# Hydrodynamics of active permeating gels

## A C Callan-Jones[1,3] and F Jülicher[2]

[1] Laboratoire Charles Coulomb, UMR 5521 CNRS-UM2,
Université Montpellier II, 34095 Montpellier Cedex 5, France
[2] Max-Planck-Institut für Physik komplexer Systeme, Nöthnitzerstrasse 38,
01187 Dresden, Germany
E-mail: andrew.callan-jones@univ-montp2.fr

**Abstract.** We develop a hydrodynamic theory of active permeating gels with viscoelasticity in which a polymer network is embedded in a background fluid. This situation is motivated by active processes in the cell cytoskeleton in which motor molecules generate elastic stresses in the network, which can drive permeation flows of the cytosol. Our approach differs from earlier ones by considering the elastic strain in the polymer network as a slowly relaxing dynamical variable. We first present the general ideas for the case of a passive, isotropic gel and then extend this description to a polar, active gel. We discuss two specific cases to illustrate the role of permeation in active gels: self-propulsion of a thin slab of gel relative to a substrate driven by filament polymerization and depolymerization; and non-equilibrium deswelling of a gel driven by molecular motors.

[3] Author to whom any correspondence should be addressed.

**IOP** Institute of Physics ⚛ DEUTSCHE PHYSIKALISCHE GESELLSCHAFT

**Contents**

Living cells are highly dynamic systems that are able to move, to divide and to generate forces. This dynamics originates from the cytoskeleton, a gel-like network of elastic filaments. The cytoskeleton is an active material in which specialized motor molecules use the hydrolysis of a chemical fuel, adenosine triphosphate (ATP), to generate directed movements and forces. Because of this internal activity, novel types of material properties arise, such as active stresses [1] and spontaneous flows [2].

Cell shape and cell mechanics are governed by the actin cytoskeleton, which serves as a motivation for the hydrodynamic theory presented in this paper. Actin networks are crosslinked by passive and active linkers, resulting in short-time elastic and long-time viscous properties. Typical short-time shear moduli are in the range of $10^3$–$10^4$ Pa; the gel flows on time scales greater than 10–100 s [3]. In addition, the cytoskeletal gel is permeated by a cytosol consisting of water and solutes. Since filaments are polar structures with two different ends, they can align on average, giving rise to an anisotropic or polar gel. In a polar gel, ATP-driven polymerization and depolymerization reactions can lead to polymer flow relative to the cytosol, a process known as treadmilling. Finally, active stresses are generated by the action of motors, which can lead to gel contraction and the expulsion of cytosol and, in polar gels, to anisotropic active stresses that induce complex flow patterns.

Theoretical approaches to describing the physics of active gels have been introduced that either start at the filament scale from basic interaction rules between filaments and motors [4–6] or take a phenomenological approach and derive dynamic equations in the hydrodynamic limit based on conservation laws and symmetries [7–12]. In these hydrodynamic approaches, the physical description of viscoelasticity and permeation in active gels poses fundamental challenges. The goal of this paper is to develop a generic hydrodynamic theory of active, polar, viscoelastic polymer networks in a solvent that describes permeation flow generated by elastic

stress in the network. Our approach differs from the one-component theory of [7], applicable to situations in which cytosolic flow causes no dissipation or in which the gel and solvent move together. We extend the multi-component theory of [9] to cases in which elastic stresses and permeation flows persist on long times even in viscoelastic systems, because of steady state active stresses. As an example, cell locomotion on a substrate involves flow of the actin polymer network and the cytosol in opposite directions, and thus permeation flow.

We show here that viscoelasticity can be introduced systematically via an internal degree of freedom that describes local elastic deformations and which relaxes during the viscoelastic relaxation time. A key result stemming from this approach is the appearance of an effective viscous stress in the polymer network at long times, which drives solvent flow and leads to couplings with the other hydrodynamic variables. Our approach provides a formal basis for the two-phase theory of [12, 13], in which the cytoskeleton is composed of a highly viscous polymer phase interpenetrated by a solvent. At the same time, our work shows that such a two-phase fluid requires viscoelastic material properties.

This paper is organized as follows. In section 1, the hydrodynamic equations of a passive, two-component viscoelastic gel consisting of a polymer network in a solvent are derived. This example reveals how the Maxwell model for the polymer component (section 2) arises from a general approach based on irreversible thermodynamics. Following the same strategy, in section 3 we present the hydrodynamics of a multi-component, active, polar viscoelastic gel, identifying novel couplings that are unique to a polar gel. We then use this description to study two problems motivated by cell biophysics: in section 4 we consider the movement of a thin active gel layer driven by filament treadmilling, and in section 5 we describe the non-equilibrium deswelling of an isotropic active gel under contractile stress. We discuss our results in section 6.

## 1. Hydrodynamics of a two-component passive viscoelastic gel

We first consider a passive viscoelastic gel to illustrate how the standard hydrodynamic approach [14, 15] can be extended to include the elastic strain in the polymer component as a slowly relaxing yet non-hydrodynamic variable. Our approach generalizes those of [16–18] by using Onsager theory to obtain generic constitutive relations that describe solvent permeation and elastic strain relaxation in a gel at long times.

### 1.1. Slow variables and continuity equations

In a two-component viscoelastic fluid, there are three conserved quantities: the masses of the two components and the total momentum. The corresponding continuity equations for the polymer and solvent mass densities, $\rho_p$ and $\rho_s$, and the total momentum density, $g_\alpha$, are

$$\partial_t \rho_p + \partial_\alpha (\rho_p v_\alpha^p) = 0, \tag{1}$$

$$\partial_t \rho_s + \partial_\alpha (\rho_s v_\alpha^s) = 0, \tag{2}$$

$$\partial_t g_\alpha - \partial_\beta \sigma_{\alpha\beta}^{tot} = f_\alpha^{ext}, \tag{3}$$

where $v_\alpha^p$ is the polymer velocity, $v_\alpha^s$ is the solvent velocity, $\sigma_{\alpha\beta}^{tot}$ is the total stress tensor and $f_\alpha^{ext}$ is an external force density. In the following, we suppose that $f_\alpha^{ext} = 0$. Introducing the total mass density $\rho = \rho_p + \rho_s$ and the center-of-mass velocity

$$v_\alpha = \frac{\rho_p}{\rho} v_\alpha^p + \frac{\rho_s}{\rho} v_\alpha^s, \tag{4}$$

**IOP** Institute of Physics $\Phi$ DEUTSCHE PHYSIKALISCHE GESELLSCHAFT

the momentum density is given by $g_\alpha = \rho v_\alpha$. The polymer and fluid velocities can be expressed in terms of $v_\alpha$ and the relative flux, $j_\alpha$:

$$v_\alpha^p = v_\alpha + \frac{j_\alpha}{\rho_p} \tag{5}$$

and

$$v_\alpha^s = v_\alpha - \frac{j_\alpha}{\rho_s}. \tag{6}$$

A two-component viscoelastic fluid is also characterized by the amount of elastic energy stored in its polymer component. As a result, the relaxation of long-wavelength disturbances of the gel will depend not only on gradients of the conserved variables, but also on the amount of elastic strain, given by the symmetric tensor $u_{\alpha\beta}$. In a perfect elastic solid, in which a reference state is well defined, $u_{\alpha\beta}$ would be the elastic strain tensor. In a viscoelastic fluid, $u_{\alpha\beta}$ is a slowly relaxing quantity, and as a result one can divide the gel volume into small elements, each of which is in a state of local equilibrium described by the free energy density $f(\rho_p, \rho_s, u_{\alpha\beta})$. We can then define $u_{\alpha\beta}$ as the quantity conjugate to the more physically tangible elastic stress, $\sigma_{\alpha\beta}^{el}$:

$$\sigma_{\alpha\beta}^{el} = \frac{\partial f}{\partial u_{\alpha\beta}}. \tag{7}$$

*1.2. Fluxes and forces*

To find the constitutive relations for the gel, we first identify the fluxes and forces that cause dissipation; to do this we follow the formalism of irreversible thermodynamics [14]. The total free energy of the gel is obtained by integrating $f$ and adding this to the kinetic energy contained in the fluid volume $V$:

$$F = \int \left[ \frac{1}{2} \rho v^2 + f(\rho_p, \rho_s, u_{\alpha\beta}) \right] dV. \tag{8}$$

In a non-equilibrium, isothermal change the time derivative of $F$ is

$$\frac{dF}{dt} = -\int_{\partial V} j_\alpha^F \, dS_\alpha - T \int_V \theta \, dV, \tag{9}$$

where $j_\alpha^F$ is the free energy flux through an element $dS$ of the bounding surface $\partial V$ and $\theta$ is the rate of internal entropy production. The time derivative of $F$ is obtained using the differential of $f$,

$$df = \mu_p dn_p + \mu_s dn_s + \sigma_{\alpha\beta}^{el} du_{\alpha\beta}, \tag{10}$$

where $\mu_i = \partial f / \partial n_i$, $i = p, s$, are the chemical potentials and $n_i = \rho_i / m_i$ and $m_i$ are the number density and molecular mass of component $i$, respectively. Using this relation and the continuity equations, we obtain

$$\frac{dF}{dt} = \int \left[ \frac{1}{2} v^2 \partial_\alpha (\rho v_\alpha) + v_\alpha \partial_\beta \sigma_{\alpha\beta}^{tot} - \mu_p \partial_\alpha (n_p v_\alpha) - \mu_s \partial_\alpha (n_s v_\alpha) - \overline{\mu} \partial_\alpha j_\alpha + \sigma_{\alpha\beta}^{el} \partial_t u_{\alpha\beta} \right] dV, \tag{11}$$

where $\overline{\mu} = \frac{\mu_p}{m_p} - \frac{\mu_s}{m_s}$ is the exchange chemical potential. Introducing the pressure $P = -f + \mu_p n_p + \mu_s n_s$, using equation (10) and integrating by parts, the above can be simplified to

$$\frac{dF}{dt} = \int \left[ -\left( \sigma_{\alpha\beta}^{tot} + \rho v_\alpha v_\beta + P \delta_{\alpha\beta} \right) \partial_\beta v_\alpha + j_\alpha \partial_\alpha \overline{\mu} + \sigma_{\alpha\beta}^{el} \left( \partial_t u_{\alpha\beta} + v_\gamma \partial_\gamma u_{\alpha\beta} \right) \right] dV + \text{surface terms}. \tag{12}$$

Noting that the antisymmetric part of the total stress, $\sigma_{\alpha\beta}^{\text{tot},a}$, is zero (see appendix A), we obtain the entropy production rate

$$T\theta = \sigma_{\alpha\beta} v_{\alpha\beta} - j_\alpha \partial_\alpha \overline{\mu} - \frac{Du_{\alpha\beta}}{Dt} \sigma_{\alpha\beta}^{\text{el}}. \tag{13}$$

In equation (13), $\sigma_{\alpha\beta}$ is the symmetric, deviatoric stress given by

$$\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{\text{tot}} + \rho v_\alpha v_\beta + P\delta_{\alpha\beta}, \tag{14}$$

$v_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta + \partial_\beta v_\alpha)$ is the symmetric part of the velocity gradient tensor,

$$\frac{Du_{\alpha\beta}}{Dt} = \frac{\partial u_{\alpha\beta}}{\partial t} + v_\gamma \partial_\gamma u_{\alpha\beta} + \omega_{\alpha\gamma} u_{\gamma\beta} + \omega_{\beta\gamma} u_{\alpha\gamma} \tag{15}$$

is the convected, co-rotational time derivative of $u_{\alpha\beta}$ and $\omega_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta - \partial_\beta v_\alpha)$ is the vorticity tensor.

