Biomechanics of Aquatic Micro-Organisms

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1 Introduction

Aquatic micro-organisms, many of which are active swimmers, play a vital role in life on earth. Phytoplankton (algae, diatoms, etc: length scale 10-100μm, are the bottom link of the food chain in oceans and lakes, absorbing energy from sunlight and elementary nutrients from the water. They contain and are surrounded by even smaller bacteria (2-10μm) which break down metabolites and detritus into those elementary nutrients and no doubt have many other effects which have not been described. The phytoplankton are themselves the prey for somewhat larger micro-organisms (zooplankton such as ciliates and heterotrophic flagellates)which in turn are eaten by larger zooplankton such as copepods (small crustacea) which are eaten by fish larvae and adult fish, and so on. The phytoplankton absorb CO_2 from the water, most of which comes from the atmosphere via complex mixing processes, and thus they play an important role in the global carbon cycle and hence in phenomena such as global warming. Every spring, in every ocean, there are massive phytoplankton blooms (population explosions) which underlie the ecology of all aquatic species and need to be understood for fisheries prediction, for example. Harmful algal blooms also occur in coastal waters ('red tides') and can lead to economic damage to coastal communities that rely on shellfish. Some micro-organisms are used by biotechnologists to make chemicals, or are used as a direct source of biomass in large bioreactors. Thus the study of micro-organism behaviour is a proper subject for scientific investigation.

The complex food web of an oceanic ecosystem does not lend itself readily to comprehensive computational simulation; the number of species is far too large, as is the number of ways in which they can interact. In order to get a feel for the sort of effects that can arise in such a web, idealised models have been proposed. One such is outlined in figure 1 [1]. Organisms are arranged in two rows of three categories each. Members of the lower row consume nutrients and are themselves consumed by members of the top row which are also linked by predator-prey interactions. A model of the interactions consists of a set of nonlinear ordinary differential equations. For example, the population density of ciliates (C) is governed by an equation of the form:

$$\frac{dc}{dt} = Y_c(g_{CA} + g_{CH})C - g_{ZC}Z \quad , \qquad (1)$$

where Y_C is the ciliate yield and the g's are functions in which g_{PQ} means the rate at which species P grazes on species Q (the symbols A,H,Z are defined in figure 1). Examples of the sort of functions involved are:

$$\begin{aligned} g_{CA} &= \frac{\lambda_c A^2}{\mu_c(A+H) + A^2 + H^2} \\ g_{BN} &= \frac{\lambda_B N}{\mu_B + N} \end{aligned} \qquad (2)$$

where the λs and μs are constants.

These are standard models, but it is worth asking where the functional forms and constants come from. In other words, how should the macroscopic, population-level model be derived from individual behaviour, which itself can be investigated in detail? This article will outline briefly some of the fluid mechanical aspects which have been or are being investigated to shed light on both the individual and the collective behaviour of swimming micro-organisms. There will be a natural but perhaps undesirable emphasis on work in which the writer has been involved; readers should take these as examples of the sort of research that may be of interest rather than an exclusive definition of the field.

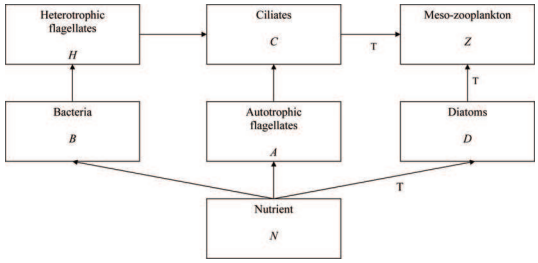

Figure 1: A "minimum model" for plankton population dynamics. Arrows between boxes represent predator-prey interactions; the letter T by an arrow means that turbulence may have an influence [1, 2].

