Interplay between energetics and dynamics in bacterial motility

C. A. Condat and Mario E. Di Salvo
IFEG-CONICET and FaMAF, Universidad Nacional de Córdoba, 5000-Córdoba, Argentina
(Received 18 March 2011; revised manuscript received 23 May 2011; published 15 July 2011)

We study how self-propelled organisms administer their energetic resources in order to optimize space exploration. Noting the existence of two very different time scales, we use a quasistatic approximation to analyze the relation between bacterial dynamics and changes in the energy stored by a bacterium. We then find both steady-state and time-dependent solutions for the bacterial speed and stored energy. The model also predicts the volume of the region that a bacterium may visit in a resource-depleted medium.

DOI: 10.1103/PhysRevE.84.011911 PACS number(s): 87.17.Jj, 05.40.Fb, 87.17.Aa

I. INTRODUCTION

The dynamics of self-propelled microorganisms is a fascinating subject. It depends on many variables, including the internal state of the organism, nutrient distribution, chemotactic interactions, interactions with walls and with other organisms, etc. Although theoretical and experimental studies of microorganism motion have been performed for decades [1–3], some leading biophysics research groups have recently focused their attention on various aspects of microorganism dynamics. The nature of the flow field in the neighborhood of a microorganism [4–7], the characterization of the hydrodynamic interactions with a wall [8], of self-organization [9] and formation of coherent structures [10], of enhanced shear adhesion [11], and the ability to create ratchet effects and directional motion when restricted to special geometries [12–16] are among the effects that have sparked an explosion of high-quality publications on the properties of microorganism motion. A review of the hydrodynamics of swimming microorganisms was published by Lauga and Powers in 2009 [17], while Berg's 2004 book describes in detail the properties of *Escherichia coli*, the prototype of bacterial studies [18]. Since an external energy supply is crucial for metabolism and space exploration, it would be of great interest to understand the interplay between nutrient intake and storage and microorganism motility. In this connection, careful studies have been performed of the relation between bacterial swimming and oxygen concentration and transport in *E. coli* [19] and *Bacillus subtilis* [9]. In particular, a sharp motility reduction has been observed to occur a few minutes after the bacteria are deprived of oxygen [19]. The model developed here allows us to estimate the size of the region a nutrient-deprived bacterium may explore. This is especially important for oceanic bacteria, which are generally immersed in a medium where the nutrient is concentrated in well-separated lumps [20,21].

In 1998 Schweitzer, Ebeling, and Tilch (SET) introduced a model in which the energy taken from available nutrients was stored and then used either for metabolic or motional purposes. Motion was considered to be the result of the combined action of Brownian forces and of the microorganism propulsion system [22,23]. This model was later used to study the effect of thermal noise on the mechanical efficiency of the propulsion system [24] and to investigate microorganism locomotion under starvation conditions [25]. Unfortunately, not much comparison with realistic parameters was pursued at that time. In the original papers, some results were obtained under the assumption that equilibration was faster for the energetic stores than for the microorganism speed. However, a detailed analysis of the experimental data for bacteria reveals that this assumption does not generally hold for realistic systems. For instance, an upper estimate of the time required to fill the energy depot can be made by assuming an uptake of 30 glucose molecules per second. This is in agreement with theoretical predictions [3] and experimental measurements [26] in a concentration of 1 nM, a concentration typically found in the ocean. If, according to Mitchell [27], we assume that 1% of the cell volume is energy reserve in the form of glucose at maximum density, then the time required for a 0.5 μm bacterium to fill its stores is about 250 hours (of course, the organism must find a higher concentration source). If, under more favorable conditions, the concentration were 0.1 μM with 10% uptake efficiency, i.e., if 10% of the bacterium surface behaved as a perfect absorber, then the time would drop to 45 minutes. We can thus estimate that substantial variation of the bacterial energetic stores occurs over times of the order of hours. Note also that nutrient intake per unit mass depends on bacterial size [28]. On the other hand, observation shows that bacteria change their speed substantially in small fractions of a second, for instance, accelerating from zero to their run speed and stopping every time between two tumbles. This time is even much shorter than the stopping time observed in Ref. [19] for oxygen-deprived cells. There are, therefore, two very different time scales: A long time scale (typically a few hours) characterizes the filling and emptying of the energetic stores, while a much shorter time scale (fractions of a second) characterizes speed variations. A quasistatic (QS) approximation can thus be implemented, which allows us to work out some important properties of the model analytically. The purpose of this paper is to adapt and correct the SET model in order to investigate how the motion of self-propelled microorganisms can be related to the availability of nutrient sources and how it can be used to optimize space exploration.

