# Modeling a spheroidal squirmer through a complex fluid

Zhenyu Ouyang<sup>0</sup>,<sup>1</sup> Chen Liu<sup>1</sup>,<sup>1</sup> Zhaowu Lin<sup>1</sup>,<sup>2,\*</sup> and Jianzhong Lin<sup>1,2</sup>

<sup>1</sup>Laboratory of Impact and Safety Engineering (Ningbo University), Ministry of Education, Ningbo 315201, China

<sup>2</sup>Department of Mechanics, State Key Laboratory of Fluid Power and Mechatronic Systems, Zhejiang University, Hangzhou 310027, China

(Received 29 February 2024; accepted 24 June 2024; published 23 July 2024)

We simulate a spheroidal swimmer through a complex fluid, modeled by the Giesekus constitutive equation incorporating fluid inertia. We develop a spheroidal swimmer model and exert it in a direct-forcing fictitious domain method framework. This model extends the conventional spherical "squirmer," representing a microswimmer generating self-propulsion through tangential surface waves at its boundaries. We vary the swimmer's aspect ratio (AR) and Weissenberg number (Wi; the ratio of fluid elastic force to viscous force), respectively, in the range of  $1.5 \leq AR \leq 8$  and  $0.5 \leq Wi \leq 10$ . Our results show that, an inertial spheroidal puller with a small  $|\beta|$  (a swimming intensity parameter) swims faster than the counterpart subjected to the Stokes flow regime-a departure from the observed pattern in spherical pullers. Within the Giesekus fluid medium, an augmented mobility factor  $\alpha$  correlates with an increased squirmer velocity, while a larger AR contributes significantly to the speed enhancement of a neutral squirmer in the presence of fluid inertia. Meanwhile, we explore the squirmer's energy expenditure and hydrodynamic efficiency, finding that a slenderer, inertial squirmer with a vigorous swimming intensity expends more energy, contrasting with the reduced energy expenditure associated with a smaller intensity. Notably, a larger AR positively correlates with squirmer efficiency, displaying an advantageous relationship with swimming speed.

DOI: 10.1103/PhysRevFluids.9.073303

# I. INTRODUCTION

Locomotion of microswimmers in complex (nonlinear) fluids causes considerable attention due to their relevance in various biological processes, medicine, and technological applications [1–5]. Examples of such typical problems include the mammalian sperm swimming in the fallopian tubes [6], the diffusion and reproduction of algae in lakes [7], and utilizing micro/nanorobots for directed drug delivery and precision surgery [8]. Specifically, the active system composed of a large number of microswimmers exhibits remarkable nonequilibrium phenomena and emergent behavior like swarming [9], turbulence [10,11], and activity-induced clustering and phase transitions [12,13]. A comprehensive grasp of the hydrodynamics of individual microswimmers within complex fluids holds significance in advancing scientific understanding by elucidating collective behaviors and, in practical terms, designing efficient swimming devices in various applications.

Many natural microswimmers utilize synergistic oscillating flagella and cilia (short flagella) for locomotion. For example, *Chlamydamonas* (green algae) uses its cilia to generate thrust from the front, performing a breast-stroke-like motion. *Escherichia coli* employs the oscillating flagella to generate thrust from the rear for self-propelling. These microswimmers can be classified

<sup>\*</sup>Contact author: linzhaowu@zju.edu.cn

into pullers (*Chlamydamonas*) and pushers (*E. coli*) based on their different thrust types. The "squirmer," a classical microswimming model established by Lighthill [14] and extended by Blake [15], is widely adopted to mimic the self-propulsion of a swimmer with a dense array of cilia on its surface. This model can reoccur the flow field around both the puller and the puller-type microswimmers by adjusting a swimming parameter [16–20], and it has successfully simulated many microswimming scenarios, including the microorganisms' nutrient uptake [21,22], their swimming in a non-Newtonian fluid [23], swirling motion [24], hydrodynamic interactions with a wall [25,26], the two-body hydrodynamic interactions [27–30], and the collective swimming dynamics [13,31,32].

While the squirmer model is adequate for microswimmers like Volvox, many organisms such as E. coli, Chlamydomonas, Paramecium, and Tetrahymena appear as nonspherical shapes in nature. Hence, to better represent the ciliates of these microswimmers, an appropriate extension of the squirmer model adapted to the spheroidal objects is desirable. To investigate the effect of geometrical shape on ciliary locomotion, Keller and Wu [33] first generalize the squirmer model to a prolate spheroidal body of arbitrary eccentricity. This model can mimic the swimming of biological microswimmers such as Tetrahymenapyriformis, Spirostomum ambiguum, and Paramecium multimicronucleatum. Subsequently, a force-dipole mode has been incorporated into the spheroidal model, successfully simulating other types of swimmers. Ishimoto and Gaffney [25] have theoretically explored the boundary behavior of axisymmetric squirmers in an inertialess Newtonian fluid near a no-slip interface and also a free surface, demonstrating the stable and unstable limit cycles. Theers et al. [34] implement the spheroidal squirmer model into the multiparticle collision dynamics approach and study the cooperative swimming in a narrow slit, finding that two pullers can swim cooperatively, forming a wedgelike conformation with a small constant angle. Pöhnl et al. [35] study the motion of a spheroidal and axisymmetric squirmer in an unbounded fluid analytically. They conclude that the squirming modes beyond the second can be as important as the first two concerning the contributions to the velocity and stresslet of the particle. More recently, van Gogh et al. [36] examined the effect of geometrical shape upon locomotion in a shear-thinning fluid using the prolate spheroidal squirmer model, finding that the spheroidal squirmers have advantages over spherical ones in terms of both swimming speed and energetic efficiency. In contrast, a recent work [37] indicates that a swimmer with a large aspect ratio (AR; a larger AR indicates a slenderer body) yields a slow swimming speed, and an aspect ratio of 2 is found to be the most hydrodynamically efficient. This controversy requires clarification.

While numerous studies have explored the swimming behavior of spheroidal squirmers in a Newtonian fluid, it is noteworthy that these investigations have primarily focused on the limit of the Stokes flow regime (the problem is linear, neglecting the effect of fluid inertia). In nature, many micron-sized aquatic microorganisms swimming in their escape from predators achieve a finite Reynolds number ranging from 1 to10 [38–43]. Larger microorganisms, such as the millimeter-sized copepods and *Pleurobrachia*, commonly achieve Re(10) [40]. This swimming is beyond the Stokes flow regime, and the fluid inertia can remarkably affect the microswimmers' motion, both enhancing or hindering their speed [44–47], unstabilizing the puller-type swimmers [17,48], modifying the contact time between a swimmer with solid boundaries and another swimmer [49,26], and weakening the collective dynamics [50]. Consequently, a need arises to comprehend how finite fluid inertia (a typical nonlinear behavior of fluids) and the geometric configuration of microswimmers may interact competitively or synergistically, impacting their swimming speed and hydrodynamic efficiency.

The investigation of squirming dynamics in non-Newtonian fluids has garnered significant attention recently, primarily driven by its relevance to numerous physiological processes. For instance, the bacteria *E. coli* resides in the mucus of the intestine [51] and *Borrelia burgdorferi* traverses the extracellular matrix of mammalian skin [52]. The fluids where the microswimmers are immersed commonly exhibit another typical nonlinear behavior—viscoelasticity. Recent efforts indicate that fluid viscoelasticity can significantly modify the microswimmers' speed [53], the flow structure near the body [37], and the rheological behavior of the fluid [54]. More importantly, there is controversy over whether fluid elasticity increases or hinders the movement of microorganisms. For instance, the bacteria *Chlamydomonas reinhardtii* and *E. coli* appear to swim significantly faster in viscoelastic fluids or a polymer solution than in a Newtonian fluid [55], in contrast to the hindrance of the viscoelasticity for the algal cell *C. reinhardtii* [56]. Researchers have tried to clarify this controversy using the spherical squirmer model, in which the induced wake behind the neutral squirmer may lead to a slower speed in a viscoelastic fluid than in a Newtonian fluid [37]. However, a contrary result can be achieved by adding a swirling motion at the squirmer [24]. In summary, the coupling effects of microswimmers' geometrical features and the fluid viscoelastic nature complicate their swimming. Moreover, hydrodynamic interactions with diverse self-propulsion modes exert a substantial impact on swimming velocity, energy consumption, and hydrodynamic efficiency [57,58]. Thus, further exploration into the intricate relationship between fluid viscoelasticity and microswimmer geometry is warranted. Understanding how these factors competitively or synergistically alter the hydrodynamic interaction between the squirmer and fluids is crucial for comprehending variations in swimming speed and hydrodynamic efficiency.

This paper utilizes a direct-forcing fictitious domain (DF-FD) method to examine the propulsion dynamics of a spheroidal swimmer in the presence of both viscoelastic and fluid inertia effects. We aim to elucidate how the fluid inertia, elasticity, and the microswimmers' geometrical shape competitively or synergistically affect the swimmer's hydrodynamics. To achieve this objective, we initially derived the solution for the flow within the spheroidal squirmer by incorporating the tangential velocity boundary condition, thereby adapting the model to the current DF-FD method framework. The remainder of this paper is organized as follows. Section II briefly states the DF-FD method and the dynamics of the spheroidal squirmer. Following this, we meticulously validate the steady speed of our spheroidal squirmer model against existing analytical solutions and establish the parameters for calculations in Sec. III. Section IV presents the results, including the squirmers' swimming speeds, the force decoupling analysis, energy expenditure, and hydrodynamic efficiency. In Sec. V, some concluding remarks are finally given.

