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Locomotion in complex fluids: Integral theorems

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The biological fluids encountered by self-propelled cells display complex microstructures and rheology. We consider here the general problem of low-Reynolds number locomotion in a complex fluid. Building on classical work on the transport of particles in viscoelastic fluids, we demonstrate how to mathematically derive three integral theorems relating the arbitrary motion of an isolated organism to its swimming kinematics in a non-Newtonian fluid. These theorems correspond to three situations of interest, namely, (1) squirming motion in a linear viscoelastic fluid, (2) arbitrary surface deformation in a weakly non-Newtonian fluid, and (3) small-amplitude deformation in an arbitrarily non-Newtonian fluid. Our final results, valid for a wide-class of swimmer geometry, surface kinematics, and constitutive models, at most require mathematical knowledge of a series of Newtonian flow problems, and will be useful to quantity the locomotion of biological and synthetic swimmers in complex environments. © *2014 AIP Publishing LLC*. [http://dx.doi.org/10.1063/1.4891969]

I. INTRODUCTION

Among all active fields of fluid mechanics, the biological hydrodynamics of cellular life has recently undergone a bit of a renaissance.[1] This is due to three facts. First, while the hydrodynamics of swimming cells primarily interested scientists from traditional continuum mechanics,[2–6] many problems in collective locomotion have found traction in the condensed matter physics community, with a number of questions still under active debate.[7] Second, new quantitative data from the biological world have led to renewed interest in classical questions, in particular, regarding the synchronization of cellular appendages.[8] The third reason, and the one at the center of our study, concerns locomotion in fluids displaying non-Newtonian characteristics.

In most biological situations, the fluids encountered by self-propelled cells display complex microstructures and rheology. Some bacteria progress through multi-layered host tissues while others live in open water surrounded by particle suspensions.[9] Lung cilia have to transport viscoelastic, polymeric mucus.[10] Mammalian spermatozoa have to overcome the resistance of cervical mucus in order to qualify for the race to the finish line.[11] In all these situations, a non-Newtonian fluid is being transported, or being exploited to induce fluid transport, and it is of fundamental importance to quantify the relationship between kinematics and the resulting transport.

The problem of predicting the swimming speed of a low-Reynolds swimmer in a complex fluid was first addressed in three pioneering studies focusing on a two-fluid model,[12] second-order fluid,[13] and linearly viscoelastic fluids.[14] Recent work started by looking at the asymptotic regime of small-amplitude waving motion in Oldroyd-like fluids,[15–17] predicting that, for a fixed swimming gait, the swimming speed is always smaller than in a Newtonian fluid. Importantly, that result does not appear to depend on the detail of the continuum description for the viscoelastic fluid, and is unchanged for more advanced nonlinear relationships such as FENE (finitely extensible nonlinear elastic) or Giesekus in the same asymptotic limit.[15] Numerical computations in two dimensions were then employed to probe the limit of validity of these results. While they confirmed the low-amplitude

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results, they also demonstrated that for some large-amplitude motion viscoelasticity could actually enhance the swimming speed of the model cell.[18] In contrast, simulations for spherical squirmers—swimmers acting on the surrounding fluid tangentially to their shape—showed that viscoelastic swimming was systematically slower than its Newtonian counterpart even at high Weissenberg number.[19,20]

Beyond polymeric fluids, analytical modeling was also proposed for locomotion in fluids displaying other rheological behavior. The two-dimensional approach was applied to swimming in a gel,[21] a two-phase fluid,[22] and yield stress materials.[23] A series of models was exploited to demonstrate that locomotion in a heterogeneous media—one made of stationary rigid inclusions—could systematically enhance self-propulsion.[24] Inelastic fluids with shear-dependent viscosities were also considered. While they necessarily impact the fluid motion at a higher order than polymeric stresses,[25] it was shown that shear and therefore rheological gradients along the swimmer could lead to swimming enhancement.[26,27] Different setups were also proposed and tested to demonstrate that nonlinearities in the fluid rheology could be exploited to design novel actuation and swimming devices.[28–32]

In contrast with theoretical studies, detailed experimental work on the fluid mechanics of swimming in complex fluids has been limited to a small number of investigations. A study of the nematode *C. elegans* self-propelling in synthetic polymeric solutions behaving as Boger fluids (constant shear viscosities) showed a systematic decrease of their swimming speed[33] consistent with asymptotic theoretical predictions.[15,16] In contrast, recent work on a two-dimensional rotational model of a swimming sheet demonstrated that Boger fluids always lead to an increase of the swimming speed while elastic fluids with shear-thinning viscosities lead to a systematic decrease.[34] The swimming increase in Boger fluid was also obtained in the case of force-free flexible swimmers driven by oscillating magnetic fields.[35] Translating rigid helices used as a model for free-swimming of bacteria were further shown to also decrease their swimming speed at small helix amplitude but displayed a modest speed increase for larger helical amplitude.[36] This increase is consistent with earlier computations[18] and was further confirmed by a detailed numerical study.[37]

In this paper, we consider theoretically the general problem of low-Reynolds number locomotion in a non-Newtonian fluid. Following classical work proposing integral formulations to quantify cell locomotion in Newtonian flows[38] and the motion of solid particles in viscoelastic fluids[39–44] (themselves adapted from earlier work on inertial effects[45–48]), we demonstrate how to mathematically derive three integral theorems relating the arbitrary motion of an organism to its swimming kinematics. After introducing the mathematical setup (Sec. II) and recalling the classical results for locomotion in a Newtonian fluid (Sec. III), the first theorem considers the classical tangential squirmer model of Lighthill and Blake (Sec. IV). We demonstrate that in this case, in an arbitrary linear viscoelastic fluid the swimming kinematics are the same as in a Newtonian fluid. The second theorem considers the asymptotic limit of small deviation from the Newtonian behavior (low Deborah number limit) with no asymptotic constraint on the amplitude of the deformation (Sec. V). We compute analytically in this weakly non-Newtonian regime the first-order effect of the non-Newtonian stresses on the swimming kinematics. In the final, and more general, theorem we address an arbitrary nonlinear viscoelastic fluid and derive the swimming kinematics in the limit of small-amplitude deformation (Sec. VI). The theorems in Secs. V and VI address therefore two complementary asymptotic limits: small deformation rate in Sec. V (low Deborah number) vs. small deformation amplitude in Sec. VI (low Weissenberg number, arbitrary Deborah number). The implications of our results for Purcell's scallop theorem are then discussed in Sec. VII. Finally, we apply the general theorem from Sec. VI to the locomotion of a sphere in an Oldroyd-B fluid in Sec. VIII. We show in particular that we can construct swimming kinematics which are either enhanced or reduced by the presence of viscoelastic stresses, thereby further demonstrating that the impact of non-Newtonian rheology on swimming is kinematics-dependent.

II. MATHEMATICAL SETUP

The mathematical setup for the swimming problem is illustrated in Fig. 1. We consider a closed surface S_0 undergoing periodic deformation into a shape denoted $S(t)$. This shape is that

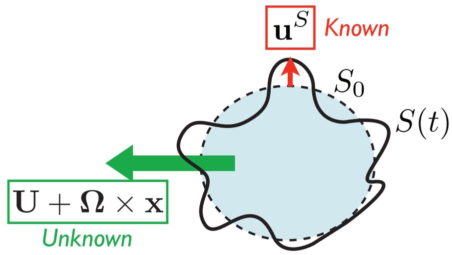

FIG. 1. Schematic representation of the swimming problem: Material points on a surface S_0 are moving periodically to a time-dependent shape $S(t)$. The instantaneous velocity on the surface is denoted $\mathbf{u}^S$, and is the swimming gait. As a result of free swimming motion, the shape $S(t)$ moves instantaneously with three-dimensional solid body velocity $\mathbf{U}(t)$ and rotation rate $\mathbf{\Omega}(t)$.

of an isolated three-dimensional swimmer self-propelling in an infinite fluid. We use the notation $\mathbf{x}^S$ for the instantaneous location of the material points on the surface of the swimmer and $\mathbf{n}$ the instantaneous normal to the surface $S(t)$. The velocity field and stress tensor in the fluid are written $\mathbf{u}$ and $\boldsymbol{\sigma}$, respectively. The stress is given by $\boldsymbol{\sigma} = -p\mathbf{1} + \boldsymbol{\tau}$ where p is the pressure, $\mathbf{1}$ the identity tensor, and $\boldsymbol{\tau}$ the deviatoric stress, modeled by specific constitutive relationships considered in Secs. III–VIII. The equations to solve for the fluid are the incompressibility condition, $\nabla \cdot \mathbf{u} = 0$, and Cauchy's equation of motion in the absence of inertia

$$\nabla p = \nabla \cdot \boldsymbol{\tau}. \tag{1}$$

The boundary conditions for Eq. (1) are given by

$$\mathbf{u}(\mathbf{x}^S, t) = \mathbf{U} + \mathbf{\Omega} \times \mathbf{x}^S + \mathbf{u}^S, \tag{2}$$

where the imposed surface velocity, $\mathbf{u}^S(\mathbf{x}^S, t)$, is the swimming gait, and $\{\mathbf{U}, \mathbf{\Omega}\}$ are the unknown swimming kinematics, i.e., the instantaneous solid body translation and rotation of the shape $S(t)$. Both are to be determined by enforcing the instantaneous condition of no net force or torque on the swimmer as

$$\iint_{S(t)} \boldsymbol{\sigma} \cdot \mathbf{n} \, \mathrm{d}S = \iint_{S(t)} \mathbf{x}^S \times (\boldsymbol{\sigma} \cdot \mathbf{n}) \, \mathrm{d}S = \mathbf{0}. \tag{3}$$

Note that throughout the paper we will use the notation $\dot{\boldsymbol{\gamma}} = \nabla \mathbf{u} + {}^t\nabla \mathbf{u}$ for the shear rate tensor, $\dot{\boldsymbol{\gamma}}$, equal to twice the symmetric rate-of-strain tensor (^{t} denotes the transpose of a tensor). Note also that surface motion ($\mathbf{u}^S \neq \mathbf{0}$) does not necessarily imply a change in shape as only the components of $\mathbf{u}^S$ normal to the surface, $\mathbf{u}^S \cdot \mathbf{n}$, contribute to the deformation of the shape.

III. NEWTONIAN CASE

Before addressing the non-Newtonian case, we briefly summarize here the integral theorem in the Newtonian case for which $\boldsymbol{\tau} = \mu \dot{\boldsymbol{\gamma}}$. This is work originally presented by Stone and Samuel[38] based on an application of Lorentz' reciprocal theorem.

We consider two solutions of Stokes flow with the same viscosity around the instantaneous surface $S(t)$. The first one has velocity and stress fields given by $(\mathbf{u}, \boldsymbol{\sigma})$ and is that of the swimming problem. Its boundary conditions are thus yet to be determined. The second solution, denoted $(\hat{\mathbf{u}}, \hat{\boldsymbol{\sigma}})$, is the problem of solid body motion with instantaneous shape $S(t)$, with force $\hat{\mathbf{F}}$,

$$\hat{\mathbf{F}} = \iint \hat{\boldsymbol{\sigma}} \cdot \mathbf{n} \, \mathrm{d}S, \tag{4}$$

and torque $\hat{\mathbf{L}}$ with respect to some origin in the body,

$$\hat{\mathbf{L}} = \iint \mathbf{x}^S \times (\hat{\boldsymbol{\sigma}} \cdot \mathbf{n}) \, \mathrm{d}S. \tag{5}$$

In the hat problem, the shape $S(t)$ moves thus instantaneously like a solid body with velocity $\hat{\mathbf{U}}$ and rotation speed $\hat{\boldsymbol{\Omega}}$, and thus on the surface we have

$$\hat{\mathbf{u}} = \hat{\mathbf{U}} + \hat{\boldsymbol{\Omega}} \times \mathbf{x}^S, \tag{6}$$

for all material points $\mathbf{x}^S$.

