Enhanced Diffusion by Reciprocal Swimming

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Purcell's scallop theorem states that swimmers deforming their shapes in a time-reversible manner ("reciprocal" motion) cannot swim. Using numerical simulations and theoretical calculations we show here that, in a fluctuating environment, reciprocal swimmers undergo, on time scales larger than that of their rotational diffusion, diffusive dynamics with enhanced diffusivities, possibly by orders of magnitude, above normal translational diffusion. Reciprocal actuation does therefore lead to a significant advantage over nonmotile behavior for small organisms such as marine bacteria.

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In addition to its importance in our macroscopic world, fluid mechanics plays a crucial role in many cellular processes. One example is the hydrodynamics of motile cells such as bacteria, spermatozoa, algae, and half of the microorganisms on Earth [1,2]. Most of them exploit the bending or rotation of a few flagella (short whiplike organelles, length scale from a few to tens of microns) to create fluid-based locomotion [3]. In contrast, ciliated microorganisms swim by using the coordinated beating of many short flagella termed *cilia* distributed along their surface [3].

Two physical ideas govern the fluid mechanics of cell locomotion on small scales. The first one is the exploitation by cells of anisotropic drag-based thrust to generate instantaneous propulsive forces [2]. The second one is the requirement to distribute this local propulsion along the surfaces of organisms in a manner that does not average to zero over one period of cellular actuation [4]. Indeed, on very small scales, the inertialess equations governing the surrounding fluid are linear and independent of time (Stokes equation), and thus any actuation on the fluid remaining identical under a reversal of time (so-called reciprocal actuation) cannot generate any net motion. This is known as Purcell's scallop theorem [4,5].

To overcome the constraints of the scallop theorem, microorgansims swim using wavelike deformations of their appendages or bodies, be it prokaryotes, eukaryotes with small numbers of flagella, or ciliates [1,2]. For deformation of synthetic swimmers, at least 2 degrees of freedom of shape change are required [4–8], or further physical effects need to be exploited, for example, those leading to nonlocality (hydrodynamic interactions [9]), relaxation (actuation of flexible filaments [10]), or nonlinearity (in particular, non-Newtonian stresses [11]).

In contrast to large organisms able to sustain directional swimming for long periods of times, small bacteria quickly lose their orientation due to rotational Brownian motion. If a is the typical hydrodynamic size of an organism in a fluid of viscosity η and temperature T, this thermal orientation loss occurs on a typical time scale $\tau \sim \eta a^3/k_B T$, of about 1 s for a 1 μm bacterium in water, and tens of seconds for *E. coli*. On time scales $t \gg \tau$, the coupling between locomotion at a typical speed U and orientation loss [12,13] leads to diffusive behavior for the cells with an effective diffusivity $D \sim U^2\tau$, usually much larger than that due to normal Brownian motion. For example, dead *E. coli* bacteria have diffusivities of $\approx 0.1\ \mu\text{m}^2/\text{s}$ while those of swimming cells are at least 3 orders of magnitude larger [13]. This transition from directional motion to diffusive dynamics was further addressed in recent work [14].

For small organisms significantly affected by Brownian diffusivity, we thus have the following intriguing observation. The scallop theorem dictates how cells should deform in order to undergo nonzero time-average displacements, but at long times, cells always diffuse, and thus always display zero time-average displacement. Would it then be possible that similar enhanced diffusive motion could be obtained within the constraints of the theorem?

In this Letter we consider swimmers undergoing reciprocal actuation in a fluctuating environment. Although the scallop theorem prevents swimming on average, we show that, on time scales larger than that of rotational diffusion, these reciprocal nonswimmers undergo diffusive motion with enhanced diffusivities, possibly by orders of magnitude, above their normal Brownian diffusion. This result is demonstrated computationally using Brownian dynamics simulations, and analytically using exact calculations for the long-time effective diffusivity of reciprocal unidirectional swimmers. The different regimes obtained are also captured by physical scalings. These new results demonstrate thus that reciprocal actuation, useless at zero temperature, does in fact lead to a significant advantage over nonmotile behavior for small organisms such as marine bacteria. There is thus no rms scallop theorem.

