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Mechanics of active surfaces

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We derive a fully covariant theory of the mechanics of active surfaces. This theory provides a framework for the study of active biological or chemical processes at surfaces, such as the cell cortex, the mechanics of epithelial tissues, or reconstituted active systems on surfaces. We introduce forces and torques acting on a surface, and derive the associated force balance conditions. We show that surfaces with in-plane rotational symmetry can have broken up-down, chiral, or planar-chiral symmetry. We discuss the rate of entropy production in the surface and write linear constitutive relations that satisfy the Onsager relations. We show that the bending modulus, the spontaneous curvature, and the surface tension of a passive surface are renormalized by active terms. Finally, we identify active terms which are not found in a passive theory and discuss examples of shape instabilities that are related to active processes in the surface.

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Biological systems exhibit a stunning variety of complex morphologies and shapes. Organisms form from a fertilized egg in a dynamic process called morphogenesis. Such shape forming processes in biology involve active mechanical events during which surfaces undergo shape changes that are driven by active stresses and torques generated in the material. Important examples are two-dimensional tissues, so called epithelia. They represent surfaces that can deform their shape as a result of active cellular processes [1]. Cells also exhibit a variety of different shapes and can undergo active shape changes. For example, during cell division, cells round up to a spherical shape due to an increase of active surface tension [2]. Cell shapes are governed by the cell cortex, a thin layer of an active contractile material at the surface of the cell [3]. Epithelial tissues and the cell surface are examples of active surfaces. In addition, recent experiments have reconstituted thin shells of active material *in vitro* [4]. These are thin sheets of active matter that can deform due to the generation of internal forces and torques that are balanced by external forces [Fig. 1(a)].

The theory of active gels describes the large-scale properties of viscoelastic matter driven out of equilibrium due to a source of chemical free energy in the system [5]. A number of processes in living systems have been successfully described using this theoretical framework [6]. Living or artificial active systems often assemble into nearly two-dimensional surfaces. To understand the physics of such active surfaces requires a systematic analysis of force and torque balances in curved two-dimensional geometries, taking into account active stresses and material properties. The shapes of passive fluid membranes have been described with considerable success by the Helfrich free energy, a coarse-grained description of membranes with an expansion of the free energy in powers of the curvature tensor [7]. Expressions for the stress and torque tensors within a Helfrich membrane have been obtained. The associated force and torque balance equations are equivalent to shape equations for minimal energy shapes [8,9]. Active membrane theories have expanded the description of passive membranes to include external forces induced by pumps contained in a membrane [10–12].

The morphogenesis of epithelial tissues is a highly complex problem involving forces generated actively within the cells. Distribution of forces acting along the cross section of a sheetlike tissue give rise to in-plane tensions, but also to internal torques resulting from differential stresses acting along the cross section of the tissue [Fig. 1(b)]. These differential stresses are crucial to generate tissue shape changes [13]. However, no framework currently allows to describe the mechanics of active thin surfaces with internal stresses and torque densities.

In this work, we present such a general framework for the mechanics of active surfaces, driven internally out of equilibrium by molecular processes such as a chemical reaction. We start by considering forces and torques generated in a surface of arbitrary shape. The corresponding expression for the virtual work shows that components of the tension and torque tensors are coupled to the variation of the metric, of the curvature tensors, and of the Christoffel symbols defined for the surface [Eq. (15)]. Using these expressions, we then derive the entropy production for a fluid surface undergoing chemical reactions. We analyze the symmetries of surfaces with rotational symmetry in the plane, and show that they can have up-down, chiral, or planar-chiral broken symmetry. We write the corresponding constitutive equations for the components of the tension and torque tensors and for the fluxes of the chemical species. Interestingly, the generic constitutive equations involve couplings of the curvature tensor with the chemical potential of the surface chemical species. We then discuss the stability of a flat active fluid with broken up-down symmetry. Finally, we show that generic equations for an active elastic thin shell can be obtained using the same framework.

I. FORCE AND TORQUE BALANCE ON A CURVED SURFACE

We consider a curved surface $\mathbf{X}(s^1,s^2)$ parametrized by two generalized coordinates s^1, s^2 [Fig. 1(c)]. We use Latin indices to refer to surface coordinates and Greek indices to refer to

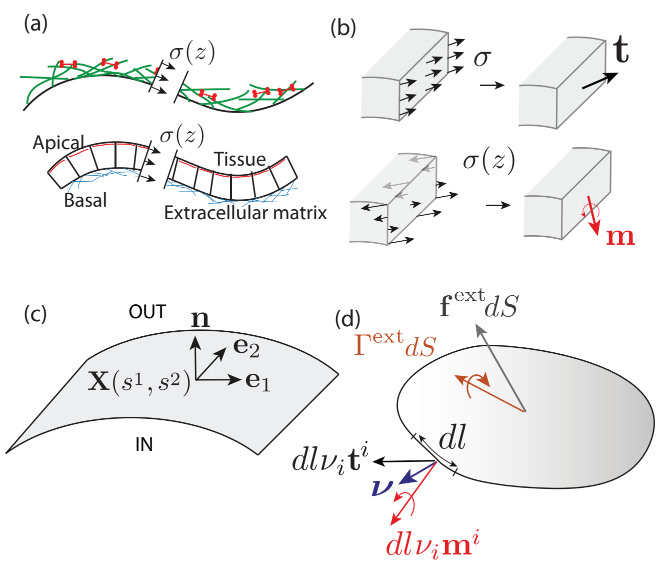

FIG. 1. (a) Filaments and motors near a surface and epithelial tissues are examples of active surfaces. (b) The distribution of stresses within a thin layer give rise to stresses and torques when integrated across the thickness of the layer. (c) Local basis of tangent vectors $\mathbf{e}_1$, $\mathbf{e}_2$ and normal vector $\mathbf{n}$ associated to the surface $\mathbf{X}(s^1,s^2)$. (d) Internal and external forces and torques acting on a surface element with surface area dS.

three-dimensional (3D) Euclidean coordinates. We introduce the metric tensor $g_{ij} = \mathbf{e}_i \cdot \mathbf{e}_j$ where $\mathbf{e}_i = \partial_i \mathbf{X}$ with $\partial_i = \partial/\partial s^i$. The curvature tensor is defined as $C_{ij} = -(\partial_i\partial_j\mathbf{X})\cdot\mathbf{n}$, where $\mathbf{n} = \mathbf{e}_1 \times \mathbf{e}_2/|\mathbf{e}_1 \times \mathbf{e}_2|$ is the unit normal vector, which we usually consider to point outward for a closed surface. We denote dl with $dl^2 = g_{ij}ds^i ds^j$ a line element on the surface, and $dS = \sqrt{g}ds^1ds^2$ a surface element, where $g = \det g_{ij}$ is the determinant of the metric tensor (Appendix A).

The force $\mathbf{f}$ and torque $\boldsymbol{\Gamma}$ across a line of length dl with *unit* vector $\boldsymbol{\nu} = \nu^i\mathbf{e}_i$, tangential to the surface and normal to the line, can be expressed as

$$\mathbf{f} = dl\ \nu^i\mathbf{t}_i = dl\ \nu_i\mathbf{t}^i, \tag{1}$$

$$\boldsymbol{\Gamma} = dl\ \nu^i\mathbf{m}_i = dl\ \nu_i\mathbf{m}^i, \tag{2}$$

where we have introduced the tension $\mathbf{t}_i$ and moment $\mathbf{m}_i$ per unit length [Figs. 1(b) and 1(d)]. Decomposing $\mathbf{t}^i$ and $\mathbf{m}^i$ in tangential and normal components as

$$\mathbf{t}^i = t^{ij}\mathbf{e}_j + t_n^i\mathbf{n}, \tag{3}$$

$$\mathbf{m}^i = m^{ij}\mathbf{e}_j + m_n^i\mathbf{n} \tag{4}$$

defines the tension and moment per unit length tensors t^{ij}, t_n^i, m^{ij}, and m_n^i. For simplicity, here and in the following we do not explicitly state if tensors are ordinary or pseudo tensors.

By expressing the total force acting on a region of surface $\mathcal{S}$ with contour $\mathcal{C}$ and using Newton's law, one finds

$$\int_{\mathcal{S}} dS\ \rho\mathbf{a} = \oint_{\mathcal{C}} dl\ \nu_i\mathbf{t}^i + \int_{\mathcal{S}} dS\ \mathbf{f}^{\rm ext}, \tag{5}$$

where ρ is the surface mass density, $\mathbf{a}$ is the local center-of-mass acceleration, $\mathbf{f}^{\rm ext}$ is an external force surface density. When the surface is embedded in a medium, the external force surface density is related to stresses exerted by the medium on the surface $f_\alpha^{\rm ext} = \sigma_{\beta\alpha}n_\beta$ with $\sigma_{\alpha\beta}$ the three-dimensional stress tensor in the medium. The total torque obeys

$$\int_{\mathcal{S}} dS[\mathbf{X}\times\rho\mathbf{a}] = \oint_{\mathcal{C}} dl\ \nu_i[\mathbf{m}^i + \mathbf{X}\times\mathbf{t}^i] + \int_{\mathcal{S}} dS[\boldsymbol{\Gamma}^{\rm ext} + \mathbf{X}\times\mathbf{f}^{\rm ext}], \tag{6}$$

where $\boldsymbol{\Gamma}^{\rm ext}$ is the external torque surface density, and where the left-hand side is the torque stemming from inertial forces. Here, we ignore the moment of inertia tensor for simplicity. This results in the force balance expression (Appendix C)

$$\nabla_i\mathbf{t}^i = -\mathbf{f}^{\rm ext} + \rho\mathbf{a}, \tag{7}$$

$$\nabla_i\mathbf{m}^i = \mathbf{t}^i\times\mathbf{e}_i - \boldsymbol{\Gamma}^{\rm ext}. \tag{8}$$

These equations can be expressed in terms of the components of the tension and torque tensors:

$$\nabla_i t^{ij} + C_i{}^j t_n^i = -f^{{\rm ext},j} + \rho a^j, \tag{9}$$

$$\nabla_i t_n^i - C_{ij}t^{ij} = -f_n^{\rm ext} + \rho a_n, \tag{10}$$

$$\nabla_i m^{ij} + C_i{}^j m_n^i = \epsilon_i{}^j t_n^i - \Gamma^{{\rm ext},j}, \tag{11}$$

$$\nabla_i m_n^i - C_{ij}m^{ij} = -\epsilon_{ij}t^{ij} - \Gamma_n^{\rm ext}, \tag{12}$$

where the tangential and normal components of a vector $\mathbf{v}$ on the surface are written $v^i = \mathbf{v}\cdot\mathbf{e}^i$ and $v_n = \mathbf{v}\cdot\mathbf{n}$.

II. VIRTUAL WORK

We introduce the virtual work δW, which is the mechanical work acting on a region of surface $\mathcal{S}$ enclosed by a contour $\mathcal{C}$, upon a small deformation $\delta\mathbf{X}$ of the surface, with $\mathbf{X}'(s^1,s^2) = \mathbf{X}(s^1,s^2) + \delta\mathbf{X}(s^1,s^2)$. Here, $\delta\mathbf{X}(s^1,s^2)$ represents a displacement of a material point on the surface specified by (s^1,s^2). The virtual work can be defined as

$$\delta W = \oint_{\mathcal{C}} dl\ \nu_i\left[\mathbf{t}^i\cdot\delta\mathbf{X} + \frac{1}{2}\boldsymbol{m}^i\cdot(\nabla\times\delta\mathbf{X})\right] + \int_{\mathcal{S}} dS\left[(\mathbf{f}^{\rm ext} - \rho\mathbf{a})\cdot\delta\mathbf{X} + \frac{1}{2}\boldsymbol{\Gamma}^{\rm ext}\cdot(\nabla\times\delta\mathbf{X})\right], \tag{13}$$

where $\mathcal{S}$ is the surface region enclosed by $\mathcal{C}$, and we have introduced the curl operator in Euclidian space [Eq. (A29)]:

$$(\nabla\times\delta\mathbf{X})_\alpha = \epsilon_{\alpha\beta\gamma}e_\beta^i(\partial_i\delta X_\gamma) + \epsilon_{\alpha\beta\gamma}n_\beta(\partial_n\delta X_\gamma). \tag{14}$$

In Eq. (14), we have introduced the normal derivative of the surface deformation $\partial_n\delta\mathbf{X}$. We consider here $\partial_n\delta\mathbf{X} = -(\partial_i\delta\mathbf{X}\cdot\mathbf{n})\mathbf{e}^i$ (Appendix B).

The terms in the expression of the virtual work (13) describe the work due to forces and torques acting at the boundary $\mathcal{C}$ as well as external forces and torques acting on the surface $\mathcal{S}$. Using force balance and the divergence theorem, the virtual work can be reexpressed as (see Appendix D)

$$\delta W = \int_{\mathcal{S}} dS\left[\bar{t}^{ij}\frac{\delta g_{ij}}{2} + \overline{m}^i{}_j\delta C_i{}^j + m_n^i\frac{\epsilon^j{}_k\delta\Gamma_{ij}^k}{2}\right]. \tag{15}$$

Here, the explicit expression of the metric variation δg_{ij}, curvature variation $\delta C_i{}^j$, and variation of Christoffel symbols $\delta\Gamma_{ij}^k$ as a function of the surface variation $\delta\mathbf{X}$ are given in Appendix B. We have introduced the in-plane tension and bending moment tensors

$$\bar{t}^{ij} = t_s^{ij} + \tfrac{1}{2}\left(\bar{m}^{ki}C_k{}^j + \bar{m}^{kj}C_k{}^i\right), \tag{16}$$

$$\overline{m}^{ij} = -m^{ik}\epsilon_k{}^j, \tag{17}$$

where the s subscript denotes the symmetric part of the tensor [Eq. (A14)]. In Eq. (15), we have used a reference frame that deforms with the material.

The virtual work given by Eq. (15) can be interpreted physically as the mechanical work due to different types of deformations. The in-plane surface stress tensor $\bar{t}^{ij}$ is conjugate to the variation of the metric tensor δg_{ij}, describing internal shear and area compression. The in-plane tension tensor $\bar{t}_{ij}$ introduced in Eq. (16) differs from the tension tensor t_{ij} introduced in Eq. (3): this is because in a thin shell, a deformation leading to a change of metric of the surface midplane corresponds to a three-dimensional shear within the shell. As a result, the work to deform the surface midplane depends on the in-plane bending moment tensor, which reflects the distribution of stresses across the thickness of the shell. The in-plane tensor $\bar{m}^i{}_j$ of bending moments is conjugate to the variation of the curvature tensor $\delta C_i{}^j$ due to bending of the surface. The normal torque m_n^i is conjugate to gradients of local rotations $\epsilon^j{}_k\delta\Gamma_{ij}^k$. The expression of the virtual work (15) does not include shear perpendicular to the surface: this would require the introduction of an additional variable.

The virtual work given in Eq. (15) is very general. In order to evaluate the virtual work for a given surface deformation, the values of the internal stresses characterized by the in-plane stress tensor $\bar{t}^{ij}$, the in-plane bending moment tensor $\overline{m}^{ij}$, and the normal torque $\mathbf{m}_n$, have to be known. In general, they are provided by constitutive relations describing the properties of the material associated with the surface.

We now discuss constitutive relations for active fluid and elastic curved surfaces. The case of a passive membrane is discussed in Appendix H.

III. CURVED ACTIVE FILM

We now use concepts for irreversible thermodynamics to derive constitutive equations for a curved isotropic fluid. We consider a fluid consisting of several species $\alpha = 1\ldots N$ with concentrations c^α. The local mass density is given by $\rho = \sum_\alpha m^\alpha c^\alpha$ with m^α the molecular mass of species α. The free energy density in the rest frame is denoted $f_0(c^\alpha, C_i{}^j, T)$ where $C_i{}^j$ is the curvature tensor of the film in mixed coordinates, and T the temperature. The differential of f_0 is

$$df_0 = \mu^\alpha dc^\alpha + K^i{}_j dC_i{}^j - s\,dT, \tag{18}$$

where μ^α is the chemical potential of component α, $K^i{}_j$ is the passive bending moment, and s the entropy density. The total free energy density is

$$f = \tfrac{1}{2}\rho v^2 + f_0, \tag{19}$$

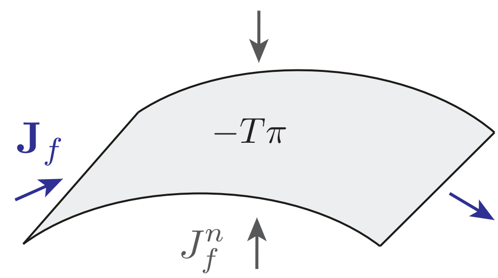

FIG. 2. Free energy balance on a surface element in the isothermal case. Free energy density is exchanged between the surface element and the surrounding surface with a flux $\mathbf{J}^f$, with the surrounding bulk with flux J_n^f, and is produced with rate $-T\pi$.

where the kinetic energy density is given by $\frac{1}{2}\rho v^2 = \frac{1}{2}\rho[v_i v^i + (v_n)^2]$. We denote $\mu_{\text{tot}}^\alpha = df/dc^\alpha = \mu^\alpha + m^\alpha v^2/2$ the total chemical potential of the chemical species α.

