

Locomotion of a microorganism in weakly viscoelastic liquids

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In the present work we study the motion of microorganisms swimming by an axisymmetric distribution of surface tangential velocity in a weakly viscoelastic fluid. The second-order fluid constitutive equation is used to model the suspending fluid, while the well-known “squirmers model” [M. J. Lighthill, *Comm. Pure Appl. Math.* **5**, 109 (1952); J. R. Blake, *J. Fluid Mech.* **46**, 199 (1971)] is employed to describe the organism propulsion mechanism. A regular perturbation expansion up to first order in the Deborah number is performed, and the generalized reciprocity theorem from Stokes flow theory is then used, to derive analytical formulas for the squirmer velocity. Results show that “neutral” squirmers are unaffected by viscoelasticity, whereas “pullers” and “pushers” are slowed down and hastened, respectively. The power dissipated by the swimming microorganism and the “swimming efficiency” are also analytically quantified.

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I. INTRODUCTION

The locomotion of small organisms in Newtonian fluids at low Reynolds numbers (Re) displays very different features with respect to that used by larger organisms. Indeed, in the $Re \ll 1$ regime, viscous forces are dominant over inertial ones, and propulsion is only possible through non time-reversible swimming strokes, a feature that has been brilliantly discussed by Purcell in enunciating the so-called “*Scallop Theorem*” [1]. Different swimming mechanisms are exploited by microorganisms to generate their own propulsion. One of them is the undulatory movement of flagella, notable examples being *Spermatozoa* and *Escherichia Coli*, among others; another mechanism is the undulatory movement of many small flagella, called cilia, on the organism surface, as exploited by *Paramecium*, *Volvox*, or *Opalina*. A theoretical model for the former mechanism of propulsion has been proposed by Taylor [2], whereas the latter mechanism has been investigated in the pioneering works of Lighthill [3] and Blake [4]. The model proposed by those latter authors has been widely used in the literature, e.g., to study hydrodynamic interactions between two ciliated organisms [5], suspensions of active organisms [6,7], and the behavior of single and many “active particles” near boundaries [8,9]. Organisms modeled through this approach have usually been termed *squirmers* in the literature.

In many situations of interest, small organisms are propelling themselves through non-Newtonian fluids such as mucus [10] or biofilms [11], which can display highly viscoelastic properties. Viscoelasticity in the suspending fluid breaks the above cited *scallop theorem*, and locomotion with time-reversible strokes becomes possible, as shown by

Lauga [12]. The impact of viscoelasticity in the constitutive equation of the suspending fluid is typically quantified by introducing the Deborah number De , which is the ratio of the fluid and the flow characteristic times.

For the viscoelastic case, most of the work has dealt with flagellar-based propulsion: small amplitude theories for swimming sheets [13,14] and filaments [15] have been reported, together with numerical simulations for large amplitude swimming [16], and for motions of helicoidally shaped flagella [17,18]. On the other hand, theoretical studies on the swimming of ciliated organisms in viscoelastic fluids are limited to the above-cited work of Lauga [12,19], with results valid for small-amplitude time-dependent swimming strokes, and to recent numerical simulations of steady squirmers, performed at rather high Deborah numbers [20,21].

In this paper, we investigate the effects of a low viscoelasticity of the suspending medium on the locomotion of ciliated microorganisms. Indeed, in several realistic situations, such as in marine water or ponds [22], protozoa and algae swim in dilute suspensions of other microorganisms, in which exopolymeric substances (mostly consisting of high molecular weight polysaccharides) are dissolved [23]. The resulting dilute polymeric solution can therefore conveniently be modeled as a slightly viscoelastic fluid [22,23]. In this situation, viscoelasticity effects on the swimming behavior of ciliated microorganisms can be computed analytically, which is the aim of the present work. Specifically, we use a perturbative analysis in the Deborah number to study the swimming behavior of a single squirmer propelling itself in a *second-order fluid* (SOF), i.e., the “basic” viscoelastic liquid [24]. In the derivation, the so-called *generalized reciprocity theorem* [25] from Stokes flow theory is used. We obtain analytical expressions for the organism velocity and the dissipated power, valid to first order in De . To the best of our knowledge, these are the first analytical

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expressions derived for a steady squirmer in a viscoelastic fluid.

The paper is organized as follows. In Sec. II, we briefly review the organism propulsion model adopted, i.e., the Lighthill-Blake model. In Secs. III and IV the governing fluid-dynamics equations are reported, together with the perturbative procedure. In Secs. V–VI the reciprocity theorem is applied to compute both the swimmer velocity and the power dissipated by the swimmer in a second-order fluid. Some conclusions are drawn in Sec. VII. For sake of completeness, the explicit calculation of the velocity and pressure fields at order De is reported in the Appendix.

II. SWIMMER MODEL

It is apparent that a description of the dynamics of a ciliated organism through a detailed analysis of the individual cilia motions is by far too complex. For this reason, different models have been proposed, where actual cilia motions are replaced, e.g., by an overall motion of a deformable surface (a sort of “envelope” of the cilia population) [26], or, in an even simpler way, by a steady tangential “slip velocity” on a rigid boundary representing the microorganism surface [27]. In this latter case, the slip velocity is in fact an ultrasimplified modeling of the time-averaged ciliary propulsion [5], introduced for the first time by Lighthill and Blake [3,4]. In the rest of the paper, we will refer to this model microorganism as a “squirmer.”

In the context of the Lighthill-Blake model, we consider the squirmer as a sphere propelling itself only by axisymmetric surface tangential velocities. In spherical comoving coordinates, with origin at the microorganism center, and the z axis coinciding with the direction of motion, the slip velocity on the surface can then be written as [3,4]

$$v_r = 0, \quad (1a)$$

$$v_\theta = \sum_{n=1}^{\infty} \frac{-2}{n(n+1)} B_n P_n^1[\cos(\theta)], \quad (1b)$$

$$v_\phi = 0, \quad (1c)$$

where θ is the azimuthal angle (and ϕ is the angle of revolution), $P_n^1[\cos(\theta)]$ are the n th associated Legendre polynomials, and the B_n s, which have units of velocity, are the “swimming modes” [5]. In the present work we consider $B_n = 0$ for $n > 2$, as commonly assumed in literature [5,20,21]. Thus, the specification of the coefficients B_1 and B_2 completely determines the type of swimming. A squirmer with a positive ratio $\frac{B_2}{B_1}$ is called *puller*, as its maximum tangential velocity is on the frontal hemisphere; in other words, a puller generates propulsion from the front. Squirmers with a negative ratio $\frac{B_2}{B_1}$ are called *pushers*, as they generate propulsion from the rear. When $B_2 = 0$, the organism is called *neutral*.

In Newtonian fluids, the swimming velocity V is given by $V_N = \frac{2}{3} B_1$ [3,4], hence is the same for all squirmers. The coefficient B_2 will only enter the expression of the swimming dissipated power [4] (see Eq. (35)).