#### **II. NUMERICAL SCHEME AND SPHEROIDAL SQUIRMER MODEL**

An interface-resolved DF-FD method proposed by Yu and Shao [59] is employed here to simulate a spheroidal squirmer through a fluid. The basic strategy of this method is that the interior of the body (e.g., solid squirmer) fills with a fictitious fluid, and a pseudo-body force is considered over the body's inner domain to enforce the fictitious fluid to satisfy the rigid-body motion constraint when dealing with hydrodynamic interactions between the body and the fluid. Briefly, we demonstrate the following nondimensional FD formulation for an incompressible fluid which contains three parts. Let  $P_0$  denote the solid domain and  $\Omega$  the entire domain including the interior and exterior of the solid body. We adopt the following scales for the nondimensionalization: H for length,  $U_0$  for velocity,  $H/U_0$  for time,  $\rho_f U_0^2$  for the pseudo-body force with  $\rho_f$  being the fluid density. For the present problem, the following equation must be coupled and solved in full.

(a) Fluid momentum equations

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} = \frac{\eta_r \nabla^2 \mathbf{u}}{\text{Re}} - \nabla p + \frac{(1 - \eta_r) \nabla \cdot \mathbf{B}}{\text{Re Wi}} + \lambda \text{ in } \Omega, \qquad (2.1)$$

where **u** and *p* are the fluid velocity and pressure, respectively;  $\lambda$  is the vectorial Lagrange multiplier (pseudo-body force); the Reynolds number is defined by Re =  $\rho_f U_0 H/\eta_0$  ( $\eta_0$  denoting the total zero-shear-rate viscosity of the fluid  $\eta_0 = \eta_s + \eta_p$ , and  $U_0$  representing the characteristic velocity of a spheroidal squirmer which we will introduce later).  $\eta_s$  and  $\eta_p$  are, respectively, the fluid solvent viscosity and polymer viscosity, and  $\eta_r$  denotes the ratio of the solvent viscosity ( $\eta_s$ ) to the total zero-shear-rate viscosity of the fluid ( $\eta_0$ ). When  $\eta_r = 1$ , the medium degenerates into Newtonian fluids. For a viscoelastic fluid, the Weissenberg number Wi =  $\lambda_t U_0/H$  ( $\lambda_t$  being the fluid relaxation time) is adopted here. **B** denotes the polymer configuration tensor related to the polymer stress tensor  $\tau = \eta_p (\mathbf{B} - \mathbf{I})/\lambda_t$ . The fluids in the solid domain satisfy the rigid-body motion constraints:

$$\mathbf{u} = \mathbf{U} + \boldsymbol{\omega}_s \times \mathbf{r} + \mathbf{u}_s \text{ in } P_0, \tag{2.2}$$

$$(\rho_r - 1)V_s^* \frac{\mathrm{d}\mathbf{U}}{\mathrm{d}t} = -\int_{P_0} \boldsymbol{\lambda} \,\mathrm{d}\mathbf{x},\tag{2.3}$$

$$(\rho_r - 1)\mathbf{J}^* \frac{\mathrm{d}\boldsymbol{\omega}_s}{\mathrm{d}t} = -\int_{P_0} \mathbf{r} \times \mathbf{\lambda} \,\mathrm{d}\mathbf{x},\tag{2.4}$$

where **r** is the position vector concerning the spheroidal squirmer's mass center; **U** and  $\boldsymbol{\omega}_s$  are its translational and angular velocities; **u**<sub>s</sub> denotes the velocity distribution for the spheroidal squirmer dynamics which we will introduce later;  $\rho_r$  is the squirmer-fluid density ratio,  $\rho_r = \rho_s/\rho_f$ , here  $\rho_r = 1$ ;  $V_p^*$  is the dimensionless volume defined by  $V_p^* = V_p/H^3$  with  $V_p$  being the squirmer's volume, and **J**<sup>\*</sup> is the dimensionless moment of inertia with  $\mathbf{J}^* = \mathbf{J}/\rho_s H^5$ .

(b) Continuity equation:

$$\nabla \cdot \mathbf{u} = 0 \text{ in } \Omega. \tag{2.5}$$

(c) For a viscoelastic fluid, we employed the Giesekus constitutive model here:

$$\frac{\partial \mathbf{B}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{B} - \mathbf{B} \cdot \nabla \mathbf{u} - (\nabla \mathbf{u})^T \cdot \mathbf{B} + \frac{\alpha}{W_i} (\mathbf{B} - \mathbf{I})^2 + \frac{\mathbf{B} - \mathbf{I}}{W_i} = 0 \text{ in } \Omega, \qquad (2.6)$$

where  $\alpha$  is the mobility parameter to quantify the shear-thinning effect ( $\alpha = 0$  gives the Oldroyd-B constitutive model with constant viscosity). We decouple Eqs. (2.1)–(2.6) into the fluid, particle, and viscoelastic subproblems using a fractional-step time method. For more details on the discrete schemes, one can refer to the work of [59,60]. Note that for a high Wi problem, numerical instability or low-accurate results may occur, mainly due to the lack of symmetry and positive definiteness of the configuration tensor **B** when calculating Eq. (2.6). Hence, we employ the scheme proposed by Vaithianathan and Collins [61] to solve Eq. (2.6), using the usual Cholesky analysis for a real symmetric and positive-definite matrix. One can refer to our previous work for more details of our code's implementation and validations [23]. In this study, we discretize the convection term using the MUSCL (a high-precision monotone upstream-centered scheme for conservation laws) scheme, and the fourth-order Runge-Kutta method is employed for time integration.

In the spherical squirmer model, a progressive waving envelope is introduced to mimic both radial and angular oscillations at the boundary of a microswimmer with arrays of cilia like *Volvox* [18]. A reduced-order squirmer, which only considers the steady tangential motion on its surface, has been extensively adopted to investigate the microswimming mechanisms under various background flows. This reduced-order squirmer model gives a tangential boundary condition at a spherical body's surface (in the framework of reference moving with the body) for self-propelling, and it reads

$$\mathbf{u}_{s}^{b} = u_{\theta}^{s}(\theta)\mathbf{e}_{\theta} = (B_{1}\sin\theta + B_{2}\sin\theta\cos\theta)\mathbf{e}_{\theta}, \qquad (2.7)$$

where  $\theta$  is the angle concerning the swimming direction, and  $B_1$  and  $B_2$  are the first two squirming modes (parameters).  $\mathbf{e}_{\theta}$  is the unit vector along the polar direction. The squirmer can be categorized into a puller ( $\beta > 0$ , e.g., *Chlamydomonas*), pusher ( $\beta < 0$ , e.g., *E. coli*), and neutral squirmer ( $\beta = 0$ ), respectively, based on the values of  $\beta = B_2/B_1$  ( $B_1 > 0$ ) [31]. In the Stokes flow regime, the steady swimming speed of a squirmer through a Newtonian fluid is  $U_0 = 2B_1/3$  [14]. In the framework of the present DF-FD method, a solenoidal volumetric velocity  $\mathbf{u}_s$  is derived [using the boundary condition, Eq. (2.7)] and exerted at the whole spherical solid domain (inside) to realize the self-propelling of the body [47,48,50,62], and it reads

$$\mathbf{u}_{s} = \left[ \left(\frac{r}{a}\right)^{m} - \left(\frac{r}{a}\right)^{m+1} \right] \left( u_{\theta}^{s} \cot \theta + \frac{du_{\theta}^{s}}{d\theta} \right) \mathbf{e}_{r} + \left[ (m+3) \left(\frac{r}{a}\right)^{m+1} - (m+2) \left(\frac{r}{a}\right)^{m} \right] u_{\theta}^{s} \mathbf{e}_{\theta}, \quad (2.8)$$



FIG. 1. Schematic of a spheroidal squirmer swimming in an infinite flow (the gray arrow indicates the swimming direction).

where *a* is the radius of the spherical squirmer, *r* is the distance from the squirmer's center, and  $\mathbf{e}_r$  is the unit vector along the radial direction; *m* is an arbitrary positive integer, and usually m = 5 is adopted.

