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The mechanism of propulsion of a model microswimmer in a viscoelastic fluid next to a solid boundary

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In this paper, we study the swimming of a model organism, the so-called Taylor's swimming sheet, in a viscoelastic fluid close to a solid boundary. This situation comprises natural habitats of many swimming microorganisms, and while previous investigations have considered the effects of both swimming next to a boundary and swimming in a viscoelastic fluid, seldom have both effects been considered simultaneously. We re-visit the small wave amplitude result obtained by Elfring and Lauga ["Theory of locomotion through complex fluids," in *Complex Fluids in Biological Systems*, Biological and Medical Physics, Biomedical Engineering, edited by S. E. Spagnolie (Springer New York, New York, NY, 2015), pp. 283–317] and give a mechanistic explanation to the decoupling of the effects of viscoelasticity, which tend to slow the sheet, and the presence of the boundary, which tends to speed up the sheet. We also develop a numerical spectral method capable of finding the swimming speed of a waving sheet with an arbitrary amplitude and waveform. We use it to show that the decoupling mentioned earlier does not hold at finite wave amplitudes and that for some parameters the presence of a boundary can cause the viscoelastic effects to increase the swimming speed of microorganisms. *Published by AIP Publishing*. https://doi.org/10.1063/1.4996839

I. INTRODUCTION

Many microorganisms are able to propel themselves through fluid environments by deforming their bodies. The small size of these organisms, ranging from a few micrometers in the case of most bacteria, to tens or hundreds of micrometers in the case of eukaryotes, and their relatively small propulsion speeds dictate that their swimming typically occurs in the low-Reynolds-number regime and that the fluid flow around them obeys the Stokes equation.¹ As was pointed out by Purcell,² this poses a severe restriction on how microorganisms move since they have to break the intrinsic time-reversibility of the Stokes equation-a result commonly known as Purcell's scallop theorem. In order to propel, microorganisms have to either deform their bodies or move parts of their bodies in a non-time-reversible fashion, and a vast number of studies considered how various modes of propulsion work, and what the resulting properties of microorganisms' motion are (see Refs. 1, 3, and 4, and references therein).

Arguably the most influential model of swimming at low Reynolds numbers is Taylor's swimming sheet model⁵ that guided the later studies of microorganism propulsion. It comprises an infinite inextensible two dimensional sheet, periodic in space, that can change its shape by propagating a wave with a speed *c* along its waveform. From the point of view of an external observer, its shape traces out the curve y_s in the *xy*-plane, given by

$$y_s(x,t) = f(x - (c - U)t),$$
 (1)

where the wave is traveling in the positive x-direction and the organism swims at speed U along the same axis. The waveform f(x) is a periodic function with the period $2\pi/k$, where k is the associated wavenumber. For sheets with sinusoidal waveforms, $f(x) = b \sin(kx)$, and small amplitudes, $bk \ll 1$, Taylor demonstrated that the sheet moves with the speed $U_{BN} = c b^2 k^2/2$ in the direction opposite to the direction of wave propagation.⁵

This result was extended by $Katz^6$ who considered a Taylor sheet swimming next to a solid boundary and showed that to lowest order in *bk* its swimming speed is given by

$$U_N = c \frac{b^2 k^2}{2} \left(\frac{\sinh^2(hk) + h^2 k^2}{\sinh^2(hk) - h^2 k^2} \right),$$
 (2)

where *h* is the distance between the middle line of the organism and the boundary. Notably, this speed is larger than U_{BN} , the swimming speed in the bulk, for any finite value of *h*, although this conclusion relies on the assumption that the organism keeps the same kinematics in the bulk and next to a wall. The studies by Taylor⁵ and Katz⁶ were instrumental in guiding later studies of low-Reynolds propulsion of various model swimmers, both in the bulk^{7–27} and close to surfaces.^{28–35}

Another important extension of Taylor's result was derived by Lauga³⁶ who studied a waving sheet swimming in the bulk of a viscoelastic fluid. Lauga showed³⁶ that for a range of constitutive models, the small-amplitude swimming speed is given by

$$U_B = c \frac{b^2 k^2}{2} \left(\frac{1 + \beta \text{De}^2}{1 + \text{De}^2} \right).$$
(3)

Here, $\beta = \eta_s/(\eta_s + \eta_p)$, with η_s and η_p being the viscosity of the solvent and the polymer components, respectively, and

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De = λck is the Deborah number of the problem, where λ is the longest relaxation time of the fluid. For the fixed kinematics of the organism, this result suggests that viscoelasticity reduces the propulsion speed of a small-amplitude sheet compared to its Newtonian value, reaching for large Deborah numbers the limit βU_{BN} . These conclusions were extended to other swimmers^{37–52} or fluids with different rheological properties^{53–58} and were used as a motivation for experimental studies.^{59–67}

While the previous studies provide understanding of how individual effects influence microswimming (with a notable exception of Refs. 68–71), the actual ecological situation of many microorganisms often comprises a combination of these effects. Examples range from sperms moving in mucus along the cervix wall^{72–74} to bacterial pathogens invading biofilms of different bacterial species.⁷⁵ The simplest model to study such systems should include both viscoelasticity of the suspending fluid and the presence of a solid boundary, i.e., be a combination of the effects discussed earlier. The first step in this direction was taken by Elfring and Lauga⁷⁶ who calculated the swimming speed of a small-amplitude Taylor sheet swimming next to a boundary in an Oldroyd-B fluid. Surprisingly, the swimming speed they obtain,

$$U = c \frac{b^2 k^2}{2} \left(\frac{1 + \beta \text{De}^2}{1 + \text{De}^2} \right) \left(\frac{\sinh^2(hk) + h^2 k^2}{\sinh^2(hk) - h^2 k^2} \right), \quad (4)$$

is simply a combination of the swimming speeds U_{BN} , U_N , and U_B , i.e., the effects of viscoelasticity and the boundary factorise. While Eqs. (2)–(4) are often cited, there is currently no simple understanding of the corresponding effects.

The purpose of this work is to provide a mechanistic explanation of the interplay between viscoelasticity of the fluid and the presence of a solid wall. Our paper is organised as follows. In Sec. II, we consider a small-amplitude Taylor sheet model swimming next to a boundary in an Oldroyd-B fluid. We re-derive the result obtained by Elfring and Lauga,⁷⁶ Eq. (4), and obtain explicit expressions for the velocity and stress fields around the swimmer which we will use to develop a small-amplitude physical mechanism in Sec. IV. In Sec. III, we develop a numerical method based on a spectral representation of hydrodynamic fields to calculate the swimming speed of a Taylor sheet of any amplitude and shape and apply it to the situation discussed earlier. Finally, in Sec. IV, we use the velocity and stress fields calculated in Secs. II and III to explain the origin of Eqs. (2) and (3), and Eq. (4), and discuss the emerging mechanism of propulsion.

II. SMALL-AMPLITUDE SWIMMING: ANALYTICAL SOLUTION

In this section, we consider a Taylor's waving sheet swimming in a viscoelastic fluid next to a boundary in the smallamplitude limit, see Fig. 1. In the low-Reynolds-number limit, the flow of the fluid around the organism is governed by the Stokes equation, $\nabla \cdot \Sigma = 0$, where Σ is the total stress in the fluid given by

$$\boldsymbol{\Sigma} = -p\mathbf{1} + 2\eta_s \mathbf{D} + \boldsymbol{\tau}.$$
 (5)

Here, *p* is the pressure, **1** is the identity matrix, **D** = $(\nabla \mathbf{u} + \nabla \mathbf{u}^T)/2$ is the symmetric strain rate tensor, **u** is the velocity of the fluid, η_s is the solvent viscosity, and $(\dots)^T$ denotes



FIG. 1. Schematic of a cross section of a sheet of a distance *h* below a wall with the waveform f(x).

the transpose. The polymeric contribution to the total stress, τ , arises due to the polymers being stretched and oriented by local velocity gradients. Here we use one of the simplest viscoelastic constitutive equations, the Oldroyd-B model,^{77,78} that develops large normal stresses in shear flows that are responsible for many non-trivial effects exhibited by viscoelastic fluids,⁷⁷ but the model does not have any shear thinning effects, i.e., its material properties are independent of local velocity gradients. Combined together, the governing equations are given by

$$-\nabla p + 2\eta_s \nabla \cdot \mathbf{D} + \nabla \cdot \boldsymbol{\tau} = \mathbf{0}, \tag{6a}$$

$$\nabla \cdot \boldsymbol{u} = \boldsymbol{0},\tag{6b}$$

$$\boldsymbol{\tau} + \lambda \overset{\diamond}{\boldsymbol{\tau}} = 2\eta_p \mathbf{D},\tag{6c}$$

where η_p is the polymeric contribution to the fluid's viscosity, λ is the longest relaxation time of the solution, and we assumed the fluid to be incompressible. The upper-convected Maxwell derivative is given by

$$\nabla^{\mathbf{\nabla}}_{\boldsymbol{\tau}} = \partial_t \boldsymbol{\tau} + \boldsymbol{u} \cdot \boldsymbol{\nabla} \boldsymbol{\tau} - \boldsymbol{\nabla} \boldsymbol{u}^T \cdot \boldsymbol{\tau} - \boldsymbol{\tau} \cdot \boldsymbol{\nabla} \boldsymbol{u}.$$

The boundary conditions are given by the no-slip boundary conditions at the sheet and the wall,

$$\boldsymbol{u}|_{\boldsymbol{y}=\boldsymbol{y}_s} = \boldsymbol{u}_s, \tag{7a}$$

$$\boldsymbol{u}|_{\boldsymbol{v}=\boldsymbol{h}} = \boldsymbol{u}_{\boldsymbol{w}},\tag{7b}$$

where u_s and u_w are the velocity of the material points of the sheet and the wall, respectively.