2 Individual behaviour

The question of how micro-organisms swim has attracted fluid dynamicists for over 50 years, the pioneers being G.I. Taylor [3] and James Lighthill [4]. The Reynolds numbers of the cells in question, and of their moving appendages, are very small so inertia is negligible. It follows that the appendages cannot execute purely reversible motions if the cells are to make progress. Biflagellate algae such as *Chlamydomonas spp* execute a sort of low-Reynolds-number breaststroke; monoflagellates and sperm send unidirectional waves along their flagella; bacteria generate thrust from a bundle of *rotating*, fairly rigid flagella; ciliates beat large numbers of cilia in the form of co-ordinated waves. The hydrodynamics of such propulsive devices was first investigated using the rather crude (but extremely useful) *resistive force theory* [5,6], according

to which the normal and tangential components of the force exerted on the fluid by one short segment of a beating flagellum are directly proportional to the normal and tangential components of the velocity of that segment relative to the fluid far away, but with different, constant, coefficients of proportionality K_N and K_T(K_N is nearly twice as large as K_T for a segment of a circular cylinder). The next level of sophistication is to use slender body theory [4,7,8,9], and these days it is feasible to do complete simulations using the boundary element method [10].

If an organism is neutrally buoyant then the net force acting on the whole organism is zero, an important constraint in the theory. If it is homogeneous, then the net torque on the organism must also be zero. However, most micro-organisms are denser than water and tend to sediment, though at a speed that is much smaller than their swimming speed. For example, dead *Chlamydomanas nivalis* sediment at about 3μm s^{-1} while live ones swim at over 50μm s^{-1}. In addition, *C. nivalis* naturally tend to swim upwards, on average, against gravity (though individual trajectories are very erratic). This is probably not because they have a sophisticated molecular "gravi sensor": there are at least two passive mechanical mechanisms that can cause them to do so.

The first and most popular is that they are bottom-heavy, so a deviation from the vertical generates a gravitational torque that rotates them back towards the vertical again (albeit slowly, against the viscous torque set up by such rotation) [11, 12]. An alternative proposed mechanism, that has the same effect, is based on a cell's asymmetric shape rather than its asymmetric mass distribution: as *C. nivalis*, for example, sediments slowly relative to the fluid, the drag on its (beating)flagella will exert a torque to rotate them towards the upwards vertical, thus causing the cell to swim upwards in still water without being bottom-heavy [13]. Sperm, with the flagellum behind, would presumably tend to swim downwards. A consequence of either of these upswimming mechanisms is that the swimming direction, relative to the fluid, will change when the cell is put into a shear flow which exerts a viscous torque on the cell. For example, in a vertically downwards shear flow, cells will tend to swim towards the zone of largest downwards velocity. Having predicted the effect, Kessler observed it in a downwards pipe flow, in which cells were focused in a thin green line on the axis [11].

As stated above, bacteria generate thrust and thereby swim in a roughly straight line, by rotating a sort of corkscrew behind them. This corkscrew is formed from a number of individual flagella each of which rotates in its socket in the cell membrane. They come together when the rotation is counter clockwise. From time to time (stochastically) the flagellar motors turn clockwise. Then the flagella can no longer fit together; they fly apart, and the cell tumbles, setting off on a run in a new direction [14]. The details of this process have been thoroughly investigated only for *Escherichia coli* (a gut bacterium) but it is presumed that other bacteria behave similarly. How the rotating flagella come together in a bundle when rotating counter clockwise is itself a fluid mechanical problem. Recent studies suggest that bundling could occur passively if the flagella were slightly flexible [15,16], but there is more detailed work to be done.

It is known that bacteria exhibit chemotaxis - a tendency to swim up gradients of chemoattractant (food). However, they are too small to be able to measure concentration gradients directly [17], so how do they know to swim up the gradient? The mechanism (in *E. coli at least*) requires (a) that they can measure concentration (i.e. "knowing" how many chemoreceptors on their surface are occupied), (b) they they can remember it for a short time, so that they can tell whether the concentration is rising or falling with time, and (c) they can, in consequence, alter the probability of tumbling according to the answer to (b). In fact this is what they do: the tumbling rate falls when they are swimming up a gradient, and rises when they are swimming down it [18]. How the chemotaxis process is affected when the bacteria are in a shear flow, which will rotate them, has not been investigated experimentally, but has been analysed theoretically [19,20]. It is predicted that there are circumstances in which they swim the wrong way!

