

# KINETIC MODELS FOR BIOLOGICALLY ACTIVE SUSPENSIONS

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**Abstract.** Biologically active suspensions, such as suspensions of swimming microorganisms, exhibit fascinating dynamics including large-scale collective motions and pattern formation, complex chaotic flows with good mixing properties, enhanced passive tracer diffusion, among others. There has been much recent interest in modeling and understanding these effects, which often result from long-ranged fluid-mediated interactions between swimming particles. This paper provides a general introduction to a number of recent investigations on these systems based on a continuum mean-field description of hydrodynamic interactions. A basic kinetic model is presented in detail, and an overview of its applications to the analysis of coherent motions and pattern formation, chemotactic interactions, and the effective rheology in active suspensions, is given.

**Key words.** suspensions, microorganisms, kinetic theory, collective dynamics

**AMS(MOS) subject classifications.** 35Q35, 35Q92, 76D07, 76T20, 76Z99

**1. Introduction.** Microorganisms are present in every part of the biosphere, ranging from harmful and beneficial bacteria in our bodies to phytoplankton in the oceans. They play a central role in many biological and ecological phenomena, among which pathogenic infection, digestion, reproduction, CO<sub>2</sub> capture and mixing in the oceans, and they are also at the base of the marine food web. Understanding their behavior, motility, dynamics, and interactions, is therefore a central step in the modeling of these various phenomena.

Much previous work in this field has focused on the hydrodynamics of single swimming microorganisms [27], which exhibit interesting and unusual strategies for locomotion in environments where viscous effects dominate and inertia is negligible. In this regime of low Reynolds numbers, the disturbance flows generated by moving particles (such as swimming microorganisms) decay very slowly with the distance from the particle center, thereby resulting in strong particle-particle hydrodynamic interactions in suspensions of many swimmers. These interactions in turn are known to result in a variety of complex and fascinating phenomena that have been reported in experiments, including: enhanced passive tracer diffusion [49, 26, 28, 30] and swimming speeds [13], large-scale chaotic flows with unsteady jets and vortices [29, 13, 11, 44], emergence of density fluctuations and patterns [13, 11], etc. Direct numerical simulations of these systems have also been performed, using various models and levels of approximation, including: simple dumbbell models [19, 20], boundary integral simulations [25], slender-body models [37, 43], and Stokesian dynamics

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simulations [24]. These simulations are often successful at capturing the qualitative features observed experimentally, and provide a wealth of useful information on the details of interactions and on the structure of the suspensions. Yet, they sometimes fail at elucidating the fundamental mechanisms leading to collective motion.

A different and complementary approach consists of developing continuum equations to capture the dynamics of various field variables such as swimmer concentration and orientation. These models are typically variants of existing kinetic theories for passive suspensions, liquid crystals, or polymer solutions, which all share similarities with active suspensions. The first notable model of this kind was proposed by Aditi Simha & Ramaswamy in a seminal paper [1], in which they adapted equations for the dynamics of liquid crystals, coupled to the Navier-Stokes equations for the fluid flow, to study the stability of aligned suspensions of active particles. A number of similar models have been developed since then [4, 6, 31, 33, 48], which have been applied to investigate collective effects in concentrated active suspensions. These models, however, often include ad hoc terms to account for near-field steric interactions, so that they are not always appropriate to study the sole effect of hydrodynamic interactions.

Another simpler kinetic model was developed recently by Saintillan & Shelley [38, 39], and is the focus of this paper.<sup>1</sup> The model is based on the use of a probability distribution function  $\Psi(\mathbf{x}, \mathbf{p}, t)$  of finding a particle at position  $\mathbf{x}$  with orientation  $\mathbf{p}$  in the suspension (here  $\mathbf{p}$  is a unit vector pointing in the direction of swimming). A conservation equation is written for the distribution function, with fluxes that depend on the local fluid velocity. This fluid velocity is in turn obtained by solving the Stokes equations with a coarse-grained effective stress tensor capturing the effect of the swimming particles on the flow. These basic equations can then either be analyzed theoretically (for instance in a stability analysis) or integrated numerically in simulations.

Here, we review this basic kinetic model and some of its applications. We briefly discuss single-particle hydrodynamics and derive an expression for the effective stress tensor induced by a collection of particles in section 2. The governing equations for the kinetic theory are exposed in section 3. We then describe their application to the study of instabilities and coherent motions in active suspensions in section 4, chemotaxis in thin bacterial films in section 5, and the effective rheology of active suspensions in section 6. We conclude and discuss directions for future work in section 7.

**2. Single-particle hydrodynamics and coarse-graining.** A large body of work exists on the analysis and modeling of propulsion mechanisms for microorganisms and on single-organism hydrodynamics, e.g. [27]. Here, we only review a few basic features that we will use to construct an expres-

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<sup>1</sup>Note that a very similar model was also proposed independently and around the same time by Subramanian & Koch [47].

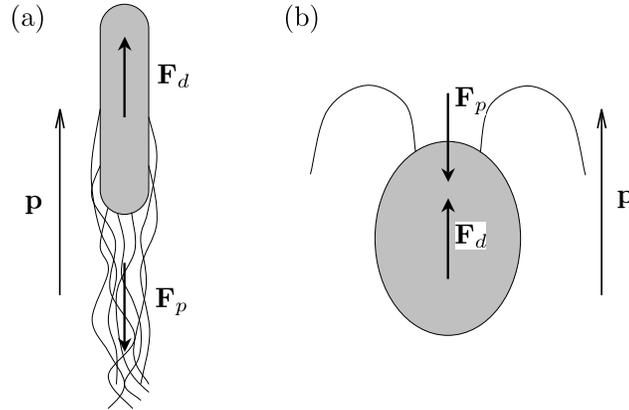


FIG. 1. Propulsion of two model swimming microorganisms: (a) a pusher (such as a bacterium) exerts a propulsive force near its tail, whereas (b) a puller (such as a microalga) exerts a thrust near its head.

sion for the mean-field stress tensor generated by a collection of swimmers. In nature, numerous swimming mechanisms exist at low Reynolds numbers, which all rely on non-reciprocal shape deformations as prescribed by Purcell's famous scallop theorem [34]. Most microorganisms make use of flexible appendages named flagella, which are actuated in a non-reciprocal fashion, thereby exerting a net thrust on the surrounding fluid. This is the case of many types of bacteria such as the common *Escherichia coli* and *Bacillus subtilis*, which use a bundle of flagella for propulsion, and of some types of microphytes such as *Chlamydomonas reinhardtii*, which beats two flagella in a breaststroke-like fashion (FIG. 1).

