

REVIEW

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## Review

# Hydrodynamic theory of active matter

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## Abstract

We review the general hydrodynamic theory of active soft materials that is motivated in particular by biological matter. We present basic concepts of irreversible thermodynamics of spatially extended multicomponent active systems. Starting from the rate of entropy production, we identify conjugate thermodynamic fluxes and forces and present generic constitutive equations of polar active fluids and active gels. We also discuss angular momentum conservation which plays a role in the physics of active chiral gels. The irreversible thermodynamics of active gels provides a general framework to discuss the physics that underlies a wide variety of biological processes in cells and in multicellular tissues.

Keywords: \*\*, active matter, hydrodynamics, nonequilibrium processes, active gels, molecular motors, irreversible thermodynamics

(Some figures may appear in colour only in the online journal)

## 1. Introduction

Cells and tissues provide extraordinarily complex examples for active condensed matter far from thermodynamic equilibrium. Cells are inherently dynamic and exhibit force generation by active molecular processes and the generation of spontaneous movements [1]. Active processes on the molecular scale are driven by chemical free energy provided by metabolic processes [2]. Examples are cell motility such as the gliding of cells on a solid substrate, and cell division. An important phenomenon is the ability of cells to generate forces and to control their shape. The prototype example for active molecular processes are motor molecules which interact with filaments of the cytoskeleton [3]. Motors bind to specific filaments. These have two different ends and thus display a polar asymmetry, providing a local direction for the motion of motors. Motor molecules catalyze the hydrolysis of Adenosinetriphosphate (ATP) to Adenosinediphosphate (ADP) and inorganic phosphate. ATP serves as a chemical fuel, and motor molecules generate spontaneous movements along

filaments driven by the chemical free energy provided by ATP hydrolysis. These movements proceed even in the presence of an external load and the motors can perform mechanical work [3]. Dynamic processes on the cell scale arise as collective behaviors of many molecular components, including motor proteins, in the cell cytoskeleton.

The cytoskeleton governs the material properties of cells and their response to external forces [4]. Filaments of the cytoskeleton turn over by polymerization and depolymerization processes [5]. They can be cross-linked by a number of associated proteins. A first class of cytoskeletal filaments are microtubules, which are stiff filaments that can become tens of micrometers long. They play a key role to organize the mitotic spindle and they form the basis of motile cilia. Kinesin and dynein motor proteins exert forces and movements along microtubules. A second important class of cytoskeletal filaments that can form active materials are actin filaments. Actin filaments are semiflexible, less stiff and typically shorter than microtubules. They often form gel-like materials in the cell, assembling into contractile bundles such as stress fibers. In

the presence of myosin motor proteins and ATP, mechanical stresses and movements are generated in actin filaments systems. The actin cytoskeleton also plays a key role to determine the mechanical properties of cells and the cell shape. It forms a thin layer of an actin gel below the outer plasma membrane of cells, the cell cortex, which generates contractile tension that governs cell surface tension. The actin cytoskeleton thus forms a complex material based on a network of filaments, motors and other molecular components. This network is dynamically organized in space and time and governs cellular material properties and cell mechanics. In many situations, this material is anisotropic. When filaments align on average, the network can be locally characterized by polar or nematic order [6], see figure 1. The associated order parameter can couple to force generation and movement [7–12]. Cytoskeletal networks thus are important examples for active materials with complex dynamics and unconventional material properties. This class of systems has been termed active gels, see figure 2. These are gel-like materials that are subject to active processes that give rise to active stresses and spontaneous flows [10, 11, 13–18]. Similar concepts describe material properties of multicellular systems and tissues, and it has been shown that tissues can also exhibit properties of active matter, both as active solids or as active liquids [19–31].

An important conceptual approach to active biological matter is to identify general physical principles and robust properties of active matter. This can be achieved using a hydrodynamic approach that captures the slow dynamics of modes that correspond to conservation laws or broken symmetries [17, 32, 33]. Here we review the general hydrodynamic theory of active gels and fluids based on irreversible thermodynamics. We discuss the basic thermodynamic concepts and derive expressions for entropy production in such systems. Using linear constitutive relations between generalized thermodynamic fluxes and forces we obtain a generic theory of active fluids and gels with polar or nematic asymmetries. This hydrodynamic theory generalizes the hydrodynamics and statistical mechanics of liquid crystals [6, 34–39] to systems maintained away from thermodynamic equilibrium by chemical processes driven by fuels provided in external reservoirs. Coupling soft materials to chemical reactions leads to mechano-chemical couplings and the transduction of chemical free energy to active mechanical stresses and spontaneous material flows. In addition to active polar and nematic systems, we also discuss active processes in chirally asymmetric systems. The hydrodynamic approach shows that chiral active processes such as motors interacting with chirally asymmetric filaments can give rise to pronounced chirality at larger scales and active chiral hydrodynamic processes. In order to discuss active chiral processes, the conservation of angular momentum plays an important role. This is different from hydrodynamics of passive fluids, where intrinsic rotations do not play significant roles on long time scales.

The paper is organized as follows. After the introduction, we present in section 2 the key conservation laws of mass, energy, momentum and angular momentum. Chemical reactions specify the number of conservation laws for molecular

components in a given system. In section 3, we define thermodynamic quantities and discuss the balance of entropy and free energy. To build the hydrodynamic theory of active matter, we identify pairs of conjugate thermodynamic fluxes and forces that determine the rate of entropy production. Section 4 presents the constitutive relations for active matter using linear response theory and symmetry arguments. The cases of polar active gels, active nematics and active chiral gels are discussed. Examples for the application of continuum theories to cellular processes and tissue dynamics are discussed in section 5. The paper concludes with a discussion in section 6.

## 2. Conservation laws

We construct the general theory of active matter starting from fundamental conservation laws. We consider a spatially extended macroscopic system of soft condensed matter in the presence of chemical reactions. We use a coarse-grained description that is based on a large number of local volume elements in which densities of molecular components, of the momentum and of the energy are defined. We consider a continuum limit that is valid on large length scales as compared to the size of volume elements. The microscopic equations of motion of the molecular components satisfy several conservation laws. These conservation laws are generally valid both in and out of thermodynamic equilibrium and at all scales. On a coarse grained level they can be expressed as continuity equations for conserved densities.

*Mass conservation.* First, we consider mass conservation which can be expressed as

$$\partial_t \rho + \partial_\alpha (\rho v_\alpha) = 0. \quad (1)$$

Here  $\rho$  is the mass density or mass per volume. We use a summation convention where summation over repeated vector indices is implied. Equation (1) defines the local center-of-mass velocity  $v_\alpha$ . The mass flux is given by the momentum density  $g_\alpha = \rho v_\alpha$ .

*Energy conservation.* Energy conservation implies that the energy density  $e$  in local volume elements obeys

$$\partial_t e + \partial_\alpha J_\alpha^e = 0, \quad (2)$$

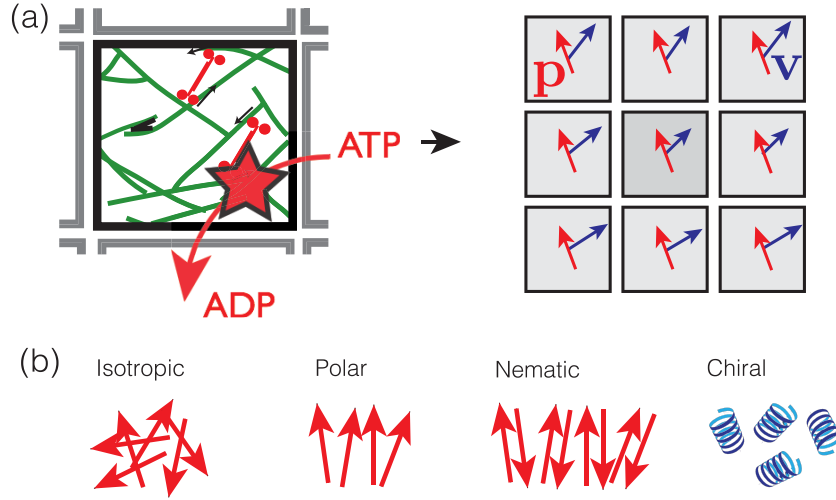
where  $J_\alpha^e = e v_\alpha + j_\alpha^e$  is the energy flux. Here we have introduced the relative energy flux  $j_\alpha^e$  in a reference frame that moves with the local volume elements.

*Momentum conservation.* Momentum conservation can be expressed as a continuity equation for the momentum balance  $g_\alpha$  which reads

$$\partial_t g_\alpha - \partial_\beta \sigma_{\alpha\beta}^{\text{tot}} = 0. \quad (3)$$

Here, the momentum flux is the negative total stress  $-\sigma_{\alpha\beta}^{\text{tot}}$ . We write  $\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta} - g_\alpha v_\beta$ , where  $\sigma_{\alpha\beta}$  denotes the stress in a reference frame moving with local volume elements.

*Angular momentum conservation.* Similarly, angular momentum conservation can be expressed as



**Figure 1.** (a) Coarse graining of an active gel. The gel is a dynamic meshwork of filaments that interact with molecular motors. Filaments have an average direction that can be characterized by a polarity vector  $p$ . Motors consume the fuel ATP which is hydrolyzed to ADP and inorganic phosphate. The chemical free energy provided by this reaction drives force generation of motors. Averaging filament polarity (red), and center of mass movements (blue) in small volume elements provides the basis for a coarse grained hydrodynamic description on large scales. (b) The hydrodynamic theory of active gels is based on broken symmetries that are characterized by order parameters. A filament system can be isotropic or it can for example exhibit polar or nematic anisotropies. Since individual filaments are chiral, chiral asymmetries in active gels can also play a role.

$$\partial_t l_{\alpha\beta}^{\text{tot}} - \partial_\gamma M_{\alpha\beta\gamma}^{\text{tot}} = 0. \quad (4)$$

Here, the antisymmetric tensor  $l_{\alpha\beta}^{\text{tot}} = \epsilon_{\alpha\beta\gamma} l_\gamma^{\text{tot}}$  describes the angular momentum density and  $l_\gamma^{\text{tot}}$  is the angular momentum density pseudo vector. We denote the total angular momentum flux by  $M_{\alpha\beta\gamma}^{\text{tot}}$ , which is antisymmetric in the first two indices. The angular momentum density can be decomposed in an intrinsic or spin angular momentum density  $l_{\alpha\beta}$  and an orbital contribution which corresponds to the angular momentum of the center-of-mass motion:  $l_{\alpha\beta}^{\text{tot}} = l_{\alpha\beta} + (x_\alpha g_\beta - x_\beta g_\alpha)$ , where the position vector is denoted  $x_\alpha$ . We also decompose the angular momentum flux into an intrinsic or spin angular momentum flux  $M_{\alpha\beta\gamma}^\pi$  and the flux of orbital angular momentum as  $M_{\alpha\beta\gamma}^{\text{tot}} = M_{\alpha\beta\gamma}^\pi + x_\alpha \sigma_{\beta\gamma}^{\text{tot}} - x_\beta \sigma_{\alpha\gamma}^{\text{tot}}$ .

Using these definitions, angular momentum conservation can be rewritten in the form [33, 39]

$$\partial_t (x_\alpha g_\beta - x_\beta g_\alpha) - \partial_\gamma (x_\alpha \sigma_{\beta\gamma}^{\text{tot}} - x_\beta \sigma_{\alpha\gamma}^{\text{tot}}) = 2\sigma_{\alpha\beta}^a \quad (5)$$

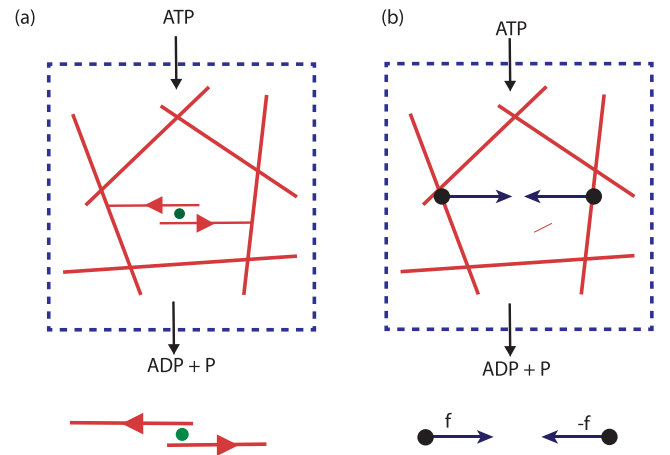
$$\partial_t l_{\alpha\beta} - \partial_\gamma M_{\alpha\beta\gamma}^\pi = -2\sigma_{\alpha\beta}^a \quad (6)$$

where

$$\sigma_{\alpha\beta}^a = \frac{1}{2} (\sigma_{\alpha\beta}^{\text{tot}} - \sigma_{\beta\alpha}^{\text{tot}}) \quad (7)$$

is the antisymmetric part of the stress. Note that equations (5) and (6) follow directly from equations (3) and (4).

*Particle number balance—chemical reactions.* In addition to mass balance, the particle number densities of molecular species can obey conservation laws. We write balance equations for the particle number densities  $n_i$  of molecular species  $i$  with  $i = 0, \dots, N$ :



**Figure 2.** (a) The cell cytoskeleton is a filament network in which molecular motors can act as active cross-linkers. When a filament pair (red arrows) interacts with a small aggregate of molecular motors (green), the motors introduce a force and a counter force in the network in the presence of the fuel ATP. The material can be maintained away from thermodynamic equilibrium if the fuel and reaction products are kept at constant concentration by external reservoirs. (b) The force exerted by motor on a pair of filaments introduces a force dipole in the material. On larger scales, the average density of force dipoles corresponds to the active stress.

$$\partial_t n_i + \partial_\alpha J_\alpha^i = r_i \quad (8)$$

where  $J_\alpha^i = n_i v_\alpha + j_\alpha^i$  are particle currents and we have defined the relative fluxes  $j_\alpha^i$ . In the absence of chemical reactions, these densities are all conserved. Chemical reactions contribute to sources  $r_i$  in equation (8). We denote chemical reactions by the index  $I = 1, \dots, M$ , where  $M$  is the number of reactions. These chemical reactions can in general be expressed in the form

$$\sum_{i=0}^N a_i^l A_i \rightleftharpoons 0. \quad (9)$$

Here,  $A_i$  denotes the chemical symbol of molecule species  $i$ . The numbers  $a_i^l$  are the stoichiometric coefficients for reaction  $l$  which obey  $\sum_{i=0}^N a_i^l m_i = 0$ , where  $m_i$  are the masses of molecules of species  $i$ . For  $a_i^l > 0$ , molecular species  $i$  is a reaction substrate, for  $a_i^l < 0$ , species  $i$  is a reaction product. For  $a_i^l = 0$  the molecular species  $i$  is not taking part in reaction  $l$ . The rates  $r_i$  at which molecular species  $i$  is generated by chemical reactions can thus be written as a sum over contributions from different reactions

$$r_i = - \sum_{l=1}^M a_i^l r^l, \quad (10)$$

where we have introduced the chemical fluxes  $r^l$ , which are the rates at which chemical reactions  $l$  proceed.

The currents  $j_\alpha^i$  describe relative movements of different molecular species. The mass density can be written as  $\rho = \sum_{i=0}^N m_i n_i$ . Mass conservation (1) then implies

$$\sum_{i=0}^N m_i j_\alpha^i = 0 \quad \text{and} \quad \sum_{i=0}^N m_i r_i = 0. \quad (11)$$

We can therefore express the current and the source rate of one molecular species (we choose the solvent  $i = 0$ ) by the remaining currents and rates:

$$j_\alpha^0 = - \frac{1}{m_0} \sum_{i=1}^N m_i j_\alpha^i \quad (12)$$

$$r_0 = - \frac{1}{m_0} \sum_{i=1}^N m_i r_i. \quad (13)$$

The reaction rate  $r_0$  and flux  $j_\alpha^0$  are thus not independent variables and can be eliminated. In addition to overall mass conservation, for  $N + 1$  molecular species and  $M$  linearly independent chemical reactions there are thus  $N - M$  conservation laws for molecule number densities.

### 3. Irreversible thermodynamics of active matter

#### 3.1. Balance of entropy and free energy

In order to understand the dynamics of a complex system of condensed matter, one has in principle to solve microscopic equations of motion. At thermodynamic equilibrium, the behaviours of a many-particle system can be understood to a large extent from the knowledge of thermodynamic potentials which are functions of only a few thermodynamic variables. Here we employ the framework of irreversible thermodynamics in order to discuss the dynamics of a complex system in the vicinity of a thermodynamic equilibrium [33]. More precisely, we describe the case where a system is locally at equilibrium while being maintained away from equilibrium globally. Such local thermodynamic equilibrium can be considered if small

volume elements equilibrate at times that are short compared to the slow dynamics of hydrodynamic modes at large scales. We discuss the equilibrium thermodynamics of local volume elements of volume  $V$  at temperature  $T$  containing  $N_i = n_i V$  particles of type  $i$  with free energy density  $F = fV$  and entropy  $S = sV$ , where  $f$  and  $s$  denote the densities of free energy and entropy, respectively. We have  $s = -\partial f / \partial T$  and the chemical potentials are given by  $\mu_i = \partial f / \partial n_i$  in each local volume element. The system as a whole is in general not at a global thermodynamic equilibrium. However its total free energy  $F = \int d^3x f$  and entropy  $S = \int d^3x s$  are always well defined as the sum of the contributions of locally equilibrated volume elements.

For such a non equilibrium system, the total entropy  $S$  in general increases over time according to the second law of thermodynamics. Accordingly, we can express changes of entropy in the system with a balance equation for the entropy density:

$$\partial_t s + \partial_\alpha J_\alpha^s = \theta \quad (14)$$

where  $\theta > 0$  denotes the entropy production rate per unit volume due to irreversible processes and  $J_\alpha^s = s v_\alpha + j_\alpha^s$  is the entropy flux. Here we have introduced the relative entropy flux  $j_\alpha^s$ . We can also write a balance equation for the free energy density  $f$

$$\partial_t f + \partial_\alpha J_\alpha^f = \theta_f \quad (15)$$

where we have introduced the free energy flux  $J_\alpha^f$  and the source of free energy  $\theta_f$ . The free energy density obeys the local thermodynamic relation  $f = e - Ts$  between densities of energy, entropy and free energy. We express the free energy flux also as a convected part and the flux  $j_\alpha^f$  relative to the center of mass,  $J_\alpha^f = f v_\alpha + j_\alpha^f$ . The total energy flux is then the sum of free energy transport and heat transport  $J_\alpha^e = (f + Ts)v_\alpha + j_\alpha^f + j_\alpha^e$ . Here, we define the heat flux as  $j_\alpha^e = T j_\alpha^s$ , which is the entropy flux with respect to the center of mass motion (note that other definitions of the heat flux are also sometimes used [33]). Thus, the relative free energy flux  $j_\alpha^f = j_\alpha^e - j_\alpha^e$  is the part of the relative energy flux that is not in the form of heat. The projected free energy flux at the system boundaries  $-j_\alpha^f n_\alpha$  can be interpreted as work performed per unit area by the environment on the system. Here  $n_\alpha$  is a unit vector normal to the boundary pointing outwards. In isothermal systems which are maintained everywhere at temperature  $T$  by a thermostat, the local reduction rate of free energy is directly related to the rate of entropy production:  $T\theta = -\theta_f$ , which follows using equation (2), see equation (A.22). In the following, we will limit our discussion for simplicity to this isothermal case. The irreversible thermodynamics of a multi-component fluid, taking into account temperature variations, is reviewed in appendix A.

#### 3.2. Equilibrium thermodynamics of a polar fluid

We consider a polar fluid that is characterised by a local vectorial anisotropy described by the vector  $p_\alpha$ . In the context of the cell cytoskeleton, the vector

$$p_\alpha = \langle p_\alpha^n \rangle \quad (16)$$

could for example correspond to the average in a local volume element of vectors  $p_\alpha^n$  that define the directions of individual filaments  $n$  in a filament network, see figure 1. Considering a local equilibrium, we denote the free energy per volume in the reference frame moving with the center of mass velocity  $v_\alpha$  by  $f_0(p_\alpha, \partial_\beta p_\alpha, n_i, T)$ , which in general depends on the local polarity anisotropy  $p_\alpha$ . For inhomogeneous systems, we also have to consider the dependence of the free energy on gradients of the polarity field  $\partial_\alpha p_\beta$ . The total free energy then reads

$$F = \int d^3x \left( \frac{g_\alpha^2}{2\rho} + f_0(p_\alpha, \partial_\alpha p_\beta, n_i) \right), \quad (17)$$

and we define the total free energy density  $f(p_\alpha, \partial_\alpha p_\beta, n_i, g_\alpha) = g_\alpha^2/(2\rho) + f_0(p_\alpha, \partial_\alpha p_\beta, n_i)$  which also contains the kinetic energy of center-of-mass motion. The conjugate field to the polarity  $p_\alpha$  is  $h_\alpha = -\delta F_0/\delta p_\alpha$  where the functional derivative can be expressed as

$$h_\alpha = -\frac{\partial f_0}{\partial p_\alpha} + \partial_\beta \frac{\partial f_0}{\partial (\partial_\beta p_\alpha)} \quad (18)$$

and  $F_0 = \int d^3x f_0$ . Furthermore, we introduce the total chemical potential  $\mu_i^{\text{tot}} = \delta F/\delta n_i$  with

$$\mu_i^{\text{tot}} = -\frac{1}{2} m_i v_\alpha^2 + \mu_i \quad (19)$$

where  $\mu_i = \partial f_0/\partial n_i$  is the conventional chemical potential. In an anisotropic system, the stress at equilibrium is not an isotropic pressure but an anisotropic stress. The equilibrium stress tensor can be obtained from considering translation invariance.