Similarly, we employ the tangential boundary condition of the spherical squirmer with the first  $(B_1)$  and second  $(B_2)$  modes and generalize to the spheroidal squirmer model. The tangential boundary condition at the surface of the spheroidal squirmer reads [34]

$$\mathbf{u}_{\mathbf{s}}^{b_{-}e} = -B_1(\mathbf{s} \cdot \mathbf{e}_z)\mathbf{s} - B_2\zeta(\mathbf{s} \cdot \mathbf{e}_z)\mathbf{s}$$
$$= -B_1\tau_0(1+\beta\zeta)\sqrt{\frac{1-\zeta^2}{\tau_0^2-\zeta^2}}\mathbf{e}_\zeta, \qquad (2.9)$$

where unit tangent vectors on the spheroidal surface are given by the basis vector as  $\mathbf{s} = -\mathbf{e}_{\zeta}$ , and  $\mathbf{e}_z$  denotes the unit vector in the *z*-axis direction. Here, we define  $\tau_0 = 1/e$  ( $e = c/b_z$  is the eccentricity with  $c = \sqrt{b_z^2 - b_x^2}$ ) with  $\tau > \tau_0$  corresponding to the fluid domain exterior to the surface ( $\tau = \tau_0$ ) of the squirmer (see Fig. 1). In the spherical limit  $\mathbf{s} \to \mathbf{e}_{\theta}$ , the present squirming velocity [Eq. (2.9)] reduces to the spherical squirmer boundary condition [Eq. (2.7)]. To implement the spheroidal squirmer model in our DF-FD method, one needs to derive the solenoidal volumetric velocity within the spheroidal body [similar to Eq. (2.8)] based on the boundary condition, Eq. (2.9). Having meticulously addressed the flow problem, we have successfully obtained the velocity results within the reference framework moving with the body (see the Appendix for the details of the derivation). It reads

$$\mathbf{u}_{\mathrm{s}}^{e} = \mathbf{v},\tag{2.10}$$

where  $\mathbf{v}$  is denoted as Eq. (A6). We employ the periodic boundary conditions at all the boundaries to simulate the infinite flow field, and it reads

$$f(x,t) = f(x+K,t),$$
 (2.11)

where f(x) denotes any physical quantity, and K is the period length of the flow field (see Fig. 1; K = W, R, and L in the x, y, and z axis, respectively). The motion of a spheroidal squirmer is governed by Eqs. (2.3) and (2.4). One can refer to our previous work [23,50,62,63] for the details of the squirmer dynamics in the framework of the DF-FD method.

# **III. VALIDATION OF A SPHEROIDAL SQUIRMER**

The present DF-FD method has shown to be accurate in coping with the swimming of a spherical squirmer in a Newtonian fluid at Re = 0 [50] and the finite Re [62], as well as in the Giesekus viscoelastic fluids [23] when compared with the available theoretical solution and the numerical results. This section first validates a spheroidal squirmer through a Newtonian fluid. For a spherical



FIG. 2. Comparing the steady swimming speed of a spheroidal squirmer with AR (Re = 0.01).

squirmer, a computational domain with  $R \times W \times L = [-16a, 16a] \times [-16a, 16a] \times [-16a, 16a]$ , is shown to be convergent in simulating a viscoelastic and infinite flow field [23]. Accordingly, we adopt the adjustable calculation domains to ensure that the flow field in each axial direction of the spheroidal squirmer is greater than  $16a_e$ , in which  $a_e$  denotes a radius in the corresponding axis. Note that the squirmer's translation and rotation in the x and y axes are restricted, if not otherwise specified. For this squirming problem, the spheroidal squirmer's equivalent radius a and the self-propelling parameter  $B_1$  [see Eq. (2.9)] are adopted as the characteristic length and velocity, respectively. Hence, the Reynolds and Weissenberg numbers are respectively defined by  $Re = \rho_f aB_1/\eta_0$  and  $Wi = \lambda_t B_1/a$ . Upon enforcing the force-free condition for steady swimming, the speed of a spheroidal squirmer in a Newtonian fluid is given as [33,34]

$$U_0 = B_1 \tau_0 [\tau_0 - (\tau_0^2 - 1) \operatorname{coth}^{-1} \tau_0], \qquad (3.1)$$

where  $\tau_0 = 1/e$  with *e* being the eccentricity of the squirmer [see Eq. (2.9)]. Note that this expression is derived in the Stokes flow regime, and it applies to the swimming of a neutral spheroidal squirmer ( $\beta = 0$ ) in an inertial flow since it generates no vorticity [48]. The swimming Reynolds number here is set to Re = 0.01 at which the effects of the inertia on the swimming speed can be neglected [44]. The spheroidal squirmer is initially released at the center (origin of the coordinate system) of the domain with its orientation directed along the *z* axis, and its velocity reaches a steady state after the initial transient dynamics. A mesh size of more than  $18\Delta x$  across the spheroidal squirmer's radius of the rotational axis and a time step  $\Delta t = 5 \times 10^{-4}$  are adopted here. As shown in Fig. 2, the steady swimming speeds of the squirmer with AR agree well with the theoretical result.

Subsequently, we consider the effect of the mesh resolution on a neutral squirmer through the Giesekus viscoelastic fluids at Wi = 2, employing the maximum aspect ratio (AR = 8) utilized in this study. The viscosity ratio  $\eta_r = 0.5$  and mobility factor  $\alpha = 0.2$  are employed, if not otherwise specified. Figure 3 presents the transient dynamics, demonstrating excellent agreement in the evolution of the squirmers' speed across two different resolutions (the relative error is less than 1%). This observation suggests that a resolution of  $18\Delta x$  across the radius of the rotational axis of the spheroidal squirmer, which is employed as a minimum requirement in subsequent calculations, yields convergent results.



FIG. 3. (a) Comparing the transient speed of a spheroidal squirmer (AR = 8) with different mesh resolutions (Re = 0.01; Wi = 2); (b) steady velocity contour lines around the spheroidal squirmer in the swimming direction velocity (top half:  $a_r = 9\Delta x$ ; bottom half:  $a_r = 18\Delta x$ ).  $a_r$  denotes the spheroidal squirmer's radius of the rotational axis.

## **IV. RESULTS AND DISCUSSION**

In this section, we simulate the swimming of a spheroidal squirmer under the influence of fluid inertia and/or elasticity. The AR and Wi are varied within the respective ranges of  $1.5 \leq AR \leq 8$  and  $0.5 \leq Wi \leq 10$ . The calculation parameters outlined in Sec. III are applied unless otherwise specified. In the subsequent subsections, we initially examine the effect of fluid inertia on the swimming behavior of a spheroidal squirmer. Subsequently, we investigate the hydrodynamics of a spheroidal squirmer through the Giesekus fluids. The force contributions on the squirmer are later decoupled and analyzed. Finally, we discuss the energy expenditure and hydrodynamic efficiency.

# A. Fluid inertia can speed up a spheroidal puller with a small swimming intensity $\beta$

The steady swimming speed of the squirmers in an unconfined flow is achieved after transient dynamics, as shown in Fig. 4. As the Navier-Stokes equations are resolved fully in this study, Re determines the nonlinearity of the Newtonian fluids. The theoretical solutions and our results show that the increased AR results in a monotonic increase in a squirmer's speed at the Stoke flow regime (all the squirmers have an identical volume). However, in the work of Zhu et al. [37], the spheroidal squirmer with a larger AR yields a slower speed. This is because their definition of the tangential velocity distribution on the spheroidal body for self-propelling is different from ours (their model is not based on a generalization under the strict ellipsoidal coordinate systems, and the velocity distribution of the swimmer surface may not guarantee that it is tangent to the surface), while both the spheroidal squirmers degenerate to the classical spherical squirmer as the AR tends to be 1. With the inclusion of fluid inertia (e.g., Re = 5), the speed of the spheroidal puller (pusher) with  $|\beta| = 3$  is hindered (enhanced), in contrast to the behavior observed in the Stokes flow regime (no variation for all squirmers). This pattern is similar to that of a spherical squirmer [17,62]. The main finding in this section is that the inertial puller (Re = 5) with a small swimming intensity ( $\beta = 0.5$ ) swims faster than the counterpart subjected to the Stokes flow regime (compared to the theoretical solution). To illustrate the possible mechanism for this result, we plot a schematic, as shown in Fig. 5. Generally, an inertial puller is "pulled" by the flows it induced earlier [denoted by the solid arrows as in Fig. 5(b)], leading to the hindrance in its speed [48]. This contrasts with a puller falling into the Stoke flow regime [see Fig. 5(a)]. This mechanism applies to the spherical puller regardless of  $\beta$ . Note that for a spherical puller with a small  $\beta$  (e.g.,  $\beta = 0.5$ ), the flows inside the body should be more significant than those with a large  $\beta$  (but the inside flows are still weaker than the induced



FIG. 4. Steady swimming speed of a spheroidal squirmer through a fluid at Re = 5. (a) Effect of the AR; (b) effect of the puller's swimming intensity  $\beta$ . The red curve in (a) denotes Eq. (3.1); the dotted curves in (b) indicate the specified values of Eq. (3.1) at different AR.

flows near the boundaries [as shown in Fig. 5(c), the effect of the green arrows is still weaker than that of the solid blue arrows]) since the flows should be similar to that of a neutral squirmer ( $\beta = 0$ ). However, with the stretch of the body, the flows inside the spheroidal puller become more significant than the induced flows [see Fig. 5(d); the effect of the green arrows is more significant than that of the solid blue arrows]. Hence, the total effect of fluid inertia on the speed of a puller with a large AR but small  $\beta$  is positive. This answers why the spheroidal inertial puller with a small  $\beta$  can swim faster than the inertialess counterpart.



FIG. 5. Schematic to compare the swimming mechanisms for an inertial puller swimming in a fluid. (a) A spherical puller at the Stokes flow regime; (b) a spherical puller swimming in an inertial flow; (c) a spherical puller with a small swimming intensity ( $\beta$ ) at an inertial flow; (d) a spheroidal puller with a small swimming intensity ( $\beta$ ) at an inertial flow. The dashed and solid squirmers, respectively, denote them at the previous and current instants. All the blue and dashed arrows indicate the flows induced at the previous instant, and the blue and solid arrows denote the flows affecting the squirmers at the current instant. The green arrows denote the flows inside the pullers when the swimming intensity ( $\beta$ ) is small, and the black arrows indicate the swimming direction.



