Recently, there has been renewed interest in the swimming of microorganisms for applications that include artificial swimmers, novel materials, drug delivery, and micro-robotics. Due to small length scales, the fluid mechanics of swimming of microorganisms are governed by low Reynolds number (Re) hydrodynamics. In such a regime, linear viscous forces dominate over nonlinear inertial forces. While our current understanding of locomotion at low Re is derived mainly from investigations in simple, Newtonian fluids (e.g. water), many of the fluids in which locomotion occurs contain solids or (biological) polymers that are instead not Newtonian. Examples include wet soils, human mucus, and fluids in the cervix and female reproductive tract amongst other. A major challenge remains to understand and determine the propulsion mechanisms in fluids that display both solid- and fluid-like behavior (i.e., viscoelastic media).

1 Introduction

Microorganisms are surrounded by fluids. They cope and take advantage of water or wind currents to move, feed, and reproduce. Many, if not most, living organisms evolve in the realm of low Reynolds numbers (Re) [112], usually defined as $Re = \rho UL/\mu$, where $U$ is a characteristic speed, $L$ a characteristic length (e.g., body size), and $\rho$ and $\mu$ are the fluid’s density and dynamic viscosity, respectively. This is specially true for mili- and micro-organisms due to their small length scales $L$ spanning approximately $O(10^{-6})$ m to $O(10^{-3})$ m. Examples include include vari-
ous single-cell eukaryotic protozoa (e.g., sperm cells [18, 52, 53]), prokaryotes (e.g., bacteria [26]), and multi-cellular organisms (e.g., nematodes [26, 54]). By contrast, humans when swimming in the ocean or water pools can reach Re of approximately $10^4$. This means that humans can rely on inertial forces for propulsion due to relatively large length scales, while microorganisms simply cannot. Small living organisms instead have to overcome the linear viscous forces and drag arising from the fluid in order to achieve any appreciable net motion. The picture that emerges is that moving (and living) at low Reynolds number is drastically different from what we are accustomed to; namely, the nonlinear forces that we humans rely on for locomotion, that is inertia, are entirely absent in the realm of low Re. For the case of swimming microorganisms in simple fluids such as water, the equations of fluid motion become time-reversible. As a result, net locomotion can only be generated from non-reciprocal kinematics in order to break time-reversal symmetry [18, 85, 89]; this phenomenon is also known as the “scallop theorem” [112] which states that organisms that rely on reciprocal motion for locomotion cannot achieve net motion in the limit of vanishing Re.

Microorganisms have developed diverse strategies to break time-symmetry and create non-reciprocal motion (Fig. 1). Such strategies include body undulations and the presence of moving flagella. For example, the motility of various multi-cellular organisms including the worm nematode *Caenorhabditis elegans* originates from the propagation of undulatory waves from head to tail as a result of patterns of muscle activation and neuromuscular control [29, 154, 157]. In the specific case of *C. elegans*, body bending is generated by alternating contractions and relaxations of dorsal and ventral muscle groups running along the worm’s body length [104, 149]. Locomotion may also result from flagellar motility where one or several bundled appendages protrude from the cell body of certain prokaryotic and eukaryotic cells. Although there exist many interspecies variations within flagellar motility, one can typically distinguish between bacterial flagella that are helical filaments (e.g., *Escherichia coli* [10]), each with a rotary motor at its base which can turn clockwise or counterclockwise [8, 9, 11], and eukaryotic flagella that are flexible filaments undergoing “whip-like” motions resulting from the action of molecular motors distributed along the filament length; this latter mode of flagellar actuation is seen for example in many sperm cells [17, 98, 153]. Other eukaryotic organisms (e.g., *Paramecium*), have instead their body surface covered with thousands of small hair-like protrusions (*cilia*) that beat in a coordinated manner [17, 49].

Beyond the vast world of self-propelled microorganisms, we note a number of other cellular environments that are characterized by low Re locomotion. In mammals, for instance, cells featuring motile cilia include the epithelium of the female Fallopian tubes, where rhythmic beating guarantees translocation of the ovum from the ovary into the uterus [93, 94, 102]. Motile cilia are also found in the epithelial lining of the tracheobronchial airways of the lungs [120]. There, the ciliated epithelium prevents mucus accumulation in the airway lumen and serves importantly as an immune barrier against pathogens and foreign particulate matter by action of the so-called mucociliary escalator [76, 107]. Such synchronous waves of ciliary beating
Fig. 1 Examples of micro-organisms. (a) The green alga Chlamydomonas reinhardtii, a model eukariotic organism, (b) sperm cells moving next to boundaries, and (c) the bacterium E. coli, one the most widely studied prokaryotic model organism

effectively transport mucus secretions towards the laryngopharynx for expectoration or swallowing to the stomach.

It is clear from everyday observation and from the few examples cited above that nature has found many fascinating ways to break time-reversibility and achieve net motion at the microscopic scale. One can of course spend a lifetime attempting to map out in detail the various motility strategies found in nature. Here rather, we seek to deliver a physical understanding of how microorganisms move (or swim) in fluids at low Re. To do so, we first turn our attention to the equations of fluid motion that govern the motility of microorganisms at low Re.

2 Basic Principles: Fluid Dynamics of Swimming at Low Re

We begin here by briefly discussing the underlying hydrodynamic principles of swimming at low Re; a more thorough review of the subject can be found elsewhere [18, 26, 58, 85]. The general form of the equation of motion for fluids is given as

$$\rho \left( \frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla p + \nabla \cdot \mathbf{T} + \rho \mathbf{g},$$

(1)

where \( \mathbf{u} \) is the velocity vector, \( \rho \) is the fluid density, \( p \) is the pressure, \( \mathbf{T} \) is the deviatoric component of the total stress tensor, \( \mathbf{g} \) is the gravity field, and \( \nabla \) is the divergence operator. Here, we restrict our discussion to incompressible fluids (\( \rho = \text{constant} \)) such that

$$\nabla \cdot \mathbf{u} = 0.$$  

(2)

We will now make a series of simplifications to the above equations by considering the propulsion of a bacterium such as E. coli in water. Because the fluidic medium considered is a Newtonian liquid, the shear-stress \( \tau \) is linearly proportional to the fluid strain-rate \( \dot{\gamma} \), the constant of proportionality being the fluid shear viscosity \( \mu \) such that

$$\tau = \mu \dot{\gamma} = \mu(\nabla \mathbf{u} + \nabla \mathbf{u}^T),$$

where the superscript \( T \) represents the transpose of the vector. Let us now estimate the representative Reynolds number of an E. coli bacterium swimming in water. The shear viscosity (\( \mu \)) of water is 1 mPa·s.
(or 1 cP) and independent of shear-rate \( \dot{\gamma} \). The characteristic size \( L \) of \( E. coli \) is approximately 2 \( \mu \)m, and the bacterium is known to achieve net swimming speeds \( U \) of approximately 25 \( \mu \)m/s \[22\]. Following these parameters, we can estimate the Reynolds number for \( E. coli \) to be approximately \( \text{Re} = \rho U L / \mu = 5 \times 10^{-5} \ll 1 \). Such low value of \( \text{Re} \) implies that linear viscous forces dominate over inertial forces, and the nonlinear convective term \((\mathbf{u} \cdot \nabla \mathbf{u})\) in Eq. (1) can be safely ignored.

Additionally, one can compute the frequency-based Reynolds number, typically defined as \( \text{Re}_{\text{freq}} = \rho L^2 \omega / \mu \), to assess unsteady flow effects (i.e., \( \partial \mathbf{u} / \partial t \)), where \( \omega \) is the frequency at which the bacterium flagella rotate (\( \sim 100 \) Hz). We find again for \( E. coli \) that \( \text{Re}_{\text{freq}} \ll 0.1 \), and thus one can assume the flow to be steady. Using the above arguments, Eq. (1) effectively reduces to

\[
\nabla p = \nabla \cdot \tau.
\]

The above equation is often referred to as the Stokes equation (named after the mathematician Sir George Stokes) or alternatively as the creeping equations of fluid motion. For a Newtonian fluid, the stress tensor is given as \( \tau = \mu \dot{\gamma} = \mu (\nabla \mathbf{u} + (\nabla \mathbf{u})^T) \) and Eq. (3) reduces to

\[
\nabla p = \mu \nabla^2 \mathbf{u}.
\]

It is important to note that the above result is instantaneous in the sense that Eq. (4) has no dependence on time other than via boundary conditions. Equation (4) is also linear in both velocity and pressure. Furthermore, it is time-reversible in the sense that any time-reversed Stokes flow solves the same equations as the original Stokes flow. This time-reversibility, or kinematic reversibility, forms the hydrodynamic basis of the “scallop theorem” introduced earlier \[112\]. These hydrodynamic properties illustrate that swimming at low \( \text{Re} \) can seem at first as a highly confined phenomenon, yet microorganisms have found a variety of ways to overcome the constraints of the “scallop theorem” including the semi-flexible, helical-shaped flagella of \( E. coli \) or body undulations in the form of traveling waves for the nematode \( C. elegans \). In what follows, we briefly review some of the classical theories that have shed light on the hydrodynamic mechanisms leading to net propulsion at low \( \text{Re} \).

Over half a century ago, G.I. Taylor demonstrated in his seminal work that a slender body such as an (infinite) waving sheet (Fig. 2a) could swim in an incompressible, Newtonian fluid by generating traveling waves in the absence of inertia \[137, 138\]; that is, at vanishing values of \( \text{Re} \). In Taylor’s work, the planar sheet oscillates in time in a prescribed form according to \( y(x,t) = a \sin(kx - \omega t) \), where \( a \) is the traveling wave amplitude, \( \lambda = 2\pi / k \) is the wavelength, \( c = \omega / k \) is the traveling wave speed and \( k \) is the wavenumber. For vanishing \( \text{Re} \), Taylor found that the sheet oscillations induce a forward velocity \( U = \omega a^2 k / 2 + O(ka)^4 \) \[137\], where the sheet is propelled in the direction opposite to that of the propagating wave (Fig. 2a). Many important investigations followed Taylor’s landmark contribution. Of particular relevance, we highlight the well-known resistive force theory (RFT) introduced by Gray and Hancock in analyzing the locomotion of sperm cells \[52\]. There, the authors assumed that the hydrodynamic forces experienced by the organism would
be approximately proportional to the local body velocity such that the force exerted by a body or flagellar segment is given by $F = C_N U_N + C_T U_T$, where $C$ corresponds to the local drag coefficient per unit length (dependent on geometry and fluid viscosity), and $N$ and $T$ are the normal and tangential components, respectively (see Fig. 2b). Hence, the total thrust can then be obtained by integrating the propulsive force over the entire body or flagellum length. It is namely the anisotropy between the normal and tangential drag coefficients, with $C_N > C_T$, that lies at the origin of drag-based thrust.

