Hydrodynamics of Confined Active Fluids

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We theoretically describe the dynamics of swimmer populations in rigidly confined thin liquid films. We first demonstrate that hydrodynamic interactions between confined swimmers depend solely on their shape and are independent of their specific swimming mechanism. We also show that, due to friction with the nearby rigid walls, confined swimmers do not just reorient in flow gradients but also in uniform flows. We then quantify the consequences of these microscopic interaction rules on the large-scale hydrodynamics of isotropic populations. We investigate in detail their stability and the resulting phase behavior, highlighting the differences with conventional active, three-dimensional suspensions. Two classes of polar swimmers are distinguished depending on their geometrical polarity. The first class gives rise to coherent directed motion at all scales, whereas for the second class we predict the spontaneous formation of coherent clusters (swarms).

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Soft materials composed of motile particles have seen a surge of interest over the last couple of years. They encompass autophoretic colloids [1], self-propelled droplets [2], and vibrated grains [3,4]. This interest was triggered by their remarkable structural and transport properties akin to the one found in biological systems such as bacterial suspensions, migrating cells, and cytoskeletal extracts (see Ref. [5] and references therein). These so-called active fluids are ensembles of self-driven particles capable of self-propulsion in the absence of any external actuation [5–9].

From a theoretical perspective, such systems are commonly separated into two classes depending on the way they exchange momentum with their surroundings [5–7]. ''Dry'' systems, typically walkers or crawlers, achieve locomotion by transferring momentum to a rigid substrate and interact via short-range contact interactions. In contrast, ''wet'' systems, typically suspensions of swimmers, conserve momentum, and the particles interact at finite distance via long-range hydrodynamic interactions. A number of experimentally relevant situations involve monolayers of active particles living in rigidly confined fluid films and thus belong to both classes—e.g., bacteria swimming in micrometer-thick films at the surface of cell-culture gels [10–12] or active colloids and droplets moving in microfluidic channels [2].

In this Letter, we describe the phase behavior of active fluids confined, at least by one rigid wall, in two-dimensional (2D) geometries. In order to do so, we first revisit the description of hydrodynamic interactions under rigid confinement. We demonstrate that the far-field flow induced by a swimmer does not depend on the specifics of its swimming mechanism. The notions of pushers and pullers, for instance, prevalent in three dimensions (3D), are found to no longer be relevant in rigidly confined thin films [13]. In addition, on the basis of a prototypal microscopic model, we show that, due to friction with the walls, rigidly confined polar swimmers are not only prone to align along the local elongation axis but with the flow field itself. We then exploit these new interaction rules in 2D to address the large-scale dynamics of confined populations of swimmers. We establish a novel set of hydrodynamic equations for confined active films that qualitatively differ from the modified Leslie-Eriksen equations for active liquid crystals [5]. An investigation of the resulting phase behavior leads to the distinction between two classes of polar swimmers depending on their geometrical polarity. The first class (large head), gives rise to the emergence of coherent particle motion along the same direction at all scales, whereas, for the second class (large tail), we predict the spontaneous formation of coherent clusters (swarms).

Let us consider an ensemble of self-propelled particles confined in a thin film of a Newtonian liquid between two rigid walls or by one rigid wall and a free surface. We address strongly confined geometries where the particle height is comparable to the film thickness, h; see Fig. 1 (left). At scales larger than h, the fluid flow is characterized by the projection of the z-averaged velocity field in the (x, y) plane. Far from a swimmer, the projected flow field $\mathbf{u}(\mathbf{r}, t)$ is potential

$$\mathbf{u}(\mathbf{r}) = -G\nabla\Pi(\mathbf{r}), \tag{1}$$

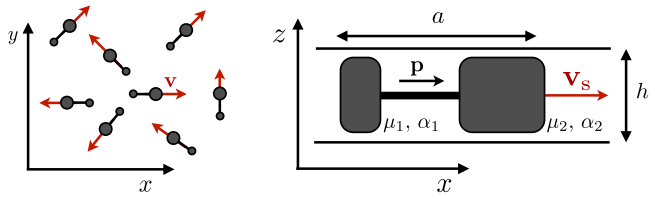

FIG. 1 (color online). Left: sketch of a confined suspension of active particles swimming freely in the (x, y) plane. Right: close-up on a single polar swimmer (see the text for notation). The active particles are confined between two rigid walls in the z direction.

where $\Pi(\mathbf{r})$ is the pressure at $\mathbf{r} = (x, y)$. The Darcy factor G scales as $G \sim h^2/\eta$, where η is the fluid viscosity.