For a first illustration of our results, we use numerical computations. We performed Brownian dynamics simulations [15] of a spherical swimmer (radius $a = 1\ \mu$m), in water at $T = 300$ K and during a time interval of 100 s, with results shown in Fig. 1. The instantaneous velocity, $\mathbf{U}$,

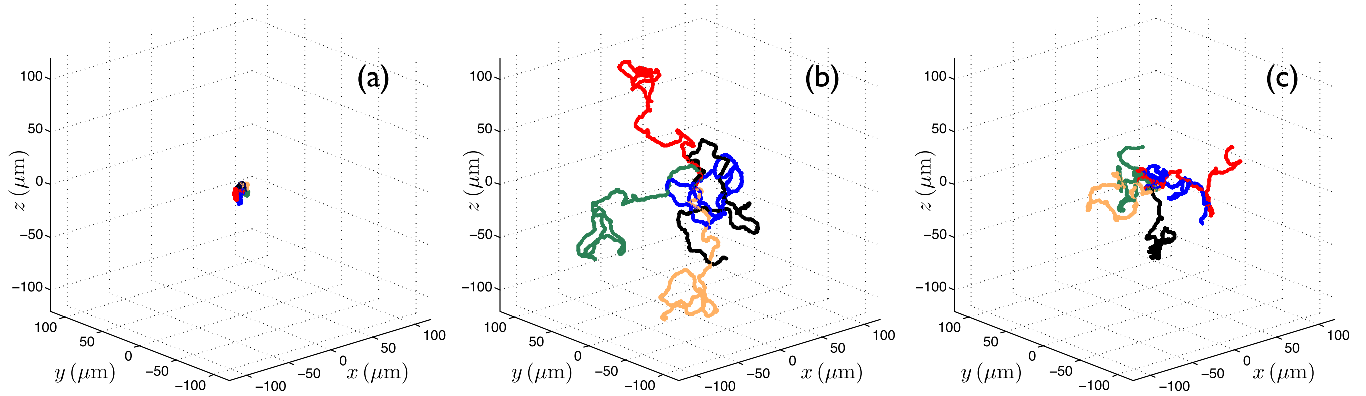

FIG. 1 (color online). Brownian dynamics simulation of a spherical swimmer (radius $a = 1\ \mu$m), in water at $T = 300$ K during a time interval of 100 s (5 realizations are superimposed). (a) No swimming, (b) steady swimming at speed $U = 5\ \mu$m/s, (c) reciprocal swimming at speed $\bar{U}\cos\omega t$ with $\bar{U} = 5\ \mu$m/s and $\omega = 2D_R$ (D_R is the rotational diffusivity of the swimmer, $\omega = 0.33$ rad/s). Case (a) is pure Brownian motion while both (b) and (c) show enhanced diffusivities.

and rotation rate, $\boldsymbol{\Omega}$, of the sphere satisfy the dynamics: $\mathbf{R}_{FU}\cdot(\mathbf{U}-\mathbf{U}_{\rm swim}) = \mathbf{F}^B$, $\mathbf{R}_{L\Omega}\cdot\boldsymbol{\Omega} = \mathbf{L}^B$, where $\mathbf{U}_{\rm swim}$ is the swimming speed, $\mathbf{R}_{FU} = 6\pi\eta a\mathbf{1}$ and $\mathbf{R}_{L\Omega} = 8\pi\eta a^3\mathbf{1}$ are the viscous resistances in translation and orientation ($\mathbf{1}$ is the identity tensor), and $\mathbf{F}^B$ and $\mathbf{L}^B$ are, respectively, zero-mean Brownian forces and torques, with correlations governed by the fluctuation-dissipation theorem, i.e., $\langle\mathbf{F}^B(t)\mathbf{F}^B(t')^T\rangle = 2k_BT\mathbf{R}_{FU}\delta(t-t')$ and $\langle\mathbf{L}^B(t)\mathbf{L}^B(t')^T\rangle = 2k_BT\mathbf{R}_{L\Omega}\delta(t-t')$.

Simulations were performed for three different swimming behaviors; in each case five realizations are superimposed in Fig. 1. In Fig. 1(a), the spheres do not swim ($\mathbf{U}_{\rm swim} = \mathbf{0}$) and thus undergo pure Brownian motion. In Fig. 1(b), the spheres swim steadily at speed $\mathbf{U}_{\rm swim} = U\mathbf{e}$ where $\mathbf{e}$ is a unit vector fixed to the swimmers, and $U = 5\ \mu$m/s. With these parameters, the time scale for thermal orientation loss is on the order of $\tau \approx 3$ s; we are thus in the regime where $t \gg \tau$, and the steady swimmers show diffusive behavior with a diffusion constant significantly larger than the Brownian one from Fig. 1(a).

