Evolution of microorganism locomotion induced by starvation

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The search strategies of many organisms play a fundamental role in their competition to survive in a given environment. In this context, the propulsion systems of microorganisms have evolved during life history, to optimize the suitable use of energy they take from nutrients. Starting from a model for the motion of Brownian objects with internal energy depot, we show that the propulsion system of microorganisms has an optimal regimen while searching for new sources of food. Bacteria with a too low or too high energy expenditure in propulsion, moving in a nutrient-depleted environment, do not reach remote distances. In this sense, the mean square displacement has a maximum for a finite value of the propulsion rate. Species using the most efficient locomotion system have a considerable advantage for survival in hostile environments, a common situation in the ocean. Moreover, we found the existence of a lower size limit for useful locomotion. This suggests that, for organisms whose linear dimensions are below a certain threshold, it is advantageous not to use any propulsion mechanism at all, a result that is in agreement with what is observed in nature.

I. INTRODUCTION

Considerable effort is being devoted to the understanding of molecular motors, which have been shown to play a crucial role in the dynamics of diverse biological objects, from myosin fibers to bacteria [1,2]. For instance, there are many works studying the molecular mechanism of force generation for the flagellar movement of bacteria [3], but what is the relationship between the acquired energy and the bacterial movement? Motility is important for many organisms that dedicate a substantial portion of their energetic resources to exploring space, searching for the nutrient sources needed to replenish the energetic stores used for their metabolic processes [4,5]. These entities must have evolved to survive when the environmental conditions are hostile, learning to carry out their functions efficiently. Examples of such hostile environments are micropatches in the ocean; point sources of nutrients that are available for a limited time [6]. In marine waters there are also organic and inorganic surfaces where the aggregation of macromolecules and nutrient ions generates a zone of substrate elevation surrounded by a nutrient-deficient environment [7]. It is in these media of low nutrient concentrations that motility is crucial for surviving.

Several authors have analyzed the circumstances in which locomotion benefits the organism. Purcell [8] showed that the energetic cost of motility is negligible in bacteria, but he considered only movement in culture media, where resources are unlimited. If the nutrient limitation is extreme, small cells get a larger portion of the maximum possible uptake per receptor than large cells. Independent of mobility, this is a possible explanation for the tendency toward microbacterial sizes in seawater [9]. Torrella and Morita [10] suggest that the ability of the nutrient-depleted bacteria to respond to substrate addition may influence the survival capacity of the organism. Mitchell studied the influence of body size in the

energetic cost of movement [11]. He compared the cost of four chemotactic strategies for different-sized bacteria by adding the cost of translating and rotating. He found the same power law behavior for bacteria as for the swimming animals, proposing a universal allometric equation for all swimming organisms.

For small microorganisms (sizes of the order of a micrometer or smaller), Brownian forces have a non-negligible effect on the motion. In fact, run-and-stop and run-and-reverse chemotactic strategies are common in marine bacteria, whose unusually long runs and high speeds, up to 400 μm/s [12], are needed to defeat fast noise-induced directional changes [13]. In a previous work [14] we found that external fluctuations can increase the mechanical efficiency of a microorganism's propulsion system. Our analytical results and Monte Carlo simulations suggest that, under certain circumstances, microorganisms can take advantage of Brownian forces to search more efficiently for a favorable environment. Furthermore, according to those results, for smaller particles the synergy between noise and propulsion will increase, leading to the absence of a minimum size limit for useful locomotion. However, the smallest motile bacterium is found to have a diameter of 0.84 μm [15]. All the bacterial genera with sizes smaller than this value (in the range between 0.14 and 0.84 μm) are nonmotile, being moved only by the action of Brownian forces. How these two results are correlated is the topic of this work.

We analyze further the relationship between propulsion and nutrient availability for a bacterium. We performed Monte Carlo simulations of the movement of a bacterium in a nutrient-depleted (hostile) environment, based on the model of Schweitzer, Ebeling, and Tilch (SET) [16]. They use an internal energy depot to relate the Brownian object (BO) motion with the rate of resource utilization in the propulsion system. We find that, for a given set of the parameters, the mean square displacement has a maximum for a finite value of the energy reconversion rate d_2^*. In this way, we show that there is an optimum propulsion configuration that maximizes the search for a new nutrient source. Further-

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more, we find that there is a finite critical noise value for which d_2^* tends to zero. This indicates that for organisms smaller than a certain threshold size (for which the influence of noise is strong) the best strategy is not to use any propulsion system at all, a result in agreement with the situation observed in nature by Dusenbery [15].

In the next section we propose an explanation for the existence of the size threshold, based on simple physics. In Sec. III we review the SET model and its approximations, while in Sec. IV we present some analytical solutions for the microorganism movement in a hostile environment. We present the simulation results in Sec. V, summarizing our conclusions in Sec. VI.