### 3.3. Translation invariance of the free energy: the equilibrium stress tensor

Using the invariance of the free energy with respect to translations in space results in a generalized Gibbs–Duhem equation and an expression for the equilibrium stress. The free energy change due to an infinitesimal translation by a vector  $\delta x_\alpha$  is given by (see appendix B)

$$\begin{aligned} \delta F = & \int d^3x \left[ (\partial_\beta v_\alpha) g_\alpha + (\partial_\beta \mu_i^{\text{tot}}) n_i + h_\alpha \partial_\beta p_\alpha \right] \delta x_\beta \\ & + \oint dS_\alpha \left[ (f - v_\gamma g_\gamma - \mu_i^{\text{tot}} n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\alpha p_\gamma)} \partial_\beta p_\gamma \right] \delta x_\beta. \end{aligned} \quad (20)$$

Here and in the following we imply summation over repeated indices  $i$  from  $i = 0$  to  $N$ . The area element  $dS_\alpha$  is a vector pointing in the direction normal to the surface in outward direction. From the surface contribution we identify the equilibrium stress, also called Ericksen stress

$$\sigma_{\alpha\beta}^e = (f_0 - \mu_i n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\beta p_\gamma)} \partial_\alpha p_\gamma. \quad (21)$$

Translational invariance  $\delta F = 0$  implies the Gibbs–Duhem relation

$$-\partial_\beta \sigma_{\alpha\beta}^e = (\partial_\alpha \mu_i) n_i + h_\beta \partial_\alpha p_\beta. \quad (22)$$

The generalized Gibbs–Duhem relation (22) shows that the equilibrium stress obeys a force balance condition  $\partial_\beta \sigma_{\alpha\beta}^e = 0$  at thermodynamic equilibrium when  $\partial_\alpha \mu_i$  and  $h_\beta$  vanish. However, in an out of equilibrium situation, the equilibrium stresses do not obey a force balance and out of equilibrium contributions to the stress must exist.

### 3.4. Rotation invariance and equilibrium angular momentum flux

Rotation invariance of the free energy provides an additional condition that is related to angular momentum conservation. The change of free energy under an infinitesimal rotation reads

$$\delta F = \int d^3x \left[ (\sigma_{\beta\alpha}^e - h_\beta p_\alpha) \epsilon_{\beta\gamma\alpha} \theta_\gamma \right] + \oint dS_\delta \frac{\partial f_0}{\partial (\partial_\delta p_\beta)} p_\alpha \epsilon_{\beta\gamma\alpha} \theta_\gamma. \quad (23)$$

Equation (23) describes the vanishing net torque and we identify the equilibrium intrinsic angular momentum flux

$$M_{\alpha\beta\gamma}^e = \frac{\partial f_0}{\partial (\partial_\gamma p_\beta)} p_\alpha - \frac{\partial f_0}{\partial (\partial_\gamma p_\alpha)} p_\beta. \quad (24)$$

From the condition that  $\delta F$  in equation (23) must vanish for any small rotations  $\theta_\beta$ , we obtain

$$\partial_\gamma M_{\alpha\beta\gamma}^e = 2\sigma_{\alpha\beta}^{e,a} + (p_\alpha h_\beta - p_\beta h_\alpha). \quad (25)$$

Note that the Ericksen stress can have an antisymmetric part  $\sigma_{\alpha\beta}^{e,a} = (\sigma_{\alpha\beta}^e - \sigma_{\beta\alpha}^e)/2$ . At equilibrium with  $h_\alpha = 0$  and  $\partial_t l_{\alpha\beta} = 0$ , we have  $M_{\alpha\beta\gamma}^\pi = M_{\alpha\beta\gamma}^e$  and the torque balance equation (6) reads  $\partial_\gamma M_{\alpha\beta\gamma}^e = 2\sigma_{\alpha\beta}^{e,a}$ .

### 3.5. Entropy production rate of a polar fluid

*Rate of change of the free energy.* For an isothermal system, the rate of entropy production obeys  $TdS/dt = -dF/dt$  is related to the rate of change of the free energy. We derive in several steps a general expression for the rate of change of the free energy for the case of a polar isothermal system. Within a volume  $V$  of fixed shape we have

$$\begin{aligned} \frac{dF}{dt} = & \int_V d^3x \left[ v_\alpha \partial_t g_\alpha + \mu_i^{\text{tot}} \partial_t n_i - h_\alpha \partial_t p_\alpha \right] + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \partial_t p_\beta \\ = & \int_V d^3x \left( -(\partial_\beta v_\alpha) \sigma_{\alpha\beta}^{\text{tot}} + \mu_i^{\text{tot}} r_i + (j_\alpha^i + n_i v_\alpha) \partial_\alpha \mu_i^{\text{tot}} - h_\alpha \partial_t p_\alpha \right) \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha}^{\text{tot}} - \mu_i^{\text{tot}} j_\alpha^i + \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \partial_t p_\beta \right), \end{aligned} \quad (26)$$

where we have used the conservation laws for mass and momentum. Using the Gibbs–Duhem relation (22), we can rewrite this as

$$\begin{aligned} \frac{dF}{dt} = & \int d^3x \left( -\partial_\beta v_\alpha (\sigma_{\alpha\beta} - \sigma_{\alpha\beta}^e) + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \frac{dp_\alpha}{dt} \right) \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \frac{dp_\beta}{dt} \right) \end{aligned} \quad (27)$$

where  $d/dt = \partial_t + v_\gamma \partial_\gamma$  is a convected time derivative and  $\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{\text{tot}} + v_\alpha g_\beta$ . We can

decompose the velocity gradient  $\partial_\beta v_\alpha = v_{\alpha\beta} - \omega_{\alpha\beta}$  in a symmetric part  $v_{\alpha\beta} = (1/2)(\partial_\alpha v_\beta + \partial_\beta v_\alpha)$  and the vorticity  $\omega_{\alpha\beta} = (1/2)(\partial_\alpha v_\beta - \partial_\beta v_\alpha)$  and write

$$\begin{aligned} \frac{dF}{dt} = & \int d^3x (-v_{\alpha\beta}(\sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^{e,s}) + \omega_{\alpha\beta}(\sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a}) + h_\alpha p_\beta) \\ & + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \frac{Dp_\alpha}{Dt} \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{dp_\beta}{dt} \right) \end{aligned} \quad (28)$$

where  $\sigma_{\alpha\beta}^s = (\sigma_{\alpha\beta} + \sigma_{\beta\alpha})/2$  the symmetric part of the stress and we have introduced the convected corotational time derivative

$$\frac{Dp_\alpha}{Dt} = \partial_i p_\alpha + v_\gamma \partial_\gamma p_\alpha + \omega_{\alpha\beta} p_\beta \quad (29)$$

of the vector  $p_\alpha$ , which is the time derivative evaluated in a co-rotating and co-moving reference frame. We still have to use angular momentum conservation to obtain the final expression that allows us to identify the local entropy production rate. In the free energy (17) we do not take into account the kinetic energy associated with intrinsic angular momentum. This corresponds to the case where the density of intrinsic angular momentum can be neglected,  $l_{\alpha\beta} = 0$ . In this simple case angular momentum conservation implies

$$\partial_\gamma M_{\alpha\beta\gamma}^\pi - \partial_\gamma M_{\alpha\beta\gamma}^e = 2(\sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a}) - (p_\alpha h_\beta - p_\beta h_\alpha), \quad (30)$$

where we have used equation (24). Expression (30) permits us to eliminate the antisymmetric stress from equation (28). The rate of change of the free energy finally reads

$$\begin{aligned} \frac{dF}{dt} = & \int d^3x (-v_{\alpha\beta} \sigma_{\alpha\beta}^{d,s} - \frac{1}{2}(\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \frac{Dp_\alpha}{Dt}) \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} + \frac{1}{2} M_{\beta\gamma\alpha}^\pi \omega_{\beta\gamma} - v_\alpha f - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{Dp_\beta}{Dt} \right). \end{aligned} \quad (31)$$

Here we have introduced the symmetric deviatoric stress

$$\sigma_{\alpha\beta}^{d,s} = \sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^{e,s} \quad (32)$$

and the deviatoric part of the angular momentum flux

$$M_{\alpha\beta\gamma}^d = M_{\alpha\beta\gamma}^\pi - M_{\alpha\beta\gamma}^e. \quad (33)$$

The rate of change of the free energy given by equation (31) has a bulk and a surface contribution. The bulk term vanishes at thermodynamic equilibrium and can be identified with the free energy source  $\int d^3x \theta_f$ . In isothermal systems it is directly related to entropy production  $T\theta = -\theta_f$ . The surface contribution describes the mechanical and chemical work performed on the system at the surface. It is of the form  $-\oint dS_\alpha J_\alpha^f$  with  $J_\alpha^f = f v_\alpha + j_\alpha^f$ . From equation (31), we thus identify the relative free energy flux

$$j_\alpha^f = -v_\beta \sigma_{\beta\alpha} - \frac{1}{2} \omega_{\beta\gamma} M_{\beta\gamma\alpha}^\pi + \mu_i j_\alpha^i - \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{Dp_\beta}{Dt}. \quad (34)$$

The first term describes the mechanical work of surface forces. The second term accounts for the work of surface torques. The remaining terms describe chemical work on the surface and the work associated with changes of the polarity field.

*Rate of entropy production.* The form of equation (31) ensures that all bulk contributions to free energy changes involve conjugate pairs of thermodynamic fluxes and of generalized forces that all vanish for thermodynamic equilibrium states. Equilibrium states correspond either to systems with zero or constant velocity  $v_\alpha$  or to situations with constant vorticity  $\omega_{\alpha\beta}$  corresponding to a spinning equilibrium system. For nonequilibrium situations the entropy production reads

$$\begin{aligned} T\theta = & v_{\alpha\beta} \sigma_{\alpha\beta}^{d,s} + \frac{1}{2} (\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d + \sum_{I=1}^M r^I \Delta\mu^I \\ & - \sum_{i=1}^N j_\alpha^i \partial_\alpha \bar{\mu}_i + h_\alpha \frac{Dp_\alpha}{Dt}. \end{aligned} \quad (35)$$

Here we have introduced the the relative chemical potentials

$$\bar{\mu}_i = \mu_i - \frac{m_i}{m_0} \mu_0, \quad (36)$$

and the chemical free energy change associated with reaction  $I$  is  $\Delta\mu^I = \sum_{i=0}^N a_i^I \mu_i$ . From mass conservation  $\sum_{i=0}^N m_i a_i^I = 0$  it follows that

$$\Delta\mu^I = \sum_{i=1}^N a_i^I \bar{\mu}_i. \quad (37)$$

From equation (13) we also have  $\sum_{i=0}^N j_\alpha^i \mu_i = \sum_{i=1}^N j_\alpha^i \bar{\mu}_i$  and thus only  $N$  diffusion fluxes dissipate. The contributions of the chemical reactions  $I = 1 \dots M$  to entropy production are written explicitly. Each chemical reaction  $I$  is driven by the chemical free energy changes  $\Delta\mu^I$  associated with the corresponding reaction. Note that  $\sum_{I=1}^M r^I \Delta\mu^I = -\sum_{i=1}^N r_i \bar{\mu}_i$ .

### 3.6. Irreversible thermodynamics of a nematic fluid

If the local order of filaments is not polar but nematic, the relevant order parameter becomes a traceless symmetric tensor

$$Q_{\alpha\beta} = \langle p_\alpha^n p_\beta^n \rangle - \frac{1}{3} \langle p_\gamma^n p_\gamma^n \rangle \delta_{\alpha\beta}, \quad (38)$$

where the average is over the directions  $p_\alpha^n$  of individual filaments in a local volume element. The free energy density  $g_\alpha^2/(2\rho) + f_0(n_i, Q_{\alpha\beta}, \partial_\gamma Q_{\alpha\beta})$  now depends on the nematic order parameter and its gradients. The field  $H_{\alpha\beta} = -\frac{\delta F_0}{\delta Q_{\alpha\beta}}$ , conjugate to the nematic order, is given by

$$H_{\alpha\beta} = -\frac{\partial f_0}{\partial Q_{\alpha\beta}} + \partial_\gamma \frac{\partial f_0}{\partial(\partial_\gamma Q_{\alpha\beta})}. \quad (39)$$

Here, the tensor  $H_{\alpha\beta}$  is traceless because only traceless variations of  $Q_{\alpha\beta}$  are permitted when determining the functional derivative. The equilibrium stress then reads

$$\sigma_{\alpha\beta}^e = (f_0 - \mu_i n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\beta Q_{\gamma\nu})} \partial_\alpha Q_{\gamma\nu} \quad (40)$$

and the Gibbs–Duhem relation is given by

$$-\partial_\beta \sigma_{\alpha\beta}^e = (\partial_\alpha \mu_i) n_i + H_{\gamma\nu} \partial_\alpha Q_{\gamma\nu}. \quad (41)$$

Invariance under infinitesimal rotations implies the relations (B.6) and (B.7). The rate of change of free energy then reads

$$\begin{aligned} \frac{dF}{dt} = & \int d^3x \left( -v_{\alpha\beta} \sigma_{\alpha\beta}^{d,s} - \frac{1}{2} (\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d + \mu_i r_i \right. \\ & \left. + j_\alpha^i \partial_\alpha \mu_i - H_{\alpha\beta} \frac{DQ_{\alpha\beta}}{Dt} \right) \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} + \frac{1}{2} M_{\beta\gamma\alpha}^\pi \omega_{\beta\gamma} - v_\alpha f \right. \\ & \left. - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial (\partial_\alpha Q_{\beta\gamma})} \frac{DQ_{\beta\gamma}}{Dt} \right) \end{aligned} \quad (42)$$

where the convected co-rotational time derivative of a tensor is defined as [40]

$$\frac{DQ_{\alpha\beta}}{Dt} = \partial_t Q_{\alpha\beta} + v_\gamma \partial_\gamma Q_{\alpha\beta} + \omega_{\alpha\gamma} Q_{\gamma\beta} + \omega_{\beta\gamma} Q_{\alpha\gamma}. \quad (43)$$

Note that there exist several definitions of corotational time derivatives of a tensor. Equation (43) is often called upper convected time derivative. It represents a material time derivative taken in a reference frame that is convected and co-rotated with the center of mass motion.

### 3.7. Irreversible thermodynamics of a visco-elastic gel

So far we have discussed the thermodynamics of fluids with polar or nematic order. Cytoskeletal networks are gel-like materials which in general have visco-elastic properties. Such visco-elastic material properties can also be captured by the generic thermodynamic approach. We thus discuss the physics of viscoelastic systems for simplicity for the case of a viscoelastic gel or filament network that is isotropic at equilibrium. Such materials can exhibit transient elastic shear stress  $\sigma_{\alpha\beta}^{\text{el}}$  and elastic shear strain  $\tilde{u}_{\alpha\beta}$ , which is a traceless symmetric tensor describing local network anisotropies. The elastic stress relaxes via network rearrangements within a finite relaxation time. To describe the thermodynamics of such systems, we introduce a thermodynamic ensemble with prescribed strain and corresponding free energy density  $f = g_\alpha^2 / (2\rho) + f_0(n_i, \tilde{u}_{\alpha\beta})$  which is a function of densities  $n_i$  and of the prescribed shear strain  $\tilde{u}_{\alpha\beta}$ . The conjugate thermodynamic field

$$\sigma_{\alpha\beta}^{\text{el}} = \frac{\partial f_0}{\partial \tilde{u}_{\alpha\beta}} \quad (44)$$

is the traceless elastic stress associated with  $\tilde{u}_{\alpha\beta}$ . The equilibrium stress  $\sigma_{\alpha\beta}^e = -P^e \delta_{\alpha\beta}$  is isotropic and given by

$$\sigma_{\alpha\beta}^e = (f_0 - n_i \mu_i) \delta_{\alpha\beta} \quad (45)$$

where  $P^e$  is the equilibrium hydrostatic pressure. It obeys the Gibbs–Duhem relation

$$\partial_\alpha P^e = n_i \partial_\alpha \mu_i - \sigma_{\beta\gamma}^{\text{el}} \partial_\alpha \tilde{u}_{\beta\gamma}. \quad (46)$$

The rate of change of the free energy change is

$$\begin{aligned} \frac{dF}{dt} = & \int d^3x \left( -\partial_\beta v_\alpha (\sigma_{\alpha\beta} + P^e \delta_{\alpha\beta}) + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i + \sigma_{\alpha\beta}^{\text{el}} \frac{D\tilde{u}_{\alpha\beta}}{Dt} \right) \\ & + \oint dS_\alpha (v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i), \end{aligned} \quad (47)$$

where the convected corotational time derivative of  $\tilde{u}_{\alpha\beta}$  is defined in equation (43).

### 3.8. Irreversible thermodynamics of systems with intrinsic rotations

So far, we have simplified angular momentum conservation and have ignored the density  $l_{\alpha\beta} = \epsilon_{\alpha\beta\gamma} l_\gamma$  of intrinsic angular momentum in the free energy. In general, the free energy density in the center of mass reference frame  $f_0(p_\alpha, \partial_\beta p_\alpha, n_i, l_{\alpha\beta})$  depends on the density of intrinsic angular momentum  $l_{\alpha\beta}$  [41]. This dependence accounts for the kinetic energy contributions that are associated with intrinsic rotations. The intrinsic rotation rate is defined as

$$\Omega_{\alpha\beta} = 2 \frac{\partial f_0}{\partial l_{\alpha\beta}}, \quad (48)$$

with  $\Omega_{\alpha\beta} = \epsilon_{\alpha\beta\gamma} \Omega_\gamma$  and  $\Omega_{\alpha\beta} l_{\alpha\beta} = 2\Omega_\alpha l_\alpha$ . The derivation of the rate of entropy production taking into account the kinetic energy of intrinsic rotations is given in appendix B. The entropy production rate reads

$$\begin{aligned} T\theta = & v_{\alpha\beta} \sigma_{\alpha\beta}^{d,s} + (\Omega_{\alpha\beta} - \omega_{\alpha\beta}) \sigma_{\alpha\beta}^{d,a} + \frac{1}{2} (\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d \\ & + \sum_{I=1}^M r^I \Delta \mu^I - \sum_{i=1}^N j_\alpha^i \partial_\alpha \bar{\mu}_i + h_\alpha \frac{Dp_\alpha}{Dt}. \end{aligned} \quad (49)$$

Here, the deviatoric antisymmetric stress is defined as

$$\sigma_{\alpha\beta}^{d,a} = \sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a} - \frac{1}{2} (p_\alpha h_\beta - p_\beta h_\alpha) - \frac{1}{2} \partial_\gamma M_{\alpha\beta\gamma}^d. \quad (50)$$

The total stress is then given by

$$\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta}^{d,s} + \sigma_{\alpha\beta}^{d,a} - \rho v_\alpha v_\beta + \sigma_{\alpha\beta}^e + \frac{1}{2} (p_\alpha h_\beta - p_\beta h_\alpha) + \frac{1}{2} \partial_\gamma M_{\alpha\beta\gamma}^d. \quad (51)$$

The total stress has an antisymmetric part  $\sigma_{\alpha\beta}^a = \sigma_{\alpha\beta}^{e,a} + \frac{1}{2} (p_\alpha h_\beta - p_\beta h_\alpha) + \frac{1}{2} \partial_\gamma M_{\alpha\beta\gamma}^d + \sigma_{\alpha\beta}^{d,a}$ . Often only the reactive or equilibrium part of this antisymmetric stress  $\sigma_{\alpha\beta}^{e,a} + \frac{1}{2} (p_\alpha h_\beta - p_\beta h_\alpha)$  is discussed. However in general dissipative contributions to the antisymmetric stress can exist [41, 42].

### 3.9. Conjugate pairs of thermodynamic fluxes and generalized forces

By combining the different cases discussed above, we can now extend equation (35) and write a general form of the entropy production rate. We decompose the symmetric part of the stress tensor  $\sigma_{\alpha\beta}^s = (\sigma_{\alpha\beta} + \sigma_{\beta\alpha})/2$  in the form



$\sigma_{\alpha\beta}^s = \tilde{\sigma}_{\alpha\beta}^s + \sigma\delta_{\alpha\beta}$ , where  $\tilde{\sigma}_{\alpha\beta}^s$  is the traceless symmetric shear stress and  $\sigma = (1/d)\sigma_{\gamma\gamma}^s$  denotes the isotropic stress with  $d$  the number of space dimensions. Similarly, the deviatoric part of the symmetric stress that enters the total stress in equation (51) is decomposed as  $\sigma_{\alpha\beta}^{d,s} = \tilde{\sigma}_{\alpha\beta}^d + \sigma^d\delta_{\alpha\beta}$  in a traceless part  $\tilde{\sigma}_{\alpha\beta}^d$  and the isotropic part  $\sigma^d$ , with  $\sigma^d = \sigma + P^e$ , where  $P^e = -(1/d)\sigma_{\gamma\gamma}^{e,s}$  denotes the equilibrium pressure. Finally, we decompose the symmetric part of the velocity gradient  $v_{\alpha\beta} = \tilde{v}_{\alpha\beta} + (\partial_\gamma v_\gamma)\frac{1}{d}\delta_{\alpha\beta}$  in a traceless rate of pure shear  $\tilde{v}_{\alpha\beta}$  and local expansion rate, which is the divergence  $\partial_\gamma v_\gamma$  of the flow velocity. The total entropy production rate then reads

$$\begin{aligned} T\theta = & v_{\gamma\gamma}\sigma^d + \tilde{v}_{\alpha\beta}\tilde{\sigma}_{\alpha\beta}^{d,s} + (\Omega_{\alpha\beta} - \omega_{\alpha\beta})\sigma_{\alpha\beta}^{d,a} \\ & + \frac{1}{2}(\partial_\gamma\omega_{\alpha\beta})M_{\alpha\beta\gamma}^d + \sum_{l=1}^M r^l\Delta\mu^l - \sum_{i=1}^N J_\alpha^i\partial_\alpha\bar{\mu}_i \\ & + h_\alpha\frac{Dp_\alpha}{Dt} + H_{\alpha\beta}\frac{DQ_{\alpha\beta}}{Dt} - \sigma_{\alpha\beta}^{el}\frac{D\tilde{u}_{\alpha\beta}}{Dt}, \end{aligned} \quad (52)$$

where we consider the isothermal case for simplicity. The rate of entropy production (52) is a sum of independent contributions which are products of a generalized thermodynamic force  $F_n$  and a conjugate thermodynamic flux  $J_n$  of the form

$$T\theta = \sum_n J_n F_n. \quad (53)$$

Here, the index  $n$  specifies a thermodynamic variable or a tensor or vector component of a given variable. From equation (52) we can identify the set of conjugate pairs of thermodynamic fluxes and generalized forces given in table 1.

