Clustering of gyrotactic microorganisms in turbulent flows

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We study the spatial distribution of gyrotactic microorganisms transported by a three-dimensional turbulent flow generated by direct numerical simulations. We find that gyrotaxis combines with turbulent fluctuations to produce small scales (multi-)fractal clustering. We explain this result by showing that gyrotactic swimming cells behave like tracers in a compressible flow. The effective compressibility is derived in the limits of fluid acceleration much larger and smaller than the gravity.

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Microbial patchiness in oceans is important for ecological and evolutionary dynamics and for biogeochemical processes. In motile aquatic microorganisms, self-propulsion provides a mechanism to escape fluid pathways, potentially leading to small-scale patchiness. Remarkably, motility combined with fluid flows can also generate large-scale inhomogeneities. For instance, spectacular aggregation of phytoplankton cells (in layers centimeters to meters thin, horizontally extending from hundreds of meters to kilometers) can result from vertical shears and gyrotactic swimming. Gyrotaxis characterizes several species of motile microalgae whose swimming direction is determined by the balance of viscous and gravitational torques, due to the displacement between the cell center of mass and buoyancy. As an effect of such balance, for example, gyrotactic algae aggregate in the center (wall) of descending (ascending) vertical pipe flows. Gyrotaxis is observed in algae, e.g., of the genus *Chlamydomonas*, which can be engineered to transport microloads, or *Dunaliella*, employed in biofuels. So far most studies focused on the dynamics of gyrotactic microorganisms in simple stationary flows or kinematic models. In this Letter, we investigate the interplay between gyrotactic motility and realistic turbulent flows, as occurring in the sea. We find that turbulence and gyrotaxis combine to generate inhomogeneous distributions with small-scale (multi-)fractal statistics (see Fig. 1). We study the limit of gravitational acceleration much smaller or larger than turbulent accelerations to identify the mechanisms responsible for gyrotactic clustering in terms of an effective compressible velocity field.

In this Letter, we consider dilute suspensions of non interacting motile microorganisms, much smaller than the smallest scale of turbulence, the Kolmogorov length $\eta$. We can thus model them as self-propelled particles with velocity, given by the sum of the fluid velocity $u$ at the particle position $X$ and the swimming contribution $v_s p$, where the swimming speed $v_s$ is assumed constant.

$$\ddot{X} = u(X, t) + v_s p,$$

where $\omega$ is the fluid vorticity and $v_o = 3v/h$ is the orientation speed for spherical cells subject to the acceleration $A$. In a fluid at rest, besides viscous forces, only gravity (and buoyancy) $g$ is acting and thus $A = -g$. Parameters correspond to circled symbols in Fig. 1 and Fig. 3, respectively.

We consider the fluid acceleration given by the Navier-Stokes equations ruling the velocity $u$ of an incompressible fluid with viscosity $\nu$, pressure $p$ and stirred by an external forcing $f$. Previous studies on gyrotactic swimmers disregarded fluid acceleration, as mainly focused on simple, non-turbulent flows where $|a| \ll g$. In turn-
bulence, fluid acceleration can locally exceed $g$ and therefore its contribution has to be taken into account.

The first term on the rhs of Eq. 2 causes the direction of swimming $\mathbf{p}$ to align with $\mathbf{A}$ on a time scale $v_\nu/A$. When the contribution of fluid acceleration can be neglected, cells tend to orient vertically ($\mathbf{p} \to \hat{z}$) on a time scale $B = v_\nu/g$. The alignment is contrasted by the vorticity term $\omega \times \mathbf{p}$ and, depending on $B\omega$ being smaller or larger than 1, cells may swim along a resulting local equilibrium direction or tumble randomly as the orientation becomes unstable due to vorticity. In principle, the swimming direction may be modified also by rotational Brownian motion and tumbling due to flagella desynchronization during swimming, which are here neglected. The former effect is very small for typical algae (having size $O(10\mu m)$); the latter can be neglected whenever the tumbling time is longer than the reorientation one.

