Various Findings related to Bioconvection Phenomenon - a detailed Study

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1. Bioconvective phenomenon

The phenomenon of bioconvection patterns in suspensions of swimming cells have been observed several decades ago. Ever since common algae, such as Chlamydomonas nivalis, Euglena viridis, Crypthecodinium cohnii and the ciliated protozoan Tetrahymena pyriformis were isolated, plumes of aggregating cells have been noticed in the culturing flasks. Platt (1961) coined the term ''bioconvection'' to describe the phenomenon of pattern formation in shallow suspensions of motile micro-organisms at constant temperature, on par with those found in convection experiments. However, this is by no means the first documented observation, which goes back to at least 1848 e.g., Wager (1911). Other experimental investigators include Loeffer and Mefferd (1952) Nultsch and Hoff (1972) Plesset and Winet (1974) and, more recently, Kessler,(1984, 1985b) Bees(1996) and Bees and Hill.(1998). Bioconvection is generally due to an overturning instability caused by micro-organisms swimming towards the upper surface of a fluid which has a lower density than the micro-organisms. The first models of bioconvection were developed by Plesset and Winet (1974). They considered a Rayleigh-Taylor instability in a continuously stratified, two-layer model and were able to investigate the preferred pattern wavelength as a function of the upper layer depth and the cell concentration. Levandowsky *et al.*(1975) investigated bioconvection patterns and proposed a more realistic model. In the case of Childress *et al.*(1975) the micro-organisms could swim but, were constrained to swim upwards only, due to their asymmetric density distribution.

Bioconvection is the name given to pattern formation in suspensions of micro organisms, such as bacteria and algae, due to up-swimming of the micro-organisms and is relatively new area of fluid mechanics (Pedley & Kessler 1992). In all cases the micro-organisms are denser than water and on average they swim upwards (although the reasons for up-swimming may be different for different species). The algae (e.g. Chlamydomonas) are approximately 5% denser than water

(Ghorai and Hill (1999)), whereas the bacteria are nearly 10% denser than water. Micro organisms respond to certain stimuli by tending to swim in particular directions. These responses are called taxes; examples being gravitaxis, phototaxis, chemotaxis and gyrotaxis. Gravitaxis indicates swimming in the opposite sense to gravity, phototaxis denotes swimming towards or away from light, and chemotaxis corresponds to swimming up chemical gradients. Gyrotaxis is swimming directed by the balance between the torque due to gravity acting on a bottom-heavy cell and the torque due to viscous forces arising from local shear flows. Depending on the particular species, the direction of swimming of motile microorganisms may be dictated by different stimuli, such as gravity (gravitaxis), light (phototaxis), or chemical gradients (chemotaxis) as discussed earlier. This thesis considers micro organisms exhibiting gyrotactic behaviour, which is typical for many species of algae. Gyrotactic micro organisms swim generally upward. The exact direction of swimming of these microorganisms is determined by the balance of two torques. The first is the viscous torque that acts on a body placed in a shear flow. The second torque is generated by the gravity because the center of mass of a typical micro organisms is displaced from its center of buoyancy. According to Pedley et.al [1988], the effect of gyrotaxes on bottom heavy microorganisms is to cause their motion toward the regions of down flow and away from the regions of up flow. Algae are typically 5% denser than water, therefore the regions of down flow become denser than the regions of up flow. Buoyancy then increases the upward velocity in the regions of up flow and downward velocity in the regions of down flow, thus enhancing the velocity fluctuations.