In the absence of body forces, Lorentz' reciprocal theorem states if both problems concern a fluid with identical viscosity we have the equality of virtual powers

$$\iint_S \mathbf{u} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S = \iint_S \hat{\mathbf{u}} \cdot \boldsymbol{\sigma} \cdot \mathbf{n}\, \mathrm{d}S. \tag{7}$$

Since $\hat{\mathbf{u}}$ is known everywhere on the surface, Eq. (6), the left term in Eq. (7) gives

$$\iint_S \hat{\mathbf{u}} \cdot \boldsymbol{\sigma} \cdot \mathbf{n}\, \mathrm{d}S = \hat{\mathbf{U}} \cdot \iint_S \boldsymbol{\sigma} \cdot \mathbf{n}\, \mathrm{d}S + \hat{\boldsymbol{\Omega}} \cdot \iint_S \mathbf{x}^S \times (\boldsymbol{\sigma} \cdot \mathbf{n})\, \mathrm{d}S = 0, \tag{8}$$

because swimming is force- and torque-free at all instants, see Eq. (3). Consequently, Eq. (7) simplifies to

$$\iint_S \mathbf{u} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S = 0. \tag{9}$$

By using the kinematic decomposition on the swimmer surface in Eq. (2), Eq. (9) becomes

$$\iint_S \mathbf{u} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S = \mathbf{U} \cdot \iint_S \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S + \boldsymbol{\Omega} \cdot \iint_S \mathbf{x}^S \times (\hat{\boldsymbol{\sigma}} \cdot \mathbf{n})\, \mathrm{d}S + \iint_S \mathbf{u}^S \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S = 0 \tag{10}$$

and thus, using Eqs. (4) and (5) we finally obtain

$$\hat{\mathbf{F}} \cdot \mathbf{U} + \hat{\mathbf{L}} \cdot \boldsymbol{\Omega} = -\iint_S \mathbf{u}^S \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{n}\, \mathrm{d}S. \tag{11}$$

The final result, Eq. (11), is an equation for the swimming kinematics, $\{\mathbf{U}, \boldsymbol{\Omega}\}$. In order to solve that equation, one needs to know the distribution of stress, $\hat{\boldsymbol{\sigma}} \cdot \mathbf{n}$, on the surface S for solid body motion in a Newtonian flow under and external force $\hat{\mathbf{F}}$ and torque $\hat{\mathbf{L}}$, which we assume is known. Since the values of $\hat{\mathbf{F}}$ and $\hat{\mathbf{L}}$ are arbitrary, Eq. (11) allows us to solve for all components of $\mathbf{U}$ and $\boldsymbol{\Omega}$.

As a side note which will be exploited later in the paper, we remind that the two velocity and stress fields in the application of Lorentz' reciprocal theorem correspond to two problems in the same Newtonian fluid. However, this constraint is relaxed in the final result quantified by Eq. (11). This is because the left-hand side of Eq. (7) turns out to be identically zero and a solid body motion implies zero virtual rate of work against a distribution of stress from force-free and torque-free swimming. Another way to see this is to note that by changing the fluid viscosity in Eq. (11), both sides of the equation are modified by the same prefactor since forces, torque, and stresses all scale proportionally with the viscosity in the Stokes regime.

IV. SQUIRMING IN A LINEARLY VISCOELASTIC FLUID

A. Squirming

In this section, we present the derivation for the first of our integral theorems. We consider here the class of swimmers known as squirmers which deform their surfaces everywhere in the direction parallel to their shapes, i.e., for which $\mathbf{u}^S \cdot \mathbf{n} = 0$ for all times. The shape of the swimmer is therefore fixed in time, S_0, and the distribution of velocity $\mathbf{u}^S$ is assumed to be known on S_0 ($\mathbf{u}^S$ does not have to be steady, as we see below). This squirmer model, most often used when S_0 is a sphere, was first proposed by Lighthill,[49] with corrections by Blake,[50] and is one of the very few analytical solutions to low-Reynolds swimming. As such, it has proven very popular to address a larger number of fundamental problems in cell locomotion, including hydrodynamic interactions,[51] the rheology of swimmer suspensions,[52] optimal locomotion,[53] nutrient uptake,[54,55] inertial swimming,[56] and locomotion in polymeric fluids.[19,20]

B. Generalized linear viscoelastic fluid

For the constitutive relationship, we assume in this section that the fluid is a generalized linear viscoelastic fluid.[57,58] Admittedly, this is a very idealized assumption as the flow around a swimming cell is non-viscometric while the linear constitutive equation only applies to small-amplitude viscometric motions. However, within this idealized class of fluids, we are able to obtain the solution for the swimming problem exactly without requiring any asymptotic expansion, which makes it a valuable exercise. Furthermore, the work in this section will in fact represent the leading-order behavior for a fluid with a more complex, nonlinear rheology as addressed in Sec. VI asymptotically, and therefore the mathematical details outlined below are important preliminaries.

A generalized linear viscoelastic fluid is characterized by arbitrary relaxation modulus, G, such that the stress is linearly related to the history of the rate of train in the most general form as

$$\boldsymbol{\tau}(\mathbf{x}, t) = \int_{-\infty}^{t} G(t - t')\dot{\boldsymbol{\gamma}}(\mathbf{x}, t')\,\mathrm{d}t', \tag{12}$$

or, using index notation,

$$\tau_{ij}(\mathbf{x}, t) = \int_{-\infty}^{t} G(t - t')\dot{\gamma}_{ij}(\mathbf{x}, t')\,\mathrm{d}t'. \tag{13}$$

In order to derive the integral theorem in this section we are going to use Eq. (13) written in Fourier space. This will allow us to derive an integral theorem for each Fourier components of the swimming kinematics (see earlier work on the so-called correspondence principle for linear viscoelasticity[59]). The one-dimensional Fourier transform and its inverse are defined for any function $f(t)$ as

$$\tilde{f}(\omega) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} f(t)e^{-i\omega t}\,\mathrm{d}t, \quad f(t) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} \tilde{f}(\omega)e^{i\omega t}\,\mathrm{d}t. \tag{14}$$

Following a classical textbook approach,[58] we apply the Fourier transform to Eq. (13), leading to

$$\tilde{\tau}_{ij}(\mathbf{x}, \omega) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} \tau_{ij}(\mathbf{x}, t)e^{-i\omega t}\,\mathrm{d}t = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}\left[\int_{-\infty}^{t} G(t - t')\dot{\gamma}_{ij}(\mathbf{x}, t')\,\mathrm{d}t'\right]e^{-i\omega t}\,\mathrm{d}t. \tag{15}$$

Change the order of time-integration allows us to obtain

$$\tilde{\tau}_{ij}(\mathbf{x}, \omega) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}\left[\int_{t'}^{\infty} G(t - t')e^{-i\omega t}\,\mathrm{d}t\right]\dot{\gamma}_{ij}(\mathbf{x}, t')\,\mathrm{d}t'. \tag{16}$$

We then write $e^{-i\omega t} = e^{-i\omega(t-t')}e^{-i\omega t'}$ and get

$$\tilde{\tau}_{ij}(\mathbf{x}, \omega) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}\left[\int_{t'}^{\infty} G(t - t')e^{-i\omega(t-t')}\,\mathrm{d}t\right]\dot{\gamma}_{ij}(\mathbf{x}, t')e^{-i\omega t'}\,\mathrm{d}t'. \tag{17}$$

A final change of variable $\bar{t} = t - t'$ in the bracketed integral leads to

$$\tilde{\tau}_{ij}(\mathbf{x}, \omega) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}\left[\int_{0}^{\infty} G(\bar{t})e^{-i\omega\bar{t}}\,\mathrm{d}\bar{t}\right]\dot{\gamma}_{ij}(\mathbf{x}, t')e^{-i\omega t'}\,\mathrm{d}t'. \tag{18}$$

Defining

$$\mathcal{G}(\omega) = \int_{0}^{\infty} G(\bar{t})e^{-i\omega\bar{t}}\,\mathrm{d}\bar{t}, \tag{19}$$

we are able to take $\mathcal{G}(\omega)$ out of the integral relationship in Eq. (18), leading to

$$\tilde{\tau}_{ij}(\mathbf{x}, \omega) = \mathcal{G}(\omega)\tilde{\dot{\gamma}}_{ij}(\mathbf{x}, \omega). \tag{20}$$

The statement in Eq. (20) is the constitutive relationship written in Fourier space, while Eq. (19) is the classical approach to relate the relaxation modulus of the fluid to the storage and loss modulus in Fourier space.[58]

C. Integral theorem

In order to derive the integral theorem, we first rewrite the swimming problem in Fourier space. Since the kinematics is restricted to squirming motion, the shape of the swimmer does not change, and $\mathbf{u}^S$ is known with no ambiguity in the Eulerian frame for each point $\mathbf{x}^S$ and for all times. We therefore decompose the surface velocity in Fourier modes as

$$\mathbf{u}^S(\mathbf{x}^S, t) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \tilde{\mathbf{u}}^S(\mathbf{x}^S, \omega) e^{i\omega t}\, \mathrm{d}t, \tag{21}$$

and do similarly for the swimming kinematics as

$$\{\mathbf{U}(t), \boldsymbol{\Omega}(t)\} = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \{\tilde{\mathbf{U}}(\omega), \tilde{\boldsymbol{\Omega}}(\omega)\} e^{i\omega t}\, \mathrm{d}t. \tag{22}$$

The Fourier transforms of the velocity and pressure fields are similarly defined.

Using Eq. (20), we then see that the incompressible Cauchy's equation, Eq. (1), becomes in Fourier space

$$\nabla \tilde{p}(\mathbf{x}, \omega) = \mathcal{G}(\omega) \nabla^2 \tilde{\mathbf{u}}(\mathbf{x}, \omega), \quad \nabla \cdot \tilde{\mathbf{u}}(\mathbf{x}, \omega) = 0. \tag{23}$$

Consequently, the swimming problem consists in solving Eq. (23) with the boundary condition

$$\tilde{\mathbf{u}}(\mathbf{x}^S, \omega) = \tilde{\mathbf{U}}(\omega) + \tilde{\boldsymbol{\Omega}}(\omega) \times \mathbf{x}^S + \tilde{\mathbf{u}}^S(\mathbf{x}^S, \omega). \tag{24}$$

The problem defined by Eqs. (23) and (24) is a Stokes flow locomotion problem with (complex) viscosity $\mathcal{G}(\omega)$. The integral theorem of Sec. III is then directly applicable, and we have

$$\hat{\mathbf{F}} \cdot \tilde{\mathbf{U}}(\omega) + \hat{\mathbf{L}} \cdot \tilde{\boldsymbol{\Omega}}(\omega) = -\iint_S \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \tilde{\mathbf{u}}^S(\mathbf{x}^S, \omega)\, \mathrm{d}S. \tag{25}$$

The final step allowing us to go back from Fourier to real space is to take advantage of the fact that the hat problem in Eq. (25) is a Newtonian Stokes flow with arbitrary viscosity (see the discussion at the end of Sec. III). We can take it to be a constant reference viscosity, μ_0, independent of the frequency ω. Furthermore, the shape S of the swimmer is not a function of time. We therefore see that none of the terms in Eq. (25) depend on the frequency except for the three Fourier components: $\mathbf{U}(\omega)$, $\boldsymbol{\Omega}(\omega)$, and $\tilde{\mathbf{u}}^S(\mathbf{x}^S, \omega)$. The inverse Fourier transform in Eq. (14) can directly be applied to Eq. (25) leading to the same integral equation as for the Newtonian case

$$\hat{\mathbf{F}} \cdot \mathbf{U} + \hat{\mathbf{L}} \cdot \boldsymbol{\Omega} = -\iint_S \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}^S\, \mathrm{d}S. \tag{26}$$

In summary, for squirming in an arbitrary linear viscoelastic fluid we obtain an exact integral theorem for the swimming kinematics, Eq. (26), identical to the Newtonian one. The squirming velocity and rotation rate in a linearly viscoelastic fluid are thus identical to those in a Newtonian fluid. In Eq. (26) the hat problem is in a different fluid though, namely, a Newtonian Stokes flow with constant, arbitrary, viscosity. It is notable that no asymptotic assumption was required to derive Eq. (26).

Two hypotheses were necessary in order to derive this result. First, we assumed that the motion was always tangential to the shape, allowing us to write the boundary condition on the swimmer surface in Fourier space and to take the inverse Fourier transform of Eq. (25) with no ambiguity. Second, we assumed that the fluid was linearly viscoelastic with no nonlinear rheological response (despite the shortcomings of this hypothesis, as outlined above). Beyond this, no restriction was required on the distribution of surface velocity, $\mathbf{u}^S$, and in particular it could be unsteady. If either hypothesis breaks down, and the fluid is nonlinear (as most fluids are) or the swimmer undergo normal shape deformation, an asymptotic analysis will be required, as we show in Secs. V–VI.

V. SWIMMING IN WEAKLY NON-NEWTONIAN FLUIDS

A. Weakly non-Newtonian rheology

In this section, we consider fluids whose rheological behaviors are close to that of a Newtonian fluid. If a fluid displays a zero-shear-rate Newtonian behavior, then we are concerned here in situations in which the fluid is deformed at small shear rate, and we will quantify the first effect of non-Newtonian rheology.