![Fig. 2](a). Two-dimensional waving sheet in a viscous fluid illustrating the traveling wave of velocity $c$ progressing in the $x$-direction and the forward swimming speed ($U$) in opposite direction. (b) Resistive Force Theory (RFT) diagram illustrating the normal and tangential components of the velocity $U$ and force $F$, and the resulting net propulsive force.

Using RFT, Gray and Hancock obtained for the case of large amplitude displacements a closed-form solution for the swimming speed of an undulating filament given by the expression $U = \frac{\pi c (a/\lambda)^2 (C_N/C_T - 1)}{(1 + 2\pi^2 (C_N/C_T)(a/\lambda)^2)}$. Here, $C_N = 2C_N = 4\pi \mu / \ln(L/a)$ for a straight rod of length $L$ such that the ratio of normal to tangential drag coefficients yields $C_N/C_T = 2$ for a sine wave of wavelength $\lambda$. For example, more recent experiments using the nematode *C. elegans* estimated this ratio at $C_N/C_T = 1.4$ [133]; such value lies closely with earlier estimates reported by Gray and Lissmann [54] who dropped thin wires into viscous fluids ($C_N/C_T = 1.4-1.6$).

With the emergence of resistive force theory, Lighthill [89] later recognized the importance of long-range hydrodynamics interactions and improved RFT the by incorporating slender-body approximations. Such improvements led to $C_N/C_T = 1.5$ for the case of an undulating filament swimming in an infinite fluid medium. When incorporating wall-effects into the analysis, a significantly larger value of the drag coefficient ratio ($C_N/C_T = 4.1$) was subsequently obtained using the corrections of Katz et al. [66].

As noted earlier, the flow disturbances driven by the kinematic motion of a swimming microorganism in a Newtonian fluid will depend linearly upon the stresses exerted by the moving body on the fluid (see Eq. (4)). These boundary-driven flows are known to decay very slowly with the distance $r$ away from the body [18, 85, 119]. Most often, such flow disturbances are mathematically cast as linear superpositions
of fundamental solutions of the Stokes equation and decay with inverse powers of \( r \). The first solution, referred to as a “Stokeslet”, arises from the net force on the fluid, and has a velocity field that decays as \( 1/r \). The next solution, also known as a “stresslet” flow, is induced by the first force moment exerted by the body on the fluid and decays more rapidly (\( 1/r^2 \)); higher-order solutions decay even more rapidly (\( 1/r^3 \)). As a result, linear combinations of basic solutions of the creeping equations of fluid motion can generate a multitude of complex flow fields, exhibiting contrasting near- and far-field behaviors [119].

3 Experiments in Newtonian Fluids

Experimental studies on low Reynolds number locomotion in Newtonian fluids have undoubtedly complimented early theories on the topic [52, 53, 54, 89, 137, 138]. Many of these works have aimed at addressing the validity of classical theoretical models at least qualitatively, including RFT. In the section below, we briefly review a number of relevant experimental efforts that have helped over time characterize low Re propulsion in Newtonian media.

3.1 From scaled-up models to live microorganisms

Experiments with live microorganisms are generally challenging due to difficulties with imaging and optical setups, as well as the lack of control over the organisms themselves. One attractive experimental approach to circumvent some of these issues relies on leveraging scaled-up systems, often designed to mimic the organism’s main swimming kinematics (Fig. 3). Scaled-up models provide much valuable insight into the main physical mechanisms governing microswimming phenomena; they have brought valuable insight in understanding the net motion resulting from traveling waves along elastic tails [74, 113, 163], helical flagella [118, 165] and flagellar bundles [70, 71], as well as in uncovering the motility resulting from surface traveling waves along cylindrical shells [122].

Beyond fundamental research into microorganism locomotion, a broad range of scaled-up designs has been employed in the context of artificial swimming strategies at low Re [85], including Purcell’s seminal “three-link swimmer” which possesses two hinges actuated with both time and phase differences [151] and a flapping body performing reciprocal motions near a deformable free surface [143]. Smaller mechanical systems have also been investigated. For example, the shapes of an oscillating passive actin filament have been experimentally probed [155] and more recently, a three-sphere design has been implemented using colloidal beads and optical tweezers [87].

Despite challenges in working with live microorganisms, microscopy imaging of bacterial flagella has gained tremendous traction following the pioneering work
of H.C. Berg [6, 7, 8, 10, 12]. Of utmost relevance, flagellar kinematics of individual bacteria have been visualized in real time using fluorescent staining of both cells and flagellar filaments [146]. In more recent years, these initial microscopy techniques have been further developed to obtain time-resolved imaging of flagellar motility using setups with high-speed cameras [88] as well as to track swimming microorganisms three-dimensionally (3D), for instance in a fluid far from surfaces [36].

Since, however, microorganisms evolve constantly near solid boundaries (e.g., migration of infectious bacteria through tissues), a growing number of experiments has shown that the presence of surfaces is crucial to consider in low Re locomotion; namely, surfaces and wall effects drastically alter the kinematics of live swimming microorganisms relative to ideal unbounded swimming conditions. A best-known example is perhaps illustrated for helical flagella (e.g., *E. coli*): swimming trajectories are modified from straight to circular in the vicinity of boundaries, clockwise when the wall is rigid [84] and anticlockwise near a free surface [31]. In particular, solid surfaces not only lead to the reorientation of microorganisms in the direction parallel to the surfaces, they also attract the organism to the closest wall [14].

Uncovering the fundamental hydrodynamic interactions between surfaces and swimming microorganisms has helped shed light on experimental observations of the accumulation of confined spermatozoa on boundaries [28, 117, 158]. It was
recently observed [62] that ciliated *Paramecium* swimming in capillary tubes execute helical trajectories that slowly transition to straight lines as the tube diameter decreases (Fig. 4). Further experimental studies mimicking bio-locomotion in confined environments (e.g., female reproductive tract) have also revealed that the migration of motile spermatozoa in 3D microchannels is strongly influenced by specific wall shapes, including the turning angles at corners [30]. Beyond single-cell eukaryotic and prokaryotic microorganisms, it has also been noted that multi-cellular organisms, such as *C. elegans*, may display some finite attraction to the presence of boundaries [51] and certainly exhibit changes in their swimming kinematics under confinement conditions (e.g., setups with parallel-wall cells) [86].

![Fig. 4](image)

**Fig. 4** Swimming of *Paramecium* in tubes of different diameters [62]. Here, $\Lambda$ denotes the wavelength, $c$ denotes the radius of the organism and $A$ the amplitude of the helical trajectory traced by the organism in tubes of different diameter. (a) *Paramecium* swimming in large tube ($R/c = 2.63$) where the trajectory of the motion is helical. (b) Small wavelength helices are seen inside tubes of intermediate diameters ($R/c = 1.67$). (c) In very small tubes ($R/c = 0.9$), *Paramecium* swims in a straight line. Figure reproduced with permission from the American Institute of Physics.

### 3.2 Propulsive force & flow measurements

Beyond microscopy visualizations of low Re motility including measurements of swimming kinematics, experimental efforts have strived to deliver measurements of the propulsive forces (i.e., thrust) directly at the scale of single organisms. For instance, optical traps have been used to measure the forces required to tether sperm cells and bacteria [22, 75, 134]. In parallel, atomic force microscopy (AFM) has enabled the measurements of forces exerted by mucus-propelling cilia that lie on the order of $< 1$ nN per cilium during the effective stroke [139]. Recently, force measurements using optical tweezers have been obtained on individual bacteria to test the validity of RFT and determine the swimming efficiency of *E. coli* [23]. These
latter measurements have revealed for the first time that long-range hydrodynamic interactions are indeed critical in capturing accurately single-cell propulsion; in contrast, relying on RFT assumes a stationary background fluid while ignoring local flows induced from the other moving parts of the cell. Such observations have been most recently corroborated in scaled-up models of helical flagella, where the validity of RFT breaks down for increasing pitch angles of the helix [165]: a property attributed to the hydrodynamic interactions among helical loops at higher pitch angles. Concurrently, experiments on macroscopic swimmers for the range of helical wavelengths $\lambda$, radii $R$, and lengths $L$ relevant to bacterial flagella have also highlighted the qualitative and quantitative discrepancies with RFT predictions [116].

Despite the tremendous experimental progress brought on low Re locomotion in Newtonian fluids, there are still few available data on the dynamics of the fluid flows surrounding individual swimming microorganisms. One limiting reason remains the difficulty to resolve the microflows generated by individual swimmers such as $E. \text{coli}$ bacteria and spermatozoa. In turn, scaled-up studies have offered an attractive path to obtain time-resolved quantitative flow visualizations of the velocity fields using particle image velocimetry (PIV) techniques [71, 165]. For live organisms, perhaps the most well-known flow visualizations of individual undulatory swimming microorganisms date back historically to Gray and Lissmann [54], where the authors presented qualitative pathlines of freely swimming nematodes in water seeded with starch grains.

Since these seminal flow visualizations, the implementation of modern micro-PIV (µPIV) techniques [152] has begun paving the way toward quantitative flow measurements at the level of individual microorganisms. Most recently, pathlines of particles seeded in flows generated by an individual ciliated Paramecium have been imaged [62]. However, it is only by combining high-speed microscopy imaging with µPIV that the planar (2D) flows generated by individual unicellular microorganisms [88] and multi-cellular nematodes [133] have been resolved. In the latter case, the authors demonstrated that velocity magnitudes of fluid motion follow closely an exponential decay of the form $\exp\left(-\frac{2\pi r}{\lambda}\right)$ as a function of the distance $r$ away from the nematode body (see Fig. 5); this analytical solution was originally derived by Lighthill [89] for an undulating sheet of wavelength $\lambda$ in Stokes flow. Further extension of high-speed imaging techniques using for example tomographic PIV, where multiple cameras image simultaneously the interrogation volume from different angles [101], has enabled measurements of 3D time-resolved flow fields surrounding millimeter-sized copepods ($Calanus \text{finmarchicus}$).

