Extensile stress promotes out-of-plane flows in active layers

Mehrana R. Nejad\(^1\) and Julia M. Yeomans\(^1\)

\(^1\)The Rudolf Peierls Centre for Theoretical Physics, Department of Physics, University of Oxford, Parks Road, Oxford OX1 3PU, UK

We use numerical simulations and linear stability analysis to study an active nematic layer where the director is allowed to point out of the plane. Our results highlight the difference between extensile and contractile systems. Contractile stress suppresses the flows perpendicular to the layer and favours in-plane orientations of the director. By contrast extensile stress promotes instabilities that can turn the director out of the plane, leaving behind a population of distinct, in-plane regions that continually elongate and divide. Our results suggest a mechanism for the initial stages of layer formation in living systems, and explain the propensity of dislocation lines in three-dimensional active nematics to be of twist-type in extensile or wedge-type in contractile materials.

Because living systems exist out of equilibrium \([1]\) they can exhibit novel behaviors that cannot be captured by conventional equilibrium statistical mechanics \([2]\) such as coherent animal flocks \([3]\) and cell crawling and division \([4, 5]\).

The hydrodynamics of active particles, such as bacteria, cells and microtubules driven by kinesin motors lies in the low Reynolds number regime and they can be modeled as force dipoles with nematic symmetry. The direction of the force dipoles can be inwards along the dipolar axis (contractile systems) or outwards (extensile systems). Both extensile and contractile systems are found in nature: actomyosin suspensions are contractile, microtubule-kinesin motor suspensions and bacteria are extensile, while confluent cell layers can be either \([6, 7]\).

Active stresses destabilise the nematic phase resulting in a state of chaotic flows, with prominent vorticity and fluid jets, known as active turbulence \([8–15]\). In two dimensions active turbulence is characterized by the continuous creation and annihilation of +1/2 and -1/2 topological defect pairs in the nematic director field \([16–18]\). The +1/2 defects have polar symmetry and hence are self-propelled. Recently, three-dimensional active suspensions have also attracted a considerable amount of interest. In contrast to 2D, 3D active flows are governed by the creation and annihilation of disclination lines and loops \([19–21]\).

There is significant understanding of completely 2D or 3D active materials. However many biological systems evolve from 2D to 3D structures during their life cycle. The growth of a 2D layer into the third dimension leads to the formation of biofilms \([22, 23]\), where the transition is often initiated by the formation of a vertically aligned core of bacteria \([24, 25]\). Gastrulation is a vital step in the early development of most animals when a single layer epithelium is reorganised into a multilayer structure of differentiated cells that will form specific tissues and organs \([26]\). To understand these processes further, in this paper we study the transition from 2D to 3D in active nematics showing that extensile and contractile materials demonstrate remarkably different behaviours.

Equations of motion: We consider an active nematic layer in the \(x-y\) plane. Allowing the director and velocity fields to have components along \(x, y\) and \(z\) directions, we numerically solve the active nematic hydrodynamic equations of motion \([27]\).

The nematic order is defined by the 3D tensor \(Q = 3S(nn - I/3)/2\), with director field \(n\) and scalar order parameter \(S\), and evolves according to \(D_t Q - S = H/\gamma\) \([28]\). The nematic tensor relaxes towards equilibrium at a rate determined by the rotational viscosity \(\gamma\), and \(D_t\) and \(S\) describe the material derivative and co-rotational advection due to gradients of the velocity field \([27]\).

The nematic equilibrium follows from the molecular field \(H\), which is a functional derivative of the free energy. The free energy density includes a Landau-de Gennes term \(F_{\text{bulk}} = \frac{\kappa}{2} Q^2 + \frac{\lambda}{4} Q^4 + \frac{\mu}{2} Q^3\) where we choose the prefactors so that the equilibrium is in the nematic phase. We also include a distortion energy density that penalizes deformations in the orientation field, choosing the one-constant elastic approximation \(F_{\text{el}} = \frac{K}{2} (\nabla Q)^2\).

