Fingering instability of active nematic droplets

Ricard Alert

Max Planck Institute for the Physics of Complex Systems, Nöthnitzerstr. 38, 01187 Dresden, Germany
Center for Systems Biology Dresden, Pfotenhauerstr. 108, 01307 Dresden, Germany

E-mail: ralert@pks.mpg.de

Received 28 February 2022, revised 19 April 2022
Accepted for publication 3 May 2022
Published 18 May 2022

Abstract

From the mitotic spindle up to tissues and biofilms, many biological systems behave as active droplets, which often break symmetry and change shape spontaneously. Here, I show that active nematic droplets can experience a fingering instability. I consider an active fluid that acquires nematic order through anchoring at the droplet interface, and I predict its morphological stability in terms of three dimensionless parameters: the anchoring angle, the penetration length of nematic order compared to droplet size, and an active capillary number. Droplets with extensile (contractile) stresses and planar (homeotropic) anchoring are unstable above a critical activity or droplet size. This instability is interfacial in nature: it arises through the coupling of active flows with interface motion, even when the bulk instability of active nematics cannot take place. In contrast to the dynamic states characteristic of active matter, the instability could produce static fingering patterns. The number of fingers increases with activity but varies non-monotonically with the nematic penetration length. Overall, these results pave the way towards understanding the self-organized shapes of biological systems, and towards designing patterns in active materials.

Keywords: active fluids, fingering instability, active droplets, active nematics, interfacial phenomena, morphogenesis

(Some figures may appear in colour only in the online journal)
Active matter is driven internally by its own constituents, be they molecular motors, cells, animals, or artificial self-propelled particles. As a result, active fluids exhibit striking phenomena such as spontaneous flows without external driving [1, 2], turbulence at low Reynolds numbers [3], and phase separation of repulsive particles [4]. These distinctive phenomena arise from activity-induced bulk instabilities.

Very often, however, active fluids form finite droplets. Examples abound in biological systems (figure 1), including biomolecular condensates [5], the mitotic spindle [6–8], cell aggregates and monolayers [9–11], and bacterial biofilms [12]. Active droplets can also be made artificially [13], for example by preparing vesicles containing either microswimmers [14–18], an actomyosin cortex [19, 20], or microtubule-kinesin films [21–24] (figure 1(a)). In all these systems, active droplets are commonly observed to spontaneously break symmetry and undergo shape changes. Interestingly, these shape dynamics could provide basic mechanisms for the onset of cell motility [25–38] as well as for cell and tissue morphogenesis [39–45] (figure 1(b)).

A key feature of active droplets is that they have an interface. As in passive fluids, interfaces have important consequences such as setting the kinetics of phase separation [5, 26, 46], driving wetting phenomena [9, 47], and allowing for interfacial instabilities. Here, I predict a generic interfacial instability of active nematic fluids. Thus, the results provide an active counterpart to paradigmatic interfacial instabilities in passive fluids, such as the Saffmann–Taylor instability underlying viscous fingering [48, 49].

In active and living fluids, interfacial instabilities and patterns emerge in a wide variety of systems: phase-separated droplets driven by chemical reactions [50, 51], microswimmer suspensions [52–54], chemotactic cells [55, 56], growing tumors [57–62] and bacterial biofilms [63–73], as well as in epithelial monolayers, either in mechanical competition [74, 75] or spreading freely [9, 10, 76, 77]. The instability mechanisms are varied; sometimes they rely on activity regulation, for example through nutrient depletion [57, 71], surfactant production [72], mechanical regulation of cell growth [62, 74], and limitations in chemical sensing [56]. In other cases, the instability results just from the interplay of active forces and interface dynamics. For example, active polar forces can produce waves on the surface of fluid films and membranes [78–82], and they can destabilize the interface of a spreading tissue [76]. Similarly, the free surface of an active nematic can also be destabilized by its bulk activity [83–88], and many simulations showcased the unsteady shape dynamics of active nematic interfaces [70, 88–97].

Crucially, the interface of active droplets not only provides a free boundary but can also localize activity. Activity localization can happen either because the interface induces nematic order, as when cells align at the tissue boundary [98–103] (figure 1(c)), or because the active material adsorbs at the interface, as is the case of the cell cortex and of synthetic active films in either vesicles or at oil–water interfaces [21–24]. Here, I take this localization effect into account by considering a fluid that is isotropic in the bulk but acquires nematic order at the interface. The order then decays inward over a penetration length. Tuning this penetration length with respect to droplet size allows the theory to encompass situations in which the order either remains interfacial or spans the entire droplet.

Similarly, I also account for an arbitrary anchoring angle, i.e., the angle between the local axis of nematic order and the interface. This is relevant as biological systems can exhibit a wide variety of anchoring angles. For example, microtubules tend to orient parallel to oil–water interfaces [24] (figure 1(a)). Actin filaments typically orient roughly parallel to the membrane in the cell cortex but roughly perpendicular to the membrane in protrusions like the lamellipodium [104]. Similarly, the orientation of stress fibers is dynamical and coupled to cell shape [105]. At the multicellular scale, depending on the cell type and experimental conditions,
Figure 1. Examples of active nematic droplets. (a) An active nematic film made of microtubules and molecular motors is encapsulated within a lipid vesicle. The active film undergoes spontaneous flows, which drive vesicle shape deformations. Dots indicate topological defects of the nematic order. The two images on the right are top and bottom hemisphere projections obtained through confocal microscopy. From [22]. Reprinted with permission from AAAS. (b) A mature Hydra, a small aquatic animal, has supracellular actin fibers that form an active nematic film in the external cell layer (top). Strikingly, the animal can regenerate from a tissue fragment that initially folds into a closed spheroidal shell (bottom). Adapted from [42], with permission from Springer Nature. (c) Phase-contrast image (left) and cell boundaries (right) of a circular monolayer of 3T3 fibroblasts. Cells align parallel to the tissue boundary, which induces nematic order that is maximal at the edge and decreases toward the center. Reproduced from [102]. CC BY 4.0. (d) A growing biofilm of Escherichia coli bacteria. Cells tend to orient parallel to the boundary and with one another, and growth-induced active nematic forces drive biofilm shape changes. The image has no scale bar, but the average cell length is $\sim 2\text{–}3\ \mu m$. Reproduced from [12]. CC BY 4.0.

epithelial and mesenchymal cells can align either parallel [98–102] (figure 1(c)), perpendicular [9], or at an intermediate angle [106] with respect to the tissue boundary. Cell monolayers can even dynamically reorganize from one boundary condition to another [107]. Instead, bacteria tend to orient parallel to the biofilm edge [12, 103] (figure 1(d)), partly as a result of the active...
anchoring phenomenon [83, 90]. Finally, because of hydrodynamic torques, pusher and puller swimmers reorient differently at interfaces [108]. To account for this diversity of anchoring conditions, here we can tune the anchoring angle to interpolate between planar (parallel) and homeotropic (perpendicular) anchoring.

Altogether, I obtain results in terms of three dimensionless parameters: the nematic penetration length relative to droplet size, the anchoring angle, and the active capillary number, which compares active forces to surface tension. Depending on the anchoring angle and the extensile/contractile nature of the active stresses, droplets can break their initial circular symmetry above a critical active capillary number, which can be reached by increasing either activity or droplet size. Increasing activity localization, for example by decreasing the nematic penetration length, favors stability. The selected mode of the instability, which determines the number of fingers in the resulting pattern, increases with activity but varies non-monotonically with the nematic penetration length. The number of fingers increases as the nematic penetration increases while remaining small compared to droplet size. However, when the penetration length becomes comparable to the droplet size, the range of unstable modes shrinks, and modes with fewer fingers are selected again. Overall, this work provides a minimal analytical theory for the morphological stability of active nematic droplets, which exposes the underlying mechanisms, complements existing simulations, and paves the way towards interpreting experimental observations.

1. Model of an active nematic droplet

To analyze basic mechanisms of their morphological stability, I study a minimal model of active nematic droplets. I consider a two-dimensional circular droplet of incompressible fluid on a substrate.

**Nematic order.** The orientational degrees of freedom of the fluid are described in terms of the nematic order parameter tensor $Q$. In two dimensions, $Q_{\alpha\beta} = S [2 \hat{n}_\alpha \hat{n}_\beta - \delta_{\alpha\beta}]$, where $S$ is the scalar strength of the order parameter, and $\hat{n} = (\cos \theta, \sin \theta)$ is the unitary director field, with $\theta$ the orientation angle [109]. The Cartesian components of $Q$ are $Q_{xx} = -Q_{yy} = S \cos(2\theta)$ and $Q_{xy} = Q_{yx} = S \sin(2\theta)$. In terms of $Q$, and in the usual one-constant approximation of the Frank elastic energy, the nematic free energy reads [110, 111]

$$F = \int \left[ \frac{a}{2} Q_{\alpha\beta} Q_{\alpha\beta} + \frac{L}{2} (\partial_\alpha Q_{\beta\gamma}) (\partial_\alpha Q_{\beta\gamma}) \right] d^2r,$$

(1)

where I take $a > 0$ to stabilize the isotropic phase in the bulk, and $L$ is the orientational elastic modulus, which is directly related to the Frank elastic constant.

