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Effect of inertia on model flocks in a turbulent environment

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Abstract – We study flocking of self-propelled, interacting microorganisms with finite sizes and mass immersed in a turbulent flow. In the presence of the competing interactions of self-propulsion and the carrier turbulent flow, as is typical in nature, we show that including the effect of inertia is essential for the stability of flocks. We examine the problem from the point of view of global as well as local order and the statistics of the velocity of the microorganisms as a function of the inertia, the interaction radius, the level of self-propulsion as well as noise.



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Introduction. – The collective, organised motion of individuals having strongly aligned and correlated velocities, is a prototypical example of self-organized collective behaviour in biological systems and active matter. One of the key reasons behind the need to understand this phenomenon, often called flocking or swarming, is the presence of collective motion in the natural world amongst a variety of organisms, from fish and birds to microorganisms like bacteria and plankton [1]. Given the ubiquity of this phenomenon, it is not only important to investigate the evolutionary or ecological advantages for individuals and groups, but also to recognise this as a natural setting for the understanding of self-organised behaviour in general. Hence the importance of the problem of how ordered behaviour of a group of individuals can arise in various random and noisy settings is a problem of immense importance for not only biologists but also for physicists and engineers. As a result of this, in recent years several studies have tried to understand the dynamics of coordinated motion in a group of animals, birds, and even microorganisms through approaches as varied as cellular automata to partial differential equations [2-4]. The basis for many such approaches has been to prescribe rules for the motion of individuals in a large population which combines elements of both long-range attraction and short-range repulsions, as well as self-propulsion and self-alignment over appropriate spatial scales [5]. It is indeed remarkable that from such simple, mechanical rules self-organisation emerges, and various predictions have been borne out in controlled experiments.

In nature, however, organisms move in an environment which has a high degree of spatio-temporal complexity. In spite of this, observations have shown that for a wide class of living organisms, the flocking behaviour is persistent and is able to overcome seemingly strong perturbation coming from the environment. Hence to gain a better understanding of what are the optimal conditions for the stability of a flock, it is important to model the effect of the environment or the ambient flow and not treat the collective motion of self-propelled individuals in isolation. A natural choice to incorporate the complexity and randomness of the environment is to use an external stochastic noise which are uncorrelated between individuals in a flock. However, flocking in the natural world occurs in the presence of strong external flow which is often turbulent. Thus it behooves us to study the conditions and nature of flocking in the presence of fluid turbulence.

The role of an external fluid flow on the flocking behaviour has received attention only very recently. However given the added difficulty of resolving fully developed turbulent flows —without ignoring the importance of it—has lead to studies limited only to model flows, which are by themselves not solutions of the Navier-Stokes equation [6,7]. Similarly, the role of turbulence in small-scale patchiness has also received attention in recent work [8]. Furthermore, self-propelled microorganisms —such as zooplankton— have sizes much smaller than the associated Kolmogorov scale of such flows; hence accounting for a linear Stokes drag on such microorganisms should be important for a realistic modelling of their dynamics. We return to the validity of our model in the context of the natural world in a later section.

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In this letter, we address both these questions by considering microorganisms suspended in a turbulent, two-dimensional flow with a Kolmogorov scale larger than that of the organism. We thus deal with collective motion of organisms in a turbulent environment where the drag stemming from their finite size and the spatio-temporally chaotic flow competes with the self-alignment and selfpropulsion of the individual, to either enhance or decrease the level of flocking and self-organisation. Furthermore we argue that the taking into account of the inertia of the individual microorganism allows for spatially clustering groups of individuals, leading to a more effective flocking behaviour. In the area of turbulent transport, this phenomenon is well known and has been a subject of extensive research over the last decade. In this letter, we therefore bring together for the first time, to the best of our knowledge, ideas of preferential concentration of inertial particles [9] (which must play a crucial role for microorganisms such as plankton) with the ideas of self-alignment, to provide a more complete picture of the origins and stability of model flocks.