Our new result is illustrated in Fig. 1(c), where we show the dynamics of swimmers undergoing reciprocal motion with velocity $\mathbf{U}_{\rm swim} = U(t)\mathbf{e}$ and $U(t) = \bar{U}\cos\omega t$ with $\bar{U} = 5\ \mu$m/s and $\omega = 2D_R$ where D_R is the rotational diffusivity of the swimmer ($\omega = \tau^{-1} = 0.33$ rad/s). Although the swimmers display no net motion even at short times (by construction the swimming speed averages to zero over one period of actuation), it is apparent from the numerical results that they diffuse much faster than pure Brownian motion [Fig. 1(a)].

How can we physically account for the increase in swimmer diffusion? The simplest approach involves recalling the dynamics of three-dimensional (3D) random walks [16,17]. If a particle at position x undergoes a 3D random walk where steps of size ℓ are followed along a random direction during time intervals δt, the particle shows no average motion, $\langle x\rangle = 0$, but undergoes rms spread as $\langle x^2\rangle \sim N\ell^2$. Since time increases as $t \sim N\delta t$, we get diffusive motion with $\langle x^2\rangle \sim Dt$ with the diffusion constant, D, scaling as $D \sim \ell^2/\delta t$. In the previously-understood case of steady swimming at speed U, the step size is the swimming speed times the time step, $\ell = U\delta t$, and the relevant time step for change of direction is the time scale over which the swimming direction is lost, i.e., $\delta t = \tau$, leading to the well-known scaling $D \sim U^2\tau$ [12].

Reciprocal nonswimmers subject to Brownian noise also behave as 3D random walkers, and to estimate their effective diffusivity, we have to consider the appearance of a new time scale, namely, the period ω^{-1} of reciprocal actuation over which the reversal of swimming direction occurs. We denote by $\bar{U}$ the amplitude of the swimming velocity. If the period of actuation is much larger than the loss-of-orientation scale, i.e., $\omega^{-1} \gg \tau$, then the step size is expected to be limited by the orientation loss and scales as $\ell \sim \bar{U}\tau$, leading to diffusive motion with an expected scaling $D \sim \bar{U}^2\tau$. In this low-frequency limit, the effective diffusion should thus show the same scaling as the one for steady swimmers with the velocity amplitude replacing the steady swimming speed. In contrast, in the limit where the time for reorientation is long compared to the period of actuation, $\omega^{-1} \ll \tau$, then the size of the 3D random walk step should be limited by the swimming amplitude, $\ell \sim \bar{U}/\omega$, while the relevant time scale for change of orientation remains τ, leading to an expected high-frequency scaling for the diffusivity as $D \sim \bar{U}^2/\omega^2\tau$.

We now proceed to calculate exactly the effective diffusion constant for reciprocal nonswimmers in a noisy environment. We consider instantaneous unidirectional motion with speed $U(t)$ along a direction quantified by a unit vector $\mathbf{e}(t)$ attached to the swimming frame—this direction is allowed to change due to rotational diffusion. As the swimmer is subject to noise, its position, denoted $\mathbf{x}(t)$, follows, in the absence of inertia, the dynamics

$$\dot{\mathbf{x}}(t) = U(t)\mathbf{e}(t) + \boldsymbol{\xi}(t), \tag{1}$$

where the zero-mean noise term $\boldsymbol{\xi}$ has a magnitude set by the fluctuation-dissipation theorem $\langle \boldsymbol{\xi}(t)\cdot\boldsymbol{\xi}(t')\rangle = 6D_{k_BT}\delta(t-t')$. Here D_{k_BT} is the Brownian diffusivity of the nonswimming particle ($D_{k_BT} = k_BT/6\pi\eta a$ for a sphere of radius a). In the absence of swimming ($U = 0$), the swimmer displays purely Brownian motion and $\langle \mathbf{x}\cdot\mathbf{x}\rangle \approx 6D_{k_BT}t$ in the limit $t\to\infty$. When $U\neq 0$, the swimmer position, Eq. (1), can be integrated in time to give

$$\mathbf{x}(t) = \int_0^t U(t')\mathbf{e}(t')dt' + \int_0^t \boldsymbol{\xi}(t')dt'. \qquad (2)$$

The swimming direction, $\mathbf{e}$, varies in time according to 3D rotational diffusion [17]. We thus expect no mean direction, $\langle\mathbf{e}\rangle = \mathbf{0}$, and an exponential loss of swimming direction over time as quantified by the correlation

$$\langle \mathbf{e}(t_1+t_2)\cdot\mathbf{e}(t_1)\rangle = e^{-t_2/\tau}, \qquad (3)$$

where $\tau^{-1} = 2D_R$ and D_R is the rotational diffusion coefficient for the swimmer ($D_R = k_BT/8\pi\eta a^3$ for a sphere). From Eq. (1) we thus first get that $\langle\mathbf{x}\rangle = \mathbf{0}$ and as expected, in the long-time limit, there is no net swimming.

