Swimming in an anisotropic fluid: How speed depends on alignment angle

Juan Shi and Thomas R. Powers

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Swimming in an anisotropic fluid: how speed depends on alignment angle

Juan Shi[1] and Thomas R. Powers[1,2]

[1] *School of Engineering, Brown University, Providence, RI 02912 USA and*

[2] *Department of Physics, Brown University, Providence, RI 02012 USA*

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Abstract

Orientational order in a fluid affects the swimming behavior of flagellated microorganisms. For example, bacteria tend to swim along the director in lyotropic nematic liquid crystals. To better understand how anisotropy affects propulsion, we study the problem of a sheet supporting small-amplitude traveling waves, also known as the Taylor swimmer, in a nematic liquid crystal. For the case of weak anchoring of the nematic director at the swimmer surface, and in the limit of a minimally anisotropic model, we calculate the swimming speed as a function of the angle between the swimmer and the nematic director. The effect of the anisotropy can be to increase or decrease the swimming speed, depending on the angle of alignment. We also show that elastic torque dominates the viscous torque for small-amplitude waves, and that the torque tends to align the swimmer along the local director.

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I. INTRODUCTION

Propulsion mechanisms depend strongly on the nature of the ambient fluid. For swimming microorganisms, a key property of water on the micron scale is that viscous effects dominate inertial effects: water is very viscous for the length and time scales characteristic of a swimming cell [1–3]. But it is also common for swimming microorganisms to be found in complex fluids such as polymer solutions and gels. These fluids have additional distinctive features. For example, the effects of the elasticity of the polymers or the shear-thinning of the viscosity on swimming speed in these fluids have been the subject of several theoretical and experimental investigations (see e.g. [4–11]). Recently, attention has turned toward bacteria in anisotropic fluids, such as biofilms [12], where rod-like swimming bacteria tend to orient with the long axis parallel with aligned polymers [13]. Bacteria also align in artificial environments, such as the chromonic liquid crystal DSCG [14–16]. Bacteria in DSCG tend to swim along the local director, even when the director pattern is nonuniform [16], and they are attracted to or repelled by the cores of topological defects, depending on the sign of the defect [17]. These observations suggest that an anisotropic medium can be used to guide natural and artificial swimmers alike [18]. In this article we study how swimming speed depends on the angle between a swimmer and the director in a nematic liquid crystal. The model we use is the Taylor swimmer [1], which is a sheet which deforms via internally-generated low-amplitude plane waves of fixed frequency and wavelength (Fig. 1). We consider the two-dimensional case, in which there is no change in the sheet deformation, flow field, or liquid crystal configuration in the direction perpendicular to the xy plane. Our work is a generalization of the problems treated in reference [19] and [20], where one of us studied the Taylor swimmer aligned along one of the sixfold axes in a hexatic liquid crystal, and along the director in a nematic liquid crystal. Our work is also related to the work of reference [21], which was a study of the propulsion of the Taylor swimmer in both passive and active transversely isotropic materials. The passive case of the transversely isotropic fluid is the same as our model when our elastic terms and anchoring effects are set to zero. Although the limiting value of our swimming speed when the elastic and anchoring constants are taken to be small agrees with the swimming speed of reference [21] in their passive case, we also find that this limit is singular. We show that when the full time-dependences of the flow field and the nematic director field are calculated to second order in swimmer deflection,

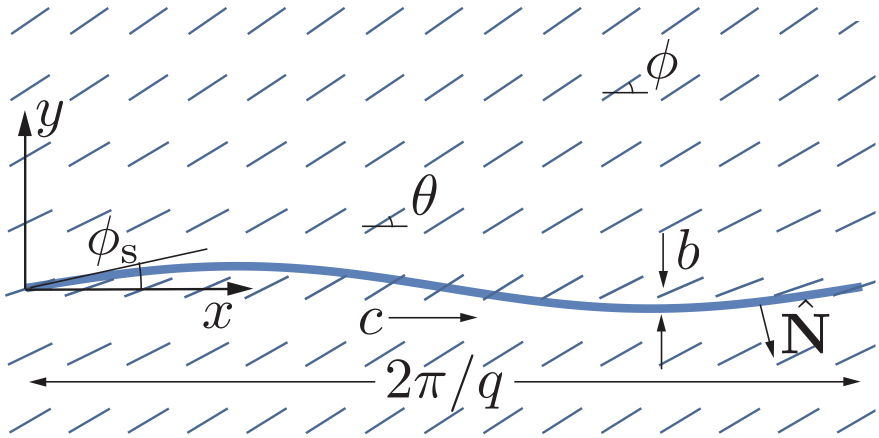

FIG. 1. (Color online). Taylor swimmer with wavevector q, amplitude b, and wavespeed c in a two-dimensional liquid crystal. The local tangent vector of the swimmer makes an angle ϕ_s with the x axis, and $\hat{\mathbf{N}}$ is the outward pointing normal for the region on the side of the swimmer with $y > 0$. The director $\mathbf{n}$ makes an angle θ with the x-axis, and the director has a fixed angle ϕ for large $|y|$.

the transversely isotropic theory has a secular term arising because the aligning effects of the liquid crystal Frank elasticity are absent.

II. TAYLOR SWIMMER IN A NEMATIC LIQUID

Figure 1 shows the Taylor swimmer in a two-dimensional nematic liquid crystal. The swimmer is an idealized model of planar flagellar beating, and it consists of an infinite flexible sheet with an internally generated transverse wave of amplitude b and wavenumber q, described by $y_s = b\sin(qx - \omega t)$. Here $\omega = cq$ is the frequency, and c is the wave speed. The amplitude is taken to be small relative to the wavelength, $bq \ll 1$, and following Taylor we calculate the leading order swimming speed in an expansion in bq [1]. We work in the reference frame of the swimmer, and take the swimmer to be aligned with the x-axis.

Experiments on swimming bacteria often employ a thin layer of nematic liquid crystal sandwiched between two glass plates [17], each parallel to the xy-plane of our Fig. 1, and with the plates treated to prefer anchoring of the director $\mathbf{n} = \hat{\mathbf{x}}\cos\theta + \hat{\mathbf{y}}\sin\theta$ along a certain direction $\mathbf{p} = \hat{\mathbf{x}}\cos\phi + \hat{\mathbf{y}}\sin\phi$. We suppose uniform treatment of the plates so that the angle ϕ is constant. At the the surface of the swimmer, there is also an anchoring potential which we take to give a preference for the directors to align parallel to the swimmer body. Far from the swimmer, the effects of the swimmer anchoring potential die off and $\theta \to \phi$. We model the alignment due to the anchoring potential at the plates by an effective external field. The elastic energy cost is thus

$$F_{\mathrm{el}}/d = \int \mathrm{d}x\mathrm{d}y\mathcal{F} - \frac{W}{4}\int \mathrm{d}s \cos\left[2(\theta - \phi_{\mathrm{s}})\right], \tag{1}$$

where d is the spacing between the plates. In Eq. (1), the elastic energy density is given by

$$\mathcal{F} = \frac{K}{2}\partial_\alpha \mathbf{n} \cdot \partial_\alpha \mathbf{n} - \frac{\xi}{2}(\mathbf{p} \cdot \mathbf{n})^2, \tag{2}$$

where K is the Frank elastic modulus in the commonly used one-coupling constant approximation [22], ξ is the effective aligning field due to the treatment of the glass plates, W is the anchoring strength at the swimmer, s is arclength along the swimmer, and ϕ_{s} is the angle the local swimmer tangent vector makes with the x axis. The competition between Frank elasticity and the aligning effect leads to a characteristic length $\ell_\xi \equiv \sqrt{K/\xi}$ for the decay of the director field from the value preferred by the anchoring potential near the swimmer to the value far preferred by the aligning term.

