Hydrodynamic theory for multi-component active polar gels

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Abstract. We develop a generic hydrodynamic theory of active fluids with several components. We take into account polar order and consider the case when one component is viscoelastic. Our theory is motivated by the cytoskeleton which is a network of elastic filaments that are coupled to active processes such as the action of motor proteins which can generate relative forces between filaments as they hydrolyze a fuel (ATP). In addition to the filament gel, the system is embedded in a solvent component and free monomers constitute a third component. We derive constitutive material equations for the combined system which include reactive and dissipative couplings as well as the chemical driving by ATP hydrolysis and a possible chiral symmetry of the filaments. As an illustration of these equations, we discuss an active liquid in a simple shear gradient.

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1. Introduction

The cytoskeleton is a network of filaments present in all eukaryotic cells [1, 2]. It is largely responsible for the mechanical and material properties of cells [3]. The most important filaments are actin filaments and microtubules which form by assembly of actin and tubulin proteins, respectively. In the presence of cross-linking proteins such as filamin, fascin or α-actinin the polymer network turns into a viscoelastic physical gel [4]. In the presence of filamin, for example, an actin network displays on short timescales smaller than 10–100 s a shear modulus of the order of 10^3–10^4 Pa. At long times, the gel behaves as a fluid with a viscosity of the order of 10^4–10^5 Pa s. A key property of actin filaments and microtubules is their structural polarity, which results from differences between the two ends of such a filament, commonly referred to as plus- and minus-end, respectively. On a larger scale, the filament network can therefore be structurally polar if filaments are oriented on an average along a certain direction.

In order to describe the dynamics and mechanics of the cytoskeleton in cells, it is essential to take into account the inherent activity of the system. This activity results, for example, from specialized motor proteins which specifically bind to filaments [2, 3]. Motor proteins transduce the chemical energy liberated during the hydrolysis of adenosine triphosphate (ATP) yielding adenosine diphosphate (ADP) and inorganic phosphate (P_i) to generate motion and forces along the filaments in a direction imposed by the filaments' polarity. Small aggregates of motors can form mobile cross-linkers in the gel which generate filament flows and active stresses in the system [5]. In a gel with net polarity, motors can generate net transport. Another important process driven by ATP hydrolysis is filament treadmilling. In this case, filaments turn over by being polymerized at the plus-end while depolymerizing at the minus-end.

In addition to transport by motor proteins, the cytoskeleton can induce transport in an indirect way by inducing flows in the cytosol, i.e. the solvent surrounding the filament network. Such a situation occurs, for example, at the leading edge of a cell crawling on a substrate [6, 7]. The front part of such a cell is called lamellipodium. It is a thin layer of cytoskeletal gel which protrudes forward by polymerizing and cross-linking new actin filaments. This process is promoted by proteins like Wiskott–Aldrich syndrome protein (WASP) located in

the cell membrane at the tip. The actin network density is controlled by the density of proteins which promote gel polymerization. Subsequently, though, the polymerized gel must reach its equilibrium swelling, which requires a flux of the cytosol with respect to the gel.

Physical descriptions of cytoskeletal dynamics have included different aspects of this dynamics. In microscopic descriptions of the dynamics of filaments induced by molecular motors, relative movements of filaments and solvent are described, but the solvent is assumed to be immobile [8]–[16]. This assumption is justified in situations where the cytoskeletal gel is close to a solid substrate. Macroscopic, phenomenological descriptions were either based on the same assumption or described the cytoskeletal gel together with the surrounding fluid as a single effective component [17]–[20]. In [18], we proposed a systematic approach to the dynamics of one-component active polar gels, based on the hydrodynamic theories of liquid crystals initiated by Martin *et al* [21]. It considers only macroscopic variables such as the stress or the rate of change of the polarization. The most general linear relations between fluxes and forces and consistent with the symmetries of the system are expressed. Both reactive and dissipative terms are considered and geometric nonlinearities and convective as well as co-rotational terms are included. Because of the general nature of this approach, this theory also captures the large length and long timescale dynamics of other systems with the same symmetries. An example is provided by suspensions of self-propelling bacteria, discussed for example in [22]. Here, the polarity results from the direction of motion of single bacteria. However, since the dominant interactions between bacteria are hydrodynamic and mediated by the solvent, a two-component phenomenological theory has been proposed for the long time and large length scale behavior [23, 24]. In comparison to our hydrodynamic theory of active polar gels, the theory developed by Ramaswamy and Simha takes viscoelastic effects into account via the relaxation time of the orientational order parameter, and does not consider explicitly the role of ATP hydrolysis.

In the present work, we extend our one-component hydrodynamic description of the cytoskeleton to that of a three-component fluid which distinguishes between the viscoelastic polar filament network, the surrounding solvent as well as the filament subunits dissolved in the solvent. In addition to permeation effects, this theory also allows us to account for the gel compressibility. These features are important for a physical description of filament polymerization and depolymerization in the bulk.

In the following section, we introduce the general framework by discussing a standard two-component fluid which is passive, viscous and non-polar. This illustrative example introduces the basic concepts and notations. In the same section, we also discuss the passive permeation of a liquid through an elastic gel. In section 3, we turn to the case of a three-component viscous polar fluid which is driven by inherent active processes and derive general constitutive equations. The following section discusses the shear flow of an active gel between two plates as a simple example. In section 5, we extend our theory to viscoelastic gels and consider the effects of filament chirality. The paper closes with a discussion and relates the present work to earlier descriptions.

2. Passive two-component fluids

We first consider a passive fluid consisting of two components to illustrate the general hydrodynamic approach and we follow closely the lines of arguments given by De Groot and Mazur [25]. In a two-component fluid, there are three conserved quantities, namely the masses

of the two components and the total momentum. The corresponding conservation laws for the masses are

$$\partial_t \rho_i + \nabla \cdot \rho_i \mathbf{v}_i = 0, \tag{1}$$

where ρ_i, $i = 1, 2$ are the respective mass densities of the two components and $\rho_i \mathbf{v}_i$ the corresponding currents. Momentum conservation can be written as

$$\partial_t \mathbf{g} - \nabla \cdot \sigma = \mathbf{f}_{\text{ext}}, \tag{2}$$

where $\mathbf{g}$ is the total momentum density, and where the momentum flux density is equal to the negative of the total stress tensor σ. The external force density is denoted by $\mathbf{f}_{\text{ext}}$. Introducing the total mass density $\rho = \rho_1 + \rho_2$ and the center-of-mass velocity $\mathbf{v} = (\rho_1 \mathbf{v}_1 + \rho_2 \mathbf{v}_2)/\rho$ of small volume elements, the total momentum density can be expressed as $\mathbf{g} = \rho \mathbf{v}$. Note that since molecular masses m_i are constant, conservation of mass is equivalent to conservation of particle numbers for each component. The continuity equations for the particle number densities n_i, where $\rho_i = m_i n_i$, are

$$\partial_t n_i + \nabla \cdot \mathbf{J}_i = 0 \tag{3}$$

with particle currents $\mathbf{J}_i = \rho_i \mathbf{v}_i / m_i$. It is helpful to split the particle currents into a convective part moving with the center-of-mass velocity $\mathbf{v}$ and a diffusive part associated to the relative flux between the two components:

$$\mathbf{J}_i = n_i \mathbf{v} + \frac{\mathbf{j}_i}{m_i}, \tag{4}$$

where $\mathbf{j}_1 = -\mathbf{j}_2 \equiv \mathbf{j}$.