II. THE MODEL

A. Formulation

SET investigated the motion of microorganisms due to the combined action of their propulsion system and of Brownian forces using a Langevin formalism [22]. The model assumes that the microorganism can take up energy from the environment at a rate q and store it internally. The stored

 ©2011 American Physical Society

energy $E(t)$ can be either reconverted into kinetic energy, at a rate $k(v)E$, or dissipated at a rate cE. This dissipation rate is assumed to account for the nonmechanical expenditure of the available energy. Therefore, the amount of stored energy evolves according to the equation,

$$\frac{dE(t)}{dt} = q - [c + k(v)]\, E(t)\,. \tag{1}$$

The bacterial velocity $\vec{v}$ is assumed to satisfy the modified Langevin equation,

$$m\frac{d\vec{v}}{dt} = -\gamma\vec{v} + \frac{k(v)}{v^2}E(t)\vec{v} + \vec{F}(t)\,. \tag{2}$$

Here, γ is the friction coefficient and $\vec{F}(t)$ is a stochastic force.

Equations (1) and (2) are rather general. To obtain concrete predictions we will make some additional assumptions:

(1) Equation (2) is valid for the speed, i.e., we treat it as a scalar equation. Since we are interested in the relation between energy absorption and microorganism speed, we will consider only motion in the bacterial run phase, and the space variable will describe the displacement along the run trajectory. Of course, this assumption does not mean that the microorganism is actually swimming in one dimension but embodies the idea that changes in direction have little influence on the relation between stored energy and kinetic energy.

(2) The rate of energy conversion, $k(v)$, has a power-law dependence on the speed, $k(v) = d_\xi v^\xi$. This keeps the problem relatively simple while allowing us to generate a reasonably general family of models. Other functional forms could be analyzed by methods that parallel those used here.

(3) Thermal noise can be neglected. The main effect of thermal noise is to generate rotational diffusion, its influence on speed being, in general, negligible. Since in this work we are concerned only with the speed of the microorganisms, but not with their direction changes, we can safely ignore noise. Of course, the influence of noise could be important for small bacteria moving at very low speeds, or for bacteria lacking a propulsion system, but these are not the object of the present study.

If, according to assumption 2, $k(v) = d_\xi v^\xi$, it can be readily verified that the leading contribution to the low-speed acceleration experienced by the microorganism has the form $A \approx (q/mc)\, d_\xi v^{\xi-1}$. Since the acceleration must be finite, but not too small, we can thus argue that, *at low speeds*, ξ must be close to unity: In the absence of noise, $\xi = 1$ leads to constant acceleration, while $\xi < 1$ and $\xi > 1$ would require, respectively, enormous torques and very long speed-up times.

Available experimental data can be used to refine the model: Margariyama and coworkers measured simultaneously the flagellar rotational speed ω and the swimming speed v of *Vibrio alginolyticus*, showing that there is, approximately, a linear relation between them ($v \approx \alpha\omega$), except at the highest rotational speeds, for which the swimming speed saturates [29]. If we accept the proportionality between v and ω, and remember that the power delivered by the bacterial motor is $\Pi = \omega M$, we see that the choice $\xi = 1$ is consistent with results obtained from measurements of the torque M generated by individual bacterial motors in *E. coli*, which indicate that the torque is approximately constant up to high flagellar rotation frequencies [18,30,31]. Of course, this does not imply that other bacterial motors necessarily have the same torque-speed relationship, or even that this is the case when *E. coli* is propelled by the flagellar bundle during a run, which justifies considering more general functional forms.

B. Steady state

In the absence of noise, and assuming that the energy transformation rate has the form $k(v) = d_\xi v^\xi$, the steady-state solution of Eq. (2) satisfies

$$\gamma d_\xi v_s^{\xi+1} + \gamma c v_s - q d_\xi v_s^{\xi-2} = 0\,. \tag{3}$$

If $\xi > 0$, there is always a nontrivial solution. For $0 < \xi < 2$, this solution is stable for every value of q. If $\xi \geqslant 2$, the stationary speed is stable if the absorption rate is above a ξ-dependent minimum absorption rate $q_c^{(\xi)}$, given by

$$q_c^{(\xi)} = \frac{\gamma\xi}{\xi-2}\left[\frac{c\,(\xi-2)}{2d_\xi}\right]^{\frac{2}{\xi}}; \quad \xi \geqslant 2\,. \tag{4}$$

If $\xi > 1$, $v = 0$ is a solution of Eq. (3) and a bifurcation occurs. This trivial solution is always unstable for $1 < \xi < 2$ and always stable for $\xi > 2$. There is a stability threshold at the crossover point $\xi = 2$.

