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Bioconvection

T.J. Pedley and J.O. Kessler

Bioconvection is the name given to pattern-forming motions set up as a result of hydrodynamic instabilities in suspensions of swimming micro-organisms. Examples of the patterns are shown for suspensions of motile algae and of bacteria; in all cases the cells swim upwards, on average, in still water and are slightly denser than the water. One mechanism of instability, dominant in a shallow chamber, is that the upswimming causes cells to accumulate in a thin layer near the upper surface, which therefore becomes denser than lower regions. This density distribution is unstable, and convective motions are set up as in a shallow fluid heated from below. In the case of the algae there is another mechanism which can operate in a deep fluid, unaffected by horizontal surfaces, and is called gyrotaxis. It is a

consequence of the fact that the cells are bottom heavy (which causes them to swim upwards in the first place) so that their average swimming direction is determined by a balance between gravitational and viscous torques. The bacteria consume oxygen and swim up gradients of oxygen concentration, so that the bioconvective motions carry oxygen around with them, changing the concentration gradient up which the cells swim. This article describes the observed phenomena and the mechanisms which underlie them, and outlines the important features that a quantitative (mathematical) description of them must possess. A recent contribution of interest has been the rational analysis of the manifestly random distribution of swimming directions in a population of motile cells.

Introduction: observations

Multitudes of micro-organisms exist in almost every conceivable aqueous environment on earth and have been estimated to form a major part (more than 50%) of the world's biomass. Most individuals live in the oceans, because that is where most of the water is. A large fraction of them constitute the phytoplankton, the light-converting bottom link of the food chain, but many similar species also live in large or small bodies of fresh water. These micro-organisms, mostly blue-green algae, green algae, dinoflagellates, diatoms, etc, are of

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considerable scientific interest for various reasons: they are thought to absorb more carbon dioxide, *in toto*, than terrestrial plants, so understanding their biology and correctly estimating their numbers is vital to forecasts of the greenhouse effect; patchiness in their populations can have significant effects on populations of higher organisms, either beneficial (e.g. stimulating the schooling of krill, exploited as food by even larger animals such as whales or men) or deleterious (e.g. red tides, which poison coastal seafood industries); some of them are harvested for their food value or for the chemicals they produce (*Dunaliella salina*, for example, is used as a source of beta-carotene, a popular red food colouring—it is more ‘green’ for food-colouring to be manufactured by algae than by chemists); others, which swim, are used as a means of bio-assay of water quality (if they stop swimming then the concentration of something harmful is too large—they can be thought of as small green canaries). The phenomena to be described in this article were observed during straightforward experiments to study populations of swimming micro-organisms, suspended in aqueous growth medium in the laboratory.

A number of authors have observed that such suspensions, when sufficiently concentrated, spontaneously form patterns, and it is this pattern-formation process that is called bioconvection (Fig. 1.) An extremely detailed series of observations were recorded by Wager¹⁵ in 1911, though he noted that there had been reports as early as 1848. Wager used several species, but the most detail was given for the flagellated alga *Euglena viridis*, about 50 μm in length and 20 μm across. He placed a well-stirred suspension in a chamber about 50 mm across and 6 mm deep and, from above, observed that patterns with a horizontal length scale of a few mm formed within about 1 min. The pattern changed substantially with time, the pattern spacing falling from about 7 mm to about 2 mm, before settling down after about 10 min to an apparently steady state. A similar sequence of observations in a shallow chamber, using the biflagellate alga *Chlamydomonas nivalis* (about 15 μm long), is reproduced in Fig 1. In this figure, dark regions represent relatively large concentrations of organisms, forming vertical columns (dots) or sheets (lines). Note that both the length-scale and the nature of the patterns change with time; they also depend on the depth of the chamber and the average concentration of suspended organisms.^{6,8} It should be pointed out that the times for formation and modification of the patterns are much smaller than those required for reproductive population changes or consumption of dissolved nutrients, and that the patterns are formed in the dark, so the organisms’ response to light cannot be the driving mechanism although the patterns are affected by light.^{6,15} Bioconvection is not restricted to suspensions of motile algae,

Fig. 1. (*Opposite*) A time sequence of bioconvection patterns viewed from above in a suspension of algae, *Chlamydomonas nivalis*. Chamber width 37 x 67 mm; fluid depth 4 mm; mean cell concentration $3 \times 10^6 \text{ cm}^{-3}$. Times between frames: from well-stirred to first and first to second, 20 s, then 30–40 s; final frame, 10 minutes.



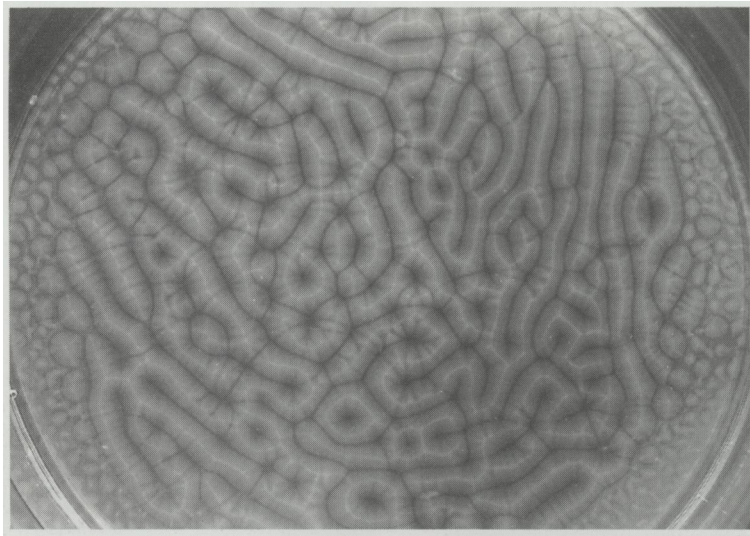


Fig. 2. *A fully developed bioconvection pattern in a suspension of bacteria, *Bacillus subtilis* near end of exponential growth phase. Chamber diameter 7 cm; chamber depth 2.5 mm; mean cell concentration 5×10^8 cells/cm³ (approx.).*

but has also been found with ciliated protozoa^{8,13} and bacteria^{12,15} (Fig. 2, taken using dark-field photography so that large cell concentrations are whiter than their surroundings).