While the resulting propulsive force  $\mathbf{F}_p$  will in general be time-dependent, we will assume here for simplicity that it is steady: its value may be interpreted as a time average over one beat cycle (an approximation that is not necessarily easy to justify as unsteady effects may also have an impact on hydrodynamic interactions). If gravitational effects can be neglected, i.e. if the microorganism and the fluid have nearly matching densities, the swimmer is force-free and must therefore exert an equal and opposite drag force  $\mathbf{F}_d = -\mathbf{F}_p$  on the fluid: this drag force is likely to be exerted mostly by those parts of the body that do not contribute to propulsion (i.e. the cell body for bacteria and microalgae). Because the application points of  $\mathbf{F}_p$  and  $\mathbf{F}_d$  differ by a distance  $l$  (of the order of the organism size), the net leading-order effect on the surrounding fluid is that of a force dipole, whose sign may depend on the mechanism for swimming. In the case of a bacterium (FIG. 1(a)), the propulsive force is exerted near the rear of the particle, and such a swimmer will be called a *pusher*. Conversely, an alga swimming the breaststroke (FIG. 1(b)) exerts a thrust near its front, and will be called a *puller*.

The force dipole exerted by a swimmer can be characterized by the so-called stresslet  $\mathbf{S}$ , which is a second-order tensor defined as the symmetric first moment of the two forces:

$$\mathbf{S} = - \sum_i \left[ \frac{1}{2}(\mathbf{x}_i \mathbf{F}_i + \mathbf{F}_i \mathbf{x}_i) - \frac{1}{3}(\mathbf{x}_i \cdot \mathbf{F}_i) \mathbf{I} \right], \quad (2.1)$$

where the sum is over the two forces  $\mathbf{F}_p$  and  $\mathbf{F}_d$ . In equation (2.1),  $\mathbf{x}_i$  is the point of application of force  $\mathbf{F}_i$ , and the last term on the right-hand side involving the idem tensor  $\mathbf{I}$  is added to make  $\mathbf{S}$  traceless. In the case of the two swimmers illustrated in FIG. 1, and defining the director  $\mathbf{p}$  as a unit vector pointing in the direction of swimming, it is straightforward to simplify this expression to:

$$\mathbf{S} = \pm Fl \left( \mathbf{p}\mathbf{p} - \frac{\mathbf{I}}{3} \right), \quad (2.2)$$

with  $F = |\mathbf{F}_p|$ , and where the minus sign corresponds to the case of a pusher and the plus sign is for a puller. In the following, we introduce the dipole strength  $\sigma_0 = \pm Fl$ , with  $\sigma_0 < 0$  for a pusher and  $\sigma_0 > 0$  for a puller. Note that the magnitude of  $\sigma_0$  is also related to the swimming speed  $U_0$  of the particle. Indeed, a force balance on the body of the organism yields  $F \propto \mu U_0 l$  where the proportionality constant depends on the exact shape, which leads to  $\sigma_0 \propto \mu U_0 l^2$ . In the following, it will be convenient to define a dimensionless stresslet strength as  $\alpha = \sigma_0 / \mu U_0 l^2$ , which is an  $O(1)$  constant of the same sign as  $\sigma_0$ .

Of course, the description of FIG. 1 in terms of two equal and opposite point forces is simplistic, and in reality the microorganism exerts a distribution of stresses over the entire surface of its body. The definition of the stresslet (2.1) is then easily generalized as

$$\mathbf{S} = - \int_S \left[ \frac{1}{2}(\mathbf{x}\mathbf{f} + \mathbf{f}\mathbf{x}) - \frac{1}{3}(\mathbf{x} \cdot \mathbf{f}) \mathbf{I} \right] dS, \quad (2.3)$$

where the integral is over the surface of body, and  $\mathbf{f}(\mathbf{x})$  is the traction (force per unit area) at any point  $\mathbf{x}$  on the body. For an axisymmetric microorganism, this expression must also simplify to

$$\mathbf{S} = \sigma_0 \left( \mathbf{p}\mathbf{p} - \frac{\mathbf{I}}{3} \right), \quad (2.4)$$

where the value of  $\sigma_0$  will depend on the details of the traction distribution. This approach provides a more general and rigorous definition of pushers and pullers than that provided above: a pusher can be defined as a self-propelled particle for which  $\sigma_0 < 0$  in equation (2.4), whereas a puller is a particle for which  $\sigma_0 > 0$ . The case  $\sigma_0 = 0$ , which corresponds to a zero net force dipole, is unlikely to occur in nature as any small fore-aft asymmetry

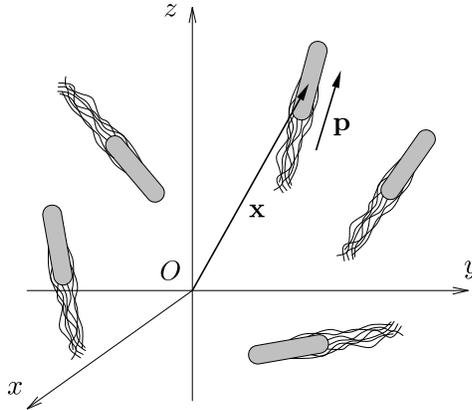


FIG. 2. *Active suspension: the configuration of the particles at time  $t$  is modeled in terms of a distribution function  $\Psi(\mathbf{x}, \mathbf{p}, t)$  of the center-of-mass  $\mathbf{x}$  and director  $\mathbf{p}$  of the swimmers.*

will result in  $\sigma_0 \neq 0$ , but it may occur for some types of artificial swimmers. This case will not be considered further, as the kinetic model we introduce below is based on a non-zero stresslet.