To address the situation sketched in Fig. 1, we solve a slightly more general problem of the sheet in a channel with walls both above and below it, placed at distances h_+ and h_- from the centreline, respectively. We then return to the original single-wall problem by taking $h_+ \rightarrow h$ and $h_- \rightarrow \infty$.

We start by simultaneously introducing dimensionless variables and removing any explicit time dependence with the help of the following transformation to starred quantities:

$$x^* = k(x - ct), \ y^* = ky, \ h^*_{\pm} = h_{\pm}k,$$
$$U^* = \frac{U}{c}, \ u^* = 1 + \frac{u}{c}, \ v^* = \frac{v}{c},$$
$$p^* = \frac{p}{\eta ck}, \ \tau^* = \frac{\tau}{\eta_p ck}, \ \Sigma^* = \frac{\Sigma}{\eta ck}.$$

In these coordinates, the velocity of the walls is $u_w^* = -e_x$ and the shape of the sheet is approximately fixed in time such that $y_s^*(x^*) = \epsilon \sin(x^*) + O(\epsilon^3)$, where $\epsilon = bk$ is the dimensionless wave amplitude. Our goal then is to find the steady velocity field surrounding the sheet and, from this, to calculate the sheet's swimming speed. From now on, we will drop the *s. We expand the fields p, u, and τ into the Taylor series about $\epsilon = 0$. For example, the pressure field is given by

$$p = \sum_{n=0}^{\infty} p^{(n)} \epsilon^n, \tag{8}$$

where $p^{(n)}$ is the "*n*th-order" contribution to the pressure field.

The velocity field is the solution to Eq. (6), subject to the no-slip boundary conditions of Eq. (7). This solution is periodic in *x*, reflecting the symmetry of the underlying problem. As we are only interested in the lowest order of the small- ϵ expansion of the swimming speed, we only need the boundary conditions to the lowest order in ϵ . From Taylor's original paper,⁵ we can show that, to the lowest order, the velocity of the material points of the sheet, u_s , is given in our coordinates, where we are co-moving with the wave, by

$$u_s = -1 + \mathcal{O}(\epsilon^2), \tag{9a}$$

$$v_s = -\epsilon \cos(x) + \mathcal{O}(\epsilon^2).$$
 (9b)

In our coordinate system, the swimming speed of the sheet can be found by averaging the velocity field along the length of the sheet. Thus, up to the second order in ϵ , the swimming speed of the sheet is given by

$$U = \langle u^{(1)} |_{y=y_s} \rangle \epsilon + \langle u^{(2)} |_{y=0} \rangle \epsilon^2 + \mathcal{O}(\epsilon^3).$$
(10)

To the lowest order in ϵ , averages over the line $y = y_s = \epsilon \sin(x)$ are equal to averages over the line y = 0; thus we take the $\langle \rangle$ above as simple *x*-averages.

We find the first and second order velocity fields by substituting the Taylor expansion of each of the fields into Eq. (6) and considering each power of ϵ separately. To the zeroth order, this procedure yields the following set of equations:

$$-\nabla p^{(0)} + \beta \nabla^2 \boldsymbol{u}^{(0)} + (1 - \beta) \nabla \cdot \boldsymbol{\tau}^{(0)} = \boldsymbol{0},$$
$$\nabla \cdot \boldsymbol{u}^{(0)} = \boldsymbol{0},$$
$$\boldsymbol{\tau}^{(0)} = \boldsymbol{D}^{(0)},$$
$$\boldsymbol{u}^{(0)}\Big|_{y=y_x} = \boldsymbol{u}^{(0)}\Big|_{y=h_+} = \boldsymbol{u}^{(0)}\Big|_{y=-h_-} = -\boldsymbol{e}_x,$$

which has the trivial solution $p^{(0)} = 0$, $\tau^{(0)} = 0$, and $u^{(0)} = -e_x$. Note that the zeroth order velocity field does not contribute to the swimming speed of the sheet as the latter is given by the difference between the average velocities of the fluid at the sheet and at the wall, which vanishes at the zeroth order.

The first order velocity field is in fact the same for an Oldroyd-B fluid as for a Newtonian one.³⁶ To demonstrate this, we consider the first order equations,

$$-\nabla p^{(1)} + \nabla \cdot (2\beta \mathbf{D}^{(1)} + (1-\beta)\boldsymbol{\tau}^{(1)}) = \mathbf{0}, \qquad (11a)$$

$$\nabla \cdot \boldsymbol{u}^{(1)} = 0, \tag{11b}$$

$$(1 - \operatorname{De} \partial_x)\boldsymbol{\tau}^{(1)} = \mathbf{D}^{(1)}, \qquad (11c)$$

$$\boldsymbol{u}^{(1)}\Big|_{y=y_s} = -\cos(x)\boldsymbol{e}_y, \ \boldsymbol{u}^{(1)}\Big|_{y=h_+} = \boldsymbol{u}^{(1)}\Big|_{y=-h_-} = \boldsymbol{0}.$$
 (11d)

Here we have used the previous solution, $u^{(0)} = -1$, in Eq. (11c), and we have re-arranged Eq. (11a) using $\nabla^2 u^{(1)} = 2\nabla \cdot \mathbf{D}^{(1)}$. Let \mathcal{L} be the linear operator defined by

$$\mathcal{L}(\boldsymbol{a}) = (1 - \operatorname{De} \partial_x) \nabla \cdot \mathcal{E} \cdot \boldsymbol{a}, \qquad (12)$$

where $\mathcal{E} = e_x e_y - e_y e_x$. Applying \mathcal{L} to Eq. (11a), we obtain

$$\nabla \cdot \mathcal{E} \cdot \nabla \cdot \left((1 - \operatorname{De} \partial_x) (2\beta \mathbf{D}^{(1)} + (1 - \beta)\tau^{(1)}) \right)$$
$$= 2\nabla \cdot \mathcal{E} \cdot \nabla \cdot (1 - \beta \operatorname{De} \partial_x) \mathbf{D}^{(1)} = 0, \quad (13)$$

where we have used the commutativity of differential operators and Eq. (11c) to remove $\tau^{(1)}$. This equation is satisfied either by a $\mathbf{D}^{(1)}$ for which $\nabla \cdot \mathcal{E} \cdot \nabla \cdot \mathbf{D}^{(1)} = 0$ or by a $\mathbf{D}^{(1)}$ for which $(1 - \beta De \partial_x)\mathbf{D}^{(1)} = 0$. The first of these conditions is satisfied by the Newtonian solution, while the second has no non-trivial solutions which are periodic in *x*. Moreover, since the boundary conditions are the same as in the Newtonian case, we conclude that the first order velocity field in an Oldroyd-B fluid is that the same as its Newtonian counterpart.

In his original analysis of a Taylor sheet swimming next to a wall, Katz⁶ showed that the first order velocity field, $u_{\pm}^{(1)}$, in the Newtonian fluid above (+) and below (-) the sheet is given by

$$u_{\pm}^{(1)} = (1 + A_{\pm} - B_{\pm}y)\sin(x)\sinh(y) + A_{\pm}y\sin(x)\cosh(y),$$
(14a)

$$v_{\pm}^{(1)} = -(A_{\pm}y + B_{\pm})\cos(x)\sinh(y) - (1 - B_{\pm}y)\cos(x)\cosh(y),$$
(14b)

where

$$A_{\pm} = \frac{\sinh^2(h_{\pm})}{\sinh^2(h_{\pm}) - h_{+}^2}, \ B_{\pm} = \frac{\pm \sinh(h_{\pm})\cosh(h_{\pm}) \pm h_{\pm}}{\sinh^2(h_{\pm}) - h_{+}^2}$$

The contribution of this field to the swimming speed is given by the first term of Eq. (10), which reads

$$\langle u^{(1)} |_{y=y_s} \rangle \epsilon = \epsilon^2 (A + \frac{1}{2}) + \mathcal{O}(\epsilon^3).$$
 (15)

Here we have dropped the explicit \pm notation, but we note that this contribution to the swimming speed is different for each region of the fluid. Below, we ensure that the total swimming speed is the same regardless of whether we use the fluid velocity above or below the sheet, but first we calculate the second term in Eq. (10).