The functions of equation (2) require that we know the rate at which organisms take up nutrient from the water (an equivalent problem concerns the output of unwanted metabolites, or mate-attracting pheromones). Even for individual cells, this problem exhibits interesting features which have not all been resolved. If the organism is small enough then adequate nutrient uptake can be achieved, in still water, by pure diffusion. However, larger organisms need to enhance this rate, and can do so by moving through or stirring the fluid around them [21].

A precise analysis of how low-Reynolds-number stirring motions can enhance nutrient uptake has been undertaken for a very simple model of a microorganism: a spherical 'squirmer', which propels itself through th fluid by driving a tangential motion along its surface [22,23]. This model was chosen for its simplicity, not because it was meant to represent a real organism (though it is not too bad a representation of the envelope of cilia tips in certain ciliates, or algal colonies like *Volvox*, or cyanobacteria such as the *Oscillatoriaceae*. The velocity field of a 'steady squirmer' is represented by a two-term series of solutions to the Stokes equations, in which the surface velocity on $r = a$ is given by:

$$\begin{aligned} U_r &= 0, U_\theta = \sum_{n=1}^{2} B_n V_n(\theta); V_n(\theta) \\ &= \frac{2}{n(n+1)} sin\theta P_n'(cos\theta) \end{aligned} \tag{3}$$

where (r, θ) are spherical polar co-ordinates, a is the sphere's radius, and the P_n are Legendre polynomials. In this two-term series, B_1 is proportional to the speed at which the squirmer swims, U, and B_2 is proportional to the force-dipole, or stresslet, that it exerts on the fluid.

In [22] the advection-diffusion equation for solute concentration C, in the velocity field of the squirmer, was solved numerically subject to the boundary conditions $C \to 1$ as $r \to \infty$, $C = 0$ on $r = a$. After non-dimensionalisation the results could be expressed as plot of the Sherwood number Sh as a function of the Péclet number Pe for different values of the 'squirming parameter', $\beta = B_2/B_1$. Here Sh is the ratio of the actual nutrient uptake to the value it would have through pure diffusion in a still fluid ($4\pi aD$), where D is the solute diffusivity); $Pe = Ua/D$ is the ratio of advection to diffusion. Asymptotic solutions can be found for small and for large Pe. The results are compared with those for a rigid sphere driven through the water at the same speed, U, by an external force. The results confirm that squirming has negligible ef-

fect on the mass transport unless $Pe > 0.2$, but as Pe rises the effect of squirming becomes more and more important, as the concentration boundary layer on the body surface becomes thinner. Indeed, for large Pe it is shown that $Sh \propto Pe^{1/2}$, not $Pe^{1/3}$ as for a rigid sphere.

One question that needs to be addressed is whether a constant C boundary condition is appropriate on the surface of a micro-organism? There may be some parts of an organism's surface across which uptake is much faster than others so the surface concentration is non-uniform. Alternatively, it might be more appropriate to consider the organelles within the cell as sinks of solute, consuming it at a rate proportional to its concentration. Then, at high Péclet number, when the resistance to mass transport in the fluid is low, the rate-limiting step would be the rate at which the cell could metabolise the solute. It was shown in [22] that in that case the Sherwood number at high Péclet number does not increase indefinitely but tends to a constant (albeit much greater than 1).

The value of Pe for an algal cell of radius $10\mu m$, swimming at $50\mu m s^{-1}$, with a small solute of diffusivity $10^{-9} m^2 s^{-1}$, is only 0.5, so the effect of swimming or stirring is small. However, spherical colonies of *Volvox* can be as big as $150\mu m$ in radius, and generate fluid motions of $100\mu m s^{-1}$, so for them the Péclet number is quite large and the fluid flow driven by their flagella is very important for nutrient uptake[24].