The elastic torques that arise when the director field is not uniform or not aligned with the direction preferred by the treated plates may be calculated from the free energy using the molecular field $\mathbf{H} = -\delta F_{\mathrm{el}}/\delta \mathbf{n}$ [23]:

$$\mathbf{H} = K\Delta\mathbf{n} + \xi\mathbf{p}\left(\mathbf{p} \cdot \mathbf{n}\right), \tag{3}$$

where Δ denotes the Laplacian. Only the transverse part $\mathbf{h}$ of the molecular field contributes to the elastic torque:

$$\mathbf{h} = \mathbf{H} - \mathbf{n}\left(\mathbf{n} \cdot \mathbf{H}\right) \tag{4}$$

$$= K\mathbf{n}_\perp \Delta\theta + \frac{\xi}{2}\mathbf{n}_\perp \sin[2(\phi - \theta)], \tag{5}$$

where $\mathbf{n}_\perp = -\hat{\mathbf{x}}\sin\theta + \hat{\mathbf{y}}\cos\theta$ is perpendicular to $\mathbf{n}$. The boundary condition on the director at the swimmer is

$$K\hat{\mathbf{N}} \cdot \boldsymbol{\nabla}\theta + \frac{W}{2}\sin\left[2(\theta - \phi_{\mathrm{s}})\right] = 0, \tag{6}$$

where ϕ_{s} is the angle the local tangent vector of the swimmer makes with the x axis.

The stress tensor corresponding to the elastic energy (2) is [23]

$$\sigma^{\mathrm{r}}_{\alpha\beta} = -K\partial_\alpha n_\gamma \partial_\beta n_\gamma - \frac{\lambda}{2}(n_\alpha h_\beta + n_\beta h_\alpha) + \frac{1}{2}(n_\alpha h_\beta - n_\beta h_\alpha), \tag{7}$$

where λ is a kinetic coefficient, positive for rod-like molecules and negative for disk-like molecules. The value $\lambda = 1$ is special; nematic liquid crystals with $\lambda < 1$ tend to have their directors continuous rotate in a shear flow, whereas nematic liquid crystals with $\lambda > 1$ tend to have the directors align at a fixed angle relative to the principal direction of shear. Note that the balance of torques $\mathbf{h} = \mathbf{0}$ implies the balance of forces, $-\partial_\alpha p_{\mathrm{eq}} + \partial_\beta \sigma^{\mathrm{r}}_{\alpha\beta} = 0$, where the equilibrium pressure is $p_{\mathrm{eq}} = -\mathcal{F}$ [22]. The dynamic equation for the director is

$$\partial_t n_\alpha + \mathbf{u} \cdot \boldsymbol{\nabla} n_\alpha - \frac{1}{2}\left[(\boldsymbol{\nabla} \times \mathbf{u}) \times \mathbf{n}\right]_\alpha = \lambda(\delta_{\alpha\beta} - n_\alpha n_\beta) E_{\beta\gamma} n_\gamma + h_\alpha/\gamma, \tag{8}$$

where $\mathbf{u}$ is the velocity field, $E_{\alpha\beta} = (\partial_\alpha u_\beta + \partial_\beta u_\alpha)/2$ is the rate of strain tensor and γ is the rotational viscosity [23].

To complete the specification of the equations of motion, we need the viscous stress tensor

$$\sigma^{\mathrm{v}}_{\alpha\beta} = 2\mu E_{\alpha\beta} + 2\mu_1 n_\alpha n_\beta n_\gamma n_\delta E_{\gamma\delta} + \mu_2 (n_\alpha E_{\beta\gamma} n_\gamma + n_\gamma E_{\gamma\alpha} n_\beta), \tag{9}$$

where μ is the shear viscosity and μ_1 and μ_2 are anisotropic shear viscosities. For the zero Reynolds number limit appropriate for microscopic swimmers, the forces must balance:

$$-\partial_\alpha p + \partial_\beta(\sigma^{\mathrm{r}}_{\alpha\beta} + \sigma^{\mathrm{v}}_{\alpha\beta}) = 0, \tag{10}$$

where p is the pressure associated with the constraint of incompressibility, $\partial_\alpha u_\alpha = 0$. The no-slip boundary condition on the flow is

$$\mathbf{u}(x, y = y_{\mathrm{s}}) = \hat{\mathbf{y}} \partial y_{\mathrm{s}} / \partial t. \tag{11}$$

Since our problem is two-dimensional, it will be convenient to enforce incompressibility by using the stream function ψ, defined such that $\mathbf{u} = \boldsymbol{\nabla} \times (\psi \hat{\mathbf{z}})$.

There are many terms in the governing equations, leading to complicated expressions for swimming speed. To keep the calculation manageable and to illustrate only the essential physics, we make several simplifying calculations. We have already noted that we use the one-coupling constant approximation for the Frank energy. We assume that the anchoring strength is weak, $W \ll qK$, so that the angle between the director and the far-field director is always small: $\theta - \phi \ll 1$. In this limit, the director never turns through a large angle, but the elastic torque can be nonzero. We set $\mu_2 = 0$, and assume that the remaining anisotropic viscosity is small, $\mu_1 \ll \mu$. Also, note that when $\gamma = 0$, the elastic and the viscous parts of the problem become partially decoupled; inspection of Eq. (8) reveals that when $\gamma = 0$, the molecular field vanishes, $\mathbf{h} = \mathbf{0}$, and the director configuration is in equilibrium for the instantaneous shape of the swimmer. Even with these simplifications, there are still several small parameters. We reduce the number of small parameters by assuming that γ and μ_1 are proportional to the same small dimensionless parameter δ. Finally, we limit our analysis to the special cases of $\lambda = 0$ and $\lambda = 1$. Thus we expand the angle field and flow velocity to second order in dimensionless amplitude $\epsilon = bq$, first order in dimensionless anchoring strength $w = W/(Kq)$, and first order in anisotropy δ:

$$\begin{aligned}\theta &\approx \phi + w\theta^{(010)} + \epsilon\left(\theta^{(100)} + \delta\theta^{(101)} + w\theta^{(110)} + w\delta\theta^{(111)}\right)\\ &\quad +\epsilon^2\left(\theta^{(200)} + \delta\theta^{(201)} + w\theta^{(210)} + w\delta\theta^{(211)}\right) \qquad (12)\\ \psi &\approx \epsilon\left(\psi^{(100)} + \delta\psi^{(101)} + w\psi^{(110)} + w\delta\psi^{(111)}\right)\\ &\quad +\epsilon^2\left(\psi^{(200)} + \delta\psi^{(201)} + w\psi^{(210)} + w\delta\psi^{(211)}\right). \qquad (13)\end{aligned}$$

Note that the superscript (abc) denotes ath order in ϵ, bth order in w, and cth order in δ. No assumption is made about the relative smallness of ϵ, w, and δ. The final simplification is to measure length in units of $1/q$ and time in units of $1/\omega$. The dimensionless number which characterizes the ratio of typical viscous stresses to typical elastic stresses is known as the Ericksen number, $\mathrm{Er} = \mu\omega/(Kq^2)$ [24]. The Ericksen number appears in the dimensionless equations.