Thus, if $\xi \geqslant 2$, there is a lower threshold in the amount of nutrient uptake required to keep the microorganism moving. If it finds itself in a large region where nutrient concentration is so low that $q < q_c^{(\xi)}$, all organized motion must eventually stop.

Analytical forms for the nontrivial steady-state solution can be easily found for $\xi = 0,1,2$. The case $\xi = 2$ was studied in Refs. [22] and [24], and v_s has the simple form

$$v_s^{(2)} = \sqrt{\frac{q}{\gamma} - \frac{c}{d_2}}\,, \tag{5}$$

provided that $\Phi \equiv \frac{qd_2}{\gamma c} > 1$, in agreement with Eq. (4).

For $\xi = 1$, the nontrivial stationary speed is

$$v_s^{(1)} = -\frac{c}{2d_1} + \sqrt{\frac{q}{\gamma} + \left(\frac{c}{2d_1}\right)^2}\,, \tag{6}$$

while for $\xi = 0$,

$$v_s^{(0)} = \sqrt{\frac{qd_0}{\gamma(c+d_0)}}\,. \tag{7}$$

The stability of the nontrivial solution can be oscillatory for $\xi \geqslant 2$, i.e., the fixed point is a stable focus if the parameters satisfy the condition

$$\left[(\xi-2)\frac{\gamma}{m} + c + d_\xi v_s^\xi\right]^2 - \frac{4\xi d_\xi \gamma v_s^\xi}{m} < 0\,. \tag{8}$$

Here, v_s is the steady-state solution satisfying Eq. (3). For the case $\xi = 2$, this condition reduces to

$$\frac{\Phi^2}{\Phi - 1} - \frac{8\gamma}{mc} < 0\,. \tag{9}$$

The microorganism speed will seldom be equal to v_s: not only will it try to adapt to the instantaneous value of the stored energy, but it will also fluctuate due to changes in the bacterial state or in the flagellar configuration.

C. QS approximation

An exact analytical solution to the system of Eqs. (1) and (2), in the absence of noise, is possible only in the case $\xi = 0$. The model equations can be solved numerically for other values of ξ, but it is convenient to investigate their solutions using analytical approximations. Since the variation in $E(t)$ is much slower than the variation in $v(t)$, the system of equations (1) and (2) can be separated. That this is the case can be surmised from the fact that $m \sim 10^{-12}$ g and from the discussion in the Introduction; we will later see that this assumption is generally correct for bacteria. For each given value of the slow variable E, the fast variable rapidly reaches its quasiequilibrium value,

$$v_Q(t) = \left[\frac{d_\xi E(t)}{\gamma}\right]^\psi , \tag{10}$$

with $\psi = (2-\xi)^{-1}$ and $\xi \neq 2$. For simplicity, in the following we omit the superscripts specifying the value of ξ. Note that the QS approximation breaks down for small speeds if $\xi > 2$ and that a QS solution cannot be determined for $\xi = 2$.

By using assumption 2 and inserting Eq. (10) into Eq. (1), we obtain an equation for the time evolution of the available energy:

$$\frac{dE(t)}{dt} = q - d_\xi^{2\psi}\gamma^{-\xi/\psi}E(t)^{2\psi} - cE(t)\,. \tag{11}$$

Usually, the measurement interval Δt is much shorter than the characteristic time for energy storage; then, the speed at time $t + \Delta t$ is given, for any $\xi < 2$, by,

$$v_Q^{2-\xi}(t+\Delta t) = e^{-\Delta t/T_\xi}v_Q^{2-\xi}(t) + \frac{d_\xi E(t)}{\gamma}(1 - e^{-\Delta t/T_\xi}), \tag{12}$$

where $T_\xi = m/[\gamma(2-\xi)]$ is the speed equilibration time, i.e., the time required for the speed to reach the quasistatic value corresponding to the instantaneous amount $E(t) \approx E(t + \Delta t)$ of available stored energy. Assuming, for simplicity, a spherical microorganism of density ρ and radius a, and writing $\gamma = 6\pi\eta a$, where η is the viscosity, we find that $T_\xi \sim 2a^2\rho[9\eta(2-\xi)]^{-1}$. This equilibration time is very short for microorganisms, except in the case $\xi \to 2$. For instance, for $\xi = 1$ and a small bacterium ($a \sim 0.3\ \mu$m), $T_1 \sim 2 \times 10^{-8}$ s, while for a large bacterium ($a \sim 10\ \mu$m), $T_1 \sim 2 \times 10^{-5}$s.