Hydrodynamic flows orient and convect. Bioconvection is therefore an exciting, complex, yet experimentally tractable, approach for studying the mutual interdependence of physics and biology, where the overall phenomenology greatly exceeds its primitive components (Kessler, 1989; Kessler and Hill, 1997). The distinguishability of microbial species by their bioconvection patterns is a very significant result that lends motivation to the experiments and to the analysis described here. Classes of bioconvective systems can be distinguished on the basis of the mechanism of directional motion, or taxis, of the cells. (i) Some micro-organisms swim upwards because they are bottom-heavy (geotaxis or gravitaxis). (ii) The oxygen concentration gradient, generated by the oxygen consumption of the cells and by supply from the air interface, can induce upward swimming towards regions of higher oxygen concentration (aerotaxis, oxygen taxis or, in general, chemotaxis). During fully developed bioconvection, oxygen charged water is convected downwards from the air/water interface, so the bacteria swim towards a complex, convection dependent (usually not vertical), gradient. (iii) In phototaxis, organisms swim towards or away from a source of light. Self shading of concentrated organism populations is a type of consumption (of photons), and is analogous to the consumption of oxygen molecules in aero taxis. Childress et al. (1975) proposed the first extensive theory for bioconvection of gravitactic swimmers. Their equations included both directional and stochastic aspects of the swimming velocity, but did not take into account the effect of local vorticity on swimming direction. A continuum theory for bioconvection of suspensions of aerotactic bacteria that swim upwards in molecular gradients created by consumption must include three sets of coupled equations: (i) the continuity and Navier–Stokes equations, driven by variations in the concentration of the micro-organisms that correspond to locally averaged variations in the 'external' driving force density, (ii) the equation for conservation of organisms, including directional and stochastic aspects of swimming together with advection by the motion of the water in which they are suspended, and (iii) the equation for conservation of the molecules that the organisms consume, including the rate of consumption by the cells, due to diffusive supply and advection. This set of coupled nonlinear equations and the methods for modeling the part of the organism flux that is due to swimming have been discussed by Kessler and Wojciechowsi (1997) and Kessler et al. (2000). A full solution of these equations has not been attempted.

Many swimming micro-organisms are bottom-heavy and so, although their swimming directions are fairly random, they naturally tend to swim upwards (negative gravitaxis or geotaxis). Such creatures tend to aggregate at the upper boundaries of the fluid and, in sufficiently shallow layers and at low concentrations, may form a horizontally uniform, top heavy equilibrium distribution in which the flux of cells due to upswimming is balanced by diffusion down cell concentration gradients, due to a degree of randomness in their swimming behavior. If the micro-organisms have a higher density than the ambient fluid, then aggregations of the cells at the upper surface can initiate an overturning instability, reminiscent of thermal or Rayleigh–Bénard convection, and thus produce spatial concentration patterns. The bulk motion of the fluid exerts viscous (or frictional) torques on the micro-organisms and the resulting balance with the gravitational torque is called gyrotaxis (Kessler, 1984*b*, 1985*a*,*b*). The micro-organisms' geometry and mass distribution imply that a component of their swimming velocity is towards regions of down welling fluid and away from upwelling fluid. In this way, the microorganisms increase the average density of down welling regions of fluid and cause them to sink faster. This second ‘gyrotactic’ instability mechanism, together with the overturning instability, drives complex patterns in suspensions of the micro-organisms which are termed bioconvection. When viewed from above, the patterns are characterized by highly concentrated aggregations of cells in both one- and two dimensional structures.

Populations of algae or bacteria swimming in a quiescent body of water often generate the collective phenomenon called ‘‘bioconvection’’ [Platt (1961), Bees and Hill (1997)]. In fully developed bioconvection, the mean local concentration and sometimes the swimming direction [Kessler1985] of the organisms is coupled with the local fluid velocity of the convection cells. As in thermally driven convection, the continuous motion of the fluid is due to the non-uniformity of its mean density. In thermal convection this non-uniformity is supplied by heat flux through the boundaries. In bioconvection, which is isothermal, the non-uniformity of the density is generated and maintained by the directional swimming of the ‘‘heavy’’ organisms suspended in the fluid. They are advected with the fluid and also swim relative to it.

Populations of swimming, swarming, or gliding bacteria are capable of spontaneous self-organization into states that exhibit cooperative behavior. In systems such as the multicellular forms of myxobacteria and the complex colonial patterns produced by motile strains of Escherichia coli and Salmonella, cellular aggregation arises in response to signaling by certain cells that excrete attractants (Budrene and Berg(1991),Kessler(1989),Shapiro (1997)). Responding cells accumulate and together display features that distinguish them from their individual cell progenitors. Another form of cellular organization has been found in fluid cultures of swimming *Bacillus subtilis* strains. This form also results in the accumulation of cells in spatially restricted regions by bringing together individual cells initially distributed throughout a larger region. The spatial and temporal order of cells in this case, however, appears not to require cell-cell signaling. Instead, external constraints set into play by the swimming of cells upwards and the force of gravity acting on the accumulated cell mass beneath the fluid surface give rise to a bioconvection process that is responsible for organizing the cells into discrete regions of high density (Childress et al.(1975),Hill et al.(1989), Kessler and Wojciechowsi (1997), Pedley et al.(1988-1961),Wager(1911)).