A. Director field at zero amplitude

The expanded equations quickly get too complicated to display for the case of general λ, and even for $\lambda = 1$. Therefore, we will only display the final results for $\lambda = 1$; the method used to solve the equations is the same for both $\lambda = 0$ and $\lambda = 1$. First consider the case in which the swimmer has zero amplitude, $b = 0$. If the swimmer is not aligned with the far-field director field, then there will be an aligning torque due to the Frank elasticity. There is a discussion of this torque in [22], which we review here for completeness. To calculate the torque, we find the director field to zeroth order in ϵ, and first order in each of w and δ, i.e. $\mathcal{O}(\epsilon^0 w\delta)$. The director equation (8) at this order becomes

$$\Delta\theta^{(001)} - \frac{1}{q^2\ell_\xi^2}\theta^{(001)} = 0 \tag{14}$$

$$\Delta\theta^{(010)} - \frac{1}{q^2\ell_\xi^2}\theta^{(010)} = 0 \tag{15}$$

$$\Delta\theta^{(011)} - \frac{1}{q^2\ell_\xi^2}\theta^{(011)} = 0, \tag{16}$$

and the boundary condition (6) leads to

$$\partial_y\theta^{(001)}|_{y=0} = 0 \tag{17}$$

$$-\left.\frac{\partial\theta^{(010)}}{\partial y}\right|_{(x,y=0)} + \frac{1}{2}\sin(2\phi) = 0 \tag{18}$$

$$\partial_y\theta^{(011)}|_{y=0} = 0. \tag{19}$$

Thus we find that when $\epsilon = 0$,

$$\theta^{(001)} = 0 \tag{20}$$

$$\theta^{(010)} = -\frac{q\ell_\xi}{2}\exp\left[-y/(q\ell_\xi)\right]\sin(2\phi) \tag{21}$$

$$\theta^{(011)} = 0. \tag{22}$$

The director field for a zero-amplitude swimmer decays exponentially to its far-field value $\theta = \phi$ over a decay length ℓ_ξ.

To calculate the torque, note that the boundary condition (6) amounts to the statement that the torque per unit length exerted via the anchoring potential is equal to the elastic torque per unit length on the liquid crystal molecules. Thus, the dimensional torque per unit length of the swimmer, acting on the swimmer (spanning a distance d between the glass plates in the direction perpendicular to the xy plane) is $\tau d = K\hat{\mathbf{N}}\cdot\nabla\theta|_{y=0}$, or [22]

$$\tau d = -\frac{W}{2}\sin(2\phi). \tag{23}$$

The torque on the swimmer vanishes when the swimmer is aligned with the liquid crystal director, and also when the swimmer is perpendicular to the liquid crystal director. Alignment of the swimmer axis along the director is stable: when ϕ is small in magnitude, the torque tends to restore ϕ to zero. Alignment of the swimmer axis perpendicular to the director is unstable: when ϕ is close to $\pi/2$, the torque tends to rotate the swimmer away from the director. Since there is no flow when the swimmer amplitude vanishes ($b = 0$), any hydrodynamic contribution to the torque will be at least of order ϵ. Therefore, the elastic torque always dominates the viscous torque for the Taylor swimmer at small amplitude.

B. Flow and angle field to first order in amplitude; power dissipated

The order ϵ equations are complicated. The $\mathcal{O}(\epsilon w^0 \delta^0)$ equation for the stream function is the same as that for Stokes flow, but there are increasingly more terms as we expand to first order in w, δ, and $w\delta$. The details are presented in Appendix A. As in the case of the Taylor swimmer in a viscous fluid [1], the swimming speed vanishes to first order in ϵ. The $\mathcal{O}(\epsilon)$ angle field also has no mean part. The power dissipated by the flows and director deformations induced by the swimmer is given by

$$2R = \int \mathrm{d}x \int_{y_\mathrm{s}}^{\infty} \mathrm{d}y \left(\sigma^{\mathrm{v}}_{\alpha\beta} E_{\alpha\beta} + \mathbf{h}\cdot\mathbf{h}/\gamma\right). \tag{24}$$

To leading order, the power is $\mathcal{O}(\epsilon^2)$, but since $E_{\alpha\beta}$, $\sigma^{\mathrm{v}}_{\alpha\beta}$, and $\mathbf{h}$ are each $\mathcal{O}(\epsilon)$, we can calculate the leading order power dissipated from the $\mathcal{O}(\epsilon)$ expressions. To leading order in the anisotropy, the dimensional contribution to the power generated in each wavelength of the swimmer (for $\lambda = 0$) is

$$2R = \mu\omega^2 b^2 \left[1 + \frac{\mu_1 + \mathrm{Er}\gamma}{\mu} + wq^2\ell_\xi^2 \mathrm{Er}\frac{\gamma}{\mu}\left(\frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}} - 1\right)\cos(2\phi)\right]. \tag{25}$$

Since our approximation is that μ_1/μ, γ/μ, and w are all small, the change in the power dissipated due to the anisotropic medium is dominated by the power for the isotropic case. However we can see that the effect of the viscosity μ_1 in this limit is always to increase the power dissipated, and that the rotational viscosity γ can lead to either increased or decreased dissipation, depending on the alignment angle ϕ.

C. Flow and angle field to second order in amplitude: swimming speed

Next we consider the flow fields and angle field to second order in amplitude, $\mathcal{O}(\epsilon^2)$. Since there are even more terms than in the first-order expansion, we only consider the $\mathcal{O}(\epsilon^2)$ equations averaged over a period in x. We denote the average over one spatial period by angle brackets: $\langle F(x,y,t)\rangle = \int_0^{2\pi} \mathrm{d}x F/(2\pi)$. This averaging procedure eliminates terms which are oscillatory in $x-t$, which are by far the majority of the terms. However, as we discuss below, in a separate calculation (for the case $\lambda = 0$) we included the full t-dependence to verify that there are no secular terms (e.g. of the form $t\cos[2(x-t)]$) at $\mathcal{O}(\epsilon^2)$. Physically, we expect that the aligning field and Frank elasticity prevents the director