We study gyrotactic swimming in homogeneous and isotropic turbulent velocity fields of moderate intensity ($Re_\lambda \approx 65 - 100$) by means of direct numerical simulations of Navier-Stokes equations. In particular, Eq. 1 is solved by means of a standard pseudospectral algorithm with 2nd order Runge-Kutta time-stepping, on a tri-periodic cubic grid of size $N^3$ (for $N = 128$ and 256). Statistical stationarity is guaranteed by means of a zero mean, Gaussian and white in time random forcing $\mathbf{f}$ restricted to large scales. Viscosity $\nu$ is such that the Kolmogorov length $\eta$ is of the order of the grid spacing, ensuring well resolved small-scale velocity dynamics. For different values of $g$, several populations of swimmers, characterized by different values of $v_\nu$ and $v_\eta$ are injected with random positions and orientations. At each time step, velocity and acceleration at the swimmers positions, needed to integrate Eqs. 1, 2, are obtained by interpolation. The self-propelled particles are then evolved, and their distribution and orientation studied in statistically steady conditions. In the sequel, we mostly focus on the dependence on the orientation speed $v_\nu$ by fixing $v_\eta \approx 0.3u_\eta$, $u_\eta$ being the typical fluid velocity fluctuation at the Kolmogorov scale.

Formally, Eqs. 1, 2 define a dissipative dynamical system evolving in the 2d-dimensional (actually 2d−1 because $p^2 = 1$ and $d = 3$) phase space ($X, \mathbf{p}$) with phase-space contraction rate

$$\Gamma = \sum_{i=1}^d \frac{\partial X_i}{\partial X_i} + \sum_{i=1}^d \frac{\partial p_i}{\partial X_i} = -\frac{d+1}{2v_\nu} (g p_z + a \cdot \mathbf{p}).$$  \ (4)

As $\mathbf{p}$ orients in the direction $a - g$, $\Gamma$ is expected to be negative on average, meaning that swimmers will evolve onto a dynamical attractor of dimension smaller than the whole phase space, which explains why clustering can be observed: if the fractal dimension of the attractor is smaller than $d$, clustering in position space (as in Fig. 1) is possible (see Ref. 14 for a conceptually similar phenomenon occurring for inertial particles). We remark that clustering is a consequence of swimming: indeed for $v_\nu = 0$ Eqs. 1 and 2 decouple, thus cells become tracer advected by an incompressible velocity and cannot cluster. Moreover, in the limit $v_\nu \to \infty$ we have $\Gamma \to 0$ and therefore swimmers cannot cluster. Nonetheless, even in this limit, if $v_\eta > 0$ they deviate from fluid trajectories and generate interesting dynamics [18].

We now discuss the physical mechanisms of clustering which, as anticipated, depend on whether the dominating effect comes from the gravitational ($g$) or fluid acceleration (which we quantify in terms of its rms value $a_{rms}$).

We start considering the case $a_{rms} \gg g$ and therefore we take $\mathbf{A} = \mathbf{a}$ in Eq. 2. Figure 2 summarizes the behavior of the main observables as a function of the dimensionless number $B\omega_{rms}$ (now $B = v_\nu/a_{rms}$) measuring the ratio of the alignment timescale to rotation timescale induced by vorticity. When the alignment is very fast, the swimming direction $\mathbf{p}$ becomes parallel to the local direction of the fluid acceleration $\hat{a} = a/a$, as confirmed by Fig. 2b showing that $\langle \mathbf{a} \cdot \mathbf{p} \rangle \to 1$ for $B\omega_{rms} \ll 1$ (here and in the following $\langle \cdot \rangle$ denotes average over particle distribution). In this limit, swimming cells behave like tracers advected by an effective velocity $\mathbf{v} \approx \mathbf{a} + v_\nu \hat{a}$. While $\mathbf{u}$ is incompressible, the effective velocity field $\mathbf{v}$ is not: $\nabla \cdot \mathbf{v} \propto v_\nu \nabla \cdot \mathbf{a}$ being negative (positive) in high vorticity (strain) regions. Therefore, as it occurs for inertial particles lighter than fluid [14, 20], the swimmers cluster inside vortical structures (Fig. 1b and Fig. 2a). The divergence of $\mathbf{v}$ is proportional to $v_\nu$, clustering is thus expected to increase with the swimming speed. In the opposite limit of slow alignment, when $B\omega_{rms} \gg 1$, random tumbling due to fluid vorticity dominates, hence swimming orientation cannot align to the local acceleration ($\langle \mathbf{a} \cdot \mathbf{p} \rangle \to 0$, see Fig. 2a): the compressible effect is
lost and particles distribute uniformly in the volume. To quantify clustering we measured the correlation dimension \(D_2\), ruling the small-distance \((r \to 0)\) behavior of the probability to find two swimmers at separation less than \(r\): \(P_2(|x_1 - x_2| < r) \propto r^{D_2}\) \[22\]. For uniformly distributed particles \(D_2 = d\), while when clustering is present the probability to find close pairs increases and \(D_2 < d\) (see e.g. \[22\] for a similar study in the case of inertial particles). In Fig. 2 we show \(D_2\) as a function of \(B\omega_{rms}\): for \(B\omega_{rms} \ll 1\), \(D_2 \approx 1.5\), indicating strong clustering in almost filamentary structures; conversely, when \(B\omega_{rms} > 1\), the correlation dimension approaches the uniform-distribution value \(D_2 \approx 3\).