A. Conservation equations

We start by deriving conservation equations for the surface mass, concentration of chemical species, energy, entropy, and free energy. Using a Eulerian representation (Appendix E), mass balance reads as

$$\partial_t\rho + \nabla_i(\rho v^i) + v_n C_i{}^i\rho = J_n^\rho, \tag{20}$$

where J_n^ρ is a source term due to mass exchange with the environment and $\mathbf{v} = v^i\mathbf{e}_i + v_n\mathbf{n}$ is the center-of-mass velocity.

The concentrations c^α obey the balance equation

$$\partial_t c^\alpha + \nabla_i J^{\alpha,i} + v_n C_i{}^i c^\alpha = J_n^\alpha + r^\alpha, \tag{21}$$

where $J^{\alpha,i} = c^\alpha v^i + j^{\alpha,i}$ is the tangential flux in the surface of molecule α with $j^{\alpha,i}$ the flux relative to the center of mass, J_n^α describes exchanges between the surface and its surrounding environment, and r^α denote source and sink terms corresponding to chemical reactions in the surface. Mass conservation implies the following relation between fluxes of molecules and chemical rates:

$$\sum_\alpha m^\alpha J_n^\alpha = J_n^\rho, \tag{22}$$

$$\sum_\alpha m^\alpha j^{\alpha,i} = 0, \tag{23}$$

$$\sum_\alpha m^\alpha r^\alpha = 0. \tag{24}$$

In the remaining of this work, summation over α is implicit. The conservation of energy and the balance of entropy and free energy density have the form (Fig. 2)

$$\partial_t e + \nabla_i J^{e,i} + v_n C_i{}^i e = J_n^e, \tag{25}$$

$$\partial_t s + \nabla_i J^{s,i} + v_n C_i{}^i s = J_n^s + \pi, \tag{26}$$

$$\partial_t f + \nabla_i J^{f,i} + v_n C_i{}^i f = J_n^f - T\pi - J_s^i\nabla_i T - (\partial_t T)s, \tag{27}$$

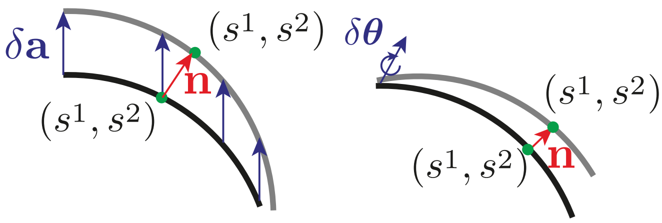

FIG. 3. Two Gibbs-Duhem relations for a fluid surface are obtained by considering a rigid translation of the surface by a uniform infinitesimal vector $\delta\mathbf{a}$ or a rigid rotation with infinitesimal vector $\delta\boldsymbol{\theta}$. Coordinates on the new surface are obtained by following the normal $\mathbf{n}$ of the original surface.

where e and s are the energy and entropy density, respectively, J_n^e and J_n^s are energy and entropy fluxes entering the surface from the adjacent bulk, $J^{e,i}$ and $J^{s,i}$ are tangential energy and entropy fluxes within the surface, and $J_n^f = J_n^e - TJ_n^s$ and $J^{f,i} = J^{e,i} - TJ^{s,i}$ are the normal and tangential fluxes of free energy. The entropy production rate within the surface is denoted π. Equation (27) is obtained from the relation $f = e - Ts$ and Eqs. (25) and (26). In the following, we consider for simplicity the isothermal case.

B. Translation and rotation invariance

We now discuss relations between equilibrium tensions and torques implied by invariance of the surface properties under a rigid translation or rotation.

1. Gibbs-Duhem relation

Using translation invariance of the free energy, we can derive a Gibbs-Duhem relation. We consider an infinitesimal translation of the surface by a constant vector $\delta\mathbf{a}$. The condition $\partial_i \delta\mathbf{a} = 0$ implies, using Eq. (A20),

$$\nabla_i \delta a^j + C_i{}^j \delta a_n = 0, \tag{28}$$

$$\partial_i \delta a_n - C_{ij}\delta a^j = 0. \tag{29}$$

During translation, we reparametrize the new surface such that each point (s^1,s^2) moves normal to the original surface on the new translated surface (Fig. 3). Translation invariance then implies the relation (see Appendix F)

$$\nabla_j\left[(f_0 - \mu^\alpha c^\alpha)g_i{}^j - K^{jk}C_{ik}\right] + C_{ik}\nabla_j K^{jk} = -c^\alpha \partial_i \mu^\alpha. \tag{30}$$

Equation (30) is a covariant generalization for surfaces of the Gibbs-Duhem relation for a three-dimensional multicomponent fluid [14,15], with an additional term arising from the passive bending moment tensor.

2. Rotation invariance

We can derive a generalized Gibbs-Duhem relation describing torque balances using infinitesimal rotation described by the pseudovector $\delta\boldsymbol{\theta}$, such that the surface is deformed as

$$\delta X_\alpha = \epsilon_{\alpha\beta\gamma}\delta\theta_\beta X_\gamma. \tag{31}$$

The deformation defines a new surface $\mathbf{X}' = \mathbf{X} + \delta\mathbf{X}$, which is reparametrized such that (s^1,s^2) is constant along the normal to the original surface. Rotation invariance then implies (see Appendix F)

$$K^{ij}\epsilon_{jk}C_i{}^k = 0, \tag{32}$$

implying that the tensor $K^{ij}C_i{}^k$ is symmetric.

3. Equilibrium tensions and torques

The equilibrium tension and bending moment tensors can be obtained by calculating the change of free energy under a surface deformation and using the expression of the virtual work (15) (Appendix H). The equilibrium tension and bending moments are given by

$$\bar{t}_e^{ij} = (f_0 - \mu^\alpha c^\alpha)g^{ij}, \tag{33}$$

$$\bar{m}_e^{ij} = K^{ij}, \tag{34}$$

$$m_{n,e}^i = 0. \tag{35}$$

Using Eqs. (16) and (17), one also obtains the symmetric part of the equilibrium tension tensor $t_{e,s}^{ij} = (f_0 - \mu^\alpha c^\alpha)g^{ij} - (K_k{}^i C^{kj} + K_k{}^j C^{ki})/2$ and the bending moment tensor $m_e^{ij} = K^{ik}\epsilon_k{}^j$. Note that the surface tension can be defined by $\gamma = t_i{}^i/2 = f_0 - \mu^\alpha c^\alpha - K_{ij}C^{ij}/2$. Using the tangential torque balance equation (11) then yields the equilibrium tension $t_{e,n}^i = \nabla_j K^{ji} - \epsilon_j{}^i \Gamma^{\text{ext},j}$. Using Eqs. (32) and (35), the normal torque balance equation (12) yields the equilibrium antisymmetric part of the stress $\epsilon_{ij}t^{ij} = -\Gamma_n^{\text{ext}}$.

Combining the Gibbs-Duhem relation (30) and the tangential force balance given by Eq. (9), taking into account the symmetry relation (32), leads to the equilibrium condition relating chemical equilibrium gradients to external forces:

$$\begin{aligned} c^\alpha \partial_j \mu^\alpha &= f_j^{\text{ext}} - \tfrac{1}{2}\epsilon^i{}_j\left(\partial_i \Gamma_n^{\text{ext}}\right) - C_{ij}\epsilon_k{}^i \Gamma^{\text{ext},k} \\ &= -c^\alpha[\partial_j U^\alpha + C_{ij}(\partial U^\alpha/\partial\mathbf{n})\cdot\mathbf{e}^i]. \end{aligned} \tag{36}$$

In the second line, the external force and torque surface densities derive from a potential $U^\alpha(s^1,s^2,\mathbf{n})$ acting on component α [Eqs. (H10) and (H11)]. Equation (36) shows that one can then introduce the effective chemical potential $\mu_{\text{eff}}^\alpha(s^1,s^2) = \mu^\alpha(s^1,s^2) + U^\alpha(s^1,s^2,\mathbf{n}(s^1,s^2))$, for which $c^\alpha\partial_i\mu_{\text{eff}}^\alpha = 0$.

The remaining normal force balance equation (10) then provides a shape equation for the equilibrium surface shape.

C. Entropy production rate

We can now calculate the entropy production rate using the variation of the free energy and the Gibbs-Duhem relation derived above. We consider a region of surface $\mathcal{S}$ enclosed by a fixed contour $\mathcal{C}$, which can deform in three dimensions. The rate of change of the free energy F can be written as (see Appendix I)

$$\begin{aligned} \frac{dF}{dt} = \int_{\mathcal{S}} dS\Big[&-\left(\bar{t}^{ij} - \bar{t}_e^{ij}\right)v_{ij} - (\bar{m}^{ij} - K^{ij})\frac{DC_{ij}}{Dt} \\ &- m_n^i(\partial_i\omega_n - C_{ij}\omega^j) + (\partial_i\mu^\alpha)j^{\alpha,i} + \mu^\alpha r^\alpha \\ &+ \mu_{\text{tot}}^\alpha J_n^\alpha + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + \boldsymbol{\Gamma}^{\text{ext}}\cdot\boldsymbol{\omega}\Big] \\ &+ \int_{\mathcal{C}} dl\, \nu_i[-fv^i - \mu^\alpha j^{\alpha,i} + \mathbf{t}^i\cdot\mathbf{v} + \mathbf{m}^i\cdot\boldsymbol{\omega}], \end{aligned} \tag{37}$$

where we have introduced the symmetric in-plane shear tensor v_{ij}, the curl of the flow $\boldsymbol{\omega} = \omega^i \mathbf{e}_i + \omega_n \mathbf{n}$, and the corotational derivative of the curvature tensor:

$$v_{ij} = \tfrac{1}{2}(\nabla_i v_j + \nabla_j v_i) + C_{ij} v_n, \tag{38}$$

$$\boldsymbol{\omega} = \epsilon^{ij}(\partial_j v_n - C_{jk} v^k)\mathbf{e}_i + \tfrac{1}{2}\epsilon^{ij}(\nabla_i v_j)\mathbf{n}, \tag{39}$$

$$\frac{DC_{ij}}{Dt} = -\nabla_i(\partial_j v_n) - v_n C_{ik} C^k{}_j + v^k \nabla_k C_{ij} + \omega_n\left(\epsilon_i{}^k C_{kj} + \epsilon_j{}^k C_{ki}\right). \tag{40}$$

Note that the in-plane shear tensor v_{ij} is the sum of a contribution from in-plane flows, equal to the symmetric part of the covariant gradient of flow $\nabla_i v_j$, and a contribution arising from normal flows v^n, corresponding to in-plane shear induced by the deformation of the surface in three dimensions. The vorticity $\boldsymbol{\omega}$ of the flow has a normal part arising from the two-dimensional vorticity of the flow $\epsilon^{ij}\nabla_i v_j/2$, and a tangential part specific to curved surfaces. The bending rate tensor DC_{ij}/Dt has the form of a corotational derivative, with the third term in Eq. (40) corresponding to advection of the curvature, and the last two terms to a corotational term. In Eq. (37), we have not included contributions from the antisymmetric part of $\bar{m}_{ij}$. Note that the bending moment tensor can always be chosen to be symmetric in the force balance equations (see Appendix I).

We can read off the entropy production rate in the surface per unit area from Eq. (37):

$$T\pi = \bar{t}^{ij}_d v_{ij} + \bar{m}^{ij}_d \frac{DC_{ij}}{Dt} + m^i_n(\partial_i \omega_n - C_{ij}\omega^j) - (\partial_i \mu^\alpha) j^{\alpha,i} - \mu^\alpha r^\alpha, \tag{41}$$

where $\bar{t}^{ij}_d = \bar{t}^{ij} - \bar{t}^e_{ij}$ and $\bar{m}^{ij}_d = \bar{m}^{ij} - K^{ij}$ are the deviatoric parts of the in-plane stress and bending moment tensor. The mechanical contribution to dissipation can be also understood starting from Eq. (15) using $T\pi_m = \delta W_d/\delta t$, where δW_d is the work done by dissipative forces, together with Eqs. (E6)–(E8). The entropy production rate is a sum of products of conjugate thermodynamic fluxes and forces, which all vanish at thermodynamic equilibrium. The pairs of conjugate fluxes and forces are listed in Table I. Because of the balance equations (23) and (24), the N fluxes $j^{\alpha,i}$ and rates r^α are not independent and the current and source rate of one molecular species can be expressed as a function of the others.

We now briefly discuss the conjugate fluxes and forces. The deviatoric in-plane tension tensor $\bar{t}^{ij}_d$ is conjugate to the in-plane shear rate v_{ij}, corresponding to the dissipative cost of introducing in-plane deformations in the surface. The coupling between the deviatoric in-plane bending moment $\overline{m}^{ij}_d$ and the bending rate tensor DC_{ij}/Dt arises only for curved surfaces and is associated to the dissipative cost of changing the surface shape in three dimensions. The coupling between the normal moment m^i_n and the vorticity gradient of flow $(\partial_i\boldsymbol{\omega})\cdot\mathbf{n} = \partial_i\omega_n - C_{ij}\omega^j$ is a generalization to curved surfaces of a coupling which also arises for planar surfaces, and is associated to the dissipative cost of gradients of rotations within the surface [16]. Finally, the two last terms in Eq. (41) correspond to couplings of the chemical potential and its gradient to the rates of reactions and the flux of diffusion of species in the surface [15].

The flux of free energy entering the surface from the adjacent bulk reads as

$$J^f_n = \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + \boldsymbol{\Gamma}^{\text{ext}}\cdot\boldsymbol{\omega} + \mu^\alpha_{\text{tot}} J^\alpha_n, \tag{42}$$

which corresponds to the sum of the mechanical power acting on the surface and of the influx of chemical energy in the surface. The flux of free energy tangential to the surface reads as

$$J^{f,i} = f v^i - \mathbf{t}^i\cdot\mathbf{v} - \mathbf{m}^i\cdot\boldsymbol{\omega} + \mu^\alpha j^{\alpha,i}, \tag{43}$$

where $f v^i$ is the advection of free energy, $\mu^\alpha j^{\alpha,i}$ is the flux of chemical free energy, and the remaining terms describe the mechanical power tangential to the surface at its boundaries.

D. Mirror and rotation symmetries of surfaces

Constitutive relations describing the active surface must respect the symmetries satisfied by the surface [17]. We therefore classify surfaces by asking whether the state of an element of surface is preserved under application of symmetries (Fig. 4).

We restrict ourselves to surfaces with rotation symmetry in the plane. We then find that three sets of discrete symmetries can be associated to thin shells: up-down mirror symmetry M_n, mirror symmetry with respect to a plane normal to the surface M_t, and up-down rotation symmetry R_t [Fig. 4(a)]. M_t corresponds to a mirror symmetry by a normal plane going along an arbitrary tangent vector $\mathbf{t}$, R_t to a rotation of π around an arbitrary tangent vector $\mathbf{t}$. The corresponding transformations rules are given in Appendix G. Because inversion of space can be written as the combination of M_n and the rotation of π around the normal R_n, inversion of space and M_n are broken or preserved simultaneously for a surface with in-plane rotation symmetry. Furthermore, combination of two of the symmetries M_n, M_t, and R_t yields the third one, such that at least two of these symmetries must be broken. As a result, surfaces can be classified into five different classes: (i) up-down symmetric, nonchiral surfaces (type 0) preserve all three symmetries, (ii) nonchiral surfaces with broken up-down symmetry (type UD) preserve M_t but break M_n and R_t, (iii) chiral surfaces with up-down rotation symmetry break all mirror symmetries M_t and M_n but preserve R_t (type C), (iv) planar-chiral surfaces preserve up-down mirror symmetry M_n but break M_t and R_t (type PC), (v) up-down asymmetric and chiral surfaces break M_n, M_t and R_t (Fig. 4). Note that we choose to denote surfaces breaking M_t and not M_n

TABLE I. List of pairs of conjugate thermodynamics fluxes and forces in a thin active surface.