The second order set of governing equations is given by

$$-\nabla p^{(2)} + \beta \nabla^2 \boldsymbol{u}^{(2)} + (1 - \beta) \nabla \cdot \boldsymbol{\tau}^{(2)} = \boldsymbol{0}, \quad (16a)$$

$$\nabla \cdot \boldsymbol{u}^{(2)} = 0, \tag{16b}$$

$$(1 - \operatorname{De} \partial_x)\boldsymbol{\tau}^{(2)} = \mathbf{D}^{(2)} - \operatorname{De} \left[\boldsymbol{u}^{(1)} \cdot \nabla \boldsymbol{\tau}^{(1)} - (\nabla \boldsymbol{u}^{(1)})^T \right]$$
$$\cdot \boldsymbol{\tau}^{(1)} - \boldsymbol{\tau}^{(1)} \cdot \nabla \boldsymbol{u}^{(1)} .$$
(16c)

We have left out the boundary conditions, which we will deal with later. Note that in the second term of Eq. (10), the *x*-average commutes with the *y*-substitution, as the substitute is independent of *x*. Thus, we only have to solve the *x*-average of Eq. (16) to find the second order swimming speed. Considering the *x*-averages of the *x*-component of Eq. (16a) and the *xy*-component of Eq. (16c), we have

$$\beta \partial_{yy} \langle u^{(2)} \rangle + (1 - \beta) \partial_y \langle \tau_{xy}^{(2)} \rangle = 0, \qquad (17a)$$

$$\langle \tau_{xy}^{(2)} \rangle = \partial_y \langle u^{(2)} \rangle - \text{De} [\langle u^{(1)} \partial_x \tau_{xy}^{(1)} \rangle + \langle v^{(1)} \partial_y \tau_{xy}^{(1)} \rangle - \langle D_{xy}^{(1)} (\tau_{xx}^{(1)} + \tau_{yy}^{(1)}) \rangle + \langle \Omega_{xy}^{(1)} (\tau_{xx}^{(1)} - \tau_{yy}^{(1)}) \rangle],$$
 (17b)

where $\Omega = (\nabla u^T - \nabla u)/2$ is the vorticity tensor, and we have ignored the *x*-averages of *x*-derivatives of *x*-periodic functions, which must vanish. Since the first order fields are known, Eq. (17) is simply an ordinary differential equation for $\langle u^{(2)} \rangle$, and the solution to which is given by

$$\langle u_{\pm}^{(2)} \rangle = E_{\pm} + F_{\pm}y + \frac{(1 - \beta)\text{D}e^2}{4(1 + \text{D}e^2)} \times [G_{\pm}\cosh(2y) + H_{\pm}\sinh(2y)],$$
 (18)

where

$$\begin{split} G_{\pm} &= (2 + 4A_{\pm} + A_{\pm}^2 - B_{\pm}^2) - 4B_{\pm}(1 + A_{\pm})y + 2(A_{\pm}^2 + B_{\pm}^2)y^2, \\ H_{\pm} &= 2A_{\pm}(B_{\pm} + 2(1 + A_{\pm})y - 2B_{\pm}y^2). \end{split}$$

Here, E_{\pm} and F_{\pm} are arbitrary constants.

Until now, the solutions in the domains above and below the sheet were completely independent. Their coupling is now ensured by applying appropriate boundary conditions, which determine the constants E_{\pm} and F_{\pm} . Similar to the solution developed by Katz for swimming of a Taylor sheet next to a wall in a Newtonian fluid,⁶ we require that (i) the swimming speeds we calculate from the upper and lower fluids match and that (ii) the sheet is, on average, force-free to the second order in the *x*-direction. The first order flow field, which is the same as the first order Newtonian flow field, does not apply a net-force to the sheet,⁶ while the second order flow field contributes a force $\Sigma^{(2)} \cdot n_{\pm}|_{y=0}$, where $n_{\pm} = \pm e_y + \mathcal{O}(\epsilon)$ is the inward-normal of the sheet in the upper/lower fluid. To the second order, these boundary conditions are given by

$$\left\langle u_{\pm}^{(2)} \right\rangle \Big|_{y=\pm h_{\pm}} = 0, \tag{19a}$$

$$\left\langle u_{+}^{(1)} \right|_{y=y_{s}} \right\rangle \epsilon + \left\langle u_{+}^{(2)} \right\rangle \Big|_{y=0} \epsilon^{2}$$

= $\left\langle u_{-}^{(1)} \right|_{y=y_{s}} \right\rangle \epsilon + \left\langle u_{-}^{(2)} \right\rangle \Big|_{y=0} \epsilon^{2} + \mathcal{O}(\epsilon^{3}),$ (19b)

$$-\beta \partial_{y} \langle u_{+}^{(2)} \rangle \Big|_{y=0} + (1-\beta) \langle \tau_{xy,+}^{(2)} \rangle \Big|_{y=0}$$

= $-\beta \partial_{y} \langle u_{-}^{(2)} \rangle \Big|_{y=0} + (1-\beta) \langle \tau_{xy,-}^{(2)} \rangle \Big|_{y=0}$, (19c)

which result in

$$E_{\pm} = \frac{(1+\beta \text{De}^2)}{(1+\text{De}^2)} \frac{h_{\pm}(A_{\mp} - A_{\pm})}{(h_{+} + h_{-})} + \frac{(1-\beta)\text{De}^2}{(1+\text{De}^2)} (A_{\pm}^2 - B_{\pm}^2),$$
(20a)

$$F_{\pm} = \frac{(1+\beta \text{De}^2)}{(1+\text{De}^2)} \frac{(A_{\mp} - A_{\pm})}{(h_{+} + h_{-})} + \frac{(1-\beta)\text{De}^2}{h_{\pm}(1+\text{De}^2)} \times (J_{\pm}\cosh^2(h_{\pm}) + K_{\pm}\sinh^2(h_{\pm})),$$
(20b)

where

$$\begin{split} J_{\pm} &= (1 - 2h_{\pm}B_{\pm}) + h_{\pm}^2 (A_{\pm}^2 - B_{\pm}^2), \\ K_{\pm} &= (1 + 2A_{\pm})(1 - 2h_{\pm}B_{\pm}) + (1 - h_{\pm}^2)(A_{\pm}^2 - B_{\pm}^2). \end{split}$$

Substituting the first and second order velocity fields into Eq. (10), we finally arrive at

$$U = \frac{\epsilon^{2}(1+\beta \text{De}^{2})}{(h_{+}+h_{-})(1+\text{De}^{2})} \left[h_{-} \left(A_{+} + \frac{1}{2} \right) + h_{+} \left(A_{-} + \frac{1}{2} \right) \right]$$

$$= \frac{\epsilon^{2}(1+\beta \text{De}^{2})}{2(h_{+}+h_{-})(1+\text{De}^{2})} \left[h_{-} \left(\frac{\sinh^{2}(h_{+}) + h_{+}^{2}}{\sinh^{2}(h_{+}) - h_{+}^{2}} \right) + h_{+} \left(\frac{\sinh^{2}(h_{-}) + h_{-}^{2}}{\sinh^{2}(h_{-}) - h_{-}^{2}} \right) \right].$$
(21)

In the limit of $h_+ \rightarrow hk$ and $h_- \rightarrow \infty$, we recover Eq. (4) as mentioned earlier. The main implication of this result is the observation that the effects of swimming next to a wall and swimming in an Oldroyd-B fluid decouple at small wave amplitudes. The mechanism of this decoupling is discussed in Sec. IV, but first we develop a numerical method capable of calculating the swimming speed for any value of the wave amplitude.

III. LARGE-AMPLITUDE SWIMMING: NUMERICAL METHOD

Here we develop a numerical method to solve Eq. (6) subject to the boundary conditions of Eq. (7) for an arbitrary wave, with any amplitude or shape. As in Sec. II, we in fact solve the more general problem of the sheet in a channel, with the walls above and below the sheet at a distance h_+ and h_- from the centreline, respectively. We perform the following transformation to the starred variables:

$$\begin{aligned} x^* &= k(x - (c - U)t), \ y^* &= ky, \ h_{\pm}^* &= h_{\pm}k, \\ U^* &= \frac{U}{c}, \ u^* &= 1 - U^* + \frac{u}{c}, \ v^* &= \frac{v}{c}, \\ p^* &= \frac{p}{\eta ck}, \ \tau^* &= \frac{\tau}{\eta_p ck}, \ \Sigma^* &= \frac{\Sigma}{\eta ck}, \end{aligned}$$

that render the problem dimensionless. This transformation is different from the small-amplitude transformation because in this frame of reference the shape of the sheet is exactly independent of time, as opposed to being independent of time only in the limit of small wave amplitudes. Again, we drop the *s in what follows.