The generalized forces and fluxes can be characterized by their signature  $\epsilon$  under time reversal. We denote by  $\epsilon_n$  the time reversal signatures of the generalized thermodynamic forces  $F_n$ , which are given in table 1. For example, under the transformation  $t \rightarrow -t$ , we have  $\tilde{v}_{\alpha\beta} \rightarrow -\tilde{v}_{\alpha\beta}$  which corresponds to  $\epsilon_v = -1$  while  $h_\alpha \rightarrow h_\alpha$  and  $\epsilon_h = 1$ . Because the entropy production  $\theta$  has signature  $\epsilon_\theta = -1$ , the time reversal signature of the conjugate thermodynamic fluxes  $J_n$  is given by  $-\epsilon_n$ , opposite to those of  $F_n$ . The time reversal signatures of thermodynamic forces are listed in table 1.

## 4. Constitutive relations and hydrodynamic equations

### 4.1. Onsager relations

At thermodynamic equilibrium all thermodynamic fluxes  $J_n$  and generalized forces  $F_n$  vanish and no entropy is produced,  $T\theta = 0$ . Irreversible thermodynamics provides a systematic expansion of the fluxes  $J_n$  in terms of the generalized forces  $F_n$  in the vicinity of equilibrium. These relations define the dynamic properties of the system and represent constitutive relations characterizing the material properties. To linear order, we have [43–46]

$$J_n = \sum_m O_{nm} F_m, \quad (54)$$

**Table 1.** List of the pairs of conjugate thermodynamic fluxes  $J_n$  and forces  $F_n$ . The signatures of the thermodynamic forces  $F_n$  under time reversal  $\epsilon_n$  are given. The time reversal signature of the corresponding thermodynamic flux  $J_n$  is  $-\epsilon_n$ . Scalars, vectors and tensorial objects differ in their transformation behaviours under coordinate rotations.

Flux	$J_n \leftrightarrow$ force	$F_n$	Time-reversal signature $\epsilon_n$ of $F_n$	Rotation symmetry
$\tilde{\sigma}_{\alpha\beta}^{d,s} \leftrightarrow \tilde{v}_{\alpha\beta}$			-1	Traceless symmetric tensor
$\sigma^d \leftrightarrow \partial_\gamma v_\gamma$			-1	Scalar
$\frac{Dp_\alpha}{Dt} \leftrightarrow h_\alpha$			+1	Vector
$\frac{DQ_{\alpha\beta}}{Dt} \leftrightarrow H_{\alpha\beta}$			+1	Traceless symmetric tensor
$J_\alpha^i \leftrightarrow -\partial_\alpha \bar{\mu}_i$			+1	Vector
$r^l \leftrightarrow \Delta\mu^l$			+1	Scalar
$M_{\alpha\beta\gamma}^d \leftrightarrow \frac{1}{2}\partial_\gamma\omega_{\alpha\beta}$			-1	Rank three tensor
$\sigma_{\alpha\beta}^{d,a} \leftrightarrow (\Omega_{\alpha\beta} - \omega_{\alpha\beta})$			-1	Antisymmetric tensor
$\frac{D\tilde{u}_{\alpha\beta}}{Dt} \leftrightarrow -\sigma_{\alpha\beta}^{el}$			+1	Traceless symmetric tensor

which ensures that all  $J_n$  vanish when the  $F_n$  are zero. This linear relation between thermodynamic fluxes and generalized forces defines the constitutive relations that describe the properties of a given material or system. Here we have introduced the matrix of Onsager coefficients  $O_{nm} = O_{nm}^d + O_{nm}^r$  which can be decomposed in a dissipative part  $O_{nm}^d$  and a reactive part  $O_{nm}^r$ . Only the dissipative part  $O_{nm}^d$  with the Onsager symmetry property  $O_{nm}^d = O_{mn}^d$  contributes to entropy production and dissipation. The reactive part is antisymmetric and obeys  $O_{nm}^r = -O_{mn}^r$ . Because of this antisymmetry the reactive coefficients do not contribute to entropy production and describe reversible phenomena. Time reversal symmetry implies that the dissipative coefficients  $O_{nm}^d$  are nonzero if the generalized force  $F_n$  and the flux  $J_m$  have opposite time reversal signature (and thus  $F_n$  and  $F_m$  have the same signature):  $\epsilon_n\epsilon_m = 1$  and vanish if  $F_n$  and the flux  $J_m$  have the same signature. Similarly, the reactive coefficients  $O_{nm}^r$  are nonzero only in the case where  $F_n$  and  $J_m$  have the same time reversal signature (and thus  $F_n$  and  $F_m$  have opposite signature) or  $\epsilon_n\epsilon_m = -1$ .

In addition to time reversal symmetry, the coefficients  $O_{nm}^d$  and  $O_{nm}^r$  have to reflect the spatial symmetries of a given system. This is called the Curie principle. The Curie principle provides a guide to determine the form of the matrix  $O_{nm}$  based on the symmetries of a system [47]. In particular, the Curie principle demands that the transformation properties of scalars, vectors and tensors under coordinate changes have to be respected. The thermodynamic fluxes  $J_n$  can be scalars, vectors or tensors, see table 1. If a particular constitutive equation describes a scalar flux, this flux can involve vector quantities only via scalar products. Similarly, a thermodynamic flux which is a vector can be constructed from other vectors or from the contraction of a second rank tensor with a vector. The coefficients  $O_{nm}$  can themselves be vectors or tensors if the system exhibits vectorial or tensorial asymmetries such as polar or nematic order parameters. We will now discuss the constitutive relations of different classes of active systems

using the Curie principle to express the Onsager relations given by equation (54).

#### 4.2. Active gels

*Active polar gels.* Using this formalism, we can now construct the theory of active polar gels. We consider the simple case of an incompressible medium with divergence free flow,  $\partial_\gamma v_\gamma = 0$ . In this case, the isotropic stress  $\sigma = -P$  or the hydrostatic pressure  $P$  becomes a Lagrange multiplier to impose the incompressibility constraint. We are left with the pairs of conjugate variables  $\tilde{\sigma}_{\alpha\beta}^{d,s} \leftrightarrow \tilde{v}_{\alpha\beta}$ ,  $Dp_\alpha/Dt \leftrightarrow h_\alpha$ ,  $j_\alpha^i \leftrightarrow -\partial_\alpha \bar{\mu}_i$ ,  $r^I \leftrightarrow \Delta\mu^I$  and  $D\tilde{u}_{\alpha\beta}/Dt \leftrightarrow -\sigma_{\alpha\beta}^{\text{el}}$ . Here we neglect for simplicity dissipative contributions to the antisymmetric stress which are irrelevant in the hydrodynamic limit, see also section 4.4 below and appendix C.3 [39, 41].

Writing terms obeying scalar, vectorial or tensorial symmetries only, the Onsager relations (54) of an active polar gel read [11, 16, 18, 48, 49]

$$\begin{aligned} \tilde{\sigma}_{\alpha\beta}^{d,s} &= \sigma_{\alpha\beta}^{\text{el}} + 2\eta\tilde{v}_{\alpha\beta} + \frac{\nu_1}{2}(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta}) + \zeta^I \Delta\mu^I \tilde{q}_{\alpha\beta} \\ &\quad - \frac{\nu^i}{2}(p_\beta \partial_\alpha \bar{\mu}_i + p_\alpha \partial_\beta \bar{\mu}_i - \frac{2}{3}p_\gamma \partial_\gamma \bar{\mu}_i \delta_{\alpha\beta}) \end{aligned} \quad (55)$$

$$\begin{aligned} \frac{Dp_\alpha}{Dt} &= \frac{1}{\gamma_1} h_\alpha - \nu_1 p_\beta \tilde{v}_{\alpha\beta} - \chi p_\beta \sigma_{\alpha\beta}^{\text{el}} + \lambda^I p_\alpha \Delta\mu^I \\ &\quad + \lambda_1^I \Delta\mu^I p_\alpha \partial_\gamma p_\gamma + \lambda_2^I \Delta\mu^I p_\gamma \partial_\gamma p_\alpha + \lambda_3^I \Delta\mu^I p_\gamma \partial_\alpha p_\gamma + \kappa^i \partial_\alpha \bar{\mu}^i \end{aligned} \quad (56)$$

$$\begin{aligned} j_\alpha^i &= -\Lambda^{ij} \partial_\alpha \bar{\mu}_j - \chi^i p_\beta \sigma_{\alpha\beta}^{\text{el}} - \nu^i p_\beta \tilde{v}_{\alpha\beta} + \lambda^i p_\alpha \Delta\mu^I + \chi_1^i \partial_\beta \sigma_{\alpha\beta}^{\text{el}} \\ &\quad + \epsilon_1^i \Delta\mu^I p_\alpha \partial_\gamma p_\gamma + \epsilon_2^i \Delta\mu^I p_\gamma \partial_\gamma p_\alpha - \kappa^i h_\alpha \end{aligned} \quad (57)$$

$$\begin{aligned} r^I &= \bar{\Lambda}^{IJ} \Delta\mu^J - \zeta^I \tilde{q}_{\alpha\beta} \tilde{v}_{\alpha\beta} - \psi^I \tilde{q}_{\alpha\beta} \sigma_{\alpha\beta}^{\text{el}} + \lambda^I p_\alpha h_\alpha \\ &\quad + \lambda_1^I h_\alpha p_\alpha \partial_\gamma p_\gamma + \lambda_2^I h_\alpha p_\gamma \partial_\gamma p_\alpha \\ &\quad + \lambda_3^I h_\alpha p_\gamma \partial_\alpha p_\gamma - \lambda^i p_\alpha \partial_\alpha \bar{\mu}_i - \epsilon_1^i (\partial_\alpha \bar{\mu}_i) p_\alpha \partial_\gamma p_\gamma \\ &\quad - \epsilon_2^i (\partial_\alpha \bar{\mu}_i) p_\gamma \partial_\gamma p_\alpha \end{aligned} \quad (58)$$

$$\begin{aligned} \frac{D\tilde{u}_{\alpha\beta}}{Dt} &= \tilde{v}_{\alpha\beta} - \Gamma \sigma_{\alpha\beta}^{\text{el}} + \frac{\chi}{2}(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta}) \\ &\quad + \psi^I \Delta\mu^I \tilde{q}_{\alpha\beta} \\ &\quad - \frac{\chi^i}{2}(p_\alpha \partial_\beta \bar{\mu}_i + p_\beta \partial_\alpha \bar{\mu}_i - \frac{2}{3}p_\gamma \partial_\gamma \bar{\mu}_i \delta_{\alpha\beta}) \\ &\quad - \chi_1^i (\partial_\alpha \partial_\beta \bar{\mu}_i - \frac{1}{3} \partial_\gamma \partial_\gamma \bar{\mu}_i \delta_{\alpha\beta}) \end{aligned} \quad (59)$$

where we have defined the traceless symmetric tensor

$$\tilde{q}_{\alpha\beta} = p_\alpha p_\beta - \frac{1}{3} p_\gamma p_\gamma \delta_{\alpha\beta}. \quad (60)$$

We have introduced dissipative and reactive Onsager coefficients that obey symmetric relations: The viscosity  $\eta$ , the polarity-flow-coupling coefficient  $\nu_1$ , the coefficients  $\zeta^I$  describing the generation of active stress by reaction  $I$ , a coefficient  $\nu^i$  coupling the chemical potential gradients to the stress as well as  $\gamma_1$  describing dissipation associated to

polarity changes. The coefficient  $\chi$  couples elastic stresses to polarity while the coefficient  $\lambda^I$  can serve as a Lagrange multiplier to impose the constraint  $p_\alpha^2 = 1$ . We included the coefficients  $\lambda_1^I$ ,  $\lambda_2^I$  and  $\lambda_3^I$  of second order terms in  $p_\alpha$  that can exist in polar systems. While a term proportional to  $p_\gamma \partial_\alpha p_\gamma$  described by the coefficient  $\lambda_3^I$  also exists in passive polar systems, the other two coefficients  $\lambda_1^I$  and  $\lambda_2^I$  are specific to active systems and generate interesting physics [12, 17, 50]. The coefficients  $\kappa^i$  describe the coupling between diffusion fluxes and polarity. The matrix  $\Lambda^{ij}$  describes diffusion coefficients and cross-diffusion and we take into account the coupling of elastic stresses to diffusion fluxes via the coefficients  $\chi_i$  and  $\chi_{1i}$  and couplings to polarity gradients via the coefficients  $\epsilon_1^i$  and  $\epsilon_2^i$ . The coefficients  $\lambda^{ii}$  describe molecular fluxes generated by chemical reactions such as the effects of molecular motors. The coefficient  $\Gamma$  describes the relaxation of elastic strain and  $\psi^I$  captures the generation of active elastic stresses by chemical reactions. Finally, the coefficients  $\bar{\Lambda}^{IJ}$  describe the chemical reaction rates. Note that in the constitutive equations (55)–(59), the component indices run from  $i = 1, \dots, M$  and do not include the solvent  $i = 0$ . The solvent flux  $j_\alpha^0$  follows from other fluxes through the mass conservation equation (equation (12)).

Note that the elastic stress  $-\sigma_{\alpha\beta}^{\text{el}}$  enters in equation (55) with Onsager coefficient  $-1$  and  $\tilde{v}_{\alpha\beta}$  in equation (59) with coefficient  $1$ , consistent with a reactive coupling. The magnitude of the dimensionless coefficients can be chosen without loss of generality to be  $\pm 1$ . The total stress is given by

$$\sigma_{\alpha\beta}^{\text{tot}} = -\rho v_\alpha v_\beta + \tilde{\sigma}_{\alpha\beta}^e - P \delta_{\alpha\beta} + \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha) + \tilde{\sigma}_{\alpha\beta}^{d,s}, \quad (61)$$

where  $\tilde{\sigma}_{\alpha\beta}^e$  denotes the traceless part of the equilibrium stress  $\sigma_{\alpha\beta}^{\text{el}}$  defined in equation (21).

*Hydrodynamic limit.* In the hydrodynamic limit, the system is governed by the slow dynamics of hydrodynamic modes which follow from conservation laws. The relaxation time of these modes diverges in the limit of long wave-lengths. Because the strain variable relaxes on a finite time scale, in the hydrodynamic limit it has relaxed to a steady state value with  $D\tilde{u}_{\alpha\beta}/Dt = 0$ . The elastic stress  $\sigma_{\alpha\beta}^{\text{el}}$  can then be determined from equation (59). The gel then behaves as a viscous fluid. On long length scales all terms proportional to spatial gradients can be neglected. After eliminating the elastic stress  $\sigma_{\alpha\beta}^{\text{el}}$  in equation (55), we arrive at the hydrodynamic theory of an active polar fluid [11, 16, 18, 48]

$$\tilde{\sigma}_{\alpha\beta}^{d,s} = 2\eta^{\text{eff}} \tilde{v}_{\alpha\beta} + \frac{\nu_1^{\text{eff}}}{2}(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta}) + \zeta_{\text{eff}}^I \Delta\mu^I \tilde{q}_{\alpha\beta} \quad (62)$$

$$\begin{aligned} \frac{Dp_\alpha}{Dt} &= \left( \frac{1}{\gamma_1} - \frac{\chi^2 p_\beta p_\beta}{2\Gamma} \right) h_\alpha - \frac{\chi^2}{6\Gamma} p_\alpha h_\beta p_\beta - \nu_1^{\text{eff}} p_\beta \tilde{v}_{\alpha\beta} \\ &\quad + \lambda^I p_\alpha \Delta\mu^I + \lambda_1^I \Delta\mu^I p_\alpha \partial_\gamma p_\gamma \\ &\quad + \lambda_2^I \Delta\mu^I p_\gamma \partial_\gamma p_\alpha + \lambda_3^I \Delta\mu^I p_\gamma \partial_\alpha p_\gamma - \frac{\psi^I \chi}{\Gamma} \Delta\mu^I p_\beta \tilde{q}_{\alpha\beta} \end{aligned} \quad (63)$$

$$j_\alpha^i = -\Lambda^{ij} \partial_\alpha \bar{\mu}^j + \lambda^i p_\alpha \Delta\mu^I \quad (64)$$

$$r^I = (\bar{\Lambda}^I - \frac{\psi^I \psi^I}{\Gamma} \tilde{q}_{\alpha\beta} \tilde{q}_{\alpha\beta}) \Delta\mu^I - \zeta_{\text{eff}}^I \tilde{q}_{\alpha\beta} \tilde{v}_{\alpha\beta} - \frac{\chi \psi^I}{\Gamma} \tilde{q}_{\alpha\beta} p_\alpha h_\beta + \lambda^I p_\alpha h_\alpha + \lambda_1^I h_\alpha p_\alpha \partial_\gamma p_\gamma + \lambda_2^I h_\alpha p_\gamma \partial_\gamma p_\alpha + \lambda_3^I h_\alpha p_\gamma \partial_\alpha p_\gamma - \lambda^I p_\alpha \partial_\alpha \bar{\mu}_i. \quad (65)$$

Here we have introduced the effective gel viscosity  $\eta^{\text{eff}} = \eta + 1/(2\Gamma)$  as well as the effective Onsager coefficient  $\nu_1^{\text{eff}} = \nu_1 + \chi/\Gamma$  and the coefficient  $\zeta_{\text{eff}}^I = \zeta^I + \psi^I/\Gamma$  describing active stresses. For simplicity, we have considered the case  $\chi^i = 0$ ,  $\chi_1^i = 0$ ,  $\nu^i = 0$ ,  $\kappa^i = 0$ , and  $\epsilon_k^i = 0$  with  $k = 1, 2$ .

*Active stress.* A key feature of the constitutive equations of active polar gels given by equations (55) and (62) is the traceless and symmetric contribution to the stress

$$\tilde{\sigma}_{\alpha\beta}^{\text{act}} = \zeta^I \Delta\mu^I \tilde{q}_{\alpha\beta} \quad (66)$$

due to active chemical processes. This active stress plays a fundamental role for the dynamics of active gels and fluids and implies that in the absence of external stresses the gel can undergo spontaneous shear. Furthermore the system can perform mechanical work against external stresses which are powered by chemical energy related to chemical potential differences  $\Delta\mu^I$ . Because of Onsager symmetries of the coupling coefficients, the coefficients  $\zeta^I$  also enter the chemical reaction rates (58) and (65), which effectively become mechanosensitive.

In the biological context, the molecular processes that generate active stresses are often mediated by molecular motors. These motors are fueled by the hydrolysis reaction of ATP to ADP and inorganic phosphate. This hydrolysis reaction therefore is the dominant chemical reaction  $I$  that couples via the coefficient  $\zeta^I$  to active stress. The active stress  $\sigma_{\alpha\beta}^{\text{act}}$  emerges from a large number of force generating events that occur in the anisotropic material. A small assembly of molecular motors that locally interacts for example with two aligned filaments in the presence of ATP generates a pair of equal and opposite forces  $\pm f^n p_\alpha^n$  in the material, see figures 2(a) and (b). Here  $\pm p_\alpha^n$  are unit vectors, characterizing the opposite orientations of the two aligned filaments and  $n$  is an index over such pairs of aligned filaments that are cross-linked by active motors. This force and counter force correspond to a force dipole with force density

$$\phi_\alpha = f^n p_\alpha^n \left( \delta(\mathbf{x} - \mathbf{x}_0 + \frac{a}{2} \mathbf{p}^n) - \delta(\mathbf{x} - \mathbf{x}_0 - \frac{a}{2} \mathbf{p}^n) \right) \quad (67)$$

at position  $\mathbf{x}_0$  in the material. Here  $a$  denotes the distance at which force and counter-force act. On large length scales or in a continuum limit, this can be expanded in the microscopic length  $a$ . To first order it corresponds to the point dipole

$$\phi_\alpha \simeq a f^n p_\alpha^n p_\beta^n \partial_\beta \delta(\mathbf{x} - \mathbf{x}_0) = \partial_\beta \sigma_{\alpha\beta}^n \quad (68)$$

with the corresponding stress [15]

$$\sigma_{\alpha\beta}^n = f a p_\alpha^n p_\beta^n. \quad (69)$$

In a continuum description, the density of these force dipoles in a local volume elements  $V$  is the active stress

$$\sigma_{\alpha\beta}^{\text{act}} = \frac{1}{V} \sum_n f^n a p_\alpha^n p_\beta^n \quad (70)$$

where the sum is over motor-induced force dipoles in the volume  $V$ . The anisotropic part of this active stress is given in equation (66) to linear order in the chemical force  $\Delta\mu^I$ . In the context for motor protein generated active stress the ATP hydrolysis reaction drives the generation of the active stress and  $\Delta\mu^I$  corresponds to the chemical potential difference of the fuel ATP and its reaction products.

