Low-Reynolds-number swimming in gels

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Abstract – Many microorganisms swim through gels, materials with nonzero zero-frequency elastic shear modulus, such as mucus. Biological gels are typically heterogeneous, containing both a structural scaffold (network) and a fluid solvent. We analyze the swimming of an infinite sheet undergoing transverse traveling-wave deformations in the “two-fluid” model of a gel, which treats the network and solvent as two coupled elastic and viscous continuum phases. We show that geometric nonlinearities must be incorporated to obtain physically meaningful results. We identify a transition between regimes where the network deforms to follow solvent flows and where the network is stationary. Swimming speeds can be enhanced relative to Newtonian fluids when the network is stationary. Compressibility effects can enhance swimming velocities. Finally, microscopic details of sheet-network interactions influence the boundary conditions between the sheet and network and the boundary conditions significantly impact swimming speeds.

While biological locomotion at low Reynolds number is a well-established and active field (see [1] for a review), only recently has swimming in complex, non-Newtonian media started to be systematically explored. Indeed, many microorganisms routinely swim through complex or non-Newtonian media. Bacteria in the stomach such as Helicobacter pylori encounter gastric mucus [2]; mammalian sperm swim through viscoelastic mucus in the female reproductive tract [3,4]; and spirochetes burrow into the tissues they infect [5]. Most prior theoretical work on swimming in complex media has focused on viscoelastic fluids [6–14]. Because prescribed swimming strokes lead to the same swimming speed in linearly viscoelastic fluids as in Newtonian fluids [7,13], these studies have focused on the effects of nonlinear viscoelasticity [6,8,9,11–14] and the effect of altered medium response on swimming strokes via fluid-structure interactions [9,10]. However, many biological viscoelastic materials contain crosslinked polymer networks, and are thus solid rather than fluid. In this paper we focus on swimming in such crosslinked materials, which have a nonzero zero-frequency elastic shear modulus, and which we refer to using the term “gel”.

Generally, viscoelastic materials have frequency-dependent response, while the distinction we make between solid and fluid is a zero-frequency property. Some of the issues addressed by studies of viscoelastic fluids carry over straightforwardly to gels. For example, the fluid-structure interactions which determine the beating patterns of sperm flagella depend on the viscoelastic response at the beating frequency, not at zero frequency. However, a simple physical argument demonstrates a fundamental difference between swimming in a gel versus swimming in a fluid. In fluid dynamics, one uses no-slip boundary conditions, but for a swimmer in a solid, no-slip boundary conditions do not allow swimming because under no-slip boundary conditions a swimmer would drag solid material along with it, leading to large deformations and restoring forces which oppose translation. Thus, swimming in a gel requires the swimmer to slip past the medium. This simple consideration highlights the impact of boundary conditions on swimming in gels, a major theme of this paper.

Another motivation for studying swimming in gels is the search for mechanisms that enhance swimming speeds in complex materials. Since spirochetes have been observed to swim faster in fluids with an elastic response component [15], there has been interest in how viscoelastic media increase or decrease swimming velocities. For filamentous geometries, it has been suggested that polymeric fluids may have higher effective anisotropies in resistive-force theories, leading to increased swimming speeds [16,17]. Furthermore, the breaking of kinematic reversibility [18] in nonlinearly viscoelastic fluids makes certain reciprocal swimming strokes more effective than in Newtonian fluids [11,13]. Restricting attention to
sheet-like geometries with traveling-wave deformations (the subject of this paper), infinite sheets in nonlinearly viscoelastic fluids swim more slowly than in Newtonian fluids [8]. However, finite-length sheet-like swimmers in viscoelastic fluids [14], and infinite swimmers in a Brinkmann fluid have increased swimming velocities [17,19].

