

Stochastic kinetic theory for collective behavior of hydrodynamically interacting active particles

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Self-propelled particles with hydrodynamic interactions (microswimmers) have previously been shown to produce long-range ordering phenomena. Many theoretical explanations for these collective phenomena are connected to instabilities in the hydrodynamic or kinetic equations. By incorporating stochastic fluxes into the mean field kinetic equation, we quantify the dynamics of a suspension of microswimmers in the parameter regime where the deterministic equation is stable. We can thereby compute nontrivial collective phenomena concerning spatial correlations of orientation and stress as well as the enhanced diffusion of tracer particles. Our analysis here focuses primarily on two-dimensional systems, though we also show how superdiffusion of tracers in three dimensions can occur by our framework.

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I. INTRODUCTION

Bacteria, algal cells, and synthetic microscale motors can be conceptualized as hydrodynamically interacting self-propelled particles, which we will refer to as microswimmers [1–9]. The flows created by them can influence their own motion and the motion of passive objects suspended within the fluid. If the long-ranged hydrodynamics largely determine the behavior of such a system, the response can be understood by examining a suspension of dipole microswimmers. In this article, we develop a fluctuation theory for a model consisting of an idealized system of point dipole microswimmers.

Continuum field theories have been a fruitful approach to understanding collective phenomena in active suspensions with hydrodynamic interactions [10–14]. Such theories indicate that the linear stability of the uniform isotropic state depends on the sign of the force dipole, which classifies the “puller” and “pusher” mechanisms of swimming. The uniform isotropic configuration of pullers is always linearly stable, while for pushers it can suffer an instability when rotational diffusion is weak enough relative to the hydrodynamic coupling of orientations [15–23]. Much attention has been focused on patterning phenomena proceeding nonlinearly from the instability, including the associated long-ranged correlations [20,24], giant fluctuations [25,26], turbulence [27], and other factors that influence the instability and nonlinear oscillatory dynamics [28,29]. Indeed, the continuum mean-field equations describe only trivial dynamics in the linearly stable regime, which includes the general dynamics of pullers.

Experimental [30–33] and particle-based computational realizations [10,34–38] in the stable regime clearly demonstrate nontrivial flow and enhanced mixing even though the activity is less organized and vigorous than in unstable pusher systems. Such nontrivial dynamics can be described only by including the finite particulate nature of the microswimmers. One theoretical approach is to analyze a sample pair of microswimmers to understand the role of particle interactions [34,39–42] or a microswimmer and tracer to understand mixing in the dilute limit [32,35,43,44]. We will adopt the complementary approach of adding stochastic fluxes to the continuum field equations to represent the mesoscopic fluctuations. In addition to being more amenable to theoretical analysis, continuum field models are typically much less computationally expensive than direct particle simulations [45], though at the price of coarse-graining some interaction details.

The approach of adding physically appropriate mesoscopic noise to the diffusion equation has been used previously for a thermal equilibrium bath by Dean [46], Yoshimori [47], and Biroli

[48]. Cates [49,50] applied this concept to some systems of active Brownian particles without explicit hydrodynamic interactions. A related approach was used by Lau and Lubensky [31,51] who incorporated stochastic fluxes in a hydrodynamic model for microswimmers as a basis for computing statistical fluctuations and enhanced tracer diffusion. In this article, we pursue similar objectives but proceed instead from a mesoscopic stochastic equation which can be more transparently derived from an underlying particle-level model, and which can be viewed as a stochastic variation of the mean-field kinetic equation of [15]. Our results quantifying enhanced tracer diffusion are similar to, but not in complete agreement with, those obtained by Ref. [51].

II. MODEL EQUATIONS

Our model consists of a suspension of N_p rodlike dipole microswimmer particles in an incompressible, Newtonian fluid occupying a two-dimensional periodic square of side length L . We assume a concentration large enough for a continuum approximation to be reasonable but not so large that near-field and steric effects should be taken into account. The phase space number density $\psi(\mathbf{x}, \mathbf{n}, t)$ of microswimmers with position \mathbf{x} and the unit vector of orientation \mathbf{n} at time t is governed by a mesoscopic field kinetic equation. This equation can be derived from hydrodynamically coupled Langevin equations for the individual microswimmers, following the procedures described for other models [46,50,52], with the result

$$\frac{\partial \psi}{\partial t} = -\nabla_{\mathbf{x}} \cdot (\dot{\mathbf{x}}\psi) - \nabla_{\mathbf{n}} \cdot (\dot{\mathbf{n}}\psi) + D_t \nabla_{\mathbf{x}}^2 \psi + D_r \nabla_{\mathbf{n}}^2 \psi + \Xi(\mathbf{x}, \mathbf{n}, t), \quad (1)$$

$$\dot{\mathbf{x}} = v\mathbf{n} + \mathbf{u}(\mathbf{x}, t), \quad (2)$$

$$\dot{\mathbf{n}} = (\mathbf{I} - \mathbf{n}\mathbf{n}) \cdot [\gamma \mathbf{E}(\mathbf{x}, t) - \boldsymbol{\Omega}(\mathbf{x}, t)] \cdot \mathbf{n}. \quad (3)$$