*Visco-elastic gel.* On shorter time scales, the active gel exhibits elastic behaviors. Writing  $\sigma_{\alpha\beta}^{\text{el}} = K \tilde{u}_{\alpha\beta}$ , where  $K$  is an elastic modulus, The equation (59) for the elastic stress becomes [49]

$$(1 + \tau \frac{D}{Dt}) \sigma_{\alpha\beta}^{\text{el}} = \frac{1}{\Gamma} \tilde{v}_{\alpha\beta} + \frac{\chi}{2\Gamma} (p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta}) + \frac{\psi^I \Delta\mu^I}{\Gamma} \tilde{q}_{\alpha\beta} \quad (71)$$

where  $\tau = 1/(K\Gamma)$  is a Maxwell relaxation time. Equation (71) thus is the generalization of a Maxwell model of viscoelastic gels to the case of polar and active gels. Permeation of this Maxwell gel by solvent is captured in this theory when we include the coefficient  $\chi_1^i$  from equation (57) in equation (64) for  $i = g$ , where  $g$  denotes the gel material. We then have

$$j_\alpha^g = -\bar{\Lambda}^{gj} \partial_\alpha \bar{\mu}_j + \lambda^{gI} p_\alpha \Delta\mu^I + \chi_1^g \partial_\beta \sigma_{\alpha\beta}^{\text{el}}. \quad (72)$$

Using  $J_\alpha^g = j_\alpha^g + n_g v_\alpha$  and  $J_\alpha^g = n_g v_\alpha^g$ , this can be written as a permeation equation

$$\lambda^g (v_\alpha^g - v_\alpha) = -\bar{\Lambda}^{gj} \partial_\alpha \bar{\mu}_j + \bar{\lambda}^{gI} p_\alpha \Delta\mu^I + \partial_\beta \sigma_{\alpha\beta}^{\text{el}}, \quad (73)$$

which describes the effects of the elastic force density  $\partial_\beta \sigma_{\alpha\beta}^{\text{el}}$  pushing the fluid through the gel [51]. Here, the permeation coefficient is  $\lambda^g = n_g/\chi_1^g$ . Furthermore,  $\bar{\Lambda}^{gj} = \Lambda^{gj}/\chi_1^g$  and  $\bar{\lambda}^{gI} = \lambda^{gI}/\chi_1^g$ . The contribution  $\bar{\lambda}^{gI} p_\alpha \Delta\mu^I$  describes the force density due to the action of chemical reactions or molecular motors.

In the long-time limit, the elastic stress is governed by gel viscosity and active stresses and is of the form [49]

$$\sigma_{\alpha\beta}^{\text{el}} \simeq \eta_g (\partial_\alpha v_\beta^g + \partial_\beta v_\alpha^g - \frac{2}{3} \partial_\gamma v_\gamma^g \delta_{\alpha\beta}) + \frac{\psi^I \Delta\mu^I}{\Gamma} \tilde{q}_{\alpha\beta} + \frac{\chi}{2\Gamma} (p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta}). \quad (74)$$

Gel viscosity and gel permeation coefficient introduce a characteristic length  $\ell = (\eta_g/\lambda^g)^{1/2}$ . On length scales large compared to  $\ell$ , the contribution  $\partial_\beta \sigma_{\alpha\beta}^{\text{el}}$  can be neglected in equation (72) and we recover in the hydrodynamic limit the form of equation (64). On short length scales, however, the friction due to permeation  $\lambda^g (v_\alpha^g - v_\alpha)$  can be neglected. In this limit, the permeating fluid can be ignored and equation (73) for  $\lambda^g = 0$  describes the force balance of the gel alone. In this limit a simplified one-component model of only the gel [11, 16, 52] can be used to capture the main features of the active gel.

### 4.3. Active nematics

Nematic liquid crystals are characterized by the tensor order parameter  $Q_{\alpha\beta}$ , which is traceless and characterizes local anisotropies. In the presence of active processes and on time scales when elastic stresses have relaxed, we consider the conjugate variables  $\tilde{\sigma}_{\alpha\beta}^{d,s} \leftrightarrow \tilde{v}_{\alpha\beta}$ ,  $DQ_{\alpha\beta}/Dt \leftrightarrow H_{\alpha\beta}$ ,  $j_{\alpha}^i \leftrightarrow -\partial_{\alpha}\bar{\mu}_i$  and  $r^I \leftrightarrow \Delta\mu^I$ . We again describe an incompressible system and the pressure  $P$  serves as a Lagrange multiplier to impose incompressibility. An active nematic fluid is then characterized by the following constitutive relations [53, 54]

$$\tilde{\sigma}_{\alpha\beta}^{d,s} = 2\eta\tilde{v}_{\alpha\beta} + \nu_1 H_{\alpha\beta} + \zeta^I \Delta\mu^I Q_{\alpha\beta} \quad (75)$$

$$\frac{DQ_{\alpha\beta}}{Dt} = \frac{1}{\gamma_1} H_{\alpha\beta} - \nu_1 \tilde{v}_{\alpha\beta} + \lambda^I Q_{\alpha\beta} \Delta\mu^I \quad (76)$$

$$j_{\alpha}^i = -\Lambda^{ij} \partial_{\alpha}\bar{\mu}_j + \epsilon^{il} \Delta\mu^l \partial_{\beta} Q_{\alpha\beta} \quad (77)$$

$$r^I = \bar{\Lambda}^{IJ} \Delta\mu^J - \zeta^I Q_{\alpha\beta} \tilde{v}_{\alpha\beta} + \lambda^I Q_{\alpha\beta} H_{\alpha\beta} - \epsilon^{il} (\partial_{\alpha}\bar{\mu}_i) \partial_{\beta} Q_{\alpha\beta}, \quad (78)$$

where we have introduced phenomenological coupling coefficients  $\nu_1$ ,  $\gamma_1$ ,  $\lambda^I$ ,  $\epsilon^{il}$ . They are related to coefficients with the same name in the polar case given in equations (55)–(59), but correspond here to a nematic system and do not have the same values. The total stress is given by

$$\sigma_{\alpha\beta}^{\text{tot}} = \rho v_{\alpha} v_{\beta} + \tilde{\sigma}_{\alpha\beta}^e - P \delta_{\alpha\beta} + Q_{\alpha\gamma} H_{\beta\gamma} - Q_{\beta\gamma} H_{\alpha\gamma} + \tilde{\sigma}_{\alpha\beta}^{d,s}, \quad (79)$$

with the equilibrium stress  $\sigma_{\alpha\beta}^e$  defined in (40).

### 4.4. Active chiral systems

The molecular building blocks of biological systems are chiral. In particular, the filaments of the cytoskeleton form helical structures along which molecular motors move. As a consequence active processes that generate forces and movements at molecular scales are chirally asymmetric. This implies that in the constitutive material equations terms are allowed that are chirally asymmetric. Such terms can involve the totally antisymmetric pseudo tensor  $\epsilon_{\alpha\beta\gamma}$  which can couple antisymmetric tensors with vectors.

Active chiral processes generate torques. More precisely, they introduce torque dipoles in the active gel which contribute to fluxes of angular momentum. To capture the physics of such active torque dipoles, we include the variables describing intrinsic rotations and angular momentum fluxes in the discussion of active chiral systems [42, 55]. We thus consider an active chiral polar fluid and focus on the pairs of conjugate variables  $\tilde{\sigma}_{\alpha\beta}^{d,s} \leftrightarrow \tilde{v}_{\alpha\beta}$ ,  $Dp_{\alpha}/Dt \leftrightarrow h_{\alpha}$ ,  $r^I \leftrightarrow \Delta\mu^I$ ,  $M_{\alpha\beta\gamma}^d \leftrightarrow \partial_{\gamma}\omega_{\alpha\beta}/2$  and  $\sigma_{\alpha\beta}^{d,a} \leftrightarrow (\Omega_{\alpha\beta} - \omega_{\alpha\beta})$ .

The constitutive relations then read

$$\tilde{\sigma}_{\alpha\beta}^{d,s} = 2\eta\tilde{v}_{\alpha\beta} + \frac{\nu_1}{2} (p_{\alpha} h_{\beta} + p_{\beta} h_{\alpha} - \frac{2}{3} p_{\gamma} h_{\gamma} \delta_{\alpha\beta}) + \zeta^I \Delta\mu^I \tilde{q}_{\alpha\beta} \quad (80)$$

$$\begin{aligned} \sigma_{\alpha\beta}^{d,a} &= 2\eta'(\Omega_{\alpha\beta} - \omega_{\alpha\beta}) + \frac{\bar{\eta}}{2} p_{\gamma} \partial_{\gamma} \omega_{\alpha\beta} \\ &+ \frac{\nu_2}{2} (p_{\alpha} h_{\beta} - p_{\beta} h_{\alpha}) + \nu_3 \epsilon_{\alpha\beta\gamma} h_{\gamma} \\ &+ \zeta_a^I \Delta\mu^I p_{\gamma} \epsilon_{\alpha\beta\gamma} \end{aligned} \quad (81)$$

$$\begin{aligned} \frac{Dp_{\alpha}}{Dt} &= \frac{1}{\gamma_1} h_{\alpha} - \nu_1 p_{\beta} \tilde{v}_{\alpha\beta} + \nu_2 p_{\beta} (\Omega_{\alpha\beta} - \omega_{\alpha\beta}) - \nu_3 \epsilon_{\alpha\beta\gamma} (\Omega_{\beta\gamma} - \omega_{\beta\gamma}) \\ &+ \frac{\bar{\nu}_2}{2} p_{\gamma} p_{\beta} \partial_{\gamma} \omega_{\alpha\beta} - \frac{\bar{\nu}_3}{2} \epsilon_{\gamma\beta\alpha} p_{\delta} \partial_{\delta} \omega_{\gamma\beta} - \frac{\bar{\nu}_4}{2} \epsilon_{\gamma\beta\delta} p_{\alpha} \partial_{\delta} \omega_{\gamma\beta} \\ &+ \lambda^I p_{\alpha} \Delta\mu^I + \lambda_1^I \Delta\mu^I p_{\alpha} \partial_{\gamma} p_{\gamma} + \lambda_2^I \Delta\mu^I p_{\gamma} \partial_{\gamma} p_{\alpha} \end{aligned} \quad (82)$$

$$\begin{aligned} M_{\alpha\beta\gamma}^d &= \kappa \partial_{\gamma} \omega_{\alpha\beta} + \bar{\eta} p_{\gamma} (\Omega_{\alpha\beta} - \omega_{\alpha\beta}) \\ &+ \frac{\bar{\nu}_2}{2} p_{\gamma} (p_{\alpha} h_{\beta} - p_{\beta} h_{\alpha}) + \bar{\nu}_3 \epsilon_{\alpha\beta\delta} h_{\delta} p_{\gamma} + \bar{\nu}_4 \epsilon_{\alpha\beta\gamma} p_{\delta} h_{\delta} \\ &+ \zeta_1^I \Delta\mu^I \epsilon_{\alpha\beta\gamma} + \zeta_2^I \Delta\mu^I \epsilon_{\alpha\beta\nu} p_{\nu} p_{\gamma} \\ &+ \zeta_3^I \Delta\mu^I (\epsilon_{\alpha\gamma\delta} p_{\delta} p_{\beta} - \epsilon_{\beta\gamma\delta} p_{\delta} p_{\alpha}) + \zeta_4^I \Delta\mu^I (\delta_{\alpha\gamma} p_{\beta} - \delta_{\beta\gamma} p_{\alpha}) \end{aligned} \quad (83)$$

$$\begin{aligned} r^I &= \bar{\Lambda}^{IJ} \Delta\mu^J - \zeta^I \tilde{q}_{\alpha\beta} \tilde{v}_{\alpha\beta} + \lambda^I p_{\alpha} h_{\alpha} + \lambda_1^I h_{\alpha} p_{\alpha} \partial_{\gamma} p_{\gamma} \\ &+ \lambda_2^I h_{\alpha} p_{\gamma} \partial_{\gamma} p_{\alpha} + \zeta_a^I (\omega_{\alpha\beta} - \Omega_{\alpha\beta}) p_{\gamma} \epsilon_{\alpha\beta\gamma} \\ &- \frac{\partial_{\gamma} \omega_{\alpha\beta}}{2} [\zeta_1^I \epsilon_{\alpha\beta\gamma} + \zeta_2^I \epsilon_{\alpha\beta\nu} p_{\nu} p_{\gamma} + \zeta_3^I (\epsilon_{\alpha\gamma\delta} p_{\delta} p_{\beta} - \epsilon_{\beta\gamma\delta} p_{\delta} p_{\alpha}) \\ &+ \zeta_4^I (\delta_{\alpha\gamma} p_{\beta} - \delta_{\beta\gamma} p_{\alpha})]. \end{aligned} \quad (84)$$

Here, we have introduced new Onsager coefficients that describe antisymmetric stresses, angular momentum fluxes and active chiral terms. The dissipative coefficients  $\eta'$ ,  $\bar{\eta}$ ,  $\kappa$  and the reactive coefficients  $\nu_2$  and  $\bar{\nu}_2$  also exist in nonchiral passive systems and are irrelevant in the hydrodynamic limit. The chiral terms described by the coefficients  $\nu_3$ ,  $\bar{\nu}_3$  and  $\bar{\nu}_4$  are passive and also irrelevant in the hydrodynamic limit. Active chiral terms are described by the coefficients  $\zeta_a^I$ ,  $\zeta_1^I$ ,  $\zeta_2^I$  and  $\zeta_3^I$ . The active term with coefficient  $\zeta_4^I$  also exists in nonchiral active systems [42].

What are the roles of the new variables  $\Omega_{\alpha\beta}$ ,  $\sigma_{\alpha\beta}^{d,a}$  and  $M_{\alpha\beta\gamma}^d$ ? The total antisymmetric stress depends on  $\sigma_{\alpha\beta}^{d,a}$  and  $M_{\alpha\beta\gamma}^d$  through equation (50). Therefore both the dissipative antisymmetric stress and the angular momentum flux enter the momentum conservation equation (3), which generalizes the Stokes equation and determines the velocity field. These new variables thus capture the effects of active chiral processes on the flow field. Using the angular momentum conservation equation (6) and the definition of the dissipative antisymmetric stress (50), one obtains an equation for the angular momentum density (appendix C.2)

$$\partial_t l_{\alpha\beta} + \partial_{\gamma} (v_{\gamma} l_{\alpha\beta}) - (\Omega_{\alpha} l_{\beta} - \Omega_{\beta} l_{\alpha}) = -2\sigma_{\alpha\beta}^{d,a}. \quad (85)$$

Therefore, the dissipative antisymmetric stress  $\sigma^{d,a}$  provides a source for the angular momentum density and influences the intrinsic rotation rate  $\Omega_{\alpha\beta}$ . In passive fluids or liquid crystals, the intrinsic rotation rate approaches the vorticity field,  $\Omega_{\alpha\beta} \simeq \omega_{\alpha\beta}$  in the hydrodynamic limit and  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$  becomes irrelevant. As we show now, the intrinsic rotation mismatch  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$  can persist in active chiral systems.

We consider the limit where the angular momentum density  $l_{\alpha\beta}$  is small and can be neglected in equation (85) as compared to terms proportional to the rotational viscosity  $\eta'$  that contribute to  $\sigma_{\alpha\beta}^{a,d}$ . In that case equation (85) reduces to  $\sigma_{\alpha\beta}^{a,d} = 0$ . From equation (81) we then obtain an equation for the intrinsic rotation rate mismatch:

$$\begin{aligned} \Omega_{\alpha\beta} - \omega_{\alpha\beta} = & -\frac{\bar{\eta}}{4\eta'} p_\gamma \partial_\gamma \omega_{\alpha\beta} - \frac{\nu_2}{4\eta'} (p_\alpha h_\beta - p_\beta h_\alpha) \\ & - \frac{\nu_3}{2\eta'} \epsilon_{\alpha\beta\gamma} h_\gamma - \frac{\zeta_a^I}{2\eta'} \Delta\mu^I p_\gamma \epsilon_{\alpha\beta\gamma}. \end{aligned} \quad (86)$$

The intrinsic rotation mismatch corresponds to differences between the intrinsic rotation rate and the local rotation vorticity. Here, terms on the right-hand side correspond to different processes generating a rotation mismatch when the fluid is out of equilibrium. The last term corresponds to an active term describing chemical reactions driving such rotation deviations. Note that equation (86) shows that for active systems with  $\zeta_a^I$  nonzero, the rotation mismatch  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$  can persist in the hydrodynamic limit and for long times. This is a novel and original feature of active chiral systems.

In situations where the intrinsic rotation rate mismatch is not experimentally accessible or not of interest, equation (86) can be used to eliminate the intrinsic rotation rate  $\Omega_{\alpha\beta}$  from the constitutive equations. The equations for the rate of polarity change and for the dissipative part of the angular momentum flux then take the form

$$\begin{aligned} \frac{Dp_\alpha}{Dt} = & \left( \frac{1}{\gamma_1} + \frac{\nu_2^2 p_\gamma p_\gamma + 4\nu_3^2}{4\eta'} \right) \delta_{\alpha\beta} - \frac{\nu_2^2}{4\eta'} p_\alpha p_\beta \Big) h_\beta - \nu_1 p_\beta \tilde{\nu}_{\alpha\beta} \\ & + \frac{\bar{\nu}_2^{\text{eff}}}{2} p_\gamma p_\beta \partial_\gamma \omega_{\alpha\beta} - \frac{\bar{\nu}_3^{\text{eff}}}{2} \epsilon_{\gamma\beta\alpha} p_\delta \partial_\delta \omega_{\gamma\beta} - \frac{\bar{\nu}_4}{2} \epsilon_{\gamma\beta\delta} p_\alpha \partial_\delta \omega_{\gamma\beta} \\ & + \lambda^{I,\text{eff}} p_\alpha \Delta\mu^I + \lambda_1^I \Delta\mu^I p_\alpha \partial_\gamma p_\gamma + \lambda_2^I \Delta\mu^I p_\gamma \partial_\gamma p_\alpha \end{aligned} \quad (87)$$

$$\begin{aligned} M_{\alpha\beta\gamma}^d = & \left( \kappa \delta_{\gamma\delta} - \frac{\bar{\eta}^2}{4\eta'} p_\gamma p_\delta \right) \partial_\delta \omega_{\alpha\beta} + \frac{\bar{\nu}_2^{\text{eff}}}{2} p_\gamma (p_\alpha h_\beta - p_\beta h_\alpha) \\ & + \bar{\nu}_3^{\text{eff}} p_\gamma h_\delta \epsilon_{\alpha\beta\delta} \\ & + \bar{\nu}_4 \epsilon_{\alpha\beta\gamma} p_\delta h_\delta + \zeta_1^I \Delta\mu^I \epsilon_{\alpha\beta\gamma} + \zeta_2^{I,\text{eff}} \Delta\mu^I \epsilon_{\alpha\beta\nu} p_\nu p_\gamma \\ & + \zeta_3^I \Delta\mu^I (\epsilon_{\alpha\gamma\delta} p_\delta p_\beta - \epsilon_{\beta\gamma\delta} p_\delta p_\alpha) \\ & + \zeta_4^I \Delta\mu^I (\delta_{\alpha\gamma} p_\beta - \delta_{\beta\gamma} p_\alpha), \end{aligned} \quad (88)$$

where we have introduced the effective coefficients  $\bar{\nu}_2^{\text{eff}} = \bar{\nu}_2 - \bar{\eta}\nu_2/(2\eta')$ ,  $\bar{\nu}_3^{\text{eff}} = \bar{\nu}_3 - \bar{\eta}\nu_3/(2\eta')$ ,  $\lambda^{I,\text{eff}} = \lambda^I + \nu_3\zeta_a^I/\eta'$  and  $\zeta_2^{I,\text{eff}} = \zeta_2^I - \bar{\eta}\zeta_a^I/(2\eta')$ . Eliminating the rotation mismatch thus leads to a renormalization of phenomenological coefficients. In addition, new anisotropies are introduced in the term proportional to  $h_\beta$  in equation (87) and proportional to  $\partial_\delta \omega_{\alpha\beta}$  in equation (88). These terms are allowed by symmetry in equations (82) and (83) but were neglected for simplicity. The corresponding antisymmetric part of the total stress is given by  $\sigma_{\alpha\beta}^a = \sigma_{\alpha\beta}^{e,a} + \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha) + \frac{1}{2}\partial_\gamma M_{\alpha\beta\gamma}^d$ .