II. EXISTENCE OF A MINIMUM SIZE

Many authors tried to explain the existence of this minimum size threshold for useful locomotion. Dusenbery [15] concluded that a free-floating organism smaller than 0.6 μm diameter is unlikely to obtain any advantage by expending energy on swimming. His prediction arises as a consequence of considering the energy balance (between the increment in nutrient uptake and the cost of locomotion) for an organism with directed locomotion toward a stimulus. Previously, Karp-Boss *et al.* predicted a minimum value of 8.5 μm, and Berg and Purcell a minimum diameter of 3.7 μm, considering the increment in the nutrient flux due to motion of the bacterium or due to stirring of the medium by the organism, respectively [17,18]. Mitchell analyzed the energetic cost of flagellar stabilization needed by small bacteria to overcome the Brownian forces [11,13]. He concluded that the high energetic cost of flagella production in small bacteria should be a strong constraint in competitiveness, in the sense that small bacteria could not acquire enough nutrients to build and maintain a flagellum. But in a nutrient-rich environment the situation could be the opposite. Berg [19] mentions the case of some *Escherichia coli* strains grown in the laboratory that are nonmotile due to the excess of nutrients: "If there is not need to hunt for food, then why bother to build the chemotaxis apparatus?"

Our goal is to show that nutrient availability is also a factor to be included in the explanation of the minimum size threshold. In this sense our line of thinking is to consider a bacterium in an environment without nutrients that has to maximize, before starving, the mean square displacement ($\langle r^2 \rangle$) in its wandering for a new nutrient source. If for simplicity we consider that $\langle r^2(t) \rangle$ is the sum of the contributions from the Brownian motion and from the run-and-tumble mechanism, then[1]

$$\langle r^2(t) \rangle = 4t\left(\frac{k_B T}{6\pi\eta R} + v^2\tau\right) \tag{1}$$

with k_B the Boltzmann's constant, T the temperature of the system, η the viscosity of the fluid (10^{-2} cm^2/s for water), R the characteristic size of the bacterium, v the mean speed during a run, and τ the mean time between tumbles.

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[1]The following argument was suggested by an anonymous referee.

Considering a bacterium with a constant metabolic rate G, and a constant rate of energy consumption for swimming, d, then the time needed to consume the initial stored energy e_0 is

$$t = \frac{e_0}{G+d}. \tag{2}$$

The minimum power required to swim is just the one required to overcome the drag force. Therefore, assuming the bacterium to be a sphere, we can estimate $d = 6\pi\eta R v^2$. Considering that the initial energy and the metabolic rate are proportional to the volume of the bacterium we can write the mean square displacement as

$$\langle r^2(t) \rangle = \frac{8c_e R^2(k_B T/6\pi\eta R + v^2\tau)}{2c_m R^2 + 9\eta v^2} \tag{3}$$

with c_e and c_m the proportionality constants for the initial energy and for the metabolic rate, respectively. A bacterium without a propulsion system will spend energy only through the metabolic channel and then the mean square displacement before starving is

$$\langle r^2(t) \rangle = \frac{4c_e k_B T}{6\pi\eta c_m R}. \tag{4}$$

We can see that, as R tends to zero, the mean square speed with propulsion [Eq. (3)] also tends to zero while Eq. (4) diverges as $1/R$, showing that there must exist an intermediate size for which the usefulness of a propulsion system begins. Setting Eq. (3) equal to Eq. (4), we get an equation for R that defines the threshold,

$$R = \left(\frac{3k_B T}{4\pi c_m \tau}\right)^{1/3}. \tag{5}$$

In other words the threshold is set at the point where the energy expended for living equals $k_B T$. Assuming the approximate values $\tau \sim 1$ s [19] and $c_m \sim 5.6 \times 10^4$ erg cm^{-3} s^{-1} [15] then the minimum bacterial size for useful locomotion is $R = 0.006$ μm. This value is low compared with that observed in nature, but we have underestimated the power to drive motility; the molecular motor requires more energy due to the propulsion efficiency, which is around 10% for bacteria.

III. THE SET FORMALISM

The first attempt to relate the efficiency of the BO motion with the rate of resource utilization was the SET model [16]. In this work the authors use a Langevin formalism to investigate the motion of microorganisms modeled as a BO with an energy depot. The basic assumption is that the BO can take up energy from the environment at a rate q, store it in an internal energy depot, and reconvert part of it into kinetic energy at a rate d, which is, generally, a function of the speed v. The depot energy $e(t)$ is dissipated at a rate $G[e(t)]$, which depends on the particular metabolic processes, and is meant to account for all the nonmechanical use of the available energy. The amount of stored energy is therefore described by the equation

$$\frac{de}{dt} = q[\vec{r}, v, \mu; e(t)] - G[e(t)] - d[v, e(t), \mu], \qquad (6)$$

where μ is the metabolic state, e.g., the stage of the reproductive cycle, or, in the case of a bacterium, the creation of flagella. Then, the total energy of the active particle of mass m is $E(t) = (m/2)v^2 + e(t)$.

The uptake rate could depend on the local nutrient availability and on the internal state of the microorganism, but, to simplify the analysis, we previously assumed a constant q [14]. This is also a reasonable assumption for this work, considering that our objective is to study the movement in a region without nutrients. We further assume that the dissipation rate is proportional to the stored energy, $G[e(t)] = ce$. SET proposed the following ansatz: the rate of conversion to kinetic energy is proportional to both the instantaneous depot energy and the instantaneous kinetic energy, and in consequence they wrote $d[v, e(t)] = d_2 e v^2$. Records of bacterial motion [20] show that bacterial speeds during the run phase increase slowly, suggesting that the bacterial motors pass through many states that would correspond to successively higher speeds and higher rates of energy conversion. In fact, simulations performed using SET's ansatz give results in agreement with the experimental data of Berg and Brown [21].