In these shallow chambers, observation from the side would reveal a high concentration of cells at the top surface, with tapered columns or plumes of cells extending over the whole depth. However, when a much deeper suspension is viewed from the side, more or less vertical streaks are observed to form in the body of the chamber, but as time passes they become more regularly spaced and migrate towards the bottom of the chamber where once more an approximately steady state pattern is formed (Fig. 3). Such ‘bottom-standing plumes’¹² were also observed by Wager.¹⁵

Mechanisms

Organisms exhibiting bioconvection share two common characteristics: (1) they are slightly denser than water and (2) isolated individuals on average swim upwards (exhibiting negative ‘geotaxis’ or ‘gravitaxis’). In a shallow chamber and in the absence of any bulk fluid motion, therefore, greater cell concentration will develop towards the top of the chamber than the bottom and in consequence the average density (of cells plus fluid) will be greater at the top. Such a stratification, with denser fluid above less dense fluid, is well-known to be unstable if the density gradient is large enough, and to lead to the recirculating bulk

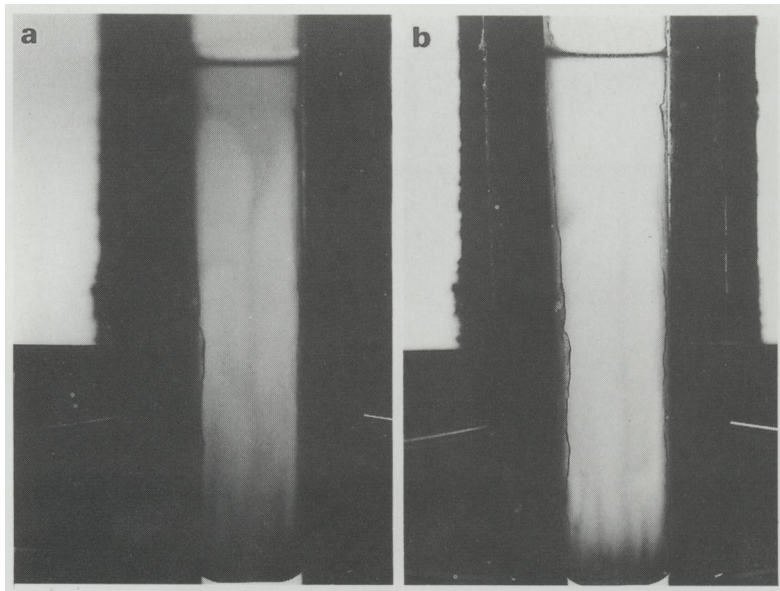


Fig. 3. 'Bottom-standing plumes' in a suspension of algae, *C. nivalis*. Chamber width: 1 cm; depth (front to back) 3 mm. (a) Two minutes after stirring. Note the plume descending

from the dense, upper cell-laden fluid through the middle region from which the cells have already formed the plumes standing in the lower part of the cuvette. (b) Two minutes later.

motions called convection (Fig. 4). This is what happens in a layer of fluid heated from below, when the motion is called *thermal convection* or *Rayleigh-Bénard convection*. Platt¹³ was the first to recognise that density stratification was the (or at least a) mechanism for pattern-formation in suspensions of swimming micro-organisms, and he coined the term bioconvection. An additional mechanism for the initiation of bioconvection is discussed below.

Let us go back to ask what is the mechanism by which a cell is enabled to respond to gravity and swim upwards? One possibility is a response to light ('phototaxis'). However, upswimming and hence bioconvection can take place in the dark. Another possibility is chemotaxis, or the tendency to swim along concentration gradients of some chemical: we believe that it is the tendency of the bacteria to swim up an oxygen gradient towards the free surface that is responsible for the bacterial bioconvection depicted in Fig. 2. However, chemotaxis has been eliminated as the upswimming mechanism for algal species which have been studied in the laboratory.

The simplest mechanism for orienting cells so that they swim upwards is entirely passive, not requiring any sophisticated sensors: it is that the cells are bottom-heavy.^{5,6} Consider for example a biflagellate algal cell such as *C. nivalis* or *D. tertiolecta*, in a fluid without bulk motion. It

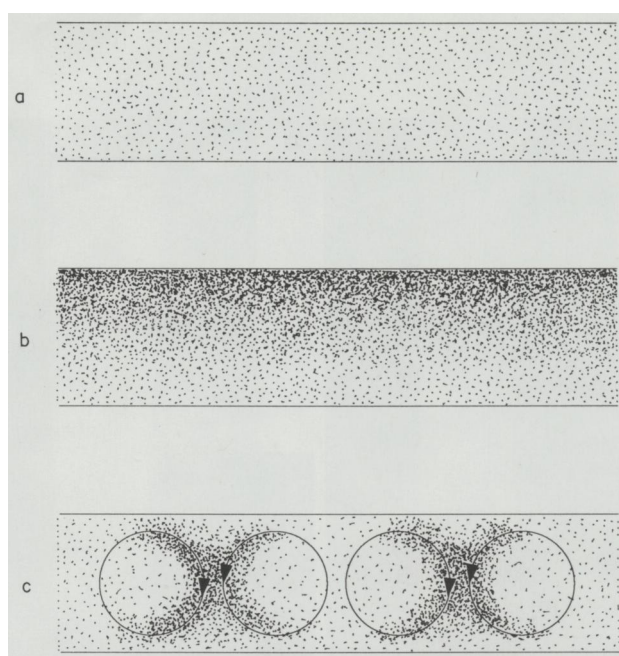


Fig. 4. *Upswimming in an initially uniform, shallow suspension causes cells to accumulate at the top. The top layer therefore becomes denser than the regions below, and a convective*

instability ensues, in which bulk motions throughout the fluid redistribute the cells into bioconvection patterns.