FIG. 6. Vorticity contours around the spheroidal squirmers at Re = 5. (a) AR = 1.5,  $\beta$  = 3; (b) AR = 4,  $\beta$  = 3; (c) AR = 4,  $\beta$  = 0.5; (d) AR = 1.5,  $\beta$  = -3; (e) AR = 4,  $\beta$  = -3; (f) AR = 4,  $\beta$  = -0.5.

To further understand this finding, we plot the different spheroidal pullers' steady speeds with  $\beta$ , as shown in Fig. 4(b). It is seen that an inertial puller with a higher AR swims slower than the counterpart theoretical solution (under a Stokes flow) in a larger range of  $\beta$ . Based on this pattern, it is reasonable to predict that the speeds of the spherical (AR = 1), inertial puller with different  $\beta$  are entirely below its theoretical solution at Re = 0, in agreement with the available results [17,44]. Interestingly, with the increase of  $\beta$  (e.g.,  $\beta \ge 3$ ), the speeds are restored after dropping into the valleys, especially for a large AR. This finding indicates the different inertial hydrodynamics between a spheroidal and spherical squirmers, in which the spherical one's speed decreases monotonically with  $\beta$ . This phenomenon could be attributed to the more pronounced enhancement in the ratio of flows within the body with  $\beta$  compared to the induced flows in the outer region [see Fig. 5(d); the solid green arrows may become stronger than the counterpart solid blue ones with  $\beta$ ]. Moreover, the significance of this mechanism becomes more pronounced with increasing AR.

Figure 6 presents the vorticity distributed around the spheroidal squirmers at Re = 5. It is recalled that a spherical squirmer with different self-propelled modes (depending on  $\beta$ ) displays divergent speeds with finite fluid inertia [48,62]. This leads to the conclusion that, with increasing Re, a puller "pulls" the vorticity (generated by the puller) to accumulate around the body, hence hindering its speed. In contrast, a pusher "pushes" the vorticity (generated by the pusher) downstream, speeding up its speed. This mechanism applies to the present spheroidal squirmers [see Figs. 6(a), 6(b), 6(d), and 6(e); the vorticity bubbles at the rears of the pullers are expanded more significantly than that of the pushers]. Note that this mechanism only applies to inertial swimming since the fluid inertia breaks the fore-and-aft symmetry of the induced flows (velocity and vorticity) around the bodies. Referring back to Fig. 4, we find that a larger AR may be more beneficial to strengthening (weakening) the effect of fluid inertia in speeding up (hindering) a pusher (puller). For example, the



FIG. 7. Steady swimming speed of a spheroidal squirmer through a viscoelastic fluid with Wi (Re = 0.01).

speed of a pusher (puller) with  $\beta = -3$  ( $\beta = 3$ ) and AR = 4 increases (decreases) approximately by 68% (9%) from Re = 0 to 5; in contrast to that, the counterpart squirmer with AR = 1.5 increases (decreases) by 43% (16.8%). This may be because the slender-shaped body is more beneficial in the convection of the vorticity than the blunt-shaped one [see Figs. 6(a), 6(b), 6(d), and 6(e)]. Figures 6(c) and 6(f) show the vorticity around the squirmers with  $|\beta| = 0.5$ . The vorticity around the pusher and puller is not very notable, similar to that of the neutral squirmer. This indicates the possible mechanism for the finding above that the inertial puller (Re = 5) with  $\beta = 0.5$  swims faster than at Re = 0, as the inside flows may become more significant than the outer ones.

## B. How do fluid inertia and elasticity jointly affect the swimming of a spheroidal squirmer?

This section first considers a squirmer through the Giesekus fluids, excluding the influence of fluid inertia (Re = 0.01). We employ the viscosity ratio  $\eta_r = 0.5$  and mobility factor  $\alpha = 0.2$ , if not otherwise specified. As shown in Fig. 7, the speed of the neutral squirmer ( $\beta = 0$ ) increases monotonically with Wi (the puller, not shown, also adheres to this pattern). Regarding the pusher with  $\beta = -3$ , its speed exhibits a decrease followed by a subsequent recovery with Wi. These patterns are similar to that of a spherical squirmer swimming in the Giesekus fluids [37], indicating the qualitative rationality of the present results. A unified increase of their speeds at a high Wi (e.g., Wi  $\ge 6$ ) is due to the elongation effect of a viscoelastic shear-thinning medium at the rear of the squirmer, leading to a reduced elastic resistance with Wi [37]. In a viscoelastic shear-thinning fluid (Re = 0.01), the squirmer with a larger AR yields a faster speed, consistent with the pattern observed in a Newtonian fluid. When altering the mobility factor  $\alpha$ , the tendency of the speeds with Wi persists. But, a larger  $\alpha$  results in a faster speed. For example, by increasing  $\alpha$  from 0.05 to 0.2, the speed of a neutral squirmer (pusher with  $\beta = -3$ ) increases in a range of 2%-3% (8%-15%) according to different Wi adopted here. This pattern is similar to the result that the speed of a neutral squirmer ( $\beta = 0$ ) increases with  $\alpha$  at a relatively high Wi (Wi = 3) [24]. We have also conducted a simulation in the Oldroyd-B fluid ( $\alpha = 0$ ), yielding results that exhibit strong consistency with decreasing  $\alpha$ . This observation suggests that Giesekus fluids effectively capture the fundamental characteristics of Oldroyd-B fluids when simulating microswimmers within viscoelastic shear-thinning fluids.

#### MODELING A SPHEROIDAL SQUIRMER THROUGH A ...



FIG. 8. Velocity magnitudes and vorticity contours around the spheroidal squirmers with AR = 1.5 (Re = 0.01, Wi = 6). (a) and (b) Velocity magnitude around the neutral squirmer ( $\beta = 0$ ); (c) and (d) vorticity contours around the spheroidal pusher ( $\beta = -3$ ). (a) and (c)  $\alpha = 0.2$ ; (b) and (d)  $\alpha = 0.05$ . Note that the velocity is normalized with  $B_1$ .

To illustrate the possible mechanism for the effect of  $\alpha$  on the speed, we plot the velocity magnitudes and vorticity contours around the spheroidal squirmers, as shown in Fig. 8. For a neutral squirmer (AR = 1.5), it is seen that the fluid elasticity breaks the front-back symmetry of flows, a pattern that typically holds when swimming in a Newtonian fluid [17]. This front-back asymmetry is more pronounced for the case with a smaller  $\alpha$  [see Figs. 8(a) and 8(b); a smaller  $\alpha$  yields a longer extended wake at the rear of the body]. This longer extended wake may result in more lagging stresses generated at the rear of the squirmer for driving the flow toward the body [37], leading to a lower speed. On a larger  $\alpha$  yielding a faster speed for the counterpart pusher, we expect to illustrate the mechanism by analyzing the vorticity distribution around the squirmer, as shown in Figs. 8(c) and 8(d). Previous works indicate that the efficient downstream advection of the vorticity generated on the squirmer's surface increases its speed [47,62]. This physics is applicable to the current pusher scenario, where an increase in  $\alpha$  leads to a greater accumulation of vorticity at the rear of the body (a larger  $\alpha$  leads to better convection). Simultaneously, we observe a small yet discernible vorticity bubble at the rear of the pusher, a phenomenon not previously reported in a Newtonian fluid context.

This could be attributed to the extensional polymer stress behind the swimmer, and the stronger the shear thinning characteristics (the larger  $\alpha$ ) of the fluid, the smaller the impact of this stress. The



FIG. 9. Component of polymer stress  $\tau_{zz}$  distribution around the neutral squirmers ( $\beta = 0$ , Wi=0.5, Re=0.01, AR = 1.5). (a)  $\alpha = 0.2$ ; (b)  $\alpha = 0.05$ .

polymer stress is reported to be responsible for speed hindrance [37], suggesting that its diminution leads to an increase in swimming speed [24]. This conclusion is also beneficial in understanding our results when changing  $\alpha$ . Figure 9 illustrates the contours of the polymer stress component  $\tau_{zz}$  around the neutral squirmers with AR = 1.5. It is seen that the larger  $\alpha$  yields the smaller extensional polymer stress tail, confirming our discussion.

Since the increasing fluid inertia leads to divergent speed variations for a spherical squirmer with different self-propelled modes [48], one may then ask how do fluid inertia and elasticity jointly impact the swimming of a spheroidal squirmer? For a neutral squirmer ( $\beta = 0$ ), as shown in Fig. 10(a), its speed increases with Wi when fluid inertia is considered (Re = 5). This pattern bears similarities to the swimming behavior of an inertial, spherical neutral squirmer in a Giesekus fluid [23], even though pure fluid inertia exerts no net effect on the neutral squirmer's speed [44]. Furthermore, we find that a larger AR results in a more substantial enhancement in the speed of a neutral, inertial squirmer. For example, at the specified Wi = 2, the speed of the neutral squirmer with AR = 4 (1.5) increases by 17% (6%) from Re = 0.01 to 5. This may be because the fluid inertia amplifies the asymmetry of the flow field (around the squirmer) caused by the fluid elastic stress [23], and a larger AR contributes to a more pronounced amplification. Regarding the spheroidal pullers at Re = 5, as shown in Fig. 10(b), their speeds initially exhibit a decrease with Wi (starting from Wi = 0.2), followed by a subsequent restoration with further increases in Wi. This contrasts with the pattern of a counterpart puller swimming at Re = 0.01, in which its speed increases monotonically. Recalling that an inertial puller (pusher) is "pulled" ("pusher") by the flows it induced earlier, leading to the hindrance (enhancement) in its speed [48]. This pattern applies to the swimming in a viscoelastic fluid with inertia here, as shown in Figs. 10(b) and 10(c). Moreover, with the increase of Re (from 0.01 to 5), a larger AR leads to a more significant increase in a pusher's speed (e.g., at Wi = 2, it increases by 52% for AR = 1.5 and by 89% for AR = 4) but not a very appreciable decrease in a puller's speed.