To exploit the two-dimensional nature of the problem, we introduce a stream-function $\psi(x, y)$, which is defined via its relationship to the flow field $u: u = \partial_y \psi$ and $v = -\partial_x \psi$. This substitution satisfies Eq. (6b) for any choice of ψ . To reformulate Eq. (6) in terms of the stream-function, we take the curl and divergence of Eq. (6a) to obtain the complete set of governing equations given by

$$\beta \nabla^4 \psi - (1 - \beta) [\partial_{xy}(\tau_{yy} - \tau_{xx}) + \Box^2 \tau_{xy}] = 0, \qquad (22a)$$

$$\nabla^2 p - (1 - \beta) \left[\partial_{xx} \tau_{xx} + 2 \partial_{xy} \tau_{xy} + \partial_{yy} \tau_{yy} \right] = 0, \qquad (22b)$$

$$\tau_{xx} - 2\partial_{xy}\psi + \operatorname{De}\left[(\partial_{y}\psi\partial_{x} - \partial_{x}\psi\partial_{y})\tau_{xx} - 2\tau_{xx}\partial_{xy}\psi - 2\tau_{xy}\partial_{yy}\psi\right] = 0, \qquad (22c)$$

$$\tau_{xy} + \Box^2 \psi + \text{De} \left[(\partial_y \psi \partial_x - \partial_x \psi \partial_y) \tau_{xy} + \tau_{xx} \partial_{xx} \psi - \tau_{yy} \partial_{yy} \psi \right] = 0, \qquad (22d)$$

$$\tau_{yy} + 2\partial_{xy}\psi + \text{De}[(\partial_y\psi\partial_x - \partial_x\psi\partial_y)\tau_{yy} + 2\tau_{xy}\partial_{xx}\psi + 2\tau_{yy}\partial_{xy}\psi] = 0, \qquad (22e)$$

where $\Box^2 = \partial_{xx} - \partial_{yy}$, $\beta = \eta_s / (\eta_s + \eta_p)$ is the viscosity ratio and $De = \lambda ck$ is the Deborah number of the fluid. There are five differential equations, three of which are non-linear, with five fields to solve for $(\psi, p, \tau_{xx}, \tau_{xy}, \tau_{yy})$.

To solve Eq. (22) numerically, we developed a spectral method adapted for our geometry, where the two-dimensional stream-function, pressure, and polymeric stress fields are represented by Fourier-Chebyshev series.⁷⁹ Since convergence properties of the Fourier-Chebyshev basis are optimal in rectangular domains, we perform two independent coordinate transformations, one for the fluid above the sheet and the other for the fluid below, that project the corresponding domains onto rectangular strips, periodic in one direction. These transformations from the original coordinates (*x*, *y*) to the new ones (η_{\pm}, ξ_{\pm}) are given by

$$\eta_{\pm} = x, \tag{23a}$$

$$\xi_{\pm} = 1 - 2 \frac{\pm h_{\pm} - y}{\pm h_{\pm} - f(x)},$$
(23b)

where "+" and "-" denote the regions above and below the sheet, respectively. In each domain, $\xi_{\pm} = 1$ corresponds to the domain's wall, while $\xi_{\pm} = -1$ corresponds to the sheet, i.e., the lower domain has been flipped. The two domains can be treated equivalently and from now on we will drop \pm unless it is necessary. The solutions in these domains only couple to each other through the boundary conditions at the sheet.

In each deformed domain $(\eta, \xi) \in [0, 2\pi) \times [-1, 1]$, the hydrodynamic variables are represented by truncated Fourier-Chebyshev series. For example, the pressure field, *p*, is given by

$$p(\eta,\xi) = \sum_{n=0}^{N-1} \sum_{m=0}^{M-1} p^{(nm)} F_n(\eta) T_m(\xi),$$
(24)

where $T_m(\xi) = \cos(m \arccos(\xi))$ is the *m*th Chebyshev polynomial and

$$F_n(\eta) = \begin{cases} \sin(\frac{n+1}{2}\eta), & n \text{ odd} \\ \cos(\frac{n}{2}\eta), & n \text{ even,} \end{cases}$$

is the *n*th Fourier mode. We choose the resolution (N, M) such that the error on truncating the series in Eq. (24) is small; for each set of physical parameters, this is assessed by increasing the resolution (N, M) until the value of the swimming speed of the sheet does not change by more than 0.5% between the two highest resolutions. Typically, this precision is achieved by N = 33 and M = 80.

The spatial derivatives ∂_{η} and ∂_{ξ} of the Fourier-Chebyshev representations are calculated by multiplying vectors containing spectral coefficients with the *NM* × *NM* spectral derivative matrices.^{79–81} The spatial derivatives in the original (*x*, *y*)-space are then trivially constructed with the help of Eq. (23), giving for each domain,

$$\left(\frac{\partial}{\partial x}\right)_{\pm} = \frac{\partial}{\partial \eta_{\pm}} + (\xi_{\pm} - 1) \frac{f'(\eta_{\pm})}{\pm h_{\pm} - f(\eta_{\pm})} \frac{\partial}{\partial \xi_{\pm}}, \quad (25a)$$

$$\left(\frac{\partial}{\partial y}\right)_{\pm} = \frac{2}{\pm h_{\pm} - f(\eta_{\pm})} \frac{\partial}{\partial \xi_{\pm}}.$$
 (25b)

To calculate products of the fields represented in the spectral space, we use the fast Fourier transform⁸⁰ with the following collocation points:

$$\eta_{n_c} = \frac{2\pi n_c}{N_c},\tag{26a}$$

$$\xi_{m_c} = \cos\left(\frac{\pi m_c}{M_c - 1}\right),\tag{26b}$$

to evaluate the fields in the real space, calculate their product, and transform the result back to the spectral space. Here, $n_c \in [0, N_c)$, $m_c \in [0, M_c)$, and the collocation resolution (N_c, M_c) is selected to satisfy $N_c > 1.5N$ and $M_c > 1.5M$ in order to avoid aliasing issues.^{79,80}

Representing five governing equations in the truncated Fourier-Chebyshev basis for each fluid domain yields a set of 10*NM* non-linear algebraic equations that need to be complemented by the boundary conditions. By using Fourier modes, we have implicitly imposed periodic boundary conditions in the η -direction, which correctly reflects the symmetry of the underlying problem. We still need, however, six boundary conditions (four for ψ and two for p) along the lines $\xi = \pm 1$. These boundary conditions are expanded in the Fourier basis (as they are functions of η), generating 12*N* discretised boundary conditions to substitute into the original set of 10*NM* discretised governing equations.

The first boundary conditions to consider are the no-slip boundary conditions at both the sheet and the wall, Eq. (7), where the velocities of the material points of the sheet and the walls are given by⁵

$$u_s(x) = -\frac{Q}{\sqrt{1+f'(x)^2}},$$
 (27a)

$$v_s(x) = -\frac{Qf'(x)}{\sqrt{1+f'(x)^2}},$$
 (27b)

$$\boldsymbol{u}_w = (U-1)\boldsymbol{e}_x,\tag{27c}$$

and

$$Q = \int_0^{2\pi} \sqrt{1 + f'(x)^2} \, \mathrm{d}x.$$

The four boundary conditions are, therefore,

$$\partial_y \psi \Big|_{\mathcal{E}=-1} = u_s, \tag{28a}$$

$$-\partial_x \psi|_{\xi=-1} = v_s, \tag{28b}$$

$$\partial_y \psi \Big|_{\mathcal{E}=1} = U - 1, \tag{28c}$$

$$-\partial_x \psi|_{\xi=1} = 0. \tag{28d}$$

Note that the x-derivative of the n = 0 Fourier mode vanishes and that the sheet's swimming speed U, which is unknown, appears in the n = 0 mode of Eq. (28); thus different sets of boundary conditions are required for the n = 0and the $n \neq 0$ Fourier modes. We address this below. First, we consider the other two boundary conditions required for the $n \neq 0$ case.

