

Active caustics

Rahul Chajwa ^{1,2} C. Rajarshi ² Rama Govindarajan ² and Sriram Ramaswamy ^{3,2}¹*Department of Bioengineering, Stanford University, Stanford, California 94305, USA*²*International Centre for Theoretical Sciences, Tata Institute of Fundamental Research, Bengaluru 560 089, India*³*Centre for Condensed Matter Theory, Department of Physics, Indian Institute of Science, Bengaluru 560 012, India*

(Received 17 March 2024; accepted 11 February 2026; published 20 March 2026)

Inertial particles (IPs) in vortical fluid flow cluster strongly, forming singular structures termed *caustics* for their resemblance to focal surfaces in optics. Here we show that such extreme aggregation onto low-dimensional submanifolds can arise *without* mechanical inertia for self-propelled particles (SPPs), through a formal correspondence between the dynamics of IPs and SPPs in a generic background flow. We establish that a singular perturbation underlies caustics formation by SPPs around a single vortex, and numerical studies of SPPs in two-dimensional Navier-Stokes turbulence reveal intense caustics in straining regions of the flow, peaking at intermediate levels of self-propulsion. Our work offers a route to singularly high local concentrations in a macroscopically dilute suspension of zero-Reynolds-number swimmers. Caustics generate burstlike encounters through large relative velocities between neighboring swimmers, with potentially significant implications for communication and sexual reproduction. An intriguing open direction is whether the active turbulence of a suspension of swimming microbes could serve to generate caustics in its own concentration.

DOI: [10.1103/m3v2-bdvj](https://doi.org/10.1103/m3v2-bdvj)

I. INTRODUCTION

In geometrical optics, the boundary of a family of focused light rays is termed a *caustic*. The extremal character of such a limiting surface or curve (in three or two dimensions, respectively) implies a divergent intensity [1]. By precise analogy the term caustic is applied to singularities in particle concentration arising from the crossing of trajectories—of dark matter on cosmic scales [2] or of solute in suspensions [3], the latter being the focus here. The growth of raindrops in clouds [4], the settling of atmospheric pollutants [5], the strength of the biological pump in the oceans [6], and a wide range of industrial processes [7], hinge on collisions and coalescence between particles or droplets suspended in background flows. When particles have appreciable inertia, the coupling between their velocity and the local flow profile can lead to inhomogeneities in their spatial distribution [8]. Heavy particles in a turbulent flow are known to get centrifuged out of regions of high vorticity, displaying finite-time singularities in particle trajectories that amplify collision rates, aggregation, and caustics [3,9–11], offering a mechanism for droplet growth in clouds [12,13], for example. In this article we explore theoretically the possibility of such singular enhancement of encounters in suspensions of motile particles [14] *without* particle inertia.

Swimmers in vortical and turbulent flows, through the coupling of their orientation to velocity gradients, present rich dynamical behaviors: accumulation at vortex boundaries [15], gyrotactic patchiness in vortical and turbulent flows [16–18], crossing of transport barriers in chaotic flows [19], and preferential sampling of downwelling regions by marine microorganisms [17,20,21]. Microswimmers in externally driven flows display focusing [22], aggregation [23,24], and expulsion

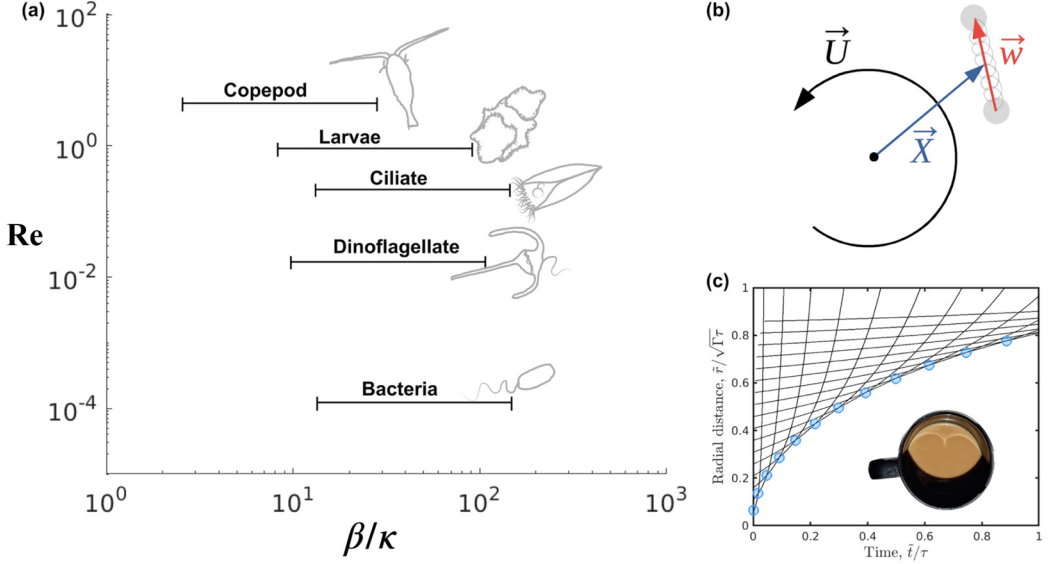


FIG. 1. Active dimer model for self-propelled particles in ambient flow. (a) We depict typical values of the ratio of flow timescale $1/\|\nabla\mathbf{U}\|$ to swimming timescale $1/\beta$, and Reynolds number Re for the marine bacterium *Vibrio alginolyticus* [29], various dinoflagellates, ciliates [30], invertebrate larvae [31], and copepods [31]. For $\|\nabla\mathbf{U}\|$ we substitute the Kolmogorov shear rate for the range of previously measured energy dissipation rates in the upper mixed layer of the ocean 10^{-8} – 10^{-6} $\text{m}^2 \text{s}^{-3}$ [32] (see Appendix B). (b) Schematic of an active dimer of extension $\mathbf{w}$ in a flow $\mathbf{U}$. (c) Caustics based on the inner solution are marked by the intersection of representative trajectories (blue circles) of particles starting at closely separated initial radial distances, with $\alpha = 0.1$. A continuous variation in $\tilde{r}_0$ would give a continuous curve. The inset is an image of optical caustics with a similar cusp on the surface of coffee in a mug (photo credit: R. Chajwa).

out of vortical regions [25], in a manner reminiscent of inertial particles [3,11]. These works established that motility and shape when coupled to background vortical flows generate clustering and transport phenomena absent for passive tracers. Durham *et al.* [17], for example, remark on the visual similarity of fractal clustering of active particles in flow and cloud formation by droplets [12]. Here we establish a more formal correspondence by identifying caustics as a unifying dynamical mechanism.

Biological motility in a fluid medium [26] is dynamic, and flows can strongly influence the dispersal of swimmers [27,28]. The competition between autonomous motion and systematic reorientation by the ambient flow field $\mathbf{U}$ is characterized by the local ratio $\beta/\|\nabla\mathbf{U}\|$ where $1/\beta$ is the time it takes for a swimmer to move its own body length. When $\mathbf{U}$ is unsteady and/or spatially heterogeneous, this ratio is dynamic along a swimmer trajectory, and thus it is convenient to define an average quantity β/κ , where $\kappa \equiv \sqrt{\langle \nabla\mathbf{U} : \nabla\mathbf{U} \rangle}$ is the root-mean-square value. Figure 1(a) depicts typical values of β/κ and Reynolds (Re) numbers for various swimmers, based on published data on swimming speed and size, and typical shear rates in the upper mixed layer of the open ocean [32] (see Appendix B). In complex natural environments, such as oceans, neither particle inertia nor activity can be directly controlled, and "collisional" aggregation [33] may arise from both inertia and activity [hence Re as a separate axis in Fig. 1(a)]. We focus on swimmers for which Re and Stokes numbers St are vanishingly small, with self-propelling stresses small compared to those created by the ambient flow. We therefore ignore particle inertia as well as the effect of the particles on the flow, neglecting interparticle hydrodynamic and steric interactions. Although their inertia is negligible, their motion is persistent because of self-propulsion [17].

We ask whether inertialess swimmers in flow [20] can display caustics analogous to those of inertial particles (IPs) [3,11], where the calculated world lines of suspended particles cross, rendering the solute velocity field multivalued. We investigate this previously unexplored possibility theoretically, and show that a mathematically divergent particle number density can emerge in the minimal setting of a dilute suspension of neutrally buoyant self-propelled particles, *without* particle inertia, in two-dimensional vortical flows. We examine the flow-coupled dynamics of two simple models of single motile particles: Hookean and preferred-length active dimers. In the presence of external noise, these correspond to active Ornstein-Uhlenbeck particles (AOUPs) [34,35] and active Brownian particles (ABPs) [36], respectively, and we will occasionally use these acronyms for brevity even when no noise is present. Only the ABP has a well-defined speed, but both possess persistence of motion. The AOUP offers the simplest realization of active movement, and its dynamics in flow, as we show below, is analogous to the Gagnol-Maxey-Riley [9,37] (hereafter GMR) model. We will therefore begin by using the AOUP to illustrate general features of the interplay of self-propulsion and ambient flow. Using a singular perturbation analysis, we show that noninertial active particles, like passive IPs, can display caustics even near a single vortex, a building block of turbulence. We establish how far the analogy with IPs may be carried and where the two differ fundamentally. We extend these findings to a continuous particle phase of dimer suspensions, which removes interparticle separation as a free parameter and allows an unambiguous demarcation of the regimes of caustic formation.

The dynamics around a single vortex forms the basis for understanding the behavior of active particles in unsteady vortical flows. We study the dynamics of preferred-length active dimers in homogeneous, isotropic turbulence through a pseudospectral direct numerical simulation, and establish caustic formation, with an intensity that peaks at an intermediate value of β/κ and show bounds on its structural stability with respect to orientational noise. The coupling of motility to ambient flow plays a central role in the lives of microscopic marine plankton [26,38,39]. By cataloging previously collected data on β/κ of such microswimmers in marine environments, we predict that they can display caustics in a vortex-laden turbulent ecosystem in the upper ocean. Active caustics produces sudden burstlike encounters between nearby particles, offering a route to increased opportunities for communication and sexual reproduction [40] among swimmers in marine environments [26,32].

Our study reveals the minimal conditions for the occurrence of active caustics: (1) activity acts as a singular perturbation to the dynamics, that is, an arbitrarily small level of activity is sufficient to generate caustics, (2) vortical flows with Jeffery-type coupling between swimmer orientation and flow ($\alpha \neq 0$) are adequate to induce caustics and turbulence is not a prerequisite, and (3) active caustics can arise even in the absence of organism-specific behaviors such as gyrotaxis or chemotaxis [20], which are not included in our model. We further demonstrate that (4) neither the coupling of the particle orientation vector to inhomogeneity in velocity gradients [the parameter ℓ in (1)] nor particle extensibility is essential, and that (5) caustics remain robust to orientational noise.

II. CORRESPONDENCE BETWEEN ACTIVE AND INERTIAL PARTICLES IN A FLOW

The motion of an IP with position vector $\mathbf{X}$ in a background flow field $\mathbf{U}$ is governed by the GMR [9,37] equation, which, to leading order in gradients, reads $\dot{\mathbf{X}} = \mathbf{v}$ and $\text{St} \dot{\mathbf{v}} = (\mathbf{U} - \mathbf{v})$, when nondimensionalized using a characteristic particle length scale d and a flow velocity scale U_0 . The Stokes number $\text{St} = \tau U_0/d$ is a nondimensional measure of inertia, characterized by the relaxation time τ ($= \text{mass}/\text{Stokes drag coefficient}$) of a particle. The centrifugation of these particles away from the vortex center results in the formation of caustics within a critical distance from the vortex origin [11]. Setting $\text{St} = 0$ yields tracer particles, which move with $\mathbf{v} = \mathbf{U}$.

The Hamiltonian structure of bound orbits of microswimmers in certain flows [41–44] points to an effective inertial character in the dynamics of active Stokesian suspensions under imposed flows, wherein the orientation vector plays a role analogous to momentum [45–47]. Building on this observation, we construct below an effective inertial description for active particles in a generic

background flow. The active particles of interest to us are orientable objects with negligible inertia, whose dynamics involves a centroid position $\mathbf{X}$ and an end-to-end vector $\mathbf{w}$ that describes their spatial extension and the direction in which they propel themselves [Fig. 1(b)]. One can model, and smoothly interpolate between, different types of particle by choosing different dynamical rules for $\mathbf{w}$, defined by the potential for its purely relaxational dynamics. In this paper we consider two cases: (1) a potential with a deep narrow minimum on the shell $|w| = w_0 \neq 0$, describing a preferred-length dimer, which, with noise becomes the active Brownian particle (ABP) [36]) and (2) a quadratic potential centered at 0, constituting a Hookean dimer, which self-propels transiently, and is called the Active Ornstein-Uhlenbeck Particle (AOUP) [34,35] when white noise is added to the dynamics because $\mathbf{w}$ is then an Ornstein-Uhlenbeck process, an instructive and analytically tractable test bed for the development of ideas in active matter.