has a roughly spheroidal body and swims by means of a sort of breast-stroke of the flagella, towards the ‘front’ where the flagella are mounted. Suppose that the denser of the cell contents are displaced towards the rear (Fig. 5), for which there is some direct observational evidence, so that the centre of mass is behind the centre of buoyancy. Then suppose that the cell’s axis is disturbed from the vertical: gravity now exerts a torque on the cell, tending to restore the axis to the vertical whether the cell is swimming or not.

Now consider what happens when the cell is in a fluid which is in motion, in particular a vertical shear flow such as that set up in a vertical pipe by gravity or a pressure difference between the ends. The fluid velocity increases from the walls (where it is zero) to the centre of the pipe (Fig. 6). This shearing motion causes every fluid element to rotate; thus a viscous torque is exerted on any small body, suspended in the fluid, that is not rotating at the same angular velocity. A bottom-heavy cell will thus experience competing torques, viscous and gravitational, and the angle, θ , that its axis makes with the vertical will be determined by a balance between the two. Since a cell swims in the direction of its axis (approximately), it follows that when the pipe flow is directed vertically downwards the cells will all tend to swim in towards the centreline (towards the wall when the flow is upwards), as well as upwards relative to the fluid. Such radial focussing of cells is

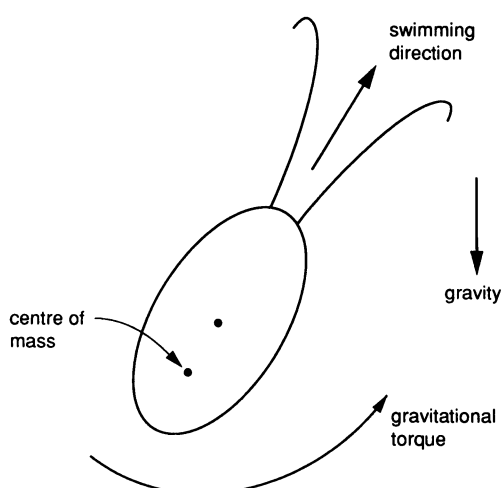


Fig. 5. A bottom-heavy cell displaced from the vertical orientation experiences a gravitational torque which tends to restore it to the vertical.

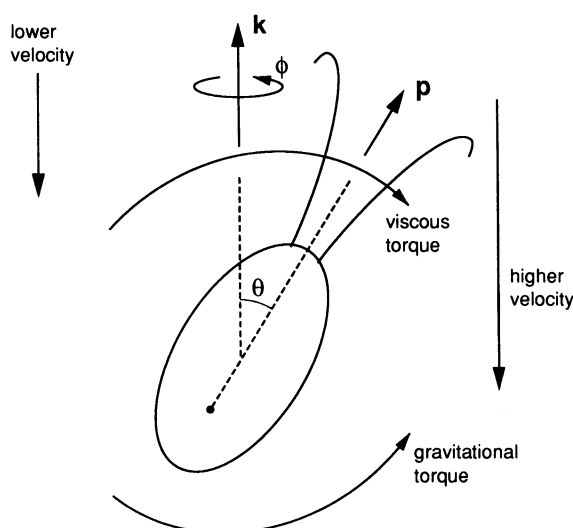


Fig. 6. Gyrotaxis. A bottom-heavy cell in a vertical shear flow experiences a viscous torque as well as a gravitational one. Its orientation (i.e. swimming direction) \mathbf{p} is therefore inclined to the

vertical \mathbf{k} (on average) by an angle θ ; ϕ is the angle the vertical plane containing the axis \mathbf{p} makes with a fixed vertical plane.

indeed observed,⁵ and constitutes an experimental verification of the hypothesis of bottom-heaviness—no other mechanism has been proposed which can account for the focussing phenomenon.

The swimming of cells oriented by such a balance between viscous

and gravitational torques is termed *gyrotaxis*;^{5,6} the swimming of head-heavy spermatozoa provides another example of it, though in that context the phenomenon is termed *rheotaxis*.¹⁴ Not all micro-organisms that exhibit bioconvection are oriented by gyrotaxis, as can be inferred from the fact that they do not become focussed in downwards pipe flow. The mechanism which drives bioconvection of chemotactic bacteria has already been mentioned. The ciliated protozoan, *Tetrahymena pyriformis*, appears not to be gyrotactic since it has so far not been possible to focus it, yet it is one of the most popular organisms for demonstrating bioconvection.^{2,8,13} Its behaviour must include gravitaxis and may result from active sensing of the gravitational force.

The presence of gyrotaxis provides a separate mechanism for the initiation of bioconvection which is independent of the generation of an unstable density stratification and can take place in an unbounded suspension (i.e. the top and bottom are so far away that their effect will not be felt in the middle for a very long time) which is initially uniform and at rest. Consider a blob of fluid in which, as a result of a natural small fluctuation, the cell concentration is slightly greater than in its surroundings. Since the effective density of the fluid increases with cell concentration, this blob will be somewhat denser than the surroundings and will tend to sink. In sinking, the blob will drag down the fluid around it, by the action of viscous forces, thereby setting up a sheared, downwards velocity distribution as shown in Fig. 7. The cells experiencing this shear will then be oriented by gyrotaxis so that they tend to swim in towards the blob and its wake, thus reinforcing the initial fluctuation in cell concentration which will become more and more marked. This is a positive feedback process, the concentrated region falling more and more rapidly and focussing more and more cells into itself. We thus have a mechanism for the spontaneous generation of falling plumes in the interior of the suspension, as observed in a deep chamber (Fig. 3a).