The entropy production rate given by equation (13) is a sum of terms, each consisting of a thermodynamic flux multiplied by its conjugate force. The deviatoric stress, $\sigma_{\alpha\beta}$, is conjugate to the symmetrized velocity gradient, $v_{\alpha\beta}$. The relative polymer current, $j_\alpha$, is conjugate to the gradient of the exchange chemical potential, $\partial_\alpha \overline{\mu}$. Finally, the elastic strain rate, $Du_{\alpha\beta}/Dt$, is conjugate to the elastic stress, $\sigma_{\alpha\beta}^{\text{el}}$.

To help enumerate flux–force pairs, the product of a rank two tensorial flux and a rank two tensorial force can be decomposed into scalar (trace) and tensorial (traceless) terms. In our case,

$$\sigma_{\alpha\beta} v_{\alpha\beta} = \tilde{\sigma}_{\alpha\beta} \tilde{v}_{\alpha\beta} + \tfrac{1}{3}\sigma v, \tag{16}$$

$$\frac{Du_{\alpha\beta}}{Dt}\sigma_{\alpha\beta}^{\text{el}} = \frac{D\tilde{u}_{\alpha\beta}}{Dt}\tilde{\sigma}_{\alpha\beta}^{\text{el}} + \frac{1}{3}\frac{du}{dt}\sigma^{\text{el}}, \tag{17}$$

where $\tilde{A}_{\alpha\beta} \equiv A_{\alpha\beta} - \frac{1}{3}A_{\gamma\gamma}\delta_{\alpha\beta}$ is the traceless part of a tensor $A_{\alpha\beta}$, $A \equiv A_{\gamma\gamma}$ is its trace and $\frac{d}{dt} = \frac{\partial}{\partial t} + v_\alpha \partial_\alpha$ is the convected time derivative. As a result, the conjugate flux–force pairs are

$$
\begin{aligned}
\text{Flux} \;\; &\leftrightarrow \text{Force} \\[4pt]
\tilde{\sigma}_{\alpha\beta} &\leftrightarrow \tilde{v}_{\alpha\beta} \\[4pt]
\sigma \;\; &\leftrightarrow \tfrac{1}{3}v \\[4pt]
j_\alpha &\leftrightarrow -\partial_\alpha \overline{\mu} \\[4pt]
\frac{D\tilde{u}_{\alpha\beta}}{Dt} &\leftrightarrow -\tilde{\sigma}_{\alpha\beta}^{\text{el}} \\[4pt]
\frac{du}{dt} &\leftrightarrow -\frac{1}{3}\sigma^{\text{el}}.
\end{aligned}
\tag{18}
$$

### 1.3. Constitutive relations

The constitutive relations for the passive gel are obtained by expanding the fluxes to linear order in the forces, writing all terms allowed by symmetry [14]. We note that each flux contains a dissipative part and a reactive part, i.e. $\tilde{\sigma}_{\alpha\beta} = \tilde{\sigma}_{\alpha\beta}^{\text{d}} + \tilde{\sigma}_{\alpha\beta}^{\text{r}}$, etc. The dissipative part contributes to the entropy production rate, while the reactive, or reversible, part does not. The dissipative and

reactive parts are identified by their signatures under time reversal. Noting that the forces $\tilde{v}_{\alpha\beta}$ and $v/3$ are odd under time reversal and $-\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta}$, $-\sigma^{\mathrm{el}}/3$ and $-\partial_\alpha\overline{\mu}$ are even, the dissipative parts of the fluxes are given by

$$\tilde{\sigma}^{\mathrm{d}}_{\alpha\beta} = 2\eta\tilde{v}_{\alpha\beta}, \tag{19}$$

$$\sigma^{\mathrm{d}} = 3\overline{\eta}v, \tag{20}$$

$$j^{\mathrm{d}}_\alpha = -\gamma\,\partial_\alpha\overline{\mu} + \chi_1\partial_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \frac{\overline{\chi}_1}{3}\partial_\alpha\sigma^{\mathrm{el}}, \tag{21}$$

$$\frac{\mathrm{D}\tilde{u}^{\mathrm{d}}_{\alpha\beta}}{\mathrm{D}t} = -\chi_1\left(\partial_\alpha\partial_\beta\overline{\mu} - \frac{1}{3}\partial^2_\gamma\overline{\mu}\delta_{\alpha\beta}\right) - \Gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \frac{\Gamma_1}{2}\left(\partial_\alpha\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\rho\gamma}\right)$$
$$+ \frac{\Gamma'_1}{3}\left(\partial_\alpha\partial_\beta\sigma^{\mathrm{el}} - \frac{1}{3}\partial^2_\gamma\sigma^{\mathrm{el}}\delta_{\alpha\beta}\right), \tag{22}$$

$$\frac{\mathrm{d}u^{\mathrm{d}}}{\mathrm{d}t} = -\overline{\chi}_1\partial^2_\alpha\overline{\mu} + \Gamma'_1\partial_\alpha\partial_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} - \overline{\Gamma}\sigma^{\mathrm{el}} + \frac{\overline{\Gamma}_1}{3}\partial^2_\alpha\sigma^{\mathrm{el}}. \tag{23}$$

These relations contain several Onsager coefficients, in addition to the shear and bulk viscosities $\eta$ and $\overline{\eta}$, already arising in a simple fluid. Filament diffusion through the solvent is related to the osmotic mobility, $\gamma$, in equation (21). Elastic forces drive flow of polymer relative to solvent, in proportion to the mobilities $\chi_1$ and $\overline{\chi}_1$ appearing in equation (21). Finally, viscoelastic relaxation in the polymer network is described by the coefficients $\Gamma$, $\Gamma_1$, $\Gamma'_1$, $\overline{\Gamma}$ and $\overline{\Gamma}_1$ in equations (22) and (23). Onsager reciprocity for dissipative couplings has been respected in equations (19)–(23), noting that the $\chi_1$-terms in equations (21) and (22), when multiplied by their conjugate force, only differ by a partial integration whose boundary term is irrelevant to the entropy production rate. The same is true for the $\overline{\chi}_1$ terms.

The reactive parts of the fluxes are

$$\tilde{\sigma}^{\mathrm{r}}_{\alpha\beta} = \pi_1\left(\partial_\alpha\partial_\beta\overline{\mu} - \frac{1}{3}\partial^2_\gamma\overline{\mu}\delta_{\alpha\beta}\right) + \nu\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \frac{\nu_2}{2}\left(\partial_\alpha\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\rho\gamma}\right)$$
$$+ \frac{\overline{\nu}_2}{3}\left(\partial_\alpha\partial_\beta\sigma^{\mathrm{el}} - \frac{1}{3}\partial^2_\gamma\sigma^{\mathrm{el}}\delta_{\alpha\beta}\right), \tag{24}$$

$$\sigma^{\mathrm{r}} = \overline{\pi}_1\partial^2_\gamma\overline{\mu} + \frac{\nu'_2}{3}\partial_\alpha\partial_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \overline{\nu}\sigma^{\mathrm{el}} + \frac{\overline{\nu}'_2}{3}\partial^2_\gamma\sigma^{\mathrm{el}}, \tag{25}$$

$$j^{\mathrm{r}}_\alpha = -\pi_1\partial_\beta\tilde{v}_{\alpha\beta} - \frac{\overline{\pi}_1}{3}\partial_\alpha v, \tag{26}$$

$$\frac{\mathrm{D}\tilde{u}^{\mathrm{r}}_{\alpha\beta}}{\mathrm{D}t} = \nu\tilde{v}_{\alpha\beta} + \frac{\nu_2}{2}\left(\partial_\alpha\partial_\gamma\tilde{v}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{v}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{v}_{\rho\gamma}\right) + \frac{\nu'_2}{3}\left(\partial_\alpha\partial_\beta v - \frac{1}{3}\partial^2_\gamma v\delta_{\alpha\beta}\right), \tag{27}$$

$$\frac{\mathrm{d}u^{\mathrm{r}}}{\mathrm{d}t} = \overline{\nu}_2\partial_\alpha\partial_\beta\tilde{v}_{\alpha\beta} + \overline{\nu}v + \frac{\overline{\nu}'_2}{3}\partial^2_\gamma v. \tag{28}$$

These relations contain all possible reactive couplings of a passive viscoelastic gel up to second derivatives in the exchange chemical potential, the elastic stress and the symmetrized velocity gradient. We note that Onsager reciprocity for reactive couplings has been respected. We observe first that the elastic stress contributes reactively to the deviatoric stress, with coefficients $\nu$ and $\overline{\nu}$ in equations (24) and (25). The reciprocal couplings, that is, the $\nu$- and $\overline{\nu}$-terms in equations (27) and (28), describe convection of the elastic strain by the center-of-mass velocity. We note also that a non-homogeneous center-of-mass velocity gradient contributes to the polymer flux. This effect, described here by the coefficients $\pi_1$ and $\overline{\pi}_1$, has been obtained earlier from kinetic theory arguments for flexible polymers in a solvent [19]. The remaining terms, and terms involving second derivatives of $\overline{\mu}$ and $\sigma_{\alpha\beta}^{\mathrm{el}}$ in the dissipative relations, have been included here because they are relevant for obtaining a simple Maxwell model.