To demonstrate analytically that caustics and the consequent discontinuities in particle number densities can arise due to activity, even without inertia, we will begin with the Hookean active dimer, placed in an imposed background flow field $\mathbf{U}$. We work at zero Stokes number and thus neglect particle inertia, but, as we see below, self-propulsion allows the particle to cross streamlines. In the absence of translational diffusion the equations of motion for $\mathbf{X}$ and $\mathbf{w}$ then take the first-order form

$$\dot{\mathbf{X}} = \mu \mathbf{F} + \mathbf{U} + \beta \mathbf{w} \equiv \mathbf{v}, \quad (1a)$$

$$\dot{\mathbf{w}} = -\frac{\mathbf{w}}{\tau} + (\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{w} - \ell^2 \nabla^2 \mathbf{U} + \sqrt{2D} \boldsymbol{\eta}, \quad (1b)$$

where μ is the Stokesian mobility of the particle, and $\mathbf{U}$, $\nabla^2 \mathbf{U}$, and the external force field $\mathbf{F}$ are evaluated at $\mathbf{X}(t)$. In (1a) β , with units of inverse time but indefinite sign, endows a dimer with self-propulsion proportional to its extension, parallel or antiparallel to $\mathbf{w}$ depending on $\text{sgn}(\beta)$. When $\mathbf{U} = 0$, self-propulsion in (1a) is a correlated noise, with persistence time given by τ . The mobility μ has no corresponding memory; this mismatch means the AOUP (and of course ABP) is out of equilibrium. The disequilibrium of the AOUP, though mild and not characterized by a well-defined speed of self-propulsion, suffices to demonstrate many active-matter phenomena. It is also realized physically in the displacements of passive colloids mobilized by active swimmers (see discussion in [34]), and of disks that propel themselves on a solid surface by transducing its vibrations via their tilt [48].

The polar flow-alignment parameter ℓ , with units of length, orients the dimer along a locally parabolic flow and vanishes for an apolar, i.e., fore-aft symmetric, particle. A term of the ℓ type appears in the context of the dynamics of a *collective* orientation vector in [49]. Mathematically, in a gradient expansion, it is the lowest-order coupling of orientation to flow that is sensitive to the orientation *vector* rather than simply the headless *axis* of the particle. Physically, locally in an unbounded fluid an object characterized by a vector $\mathbf{w}$ can align not with $\mathbf{U}$ itself, as that is not a frame-invariant notion, but with a Galilean-invariant vector made from $\mathbf{U}$, the simplest being $\nabla^2 \mathbf{U}$. For a system confined between planar walls, which provide an absolute frame of reference, a term simply proportional to $\mathbf{U}$ is permitted, as discussed in [50–52]. For a review of microswimmers in imposed flow fields, though without the polar coupling ℓ , see [41]. Apolar flow-orientation couplings [53] enter through the strain rate and vorticity tensors $\mathbf{S} \equiv (\nabla \mathbf{U} + \nabla \mathbf{U}^\top)/2$ and $\mathbf{A} \equiv (\nabla \mathbf{U} - \nabla \mathbf{U}^\top)/2$, respectively, with a response parameter α . While the original Jeffery equations are for a rigid ellipsoid, in this study $\mathbf{w}$ does not follow a rigidity constraint, relaxing the requirement of a transverse projection operator $(\mathbb{I} - \mathbf{w}\mathbf{w})$ [53] in (1b). Since the shape of the dimer depends on $|\mathbf{w}|$, α in our model does not admit the direct geometric interpretation that underlies the shape-dependent coupling in [53]. In (1b) $\boldsymbol{\eta}$ is a zero-mean, isotropic, Gaussian white noise with unit variance. With this preamble we proceed to derive an effective inertial equation of an active particle in a background flow.

For $\beta \neq 0$, (1a) and (1b) yield an equation for the total active-particle velocity $\mathbf{v}$ [see (1a)] viewed as a dynamical variable

$$\begin{aligned} \frac{d\mathbf{v}}{dt} &= \mu \mathbf{v} \cdot \nabla \mathbf{F} + \mathbf{v} \cdot \nabla \mathbf{U} - \frac{\beta}{\tau} \mathbf{w} + \beta(\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{w} + \partial_t \mathbf{U} - \beta \ell^2 \nabla^2 \mathbf{U} + \beta \sqrt{2D} \boldsymbol{\eta} \\ &= \left[-\frac{1}{\tau} \mathbf{I} + (\alpha \mathbf{S} + \mathbf{A}) \right] \cdot (\mathbf{v} - \mathbf{U} - \mu \mathbf{F}) + [\mu(\nabla \mathbf{F})^\top + (\nabla \mathbf{U})^\top] \cdot \mathbf{v} + \partial_t \mathbf{U} - \beta \ell^2 \nabla^2 \mathbf{U} + \beta \sqrt{2D} \boldsymbol{\eta}. \end{aligned}$$

Using

$$\begin{aligned} \mathbf{A} \cdot \mathbf{v} + (\nabla \mathbf{U})^\top \cdot \mathbf{v} &= \frac{1}{2} [\nabla \mathbf{U} - (\nabla \mathbf{U})^\top] \cdot \mathbf{v} + (\nabla \mathbf{U})^\top \cdot \mathbf{v} \\ &= \frac{1}{2} [\nabla \mathbf{U} + (\nabla \mathbf{U})^\top] \cdot \mathbf{v} \\ &= \mathbf{S} \cdot \mathbf{v}, \end{aligned}$$

and multiplying both sides by τ/μ , gives

$$\begin{aligned} \frac{\tau}{\mu} \frac{d\mathbf{v}}{dt} &= [\mathbf{I} - \tau(\alpha \mathbf{S} + \mathbf{A})] \cdot \left(\mathbf{F} + \frac{1}{\mu} \mathbf{U} \right) + \frac{\tau}{\mu} (\partial_t - \beta \ell^2 \nabla^2) \mathbf{U} \\ &\quad + \left[-\frac{1}{\mu} \mathbf{I} + \frac{\tau}{\mu} (\alpha + 1) \mathbf{S} + \tau (\nabla \mathbf{F})^\top \right] \cdot \mathbf{v} + \frac{\tau \beta}{\mu} \sqrt{2D} \boldsymbol{\eta}, \end{aligned} \quad (2)$$

where the first two terms on the right-hand side present a generalized reversible force, the third term is a generalized velocity-dependent force and the last term contains the noise. Thus (2) becomes

$$\frac{\tau}{\mu} \dot{\mathbf{v}} = \left[-\frac{1}{\mu} \mathbf{I} + \frac{\tau}{\mu} (\alpha + 1) \mathbf{S} \right] \cdot (\mathbf{v} - \mathbf{U}) + \mathbf{F}_{\text{eff}} + \frac{\tau}{\mu} (D_t - \beta \ell^2 \nabla^2) \mathbf{U} + \frac{\tau \beta}{\mu} \sqrt{2D} \boldsymbol{\eta}, \quad (3)$$

where $D_t = \partial_t + \mathbf{U} \cdot \nabla$, $\mathbf{F}_{\text{eff}} = \mathbf{F} + \tau \dot{\mathbf{F}} - \tau(\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{F}$, is the effective external force on the particle, and all fields are evaluated at $\mathbf{X}(t)$. In the absence of $\ell^2 \nabla^2 \mathbf{U}$ and $\boldsymbol{\eta}$ (1b) is homogeneous, so that β can be absorbed into $\mathbf{w}$ in (1). This is why β appears only as a prefactor of $\nabla^2 \mathbf{U}$ and $\boldsymbol{\eta}$ in (3). However, (1) can be recast as (3) only if $\mathbf{w}$, i.e., self-propulsion, enters (1a); the degree to which it does so is governed by τ in (1b). For $\tau \rightarrow 0$, (1b) implies $\mathbf{w} = 0$.

The presence in (3) of the external force and the drag, unmodified by prefactors, means that τ/μ plays the role of an effective mass for this inertialess active system. Indeed, (3) resembles the GMR [9,37] equation for inertial particles in a flow. There are differences, such as the absence in (3) of the Basset-Boussinesq history term [9,37,54], but the similarities prompt us to explore analogs to passive inertial-particle behavior in the dynamics of active inertialess particles in external flows.

III. CAUSTICS NEAR A POINT VORTEX FLOW: SINGULAR PERTURBATION ANALYSIS

We begin with the classical case of motion in the flow field of a point vortex. In plane polar coordinates (r, θ) , $\mathbf{U} = \hat{\theta} \tilde{\Gamma}/r$, with circulation $2\pi \tilde{\Gamma}$. Note that $\mathbf{A} = 0$ for this flow everywhere except at the origin. To demonstrate caustics even for simple fore-aft symmetric particles in the absence of external forcing and noise, we set $\ell = 0$, $\eta = 0$, and $\mathbf{F} = 0$. Nondimensionalizing (3) using the natural length $\sqrt{\tilde{\Gamma} \tau}$ [11] and time τ , we get the coupled equations

$$\ddot{r} - \frac{L^2}{r^3} = -\dot{r} + \frac{\alpha}{r^3} - \frac{(1 + \alpha)L}{r^3}, \quad (4a)$$

$$\dot{L} = 1 - L - \frac{(1 + \alpha)\dot{r}}{r}, \quad (4b)$$

where the overdot denotes d/dt . Equations (4) govern the Lagrangian dynamics of an active particle whose centroid is at a radial distance of r from a point vortex. Here $L \equiv r^2 \dot{\theta}$ is the angular momentum per unit mass of the particle. For a detailed derivation of (4), see Appendix C.

An effective centrifugal acceleration, reinforcing the similarity to an IP, arises through the L^2/r^3 term. Due to the terms containing α , our equations are distinct from those for true IP [11]. We treat the nonlinearities in (4a) and (4b) perturbatively. A *regular* perturbation approach yields absurd solutions near the origin; in fact, Eqs. (4a) and (4b) constitute a singular perturbation problem [55]. The behavior at very small times and small distances away from the vortex is singular, and relatively violent, unlike the more gentle relaxation to the final state at late times. We exploit this feature to understand the different physics at small and large time.

We seek an inner solution at the lowest order for $t \ll 1$ and $r \ll 1$, and an outer solution for $t \gg 1$, where r could be $O(1)$ or larger. In contrast to an IP which centrifuges out forever, the outer solution for an active Hookean dimer is steady rotation with $\mathbf{w}$ and $\dot{\theta} = 1/r_f^2$ at a constant final distance r_f from the vortex, rendering the particle passive at large times. The unexpected physics that appears in the inner region sets the stage for the rest of this article.

A. Inner solution, $r \ll 1$

A particle starting near the vortex origin spends little time in its vicinity, centrifuging out quickly to large distances. We may write a dominant balance equation applicable to this region. As is standard in singular perturbation theory, we recast (4a) and (4b) in the stretched spatial $\tilde{r} \equiv r/\delta_i$ and temporal $\tilde{t} \equiv t/\epsilon_i$ variables, where ϵ_i and δ_i are as yet unknown, but will be selected to ensure that all derivatives in the stretched variables are $O(1)$. This rescaling preserves the angular momentum per unit mass, $\tilde{L} = L$. Examining Eqs. (4a) and (4b) tells us that, for centrifugation to occur, the time derivatives must be much larger than $O(1)$ in the $r \rightarrow 0$ limit. Dominant balance gives the following asymptotic equation for L ,

$$\dot{L} = -\frac{(1+\alpha)\dot{\tilde{r}}}{\tilde{r}}, \quad (5)$$

with solution $L(\tilde{r}) = L_0 - (1+\alpha) \log \tilde{r}/\tilde{r}_0$, where $L = L_0$ when $r = r_0$, a constant. The subscript 0 indicates an initial value. Similarly, the equation for $\tilde{r}$ becomes

$$\frac{\delta_i}{\epsilon_i^2} \left(\ddot{\tilde{r}} - \frac{L^2}{\tilde{r}^3} \right) = \frac{\delta_i}{\epsilon_i} \dot{\tilde{r}} + \frac{1}{\delta_i^3 \tilde{r}^3} \left(\alpha - \frac{\delta_i^2}{\epsilon_i} (\alpha + 1)L \right), \quad (6)$$

which immediately provides the relationship $\epsilon_i \sim \delta_i^2$ between the two small quantities. Making the choice $\epsilon_i = \delta_i^2$ in (6) leads, at $O(1)$, to the autonomous equation

$$\tilde{r}^3 \ddot{\tilde{r}} = (L-1)(L-\alpha). \quad (7)$$

Equations (5) and (7) yield the dynamics $\dot{\tilde{r}} = \partial \mathcal{H} / \partial p$ and $\dot{p} = -\partial \mathcal{H} / \partial \tilde{r}$ with an effective Hamiltonian

$$\mathcal{H} = \frac{p^2}{2} + \frac{\alpha + [L(\tilde{r}) - 1 - \alpha]^2}{2\tilde{r}^2}, \quad (8)$$

where $p \equiv d\tilde{r}/d\tilde{t}$ is the radial momentum per unit mass of the particle. Hamiltonian structure in an overdamped dynamical system has been observed in self-propelled [41–44,46] and externally driven [45,47] particles. Integrating Eq. (7), using the chain rule $\ddot{\tilde{r}} = p dp/d\tilde{r}$ and the inner solution $L(\tilde{r})$ of (5) gives the constant-energy manifolds

$$p^2 = p_0^2 - \frac{\alpha + (L-1-\alpha)^2}{\tilde{r}^2} + \frac{\alpha + (L_0-1-\alpha)^2}{\tilde{r}_0^2}, \quad (9)$$

in the effective $(\tilde{r}, p)$ phase space, where each level set corresponds to a ray in the (t, r) plane, acquired by integrating (9). We start with two rings of particles around the vortex at initial radii r_0 and $r_0 + \Delta r$. The intersection of their rays in the r, t plane represents an overtaking of the outer ring by the inner, i.e., the occurrence of caustics.

