

Self-organized dynamics and emergent shape spaces of active isotropic fluid surfaces

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Theories of self-organized active fluid surfaces have emerged as an important class of minimal models for the shape dynamics of biological membranes, cells, and tissues. However, due to their inherent geometric nonlinearities and the absence of general minimization principles in active systems, it remains a major challenge to systematically study the emergent shape spaces that such theories give rise to. Here, we introduce a variational approach that allows for a direct computation of stationary surface geometries and flows, which enables the classification of nonequilibrium phase transitions in shape spaces described by active surface theories. To achieve this, we construct a dissipation functional systematically from the entropy production in active surfaces and show how generic symmetries imposed by Onsager relations can be exploited to also account for reactive nondissipative terms in constitutive laws. This functional is supplemented by Lagrange multipliers that relax nonlinear geometric constraints, which leads to a tractable variational problem suitable for implicit dynamic simulations and explicit calculations of nontrivial steady state geometries and flows. We apply this framework to study the dynamics of open fluid membranes and closed active fluid surfaces, and characterize the space of stationary solutions that corresponding surfaces and flows occupy. These analyses rationalize the interplay of first-order shape transitions of internally and externally forced fluid membranes, reveal degenerate regions in stationary shape spaces of mechanochemically active surfaces, and identify a mechanism by which hydrodynamic screening controls the geometry of active surfaces undergoing cell divisionlike shape transformations.

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I. INTRODUCTION

Many crucial processes in living systems rely on the geometric control of two-dimensional structures with fluidlike properties. Membranes, for example, are made of thin lipid bilayer sheets and are critical in regulating traffic into and out of cells via endocytosis and exocytosis [1–3]. Due to weak hydrophobic interactions [4,5], these lipid sheets behave as two-dimensional fluids [6], while orientational order in lipid packing allows membranes to resist bending. The cortex of eukaryotic cells is a thin polymer filament network beneath the cell membrane [4] that can also behave as an effectively two-dimensional viscous fluid due to filament and cross-linker turnover on timescales of seconds [7]. Active mechanical forces generated by motor proteins lead to cortical flows [8,9] and play a crucial role in maintaining cell shape and enabling dynamic cellular processes such as migration and division [7,9–12]. Finally, epithelial tissues are effectively two-dimensional cell monolayers that are critical for embryonic development and morphogenesis [10,13]. This role is

facilitated by active cellular processes that allow epithelial tissues to autonomously change their shape [14]. Cellular rearrangements, cell division, and cell death lead to viscous material properties on the timescale of hours [15]. The ability to resist bending plays an important role in both the cellular cortex [16] and in epithelial tissues [17].

Given the abundance of fluid surfaces involved in the shape regulation of cells and tissues, minimal models of self-organizing active fluid surfaces have become an essential framework to understand the emergence of shape in living systems [18–23]. An often encountered bottleneck in investigating such theories is the inevitably nonlinear nature of surface force balance equations that involve *a priori* unknown, or even dynamic, domain geometries. Restricting oneself to axisymmetric geometries and surfaces that exhibit a purely passive response to bending, this bottleneck has been addressed within a historical body of work starting from the formulation of the Helfrich bending free energy [24–26] over the derivation of highly nonlinear shape equations [27,28] to the formulation of a variational approach that converts the shape equation into a tractable boundary value problem [29–32]. The success of this variational formulation in explaining many experimental observations [33–39] arose from its ability to systematically characterize the space of stationary surface shapes a given membrane theory gives rise to.

Active materials can in general not be described in terms of an energy functional, which raises the question if and how variational formulations—analogue to those previously developed for passive membranes—can be systematically

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developed for out-of-equilibrium fluid surfaces. A promising route to address this question has been pioneered in Refs. [40–42] using Onsager’s variational principle. In this formulation, a Rayleigh functional is constructed that includes the free-energy change rate and dissipative energy losses. Variation of the Rayleigh functional then gives rise to a set of dynamic equations [42] that should be equivalent to force and moment balance equations in terms of some constitutive laws. However, while suitable expressions for common contributions to dissipation, such as viscous shear stresses, can essentially be guessed, there exists currently no systematic way to start from more general constitutive laws of active surfaces [18,43] and formulate a corresponding functional. Additionally, because the minimization of dissipation is not a fundamental principle [44], we have to ask whether such functionals exist at all in more general cases.

Here, we build on recent theoretical advances in applying the framework of irreversible thermodynamics to curved and deforming surfaces [18,43] to address these questions. Exploiting the symmetries imposed by Onsager relations [45–47], we show that the entropy production of active deforming surfaces derived in these works can indeed be used to construct suitable Rayleigh functionals. Specifically, variations of the latter give rise to a boundary value problem that is equivalent to the force and moment balance equations for the full set of *a priori* defined constitutive laws, including those describing the out-of-equilibrium maintenance of chemical potentials, and even if nondissipative active couplings are present.

A key numerical challenge when solving for the shape dynamics of a deforming surface is that its parametrization will also depend on time. This potentially results in a lack of computational control over the accuracy with which the physical surface can be represented and is often addressed using arbitrary Lagrangian-Eulerian (ALE) parametrizations [48,49,69]. In this work, we design an ALE parametrization that can directly be integrated into the dissipation functional, facilitates a numerically robust implicit solution of the shape dynamics, and ensures points on the deforming surface are mapped to fixed reference coordinates via a simple scaling. We will use this integrated framework to study both the dynamics and the space of stationary geometries and flows of active fluid surfaces undergoing biologically relevant shape transformations. The numerical implementations of this framework can be found on GitHub [50].

II. DYNAMICS OF PARAMETRIZED CURVED SURFACES

We describe a surface Ω by the vector field $\mathbf{X}(s^1, s^2, t) \in \mathbb{R}^3$ that is parametrized by two generalized coordinates s^i ($i \in \{1, 2\}$) and time t . Tangent vectors and surface normal are given by $\mathbf{e}_i = \partial_i \mathbf{X}$ and $\mathbf{n} = \mathbf{e}_1 \times \mathbf{e}_2 / |\mathbf{e}_1 \times \mathbf{e}_2|$, respectively, where we denote $\partial_i := \partial / \partial s^i$. Metric tensor and curvature tensors are defined by $g_{ij} = \mathbf{e}_i \cdot \mathbf{e}_j$ and $C_{ij} = -\mathbf{n} \cdot \partial_i \partial_j \mathbf{X}$. The surface area element is given by $dA = \sqrt{g} ds^1 ds^2$, where $g = \det(g_{ij})$. Vector fields on the surface $\mathbf{w} = \mathbf{w}_\parallel + \mathbf{w}_\perp$ can be expanded in terms of their in-plane components $\mathbf{w}_\parallel = w^i \mathbf{e}_i$ and their normal components $\mathbf{w}_\perp = w_n \mathbf{n}$. We denote Euclidean representations of metric and curvature tensor by $\mathbf{G} = g_{ij} \mathbf{e}^i \otimes$

$\mathbf{e}^j$ and $\mathbf{C} = C_{ij} \mathbf{e}^i \otimes \mathbf{e}^j$, respectively, and similarly for other tangential tensors.

A. Parametrization of deforming surfaces

Any motion and deformation of the surface can be described by a local center-of-mass velocity field $\mathbf{v} = v^i \mathbf{e}_i + v_n \mathbf{n}$, where the components (v^i) and (v_n) correspond to in-plane flow surface deformations, respectively. The general surface dynamics is given by

$$\frac{d\mathbf{X}}{dt} = \mathbf{v}, \quad (1)$$

where $\frac{d}{dt}(\cdot)$ denotes the total time derivative. To discuss the appearance of a time-dependent parametrization in Eq. (1) explicitly, we expand the total time derivative as

$$\partial_t \mathbf{X} + q^i \partial_i \mathbf{X} = \mathbf{v}. \quad (2)$$

The components q^i of the coordinate flow $\mathbf{q} = q^i \mathbf{e}_i$ capture the in-plane motion of a surface point $\mathbf{X}$ at fixed coordinates s^i , relative to its actual in-plane center-of-mass velocity $\mathbf{v}_\parallel = v^i \mathbf{e}_i$. For example, for a fixed material coordinate S , a surface point $\mathbf{X}$ moves by definition already with in-plane center-of-mass velocity $\mathbf{v}_\parallel$, which implies $q^i = 0$. This corresponds to a Lagrangian parametrization for which the surface dynamics [Eq. (1)] becomes $\partial_t \mathbf{X} = \mathbf{v}$ [12,18,22]. Another common parametrization choice is to set $q^i = v^i$, corresponding to an Eulerian parametrization for which the surface dynamics [Eq. (1)] becomes $\partial_t \mathbf{X} = v_n \mathbf{n}$ [18,19]. In both cases, it is the surface flow that dictates the dynamics of the parametrization. In general, however, either of the two— $q^i(s^i, t)$ or $s^i(S, t)$ —can be chosen freely and are related by

$$q^i = \left. \frac{\partial s^i}{\partial t} \right|_S. \quad (3)$$

The parametrizations resulting from different choices will typically be neither Lagrangian nor Eulerian, but as such may be fully decoupled from flows and deformations. Analog approaches in “flat” Euclidean space are called ALE methods [51], a terminology that we will adopt in the present work when extending it to embedded curved surfaces.

B. Conservation laws on ALE-parametrized curved surfaces

To formulate conservation laws and transport equations on ALE-parametrized curved surfaces, one has to determine the dynamics of area integrals of the form

$$F(t) = \int_{\omega(t)} ds^1 ds^2 \sqrt{g} f(s^1, s^2, t), \quad (4)$$

where the integration domain $\omega(t)$ is some coordinate region that parametrizes a fixed set of material elements. Importantly, $\omega(t)$ is only independent of time if Lagrangian material coordinates are used. We show in Appendix III A of the Supplemental Material [52] that for an ALE-parametrized curved surface

$$\frac{dF}{dt} = \int_{\Omega} dA \left[\frac{1}{\sqrt{g}} \partial_t (f \sqrt{g}) + \nabla_i (f q^i) \right], \quad (5)$$

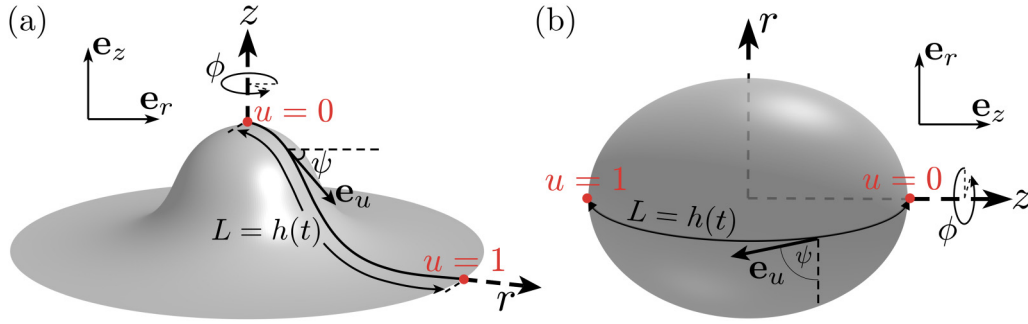


FIG. 1. Parametrization of open [panel (a)] and closed [panel (b)] axisymmetric surfaces $\mathbf{X}(u, \phi, t)$ considered in this work [see Eq. (8)]. We introduce a scaling Lagrangian-Eulerian parametrization (Sec. IID) that maps fixed mesh coordinates $u \in [0, 1]$ to physical arc length coordinates s on the deforming surface via $s = h(t)u$. ψ denotes the tangent angle and $\mathbf{e}_u = \partial_u \mathbf{X}$ the meridional tangent vector. Cylindrical coordinates (r, ϕ, z) parametrize the embedding Euclidean space. The total length $L = h(t)$ of the meridional outline changes in time as surfaces deform.

where ∇_i denotes the covariant derivative. Using the covariant Stokes theorem [18], the second term can be identified as a boundary term that results from the dynamics of the coordinate region $\omega(t)$. As expected, this boundary contribution vanishes for a Lagrangian parametrization ($q^i = 0$) and it can be interpreted as a flux $j_f^i = f v^i$ across the boundary for an Eulerian parametrization ($q^i = v^i$). In general, however, it is not a physical flux but an artifact of any parametrization that is decoupled from the local center-of-mass motion.

As an important example, we consider $f = \rho$, where ρ is the mass density of the surface, we have the total mass $F(t) = M(t)$ and mass conservation directly follows from Eq. (5) (see Appendix III B 1 of the Supplemental Material [52]). If multiple chemical species α of concentration $c_\alpha(s^1, s^2, t)$ are present, this leads to continuity equations for each species of the form

$$\partial_t c_\alpha + q^i \partial_i c_\alpha + c_\alpha \text{div}(\mathbf{v}) + \text{div}(\mathbf{j}_\alpha) = r_\alpha + J_{n,\alpha}, \quad (6)$$

where $\text{div}(\cdot) := \mathbf{e}^i \cdot \partial_i(\cdot)$ denotes the divergence operator on the surface, implying

$$\text{div}(\mathbf{v}) = \nabla_i v^i + C_i^i v_n, \quad (7)$$

$\mathbf{j}_\alpha = j_\alpha^i \mathbf{e}_i$ are diffusive fluxes relative to the in-plane center-of-mass flux $c_\alpha v^i$, r_α denotes chemical reaction rates among species, and $J_{n,\alpha}$ denotes fluxes between the surface and its environment.