How does confinement affect hydrodynamic interactions between swimmers? In unbounded fluids, the flow induced by a swimmer depends on the microscopic details of the propulsion mechanism [14–16]. In the far field, this flow is often well approximated at leading order by a force-dipole singularity, with a $\sim 1/r^2$ spatial decay, and as such has been used in most theoretical models [13,17–19]. This description results in the distinction between so-called pushers (or extensile swimmers) and pullers (or contractile swimmers). They correspond to force dipoles having opposite signs and displaying different large-scale dynamics [13,17,18]. When confined by solid walls, these flows are screened algebraically and decay as $\sim 1/r^3$, while retaining their angular symmetry. This screening of hydrodynamic interactions was shown to suppress generic instabilities, which are the hallmark of isotropic pusher suspensions [5].

As it turns out, however, the two main consequences of confinement have actually been overlooked so far. Any multipolar stress distribution on the surface of the swimmer actually yields only subdominant contributions to the flow in the far field. For any particle-transport mechanism (swimming, driving, advection), the far-field flow induced by a particle moving in a confined fluid has instead the symmetry of a potential source dipole and decays as $\sim 1/r^2$ [20,21]. The usual distinction done between pushers and pullers thus becomes irrelevant under rigid confinement [13,17]. Irrespective of the propulsion mechanism, the flow induced by a swimmer located at $\mathbf{r} = \mathbf{R}(t)$ is defined by Eq. (1) and by a modified incompressibility relation,

$$\nabla \cdot \mathbf{u}(\mathbf{r}) = -\boldsymbol{\sigma} \cdot \nabla \delta[\mathbf{r} - \mathbf{R}(t)], \tag{2}$$

where the dipole strength is $\boldsymbol{\sigma} \equiv \sigma[\dot{\mathbf{R}}(t) - \mathbf{u}^{(0)}(\mathbf{R}(t))]$, where $\mathbf{u}^{(0)}$ is the velocity field in the absence of the particle and σ scales as the square of the particle size (for a disk-shaped particle, σ is twice the particle area) [21]. The dipolar solution, $\mathbf{u}^d(\mathbf{r}|\mathbf{R}(t), \boldsymbol{\sigma})$, of Eqs. (1) and (2) is given, for a particle located at the origin, by

$$\mathbf{u}^d(\mathbf{r}|\mathbf{0}, \boldsymbol{\sigma}) = \frac{1}{2\pi|\mathbf{r}|^2}(2\hat{\mathbf{r}}\,\hat{\mathbf{r}} - \mathbf{I}) \cdot \boldsymbol{\sigma}, \tag{3}$$

where $\hat{\mathbf{r}} \equiv \mathbf{r}/|\mathbf{r}|$ and $\mathbf{I}$ is the identity tensor [20,21]. This framework has proven to accurately describe the interactions between confined advected droplets even in concentrated systems [21,22]. Importantly, the angular symmetry of $\mathbf{u}^d$ is different from the one of a force dipole: It is a polar flow field displaying the same angular dependence as that of a force *monopole* under confinement [20] despite the swimmers being self-driven. The reason for this apparent paradox lies in the continuous momentum exchange with the confining rigid walls, via the shear flow in the thin films that lubricate the swimmer-wall contacts (Fig. 1).