The latter two studies [17,19] are closest in spirit to this letter. Both investigate Taylor’s swimming sheet [20], an infinite sheet with a small amplitude traveling-wave deformation, in the Brinkmann model, which treats the effect of a stationary porous phase on fluid flows in an effective medium approach. Instead, we solve for the flows induced by the moving sheet in the “two-fluid model” [21–24], which represents the gel as two phases. One phase describes an elastic polymer network with displacement field \( u \) and Lamé coefficients \( \mu \) and \( \lambda \), and the other phase describes a viscous fluid solvent with velocity field \( v \) and viscosity \( \eta \). Throughout this paper we will be concerned with the zero-Reynolds-number limit appropriate for swimming microorganisms, and hence always ignore inertial effects. The two phases are coupled by a drag force proportional to their relative local velocity, with drag coefficient \( \Gamma \), giving the governing equations

\[
\nabla \cdot \sigma = \Gamma \left( \frac{d}{dt} u - v \right), \quad (1)
\n\nabla \cdot \sigma = -\Gamma \left( \frac{d}{dt} u - v \right), \quad (2)
\n\sigma^n = \mu \left[ (\nabla u + (\nabla u)^T) + I \right] \nabla \cdot u + \bar{\sigma}^n, \quad (3)
\n\sigma^n = \eta \left[ (\nabla v + (\nabla v)^T) - p I \right]. \quad (4)
\]

Here the network and solvent stress tensors are \( \sigma^n \) and \( \sigma^s \), respectively. The moduli in the network stress tensor are effective, macroscopic moduli —for example, they incorporate osmotic effects, and they depend implicitly on the volume fraction of the network. The network stress tensor incorporates nonlinear terms (involving products of \( \mathbf{u} \)) explicitly in \( \sigma^n \). We do not specify the form of \( \sigma^n \) because the precise form does not turn out to affect the swimming speed. Volume conservation for the network with volume fraction \( \varphi \) and solvent with volume fraction \( 1 - \varphi \) are written as \( -\partial_t \varphi = \nabla \cdot \left[ \varphi \frac{d}{dt} \mathbf{u} \right] \) and \( -\partial_t (1 - \varphi) = \nabla \cdot (1 - \varphi) \mathbf{v} \), respectively, assuming that the individual solvent and network phases are incompressible. Combining the two yields

\[
0 = \nabla \cdot \left[ (1 - \varphi) \mathbf{v} + \varphi \frac{d}{dt} \mathbf{u} \right]. \quad (5)
\]

In the rest of the paper, we work in the regime where network volume fraction \( \varphi \) can be ignored, yet the macroscopic network stresses cannot be ignored, i.e. expanding the solutions in \( \varphi \), we obtain the zeroth-order solutions in \( \varphi \). In this \( \varphi \rightarrow 0 \) limit, eq. (5) reduces to \( \nabla \cdot \mathbf{v} = 0 \). The drag coefficient \( \Gamma \) can be estimated as \( \Gamma \approx \eta/\xi^2 \), where \( \xi \) is the mesh size of the network [21].

Our use of the two-fluid model explicitly recognizes the role of heterogeneity in complex media, while still retaining a continuum description. Reference [17] emphasizes that polymers in a viscoelastic fluid may be viewed as heterogeneous inclusions in a viscous fluid. Treating the inclusions as a stationary background results in the Brinkmann fluid as an effective model. The two-fluid model allows us to describe the heterogeneous phase more realistically as a dynamic component, and understand when it is appropriate to think of heterogeneities as stationary or dynamic.

Our investigation leads to three main conclusions. First, network dynamics determine when heterogeneities lead to increased swimming velocities. Roughly speaking, network deformations are a result of drag forces arising from solvent flow, and are opposed by the stiffness of the network. For fast flows or compliant networks, the network moves with the flows and does not attenuate the flow, while for slow flows or stiff networks, the network acts like a stationary phase, leading to enhanced swimming velocities. Network compressibility can also lead to additional enhancement of swimming velocities.

Second, a consistent treatment of swimming velocities requires proper treatment of nonlinearities. We show that nonlinearities in the constitutive relationship \( \sigma^n \) in eq. (3) of the elastic phase of a gel do not affect swimming speeds. However, geometric nonlinearities arise from the terms of eqs. (1) and (2) that involve the velocity of material points of the network, \( \frac{d}{dt} \mathbf{u} \). The displacement field is a function of current coordinates —i.e., the position of a material element originally at \( \mathbf{x}_0 \) is \( \mathbf{x}(\mathbf{x}_0, t) = \mathbf{x}_0 + \mathbf{u}(\mathbf{x}, t) \)— so the velocity of material elements is the material derivative, defined implicitly via \( \frac{d}{dt} \mathbf{u} = \partial_t \mathbf{u} + \frac{d}{dt} \mathbf{u} \cdot \nabla \mathbf{u} \). In the remainder of the paper we refer to the term \( \frac{d}{dt} \mathbf{u} \cdot \nabla \mathbf{u} \) as the “convective” nonlinearity. Without it one cannot obtain physically meaningful swimming velocities.