C. Deforming axisymmetric surfaces

Purely Lagrangian and Eulerian parametrizations relate the coordinate flow q^i only to the in-plane center-of-mass velocity $\mathbf{v}_\parallel$ and are consequently slave to the system dynamics, precluding any explicit level of control whenever surface movements and deformations occur. When solving Eq. (1) numerically, this lack of control over the parametrization is typically countered by adaptive remeshing [12,69], which repeatedly interpolates the surface state and effectively resets the parametrization. By integrating surface deformations into the coordinate flow q^i , we develop and apply in the following an approach that reduces the dependence of the parametrization on the surface dynamics to a global scaling, which naturally eliminates the need for flow-dependent remeshing. To make this concrete, we consider a deforming axisymmetric

surface described by

$$\mathbf{X}(u, \phi, t) = [r(u, t) \cos \phi, r(u, t) \sin \phi, z(u, t)], \quad (8)$$

where $r(u, t)$ and $z(u, t)$ denote time-dependent components of points on the surface, and $u \in [0, 1]$ and $\phi \in [0, 2\pi]$ are time-independent coordinates we refer to as *mesh coordinates* (Fig. 1). For general center of mass flows

$$\mathbf{v}(u, \phi, t) = v^u(u, t) \mathbf{e}_u + v^\phi(u, t) \mathbf{e}_\phi + v_n(u, t) \mathbf{n}, \quad (9)$$

the components of the surface dynamics implied by Eqs. (2) and (8) are given by

$$\partial_t r = (v^u - q^u) r' - \frac{z'}{\sqrt{r'^2 + z'^2}} v_n, \quad (10)$$

$$\partial_t z = (v^u - q^u) z' + \frac{r'}{\sqrt{r'^2 + z'^2}} v_n, \quad (11)$$

where primes “’” denote partial derivatives with respect to u and azimuthal flows v^ϕ do by construction not contribute. Reparametrizing $\{r'(u, t), z'(u, t)\} \rightarrow \{(h(u, t), \psi(u, t))\}$, where $h = \sqrt{r'^2 + z'^2}$ and ψ is determined by

$$r' = h \cos \psi, \quad (12)$$

$$z' = -h \sin \psi, \quad (13)$$

the shape dynamics [Eqs. (10) and (11)] become

$$\partial_t r = (v^u - q^u) h \cos \psi + v_n \sin \psi, \quad (14)$$

$$\partial_t z = (q^u - v^u) h \sin \psi + v_n \cos \psi. \quad (15)$$

Note that ψ can be geometrically interpreted as the tangent angle (Fig. 1) [30], and is related to the meridional curvature tensor component by $C_u^u = \psi'/h$. We find from the definition of h and Eqs. (12)–(15) that

$$\partial_t h = [(v^u - q^u) h]' + v_n \psi'. \quad (16)$$

The significance of Eq. (16) for this work is as follows: From $h = |\partial_u \mathbf{X}|$, we see that $h(u, t)$ mediates via

$$s(u, t) = \int_0^u d\bar{u} h(\bar{u}, t). \quad (17)$$

A relationship between the fixed mesh coordinates u used to parametrize numerical solutions and the physical arc length

TABLE I. Comparison of parametrizations classified by their coordinate flow q'' [see Eq. (2)]. $h(u, t)$ maps fixed mesh coordinates u to physical arc length coordinates [see Eq. (16)] and develops unpredictable flow- and shape-dependent inhomogeneities when purely Eulerian or Lagrangian parametrizations are used. The SLE parametrization is independent of local flows v'' , deformations v_n , and curvature ψ' , and amounts to a simple scaling between mesh and arc length coordinates.

Parametrization	q''	$\partial_t h$	References
Eulerian	v''	$\psi' v_n$	[19]
Lagrangian	0	$(v'' h)' + \psi' v_n$	[12,22]
SLE	s.t. $h' = 0$	dL/dt	This work

$s(u, t)$ along the meridional outline [19]. Consequently, the numerical resolution of the physical surface directly depends on the dynamic properties of $h(u, t)$.

D. Scaling Eulerian-Lagrangian parametrization

For purely Eulerian ($q'' = v''$) or Lagrangian ($q'' = 0$) parametrizations the dynamics of $h(u, t)$ [Eq. (16)], and consequently the resolution of the physical surface, is slave to the local surface flows $\mathbf{v}$ (Table I). To mitigate this lack of control, we choose a different approach in which the coordinate flow field q'' is determined by the constraint that the map $h(u, t) = h(t)$ used in Eq. (17) has to remain spatially constant and thus becomes fully independent of local surface flows or deformations. If this can be achieved, the resulting parametrization will in general be neither Eulerian nor Lagrangian and $L(t) = s(1, t) = h(t)$, where $L(t)$ is the total length of the meridional surface outline. Hence, $s(u, t) = L(t)u$ and $h(t)$ becomes a simple scaling factor that translates numerical mesh to physical arc length coordinates. We will refer to the resulting parametrization as scaling Lagrangian-Eulerian (SLE) parametrization.

To show a coordinate flow q'' for such an SLE always exists, we impose $h' = 0$ in Eq. (16) and solve for q'' , which yields

$$q''(u, t) = v''(u, t) + \frac{1}{h(t)} \int_0^u d\bar{u} v_n(\bar{u}, t) \psi'(\bar{u}, t) + c_1(t) + c_2(t)u, \quad (18)$$

where $c_1(t)$ and $c_2(t)$ are integration constants that depend on the boundary conditions for q'' and v'' . The coordinate flow q'' given in Eq. (18) specifies the SLE parametrization and leads with Eq. (16) to

$$\partial_t h = (v'' - q'')h|_0^1 + \int_0^1 du v_n \psi'. \quad (19)$$

Equation (19) explicitly shows that an initially constant $h = L_0$ will remain spatially constant over time and only changes as the length $L(t) = h(t)$ of the meridional outline changes (see Fig. 1) due to boundary flows (first term) and surface deformations (second term). Boundary conditions $q''(u_b, t)$ for $u_b = 0, 1$ can in principle be chosen arbitrarily, but two natural choices are to treat a boundary point either as Lagrangian [$q''(u_b, t) = 0$] or Eulerian point [$q''(u_b, t) =$

$v''(u_b, t)$]. Both cases will be considered in the examples discussed below.

III. MECHANICS OF DEFORMING ACTIVE FLUID SURFACES

A. Force and torque balance

The mechanical state of a curved surface is described by its tension and moment tensor, $\mathbf{T} = \mathbf{e}_i \otimes \mathbf{t}^i$ and $\mathbf{M} = \mathbf{e}_i \otimes \mathbf{m}^i$, where $\mathbf{t}^i = t^{ij} \mathbf{e}_j + t_n^i \mathbf{n}$ and $\mathbf{m}^i = m^{ij} \mathbf{e}_j + m_n^i \mathbf{n}$ are tension and moment vectors whose components describe in-plane (t^{ij}, m^{ij}) and out-of-plane or normal (t_n^i, m_n^i) contributions. In particular, for any line element of length ds on the surface with an in-plane unit vector $\mathbf{v} = v_i \mathbf{e}^i$ orthogonal to it, vectors $\mathbf{F} = ds \mathbf{v} \cdot \mathbf{T} = ds v_i \mathbf{t}^i$ and $\boldsymbol{\tau} = ds \mathbf{v} \cdot \mathbf{M} = ds v_i \mathbf{m}^i$ yield the total force and the total torque, respectively, that act on the line element. Force and torque balance equations for the surface are given by [18]

$$\text{div}(\mathbf{T}) = -\mathbf{f}^{\text{ext}}, \quad (20)$$

$$\text{div}(\mathbf{M}) = -\boldsymbol{\epsilon} : \mathbf{T}. \quad (21)$$

Here, $\text{div}(\mathbf{T}) := \mathbf{e}^i \cdot \partial_i \mathbf{T}$ denotes the in-plane divergence of the tension tensor (analog for $\mathbf{M}$), $(\boldsymbol{\epsilon} : \mathbf{T})_\alpha = \epsilon_{\alpha\beta\gamma} T_{\beta\gamma}$, where $\epsilon_{\alpha\beta\gamma}$ is fully antisymmetric Levi-Civita tensor (Greek indices reference Cartesian components) and we do not include inertial forces or external torques. In the force balance [Eq. (20)], $\mathbf{f}^{\text{ext}} = f_i^{\text{ext}} \mathbf{e}^i + f_n^{\text{ext}} \mathbf{n}$ are external forces, and we have neglected inertia, as we are interested in the typically overdamped dynamics of biological cells and tissues. In this work, we will consider external tangential friction forces

$$f_i^{\text{ext}} = -\Gamma v_i, \quad (22)$$

with friction constant Γ . A general derivation of momentum conservation of curved surfaces described by an arbitrary Lagrangian-Eulerian parametrization is provided in Appendix III B 2 of the Supplemental Material [52]. The torque balance [Eq. (21)] implies that inhomogeneous surface moments give rise to antisymmetric components of the tension tensor $\mathbf{T}$, which correspond to contributions from antisymmetric in-plane tensions t_{ij} and from normal forces t_n^i . In the absence of moments, $\mathbf{M} = 0$, $\mathbf{T}$ must be symmetric, which is equivalent to a symmetric in-plane tension tensor t_{ij} and vanishing normal forces, $t_n^i = 0$. Center-of-mass velocities $\mathbf{v}$ that drive the surface dynamics [Eq. (1)] will be determined by solving the force and torque balance equations (20) and (21). In the next step, we introduce the constitutive laws that relate tension $\mathbf{T}$ and moments $\mathbf{M}$ in the surface to its geometry and local center-of-mass velocity $\mathbf{v}$.

B. Constitutive laws

We discuss in this work open and closed active fluid surface models that capture essential physical features of membranes, the cell cortex, and epithelial tissues. In anticipation of formulating a dissipation functional for such surfaces, we introduce constitutive laws by closely following their systematic construction within the framework of irreversible thermodynamics [18,47]. We start by introducing the free-energy density of the surface. The first contribution is given

by the Helfrich free-energy density [25]

$$f_H = \gamma_H + f_\kappa, \quad (23)$$

where γ_H denotes a passive isotropic surface tension and

$$f_\kappa = \frac{1}{2}\kappa(2H - C_0)^2 \quad (24)$$

includes a bending rigidity κ , the spontaneous curvature C_0 , and $H = \text{tr}(\mathbf{C})/2$ denotes the mean curvature. Second, we include the chemical free-energy density $f_c(c_f, c_p)$ associated with surface concentrations c_f and c_p of chemical fuel and product species, respectively. In a biological system, these could be the reactant and product species involved in ATP hydrolysis [53,54]. The chemical potential difference $\Delta\mu = \mu_f - \mu_p$ with $\mu_n = \partial f_c / \partial c_n$ ($n = f, p$) provides the chemical energy to generate active stresses in the surface. The free energy of the whole surface Ω is then given by

$$F = \int_{\Omega} dA(f_H + f_c). \quad (25)$$

Such a free energy gives rise to well-defined, curvature-dependent equilibrium tensions and moments in the surface [18,20] that are in the following denoted by $\mathbf{T}_e$ and $\mathbf{M}_e$.

To introduce dissipative contributions, we use the symmetrized strain rate tensor $S_{ij} = (v_{ij} + v_{ji})/2$, where $v_{ij} = \mathbf{e}_j \cdot (\partial_i \mathbf{v})$, and denote its traceless part by

$$\tilde{\mathbf{S}} = \mathbf{S} - \frac{1}{2}\text{tr}(\mathbf{S})\mathbf{G}, \quad (26)$$

with $\mathbf{S} = S_{ij}\mathbf{e}^i \otimes \mathbf{e}^j$. Note also that $\text{tr}(\mathbf{S}) = \text{div}(\mathbf{v})$. We consider a dissipative contribution to the tension tensor given by

$$\mathbf{T}_d = 2\eta_s \tilde{\mathbf{S}} + \eta_b \text{div}(\mathbf{v})\mathbf{G} + \xi \Delta\mu \mathbf{G}, \quad (27)$$

where we have introduced shear viscosity and bulk viscosities η_s and η_b , respectively, as well as an active isotropic tension $\xi \Delta\mu$ that captures the conversion of chemical free energy into mechanical work. We do not consider dissipative moments, such that the tension and moment tensors used in this work are given by

$$\mathbf{T} = \mathbf{T}_e + \mathbf{T}_d, \quad (28)$$

$$\mathbf{M} = \mathbf{M}_e. \quad (29)$$

From Onsager's symmetry relations [45–47], we expect from Eq. (27) an additional constitutive law for the thermodynamic variable conjugate to the chemical potential difference $\Delta\mu$. Introducing such a constitutive law in a way that is compatible with the formulation of a dissipation functional involves a crucial subtlety that will be discussed in the next step.

IV. VARIATIONAL FORMULATION

A. Motivation

For any given surface geometry and distribution of active tension $\sim \xi \Delta\mu$, force and torque balance [Eqs. (20) and (21)] with constitutive laws (28) and (29) determine in-plane flows and deformations $\mathbf{v}$. To characterize such an active surface theory systematically, we have to explore the space of nontrivial stationary geometries it gives rise to. To this end, we take inspiration from previous work on equilibrium membranes,

for which phase diagrams of stationary equilibrium shapes have been determined using a variational formulation based on the free energy [Eq. (23)] with $f_c = 0$ [36]. In these works, the free energy was complemented by Lagrange multipliers to impose the nonlinear geometric relations [Eqs. (12) and (13)]. While this yields a larger system of equations that is altogether still equivalent to the normal component of the force balance [Eq. (20)], it allows for direct calculations of stationary surface geometries described by energies like Eq. (23) via a much simpler boundary value problem. Here, we generalize this approach to out-of-equilibrium surfaces by constructing a Rayleigh dissipation functional $\mathcal{R}$ that imposes nonlinear geometric constraints, as well as an SLE parametrization, via suitable Lagrange multipliers and whose stationary points defined by the variation

$$\frac{\delta \mathcal{R}}{\delta \mathbf{v}} = 0 \quad (30)$$

are surfaces and flows that satisfy the force and torque balance [Eqs. (20) and (21)] for constitutive laws (28) and (29).

