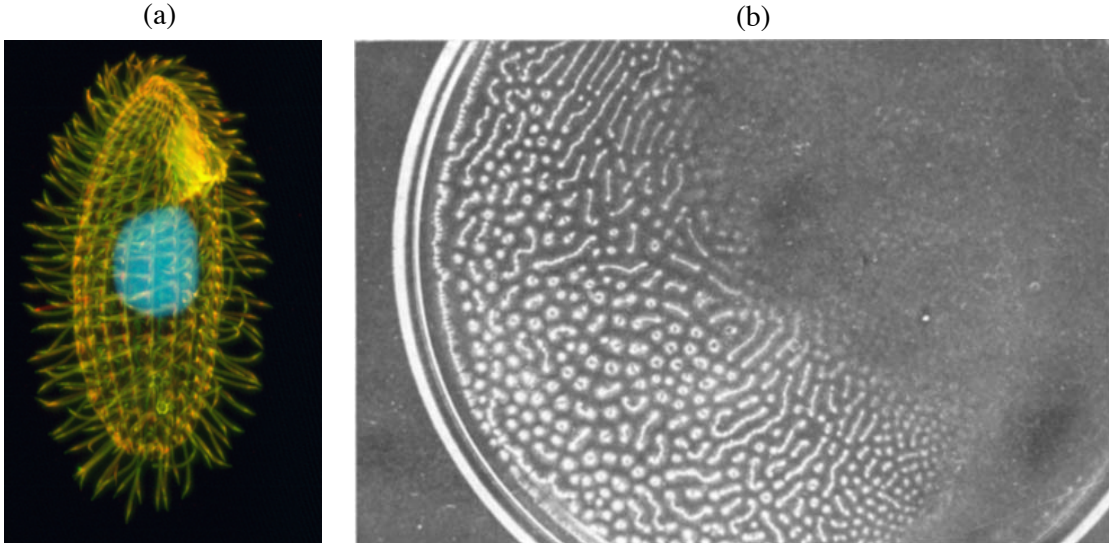


FIG. 1: (a), The ciliated protozoan, *Tetrahymena pyriformis* (source:wikipedia.org). (b) Spontaneous pattern formation in a suspension of *Tetrahymena*. The dish is viewed from above, and the fluid is deeper in the lower left corner, where convection cells appear.¹.

II. INTRODUCTION

Early work describing bioconvection was done by Childress et al.¹ (a copy of this paper in your project folder.) Apply the Boussinesq approximation, and treat the organism concentration, $c(\mathbf{x}, t)$, as a continuous scalar variable.

The dimensional governing equations that we will consider can then be written

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} = -\frac{1}{\rho_0} \nabla p + \nu \nabla^2 \mathbf{u} - g(1 + \alpha c) \hat{j}, \quad (1)$$

$$\frac{\partial c}{\partial t} + \mathbf{u} \cdot \nabla c = \kappa \nabla^2 c - \frac{\partial}{\partial z}(c U_s), \quad (2)$$

$$\nabla \cdot \mathbf{u} = 0, \quad (3)$$

where \mathbf{u} is the fluid velocity, and U_s is the upward swimming speed. Note that the notation differs slightly from Childress et al. in that here y is the vertical direction, to be consistent with Diablo's notation. Although the concentration diffusivity, κ , is primarily due to organism swimming, and should in general be a spatially variable tensor, for simplicity we will assume that it is isotropic and constant. The relative density of the organisms is controlled by the parameter $\alpha = \rho_0/\rho_c - 1$, where ρ_0 is the fluid density, and ρ_c is the mean density of each organism. Here, start by considering a relatively simple case with a constant swimming speed, $U_s = \text{const}$. In the limit of no flow, steady-state solutions require a balance between swimming and diffusion, with an equilibrium profile of the form

$$c_{eq} = c_0 e^{U_s y / \kappa}. \quad (4)$$

Your first objective will be to determine whether this equilibrium state is stable or unstable to small perturbations for a variety of parameters.

