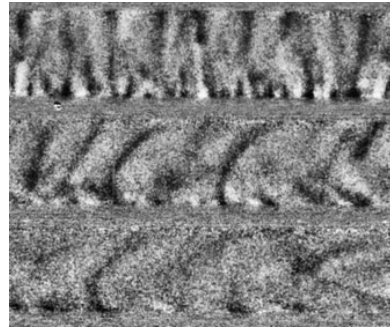


## Swimming in shear

David Saintillan†

Department of Mechanical and Aerospace Engineering,  
University of California, San Diego, La Jolla,  
CA 92093, USA



The complex patterns observed in experiments on suspensions of swimming cells undergoing bioconvection have fascinated biologists, physicists and mathematicians alike for over a century. Theoretical models developed over the last few decades have shown a strong similarity with Rayleigh–Bénard thermal convection, albeit with a richer dynamical behaviour due to the orientational degrees of freedom of the cells. In a recent paper, Hwang & Pedley (*J. Fluid Mech.*, vol. 738, 2014, pp. 522–562) revisit previous models for bioconvection to investigate the effects of an external shear flow on pattern formation. In addition to casting light on new mechanisms for instability, their study demonstrates a subtle interplay between shear, swimming motions and bioconvection patterns.

**Key words:** bioconvection, instability, micro-organism dynamics

### 1. Introduction

In a classic experimental paper, Platt (1961) reported the formation of polygonal concentration patterns at the free surface of a shallow suspension of swimming micro-organisms. Noting a striking similarity with the Bénard cells observed in thermal convection, he coined the term ‘bioconvection’ to describe this peculiar phenomenon, which had in fact been known for over a century. The analogy with the Rayleigh–Bénard instability was not formalized until Childress, Levandowsky & Spiegel (1975) posed a continuum model for a suspension of non-neutrally-buoyant gravitactic micro-organisms (organisms that swim in the direction opposite gravity) coupled to the Navier–Stokes equations for the fluid motion with a Boussinesq forcing arising from the weight of the suspension. A linear stability analysis elucidated a simple ‘gravitational overturning’ mechanism for this phenomenon: upward-swimming micro-organisms tend to accumulate at the free surface, leading to an unstable stratification in which weak density fluctuations can destabilize the system and drive horizontal convection rolls. The model by Childress *et al.* (1975), while providing

† Email address for correspondence: [dstn@ucsd.edu](mailto:dstn@ucsd.edu)

a potential mechanism for bioconvection, is based on a simplified description of the suspension dynamics that neglects details of the swimming motions.

A number of other more realistic and sophisticated models were subsequently proposed, most notably by Pedley, Kessler and coworkers (e.g. Pedley, Hill & Kessler 1988; Pedley & Kessler 1990; Pedley 2010). These studies focused primarily on one specific mechanism for upward swimming typical of many algal cells called ‘gyrotaxis’, in which a bottom-heavy motile cell is subject to a gravitational torque that tends to align it against gravity. The accurate modelling of a suspension of gyrotactic cells requires accounting for particle orientations but is still amenable to analytical or computational treatment. Linear stability analyses of this more complex model have confirmed the existence of the gravitational overturning instability (Pedley *et al.* 1988; Bees & Hill 1998) but also revealed new instability mechanisms specific to gyrotactic cells as we further discuss below.

These various continuum models have been quite successful at explaining controlled experimental observations in quiescent suspensions, and in particular at predicting the onset of instability in terms of a critical bioconvection Rayleigh number expressing the ratio of the Boussinesq forcing to diffusive processes. In nature, however, micro-organisms often evolve in complex environments where swimming motions are affected by external flows (Guasto, Rusconi & Stocker 2012), yet very little is known on the interaction of bioconvection patterns with even the simplest of flow fields. In recent experiments, Croze, Ashraf & Bees (2010) showed that an imposed pressure-driven pipe flow tends to deform bioconvection patterns at low to moderate flow rates, and eventually disrupts pattern formation at high flow rates, as shown in the figure by the title where the flow rate increases downwards in the three panels, which are adapted from figure 6 of Croze *et al.* (2010), used with permission. These experiments motivate the theoretical study by Hwang & Pedley (2014), which extends the previous model of Pedley & Kessler (1990) to account for the effects of an externally imposed simple shear flow.

