# Bioconvection

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**Abstract**

Bioconvection patterns are usually observed in the laboratory in shallow suspensions of randomly, but on average upwardly, swimming micro-organisms which are a little denser than water, but have also been found *in situ* in micropatches of zooplankton (Kils 1993). The mechanism of upswimming differs between bottom-heavy algae and oxytactic bacteria. Rational continuum models have been formulated and analysed in each of these cases for low cell volume fraction. These will be described, as will new theoretical and experimental developments, including nonlinear analysis of the patterns, dispersion in shear flows, measurements of algal cell swimming behaviour, and new attempts to set up a model for more concentrated suspensions. The paper will review all work in this area since 1992, the year of the publication of the article "Hydrodynamic phenomena in suspensions of swimming micro-organisms" by T.J. Pedley & J.O. Kessler (1992b) in the Annual Review of Fluid Mechanics.

*Key words:* Bioconvection; swimming micro-organisms; pattern formation; biofluiddynamics; bacteria, algae, *Chlamydomonas nivalis*, *Bacillus subtilis*

## 1 Introduction

Bioconvection patterns are observed in shallow suspensions of randomly, but on average upwardly, swimming micro-organisms which are a little denser than water. Excellent images of typical bioconvection patterns formed by suspensions of single-celled algae and bacteria can be found in the article by Pedley & Kessler (1992a). The basic mechanism is analogous to that of Rayleigh–Bénard convection, in which an overturning instability develops when the upper regions of fluid become denser than the lower regions. The reason for the upswimming however depends on the species of micro-organism: certain

biflagellate algae are bottom-heavy, and therefore experience a gravitational torque when they are not vertical; certain oxytactic bacteria, such as *Bacillus subtilis*, swim up oxygen gradients that they generate by their consumption of oxygen (Kessler 1985a; Pedley & Kessler 1992a; Platt 1961; Wager 1911).

Two micro-organisms that are commonly used in bioconvection experiments are the bottom-heavy alga, *Chlamydomonas nivalis* which is found in snow fields and is active when the snow is melting, and the common soil bacterium *B. subtilis*. The cell bodies of *C. nivalis* are slightly-prolate spheroids about $10\,\mu$m in diameter. They have two flagella about $15\,\mu$m in length at the anterior end of the cell which are moved in a breast-stroke-like fashion to enable the cells to swim at speeds of up to 10 body lengths per second. Figure 1 in Pedley & Kessler (1990) gives images of the alga *C. nivalis*, which clearly show the flagella. An example of a *B. subtilis* cell is shown in Fig. 1 in this review. The cells are rod-like and typically 2 to $4\,\mu$m in length. They have many flagella which wind together to form a helical flagellar bundle that rotates to propel the cell forward. Again they can reach speeds of over 10 body lengths per second. Populations of both species contain cells of a variety of ages, sizes and swimming speeds.

Rational (i.e. systematically-derived from scientific data as opposed to *ad hoc*) continuum models have been formulated and analysed in each of these cases, on the assumption that the cell volume fraction $\phi$ is low enough for hydrodynamic or other cell-cell interactions to be neglected ($\phi \leq 0.1\%$) (Hillesdon *et al* 1995; Pedley & Kessler 1992b). Another sort of pattern-formation ("whorls and jets") is observed in very concentrated, very shallow cultures of swimming bacteria (Kessler & Hill 1997; Kessler & Wojciechowski 1997; Mendelson *et al* 1999). Here upwards swimming is not required but cell-cell interactions are crucial; however it is not clear how to derive an appropriate macroscopic model that is consistent with the laws of mechanics at the cellular level. In this review, we shall concentrate primarily on research in bioconvection for dilute suspensions published since the major review by Pedley & Kessler (1992b). The main themes have been: (a) further developments of the new continuum model introduced by Pedley & Kessler (1990); (b) modelling of bioconvection in suspensions of oxytactic bacteria; (c) numerical solutions of the continuum equations; and (d) experimental studies of both algal and bacterial bioconvection. The layout of the review is as follows. In Section 2, the basic continuum and linear stablility theory is reviewed and the developments for oxytactic bacteria and chemotaxis in a shear flow are described. Nonlinear extensions to these models, are described in Section 3. An overview of numerical solutions for bioconvection is given in Section 4, followed in Section 5 by a review of experimental work. The review concludes with comments on the progress in modelling concentrated suspensions of micro-organisms in Section 6, and with a brief discussion of future challenges in Section 7.

