

Kinematic matrix theory and universalities in self-propellers and active swimmers

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We describe an efficient and parsimonious matrix-based theory for studying the ensemble behavior of self-propellers and active swimmers, such as nanomotors or motile bacteria, that are typically studied by differential-equation-based Langevin or Fokker-Planck formalisms. The kinematic effects for elementary processes of motion are incorporated into a matrix, called the “kinematrix,” from which we immediately obtain correlators and the mean and variance of angular and position variables (and thus effective diffusivity) by simple matrix algebra. The kinematrix formalism enables us recast the behaviors of a diverse range of self-propellers into a unified form, revealing universalities in their ensemble behavior in terms of new emergent time scales. Active fluctuations and hydrodynamic interactions can be expressed as an additive composition of separate self-propellers.

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I. INTRODUCTION

Self-propellers are a wide class of far-from-equilibrium systems including motile cells and bacteria [1–19], artificial nanomotors [20–31], aquatic swimmers [32–35], insects, birds, and other animals [36–41], and even pedestrians [42]. Their motion naturally decomposes into distinct elementary processes such as deterministic translation and rotation, plus stochastic components such as orientational diffusion, flipping about an axis, or tumbling (Fig. 1). The phenomenological kinematic parameters of these elementary processes are typically obtained by comparing experimental observations to theoretical models that are developed using Langevin or Fokker-Planck differential equations [3–8,41–56]. These mathematical formalisms grow more cumbersome as the number of elementary processes increases, with distinct processes often being treated in a nonuniform manner by a menu of methods. Here we introduce an alternative approach based on matrix algebra, which treats all elementary motive processes on an equal footing and remains tractable for complex motor behavior. By inspection, we compile the kinematic effects of the elementary processes into a kinematic matrix, called the *kinematrix*, from which we immediately obtain the ensemble behavior of self-propellers by simple matrix algebra. The kinematrix consolidates the behavior of many classes of self-propellers [14–17,47–50,57–59] into a single unified form with newly emergent composite time scales, thus revealing universalities in the ensemble behavior of diverse self-propellers that had previously been considered “different” systems. The analytical and computational simplicity of the kinematrix should also facilitate further advances in the analysis of large complex datasets, such as the inverse problem of extracting the correct elementary motive processes from complex trajectory data. The effects of active fluctuations and rotation-translation coupling at the level of ensemble properties can be recast as effectively additive contributions arising from independent self-propellers.

The key to the kinematrix approach is a body-frame description of the motion. A self-propeller, while translating, may rotate deterministically due to structural imperfection [46,60,61], hydrodynamic interaction with a substrate [9–13], or purposeful engineering [62–69]; they may also suffer stochastic events that influence the direction of motion such as tumbling or orientational diffusion. We build an empirical body frame that is anchored in dynamical (rather than geometrical) properties: The self-propeller translates at velocity $\mathbf{v} = v\hat{v}$ while rotating at angular velocity $\boldsymbol{\omega} = \omega\hat{\omega}$ at a position $\mathbf{p} = \frac{v}{\omega}\hat{p}$ with respect to the center of its instantaneous circular orbit, thus yielding an orthonormal triple $[\hat{p}, \hat{v}, \hat{\omega}]$ as a right-handed empirical body frame fixed to the self-propeller. We choose a fixed laboratory frame $[\hat{x}, \hat{y}, \hat{z}]$ that coincides with $[\hat{p}, \hat{v}, \hat{\omega}]$ at $t = 0$. The orientation of body frame at time t is related to its initial orientation by a propagator $U(t)$ such that $\hat{\xi}(t) = U(t)\hat{\xi}(0)$ for $\hat{\xi}$ being any of \hat{p} , \hat{v} , or $\hat{\omega}$. The propagator represents the net deterministic and stochastic rotation of the body frame from $0 \rightarrow t$; from its ensemble average $\langle U(t) \rangle$ we can obtain pair correlators, finite-time

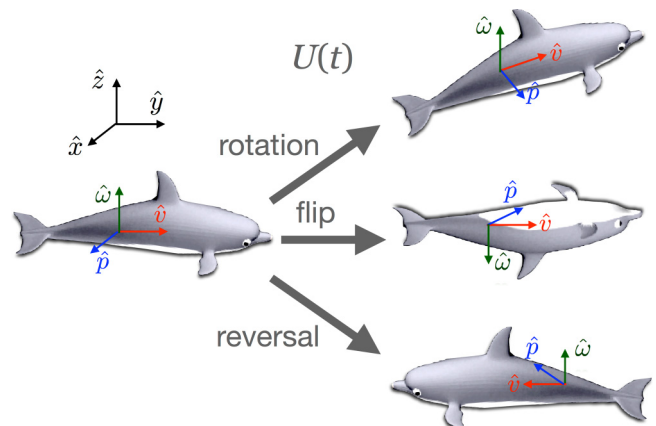


FIG. 1. (Color online) At $t = 0$ the laboratory frame and body frame coincide. During $[0, dt]$ a self-propeller can experience small turns about $\hat{\omega}$ due to deterministic rotation, stochastic orientational diffusion, or tumbling; it can also flip about \hat{v} or reverse the direction of motion. The operator $U(t)$ represents this evolution.

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average displacement, finite-time mean-square displacement, and asymptotic effective diffusivity. The stochastic component of the dynamics leads to an ensemble of possible body-frame orientations at time t , and each orientation connects to the initial orientation through an ensemble of different paths. The core of kinematrix theory is to overcome the difficulty of obtaining $\langle U(t) \rangle$ over these ensembles by turning $\langle U(t) \rangle$ into the product of ensemble averages of independent incremental rotations in the body frame, as explained below.

II. THEORY FORMULATION

Divide the time line $[0, t)$ into infinitesimal increments $dt = t/n$ (large integer n) with end points $t_i \equiv i dt$ (integer i). With $U_i \equiv U(t_i)$ and \mathcal{R}_i as the net rotation in the laboratory frame during the infinitesimal interval $[t_i, t_{i+1})$, the propagator takes the recursive form $U_n = \mathcal{R}_{n-1} U_{n-1}$. Now we transform the rotations \mathcal{R}_i in the laboratory frame into rotations in the body frame $\tilde{\mathcal{R}}_i = U_i^{-1} \mathcal{R}_i U_i$, yielding, $U_n = \mathcal{R}_{n-1} U_{n-1} = U_{n-1} \tilde{\mathcal{R}}_{n-1} = \tilde{\mathcal{R}}_0 \tilde{\mathcal{R}}_1 \cdots \tilde{\mathcal{R}}_{n-1}$. For processes with negligible correlation time, the $\tilde{\mathcal{R}}_i$'s are independent and identically distributed, $\langle \tilde{\mathcal{R}}_i \rangle = \langle \tilde{\mathcal{R}}_0 \rangle$, resulting in

$$\langle U(t) \rangle \simeq \langle \tilde{\mathcal{R}}_0 \rangle^{t/dt}. \quad (1)$$