It is worthwhile noting that experiments have gone beyond highlighting the limitations of classic analytical models such as RFT. Indeed, experiments resolving flow fields surrounding freely swimming microalgae have demonstrated that local fluid motions are much more complex than analytical models would initially suggest [35, 57]. This observation is particularly true in the near field, where the largest flow velocities occur. For example, Drescher et al. [35] detailed quantitative measurements of time-averaged flows using µPIV for two different types of microalgae: Volvox carteri, a ciliated multicellular spherical alga, and Chlamydomonas reinhardtii, a unicellular alga featuring two flagella that beat in a breaststroke-like
fashion. Guasto et al. [57] resolved rather the oscillatory nature of the flow field driven by *Chlamydomonas reinhardtii* over one period of motion using high-speed imaging, where the swimming microorganisms were confined in thin liquid films. Both studies have emphasized how distinct species are likely to drive qualitatively different disturbance flows, as recently highlighted by Saintillan [119]. This flow feature remains true in the far field as well, where it is commonly assumed that there, flow fields can be described in terms of a stresslet. As a final word, we note that the representation of these driven flows using time-averaged velocity fields fall short of capturing the true nature of the flow, since time fluctuations can be of the same order as the mean.

### 3.3 Individual organisms & collective behavior

Until now, we have stressed the unique swimming features of individual microorganisms. Beyond such individual motion, a number of experimental studies have focused in recent years on collective behavior phenomena that arise at low Re [3, 85, 148]. Here, we highlight collective motions that result in flows affecting
the dynamics of entire populations in contrast to single microorganisms, as seen for instance in sperm cells [100, 114, 132]. Moreover, collective behavior may also be noted in the non-reciprocal motion of cilia that is at the origin of the mucociliary escalator and guarantees net fluid flow towards the trachea [40]. Most noticeably, experiments using flow velocimetry and tracking techniques in bacterial suspensions have demonstrated the existence of transient patterns of coherent locomotion with correlation lengths much larger than the size of individual organisms (i.e., from a few tens to several hundreds of microns) and the presence of recurring swirls and jets [25, 33, 129, 159].

In analogy to analysis methods dedicated for high-Reynolds-number fluid turbulence, the dynamics of so-called ‘bacterial turbulence’ have been recently characterized in terms of kinetic energy, dissipation (quantified by the enstrophy, or mean-squared flow vorticity) and spatio-temporal correlation functions due to the transient, large-scale nature of such collective motions [38]. In this latter study, the authors successfully probed for the first time the fluid and bacterial dynamics independently by applying bright-field microscopy to analyze the movement of the bacteria whereas micron-sized fluorescent markers were seeded to visualize the flow of the suspending fluid (see Fig. 6). From a practical standpoint, collective motion has drawn attention as a strategy to achieve controlled mixing and pumping action in microfluidic devices using bacterial suspensions [72, 73] and artificial cilia [21, 126].

Fig. 6 Collective dynamics of suspensions of bacteria. Adapted from Dunkel et al. [38]. (a) Streamlines and normalized vorticity field determined from PIV in a very dense homogeneous suspension of B. subtilis. (b) Turbulent “Lagrangian” flow of fluorescent tracer particles (false-color) in the same suspension, obtained by integrating emission signals over 1.5 s. Scalebar represents 70 µm. Figure reproduced with permission from the American Physical Society.
4 From Newtonian to Complex Fluids

Much of our understanding of low Re locomotion arises from considerations in simple, Newtonian fluids like water [18, 52, 53, 89]. But such fluids do not capture the diversity of habitats characterizing locomotion in the low Re realm. Indeed, many microorganisms evolve within complex fluids that contain particulates and/or biopolymers [39, 131, 145]. But, what are complex fluids? Here, we define complex fluids as a broad class of materials that are usually homogeneous at the macroscopic scale and disordered at the microscopic scale, but possess structure at an intermediate scale (typically, a few sizes of its particles). Examples include colloidal suspensions, foams and emulsions, polymeric fluids, gels, human mucus, and blood. In colloidal crystals, for example, the intermediate scale is set by the size of the organized crystalline structure; that is, if one considers a cup of a cornstarch suspension, then the microscopic scale is the matrix that includes both the water molecules and the cornstarch grains (∼1 µm), and the macroscopic scale is the size of the cup (∼10 cm), while the intermediate scale is set by the structural length scale (if any) of the cornstarch grains. The cornstarch suspension will respond quite differently to an applied stress, depending on the grain size, concentration, and the grain arrangement in the suspending liquid. Thus, the macroscopic flow behavior, otherwise known as the rheology of complex fluids, is a strong function of the fluid microstructure.

Shear-Thinning Viscosity: Complex fluids such as human mucus, blood, wet soil, and gels often display non-Newtonian rheological behavior such as strain-rate dependent viscosity (e.g., shear-thinning) and viscoelasticity. For example, one of the most common non-Newtonian behavior found in polymeric solutions and colloidal suspensions is rate-dependent viscosity in which the fluid viscosity is a function of the shear-rate; viscoelasticity can also be found in such fluids. This non-Newtonian viscosity behavior can be captured by an empirical power law model of the type \( \eta = \eta_0 |\dot{\gamma}|^{n-1} \), where \( \eta \) is the non-Newtonian viscosity, \( \eta_0 \) is the viscosity factor, and \( n \) is the power law index. If \( n > 1 \), the fluid is shear thickening whereas if \( n < 1 \) the fluid is shear-thinning. For the particular case \( n = 1 \), the model reduces to Newtonian. Recall that for Newtonian fluids, the stress is linearly proportional to the strain-rate and \( \mu \) is a constant independent of \( \dot{\gamma} \); note that we use the symbol \( \mu \) for Newtonian viscosity and \( \eta \) for non-Newtonian viscosity. Another common empirical rheological model is the Carreau viscosity model usually given as:

\[
\eta = \eta_0[1 + \lambda_c|^\dot{\gamma}|^2]^{(n-1)/2},
\]

where \( \lambda_c \) is a time-scale associated with the shear-rate (1/s) at which the fluid viscosity departs from Newtonian behavior. The Carreau number \( Cr = \lambda_c \dot{\gamma} \) is often used to characterize such transition; \( Cr = 1 \) marks the departure from low shear-rate Newtonian viscosity. This model offers some advantages over the power law model discussed above. The most significant perhaps is that the Carreau model is able to capture the frequently observed viscosity transition from a low-shear-rate Newtonian plateau to the power-law region as the shear-rate \( \dot{\gamma} \) is gradually increased. A
drawback of the Carreau model, however, is that it assumes the fluid infinite-shear-viscosity $\eta_\infty$ to be effectively zero. That is, the transition from the power-law region to this high-shear, Newtonian plateau is not captured by Eq. (5). An alternative is to use the more general Carreau-Yassuda model [15]. Nevertheless, Eq. (5) offers a great improvement over the power-law model.

The nonlinear relationship between $\tau$ and $\dot{\gamma}$ seen in shear-thinning fluids can have significant consequences to locomotion at low Re including (i) a breakdown of the “scallop” theorem, (ii) kinematic changes in the organism’s swimming motion, and (iii) changes in the drag forces experienced by the organism. In fact, it was recently shown that shear-thinning viscosity may enhance both the efficiency and the swimming speed of swimming microorganisms [99, 147]. Using Taylor’s waving sheet with prescribed kinematics along with a Carreau fluid model, Vélez-Cordero and Lauga [147] showed that the swimming speed for an inextensible sheet is the same for shear-thinning and Newtonian fluids, but the swimmer (i.e., sheet), however, is more efficient in the shear-thinning fluid. A numerical simulation by Montenegro-Johnson, Smith, and Loghin [99] showed that for large amplitude waves the swimming speed increases in shear-thinning fluids compared to that in Newtonian fluids. These recent studies have shown that even relatively simple non-Newtonian fluid behavior can have a significant impact on the swimming kinematics of microorganisms.

### 4.1 Viscoelasticity

A common fluid rheological behavior is viscoelasticity and is typically found in liquids containing polymers or bio-polymers, gels, mud, intestinal fluid, and mucus. Such viscoelastic fluids possess both fluid-like and solid-like behavior, as well as time-dependent rheology. A very simple (and linear) constitutive model to describe fluid viscoelasticity is the Maxwell model which is represented by a purely viscous damper and a purely elastic spring connected in series [41, 81]. The Maxwell model is usually expressed as

$$\tau + \lambda \frac{\partial \tau}{\partial t} = \mu \dot{\gamma},$$  \hspace{1cm} (6)

where $\lambda = \mu / G$ is the fluid relaxation time and $G$ is the elastic modulus (of the spring). This simple model predicts that the stress relaxes exponentially in time, which is accurate for many liquids containing polymers. However, Eq. (6) predicts that stress will increase linearly with time under constant stress, a trend not observed in real polymeric solutions. In addition, the Maxwell model is only valid for small deformations. For larger deformations, one should instead turn to nonlinear models such as the Oldroyd-B and the finite extensibility non-linear elasticity (FENE) models [81]. Such models are known to capture many nontrivial viscoelastic phenomena such as the development of hoop-stresses and hydrodynamic instabilities [123].
Despite its simplicity and limited applicability, the Maxwell model (Eq. 6) is useful in illustrating one of the main features of fluid viscoelasticity, namely that the shear-stress is time dependent and that it depends on the history of deformation. Such features give rise to flow behavior that is markedly different from that of Newtonian fluids even at low Re [15, 81, 123], and they can even lead to the breakdown of the scallop theorem [69]. Indeed, flow instabilities and nonlinear dynamics have long been observed in viscoelastic fluids [4, 123, 160], particularly those containing polymers. Most of the nonlinear flow behavior observed in these studies arises from the extra elastic stresses due to the presence of polymer molecules in the fluid. Mechanical stresses in these fluids are history-dependent and depend namely on a characteristic time $\lambda$ that in dilute solutions is proportional to the relaxation time of a single polymer molecule. In semi-dilute solutions, $\lambda$ depends also on molecular interactions.

As mentioned earlier, many microorganisms live in complex fluid environments that are viscoelastic. The bulk and local nonlinear behavior response of such viscoelastic fluids is expected to play a significant role on small swimmers. Consider for example the swimming behavior of motile sperm cells [60, 67, 68] that usually swim as a result of (single) flagellar beating. For freely swimming spermatozoa in Newtonian semen (Fig. 7a), the flagellum exhibits a regular sinusoidal beating pattern [131]. But once the organism encounters a viscoelastic medium (i.e., cervical mucus), the regular beating pattern is transformed into high-amplitude, asymmetric bending of the flagellum (Fig. 7b). This ‘hyper-activated’ sperm is believed to be dramatically influenced by its fluidic environment [60, 131], which in turn can affect human fertility [39, 97]. Other examples of motility in viscoelastic media include the removal of mucus in the human respiratory track by beating cilia [107, 120], the locomotion of bacteria in biofilms [61, 162], and the burrowing of organisms in wet soil [65, 156]. Understanding how microorganisms move in viscoelastic fluids is, therefore, of both scientific and practical importance.