Here $\dot{\mathbf{x}}$ is the velocity of the microswimmer, $\dot{\mathbf{n}}$ is the angular velocity, the noise term Ξ describes the divergence of stochastic fluxes from translational and rotational diffusion [46], v is the swimming speed of an isolated swimmer, \mathbf{u} is the local fluid velocity, D_t is the translational diffusivity, D_r is the rotational diffusivity, \mathbf{I} is the identity tensor, \mathbf{E} is the rate of strain tensor, $\boldsymbol{\Omega}$ is the vorticity tensor, and γ is a shape parameter. For the case of long slender organisms including flagella, the shape parameter is $\gamma \approx 1$. The swimming and flow lead to an advective flux while the diffusion leads to a stochastic flux. The Laplacian terms describe the mean divergence of these stochastic fluxes, while Ξ has zero mean and represents the fluctuations about the mean.

In the stochastic kinetic theory model, the instantaneous noise term in two-dimensional physical space is given by [46]

$$\Xi dt = \nabla_{\mathbf{x}} \cdot [\sqrt{2D_t\psi} d\mathbf{U}(\mathbf{x}, \theta, t)] + \partial_{\theta} [\sqrt{2D_r\psi} dV(\mathbf{x}, \theta, t)]. \quad (4)$$

The variables $d\mathbf{U}$ and dV are independent Brownian motion processes following a Gaussian distribution with zero mean. The spatial noise contains x and y Cartesian components that are independent. The correlations are given by

$$\begin{aligned} \langle dU_x(\mathbf{x}, \theta, t) dU_x(\mathbf{x}', \theta', t') \rangle &= \langle dU_y(\mathbf{x}, \theta, t) dU_y(\mathbf{x}', \theta', t') \rangle = \langle dV(\mathbf{x}, \theta, t) dV(\mathbf{x}', \theta', t') \rangle \\ &= \delta(\mathbf{x} - \mathbf{x}') \delta(\theta - \theta') \delta(t - t') dt dt', \end{aligned} \quad (5)$$

and the stochastic differential equation is to be interpreted in the Itô sense. This noise on microswimmers is generally considered to be dominated by nonthermal effects such as noise from the operation of the molecular motors driving the swimming [9,14,51,53].

The fluid flow is obtained from the time-independent Stokes equation for an incompressible fluid

$$-\eta \nabla_{\mathbf{x}}^2 \mathbf{u} + \nabla_{\mathbf{x}} q = \nabla_{\mathbf{x}} \cdot \boldsymbol{\Sigma}, \quad (6)$$

where η is the dynamic viscosity and q is the pressure. The active stress is

$$\boldsymbol{\Sigma} = d \int \psi(\mathbf{n}\mathbf{n} - \mathbf{I}/2) d\mathbf{n}, \quad (7)$$

where d is the stresslet coefficient of the force dipole, which is positive for pullers and negative for pushers. By using the time-independent Stokes equation, we are assuming the time scale of stress fluctuations induced by the microswimmer dynamics is slow relative to viscous relaxation, which amounts roughly to $D_t \ll \eta/\rho$, where ρ is the fluid density, and wave numbers k such that $k \gg v\rho/\eta$, $\sqrt{D_r\rho/\eta}$, $\sqrt{|d|N_p\rho/(\eta L)}$.

These field equations lead to nontrivial dynamics even when the phase space density fluctuates around the uniform isotropic state. If these fluctuations are small enough, the field equations can be linearized, which is the subject of the rest of this article. In two dimensions, we can express the orientation vector as $\mathbf{n} = (\cos\theta, \sin\theta)$. We nondimensionalize the system using the time scale $t_c = \eta L^2/(N_p|d|)$ [54] and the length scale $l_c = vt_c = v\eta L^2/(N_p|d|)$ and scale the dimensional phase space density by its mean value $N_p/(2\pi L^2)$. The key dimensionless parameters are $\tilde{L} = L/l_c$, $\tilde{D}_t = D_t t_c/l_c^2$, $\tilde{D}_r = D_r t_c$. For simplicity of notation, in the rest of the article all other variables are nondimensional unless otherwise stated.

