SELF-PROPULSION & SWIMMING IN VISCOELASTIC FLUIDS

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Summary The effects of fluid elasticity on the swimming behaviour of the nematode *Caenorhabditis elegans* are experimentally investigated by tracking the nematode's motion and measuring velocity fields. We find that fluid elasticity hinders self-propulsion, compared to Newtonian solutions, and leads to up to 35% slower propulsion speed. Furthermore, self-propulsion decreases as elastic stresses grow in magnitude in the fluid, and this decrease is related to the stretching of molecules near hyperbolic points in the flow.

INTRODUCTION

Life immersed in a fluid is nothing unusual for live organisms. They navigate and take advantage of water or wind currents to move, feed, and reproduce. Many, if not most, organisms move in the regime of low Reynolds (*Re*) numbers, usually defined as $Re=\rho U L/\mu$, where ρ and μ are the fluid density and viscosity respectively, and U and L are the organism's speed and characteristic length scale. Due to small length scales, microorganisms such as bacteria, sperm cells, and various kinds of protozoa move at low *Re*. In this regime, linear viscous forces dominate over nonlinear inertial forces and locomotion results from non-reciprocal deformations in order to break time-reversal symmetry [1].
However, the fluid stresses acting on a microorganism need not be purely viscous. Many microorganisms live in complex fluid media that contain solids and/or polymers [2]. Fluids such as gels, mud, intestinal fluid, and human mucus are not Newtonian, and often possess viscoelastic behavior. The effects of fluid elasticity on swimming at low *Re* have been considered in theory and numerical simulation. For an infinite waving sheet immersed in a second-order fluid [3], it was shown that elasticity augments propulsion speed. Recently, it was shown that, for the case of an infinite undulating sheet [2] and cylinder [4], viscoelasticity decreases swimming speed compared to Stokesian Newtonian cases. By contrast, a two-dimensional numerical simulation for a *finite* undulating sheet using the Oldroyd-B model [5] showed that fluid elasticity could in fact augment swimming speed when the beating frequency f is equal to the inverse of the fluid relaxation time λ that is, the Deborah number $De=\lambda f$. Despite these recent efforts, there is a dearth of experimental investigations of swimming in viscoelastic fluids, and the effects of fluid elasticity on swimming are still not clear. Here, the effects of fluid elasticity on an undulatory swimmer are experimentally investigated at low *Re* by tracking the swimmer and tracer particles in the flow (Fig. 1). The organism is the nematode *Caenorhabditis elegans*, a roundworm widely used for biological research [6] that swims by generating traveling waves.

METHODS

Experiments are performed in fluid-filled channels that are 15 mm wide and 600 μm deep. Newtonian fluids of different shear viscosities μ are prepared by mixing low molecular weight oils (Halocarbon oil). Viscoelastic fluids are prepared by adding small amounts of carboxymethyl cellulose (CMC, 7 x 10^5 MW) into water. CMC is a long, flexible polymer with an overlap concentration of approximately 10^4 ppm. The polymer concentration in solution ranges from 1000 to 6000 ppm resulting in fluid relaxation times λ that range from 0.4 s to 5.6 s. These solutions are dilute and do not show significant shear-thinning viscosity, particularly in the range of typical swimming shear-rates of 1 s^{-1} to 20 s^{-1}.
The swimming motion of *C. elegans* is imaged using bright-field microscopy at 125 frames per second. The nematode is approximately 1 mm long and 80 μm in diameter. The objective focal plane is set on the longitudinal axis of the nematode body. All data presented here pertain to nematodes swimming at the center plane of the fluidic channel. An average of 15 nematodes is recorded for each experiment. More detailed information on the experimental methods can be found in [7].

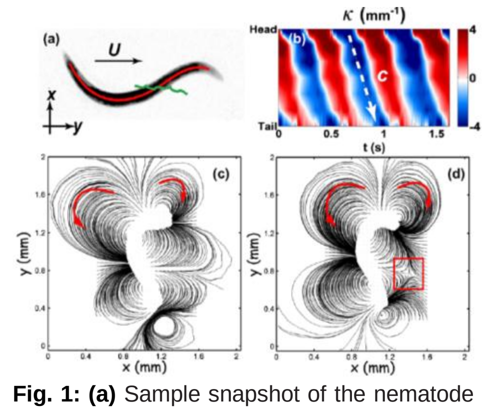

Fig. 1: (a) Sample snapshot of the nematode *C. elegans* swimming in buffer, water-like solution. Lines represent nematode's "skeleton" and its centroid path. **(b)** Curvature contour plot. **(c,d)** Flow streamlines in Newtonian (c) and viscoelastic (d) fluids.