Two specific examples of such fluids can be given. For an inelastic fluid with shear-dependent viscosity η (so-called Generalized Newtonian fluids), we are interested in the limit where $(\eta - \eta_0)/\eta_0 \ll 1$ when η_0 is the zero-shear-rate viscosity.[58] Another example is that of elastic fluids at small Deborah numbers, De $\ll 1$, for which the constitutive relationship is the retarded motion expansion.[57]

In all cases, we assume that the non-Newtonian rheology of the fluid is a small perturbation, of dimensionless size ϵ, on an otherwise Newtonian dynamics. We thus write the constitutive relationship in the most general form as

$$\boldsymbol{\tau} = \eta \dot{\boldsymbol{\gamma}} + \epsilon \boldsymbol{\Sigma}[\mathbf{u}], \tag{27}$$

where $\boldsymbol{\Sigma}[\mathbf{u}]$ is a symmetric tensor and an arbitrary nonlinear functional of $\mathbf{u}$ with units of stress and $\epsilon \ll 1$ quantifies the small deviation from Newtonian behavior. For example, ϵ could be a small Deborah number in the case of viscoelastic fluids, or a small Carreau number for a shear-thinning fluid. Importantly, since we assume a small value for ϵ we have no time-history in the constitutive relationship and therefore the shape $S(t)$ will be allowed to vary arbitrarily in time.

B. Integral theorem

In order to derive the integral theorem in this case, we adapt below classical work on the first effect of non-Newtonian rheology on the dynamics of small particles in externally-driven flows (see, e.g., classical studies in Refs. 39–42 and reviews in Refs. 43 and 44) to the case of self-propulsion. The reader already familiar with these works will not be surprised by the final form of the non-Newtonian component of the swimming speed derived in Eq. (44).

1. Asymptotic expansion

We look for regular perturbation expansions for all variables under the form

$$\{\mathbf{u}, \boldsymbol{\tau}, p, \boldsymbol{\sigma}\} = \{\mathbf{u}_0, \boldsymbol{\tau}_0, p_0, \boldsymbol{\sigma}_0\} + \epsilon\{\mathbf{u}_1, \boldsymbol{\tau}_1, p_1, \boldsymbol{\sigma}_1\} + \dots \tag{28}$$

and similarly for the resulting locomotion kinematics

$$\{\mathbf{U}, \boldsymbol{\Omega}\} = \{\mathbf{U}_0, \boldsymbol{\Omega}_0\} + \epsilon\{\mathbf{U}_1, \boldsymbol{\Omega}_1\} + \dots, \tag{29}$$

which, in the most general case, are allowed to depend in time.

The swimming gait, $\mathbf{u}^S$, is imposed at order ϵ^0 and has no component at higher orders. In other words, the swimming gait is fixed and independent of the rheological behavior of the fluid. On the swimmer surface we thus have the instantaneous boundary conditions at order ϵ^0 and ϵ given by

$$\mathbf{u}_0 = \mathbf{U}_0 + \boldsymbol{\Omega}_0 \times \mathbf{x} + \mathbf{u}^S, \tag{30a}$$

$$\mathbf{u}_1 = \mathbf{U}_1 + \boldsymbol{\Omega}_1 \times \mathbf{x}. \tag{30b}$$

The hydrodynamic force and torque on the swimmer are given by

$$\mathbf{F}(t) = \iint_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma}\, \mathrm{d}S, \quad \mathbf{L}(t) = \iint_{S(t)} \mathbf{x}^S \times (\boldsymbol{\sigma} \cdot \mathbf{n})\, \mathrm{d}S, \tag{31}$$

where the torque can be computed with respect to an arbitrary origin since $\mathbf{F} = \mathbf{0}$. Expanding both in powers of ϵ we obtain

$$\{\mathbf{F}, \mathbf{L}\} = \{\mathbf{F}_0, \mathbf{L}_0\} + \epsilon\{\mathbf{F}_1, \boldsymbol{\Omega}_1\} + \dots, \tag{32}$$

and we see that the force- and torque-free requirements lead to $\mathbf{F}_i = \mathbf{\Omega}_i = \mathbf{0}$ at any order i for all times.

2. Order ϵ^0

At order ϵ^0, the flow is Newtonian, $\boldsymbol{\sigma}_0 = -p_0\mathbf{1} + \eta\dot{\boldsymbol{\gamma}}_0$, and we can directly apply the integral result from Sec. III

$$\hat{\mathbf{F}} \cdot \mathbf{U}_0 + \hat{\mathbf{L}} \cdot \mathbf{\Omega}_0 = -\iint_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}^S \, \mathrm{d}S, \tag{33}$$

where $S(t)$ is the instantaneous shape of the swimmer (note that we placed no restriction on the amplitude of the surface motion).

3. Order ϵ

At next order, we are interested in deriving the new formulae leading to $\mathbf{U}_1$ and $\mathbf{\Omega}_1$. At order ϵ, the constitutive relationship is written as

$$\boldsymbol{\sigma}_1 = -p_1\mathbf{1} + \eta\dot{\boldsymbol{\gamma}}_1 + \mathbf{\Sigma}[\mathbf{u}_0]. \tag{34}$$

In order to derive the integral result, we first have to use a modified version of Lorentz reciprocal theorem. We start by noting that we have, at each instant,

$$\nabla \cdot \boldsymbol{\sigma}_1 = 0 = \nabla \cdot \hat{\boldsymbol{\sigma}}, \tag{35}$$

where the hat stress field, $\hat{\boldsymbol{\sigma}}$, refers to the Stokes flow where the body is subject to external force, $\hat{\mathbf{F}}$, and an external torque, $\hat{\mathbf{\Omega}}$, in Newtonian fluid of viscosity η (same notation as in Sec. III). We then dot Eq. (35) with the velocity fields $\hat{\mathbf{u}}$ and $\mathbf{u}_1$ as

$$\hat{\mathbf{u}} \cdot \nabla \cdot \boldsymbol{\sigma}_1 = \mathbf{u}_1 \cdot \nabla \cdot \hat{\boldsymbol{\sigma}}, \tag{36}$$

which states that the virtual rates of working of each flow in the opposite stress field are equal. Integrating Eq. (36) over the entire fluid volume, $V(t)$, and using the divergence theorem leads to the equality

$$\iint_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}_1 \, \mathrm{d}S - \iint_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma}_1 \cdot \hat{\mathbf{u}} \, \mathrm{d}S = \iiint_{V(t)} \boldsymbol{\sigma}_1 : \nabla\hat{\mathbf{u}} \, \mathrm{d}V - \iiint_{V(t)} \hat{\boldsymbol{\sigma}} : \nabla\mathbf{u}_1 \, \mathrm{d}V, \tag{37}$$

where the normal $\mathbf{n}$ is directed into the fluid. Examining the right-hand side of Eq. (37) we can rewrite it as

$$\begin{aligned}\iiint_{V(t)} \boldsymbol{\sigma}_1 : \nabla\hat{\mathbf{u}} \, \mathrm{d}V - \iiint_{V(t)} \hat{\boldsymbol{\sigma}} : \nabla\mathbf{u}_1 \, \mathrm{d}V &= \iiint_{V(t)} \mathbf{\Sigma}[\mathbf{u}_0] : \nabla\hat{\mathbf{u}} \, \mathrm{d}V \\ &+ \iiint_{V(t)} \left[(-p_1\mathbf{1} + \eta\dot{\boldsymbol{\gamma}}_1) : \nabla\hat{\mathbf{u}} - (-\hat{p}\mathbf{1} + \eta\hat{\dot{\boldsymbol{\gamma}}}) : \nabla\mathbf{u}_1\right] \mathrm{d}V. \end{aligned} \tag{38}$$

Using incompressibility for the fields $\mathbf{u}_1$ and $\hat{\mathbf{u}}$ (i.e., $\nabla \cdot \mathbf{u}_1 = \nabla \cdot \hat{\mathbf{u}} = 0$), it is straightforward to show that

$$\iiint_{V(t)} \{(-p_1\mathbf{1} + \eta\dot{\boldsymbol{\gamma}}_1) : \nabla\hat{\mathbf{u}} - (-\hat{p}\mathbf{1} + \eta\hat{\dot{\boldsymbol{\gamma}}}) : \nabla\mathbf{u}_1\} \, \mathrm{d}V = \iiint_{V(t)} \eta\{\dot{\boldsymbol{\gamma}}_1 : \nabla\hat{\mathbf{u}} - \hat{\dot{\boldsymbol{\gamma}}} : \nabla\mathbf{u}_1\} \, \mathrm{d}V, \tag{39}$$

which is zero by symmetry, so that Eq. (37) becomes

$$\iint_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}_1 \, \mathrm{d}S - \iint_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma}_1 \cdot \hat{\mathbf{u}} \, \mathrm{d}S = \iiint_{V(t)} \mathbf{\Sigma}[\mathbf{u}_0] : \nabla\hat{\mathbf{u}} \, \mathrm{d}V. \tag{40}$$

In the hat problem, the surface instantaneously moves with solid-body motion with velocity $\hat{\mathbf{U}}$ and rotational speed $\hat{\mathbf{\Omega}}$, and therefore on the surface of the swimmer, we have $\hat{\mathbf{u}} = \hat{\mathbf{U}} + \hat{\mathbf{\Omega}} \times \mathbf{x}^S$. Consequently, the second integral on the left-hand-side of Eq. (37) is given by

$$\iint_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma}_1 \cdot \hat{\mathbf{u}} \, \mathrm{d}S = \hat{\mathbf{U}} \cdot \iint_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma}_1 \, \mathrm{d}S + \hat{\mathbf{\Omega}} \cdot \iint_{S(t)} \mathbf{x}^S \times (\mathbf{n} \cdot \boldsymbol{\sigma}_1) \, \mathrm{d}S. \tag{41}$$

The two integrals on the right-hand side of Eq. (41) are the instantaneous first-order force and torque on the swimmer, which, as was shown above, are both zero and thus we obtain

$$\iint_{S(t)} \mathbf{n}\cdot\boldsymbol{\sigma}_1\cdot\hat{\mathbf{u}}\,\mathrm{d}S = 0. \tag{42}$$

As a consequence, Eq. (40) simplifies to

$$\iint_{S(t)} \mathbf{n}\cdot\hat{\boldsymbol{\sigma}}\cdot\mathbf{u}_1\,\mathrm{d}S = \iiint_{V(t)} \boldsymbol{\Sigma}[\mathbf{u}_0]:\nabla\hat{\mathbf{u}}\,\mathrm{d}V. \tag{43}$$

On the swimmer surface, we then apply the boundary condition at order ϵ from Eq. (30b) and obtain the final integral relationship

$$\hat{\mathbf{F}}\cdot\mathbf{U}_1 + \hat{\mathbf{L}}\cdot\boldsymbol{\Omega}_1 = \iiint_{V(t)} \boldsymbol{\Sigma}[\mathbf{u}_0]:\nabla\hat{\mathbf{u}}\,\mathrm{d}V. \tag{44}$$

This second integral theorem, Eq. (44), allows us to compute the first non-Newtonian correction to the Newtonian swimming kinematics, namely, $\mathbf{U}_1$ and $\boldsymbol{\Omega}_1$, using only the knowledge from Newtonian solution. Importantly, the derivation is instantaneous, and it is thus valid for both steady and unsteady problems. In contrast to the Newtonian integral theorem, we notice that we need to know more than just the solution to the hat problem and the entire velocity field, $\mathbf{u}_0$, for the instantaneous Newtonian swimming problem also needs to be known. Given Eq. (11), we know the boundary conditions for $\mathbf{u}_0$ and thus solving for it is the same level of complexity as solving for $\hat{\mathbf{u}}$. With the knowledge of both $\mathbf{u}_0$ and $\hat{\mathbf{u}}$, the volume integral on the right-hand side of Eq. (44) can be computed, giving access to the swimming kinematics. As a side note, it is clear that the antisymmetric part of $\nabla\hat{\mathbf{u}}$ does not contribute to Eq. (44) since $\boldsymbol{\Sigma}$ is a symmetric tensor, and thus the integral theorem can also be rewritten as

$$\hat{\mathbf{F}}\cdot\mathbf{U}_1 + \hat{\mathbf{L}}\cdot\boldsymbol{\Omega}_1 = \iiint_{V(t)} \boldsymbol{\Sigma}[\mathbf{u}_0]:\hat{\mathbf{e}}\,\mathrm{d}V, \tag{45}$$

where $\hat{\mathbf{e}} = \frac{1}{2}({}^t\nabla\hat{\mathbf{u}} + \nabla\hat{\mathbf{u}})$ is the symmetric rate-of-strain tensor for the hat problem.

VI. SMALL-AMPLITUDE SWIMMING IN NONLINEAR FLUIDS

For the two integral theorems above we considered very specific constitutive relationships. Specifically, in order to derive Eq. (26) we assumed that the fluid rheology was linear while, in order to obtain Eq. (44), we allowed some nonlinearity in the constitutive relationship but assumed it was always small. It would be desirable to have a theorem valid when the rate of deformation of the fluid is comparable to its relation time, thereby displaying possible nontrivial nonlinear effects on the swimming kinematics. In order to allow finite values of the Deborah number while deriving the result analytically we consider another asymptotic limit, namely that of small-amplitude deformations. The results presented below are the most important results of this paper and are broadly applicable to different fluids and geometry. An earlier form of the theorem focusing solely on time-averaged motion was presented in Ref. 29. Furthermore, as we detail below, the results from Sec. IV will be used at leading order.