III. SPECIAL CASES

Next, we present results for some special cases. While an exact solution is possible for $\xi = 0$, we use the QS approximation for $\xi = 1$ and a numerical solution for $\xi = 2$.

A. $\xi = 0$

As mentioned earlier, it is possible to find an exact analytical solution for the case $\xi = 0$. If E_0 and v_0 are, respectively, the initial values of the stored energy and the speed, their values for all times are given by

$$E(t) = q\tau_0 + (E_0 - q\tau_0)e^{-t/\tau_0} \tag{13}$$

and

$$v(t) = \left\{v_0^2 e^{-t/T_0} + \frac{d_0}{\gamma}\left[q\tau_0 + \frac{(E_0 - q\tau_0)e^{-t/\tau_0}}{1 - T_0/\tau_0} + \left(\frac{q\tau_0 - E_0}{1 - T_0/\tau_0} - q\tau_0\right)e^{-t/T_0}\right]\right\}^{1/2}, \tag{14}$$

where $T_0 = m/2\gamma$ is the speed equilibration time defined above and $\tau_0 = (c + d_0)^{-1}$ is the energy-storage characteristic time.

B. $\xi = 1$

As we have seen in Sec. II A, the case $\xi = \psi = 1$ is especially important. In this case, Eq. (11) has an analytical solution,

$$E(t) = \frac{E_0 + (q - cE_0/2)\tau_1 \tanh(t/\tau_1)}{1 + \left(d_1^2 E_0/\gamma + c/2\right)\tau_1 \tanh(t/\tau_1)}, \tag{15}$$

where τ_1 is the characteristic time for the energy storage

$$\tau_1 = \left[\frac{qd_1^2}{\gamma} + \left(\frac{c}{2}\right)^2\right]^{-1/2}.$$

We can investigate the dependence of τ_1 with bacterial size by assuming that the microorganism is a sphere uniformly covered with absorbers in a diffusion-limited medium; in this case, $q \propto a$ [3]. If we also assume that the nonmechanical expenditure of the energy is proportional to the cell volume, c is size-independent. As a result, τ_1 is only weakly dependent on size and we can estimate the characteristic time for the filling of the energy depot in about 6.5 hours. This time should be compared with the much shorter speed equilibration time T_1 calculated above, which validates the QS approximation.

From Eq. (10), we see that, for $\xi = 1$, the quasistatic value of the bacterial speed varies linearly with E, $\bar{v}(t) = (d_1/\gamma)E(t)$. The $t \to \infty$ limit yields the steady states E_s for the stored energy and v_s for the bacterial speed, which is that given by Eq. (6). A comparison between the QS approximation used in this paper, and that used in older work can be seen in Fig. 1, where it is clear that the new approximation agrees precisely with the exact numerical solution for Eqs. (1) and (2), while the old SET approximation (inset) leads to the correct asymptotic values, but over times that are about 11 orders of magnitude shorter than for the exact solution. This occurs when the depot is initially empty: the speed then adapts itself to the value of the stored energy and it takes hours to reach a steady state. If the depot is initially full, the old SET approximation works better.

C. $\xi = 2$

In this case, the QS approximation is not valid, and we must obtain numeric solutions of Eqs. (1) and (2). The bacterium reaches the stationary speed given by Eq. (5) if $\Phi > 1$; otherwise the stationary solution is $v = 0$, because the energy intake is too low to keep the bacterium moving. As shown by the numerical results presented in Fig. 2, if $\Phi < 1$, the bacterial speed goes smoothly to zero. If $\Phi > 1$, the speed can either go smoothly to the nonzero stationary solution (for high masses) or oscillate before stabilizing into its stationary speed