It is also possible to derive the constitutive equations of an active chiral fluid using symmetric stresses only. In fact, using a specific redefinition  $g'$  of the momentum density

and using a redefined angular momentum density  $l'_{\alpha\beta}$  and angular momentum flux  $M'_{\alpha\beta\gamma}$  with  $l'_{\alpha\beta} = 0$  and  $M'_{\alpha\beta\gamma} = 0$ , the corresponding redefined stress tensor  $\sigma'_{\alpha\beta}$  becomes symmetric [39], see appendix C.3. With these redefinitions one obtains a hydrodynamic theory in which the stress tensor is symmetric. In the case of passive systems with  $\Delta\mu^I = 0$ , this theory with symmetric stress tensor  $\sigma'_{\alpha\beta}$  contains the same physics on large scales as the theory presented in the previous sections that is based on asymmetric stress tensors. However, differences can arise on smaller scales. Importantly, for an active system with active chiral terms differences between both approaches can arise even in the hydrodynamic limit. This is because a theory based on a symmetrized stress tensor misses the physics of internal rotations and it does not contain the internal rotation mismatch  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$ . However this term can be critical: while for passive systems this internal rotation mismatch vanishes in the hydrodynamic limit, this is not so in the presence of active chiral processes where it can persist at long times as described by equation (86).

#### 4.5. Fluctuations and noise

We have presented a systematic procedure to construct constitutive equations for polar, nematic and visco-elastic active gels based on the principles of irreversible thermodynamics and Onsager relations governing conjugate thermodynamic fluxes and forces. In this framework, one can systematically add the effects of fluctuations, taking into account the fluctuation dissipation theorem that applies at thermodynamic equilibrium. Realistic biological systems operate far from thermodynamic equilibrium and the fluctuation dissipation theorem is broken. However introducing noise according to rules from irreversible thermodynamics is a useful starting point [56]. Far from equilibrium specific arguments are needed to characterize the properties of the nonequilibrium noise [57].

The linear response relations (54) can be extended to include noise terms which then leads to noisy hydrodynamic equations. The extended linear response reads [32]

$$J_n = \sum_m O_{nm} F_m + \eta_n(t). \quad (89)$$

The noises  $\eta_n(t)$  are Gaussian stochastic variables with average  $\langle \eta_n(t) \rangle = 0$  and variance

$$\langle \eta_n(t) \eta_m(t') \rangle = 2k_B T O_{nm}^d \delta(t - t') \quad (90)$$

where  $O_{mn}^d = (O_{mn} + O_{nm})/2$  is the symmetric part of  $O_{mn}$  and the fluctuation dissipation theorem has been used to set the noise amplitude. Higher order correlations follow from the Gaussian statistics of these variables.

We illustrate this principle by adding appropriate noise terms to the constitutive equations of a polar active gel (55)–(59) which read [56]

$$\begin{aligned} \tilde{\sigma}_{\alpha\beta}^{d,s} = & \sigma_{\alpha\beta}^{eI} + 2\eta\tilde{\nu}_{\alpha\beta} + \frac{\nu_1}{2}(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta}) + \zeta^I \Delta\mu^I \tilde{q}_{\alpha\beta} \\ & - \frac{\nu_i}{2}(p_\beta \partial_\alpha \bar{\mu}_i + p_\alpha \partial_\beta \bar{\mu}_i - \frac{2}{3}p_\gamma \partial_\gamma \bar{\mu}_i \delta_{\alpha\beta}) + \zeta_{\alpha\beta}^{(\sigma)} \end{aligned} \quad (91)$$

$$\begin{aligned} \frac{Dp_\alpha}{Dt} &= \frac{1}{\gamma_1} h_\alpha - \nu_1 p_\beta \tilde{v}_{\alpha\beta} - \chi p_\beta \sigma_{\alpha\beta}^{\text{el}} + \lambda^I p_\alpha \Delta \mu^I \\ &+ \lambda_1^I \Delta \mu^I p_\alpha \partial_\gamma p_\gamma + \lambda_2^I \Delta \mu^I p_\gamma \partial_\gamma p_\alpha \\ &+ \lambda_3^I \Delta \mu^I p_\gamma \partial_\alpha p_\gamma + \kappa^i \partial_\alpha \bar{\mu}^i + \xi_\alpha^{(p)} \end{aligned} \quad (92)$$

$$\begin{aligned} j_\alpha^i &= -\Lambda^{ij} \partial_\alpha \bar{\mu}^j - \chi^i p_\beta \sigma_{\alpha\beta}^{\text{el}} - \nu^i p_\beta \tilde{v}_{\alpha\beta} \\ &+ \lambda^i p_\alpha \Delta \mu^I + \chi_1^i \partial_\beta \sigma_{\alpha\beta}^{\text{el}} \\ &+ \epsilon_1^{ii} \Delta \mu^I p_\alpha \partial_\gamma p_\gamma + \epsilon_2^{ii} \Delta \mu^I p_\gamma \partial_\gamma p_\alpha - \kappa^i h_\alpha + \xi_\alpha^{i(j)} \end{aligned} \quad (93)$$

$$\begin{aligned} r^I &= \bar{\Lambda}^{IJ} \Delta \mu^J - \zeta^I \tilde{q}_{\alpha\beta} \tilde{v}_{\alpha\beta} - \psi^I \tilde{q}_{\alpha\beta} \sigma_{\alpha\beta}^{\text{el}} + \lambda^I p_\alpha h_\alpha \\ &+ \lambda_1^I h_\alpha p_\alpha \partial_\gamma p_\gamma + \lambda_2^I h_\alpha p_\gamma \partial_\gamma p_\alpha \\ &+ \lambda_3^I h_\alpha p_\gamma \partial_\alpha p_\gamma - \lambda^i p_\alpha \partial_\alpha \bar{\mu}^i - \epsilon_1^{ii} (\partial_\alpha \bar{\mu}^i) p_\alpha \partial_\gamma p_\gamma \\ &- \epsilon_2^{ii} (\partial_\alpha \bar{\mu}^i) p_\gamma \partial_\gamma p_\alpha + \xi^{I(r)} \end{aligned} \quad (94)$$

$$\begin{aligned} \frac{D\tilde{u}_{\alpha\beta}}{Dt} &= \tilde{v}_{\alpha\beta} - \Gamma \sigma_{\alpha\beta}^{\text{el}} + \frac{\chi}{2} (p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta}) \\ &+ \psi^I \Delta \mu^I \tilde{q}_{\alpha\beta} \\ &- \frac{\chi^i}{2} (p_\alpha \partial_\beta \bar{\mu}^i + p_\beta \partial_\alpha \bar{\mu}^i - \frac{2}{3} p_\gamma \partial_\gamma \bar{\mu}^i \delta_{\alpha\beta}) \\ &+ \chi_1^i (\partial_\alpha \partial_\beta \bar{\mu}^i - \frac{1}{3} \partial_\gamma \partial_\gamma \bar{\mu}^i \delta_{\alpha\beta}) + \xi_{\alpha\beta}^{(u)}. \end{aligned} \quad (95)$$

The Gaussian noises are the stress fluctuation  $\xi_{\alpha\beta}^{(\sigma)}$ , the polarity fluctuations  $\xi_\alpha^{(p)}$ , the current fluctuations  $\xi_\alpha^{i(j)}$ , the reaction rate fluctuations  $\xi^{I(r)}$  and the strain fluctuations  $\xi_{\alpha\beta}^{(u)}$ . They all vanish on average and have the correlations

$$\langle \xi_{\alpha\beta}^{(\sigma)}(t, \mathbf{x}) \xi_{\gamma\delta}^{(\sigma)}(t', \mathbf{x}') \rangle = 2k_B T \eta \left[ \delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma} - \frac{2}{3} \delta_{\alpha\beta} \delta_{\gamma\delta} \right] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \quad (96)$$

$$\langle \xi_\alpha^{(p)}(t, \mathbf{x}) \xi_\beta^{(p)}(t', \mathbf{x}') \rangle = \frac{2k_B T}{\gamma_1} \delta_{\alpha\beta} \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \quad (97)$$

$$\langle \xi_\alpha^{k(j)}(t, \mathbf{x}) \xi_\beta^{l(j)}(t', \mathbf{x}') \rangle = 2k_B T \Lambda^{kl} \delta_{\alpha\beta} \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \quad (98)$$

$$\langle \xi^{I(r)}(t, \mathbf{x}) \xi^{J(r)}(t', \mathbf{x}') \rangle = 2k_B T \bar{\Lambda}^{IJ} \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \quad (99)$$

$$\begin{aligned} \langle \xi_{\alpha\beta}^{(u)}(t, \mathbf{x}) \xi_{\gamma\delta}^{(u)}(t', \mathbf{x}') \rangle &= 2k_B T \Gamma \left[ \delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma} \right. \\ &\left. - \frac{2}{3} \delta_{\alpha\beta} \delta_{\gamma\delta} \right] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}'). \end{aligned} \quad (100)$$

There are further dissipative couplings which imply the cross-correlations

$$\begin{aligned} \langle \xi_\alpha^{(p)}(t, \mathbf{x}) \xi_{\beta\gamma}^{(u)}(t', \mathbf{x}') \rangle &= k_B T \chi [\delta_{\alpha\beta} p_\gamma \\ &+ \delta_{\alpha\gamma} p_\beta - \frac{2}{3} \delta_{\beta\gamma} p_\alpha] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \end{aligned} \quad (101)$$

$$\begin{aligned} \langle \xi_\alpha^{(p)}(t, \mathbf{x}) \xi^{I(r)}(t', \mathbf{x}') \rangle &= 2k_B T \left[ \lambda^I p_\alpha + \lambda_1^I p_\alpha (\partial_\gamma p_\gamma) \right. \\ &+ \lambda_2^I p_\gamma (\partial_\gamma p_\alpha) + \lambda_3^I p_\gamma (\partial_\alpha p_\gamma) \left. \right] \\ &\times \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \end{aligned} \quad (102)$$

$$\langle \xi_\alpha^{(p)}(t, \mathbf{x}) \xi_\beta^{k(j)}(t', \mathbf{x}') \rangle = -2k_B T \kappa^k \delta_{\alpha\beta} \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \quad (103)$$

$$\begin{aligned} \langle \xi_\alpha^{i(j)}(t, \mathbf{x}) \xi_{\beta\gamma}^{(u)}(t', \mathbf{x}') \rangle &= k_B T \chi^i [\delta_{\alpha\beta} p_\gamma + \delta_{\alpha\gamma} p_\beta \\ &- \frac{2}{3} \delta_{\beta\gamma} p_\alpha] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \\ &- k_B T \chi_1^i [\delta_{\alpha\beta} \partial_\gamma + \delta_{\alpha\gamma} \partial_\beta - \frac{2}{3} \delta_{\beta\gamma} \partial_\alpha] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \end{aligned} \quad (104)$$

$$\begin{aligned} \langle \xi_\alpha^{k(j)}(t, \mathbf{x}) \xi^{I(r)}(t', \mathbf{x}') \rangle &= 2k_B T \left[ \lambda^{kl} p_\alpha + \epsilon_1^{kl} p_\alpha (\partial_\gamma p_\gamma) \right. \\ &+ \epsilon_2^{kl} p_\gamma (\partial_\gamma p_\alpha) \left. \right] \\ &\times \delta(t-t') \delta(\mathbf{x}-\mathbf{x}') \end{aligned} \quad (105)$$

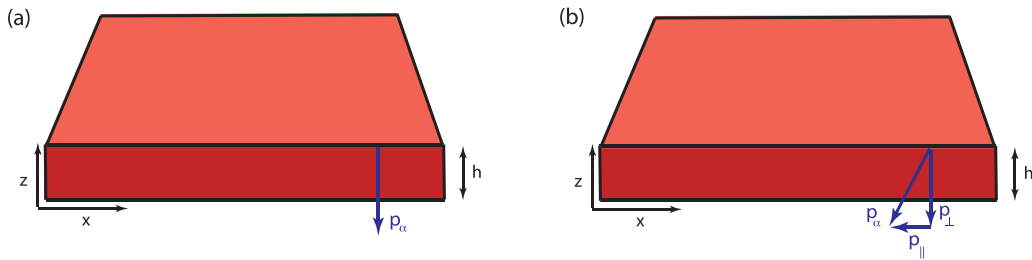
$$\langle \xi_{\alpha\beta}^{(u)}(t, \mathbf{x}) \xi^{I(r)}(t', \mathbf{x}') \rangle = 2k_B T \psi^I \tilde{q}_{\alpha\beta} \delta(t-t') \delta(\mathbf{x}-\mathbf{x}'). \quad (106)$$

The noisy constitutive relations characterized by the noise correlations equations (101)–(106) together with the conservation laws provides stochastic dynamic equations for active gels in the vicinity of thermal equilibrium. Note that some noise correlations depend on the polarity field  $p_\alpha(\mathbf{x}, t)$  and the noise is therefore state dependent or multiplicative. In this case, the specific conventions that are used when defining time integrals of these stochastic variables become relevant. Using Stratonovich or Ito conventions requires the addition of compensating drift terms in the stochastic differential equations in order to satisfy the fluctuation dissipation theorem. When using the isothermal convention, such compensating terms do not occur in the Langevin equations [58–60].

## 5. Nonequilibrium processes in cells and tissues

### 5.1. Active gels in cell biology

The hydrodynamic theory presented in the previous sections provides a general framework to capture key aspects of material properties and the dynamics of biological matter. On mesoscopic scales, cellular materials and in particular the cell cytoskeleton can be considered as active gels. Such systems can exhibit unconventional material properties of active matter. In situations where the filaments are short compared to mesoscopic length scales of cellular structures, a hydrodynamic or continuum approach can capture the key features of intracellular flows and force generation. Actin filaments together with myosin molecular motors and many associated proteins form very dynamic gels with contractile properties. Early continuum approaches to cellular gels that are permeated by a solvent were based on two phase descriptions [13]. In many situations, filaments are organized in anisotropic arrangements that can be polar or nematic. Here, the full properties of active polar or active nematic gels become relevant. Cell locomotion and cellular shape changes are key examples for processes that are governed by the mechanics and hydrodynamics of active gels. Cells crawling on a solid substrates such as fish keratocytes have been studied extensively [2, 52, 61–63]. The emerging motion of such cells is a complex biophysical process involving the interplay of adhesion,



**Figure 3.** The cell cortex can be represented as a thin layer of an active gel of thickness  $h$  below the cell membrane. (a) In the simplest case, the average filament polarity vector  $p_\alpha$  is normal to the surface. By integrating over the thin dimension  $z$  one can obtain an effective two-dimensional hydrodynamic theory of the system in the  $x - y$  plane with an isotropic active tension  $T^{\text{act}}\delta_{ij}$  in the plane. (b) In the general case, a normal component  $p_\perp$  and a tangential component  $p_\parallel$  of average filament orientation with respect to the surface exist. In this case, the active tension  $T_{ij}^{\text{act}}$  is anisotropic.

active contractile stresses in an actomyosin gel that undergoes polymerization and depolymerization. Importantly, all these processes are organized in space and time. Continuum theories of active gels allow to capture the essential force balances involved in lamellipodium protrusion and can explain the origin of retrograde flows as a consequence of contractile active stresses in the polarized actomyosin gel [52].

The actomyosin cell cortex is an important intracellular structure where continuum approaches to active gels have been useful for describing cytoskeletal deformations and flows [53, 64–70]. The cell cortex is a thin layer of actomyosin gel associated with the cell membrane [4]. The height of the layer is small compared to its lateral extents, and an effective two-dimensional theory of the dynamic cell cortex can be obtained [53, 64, 71] with equations for the densities of actin filaments and actin monomers that are contained in the balance equations equation (8).

To illustrate the basic ideas, we consider a thin layer of an active gel on a solid support. The active film equations can be found most easily by writing the active gel theory in two dimensions. Alternatively, one can derive these equations taking the thin film limit of a three dimensional gel layer of thickness  $h \sim v_p/k$ , see figure 3. This thickness is set by a balance of filament polymerisation with velocity  $v_p$  and depolymerisation which eliminates filaments at a rate  $k$ . The planar geometry below the membrane implies that an axis of anisotropy is provided by the normal to the surface. In the simplest case, the filaments are on average oriented normal to the surface, see figure 3(a). In general, one can distinguish a normal and a tangential component of the average polarity, see figure 3(b). While in three dimensions we usually consider the active material to be incompressible, no incompressibility condition exists in the effective film equations in two dimensions. This is because material can be exchanged between the two dimensional film and its surroundings. Integrating the incompressibility condition  $\partial_\alpha v_\alpha = 0$  along the  $z$ -axis perpendicular to the film, we have

$$v_z \simeq -h(\partial_x \bar{v}_x + \partial_y \bar{v}_y) \quad (107)$$

Thus, the resulting average two-dimensional flow field  $\bar{v}_i$  with  $i = x, y$  is not divergence free. The divergence  $\partial_i \bar{v}_i$  in two dimensions defines a velocity  $v_z$  that for a gel with constant density corresponds to the rate of height changes. For a thin

gel in which the dynamics of filaments maintains a preferred film height  $h$ ,  $v_z$  becomes proportional to the net flow velocity of material leaving the gel and entering the cytosol after depolymerisation.

In order to discuss the dynamic equations of the active film we write the constitutive equations of an active gel in the long time limit (62) in  $d = 2$ . For simplicity, we consider the case where the system is isotropic in the plane of the film and we therefore do not introduce a polarity field  $p_\alpha$  and the conjugate field  $h_\alpha$  in the plane, corresponding to figure 3(a). Because the active gel turns over and material can escape in the third dimension the active gel is compressible in two dimensions. The film tension tensor can be defined as an integral of the stress over the film thickness

$$T_{ij} = \int_0^h dz \sigma_{ij}. \quad (108)$$

The stress tensor in two dimensions  $T_{ij}$ , where  $i, j = x, y$  are indices in two dimensions has units of energy per area. The constitutive equation for the active film read

$$T_{ij} = 2\bar{\eta}(v_{ij} - \frac{1}{2}v_{kk}\delta_{ij}) + \eta_b v_{kk}\delta_{ij} + (\bar{\zeta}\Delta\mu - P^{2d})\delta_{ij}. \quad (109)$$

Here, we have introduced the two-dimensional shear and bulk viscosities  $\bar{\eta}$  and  $\eta_b$ , respectively,  $P^{2d}$  is the two dimensional pressure and the two-dimensional active tension is  $T^{\text{act}} = \bar{\zeta}\Delta\mu$ . Material balance of the film can be expressed as an equation for its two dimensional actin density  $\rho$

$$\frac{d\rho}{dt} = -\rho\partial_k v_k - k(\rho - \rho_0) \quad (110)$$

where  $d/dt$  denotes a convected time derivative. The film turns over at a rate  $k$  by polymerization and depolymerization and has a steady state area density  $\rho_0$ . The film pressure is  $P^{2d} = \chi(\rho - \rho_0)/\rho_0$ , where  $\chi$  is a compressibility in two dimensions. On times long compared to the turnover rate  $k$ , the density is stationary,  $d\rho/dt \simeq 0$  and we have

$$P^{2d} \simeq -\frac{\chi}{k}\partial_k v_k. \quad (111)$$

Therefore, the 2d pressure effectively renormalizes the bulk viscosity in equation (109) and we have

$$T_{ij} = 2\eta(v_{ij} - \frac{1}{2}v_{kk}\delta_{ij}) + \bar{\eta}v_{kk}\delta_{ij} + T^{\text{act}}\delta_{ij} \quad (112)$$

with the effective two dimensional bulk viscosity  $\bar{\eta} = \eta_b + \chi/k$ . The force balance can then be written as

$$\partial_j T_{ij} = \gamma v_i \quad (113)$$

where  $\gamma$  is a coefficient describing friction forces with respect to a substrate.

A simple case is an effectively one-dimensional geometry, where gradients are all in  $x$  – direction and vanish in the  $y$  – direction. In this case,  $T_{xx} = (\eta + \bar{\eta})\partial_x v_x + T^{\text{act}}$ . Using  $\partial_x T_{xx} = \gamma v_x$ , we finally obtain the hydrodynamic equation for the flow velocity in  $x$  – direction

$$\partial_x T^{\text{act}} = \gamma v_x - (\eta + \bar{\eta})\partial_x^2 v_x. \quad (114)$$

It is interesting to consider the simple case where the active stress is piecewise constant with  $T^{\text{act}} = T_A$  for  $x < 0$  and  $T^{\text{act}} = T_P$  for  $x > 0$ . In this case,  $\partial_x T^{\text{act}} = (T_P - T_A)\delta(x)$  and the flow field is given by

$$v_x = (T_P - T_A) \frac{\ell/2}{\eta + \bar{\eta}} e^{-|x|/\ell}. \quad (115)$$

Thus, gradients of active stresses induce flow patterns in the active film governed by the hydrodynamic length

$$\ell = \left( \frac{\eta + \bar{\eta}}{\gamma} \right)^{1/2}. \quad (116)$$

The magnitude of these flows increases linearly with this length scale.

Actomyosin flows that serve to establish cell polarity in the *Caenorhabditis elegans* embryo can be described within this framework, by considering the spatial distribution of active stress generated by myosin molecular motors in the thin cortical layer together with viscous stresses as well as external friction forces acting on the cortex when it moves relative to the outer egg shell [64]. Flows within an actin ring powering zebrafish epiboly can be understood with a similar approach [72]. Myosin induced cortical flows also provide a physical mechanism for stable bleb amoeboid motion [73] and for the adhesion independent migration of cells in narrow tubes [74]. Furthermore cell division is driven by actin filaments assembling into a contractile ring [53, 70, 71]. Actin filaments are aligned along the cell equator, and this alignment can be generated by actomyosin flows converging upon the equatorial region and compressing the network which in turn will generate alignment. A continuum theory of an active nematic gel can capture this flow-alignment coupling and the corresponding dynamics as measured in the one cell stage *Caenorhabditis elegans* embryo [70].