Finally, we highlight the importance of boundary conditions (BC) between the sheet and elastic phase. There is a long history of experimental support for the validity of no-slip BC for fluids, and we use no-slip BC between the sheet and solvent, \( \mathbf{v}(x, h(x, t), t) = \partial_t h(x, t) \mathbf{y} \), where \( h(x, t) \) is height of the sheet at \( (x, t) \). However, there is no a priori selection of BC between the sheet and network in our macroscopic theory. In this paper, we consider two types of network-sheet BC that may plausibly result from microscopic interactions at a swimmer surface.

The first class of boundary conditions applies when the network is dense on the scale of swimmer undulations (fig. 1(a)). Then we imagine that the sheet presses directly against the polymer network and the network must conform to the sheet,

\[
u(x, h(x, t), t) = h(x, t). \quad (6)
\]

The remaining boundary condition is applied to the tangential network stress via a kinetic (Navier) friction
law, with tangential stress proportional to the tangential velocity of the polymer relative to the sheet:

\[ \dot{\mathbf{t}} \cdot \sigma^{n}(x, h, t) \cdot \dot{\mathbf{n}} = \Xi \dot{\mathbf{t}} \cdot \left( \frac{d}{dt} \mathbf{u}(x, h, t) - \partial_{h} \mathbf{y} \right), \]

where \( \dot{\mathbf{t}} \) and \( \dot{\mathbf{n}} \) are the tangent and normal to the sheet. \( \Xi \rightarrow 0 \) corresponds to free tangential slip, while \( \Xi \rightarrow \infty \) corresponds to no-slip.

In the second class of boundary conditions, the network is dilute on the scale of swimmer undulations (fig. 1(b)), so the sheet exerts no forces directly on the network. Instead all forces on the network are mediated by the solvent, and the network traction on the sheet vanishes:

\[ \sigma^{n}(x, h, t) \cdot \dot{\mathbf{n}} = 0. \tag{8} \]

Both “direct” BC (eqs. (6), (7)) and “solvent-mediated” BC (eq. (8)) allow the swimmer to slide past the network, in accordance with our physical discussion above.

**Solutions.** – In the frame where the sheet is stationary, the transverse undulations are described by \( h(x, t) = \text{Re} \{ \exp(i(kx - wt)) \} \). The sheet swims with velocity \( V_{x} \), but sufficiently far from the sheet in the lab frame the elastic phase is stationary. Thus, we write the displacement field in the frame of the sheet as \( \mathbf{u}(x, t) = V_{x} t \mathbf{x} + \delta \mathbf{u}(x, t) \), with \( \delta \mathbf{u} \) small. As we will see \( \delta \mathbf{u} \) turns out to be second order in the displacements.

The solution strategy follows Taylor [20], which we review briefly here. In the Newtonian case the governing equations are eqs. (2) and (4) with \( \Gamma = 0 \), plus \( \nabla \cdot \mathbf{v} = 0 \). For small traveling-wave amplitudes relative to wavelengths, we determine the velocity field order by order in \( \delta \mathbf{u} \). We write \( \mathbf{v} = \mathbf{v}^{(1)} + \mathbf{v}^{(2)} + \ldots \), with \( \mathbf{v}^{(1)} \) first order in \( \delta \mathbf{u} \), etc. The fields satisfy the governing equations and no-slip boundary conditions, also expanded order by order in \( \delta \mathbf{u} \).