III. GOVERNING EQUATIONS

The investigation of the behavior of a steady squirmer in a non-Newtonian fluid of course requires the specification of a

constitutive equation for the fluid stress tensor. In this work, as mentioned in the Introduction, we will employ the second-order fluid (SOF) constitutive model [24], since we are only interested in small deviations from the Newtonian behavior. The second-order fluid is the asymptotic approximation of most viscoelastic fluids in slow and slowly varying flows [28]. The stress tensor \mathbf{T} for an incompressible SOF is given by

$$\mathbf{T} = -p\mathbf{I} + \mu\mathbf{A} + \alpha_1\mathbf{B} + \alpha_2\mathbf{A}^2. \quad (2)$$

In Eq. (2), p is the pressure, μ is the viscosity, \mathbf{A} is the symmetric part of the velocity gradient,

$$\mathbf{A} = \nabla\mathbf{v} + \nabla\mathbf{v}^T, \quad (3)$$

and \mathbf{B} is given by

$$\mathbf{B} = \frac{\partial\mathbf{A}}{\partial t} + (\mathbf{v} \cdot \nabla)\mathbf{A} + \mathbf{A} \cdot \nabla\mathbf{v} + \nabla\mathbf{v}^T \cdot \mathbf{A}. \quad (4)$$

The constitutive coefficients α_1 and α_2 in Eq. (2) are related to “normal stresses” of the viscoelastic liquid. Specifically, for a steady shear flow with shear rate $\dot{\gamma}$, the first and second normal stress differences are $N_1 = \Psi_1\dot{\gamma}^2$ and $N_2 = \Psi_2\dot{\gamma}^2$, respectively, and it is $\alpha_1 = -\frac{\Psi_1}{2}$ and $\alpha_2 = \Psi_1 + \Psi_2$.

Under the assumption of negligible Reynolds number, the steady-state dimensionless mass balance and momentum balance are

$$\nabla \cdot \mathbf{v} = 0, \quad (5)$$

$$\nabla \cdot \mathbf{T} = \mathbf{0}, \quad (6)$$

with the dimensionless stress tensor given by

$$\mathbf{T} = -p\mathbf{I} + \mathbf{A} - \text{De}(\mathbf{B} + b\mathbf{A}^2), \quad (7)$$

where $b = \frac{\alpha_2}{\alpha_1}$ and $\text{De} = -\frac{\alpha_1}{\mu} \frac{2B_1}{3a}$. In defining the Deborah number, we considered $-\frac{\alpha_1}{\mu}$ as the characteristic viscoelastic timescale, and we choose as flow timescale the ratio of the microorganism radius a and the Newtonian swimmer velocity $\frac{2B_1}{3}$. Finally, notice that the viscosity of the suspending fluid has also been used in making the stress nondimensional in Eq. (7), through the choice of a characteristic stress $\mu \frac{2B_1}{3a}$.

In addition to the above equations, we assume that the microorganism is “force-free,” i.e., that the fluid exerts a zero force on it:

$$\int_{4\pi} \mathbf{T} \cdot \mathbf{n} dS = \mathbf{0}. \quad (8)$$

(\mathbf{n} in Eq. (8) is the inwardly directed normal to the sphere surface 4π , as a is the characteristic length.)

We seek a solution for the dynamical Eqs. (5)–(7), plus the force-free condition Eq. (8), in the limit of $\text{De} \ll 1$. Of course, appropriate boundary conditions will be required; see the next section.

IV. PERTURBATIVE PROCEDURE

In this section we proceed with the perturbative analysis of non-Newtonian effects on the squirmer motion, with De as the expansion parameter. We therefore write the unknown velocity and pressure fields as regular expansions in De , that is to say

$$\mathbf{v} = \mathbf{v}_N + \text{De} \mathbf{v}_{\text{SOF}} + \mathcal{O}(\text{De}^2), \quad (9a)$$

$$p = p_N + \text{De} p_{\text{SOF}} + \mathcal{O}(\text{De}^2). \quad (9b)$$

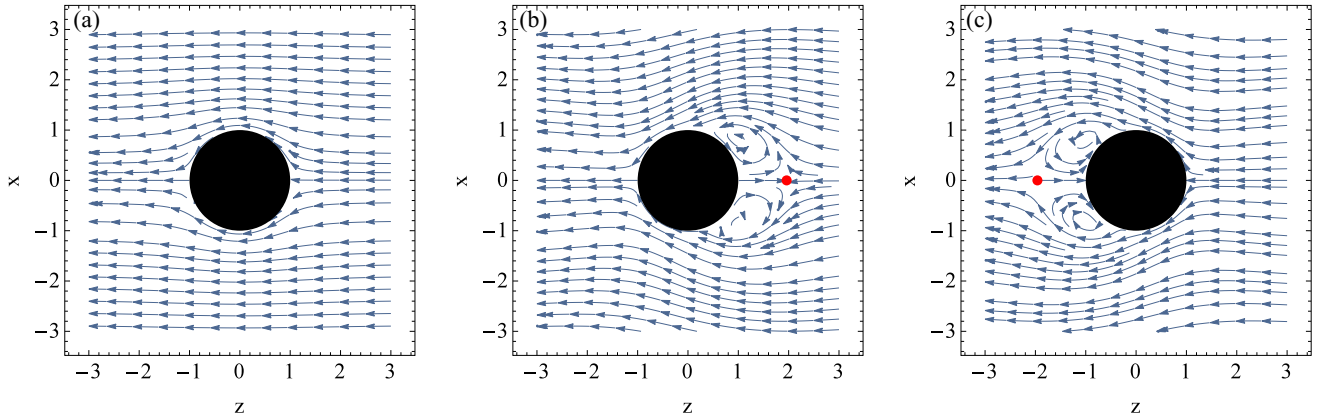


FIG. 1. (Color online) Comoving frame streamlines generated by microorganisms in a Newtonian fluid: (a) neutral swimmer, (b) pusher with $\beta = -3$, (c) puller with $\beta = 3$. (Somehow unrealistic high values of β are chosen, merely to highlight the flow field features.) The solid dot represents the position of a stagnation point.