Another aspect of nutrient uptake by small organisms is that of predator-prey dynamics. At what rate do microzooplankton encounter and consume their phytoplankton prey? And how is this affected by turbulence in the ambient fluid? The first coherent models of these processes, in two papers that are already classics, were by Gerritsen & Strickler and by Rothschild & Osborn [25,26]. The model was based on a consideration of the volume of fluid swept out by a swimming predator. If it swims in a straight line at constant speed in still fluid, and if the prey do not swim, then it will encounter all prey within a cylinder of radius R around its trajectory, where R is the "contact radius", the furthest distance at which it perceives its prey. Thus the encounter rate (number of contacts per unit time) is $\pi R^2 V_p N_H$, where V_p is the predator's swimming speed and N_H is the number density of prey. This simple swept-volume model can be modified to account for randomly oriented prey swimming and for turbulence; Rothschild & Osborn obtained the following formula for the contact rate;

$$CR = \pi R^2 N_H (V_p^2 + V_H^2 + 2W^2(r))^{1/2}, \qquad (4)$$

where V_p, V_H are the *average* predator and prey swimming speeds and $W(r)$ is a scale for the difference in turbulent fluid velocities at two points separated by a distance r. It was not clear whether r should be chosen equal to R or not.

There were some over-simplifications in the Rothschild and Osborn model, so Lewis & Pedley [27] set out to modify it and, more importantly, to test the modified model against a numerical simulation. The simulation consisted in placing a number of predator and prey individuals randomly in a periodic box and allowing them to swim with random speeds and orientations (according to specified probability distributions), recording an encounter when they came within a distance R of each other. The fluid was also moving randomly, with a turbulent-like incompressible velocity field specified by a Fourier series, whose terms had randomly selected wave number, frequency and amplitude such that the energy spectrum was the same as for isotropic, homogeneous turbulence. Two-point correlations were not controlled so this velocity field was different from real turbulence. However, that would have required enormous computer resources, for reasonable Reynolds numbers, as can be seen from the corresponding work of Yamazaki [28]. The main result, in the event, was that the modified swept-volume model (with $V = R$ in equation (4)) agreed rather well with the full simulations in predicting encounter rates; the value of the model is that it is analytical and can be used to specify the functional forms required in equation (1).

However, encounter is not the whole story. To predict prey capture it is necessary to specify the probability of capture, given that encounter has occurred. A simple model for this [29] led to the interesting, if not surprising, result that if turbulence is weak or the time taken for capture is small, then it pays the predator to swim in order to catch prey. However, if turbulence is strong or capture efficiency low, there is a tendency for the prey to be swept away before it can be captured, so it does not pay to swim; it is better to stay still (relative to the fluid) and wait for prey to come to you. Examples of both 'cruise' and 'ambush' predators are recorded in the literature.

3 Collective behaviour

We turn now to the fluid dynamic behaviour of populations of swimming micro-organisms, in particular the phenomena of *bioconvection*. Bioconvection patterns are observed in shallow suspensions of randomly, but on average upwardly, swimming microorganisms which are a little denser than water. Images of typical bioconvection patterns formed by suspensions as single-celled algae and bacteria can be found in [12]. 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: some algae are bottom-heavy, (see above) while certain oxytactic bacteria, such as *Bacillus subtilis*, swim on average up oxygen gradients that they generate by their consumption of oxygen.

The rational continuum modelling of bioconvection is dilute suspensions (volume fraction of cells $<$ 0.001) has been fully described in many original papers and, in particular, in two review articles [30,31]. Here we concentrate on aspects of the phenomena or the modelling that are not completely understood.

In a continuum model it is assumed that every volume element, small compared with the scale of the bulk flow, contains very many cells, so that variables such as the cell number density n or the bulk velocity $\mathbf{u}$ can be represented by their averages over the volume element. They can thus be taken to be smooth functions of position and time t.

Averaging has to be done with care, because the cells swim randomly - i.e. each cell undergoes a (biased) random walk, and each random walk is independent of the trajectories of other cells. Data on the trajectories of *C. nivalis* in still fluid are shown in figure 2, from the authors of [32], where the vector from the origin to a cross represents the vertical projection of a 1.1 second segment of a trajectory. The bias to upswimming is clear.