Having obtained the stresslet  $\mathbf{S}$ , it is then possible to determine the effective extra stress induced by a collection of swimmers as a volume average. This classic result, sometimes known as the Kirkwood formula, was originally derived to model the stress in polymer solutions [12]. It was adapted to the case of suspensions by Batchelor [7], who expressed the extra stress tensor  $\boldsymbol{\Sigma}^p$  for a suspension of torque-free particles in a volume  $V$  as a volume average of the stresslets on all the particles (with index  $\alpha$ ):

$$\boldsymbol{\Sigma}^p = \frac{1}{V} \sum_{\alpha} \mathbf{S}_{\alpha}. \quad (2.5)$$

If we model the configuration of a suspension at time  $t$  in terms of a probability distribution function  $\Psi(\mathbf{x}, \mathbf{p}, t)$  of finding a particle with center-of-mass  $\mathbf{x}$  and director  $\mathbf{p}$  (see FIG. 2), the particle extra stress at point  $\mathbf{x}$  is then more readily expressed as

$$\boldsymbol{\Sigma}^p(\mathbf{x}, t) = \int_{\Omega} \Psi(\mathbf{x}, \mathbf{p}, t) \mathbf{S} \, d\mathbf{p} = \sigma_0 \int_{\Omega} \Psi(\mathbf{x}, \mathbf{p}, t) \left( \mathbf{p}\mathbf{p} - \frac{\mathbf{1}}{3} \right) \, d\mathbf{p}, \quad (2.6)$$

where  $\Omega$  denotes the unit sphere. The expression (2.6) for the coarse-grained particle stress tensor is valid for describing the flow generated by a suspension of swimmers on length scales much greater than the particle dimensions, and will be the basis of the kinetic model of section 3. Also note that the stress tensor (2.6) can also be interpreted as a local nematic order parameter: indeed,  $\boldsymbol{\Sigma}^p = \mathbf{0}$  for a suspension that is locally isotropic, whereas  $\boldsymbol{\Sigma}^p \neq \mathbf{0}$  for a suspension exhibiting a local nematic alignment.

A few comments on the generality of the above results are in order. The main assumption that allowed us to derive equation (2.6) for the active stress tensor is that the swimmers are force- and torque-free and exert a steady force dipole on the fluid. While this may be a good approximation for some types of microorganisms, others do not satisfy all of these assumptions [42]. In particular, some microorganisms have a density that is significantly different from that of water, so that they exert a net force on the fluid and have interactions that may resemble those between sedimenting particles: this is the case of *Volvox carteri*, which exerts a net force on the fluid and has a negligible stresslet [14]. Other microorganisms, called gyrotactic, are subject to a buoyant torque as their center of mass and center of buoyancy do not coincide [32]. Finally, some microorganisms, including *Chlamydomonas reinhardtii*, drive oscillatory flows in time as they swim, that sometimes even result in a reversal of the stresslet over the course of one swimming stroke [16]. For simplicity, all of these effects are neglected here, though we realize that they should be incorporated into more detailed theories.

**3. Basic kinetic model.** The basic model of interest here was first introduced by Saintillan & Shelley [38, 39] and is based on an evolution equation for the distribution function  $\Psi(\mathbf{x}, \mathbf{p}, t)$  defined in section 2, coupled to an equation for the fluid motion. By conservation of particles,  $\Psi$  must indeed satisfy a Smoluchowski equation [12]:

$$\frac{\partial \Psi}{\partial t} + \nabla_x \cdot (\dot{\mathbf{x}} \Psi) + \nabla_p \cdot (\dot{\mathbf{p}} \Psi) = 0, \quad (3.1)$$

where  $\nabla_p$  is the gradient on the unit sphere  $\Omega$ .  $\Psi$  is also normalized as

$$\frac{1}{V} \int_V \int_{\Omega} \Psi(\mathbf{x}, \mathbf{p}, t) \, d\mathbf{p} \, d\mathbf{x} = n, \quad (3.2)$$

where  $V$  is the volume of interest and  $n$  is the number density (number of particles per unit volume). The solution of equation (3.1) requires knowledge of the center-of-mass and rotational flux velocities  $\dot{\mathbf{x}}$  and  $\dot{\mathbf{p}}$ , which describe the dynamics of a given swimmer. In a dilute suspension, these can be modeled as

$$\dot{\mathbf{x}} = U_0 \mathbf{p} + \mathbf{u}(\mathbf{x}) - D \nabla_x (\ln \Psi), \quad (3.3)$$

$$\dot{\mathbf{p}} = (\mathbf{I} - \mathbf{p}\mathbf{p}) \cdot \nabla_x \mathbf{u} \cdot \mathbf{p} - d \nabla_p (\ln \Psi). \quad (3.4)$$

Specifically, the center-of-mass velocity of a particle is modeled as the sum of its swimming velocity  $U_0 \mathbf{p}$ , which is assumed to be unchanged by interactions, and of the local fluid velocity  $\mathbf{u}(\mathbf{x})$ , which may result from an external flow or from hydrodynamic interactions. Similarly, the particle rotational velocity is modeled using Jeffery's equation [10] in terms of the velocity gradient  $\nabla_x \mathbf{u}$ . Both flux velocities also account for diffusion, with

isotropic diffusivities  $D$  and  $d$  which are assumed to be independent of  $\mathbf{x}$  and  $\mathbf{p}$ . These may model hydrodynamic fluctuations in the suspension [37], or thermal fluctuations if the swimmers are small enough to be affected by Brownian motion (generally not the case for microorganisms).

To close the equations, a model for the fluid velocity  $\mathbf{u}$  appearing in equations (3.3)–(3.4) is needed. Here we consider the situation where there is no external flow, in which case  $\mathbf{u}$  is simply the velocity driven by the swimming particles themselves. As we argued in section 2, swimming particles (in most cases) exert force dipoles on the surrounding fluid, which can be captured in a mean-field description using the active stress tensor of equation (2.6). More precisely, the flow field driven by the distribution of dipoles on all the particles satisfies the momentum and continuity equations:

$$-\mu \nabla_x^2 \mathbf{u} + \nabla_x q = \nabla_x \cdot \boldsymbol{\Sigma}^P, \quad \nabla_x \cdot \mathbf{u} = 0, \quad (3.5)$$

where  $\boldsymbol{\Sigma}^P$  is obtained in terms of  $\Psi$  using equation (2.6). Equations (3.1), together with (3.3)–(3.5), form a closed system that may in principle be integrated in time for the distribution function  $\Psi$  and fluid velocity  $\mathbf{u}$  in the suspension, given an initial condition.