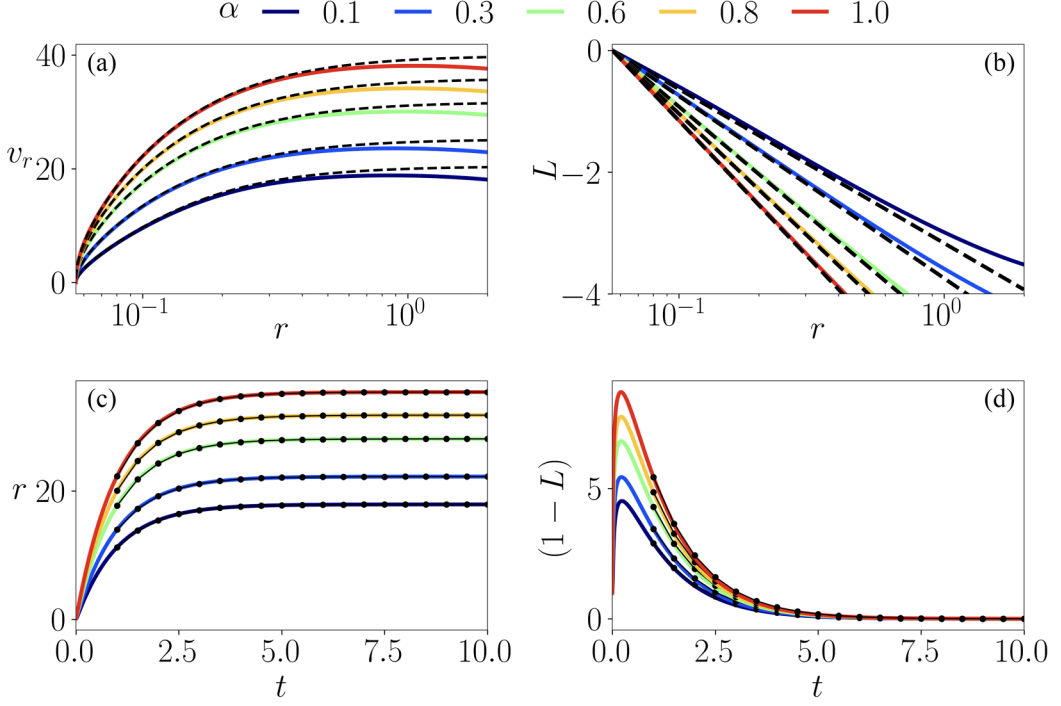


FIG. 2. Comparison between asymptotic analysis and full numerical solution. (a), (b) Comparing trajectories obtained analytically from the inner solution in (9) (dashed lines), and from evolving the full system following (4) (curves). Both the radial velocity in (a) and angular momentum in (b) follow the analytical solution till particles reach $O(1)$ distance from the vortex origin, where the inner solution is no longer valid. (c), (d) The outer solution in black dotted lines following (12) also matches well the numerical solution of the full system at late times. At such times, particles are far away from the vortex origin (c), and their angular momentum saturates to the background fluid angular velocity (d).

Caustics for a few chosen r_0 are shown by the blue circles in Fig. 1(c), along with the envelope (continuous line) for all r_0 , representing the smallest radial distance at a given time for the occurrence of caustics. For the purpose of demonstration we have taken $L_0 = -(1 + \alpha) \log \tilde{r}_0$, and equal initial speeds. This picture is akin to geometrical optics, where caustics form an envelope tangent to the light rays [56].

Figures 2(a) and 2(b) compare the inner solution with the full solution obtained by numerically time integrating (4) in the form of particle trajectories for different α s averaged over initial particle velocity. For all activity values, the inner solution in dashed lines matches well when $r \ll 1$. Around r of order unity, the inner solution expectedly deviates from the numerical solution as higher order corrections of ϵ_i become significant. Following Fig. 2(a), we see that particles with higher activity centrifuge out with larger velocities. This is expected from (4a), as α is involved in terms that have r^3 in the denominator, which control centrifugation. α also controls the slope in (4b), and therefore we see L decreases faster with larger α in Fig. 2(b).

B. Outer solution, $r \gg 1$

At long times, particles move far away from the vortex origin. i.e., $r \gg 1$ for $t \gg 1$. This motivates us to rescale r and t in (4) such that the rescaled outer variables $\tilde{t} = t\epsilon_o$ and $\tilde{r} = r\delta_o$ are $O(1)$ for small ϵ_o and δ_o . Substituting this in (4a) gives a constant $\tilde{r}(t)$, with no caustics and no activity. Thus, there is a critical initial radial distance r_0 above which particles asymptotically

approaches a final radius r_f , without caustics with final angular momentum per unit mass, $L_f = 1$. To explore this dynamics in detail, we expand r in series of δ_o ,

$$r(t) = \frac{\tilde{r}_f}{\delta_o} - \tilde{r}(t) + O(\delta_o), \quad (10)$$

where $\tilde{r}_f = r_f \delta_o$, and $\delta_o \ll 1$. The nondimensional equation (4) can be recast as

$$\begin{aligned} -\ddot{\tilde{r}} &= \tilde{r} + O(\delta_o^3), \\ \dot{L} &= 1 - L + \frac{\delta_o(\alpha + 1)}{\tilde{r}_f} \tilde{r} + O(\delta_o^2). \end{aligned} \quad (11)$$

Using the boundary conditions $r(t^*) = r^*$, $\dot{r}(t^*) = v_r^*$, and $L(t^*) = L^*$, we obtain the leading order solution of r and L ,

$$L = 1 - [1 - L^*(\alpha)]e^{-(t-t^*)} + (t - t^*) + (\alpha + 1)\frac{v_r^*}{r_f}e^{-(t-t^*)} + O(\delta_o^2), \quad (12a)$$

$$r = r_f - v_r^*e^{-(t-t^*)} + O(\delta_o^2). \quad (12b)$$

For every particle, r_f , L^* , and v_r^* vary with α , as shown in Figs. 2(c) and 2(d), which compares the above outer solution to the full numerical solution for various values of α . Choosing the t^* carefully such that the particle is far from the origin, we see that the outer solution in dotted lines matches well the full numerical solution. The inner and outer solutions uncover two qualitatively distinct dynamics, one near and the other far from the vortex origin. The inner solution presents rapid centrifugation and caustics, whereas the outer solution yields exponential relaxation of the particle trajectories to the background flow. We explore the caustics in the inner region and their dependency on α in the next section.

IV. ACTIVE DIMER CLOUD IN A POINT VORTEX: NUMERICAL SOLUTION

We now numerically solve the full equations (1a) and (1b), with the noise, the external force $\mathbf{F}$, and the polar flow coupling λ set to zero (see Video 1 [57]; all supplemental videos are described in Appendix A). In this case the self-propulsion β can be absorbed in the definition of $\mathbf{w}$. Early in the process, for times t less than or comparable to τ , we find that noiseless AOUP, i.e., active Hookean dimers, behave similar to IP, in that they both display centrifugation close to the vortex [see middle panel of Fig. 3(a)]. Such voiding of vortical regions has been observed previously for rigid gyrotactic swimmers [16] and bacteria [25], and is shown to be critical for their transport in turbulent environments [15,18]. However, the identification of a singularity, namely, caustics, for this flow- and motility-induced dynamics was missing. At long times, the radial profile of number density reaches a steady state, with a peak at a particular radius [Fig. 3(b)] The extension of the dimer relaxes to zero, so in the absence of noise, the AOUP at long time behaves like a tracer particle, consistent with our asymptotic analysis. In contrast, IPs centrifuge out forever, though more slowly as time progresses (see Supplemental Material Video 1 [57]) since the drag force balances the centrifugal force and radial velocity decays as r^{-3} [57,58]. This feature of IPs is closely mimicked by a more robust motile particle (see SM Video 2 [57]), which we discuss below. The sharp peak in the number density at a particular radial distance coincides with the formation of caustics, which we obtain by averaging over uniformly random initial orientations. The caustics are seen in Fig. 3(c) with an envelope as predicted by the inner solution in the discussion before (8). The scaling of this caustics curve near the vortex singularity is $r \sim t^{2/3}$ [green curve in Fig. 3(c)], similar to the power-law scaling of the optical caustics near its singular tip [56] [Fig. 1(c) inset], and distinct from the scaling in IP.

We demarcate the regions in the $r_0 - \alpha$ plane where caustics occur as those where an intersection of adjacent rays [see Fig. 3(e)] takes place in finite time, t_x . At a particular $r_0 = r_c$, t_x diverges [see Fig. 3(d)], and caustics do not occur when the initial particle position is beyond this critical radius.

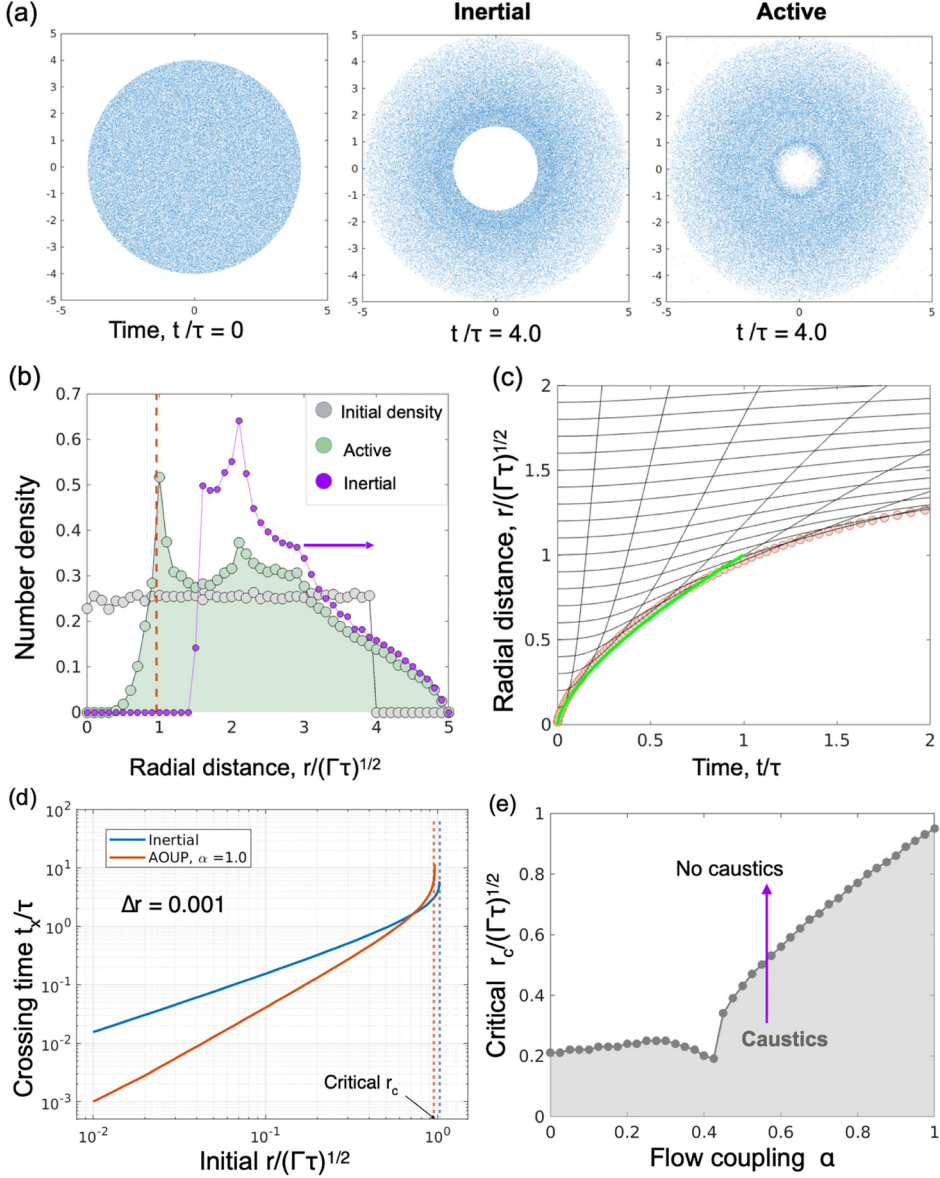


FIG. 3. Centrifugation and caustics of a Hookean dimers in point vortex. (a) Time frames showing the positions of the particles (blue dots) around a point vortex at the origin for IP and noiseless AOUP, by numerically solving the GMR [9,37] equation and Eqs. (1a) and (1b), respectively (see SM Video 1 [57]). $N = 10^5$ particles were initialized with uniformly random initial positions and orientations and velocities. (b) An initially homogeneous number-density (gray circles) peaks near a critical radial distance (green) in the steady state, compared to unsteady density of IP (purple) at a representative $t \gg 1$. (c) Trajectory (rays) of particles averaged over all initial orientations. The envelope of rays, for particles starting at various initial r , gives rise to caustics (red circles). The green curve shows $R = t^\nu$, with $\nu = 2/3$. In (b), (c), and (d), $\alpha = 1$. (d) The crossing time of adjacent rays separated by $\Delta r = 0.001$ starting at various radial distances r , averaged over uniformly random initial orientations, diverges at a finite critical radius r_c for an active particle (red) and for an inertial particle (blue) averaged over uniformly random initial velocity of unit magnitude. (e) For various α , plotting r_c demarcates the region of caustics, which is the radial distance below which adjacent rays cross each other in a finite time.