To account for the energy reconversion contribution to the BO motion, we followed SET and postulated the modified Langevin equation,

$$m\frac{d\vec{v}}{dt} = -\gamma\vec{v} + d_2 e\vec{v} + \vec{F}(t), \qquad (7)$$

where γ is the friction coefficient and $\vec{F}$ is a stochastic force satisfying,

$$\langle\vec{F}(t)\rangle = 0, \quad \langle F_i(t)F_j(t')\rangle = \epsilon\delta_{ij}\delta(t - t'). \qquad (8)$$

Here $\epsilon = 2\gamma k_B T$ is the noise intensity [22], due to the energy compensation between the friction loss and the gain due to the stochastic force.

To estimate the mean square speed for some special cases we assumed that the depot energy reaches its quasistatic equilibrium e_s fast enough compared to the motion time scale, obtaining the value of e_s as a function of the speed

$$e_s = \frac{q}{c + d_2 v^2}. \qquad (9)$$

Replacing this expression in Eq. (7) we get a stochastic differential equation that can be solved analytically for different situations.

(1) If there is no internal dissipation, $c = 0$, all the depot energy is eventually transformed into kinetic energy, and we can then easily solve the deterministic ($\vec{F} = \vec{0}$) equation. If v_0 is the velocity at $t = 0$, the resulting velocity in one dimension is [21]

$$v_D(t) = \left(\frac{q}{\gamma}\right)^{1/2}\left[1 + \left(-1 + \frac{\gamma v_0^2}{q}\right)e^{-2\gamma t/m}\right]^{1/2}. \qquad (10)$$

At long times and including the noise contribution for a d-dimensional system, we obtain the mean square speed

$$\langle v^2(t \to \infty)\rangle = \frac{q}{\gamma} + d\frac{k_B T}{m}. \qquad (11)$$

Here we note that in this regime the contribution of the two energy sources is additive.

(2) If most of the depot energy is consumed internally without being transformed into mechanical energy [$c \gg d_2 v^2$], the asymptotic mean square speed is [21]

$$\langle v^2(t)\rangle = \frac{k_B T}{m(1 - Q)} + \left(v_0^2 - \frac{k_B T}{m(1 - Q)}\right)e^{-2\gamma(1-Q)t/m}, \qquad (12)$$

where $Q = qd_2/\gamma c$ is a parameter used to characterize the dynamics. We calculated also the mean square displacement, finding that for long times the motion becomes diffusive, despite the effect of the propulsion system, even in the case of a nonzero energy uptake.

A different perspective was obtained by solving the Fokker-Planck equation associated with the stochastic differential equation [23]. For the steady state in one dimension, the probability density takes the form [14]

$$W_s(v) = W_0 e^{-mv^2\gamma/\epsilon}\left(1 + \frac{d_2}{c}v^2\right)^{mq/\epsilon}, \qquad (13)$$

where W_0 is a normalization constant. This distribution exhibits a bifurcation at $Q = 1$; for $Q < 1$ it has one maximum located at $\hat{v} = 0$, while for $Q > 1$ there are two maxima, located at

$$\hat{v}_\pm = \pm\left(\frac{c}{d_2}\right)^{1/2}(Q - 1)^{1/2}, \qquad (14)$$

which suggests that the presence of the depot has introduced a degree of organization in the motion.

IV. THE HOSTILE ENVIRONMENT

But what happens if there are no nutrients in the environment? Taking $q = 0$ in the previous analysis [Eqs. (10)–(12)] we see that at long times the particle becomes a BO, simply diffusing in the medium. Due to the low Reynolds numbers, the viscous forces dominate the motion, and the microorganism will have to wait for long times to record a change in the surroundings [8]; then the probability to find a new source of nutrients in a finite time will tend to zero, leading to starvation. To analyze the effect of a nutrient-depleted environment on the movement of a BO with energy depot, we have to evaluate the whole evolution of the movement, since the asymptotic regime will always be diffusive.

Considering that any biological entity must have evolved to perform the search of new nutrient sources more efficiently, it will be of interest to analyze the mean square displacement for a particle that departs from a nutrient point source that has been depleted. In this sense, the BO energy

depot is initially not empty, and thus the microorganism must optimize the use of the stored energy to cover the biggest possible area in its search for a new source, before starving.

In the absence of a motor ($d_2 = 0$) the mean square displacement at long times is $\langle r^2(t) \rangle \sim 2Dt$ [22], where the diffusion coefficient is given by $D = \epsilon/2\gamma^2$. If we consider that there is a threshold value of the depot energy, e_d, below which the biological entity cannot maintain its primary metabolic functions and dies, the surviving time T_s can be computed by simply integrating Eq. (6), getting

$$T_s = \frac{1}{c} \ln\left(\frac{e_0}{e_d}\right) \qquad (15)$$

with e_0 the initial value of the depot energy. This result is quite obvious: the particle consumes its stored energy at a constant rate through the metabolic channel alone.