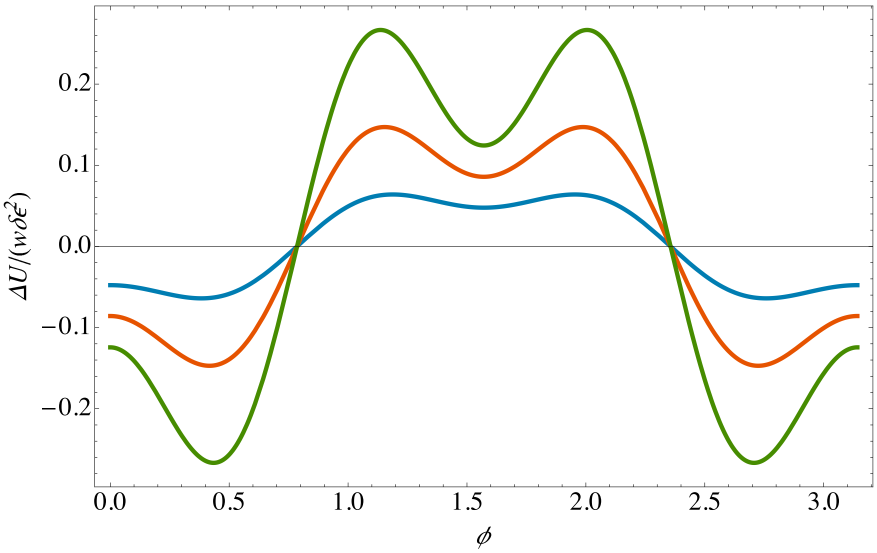

FIG. 2. (Color online). Dimensionless change in swimming speed as a function of the angle ϕ between the swimmer and the nematic direction, for $\lambda = 0$ and various values of the dimensionless penetration depth $q\ell_\xi$: $q\ell_\xi = 0.5$ (blue, bottom curve at $\phi = \pi/2$), $q\ell_\xi = 1$ (red, middle curve), and $q\ell_\xi = 10$ (green, top curve at $\phi = \pi/2$). The $q\ell_\xi = 10$ curve is indistinguishable from the $q\ell_\xi = \infty$ curve.

fields from rotating continuously, as it does in the transversely isotropic case without these aligning effects (Appendix B). This calculation with the full t-dependence is too unwieldy to include in this article.

Although the calculation of the averaged quantities is much simpler, some of the equations have many terms and we again put the details in the appendix. The final result is that the dimensionless swimming speed is

$$U = \frac{\epsilon^2}{2} + \Delta U, \tag{26}$$

where ΔU is given by

$$\Delta U(\lambda = 0) = \epsilon^2 w\delta \cos(2\phi)\left[V_1 + V_2\cos(4\phi)\right] \tag{27}$$

$$V_1 = -\frac{\gamma\left[2q\ell_\xi\left(2+3q^2\ell_\xi^2\right) + (1+6q^2\ell_\xi^2)\sqrt{1+q^2\ell_\xi^2}\right]}{2\mu\sqrt{1+q^2\ell_\xi^2}\left(q\ell_\xi + \sqrt{1+q^2\ell_\xi^2}\right)^4} \tag{28}$$

$$V_2 = \frac{\mu_1 q\ell_\xi\left(1+2q^2\ell_\xi^2 + 2q\ell_\xi\sqrt{1+q^2\ell_\xi^2}\right)}{\mu\sqrt{1+q^2\ell_\xi^2}\left(q\ell_\xi + \sqrt{1+q^2\ell_\xi^2}\right)^4}. \tag{29}$$

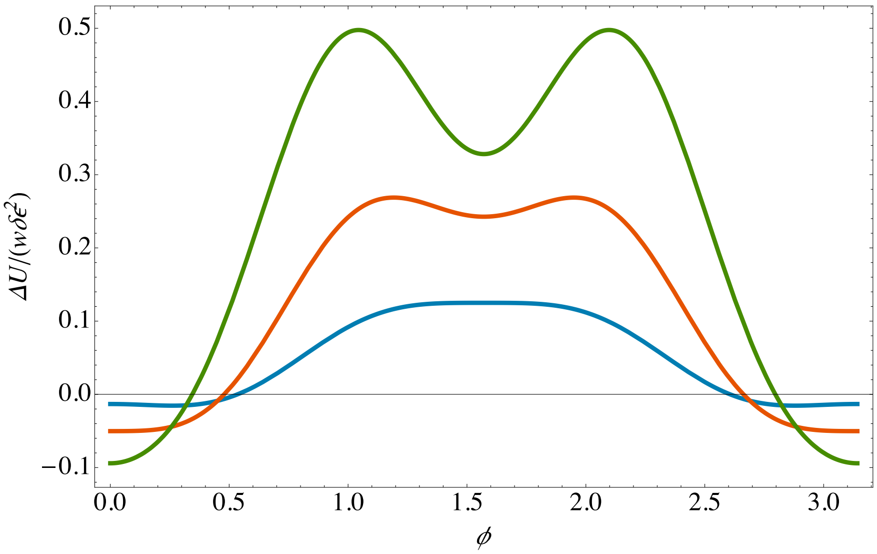

FIG. 3. (Color online). Dimensionless change in swimming speed as a function of the angle ϕ between the swimmer and the nematic direction, for $\lambda = 1$ and various values of the dimensionless penetration depth $q\ell_\xi$: $q\ell_\xi = 0.5$ (blue, bottom curve at $\phi = \pi/2$), $q\ell_\xi = 1$ (red, middle curve), and $q\ell_\xi = 2$ (green, top curve at $\phi = \pi/2$).

III. DISCUSSION AND CONCLUSION

Figures 2 and 3 show the dimensionless correction to the swimming speed for $\lambda = 0$ and $\lambda = 1$, respectively, as a function of the alignment angle ϕ. The swimming speed is symmetric under $\phi \mapsto \phi + \pi$, in accord with the nematic symmetry. First let us focus on the case of $\lambda = 0$. When the swimmer is aligned with the director field, the effect of the nematic liquid crystal is to reduce the propulsion speed from its isotropic value. For $\pi/4 < \phi < 3\pi/4$ (and $5\pi/4 < \phi < 7\pi/4$), the swimming speed is enhanced (Fig. 2). The limit of zero anchoring field is problematic, since in this limit $\ell_\xi \to \infty$, causing several of the fields ($\theta^{(010)}$, $\theta^{(101)}$, $\psi^{(111)}$...) to diverge. Nevertheless, the $\ell_\xi \to \infty$ limit of the correction to the swimming speed is well-behaved for $\lambda = 0$, and already attained by the time $q\ell_\xi = 10$; therefore the large ℓ_ξ limit is relevant even if ℓ_ξ is not numerically large. The change in the swimming speed for weak alignment is

$$\lim_{\ell_\xi \to \infty} \Delta U(\lambda = 0) = \frac{1}{8} w\delta\epsilon^2 \cos(2\phi) \left[2\mu_1 \cos(4\phi) - 3\gamma\right]. \tag{30}$$

We can check one limit of this expression with previously published results. When $\mu_1 = 0$ and $\phi = 0$, we have the situation of a swimmer in a hexatic liquid crystal with weak anchoring.

This limit (30) agrees with the weak-anchoring, low Ericksen number limit studied in [19]. Note that it has previously been pointed out that a sufficiently large rotational viscosity γ can reverse the direction of swimming when the swimmer is aligned with the order [19]. Equation (30) suggests that whether or not γ can reverse the swimming direction depends on the alignment angle ϕ.

Turning now to the case of $\lambda = 1$, Fig. 3 shows that the ϕ-dependence of ΔU is qualitatively similar to that of $\lambda = 0$, with enhancement for ϕ near $\pi/2$, and reduction for $\phi \approx 0$. However the points at which $\Delta U = 0$ depend on the value of ℓ_ξ for $\lambda = 1$. A more important difference between $\lambda = 0$ and $\lambda = 1$ is that the correction to the swimming speed increases linearly with ℓ_ξ for large ℓ_ξ for $\lambda = 1$, diverging in the limit of zero aligning field:

$$\Delta U(\lambda = 1) \sim \frac{\gamma}{8} w\delta\epsilon^2 q\ell_\xi \left[1 - \cos(4\phi)\right]. \tag{31}$$

Although the corrections to the swimming speed are small since we work in the limit of weak anchoring strength, weak coupling, and weak anisotropy, the strong dependence of the correction on the orientation shown in Figs. 2 and 3 suggest that when the swimming speed will have a strong dependence on orientation when the couplings are not small.