Flux	Force
In-plane shear tensor v_{ij}	In-plane tension tensor $\bar{t}^{ij}_d$
Bending rate tensor $\frac{DC_{ij}}{Dt}$	In-plane bending moment tensor $\bar{m}^{ij}_d$
Vorticity gradient $(\partial_i\boldsymbol{\omega})\cdot\mathbf{n}$	Normal moment m^i_n
Diffusion flux $j^{i,\alpha}$	Chemical potential gradient $-\partial_i\mu^\alpha$
Chemical reaction rate $-r^\alpha$	Chemical potential μ^α

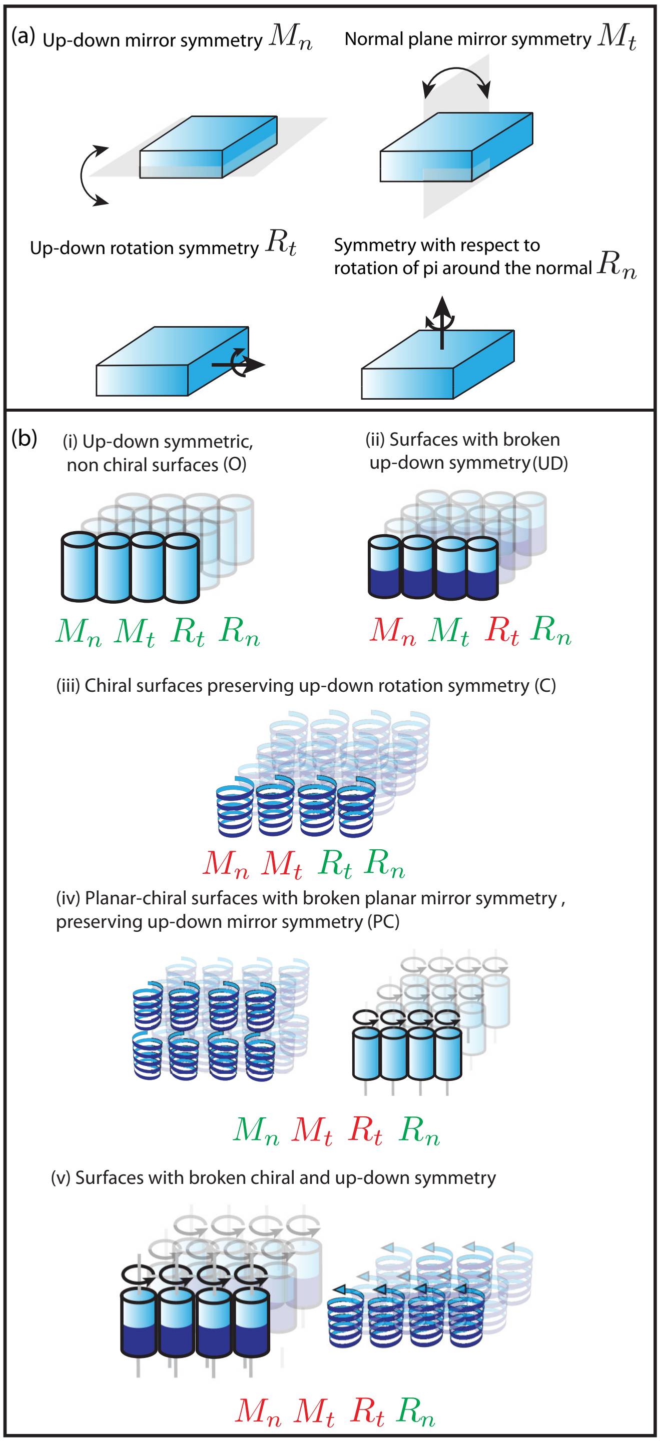

FIG. 4. Classification of surfaces with in-plane rotation symmetry. (a) The surface state can change under up-down mirror symmetry M_n, mirror symmetry M_t, up-down rotation symmetry R_t, and rotation by π around the normal R_n. The symmetry R_n is not broken for a surface with in-plane rotation symmetry. (b) Surfaces with in-plane rotation symmetry can be categorized in five classes according to their symmetries. Schematics give examples of actual surfaces belonging to each category. Red and green letters indicate, respectively, broken and preserved symmetries.

planar-chiral surfaces because they break mirror symmetry with respect to a plane perpendicular to the surface, but these surfaces are not necessarily made of chiral molecules [Fig. 4(b)].

E. Constitutive and hydrodynamic equations

Using the conjugate thermodynamic forces and fluxes obtained from Eq. (41) and listed in Table I, we write a generic linear response theory taking into account the symmetries of an active fluid surface. For simplicity, we consider that a single chemical reaction occurs in the surface converting a fuel species F into a product species P. The fuel and product species have the same mass, and we neglect here for simplicity reaction rates and fluxes relative to the center of mass of other components. We denote $\Delta\mu = \mu^F - \mu^P$ the difference of chemical potential between the field and product species, $r = -r^F = r^P$ the rate of fuel consumption and $\mathbf{j} = \mathbf{j}^F = -\mathbf{j}^P$ its flux, where we have used Eqs. (23) and (24). We also assume that no chemical exchange exists between the membrane and its surrounding, such that the normal fluxes J_n^α and J_n^ρ vanish. In the linear response theory, we expand the tensors $\bar{t}_d^{ij}$, $\bar{m}_d^{ij}$, m_n^i, diffusion flux $j^{i,\alpha}$, and chemical reaction rate r^α to linear order in the rates of deformation v_{ij}, $DC_i{}^j/Dt$, $(\partial_i \boldsymbol{\omega})\cdot\mathbf{n}$, chemical potential gradient $\partial_i\Delta\mu$, and chemical potential $\Delta\mu$.

The stress and moment tensors can then be decomposed as

$$\begin{aligned} \bar{t}_d^{ij} &= \bar{t}_0^{ij} + \bar{t}_{\mathrm{UD}}^{ij} + \bar{t}_{\mathrm{C}}^{ij} + \bar{t}_{\mathrm{PC}}^{ij}, \\ \overline{m}_d^{ij} &= \overline{m}_0^{ij} + \overline{m}_{\mathrm{UD}}^{ij} + \overline{m}_{\mathrm{C}}^{ij} + \overline{m}_{\mathrm{PC}}^{ij}, \\ m_n^i &= m_{n0}^i + m_{n\mathrm{UD}}^i + m_{n\mathrm{C}}^i + m_{n\mathrm{PC}}^i, \end{aligned} \tag{44}$$

where $\bar{t}_0^{ij}$ is the part of the stress tensor that exists for any surface, $\bar{t}_{\mathrm{UD}}^{ij}$ correspond to terms present when the surface breaks up-down symmetry, $\bar{t}_{\mathrm{C}}^{ij}$ exist for chiral surfaces, and $\bar{t}_{\mathrm{PC}}^{ij}$ for planar-chiral surfaces. Similar rules apply for the decomposition of the bending moment tensor and normal moment tensor.

To express constitutive equations for each of the components, we then write all possible terms of the expansion of the generalized forces in the fluxes at linear order, and ask whether the corresponding terms break the symmetry M_n, M_t, R_t according to the signatures given in Appendix G. We consider here an active surface close to equilibrium and use the Onsager symmetry relations [18]. The contributions to the deviatoric part of the tension tensor then read as

$$\begin{aligned} \bar{t}_0^{ij} &= 2\eta\tilde{v}^{ij} + \eta_b v_k{}^k g^{ij} + \zeta g^{ij}\Delta\mu, \\ \bar{t}_{\mathrm{UD}}^{ij} &= 2\bar{\eta}\frac{D\tilde{C}^{ij}}{Dt} + \bar{\eta}_b\frac{DC_k{}^k}{Dt}g^{ij} + 2\tilde{\zeta}\tilde{C}^{ij}\Delta\mu + \zeta' C_k{}^k g^{ij}\Delta\mu, \\ \bar{t}_{\mathrm{C}}^{ij} &= \eta_{\mathrm{C}}\left(\epsilon^{ik}\frac{DC_k{}^j}{Dt} + \epsilon^{jk}\frac{DC_k{}^i}{Dt}\right) + \zeta_{\mathrm{C}}(\epsilon^i{}_k C^{kj} + \epsilon^j{}_k C^{ki})\Delta\mu, \\ \bar{t}_{\mathrm{PC}}^{ij} &= \eta_{\mathrm{PC}}(\epsilon^i{}_k v^{kj} + \epsilon^j{}_k v^{ki}), \end{aligned} \tag{45}$$

where we have introduced the notation $\tilde{A}_{ij} = A_{ij} - \frac{1}{2}A_k{}^k g_{ij}$ for the traceless part of a tensor $\mathbf{A}$. The deviatoric part of the moment tensor reads as

$$\begin{aligned}
\overline{m}_0^{ij} &= 2\eta_c \frac{D\tilde{C}^{ij}}{Dt} + \eta_{cb}\frac{DC_k{}^k}{Dt} g^{ij} + 2\tilde{\zeta}_c \tilde{C}^{ij}\Delta\mu + \zeta_c' C_k{}^k g^{ij}\Delta\mu, \\
\overline{m}_{\rm UD}^{ij} &= 2\bar{\eta}\tilde{v}^{ij} + \bar{\eta}_b v_k{}^k g^{ij} + \zeta_c g^{ij}\Delta\mu, \\
\overline{m}_{\rm C}^{ij} &= -\eta_{\rm C}(\epsilon^i{}_k v^{kj} + \epsilon^j{}_k v^{ki}), \\
\overline{m}_{\rm PC}^{ij} &= \eta_{\rm cPC}\left(\epsilon^{ik}\frac{DC_k{}^j}{Dt} + \epsilon^{jk}\frac{DC_k{}^i}{Dt}\right) \\
&\quad + \zeta_{\rm PC}(\epsilon^i{}_k C^{kj} + \epsilon^j{}_k C^{ki})\Delta\mu. \qquad (46)
\end{aligned}$$

In Eq. (46), we have only introduced symmetric contributions to the bending moment tensor. The normal moment reads as

$$\begin{aligned}
m_{n0}^i &= \lambda(\partial^i\omega_n - C^{ij}\omega_j) + \chi\epsilon^{ij}\partial_j\Delta\mu \\
m_{n\rm UD}^i &= (\bar{\chi}_1\epsilon^i{}_k C^{kj} + \bar{\chi}_2 C^i{}_k\epsilon^{kj})\partial_j\Delta\mu \\
m_{n\rm C}^i &= \chi_{\rm C} C^{ij}\partial_j\Delta\mu + \chi_{\rm C}' C_k{}^k\partial^i\Delta\mu \\
m_{n\rm PC}^i &= \lambda_{\rm PC}\epsilon^{ij}(\partial_j\omega_n - C_{jk}\omega^k) + \chi_{\rm PC}\partial^i\Delta\mu. \qquad (47)
\end{aligned}$$

The rate of fuel consumption then reads as

$$\begin{aligned}
r &= -(\zeta + \zeta' C_k{}^k)v_k{}^k - 2\tilde{\zeta}\tilde{C}^{ij}\tilde{v}_{ij} - 2\zeta_{\rm C}\epsilon^i{}_k C^{kj} v_{ij} \\
&\quad - (\zeta_c + \zeta_c' C_k{}^k)\frac{DC_k{}^k}{Dt} - 2\tilde{\zeta}_c\tilde{C}^{ij}\frac{D\tilde{C}_{ij}}{Dt} \\
&\quad - 2\zeta_{\rm PC}\epsilon^i{}_k C^{kj}\frac{DC_{ij}}{Dt} + \Lambda\Delta\mu \qquad (48)
\end{aligned}$$

and the fuel flux relative to the center of mass is given by

$$\begin{aligned}
j^i &= -L\partial^i\Delta\mu + L_{\rm PC}\epsilon^{ij}\partial_j\Delta\mu + (-\chi\epsilon^{ij} + \chi_{\rm C} C^{ij} \\
&\quad -\bar{\chi}_2\epsilon^i{}_k C^{kj} - \bar{\chi}_1 C^i{}_k\epsilon^{kj} + (\chi_{\rm PC} + \chi_{\rm C}' C_k{}^k)g^{ij}) \\
&\quad \times(\partial_j\omega_n - C_{jk}\omega^k). \qquad (49)
\end{aligned}$$

$\eta, \eta_b, \bar{\eta}, \bar{\eta}_b, \eta_c, \eta_{cb}, \eta_{\rm C}, \lambda, \Lambda$, and L are dissipative couplings, ζ, ζ', $\tilde{\zeta}$, ζ_c, $\tilde{\zeta}_c$, ζ_c', $\zeta_{\rm C}$, $\zeta_{\rm PC}$, χ, $\bar{\chi}_1$, $\bar{\chi}_2$, $\chi_{\rm C}$, $\chi_{\rm C}'$, and $\chi_{\rm PC}$ are reactive couplings. The viscosities depend in general on the curvature tensor C_{ij}; here we have not taken this dependency into account for simplicity. We have introduced terms proportionals to $\eta_{\rm PC}$, $\eta_{\rm cPC}$, $\lambda_{\rm PC}$, and $L_{\rm PC}$ corresponding to odd or Hall viscosities which do not contribute to dissipation. These are reactive coefficients, and the time signatures of the constitutive equations imply that they change sign under time reversal, which could exist for example in the presence of a magnetic field [19]. Active tensions and bending moments proportional to the difference of chemical potential $\Delta\mu$ depend on the curvature tensor. In the constitutive equations (45)–(49), we have expanded these terms to first order in the curvature tensor C_{ij}. Although we have not written explicitly this dependency here, the phenomenological coefficients also depend in general in the concentration fields c^α. Positivity of entropy productions implies that the viscosities η, η_b, η_c, η_{cb}, and λ are positive, however, the up-down asymmetric viscosities $\bar{\eta}$, $\bar{\eta}_b$ and chiral viscosity $\eta_{\rm C}$ can be positive or negative.

In the equations above, the contribution to the two-dimensional stress $\bar{t}_0^{ij}$ is the generalization for curved surfaces of the generic hydrodynamic equations of a three-dimensional active gel [5]: η and η_b are, respectively, the planar shear and bulk viscosity of the surface, and $\zeta\Delta\mu$ is an active tension arising in the surface from active processes. Additional viscous tensions proportional to $\bar{\eta}$, $\bar{\eta}_b$, and η_C arise for a curved surface due to the dissipative cost of changing the surface curvature. We also find new active terms for the tension tensor of a curved surface proportional to $\tilde{\zeta}$, ζ', ζ_C, that depend on the curvature tensor C_{ij}. In particular, anisotropic active stresses can arise in a curved surface isotropic in the plane, due to the anisotropy of the curvature.

Active terms for the moment tensor introduced in Eq. (46) are specific to thin films and correspond to actively induced torques in the film. The active torque ζ_c, arising in a surface with broken up-down symmetry, can induce active bending of a flat surface. Combining the constitutive equations (45)–(49), the force and torque balance equations (7) and (8), and the concentration balance equations (21) yield dynamic equations for the surface shape, the velocity field on the surface **v**, and the concentration fields on the surface c^α. While the constitutive equations obtained here are linear in the fluxes, the dynamics equations for the surface shape are in general nonlinear due to geometric couplings.

F. Instabilities of a homogeneous active Helfrich membrane

In this section, we restrict ourselves to nonchiral surfaces with broken up-down symmetry and discuss low Reynolds numbers where inertial terms can be neglected. Starting from a description of a passive surface with the Helfrich free energy, we consider effects introduced by additional active terms.

1. General equations

A passive fluid membrane described by the Helfrich energy with membrane tension γ_H, bending modulus κ, Gaussian bending modulus κ_g, and spontaneous curvature C_0 has the equilibrium tension and bending moment tensor (Appendix H)

$$\bar{t}_{ij} = \left[\gamma_H + \left(\frac{\kappa+\kappa_g}{2}\right)(C_k{}^k)^2 - \kappa C_k{}^k C_0 - \frac{\kappa_g}{2}C_l{}^k C_k{}^l\right]g_{ij}, \qquad (50)$$

$$\bar{m}_i{}^j = [(\kappa+\kappa_g)C_k{}^k - \kappa C_0]g_i{}^j - \kappa_g C_i{}^j. \qquad (51)$$

Starting from such a passive fluid membrane, the constitutive relation for the tension and bending moment tensor of an active surface reads as, neglecting viscous terms for this discussion and keeping terms only to first order in the curvature,

$$\bar{t}^{ij} \simeq [\gamma_H + \zeta\Delta\mu + (-\kappa C_0 + \zeta'\Delta\mu)C_k{}^k]g^{ij} + 2\tilde{\zeta}\Delta\mu\tilde{C}^{ij}, \qquad (52)$$

$$\begin{aligned}
\bar{m}^{ij} &\simeq \{[\kappa + \kappa_g + (\zeta_c' - \tilde{\zeta}_c)\Delta\mu]C_k{}^k + (\zeta_c\Delta\mu - \kappa C_0)\}g^{ij} \\
&\quad - (\kappa_g - 2\tilde{\zeta}_c\Delta\mu)C^{ij}. \qquad (53)
\end{aligned}$$

Introducing a surface tension renormalized by activity $\bar{\gamma} = \gamma_H + \zeta\Delta\mu$, and similarly the renormalized bending moduli $\bar{\kappa}_g = \kappa_g - 2\tilde{\zeta}_c\Delta\mu$, $\bar{\kappa} = \kappa + (\tilde{\zeta}_c + \zeta_c')\Delta\mu$ and spontaneous curvature $\bar{C}_0 = \kappa C_0/\bar{\kappa} - \zeta_c\Delta\mu/\bar{\kappa}$, one obtains

$$\bar{t}^{ij} = \{\bar{\gamma} + [-\bar{\kappa}\bar{C}_0 + (\zeta' - \zeta_c)\Delta\mu]C_k{}^k\}g^{ij} + 2\tilde{\zeta}\Delta\mu\tilde{C}^{ij}, \qquad (54)$$

$$\bar{m}^{ij} = [(\bar{\kappa} + \bar{\kappa}_g)C_k{}^k - \bar{\kappa}\bar{C}_0]g^{ij} - \bar{\kappa}_g C^{ij}. \qquad (55)$$

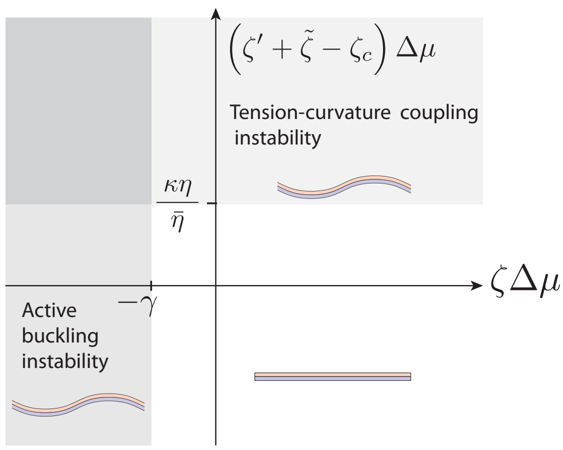

FIG. 5. Phase diagram for the stability of a flat active Helfrich membrane with up-down asymmetry, as a function of the active tension $\zeta\Delta\mu$ and the active tension-curvature coupling term $(\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu$, for $\bar{\eta} > 0$. For simplicity, we consider here the case $\tilde{\zeta}_c = \zeta_c' = 0$ and $\eta_b = \bar{\eta}_b = \eta_{cb} = 0$.