This behavior is similar to that of IPs [11]. The flow coupling α has a dual role at small to moderate distances from the vortex: (1) it aligns the dimer along the stable principal axis of $\mathbf{S}$, which has a nonzero radial component, and (2) once aligned, it extends the dimer along this axis, thus competing with the $1/\tau$ relaxation to zero motility. However, when the dimers have been centrifuged out to large r , the relaxation term takes over, leading to tracer-like dynamics, and the caustics radii lie at intermediate values of r [see Fig. 3(b)].

V. CAUSTICS FROM THE CONTINUUM LIMIT OF ACTIVE PARTICLES

Thus far we have obtained caustics by evolving pairs of particles close to each other and then checking if their paths cross, where the initial separation between the two particles, Δr , is a free parameter that is fixed arbitrarily. In this section, by turning to an alternative formulation of caustics, we establish that our choice of Δr does not affect our answers. We transition from a discrete particle system to a continuous particle phase, an approach common for studying IP caustics [12, 59, 60]. Consider a continuum of Hookean active dimers, each obeying (3) without noise. Their dynamics can be described by a velocity field $\mathbf{v} = \mathbf{v}(\mathbf{x}, t)$, whose equation follows directly from (3),

$$\frac{\tau}{\mu} d_t v_i = - \left[\frac{1}{\mu} - \frac{\tau}{\mu} (\alpha + 1) \mathbf{S}_{ik} \right] (v_k - U_k) + (\mathbf{F}_{\text{eff}})_i + \frac{\tau}{\mu} (D_t - \beta \ell^2 \nabla^2) U_i, \quad (13)$$

using the Einstein summation convention, where $d_t \equiv \partial_t + v_k \partial_k$ is the particle-phase material derivative. Note that (13) is identical in form to (3) except in the definition of d_t . The particle velocity field generally has a nonzero divergence since the particle flow is compressible. However, it is continuous everywhere except in caustics regions where this divergence $\nabla \cdot \mathbf{v} \rightarrow -\infty$ [59], that is, $\text{Tr}(\mathbf{Z}) \rightarrow -\infty$ where $\mathbf{Z} = \tau \nabla \mathbf{v}$ is a nondimensional particle-velocity gradient tensor. The dynamics of $\mathbf{Z}$ readily follows from Eq. (13),

$$\begin{aligned} d_t Z_{ij} = & -\frac{1}{\tau} (Z_{ij} - \tilde{O}_{ij} + Z_{ik} Z_{kj}) + \mu \partial_j (\mathbf{F}_{\text{eff}})_i + (D_t - \beta \ell^2 \nabla^2) \tilde{O}_{ij} + \frac{1}{\tau} \tilde{O}_{ik} \tilde{O}_{kj} \\ & + \frac{\alpha + 1}{2} [(v_k - U_k) \cdot \partial_k \tilde{O}_{ij} + (v_k - U_k) \partial_i \tilde{O}_{kj} + 2S_{ik} (Z_{kj} - \tilde{O}_{kj})], \end{aligned} \quad (14)$$

where $\tilde{\mathbf{O}} = \tau \nabla \mathbf{u} = \tau (\mathbf{S} + \mathbf{A})$ is the nondimensional fluid gradient tensor with $\tilde{\mathbf{S}} = \tau \mathbf{S}$ and $\tilde{\mathbf{A}} = \tau \mathbf{A}$ being its symmetric and antisymmetric part, respectively. The benefit of Eq. (14) is that it can be solved in the Lagrangian frame of individual particles and can thus predict whether a given particle will experience a caustic. Furthermore, $\mathbf{Z}$ at a single point quantifies the differences in particle velocities in the neighbourhood of that point.

In the following, we show caustics formation by active Hookean Dimers near a point vortex using both Eqs. (13) and (14) and confirm that they both yield the same result. We consider fore-aft symmetric particles without external forcing, i.e., $\ell = \mathbf{F}_{\text{eff}} = 0$, just as in Sec. III. Using the characteristic length and timescale of $\sqrt{\Gamma \tau}$ and τ , respectively, Eq. (13) reduces to the nondimensional form

$$d_t v_i = -[1 - (\alpha + 1) \tilde{S}_{ik}] (v_k - U_k) + D_t U_i, \quad (15)$$

where, for a point vortex,

$$\tilde{\mathbf{S}} \equiv -\frac{1}{r^2} \begin{bmatrix} -\sin 2\theta & \cos 2\theta \\ \cos 2\theta & \sin 2\theta \end{bmatrix} = \tilde{\mathbf{O}}, \quad (16)$$

which is well defined everywhere except at the origin, with $\theta = \tan^{-1} y/x$ in terms of Cartesian x, y coordinates. Similarly, Eq. (14) becomes

$$d_t \mathbf{Z} = -(\mathbf{Z} - \tilde{\mathbf{S}} + \mathbf{Z}^2) + D_t \tilde{\mathbf{S}} + \tilde{\mathbf{S}}^2 + (\alpha + 1)[(\mathbf{v} - \mathbf{U}) \cdot \nabla \tilde{\mathbf{S}} + \tilde{\mathbf{S}} \cdot (\mathbf{Z} - \tilde{\mathbf{S}})]. \quad (17)$$

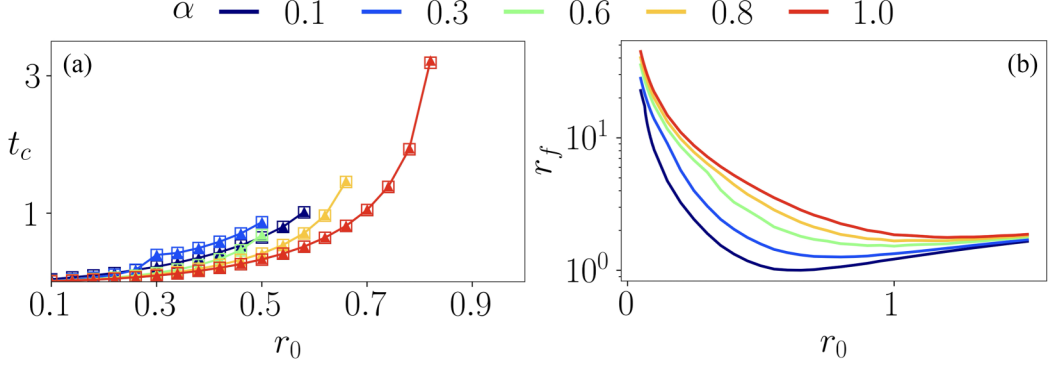


FIG. 4. Caustics in continuum limit. (a) Caustics times for particles starting from different initial radii as obtained from trajectories obeying Eqs. (15) (triangles), and from blowup of $\text{Tr}(\mathbf{Z})$ by evolving (17) (squares). The two definitions of caustics give the same answer. (b) Average final radius for a range of initial radius, for different activity levels α , of particles starting near a point vortex.

For a stationary background flow, such as a point vortex,

$$D_t U_i = \mathbf{U} \cdot \nabla U_i \quad \text{and} \quad D_t \tilde{\mathbf{S}} = \mathbf{U} \cdot \nabla \tilde{\mathbf{S}}. \quad (18)$$

With these equations, we initialize active Hookean particles at different radii, with initial velocity $\mathbf{v}(0) = \sin(r)\mathbf{U}$, and evaluate where and when they form caustics. Figure 4(a) shows the time taken for different particles to form caustics starting from a radius r_0 for different values of α . The caustics detected by the $\text{Tr}(\mathbf{Z}) \rightarrow -\infty$ (squares) practically overlap with those obtained from crossing of particle trajectories (triangles).

Another way of looking at whether particles starting from a particular radius formed caustics is the following. If two rings of particles start with initial radii r_{01} and r_{02} with $r_{01} < r_{02}$ and end at final radii r_{f1} and r_{f2} respectively, with $r_{f1} > r_{f2}$, they must have undergone caustics during their evolution. We can thus identify, from the regions of negative slope, that caustics occur almost everywhere in the range of initial locations shown in Fig. 4(b) for particles with different activity with $r_0 \ll 1$.

VI. ACTIVE PREFERRED-LENGTH DIMER IN A POINT VORTEX

Although Active Hookean dimers are analytically tractable and offer a conceptual understanding of the coupling between flow and the activity of deformable swimmers, their extension, and hence their intrinsic speed, relax to zero in the absence of noise and flow. The motility parameter β defines a speed only when multiplied by a preferred scale of $\mathbf{w}$, say, its RMS value. In nature, motile organisms generally possess an intrinsic speed independent of noise. To study such a case, we consider the equations for position $\mathbf{X}$ and extension $\mathbf{w}$ for an active dimer with a strongly preferred value of $|\mathbf{w}| = w_0$ and speed $v = \beta w_0$,

$$\dot{\mathbf{X}} = \mu \mathbf{F} + \mathbf{U} + \beta \mathbf{w}, \quad (19)$$

$$\dot{\mathbf{w}} = \frac{1}{\tau} \left(1 - \frac{|\mathbf{w}|^2}{w_0^2} \right) \mathbf{w} + (\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{w} - \ell^2 \nabla^2 \mathbf{U} + \sqrt{2D} \boldsymbol{\eta}(t). \quad (20)$$

Equations (19) and (20) describe an active Brownian particle (ABP) in a flow. Note that instead of a projection operator $\mathbb{I} - \mathbf{w}\mathbf{w}$ on $(\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{w}$ that imposes a rigidity constraint [53], the τ -dependent term in (20) allows soft distortions about the preferred length w_0 . This difference between our preferred-length model and the traditional rigid ABP, in which $|\mathbf{w}|$ is constant, is unimportant. Similar to Secs. III and IV, we study the dynamics of a suspension of active preferred-length dimers