A. Zeroth-order solution

The fundamental solution (the Newtonian case), has been given by Lighthill and Blake [3,4]. By adopting a “comoving” spherical coordinate system with its origin coinciding with the sphere center, the nondimensional boundary conditions on the sphere surface $r = a = 1$ are given by

$$v_{r,N} = 0, \quad (10a)$$

$$v_{\theta,N} = \frac{3}{2}\sin(\theta) + \frac{3}{2}\beta\cos(\theta)\sin(\theta), \quad (10b)$$

$$v_{\phi,N} = 0 \quad (10c)$$

[see Eq. (1)], where we defined $\beta = \frac{B_2}{B_1}$. Values of β for real microorganisms that have been reported in literature range between -1 and 1 [7,8,29,30]. Always in the comoving frame, as $r \rightarrow \infty$, the pressure is zero, and the velocity is

$$v_{r,N} = -V_N \cos(\theta), \quad (11a)$$

$$v_{\theta,N} = V_N \sin(\theta), \quad (11b)$$

$$v_{\phi,N} = 0, \quad (11c)$$

where V_N is the (nondimensional) Newtonian swimming velocity, to be determined. As already stated above, the dimensional velocity calculated by Lighthill and Blake is $V_N = \frac{2B_1}{3}$ (along z), and is the same for all swimmers (i.e., it is independent from β). Hence, the nondimensional zeroth-order (Newtonian) squirmer velocity in Eq. (11) is 1, and the zeroth-order complete dimensionless velocity and pressure fields in the comoving frame are given by

$$v_{r,N} = \left(\frac{1}{r^3} - 1\right)\cos(\theta) + \frac{3}{4}\left(\frac{1}{r^4} - \frac{1}{r^2}\right)\beta[3\cos(\theta)^2 - 1], \quad (12a)$$

$$v_{\theta,N} = \left(1 + \frac{1}{2r^3}\right)\sin(\theta) + \frac{3}{2}\frac{1}{r^4}\beta\cos(\theta)\sin(\theta), \quad (12b)$$

$$v_{\phi,N} = 0, \quad (12c)$$

$$p_N = \frac{3}{2}\frac{1}{r^3}\beta[3\cos(\theta)^2 - 1]. \quad (12d)$$

In Fig. 1, we report the streamlines generated by three different organisms in a Newtonian fluid, in the comoving frame. The motion of the swimmers in the laboratory frame is to the right, hence, velocity is negative at large positive z for all three swimmers in Fig. 1 (comoving frame). A neutral squirmer, Fig. 1(a), generates a front-rear antisymmetric flow field, whereas such symmetry is broken for pusher and puller organisms, Figs. 1(b) and 1(c), where stagnation points can be seen ahead and behind the swimmer, respectively.

For later use, we define the zeroth-order stress tensor resulting from the velocity and pressure fields given in Eq. (12) as

$$\mathbf{T}_N = -p_N \mathbf{I} + \mathbf{A}_N. \quad (13)$$

B. First-order problem

The governing equations of the first-order problem are

$$\nabla \cdot \mathbf{v}_{\text{SOF}} = 0, \quad (14)$$

$$\nabla \cdot \mathbf{T}_{\text{SOF}} = \nabla \cdot (\mathbf{B}_N + b\mathbf{A}_N^2), \quad (15)$$

where the stress tensor \mathbf{T}_{SOF} is defined by

$$\mathbf{T}_{\text{SOF}} = -p_{\text{SOF}} \mathbf{I} + \mathbf{A}_{\text{SOF}}, \quad (16)$$

and the tensors \mathbf{B}_N and \mathbf{A}_N are evaluated with the zeroth-order flow field.

Of course, the force-free condition has to be imposed also for the first-order problem and is written as

$$\int_{4\pi} [\mathbf{T}_{\text{SOF}} - (\mathbf{B}_N + b\mathbf{A}_N^2)] \cdot \mathbf{n} dS = \mathbf{0}. \quad (17)$$

Notice that, although the force-free condition of Eq. (17) is at order De , the stress tensor appearing in the equation (in square brackets) also includes a contribution from the Newtonian solution.

In writing down the boundary conditions for the first-order problem, we retain the choice of the previous subsection for the reference frame, i.e., we remain in the (Newtonian) comoving frame. As a consequence, the boundary conditions at infinity

are simply

$$v_{r,\text{SOF}} = 0, \quad (18a)$$

$$v_{\theta,\text{SOF}} = 0, \quad (18b)$$

$$v_{\phi,\text{SOF}} = 0, \quad (18c)$$

$$p_{\text{SOF}} = 0, \quad (18d)$$

whereas the first-order problem boundary condition on the sphere surface is given by

$$v_{r,\text{SOF}} = V_{\text{SOF}} \cos(\theta), \quad (19a)$$

$$v_{\theta,\text{SOF}} = -V_{\text{SOF}} \sin(\theta), \quad (19b)$$

$$v_{\phi,\text{SOF}} = 0, \quad (19c)$$

where the nondimensional V_{SOF} , to be determined, is the order De correction to the swimmer velocity. Notice that the adoption of the boundary condition Eqs. (19) expresses in fact the hypothesis that the propulsion mechanism at the microorganism surface is not affected by the suspending fluid. Notice further that, in the laboratory frame, the overall nondimensional velocity of the squirmer is given by

$$V = 1 + \text{De} V_{\text{SOF}} + \mathcal{O}(\text{De}^2). \quad (20)$$

V. SWIMMER VELOCITY

In principle, the unknown fields p_{SOF} and \mathbf{v}_{SOF} plus the first-order squirmer velocity V_{SOF} can be obtained from the solution of Eqs. (14)–(17). In what follows, on the other hand, we show that the first-order squirmer velocity V_{SOF} can in fact be obtained without the explicit knowledge of the first-order velocity and pressure fields, by making use of the *generalized reciprocity theorem* [25] from Stokes flow theory.

We proceed by defining an *auxiliary* Stokes problem, namely, the translation of a sphere, suspended in an unbounded quiescent Newtonian fluid, in the same direction of the squirmer. For simplicity, we will assume that the sphere translation in the auxiliary problem is occurring with velocity $V_{\text{N}} = 1$, i.e., with the same velocity of the Newtonian squirmer. The equations governing this problem are

$$\nabla \cdot \hat{\mathbf{v}} = 0, \quad (21)$$

$$\nabla \cdot \hat{\mathbf{T}} = \mathbf{0}. \quad (22)$$

(All the quantities related to the *auxiliary* problem are denoted with a caret.) The stress tensor of the auxiliary problem is given by

$$\hat{\mathbf{T}} = -\hat{p}\mathbf{I} + \hat{\mathbf{A}}, \quad (23)$$

and the boundary conditions on the sphere surface (in the comoving frame) are

$$\hat{v}_r = 0, \quad (24a)$$

$$\hat{v}_\theta = 0, \quad (24b)$$

$$\hat{v}_\phi = 0. \quad (24c)$$

Always in the comoving frame, the boundary conditions at infinity are

$$\hat{v}_r = -\cos(\theta), \quad (25a)$$

$$\hat{v}_\theta = \sin(\theta), \quad (25b)$$

$$\hat{v}_\phi = 0, \quad (25c)$$

$$\hat{p} = 0. \quad (25d)$$

The generalized reciprocity theorem in our case reads

$$\begin{aligned} & - \int_{4\pi} \hat{\mathbf{v}} \cdot \mathbf{n} \cdot \mathbf{T}_{\text{SOF}} dS + \int_{4\pi} \mathbf{v}_{\text{SOF}} \cdot \mathbf{n} \cdot \hat{\mathbf{T}} dS \\ & = - \int_V \hat{\mathbf{v}} \cdot (\nabla \cdot \mathbf{T}_{\text{SOF}}) dV + \int_V \mathbf{v}_{\text{SOF}} \cdot (\nabla \cdot \hat{\mathbf{T}}) dV. \end{aligned} \quad (26)$$