The physical elastic stresses that contribute to the total stress, $\sigma_{\alpha\beta}^{\mathrm{tot}}$, are $\nu\tilde{\sigma}_{\alpha\beta}^{\mathrm{el}}$ and $\overline{\nu}\sigma^{\mathrm{el}}$, with conjugate strains $\tilde{u}_{\alpha\beta}/\nu$ and $u/\overline{\nu}$. As a result, we may write Onsager relations for $\tilde{u}_{\alpha\beta}/\nu$ and $u/\overline{\nu}$ and simply renormalize the Onsager coefficients as follows: $\chi_1 \to \chi_1/\nu$, $\overline{\chi}_1 \to \overline{\chi}_1/\overline{\nu}$, $\Gamma \to \Gamma/\nu^2$, $\Gamma_1 \to \Gamma_1/\nu^2$, $\Gamma_1' \to \Gamma_1'/(\nu\overline{\nu})$, $\overline{\Gamma} \to \overline{\Gamma}/\overline{\nu}^2$, $\overline{\Gamma}_1 \to \overline{\Gamma}_1/\overline{\nu}^2$, $\nu_2 \to \nu_2/\nu$, $\nu_2' \to \nu_2'/\nu$, $\overline{\nu}_2 \to \overline{\nu}_2/\overline{\nu}$ and $\overline{\nu}_2' \to \overline{\nu}_2'/\overline{\nu}$. We may therefore take $\nu = \overline{\nu} = 1$ without loss of generality.

The constitutive relations for the passive, two-component, viscoelastic gel are obtained by adding the dissipative and reactive parts of each flux, i.e. $\tilde{\sigma}_{\alpha\beta} = \tilde{\sigma}_{\alpha\beta}^{\mathrm{d}} + \tilde{\sigma}_{\alpha\beta}^{\mathrm{r}}$, etc. These constitutive relations, together with the continuity equations, (1)–(3), complete the description of the passive viscoelastic gel. When inertial terms are neglected in the momentum conservation equation, the force balance condition

$$\partial_\beta(\sigma_{\alpha\beta} - P\delta_{\alpha\beta}) = 0 \tag{29}$$

is obtained. Note that the pressure $P$ is different from the hydrostatic pressure $P - \sigma^{\mathrm{el}}$.

To summarize, Onsager relations, given by equations (19)–(23) and (24)–(28), have been obtained that describe strain relaxation and permeation in an isotropic, passive, two-component viscoelastic fluid. By treating $u_{\alpha\beta}$ as a slow dynamical variable, viscoelastic relaxation in the polymer component of the gel is contained in the dissipative relations for $\mathrm{D}\tilde{u}_{\alpha\beta}^{\mathrm{d}}/\mathrm{D}t$ and $\mathrm{d}u^{\mathrm{d}}/\mathrm{d}t$. When elastic stresses are not fully relaxed, the flux of polymer relative to the center-of-mass is seen to be driven by the elastic force $\partial_\beta\tilde{\sigma}_{\alpha\beta}^{\mathrm{el}}$, in addition to the osmotic force $\partial_\alpha\overline{\mu}$.

Equations (19)–(23) and (25)–(28) are completely general relations describing a viscoelastic gel; if certain conditions are imposed among the Onsager coefficients, specific model behaviors can be obtained. The simplest such model is the Maxwell model of viscoelasticity. In the next section, we show how this model behavior arises from our general description.

## 2. Maxwell model with permeation

The Maxwell model is a simple description of stress relaxation on a single time scale, $\tau$, such that the response of the viscoelastic fluid is solid-like on time scales shorter than $\tau$ and liquid-like on time scales greater than $\tau$. Some care, however, must be taken in writing down the Maxwell model for stress relaxation in the polymer network, since in general the polymer velocity and the center-of-mass velocity are different. The Maxwell model for the polymer

component is written as

$$\left(1 + \tau \frac{D}{Dt}\right) \tilde{\sigma}_{\alpha\beta}^{el} = 2\eta_p \tilde{v}_{\alpha\beta}^p, \tag{30}$$

$$\left(1 + \overline{\tau} \frac{d}{dt}\right) \sigma^{el} = \overline{\eta}_p v^p, \tag{31}$$

where $\eta_p$ and $\overline{\eta}_p$ are the shear and bulk polymer viscosities and $\tilde{v}_{\alpha\beta}^p$ and $v^p$ are the traceless part and trace of the polymer velocity tensor $v_{\alpha\beta}^p = \frac{1}{2}\left(\partial_\alpha v_\beta^p + \partial_\beta v_\alpha^p\right)$. In equations (30) and (31), we have distinguished shear and isotropic relaxation by the two relaxation times $\tau$ and $\overline{\tau}$.

## 2.1. Simplification of Onsager relations

To obtain equations (30) and (31) from our theory, we first assume Hookean elasticity:

$$\tilde{\sigma}_{\alpha\beta}^{el} = 2G\tilde{u}_{\alpha\beta}, \tag{32}$$

$$\sigma^{el} = Ku, \tag{33}$$

where $G$ and $K$ are the shear and bulk moduli. The Maxwell model is then obtained from the constitutive equations for $D\tilde{u}_{\alpha\beta}/Dt$ and $du/dt$. Using the Onsager relations equations (21)–(23) and (26)–(28), we obtain

$$\left(1 + \frac{1}{2G\Gamma} \frac{D}{Dt}\right) \tilde{\sigma}_{\alpha\beta}^{el} = \frac{\tilde{v}_{\alpha\beta}^p}{\Gamma} + \frac{1}{\Gamma}\left[\left(\frac{\nu_2}{2} + \frac{\pi_1}{2\rho_{p0}}\right)\left(\partial_\alpha \partial_\gamma \tilde{v}_{\beta\gamma} + \partial_\beta \partial_\gamma \tilde{v}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho \partial_\gamma \tilde{v}_{\rho\gamma}\right)\right.$$

$$+ \left(\frac{\nu_2'}{3} + \frac{\overline{\pi}_1}{3\rho_{p0}}\right)\left(\partial_\alpha \partial_\beta v - \frac{1}{3}\partial_\gamma^2 v \delta_{\alpha\beta}\right) + \left(\frac{\gamma}{\rho_{p0}} - \chi_1\right)\left(\partial_\beta \partial_\alpha \overline{\mu} - \frac{1}{3}\delta_{\alpha\beta}\partial_\gamma^2 \overline{\mu}\right)$$

$$+ \left(\frac{\Gamma_1}{2} - \frac{\chi_1}{2\rho_{p0}}\right)\left(\partial_\alpha \partial_\gamma \tilde{\sigma}_{\beta\gamma}^{el} + \partial_\beta \partial_\gamma \tilde{\sigma}_{\alpha\gamma}^{el} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho \partial_\gamma \tilde{\sigma}_{\rho\gamma}^{el}\right)$$

$$\left. + \left(\frac{\Gamma_1'}{3} - \frac{\overline{\chi}_1}{3\rho_{p0}}\right)\left(\partial_\alpha \partial_\beta \sigma^{el} - \frac{1}{3}\partial_\gamma^2 \sigma^{el} \delta_{\alpha\beta}\right)\right], \tag{34}$$

$$\left(1 + \frac{1}{K\overline{\Gamma}} \frac{d}{dt}\right) \sigma^{el} = \frac{v^p}{\overline{\Gamma}} + \frac{1}{\overline{\Gamma}}\left[\left(\overline{\nu}_2 + \frac{\pi_1}{\rho_{p0}}\right)\partial_\alpha \partial_\beta \tilde{v}_{\alpha\beta} + \left(\frac{\overline{\nu}_2'}{3} + \frac{\overline{\pi}_1}{3\rho_{p0}}\right)\partial_\gamma^2 v\right.$$

$$\left. + \left(\frac{\gamma}{\rho_{p0}} - \overline{\chi}_1\right)\partial_\alpha^2 \overline{\mu} + \left(\Gamma_1' - \frac{\chi_1}{\rho_{p0}}\right)\partial_\alpha \partial_\beta \tilde{\sigma}_{\alpha\beta}^{el} + \left(\frac{\overline{\Gamma}_1}{3} - \frac{\overline{\chi}_1}{3\rho_{p0}}\right)\partial_\alpha^2 \sigma^{el}\right]. \tag{35}$$

To obtain the above, we have used $v_{\alpha\beta} \simeq v_{\alpha\beta}^p - (\partial_\alpha j_\beta + \partial_\beta j_\alpha)/2\rho_{p0}$ and the constitutive relation for $j_\alpha$ to rewrite the first term on the right-hand side of equation (27) and the second term on the right-hand side of equation (28) in terms of gradients of the polymer velocity. Here, $\rho_{p0}$ is the polymer mass density at equilibrium.

Equations (34) and (35) represent a generalized Maxwell model with the polymer viscosities $\eta_p = 1/(2\Gamma)$ and $\overline{\eta}_p = 1/\overline{\Gamma}$ and the viscoelastic relaxation times $\tau = \eta_p/G$ and $\overline{\tau} = \overline{\eta}_p/K$. To recover the simplified Maxwell model, we set the osmotic and mechanical mobilities equal to each other: $\chi_1 = \overline{\chi}_1 = \gamma/\rho_{p0}$, a choice made in two-fluid models of polymer solutions [20]. If, furthermore, $\Gamma_1 = \Gamma_1' = \overline{\Gamma}_1 = \gamma/\rho_{p0}^2$, $\nu_2 = \overline{\nu}_2 = -\pi_1/\rho_{p0}$ and $\nu_2' = \overline{\nu}_2' = -\overline{\pi}_1/\rho_{p0}$, all but the first terms on the right-hand sides of equations (34) and (35) vanish, and we recover equations (30) and (31).

## 2.2. Two-fluid description of permeation

With these choices of Onsager coefficients and $\pi_1 = \overline{\pi}_1 = 0$, we obtain a two-fluid description of permeation in the gel. From the constitutive relation for $j_\alpha$,

$$\partial_\beta(\sigma^{\text{el}}_{\alpha\beta} - \rho_{\text{p0}}\overline{\mu}\delta_{\alpha\beta}) - \frac{\rho^2_{\text{p0}}}{\gamma}(v^{\text{p}}_\alpha - v_\alpha) = 0. \tag{36}$$

Equation (36) can be interpreted as the force balance equation on the polymer component of the gel, where the first bracketed term contains the elastic and osmotic forces and the second bracketed term contains the drag force between the polymer and the solvent and describes permeation. Subtracting equation (36) from the total force balance, equation (29), we obtain the force balance on the solvent:

$$\partial_\beta(2\eta\tilde{v}_{\alpha\beta} + \overline{\eta}v\delta_{\alpha\beta} - P_{\text{s}}\delta_{\alpha\beta}) - \frac{\rho^2_{\text{p0}}}{\gamma}(v_\alpha - v^{\text{p}}_\alpha) = 0, \tag{37}$$

where $P_{\text{s}} = P - \rho_{\text{p0}}\overline{\mu}$ is identified as the solvent pressure. For small polymer mass fractions, $v^{\text{s}}_\alpha \simeq v_\alpha$, and it becomes clear that in equation (37) the first bracketed term contains the viscous forces and the pressure force on the solvent, and the second bracketed term contains the reaction force of the polymer network on the solvent. We see that the Onsager approach generates a Maxwell model of the polymer component of the gel, equations (30) and (31), whose elastic stresses drive permeation of a solvent, described by equations (36) and (37).