As already mentioned earlier, we do not directly solve the force balance equation, Eq. (6a), but instead solve its derivatives [specifically its curl and divergence, see Eq. (22)]. The solutions to both problems may differ, at most, by curl-free and divergence-free terms. To fix those terms, we explicitly ensure that the force balance equation is satisfied at the boundaries. Specifically, at both the sheet and the wall, we require that $n \cdot \nabla \cdot \Sigma = 0$, where *n* is the normal to the surface. This yields the final two boundary conditions for the $n \neq 0$ Fourier modes,

$$[f'(\eta)\partial_x p - \partial_y p + \beta(f'(\eta)\partial_y - \partial_x)\nabla^2 \psi + f'(\eta)\partial_x \tau_{xx} + (f'(\eta)\partial_y + \partial_x)\tau_{xy} + \partial_y \tau_{yy}]_{\xi=-1} = 0,$$
(29a)

$$\left[\partial_{y}p + \beta \partial_{x} \nabla^{2} \psi - \partial_{x} \tau_{xy} - \partial_{y} \tau_{yy}\right]_{\xi=1} = 0, \qquad (29b)$$

where $(0, -1)^T$ is the normal to the wall and $(-f'(\eta), 1)^T$ is the normal to the surface of the sheet.

For the n = 0 mode, we replace Eqs. (28a), (28b), (28d), and (29b) with alternative boundary conditions. First of all, we note that ψ and p are defined up to a constant as only their derivatives are physical, and we set those constants to some arbitrary value. The other two boundary conditions ensure that the average x-force being applied to each of the walls is zero. And similarly to the small amplitude case, we have to couple the two domains by requiring that the swimming speed of the sheet as calculated by each domain is the same and that the sheet is a force-free swimmer. Thus, we have

$$p|_{\xi=1} = 0,$$
 (30a)

$$\psi|_{\mathcal{E}=1} = 0, \tag{30b}$$

$$[\beta \Box^2 \psi - \tau_{xy}]_{\xi=1} = 0, \qquad (30c)$$

$$[f'(\eta_{+})p_{+} - 2\beta f'(\eta_{+})\partial_{xy}\psi_{+} - \beta \Box^{2}\psi_{+} - f'(\eta_{+})\tau_{xx,+} + \tau_{xy,+}]_{\xi_{+}=-1}$$

= $[f'(\eta_{-})p_{-} - 2\beta f'(\eta_{-})\partial_{xy}\psi_{-} - \beta \Box^{2}\psi_{-} - f'(\eta_{-})\tau_{xx,-}$
+ $\tau_{xy,-}]_{\xi_{-}=-1},$ (30d)

$$\partial_y \psi_+ \Big|_{\xi_+=1} = \partial_y \psi_- \Big|_{\xi_-=1}, \qquad (30e)$$

where the absence of \pm implies that the boundary condition applies to both domains.

In the spirit of the Chebyshev-tau method,⁸⁰ for each Fourier mode, we replace the four highest Chebyshev modes of the discretised equation (22a) and the two modes of Eq. (22b) with the boundary conditions presented earlier. Combining everything together leads to the set of 10*NM* non-linear discretised equations, with the structure outlined in Table I. With the solution to this set of equations, the swimming speed of the sheet is given by

$$U = \left. \partial_y \psi \right|_{\xi=1} + 1. \tag{31}$$

To actually solve this set of non-linear equations, we use the Newton-Raphson method⁸⁰ with an analytically calculated Jacobian. In general, for De > 0, starting from an arbitrary initial guess does not lead to convergence of the Newton-Raphson algorithm, and therefore, we employ a simple continuation Phys. Fluids 29, 121612 (2017)

	n = 0	0 < n < N
$0 \le m < M - 4$	Equations (22a)-(22e)	Equations (22a)-(22e)
m = M - 4	Equations (30d)(+) (30e)(-)	Equation (28d)
	Equations (22b)-(22e)	Equations (22b)-(22e)
m = M - 3	Equation (30c)	Equation (28c)
	Equations (22b)–(22e)	Equations (22b)-(22e)
m = M - 2	Equation (30b)	Equation (28b)
	Equation (30a)	Equation (29b)
	Equations (22c)-(22e)	Equations (22c)-(22e)
m = M - 1	Equation (28a)	Equation (28a)
	Equation (29a)	Equation (29a)
	Equations (22c)-(22e)	Equations (22c)-(22e)

strategy. For each set of parameters, we start from the Newtonian case, De = 0, which is linear and can always be solved, and use its solution as the initial guess for a slightly higher De. This process is continued until we either reach the target value of De or the algorithm fails to converge, in which case a smaller step ΔDe is selected. In practice, ΔDe required for continuation becomes very small at sufficiently large De, leading to unreasonable computation times in which case we only report the results up to that value of De.

We verify that our numerical method correctly reproduces the small-amplitude prediction equation (4). In Fig. 2, we plot the swimming speed for a sheet with bk = 0.01 as a function of the Deborah number De for various distances to the wall and viscosity ratios. As expected, for this amplitude, the numerically computed swimming speeds (symbols) agree well with the analytical prediction of Eq. (4) (solid line), again demonstrating that the effects of swimming next to a wall decouple



FIG. 2. The swimming speed U of a small-amplitude (bk = 0.01) Taylor sheet swimming next to a wall as the function of the Deborah number De for various values of the solvent viscosity ratio β and the distance from the wall h. The swimming speeds are normalised by the swimming speed, U_N , of the same geometric situation in a Newtonian fluid of the same viscosity. The symbols are the results of our numerical calculations, while the solid black lines are the small amplitude predictions from Eq. (4).



from the effects of swimming in a viscoelastic fluid at small amplitudes.

The situation changes significantly for finite values of the wave amplitude. In Fig. 3, we plot the swimming speed for a sheet with bk = 0.5 as a function of the Deborah number De for various distances to the wall and viscosity ratios. We observe that the numerical data now deviate significantly from the small-amplitude prediction equation (4). Despite this deviation, for most values of h and β , the swimming speed follows the same trend as predicted by Eq. (4): starting from its Newtonian value, it decreases monotonically with De and reaches a plateau value at large Deborah numbers. However, for sufficiently small h (hk = 1.05, 1.1) at $\beta = 0.5$ and $\beta = 0.9$, the swimming speed breaks this trend and exhibits a non-monotonic dependence on De. This effect seems to be the stronger for larger values of β , which corresponds to more dilute solutions, reaching speeds faster than the Newtonian case for $\beta = 0.9$. Also, there are indications that at lower values of β the swimming speed starts to increase with De at sufficiently large values of the Deborah number. These results are further discussed in Sec. IV.

IV. DISCUSSION

As we have demonstrated earlier, at small wave amplitudes, the influence of the polymeric stress on the swimming speed is the same for both swimming in the bulk and next to a wall. In other words, the effects of the boundary and polymers decouple and the swimming speed is given by the product of the corresponding contributions, see Eq. (4). Let us discuss the mechanism of this behavior.

We start by considering the kinematics of a Taylor sheet swimming in the bulk of a Newtonian fluid. As noted by Taylor⁵ and Lauga and Powers,¹ at small wave amplitudes, every point of the sheet is oscillating approximately up and down, generating locally a vertical motion of the surrounding fluid. Along one period of the sheet's waveform, for every point moving up, there is another point moving down with the same speed. Since the fluid is incompressible, this sets an array of counter-rotating vortices along the sheet, two vortices per period, see Fig. 4. We will be referring to them as the "sheet vortices." As can be seen from Fig. 4, the presence of these vortices implies a velocity component along the surface of the sheet, which on average drags the sheet along the horizontal direction. FIG. 3. The swimming speed U of a finite-amplitude (bk = 0.5) Taylor sheet swimming next to a wall as the function of the Deborah number De for various values of the solvent viscosity ratio β and the distance from the wall h. The swimming speeds are normalised by the swimming speed, U_N , of the same geometric situation in a Newtonian fluid of the same viscosity. The symbols are the results of our numerical calculations, while the solid black lines are the small amplitude predictions from Eq. (4).

When this configuration of sheet vortices is placed next to a solid boundary, as shown in Fig. 4, it generates a non-zero velocity at the boundary which obviously does not satisfy the no-slip boundary condition at this boundary. This velocity is canceled by the creation of an array of vortices localised at the boundary with the same periodicity as the sheet vortices. Along the boundary, the velocity of these "wall vortices" has the same magnitude but opposing direction of the velocity of the sheet vortices. And thus, the no-slip boundary condition is satisfied for the total velocity field. In turn, the wall vortices have a contribution along the surface of the sheet that effectively increases the speed of the sheet vortices, which in turn causes the sheet to speed up. Effectively, this implies that a small-amplitude sheet swimming next to a wall can be viewed as a free-swimming sheet with faster sheet vortices.