**4. Instabilities and coherent motions.** The first study of interest that we describe here concerns the evolution of an initially isotropic and uniform suspension of swimmers [38, 39, 22]. This situation can first be analyzed as a stability problem: given a small perturbation in such a system, under which conditions will this perturbation grow or decay? This question was addressed by Saintillan & Shelley [38, 39], who considered a plane-wave perturbation at wavenumber  $\mathbf{k}$ :

$$\Psi(\mathbf{x}, \mathbf{p}, t) = \frac{n}{4\pi} \left[ 1 + \epsilon \tilde{\Psi}(\mathbf{p}, \mathbf{k}) \exp(i\mathbf{k} \cdot \mathbf{x} + \sigma t) \right]. \quad (4.1)$$

By substituting (4.1) into the kinetic equations of section 3, linearizing to order  $\epsilon$ , and neglecting rotational diffusion, it is possible to reduce the equations to an eigenvalue problem for the active particle stress tensor [38]:

$$\tilde{\boldsymbol{\Sigma}}^P(\mathbf{k}) = \boldsymbol{\Pi}(\mathbf{k}, \sigma) : \tilde{\boldsymbol{\Sigma}}^P(\mathbf{k}), \quad (4.2)$$

where

$$\tilde{\boldsymbol{\Sigma}}^P(\mathbf{k}) = \int_{\Omega} \tilde{\Psi}(\mathbf{p}, \mathbf{k}) \left( \mathbf{p}\mathbf{p} - \frac{\mathbf{I}}{3} \right) d\mathbf{p}, \quad (4.3)$$

and the operator  $\boldsymbol{\Pi}(\mathbf{k}, \sigma)$  is a fourth-order tensor. A dispersion relation for this eigenvalue problem can be obtained as [38, 39, 22]

$$-\frac{3\alpha}{4} \int_0^\pi \frac{\cos^2 \theta \sin^3 \theta}{\sigma + k^2 D + ik \cos \theta} d\theta = 1. \quad (4.4)$$

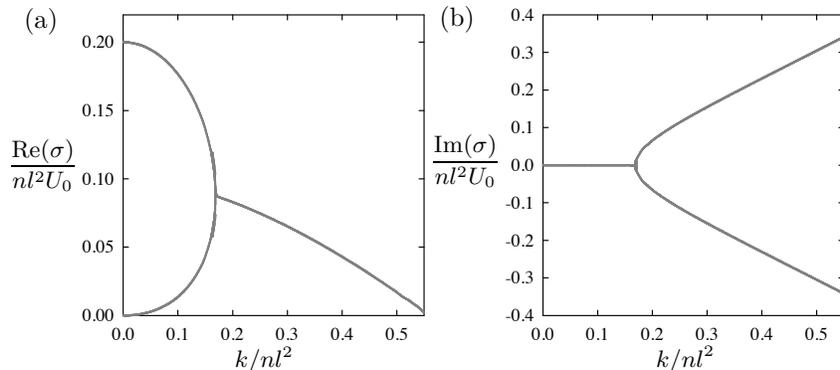


FIG. 3. (a) Real and (b) imaginary parts of the complex growth rate  $\sigma$  (normalized by  $nl^2U_0$ ), as functions of the wavenumber  $k$  in a suspension of pushers with  $\alpha = -1$  and  $D = d = 0$ . Adapted with permission from [39].

This equation can be solved numerically for the complex growth rate  $\sigma$  in terms of the wavenumber  $k = |\mathbf{k}|$ , and such a solution is shown in FIG. 3 for a suspension of pushers ( $\alpha = -1$ ) in the absence of diffusion ( $D = d = 0$ ). The main conclusion of this study is the existence of a positive growth rate  $\text{Re}(\sigma)$  below a critical wavenumber  $k_c \approx 0.55 nl^2$  in suspensions of pushers. The case of pullers ( $\alpha > 0$ ) is simply obtained by changing the sign of  $\text{Re}(\sigma)$  and is therefore characterized by a negative growth rate. Beyond the critical wavenumber  $k_c$ , a more detailed analysis by Hohenegger & Shelley [22] demonstrated that both types of suspensions are stable when diffusion is included. Also note that the numerical factor in the expression for  $k_c$  depends on diffusion, and decreases as either  $D$  or  $d$  increases.

This critical wavenumber can be interpreted as corresponding to the smallest linear system size  $L$  above which an instability will occur in a suspension of pushers. In other words, the fluctuations in equation (4.1) will grow if the system size  $L$  satisfies:

$$\frac{2\pi}{L} < 0.55 nl^2, \quad (4.5)$$

or equivalently,

$$\left(\frac{L}{l}\right) \times nl^3 > \frac{2\pi}{0.55}, \quad (4.6)$$

i.e. when the product of the system size  $L$  (normalized by the characteristic dimension  $l$  of the swimmers) by the effective volume fraction  $nl^3$  exceeds a given threshold. It is important to realize that this linear instability pertains to the active stress tensor (4.3), which as we mentioned earlier can be viewed as a nematic order parameter: the instability will therefore result in a local nematic alignment of the particles, but the linear eigenmodes

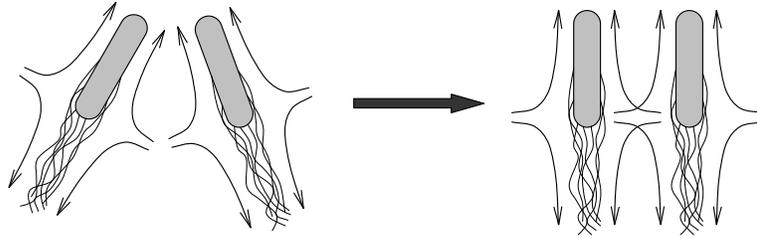


FIG. 4. *Hydrodynamic interaction of two pushers. The arrows illustrate the disturbance flow field driven by the force dipole exerted on the fluid, in the reference frame of the particle. When two pushers come together, they tend to align as a result of these flows.*

can be shown not to be associated with spatial concentration fluctuations [39, 22]. This local alignment of pushers can be understood qualitatively by simply considering the disturbance flow induced by the force dipole exerted by a pusher on the fluid (FIG. 2): as two pushers come together, it is easy to see that their disturbance flows will tend to align them, whereas the disturbance flow driven by a puller is of opposite direction. This effect was also observed in direct numerical simulations [37].