![Fig. 7 Snapshot of sperm cells moving in (a) Newtonian fluid (semen) and viscoelastic fluid (mucus); adapted from Ho and Suarez [60].](image)
Locomotion in Complex Fluids: Experiments

Despite many recent efforts to be discussed below, the effects of bulk fluid elasticity on the motility behavior of live organisms at low Re are still not clear and well understood. In order to provide the reader with some basic insight into this issue, we turn to our favorite dimensionless parameters and their physical meaning. The first, of course, is the Reynolds number defined earlier as $Re=\frac{\rho U L}{\mu}$; Re is a measure of the relative importance of the fluid inertia to viscous forces. Because the length scale $L$ of microorganisms is very small, magnitudes of Re are also small ($Re \ll 1$) and viscous forces dominate over inertial forces. We saw earlier that for $E. coli$ swimming, Re is estimated to be approximately $10^{-4}$. The effects of fluid elasticity are often measured using the Deborah number, defined as $De=\lambda f$ where $\lambda$ is the fluid relaxation time and $f$ is the organism’s beating frequency. Note that $De=0$ for Newtonian fluids and $De \to \infty$ for purely elastic solids. One could imagine that fluid elasticity may begin to play a dominant role for $De > 1$. If one considers the beating frequency $f$ of sperm cells to range from 20 to 50 Hz and the relaxation time $\lambda$ of cervical mucus to range from 1 to 10 s (depending on factors like hydration, among others), one can expect fluid elasticity to play a significant role on the motility of spermatozoa. One can also compare the ratio of the (fluid) elastic time scale $\lambda$ to the (fluid) viscous time scale $\rho L^2/\mu$. This is the so-called Elasticity number, defined as $El=\frac{\lambda \mu}{\rho L^2}$. Elastic effects are expected to dominate for $El > 1$. Because of the nonlinear (squared) dependence of $El$ on the (swimmer) length scale $L$, one anticipates the effects of fluid elasticity to become increasingly important for swimming microorganisms.

4.1.1 Swimming in Viscoelastic Fluids: Expectations

In 1979, Chaudhury [24] attempted to incorporate the effects of fluid elasticity on animal locomotion using a series of expansions similar to Taylor’s analysis and a second-order fluid. It was then predicted that fluid elasticity could either increase or decrease the propulsion speed of the waving sheet (Fig. 2), depending on the value of Re. Later, inspired by experimental observations of spermatozoa swimming in mucus [60, 131], the effects of elasticity on beating flagellar structures were considered in Stokes flow using the Maxwell model [46]. It was shown that self-propulsion was not affected by viscoelasticity even at large Deborah numbers ($De$), where $De=\lambda f$. Here, $\lambda$ is the fluid relaxation time and $f$ is the beating frequency. However, the total work decreased with increasing $De$. It was then suggested that a microorganism could swim faster in a viscoelastic fluid with the same expenditure of energy compared with a Newtonian fluid.

More recently, Lauga [82] showed that, for a 2D waving sheet (Fig. 2), elastic stresses could significantly alter the organism speed and the work required to achieve net motion. Using nonlinear viscoelastic fluid models such as the Oldroyd-B and the FENE-P models, it was shown that the sheet’s forward speed $U$ in a purely elastic fluids is given by [82]
\[
\frac{U}{U_N} = 1 + De^2 \left( \frac{\eta_s}{\eta} \right) \quad 1 + De^2,
\]

where \( U_N \) is the swimming speed of the sheet in a viscous Newtonian fluid (i.e., Taylor’s original result) and \( \eta_s \) is the solvent viscosity; note that the solution viscosity \( \eta \) is assumed to be the sum of the solvent viscosity and the polymer viscosity such that \( \eta = \eta_s + \eta_p \). Hence, for a given (i.e. prescribed) swimming gait \( U_N \geq U \), that is, elastic stresses reduce the overall speed of the waving sheet. A similar result was also obtained for a waving cylinder by Fu et al. [45]. These important results imply that fluid elasticity can reduce the swimming speed of microorganisms when compared to simple, Newtonian fluids. An important caveat, of course, is that organisms may compensate the reduction in velocity by increasing their beating frequency and/or concurrently decreasing their body wavelength. In other words, microorganisms can alter their swimming kinematics to adjust or adapt to varying fluidic environments.

Numerical simulations have also been used to address the role of fluid elasticity on the swimming behavior of microorganisms. In particular, Teran and co-workers [140] considered two-dimensional swimming “free” sheets (i.e., with free head and tail) of finite length \( L \) in viscoelastic fluids. The simulations were performed by solving Stokes equation using the Oldroyd-B model as the constitutive equation using an immersed boundary method. The simulations show that, for accentuated tail motions, the sheet swims faster at \( De \approx 1 \) than in a Newtonian fluid. This regime corresponds to where “swimmer” stroke frequency matches the fluid relaxation time. This is unlike Eq. (7) which predicts that the swimmer speed in viscoelastic fluids is always slower than in Newtonian fluids. The simulations do show that for \( De > 1 \), the swimming speed decreases as \( De \) increases.

As briefly discussed above, fluid elasticity can strongly affect both the swimming dynamics and kinematics of small organisms even at low \( Re \). Recent ana-
lytical works predict that fluid elasticity hinders swimming speed while numerical simulations show that it is possible to obtain an enhancement in self-propulsion in a regime where the fluid relaxation time matches the swimmer stroke frequency, that is $De \approx 1$. Despite such important advances, it is still not clear whether elastic stresses enhance or hamper self-propulsion since theoretical and numerical results are model dependent. So the question still stands: does fluid elasticity enhance or hinder self-propulsion at low Re? Perhaps experiments will shed more light into this important question.

5 Experiments in Viscoelastic Fluids

5.1 Scaled-up experiments

While some specific aspects of the role of elastic stresses on the swimming behavior of microorganisms have been recently addressed both theoretically and numerically, there is still a dearth of systematic experiments addressing the role of viscoelasticity on swimming of microorganisms at low Re. Part of the problem is undoubtedly the difficulty in identifying a model organism or swimmer that is both able to move in different types of media and relatively easy to image and track. To circumvent some of these difficulties, many investigators choose to build instead macroscopic-scaled versions of the microorganisms’ propulsion mechanism [71, 73, 74, 91]. Such scaled-up experiments can provide a wealth of information that would be otherwise difficult to obtain with live microorganisms (e.g., detailed velocity fields). In this section, we discuss an interesting experimental setup proposed by Liu and co-workers [91] in which a scaled-up model of bacterial filaments is investigated.

The experimental setup is shown in Fig. 9 and consists of a large cylindrical tank filled with either a viscous Newtonian fluid (silicon oil) or a viscoelastic fluid (polymeric solution). A rigid helix rotating at speed $\omega$ is slowly immersed or plunged at a constant speed $V$ into the fluid-filled tank. Helices of varying pitch angles are used to mimic the geometry of bacterial flagellar filaments (e.g., E. coli). The hydrodynamic force exerted on the helices by the fluid is measured by placing the tank on top of a sensitive digital balance. In these experiments, zero-force swimming is achieved by adjusting the translation speed until the measured axial force is zero. Because the helix is inserted from above, a positive vertical force on the helix represents a drag, and a negative vertical force on the helix is a thrust. The force-free swimming speed is measured as a function of helix rotation rate, helix geometry (i.e., pitch angle), and fluid properties (i.e., Newtonian vs. viscoelastic).

Because the fluids are very viscous, the Reynolds number is well below 0.01 and inertial effects are negligible. In order to decouple the effects of fluid elasticity from those of rate dependent viscosity (e.g., shear-thinning) common in polymeric solutions, a nearly constant-viscosity, elastic fluid was prepared. Such fluids are often called “Boger fluids” in reference to David Boger who first proposed the use
Boger fluids are constructed by using a small quantity (usually in part per millions) of high molecular weight (MW) flexible polymer dissolved in a very viscous solvent. Because the polymer contribution to the overall solution viscosity is small, the solution viscosity is overwhelmed by the viscosity of the Newtonian solvent. The addition of high MW flexible polymers is able to add elasticity to the fluids. As a result, Boger fluids have nearly-constant viscosity while still possessing elasticity. In the work of Liu et al [91], Boger fluids are prepared by dissolving either 3000 ppm or 6000 ppm of poly-isobutylene (PIB) in polybutene (solvent). The average relaxation time $\lambda$ for both polymeric solutions is approximately 0.6 s.

The main result of the scaled-up experiment is shown in Fig. 9 (rightmost panel). The investigators find an enhancement of the measured swimming speed of a rotating helix in a viscoelastic fluid near $De=1$, where $De=\omega \lambda / 2\pi$. This result is similar to the enhancement observed in numerical simulations of 2D flexible filaments in Oldroyd-B fluids by Teran and co-workers [140] and of helical filaments [128], but is in contrast with the decrease observed in analytical calculations [43, 82] and experiments with live organisms [124]. As the rotating speed (and $De$) increases, the helix propulsion speed decreases even below the purely viscous Newtonian speed.

An important take-away message from these scale up experiments is that it appears that the nature of the dependence of propulsion speed on fluid elasticity (or $De$) depends strongly on the geometry of the waveform used for swimming. This is made obvious by the sensitivity of the peak enhancement of swimming speed on the pitch angle of the helix, as shown in Fig. 9 (rightmost panel). This is an important point which we will further discuss later in this chapter.
While scale-up or mechanical mock experiments can provide much useful information, they cannot fully capture the complexity of live organisms. Therefore, it is important to perform systematic studies using live organisms. In the next section, we will discuss experiments using a well known biological model system, namely, the nematode *Caenorhabditis elegans*.

### 5.2 Experiments with live organisms

As discussed above (and in other parts of this book), there has been much interest in understanding the swimming behavior of microorganisms in complex fluids, in particular fluids possessing elasticity. Example of such fluids include materials made up of organic components such as glucose, amino acids, and soluble proteins amongst other. This is the case for internal body linings including gastrointestinal [27], respiratory [111] and urogenital mucus [39]. Many microorganisms live in such complex fluidic environments including sperm cells as well as many types of bacteria and algae. Clearly, understanding the effects of fluid elasticity on the swimming behavior of microorganisms is of both scientific and practical interest.

Both numerical simulations and theoretical analyses have been used to gain insight into the problem of swimming in viscoelastic fluids. Results seem to vary depending on the type of constitutive model and on the swimmer waveform. For example, it was shown that elasticity augments propulsion speed for an infinite waving sheet immersed in a second-order fluid [24]. But recent analyses using both Oldroyd-B and FENE models showed that for the case of an infinite undulating sheet [82] and cylinder [43], 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 showed that fluid elasticity could in fact augment swimming speed when the Deborah number (De) is approximately 1 [140]. A recent experiment using a mechanical scale up model of a helical flagellum, showed that there is indeed an enhancement in propulsion speed at De ≈ 1 [128].