The net rotation $\tilde{\mathcal{R}}_0 = \tilde{\mathcal{R}}_0^{(1)} \cdots \tilde{\mathcal{R}}_0^{(N)}$ is the product of N independent elementary processes $\tilde{\mathcal{R}}_0^{(j)}$ (such as flipping, tumbling or orientational diffusion) involved in self-propeller's motion during $[0, dt)$. Expanding their expectations to first order in dt , $\langle \tilde{\mathcal{R}}_0^{(j)} \rangle = \mathcal{I} - \mathcal{K}^{(j)} dt + \mathcal{O}(dt^2)$ for $j = 1, \dots, N$, we obtain

$$\langle \tilde{\mathcal{R}}_0 \rangle = \mathcal{I} - \mathcal{K} dt + \mathcal{O}(dt^2). \quad (2)$$

We call $\mathcal{K} = \mathcal{K}^{(1)} + \cdots + \mathcal{K}^{(N)}$ the *kinematrix*. It is the sum of the first-order contributions $\mathcal{K}^{(i)}$ of elementary rotations and contains the kinematic effects of all such processes. In the limit $t \gg dt$, Eqs. (1) and (2) yield

$$\langle U(t) \rangle = e^{-\mathcal{K}t}. \quad (3)$$

Using the initial condition $[\hat{x}, \hat{y}, \hat{z}] \equiv [\hat{p}(0), \hat{v}(0), \hat{\omega}(0)]$ and $\hat{\xi}(t) = U(t) \hat{\xi}(0)$ for $\hat{\xi}$ any of \hat{p} , \hat{v} , or $\hat{\omega}$, we obtain the correlators for linear ($v\hat{v}$) and angular ($\omega\hat{\omega}$) velocities,

$$C_{vv}(t) = \langle v(0) \cdot v(t) \rangle = \langle v(0)v(t) \rangle [e^{-\mathcal{K}t}]_{22}, \quad (4)$$

$$C_{\omega\omega}(t) = \langle \omega(0) \cdot \omega(t) \rangle = \langle \omega(0)\omega(t) \rangle [e^{-\mathcal{K}t}]_{33}. \quad (5)$$

The subscripts on $[e^{-\mathcal{K}t}]$ identify matrix elements. The off-diagonal elements of $e^{-\mathcal{K}t}$ give the correlators between different directions \hat{p} , \hat{v} , $\hat{\omega}$.

The magnitude and direction of the velocity may fluctuate as a result of random disturbances, but since the sources of these fluctuations generally differ, the fluctuations of v and \hat{v} are typically independent. Before discussing the effect of active speed fluctuations, we explain the formalism with a speed $v(t)$ fluctuating weakly around a mean $\langle v(t) \rangle = \bar{v}$ with negligible correlation time, so that $\langle v(0)v(t) \rangle \simeq \bar{v}^2$ (the common assumption of constant speed [46–50,57,70] is a special case). Thus, the ensemble average and mean-squared displacements are

$$\langle \Delta \mathbf{r}(t) \rangle = \bar{v} \int_0^t e^{-\mathcal{K}t'} \cdot \hat{v}(0) dt' = \bar{v} \mathcal{K}^{-1} (\mathcal{I} - e^{-\mathcal{K}t}) \cdot \hat{v}(0), \quad (6)$$

$$\langle |\Delta \mathbf{r}(t)|^2 \rangle = 2\bar{v}^2 [t \mathcal{K}^{-1} - \mathcal{K}^{-1} \mathcal{K}^{-1} (\mathcal{I} - e^{-\mathcal{K}t})]_{22}. \quad (7)$$

The interplay of deterministic and stochastic dynamics creates effective diffusion at long times; the observed diffusivity of a self-propeller is the sum of its effective and passive Brownian diffusivities. The effective diffusivity $D_{\text{eff}} = \frac{1}{2d} \lim_{t \rightarrow \infty} t^{-1} \langle |\Delta \mathbf{r}(t)|^2 \rangle$ in d dimensional space is

$$D_{\text{eff}} = \frac{\bar{v}^2}{d} [\mathcal{K}^{-1}]_{22} = \frac{\bar{v}^2}{d} \frac{\mathcal{K}_{11}\mathcal{K}_{33} - \mathcal{K}_{13}\mathcal{K}_{31}}{\det \mathcal{K}}. \quad (8)$$

If motion is strictly restricted to a plane such that $\det \mathcal{K} = 0$, we make the replacement $\mathcal{K} \rightarrow \mathcal{K} + \varepsilon \mathcal{I}$, calculate Eqs. (4)–(8), and take $\varepsilon \rightarrow 0$ at the end.

Unsteady operation of the self-propeller's engine leads to speed fluctuations $\delta v(t)$. Since $\langle v(t)v(0) \rangle = \bar{v}^2 + \langle \delta v(t) \delta v(0) \rangle$, as far as velocity correlations (4), mean-square displacement (7), and effective diffusivity (8) are concerned, the velocity fluctuations $\delta v(t) \hat{v}(t)$ make an uncorrelated additive contribution. For models [7] where $\langle \delta v(t) \delta v(0) \rangle = [v^2 - \bar{v}^2] e^{-\kappa_v t}$, such contributions are equal to the corresponding properties of a self-propeller with mean speed $\sqrt{v^2 - \bar{v}^2}$ and kinematrix $\mathcal{K}' = \mathcal{K} + \kappa_v \mathcal{I}$.

III. ELEMENTARY PROCESSES

Equations (4)–(8) show how important physical quantities follow immediately from the kinematrix \mathcal{K} . Next, we show how to build \mathcal{K} from the contributions $\mathcal{K}^{(j)}$ of elementary processes by inspection of motion during the interval $[0, dt)$. We write \mathcal{K} in terms of a linear combination of matrices \mathcal{J}_k , \mathcal{P}_k , and \mathcal{P}_k^\perp . \mathcal{J}_k is the generator of infinitesimal rotation about an axis \hat{k} ,

$$\begin{aligned} \mathcal{J}_x &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & -1 \\ 0 & 1 & 0 \end{bmatrix}, & \mathcal{J}_y &= \begin{bmatrix} 0 & 0 & 1 \\ 0 & 0 & 0 \\ -1 & 0 & 0 \end{bmatrix}, \\ \mathcal{J}_z &= \begin{bmatrix} 0 & -1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \end{aligned} \quad (9)$$