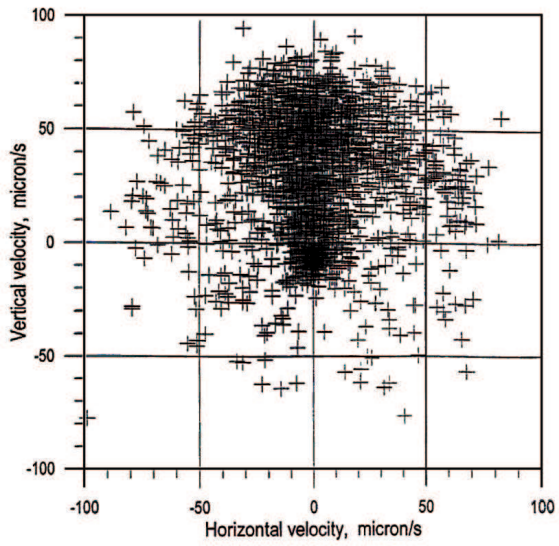

Figure 2: Projections of the velocity vectors of 1.1 sec segments of trajectories of C. nivalis, represented by the vector from the origin to the centre of each cross (see [32]).

Perhaps the most important equation in the continuum model is the cell conservation equation:

$$\frac{\partial_n}{\partial t} = -\nabla \cdot [n(\mathbf{u} + \mathbf{V}_c) - \mathbf{D} \cdot \nabla n], \qquad (5)$$

where $\mathbf{V}_c$ is the average cell swimming speed, representing directed cell swimming, and the last term represents the flux due to random cell swimming, here modelled as a diffusive process. Both $\mathbf{V}_c$ and $\mathbf{D}$ can be calculated if we know the probability distribution for cell swimming velocity, incorporating both magnitude and direction. The data in figure 2 provide information on this distribution, in one case. However, assuming that the cell swimming *speed* was constant, that the random reorientation experienced by a cell was independent of its current orientation and that the time-scale for such reorientation was small compared with any other time-scale of interest, Pedley & Kessler [33] proposed that the p.d.f. f(**p**)for swimming direction **p** (a unit vector) should satisfy a quasi steady Fokker-Planck equation. The solution of that equation for bottom-heavy algae in a still fluid is

$$f(\mathbf{p}) = \mu e^{\lambda \mathbf{k} \cdot \mathbf{p}} \qquad (6)$$

where the unit vector $\boldsymbol{k}$ is vertically upwards, and λ, μ are constants, which is reasonably consistent with figure 2.

When the fluid is moving, the Fokker-Planck equation can still be used to find f **(p)** if it is possible to write down an equation for ($\dot{\mathbf{p}}$), the rate of change of , in the absence of the random reorientations. This is straight-forward for the bottom heavy algae, because $\dot{\mathbf{p}}$ is determined by the balance between gravitational and viscous torques and the latter can be evaluated for any ambient shear flow. However, we do not have an equation for $\dot{\mathbf{p}}$ in the case of chemotactic bacteria, because the chemotaxis process cannot be expressed in terms of a torque balance. In addition, there is no general guarantee that random swimming can be represented as a diffusion process.

In the standard model of chemotaxis in a still fluid, first proposed by Keller and Segel [35], the cell swimming term in (5) is given by $V_c = \chi \nabla C$, where C is the chemoattractant distribution (for which, in general, another conservation equation is required) and χ is a scalar chemotaxis parameter. The main objective of the thesis work of Bearon [19,35] was to see under what circumstances equation (5) can still be used for run-and-tumble, chemotaxis in a shear flow, with some rational choice for V_c. The investigation was highly probabilistic, starting from a master equation for $\Psi(\mathbf{p}, \mathbf{x}, \mathbf{t})$, the number density of cells with swimming direction $\mathbf{p}$ at position $\mathbf{x}$ and time t.

The master equation can be integrated to give an equation of the form

$$\frac{\partial n}{\partial t} = -\mathbf{u} \cdot \nabla n - \nabla \cdot \mathbf{J} \qquad (7)$$

(cf eq.(5)), where $n = \int \Psi d^2\mathbf{p}$ and the flux $\mathbf{J}$ is the first moment of the Ψ distribution ($\mathbf{J} = \int \Psi \mathbf{p} d^2\mathbf{p}$). One can also obtain an equation for $\partial \mathbf{J}/\partial t$ but that involves the second moment, etc. It is a particular closure assumption that the second moment can be represented as a diffusive term; in general this may not be done. The findings of [35], briefly, were that the closure could be performed, and the Keller-Segel model used in a general shear flow, only if the perturbation to isotropic tumbling were small enough and if the vorticity in the flow were much less than the tumble rate. What to do in a general flow is still very unclear.