In order to derive the constitutive equations, space is divided into volume elements that are small compared to the length scales of the spatial structures under study. The central assumption is that each volume element is in a state of local thermodynamic equilibrium. The total free energy of such a volume element can then be written as

$$F = \tfrac{1}{2} M v^2 + F_0(N_1, N_2, V). \tag{5}$$

The first term is the kinetic energy associated with the volume element that moves in space with center-of-mass velocity $\mathbf{v}$ and that contains particles of total mass M. The second term on the left-hand side describes the free energy of the system in the volume element, which depends on the numbers N_1 and N_2 of particles of the respective two components as well as on the volume V. The local particle number densities are $n_i = N_i/V$. As usual, the pressure in the volume element is given by $P = -\partial F_0/\partial V$ while the respective chemical potentials of the two components are given by $\mu_i = \partial F_0/\partial N_i$, $i = 1, 2$. These intensive quantities are related by the Gibbs–Duhem relation

$$\mathrm{d}P = n_1 \mathrm{d}\mu_1 + n_2 \mathrm{d}\mu_2. \tag{6}$$

The energy of the full system is obtained by summing over the contributions of all volume elements. In the continuum limit this yields

$$F = \int \mathrm{d}^3 \mathbf{r} \left\{ \tfrac{1}{2} \rho v^2 + f_0(n_1, n_2) \right\}, \tag{7}$$

where $f_0 = F_0/V$ is the free energy density that only depends on the densities of the two components.

We consider now the rate of change of the full free energy of the system

$$\frac{\mathrm{d}}{\mathrm{d}t}F = \int \mathrm{d}^3\mathbf{r} \left\{ \partial_t \tfrac{1}{2}\rho v^2 + \partial_t f_0 \right\} = \int \mathrm{d}^3\mathbf{r} \left\{ v_\alpha \partial_t g_\alpha - \tfrac{1}{2}v_\alpha^2 \partial_t \rho + \mu_1 \partial_t n_1 + \mu_2 \partial_t n_2 \right\}. \tag{8}$$

Using the conservation laws for the two components, this can be rearranged as

$$\frac{\mathrm{d}}{\mathrm{d}t}F = \int \mathrm{d}^3\mathbf{r} \left\{ v_\alpha \partial_\beta \sigma_{\alpha\beta} + \tfrac{1}{2}v_\alpha^2 \partial_\beta(\rho v_\beta) - \mu_1 \partial_\alpha \left[n_1 v_\alpha + \frac{j_\alpha}{m_1} \right] - \mu_2 \partial_\alpha \left[n_2 v_\alpha - \frac{j_\alpha}{m_1} \right] \right\}. \tag{9}$$

Partial integration, use of the Gibbs–Duhem relation and taking into account the symmetry of the stress tensor for an isotropic liquid finally yields

$$\frac{\mathrm{d}}{\mathrm{d}t}F = \int \mathrm{d}^3\mathbf{r} \left\{ -\sigma_{\alpha\beta}^{\mathrm{d}} v_{\alpha\beta} + j_\alpha \partial_\alpha \bar{\mu} \right\}, \tag{10}$$

where we have introduced the strain rate tensor $v_{\alpha\beta} = (\partial_\alpha v_\beta + \partial_\beta v_\alpha)/2$. The dissipative stress is defined as $\sigma_{\alpha\beta}^{\mathrm{d}} = \sigma_{\alpha\beta} + \rho v_\alpha v_\beta + P\delta_{\alpha\beta}$ and the relative chemical potential $\bar{\mu} = \frac{\mu_1}{m_1} - \frac{\mu_2}{m_2}$. The rate of change of the total free energy is thus a sum of products of generalized fluxes, σ and $\mathbf{j}$, and generalized forces, $v_{\alpha\beta}$ and $-\partial_\alpha \bar{\mu}$.

The constitutive equations of the fluid are obtained by expanding the fluxes as functions of the forces. At linear order we obtain

$$\sigma_{\alpha\beta}^{\mathrm{d}} = 2\eta \left[v_{\alpha\beta} - \tfrac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta} \right] + \bar{\eta} v_{\gamma\gamma}\delta_{\alpha\beta}, \tag{11}$$

$$j_\alpha = -\gamma \, \partial_\alpha \bar{\mu}. \tag{12}$$

The phenomenological parameters (the Onsager transport coefficients) η and $\bar{\eta}$ are, respectively, the shear and bulk viscosity and $\gamma > 0$ is a mobility. Note that there is no coupling to linear order between the two pairs of conjugate fluxes and forces. This is due to the different tensorial order of the fluxes and to the isotropy of the fluid. Furthermore, the dissipative stress tensor is symmetric. An asymmetric component would yield a surface term corresponding to an externally applied torque.

The mobility γ is related to the usual diffusion constant. Indeed, expressing $\bar{\mu}$ in terms of the mass fraction $\phi = \rho_1/(\rho_1 + \rho_2)$ and the pressure P we find

$$\partial_\alpha \bar{\mu} = \frac{\partial \bar{\mu}}{\partial \phi}\partial_\alpha \phi + \frac{\partial \bar{\mu}}{\partial P}\partial_\alpha P, \tag{13}$$

$$= \frac{\partial \bar{\mu}}{\partial \phi}\partial_\alpha \phi + \left(\frac{\omega_1}{m_1} - \frac{\omega_2}{m_2} \right)\partial_\alpha P, \tag{14}$$

where $\omega_i = \frac{\partial \mu_i}{\partial P}$ is the molecular partial volume of component i; we therefore obtain

$$j_\alpha = -\rho D \partial_\alpha \phi - \tilde{\gamma}\partial_\alpha P, \tag{15}$$

where $D = (\gamma/\rho)\partial \bar{\mu}/\partial \phi$ is the diffusion constant and $\tilde{\gamma} = [\omega_1/m_1 - \omega_2/m_2]\gamma$.

As mentioned in the introduction, the cytoskeleton is a physical gel with elastic behavior on short timescales. Its dynamics thus involves permeation by the cytosol, the fluid component of the cell interior in which the cytoskeleton gel is immersed. The permeation flow is driven by fluid pressure and by elastic forces present in the gel. We will now briefly consider the

hydrodynamics of a two-component system consisting of an elastic gel and a fluid. Let n_f denote the density of the fluid and x_α the displacement field of the gel component. The free energy of the system depends on the fluid density n_f and on the strain tensor $x_{\alpha\beta} = \frac{1}{2}(\partial_\alpha x_\beta + \partial_\beta x_\alpha)$. It can be written as

$$F = \int \mathrm{d}^3\mathbf{r} \left\{ \tfrac{1}{2}\rho v^2 + f(n_f, x_{\alpha\beta}) \right\}, \tag{16}$$

where v_α is again the center-of-mass velocity of the system. Using the same logic as described above, we find for the rate of change of the free energy

$$\frac{\mathrm{d}}{\mathrm{d}t}F = \int \mathrm{d}^3\mathbf{r} \left\{ -\sigma_{\alpha\beta}^d v_{\alpha\beta} - (u_\alpha - v_\alpha)\left(\partial_\beta \sigma_{\alpha\beta}^{el} + \frac{\phi_g}{\phi_f} \partial_\alpha P_f \right) \right\}, \tag{17}$$