This argument is further corroborated by rearranging the first order velocity field equation (14) in the following form, with dimensional quantities:

$$u^{(1)} = \frac{c}{2}((A+B)ky - A - 1)\sin(k(x-ct))\exp(-ky) + \frac{c}{2}((A-B)ky + A + 1)\sin(k(x-ct))\exp(ky), v^{(1)} = \frac{c}{2}((A+B)ky + B - 1)\cos(k(x-ct))\exp(-ky) + \frac{c}{2}((B-A)ky - B - 1)\cos(k(x-ct))\exp(ky),$$

where we have dropped \pm , as the fluid domains are equivalent and the distinction between them is unimportant. In the upper domain, the terms proportional to $\exp(-ky)$ and $\exp(ky)$ correspond to the sets of vortices which are localised at the sheet



FIG. 4. Gedankenexperiment demonstrating the sheet vortices (blue isolines) generated by the small-amplitude vertical motion of the material points of the sheet and the velocity field it generates at an imaginary surface, as the wave travels to the right. Note that this velocity field does not satisfy the no-slip boundary conditions. The surface velocity is canceled by the wall vortices (green isolines), as discussed in the text.

and at the wall, respectively. The centres of these vortices are located along the lines $ky = \omega_s$ and $ky = \omega_w$, where

$$\omega_s = \frac{A+1}{A+B} = \frac{2\sinh^2(hk) - h^2k^2}{hk + \sinh(hk)\cosh(hk) + \sinh^2(hk)},$$
$$\omega_w = \frac{A+1}{B-A} = \frac{2\sinh^2(hk) - h^2k^2}{hk + \sinh(hk)\cosh(hk) - \sinh^2(hk)}.$$

For hk > 1, $\omega_s \ll hk$ and $\omega_w \approx hk$, thus justifying the sheet and wall label of the arrays of vortices. Note that the vertical location of the sheet vortices is moved from its bulk location, ky = 0, to the line $ky = \omega_s \ll hk$.

Now we turn to the effect that the viscoelasticity of the fluid has on the swimming speed. We have recently studied the mechanism of the polymer-induced slowing down of a Taylor sheet in the bulk⁸² that we briefly summarise here. As we have seen in Sec. II, the first order velocity field is the same for a Newtonian and Oldroyd-B fluids, and we start by considering its effect on the polymeric stresses. While this vortical velocity field is locally a simple shear flow in most parts of the domain, the regions in-between the vortices correspond to locally extensional flows around stagnation points, similar to the ones observed in PIV (Particle Image Velocimetry) measurements by Shen and Arratia.⁶⁷ These extensional flows generate large normal components of the polymer stresses, τ_{xx} and τ_{yy} , that are advected downstream by the fluid flow and, in turn, generate significant shear stresses in the fluid that drive the sheet horizontally, in the direction of the wave propagation.⁸² Since the Taylor sheet swims in the direction opposite to the direction of its wave propagation, this results in slowing down of the sheet compared to a Newtonian fluid. See also Ref. 48 for a discussion of the interaction between the multiple waves propagating in the opposite directions and viscoelasticity.

Next to a boundary, the same mechanism applies at small wave amplitudes since, as we have argued above, a Newtonian sheet swimming next to a wall is equivalent to a free-swimming sheet with faster sheet vortices and, hence, with a larger swimming speed given by Eq. (2). This "effective" free-swimming sheet would experience the same slowing down as discussed earlier and would swim with the speed set by Eq. (3), where the Newtonian swimming speed $cb^2k^2/2$ should be replaced with

Eq. (2), arriving finally at Eq. (4). This is the fundamental reason behind the factorisation of the effects of viscoelasticity and the boundary.

Now we turn to the case of finite-amplitude swimming. As shown in Fig. 3, at bk = 0.5, the swimming speed deviates significantly from the small amplitude prediction of Eq. (4). Although, in the majority of cases the trend of the velocity decreasing with the Deborah number persists, the high-De value of the swimming speed U_{∞} is larger than the asymptotic prediction of Eq. (4), $U_{\infty} > \beta U_N$, and increases as the boundary is brought closer to the swimmer. Moreover, in some cases, the swimming speed no longer decreases monotonically and can even increase to swimming speeds greater than the Newtonian value.

To understand this behavior, we analyze the spatial distribution of the elastic stresses in the fluid. Additionally, we plot the flow type parameter χ defined as $\chi = \frac{|\mathbf{D}| - |\Omega|}{|\mathbf{D}| + |\Omega|}$.⁸³ Based on the invariants of the velocity gradient tensor, it is designed to determine the velocity type at every point in space, independent of its local orientation: $\chi = 1$ corresponds to purely extensional, $\chi = 0$ corresponds to shear, and $\chi = -1$ corresponds to purely rotation flows. Note that the flow type parameter does not measure the magnitude of the flow, only its topology.

First, we consider the case of a moderate viscosity ratio and distance to the wall, $\beta = 0.5$ and $h_+k = 1.2$. In Fig. 5, we plot the shear stress τ_{xy} , the difference between normal stresses $\tau_{xx} - \tau_{yy}$, and the flow type parameter for the Newtonian case De = 0 and two values of the Deborah number, De = 0.5 and 3.2, corresponding to the monotonic decrease of the swimming speed from its Newtonian value. The plots are superimposed with the isolines of the stream-function ψ (black lines) and the local direction of the velocity field (black arrows). Note that we plot the total velocity field but will discuss it as consisting of the sheet and wall vortices, when useful.

In line with the small-amplitude mechanism discussed earlier, we observe formation of lines of strong extensional flows that generates large normal stresses $\tau_{xx} - \tau_{yy}$, which are advected by the local flow. The main difference between this case and the small-amplitude one is the fact that the normal stresses generated in-between the wall vortices are now advected by the vortices toward the sheet and also contribute to the shear stress τ_{xy} that generates an additional average flow



FIG. 5. The polymeric stress, τ , surrounding a sheet with amplitude bk = 0.5 near a wall at a distance $h_{+}k = 1.2$ above it in an Oldroyd-B fluid with $\beta = 0.5$ and De = 0.0 (left), De = 0.5 (middle), and De = 3.2 (right). The wall below the sheet is at $h_{-}k = 13.0$ which is far enough away to have no effect; however, the fluid domain is only shown until ky = -5.0. The swimming speed of the sheet in each situation is $U = U_N = 0.362c$ (left), $U = 0.959U_N$ (middle), $U = 0.854U_N$ (right).



FIG. 6. The polymeric stress, τ , surrounding a sheet with amplitude bk = 0.01 near a wall at a distance $h_+k = 0.11$ above it in an Oldroyd-B fluid with $\beta = 0.5$ and De = 0.0 (left), De = 0.5 (middle), and De = 3.2 (right). The wall below the sheet is at $h_-k = 13.0$ which is far enough away to have no effect; however, the fluid domain is only shown until ky = -0.5. The swimming speed of the sheet in each situation is $U = U_N = 0.0242c$ (left), $U = 0.905U_N$ (middle), $U = 0.559U_N$ (right).

FIG. 7. Comparison between the stress distributions around a sheet with the amplitude bk = 0.5 at a distance $h_+k = 1.05$ from the upper wall with De = 2.7: $\beta = 0.5$ (left) and $\beta = 0.9$ (right). The wall below the sheet is at $h_-k = 13.0$ which is far enough away to have no effect; however, the fluid domain is only shown until ky = -5.0. The swimming speed in each case is $U = 0.992U_N$ (left) and $U = 1.020U_N$ (right) with $U_N = 0.440c$.

that, in turn, drags the sheet in the direction of the wave. At small Deborah number, De = 0.5, the negative value (blue) of the normal stresses $\tau_{xx} - \tau_{yy}$ is rotated into extra positive (red) τ_{xy} , which is responsible for the slow down of the sheet relative to swimming in a Newtonian fluid. This only happens in the vortices in the troughs of the sheet, where the vortices are not restricted too much by the presence of the wall. At a larger Deborah number, De = 3.2, in addition to a region with extra positive τ_{xy} , there is a region with extra negative τ_{xy} which pushes the sheet in the direction of its swimming, in competition with the positive region. The growth of this region of negative polymeric shear stress is absent from the small amplitude solution (shown in Fig. 6) and is responsible for the increased swimming speed compared to the small amplitude prediction equation (4).

Now we turn to the case of non-monotonic behavior of the swimming speed with the Deborah number. In Fig. 7, we compare the stress distributions for $\beta = 0.5$ and $\beta = 0.9$ for hk = 1.05and De = 2.7. For β = 0.5, these values approximately correspond to the local maximum of the swimming speed, although its value is still smaller than the Newtonian one, while at these parameters the case with $\beta = 0.9$ exhibits swimming speeds larger than U_N , see Fig. 3. First, we note that now both the trough and crest vortices are equally close to the wall, somewhat in contrast to Fig. 5. This behavior is also observed in the Newtonian case De = 0, not shown. However, in Fig. 7, there are no significant differences between the stress distributions for $\beta = 0.5$ and $\beta = 0.9$ cases besides the numerical values of the stresses, and we conclude that whether the swimming speed is larger or smaller than its Newtonian counterpart is determined by a numerical competition between the wall and sheet stresses that cannot be deduced from hand-waving arguments.