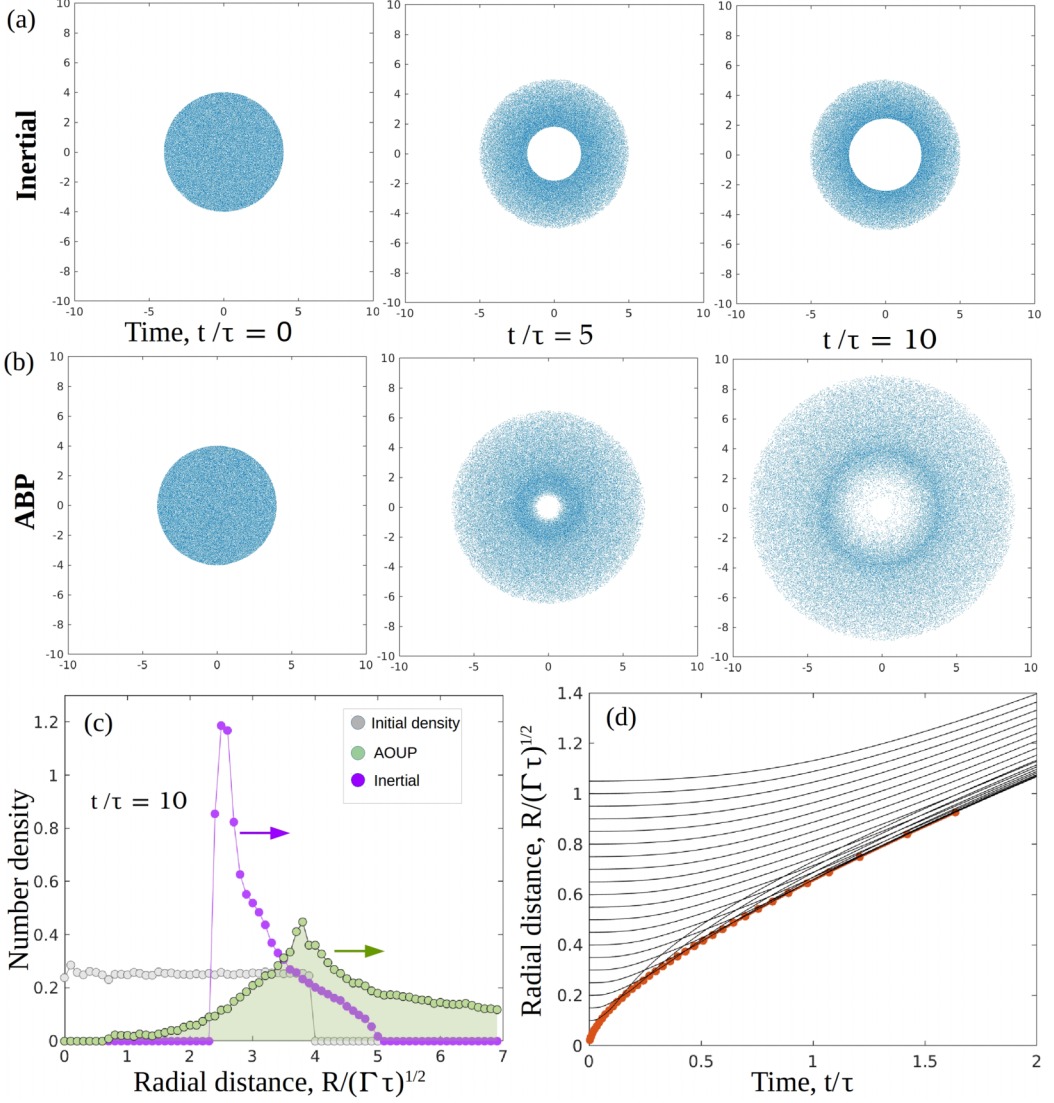


FIG. 5. Centrifugation and caustics of active preferred-length dimers in a point vortex. Panels (a) and (b) show time frames of particle positions around a point vortex for inertial particles and preferred-length dimers (or ABP without noise), respectively, shown for $\tilde{\beta} = 0.5$ and $\alpha = 1.0$ in (19) and (20). (c) Radial number density of active particles (green) compared with inertial particles (purple) shown for time 10τ , and the number density at $t = 0$ (gray). Arrows schematically depict the radial drift of the unsteady state. (d) Intersections of adjacent trajectories marking the caustics curve (red circles) obtained for $\tilde{\beta} = 0.5$, $\alpha = 1.0$, and $\Delta r = 0.01$.

in a point vortex (see Appendix D). Setting $\ell = 0$ and $\boldsymbol{\eta} = \mathbf{0}$, and integrating Eqs. (19) and (20) with uniformly random initial orientations and positions, distributed on a disk of radius $4\sqrt{\Gamma}\tau$, gives rise to caustics in the inner region, with the motility β playing a more conspicuous role than in the active Hookean case. Figures 5(a) and 5(b) compare the effective centrifugation of inertial and active particles, with $\tilde{\beta} = 0.5$ and $\alpha = 1.0$ for various time frames, where $\tilde{\beta} \equiv \beta\sqrt{\tau/\Gamma}$ is the nondimensional motility. The radial number density of a preferred-length dimer does not have a

TABLE I. Spectral parameters for the DNS.

Domain	k_f	F_0	ν	μ
512^2	3 m^{-1}	0.1 m s^{-2}	$5 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$	0.01 s^{-1}

steady state [see Fig. 5(c)], and particles keep drifting radially outward on average, akin to inertial particles, and unlike the Hookean dimers. A crucial distinction is the display of sharper caustics by the inertial particles, with a complete expulsion of particles within a ring that expands radially outwards with a velocity that asymptotically decays to 0 as $r \rightarrow \infty$ [11]. In contrast, the radial drift of active particles approaches a constant velocity for $r \gg 1$ (see SM Video 2 [57]). The outer solution from the asymptotic analysis of (D6)–(D9) (see Appendix D) predicts this constant radial velocity to be the nondimensional motility $\tilde{\beta}$ of a “free” particle independent of α , consistent with the linearity of the rays at late times in Fig. 5(d). We also find a caustics curve in the r - t plane by measuring the intersection of adjacent trajectories with $\Delta r = 0.01$, where the critical radius for caustics [defined in Fig. 3(d)] also depends on α and $\tilde{\beta}$.

VII. ACTIVE CAUSTICS IN TURBULENCE: DIRECT NUMERICAL SIMULATION

To study the dynamics of a collection of ABPs in unsteady vortical flows, we write a pseudospectral code to solve the Navier-Stokes equations with a deterministic external forcing $F_0 q \cos qx$ on the background flow $\mathbf{U}$, in the stream-function-vorticity formulation [61]. In two dimensions, the inverse cascade feeds energy into long wavelengths, which we avoid by including an Ekman friction μ [62], in addition to the viscous dissipation ν . The spectral Direct Numerical Simulations (DNS) are performed in a 2π periodic domain with 512×512 collocation points, and the parameters given in Table I.

This gives the flow velocity field $\mathbf{U}$ that drives the particle dynamics. A one-way coupling is assumed, wherein the ambient flow stirs the particles but particles do not generate flows. We use w_0 and the inverse of the root-mean-square velocity gradient $\kappa \equiv \sqrt{\langle \nabla \mathbf{U} : \nabla \mathbf{U} \rangle}$ of the background flow in the turbulent steady state as length and time scales, respectively, which gives the nondimensional parameters, $(\beta/\kappa, \tau\kappa, \alpha, \ell^2/w_0^2)$ and noise strength $\sqrt{2D/w_0^2\kappa}$. We fix $\alpha = 1$, which in the geometric interpretation of [53] corresponds to a needle-shaped particle, and $\tau = 1$, with $\tau\kappa = 0.8454$. This leaves a two-dimensional parameter space $(\beta/\kappa, \ell^2/w_0^2)$ of activity and polar alignability, respectively.

In a turbulent steady state, we initialize the particles with uniformly random initial positions and orientations. In the steady state of particle dynamics, we find tracer-like behavior for small values of motility strength β/κ in which swimmers get trapped within the vortices, consistent with the single vortex study. For large values of β/κ , swimmers exhibit ballistic dynamics, leading to a homogeneous number density of particles. Caustics appear sharply at intermediate values of β/κ (see SM Video 3 [57]), where we see preferential sampling and clustering [see Figs. 6(a) and 6(b)]. We quantify caustics-induced clustering by measuring the density fluctuation with respect to the initial homogeneous state (see Appendix E), and find pronounced caustics for a range of ℓ^2/w_0^2 and β/κ [see Fig. 6(c)]. We find that for intermediate values of activity β/κ , increasing ℓ^2/w_0^2 sharpens the caustics filaments (see SM Video 4 [57]). The density fluctuation exhibits a peak around $\beta/\kappa \simeq 10^2$ [see Fig. 6(d)], which is similar to the dynamics of IP, where for intermediate values of Stokes number St , particles display clustering [63] and sharp caustics [3], as compared to large and small values of St .

We quantify how swimmers sample the flow by calculating the Okubo-Weiss parameter, $\mathcal{W} = \omega^2 - 2\mathbf{S} : \mathbf{S}$ at the location of particles, where $\mathbf{S}$ is the symmetric part of the velocity gradient tensor [64] and ω the vorticity. $\mathcal{W} > 0$ implies that the particles are in a vortical region, and $\mathcal{W} < 0$ indicates localization of particles in the straining region. The distribution of the Okubo-Weiss

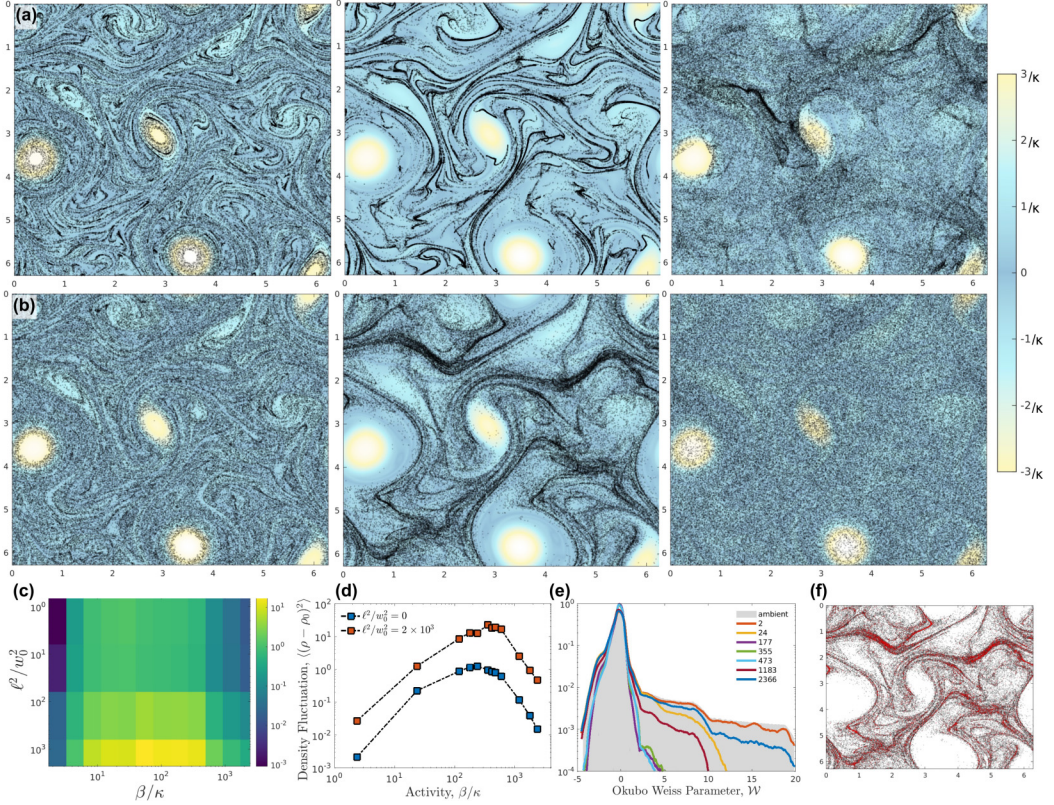


FIG. 6. Caustics in turbulent flow. The blue-yellow colorbar represents the vorticity magnitude in the ambient turbulent flow scaled by the root-mean-square velocity gradient $\kappa = 0.8454 \text{ s}^{-1}$ and black speckles are the locations of the geometric centers of 10^5 active dimers with preferred length $w_0 = 500 \mu\text{m}$. (a) $\ell^2/w_0^2 = 2 \times 10^3$ with (from left to right) $\beta/\kappa = 23.6, 236$, and 2360 . (b) $\ell^2/w_0^2 = 0$ with (left to right) $\beta/\kappa = 23.6, 236$, and 2360 . For intermediate activity the particles display pronounced caustics (see SM Videos 3 and 4 [57]). (c) Heat map of the number-density fluctuation plotted in $(\beta/\kappa, \ell^2/w_0^2)$ plane. For comparison with plankton motility see Fig. 1(a). (d) Number-density fluctuation as a function of activity, showing pronounced agglomeration for intermediate levels of activity. (e) Okubo-Weiss parameter plotted for $\ell = 0$ and various values of activity β/κ . (f) For $\ell^2/w_0^2 = 0$ and $\beta/\kappa = 236$, the colliding pairs of particles are colored red and are pronounced in caustics regions.

parameter $\mathcal{W}$ sampled over all particle locations gives the deviation from homogeneous sampling of the flow; when compared with the distribution of $\mathcal{W}$ over the entire flow domain [see Fig. 6(e)]. We find that particles cluster preferentially in the straining regions, in a manner similar to that of gyrotactic swimmers [17,21]. This clustering coincides with pronounced collisions or path crossing [see Fig. 6(f) and SM Video 5 [57]] that mark caustics of active particles in flow, akin to the inertial case [3], as might have been anticipated from our stationary vortex studies, and as argued to arise for gyrotactic swimmers in turbulence [21]. Furthermore, to demonstrate the robustness of caustics to noise in Eq. (20), we include a uniformly random, uncorrelated noise η with zero mean and unit width. For realistic levels of nondimensional noise strength $\sqrt{2D/w_0^2\kappa}$, we find softening of caustics that retains its qualitative features (see Fig. 7 and Appendix A [57]), and high values of noise strength $\sqrt{2D/w_0^2\kappa} \simeq O(10^2)$ randomize the particle positions to produce a uniform state.