Further insight can be gained into the effects of nonlinearities and into the long-time dynamics in the suspensions by calculating numerical solutions of the kinetic equations, starting from a weakly perturbed homogeneous and isotropic distribution function. Such simulations were performed in two dimensions by Saintillan & Shelley [38, 39], and in three dimensions by Alizadeh Pahlavan & Saintillan [2]. These simulations confirm the stability of puller suspensions, and the instability criterion (4.6) for pusher suspensions. In unstable suspensions, local nematic alignment of the particles is observed in agreement with the prediction of the linear analysis, but this alignment is followed by the growth of density fluctuations on the scale of the system. These fluctuations eventually saturate as a result of diffusion, and undergo complex time dynamics in which dense sheet-like structures form and break up repeatedly in time, see FIG. 5(a). This growth of concentration fluctuations, which is a nonlinear effect, can be explained as a result of the swimming of the particles, which causes them to aggregate in regions of negative divergence of the mean director field [39]. The dynamics in the unstable suspensions are complex and chaotic, and are characterized by large-scale flows with jets and vortices, efficient fluid mixing, enhanced swimming speeds, and correlated dynamics on length scales of the order of the system size, in good qualitative agreement with experimental observations.

Note that the prediction of equation (4.6) was also recently tested in direct particle simulations using a slender-body model [43]. In these simulations, where individual particles are tracked and interact hydrodynamically, a transition from uncorrelated to correlated motions is also observed

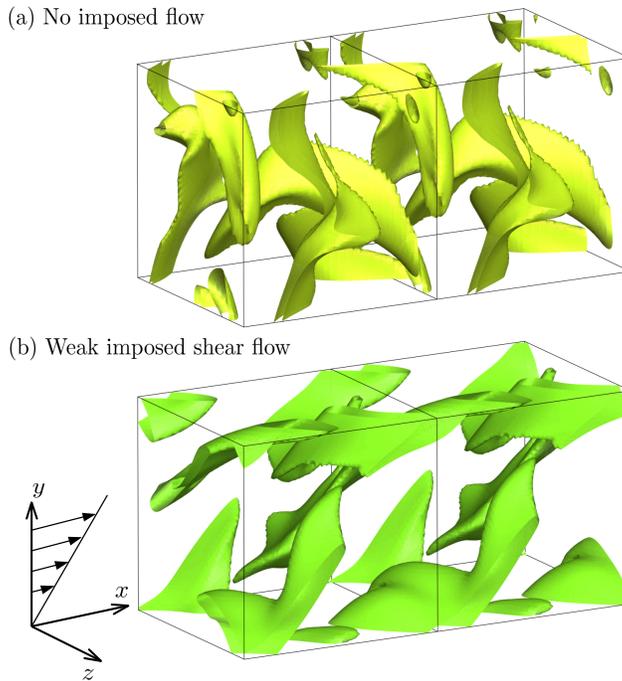


FIG. 5. Pattern formation in suspensions of swimming microorganisms: concentration iso-surfaces at  $c = 1.5$ , (a) in a quiescent suspension (no imposed flow), and (b) when a weak external shear flow is imposed. Adapted with permission from [2].

at a critical volume fraction (for a fixed system size) that matches the prediction of (4.6) within a factor of 2. The transition manifests itself in many different ways, and for instance affects velocity correlation lengths and times, swimming velocities, density fluctuations, passive tracer mixing rates and diffusivities, among others.

While the analysis and simulations described above considered swimmer dynamics and interactions in a quiescent fluid, microorganisms in nature often evolve in complex flow environments, e.g. in the oceans. It is therefore interesting and important to understand how an external flow may affect these instabilities and dynamics. Such a study is also important to understand the effective rheology of microorganism suspensions, as we discuss further in section 6. The case of a simple shear flow was recently analyzed by Alizadeh Pahlavan & Saintillan [2], using both a stability theory and continuum simulations. The main finding of this study is that an external shear flow tends to stabilize the suspensions by controlling the orientation of the particles. A sample simulation in a weak shear flow is illustrated in FIG. 5(b), and shows alignment of the density patterns with a  $45^\circ$  axis with respect to the flow direction. As shear rate increases, the instabilities can be shown to become weaker and are eventually suppressed.

**5. Chemotaxis.** The previous analysis, in which boundaries and external fields were entirely neglected, provides useful insight into the dynamics in active suspensions, but is highly idealistic and may be difficult to recreate in a laboratory experiment. Swimming microorganisms indeed often interact with boundaries and chemical cues. Here, we describe how the kinetic model of section 3 can be amended to include some of these effects, and we specifically discuss the modeling of a thin active suspension film surrounded on both sides by an oxygen bath [3]. This study is motivated by the many experiments on active suspensions that have been performed in stabilized liquid films [49, 44, 16], and more specifically by the recent investigation of Sokolov *et al.* [45]. In this latter study, the dynamics in a free-standing thin film containing a suspension of *Bacillus subtilis* were observed, and demonstrated a transition from quasi-two-dimensional collective motion to three-dimensional chaotic behavior as the film thickness was increased. Migration of the bacteria towards the boundaries where the strongest concentration in oxygen occurs was also reported. The existence of this transition is not too surprising in light of equation (4.6), which predicts instabilities only above a critical system size, but a more accurate model should include coupling with the oxygen field and interactions with the free surfaces.