In conclusion, we have provided a mechanistic explanation for the small-wave-amplitude swimming speed of a Taylor sheet derived by Elfring and Lauga⁷⁶ and explain why the effects of fluid's viscoelasticity and the presence of a solid boundary decouple. We also developed a numerical method with spectral accuracy that allows us to study finite-amplitude sheets of various waveforms close to and away from solid walls. We observe that at finite amplitudes the swimming speed is no longer a monotonic function of the Deborah number and can even become larger than the corresponding Newtonian value. Interestingly, this effect seems to be the stronger, the more dilute the viscoelastic solution is (large values of β), although there are indications that at lower values of β the swimming speed starts to increase with De at sufficiently large values of the Deborah number. This result suggests that even small amounts of polymer, either excreted or naturally present in the solution, can aid propulsion next to solid boundaries, although the speed increase reported in this work is minute. Our numerical data are not sufficient to determine whether this increase would eventually lead to swimming speeds larger than the Newtonian values for all values of β , at what values of De this can be achieved, and how significant this speed up might be. Further study is required to address these questions.

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¹E. Lauga and T. R. Powers, "The hydrodynamics of swimming microorganisms," Rep. Prog. Phys. **72**(9), 096601 (2009).

²E. M. Purcell, "Life at low Reynolds number," Am. J. Phys. **45**(1), 3–11 (1977).

- ³C. Brennen and H. Winet, "Fluid mechanics of propulsion by cilia and flagella," Annu. Rev. Fluid Mech. **9**(1), 339–398 (1977).
- ⁴J. S. Guasto, R. Rusconi, and R. Stocker, "Fluid mechanics of planktonic microorganisms," Annu. Rev. Fluid Mech. **44**(1), 373–400 (2012).
- ⁵G. Taylor, "Analysis of the swimming of microscopic organisms," Proc. R. Soc. A 209(1099), 447–461 (1951).
- ⁶D. F. Katz, "On the propulsion of micro-organisms near solid boundaries," J. Fluid Mech. **64**(01), 33 (1974).
- ⁷L. Li and S. E. Spagnolie, "Swimming and pumping of rigid helical bodies in viscous fluids," Phys. Fluids **26**(4), 041901 (2014).
- ⁸F. Alouges, A. DeSimone, and A. Lefebvre, "Optimal strokes for low Reynolds number swimmers: An example," J. Nonlinear Sci. **18**(3), 277–302 (2008).
- ⁹J. R. Blake, "A spherical envelope approach to ciliary propulsion," J. Fluid Mech. 46(1), 199–208 (1971).
- ¹⁰R. S. Berman, O. Kenneth, J. Sznitman, and A. M. Leshansky, "Undulatory locomotion of finite filaments: Lessons from Caenorhabditis elegans," New J. Phys. **15**(7), 075022 (2013).
- ¹¹J. E. Drummond, "Propulsion by oscillating sheets and tubes in a viscous fluid," J. Fluid Mech. **25**(04), 787 (1966).
- ¹²J. Gray and G. J. Hancock, "The propulsion of sea-urchin spermatozoa," J. Exp. Biol. **32**(4), 802–814 (1955).
- ¹³G. J. Hancock, "The self-propulsion of microscopic organisms through liquids," Proc. R. Soc. A **217**(1128), 96–121 (1953).
- ¹⁴T. D. Montenegro-Johnson and E. Lauga, "Optimal swimming of a sheet," Phys. Rev. E 89(6), 060701 (2014).
- ¹⁵O. S. Pak and E. Lauga, "The transient swimming of a waving sheet," Proc. R. Soc. A **446**(2113), 107–126 (2010).
- ¹⁶O. Pironneau and D. F. Katz, "Optimal swimming of flagellated microorganisms," J. Fluid Mech. **66**(02), 391 (1974).
- ¹⁷E. M. Purcell, "The efficiency of propulsion by a rotating flagellum," Proc. Natl. Acad. Sci. U. S. A. **94**(21), 11307–11311 (1997).
- ¹⁸A. J. Reynolds, "The swimming of minute organisms," J. Fluid Mech. 23(2), 241–260 (1965).
- ¹⁹E. O. Tuck, "A note on a swimming problem," J. Fluid Mech. **31**(02), 305 (1968).
- ²⁰M. Sauzade, G. J. Elfring, and E. Lauga, "Taylor's swimming sheet: Analysis and improvement of the perturbation series," Phys. D 240(20), 1567–1573 (2011).
- ²¹J. Sznitman, X. Shen, P. K. Purohit, and P. E. Arratia, "The effects of fluid viscosity on the kinematics and material properties of *C. elegans* swimming at low Reynolds number," Exp. Mech. **50**(9), 1303–1311 (2010).
- ²²D. Tam and A. Hosoi, "Optimal stroke patterns for Purcell's three-link swimmer," Phys. Rev. Lett. **98**(6), 068105 (2007).
- ²³O. Wiezel and Y. Or, "Optimization and small-amplitude analysis of Purcell's three-link microswimmer model," Proc. R. Soc. A 472(2192), 20160425 (2016).
- ²⁴G. Taylor, "The action of waving cylindrical tails in propelling microscopic organisms," Proc. R. Soc. A **211**(1105), 225–239 (1952).
- ²⁵G. J. Elfring, "A note on the reciprocal theorem for the swimming of simple bodies," Phys. Fluids 27(2), 023101 (2015).
- ²⁶M. A. Jalali, M.-R. Alam, and S. H. Mousavi, "Versatile low-Reynoldsnumber swimmer with three-dimensional maneuverability," Phys. Rev. E 90(5), 053006 (2014).
- ²⁷M. J. Lighthill, "On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers," Commun. Pure Appl. Math. 5(2), 109–118 (1952).
- ²⁸A. P. Berke, L. Turner, H. C. Berg, and E. Lauga, "Hydrodynamic attraction of swimming microorganisms by surfaces," Phys. Rev. Lett. **101**(3), 038102 (2008).
- ²⁹D. F. Katz, J. R. Blake, and S. L. Paveri-Fontana, "On the movement of slender bodies near plane boundaries at low Reynolds number," J. Fluid Mech. **72**(03), 529 (1975).
- ³⁰F. Lebois, P. Sauvage, C. Py, O. Cardoso, B. Ladoux, P. Hersen, and J.-M. D. Meglio, "Locomotion control of *Caenorhabditis elegans* through confinement," Biophys. J. **102**(12), 2791–2798 (2012).
- ³¹D. Lopez and E. Lauga, "Dynamics of swimming bacteria at complex interfaces," Phys. Fluids 26(7), 071902 (2014).