For simplicity, I ignore flow alignment of the nematic orientation. Moreover, I focus on flows over time scales longer than the nematic relaxation time $\gamma_r/t$, with $\gamma_r$ the rotational viscosity, so that the order parameter field rapidly relaxes to the equilibrium configuration given by $\delta F/\delta Q_{\alpha\beta} = 0$. Given that $Q$ is a rank-2 symmetric and traceless tensor, it can be described in terms of a single complex field $\chi = Q_{xx} + i Q_{xy} = S e^{2i\theta}$. In terms of this field, the equilibrium condition reads

$$\ell^2 \nabla^2 \chi = \chi,$$

(2)

where I have defined the nematic length $\ell = \sqrt{L/a}$ that controls variations in nematic order through the droplet.

As motivated in the introduction, I assume that the fluid acquires nematic order at the droplet interface. Specifically, I impose that the nematic order has maximal strength at the droplet
boundary: \( S|_{r=R} = 1. \) Solving equation (2), I obtain (appendix A1)

\[
S_0(r) = \frac{I_2(r/\ell)}{I_2(R_0/\ell)},
\]

where the subscript 0 indicates that this is the reference solution for an unperturbed circular droplet of radius \( R_0. \) This solution shows that nematic order decays from the edge toward the center over a length \( \ell \) to achieve the isotropic bulk state imposed by the free energy in equation (1) (figure 2).

Respectively, the director \( \hat{n} \) anchors to the interface at an angle \( \theta_a \) with respect to the normal vector \( \hat{m}: \)

\[
\hat{n} \cdot \hat{m}|_{r=R} = \cos \theta_a.
\]

Thus, planar (parallel) anchoring corresponds to \( \theta_a = \pi/2, \) and homeotropic (perpendicular) anchoring corresponds to \( \theta_a = 0 \) (figure 2). For an unperturbed circular droplet, the nematic angle throughout the droplet is independent of the radial coordinate and reads

\[
\theta_0(\phi) = \theta_a + \phi.
\]

**Force balance.** Active nematics generate an active anisotropic stress \( \sigma^{a}_{\alpha\beta} = -\zeta Q_{\alpha\beta}, \) with coefficient \( \zeta > 0 \) for extensile and \( \zeta < 0 \) for contractile active stresses. I ignore antisymmetric nematic stresses, which are of higher order in gradients as compared to active stresses. In the limit of fast nematic relaxation, as assumed to obtain equation (2), flow-alignment stresses vanish. In the thin-film limit, viscous stresses are dominated by velocity gradients perpendicular to the film, which lead to a Darcy friction term \( \xi v \) when the flow is averaged over the film height. Altogether, force balance reduces to

\[
-\nabla P + f^a = \xi v,
\]

where \( f^a = -\partial_\beta \sigma^{a}_{\alpha\beta} \) is the active force density arising from gradients of the active stress, and \( P \) is the pressure field that enforces the incompressibility condition \( \nabla \cdot v = 0. \) To leverage this condition, I take the divergence of equation (6) and obtain

\[
\nabla^2 P = \nabla \cdot f^a \equiv s.
\]
Equation (7) is a Poisson equation for the pressure field, where the divergence of the active force density acts as a pressure source $s$.

At the droplet interface, with normal vector $\hat{m}$, I impose a 2D surface tension $\gamma$, which gives a discontinuity of the normal stress as prescribed by the Young–Laplace law:

$$
\hat{m}_\alpha \sigma_{\alpha\beta} \hat{m}_\beta|_{r=R} = -\gamma \nabla \cdot \hat{m}|_{r=R}.
$$

(8)

Here, $\sigma_{\alpha\beta} = -P\delta_{\alpha\beta} + \zeta Q_{\alpha\beta}$ is the total stress tensor of the active fluid. I have assumed that the external fluid is ideal, and I have set the pressure origin so that $P_{\text{ext}} = 0$.

In addition to Laplace pressure due to surface tension, the curvature of the interface creates distortions of the director field. These distortions lead to radial active forces (appendix A2, equation (A3)), which produce either pure extension or compression. As the fluid is incompressible, these forces do not drive flow but instead lead to a buildup of pressure. Solving equation (7) with the boundary conditions in equation (8), I obtain a pressure profile (appendix A2)

$$
P_0(r) = \frac{\gamma}{R_0} - \zeta \cos(2\theta_a) \left[ 1 - \frac{I_0(R_0/\ell) - I_0(r/\ell)}{I_2(R_0/\ell)} \right].
$$

(9)

Introducing this solution into the force balance equation (6) confirms that the velocity vanishes: $v^0_r(r) = 0$. The unperturbed droplet is quiescent: the pressure gradient exactly compensates the active force without inducing flow. Thus, this base state shows that active fluids can remain quiescent even when generating net active force.

2. Morphological stability

Shape perturbations and growth rate. To analyze the linear stability of the circular droplet shape, I introduce morphological perturbations by allowing the droplet radius to vary with the polar angle (figure 3): $R(\phi) = R_0 + \delta R(\phi)$. Accordingly, the strength and orientation of the nematic order are also perturbed (appendix B1), as are the forces and flows (appendix B2). The flow induced by the perturbations then drives interface motion through the kinematic condition

$$
\frac{dR(\phi)}{dt} = v \cdot \hat{m}|_{r=R} \approx \delta v_\phi(R_0, \phi),
$$

(10)

where $\hat{m}$ is the normal vector, and I have expanded to first order in perturbations and used that $v^0_\phi(r) = v^0_\phi(R_0) = 0$. To analyze the interface dynamics, I decompose all fields in angular Fourier modes labelled by the index $k$, which indicates the number of protrusions of the perturbed droplet contour (figure 3). The growth rate of the morphological perturbations is given by $\omega_k = \delta v_\phi(R_0)/\delta R_k$. Introducing all the perturbation results obtained in appendix B, I obtain the final result for the growth rate, whose complete expression is given in appendix B3.

The result shows that the stability of droplets with planar anchoring and extensile stresses is equivalent to that of droplets with homeotropic anchoring and contractile stresses. More generally, the growth rate is invariant under the transformation $\zeta, \theta_a \to -\zeta, \theta_a + \pi/2$. For clarity, hereafter I discuss the results for planar anchoring $\theta_a = \pi/2$. In this case, the growth rate simplifies to

$$

$$
Figure 3. Shape perturbations of a circular droplet. The dashed circle indicates the unperturbed shape.

\[
\omega_k = \frac{k(k-1)}{\xi R_0^3} \left\{ -\gamma(k+1) + 2\zeta R_0 \left[ \frac{2(k-1)\ell}{R_0} + \frac{I_1(R_0/\ell)}{I_2(R_0/\ell)} \frac{I_{k-1}(R_0/\ell)}{I_{k-2}(R_0/\ell)} - 1 \right] \right\}. \tag{11}
\]

The prefactor ensures that both the dilation/contraction mode \( k = 0 \) and the translation mode \( k = 1 \) are marginal, \( \omega_0 = \omega_1 = 0 \), as a consequence of the fluid’s incompressibility and translational invariance, respectively. Beyond the prefactor, the first term in equation (11) corresponds to the stabilizing contribution of surface tension, whereas the second term accounts for the active effects, which are stabilizing (destabilizing) for contractile (extensile) stresses (figure 4).