Two active terms proportional to $\Delta\mu$ remain in the constitutive equation (54). Active terms therefore do not simply renormalize the physical parameters of the Helfrich membrane, but introduce other physical effects. To clarify the role of these terms, we discuss below the instabilities of a flat active Helfrich membrane.

2. *Instabilities of a flat surface*

We consider here a flat, homogeneous, and compressible membrane. We ignore here the surrounding medium and the membrane is therefore free from external forces and torques. Perturbations of the flat shape are described in the Monge gauge by the height $h(x,y)$, such that the surface position is given by $\mathbf{X}(x,y) = x\mathbf{u}_x + y\mathbf{u}_y + h(x,y)\mathbf{u}_z$. We take here for simplicity the bulk viscosities $\eta_b = \bar{\eta}_b = \eta_{cb} = 0$ and we obtain the shape equation (Appendix J)

$$q^4\left[\left(\eta_c - \frac{\bar{\eta}^2}{\eta}\right)\partial_t + \kappa + (\tilde{\zeta}_c + \zeta_c')\Delta\mu + \frac{\bar{\eta}(\zeta_c - \zeta' - \tilde{\zeta})\Delta\mu}{\eta}\right]\tilde{h} + q^2(\gamma_H + \zeta\Delta\mu)\tilde{h} = 0, \tag{56}$$

where we have introduced the Fourier transform of the height $\tilde{h}(q_x,q_y) = \frac{1}{2\pi}\int dx\, dy\, h(x,y)e^{-i(q_x x + q_y y)}$, and $q = \sqrt{q_x^2 + q_y^2}$. The second law of thermodynamics imposes that $\eta_c\eta > \bar{\eta}^2$. We find that the active flat surface undergoes shape instabilities for (Fig. 5)

$$\zeta\Delta\mu < -\gamma_H, \tag{57}$$

$$\frac{\bar{\eta}(\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu}{\eta} > \kappa + (\tilde{\zeta}_c + \zeta_c')\Delta\mu. \tag{58}$$

The first condition corresponds to the classical buckling instability occurring when active stresses are compressive and establish a negative surface tension $\bar{\gamma} = \gamma_H + \zeta\Delta\mu < 0$ in the membrane.

In the second condition, the instability is favored by negative values of $\tilde{\zeta}_c + \zeta_c'$ or positive values of $\bar{\eta}(\zeta' + \tilde{\zeta} - \zeta_c)$. Negative values of $\tilde{\zeta}_c + \zeta_c'$ lower the effective bending modulus $\bar{\kappa}$. Positive values of $\bar{\eta}(\zeta' + \tilde{\zeta} - \zeta_c)$ induce an instability coupling the membrane shape to tangential flows. This instability can be understood from the dependency of the tension on curvature [Eqs. (16) and (45)]. Because of this dependency, a perturbation of the surface shape results in regions of low and high surface tension, depending on the sign of the local mean curvature and the sign of the coefficient $\zeta' + \tilde{\zeta} - \zeta_c$ which couples the tension tensor to the curvature tensor. Differences of surface tensions result in flows towards region of higher surface tension. These flows generate further in-plane torques when the surface has a nonzero up-down asymmetric viscosity $\bar{\eta}$ or $\bar{\eta}_b$. A shape instability occurs when the sign of this additional torque leads to further deformation of the surface.

IV. ACTIVE ELASTIC THIN SHELL

In addition to fluid surfaces, the formalism presented here can also be used for elastic surfaces. We discuss here isotropic active elastic thin shells.

A. Hookean elasticity

We first write generic constitutive equations for a Hookean elastic shell. Rather than inferring tensions and moment tensors from three-dimensional stresses, we directly obtain generic two-dimensional constitutive equations [20,21]. We consider a surface with reference shape $\mathbf{X}_0$ and a deformation field $\mathbf{u}$, such that the deformed surface has position $\mathbf{X} = \mathbf{X}_0 + \mathbf{u}$. In the following, the subscript 0 refers to quantities associated to the reference surface. Using the differential virtual work expression (15), the change of virtual work induced by a change in the deformation field $\mathbf{u}$ reads as, to first order in the deformation field,

$$\delta W \simeq \int_S dS\left[\bar{t}^{ij}\delta u_{ij} + \bar{m}^{ij}\delta c_{ij} + m_n^i\delta\Omega_i\right], \tag{59}$$

where we have introduced the deformation tensors $u_{ij} = \Delta g_{ij}/2$, $c_{ij} = (g_{0ik}\Delta C_j{}^k + g_{0jk}\Delta C_i{}^k)/2$, and $\Omega_i = \epsilon_0{}^j{}_k\Delta\Gamma_{ij}^k/2$, with $\Delta g_{ij} = g_{ij} - g_{0ij}$, $\Delta C_i{}^j = C_i{}^j - C_{0i}{}^j$, $\Delta\Gamma_{ij}^k = \Gamma_{ij}^k - \Gamma_{0ij}^k$, and we have assumed as for the fluid case that $\bar{m}_{ij}$ can be taken to be symmetric. The deformation tensors read as, to first order in the deformation field,

$$u_{ij} = \tfrac{1}{2}(\nabla_i u_j + \nabla_j u_i) + C_{0ij}u^n, \tag{60}$$

$$c_{ij} = -\nabla_i(\partial_j u_n) - u_n C_{0ik}C_0{}^k{}_j + (\nabla_k C_{0ij})u^k + \tfrac{1}{2}\epsilon_{0kl}(\nabla^k u^l)\left(\epsilon_{0i}{}^k C_{0kj} + \epsilon_{0j}{}^k C_{0ki}\right), \tag{61}$$

$$\Omega_i = \tfrac{1}{2}\nabla_i(\epsilon_0{}^j{}_k\nabla_j u^k) - C_{0ij}\epsilon_0{}^{jk}(\partial_k u_n - C_{0kl}u^l), \tag{62}$$

where we have used Eqs. (B13), (B17), and (D10), the covariant derivatives are taken on the undeformed surface, and the components of the deformation tensor are projected on the basis of the reference surface. We can then identify that the in-plane stress $\bar{t}_{ij}$, in-plane bending moments $\bar{m}_{ij}$, and normal moments m_n are conjugate to the deformation tensor u_{ij}, c_{ij}, and Ω_i. We can therefore express Hookean elasticity by the following constitutive relations:

$$\bar{t}^{e}_{ij} = E_{ijkl}u^{kl} + G_{ijkl}c^{kl}, \tag{63}$$

$$\bar{m}^{e}_{ij} = K_{ijkl}u^{kl} + F_{ijkl}c^{kl}, \tag{64}$$

$$m^{i}_{n} = H^{ij}\Omega_j, \tag{65}$$

where we have introduced the Hookean elastic moduli tensors E, F, G, K, and H. For a shell in thermodynamic equilibrium with free energy density on the reference surface f, $E^{ijkl} = \partial^2 f/\partial u_{kl}\partial u_{ij} = \partial^2 f/\partial u_{ij}\partial u_{kl} = E^{klij}$, $F^{ijkl} = \partial^2 f/\partial c_{kl}\partial c_{ij} = \partial^2 f/\partial c_{ij}\partial c_{kl} = F^{klij}$, $G^{ijkl} = \partial^2 f/\partial c_{kl}\partial u_{ij} = \partial^2 f/\partial u_{ij}\partial c_{kl} = K^{klij}$, and $H^{ij} = \partial^2 f/\partial\Omega_i\partial\Omega_j = \partial^2 f/\partial\Omega_j\partial\Omega_i = H^{ji}$. On a homogeneous elastic shell, the metric, curvature, and Levi-Civita tensors can be used to define these elasticity tensors. We therefore simplify the general relations above in the form

$$\begin{aligned}
\bar{t}^{ij}_{0} &= E_1 u^{ij} + E_2 u_k{}^k g_0{}^{ij}\\
\bar{t}^{ij}_{\mathrm{UD}} &= G_1 c^{ij} + G_2 c_k{}^k g_0{}^{ij}\\
\bar{t}^{ij}_{\mathrm{C}} &= G_{\mathrm{C}}\left[\epsilon_0{}^i{}_k c^{kj} + \epsilon_0{}^j{}_k c^{ki}\right]\\
\bar{t}^{ij}_{\mathrm{PC}} &= E_{\mathrm{PC}}\left[\epsilon_0{}^i{}_k u^{kj} + \epsilon_0{}^j{}_k u^{ki}\right],
\end{aligned} \tag{66}$$

$$\begin{aligned}
\overline{m}^{ij}_{0} &= F_1 c^{ij} + F_2 c_k{}^k g_0{}^{ij}\\
\overline{m}^{ij}_{\mathrm{UD}} &= K_1 u^{ij} + K_2 u_k{}^k g_0{}^{ij}\\
\overline{m}^{ij}_{\mathrm{C}} &= -K_{\mathrm{C}}\left[\epsilon_0{}^i{}_k u^{kj} + \epsilon_0{}^j{}_k u^{ki}\right]\\
\overline{m}^{ij}_{\mathrm{PC}} &= F_{\mathrm{PC}}\left[\epsilon_0{}^i{}_k c^{kj} + \epsilon_0{}^j{}_k c^{ki}\right],
\end{aligned} \tag{67}$$

$$\begin{aligned}
m^{i}_{n0} &= H_1\Omega^i\\
m^{i}_{n\mathrm{UD}} &= \bar{H}_1 C_0^{ij}\Omega_j + \bar{H}_2 C_{0k}{}^k\Omega^i\\
m^{i}_{n\mathrm{C}} &= H_{\mathrm{C}}\epsilon_0{}^i{}_k C_0^{kj}\Omega_j + \bar{H}_{\mathrm{C}}\epsilon_{0jk}C_0^{ki}\Omega^j\\
m^{i}_{n\mathrm{PC}} &= H_{\mathrm{PC}}\epsilon_0{}^{ij}\Omega_j,
\end{aligned} \tag{68}$$

where we have decomposed the tension and bending moment tensors according to the symmetry class of the shell, as in the fluid case [Eq. (44)]. The coefficients E_k, F_k, G_k, K_k, and H_k are elastic moduli, and we have written all terms allowed by symmetry for a homogeneous isotropic elastic material, at lowest order in the curvature tensor of the reference surface C_0^{ij}. For an elastic shell at thermodynamic equilibrium, $G_1 = K_1$, $G_2 = K_2$, $G_{\mathrm{C}} = K_{\mathrm{C}}$, $H_{\mathrm{C}} = \bar{H}_{\mathrm{C}}$, as a result of the tensor symmetries $G_{ijkl} = K_{klij}$ and $H_{ij} = H_{ji}$ [see after Eq. (65)]. A linear shell theory for a homogeneous elastic shell yields $E_1 = Eh/(1+\nu)$, $E_2 = Eh\nu/(1-\nu^2)$, $F_1 = Eh^3/[12(1+\nu)]$, $F_2 = Eh^3\nu/[12(1-\nu^2)]$ and other coefficients equal to zero, with E,ν the 3D elastic modulus and Poisson ratio of the shell material and h the thickness of the shell [21,22]. The elastic moduli E_{PC}, F_{PC}, and H_{PC} do not contribute to the work (59) and only exist for nonequilibrium systems: they vanish for an elastic shell at equilibrium as they do not derive from a free energy.

B. Constitutive relations for an active elastic shell

For an active elastic shell, an active contribution to the tension and bending moment tensors can be added to the elastic contribution in Eqs. (66)–(68):

$$\bar{t}^{a}_{ij} = \left(\zeta g_{ij} + \zeta' C_k{}^k g_{ij} + 2\tilde{\zeta}\tilde{C}_{ij}\right)\Delta\mu, \tag{69}$$

$$\bar{m}^{a}_{ij} = \left(\zeta_c g_{ij} + \zeta'_c C_k{}^k g_{ij} + 2\tilde{\zeta}_c\tilde{C}_{ij}\right)\Delta\mu, \tag{70}$$

where we restrict ourselves here for simplicity to the case of a nonchiral surface with broken up-down symmetry. The metric and curvature tensors g_{ij} and C_{ij} are taken on the deformed surface. In the expansions above, the terms proportional to ζ and ζ_c, which are to lowest order in the curvature, introduce, respectively, an active tension and an active torque within the elastic shell.

We can perform a stability analysis of a nonchiral elastic flat active surface subjected to spatially uniform active stress and torques, similar to the calculation of Sec. III F 2 for the fluid case (Appendix J). We find

$$\xi\partial_t\tilde{h} = -\zeta\Delta\mu q^2\tilde{h} - \left\{F + (\zeta'_c + \tilde{\zeta}_c)\Delta\mu - \frac{K}{E}[G + (\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu]\right\}q^4\tilde{h}, \tag{71}$$

where we have introduced an effective external friction force normal to the surface, with friction coefficient ξ, the Fourier transform of the height $\tilde{h}$, and the coefficients $F = F_1 + F_2$, $K = K_1 + K_2$, $E = E_1 + E_2$, and $G = G_1 + G_2$. The elastic surface is then unstable for

$$\zeta\Delta\mu < 0, \tag{72}$$

$$\frac{K(\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu}{E} > F - \frac{KG}{E} + (\zeta'_c + \tilde{\zeta}_c)\Delta\mu. \tag{73}$$

As for the fluid case [Eqs. (57) and (58)], an instability can arise from active compressive stresses in the surface, or from active couplings between tension and curvature.

The deformation induced by a gradient of active stress and torques in a cylindrical elastic shell has been discussed in Ref. [23]. In this work, it was shown that deformation profiles depend on two characteristic lengths which depend on the shell bending modulus, elastic modulus, cylinder radius, and on the active tension acting within the shell.

V. DISCUSSION

We have developed a general, covariant theory for the dynamics of active surfaces. Starting from balances of forces and torques, we have derived an expression for the virtual work. We have identified the entropy production on a curved surface which generalizes the entropy production of bulk fluids known from irreversible thermodynamics to surfaces of arbitrary shapes [18]. Using this entropy production, we have identified conjugate fluxes and forces for an active fluid membrane. Our approach can also be directly applied to the study of active elastic surfaces. Our constitutive relations for active surfaces include the derivation of a fully generalized Hooke's law for elastic thin shells. We have classified active surfaces in five different symmetry classes: (i) up-down symmetric, nonchiral surfaces, (ii), nonchiral surfaces with broken up-down symmetry, (iii) chiral surfaces, (iv) planar-chiral surfaces, and (v) chiral surfaces with broken up-down symmetry. Classes (i) and (ii) have been characterized before. Chiral surfaces (iii) must consist of chiral constituents and are up-down asymmetric, while planar-chiral surfaces (iv) do not have to be built from chiral subunits and only appear chiral when viewed from one side (Fig. 4). The constitutive equations for the surface have to obey these symmetries and coupling terms in the constitutive equation can be associated with these symmetry classes.

We have neglected here some degrees of freedom of the surface, such as the local rotation rate of molecules Ω_{ij} which relaxes rapidly to the vorticity flow ω_{ij} [16]. We have also identified the normal derivative of the surface deformation with the rotation of the normal vector to the surface [Eqs. (B21) and (14)]. This corresponds to neglecting a component of the shear normal to the surface. This additional contribution could be taken into account by adding an additional polar field tangential to the surface. We have considered the physics of an isolated surface, not taking into account the environment and external forces. Furthermore, we have restricted ourselves to isotropic surfaces. It will be interesting to expand the theory presented here to the case of active nematic or polar surfaces.

When the surface is embedded in a viscous fluid, external forces and torques acting on the surface arise from stresses acting within the bulk fluid. The hydrodynamics of the 3D fluid and of the membrane are then coupled to each other. It would be interesting to expand the theory obtained here to include these couplings between the surface and the bulk fluid.

Our work is related to previous works on active membrane and membrane dynamics [10–12,14,24–30] as well as on works on thin active films [31–33]. We propose here a generic framework for active surfaces that captures many aspects of the physics discussed in earlier works. In addition, we identify new active terms associated with internal tensions and bending moments. In particular, we show the existence of active torque terms that can induce curvature changes.

Our general approach provides a framework for the study of complex morphological changes of active surfaces in biology, for example, during morphogenesis of an organism or the formation of complex cell shapes. We have introduced a limited number of phenomenological parameters which capture the generic effects of a large variety of molecular processes in cells and tissues. We expect in particular that biological processes such as tissue folding, invagination, and twisting can be captured by our theory [34,35]. Fold formation could occur through apical constriction [13], which corresponds to the establishment of a difference in apical and basal surface tension in an epithelium, resulting in a gradient of active bending moment. Our theoretical framework provides a formalism to study how such gradients can result in tissue folding. By quantifying forces and deformations in tissues, the phenomenological parameters we introduce could be experimentally measured. Active tensions and bending moments could be related to the spatial and temporal distribution of force-generating elements such as myosin molecular motors in a tissue, as has been done to estimate active stresses distribution in the cell cortex [36–38].