\mathcal{P}_k is the orthogonal projection onto the k th coordinate,

$$\begin{aligned} \mathcal{P}_x &= \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, & \mathcal{P}_y &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \\ \mathcal{P}_z &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix}, \end{aligned} \quad (10)$$

and $\mathcal{P}_k^\perp = \mathcal{I} - \mathcal{P}_k$ is the projection onto the plane perpendicular to \hat{k} ,

$$\begin{aligned} \mathcal{P}_x^\perp &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}, & \mathcal{P}_y^\perp &= \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix}, \\ \mathcal{P}_z^\perp &= \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{bmatrix}. \end{aligned} \quad (11)$$

We study four elementary processes: tumbles, flips, deterministic rotation, and orientational diffusion; these four processes cover a wide variety of self-propeller dynamics from artificial nanomotors to motile single-cell organisms and macroscopic movers. A tumble is a sudden rotation of angle θ with distribution $P(\theta)$ about an axis k , occurring at a rate f . We model tumbles by a Poisson process $\tilde{\mathcal{R}}_0^{\text{tumble}} = \mathcal{I} + s_0[(\cos\theta - 1)\mathcal{P}_k^\perp + \sin\theta\mathcal{J}_k]$, where s_0 is 0 or 1 with probabilities $(1 - f)dt$ or $f dt$, respectively. The contribution of tumbling is then

$$\mathcal{K}_k^{\text{tumble}} = f(1 - \langle \cos\theta \rangle_p)\mathcal{P}_k^\perp - f\langle \sin\theta \rangle_p\mathcal{J}_k, \quad (12)$$

where the averages $\langle \cos\theta \rangle_p$ and $\langle \sin\theta \rangle_p$ are with respect to $P(\theta)$. Flipping is tumbling by $\theta = \pi$ about an axis k :

$$\mathcal{K}_k^{\text{flip}} = 2f\mathcal{P}_k^\perp. \quad (13)$$

Deterministic rotation at angular speed ω about axis k during dt is described by $e^{\omega dt\mathcal{J}_k} = \mathcal{I} - (-\omega\mathcal{J}_k)dt + \mathcal{O}(dt^2)$; thus,

$$\mathcal{K}_k^{\text{det}} = -\omega\mathcal{J}_k. \quad (14)$$

Orientational diffusion with diffusivity D_k about an axis k during dt is described by $\tilde{\mathcal{R}}_0^{\text{ort}} = e^{d\phi\mathcal{J}_k}$ where the incremental rotational angle $d\phi$ is a Wiener process of mean zero and standard deviation $\sqrt{2D_k dt}$. The contribution of $\langle \tilde{\mathcal{R}}_0^{\text{ort}} \rangle = \mathcal{I} - D_k\mathcal{P}_k^\perp dt + \mathcal{O}(dt^2)$ to the kinematrix is

$$\mathcal{K}_k^{\text{ort}} = D_k\mathcal{P}_k^\perp. \quad (15)$$

IV. FOUR SELF-PROPELLER SCENARIOS

Having established the formalism, we now demonstrate how the elementary processes of Eqs. (12)–(15) combine to describe four different classes of self-propellers, building \mathcal{K} by inspection. We start by illustrating the application of our formalism to the previously studied classes of diffusing-and-flipping self-propellers and magnetotactic bacteria in a rotating magnetic field, calculating the asymptotic D_{eff} (8) as an example of ensemble properties (4)–(8). Next we study run-and-tumble motion via our continuous model—rather than traditional discrete random walks [18,19,33,71,72]—and demonstrate how to incorporate speed fluctuations. Last, we analyze a 3D swimmer and discuss the effect of rotation-translation coupling. After discussing these individual classes of self-propellers, we recast the kinematrices into a form that covers all motor types; the clarity of the formalism reveals new emergent time scales with universal short and long time behavior. In building \mathcal{K} for each class, keep in mind that we inspect the motion during $[0, dt)$; hence, $\mathcal{P}_p^\perp = \mathcal{P}_x^\perp, \mathcal{P}_v^\perp = \mathcal{P}_y^\perp, \mathcal{P}_\omega^\perp = \mathcal{P}_z^\perp$, and $\mathcal{J}_\omega = \mathcal{J}_z$ in Eqs. (12)–(15).

Diffusion-flip (DF) self-propellers include biological “circle swimmers” as well as artificial nanomotors [46–50,57]. Steric hinderance from a two dimensional (2D) planar substrate resists free orientational diffusion about any axis parallel to the substrate and forces the self-propeller to perform only sudden flips about \hat{v} . While translating and rotating in a 2D plane, the swimmer undergoes orientational diffusion with diffusivity D_ω about $\hat{\omega}$ perpendicular to the substrate while flipping with frequency f about \hat{v} and changing its rotation chirality. The contributions to \mathcal{K} are $-\omega\mathcal{J}_z$ for deterministic rotation about $\hat{\omega}$, $D_\omega\mathcal{P}_z^\perp$ for orientational diffusion about $\hat{\omega}$, and

$2f\mathcal{P}_y^\perp$ for flipping about \hat{v} , so that $\mathcal{K}_{2D} = -\omega\mathcal{J}_z + D_\omega\mathcal{P}_z^\perp + 2f\mathcal{P}_y^\perp$. Eq. (8) then yields (see Sec. 1 of the Appendix)

$$D_{\text{eff},2D} = \frac{\bar{v}^2}{2} \frac{D_\omega + 2f}{\omega^2 + D_\omega(D_\omega + 2f)}. \quad (16)$$

For a fast flipping rotor ($f \gg \omega$), the rotation rapidly averages out and the rotor acts like a linear motor ($D_{\text{eff},2D}^{\text{linear}} = \frac{\bar{v}^2}{2D_\omega}$).

Magnetotactic bacteria (MB) can move near a substrate and rotate in synchrony with a rotating magnetic field at angular speed ω [14–17]. The rotation contributes $-\omega\mathcal{J}_z$. The trajectory is a set of U-shaped segments due to occasional reversals of \hat{v} with frequency f while preserving the chirality of the orbit (contributing $2f\mathcal{P}_z^\perp$), plus orientational diffusion about $\hat{\omega}$ (contributing $D_\omega\mathcal{P}_z^\perp$). From $\mathcal{K}_{\text{MB}} = (2f + D_\omega)\mathcal{P}_z^\perp - \omega\mathcal{J}_z$ we obtain (see Sec. 2 of the Appendix)

$$D_{\text{eff},\text{MB}} = \frac{\bar{v}^2}{2} \frac{D_\omega + 2f}{\omega^2 + (D_\omega + 2f)^2}. \quad (17)$$