The first modification consists in coupling the equations of motion to the dynamics of the oxygen field, whose concentration we denote by  $s(\mathbf{x}, t)$ . It obeys an advection-diffusion equation:

$$\frac{\partial s}{\partial t} + \mathbf{u}(\mathbf{x}) \cdot \nabla_x s - d_0 \nabla_x^2 s = -\kappa s(\mathbf{x}, t) c(\mathbf{x}, t), \quad (5.1)$$

which expresses transport of the oxygen by the disturbance flow  $\mathbf{u}(\mathbf{x})$  driven by the microorganisms, and diffusion with constant diffusivity  $d_0$ . The last term on the right-hand side of equation (5.1) models consumption of oxygen by the swimmers as a second-order reaction. If we were to model the release of a chemical cue by the swimmers (as would arise in a simulation of quorum sensing [36]), this term may be replaced by  $+\kappa c(\mathbf{x}, t)$ .

Secondly, the effect of the oxygen concentration on the microorganism dynamics must also be modeled. This coupling is more subtle, and here we mention two different approaches:

- *Gradient-detecting model:* this model, which is the simplest of the two but also the least realistic, assumes that the swimmers are able to detect the local oxygen gradient and adjust their orientation to swim towards the regions of high oxygen concentration. This is achieved by adding an extra deterministic torque that aligns particles with the oxygen gradient in equation (3.4) for the rotational velocity, which becomes:

$$\dot{\mathbf{p}} = (\mathbf{I} - \mathbf{p}\mathbf{p}) \cdot [\nabla_x \mathbf{u} \cdot \mathbf{p} + \chi \nabla_x s] - d \nabla_p (\ln \Psi). \quad (5.2)$$

- *Run-and-tumble model*: In reality, bacteria for instance are unable to sense local concentration gradients, but instead use a stochastic process of random orientation changes (so-called ‘tumbling’ events) whose characteristic frequency depends on the local oxygen concentration. The net effect of this biased random walk is a migration towards the regions of high oxygen concentration [9]. As explained in detail by Bearon & Pedley [8], this effect may be captured by a modification of the conservation equation (3.1) as follows:

$$\frac{\partial \Psi}{\partial t} + \nabla_x \cdot (\dot{\mathbf{x}} \Psi) + \nabla_p \cdot (\dot{\mathbf{p}} \Psi) = -\lambda \Psi + \int_{\Omega} \lambda \Psi(\mathbf{x}, \mathbf{p}', t) d\mathbf{p}', \quad (5.3)$$

where the quantity  $\lambda(\mathbf{x}, \mathbf{p}, t)$  is the stopping rate and is related to the probability for a bacterium to undergo a tumbling event over a fixed time interval. This stopping rate depends on the oxygen field sampled by the bacterium as it swims, and is modeled as

$$\lambda(\mathbf{x}, \mathbf{p}, t) = \lambda_0 \left( 1 - \xi \frac{Ds}{Dt} \right), \quad (5.4)$$

where

$$\frac{Ds}{Dt} = \frac{\partial s}{\partial t} + [U_0 \mathbf{p} + \mathbf{u}(\mathbf{x})] \cdot \nabla_x s \quad (5.5)$$

is akin to a material derivative, and denotes the rate of change of  $s(\mathbf{x}, t)$  sampled by a swimmer along its trajectory.

Thirdly, non-periodic boundary conditions need to be implemented to account for the free surfaces of the liquid film. A natural boundary condition for the disturbance velocity field is zero shear stress (although the no-slip boundary condition may be more appropriate if surfactants are present). Boundary conditions for the distribution function  $\Psi$  are slightly more subtle and must express the inability of the swimmers to cross the boundaries. This can be achieved by letting the normal component of the center-of-mass flux velocity (3.3) vanish at the free surface:  $\mathbf{n} \cdot \dot{\mathbf{x}} = 0$ , where  $\mathbf{n}$  is the unit normal at the boundary. A slightly weaker condition consists in prescribing zero net concentration flux, and is expressed as

$$\mathbf{n} \cdot \int_{\Omega} \dot{\mathbf{x}} d\mathbf{p} = 0. \quad (5.6)$$

The zero-shear-stress boundary condition, together with (5.6), can be implemented in simulations using a reflection method, and details of the numerical algorithm are forthcoming [3].

Two typical simulations are illustrated in FIG. 6 for two different film thicknesses: (a)  $L_y = 20(nl^2)^{-1}$ , and (b)  $L_y = 20(nl^2)^{-1}$ . These simulations were performed using the run-and-tumble model of equation (5.3), although the gradient detecting method is found to qualitatively produce

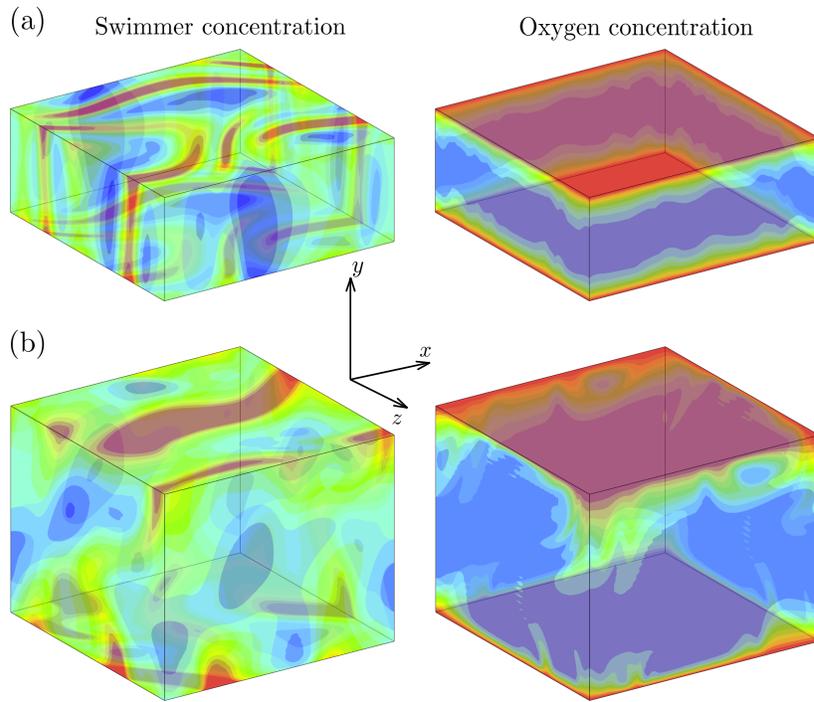


FIG. 6. Simulations of chemotaxis performed using the run-and-tumble model of equation (5.3). The domains are doubly-periodic in the  $x$  and  $z$  directions, with interfaces in the  $y$ -direction. Two film thicknesses are shown: a)  $L_y = 20(nl^2)^{-1}$ , and (b)  $L_y = 20(nl^2)^{-1}$ . The left column shows the local swimmer concentration, whereas the right panel shows the oxygen concentration.