B. Free-energy dynamics

The dissipation functional consists of contributions from both the equilibrium properties of the surface and its dissipative properties. The former result from changes of the free energy given in Eq. (25), which follow from Eqs. (5) and (6) as

$$\begin{aligned} \frac{dF}{dt} = \int_{\Omega} dA \left(\frac{1}{\sqrt{g}} \partial_t (f_H \sqrt{g}) - r_p \Delta\mu \right. \\ \left. + \gamma_e \text{div}(\mathbf{v}) + J_n^{\text{ext}} \right) + \oint_{\partial\Omega} f_H q^i v_i ds, \end{aligned} \quad (31)$$

where $r_p = -r_f$ denotes the rate at which the product species is produced due to fuel consumption, $\gamma_e = f_c - \mu_f c_f - \mu_p c_p$ is an equilibrium surface tension [18], and $J_n^{\text{ext}} = J_{n,f} \mu_f + J_{n,p} \mu_p$ denotes the influx of chemical free energy due to reactions with the surrounding. We assume that the flux J_n^{ext} is such that the chemical potential difference $\Delta\mu$ on the surface is maintained constant in space and time. Consequently, γ_e only renormalizes the isotropic surface tension γ_H and we denote the total passive tension by $\gamma = \gamma_H + \gamma_e$. The boundary term in Eq. (31), which is a consequence of the ALE parametrization, contributes to boundary conditions on open surfaces when performing variation of $\frac{dF}{dt}$. The Helfrich free-energy dynamics in terms of an Eulerian parametrization has previously been derived in Ref. [40].

C. Entropy production

The dissipative tension tensor in Eq. (27) can be obtained as an Onsager expansion of the entropy production Θ_{int} for an active isotropic fluid surface [18,43]:

$$\Theta_{\text{int}} = \int dA (\mathbf{T}_d : \mathbf{S} + r_p \Delta\mu), \quad (32)$$

where each pair of conjugate thermodynamic variables contains one factor that is even ($\mathbf{T}_d, \Delta\mu$), and one that is odd ($\mathbf{S}, r_p$), under time reversal. After designating for each pair one thermodynamic flux and one thermodynamic force, all

fluxes can be expanded near thermodynamic equilibrium in terms of forces following Onsager theory [45,46]. This procedure yields constitutive laws such as Eq. (27), where η_s , η_b , and ξ represent phenomenological Onsager coefficients [18,43,47]. Given the most commonly made choice of treating $\Delta\mu$ as thermodynamic force [53], as done in Eq. (27), the constitutive law for the thermodynamic flux r_p reads

$$r_p = \Lambda \Delta\mu - \xi \operatorname{div}(\mathbf{v}). \quad (33)$$

Onsager reciprocity relations require the cross-coupling with coefficient $-\xi$: Because flux $\mathbf{T}_d$ and force $\Delta\mu$ have the same time-reversal symmetry—the same is necessarily true for their cross-coupled conjugate partners $\operatorname{div}(\mathbf{v})$ and r_p —the coupling ξ is a reactive coefficient that must appear with opposite signs in the constitutive laws [Eqs. (27) and (33)] [47]. In the following, we will denote the entropy production [Eq. (32)] expressed in terms of constitutive laws [Eqs. (27) and (33)] as functional $\Theta_{\text{int}}(\mathbf{v}, \Delta\mu)$. Dissipative external forces, such as the effective friction introduced in Eq. (22), will additionally contribute to the entropy production with

$$\Theta_{\text{ext}} = - \int dA \mathbf{v} \cdot \mathbf{f}^{\text{ext}}. \quad (34)$$

D. Flux-force choice and dissipation functional

Unfortunately, variations of the “naive” entropy production [Eq. (32)] cannot recover the constitutive law [Eq. (27)]: Reactive couplings, such as the Onsager coefficient ξ in Eqs. (27) and (33), do by construction not contribute to the entropy production. This can easily be verified by plugging Eqs. (27) and (33) into the entropy production $\Theta_{\text{int}}(\mathbf{v}, \Delta\mu)$ given in Eq. (32). We therefore adapt our strategy and try to formulate an equivalent set of constitutive laws exclusively in terms of dissipative Onsager coefficients. Here, this can be realized by choosing—instead of $\Delta\mu$ —the chemical production rate r_p as the thermodynamic force. We write the resulting constitutive laws as

$$\hat{\mathbf{T}}_d = 2\eta_s \hat{\mathbf{S}} + \left(\eta_b + \frac{\xi^2}{\Lambda} \right) \operatorname{div}(\mathbf{v}) \mathbf{G} + \frac{\xi}{\Lambda} r_p \mathbf{G}, \quad (35)$$

$$\Delta\hat{\mu} = \frac{1}{\Lambda} r_p + \frac{\xi}{\Lambda} \operatorname{div}(\mathbf{v}), \quad (36)$$

where we have parametrized Onsager coefficients that would appear such that Eqs. (35) and (36) are equivalent to the desired constitutive laws [Eq. (27) and (33)], i.e., $\hat{\mathbf{T}}_d = \mathbf{T}_d$ and $\Delta\hat{\mu} = \Delta\mu$. We denote the entropy production associated with constitutive laws [Eqs. (35) and (36)] as functional

$$\hat{\Theta}_{\text{int}}(\mathbf{v}, r_p) = \int dA (\hat{\mathbf{T}}_d : \mathbf{S} + r_p \Delta\hat{\mu}). \quad (37)$$

Note that, consistent with Onsager reciprocity relations, the Onsager coefficient ξ/Λ now appears as a dissipative term with the same sign in both constitutive laws [Eqs. (35) and (36)] and cross-couples flux-force pairs with opposite time-reversal signature. Consequently, it will contribute to the entropy production $\hat{\Theta}_{\text{int}}(\mathbf{v}, r_p)$. One can directly verify that if coefficients η , η_b , and ξ in are such that the second law is respected in the original entropy production, i.e., $\Theta_{\text{int}}(\mathbf{v}, \Delta\mu) \geq 0$, then it will also be respected by $\hat{\Theta}_{\text{int}}(\mathbf{v}, r_p)$ in Eq. (37).

It has been pointed out that the designation of thermodynamic fluxes and forces is essentially arbitrary [44,55], and the physics described by the resulting constitutive laws will be equivalent in the thermodynamic limit for every choice. It is therefore not surprising that the transformation of the constitutive laws into Eqs. (35) and (36), based on a modified flux-force pair choice, exists. The fact that associated entropy productions take different forms for different flux-force choices and only some choices yield a suitable dissipation functional does also not contradict any physical principle: In contrast to a principle such as energy minimization, the minimization of dissipation invoked by Rayleigh functionals is not a first physical principle and the existence of a suitable functional for any set of constitutive laws describing an out-of-equilibrium system is not guaranteed [44]. However, for constitutive laws that are linear in thermodynamic forces, Onsager relations guarantee an invertible coefficient matrix and thus ensure the existence of equivalent constitutive laws in terms of exclusively dissipative phenomenological coefficients.

The total dissipation rate used in this work is given by

$$\mathcal{D}(\mathbf{v}, r_p) = \frac{1}{2} (\hat{\Theta}_{\text{int}} + \Theta_{\text{ext}}), \quad (38)$$

where $\hat{\Theta}_{\text{int}}(\mathbf{v}, r_p)$ denotes the entropy production given in Eq. (37) with $\hat{\mathbf{T}}_d$ and $\Delta\hat{\mu}$ given in Eqs. (35) and (36), respectively, as well as Θ_{ext} given in Eq. (34). Together with contributions from the free energy in Eq. (31), we arrive at the final Rayleigh dissipation functional

$$\mathcal{R}(\mathbf{v}, r_p) = \frac{dF}{dt} + \mathcal{D}. \quad (39)$$

We show in Appendix V of the Supplemental Material [52] that variational equations (30) derived from $\mathcal{R}(\mathbf{v}, r_p)$ correspond exactly to force and torque balance equations (20) and (21) with tension and moments given by Eqs. (28) and (29). Variation $\delta\mathcal{R}/\delta r_p = 0$ yields the remaining constitutive law [Eq. (33)]; see Appendix V D of the Supplemental Material [52].

E. Enforcing geometric relations and SLE parametrization via Lagrange multipliers

The Rayleigh functional $\mathcal{R}(\mathbf{v}, r_p)$ [Eq. (39)] can now be supplemented by suitable Lagrange multipliers that dynamically impose nonlinear geometric relations and the SLE parametrization introduced above (Sec. II D). This will provide us with an approach to directly solve for stationary surface geometries and flows, and to compute the shape dynamic [Eq. (1)] in an implicit fashion. To discuss this in detail, we express Eq. (39) on an axisymmetric surface:

$$\mathcal{R}(\mathbf{v}, r_p) = 2\pi \int_0^1 du R(\mathbf{v}, r_p) + 2\pi (f_\kappa q^u r h)|_0^1, \quad (40)$$

where the explicit form of $R(\mathbf{v}, r_p)$ reads

$$R(\mathbf{v}, r_p) = \left[\partial_t f_\kappa + f_\kappa \frac{\partial_t(rh)}{rh} - r_p \Delta\mu + J_n^{\text{ext}} - \mathbf{f}^{\text{ext}} \cdot \mathbf{v} \right] rh + \left[\gamma \operatorname{div}(\mathbf{v}) + \frac{1}{2} (S_1 + S_2 + S_3) + \frac{1}{2} \Gamma \mathbf{v}_\parallel^2 \right] rh. \quad (41)$$

All terms in the first line of Eq. (41), as well as $\gamma \text{div}(\mathbf{v})$ with the effective membrane tension $\gamma = \gamma_H + \gamma_e$, are part of the free-energy change rate dF/dt [see Eq. (31)]. The Helfrich free-energy density f_κ reads for an arc length parametrization:

$$f_\kappa = \frac{\kappa}{2} \left(\frac{\sin \psi}{r} + \frac{\psi'}{h} - C_0 \right)^2. \quad (42)$$

Its time derivative has to be expanded as

$$\partial_t f_\kappa = \frac{\partial f_\kappa}{\partial r} \partial_t r + \frac{\partial f_\kappa}{\partial \psi} \partial_t \psi + \frac{\partial f_\kappa}{\partial \psi'} \partial_t \psi' + \frac{\partial f_\kappa}{\partial h} \partial_t h + \frac{\partial f_\kappa}{\partial C_0} \partial_t C_0. \quad (43)$$

The dissipative terms

$$S_1 = \eta_b (\bar{S}_{uu} + \bar{S}_{\phi\phi})^2, \quad (44)$$

$$S_2 = \eta_s [(\bar{S}_{uu} - \bar{S}_{\phi\phi})^2 + (2\bar{S}_{u\phi})^2], \quad (45)$$

$$S_3 = \frac{1}{\Lambda} [r_p + \xi (\bar{S}_{uu} + \bar{S}_{\phi\phi})]^2, \quad (46)$$

contribute with density $\hat{\Theta}_{\text{int}} = S_1 + S_2 + S_3$ to the internal entropy production rate $\hat{\Theta}_{\text{int}}$ given in Eq. (37). Explicit expressions for the strain rate tensor components $\bar{S}_{uu}$, $\bar{S}_{u\phi}$, $\bar{S}_{\phi\phi}$ are given in Appendix V of the Supplemental Material [52]. In addition to the dissipative contribution of friction $\sim \Gamma$ in Eq. (41), we have for generality also included velocity-independent external forces (denoted also by $\mathbf{f}^{\text{ext}}$ for simplicity).

Equation (40) represents a functional of a number of functions $R[v'', v^\phi, v_n, \partial_t r, \partial_t h, \partial_t \psi, q'', r_p]$. For Eulerian or Lagrangian parametrizations, $\partial_t r$, $\partial_t h$, and $\partial_t \psi$ can be expressed in terms of flow velocities (see Appendix V A of the Supplemental Material [52]), and the coordinate flow q'' becomes fixed, such that the functional is reduced to $R[v'', v^\phi, v_n, r_p]$. While variations with respect to velocity components do recover force and moment balance equations (see Appendix V C 1 of the Supplemental Material [52]), it disconnects from the shape dynamics in the embedding space and excludes explicit control over the mapping $h(u, t)$ between fixed mesh coordinates u and physical space [see Eq. (17)]. However, imposing the SLE parametrization by directly fixing the coordinate flow q'' to Eq. (18) leads to impractical integro-differential equations when performing the variation and is therefore also not feasible. To sidestep an explicit specification of the coordinate flow q'' entirely, while still imposing an SLE parametrization, we proceed as follows. From the shape dynamics of an axisymmetric surface [Eqs. (14) and (15)], we find

$$v_n = \sin \psi \partial_t r + \cos \psi \partial_t z, \quad (47)$$

$$q'' = v'' + h^{-1} (\sin \psi \partial_t z - \cos \psi \partial_t r). \quad (48)$$

Using those identities to eliminate v_n and q'' from the Rayleigh functional (40) leads to remaining dependencies $R[v'', v^\phi, \partial_t r, \partial_t z, \partial_t h, \partial_t \psi, r_p]$.