In the opposite case, in which both the internal consumption of nutrients and the noise intensity are negligible, Eqs. (6) and (7) can be transformed into

$$\frac{de}{dt} = -d_2 e(t) v^2, \qquad (16)$$

$$m \frac{dv^2}{dt} = 2v^2[-\gamma + d_2 e(t)]. \qquad (17)$$

From these we can find the relationship

$$\frac{dv^2}{de} = -\frac{2}{m}\left(1 - \frac{\Gamma}{\Lambda}\right) \qquad (18)$$

with $\Lambda = e/e_0$ and $\Gamma = \gamma/(d_2 e_0)$. A first observation arises from this equation: If the initial depot energy is lower than γ/d_2, the particle will decrease its velocity or simply will not move at all if it starts at zero speed. The explanation of this effect is quite straightforward; the transfer of energy to the kinetic channel must be high enough to overcome the dissipation. If the initial depot energy is higher than γ/d_2, the particle will increase its speed while decreasing its stored energy, until the moment when $\Lambda = \Gamma$, when the speed will reach its maximum value.

Integrating Eq. (18) we get

$$v^2 = v_0^2 + \frac{2e_0}{m}(1 - \Lambda + \Gamma \ln \Lambda). \qquad (19)$$

Thus, for high energy transfer rates or low dissipation, so that $\Lambda \gg \Gamma$, the kinetic energy will increase as a linear function of the depot energy. In particular, this will be the case at short times, when the depot energy is close to its initial value. For long times, on the contrary, when the depot starts to deplete, the speed evolution will be governed by the logarithmic term, leading to a fast reduction of the movement. Following the previous considerations, after replacing Λ with Γ, we find the maximum mean square speed as

$$v_{max}^2 = v_0^2 + \frac{2e_0}{m}[1 + \Gamma(\ln \Gamma - 1)]. \qquad (20)$$

A possible first approximation is to consider only the linear term in Eq. (19), which is the case of high mechanical

use of the energy $[d_2 \gg \gamma \ln(e_0/e_d)]$, obtaining the depot energy evolution as

$$e(t) = e_0 - \frac{1}{2}mv^2(t). \qquad (21)$$

The conclusion is straightforward: Under this approximation, the decrement of the energy stored in the depot is due only to its kinetic use, and the total energy is conserved. The survival time can be obtained using the same approximation, simply replacing the linear term of Eq. (19) in Eq. (16) and integrating. Considering that at the moment of the departure from the depleted nutrient source the initial speed of the particle is zero, the T_s value obtained is infinite because we neglected the noise term. If there is no noise and the initial speed is zero, the particle is initially in a steady state according to the speed evolution equation (7) and it will never move. Without the noise term, the speed will never increase because the kinetic transfer of the depot energy will never occur [see the definition of $d(v,e)$ after Eq. (6)]. Nevertheless, if we divide the movement into two stages, a first one where the evolution is governed only by the noise term and a second one where the noise is overcome by the propulsion system, we can assure that the survival time of the particle will be proportional to d_2^{-1}. The reason for this behavior is that the threshold time between the two stages depends only on ε and γ. This result has been confirmed by numerical simulations (see Sec. IV).

What happens if we add noise? We consider that the propulsion and noise contributions to the energy are additive [as was obtained previously, in Eq. (11) for the stationary case [14]], adding directly the noise contributions at the end of the mean square speed evolution equation [Eq. (17)]. After considering the same approximation introduced in the previous analysis, replacing the depot energy value with Eq. (21), we get

$$m \frac{d\langle v^2 \rangle}{dt} = [-2\gamma + d_2(2e_0 - m\langle v^2 \rangle)]\langle v^2 \rangle + \epsilon, \qquad (22)$$

with ϵ the noise parameter. Solving this equation we, find

$$\langle v^2(t) \rangle = \frac{1}{2d_2}\left(\lambda + s \frac{\lambda(1 + e^{-st}) - s(1 - e^{-st})}{\lambda(1 - e^{-st}) - s(1 + e^{-st})}\right), \qquad (23)$$

where $\lambda = 2(d_2 e_0 - \gamma)/m$, and $s = \sqrt{\lambda^2 + 4d_2\epsilon/m}$. In the short-time limit the mean square speed grows as ϵt, being governed only by the noise contribution. In the long-time limit (before starving) the situation is reversed, because it is the motor that controls the evolution of the movement. A typical mean square speed evolution described by Eq. (23) is depicted in Fig. 1(b). Replacing the previous equation in Eq. (21), it is straightforward to find the survival time of the biological entity as

$$T_s = \frac{1}{s} \ln\left(\frac{(\lambda + s)[\lambda - s - 4d_2(e_0 - e_d)/m]}{(\lambda - s)[\lambda + s - 4d_2(e_0 - e_d)/m]}\right). \qquad (24)$$