In general, biological systems have both elastic and viscous properties that could be captured by a viscoelastic generalization of our theory. However, in many cases either elastic or viscous properties dominate: plant morphogenesis is often described as an active elastic medium, while long-time behavior of tissue flows during animal morphogenesis can be captured by a viscous limit, on time scales where cells can rearrange their neighbors [39,40]. It will be a future challenge to find analytic and numerical solutions for the complex shape changes predicted by our theory.

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APPENDIX A: DIFFERENTIAL GEOMETRY

We give here definitions of differential geometry quantities used in the text. We consider a two-dimensional surface parametrized by two coordinates $\mathbf{X}(s^1,s^2)$. Two tangent vectors and a normal vector are associated to every point on the surface, according to

$$\mathbf{e}_1 = \frac{\partial \mathbf{X}}{\partial s^1},\ \mathbf{e}_2 = \frac{\partial \mathbf{X}}{\partial s^2},\ \mathbf{n} = \frac{\mathbf{e}_1 \times \mathbf{e}_2}{|\mathbf{e}_1 \times \mathbf{e}_2|}. \tag{A1}$$

Lower indices correspond to covariant coordinates and upper indices to contravariant coordinates. The metric g_{ij} and curvature tensor C_{ij} associated to $\mathbf{X}$ are defined by

$$g_{ij} = \mathbf{e}_i \cdot \mathbf{e}_j,\ C_{ij} = -(\partial_i \partial_j \mathbf{X}) \cdot \mathbf{n}, \tag{A2}$$

and $C_i{}^j = C_{ik} g^{kj}$. The inverse of the metric tensor $g^{ij} = g_{ij}{}^{-1}$ verifies

$$g_{ij} g^{jk} = \delta_i{}^k. \tag{A3}$$

The contravariant basis is defined by

$$\mathbf{e}_i \cdot \mathbf{e}^j = \delta_i{}^j, \tag{A4}$$

with $\mathbf{e}^i = g^{ij}\mathbf{e}_j$. Indices can be raised and lowered by contraction with the metric tensor according to $a^i = g^{ij} a_j$ and $a_i = g_{ij} a^j$ for a tangent vector $\mathbf{a} = a^i \mathbf{e}_i = a_i \mathbf{e}^i$.

The derivatives of the basis and normal vectors are given by the Gauss-Weingarten equations

$$\partial_i \mathbf{n} = C_i{}^j \mathbf{e}_j, \tag{A5}$$

$$\partial_i \mathbf{e}_j = -C_{ij}\mathbf{n} + \Gamma_{ij}^k \mathbf{e}_k, \tag{A6}$$

where the Christoffel symbols Γ_{ij}^k are obtained from the metric by

$$\Gamma_{ij}^k = \tfrac{1}{2} g^{km} [\partial_j g_{im} + \partial_i g_{jm} - \partial_m g_{ij}]. \tag{A7}$$

The surface area element is denoted $dS = \sqrt{g} ds^1 ds^2$ where $g = \det(g_{ij})$ is the determinant of the metric.

The Levi-Civita tensor on the curved surface can be defined as

$$\epsilon_{ij} = \mathbf{n} \cdot (\mathbf{e}_i \times \mathbf{e}_j). \tag{A8}$$

It is antisymmetric when expressed in a purely contravariant or covariant basis:

$$\epsilon_{ij} = \sqrt{g}\begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix},\ \epsilon^{ij} = \frac{1}{\sqrt{g}}\begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}. \tag{A9}$$

Furthermore, it satisfies the identity

$$\epsilon_{ij}\epsilon^{jk} = -\delta_i^k. \tag{A10}$$

The Levi-Civita tensor can be used to express vectorial products of the basis vectors:

$$\mathbf{n} \times \mathbf{e}_i = \epsilon_i{}^j \mathbf{e}_j, \tag{A11}$$

$$\mathbf{e}_i \times \mathbf{e}_j = \epsilon_{ij}\mathbf{n}. \tag{A12}$$

The second relation implies

$$|\mathbf{a} \times \mathbf{b}| = \epsilon_{ij} a^i b^j, \tag{A13}$$

for two tangent vectors **a** and **b**. A tensor with two indices can generally be decomposed into a symmetric and antisymmetric part:

$$A^{ij} = A_s^{ij} + A_a^{ij} \tag{A14}$$

$$= A_s^{ij} + \tfrac{1}{2} A^{kl}\epsilon_{kl}\epsilon^{ij}. \tag{A15}$$

We denote $\partial_i = \partial/\partial s^i$ and ∇_i the covariant derivative, which has the property for a *tangent* vector $\mathbf{a} = a^i \mathbf{e}_i$ and tensor $\mathbf{t} = t^{ij}\mathbf{e}_i \otimes \mathbf{e}_j$:

$$\nabla_i a^j = (\partial_i \mathbf{a}) \cdot \mathbf{e}^j, \tag{A16}$$

$$\nabla_i t^{jk} = \mathbf{e}^j \cdot (\partial_i \mathbf{t}) \cdot \mathbf{e}^k. \tag{A17}$$

The definitions above then correspond to the following expressions:

$$\nabla_i v^j = \partial_i v^j + \Gamma_{ik}^j v^k, \tag{A18}$$

$$\nabla_i t^{jk} = \partial_i t^{jk} + \Gamma_{il}^j t^{lk} + \Gamma_{il}^k t^{jl}. \tag{A19}$$

For a general vector $\mathbf{f} = f^i \mathbf{e}_i + f_n \mathbf{n}$, we have

$$\partial_i \mathbf{f} = \left(\nabla_i f^j + C_i{}^j f_n\right)\mathbf{e}_j + (\partial_i f_n - C_{ij} f^j)\mathbf{n}. \tag{A20}$$

The curvature tensor satisfies the Mainardi-Codazzi equation [41]

$$\nabla_i C_{jk} = \nabla_j C_{ik}. \tag{A21}$$

The curvature tensor also satisfies the identity

$$\nabla_i \left(C^i{}_j - C_k{}^k \delta^i{}_j\right) = 0, \tag{A22}$$

as well as the relation

$$C_{ik} C^k{}_j = C_k{}^k C_{ij} - g_{ij} \det\left(C_k{}^l\right). \tag{A23}$$

The covariant derivatives of the metric and of the Levi-Civita antisymmetric tensor vanish:

$$\nabla_i g^{jk} = 0, \tag{A24}$$

$$\nabla_i \epsilon^{jk} = 0. \tag{A25}$$

The coordinates of the tangent vectors in the 3D space with Cartesian Euclidian basis $\mathbf{u}_\alpha$ are written

$$\mathbf{e}_i = e_{i,\alpha}\mathbf{u}_\alpha, \tag{A26}$$

$$\mathbf{e}^i = e_\alpha^i \mathbf{u}_\alpha. \tag{A27}$$

The gradient of a vector field $\mathbf{v}(x_\alpha)$ in the 3D space can be evaluated on the surface **X** through

$$\frac{\partial v_\beta}{\partial x_\alpha} = (\partial_i v_\beta) e_\alpha^i + (\partial_n v_\beta) n_\alpha, \tag{A28}$$

where $\partial_n \mathbf{v}$ is the derivative normal to the surface. In particular, the curl of a vector field on the surface is given by

$$(\nabla \times \mathbf{v})_\alpha = \epsilon_{\alpha\beta\gamma} e_\beta^i \partial_i v_\gamma + \epsilon_{\alpha\beta\gamma} n_\beta \partial_n v_\gamma. \tag{A29}$$

The divergence theorem on a curved surface can be expressed using the covariant derivative [8]:

$$\int_{\mathcal{S}} dS\, \nabla_i f^i = \int_{\mathcal{C}} dl\, \nu_i f^i, \tag{A30}$$

where $\mathcal{S}$ is the surface enclosed by $\mathcal{C}$, $\boldsymbol{\nu}$ is a unit vector tangent to $\mathcal{S}$, outward-pointing and normal to the contour $\mathcal{C}$, and dl is an infinitesimal line element going along the contour $\mathcal{C}$. Equation (A30) results from the identity [41]

$$\partial_i \sqrt{g} = \sqrt{g}\Gamma_{ki}^k. \tag{A31}$$

Indeed, denoting s a coordinate going along the closed contour $\mathcal{C}$ in a trigonometric orientation around the normals to the surface $\mathcal{S}$, one obtains

$$\begin{aligned} \int_{\mathcal{S}} dS\, \nabla_i f^i &= \int_{\mathcal{S}} ds^1 ds^2 \partial_i(\sqrt{g} f^i) \\ &= \int_{\mathcal{C}} ds \sqrt{g}\left[\frac{\partial s^2}{\partial s} f^1 - \frac{\partial s^1}{\partial s} f^2\right] \\ &= -\int_{\mathcal{C}} ds \frac{\partial s^i}{\partial s} \epsilon_{ij} f^j \\ &= \int_{\mathcal{C}} dl\, \nu_i f^i, \end{aligned} \tag{A32}$$

where the second line results from the usual divergence theorem, the third line from Eq. (A9), and the fourth line from the relations

$$dl = ds|\mathbf{e}_s|, \tag{A33}$$

$$\boldsymbol{\nu} = \frac{\mathbf{e}_s \times \mathbf{n}}{|\mathbf{e}_s \times \mathbf{n}|} = -\frac{\partial s^i}{\partial s}\epsilon_i{}^j \mathbf{e}_j / |\mathbf{e}_s|, \tag{A34}$$

with $\mathbf{e}_s = \partial_s \mathbf{X} = (\partial s^i/\partial s)\mathbf{e}_i$ the vector tangent to the contour $\mathcal{C}$.

APPENDIX B: VARIATION OF SURFACE QUANTITIES

We consider here that the surface **X** is modified to a new surface $\mathbf{X}'$:

$$\mathbf{X}'(s^1,s^2) = \mathbf{X}(s^1,s^2) + \delta\mathbf{X}(s^1,s^2). \tag{B1}$$

We derive here expressions for the perturbations of the associated differential geometry quantities. The tangent vector variation reads as

$$\delta \mathbf{e}_i = \partial_i \delta \mathbf{X}. \tag{B2}$$

Using $g_{ij} = (\partial_i \mathbf{X}) \cdot (\partial_j \mathbf{X})$, one finds

$$\delta g_{ij} = (\partial_i \delta \mathbf{X}) \cdot \mathbf{e}_j + (\partial_j \delta \mathbf{X}) \cdot \mathbf{e}_i. \tag{B3}$$

Using $\mathbf{n}\cdot\mathbf{e}_i = 0$ and $\mathbf{n}\cdot\mathbf{n} = 1$,

$$\delta\mathbf{n} = -[(\partial_i\delta\mathbf{X})\cdot\mathbf{n}]\mathbf{e}^i. \tag{B4}$$

Using $\mathbf{e}^i\cdot\mathbf{e}_j = \delta^i_j$, resulting in $\mathbf{e}^i\cdot\delta\mathbf{e}_j + \delta\mathbf{e}^i\cdot\mathbf{e}_j = 0$,

$$\delta\mathbf{e}^i = -[(\partial_j\delta\mathbf{X})\cdot\mathbf{e}^i]\mathbf{e}^j + [(\partial^i\delta\mathbf{X})\cdot\mathbf{n}]\mathbf{n}. \tag{B5}$$

Using $C_{ij} = -(\partial_i\partial_j\mathbf{X})\cdot\mathbf{n}$ and $C_i{}^j = C_{ik}g^{kj}$,

$$\delta\hat{C}_{ij} = -(\nabla_i\partial_j\delta\mathbf{X})\cdot\mathbf{n}, \tag{B6}$$

$$\delta C_i{}^j = \delta\hat{C}_{ik}g^{kj} + C_{ik}\delta g^{kj}. \tag{B7}$$

Note that we distinguish $\delta\hat{C}_{ij} = C'_{ij} - C_{ij}$ and $\delta C_i{}^j = C_i'^j - C_i{}^j$, which are two different tensors, related by Eq. (B7).

Using $\Gamma^k_{ij} = (\partial_i\partial_j\mathbf{X})\cdot\mathbf{e}^k$,

$$\delta\Gamma^k_{ij} = (\nabla_i\partial_j\delta\mathbf{X})\cdot\mathbf{e}^k - C_{ij}(\partial^k\delta\mathbf{X})\cdot\mathbf{n}. \tag{B8}$$

Separating $\delta\mathbf{X}$ into a tangent and normal part

$$\delta\mathbf{X} = \delta X^i\mathbf{e}_i + \delta X_n\mathbf{n}, \tag{B9}$$

we obtain the expressions in terms of components of the shape perturbation:

$$\delta\mathbf{e}_i = (\nabla_i\delta X^j + C_i{}^j\delta X_n)\mathbf{e}_j + (\partial_i\delta X_n - C_{ij}\delta X^j)\mathbf{n}, \tag{B10}$$

$$\delta\mathbf{e}^i = -(\nabla^j\delta X^i + C^{ij}\delta X_n)\mathbf{e}_j + (\partial^i\delta X_n - C^i{}_j\delta X^j)\mathbf{n}, \tag{B11}$$

$$\delta\mathbf{n} = (-\partial_i\delta X_n + C_{ij}\delta X^j)\mathbf{e}^i, \tag{B12}$$

$$\delta g_{ij} = \nabla_i\delta X_j + \nabla_j\delta X_i + 2C_{ij}\delta X_n, \tag{B13}$$

$$\delta g^{ij} = -\nabla^i\delta X^j - \nabla^j\delta X^i - 2C^{ij}\delta X_n, \tag{B14}$$

$$\delta\sqrt{g} = \frac{1}{2}\sqrt{g}g^{ij}\delta g_{ij}, \tag{B15}$$

$$\delta\hat{C}_{ij} = -\nabla_i(\partial_j\delta X_n) + (\nabla_j\delta X^k)C_{ik} + (\nabla_i\delta X^k)C_{kj} + (\nabla_i C_{jk})\delta X^k + \delta X_n C_{ik}C^k{}_j, \tag{B16}$$

$$\delta C_i{}^j = -\nabla_i(\partial^j\delta X_n) + (\nabla_i\delta X^k)C_k{}^j - (\nabla^k\delta X^j)C_{ik} + (\nabla_i C^j{}_k)\delta X^k - \delta X_n C_{ik}C^{kj}, \tag{B17}$$

$$\delta\Gamma^k_{ij} = \nabla_i(\nabla_j\delta X^k) + (C_{ij}C^k{}_l - C_{jl}C_i{}^k)\delta X^l + C_j{}^k(\partial_i\delta X_n) + C_i{}^k(\partial_j\delta X_n) - C_{ij}(\partial^k\delta X_n) + (\nabla_i C_j{}^k)\delta X_n. \tag{B18}$$

In order to define the the normal derivative of an infinitesimal surface deformation $\partial_n\delta\mathbf{X}$, we introduce material coordinates for the points in the volume around the surface:

$$\overline{\mathbf{X}}(s^1,s^2,z) = \mathbf{X}(s^1,s^2) + z\mathbf{n}, \tag{B19}$$

with z a coordinate going along the normal to the surface. When the surface is deformed with infinitesimal vector deformation $\delta\mathbf{X}$, we assume that the volume around the surface is deformed by

$$\delta\overline{\mathbf{X}}(s^1,s^2,z) = \delta\mathbf{X}(s^1,s^2) + z\delta\mathbf{n}. \tag{B20}$$

This choice implies that only in-plane shear occurs. We then obtain

$$\partial_z\delta\overline{\mathbf{X}} = \delta\mathbf{n} = -[(\partial_i\delta\mathbf{X})\cdot\mathbf{n}]\mathbf{e}^i. \tag{B21}$$

We identify $\partial_n\delta\mathbf{X}$ with $\partial_z\delta\overline{\mathbf{X}}$ in Eq. (14). This choice is equivalent to assume that points along the normal to the initial surface before deformation are along the normal to the new surface after deformation.