Run-and-tumble self-propellers (RT) such as *E. coli* [1] and *Daphnia* [33–35] undergo intermittent tumbles due to stochastic forces or switching of flagellar beating between the synchronous and asynchronous modes [58,59]. They have been studied by *ad hoc* models of discrete random walks [18,19,33,72] in quasi-2D with a distribution of turning angles. Although mathematically functional for experimental analysis, such an approach does not unfold the physical processes underlying the motion in continuous time. Here we build a continuous-time model and extend it further to include the effects of engine fluctuations. The velocity direction \hat{v} lies in the plane of motion and $\hat{\omega}$ represents an axis perpendicular to this plane about which the self-propeller undergoes orientational diffusion (contributing $D_\omega\mathcal{P}_z^\perp$) and tumbling with frequency f [contributing $f(1 - \langle \cos\theta \rangle_p)\mathcal{P}_z^\perp - f\langle \sin\theta \rangle_p\mathcal{J}_z$ to the kinematrix]. The kinematrix $\mathcal{K}_{\text{RT}} = [D_\omega + f(1 - \langle \cos\theta \rangle_p)]\mathcal{P}_z^\perp - f\langle \sin\theta \rangle_p\mathcal{J}_z$ yields the effective diffusivity for a run-and-tumbler at mean speed \bar{v} (noted by the superscript “ms”),

$$D_{\text{eff,RT}}^{\text{ms}} = \frac{\bar{v}^2}{2} \frac{D_\omega + f(1 - \langle \cos\theta \rangle_p)}{[f\langle \sin\theta \rangle_p]^2 + [D_\omega + f(1 - \langle \cos\theta \rangle_p)]^2}. \quad (18)$$

We can extend this model to take into account speed fluctuations $\delta v(t)$ with autocorrelation $\langle \delta v(t)\delta v(0) \rangle = [(v^2) - \bar{v}^2]e^{-\kappa_v t}$ [7]. Then, the additive modification to effective diffusivity due to fluctuations (noted by the superscript “fluc”) is equal to the effective diffusivity of a self-propeller with kinematrix $\mathcal{K}_{\text{RT}}^{\text{fluc}} = \mathcal{K}_{\text{RT}} + \kappa_v\mathcal{I}$ and mean speed $\sqrt{(v^2) - \bar{v}^2}$; that is,

$$D_{\text{eff,RT}}^{\text{fluc}} = \frac{((v^2) - \bar{v}^2)[\kappa_v + D_\omega + f(1 - \langle \cos\theta \rangle_p)]}{2\{[f\langle \sin\theta \rangle_p]^2 + [\kappa_v + D_\omega + f(1 - \langle \cos\theta \rangle_p)]^2\}}. \quad (19)$$

Combining these, the effective diffusivity for a run-and-tumbler with speed fluctuations is $D_{\text{eff,RT}}^{\text{ms}} + D_{\text{eff,RT}}^{\text{fluc}}$. The same procedure holds for velocity autocorrelation (5) and mean-square displacement (7). We can advance the model further by including more elementary processes in the model and fitting multiple models in parallel to an experimental dataset to find the best model and elucidate the underlying continuous-time motion of the run-and-tumbler.

3D self-propeller: The motion of biological and artificial self-propellers in 3D is also of interest [73–75]. In contrast to the fixed rotation plane in 2D motion, the plane of rotation for a 3D self-propeller wanders in 3D space. The kinematrix for a self-propeller moving at \bar{v} while rotating at angular speed ω and suffering orientational diffusion about the three axes of the body frame is $\mathcal{K}_{3D} = D_{\hat{p}}\mathcal{P}_x^\perp + D_{\hat{v}}\mathcal{P}_y^\perp + D_{\hat{\omega}}\mathcal{P}_z^\perp - \omega\mathcal{J}_z$. Equation (8) then yields

$$D_{\text{eff},3D} = \frac{\bar{v}^2}{3} \frac{D_{\hat{\omega}} + D_{\hat{v}}}{[D_{\hat{\omega}} + D_{\hat{p}}][D_{\hat{\omega}} + D_{\hat{v}}] + \omega^2}. \quad (20)$$

For a 3D linear motor, setting $\omega = 0$ eliminates $D_{\hat{v}}$ from $D_{\text{eff},3D}$, since rotation about \hat{v} has no observable effect for a linear motor. In that case, $D_{\hat{p}}$ and $D_{\hat{\omega}}$'s new meanings are orientational diffusion coefficients about two perpendicular axes orthogonal to \hat{v} . Although the effects of rotation-translation coupling in 2D are included implicitly in the phenomenological kinematic parameters, in 3D such hydrodynamic interactions can lead to nonorthogonality of the propulsive velocity and rotation axis. Hence, the velocity has a component $\bar{v}\hat{v}$ in the instantaneous plane of rotation as well as a component $\bar{v}_\omega\hat{\omega}$ along the rotation axis, so the speed is $\sqrt{\bar{v}^2 + \bar{v}_\omega^2}$. The effective diffusivity depends on both diagonal

and off-diagonal elements of \mathcal{K}^{-1} in the form

$$D_{\text{eff},3D}^{\text{non}\perp} = \frac{\bar{v}^2}{d}[\mathcal{K}^{-1}]_{22} + \frac{\bar{v}\bar{v}_\omega}{d}[\mathcal{K}^{-1}]_{23} + \frac{\bar{v}_\omega\bar{v}}{d}[\mathcal{K}^{-1}]_{32} + \frac{\bar{v}_\omega^2}{d}[\mathcal{K}^{-1}]_{33}. \quad (21)$$

For the 3D example here, off-diagonal terms are zero and the correction to $D_{\text{eff},3D}$ is an additional term $(\bar{v}_\omega^2/d)[\mathcal{K}^{-1}]_{33} = \bar{v}_\omega^2/3(D_{\hat{p}} + D_{\hat{v}})$, which is the effective diffusivity of a 3D linear motor with speed \bar{v}_ω .

V. UNIVERSALITIES

The clarity of kinematrix formalism facilitates further insights into universalities that previously had been hiding in the complexities required of differential-equation-based analysis. We can consolidate and recast these four scenarios into a *unified* form,

$$\mathcal{K}_{\text{uni}} = \gamma_\omega\mathcal{P}_z + \gamma\mathcal{P}_z^\perp - \omega_z\mathcal{J}_z + \delta(\mathcal{P}_x - \mathcal{P}_y) \quad (22a)$$

$$= \begin{bmatrix} \gamma + \delta & \omega_z & 0 \\ -\omega_z & \gamma - \delta & 0 \\ 0 & 0 & \gamma_\omega \end{bmatrix}, \quad (22b)$$

where the scenario-dependent parameters are

	γ_ω	γ	δ	ω_z
2D	$2f$	$D_{\hat{\omega}} + f$	f	ω
RT	0	$D_{\hat{\omega}} + f(1 - \langle \cos \theta \rangle)$	0	$f \langle \sin \theta \rangle$
MB	0	$D_{\hat{\omega}} + 2f$	0	ω
3D	$D_{\hat{p}} + D_{\hat{v}}$	$D_{\hat{\omega}} + \frac{D_{\hat{p}} + D_{\hat{v}}}{2}$	$\frac{D_{\hat{v}} - D_{\hat{p}}}{2}$	ω