where ϕ_g and ϕ_f are the mass fractions of fluid and gel, $\sigma_{\alpha\beta}^{el} = \delta F / \delta x_{\alpha\beta}$ is the elastic stress tensor of the gel and $u_\alpha = \dot{x}_\alpha$ is the gel velocity. The fluid pressure is defined as $P_f = n_f \mu_f - f$, where the fluid chemical potential is $\mu_f = \delta F / \delta n_f$. It is related to the total pressure by $P = P_f - \frac{1}{3}\sigma_{\gamma\gamma}^{el}$. The dissipative stress tensor given by $\sigma_{\alpha\beta}^d = \sigma_{\alpha\beta} - \sigma_{\alpha\beta}^{el} + P_f \delta_{\alpha\beta} + \rho v_\alpha v_\beta$. The force balance condition is

$$\partial_\beta(\sigma_{\alpha\beta}^d + \sigma_{\alpha\beta}^{el} - P_f \delta_{\alpha\beta}) = 0, \tag{18}$$

where inertial forces have been neglected. Identifying $(u_\alpha - v_\alpha)$ and $\sigma_{\alpha\beta}^d$ as fluxes and $v_{\alpha\beta}$ and $\partial_\beta(\sigma_{\alpha\beta}^{el} + \frac{\phi_g}{\phi_f}P_f\delta_{\alpha\beta})$ as forces, we write the constitutive equations as

$$\sigma_{\alpha\beta}^d = 2\eta_s(v_{\alpha\beta} - \tfrac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}) + \bar{\eta}_s v_{\gamma\gamma}\delta_{\alpha\beta}, \tag{19}$$

$$\lambda_p(u_\alpha - v_\alpha) = \partial_\beta\left(\sigma_{\alpha\beta}^{el} + \frac{\phi_g}{\phi_f}P_f\delta_{\alpha\beta} \right), \tag{20}$$

here η_s and $\bar{\eta}_s$ are the viscosities of the solvent and λ_p is a permeation coefficient. According to equation (20), permeation flows of the fluid through the gel are driven by elastic stresses and fluid pressure gradients. These are the classical equations obtained for gel permeation in a so-called two-fluid model [26].

3. Active polar three-component fluids

We now apply the approach of the previous section to derive the hydrodynamic equations for a fluid sharing essential features with the cytoskeleton. The fluid is composed of three components: the first component describes a polar polymer network with a number density n_0 of monomeric subunits. The second component represents the monomeric subunits with number density n_1, while the third component describes the solvent which has a number density n_2 of solvent molecules. Furthermore, we also take into account the effects of active processes driven by the hydrolysis of ATP. In a first step, we identify the conserved quantities and the broken continuous symmetries in the system and then calculate the change in free energy per unit time. We identify the fluxes and forces and express the phenomenological constitutive equations. This is done for a viscous response. The viscoelastic case is discussed later in section 5.

3.1. Conservation laws and order parameters

Key quantities which satisfy conservation laws are the particle densities n_0, n_1 and n_2 of the three components. They satisfy the conservation equations

$$\partial_t n_0 + \nabla \cdot \mathbf{J}_0 = S, \tag{21}$$

$$\partial_t n_1 + \nabla \cdot \mathbf{J}_1 = -S, \tag{22}$$

$$\partial_t n_2 + \nabla \cdot \mathbf{J}_2 = 0. \tag{23}$$

The source term S accounts for the polymerization and depolymerization reactions which lead to an exchange of monomers between the gel and the solvent. The particle currents $\mathbf{J}_i$ can be expressed by the center-of-mass velocity $\mathbf{v}$ and the diffusion currents $\mathbf{j}_0$ and $\mathbf{j}_1$:

$$\mathbf{J}_0 = n_0 \mathbf{v} + \frac{\mathbf{j}_0}{m_0}, \tag{24}$$

$$\mathbf{J}_1 = n_1 \mathbf{v} + \frac{\mathbf{j}_1}{m_1}, \tag{25}$$

$$\mathbf{J}_2 = n_2 \mathbf{v} - \frac{\mathbf{j}_0}{m_2} - \frac{\mathbf{j}_1}{m_2}. \tag{26}$$

Here, m_i, $i = 0, 1, 2$ are the respective molecular masses of monomers in the gel, dissociated monomers in solution as well as of the solvent molecules. The dynamics of the concentrations of ATP and its hydrolysis products (ADP and P_i) will not be considered explicitly. For simplicity, we assume them to be homogeneous in space and constant in time.

Due to the polar nature of the cytoskeletal filaments, the system can be locally anisotropic. This introduces a hierarchy of order parameters, the most important ones are polar and nematic order. They result from breaking a continuous symmetry (rotational invariance) and thus contribute to the hydrodynamic modes. Here, for simplicity, we consider only the polar order described by a vector field $\mathbf{p}$. Note that a generalization to nematic order and order parameters of higher order is straightforward.

3.2. Fluxes and forces

The free energy associated with a volume element depends on the numbers of the three kinds of particles contained in the element, but also on the polarization and the numbers of ATP, ADP and P_i. The field $\mathbf{h}$ conjugate to the local polarization is given by the functional derivative of the free energy density with respect to the local polarization as $h_\alpha = -\frac{\delta f}{\delta p_\alpha}$. The rate of change of the full free energy of the system can be written as

$$
\begin{aligned}
\frac{\mathrm{d}F}{\mathrm{d}t} &= \int \mathrm{d}^3\mathbf{r} \left\{ \partial_t \tfrac{1}{2} \rho v^2 + \sum_{i=0}^{2} \mu_i \partial_t n_i - h_\alpha \partial_t p_\alpha - r\Delta\mu \right\} \\
&= \int \mathrm{d}^3\mathbf{r} \left\{ -\left[\sigma_{\alpha\beta} - \rho v_\alpha v_\beta\right] \partial_\alpha v_\beta + \sum_{i=0}^{2} n_i v_\alpha \partial_\alpha \mu_i + j_{0,\alpha} \partial_\alpha \bar{\mu}_0 + j_{1,\alpha} \partial_\alpha \bar{\mu}_1 - (\partial_t p_\alpha) h_\alpha - r\Delta\mu \right\}.
\end{aligned}
\tag{27}
$$

Here, we have used the conservation equations and introduced the effective chemical potentials $\bar{\mu}_i = (\mu_i/m_i - \mu_2/m_2)$ for $i = 0, 1$. Furthermore, we have included the contribution of ATP

hydrolysis to the change in free energy given by the term $r\,\Delta\mu$. Here, r is the rate at which ATP molecules are hydrolyzed and $\Delta\mu = \mu_{\text{ATP}} - \mu_{\text{ADP}} - \mu_{\text{P}}$ is the difference in chemical potentials of ATP and the product molecules ADP and P_i, respectively.