To quantify the effective diffusivity, we need to compute the mean square displacements. As $t\to\infty$, we expect $\langle\mathbf{x}\cdot\mathbf{x}\rangle \approx 6Dt$ in 3D, and the effective diffusion constant, D, can thus be inferred from the limit

$$D = \frac{1}{3}\lim_{t\to\infty}\langle \mathbf{x}\cdot\dot{\mathbf{x}}\rangle. \qquad (4)$$

Given the integration for $\mathbf{x}$, Eq. (2), we can compute

$$(\mathbf{x}\cdot\dot{\mathbf{x}})(t) = U(t)\left[\int_0^t [U(t')\mathbf{e}(t)\cdot\mathbf{e}(t') + \mathbf{e}(t)\cdot\boldsymbol{\xi}(t')]dt'\right] + \int_0^t U(t')\boldsymbol{\xi}(t)\cdot\mathbf{e}(t')dt' + \int_0^t \boldsymbol{\xi}(t)\cdot\boldsymbol{\xi}(t')dt'. \qquad (5)$$

Since for any times t_1 and t_2 we have no correlation $\langle\mathbf{e}(t_1)\cdot\boldsymbol{\xi}(t_2)\rangle = 0$, we obtain

$$\langle \mathbf{x}(t)\cdot\dot{\mathbf{x}}(t)\rangle = U(t)\int_0^t U(t')\langle\mathbf{e}(t)\cdot\mathbf{e}(t')\rangle dt' + 3D_{k_BT}, \qquad (6)$$

which, using Eq. (3), and recalling Eq. (4), leads to

$$D = D_{k_BT} + \frac{1}{3}\left[\lim_{t\to\infty}\int_0^t U(t)U(t')e^{-(t-t')/\tau}dt'\right]. \qquad (7)$$

The effective swimmer diffusivity, Eq. (7), is thus given by the swimming velocity correlation function modulated by an exponential loss [for periodic swimming, Eq. (7) should be understood as mean value over a period] [18].

With our exact calculation, we can now compute the effective diffusivity for some simple cases. For steady swimming $U(t) = U$, Eq. (7) leads to

$$D = D_{k_BT} + \frac{1}{3}U^2\tau, \qquad (8)$$

which is the classical result [12,13]. In the case of harmonic reciprocal swimming, $U(t) = \bar{U}\cos\omega t$, we get

$$D = D_{k_BT} + \frac{1}{6}\frac{\bar{U}^2\tau}{1+\omega^2\tau^2}. \qquad (9)$$

More generally, for periodic swimming of the form $U = U_0\Re\{\sum_{n\geq 0}a_n\exp(in\omega t)\}$, where a_0 is real, we obtain

$$D = D_{k_BT} + \frac{U_0^2\tau}{3}\left(a_0^2 + \frac{1}{2}\sum_{n\geq 1}\frac{|a_n|^2}{1+(n\tau\omega)^2}\right), \qquad (10)$$

which displays both scalings for $\omega\tau \gg 1$ and $\omega\tau \ll 1$ discussed above. We also get from Eq. (10) that we always have $D > D_{k_BT}$. For example, for a periodic square swimming with $U(t) = -\bar{U}$ during $t\in(-\pi/\omega, 0)$ and then instantaneous reversal $U(t) = +\bar{U}$ for $t\in(0,\pi/\omega)$, we have $U_0 = \bar{U}$, $a_{2p} = 0$, and $a_{2p+1} = -4i/\pi(2p+1)$, leading to $D = D_{k_BT} + \bar{U}^2\tau[1 - 2\tau\omega\tanh(\pi/2\tau\omega)/\pi]/3$.

In Fig. 2 we show a comparison between simulations and theory. We plot the mean square displacement of 500 realizations of the swimmers with the same three cases as in Fig. 1 over 200 s. For these three cases (no swimming, steady swimming, and reciprocal swimming), we also plot as straight lines the theoretical prediction [where D is given, respectively, by D_{k_BT}, Eqs. (8) and (9)]. We obtain excellent quantitative agreement, confirming the validity of our theoretical approach.