Model. – In this study, our strategy is the following: Our organisms, small but finite-sized, are self-propelled as well as affected by the environment of a two-dimensional turbulent flow and a Stokesian drag. In the absence of any interactions, or self-propulsion, these particles would have clustered and shown a non-monotonic degree of preferential concentration (characterised by a correlation dimension) as a function of their size (measured via the Stokes number St). However, in order to study their collective behaviour, we adapt the most common flocking model due to Vicsek et al. [5], to mimic interactions between different individuals. Thus our simple model is rich enough to allow for the competing interactions of i) Vicsek-like alignment, ii) self-propulsion with a specified velocity vector, and iii) the effect of the turbulent flow (which tries to randomize the velocity vector of each individual and hence destabilize the flock) as well as inertia (which lead to individuals coming close to each other in space).

Organism. Microorganisms such as zooplankton have a finite mass and a finite size. Hence it is natural for us to model our organisms as finite-sized, heavy inertial particles with a finite Stokes time τ_p . Each individual i, at position \mathbf{x}_i , moves with a velocity \mathbf{v}_i which is composed of an intrinsic, self-propelled part \mathbf{V}_i^p as well as an inertial contribution \mathbf{V}_i^{st} due to the effect of the surrounding flow, such that $\mathbf{v}_i = \mathbf{V}_i^p + \mathbf{V}_i^{\text{st}}$. We set the speed $|\mathbf{V}_i^p|$ of the self-propelled part of the individual such that $\mathbf{V}_i^p = |\mathbf{V}_i^p| \hat{\mathbf{n}}_i$, where the orientation vector $\hat{\mathbf{n}}_i = \mathbf{V}_i^{\text{st}}/|\mathbf{V}_i^{\text{st}}|$. The inertial contribution to the velocity of the individual is obtained from the linear Stokes drag model, via the simplified Maxey-Riley equation [10]:

$$\frac{\mathrm{d}\mathbf{V}_{i}^{\mathrm{st}}}{\mathrm{d}t} = -\frac{\mathbf{V}_{i}^{\mathrm{st}} - \mathbf{u}(\mathbf{X}_{i}, t)}{\tau_{p}}.$$
(1)

In order for this to be a valid description, we, of course, consider the size of the organisms to be smaller than the dissipative scales of the ambient fluid environment as well as their number density to be sufficiently low.

To allow for the emergence of a flocking behaviour, we adapt the so-called Vicsek model. Hence, after discrete time intervals ΔT , individual i calculates the average orientation

$$\bar{\theta}_i = \frac{1}{N_{\text{int}}} \sum_{j \in r_{\text{int}}} \tan^{-1} \left(\frac{v_{y,j}}{v_{x,j}} \right)$$
 (2)

of all individuals $N_{\rm int}$ within an interaction radius $r_{\rm int}$. It is to be recalled that the interaction radius is the maximum length scale over which a given individual organism in the flock can "see" any other individual organism of the flock (i.e., sense its instantaneous orientation). $v_{x,j}$ and $v_{y,j}$ are the x and y components of the velocity vector \mathbf{v}_j of the j-th individual. To allow for further fluctuations, we add a random noise $\sigma \in [-\eta, \eta]$ to the average angle calculated in (2), to obtain

$$\theta_i^{\text{avg}} = \bar{\theta}_i + \sigma. \tag{3}$$

Thus, the individual i then reorients its velocity vector in the new direction θ_i^{avg} without changing its speed, such that at times $t_{\star} = m\Delta T$ (where m is an integer),

$$\mathbf{v}_i(t_\star) = |\mathbf{v}_i(t_\star)|\hat{\mathbf{n}}_i^{\text{avg}},\tag{4}$$

where $\hat{\mathbf{n}}_i^{\text{avg}} = \cos \theta_i^{\text{avg}} \hat{\mathbf{i}} + \sin \theta_i^{\text{avg}} \hat{\mathbf{j}}$; the unit vectors in Cartesian coordinates being represented by $\hat{\mathbf{i}}$ and $\hat{\mathbf{j}}$. In the time interval between successive t_{\star} , each individual evolves according to the simplified Maxey-Riley eq. (1) and its own self-propelled velocity as described above.