We now consider the limit \(a_{rms} \ll g\) when we can take \(A = -g\) and Eq. \[2\] reads

\[
\mathbf{\dot{p}} = \frac{1}{2B}\mathbf{\ddot{z}} - \mathbf{p} \times \mathbf{p} + \frac{1}{2} \mathbf{\omega} \times \mathbf{p}, \tag{5}
\]

with \(B = v_0/g\). Similarly to the previous case, when \(B\omega_{rms} \to 0\) the cells orient in the preferred direction \(\mathbf{z}\), which is now fixed in space. The effective velocity thus becomes \(\mathbf{v} = \mathbf{u} + v_s \mathbf{z}\) which, unlike the previous case, is incompressible \((\nabla \cdot \mathbf{v} = 0)\). Therefore, now we expect that not only for \(B\omega_{rms} \gg 1\) but also for \(B\omega_{rms} \to 0\) swimmers distribute uniformly, as confirmed by Fig. 3a showing that \(D_2 \to 3\) in both limits. Remarkably, Fig. 3a shows that also in this case gyrotactic swimmers cluster on a fractal set (see Fig. 1b) for intermediate values, with a well defined minimum of the correlation dimension \((D_2 \approx 2.7)\) for \(B\omega_{rms} \sim O(1)\). We remark that an optimal orientation timescale for aggregation is also observed in steady kinematic vortical flows \[6\] where, however, a vast class of trajectories is integrable.

We can understand the origin of the observed clustering by considering the limit \(B\omega_{rms} \ll 1\). In such limit, cell orientation being very fast we can assume that the swimming direction \(\mathbf{p}\) is always at an equilibrium orientation with \(p_x, p_y \ll p_z \approx 1\) (see Fig. 3a). In particular, solving Eq. \[5\] for \(\mathbf{\dot{p}} = 0\), at first order in \(p_x, p_y\), one finds \(p_x \simeq B\omega_{y}\) and \(p_y \simeq -B\omega_{x}\) (which is confirmed by simulations). As a consequence, the effective swimmer velocity field \(\mathbf{v} = \mathbf{u} + v_s \mathbf{p}\) with \(p \simeq (B\omega_{x}, -B\omega_{y}, 1)\) has a compressible component with divergence

\[
\nabla \cdot \mathbf{v} \simeq -v_s B\nabla^2 u_z, \tag{6}
\]

which, unlike the previous case, is unrelated to fluid acceleration so that swimmers will cluster in regions different from those of high vorticity (compare Fig. 1a and b). We notice that \[6\] generalizes the well known mechanism of cell focusing in the center (walls) of downward (upward) vertical pipe flows \[8\]. Notice that in the above argument the vertical component of the vorticity plays no role, as it does not change \(p_z\).