Despite these important recent developments, experiments with live organisms have been lacking and the effects of fluid elasticity on swimming behavior of microorganisms are still not clear [78]. In this section, we will focus on swimming experiments with a biological model system, namely the nematode *Caenorhabditis elegans*. Model organisms are non-human species which are extensively studied to understand particular biological phenomena. Examples include the zebra fish, *E. coli*, fruit fly (*Drosophila melanogaster*), and mice, among many others. The idea is that discoveries made in model organisms will provide insight into the workings of other non-model organisms. In the case of swimming, the hope is that by choosing a model organisms, discoveries made with the nematode *C. elegans* can be used to understand other organisms.
5.2.1 *C. elegans*: an attractive model organism for swimming studies

An interesting model system that has received much attention in the biological community is the nematode *Caenorhabditis (C.) elegans*, which is a small, multi-cellular, free-living roundworm found in soil environments. Much is known about the nematode’s genetics and physiology; its genome has been completely sequenced [19] and a complete cell lineage has been established [20]. These nematodes are equipped with 95 muscle cells that are highly similar in both anatomy and molecular makeup to vertebrate skeletal muscle [154]. Their neuromuscular system controls their body undulations which allows *C. elegans* to swim, dig, and crawl through diverse environments. The wealth of biological knowledge accumulated to date makes *C. elegans* ideal candidates for investigations that combine aspects of biology, biomechanics, and the fluid mechanics of propulsion.

Figure 10 shows an image of an adult, wild-type *C. elegans* swimming in a water-like buffer (M9) solution. The nematode is characterized by a relatively long and quasi-cylindrical body shape (Fig. 10). Its length can vary from 50 µm (infants) to 1 mm (adults) while its radius is approximately 80 µm. The nematode length-scale is an important feature, since imaging the motion of micro-organisms and the flow induced by them is not a trivial task.
5.2.2 Swimming experiments with *C. elegans*: Dilute polymeric solutions

We now discuss swimming experiments using the nematode *C. elegans* in some detail. Experiments with two main type of fluids, namely Newtonian and viscoelastic, are discussed. Experiments are performed in small channels that are made of acrylic and are 1.5 mm wide and 500 µm deep; they are sealed with a thin (0.13 mm) cover glass. In order to minimize three-dimensional motion, the channels are relatively shallow, yet the nematode is able to freely move. The swimming motion of *C. elegans* are imaged using standard bright-field microscopy using a fast CMOS camera. The image acquisition rate are kept constant at 125 frames per second to guarantee small linear displacements along the nematodes body between consecutive frames. All data presented here pertain to nematodes swimming at the center plane of the fluidic channel. Out-of-plane recordings are discarded. An average of 15 nematodes is recorded for each experiment.

An important consideration in swimming experiments with live organisms is the fluid medium. Fluids must be "constructed" or developed such that they possess the desirable rheological property (elasticity, shear-thinning, etc) but without being toxic to the organism. In the experiments to be discussed here, Newtonian fluids of different shear viscosities \( \mu \) are prepared by mixing two low molecular weight oils (Halocarbon oil, Sigma-Aldrich). Viscoelastic fluids are prepared by adding small amounts of carboxymethyl cellulose (CMC, \( 7 \times 10^5 \) MW) into de-ionized water. CMC is a long, flexible polymer with an overlap concentration \( (c^*) \) of approximately \( 10^4 \) ppm. In order to rule out the effects of shear-rate dependent viscosity, an aqueous solution of the stiff polymer Xanthan Gum (XG) that is shear-thinning but possesses negligible elasticity is also used in experiments.

Fig. 11

(Left) Fluid shear viscosity curves for the flexible carboxy-methyl cellulose (CMC) and semi-rigid xanthan gum (XG) solutions. The concentrations of CMC solution ranges from 1000 ppm to 8000 ppm by weight, from bottom to top in the plot. Solid circles represent the 3000 ppm XG aqueous solution. The values of the power law index \( n \) are 0.65 and 0.35 for the 8000 ppm CMC and the 3000 ppm XG solutions, respectively. Table: The power law indexes of the CMC aqueous solutions.
Fluid Rheology - Viscosity Data: An important step in these experiments is fluid rheological characterization. How viscous or elastic are the fluids? A strain-controlled rheometer RSF III (TA Instruments) with a cone-and-plate geometry is used to characterize the rheological properties of the CMC and XG solutions. As shown in Fig. 11, the viscosities of these polymeric solutions share similar monotonic decrease as the shear rate increases, that is they are slightly shear-thinning. The viscosity curve of polymeric solutions are fitted with the power-law fluid model of the type \( \mu = \mu_0 |\dot{\gamma}|^{n-1} \), where \( \mu_0 \) is the viscosity factor and \( n \) is the power law index. The power law index \( n \) is fitted to all CMC and XG solutions (see table in Fig. 11). The CMC solutions show relatively weak shear-thinning behavior, particularly in the shear rate range of 1 s\(^{-1}\) to 20 s\(^{-1}\). This is the range of shear-rates produced by the swimming \textit{C. elegans} in fluids. As the CMC concentration in solution increases, shear-thinning effects also increases. In the most concentrated CMC solution, i.e. at 8000 ppm, the power law index is approximately 0.65. As a comparison, the xanthan gum solution at 3000 ppm shows much stronger shear-thinning behavior, and the power law index for this xanthan gum solution is 0.35. Note that the mixture of low molecular weight Halocarbon oils show constant shear viscosity and are not shown.

Fluid Rheology - Relaxation Times: Shear-viscosity or flow curves are not sufficient to describe the material properties of viscoelastic fluids which are inherently time-dependent (see Eq. 6). An important quantity used to characterize viscoelastic fluids is the fluid relaxation time \( \lambda \). Measuring \( \lambda \) is not a trivial task for several reasons including the fact that most real viscoelastic fluids have not one but an spectrum of relaxation times; \( \lambda \) can also be shear-rate dependent. What is usually reported in the literature (and used in many models) is the longest, most dominant value of \( \lambda \). There are several ways to obtain \( \lambda \) including (i) measurements of first normal stress difference \( N_1 \) from steady rheology combined with an appropriate constitutive model, (ii) oscillatory or frequency dependent measurements in which both the viscous \( G'' \) and elastic \( G' \) moduli are measured for small strains, and (iii) stress relaxation experiments. For more detail information on rheological measurements and applications, please see [124].

For the experiments discussed in this section, the values of \( \lambda \) for all the viscoelastic CMC solutions are obtained using a stress relaxation technique after a sudden applied strain or shearing displacement. This technique is sometimes referred to as step-strain stress relaxation. In the experiment, the time decay of the shear stress is described by a relaxation modulus \( G(t) \) (Fig. 12), which is fitted with the generalized linear viscoelastic model of a single relaxation time of the type \( G(t) = G_0 e^{-t/\lambda} \). By varying the polymer concentration in solution, the values of \( \lambda \) can range by as much as an order of magnitude from 0.4 s for the most dilute concentration (1500 ppm) to about 5.6 s for the most concentrated solution (8000 ppm). The value of \( \lambda \) for all CMC solutions are shown in the Table in Fig. 12.

Swimming Kinematics: Now that the fluids have been characterized, we can begin to discuss the swimming experiments using \textit{C. elegans}. Because it is important to establish a baseline, results obtained with the viscoelastic fluids (CMC solutions) are compared to swimming in Newtonian fluids (halocarbon oils). An important quan-
Locomotion in Complex Fluids: Experiments

Fig. 12 (Left) Stress relaxation data and (Table) fluid relaxation time $\lambda$ for all polymeric (CMC) solutions.

- $\kappa(s,t) = \frac{d\phi}{ds}$
- $\phi$ is the angle made by the tangent to the x-axis in the laboratory frame at each point along the body centerline, and $s$ is the arc length coordinate spanning the head of the nematode ($s = 0$) to its tail ($s = L$).

The contour plots show the existence of periodic, well-defined diagonally oriented lines characteristic of bending waves, which propagate in time along the nematode body length. By taking the Fourier transform of the contour plots (along the axis of time), a single peak at 2 Hz is found indicating that the nematode beating is periodic in time (Fig. 13b). Other kinematic metrics such as wavelength (1 mm) and wave speed (5 mm/s) can also be extracted from the contour plots.

**Propulsion Speed: Newtonian vs Viscoelastic**: Now, it is possible to address the question of whether fluid elasticity hinders or enhances the propulsion speed of live organisms using *C. elegans*. The average nematode forward velocity $U$ is calculated by differentiating the nematode’s centroid position with respect to time (Fig. 10). For nematodes swimming in a Newtonian fluid of shear-viscosity $\mu$ of 5 mPa·s (or 5 × the viscosity of water), the value of $U$ is approximately 0.4 mm/s and the Reynolds number ($Re=\rho UL/\mu$) is approximately 0.05. Hence, the model organism *C. elegans* can be considered a low Re swimmer.

The nematode’s swimming speed as a function of fluid viscosity for both Newtonian and viscoelastic (CMC) solutions is shown in Fig. 14a. For relatively low viscosity values, the swimming speed is independent of fluid viscosity $\mu$ and the values of $U$ are nearly identical for both cases. For $\mu > 30$ mPa·s, the swimming speed decreases with increasing $\mu$ even for Newtonian fluids. This decrease in $U$ is most likely due to the nematode’s finite power. Note that, for a nematode swimming with constant power at low Re, $P \sim \mu U^2$ where $P$ is power. Results show that,
Fig. 13 The kinematics of swimming *C. elegans* at low Re number in viscous Newtonian fluids (Re ≈ 0.1). (a) Contour plot of the measured curvature (κ) along the nematodes “skeleton” or body centerlines as a function of time. The y-axis corresponds to the dimensionless position s/L along the nematode’s body where s = 0 is the head and s = L the tail. (b) Frequency spectra of κ at different selected positions s/L. The nematodes beating frequency peaks at a single value (~2.0 Hz), irrespective of the location s/L.

over the admittedly limited range of μ, the nematode’s propulsion speed shows a decay that is slower than μ⁻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, calculated for μ = 30 mPa·s.

Importantly, the values of U for viscoelastic fluids are found to be 35 % lower than the Newtonian fluid of same shear viscosity (Fig. 14a). 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 shear viscosity for both fluids is 300 mPa·s (Fig. 14a). The decrease in swimming speed in CMC (polymeric) solutions does not seem to be due to shear-thinning effects since nematode swimming in the non-viscoelastic, shear-thinning fluid (XG) showed no apparent decrease in propulsion speed (Fig. 14a, triangle symbol) compared to the Newtonian case.