## 2. Overview

In the model described by Hwang & Pedley (2014), the configuration of the particles in suspension is captured using a distribution function  $\Psi(\mathbf{x}, \mathbf{e}, t)$  of cell positions  $\mathbf{x}$  and swimming directions  $\mathbf{e}$  at time  $t$ . This distribution function satisfies a conservation equation including the effects of gyrotaxis, cell swimming and sedimentation, transport and reorientation by the suspending liquid, as well as translational and rotational diffusion. As discussed by Hwang & Pedley, translational diffusion plays a critical role in the stability of the system. In a suspension of swimming micro-organisms, diffusion in space is primarily a consequence of the coupling between self-propulsion and orientation decorrelation mechanisms such as rotational diffusion or cell tumbling (Berg 1993), with a diffusion tensor modelled as  $\mathbf{D}_T = V_c^2 \tau (\langle \mathbf{e}\mathbf{e} \rangle - \langle \mathbf{e} \rangle \langle \mathbf{e} \rangle)$ , where  $V_c$  is the swimming speed,  $\tau$  is the correlation timescale for a cell’s swimming direction, and  $\langle \mathbf{e} \rangle$  and  $\langle \mathbf{e}\mathbf{e} \rangle$  are the first and second moments of particle orientations. The model thus posed is quite general and can be linearized for the purpose of performing a stability analysis, yielding an eigenvalue problem that shares similarities with other well-known systems: in the absence of shear, it is identical to the previous model of Pedley & Kessler (1990) and is also reminiscent of the classic equations for thermal convection (Drazin & Reid 1981), whereas it simplifies to the Orr–Sommerfeld equation for the stability of a viscous shear flow when the cell density vanishes.

Before examining the effects of shear, Hwang & Pedley first revisit the mechanisms leading to bioconvection in a quiescent suspension. Their analysis captures the

gravitational overturning mechanism arising from unstable stratification, but also exposes two other instability mechanisms that are unique to gyrotactic cells and are in fact expected to be dominant at most wavenumbers. First, they argue that a horizontal vortical perturbation induced by the settling of a dense blob of cells leads to a net horizontal swimming flux that reinforces the initial density fluctuations. This ‘gyrotactic instability’, first described in prior work by Pedley *et al.* (1988), is a direct consequence of the rotation of the cells in the vortical field, which causes them to swim towards the wake of the blob. More curiously perhaps, Hwang & Pedley also describe a third mechanism in which the downward flow driven by a blob of cells couples with the unstable stratification to drive a cross-diffusion particle flux from the less-dense surrounding regions towards the blob and its wake. The unexpected direction of this flux is a consequence of the sign of the off-diagonal components of the diffusion tensor, which are predicted to be negative both by the above model and by generalized Taylor dispersion theory (Bearon, Bees & Croze 2012). The robustness of this ‘diffusion-oriented instability’ is questionable, as it appears to depend critically on the choice of model for the translational diffusion tensor.

Hwang & Pedley then proceed to analyse the influence of shear on the onset of instability and on the form of the unstable eigenmodes. The effects of the flow are in fact quite complex and can either be stabilizing or destabilizing depending on shear rate and wavenumber. In weak flows, a numerical solution of the eigenvalue problem predicts destabilization of low-wavenumber perturbations, but stabilization of high wavenumbers. The destabilization is attributed to the gravitational overturning mechanism and is explained as a consequence of the thickening of the unstably stratified layer near the free surface due to shear. The high-wavenumber stabilization, on the other hand, is related to the gyrotactic instability and results from the disruption of the horizontal swimming flux due to the rotation of the cells in the imposed vortical field. In stronger flows, however, cell rotation becomes so important that the net upward motility of the gyrotactic cells is hindered (Durham, Kessler & Stocker 2009), leading to a stably stratified base state due to sedimentation, and to the stabilization of the gravitational overturning as a result. Therefore, above a critical shear rate, all wavenumbers are stabilized and bioconvection is entirely suppressed. In the unstable regime, the shape of the eigenfunctions is affected by the flow, which causes the convection rolls to tilt in the flow-gradient plane as shown in figure 1, in good qualitative agreement with the experimental observations of Croze *et al.* (2010). It should be noted finally that the effects of shear on bioconvection differ quite significantly from the case of Rayleigh–Bénard convection (Gallagher & Mercer 1965), notably because the base-state unstable stratification in thermal convection is driven by the vertical temperature gradient, which is unaffected by the horizontal shear flow.

### 3. Future

The paper by Hwang & Pedley (2014) provides a novel understanding of gyrotactic bioconvection and its interaction with an imposed flow, while also opening the door for future studies on more complex systems. One natural extension would consider other types of flow fields, including unsteady or chaotic flows. Recent computational studies have shown unusual dynamics and aggregation patterns of gyrotactic cells in complex flow fields (Durham *et al.* 2013), although the richness of interaction modes between motile micro-organisms and fluid flows and their biological and ecological implications have yet to be fully explored. Other possible extensions could also include: the effects of cell shape anisotropy, which may lead to additional instabilities (Koch & Shaqfeh 1989); hydrodynamic interactions due to self-propulsion (Pedley 2010; Saintillan & Shelley 2013); as well as other types of taxis phenomena such as chemotaxis and phototaxis.

