A model for gyrotactic pattern formation of motile micro-organisms in turbulence

K. Gustavsson\(^1\), F. Berglund\(^1\), P.R. Jonsson\(^2\), and B. Mehlig\(^1\)

\(^1\) Department of Physics, Gothenburg University, SE-41296 Gothenburg, Sweden
\(^2\) Department of Biological and Environmental Sciences - Tjärnö, SE-45296 Strömstad, Sweden

Recent studies show that spherical motile micro-organisms in turbulence subject to gravitational torques gather in down-welling regions of the turbulent flow. By analysing a statistical model we analytically compute how shape affects this preferential sampling and small-scale spatial clustering (determining local encounter rates). By recursively refining approximations for the paths the organisms take through the flow we determine how preferential sampling and small-scale clustering in the model depend upon the dimensionless parameters of the problem. We show that singularities (‘caustics’) affect the dynamics of motile micro-organisms.

PACS numbers: 05.40.-a, 47.63.Gd, 47.27.-i, 92.20.jf

Patchiness in suspensions of micro-organisms is frequently observed on a range of spatial scales. There is a long-standing debate about the underlying mechanisms, for instance density stratification and vertical shears \(^1\), predator-prey cycles, and interactions between the organisms with water-column gradients — in light, chemistry, turbulence, and in hydrostatic pressure \(^2\). The resulting small-scale inhomogeneities in the number density are important because many biological processes (maturing, feeding, predation) rely on encounters between individuals \(^3\), and the encounter rate is strongly influenced by local number-density fluctuations.

Gravitaxis may cause inhomogeneities in the spatial distribution of motile micro-organisms. Density- or drag-asymmetries of the body give rise to torques affecting the swimming direction \(^4\)\(^6\). When the effects of gyrotactic torques and fluid-velocity gradients balance, inhomogeneities may form in the spatial distribution, as shown by the micro-alga *Chlamydomonas nivalis* swimming up against a down-welling pipe flow. The micro-algae gather in the centre of the pipe where the down-welling velocity is largest \(^7\). Gyrotaxis may trap motile organisms in macroscopic shear gradients \(^8\)\(^9\), and fluctuating vorticity may cause patchiness \(^10\). This is confirmed by recent direct numerical simulations (DNS) of motile, spherical micro-organisms in turbulence \(^11\) that reveal spatial inhomogeneities, the organisms preferentially sample down-welling regions of the turbulent flow.

These results raise three fundamental questions that we address and answer in this Letter. We solve a statistical model, taking into account recursively \(^20\)\(^22\) how gyrotaxis and fluid-velocity gradients determine the trajectories of the organisms through the flow.

First, how does shape affect the dynamics of motile micro-organisms in turbulence subject to gyrotaxis? The organisms in \(^11\) were assumed to be spherical. Non-spherical organisms respond not only to turbulent vorticity but also to turbulent strain \(^12\)\(^15\). This causes passive rods to exhibit intricate orientational patterns on the surface of turbulent and other complex flows \(^16\)\(^18\). Also, shape strongly affects the trajectories of active particles in model flows \(^19\)\(^20\), and recent DNS indicate that prolate gyrotactic organisms cluster less than spherical ones when gyrotaxis is strong \(^21\). But what happens in other parameter regimes? Second, are there circumstances where the organisms may not gather in down-welling regions? Are there other, independent, criteria that determine where the organisms go in the turbulence? Third, noting that particles tend to gather in certain regions of the flow does not explain which mechanisms actually cause them to get in contact. Small-scale fluctuations in the number density of the organisms, on scales of the order of their size, directly affect encounter rates. How are such fluctuations related to preferential sampling of the turbulent velocities and their gradients?

Our calculations also show that singularities in the motion of nearby micro-organisms randomise their swimming directions, similar to ‘caustics’ for heavy particles in turbulence \(^22\)\(^24\). How can the effect of these singularities be incorporated in phenomenological models for encounter rates \(^25\)?