The second important difference with 3D suspensions concerns hydrodynamic interactions between swimmers. In order to account for these interactions, we first establish the equations of motion of an isolated swimmer in an arbitrary fluid flow. We focus on swimming bodies with polar shapes (i.e., front-back asymmetric), as is the case for most motile cells. For a swimmer at position $\mathbf{R}(t)$, we denote as $\mathbf{p}(t)$ its orientation ($|\mathbf{p}|^2 = 1$) and v_s the magnitude of its swimming velocity along $\mathbf{p}$. From symmetry considerations and at leading order in $|\nabla \mathbf{u}|$, the equations of motion of a polar swimmer for $\{\mathbf{R}(t), \mathbf{p}(t)\}$ take the generic form

$$\dot{R}_\alpha = v_s p_\alpha + \mu_\perp(\delta_{\alpha\beta} - p_\alpha p_\beta)u_\beta + \mu_\parallel(p_\alpha p_\beta)u_\beta, \tag{4}$$

$$\dot{p}_\alpha = \nu(\delta_{\alpha\beta} - p_\alpha p_\beta)u_\beta + \nu'(\delta_{\alpha\beta} - p_\alpha p_\beta)(\nabla_\gamma u_\beta)p_\gamma, \tag{5}$$

where $\mu_\perp$ (respectively, $\mu_\parallel$) is a transverse (respectively, longitudinal) mobility coefficient and ν and ν' are two rotational mobility coefficients. To better understand the effect of confinement on particle motion, let us first consider the advection of a passive particle by a uniform, unbounded flow. In that case, the velocity field is uniform everywhere in space and the passive particle undergoes translation at the same speed as the fluid. In unbounded fluids, we therefore have $\nu = 0$, $\mu_\perp = \mu_\parallel = 1$, and Eq. (5) then reduces to Jeffrey's equation that is commonly used to quantify the orientation of anisotropic particles with the flow-elongation axis [13,14].

In contrast, rigidly confined suspensions offer the possibility of having a nonzero value for ν. Instead of reorienting due to flow gradients, swimmers can reorient because of the flow itself, a new type of orientational dynamics that has not been considered so far. To provide insight into the conditions for nonzero values of ν, we derive the equations of motion above for a prototypal microscopic model (dumbbell). We show how the lubricated friction with the walls induces both anisotropic mobility ($\mu_\perp \neq \mu_\parallel$) and a direct coupling between the flow velocity and the particle orientation ($\nu \neq 0$). Consider a rigid-dumbbell swimmer, composed of two disks of radius b_1 (respectively, b_2) located at $\mathbf{R}_1$ (respectively, $\mathbf{R}_2$), and connected by a frictionless rigid rod of length $a \gg \{b_1, b_2\}$

(see Fig. 1, right). The lubrication forces between a disk-shaped particle and the solid walls hinder its advection by the fluid. Passive disks would be transported at a velocity $\dot{\mathbf{R}}_i(t) = \mu_i \mathbf{u}(\mathbf{R}_i)$ $(i = 1, 2)$, where the mobility coefficient μ_i is comprised between 0 (fixed obstacle) and 1 (passive tracer). We also introduce the drag coefficients α_i: When a disk is pulled by an external force $\mathbf{F}$ in a quiescent fluid, it moves at a velocity $\dot{\mathbf{R}}_i(t) = \alpha_i \mathbf{F}$. Let us now assume that the two disks would propel at a velocity $v_s^{(0)}\mathbf{p}$ when alone and let us compute the swimming speed and mobility coefficients from Eqs. (4) and (5) for the dumbbell.

The displacement of each disk results from the competition between (i) self-propulsion, (ii) the advection by the external flow $\mathbf{u}^{(0)}$, (iii) the advection of the disk i by the dipolar perturbation induced by the motion of the disk j, $\mathbf{u}^d(\mathbf{R}_i|\mathbf{R}_j, \boldsymbol{\sigma}_j)$, and (iv) the inextensibility constraint, $\mathbf{R}_2 - \mathbf{R}_1 = a\mathbf{p}$. At leading order in b_i/a, these contributions yield the following equations of motion for the "head" $(i = 2)$ and the "tail" $(i = 1)$ of the swimmer:

$$\dot{\mathbf{R}}_1 = v_s^{(0)}\mathbf{p} + \mu_1[\mathbf{u}^{(0)}(\mathbf{R}_1) + \mathbf{u}^d(\mathbf{R}_1|\mathbf{R}_2, \boldsymbol{\sigma}_2)] + \alpha_1 \mathbf{T}, \tag{6}$$

$$\dot{\mathbf{R}}_2 = v_s^{(0)}\mathbf{p} + \mu_2[\mathbf{u}^{(0)}(\mathbf{R}_2) + \mathbf{u}^d(\mathbf{R}_2|\mathbf{R}_1, \boldsymbol{\sigma}_1)] - \alpha_2 \mathbf{T}, \tag{7}$$

where the tension $\mathbf{T}$ ensures the inextensibility condition, $\mathbf{p} \cdot (\dot{\mathbf{R}}_2 - \dot{\mathbf{R}}_1) = 0$. Defining the center of drag of the swimmer as $\mathbf{R} \equiv (\alpha_1\mathbf{R}_2 + \alpha_2\mathbf{R}_1)/(\alpha_1 + \alpha_2)$, Eqs. (6) and (7) are readily recast into the form of Eqs. (4) and (5) with a dumbbell velocity and mobility coefficients given at leading order by $v_s = v_s^{(0)} + \mathcal{O}((b_i/a)^2)$, $\mu_\perp = \alpha_2\mu_1(1 - \gamma_2) + \alpha_1\mu_2(1 - \gamma_1)$, $\mu_\parallel = \alpha_2\mu_1(1 + \gamma_2) + \alpha_1\mu_2(1 + \gamma_1)$, and $\nu = [(\mu_2 + \mu_1\gamma_2) - (\mu_1 + \mu_2\gamma_1)]/a$, where $\gamma_i \equiv b_i^2(\mu_i - 1)/a^2$. We first see that the translational mobility coefficients $\mu_{\perp,\parallel}$ depend only on the anisotropy of the swimmer and are independent of its geometrical polarity (they remain unchanged upon a $1 \leftrightarrow 2$ permutation). In addition, as $\mu_\parallel < \mu_\perp$, a nonswimming dumbbell making a finite angle with a uniform flow field would drift at a finite angle from the flow direction. We also obtain that indeed $\nu \neq 0$ for polar swimmers. Since the μ_i's are decreasing functions of the particle radius, ν is negative for large-head swimmers $(b_2 > b_1)$ and positive otherwise. From Eq. (5), we thus get that, in a uniform flow, large-head swimmers would reorient against the flow and thus self-propel upstream. In contrast, large-tail swimmers $(b_1 > b_2)$ would swim downstream. These results are to be contrasted with the dynamics in unbounded fluids where, as discussed above, no such reorientation is present. In confinement, ν vanishes for apolar swimmers, and the orientation of a symmetric dumbbell evolves according to the Jeffrey's orbits, Eq. (5), where $\nu = 0$ and $\nu' = a[\mu_2(1 + \gamma_1) + \mu_1(1 + \gamma_2)]/2$. Note that, since $\mathbf{u}$ is irrotational, the orientation of an isotropic swimmer made of a single disk is not coupled to the background flow. In the rest of the Letter, we discard the conventional ν' contribution to the orientational dynamics. It only yields short-wavelength corrections to the large-scale description of polar-swimmer suspensions described below.

We now turn to the dynamics of a dilute population of interacting swimmers in a quiescent fluid. We introduce the one-point probability distribution function, $\Psi(\mathbf{r}, \mathbf{p}, t)$, for swimmers with orientation $\mathbf{p}$ at position $\mathbf{r}$ and time t. The dynamics of the active particles is defined by Eqs. (4) and (5), with the fluid velocity field, $\mathbf{u}(\mathbf{r}, t)$, resulting from the linear superposition of force dipoles induced by each swimmer, $\mathbf{u}(\mathbf{r}, t) = \int d\mathbf{p}d\mathbf{r}'\Psi(\mathbf{r}', \mathbf{p}, t)\mathbf{u}^d(\mathbf{r}|\mathbf{r}', \boldsymbol{\sigma}')$, where $\boldsymbol{\sigma}' = \sigma v_s \mathbf{p}$. Assuming that swimmers are subject to translational and rotational diffusion, $\Psi(\mathbf{r}, \mathbf{p}, t)$ obeys the continuity equation