The gradients of the chemical potentials can be eliminated by using the Gibbs–Duhem relation for a multi-component polar fluid

$$\partial_\beta \sigma_{\alpha\beta}^{\text{e}} = -\sum_{i=0}^{2} n_i \partial_\alpha \mu_i - h_\gamma \partial_\alpha p_\gamma. \tag{28}$$

It involves the Ericksen stress σ^{e} which in this system generalizes the pressure as the variable conjugate to the volume. It is given by

$$\sigma_{\alpha\beta}^{\text{e}} = \left(f - \sum_{i=0}^{2} \mu_i n_i \right) \delta_{\alpha\beta} - \frac{\partial f}{\partial(\partial_\beta p_\gamma)} \partial_\alpha p_\gamma. \tag{29}$$

This expression is derived in appendix A.

Using the Gibbs–Duhem relation (28) we can rewrite the rate of change of the free energy (27) as

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \int \mathrm{d}^3\mathbf{r} \left\{ -\sigma_{\alpha\beta}^{\text{s}} v_{\alpha\beta} + j_{0,\alpha} \partial_\alpha \bar\mu_0 + j_{1,\alpha} \partial_\alpha \bar\mu_1 - P_\alpha h_\alpha - r\,\Delta\mu \right\}. \tag{30}$$

Here, we have introduced the symmetric part of the deviatory stress

$$\sigma_{\alpha\beta}^{\text{s}} = \sigma_{\alpha\beta} + \rho v_\alpha v_\beta - \sigma_{\alpha\beta}^{\text{a}} - \sigma_{\alpha\beta}^{\text{e,s}}, \tag{31}$$

where $\sigma^{\text{e,s}}$ is the symmetric part of the Ericksen stress and σ^{a} the antisymmetric part of the total stress. The antisymmetric part of the stress tensor can be determined independently using angular momentum conservation. It is given by the torque density that is generated by the molecular field $\mathbf{h}$ on the polarization vector $\mathbf{p}$ [27]

$$\sigma_{\alpha\beta}^{\text{a}} = \left(p_\alpha h_\beta - p_\beta h_\alpha \right)/2. \tag{32}$$

In equation (30), $\mathbf{P}$ denotes the convected co-rotational derivative of the polarization vector

$$P_\alpha = \frac{\mathrm{D}}{\mathrm{D}t} p_\alpha = \partial_t p_\alpha + v_\beta \partial_\beta p_\alpha + \omega_{\alpha\beta} p_\beta, \tag{33}$$

where $\omega_{\alpha\beta} = (\partial_\alpha v_\beta - \partial_\beta v_\alpha)/2$ is the vorticity of the velocity field $\mathbf{v}$.

From expression (30) for the rate of change of the free energy change we find the following pairs of conjugated fluxes and forces:

$$
\begin{aligned}
&\text{flux} \leftrightarrow \text{force} \\
&\sigma_{\alpha\beta}^{\text{s}} \leftrightarrow v_{\alpha\beta} \\
&j_{i,\alpha} \leftrightarrow -\partial_\alpha \bar\mu_i \\
&P_\alpha \leftrightarrow h_\alpha \\
&r \leftrightarrow \Delta\mu.
\end{aligned} \tag{34}
$$

3.3. Phenomenological constitutive equations—viscous response

The phenomenological constitutive equations are obtained by expressing the fluxes to linear order in terms of the forces. In contrast to the case of two fluids discussed in the previous

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section, a coupling between quantities of different tensorial ranks is now possible, because the fluid can be polarized which locally leads to anisotropies characterized by the vector **p**. The corresponding coupling constants are tensors that are constructed using the polarization vector **p**. For simplicity, we neglect here the chirality of the filaments. For completeness, we give in appendix B the generalization of the constitutive equation for a polar chiral material. Note, that the generalized forces have different signatures under time inversion. While $v_{\alpha\beta}$ changes sign, the other forces do not. Therefore we distinguish between the components of the fluxes that show the same behavior under time inversion as the conjugated force, called dissipative, and those that show the opposite behavior called reactive. We denote the various components by superscripts 'd' and 'r', respectively.

The phenomenological equations for the dissipative currents can then be written as

$$\sigma_{\alpha\beta}^{\mathrm{s,d}} = 2\eta\left(v_{\alpha\beta} - \tfrac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}\right) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta}, \tag{35}$$

$$j_{i,\alpha}^{\mathrm{d}} = -\sum_{j=0}^{1}\gamma_{ij}\partial_{\alpha}\bar{\mu}_{j} + \bar{\lambda}_{i}h_{\alpha} + \kappa_{i}p_{\alpha}\Delta\mu, \tag{36}$$

$$P_{\alpha}^{\mathrm{d}} = -\bar{\lambda}_{i}\partial_{\alpha}\bar{\mu}_{i} + \frac{1}{\gamma_{1}}h_{\alpha} + \lambda_{1}p_{\alpha}\Delta\mu, \tag{37}$$

$$r^{\mathrm{d}} = -\sum_{i=0}^{1}\kappa_{i}p_{\alpha}\partial_{\alpha}\bar{\mu}_{i} + \lambda_{1}p_{\alpha}h_{\alpha} + \Lambda\Delta\mu. \tag{38}$$

These equations are very similar to the constitutive equations of the one component active polar gel that we have derived previously. In the absence of activity, $\Delta\mu = 0$, they include a non-diagonal mobility matrix γ_{ij} as in all multicomponent systems and a dissipative coupling between the currents and the polarization field (characterized by $\bar{\lambda}_{i}$). There are two types of active terms: an active orientational field $\lambda_{1}\Delta\mu$ which also exists for a single component active fluid, but also active currents $\kappa_{i}p_{\alpha}\Delta\mu$. These currents could for example result from interactions between motors walking on filaments and the surrounding fluids. Hydrodynamic couplings can induce such relative motions between the various components and the solvent as shown in [28].

The reactive terms in turn can be written as

$$\sigma_{\alpha\beta}^{\mathrm{s,r}} = -\sum_{j=0}^{1}\frac{\epsilon_{j}}{2}(p_{\alpha}\partial_{\beta}\bar{\mu}_{j} + p_{\beta}\partial_{\alpha}\bar{\mu}_{j}) - \sum_{j=0}^{1}\bar{\epsilon}_{j}p_{\gamma}\partial_{\gamma}\bar{\mu}_{j}\delta_{\alpha\beta} + \frac{\nu_{1}}{2}(p_{\alpha}h_{\beta} + p_{\beta}h_{\alpha})$$
$$+ \bar{\nu}_{1}p_{\gamma}h_{\gamma}\delta_{\alpha\beta} - \bar{\zeta}\delta_{\alpha\beta}\Delta\mu - \zeta p_{\alpha}p_{\beta}\Delta\mu - \zeta'p_{\gamma}p_{\gamma}\delta_{\alpha\beta}\Delta\mu, \tag{39}$$

$$j_{i,\alpha}^{\mathrm{r}} = -\epsilon_{i}p_{\beta}v_{\alpha\beta} - \bar{\epsilon}_{i}p_{\alpha}v_{\beta\beta}, \tag{40}$$

$$P_{\alpha}^{\mathrm{r}} = -\nu_{1}p_{\beta}v_{\alpha\beta} - \bar{\nu}_{1}p_{\alpha}v_{\beta\beta}, \tag{41}$$

$$r^{\mathrm{r}} = \zeta p_{\alpha}p_{\beta}v_{\alpha\beta} + \bar{\zeta}v_{\alpha\alpha} + \zeta'p_{\alpha}p_{\alpha}v_{\beta\beta}. \tag{42}$$