Following Childress et al.¹, it is useful to consider non-dimensional equations, normalizing by U_s , κ , and c_0 :

$$\frac{1}{Pr} \left(\frac{\partial \mathbf{u}^*}{\partial t^*} + \mathbf{u}^* \cdot \nabla_* \mathbf{u}^* \right) = -\nabla_* p^* + \nabla_*^2 \mathbf{u}^* - Ra c^* \hat{j}, \quad (5)$$

$$\frac{\partial c^*}{\partial t^*} + \mathbf{u}^* \cdot \nabla_* c^* = -\frac{\partial c^*}{\partial y^*} + \nabla_*^2 c^*, \quad (6)$$

$$\nabla_* \cdot \mathbf{u}^* = 0. \quad (7)$$

where the Prandtl number and Rayleigh numbers are defined as

$$Pr \equiv \frac{\nu}{\kappa}, \quad Ra \equiv \frac{\alpha g c_0 \kappa^2}{\nu U_s^3}. \quad (8)$$

III. LINEAR STABILITY ANALYSIS

Consider the stability of small perturbations the equilibrium state defined above: $\mathbf{u} = \epsilon \mathbf{u}'$, $c = c_{eq} + \epsilon c'$ (here all quantities will be non-dimensional, but the $*$ is omitted.) After linearizing the perturbation equations about the basic state, we can look for 2D solutions of the form

$$c' = \hat{c}(z) e^{ikx + \sigma t}, \quad v' = \hat{v}(y) e^{ikx + \sigma t}. \quad (9)$$

After eliminating the horizontal velocity and using the perturbation form defined above, we arrive at two coupled ODEs (equivalent to Eqns. 2.17 and 2.18 in Childress et al.¹):

$$\left(\frac{\sigma}{Pr} \right) (d_y^2 - k^2) \hat{w} = (d_y^2 - k^2)^2 \hat{v} + k^2 \hat{c} R, \quad (10)$$

$$\sigma \hat{c} = -\hat{v} \hat{c}_y - U \hat{c}_y + (d_y^2 - k^2) \hat{c}, \quad (11)$$

where $d_y = d/dy$ and subscripts are also used to denote a y -derivative. These coupled equations form an eigenvalue problem for the growth rate, σ , and the vertical velocity and concentration profiles \hat{v} and \hat{c} . Notice that these equations are very similar to the equations that we solved for stratified shear flow. In fact, you can use a slightly modified version of the same solver to numerically calculate the maximum growth rate.

The MATLAB script, *bioconvect.m*, which is inside the project folder, solves the eigenvalue problem given above, returning the vertical velocity and buoyancy eigenfunctions, $\hat{v}(y)$ and $\hat{b}(y)$, and the corresponding growth rates, σ . At its core is a slightly modified version of the same solver that we used to study stratified shear flow. As before, at the beginning of *bioconvect.m* you can specify several parameters including the non-dimensional vertical domain size, LY , the number of gridpoints, NY , and the Prandtl and Rayleigh numbers, Pr and Ra .

Childress et al.¹ give estimates for the following dimensional parameters for *Tetrahymena pyriformis*:

$$\nu = 0.01 \text{ cm}^2/\text{s}, \quad \alpha = 0.09, \quad c_0 = 1.8 \times 10^{-3}, \quad U_s = 0.045 \text{ cm/s}. \quad (12)$$

- Starting with $Pr = 1$, calculate the corresponding Rayleigh number.
- Set the input parameters in *bioconvect.m*, along with a non-dimensional fluid depth, $LY = 5$, and run the script.
- Is the equilibrium state stable or unstable in this case?
- If it is unstable, make note of the maximum growth rate and the corresponding wavenumber.
- Change the Rayleigh number from a single number to an array of values. The script will then calculate the maximum growth rate for each Rayleigh number. Use this to estimate the critical Rayleigh number. (The script will take a while to run, so you may want to start with 10 values of the Rayleigh number, and tighten your search window several times to get the critical value).

IV. NONLINEAR SIMULATIONS

Now, let's try to re-create bioconvection using Diablo. Here, we will consider flow in a 2D horizontal/vertical slice. Start with periodic boundary conditions at both ends of the x -domain for all variables, and place no-slip, no normal flow walls at the top and bottom in the y -direction with gravity pointing down (in the negative y -direction). Here, we will effectively be solving the non-dimensional equations Eqns. (5)-(7).