The scaled phase space density in a spectral expansion decouples the spatial Fourier modes for each spatial wave vector $\mathbf{k} = (k_x, k_y)$. In the spectral (Fourier) expansion, the phase space density is

$$\psi(\mathbf{x}, \mathbf{n}, t) = \sum_{\mathbf{k} \in 2\pi\tilde{L}^{-1}\mathbb{Z}^2} \sum_{l=-\infty}^{\infty} \hat{\psi}_{\mathbf{k},l} e^{i(\mathbf{k}\cdot\mathbf{x} + l\theta)}. \quad (8)$$

The Fourier coefficients for different angular modes l are coupled and can be written in matrix form as a vector $\hat{\boldsymbol{\psi}}_{\mathbf{k}}$ with components $\hat{\psi}_{\mathbf{k},l}$ for $l = \dots, -1, 0, 1, \dots$. The evolution equation is

$$\frac{\partial \hat{\boldsymbol{\psi}}_{\mathbf{k}}}{\partial t} = \mathbf{L}_{\mathbf{k}} \hat{\boldsymbol{\psi}} + ik_x \sqrt{\frac{2\tilde{D}_t}{N_p}} \frac{d\mathbf{U}_{x,\mathbf{k}}}{dt} + ik_y \sqrt{\frac{2\tilde{D}_t}{N_p}} \frac{d\mathbf{U}_{y,\mathbf{k}}}{dt} + i \sqrt{\frac{2\tilde{D}_r}{N_p}} \mathbf{R}_{\mathbf{k}} \frac{d\mathbf{V}_{\mathbf{k}}}{dt}, \quad (9)$$

where $\mathbf{R}_{\mathbf{k}}$ is diagonal with components $R_{k,l,l'} = l\delta_{l,l'}$, while the matrix $\mathbf{L}_{\mathbf{k}}$ is an infinite matrix with components given, for $\mathbf{k} \neq \mathbf{0}$, by

$$\begin{aligned} L_{k,l,l'} = & -\frac{i}{2} k e^{-i\theta_k} \delta_{l,l'-1} - \frac{i}{2} k e^{i\theta_k} \delta_{l,l'+1} - \tilde{D}_t k^2 \delta_{l,l'} - \tilde{D}_r l^2 \delta_{l,l'} + \delta_{l,2} \frac{p\gamma}{8} (-\delta_{l',2} + e^{-i4\theta_k} \delta_{l',-2}) \\ & + \delta_{l,-2} \frac{p\gamma}{8} (\delta_{l',2} e^{i4\theta_k} - \delta_{l',-2}), \end{aligned} \quad (10)$$

where θ_k is the angle between the x axis and \mathbf{k} , and $p = d/|d|$ is the sign of the stresslet strength.

The noise terms are also written in Fourier space and collected in vectors $d\mathbf{U}_{x,\mathbf{k}}$, $d\mathbf{U}_{y,\mathbf{k}}$, and $d\mathbf{V}_{\mathbf{k}}$ that are proportional to the Fourier transform of the physical space noise. These vectors have components $dU_{x,\mathbf{k},l}$, $dU_{y,\mathbf{k},l}$, and $dV_{\mathbf{k},l}$. All components are independent differentials of standard complex-valued Brownian motion, namely, Gaussian random functions with zero means and correlation functions given by

$$\langle dU_{x,\mathbf{k},l}^*(t) dU_{x,\mathbf{k},l}(t') \rangle = \langle dU_{y,\mathbf{k},l}^*(t) dU_{y,\mathbf{k},l}(t') \rangle = \langle dV_{\mathbf{k},l}^*(t) dV_{\mathbf{k},l}(t') \rangle = \delta(t - t') dt dt'. \quad (11)$$

The linear evolution equation for $\hat{\boldsymbol{\psi}}_{\mathbf{k}}$ for each \mathbf{k} contains all the information about how the active motion and hydrodynamic interactions of the microswimmers lead to coordinated motion provided the phase space density remains close enough to the uniform isotropic state that the linear approximation is valid. Within this approximation, we will focus on the properties of the long-time statistically stationary state [or nonequilibrium steady state (NESS)] of the fluctuations and whose Fourier space amplitude will be proportional to $N_p^{-1/2}$.