**Statistical model.** We use a simplified equation \(^7\)\(^11\)\(^21\) for the translation and rotation of small axisymmetric active particles subject to turbulence and gyrotaxis:

\[
\dot{r} = \mathbf{v} = \mathbf{u}(r,t) + v_n\mathbf{n} \quad \text{and} \quad \dot{n} = \mathbf{\omega}(r,t) \wedge \mathbf{n}.
\]

(1)

Dots denote derivatives w.r.t. time \(t\), \(r\) is the particle position. It swims with constant speed \(v_n\) in the direction of the unit vector \(\mathbf{n}\) aligned with the symmetry axis of the particle. The turbulent velocity field is denoted by \(\mathbf{u}(r,t)\), and the angular velocity of the particle is

\[
\mathbf{\omega}(r,t) = -(\mathbf{n} \wedge \mathbf{g})/(2\mathcal{B}) + \mathbf{\Omega}(r,t) + \Lambda\mathbf{n} \wedge [\mathbf{S}(r,t)n].
\]

(2)

The first term on the r.h.s describes gyrotaxis. The unit vector \(\mathbf{g}\) points in the direction of gravity (\(-e_z\) in the three-dimensional model), \(\mathcal{B}\) is the gyrotactic re-orientation time \(^7\)\(^11\). It depends on the mass distribution within the particle, and also on its shape. The other terms on the r.h.s. of Eq. (2) represent the effect of the turbulent velocity gradients upon the particle orientation \(^12\). The vector \(\mathbf{\Omega} = (\nabla \wedge \mathbf{u})/2\) equals half the flow vorticity, \(\mathbf{S}\) is the strain-rate matrix, the symmetric part of
the matrix $A$ with elements $A_{ij} = \partial u_i / \partial r_j$. The parameter $\Lambda$ characterises the shape of the particle: $\Lambda = 0$ for spheres, and $\Lambda = 1$ for infinitely thin rods. Eq. (2) disregards turbulent accelerations. In most marine conditions this is an excellent approximation [29]. We model the turbulent fluctuations in the dissipative range by 2- and 3-dimensional, incompressible, homogeneous, and isotropic Gaussian random velocity fields with correlation length $\eta$, correlation time $\tau$, and typical speed $u_0$ [28]. The model is appropriate for organisms smaller than the Kolmogorov length of the turbulence. For larger organisms inertial-range properties become important [30]. We use dimensionless variables $t' = t/\tau$, $r' = r/\eta$, $u' = u/u_0$, and drop the primes in the following.

There are four dimensionless parameters: the shape parameter $\Lambda$, the dimensionless swimming speed $\Phi = v_s/u_0$, and the inverse strength of gyrotaxis $\Psi = 1/\eta \tau$. We vary $\Psi$ and $\Lambda$ independently, keeping $\beta$ constant as $\Lambda$ is varied. The parameters $\Phi$ and $\Psi$ can assume values of order unity in fully-developed turbulence. In most marine conditions, and $\Lambda = 1$ for infinitely thin rods. Eq. (2) disregards turbulent accelerations. In most marine conditions this is an excellent approximation [29].

**Method.** The non-linear problem (1,2) can be solved by iteratively refining approximations for the path a particle takes through the flow [28]. This results in expansions of steady-state averages in powers of $Ku$ and allows to determine how the remaining parameters ($\Phi$, $\Psi$, and $\Lambda$) affect preferential sampling and small-scale clustering at finite but small Kubo numbers. The first step is to insert the ansatz $n(r_1, t) = \sum_{q=0}^{\infty} n_q(r_0, t) Ku^q$ into (1). Identifying terms of order $Ku^p$ results in equations for $n_q$ that can be solved in terms of integrals over $n_p$ for $p < q$. The lowest-order solution in $Ku$, $n_0$, is deterministic and independent of $u$ and gradients of $u$. It approaches $-\mathbf{\dot{g}}$ as $t \to \infty$. Since the steady state of the dynamics must be independent of the initial orientations we can simply put $n_0 = -\mathbf{\dot{g}}$. This yields a lowest-order deterministic approximation $r^{(d)}$ for the particle position at time $t$, $r^{(d)}_i = r_0 - Ku \Phi \mathbf{\dot{g}} t$. Second we substitute the recursive solution for $n_i$ into the implicit solution of (1):

$$r = r^{(d)} + Ku \int_0^t dt' \left( u(r_{t'}, t') + \Phi \sum_{q=1}^{\infty} n_q(r_{t'}, t') Ku^q \right), \quad (3)$$

and expand all quantities in Eqs. (1) that depend on $r_i$ in terms of $\delta r_i \equiv r_i - r^{(d)}_i$ as described in Ref. [28]. Third we average over the fluid-velocity fluctuations in the statistical model. In the remainder of this Letter we summarise the results obtained in this way.