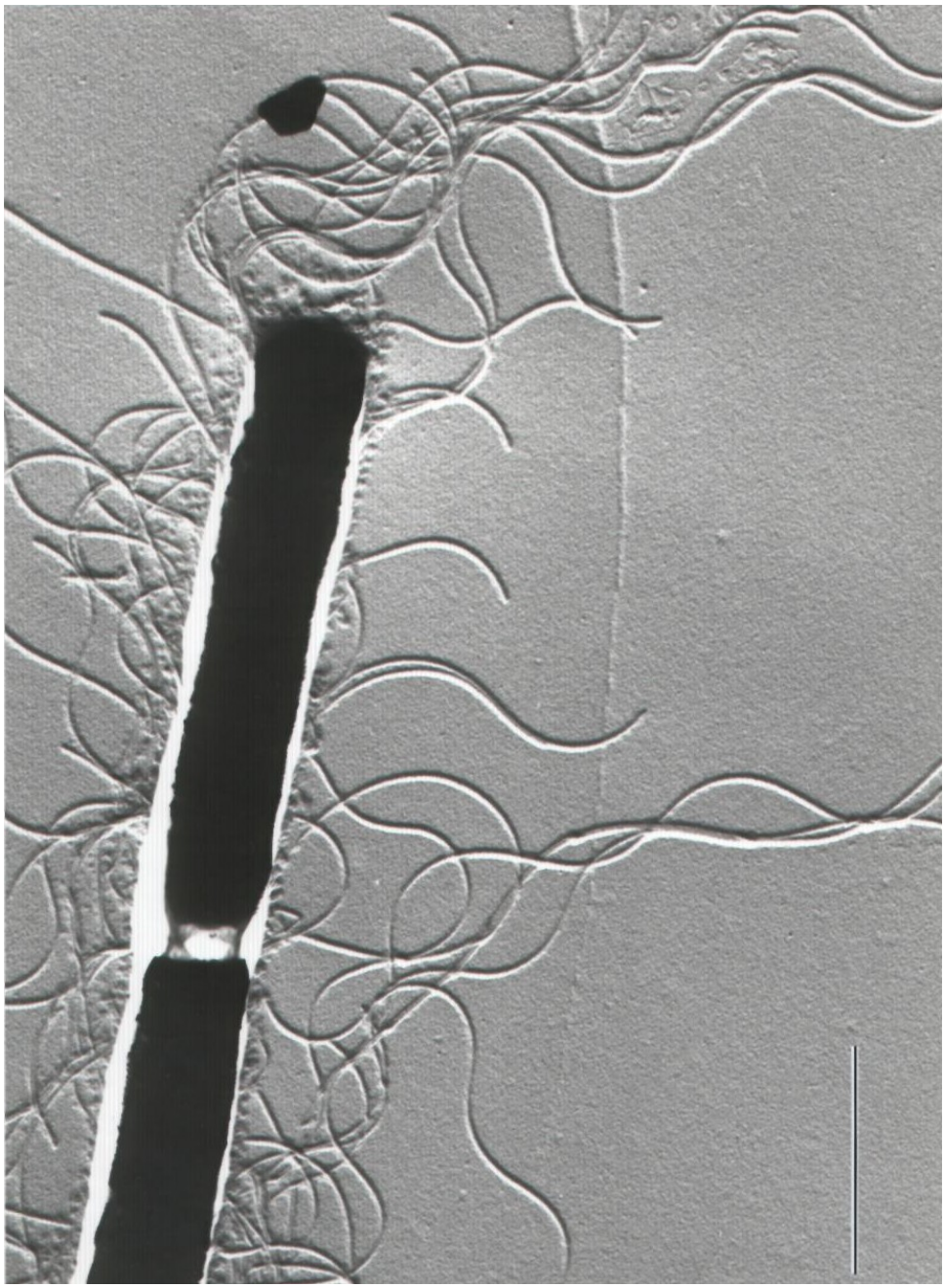

Fig. 1. Electron micrograph of the oxytactic bacterium *Bacillus subtilis*. The picture shows a cell about to divide into two. Clearly visible are the multiple flagella, which coalesce to form the 'flagellar bundle' when the cell swims. The scale bar is $1\,\mu$m. Platinum was evaporated at a shallow angle on a dried sample and then imaged using a transmission electron microscope. *Image kindly provided by C. Dombrowski, J.O. Kessler & D. Bentley, University of Arizona.*

## 2 Continuum models for dilute micro-organism suspensions

### *2.1 General*

In a continuum model one assumes that volume elements, which are small compared with the scale of the flow or the container, contain very many cells, so that variables can be represented by their averages over the volume element. These averages can be represented as functions of spatial position $\mathbf{x}$ and time $t$, e.g. the concentration (number density) of cells, $n(\mathbf{x}, t)$. The averaging of some quantities may not be straightforward, because cells typically swim in random directions.

For a dilute suspension of cells, the volume fraction of cells is small, i.e. $n\upsilon = \phi \ll 1$ (where $\upsilon$ is the average volume of a cell). In that case the bulk velocity field $\mathbf{u}(\mathbf{x}, t)$ satisfies the continuity and Navier–Stokes equations subject to the Boussinesq approximation, in which the variation in suspension density with $n$ is negligible except in the gravitational (negative) buoyancy term:

$$\rho \frac{D\mathbf{u}}{Dt} = -\nabla p_e - n\rho g' \mathbf{k} + \nabla.\mathbf{\Sigma} \tag{1}$$

$$\nabla.\mathbf{u} = 0. \tag{2}$$

Here $p_e$ is the pressure excess over hydrostatic, $g'$ is the reduced gravity ($= g\Delta\rho/\rho$, where $\rho$ is water density and $\rho + \Delta\rho$ is mean cell density), $\mathbf{k}$ is the vertical (upward) unit vector, $\mathbf{\Sigma}$ is the deviatoric stress tensor, and $D/Dt$ is the material time derivative ($D\mathbf{u}/Dt \equiv \partial\mathbf{u}/\partial t + (\mathbf{u}.\nabla)\mathbf{u}$). For a dilute suspension, $\mathbf{\Sigma}$ is approximately equal to its Newtonian value, and it was shown by Pedley & Kessler (1990) that the first correction for swimming algae would be due to the average stresslet strength of the swimmers, $\mathbf{\Sigma}^s$, not to the 'Batchelor' suspension stresses (Batchelor 1970). Thus

$$\mathbf{\Sigma} \approx \mu \left( \nabla\mathbf{u} + \nabla\mathbf{u}^T \right) + \mathbf{\Sigma}^s, \tag{3}$$

where $\mu$ is the viscosity of the fluid and the second term is neglected for the remainder of this section.

The other key equation of the model is the equation of conservation of cells. Neglecting birth or death processes, for which the time-scale is much longer than that of the bioconvective flows, and neglecting gravitational sedimentation, because the terminal sinking speed of a cell is much smaller than its swimming speed, this equation is

$$\frac{Dn}{Dt} = \left( \frac{\partial}{\partial t} + \mathbf{u}.\nabla \right) n = -\nabla. \left( n\mathbf{V}_c - \mathsf{D}.\nabla n \right). \tag{4}$$

Here the terms on the right hand side both represent the effect of cell swimming; $\mathbf{V}_c$ is the average cell swimming velocity (due to gravitaxis, chemotaxis, etc) and $-\mathsf{D}.\nabla n$ is the flux due to random cell swimming motions, modelled as a diffusive process with diffusivity tensor $\mathsf{D}$. See Kessler & Hill (1997) for data on typical swimming speed distributions. The specification of these terms depends on the type of cells being considered, and the next subsection deals with gyrotactic (bottom-heavy) algae. The modelling of chemotactic bacteria is described later.

### *2.2 Gyrotactic algae*

The biflagellate algae which form bioconvection patterns in Kessler's (1985a) experiments (with $n \sim 10^6$ ml$^{-1}$), *Chlamydomonas nivalis*, have been observed to perform random walks in otherwise still fluid, and these have been quantified by Hill & Häder (1997) and by Vladimirov *et al.* (2000, 2004). From the measured velocity distributions of the cells, it can be seen that the cells swim upwards on average. The reason for this has been shown by Kessler (1985a) to be that the cells are bottom heavy; their centre of mass is displaced from the centre of buoyancy in a direction opposite to the direction of cell swimming.

A cell's instantaneous swimming velocity can be written $V_s\mathbf{p}$, where $V_s$ is the swimming speed and $\mathbf{p}$ is a unit vector in the swimming direction. The random swimming can be represented in terms of a probability density function (pdf) for $\mathbf{p}$, $f(\mathbf{p})$, and another for $V_s$, assuming $\mathbf{p}$ and $V_s$ are independent random variables. For clarity we will ignore the variability of $V_s$ and treat it as a constant. Then the ensemble average of a quantity is defined by

$$< \cdot\cdot >= \int_{S_2} \cdot\cdot f(\mathbf{p}) d^2\mathbf{p}, \tag{5}$$

where the integral is over $\mathbf{p}$-space, i.e. the unit sphere $S_2$. Thus the average swimming velocity in the absence of fluid motion is

$$\mathbf{V}_c = V_s < \mathbf{p} > . \tag{6}$$

The accurate representation of $\mathsf{D}$ is more complicated (Bees *et al* 1998; Hill & Bees 2002); Pedley & Kessler (1990, 1992b) used the following approximation:

$$\mathsf{D} = \mathrm{sym}\left[\int_0^\infty < \mathbf{V}_{rel}(t)\mathbf{V}_{rel}(t-t') > dt'\right] \approx V_s^2\tau < (\mathbf{p} - < \mathbf{p} >)(\mathbf{p} - < \mathbf{p} >) >, \tag{7}$$

where $\mathbf{V}_{rel} = V_s\mathbf{p} - \mathbf{V}_c$ and $\tau$ is a fixed correlation time. Here sym is the symmetric part of the tensor.