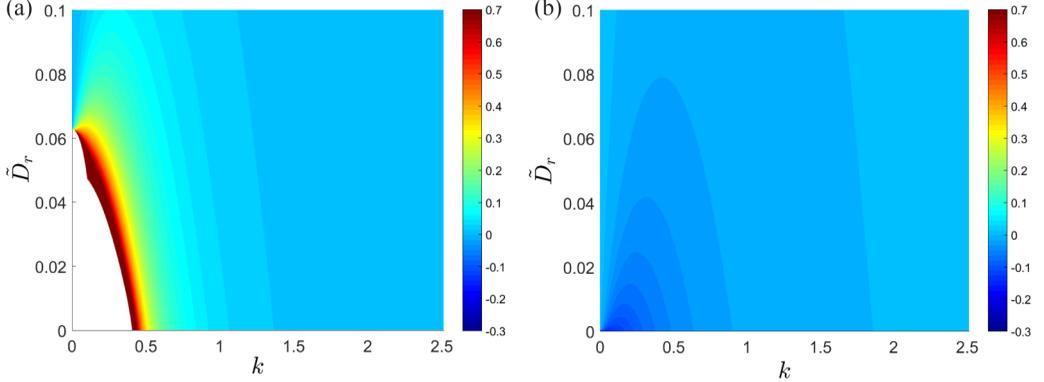


FIG. 1. Fourier mode amplitudes of orientation correlation function, $\log_{10}(N_p \hat{C}_{o,k})$, for pushers (a) and pullers (b) as a function of wave number k and nondimensional rotational diffusivity \tilde{D}_r . The blank region in panel (a) corresponds to the region of linear instability of the pusher system. For both cases, the microswimmers are rodlike and slender ($\gamma = 1$) with translational diffusivity of $\tilde{D}_t = 0.45$.

III. MICROSWIMMER FLUCTUATIONS AND CORRELATIONS

One important measure of group behavior is the local orientation of microswimmers, which for our nondimensionalization is

$$N(\mathbf{x}, t) = \frac{1}{2\pi} \int \mathbf{n} \psi(\mathbf{x}, \mathbf{n}) d\mathbf{n}. \quad (12)$$

Its spatial correlation function is defined as

$$C_o(\mathbf{x}') = \langle N(\mathbf{x}, t) \cdot N(\mathbf{x} + \mathbf{x}', t) \rangle, \quad (13)$$

with its Fourier spectrum given by

$$\hat{C}_{o,k} = \frac{1}{\bar{L}^2} \int_{0 \times 0}^{\bar{L} \times \bar{L}} C_o(\mathbf{x}') \exp(-i\mathbf{k} \cdot \mathbf{x}') d\mathbf{x}'. \quad (14)$$

Figure 1 shows the spectrum from truncation of Eq. (9) to components $|l| \leq 32$, and solving the deterministic Lyapunov matrix equation characterizing the NESS statistics.

At large \tilde{D}_r , the spectrum of the orientation fluctuations approaches the flat profile $\hat{C}_{o,k} = N_p^{-1}$ corresponding to independent microswimmers, while for sufficiently small \tilde{D}_r and wave number k , the linearized theory is inapplicable for pushers due to the instability of the uniform isotropic state [15,23]. At intermediate \tilde{D}_r , the fluctuations in the orientation correlation field are enhanced for pushers and depressed for pullers, corresponding to their respective aligning and antialigning tendencies [7,38]. This can be understood by noting the polar orientation correlations can only be induced from the symmetric force dipole flows through coupling to swimming [first two terms $\propto k$ in Eq. (10)]. Translational diffusion destroys correlations at larger k .

To obtain further insight, we developed a “slow-swimming approximation” in which the first two terms representing swimming in Eq. (10) are perturbations to the remaining terms involving diffusion and active stress. This approximation is formally valid for wave numbers $k \ll \min(\tilde{D}_r, 4\tilde{D}_r + p\gamma/4)$ or $k \gg \tilde{D}_r^{-1}$, provided a singular perturbation expansion is developed to handle the degeneracy of rotational diffusion in the $l = 0$ angular mode. Under the slow-swimming approximation, the orientation fluctuation spectrum is

$$N_p \hat{C}_{o,k} = 1 - \frac{p\gamma k^2 / 640}{(\tilde{D}_r + \frac{k^2 \tilde{D}_t}{4} + \frac{p\gamma}{16})(\tilde{D}_r + \frac{2k^2 \tilde{D}_t}{5} + \frac{p\gamma}{20})(\tilde{D}_r + k^2 \tilde{D}_t)} + \dots \quad (15)$$