The only active term is the active stress characterized by the activity coefficient ζ and there is no new active contribution compared to a one component polar active fluid. The main new passive effect is the coupling between the composition gradient and the mechanical variables characterized by the transport coefficients ϵ_{i}.
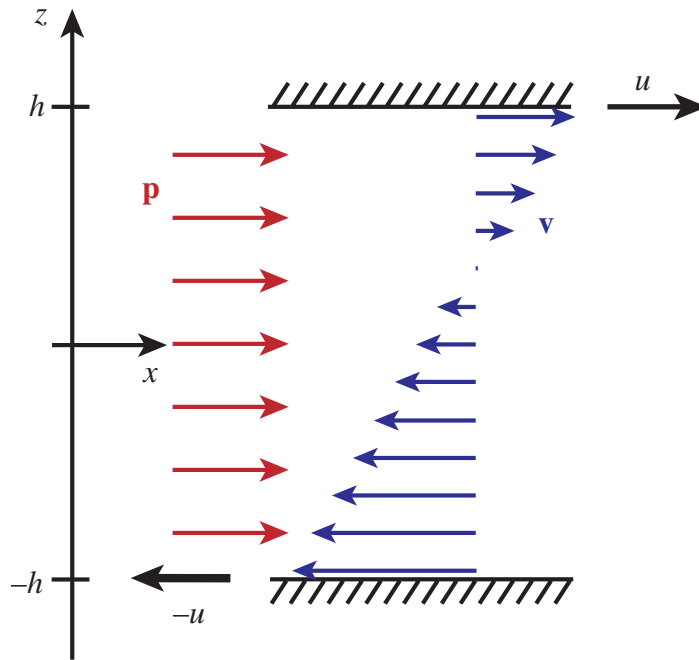
Figure 1. Illustration of the shear flow geometry and the corresponding solution for the center-of-mass velocity v. The polarization p points into the x-direction, the upper plate moves at velocity u, the lower at velocity $-u$ in the x-direction.

4. Shear flow

As an illustration of the multicomponent active gel equations, we consider a flow confined between two parallel plates, see figure 1. The plates are placed at $z = -h$ and $z = h$ and are sheared with a relative velocity $2u$ in the x-direction. For the sake of simplicity, we do not consider filament polymerization and depolymerization and we do not consider explicitly the free actin monomers which are included in an effective solvent. The polarization vector is assumed to be fixed with $p_x = 1$ and $p_z = 0$. The fluid is incompressible, such that $\partial_x v_x + \partial_z v_z = 0$, where $\mathbf{v}$ is the center-of-mass velocity. The system is invariant with respect to translations in the x-direction and $v_z = 0$. In the following v_x is denoted by v.

According to equations (31), (35) and (39), the transverse component of the stress tensor σ can be written as

$$\sigma_{xz} = \eta \frac{\mathrm{d}}{\mathrm{d}z} v - \frac{\epsilon}{2} \frac{\mathrm{d}}{\mathrm{d}z} \bar{\mu}. \tag{43}$$

In the expression for σ_{xz}, $\bar{\mu}$ denotes the exchange chemical potential given by $\bar{\mu} = (\mu_g/m_g - \mu_s/m_s)$, where the subscripts 'g' and 's' refer to quantities related to the gel and the solvent, respectively. In a two-component fluid, there is only one independent particle flux and we omit here the subscript 'i' corresponding to the various independent fluxes $\mathbf{j}_i$. The components of the diffusive current $\mathbf{j}$ are given by equations (36) and (40).

$$j_x = \kappa \, \Delta \mu, \tag{44}$$

$$j_z = -\gamma \frac{\mathrm{d}}{\mathrm{d}z} \bar{\mu} - \frac{\epsilon}{2} \frac{\mathrm{d}}{\mathrm{d}z} v. \tag{45}$$

We now use the conservation laws for the particle numbers and the momentum to obtain the flow field in the fluid. In a steady state, the diffusive current in the z-direction must be constant. Since filaments are assumed not to polymerize or depolymerize in the system, the conservation of the gel mass implies $j_z = 0$, so that

$$\bar{\mu} + \frac{\epsilon}{2\gamma} v = \mu_0, \tag{46}$$

where μ_0 is an integration constant.

Cytoskeletal dynamics occurs at low Reynolds numbers and we therefore neglect in the following inertial terms. Consequently, momentum conservation reduces to the force balance $\partial_\beta \sigma_{\alpha\beta} = 0$. The force balance in the x-direction implies

$$\eta v(z) - \epsilon \bar{\mu}/2 = \sigma_0 z + b \tag{47}$$

with two integration constants σ_0 and b. The constants σ_0 and b are fixed by the boundary conditions on the shear stress σ_{xz} at the plates, $z = \pm h$. Several slip conditions are possible. We consider here the case where the stress is imposed by the friction of the gel at the plates. In the reference system, where the upper plate moves with velocity u and the lower plate with a velocity $-u$, we get

$$\sigma_{xz}(h) = -\xi(v_g(h) - u), \tag{48}$$

$$\sigma_{xz}(-h) = -\xi(v_g(-h) + u). \tag{49}$$

We have defined here the gel velocity v_g from the number current $\mathbf{J}_g = n_g \mathbf{v}_g$ so that $\mathbf{v}_g = \mathbf{v} + \mathbf{j}/\rho_g$. As $\sigma_{xz}(h) = -\sigma_{xz}(-h)$, we obtain for the gel velocity at the upper and lower plates $v_g(-h) = -v_g(h)$. Hence, the center-of-mass velocity obeys $v(-h) = -v(h) - 2\kappa \Delta \mu/\rho_g$. This allows for the calculation of the two integration constants. The center-of-mass velocity then reads

$$v(z) = \frac{\xi u}{\xi h + \eta + \epsilon^2/(4\gamma)} z - \frac{\kappa}{\rho_g} \Delta \mu. \tag{50}$$

The exchange potential is

$$\bar{\mu} = \mu_0 + \frac{\epsilon \kappa \Delta \mu}{2\gamma \rho_g} - \frac{\epsilon}{2\gamma} \frac{\xi u}{\xi h + \eta + \epsilon^2/(4\gamma)} z. \tag{51}$$

For a passive non-polar system ($\Delta \mu = 0$, $\epsilon = 0$), we find the classical results for a sheared incompressible homogeneous fluid. The exchange chemical potential $\bar{\mu}$ is constant and therefore the mass fraction ϕ is constant. There is no macroscopic flux of liquid. If, however, the system is active, $\Delta \mu \neq 0$, a macroscopic flux of liquid is generated. Due to the actin polarity there is also a gradient of exchange potential and therefore a gradient of mass fraction. The integration constant μ_0 is fixed by the average mass fraction in the slab ϕ_0. If we assume that the exchange potential varies linearly with the mass fraction, $\mu_0 + \frac{\epsilon \kappa \Delta \mu}{2\gamma \rho_g} = \bar{\mu}(\phi_0)$ and $\phi(z = 0) = \phi_0$. The mass fraction $\phi - \phi_0$ is antisymmetric around the center of the liquid slab $z = 0$.

5. Multicomponent chiral viscoelastic gels

As was mentioned in the introduction, the cytoskeleton shows viscoelastic behavior. The filaments are passively and actively cross-linked yielding elastic behavior on timescales that are short compared to the average life-time of a cross-link, while it exhibits viscous behavior on

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longer time-scales. The hydrodynamic theory of a multicomponent active polar fluid presented in the previous section, neglects the elastic behavior on short timescales.