The first-order solutions must satisfy \( \eta \nabla^{2} \mathbf{v}^{(1)} - \nabla p^{(1)} = 0 \), \( \nabla \cdot \mathbf{v}^{(1)} = 0 \), and take the form \( \mathbf{v}^{(1)} = \text{Re} \{ -b \omega y \exp(-ky + i(kx - wt)) \} \) and \( \mathbf{v}^{(1)} = \text{Re} \{ -i b \omega (1 + y) \exp(-ky + i(kx - wt)) \} \). Once the first-order solutions are obtained the swimming velocity is found by solving the second-order equations. The swimming velocity is determined by the \( x \)-component of the time- and \( x \)-averaged velocity field. Any overall time- or \( x \)-derivative vanishes upon averaging, so the time-averaged \( x \)-component of the 2nd-order pieces of eq. (2) is \( -\eta \nabla^{2} \mathbf{v}^{(2)(1)} = 0 \), while the second-order BC is

\[ \langle v_{x}^{(2)}(y = 0) \rangle = -\langle h \partial_{y} v_{x}^{(1)}(y = 0) \rangle. \tag{9} \]

Here the brackets denote time- and \( x \)-averaging. The second-order solution is \( \langle v_{x}^{(2)}(y = \infty) \rangle = -d_{2}/(h \partial_{y} v_{x}^{(1)}) = b^{2} \omega k/2 \).

For the two-fluid model, the first-order governing equations are

\[ \mu \nabla^{2} \mathbf{u}^{(1)} + (\lambda + \mu) \nabla (\nabla \cdot \mathbf{u}^{(1)}) = \Gamma (\partial_{t} \delta \mathbf{u}^{(1)} - \mathbf{v}^{(1)}), \]

\[ \eta \nabla^{2} \mathbf{v}^{(1)} - \nabla p = -\Gamma (\partial_{t} \delta \mathbf{u}^{(1)} - \mathbf{v}^{(1)}). \]

The first-order solutions take the form \( \delta \mathbf{u}^{(1)} = \text{Re} \{ \delta \mathbf{u}(y) \exp(i(kx - wt)) \} \) (for example) and can be found by introducing stream and potential functions, \( \mathbf{v}^{(1)} = \text{curl} \{ \mathbf{f}(y) \} \) and \( \delta \mathbf{u}^{(1)} = \text{curl} \{ \mathbf{f}(y) \} + \nabla \chi \), and then following the methods detailed in [24]. As in the Newtonian case, once the first-order solutions are obtained, the swimming velocity is found by solving the \( x \)-component of the time- and \( x \)-averaged second-order pieces of eqs. (1) and (2),

\[ -\eta \partial_{y}^{2} \langle v_{x}^{(2)(1)} \rangle = \mu \partial_{y}^{2} \langle \delta u_{x}^{(2)} \rangle + \partial_{y} \langle \sigma_{y x}^{(2)} \rangle \]

\[ = \Gamma \left[ V_{x} - \langle v_{x}^{(2)} \rangle + \langle (\partial_{y} \delta \mathbf{u}^{(1)}) \cdot \nabla \rangle \delta u_{x}^{(1)} \rangle. \tag{10} \]

Here \( \sigma_{y x}^{(2)} \) includes the 2nd-order contributions to the network stress involving products of two first-order fields. The solutions to these second-order equations are \( \langle v_{x}^{(2)} \rangle = V_{x} + c_{1} \exp(-\sqrt{\Gamma/\eta} y) + f(y) \) and \( \delta u_{x}^{(2)} = -((\eta/\mu) \langle v_{x}^{(2)} \rangle + g(y)), \) where \( f(y) \) is the inhomogeneous solution satisfying \( (\eta \partial_{y}^{2} - \Gamma) f = -\Gamma (\partial_{y} \delta \mathbf{u}^{(1)}) \cdot \nabla \delta u_{x}^{(1)} \) and \( g(y) \) is the inhomogeneous solution satisfying \( \mu \partial_{y} g = -\langle \sigma_{y x}^{(2)} \rangle \).

Boundary conditions at infinity rule out other possible solutions.