A. Domain perturbation

The tool used to derive the approximate solution in this case is that of domain perturbation, as originally proposed by Taylor in his pioneering study of the two-dimensional swimming sheet swimming in a Newtonian fluid.[60] We now denote by ϵ the dimensionless amplitude of the surface deformation and are interested in deriving the results asymptotically in the limit $\epsilon \ll 1$.

In this domain-perturbation approach we have to make explicit the link between the Lagrangian deformation of the surface and the resulting Eulerian boundary conditions for the solution to the fluid dynamics problem. The reference surface, S_0, is described by the field $\mathbf{x}_0^S$, and we then write the Lagrangian location of material points, $\mathbf{x}^S$, on the surface as

$$\mathbf{x}^S(t) = \mathbf{x}_0^S + \epsilon \mathbf{x}_1^S(\mathbf{x}_0^S, t), \tag{46}$$

where $\mathbf{x}_1^S$ represents thus the dimensional change in position of each reference point $\mathbf{x}_0^S$. While $\mathbf{n}$ denotes the normal to the surface S into the fluid, we denote by $\mathbf{n}_0$ the normal to the reference surface S_0.

We then proceed to solve the problem as a perturbation expansion in powers of ϵ. At order ϵ^0 there is no motion, so we have to go to order ϵ to obtain the leading-order fluid motion as well as ϵ^2 since we expect the swimming kinematics to scale quadratically with the amplitude of the surface motion.[60] We thus write the swimming kinematics as

$$\{\mathbf{U}, \boldsymbol{\Omega}\} = \epsilon\{\mathbf{U}_1, \boldsymbol{\Omega}_1\} + \epsilon^2\{\mathbf{U}_2, \boldsymbol{\Omega}_2\} + \ldots \tag{47}$$

and look similarly for velocity and stress fields as

$$\{\mathbf{u}, \boldsymbol{\tau}, p, \boldsymbol{\sigma}\} = \epsilon\{\mathbf{u}_1, \boldsymbol{\tau}_1, p_1, \boldsymbol{\sigma}_1\} + \epsilon^2\{\mathbf{u}_2, \boldsymbol{\tau}_2, p_2, \boldsymbol{\sigma}_2\} + \ldots, \tag{48}$$

which are defined, in the domain-perturbation framework, with boundary conditions on the zeroth-order surface S_0. Note that the domain-perturbation approach does rigorously take into account all terms of the dynamics balance for the swimmer, even nonlinear interactions at all orders, as shown below.

B. Boundary conditions

In order to derive the correct boundary conditions for the velocity field in Eq. (48), we have to pay attention to the kinematics of the surface. The instantaneous boundary condition on the surface of the swimmer is given by

$$\mathbf{u}(\mathbf{x}^S, t) = \mathbf{U} + \boldsymbol{\Omega} \times \mathbf{x}^S + \mathbf{u}^S, \tag{49}$$

an equation in which all four terms need to be properly expanded in powers of ϵ. The swimming velocity, $\mathbf{U}$, and rotation rate, $\boldsymbol{\Omega}$, are expanded in Eq. (47) while the expansion for the surface shape is given in Eq. (46). The expansion for the swimming gait, $\mathbf{u}^S$, is carried out using a Taylor expansion on the swimmer surface. The instantaneous boundary condition on the swimmer surface defining the swimming gait is given by

$$\mathbf{u}^S(\mathbf{x}^S, t) = \frac{\partial \mathbf{x}^S}{\partial t}\cdot \tag{50}$$

The Lagrangian partial derivative on the right-hand side of Eq. (50) is order ϵ while the Eulerian velocity on the left-hand side of the equation contains terms at all order in ϵ since it is evaluated on a moving shape defined by Eq. (46). A Taylor expansion of Eq. (50) up to order ϵ^2 allows us to obtain the two boundary conditions as

$$\mathbf{u}_1 = \mathbf{U}_1 + \boldsymbol{\Omega}_1 \times \mathbf{x}_0^S + \mathbf{u}_1^S, \tag{51a}$$

$$\mathbf{u}_2 = \mathbf{U}_2 + \boldsymbol{\Omega}_2 \times \mathbf{x}_0^S + \mathbf{u}_2^S, \tag{51b}$$

where $\mathbf{u}_1^S = \partial \mathbf{x}_1^S / \partial t|_{\mathbf{x}_0^S}$ and $\mathbf{u}_2^S = -\mathbf{x}_1^S \cdot \nabla \mathbf{u}_1|_{\mathbf{x}_0^S} + \boldsymbol{\Omega}_1 \times \mathbf{x}_1^S$.

A final important point to note is that since we are using an approach in domain perturbation, all fields are defined with boundary conditions on the $O(\epsilon^0)$ shape S_0. This shape is fixed in time, a fact which as we see below is critical.

C. Constitutive relationship

For this integral theorem, we place no restriction on the Deborah number for the flow, and will allow the period of the surface motion to be on the same order as the fluid relaxation time, but the small value of ϵ will ensure that the Weissenberg number remains small. We consider fluids obeying a general, multi-mode, differential relationship with a spectrum of relaxation times in which the deviatoric stress, $\boldsymbol{\tau} = \boldsymbol{\sigma} + p\mathbf{1}$, is written as a sum

$$\boldsymbol{\tau} = \sum_i \boldsymbol{\tau}^i. \tag{52}$$

Each stress, $\boldsymbol{\tau}^i$, is assumed to be following a nonlinear evolution equation of the form

$$(1 + \mathcal{A}_i)\boldsymbol{\tau}^i + \mathbf{M}_i(\boldsymbol{\tau}^i, \mathbf{u}) = \eta_i(1 + \mathcal{B}_i)\dot{\boldsymbol{\gamma}} + \mathbf{N}_i(\dot{\boldsymbol{\gamma}}, \mathbf{u}), \tag{53}$$

where the repeated indices i do not imply Einstein summations. In Eq. (53), $\mathcal{A}_i$ and $\mathcal{B}_i$ are arbitrary linear differential operators in time (for example, a time scale times a time derivative giving Maxwell-like terms); the symmetric tensors $\mathbf{M}_i$ and $\mathbf{N}_i$ are arbitrary nonlinear differential operators in space (for example, upper-convective derivatives) which are differentiable and contain no linear part (so at least quadratic); and η_i is the zero-shear rate viscosity of the ith mode.

The assumed constitutive relationship, Eqs. (52) and (53), is very general, and includes all classical non-Newtonian models from continuum mechanics, including all Oldroyd-like models (upper- and lower-convected Maxwell, corotational Maxwell and Oldroyd, Oldroyd-A and -B, Oldroyd 8-constant model, Johnson-Segalman-Oldroyd), Giesekus and Phan-Thien-Tanner nonlinear polymeric models, the second and nth order fluid approximation, all generalized Newtonian fluids, and all multi-mode version of these constitutive models.[57,58,61–65] Furthermore, although the FENE-P constitutive relationship does not exactly take the form in Eqs. (52) and (53), it agrees with it for small deformations,[15] so our approach is valid for the FENE class of models too.

D. First order solution

At leading order, the constitutive equation for each mode is linearized and becomes

$$(1 + \mathcal{A}_i)\boldsymbol{\tau}_1^i = \eta_i(1 + \mathcal{B}_i)\dot{\boldsymbol{\gamma}}_1. \tag{54}$$

For each mode, we obtain therefore a linearly viscoelastic fluid on a fixed shape, S_0, a problem which was almost already solved in Sec. IV.

In order to proceed in the analysis we will make the assumption, relevant to all small-scale biological swimmers, that the shape change occurs periodically in time with a fixed period, denoted T. We thus use Fourier series, and we write for all functions h of period $T = 2\pi/\omega$

$$h(t) = \sum_{n=-\infty}^{\infty} \tilde{h}^{(n)} e^{in\omega t}, \quad \tilde{h}^{(n)} = \frac{1}{T}\int_0^T h(t)e^{-in\omega t}\,\mathrm{d}t. \tag{55}$$

Evaluating Eq. (54) in Fourier space leads to

$$[1 + \mathcal{A}_i(n)]\tilde{\boldsymbol{\tau}}_1^{i,(n)}(\mathbf{x}) = \eta_i[1 + \mathcal{B}_i(n)]\tilde{\dot{\boldsymbol{\gamma}}}_1^{(n)}(\mathbf{x}), \tag{56}$$

where $\mathcal{A}_i(n)$ and $\mathcal{B}_i(n)$ are multiplicative operators obtained by evaluating the differential operators $\mathcal{A}_i$ and $\mathcal{B}_i$ in Fourier space. We can write Eq. (56) compactly as

$$\tilde{\boldsymbol{\tau}}_1^{i,(n)}(\mathbf{x}) = \mathcal{G}_i(n)\tilde{\dot{\boldsymbol{\gamma}}}_1^{(n)}(\mathbf{x}), \tag{57}$$

where

$$\mathcal{G}_i(n) = \eta_i \frac{1 + \mathcal{B}_i(n)}{1 + \mathcal{A}_i(n)}. \tag{58}$$

Summing on all the modes i we then obtain the Fourier components of the total stress as Newtonian-like

$$\tilde{\boldsymbol{\tau}}_1^{(n)}(\mathbf{x}) = \mathcal{G}(n)\tilde{\dot{\boldsymbol{\gamma}}}_1^{(n)}(\mathbf{x}), \tag{59}$$

with effective complex viscosity

$$\mathcal{G}(n) = \sum_i \mathcal{G}_i(n). \tag{60}$$

To within a rescaling of the pressure, the problem posed by Eq. (59) is that of force- and torque-free swimming a linear viscoelastic fluid with a surface velocity defined on a fixed shape, S_0. This is therefore the same problem as in Sec. IV, and thus the swimming kinematics at order ϵ are the same as the Newtonian one and we obtain for each Fourier component

$$\hat{\mathbf{F}} \cdot \tilde{\mathbf{U}}_1^{(n)} + \hat{\mathbf{L}} \cdot \tilde{\mathbf{\Omega}}_1^{(n)} = -\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}} \cdot \tilde{\mathbf{u}}_1^{S,(n)}\, \mathrm{d}S. \tag{61}$$

Given that the shape S_0 does not vary with time, one can invert the Fourier transform in Eq. (61) to obtain

$$\hat{\mathbf{F}} \cdot \mathbf{U}_1 + \hat{\mathbf{L}} \cdot \mathbf{\Omega}_1 = -\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}_1^{S}\, \mathrm{d}S. \tag{62}$$

Notice that, similarly to the problem addressed in Sec. IV, all material properties of the fluid have disappeared at leading order. They will however matter at next order.

The result of Eq. (62) can also be used to show that the time-averaged locomotion at leading order is always zero. From Eq. (51a), we see that $\mathbf{u}_1^S$ is an exact time-derivative. We therefore have $\langle \mathbf{u}_1^S(\mathbf{x}_0^S, t)\rangle = \mathbf{0}$ and thus taking the time-average of Eq. (62) leads to

$$\hat{\mathbf{F}} \cdot \langle \mathbf{U}_1 \rangle + \hat{\mathbf{L}} \cdot \langle \mathbf{\Omega}_1 \rangle = 0, \tag{63}$$

and therefore $\langle \mathbf{U}_1 \rangle = \langle \mathbf{\Omega}_1 \rangle = \mathbf{0}$. Similarly to the Newtonian case, net swimming occurs therefore at order ϵ^2 at least.[3,15,60]

E. Second-order solution

We now consider the expansion at second order.