## 3. Hydrodynamics of an active, polar, viscoelastic gel with permeation

In this section, we account for two key features of active gels: polar order and active processes driven by ATP hydrolysis [7, 9]. Active processes in the cytoskeleton, whether forces exerted by myosin motors or filament turnover, are introduced via the difference in chemical potentials between ATP and ADP and inorganic phosphate, P$_{\text{i}}$, $\Delta\mu = \mu_{\text{ATP}} - \mu_{\text{ADP}} - \mu_{\text{P}}$. When $\Delta\mu > 0$ a free energy $\Delta\mu$ is released per molecule of hydrolyzed ATP. We suppose for simplicity that the concentrations of ATP, ADP and P$_{\text{i}}$ are uniform in space and time in the cell, and therefore $\Delta\mu$ is also constant.

In the hydrodynamic description presented below, several new couplings arise due to the elastic stress in the network and to filament turnover that were not considered in earlier theories of active, polar gels [7, 9, 21, 22]. To find these couplings, we follow the same procedure as that used in section 1.

## 3.1. Continuity equations and polar order parameter

To account for filament turnover, we introduce the monomer mass density, $\rho_{\text{m}}$, in addition to the polymer and solvent densities, $\rho_{\text{p}}$ and $\rho_{\text{s}}$. The continuity equations are then given by

$$\partial_t\rho_{\text{p}} + \partial_\alpha(\rho_{\text{p}}v^{\text{p}}_\alpha) = -s, \tag{38}$$

$$\partial_t\rho_{\text{m}} + \partial_\alpha(\rho_{\text{m}}v^{\text{m}}_\alpha) = s, \tag{39}$$

$$\partial_t\rho_{\text{s}} + \partial_\alpha(\rho_{\text{s}}v^{\text{s}}_\alpha) = 0, \tag{40}$$

$$\partial_t g_\alpha - \partial_\beta\sigma^{\text{tot}}_{\alpha\beta} = 0, \tag{41}$$

where $s$ describes polymerization and depolymerization reactions that lead to an exchange of monomers between polymer filaments and the solvent. The total mass density is $\rho = \rho_p + \rho_m + \rho_s$, the center-of-mass velocity is $v_\alpha = (\rho_p v_\alpha^p + \rho_m v_\alpha^m + \rho_s v_\alpha^s)/\rho$, and hence the total momentum density is $g_\alpha = \rho v_\alpha$. Next, the polymer and monomer relative fluxes $j_\alpha^p$ and $j_\alpha^m$ are defined by

$$v_\alpha^p = v_\alpha + \frac{j_\alpha^p}{\rho_p}, \tag{42}$$

$$v_\alpha^m = v_\alpha + \frac{j_\alpha^m}{\rho_m}, \tag{43}$$

$$v_\alpha^s = v_\alpha - \frac{(j_\alpha^p + j_\alpha^m)}{\rho_s}. \tag{44}$$

Polymer filaments that make up active gels are generally polar, which can give rise to local anisotropy in the gel. Polar order is described here by the vector order parameter $p_\alpha$, similar to the director in nematic liquid crystals [15]; as it represents broken rotational invariance of the gel, $p_\alpha$ is a hydrodynamic variable.

### 3.2. Fluxes and forces

The free energy for the multi-component, polar fluid is given by

$$F = \int \left[ \frac{1}{2}\rho v^2 + f(\rho_p, \rho_m, \rho_s, u_{\alpha\beta}, p_\alpha, \partial_\alpha p_\beta) \right] dV. \tag{45}$$

The time derivative of $F$ is obtained using the differential of $f$,

$$df = \sum_{i=p,m,s} \mu_i dn_i + \sigma_{\alpha\beta}^{el} du_{\alpha\beta} - h_\alpha dp_\alpha + \partial_\alpha(\pi_{\alpha\beta} dp_\beta), \tag{46}$$

where $\mu_i = \partial f/\partial n_i$, $i = p, m, s$, are the chemical potentials, $n_i = \rho_i/m_i$ and $m_i$ are, respectively, the number density and molecular mass of component $i$, $\pi_{\alpha\beta} = \frac{\partial f}{\partial(\partial_\alpha p_\beta)}$ and $h_\alpha = -\frac{\partial f}{\partial p_\alpha} + \partial_\beta \pi_{\beta\alpha}$ is the field conjugate to $p_\alpha$ [15]. Using equation (46), the continuity equations and integrating by parts, we find that

$$\frac{dF}{dt} = \int dV \left[ -(\sigma_{\alpha\beta}^{tot} + \rho v_\alpha v_\beta)\partial_\beta v_\alpha + j_\alpha^p \partial_\alpha \overline{\mu}_p + j_\alpha^m \partial_\alpha \overline{\mu}_m - \sum_{i=p,m,s} \mu_i \partial_\alpha (n_i v_\alpha) \right.$$

$$\left. + \sigma_{\alpha\beta}^{el} \partial_t u_{\alpha\beta} - h_\alpha \partial_t p_\alpha - r\Delta\mu - s\Delta\mu_{pm} \right] + \text{surface terms}, \tag{47}$$

where $\overline{\mu}_i = \frac{\mu_i}{m_i} - \frac{\mu_s}{m_s}$, $i = p, m$, are exchange chemical potentials, $r$ is the number of ATP molecules hydrolyzed per unit time and $\Delta\mu_{pm} = \mu_p - \mu_m$. Introducing the pressure $P = -f + \sum_{i=p,m,s} \mu_i n_i$ and using equation (46), the above can be simplified to

$$\frac{dF}{dt} = \int dV \left[ -\sigma_{\alpha\beta}^s v_{\alpha\beta} + \left( \sigma_{\alpha\beta}^a + 2\sigma_{\alpha\gamma}^{el} u_{\gamma\beta} + h_\alpha p_\beta \right) \omega_{\alpha\beta} + j_\alpha^p \partial_\alpha \overline{\mu}_p + j_\alpha^m \partial_\alpha \overline{\mu}_m \right.$$

$$\left. + \sigma_{\alpha\beta}^{el} \frac{Du_{\alpha\beta}}{Dt} - h_\alpha \frac{Dp_\alpha}{Dt} - r\Delta\mu - s\Delta\mu_{pm} \right] + \text{surface terms}. \tag{48}$$

In equation (48), $\sigma_{\alpha\beta}^s$ and $\sigma_{\alpha\beta}^a$ are the symmetric and antisymmetric parts of the deviatoric stress

$$\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{tot} + \rho v_\alpha v_\beta - \sigma_{\alpha\beta}^e + P\delta_{\alpha\beta}, \tag{49}$$

where $\sigma_{\alpha\beta}^{\mathrm{e}} = -\pi_{\beta\gamma}\partial_\alpha p_\gamma$ is the Ericksen stress [15], and

$$\frac{\mathrm{D}p_\alpha}{\mathrm{D}t} = \partial_t p_\alpha + v_\beta \partial_\beta p_\alpha + \omega_{\alpha\beta} p_\beta \qquad (50)$$

the convected, co-rotational time derivative of $p_\alpha$. The Ericksen stress is an equilibrium stress that generalizes the hydrostatic pressure to anisotropic fluids [15]. Since no dissipation occurs in a rotational flow ($v_{\alpha\beta} = 0$) in which the fields $u_{\alpha\beta}$ and $p_\alpha$ move and rotate with the fluid ($\mathrm{D}u_{\alpha\beta}/\mathrm{D}t = 0$, $\mathrm{D}p_\alpha/\mathrm{D}t = 0$), it follows that

$$\sigma_{\alpha\beta}^{\mathrm{a}} = \tilde{\sigma}_{\beta\gamma}^{\mathrm{el}}\tilde{u}_{\gamma\alpha} - \tilde{\sigma}_{\alpha\gamma}^{\mathrm{el}}\tilde{u}_{\gamma\beta} + \tfrac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha) \qquad (51)$$

and that the entropy production rate is given by

$$T\theta = \sigma_{\alpha\beta}^{\mathrm{s}} v_{\alpha\beta} - j_\alpha^{\mathrm{p}} \partial_\alpha \overline{\mu}_p - j_\alpha^{\mathrm{m}} \partial_\alpha \overline{\mu}_m - \frac{\mathrm{D}u_{\alpha\beta}}{\mathrm{D}t}\sigma_{\alpha\beta}^{\mathrm{el}} + \frac{\mathrm{D}p_\alpha}{\mathrm{D}t}h_\alpha + r\Delta\mu + s\Delta\mu_{\mathrm{pm}}. \qquad (52)$$

From equation (52), we identify the flux–force pairs new to this section. Firstly, the relative monomer current, $j_\alpha^{\mathrm{m}}$, is conjugate to the gradient of the monomer exchange chemical potential, $\partial_\alpha \overline{\mu}_{\mathrm{m}}$. Secondly, the convected, co-rotational time derivative of the polarity vector, $\mathrm{D}p_\alpha/\mathrm{D}t$, is conjugate to the molecular field, $h_\alpha$. Thirdly, the reaction rate of the chemical fuel, $r$, is conjugate to the chemical potential difference between the fuel and its products, $\Delta\mu$. Finally, the polymer–monomer exchange rate, $s$, is conjugate to the difference in chemical potential between polymer and monomer. We note that in a passive system, a nonzero $\Delta\mu_{\mathrm{pm}}$ will relax in a finite time. In non-equilibrium steady states, the chemical potential difference $\Delta\mu_{\mathrm{pm}}$ will be a function of $\Delta\mu$.

The flux–force pairs for the gel may thus be summarized as

$$
\begin{aligned}
&\text{Flux} &&\leftrightarrow &&\text{Force} \\
&\tilde{\sigma}_{\alpha\beta}^{s} &&\leftrightarrow &&\tilde{v}_{\alpha\beta} \\
&\sigma^{\mathrm{s}} &&\leftrightarrow &&\tfrac{1}{3}v \\
&j_\alpha^{i} &&\leftrightarrow &&-\partial_\alpha\overline{\mu}_i \\
&\frac{\mathrm{D}\tilde{u}_{\alpha\beta}}{\mathrm{D}t} &&\leftrightarrow &&-\tilde{\sigma}_{\alpha\beta}^{\mathrm{el}} \\
&\frac{\mathrm{d}u}{\mathrm{d}t} &&\leftrightarrow &&-\frac{1}{3}\sigma^{\mathrm{el}} \\
&\frac{\mathrm{D}p_\alpha}{\mathrm{D}t} &&\leftrightarrow &&h_\alpha \\
&r &&\leftrightarrow &&\Delta\mu \\
&s &&\leftrightarrow &&\Delta\mu_{\mathrm{pm}},
\end{aligned}
\qquad (53)
$$

where $i$ is equal to $p$ or $m$.