**Preferential sampling.** To leading order in $Ku$ we find for the steady-state averages of the fluid velocity and gradients evaluated at the particle position $(i, j = x, y, z)$:

$$\langle u_i \rangle = \frac{\sum_{q=1}^{\infty} n_q(r_{t'}, t') Ku^q}{\sum_{q=0}^{\infty} n_q(r_{t'}, t') Ku^q}, \quad (4a)$$

$$\langle A_{ij} \rangle = \frac{\sum_{q=1}^{\infty} \frac{1}{4\sqrt{2} F^3} \left( [1+4\Psi+4\Psi^2(1-(d+1)^2) + \Lambda (1+4\Psi+4\Psi^2 (1+(d+1)^2))] F \left[ 1+2\Psi \sqrt{\frac{1}{2} F} \Psi \right] \right)}{\sum_{q=0}^{\infty} \frac{1}{4\sqrt{2} F^3} \left( [1+4\Psi+4\Psi^2(1-(d+1)^2) + \Lambda (1+4\Psi+4\Psi^2 (1+(d+1)^2))] F \left[ 1+2\Psi \sqrt{\frac{1}{2} F} \Psi \right] \right)}, \quad (4b)$$

with $\mathcal{F}(x) = \sqrt{\pi} \exp(x^2) \text{erfc}(x)$ and $F \equiv Ku \Phi = v_s \tau / \eta$. Eqs. (4) allow us to determine how shape affects preferential sampling in the statistical model at finite (but small) Kubo numbers. Fig. [2] shows the steady-state average $\langle u_z \rangle$ of the $z$-component of the fluid velocity for the 2-dimensional statistical model for $Ku = 0.1$. The same is found in $d = 3$ for small Ku, as Eq. (4b) shows.

**Gyrotaxis and motility.** Gyrotaxis and motility break the up-down and fore-aft symmetry of the problem. When $\Psi$ is small the particles swim essentially upwards and are expected to collect in the sinks of the transversal flow-velocity field characterised by $\text{Tr}_S < 0$ (in 3 spatial dimensions $\text{Tr}_S = \partial \times u_x + \partial_u u_y$). Fig. [2] shows that $\langle\text{Tr}_S \rangle \sim 0$ indicating that the particles gather in transversal sinks, irrespective of the shape ($0 \leq \Lambda \leq 1$). For small Ku the same is true for $d = 3$ as Eq. (4b) shows. Note that $\text{Tr}_S = -S_{zz}$ since $u$ is incompressible.

**Small-scale clustering.** Which mechanisms cause two
particles caught in the same flow region to actually collide? This is a two-particle problem. Fluctuations in the separations between nearby particles are determined by the dynamics of the matrix \( Z \) of particle-velocity gradients \( Z_{ij} = \partial v_i / \partial r_j \). Eq. \( \ref{eq:matrix} \) shows that \( Z = \Lambda + \Phi Y \) where \( Y \) has elements \( Y_{ij} = \partial n_i / \partial r_j \). The statistics of \( Y \) is given by the history of fluid-velocity gradients encountered by the particles, and small-scale clustering (on scales of the order of the particle size) is determined by \( \text{Tr} \, Z = \nabla \cdot v \) and not directly by the fluctuations of \( \Lambda \). Our theory allows us to compute \( \langle \nabla \cdot v \rangle_\infty \) to order \( Ku^2 \):
pointing along the separation $\vec{R}$ between two nearby particles. For $d = 2$ we find:

$$
\langle (\vec{R} \cdot \hat{g})^{2p} \rangle_\infty = \frac{(2p-1)!!}{2^p p!} \left[ 1 + \frac{p F^2}{p+1} - \frac{p(41+19p) F^4}{4(p+1)(p+2)} \right]
$$

(11)

(the same expression is found for the moments of $\vec{R} \cdot \hat{g}$ for particles settling in a turbulent aerosol [27]).