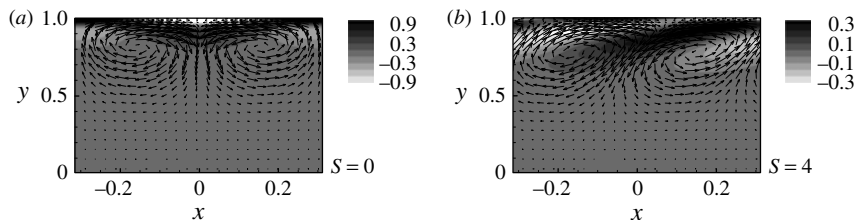


FIGURE 1. Unstable eigenfunctions in the flow-gradient plane without and with shear: (a)  $S=0$ , (b)  $S=4$ . The contours show the perturbed cell density, and the arrows indicate the streamwise and wall-normal velocities. Application of a shear flow tends to tilt the counter-rotating convection rolls, in qualitative agreement with the experiments of Croze *et al.* (2010). Adapted from Hwang & Pedley (2014), figure 11.

## References

- BEARON, R. N., BEES, M. A. & CROZE, O. A. 2012 Biased swimming cells do not disperse in pipes as tracers: a population model based on microscale behaviour. *Phys. Fluids* **24**, 121902.
- BEES, M. A. & HILL, N. A. 1998 Linear bioconvection in a suspension of randomly swimming, gyrotactic micro-organisms. *Phys. Fluids* **10**, 1864–1881.
- BERG, H. C. 1993 *Random Walks in Biology*. Princeton University Press.
- CHILDRESS, S., LEVANDOWSKY, M. & SPIEGEL, E. A. 1975 Pattern formation in a suspension of swimming micro-organisms: equations and stability theory. *J. Fluid Mech.* **63**, 591–613.
- CROZE, O. A., ASHRAF, E. E. & BEES, M. A. 2010 Sheared bioconvection in a horizontal tube. *Phys. Biol.* **7**, 046001.
- DRAZIN, P. G. & REID, W. H. 1981 *Hydrodynamic Stability*. Cambridge University Press.
- DURHAM, W. M., CLIMENT, E., BARRY, M., DE LILLO, F., BOFFETTA, G., CENCINI, M. & STOCKER, R. 2013 Turbulence drives microscale patches of motile phytoplankton. *Nat. Commun.* **4**, 2148.
- DURHAM, W. M., KESSLER, J. O. & STOCKER, R. 2009 Disruption of vertical motility by shear triggers formation of thin phytoplankton layers. *Science* **323**, 1067–1070.
- GALLAGHER, A. P. & MERCER, A. MCD. 1965 On the behavior of a small disturbance in plane Couette flow with a temperature gradient. *Proc. R. Soc. Lond.* **286**, 117–128.
- GUASTO, J. S., RUSCONI, R. & STOCKER, R. 2012 Fluid mechanics of planktonic microorganisms. *Annu. Rev. Fluid Mech.* **44**, 373–400.
- HWANG, Y. & PEDLEY, T. J. 2014 Bioconvection under uniform shear: linear stability analysis. *J. Fluid Mech.* **738**, 522–562.
- KOCH, D. L. & SHAQFEH, E. S. G. 1989 The instability of a dispersion of sedimenting spheroids. *J. Fluid Mech.* **209**, 521–541.
- PEDLEY, T. J. 2010 Instability of uniform microorganism suspensions revisited. *J. Fluid Mech.* **647**, 335–359.
- PEDLEY, T. J., HILL, N. A. & KESSLER, J. O. 1988 The growth of bioconvection patterns in a uniform suspension of gyrotactic micro-organisms. *J. Fluid Mech.* **195**, 223–237.
- PEDLEY, T. J. & KESSLER, J. O. 1990 A new continuum model for suspensions of gyrotactic micro-organisms. *J. Fluid Mech.* **212**, 47–70.
- PLATT, J. R. 1961 Bioconvection patterns in cultures of free-swimming organisms. *Science* **133**, 1766–1767.
- SAINTILLAN, D. & SHELLEY, M. J. 2013 Active suspensions and their nonlinear models. *C. R. Physique* **14**, 497–517.