These solutions must satisfy the second-order boundary conditions, obtained by expanding eqs. (7) and (8) using \( \mathbf{u} \approx \mathbf{u}_{\infty} + \partial_{y} \mathbf{h} \mathbf{x} \) and \( \dot{\mathbf{u}} \approx \dot{\mathbf{u}}_{\infty} + \partial_{y} \mathbf{h} \mathbf{y} \). For direct sheet-network interactions, the relevant BC are eq. (9) and

see eq. (11) on the next page

with all quantities evaluated at \( y = 0 \). Equations (9) and (11) also apply for solvent-mediated BC if we set \( \Xi = 0 \) in eq. (11). In eq. (11), all pieces involving \( \langle \sigma_{y x}^{(2)} \rangle \) cancel due to the form of \( \delta u_{x}^{(2)} \). Therefore nonlinearities in the constitutive relation for the polymer stress (i.e., \( \bar{\sigma}^{n} \)) do not affect the swimming velocity at second order. Similar cancellations help to show that these solutions satisfy overall force balance on the swimmer.

Substituting the solutions for \( \langle v_{x}^{(2)} \rangle \) and \( \delta u_{x}^{(2)} \) into eqs. (9) and (11) and eliminating \( c_{1} \) yields \( V_{x} \) in terms of 1st-order quantities. For direct network-sheet BC,

see eq. (12) on the next page

Note that although many terms in these equations involve products of two first-order solutions, most would be
present even if the governing equations were completely linear. We use the terminology “nonlinear” to refer to the terms that are only present due to nonlinearities in the governing equations. Since the nonlinearity $\sigma$ does not affect the swimming velocity, the only such nonlinear term is the fourth term on the right hand side, $\langle \partial_t \sigma^{(1)} \rangle \cdot \nabla \delta u^{(1)}$, which arises from the convective nonlinearity. For the solvent-mediated BC, the swimming velocity is given by eq. (12) with $\Xi = 0$. However, the averages for solvent-mediated BC are different from those for direct BC and $\Xi = 0$, since the first-order solutions differ, and furthermore the inhomogeneous solution $f$ is nonzero only when the convective nonlinearity is included.

Although in general evaluating eq. (12) in terms of model parameters leads to unilluminating expressions, two limiting cases serve to illustrate the application of eq. (12). For an incompressible network ($\lambda = \infty$) with direct network-solvent BC, the first-order solutions do not depend on $\Xi$; the velocity field $V^{(1)}$ is identical to the Newtonian case while $\delta u^{(1)} = \Re\{-ib y \exp(-ky + i(kx - \omega t))\}$ and $\delta u_y^{(1)} = \Re\{b(1 + y)\exp(-ky + i(kx - \omega t))\}$, describing network and solvent moving together and in phase. For the first case, neglect the convective nonlinearity. Then $f(y) = 0$, and the averages in eq. (12) are $\langle \partial_t h \partial_x h \rangle = \langle \partial_t h \partial_y h \rangle = \langle \partial_t \delta u_y^{(1)} \rangle = \langle \partial_t \delta u_x^{(1)} \rangle = -b^2 \omega k^2 / 2$, and $\langle \partial_t \delta u_y^{(1)} \rangle = \langle \partial_t h \delta u_y^{(1)} - \sigma^{(1)} \rangle = 0$, yielding a swimming speed which is the same as in a Newtonian fluid, $V_N = b^2 \omega k^2 / 2$. For the second case, include the convective nonlinearity. The first-order solutions are the same, but now we need to also include $\langle \partial_t \sigma^{(1)} \cdot \nabla \delta u^{(1)} \rangle = b^2 \omega k^2 / 2$, $f(0) = b^2 \omega k \gamma (-32 - 12 \gamma + \gamma^2)/[2(-4 + \gamma)^3]$, and $\partial_y f(0) = -b^2 \omega k^2 \gamma^2 (-20 + \gamma)/(-4 + \gamma)^3$, with $\gamma = \Gamma / \langle \eta k^2 \rangle$, yielding

$$V_N = b^2 \omega k \sqrt{\frac{4\sqrt{\Gamma\eta} + 4\sqrt{\Gamma/\langle \eta k^2 \rangle} + \Gamma / \langle \eta k^2 \rangle}{\Xi + \sqrt{\Gamma\eta}}}.\quad(13)$$

**Results and discussion.** – Our solutions show how the heterogeneous nature of gels leads to behavior not captured by modeling viscoelastic media as single-phase fluids. This is apparent even in the first-order solutions. In a viscoelastic fluid, the first-order solutions are the same as in a Newtonian fluid, while in our solutions, once the network becomes compressible, or once one uses solvent-mediated sheet-network BC, there is relative motion between the solvent and network and both phases move differently from a Newtonian fluid.