Environment. The environment that the organisms interact with is a two-dimensional turbulent flow, as is typically the surrounding for microorganisms in ocean surfaces. Thus the fluid velocity $\mathbf{u}(\mathbf{X}_i,t)$, which mimics the typical environment in a natural setting and affects the organisms via (1), is a solution of the forced two-dimensional Navier-Stokes equation, with periodic boundary conditions and Ekman friction. The forcing and the damping ensure that our flow remains in a statistical steady state. The two-dimensional Navier-Stokes equation is best written in terms of the pseudo-scalar vorticity $\omega \equiv \nabla \times \mathbf{u}$ and the stream-function ψ

$$\nabla \cdot \mathbf{u} = 0, \tag{5}$$

$$\frac{\partial \omega}{\partial t} - J(\psi, \omega) = \nu \nabla^2 \omega - \mu \omega + \mathbf{f}, \tag{6}$$

where $\nabla^2 \psi = \omega$, $J(\psi, \omega) \equiv (\partial_x \psi)(\partial_y \omega) - (\partial_x \omega)(\partial_y \psi)$, **f** is the forcing term, and μ is the coefficient of the Ekman friction.

Details of the simulations. – We solve eq. (6) augmented by the incompressibility constraint (6) for the fluid velocity field u on a 2π periodic domain, by using a standard pseudo-spectral method and a second-order Runge-Kutta scheme for time marching. Our square grid

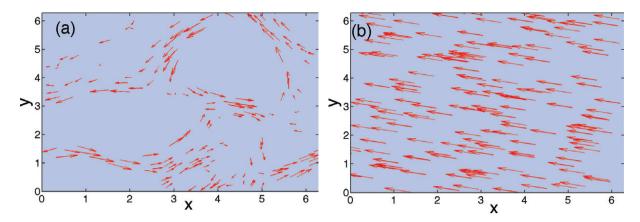


Fig. 1: (Color online) Velocity vectors of the microorganisms in a statistically stationary state for (a) $v_p = 0.02$, St = 0.05, and $\xi = 1.005$ and (b) $v_p = 0.8$, St = 2.0, and $\xi = 0.0006$. The noise strength $\eta = 0.01$ is held fixed for both the panels. The relative sizes of the arrows are a measure of the magnitude of the velocity for each microorganism. For clarity, we have only shown a representative subset of the all the microorganisms in our simulations.

has 1024^2 collocation points, a time step of size $\delta t = 10^{-3}$, a deterministic forcing on wavenumber k = 2, viscosity $\nu = 10^{-3}$, and a coefficient of friction $\mu = 0.01$ (see refs. [11,12] for details). With these parameters, we obtain homogeneous, isotropic turbulence with a Taylor-scale Reynolds number $R_{\lambda} \approx 500$. We perform several simulations with different population sizes N_p , but report here representative values for $N_p = 5000$. We choose three different values of the noise $\eta = 0.01, 0.1, 0.5$; and four different values of the speed of self-propulsion $|\mathbf{V}_i^p|$ 0.02, 0.2, 0.8, 2.2. In order to see the dependence of flocking on the inertia of the individuals (which, in the absence of interactions and self-propulsion, would affect the preferential concentration of the microorganisms), measured via the Stokes number $\mathrm{St} = \tau_p/\tau_\eta$ (where τ_p is the Stokes time and τ_{η} is the characteristic (small) time scale associated with the enstrophy cascade [13]), we perform simulations with 9 different values of St. We have also checked that in our simulations the number density of organisms remain sufficiently dilute to justify the use of eq. (1), and that there is no overlapping or crossing between organisms leading to unphysical results. Apart from the Stokes number, which aids or dissuades individuals from coming close to each other, the level of flocking crucially depends on the interaction radius $r_{\rm int}$, defined above, and which is best expressed (following ref. [6]), in terms of the non-dimensional variable $\xi = \frac{1}{N_0 \pi r_{\rm int}^2}$, where the number density $N_0 = N_p/(2\pi)^2$.