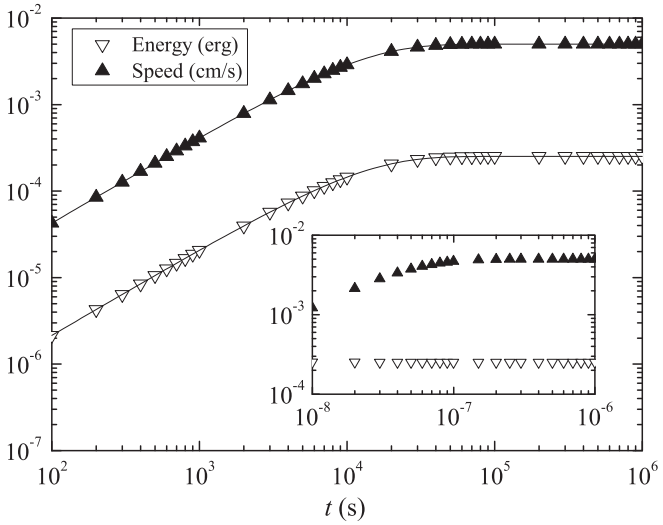

FIG. 1. Predicted speed and energy increase for a bacterium starting with an empty energy storage. Here, $\xi = 1$, $a = 0.4$ μm, $\gamma = 7.54 \times 10^{-6}$ g/s, $q = 2.15 \times 10^{-8}$ erg/s, $d_1 = 1.5 \times 10^{-4}$ s/cm^2, $c = 8.49 \times 10^{-5}$ s^{-1}, and $v_0 = 0$. The current QS approximation (solid lines) agrees extremely well with the simulation results (triangles). Note that the old QS approximation (E instantaneously follows the value of v) is inadequate except under stationary conditions (inset, note the time scale).

(for low masses), in accordance with the condition specified by Eq. (9). The parameters used in Fig. 2 have been chosen to show the transition between the smooth and oscillatory regimes. If real bacterial parameters were chosen, we would be well in the oscillatory regime on account of the small mass of the organism.

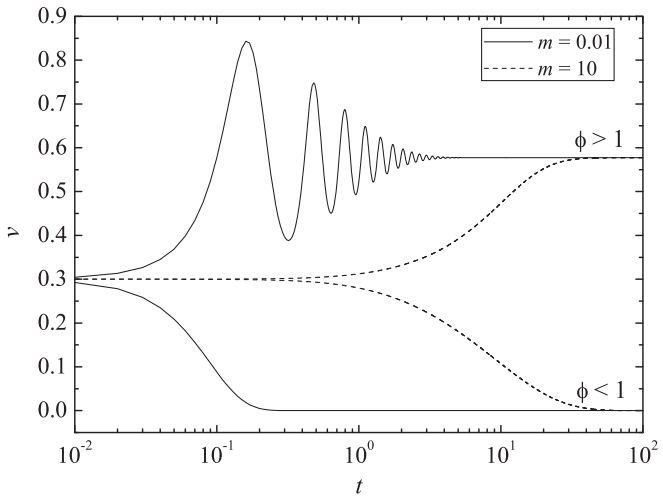

FIG. 2. Speed as a function of time (arbitrary units) for $\xi = 2$. If $\Phi < 1$, the bacterial speed goes smoothly to zero. If $\Phi > 1$, the speed of a high-mass organism goes smoothly to the steady state, while a low-mass organism would undergo a large number of speed oscillations before stabilizing into its "cruising" speed. Parameters were chosen to exhibit the transition between smooth and oscillating accelerations.

IV. STARVING BACTERIUM

In the ocean, individual patches of dissolved organic matter are small but abundant [21]. It is important that the bacterial energy stores last long enough to allow it to find neighboring patches. Therefore, we can ask ourselves what is the volume that a given bacterium can explore in a nutrient-depleted medium. This can be done by setting $q = 0$ in Eq. (1). If $\xi < 2$, the QS approximation can be used to find $v_Q(t)$, which, after further integration, yields the total displacement. Next we present explicit results for the case $\xi = 1$.

Taking $q = 0$ in Eq. (15), we obtain an equation for the depletion of available energy in a starving bacterium. Using Eq. (10), we then get an explicit expression for the QS speed,

$$v_Q(t) = \frac{(d_1 E_0/\gamma)\,[1 - \tanh(ct/2)]}{1 + \left(1 + 2d_1^2 E_0/c\gamma\right)\tanh(ct/2)}\,. \qquad (16)$$

This speed goes smoothly to zero as $t \to \infty$ (of course, it is reasonable to expect that the bacterium will either die or stop completely when the available energy goes below a threshold E_+). To find the (linear) distance $x(t)$ covered by the bacterium from time $t = 0$ up to a time t, we can integrate Eq. (16) between these limits, obtaining

$$x(t) = \frac{1}{d_1}\ln\left\{\frac{c\gamma + \tanh(ct/2)\left(c\gamma + 2d_1^2 E_0\right)}{c\gamma\,[\tanh(ct/2) + 1]}\right\}\,. \qquad (17)$$

In Fig. 3, we show $x(t)$ at various times as a function of d_1.