Fig. 2: (Colour on-line) Swimming speed normalized by Newtonian swimming speed, $V_s / V_N$, as a function of $\eta k / \Xi$. Only when convective nonlinearities are included does the swimming velocity vanish for no-slip BC ($\eta k / \Xi \to 0$). All curves use direct network-sheet BC. Thick-black (dots) and thick-black (solid): incompressible network with $\Gamma / \langle \eta k^2 \rangle = 1$. Red (long dashes): $\eta_0 / \mu = 0.01, \lambda = \mu, \Gamma / \langle \eta k^2 \rangle = 10$. Magenta (dash-dots): $\eta_0 / \mu = 10, \lambda = \mu, \Gamma / \langle \eta k^2 \rangle = 10$. Blue (short dashes): $\eta_0 / \mu = 0.01, \lambda = \mu, \Gamma / \langle \eta k^2 \rangle = 10$. Green (medium dashes): $\eta_0 / \mu = 10, \lambda = \mu, \Gamma / \langle \eta k^2 \rangle = 10$. Thick-black, red, and green curves include the convective nonlinearity; thin-black, magenta, and blue curves do not.

Turning to the swimming velocities, we see the importance of correctly accounting for nonlinearities. As in previous studies of nonlinearities in single-phase viscoelastic fluids [8,9,11], for small amplitude swimming stokes the swimming speed is a second-order effect, and so a consistent description must take into account any nonlinearities in constitutive laws. In the case of a gel described using a two-fluid model, we saw that for both types of sheet-network BC, nonlinearities in the constitutive law for the elastic phase do not affect the swimming velocity. However, the geometric convective nonlinearity must be taken into account to obtain physically meaningful swimming velocities. Figure 2 shows the swimming velocity as a function of inverse friction $1/\Xi$. Previously we argued that no-slip sheet-network BC prevent a sheet from swimming, which implies that the swimming velocity should vanish as $1/\Xi \to 0$, (the no-slip limit). This expected behavior is only obtained when the convective nonlinearities are included. In Fig. 2 we demonstrate this for 3 representative cases: stiff networks (small $\eta_0 / \mu = 0.01$), compare red and blue curves; compliant networks (large $\eta_0 / \mu = 10$), compare
magenta and green curves; and incompressible networks ($\lambda \to \infty$), compare black curves. The results for the incompressible network can also be deduced by directly comparing the analytic swimming speeds in eq. (13) and the text above it.

Compressibility effects are a possible mechanism for swimming speed enhancement. Figure 3 show the swimming speed as a function of Lamé coefficient $\lambda$, a measure of incompressibility (the bulk modulus of compression is $2\mu + \lambda$). For direct sheet-network BC, the strongest enhancement of swimming speed occurs for a material with large shear modulus ($\mu \to \infty$) but which for given $\mu$ is maximally compressible ($\lambda = 0$), and for a network which slips freely past the swimming sheet ($\Xi = 0$). Compressibility does not strongly affect the swimming speed for solvent-mediated sheet-network BC. Swimming speeds can be faster than in Newtonian fluids for stiff networks/low frequencies (small $\eta \omega/\mu$). Red and green curves are for solvent-mediated network-sheet BC. Swimming speeds are faster than in Newtonian fluids for stiff networks/low frequencies (small $\eta \omega/\mu$). Magazine curves are for solvent-mediated network-sheet BC. Red (long dashes): $\eta \omega/\mu = 0.01$, $\Gamma/\eta k^2 = 10$. Green (medium dashes): $\eta \omega/\mu = 10$, $\Gamma/\eta k^2 = 10$. Blue (short dashes): $\eta \omega/\mu = 0.01$, $\Gamma/\eta k^2 = 10$. Magenta (dash-dots): $\eta \omega/\mu = 10$, $\Gamma/\eta k^2 = 10$. Magenta and green curves overlap.