We can also compare our expression to the passive transversely isotropic fluid considered in [21]. The tranversely isotropic fluid does not have elastic moduli or anchoring terms; setting $w = 0$ in our formula leads to $\Delta U = 0$, in agreement with the results of [21]. However, our previous results on swimming in a hexatic liquid crystal indicated that the limit of zero elastic moduli is a singular limit, such that the swimming speed in a hexatic liquid crystal with zero elastic modulus is not the same as the limit of the swimming speed in a hexatic liquid crystal as the elastic modulus goes to zero [19]. Thus, although we agree with the final results of [21] for a swimmer in a passive medium with no elastic moduli, our calculations are in disagreement; we find a nonzero correction to the isotropic swimming speed, as a function of ϕ in the transversely isotropic fluid model. We discuss this subtle issue in Appendix B.

To conclude, we studied the problem of a swimmer with a prescribed gait in a nematic liquid crystal, allowing the swimmer to be oriented at an arbitrary angle to the direction of nematic order. In the limit of weak anchoring of the liquid crystal at the surface of the swimmer, small rotational viscosity, small anisotropic shear viscosity, and small amplitude, we found that the elastic torque dominates the viscous torque, and tends to align the swimmer with the direction of order. We also found that if the swimmer is held at a fixed angle ϕ relative to the nematic director, the swimmer tends to swim slower than it would in an isotropic viscous liquid if it is held with its axis close to alignment, and faster if it is held with its axis close to perpendicular to the nematic directors. Computing the trajectory of a swimmer that is torque free and reorienting to align with the directors is a transient problem like the startup problem studied in [25]; due to the complexity arising from the anisotropy, the torque-free problem is likely best addressed with numerical methods.

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Appendix A: Details of the calculation for $\lambda = 0$

We calculate the angle field and flow to first order in ϵ. At $\mathcal{O}(\epsilon w^0 \delta^0)$, the governing equations are

$$\Delta\theta^{(100)} - \theta^{(100)}/\ell_\xi^2 = 0 \tag{A1}$$

$$\Delta^2\psi^{(100)} = 0. \tag{A2}$$

The boundary conditions at this order are $\partial\theta^{(100)}/\partial y|_{y=0} = 0$ and $-\partial\psi^{(100)}/\partial y = \partial y_\mathrm{s}/\partial t$, leading to $\theta^{(100)} = 0$ and $\psi^{(100)} = (1+y)\exp(-y)\sin(x-t)$, just as in the Taylor problem for a viscous fluid [1].

At $\mathcal{O}(\epsilon w^0 \delta)$ we find

$$\Delta\theta^{(101)} - \theta^{(101)}/\ell_\xi^2 + \mathrm{Er}\frac{\gamma}{\mu}\exp(-y)\sin(x-t) = 0 \tag{A3}$$

$$\mu\Delta^2\psi^{(101)} + 2\mu_1(2-y)\exp(-y)\sin(x-t+4\phi) = 0. \tag{A4}$$

The parameter δ does not enter the boundary condition for the angle field, implying that

$\partial\theta^{(101)}/\partial y|_{y=0} = 0$, and

$$\theta^{(101)} = \mathrm{Er}\gamma q^2\ell_\xi^2 \left[\exp(-y) - \frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}} \exp\left(-\frac{y\sqrt{1+q^2\ell_\xi^2}}{q\ell_\xi}\right)\right] \sin(x-t). \tag{A5}$$

Likewise, since δ does not enter the no-slip boundary condition, $\psi^{(101)}(x, y=0) = 0$, and

$$\psi^{(101)} = \frac{\mu_1}{12\mu} y^3 \exp(-y) \sin(x - t + 4\phi). \tag{A6}$$

At $\mathcal{O}(\epsilon w \delta^0)$, the equation for the angle field is again homogeneous,

$$\Delta\theta^{(110)} - \theta^{(110)}/\ell_\xi^2 = 0 \tag{A7}$$

with the boundary condition

$$\partial\theta^{(110)}/\partial y + \cos(2\phi)\cos(x-t) = 0. \tag{A8}$$

Solving yields

$$\theta^{(110)} = \frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}} \exp\left[-\frac{y\sqrt{1+q^2\ell_\xi^2}}{q\ell_\xi}\right] \cos(2\phi)\cos(x-t). \tag{A9}$$

The force balance equation at $\mathcal{O}(\epsilon w \delta^0)$ is simply that $\psi^{(110)}$ is biharmonic, $\Delta^2\psi^{(110)} = 0$. Since δ does not enter the no-slip boundary condition, $\psi^{(110)} = 0$ everywhere.

At $\mathcal{O}(\epsilon w \delta)$, the angle equation is

$$\Delta\theta^{(111)} - \frac{1}{q^2\ell_\xi^2}\theta^{(111)} + f = 0, \tag{A10}$$

where

$$f = f_1 \sin(2\phi)\cos(x-t) + f_2 \cos(2\phi)\sin(x-t) \tag{A11}$$

$$f_1 = \frac{\gamma \mathrm{Er}}{2\mu}(1+y)\mathrm{e}^{-y-y/(q\ell_\xi)} \tag{A12}$$

$$f_2 = -\frac{\gamma \mathrm{Er}}{\mu\sqrt{1+q^2\ell_\xi^2}} q\ell_\xi \mathrm{e}^{-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)}. \tag{A13}$$

Since the boundary condition for the angle field is independent of w and δ, we have $\partial_y\theta^{(111)}|_{y=0} = 0$. Solving for $\theta^{(111)}$ yields

$$\theta^{(111)} = \theta_1 \sin(2\phi)\cos(x-t) + \theta_2\cos(2\phi)\sin(x-t), \tag{A14}$$

where

$$\theta_1 = \frac{\gamma q\ell_\xi \mathrm{Er}}{4\mu}\left[\frac{2+q\ell_\xi(2+q\ell_\xi)}{\sqrt{1+q^2\ell_\xi^2}}\mathrm{e}^{-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)} - (2+y+q\ell_\xi)\mathrm{e}^{-y-y/(q\ell_\xi)}\right] \tag{A15}$$

$$\theta_2 = -\frac{\gamma\ell_\xi^2 \mathrm{Er}\,\mathrm{e}^{-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)}}{2\mu(1+q^2\ell_\xi)^{3/2}}\left\{y\sqrt{1+q^2\ell_\xi^2}+q\ell_\xi\left[3+2q\ell_\xi(q\ell_\xi-\sqrt{1+q^2\ell_\xi^2})\right]\right\} \tag{A16}$$