So far, experiments using an undulatory, low Re swimmer (i.e. *C. elegans*) show that for similar viscosities fluid elastic stresses seem to hinder the organisms’ propulsion speed. An important question is whether the organism is responding or adapting to the extra elastic stresses present in the fluid or are the polymer molecules toxic to the organism? In other words, is the observed decrease in swimming speed due to hydrodynamics or biology? This is a difficult question to answer with certainty, but one can address it at least in part by comparing the swimming phenotypic behavior (i.e. kinematics) between Newtonian and viscoelastic fluids. The wave-speed c produced by the nematode is of particular interest since it has been shown that the values of c seem to change significantly once the nematode adopts a different swimming gait, i.e. swimming versus crawling [125]. The wave-speed can be easily measured from the curvature contour plots. The inset of In Fig. 14a shows the nematode’s bending wave speed c as a function of fluid viscosity. Results indicate
that viscoelasticity has negligible effect on the nematode’s swimming kinematics. That is, the changes in kinematics including the decrease in beating frequency and wave speed are due to viscous effects only. In addition, there is no evidence of change in motility gait (e.g. swimming to crawling) as \( \mu \) increases since the beating amplitudes remain constant \( (A = 0.26 \text{ mm}) \) even for the most viscous fluid \( (\mu = 400 \text{ mPa} \cdot \text{s}) \).

The effects of fluid elasticity on the nematode’s swimming behavior are best illustrated by plotting the normalized swimming speed \( \frac{U}{U_N} \) as a function of the Deborah number \( (De = \lambda f) \), where \( U_N \) is the Newtonian speed. Figure 14(b) shows that the normalized swimming speed decreases monotonically with \( De \), and reaches an asymptotic value of 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.

Comparing Experiments to Calculations: We can now compared the experimental results to the numerical and theoretical prediction discussed above. Of course, such comparisons is not quite fair because there are significant differences between the experiments and the calculations. For example, most calculations are two-dimensional (2D) while the nematode is allowed to swim in 3D. Most importantly, while the calculations assume a prescribe kinematics or waveform, the nematode is free to choose its own. Nevertheless, qualitative assessments can be made.
We begin by noting that for all the experiments presented in this section, the ratio of the solvent viscosity to the total solution viscosity is below 0.05, which is similar to the calculations [82, 43]. As mentioned before, for the case of an infinitely long, 2D waving sheet and cylinder with prescribed beating pattern, it is predicted that $U$ decreases with increasing $De$. While the experimental data supports the predicted trend, at least qualitatively, there are quantitative discrepancies between the experimental and theoretical results as shown in Figure 14(b). Of course, quantitative agreement is not expected. Some of the possible reasons for the observed discrepancies may be the finite length of the swimmer and the assumption of small beating amplitude in the theoretical works. That is, only small deflections are considered for both the waving sheet and cylinder while the nematode shows significant bending. Nevertheless, the theoretical models are able to capture the main trends in the experimental data and perform surprisingly well.

How do the experimental results compare to the 2D numerical simulations [140, 128]? Remember that the simulations predict an interesting enhancement of the sheet swimming speed at $De = 1$. The experimental results do not reveal such swimming speed enhancement, although a scale up mechanical experiment did find such enhancement [91]. Nevertheless, for $De > 1$, the simulation predicts a gradual decrease in $U$. The discrepancies between the experiment and the simulations are most likely due to the difference in the swimming beating patterns. While simulations used a left-moving traveling wave with an amplitude that increased from head to tail, the experiments with *C. elegans* reveal a traveling wave with an exponential decay from head to tail.

**A Possible Mechanism - The Role of Extensional Viscosity**: So what could explain the decrease in swimming speed for nematodes moving in viscoelastic fluids? One possible explanation may be related to the *extensional viscosity* of polymeric fluids. The reader may be very familiar with the concept of shear viscosity $\mu$, which is the fluid resistance to a shear deformation. The concept of extensional viscosity may be less familiar because it is not usually taught in standard fluid dynamics textbooks. Simply put, extensional viscosity $\eta_e$ is the fluid resistance to an extensional deformation that is devoid of shear; such flows are sometimes called shear-free. Hence, the material property of interest in shear-free flows such as biaxial stretching and elongation flows is the fluid extensional viscosity $\eta_e$.

For Newtonian fluids, the extensional viscosity is equal to three times the shear viscosity such that $\eta_e = 3\mu$. This result was first reported by Trouton over a century ago in 1906 [144], and the quantity $\eta_e/\mu$ is often referred to as the Trouton ratio; for Newtonian liquids, the Trouton ratio is constant ($Tr = \eta_e/\mu = 3$). Viscoelastic fluids such as solutions containing flexible polymers, however, behave quite differently. Many experiments have shown that the extensional viscosity of liquids containing flexible polymers can be orders of magnitude larger than the extensional viscosity of Newtonian fluids [5, 96]. This is true even for viscoelastic and Newtonian fluids that have similar values of $\mu$. In addition, while Newtonian fluids exhibit $\eta_e$ values that are independent of strain, viscoelastic fluids show strain hardening behavior. It should be evident that viscoelastic and Newtonian fluids will behave quite differently in flows with a strong extensional component.
But, how can extensional viscosity explain the reduced swimming speed of \textit{C. elegans} in viscoelastic fluids? A clue maybe in the velocity fields produced by the swimming nematodes. Figure 15 show typical streamlines computed from experimentally measured velocity fields using particle tracking methods for both the (a) Newtonian and (b) the viscoelastic cases. Overall, the streamlines display large recirculation flow structures, or vortices, that are attached to the nematode’s body. While the large scale patterns are similar for both cases, detail inspections shows the appearance of a distinct \textit{hyperbolic point} near the nematode for the viscoelastic case. It is important to note that flow near such hyperbolic points is purely extensional. The hypothesis that the decreased in swimming speed (in the nematode case, at least) is mostly likely due to the sudden increase of elastic stresses near regions of high velocity gradients such as hyperbolic points. Near such regions, the extensional viscosity of a solution of flexible polymers can be orders of magnitude larger than a Newtonian fluid. Polymer molecules can be easily aligned and stretched, which results in an increase in hydrodynamic drag along the molecules and poses an additional resistance to fluid transport and swimming.

![Fig. 15](image)

Fig. 15 (a) Streamlines computed from instantaneous velocity fields of Newtonian (\(Re < 10^{-3}\)) and (b) polymeric (\(Re < 10^{-3}; De = 3.0\)) fluids. Arrows in (a,b) indicate flow direction and the box in (b) shows a hyperbolic point in the flow.

In summary, experiments with the nematode \textit{C. elegans} shows that fluid elasticity can hinder its swimming speed. Further, it appears that the nematode’s swimming speed decreases with increasing fluid elasticity, that is, \(U\) decreases as the Deborah number is increased. This trend is predicted by both numerical simulations [refs] and theory [refs], but the agreement is only qualitative. Hence, there is plenty of room for refining the experiments, theory, and simulations. It is clear that knowledge of the velocity fields is important in determining how fluid elasticity affects the organism’s swimming kinematics and dynamics. In the case of dilute polymeric solutions, one is interested in the interactions between the polymer molecules (fluid microstructure) and the velocity field produced by the swimmer, as discussed above. In the next section, we will discuss the undulatory swimming of \textit{C. elegans} in non-dilute (i.e.
semi-dilute and concentrated) solutions, where polymer networks rather than single molecules are of interest.

5.2.3 Swimming experiments with \textit{C. elegans}: Beyond the dilute regime

In this section, we will briefly discuss the swimming behavior of \textit{C. elegans} in semi-dilute and concentrated polymeric solutions. Such solutions are characterized by the formation of polymer networks, and the interplay between the fluid’s internal structure (e.g. polymer networks) and self-propulsion is critical to many biological processes such as reproduction [59], bacterial infection [63], and bio-degradation in soil [2]. Early experimental observations have revealed that polymer networks can enhance the swimming speed of flagellated bacteria moving in solutions containing long-chain polymer molecules [13, 121]. For these small organisms ($L < 10 \mu m$), it has been argued that the main mechanism for this propulsion enhancement is due to the benefits of pushing against a quasi-rigid polymer network [13, 95]. It is worth noting that the exact mechanism responsible for the observed propulsion enhancement is still not clear.

The flow behavior of non-dilute, concentrated polymeric solutions are strong function of the mechanical properties of the network. The role of the mechanical properties of fluid internal networks on an organism’s swimming behavior has recently been investigated in numerical [42, 37, 95, 103] and theoretical [90] studies. Numerical studies of swimming in structured fluids have postulated that the shapes and dynamics of internal networks are accounted for by two effective anisotropic viscosities [95, 103], which qualitatively explain some of the observed propulsion enhancement in microorganisms [13, 121]. Such anisotropic viscosities, however, are difficult to measure and apply to quantitative analysis. In heterogeneous, gel-like environments, modeled by embedding stationary objects in an incompressible viscous fluid, the swimming speed of a microorganism can be enhanced by the underlying structures in the fluid [90]. For internal networks made of small molecules, such as a binary blend of two intermixed fluids, a two-fluid model predicts an enhancement in swimming speed for stiff and compressible networks [42], and a reduction in swimming speed when local distributions of volume fractions of the two phases scale differently for thrust and drag [37]. Overall, the observed propulsion speed variations in these studies underscore the important role of the fluid internal structures on the swimming behavior of microorganisms.

But let’s see how the fluid internal structures, in this case polymer networks, affect the swimming behavior of \textit{C. elegans}. In this subsection we will discuss a recent experimental investigation similar to the one just discussed above, except that the polymeric solutions are non-dilute and possess networks; more details can be found elsewhere [48]. Polymer networks are formed by controlling the concentration of the bio-compatible rod-like polymer xanthan gum (XG) in water. Polymer concentration ranges from 300 ppm to 5000 ppm by weight. These XG solutions transition from the semi-dilute to the concentrated regime at a concentration of approximately 3000 ppm [48]. This is made clear by plotting the solutions zero-shear
viscosity $\mu_0$ as a function of polymer concentration, as shown in 16(a). Note that the values of $\mu_0$ increase as the polymer concentration $c$ is increased, as expected. But we find a change in slope as the solution transitions from the semi-dilute to the concentrated regime at a concentration of approximately 2800 ppm. This transition is commonly interpreted as a structural transition [115, 32]. In concentrated solution, the shape and dynamic properties of polymer networks dominate flow behaviors; in semi-dilute solution, the hydrodynamic interactions among individual polymers dominate flow behaviors [32].