RESULTS

Figure 1(a) shows a sample snapshot of a nematode swimming in a water-like solution at *Re*=0.2 as well as the nematode's shape-line or "skeleton" and its centroid path. Here, swimming speed U is calculated by differentiating the nematode centroid position over time. Figure 1(b) shows the spatio-temporal evolution of the nematode's body curvature $\kappa(s,t)$ for 3T, or 3 swimming cycles. The contour plots show the existence of periodic, well-defined diagonally oriented

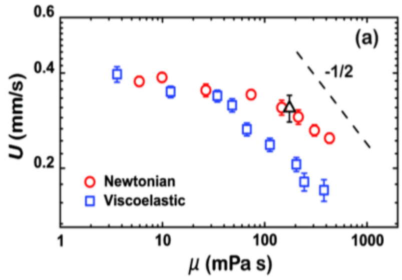

Fig. 2: Swimming speed of *C. elegans* in Newtonian (red circles) and viscoelastic (blue squares) fluids as a function of fluid viscosity. Triangle symbol represents the non-elastic xanthan gum solution. The data show that fluid elasticity decreases the nematode's swimming speed and efficiency when compared to a Newtonian fluid of same viscosity.

lines characteristic of bending waves, which propagate in time along the nematode body length. From such contour plots, we can extract kinematic quantities such as the nematode's swimming frequency f and wavelength λ_w as well as the wave speed $c= \lambda_w f$. For the nematode shown in Fig. 1b, $f\approx 2$ Hz, λ_w=2.5 mm, and c=5 mm/s.

The flow fields produced by the nematode are investigated using particle tracking velocimetry [7]. Examples of streamlines computed from instantaneous velocity fields are shown in Fig. 1(c) and 1(d) for the Newtonian and viscoelastic cases, respectively. Here, $Re<10^{-3}$ for both fluids, and De=3.0 for the viscoelastic fluid. The streamlines display large recirculating structures, or vortices, attached to the nematode's body. Such recirculation zones are usually associated with regions of maximum transverse nematode body displacement. The streamlines for the Newtonian and viscoelastic cases are qualitatively different, with the appearance of a distinct hyperbolic point near the nematode for the latter case.

We now address the question of whether fluid elasticity hinders or enhances swimming speed. The nematode's swimming speed as a function of fluid viscosity for both Newtonian and polymeric fluids is shown in Fig. 2. For relatively low viscosity values, the swimming speed is independent of fluid viscosity, and the values of U are nearly identical for both cases. For μ>30 mPa s, the swimming speed decreases with increasing μ even for Newtonian fluids. The decrease in U with increasing μ at low Re is most likely due to the nematode's finite power. Results show that, over the limited range of U, the *C. elegans*' propulsion speed shows a decay that is slower than $\mu^{-1/2}$, which strongly suggests that the nematode does not swim with constant power. The maximum power generated by the organism is approximately 200 pW (μ=30 mPa s). Nevertheless, we find that the values of U for viscoelastic fluids can be 35% lower than the Newtonian fluid of same shear viscosity. For example, the nematode's swimming speeds for the viscoelastic and Newtonian cases are 0.18 mm/s and 0.25 mm/s, respectively, even though the viscosity for both fluids is 300 mPa s (Fig. 2). The decrease in swimming speed in CMC (polymeric) solutions is not due to shear-thinning effects since nematode swimming in the non-elastic, shear-thinning fluid (xanthan gum) showed no apparent decrease in propulsion speed (Fig. 2, triangle symbol) compared to the Newtonian case.

The effects of fluid elasticity on the nematode's swimming behaviour are best illustrated by plotting the normalized swimming speed U/U_N as a function of the Deborah number ($De=f\lambda$), where U_N is the Newtonian speed (Fig. 3). Results show that the normalized swimming speed decreases monotonically with De, and reaches an asymptotic value of approximately 0.4 as De is further increased. In other words, as the elastic stresses increase in magnitude in the fluid, it introduces a larger resistance to propulsion, therefore decreasing the nematode's swimming speed. The trends observed in the experiments are similar to numerical and theoretical predictions [2, 4, 5].

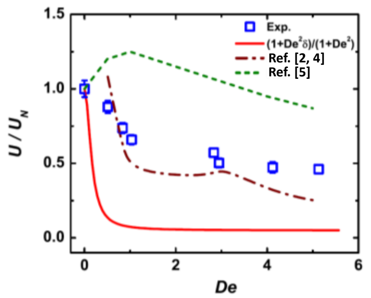

Fig. 3: Nematode's normalized swimming speed as function of Deborah number. The data (squares) show that propulsion speed decreases as elasticity in the fluid increases. Lines represent recent predictions.

CONCLUSIONS

We investigated the effects of fluid elasticity on the swimming behaviour of undulatory swimmers at low Re. We find that fluid elasticity *hinders* the propulsion of *C. elegans* at low Re. The swimming speed decreases as elasticity is increased. This trend is qualitatively similar to theoretical and numerical results [2, 4, 5]. Furthermore, fluid elastic stresses can alter the flow field generated by nematodes, and hyperbolic points in viscoelastic flows can result in large extensional viscosities and resistance to flow. This implies that foraging, feeding, and mixing may become difficult in strongly viscoelastic media. We note that generally, elastic response is not limited to extensional effects; it could also take the form of the hoop stresses associated with circulating flows. We therefore expect the dynamics of swimming in viscoelastic media to depend very much on the type of the swimming stroke.

References

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