At this stage, before we present our results, it is important to ask if our model and working equations are indeed valid in natural settings beyond that of artificial microswimmers. In recent years several studies (see, e.g., [14]) have observed collective motion and flocking in a wide variety of zooplankton. For most aquatic (ocean or sea) surfaces, the Kolmogorov scale for the flow is typically in the range from 0.1 to 10 mm [15] whereas the size of zooplankton, which interact with this marine environment, varies in the range from 1 $\mu{\rm mm}$ to 10 mm. Thus for a

wide class of such microorganisms, the central assumption in writing down the Stokes drag model, *i.e.*, the size of the organism (particle) is smaller than the Kolmogorov scale of the flow, holds. Furthermore, if we consider the Stokes time associated with such organisms —which ranges from $1\,\mu\mathrm{s}$ to $1\,\mathrm{s}$ — and the relevant time scales of the flow, we find that the Stokes numbers of the microorganisms vary from essentially tracer-like $\mathrm{St}=0$ to inertial with finite Stokes numbers. This is precisely why, given the variability in these numbers, our study explores the dependence flocking on St (including the tracer-limit) in detail. It is this dependence and the importance of finite Stokes number that have been neglected in previous studies.

Results. – We begin our simulations with a statistically stationary, driven turbulent flow in which N_p microorganisms are placed at random locations, with velocity vectors matching that of the local fluid velocity field. We then let the system evolve for a very long time to see the emergent dynamical behaviour. At sufficiently large times (which are comparable to several large-eddy-turnover times of the fluid), the motion of the microorganisms organises itself depending on, crucially, the Stokes number St and the normalised interaction radius ξ . Statistically speaking, the behaviour of these microorganisms at such times is stationary and several measures can be defined, as below, to characterise their motion. Therefore, we ignore the transient stage and comment below on the final evolved system at late times.

Let us begin by understanding qualitatively the effect of turbulence, self-propulsion, and inertia on the flocking of these microorganisms, as shown in fig. 1. By comparing fig. 1(a) (for small values of $|\mathbf{V}_i^p|$ and St, and large values of ξ) with fig. 1(b) (for large values of $|\mathbf{V}_i^p|$ and St, and small values of ξ), we find that the level of flocking is strongly dependent on the physical parameters of the problem. In order to develop a detailed understanding of this effect, let us first define a measure for this level of flocking, or global ordering.

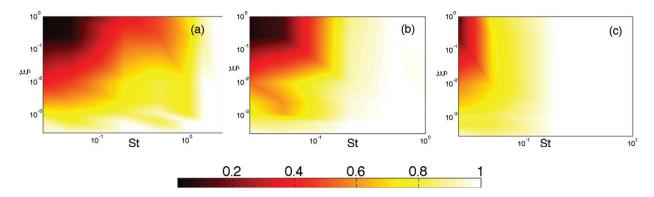


Fig. 2: (Color online) Pseudocolor plots of the global order ϕ as a function of log ξ and log St for (a) $v_p = 0.02$, (b) $v_p = 0.2$, and (c) $v_p = 0.8$. The value of the noise $\eta = 0.01$ for all these plots.

Global ordering can be characterised most conveniently [5] by quantifying the level of alignment of the velocity vectors of individuals via

$$\phi = \frac{\left|\sum_{i=1}^{N_p} \mathbf{v}_i\right|}{\sum_{i=1}^{N_p} |\mathbf{v}_i|}.$$
 (7)

As can be easily seen from the above definition, perfect global ordering or flocking yields $\phi=1$ and a complete absence of any flocking yields $\phi=0$. Furthermore, to smoothen out fluctuations, we take average ϕ over time in the statistically stationary phase.

Let us now understand how the nature of flocking changes as a function of ξ , St, and $|\mathbf{V}_{i}^{p}|$ for a given noise. In fig. 2 we show pseudocolor plots for ϕ as a function of ξ and St, for different values of $|\mathbf{V}_{i}^{p}|$, which increases as we go from fig. 2(a) to fig. $2(c)^{1}$. These figures reveal a hitherto unknown mechanism which might provide a mechanical explanation for the ubiquitous nature of flocking in some microorganisms. For any given value of $|\mathbf{V}_{i}^{p}|$, it is well known since the work of Vicsek et al. [5] and various other authors [6,16–19], that the global order gets destroyed (i.e., $\phi \to 0$) as the interaction distance becomes smaller and smaller (or ξ becomes larger and larger). We find that, remarkably, global order can be restored even for large ξ (as shown in fig. 2), because of the effect of the finite size of the microorganism (as characterised by the Stokes number). Therefore we find that, even for large $\xi \to 1$ although $\phi \to 0$ for small Stokes numbers, as we increase St the global order is restored $(\phi \to 1)$. This is true qualitatively for all our values of $|\mathbf{V}_i^p|$, although the precise dependence of ϕ on St and ξ depends weakly on the self-propelled velocity: with increasing $|\mathbf{V}_{i}^{p}|$, the onset of global order happens for smaller St.