$$\partial_t \Psi = -\nabla \cdot (\Psi\dot{\mathbf{R}}) - \nabla_{\mathbf{p}} \cdot (\Psi\dot{\mathbf{p}}) + D\nabla^2\Psi + D_R\nabla_{\mathbf{p}}^2\Psi, \tag{8}$$

where $\dot{\mathbf{R}}$ and $\dot{\mathbf{p}}$ are defined by Eqs. (4) and (5), D and D_R are the translational and the rotational diffusion coefficients, respectively, and $\nabla_{\mathbf{p}}$ stands for the gradient on the unitary circle. For simplicity, we neglect translational diffusion. Specifically, anticipating our results, we assume that $D \ll v_s^2/D_R$, which is true for most biological and artificial microsize swimmers. Note that, for homogeneous suspensions and due to the symmetry of the dipolar coupling, the sum of all hydrodynamic interactions vanishes: Indeed, when $\nabla\Psi(\mathbf{r}, \mathbf{p}, t) = 0$, we have $\int d\mathbf{r}'\mathbf{u}^d(\mathbf{r}|\mathbf{r}', \boldsymbol{\sigma}') = 0$, and thus from Eqs. (4) and (5) it follows that $\dot{\mathbf{p}} = 0$ and $\nabla \cdot \dot{\mathbf{R}} = 0$. The dynamics of a homogeneous population, from Eq. (8), reduces thus to the orientational diffusion of an isolated swimmer, and homogeneous phases relax toward an isotropic state over a time $\sim D_R^{-1}$.

We now investigate the dynamic response of the homogeneous and isotropic phases to spatial fluctuations of the concentration and orientation of the active particles. The phase behavior is described in terms of (i) the concentration field, $c(\mathbf{r}, t) \equiv \int \Psi(\mathbf{r}, \mathbf{p}, t)d\mathbf{p}$; (ii) the local polarization, $\mathbf{P}(\mathbf{r}, t) \equiv \frac{1}{c}\int \mathbf{p}\Psi(\mathbf{r}, \mathbf{p}, t)d\mathbf{p}$; and (iii) the local nematic-orientation tensor, $\mathbf{Q}(\mathbf{r}, t) \equiv \frac{1}{c}\int(\mathbf{pp} - \frac{1}{2}\mathbf{I})\Psi(\mathbf{r}, \mathbf{p}, t)d\mathbf{p}$. To establish their equation of motion, we need to add a closure relation to Eq. (8). As we focus on deviations from isotropic and homogeneous states, we expand Ψ linearly in its three first moments [17,18],

$$\Psi(\mathbf{x}, \mathbf{p}, t) = \frac{1}{2\pi} c(1 + 2p_\alpha P_\alpha + 4p_\alpha p_\beta Q_{\alpha\beta}), \tag{9}$$

where the numerical coefficients are chosen so that c, $\mathbf{P}$, and $\mathbf{Q}$ are defined in a self-consistent fashion. Defining $\bar{\mu} \equiv \frac{1}{2}(\mu_\parallel + \mu_\perp)$ and $\tilde{\mu} \equiv (\mu_\parallel - \mu_\perp)$, and after some elementary but tedious algebra, the three nonlinear equations of motion are inferred from Eqs. (8) and (9) as

$$\partial_t c = -\nabla_\alpha [v_s c P_\alpha + \bar{\mu} c u_\alpha + \tilde{\mu} c Q_{\alpha\beta} u_\beta], \quad (10)$$

$$\partial_t (c P_\alpha) = \frac{\nu}{2} u_\alpha c - \nu c u_\beta Q_{\beta\alpha} - D_R c P_\alpha - \nabla_\beta \mathcal{I}_{\beta\alpha}, \quad (11)$$