The maximum theoretical distance X the bacterium can cover in a nutrient-depleted medium is

$$X = x(\infty) = \frac{1}{d_1}\ln\left(1 + \frac{d_1^2}{c\gamma}E_0\right)\,. \qquad (18)$$

The maximum reachable distance grows logarithmically with the initial energy: it decreases if more energy is either spent metabolically (c) or due to external friction (γ). More interesting is the dependence with the coefficient d_1 of energy

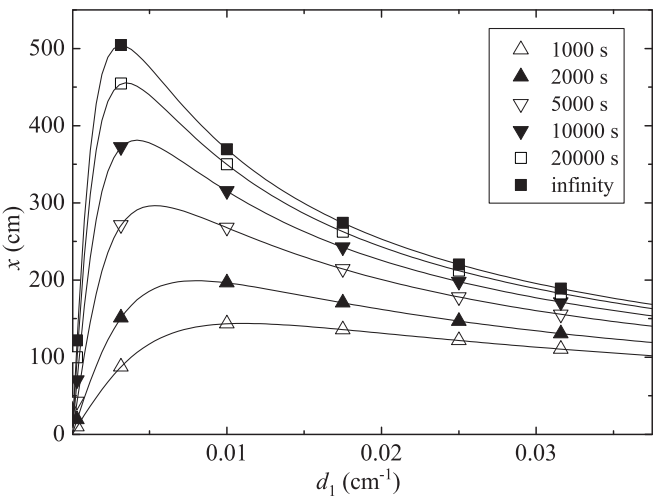

FIG. 3. Linear distance covered by a starving bacterium as a function of d_1 for the indicated times. The bacterium starts with a full energy storage, $E_0 = 2.52 \times 10^{-4}$ erg. The rest of the parameters are as described in the legend of Fig. 1. Again our QS approximation (solid lines) agrees very well with the simulation results.

transference to the motors. If d_1 is small, the speed is very low and the bacterium cannot go far; most of the energy is spent metabolically. If d_1 is large, v is high, and a lot of energy is spent against dissipation. Therefore, there is an optimum value of the coefficient that maximizes X. Numerically, we find that this optimal value is $d_{1M} = 1.9803(c\gamma/E_0)^{1/2}$, and the corresponding distance, $X_{\mathrm{MAX}} = 0.8047\sqrt{E_0/c\gamma}$. The value of d_1 that optimizes $x(t)$ depends on t, as it can be seen from Fig. 3. Of course, since d_{1M} was obtained without setting any constraints on the system efficiency, this "optimal" value for d_1 gives only an upper bound for the true maximum covered distance X_{MAX}.

We have just estimated the linear distance covered by a starving bacterium before it stops. Because of its run-and-tumble strategy [32], the bacterium effectively performs a random walk and we can also estimate the size of the region that it explores. A measure of this size is given by the mean square displacement (MSD), $\langle x^2(t)\rangle$. Since the speed decreases with time, the diffusion coefficient D will also depend on time. Neglecting the time and energy loss due to the tumbles, and considering the run duration θ to be a constant, we can calculate the MSD as

$$\langle x^2(t)\rangle = 2n\int_0^t D(t')dt' = \frac{1}{\theta}\int_0^t\left[\int_{t'}^{t'+\theta} v(t'')dt''\right]^2 dt'. \tag{19}$$

Here, n is the system dimensionality. A numerical integration of Eq. (19) is shown in Figs. 4 and 5. After a normal diffusion period, which is longer for larger bacteria, the motion becomes subdiffusive. The effective bacterial search time is taken as the time at which the corresponding curve becomes horizontal, i.e., when the bacterium has run down its energetic stores. We see that the radius of the region covered by an $a = 1$ μm bacterium is about 1 cm, while a 0.5 μm bacterium can cover a 0.5 cm region.