Gyrotaxis also provides an explanation for the development of bottom-standing plumes (Fig. 3b and Fig. 8). The tendency of cells to end up near the bottom of a chamber once they are mostly (self-)

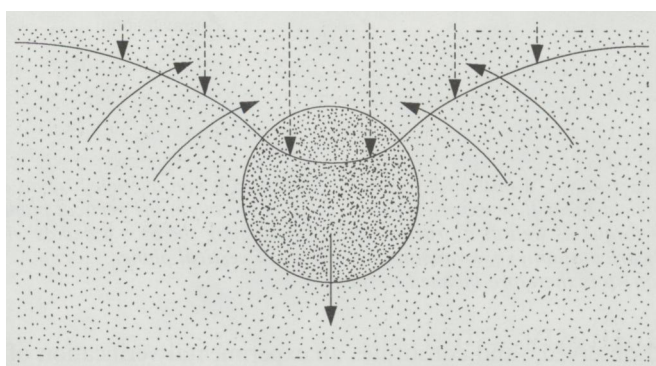


Fig. 7. The mechanism for gyrotactic instability of a uniform suspension: a blob with a high cell concentration

falls, generating a sheared velocity profile which causes other cells to be focussed into its wake.

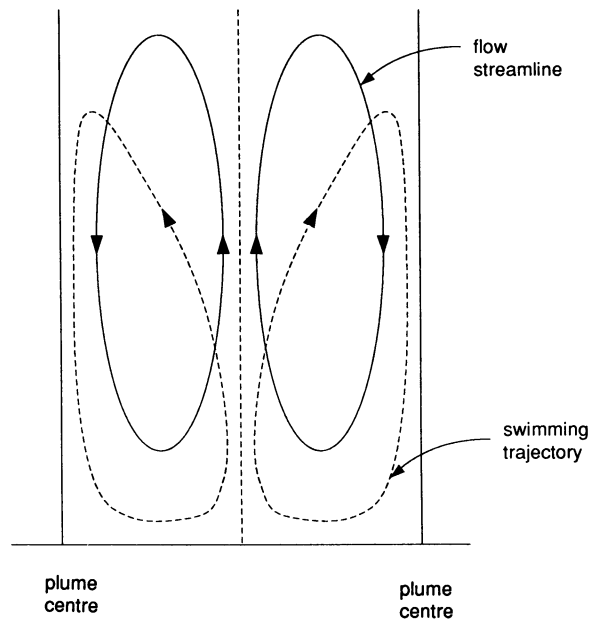


Fig. 8. The mechanism for the persistence of 'bottom-standing plumes:' cells in the dense falling plume are carried round at the bottom into the upflow, but they swim across, by gyrotaxis, and enter the plume again higher up. Cell trajectories: — — —; flow streamlines: ———.

concentrated into plumes, although they swim upwards relative to the fluid, follows from the fact that the gravity-driven sinking velocity, which can reach the order of millimetres per second (measured by watching the motion of individual cells), greatly exceeds a typical cell swimming speed relative to the fluid ($70 \mu\text{m s}^{-1}$ for *C. nivalis*). (Incidentally the sedimentation speed of a dead cell relative to the fluid is at least ten times smaller.) Near the bottom of the chamber, then, there will be a strong downflow driven by the plumes, compensated for by an upflow in the fluid between the plumes. Cells will be swept round with the flow, near the bottom boundary, from a downflow zone to an upflow zone. In the upflow zone the cells continue to swim upwards relative to the fluid, but gyrotaxis means that they also have a horizontal component of velocity, V_H , in towards the plume. After a time, T , roughly equal to half the plume-spacing divided by V_H , all the cells will have been guided back into the downflow plume, and none will be able to rise higher. This gives an estimate of the height of the bottom-standing plumes equal to T multiplied by the maximum upflow velocity (Fig. 8).

Quantitative analysis

If the phenomena described above are to be more than a curiosity we must be able to use them to learn something about the ecology or biology of the organisms concerned. Some useful things have already

been learnt. In the context of algal ponds it might have been thought that upswimming meant that it would be easy to harvest the algae from the top surface of the pond; however, bioconvection means that the pond is constantly stirred up, so harvesting is more difficult. Gyrotactic guidance provides a mechanism for the selective withdrawal of the best swimmers from the axis of a vertical pipe, and hence a means for manipulation of algal populations.^{5,6} However, in the open ocean bioconvection patterns are likely to be destroyed by the much more vigorous, turbulent stirring generated by wind and waves, at least in the upper levels.

In order to learn more from the laboratory experiments we must be able to relate easily measurable quantities, like the size and shape of the bioconvection patterns, to average properties of the individual cells, which are much harder to measure. To do that we need quantitative models of the phenomena of interest.