(23)

Using Eqs. (4), (5), (22) and defining

$$\Omega^2 = \omega_z^2 - \delta^2, \quad (24)$$

the autocorrelators of angular and linear velocities are

$$C_{\omega\omega}(t) = \omega^2 e^{-\gamma\omega t}, \quad (25)$$

$$C_{vv}(t) = \bar{v}^2 e^{-\gamma t} \{\cos(\Omega t) + \delta \sin \Omega t / \Omega\}. \quad (26)$$

Five newly emergent time scales γ_ω^{-1} , γ^{-1} , δ^{-1} , ω_z^{-1} , and Ω^{-1} govern the behavior of all these self-propellers. In 3D $C_{\omega\omega}$ measures the wandering of the orbital plane, with an exponential decay at characteristic time γ_ω^{-1} . In 2D it measures the loss of memory of the sense of rotation (i.e., chirality), since $\hat{\omega}$ orients to the orbit by a right-hand rule. C_{vv} measures how fast the velocity forgets its orientation, with characteristic time γ^{-1} . The temporal behavior is not governed by ω^{-1} , but Ω^{-1} which can be real or imaginary depending on δ and ω_z . For imaginary Ω , C_{vv} does not oscillate but has a longer correlation time $(\gamma - |\Omega|)^{-1}$ as for linear nanomotors. These time scales also determine the extent to which $\langle \Delta \mathbf{r}(\infty) \rangle = (\gamma^2 + \Omega^2)^{-1} \bar{v} [-\omega \hat{p}(0) + (\delta + \gamma) \hat{v}(0)]$ depends on the direction of initial velocity and, therefore, initial direction of rotation. This is the generalization of the

“chiral diffusion” of 2D nanorotors [49], even though there is no well-defined chirality for a 3D rotary swimmer.

Equations (8) and (22) yield a unified expression for the effective diffusion coefficient in terms of the new time scales:

$$D_{\text{eff,uni}} = \left(\frac{\bar{v}^2}{d} \right) \frac{\gamma + \delta}{\gamma^2 + \Omega^2}. \quad (27)$$

We can obtain D_{eff} for any class of self-propeller by substituting the appropriate parameters from Eq. (23) into Eq. (27). The mean-square displacement (7) takes a unified form,

$$\begin{aligned} \langle |\Delta \mathbf{r}(t)|^2 \rangle_{\text{uni}} &= 2dD_{\text{eff}}t - 2\bar{v}^2(\gamma^2 - \Omega^2 + 2\gamma\delta)/(\gamma^2 + \Omega^2)^2 \\ &+ \frac{2\bar{v}^2 e^{-\gamma t}}{(\gamma^2 + \Omega^2)^2} \{(\gamma^2 - \Omega^2 + 2\gamma\delta) \cos \Omega t \\ &+ [(\gamma^2 - \Omega^2)\delta - 2\gamma\Omega^2] \sin \Omega t / \Omega\}. \end{aligned} \quad (28)$$

It behaves ballistically (i.e., $\bar{v}^2 t^2$) at short times $t \ll \min(\Omega^{-1}, \gamma^{-1})$ and diffusively ($2dD_{\text{eff}}t$) at long times. For real $\Omega^{-1} < \gamma^{-1}$ the crossover between the two limits is oscillatory. However, for $\Omega^{-1} > \gamma^{-1}$ the rate at which the velocity forgets its orientation is faster than the oscillation, and the oscillatory crossover is suppressed. For an imaginary Ω , on the other hand, the characteristic time of the exponential decay is $(\gamma - |\Omega|)^{-1} > \gamma^{-1}$ with no oscillatory crossover

between ballistic and diffusive regimes. The special cases of 2D self-propellers with flipping [46] and without flipping [50] and magnetotactic bacteria [16] have been compared thoroughly with numerical experimental data.

VI. CONCLUSION

The kinematrix formalism elegantly handles a variety of self-propellers with active fluctuations and rotation-translation coupling and reveals universalities in self-propeller behavior. As a parsimonious means to construct models with different sets of elementary processes, the kinematrix could enable new types of analysis beyond the traditional mode of feeding forward from dynamical model to motor trajectory. For example, distinct stochastic processes that are lumped together in current treatments could be distinguished, such as local environmental noise and internal engine fluctuations which contribute towards a single distribution of turning angles within a traditional discrete model with a fixed-length random walker. In the longer term, memory effects could be disentangled from complex composite behaviors by identifying an optimal memory-free kinematrix description and then extracting the residual memory-dependent phenomena. Extension of the formalism to explicitly handle memory effects is also a natural next step; the generality and intuitive clarity of this formalism provides a strong conceptual underpinning to further advances in the analysis of self-propellers.

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APPENDIX: CALCULATING ENSEMBLE AVERAGE PROPERTIES AND EMERGENT TIME SCALES

In this appendix we provide a detailed step-by-step walk through of the application of our theory to two scenarios: the diffusion-flip self-propeller and the magnetotactic bacterium. We build the kinematrix by inspection and calculate the corresponding effective diffusivity using Eq. (8). We also find the emergent new time scales, γ_ω^{-1} , ω_z^{-1} , γ^{-1} , δ^{-1} , and Ω^{-1} , by comparing the scenario-specific kinematrix with the general kinematrix form (22). Then we can calculate the effective diffusivity and mean-square displacement

simply by plugging these parameters into Eqs. (27) and (28), respectively.

1. Diffusion-flip self-propellers

The DF self-propeller moves with speed \bar{v} and rotates with angular speed ω while diffusing orientationally about the axis of rotation $\hat{\omega}$ with diffusion coefficient D_ω and flipping at a rate of f about the direction of the velocity \hat{v} . The kinematrix includes contributions of three elementary processes: deterministic rotation about $\hat{\omega}$, $\mathcal{K}_\omega^{\text{det}} = -\omega\mathcal{J}_\omega$, orientational diffusion about $\hat{\omega}$, $\mathcal{K}_\omega^{\text{ort}} = D_\omega\mathcal{P}_\omega^\perp$, and flipping around \hat{v} , $\mathcal{K}_v^{\text{flip}} = 2f\mathcal{P}_v^\perp$. As discussed in the body of the paper, we inspect the motion during $[0, dt)$, where $\mathcal{P}_v^\perp = \mathcal{P}_y^\perp$, $\mathcal{P}_\omega^\perp = \mathcal{P}_z^\perp$, and $\mathcal{J}_\omega = \mathcal{J}_z$. Using the explicit forms of these matrices [Eqs. (9)–(11)], the kinematrix becomes