APPENDIX C: FORCE BALANCE DERIVATION

We discuss here the force and torque balance for an element of surface. We consider a force balance equation taking into account the contribution of mass accretion or ejection from the surface. For simplicity, we assume here that mass accretion or ejection occurs only on one side of the surface. Applying the law of Newton on a surface region $\mathcal{S}$ of contour $\mathcal{C}$ yields

$$\partial_t\left(\int_{\mathcal{S}} dS\,\rho\mathbf{v}\right) = \int_{\mathcal{S}} dS\,J_n^\rho(\mathbf{v}+\mathbf{u}) + \oint_{\mathcal{C}} dl\,\nu_i(\mathbf{t}^i - \rho v^i\mathbf{v}) + \int_{\mathcal{S}} dS\,\mathbf{f}_0^{\text{ext}}, \tag{C1}$$

where the second term arises from the change of momentum due to mass being absorbed by the surface with velocity $\mathbf{u}$ relative to the surface. The third term arises from the force acting on the surface $\mathcal{S}$ from the surface outside of $\mathcal{S}$ and includes the flux of momentum at the contour $\mathcal{C}$ that is lost by advection. $\mathbf{f}_0^{\text{ext}}$ is the external stress acting on the surface in addition to the momentum of incoming molecules. The flux of mass towards the surface J_n^ρ is introduced in Eq. (20). The surface momentum rate of change can be rewritten using Eqs. (E15), (20), and the divergence theorem (A30):

$$\begin{aligned}\partial_t\left(\int_{\mathcal{S}} dS\,\rho\mathbf{v}\right) + \oint_{\mathcal{C}} dl\,\nu_i v^i\rho\mathbf{v} &= \int_{\mathcal{S}} dS\big[\partial_t(\rho\mathbf{v}) + v_n C_k{}^k\rho\mathbf{v}\big] + \oint_{\mathcal{C}} dl\,\nu_i v^i\rho\mathbf{v}\\ &= \int_{\mathcal{S}} dS\big[\rho\partial_t\mathbf{v} - \nabla_i(\rho v^i)\mathbf{v} + J_n^\rho\mathbf{v} + \nabla_i(\rho v^i\mathbf{v})\big]\\ &= \int_{\mathcal{S}} dS[\rho(\partial_t\mathbf{v} + v^i\nabla_i\mathbf{v}) + J_n^\rho\mathbf{v}],\end{aligned} \tag{C2}$$

such that the force balance equation (C1) can be rewritten

$$\int_{\mathcal{S}} dS\,\rho\mathbf{a} = \oint_{\mathcal{C}} dl\,\nu_i\mathbf{t}^i + \int_{\mathcal{S}} dS\,\mathbf{f}^{\text{ext}}, \tag{C3}$$

where we have introduced the total external force $\mathbf{f}^{\text{ext}} = \mathbf{f}_0^{\text{ext}} + J_n^\rho\mathbf{u}$, and the acceleration $\mathbf{a}$ is defined by

$$\mathbf{a} = \frac{d\mathbf{v}}{dt}, \tag{C4}$$

with $d/dt = \partial_t + v^i\nabla_i$ the convected derivative. Using the divergence theorem (A30), Eq. (C3) can be rewritten

$$\int_{\mathcal{S}} dS[\rho\mathbf{a} - \nabla_i\mathbf{t}^i - \mathbf{f}^{\text{ext}}] = 0. \tag{C5}$$

Because this equation has to be valid for any surface element, this results in Eq. (7), which can also be written in the form of a local conservation of momentum:

$$\frac{1}{\sqrt{g}}\partial_t(\sqrt{g}\rho\mathbf{v}) = \nabla_i(\mathbf{t}^i - \rho v^i\mathbf{v}) + \mathbf{f}_0^{\text{ext}} + J_n^\rho(\mathbf{v}+\mathbf{u}). \tag{C6}$$

Here, the two last terms arise from exchange of momentum between the surface and its environment.

Ignoring the moment of inertia tensor for simplicity, the total torque acting on a surface region $\mathcal{S}$ of contour $\mathcal{C}$ vanishes:

$$\oint_{\mathcal{C}} dl\, \nu_i \mathbf{m}^i + \oint_{\mathcal{C}} dl\, \mathbf{X} \times \nu_i \mathbf{t}^i + \int_{\mathcal{S}} dS\, \mathbf{X} \times (\mathbf{f}^{\text{ext}} - \rho \mathbf{a}) + \int_{\mathcal{S}} dS\, \mathbf{\Gamma}^{\text{ext}} = 0, \quad \text{(C7)}$$

where $\mathbf{\Gamma}^{\text{ext}}$ is the external torque density acting on the surface. Using the divergence theorem and the force balance equation (7), the torque balance equation can be rewritten

$$\int_{\mathcal{S}} dS[\nabla_i \mathbf{m}^i + \mathbf{e}_i \times \mathbf{t}^i + \mathbf{\Gamma}^{\text{ext}}] = 0, \quad \text{(C8)}$$

which results in the torque balance expression Eq. (8).

We note that the force balance equations (9)–(12) are invariant under the variable transformation

$$t^{ij} \rightarrow t^{ij} + m\epsilon^i{}_k C^{kj}, \quad \text{(C9)}$$

$$t_n^i \rightarrow t_n^i + \epsilon^{ij}(\partial_j m), \quad \text{(C10)}$$

$$m^{ij} \rightarrow m^{ij} + m g^{ij}. \quad \text{(C11)}$$

where m is an arbitrary function on the surface, and we have used Eqs. (A21) and (A23).

APPENDIX D: DIFFERENTIAL WORK

The virtual work defined in Eq. (13) can be rewritten using the divergence theorem on a curved surface (A30) and the force and torque balance equations (7) and (8):

$$\delta W = \int_{\mathcal{S}} dS\Big[\mathbf{t}^i \cdot \partial_i \delta \mathbf{X} + \frac{1}{2}\mathbf{m}^i \cdot \partial_i(\nabla \times \delta \mathbf{X}) + \frac{1}{2}(\mathbf{t}^i \times \mathbf{e}_i)\cdot(\nabla \times \delta \mathbf{X})\Big]. \quad \text{(D1)}$$

Projecting t^i and m^i along the tangent and normal directions and using Eqs. (A11) and (A12), one finds

$$\delta W = \int_{\mathcal{S}} dS\Big[t^{ij}\mathbf{e}_j \cdot \partial_i \delta \mathbf{X} + t_n^i \mathbf{n}\cdot \partial_i \delta \mathbf{X} + \frac{1}{2}m^{ij}\mathbf{e}_j \cdot \partial_i(\nabla \times \delta \mathbf{X}) + \frac{1}{2}m_n^i \mathbf{n}\cdot\partial_i(\nabla \times \delta\mathbf{X}) - \frac{1}{2}t^{ij}\epsilon_{ij}\mathbf{n}\cdot(\nabla\times\delta\mathbf{X}) + \frac{1}{2}t_n^i \epsilon_{ij}\mathbf{e}^j \cdot (\nabla \times \delta \mathbf{X})\Big]. \quad \text{(D2)}$$

Using the definition of the curl operator (14), the relations (A11) and (A12), the expression of the normal derivative of the displacement (B21), the variation of the curvature tensor (B6), and of the Christoffel symbols (B8), the following identities can be obtained:

$$\mathbf{n}\cdot(\nabla \times \delta\mathbf{X}) = \epsilon^i{}_j(\partial_i \delta \mathbf{X})\cdot \mathbf{e}^j, \quad \text{(D3)}$$

$$\mathbf{e}^i \cdot (\nabla \times \delta \mathbf{X}) = 2\epsilon^{ij}(\partial_j \delta\mathbf{X})\cdot \mathbf{n}, \quad \text{(D4)}$$

$$\mathbf{e}_j \cdot \partial_i(\nabla\times\delta\mathbf{X}) = \big(2C_i{}^l\epsilon_j{}^k + C_{ij}\epsilon^{kl}\big)(\partial_k\delta\mathbf{X})\cdot\mathbf{e}_l - 2\epsilon_j{}^k\delta\hat{C}_{ik}, \quad \text{(D5)}$$

$$\mathbf{n}\cdot\partial_i(\nabla\times\delta\mathbf{X}) = \epsilon^j{}_k\delta\Gamma^k_{ij}. \quad \text{(D6)}$$

Using these relations, the virtual work can be rewritten

$$\delta W = \int_S dS\Big[\Big(t^{ij} - \frac{1}{2}t^{kl}\epsilon_{kl}\epsilon^{ij} + m^{kl}C_k{}^j\epsilon_l{}^i + \frac{1}{2}m^{kl}C_{kl}\epsilon^{ij}\Big) \times (\partial_i\mathbf{X})\cdot\mathbf{e}_j - m^{ij}\epsilon_j{}^k\delta\hat{C}_{ik} + \frac{1}{2}m_n^i\epsilon^j{}_k\delta\Gamma^k_{ij}\Big]. \quad \text{(D7)}$$

Using the in-plane torque tensor introduced in Eq. (17) $\bar{m}^{ij} = -m^{ik}\epsilon_k{}^j$ (with inverse relation $m^{ij} = \bar{m}^{ik}\epsilon_k{}^j$) and using the expression for the variation of the metric (B3), one finds

$$\delta W = \int_S dS\Big\{\frac{1}{2}\Big[t_s^{ij} - \frac{1}{2}(\bar{m}^{ki}C_k{}^j + \bar{m}^{kj}C_k{}^i)\Big]\delta g_{ij} + \bar{m}^{ij}\delta\hat{C}_{ij} + \frac{1}{2}m_n^i\epsilon^j{}_k\delta\Gamma^k_{ij}\Big\}. \quad \text{(D8)}$$

Using Eq. (B7) leads to the alternative expression of the virtual work

$$\delta W = \int_S dS\Big\{\frac{1}{2}\Big[t_s^{ij} + \frac{1}{2}(\bar{m}^{ki}C_k{}^j + \bar{m}^{kj}C_k{}^i)\Big]\delta g_{ij} + \bar{m}^i{}_j\delta C_i{}^j + \frac{1}{2}m_n^i\epsilon^j{}_k\delta\Gamma^k_{ij}\Big\}, \quad \text{(D9)}$$

which leads to Eq. (15) with the definition (16).

The deformation term in factor of m_n^i is a generalization to curved surfaces of the gradient of rotations [16]. This can be seen from its explicit expression in term of the deformation coordinates

$$\epsilon^j{}_k\delta\Gamma^k_{ij} = \nabla_i(\epsilon^j{}_k\nabla_j\delta X^k) - 2C_{ij}\epsilon^{jk}(\partial_k\delta X_n - C_{kl}\delta X^l), \quad \text{(D10)}$$

where we have used Eq. (B18).

APPENDIX E: EULERIAN AND LAGRANGIAN REPRESENTATIONS OF SURFACE FLOWS

1. Lagrangian representation

In a Lagrangian representation, the parameters s^1 and s^2 label the center of mass of a specific volume element. The surface is characterized by the time-dependent parametrization $\mathbf{X}(s^1,s^2,t)$. The center-of-mass velocity is given by

$$\mathbf{v} = \partial_t \mathbf{X}(s^1,s^2,t). \quad \text{(E1)}$$

The mass density conservation equation without exchange between the surface and its environment reads as in Lagrangian coordinates

$$\partial_t\rho + \rho\big(\nabla_i v^i + C_i{}^i v_n\big) = 0. \quad \text{(E2)}$$

This can be seen from the conservation of mass of a region of surface $\mathcal{S}$:

$$\frac{d}{dt}\left[\int_{\mathcal{S}} dS\, \rho(s^1,s^2)\right] = 0, \tag{E3}$$

$$\int_{\mathcal{S}} ds^1 ds^2[\rho\partial_t(\sqrt{g}) + \sqrt{g}\partial_t\rho] = 0, \tag{E4}$$

$$\int_{\mathcal{S}} dS\big[\big(\nabla_i v^i + v_n C_i^i\big)\rho + \partial_t\rho\big] = 0, \tag{E5}$$

which leads to Eq. (E2). In this derivation, we have obtained $d\sqrt{g}/dt$ by setting $\delta\mathbf{X} = \mathbf{v}dt$ in Eq. (B15).

The rate of change of metric in Lagrangian coordinates

$$\partial_t g_{ij} = \nabla_i v_j + \nabla_j v_i + 2v_n C_{ij}, \tag{E6}$$

obtained by setting $\delta\mathbf{X} = \mathbf{v}dt$ in Eq. (B13), relates to the gradient of flow defined in Eq. (38) through $\partial_t g_{ij} = 2v_{ij}$. Similarly, the rate of change of the curvature tensor in Lagrangian coordinates, obtained by setting $\delta\mathbf{X} = \mathbf{v}dt$ in Eq. (B17), defines a convected Lagrangian derivative $\bar{D}/\bar{D}t$ of the curvature tensor:

$$\frac{\bar{D}C_i{}^j}{\bar{D}t} = -\nabla_i(\partial^j v_n) - v_n C_{ik}C^{kj} + \big(\nabla_i C^j{}_k\big)v^k + (\nabla_i v^k)C_k{}^j - (\nabla_k v^j)C_i{}^k, \tag{E7}$$

and its symmetric part is introduced in Eq. (40). The rate of change of the Christoffel symbols is related to the gradient of rotations introduced in Eqs. (37) and (39) through the identity

$$\frac{1}{2}\epsilon^j{}_k\frac{\bar{D}\Gamma^k_{ij}}{\bar{D}t} = \partial_i\omega_n - C_{ij}\omega^j = (\partial_i\boldsymbol{\omega})\cdot\mathbf{n}, \tag{E8}$$

where we have used Eq. (B18).

2. Eulerian coordinates

In Eulerian coordinates, the center-of-mass velocity field is given by

$$\mathbf{v} = v^i\mathbf{e}_i + v_n\mathbf{n}, \tag{E9}$$

where $v^i\mathbf{e}_i$ is the tangential velocity field, and the normal velocity field is given by

$$v_n = (\partial_t\mathbf{X}(s^1,s^2,t))\cdot\mathbf{n}. \tag{E10}$$

In addition, one requires the condition

$$(\partial_t\mathbf{X}(s^1,s^2,t))\cdot\mathbf{e}^i = 0, \tag{E11}$$

such that coordinates do not change when the shape of the surface is not changing. Here, s^1 and s^2 do not describe a specific material element.

In the Eulerian perspective, the time derivative of the tangent vectors, normal, metric, surface element area, and curvature are given by

$$\partial_t\mathbf{e}_i = v_n C_i{}^j\mathbf{e}_j + (\partial_i v_n)\mathbf{n}, \tag{E12}$$

$$\partial_t\mathbf{n} = -(\partial_i v_n)\mathbf{e}^i, \tag{E13}$$

$$\partial_t g_{ij} = 2v_n C_{ij}, \tag{E14}$$

$$\partial_t\sqrt{g} = \sqrt{g}v_n C_i{}^i, \tag{E15}$$

$$\partial_t C_i{}^j = -\nabla_i(\partial^j v_n) - v_n C_{ik}C^{kj}, \tag{E16}$$

where we have used Eqs. (B10), (B12), (B13), (B15), and (B17) with $\delta X^i = 0$ and $\delta X_n = v_n dt$.

Mass conservation without exchange between the surface and its environment has the form

$$\partial_t\rho + \nabla_i(\rho v^i) + \rho C_i{}^i v_n = 0, \tag{E17}$$

which follows from the mass conservation of an element of surface $\mathcal{S}$ with fixed contour $\mathcal{C}$:

$$\frac{d}{dt}\left(\int_{\mathcal{S}} dS\,\rho\right) = -\oint_{\mathcal{C}} dl\,\boldsymbol{\nu}\cdot\mathbf{v}\rho = -\int_{\mathcal{S}} dS\,\nabla_i(v^i\rho),$$

$$\int_{\mathcal{S}} ds^1ds^2[(\partial_t\sqrt{g})\rho + \sqrt{g}\partial_t\rho] = -\int_{\mathcal{S}} dS\,\nabla_i(v^i\rho),$$

$$\int_{\mathcal{S}} dS\big[\big(v_n C_i{}^i\big)\rho + \partial_t\rho + \nabla_i(\rho v^i)\big] = 0, \tag{E18}$$

which leads to Eq. (E17). The acceleration reads as [Eq. (C4)]

$$\mathbf{a} = \partial_t\mathbf{v} + v^i\partial_i\mathbf{v} \tag{E19}$$

$$= \big[\partial_t v^i + v^j\nabla_j v^i + 2v_n v^j C_j{}^i - v_n\partial^i v_n\big]\mathbf{e}_i + [\partial_t v_n + 2v^i\partial_i v_n - v^i v^j C_{ij}]\mathbf{n}, \tag{E20}$$

where we have used Eqs. (E12) and (E13).

APPENDIX F: TRANSLATION AND ROTATION INVARIANCE

We derive here relations for the stress and torque tensor of a fluid surface, obtained from the invariance of the free energy under rigid translation and rotations of the surface. We consider for this derivation a surface in the absence of external forces. The fluid surface contains N species $\alpha = 1\ldots N$ with concentration c^α and its free energy density is given by Eq. (19). The deformation by an infinitesimal rigid translation or rotation defines a new surface $\mathbf{X}' = \mathbf{X} + \delta\mathbf{X}$. The new surface is then reparametrized by new coordinates, such that a point (s^1,s^2) on the initial surface finds its new position on the new surface by going along the normal to the initial surface (Fig. 3):

$$\mathbf{X}''(s^1,s^2) = \mathbf{X}(s^1,s^2) + (\delta\mathbf{X}\cdot\mathbf{n})\mathbf{n}. \tag{F1}$$

1. Invariance by translation

We consider here a rigid translation of the surface by an infinitesimal uniform vector $\delta\mathbf{a}$, implying $\partial_i\delta\mathbf{a} = 0$ and the relations (28) and (29). With the choice of coordinates (F1), the concentration and kinetic energy density fields on the surface are modified only by the tangential contributions of displacement:

$$\delta c^\alpha = -(\partial_i c^\alpha)\delta a^i, \tag{F2}$$

$$\tfrac{1}{2}\delta(\rho v^2) = -\tfrac{1}{2}[\partial_i(\rho v^2)]\delta a^i. \tag{F3}$$

The geometric quantities on the new surface can be obtained by using Eqs. (B15) and (B17), with the normal displacement (F1), and using Eqs. (28), (29), and (A21):

$$\delta\sqrt{g} = \sqrt{g}C_i{}^i\delta a_n, \tag{F4}$$

$$\delta C_j{}^k = -\big(\nabla_i C_j{}^k\big)\delta a^i. \tag{F5}$$

The variation of surface free energy after the rigid translation must vanish, and is given by

$$\begin{aligned}\delta F &= \int_S dS\big[f\delta a_n C_k{}^k + \delta f\big] + \oint_{\mathcal{C}} dl\,\nu_i[f\delta a^i] \\ &= \int_S dS\bigg\{f\delta a_n C_k{}^k - \mu^\alpha(\partial_i c^\alpha)\delta a^i - \bigg[\frac{1}{2}\partial_i(\rho v^2)\bigg]\delta a^i \\ &\quad - K^{jk}(\nabla_i C_{jk})\delta a^i + \nabla_i(f\delta a^i)\bigg\} \\ &= \delta a^i \int_S dS[-(\mu^\alpha\partial_i c^\alpha + K^{jk}\nabla_i C_{jk}) + \partial_i f_0] \\ &= \delta a^i \int_S dS\{\partial_i \mu^\alpha c^\alpha + (\nabla_j K^{jk})C_{ik} \\ &\quad + \nabla_j[(f_0 - \mu^\alpha c^\alpha)g_i{}^j - K^{jk}C_{ik}]\} \\ &= 0, \end{aligned} \tag{F6}$$

where we have used the expression of the differential of the free energy density (19) at constant temperature, Eq. (28), and the Mainardi-Coddazi equation (A21). Because Eq. (F6) is valid for any surface element and any infinitesimal vector $\delta\mathbf{a}$, we obtain Eq. (30).