Another consequence of the expansion \(p \simeq (B\omega_{x}, -B\omega_{y}, 1)\) is that \(p_z\) (resp. \(p_y\)) and \(\omega_{y}\) (\(\omega_{x}\)) have locally the same (opposite) sign. Numerical simulations show that this remains true also for larger values of \(B\omega_{rms}\), on average. Indeed, at stationarity, by averaging Eq. \[5\] and using isotropy on the \((x, y)\) plane (guaranteed by the isotropy of the fluid velocity field) we obtain \(\langle p_x^2 \rangle = \langle p_y^2 \rangle = B \langle p_z^2 \rangle = -B \langle p_\omega^2 \rangle\). The correlation between the horizontal components of \(\mathbf{p}\) and \(\mathbf{\omega}\) implies that the swimmers will stay longer in regions of the flow characterized by positive vertical velocity and negative vertical acceleration (Fig. 3b). This can be easily seen in a case with, say, a vortex aligned with the \(x\)-axis, where the above argument with \(\omega_x \geq 0\) implies \(\langle p_x \rangle > 0\), \(\langle p_y \rangle < 0\), so that the trajectories spend more time in regions where \(a_z > 0, u_z < 0\) as there the swimming velocity opposes that of the fluid. The preferential concentration in these regions of the flow will be maximal (and correspondingly the correlation dimension minimal, i.e. clustering stronger) for \(B\omega_{rms} \sim O(1)\) where the correlation between swimming direction and vorticity

![FIG. 3. (color online) Clustering properties as a function of \(B\omega_{rms}\), for \(g \gg |A|\) \((B = v_0/g)\). (a) Correlation dimension \(D_2\) of the swimmer positions. Circled symbol corresponds to the data shown in Fig. 1b. (b) Variances of swimming direction components \((\langle p_x^2 \rangle, \langle p_y^2 \rangle, \langle p_z^2 \rangle)\). The dashed blue curve is the parabola \((B\omega_{rms})^2\). The solid horizontal line represents the random orientation value 1/3.](image)
be strongly inhibited by the bias towards downwelling
We observe that the swimmer vertical migration can
ling the probability to find
vorticity dominated ones where
depends on the moment
Summarizing, we have shown that gyrotactic motil-
rection, and the correlation between vorticity and swimming
direction on the plane perpendicular to gravity leading
to preferentially explore downwelling, upward
velops position normalized to the volume average value at varying the ratio \( \alpha = a_{\text{rms}} / g \) \( \alpha = 0 \) corresponds to data of Fig. 5; (b) correlation dimension \( D_2 \) vs \( \alpha \); (c) \( D_2 \) vs swimming speed \( v_s / u_q \), the circled symbol corresponds to the circled one in (b); (d) generalized dimensions \( D_q \) vs \( q \) for circled data in (b), notice that the case \( \alpha = 0 \) (filled black circles) appears to be less multifractal than when also the fluid acceleration is
the fluid acceleration is
rtorial fluctuations \( (v_s / u_q) \) and the reorientation time scale with respect to vorticity intensity \( (B \omega_{\text{rms}}) \). For
be less multifractal
in the ocean. The turbulence intensity, measured in terms of kinetic energy dissipation \( \epsilon \), varies from \( \epsilon \sim 10^{-4} \) to \( 10^{-5} W/Kg \) in the upper mixing layer down to \( \epsilon \sim 10^{-6} \) to \( 10^{-7} W/Kg \) a few meters deeper. We can thus estimate that \( v_s / u_q \in [0.02 : 0.4] \) and \( B \omega_{\text{rms}} \in [0.1 : 50] \) therefore the effects discussed in this Letter are relevant in realistic conditions and can
can definitely be tested in laboratory by tuning turbulence
We conclude by remarking that for non-spherical cells
stable spheroids the term \( \gamma \cdot S \cdot (1 - \rho \cdot S) \) should be added to Eq. (2) \( (\gamma \) being the eccentricity, and \( S \) and \( I \) the symmetric rate of strain tensor and identity matrix, resp.) \[9\]. Such term is also contributing to the phase-space contraction rate \[1\] providing an additional mechanism for clustering \[5\]. It will thus be interesting to study if and how gyrotactic clustering in turbulence is modified at varying the cell shape.
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