To complete the model set of equations it is necessary to find a way of determining $f(\mathbf{p})$, preferably theoretically since particle-tracking experiments are

extremely time-consuming. Some early models (Childress *et al* 1975; Pedley *et al* 1988) were inconsistent, postulating a deterministic cell swimming direction but still incorporating cell diffusion. Pedley & Kessler (1990) proposed a more rational model, treating the suspension of swimmers as analogous to a suspension of colloidal particles subjected to Brownian motion. Thus they proposed that the random walks (assumed Markovian) would imply that $f(\mathbf{p}, t)$ should satisfy a Fokker–Planck equation in $(\mathbf{p}, t)$-space:

$$\frac{\partial f}{\partial t} + \nabla_p.(\dot{\mathbf{p}} f) = D_r \nabla_p^2 f, \tag{8}$$

where $D_r$ is a rotational diffusivity, assumed isotropic, to represent the randomising process in the cells' swimming behaviour, and $\dot{\mathbf{p}}$ is the rate of change of $\mathbf{p}$ as a result of deterministic reorientation arising from the inertia-free balance between gravitational and viscous torques (gyrotaxis). If the cells are spheroidal, it can be shown that

$$\dot{\mathbf{p}} = \frac{1}{B}[\mathbf{k} - (\mathbf{k}.\mathbf{p})\mathbf{p}] + \frac{1}{2}\boldsymbol{\omega} \wedge \mathbf{p} + \alpha_0 \mathbf{p}.\mathsf{E}.(\mathsf{I} - \mathbf{pp}), \tag{9}$$

where $\boldsymbol{\omega}$ is the local vorticity, $\mathsf{E}$ is the rate of strain tensor, $\mathsf{I}$ is the identity tensor, and $\alpha_0 = (a^2 - b^2)/(a^2 + b^2)$ is the eccentricity of a spheroid with semi-major axis $a$ and semi-minor axis $b$. $B \propto \mu/\rho g h$ is a time-scale for gyrotactic reorientation, $h$ being the distance from the centre of the spheroid to its centre of mass. If the time-scale for the bulk bioconvective motions is much larger than $B$, then the first term in (8) will be negligible and $f(\mathbf{p})$ will be quasi-steady. This has been generally assumed (Bees & Hill 1998; Pedley & Kessler 1990, 1992b), but more for convenience than for validity.

The solution of (8) in still fluid, for which $\boldsymbol{\omega}$ and $\mathsf{E} = 0$ in (9), is simply found to be the Fisher distribution:

$$f(\mathbf{p}) = \mu \exp(\lambda \mathbf{k}.\mathbf{p}), \tag{10}$$

where $\lambda = (BD_r)^{-1}$ and $\mu = \lambda/(4\pi \sinh \lambda)$ is a normalisation constant. The experimental data can be used to test this prediction and a value of $\lambda \approx 2.2$ was deduced by Pedley & Kessler (1992b) from the data of Hill & Häder (1997).

In order to investigate bioconvection, the equilibrium cell concentration distribution $n_0(\mathbf{x})$ has to be calculated first, using equations (4), (6), (7) and (10). In an unbounded medium $n_0$ is uniform, while in a shallow layer it depends exponentially on the vertical coordinate $z$. Then the linear instability of that equilibrium is investigated by postulating a small initial disturbance of general form, separated into Fourier modes in the horizontal plane, and calculating whether the disturbance will grow or not. If every such disturbance dies away, the original state is stable; if at least one mode grows, the state is unstable.

When some modes grow, the one that grows most quickly is likely to be the one initially observed. Such linear theory has been applied to both uniform (Pedley & Kessler 1990) and shallow (Bees & Hill 1998) suspensions of *C. nivalis*. In both cases the most unstable disturbance was predicted to have a horizontal lengthscale of around 9 mm. This is considerably larger than the 2 mm observed in approximately steady-state bioconvection patterns; however, observation has also shown that the initial length scale of 4–7 mm is considerably larger than the final one (Bees & Hill 1997; Wager 1911), presumably as a consequence of nonlinear effects.

Bees *et al.* (1998) derived general expressions for the approximation (7) for $\mathsf{D}$ for spheroidal cells in both two-dimensional flows and three-dimensional flows with no vertical component of vorticity. The solutions were found by expanding the Fokker–Planck equation (9) in terms of spherical harmonic functions. The resulting system of equations was truncated and then solved using computer algebra. These results were used by Bees & Hill (1998) to re-examine the linear stability of a suspension of finite depth. They found the predicted wavelengths ($\approx 1$ mm) for the onset of bioconvection to be smaller than observed values ($\approx$ 4–7 mm) for their *best* estimates of parameter values. However, the predictions are sensitive to choices of $B$ and $\tau$, and good agreement can be obtained by tuning these parameters within realistic bounds. Independent measurements of $B$ and $\tau$ are needed to resolve this issue. They also showed that a distribution of swimming speeds increases the diffusivity due to swimming.

### *2.3 Oxytactic bacteria*

The other species of swimming micro-organism for which Kessler has recorded reproducible and interestingly intricate bioconvection patterns (with $n \sim 10^8$ ml$^{-1}$) is the bacterium *Bacillus subtilis* (Kessler & Hill 1995; Kessler *et al* 1994). These small ($\sim 4\,\mu$m) organisms consume oxygen and are active swimmers when the ambient oxygen concentration exceeds a (small) critical value (a process known as chemokinesis). Moreover, on average, they swim up oxygen gradients (chemo- or oxy-taxis). In a chamber whose upper surface is open to the atmosphere, so that it is supplied with oxygen at a given concentration, the consumption of oxygen gives rise to an oxygen concentration gradient, up which the cells swim. Since they, too, are denser than the culture medium, a bioconvective instability can and does occur.

A continuum model has been developed and analysed for a dilute suspension of these bacteria (dilute because, even with $n \approx 10^8$ ml$^{-1}$, the volume fraction $nv$ is only around $3\times10^{-3}$) (Hillesdon *et al* 1995). The momentum and continuity equations are again (1) and (2), $\boldsymbol{\Sigma}$ is given by (3) with $\boldsymbol{\Sigma}^{(s)} = 0$, and the cell conservation equation is still (4), with the cell diffusivity tensor being assumed

isotropic. However, the average cell swimming velocity arises as a result of chemotaxis, and it was assumed that this was directly proportional to the gradient in oxygen concentration $C$, as proposed by Keller & Segel 1971):

$$\mathbf{V}_c = \chi \nabla C, \tag{11}$$

where $\chi$ is a constant. This then requires a further equation for $C$, which also diffuses and is advected by the flow, and is consumed by the bacteria. Thus the $C$-equation is taken to be

$$\frac{DC}{Dt} = D_c \nabla^2 C - Kn, \tag{12}$$

where $D_c$ is the oxygen diffusivity which is usually very different in magnitude to the cell diffusivity.

The equilibrium cell distribution was analysed in (Hillesdon *et al* 1995) — this is not as simple as for algae because if the chamber is deep enough, cells lower down run out of oxygen before they 'know' there is a gradient to swim up, and this can lead to a sharp interface between such dormant cells and the region just above from which the cells have swum upwards. Such an interface has frequently been observed experimentally. The linear instability of the equilibrium was analysed in (Hillesdon & Pedley 1996) and a weakly nonlinear analysis in (Metcalfe & Pedley 1998), leading to a prediction of the form of the convection pattern (hexagonal) that agrees with observations. Fully nonlinear computations have not been made for this system, and the observed patterns in experiments where the bacterial-cell concentrations are considerably higher than the critical value for pattern formation can be very complex and unsteady (Kessler 1996).

The theoretical understanding of bioconvection provided by the continuum models is on the whole satisfactory but, especially in the bacterial context, there are two worrying deficiencies. One is shared by the algal system, and is a doubt about the validity of the dilute-suspension assumption. In the dense, downflowing plumes of a nonlinear bioconvection pattern, the cell concentration becomes significantly higher than its initial value and cell-cell interactions must begin to be important. Concentrated suspensions are briefly discussed in the next section.