Fig. 2 shows that the resulting fractal Lyapunov dimension $d_\lambda$ is in good agreement with numerical simulations of the statistical model ($d = 2$) as a function of $\Phi$ for $\text{Ku} = 0.1$ and different values of $\Psi$. We see that spherical organisms cluster more than rods, as mentioned above. But when the effect of the gravitational torque is small then prolate organisms cluster more as explained above. Panel b in Fig. 2 demonstrates this crossover. It shows $d_\lambda$ for $\Phi = 2$, $\text{Ku} = 1$ as a function of $\Psi$. The cross-over occurs at $\Psi_c \approx 0.26$ for the parameter values shown. We arrive at qualitatively similar conclusions by numerically computing the fractal correlation dimension $d_\gamma$ [28]. But the numerical values found for $d_\gamma$ differ from $d_\lambda$ (the cross-over value $\Psi_c$ differs too). This shows that the spatial distribution is multifractal [22].

**Caustics.** The dynamics of $Y$ exhibits singularities. In the deterministic limit the $n$-dynamics has a stable fixed point at $n^* = -\hat{g}$. In two dimensions there are only two independent elements of $Y$, with dynamics

$$
\dot{Y}_{11} = -\frac{Y_{11}}{2\Psi} - \text{Ku}_{\Phi} Y_{11}^2, \quad \dot{Y}_{12} = -\frac{Y_{12}}{2\Psi} - \text{Ku}_{\Phi} \Phi Y_{12} Y_{11}.
$$

(12)

For $\Psi < \infty$ his system has a stable fixed point at $(0,0)$ and a line of marginal fixed points at $Y_{11} = -1/(2\text{Ku}_{\Phi}\Psi)$. Weak turbulent fluctuations cause $Y_{11}$ and $Y_{12}$ to repeatedly diverge to $-\infty$. These singularities are analogous to caustics in inertial-particle dynamics [22,24] and correspond to instances where the $n$-field becomes multi-valued so that nearby particles can have very different orientations, leading to a defocusing of the swimming directions. The rate of caustic formation is larger for larger $\Phi$ and $\Psi$ (not shown). At small $\Psi$ the problem of calculating the rate of caustic formation can be mapped onto a Kramers escape problem [30].

**Conclusions.** First, our statistical-model calculations show how the dynamics of gyrotactic motile microorganisms depends on the dimensionless parameters of the problem: $\Lambda$ (shape), $\Phi$ (swimming speed), and $\Psi$ (inverse strength of gyrotaxis), for finite but small values of the Kubo number. Second, the particles tend to preferentially sample positive values of $S_{zz}$, corresponding to sinks in the transversal flow. Spherical particles are more often found in regions where $u_z$ is negative, for rod-like particles this effect is weaker. In the statistical model rods may in fact sample up-welling regions of the flow for larger swimming speeds, albeit weakly. Third, we have analytically computed how the degree of small-scale spatial clustering determined by the history of fluid-velocity gradients that the particles have encountered depends on their shape. This is important because small-scale fractal clustering enhances encounter rates of the particles. For spherical particles and small values of $\Psi$ and $\Phi\Psi$ our results are consistent with those of Ref. [11]. Since $\text{Ku} \sim 1$ in turbulence it is necessary to determine to which extent the new results derived in this Letter (and the corresponding mechanisms) explain patchiness and encounter rates of motile micro-organisms in the ocean. A detailed comparison between the statistical-model results and DNS in turbulence would also show how time-reversal symmetry breaking, vortex tubes, and intermittency affect the dynamics of motile micro-organisms. It would be of interest to analytically calculate the fractal correlation dimension $d_\gamma$ for the statistical model, in particular for large values of $\Phi$ and $\Psi$.

Finally we have shown that singularities (caustics) occur in the particle dynamics. How the rate of caustic formation depends on the dimensionless parameters $\Lambda$, $\Phi$ and $\Psi$ is not yet known. Caustics may significantly enhance encounter rates and it is of great interest to quantify this effect, in DNS of active particles in turbulence, and in the statistical model.

**Acknowledgments.** This work was supported by Veten-
skapsrådet (VR), by a Linnaeus-grant from VR and Formas (http://www.cemeb.science.gu.se), and by the Göran Gustafsson Foundation for Research in Natural Sciences and Medicine. The numerical computations were performed using resources provided by C3SE and SNIC.