Importantly, this substitution expresses two velocities, v_n and q'' , in terms of three other velocities $\partial_t r$, $\partial_t z$ and v'' . The relationship between v_n , $\partial_t r$, $\partial_t z$, and v'' becomes only unique once the coordinate flow q'' has been specified by a suitable constraint. This constraint is naturally given by $h' = 0$, which

TABLE II. List of fields with respect to which the dissipation functional $\bar{\mathcal{R}} = \mathcal{R} + \mathcal{L}$, with $\mathcal{R}$ and $\mathcal{L}$ given in Eqs. (40) and (49), is varied and the differential equations implied by the corresponding variations. For an open incompressible surface variation with respect to the tension $\gamma_H(u)$ implies an additional ODE, which is not present in the compressible surface (n.a.). The explicit ODE equations resulting from these variations are given in Appendix V of the Supplemental Material [52].

Variation	Implied ODE
$\partial_t r$	$\alpha' = \dots$
$\partial_t z$	$\beta' = \dots$
$\partial_t \psi$	$\psi'' = \dots$
$\partial_t h$	$\zeta' = \dots$
$\partial_t \alpha$	$r' = \dots$
$\partial_t \beta$	$z' = \dots$
$\partial_t \zeta$	$h' = 0$
v''	$\gamma_H' = \dots / (v'')'' = \dots$
v^ϕ	$(v^\phi)'' = \dots$
γ_H	$(v'')' = \dots / \text{n.a.}$

we know leads to the SLE coordinate flow derived in Eq. (18). However, the coordinate map h depends itself on r, z, ψ via the nonlinear geometric identities [Eqs. (12) and (13)] and can therefore not be treated as an independent variable we would be allowed to constrain. To resolve this, we generalize an idea from work on passive membranes [30] and introduce Lagrange multipliers instead to impose the geometric identities [Eqs. (12) and (13)]. The full set of constraint terms is given by

$$\mathcal{L} = 2\pi \int_0^1 du \partial_t [\zeta h' + \alpha(r' - h \cos \psi) + \beta(z' + h \sin \psi)], \quad (49)$$

where α, β , and ζ represent Lagrange multipliers that dynamically enforce geometric relations [Eqs. (12) and (13)] and implicitly impose the SLE parametrization [Eq. (18)]. The final constrained Rayleigh dissipation functional is then given by

$$\bar{\mathcal{R}} = \mathcal{R} + \mathcal{L}, \quad (50)$$

with $\mathcal{R}$ and $\mathcal{L}$ given in Eqs. (40) and (49), respectively. This functional is varied with respect to the independent fields $\Phi \in \{v'', v^\phi, \partial_t r, \partial_t z, \partial_t h, \partial_t \psi, \partial_t \alpha, \partial_t \beta, \partial_t \zeta\}$ to determine equations of motion. The structure of the resulting system of ordinary differential equations (ODEs) obtained from

$$\frac{\delta \bar{\mathcal{R}}}{\delta \Phi} = 0 \quad (51)$$

is indicated in Table II. Their explicit form is derived in Appendix V C 2 of the Supplemental Material [52], where we also show that the resulting ODE system is again equivalent to the force balance equations of the active fluid surface. The bare ODE system yields for both incompressible and compressible fluid surfaces 12 first-order equations. It must therefore be complemented by 12 boundary conditions, which are listed in Table III and can be derived from the boundary terms of the functional variation [Eq. (51)]; see Appendix VI

TABLE III. Boundary conditions for open and closed surfaces, which follow from the boundary terms of $\delta\mathcal{R} = 0$ (see Appendix VI of the Supplemental Material [52]). The explicit ODE equations resulting from these variations are also given in Appendix V of the Supplemental Material [52].

Variation	Boundary conditions	
	Open surface	Closed surface
$\partial_t r$	$r(0) = 0, r(1) = R_b$	$r(0) = 0, r(1) = 0$
$\partial_t z$	$\beta(0) = 0, z(1) = 0$	$\beta(0) = 0, \beta(1) = 0$
$\partial_t \psi$	$\psi(0) = 0, \psi(1) = 0$	$\psi(0) = 0, \psi(1) = \pi$
$\partial_t h$	$\zeta(0) = 0, \zeta(1) = 0$	
v^u	$v^u(0) = 0, \gamma_H(1) = \gamma_0$	$v^u(0) = 0, v^u(1) = 0$
v^ϕ	$v^\phi(0) = 0, v^\phi(1) = 0$	

of the Supplemental Material [52]. In cases where closed surfaces with a conserved enclosed volume V_0 are considered (see Secs. VB 1 and VB 2), this ODE system is complemented by an equation $V'(u) = \pi r^2 h \sin \psi$, which is by construction satisfied by the cumulative volume $V(u)$ [30]. The boundary condition $V(1) = V_0$ imposes the volume constraint. A second boundary condition, $V(0) = 0$, fixes a degree of freedom that can directly be included as an external normal force $f_n^{\text{ext}} = p$ and corresponds to the pressure difference p between the enclosed volume and the surrounding.

F. Implicit dynamics and direct computation of stationary states

Having obtained a formulation that simultaneously evolves surface coordinates in the embedding space (r, z) and in-plane geometric properties (ψ, h) enables us now to conveniently—and robustly—perform dynamic simulations of deforming fluid surfaces, as well as to directly compute stationary surface geometries and flows.

1. Implicit time-stepping method for the surface dynamics

For the ODEs listed in Table II, the right-hand side contains the time derivatives $\partial_t r, \partial_t z, \partial_t \psi$, which enter all equations by construction linearly. We can therefore design a fully implicit time integration scheme to evolve the surface shape by replacing

$$\begin{aligned}\partial_t r &= \frac{r(u, t) - r(u, t - \Delta t)}{\Delta t}, \\ \partial_t z &= \frac{z(u, t) - z(u, t - \Delta t)}{\Delta t}, \\ \partial_t \psi &= \frac{\psi(u, t) - \psi(u, t - \Delta t)}{\Delta t},\end{aligned}\quad (52)$$

and using $r(u, t - \Delta t), z(u, t - \Delta t), \psi(u, t - \Delta t)$ from the previous time step. Solutions $[r(u, t), z(u, t), \psi(u, t), v_u, v_\phi]$ of the ODE system derived from the variational formulation then directly correspond to surface geometries and flows at the next time point. Throughout this work, we use $\Delta t = 4 \times 10^{-4} \tau_\eta$ and $\Delta t = 10^{-3} \tau_\eta$ for simulations of open (see Table IV) and closed surfaces (see Table V), respectively. We provide a MATLAB implementation [50] to perform these iterative computations using standard boundary value solver [56].

TABLE IV. Parameters used in open membrane examples shown in Figs. 2 and 3; the characteristic time is defined as $\tau_\eta = \eta_s R_b^2 / \kappa$.

Parameter	Value	Unit
κ	Bending rigidity	1
η_s	Shear viscosity	1
R_b	Base radius	1
τ_η	Timescale	$\eta_s R_b^2 / \kappa$
Γ	Friction	0.25
γ_0	Boundary tension	12.5
A_p	Area of coating	2/25
σ_p	Coating profile sharpness	25
A_f	Area of external force	2/250
σ_f	Force profile sharpness	250

2. Direct computation of stationary geometries and flows

While dynamic simulations are useful to explore the parameter dependence of a given model, they are not practical to systematically characterize the space of nontrivial stationary surface geometries and flows or the bifurcation structure of this space. With the formulation derived above, we can directly compute these features by setting instead

$$\begin{aligned}\partial_t r &= 0, \\ \partial_t z &= v_0, \\ \partial_t \psi &= 0,\end{aligned}\quad (53)$$

where v_0 is an additional parameter that represents a possible translational velocity of the surface along the symmetry axis. For open surfaces that are fixed at the base by boundary condition $z(1) = 0$, we have $v_0 = 0$ (see Table III). For closed surfaces with asymmetric surface flows and in the presence of friction, v_0 is an unknown parameter determined as part of the boundary value problem. In the latter case, the boundary condition $z(0) + z(1) = 0$ is added to fix a reference frame

TABLE V. Parameters used in closed active fluid surface examples shown in Figs. 4–7 (parameters k and c_s are only used in Figs. 6 and 7). The characteristic time in these simulations is defined as $\tau_\eta = \eta_b R_0^2 / \kappa$. Characteristic length scale R_0 is related to the enclosed conserved volume by $V = 4\pi R_0^3 / 3$.

Parameter	Value	Unit
κ	Bending rigidity	1
η_b	Bulk viscosity	1
η_s	Shear viscosity	1
R_0	Spherical radius	1
τ_η	Timescale	$\eta_b R_0^2 / \kappa$
$(\xi \Delta \mu)_0$	Active contractility	450
Γ	Friction	0.09
$\gamma = \gamma_H + \gamma_e$	Passive tension	9
D	Diffusion constant	1
k	Turnover rate	45
c_0	Steady state concentration	1
c_s	Saturation concentration	10
w	Preferred concentration profile width	0.02

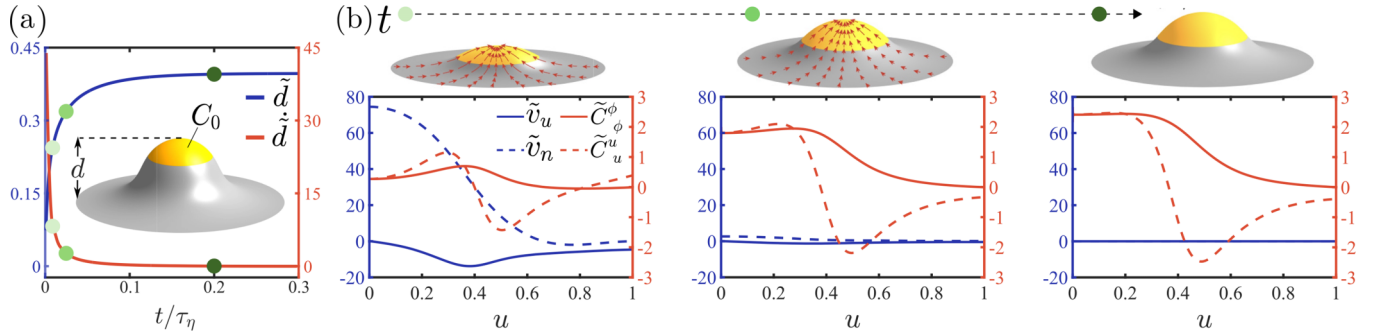


FIG. 2. Dynamics of an open membrane with local spontaneous curvature coating [yellow patches; see Eq. (55)]. (a) Starting from a flat disk geometry, the membrane height $\tilde{d} = d/R_b$ (blue curve) grows in time t due to the coating ($\tau_\eta = \eta_s R_b^2/\kappa$, R_b is the fixed base radius). Red curve depicts growth speed. (b) Snapshots of evolving geometry with tangential components of local center-of-mass flow velocities indicated by red arrows (top row; Movie S1 of the Supplemental Material [52]). Bottom row shows flow velocity and curvature tensor components: tangential velocity $\tilde{v}_u = \tilde{v}_u \tau_\eta/R_b$, normal velocity $\tilde{v}_n = v_n \tau_\eta/R_b$, azimuthal curvature $\tilde{C}_\phi = C_\phi^\phi R_b$, and meridional curvature $\tilde{C}_u = C_u^u R_b$. Last time point shows final stationary geometry ($v_n = 0$). Spontaneous curvature $\tilde{C}_0 = \tilde{C}_0 R_b$ is set to $\tilde{C}_0 = 9$. All other parameters are listed in Table IV.

that is comoving with the surface [19]. We test the stability of stationary solution by applying a small perturbation and using the resulting geometry as initial condition in dynamic simulations (Fig. S2 of the Supplemental Material [52]). We note that the direct computation of stationary solutions, even those that may still exhibit tangential flows, is only made possible by using the SLE parametrization.

V. SURFACE DYNAMICS AND SHAPE SPACES

A. Formation of membrane protrusion via internal and external forces

To illustrate the flexibility of our method and its capacity to characterize emergent shape spaces, we first study deformations of an open circular patch of membrane in response to internal and external forces, and neglect contributions from the chemical free energy [consequently $\xi \Delta\mu = 0$ in Eq. (27)]. In all cases, we consider an incompressible membrane for which the isotropic tension γ_H in the Helfrich free energy [Eq. (23)] becomes a Lagrange multiplier that has to be dynamically solved for (see Table II). The free-energy dynamics [Eq. (31)] simplifies on the axisymmetric semiopen surface [Fig. 1(a)] to

$$\frac{dF}{dt} = 2\pi \int_0^1 du [\partial_t(rh f_\kappa) + rh \gamma_H \text{div}(\mathbf{v})] + 2\pi f_H q^u hr|_{u=1}, \quad (54)$$

where $\text{div}(\mathbf{v})$ and the Helfrich density f_κ on axisymmetric surfaces are given in Eq. (S13) of the Supplemental Material [52] and Eq. (42), respectively.

1. Local spontaneous curvature

We first assign a finite spontaneous curvature “coating” to a subregion of the membrane [Fig. 2(a), inset], as can be induced by, for example, protein patches on lipid membranes that play a role in clathrin-mediated endocytosis [37,38,57]. We assume this coating occupies the same material points at

all times. Starting from an initial profile [58]

$$C_0(u) = \frac{\tilde{C}_0}{2} (1 - \tanh[\sigma_p[A(u) - A_p]]), \quad (55)$$

where $A(u) = 2\pi \int_0^u du' r h$ denotes the cumulative surface area up to mesh coordinate u , the coating must therefore satisfy $\frac{dC_0}{dt} = 0$ or, explicitly,

$$\partial_t C_0 = -q^u \partial_u C_0, \quad (56)$$

where q^u is the SLE coordinate flow given in Eq. (48).