The other worry about the bacterial model is that the chemotaxis term (11) takes no account of the reorientation of cell swimming trajectories by shear in the ambient flow; there is no chemo-gyrotactic torque balance analogous to (9) (Kessler 1986). Nor is there explicit analysis of the probability density function of swimming direction, as led to (8) for the algae.

Part of the difficulty is that, as far as we are aware, there have been no detailed measurements of the swimming trajectories of *B. subtilis* cells in a well-defined oxygen gradient, even in a still fluid. We do not know the mechanism for chemotaxis in that species, though we can be fairly certain that it does not consist of a balance of mechanical torques.

The only bacterial species for which the mechanism of chemotaxis is well understood is the familiar *Escherichia coli*. This performs run-and-tumble swimming, in which the cell swims in a straight line while its flagella rotate in one sense (anti-clockwise), but every now and then they reverse the sense of the rotation, the flagella fly apart, and the cell tumbles randomly so that when it starts swimming forwards again all directions are equally likely (Berg & Brown 1972). Chemotaxis is achieved because the tumbling frequency, or stopping rate, decreases if the cell finds itself swimming up a gradient of chemo-attractant (not oxygen for *E.coli*), and vice versa.

We outline here an analysis by Bearon & Pedley (2000) and Bearon (2001) of run-and-tumble chemotaxis in an ambient shear flow. We again assume the cells to be spherical so that only the vorticity of the ambient flow has an effect on their orientation.

Let $\Psi(\mathbf{p}, \mathbf{x}, t)$ be the number density of cells with swimming direction $\mathbf{p}$, position $\mathbf{x}$ and time $t$. Let $\lambda(\mathbf{p})$ be the tumble rate and let $V_s$ be the cell swimming speed (assumed constant). Then

$$\frac{\partial \Psi}{\partial t} = -\nabla.[(\mathbf{u}+V_s\mathbf{p})\Psi] - (\boldsymbol{\omega}\wedge\mathbf{p}).\nabla_p\Psi - \lambda\Psi + \int \lambda(\mathbf{p}')\widetilde{T}(\mathbf{p},\mathbf{p}')\Psi(\mathbf{p}')\,d^2\mathbf{p}' \quad (13)$$

where $\widetilde{T}(\mathbf{p},\mathbf{p}')$ is the transition probability, that a bacterium that was swimming in direction $\mathbf{p}'$ prior to tumbling swims in direction $\mathbf{p}$ afterwards, c.f. Alt (1980). If we assume this to be isotropic, as is suggested by the above discussion but is not borne out by careful observation (Berg 1983), then $\widetilde{T} = 1/4\pi$. We also assume that

$$\lambda = \lambda_0(1 - \alpha\nabla C.\mathbf{p}) \quad (14)$$

where $\nabla C$ is the $O_2$-concentration gradient, $\alpha$ is an $O(1)$ constant and $\delta \ll 1$. Now define $n = \int \Psi\, d^2\mathbf{p}$, the volume concentration of cells, and $\mathbf{J} = \int \Psi\mathbf{p}\, d^2\mathbf{p}$, the cell flux vector.

Non-dimensionalise, and integrate equation (13) to obtain its zeroth and first moments:

$$\frac{1}{T}\frac{\partial n}{\partial t} = -\Gamma\mathbf{u}.\nabla n - \frac{1}{X}\nabla.\mathbf{J} \quad (15)$$

$$\frac{1}{T}\frac{\partial \mathbf{J}}{\partial t} = -\Gamma\mathbf{u}.\nabla\mathbf{J} + \frac{1}{X}(\alpha\nabla C - \nabla).\int \mathbf{p}\mathbf{p}\Psi\, d^2\mathbf{p} - \boldsymbol{\omega}\wedge\mathbf{J}, \quad (16)$$

where $T(\gg 1)$ is the ratio of time-scale of density variation to $1/\lambda_0$, a typical run duration, $X(\gg 1)$ is the ratio of length-scale, $h$, (e.g. chamber depth) to $V_s/\lambda_0$, a typical run displacement, and $\Gamma = \overline{U}/\lambda_0 h$, $\overline{U}$ being a fluid velocity scale. Equation (15) is just the cell conservation equation (4) again, while (16) is the equation from which $\mathbf{J}$ should be determined. However, this equation depends on the second moment of $\Psi$ in $\mathbf{p}$-space, the equation for the second moment depends on the third moment, etc. Some form of closure is required. In general it is not possible to reduce the equations to a single partial differential (advection-reaction-diffusion) equation for $n(\mathbf{x}, t)$.

A simple closure is possible for weak chemotaxis and weak flow, as follows. Define $1/T = \Gamma \ll 1$ and $1/X = \alpha \ll 1$ and let $|\nabla C| = O(1)$. Then to leading order, equations (15) and (16) give the standard Keller–Segel equation (Keller & Segel 1971)

$$\Gamma\left(\frac{\partial n}{\partial t} + \mathbf{u}.\nabla n\right) = -\frac{\alpha^2}{3}\nabla.[n\nabla C - \nabla n]. \tag{17}$$

Here the diffusivity and the chemotaxis constant appear the same ($\alpha^2/3$) only because of the non-dimensionalisation. The ambient flow comes in only at the next order:

$$\Gamma\left(\frac{\partial n}{\partial t} + \mathbf{u}.\nabla n\right) = -\frac{\alpha^2}{3}\nabla.[(1+\Gamma\boldsymbol{\omega}\wedge)(n\nabla C - \nabla n)] + \frac{\alpha^2\Gamma}{3}\nabla.\left[\left(\frac{\partial}{\partial t} + \mathbf{u}.\nabla\right)(n\nabla C - \nabla n)\right]. \tag{18}$$

Thus rotation of the flow has an effect, both directly ($\Gamma\boldsymbol{\omega}\wedge$) and through its interaction with chemotaxis (the last term). Note, however, that if the shear flow is strong enough for $\Gamma$ not to be small, it is not possible to reduce the equations to a single partial differential equation for $n$. Thus, even for a dilute suspension, the model is not as simple as previously supposed.

## 3 Developments of and extensions to the continuum theory

### *3.1 Nonlinear analysis*

Nonlinear analysis of gyrotactic bioconvection given by equations (1)–(9) was carried out by Bees and Hill (1999) for a deep layer. They considered long-vertical-wavelength disturbances to an initially uniform suspension in an infinitely deep layer. In the absence of any vertical variation, a weakly nonlinear analysis shows that the bifurcation to instability is supercritical, which gives some justification for the use of linear stability theory to predict initial bioconvection pattern wavelengths. Fully nonlinear, stable and travelling wave solutions were also found for the case of no vertical variation. These predict

the long plume-like solutions that are routinely observed in deep suspensions of *C. nivalis*. They were also able to predict the speed of long vertical wavelength instabilities of these plumes. Metcalfe & Pedley (2001) have derived asymptotic solutions for a steady plume in a suspension of oxytactic bacteria.

Yannacopoulos & Rowlands (1999) calculated the effective drift velocity and diffusivity for gyrotactic algae swimming in a weak, periodic external flow, assuming that the suspension is sufficiently dilute that there is no bioconvection. Because the flow is inhomogeneous, $\mathbf{V}_c$ and $\mathsf{D}$ in (4) are spatially dependent, and a multiple-scales expansion is used to evaluate their spatial averages. It was found that both effective transport coefficients can be enhanced or reduced depending on the parameter values and the shape of the cells.