It can be shown from Eq. (24) that the survival time of the BO is again proportional to the inverse of the rate of energy
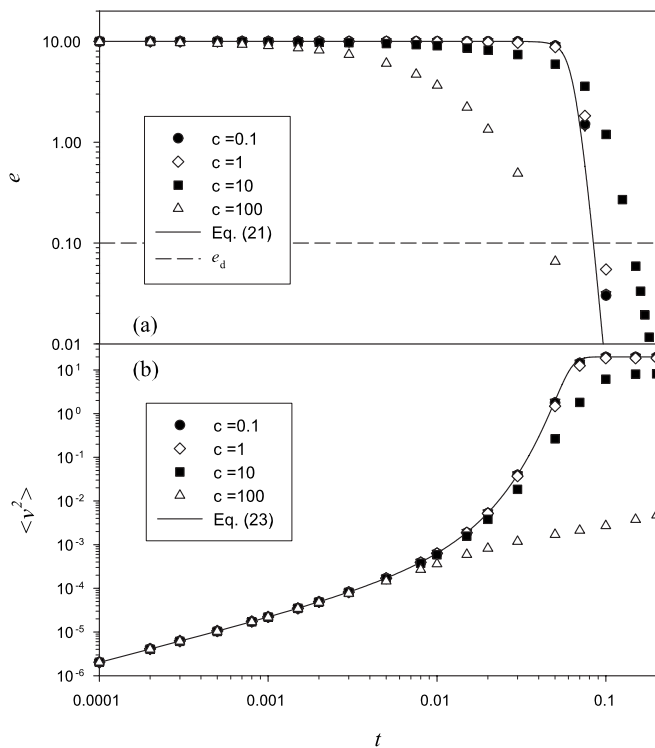
FIG. 1. Simulation results of the time evolution of the mean square speed (circles) and depot energy (squares) for $d_2=10$, $c=0.01$, $\gamma=0.01$, $\varepsilon=0.01$, $e_0=10$, and $e_d=0.1$. The solid lines correspond to the analytical solutions obtained from Eq. (23), showing an excellent agreement, especially at short times.

reconversion when the propulsion system dominates the kinetics.

In the limit of high dissipation or low rate of energy reconversion, $\gamma \gg d_2 e_0$, we can consider the exact solution of the stochastic differential equation (7) [22], and, after replacing it in Eq. (19), we get that the survival time is again proportional to d_2^{-1}:

$$T_s = \frac{2\gamma}{d_2\epsilon} \ln\left(\frac{e_0}{e_d}\right). \qquad (25)$$

Note that the survival time is inversely proportional to the noise intensity. This is a direct implication of the increase in the mechanical efficiency of a microorganism's propulsion system that we found previously [14]. An increment in the noise intensity enhances the propulsion function, leading to a faster expenditure of the stored energy, which in turn decreases the survival time. The survival time as a function of the energy reconversion term, for both high- and low-dissipation limits [Eqs. (24) and (25)], is depicted in Figs. 2 and 3.

V. SIMULATION RESULTS

We have performed extensive Monte Carlo simulations of Eqs. (6)–(8). We discretize the equations by using the standard Euler numerical method for Eq. (6), combined with Heun's algorithm [24] for Eq. (7). To generate the stochastic force [Eq. (8)] we used the Box-Mueller method [25]. The
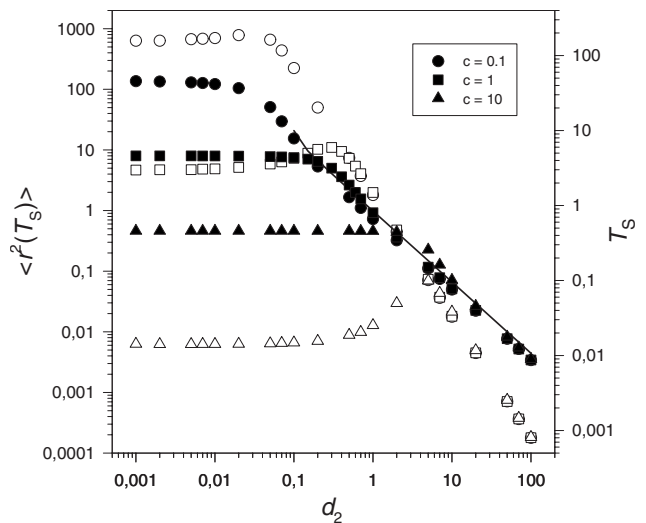

FIG. 2. Mean square displacement (empty shapes) and survival time T_s (filled shapes) as functions of the rate of energy transfer to the propulsion system. Here we take $\gamma=0.1$, $\varepsilon=0.1$, $e_0=10$, and $e_d=0.1$, and the indicated values of c. The solid line corresponds to the T_s approximation obtained in Eq. (24).

results presented here were obtained by averaging over 20 000 random walkers, while the time discretization was chosen between 0.1 and 10^{-6}, to ensure good convergence and stability. We consider, as the initial setup, that the particles are at rest ($v=0$) at the origin of the coordinate system, where the just depleted nutrient source was located. Therefore, the BOs have a nonzero initial value e_0 of energy stored in the depot.
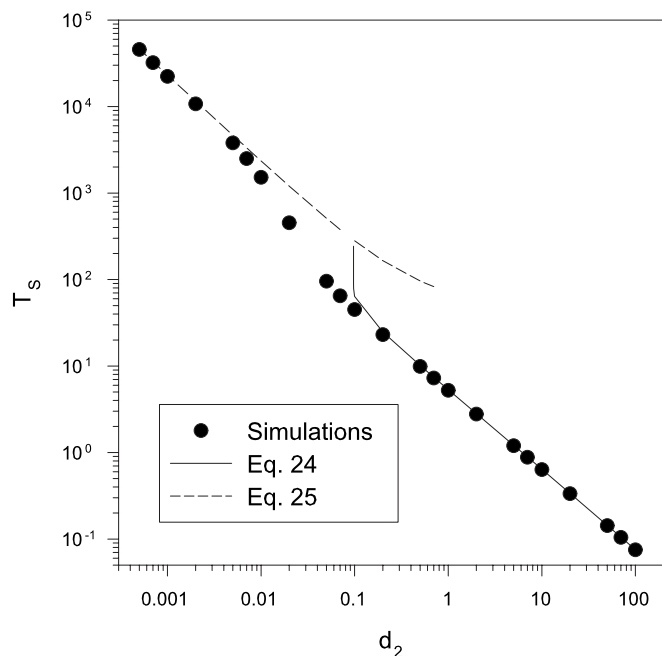

FIG. 3. Lifetime of the BO as a function of the rate of energy transfer to the propulsion system for the no internal dissipation case, $c=0$. The rest of the parameters are the same as in Fig. 2. Note the excellent agreement obtained between the simulations and the analytical expressions.