This result is remarkable, principally because it shows for the first time that even if there is a limitation to the visual mechanism to flock, inertial effects or finiteness of the organisms will lead them to come closer and closer to each other, and hence overcome the barrier imposed by the limited range of them picking up visual cues on the preferred collective orientation. In other words, in the absence of inertia such organisms would never have been able to flock.

Along with the onset of global order and stable flocks, a second feature emerges. Qualitatively this is already seen in fig. 1; organisms with a smaller self-propelled velocity tend to a have greater variation in their speeds than the ones with a larger $|\mathbf{V}_i^p|$ (fig. 1(a)). This leads us to ask: is it possible that flocking is accompanied with a homogenisation of velocities of the individual organisms? Physically this should certainly be the case, because for a flock to be stable each organism should move not only in the same average direction but also with the same speed. We investigate, within our model, a quantitative measure to see how inertia helps in stabilising a flock.

In figs. 3(a) and (b), we show the mean velocity of the N_p microorganisms and the standard deviation of their velocities respectively, as a function of St and ξ for $|\mathbf{V}_{i}^{p}| = 0.02$; in figs. 3(c) and (d) the corresponding plots for $|\mathbf{V}_{i}^{p}| = 2.2$ are shown. These figures are remarkable for a variety of reasons. The mean speed for any given Stokes number has a weak dependence on ξ , and as $|\mathbf{V}_{i}^{p}|$ increases this dependence grows even weaker. As can be easily seen from figs. 3(a) and (c), the mean speed increases by close to a factor of 5 as we go from tracer-like particles (size and massless organisms) to those with finite Stokes numbers. Even more remarkable, by comparing figs. 3(b) and (d), we find that the variation in the speeds amongst individuals for any St and ξ becomes increasingly weaker as $|\mathbf{V}_{i}^{p}|$ increases. This is a quantitative measure of what was already observed qualitatively in fig. 1. Furthermore we find a non-trivial and non-monotonic dependence of the variations in speeds (figs. 3(b) and (d)) as a function of St and ξ . This dependence however becomes more monotonic as $|\mathbf{V}_{i}^{p}|$ increases (as can be seen by comparing figs. 3(b) and (d)). Thus a measurement of the statistics of the speeds of individual organisms gives us an insight as to the stability of flocks and emergence of global order when

 $^{^{1}}$ The noise is fixed to the smallest value used in our simulations for these figures; we have checked that the qualitative features seen here are independent of the noise strength.

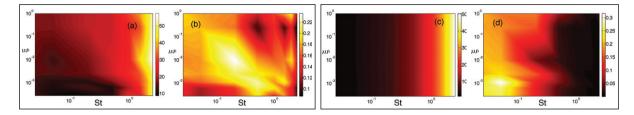


Fig. 3: (Color online) Pseudocolor plots of the mean velocity (a) and (c) and the standard deviation (b) and (d) as a function of $\log \xi$ and $\log St$; the left panels (a) and (b) are for $|\mathbf{V}_i^p| = 0.02$; the right panels (c) and (d) are for $|\mathbf{V}_i^p| = 2.2$. The velocities have been normalised by the value of the self-propelled velocity $|\mathbf{V}_i^p|$. We choose the largest value of the noise and $\eta = 1.0$ for these plots.