Figure 11 illustrates the steady swimming speed of a squirmer through a Giesekus fluid ( $\alpha = 0.2$ ) with Re. The observed pattern of speed variation aligns consistently with the results depicted in Fig. 10. Notably, our investigation reveals intersecting data points when considering two distinct Wi of 0.5 and 2. Chaudhury [64] employed Taylor's swimming sheet model [65] to simulate the locomotion of a microorganism, revealing that fluid elasticity can either positively enhance (0 < Re < 15) or hinder (15 < Re < 60) propulsion. It is noteworthy that the Taylor swimming sheet model resembles a pusher-type self-propelling mechanism, hence exhibiting a similar speed tendency to that of our pusher ( $\beta = -3$ ) within the range of ( $1 < \text{Re} \le 5$ ). However, discrepancies



FIG. 10. Comparing the steady speed of inertial and inertialess spheroidal squirmers in the Giesekus fluids. (a)  $\beta = 0$ ; (b)  $\beta = 3$ ; (c)  $\beta = -3$ .



FIG. 11. Effect of fluid inertia on steady swimming speed of a squirmer through a Giesekus fluid ( $\alpha = 0.2$ ).

emerge when Re < 1. Chaudhury [64] reported that the solution converges to unity regardless of fluid elasticity at Re = 0. In contrast, our results indicate that a higher Wi leads to a reduction in pusher speed at Re = 0.01. Zhu *et al.* [37] have carefully investigated divergent speeds at different Wi (Re = 0), and they concluded that different swimming modes for a squirmer generate different polymer dynamics (by modifying the polymer stretching) around the swimmer and this, in turn, influences the swimming speed. At Re = 0.01, we also find that the neutral squirmer maintains a faster speed at a larger Wi. For a puller, its speed contrasts to that of a pusher, in agreement with the results of Zhu *et al.* [37]. Chaudhury [64] suggested that fluid elasticity reverses its role and hampers propulsion (reduces induced velocity) when the Reynolds number is sufficiently increased, that is, the flow is of the boundary-layer type. However, owing to the constraints of the current algorithm, analyzing the particle boundary layer presents a considerable challenge. Our future endeavors will focus on implementing body-fitted grids to facilitate the examination of flow dynamics in the vicinity of the boundary layer.

## C. Force decoupling analysis

To better understand the possible mechanism underlying the above findings, we decouple the forces acting on the surface of the squirmers with steady swimming. Swimming through a Giesekus fluid, the net force on the body can be decomposed into pressure, viscous, and polymeric contributions, and it has  $F_z = F_z^{\text{pres}} + F_z^{\text{visc}} + F_z^{\text{poly}} = 0$  (force-free) in the swimming direction (*z* axis). Specifically, the pressure, the viscous, and the polymeric forces are respectively calculated in the following forms:

$$F_z^{\text{pres}} = -\int_{\partial P_0} n_z p \,\mathrm{d}S,\tag{4.1}$$

$$F_{z}^{\text{visc}} = \eta_{s} \int_{\partial P_{0}} \left[ 2n_{z} \frac{\partial u_{z}}{\partial z} + n_{x} \left( \frac{\partial u_{z}}{\partial x} + \frac{\partial u_{x}}{\partial z} \right) + n_{y} \left( \frac{\partial u_{z}}{\partial y} + \frac{\partial u_{y}}{\partial z} \right) \right] \mathrm{d}S, \tag{4.2}$$

$$F_z^{\text{poly}} = \int_{\partial P_0} [n_z \tau_{zz} + n_y \tau_{yz} + n_x \tau_{xz}] \mathrm{d}S, \qquad (4.3)$$

where  $\eta_s$  denotes the fluid viscosity and **n** is the unit normal outward of the surface *S* of the body. In Eq. (4.3), the polymer force can be further decomposed into the normal polymeric force,  $F_{zn}^{\text{poly}}$ , and the polymeric shear force,  $F_{zn}^{\text{poly}}$ :

$$F_{zn}^{\text{poly}} = \int_{\partial P_0} n_z \tau_{zz} \mathrm{d}S, \qquad (4.4)$$

$$F_{zs}^{\text{poly}} = \int_{\partial P_0} [n_y \tau_{yz} + n_x \tau_{xz}] \mathrm{d}S.$$
(4.5)

Figure 12 presents the force contributions for an inertial squirmer swimming in a Newtonian fluid, in which the forces can only be decomposed into the pressure and viscous contributions (normalized by  $\eta_0 U_0 a$ ). It is seen that the viscous force  $F_z^{\text{visc}}$  decreases monotonically with the AR and maintains negative contributions. This suggests that a slenderer squirmer is more prone to break the fore-and-aft symmetry of the flows around the body, and the positive pressure (not shown) may be significant in speeding up a squirmer (recalling that the spheroidal squirmer with a larger AR yields a faster speed in Fig. 4). We infer that the viscous force contribution is associated with the squirmer's surface area as a larger AR corresponds to a larger surface area. Interestingly, in the case of an inertial puller with AR  $\ge 2$ , the magnitude of the viscous force contribution is larger than that of the counterpart pusher. This pattern is particularly pronounced for scenarios with a strong swimming intensity ( $|\beta|$ ). This mechanism can be elucidated by examining the distinct characteristics between the swimming modes of a pusher and a puller in an inertial flow. The pusher is more significantly affected by fluid inertia than the puller [17]; hence the effect of fluid viscosity on a pusher is weaker than the counterpart puller. However, this conclusion does



FIG. 12. Effect of aspect ratio (AR) on an inertial squirmer's force contribution in a Newtonian fluid (Re = 5).

not hold for a squirmer with AR = 1.5, as a relatively large body curvature may subtly alter the pressure distribution and, consequently, the contributions of viscous forces for the pusher and puller.

Regarding a neutral squirmer swimming in the Giesekus fluids, we find that viscous force,  $F_z^{\text{visc}}$ , and polymeric forces,  $F_z^{\text{poly}}$ , maintain negative contributions, as shown in Fig. 13. As the neutral squirmer swims within the viscous flow regime (Re = 0.01), it is evident that the negative contribution is predominantly dominated by the viscous force. This pattern is more pronounced for a neutral squirmer with a larger AR. For the polymeric forces,  $F_{zs}^{\text{poly}}$  exhibits a more considerable negative contribution than  $F_{zn}^{\text{poly}}$ , in agreement with the results of Binagia *et al.* [24].



FIG. 13. Effect of aspect ratio (AR) on a neutral squirmer's force contribution in the Giesekus fluids (Wi=0.5, Re=0.01).



FIG. 14. Energy expenditure for the steady swimming of a spheroidal squirmer through a fluid. (a) Newtonian medium; (b) Giesekus medium.

## D. Energy expenditure and hydrodynamic efficiency

Finally, we would like to discuss the spheroidal squirmer's energy expenditure and hydrodynamic efficiency in a fluid. The rate of work P can be written as

$$P = -\int_{\partial P_0} \mathbf{u} \cdot \boldsymbol{\sigma} \cdot \boldsymbol{n} \, \mathrm{d}S,\tag{4.6}$$

where *n* is the unit normal outward of the surface S of the swimmer, and  $\sigma$  denotes the total stress tensor. Figure 14 presents the energy expenditure for the steady swimming of a spheroidal squirmer through a fluid, in which P is normalized with  $P_N$ .  $P_N = 12\pi$  (normalized by  $4B_1^2 a\eta_0/9$ ) denotes the energy expenditure for a neutral spherical squirmer ( $\beta = 0$ ) in a Newtonian fluid, and it is obtained by integrating Eq. (4.6) in Stoke flow [44]. The main finding in this section is that, as shown in Fig. 14(a), a slenderer inertial squirmer (Re = 5) with a large swimming intensity ( $|\beta| = 3$ ) expends more energy in a Newtonian fluid. This contrasts with the inertial squirmer with a small swimming intensity ( $|\beta| = 0.5$ ). Since the power expended by the squirmer is dissipated viscously by the fluid, the decoupling of integrating Eq. (4.6) may provide insight into understanding the mechanism. At steady swimming, the dimensionless viscous dissipation rate in the flow around a tangentially deforming body and P are equivalent, and it involves the contributions of the vorticity and surface velocity [66,67]. At a large  $|\beta|$  (e.g.,  $|\beta| = 3$ ), the vorticity around the body dominates the energy expenditure as the right second term  $(B_2)$  of Eq. (2.7) is responsible for vorticity generation [17]. This explains why a larger  $|\beta|$  expends more energy for the squirmers with the same geometry. Moreover, a slenderer body indicates a larger surface area, thus expending more energy. At a small  $|\beta|$  (e.g.,  $|\beta| = 0.5$ ), the hydrodynamics of a squirmer resembles that of a neutral squirmer ( $\beta = 0$ ). In this scenario, the effect of vorticity is relatively weak, with the remaining contribution of velocity around the body accounting for energy expenditure. Keller and Wu [33] have derived the energy expenditure of the neutral spheroidal squirmer in a Newtonian and Stokes flow, and it reads

$$P = \frac{4\pi \left(\tau_0^2 - 1\right) \left[ \left(1 + \tau_0^2\right) \coth^{-1} \tau_0 - \tau_0 \right]}{\tau_0}.$$
(4.7)

This analytical solution is plotted in Fig. 14(a), showing a monotonic decrease with the AR.