**Fig. 16** (Left) Xanthan gum (XG) zero-shear viscosity $\mu_0$ as a function of polymer concentration $c$. The values of $\mu_0$ increases with polymer concentration, as expected. The change in slope at $c \approx 2800$ ppm is often associated with a structural transition. (Right) Nematode swimming speed $U$ as a function of concentration. Swimming speed exhibits a rapid increase as the solution enters the concentrated regime at approximately 2800 ppm.

**Effects of polymer networks on swimming speed:** The swimming speed of *C. elegans* in XG solutions is investigated as a function of polymer concentration, as shown in Figure 16(b). Results show that $U$ remains relatively constant for polymer concentrations below 3000 ppm. Surprisingly, however, the data shows sudden increase in $U$ for concentrations above 3000 ppm. The values of $U$ are maintained around 0.15 mm/s in semi-dilute solutions ($c < 2800$ ppm) but they quickly rise by 65% to about 0.25 mm/s in concentrated solutions ($c > 2800$ ppm) despite a significant increase in solution viscosity. As expected, the swimming speed ultimately decreases as the concentration is further increased due to the nematode’s finite power output [124]. An increase in $U$ with viscosity has been previously reported for microorganisms moving in structured gel-like media, but the mechanisms are still not well understood [13, 121]. A recent theoretical work suggests that such increase may be due to the presence of polymer networks in the media and that microorganisms may be able to push against such quasi-static networks and move more efficiently [95]. However, because of the large difference in length scales between the nematode ($\approx 1$ mm) and the polymer networks ($\approx 10$ $\mu$m), this notion does not adequately explain the observed propulsion enhancement.
By comparing the velocity fields produced by the nematodes in semi-dilute and concentrated regimes (not shown here), a recent experimental investigation [48] showed that the observed enhancement in $U$ for *C. elegans* swimming in concentrated polymer solutions is most likely related to shear-induced fluid anisotropy. That is, the increase in $U$ observed in Fig. 16(b) is probably due to the anisotropic response of the fluid microstructure to applied stress due to the nematodes swimming motion. In short, the undulatory swimming motion of *C. elegans* induces a structural anisotropy which leads to an increase in the effective drag coefficient ratio $C_d/C_t$ (see RFT equation in Section 1) and consequently an enhancement in $U$.

The above results show that the nematode *C. elegans* can swim faster in concentrated solutions than in semi-dilute solutions. This is an unexpected result since the fluid viscosity increases as polymeric solution transitions from the semi-dilute to the concentrated regime. This sudden increase in $U$ in fluids with polymer networks is thought to be connected to the anisotropic response of the fluid microstructure to applied shear stresses due the nematode’s motion [48]. While intriguing, the proposed mechanism is speculative due to the difficulty to measure or visualize the polymer microstructure during swimming. In this cases, numerical simulations and theoretical calculations can provide much needed clarity and understanding to the problem.

### 5.2.4 Swimming experiments with *C. elegans*: Final Remarks

In this section, we discussed the swimming behavior of the nematode *C. elegans* in Newtonian and viscoelastic (i.e. polymeric) fluids. For dilute polymeric solutions, a recent experiment show that fluid elasticity hinders the swimming speed of nematodes by 40% compared to Newtonian fluids. The swimming speed is also shown to decrease as elasticity (i.e. Deborah number) increases. On the other hand, for concentrated polymeric solutions, the presence of polymer networks seem to enhance swimming speed by as much as 65% when compared to semi-dilute and dilute polymeric solutions. These results underscore the importance of the fluid microstructure and its interactions with the applied stresses generated by the swimmer. Perhaps the main message so far is that it is difficult to quantitatively describe *a priori* the motility of microorganisms in complex fluids without knowledge of the interactions between the fluid microstructure and the applied stresses. It becomes clear that these non-trivial interactions need to be accounted for in theoretical calculations and numerical simulations.

### 5.3 Fluid-assisted locomotion in complex fluids: Artificial swimmers

As shown above, fluid elasticity can significantly affect the swimming behavior of live organisms. In the case of a slender undulatory swimmer (e.g. *C. elegans*),
Locomotion in Complex Fluids: Experiments

fluid elasticity is shown to hinder the organism propulsion speed. In this section, we will explore a different, and perhaps simpler, question: Can fluid elasticity enable propulsion?

To answer the above question, one needs to think back to the “scallop theorem”, which tells us that only non-reciprocal deformations of the swimmer can break time-reversal symmetry and result in net motion [112]. The main assumptions of the theorem is that the swimmer is moving at low Reynolds numbers ($Re < 0.1$) and that the fluid is purely viscous or Newtonian. So, in order to break the “scallop theorem” or kinematic reversibility one needs to increase the amount of inertia in the system (i.e. increase $Re$) and/or to use fluids that are not Newtonian and possess nonlinear rheological behavior. In this section, we will review recent experiments [69] in which artificial particles with reciprocal swimming strategies are able to break the scallop theorem once immersed in complex fluids. Net motion happens even in the absence of inertia (low $Re$). The experiments focus mainly on the role of viscoelasticity, and two main types of fluids will be used: (i) dilute polymeric solutions [69] and (ii) wormlike micellar solutions [47].

Before we begin, it is worth noting that the possibility that fluid elasticity can enable rather than modify propulsion circumventing the scallop theorem is still largely unexplored. Propulsion enabled by fluid elasticity has been predicted for three special cases of reciprocal motion: a flapping surface extending from a plane [106, 108]; a sphere which generates small-amplitude sinusoidal motion of fluid along its surface [85]; and a “wriggling” cylinder with reciprocal forward and backward strokes at different rates [45]. However, there remains little experimental demonstration, and such propulsion of free, finite-amplitude swimmers have been seldom studied.

5.3.1 Experiments with reciprocal swimmers: Can fluid elasticity enable propulsion?

Here, we briefly discuss recent experiments [69, 47] in which a single rigid object, in this case a dumbbell particle or dimer, is actuated in a reciprocal manner in very viscous fluids. In the experiments, the dimer such as the one shown in Fig. 17 is immersed in a fluid and repeatedly reoriented by a magnetic field. The effects of inertia are absent due to the high fluid viscosity ($\sim 10 \text{ Pa·s}$), resulting in $Re \ll 0.1$ comparable to that of a swimming microorganism. By applying only magnetic torques, the apparatus reciprocally actuates just one degree of freedom in the system, the dimer’s orientation $\hat{a}$. For a purely viscous Newtonian fluid at low $Re$, the authors found no net motion because $\hat{a}(t)$ is cyclic; this is as expected. Yet when a small amount of polymer or surfactants are added to the fluid, making it viscoelastic, the same cyclic stroke results in propulsion, in a direction set by the dimer’s shape and boundary conditions.

Experimental Setup: Before diving into the discussion, let us briefly describe the experimental setup. More details can be found elsewhere [69, 47]. The artificial swimmer is a polar (asymmetric) dimer (Fig. 17a); symmetric dimers are also used for control but no net motion is expected. The polar dimer consists of a piece of
Fig. 17 (a) Snapshot of polar dimer. An epoxy bead is attached to a steel wire to form polar (asymmetric) dimers. (b) Top view of experiment. Two aligning electromagnets at constant current are orthogonal to two driving magnets, controlled by a computer. (c) The dimer with magnetization \( \mathbf{m} \) experiences torque \( \tau_{\text{mag}} \) to align with the magnetic field. Dimer orientation \( \hat{a} \) oscillates around \( \langle \hat{a} \rangle \), which is parallel to \( B_{\text{align}} \).

Carbon steel wire of length \( 2R_{\text{dimer}} = 2.5-3 \) mm and diameter 230 \( \mu m \), with an epoxy bead of diameter \( 2R_{\text{dimer}} \approx 500 \) \( \mu m \) at one end. The dimer is then immersed in a fluid bath that is surrounded by four electromagnets; a schematic of the apparatus is shown in Fig. 17(b). The dimer has orientation \( \hat{a} \) and is magnetized with moment \( \mathbf{m} = \hat{a} \mathbf{m} \), so that a uniform magnetic field \( \mathbf{B} \) reorients it with torque \( \tau_{\text{mag}} = \mathbf{m} \times \mathbf{B} \), as depicted in Fig. 17(c). In short, four electromagnets reorient the dimer in a fluid cell. A reciprocal “wiggling” motion is achieved with two diametrically opposed electromagnets generating a constant field \( B_{\text{align}} \), and a pair of orthogonal magnets generating the AC field component \( B_{\text{drive}} \). The driving magnet current is controlled by a computer via a power amplifier. The magnitude of \( B_{\text{align}} \) and amplitude of \( B_{\text{drive}} \) are \( \mathcal{O}(10^3 \text{ G}) \). The dimer has orientation \( \hat{a} \) and is magnetized with moment \( \mathbf{m} = \hat{a} \mathbf{m} \), so that a uniform magnetic field \( \mathbf{B} \) reorients it with torque \( \tau_{\text{mag}} = \mathbf{m} \times \mathbf{B} \), as depicted in Fig. 17(c).

**Working Fluids:** The dimer is immersed in a container (50 mm tall, 30 mm in diameter) of either Newtonian or viscoelastic fluid (Fig. 17(b)). The Newtonian fluid is a 96%-corn syrup aqueous solution (by mass) with a kinematic viscosity \( \mu/\rho \) of approximately \( 4 \times 10^4 \) cSt. Two viscoelastic solutions are prepared: a dilute polymeric solution and a wormlike micellar (WLM) solutions. The polymeric solution is made by adding 0.17% (by mass) of high-molecular-weight polyacrylamide (PAA, \( M_W = 1 \times 10^6 \)) to a viscous Newtonian solvent (93%-corn syrup aqueous solution). The solution has nearly constant shear viscosity of approximately 50 Pa·s and a relaxation time \( \lambda \) of approximately 2 s.

The WLM solution is prepared by slowly adding 130 mM hexadecyltrimethy lammonium bromide (CTAB) to an aqueous solution of 130 mM sodium salicylate (NaSal). This type of WLM solutions is known to form long wormlike micelles that continuously break and reform due to thermal fluctuations leading to viscoelastic stress relaxation. The relaxation time \( \lambda \) of the WLM solution is approximately 1.5 s [47]. Because the main rheological property of interest is viscoelasticity and the fluid relaxation times \( \lambda \) of both solutions are known, it is possible to define a Deborah number (\( De \)). For this oscillating (time-dependent) system, it is customary
to define $De$ as the product of the longest relaxation time of the fluid $\lambda$ and the driving frequency $f_{\text{drive}}$.