Bioconvection is the term used to describe the phenomenon of spontaneous pattern formation in suspension of microorganisms such as bacteria and algae (Pedley and Kessler [1992], Kessler [1985,1985].the microorganisms are always denser than water and, on average, they swim upwards. The algae are approximately 5% denser than water, whereas the bacteria are nearly 10% denser than water (Ghorai and Hill [1999]). Upswimming is usually a response to an external force field such as gravity or biochemical stimulus such as the gradient of oxygen concentration .The response to gravity is called "gravitaxis" The center of mass of a typical upswimming organism is displaced from the center of buoyancy in a direction opposite to the swimming direction, which means that the cell is bottom-heavy. Gravitaxis causes bottom heavy cells to be concentrated in the layers near the top of the enclosure. The top fluid layer thus becomes denser than the fluid beneath it. This is the reason for the spontaneous growth of concentration fluctuation, which can presumably develop into observable convection patterns, even in the absence of a mean vertical concentration gradient.

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– B´enard 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 μm in diameter. They have two flagella about 15 μm 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.

Bioconvection is a collective behavior of microorganisms. It refers to the spatial patterns that develop in suspensions of swimming microorganisms, including bacteria, ciliate and flagellate protozoa and the planktonic larvae of some invertebrates (Platt, 1961; Levandowsky et al., 1975; Kessler, 1989; Pedley and Kessler, 1992). When viewed from above, the patterns are characterized by the highly concentrated aggregation of microorganisms into two-dimensional structures with a scale much greater than the size of the microorganisms. This phenomenon is related to the swimming behavior of microorganisms, with special reference to gravity. Many aquatic microorganisms swim preferentially upwards: negative gravitaxis. Due to the orientation torque generated on the basis of mechanical (Mogami et al., 2001) as well as physiological mechanisms (Mogami et al., 1988b; Machemer et al., 1991; Ooya et al., 1992), microorganisms tend to propel themselves upwards, irrespective of their mass density being greater than that of water. The suspension of such organisms does not remain homogeneous but forms a layer of organisms accumulated at the top of the water column. This stratification, however, can be unstable when the potential energy released by the downward movement of a lump of the accumulated organisms is sufficient to overcome the associated viscous dissipation. As noted by Plesset and Winet (1974), such instability is therefore the viscous counterpart to the Rayleigh–Taylor instability of a stratified fluid.

Many living microorganisms (many species of bacteria and algae) can propel themselves by rotating flagella which are driven by reversible molecular motors that are embedded in the cell wall. Because these microorganisms are generally heavier than water, the fluid regions with higher – number density of the motile cells become heavier than fluid regions with smaller number density of the cells. Since the cells tend to swim in a particular direction in response to certain stimuli such as gravity (gravitaxis), light (phototaxis), or chemical gradients (chemotaxis), they concentrate in certain regions of the fluid domain. This causes density gradients in the fluid which may result in the development of convection instability. This instability leads to a spontaneous pattern formation in suspensions of motile microorganisms, which is called bioconvection (Pedley and Kessler [1992]). In the case of upswimming microorganisms, the mechanism of development of bioconvection is somewhat similar to the mechanism of the Rayleigh-$Be'nard$ convection instability, yet the development of bioconvection does not require the vertical temperature gradient (Bees and Hill [1997], Kessler et.al.[2000], Harashima et.al.[1998].)

There are two typical types of up swimming micro-organisms that are usually used in bioconvection experiments: bottom-heavy alga and certain oxytactic bacteria. Although the bioconvection patterns formed by them are very similar, the mechanisms of orientation are different (Hill and Pedley, 2005). Bottom-heavy micro-organisms swim upward in still water because of the asymmetric mass distribution. When such micro-organisms are in a flow field, the swimming direction is determined by the balance between the toques due to viscous drag arising from shear flow and gravity acting on the cell (Pedley *et al*., 1988). Cells tend to swim towards regions of down -welling fluid, which is known as gyrotaxis as discussed earlier.

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