very similar results. The figure shows both swimmer concentration and oxygen concentration. In thin films (FIG. 6(a)), the dynamics are found to be quasi two dimensional: the swimming microorganisms still organize into dense patterns that form and break up repeatedly in time, but these patterns are nearly uniform in the  $y$ -direction, and all the dynamics take place in the  $x$ - $z$  plane. As the film thickness increases (FIG. 6(b)), a transition occurs to three-dimensional chaotic behavior: the density patterns are no longer uniform in the  $y$ -direction, and the dynamics near both interfaces become uncorrelated on average. This also leads to the emergence of three-dimensional flows, which drive more fluctuations in the oxygen field, with the formation of oxygen plumes that penetrate into the bulk of the film. This has in turn the effect of enhancing oxygen transport and mixing into the film [3], with clear benefits to the microorganisms. This transition as film thickness increases is qualitatively similar to that reported in the experiments of Sokolov *et al.* [45], suggesting that the effect is likely a result of hydrodynamic interactions between swimmers.

**6. Effective rheology.** As a final application, we discuss the effective rheology of suspensions of microorganisms, which has recently received significant attention. Only a few attempts have been made at measuring the effective viscosity of active suspensions, and have demonstrated very peculiar trends. In a first study, Sokolov & Aranson [46] measured the drag on a rotating magnetic particle immersed in a liquid film containing swimming bacteria, and used it to infer a value for the effective viscosity of the suspension. The value they obtained was significantly lower than that for pure solvent, by up to a factor of 7, and this decrease was found to correlate with the swimming speed of the bacteria. This decrease in viscosity is quite unusual, as particulate suspensions typically exhibit enhanced viscosities owing to the additional viscous dissipation taking place near the particle surfaces. In a second study, Rafai *et al.* [35] measured the viscosity of a suspension of swimming microalgae, and compared it to that of a suspension of dead algae: they observed a significant increase in viscosity as a result of the swimming activity. While the results of both studies seem to contradict each other, this discrepancy is easily resolved by realizing that bacteria are pushers whereas microalgae are pullers.

A number of models [18, 17, 15] and numerical simulations [23] have been proposed to address this problem. Here, we briefly discuss the analysis of Saintillan [40, 41], which uses a model very similar to that of section 3. In a dilute suspension, hydrodynamic interactions between microorganisms can be neglected to a first approximation, and particle positions become uncorrelated. In this limit, the configuration of a spatially homogeneous suspension is entirely captured by an orientation distribution  $\Psi(\mathbf{p}, t)$ , which satisfies a special case of equation (3.1):

$$\frac{\partial \Psi}{\partial t} + \nabla_p \cdot (\dot{\mathbf{p}} \Psi) = 0. \quad (6.1)$$

If an external linear flow with constant velocity gradient  $\mathbf{A}$  is applied, the angular flux velocity  $\dot{\mathbf{p}}$  captures the rotation and alignment of the swimmers in the flow:

$$\dot{\mathbf{p}} = (\mathbf{I} - \mathbf{p}\mathbf{p}) \cdot \mathbf{A} \cdot \mathbf{p} - d\nabla_p(\ln \Psi). \quad (6.2)$$

Steady-state solutions  $\Psi(\mathbf{p})$  of equations (6.1)–(6.2) can be obtained analytically for irrotational flows [41], and numerically for other types of linear flows such as a simple shear flow [40]. Once  $\Psi(\mathbf{p})$  is known, it can be used to calculate the effective particle stress tensor  $\boldsymbol{\Sigma}^p$  in the suspension as a configurational average of the force dipoles (or stresslets) on the swimmers according to equation (2.5). Note that for particles in an external flow, an additional stresslet must be included, which arises from the inability of the particles to stretch under flow. This flow-induced stresslet, which is added to the permanent stresslet (2.4), can be shown to be of the form [21]:

$$\mathbf{S} = C(\mathbf{p}\mathbf{p} : \mathbf{A}) \left( \mathbf{p}\mathbf{p} - \frac{\mathbf{I}}{3} \right), \quad (6.3)$$

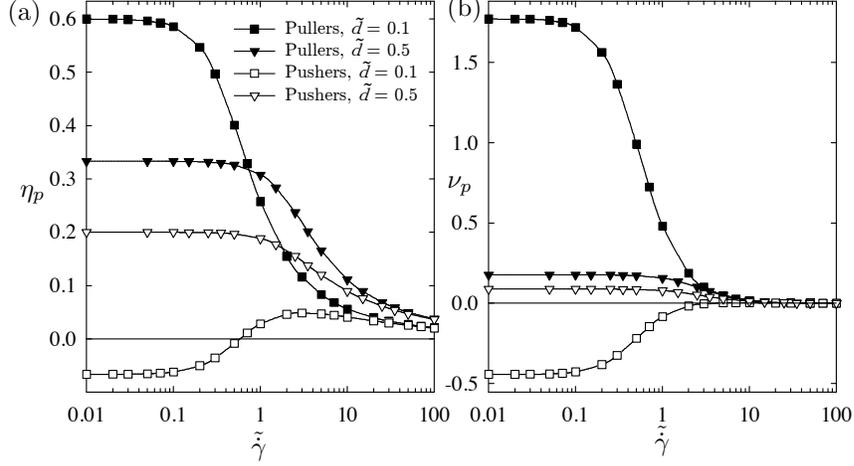


FIG. 7. (a) Effective viscosity  $\eta_p$ , and (b) first normal stress difference coefficient  $\nu_p$ , as functions of dimensionless shear rate  $\tilde{\gamma}$  in suspensions of pushers and pullers in a simple shear flow. Adapted with permission from [41].