We will capture viscoelastic effects by making use of the Maxwell model for viscoelastic materials with an elastic response on short and a viscous response on long timescales. It is given by the linear constitutive equation

$$\left(1 + \tau \frac{D}{Dt}\right) \sigma_{\alpha\beta} = 2\eta \left(v_{\alpha\beta} - \tfrac{1}{3}\delta_{\alpha\beta}v_{\gamma\gamma}\right) + \bar{\eta}\delta_{\alpha\beta}v_{\gamma\gamma}, \tag{52}$$

here, $\tau = E/\eta$, is the viscoelastic relaxation time and E denotes the elastic modulus observed on short timescales. We use the simplifying assumption of only one relaxation time, but note that there is experimental evidence for a power law distribution of relaxation times in the cytoskeleton [29, 30]. The Maxwell model can be rewritten as Onsager relations for the reactive and dissipative component of the stress, with $\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{d} + \sigma_{\alpha\beta}^{r}$ and the relations:

$$\left(1 - \tau^2 \frac{D^2}{Dt^2}\right) \sigma_{\alpha\beta}^{d} = 2\eta \left(v_{\alpha\beta} - \tfrac{1}{3}\delta_{\alpha\beta}v_{\gamma\gamma}\right) + \bar{\eta}\delta_{\alpha\beta}v_{\gamma\gamma}, \tag{53}$$

$$\sigma_{\alpha\beta}^{r} = -\tau \frac{D}{Dt}\sigma_{\alpha\beta}^{d}. \tag{54}$$

Based on this Maxwell model, we can generalize the expansion of the dissipative fluxes given by equations (35)–(38) and of the reactive fluxes given by equations (39)–(42). These generalized relations are presented in appendix B in equations (B.1)–(B.8). As in [19], we have assumed here that there is a single relaxation time for the stress relaxation and for the rate of change of the polarization. The resulting constitutive material equations for a viscoelastic active gel are presented in equations (B.9)–(B.12). Note that in the limits of long times, these equations simplify and become those discussed in the previous section. In the limit of short times, they contain the elastic properties of the Maxwell model.

However, for short times we do not recover the full physics of permeation of an elastic gel immersed in a fluid discussed in section 2. In order to capture this physics described by equation (20), we modify equation (B.10) by assuming that there is a single relaxation time. The correct asymptotic behaviors in both the liquid and the solid limit are found if the currents $\mathbf{j}_i$ satisfy

$$\left(1 - \tau^2 \frac{D^2}{Dt^2}\right) \left(j_{i,\alpha} + \sum_{j=0}^{1} \gamma_{ij}\partial_\alpha\bar{\mu}_j - \bar{\lambda}_i h_\alpha - \kappa_i p_\alpha \Delta\mu + \epsilon_i p_\beta v_{\alpha\beta} + \bar{\epsilon}_i p_\alpha v_{\beta\beta}\right)$$
$$= -\frac{\tau^2 \phi_g}{\lambda_p} \frac{D}{Dt}\partial_\beta \left(2\eta \left(v_{\alpha\beta} - \tfrac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}\right) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta}\right). \tag{55}$$

This equation introduces new crossed terms between the diffusive currents and the stress. Note that the constitutive equation for the stress should also be modified accordingly in order to satisfy the Onsager relations.

Actin filaments and microtubules are helical objects. This symmetry allows for chiral terms which can be included in the theory as additional terms in the constitutive equations which involve the totally antisymmetric tensor $\epsilon_{\alpha\beta\gamma}$. The chiral terms permitted to linear order in the forces are included in the constitutive relations (B.1)–(B.12). Note that all the chiral terms have a passive character.

6. Discussion

Motivated by the description of the actin cytoskeleton, we have presented in this paper a hydrodynamic theory of three component active fluids, one of which is active and polar and represents the filamentous actin phase, while the other two represent monomeric actin and the cytosol (the solvent). Built on conservation laws and symmetry relations, the theory captures the essential features of the cytoskeleton and allows to address physical aspects of cytoskeletal dynamics. The description extends our earlier work [18], where the cytoskeleton was approximated by a one component active polar gel. This description thus ignored the relative permeation motion of the cytosol through the network of actin filaments.

Although in some cases this permeation motion does not seem to be essential it is clearly important for example for the motion of a lamellipodium discussed in [31]. In the front part of the lamellipodium, the actin network displays retrograde motion into the direction opposite to that of the lamellipodium leading edge. The cytosolic flow, though, follows the leading edge, implying a permeation flow through the actin gel. As the active gel is in general dilute, the center-of-mass velocity is then in the direction of the cytosol velocity and thus in the direction of the global lamellipodium motion. Note that in the one component description of [18] the cytosol is entirely ignored and the center-of-mass velocity coincides with the actin velocity.

In addition to the actin gel and the cytosol, our description explicitly accounts for the density of actin monomers. This is relevant for the description of processes, in which the effects of actin polymerization and depolymerization play an important role. The cytosol still contains other components, which in some situations should be described explicitly. This holds notably for molecular motors, as the active stress generated by these proteins depends on their density. In fact, two concentrations of motors attached and not attached to actin filaments, respectively, should be considered. However, in the linear theory, which we consider here, the active stress $\zeta \Delta \mu$ remains constant. Therefore, to linear order, it is appropriate not to consider the motor concentration explicitly. This is no longer true in nonlinear theories, where the dependence of the active stress on the motor density might lead to interesting effects.

Another important difference between the one component active gel theory and the multicomponent theory of this paper is the role played by polarity. The one component theory of [18] is in fact not a polar theory. All the equations are invariant by change of the polarization vector $\mathbf{p}$ to $-\mathbf{p}$. It can therefore be applied also to systems with a nematic symmetry. The multicomponent theory that we propose is indeed polar. Both the dissipative and the reactive components of the diffusive currents j_i contain polar terms proportional to the polarization vector p_α. The role of these polar terms is well illustrated by the example of a two-component active liquid under shear treated in section 4. The passive reactive component of the diffusive current proportional to ϵ drives the composition gradient in the fluid layer (the mass fraction is not constant) and the active dissipative current creates the global flux of the total fluid along the slab. Note that the boundary conditions are very important here. If we choose different boundary conditions with the tangential stress on the surface being proportional to the center-of-mass velocity and not to the gel velocity, there is no fluid flux (the average center-of-mass velocity over the thickness vanishes) but there is a flux of the active gel in one direction and an opposite flux of the other fluid in the other direction.

Finally, it is appropriate to compare our active gel theory to other active theories proposed for very different systems. In [23, 24], Simha *et al* propose a generalized hydrodynamic theory for suspensions of self-propelled particles. Even though they do not use a systematic derivation

of the constitutive equations based on Onsager relations, their theory to linear order and for large wavelengths is equivalent to the equations that we propose here.

Continuum equations were proposed by Toner and Tu [32] to describe flocks of birds by a one-component theory not including the hydrodynamics of the solvent. There, the dynamic equations are expanded with respect to a non-equilibrium reference state. The differences between the physical systems considered in these works and the similarity between macroscopic descriptions of them emphasize the generic character of our equations.