We can make some simplifications in the above equation: (i) the last integral of the right-hand side is identically zero [see Eq. (22)]; (ii) the first integral of the left-hand side is identically zero [see Eq. (24)]; (iii) in the surviving volume integral, $\nabla \cdot \mathbf{T}_{\text{SOF}}$ is substituted by the known expression $\nabla \cdot (\mathbf{B}_{\text{N}} + b\mathbf{A}_{\text{N}}^2)$, using Eq. (15); (iv) since the velocity \mathbf{v}_{SOF} on the sphere surface is equal to $\mathbf{v}_{\text{SOF}} = V_{\text{SOF}}\mathbf{k}$ (\mathbf{k} is the unit vector of the z axis), the second surface integral on the left-hand side of Eq. (26) is simply equal to $V_{\text{SOF}}\hat{F}$, where \hat{F} is the force required to sustain the sphere motion in the auxiliary problem. From Stokes law, it is $\hat{F} = 6\pi\hat{V} = 6\pi V_{\text{N}} = 6\pi$ along the axis of motion. Hence, Eq. (26) becomes

$$6\pi V_{\text{SOF}} = - \int_V \hat{\mathbf{v}} \cdot [\nabla \cdot (\mathbf{B}_{\text{N}} + b\mathbf{A}_{\text{N}}^2)] dV. \quad (27)$$

By using the identity $\mathbf{w} \cdot \nabla \cdot \mathbf{W} = \nabla \cdot (\mathbf{w} \cdot \mathbf{W}) - \nabla \mathbf{w} : \mathbf{W}$ (\mathbf{w} and \mathbf{W} are a vector and a tensor, respectively), we rewrite the volume integral in Eq. (27) as the sum of two volume integrals, and we transform the volume integral containing the overall divergence into a surface integral to obtain

$$\begin{aligned} & \int_{4\pi} \hat{\mathbf{v}} \cdot \mathbf{n} \cdot (\mathbf{B}_{\text{N}} + b\mathbf{A}_{\text{N}}^2) dS + 6\pi V_{\text{SOF}} \\ & = \int_V \nabla \hat{\mathbf{v}} : (\mathbf{B}_{\text{N}} + b\mathbf{A}_{\text{N}}^2) dV. \end{aligned} \quad (28)$$

Again, the surface integral is zero because of Eq. (24). We then obtain

$$V_{\text{SOF}} = \frac{1}{6\pi} \int_V \nabla \hat{\mathbf{v}} : (\mathbf{B}_{\text{N}} + b\mathbf{A}_{\text{N}}^2) dV. \quad (29)$$

We emphasize that, because of our choice of the Newtonian comoving frame, the time derivative included in \mathbf{B}_{N} is zero; see Eq. (4). Thus, the integral Eq. (29) involves only known quantities, from the zeroth-order problem and the auxiliary problem, and can be analytically computed to give

$$V_{\text{SOF}} = \frac{3}{10}(1+b)\beta \quad (30)$$

for the the $\mathcal{O}(\text{De})$ organism velocity correction. The total microorganism velocity is then given by

$$V = 1 + \frac{3}{10}(1+b)\beta \text{De} + \mathcal{O}(\text{De}^2) \quad (31)$$

[see Eq. (20)] or, in dimensional variables,

$$V = \frac{2}{3}B_1 \left[1 - \frac{1}{10} \frac{B_2}{a} \frac{\Psi_1}{\mu} \left(1 + \frac{\Psi_2}{\Psi_1} \right) \right]. \quad (32)$$

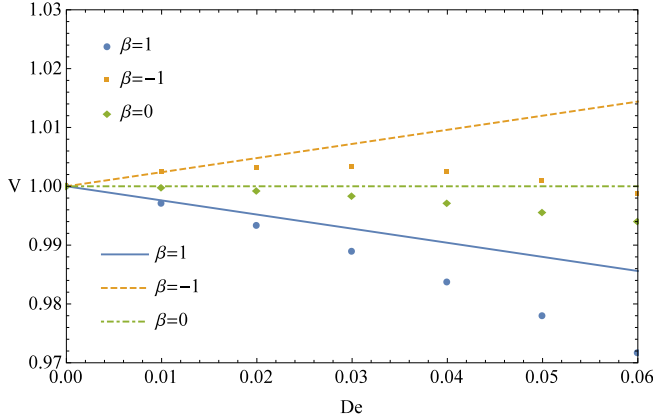


FIG. 2. (Color online) Squirmer swimming velocity as a function of De . Solid lines represent the analytical solution, Eq. (31), for $b = -1.8$; solid symbols are numerical solution for a Giesekus fluid with $b = -1.8$.

Similar to what was found by Wang and Ardekani [31] for a ciliated organism swimming in a Newtonian fluid at small, but nonzero, Reynolds number, the swimming speed depends linearly on the parameter β . Our analysis shows that the order De correction, Eq. (30), also depends on the constitutive parameter b . We remark that realistic values for b range from -2 , for a fluid with $\Psi_2 = 0$ (no second normal stress difference), to -1 , when $\Psi_2 = -\frac{\Psi_1}{2}$. Thus, $(1+b)$ is always negative, and the sign of the velocity correction at order De will depend on the sign of β . (A qualitatively similar result was obtained by Wang and Ardekani [31] for small nonzero Reynolds numbers; indeed, they found $V_{Re} = -0.11\beta$ for the $\mathcal{O}(Re)$ correction to the Newtonian velocity with no inertia.)

The total organism velocity V is shown in Fig. 2, as a function of De , for three different β values. We find that a puller is slower in a viscoelastic fluid than in a Newtonian one, while a pusher is faster. We emphasize that the speed of a neutral squirmer ($\beta = 0$) is unchanged by viscoelasticity up to $\mathcal{O}(De)$. Recent numerical simulations at high De [20,21] showed that pusher, puller, and neutral squirmers are all slower in a viscoelastic fluid than in a Newtonian fluid. On the other hand, our analytic results show that a pusher swims faster at $\mathcal{O}(De)$, while a neutral squirmer is unaffected by viscoelasticity at $\mathcal{O}(De)$. In order to verify our analytical solution we computed the squirmer swimming velocity in a Giesekus viscoelastic fluid [24] through numerical simulations at small Deborah numbers. The rheological parameters were chosen so as to match a second-order fluid with $b = -1.8$. The results are shown as solid symbols in Fig. 2. Data obtained from numerical simulations are in agreement with our analytical solution for very low De values. In Fig. 2 it is clearly shown from simulation results that the velocity of a pusher squirmer goes through a maximum and then decreases, while, for a neutral squirmer, the velocity shows an initially flat behavior and then decreases with increasing De . It is apparent that, for Deborah numbers larger than ≈ 0.02 , the numerical results start to deviate from the analytical theory, which means that higher-order viscoelastic effects (i.e., higher powers of De) come into play. The organism velocity obtained from the numerical simulations, being always lower than the analytical

velocity at order De , suggests that higher-order De effects always reduce the velocity of the microorganism regardless if it is a puller, pusher, or neutral, compatibly with what found by Zhu *et al.* [20,21] at large Deborah numbers.