$$\begin{aligned}\mathcal{K}_{2D} &= \mathcal{K}_\omega^{\text{det}} + \mathcal{K}_\omega^{\text{ort}} + \mathcal{K}_v^{\text{flip}} \\ &= -\omega\mathcal{J}_\omega + D_\omega\mathcal{P}_\omega^\perp + 2f\mathcal{P}_v^\perp \\ &= -\omega\mathcal{J}_z + D_\omega\mathcal{P}_z^\perp + 2f\mathcal{P}_y^\perp \\ &= \begin{bmatrix} D_\omega + 2f & \omega & 0 \\ -\omega & D_\omega & 0 \\ 0 & 0 & 2f \end{bmatrix},\end{aligned}\quad (\text{A1})$$

from which we obtain

$$\mathcal{K}_{11}\mathcal{K}_{33} - \mathcal{K}_{13}\mathcal{K}_{31} = (2f + D_\omega)(2f) - 0 = 2f(2f + D_\omega) \quad (\text{A2})$$

and

$$\begin{aligned}\det\mathcal{K}_{2D} &= 2f \begin{vmatrix} 2f + D_\omega & \omega \\ -\omega & D_\omega \end{vmatrix} \\ &= 2f[D_\omega(2f + D_\omega) + \omega^2].\end{aligned}\quad (\text{A3})$$

Employing now Eq. (8) yields

$$\begin{aligned}D_{\text{eff},2D} &= \frac{\bar{v}^2}{d} \frac{\mathcal{K}_{11}\mathcal{K}_{33} - \mathcal{K}_{13}\mathcal{K}_{31}}{\det\mathcal{K}} \\ &= \frac{\bar{v}^2}{2} \frac{2f + D_\omega}{D_\omega(2f + D_\omega) + \omega^2},\end{aligned}\quad (\text{A4})$$

which is expression (16). Comparing the kinematrix (A1) with the unified kinematrix (22b) immediately yields $\gamma_\omega = 2f$, $\omega_z = \omega$, $\gamma = D_\omega + f$, $\delta = f$, and $\Omega^2 = \omega^2 - f^2$, as tabulated in (23). Plugging these parameters into the unified form $\langle |\Delta\mathbf{r}(t)|^2 \rangle_{\text{uni}}$ (28) gives the mean-square displacement for diffusion-flip self-propellers,

$$\begin{aligned}\langle |\Delta\mathbf{r}(t)|^2 \rangle_{2D} &= 2\bar{v}^2 t \frac{2f + D_\omega}{D_\omega(2f + D_\omega) + \omega^2} - 2\bar{v}^2 \frac{(2f + D_\omega)^2 - \omega^2}{[D_\omega(2f + D_\omega) + \omega^2]^2} + 2\bar{v}^2 e^{-(D_\omega + f)t} \frac{(2f + D_\omega)^2 - \omega^2}{[D_\omega(2f + D_\omega) + \omega^2]^2} \cos(t\sqrt{\omega^2 - f^2}) \\ &\quad + 2\bar{v}^2 e^{-(D_\omega + f)t} \frac{f(2f + D_\omega)^2 - \omega^2(3f + 2D_\omega)}{[D_\omega(2f + D_\omega) + \omega^2]^2} \frac{\sin(t\sqrt{\omega^2 - f^2})}{\sqrt{\omega^2 - f^2}}.\end{aligned}\quad (\text{A5})$$

2. Magnetotactic bacteria

In this scenario, motion is restricted to a plane and $\det\mathcal{K} = 0$. Magnetotactic bacteria move with speed \bar{v} and rotate in

synchrony with a rotating magnetic field at angular speed ω while suffering orientational diffusion about $\hat{\omega}$ and occasional chirality-preserving reversals of \hat{v} with frequency f . Three

elementary processes contribute to the kinematrix: deterministic rotation about $\hat{\omega}$, $\mathcal{K}_{\hat{\omega}}^{\text{det}} = -\omega\mathcal{J}_{\omega}$, orientational diffusion about $\hat{\omega}$, $\mathcal{K}_{\hat{\omega}}^{\text{ort}} = D_{\hat{\omega}}\mathcal{P}_{\omega}^{\perp}$, and reversals of \hat{v} with frequency f while preserving the chirality which is equivalent to 180° rotation of \hat{v} about $\hat{\omega}$, so that $\mathcal{K}_{\hat{\omega}}^{\text{flip}} = 2f\mathcal{P}_{\omega}^{\perp}$. Summing up these contributions and keeping in mind that $\mathcal{P}_{\omega}^{\perp} = \mathcal{P}_z^{\perp}$ and $\mathcal{J}_{\omega} = \mathcal{J}_z$, we obtain the kinematrix for the magnetotactic bacteria,

$$\begin{aligned} \mathcal{K}_{\text{MB}} &= \mathcal{K}_{\hat{\omega}}^{\text{det}} + \mathcal{K}_{\hat{\omega}}^{\text{ort}} + \mathcal{K}_{\hat{\omega}}^{\text{flip}} \\ &= -\omega\mathcal{J}_{\omega} + D_{\hat{\omega}}\mathcal{P}_{\omega}^{\perp} + 2f\mathcal{P}_{\omega}^{\perp} \\ &= -\omega\mathcal{J}_z + D_{\hat{\omega}}\mathcal{P}_z^{\perp} + 2f\mathcal{P}_z^{\perp} \\ &= \begin{bmatrix} D_{\hat{\omega}} + 2f & \omega & 0 \\ -\omega & D_{\hat{\omega}} + 2f & 0 \\ 0 & 0 & 0 \end{bmatrix}. \end{aligned} \quad (\text{A6})$$

In this example, the motion is strictly in the xy plane and $\det \mathcal{K}_{\text{MB}} = 0$, such that Eq. (8) for effective diffusivity gives the indeterminate form $0/0$. To resolve this problem, as discussed following Eq. (8), we replace $\mathcal{K} \rightarrow \mathcal{K}^{(\varepsilon)} \equiv \mathcal{K} + \varepsilon\mathcal{I}$, perform the calculations, and then take the limit $\varepsilon \rightarrow 0$. Therefore, we write

$$\begin{aligned} \mathcal{K}_{\text{MB}}^{(\varepsilon)} &= \mathcal{K}_{\text{MB}} + \varepsilon\mathcal{I} \\ &= \begin{bmatrix} D_{\hat{\omega}} + 2f + \varepsilon & \omega & 0 \\ -\omega & D_{\hat{\omega}} + 2f + \varepsilon & 0 \\ 0 & 0 & \varepsilon \end{bmatrix}, \end{aligned} \quad (\text{A7})$$

from which we obtain

$$\begin{aligned} \mathcal{K}_{11}^{(\varepsilon)}\mathcal{K}_{33}^{(\varepsilon)} - \mathcal{K}_{13}^{(\varepsilon)}\mathcal{K}_{31}^{(\varepsilon)} &= \varepsilon(D_{\hat{\omega}} + 2f + \varepsilon) - 0 \\ &= \varepsilon(D_{\hat{\omega}} + 2f + \varepsilon) \end{aligned} \quad (\text{A8})$$

and

$$\begin{aligned} \det \mathcal{K}_{\text{MB}}^{(\varepsilon)} &= \varepsilon \begin{vmatrix} D_{\hat{\omega}} + 2f + \varepsilon & \omega \\ -\omega & D_{\hat{\omega}} + 2f + \varepsilon \end{vmatrix} \\ &= \varepsilon[(D_{\hat{\omega}} + 2f + \varepsilon)^2 + \omega^2]. \end{aligned} \quad (\text{A9})$$