The growth rate equation (11) depends on four parameter combinations: a capillary time \( \tau \equiv \xi R_0^3/\gamma \), the ratio of nematic length and droplet size \( \bar{\ell} \equiv \ell/R_0 \), the sign of the active stress \( \zeta/|\zeta| \), and the active capillary number \( \text{Ca}_A \equiv |\zeta| R_0/\gamma \). Using the capillary time as the time unit, the rescaled growth rate \( \bar{\omega}_k \equiv \omega_k \tau \) can be recast in terms of the other three (dimensionless) parameters:

\[
\bar{\omega}_k = k(k-1) \left\{ -(k+1) + 2\text{Ca}_A \frac{\zeta}{|\zeta|} \left[ \frac{2(k-1)\bar{\ell}}{1} + \frac{I_1(1/\bar{\ell})}{I_2(1/\bar{\ell})} \frac{I_{k-1}(1/\bar{\ell})}{I_{k-2}(1/\bar{\ell})} - 1 \right] \right\}. \tag{12}
\]

**Active capillary number.** The active capillary number compares active stresses to surface tension [83, 84, 91, 92]. It is an active variant of the ordinary capillary number \( \text{Ca} \equiv \eta V/\gamma \), which compares dissipative viscous forces to surface tension [112]. Here, \( \eta \) is the shear viscosity, \( V \) is a characteristic flow velocity, and \( \gamma \) is the surface tension. In the present work, dissipation is due to friction, and hence the capillary number is instead defined as \( \text{Ca} \equiv \xi VL^2/\gamma \),
Figure 4. Growth rate of shape perturbations of active nematic droplets. When rescaled by the capillary time \( \tau \equiv \xi R_0^3/\gamma \), the growth rate depends only on three dimensionless parameter combinations: the extensile or contractile sign of active stresses, the rescaled nematic length \( \bar{\ell} \equiv \ell/R_0 \), and the active capillary number \( \text{Ca}_A \equiv |\zeta| R_0/\gamma \). These plots are for planar anchoring (figure 2(a)). For homeotropic anchoring (figure 2(b)), the results are equivalent upon exchanging extensile for contractile. (a) For extensile (contractile) active stresses, increasing the active capillary number leads to a further destabilization (stabilization) of the droplet shape. The values of the active capillary number are \( \text{Ca}_A = 5n; n = 1, \ldots, 4 \). (b) A similar trend holds as the rescaled nematic length increases. Its values are \( \bar{\ell} = 2^n/20; n = 0, \ldots, 3 \).

where \( L \) is a characteristic length of the droplet. Introducing the characteristic velocity of active flows, \( V_A = |\zeta|/(\xi R_0) \), yields the active capillary number used here: \( \text{Ca}_A \equiv |\zeta| R_0/\gamma \).

Alternatively, this quantity can also be thought of as an active Bond number. The ordinary Bond number, also known as the Eötvös number, compares gravitational to surface tension forces, and it is used to characterize the shape of drops, for example during gravity-driven wetting [112]. It is defined as \( \text{Bo} \equiv \Delta \rho g L^2/\gamma \), where \( \Delta \rho \) is the density difference between two media (e.g., the liquid of the droplet and the surrounding fluid), and \( g \) is the gravitational acceleration. Unlike the ordinary capillary number, the Bond number compares a driving force (gravity) to surface tension, parallel to how the active capillary number compares active driving forces to surface tension. Furthermore, the active capillary number can be written as \( \text{Ca}_A = R_0/\ell_{ac} \), where \( \ell_{ac} \equiv \gamma/|\zeta| \) is an active capillary length. This length is an active variant of the ordinary capillary length \( \ell_c \equiv \sqrt{\gamma/(\Delta \rho g)} \) defined by the balance of gravitational and surface tension forces, which allows to write the Bond number as \( \text{Bo} = L^2/\ell_c^2 \). Overall, the active capillary number, which here controls droplet shape stability, has conceptual parallels with both the capillary and Bond numbers of passive fluids.

**Stability diagram and mode selection.** How do these dimensionless parameters control droplet stability? For planar anchoring, figure 4 shows that droplets with contractile stresses \( (\zeta < 0) \) are stable \( (\omega_k < 0) \), whereas droplets with extensile stresses \( (\zeta > 0) \) experience a morphological instability (some modes \( k \) with \( \omega_k > 0 \)). The competition between active forces and surface tension, controlled by both \( \text{Ca}_A \) and \( \bar{\ell} \), governs the range of unstable modes and selects the mode with the fastest growth rate, which determines the initial number of fingers resulting from the instability.

For contractile stresses, both increasing the active capillary number (figure 4(a)) and increasing the rescaled nematic length (figure 4(b)) result in a further stabilization of the droplet shape. In contrast, for extensile stresses, as the active capillary number \( \text{Ca}_A \) increases, more modes become unstable, and the selected mode becomes higher (figure 4(a)). The same trend
Figure 5. Morphological stability diagram of active nematic droplets. Below the critical active capillary number (equation (14)), a circular active nematic droplet is stable. Above the critical value, the droplet experiences a fingering instability. The selected (fastest-growing) mode increases monotonically with the active capillary number, but it exhibits a non-monotonic dependence on the nematic length. This plot is for either extensile stresses and planar anchoring (figure 2(a)), or equivalently contractile stresses and homeotropic anchoring (figure 2(b)). In the remaining combinations, the droplet is stable. In cases with intermediate anchoring angles, the results follow from the expressions in appendix B3.

is obtained when increasing the rescaled nematic length $\ell$ while keeping it small, $\ell \ll 1$. However, when the nematic length becomes comparable to the droplet radius, this behavior changes. As the rescaled nematic length is increased further, the range of unstable modes shrinks a bit, and the selected mode becomes lower again (figure 4(b)). Eventually, in the limit of large nematic length $\ell \to \infty$, which corresponds to nematic order extending throughout the droplet, the growth rate becomes independent of $\ell$:

$$\lim_{\ell \to \infty} \omega_k = -k(k^2 - 1) + 4Ca_\lambda \frac{\zeta}{|\zeta|} k. \quad (13)$$

As seen in either equation (11) or equation (12), the destabilizing active effects dominate at long wavelengths (low mode number $k$). Hence, an infinite interface would always be unstable. However, for the interface of a finite droplet, the first mode that might become unstable is the elliptic mode $k = 2$. Therefore, for a droplet, the instability has a finite threshold, given by $\omega_2 = 0$. The critical value of the active capillary number is

$$Ca_\lambda = \frac{3}{2} \frac{I_0(1/\ell)I_2(1/\ell)}{I_1^2(1/\ell) - I_2^2(1/\ell)}. \quad (14)$$

which monotonically decreases with the rescaled nematic length (black curve in figure 5). Instability is most favorable in the limit of large nematic length compared to droplet size, in which the critical active capillary number tends to its minimum: $\lim_{\ell \to \infty} Ca_\lambda = 3/4$. In the unstable region, the stability diagram in figure 5 also shows the selected mode. As explained earlier, the selected mode increases monotonically with the active capillary number, but it features a non-monotonic behavior with the nematic length $\ell$. Respectively, increasing droplet size $R_0$ decreases $\ell = \ell/ R_0$ but increases $Ca_\lambda = |\zeta| R_0 / \gamma$, and hence it corresponds to moving up along a hyperbola in the stability diagram in figure 5. Thus, the selected mode also varies non-monotonically with droplet size.
Figure 6. Instability mechanism. Schematic of the interface (black), the underlying director field (blue), and the active forces that it generates on the interface (red). Certain combinations of anchoring conditions and active stresses amplify shape perturbations, leading to droplet shape instability. The figure depicts the unstable cases of (a) planar anchoring ($\theta_a = \pi/2$) and extensile stresses ($\zeta > 0$), and (b) homeotropic anchoring ($\theta_a = 0$) and contractile stresses ($\zeta < 0$).

3. Discussion and outlook

I have shown that active nematic droplets can experience a morphological instability. The mechanism is simple: droplet shape perturbations distort the nematic order, which generates an active force that further deforms the droplet (figure 6). This mechanism is similar to that of the well-known bulk instability of active nematics, which leads to spontaneous flows even in unbounded systems without an interface [1–3]. Despite the similarities, the instability presented here is interfacial in nature, and thus it is fundamentally different from the bulk instability.

In the bulk instability, a perturbation in the nematic director generates active flows that further rotate the director. Similarly, bulk nematic order can emerge spontaneously from the isotropic state through a positive feedback from active flows [113]. These feedbacks require the director field to have a dynamics, which couples it directly to the flow. Here, instead, I have taken the nematic order to instantaneously relax to its equilibrium configuration (equation (2)), and hence the director has no intrinsic dynamics [87]. Therefore, the active nematic considered here cannot experience a bulk instability. Yet, it can be unstable in the presence of an interface. Through anchoring, interface motion affects the director field, and therefore it provides the missing dynamical field that enables the feedback between the director and active flows. Previous works considered similar interfacial instabilities but retained one additional dynamical field, either the concentration of microswimmers [84], the director [85], or the density in a compressible active nematic [87]. Thus, the theory presented here provides a minimal description of morphological instability in active nematics, in which interface motion is the only dynamical field.

The instability takes place only for appropriate combinations of the anchoring angle and the sign of the active stresses, as illustrated in figure 6. For these combinations, active stresses
tend to extend the interface, which consequently undulates and forms finger-like protrusions. Beyond the initial, linear stage of the instability, non-linear effects arising from surface tension and incompressibility could potentially saturate finger growth. In this case, an active instability would lead to a static fingering pattern, similar to the recently-found buckling instability in active nematic films [114], but in stark contrast to the flowing steady states characteristic of active matter. Alternatively, the fingering process could lead to pinch-off events and droplet splitting [91].