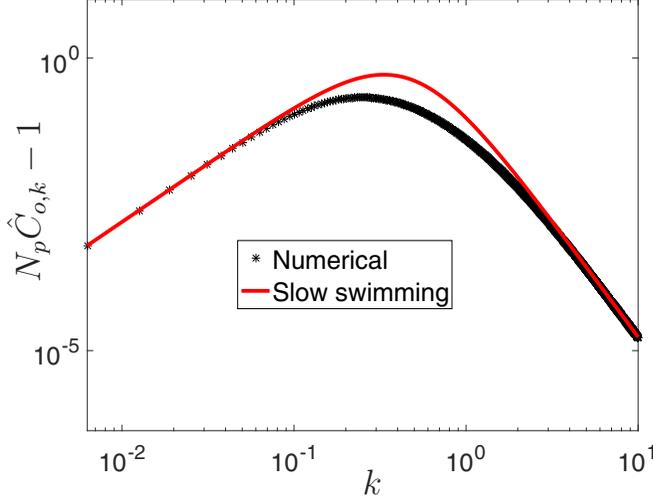


FIG. 2. Comparison of $N_p \hat{C}_{o,k} - 1$ between the numerical results from Fig. 1(a) and the slow-swimming perturbation approximation. The translational diffusivity is $\tilde{D}_t = 0.45$, and the rotational diffusivity is $\tilde{D}_r = 0.09$.

Figure 2 compares the slow-swimming approximation for slender pushers ($p\gamma = -1$) with $\tilde{D}_r = 0.09$ and $\tilde{D}_t = 0.45$ against the results from Fig. 1. We see agreement with both the k^2 scaling due to swimming at small k and k^{-4} scaling at large k from translational diffusion. For $\tilde{D}_r \gg \gamma/16$, the correlations peak at a wave number $k_p \sim (\tilde{D}_t/\tilde{D}_r)^{-1/2}$, where translational diffusion and rotational diffusion balance. For pushers ($p = -1$), the hydrodynamic interactions cause the correlation length to increase as \tilde{D}_r decreases and to diverge to the system size at the stability limit $\tilde{D}_r = \gamma/16$ of the uniform isotropic state.

In addition to orientation correlations, another important measure of fluctuations is the concentration of organisms relative to the mean concentration. Fluctuations in the spatial concentration defined as

$$C(\mathbf{x}, t) = \frac{1}{2\pi} \int \psi(\mathbf{x}, \mathbf{n}, t) d\mathbf{n} \quad (16)$$

in our nondimensional scaling are found to be negligibly small in the linearized model. This is supported by the slow-swimming perturbation expansion which shows that the spatial autocorrelation function of the concentration fluctuations is delta-correlated in real space to the first three orders. Recall that it is typically nonlinear effects or near-field effects that are responsible for the substantial concentration fluctuations seen in other studies [25, 29, 55–57], while near-field effects are neglected here.

We consider next the shear component of the active stress, which under the deterministic mean field theory is the driver of the instability of the uniform isotropic state. The results will be reported for the dimensional stress scaled by $\eta/t_c = N_p |d|/L^2$, so the dimensionless stress is given by

$$\Sigma = \frac{P}{2\pi} \int \psi(\mathbf{nn} - \mathbf{I}/2) d\mathbf{n}. \quad (17)$$

The shear stress correlation function in the nonequilibrium steady state (NESS) is

$$C_s(\mathbf{x}') = \langle \Sigma_{xy}(\mathbf{x}, t) \Sigma_{xy}(\mathbf{x} + \mathbf{x}', t) \rangle. \quad (18)$$

This choice of shear component leads to a stress correlation that depends on θ_k , so we will focus here on $\theta_k = 0$. Similar to our approach with orientation correlations, the Fourier spectrum was

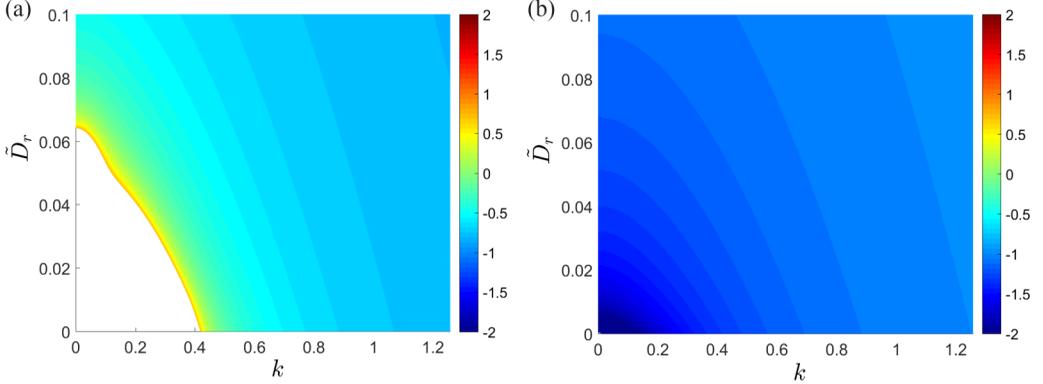


FIG. 3. Fourier mode amplitudes of active stress correlation function, $\log_{10}(N_p \hat{C}_{s,k}|_{\theta_k=0})$, for pushers (a) and pullers (b) as a function of wave number k and nondimensional rotational diffusivity \tilde{D}_r . The blank region in panel (a) corresponds to the region of linear instability of the pusher system. For both cases, the microswimmers are rodlike and slender ($\gamma = 1$) with translational diffusivity of $\tilde{D}_t = 0.45$.