$$\partial_t (c Q_{\alpha\beta}) = \frac{\nu}{2} c u_\gamma (2\delta_{\gamma(\alpha} P_{\beta)} - \delta_{\alpha\beta} P_\gamma) - 4 D_R c Q_{\alpha\beta} - \nabla_\gamma \mathcal{J}_{\gamma\alpha\beta}, \quad (12)$$

where the (potential) fluid velocity satisfies

$$\partial_\alpha u_\alpha = -\sigma v_s \partial_\alpha (c P_\alpha) \quad (13)$$

and where the expressions for the fluxes $\mathcal{I}$ and $\mathcal{J}$ are given in the Supplemental Material [23].

Equations (10)–(13) fully describe the dynamics of the isotropic phase. We investigate their linear stability with respect to plane-wave excitations of the form $(\delta c, \delta \mathbf{P}, \delta \mathbf{Q}) \exp(i\mathbf{k}\cdot\mathbf{r} - i\omega t)$, with $\mathbf{k} = k\hat{\mathbf{x}}$. At linear order, we can integrate Eq. (13) for the fluid velocity and recast the equations of motion into a set of two uncoupled linear systems having the form $\partial_t(\delta P_y, \delta Q_{xy}) = M_{\text{bend}}(\delta P_y, \delta Q_{xy})$ and $\partial_t(\delta c, \delta P_x, \delta Q_{xx}) = M_{\text{splay}}(\delta c, \delta P_x, \delta Q_{xx})$. The first system couples the transverse polarization and the bend modes only. These modes are stable for all k; they correspond to damped sound waves. The associated dispersion relation is deduced from the eigenvalues of M_{bend} as $i\omega = \frac{1}{2}[5D_R \pm i\sqrt{-9D_R^2 + (k v_s/2)^2}]$. In contrast, long-range hydrodynamic interactions between swimmers can destabilize the concentration (c), the longitudinal polarization (P_x), and the splay modes (Q_{xx}). To convey an intuitive description of this instability, we introduce the two governing dimensionless numbers. First, $\mathrm{Pe} \equiv \nu c_0 \sigma v_s/(2D_R)$ is a signed Péclet number comparing the rotational diffusion constant, D_R, to the rate of rotation of a polar swimmer induced by a source dipole of magnitude $\sigma c_0 v_s$ (c_0 being the average concentration); large-tail swimmers (respectively, large-head swimmers) correspond to $\mathrm{Pe} > 0$ (respectively, $\mathrm{Pe} < 0$). The second dimensionless number, $H \equiv (\bar{\mu}\sigma c_0 v_s)/v_s$, compares the swimming speed, v_s, to the advection velocity induced by a source dipole of magnitude $\sigma c_0 v_s$. In the long-wavelength limit ($k \to 0$), the eigenfrequencies associated with the stability matrix M_{splay} then take the form

$$\omega_c = -i \frac{v_s^2}{2D_R} \left(\frac{1-H}{1+\mathrm{Pe}}\right) k^2, \quad (14)$$

$$\omega_P = -iD_R(1+\mathrm{Pe}) + \mathcal{O}(k^2), \quad (15)$$

$$\omega_Q = -4iD_R + \mathcal{O}(k^2). \quad (16)$$

At zeroth order in k, the total number of swimmers being a conserved quantity, we have $\omega_c = 0$, and M_{splay} has only two nontrivial eigenvalues. Whereas rotational diffusion always stabilizes the nematic orientation ($-i\omega_Q < 0$), hydrodynamic interactions can in fact destabilize the isotropic state. From Eq. (15), we see that large-head swimmers with $\mathrm{Pe} < -1$ experience a generic instability: Fluctuations of the local polarization are amplified when the rotation induced by the hydrodynamic couplings overcomes the diffusional relaxation of P_x (see Fig. 2).