The fingering instability presented here has implications for both biological and synthetic active systems. Foremost, it provides a symmetry-breaking mechanism for the spontaneous shape changes observed in multiple systems, from the sub-cellular scales of the mitotic spindle and the cell cortex to the scale of entire organisms such as Hydra, and including reconstituted systems such as active vesicles (figure 1). The findings might be particularly relevant for epithelial cell monolayers. In situations such as wound healing, cells at the tissue edge polarize perpendicularly to the interface, which produces active fingering instabilities [76]. In other situations, however, cells align parallel to the interface. The results of this work could provide the conceptual basis to understand the tissue shape changes observed in these cases [101]. The reported fingering instability could also be exploited to pattern active materials, for example to design corrugated surfaces with potential applications as reconfigurable substrates to study tissue dynamics.

Looking forward, this work could be extended to capture the three-dimensional profile of the droplet [47], which would bring in additional effects such as wetting energies [115, 116] and out-of-plane nematic order [45, 117]. Other interesting extensions would be to include chiral flows [118], mechanochemical processes [40, 41], and an external elastic medium, which is relevant to study the growth of biofilms in mucus-like gels and in host tissues [103].

Acknowledgments

I thank Jaume Casademunt, John D McEnany, Howard A Stone, Ned S Wingreen, and Jing Yan for discussions.

Data availability statement

No new data were created or analysed in this study.

Appendix A. Unperturbed state. Circular droplet

As a reference, I consider a circular droplet of radius $R_0$.

A1. Nematic order

In polar coordinates, the equilibrium condition equation (2) for the nematic order reads

$$\left[\partial_r^2 + \frac{1}{r} \partial_r + \frac{1}{r^2} \partial_\phi^2 - \frac{1}{r^2}\right] \chi(r, \phi) = 0.$$  \hspace{1cm} (A1)

The anchoring condition imposes the nematic angle at the droplet boundary: $\theta(R_0, \phi) = \theta_a + \phi$, where $\phi$ is the polar angle. Because there is no reason for the nematic angle to change along the radial coordinate, the nematic angle is a function of the polar angle only, as given in...
equation (5). Similarly, axial symmetry implies that the strength of the nematic order depends only on the radial coordinate, \( S = S_0(r) \). Therefore, \( \chi(r, \phi) = S_0(r)e^{i2\phi} \), and equation (A1) reduces to

\[
S''_0(r) + \frac{1}{r} S'_0(r) - \left[ \frac{1}{r^2} + \frac{4}{r^2} \right] S_0(r) = 0. \tag{A2}
\]

The solutions to this equation are modified Bessel functions of order \( n = 2 \) and scale factor \( \ell \).

Imposing that the nematic order has a maximal strength \( S_0(R_0) = 1 \) at the boundary, I obtain the solution in equation (3), which is displayed in figure 2.

A2. Forces and flows

For the nematic order of the unperturbed droplet, given by equations (3) and (5), the active force density has components

\[
f_{r0}(r) = -\zeta \cos(2\theta_a) \left[ S'_0(r) + \frac{3}{r} S_0(r) \right], \tag{A3a}
\]

\[
f_{\phi0}(r) = 0. \tag{A3b}
\]

Given that the active force has axial symmetry, the pressure is also axially symmetric, \( P_0(r, \phi) = P_0(r) \). Hence, the Poisson equation for the pressure field reads as

\[
\left[ \frac{d^2}{dr^2} + \frac{1}{r} \frac{d}{dr} \right] P_0(r) = -\zeta \cos(2\theta_a) \left[ S''_0(r) + \frac{3}{r} S'_0(r) \right]. \tag{A4}
\]

To solve this equation, we need to impose boundary conditions as specified by the Young–Laplace relation in equation (8).

The stress tensor of the active fluid is given by

\[
\sigma_{\alpha\beta} = -P\delta_{\alpha\beta} - \zeta Q_{\alpha\beta}, \tag{A5}
\]

and its components in a cylindrical-coordinate basis are

\[
\sigma_{rr} = -P - \zeta S \cos(2(\theta - \phi)), \tag{A6a}
\]

\[
\sigma_{r\phi} = \sigma_{\phi r} = -\zeta S \sin(2(\theta - \phi)), \tag{A6b}
\]

\[
\sigma_{\phi\phi} = -P + \zeta S \cos(2(\theta - \phi)). \tag{A6c}
\]

For the unperturbed circular droplet, \( \sigma_{r0}''(r) = -P_0(r) - \zeta \cos(2\theta_a)S_0(r) \), and hence, the Young–Laplace boundary condition equation (8) becomes

\[
P_0(R_0) = \frac{\gamma}{R_0} - \zeta \cos(2\theta_a). \tag{A7}
\]

With this boundary condition, the solution to equation (A4) is given in equation (9).

Appendix B. Perturbed state. Non-circular droplet

Here, I obtain the perturbations in nematic order, forces, and flows induced by perturbations in droplet shape, which are introduced as a radius that varies along the droplet contour, i.e. with the polar angle \( \phi: R(\phi) = R_0 + \delta R(\phi) \).
B1. Nematic order

As a result of the morphological perturbations, the strength and orientation of the nematic order are perturbed as

\[ S(r, \phi) = S_0(r) + \delta S(r, \phi), \]
\[ \theta(r, \phi) = \theta_0(\phi) + \delta \theta(r, \phi). \]

Hence, to first order in the perturbations, the complex field \( \chi \) reads

\[ \chi(r, \phi) = S(r, \phi) e^{i2\theta(r, \phi)} \approx \left[ S_0(r) + \delta S(r, \phi) + 2i S_0(r) \delta \theta(r, \phi) \right] e^{i2\theta_0(\phi)}. \]

Using this expression, the nematic equilibrium condition equation (A1) becomes a complex equation for the perturbation fields \( \delta S \) and \( \delta \theta \). The real and imaginary parts of this equation must vanish separately, which leads to the following pair of coupled partial differential equations (PDEs):

\[ \left[ \frac{\partial^2}{\partial r^2} + \frac{1}{r} \frac{\partial}{\partial r} + \frac{1}{r^2} \left( 4 - \frac{1}{r^2} \right) \right] \delta S(r, \phi) - \frac{8i}{r^2} S_0(r) \delta \theta(r, \phi) = 0, \]
\[ \frac{2i}{r^2} \delta \theta(r, \phi) + \left[ S_0(r) \frac{d^2}{dr^2} + \left( 2 \frac{S_0'(r)}{r} + \frac{1}{r} S_0(r) \right) \frac{d}{dr} - \frac{k^2}{r^2} \right] \delta \theta(r, \phi) = 0. \]

To solve these equations, we introduce the angular Fourier decomposition of the perturbation fields:

\[ \delta S(r, \phi) = \sum_{k=0}^{\infty} \delta S_k(r) e^{ik\phi}, \]
\[ \delta \theta(r, \phi) = \sum_{k=0}^{\infty} \delta \theta_k(r) e^{ik\phi}. \]

In terms of their Fourier components, the pair of coupled PDEs becomes a pair of coupled ordinary differential equations:

\[ \left[ \frac{d^2}{dr^2} + \frac{1}{r} \frac{d}{dr} - \frac{k^2 + 4}{r^2} - \frac{1}{r^2} \right] \delta S_k(r) - \frac{8ik}{r^2} S_0(r) \delta \theta_k(r) = 0, \]
\[ \frac{2ik}{r^2} \delta S_k(r) + \left[ S_0(r) \frac{d^2}{dr^2} + \left( 2 \frac{S_0'(r)}{r} + \frac{1}{r} S_0(r) \right) \frac{d}{dr} - \frac{k^2}{r^2} \right] \delta \theta_k(r) = 0. \]

Even though the coefficients of the differential operators involve non-linear functions, these equations can be solved analytically. The solution can be guessed by looking at the operator on \( \delta S_k(r) \) in equation (B5a). Adding an appropriate term, this operator would correspond to a modified Bessel operator of integer order. There are two symmetric ways to complete this
operator to this end: either to add or to subtract a term \(4k/r^2 \delta \tilde{S}_k(r)\), which respectively transform the operator into a modified Bessel operator of order \(k \mp 2\). Hence, I propose the ansatz

\[
\delta \tilde{S}_k(r) = AI_{k+2}(r/\ell) + BI_{k-2}(r/\ell).
\] (B6)

The corresponding modified Bessel functions of second species are also solutions of the equations. However, because they diverge at \(r = 0\), their integration constants must be set to zero. Introducing the ansatz into equation (B5a) yields an algebraic equation for \(\delta \tilde{\theta}_k(r)\), whose solution is

\[
\delta \tilde{\theta}_k(r) = i \frac{I_2(R_0/\ell)}{2 I_2(r/\ell)} \left[ BI_{k-2}(r/\ell) - AI_{k+2}(r/\ell) \right].
\] (B7)

Although they were proposed for equation (B5a), the solutions in equations (B6) and (B7) turn out to satisfy equation (B5b). Therefore, they are solutions to the full equation (B5).