We have simulated the neutral squirmers at Re = 0.01 to validate our calculation results further. The energy expenditure of the neutral spheroidal squirmers agrees well with the analytical solution. In the presence of finite fluid inertia (e.g., Re = 5), it is observed that a spheroidal pusher expends



FIG. 15. Hydrodynamic efficiency for the steady swimming of a spheroidal squirmer through a fluid. (a) Newtonian medium; (b) Giesekus medium.

more energy than the counterpart puller. This pattern is similar to an inertial squirmer across a shear-dependent fluid [46]. The result may be relevant to their swimming speeds [see Fig. 4(a)], where the faster counterpart squirmer tends to expend more energy. Comparing Figs. 14(a) and 14(b), it is seen that a neutral squirmer in a Giesekus fluid (Wi = 0.5) expends less energy than its Newtonian counterpart. A similar conclusion has been reported for a squirmer dumbbell and swirling squirmer swimming in a viscoelastic fluid [23,24].

We extend our investigation to the spheroidal squirmer's hydrodynamic efficiency  $\eta = P^*/P$ , as shown in Fig. 15, where  $P^*$  denotes the power necessary to move a counterpart spheroidal body at its swimming speed U. Note that  $P^*$  is obtained numerically using our DF-FD code. For a neutral spheroidal squirmer, its hydrodynamic efficiency in a Newtonian and Stokes flow follows this expression [33]:

$$\eta = \frac{2\tau_0^2 \left[\tau_0 + \left(1 - \tau_0^2\right) \coth^{-1} \tau_0\right]^2}{\left(\tau_0^2 - 1\right) \left[\tau_0 - \left(1 + \tau_0^2\right) \coth^{-1} \tau_0\right]^2}.$$
(4.8)

In Eq. (4.8),  $\eta$  converges to 0.5 as  $\tau_0 \to \infty$  [see Fig. 15(a)], corresponding to the hydrodynamic efficiency of a neutral spherical squirmer, which has been derived by Wang and Ardekani [44]. Since the hydrodynamic efficiency of a neutral squirmer increases monotonically with Re [17],  $\eta$  at Re = 5 should be above the plotted curve [Eq. (4.8)] in Fig. 15(a). This concludes that a neutral squirmer is more efficient than other squirmers at Re = 5, as it expends the least energy due to its generation of no vorticity [17]. A pusher is more efficient than the counterpart puller in a Newtonian and inertial flow [see Fig. 15(a)]. This is because the fluid inertia speeds up a pusher but hinders a puller [48]. Meanwhile, a larger AR leads to a higher efficiency, highlighting a positive correlation with the swimming speed of the corresponding swimmers.

## V. CONCLUSION

We have numerically investigated the hydrodynamics of a spheroidal squirmer within a complex fluid characterized by nonlinear behaviors, encompassing both fluid inertia and viscoelasticity (using the Giesekus model). Through a systematic examination of the swimmer's speed, energy expenditure, and hydrodynamic efficiency, our aim is to provide insights into how the combined influence of the fluid's nonlinear behaviors and the swimmer's geometry modify its hydrodynamic behaviors. We first develop a spheroidal swimmer model based on a spherical squirmer model, which imparts a specified tangential velocity at its boundaries to achieve self-propulsion. To integrate the model into the current DF-FD, we have derived the solution for flows within the spheroidal squirmer based on the tangential velocity boundary condition.

Our results indicate that, a spheroidal puller in a Newtonian and inertial flow swims faster than its counterpart subjected to the Stokes flow regime when its swimming intensity is weak. This pattern differs from the behavior observed in spherical counterparts. This phenomenon can be attributed to the fact that a slender body enhances the flows inside the spheroidal puller more significantly than in the case of a spherical one. On swimming in the Giesekus fluids, a greater mobility factor  $\alpha$  results in a faster squirmer, and a larger AR yields a more significant enhancement in the speed of a neutral squirmer when fluid inertia is considered. This may be because the fluid elasticity breaks the flow's front-back symmetry, which holds the pattern when swimming in a Newtonian fluid. The front-back asymmetry is more pronounced for the case with a smaller  $\alpha$ , leading to lagging stresses that hinder the body. Moreover, the fluid inertia amplifies the asymmetry of the flow field (around the squirmer) caused by the fluid elastic stress, and a larger AR contributes to a more pronounced amplification. We further decouple the net force acting on the body, finding that the viscous force in a Newtonian fluid decreases monotonically with the AR. Regarding a neutral squirmer swimming in the Giesekus fluids, viscous and polymeric forces maintain negative contributions. This pattern is particularly accentuated with a larger AR.

Our observations reveal that a slenderer, inertial squirmer swimming in a Newtonian fluid with a vigorous swimming intensity ( $|\beta| = 3$ ), expends more energy. However, it expends less energy when the swimming intensity is small ( $|\beta| = 0.5$ ). The disparate patterns may arise from the distinct dominance of contributions, where the generation of vorticity and the friction between the fluid and the body respectively determine the energy expenditure of a squirmer with a large and small  $|\beta|$ . Our findings suggest that a neutral squirmer swimming in a Giesekus fluid expends less energy than in a Newtonian fluid. Additionally, we observe that an inertial pusher is more efficient than the counterpart puller in a Newtonian fluid. This is attributed to the fact that fluid inertia speeds up a pusher but hinders a puller. Furthermore, a larger AR results in higher efficiency, displaying a positive relationship with the corresponding swimmers' speed.

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ACKNOWLEDGMENTS

The authors would like to thank the National Natural Science Foundation of China (Grants No. 12302333, No. 12132015, and No. 12172327). We thank Gaojin Li for the helpful discussions. The authors report no conflict of interest.

# APPENDIX: IMPOSED SOLENOIDAL VOLUMETRIC VELOCITY

In this part, we have carefully derived the analytical solution for the solenoidal volumetric velocity inside a spheroidal squirmer, enabling the model to be implemented in our DF-FD method framework. In Cartesian coordinates (x, y, z), the surface equation of a spheroid is

$$\frac{x^2 + y^2}{b_x^2} + \frac{z^2}{b_z^2} = 1,$$
(A1)

where  $b_z$  and  $b_x$  denote the semimajor and semiminor axis, respectively ( $b_z \ge b_x$ ; see Fig. 16). Here, we define  $\tau_0 = 1/e$  ( $e = c/b_z$  is the eccentricity with  $c = \sqrt{b_z^2 - b_x^2}$ ) with  $\tau > \tau_0$  corresponding to the fluid domain exterior to the surface ( $\tau = \tau_0$ ) of the squirmer. In terms of spheroidal coordinates ( $\tau, \zeta, \varphi$ ), the Cartesian coordinates denote

$$x = c\sqrt{\tau^2 - 1}\sqrt{1 - \zeta^2}\cos\varphi,$$
  

$$y = c\sqrt{\tau^2 - 1}\sqrt{1 - \zeta^2}\sin\varphi,$$
  

$$z = c\tau\zeta,$$
  
(A2)



FIG. 16. Schematic of normal and tangent vectors of a spheroidal squirmer. The self-propulsion (in the z direction) is achieved by a prescribed tangential surface velocity in the direction of the tangent vector **s**.

where  $1 \le \tau \le \infty$ ,  $-1 \le \zeta \le 1$ , and  $0 \le \varphi \le 2\pi$ . All points with  $\tau = \tau_0$  lie on the spheroid's surface. The intersection of the spheroid and a meridian plane, where  $\phi$  is constant, is an ellipse. For simplicity, a sketch of the normal  $(\mathbf{e}_{\tau})$  and tangent  $(-\mathbf{e}_{\zeta})$  vectors of a spheroidal squirmer in this plane is shown in Fig. 16. The Lamé metric coefficients for prolate spheroidal coordinates are

$$h_{\zeta} = c \frac{\sqrt{\tau^2 - \zeta^2}}{\sqrt{1 - \zeta^2}}, \quad h_{\tau} = c \frac{\sqrt{\tau^2 - \zeta^2}}{\sqrt{\tau^2 - 1}}, \quad h_{\varphi} = c \sqrt{\tau^2 - 1} \sqrt{1 - \zeta^2}.$$
 (A3)

The Jacobian determinant is defined as  $J = h_{\zeta}h_{\tau}h_{\varphi} = c^3(\tau^2 - \zeta^2)$ . The internal flow field **v** of a spheroidal squirmer is governed by the Stokes equation and incompressibility condition. On the surface of the swimmer, the boundary condition satisfies Eq. (2.9). We note that the steady internal flow results in a zero translational and rotational velocity as

$$\iiint \mathbf{v} J \,\mathrm{d}\zeta \,\mathrm{d}\tau \,\mathrm{d}\varphi = 0,\tag{A4}$$

$$\iiint \mathbf{r} \times \mathbf{v} J \,\mathrm{d}\zeta \,\mathrm{d}\tau \,\mathrm{d}\varphi = 0. \tag{A5}$$