This solution for the angle field leads to the stream function equation

$$\Delta^2\psi^{(111)} + g = 0, \tag{A17}$$

where

$$g = g_1\sin(2\phi)\cos(x-t) + g_2\cos(2\phi)\sin(x-t) + g_3\sin(2\phi)\cos(x-t+4\phi) \tag{A18}$$

$$g_1 = -\frac{\gamma}{4\mu q^2\ell_\xi^2}\mathrm{e}^{-y-y/(q\ell_\xi)}(1+y+2yq\ell_\xi) \tag{A19}$$

$$g_2 = -\frac{2\gamma}{4\mu q\ell_\xi\sqrt{1+q^2\ell_\xi^2}}\mathrm{e}^{-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)} \tag{A20}$$

$$g_3 = \frac{\mu_1}{\mu q\ell_\xi\sqrt{1+q^2\ell_\xi^2}}\mathrm{e}^{-y-y/(q\ell_\xi)}\left[y+2(y-1)\ell_\xi\right]. \tag{A21}$$

Since w and δ do not enter the no-slip boundary condition, we have $(\partial_y\psi^{(111)}, -\partial_x\psi^{(111)})|_{y=0} = 0$, and the stream function takes the form

$$\psi^{(111)} = \psi_1^{(111)}\cos(x-t) + \psi_2^{(111)}\sin(x-t), \tag{A22}$$

where

$$\psi_1^{(111)} = -\frac{q\ell_\xi}{4(1+2q\ell_\xi)}\left[\frac{\gamma}{\mu}b_1 + \frac{\mu_1}{\mu}b_2\cos(4\phi)\right]\sin(2\phi) \tag{A23}$$

$$b_1 = \mathrm{e}^{-y-y/(q\ell_\xi)}q\ell_\xi(1+y+2q\ell_\xi) + \mathrm{e}^{-y}\left[y+(y-1)q\ell_\xi - 2q^2\ell_\xi\right] \tag{A24}$$

$$b_2 = -4\mathrm{e}^{-y-y/(q\ell_\xi)}q^2\ell_\xi^2(1+2q\ell_\xi)\left[y+\mathrm{e}^{-y}(y-2q\ell_\xi)+2q\ell_\xi\right] \tag{A25}$$

$$\psi_2^{(111)} = \frac{q^2\ell_\xi^2}{2}\left[\frac{\gamma}{\mu}c_1\cos(2\phi) + \frac{\mu_1}{\mu}c_2\sin(2\phi)\sin(4\phi)\right] \tag{A26}$$

$$c_1 = \frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}}e^{-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)} + \mathrm{e}^{-y}\left[y - \frac{(1+y)q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}}\right] \tag{A27}$$

$$c_2 = -2\mathrm{e}^{-y-y/(q\ell_\xi)}q\ell_\xi\left[y(1+\mathrm{e}^{y/(q\ell_\xi)})+2q\ell_\xi\right]\sin(4\phi). \tag{A28}$$

Turning now to the second order in ϵ, at $\mathcal{O}(\epsilon^2 w^0 \delta^0)$ we find

$$\frac{\mathrm{d}^2\langle\theta^{(200)}\rangle}{\mathrm{d}y^2} - \frac{1}{q^2\ell_\xi^2}\langle\theta^{(200)}\rangle = 0 \tag{A29}$$

$$\frac{\mathrm{d}^2\langle u_x^{(200)}\rangle}{\mathrm{d}y^2} = 0, \tag{A30}$$

with boundary condition $\mathrm{d}\langle\theta^{(200)}\rangle/\mathrm{d}y|_{y=0} = 0$ and $\langle u_x^{(200)}\rangle|_{y=0} = 1/2$. Therefore, $\langle\theta^{(200)}\rangle = 0$, and $\langle u_x^{(200)}\rangle = 1/2$, just as in the isotropic viscous case [1]. At the next order, $\mathcal{O}(\epsilon^2 w^0 \delta)$, the governing equations are

$$\frac{\mathrm{d}^2\langle\theta^{(201)}\rangle}{\mathrm{d}y^2} - \frac{1}{q^2\ell_\xi^2}\langle\theta^{(201)}\rangle = 0 \tag{A31}$$

$$\frac{\mathrm{d}^2\langle u_x^{(200)}\rangle}{\mathrm{d}y^2} + 2\frac{\mu_1}{\mu}\cos\phi\sin^3\phi\frac{\mathrm{d}^2\langle u_y^{(200)}\rangle}{\mathrm{d}y^2} = 0. \tag{A32}$$

Note however that the incompressibility condition implies $\partial_x u_x^{(200)} + \partial_y u_y^{(200)} = 0$, which leads to $\mathrm{d}\langle u_y^{(200)}\rangle/\mathrm{d}y = 0$. Thus, Eq. (A32) reduces to $\mathrm{d}^2\langle u_x^{(200)}\rangle/\mathrm{d}y^2 = 0$. The $\mathcal{O}(\epsilon^2 w^0 \delta)$ boundary conditions are

$$\left.\frac{\mathrm{d}\langle\theta^{(201)}\rangle}{\mathrm{d}y}\right|_{y=0} - \frac{\gamma}{2\mu}\mathrm{Er}\, q^2\ell_\xi^2\left(1 - \frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}}\right) = 0 \tag{A33}$$

$$\langle u_x^{(201)}\rangle|_{y=0} = 0, \tag{A34}$$

leading to

$$\langle\theta^{201}\rangle = \frac{\gamma q^3\ell_\xi^3\mathrm{Er}}{2\mu}\mathrm{e}^{-y/(q\ell_\xi)}\left(1 - \frac{q\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}}\right) \tag{A35}$$

$$\langle u_x^{(201)}\rangle = 0 \tag{A36}$$

$$\langle u_y^{(201)}\rangle = 0. \tag{A37}$$

The $\mathcal{O}(\epsilon^2 w \delta^0)$ equations are

$$\frac{\mathrm{d}^2\langle\theta^{(210)}\rangle}{\mathrm{d}y^2} - \frac{1}{q^2\ell_\xi^2}\langle\theta^{(210)}\rangle = 0 \tag{A38}$$

$$\frac{\mathrm{d}^2\langle u_x^{(210)}\rangle}{\mathrm{d}y^2} = 0 \tag{A39}$$

with boundary conditions

$$\left.\frac{\mathrm{d}\langle\theta^{(210)}\rangle}{\mathrm{d}y}\right|_{y=0} + \frac{3}{8}\sin(2\phi) = 0 \tag{A40}$$

$$\langle u_x^{(210)}\rangle = 0. \tag{A41}$$

and solutions

$$\langle\theta^{(210)}\rangle = \frac{3}{8}q\ell_\xi \mathrm{e}^{-y/(q\ell_\xi)}\sin(2\phi) \tag{A42}$$

$$\langle u_x^{(210)}\rangle = 0. \tag{A43}$$

Again, the constraint of incompressibility yields $\langle u_y^{(210)}\rangle = 0$.