Active stresses in the actin cytoskeleton of cells are controlled by regulatory pathways. These pathways are based on sets of regulatory molecules that typically diffuse in the cell. Specific regulators control molecular processes in the actomyosin gel. They can for example regulate myosin density and thereby control overall myosin activity and the amount of myosin-based force generation. In general, regulatory

processes therefore modify and control active and passive material properties in the cell cortex. This in turn implies that couplings and feedbacks exist between active mechanical processes in the material and chemical processes. These couplings can arise through mechano-sensing, but also through advective transport where the regulators that control molecular processes in the gel are transported by gel flows [75–77]. From the point of view of physics, morphogenesis in biological systems is fundamentally a mechano-chemical process. On the scale of a cell, such mechano-chemical processes create patterns and cell flows that break cellular symmetries and can lead for example to the emergence of cell polarity and cell chirality [64, 78]. On a multicellular level, structures such as tissues, organs and eventually organisms form via the collective organization of large numbers of cells in space and time. The dynamics of tissues also involves a coupling of active mechanical events with regulatory pathways and chemical signals. Thus, tissue morphogenesis and the development of organisms from a fertilized egg are examples of specific mechano-chemical patterning processes that serve to build tissue-scale structures. These processes are guided by upstream genetic programs that define the dynamic rules of the cellular behaviors, ensuring that appropriate structures are formed at the right place and time.

Mechano-chemical pattern and structure formation provides a paradigm for biological morphogenesis. This mechanism of pattern formation is qualitatively different from classical concepts, such as pattern formation via reaction–diffusion processes and Turing patterns. These are essentially chemical in nature and do not take into account force balances and actively generated material flows and deformations [79–81]. Hence, mechano-chemical self-organization represents a novel class of pattern formation processes in Physics. General and simple features of mechano-chemical pattern formation can be best studied in minimal systems and simplified models. An example consists of a thin active gel or fluid in which a regulator of active stress diffuses and is convected by flows. The behavior of this system is characterized by a Peclet number that measures the ratio of diffusive and convected transport. Steady states exist in which concentration and stress profiles are homogeneous and no flows occur. Homogeneous quiescent states can become unstable with respect to wave-like perturbations of the regulator concentration field. Increased concentrations of the regulator lead to increased active stress, and beyond a critical coupling strength between regulator concentration and active stress, flows can arise spontaneously. These flows transport stress regulators towards regions where stress is already increased. This gives rise to an instability. Beyond this instability, the system reaches a steady state exhibiting a spatial concentration profile and a flow patterns [76]. Introducing two diffusing species which activate and inhibit active stress can lead to oscillatory patterns. Such dynamic instabilities might also be at the heart of transient aggregations of myosin into so-called foci that are often observed in highly contractile actomyosin cortices during the development of organisms [82–84].



## 5.2. Continuum theories of tissues

The hydrodynamic equations governing the dynamics of active gels discussed in this review are generic and depend only on the symmetries and conservation laws that characterize a given system. Beside the cell cytoskeleton, which is a biological example of an active gel, tissues are also soft active materials. Furthermore, tissues can exhibit vectorial, nematic or chiral asymmetries similar to the asymmetries encountered in the cytoskeleton. As a result, the equations for active gels can also be applied to tissue dynamics. However there are a few specific considerations.

Tissues are assemblies of many cells which adhere to each other and which are often also associated to an extracellular matrix. The extracellular matrix is an extracellular soft polymeric material, the components of which are secreted by cells [85, 86]. Cells exhibit anisotropies such as cell polarity or they may take elongated shapes, which correspond to a nematic anisotropy. In a continuum approach, tissue anisotropies can thus be captured by nematic or polar order parameter fields [25, 87–89]. In addition, tissues generate active stresses and flows. Cells may exert contractile stresses which often are mediated by the cellular acto-myosin cytoskeleton. For example, stress fibers in cells can contract and induce a force dipole and thus an active stress in the tissue [90]. Growth processes and in particular cell growth is typically associated with isotropic active stresses [22]. Cell division is an anisotropic process. Mechanical events during cell division are active and typically contribute to anisotropic active stresses [24].

An important feature of tissues is cell division and cell death. Cell death often occurs via a regulated process called apoptosis. A key characteristics of tissues is the number density  $n(\mathbf{x})$  of cells which obeys the balance equation

$$\partial_t n + \partial_\alpha (n v_\alpha^c) = (k_d - k_a)n, \quad (117)$$

where  $k_d$  and  $k_a$  denote the average division and apoptosis rates in local volume elements. Here, we have introduced the cell velocity  $v_\alpha^c$ .

The material properties of a tissue can be elastic or visco-elastic. Cell turnover and cell divisions can fluidify an elastic tissue [24]. In order to discuss these properties, we start from a tissue characterized by compression and shear elastic moduli  $\chi$  and  $E$ , respectively. Using equation (117), the isotropic stress then obeys

$$\frac{d\sigma}{dt} \simeq \chi(v_{\gamma\gamma}^c - (k_d - k_a)), \quad (118)$$

where  $d/dt$  denotes a convected time derivative. Typically, division and apoptosis rates are regulated by growth factors and related chemical signals. However in general, they also depend on local stresses and in particular the local cell pressure. At homeostatic conditions,  $k_d - k_a = 0$ . If such homeostatic condition exist for some pressure  $P_h$ , we can expand the division and apoptosis rates to lowest order in the vicinity of the homeostatic state:

$$k_d - k_a \simeq \bar{\eta}^{-1}(P_h + \sigma). \quad (119)$$

We then obtain a constitutive equation for the isotropic stress

$$\left(1 + \tau \frac{d}{dt}\right) \sigma = \bar{\eta} v_{\gamma\gamma}^c - P_h, \quad (120)$$

where the coefficient  $\bar{\eta}$  describing the pressure dependence of  $k_d - k_a$  plays the role of the bulk viscosity. The relaxation time for isotropic stresses is  $\tau = \bar{\eta}/\chi$ .

When considering the anisotropic stress, cell division and apoptosis events generally introduce force dipoles that can relax existing elastic stresses

$$\frac{D}{Dt} \tilde{\sigma}_{\alpha\beta} = 2E v_{\alpha\beta}^c - n(d_d k_d + d_a k_a) \tilde{q}_{\alpha\beta}. \quad (121)$$

Here,  $d_d$  and  $d_a$  denote the magnitudes of force dipoles associated with individual division and apoptosis events, see equation (69). The traceless tensor  $\tilde{q}_{\alpha\beta}$  describes the average orientation of these force dipoles. Taking into account that existing stress anisotropies bias the orientation of division events, we use  $\tilde{q}_{\alpha\beta} \simeq \tilde{q}_{\alpha\beta}^0 + \tilde{\sigma}_{\alpha\beta}/\sigma_0$ , where  $\tilde{q}_{\alpha\beta}^0$  captures stress independent anisotropies of division and apoptosis events. We then arrive at a viscoelastic constitutive equation for the anisotropic stress

$$\left(1 + \tau_a \frac{D}{Dt}\right) \tilde{\sigma}_{\alpha\beta} = 2\bar{\eta} \tilde{v}_{\alpha\beta}^c - \sigma_0 \tilde{q}_{\alpha\beta}^0, \quad (122)$$

which takes the form of an active visco-elastic material with relaxation time  $\tau_a^{-1} = n(d_d k_d + d_a k_a)/\sigma_0$  of anisotropic stresses, viscosity  $\eta = E\tau_a$  and an active stress of magnitude  $\sigma_0$ .

Many tissues are sheet-like epithelia. These are two dimensional cell layers which play a key role in many developmental processes [91, 92]. An advantage of the study of epithelia is that the cell shape can often be directly observed. The local average cell shape can be characterized by a traceless symmetric cell shape tensor  $\tilde{Q}_{\alpha\beta}$  which in two dimensions is a  $2 \times 2$  matrix. If both the cell shape tensor and the tissue deformation rate  $v_{\alpha\beta}^c$  are observed, this provides information about the decomposition of tissue shear deformations  $\tilde{v}_{\alpha\beta}^c$  in contributions from cell shape changes and from cell rearrangements [23, 28–30, 93]

$$\tilde{v}_{\alpha\beta}^c = \frac{D\tilde{Q}_{\alpha\beta}}{Dt} + \tilde{R}_{\alpha\beta}. \quad (123)$$

Here,  $\tilde{R}_{\alpha\beta}$  is a traceless symmetric tensor that captures the contributions of tissue shear stemming from cell rearrangements. Using this decomposition in a continuum approach, one can start from a constitutive equation describing elastic cell mechanics

$$\tilde{\sigma}_{\alpha\beta} = 2E\tilde{Q}_{\alpha\beta} + \zeta\Delta\mu\tilde{q}_{\alpha\beta}, \quad (124)$$

where  $\zeta\Delta\mu\tilde{q}_{\alpha\beta}$  is an active stress or equivalently a spontaneous cell elongation. We then also require a constitutive material equation for cell rearrangements. Using the simplest choice

$$\tilde{R}_{\alpha\beta} = \tau_a^{-1}\tilde{Q}_{\alpha\beta} + \gamma\Delta\mu\tilde{q}_{\alpha\beta}, \quad (125)$$

where  $\tau_a$  is a timescale and  $\gamma$  a phenomenological coefficient, we again obtain equation (122). However, in tissues we have

the possibility to directly measure the cell shape  $\tilde{Q}_{\alpha\beta}$  which is related to the elastic deformation as separate observables. In typical Maxwell gels this variable is not easily accessible. Furthermore, the constitutive equation for  $\tilde{R}_{\alpha\beta}$  in typical tissues can be more complex than equation (125) and may involve further relaxation processes and memory effects. In such cases the tissue rheology becomes complex and can exhibit unconventional features [29, 30].

## 6. Discussion

We have reviewed a generic approach to active matter based on fundamental concepts of irreversible thermodynamics. Irreversible thermodynamics captures the dynamics of macroscopic systems in the vicinity of thermodynamic equilibrium when only a few degrees of freedom are driven away from equilibrium. This corresponds to a local equilibrium approximation. The constitutive equations of active matter which we discussed are based on linear Onsager relations which are rigorously valid in a regime close to equilibrium. In the limit of large length scales, slow hydrodynamic modes govern the dynamics of spatially extended systems. Such hydrodynamic modes emerge as a result of conservation laws for mass, momentum and energy. Furthermore, broken symmetries that are for example associated with polar or nematic order can also give rise to hydrodynamic modes. Hydrodynamic modes are generic and independent of the microscopic details that underlie a particular system. Therefore, systems that can be observed over long times and in the limit of large system sizes exhibit robust behaviours governed by such a hydrodynamic theory [32, 94].

The irreversible thermodynamics of hydrodynamic systems provides a powerful framework for the study of active matter. Hydrodynamic modes represent a small number of slow degrees of freedom of the system that are well captured by irreversible thermodynamics. Because hydrodynamic modes are slow, a large number of faster relaxing modes become equilibrated when considering dynamics on large lengths scales and in a continuum limit. Thus the local equilibrium approximation becomes valid. Irreversible thermodynamics therefore captures the behaviours of hydrodynamic modes accurately. In real systems one is often also interested in the dynamics of collective modes that relax more rapidly. In such cases the hydrodynamic approach can be extended to faster relaxing modes, however in such cases the local equilibrium condition is not always a good approximation. In addition, a continuum limit may not be always appropriate to capture the physics of mesoscopic systems. Noise and fluctuations can be systematically introduced to the irreversible thermodynamics approach to capture fluctuations on mesoscopic scales. However, only in the vicinity of equilibrium is there a rigorous procedure to specify the properties of such noise via the fluctuation–dissipation theorem. Thus, the conceptual framework discussed here has a number of limitations in particular when it is applied to active biological systems. One important point is that irreversible thermodynamics is valid in the vicinity of a thermodynamic equilibrium and may not capture some

features of a system far from equilibrium. Furthermore, the approach of irreversible thermodynamics discussed here is based on linear response theory and expresses dynamic equations to first order in the thermodynamic forces that drive the dynamics.

Biological systems typically differ from such ideal regimes in several ways. Cells are mesoscopic systems and a large length scale limit can often not be taken. Filaments of the cytoskeleton can have lengths of a micrometer and more which implies that a continuum limit may emerge only on scales beyond the cell size. Biological systems also exhibit very important dynamics on intermediate time scales, for example the process of cell division. Events that take place on fixed time scales do not correspond to hydrodynamic modes. Also, biological systems are examples of matter that is driven far from thermodynamic equilibrium. In a typical cell many variables are dynamic and are kept away from thermodynamic equilibrium, and many of these variables do not correspond to classical hydrodynamic modes. This is particularly clear for dynamic cellular processes such as cell polarization, cell division and cellular signalling. Hence, to capture important biological phenomena a theory based on the generic properties of hydrodynamic modes needs to be complemented by models for non-hydrodynamic variables.

Furthermore, some dynamic processes in living cells are expected to operate further away from equilibrium that can be accurately captured by linear response theory. However local equilibrium concepts do still have much value when applied to reconstituted cellular systems or when used inside cells. In fact, many degrees of freedom are equilibrated on time scales relevant to cellular dynamics. For example, a local temperature remains a key concept, and temperatures as well as heat produced in biological systems and organisms can be measured [95, 96]. Key features of many collective processes, such as the assembly of molecular compartments by phase separation, can in many cases be described using irreversible thermodynamics and local equilibrium approximations [97, 98]. To capture the essence of the physics of biological dynamics and self-organization, it is therefore important for a given biological process to identify the relevant dynamic variables. The number of such relevant variables can be significantly larger than the number of conventional hydrodynamic modes, but this number will still be orders of magnitudes smaller than the total number of microscopic degrees of freedom. As a result, models for biological dynamics are often not fully generic but can depend in important ways on details of biological interaction networks and signalling pathways. To conclude, the framework described in this review provides a systematic and physically coherent approach to non-equilibrium dynamics of active systems that obeys important conservation laws and basic physical principles. It also provides the correct equilibrium physics in the absence of active processes.

An alternative approach to develop a hydrodynamic theory of active matter is to directly provide an expansion of dynamic variables writing all terms allowed by the symmetries of a given system [15, 17]. Such a general theory must still be based on fundamental conservation laws but may not make use of equilibrium thermodynamics. An advantage of such an

approach is that it is not restricted to the regime in the vicinity of a thermodynamic equilibrium. This advantage, however, comes at the cost that there is no longer a systematic procedure that helps to identify relevant variables that govern the dynamics, apart from the slow modes stemming from conservation laws and symmetries. Furthermore, a theory constructed far from equilibrium does not necessarily provide the correct limits when approaching equilibrium. In general, theories developed using more general approaches and theories based on irreversible thermodynamics share many features in common and often exhibit the same physics. An important example is the active stress, which is a central concept to active matter that was introduced independently using different approaches [11, 15]. The active matter equations discussed in this review can lead to the spontaneous formation of complex structures. These include spontaneous flows, topological defects, and spatiotemporal structures such as traveling waves [11, 76, 99]. Numerical simulations of active nematic fluids have shown that low Reynolds number turbulence can arise in an active system [100–102].

The hydrodynamic theory of active matter outlined here generalizes the classic hydrodynamic theories of passive liquid crystals [6, 34–39] to the case where chemical processes maintain such liquid crystals away from equilibrium. In the biological context, active materials are often based on the cytoskeleton where molecular motors interact with filaments and form an active gel. An important property of biological matter is that it is fundamentally chiral. This results from the chirality of biomolecules. Active chiral processes mediated by motor molecules and chiral filaments contribute to movements and flows that are generated in cells and in tissues. The resulting chirality of cellular processes in turn plays a key role for the breaking of left–right symmetry in cells and in developing organisms [103–106].

Equations for the hydrodynamics of active matter have been expressed here in cartesian coordinates. Morphogenesis in biology can also occur through deformation of thin layers of active material, such as the cell cortex or two-dimensional tissues called epithelia. In that case, the shape of the system is well-described by approximating it by a moving surface. The hydrodynamics of active matter can be generalized to consider flows on a deformable manifold. A new feature is that active internal bending moments generated in the thin layer play a role, in addition to active stresses [107].

The approach to investigate the irreversible thermodynamics of hydrodynamic systems has been powerful for shedding light on the physical basis of biological processes ranging from the intracellular activities to the dynamics of tissues. In the one cell-stage *Caenorhabditis elegans* embryo, flows that serve to polarize the zygote were shown to be driven by inhomogeneities in the distribution of myosin motor proteins [53, 64]. These flows serve to trigger the formation of a cell polarity pattern, by transporting markers of polarity along the cell surface [75, 108]. Cell division occurs via active contraction in a contractile ring. Active gel can capture the mechanics of the cell cortex and the resulting cell shape changes [71]. At the multicellular scale, actomyosin flows into a supra-cellular ring-like structure generate the forces that drive

epithelial spreading and epiboly progression in the developing zebrafish embryo [72]. In these cases, active gel theory was used to characterize the force-balance that underlie the associated actomyosin dynamics. The structure of myosin in a highly contractile cortex is known to be non-homogeneous, myosin is concentrated into aggregates called myosin foci that undergo a pulsatile activity, with new ones forming and old foci disappearing on a time scale of one minute [83, 84]. Such processes result from the dynamic interplay of chemical oscillations and active gel dynamics in a mechano-chemical process [84]. Generally, cell dynamics typically emerges from mechano-chemical processes that combine active gels with chemical patterns [81].

Similar principles operate at the scale of tissues. Chemical patterns emerge from signalling processes and such chemical patterns can influence mechanical events. A reaction–diffusion system consisting of several specific signalling molecules drives digit formation in the mouse [109]. However, if and how growth and deformation feeds back on the pattern forming process in this system is not yet known. Interestingly, the process of positioning skin follicles, the structures of the skin that grow hairs in humans and feathers in chicken, is dependent on a patterning process where mechanical and regulatory pathways cannot be separated. The dermis of the skin, which is a tissue layer that is below the epidermis, appears to undergo a contractile instability, which causes compression and mechano-transduction of  $\beta$ -catenin in the epidermis and hair follicle specification [110]. We think that theoretical approaches based on continuum theories of active matter will play an increasing role to shed further light on mechanochemical patterning processes in biology from the scales of cells to tissues.

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## Appendix A. Irreversible thermodynamics of multicomponent fluids

### A.1. Thermodynamic potentials and thermodynamic variables

We briefly review the irreversible thermodynamics of multicomponent fluids [33]. We first consider the equilibrium thermodynamics of a multicomponent fluid with local concentrations  $n_i = N_i/V$  of molecular species  $i$  and mass density  $\rho = \sum_{i=0}^N m_i n_i$  in a volume element of volume  $V$ . The center of mass velocity is given by

$$v_\alpha = \frac{1}{M} \sum_i m_i N_i v_\alpha^i, \quad (\text{A.1})$$

where  $M = \sum_{i=0}^N N_i m_i$  is the total mass and  $v_\alpha^i$  the local average velocity of molecules of type  $i$ . The total momentum of the volume element is  $G_\alpha = M v_\alpha$ , the momentum density is  $g_\alpha = \rho v_\alpha$ .

As a result of Galilei invariance of the microscopic equations of motion, the thermodynamics of a local element of volume  $V$  can always be studied in the the center of mass reference frame in which  $v_\alpha = 0$ , the momentum vanishes  $G_\alpha = 0$  and the free energy is denoted  $F_0$ . The free energy with centre of mass motion then has the form

$$F(T, V, N_i, G_\alpha) = \frac{G_\alpha^2}{2M} + F_0(T, V, N_i), \quad (\text{A.2})$$

where  $N_i$  denotes the number of particles of species  $i$  and  $T$  denotes temperature. Similarly, we define the free energy density  $f(T, n_i, g_\alpha) = g_\alpha^2/2\rho + f_0(T, n_i)$ , with  $f_0 = F_0/V$ . We then have

$$v_\alpha = \left. \frac{\partial F}{\partial G_\alpha} \right|_{V, N_i, T} = \left. \frac{\partial f}{\partial g_\alpha} \right|_{n_i, T}. \quad (\text{A.3})$$

We define the following thermodynamic quantities:

$$P_0 = - \left. \frac{\partial F_0}{\partial V} \right|_{T, N_i} = -f_0 + \sum_i \mu_i^{(0)} n_i \quad (\text{A.4})$$

$$\mu_i^{(0)} = \left. \frac{\partial F_0}{\partial N_i} \right|_{T, V, N_j} = \left. \frac{\partial f_0}{\partial n_i} \right|_{T, n_j} \quad (\text{A.5})$$

$$S = - \left. \frac{\partial F_0}{\partial T} \right|_{V, N_i} = -V \left. \frac{\partial f_0}{\partial T} \right|_{n_i}, \quad (\text{A.6})$$

where  $P_0$  is the hydrostatic pressure and  $\mu_i^{(0)}$  are the chemical potentials of a homogeneous system.

Inhomogeneous systems which are locally at equilibrium can be captured using a free energy density  $f_0$ , where we also include contributions of concentration gradients to the free energy. The free energy reads

$$F = \int d^3x \left( \frac{g_\alpha^2}{2\rho} + f_0(T, n_i, \partial_\alpha n_i) \right), \quad (\text{A.7})$$

where  $f(T, n_i, \partial_\alpha n_i, g_\alpha) = g_\alpha^2/2\rho + f_0(T, n_i, \partial_\alpha n_i)$  is the total free energy density. In inhomogeneous systems, we generalise the definition of the chemical potential as  $\mu_i = \delta F_0 / \delta n_i$  and thus write

$$\mu_i = \frac{\partial f_0}{\partial n_i} - \partial_\alpha \frac{\partial f_0}{\partial (\partial_\alpha n_i)}. \quad (\text{A.8})$$

We also introduce the total chemical potential  $\mu^{\text{tot}} = \delta F / \delta n_i$  with

$$\mu_i^{\text{tot}} = -\frac{1}{2} m_i v_\alpha^2 + \mu_i. \quad (\text{A.9})$$

In the case of inhomogeneous systems, we also need to generalise the concept of equilibrium pressure which becomes an equilibrium stress. This equilibrium stress follows from translation invariance considerations.