## 3.3. Constitutive relations

In a polar gel, fluxes and forces of different tensorial order may couple to each other by allowing the Onsager coefficients to be functions of $p_\alpha$. Based on the flux–force pairs, equation (53),

**IOP** Institute of Physics Φ DEUTSCHE PHYSIKALISCHE GESELLSCHAFT

a number of dissipative and reactive couplings arise; see appendix B. Here, we only list the couplings that are relevant for the discussion of active, polar, viscoelastic gels. The dissipative relations are

$$j_\alpha^{i,d} = \chi_i p_\beta \tilde{\sigma}_{\alpha\beta}^{el} + \frac{\overline{\chi}_i}{3} p_\alpha \sigma^{el} + \kappa_i p_\alpha \Delta\mu + \kappa_i' p_\alpha \Delta\mu_{pm} + o.c., \tag{54}$$

$$\frac{D\tilde{u}_{\alpha\beta}^d}{Dt} = \sum_{i=p,m} \frac{\chi_i}{2} \left( p_\alpha \partial_\beta \overline{\mu}_i + p_\beta \partial_\alpha \overline{\mu}_i - \frac{2}{3} p_\gamma \partial_\gamma \overline{\mu}_i \delta_{\alpha\beta} \right) + \frac{\omega_1}{2} \left( p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta} \right)$$
$$+ \psi \tilde{q}_{\alpha\beta} \Delta\mu + \psi' \tilde{q}_{\alpha\beta} \Delta\mu_{pm} + o.c., \tag{55}$$

$$\frac{du^d}{dt} = \sum_{i=p,m} \overline{\chi}_i p_\alpha \partial_\alpha \overline{\mu}_i + \overline{\omega}_1 p_\alpha h_\alpha + \overline{\psi} \Delta\mu + \overline{\psi}_1 p_\alpha p_\alpha \Delta\mu + \overline{\psi}' \Delta\mu_{pm} + \overline{\psi}_1' p_\alpha p_\alpha \Delta\mu_{pm} + o.c., \tag{56}$$

$$\frac{Dp_\alpha^d}{Dt} = -\omega_1 p_\beta \tilde{\sigma}_{\alpha\beta}^{el} - \frac{\overline{\omega}_1}{3} p_\alpha \sigma^{el} + \lambda_1' p_\alpha \Delta\mu_{pm} + o.c., \tag{57}$$

$$r^d = -\psi \tilde{q}_{\alpha\beta} \tilde{\sigma}_{\alpha\beta}^{el} - \frac{\overline{\psi}}{3} \sigma^{el} - \frac{\overline{\psi}_1}{3} p_\alpha p_\alpha \sigma^{el} + \Lambda' \Delta\mu_{pm} + o.c., \tag{58}$$

$$s^d = -\sum_{i=p,m} \kappa_i' p_\alpha \partial_\alpha \overline{\mu}_i - \psi' \tilde{q}_{\alpha\beta} \tilde{\sigma}_{\alpha\beta}^{el} - \frac{\overline{\psi}'}{3} \sigma^{el} - \frac{\overline{\psi}_1'}{3} p_\alpha p_\alpha \sigma^{el} + \lambda_1' p_\alpha h_\alpha + \Lambda' \Delta\mu + \Lambda_1 \Delta\mu_{pm}, \tag{59}$$

where $\tilde{q}_{\alpha\beta} = p_\alpha p_\beta - \frac{1}{3} p_\gamma p_\gamma \delta_{\alpha\beta}$ and 'o.c.' stands for other couplings that have already been presented in section 1 or in earlier studies [7, 9]. Note that there are no new reactive couplings as compared with section 1 and those found earlier for active, polar fluids [7, 9]. The constitutive equations are obtained by adding the dissipative and reactive parts of each flux given in equations (B.1)–(B.16), i.e. $\tilde{\sigma}_{\alpha\beta}^s = \tilde{\sigma}_{\alpha\beta}^{s,d} + \tilde{\sigma}_{\alpha\beta}^{s,r}$, etc. The hydrodynamic behavior of the gel is then fully described by these equations and the continuity equations, equations (38)–(41). Neglecting inertial terms in the momentum conservation equation, the force balance condition is given by

$$\partial_\beta(\sigma_{\alpha\beta}^s + \sigma_{\alpha\beta}^a + \sigma_{\alpha\beta}^e - P\delta_{\alpha\beta}) = 0. \tag{60}$$

We discuss now the physical meaning of the couplings in equations (54)–(59). Firstly, in a polar gel, the relative fluxes couple directly to the elastic stress in equations (54), with coefficients $\chi_i$ and $\overline{\chi}_i$. Onsager reciprocity indicates that terms with the same coefficients appear in the constitutive relations for the elastic strain rate, equations (55) and (56). Secondly, the $\omega_1$- and $\overline{\omega}_1$-terms in equations (55) and (56) describe elastic strain relaxation or production caused by the molecular field, $h_\alpha$. The reciprocal terms in equation (57) account for alignment of the polarity vector by the elastic stress. Thirdly, active elastic stresses arise from terms proportional to $\Delta\mu$ in the elastic strain rate equations, equation (55) and (56). There are isotropic and anisotropic active terms in these equations, and they describe relaxation or production of elastic strain by active processes, such as polymer assembly and disassembly and the effects of molecular motors. Next, the elastic stress couples to the reaction rate of chemical fuel, $r$, in equation (58),
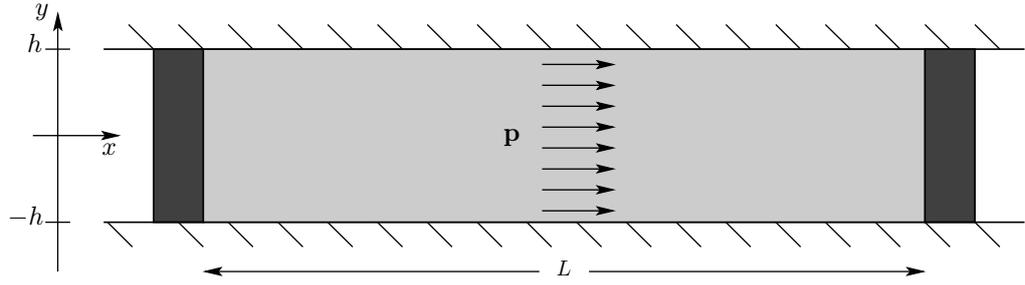
**Figure 1.** A thin film of active gel positioned between two pistons sets itself into motion.

with coefficients $\psi$, $\overline{\psi}$, and $\overline{\psi}_1$. Finally, equation (59) contains couplings, with coefficients $\psi'$, $\overline{\psi}'$ and $\overline{\psi}'_1$, that describe at linear order the effects of elastic stress on the polymerization rate $s$.

Polymer treadmilling is a biologically relevant phenomenon in which filaments polymerize at one end and depolymerize at the other end at constant length [23, 24]. It requires asymmetric filaments and ATP consumption, and is described here by the active current $\kappa_p p_\alpha \Delta \mu$. The term $\kappa'_p p_\alpha \Delta \mu_{\mathrm{pm}}$ describes polymerization and depolymerization reactions driven by chemical potential differences between polymers and monomers. This current could also exist as a transient effect in a passive, polar gel. In an active, polar gel, treadmilling may arise even if the net turnover rate, $s$, is zero, as might occur in a uniform, steady state.

## 4. Self-propulsion of a thin active gel

In this section, we present a simple model of self-generated motion of an active gel. This problem is motivated by cell locomotion on a solid substrate. We consider a thin layer of an incompressible, active, polar gel between two parallel surfaces located at $y = -h$ and $y = h$; see figure 1. The active gel is bounded in the $x$-direction by two pistons separated by a distance $L$ much greater than $h$, and is spatially homogeneous in the $z$-direction. The layer of gel could, for instance, represent the thin film-like lamellipodium of a crawling cell [25], while the pistons represent the trailing cell body and a load at the leading edge that the lamellipodium moves against. The fluid is assumed to be polarized in the $x$-direction with unit magnitude: $|\mathbf{p}| = 1$.

We describe the gel flow at steady state using a two-component description in which free monomers are included in an effective solvent; for simplicity, we do not consider polymerization and depolymerization at the surfaces but instead consider filament treadmilling in the bulk. The fluid is described by the following constitutive relations, simplified from section 3:

$$\sigma_{\alpha\beta} = 2\eta v_{\alpha\beta} + \sigma_{\alpha\beta}^{\mathrm{el}}, \tag{61}$$

$$j_\alpha = -\gamma \, \partial_\alpha \overline{\mu} + \chi_1 \partial_\beta \sigma_{\alpha\beta}^{\mathrm{el}} + \kappa p_\alpha \Delta \mu, \tag{62}$$

$$0 = -\sigma_{\alpha\beta}^{\mathrm{el}} + 2\eta_{\mathrm{p}} v_{\alpha\beta}^{\mathrm{p}}, \tag{63}$$

where we have used the notation $j_\alpha = j_\alpha^{\mathrm{p}}$, $\gamma = \gamma_p$, $\overline{\mu} = \overline{\mu}_p$, $\chi_1 = \chi_{1p} = \overline{\chi}_{1p}$, $\kappa = \kappa_p$ and have used the simple case $\overline{\eta} = 2\eta/3$ and $\overline{\eta}_{\mathrm{p}} = 2\eta_{\mathrm{p}}/3$.

Mass conservation, force balances and the incompressibility condition of the medium read

$$\frac{d}{dy}\left(\rho_p v_y^p\right) = 0, \tag{64}$$

$$\frac{d\sigma_{xy}}{dy} - \partial_x P = 0, \tag{65}$$

$$\frac{d\sigma_{yy}}{dy} - \partial_y P = 0, \tag{66}$$

$$\frac{dv_y}{dy} = 0. \tag{67}$$

In the above, we have assumed that the system is homogeneous along the $x$-direction. As a result, the stresses, velocities and densities are independent of $x$. Note that we neglect the dependence of the exchange chemical potential $\overline{\mu}$ on pressure, which is valid if the specific volumes of the solvent and polymer components are equal [9, 26]. Integrations of equation (65) with respect to $x$ and $y$ imply that $P = P_0 + \alpha(y)x$ and $\sigma_{xy} = \sigma_0 + \int dy \, \alpha(y)$, where $P_0$ and $\sigma_0$ are integration constants. Integrations of equations (64) and (67) with respect to $y$ and using no-flux conditions at the surfaces show that $v_y = v_y^p = 0$. It follows that $\sigma_{yy} = 0$ and $\partial_y P = 0$, implying that $\alpha$ is a constant. Furthermore, the no-flux condition at $y = \pm h$ leads to $j_y = 0$; as a result, $\overline{\mu}$ and, therefore, $\rho_p$ are constants.