1. Constitutive relationship

The constitutive relationship, Eq. (53), is written at order ϵ^2 as

$$(1 + \mathcal{A}_i)\boldsymbol{\tau}_2^i = \eta_i(1 + \mathcal{B}_i)\dot{\boldsymbol{\gamma}}_2 + \mathbf{H}_i[\mathbf{u}_1]. \tag{64}$$

Unlike the expansion considered in Sec. V for weakly non-Newtonian flows, the general model considered in this section does allow for history terms in the evolution of the fluid stress ($\mathcal{A}_i \neq 0$) and thus the problem requires us to consider each Fourier mode separately. In Eq. (64), the nonlinear operator, $\mathbf{H}_i$, is only a functional of $\mathbf{u}_1$ and is formally written using gradients in the operators $\mathbf{N}_i$ and $\mathbf{M}_i$ as

$$\mathbf{H}_i[\mathbf{u}_1] = \dot{\boldsymbol{\gamma}}_1 : \left[(\nabla_{\dot{\boldsymbol{\gamma}}} \nabla_{\mathbf{u}} \mathbf{N}_i)\big|_{\mathbf{0},\mathbf{0}}\right] \cdot \mathbf{u}_1 - \boldsymbol{\tau}_1^i : \left[(\nabla_{\boldsymbol{\tau}^i} \nabla_{\mathbf{u}} \mathbf{M}_i)\big|_{\mathbf{0},\mathbf{0}}\right] \cdot \mathbf{u}_1, \tag{65}$$

with the relationship between $\boldsymbol{\tau}_1^i$ and $\dot{\boldsymbol{\gamma}}_1$ given by Eq. (54), and where we recall that $\dot{\boldsymbol{\gamma}}_1 = \nabla \mathbf{u}_1 + \nabla \mathbf{u}_1^T$. Using Fourier series and using the same notation as in Sec. VI D, we can then rewrite Eq. (64) as

$$[1 + \mathcal{A}_i(n)]\tilde{\boldsymbol{\tau}}_2^{i,(n)}(\mathbf{x}) = \eta_i[1 + \mathcal{B}_i(n)]\tilde{\dot{\boldsymbol{\gamma}}}_2^{(n)}(\mathbf{x}) + \widetilde{\mathbf{H}_i[\mathbf{u}_1]}^{(n)}(\mathbf{x}), \tag{66}$$

or

$$\tilde{\boldsymbol{\tau}}_2^{i,(n)}(\mathbf{x}) = \mathcal{G}_i(n)\tilde{\dot{\boldsymbol{\gamma}}}_2^{(n)}(\mathbf{x}) + \frac{1}{[1 + \mathcal{A}_i(n)]}\widetilde{\mathbf{H}_i[\mathbf{u}_1]}^{(n)}(\mathbf{x}). \tag{67}$$

Summing up Eq. (67) for all indices i, we obtain explicitly the second order deviatoric stress as

$$\tilde{\boldsymbol{\tau}}_2^{(n)}(\mathbf{x}) = \mathcal{G}(n)\tilde{\dot{\boldsymbol{\gamma}}}_2^{(n)}(\mathbf{x}) + \widetilde{\mathbf{\Sigma}[\mathbf{u}_1]}^{(n)}(\mathbf{x}), \tag{68}$$

where we have defined

$$\widetilde{\mathbf{\Sigma}[\mathbf{u}_1]}^{(n)}(\mathbf{x}) = \sum_i \frac{1}{1 + \mathcal{A}_i(n)}\widetilde{\mathbf{H}_i[\mathbf{u}_1]}^{(n)}(\mathbf{x}). \tag{69}$$

2. Principle of virtual work

After Eq. (68), we see that total stress in the fluid is given by

$$\tilde{\boldsymbol{\sigma}}_2^{(n)}(\mathbf{x}) = -\tilde{p}_2^{(n)}(\mathbf{x})\mathbf{1} + \mathcal{G}(n)\tilde{\dot{\boldsymbol{\gamma}}}_2^{(n)}(\mathbf{x}) + \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)}(\mathbf{x}). \tag{70}$$

We now apply the principle of virtual work to the $\{\tilde{\mathbf{u}}_2^{(n)}, \tilde{\boldsymbol{\sigma}}_2^{(n)}\}$ problem, together with a solid body motion which takes place with the viscosity $\mathcal{G}(n)$, which we denote $\{\hat{\mathbf{u}}_{(n)}, \hat{\boldsymbol{\sigma}}_{(n)}\}$ (note that the flow field $\hat{\mathbf{u}}_{(n)}$ is not a Fourier component nor a series expansion; the subscript (n) is simply used as a reminder that the associated viscosity is $\mathcal{G}(n)$). The solid body motion is associated with complex forces and torques given by $\hat{\mathbf{F}}_{(n)}$ and $\hat{\mathbf{L}}_{(n)}$, resulting in solid body kinematics given by $\hat{\mathbf{U}}_{(n)}$ and $\hat{\boldsymbol{\Omega}}_{(n)}$. As a difference with the calculation in Sec. IV, here the value of the complex viscosity matters and thus the solid body motion in the hat problem will always be a function of the order, n, of the Fourier mode considered (hence the notation chosen).

Since both problems satisfy that the divergence of the stress tensor is zero, we compute the virtual work and obtain

$$\hat{\mathbf{u}}_{(n)} \cdot \nabla \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)} = \tilde{\mathbf{u}}_2^{(n)} \cdot \nabla \cdot \hat{\boldsymbol{\sigma}}_{(n)}, \tag{71}$$

which we then integrate in the entire fluid volume and use the divergence theorem to obtain

$$\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}}_{(n)} \cdot \tilde{\mathbf{u}}_2^{(n)}\, \mathrm{d}S - \iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)} \cdot \hat{\mathbf{u}}_{(n)}\, \mathrm{d}S = \iiint_{V_0} \tilde{\boldsymbol{\sigma}}_2^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\, \mathrm{d}V - \iiint_{V_0} \hat{\boldsymbol{\sigma}}_{(n)} : \nabla\tilde{\mathbf{u}}_2^{(n)}\, \mathrm{d}V. \tag{72}$$

We then plug Eq. (70) into the right-hand side of Eq. (72) to get

$$\iiint_{V_0} \tilde{\boldsymbol{\sigma}}_2^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\, \mathrm{d}V - \iiint_{V_0} \hat{\boldsymbol{\sigma}}_{(n)} : \nabla\tilde{\mathbf{u}}_2^{(n)}\, \mathrm{d}V = \iiint_{V_0} \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\, \mathrm{d}V, \tag{73}$$

where the symmetric terms have disappeared due to incompressibility and by equality of their viscosity, similarly to Eq. (39), so that we obtain

$$\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}}_{(n)} \cdot \tilde{\mathbf{u}}_2^{(n)}\, \mathrm{d}S - \iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)} \cdot \hat{\mathbf{u}}_{(n)}\, \mathrm{d}S = \iiint_{V_0} \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\, \mathrm{d}V. \tag{74}$$

On the left-hand side of Eq. (72) we write, on S_0, the Fourier components of the boundary condition at order ϵ^2, namely, $\tilde{\mathbf{u}}_2^{(n)}(\mathbf{x}_0^S) = \tilde{\mathbf{U}}_2^{(n)} + \tilde{\boldsymbol{\Omega}}_2^{(n)} \times \mathbf{x}_0^S + \tilde{\mathbf{u}}_2^{S,(n)}(\mathbf{x}_0^S)$, so that the integral formulation, Eq. (74), becomes

$$\begin{aligned}\hat{\mathbf{F}}_{(n)} \cdot \tilde{\mathbf{U}}_2^{(n)} + \hat{\mathbf{L}}_{(n)} \cdot \tilde{\boldsymbol{\Omega}}_2^{(n)} = &-\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}}_{(n)} \cdot \tilde{\mathbf{u}}_2^{S,(n)}\, \mathrm{d}S + \iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)} \cdot \hat{\mathbf{u}}_{(n)}\, \mathrm{d}S \\ &+ \iiint_{V_0} \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\, \mathrm{d}V,\end{aligned} \tag{75}$$

where $\hat{\mathbf{F}}_{(n)}$ and $\hat{\mathbf{L}}_{(n)}$ depend on n through the complex viscosity $\mathcal{G}(n)$. The final term we have to evaluate in Eq. (75) is the integral

$$\mathcal{I} = \iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)} \cdot \hat{\mathbf{u}}_{(n)}\, \mathrm{d}S, \tag{76}$$

and since the boundary condition for the hat problem on the surface is $\hat{\mathbf{u}}_{(n)} = \hat{\mathbf{U}}_{(n)} + \hat{\boldsymbol{\Omega}}_{(n)} \times \mathbf{x}_0^S$, $\mathcal{I}$ is given by

$$\mathcal{I} = \left[\iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)}\, \mathrm{d}S\right] \cdot \hat{\mathbf{U}}_{(n)} + \left[\iint_{S_0} \mathbf{x}_0^S \times (\mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)})\, \mathrm{d}S\right] \cdot \hat{\boldsymbol{\Omega}}_{(n)}. \tag{77}$$

The terms multiplying the solid-body kinematics in Eq. (77) seem to involve the $O(\epsilon^2)$ forces and torques on the swimmer. In Sec. VI E 3, we show how to use arguments of vector calculus and differential geometry to evaluate them explicitly.

3. Differential geometry

Since we are using a domain expansion method, particular attention needs to be paid to the expressions for the hydrodynamic forces and moments acting on the swimmer. Indeed, these are to be evaluated on a shape changing in time, and thus the application of the force- and moment-free condition is not straightforward.

Since motion of the swimmer tangential to its surface does not lead to changes in its shape, only the normal component of the surface motion will contribute. We thus write the shape variation of the periodically moving interface, $S(t)$, as the normal projection to the motion of the material points, and thus we describe the surface as $\mathbf{x} = \mathbf{x}_0^S + \epsilon\delta_1(\mathbf{x}_0^S, t)\mathbf{n}_0(\mathbf{x}_0^S)$, where $\mathbf{n}_0$ is the normal to the surface S_0 at point $\mathbf{x}_0^S$, and the function δ_1, with units of length, represents the normal shape deformation of the reference surface. Given that we have material points whose dynamics is given by Eq. (46) we necessarily have $\delta_1 = \mathbf{x}_1^S \cdot \mathbf{n}_0$. Note that for a squirming motion, we have by definition $\delta_1 = 0$, so $\mathbf{x} = \mathbf{x}_0^S$ and thus $S(t) = S_0$ for all times. Associated with this shape variation is the normal to the surface, which is expanded as $\mathbf{n} = \mathbf{n}_0(\mathbf{x}_0^S) + \epsilon\mathbf{n}_1(\mathbf{x}_0^S) + \ldots$, with all fields described on the undeformed surface, S_0. On the swimmer surface we thus have the expansion

$$\mathbf{n}\cdot\boldsymbol{\sigma} = \epsilon\mathbf{n}_0\cdot\boldsymbol{\sigma}_1 + \epsilon^2(\mathbf{n}_0\cdot\boldsymbol{\sigma}_2 + \mathbf{n}_1\cdot\boldsymbol{\sigma}_1). \tag{78}$$

Using this description, we can calculate the asymptotic value of the surface integral W of an arbitrary scalar field $w(\mathbf{x})$

$$W = \iint_{S(t)} w(\mathbf{x})\,\mathrm{d}S. \tag{79}$$

Expanding the integrand as $w(\mathbf{x}) = \epsilon w_1(\mathbf{x}) + \epsilon^2 w_2(\mathbf{x}) + \ldots$ and using Taylor expansion to evaluate the integral on the reference S_0 we obtain $W = \epsilon W_1 + \epsilon^2 W_2 + \ldots$ with

$$W_1 = \iint_{S_0} w_1(\mathbf{x}_0^S)\,\mathrm{d}S, \quad \text{and} \quad W_2 = \iint_{S_0}\left(w_2 + \delta_1\frac{\partial w_1}{\partial n}\right)(\mathbf{x}_0^S)\,\mathrm{d}S, \tag{80}$$

where the normal derivative is understood as normal to the unperturbed surface, i.e., $\partial w_1/\partial n = \mathbf{n}_0\cdot\nabla w_1$.

The force and torque on the swimmer are formally given by the integrals

$$\mathbf{F} = \iint_{S(t)} \mathbf{n}\cdot\boldsymbol{\sigma}\,\mathrm{d}S, \quad \boldsymbol{\Omega} = \iint_{S(t)} \mathbf{x}\times(\mathbf{n}\cdot\boldsymbol{\sigma})\,\mathrm{d}S, \tag{81}$$

for which we will have the expansion

$$\{\mathbf{F},\mathbf{L}\} = \epsilon\{\mathbf{F}_1,\mathbf{L}_1\} + \epsilon^2\{\mathbf{F}_2,\boldsymbol{\Omega}_2\} + \ldots \tag{82}$$

with the forces and torques equal to zero at each order. Applying the results above with w equal to each component of the force per unit area on the swimmer, $\boldsymbol{\sigma}\cdot\mathbf{n}$, expanded as in Eq. (78) we obtain at fist order the expected integrals

$$\mathbf{F}_1 = \iint_{S_0} \mathbf{n}_0\cdot\boldsymbol{\sigma}_1\,\mathrm{d}S = \mathbf{0}, \tag{83a}$$

$$\mathbf{L}_1 = \iint_{S_0} \mathbf{x}_0^S\times(\mathbf{n}_0\cdot\boldsymbol{\sigma}_1)\,\mathrm{d}S = \mathbf{0}, \tag{83b}$$

while at order ϵ^2 it leads to additional terms and

$$\mathbf{F}_2 = \iint_{S_0}\left(\mathbf{n}_0\cdot\boldsymbol{\sigma}_2 + \mathbf{n}_1\cdot\boldsymbol{\sigma}_1 + \delta_1\mathbf{n}_0\cdot\frac{\partial\boldsymbol{\sigma}_1}{\partial n}\right)\mathrm{d}S = \mathbf{0}, \tag{84a}$$

$$\mathbf{L}_2 = \iint_{S_0} \mathbf{x}_0^S\times\left(\mathbf{n}_0\cdot\boldsymbol{\sigma}_2 + \mathbf{n}_1\cdot\boldsymbol{\sigma}_1 + \delta_1\mathbf{n}_0\cdot\frac{\partial\boldsymbol{\sigma}_1}{\partial n}\right)\mathrm{d}S + \iint_{S_0}\delta_1\mathbf{n}_0\times(\mathbf{n}_0\cdot\boldsymbol{\sigma}_1)\,\mathrm{d}S = \mathbf{0}, \tag{84b}$$

for all times.