Now, using Eqs. (8), (A8), and (A9) we can calculate the effective diffusivity in the limit $\varepsilon \rightarrow 0$,

$$\begin{aligned} D_{\text{eff,MB}} &= \lim_{\varepsilon \rightarrow 0} \frac{\bar{v}}{2} \frac{\varepsilon(D_{\hat{\omega}} + 2f + \varepsilon)}{\varepsilon[(D_{\hat{\omega}} + 2f + \varepsilon)^2 + \omega^2]} \\ &= \frac{\bar{v}^2}{2} \frac{D_{\hat{\omega}} + 2f}{(D_{\hat{\omega}} + 2f)^2 + \omega^2}, \end{aligned} \quad (\text{A10})$$

which is Eq. (17). An alternative approach is to compare the kinematrix (A6) with the unified form (22b), which yields $\omega_z = \omega$, $\gamma = D_{\hat{\omega}} + 2f$, $\delta = \gamma\omega = 0$, and $\Omega = \omega$. Plugging these parameters into Eq. (27) directly gives Eq. (17) without need for the substitution $\mathcal{K} \rightarrow \mathcal{K} + \varepsilon\mathcal{I}$. Moreover, similar to diffusion-flip self-propellers, by plugging these parameters into Eq. (28) we obtain the mean-square displacement of magnetotactic bacteria.

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- [1] H. C. Berg, *Phys. Today* **53**, 24 (2000).
 - [2] V. Zaburdaev, S. Uppaluri, T. Pfohl, M. Engstler, R. Friedrich, and H. Stark, *Phys. Rev. Lett.* **106**, 208103 (2011).
 - [3] H. U. Bödeker, C. Beta, T. D. Frank, and E. Bodenschatz, *Europys. Lett.* **90**, 28005 (2010).
 - [4] L. Li, S. F. Nørrelykke, and E. C. Cox, *PLoS ONE* **3**, e2093 (2008).
 - [5] L. Li, E. C. Cox, and H. Flyvbjerg, *Phys. Biol.* **8**, 046006 (2011).
 - [6] M. Sadati, A. Nourhani, J. J. Fredberg, and N. Taheri Qazvini, *WIREs Syst. Biol. Med.* **6**, 137 (2014).
 - [7] F. Peruani and L. G. Morelli, *Phys. Rev. Lett.* **99**, 010602 (2007).
 - [8] D. Campos, V. Mendez, and I. Llopis, *J. Theor. Biol.* **267**, 526 (2010).
 - [9] G. Li, L.-K. Tam, and J. Tang, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 18355 (2008).
 - [10] P. D. Frymier, R. M. Ford, H. C. Berg, and P. T. Cummings, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 6195 (1995).
 - [11] E. Lauga, W. R. Diluzio, G. M. Whitesides, and H. A. Stone, *Biophys. J.* **90**, 400 (2006).
 - [12] S. Kudo, N. Imai, M. Nishitoba, S. Sugiyama, and Y. Magariyama, *FEMS Microbiol. Lett.* **242**, 221 (2005).
 - [13] I. H. Riedel, K. Kruse, and J. Howard, *Science* **309**, 300 (2005).
 - [14] B. Steinberger, N. Petersen, H. Petermann, and D. G. Weiss, *J. Fluid Mech.* **273**, 189 (1994).
 - [15] A. Cēbers and M. Ozols, *Phys. Rev. E* **73**, 021505 (2006).
 - [16] K. Ērglis, Q. Wen, V. Ose, A. Zeltins, A. Sharipo, P. A. Janmey, and A. Cēbers, *Biophys. J.* **93**, 1402 (2007).
 - [17] A. Cēbers, *J. Magn. Magn. Mater.* **323**, 279 (2011).
 - [18] D. Selmeczi, S. Mosler, P. H. Hagedorn, N. B. Larsen, and H. Flyvbjerg, *Biophys. J.* **89**, 912 (2005).
 - [19] D. Selmeczi, L. Li, L. I. Pedersen, S. F. Nørrelykke, P. H. Hagedorn, S. Mosler, N. B. Larsen, E. C. Cox, and H. Flyvbjerg, *Eur. Phys. J. Spec. Top.* **157**, 1 (2008).
 - [20] J. R. Howse, R. A. L. Jones, A. J. Ryan, T. Gough, R. Vafabakhsh, and R. Golestanian, *Phys. Rev. Lett.* **99**, 048102 (2007).
 - [21] W. Paxton, K. Kistler, C. Olmeda, A. Sen, S. S. Angelo, Y. Cao, T. Mallouk, P. Lammert, and V. Crespi, *J. Am. Chem. Soc.* **126**, 13424 (2004).
 - [22] W. Paxton, A. Sen, and T. Mallouk, *Chem.: Eur. J.* **11**, 6462 (2005).
 - [23] W. F. Paxton, S. Sundararajan, T. E. Mallouk, and A. Sen, *Angew. Chem. Int. Ed.* **45**, 5420 (2006).
 - [24] J. Wang, *ACS Nano* **3**, 4 (2009).
 - [25] J. Wang and K. M. Manesh, *Small* **6**, 338 (2010).
 - [26] J. Gibbs and Y. Zhao, *Front. Mater. Sci.* **5**, 25 (2011).
 - [27] G. Ozin, I. Manners, S. Fournier-Bidoz, and A. Arsenaault, *Adv. Mater.* **17**, 3011 (2005).
 - [28] T. Mirkovic, N. S. Zacharia, G. D. Scholes, and G. A. Ozin, *Small* **6**, 159 (2010).
 - [29] T. Mirkovic, N. S. Zacharia, G. D. Scholes, and G. A. Ozin, *ACS Nano* **4**, 1782 (2010).
 - [30] S. J. Ebbens and J. R. Howse, *Soft Matter* **6**, 726 (2010).
 - [31] R. Golestanian, *Phys. Rev. Lett.* **102**, 188305 (2009).