calculated numerically and is shown in Fig. 3. As with the orientation spectrum, the independent swimmer fluctuations are obtained for large enough \tilde{D}_r or k . The spectrum is monotonically varying in k , with the largest value for pushers at small k and the smallest value for pullers as $k \rightarrow 0$. This is consistent with the mechanism of linear instability found in the mean field theory. The flows created by pushers enhance perturbations while the flows created by pullers suppress perturbations. The magnitude of this enhancement is largest for small k .

Many of the key features are illustrated by the perturbation expansion of the shear stress fluctuation spectrum under the slow-swimming approximation, which is given by

$$\begin{aligned}
 & N_p C_{s,k}|_{\theta_k=0} \\
 &= \left(\frac{4\tilde{D}_r + k^2\tilde{D}_t}{32\tilde{D}_r + 8k^2\tilde{D}_t + 2p\gamma} \right) \\
 &\times \left[1 + \frac{2p\gamma k^2(36\tilde{D}_r + 8k^2\tilde{D}_t + p\gamma)}{(52\tilde{D}_r + 8k^2\tilde{D}_t + p\gamma)(20\tilde{D}_r + 8k^2\tilde{D}_t + p\gamma)(16\tilde{D}_r + 4k^2\tilde{D}_t + p\gamma)(4\tilde{D}_r + k^2\tilde{D}_t)} + \dots \right].
 \end{aligned} \tag{19}$$

Figure 4 compares the slow swimming approximation for slender pushers ($p\gamma = -1$) with $\tilde{D}_r = 0.09$ and $\tilde{D}_t = 0.45$ against the results from Fig. 3. The leading order term of the approximation matches qualitatively with the numerical results. The slow-swimming approximation is formally valid for wave numbers $k \ll \min(\tilde{D}_r, 4\tilde{D}_r + p\gamma/4)$ or $k \gg \tilde{D}_t^{-1}$. For these values of k , using more terms in the expansion improves the comparison to the numerical results.

IV. TRACER DYNAMICS

We next consider how the statistical dynamics of the microswimmers enhance diffusion of passive objects (tracers) suspended in the fluid. To quantify this diffusion, we have numerically integrated the stochastic equations of motion for the fluid velocity fluctuations, using the linearized equations together with non-Brownian point tracers advected by the local fluid velocity. The linearized version of Eqs. (1)–(3) are discretized on a mesh with central finite difference derivatives in position or angle and explicit first order time stepping. The mesh contains 64 elements each in x and y and 128 in θ . The time step is $\Delta t = 10^{-2}$. At each step, the active stress is evaluated on the mesh and the fluid velocity is found on the mesh from the Stokes equation using the FFTW algorithm. All of

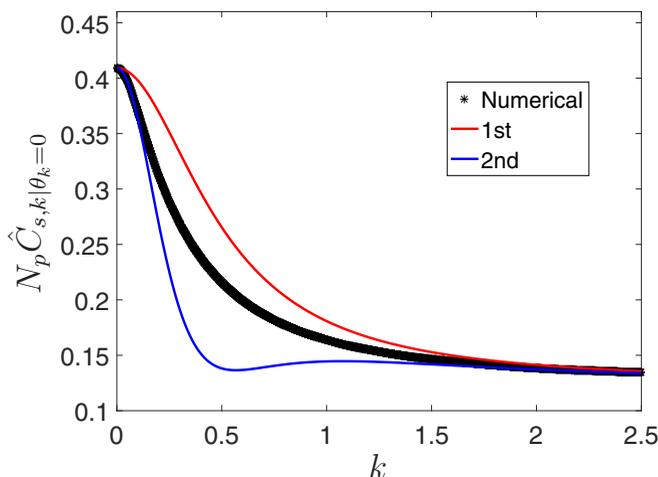


FIG. 4. Comparison of $N_p \hat{C}_{s,k} |_{\theta_k=0}$ between the numerical results from Fig. 3(a) and the slow-swimming perturbation approximation. The translational diffusivity is $\tilde{D}_t = 0.45$, and the rotational diffusivity is $\tilde{D}_r = 0.09$. The red line uses the first approximation (first term) from Eq. (19), while the blue line uses both terms shown in Eq. (19).

the results shown here have parameters $\tilde{D}_t = 0.45$, $\tilde{L} = 50$, and $N_p = 10^9$. The initial 200 units of dimensionless time of the simulations are ignored to allow the system to reach the NESS.