## A.2. Translation and rotation invariance

We consider the change in free energy of a finite volume element under infinitesimal translations  $x'_\alpha = x_\alpha + \delta x_\alpha$ , with constant translation vector  $\delta x_\alpha$ . Defining translations as  $n'_i(x'_\alpha) = n_i(x_\alpha)$ , we have  $\delta n_i(x_\alpha) = n'_i(x_\alpha) - n_i(x_\alpha)$ , or  $\delta n_i(x_\alpha) = n_i(x_\alpha - \delta x_\alpha) - n_i(x_\alpha)$ . This argument applies to all variables. The free energy can then be written as

$$\delta F = \int d^3x (v_\alpha \delta g_\alpha + \mu_i^{\text{tot}} \delta n_i - s \delta T) + \oint dS_\alpha (f \delta x_\alpha + \frac{\partial f_0}{\partial (\partial_\alpha n_i)} \delta n_i), \quad (\text{A.10})$$

where the second term takes into account that the boundary is displaced with the system. The change  $\delta F$  given by equation (A.10) must vanish in the absence of external forces because of translation invariance. Using  $\delta n_i = -\delta x_\alpha \partial_\alpha n_i$ ,  $\delta g_\alpha = -\delta x_\beta \partial_\beta g_\alpha$  and  $\delta T = -\delta x_\alpha \partial_\alpha T$ , we have

$$\delta F = \int d^3x [(\partial_\beta v_\alpha) g_\alpha + (\partial_\beta \mu_i^{\text{tot}}) n_i + s \partial_\beta T] \delta x_\beta + \oint dS_\alpha \left[ (f - v_\gamma g_\gamma - \mu_i^{\text{tot}} n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\alpha n_i)} \partial_\beta n_i \right] \delta x_\beta. \quad (\text{A.11})$$

We identify the equilibrium stress,

$$\sigma_{\alpha\beta}^e = (f_0 - \mu_i n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\beta n_i)} \partial_\alpha n_i. \quad (\text{A.12})$$

Translational invariance then imposes the Gibbs–Duhem relation

$$-\partial_\beta \sigma_{\alpha\beta}^e = (\partial_\alpha \mu_i) n_i + s \partial_\alpha T \quad (\text{A.13})$$

that ensures that  $\delta F = 0$  for pure translations. The Gibbs–Duhem relation shows that the equilibrium stress is divergence free at thermodynamic equilibrium when  $\partial_\alpha \mu_i$  and  $\partial_\alpha T$  vanish. However, in an out of equilibrium situation, local equilibrium stresses are not force balanced. In addition to translation invariance,  $F$  also obeys rotation invariance. Rotation invariance of the free energy implies that the equilibrium stress is symmetric,  $\sigma_{\alpha\beta}^e = \sigma_{\beta\alpha}^e$  and the equilibrium angular momentum flux  $M_{\alpha\beta\gamma}^e$  and the antisymmetric part of the equilibrium stress  $\sigma_{\alpha\beta}^{e,a}$  vanish.

## A.3. Rate of free energy changes

We now express the balance of free energy in several steps. The change of free energy in a volume of fixed shape (non-moving boundary) can be expressed as

$$\begin{aligned} \frac{dF}{dt} &= \int d^3x \left[ \partial_t \left( \frac{1}{2} \rho v^2 \right) + \left( \mu_i^{\text{tot}} + \frac{1}{2} m_i v_\alpha^2 \right) \partial_t n_i - s \partial_t T \right] \\ &\quad + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha n_i)} \partial_t n_i \\ &= \int d^3x [v_\alpha \partial_t g_\alpha + \mu_i^{\text{tot}} \partial_t n_i - s \partial_t T] + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha n_i)} \partial_t n_i \\ &= \int d^3x (v_\alpha \partial_\beta \sigma_{\alpha\beta}^{\text{tot}} + \mu_i^{\text{tot}} (r_i - \partial_\alpha J_\alpha^i) - s \partial_t T) \\ &\quad + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha n_i)} \partial_t n_i. \end{aligned} \quad (\text{A.14})$$

We can now use partial integrations in order to create boundary contributions that correspond to the total work performed at the surface. We first write

$$\frac{dF}{dt} = \int d^3x \left( -(\partial_\beta v_\alpha) \sigma_{\alpha\beta}^{\text{tot}} + \mu_i^{\text{tot}} r_i + (j_\alpha^i + n_i v_\alpha) \partial_\alpha \mu_i^{\text{tot}} - s \partial_t T \right) + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha}^{\text{tot}} - \mu_i^{\text{tot}} J_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \partial_t n_i \right). \quad (\text{A.15})$$

Using the Gibbs–Duhem relation (A.13) we then have

$$\begin{aligned} \frac{dF}{dt} &= \int d^3x \left( -(\partial_\beta v_\alpha) \sigma_{\alpha\beta}^{\text{tot}} + \mu_i^{\text{tot}} r_i + j_\alpha^i \partial_\alpha \mu_i^{\text{tot}} - v_\alpha \partial_\beta \sigma_{\alpha\beta}^e \right. \\ &\quad \left. - v_\alpha g_\beta (\partial_\alpha v_\beta) - s v_\alpha \partial_\alpha T - s \partial_t T \right) \\ &\quad + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha}^{\text{tot}} - (\mu_i - \frac{1}{2} m_i v^2) (j_\alpha^i + n_i v_\alpha) + \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \partial_t n_i \right) \\ &= \int d^3x \left( -\partial_\beta v_\alpha (\sigma_{\alpha\beta}^{\text{tot}} + v_\alpha g_\beta - \sigma_{\alpha\beta}^e) \right. \\ &\quad \left. + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - s (\partial_t T + v_\alpha \partial_\alpha T) \right) \\ &\quad + \oint dS_\alpha \left( v_\beta (\sigma_{\beta\alpha}^{\text{tot}} - \sigma_{\beta\alpha}^e) + v_\alpha (\frac{1}{2} \rho v^2 \right. \\ &\quad \left. - \mu_i n_i) - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \partial_t n_i \right). \end{aligned} \quad (\text{A.16})$$

Using the definition of the equilibrium stress (A.12) in the surface terms, we finally obtain

$$\begin{aligned} \frac{dF}{dt} &= \int d^3x \left( -\partial_\beta v_\alpha (\sigma_{\alpha\beta} - \sigma_{\alpha\beta}^e) + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - s \frac{dT}{dt} \right) \\ &\quad + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \frac{dn_i}{dt} \right), \end{aligned} \quad (\text{A.17})$$

where  $\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{\text{tot}} + v_\alpha g_\beta$  and we have introduced the convected time derivative  $d/dt = \partial_t + v_\gamma \partial_\gamma$ . The final expression given in (A.17) has a surface contribution to free energy changes. This surface term, except for the free energy convection  $-f v_\alpha$ , corresponds to the work performed at the boundary of the system. The bulk terms reflect the local sources of free energy.

#### A.4. Angular momentum conservation

From rotational invariance of the free energy it follows that both the antisymmetric part of the equilibrium stress and the equilibrium angular momentum flux vanish:  $\sigma_{\alpha\beta}^{e,a} = 0$  and  $M_{\alpha\beta\gamma}^e = 0$ . However, deviatoric parts  $\sigma_{\alpha\beta}^{d,a}$  and  $M_{\alpha\beta\gamma}^d$  could in principle exist in nonequilibrium conditions. For the simple case where the density of intrinsic angular momentum  $l_\alpha$  can be neglected, angular momentum conservation then implies

$$\partial_\gamma M_{\alpha\beta\gamma}^d = 2\sigma_{\alpha\beta}^{d,a}. \quad (\text{A.18})$$

This allows us to eliminate the antisymmetric stress from equation (A.17). We then have

$$\begin{aligned} \frac{dF}{dt} &= \int d^3x \left( -v_\alpha \beta (\sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^e) - \frac{1}{2} M_{\alpha\beta\gamma}^d \partial_\gamma \omega_{\alpha\beta} + \mu_i r_i \right. \\ &\quad \left. + j_\alpha^i \partial_\alpha \mu_i - s \frac{dT}{dt} \right) \\ &\quad + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i + \frac{1}{2} M_{\beta\gamma\alpha}^d \omega_{\beta\gamma} \right. \\ &\quad \left. + \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \frac{dn_i}{dt} \right), \end{aligned} \quad (\text{A.19})$$

where  $\sigma_{\alpha\beta}^s = (\sigma_{\alpha\beta} + \sigma_{\beta\alpha})/2$ ,  $v_{\alpha\beta} = (\partial_\alpha v_\beta + \partial_\beta v_\alpha)/2$  and  $\omega_{\alpha\beta} = (\partial_\alpha v_\beta - \partial_\beta v_\alpha)/2$ . Note that a contribution corresponding to the mechanical work of torques occurs at the boundary.

#### A.5. Balance of free energy, entropy and energy

The surface term of equation (A.19), defines the free energy flux  $J_\alpha^f = j_\alpha^f + f v_\alpha$  with

$$j_\alpha^f = -v_\beta \sigma_{\beta\alpha} + \mu_i j_\alpha^i - \frac{1}{2} M_{\beta\gamma\alpha}^d \omega_{\beta\gamma} - \frac{\partial f_0}{\partial(\partial_\alpha n_i)} \frac{dn_i}{dt}. \quad (\text{A.20})$$

From the bulk term, we obtain the rate of free energy production which reads

$$\theta_f = -v_\alpha \beta (\sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^e) - \frac{1}{2} M_{\alpha\beta\gamma}^d \partial_\gamma \omega_{\alpha\beta} + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - s \frac{dT}{dt}. \quad (\text{A.21})$$

The flux of free energy is related to the heat flux as  $j_\alpha^Q = j_\alpha^e - j_\alpha^f$ , where  $j_\alpha^e$  is the energy flux in the barycentric reference frame. The source of free energy  $\theta_f$  can be related to the entropy production rate  $\theta$  per unit volume. Using equations (2) with (14), (15) and  $J_\alpha^e = J_\alpha^f + T J_\alpha^s$ , we have  $\partial_t(Ts) + \partial_\alpha(TJ_\alpha^s) = -\theta_f$  and  $j_\alpha^Q = T j_\alpha^s$

$$\begin{aligned} T\theta &= -\theta_f - J_\alpha^s \partial_\alpha T - s \partial_t T \\ &= -\theta_f - j_\alpha^Q \frac{\partial_\alpha T}{T} - s \frac{dT}{dt}. \end{aligned} \quad (\text{A.22})$$

We thus obtain the entropy production rate per unit volume  $\theta$  with

$$\begin{aligned} T\theta &= v_\alpha \beta (\sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^e) + \sum_{I=1}^M r^I \Delta \mu^I \\ &\quad - \sum_{i=1}^N j_\alpha^i \partial_\alpha \bar{\mu}_i + \frac{1}{2} M_{\alpha\beta\gamma}^d \partial_\gamma \omega_{\alpha\beta} - j_\alpha^Q \frac{\partial_\alpha T}{T}, \end{aligned} \quad (\text{A.23})$$

where  $\Delta \mu^I = \sum_i d_i^I \bar{\mu}_i$ . Furthermore, we have expressed the dissipation rate in terms of the chemical potential differences  $\bar{\mu}_i = \mu_i - \mu_0 m_i / m_0$  relative to the solvent  $i = 0$ . The entropy density  $s = -\partial f^0 / \partial T$  obeys the balance equation (14) with entropy source  $\theta$  and entropy flux

$$J_\alpha^s = s v_\alpha + \frac{j_\alpha^Q}{T}. \quad (\text{A.24})$$

The energy is conserved such that the energy density

$$e = f - T \frac{\partial f_0}{\partial T} \quad (\text{A.25})$$

with energy flux

$$J_\alpha^e = e v_\alpha + j_\alpha^f + j_\alpha^Q \quad (\text{A.26})$$

obeys the conservation law (2).

#### A.6. Dynamic equations

We now use the quantities introduced so far to express dynamic equations. We obtain a dynamic equation for the temperature

using energy conservation. The conservation equation (2) for the energy density  $e = f - T\partial f_0/\partial T$  implies

$$\frac{\partial e}{\partial T}\partial_t T + \frac{\partial e}{\partial n_i}\partial_t n_i + \frac{\partial e}{\partial(\partial_\alpha n_i)}\partial_t \partial_\alpha n_i + \frac{\partial e}{\partial g_\alpha}\partial_t g_\alpha = -\partial_\alpha J_\alpha^e. \quad (\text{A.27})$$

Note that because of Galilei invariance  $\partial e/\partial g_\alpha = v_\alpha$ . We then have

$$c\partial_t T = -\frac{\partial e}{\partial n_i}\partial_t n_i - \frac{\partial e}{\partial(\partial_\alpha n_i)}\partial_t \partial_\alpha n_i - v_\alpha \partial_t g_\alpha - \partial_\alpha (e v_\alpha + j_\alpha^f + j_\alpha^Q) \quad (\text{A.28})$$

where  $c = -T\partial^2 f_0/\partial T^2$  is the specific heat.

Given a state of the system described by the functions  $n_i(\mathbf{r})$ ,  $T(\mathbf{r})$  and  $v_\alpha(\mathbf{r})$ , the time derivatives of these state variables can be determined if in addition to the free energy  $f$  the quantities  $\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta} - \rho v_\alpha v_\beta$ ,  $j_\alpha^i$ ,  $r_i$  and  $j_\alpha^Q$  are known at time  $t$ :

$$\begin{aligned} \partial_t v_\alpha &= -v_\beta \partial_\beta v_\alpha + \rho^{-1} \partial_\beta \sigma_{\alpha\beta} \\ \partial_t n_i &= -\partial_\alpha (n_i v_\alpha + j_\alpha^i) + r_i \\ \partial_t T &= c^{-1} \left( \frac{\partial e}{\partial n_i} (\partial_\alpha (n_i v_\alpha + j_\alpha^i) - r_i) \right. \\ &\quad + \frac{\partial e}{\partial(\partial_\alpha n_i)} \partial_\alpha (\partial_\beta (n_i v_\beta + j_\beta^i) - r_i) \\ &\quad \left. - v_\alpha \partial_\beta \sigma_{\alpha\beta}^{\text{tot}} - \partial_\alpha (e v_\alpha + j_\alpha^f + j_\alpha^Q) \right). \end{aligned} \quad (\text{A.29})$$

The thermodynamic fluxes  $\sigma_{\alpha\beta}^{\text{tot}}$ ,  $j_\alpha^i$ ,  $r_i$  and  $j_\alpha^Q$  in general are functions (or functionals) of  $n_i$ ,  $T$  and  $v_\alpha$  which obey translation and rotation invariance. These functions define the material properties and are called constitutive material relations. Linear response theory can be used to express these constitutive relations to linear order in the vicinity of a thermodynamic equilibrium.

### A.7. Linear response theory

The description of the system is completed by adding constitutive relations to express the quantities  $v_{\alpha\beta}$ ,  $j_\alpha^i$ ,  $r^I$  and  $j_\alpha^Q$  in terms of their conjugate thermodynamic forces  $\sigma_{\alpha\beta} - \sigma_{\alpha\beta}^e$ ,  $\partial_\alpha \bar{\mu}_i$ ,  $\Delta\mu^I$  and  $\partial_\alpha T$  using linear response theory. To linear order, we write

$$\begin{aligned} \sigma_{\alpha\beta} &= 2\eta(v_{\alpha\beta} - \frac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta} \\ &\quad + \gamma^I \Delta\mu^I \delta_{\alpha\beta} + \sigma_{\alpha\beta}^e + \frac{1}{2}\partial_\gamma M_{\alpha\beta\gamma}^\pi \\ j_\alpha^i &= -\Gamma_{ij}\partial_\alpha \bar{\mu}_j - \Gamma_i \partial_\alpha T \\ r^I &= M^{IJ}\Delta\mu^J - \gamma^I v_{\gamma\gamma} \\ j_\alpha^Q &= -\bar{\kappa}\partial_\alpha T - \Gamma_i \partial_\alpha \bar{\mu}_i \\ M_{\alpha\beta\gamma}^\pi &= \kappa\partial_\gamma \omega_{\alpha\beta}. \end{aligned} \quad (\text{A.30})$$

Here we have introduced dissipative coefficients and have neglected higher order terms. The bulk and shear viscosity are denoted  $\bar{\eta}$  and  $\eta$ . Diffusion coefficients and the cross coupling of diffusion fluxes is described by the symmetric matrix  $\Gamma_{ij}$ . Thermophoretic effects that couple temperature gradients to

diffusive fluxes are characterised by the coefficients  $\Gamma_i$ . The chemical reaction kinetics is described by the symmetric matrix  $M^{IJ}$  of coefficients that specify the reaction rates as well as a coupling  $\gamma^I$  to the divergence of the flow field which captures pressure generation by chemical reactions. The coefficient  $\bar{\kappa}$  describes heat conductivity. Interestingly, there can exist a dissipative coupling  $\kappa$  generating a contribution to the antisymmetric stress  $\sigma_{\alpha\beta}^a = (\kappa/2)\partial_\gamma \partial_\gamma \omega_{\alpha\beta}$ , which in simple fluids is irrelevant in the hydrodynamic limit and thus usually neglected. Using  $\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta} - \rho v_\alpha v_\beta$ ,  $\Delta\mu^I = \sum_i a_i^I \bar{\mu}_i$  and  $\bar{\mu}_i = \mu_i - \mu_0 m_i/m_0$ , equations (A.29) and (A.30) provide a dynamic description of the multicomponent fluid if the free energy density  $f$  is given.

## Appendix B. Translation and rotation invariance of the free energy in polar and nematic systems

### B.1. Translation invariance

We first consider a polar system with free energy density  $f = g_\alpha^2/(2\rho) + f_0(p_\alpha, \partial_\beta p_\alpha, n_i)$ . An infinitesimal translation of a volume  $V$  to  $V'$  by a small and constant translation vector  $\delta x_\alpha$  can be described by the displaced positions  $x'_\alpha = x_\alpha + \delta x_\alpha$ . To linear order in the displacement vector, the change in free energy  $\delta F = \int_{V'} d^3x f' - \int_V d^3x f$  can be expressed as

$$\begin{aligned} \delta F &= \int_V d^3x (v_\alpha \delta g_\alpha + \mu_i^{\text{tot}} \delta n_i - h_\alpha \delta p_\alpha) + \oint dS_\alpha (f \delta x_\alpha \\ &\quad + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \delta p_\beta). \end{aligned} \quad (\text{B.1})$$

Here, the first term corresponds to  $f' - f$  due to the displacement of the fields in the original volume. The second term captures the contributions to  $\delta F$  at the translated boundary when shifting from  $V$  to  $V'$ .

Expressing translations of the concentration fields with constant displacement vector  $\delta x_\alpha$  as  $n'_i(x'_\alpha) = n_i(x_\alpha)$ , we have  $\delta n_i(x_\alpha) = n'_i(x_\alpha) - n_i(x_\alpha)$ . Therefore  $\delta n_i(x_\alpha) = n_i(x_\alpha - \delta x_\alpha) - n_i(x_\alpha) \simeq -\delta x_\alpha \partial_\alpha n_i$ . Similar transformations hold for the other fields:  $\delta g_\alpha \simeq -\delta x_\beta \partial_\beta g_\alpha$  and  $\delta p_\beta \simeq -\delta x_\alpha \partial_\alpha p_\beta$ . The free energy change due to a translation is then given by

$$\begin{aligned} \delta F &= \int d^3x [(\partial_\beta v_\alpha) g_\alpha + (\partial_\beta \mu_i^{\text{tot}}) n_i + h_\alpha \partial_\beta p_\alpha] \delta x_\beta \\ &\quad + \oint dS_\alpha \left[ (f - v_\gamma g_\gamma - \mu_i^{\text{tot}} n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial(\partial_\alpha p_\gamma)} \partial_\beta p_\gamma \right] \delta x_\beta. \end{aligned} \quad (\text{B.2})$$

From the surface contribution we identify the equilibrium stress (21). Translational invariance  $\delta F = 0$  implies the Gibbs–Duhem relation (22).