Assuming the squirmer's motion is axisymmetric, the internal flow field can be expressed by the stream function  $\Psi$  as [68]

$$\mathbf{v}(\zeta, \tau, \varphi) = \operatorname{curl}\left(\frac{1}{h_{\varphi}}\Psi(\tau, \zeta)\mathbf{e}_{\varphi}\right).$$
(A6)

The stream function itself satisfies the equation

$$E^4\Psi(\tau,\zeta) = 0,\tag{A7}$$

where the operator has the following form [69]:

$$E^{2} = \frac{1}{c^{2}(\tau^{2} - \zeta^{2})} \bigg[ (\tau^{2} - 1)\frac{\partial^{2}}{\partial\tau^{2}} + (1 - \zeta^{2})\frac{\partial^{2}}{\partial\zeta^{2}} \bigg].$$
 (A8)

## 073303-19

AR	1.5	2	3	4	6	8
$a_0$	$-105.9B_{1}$	$-739.6B_{1}$	$-8222.8B_{1}$	$-41284.3B_1$	$-375334.5B_1$	$-1781709.3B_{1}$
$a_1$	$-105.9B_{1}$	$-739.6B_{1}$	$-8222.8B_{1}$	$-41284.3B_1$	$-375334.5B_1$	$-1781709.3B_{1}$
$a_2$	$117.3B_1$	855.8 <i>B</i> <sub>1</sub>	$9726.5B_1$	49156.9 <i>B</i> <sub>1</sub>	448890.7 <i>B</i> <sub>1</sub>	2134042.4 <i>B</i> <sub>1</sub>
$a_3$	$-13.4B_{1}$	$-119.5B_{1}$	$-1509.9B_{1}$	$-7881.8B_{1}$	$-73571.9B_{1}$	$-352356.6B_1$
$a_4$	$8.3B_{2}$	$26.9B_2$	$118.3B_2$	321.6 <i>B</i> <sub>2</sub>	$1278.9B_2$	$3370.0.3B_2$
$a_5$	$8.3B_2$	$26.9B_2$	118.3 <i>B</i> <sub>2</sub>	321.6 <i>B</i> <sub>2</sub>	$1278.9B_2$	$3370.0.3B_2$
$a_6$	$-4.9B_{2}$	$-20.8B_{2}$	$-106.4B_{2}$	$-303.5B_2$	$-1246.9B_2$	$-3322.6B_2$

TABLE I. Value of the constants  $a_k$  in Eqs. (A13) and (A14).

The velocity components can be derived from (A6)–(A8) as

$$\mathbf{v}_{\tau} = \frac{1}{h_{\zeta}h_{\varphi}}\frac{\partial\Psi}{\partial\zeta} = c^{-2}(\tau^2 - 1)^{-1/2}(\tau^2 - \zeta^2)^{-1/2}\frac{\partial\Psi}{\partial\zeta},$$
 (A9)

$$\mathbf{v}_{\zeta} = \frac{1}{h_{\tau}h_{\varphi}} \frac{\partial\Psi}{\partial\tau} = -c^{-2}(1-\zeta^2)^{-1/2}(\tau^2-\zeta^2)^{-1/2} \frac{\partial\Psi}{\partial\tau}.$$
 (A10)

The general solution of Eq. (A7) is given as [70]

$$\Psi(\tau,\zeta) = g_0(\tau)G_0(\zeta) + g_1(\tau)G_1(\zeta) + \sum_{n=2}^{\infty} [g_n(\tau)G_n(\zeta) + h_n(\tau)H_n(\zeta)].$$
(A11)

In Eq. (A11),  $G_n$  and  $H_n$  are the Gegenbauer functions of the first and second kind, respectively.  $g_n(\tau)$  and  $h_n(\tau)$  are  $\tau$ -dependent functions given by certain linear combinations of  $G_k(\tau)$  and  $H_k(\tau)$ [70]. For the present problem, the functions  $g_{n\geq 2}$  will be of interest, and Eq. (A11) can be simplified as

$$\Psi(\tau,\zeta) = g_2(\tau)G_2(\zeta) + g_3(\tau)G_3(\zeta).$$
(A12)

The functions  $g_2(\tau)$  and  $g_3(\tau)$  respectively have the following forms:

$$g_2(\tau) = a_0 G_0(\tau) + a_1 G_1(\tau) + a_2 G_2(\tau) + a_3 G_4(\tau),$$
(A13)

$$g_3(\tau) = a_4 G_0(\tau) + a_5 G_1(\tau) + a_6 G_3(\tau), \tag{A14}$$

where the constants  $a_k$  will be further calculated by requiring that the solution satisfies the boundary condition and the condition of no-net force and torque [i.e., Eqs. (A4) and (A5)] discussed below. For the squirmer problem, the boundary conditions of the stream function in the body-fixed frame satisfy

$$\Psi(\tau_0,\zeta) = 0,\tag{A15}$$

$$\left. \frac{\partial \Psi}{\partial \tau} \right|_{\tau=\tau_0} = (B_1 + B_2 \zeta) c^2 \tau_0 (1 - \zeta^2). \tag{A16}$$

Note that Eq. (A15) ensures  $\mathbf{v}_{\tau} = 0$  at the squirmer's surface. Since Eqs. (A4) and (A5) involve elliptic integrals, the values of  $a_k$  in Eqs. (A13) and (A14) are given below (Table I) for specific aspect ratios by a numerical method. Finally, we obtain the imposed solenoidal volumetric velocity field by Eqs. (A9) and (A10) in the prolate spheroidal coordinates.

<sup>[1]</sup> E. Lauga, Bacterial hydrodynamics, Annu. Rev. Fluid Mech. 48, 105 (2016).

<sup>[2]</sup> I. C. Yasa, H. Ceylan, U. Bozuyuk, A. M. Wild, and M. Sitti, Elucidating the interaction dynamics between microswimmer body and immune system for medical microrobots, Sci. Rob. 5, eaaz3867 (2020).

- [3] U. K. Cheang, D. Roy, J. H. Lee, and M. J. Kim, Fabrication and magnetic control of bacteria-inspired robotic microswimmers, Appl. Phys. Lett. 97, 213704 (2010).
- [4] S. Sengupta, M. E. Ibele, and A. Sen, Fantastic voyage: Designing self-powered nanorobots, Angew. Chem. Int. Ed. Engl. 51, 8434 (2012).
- [5] G. Li, E. Lauga, and A. M. Ardekani, Microswimming in viscoelastic fluids, J. Non-Newtonian Fluid Mech. 297, 104655 (2021).
- [6] E. A. Gaffney, H. Gadêlha, D. J. Smith, J. R. Blake, and J. C. Kirkman-Brown, Mammalian sperm motility: Observation and theory, Annu. Rev. Fluid Mech. 43, 501 (2011).
- [7] J. Wang, Y. Zhou, X. Bai, and W. Li, Effect of algal blooms outbreak and decline on phosphorus migration in Lake Taihu, China, Environ. Pollut. 296, 118761 (2022).
- [8] J. Li, B. Esteban-Fernández de Ávila, W. Gao, L. Zhang, and J. Wang, Micro/nanorobots for biomedicine: Delivery, surgery, sensing, and detoxification, Sci. Rob. 2, eaam6431 (2017).
- [9] D. B. Kearns, A field guide to bacterial swarming motility, Nat. Rev. Microbiol. 8, 634 (2010).
- [10] S. Thampi and J. Yeomans, Active turbulence in active nematics, Eur. Phys. J.: Spec. Top. 225, 651 (2016).
- [11] R. Alert, J. Casademunt, and J. F. Joanny, Active turbulence, Annu. Rev. Condens. Matter Phys. 13, 143 (2022).
- [12] I. Theurkauff, C. Cottin-Bizonne, J. Palacci, C. Ybert, and L. Bocquet, Dynamic clustering in active colloidal suspensions with chemical signaling, Phys. Rev. Lett. 108, 268303 (2012).
- [13] A. Zöttl and H. Stark, Hydrodynamics determines collective motion and phase behavior of active colloids in quasi-two-dimensional confinement, Phys. Rev. Lett. 112, 118101 (2014).
- [14] M. J. Lighthill, On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers, Commun. Pure Appl. Math. 5, 109 (1952).
- [15] J. R. Blake, A spherical envelope approach to ciliary propulsion, J. Fluid Mech. 46, 199 (1971).
- [16] T. Ishikawa and M. Hota, Interaction of two swimming *Paramecia*, J. Exp. Biol. 209, 4452 (2006).
- [17] N. G. Chisholm, D. Legendre, E. Lauga, and A. S. Khair, A squirmer across Reynolds numbers, J. Fluid Mech. 796, 233 (2016).
- [18] T. J. Pedley, D. R. Brumley, and R. E. Goldstein, Squirmers with swirl: A model for volvox swimming, J. Fluid Mech. 798, 165 (2016).
- [19] K. Drescher, R. E. Goldstein, N. Michel, M. Polin, and I. Tuval, Direct measurement of the flow field around swimming microorganisms, Phys. Rev. Lett. 105, 168101 (2010).
- [20] A. Doostmohammadi, R. Stocker, and A. M. Ardekani, Low-Reynolds-number swimming at pycnoclines, Proc. Natl. Acad. Sci. USA 109, 3856 (2012).
- [21] V. Magar, T. Goto, and T. J. Pedley, Nutrient uptake by a self-propelled steady Squirmer, Q. J. Mech. Appl. Math. 56, 65 (2003).
- [22] V. Magar and T. J. Pedley, Average nutrient uptake by a self-propelled unsteady squirmer, J. Fluid Mech. 539, 93 (2005).
- [23] Z. Ouyang, Z. Lin, J. Lin, Z. Yu, and N. Phan-Thien, Cargo carrying with an inertial squirmer in a Newtonian fluid, J. Fluid Mech. 959, A25 (2023).
- [24] J. P. Binagia, A. Phoa, K. D. Housiadas, and E. S. Shaqfeh, Swimming with swirl in a viscoelastic fluid, J. Fluid Mech. 900, A4 (2020).
- [25] K. Ishimoto and E. A. Gaffney, Squirmer dynamics near a boundary, Phys. Rev. E 88, 062702 (2013).
- [26] Z. Ouyang, J. Lin, and X. Ku, Hydrodynamic properties of squirmer swimming in power-law fluid near a wall, Rheol. Acta 57, 655 (2018).
- [27] T. Ishikawa, M. P. Simmonds, and T. J. Pedley, Hydrodynamic interaction of two swimming model microorganisms, J. Fluid Mech. 568, 119 (2006).
- [28] I. O. Götze and G. Gompper, Mesoscale simulations of hydrodynamic squirmer interactions, Phys. Rev. E 82, 041921 (2010).
- [29] R. M. Navarro and I. Pagonabarraga, Hydrodynamic interaction between two trapped swimming model micro-organisms, Eur. Phys. J. E 33, 27 (2010).
- [30] Z. Ouyang, J. Lin, and X. Ku, Hydrodynamic interaction between a pair of swimmers in power-law fluid, Int. J. Nonlinear Mech. 108, 72 (2019).