To determine the integration constants \(A\) and \(B\), we have to use boundary conditions. To this end, I derive the boundary conditions on the perturbed nematic order. First, I impose the anchoring condition, which depends on the normal vector \(\hat{m}\) of the perturbed boundary (figure 3).

In terms of the local angle \(\alpha\) between the perturbed and the original (circular) boundary, the normal vector reads

\[
\hat{m} = \cos \alpha \hat{r} + \sin \alpha \hat{\phi} \approx \hat{r} - \frac{1}{R_0} \frac{d\delta R}{d\phi} \hat{\phi}.
\] (B8)

Here, I have approximated \(\hat{m}\) to first order in perturbations using that \(\alpha \approx \tan \alpha = -d\delta R/ds\), where \(s = R_0 \phi\) is the arc length coordinate. Then, in terms of the nematic director field \(\hat{n}\), the anchoring condition reads

\[
\hat{n}(R, \phi) \cdot \hat{m} = \cos \theta_a.
\] (B9)

Here, \(\hat{n}(r, \phi) = \hat{n}_0(\phi) + \delta \hat{n}(r, \phi)\), where \(\hat{n}_0(\phi) = \cos \theta_a \hat{r} + \sin \theta_a \hat{\phi}\) and \(\delta \hat{n} = -\sin \theta_a \delta \theta \hat{r} + \sin(\theta_a + 2\phi) \delta \theta \hat{\phi}\). Thus, to first order in perturbations, equation (B9) implies

\[
\delta \theta(R_0, \phi) \approx -\frac{1}{R_0} \frac{d\delta R}{d\phi},
\] (B10)

which provides a boundary condition for the angle perturbations.

Next, I enforce that the strength of the nematic order remains 1 at the boundary, \(S(R, \phi) = 1\), which implies

\[
S_0(R) + \delta S(R, \phi) = 1.
\] (B11)

Taking into account that \(S_0(R) \approx S_0(R_0) + S'_0(R_0) \delta R(\phi)\), and to first order in perturbations, I obtain the boundary condition for the nematic strength perturbations,

\[
\delta S(R_0, \phi) \approx -S'_0(R_0) \delta R(\phi),
\] (B12)

where I have used that \(S_0(R_0) = 1\). The right-hand side can be evaluated using that
The active pressure source in equation (7) reads as

\[ S_0(r) = \frac{1}{\ell} \left[ \frac{I_1(r/\ell)}{I_2(R_0/\ell)} \right] - \frac{2\ell}{r} \frac{I_2(r/\ell)}{I_2(R_0/\ell)} \]. \hspace{1cm} (B13)

In Fourier space, the boundary conditions equations (B10) and (B12) read

\[
\delta \tilde{\theta}_k(R_0) = -\frac{i}{R_0} \delta \tilde{R}_k, \hspace{1cm} (B14a)
\]
\[
\delta \tilde{S}_k(R_0) = -S_0'(R_0) \delta \tilde{R}_k, \hspace{1cm} (B14b)
\]

where \( \delta \tilde{R}_k \) are the angular Fourier components of the radius perturbation \( \delta R(\phi) \). Applying these boundary conditions to the solutions equations (B6) and (B7), I obtain the final solutions

\[
\delta \tilde{S}_k(r) = \left\{ \begin{array}{l}
1 + k \frac{1}{R_0} - \frac{1}{2\ell} \frac{I_1(R_0/\ell)}{I_2(R_0/\ell)} \frac{I_{k+2}(r/\ell)}{I_{k+2}(R_0/\ell)} \\
+ \left[ 1 - k \frac{1}{R_0} - \frac{1}{2\ell} \frac{I_1(R_0/\ell)}{I_2(R_0/\ell)} \frac{I_{k-2}(r/\ell)}{I_{k-2}(R_0/\ell)} \right] \delta \tilde{R}_k.
\end{array} \right. \hspace{1cm} (B15a)
\]
\[
\delta \tilde{\theta}_k(r) = \left\{ \begin{array}{l}
1 - k \frac{1}{R_0} - \frac{1}{2\ell} \frac{I_1(R_0/\ell)}{I_2(R_0/\ell)} \frac{I_{k-2}(r/\ell)}{I_{k-2}(R_0/\ell)} \\
- \left[ 1 + k \frac{1}{R_0} - \frac{1}{2\ell} \frac{I_1(R_0/\ell)}{I_2(R_0/\ell)} \frac{I_{k+2}(r/\ell)}{I_{k+2}(R_0/\ell)} \right] \frac{I_2(R_0/\ell)}{I_2(r/\ell)} \frac{i}{2} \delta \tilde{R}_k.
\end{array} \right. \hspace{1cm} (B15b)
\]

**B2. Forces and flows**

The perturbations of the nematic order obtained above induce flows that further affect droplet shape. To obtain these flows, we first compute the pressure perturbations. The perturbations of the active pressure source in equation (7) read as

\[
\delta s(r, \phi) = -\zeta \cos(2\theta_0) \left\{ \left[ \partial_r^2 + \frac{3}{r} \partial_r - \frac{1}{r^2} \partial_\phi^2 \right] \delta S(r, \phi) \\
+ \frac{4}{r} \left\{ S_0(r) \left[ \frac{1}{r} + \partial_r \right] + S_0'(r) \right\} \partial_\phi \delta \theta(r, \phi) \\
- 2\zeta \sin(2\theta_0) \left\{ \left[ \frac{1}{r} \partial_r + \frac{1}{r^2} \right] \partial_\phi \delta S(r, \phi) \\
- \left\{ S_0(r) \partial_r^2 + \frac{3}{r} S_0(r) + 2S_0'(r) \right\} \partial_r \\
+ \frac{3}{r} S_0'(r) + S_0''(r) - \frac{1}{r^2} S_0(r) \partial_\phi^2 \right\} \delta \theta(r, \phi) \right\}. \hspace{1cm} (B16)
\]

Its angular Fourier components are given by
\[ \delta \tilde{\sigma}_k(r) = -\zeta \cos(2\theta_a) \left\{ \left[ \frac{d^2}{dr^2} + \frac{3}{r} \frac{d}{dr} + \frac{k^2}{r^2} \right] \delta \tilde{S}_k(r) \right. \]
\[ + \frac{4}{r} \left\{ S_0(r) \left[ \frac{1}{r} + \frac{d}{dr} \right] + S_0'(r) \right\} ik \delta \tilde{\theta}_k(r) \]
\[ - 2\zeta \sin(2\theta_a) \left\{ \left[ \frac{1}{r} \frac{d}{dr} + \frac{1}{r^2} \right] ik \delta \tilde{S}_k(r) \right. \]
\[ - \left\{ S_0(r) \frac{d^2}{dr^2} + \frac{3}{r} S_0'(r) + 2S_0''(r) \right\} \frac{d}{dr} \]
\[ + \frac{3}{r} S_0'(r) + S_0''(r) + \frac{k^2}{r^2} S_0(r) \right\} \delta \tilde{\theta}_k(r) \] \hspace{1cm} (B17)

In Fourier space, the Poisson equation (7) can be recast as
\[ \left[ \frac{d^2}{dr^2} + \frac{1}{r} \frac{d}{dr} - \frac{k^2}{r^2} \right] \delta \tilde{P}_k(r) = \delta \tilde{S}_k(r). \] \hspace{1cm} (B18)

Then, introducing the nematic order perturbations equation (B15) into the pressure source perturbations equation (B17), I solve equation (B18) to obtain the angular Fourier components of the pressure perturbations. For \( k > 0 \), they are given by
\[ \delta \tilde{P}_k(r) = A_k r^k + B_k \frac{r}{\ell} - \frac{\delta \tilde{R}_k}{R_0} c_\ell(R_0/\ell, \theta_a) \left[ \frac{1}{k!} \left( \frac{r}{\ell} \right)^k - I_k(r/\ell) \right], \] \hspace{1cm} (B19)

where \( A_k \) and \( B_k \) are integration constants, and
\[ c_\ell(R_0/\ell, \theta_a) = \frac{(2k/\ell R_0)^{k+1}(k+2)!}{\ell^k F_1(k+3; R_0^2/(4\ell^2))} e^{-2\theta_a} \left\{ 1 + e^{4\theta_a} + 4k(k+1) \frac{\ell^2}{R_0^2} \right\} \]
\[ - 4k \left( 1 + 2(k^2 - 1) \frac{\ell^2}{R_0^2} \right) \left[ \frac{\ell}{R_0} I_{k-1}(R_0/\ell) \right] I_k(R_0/\ell) I_{k-1}(R_0/\ell) \]
\[ + |k - 1 - (k+1)e^{4\theta_a} + 4k(k^2 - 1) \frac{\ell^2}{R_0^2} - 4k(k-1) \left( 1 + 2(k^2 - 1) \frac{\ell^2}{R_0^2} \right) I_{k-1}(R_0/\ell) I_k(R_0/\ell) \]
\[ - 4k(k-1) \left[ \frac{1}{k!} \left( \frac{r}{\ell} \right)^k - \frac{\ell}{R_0} I_{k-1}(R_0/\ell) I_k(R_0/\ell) \right] \frac{2\ell}{R_0} \} \] \hspace{1cm} (B20)

is a numerical factor. Here, \( F_1 \) is a generalized hypergeometric function. For mode \( k = 0 \), the solution for the pressure perturbation is different:
\[ \delta \tilde{P}_0(r) = A_0 + B_0 \ln r - \zeta \frac{\delta \tilde{R}_0}{R_0} c_0(R_0/\ell, \theta_a) \left[ I_0(r/\ell) - 1 \right]. \] \hspace{1cm} (B21)