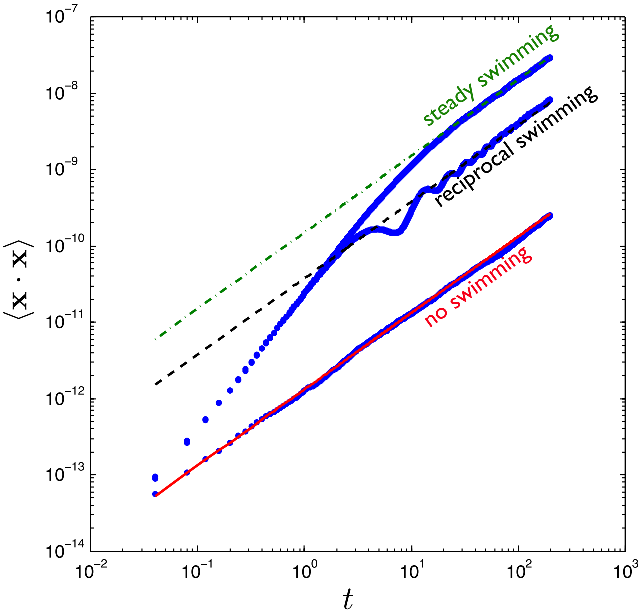

FIG. 2 (color online). Comparison between simulations and theory for a spherical swimmer. Symbols: Brownian dynamics simulations for the same three cases as in Fig. 1 (averages of 500 realizations over 200 s). Top to bottom: steady, reciprocal, and no swimming. Theoretical predictions shown as straight lines. Top (green dash-dotted line): prediction for effective diffusion for steady swimming, Eq. (8). Middle (black dashed line): prediction for diffusion by reciprocal swimming, Eq. (9). Bottom (red solid line): Brownian motion.

Biologically, our results are relevant to the dynamics of marine bacteria. Nonmarine bacteria such as *E. coli* swim in "run-and-tumble," with straight swimming paths followed by random reorientation events [19]. In contrast, marine bacteria display "run-and-reverse" (or "back-and-forth") locomotion where high speed swimming along straight paths is followed by almost complete reversal of their swimming direction [20,21]. With no bias in the characteristics of the paths, this is the example of a biological reciprocal swimmer.

To estimate the order of magnitude of our result, let us consider an elongated bacterium characterized by two length scales, b and $a \gg b$. Scaling-wise, we have $D_{k_BT} \sim k_BT/\eta a \log(a/b)$, $D_R \sim k_BT/\eta a^3 \log(a/b)$, and thus the reorientation time scales as $\tau \sim a^2/D_{k_BT}$. The maximum enhanced diffusivity occurs at low frequencies, $\omega\tau \lesssim 1$. In that case, the increase in cell diffusivity above Brownian motion is given by $D/D_{k_BT} \sim \bar{U}^2\tau/D_{k_BT} \sim \mathrm{Pe}^2$, where the Peclet number is $\mathrm{Pe} = a\bar{U}/D_{k_BT}$. For blunt swimmers where $a \approx b$, the log terms in the diffusion constants disappear, but the final scaling is unchanged. For Peclet of order 1 or above, the diffusivities are thus expected to be dominated by all swimming-induced terms, including the reciprocal ones. For a 10 μm bacterium in water at room temperature, this corresponds to a critical amplitude of reciprocal swimming of $\bar{U} \approx 10$ nm/s, less than 0.1% of the steady swimming speed of most marine bacteria [21]. For example, the micron-size marine bacterium *Shewanella putrefaciens* (CN32) has an average swimming speed of 100 μm/s and run duration of about 1 s [20], leading to an expected reciprocal diffusivity of 10 μm^2/s, over 2 orders of magnitude above its Brownian diffusivity.

Many marine bacteria are found in high-Reynolds number turbulent environments [22]. Our framework remains valid provided T is interpreted as an effective temperature, with an equation equivalent to Eq. (3) capturing the rotational dynamics of bacteria in turbulent flows. Our results could thus be used to describe the diffusion of marine bacteria in intermittent or turbulent flows. Our work could also be adapted to describe biased effective diffusion and chemotaxis in the presence of external fields, for example, if the reciprocal swimming amplitude, or its frequency, were to be coupled to an external chemical concentration. More generally, any noisy process leading to an exponential loss of cell orientation will lead to a similar enhanced diffusion for reciprocal actuation, for example, cell-cell collisions at high density [23].