2. Invariance by rotation

We now consider a uniform rotation of the surface with vector $\delta\boldsymbol{\theta}$, such that the surface is deformed by $\delta\mathbf{X} = \delta\boldsymbol{\theta}\times\mathbf{X}$. One can verify that the following identity holds for such a deformation:

$$\nabla_i \delta X^i = -C_i{}^i \delta X_n. \tag{F7}$$

As for a rigid translation, the concentration and kinetic energy density fields are modified only by tangential contributions of displacements. One finds then

$$\delta c = -(\partial_i c^\alpha)\delta X^i, \tag{F8}$$

$$\tfrac{1}{2}\delta(\rho v^2) = -\tfrac{1}{2}[\partial_i(\rho v^2)]\delta X^i. \tag{F9}$$

As for translations, changes in geometric quantities can be obtained from Eqs. (B15) and (B17), with the normal displacement (F1):

$$\delta(\sqrt{g}) = \sqrt{g}C_i{}^i\delta X_n, \tag{F10}$$

$$\delta C_i{}^j = -(\nabla_k C_i{}^j)\delta X^k - \delta\omega^{jk}C_{ki} - \delta\omega_{ik}C^{kj}, \tag{F11}$$

with $\delta\omega_{ij} = \epsilon_{ij}(\frac{1}{2}\nabla_k\delta X_l\epsilon^{kl}) = \epsilon_{ij}\delta\boldsymbol{\theta}\cdot\mathbf{n}$. The associated variation of free energy reads as

$$\begin{aligned}\delta F &= \int_S dS\big[f\delta X_n C_k{}^k + \delta f\big] + \oint_{\mathcal{C}} dl\,\nu_i[f\delta X^i] \\ &= \int_S dS\bigg\{f\delta X_n C_k{}^k - \mu^\alpha(\partial_i c^\alpha)\delta X^i - \frac{1}{2}[\partial_i(\rho v^2)]\delta X^i - K^{ij} \\ &\quad \times(\nabla_k C_{ij})\delta X^k - K^{ij}\delta\omega_{jk}C_i{}^k \\ &\quad - K^{ij}\delta\omega_{ik}C^k{}_j + \nabla_i(f\delta X^i)\bigg\} \\ &= \int_S dS\big[-(\mu^\alpha\partial_i c^\alpha + K^{jk}\nabla_i C_{jk})\delta X^i + (\partial_i f_0)\delta X^i \\ &\quad - \delta\boldsymbol{\theta}\cdot\mathbf{n}\big(K^{ij}\epsilon_{jk}C_i{}^k + K^{ij}\epsilon_{ik}C^k{}_j\big)\big] \\ &= -\delta\boldsymbol{\theta}\cdot\mathbf{n}\int_S dS\big[K^{ij}\epsilon_{jk}C_i{}^k + K^{ij}\epsilon_{ik}C^k{}_j\big] \\ &= -2\delta\boldsymbol{\theta}\cdot\mathbf{n}\int_S dS\,\epsilon_{jk}K^{ij}C_i{}^k \\ &= 0, \end{aligned} \tag{F12}$$

where we have used Eqs. (18), (19), (30), (F7), and the symmetry of K_{ij}. Because Eq. (F12) is valid for any surface element and any infinitesimal rotation vector $\delta\boldsymbol{\theta}$, this results in Eq. (32).

APPENDIX G: UP-DOWN ASYMMETRY, CHIRALITY, AND PLANAR CHIRALITY OF SURFACES

We discuss here the symmetries of a surface with rotational symmetry in the plane. The symmetries that can be broken for to these surfaces are the up-down mirror symmetry (M_n), the mirror symmetries in the plane (M_t, a mirror symmetry by a plane going along an arbitrary tangent vector $\mathbf{t}$), and the up-down rotation symmetries (R_t, a rotation of π around an arbitrary tangent vector $\mathbf{t}$). Rotations around the normal with angle π, R_n preserve the state of a surface with rotational symmetry in the plane. Composition of these symmetries is indicated in the multiplication Table II.

Because inversion of space can be written as a composition of the up-down mirror symmetry and the rotation R_n, $I = R_n M_n$, inversion of space and up-down mirror symmetry is preserved and broken simultaneously for a surface with rotation symmetry in the plane.

Under these symmetries, the stress, torque, curvature, Levi-Civita tensor, as well as vectors and pseudovectors are modified. We list in Table III signatures of transformations of components of these tensors associated to the symmetries introduced above. Vectors transform as the velocity field $\mathbf{v}$ and pseudovectors as the curl of the flow $\boldsymbol{\omega}$. In Table III, an additional set of signatures can be obtained from the product of signatures of M_t and R_n (respectively R_t and R_n). The signatures for M_t (respectively R_t) can be alternatively chosen from this additional set of signatures. An additional transformation and set of signatures arises from the combination $I = R_n M_n$, which can be considered alternatively to signatures associated to M_n.

The force and torque balance equations (9)–(12) are invariant under these transformations. One can further verify that transformations under R_n preserve all the constitutive equations (45)–(49).

TABLE II. Multiplication table of discrete symmetries. $\mathbb{1}$ denotes the identity operation, I denotes inversion of space.

	M_n	M_t	R_t	R_n
M_n	$\mathbb{1}$	R_t	M_t	I
M_t	R_t	$\mathbb{1}$	M_n	$M_t R_n$
R_t	M_t	M_n	$\mathbb{1}$	$R_t R_n$
R_n	I	$M_t R_n$	$R_t R_n$	$\mathbb{1}$

TABLE III. Signature of symmetries on vector and tensor fields of the surface. Signatures are chosen to preserve g_{ij} and t_{ij} under each transformation.

Symmetry	M_n	M_t	R_t	R_n
g_{ij}	1	1	1	1
t_{ij}	1	1	1	1
t_n^i	–1	1	–1	–1
m_{ij}	–1	–1	1	1
m_n^i	1	–1	–1	–1
C_{ij}	–1	1	–1	1
ϵ_{ij}	1	–1	–1	1
v^i	1	1	1	–1
v_n	–1	1	–1	1
∇_i	1	1	1	–1
v_{ij}	1	1	1	1
ω_i	–1	–1	1	–1
ω_n	1	–1	–1	1

APPENDIX H: EQUILIBRIUM TENSION AND MOMENT TENSORS, EXTERNAL FORCE, AND TORQUE SURFACE DENSITIES FOR A FLUID MEMBRANE

Using the expression of the virtual work given in Eq. (15), we obtain in this appendix the equilibrium tension tensor and moment tensor for a fluid membrane, first for the generic case, and then for the specific case of a Helfrich membrane. We then obtain the external force and torque surface densities induced by an external potential acting on the surface.

1. Tension and moment tensors for a generic equilibrium fluid membrane

We start here from a fluid membrane with a free energy density given by Eq. (18), such that the free energy for a region of surface $\mathcal{S}$ is given by $F = \int_{\mathcal{S}} dS\, f_0$ with $df_0 = \mu^\alpha dc^\alpha + K^i{}_j dC_i{}^j - s\, dT$. We now calculate the change of free energy following a change of shape of the surface at constant temperature. A change of the surface metric results in a dilution of the concentrations, according to $\delta c^\alpha / c^\alpha = -\delta(\sqrt{g})/\sqrt{g}$. As a result and using Eq. (B15), the free energy differential following a shape change reads as

$$\delta F = \int_{\mathcal{S}} dS \left[(f_0 - \mu^\alpha c^\alpha) g^{ij} \frac{\delta g_{ij}}{2} + K^i{}_j \delta C_i{}^j \right]. \tag{H1}$$

At equilibrium, inertial forces vanish and we have $\delta W = \delta F$ for infinitesimal deformations. Using Eq. (15), one can then identify the equilibrium tensors $\bar{t}_e^{ij}$, $\bar{m}_e^{ij}$, $m_{e,n}^i$ given in Eqs. (33)–(35).

2. Tension and moment tensors for a Helfrich membrane

The Helfrich free energy functional for a region of surface $\mathcal{S}$ of a fluid membrane reads as

$$F = \int_{\mathcal{S}} dS \left\{ \gamma_H + \frac{\kappa}{2}\left[\left(C_i{}^i\right)^2 - 2C_0 C_i{}^i \right] + \kappa_g \det\left(C_i{}^j\right) \right\}, \tag{H2}$$

where γ_H is the surface tension, κ is the bending rigidity, C_0 is the spontaneous curvature, and κ_g the Gaussian bending modulus. Using Eq. (15) and the relation $\delta W = \delta F$ for infinitesimal deformations, one finds for the in-plane stress tensor and bending moment tensor

$$\bar{t}_e^{ij} = \left\{ \gamma_H + \frac{\kappa}{2}\left[\left(C_k{}^k\right)^2 - 2C_0 C_k{}^k \right] + \kappa_g \det\left(C_k{}^l\right) \right\} g^{ij}, \tag{H3}$$

$$\bar{m}_e^{ij} = (\kappa + \kappa_g) C_k{}^k g^{ij} - \kappa C_0 g^{ij} - \kappa_g C^{ij}, \tag{H4}$$

where we have used $\det(C_i{}^j) = \frac{1}{2}[(C_k{}^k)^2 - C_{ik}C^{ki}]$ by taking the trace of Eq. (A23), and Eq. (B15). The equilibrium stress tensor t_e^{ij} and bending moment tensor m_e^{ij} are then given in the absence of external torques by

$$t_e^{ij} = \gamma_H g^{ij} - \kappa\left(C_k{}^k - C_0\right) C^{ij} + \frac{\kappa}{2} C_k{}^k \left(C_k{}^k - 2C_0\right) g^{ij}, \tag{H5}$$

$$m_e^{ij} = (\kappa + \kappa_g) C_k{}^k \epsilon^{ij} - \kappa C_0 \epsilon^{ij} - \kappa_g C^i{}_k \epsilon^{kj}, \tag{H6}$$

where we have used the identity (A23). The isotropic part of the stress tensor $\gamma = t_i{}^i/2$ is related to γ_H by $\gamma = \gamma_H - \kappa C_0 C_k{}^k/2$. From the force balance equation (11) and because of Eq. (A22), the equilibrium normal shear stress $\mathbf{t}_{e,n}$ is given in the absence of external torque by

$$t_{e,n}^j = \nabla_i \bar{m}_e^{ij} = \kappa \nabla^j C_k{}^k, \tag{H7}$$

which does not depend on the Gaussian bending modulus. Equations (H5) and (H7) are in accordance with Ref. [8], with an opposite sign convention for the force density $\mathbf{t}$.

From Eqs. (H5) and (H7), the equilibrium stress tensor $\mathbf{t}_e^i$ does not depend on the Gaussian bending modulus κ_g. While m_e^{ij} depend on κ_g, terms proportional to κ_g cancel when using force balance equations (7) and (8). Therefore, in accordance with the Gauss-Bonnet theorem, the Gaussian bending modulus only enters boundary conditions when solving the force balance equations to find the the surface shape.

3. External force and torque density for an equilibrium fluid membrane

If molecules in the surface are subjected to an external potential $U = \int_{\mathcal{S}} dS c^\alpha U^\alpha(s^1, s^2, \mathbf{n})$, where U^α acts on component α, the variation of this external potential induced by a deformation of the surface $\delta\mathbf{X}$ reads as

$$\begin{aligned} \delta U &= \int_{\mathcal{S}} dS c^\alpha \left[(\partial_i U^\alpha)\delta X^i + \frac{\partial U^\alpha}{\partial \mathbf{n}} \cdot \delta \mathbf{n} \right], \\ &= \int_{\mathcal{S}} dS c^\alpha \left[(\partial_i U^\alpha)\delta X^i + \frac{1}{2}\left(\frac{\partial U^\alpha}{\partial \mathbf{n}} \cdot \mathbf{e}^i \right) \epsilon_{ik} \mathbf{e}^k \cdot (\nabla \times \delta \mathbf{X}) \right], \end{aligned} \tag{H8}$$

where we have used the identities (B4) and (D4). The contribution of external forces and torques to the virtual work given in Eq. (13) on the other hand reads as, ignoring here inertial terms,

$$\delta W_{\rm ext} = \int_{\mathcal{S}} dS \left[\mathbf{f}^{\rm ext} \cdot \delta \mathbf{X} + \frac{1}{2} \mathbf{\Gamma}^{\rm ext} \cdot (\nabla \times \delta \mathbf{X}) \right]. \tag{H9}$$

Using $\delta W_{\text{ext}} = -\delta U$, one then obtains the external surface force density and external surface torque density:

$$\mathbf{f}^{\text{ext}} = -c^{\alpha}(\partial_i U^{\alpha})\mathbf{e}^i, \tag{H10}$$

$$\boldsymbol{\Gamma}^{\text{ext}} = -c^{\alpha}\left(\frac{\partial U^{\alpha}}{\partial \mathbf{n}} \cdot \mathbf{e}^j\right)\epsilon_{ji}\mathbf{e}^i. \tag{H11}$$

APPENDIX I: ENTROPY PRODUCTION RATE FOR A FLUID SURFACE

We derive here the entropy production rate for a region of a fluid surface $\mathcal{S}$ enclosed by a fixed contour $\mathcal{C}$. The time derivative of the free energy of the surface F is

$$\frac{dF}{dt} = \int_{\mathcal{S}} dS\left[\frac{1}{2}\partial_t(\rho v_i v^i + \rho(v_n)^2) + K^i{}_j\partial_t C_i{}^j + \mu^{\alpha}\partial_t c^{\alpha}\right] + \int_{\mathcal{S}} dS v_n C_i{}^i\left[\frac{1}{2}\rho v^2 + f_0\right]. \tag{I1}$$

Using the following relation obtained from Eq. (E14) $\partial_t v_i = \partial_t(g_{ij}v^j) = g_{ij}\partial_t v^j + 2v_n C_{ij}v^j$, as well as the mass balance equation (20), one obtains

$$\tfrac{1}{2}\partial_t(\rho v_i v^i + \rho(v_n)^2) + \tfrac{1}{2}\rho v_n C_i{}^i v^2 = \rho a^i v_i + \rho a_n v_n - \tfrac{1}{2}\nabla_i(\rho v^2 v^i) + \tfrac{1}{2}J_n^{\rho}v^2, \tag{I2}$$

where we have used the expression of the acceleration $\mathbf{a}$ obtained in Eq. (E20). Using then the force balance equation (7) and the concentration balance equation (21), we find

$$\frac{dF}{dt} = \int_{\mathcal{S}} dS\Big[-\frac{1}{2}\nabla_i(\rho v^i v^2) + \frac{1}{2}J_n^{\rho}\mathbf{v}^2 + (\nabla_j t^{ji})v_i + t_n^j C_j{}^i v_i + f^{\text{ext,i}}v_i + (\nabla_i t_n^i)v_n - t^{ij}C_{ij}v_n + f_n^{\text{ext}}v_n$$
$$+ K^i{}_j\partial_t C_i{}^j + (f_0 - \mu^{\alpha}c^{\alpha})C_i{}^i v_n - \mu^{\alpha}\nabla_i(c^{\alpha}v^i + j^{\alpha,i}) + \mu^{\alpha}(J_n^{\alpha} + r^{\alpha})\Big]. \tag{I3}$$

Using the divergence theorem (A30), this can be rewritten

$$\frac{dF}{dt} = \int_{\mathcal{S}} dS\Big[-t^{ji}\nabla_j v_i + t_n^j C_j{}^i v_i - t_n^i\partial_i v_n - t^{ij}C_{ij}v_n + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + (f_0 - \mu^{\alpha}c^{\alpha})C_i{}^i v_n + K^i{}_j\partial_t C_i{}^j$$
$$+ (\partial_i\mu^{\alpha})(c^{\alpha}v^i + j^{\alpha,i}) + \mu^{\alpha}(J_n^{\alpha} + r^{\alpha}) + \frac{1}{2}J_n^{\rho}v^2\Big] + \oint_{\mathcal{C}} dl\, \nu_i\Big[-\frac{1}{2}\rho v^2 v^i + t^{ij}v_j + t_n^i v_n - \mu^{\alpha}(c^{\alpha}v^i + j^{\alpha,i})\Big]. \tag{I4}$$