For bacterial suspensions, Lega and Mendelson (Mendelson & Lega 1998; Lega & Mendelson 1999) demonstrated that patterns derived from a generic Swift–Hohenberg equation can provide a descriptive model of bioconvection patterns and showed numerical results for the development of a phase-unstable pattern behind a moving front, as shown in experiments. They did not, however, derive the Swift–Hohenberg equation from the governing equations so it is not possible to compare their parameter values with experimental data.

### *3.2 Taylor dispersion of swimming cells in a shear flow*

Prior to the publication of the papers by Hill & Bees (2002) and Manela & Frankel (2003), all the calculations of diffusion resulting from the random swimming of micro-organisms included the effects of the local velocity gradients on the orientation of the cells, but neglected the effects of transport and dispersion by the flow. Hill & Bees applied generalised Taylor dispersion theory (Frankel & Brenner 1991) to a dilute suspension of gyrotactic cells in an unbounded linear shear flow.

The pdf $P(\mathbf{R}, \mathbf{p}, t|\mathbf{R}', \mathbf{p}')$ of finding a cell at position $\mathbf{R}$ with orientation $\mathbf{p}$ at time $t > 0$, given that it was at position $\mathbf{R}'$ with orientation $\mathbf{p}'$ at time $t = 0$ is assumed to satisfy the Fokker–Planck equation

$$\frac{\partial P}{\partial t} + \nabla_{\mathbf{R}}.\mathbf{J} + \nabla_{\mathbf{p}}.\mathbf{j} = 0, \tag{19}$$

where

$$\mathbf{J} = [\mathbf{V}(\mathbf{R}') + (\mathbf{R} - \mathbf{R}').\mathsf{G} + V_s\mathbf{p}]\, P \tag{20}$$

is the physical-space flux density and

$$\mathbf{j} = \dot{\mathbf{p}}P - d_r\nabla_{\mathbf{p}}P \tag{21}$$

is the orientational-space flux density. Here $\mathsf{G} = (\nabla_{\mathbf{R}}\mathbf{V})^T$ is the fluid velocity

gradient tensor and $d_r$ is the constant rotational diffusivity. Note that there is no translational Brownian diffusion in this model. The algae are too large for Brownian effects to be significant, and thus the dispersion occurs entirely because of the random swimming of the cells. In the far field $P$ decays to zero and to ensure that integrals of the moments of $P$ converge, we require that

$$(P, \mathbf{J}, \mathbf{j})|\mathbf{R} - \mathbf{R}'|^m \to 0 \quad \text{as} \quad |\mathbf{R} - \mathbf{R}'| \to \infty \quad \text{for} \quad m = 0, 1, 2, \dots \ . \tag{22}$$

The goal of this theory is to calculate the orientational average pdf

$$\overline{\mathbf{P}}(\mathbf{R}, t|\mathbf{R}') = \int_{S_2} P(\mathbf{R}, \mathbf{p}, t|\mathbf{R}', \mathbf{p}')\, d^2\mathbf{p}, \tag{23}$$

which satisfies the Fokker–Planck equation

$$\frac{\partial \overline{\mathbf{P}}}{\partial t} + \nabla_{\mathbf{R}}.\overline{\mathbf{J}} = 0, \tag{24}$$

where

$$\overline{\mathbf{J}} = \left[\mathbf{V}(\mathbf{R}') + (\mathbf{R} - \mathbf{R}').\mathsf{G} + \overline{\mathbf{U}}\right]\overline{\mathbf{P}} - \overline{\mathsf{D}}.\nabla_{\mathbf{R}}\overline{\mathbf{P}} \tag{25}$$

is the asymptotic long-time leading order flux of $\overline{\mathbf{P}}$. $\overline{\mathbf{U}}$ and $\overline{\mathsf{D}}$ are the phenomenological mean swimming velocity and effective diffusion. Generalised Taylor dispersion theory shows that these exist, provided that real parts of the eigenvalues of $\mathsf{G}$ are zero so that the fluid motion alone does not lead to exponentially diverging particle trajectories. $\overline{\mathbf{U}}$ and $\overline{\mathsf{D}}$ are defined in terms of codeformational derivatives of the moments of $P$:

$$\overline{\mathbf{U}} + \mathbf{V}(\mathbf{R}') = \lim_{t\to\infty} \frac{\delta \mathsf{M}_1}{\delta t} \equiv \lim_{t\to\infty} \left(\frac{d\mathsf{M}_1}{dt} - \mathsf{M}_1.\mathsf{G}\right), \tag{26}$$

$$\overline{\mathsf{D}} = \lim_{t\to\infty} \frac{1}{2}\frac{\delta}{\delta t}(\mathsf{M}_2 - \mathsf{M}_1\mathsf{M}_1) \equiv \lim_{t\to\infty} \frac{1}{2}\left[\frac{d}{dt}(\mathsf{M}_2 - \mathsf{M}_1\mathsf{M}_1) + (\mathsf{M}_2 - \mathsf{M}_1\mathsf{M}_1).\mathsf{G} - \mathsf{G}^T.(\mathsf{M}_2 - \mathsf{M}_1\mathsf{M}_1)\right] \tag{27}$$

and

$$\mathsf{M}_m \equiv \int_{\mathbf{R}_\infty}\int_{S_2} (\mathbf{R} - \mathbf{R}')^m P\, d^2\mathbf{p}\, d^3\mathbf{R} \quad \text{for} \quad m = 0, 1, 2, \dots \ . \tag{28}$$

Hill & Bees (2002) show that

$$\overline{\mathbf{U}} = \int_{S_2} P_0^\infty(\mathbf{p}) V_s \mathbf{p}\, d^2\mathbf{p} \quad \text{and} \quad \overline{\mathsf{D}} = V_s \int_{S_2} P_0^\infty(\mathbf{p}) \mathrm{sym}[\mathbf{B}\mathbf{p}]\, d^2\mathbf{p}. \tag{29}$$

Here $P_0^\infty$ is the steady long-time pdf for the orientation of the cells which satisfies

$$\nabla_{\mathbf{p}}.(\dot{\mathbf{p}} P_0^\infty - d_r \nabla_{\mathbf{p}} P_0^\infty) = 0 \tag{30}$$

and $\mathbf{B}(\mathbf{p})$ is the long-time limit of the difference between the average position of a particle, given that its instantaneous orientation is $\mathbf{p}$, and its average position averaged over all values of $\mathbf{p}$. $\mathbf{B}(\mathbf{p})$ is the solution of

$$\nabla_{\mathbf{p}}.[\dot{\mathbf{p}} P_0^\infty \mathbf{B} - d_r \nabla_{\mathbf{p}}(P_0^\infty \mathbf{B})] - P_0^\infty \mathbf{B}.\mathsf{G} = P_0^\infty (V_s \mathbf{p} - \overline{\mathbf{U}}). \tag{31}$$

High values of local vorticity can cause gyrotactic cells to tumble (Kessler 1986), and Hill & Bees (2002) give an example of dispersion of spherical cells in a linear shear flow and show e.g. that, as the vorticity tends to infinity, the effective diffusivity in the shear plane tends to zero due the more and more rapid tumbling of the cells. Manela & Frankel (2003) extend this theory to *axisymmetric* micro-organisms so that the local rate-of-strain as well as the local vorticity influences the orientation of the cells (c.f. equation 9). They also provide an important critique of the various approaches to the calculation of dispersion in suspensions of gyrotactic cells.