Starting from a flat geometry, surfaces with such a coating gradually bend and form protruding geometries (Fig. 2) as a result of the spontaneous curvature coating. At first, the normal velocity v_n has its maxima at the center $u = 0$ and decays toward the base $u = 1$. Gradients of spontaneous curvature generate inhomogeneous in-plane tension (see Appendix IV of the Supplemental Material [52]), which leads to in-plane flows v_u that accompany the protrusion process [red arrows in Fig. 2(b)]. Growth eventually saturates, leading to a nontrivial stationary membrane geometry and vanishing center-of-mass flows [Fig. 2(b), right].

We now characterize the space of emergent stationary geometries as a function of the local spontaneous curvature $\tilde{C}_0 = \tilde{C}_0 R_b$ systematically. The corresponding trajectories of stationary geometries are obtained by direct computation as described in Sec. IV F 2. This analysis reveals a nonmonotonic, nonbijective behavior, known as Gibbs loop, of the stationary membrane height d as a function of $\tilde{C}_0$ [Fig. 3(a)]. Consequently, for an intermediate range of local spontaneous curvature, three distinct stationary geometries are associated with a given spontaneous curvature imposed by the coating. Subsequent stability testing identifies two stable and one unstable region of the solution branch [solid and dashed lines, respectively, in Fig. 3(a)] in the degenerate parameter region. Such a degeneracy of membrane shapes was previously discussed in the context of a snap-through instability [37]. The trajectory of stationary surfaces terminates in a limiting geometry [dark blue circle in Fig. 3(a)] associated with a budding transition. Fixing $\tilde{C}_0 = 9$ [black vertical dashed line in Fig. 3(a)] and considering different geometries as initial

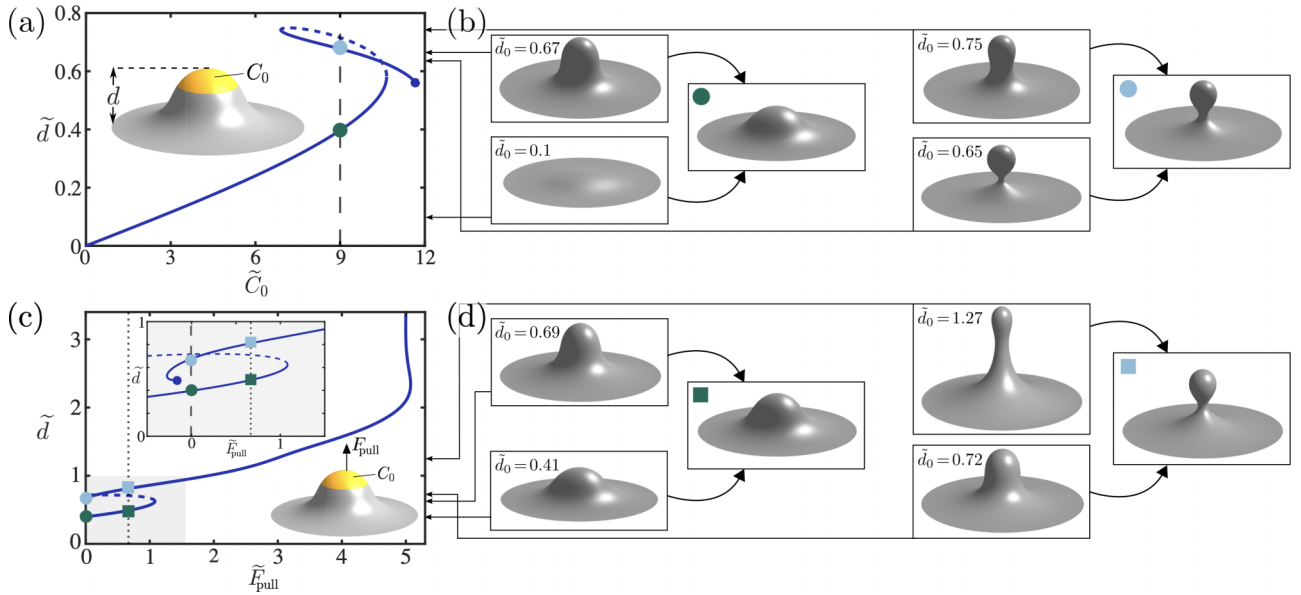


FIG. 3. Nonlinear shape space analysis of open membranes. (a) Height $\tilde{d} = d/R_b$ of stationary surfaces as a function of spontaneous curvature $\tilde{C}_0 = \hat{C}_0 R_b$ in a finite-sized patch (yellow). Solutions obtained by direct computation of stationary geometries (Sec. IV F 2) reveal a first-order transition due to a Gibbs loop with stable (solid blue line) and unstable (dashed blue line) branch regions. Solution branch terminates in limiting shape associated with a budding transition (dark blue circle). (b) Depending on initial height $\tilde{d}_0$ and geometry, membranes relax for fixed spontaneous curvature ($\tilde{C}_0 = 9$) to stationary shapes without (green circle) and with neck (blue circle). (c) Stationary shape trajectory with $\tilde{C}_0 = 9$ under additional application of external pulling forces $\tilde{F}_{\text{pull}} = F_{\text{pull}} R_b / \kappa$ [see Eq. (57)]. Inset shows close-up of gray region extended to $\tilde{F}_{\text{pull}} < 0$. The budding transition for this spontaneous curvature occurs when the membrane is pushed ($\tilde{F}_{\text{pull}} < 0$). Branch regions without and with necks become fully disconnected in the $(\tilde{F}_{\text{pull}}, \tilde{d})$ -space (inset), leading to a distinct first-order transition near $\tilde{F}_{\text{pull}} \approx 1$. Pulling forces saturate following an additional first-order transition near $\tilde{F}_{\text{pull}} \approx 5$, consistent with Ref. [35]. (d) Representative examples of shape relaxations at fixed pulling force ($\tilde{F}_{\text{pull}} = 0.7$) for different initial geometries (Movie S2 of the Supplemental Material [52]). All other parameters are listed in Table IV.

conditions, the convergence to stationary surface geometries on the stable branch is illustrated in Fig. 3(b). Stationary solutions indicate the separated stable regions correspond to protrusions with (without) a neck, defined as surfaces with (without) a region of negative Gaussian curvature [green and blue circles in Figs. 3(a) and 3(b)]. The first-order transition indicated by the Gibbs loop in the $(\tilde{C}_0, \tilde{d})$ -space is therefore a transition between these two basic protrusion geometries, consistent with previous observations [37,57]. An additional signature of this discontinuous transition is an effective shape hysteresis [see Fig. 3(b)]: A further protruded surface ($\tilde{d}_0 = 0.67$) without neck may still relax to a flatter final state (green dot), while a slightly less protruded initial surface ($\tilde{d}_0 = 0.65$) can relax to a further extended geometry (blue dot) if an initial neck is present.

2. Pulling forces

We next study membrane deformations under an external force density $\mathbf{f}^{\text{ext}} = f_z^{\text{ext}} \mathbf{e}_z$, while maintaining the spontaneous curvature coating. The external force density amounts to a total applied pulling force $F_{\text{pull}} = \int dA f_z^{\text{ext}}$. The pulling force density is parametrized by

$$f_z^{\text{ext}}(u) = \frac{f_0}{2} (1 - \tanh\{\sigma_f [A(u) - A_f]\}). \quad (57)$$

In Eq. (57), f_0 is the magnitude of the applied force density, A_f denotes the approximate total area of the region to which

it is applied, and σ_f is the inverse width of the transition between forced and unforced membrane regions. The impact of turgor pressure on such a configuration has previously been described [57]. Here, we are interested in the interplay of pulling forces and spontaneous curvature coating. Pulling forces in the absence of a spontaneous curvature coating give rise to a first-order transition after which membrane protrusions become tubular and keep growing at constant force [35]. This phenomenology is recovered in Fig. 3(c) at $\tilde{F}_{\text{pull}} \approx 5$, in quantitative agreement with results for singular point pulling forces obtained in Ref. [35], where a characteristic force $\hat{f}_0 = 2\pi\sqrt{\gamma_0\kappa}$ was used, while the characteristic force in our case is $\kappa/R_b \approx \hat{f}_0/5$ for the parameters used (see Table IV). However, we now find an additional first-order transition at smaller pulling forces ($\tilde{F}_{\text{pull}} \approx 1$) when the spontaneous curvature coating is present. Closer inspection [inset in Fig. 3(c)] reveals that solution branches without and with necks are now fully disconnected in the $(\tilde{F}_{\text{pull}}, \tilde{d})$ -space, while they form loops in the $(\tilde{C}_0, \tilde{d})$ -space when $\tilde{F}_{\text{pull}} = 0$ [see Fig. 3(a)] signifying another spontaneous curvature-associated, but physically distinct, first-order transition. We further find that the budding transition can occur for compressive forces [$\tilde{F}_{\text{pull}} < 0$; see inset Fig. 3(c), dark blue circle] when a spontaneous curvature coating is present. Exemplary transitions under fixed pulling force [$\tilde{F}_{\text{pull}} = 0.7$, black vertical dashed line in Fig. 3(c)] between different initial conditions and corresponding stationary states are shown in Fig. 3(d), which confirms the disconnected

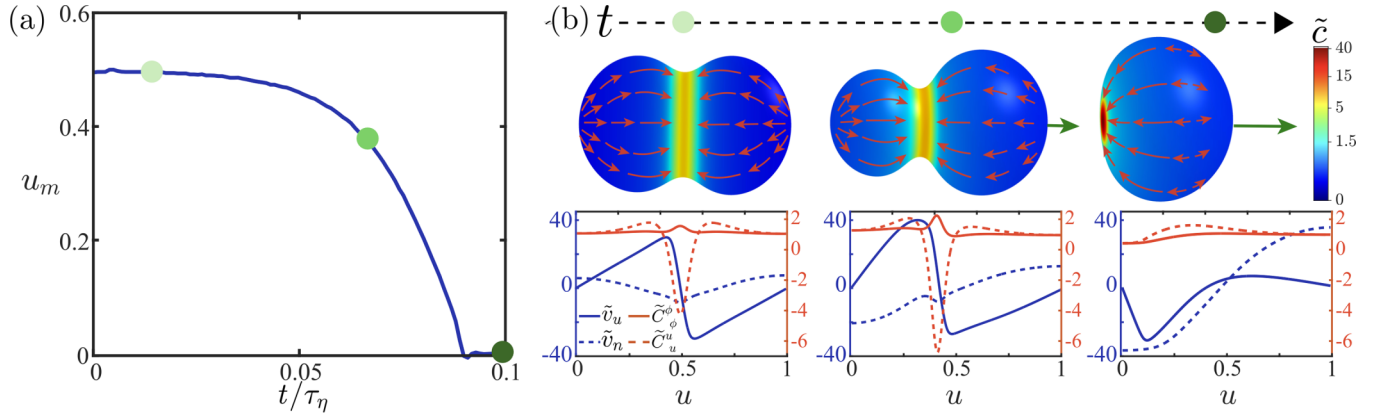


FIG. 4. Self-organization dynamics, contractile ring slipping, and propagation of a closed active isotropic fluid surface. (a) Mesh coordinate u_m of maximal stress-regulator concentration over time ($\tau_\eta = \eta_b R_0^2 / \kappa$) when initiating a centered contractile ring profile $c(u)_{t=0} = c_0[0.2 + 2 \exp(-(u - 1/2)^2/w^2)]$. The contractile ring remains initially centered but eventually slips to the pole ($u = 0$). (b) Snapshots of surface shapes with surface flow velocities indicated by red arrows; color code indicates stress regulator concentration $\tilde{c} = c/c_0$. Last snapshot shows final surface geometry. Velocity ($\tilde{v}_u = \tilde{v}_u \tau_\eta / R_0$, $\tilde{v}_n = \tilde{v}_n \tau_\eta / R_0$) and curvature ($\tilde{C}_\phi^\phi = C_\phi^\phi R_0$, $\tilde{C}_u^u = C_u^u R_0$) component profiles at corresponding time points are shown in the bottom row. Polar symmetry breaking leads to directed surface flows as previously found [19,20]. Here, due to friction with the surrounding [see Eq. (22)], these flows lead to a translation of the final stationary shape. Green arrows indicate relative swimmer speed. Surface flow velocity arrows and velocity components are shown in the laboratory frame. As a result, $v_n \neq 0$ in the last snapshot, even though the surface geometry is stationary. Parameters are listed in Table V.

solution branches in the $(\tilde{c}_0, \tilde{d})$ -space indeed correspond to stationary surfaces without and with neck [green and blue squares in Figs. 3(c) and 3(d)], as suggested by their association with the corresponding branches of the Gibbs loop when $\tilde{F}_{\text{pull}} = 0$ [circles in Figs. 3(a) and 3(c)].