The mean-squared-displacement of the tracers is calculated and a diffusivity \tilde{D}_{tr} is extracted from the slope at long time. These diffusivities are shown as symbols in Fig. 5 for suspensions of slender rodlike ($\gamma = 1$) pushers and pullers. At large \tilde{D}_r , the interactions between organisms do not significantly alter the swimmer dynamics, which leads to tracer diffusion that is the same for pushers

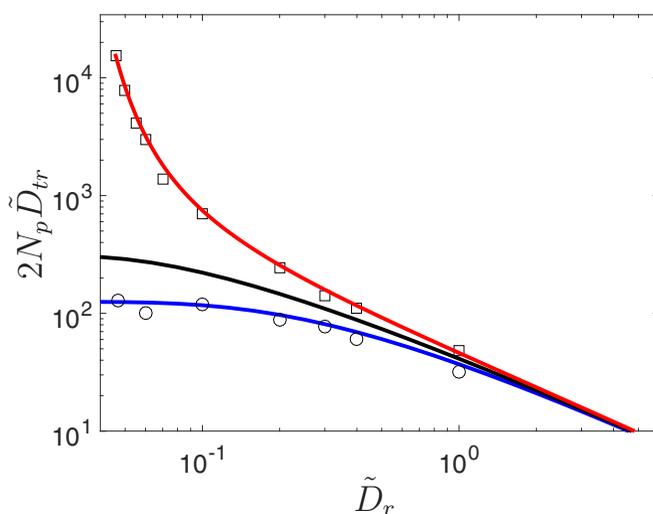


FIG. 5. The diffusivity \tilde{D}_{tr} of non-Brownian passive point-particle tracers as a function of the rotational diffusivity of the microswimmer \tilde{D}_r . The symbols are from PDE-based stochastic simulations for slender rodlike pushers (squares) and pullers (circles). The lines are the solution to deterministic matrix equations that assume zero Kubo number. The solid red line is the calculation result for pushers, while the solid blue line is for pullers, and the solid black line is for noninteracting microswimmers.

and pullers. At smaller \tilde{D}_r , the interactions between organisms can alter the effective diffusion of the tracers. The tracer diffusivity is the integral of its Lagrangian velocity correlation function, which is generally difficult to calculate analytically. However, the cases simulated in Fig. 5 have a small Kubo number $Ku = v_f \tau_f / l_f \sim 10^{-5}$, where v_f is the root-mean-square fluid velocity, τ_f is the correlation time of the fluid velocity, and l_f is the correlation length of the fluid velocity [58]. For small Kubo number, the Lagrangian velocity correlation function can be well approximated by the Eulerian one.

From the linearized stochastic equations [Eqs. (9) and (10)], we derived deterministic (truncated) matrix equations for the Eulerian velocity correlation function, and solve these numerically to obtain small Kubo number approximations for the tracer diffusivity, which are shown as solid curves in Fig. 5. Because the Kubo number of the stochastic simulations are very small, they match well with the small Kubo number approximation. If all wave numbers can be treated under the slow swimming approximation [$\tilde{D}_t^{-1} \ll \min(\tilde{D}_r, 4\tilde{D}_r + p\gamma/4)$], and we have the further condition $\tilde{L}^2 \tilde{D}_t^{-1} (4\tilde{D}_r + p\gamma/4) \gg 1$ so that the sum over modes can be well approximated by an integral, we can obtain an analytical expression for the tracer diffusivity as

$$\tilde{D}_{tr} = \frac{\tilde{L}^2}{64\pi N_p (4\tilde{D}_r + \frac{p\gamma}{4})^2} \left(\frac{p\gamma}{4} + 4\tilde{D}_r \left\{ \delta + \ln \left[\frac{\tilde{L}^2}{4\pi \tilde{D}_t} \left(4\tilde{D}_r + \frac{p\gamma}{4} \right) \right] \right\} \right), \quad (20)$$

where $\delta \approx 1.8$ is the Masser-Gramain constant. In dimensional terms this expression is

$$D_{tr} = \frac{N_p |d|^2}{256\pi \eta^2 D_r L^2 \left(1 + \frac{N_p d\gamma}{16D_r \eta L^2} \right)^2} \left\{ \frac{N_p d\gamma}{16D_r \eta L^2} + \delta + \ln \left[\frac{L^2 D_r}{\pi D_t} \left(1 + \frac{N_p d\gamma}{16D_r \eta L^2} \right) \right] \right\}. \quad (21)$$

For small concentrations the tracer diffusivity is proportional to the concentration of microswimmers and is the same for pushers and pullers. For higher concentrations, the hydrodynamic interactions of the microswimmers alter the tracer diffusion. This formula provides an analytical approximation of this effect.