Integrating the force balance equation, equation (65), twice along $x$ leads to the condition $\eta v_x + \eta_p v_x^p = \sigma_1 + \sigma_0 y + \alpha y^2/2$, where $\sigma_1$ is another integration constant and $\sigma_0 = 0$, by symmetry with respect to $y$. Using the definition $j_x = \rho_p(v_x^p - v_x)$ we obtain

$$\chi_1 \eta_p \frac{d^2 v_x^p}{dy^2} - \rho_p \left(1 + \frac{\eta_p}{\eta}\right) v_x^p = -\kappa \Delta\mu - \frac{\rho_p}{\eta}\left(\sigma_1 + \frac{\alpha}{2} y^2\right). \tag{68}$$

The boundary conditions at $y = -h$ and at $y = h$ specify how momentum is transferred between the surfaces and the gel. Assuming that the gel is linked to the surfaces by adhesion molecules that bind and detach, we introduce a surface friction coefficient for polymer, $\xi$, which implies

$$\sigma_{xy}^{el}(\pm h) = \mp \xi v_x^p(\pm h). \tag{69}$$

For simplicity we assume that the solvent can slip on the surface, leading to

$$\frac{dv_x}{dy}(\pm h) = 0. \tag{70}$$

The solution to equations (68)–(70) is

$$v_x^p(y) = -\frac{\alpha h}{\xi} + \frac{\alpha}{2(\eta + \eta_p)}(y^2 - h^2) + \frac{\alpha h}{q} \frac{\eta}{\eta_p(\eta + \eta_p)}\left[\frac{\cosh(qy) - \cosh(qh)}{\sinh(qh)}\right], \tag{71}$$

where $q^2 = \rho_p(\eta^{-1} + \eta_p^{-1})/\chi_1$. The permeation length $q^{-1}$ is related to the mesh size of the gel, $\lambda$, and to the persistence length, $L_p$, of the gel's filaments. Assuming that $\eta \ll \eta_p$ and taking $\chi_1 = \gamma/\rho_p$ (see section 2), we first obtain $q^2 = \rho_p^2/(\eta\gamma)$. Since $\gamma = \rho_p^2 D/\Pi$, where $D \approx k_B T/(\eta\lambda)$ is the cooperative filament diffusion constant, $k_B$ is Boltzmann's constant, $T$ is the temperature and $\Pi$ is the osmotic compression modulus, we find that $q^2 \approx \lambda\Pi/(k_B T)$.

For semiflexible polymers with $\lambda \ll L_p$, $\Pi \approx k_B T (\lambda/L_p)^{1/5}/\lambda^3$ [27, 28], and we finally obtain $q^{-1} \approx \lambda (\lambda/L_p)^{-1/10}$. Below, we consider separately the limits $qh \ll 1$ and $qh \gg 1$.

In the limit of small $qh$, where the solvent freely permeates the polymer network, we obtain from equation (71) Poiseuille flow with pressure gradient $\alpha$ for the polymer component:

$$v_x^p(y) \simeq \frac{\alpha}{2\eta_p}\left(y^2 - h^2\right) - \frac{\alpha h}{\xi}; \tag{72}$$

the barycentric velocity is then given by

$$v_x(y) \simeq -\frac{\kappa \Delta \mu}{\rho_p} - \frac{\alpha}{q^2}\left(\frac{1}{\eta} + \frac{1}{\eta_p}\right), \tag{73}$$

which implies a plug-flow profile of the solvent.

In the limit of large $qh$, in which the solvent moves with the polymer network, we find that

$$v_x^p(y) \simeq \frac{\alpha}{2(\eta + \eta_p)}\left(y^2 - h^2\right) - \frac{\alpha h}{\xi}, \tag{74}$$

$$v_x(y) \simeq -\frac{\kappa \Delta \mu}{\rho_p} + \frac{\alpha}{2(\eta + \eta_p)}\left(y^2 - h^2\right) - \frac{\alpha h}{\xi}. \tag{75}$$

The as yet unknown pressure gradient $\alpha$ is found from the condition of mechanical equilibrium at the two pistons, which move with a velocity $U = \Delta P/(2\xi_p)$, where $\xi_p$ is the piston friction coefficient and $\Delta P$ is the pressure drop across the piston. This implies that $\xi_p U = \alpha L/4$; in steady state $U = \frac{1}{2h}\int_{-h}^{h} v_x dy$. From this argument, we finally obtain the slab velocity

$$U = -\frac{\kappa \Delta \mu/\rho_p}{1 + 4\xi_p \chi_1/(L\rho_p)}, \quad \text{for } qh \ll 1, \tag{76}$$

$$U = -\frac{\kappa \Delta \mu/\rho_p}{1 + \dfrac{4\xi_p h}{L}\left(\dfrac{1}{\xi} + \dfrac{h}{3(\eta + \eta_p)}\right)}, \quad \text{for } qh \gg 1. \tag{77}$$

The two expressions are qualitatively similar and become identical for an infinitely long gel layer, in which the pressure gradient vanishes and forced permeation is absent.

This simple model demonstrates that a bulk treadmilling current generates center-of-mass gel motion in the opposite direction. The scenario that we have discussed could be realized experimentally by confining a film of actin gel between two surfaces. In the presence of ATP, filament treadmilling could give rise to center-of-mass motion of the film, as predicted by our model.

## 5. Deswelling of an active gel

Myosin motors interacting with actin filaments are known to actively contract the network [1], [29–31]. In this section, we describe the active deswelling of the polymer-rich phase of a phase-separated isotropic gel. We ignore polymerization and depolymerization in the following.

In an isotropic gel with no center-of-mass flow ($v_\alpha = 0$), the constitutive equations, equations (B.3)–(B.16), at steady state simplify to

$$j_\alpha = -\gamma \partial_\alpha \overline{\mu} + \frac{\overline{\chi}_1}{3}\partial_\alpha \sigma^{el}, \tag{78}$$

$$0 = -\overline{\chi}_1 \partial_\alpha^2 \overline{\mu} - \overline{\Gamma}\sigma^{\mathrm{el}} + \overline{\psi}\Delta\mu, \tag{79}$$

where $\overline{\chi}_1 \equiv \overline{\chi}_{1p}$ and the remaining notation is the same as in section 4.

We first consider equilibrium conditions, i.e. $\Delta\mu = 0$. In the uniform bulk of the network, we find that $\sigma^{\mathrm{el}} = 0$. We assume a gel with spherical symmetry. Setting $j_r = 0$ in equation (78) and integrating along the radial direction, $r$, we obtain the condition of chemical equilibrium between inside and outside of the polymer-rich region:

$$\overline{\mu} = \overline{\mu}_0, \tag{80}$$

where $\overline{\mu}_0$ is an integration constant.

Including ATP hydrolysis, $\Delta\mu > 0$, from equation (79) we find a spatially constant, steady-state value of $\sigma^{\mathrm{el}}$ in the polymer-rich region:

$$\sigma^{\mathrm{el}} = \frac{\overline{\psi}\Delta\mu}{\overline{\Gamma}}. \tag{81}$$

Integration of the force balance equation, $\partial_r(P - \sigma^{\mathrm{el}}) = 0$, gives

$$P - \sigma^{\mathrm{el}} = P_0, \tag{82}$$

where $P_0$ is an integration constant corresponding to the pressure in the solvent-rich phase. This shows that the hydrostatic pressure is the same inside and outside the gel.

Equation (81) gives the isotropic elastic stress due to motor activity. Integration of the relation $j_r = 0$ with respect to $r$ and the use of equation (81) leads to

$$\overline{\mu} - \overline{\mu}_0 = \frac{\overline{\chi}_1 \overline{\psi}\Delta\mu}{3\gamma\overline{\Gamma}}. \tag{83}$$

Equation (83) describes the chemical potential imbalance between the gel and solvent phases due to motor activity.

Experiments indicate that motors exert contractile forces on actin filaments [29–35]. This means that motors put the gel under tension, with $\sigma^{\mathrm{el}} > 0$. According to equation (81), contractile activity corresponds to $\overline{\psi} > 0$. For positive mobility $\overline{\chi}_1$, $\overline{\mu} - \overline{\mu}_0 > 0$ and the polymer volume fraction in the gel increases, given by $\delta\phi = K_0(\overline{\mu} - \overline{\mu}_0)$, where $K_0$ is the osmotic compressibility. This short example demonstrates the physics of active gel deswelling: motor activity generates an isotropic stress in the polymer network, which drives out the solvent, thus contracting the polymer component of the gel.

## 6. Discussion

Motivated by cytoskeletal dynamics in cells, we have developed a hydrodynamic theory describing active, polar, viscoelastic gels. A key result of this work is that by introducing the elastic deformation in the polymer component of the gel as a macroscopic variable, we obtained constitutive relations that describe the effects of permeation of the solvent driven by elastic stresses. In an active gel, these stresses can be generated by active processes, such as the action of motor molecules [1].

We first tested our approach by deriving constitutive relations for a passive, two-component, viscoelastic gel. Our generic approach based on Onsager theory leads to results that are close to those of [17, 18, 36], in which polymer solution dynamics are described by force balance equations for the solvent and polymer components. Our results show that the elastic

stress in the polymer network generates permeation flow. We developed generic constitutive relations and demonstrated that these relations contain the Maxwell model of viscoelasticity as a simple case, provided certain relations between the Onsager coefficients hold. In the long-time limit we found a description of the gel as two interpenetrating fluids, characterized by the viscosities $\eta$ and $\eta_p$ and by a frictional force between them proportional to their difference in velocities. This result provides a conceptual basis for the two-fluid models of the cytoskeleton introduced previously [11, 12]. We showed that to obtain this limit one needs to explicitly consider the elastic deformation in the polymer network of the gel.

Using the Onsager approach, we then developed constitutive equations for an active, polar gel. By introducing ATP hydrolysis, our theory allows a hydrodynamic description of active gels, such as the actin cytoskeleton, in which motor activity and filament treadmilling couple to polar order, viscoelasticity in the network and permeation. Our treatment of viscoelasticity and permeation generalizes an earlier active gel theory [9]. In [9], the network strain is not explicitly considered as a macroscopic variable. Instead, viscoelasticity is introduced by assuming a Maxwell model between the total stress and the center-of-mass strain rate. At long times, the theory of [9] describes the active gel as a polar fluid containing multiple diffusing components. There is no elastic stress-driven solvent permeation in this description.