Fig. 3: (Colour on-line) Swimming speed normalized by Newtonian swimming speed, $V_s/V_N$, as a function of incompressibility, $\lambda/\mu$. Compressibility effects can enhance swimming speeds for direct network-sheet BC. Swimming speed is faster than in the Newtonian case for stiff networks or low frequencies (small $\eta \omega/\mu$). Red and green curves use direct network-sheet BC and $\Xi = 0$; blue and magenta curves use solvent-mediated network-sheet BC. Red (long dashes): $\eta \omega/\mu = 0.01$, $\Gamma/\eta k^2 = 10$. Green (medium dashes): $\eta \omega/\mu = 10$, $\Gamma/\eta k^2 = 10$. Blue (short dashes): $\eta \omega/\mu = 0.01$, $\Gamma/\eta k^2 = 10$. Magenta (dash-dots): $\eta \omega/\mu = 10$, $\Gamma/\eta k^2 = 10$. Magenta and green curves overlap.

The transition between the two regimes occurs when the force/volume due to elasticity, $\sim \mu k^2$, becomes comparable to the force/volume due to elasticity, $\sim \nu k^2$, i.e. when $\eta \omega/\mu \sim \eta k^2/\Gamma$, which can be confirmed by comparing the curves in fig. 4.

We can compare our results to those for the single-phase Brinkmann fluid [17,19], which obeys $\eta \nabla^2 \mathbf{v} - \nabla p = \Gamma^B \mathbf{v}$ and has swimming speed $V_s = V_N \sqrt{\Gamma/\Gamma^B/(\eta k^2)}$. In the Brinkmann fluid the elastic phase is not a dynamic degree of freedom, but instead enters as an inert background retarding solvent motion. Thus, the two-fluid model should behave like a Brinkmann fluid when the network does not deform (i.e., $\eta \omega/\mu < \eta k^2/\Gamma$) and if $\Gamma^B = \Gamma$. This expectation is borne out in fig. 5, but only for solvent-mediated BC. When the network deforms (compliant networks/high frequencies) the network-sheet BC do not greatly affect the swimming speed (magenta and green curves).

Our results highlight the importance of understanding the proper boundary conditions for swimmers in gels. The boundary conditions need not be the same for all swimmers; they may depend on factors including swimmer morphology, surface biochemistry, or gel structure. However, one way to estimate whether a swimmer has direct interaction with the polymer network in a gel is to compare the swimmer size with the mesh size of the network. For example, sperm swimming in cervical mucus have head sizes of $3-5 \mu m$. The mesh size of the network of mucin fibers in cervical mucus varies strongly with time during the menstrual cycle, with mesh sizes of up to $25 \mu m$ around ovulation, and as small as $200 \text{nm}$ at other
Network-sheet BC and \( \Xi = 0 \), and \( \eta \omega/\mu \) network-sheet BC when the network does not deform (small \( \eta \omega/\mu \)). Blue and magenta curves use direct network-sheet BC, \( \Xi = 0 \), and \( \lambda = 0 \); red and green curves use solvent-mediated network-sheet BC and \( \lambda = 0 \). Red (long dashes): \( \eta \omega/\mu \approx 0.01 \). Green (medium dashes): \( \eta \omega/\mu \approx 10 \). Blue (short dashes): \( \eta \omega/\mu \approx 0.01 \). Magenta (dash-dots): \( \eta \omega/\mu = 10 \). Red and black curves overlap, and magenta and green curves overlap.

Fig. 5: (Colour on-line) Swimming speed normalized by Newtonian swimming speed, \( V_s/V_N \), as a function of drag coupling \( \Gamma/\eta k^2 \). The swimming speed is the same as in a Brinkmann fluid (black solid curve) for solvent-mediated network-sheet BC when the network does not deform (small \( \eta \omega/\mu \)). Blue and magenta curves use direct network-sheet BC, \( \Xi = 0 \), and \( \lambda = 0 \); red and green curves use solvent-mediated network-sheet BC and \( \lambda = 0 \). Red (long dashes): \( \eta \omega/\mu \approx 0.01 \). Green (medium dashes): \( \eta \omega/\mu \approx 10 \). Blue (short dashes): \( \eta \omega/\mu \approx 0.01 \). Magenta (dash-dots): \( \eta \omega/\mu = 10 \). Red and black curves overlap, and magenta and green curves overlap.

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