VI. POWER DISSIPATED AND SWIMMING EFFICIENCY

Another effect of fluid viscoelasticity is that of modifying the power dissipated by the organism to move. The power P consumed by the microorganism is given by

$$P = \int_{4\pi} \mathbf{T} \cdot \mathbf{n} \cdot \mathbf{v} dS. \quad (33)$$

Applying the asymptotic expansion Eq. (9) to the definition above, and retaining only the terms up to $\mathcal{O}(De)$, we obtain

$$P = \int_{4\pi} \mathbf{T}_N \cdot \mathbf{n} \cdot \mathbf{v}_N dS + De \left[\int_{4\pi} \mathbf{T}_N \cdot \mathbf{n} \cdot \mathbf{v}_{SOF} dS + \int_{4\pi} [\mathbf{T}_{SOF} - (\mathbf{B}_N + b\mathbf{A}_N^2)] \cdot \mathbf{n} \cdot \mathbf{v}_N dS \right]. \quad (34)$$

The second integral in Eq. (34) is identically zero, because $\mathbf{v}_{SOF} = V_{SOF}\mathbf{k}$ is constant on the surface 4π and can be taken out of the integral, and the resulting integral expresses the Newtonian swimmer force-free condition. In the above equation, moreover, the first integral is simply the power dissipated by a swimming microorganism in a Newtonian fluid and has been calculated by Blake [4]:

$$P_N = 6\pi(2 + \beta^2). \quad (35)$$

Thus, it is

$$P = 6\pi(2 + \beta^2) + De \int_{4\pi} [\mathbf{T}_{SOF} - (\mathbf{B}_N + b\mathbf{A}_N^2)] \cdot \mathbf{n} \cdot \mathbf{v}_N dS = P_N + De P_{SOF}. \quad (36)$$

The De first-order correction P_{SOF} is given by the surface integral in Eq. (36). For the sake of precision, a piece of this integral involves known quantities (\mathbf{A}_N , \mathbf{B}_N , and \mathbf{v}_N); hence, only the piece containing \mathbf{T}_{SOF} is still unknown. We can compute this integral without the explicit expressions of the first-order velocity and pressure fields entering \mathbf{T}_{SOF} , however, again by applying the generalized reciprocity theorem. Indeed, by considering the Newtonian zeroth-order solution as the ‘‘auxiliary’’ problem, we can write

$$\begin{aligned} \int_{4\pi} \mathbf{v}_N \cdot \mathbf{n} \cdot \mathbf{T}_{SOF} dS &= \int_{4\pi} \mathbf{v}_{SOF} \cdot \mathbf{n} \cdot \mathbf{T}_N dS \\ &+ \int_V \mathbf{v}_N \cdot (\nabla \cdot \mathbf{T}_{SOF}) dV \\ &- \int_V \mathbf{v}_{SOF} \cdot (\nabla \cdot \mathbf{T}_N) dV. \end{aligned} \quad (37)$$

Now: (i) The last volume integral in Eq. (37) is nil, because $\nabla \cdot \mathbf{T}_N = \mathbf{0}$; (ii) the surface integral in the right-hand side is nil, because $\mathbf{v}_{SOF} = V_{SOF}\mathbf{k}$ can be taken out of the integral, and the integral now expresses the force-free condition of the Newtonian problem; (iii) in the surviving volume integral of Eq. (37), we can use Eq. (15), and hence the integrand function is completely known in terms of the Newtonian fields. In

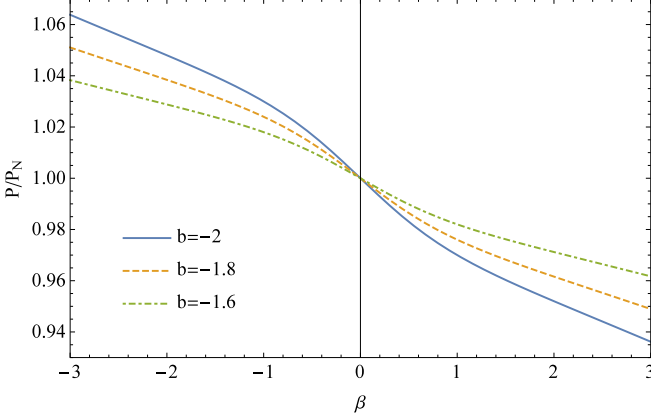


FIG. 3. (Color online) Total swimming power dissipated as a function of β , for $De = 0.02$.

conclusion, we obtain

$$P_{\text{SOF}} = - \int_{4\pi} (\mathbf{B}_N + b\mathbf{A}_N^2) \cdot \mathbf{n} \cdot \mathbf{v}_N dS + \int_V \mathbf{v}_N \cdot \nabla \cdot (\mathbf{B}_N + b\mathbf{A}_N^2) dV. \quad (38)$$

By further manipulation of the latter equation (through divergence theorem and the tensorial identity already exploited in the previous section), we get the final compact form for the first-order power correction:

$$P_{\text{SOF}} = - \int_V \nabla \mathbf{v}_N : (\mathbf{B}_N + b\mathbf{A}_N^2) dV. \quad (39)$$

By analytically performing the integration in Eq. (39), we obtain

$$P = P_N + De P_{\text{SOF}} = 6\pi(2 + \beta^2) + De \frac{27}{5} \pi (1 + b)(4\beta + \beta^3). \quad (40)$$

The first-order correction to the power dissipated by the squirmer depends cubically on β , similarly to what found by Wang and Ardekani [31] for a squirmer propelling through a Newtonian fluid at nonnegligible Reynolds number. Interestingly, we find that the power employed by a neutral organism for swimming is unchanged up to $\mathcal{O}(De)$. In Fig. 3 we plot the swimming power, normalized by the Newtonian P_N , as a function of β , and for $De = 0.02$. (For such a De value, the first-order theory is applicable; see the comparison with the numerical simulations of Fig. 2, and the discussion there.) When the organism is almost neutral (i.e., $\beta \approx 0$) the slope of $\frac{P}{P_N}$ versus β is determined by the linear term in P_{SOF} that, in turn, depends on b ; for realistic fluids, such slope is negative. Also for larger β (in absolute value) the slope stays negative. Thus, pullers swimming in a viscoelastic medium are saving energy with respect to the Newtonian case, while pushers are spending more energy. Our analysis reveals then a behavior at variance with recent numerical simulations [21], where it is found that squirmers swimming in a viscoelastic fluid always save energy with respect to the Newtonian case. It must be emphasized, however, that the simulations reported in Ref. [21] are performed at much higher De values than those considered here, in the perturbative approach.