To explore the relevance of our results in marine ecosystems, we plot the typical values of β/κ and Re for various swimmers [see Fig. 1(a)], based on published data on swimming speed and

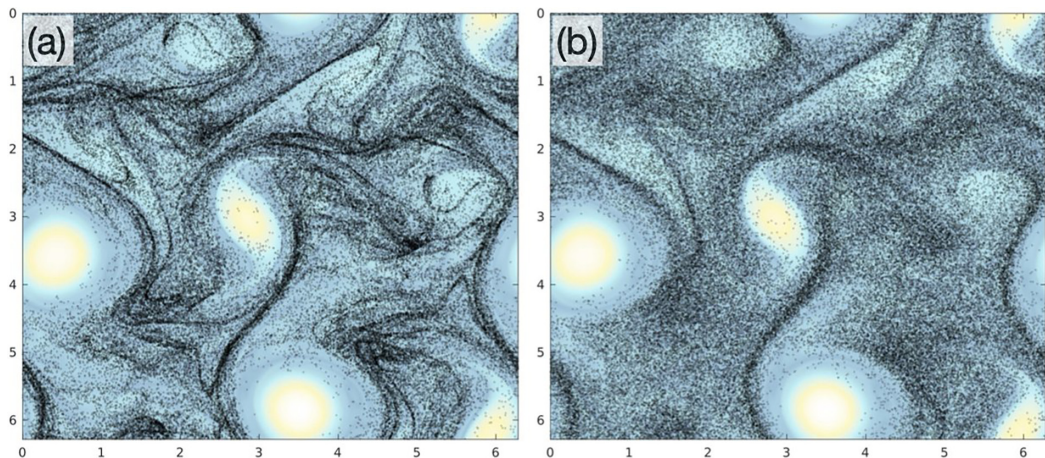


FIG. 7. Effect of Orientational Noise. Dynamics with noise in Eq. (20) for (a) $\sqrt{2D/w_0^2}\kappa = 0.91$ and (b) $\sqrt{2D/w_0^2}\kappa = 9.19$ shows softening of caustics with the coarse structure retained (see SM Video 6 [57]). The color bar for the background vorticity field is the same as Figs. 6(a) and 6(b).

size, and typical shear rates in the upper mixed layer of the open ocean [32] (see Appendix B). For small swimming organisms, like ciliates, invertebrate larvae, and copepods, when turbulence energy dissipation rates are towards the lower end of the range of values observed in the upper mixed layer of the ocean 10^{-8} – 10^{-6} $\text{m}^2 \text{s}^{-3}$ [32], β/κ can be in the intermediate regime, and from the comparison of β/κ in Figs. 1(a) and 6(c) we expect some manifestation of active caustics in these natural biological suspensions. Interparticle collisions, which can be central to sexual reproduction in suspension of swimming organisms, formally occur in our framework through a phase-space singularity, which is missing in the prior descriptions of clustering in turbulence [17,18].

VIII. CONCLUSIONS

We have shown how advection, rotation, and alignment by an ambient vortical flow can lead to a divergence in the number density of suspended self-propelled particles without mechanical inertia. We have considered two dimer models of motile particles, Hookean and preferred length, in vortical flows, corresponding, when noise is included to active Ornstein-Uhlenbeck [34,35] and active Brownian particles [36]. To facilitate future studies including exploration of the possible dependence of caustic structure on the specific microswimmer model, we have made our simulation codebase publicly available [61].

By recasting the dynamics of motile inertialess particles in a form close to that of the classic GMR [37,64] equations of inertial particles (IPs), we highlight the similarities and differences between the centrifugation of these two types of particle, in the illustrative setting of a single point vortex. We show the formation of caustics in both the dimer types mentioned above, by analyzing the intersection of rays in the r - t plane. For a range of the flow-coupling parameter α , we demarcate the regimes in the α - r plane where caustics occur. We study the effect of advection by more general vortical flows in the form of two-dimensional Navier-Stokes turbulence generated by direct numerical simulation, characterizing the preferential sampling of straining regions by the swimmers by means of the Okubo-Weiss parameter. We find that for intermediate values of the dimensionless motility β/κ , clustering and caustics are more pronounced, similar to the dynamics of IP as the Stokes number St is varied, suggesting that β/κ plays the same role as St . This hitherto unexplored caustics regime is of interest formally because crossing of active-particle worldlines renders their velocity field multiple-valued, and practically because the resulting rapid, transient collisions offer a strikingly effective natural mechanism for close encounters between organisms.

These encounters can increase mating opportunities or contact-dependent interactions at low mean concentrations, beyond the effects of elevated local concentration [17,18]. The eco-physiological impact of clustering and caustics is expected to be organism-specific and awaits experimental verification.

The biological implications of active caustics in marine ecosystems may take time to be fully understood, but the theoretical framework developed here can be of immediate value for conceptualizing field observations. As mentioned at the beginning of this article, in complex natural environments, neither inertia nor activity can be directly controlled, and collisional aggregation [33] can arise from both inertial and active caustics. Disentangling their respective contributions, both their similarities and distinctions, is therefore essential for interpreting swimmer dynamics in field settings. A unified mechanistic framework for particle aggregation (and disaggregation) in marine environments [65] remains an open problem, to which our article contributes insights. In three dimensions, accumulation is known to be weaker than in two dimensions [18], but we expect the criteria for caustics formation to remain valid, with extremal surfaces rather than curves. While optical caustics can be engineered [66], whether an analogous framework can be developed for controlling active suspensions remains a question.

Although coarse graining eliminates multivaluedness of the velocity field, the accompanying singularity in the density field persists. In natural systems, however, the divergence in particle number density would likely be regularized by interparticle hydrodynamic, steric, and/or behavioral interactions. Whether condensation driven by caustics in active suspensions constitute a bona fide nonequilibrium phase transition, and whether active turbulence generated by swimming microbes can produce caustics in their own concentration fields, remains to be explored.

ACKNOWLEDGMENTS

S.R. acknowledges a National Science Chair and, earlier, a JC Bose Fellowship from the ANRF, India, support from the Tata Education and Development Trust, an ICTS Endowed Visiting Professorship, and discussions in the Program on Complex Lagrangian Problems of Particles in Flows, ICTS-TIFR, Bangalore. R.C. and R.G. acknowledge support from the Department of Atomic Energy, Government of India, under Project No. RTI4001. S.R. thanks the Isaac Newton Institute for Mathematical Sciences, Cambridge, for support and hospitality during the program Anti-diffusive dynamics: from sub-cellular to astrophysical scales, where work on this paper was undertaken, supported by EPSRC Grant No. EP/R014604/1. C.R. thanks Saumav Kapoor and Samriddhi Sankar Ray at ICTS for insightful discussions. R.C. acknowledges support from the International Human Frontier Science Program Organization, and discussions in Active Matter in Complex Environments Conference at the Aspen Center for Physics, and thanks Prakash Lab for valuable insights into marine ecology.

APPENDIX A: SUPPLEMENTAL VIDEOS

Video 1: Active Hookean dimers with $\alpha = 1$, $\lambda = 0$ in a point vortex flow. It is compared with the dynamics of inertial particles.

Video 2: Active Preferred-length dimers with $\alpha = 1$, $\lambda = 0$, $\beta\sqrt{\tau/\Gamma} = 0.5$ in a point vortex flow.

Video 3: Preferred-length dimers in turbulence with flow parameters given in Table I, and with $\alpha = 1$, $\tau = 1$, $\ell^2/w_0^2 = 0$, $\beta/\kappa = 23.6$, 236, and 236 (increasing from left to right). The intermediate values of activity β/κ presents the regime of the most pronounced caustics as shown in Fig. 3(b).

Video 4: Preferred-length dimers in turbulence with $\alpha = 1$, $\tau = 1$, $\beta/\kappa = 236$, and $\ell^2/w_0^2 = 0$ (left) and $\ell^2/w_0^2 = 2 \times 10^3$ (right). Increasing the polar aligning parameter ℓ^2/w_0^2 intensifies the caustics [comparison between the middle column of Figs. 3(a) and 3(b)].

TABLE II. Data used to make Fig. 1(a).

Creature	size (μm)	Speed ($\mu\text{m s}^{-1}$)	β	Re	Data sources
Dinoflagellate	63.7	261.6	9.7	0.01	[30]
Ciliate	180.2	1184.2	13.1	0.2	[30]
Larvae	396.6	2275	8.2	0.9	[31,67,68]
Copepod	1284	3440	2.5	4.4	[31]
Marine bacteria	3	40	13.3	0.0001	[29,69]

Video 5: Preferred-length dimers in turbulence with $\alpha = 1$, $\tau = 1$, $\beta/\kappa = 236$, and $\ell^2/w_0^2 = 0$, where the pairs of particles whose trajectories intersect within the numerical time step 10^{-3} s are colored red, showing extreme path-crossing events in the regions of high number density.

Video 6: preferred-length dimers in turbulence with $\alpha = 1$, $\tau = 1$, $\beta/\kappa = 236$, $\ell^2/w_0^2 = 0$, and nondimensional noise strength $\sqrt{2D/w_0^2\kappa} = 9.19$.

APPENDIX B: PLOTTING REYNOLDS NUMBER AND $\beta/\|\nabla\mathbf{U}\|$ FOR VARIOUS MARINE ORGANISMS

We use the kinematic viscosity of water, $\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$ with previously measured energy dissipation rates in the upper mixed layer of the ocean, $\epsilon = 10^{-8} - 10^{-6} \text{ m}^2 \text{ s}^{-3}$ [32], to calculate the Reynolds number and shear rate using the relation $\langle \|\nabla\mathbf{U}\| \rangle_{\text{rms}} = (\epsilon/\nu)^{1/2}$.

Table II is a compilation of datasets published previously by other researchers (sources are given in the table). Each creature type exhibits a distribution of size and swimming speed. We use the average value from the known data. There are limited data on the size and swimming statistics of marine bacteria; we use the data for *Vibrio alginolyticus*, which is studied due to its bio-medical importance.

APPENDIX C: ACTIVE HOOKEAN DIMER IN A POINT VORTEX

In the absence of external force field $\mathbf{F}$, and redefining a flow-dependent relaxation time, $\tilde{\tau}^{-1} \equiv \mathbf{I}/\tau - (\alpha \mathbf{S} + \mathbf{A})$, gives the equation

$$\frac{d\mathbf{v}}{dt} - \mathbf{v} \cdot \nabla\mathbf{U} = (\mathbf{U} - \mathbf{v}) \cdot \tilde{\tau}^{-1}. \quad (\text{C1})$$

The velocity field generated by a point vortex in polar coordinates is

$$\mathbf{U} = \frac{\Gamma}{2\pi r} \hat{\theta} \equiv \frac{\bar{\Gamma}}{r} \hat{\theta}. \quad (\text{C2})$$

In polar coordinates the position derivatives are

$$\mathbf{X} = r\hat{\mathbf{r}},$$

$$\frac{d\mathbf{X}}{dt} = \frac{dr}{dt}\hat{\mathbf{r}} + r\frac{d\theta}{dt}\hat{\theta}, \quad (\text{C3})$$

$$\text{and } \frac{d^2\mathbf{X}}{dt^2} = \frac{d^2r}{dt^2}\hat{\mathbf{r}} + 2\frac{dr}{dt}\frac{d\theta}{dt}\hat{\theta} - r\left(\frac{d\theta}{dt}\right)^2\hat{\mathbf{r}} + r\frac{d^2\theta}{dt^2}\hat{\theta}. \quad (\text{C4})$$

To demonstrate the emergence of an effective centrifugal force due to the coupling of activity with the background flow, we neglect the external force, and the Gaussian white noise in (3), and consider fore-aft symmetric particles such that $\ell = 0$. For a point vortex, the antisymmetric tensor

$\mathbf{A}$ is zero everywhere except at the origin, and the symmetric part is

$$\mathbf{S} = \begin{pmatrix} 0 & -\tilde{\Gamma}/r^2 \\ -\tilde{\Gamma}/r^2 & 0 \end{pmatrix}. \quad (\text{C5})$$