B. Spontaneous polarization, propagation, and guided division of closed active fluid surfaces

We now include chemically regulated active stresses $\sim \xi \Delta \mu$ as introduced in the tension tensor [Eq. (27)] and investigate self-organized deformations and emergent shape spaces of closed active fluid surface. Following previous work [19,20,59,60], we consider a concentration field c that represents force-generating molecules and satisfies the continuity equation [Eq. (6)]. Specifically, we use a diffusive flux $j_i = -D \partial_i c$ with diffusion constant D and a normal flux $J_n = -k(c - \hat{c}_0)$ describing the exchange of molecules with the surrounding at a rate k to maintain a reference concentration $\hat{c}_0$ on the surface. The dynamics of stress regulators reads

$$\frac{dc}{dt} + \text{div}(\mathbf{v})c = D\Delta c - k(c - \hat{c}_0), \quad (58)$$

where $\frac{dc}{dt} = \partial_t c + q^i \partial_i c$, Δ is the Laplace-Beltrami operator on the curved surface, and an expression for $\text{div}(\mathbf{v})$ is provided in Eq. (S13) of the Supplemental Material [52]. We will explore a general scenario in which the reference concentration $\hat{c}_0$ profile can correspond to a centered contractile ring, i.e.,

$$\hat{c}_0(u) = c_0 \left[1 + \Delta_c \exp\left(-\frac{(u - \frac{1}{2})^2}{w^2}\right) \right]. \quad (59)$$

The cases $\Delta_c = 0$ and $\Delta_c > 0$ will be discussed in Secs. VB 1 and VB 2, respectively. In the context of a cell cortex, an externally imposed profile of the form of Eq. (59) can

result from biochemical signaling originating from the spindle [61,62]. We assume that the active isotropic stress depends on the regulator concentration according to Ref. [19]:

$$\xi \Delta \mu(c) = (\xi \Delta \mu)_0 \frac{c^2}{c^2 + c_s^2}, \quad (60)$$

where c_s denotes the saturation density.

1. Spontaneous polarization and propagation

We first discuss the case $\Delta_c = 0$ in Eq. (59) for which the reference concentration $\hat{c}_0 = c_0$ in Eq. (58) is constant. Using this model, it has been shown in the absence of friction that a spherical surface with uniform distribution of stress regulator undergoes a mechanochemical shape instability above a critical active stress [19]. As a result of this instability, chemical patterns and surface geometry break symmetry along the z axis, eventually reaching a steady state that is polarized. This polarization dynamics still occurs in the presence of friction, and even if alternative patterns are imposed initially, as we demonstrate in Fig. 4. There, we use a centered ($u = 1/2$) ringlike concentration pattern as initial condition and follow the position of the concentration maximum over time [Fig. 4(a)]. While such ring patterns remain initially centered, they eventually move toward one of the surface's poles ($u = 0, 1$; see Fig. 1). Surface snapshots of this process and quantitative information on curvature and flow speeds are provided in Fig. 4(b). The ring does initially lead to an ingress before it slips, consistent with geometric minimal models of cell division [16,63], and a polar concentration pattern and surface geometry remain. Due to the friction, and in the presence of a polarized surface state, surfaces will propagate in the laboratory frame. Green arrows in Fig. 4 indicate the relative magnitude of propagation speeds as ring slipping occurs, which shows a clear correlation between polarization

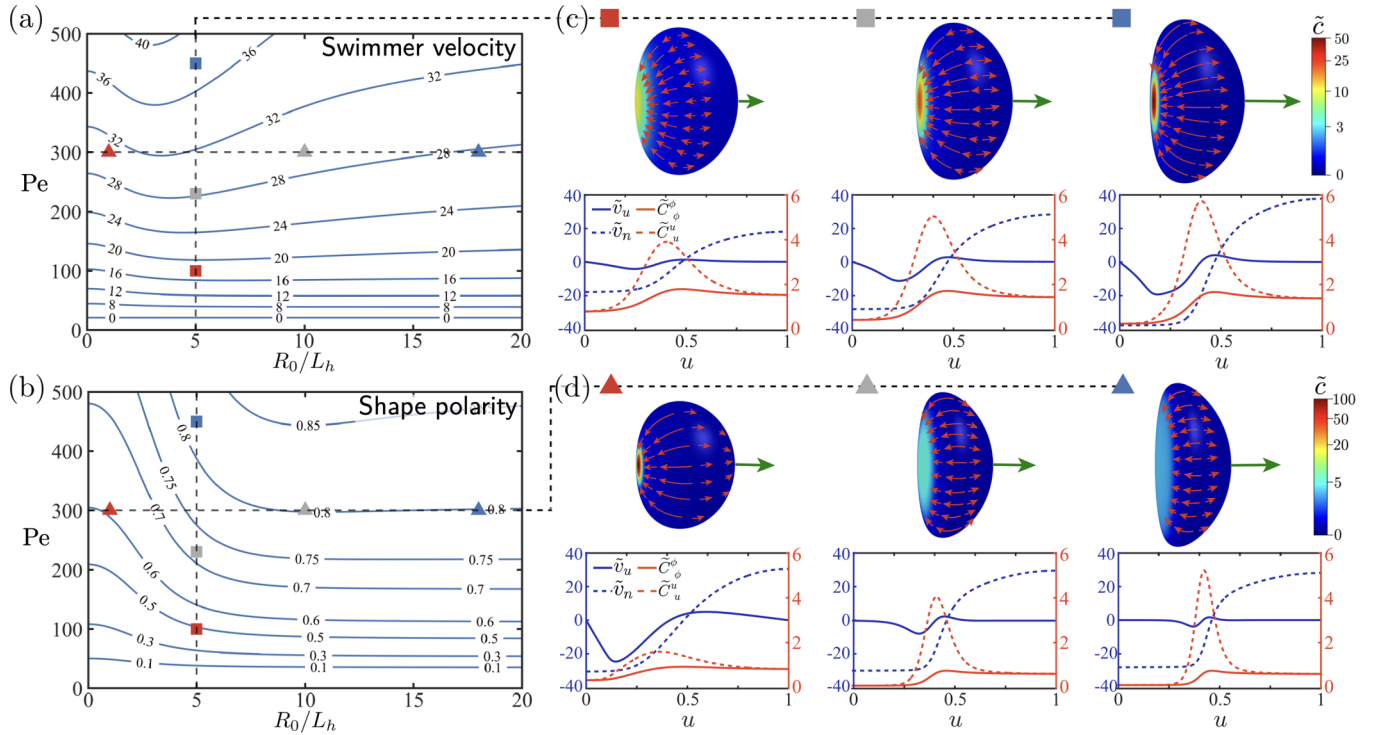


FIG. 5. Shape space characterization of polarized stationary surfaces. (a) Contour plot of swimmer velocity as a function of Péclet number $Pe = (\xi \Delta \mu)_0 R_0^2 / (D \eta_b)$ and inverse relative hydrodynamic length R_0/L_h ($L_h = \sqrt{\eta_b/\Gamma}$). Contours were obtained by direct computation of nonlinear stationary surface solutions using the approach described in Sec. IV F. (b) Surface shape polarity $P = 1 - H(0)/H(1)$ (contours), where $H(u) = C_k^k/2$ is the mean curvature in same parameter space as panel (a). (c) Exemplary stationary solutions when increasing Péclet number at fixed hydrodynamic length ($R_0/L_h = 5$): Swimming speed increases as a result of increased tangential flow velocities (Movie S3 of the Supplemental Material [52]). (d) At fixed Péclet number ($Pe = 300$), a decreasing hydrodynamic length increases the geometric shape polarity until it saturates. Panel shows exemplary stationary solutions with tangential flow velocities (red arrows), surface propagation speed (green arrows), and concentration patterns (color code). We used $k\tau_\eta = 9$ and $c_s/c_0 = 1$, all other parameters are listed in Table V.

and propagation speed. The physics of this mode of propagation is closely related to squirmer models [64,65] and droplets driven by Marangoni flows [66–68], and it can be observed when embedding active surfaces into a passive fluid [69].

We now want to exploit the capacity of our functional formulation to directly compute nonlinear stationary states in order to characterize the relationship between surface geometry, propagation velocity, and key parameters of active surface swimmers in more detail. In particular, we will focus on the interplay of the hydrodynamic length $L_h = \sqrt{\eta_b/\Gamma}$ relative to system size R_0 , and the Péclet number $Pe = \xi \Delta \mu R_0^2 / (D \eta_b)$ that characterizes the strength of active contractility [59]. To this end, we perform direct computations of stationary geometries and flows on a 500×500 grid in the $(Pe, R_0/L_h)$ space and evaluate the propagation speed [Fig. 5(a)] and a heuristic measure of geometric polarity, $P = 1 - H(u=0)/H(u=1)$, where H is the mean curvature [Fig. 5(b)]. These data provide insights into how hydrodynamic screening and activity control surface shape and propagation speed. For $Pe < Pe^*$ with $Pe^* = (2 + kR_0^2/D)/[\hat{c}_0 f'(\hat{c}_0)]$ and $f(c) = c^2/(c^2 + c_s^2)$, a spherical surface with homogeneous stress regulator pattern is linearly stable [19]. For $Pe > Pe^*$, mechanochemical shape instabilities emerge that lead to shape deformations and surface propagation. In the presence of strong hydrodynamic screening ($R_0/L_h \gg 1$), it is dominantly the Péclet number that affects shape polarity and propagation speed, which both

increase with increasing activity [Figs. 5(a) and 5(b); $Pe^* \approx 22$]. This impact of the Péclet number was expected, given that it quantifies the strength of contractility and therefore essentially the magnitude of tangential flows that move the surface forward [Fig. 5(c)]. In the regime $R_0/L_h \approx 1$, where hydrodynamic screening starts to directly affect active stress propagation across the surface, changes of the hydrodynamic length have a strong impact on the surface polarity, while still having relatively little impact on the propagation velocity. Exemplary stationary geometries, flows, and stress regulator patterns shown in Fig. 5(d) suggest an explanation for this phenomenology: Strong hydrodynamic screening for large R_0/L_h leads to stationary stress regulator patterns that put a large part of the rear surface under high tension [see, e.g., blue triangle in Fig. 5(d)]. As a result, the surface is significantly flattened on one side and shape polarity increases. The lack of change in propagation velocities when R_0/L_h is increased appears to be the result of two counteracting factors: As the area of high stress regulator concentration patch at the rear increases, contractility gradients—and therefore tangential flows—localize strongly in the equatorial region ($u \approx 1/2$). This leads to a more effective propulsion that compensates for the fact that surface flow magnitudes themselves are strongly reduced when R_0/L_h increases, such that overall surface propagation speeds remain roughly constant.

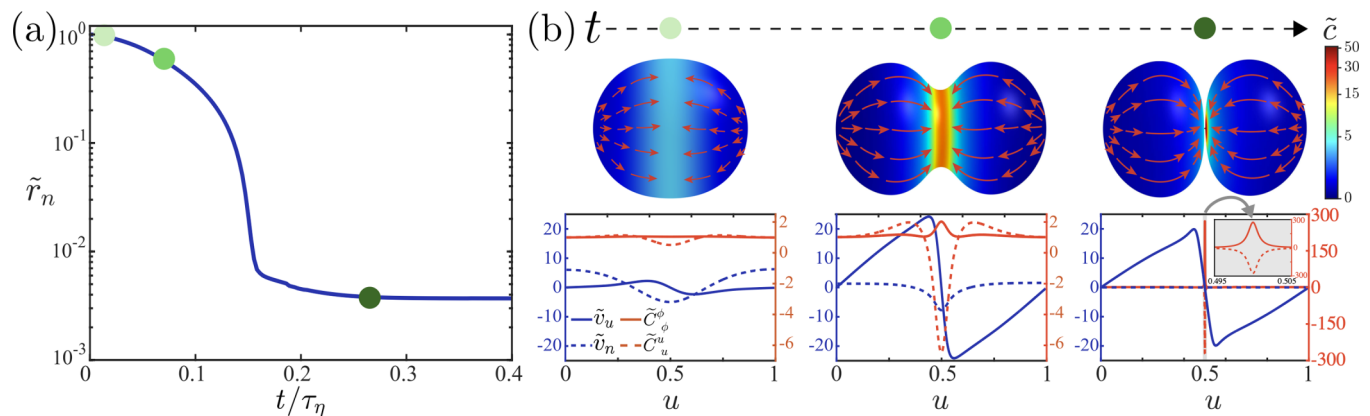


FIG. 6. Dynamics of guided furrow formation and emergence of extreme localized curvature (Movie S4 of the Supplemental Material [52]). (a) Evolution of the neck radius $\tilde{r}_n = r_n/R_0$ with $r_n := r|_{u=1/2}$ from an initially spherical surface ($\tilde{r}_n = 1$) and homogeneous concentration [$c(u)_{t=0} = c_0$], where force generator dynamics [Eq. (58)] includes an inhomogeneous pattern of preferred concentration $\hat{c}_0(u)$ [Eq. (59)]. The magnitude of the inhomogeneity is set to $\Delta_c = 4$. $\tau_\eta = \eta_b R_0^2/\kappa$. A finite neck radius remains due to bending rigidity κ . (b) Snapshots of surface shapes with surface flow velocities indicated by red arrows; color code indicates stress-regulator concentration $\tilde{c} = c/c_0$. Bottom panels show velocity ($\tilde{v}_u = \tilde{v}_u \tau_\eta/R_0$, $\tilde{v}_n = \tilde{v}_n \tau_\eta/R_0$) and curvature tensor ($\tilde{C}_\phi^u = C_\phi^u/R_0$, $\tilde{C}_u^u = C_u^u/R_0$) component profiles. An extreme localized curvature ($\Delta \tilde{C}_u^u/\Delta u \approx 5 \times 10^4$) arises in the neck region $u = 1/2$ (last time point, inset), which our approach can robustly simulate using a standard boundary value solver. All other parameters are listed in Table V.