Let us consider the torque balance on an individual, bottom-heavy cell in a given fluid flow (Fig. 6). If we ignore the presence of the flagella, it is quite a good approximation to treat the cell as a prolate spheroid, with its axis parallel to the swimming direction and the centre of mass displaced along the axis a distance h back from the centre. If the swimming direction is represented by the unit vector \mathbf{p} , and if \mathbf{k} is a unit vector directed vertically upwards, then the gravitational torque on the cell is represented by the vector product $mgh\mathbf{p}\wedge\mathbf{k}$, where m is the cell's mass and g is the gravitational acceleration. This has magnitude $mgh\sin\theta$, where θ is the angle the axis makes with the vertical. Calculation of the viscous torque on the spheroid is simplified by the fact that inertial forces are negligible compared with viscous forces for bodies as small as a cell, swimming at biologically reasonable velocities: a typical ratio of inertial to viscous forces (the *Reynolds number*) for *C. nivalis* is 0.002. The viscous torque depends on the velocity gradient in the fluid around the cell, represented by the *vorticity* (equal to twice the local angular velocity of the fluid) and the *strain-rate* (the tendency of the fluid to deform without rotation). A straining flow can exert a torque on a spheroidal body, though not on a spherical one, while if the angular velocity of the fluid is different from that of the body, a torque is exerted whatever the shape. Using formulae first derived by Jeffery⁴ in 1922, the torque balance reduces to the following equation for the rate of change of the axial direction \mathbf{p} :*

$$\dot{\mathbf{p}} = \frac{1}{2B} [\mathbf{k} - (\mathbf{k} \cdot \mathbf{p})\mathbf{p}] + \frac{1}{2} \boldsymbol{\omega} \wedge \mathbf{p} + \alpha_0 \mathbf{p} \cdot \mathbf{E} \cdot (\mathbf{I} - \mathbf{p}\mathbf{p}), \quad (1)$$

where $\boldsymbol{\omega}$ is the vorticity vector, \mathbf{E} is the strain-rate tensor, \mathbf{I} is the identity tensor, and α_0 is the measure of the eccentricity of the spheroid

* This equation is introduced for the sake of precision, and because it briefly encapsulates the torque balance in all circumstances. Readers unfamiliar with vector notation should skip to equation (2) and the discussion of the reorientation time, B . Those familiar with vectors but not tensors can avoid the latter by restricting attention to spherical cells for which $\alpha_0 = 0$.

($\alpha_0 = 0$ for a sphere; $\alpha_0 = 1$ for a rod).¹² The quantity B has the dimensions of time, and is given by

$$B = \frac{\mu v \alpha_1}{2mg h} \quad (2)$$

where μ is the fluid viscosity, v is the cell volume, and α_1 is another dimensionless constant that depends on cell shape (α_0). B represents a time-scale for the return of the cell axis to the vertical after being displaced from it in a fluid otherwise at rest; its value has been estimated to be about 3 sec for algal cells like *C. nivalis*.

Equation (1) can be used to calculate the orientation of a cell, and hence its trajectory, in an arbitrary flow field, as long as random influences on its orientation can be neglected. If it is assumed that the flow field is steady and that the cell's swimming speed is sufficiently small for the variation in the ambient flow as the cell swims to be negligible, and if equation (1) admits of a stable steady-state solution (i.e. one with $\dot{\mathbf{p}} = 0$), then a deterministic swimming direction can be computed. For example, in the case of downward flow in a pipe of radius R (in which the shear is maximum at the wall and zero on the axis), and for spherical cells (with $\alpha_0 = 0$), the angle θ that the swimming direction makes with the vertical (Fig. 6) is given by

$$\sin \theta = 2B W_0 r/R^2 \quad (3)$$

where W_0 is the maximum downwards fluid velocity (on the axis), r is the distance of the cell from the pipe axis and $\omega = 2W_0 r/R^2$ in this case. By adding the swimming velocity vector to the fluid velocity vector, the cell's velocity relative to the pipe can be computed at all points on its trajectory. Equation (3), of course, does not yield a solution for θ if the right hand side exceeds 1; in other words, if the flow is too vigorous, a stable, steady orientation does not exist. In that case, the cell will tumble over and over, its swimming direction varying with time according to equation (1) (with $\dot{\mathbf{p}} \neq 0$). There will still be a tendency to swim towards the axis *on average*, but individual cell trajectories will depend on their initial orientations.

Suppose that at some initial instant the suspension is well-stirred, so that the cell concentration is uniform everywhere in the pipe, and then the downward flow is switched on. The calculated trajectories can be used to compute the concentration distribution at later times.⁶ One predicts that there will be no cells outside a cylinder of radius $r_c(t)$ which decreases exponentially to zero; experimental evidence suggests that the focussed plume radius tends instead to a non-zero constant. One also predicts that within that cylinder the maximum concentration occurs at the outer edge, and there is a marked dip on the axis; this too is not observed experimentally. The deficiencies in the predictions are associated with the neglect of random effects (see below).

Pipe flows are not the only ones for which cell trajectories have been predicted or observed. An interesting new experiment by one of us (JOK, unpublished) concerns a planar, uniform shear flow which is

confined to a vertical plane but can be oriented at an arbitrary angle to the vertical (see Fig. 9). For this flow, the gyrotaxis angle θ is given by $\sin \theta = BS$, where S is the shear rate in the flow, and it is predicted that there is a particular flow angle at which the experiment can be set (ψ in Fig. 9 equal to $\pi/2 - \theta$), for which the cells swim along, not across, the streamlines of the flow.¹² Measurement of the cell trajectories will provide useful information about the average values of B for particular species, and about random effects in the suspension.

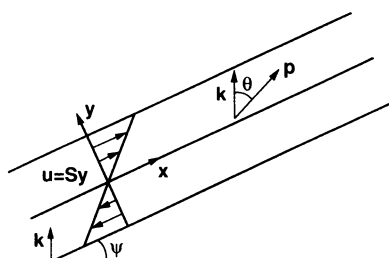


Fig. 9. A shear flow with velocity u equal to S times the transverse distance y is inclined at an angle ψ to the

horizontal. The deterministic swimming direction (\mathbf{p}) makes an angle θ with the vertical (\mathbf{k}).