To prepare the simulations, edit the following Diablo setup scripts:

set_params.m - Set $Pr = 1$, and use the same Rayleigh number, LX and LY that you did in *bioconvect.m*. (Note that in the code, $RI(n)$ is the parameter that multiplies the scalar field to add variable density effects. Although this is called the Richardson number in the code, it is actually the Rayleigh number in this application.) Start with $NX = NY = 100$ gridpoints.

set_bcs.m - Set up periodic boundary conditions at both ends of the x -domain for all variables. In the y -direction, set $U1=U2=0$ at the edges (no-slip), with $dP/dy=0$. The linear stability solver, *bioconvect.m*, applies boundary conditions only to the perturbation fields, and uses $c' = 0$ at both walls, but in Diablo, we are solving for the full concentration, not just the perturbations. Therefore in Diablo, we want the boundary conditions to match the equilibrium solution (the basic state in *bioconvect.m*), which will ensure that any departures from this state vanish at the walls. Since TH is defined on the GYF grid, and the walls are located at $GYF(2)$ and $GYF(NY-1)$ (see the Diablo User's Guide), set $TH=\exp(GYF(2))$ at the lower boundary and $TH=\exp(GYF(NY-1))$ at the upper boundary to match the non-dimensional equilibrium concentration.

create_grid.m - Here, use a uniform grid in both x and y directions. Later you can try stretching the grid in the y -direction to put more gridpoints near the upper boundary where the plumes will develop (this will be particularly useful if you try to simulate large values of LY , where the equilibrium state forms a thin boundary layer near the upper surface, or high Rayleigh numbers.)

create_flow.m - Here, in the User input area, set the velocity field to zero, and set the scalar field (TH) to the non-dimensional equilibrium solution, $TH = e^y$.

user_rhs.m - For bioconvection, we need to add the swimming term to the RHS of the TH equation. To do this, add the appropriate terms to F_TH in *user_rhs.m*.

- Now, run Diablo and compare your results with what you found from the linear stability analysis. Is the stability of the flow as you predicted? How does the scale of the plumes that develop compare with the most unstable wavelength?
- After the simulation has finished, plot one component of the *rms* velocity as a function of time during the period of exponential growth, and use the result to estimate the growth rate. How does this compare with what you found from the linear stability analysis?
- Try varying the Rayleigh number and/or the non-dimensional domain size. What happens to the scale of the plumes and the mean concentration profile?
- Run simulations at several Rayleigh numbers to find the onset of bioconvection. How well do the results

compare with the critical Rayleigh number that you found from the linear stability analysis?

V. SUGGESTED FURTHER INVESTIGATIONS

A. Variable swimming speed

One problem with using a constant swimming speed is that the equilibrium solution implies a flux of cells out of the top of the domain. For a more realistic simulation, try experimenting with different forms of U_s using Diablo, where $U_s = 0$ at both boundaries. Are the properties of the convective plumes significantly affected by your choice? Try experimenting with different forms for U_s .

B. Phytoplankton thin layer formation (ambitious)

Thin layers of phytoplankton are often seen in the ocean and in lakes. One explanation for these layers is that vertical migration of motile phytoplankton is inhibited when the fluid shear stress becomes larger than a critical value, causing the cells to tumble² (see paper in your project folder). Explore this hypothesis by making the swimming speed U_s dependent on the local shear rate. What happens if the organisms try to swim through a shear layer? If the shear layer is unstable, does that qualitatively change your results?

C. Turbulent fluxes

The Nusselt number, $-\langle v'c' \rangle / (\kappa \langle \partial c / \partial y \rangle)$, is the ratio of the turbulent to diffusive flux, and is often used to characterize the strength of turbulent convection, where angle brackets denote an average in x and time, and primes denote a departure from this average. Here, an analogous ratio is $-\langle v'c' \rangle / (U_s \langle c \rangle)$. Calculate this ratio in your simulations. How does it vary with the Rayleigh number?

VI. REFERENCES

¹ S. Childress, M. Levandowsky, and E. Spiegel, *Journal of Fluid Mechanics* **63**, 591 (1975).

² W. M. Durham, J. O. Kessler, and R. Stocker, *Science* **323**, 1067 (2009).