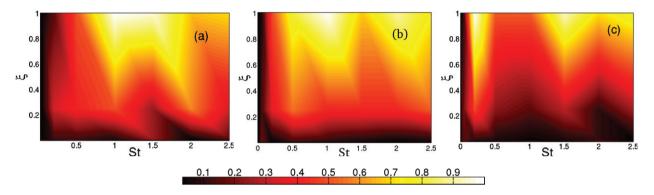


Fig. 4: (Color online) Pseudocolor plots of the local order ϕ_{local} as a function of ξ and St for (a) $|\mathbf{V}_i^p| = 0.02$, (b) $|\mathbf{V}_i^p| = 0.2$, and (c) $|\mathbf{V}_i^p| = 0.8$. The value of the noise $\eta = 0.01$ for all these plots.

inertia of the microorganisms start playing a significant role, and contrary to other theoretical models for such selforganised behaviour, we find that inertia might be more fundamental to understanding flocking behaviour than the radius of interaction.

So far we have concentrated on global features and the stability of the entire collection of microorganisms. It behooves us now to ask what happens locally. Is the population one single giant flock, or do they break up into smaller groups all of which nevertheless move in the same direction? In order to answer these questions, we need to define an individual cluster or sub-flock as a collection of $N_c > 5$ microorganisms, such that each microorganism has at least one neighbour within a distance r_{\min} and with an orientation vector in the same direction itself (within a small variation of a few degrees). The number of such sub-flocks are denoted by $N_{\text{sub-flocks}}$. We choose $r_{\min} = nN_0^{-1/2}$, where n is an integer 1 < n < 6; our results do not change qualitatively for n within this range. We define $\phi_{\text{local}} = \frac{\langle N_{\text{sub-flocks}} \rangle}{N_p}$ as the local order parameter, and examine its dependence for a given $|\mathbf{V}_{i}^{p}|$ as a function of St and ξ as well as how this behavior changes with increasing $|\mathbf{V}_{i}^{p}|$ in fig. 4. Heuristically, in the absence of inertia, $\phi_{\rm local} \rightarrow 1/N_p \approx 0$ as $\xi \rightarrow 0$ [6]. This is because, as the interaction radius increases more and more microorganisms get co-ordinated, reducing the number of sub-flocks $N_{\text{sub-flocks}}$ (and hence $\phi \to 0$). However as ξ becomes larger, the number of sub-flocks grow and

 ϕ_{local} becomes larger; indeed if we relax the definition of a sub-flock to allow $N_c = 1$, then as $r_{\text{int}} \to 0$ $\phi_{\text{local}} \to 1$.

In fig. 4 we show the behaviour of the local order; for clarity we have normalised ϕ_{local} in each panel with its largest value. For a given $|\mathbf{V}_{i}^{p}|$, the dependence on the ξ -St parameter space is far from trivial. As inertia increases particles tend to preferentially cluster, and hence there is a non-monotonic behaviour of ϕ_{local} , because of the competition between finite inertia (which tends to break up the population into smaller sub-groups via preferential concentration) and the interaction radius (which decides for a given St how global the interactions will be). Although the overall dependence on ξ -St is far from obvious, for a given value of St, we do see qualitatively the behaviour of ϕ_{local} as a function of ξ in agreement with the picture described above. The quasi-symmetry around the line St = 1 is easily understood in terms of the quasi-symmetry around St for plots of the correlation dimension D_2 vs. St, which quantifies the idea of preferential concentration in problems of turbulent transport [9]: The degree of preferential concentration on either side of the maximum of clusterization at Stokes number St_{min} is not symmetric; therefore as the Stokes number increases from St_{min} particles stay clustered more than when the Stokes number decreases from St_{min} . We conjecture that this change in the nature of clusterization around St_{min} is the reason for the assymetry seen in this figure. This quasi-symmetry slowly vanishes as $|\mathbf{V}_{i}^{p}|$ increases (fig. 4(a) to fig. 4(c)), because as microorganisms become more active they are able to overcome the dynamics dictated by pure linear drag.