We discussed two situations in which elastic stress-driven permeation plays an important role. In our model of self-propulsion of a gel film, a treadmilling current powered by ATP hydrolysis generates an elastic stress that squeezes the solvent through the polymer network and generates center-of-mass motion of the film. Note that the boundary conditions on the polymer and center-of-mass velocities at the surface are important. We discussed the simple situation where surface friction is transmitted solely to the polymer network; a different choice of boundary conditions gives similar results for the gel motion, with different elastic stress profiles and permeation flows. This model corresponds to an experimental situation in which an actin–myosin gel is confined *in vitro* between two surfaces. The physics contained in this model is also relevant to the behavior of the lamellipodium of crawling cells. There, active processes in the actin cytoskeleton and its adhesion to a substrate drive the flow of actin opposite to the direction of cell motion, and thus permeation of cytosol through the actin meshwork occurs [37]. We have identified the permeation length scale $q^{-1} \approx \lambda(\lambda/L_p)^{-1/10}$. For the actin cytoskeleton, assuming a mesh size $\lambda \simeq 50\,\text{nm}$ [38], a persistence length $L_p \simeq 10\,\mu\text{m}$ [39] and the lamellipodium thickness of $h \simeq 200\,\text{nm}$ [40], we find that $qh \sim 1$. This suggests that permeation of cytosol through the actin meshwork causes significant dissipation, which was neglected earlier [7]. In our discussion of active gel deswelling, a steady-state elastic stress in an isotropic gel results from the contractile action of motors and the remodeling of passive crosslinks. We considered a gel coexisting with an outside solvent and found that a chemical potential imbalance between the gel and the solvent is maintained by active processes. The resulting contraction of the gel is related to the contractile instability of active gels recently discussed in [41]. We note that the simplicity of our result hides the complex physics occurring at the interface of the polymer-rich and solvent-rich phases. Future work is required in order to investigate the role that interfacial dissipative phenomena play in active gel contraction.

The theory presented here is generic, and should be applicable to active systems containing a polar viscoelastic component embedded in a solvent. It thus provides a suitable framework for studying active biological gels such as the actin cytoskeleton in eukaryotic cells. In these cells, processes such as cell motility and cell division involve flows and reorientations of actin filaments, coupled to relative motion of the underlying cytosol.

## Acknowledgments

## Appendix A. Rotational invariance for a passive, viscoelastic gel

In this appendix, we show that the antisymmetric part of the total stress, $\sigma_{\alpha\beta}^{\text{tot}}$, is zero based on rotational invariance of the free energy of a passive, isotropic gel. Introducing the convected, co-rotational time derivative

$$\frac{\mathrm{D}u_{\alpha\beta}}{\mathrm{D}t} = \frac{\partial u_{\alpha\beta}}{\partial t} + v_\gamma \partial_\gamma u_{\alpha\beta} + \omega_{\alpha\gamma} u_{\gamma\beta} + \omega_{\beta\gamma} u_{\alpha\gamma}, \tag{A.1}$$

where $\omega_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta - \partial_\beta v_\alpha)$ is the vorticity tensor, equation (12) can be rewritten as

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \int \left[ -\sigma_{\alpha\beta}^{\text{s}} v_{\alpha\beta} + (\sigma_{\alpha\beta}^{\text{a}} - \sigma_{\alpha\gamma}^{\text{el}} u_{\beta\gamma} - \sigma_{\gamma\alpha}^{\text{el}} u_{\gamma\beta}) \omega_{\alpha\beta} + j_\alpha \partial_\alpha \overline{\mu} + \sigma_{\alpha\beta}^{\text{el}} \frac{\mathrm{D}u_{\alpha\beta}}{\mathrm{D}t} \right] \mathrm{d}V$$
$$+ \text{ surface terms}. \tag{A.2}$$

In equation (A.2) $v_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta + \partial_\beta v_\alpha)$ is the symmetric part of the velocity gradient tensor and $\sigma_{\alpha\beta}^{\text{s}}$ and $\sigma_{\alpha\beta}^{\text{a}}$ are the symmetric and antisymmetric parts of the deviatoric stress tensor

$$\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{\text{tot}} + \rho v_\alpha v_\beta + P \delta_{\alpha\beta}. \tag{A.3}$$

Recognizing that no change in free energy occurs if the field $u_{\alpha\beta}$ moves and rotates with the fluid in a purely rotational flow ($\mathrm{D}u_{\alpha\beta}/\mathrm{D}t = v_{\alpha\beta} = 0$), from equation (A.2) it follows that

$$\sigma_{\alpha\beta}^{\text{a}} = (\sigma_{\alpha\gamma}^{\text{el}} u_{\beta\gamma} + \sigma_{\gamma\alpha}^{\text{el}} u_{\gamma\beta})^{\text{a}}, \tag{A.4}$$

where $()^{\text{a}}$ denotes the antisymmetric part. Moreover, $-(\sigma_{\alpha\gamma}^{\text{el}} u_{\beta\gamma} + \sigma_{\gamma\alpha}^{\text{el}} u_{\gamma\beta}) \omega_{\alpha\beta}$ is the change in the free energy density, $f$, under an infinitesimal rotation $\mathrm{d}\theta_\alpha = \frac{1}{2}\epsilon_{\alpha\beta\gamma} \omega_{\beta\gamma} \mathrm{d}t$, which must also be zero. Therefore, $\sigma_{\alpha\beta}^{\text{tot,a}}$ is zero.

## Appendix B. Onsager relations for an active, polar, viscoelastic gel

In this appendix, we present the linear couplings between the fluxes and forces in equation (53). Noting that the molecular field $h_\alpha$ and the forces $\Delta\mu$ and $\Delta\mu_{\text{pm}}$ are even under time reversal, the dissipative parts of the fluxes are given by

$$\tilde{\sigma}_{\alpha\beta}^{\text{s,d}} = 2\eta \tilde{v}_{\alpha\beta}, \tag{B.1}$$

$$\sigma^{\text{s,d}} = 3\overline{\eta} v, \tag{B.2}$$

$$j_\alpha^{i,d} = -\sum_{j=p,m} \gamma_{ij} \partial_\alpha \overline{\mu}_j + \chi_i p_\beta \tilde{\sigma}_{\alpha\beta}^{\text{el}} + \chi_{1i} \partial_\beta \tilde{\sigma}_{\alpha\beta}^{\text{el}} + \frac{\overline{\chi_i}}{3} p_\alpha \sigma^{\text{el}} + \frac{\overline{\chi_{1i}}}{3} \partial_\alpha \sigma^{\text{el}}$$
$$+ \overline{\lambda}_i h_\alpha + \kappa_i p_\alpha \Delta\mu + \kappa_i' p_\alpha \Delta\mu_{\text{pm}}, \tag{B.3}$$

$$\frac{\mathrm{D}\tilde{u}^{\mathrm{d}}_{\alpha\beta}}{\mathrm{D}t} = \sum_{i=p,m} \frac{\chi_i}{2}\left(p_\alpha\partial_\beta\overline{\mu}_i + p_\beta\partial_\alpha\overline{\mu}_i - \frac{2}{3}p_\gamma\partial_\gamma\overline{\mu}_i\delta_{\alpha\beta}\right) - \sum_{i=p,m}\chi_{1i}\left(\partial_\alpha\partial_\beta\overline{\mu}_i - \frac{1}{3}\partial^2_\gamma\overline{\mu}_i\delta_{\alpha\beta}\right)$$

$$- \Gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \frac{\Gamma_1}{2}\left(\partial_\alpha\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\rho\gamma}\right) + \frac{\Gamma'_1}{3}\left(\partial_\alpha\partial_\beta\sigma^{\mathrm{el}} - \frac{1}{3}\partial^2_\gamma\sigma^{\mathrm{el}}\delta_{\alpha\beta}\right)$$

$$+ \frac{\omega_1}{2}\left(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma\delta_{\alpha\beta}\right) + \psi\tilde{q}_{\alpha\beta}\Delta\mu + \psi'\tilde{q}_{\alpha\beta}\Delta\mu_{\mathrm{pm}}, \tag{B.4}$$

$$\frac{\mathrm{d}u^{\mathrm{d}}}{\mathrm{d}t} = \sum_{i=p,m}\overline{\chi}_i p_\alpha\partial_\alpha\overline{\mu}_i - \sum_{i=p,m}\overline{\chi}_{1i}\partial^2_\alpha\overline{\mu} + \Gamma'_1\partial_\alpha\partial_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} - \overline{\Gamma}\sigma^{\mathrm{el}} + \frac{\overline{\Gamma}_1}{3}\partial^2_\alpha\sigma^{\mathrm{el}} + \overline{\omega}_1 p_\alpha h_\alpha$$

$$+ \overline{\psi}\Delta\mu + \overline{\psi}_1 p_\alpha p_\alpha\Delta\mu + \overline{\psi}'\Delta\mu_{\mathrm{pm}} + \overline{\psi}'_1 p_\alpha p_\alpha\Delta\mu_{\mathrm{pm}}, \tag{B.5}$$

$$\frac{\mathrm{D}p^{\mathrm{d}}_\alpha}{\mathrm{D}t} = -\sum_{i=p,m}\overline{\lambda}_i\partial_\alpha\overline{\mu}_i - \omega_1 p_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} - \frac{\overline{\omega}_1}{3}p_\alpha\sigma^{\mathrm{el}} + \frac{1}{\gamma_1}h_\alpha + \lambda_1 p_\alpha\Delta\mu + \lambda'_1 p_\alpha\Delta\mu_{\mathrm{pm}}, \tag{B.6}$$

$$r^{\mathrm{d}} = -\sum_{i=p,m}\kappa_i p_\alpha\partial_\alpha\overline{\mu}_i - \psi\tilde{q}_{\alpha\beta}\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} - \frac{\overline{\psi}}{3}\sigma^{\mathrm{el}} - \frac{\overline{\psi}_1}{3}p_\alpha p_\alpha\sigma^{\mathrm{el}} + \lambda_1 p_\alpha h_\alpha + \Lambda\Delta\mu + \Lambda'\Delta\mu_{\mathrm{pm}}, \tag{B.7}$$

$$s^{\mathrm{d}} = -\sum_{i=p,m}\kappa'_i p_\alpha\partial_\alpha\overline{\mu}_i - \psi'\tilde{q}_{\alpha\beta}\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} - \frac{\overline{\psi}'}{3}\sigma^{\mathrm{el}} - \frac{\overline{\psi}'_1}{3}p_\alpha p_\alpha\sigma^{\mathrm{el}} + \lambda'_1 p_\alpha h_\alpha + \Lambda'\Delta\mu + \Lambda_1\Delta\mu_{\mathrm{pm}}, \tag{B.8}$$