In summary, we have shown in this Letter that reciprocal swimmers, previously believed to display a useless form of locomotion, undergo in fact enhanced diffusion, possibly by orders of magnitude, over inert bodies of the same size. Purcell's scallop theorem, valid in the absence of noise, can therefore not be extended in a fluctuating environment, and reciprocal (or unsteady) actuation can lead to significant advantages over nonmotile behavior for small organisms.

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[1] J. Lighthill, SIAM Rev. **18**, 161 (1976).
[2] E. Lauga and T. R. Powers, Rep. Prog. Phys. **72**, 096 601 (2009).
[3] C. Brennen and H. Winet, Annu. Rev. Fluid Mech. **9**, 339 (1977).
[4] E. M. Purcell, Am. J. Phys. **45**, 3 (1977).
[5] E. Lauga, Soft Matter **7**, 3060 (2011).
[6] A. Najafi and R. Golestanian, Phys. Rev. E **69**, 062901 (2004).
[7] J. E. Avron and O. Raz, New J. Phys. **10**, 063 016 (2008).
[8] A. A. Evans, S. E. Spagnolie, and E. Lauga, Soft Matter **6**, 1737 (2010).
[9] R. Trouilloud, T. S. Yu, A. E. Hosoi, and E. Lauga, Phys. Rev. Lett. **101**, 048102 (2008); E. Lauga and D. Bartolo, Phys. Rev. E **78**, 030901 (2008); G. P. Alexander and J. M. Yeomans, Europhys. Lett. **83**, 34 006 (2008).
[10] C. H. Wiggins and R. E. Goldstein, Phys. Rev. Lett. **80**, 3879 (1998); E. Lauga, Phys. Rev. E **75**, 041916 (2007); R. Dreyfus, J. Baudry, M. L. Roper, M. Fermigier, H. A. Stone, and J. Bibette, Nature (London) **437**, 862 (2005).
[11] H. C. Fu, C. W. Wolgemuth, and T. R. Powers, Phys. Fluids **21**, 033 102 (2009); E. Lauga, Europhys. Lett. **86**, 64 001 (2009); O. S. Pak, T. Normand, and E. Lauga, Phys. Rev. E **81**, 036312 (2010).
[12] P. S. Lovely and F. W. Dahlquist, J. Theor. Biol. **50**, 477 (1975).
[13] H. C. Berg, *Random Walks in Biology* (Princeton University Press, Princeton, NJ, 1993).
[14] J. R. Howse, R. A. L. Jones, A. J. Ryan, T. Gough, R. Vafabakhsh, and R. Golestanian, Phys. Rev. Lett. **99**, 048102 (2007); V. Lobaskin, D. Lobaskin, and I. M. Kulic, Eur. Phys. J. Special Topics **157**, 149 (2008); J. Dunkel and I. M. Zaid, Phys. Rev. E **80**, 021903 (2009); M. Garcia, S. Berti, P. Peyla, and S. Rafai, Phys. Rev. E **83**, 035301 (2011).
[15] E. J. Hinch, J. Fluid Mech. **72**, 499 (1975); D. L. Ermak and J. A. McCammon, J. Chem. Phys. **69**, 1352 (1978).
[16] S. Chandrasekhar, Rev. Mod. Phys. **15**, 1 (1943); E. A. Codling, M. J. Plank, and S. Benhamou, J. R. Soc. Interface **5**, 813 (2008).
[17] M. Doi and S. F. Edwards, *The Theory of Polymer Dynamics* (Clarendon Press, Oxford, UK, 1999).
[18] The enhanced diffusion is valid in two (2D) or three dimensions (3D). In 2D, the $1/3$ coefficient in Eq. (7) becomes $1/2$, and τ is now $\tau = 1/D_R$.
[19] H. C. Berg, *E. Coli in Motion* (Springer-Verlag, New York, NY, 2004).
[20] J. G. Mitchell, L. Pearson, and S. Dillon, Appl. Environ. Microbiol. **62**, 3716 (1996).
[21] J. E. Johansen, J. Pinhassi, N. Blackburn, U. L. Zweifel, and A. Hagstrom, Aquatic Microbial Ecology **28**, 229 (2002).
[22] R. H. Luchsinger, B. Bergersen, and J. G. Mitchell, Biophys. J. **77**, 2377 (1999).
[23] T. Ishikawa and T. J. Pedley, J. Fluid Mech. **588**, 437 (2007).