Appendix A. The Ericksen stress tensor

In the following, we derive the expression for the Ericksen stress σ^{e} for a multi-component polar fluid as well as the corresponding Gibbs–Duhem relation. The free energy density f of a three component active gel depends on the number densities n_i of the N components, $i = 1, \ldots, N$ as well as on the polarization vector $\mathbf{p}$ and its derivatives $\partial_\alpha p_\beta$. If the volume of the system is changed by an amount δV, the free energy changes as

$$
\begin{aligned}
\delta F &= \int_{V+\delta V} \mathrm{d}^3\mathbf{r}\, f(\{n_i + \delta n_i\}, p_\alpha + \delta p_\alpha, \partial_\alpha p_\beta + \delta \partial_\alpha p_\beta) - \int_V \mathrm{d}^3\mathbf{r}\, f(\{n_i\}, p_\alpha, \partial_\alpha p_\beta) \\
&= \int_{\delta V} \mathrm{d}^3\mathbf{r}\, f(\{n_i\}, p_\alpha, \partial_\alpha p_\beta) + \int_V \mathrm{d}^3\mathbf{r} \left[\sum_i \mu_i \delta n_i + \frac{\partial f}{\partial p_\alpha} \delta p_\alpha + \frac{\partial f}{\partial(\partial_\beta p_\alpha)} \delta \partial_\beta p_\alpha \right] \\
&= \int_{\delta V} \mathrm{d}^3\mathbf{r}\, f(\{n_i\}, p_\alpha, \partial_\alpha p_\beta) + \int_V \mathrm{d}^3\mathbf{r} \left[\sum_i \mu_i \delta n_i - h_\alpha \delta p_\alpha \right] + \int_S \mathrm{d}S_\beta \frac{\partial f}{\partial(\partial_\beta p_\alpha)} \delta p_\alpha \\
&= -\int_V \mathrm{d}^3\mathbf{r}\, h_\alpha \delta p_\alpha + \int_S \mathrm{d}S_\beta\, u_\beta \left[f - \sum_i \mu_i n_i \right] - \int_S \mathrm{d}S_\beta \frac{\partial f}{\partial(\partial_\beta p_\alpha)} u_\gamma (\partial_\gamma p_\alpha). \quad \text{(A.1)}
\end{aligned}
$$

Here, we have made use of $\delta p_\alpha = -(\partial_\beta p_\alpha) u_\beta$, where $\mathbf{u}$ is the change from V to $V + \delta V$ in the direction normal of the original volume V, and

$$
\int_{V+\delta V} \mathrm{d}^3\mathbf{r}\, (n_i + \delta n_i) - \int_V \mathrm{d}^3\mathbf{r}\, n_i = \int_V \mathrm{d}^3\mathbf{r}\, \delta n_i - \int_{\delta V} \mathrm{d}^3\mathbf{r}\, n_i. \quad \text{(A.2)}
$$

Furthermore, we have introduced the conjugated field $\mathbf{h}$ to the polarization $\mathbf{p}$ and the chemical potentials $\mu_i = \partial f / \partial n_i$ of the different components $i = 1, \ldots, N$. From equation (A.1), we deduce the expression of the Ericksen stress tensor σ^{e}

$$
\sigma^{\mathrm{e}}_{\alpha\beta} = \left(f - \sum_i \mu_i n_i \right) \delta_{\alpha\beta} - \frac{\partial f}{\partial(\partial_\beta p_\gamma)} \partial_\alpha p_\gamma. \quad \text{(A.3)}
$$

Note that we include here the pressure (given by the first term in equation (A.3)) in the Ericksen stress tensor.

In order to derive the corresponding Gibbs–Duhem relation, we first calculate the total differential of the free energy

$$
\mathrm{d}f = -h_\alpha \mathrm{d}p_\alpha + \sum_i \mu_i \mathrm{d}n_i + \partial_\alpha \frac{\partial f}{\partial(\partial_\alpha p_\beta)} \mathrm{d}p_\beta. \quad \text{(A.4)}
$$

Using this result we get for the total differential of the Ericksen stress

$$
d\sigma^{e}_{\alpha\beta} = \left[-h_\gamma dp_\gamma + \sum_i \mu_i dn_i \right]\delta_{\alpha\beta} - \sum_i \left[\mu_i dn_i + n_i d\mu_i\right]\delta_{\alpha\beta} - \frac{\partial f}{\partial(\partial_\beta p_\gamma)}\partial_\alpha dp_\gamma
$$
$$
- (\partial_\alpha p_\gamma)d\frac{\partial f}{\partial(\partial_\beta p_\gamma)} + \partial_\gamma \frac{\partial f}{\partial(\partial_\gamma p_\delta)}dp_\gamma\delta_{\alpha\beta}, \tag{A.5}
$$

and therefore

$$
\partial_\beta\sigma^{e}_{\alpha\beta} = -\sum_i n_i\partial_\alpha\mu_i - h_\gamma\partial_\alpha p_\gamma - \frac{\partial f}{\partial(\partial_\beta p_\gamma)}\partial_\alpha\partial_\beta p_\gamma - (\partial_\alpha p_\gamma)\partial_\beta\frac{\partial f}{\partial(\partial_\beta p_\gamma)} + \partial_\gamma\frac{\partial f}{\partial(\partial_\gamma p_\delta)}\partial_\alpha p_\delta
$$
$$
= -\sum_i n_i\partial_\alpha\mu_i - h_\gamma\partial_\alpha p_\gamma, \tag{A.6}
$$

which is the sought-for Gibbs–Duhem relation (28).

Appendix B. Phenomenological equations—viscoelastic response and chirality

In the following, we provide the full expressions of the reactive and dissipative fluxes, including the viscoelastic properties and also all chiral terms permitted by symmetry. The full constitutive relations for the reactive fluxes read:

$$
\sigma^{s,r}_{\alpha\beta} = -\tau\left[\frac{D}{Dt}\sigma^{s,d}_{\alpha\beta} + A_{\alpha\beta}\right] - \bar{\zeta}\delta_{\alpha\beta}\Delta\mu - \zeta p_\alpha p_\beta\Delta\mu - \zeta' p_\gamma p_\gamma\delta_{\alpha\beta}\Delta\mu + \frac{\nu_1}{2}(p_\alpha h_\beta + p_\beta h_\alpha)
$$
$$
+ \bar{\nu}_1 p_\gamma h_\gamma\delta_{\alpha\beta} + \frac{\Pi_1}{2}\left(\epsilon_{\alpha\gamma\delta}p_\beta p_\gamma h_\delta + \epsilon_{\beta\gamma\delta}p_\alpha p_\gamma h_\delta\right) - \sum_{j=0}^{1}\frac{\epsilon_j}{2}(p_\alpha\partial_\beta\bar{\mu}_j + p_\beta\partial_\alpha\bar{\mu}_j)
$$
$$
- \sum_{j=0}^{1}\bar{\epsilon}_j p_\gamma\partial_\gamma\bar{\mu}_j\delta_{\alpha\beta} + \sum_{j=0}^{1}\frac{\Pi_2^j}{2}\left(\epsilon_{\alpha\gamma\delta}p_\beta p_\gamma\partial_\delta\bar{\mu}_j + \epsilon_{\beta\gamma\delta}p_\alpha p_\gamma\partial_\delta\bar{\mu}_j\right), \tag{B.1}
$$

$$
j^{r}_{i,\alpha} = -\epsilon_i p_\beta v_{\alpha\beta} - \bar{\epsilon}_i p_\alpha v_{\beta\beta} - \Pi_2^i\epsilon_{\beta\gamma\alpha}v_{\beta\delta}p_\gamma p_\delta, \tag{B.2}
$$

$$
\frac{D}{Dt}p^{r}_\alpha = \tau\frac{D}{Dt}\frac{h_\alpha}{\gamma_1} - \nu_1 p_\beta v_{\alpha\beta} - \bar{\nu}_1 p_\alpha v_{\beta\beta} - \Pi_1\epsilon_{\beta\gamma\alpha}v_{\beta\delta}p_\gamma p_\delta, \tag{B.3}
$$

$$
r^{r} = \zeta p_\alpha p_\beta v_{\alpha\beta} + \bar{\zeta}v_{\alpha\alpha} + \zeta' p_\alpha p_\alpha v_{\beta\beta}. \tag{B.4}
$$