Several comments are in order. First, although the growth rate of the instability does not dependent on k, the total polarization ($k = 0$) is *not* unstable. As discussed above, the sum of all the hydrodynamic interactions cancels in this limit and no global directed flow can emerge spontaneously from an isotropic suspension. The instability shows, however, that groups of particles swimming coherently along the same direction form at all scales. Second, the generic nature of the instability is specific to the dipolar symmetry of the hydrodynamic interactions and the polar shape of the particles and can be intuitively rationalized as follows. From Eq. (13), we see that any finite wavelength perturbation of P_x along x results in a fluid flow in the opposite direction, with amplitude $\sim \sigma c_0 v_s \delta P_x$. Polar swimmers align with or against the local flow direction depending on their polarity. Large-head swimmers align along $-\mathbf{u}$, thereby increasing the initial perturbation of $\mathbf{P}$ and destabilizing the isotropic state. Conversely, large-tail swimmers align in the opposite direction and the local polarization relaxes to zero. As the reorientation rate of the swimmers is set by the magnitude of the velocity only (and not by the local strain-rate tensor), the growth (or relaxation) rate of the polarization is independent of the wave vector.

This novel generic instability is qualitatively different from the one observed in unbounded suspensions of pushers that, in contrast, is suppressed by confinement [5]. They differ in both the physical mechanisms at work and the structure of the unstable modes (bend versus splay modes). The only similarity is that in both systems the generic instability is a genuine collective effect due to the long-range nature of hydrodynamic interactions.

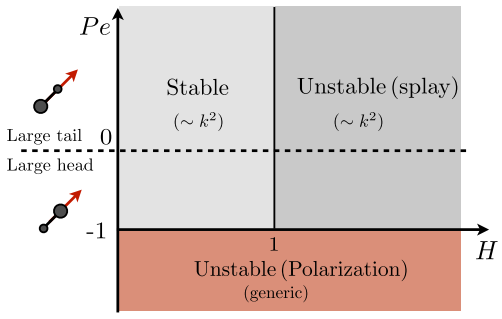

FIG. 2 (color online). Stability diagram of a nearly isotropic and homogeneous population of polar swimmers; $\mathrm{Pe} < 0$ (respectively, $\mathrm{Pe} > 0$) refers to large-head swimmers (respectively, large-tail swimmers).

To investigate the stability of the active film when $\mathrm{Pe} > -1$, we need to consider the eigenfrequencies and the eigenmodes of M_{splay} up to $O(k^2)$. From Eq. (14), we see that the combination of self-propulsion and rotational diffusion yields an effective diffusive dynamics of the suspension scaling as $\omega_c \sim (v_s^2/D_R)k^2$, as could have been anticipated from the single-swimmer problem [24]. However, hydrodynamic interactions result in a renormalization of this single-swimmer effect. These interactions control both the magnitude and the sign of the effective translational diffusion. In the regions ($\mathrm{Pe} > -1$, $H > 1$) and ($\mathrm{Pe} < -1$, $H < 1$), the effective diffusivity is negative and thus slowly destabilizes the isotropic phase (Fig. 2). The associated eigenmodes are now complex superpositions of c, P_x, and Q_{xx}, and thus clusters of aligned particles form and propel in a coherent fashion (swarms) from a homogeneous film. Notably, both large-head ($-1 < \mathrm{Pe} < 0$) and large-tail ($\mathrm{Pe} > 0$) swimmers are prone to this second splay-destabilization mechanism. In the other regions of Fig. 2, the effective diffusivity is positive and concentration fluctuations are stable.

In summary, we revisited in this Letter the theoretical description of populations of microswimmers when confined between two rigid walls. We showed that active particles interact hydrodynamically in a generic manner that is independent of the microscopic details of their propulsion mechanism and that, depending on their polarity, they may reorient in uniform flows instead of solely flow gradients. Focusing on polar swimmers, we then constructed a large-scale hydrodynamic theory from a minimal microscopic model (dumbbells). Our analysis showed that the macroscopic orientational dynamics is very different from the modified Leslie-Eriksen model of active liquid crystals due to a difference in the symmetry of the microscopic coupling between confined polar particles and the fluid flow. It results in a novel phase behavior for active films, and, in particular, spontaneous large-scale directed motion and swarming can emerge out of isotropic populations of confined swimmers.

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