We can now use differential geometry and vector calculus to simplify the results in Eq. (84a). Given that the surface shape is described by $\mathbf{x} = \mathbf{x}_0^S + \epsilon\delta_1(\mathbf{x}_0^S, t)\mathbf{n}_0(\mathbf{x}_0^S)$ then it is straightforward to see that the first perturbation of the surface normal, $\mathbf{n}_1$, is given by minus the surface gradient of the shape field δ_1, i.e., $\mathbf{n}_1(\mathbf{x}_0^S) = -\nabla_{\mathbf{x}_0^S}\delta_1$. In Eq. (84a), we therefore have

$$\mathbf{n}_1 \cdot \boldsymbol{\sigma}_1 + \delta_1 \mathbf{n}_0 \cdot \frac{\partial \boldsymbol{\sigma}_1}{\partial n} = -(\nabla_{\mathbf{x}_0^S}\delta_1)\cdot\boldsymbol{\sigma}_1 + \delta_1 \mathbf{n}_0 \cdot \frac{\partial \boldsymbol{\sigma}_1}{\partial n}\cdot \tag{85}$$

We can then use the identity from vector calculus

$$\nabla_{\mathbf{x}_0^S}\cdot(\delta_1\boldsymbol{\sigma}_1) = \delta_1(\nabla_{\mathbf{x}_0^S}\cdot\boldsymbol{\sigma}_1) + (\nabla_{\mathbf{x}_0^S}\delta_1)\cdot\boldsymbol{\sigma}_1 \tag{86}$$

to simplify Eq. (85) into

$$\mathbf{n}_1 \cdot \boldsymbol{\sigma}_1 + \delta_1 \mathbf{n}_0 \cdot \frac{\partial \boldsymbol{\sigma}_1}{\partial n} = -\nabla_{\mathbf{x}_0^S}(\delta_1\cdot\boldsymbol{\sigma}_1) + \delta_1\left(\nabla_{\mathbf{x}_0^S}\cdot\boldsymbol{\sigma}_1 + \mathbf{n}_0\cdot\frac{\partial \boldsymbol{\sigma}_1}{\partial n}\right)\cdot \tag{87}$$

The last term in parenthesis in Eq. (87) is an expression for the three-dimensional divergence of $\boldsymbol{\sigma}_1$, which is zero,

$$\nabla_{\mathbf{x}_0^S}\cdot\boldsymbol{\sigma}_1 + \mathbf{n}_0\cdot\frac{\partial\boldsymbol{\sigma}_1}{\partial n} = \nabla\cdot\boldsymbol{\sigma}_1 = \mathbf{0}, \tag{88}$$

since the flow at each order in the perturbation expansion satisfy Cauchy's equation of motion, $\nabla\cdot\boldsymbol{\sigma}_i = \mathbf{0}$. This result allows us to simplify each expression in Eq. (84a). Starting with the force in Eq. (84a), we now have

$$\mathbf{F}_2 = \iint_{S_0}\left[\mathbf{n}_0\cdot\boldsymbol{\sigma}_2 - \nabla_{\mathbf{x}_0^S}\cdot(\delta_1\boldsymbol{\sigma}_1)\right]\mathrm{d}S = \mathbf{0}. \tag{89}$$

The integral of the second term in Eq. (89) is a surface divergence integrated on a closed surface, and therefore equal to zero (this can be viewed as an application of the curl theorem). And therefore we finally obtain the simple expression for the second-order force as

$$\mathbf{F}_2 = \iint_{S_0}\mathbf{n}_0\cdot\boldsymbol{\sigma}_2\,\mathrm{d}S = \mathbf{0}. \tag{90}$$

The equation for the moment, Eq. (84b), is now written as

$$\mathbf{L}_2 = \iint_{S_0}\mathbf{x}_0^S\times(\mathbf{n}_0\cdot\boldsymbol{\sigma}_2)\,\mathrm{d}S + \iint_{S_0}\left[\delta_1\mathbf{n}_0\times(\mathbf{n}_0\cdot\boldsymbol{\sigma}_1) - \mathbf{x}_0^S\times\nabla_{\mathbf{x}_0}\cdot(\delta_1\boldsymbol{\sigma}_1)\,\mathrm{d}S\right] = \mathbf{0}. \tag{91}$$

Let us now show that the second integral in Eq. (91) is identically zero. If the shape of the swimmer does not vary, then $\delta_1 = 0$ and that second integral is trivially equal to zero. If the shape of the swimmer does change in time, then since we have freedom in how we define the reference shape S_0, we can always change how we parametrize it thus without loss of generality can assume S_0 is locally flat. We then employ Cartesian coordinates with $\mathbf{n}_0 = \mathbf{e}_z$ and the surface defined as $z = 0$, so that $\mathbf{x}_0^S = x\mathbf{e}_x + y\mathbf{e}_y$. In that case, the first integrand in the second integral in Eq. (91) is given by

$$\delta_1\mathbf{n}_0\times(\mathbf{n}_0\cdot\boldsymbol{\sigma}_1) = \delta_1\mathbf{e}_z\times(\sigma_{1,xz}\mathbf{e}_x + \sigma_{1,yz}\mathbf{e}_y) = \delta_1(\sigma_{1,xz}\mathbf{e}_y - \sigma_{1,yz}\mathbf{e}_x). \tag{92}$$

The surface divergence in second integrand is given by

$$\nabla_{\mathbf{x}_0^S}\cdot(\delta_1\boldsymbol{\sigma}_1) = \mathbf{e}_\alpha\partial_\alpha\cdot(\delta_1\sigma_{1,ij}\mathbf{e}_i\mathbf{e}_j) = \partial_\alpha(\delta_1\sigma_{1,\alpha j})\,\mathbf{e}_j, \tag{93}$$

where we have used the convention that Einstein's summation notation with Latin letters $(i, j, \ldots)$ implies a summation on all three coordinates x, y, z while a summation with Greek letters $(\alpha, \beta, \ldots)$ implies a summation only on the surface coordinates x and y. Using Eq. (93) we can then compute explicitly the second integrand as

$$-\mathbf{x}_0^S\times\nabla_{\mathbf{x}_0^S}\cdot(\delta_1\boldsymbol{\sigma}_1) = -x_\beta\mathbf{e}_\beta\times\partial_\alpha(\delta_1\sigma_{1,\alpha j})\mathbf{e}_j = -\epsilon_{m\beta j}x_\beta\partial_\alpha(\delta_1\sigma_{1,\alpha j})\,\mathbf{e}_m. \tag{94}$$

In order to force that term to take the form of a surface divergence, we can re-write it as

$$-\mathbf{x}_0^S\times\nabla_{\mathbf{x}_0^S}\cdot(\delta_1\boldsymbol{\sigma}_1) = -\partial_\alpha(\epsilon_{m\beta j}x_\beta\delta_1\sigma_{1,\alpha j})\,\mathbf{e}_m + \epsilon_{m\alpha j}\delta_1\sigma_{1,\alpha j}\,\mathbf{e}_m. \tag{95}$$

The first term on the right-hand side of Eq. (95) is a surface divergence and will thus disappear when integrate on the close surface S_0. The second term can be evaluated explicitly because for all indices j equal to x or y, since the tensor $\boldsymbol{\sigma}_1$ is symmetric and the tensor $\boldsymbol{\epsilon}$ is antisymmetric, terms with (α, j) and (j, α) will cancel out, and thus only the terms with $j = z$ survive. This leads to

$$\epsilon_{m\alpha j}\delta_1\sigma_{1,\alpha j}\,\mathbf{e}_m = \epsilon_{m\alpha z}\delta_1\sigma_{1,\alpha z}\,\mathbf{e}_m = \delta_1(\sigma_{1,yz}\,\mathbf{e}_x - \sigma_{1,xz}\,\mathbf{e}_y). \tag{96}$$

We then see that the result of Eq. (96) exactly cancels out the first integrand given in Eq. (92) and therefore the whole second integral in Eq. (91) disappears, leaving the second-order moment to be given by

$$\mathbf{L}_2 = \iint_{S_0} \mathbf{x}_0^S \times (\mathbf{n}_0 \cdot \boldsymbol{\sigma}_2)\,\mathrm{d}S. \tag{97}$$

4. Integral theorem

Using the results from Sec. VI E 3 and enforcing that swimming is force- and torque-free at order two, $\mathbf{F}_2 = \mathbf{L}_2 = \mathbf{0}$, we obtain simply

$$\iint_{S_0} \mathbf{n}_0 \cdot \boldsymbol{\sigma}_2\,\mathrm{d}S = \mathbf{0}, \quad \iint_{S_0} \mathbf{x}_0^S \times (\mathbf{n}_0 \cdot \boldsymbol{\sigma}_2)\,\mathrm{d}S = \mathbf{0}. \tag{98}$$

In Fourier space, since the reference shape S_0 is fixed, we obtain for each Fourier component

$$\iint_{S_0} \mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)}\,\mathrm{d}S = \mathbf{0}, \quad \iint_{S_0} \mathbf{x}_0^S \times (\mathbf{n}_0 \cdot \tilde{\boldsymbol{\sigma}}_2^{(n)})\,\mathrm{d}S = \mathbf{0}. \tag{99}$$

From Eq. (76), we then obtain $\mathcal{I} = 0$, and Eq. (75) leads then to the final integral theorem

$$\hat{\mathbf{F}}_{(n)} \cdot \tilde{\mathbf{U}}_2^{(n)} + \hat{\mathbf{L}}_{(n)} \cdot \tilde{\boldsymbol{\Omega}}_2^{(n)} = -\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}}_{(n)} \cdot \tilde{\mathbf{u}}_2^{S,(n)}\,\mathrm{d}S + \iiint_{V_0} \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)} : \nabla\hat{\mathbf{u}}_{(n)}\,\mathrm{d}V. \tag{100}$$

Our final result, Eq. (100), provides explicit expressions for the Fourier modes of the swimming kinematics at order 2, namely, $\mathbf{U}_2^{(n)}$ and $\boldsymbol{\Omega}_2^{(n)}$, allowing to reconstruct the whole time-dependent swimming velocity, $\mathbf{U}_2$, and rotation rate, $\boldsymbol{\Omega}_2$, at order $O(\epsilon^2)$. This is the most important result from our paper. Physically, we see that the swimming kinematics are simply given by the sum of a Newtonian component and a non-Newtonian part. Since the constitutive relationship has been left very general, the result in Eq. (100) is expected to be applicable to a wide range of complex fluids, swimmer geometry, and deformation kinematics.

In order to mathematically evaluate Eq. (100), we see that the following knowledge is required. We see to know the full velocity field at order 1, $\mathbf{u}_1$, the Fourier component of the second-order swimming gait, $\tilde{\mathbf{u}}_2^{S,(n)}$, and a dual Newtonian solution, $\{\hat{\mathbf{u}}_{(n)}, \hat{\boldsymbol{\sigma}}_{(n)}\}$, corresponding to solid body motion with net force $\mathbf{F}_{(n)}$ and moment $\boldsymbol{\Omega}_{(n)}$. The dual Newtonian problem corresponds to rigid-body motion in a Newtonian fluid of complex viscosity $\mathcal{G}(n)$, and can be deduced, by exploiting the linearity of Stokes equations, from the flow at a reference viscosity by a simple rescaling. The order 1 swimming problem, $\mathbf{u}_1$, has known boundary conditions computed in Eq. (62), and has therefore the computational complexity of a Newtonian problem. Similarly to the previous theorem, the gradient $\nabla\hat{\mathbf{u}}_{(n)}$ in Eq. (100) can be replaced by the symmetric part of the velocity gradient, giving the alternative form

$$\hat{\mathbf{F}}_{(n)} \cdot \tilde{\mathbf{U}}_2^{(n)} + \hat{\mathbf{L}}_{(n)} \cdot \tilde{\boldsymbol{\Omega}}_2^{(n)} = -\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}}_{(n)} \cdot \tilde{\mathbf{u}}_2^{S,(n)}\,\mathrm{d}S + \iiint_{V_0} \widetilde{\boldsymbol{\Sigma}[\mathbf{u}_1]}^{(n)} : \nabla\hat{\mathbf{e}}_{(n)}\,\mathrm{d}V. \tag{101}$$

F. Time-averaged swimming kinematics

The most important component of the swimming kinematics is the $n = 0$ Fourier mode giving access to the time-average of the motion. In that case, the dual Newtonian problem in Eq. (62), $\hat{\mathbf{u}}$, occurs with viscosity $\mathcal{G}(n = 0) = \sum_i \eta_i \equiv \eta$. Using the notation $\langle f \rangle = \tilde{f}^{(0)}$, to denote time averaging, the integral formula giving the time-averaged swimming kinematics is given by

$$\hat{\mathbf{F}} \cdot \langle \mathbf{U}_2 \rangle + \hat{\mathbf{L}} \cdot \langle \mathbf{\Omega}_2 \rangle = -\iint_{S_0} \mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}} \cdot \langle \mathbf{u}_2^S \rangle \, \mathrm{d}S + \iiint_{V_0} \langle \mathbf{\Sigma}[\mathbf{u}_1] \rangle : \hat{\mathbf{e}} \, \mathrm{d}V. \tag{102}$$

G. Locomotion of a sphere

A special case of interest for exact calculations is that of a swimming of a spherical body of radius a. This is the Lighthill and Blake model[49,50] addressed in Sec. IV.