The integration constants \( A_k \) and \( B_k \) in equation (B19) are determined by the Young–Laplace boundary condition equation (8). To first order in perturbations, it implies
\[ \sigma_{rr}(R) = -\frac{\gamma}{R_0} \left\{ 1 - \left[ 1 + \frac{d^2}{d\phi^2} \right] \frac{\delta R}{R_0} \right\}, \] \hspace{1cm} (B22)
where we have used that $\sigma_0^0 = 0$. Then, taking into account that $\sigma_r(R) \approx \sigma_0^0(R) + \delta \sigma_r(R)$, as well as that $\sigma_0^0 \approx -P_0 - \zeta \cos(2\theta_0) S_0$, and $\delta \sigma_r = -\delta P - \zeta \cos(2\theta_0) \delta S - 2\zeta \delta S_0 \sin(2\theta_0) \delta \theta$, equation (B22) translates into a boundary condition for the pressure perturbations

$$-[P'_0(R_0) + \zeta \cos(2\theta_0) S'_0(R_0)]\delta R(\phi) - \delta P(R_0, \phi) - \zeta \cos(2\theta_0) \delta S(R_0, \phi)$$

$$-2\zeta \sin(2\theta_0) S_0(R_0) \delta \theta(R_0, \phi) \approx \frac{\gamma}{R_0^2} \left[ 1 + \frac{d^2}{d\phi^2} \right] \delta R.$$  \hspace{1cm} (B23)

In Fourier space, this condition reads as

$$\delta \hat{P}_k(R_0) = \frac{\gamma}{R_0^2} (k^2 - 1) \delta \hat{R}_k - [P'_0(R_0) + \zeta \cos(2\theta_0) S'_0(R_0)] \delta \hat{R}_k$$

$$- \zeta \cos(2\theta_0) \delta \hat{S}_k(R_0) - 2\zeta \sin(2\theta_0) \delta \hat{\theta}_k(R_0).$$  \hspace{1cm} (B24)

For all modes, this boundary condition determines the integration constant $A_k$, whereas $B_k$ must vanish to avoid the pressure field to diverge at $r \to 0$. Introducing the values of these integration constants yields the final solutions for the pressure perturbation modes $\delta \hat{P}_k(r)$.

Next, we can obtain the flow perturbations by means of the force balance equation (6). For the radial velocity perturbations, it implies

$$\xi \delta \hat{u}_r = -\partial_r \delta P + \delta \hat{f}_r^0.$$  \hspace{1cm} (B25)

Therefore, the angular Fourier components of the radial velocity perturbations are given by

$$\delta \hat{v}_{r,k}(r) = \frac{1}{\xi} \left[ -\frac{d\delta \hat{P}_k(r)}{dr} + \delta \hat{f}_r^0(r) \right].$$ \hspace{1cm} (B26)

where

$$\delta \hat{f}_r^0(r) = -\zeta \cos(2\theta_0) \left\{ \left[ \frac{d}{dr} + \frac{2}{r} \right] \delta \hat{S}_k(r) + \frac{2ik}{r} S_0(r) \delta \hat{\theta}_k(r) \right\}$$

$$- \zeta \sin(2\theta_0) \left\{ \frac{ik}{r} \delta \hat{S}_k(r) - 2 \left[ S_0(r) \frac{d}{dr} + S'_0(r) + \frac{2}{r} S_0(r) \right] \delta \hat{\theta}_k(r) \right\}.$$  \hspace{1cm} (B27)

**B3. Interface dynamics**

The dynamics of the droplet interface is given by the free-boundary kinematic condition in equation (10). In Fourier space, it reads as

$$\frac{d\delta \hat{R}_k}{dr} \approx \delta \hat{v}_{r,k}(R_0).$$  \hspace{1cm} (B28)

Thus, the linear growth rate $\omega_k$ of the radius perturbations, defined by $d\delta \hat{R}_k/dt = \omega_k \delta \hat{R}_k$ is given by

$$\omega_k = \frac{\delta \hat{v}_{r,k}(R_0)}{\delta \hat{R}_k}.$$  \hspace{1cm} (B29)
Introducing all previous results, I obtain the final result:

\[
\omega_k = \frac{e^{-2i\theta_0}}{2\ell^2 \xi} \left[ \zeta a_k(R_0/\ell, \theta_0) - \frac{\gamma}{R_0} b_k(R_0/\ell, \theta_0) \right], \tag{B30}
\]

where the factors \(a_k\) and \(b_k\) are given by

\[
a_k(R_0/\ell, \theta_0) = \frac{I_{k+1}(R_0/\ell)}{I_k(R_0/\ell) I_{k-1}(R_0/\ell) I_{k+2}(R_0/\ell)} \left[ I_1(R_0/\ell) + 2(k-1) \frac{\ell^2}{R_0} I_2(R_0/\ell) \right] \\
\times \left[ 4k \frac{\ell}{R_0} \left( 1 + 2(k^2 - 1) \frac{\ell^2}{R_0^2} \right) I_{k+1}(R_0/\ell) + I_{k+2}(R_0/\ell) \right] \\
+ 4e^4 \frac{\ell}{R_0^4} F_1(k+3; \frac{R_0^2}{(4\ell^2)}) \left[ 2k \left( 3k - 2 - k e^{4i\theta_0} \right) _0 F_1(k+1; \frac{R_0^2}{(4\ell^2)}) \\
- 4(k-1) _0 F_1(k; \frac{R_0^2}{(4\ell^2)}) - 8k(k+1) \frac{\ell^2}{R_0^2} (3k - 2 - k e^{4i\theta_0}) \right] \\
\times \left[ _0 F_1(k; \frac{R_0^2}{(4\ell^2)}) - _0 F_1(k+1; \frac{R_0^2}{(4\ell^2)}) \right] \\
+ \frac{e^4}{R_0^4} \frac{\ell}{F_1(3; \frac{R_0^2}{(4\ell^2)})} \left[ \frac{1}{2} (e^{4i\theta_0} - 1) \frac{R_0^2}{\ell^2} + 4k(k+1) \right] _0 F_1(k+2; \frac{R_0^2}{(4\ell^2)}) \\
\times (k+2; \frac{R_0^2}{(4\ell^2)}) - 2(e^{4i\theta_0} + 1) _0 F_1(k; \frac{R_0^2}{(4\ell^2)}) \right] \right), \tag{B31}
\]