- ³²T. D. Montenegro-Johnson, H. Gadelha, and D. J. Smith, "Spermatozoa scattering by a microchannel feature: An elastohydrodynamic model," R. Soc. Open Sci. 2(3), 140475 (2015).
- ³³R. D. Schulman, M. Backholm, W. S. Ryu, and K. Dalnoki-Veress, "Undulatory microswimming near solid boundaries," Phys. Fluids 26(10), 101902 (2014).
- ³⁴R. Trouilloud, T. Yu, A. Hosoi, and E. Lauga, "Soft swimming: Exploiting deformable interfaces for low Reynolds number locomotion," Phys. Rev. Lett. **101**(4), 048102 (2008).
- ³⁵D. Crowdy, S. Lee, O. Samson, R. Lauga, and A. E. Hosoi, "A twodimensional model of low-Reynolds number swimming beneath a free surface," J. Fluid Mech. 681(2), 24–47 (2011).
- ³⁶E. Lauga, "Propulsion in a viscoelastic fluid," Phys. Fluids **19**(8), 083104 (2007).
- ³⁷M. De Corato, F. Greco, and P. L. Maffettone, "Locomotion of a microorganism in weakly viscoelastic liquids," Phys. Rev. E **92**(5), 053008 (2015).
- ³⁸M. De Corato, F. Greco, and P. L. Maffettone, "Reply to 'Comment on "Locomotion of a microorganism in weakly viscoelastic liquids"," Phys. Rev. E 94(5), 057102 (2016).
- ³⁹J. Espinosa-Garcia, E. Lauga, and R. Zenit, "Fluid elasticity increases the locomotion of flexible swimmers," Phys. Fluids **25**(3), 031701 (2013).
- ⁴⁰H. C. Fu, T. R. Powers, and C. W. Wolgemuth, "Theory of swimming filaments in viscoelastic media," Phys. Rev. Lett. **99**(25), 258101 (2007).
- ⁴¹ H. C. Fu, C. W. Wolgemuth, and T. R. Powers, "Beating patterns of filaments in viscoelastic fluids," Phys. Rev. E 78(4), 041913 (2008).
- ⁴²H. C. Fu, C. W. Wolgemuth, and T. R. Powers, "Swimming speeds of filaments in nonlinearly viscoelastic fluids," Phys. Fluids **21**(3), 033102 (2009).
- ⁴³E. Lauga, "Floppy swimming: Viscous locomotion of actuated elastica," Phys. Rev. E **75**(4), 041916 (2007).
- ⁴⁴E. Lauga, "Life at high Deborah number," EPL **86**(6), 64001 (2009).
- ⁴⁵E. Lauga, "The bearable gooeyness of swimming," J. Fluid Mech. **762**, 1–4 (2014).
- ⁴⁶E. Lauga, "Locomotion in complex fluids: Integral theorems," Phys. Fluids 26(8), 081902 (2014).
- ⁴⁷E. E. Riley and E. Lauga, "Empirical resistive-force theory for slender biological filaments in shear-thinning fluids," Phys. Rev. E **95**(6), 062416 (2017).
- ⁴⁸E. E. Riley and E. Lauga, "Small-amplitude swimmers can self-propel faster in viscoelastic fluids," J. Theor. Biol. **382**, 345–355 (2015).
- ⁴⁹E. E. Riley and E. Lauga, "Enhanced active swimming in viscoelastic fluids," EPL **108**(3), 34003 (2014).
- ⁵⁰D. Salazar, A. M. Roma, and H. D. Ceniceros, "Numerical study of an inextensible, finite swimmer in Stokesian viscoelastic flow," Phys. Fluids 28(6), 063101 (2016).
- ⁵¹J. Teran, L. Fauci, and M. Shelley, "Viscoelastic fluid response can increase the speed and efficiency of a free swimmer," Phys. Rev. Lett. **104**(3), 038101 (2010).
- ⁵²B. Thomases and R. D. Guy, "Mechanisms of elastic enhancement and hindrance for finite-length undulatory swimmers in viscoelastic fluids," Phys. Rev. Lett. **113**(9), 27 (2014).
- ⁵³J. Rodrigo Vélez-Cordero and E. Lauga, "Waving transport and propulsion in a generalized Newtonian fluid," J. Non-Newtonian Fluid Mech. **199**, 37–50 (2013).
- ⁵⁴G. Li and A. M. Ardekani, "Undulatory swimming in non-Newtonian fluids," J. Fluid Mech. **784**, R4 (2015).
- ⁵⁵J. Du, J. P. Keener, R. D. Guy, and A. L. Fogelson, "Low-Reynolds-number swimming in viscous two-phase fluids," Phys. Rev. E 85(3), 036304 (2012).
- ⁵⁶A. M. Leshansky, "Enhanced low-Reynolds-number propulsion in heterogeneous viscous environments," Phys. Rev. E 80(5), 051911 (2009).
- ⁵⁷Y. Man and E. Lauga, "Phase-separation models for swimming enhancement in complex fluids," Phys. Rev. E 92(2), 023004 (2015).
- ⁵⁸T. D. Montenegro-Johnson, D. J. Smith, and D. Loghin, "Physics of rheologically enhanced propulsion: Different strokes in generalized Stokes," Phys. Fluids **25**(8), 081903 (2013).
- ⁵⁹J. P. Celli, B. S. Turner, N. H. Afdhal, S. Keates, I. Ghiran, C. P. Kelly, R. H. Ewoldt, G. H. McKinley, P. So, S. Erramilli, and R. Bansil, "*Helicobacter pylori* moves through mucus by reducing mucin viscoelasticity," Proc. Natl. Acad. Sci. U. S. A. **106**(34), 14321–14326 (2009).
- ⁶⁰M. Dasgupta, B. Liu, H. C. Fu, M. Berhanu, K. S. Breuer, T. R. Powers, and A. Kudrolli, "Speed of a swimming sheet in Newtonian and viscoelastic fluids," Phys. Rev. E 87(1), 013015 (2013).

- ⁶¹D. A. Gagnon, N. C. Keim, and P. E. Arratia, "Undulatory swimming in shear-thinning fluids: Experiments with *Caenorhabditis elegans*," J. Fluid Mech. **758**, R3 (2014).
- ⁶²D. A. Gagnon and P. E. Arratia, "The cost of swimming in generalized Newtonian fluids: Experiments with *C. elegans*," J. Fluid Mech. **800**, 753–765 (2016).
- ⁶³S. Ishijima, S. Oshio, and H. Mohri, "Flagellar movement of human spermatozoa," Gamete Res. **13**(3), 185–197 (1986).
- ⁶⁴ V. A. Martinez, J. Schwarz-Linek, M. Reufer, L. G. Wilson, A. N. Morozov, W. C. K. Poon, and T. C. Lubensky, "Flagellated bacterial motility in polymer solutions," Proc. Natl. Acad. Sci. U. S. A. **111**(50), 17771–17776 (2014).
- ⁶⁵N. C. Keim, M. Garcia, and P. E. Arratia, "Fluid elasticity can enable propulsion at low Reynolds number," Phys. Fluids 24(8), 081703 (2012).
- ⁶⁶B. Liu, T. R. Powers, and K. S. Breuer, "Force-free swimming of a model helical flagellum in viscoelastic fluids," Proc. Natl. Acad. Sci. U. S. A. 108(49), 19516–19520 (2011).
- ⁶⁷X. N. Shen and P. E. Arratia, "Undulatory swimming in viscoelastic fluids," Phys. Rev. Lett. **106**(20), 208101 (2011).
- ⁶⁸S. Yazdi, A. M. Ardekani, and A. Borhan, "Locomotion of microorganisms near a no-slip boundary in a viscoelastic fluid," Phys. Rev. E **90**(4), 043002 (2014).
- ⁶⁹S. Yazdi, A. M. Ardekani, and A. Borhan, "Swimming dynamics near a wall in a weakly elastic fluid," J. Nonlinear Sci. 25(5), 1153–1167 (2015).
- ⁷⁰G. J. Li, A. Karimi, and A. M. Ardekani, "Effect of solid boundaries on swimming dynamics of microorganisms in a viscoelastic fluid," Rheol. Acta 53(12), 911–926 (2014).
- ⁷¹G. Li and A. M. Ardekani, "Near wall motion of undulatory swimmers in non-Newtonian fluids," Eur. J. Comput. Mech. **26**(1–2, SI), 44–60 (2017).

- ⁷²R. Bansil, "Mucin biophysics," Annu. Rev. Physiol. **57**(1), 635–657 (1995).
- ⁷³E. A. Gaffney, H. Gadelha, D. J. Smith, J. R. Blake, and J. C. Kirkman-Brown, "Mammalian sperm motility: Observation and theory," Annu. Rev. Fluid Mech. 43(1), 501–528 (2011).
- ⁷⁴J. C. Kirkman-Brown and D. J. Smith, "Sperm motility: Is viscosity fundamental to progress?," Mol. Hum. Reprod. 17(8), 539–544 (2011).
- ⁷⁵A. Houry, M. Gohar, J. Deschamps, E. Tischenko, S. Aymerich, A. Gruss, and R. Briandet, "Bacterial swimmers that infiltrate and take over the biofilm matrix," Proc. Natl. Acad. Sci. U. S. A. **109**(32), 13088–13093 (2012).
- ⁷⁶G. J. Elfring and E. Lauga, "Theory of locomotion through complex fluids," in *Complex Fluids in Biological Systems*, Biological and Medical Physics, Biomedical Engineering, edited by S. E. Spagnolie (Springer New York, New York, NY, 2015), pp. 283–317.
- ⁷⁷R. B. Bird and O. Hassager, "Dynamics of polymeric liquids: Fluid mechanics," in *Dynamics of Polymeric Liquids* (Wiley, 1987).
- ⁷⁸A. N. Morozov and S. E. Spagnolie "Introduction to complex fluids," in *Complex Fluids in Biological Systems*, Biological and Medical Physics, Biomedical Engineering, edited by S. E. Spagnolie (Springer New York, New York, NY, 2015), pp. 3–52.
- ⁷⁹J. P. Boyd, *Chebyshev and Fourier Spectral Methods*, 2nd ed., Dover books on Mathematics (Dover Publications, 2013).
- ⁸⁰C. Canuto, M. Y. Hussaini, A. Quarteroni, and T. A. Zang, *Spectral Methods in Fluid Dynamics* (Springer-Verlag, 1987).
- ⁸¹S. A. Orszag, "Accurate solution of the Orr–Sommerfeld stability equation,"
 J. Fluid Mech. 50(04), 689 (1971).
- ⁸²T. R. Ives and A. Morozov, "Swimming of wavy sheet's in Oldroyd-B fluids" (unpublished).
- ⁸³J. S. Lee, R. Dylla-Spears, N. P. Teclemariam, and S. J. Muller, "Microfluidic four-roll mill for all flow types," Appl. Phys. Lett. **90**(7), 074103 (2007).