Inside the fluid, we have the velocity field given by

$$\hat{\mathbf{u}} = \frac{3}{4} a \left[\frac{\mathbf{1}}{r} + \frac{\mathbf{rr}}{r^3} \right] \cdot \hat{\mathbf{U}} + \frac{1}{4} a^3 \left[\frac{\mathbf{1}}{r^3} - \frac{3\mathbf{rr}}{r^5} \right] \cdot \hat{\mathbf{U}} + \frac{a^3}{r^3} \hat{\mathbf{\Omega}} \times \mathbf{r}, \tag{103}$$

with boundary conditions $\hat{\mathbf{u}} = \hat{\mathbf{U}} + \mathbf{\Omega} \times \mathbf{x}_0^S$ on the sphere. The surface stress then takes the form

$$\mathbf{n}_0 \cdot \hat{\boldsymbol{\sigma}} = -\frac{3\eta}{2a} \hat{\mathbf{U}} - 3\eta \hat{\mathbf{\Omega}} \times \mathbf{n}_0. \tag{104}$$

In that case, and focusing on the time-averaged locomotion, Eq. (102) becomes

$$\hat{\mathbf{F}} \cdot \langle \mathbf{U}_2 \rangle + \hat{\mathbf{L}} \cdot \langle \mathbf{\Omega}_2 \rangle = 6\pi a \eta \, \hat{\mathbf{U}} \cdot \overline{\langle \mathbf{u}_2^S \rangle} + 8\pi a^3 \eta \, \hat{\mathbf{\Omega}} \cdot (\overline{\mathbf{x}_0^S \times \langle \mathbf{u}_2^S \rangle}) + \iiint_{V_0} \langle \mathbf{\Sigma}[\mathbf{u}_1] \rangle : \hat{\mathbf{e}} \, \mathrm{d}V, \tag{105}$$

where overline indicates surface average, $\overline{w} = (\iint_{S_0} w \, \mathrm{d}S)/(4\pi a^2)$. We have $\hat{\mathbf{F}} = -6\pi \eta a \hat{\mathbf{U}}$ and $\hat{\mathbf{L}} = -8\pi \eta a^3 \hat{\mathbf{\Omega}}$. The hat flow field in Eq. (103) can be formally written as $\hat{\mathbf{u}} = \hat{\mathbf{P}} \cdot \hat{\mathbf{U}} + \hat{\mathbf{Q}} \cdot \hat{\mathbf{\Omega}}$ leading to $\hat{\mathbf{e}} = \hat{\mathbf{E}}(\hat{\mathbf{P}}) \cdot \hat{\mathbf{U}} + \hat{\mathbf{E}}(\hat{\mathbf{Q}}) \cdot \hat{\mathbf{\Omega}}$ using the definition for, an arbitrary second-order tensor, $\mathbf{T}$, of the third order tensor $\{\hat{\mathbf{E}}(\hat{\mathbf{T}})\}_{ijk} = \frac{1}{2}(\partial_i \hat{T}_{jk} + \partial_j \hat{T}_{ik})$. Considering separately $\hat{\mathbf{U}} = \mathbf{0}$ and $\hat{\mathbf{\Omega}} = \mathbf{0}$ we then obtain from Eq. (105)

$$\langle \mathbf{U}_2 \rangle = -\overline{\langle \mathbf{u}_2^S \rangle} - \frac{1}{6\pi \eta a} \iiint_{V_0} \langle \mathbf{\Sigma}[\mathbf{u}_1] \rangle : \hat{\mathbf{E}}(\hat{\mathbf{P}}) \, \mathrm{d}V, \tag{106}$$

$$\langle \mathbf{\Omega}_2 \rangle = -\overline{\mathbf{x}_0^S \times \langle \mathbf{u}_2^S \rangle} - \frac{1}{8\pi \eta a^3} \iiint_{V_0} \langle \mathbf{\Sigma}[\mathbf{u}_1] \rangle : \hat{\mathbf{E}}(\hat{\mathbf{Q}}) \, \mathrm{d}V, \tag{107}$$

with similar formulae available for each of the Fourier modes (modulo the correct definition of the complex viscosity for mode n).

VII. APPLICATION TO THE SCALLOP THEOREM

In addition to allowing the calculation of non-Newtonian swimming of biological and synthetic swimmers, our integral results allow us to formally revisit Purcell's scallop theorem[66] in the context of complex fluids. That theorem states that deformations which are not identical under a time-reversal symmetry (so-called non-reciprocal) are required to induce locomotion in Newtonian Stokes flows. Using the formalism of the Newtonian integral theorems from Sec. III, Eq. (11), reciprocal deformations are those for which $\langle \mathbf{u}^S \rangle = \mathbf{0}$ leading to $\langle \mathbf{U} \rangle = \langle \mathbf{\Omega} \rangle = \mathbf{0}$.

When considering the scallop theorem in non-Newtonian flows, two distinct points need to be addressed. The first is answering the question: Is the scallop theorem still valid in general? The answer is obviously no. Fluids with nonlinear rheology can be exploited to generate propulsion from time-reversible motion actuation.[28,30–32] The simplest way to see this from our results is to realize that the operators $\mathbf{\Sigma}[\mathbf{u}]$ appearing in Sec. V (Eq. (44)) and Sec. VI (Eq. (100)) are nonlinear operators acting on the flow field at the previous order. If that flow includes a time-varying component $\propto e^{i\omega t}$ induced by the time-reversible motion, then $\mathbf{\Sigma}[\mathbf{u}]$ will generate harmonics, with in general a nonzero time-average. A specific example will be given in Sec. VIII.

A second, more interesting point is whether there exists a categories of non-Newtonian fluids for which the scallop theorem would be remain valid. Our integral theorems can be used to show that for any linearly viscoelastic fluid a time-reversible actuation cannot lead to any net motion. In the case where the surface actuation is tangential to the swimmer surface, as addressed in Sec. IV, we obtain by simply applying Eq. (26) in the reciprocal case that $\hat{\mathbf{F}} \cdot \langle \mathbf{U} \rangle + \hat{\mathbf{L}} \cdot \langle \boldsymbol{\Omega} \rangle = 0$ and thus $\langle \mathbf{U} \rangle = \langle \boldsymbol{\Omega} \rangle = \mathbf{0}$. That result is true for arbitrary amplitude of the motion. When the surface motion includes a nonzero component normal to the shape, and thus leads to shape changes, we can apply the small-amplitude results of Sec. VI and Eq. (100). If the fluid is linearly viscoelastic, then we have $\boldsymbol{\Sigma} = \mathbf{0}$, leading to $\hat{\mathbf{F}} \cdot \langle \mathbf{U}_2 \rangle + \hat{\mathbf{L}} \cdot \langle \boldsymbol{\Omega}_2 \rangle = 0$ and therefore $\langle \mathbf{U}_2 \rangle = \langle \boldsymbol{\Omega}_2 \rangle = \mathbf{0}$. Here again we see that reciprocal swimming is not possible in a linearly viscoelastic fluid.

VIII. LOCOMOTION IN AN OLDROYD-B FLUID

A model of particular interest for the dynamics of polymeric fluids is the Oldroyd-B fluid, which can be derived formally from a dilute solution of elastic dumbbells.[57,58,61–65] We show here how to apply Eq. (100) for the Oldroyd-B fluid and consider the special case of squirming motion.

A. General framework

The constitutive equation for the Oldroyd-B fluid is written as

$$\boldsymbol{\tau} + \lambda \overset{\triangledown}{\boldsymbol{\tau}} = (\eta_s + \eta_p)\dot{\boldsymbol{\gamma}} + \eta_s \lambda \overset{\triangledown}{\dot{\boldsymbol{\gamma}}}, \tag{108}$$

where λ is the relaxation time for the fluid, η_s the solvent viscosity, and η_p the polymeric contribution to the viscosity. In Eq. (108), for any tensor $\mathbf{a}$, we write $\overset{\triangledown}{\mathbf{a}}$ to denote the upper convected derivative defined as

$$\overset{\triangledown}{\mathbf{a}} = \frac{\partial \mathbf{a}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{a} - ({}^t\nabla \mathbf{u} \cdot \mathbf{a} + \mathbf{a} \cdot \nabla \mathbf{u}). \tag{109}$$

Writing $\eta \equiv \eta_s + \eta_p$ for the total viscosity of the fluid and using the notation $\lambda_1 \equiv \lambda$ and $\lambda_2 \equiv \lambda \eta_s/\eta$, the constitutive law can be re-written as

$$\boldsymbol{\tau} + \lambda_1 \overset{\triangledown}{\boldsymbol{\tau}} = \eta \left(\dot{\boldsymbol{\gamma}} + \lambda_2 \overset{\triangledown}{\dot{\boldsymbol{\gamma}}} \right), \tag{110}$$

and λ_2 is referred to as the retardation time scale for the fluid. Note that in this model we always have $\lambda_2/\lambda_1 < 1$.

The expansion at order one of Eq. (110) leads to

$$\boldsymbol{\tau}_1 + \lambda_1 \frac{\partial \boldsymbol{\tau}_1}{\partial t} = \dot{\boldsymbol{\gamma}}_1 + \lambda_2 \frac{\partial \dot{\boldsymbol{\gamma}}_1}{\partial t}, \tag{111}$$

while the second order term gives

$$\left(1 + \frac{\partial}{\partial t}\lambda_1\right)\boldsymbol{\tau}_2 - \eta\left(1 + \frac{\partial}{\partial t}\lambda_2\right)\dot{\boldsymbol{\gamma}}_2 = \eta\lambda_2\left[\mathbf{u}_1 \cdot \nabla\dot{\boldsymbol{\gamma}}_1 - \left({}^t\nabla\mathbf{u}_1 \cdot \dot{\boldsymbol{\gamma}}_1 + \dot{\boldsymbol{\gamma}}_1 \cdot \nabla\mathbf{u}_1\right)\right] - \lambda_1\left[\mathbf{u}_1 \cdot \nabla\boldsymbol{\tau}_1 - \left({}^t\nabla\mathbf{u}_1 \cdot \boldsymbol{\tau}_1 + \boldsymbol{\tau}_1 \cdot \nabla\mathbf{u}_1\right)\right], \tag{112}$$

from which all Fourier terms can be computed. If we assume to have only one Fourier mode, $\propto e^{i\omega t}$, in the solution at order one, then we obtain from time-averaging Eq. (112) and exploiting Eq. (111) written in Fourier space the explicit expression for the time-averaged stress as second order as

$$\langle \boldsymbol{\Sigma}[\mathbf{u}_1] \rangle = 2\eta(\lambda_2 - \lambda_1)\mathcal{R}\left\{ \frac{1}{1 + i\lambda_1\omega}\left[\tilde{\mathbf{u}}_1^{(1),*} \cdot \nabla\tilde{\dot{\boldsymbol{\gamma}}}_1^{(1)} - \left({}^t\nabla\tilde{\mathbf{u}}_1^{(1),*} \cdot \tilde{\dot{\boldsymbol{\gamma}}}_1^{(1)} + \tilde{\dot{\boldsymbol{\gamma}}}_1^{(1)} \cdot \nabla\tilde{\mathbf{u}}_1^{(1),*}\right)\right]\right\}, \tag{113}$$

where stars denote complex conjugates and $\mathcal{R}$ the real part of a complex expression.

B. Squirming motion of a sphere

We now consider that the swimmer is a sphere undergoing tangential squirming motion. We further assume that all surface motion is axisymmetric so that the sphere does not rotate and only swims along a straight line, with direction $\mathbf{e}_z$. Using cylindrical coordinates with θ the polar angle, we thus assume that its surface deforms in time as

$$\theta = \theta_0 + \epsilon[f(\theta_0)\sin\omega t + g(\theta_0)\sin(\omega t + \phi)]. \tag{114}$$

The presence of a phase ϕ in Eq. (114) allows us to combine the periodic motion of two surface modes, characterized by the functions f and g, and includes in particular standing and traveling waves as special cases.