Under the reasonable assumptions that 1% of the cell volume is energy reserve in the form of glucose at the maximum density and that all the energy goes to drive the motors, with the efficiency of the propulsion system being 1%, Mitchell estimated the length of time that a bacterium can swim at the (fixed) minimum speed required to perform chemotaxis [27]. He found that a 1 μm bacterium can swim for 9 hours and a 0.2 μm bacterium for 4 min. With the same value for the energy reserves and initial speeds, we find that a 1 μm bacterium can swim for almost 15 hours before stopping and a 0.2 μm bacterium for 7 min. We obtain a longer survival time because we consider the speed reduction due to nutrient drain. We do not require a minimum speed because the bacterium moves in a nutrient-depleted medium.

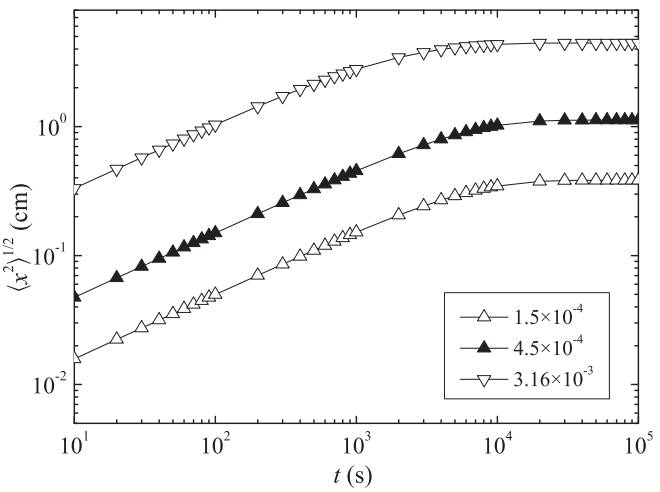

FIG. 4. Radius of the region explored by a starving bacterium ($q = 0$) for various values of the energy transfer coefficient d_1 (cm^{-1}), $v_0 = 50$ μm/s, and the rest of the parameters as described in the legend of Fig. 1. Triangles represent numerical results and the solid lines are guides to the eye.

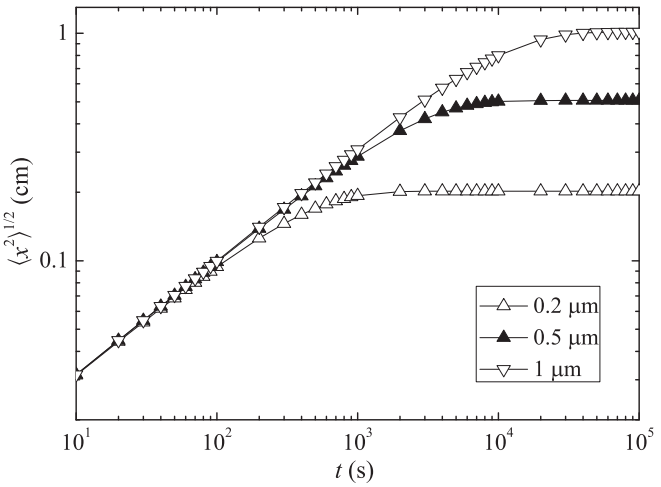

FIG. 5. Radius of the region explored by a starving bacterium ($q = 0$) for various values of the bacterial radius. Parameters were chosen so that in all cases the initial speed (which we took to be equal to the corresponding stationary speed) is 100 μm/s. Triangles represent numerical results and the solid lines are guides to the eye.

V. CONCLUSION

In this paper, we introduced a quasistatic approximation of the SET model that leads to some interesting predictions about bacterial motion. We have analyzed in some detail the implications of a power-law relation between speed and energy conversion rate. We believe that such a relation allows us to investigate the main qualitative properties of the problem. It is, of course, possible that individual bacteria may have various conversion-rate regimes, perhaps increasing the value of ξ as they speed up. For instance, we concluded that, at low speeds, the exponent of the transfer function should be unity or very close to it. This is in agreement with the experimental results of Refs. [18,30,31]. At high speeds, stronger accelerations would result for higher values of ξ, but we ignore if nature avails itself of this possibility. The numerical results for $\xi = 2$, which indicate the presence of strong speed oscillations before reaching the stationary speed, seem to indicate that microorganisms always swim in the $\xi < 2$ regime. Explicit expressions for the time evolution of the stored energy and of the bacterial speed were obtained as well as the size of the region a nutrient-deprived bacterium may explore.