With all these solutions in hand we may find the $\mathcal{O}(\epsilon^2 w\delta)$ equations. For the angle field we find

$$\frac{\mathrm{d}^2\langle\theta^{(211)}\rangle}{\mathrm{d}y^2} - \frac{1}{q^2\ell_\xi^2}\langle\theta^{(211)}\rangle - \frac{\gamma\mathrm{Er}\,\cos(2\phi)}{2\mu}\left[1+y+\frac{yq\ell_\xi}{\sqrt{1+q^2\ell_\xi^2}}\right]\exp\left[-y-\frac{y\sqrt{1+q^2\ell_\xi^2}}{q\ell_\xi}\right] = 0, \tag{A44}$$

with boundary condition

$$\left.\frac{\mathrm{d}\langle\theta^{(211)}\rangle}{\mathrm{d}y}\right|_{y=0} + \mathrm{Er}q^3\ell_\xi^3\frac{\gamma}{\mu}\cos(4\phi)H_1 = 0, \tag{A45}$$

where

$$H_1 = \frac{3-2q^3\ell_\xi^3+2\sqrt{1+q^2\ell_\xi^2}-2q\ell_\xi\left(1+\sqrt{1+q^2\ell_\xi^2}\right)+2q^2\ell_\xi^2\left(1+\sqrt{1+q^2\ell_\xi^2}\right)}{4(1+q^2\ell_\xi^2)^{3/2}}. \tag{A46}$$

The solution for the averaged angle field at this order is

$$\langle\theta^{(211)}\rangle = \frac{\gamma}{\mu}q\ell_\xi\mathrm{Er}\cos(2\phi)\left\{a_1\exp\left[-y-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)\right]+a_2\exp[-y/(q\ell_\xi)]\right\}, \tag{A47}$$

where

$$a_1 = \left\{2+3q\ell_\xi\left(q\ell_\xi+\sqrt{1+q^2\ell_\xi^2}\right)+y\left[1+2q\ell_\xi\left(q\ell_\xi+\sqrt{1+q^2\ell_\xi^2}\right)\right]\right\}/a_0 \tag{A48}$$

$$a_2 = \frac{-4q\ell_\xi-5q^3\ell_\xi^3+2q^4\ell_\xi^4+2q^6\ell_\xi^6+\left(2q^5\ell_\xi^5+2q^3\ell_\xi^3-6q^2\ell_\xi^2-2\right)\sqrt{1+q^2\ell_\xi^2}}{a_0(1+q^2\ell_\xi^2)} \tag{A49}$$

$$a_0 = 4\sqrt{1+q^2\ell_\xi^2}\left(q\ell_\xi+\sqrt{1+q^2\ell_\xi^2}\right)^2. \tag{A50}$$

Finally, the equation for u_x at $\mathcal{O}(\epsilon^2 w\delta)$ is

$$\frac{\mathrm{d}^2u_x^{(211)}}{\mathrm{d}y^2} + \frac{\mathrm{Er}}{4q\ell_\xi}\exp\left(-y-y\sqrt{1+q^2\ell_\xi^2}/(q\ell_\xi)\right)H_2 \tag{A51}$$

where

$$H_2 = -\cos(2\phi)\left[2yq\ell_\xi\frac{\gamma}{\mu}+\frac{\gamma(1+y)(1+2q^2\ell_\xi^2)}{\mu\sqrt{1+q^2\ell_\xi^2}}-\frac{4\mu_1(y-1)q^2\ell_\xi^2\cos(4\phi)}{\mu\sqrt{1+q^2\ell_\xi^2}}\right] + \frac{\mu_1}{\mu}yq\ell_\xi\csc(2\phi)\sin(8\phi). \tag{A52}$$

At this order the no-slip boundary condition takes the form

$$\langle u_x^{(211)} \rangle|_{y=0} + \frac{2q\ell_\xi\sqrt{1+q^2\ell_\xi^2} - 2q^2\ell_\xi^2 - 1}{4\mu\sqrt{1+q^2\ell_\xi^2}} q\ell_\xi \cos(2\phi) = 0. \tag{A53}$$

Solving yields a $\langle u^{(211)} \rangle$ as the sum of an term exponentially decaying in y, and a constant $\Delta U^{(211)}$, where

$$\Delta U^{(211)} = \cos(2\phi)\left[V_1 + V_2\cos(4\phi)\right] \tag{A54}$$

$$V_1 = -\frac{\gamma\left[2q\ell_\xi\left(2+3q^2\ell_\xi^2\right) + (1+6q^2\ell_\xi^2)\sqrt{1+q^2\ell_\xi^2}\right]}{2\mu\sqrt{1+q^2\ell_\xi^2}\left(q\ell_\xi + \sqrt{1+q^2\ell_\xi^2}\right)^4} \tag{A55}$$

$$V_2 = \frac{\mu_1 q\ell_\xi\left(1 + 2q^2\ell_\xi^2 + 2q\ell_\xi\sqrt{1+q^2\ell_\xi^2}\right)}{\mu\sqrt{1+q^2\ell_\xi^2}\left(q\ell_\xi + \sqrt{1+q^2\ell_\xi^2}\right)^4}. \tag{A56}$$

The expression $\Delta U^{(211)}$ is the desired correction to the Taylor swimming speed arising from the liquid-crystal nature of the medium.

Appendix B: The tranversely isotropic limit

The governing equations for the transversely isotropic fluid are a special case of the nematic liquid crystal equations, with K and $\mathbf{h}$ each set to zero, $\lambda = 1$, and $\xi = 0$. For simplicity, we will also set $\mu_2 = 0$, as we did in the main body of the text. The governing equations are thus

$$\partial_\beta \sigma_{\alpha\beta} = 0 \tag{B1}$$

$$\partial_\alpha u_\alpha = 0 \tag{B2}$$

$$\frac{\partial n_\alpha}{\partial t} + u_\beta \partial_\beta n_\alpha = n_\beta \partial_\beta u_\alpha - n_\alpha n_\beta (\partial_\beta u_\gamma) n_\gamma, \tag{B3}$$

where

$$\sigma_{\alpha\beta} = -p\delta_{\alpha\beta} + 2\mu E_{\alpha\beta} + 2\mu_1 n_\alpha n_\beta n_\gamma E_{\gamma\delta} n_\delta. \tag{B4}$$

We use the same dimensional conventions as in the text, and define $\mu_1 = \delta\mu$. Again we work to second order in ϵ and first order in δ:

$$\mathbf{u} = \epsilon\left[\mathbf{u}_0^{(1)} + \delta\mathbf{u}_1^{(1)}\right] + \epsilon^2\left[\mathbf{u}_0^{(2)} + \delta\mathbf{u}_1^{(2)}\right] \tag{B5}$$

$$\theta = \phi + \epsilon\left[\theta_0^{(1)} + \delta\theta_1^{(1)}\right] + \epsilon^2\left[\theta_0^{(2)} + \delta\theta_1^{(2)}\right]. \tag{B6}$$

We again define the stream function ψ such that $\boldsymbol{\nabla} \times (\psi \hat{\mathbf{z}}) = \mathbf{u}$.