From Eq. (114) we can compute the surface velocity as

$$\mathbf{u}_1^S = a\frac{\partial\theta}{\partial t}\mathbf{e}_\theta = a\omega[f(\theta_0)\cos\omega t + g(\theta_0)\cos(\omega t + \phi)]\mathbf{e}_\theta, \tag{115}$$

with a surface gradient given by

$$\frac{\partial \mathbf{u}_1^S}{\partial\theta} = a\omega[f'(\theta_0)\cos\omega t + g'(\theta_0)\cos(\omega t + \phi)]\mathbf{e}_\theta. \tag{116}$$

We can then use these results to compute the surface velocity as second-order using Eq. (51b) and we obtain

$$\langle \mathbf{u}_2^S\rangle = -\left\langle \theta\frac{\partial \mathbf{u}_1^S}{\partial\theta}\right\rangle = \frac{a\omega}{2}\sin\phi[f(\theta_0)g'(\theta_0) - f'(\theta_0)g(\theta_0)]\mathbf{e}_\theta. \tag{117}$$

In order to take advantage of Blake's mathematical framework[50] we then choose the dimensionless functions

$$f(\theta) = \alpha\sin\theta\cos\theta, \quad g(\theta) = \beta\sin\theta. \tag{118}$$

From Eq. (117) we then obtain

$$\langle \mathbf{u}_2^S\rangle = \frac{\alpha\beta}{2}a\omega\sin\phi\sin^3\theta\,\mathbf{e}_\theta, \tag{119}$$

giving rise to average Newtonian swimming with order-2 speed, $\langle \mathbf{U}_2\rangle_N$, as

$$\langle \mathbf{U}_2\rangle_N = -\overline{\langle \mathbf{u}_2^S\rangle} = \frac{4\alpha\beta}{15}a\omega\sin\phi\,\mathbf{e}_z. \tag{120}$$

In order to compute the non-Newtonian correction to the swimming speed we need to compute $\mathbf{u}_1$ everywhere from the knowledge of $\mathbf{u}_1^S$. From Eq. (113) we see that all we need is the Fourier component, $\tilde{\mathbf{u}}_1$, of $\mathbf{u}_1$, which we obtain from Eq. (115) as

$$\mathbf{u}_1^S(a,\theta,t) = a\omega[f(\theta_0)\cos\omega t + g(\theta_0)\cos(\omega t + \phi)]\mathbf{e}_\theta = \tilde{\mathbf{u}}_1^{S,(1)}e^{i\omega t} + \tilde{\mathbf{u}}_1^{S,(-1)}e^{-i\omega t}, \tag{121}$$

with

$$\tilde{\mathbf{u}}_1^{S,(1)}(a,\theta) = \frac{a\omega}{2}(\alpha\sin\theta\cos\theta + \beta e^{i\phi}\sin\theta)\mathbf{e}_\theta, \tag{122}$$

and $\tilde{\mathbf{u}}_1^{S,(-1)} = \tilde{\mathbf{u}}_1^{S,(1)*}$. This surface velocity leads to unsteady swimming at order one as

$$\tilde{\mathbf{U}}_1^{(1)} = \frac{a\omega}{3}e^{i\phi}\beta\mathbf{e}_z. \tag{123}$$

The total velocity at the surface of the spherical swimmer in the laboratory frame, including the component from swimming, Eq. (123), is thus given by

$$\begin{aligned}\tilde{\mathbf{u}}_1^{(1)}(a,\theta) &= \frac{a\omega}{2}(\alpha\sin\theta\cos\theta + \beta e^{i\phi}\sin\theta) + \frac{a\omega}{3}\beta e^{i\phi}(\cos\theta\mathbf{e}_r - \sin\theta\mathbf{e}_\theta)\\ &= \frac{a\omega}{6}[\alpha\tilde{\mathbf{u}}_\alpha^{(1)}(a,\theta) + \beta e^{i\phi}\tilde{\mathbf{u}}_\beta^{(1)}(a,\theta)],\end{aligned} \tag{124}$$

where we have denoted

$$\tilde{\mathbf{u}}_\alpha^{(1)}(a,\theta) = 3\sin\theta\cos\theta\,\mathbf{e}_\theta, \quad \tilde{\mathbf{u}}_\beta^{(1)}(a,\theta) = 2\cos\theta\,\mathbf{e}_r + \sin\theta\,\mathbf{e}_\theta. \tag{125}$$

The solution to the Stokes flow problem at first order with these boundary conditions is given by Blake[50] and we obtain

$$\tilde{\mathbf{u}}_\alpha(r,\theta) = \frac{3}{2}(3\cos^2\theta - 1)\left(\frac{a^4}{r^4} - \frac{a^2}{r^2}\right)\mathbf{e}_r + 3\frac{a^4}{r^4}\sin\theta\cos\theta\,\mathbf{e}_\theta, \tag{126a}$$

$$\tilde{\mathbf{u}}_\beta(r,\theta) = 2\frac{a^3}{r^3}\cos\theta\,\mathbf{e}_r + \frac{a^3}{r^3}\sin\theta\,\mathbf{e}_\theta. \tag{126b}$$

C. Non-Newtonian squirming

With this solution we can then compute the non-Newtonian term in Eq. (106). Rewriting Eq. (106) as

$$\langle \mathbf{U}_2 \rangle = \langle \mathbf{U}_2 \rangle_N + \langle \mathbf{U}_2 \rangle_{NN}, \tag{127}$$

above we computed

$$\langle \mathbf{U}_2 \rangle_N = \frac{4\alpha\beta}{15}\, a\omega \sin\phi\, \mathbf{e}_z, \tag{128}$$

and recall that we have from the integral theorem

$$\langle \mathbf{U}_2 \rangle_{NN} = -\frac{1}{6\pi\eta a}\iiint_{V_0} \langle \boldsymbol{\Sigma}[\mathbf{u}_1]\rangle : \hat{\mathbf{E}}(\hat{\mathbf{P}})\,\mathrm{d}V. \tag{129}$$

An explicit calculation for the integrand exploiting Eq. (103) leads to the final result

$$\langle \mathbf{U}_2 \rangle_{NN} = a\omega\frac{\alpha\beta}{15}\left[\frac{(\cos\phi + 4\mathrm{De}_1\sin\phi)(\mathrm{De}_2 - \mathrm{De}_1)}{\mathrm{De}_1^2 + 1}\right]\mathbf{e}_z, \tag{130}$$

where we have defined the two Deborah numbers for the flow, $\mathrm{De}_1 = \lambda_1\omega$ and $\mathrm{De}_2 = \lambda_2\omega$. The ratio between the magnitudes of non-Newtonian and Newtonian velocities is given by

$$\frac{\langle U_2\rangle_{NN}}{\langle U_2\rangle_N} = \frac{(\cos\phi + 4\mathrm{De}_1\sin\phi)(\mathrm{De}_2 - \mathrm{De}_1)}{4\sin\phi(1 + \mathrm{De}_1^2)}. \tag{131}$$

The results of Eqs. (130) and (131) can be used to obtain a number of interesting conclusions. First, we can pick the value of the phase, ϕ, which will lead to reciprocal motion (physically, a standing wave of actuation along the swimmer surface), $\sin\phi = 0$. This leads to $\langle U_2\rangle_N = 0$ while $\langle U_2\rangle_{NN} \neq 0$, indicating, as announced in Sec. VII, that an Oldroyd-B fluid can be used to induce reciprocal swimming.

For a phase $\phi = \pi/2$ where the two surface modes are completely out of phase, we then obtain a ratio

$$\frac{\langle U_2\rangle_{NN}}{\langle U_2\rangle_N} = \frac{\mathrm{De}_1(\mathrm{De}_2 - \mathrm{De}_1)}{1 + \mathrm{De}_1^2}. \tag{132}$$

This is identical to the small-amplitude result for Taylor's swimming sheet in a viscoelastic fluid[15] whose kinematics are that of a traveling wave. Indeed a traveling wave of the form $\cos(kx - \omega t)$ can be interpreted as the linear superposition of two standing waves out of phase with each other. Since we always have $\lambda_2 < \lambda_1$, this means that $\mathrm{De}_2 < \mathrm{De}_1$, and therefore the ratio $\langle U_2\rangle_{NN}/\langle U_2\rangle_N$ in Eq. (132) is negative, indicating that in this case viscoelastic stresses slow down the swimmer. By comparing the total swimming velocity to the Newtonian one we obtain in this case

$$\frac{\langle U_2\rangle_N + \langle U_2\rangle_{NN}}{\langle U_2\rangle_N} = \frac{1 + \mathrm{De}_1\mathrm{De}_2}{1 + \mathrm{De}_1^2}, \tag{133}$$

and thus non-Newtonian swimming occurs always in the same direction as its Newtonian counterpart, but with a decreased magnitude.

Third, we see by taking the limit of Eq. (131) for large values of De that

$$\lim_{\mathrm{De}\to\infty} \frac{\langle U_2\rangle_{NN}}{\langle U_2\rangle_N} = \frac{\mathrm{De}_1(\mathrm{De}_2 - \mathrm{De}_1)}{1+\mathrm{De}_1^2}, \tag{134}$$

which is the same result as Eq. (132) (and Eq. (133) remains valid in this limit). Independently of the phase, at high Deborah number the swimming speed always ends up being decreased by viscoelasticity.

Finally, we can use Eq. (131) to obtain a class of Newtonian swimmers whose propulsion speeds are increased by the presence of viscoelasticity. To obtain increase swimming we need $\langle U_2\rangle_{NN}$ and $\langle U_2\rangle_N$ to be of the same sign, and thus from Eq. (131) we see that this is equivalent to the mathematical requirement

$$\cot\phi < -4\mathrm{De}_1. \tag{135}$$

For a fixed value of De_1, we can find values of the phase between 0 and 2π which satisfy Eq. (135), leading thus to enhanced swimming at that Deborah number. Since $\langle U_2\rangle_{NN}$ is zero for zero Deborah number and since we have the asymptotic result of Eq. (134) at large values, we would obtain a maximum of the swimming speed at an intermediate value of Deborah numbers in this case. In fact, a small-De expansion of Eq. (131) shows that

$$\frac{\langle U_2\rangle_{NN}}{\langle U_2\rangle_N} \sim \frac{\mathrm{De}_2 - \mathrm{De}_1}{4\tan\phi} + O(\mathrm{De}_1^2, \mathrm{De}_1\mathrm{De}_2), \tag{136}$$

and thus we will obtain a range of Deborah numbers with enhanced viscoelastic swimming in all cases where $\tan\phi < 0$. The critical Deborah number beyond which viscoelasticity always decreases swimming is given by Eq. (135).

IX. CONCLUSION

In this paper, we derived three general integral theorems to quantity the locomotion of isolated swimmers in non-Newtonian fluids by adapting classical work on the transport of small particles in non-Newtonian flows to the case of self-propulsion. The first theorem was valid for squirmers undergoing purely tangential deformation in linearly viscoelastic fluids, and in that case the swimming kinematics were obtained to be identical to the Newtonian case. The second theorem was valid for large, arbitrary, swimmer deformation but assumed small viscoelastic behavior, for example, a small Deborah number for a viscoelastic fluid or small Carreau number for a generalized Newtonian flow. The final theorem allowed order-one Deborah number but assumed that the deformation was time-periodic and of small-amplitude. That third derivation, significantly more lengthy but more general than the previous two, exploited results of vector calculus and differential geometry to obtain a final integral formula valid for a wide class of non-Newtonian and surface-deformation models. In all three cases, the final integrals require at most the mathematical knowledge of a series of Newtonian flow problems, and will be useful to quantity the locomotion of biological and synthetic swimmers in complex environments.

Our results were then used to show that, generically, the scallop theorem should not be expected to hold in the presence of non-Newtonian stresses. An explicit example of a swimmer unable to move in a Newtonian fluid but swimming in presence of elastic stresses in an Oldroyd-B fluid was derived. We further demonstrated that there was no *a priori* relationship between the direction and magnitude of the non-Newtonian and Newtonian components of the swimming kinematics. Specific examples were derived where small-amplitude Newtonian locomotion could be either enhanced or decreased in an Olrdoyd-B fluid. Past experimental and computational results are therefore not necessarily in contradiction with each other, and changing kinematics or rheological properties can qualitatively impact the non-Newtonian influence on swimming. Future computational work will be necessary to fully untangle the relative effects of elastic vs. shear-dependent stresses.

Furthermore, and in the same way that our work was inspired by classical derivations on the motion of solid particles, the results in our paper could be adapted to address the migration of particles in oscillatory shear flows where recent experiments[67] and numerical simulations[68] under confinement have shown interesting dynamics, including an instantaneous inversion of the direction of the wall-induced force at high frequencies as well as the presence of dead zones with very little viscoelastic migration.

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