- [31] T. Ishikawa and T. J. Pedley, Coherent structures in monolayers of swimming particles, Phys. Rev. Lett. **100**, 088103 (2008).
- [32] T. Ishikawa, J. T. Locsei, and T. J. Pedley, Development of coherent structures in concentrated suspensions of swimming model micro-organisms, J. Fluid Mech. 615, 401 (2008).
- [33] S. R. Keller and T. Y. Wu, A porous prolate-spheroidal model for ciliated micro-organisms, J. Fluid Mech. 80, 259 (1977).
- [34] M. Theers, E. Westphal, G. Gompper, and R. G. Winkler, Modeling a spheroidal microswimmer and cooperative swimming in a narrow slit, Soft Matter 12, 7372 (2016).
- [35] R. Pöhnl, M. N. Popescu, and W. E. Uspal, Axisymmetric spheroidal squirmers and self-diffusiophoretic particles, J. Phys.: Condens. Matter 32, 164001 (2020).
- [36] B. van Gogh, E. Demir, D. Palaniappan, and O. S. Pak, The effect of particle geometry on squirming through a shear-thinning fluid, J. Fluid Mech. 938, A3 (2022).
- [37] L. Zhu, M. Do-Quang, E. Lauga, and L. Brandt, Locomotion by tangential deformation in a polymeric fluid, Phys. Rev. E 83, 011901 (2011).
- [38] S. Childress, Mechanics of Swimming and Flying (Cambridge University Press, Cambridge, UK, 1981).
- [39] B. S. Beckett, Biology: A Modern Introduction (Oxford University Press, New York, 1986).
- [40] T. Kiørboe, H. Jiang, and S. P. Colin, Danger of zooplankton feeding: The fluid signal generated by ambush-feeding copepods, Proc. R. Soc. B 277, 3229 (2010).
- [41] L. N. Wickramarathna, C. Noss, and A. Lorke, Hydrodynamic trails produced by *Daphnia*: Size and energetics, PLoS ONE 9, e92383 (2014).
- [42] M. M. Wilhelmus and J. O. Dabiri, Observations of large-scale fluid transport by laser-guided plankton aggregations, Phys. Fluids 26, 101302 (2014).
- [43] C. Noss and A. Lorke, Direct observation of biomixing by vertically migrating zooplankton, Limnol. Oceanogr. **59**, 724 (2014).
- [44] S. Wang and A. Ardekani, Inertial squirmer, Phys. Fluids 24, 101902 (2012).
- [45] A. S. Khair and N. G. Chisholm, Expansions at small Reynolds numbers for the locomotion of a spherical squirmer, Phys. Fluids 26, 011902 (2014).
- [46] Z. Ouyang, J. Lin, and X. Ku, The hydrodynamic behavior of a squirmer swimming in power-law fluid, Phys. Fluids 30, 083301 (2018).
- [47] R. V. More and A. M. Ardekani, Motion of an inertial squirmer in a density stratified fluid, J. Fluid Mech. 905, A9 (2020).
- [48] G. Li, A. Ostace, and A. M. Ardekani, Hydrodynamic interaction of swimming organisms in an inertial regime, Phys. Rev. E 94, 053104 (2016).
- [49] G. J. Li and A. M. Ardekani, Hydrodynamic interaction of microswimmers near a wall, Phys. Rev. E 90, 013010 (2014).
- [50] Z. Lin and T. Gao, Direct-forcing fictitious domain method for simulating non-Brownian active particles, Phys. Rev. E 100, 013304 (2019).
- [51] S. M. Sillankorva, H. Oliveira, and J. Azeredo, Bacteriophages and their role in food safety, Int. J. Microbiol. 2012, 863945 (2012).
- [52] M. W. Harman, The heterogeneous motility of the Lyme disease spirochete in gelatin mimics dissemination through tissue, Biophys. J. 102, 151a (2012).
- [53] G. J. Elfring and G. Goyal, The effect of gait on swimming in viscoelastic fluids, J. Non-Newtonian Fluid Mech. 234, 8 (2016).
- [54] M. Dasgupta, B. Liu, H. C. Fu, M. Berhanu, K. S. Breuer, T. R. Powers, and A. Kudrolli, Speed of a swimming sheet in Newtonian and viscoelastic fluids, Phys. Rev. E 87, 013015 (2013).
- [55] A. E. Patteson, A. Gopinath, M. Goulian, and P. E. Arratia, Running and tumbling with *E. coli* in polymeric solutions, Sci. Rep. 5, 15761 (2015).
- [56] D. J. Smith, E. A. Gaffney, H. Gadêlha, N. Kapur, and J. C. Kirkman-Brown, Bend propagation in the flagella of migrating human sperm, and its modulation by viscosity, Cell Motil. Cytoskeleton 66, 220 (2009).
- [57] L. A. Kroo, J. P. Binagia, N. Eckman, M. Prakash, and E. S. Shaqfeh, A freely suspended robotic swimmer propelled by viscoelastic normal stresses, J. Fluid Mech. 944, A20 (2022).

- [58] P. E. Arratia, Life in complex fluids: Swimming in polymers, Phys. Rev. Fluids 7, 110515 (2022).
- [59] Z. Yu and X. Shao, A direct-forcing fictitious domain method for particulate flows, J. Comput. Phys. 227, 292 (2007).
- [60] Z. Yu, P. Wang, J. Lin, and H. H. Hu, Equilibrium positions of the elasto-inertial particle migration in rectangular channel flow of Oldroyd-B viscoelastic fluids, J. Fluid Mech. **868**, 316 (2019).
- [61] T. Vaithianathan and L. R. Collins, Numerical approach to simulating turbulent flow of a viscoelastic polymer solution, J. Comput. Phys. 187, 1 (2003).
- [62] Z. Ouyang, Z. Lin, Z. Yu, J. Lin, and N. Phan-Thien, Hydrodynamics of an inertial squirmer and squirmer dumbbell in a tube, J. Fluid Mech. 939, A32 (2022).
- [63] Z. Ouyang, Z. Lin, J. Lin, N. Phan-Thien, and J. Zhu, Swimming of an inertial squirmer and squirmer dumbbell through a viscoelastic fluid, J. Fluid Mech. 969, A34 (2023).
- [64] T. K. Chaudhury, On swimming in a visco-elastic liquid, J. Fluid Mech. 95, 189 (1979).
- [65] G. I. Taylor, Analysis of the swimming of microscopic organisms, Proc. R. Soc. London, Ser. A 209, 447 (1951).
- [66] H. A. Stone, An interpretation of the translation of drops and bubbles at high Reynolds numbers in terms of the vorticity field, Phys. Fluids A 5, 2567 (1993).
- [67] H. A. Stone and A. D. Samuel, Propulsion of microorganisms by surface distortions, Phys. Rev. Lett. 77, 4102 (1996).
- [68] J. Happel and H. Brenner, Low Reynolds Number Hydrodynamics: With Special Applications to Particulate Media (Springer and Science Media, Berlin, 1983), Vol. 1.
- [69] G. Dassios and P. Vafeas, On the spheroidal semiseparation for Stokes flow, Phys. Res. Int. 2008, e135289 (2008).
- [70] G. Dassios, M. Hadjinicolaou, and A. C. Payatakes, Generalized eigenfunctions and complete semiseparable solutions for Stokes flow in spheroidal coordinates, Q. Appl. Math. 52, 157 (1994).