**Swimming with reciprocal motion:** Now that the methods are in place, we can ask an important question: Can the nonlinear rheological properties of a given fluid enable propulsion at low $Re$? Before we discuss the results, it is worth making sure that artifacts that could lead to net motion are not being introduced in the experiment. To that end, the investigators [47] calibrated their results against a polar and symmetrical dimer immersed in a viscous Newtonian fluid with similar shear viscosity as the polymeric and WLM solutions. As shown in Fig. 18(a), they found negligible net displacement, comparable to the effects of magnetic drift and sedimentation when driving is turned off altogether (Fig. 18a). Furthermore, the direction of displacement in a Newtonian fluid is not controlled by particle shape or boundary conditions, confirming that it is not hydrodynamic in origin. Experiments with a symmetric dimer in a viscoelastic medium far from any boundaries also yield negligible net displacement.

![Fig. 18 Centroid trajectories from $\circ$ to $+$ reciprocally actuated polar dimer (leftmost panel) in Newtonian, dilute polymeric solution, and wormlike micellar (WLM) solutions at low at high Deborah numbers. No appreciable net motion is found in the Newtonian case. Appreciable net motion is found once small amounts of polymers or surfactants (WLM) are added to a Newtonian solvent.](image)

Evidence of purely elastic propulsion is shown in Fig. 18(b)-(d) for the polar dimer immersed in dilute polymeric (b) and WLM solutions (c,d). Overall, the data show a striking contrast between performing reciprocal motion in Newtonian and in complex, viscoelastic fluids. For example, Figure 18(b) shows that in dilute polymeric solutions, far from any boundaries, the polar dimer at at $De = 5.7$ ($f_{\text{drive}} = 2.8 \text{ Hz; } Re = 1.2 \times 10^{-4}$) is able to achieve net motion at constant speed even under reciprocal forcing. The same is true for the WLM solution (Figure 18b,d). It is interesting to note that, unlike the polymeric solution case, the swimming direction in the WLM solutions seems to depend on $De$. For low elasticity values ($De < 1$), the particle moves towards the bead while the particle moves preferentially towards the rod for cases in which actuating frequency is approximately similar to the fluid relaxation time ($De \sim 1$). The dimer directional dependence on $De$ in WLM solutions is still not understood.

The net motion shown in Fig. 18 is quantified by plotting the dimer net displacement as a function of time. Figures 19(a) and (b) show the net displacement for
the dilute polymeric and WLM solutions, respectively. Both cases show dimer displacements well above the noise or drift level (shaded area). Clearly, a much larger displacement can be achieved with the WLM solutions, although the mechanisms are still unknown. The data also shows that the dimer can move either towards the bead (positive velocity) and towards the rod (negative velocity) depending on the \( De \) as discussed above.

Fig. 19  Dimer net displacement as a function of time. The reciprocally actuated dimer is immersed in (a) polymeric and (b) wormlike micellar solutions. Shaded area correspond to the dimmer drift due to small but finite magnetic gradients.

The displacement data show that fluid elasticity can indeed break the scallop theorem and produce net motion even in reciprocally actuated particles. This is fascinating because it opens the door for a new way to achieve locomotion, one that relies on the fluid itself. In order to gain further understanding on the effects of fluid elasticity on the dimer motion, it is best to plot the displacement data as a function of \( De \). Figure 20(a,b) show the dimer velocity as a function of \( De \) for the dilute polymeric and WLM solutions, respectively. Recall that the positive velocity means that the polar dimer is moving toward its bead and negative velocity means that the dimer is moving toward its rod. For the polymeric solution case, the velocity increases monotonically as a function of \( De \). In fact, the velocity seems obey a \( De^2 \) scaling.

The effects of elasticity are less obvious for the WLM solutions. While it is clear that the polar dimer speed increases as \( De \) increases, the velocity trend is more complex. It seems that for low elasticity values \((0 < De < 1)\), the trend and dimer swimming direction resemble the polymeric solution data. For for \( De \geq 1 \), the dimer dimming direction reverses, and for \( De \gg 1 \) the dimer comes to a complete stop. While the exact mechanisms leading to such behaviors in WLM solutions are not well understood, the data underscore the rich nonlinear behavior encountered in complex fluids.

In summary, we find that polar particles (dimers) undergoing reciprocal motion can indeed achieve locomotion at low Re in complex, viscoelastic fluids such as dilute polymeric and wormlike micellar (WLM) solutions. It is important to note that this type of actuation yields no net motion in a purely Newtonian fluid. But a small amount of polymer or surfactants in the fluid adds an elastic response to the driving,
Locomotion in Complex Fluids: Experiments

Fig. 20 Dependence of mean propulsion velocity on Deborah ($De$) for a reciprocally actuated dimer immersed in (a) dilute polymeric and (b) wormlike micellar (WLM) solutions.

permitting propulsion. For the case of dilute polymeric solutions, the net motion achieved by the dimers results from elastic stresses due to flow-induced changes in polymer conformation. These elastic stresses are history-dependent and do not entirely cancel out over one forcing period, but instead have a small rectified component that accumulates. In fact, Keim and Arratia [69] claim that the combination of the fluid first normal stress difference $N_1$ and the curved streamlines produced by the actuated dimer lead to a volume force (or “hoop stress”) that is able to displace the dimer. The proposed mechanism is reasonable but it is yet to be validated. The picture is less clear for WLM solutions where shear-bands are known to occur in addition to elasticity.

Finally, this type of work is proof-of-concept for an artificial “swimmer” that moves through complex fluids with only reciprocal actuation, a simple body shape, and no moving parts — a less complicated design than for other propulsive strategies [1, 34]. There may thus be a practical route to studies of collective phenomena among large numbers of such particles. These principles could also be applied to microfluidic pumps [106, 108], or to exploiting other types of nonlinear fluid rheology. Further understanding of this effect and similar ones could greatly simplify fabrication of micro-swimmers for many artificial environments, or for biological settings where viscoelasticity is ubiquitous.

6 Conclusions & Outlook

In this chapter, we briefly discussed the problem of swimming at low Reynolds numbers in complex fluids. The discussion was given from an experimental point of view and was centered on a few fundamental experiments both in living and in artificial systems that we hope illustrate the rich dynamics encountered by organisms moving in complex fluids, particularly in viscoelastic fluids. One of the main motivation emphasized here has been in understanding the effects of fluid elasticity on the propulsion speed and efficiency of microorganisms. Analysis on idealized models,
following the early work of G. I. Taylor in simple Newtonian fluids, showed that in general fluid elasticity hinders propulsion. Numerical simulations, however, found that fluid elasticity could in fact enhance propulsion under certain conditions (De $\sim 1$). Experiments seem to confirm such predictions, at least qualitatively. For example, the swimming speed and efficiency of *C. elegans* effectively decreases once the organism is immersed in dilute viscoelastic fluids, while propulsion speed increased for De $\sim 1$ in scale up mechanical experiments. In more concentrated polymeric solutions, the nematode *C. elegans* showed a remarkable increase in speed for solutions possessing polymer networks. Overall, we find that it is very hard to answer question whether fluid elasticity enhances or hinders the propulsion speed of microorganisms. In fact, it may be an unfair question altogether as the answer depends on the type of swimming kinematics (i.e., waveform) and the interactions of the swimmer with the fluid microstructure (i.e., polymer or particles). That is, the local details matter quite bit. Nevertheless, it is clear from both experiments and simulations that fluid elasticity affects, if not dramatically alters, the motility behavior of microorganisms.

Parallel to these considerations, we also discussed an exciting avenue of new developments, that is the possibility of fluid-assisted propulsion. This type of propulsion is driven by the nonlinear rheological properties of the fluid such as viscoelasticity and formation of shear-bands. We showed that even for reciprocally-actuated polar particles, the extra elastic stresses of polymeric fluids can lead to net motion at low Reynolds numbers. It is important to note that under the same conditions, the same particle in a Newtonian fluid achieves no net motion due to kinematic reversibility. The experiments show that the particle net motion and speed increases as the elasticity increases. These findings are exciting because such discovery opens a new mechanism for the study of “active” particles and collective behavior in complex fluids.

So where do we go from here? Of course there is still much to be done and understood. The question of how microorganisms move in complex fluids is still largely unanswered. We still do not know how microorganisms move in rheologically complex material that possess rate-dependent viscosity, yield stress, and thixotropy. But a picture is starting to emerge, and it seems that the interaction of the swimmer with the fluid microstructure is very important. That is in a way not surprising since microorganisms with different swimming kinematics will likely produce different velocity fields in a given fluid, and the bulk response will be determined by the way the fluid microstructure interacts with the velocity field. For example, it is well-known that extensional flows are more efficient in stretching and aligning polymer molecules than shear flows, and swimmers that produce flows with a large extensional component are dominated by the fluid extensional viscosity. On the other hand, swimmers that produce large amounts of curvature may experience a viscoelastic instability due to hoop stresses. So knowledge of the velocity field is quite important, but equally important is how the molecules or particles respond to the imposed velocity field. In a way, the swimmer may be thought of as a local probe for fluid rheology. An exciting and important direction that would allow us to gain a more complete understanding of swimming in complex fluids is to determine how
single polymer molecules, particles, and networks interact with microorganisms. This direction will ultimately take us from the continuum to a statistical mechanics description of the problem. The challenge lies in connecting the statistical representation with the continuum description.

Finally, one can also ask the question of how multiple swimmers interact in Newtonian fluids and in complex fluids. One would anticipate that the fluid microstructure will significantly alter the way multiple microorganisms interact. The type of work is related to the field of active matter or fluid in which active or live particles are present in the fluid medium. Active fluids differ from their passive counterpart in that the active particles have the ability to absorb and dissipate energy and to generate motion and mechanical stresses in the fluid medium. Importantly, these active particles can drive the system out of equilibrium even in the absence of external forcing. Active fluids exhibit novel properties not seen in conventional (passive) complex fluids such as large-scale flows and collective motion on length scales much greater than the particle dimensions [25], anomalous shear-viscosity [130], giant density fluctuations [105], and enhanced fluid mixing [77]. While much recent progress has been made, the dynamics and flow behavior (rheology) of such active complex fluids are still poorly understood. In this case, one can take advantage of a vast body of knowledge developed to understand passive complex fluids.

Acknowledgements The authors would like to thank David Gagnon, Nathan Keim, Alexander Leshansky, and Xiaoning Shen for help with the text and in drafting illustrations. This work was supported by the US-Israel Binational Science Foundation (BSF grant nr. 2011323) and J. Sznitman was supported in part by the European Commission (FP7 Program) through a Career Integration Grant (PCIG09-GA-2011-293604). P.E. Arratia was supported in part by the Army Research Office through award W911NF-11-1-0488.

References