In practice, there are many responses that bacteria may resort to when they are not in the presence of energy-yielding

substrates; these responses may modify their metabolic processes and make some results difficult to verify experimentally [33]. Our model could also be applied to describe the motion of microbots [34], for which $k(v)$ and the power intake q ($q = 0$ if battery-powered) would be precisely known.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for helpful comments. This work was supported by SECyT-UNC (Project No. 05/B354), ANPCyT (PICT 2205/33675), and CONICET (PIP 112-200801-00772) (Argentina).

[1] G. I. Taylor, Proc. R. Soc. London A **209**, 447 (1951).
[2] H. C. Berg and D. A. Brown, Nature (London) **239**, 500 (1972).
[3] H. C. Berg and E. M. Purcell, Biophys. J. **20**, 193 (1977).
[4] J. Teran, L. Fauci, and M. Shelley, Phys. Rev. Lett. **104**, 038101 (2010).
[5] K. Drescher, R. E. Goldstein, N. Michel, M. Polin, and I. Tuval, Phys. Rev. Lett. **105**, 168101 (2010).
[6] J. S. Guasto, K. A. Johnson, and J. P. Gollub, Phys. Rev. Lett. **105**, 168102 (2010).
[7] I. Rushkin, V. Kantsler, and R. E. Goldstein, Phys. Rev. Lett. **105**, 188101 (2010).
[8] T. Kaya and H. Koser, Phys. Rev. Lett. **103**, 138103 (2009).
[9] I. Tuval *et al.*, Proc. Natl. Acad. Sci. USA **102**, 2277 (2005).
[10] T. Ishikawa and T. J. Pedley, Phys. Rev. Lett. **100**, 088103 (2008).
[11] M. Whitfield, T. Ghose, and W. Thomas, Biophys. J. **99**, 2470 (2010).
[12] P. Galajda, J. Keymer, P. Chaikin, and R. Austin, J. Bacteriol. **189**, 8704 (2007).
[13] M. B. Wan, C. J. Olson Reichhardt, Z. Nussinov, and C. Reichhardt, Phys. Rev. Lett. **101**, 018102 (2008).
[14] J. Tailleur and M. E. Cates, Europhys. Lett. **86**, 60002 (2009).
[15] G. Lambert, D. Liao, and R. H. Austin, Phys. Rev. Lett. **104**, 168102 (2010).
[16] R. Di Leonardo *et al.*, Proc. Natl. Acad. Sci. USA **107**, 9541 (2010).
[17] E. Lauga and T. R. Powers, Rep. Prog. Phys. **72**, 096601 (2009).
[18] H. C. Berg, *E. coli in Motion* (Springer, New York, 2004).
[19] C. Douarche, A. Buguin, H. Salman, and A. Libchaber, Phys. Rev. Lett. **102**, 198101 (2009).
[20] J. G. Mitchell and K. Kogure, FEMS Microbiol. Ecol. **55**, 3 (2006).
[21] R. Stocker, J. R. Seymour, A. Samadani, D. E. Hunt, and M. F. Polz, Proc. Natl. Acad. Sci. USA **105**, 4209 (2008).
[22] F. Schweitzer, W. Ebeling, and B. Tilch, Phys. Rev. Lett. **80**, 5044 (1998).
[23] W. Ebeling, F. Schweitzer, and B. Tilch, BioSystems **49**, 17 (1999).
[24] C. A. Condat and G. J. Sibona, Physica A **316**, 203 (2002).
[25] G. J. Sibona, Phys. Rev. E **76**, 011919 (2007).
[26] B. E. Logan and D. K. Kirchman, Mar. Biol. **111**, 175 (1991).
[27] J. G. Mitchell, Microb Ecol. **22**, 227 (1991).
[28] H. N. Schulz and B. B. Jørgensen, Annu. Rev. Microbiol. **55**, 105 (2001).
[29] Y. Margariyama *et al.*, Biophys. J. **69**, 2154 (1995).
[30] H. C. Berg and L. Turner, Biophys. J. **65**, 2201 (1993).
[31] X. Chen and H. Berg, Biophys. J. **78**, 1036 (2000).
[32] C. A. Condat, J. Jäckle, and S. A. Menchón, Phys. Rev. E **72**, 021909 (2005).
[33] J. A. Novitsky and R. Y. Morita, Marine Biol. **48**, 289 (1978).
[34] J. E. Avron, O. Gat, and O. Kenneth, Phys. Rev. Lett. **93**, 186001 (2004).