\[
b_k(R_0/\ell, \theta_0) = \frac{8e^4}{R_0^4} \frac{\ell^2}{F_1(k+3; \frac{R_0^2}{(4\ell^2)})} \left[ _0 F_1(k+1; \frac{R_0^2}{(4\ell^2)}) \\
- 4 \frac{\ell^2}{R_0^4} (k+1) \left[ _0 F_1(k; \frac{R_0^2}{(4\ell^2)}) - _0 F_1(k+1; \frac{R_0^2}{(4\ell^2)}) \right] \right]. \tag{B32}
\]
[7] Oriola D, Jülicher F and Brugués J 2020 Active forces shape the metaphase spindle through a mechanical instability Proc. Natl Acad. Sci. USA 117 16154–9
[8] Oriola D, Needelmen D J and Brugués J 2018 The physics of the metaphase spindle Annu. Rev. Biophys. 47 655–73
[9] Pérez-González C, Alert R, Blanch-Mercader C, Gómez-González M, Kolodziej T, Bazellieres E, Casademunt J and Trepat X 2019 Active wetting of epithelial tissues Nat. Phys. 15 79–88
[10] Alert R and Trepat X 2020 Physical models of collective cell migration Annu. Rev. Condens. Matter Phys. 11 77–101
[11] Alert R and Trepat X 2021 Living cells on the move Phys. Today 74 30–6
[12] Dell’Arciprete D, Blow M L, Brown A T, Farrell F D C, Lintuvuori J S, McVey A F, Marenduzzo D and Poon W C K 2018 A growing bacterial colony in two dimensions as an active nematic Nat. Commun. 9 4190
[13] Needelmen D and Dogic Z 2017 Active matter at the interface between materials science and cell biology Nat. Rev. Mater. 2 17048
[14] Takatori S C and Sahu A 2020 Active contact forces drive nonequilibrium fluctuations in membrane vesicles Phys. Rev. Lett. 124 158102
[15] Ramos G, Cordero M L and Soto R 2020 Bacteria driving droplets Soft Matter 16 1359–65
[16] Vatavuri H R, Hoore M, Ahaurrea-Velasco C, van Buren L, Dutto A, Auth T, Fedosov D A, Gompper G and Vermant J 2020 Active particles induce large shape deformations in giant lipid vesicles Nature 586 52–6
[17] Rajabi M, Baza H, Turiv T and Lavrentovich O D 2021 Directional self-locomotion of active droplets enabled by nematic environment Nat. Phys. 17 260–6
[18] Kokot G, Faizi H A, Pradillo G E, Snezhko A and Vlahovska P M 2022 Spontaneous self-propulsion and nonequilibrium shape fluctuations of a droplet enclosing active particles Commun. Phys. 5 91
[19] Carvalho K, Tsai F-C, Lees E, Voituriez R, Koenderink G H and Sykes C 2013 Cell-sized liposomes reveal how actomyosin cortical tension drives shape change Proc. Natl Acad. Sci. USA 110 16456–61
[20] Loiseau E, Schneider J A M, Keber F C, Pelzl C, Massiera G, Salbreux G and Bausch A R 2016 Shape remodeling and blebbing of active cytoskeletal vesicles Sci. Adv. 2 e1500465
[21] Sanchez T, Chen D T N, DeCamp S J, Heymann M and Dogic Z 2012 Spontaneous motion in hierarchically assembled active matter Nature 491 431–4
[22] Keber F C, Loiseau E, Sanchez T, DeCamp S J, Gionis L, Bowick M J, Marchetti M C, Dogic Z, and Bausch A R 2014 Topology and dynamics of active nematic vesicles Science 345 1135–9
[23] Guillamat P, Kos Z, Hardouin J, Ignés-Mullol J, Ravnik M and Sagués F 2018 Active nematic emulsions Sci. Adv. 4 eaao1470
[24] Chen Y-C, Jolicoeur B, Chueh C-C and Wu K-T 2021 Flow coupling between active and passive fluids across water–oil interfaces Sci. Rep. 11 13965
[25] Ziebert F and Aranson I S 2016 Computational approaches to substrate-based cell motility npj Comput. Mater. 2 16019
[26] Cates M E and Tjhung E 2018 Theories of binary fluid mixtures: from phase-separation kinetics to active emulsions J. Fluid Mech. 836 P1
[27] Callan-Jones A C, Joanny J-F and Prost J 2008 Viscous-fingering-like instability of cell fragments Phys. Rev. Lett. 100 258101
[28] Ben Amar M, Manyuhina O V and Napoli G 2011 Cell motility: a viscous fingering analysis of active gels Eur. Phys. J. Plus 126 19
[29] Tjhung E, Marenduzzo D and Cates M E 2012 Spontaneous symmetry breaking in active droplets provides a generic route to motility Proc. Natl Acad. Sci. USA 109 12381–6
[30] Ziebert F, Swaminathan S and Aranson I S 2012 Model for self-polarization and motility of keratocyte fragments J. R. Soc. Interface 9 1084–92
[31] Blanch-Mercader C and Casademunt J 2013 Spontaneous motility of actin lamellae fragments Phys. Rev. Lett. 110 078102
[32] Whitfield C A, Marenduzzo D, Voituriez R and Hawkins R J 2014 Active polar fluid flow in finite droplets Eur. Phys. J. E 37 9962
[33] Tjhung E, Tiribocchi A, Marenduzzo D and Cates M E 2015 A minimal physical model captures the shapes of crawling cells Nat. Commun. 6 5420
[34] Khoromskaia D and Alexander G P 2015 Motility of active fluid drops on surfaces Phys. Rev. E 92 062311
[35] Whitfield C A and Hawkins R J 2016 Instabilities, motion and deformation of active fluid droplets New J. Phys. 18 123016
[36] Lavi I, Meunier N, Voituriez R and Casademunt J 2020 Motility and morphodynamics of confined cells Phys. Rev. E 101 022404
[37] Loisy A, Eggers J and Liverpool T B 2020 How many ways a cell can move: the modes of self-propulsion of an active drop Soft Matter 16 3106–24
[38] Stegemerten F, John K and Thiele U 2021 Symmetry-breaking and motion of active drops through polarization-surface coupling (arXiv:2107.08961)
[39] Al-Izzi S C and Morris R G 2021 Active flows and deformable surfaces in development Sem. Cell Dev. Biol. 120 44–52
[40] Mietke A, Jemseena V, Kumar K V, Salzarini I F and Jülicher F 2019 Minimal model of cellular symmetry breaking Phys. Rev. Lett. 123 188101
[41] Mietke A, Jülicher F and Salzarini I F 2019 Self-organized shape dynamics of active surfaces Proc. Natl Acad. Sci. USA 116 29–34
[42] Maroudas-Sacks Y, Garion L, Shani-Zerbib L, Livshits A, Braun E and Keren K 2021 Topological defects in the nematic order of actin fibres as organization centres of Hydra morphogenesis Nat. Phys. 17 251–9
[43] Fernández P A, Buchmann B, Goychuk A, Engelbrecht L K, Raich M K, Scheel C H, Frey E and Bausch A R 2021 Surface-tension-induced budding drives alveologenesis in human mammary gland organoids Nat. Phys. 17 1130–6
[44] Khoromskaia D and Salbreux G 2021 Active morphogenesis of patterned epithelial shells (arXiv:2111.12820)
[45] Hoffmann L A, Carenza L N, Eckert J and Giomi L 2022 Theory of defect-mediated morphogenesis Sci. Adv. 8 2712
[46] Fausti G, Tjhung E, Cates M E and Nardini C 2021 Capillary interfacial tension in active phase separation Phys. Rev. Lett. 127 068001
[47] Joanny J-F and Ramaswamy S 2012 A drop of active matter J. Fluid Mech. 705 46–57
[48] Saffman P G and Taylor G 1958 The penetration of a fluid into a porous medium or Hele–Shaw cell containing a more viscous liquid Proc. R. Soc. A 245 312–29
[49] Casademunt J 2004 Viscous fingering as a paradigm of interfacial pattern formation: recent results and new challenges Chaos 14 809–24
[50] Zwicker D, Seyboldt R, Weber C A, Hyman A A and Jülicher F 2017 Growth and division of active droplets provides a model for protocells Nat. Phys. 13 408–13
[51] Seyboldt R and Jülicher F 2018 Role of hydrodynamic flows in chemically driven droplet division New J. Phys. 20 105010
[52] Driscoll M, Delmotte B, Youssef M, Sacanna S, Donev A and Chaikin P 2017 Unstable fronts and motile structures formed by microrollers Nat. Phys. 13 375–9
[53] Patteson A E, Gopinath A and Arratia P E 2018 The propagation of active–passive interfaces in bacterial swarms Nat. Commun. 9 5373
[54] Miles C J, Evans A A, Shelley M J and Spagnolie S E 2019 Active matter invasion of a viscous fluid: unstable sheets and a no-flow theorem Phys. Rev. Lett. 122 098002
[55] Bhattacharjee T, Amchin D B, Alert R, Ott J A and Datta S S 2022 Chemotactic smoothing of collective migration eLife 11 e71226
[56] Alert R, Martínez-Calvo A and Datta S S 2022 Cellular sensing governs the stability of chemotactic fronts Phys. Rev. Lett. 128 148101
[57] Greenspan H P 1976 On the growth and stability of cell cultures and solid tumors J. Theor. Biol. 56 229–42
[58] Khain E and Sander L M 2006 Dynamics and pattern formation in invasive tumor growth Phys. Rev. Lett. 96 188103
[59] Basan M, Joanny J-F, Prost J and Risler T 2011 Undulation instability of epithelial tissues Phys. Rev. Lett. 106 158101
[60] Nagilla A, Prabhakar R and Jadhav S 2018 Linear stability of an active fluid interface Phys. Fluids 30 022109
[61] Bogdan M J and Savin T 2018 Fingering instabilities in tissue invasion: an active fluid model R. Soc. Open Sci. 5 181579
[62] Martin M and Risler T 2021 Visco-capillary instability in cellular spheroids New J. Phys. 23 033032
[63] Ben-Jacob E, Cohen I and Levine H 2000 Cooperative self-organization of microorganisms Adv. Phys. 49 395–554
[64] Allen RJ and Waclaw B 2019 Bacterial growth: a statistical physicist’s guide Rep. Prog. Phys. 82 016601
[65] Kitsunezaki S 1997 Interface dynamics for bacterial colony formation J. Phys. Soc. Japan 66 1544–50
[66] Müller J and van Saarloos W 2002 Morphological instability and dynamics of fronts in bacterial growth models with nonlinear diffusion Phys. Rev. E 65 061111
[67] Farrell F D C, Hallatschek O, Marenduzzo D and Waclaw B 2013 Mechanically driven growth of quasi-two-dimensional microbial colonies Phys. Rev. Lett. 111 168101
[68] Amar M B 2013 Chemotaxis migration and morphogenesis of living colonies Eur. Phys. J. E 36 64
[69] Amar M B 2016 Collective chemotaxis and segregation of active bacterial colonies Sci. Rep. 6 21269
[70] Doostmohammadi A, Thampi S P and Yeomans J M 2016 Defect-mediated morphologies in growing cell colonies Phys. Rev. Lett. 117 048102
[71] Wang X, Stone H A and Golestanian R 2017 Shape of the growing front of biofilms New J. Phys. 19 125007
[72] Trinschek S, John K and Thiele U 2018 Modelling of surfactant-driven front instabilities in spreading bacterial colonies Soft Matter 14 4464–76
[73] Yaman Y I, Demir E, Vetter R and Kocabas A 2019 Emergence of active nematics in chaining bacterial biofilms Nat. Commun. 10 2285
[74] Williamson J J and Salbreux G 2018 Stability and roughness of interfaces in mechanically regulated tissues Phys. Rev. Lett. 121 238102
[75] Büsscher T, Diez A L, Gompper G and Elgeti J 2020 Instability and fingering of interfaces in growing tissue New J. Phys. 22 083005
[76] Alert R, Blanch-Mercader C and Casademunt J 2019 Active fingering instability in tissue spreading Phys. Rev. Lett. 122 088104
[77] Trenado C, Bonilla L L and Martínez-Calvo A 2021 Fingering instability in spreading epithelial monolayers: roles of cell polarisation, substrate friction and contractile stresses Soft Matter 17 8276–90
[78] Sankararaman S and Ramaswamy S 2009 Instabilities and waves in thin films of living fluids Phys. Rev. Lett. 102 118107
[79] Sarkar N and Basu A 2012 Instabilities and diffusion in a hydrodynamic model of a fluid membrane coupled to a thin active fluid layer Eur. Phys. J. E 35 115
[80] Sarkar N and Basu A 2013 Generic instabilities in a fluid membrane coupled to a thin layer of ordered active polar fluid Eur. Phys. J. E 36 86
[81] Maitra A, Srivastava P, Rao M and Ramaswamy S 2014 Activating membranes Phys. Rev. Lett. 112 258101
[82] Yang X and Wang Q 2014 Capillary instability of axisymmetric, active liquid crystal jets Soft Matter 10 6758–76
[83] Blow M L, Agil M, Liebchen B and Marenduzzo D 2017 Motility of active nematic films driven by ‘active anchoring’ Soft Matter 13 6137–44
[84] Alonso-Matilla R and Saintillan D 2019 Interfacial instabilities in active viscous films J. Non-Newton. Fluid Mech. 269 57–64
[85] Soni H, Luo W, Pelcovits R A and Powers T R 2019 Stability of the interface of an isotropic active fluid Soft Matter 15 6318–30
[86] Liang C-C, Yasuda K, Komura S, Wu K-A and Chen H-Y 2020 Dynamics of a membrane coupled to an active fluid Phys. Rev. E 101 042601
[87] Lin L-S and Chen H-Y 2021 Dynamics and instabilities of the free boundary of a two-dimensional dry active nematic aggregate J. Phys. Commun. 5 115013
[88] Thijssen K, Kusters G L A and Doostmohammadi A 2021 Activity-induced instabilities of brain organoids Eur. Phys. J. E 44 147
[89] Mueller R and Doostmohammadi A 2021 Phase field models of active matter (arXiv:2102.05557)
[90] Blow M L, Thampi S P and Yeomans J M 2014 Biphase, isotropic, active nematics Phys. Rev. Lett. 113 248303
[91] Gioria L and DeSimone A 2014 Spontaneous division and motility in active nematic droplets Phys. Rev. Lett. 112 147802
[92] Fialho A R, Blow M L and Marenduzzo D 2017 Anchoring-driven spontaneous rotations in active gel droplets Soft Matter 13 5933–41