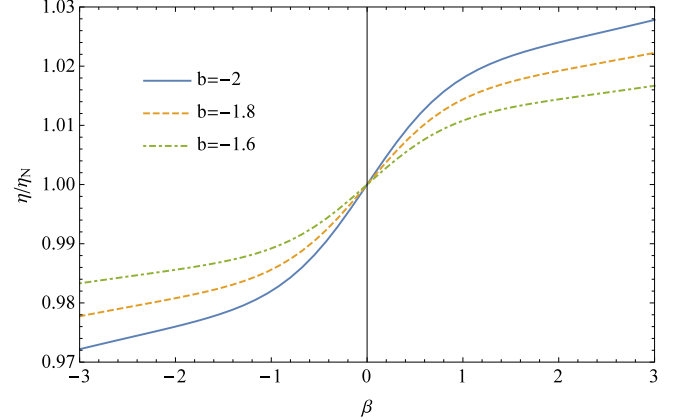


FIG. 4. (Color online) Swimming efficiency normalized with the Newtonian one, as a function of β , for $De = 0.02$.

The swimming efficiency η of a given squirmer is defined as the ratio between the power required to drag an inert sphere at the same velocity of the squirmer to that dissipated by the microorganism itself [4]:

$$\eta = \frac{V F(V)}{P(V)}. \quad (41)$$

We emphasize that the force F required to drag a sphere in a second-order fluid to first order in De is unchanged with respect to the Newtonian value [32,33]; i.e., it is $F = 6\pi V$. The efficiency, therefore, is

$$\eta = \frac{6\pi V^2}{P}, \quad (42)$$

and we calculate

$$\begin{aligned} \eta &= \eta_N \left[1 + De \left(2V_{\text{SOF}} - \frac{P_{\text{SOF}}}{P_N} \right) \right] \\ &= \frac{1}{2 + \beta^2} \left[1 + De \frac{3}{5} (1 + b) \beta \left(1 - \frac{3}{2} \frac{4 + \beta^2}{2 + \beta^2} \right) \right]. \end{aligned} \quad (43)$$

In Fig. 4 we report the squirmer efficiency η normalized with the Newtonian one $\eta_N = \frac{1}{2 + \beta^2}$ from Eq. (43), for $De = 0.02$. We find that pullers are always more efficient than pushers. It should be recalled, however, that pullers are always slower than pushers in the $\mathcal{O}(De)$ theory.

VII. CONCLUSIONS

In this paper we have studied the effects of viscoelasticity on a spherical steady squirmer swimming in a second-order fluid, through perturbative analysis. A regular perturbation expansion in the Deborah number De and the generalized reciprocity theorem have been used, to obtain analytical results. We found that the velocity of a neutral squirmer is unaffected by viscoelasticity, whereas pullers and pushers are slowed and hastened, respectively. We also quantified the power dissipated by a microorganism to swim in a second-order fluid, finding it to depend cubically on the ratio $\frac{B_2}{B_1}$, which rules the velocity at the swimmer surface in the Lighthill-Blake model. Pushers always dissipate more energy than pullers; with respect to the Newtonian case, pushers have larger dissipation, whereas pullers dissipate less.

The above-mentioned results were found at first order in De ; i.e., they represent the trends of deviations from the Newtonian results for a weak viscoelasticity of the suspending liquid. In fact, numerical computations (also reported in the paper) show that the range of applicability of the first-order theory is limited to rather low De values. We surmise, however, that our analysis can be relevant in some (selected) actual conditions. For example, for the *Volvox* microorganism it is $a \approx 100 \mu\text{m}$, $V_N \approx 100 \frac{\mu\text{m}}{\text{s}}$; hence, the flow characteristic time is 1 s. For a viscoelastic liquid with a characteristic time of 10^{-2} s, a perfectly realistic value, e.g., for a dilute macromolecular solution, the resulting Deborah number is $De \approx 10^{-2}$, inside the range of validity of our calculations. It might then be possible to observe some effects of such weak viscoelasticity, in particular for pullers, which have the largest deviations from the Newtonian case.

APPENDIX: PRESSURE AND VELOCITY FIELD CALCULATION

In this Appendix we report the “complete” solution to Eqs. (14)–(17), i.e., to the order De problem. We adopt the stream-function formulation of such equations to compute the flow and pressure fields, which is a standard way to attack axisymmetric problems [34]. The first-order radial and tangential velocity components are related to the stream-function Ψ_{SOF} as follows:

$$v_{r,\text{SOF}} = -\frac{1}{r^2 \sin\theta} \frac{\partial}{\partial\theta} \Psi_{\text{SOF}}; \quad v_{\theta,\text{SOF}} = -\frac{1}{r \sin\theta} \frac{\partial}{\partial r} \Psi_{\text{SOF}}. \quad (\text{A1})$$

In terms of Ψ_{SOF} , the momentum balance equation [Eq. (15)] becomes

$$\mathbf{i}_\phi E^4 \Psi_{\text{SOF}} = \nabla \times [\nabla \cdot (\mathbf{B}_N + b\mathbf{A}_N^2)] r \sin(\theta). \quad (\text{A2})$$

The differential operator E^4 is given by $E^4 = E^2(E^2)$, with $E^2 = \frac{\partial^2}{\partial r^2} + \frac{\sin(\theta)}{r} \frac{\partial}{\partial\theta} \left(\frac{1}{\sin(\theta)} \frac{\partial}{\partial\theta} \right)$, and \mathbf{i}_ϕ is the unit vector in the azimuthal direction. Notice that Eq. (A2) is in fact a scalar equation for the stream-function Ψ_{SOF} , since its right-hand side is itself a vector with the ϕ component only.

The first-order boundary condition Eq. (19) on the squirmer surface is also written in terms of the stream-function Ψ_{SOF} :

$$\Psi_{\text{SOF}} = -\frac{1}{2} V_{\text{SOF}} \sin^2(\theta); \quad \frac{\partial \Psi_{\text{SOF}}}{\partial r} = -V_{\text{SOF}} \sin^2(\theta), \quad (\text{A3})$$

and the quiescent condition far from the organism reads

$$\frac{\Psi_{\text{SOF}}}{r^2} \rightarrow 0 \quad \text{as } r \rightarrow \infty. \quad (\text{A4})$$

Finally, the force-free condition Eq. (17) can be written in terms of the stream function as [34]

$$\lim_{r \rightarrow \infty} \frac{\Psi_{\text{SOF}}}{r \sin^2(\theta)} = 0. \quad (\text{A5})$$