where the constant  $C$  depends on the shape of the particle. Having determined the extra stress tensor, quantities such as the effective viscosity  $\eta_p$ , and first and second normal stress difference coefficients  $\nu_p$  and  $\kappa_p$ , can be inferred as functions of flow strength as

$$\eta_p = \frac{\Sigma_{xy}^p}{\dot{\gamma}}, \quad \nu_p = \frac{\Sigma_{xx}^p - \Sigma_{yy}^p}{\dot{\gamma}^2}, \quad \kappa_p = \frac{\Sigma_{yy}^p - \Sigma_{zz}^p}{\dot{\gamma}^2}, \quad (6.4)$$

where  $\dot{\gamma}$  denotes the deformation rate and is obtained as:  $\dot{\gamma} = (\mathbf{A} : \mathbf{A})^{1/2}$ . A more detailed discussion of the model and its underlying assumptions can be found in [40, 41].

Results for the effective viscosity  $\eta_p$  and first normal stress difference coefficient  $\nu_p$  in a simple shear flow are shown in FIG. 7. In this figure, we have defined a dimensionless flow strength as  $\tilde{\gamma} = \dot{\gamma}t_c$  and a dimensionless rotary diffusivity as  $\tilde{d} = dt_c$ , where the time scale  $t_c$  is defined as

$$t_c = \frac{\pi\mu l^3}{6|\sigma_0| \ln(2/\varepsilon)}. \quad (6.5)$$

Here,  $\varepsilon$  is the inverse aspect ratio of the microswimmer, which is assumed to be an axisymmetric slender body. Suspensions of pullers (full symbols) exhibit a shear-thinning behavior and a positive first normal stress difference coefficient, much like suspensions of passive rodlike particles. As the swimming activity becomes stronger (i.e. as the dimensionless diffusivity  $\tilde{d}$  decreases), both  $\eta_p$  and  $\nu_p$  are found to increase. The trends are reversed in suspensions of pushers (open symbols): activity causes a decrease in

effective viscosity at low shear rates, which can even result in a negative value of  $\eta_p$  at low values of  $\tilde{d}$ , corresponding to a strong level of activity. Swimming activity also results in a sign change in  $\nu_p$  at low flow rates. These unusual findings are consistent with experimental observations that reported an increase in viscosity in suspensions of microalgae [35] but a decrease in suspensions of motile bacteria [46]. Similar effects have been predicted in other types of flows as well, including uniaxial extensional and compressional flows and planar extensional flow [40]. All of these previous studies have only considered dilute suspensions and have neglected particle-particle interactions; such interactions may be accounted for by including an external shear flow in the kinetic model of section 3, see FIG. 5(b) [2].

**7. Conclusions and outlook.** We have presented a simple kinetic model for suspensions of self-propelled particles such as swimming microorganisms based on a continuum description of the particle phase, that was first proposed by Saintillan & Shelley [38, 39]. This model, which is simply based on a conservation equation for the distribution of particles, coupled to the Stokes equations for the fluid motion driven by the force dipoles on the particles, was developed with the aim of understanding the effects of hydrodynamic interactions in these systems. The model was applied to study the emergence of collective motion in bacterial suspensions: as we demonstrated, such collective motion is predicted to arise when the product of the system size by the volume fraction exceeds a given threshold, in agreement with results from recent numerical simulations [43]. Other more complex applications also include the modeling of chemotaxis in external chemical fields, and the effective rheology of active suspensions.

Quite naturally, these models are only useful and valid inasmuch as they faithfully capture and explain phenomena observed in physical or biological systems. Suspensions of microorganisms are extremely complex systems, in which effects such as swimming noise, steric interactions, chemical cues, gravity, temperature variations, surfactants, among others, may all play a role in the observed dynamics. The kinetic model presented in this work neglected most of these effects, with the aim of isolating the contribution of mean-field hydrodynamic interactions. While this approach is useful from a fundamental and theoretical standpoint, attempts at quantitatively capturing the dynamics in bacterial suspensions will likely require improvements of our model to capture some of these more complex effects. Of ongoing interest to us are:

- *Steric interactions:* Experiments on bacterial suspensions are often performed at high concentrations, where excluded volume interactions between swimmers become important [11, 44]. In fact, the emergence of collective motion discussed in section 4 often occurs in the semi-dilute to concentrated regime, in which the mean-field description of interactions may no longer be appropriate. While including direct particle-particle contacts and interactions is fairly

natural in direct particle simulations [37, 43], it is far from trivial in continuum models. One possible approach is the inclusion of an interaction potential that causes particles to align with their neighbors as a result of steric interactions, in the manner of the classic model of Doi & Edwards for the isotropic-nematic transition in passive rod suspensions [12]. This additional interaction potential significantly complicates the analysis of the model, but numerical progress is still possible.

- *Confinement*: Most theoretical calculations and simulations described herein assumed periodic boundary conditions, both for convenience and as a means to model the dynamics in bulk suspensions away from boundaries. The effects of boundaries and of confinement, however, are non-trivial in real systems, as we discussed briefly in section 5. The boundary condition (5.6) of zero net concentration flux, while physically justified, does not include any details of the particle interactions with the boundary. Such details are again difficult to include in a continuum model, but may become significant in highly confined systems.
- *Unsteady swimming actuation*: Finally, as we mentioned briefly in section 3, swimming microorganisms do not exert a steady force dipole on the fluid around them, but rather perform repeated swimming cycles during which the flow field around them fluctuates periodically [16]. These fluctuations are likely to add noise to the dynamics, but their precise effects remain unknown. A previous model on a related system suggests that the effects of these fluctuations on coherent motions and ordering may be significant [5]. Amending the present kinetic model to account for unsteady swimming is not straightforward, but will be attempted in future work.

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