Here, we have introduced the coefficients Π_1 and Π_2 of chiral terms. These terms involve the totally antisymmetric tensor $\epsilon_{\alpha\beta\gamma}$ with $\epsilon_{123} = 1$. The tensor

$$
A_{\alpha\beta} = \nu_2(v_{\alpha\gamma}\sigma^{s,d}_{\gamma\beta} + \sigma^{s,d}_{\alpha\gamma}v_{\gamma\beta}) + \nu_3 v_{\gamma\gamma}\sigma^{s,d}_{\alpha\beta} + \nu_4 v_{\gamma\gamma}\sigma^{s,d}_{\delta\delta}\delta_{\alpha\beta} + \nu_5\sigma^{s,d}_{\gamma\gamma}v_{\alpha\beta} + \nu_6 v_{\gamma\delta}\sigma^{s,d}_{\delta\gamma}\delta_{\alpha\beta}
$$

contains nonlinear reactive terms to lowest order, resulting from the geometry of the flow field with corresponding phenomenological coefficients ν_i. The full constitutive relations for the dissipative fluxes are given by:

$$
\left(1 - \tau^2\frac{D^2}{Dt^2}\right)\sigma^{s,d}_{\alpha\beta} = 2\eta\left(v_{\alpha\beta} - \tfrac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}\right) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta} \tag{B.5}
$$

$$j_{i,\alpha}^{\mathrm{d}} = -\sum_{j=0}^{1} \gamma_{ij}\partial_\alpha\bar{\mu}_j + \bar{\lambda}_i h_\alpha + \kappa_i p_\alpha \Delta\mu + \Pi_3^i \epsilon_{\alpha\beta\gamma} p_\beta h_\gamma \tag{B.6}$$

$$\frac{\mathrm{D}}{\mathrm{D}t} p_\alpha^{\mathrm{d}} = \frac{h_\alpha}{\gamma_1} + \lambda_1 p_\alpha \Delta\mu - \bar{\lambda}_i \partial_\alpha\bar{\mu}_i - \sum_{j=0}^{1} \Pi_3^j \epsilon_{\alpha\beta\gamma} p_\beta \partial_\gamma\bar{\mu}_j \tag{B.7}$$

$$r^{\mathrm{d}} = -\sum_{i=0}^{1} \kappa_i p_\alpha \partial_\alpha\bar{\mu}_i + \lambda_1 p_\alpha h_\alpha + \Lambda\Delta\mu, \tag{B.8}$$

where Π_3 denotes a coefficient of chiral terms. The full dynamic equations then read:

$$2\eta\left(v_{\alpha\beta} - \tfrac{1}{3} v_{\gamma\gamma}\delta_{\alpha\beta}\right) + \bar{\eta} v_{\gamma\gamma}\delta_{\alpha\beta} = \left(1 + \tau\frac{\mathrm{D}}{\mathrm{D}t}\right)\left\{\sigma_{\alpha\beta}^{\mathrm{s}} + \bar{\zeta}\delta_{\alpha\beta}\Delta\mu + \zeta p_\alpha p_\beta\Delta\mu + \zeta' p_\gamma p_\gamma\delta_{\alpha\beta}\Delta\mu\right.$$
$$-\frac{\nu_1}{2}(p_\alpha h_\beta + p_\beta h_\alpha) - \bar{\nu}_1 p_\gamma h_\gamma\delta_{\alpha\beta} - \frac{\Pi_1}{2}\left(\epsilon_{\alpha\gamma\delta} p_\beta p_\gamma h_\delta + \epsilon_{\beta\gamma\delta} p_\alpha p_\gamma h_\delta\right)$$
$$-\sum_{j=0}^{1}\frac{\Pi_2^j}{2}\left(\epsilon_{\alpha\gamma\delta} p_\beta p_\gamma \partial_\delta\bar{\mu}_j + \epsilon_{\beta\gamma\delta} p_\alpha p_\gamma \partial_\delta\bar{\mu}_j\right) + \sum_{j=0}^{1}\frac{\epsilon_j}{2}(p_\alpha\partial_\beta\bar{\mu}_j + p_\beta\partial_\alpha\bar{\mu}_j)$$
$$\left. + \sum_{j=0}^{1}\bar{\epsilon}_j p_\gamma\partial_\gamma\bar{\mu}_j\delta_{\alpha\beta} + \tau A_{\alpha\beta}\right\}, \tag{B.9}$$

$$j_{i,\alpha} = -\sum_{j=0}^{1}\gamma_{ij}\partial_\alpha\bar{\mu}_j + \bar{\lambda}_i h_\alpha + \kappa_i p_\alpha\Delta\mu - \epsilon_i p_\beta v_{\alpha\beta} - \bar{\epsilon}_i p_\alpha v_{\beta\beta} - \Pi_2^i\epsilon_{\beta\gamma\alpha}v_{\beta\delta}p_\gamma p_\delta + \Pi_3^i\epsilon_{\alpha\beta\gamma}p_\beta h_\gamma,$$
$$\tag{B.10}$$

$$\frac{\mathrm{D}}{\mathrm{D}t}p_\alpha = \left(1 + \tau\frac{\mathrm{D}}{\mathrm{D}t}\right)\frac{1}{\gamma_1}h_\alpha + \lambda_1 p_\alpha\Delta\mu - \bar{\lambda}_i\partial_\alpha\bar{\mu}_i - \nu_1 p_\beta v_{\alpha\beta} - \bar{\nu}_1 p_\alpha v_{\beta\beta} - \Pi_1\epsilon_{\beta\gamma\alpha}v_{\beta\delta}p_\gamma p_\delta$$
$$-\sum_{j=0}^{1}\Pi_3^j\epsilon_{\alpha\beta\gamma}p_\beta\partial_\gamma\bar{\mu}_j, \tag{B.11}$$

$$r^{\mathrm{d}} = -\sum_{i=0}^{1}\kappa_i p_\alpha\partial_\alpha\bar{\mu}_i + \lambda_1 p_\alpha h_\alpha + \Lambda\Delta\mu + \zeta p_\alpha p_\beta v_{\alpha\beta} + \bar{\zeta}v_{\alpha\alpha} + \zeta' p_\alpha p_\alpha v_{\beta\beta}. \tag{B.12}$$

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