The right-hand side of Eq. (A2) is a known function, which can be written

$$\begin{aligned} \nabla \times [\nabla \cdot (\mathbf{B}_N + b\mathbf{A}_N^2)] r \sin(\theta) \\ = \mathbf{i}_\phi \frac{27}{4} (1+b)\beta \sin^2(\theta) \sum_{i=0}^3 g_i(r) P_i^0[\cos(\theta)], \end{aligned} \quad (\text{A6})$$

where the functions $g_i(r)$ are

$$g_0(r) = \frac{24}{r^8}, \quad (\text{A7a})$$

$$g_1(r) = \beta \left(\frac{88}{r^9} - \frac{24}{r^7} \right), \quad (\text{A7b})$$

$$g_2(r) = \frac{40}{r^8}, \quad (\text{A7c})$$

$$g_3(r) = \beta \left(\frac{72}{r^9} - \frac{24}{r^7} \right). \quad (\text{A7d})$$

In view of Eq. (A6), we will look for a solution for Ψ_{SOF} in the form

$$\Psi_{\text{SOF}} = \frac{27}{4} (1+b)\beta \sin^2(\theta) \sum_{i=0}^3 F_i(r) P_i^0[\cos(\theta)]. \quad (\text{A8})$$

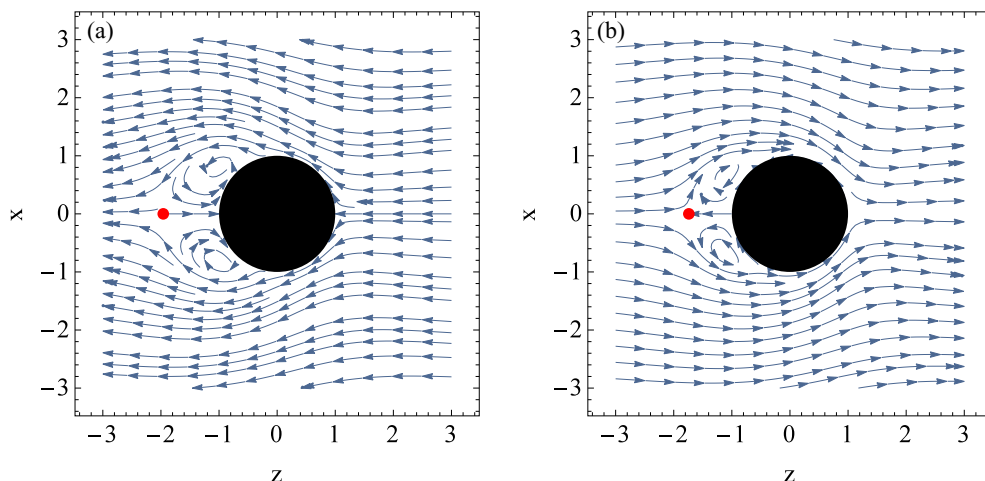


FIG. 5. (Color online) Comparison of (a) Newtonian and (b) order De streamlines generated, in the swimming frame, by a puller with $\beta = 3$, for $b = -2$. The solid circle represents the position of the stagnation point.

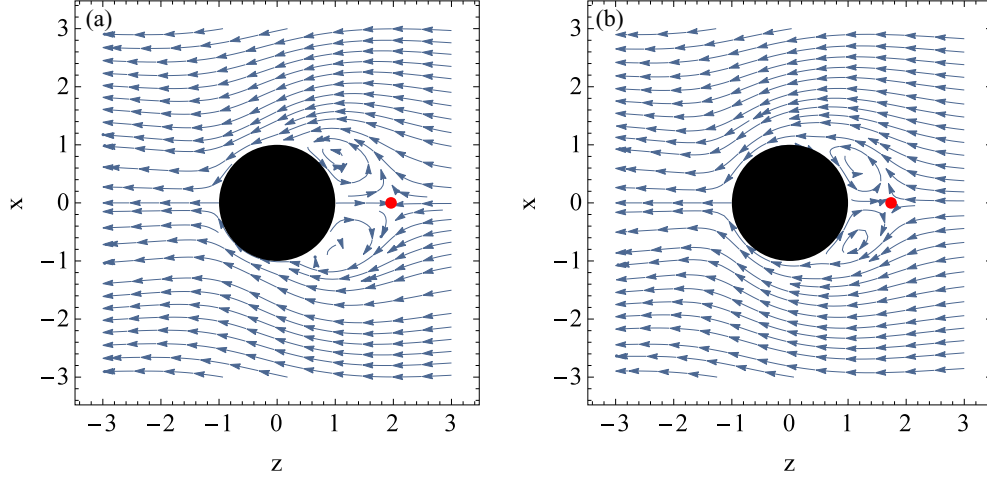


FIG. 6. (Color online) Comparison of (a) Newtonian and (b) order De streamlines generated, in the swimming frame, by a pusher with $\beta = -3$, for $b = -2$. The solid circle represent the position of the stagnation point.

The specification of the functions $F_i(r)$ in Eq. (A8) would completely determine the stream-function Ψ_{SOF} .

It is interesting to note that the stream-function Eq. (A8), and hence the flow field, is identically zero when $(1+b)\beta = 0$, which occurs when either $\beta = 0$ or $b = -1$. The former condition states that the flow field generated by a neutral squirmer is unchanged at first order in De. The latter condition, on the other hand, leads to a well-known result for fluid-dynamics problems with a second-order fluid [35], namely that, when $b = -1$, the De-order flow field is zero, and only the pressure is modified by viscoelasticity.

By inserting now Eqs. (A6) and (A8) in Eq. (A2), and by equating term-by-term the coefficients of $\sin^2(\theta)P_i^0[\cos(\theta)]$ (for $i = 0, 3$) in the resulting expression, we obtain the following system of ODEs (in r):

$$\frac{d^2}{dr^2}f_0(r) - \frac{2}{r^2}[f_0(r) + f_2(r)] = g_0(r), \quad (\text{A9a})$$

$$\frac{d^2}{dr^2}f_1(r) - \frac{6}{r^2}[f_1(r) + f_3(r)] = g_1(r), \quad (\text{A9b})$$

$$\frac{d^2}{dr^2}f_2(r) - \frac{12}{r^2}f_2(r) = g_2(r), \quad (\text{A9c})$$

$$\frac{d^2}{dr^2}f_3(r) - \frac{20}{r^2}f_3(r) = g_3(r), \quad (\text{A9d})$$

with the $g_i(r)$ given in Eq. (A7), and the $f_i(r)$ defined as

$$f_0(r) = \frac{d^2}{dr^2}F_0(r) - \frac{2}{r^2}[F_0(r) + F_2(r)], \quad (\text{A10a})$$

$$f_1(r) = \frac{d^2}{dr^2}F_1(r) - \frac{6}{r^2}[F_1(r) + F_3(r)], \quad (\text{A10b})$$

$$f_2(r) = \frac{d^2}{dr^2}F_2(r) - \frac{12}{r^2}F_2(r), \quad (\text{A10c})$$

$$f_3(r) = \frac{d^2}{dr^2}F_3(r) - \frac{20}{r^2}F_3(r). \quad (\text{A10d})$$

The set of ordinary differential Eqs. (A9) together with Eqs. (A10) yields a closed problem for the functions $F_0(r) - F_3(r)$. Elementary integration leads to