Bearon (2003) extended this theory to suspensions of run-and-tumble chemotactic bacteria. The key mathematical difference between her theory and that of Hill & Bees is that the bacteria execute discrete velocity jumps whereas the algae follow a continuous random walk so that $P(\mathbf{R}, \mathbf{p}, t|\mathbf{R}', \mathbf{p}')$ satisfies

$$\frac{\partial P}{\partial t} + \nabla_{\mathbf{R}}.\mathbf{J} + \nabla_{\mathbf{p}}.(\dot{\mathbf{p}}P) = -\lambda P + \frac{1}{4\pi}\int_{S_2} \lambda(\mathbf{p})P(\mathbf{p})\, d^2\mathbf{p} \tag{32}$$

instead of (19), where $\mathbf{J}$ is again given by (20). $\lambda$ is the turning rate and is a function of the local chemoattractant gradient. Bearon gave an example of recruitment to a biofilm and showed that the rate of attachment is significantly reduced by the dispersion.

### *3.3 Modelling phototaxis*

Phototaxis, i.e. motion towards or away from a light source depending on its intensity, is a fundamental behaviour common to most swimming algae because they depend upon photosynthesis and need to move to and remain in places in their environment where the light intensity is optimal. Indeed *C. nivalis* are both gyrotactic and phototactic (gyrophototactic). A generic description of phototaxis was given by Vincent & Hill (1996) who supposed that the cells' mean swimming velocity could be written as

$$\mathbf{V}_c = V_s < \mathbf{p} >= V_s T(I)\mathbf{k}. \tag{33}$$

The 'taxis' function, $T(I)$, depends on the light intensity $I(\mathbf{x}, t)$ and is such that

$$T(I) = \begin{cases} \geq 0 \text{ if } I(\mathbf{x}, t) \leq I_c \\ < 0 \text{ if } I(\mathbf{x}, t) > I_c, \end{cases} \tag{34}$$

where $I_c$ is the optimal (or critical) light intensity. The unit vector $\mathbf{k}$ is vertical, since the light comes from above in natural bodies of water. Vincent & Hill examined the onset of bioconvection patterns using linear stability theory for a dilute suspension in a shallow layer of infinite horizontal extent. The

suspension is initially homogeneous and illuminated uniformly from above. Cells are shaded from the light by those vertically above them. This is modelled by the Lambert–Beer law for weak scattering so that the light intensity at a point $\mathbf{x}$ in the fluid is

$$I(\mathbf{x}) = I_s \exp\left(-\alpha \int_0^{\mathbf{r}} n(\mathbf{r}')\, d\mathbf{r}'\right), \tag{35}$$

where $I_s$ is the intensity of the source, $\alpha$ is the extinction coefficient, and $\mathbf{r}$ is the vector from the cell to the light source. If the parameter values are such that $I = I_c$ at a depth $H_c$ within the layer, then cells below $H_c$ will swim upwards while those below will swim downwards leading to a concentrated horizontal layer of cells in the interior of the fluid. The suspension below this layer is unstable while the suspension above is stable. When a critical Rayleigh number is exceeded, bioconvection occurs and the flow 'penetrates' into the stable upper layer. In common with other examples of penetrative convection, oscillatory modes are predicted in certain parameter ranges.

### *3.4 Developments in the Theory of Gyrotaxis*

Jones *et al.* (1994) considered the swimming of a biflagellated, bottom-heavy micro-organism such as *Chlamydomonas* in an unbounded shear flow. The orientation of the cell is determined by gyrotaxis, i.e. the balance between viscous and gravitational torques on the cell (c.f. equation (9)), but this is the only work in which the flagella and their motion are explicitly modelled. The motion of the flagella was idealised, based on the beat patterns of *C. reinhardtii*, and the body of the cell was assumed to be a sphere. The velocity of the fluid through which the flagella move was taken to be that due to the flow around the spherical body. Gray & Hancock's (1955) resistive-force theory with Lighthill's (1976) form of the coefficients was used to calculate the forces and torques on the flagella. The model predicts realisitic swimming speeds and demonstrates that the flagellar torque has a significant effect on the cell's angular velocity, which can be substantially over-estimated if the flagella are ignored.

The orientation of gyrotactic spheroidal micro-organisms in a homogeneous isotropic turbulent flow was studied by Lewis (2003) using kinematic numerical simulations for the flow, rather than much more time-consuming solutions of the Navier–Stokes equations. Each cell in the simulations swam with a constant speed, drawn from a normal distribution, in a direction determined entirely by the gyrotactic balance given by equation (9). Parameter values typical for *C. nivalis* were used. Over long times, the distribution of the orientations of the cells were shown to be well approximated by the Fisher distribution (10) where $\lambda = (BD_{\text{eff}})^{-1}$, with the effective diffusivity $D_{\text{eff}}$ used

as a fitting parameter. The estimated values of $D_{\text{eff}}$ are of the same order of magnitude as the values of the intrinsic rotational diffusivity $D_r$ (c.f. equation (8) and Section 5.1 below), which suggests that it may be necessary to solve the time-dependent Fokker–Planck equation (8) for $f(\mathbf{p}, t)$ in future work.

### *3.5 Bioconvection in porous media*

A number of theoretical analyses of bioconvection of a suspension of gyrotactic algae in a porous medium have been carried out by Kuznetsov and coworkers (Kuznetsov & Avramenko 2002, 2003a, 2003b, 2003c; Kuznetsov *et al.* 2003; Kuznetsov & Jiang 2002, 2003; Nield *et al.* 2004). The work is based on the basic model of Pedley *et al.* in equations (1)–(4), (8) and (9) with equation (1) replaced by

$$\rho\mathbf{u} = -\kappa\nabla p_e - n\rho g'\mathbf{k}, \tag{36}$$

assuming D'Arcy's Law for the flow in a porous medium with $\kappa$ as the permeability. The onset of bioconvection has been examined using linear stability theory and there has been modelling of the clogging of the pores due to deposition of the cells. However, so far no rational justification has been given for the key assumption that on the continuum scale the swimming of the microorganisms can be adequately described by a simple gyrotactic balance law as given in equation (8). Indeed, the local vorticity generated by flow through the pores may cause the cells to tumble and drastically affect their ability to reorient if the pore sizes are not significantly larger than the cells; nor is it clear that the suspension would ever reach sufficiently high concentrations for bioconvection to occur in practice. The common observation, as reported by Pedley & Kessler (1992b, Section 5), is that cells accumulate in very high volume fractions in the porous medium environments and do not drive bioconvection flows.