Many experimental and simulation studies of passive tracers in active systems show superdiffusion at shorter times [32,37,59,60]. Yodh and coworkers [31] found the mean-squared-displacement scaled as $T^{3/2}$, where T is the lag time, and a fluctuating field model was used to deduce this scaling [31,51]. The theory developed here also produces superdiffusive scaling (nearly ballistic) of tracer motion for $T \ll (4D_r + p\gamma/4)^{-1}$ in two spatial dimensions. In particular, the dimensionless mean-squared displacement is approximately

$$\frac{\tilde{L}^2 T^2}{32\pi N_p} \left\{ c + \ln \left[\frac{1}{(4\tilde{D}_r + \frac{p\gamma}{4}) T} \right] \right\} \quad (22)$$

with

$$c = 4 - \tilde{\gamma} + \frac{4\tilde{D}_r}{4\tilde{D}_r + \frac{p\gamma}{4}} \left\{ \delta + \ln \left[\frac{\tilde{L}^2 (4\tilde{D}_r + \frac{p\gamma}{4})}{4\pi \tilde{D}_t} \right] \right\}, \quad (23)$$

where $\tilde{\gamma} \approx 0.58$ is the Euler-Mascheroni constant.

To better compare with experimental studies performed in three dimensions, we can examine the predictions of the fluctuating field theory in three dimensions. The predictions are most easily calculated analytically if we restrict attention to microswimmers which are not interacting. The long-time diffusion for non-Brownian tracers moving in these flows can be computed analytically in three dimensions under the assumptions of low Kubo number, weak swimming, and $\tilde{D}_t \tilde{L}^{-2} \ll \tilde{D}_r$ (the rotational diffusion is faster than translational diffusion across the domain). For these assumptions the long-time diffusivity is

$$\tilde{D}_{tr} = \frac{\tilde{L}^3}{90\pi \sqrt{6} N_p \tilde{D}_r^{1/2} \tilde{D}_t^{1/2}}. \quad (24)$$

In dimensional form, this tracer diffusivity is

$$D_{\text{tr}} = \frac{N_p |d|^2}{90\pi \sqrt{6} L^3 \eta^2 D_r^{1/2} D_t^{1/2}}. \quad (25)$$

The dimensional formula shows explicitly that the diffusivity is proportional to the microswimmer concentration and is independent of the sign of the dipole moment. This matches with previous theoretical work [34,35,39]. For the low Kubo number calculation to be self-consistent, it is sufficient that $D_{\text{tr}} \ll D_t$. Using the expression above, this condition is equivalent to

$$\frac{N_p}{L^3} \ll \frac{\eta^2 D_t^{3/2} D_r^{1/2}}{|d|^2}. \quad (26)$$

In dimensional terms, the point dipole approximation used throughout the article is valid when the swimmer size satisfies $l_{sw} \ll \sqrt{D_t/D_r}$. The slow swimming approximation corresponds to $v \ll \sqrt{D_r D_t}$. Our result matches exactly, including prefactors, with the slow swimming limiting behavior of the work of Ref. [35]. Relative to Ref. [35], our approach can incorporate hydrodynamic interactions of swimmers and describe the mean-square displacement of the tracers at all times in addition to the long-time diffusivity.

Indeed, for lag times $T \ll 1/\tilde{D}_r$, with the same assumptions as above, we find a superdiffusive regime with the tracer mean-square displacement behaving as $4\tilde{L}^3 T^{3/2}/(45N_p\pi^{3/2}\tilde{D}_t^{1/2})$, which is consistent with previous experimental [31,60] and theoretical [51] results. That is, superdiffusion of tracer motion in a three-dimensional flow emerges already from the long-range spatial correlations in the fluid generated by independently diffusing force dipoles, apart from any hydrodynamic interactions influencing the dynamics of those force dipoles, and does not seem to require a nonlinear theory as in Ref. [51] to obtain.

V. CONCLUSION

We have developed a stochastic kinetic theory that allows us to better understand how hydrodynamic interactions alter the behavior of suspensions of active particles. The equations can be used both when microswimmers act nearly independently and when they produce large scale group behavior. The results here have focused on situations where the uniform, isotropic state is linearly stable, and the correlations and fluctuations for the linearized dynamics have been quantified. Even within this regime, we have shown how microswimmer interactions alter the correlations and enhance the diffusion of passive tracers. This statistical structure cannot be obtained from a deterministic mean-field theory. Finally, we have shown that a simplified field theory produces the same superdiffusive scaling as observed in experiments. The stochastic kinetic theory can be used further to understand the role of fluctuations when the nonlinear terms are important and to understand the enhanced diffusion of tracers when the Kubo number is not small.

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