All the research referred to above has been restricted to dilute suspensions, in which cell-cell interactions are neglected. However, there is an increasing body of experimental evidence that some very interesting hydrodynamic phenomena arise in concentrated suspensions, mainly of swimming bacteria (*B. subtilis*). Mendelson et al [36] observed a population of *B. subtilis* swimming in a thin liquid layer on top of an agar gel, and reported a rich structure of meso-scale motions (by which is meant motions on length-scales intermediate between the population as a whole and the size or spacing of individual cells)which they called "whorls and jets". Dombrowski et al [37] also observed meso-scale motions in three-dimensional concentrated suspensions of *B. subtilis*. These are not yet understood.

One approach to modelling concentrated suspensions is by means of a continuum model in the form of a *mixture theory*, in which the cells and the suspending fluid are regarded as two co-existent continua, interacting via the laws of mechanics. This approach was well-explained in the context of shear flows of suspended rigid spheres by Nott & Brady [38]. A version of the theory was applied to two-dimensional bacterial populations by Lega & Passot [39]. Such theories raise a number of awkward questions, such as what do we mean by the concepts of "pressure" and "viscosity" in the continuum representing particles or cells? Moreover, Lega & Passot triggered the motion of their mixture by applying a random (white noise) external force to the particles, despite the fact that a neutrally buoyant swimming cell experiences zero net force. Nevertheless, the simulation reported by these authors did exhibit meso-scale motions. The mixture-theory approach needs to be followed up in greater depth.

Another approach to modelling suspensions in which hydrodynamic cell-cell interactions are important is being followed by Dr T. Ishikawa and myself. It involves simulations in which each cell is followed as it moves and in which the interaction with other

cells is analysed in a pairwise manner. Real microorganisms are too complicated for their geometry and kinematics to be represented accurately in a simulation of many cells. Instead we have gone back to the "steady squirmer" introduced above. Each 'cell' is an identical spherical squirmer, of radius a, swimming according to equation (3) with a given swimming speed U and squirming parameter β. An additional possibility is to allow the cells to be bottom-heavy, in gravity $\mathbf{g}$. The only distinction between different individuals is their orientation, or swimming direction, $\mathbf{p}$. The first step in the simulation is to calculate the trajectories of pairs of interacting squirmers in the absence of others. This is done by computing the virtual or *effective force* applied to one squirmer by the presence of another, for arbitrary initial orientations and relative position. In the far field the effective force can be calculated analytically, as it can in the very near field, when the squirmers are nearly touching and lubrication theory can be used. In between the calculation is performed numerically, using the boundary element method. A database of the results, covering the space of orientations and relative positions more-or-less uniformly, has been compiled and is used to speed up the simulations of larger numbers of spheres [40]. The macroscopic simulations are performed for random conditions in a cubic domain, extended by the use of periodic boundary conditions to represent an infinite domain. They have been used to compute (a) the effect of squirming on the rheology of a suspension of neutrally buoyant spheres in a simple shear flow [41] and (b) the mean square displacement of individual spheres: is the spreading diffusive or not [42]? In both cases a volume fraction of 0.1 is taken as typical. The answer in (a) is that squirming has a negligible effect on Batchelor's [43] results for the viscosity of a suspension of rigid spheres up to $O(C^2)$, when the squirmers are not bottom-heavy, but a significant effect when they are bottom-heavy, depending on the orientation of the shear flow relative to $\mathbf{g}$. In that case there can also be significant non-Newtonian normal stresses. In (b), the answer is that the spreading apart of non-bottom-heavy squirmers *is* correctly described as a diffusive process (i.e. their mean square displacement increases linearly with time t at large times), despite the fact that all the squirmers' motions are calculated deterministically. However, this is valid only for time-scales greater than about 30 a/U. Current research is extending these and similar results to larger volume fractions.

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