In Fig. 1 we have plotted typical time evolutions of the mean square speed [Fig. 1(a)] and the energy stored in the depot [Fig. 1(b)] for different values of the internal dissipation rate. The $\langle v^2(t) \rangle$ value has three very different behaviors. Initially, the mean square speed increases linearly due to the noise action, while the depot energy keeps its initial value. The action of the propulsion system becomes evident in the second stage, when the slope of the $\langle v^2 \rangle$ evolution increases, while the energy depot still keeps a value similar to the initial one. After a certain time the consumption of energy starts to be noticeable, leading to a fast depletion of the depot. This decrement reduces also the energy transferred to the propulsion system and then the mean square speed reaches a maximum, followed by a slowdown due to the action of the friction. The simulations stop when the value of the stored energy falls below the minimum stored energy e_d. In the figure we also compare the simulation results with Eqs. (23) and (21) after replacing the $\langle v^2 \rangle$ value. We observe a generally good agreement for $c < 1$, until the beginning of the fast depot depletion, when a slight discrepancy appears. This difference vanishes for very low values of c, when the approximation used to obtain Eqs. (23) and (21) holds. The discrepancy is not evident if we plot the evolution of the mean square speed as a function of the depot energy. The linear increase of $\langle v^2 \rangle$ is continuous, and only stops when the depot energy reaches e_d. Comparing the result of the simulation with Eq. (19), we observe an excellent agreement, concluding that the approximation of neglecting the logarithmic term in Eq. (19) is also very good at long times.

It is interesting to note in Fig. 1(a) that a bacterium can live longer by increasing its internal dissipation rate. Looking at the crossing between the different simulations varying c, it is evident that for $c = 10$ the particle will live around 50% more time than if we use $c = 1$ or lower values (the lifetime increases from 0.08 to 0.13). The explanation for this behavior is simple and lies in the strong nonlinearity of the system: if we keep the value of the internal energy high until the beginning of the second stage (when the propulsion system effect becomes evident), the speed will increase faster, leading to a faster decrement of the depot energy. Increasing the dissipation rate, the initial energy at the beginning of the second stage is reduced [see Fig. 1(a)], resulting in a lower decrement of the depot energy. Of course, if the dissipation rate is very high, the decrement of the internal energy will reduce the lifetime of the bacteria ($c = 100$ in the figure).

Figure 2 shows the time T_s at which the depot energy reaches the threshold value e_d, and the final mean square displacement $\langle r^2(T_s) \rangle$, as functions of the rate of energy reconversion d_2, for several values of the internal dissipation c. The survival time T_s (squares) has two different behaviors. For small d_2 values, T_s is constant, corresponding to the no-propulsion situation expressed by Eq. (15). After a certain value that depends on c, T_s starts to decrease approximately linearly, in agreement with Eq. (24). For a high rate of energy reconversion, the survival time is obviously reduced due to the addition of a new "channel" of energy consumption: the propulsion system. It is interesting to note that, while for small d_2 values there is a strong dependence on the
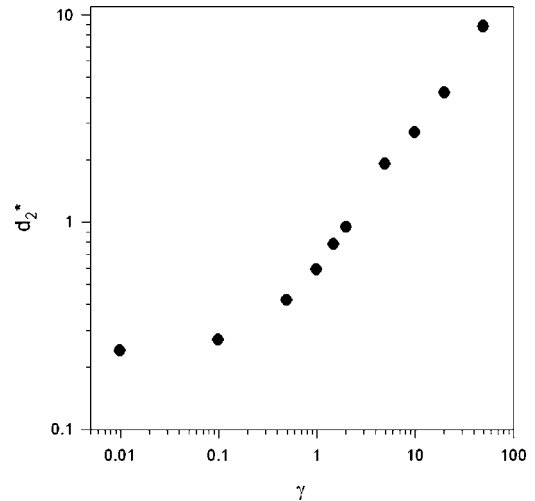

FIG. 4. Value of the rate of energy conversion at which the mean square displacement has a maximum as a function of the friction coefficient. Here $\varepsilon = 0.1$, $e_0 = 10$, and $e_d = 0.1$. In the low-friction limit d_2^* tends to a constant value, suggesting the existence of an optimum configuration of the propulsion system.

internal rate of energy consumption c, in the opposite case all the curves converge, independently of c, in complete agreement with our analytical results. The mean square displacement behavior (circles) is similar, but with the development of a maximum for intermediate d_2 values. While in the low-d_2 region the particle diffuses only due to the noise, for high reconversion rates the propulsion system is pushing the particle to farther zones. Nevertheless, due to the shorter survival times, $\langle r^2(T_s) \rangle$ tends to zero. The particle receives initially a very strong "kick" from the propulsion system that not only pushes it, but also consumes all the stored energy, killing it. In the transitional region there is a synergy between both effects, leading to a propulsion system with an optimum rate of energy utilization d_2^*. This effect is reduced if we decrease the rate of internal dissipation. In fact, if $c = 0$ the particle could live forever if there is no propulsion system at all, increasing the mean square displacement to an infinite value, just diffusing with the noise in a time that is also infinite. This situation is shown in Fig. 3, where we can see the good accuracy of our approximate solutions for low [Eq. (25)] and high [Eq. (24)] energy reconversion rates.