- [32] J. Gautrais, C. Jost, M. Soria, A. Campo, S. Motsch, R. Fournier, S. Blanco, and G. Theraulaz, *J. Math. Biol.* **58**, 429 (2009).
- [33] N. Komin, U. Erdmann, and L. Schimansky-Geier, *Fluc. Noise Lett.* **04**, L151 (2004).
- [34] A. Ordemann, G. Balazsi, and F. Moss, *Phys. A: Stat. Mech. Appl.* **325**, 260 (2003).
- [35] R. Mach and F. Schweitzer, *Bull. Math. Biol.* **69**, 539 (2007).
- [36] A. M. Edwards, R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev, M. G. E. D. Luz, E. P. Raposo, H. E. Stanley, and G. M. Viswanathan, *Nature (London)* **449**, 1044 (2007).
- [37] I. D. Couzin, J. Krause, R. James, G. Ruxton, and N. R. Franks, *J. Theor. Biol.* **218**, 1 (2002).
- [38] H.-S. Niwa, *J. Theor. Biol.* **171**, 123 (1994).
- [39] S. Bazazi, P. Romanczuk, S. Thomas, L. Schimansky-Geier, J. J. Hale, G. A. Miller, G. A. Sword, S. J. Simpson, and I. D. Couzin, *Proc. R. Soc. B* **278**, 356 (2011).
- [40] S. Bazazi, J. Buhl, J. J. Hale, M. L. Anstey, G. A. Sword, S. J. Simpson, and I. D. Couzin, *Curr. Biol.* **18**, 735 (2008).
- [41] J. Strefler, W. Ebeling, E. Gudowska-Nowak, and L. Schimansky-Geier, *Eur. Phys. J. B* **72**, 597 (2009).
- [42] D. Helbing, *Rev. Mod. Phys.* **73**, 1067 (2001).
- [43] P. Romanczuk and L. Schimansky-Geier, *Phys. Rev. Lett.* **106**, 230601 (2011).
- [44] P. Romanczuk, M. Bär, W. Ebeling, B. Lindner, and L. Schimansky-Geier, *Eur. Phys. J. Spec. Top.* **202**, 1 (2012).
- [45] J. Dunkel and I. M. Zaid, *Phys. Rev. E* **80**, 021903 (2009).
- [46] D. Takagi, A. B. Braunschweig, J. Zhang, and M. J. Shelley, *Phys. Rev. Lett.* **110**, 038301 (2013).
- [47] S. van Teeffelen and H. Löwen, *Phys. Rev. E* **78**, 020101(R) (2008).
- [48] C. Weber, P. K. Radtke, L. Schimansky-Geier, and P. Hänggi, *Phys. Rev. E* **84**, 011132 (2011).
- [49] A. Nourhani, P. E. Lammert, A. Borhan, and V. H. Crespi, *Phys. Rev. E* **87**, 050301(R) (2013).
- [50] S. Ebbens, R. A. L. Jones, A. J. Ryan, R. Golestanian, and J. R. Howse, *Phys. Rev. E* **82**, 015304 (2010).
- [51] V. Lobaskin, D. Lobaskin, and I. M. Kulic, *Eur. Phys. J. Spec. Top.* **157**, 149 (2008).
- [52] F. Schweitzer, W. Ebeling, and B. Tilch, *Phys. Rev. Lett.* **80**, 5044 (1998).
- [53] T. Si, *Physica A* **391**, 3054 (2012).
- [54] M. E. Cates and J. Tailleur, *Europhys. Lett.* **101**, 20010 (2013).
- [55] P. Romanczuk, I. D. Couzin, and L. Schimansky-Geier, *Phys. Rev. Lett.* **102**, 010602 (2009).
- [56] O. Chepizhko and F. Peruani, *Phys. Rev. Lett.* **111**, 160604 (2013).
- [57] B. M. Friedrich and F. Jülicher, *New J. Phys.* **10**, 123025 (2008).
- [58] M. Polin, I. Tuval, K. Drescher, J. P. Gollub, and R. E. Goldstein, *Science* **325**, 487 (2009).
- [59] R. R. Bennett and R. Golestanian, *Phys. Rev. Lett.* **110**, 148102 (2013).
- [60] R. Laocharoensuk, J. Burdick, and J. Wang, *ACS Nano* **2**, 1069 (2008).
- [61] P. Dhar, T. Fischer, Y. Wang, T. Mallouk, W. Paxton, and A. Sen, *Nano Lett.* **6**, 66 (2006).
- [62] A. Nourhani, Y.-M. Byun, P. E. Lammert, A. Borhan, and V. H. Crespi, *Phys. Rev. E* **88**, 062317 (2013).
- [63] Y. Wang, S. to Fei, Y.-M. Byun, P. E. Lammert, V. H. Crespi, A. Sen, and T. E. Mallouk, *J. Am. Chem. Soc.* **131**, 9926 (2009).
- [64] S. Fournier-Bidoz, A. C. Arsenault, I. Manners, and G. A. Ozin, *Chem. Commun.* **441** (2005).
- [65] L. Qin, M. J. Banholzer, X. Xu, L. Huang, and C. A. Mirkin, *J. Am. Chem. Soc.* **129**, 14870 (2007).
- [66] J. G. Gibbs, S. Kothari, D. Saintillan, and Y. P. Zhao, *Nano Lett.* **11**, 2543 (2011).
- [67] J. G. Gibbs and Y. Zhao, *Small* **6**, 1656 (2010).
- [68] J. G. Gibbs and Y.-P. Zhao, *Small* **5**, 2304 (2009).
- [69] L. F. Valadares, Y.-G. Tao, N. S. Zacharia, V. Kitaev, F. Galembeck, R. Kapral, and G. A. Ozin, *Small* **6**, 565 (2010).
- [70] S. van Teeffelen, U. Zimmermann, and H. Lowen, *Soft Matter* **5**, 4510 (2009).
- [71] L. Seuront, F. G. Schmitt, M. C. Brewer, J. R. Strickler, and S. Souissi, *Zool. Stud.* **43**, 498 (2004).
- [72] H. i Wu, B.-L. Li, T. A. Springer, and W. H. Neill, *Ecol. Model.* **132**, 115 (2000).
- [73] M. Sandoval, N. K. Marath, G. Subramanian, and E. Lauga, *J. Fluid Mech.* **742**, 50 (2014).
- [74] K. Guizien, T. Brochier, J.-C. Duchene, B.-S. Koh, and P. Marsaleix, *Mar. Ecol. Prog. Ser.* **311**, 47 (2006).
- [75] M. Uttieri, M. Grazia Mazzocchi, A. Nihongi, M. Ribera D'Alcalà, J. R. Strickler, and E. Zambianchi, *J. Plankton Res.* **26**, 99 (2004).