2. Guided division

We finally characterize surface shapes that emerge when turnover of the stress regulator is spatially inhomogeneous [$\Delta_c > 0$; see Eq. (59)] with an elevated recruitment rate around the equator ($k_{\text{on}} = k\hat{c}_0$). A representative example of the shape dynamics is depicted in Fig. 6. We set $c_s = 10c_0$ in Eq. (60) to avoid saturating local active tension in regions of high stress regulator concentration, which leads to a critical Péclet number $\text{Pe}^* \approx 2.4 \times 10^3$. For the analysis, we consider $\text{Pe} < 500$, far below the mechanochemical instability threshold. Driven by the turnover profile [Eq. (59)], a contractile ring forms and persists if the turnover rate k is sufficiently large (Fig. 6). The resulting contractile tension can lead to an almost complete ingression of the surface [neck radius $r_n := r(u = 1/2)$] over time, as shown in Fig. 6(a) for $\text{Pe} = 450$. A finite-sized neck remains due to the presence of bending rigidity κ . Snapshots of the corresponding dynamics in Fig. 6(b) show surface flows toward the contractile ring as previously described in experiment and theory [8,12,20]. The final snapshot reveals a numerically well-resolved, extreme localized curvature [$|kR_0C_u^u| \approx 300$ across $\Delta u \approx 10^{-2}$; see inset Fig. 6(b)] in the neck region, highlighting the broad geometric regimes our numerical approach can robustly capture.

To gain a deeper understanding of the overall space of emerging surface geometries, we use the approach described in Sec. IV F 2 to directly compute stationary geometries and flows on dense parameter grids, and characterize emergent surface geometries and their stability (Fig. 7 and green circles indicate parameters used in Fig. 6). Fixing $\tilde{k} = 45$ and $R_0/L_h = 0.3$, a parameter sweep in the (Δ_c, Pe) -space reveals three regimes [Fig. 7(a)]: (1) For small contractility (quantified by the Péclet number Pe) or small inhomogeneity magnitude Δ_c , final stationary surfaces are ellipsoidal with positive Gaussian curvature everywhere. (2) When both contractility and inhomogeneity magnitude are sufficiently

large, dumbbell shapes with a neck (locally negative Gaussian curvature) emerge. (3) In an intermediate regime, both ellipsoidal and dumbbell-shaped stationary surfaces can be found for fixed Pe and Δ_c [gray region in Fig. 7(a)]. Numerical shape perturbations suggest all surfaces are mechanically stable in regimes (1) and (2) [blue regions in Fig. 7(a)]. Tracking the neck radii of stationary geometries [Fig. 7(b)] for different fixed Péclet numbers [arrows in Fig. 7(a)], we find indeed overhangs in the solution branch when crossing between regions of ellipsoidal and dumbbell shapes, indicating a first-order shape transition between these geometries. Specifically, two stable and one unstable solutions [solid and dashed lines in Fig. 7(b), respectively] exist in this regime for equal parameters. Exemplary surface geometries for fixed Δ_c and Pe in this degenerate regime are shown on the right of Fig. 7(b), confirming that the first-order transition occurs between surface geometries without (yellow circle) and with (blue circle) neck.

Finally, we want to challenge the stability of the symmetrically ingressed geometries found in Figs. 7(a) and 7(b) by modifying the turnover rate k . Motivated by the observation in Fig. 5, we additionally investigate whether and how hydrodynamic screening imposed by the hydrodynamic length $L_h = \sqrt{\eta_b/\Gamma}$ affects stationary surface geometries. Fixing $\text{Pe} = 450$ and $\Delta_c = 4$, a direct computation of symmetrically ingressed stationary geometries and flows in the $(\tilde{k}, R_0/L_h)$ -space leads to the stability diagram shown in Fig. 7(c). We find that the turnover rate k has to be larger than a certain threshold for symmetrically ingressed stationary surfaces to be mechanically stable. This can be understood intuitively. We know from the previous analysis for $\Delta_c = 0$ (Figs. 4 and 5) that self-organized centered contractile rings are generally unstable and contractility patterns exhibit an inherent propensity to polarize the surface. We expect this ring slipping to occur on some timescale, which the turnover rate k has to compete against when restoring the preferred centered stress-regulator concentration profile given in Eq. (59). The interface

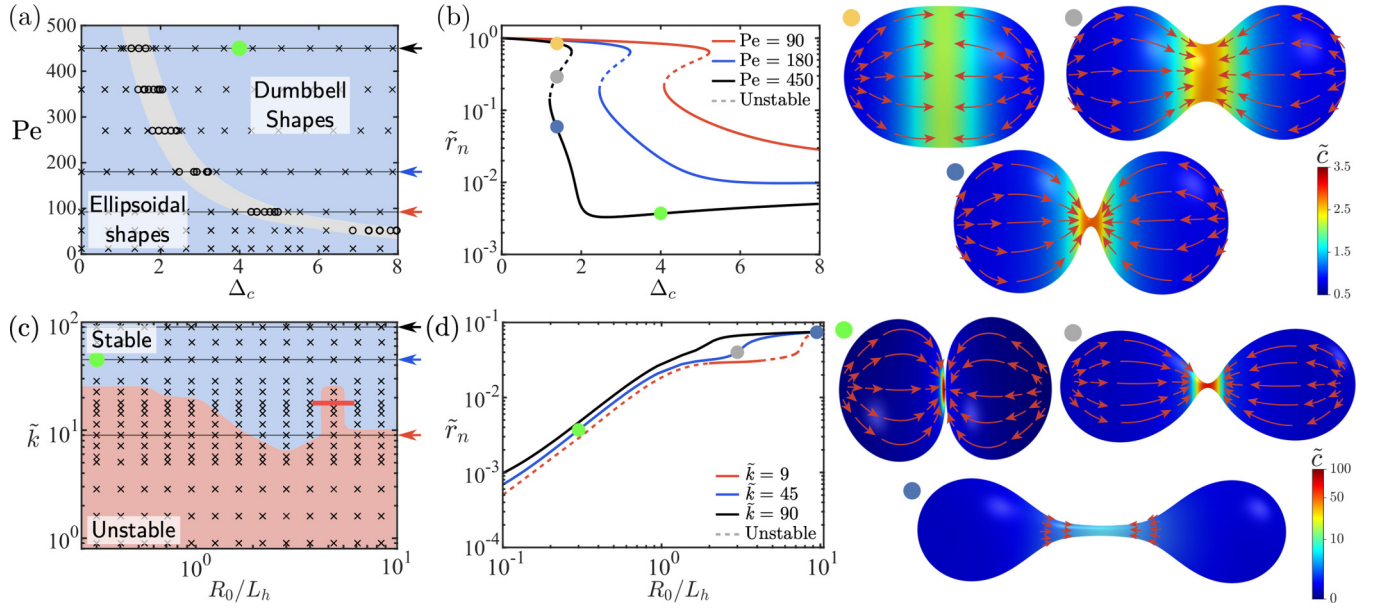


FIG. 7. Shape space analysis of guided division model with parameters used in Fig. 6 indicated by green circles. (a) Phase space of stationary surface geometries and flows—as a function of Péclet number and magnitude Δ_c of contractile ring pattern [see Eq. (59)]—obtained by direct computation of nonlinear stationary surface solutions using the approach described in Sec. IV F. Black symbols indicate complementary dynamic simulations to test stability of the stationary states. Crosses correspond to regions with unique attractors: dumbbell-shaped and ellipsoidal surfaces. Black circles identify parameter regions with multiple attractors. (b) One-dimensional slices through phase space in panel (a) show stable (solid lines) and unstable (dashed lines) regions of solution branches and reveal a first-order transition between stationary ellipsoidal and dumbbell shapes. Exemplary stationary solutions in the degenerate part of the shape space [gray region in panel (a)] are shown on the right. Red arrows indicate surface flows; color code indicates stress generator concentration $\tilde{c} = c/c_0$. (c) Stability diagram of symmetrically ingressed stationary surfaces. Black crosses depict parameters for which dynamic simulations were performed to test the mechanical surface stability (red: unstable, blue: stable). The instability “finger” (passed through by red line) corresponds to a reentrant region in which the symmetric geometry is briefly unstable, while two stable geometries with slightly asymmetrically placed rings emerge (see Fig. S1 of the Supplemental Material [52]). (d) Slices through phase space in panel (c) show stable (solid lines) and unstable (dashed lines) branches for different turnover rates (Movie S5 of the Supplemental Material [52]). Green circles depict parameters used in Fig. 6. Exemplary stationary solutions along the fully stable branch with $\tilde{k} = 45$ are shown on the right. All other parameters are listed in Table V.

between stable and unstable domains forms a rugged, non-monotonic interface in the $(\tilde{k}, R_0/L_h)$ -space. This interface includes a “finger” region in which symmetrically ingressed stationary surfaces become unstable and stable again only by changing R_0/L_h [red line in Fig. 7(c)]. A careful analysis of all stationary branches in this regime reveals the occurrence of an additional bifurcation at which the symmetric surface becomes unstable. At this point, two stable branches with a slightly asymmetrically placed ingression appear and merge again (see Fig. S1 of the Supplemental Material [52]), indicating a symmetry-breaking and symmetry-restoring reentrant behavior when changing the hydrodynamic length L_h .

Shape trajectories in terms of their neck radius for different fixed turnover rates are shown in Fig. 7(d), together with snapshots of stationary surfaces along a fully stable branch and for different hydrodynamic lengths. Analogous to the results from Fig. 3(a), changes in hydrodynamic length have the most significant impact around $R_0/L_h \approx 1$, when it changes from being irrelevant to becoming relevant on the surface, given the characteristic domain size $\sim R_0$. Emerging geometries change from sharply divided surfaces to more lengthy dumbbell geometries by the same mechanism discovered in Sec. V B 1: Hydrodynamic screening for $R_0/L_h > 1$ leads to more spread out steady state patterns of the stress regulator. This results in a broader surface region with high contractile

tension and consequently the neck region expands [blue circle, Fig. 7(d)].

VI. CONCLUSION

We have introduced a framework that integrates the nonequilibrium physics of active surfaces into an established, highly successful variational approach previously used to analyze shape spaces of equilibrium surfaces. The corresponding dissipation functional is generically constructed from the thermodynamic entropy production. A crucial methodological step in this construction is to exploit the symmetries imposed by Onsager relations to reformulate constitutive laws exclusively in terms of dissipative couplings. This requires taking into account also any off-diagonal couplings that are constrained by Onsager reciprocal relations. Specifically, for the active stress it implies that a conjugate dependence of hydrolysis rates on local material dilation has to be part of the variational functional. We note that including such a term is merely a formal necessity that ensures variations yield the correct equations of motion, but it does not have any immediate predictive power about the potential quantitative relevance of a reaction-dilation coupling in experiments. Our approach is immediately applicable to a large variety of unexplored constitutive laws for active surfaces with different broken

symmetries that have recently been derived [43]. While a limitation to linear couplings may sound restrictive, it is an acceptable limitation given the remarkably broad success of such linear constitutive laws in quantitatively explaining many biological processes [54].

We have considered two minimal models of self-organizing active fluid surfaces to exemplify the systematic analysis of stationary shape spaces that such models give rise to. For membranes that experience simultaneous internal and external forcing, we found that, surprisingly, a budding transition can occur when the membrane is being pushed instead of pulled. For a self-organized active fluid surface, we found that sufficiently small hydrodynamic screening length scale can effectively control its geometry. Extending the latter by a centered contractile ring, we find a rich phase space of nonlinear stationary solutions and identified signatures of a nonequilibrium first-order phase transition during cell-division-like shape transformations. The code to perform these analyses, using a standard boundary value solver implemented in MATLAB, is available on GitHub [50]. It is tempting to use the resulting characterization of stereotypic shape transitions as continuous or discontinuous nonequilibrium phase transitions to speculate about the biological function of either: Discontinuous transitions may be energetically more demanding to achieve, but lead to a state that is less susceptible for undesired reversals. A complementary point can be made for continuous transitions.

Many aspects of this work benefit from the simplifying restriction to axisymmetric surfaces. It will be interesting to investigate which of these insights can be carried over to surfaces without preimposed symmetry. While the unconstrained dissipation functional is valid for arbitrary surfaces, one may ask how the analog of the scaling Lagrangian-Eulerian parametrization could look like on a general surface. This could be guided by the aim to minimize the distortion in the map from a reference space to the deforming surface.

While on the axisymmetric surface this corresponds to the elimination of inhomogeneous parametric stretching along the meridional outline, one would also have to minimize the effects of shearing and twisting in the parametrization of a general two-dimensional surface.

In the future, it will also be interesting to investigate the impact of fluctuations on self-organized active surfaces. Because our approach is based on Onsager relations, it is in principle straightforward to include thermodynamically consistent fluctuations into the formulation of constitutive laws [47]. For the nonequilibrium phase transition induced by Δ_c and Pe shown in Figs. 7(a) and 7(b), for example, we anticipate that fluctuations could (1) renormalize the effective critical transition thresholds from ellipsoidal to dumbbell-shaped surfaces and (2) may lead to more rapid oscillations between these states in regions where multiple stationary shapes coexist [black circles in Fig. 7(a)]. Studying such phenomena, as well as alternative constitutive laws, promises not only to reveal a rich phenomenology in the dynamics of active surfaces, but also to advance our understanding of the physical principles that underpin shape emergence and its robustness in developing organisms.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [50].