[1] P. J. S. Franks and J. S. Jaffe, J. Marine Sys. 69, 254 (2008).
[2] C. L. Folt and C. W. Burns, Trends Ecol. Evol. 300, 14 (1999).
[3] T. Kiørboe, *A mechanistic approach to plankton ecology* (Princeton University Press, New Jersey, USA, 2008).
[4] A. M. Roberts, J. Exp. Biology 53, 687 (1970).
[5] P. Jonsson, Marine Ecol. Prog. Ser. 52, 39 (1989).
[6] A. M. Roberts and F. M. Deacon, J. Fluid. Mech. 452, 405 (2002).
[7] J. O. Kessler, Nature 313, 218 (1985).
[8] W. M. Durham, J. O. Kessler, and R. Stocker, Science 323, 1067 (2009).
[9] F. Santamaria, F. De Lillo, M. Cencini, and G. Boffetta, Phys. Fluids 26, 111901 (2014).
[10] J. G. Mitchell, A. Okubo, and J. A. Fuhrmann, Limnology and Oceanography 35, 123 (1990).
[11] W. M. Durham, E. Climent, M. Barry, F. De Lillo, G. Boffetta, M. Cencini, and R. Stocker, Nature Comm. 4, 2148 (2013).
[12] G. B. Jeffery, Proc. R. Soc. A 102, 161 (1922).
[13] S. Parsa, E. Calzavarini, F. Toschi, and G. A. Voth, Phys. Rev. Lett. 109, 134501 (2012).
[14] K. Gustavsson, J. Einarsson, and B. Mehlig, Phys. Rev. Lett. 112, 014501 (2014).
[15] M. Byron, J. Einarsson, K. Gustavsson, G. A. Voth, B. Mehlig, and E. Variano, arxiv:1412.3166 (2014).
[16] M. Wilkinson, V. Bezuglyy, and B. Mehlig, Phys. Fluids 21, 043304 (2009).
[17] V. Bezuglyy, B. Mehlig, and M. Wilkinson, Europhys. Lett. 89, 34003 (2010).
[18] M. Wilkinson, V. Bezuglyy, and B. Mehlig, J. Fluid Mech. 667, 158 (2011).
[19] W. M. Durham, E. Climent, and R. Stocker, Phys. Rev. Lett. 106, 238102 (2011).
[20] N. Khurana and N. T. Ouellette, Phys. Fluids 24, 091902 (2012).
[21] C. Zhan, G. Sardina, E. Lushi, and L. Brandt, J. Fluid Mech. 793, 22 (2014).
[22] M. Wilkinson and B. Mehlig, Europhys. Lett. 71, 186 (2005).
[23] G. Falkovich, A. Fouxon, and G. Stepanov, Nature 419, 151 (2002).
[24] K. Gustavsson, E. Meneguz, M. Reeks, and B. Mehlig, New J. Phys. 14, 115017 (2012).
[25] B. J. Rothschild and T. R. Osborn, J. Plankton Res. 10, 465 (1988).
[26] K. Gustavsson and B. Mehlig, Europhys. Lett. 96, 60012 (2011).
[27] K. Gustavsson, S. Vajedi, and B. Mehlig, Phys. Rev. Lett. 112, 214501 (2014).
[28] K. Gustavsson and B. Mehlig, arxiv:1412.4374 (2014).
[29] F. De Lillo, M. Cencini, W. M. Durham, M. Barry, R. Stocker, E. Climent, and G. Boffetta, Phys. Rev. Lett. 112, 044502 (2014).
[30] H. Pécseli, J. Trulsen, and Ø. Fiksen, Progress in Oceanography 101, 14 (2012).
[31] H. Yamazaki and K. D. Squires, Mar. Ecol. Prog. Series 144, 299 (1996).
[32] S. M. Gallager, H. Yamazaki, and K. D. Squires, Mar. Ecol. Prog. Series 267, 24 (2004).
[33] M. Cencini, talk given at ICTS-EADS discussion Meeting in Bangalore, India, 14-18 October 2013 (2013).
[34] B. Andersson, K. Gustavsson, B. Mehlig, and M. Wilkinson, Europhys. Lett. 80, 60001 (2007).
[35] J. Kaplan and J. A. Yorke, Springer Lecture Notes in Mathematics 730, 204 (1979).
[36] B. Mehlig and M. Wilkinson, Phys. Rev. Lett. 92, 250602 (2004).