21
[93] Gao T and Li Z 2017 Self-driven droplet powered by active nematics Phys. Rev. Lett. 119 108002
[94] Metselaar L, Yeomans J M and Doostmohammadi A 2019 Topology and morphology of self-deforming active shells Phys. Rev. Lett. 123 208001
[95] Coelho R C V, Araújo N A M and Telo da Gama M M 2019 Active nematic–isotropic interfaces in channels Soft Matter 15 6819–29
[96] Coelho R C V, Araújo N A M and Telo da Gama M M 2020 Propagation of active nematic–isotropic interfaces on substrates Soft Matter 16 4256–66
[97] Ruske L J and Yeomans J M 2021 Morphology of active deformable 3D droplets Phys. Rev. X 11 021001
[98] Doxzen K, Vedula S R K, Leong M C, Hirata H, Gov N S, Kabla A, Ladoux B and Lim C T 2013 Guidance of collective cell migration by substrate geometry Integr. Biol. 5 1026
[99] Ductos G, Erlenkämper C, Joanny J-F and Silberzan P 2017 Topological defects in confined populations of spindle-shaped cells Nat. Phys. 13 58–62
[100] Bade N D, Kamien R D, Assoian R K and Stebe K J 2018 Edges impose planar alignment in nematic monolayers by directing cell elongation and enhancing migration Soft Matter 14 6867–74
[101] Comelles J, Soumya S S, Lu L, Le Maout E, Anvita S, Salbreux G, Jülicher F, Inamdar M M and Riveline D 2021 Epithelial colonies in vitro elongate through collective effects eLife 10 e57730
[102] Xie T, St Pierre S R, Olaranont N, Brown L E, Wu M and Sun Y 2021 Condensation tendency and planar isotropic actin gradient induce radial alignment in confined monolayers eLife 10 e60381
[103] Zhang Q, Li J, Nijjer J, Lu H, Kothari M, Alert R, Cohen T and Yan J 2021 Morphogenesis and cell ordering in confined bacterial biofilms Proc. Natl. Acad. Sci. USA 118 e2107107118
[104] Blanchin L, Boujemaa-Paterski R, Sykes C and Plastino J 2014 Actin dynamics, architecture, and mechanics in cell motility Physiol. Rev. 94 235–63
[105] Schakenraad K, Ernst J, Pomp W, Danen E H J, Merks R M H, Schmidt T and Giomi L 2020 Mechanical interplay between cell shape and actin cytoskeleton organization Soft Matter 16 6328–43
[106] Ductos G, Blanch-Mercader C, Yashunsky V, Salbreux G, Joanny J-F, Prost J and Silberzan P 2018 Spontaneous shear flow in confined cellular nematics Nat. Phys. 14 728–32
[107] Guillamat P, Blanch-Mercader C, Pernollet G, Kruse K and Roux A 2022 Integer topological defects organize stresses driving tissue morphogenesis Nat. Mater. 21 588
[108] Huang Z, Omori T and Ishikawa T 2020 Active droplet driven by a collective motion of enclosed microswimmers Phys. Rev. E 102 022603
[109] de Gennes P-G and Prost J 1993 The Physics of Liquid Crystals 2nd edn (New York: Oxford University Press)
[110] Beris A N and Edwards B J 1994 Thermodynamics of Flowing Systems with Internal Microstructure (New York: Oxford University Press)
[111] Selinger J V 2016 Introduction to the Theory of Soft Matter. From Ideal Gases to Liquid Crystals (Heidelberg: Springer)
[112] Guyon E, Hulin J-P, Petit L and Mitescu C D 2001 Physical Hydrodynamics (New York: Oxford University Press)
[113] Santhosh S, Nejad M R, Doostmohammadi A, Yeomans J M and Thampi S P 2020 Activity induced nematic order in isotropic liquid crystals J. Stat. Phys. 180 699–709
[114] Senoussi A, Kashida S, Voituriez R, Galas J-C, Maitra A and Estevez-Torres A 2019 Tunable corrugated patterns in an active nematic sheet Proc. Natl. Acad. Sci. USA 116 22464–70
[115] Trinschek S, John K, Lecuyer S and Thiele U 2017 Continuous versus arrested spreading of biofilms at solid-gas interfaces: the role of surface forces Phys. Rev. Lett. 119 078003
[116] Trinschek S, Stegemerten F, John K and Thiele U 2020 Thin-film modeling of resting and moving active droplets Phys. Rev. E 101 062802
[117] Nejad M R and Yeomans J M 2022 Active extensional stress promotes 3D director orientations and flows Phys. Rev. Lett. 128 048001
[118] Soni V, Billilign E S, Magkiriadou S, Sacanna S, Bartolo D, Shelley M J and Irvine W T M 2019 The odd free surface flows of a colloidal chiral fluid Nat. Phys. 15 1188–94