The evolution of d_2^* as a function of the friction parameter is shown in Fig. 4. There, we can see that when the viscosity of the medium is very strong the particle must increase the energy transfer to its propulsion system to overcome diffusion. In the low-friction limit instead, the d_2^* value tends to a constant, suggesting that there is an optimum configuration of the propulsion system. In the evolution of d_2^* as a function of the noise parameter ϵ (Fig. 5), we observe the existence of a threshold value in the noise, ϵ_c. If $\epsilon > \epsilon_c$, the optimum value of the propulsion system utilization is zero, demonstrating that for particles smaller than a threshold size (for which the influence of noise is strong) it is a better strategy not to use any propulsion mechanism at all, as observed in nature [15].

Finally a last question arises: how "nutrient-depleted" does the environment have to be to validate our results? In
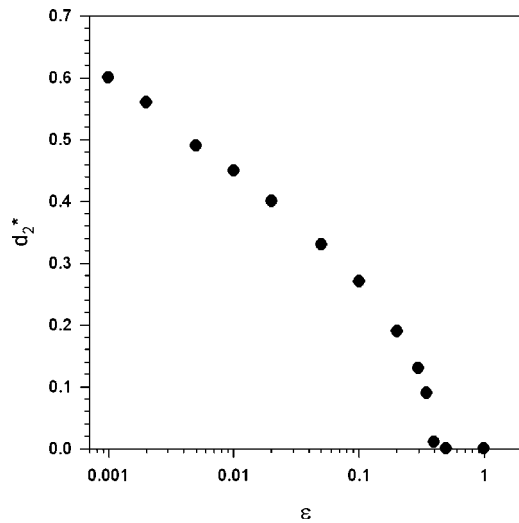
FIG. 5. Value of the rate of energy conversion at which the mean square displacement has a maximum as a function of the noise coefficient. Here $\gamma=0.1$, $e_0=10$, and $e_d=0.1$. There is a threshold value for the noise parameter at which the maximum mean square displacement starts to be obtained by simply not using any propulsion system.

Fig. 6 the evolution of the particle survival time is shown as a function of the nutrient concentration for different values of the noise intensity and a constant propulsion rate. The existence of a threshold in the nutrient uptake, q_0, is observed; a direct consequence of the synergy between propulsion and noise observed previously [14]. For values higher than q_0 the particle can survive by keeping its depot energy value higher than the minimum e_d required to sustain the
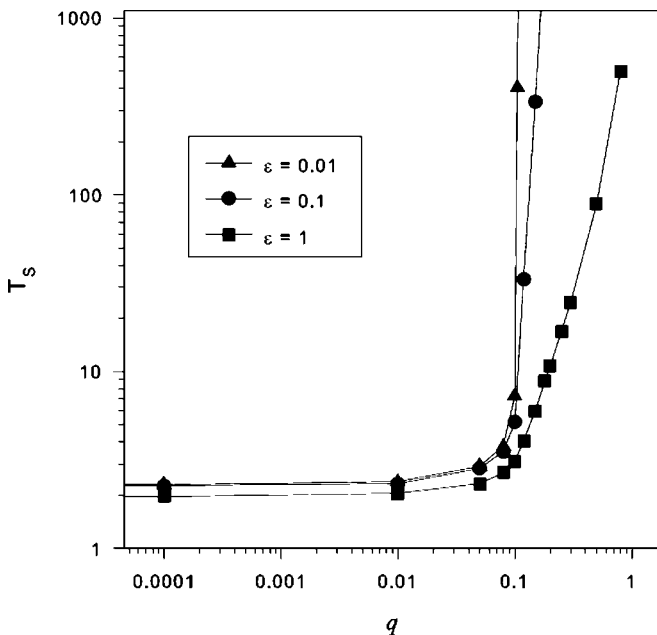

FIG. 6. Lifetime as a function of the rate of energy uptake from the medium. Here $d_2=0.1$, $c=1$, $\gamma=0.1$, $e_0=1$, and $e_d=0.1$ and the ε values indicated in the figure. The tendency to a constant for small q suggests that the results of this work can be applied also to media with low nutrient concentrations.

metabolic functions. Conversely, for $q<q_0$ the survival time of the bacteria is approximately constant, suggesting that the results obtained in this work will be valid not only in the no-nutrient regime, but also for regions of very low nutrient concentrations, as is observed in the ocean seawater.

VI. CONCLUSIONS

Based on a model that relates the movement of a particle with its resource utilization, we have analyzed several statistical properties for the evolution in a hostile environment. We found that motile organisms have an optimal regime of propulsion in their search for new sources of food. Bacteria with a too low or too high energy expenditure in propulsion will not reach remote distances, due to consumption of the energy in metabolic functions, in the first case, and a strong shortening of the survival time, in the second case. In this way, species using the most efficient locomotion system have a considerable advantage in surviving in these environments.