## 4 Numerical simulations of bioconvection

In a series of papers in the last five years, Ghorai and Hill studied gyrotactic bioconvection, using a vorticity-streamfunction formulation of the basic model first introduced by Pedley *et al.* (1998), i.e. equations (1)–(6) with $< \mathbf{p} > \equiv \mathbf{p}$, the solution of equation (9), and $\mathsf{D}$ equal to a constant times the identity tensor. The development and instabilities of a single, two-dimensional gyrotactic plume and a periodic array of such plumes were examined in (Ghorai & Hill 1999, 2000b. In sufficiently deep chambers, the plume is always unstable to both varicose and meandering modes. Away from the top and bottom of the chamber, the numerical results show that the horizontal flux of cells due to diffusion balances the horizontal flux towards the axis of the plume

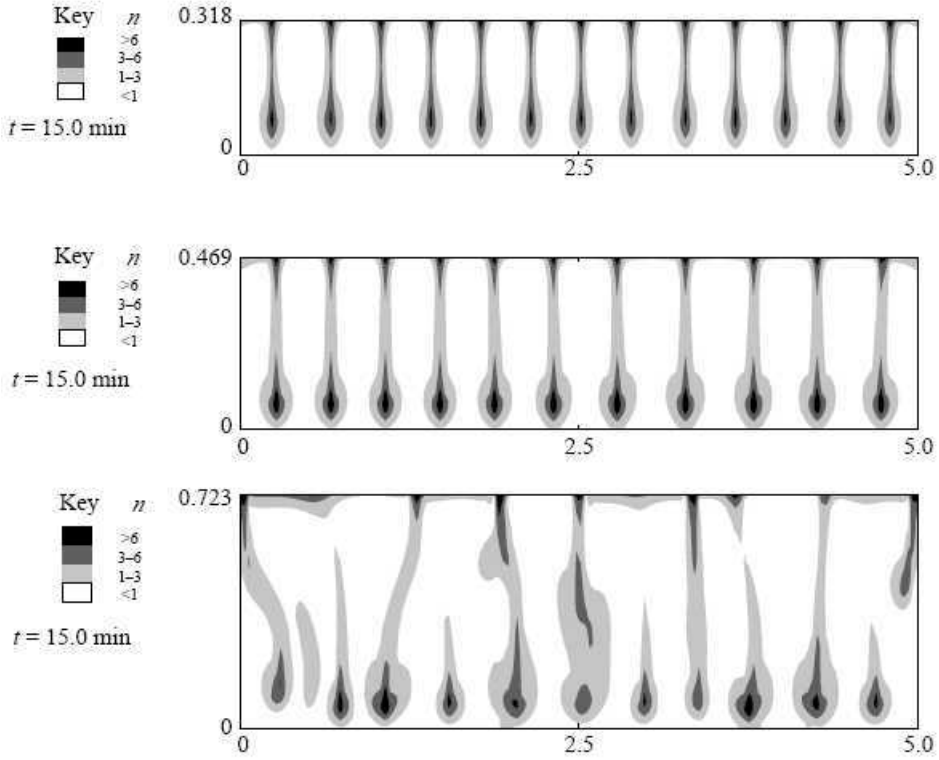


Fig. 2. Example of two-dimensional bioconvection patterns computed by Ghorai & Hill (2000a). The concentration $n$ of cells is plotted at times $t = 15$ minutes after initiation in chambers 5 cm wide and of depths $0.318, 0.460$ and $0.723$ cm. The initial conditions consist of no flow and a uniform concentration of cells subject to small random perturbations in concentration. The concentration is scaled with respect to the background concentration ($\bar{n} = 1.89 \times 10^6$ cells ml$^{-1}$). The patterns in the shallower chambers are steady, whereas the flow in the deepest layer is always unsteady and 'bottom-standing' plumes are seen.

due to gyrotaxis. Based on this, a solution for an infinitely deep plume was constructed and a linear stability analysis was performed. The linear stability analysis predicts the growth rates of the varicose and meandering instabilities, explains the mechanisms and is in good agreement with the numerical results. A similar analysis for an axisymmetric plume was given by Ghorai & Hill (2002). In Ghorai & Hill (2000b), the development of two-dimensional bioconvection patterns in a chamber sufficiently wide to accommodate about ten plumes was studied. In sufficiently deep chambers the final state is always unsteady with individual plumes continually evolving and evanescing (Fig. 2). This numerical work, albeit two-dimensional, provides the first evidence of the 'bottom-standing' plumes that are typically observed in algal bioconvection, and suggests that these are always transient, which may explain the failure to construct an analytical, self-consistent, steady solution for such a plume. Ghorai & Hill (2004) have also developed their two-dimensional numerical scheme to study phototaxis based on the model due to Vincent & Hill (1996)

and found a rich variety of bioconvection patterns.

Recently Hopkins & Fauci (2002) constructed a combined Eulerian–Lagrangian numerical scheme to simulate bioconvection in which the motion of individual cells is tracked. The potential benefit of such an approach is that the swimming behaviour of the cells can be computed directly without the need to describe the mean swimming velocity and dispersion of the cells using a pdf and a Fokker–Planck equation. However, present computer limitations mean that it is only possible to track about $10^5$ cells which is insufficient to make direct comparisons with experiments. To date, there have been no three-dimensional numerical studies of algal bioconvection, nor any on bacterial patterns.

## 5 Experimental studies

### *5.1 Swimming cells and their trajectories*

Measurement of the swimming trajectories of individual algal cells were pioneered by Hill & Häder (1997), using a computer image-recognition system that followed cells in real time and recorded their position at approximately every 0.08 s. The cells were viewed through a microscope so that it was only possible to follow cells for a few seconds before they swam out of the field of view, and also there was limited focal depth. Despite these limitations, Hill & Häder were able to analyse the directional data by measuring the statistics of the turning angles $\delta$, between the straight line segments joining data points, as a function of the absolute direction $\theta$. The means of the turning angles, $\mu_\delta(\theta, \tau)$, for *C. nivalis* were shown to be given by

$$\mu_\delta(\theta, \tau) = -d(\tau) \sin\theta, \tag{37}$$

where $\theta$ is the angle to the vertical and $d(\tau)$ is a turning amplitude that is a decreasing function of the timestep $\tau$ between data points. The sinusoidal dependence on $\theta$ is exactly as originally predicted by Kessler (1985a) for bottom-heavy cells. In contrast, for phototaxis in a horizontal layer, linear dependence,

$$\mu_\delta(\theta, \tau) = -d(\tau)\theta, \tag{38}$$

was found. The angular deviation $\sigma_\delta(\tau)$ appears to be independent of $\theta$. Apart from collisions, the swimming trajectories of these cells appear to change direction smoothly and so Hill & Häder modelled them as the continuous limit of correlated, biased random walks and were able to derive the Fokker–Planck equation (9) for the pdf of swimming directions, $f(\mathbf{p}, t)$. Explicit expressions for the coefficients, $\dot{\mathbf{p}}$ and $D_r$, were given in terms of values of $\mu_\delta(\theta)$ and $\sigma_\delta$ extrapolated from the data, in the limit as $\tau \to 0$. The swimming *speeds* were

found to be independent of $\theta$ for gyrotaxis, but there was some evidence of photokinesis. Theoretical support for the validity of extrapolating the data in this way has recently been given by Codling & Hill (2005a, 2005b) who analysed and simulated the spatial statistics of correlated, biased velocity-jump processes.

Vladimirov *et al.* (2000, 2004) have since used the more sophisticated technique of laser velocimetry to track a few hundred individual cells simultaneously. They are able to follow the cells for much longer times, and were thus able to show that there is considerable variation in swimming behaviour within the population of cells. They found good agreement with Hill & Häder's estimates of 6 s for the gyrotactic reorientation time $B$ (see equation (10)) but found $D_r$ to be between $0.018\,\mathrm{s}^{-1}$ and $0.07\,\mathrm{s}^{-1}$, which is much smaller than Hill & Häder's range of values of $0.4\,\mathrm{s}^{-1}$ to $2.2\,\mathrm{s}^{-1}$. The discrepancy may be due to the lower resolution of Hill & Häder's imaging system and to Vladimirov *et al.* being able to follow much longer trajectories.