To first order in ϵ and zeroth order in δ, the governing equations for the flow field are

$$\Delta^2 \psi_0^{(1)} = 0 \tag{B7}$$

$$\partial_t \theta_0^{(1)} + \cos^2\phi\, \partial_x^2 \psi_0^{(1)} + 2\cos\phi \sin\phi\, \partial_x \partial_y \psi_0^{(1)} + \sin^2\phi\, \partial_y^2 \psi_0^{(1)} = 0. \tag{B8}$$

The stream function at this order obeys the Stokes equation with the same no-slip boundary conditions considered by Taylor [1], and is therefore given by

$$\psi_0^{(1)} = (1+y)\mathrm{e}^{-y} \sin(x-t). \tag{B9}$$

The angle field is computed from Eq. (B8) by integrating over time:

$$\theta_0^{(1)} = \mathrm{e}^{-y} \left[\cos(x-t) + y\cos(x-t+2\phi)\right]. \tag{B10}$$

At $\mathcal{O}(\epsilon\delta)$, the governing equations are

$$\Delta^2 \psi_1^{(1)} + 2(1-y)\mathrm{e}^{-y} \sin(x-t+4\phi) = 0 \tag{B11}$$

$$\partial_t \theta_1^{(1)} + \left(\cos^2\phi\, \partial_x^2 \psi_1^{(1)} + 2\cos\phi \sin\phi\, \partial_x \partial_y \psi_1^{(1)} + \sin^2\phi\, \partial_y^2 \psi_1^{(1)}\right) = 0. \tag{B12}$$

Since the no-slip boundary condition does not involve δ, the no-slip boundary condition at this order is $\mathbf{u}_1^{(1)} = \mathbf{0}$, and the stream function is given by

$$\psi_1^{(1)} = \frac{1}{12} y^3 \mathrm{e}^{-y} \sin(x-t+4\phi). \tag{B13}$$

Solving the director equation at this order yields

$$\theta_1^{(1)} = \frac{y\mathrm{e}^{-y}}{24} \left[\left(3-6y+2y^2\right)\cos(x-t+6\phi) + (6y-6)\cos(x-t+4\phi) + 3\cos(x-t+2\phi)\right] \tag{B14}$$

Turning now to the second order in ϵ, we again find that the $\mathcal{O}(\epsilon^2\delta^0)$ stream function obeys the Stokes equation,

$$\Delta^2 \psi_0^{(2)} = 0, \tag{B15}$$

with the boundary condition $(\partial_x \psi_0^{(2)}, -\partial_y \psi_0^{(2)})|_{y=0} = (1/2 - \cos[2(x-t)], 0)$. The solution is

$$\psi_0^{(2)} = \frac{y}{2} - \frac{y}{2}\mathrm{e}^{-2y} \cos[2(x-t)]. \tag{B16}$$

The equation for the angle at this order is

$$\partial_t \theta_0^{(2)} + \cos^2\phi\, \partial_x^2 \psi_0^{(2)} + 2\sin\phi \cos\phi\, \partial_x \partial_y \psi_0^{(2)} + \sin^2\phi\, \partial_y^2 \psi_0^{(2)} + F = 0, \tag{B17}$$

where

$$F = \frac{1}{2}\mathrm{e}^{-2y}\left[F_0 + F_1\right], \tag{B18}$$

$$F_0 = 2[1 - 2y(y-1)]\sin^2\phi \tag{B19}$$

$$F_1 = \cos[2(x-t)] - 2y^2\cos[2(x-t+2\phi)] - (1+2y)\cos[2(x-t+\phi)]. \tag{B20}$$

Using the solution $\psi_0^{(2)}$ and integrating (B17) with respect to t, we find

$$\begin{aligned}\theta_0^{(2)} &= t\left[2y(y-1)-1\right]\mathrm{e}^{-2y}\sin^2\phi - \frac{1}{4}(3-2y)\mathrm{e}^{-2y}\sin\left[2(x-t+\phi)\right] \\ &- \frac{1}{2}y^2 e^{-2y}\sin\left[2(x-t+2\phi)\right] + \frac{3}{4}\mathrm{e}^{-2y}\sin\left[2(x-t)\right].\end{aligned} \tag{B21}$$

Note the secular term in (B21), increasing without bound as t increases, and eventually spoiling the assumption that θ is close to ϕ. The secular term arises because there is no aligning potential or Frank elasticity to prevent the director from rotating continuously in the transversely isotropic fluid model. Due to the secular term, the regular perturbation theory described in this appendix is only valid for times which are small compared to the beating period of the sheet. Continuing nevertheless with the calculation, the stream function at $\mathcal{O}(\epsilon\delta)$ satisfies

$$\begin{aligned}\Delta^2\psi_1^{(2)} &= \left[2+4y(y-2)\right]\mathrm{e}^{-2y}\cos(2\phi) - 4(1-y)\mathrm{e}^{-2y}\cos(4\phi) + 8\mathrm{e}^{-2y}\cos\left[2(x-t+2\phi)\right] \\ &+ \left[2 - 16y(y-1)\right]\mathrm{e}^{-2y}\cos\left[2(x-t+3\phi)\right].\end{aligned} \tag{B22}$$

Solving (B22) with the no-slip boundary condition yields

$$\begin{aligned}\psi_1^{(2)} &= \frac{y}{4}\left[\cos(2\phi)+\cos(4\phi)\right] + \frac{\mathrm{e}^{-2y}}{24}\left[(9+12y+6y^2)\cos(2\phi) + 6(1+y)\cos(4\phi)\right] \\ &+ \frac{\mathrm{e}^{-2y}}{24}\left\{2y^4\cos\left[2(x-t+3\phi)\right] + 6y^2\cos\left[2(x-t+2\phi)\right]\right\}.\end{aligned} \tag{B23}$$

Far from the swimmer, where $y \to \infty$, there is a steady streaming flow

$$\Delta U_1^{(2)} = \frac{1}{4}\left[\cos(2\phi) + \cos(4\phi)\right], \tag{B24}$$

corresponding to the correction to the swimming speed (Fig. 4). Thus, in contradiction with the work of [21] we find that the swimming speed depends on alignment angle for Ericksen's passive transversely isotropic fluid. The angle field $\theta_1^{(2)}$ at this order has an expression which is too lengthy to display; it also has secular terms proportional to t.

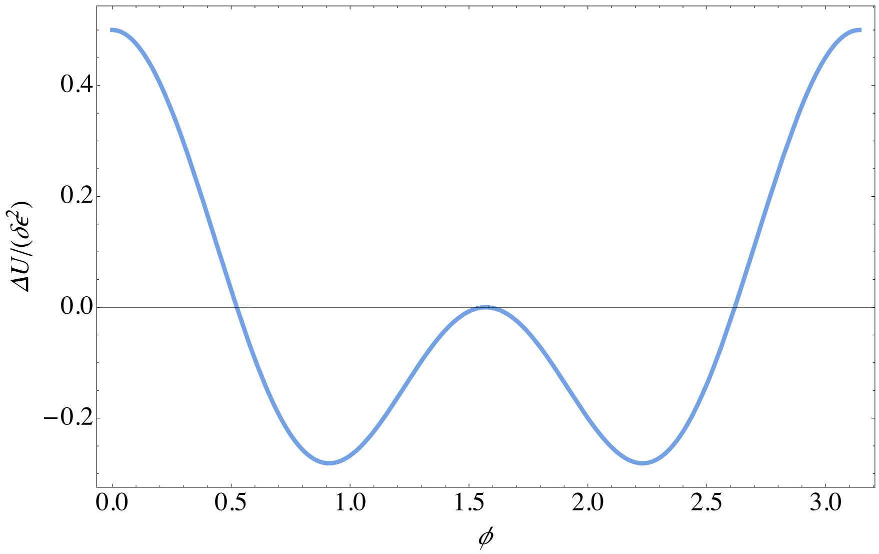

FIG. 4. (Color online). Dimensionless correction to swimming speed as a function of alignment angle for weak anisotropic viscosity in the transversely isotropic fluid model.

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