Using (C2)–(C5) in (C1) gives

$$\begin{aligned} \tau \left[\frac{d^2 r}{dt^2} \hat{\mathbf{r}} + 2 \frac{dr}{dt} \frac{d\theta}{dt} \hat{\theta} - r \left(\frac{d\theta}{dt} \right)^2 \hat{\mathbf{r}} + r \frac{d^2 \theta}{dt^2} \hat{\theta} + \frac{\tilde{\Gamma}}{r} \frac{d\theta}{dt} \hat{\mathbf{r}} + \frac{\tilde{\Gamma}}{r^2} \frac{dr}{dt} \hat{\theta} \right] \\ = \frac{\tilde{\Gamma}}{r} \hat{\theta} - \frac{dr}{dt} \hat{\mathbf{r}} - r \frac{d\theta}{dt} \hat{\theta} + \frac{\alpha \tau \tilde{\Gamma}}{r^3} \hat{\mathbf{r}} - \frac{\tau \alpha \tilde{\Gamma}}{r} \frac{d\theta}{dt} \hat{\mathbf{r}} - \frac{\tau \alpha \tilde{\Gamma}}{r^2} \frac{dr}{dt} \hat{\theta}. \end{aligned} \quad (\text{C6})$$

Separating equations in the $\hat{\mathbf{r}}$ and $\hat{\theta}$ directions in (C6), we get two coupled equations

$$\tau \frac{d^2 r}{dt^2} - \tau r \left(\frac{d\theta}{dt} \right)^2 = -\frac{dr}{dt} + \frac{\alpha \tau \tilde{\Gamma}^2}{r^3} - \frac{\tau(1+\alpha)\tilde{\Gamma}}{r} \frac{d\theta}{dt}, \quad (\text{C7})$$

$$2\tau \frac{dr}{dt} \frac{d\theta}{dt} + \tau r \frac{d^2 \theta}{dt^2} = \frac{\tilde{\Gamma}}{r} - r \frac{d\theta}{dt} - \frac{\tau(1+\alpha)\tilde{\Gamma}}{r^2} \frac{dr}{dt}. \quad (\text{C8})$$

Choosing $\sqrt{\tilde{\Gamma}\tau}$ and τ as the length and time scales, respectively, we arrive at the following nondimensional equations involving nondimensional variables r , t and $L = r^2 \dot{\theta}$:

$$\begin{aligned} \ddot{r} - \frac{L^2}{r^3} &= -\dot{r} + \frac{\alpha - (1+\alpha)L}{r^3}, \\ \dot{L} &= 1 - L - (1+\alpha) \frac{\dot{r}}{r}, \end{aligned} \quad (\text{C9})$$

where $(\dot{\cdot}) \equiv d(\cdot)/dt$.

APPENDIX D: ACTIVE PREFERRED-LENGTH DIMER IN A POINT VORTEX

The equations for an active dimer which has a preferred length are given by

$$\dot{\mathbf{X}} = \mathbf{U} + \beta \mathbf{w}, \quad (\text{D1})$$

$$\dot{\mathbf{w}} = \frac{1}{\tau} \left(1 - \frac{|\mathbf{w}|^2}{w_0^2} \right) \mathbf{w} + (\alpha \mathbf{S} + \mathbf{A}) \cdot \mathbf{w} - \ell^2 \nabla^2 \mathbf{U} + \sqrt{2D} \boldsymbol{\eta}(t). \quad (\text{D2})$$

With $\ell = 0$ and $\boldsymbol{\eta} = 0$, (D1) and (D2) can be recast as

$$\frac{d\mathbf{v}}{dt} - \mathbf{v} \cdot \nabla \mathbf{U} = (\mathbf{U} - \mathbf{v}) \cdot \tilde{\tau}^{-1}, \quad (\text{D3})$$

where $\tilde{\tau}^{-1} \equiv \frac{\mathbf{I}}{\tau} \left(\frac{\|\mathbf{V} - \mathbf{U}\|}{\beta^2} - 1 \right) - (\alpha \mathbf{S} + \mathbf{A})$. The nondimensional equations with $R = \sqrt{\tilde{\Gamma}\tau}$ and $T = \tau$ in cylindrical polar coordinates become

$$\tilde{\beta}^2 \frac{d^2 r}{dt^2} = \tilde{\beta}^2 r \left(\frac{d\theta}{dt} \right)^2 + \frac{dr}{dt} \left\{ 2 \frac{d\theta}{dt} - \left(\frac{dr}{dt} \right)^2 - r^2 \left(\frac{d\theta}{dt} \right)^2 + \tilde{\beta}^2 - \frac{1}{r^2} \right\} + \frac{\tilde{\beta}^2 \alpha}{r^3} - \frac{\tilde{\beta}^2 (1+\alpha)}{r} \frac{d\theta}{dt}, \quad (\text{D4})$$

$$\begin{aligned} \tilde{\beta}^2 r \frac{d^2 \theta}{dt^2} &= -2\tilde{\beta}^2 \frac{d\theta}{dt} \frac{dr}{dt} + \left(r \frac{d\theta}{dt} - \frac{1}{r} \right) \left[2 \frac{d\theta}{dt} - \left(\frac{dr}{dt} \right)^2 - r^2 \left(\frac{d\theta}{dt} \right)^2 + \tilde{\beta}^2 - \frac{1}{r^2} \right] \\ &\quad - \frac{\tilde{\beta}^2 (1+\alpha)}{r^2} \frac{dr}{dt}, \end{aligned} \quad (\text{D5})$$

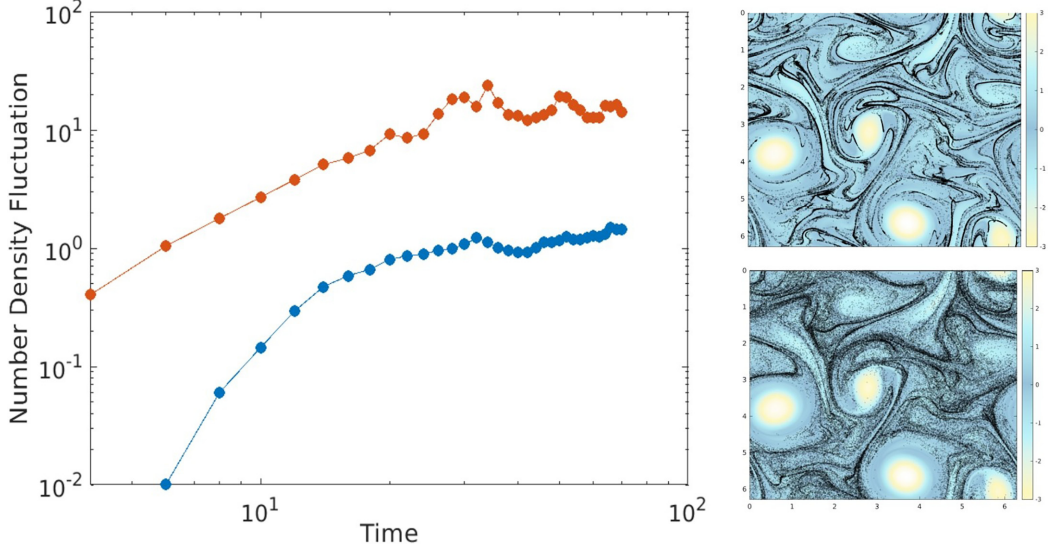


FIG. 8. Number-density fluctuations. The fluctuations saturate as a function of time as the particulate structure evolves from a uniformly random state to exhibiting caustics. Red and blue curves correspond to $\ell^2/w_0^2 = 2 \times 10^3$ and $\ell^2/w_0^2 = 0$ respectively. The activity $\beta/\kappa = 236$ in both cases. The top and bottom panels on the right correspond to the top and bottom curves on the left, respectively.

where $\tilde{\beta} \equiv \beta\sqrt{\tau/\tilde{\Gamma}}$ is the nondimensional motility. These may be recast as a system of first-order equations as

$$\frac{dr}{dt} = v_r, \quad (D6)$$

$$\tilde{\beta}^2 \frac{dv_r}{dt} = \tilde{\beta}^2 r \omega^2 + v_r \left(2\omega - v_r^2 - r^2 \omega^2 + \tilde{\beta}^2 - \frac{1}{r^2} \right) + \frac{\tilde{\beta}^2 \alpha}{r^3} - \frac{\tilde{\beta}^2 (1 + \alpha) \omega}{r}, \quad (D7)$$

$$\frac{d\theta}{dt} = \omega, \quad (D8)$$

$$\tilde{\beta}^2 \frac{d\omega}{dt} = -\frac{2\tilde{\beta}^2 v_r \omega}{r} + \left(\omega - \frac{1}{r^2} \right) \left(2\omega - v_r^2 - r^2 \omega^2 + \tilde{\beta}^2 - \frac{1}{r^2} \right) - \frac{\tilde{\beta}^2 (1 + \alpha) v_r}{r^3}. \quad (D9)$$

By calculating the divergence of crossing time, for a fixed $\tilde{\beta} = 1.0$, we get the caustics phase in the $r - \alpha$ plane, similar to the hookean case. We find that rigid spheroidal microswimmers [41,70] in vortical flow also display caustics, which we do not explore here.

APPENDIX E: NUMBER DENSITY FLUCTUATION, CLUSTERING AND COLLISIONS

Local number density fluctuations can be used as a statistical measure for the intensity of caustic-induced clustering (see Fig. 8). The space is numerically discretized into $N \times N$ cells such that there is on an average one particle per cell in the initial uniformly random state

$$\Delta \rho_{ij}^2 = \frac{1}{N^2} \sum_{i,j} (\rho_{ij} - 1)^2. \quad (E1)$$

Here i, j are the cell index corresponding to a given spatial location. The initial state itself contributes a residual density fluctuation, which we subtract to obtain purely caustic-induced clustering. To measure collisions, we find pairs of particles whose trajectories intersect within the numerical

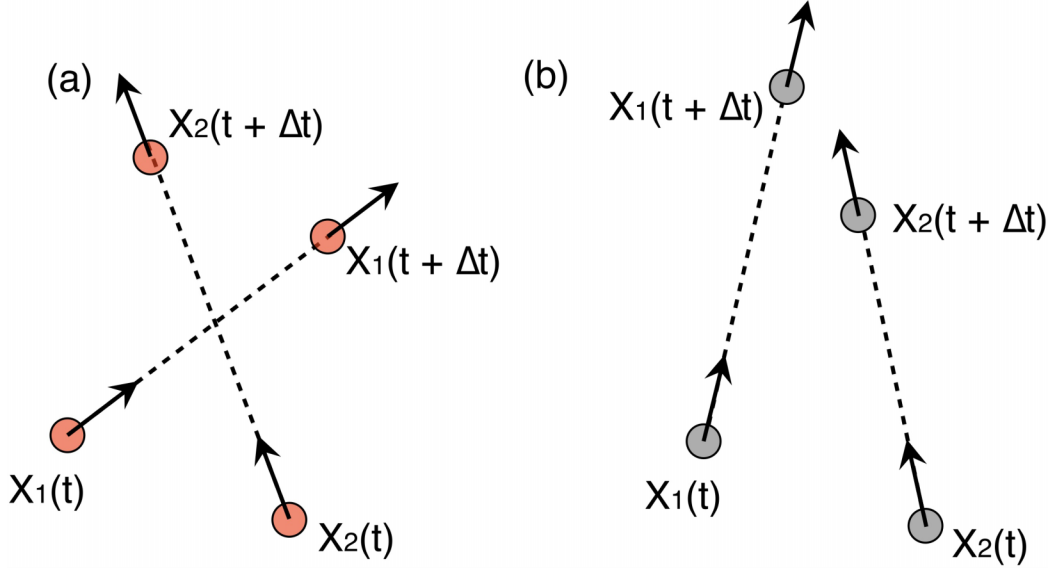


FIG. 9. Collisions: A schematic of (a) colliding (red) and (b) noncolliding (gray) pairs of particles, where the intersection of paths within the numerical time step Δt marks the collision event.

time step $\Delta t = 10^{-3}$, as shown in Fig. 9. Such particles are colored red in SM Video 5 [57]; where we one finds that the regions with high number density coincide with the crossing of particle trajectories.