The noise dependence of the optimum regime shows the existence of a threshold value, above which the better option for the biological entity is not to use any propulsion mechanism at all. Taking into account that for small microorganisms the effect of Brownian forces increases, our conclusion arises naturally: there is a minimum size for a bacterium to benefit from the use of a propulsion system, in agreement with Dusenbery's observations [15]. It is important to remark that this result appears in our model without introducing any critical size or mass, which could force the result. Of course, we do not pretend to present our argument of evolution in a hostile environment as the only explanation for the minimum size threshold of motile bacteria. Considering the previous analysis mentioned in Sec. II, we can conclude only that the absence of a locomotion mechanism in bacteria is the result of the interplay, during evolution, of many energetic constraints.

For simplicity, the work presented here is based on the original SET model; nevertheless, measurements show that the torque-speed relationship is approximately constant [19,26,27], leading to a correction in the energy conversion term in Eqs. (6) and (7). Performing simulations considering the generalized version of the model [14], we still find the existence of a threshold value in the noise term above which the most efficient locomotion system is free floating (see Fig. 7). The explanation is quite simple: When we modify the conversion rate of stored energy to mechanical energy, there is not only a velocity increase (decrease), but also a decrease (increase) in the survival time. The mean square displacement limits for high and low reconversion rates are always the same, no matter what the speed dependence, and thus there is always a value for the noise parameter that makes the mean square displacement in the absence of propulsion larger than the maximum obtained with propulsion.

To analyze the effect of the run-and-tumble mechanism in a simple (but crude) way we can work on the asymptotic results of Condat's model [28], considering a constant energy flux Φ. Under a long-time approximation, we can describe the mean square displacement as the sum of two diffusive terms ($4Dt$): one due to thermal fluctuation (independent of
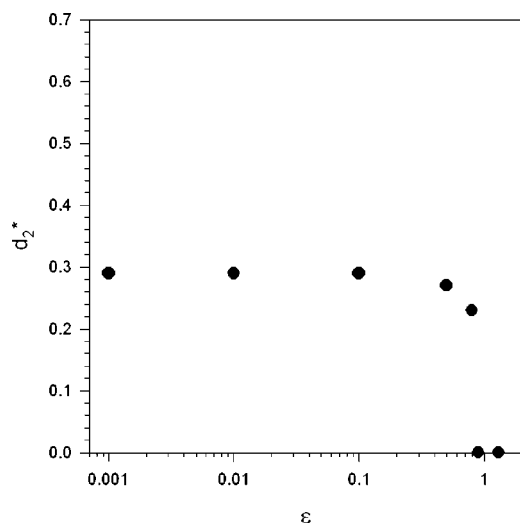
FIG. 7. Value of the rate of energy conversion at which the mean square displacement has a maximum as a function of the noise coefficient for a system with $d[v,e(t)]=d_2ev$. Here $\gamma=0.1$, $e_0=10$, and $e_d=0.1$.

Φ) and one due to motility (varies as Φ^2). Thus, there is not an optimal configuration for the propulsion: if Φ increases, $\langle r^2 \rangle$ also increases. The maximum in the mean square displacement appears only when we apply the starvation constraint. Now, the time that we have to consider corresponds to the moment at which the depot energy goes below the minimum value needed for living. Using the same model as before [28], we found that this time depends also on Φ as $1/(c+A\Phi^2)$, with c the metabolic rate of energy consumption and A a constant. Considering this term in the mean square displacement, we find a finite value of Φ that maximizes

$\langle r^2 \rangle$, from where an equation for the lower cutoff size emerges [29].

The model considered here omits two important properties of bacteria: (a) the existence of a finite lifetime (they do not live forever) independently of how many resources there are in the media; and (b) the chemotaxis mechanism [30], which optimizes the search for a new source of nutrients. We have performed simulations including both mechanisms [31], and the effect was to strengthen our findings [29]. A natural lifetime longer than the no-propulsion value, given by Eq. (15), has no effect in our results; in the opposite case, the time in which a particle has to find a new nutrient source is reduced, decreasing also the value of the area covered. This effect will be stronger for particles with low metabolic energy consumption (small c values), and thus long survival times. Now the limit for the low energy reconversion rate in the case of no internal energy dissipation [Eq. (25)] is not valid any longer. The particle cannot spend infinite time looking for nutrients. With the inclusion of the chemotactic mechanism, the particle will increase its mean square displacement due to a better strategy for nutrient searching (considering them to be far away from the origin), directing its motion to further distances. Nevertheless the consumption of energy due to the propulsion system still exists, and again a too high reconversion rate will not allow the particle to survive. Then the final effect of the chemotaxis is to "move" the optimum value d_2^* to a higher value. The bacteria can allow a higher expenditure of energy thanks to the increase in the directional efficiency of the movement.

ACKNOWLEDGMENTS

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[31] Our chemotactic scheme is based on the dynamic scheme described in [28], consisting of the known runs, separated by tumbles. During the run phase, the movement is completely described by the SET formalism, while during the tumbles the organism stops and starts a new run in a random direction. The duration of each run follows a Poisson distribution with a mean time proportional to the gradient of the chemoattractant. In this way, the runs are longer (shorter) if there is an increase (decrease) of the attractant. The gradients are computed considering the value of the chemoattractant at the actual position and the value at the position of the last tumble.