Random behaviour

The swimming direction, \mathbf{p} , of a cell is observed to be a random quantity: the direction at a given time is independent of the direction a sufficiently long time earlier. It follows that the instantaneous swimming directions of the cells in a suspension are randomly distributed. This does not mean that they are isotropically distributed: all directions are not equally likely, because of sensory or physical biases. For example, the gyrotactic torque balance is a physical bias which ensures that, whatever the present direction, there will be a tendency to return towards a particular direction, as given by equation (1). The distribution of swimming directions [which can be represented by a probability density function $f(\mathbf{p})$] results from a dynamic balance between whatever it is that causes the cells to change their orientation randomly, and the deterministic mechanisms represented by equation (1). The process is somewhat similar to a biased random walk, and can be thought of as analogous to rotary Brownian motion of bottom-heavy spheroids, which determines the orientation distribution in a suspension of colloid particles.³ An analysis of the process should result in a prediction of the mean swimming direction and the variance about it.

The principal assumption of our own recent theoretical models of micro-organism suspensions^{11,12} is that the analogy with rotary Brownian motion is exact. The theory of Brownian motion can then be used to show that the distribution $f(\mathbf{p})$ satisfies a *Fokker-Planck equation*, as follows:

$$\nabla_{\mathbf{p}} \cdot (\mathbf{p}f) = D_r \nabla_{\mathbf{p}}^2 f, \quad (4)$$

where D_r is a rotational diffusivity, with dimensions of inverse time, $\dot{\mathbf{p}}$ is given in terms of \mathbf{p} by equation (1), and $\nabla_{\mathbf{p}}$ is the two-dimensional gradient operator in \mathbf{p} - space.* In the case of thermal rotary Brownian motion, in which the random reorientations of the particles result from molecular collisions, the rotational diffusivity is proportional to kT (Boltzmann's constant times temperature) divided by the fluid viscosity. We do not know the cause of the random reorientations in micro-organism suspensions: algal cells, in particular, are certainly too large to be much affected by conventional Brownian motion. Maybe there is something like Brownian motion acting on the locomotory apparatus within the cells, giving an 'effective kT '.

There are two further assumptions that have gone into the model. First, the probability distribution is assumed to depend on the local torque balance as it would if the flow were steady. This is justified if the time required for the flow to change significantly is large compared with D_r^{-1} (if this were not justified, a $\partial f/\partial t$ term would appear on the left hand side of equation (4)). Second, the suspension is taken to be sufficiently dilute that dynamic cell-cell interactions are unimportant; if this were not true, equation (1) would be modified. Both of these assumptions are reasonably well satisfied in many of the laboratory experiments, but neither of them is accurate in all circumstances. They will have to be examined carefully in future updates of the model.

For a general flow field numerical methods are required to solve the Fokker-Planck equation (4), with $\dot{\mathbf{p}}$ given by equation (1), but analytical solutions can be found in special cases. The simplest special case is that of a suspension in which there is no bulk motion, so that ω and \mathbf{E} are zero in equation (1) and the only deterministic torque acting on a cell is gravitational. The solution, normalised so that the integral over all possible orientations is unity, is given by the so-called Fisher distribution:⁹

$$f = \frac{\lambda e^{\lambda \cos \theta}}{4\pi \sinh \lambda}, \quad (5)$$

where $\cos \theta = \mathbf{k} \cdot \mathbf{p}$ and $\lambda = (2BD_r)^{-1}$, a dimensionless constant representative of the micro-organism suspension under investigation. If λ is small, random reorientation is dominant and the distribution isotropic ($f = 1/4\pi$); if λ is large, gyrotaxis wins over randomness, and f is non-zero only in a narrow zone around $\theta = 0$, representing vertical upswimming. The distribution function given by Eq. (5) has a long history in physics. It was first derived in 1905 by Langevin, for magnetic dipoles, μ , subject to a field H , which exerts an aligning torque $\mu H \cos \theta$, and to thermal agitation kT . For that case, $\lambda = \mu H/kT$. In 1912 P. Debye

*In other words, if \mathbf{p} is represented by polar angles θ, ϕ , relative to a fixed direction such as the upwards vertical \mathbf{k} (Fig. 6), then $\nabla_{\mathbf{p}}$ has components $\frac{\partial}{\partial \theta}, \frac{1}{\sin \theta} \frac{\partial}{\partial \phi}$ in the θ, ϕ - directions respectively.

extended the theory to electric dipoles; more recent applications include thermally agitated freely jointed segments of polymers.

A solution of the Fokker–Planck equation has also been found for the case of a very weak flow in which gravity dominates and the parameter

$$\epsilon = B\omega \quad (6)$$

is small (where ω is a scale for the local vorticity). The distribution is then still close to the Fisher distribution. The equation for spherical cells ($\alpha_0 = 0$) has, moreover, been solved for strong flows (ϵ large), a case for which there is no deterministic swimming direction because the cells tumble.¹²

Equation (5) is a prediction of the model that can be tested experimentally, by measuring large numbers of cell trajectories in a very dilute suspension in which there are no bulk motions, not even bioconvection. Such measurements have been made, using the alga *Chlamydomonas nivalis*, by Professor D.-P. Häder of Erlangen, and have been analysed by Dr N. A. Hill of Leeds. The results have not yet been published, but we can report that the actual distribution is indeed reasonably well modelled by equation (5), with $\lambda \approx 0.7$ (earlier, more preliminary results, suggested $\lambda \approx 2.2$).¹¹

Cell conservation and the continuum model

Armed with the probability density function $f(\mathbf{p})$, or at least the equations from which it can be calculated, we can begin systematically to analyse the suspension as a whole. We treat it as a continuum rather than as a collection of individual cells, which is valid as long as the size and spacing of the cells (of the order of 10 and 100 μm respectively) are very much smaller than the length-scales of the phenomena of interest (e.g. bioconvection patterns, around 1 mm and above). The concentration or number density of cells, n , must be large (although the volume fraction, $n\nu$, where ν is the cell volume, must be small for the suspension to be dilute), and in the bioconvection experiments n is around 10^6 per cm^3 and above and $\nu \lesssim 10^{-9} \text{ cm}^3$.