Kessler *et al.* (1998) studied the sedimentation of micron-sized particles and the swimming of algae in a small chamber rotating about a horizontal axis, motivated by clinostat experiments. To simplify the interpretation of data, they introduced the concept of 'gravitron diagrams', in which the trajectories of particles or cells are obtained by integrating the actual velocity in the stationary frame of reference minus the component of velocity that is due to solid body rotation with the chamber. In gravitron diagrams, a sedimenting sphere moves with a constant speed along a straight line in the direction of the gravitational acceleration, and the trajectories of 'ideal' gyrotactic cells are straight lines at an angle to the vertical. Kessler *et al.* conducted preliminary experiments in which the trajectories of sedimenting spheres and the gyrotactic alga *Pleurochrysis carterae* were observed. Gravitron plots of the spheres' trajectories at rotation rates of $1.0\,\mathrm{rad\,s}^{-1}$ were indeed straight lines, but at an angle of 15° the vertical. The reasons for the discrepancy are not clear, but may be due to wall effects or to hydrodynamic interactions with other spheres. When the chamber rotated at $0.3\,\mathrm{rad\,s}^{-1}$, the gravitron trajectories of the algae were found to be distributed about a mean direction at angle to the vertical, as might be expected given the randomness seen in the trajectories of swimming cells in the absence of rotation. Surprisingly, at rotation rates of $1.0\,\mathrm{rad\,s}^{-1}$, Kessler *et al.* found that the cells' trajectories were predominantly straight lines tightly distributed around the direction of those of the sedimenting spheres, which suggests that the cells' orientations were in some way controlled by the motion of the spheres. Further experiments are needed to validate these results and could yield interesting information about the behaviour of swimming cells.

Together, these experiments have provided a basis for a fully rational continuum model of algal bioconvection. As yet, there have been no compa-

rable experiments on *B. subtilis* and current modelling assumes that they perform a run-and-tumble velocity-jump process similar to that of *E. coli* (Berg & Brown 1972).

### *5.2 Bioconvection patterns*

Bees & Hill (1997) made the first quantitative study of the patterns formed by concentrated suspensions of *C. nivalis*, $O(10^6$–$10^7)$ cells $\mathrm{ml}^{-1}$, in shallow layers up to 4 mm deep. The patterns were analysed using two-dimensional Fourier transforms of images taken from vertically above the suspensions. The dominant wavelengths of the planforms were identified from peaks in the amplitude of the Fourier transforms, and it was demonstrated that the pattern wavelength decreases as the patterns evolve towards their final state, and there is a strong dependence on the layer depth. Statistical analyses of such patterns were carried out by Taylor *et al.* (2001), who derived statistical measures for the regularity of the pattern, and by Noever and coworkers (Noever *et al* 1994a, 1995), who also considered the use of bioconvection patterns as assays for external toxins (Noever *et al* 1992, 1994b). Yamamoto *et al.* (1992) studied the effects of depth, concentration and the walls of the container on bioconvection patterns in suspensions of *C. reinhardtii*, and Mendelson (1999) compared multicellular organisation in *Bacillus subtilis* macrofibres, colonies and bioconvection patterns.

The onset of bacterial bioconvection in suspensions of *B. subtilis* was examined by Jánosi *et al.* (1998). They quantified the development of the patterns by the standard deviation of the gray levels of the pixels comprising the image, and studied the 'delay time', $T_D$, from the end of mixing of the suspension until pattern formation occurs. $T_D$ was found to be independent of the width of the chamber and inversely proportional to the concentration for a depth of 1.57 mm. This is explained by the time taken for the cells to swim upwards and form a dense layer at the upper surface which becomes gravitationally unstable. Czirók *et al.* (2000) showed later that the pattern wavelengths do not depend strongly on the depth of the layer, in contrast to algal bioconvection, presumably due to the formation of a quiescent lower layer of cells as the concentration of oxygen falls to a critical value. The consumption of oxygen during bioconvection was compared with that of a continuously shaken suspension by Jánosi *et al.* (2002). They found no significant differences despite earlier suggestions that bioconvection would enhance the transport of oxygen throughout the suspension allowing the bacteria to influence their environment by collective motion.

## 6 Concentrated suspensions

Mendelson *et al.* (1999) have conducted experiments with concentrated populations of *B. subtilis* occupying a thin water film on top of an agar gel which supplies nutrient to the cells. They observed an intricate bulk motion of "whorls and jets" with length-scale that was between that of the individual cells or cell spacing and the horizontal extent of the system (a video movie of the motion can been seen on the web site given in their paper). The motion appears to be quite random and invites a comparison with two-dimensional turbulence. Kessler & Hill (1997) and Dombrowski *et al.* (2004) have also observed such mesoscopic, random bulk motions in three-dimensional suspensions of *B. subtilis*, particularly near an air interface (horizontal, vertical or in a meniscus) (Kessler *et al.* 2000) where the oxygen concentration is high and therefore so also is the cell concentration. Since these motions are not gravitationally driven and are not observed in dilute suspensions, they must be a consequence of cell-cell interactions, but the mechanism is not properly understood. Lega & Passot (2003, 2004) have developed a two-phase model for a concentrated suspension of bacteria on top of a gel, and they have shown that small-scale random forcing can produce similar patterns to those seen in experiments. In their work, Lega and Passot propose that the swimming of the bacteria imposes a random external force on the fluid in which they swim, but the thrust generated by the flagella of individual bacteria must balance the drag as the cell moves through the fluid, since the motion occurs at a very low Reynolds number. This appears to be a fundamental problem with their theory, and it may be better to model the effects of the swimming of the bacteria as a random distribution of stresslets.

Kessler (2000) observed superdiffusion of passive particles in concentrated suspensions of bacteria in shallow layers. Related pioneering work by Wu & Libchaber (2000) on the diffusion of micron-scale beads in a concentrated suspension, or bath, of bacteria in a freely suspended soap film has found superdiffusion of the beads at small times and normal diffusion at longer times. This has led to a number of theoretical papers by Grégoire and coworkers (Grégoire *et al* 2001a, 2001b, 2003; Grégoire & Chaté 2004) using a stochastic model derived from Vicsek *et al.* (1995) in which random walkers attempt to align themselves with their neighbours at each time step but are also subject to noise in their choice of new direction, and repulsive interaction forces. These models reproduce Wu & Libchaber's (2000) observations but they are phenomenological and do not describe how bacteria interact hydrodynamically with each other (Wu & Libchaber 2001).

## 7 Discussion

Much progress has been made in the decade since Pedley & Kessler's (1992) review, especially in (a) the development of a quantitative, rational continuum model for dilute suspensions of gyrotactic algae, and (b) the construction of a rational theory for oxytactic bacteria. Such systems have become a paradigm for the interaction between physics and biology. There is much more work to be done, in particular to provide three-dimensional numerical simulations of bioconvection, to give a rational account of the combined effects of gyrotaxis and phototaxis for algae, to extend the experiments of Vladimirov *et al.* (2000, 2004) to other species of micro-organisms, and to obtain data on the trajectories of bacteria. Perhaps the most significant, outstanding challenge is the rational description of concentrated suspensions. Locally high cell concentrations do occur in bioconvection plumes even when the mean concentration is dilute. Also, another sort of pattern-formation ('whorls and jets') is observed in very concentrated cultures of swimming bacteria. Here cell-cell interactions are crucial, but it is not clear how to derive an appropriate macroscopic model that is consistent with the laws of mechanics at the cellular level.

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