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- [1] M. Kaksonen and A. Roux, Mechanisms of clathrin-mediated endocytosis, *Nat. Rev. Mol. Cell Biol.* **19**, 313 (2018).
 - [2] R. Jahn and T. C. Südhof, Membrane fusion and exocytosis, *Annu. Rev. Biochem.* **68**, 863 (1999).
 - [3] L.-G. Wu, E. Hamid, W. Shin, and H.-C. Chiang, Exocytosis and endocytosis: Modes, functions, and coupling mechanisms, *Annu. Rev. Physiol.* **76**, 301 (2014).
 - [4] B. Alberts, D. Bray, J. Lewis, M. Raff, K. Roberts, and J. Watson, *Molecular Biology of the Cell*, 4th ed. (Garland, New York, 2002).
 - [5] R. Phillips, J. Kondev, J. Theriot, and H. Garcia, *Physical Biology of the Cell* (Garland Science, New York, 2012).
 - [6] R. Dimova, S. Aranda, N. Bezlyepkina, V. Nikolov, K. A. Riske, and R. Lipowsky, A practical guide to giant vesicles. Probing the membrane nanoregime via optical microscopy, *J. Phys.: Condens. Matter* **18**, S1151 (2006).
 - [7] G. Salbreux, G. Charras, and E. Paluch, Actin cortex mechanics and cellular morphogenesis, *Trends Cell Biol.* **22**, 536 (2012).
 - [8] D. Bray and J. White, Cortical flow in animal cells, *Science* **239**, 883 (1988).
 - [9] M. Mayer, M. Depken, J. S. Bois, F. Jülicher, and S. W. Grill, Anisotropies in cortical tension reveal the physical basis of polarizing cortical flows, *Nature (London)* **467**, 617 (2010).
 - [10] T. Lecuit and P.-F. Lenne, Cell surface mechanics and the control of cell shape, tissue patterns and morphogenesis, *Nat. Rev. Mol. Cell Biol.* **8**, 633 (2007).
 - [11] P. Chugh, A. G. Clark, M. B. Smith, D. A. D. Cassani, K. Dierkes, A. Ragab, P. P. Roux, G. Charras, G. Salbreux, and E. K. Paluch, Actin cortex architecture regulates cell surface tension, *Nat. Cell Biol.* **19**, 689 (2017).
 - [12] H. Turlier, B. Audoly, J. Prost, and J.-F. Joanny, Furrow constriction in animal cell cytokinesis, *Biophys. J.* **106**, 114 (2014).
 - [13] A. C. Martin, M. Gelbart, R. Fernandez-Gonzalez, M. Kaschube, and E. F. Wieschaus, Integration of contractile forces during tissue invagination, *J. Cell Biol.* **188**, 735 (2010).
 - [14] C.-P. Heisenberg and Y. Bellaïche, Forces in tissue morphogenesis and patterning, *Cell* **153**, 948 (2013).
 - [15] J. Ranft, M. Basan, J. Elgeti, J.-F. Joanny, J. Prost, and F. Jülicher, Fluidization of tissues by cell division and apoptosis, *Proc. Natl. Acad. Sci. USA* **107**, 20863 (2010).

- [16] A. Daeden, A. Mietke, E. Derivery, C. Seum, F. Jülicher, and M. Gonzalez-Gaitan, Polarized branched actin modulates cortical mechanics to produce unequal-size daughters during asymmetric division, *Nat. Cell Biol.* **25**, 235 (2023).
- [17] M. Denk-Lobnig, J. F. Totz, N. C. Heer, J. Dunkel, and A. C. Martin, Combinatorial patterns of graded RhoA activation and uniform F-actin depletion promote tissue curvature, *Development* **148**, dev199232 (2021).
- [18] G. Salbreux and F. Jülicher, Mechanics of active surfaces, *Phys. Rev. E* **96**, 032404 (2017).
- [19] A. Mietke, F. Jülicher, and I. F. Sbalzarini, Self-organized shape dynamics of active surfaces, *Proc. Natl. Acad. Sci. USA* **116**, 29 (2019).
- [20] A. Mietke, V. Jemseena, K. V. Kumar, I. F. Sbalzarini, and F. Jülicher, Minimal model of cellular symmetry breaking, *Phys. Rev. Lett.* **123**, 188101 (2019).
- [21] A. Torres-Sánchez, M. K. Winter, and G. Salbreux, Interacting active surfaces: A model for three-dimensional cell aggregates, *PLoS Comput. Biol.* **18**, e1010762 (2022).
- [22] D. Khoromskaia and G. Salbreux, Active morphogenesis of patterned epithelial shells, *eLife* **12**, e75878 (2023).
- [23] R. Bailleul, N. Cuny, D. Khoromoskaia, S. Basu, G. Bergamini, P. Cucurachi, S. Rupp, A. Guse, C. Curantz, N. Swinhoe, P. Cleves, J. Craggs, S. Fujita, Y.-I. Nakajima, P. J. Steenbergen, A. Diz-Muñoz, G. Salbreux, and A. Ikmi, Cross-species biomechanical determinants of shape diversity, *bioRxiv*.
- [24] P. B. Canham, The minimum energy of bending as a possible explanation of the biconcave shape of the human red blood cell, *J. Theor. Biol.* **26**, 61 (1970).
- [25] W. Helfrich, Elastic properties of lipid bilayers: Theory and possible experiments, *Z. Naturforsch., C* **28**, 693 (1973).
- [26] E. A. Evans, Bending resistance and chemically induced moments in membrane bilayers, *Biophys. J.* **14**, 923 (1974).
- [27] O.-Y. Zhong-can and W. Helfrich, Instability and deformation of a spherical vesicle by pressure, *Phys. Rev. Lett.* **59**, 2486 (1987).
- [28] O.-Y. Zhong-can and W. Helfrich, Bending energy of vesicle membranes: General expressions for the first, second, and third variation of the shape energy and applications to spheres and cylinders, *Phys. Rev. A* **39**, 5280 (1989).
- [29] R. Lipowsky, The conformation of membranes, *Nature (London)* **349**, 475 (1991).
- [30] U. Seifert, K. Berndl, and R. Lipowsky, Shape transformations of vesicles: Phase diagram for spontaneous-curvature and bilayer-coupling models, *Phys. Rev. A* **44**, 1182 (1991).
- [31] H. Jian-Guo and O.-Y. Zhong-Can, Shape equations of the axisymmetric vesicles, *Phys. Rev. E* **47**, 461 (1993).
- [32] F. Jülicher and U. Seifert, Shape equations for axisymmetric vesicles: A clarification, *Phys. Rev. E* **49**, 4728 (1994).
- [33] R. Lipowsky, Domain-induced budding of fluid membranes, *Biophys. J.* **64**, 1133 (1993).
- [34] F. Jülicher and R. Lipowsky, Shape transformations of vesicles with intramembrane domains, *Phys. Rev. E* **53**, 2670 (1996).
- [35] I. Derényi, F. Jülicher, and J. Prost, Formation and interaction of membrane tubes, *Phys. Rev. Lett.* **88**, 238101 (2002).
- [36] U. Seifert, Configurations of fluid membranes and vesicles, *Adv. Phys.* **46**, 13 (1997).
- [37] J. Hassinger, G. Oster, D. Drubin, and P. Rangamani, Design principles for robust vesiculation in clathrin-mediated endocytosis, *Biophys. J.* **112**, 310a (2017).
- [38] N. Walani, J. Torres, and A. Agrawal, Endocytic proteins drive vesicle growth via instability in high membrane tension environment, *Proc. Natl. Acad. Sci. USA* **112**, E1423 (2015).
- [39] L. V. Chernomordik and M. M. Kozlov, Mechanics of membrane fusion, *Nat. Struct. Mol. Biol.* **15**, 675 (2008).
- [40] M. Arroyo and A. DeSimone, Relaxation dynamics of fluid membranes, *Phys. Rev. E* **79**, 031915 (2009).
- [41] M. Doi, Onsager's variational principle in soft matter, *J. Phys.: Condens. Matter* **23**, 284118 (2011).
- [42] M. Arroyo, N. Walani, A. Torres-Sánchez, and D. Kaurin, Onsager's variational principle in soft matter: Introduction and application to the dynamics of adsorption of proteins onto fluid membranes, in *The Role of Mechanics in the Study of Lipid Bilayers*, edited by D. Steigmann (Springer International Publishing, Cham, 2018), pp. 287–332.
- [43] G. Salbreux, F. Jülicher, J. Prost, and A. Callan-Jones, Theory of nematic and polar active fluid surfaces, *Phys. Rev. Res.* **4**, 033158 (2022).
- [44] A. Katchalsky and P. F. Curran, *Nonequilibrium Thermodynamics in Biophysics* (Harvard University Press, Cambridge, MA, 1965).
- [45] L. Onsager, Reciprocal relations in irreversible processes. I., *Phys. Rev.* **37**, 405 (1931).
- [46] L. Onsager, Reciprocal relations in irreversible processes. II., *Phys. Rev.* **38**, 2265 (1931).
- [47] F. Jülicher, S. W. Grill, and G. Salbreux, Hydrodynamic theory of active matter, *Rep. Prog. Phys.* **81**, 076601 (2018).
- [48] A. Torres-Sánchez, D. Millán, and M. Arroyo, Modelling fluid deformable surfaces with an emphasis on biological interfaces, *J. Fluid Mech.* **872**, 218 (2019).
- [49] A. Sahu, Y. A. Omar, R. A. Sauer, and K. K. Mandadapu, Arbitrary Lagrangian-Eulerian finite element method for curved and deforming surfaces: I. General theory and application to fluid interfaces, *J. Comput. Phys.* **407**, 109253 (2020).
- [50] GitHub, www.github.com/amielke/ActiveShapeSpaces.
- [51] C. Hirt, A. Amsden, and J. Cook, An arbitrary Lagrangian-Eulerian computing method for all flow speeds, *J. Comput. Phys.* **14**, 227 (1974).
- [52] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/jlps-h2qg> for detailed derivations of variational equations and of conservation laws in terms of ALE parametrizations, which includes Refs. [70,71].
- [53] F. Jülicher, A. Ajdari, and J. Prost, Modeling molecular motors, *Rev. Mod. Phys.* **69**, 1269 (1997).
- [54] J. Prost, F. Jülicher, and J. F. Joanny, Active gel physics, *Nat. Phys.* **11**, 111 (2015).
- [55] J. Meixner, Zur Thermodynamik der irreversiblen Prozesse in Gasen mit chemisch reagierenden, dissoziierenden und anregbaren Komponenten, *Ann. Phys.* **435**, 244 (1943).
- [56] J. Kierzenka and L. F. Shampine, A BVP solver based on residual control and the Matlab PSE, *ACM Trans. Math. Software* **27**, 299 (2001).
- [57] R. Ma and J. Berro, Endocytosis against high turgor pressure is made easier by partial protein coating and a freely rotating base, *Biophys. J.* **120**, 52a (2021).
- [58] A. Agrawal and D. J. Steigmann, Modeling protein-mediated morphology in biomembranes, *Biomech. Model. Mechanobiol.* **8**, 371 (2009).

- [59] J. S. Bois, F. Jülicher, and S. W. Grill, Pattern formation in active fluids, *Phys. Rev. Lett.* **106**, 028103 (2011).
- [60] M. Bonati, L. D. Wittwer, S. Aland, and E. Fischer-Friedrich, On the role of mechanosensitive binding dynamics in the pattern formation of active surfaces, *New J. Phys.* **24**, 073044 (2022).
- [61] M. Théry, A. Jiménez-Dalmaroni, V. Racine, M. Bornens, and F. Jülicher, Experimental and theoretical study of mitotic spindle orientation, *Nature (London)* **447**, 493 (2007).
- [62] N. T. L. Rodrigues, S. Lekomtsev, S. Jananji, J. Kriston-Vizi, G. R. X. Hickson, and B. Baum, Kinetochore-localized PP1–Sds22 couples chromosome segregation to polar relaxation, *Nature (London)* **524**, 489 (2015).
- [63] J. Sedzinski, M. Biro, A. Oswald, J.-Y. Tinevez, G. Salbreux, and E. Paluch, Polar actomyosin contractility destabilizes the position of the cytokinetic furrow, *Nature (London)* **476**, 462 (2011).
- [64] M. J. Lighthill, On the squirting motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers, *Commun. Pure Appl. Math.* **5**, 109 (1952).
- [65] E. Lauga and T. R. Powers, The hydrodynamics of swimming microorganisms, *Rep. Prog. Phys.* **72**, 096601 (2009).
- [66] M. Schmitt and H. Stark, Marangoni flow at droplet interfaces: Three-dimensional solution and applications, *Phys. Fluids* **28**, 012106 (2016).
- [67] A. Zöttl and H. Stark, Emergent behavior in active colloids, *J. Phys.: Condens. Matter* **28**, 253001 (2016).
- [68] C. A. Whitfield and R. J. Hawkins, Instabilities, motion and deformation of active fluid droplets, *New J. Phys.* **18**, 123016 (2016).
- [69] L. D. Wittwer and S. Aland, A computational model of self-organized shape dynamics of active surfaces in fluids, *J. Comp. Phys. X: X* **17**, 100126 (2023).
- [70] E. Kreyszig, *Introduction to Differential Geometry and Riemannian Geometry* (University of Toronto Press, Toronto, 1968).
- [71] A. Sahu, R. A. Sauer, and K. K. Mandadapu, Irreversible thermodynamics of curved lipid membranes, *Phys. Rev. E* **96**, 042409 (2017).