-
- [1] M. V. Berry and J. F. Nye, Fine structure in caustic junctions, *Nature (London)* **267**, 34 (1977).
 - [2] J. Feldbrugge, R. van de Weygaert, J. Hidding, and J. Feldbrugge, Caustic skeleton & cosmic web, *J. Cosmol. Astropart. Phys.* **2018**, 027 (2026).
 - [3] M. Wilkinson and B. Mehlig, Caustics in turbulent aerosols, *Europhys. Lett.* **71**, 186 (2005).
 - [4] M. Pinsky and A. Khain, Turbulence effects on droplet growth and size distribution in clouds—A review, *J. Aerosol Sci.* **28**, 1177 (1997).
 - [5] H. J. S. Fernando, D. Zajic, S. Di Sabatino, R. Dimitrova, B. Hedquist, and A. Dallman, Flow, turbulence, and pollutant dispersion in urban atmospheres, *Phys. Fluids* **22**, 051301 (2010).
 - [6] P. W. Boyd, H. Claustre, M. Levy, D. A. Siegel, and T. Weber, Multi-faceted particle pumps drive carbon sequestration in the ocean, *Nature (London)* **568**, 327 (2019).
 - [7] K. Samborska, S. Poozesh, A. Barańska, M. Sobulska, A. Jedlińska, C. Arpagaus, N. Malekjani, and S. M. Jafari, Innovations in spray drying process for food and pharma industries, *J. Food Eng.* **321**, 110960 (2022).
 - [8] G. Boffetta, F. De Lillo, and A. Gamba, Large scale inhomogeneity of inertial particles in turbulent flows, *Phys. Fluids* **16**, L20 (2004).
 - [9] M. R. Maxey and J. J. Riley, Equation of motion for a small rigid sphere in a nonuniform flow, *Phys. Fluids* **26**, 883 (1983).
 - [10] M. R. Maxey and S. Corrsin, Gravitational settling of aerosol particles in randomly oriented cellular flow fields, *J. Atmos. Sci.* **43**, 1112 (1986).
 - [11] S. Ravichandran and R. Govindarajan, Caustics and clustering in the vicinity of a vortex, *Phys. Fluids* **27**, 033305 (2015).

- [12] G. Falkovich, A. Fouxon, and M. Stepanov, Acceleration of rain initiation by cloud turbulence, [Nature \(London\) **419**, 151 \(2002\)](#).
- [13] P. Deepu, S. Ravichandran, and R. Govindarajan, Caustics-induced coalescence of small droplets near a vortex, [Phys. Rev. Fluids **2**, 024305 \(2017\)](#).
- [14] E. Lauga and T. R. Powers, The hydrodynamics of swimming microorganisms, [Rep. Prog. Phys. **72**, 096601 \(2009\)](#).
- [15] C. Torney and Z. Neufeld, Transport and aggregation of self-propelled particles in fluid flows, [Phys. Rev. Lett. **99**, 078101 \(2007\)](#).
- [16] W. M. Durham, E. Climent, and R. Stocker, Gyrotaxis in a steady vortical flow, [Phys. Rev. Lett. **106**, 238102 \(2011\)](#).
- [17] W. M. Durham, E. Climent, M. Barry, F. De Lillo, G. Boffetta, M. Cencini, and R. Stocker, Turbulence drives microscale patches of motile phytoplankton, [Nat. Commun. **4**, 2148 \(2013\)](#).
- [18] C. Zhan, G. Sardina, E. Lushi, and L. Brandt, Accumulation of motile elongated micro-organisms in turbulence, [J. Fluid Mech. **739**, 22 \(2014\)](#).
- [19] N. Khurana, J. Bławdziewicz, and N. T. Ouellette, Reduced transport of swimming particles in chaotic flow due to hydrodynamic trapping, [Phys. Rev. Lett. **106**, 198104 \(2011\)](#).
- [20] T. Pedley and J. O. Kessler, Hydrodynamic phenomena in suspensions of swimming microorganisms, [Annu. Rev. Fluid Mech. **24**, 313 \(1992\)](#).
- [21] K. Gustavsson, F. Berglund, P. R. Jonsson, and B. Mehlig, Preferential sampling and small-scale clustering of gyrotactic microswimmers in turbulence, [Phys. Rev. Lett. **116**, 108104 \(2016\)](#).
- [22] J. O. Kessler, Hydrodynamic focusing of motile algal cells, [Nature \(London\) **313**, 218 \(1985\)](#).
- [23] A. Genin, Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies, [J. Mar. Syst. **50**, 3 \(2004\)](#).
- [24] S. Yazdi and A. M. Ardekani, Bacterial aggregation and biofilm formation in a vortical flow, [Biomicrofluidics **6**, 044114 \(2012\)](#).
- [25] A. Sokolov and I. S. Aranson, Rapid expulsion of microswimmers by a vortical flow, [Nat. Commun. **7**, 11114 \(2016\)](#).
- [26] G. Basterretxea, J. S. Font-Munoz, and I. Tuval, Phytoplankton orientation in a turbulent ocean: A microscale perspective, [Front. Mar. Sci. **7**, 185 \(2020\)](#).
- [27] R. Monthiller, A. Loisy, M. A. R. Koehl, B. Favier, and C. Eloy, Surfing on turbulence: A strategy for planktonic navigation, [Phys. Rev. Lett. **129**, 064502 \(2022\)](#).
- [28] S. A. Berman, J. Buggeln, D. A. Brantley, K. A. Mitchell, and T. H. Solomon, Transport barriers to self-propelled particles in fluid flows, [Phys. Rev. Fluids **6**, L012501 \(2021\)](#).
- [29] K. Son, F. Menolascina, and R. Stocker, Speed-dependent chemotactic precision in marine bacteria, [Proc. Natl. Acad. Sci. USA **113**, 8624 \(2016\)](#).
- [30] M. Lisicki, M. F. Velho Rodrigues, R. E. Goldstein, and E. Lauga, Swimming eukaryotic microorganisms exhibit a universal speed distribution, [eLife **8**, e44907 \(2019\)](#).
- [31] H. L. Fuchs and G. P. Gerbi, Seascape-level variation in turbulence- and wave-generated hydrodynamic signals experienced by plankton, [Prog. Oceanogr. **141**, 109 \(2016\)](#).
- [32] J. S. Guasto, R. Rusconi, and R. Stocker, Fluid mechanics of planktonic microorganisms, [Annu. Rev. Fluid Mech. **44**, 373 \(2012\)](#).
- [33] A. Pumir and M. Wilkinson, Collisional aggregation due to turbulence, [Annu. Rev. Condens. Matter Phys. **7**, 141 \(2016\)](#).
- [34] E. Fodor, C. Nardini, M. E. Cates, J. Tailleur, P. Visco, and F. van Wijland, How far from equilibrium is active matter? [Phys. Rev. Lett. **117**, 038103 \(2016\)](#).
- [35] L. L. Bonilla, Active ornstein-uhlenbeck particles, [Phys. Rev. E **100**, 022601 \(2019\)](#).
- [36] P. Romanczuk, M. Bär, W. Ebeling, B. Lindner, and L. Schimansky-Geier, Active Brownian particles, [Eur. Phys. J.: Spec. Top. **202**, 1 \(2012\)](#).
- [37] R. Gatignol, The Faxén formulas for a rigid particle in an unsteady non-uniform stokes flow, [J. Mec. Theor. Appl. **2**, 143 \(1983\)](#).
- [38] D. Krishnamurthy, H. Li, F. B. du Rey, P. Cambournac, A. G. Larson, E. Li, and M. Prakash, Scale-free vertical tracking microscopy, [Nat. Methods **17**, 1040 \(2020\)](#).

- [39] N. Mousavi, J. Qiu, B. Mehlig, L. Zhao, and K. Gustavsson, Efficient survival strategy for zooplankton in turbulence, *Phys. Rev. Res.* **6**, L022034 (2024).
- [40] E. J. Buskey, Components of mating behavior in planktonic copepods, *J. Mar. Syst.* **15**, 13 (1998).
- [41] H. Stark, Swimming in external fields, *Eur. Phys. J.: Spec. Top.* **225**, 2369 (2016).
- [42] E. Lushi and P. M. Vlahovska, Periodic and chaotic orbits of plane-confined micro-rotors in creeping flows, *J. Nonlinear Sci.* **25**, 1111 (2015).
- [43] N. Oppenheimer, D. B. Stein, and M. J. Shelley, Rotating membrane inclusions crystallize through hydrodynamic and steric interactions, *Phys. Rev. Lett.* **123**, 148101 (2019).
- [44] J.-A. Arguedas-Leiva and M. Wilczek, Microswimmers in an axisymmetric vortex flow, *New J. Phys.* **22**, 053051 (2020).
- [45] R. Chajwa, N. Menon, and S. Ramaswamy, Kepler orbits in pairs of disks settling in a viscous fluid, *Phys. Rev. Lett.* **122**, 224501 (2019).
- [46] A. Bolitho, R. Singh, and R. Adhikari, Periodic orbits of active particles induced by hydrodynamic monopoles, *Phys. Rev. Lett.* **124**, 088003 (2020).
- [47] R. Chajwa, N. Menon, S. Ramaswamy, and R. Govindarajan, Waves, algebraic growth, and clumping in sedimenting disk arrays, *Phys. Rev. X* **10**, 041016 (2020).
- [48] Z. Zheng, C. Jiang, Y. Chen, M. Baggioli, and J. Zhang, Topological signatures of collective dynamics and turbulent-like energy cascades in apolar active granular, *Proc. Natl. Acad. Sci. USA* **123**, e2510873123 (2026).
- [49] A. Maitra, P. Srivastava, M. Rao, and S. Ramaswamy, Activating membranes, *Phys. Rev. Lett.* **112**, 258101 (2014).
- [50] N. Shimoyama, K. Sugawara, T. Mizuguchi, Y. Hayakawa, and M. Sano, Collective motion in a system of motile elements, *Phys. Rev. Lett.* **76**, 3870 (1996).
- [51] T. Broto, J.-B. Caussin, E. Lauga, and D. Bartolo, Hydrodynamics of confined active fluids, *Phys. Rev. Lett.* **110**, 038101 (2013).
- [52] N. Kumar, H. Soni, S. Ramaswamy, and A. Sood, Flocking at a distance in active granular matter, *Nat. Commun.* **5**, 4688 (2014).
- [53] G. B. Jeffery and L. N. G. Filon, The motion of ellipsoidal particles immersed in a viscous fluid, *Proc. R. Soc. London, Ser. A* **102**, 161 (1922).
- [54] S. G. Prasath, V. Vasan, and R. Govindarajan, Accurate solution method for the Maxey-Riley equation, and the effects of basset history, *J. Fluid Mech.* **868**, 428 (2019).
- [55] C. M. Bender and S. A. Orszag, *Advanced Mathematical Methods for Scientists and Engineers* (Springer, New York, 1999).
- [56] J. Eggers and M. A. Fontelos, *Singularities: Formation, Structure, and Propagation*, Cambridge Texts in Applied Mathematics (Cambridge University Press, Cambridge, 2015).
- [57] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/m3v2-bdvj> for supplemental videos, which are listed in Appendix A.
- [58] S. Ravichandran and R. Govindarajan, Waltz of tiny droplets and the flow they live in, *Phys. Rev. Fluids* **7**, 110512 (2022).
- [59] J. Meibohm, V. Pandey, A. Bhatnagar, K. Gustavsson, D. Mitra, P. Perlekar, and B. Mehlig, Paths to caustic formation in turbulent aerosols, *Phys. Rev. Fluids* **6**, L062302 (2021).
- [60] T. Bätge, I. Fouxon, and M. Wilczek, Quantitative prediction of sling events in turbulence at high Reynolds numbers, *Phys. Rev. Lett.* **131**, 054001 (2023).
- [61] R. Chajwa, GitHub repository containing necessary codes for evolving active particles in 2D turbulence (v1.0.0), Zenodo (2026), <https://doi.org/10.5281/zenodo.18882257>.
- [62] G. Boffetta and R. E. Ecke, Two-dimensional turbulence, *Annu. Rev. Fluid Mech.* **44**, 427 (2012).
- [63] J. Eaton and J. Fessler, Preferential concentration of particles by turbulence, *Int. J. Multiphase Flow* **20**, 169 (1994).
- [64] J. R. Picardo, D. Vincenzi, N. Pal, and S. S. Ray, Preferential sampling of elastic chains in turbulent flows, *Phys. Rev. Lett.* **121**, 244501 (2018).
- [65] A. B. Burd and G. A. Jackson, Particle aggregation, *Annu. Rev. Mar. Sci.* **1**, 65 (2009).

- [66] X. Zhou, H. Wang, S. Liu, H. Wang, J. Y. E. Chan, C.-F. Pan, D. Zhao, J. K. Yang, and C.-W. Qiu, Arbitrary engineering of spatial caustics with 3D-printed metasurfaces, [Nat. Commun. **15**, 3719 \(2024\)](#).
- [67] D. Wendt, Energetics of larval swimming and metamorphosis in four species of bugula (bryozoa), [Biol. Bull. **198**, 346 \(2000\)](#).
- [68] H. L. Fuchs, L. S. Mullineaux, and A. R. Solow, Sinking behavior of gastropod larvae (*Ilyanassa obsoleta*) in turbulence, [Limnol. Oceanogr. **49**, 1937 \(2004\)](#).
- [69] M. Chen, Z. Zhao, J. Yang, K. Peng, M. A. Baker, F. Bai, and C.-J. Lo, Length-dependent flagellar growth of *Vibrio alginolyticus* revealed by real time fluorescent imaging, [eLife **6**, e22140 \(2017\)](#).
- [70] A. Zöttl and H. Stark, Nonlinear dynamics of a microswimmer in poiseuille flow, [Phys. Rev. Lett. **108**, 218104 \(2012\)](#).