Conclusions. – In this letter we have studied the ubiquitous phenomena of flocking by taking into consideration, for the first time, the effects of inertia as well as a turbulent environment. Given the exploratory nature of this work, we study this problem in detail for twodimensional flows —in the spirit of the pioneering work of Vicsek et al. [5]— because it allows for a clearer understanding of the problem. Moreover in a variety of natural settings—in the ocean or in the atmosphere—flows can be effectively modelled by the two-dimensional, incompressible Navier-Stokes equation. We have been able to show that flocking can arise purely because of inertia even when visual cues (quantified by using a radius of interaction) are weak. This is a striking result and can be used to explain emergence of co-ordinated behaviour in environments such as ocean surfaces or deep seas. We were also able to show the complex local dynamics of individual sub-flocks and individual microorganisms, which are key to understanding this phenomena. Thus the importance of this work lies in coupling problems of passive transport in flows to what we see in active matter that abound in nature.

Often in nature, organisms are embedded in threedimensional flows. Although we believe our results in two-dimensional flows will not qualitatively change in three dimensions, this problem, along with the issue of finite-size effects, merits a detailed study. Additionally, more realistic microorganisms should be modelled beyond the point-particle spherical approximation, by including shape and internal degrees of freedom. Also flocking amongst large animals (such as birds) cannot be captured in this framework; to do so, we will need to model large structures in flows by resolving boundaries. Furthermore, our model can also be adapted to understand the predatorprey behaviour from the point of view of mechanics as well as foraging in a random environment, by suitably adapting the model developed in this letter. Therefore, these and many others are outstanding questions that remain unanswered and will be the subject of future work, which we hope will be inspired by the fluid-mechanical transport approach developed in this paper.

* * *

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REFERENCES

- PARRISH J. K. and EDELSTEIN-KESHET L., Science, 284 (1999) 99.
- [2] TOPAZ C. M., BERTOZZI A. L. and LEWIS M. A., Bull. Math. Biol., 68 (2006) 1601.
- [3] Eftimie R., de Vries G., Lewis M. A. and Lutscher F., Bull. Math. Biol., 69 (2007) 1537.
- [4] GIARDINA I., HFSP J., 2 (2008) 205.
- [5] VICSEK T., CZIRÓK A., BEN-JACOB E., COHEN I. and SHOCHET O., Phys. Rev. Lett., 75 (1995) 1226.
- [6] KHURANA N. and OUELLETTE N., New J. Phys., 15 (2013) 095015.
- [7] Baggaley A. W., Phys. Rev. E, **91** (2015) 053019.
- [8] Durham W. M., Climent E., Barry M., De Lillo Filippo, Boffetta G., Cencini M. and Stocker R., *Nat. Commun.*, 4 (2013) 2148.
- [9] BEC J., BIFERALE L., CENCINI M., LANOTTE A., MUSACCHIO S. and TOSCHI F., Phys. Rev. Lett., 98 (2007) 084502.
- [10] MAXEY M. R. and RILEY J. J., Phys. Fluids, 26 (1983) 883.
- [11] PERLEKAR P., RAY S. S., MITRA D. and PANDIT R., Phys. Rev. Lett., 106 (2011) 054501.
- [12] RAY S. S., MITRA D., PERLEKAR P. and PANDIT R., Phys. Rev. Lett., 107 (2011) 184503.
- [13] BOFFETTA G. and SOKOLOV I. M., Phys. Fluids, 14 (2002) 3224.
- [14] Yen J. and Bundock E. A., Aggregate behavior in zooplankton: Phototactic swarming in four developmental stages of Coullana canadensis (Copepoda, Harpacticoida), in Animal Groups in Three Dimensions, edited by Parrish J. K. and Hamner W. M. (Cambridge University Press) 1997, pp. 143–162; Ambler J. W., Hydrobiologia, 480 (2002) 155164.
- [15] JIMÉNEZ J., Sci. Mar., 61, Suppl. 1 (1997) 47.
- [16] CHEN X., DONG X., BE'ER A., SWINNEY H. L. and ZHANG H. P., Phys. Rev. Lett., 108 (2012) 148101.
- [17] BUHL J., SUMPTER D. J. T., COUZIN I. D., HALE J. J., DESPLAND E., MILLER E. R. and SIMPSON S. J., Science, 312 (2006) 1402.
- [18] COUZIN I. D., KRANSE J., JAMES R., RUNTON G. D. and FRANKS N. R., J. Theor. Biol., 218 (2002) 1.
- [19] KELLEY D. H. and OUELLETTE N. P., Sci. Rep., 3 (2013) 1073.