where $\tilde{q}_{\alpha\beta} = p_\alpha p_\beta - \frac{1}{3}p_\gamma p_\gamma\delta_{\alpha\beta}$. To keep the presentation simple, anisotropic viscosity and strain relaxation terms, such as $\alpha_1 p_\alpha p_\beta p_\gamma p_\rho\tilde{v}_{\gamma\rho}$, etc, have not been included. The reactive parts of the fluxes are

$$\tilde{\sigma}^{\mathrm{s,r}}_{\alpha\beta} = -\sum_{i=p,m}\frac{\epsilon_i}{2}\left(p_\alpha\partial_\beta\overline{\mu}_i + p_\beta\partial_\alpha\overline{\mu}_i - \frac{2}{3}p_\gamma\partial_\gamma\overline{\mu}_i\delta_{\alpha\beta}\right) + \sum_{i=p,m}\pi_{1i}\left(\partial_\alpha\partial_\beta\overline{\mu}_i - \frac{1}{3}\partial^2_\gamma\overline{\mu}_i\delta_{\alpha\beta}\right)$$

$$+ \tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \frac{\nu_2}{2}\left(\partial_\alpha\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{\sigma}^{\mathrm{el}}_{\rho\gamma}\right) + \frac{\overline{\nu}_2}{3}\left(\partial_\alpha\partial_\beta\sigma^{\mathrm{el}} - \frac{1}{3}\partial^2_\gamma\sigma^{\mathrm{el}}\delta_{\alpha\beta}\right)$$

$$+ \frac{\nu_1}{2}\left(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma\delta_{\alpha\beta}\right) + \zeta\tilde{q}_{\alpha\beta}\Delta\mu + \zeta_1\tilde{q}_{\alpha\beta}\Delta\mu_{\mathrm{pm}}, \tag{B.9}$$

$$\sigma^{\mathrm{s,r}} = \sum_{i=p,m}\overline{\pi}_{1i}\partial^2_\gamma\overline{\mu}_i - \sum_{i=p,m}3\overline{\epsilon}_i p_\gamma\partial_\gamma\overline{\mu}_i + \frac{\nu'_2}{3}\partial_\alpha\partial_\beta\tilde{\sigma}^{\mathrm{el}}_{\alpha\beta} + \sigma^{\mathrm{el}} + \frac{\overline{\nu}'_2}{3}\partial^2_\gamma\sigma^{\mathrm{el}}$$

$$+ 3\overline{\nu}_1 p_\gamma h_\gamma + 3\overline{\zeta}\Delta\mu + 3\zeta' p_\gamma p_\gamma\Delta\mu + 3\overline{\zeta}_1\Delta\mu_{\mathrm{pm}} + 3\zeta'_1 p_\gamma p_\gamma\Delta\mu_{\mathrm{pm}}, \tag{B.10}$$

$$j^{i,\mathrm{r}}_\alpha = -\epsilon_i p_\beta\tilde{v}_{\alpha\beta} - \pi_{1i}\partial_\beta\tilde{v}_{\alpha\beta} - \overline{\epsilon}_i p_\alpha v - \frac{\overline{\pi}_{1i}}{3}\partial_\alpha v, \tag{B.11}$$

$$\frac{\mathrm{D}\tilde{u}^r_{\alpha\beta}}{\mathrm{D}t} = \tilde{v}_{\alpha\beta} + \frac{\nu_2}{2}\left(\partial_\alpha\partial_\gamma\tilde{v}_{\beta\gamma} + \partial_\beta\partial_\gamma\tilde{v}_{\alpha\gamma} - \frac{2}{3}\delta_{\alpha\beta}\partial_\rho\partial_\gamma\tilde{v}_{\rho\gamma}\right) + \frac{\nu_2'}{3}\left(\partial_\alpha\partial_\beta v - \frac{1}{3}\partial_\gamma^2 v\delta_{\alpha\beta}\right), \tag{B.12}$$

$$\frac{\mathrm{d}u^r}{\mathrm{d}t} = \overline{\nu}_2\partial_\alpha\partial_\beta\tilde{v}_{\alpha\beta} + v + \frac{\overline{\nu}_2'}{3}\partial_\gamma^2 v, \tag{B.13}$$

$$\frac{\mathrm{D}p^r_\alpha}{\mathrm{D}t} = -\nu_1 p_\beta\tilde{v}_{\alpha\beta} - \overline{\nu}_1 p_\alpha v, \tag{B.14}$$

$$r^r = -\zeta\tilde{q}_{\alpha\beta}\tilde{v}_{\alpha\beta} - \zeta' p_\alpha p_\alpha v - \overline{\zeta}v, \tag{B.15}$$

$$s^r = -\zeta_1\tilde{q}_{\alpha\beta}\tilde{v}_{\alpha\beta} - \zeta_1' p_\alpha p_\alpha v - \overline{\zeta}_1 v. \tag{B.16}$$

The constitutive equations for the active, polar, three-component viscoelastic gel are obtained by adding together the dissipative and reactive parts of each flux, i.e. $\tilde{\sigma}^s_{\alpha\beta} = \tilde{\sigma}^{s,d}_{\alpha\beta} + \tilde{\sigma}^{s,r}_{\alpha\beta}$, etc. We note that we have kept higher derivative forces (such as $\partial_\alpha\partial_\beta\overline{\mu}_i$) in the constitutive relations for the fluxes introduced in section 1, but have not included them in the relations for $\mathrm{D}p_\alpha/\mathrm{D}t$, $r$ and $s$. We remark that the above couplings between $\sigma^s_{\alpha\beta}$ and $h_\alpha$ and between $\mathrm{D}p_\alpha/\mathrm{D}t$ and $v_{\alpha\beta}$ are the same as those occurring in the hydrodynamic theory of nematic liquid crystals [15]. The couplings between $\sigma^s_{\alpha\beta}$ and $\partial_\alpha\overline{\mu}_i$, between $\sigma^s_{\alpha\beta}$ and $\Delta\mu$, between $j_\alpha$ and $v_{\alpha\beta}$ and between $j_\alpha$ and $\Delta\mu$ were obtained earlier in the hydrodynamic description of multi-component, active, polar fluids [9].

## References

[1] Koenderink G H, Dogic Z, Nakamura F, Bendix P M, MacKintosh F C, Hartwig J H, Stossel T P and Weitz D A 2009 *Proc. Natl Acad. Sci. USA* **106** 15192
[2] Nédélec F J, Surrey T, Maggs A C and Leibler S 1997 *Nature* **389** 305
[3] Wottawah F, Schinkinger S, Lincoln B, Ananthakrishnan R, Romeyke M, Guck J and Käs J 2005 *Phys. Rev. Lett.* **94** 098103
[4] Kruse K and Jülicher F 2000 *Phys. Rev. Lett.* **85** 1778
[5] Liverpool T B and Marchetti M C 2003 *Phys. Rev. Lett.* **90** 138102
[6] Aronson I S and Tsimring L S 2005 *Phys. Rev.* E **71** 050901
[7] Kruse K, Joanny J-F, Jülicher F, Prost J and Sekimoto K 2005 *Eur. Phys. J.* E **16** 5
[8] Kruse K, Joanny J-F, Jülicher F, Prost J and Sekimoto K 2004 *Phys. Rev. Lett.* **92** 078101
[9] Joanny J-F, Jülicher F, Kruse K and Prost J 2007 *New J. Phys.* **9** 422
[10] Simha R A and Ramaswamy S 2002 *Phys. Rev. Lett.* **89** 058101
[11] Dembo M and Harlow F 1986 *Biophys. J.* **50** 109
[12] Alt W and Dembo M 1999 *Math. Biosci.* **156** 207
[13] Herant M, Heinrich V and Dembo M 2006 *J. Cell Sci.* **119** 1903
[14] de Groot S R and Mazur P 1984 *Non-Equilibrium Thermodynamics* (New York: Dover)
[15] de Gennes P-G and Prost J *The Physics of Liquid Crystals* 2nd edn (Oxford: Oxford University Press)
[16] Brand H R, Pleiner H and Renz W 1990 *J. Phys.* **51** 1065
[17] Milner S T 1995 *Phys. Rev.* E **48** 3674
[18] Ji H and Helfand E 1995 *Macromolecules* **28** 3869
[19] Aubert J H and Tirrell M 1980 *J. Chem. Phys.* **72** 2694
[20] Brochard F and De Gennes P-G 1977 *Macromolecules* **10** 1157
[21] Ahmadi A, Marchetti M C and Liverpool T B 2006 *Phys. Rev.* E **74** 061913
[22] Liverpool T B and Marchetti M C 2006 *Phys. Rev. Lett.* **97** 268101
[23] Wegner A 1976 *J. Mol. Biol.* **108** 139

**IOP** Institute of Physics ⟐ DEUTSCHE PHYSIKALISCHE GESELLSCHAFT

[24]  Pollard T D 1986 *J. Cell. Biol.* **103** 2747
[25]  Pollard T and Borisy G 2003 *Cell* **112** 453
[26]  Jülicher F and Prost J 2009 *Eur. Phys. J.* E **29** 27
[27]  Isambert H and Maggs A C 1996 *Macromolecules* **29** 1036
[28]  Kroy K and Frey E 1996 *Phys. Rev. Lett.* **77** 306
[29]  Szent-Györgyi A 1945 *Acta Physiol. Scand. (Suppl. XXV)* **9** 1
[30]  Spicer S S 1951 *J. Biol. Chem.* **190** 257
[31]  Bendix P M, Koenderink G H, Cuvelier D, Dogic Z, Koeleman B N, Brieher W M, Field C M, Mahadevan L
        and Weitz D A 2008 *Biophys. J.* **94** 3126
[32]  Weber A and Winicur S 1961 *J. Biol. Chem.* **236** 3198
[33]  Condeelis J S and Taylor D L 1997 *J. Cell Biol.* **74** 901
[34]  Pollard T D 1976 *J. Cell Biol.* **68** 579
[35]  Ebashi S, Ebashi F and Maruyama K 1964 *Nature* **203** 645
[36]  Doi M and Onuki A 1992 *J. Physique II* **2** 1631
[37]  Vallotton P 2005 *Mol. Biol. Cell* **16** 1223
[38]  Fleischer F, Ananthakrishnan R, Eckel S, Schmidt H, Kas J, Svitkina T M, Schmidt V and Beil M 2007
        *New J. Phys.* **9** 420
[39]  Isambert H, Venier P, Maggs A C, Fattoum A, Kassab R, Pantaloni D and Carlier M F 1995 *J. Biol. Chem.*
        **270** 11437
[40]  Anderson K I, Wang Y L and Small J V 1996 *J. Cell. Biol.* **134** 1209
[41]  Banerjee S M and Marchetti C 2011 *Soft Matter* **7** 463