Perhaps the most important equation of the continuum model is that which represents *conservation of cells*. This says that the rate of increase of cell number in a given volume of space is equal to the net flow of cells into the volume as a result (a) of being carried along by the bulk flow, and (b) of cell swimming. We neglect sedimentation, because the sedimentation speed is much less than the swimming speed (see above). The cell swimming contribution can be further subdivided into a contribution determined by the mean cell swimming velocity \mathbf{V}_c and another contribution due to the random motion of the cells relative to that mean, which is naturally modelled as a diffusion process. Converted to a differential equation, this says that the rate of change of n at a point is equal to the negative of the divergence of cell flux, or

$$\frac{\partial n}{\partial t} = -\nabla \cdot \left\{ n(\mathbf{u} + \mathbf{V}_c) - D\nabla n \right\} \quad (7)$$

where \mathbf{u} is the bulk fluid velocity and \mathbf{D} is the cell swimming diffusivity tensor (the latter is a tensor because, for example, the horizontal and vertical diffusivities in a gravitational field are different). The mean cell swimming velocity vector is equal to the mean cell swimming *speed*, V_s , say, multiplied by the mean of the cell swimming direction, $\langle \mathbf{p} \rangle$, which is the integral over all of \mathbf{p} – space (the surface of the unit sphere) of \mathbf{p} , weighted by the probability density function $f(\mathbf{p})$:

$$\mathbf{V}_c = V_s \langle \mathbf{p} \rangle = V_s \iint \mathbf{p} f(\mathbf{p}) d^2\mathbf{p}. \quad (8)$$

We thus see how the orientational probability density function comes into the cell conservation equation. (In their pioneering continuum model Childress *et al*² took \mathbf{V}_c to be vertically upwards at all times.) The diffusivity tensor \mathbf{D} can also be represented as an integral in \mathbf{p} – space, and in fact is proportional to the variance of the \mathbf{p} – distribution, $\langle (\mathbf{p} - \langle \mathbf{p} \rangle)(\mathbf{p} - \langle \mathbf{p} \rangle) \rangle$.¹² The development presented here assumes that λ has a fixed value, i.e. that the population consists of cells which are identical in shape and behaviour. Actually λ values are also distributed statistically. A complete, practically applicable theory will have to include a further averaging of the results, over the λ distribution.

If the flow field \mathbf{u} is known, as for example in the experiments using steady, downwardly directed pipe flow, equation (7) can be used to calculate the cell concentration everywhere. Doing this for pipe flow yields a steady concentration distribution with a maximum on the pipe axis, and exponential drop-off with distance away from the axis, which is qualitatively much closer to the observed focussed plume of cells than the distribution computed from deterministic trajectories.

If the flow field is not known in advance, as for example in bioconvection experiments, it has to be found by the solution of further equations. These are the standard equations of fluid dynamics, the equation of conservation of mass ($\nabla \cdot \mathbf{u} = 0$ for an incompressible fluid) and the Navier-Stokes equation representing momentum conservation.* The cells drive the flow through the gravitational body force, or negative buoyancy force, $-nv\Delta\rho g\mathbf{k}$ per unit volume, where $\Delta\rho$ is the density difference between the cells and the surrounding fluid. Dynamic pressure gradients are generated by the flow, or can be set up by the experimenter so as to drive it (as in a pipe). The motion is resisted by viscous stresses. In a simple, Newtonian fluid these are proportional to the strain-rate tensor ($\Sigma = 2\mu \mathbf{E}$), but in a suspension there are additional contributions in general.¹ In our case the most important additional contribution comes from the swimming motion of the cells themselves: although the total force on a cell is zero, the combination of the thrust

* In vector form the Navier-Stokes equation for a fluid of density ρ is

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} \right) = -\nabla p_e - nv\Delta\rho g\mathbf{k} + \nabla \cdot \Sigma \quad (9)$$

where, on the right hand side, the three terms are the effective pressure gradient, the gravitational body force, and the divergence of the viscous part of the stress tensor, respectively.

produced by the flagella and the drag on the body is equivalent to a force-dipole or ‘stresslet’, and the aggregate of many stresslets influences the bulk stress. Fortunately, perhaps, it appears that when the suspension is dilute enough for the other assumptions of the model to be valid, all the additional contributions to the stress are relatively small and the Newtonian approximation is reasonable.

Instability analysis

The full continuum model just outlined can in principle be used to analyse any bioconvective flow of a suspension of gyrotactic micro-organisms. Hitherto, however, it has been used only for analysing the instability of a uniform suspension, unstable because of gyrotaxis as discussed above.¹¹ Stability analyses are based on the assumption that the values of all variables are close to those that obtain in the undisturbed basic state, and that the small departures from the basic state are scaled by some suitable small parameter. The quantity ϵ defined by equation (6) is a suitable small parameter here, since the basic state is taken as one with no fluid motion, and hence zero vorticity. The vorticity ω , which appears in ϵ , is a small perturbation away from the basic state. All perturbations, including the fluid velocity, are therefore proportional to ϵ : the cell concentration n differs from its undisturbed value n_0 by an amount proportional to ϵ , and the orientation distribution function $f(\mathbf{p})$ differs from the Fisher distribution of equation (5) by a similar amount. The linearised equations that result when all terms involving ϵ^2 or higher powers are eliminated can be further simplified by Fourier analysis. It is assumed that the variables have sinusoidal variation with space coordinates and exponential dependence on time, so, for example, we might have

$$n - n_0 = \epsilon n_1 \cos kx \cos mz e^{\sigma t}, \quad (10)$$

where n_1 is a constant, k and m are the horizontal and vertical wave numbers, and σ is the temporal growth rate. Solution of the problem results in an algebraic expression from which σ can be calculated for any k and m . If a disturbance, i.e. a set of particular values of k and m , can be found for which σ (or its real part if it is complex) is positive, then that disturbance would grow. Assuming that infinitesimal amounts of all possible disturbances are present initially, it follows that the basic state is unstable. If no growing disturbance can be found, the basic state is stable.