Using the Gibbs-Duhem equality (30) and the balance of fluxes (22),

$$\frac{dF}{dt} = \int_{\mathcal{S}} dS\Big\{-t^{ij}\nabla_i v_j - t^{ij}C_{ij}v_n + t_n^i(C_i{}^j v_j - \partial_i v_n) + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + (f_0 - \mu^{\alpha}c^{\alpha})C_i{}^i v_n + K^i{}_j\partial_t C_i{}^j$$
$$+ v^i K_{jk}\nabla_i C^{jk} - [\partial_i(f_0 - \mu^{\alpha}c^{\alpha})]v^i + (\partial_i\mu^{\alpha})j^{\alpha,i} + \left(\mu^{\alpha} + \frac{1}{2}m^{\alpha}v^2\right)J_n^{\alpha} + \mu^{\alpha}r^{\alpha}\Big\}$$
$$+ \oint_{\mathcal{C}} ds_i\Big[-\frac{1}{2}\rho v^2 v^i + \mathbf{t}^i\cdot\mathbf{v} - \mu^{\alpha}(c^{\alpha}v^i + j^{\alpha,i})\Big]. \tag{I5}$$

Reorganizing, performing an integration by part, introducing the convected derivative of the curvature tensor

$$\frac{dC_i{}^j}{dt} = \partial_t C_i{}^j + v^k\nabla_k C_i{}^j, \tag{I6}$$

and using the total chemical potential $\mu_{\text{tot}}^{\alpha} = \mu^{\alpha} + \frac{1}{2}m^{\alpha}v^2$, one finds

$$\frac{dF}{dt} = \int_{\mathcal{S}} dS\Big\{-[t^{ij} - (f_0 - \mu^{\alpha}c^{\alpha})g^{ij}]\nabla_i v_j - t^{ij}C_{ij}v_n + t_n^i(C_i{}^j v_j - \partial_i v_n)$$
$$+ \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + (f_0 - \mu^{\alpha}c^{\alpha})C_i{}^i v_n + K^i{}_j\frac{dC_i{}^j}{dt} + (\partial_i\mu^{\alpha})j^{\alpha,i} + \mu_{\text{tot}}^{\alpha}J_n^{\alpha} + \mu^{\alpha}r^{\alpha}\Big\}$$
$$+ \oint_{\mathcal{C}} ds_i\Big[-\frac{1}{2}\rho v^2 v^i + \mathbf{t}^i\cdot\mathbf{v} - \mu^{\alpha}j^{\alpha,i} - f_0 v^i\Big]. \tag{I7}$$

Using the torque balance equation (11), splitting the tension tensor t^{ij} into a symmetric and an antisymmetric part, and introducing the equilibrium tension tensor $\bar{t}_e^{ij} = (f_0 - \mu^\alpha c^\alpha) g^{ij}$, we obtain

$$\frac{dF}{dt} = \int_S dS\Big[-(t_s^{ij} - \bar{t}_e^{ij})v_{ij} - \frac{1}{2}t^{kl}\epsilon_{kl}\epsilon^{ij}\nabla_i v_j + \big(\nabla_k \bar{m}^{ki} - C_l{}^k m_n^l \epsilon_k{}^i - \Gamma^{\text{ext},k}\epsilon_k{}^i\big)\big(C_i{}^j v_j - \partial_i v_n\big) + K^i{}_j \frac{dC_i{}^j}{dt} + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + (\partial_i \mu^\alpha)j^{\alpha,i} + \mu_{\text{tot}}^\alpha J_n^\alpha + \mu^\alpha r^\alpha\Big] + \oint_C dl\, \nu_i[-f v^i + \mathbf{t}^i\cdot\mathbf{v} - \mu^\alpha j^{\alpha,i}], \tag{I8}$$

where we have introduced the symmetric velocity gradient v_{ij} defined in Eq. (38). Using the torque balance equation (12), performing an integration by part, and using the definition of the vorticity of the flow [Eq. (39)],

$$\frac{dF}{dt} = \int_S dS\Big[-\big(t_s^{ij} - \bar{t}_e^{ij}\big)v_{ij} + \big(\nabla_i m_n^i - C_{ij}\bar{m}^{ik}\epsilon_k{}^j + \Gamma_n^{\text{ext}}\big)\omega_n - \bar{m}^{ki}\nabla_k\big(C_i{}^j v_j - \partial_i v_n\big) + m_n^j C_j{}^i \omega_i + K^i{}_j\frac{dC_i{}^j}{dt} + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + \Gamma^{\text{ext},i}\omega_i + (\partial_i\mu^\alpha)j^{\alpha,i} + \mu_{\text{tot}}^\alpha J_n^\alpha + \mu^\alpha r^\alpha\Big] + \oint_C dl \nu_i\big[-f v^i + \mathbf{t}^i\cdot\mathbf{v} + \bar{m}^{ik}\big(C_k{}^j v_j - \partial_k v_n\big) - \mu^\alpha j^{\alpha,i}\big]. \tag{I9}$$

Rearranging and performing an integration by part,

$$\frac{dF}{dt} = \int_S dS\Big\{-\big(t_s^{ij} - \bar{t}_e^{ij} + C_k{}^j\bar{m}^{ki}\big)v_{ij} - \bar{m}^i{}_j\big[-\nabla_i(\partial^j v_n) - C_{ik}C^{jk}v_n + v_k\nabla_i C^{jk} + (\nabla_i v_k)C^{kj} - (\nabla_k v^j)C_i{}^k\big] - m_n^i\partial_i\omega_n + m_n^i C_i{}^j\omega_j + K^i{}_j\frac{dC_i{}^j}{dt} + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + \mathbf{\Gamma}^{\text{ext}}\cdot\boldsymbol{\omega} + (\partial_i\mu^\alpha)j^{\alpha,i} + \mu_{\text{tot}}^\alpha J_n^\alpha + \mu^\alpha r^\alpha\Big\} + \oint_C dl\, \nu_i\big[-f v^i + \mathbf{t}^i\cdot\mathbf{v} + m^{ij}\omega_j + m_n^i\omega_n - \mu^\alpha j^{\alpha,i}\big]. \tag{I10}$$

In Eq. (I10), the term in factor of $\bar{m}^i{}_j$ corresponds to the Lagrangian convected derivative of the curvature tensor $\bar{D}C_i{}^j/\bar{D}t$, defined in Eq. (E7):

$$\frac{\bar{D}C_i{}^j}{\bar{D}t} = \frac{dC_i{}^j}{dt} + (\nabla_i v^k)C_k{}^j - (\nabla_k v^j)C_i{}^k, \tag{I11}$$

where we have used the Mainardi-Coddazzi equation (A21). We define the bending rate tensor as the symmetric part of this tensor:

$$\frac{DC_{ij}}{Dt} = \frac{1}{2}\left(g_{jk}\frac{\bar{D}C_i{}^k}{\bar{D}t} + g_{ik}\frac{\bar{D}C_j{}^k}{\bar{D}t}\right), \tag{I12}$$

whose explicit expression is given in Eq. (40). In addition, one can verify that $K^i{}_j\bar{D}C_i{}^j/\bar{D}t = K^i{}_j dC_i{}^j/dt$; indeed

$$K^i{}_j\big[(\nabla_i v_k)C^{kj} - (\nabla_k v^j)C^k{}_i\big] = \nabla_i v_j\big(K^{ik}C^j{}_k - K^{kj}C^i{}_k\big) = 0, \tag{I13}$$

as a result of the invariance by rotation [Eq. (32)] and the symmetry of K^{ij}. Using these relations and the symmetry of the tensor K^{ij}, we then find the expression for the rate of change of free energy:

$$\frac{dF}{dt} = \int_S dS\Big\{-\Big[\bar{t}^{ij} - \bar{t}_e^{ij} + \frac{1}{2}\epsilon_{ln}\bar{m}^{ln}\big(\epsilon^{ik}C_k{}^j + \epsilon^{jk}C_k{}^i\big)\Big]v_{ij} - (\bar{m}^{ij} - K^{ij})\frac{DC_{ij}}{Dt} - m_n^i\big(\partial_i\omega_n - C_i{}^j\omega_j\big) + \mathbf{f}^{\text{ext}}\cdot\mathbf{v} + \mathbf{\Gamma}^{\text{ext}}\cdot\boldsymbol{\omega} + (\partial_i\mu^\alpha)j^{\alpha,i} + \mu_{\text{tot}}^\alpha J_n^\alpha + \mu^\alpha r^\alpha\Big\} + \oint_C dl\, \nu_i[-f v^i + \mathbf{t}^i\cdot\mathbf{v} + \mathbf{m}^i\cdot\boldsymbol{\omega} - \mu^\alpha j^{\alpha,i}]. \tag{I14}$$

In Eq. (37), we have not included the contribution $\epsilon_{ln}\bar{m}^{ln}$ of the antisymmetric part of $\bar{m}^{ij}$. The antisymmetric part of $\bar{m}^{ij}$ is related to the trace of m^{ij} through the relation $m_k{}^k = -\bar{m}_{ij}\epsilon^{ij}$. The transformation invariance in Eqs. (C9)–(C11) implies that the contribution of the antisymmetric part of the bending moment tensor $\bar{m}_{ij}$ to the force balance equation can be absorbed in a redefinition of the stress tensor.

APPENDIX J: STABILITY OF A HOMOGENEOUS FLAT ACTIVE SURFACE

We discuss here the stability of a homogeneous flat active surface, in the absence of external forces and torques.

1. Fluid surface

Perturbations of the flat shape of the fluid surface are described in the Monge gauge by the height $h(x,y)$ such that the surface position is given by $\mathbf{X}(x,y) = x\mathbf{u}_x + y\mathbf{u}_y + h(x,y)\mathbf{u}_z$.

Calculations are performed for a weakly bent surface, $|\partial_i h| \ll 1$, at linear order in the height h and velocity field $\mathbf{v}$. In this limit, covariant and contravariant indices can be used indifferently, and

$$g_{ij} \simeq \delta_{ij}, \tag{J1}$$

$$C_{ij} \simeq -\partial_i \partial_j h. \tag{J2}$$

The rate of deformation tensors are given by

$$v_{ij} \simeq \frac{1}{2}(\partial_i v_j + \partial_j v_i), \tag{J3}$$

$$\frac{DC_{ij}}{Dt} \simeq -\partial_t \partial_i \partial_j h, \tag{J4}$$

$$\omega_n \simeq \frac{1}{2}\epsilon_{ij}\partial_i v_j, \tag{J5}$$

$$\omega_i \simeq \epsilon_{ij}\partial_j v_n. \tag{J6}$$

The tensions and torque tensors are given by

$$\begin{aligned}\bar{t}_{ij} = {} & \eta(\partial_i v_j + \partial_j v_i) + (\eta_b - \eta)(\partial_k v_k)\delta_{ij} - 2\bar{\eta}\partial_i\partial_j\partial_t h \\ & - (\bar{\eta}_b - \bar{\eta})(\partial_t \Delta h)\delta_{ij} + \{\gamma_H + \zeta\Delta\mu \\ & - [-\kappa C_0 + (\zeta' - \tilde{\zeta})\Delta\mu]\Delta h\}\delta_{ij} - 2\tilde{\zeta}\Delta\mu\partial_i\partial_j h,\end{aligned} \tag{J7}$$

$$\begin{aligned}\bar{m}_{ij} = {} & -2\eta_c\partial_i\partial_j\partial_t h - (\eta_{cb} - \eta_c)(\partial_t\Delta h)\delta_{ij} + \bar{\eta}(\partial_i v_j + \partial_j v_i) \\ & + (\bar{\eta}_b - \bar{\eta})\partial_k v_k \delta_{ij} \\ & + \{\zeta_c\Delta\mu - \kappa C_0 - [\kappa + \kappa_g + (\zeta_c' - \tilde{\zeta}_c)\Delta\mu]\Delta h\}\delta_{ij} \\ & - [-\kappa_g + 2\tilde{\zeta}_c\Delta\mu]\partial_i\partial_j h,\end{aligned} \tag{J8}$$

$$m_{n,i} = \frac{\lambda}{2}\partial_i\epsilon_{kl}\partial_k v_l, \tag{J9}$$

where we have used the Laplacian operator $\Delta = \partial_x^2 + \partial_y^2$. The force and torque balance equations then yield, neglecting inertial terms at low Reynolds number,

$$\begin{aligned}& \eta\Delta v_j + \eta_b\partial_j\partial_k v_k - (\bar{\eta}_b + \bar{\eta})\partial_j\partial_t\Delta h - (\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu\partial_j\Delta h \\ & = -\frac{1}{2}\epsilon_{ij}\partial_i(\epsilon_{kl}t_{kl}),\end{aligned} \tag{J10}$$

$$\partial_i t_{n,i} = -\Delta h[\gamma_H + \zeta\Delta\mu], \tag{J11}$$

$$\begin{aligned}t_{n,j} = {} & -(\eta_{cb} + \eta_c)\partial_j\partial_t\Delta h + \bar{\eta}\Delta v_j + \bar{\eta}_b\partial_j\partial_i v_i \\ & - [\kappa + (\zeta_c' + \tilde{\zeta}_c)]\partial_j\Delta h,\end{aligned} \tag{J12}$$

$$\epsilon_{ij}t_{ij} = -\frac{\lambda}{2}\Delta(\epsilon_{kl}\partial_k v_l). \tag{J13}$$

We then obtain the shape equation

$$\begin{aligned}& \left[\eta_{cb} + \eta_c - \frac{(\bar{\eta} + \bar{\eta}_b)^2}{\eta + \eta_b}\right]\partial_t\Delta\Delta h \\ & = -\left\{\kappa + \left[\zeta_c' + \tilde{\zeta}_c + \frac{\bar{\eta} + \bar{\eta}_b}{\eta + \eta_b}(\zeta_c - \zeta' - \tilde{\zeta})\right]\Delta\mu\right\}\Delta\Delta h \\ & \quad + (\gamma_H + \zeta\Delta\mu)\Delta h.\end{aligned} \tag{J14}$$

2. Elastic surface

Perturbations of the flat shape of the elastic surface are described in the Monge gauge by the height $h(x,y)$ and the tangential deformation field $\mathbf{u}$ such that the surface position is given by $\mathbf{X}(x,y) = [x + u_x(x,y)]\mathbf{u}_x + [y + u_y(x,y)]\mathbf{u}_y + h(x,y)\mathbf{u}_z$. Calculations are performed for a weakly bent surface, $|\partial_i h| \ll 1$, at linear order in the height h and deformation field $\mathbf{u}$. The deformation fields are given by

$$u_{ij} \simeq \tfrac{1}{2}(\partial_i u_j + \partial_j u_i), \tag{J15}$$

$$c_{ij} \simeq -\partial_i\partial_j h, \tag{J16}$$

$$\Omega_i \simeq \tfrac{1}{2}\epsilon_{jk}\partial_i\partial_j u_k. \tag{J17}$$

On the deformed surface, the metric and curvature tensors are given by $g_{ij} \simeq \delta_{ij} + 2u_{ij}$, $C_{ij} \simeq c_{ij}$, and the Christoffel symbols by $\Gamma_{ij}^k \simeq \partial_i\partial_j u^k$. The tensions and torque tensors are given in the limit of small displacements by

$$\begin{aligned}\bar{t}^{ij} = {} & E_1\tfrac{1}{2}(\partial_i u_j + \partial_j u_i) + E_2\partial_k u_k\delta_{ij} - G_1\partial_i\partial_j h - G_2\Delta h\delta_{ij} \\ & + \Delta\mu[\zeta\delta_{ij} - (\zeta' - \tilde{\zeta})\Delta h\delta_{ij} - 2\tilde{\zeta}\partial_i\partial_j h] \\ & - \zeta\Delta\mu(\partial_i u_j + \partial_j u_i),\end{aligned} \tag{J18}$$

$$\begin{aligned}\overline{m}^{ij} = {} & -F_1\partial_i\partial_j h - F_2\Delta h\delta_{ij} + K_1\tfrac{1}{2}(\partial_i u_j + \partial_j u_i) + K_2\partial_k u_k\delta_{ij} \\ & + \Delta\mu[\zeta_c\delta_{ij} - (\zeta_c' - \tilde{\zeta}_c)\Delta h\delta_{ij} - 2\tilde{\zeta}_c\partial_i\partial_j h] \\ & - \zeta_c\Delta\mu(\partial_i u_j + \partial_j u_i),\end{aligned} \tag{J19}$$

$$m_{n,i} = H_1\tfrac{1}{2}\epsilon_{jk}\partial_i\partial_j u_k. \tag{J20}$$

A calculation similar to the fluid case then yields the equation for the surface height

$$\begin{aligned}\xi\frac{dh}{dt} = {} & \zeta\Delta\mu\Delta h - \left\{F_1 + F_2 + (\zeta_c' + \tilde{\zeta}_c)\Delta\mu - \frac{K_1 + K_2}{E_1 + E_2}\right. \\ & \left.\times[G_1 + G_2 + (\zeta' + \tilde{\zeta} - \zeta_c)\Delta\mu]\right\}\Delta\Delta h,\end{aligned} \tag{J21}$$

where we have introduced an effective external friction force $\mathbf{f}^{\text{ext}} = -\xi\mathbf{v}\cdot\mathbf{n}$.

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