For the case of a system with nematic order  $Q_{\alpha\beta}$  and  $f = g_\alpha^2/(2\rho) + f_0(Q_{\alpha\beta}, \partial_\gamma Q_{\alpha\beta}, n_i)$ , one finds using the same arguments the equilibrium stress

$$\sigma_{\alpha\beta}^e = (f_0 - \mu_i n_i) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial (\partial_\beta Q_{\gamma\nu})} \partial_\alpha Q_{\gamma\nu}. \quad (\text{B.3})$$

The Gibbs–Duhem relation is given by

$$-\partial_\beta \sigma_{\alpha\beta}^e = (\partial_\alpha \mu_i) n_i + H_{\gamma\nu} \partial_\alpha Q_{\gamma\nu}. \quad (\text{B.4})$$

### B.2. Rotation invariance

We consider the behavior of the free energy under infinitesimal rotations described by  $\delta x_\alpha = \epsilon_{\alpha\beta\gamma} \theta_\beta x_\gamma$  with infinitesimal rotation pseudo vector  $\theta_\beta$ . The polarity field then transform as  $\delta p_\alpha = -\delta x_\beta \partial_\beta p_\alpha + \epsilon_{\alpha\beta\gamma} \theta_\beta p_\gamma$  and a similar expression holds for  $\delta g_\alpha$ . Scalar fields transform as  $\delta n_i = -\delta x_\beta \partial_\beta n_i$ . Using equation (B.1), we find

$$\begin{aligned} \delta F &= \int d^3x [(\partial_\beta \mu_i) n_i + h_\alpha (\partial_\beta p_\alpha) \delta x_\beta - h_\alpha \epsilon_{\alpha\beta\gamma} \theta_\beta p_\gamma] \\ &+ \oint dS_\alpha ((f_0 - \mu_i n_i) \delta x_\alpha - \frac{\partial f_0}{\partial (\partial_\alpha p_\gamma)} (\delta x_\beta \partial_\beta p_\gamma - \epsilon_{\gamma\beta\delta} \theta_\beta p_\delta)) \\ &= \int d^3x [(-\partial_\alpha \sigma_{\beta\alpha}^e) \epsilon_{\beta\gamma\delta} \theta_\gamma x_\delta - h_\beta \epsilon_{\beta\gamma\delta} \theta_\gamma p_\delta] \\ &+ \oint dS_\alpha (\sigma_{\beta\alpha}^e \epsilon_{\beta\gamma\delta} \theta_\gamma x_\delta + \frac{\partial f_0}{\partial (\partial_\alpha p_\gamma)} \epsilon_{\gamma\beta\delta} \theta_\beta p_\delta) \\ &= \int d^3x [(\sigma_{\beta\alpha}^e - h_\beta p_\alpha) \epsilon_{\beta\gamma\alpha} \theta_\gamma] + \oint dS_\delta \frac{\partial f_0}{\partial (\partial_\delta p_\beta)} p_\alpha \epsilon_{\beta\gamma\alpha} \theta_\gamma, \end{aligned} \quad (\text{B.5})$$

where we have used the Gibbs–Duhem relation (22). From the condition that  $\delta F$  in equation (B.5) must vanish for small rotations  $\theta_\beta$ , we obtain the relation (25) with the definition (24).

For a nematic system, the order parameter transforms as  $\delta Q_{\alpha\beta} = -\delta x_\gamma \partial_\gamma Q_{\alpha\beta} + \epsilon_{\alpha\gamma\nu} \theta_\gamma Q_{\nu\beta} + \epsilon_{\beta\gamma\nu} \theta_\gamma Q_{\alpha\nu}$  under rotations. We then find

$$\partial_\gamma M_{\alpha\beta\gamma}^e = 2\sigma_{\alpha\beta}^{e,a} + 2(Q_{\alpha\nu} H_{\beta\nu} - Q_{\beta\nu} H_{\alpha\nu}) \quad (\text{B.6})$$

with

$$M_{\alpha\beta\gamma}^e = 2\left(\frac{\partial f_0}{\partial (\partial_\gamma Q_{\beta\nu})} Q_{\alpha\nu} - \frac{\partial f_0}{\partial (\partial_\gamma Q_{\alpha\nu})} Q_{\beta\nu}\right). \quad (\text{B.7})$$

## Appendix C. Irreversible thermodynamics with intrinsic angular momentum

### C.1. Local thermodynamics with angular momentum

We can also take angular momentum conservation explicitly into account following [41]. We introduce the the angular momentum  $L_{\alpha\beta}$  of each volume element  $V$ . In the ensemble where total momentum and angular momentum are given, we can define the free energy  $F(V, N_i, T, G_\alpha, L_{\alpha\beta}) = V f(n_i, T, g_\alpha, l_{\alpha\beta})$  where  $l_{\alpha\beta}$  denotes the free energy density. We have

$$\frac{1}{2} \Omega_{\alpha\beta} = \frac{\partial F}{\partial L_{\alpha\beta}} \Big|_{V, N_i, T, G_\alpha} = \frac{\partial f}{\partial l_{\alpha\beta}} \Big|_{n_i, T, g_\alpha}. \quad (\text{C.1})$$

The factor 1/2 stems from the relation  $\Omega_{\alpha\beta} L_{\alpha\beta} = 2\Omega_\alpha L_\alpha$ . Using Gallilei invariance, the free energy can be written in the form

$$F(V, N_i, T, G_\alpha, L_{\alpha\beta}) = \frac{G_\alpha^2}{2M} + F_0(V, N_i, T, L_{\alpha\beta}). \quad (\text{C.2})$$

Similarly, we write  $f(n_i, T, g_\alpha, l_{\alpha\beta}) = g_\alpha^2 / (2\rho) + f_0(n_i, T, l_{\alpha\beta})$ , with  $f_0 = F_0/V$  and  $\rho = \sum_i m_i n_i$ . We define the following thermodynamic quantities:

$$P_0 = - \frac{\partial F_0}{\partial V} \Big|_{T, N_i, L_{\alpha\beta}} = -f_0 + \sum_i \mu_i n_i + \frac{1}{2} \Omega_{\alpha\beta} l_{\alpha\beta} \quad (\text{C.3})$$

$$\mu_i = \frac{\partial F_0}{\partial N_i} \Big|_{T, V, N_j, L_{\alpha\beta}} = \frac{\partial f_0}{\partial n_i} \Big|_{T, l_{\alpha\beta}} \quad (\text{C.4})$$

$$S = - \frac{\partial F_0}{\partial T} \Big|_{V, N_i, L_{\alpha\beta}} = -V \frac{\partial f_0}{\partial n_i} \Big|_{n_i, l_{\alpha\beta}} \quad (\text{C.5})$$

where  $P_0$  is hydrostatic pressure and  $\mu_i$  denotes chemical potential.

### C.2. Rate of free energy change in a polar system with spin

The thermodynamics of an isothermal polar system with spin can be described by the free energy density  $f = g_\alpha^2 / (2\rho) + f_0(l_{\alpha\beta}, p_\alpha, \partial_\alpha p_\beta, n_i)$ . Following the derivation given in equation (26), we have

$$\begin{aligned} \frac{dF}{dt} &= \int d^3x \left[ v_\alpha \partial_t g_\alpha + \frac{1}{2} \Omega_{\alpha\beta} \partial_t l_{\alpha\beta} + \mu_i^{\text{tot}} \partial_t n_i - h_\alpha \partial_t p_\alpha \right] + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \partial_t p_\beta \\ &= \int d^3x (v_\alpha \partial_\beta \sigma_{\alpha\beta}^{\text{tot}} + \frac{1}{2} \Omega_{\alpha\beta} (\partial_\gamma M_{\alpha\beta\gamma}^\pi - 2\sigma_{\alpha\beta}^a) + \mu_i^{\text{tot}} (r_i - \partial_\alpha J_\alpha^i) - h_\alpha \partial_t p_\alpha) + \oint dS_\alpha \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \partial_t p_\beta \\ &= \int d^3x (-(\partial_\beta v_\alpha) \sigma_{\alpha\beta}^{\text{tot}} + \frac{1}{2} \Omega_{\alpha\beta} (\partial_\gamma M_{\alpha\beta\gamma}^\pi - 2\sigma_{\alpha\beta}^a) + \mu_i^{\text{tot}} r_i + (J_\alpha^i + n_i v_\alpha) \partial_\alpha \mu_i^{\text{tot}} - h_\alpha \partial_t p_\alpha) \\ &+ \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha}^{\text{tot}} - \mu_i^{\text{tot}} J_\alpha^i + \frac{\partial f_0}{\partial (\partial_\alpha p_\beta)} \partial_t p_\beta \right), \end{aligned} \quad (\text{C.6})$$

where  $h_\alpha = -\delta F_0/\delta p_\alpha$ ,  $\mu_i = \partial f_0/\partial n_i$  and  $\Omega_{\alpha\beta} = 2\partial f_0/\partial l_{\alpha\beta}$ . Note that because  $f_0$  contains contributions of kinetic energy associated with internal angular momentum, the field  $h_\alpha$  defined here contains contributions that depend on spin [41]. The equilibrium stress now reads

$$\sigma_{\alpha\beta}^e = (f_0 - \mu_i n_i - l_\gamma \Omega_\gamma) \delta_{\alpha\beta} - \frac{\partial f_0}{\partial(\partial_\beta p_\gamma)} \partial_\alpha p_\gamma \quad (\text{C.7})$$

and the Gibbs–Duhem relation becomes

$$-\partial_\beta \sigma_{\alpha\beta}^e = \frac{1}{2}(\partial_\alpha \Omega_{\beta\gamma}) l_{\beta\gamma} + (\partial_\alpha \mu_i) n_i + h_\beta \partial_\alpha p_\beta. \quad (\text{C.8})$$

At equilibrium with  $\partial_\alpha \Omega_{\beta\gamma} = 0$ ,  $\partial_\alpha \mu_i = 0$  and  $h_\alpha = 0$ , the equilibrium stress satisfies the force balance  $\partial_\beta \sigma_{\alpha\beta}^e = 0$ . Rotational invariance now implies the rotational Gibbs–Duhem relation

$$\partial_\gamma M_{\alpha\beta\gamma}^e = 2\sigma_{\alpha\beta}^{e,a} + (p_\alpha h_\beta - p_\beta h_\alpha) + (\Omega_\alpha l_\beta - \Omega_\beta l_\alpha). \quad (\text{C.9})$$

At a thermodynamic equilibrium,  $h_\alpha$  vanishes and  $\Omega_\alpha l_\beta - \Omega_\beta l_\alpha = 0$ . In this case  $\partial_\gamma M_{\alpha\beta\gamma}^e = 2\sigma_{\alpha\beta}^{e,a}$  becomes the equilibrium torque balance. Indeed, from equations (6) and (C.9) it follows that at equilibrium  $\partial_\gamma l_{\alpha\beta} = \Omega_\alpha l_\beta - \Omega_\beta l_\alpha$ . For an equilibrium state,  $\partial_\gamma l_{\alpha\beta} = 0$ . Therefore  $\Omega_\alpha l_\beta - \Omega_\beta l_\alpha$  must vanish for a global thermodynamic equilibrium. In the context of a spinning top, the same condition implies that a top spins in a steady state around a fixed axis [111]. Only in this case does a thermodynamic equilibrium exist.

Using the Gibbs–Duhem relation (C.8) and the relation (C.9) we have

where we have used the convected time derivative  $d/dt = \partial_t + v_\gamma \partial_\gamma$ . Since a system with finite but constant  $\Omega_{\alpha\beta}$  can be at equilibrium, we rewrite this as

$$\begin{aligned} \frac{dF}{dt} = \int d^3x & (-v_{\alpha\beta}(\sigma_{\alpha\beta}^s - \sigma_{\alpha\beta}^{e,s}) \\ & + (\omega_{\alpha\beta} - \Omega_{\alpha\beta})(\sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a} - p_\alpha h_\beta - \frac{1}{2}\partial_\gamma M_{\alpha\beta\gamma}^d) \\ & - \frac{1}{2}(\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \frac{Dp_\alpha}{Dt} \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha} - v_\alpha f - \mu_i j_\alpha^i + \frac{1}{2}\omega_{\beta\gamma} (M_{\beta\gamma\alpha}^\pi + v_\alpha l_{\beta\gamma}) \right. \\ & \left. + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{Dp_\beta}{Dt} \right), \end{aligned} \quad (\text{C.12})$$

where  $\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^{\text{tot}} + v_\alpha g_\beta$ ,  $M_{\alpha\beta\gamma}^d = M_{\alpha\beta\gamma}^\pi - M_{\alpha\beta\gamma}^e + v_\gamma l_{\alpha\beta}$ . We finally identify the free energy flux

$$j_\alpha^f = -v_\beta \sigma_{\beta\alpha} - \frac{1}{2}\omega_{\beta\gamma} (M_{\beta\gamma\alpha}^\pi + v_\alpha l_{\beta\gamma}) + \mu_i j_\alpha^i - \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{Dp_\beta}{Dt}. \quad (\text{C.13})$$

The entropy production rate is

$$\begin{aligned} T\theta = v_{\alpha\beta} \sigma_{\alpha\beta}^{s,d} + (\Omega_{\alpha\beta} - \omega_{\alpha\beta}) \sigma_{\alpha\beta}^{a,d} + \frac{1}{2}(\partial_\gamma \omega_{\alpha\beta}) M_{\alpha\beta\gamma}^d \\ + \sum_{l=1}^M r^l \Delta \mu^l - \sum_{i=1}^N j_\alpha^i \partial_\alpha \bar{\mu}_i + h_\alpha \frac{Dp_\alpha}{Dt} \end{aligned} \quad (\text{C.14})$$

with the deviatoric part of the antisymmetric stress

$$\begin{aligned} \frac{dF}{dt} = \int d^3x & (-\partial_\beta v_\alpha) \sigma_{\alpha\beta}^{\text{tot}} + \frac{1}{2} \Omega_{\alpha\beta} (\partial_\gamma M_{\alpha\beta\gamma}^\pi - 2\sigma_{\alpha\beta}^a) \\ & + \mu_i^{\text{tot}} r_i + j_\alpha^i \partial_\alpha \mu_i^{\text{tot}} - v_\alpha \partial_\beta \sigma_{\alpha\beta}^e - v_\alpha g_\beta (\partial_\alpha v_\beta) - h_\alpha \partial_t p_\alpha - v_\alpha h_\beta \partial_\alpha p_\beta - \frac{1}{2} v_\alpha (\partial_\alpha \Omega_{\beta\gamma}) l_{\beta\gamma} \\ & + \oint dS_\alpha \left( v_\beta \sigma_{\beta\alpha}^{\text{tot}} - (\mu_i - \frac{1}{2} m_i \mathbf{v}^2) (j_\alpha^i + n_i v_\alpha) + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \partial_t p_\beta \right) \\ & = \int d^3x (-\partial_\beta v_\alpha (\sigma_{\alpha\beta}^{\text{tot}} + v_\alpha g_\beta - \sigma_{\alpha\beta}^e) + \omega_{\alpha\beta} h_\alpha p_\beta \\ & + \frac{1}{2} \Omega_{\alpha\beta} (\partial_\gamma (M_{\alpha\beta\gamma}^\pi - M_{\alpha\beta\gamma}^e) - 2(\sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a}) + (p_\alpha h_\beta - p_\beta h_\alpha) + (\Omega_\alpha l_\beta - \Omega_\beta l_\alpha)) \\ & + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \partial_t p_\alpha - v_\alpha h_\beta \partial_\alpha p_\beta - h_\alpha \omega_{\alpha\beta} p_\beta - \frac{1}{2} v_\alpha l_{\beta\gamma} \partial_\alpha \Omega_{\beta\gamma}) \\ & + \oint dS_\alpha \left( v_\beta (\sigma_{\beta\alpha}^{\text{tot}} - \sigma_{\beta\alpha}^e) + v_\alpha (\frac{1}{2} \rho \mathbf{v}^2 - \mu_i n_i) - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \partial_t p_\beta \right). \end{aligned} \quad (\text{C.10})$$

Rewriting the expressions and using equation (29) and the definition of the Ericksen stress (C.7) in the surface terms, we obtain

$$\begin{aligned} \frac{dF}{dt} = \int d^3x & (-v_{\alpha\beta} (\sigma_{\alpha\beta}^{\text{tot},s} + v_\alpha g_\beta - \sigma_{\alpha\beta}^{e,s}) + (\omega_{\alpha\beta} - \Omega_{\alpha\beta}) (\sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a} - p_\alpha h_\beta) \\ & + \frac{1}{2} \Omega_{\alpha\beta} \partial_\gamma (M_{\alpha\beta\gamma}^\pi - M_{\alpha\beta\gamma}^e) - \frac{1}{2} v_\gamma (\partial_\gamma \Omega_{\alpha\beta}) l_{\alpha\beta} + \mu_i r_i + j_\alpha^i \partial_\alpha \mu_i - h_\alpha \frac{Dp_\alpha}{Dt}) \\ & + \oint dS_\alpha \left( v_\beta (\sigma_{\beta\alpha}^{\text{tot}} + v_\beta g_\alpha) - v_\alpha (f - l_\gamma \Omega_\gamma) - \mu_i j_\alpha^i + \frac{\partial f_0}{\partial(\partial_\alpha p_\beta)} \frac{dp_\beta}{dt} \right), \end{aligned} \quad (\text{C.11})$$



$$\sigma_{\alpha\beta}^{a,d} = \sigma_{\alpha\beta}^a - \sigma_{\alpha\beta}^{e,a} - \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha) - \frac{1}{2}\partial_\gamma M_{\alpha\beta\gamma}^d. \quad (\text{C.15})$$

Angular momentum conservation (6) then implies a dynamic equation for the intrinsic angular momentum

$$\partial_t l_{\alpha\beta} + \partial_\gamma (v_\gamma l_{\alpha\beta}) = -2\sigma_{\alpha\beta}^{a,d} + (\Omega_\alpha l_\beta - \Omega_\beta l_\alpha). \quad (\text{C.16})$$

Note that the intrinsic angular momentum does not introduce a separate hydrodynamic variable because the balance equation has a source term. Therefore, the intrinsic rotation rate  $\Omega$  relaxes on non-hydrodynamic time scales [41].

### C.3. Symmetrization of the stress tensor

The antisymmetric part of the stress can be eliminated by the following redefinition of stress and momentum density [39]

$$g'_\alpha = g_\alpha + \frac{1}{2}\partial_\beta l_{\alpha\beta} \quad (\text{C.17})$$

$$l'_{\alpha\beta} = 0 \quad (\text{C.18})$$

$$\sigma_{\alpha\beta}^{\text{tot}'} = \sigma_{\alpha\beta}^{\text{tot}} - \sigma_{\alpha\beta}^a + \frac{1}{2}\partial_\gamma M_{\alpha\gamma\beta}^\pi + \frac{1}{2}\partial_\gamma M_{\beta\gamma\alpha}^\pi \quad (\text{C.19})$$

$$M_{\alpha\beta\gamma}^{\pi'} = 0. \quad (\text{C.20})$$

The redefined stress tensor  $\sigma'_{\alpha\beta}$  is symmetric and obeys the momentum conservation equation  $\partial_t g'_\alpha = \partial_\beta \sigma_{\alpha\beta}^{\text{tot}'}$  as well as the angular momentum conservation (4). Note that the physics does not change under this redefinition which amounts to a use of different variables. The pairs of conjugate thermodynamic forces and fluxes remain the same but have to be expressed in the new variables. For passive systems, the redefined quantities approach the original ones in the hydrodynamic limit. One can then express in the hydrodynamic limit the thermodynamic fluxes and forces directly in the redefined variables. This suggests that in the hydrodynamic limit the thermodynamic flux  $\sigma_{\alpha\beta}^{a,d}$  is not significant, and the corresponding dissipative and reactive couplings do not matter. However, while this is true for passive systems, relevant active chiral terms can be missed by the symmetrisation of the stress tensor.

To illustrate these points, we briefly discuss the effects of the redefinition (C.17)–(C.20) of the stress tensor in the case of active chiral systems discussed in section 4.4. We consider for simplicity the limit when the intrinsic angular momentum density can be neglected,  $l_{\alpha\beta} \simeq 0$ . Using equations (80) and (88) the redefined dissipative part of the traceless symmetric stress reads

$$\begin{aligned} \bar{\sigma}_{\alpha\beta}^{d,s'} &= 2\eta\tilde{\nu}_{\alpha\beta} + \frac{\nu_1}{2}(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta}) + \zeta^I \Delta\mu^I \tilde{q}_{\alpha\beta} \\ &+ \frac{1}{2}(\zeta_2^{I,\text{eff}} + \zeta_3^I)\Delta\mu^I (\epsilon_{\alpha\gamma\nu}\partial_\gamma \tilde{q}_{\nu\beta} + \epsilon_{\beta\gamma\nu}\partial_\gamma \tilde{q}_{\nu\alpha}) \\ &- \frac{1}{2}\zeta_4^I \Delta\mu^I (\partial_\beta p_\alpha + \partial_\alpha p_\beta - \frac{2}{3}\partial_\gamma p_\gamma \delta_{\alpha\beta}) \quad , \quad (\text{C.21}) \end{aligned}$$

where for simplicity, we have set  $\kappa = \bar{\eta} = \bar{\nu}_2^{\text{eff}} = \bar{\nu}_3^{\text{eff}} = \bar{\nu}_4 = 0$  and have omitted terms proportional to gradients of  $\Delta\mu^I$ . The

last two terms in equation (C.21) are active terms proportional to gradients of the polarity field. Such terms in general also exist when including all terms allowed by symmetry in the constitutive equation (80). However in equation (80) these terms were not written for simplicity because they are unimportant in the hydrodynamic limit. This shows that active terms that contribute to the antisymmetric stress and to angular momentum flux effectively renormalize active terms in the redefined symmetric stress and the physics does not change.

However, the physics described by the active coefficients  $\zeta_a^I$ , which generate relative internal rotations described by equation (86) is missing when using symmetric stress tensors only. The reason is that after redefining the stress to be symmetric, information about the difference of rotation rates  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$  is lost. Note that while  $\Omega_{\alpha\beta} - \omega_{\alpha\beta}$  vanishes in passive fluids in the hydrodynamic limit, it can be finite at long times in active chiral fluids where it is thus a relevant variable. In this case a redefinition of the stress tensor to be symmetric misses physics of the system even in the hydrodynamic limit.

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