In the present example, it turns out that for any value of k the corresponding real part of σ is largest when $m = 0$, so vertically uniform disturbances will grow more rapidly than others and will therefore be more likely to be observed. Furthermore, if k exceeds a critical value, k_c , the real part of σ is negative, which means that sufficiently short wavelength disturbances die out (because viscous action damps out motions with too rapid a spatial variation). Finally, there is a value of k , k_m , between 0 and k_c , for which the real part of σ is greatest: this

corresponds to the most rapidly growing disturbance which will in principle dominate and be observed in an experiment.

From the best available data for all the parameters of the model, the value of k_m for a uniform suspension of *C. nivalis* was calculated to be 0.7 mm^{-1} , corresponding to a pattern wavelength ($2\pi/k_m$) of 9.0 mm.¹¹ This spacing is considerably greater than the approximately 2 mm observed between bottom-standing plumes (the ultimate bioconvection pattern in a deep chamber). The patterns of plumes and sheets seen early in the experiment, when linear theory is most likely to be relevant, are more widely spaced, in deep or in shallow chambers (Figs 1 and 3). However, because the early observations may be strongly influenced by the remnants of the stirring used to make the suspension initially uniform (Fig. 1), and because by the time it is observable a disturbance is unlikely to be small enough for linear theory to be accurate, no reliance should be placed on agreement or otherwise between that theory and the observations. An approximate theory⁷ of adjacent tall plumes does yield the appropriate final steady state plume spacing. However, a quantitative comparison of theory and experiment must await a more rigorous non-linear analysis of steady state bioconvection patterns and their evolution.

Future developments

We hope it has become clear that the fluid dynamical study of bioconvection is a fascinating enterprise which has as yet barely been started. There are many things still to be done for suspensions of gyrotactic algae, using the continuum model outlined above: linear stability analysis of a shallow layer; nonlinear analysis of bioconvection, using both large numerical computations and sophisticated modern non-linear theory (used to investigate pattern-selection in other convection problems); modification of equation (1) to incorporate the effect of the moving flagella themselves on the viscous torque; investigation of (a) hydrodynamic and (b) biological or chemical interactions between cells, likely to be important in regions of high cell concentration (such as falling plumes); investigation of non-quasi-steady orientation distribution functions. Then there is the whole question of how to incorporate a second, independent orienting influence such as phototaxis into the quantitative model. It is known that many algal species swim towards the light if it is weak, but they shun it if it is too strong; this behaviour combines with bioconvection to modify the pattern geometry. There is also the analysis of bioconvection in chemotactic bacteria (Fig. 2), complicated by fluid transport of oxygen, which the cells consume and up gradients of which they swim.¹²

All these developments will be fun to do and comparison between theory and experiment will not only test the theory but will yield quantitative data on parameters intrinsic to the cells' behaviour which would be extremely difficult to measure otherwise. Examples from the gyrotactic algae include the centre of mass offset, h , and the rotational

diffusivity D_r . But can we use our understanding of these bioconvective systems to discover anything of deeper scientific significance? Any such possibilities are likely to be rather speculative, but speculation is essential to the development of new science. For example, one exciting prospect is the development of a new statistical mechanics of active particles, automata that drive their collective motions without the constraints of energy conservation (at least over short time scales). Biotechnological exploitation of gyrotactic focussing has also already been proposed.⁶ We expect too that the insight reported here will guide fundamental biological research concerning when and how active sensing of environmental stimuli combines with physical orienting mechanisms to yield complex behaviour in the real world.

Are bioconvection patterns widespread in nature and, if so, what is their significance? There are virtually no formal, as opposed to anecdotal, reports of bioconvection in natural settings (one exception occurs in dinoflagellate blooms in the sea of Galilee).⁶ However, we have seen that the phenomenon arises in concentrated populations of upswimming micro-organisms, as a direct consequence of fluid dynamics and good growth conditions. Since almost all algae swim upwards, green or brown plumes and bioconvection patterns, covering substantial areas, ought to occur commonly. The fact that they are not generally observed presumably reflects the difficulty in observing them: high cell concentrations, good optical contrast and relatively still water are required. One of us (JOK) has, on numerous occasions, found green puddles whose contents, when scooped into containers, exhibit easily visible bioconvection.

Some likely natural consequences of bioconvection in algal suspensions are (i) a greatly increased rate of descent of cells in concentrated plumes; (ii) the control of light intensity by self-shading; (iii) the modification of chemotactic swarms which accompany sexual reproduction; and (iv) the formation and exploitation of focussed regions of cells by planktivores.¹⁰ In bacterial suspensions we have seen that bioconvection causes the oxygen on which the cells depend to be mixed more deeply into the bulk of the suspension than could be achieved by pure diffusion, thereby keeping more of the cells oxygenated and active. Collective patterns thus provide a mechanism for the ventilation of a multi-celled community.

Bioconvective plumes or patterns modify the local ecosystems which support a given population of micro-organisms. The self-organization produces new sub-environments, in effect niches, of light and shade, oxygenated and depleted fluid. A corresponding diversity of physiological states among the occupants might then be expected to arise. We hope that this article will create awareness of such possibilities, and provoke new directions of investigation, in nature and in the laboratory.

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