$$F_0(r) = \frac{c_3r^{10} + 9(c_7 + 2c_{11})r^8 + 90c_{15}r^6 - 45c_8r^5 + 90c_{16}r^3 + 18c_{12}r + 5}{90r^4}, \quad (\text{A11a})$$

$$F_1(r) = \frac{5r(9c_1r^{11} + 33(c_5 + 6c_9)r^9 + 462c_{13}r^7 - 77c_6r^4 + 462c_{14}r^2 + 198c_{10}) + 77\beta(r^2 + 4)}{2310r^5}, \quad (\text{A11b})$$

$$F_2(r) = c_{11}r^4 + \frac{c_{12}}{r^3} + \frac{5c_3r^{10} - 9c_4r^3 + 15}{90r^4}, \quad (\text{A11c})$$

$$F_3(r) = c_9r^5 + \frac{c_{10}}{r^4} + \frac{154\beta + 35c_1r^{12} - 55c_2r^3 + 231\beta r^2}{770r^5}. \quad (\text{A11d})$$

The constants c_1 – c_{16} are determined by applying the boundary conditions, Eqs. (A3) and (A4). We find

$$c_2 = \frac{7\beta}{10}, \quad (\text{A12a})$$

$$c_4 = -\frac{5}{6}, \quad (\text{A12b})$$

$$c_6 = -\frac{\beta}{7}, \quad (\text{A12c})$$

$$c_8 = -\frac{3(b+1)\beta - 10V_{\text{SOF}}}{45(b+1)\beta}, \quad (\text{A12d})$$

$$c_{10} = -\frac{9\beta}{20}, \quad (\text{A12e})$$

$$c_{12} = -\frac{1}{4}, \quad (\text{A12f})$$

$$c_{14} = \frac{\beta}{420}, \quad (\text{A12g})$$

$$c_{16} = -\frac{21(b+1)\beta - 20V_{\text{SOF}}}{540(b+1)\beta}, \quad (\text{A12h})$$

$$c_1 = c_3 = c_5 = c_7 = c_9 = c_{11} = c_{13} = c_{15} = 0. \quad (\text{A13})$$

We still need to determine the velocity V_{SOF} of the squirmer. To this end we simply insert Ψ_{SOF} , as previously obtained, in Eq. (A5) (the force-free condition), which gives

$$V_{\text{SOF}} = \frac{3}{10}(1+b)\beta. \quad (\text{A14})$$

Equation (A14) is the same result obtained in Sec. V, Eq. (30), thus giving an independent verification of the results obtained in the main text of the present paper.

According to Eq. (A1), the first-order radial and tangential velocity components are

$$\begin{aligned} v_{r,\text{SOF}} = & 3(b+1)\beta \left(\frac{1}{5r^3} - \frac{1}{10r^6} \right) P_1^0[\cos(\theta)] + 9(b+1)\beta^2 \left(-\frac{1}{14r^7} + \frac{1}{7r^5} - \frac{1}{28r^4} - \frac{1}{28r^2} \right) P_2^0[\cos(\theta)] \\ & + 27(b+1)\beta \left(-\frac{1}{10r^6} + \frac{3}{20r^5} - \frac{1}{20r^3} \right) P_3^0[\cos(\theta)] + 27(b+1)\beta^2 \left(-\frac{1}{7r^7} + \frac{9}{28r^6} - \frac{3}{14r^5} + \frac{1}{28r^4} \right) P_4^0[\cos(\theta)], \end{aligned} \quad (\text{A15})$$

$$\begin{aligned} v_{\theta,\text{SOF}} = & 3(b+1)\beta \left(\frac{1}{5r^6} - \frac{1}{10r^3} \right) P_1^1[\cos(\theta)] + 3(b+1)\beta^2 \left(\frac{5}{28r^7} - \frac{3}{14r^5} + \frac{1}{28r^4} \right) P_2^1[\cos(\theta)] \\ & + 9(b+1)\beta \left(\frac{1}{10r^6} - \frac{9}{80r^5} + \frac{1}{80r^3} \right) P_3^1[\cos(\theta)] + 27(b+1)\beta^2 \left(\frac{1}{28r^7} - \frac{9}{140r^6} + \frac{9}{280r^5} - \frac{1}{280r^4} \right) P_4^1[\cos(\theta)]. \end{aligned} \quad (\text{A16})$$

The first-order pressure field is readily calculated from the equation

$$\nabla p_{\text{SOF}} = \nabla^2 \mathbf{v}_{\text{SOF}} - \nabla \cdot (\mathbf{B}_N + b\mathbf{A}_N^2), \quad (\text{A17})$$

where the right-hand side is now a known function. The radial and tangential components of Eq. (A17) (the azimuthal component of the equation is an identity) are readily integrated. Keeping into account the boundary condition $p_{\text{SOF}} \rightarrow 0$ for $r \rightarrow \infty$, it is

$$\begin{aligned} p_{\text{SOF}} = & -\frac{3\{140(2b+3)\beta^2 + 3(17b+20)\beta^2 r^4 - 10r^2[33\beta^2 + 2b(12\beta^2 - 5) - 15]\}}{20r^{10}} \\ & + P_1^0[\cos(\theta)] \left[\frac{18\beta(9br^2 - 20b + 12r^2 - 30)}{5r^9} \right] \\ & + P_2^0[\cos(\theta)] \left(-\frac{3\{200(2b+3)\beta^2 + 6(b+1)\beta^2 r^7 + 3(31b+34)\beta^2 r^4 - 8r^2[66\beta^2 + 2b(24\beta^2 - 7) - 21]\}}{28r^{10}} \right) \\ & + P_3^0[\cos(\theta)] \left\{ -\frac{9\beta[b(15r^5 - 96r^2 + 160) + 15r^5 - 128r^2 + 240]}{40r^9} \right\} \\ & + P_4^0[\cos(\theta)] \left\{ \frac{27\beta^2[b(7r^5 - 36r^4 + 80r^2 - 60) + 7r^5 - 30r^4 + 110r^2 - 90]}{70r^{10}} \right\}. \end{aligned} \quad (\text{A18})$$

The order De velocity field given in Eqs. (A15) and (A16) is visualized in Fig. 5 (right panel) for a puller with $\beta = 3$. In the same figure, the order-zero velocity field (the Newtonian case) is also reported (left panel). The velocity

fields clearly share the same features, with a stagnation point behind the advancing squirmer. The first-order field, however, shows velocities directed opposite with respect to the Newtonian case. The overall effect will be that of

reducing the velocity of the squirmer, as indeed reported in Eq. (30) of the main text. In Fig. 6, the Newtonian and SOF velocity fields are reported for a pusher $\beta = -3$.

The first-order velocity is now in the same direction as the Newtonian velocity, and hence the pusher velocity will increase.

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