The velocity field \(u\) obeys the incompressible Navier-Stokes equation \(D_t u = \nabla \cdot \Pi/\rho\), where \(\rho\) is the density and the generalized stress \(\Pi\) has viscous, elastic, and active components \([29]\). The active stress is described by \(-\zeta Q\) \([30]\) where the divergence of \(Q\) drives active forcing which destabilises the nematic ordering. The equations of motion are solved using a hybrid lattice Boltzmann method \([27]\). For details and parameter values see the Supplemental Material (SM).

Results: In Fig. 1 we compare the behaviour of an extensile system with activity \(\zeta = 0.008\) with that of a contractile system with \(\zeta = -0.008\). The figure shows that contractile stresses suppress perturbations of the director field in the direction perpen-
FIG. 1. Snapshots from simulations of 2D active nematics layers. Color denotes the magnitude of the in-plane order \( S_{in} = |1 - n_z|^2 \) from in-plane (black) to out-of-plane (white): a) extensile stress, defects in cyan. 3D twist-type defects are represented by circles, \( +1/2 \) and \( -1/2 \) in-plane wedge-type defects are shown by one and three arrows, respectively. b) contractile stress, 2D \( \pm 1/2 \) topological defects are shown in white. c) Area fraction of regions with out of plane director as a function of activity. d) In-plane \( u_{in} \) and out-of-plane \( u_z \) velocities for contractile (yellow, \( u_z = 0 \)) and extensile (pink, orange) driving.

dicular to the layer, leading to the usual 2D active dynamics (Fig. 1(b)). In extensile systems, however, the director has non-zero out-of-plane components except within dynamic, elongated domains (Fig. 1(a) and Movie 1). This behaviour is quantified in Fig. 1(c) where we plot the area fraction of the out-of-plane regions as a function of activity, showing that this quantity remains zero for the contractile case, but increases with activity in extensile systems. Histograms of the corresponding in-plane and out-of-plane flow fields are shown in Fig. 1(d). In contractile systems flows remain in the \( x-y \) plane whereas in the extensile case the flow develops substantial components along \( z \) which act to drive the director into the third dimension.

We will discuss the dynamics of the in-plane domains in the extensile case below, but first we perform a linear stability analysis of the nematohydrodynamic equations around the fully-aligned in-plane nematic phase to further understand the different behaviour of extensile and contractile systems. Denoting the Fourier transform of any fluctuating field by \( \delta f(\mathbf{r},t) = \int d\mathbf{q} \tilde{f}(\mathbf{q},\omega) e^{i\mathbf{q}\cdot\mathbf{r}+\omega t} \), in the long-wave-length and zero Reynolds number limit the growth rate of a perturbation reads:

\[
\omega_{out} = \frac{3\zeta}{4\eta} \cos^2 \theta, \quad \omega_{in} = \frac{3\zeta}{4\eta} \cos 2\theta, \quad (1)
\]

where \( \omega_{out} \) and \( \omega_{in} \) are the growth rates of the out-of-plane and in-plane components of the director, \( \theta \) is the angle between the wavevector of the perturbation and the direction of the order and \( \eta \) is the viscosity. Details of the calculations and the full form of the growth rates (including the flow-aligning dependence) can be found in the SM.

The onset of instability is given by the condition \( \omega_{in/out} > 0 \). The in-plane component shows the well-known instability of 2D active nematics to bend
FIG. 2. a) Variation of the number of snakes with time. b) Number of snakes as a function of activity at steady state. c) Director in a snake. Cyan outline: moving along the blue dashed arrow, crossing the width of a snake, the director twists by $\pi$. Yellow outline: top view of the director across the width of a snake. Magenta outline: 3D twist type defects are commonly found at the ends of the snakes. The blue circle shows the core of the defect, $\hat{t}$ represents the normal to the layer, and the blue dashed line connects the center of the twist type defect to the position with an in-plane director. $\alpha$ is the angle between this line and the local director. The director rotates out of the plane around the rotation vector $\Omega$ to form the twist defect. d) Distribution of the angle between the director and the tangent to the boundary of snakes. The histogram peaks at $\cos(\delta) = 1$, indicating parallel alignment of the director with the boundary. e) Distribution of the angle $\alpha$ in extensile systems.

(splay) perturbations in extensile (contractile) systems [30]. By contrast the growth rate of the out-of-plane component does not change sign for different values of $\theta$ and is positive (negative) for extensile (contractile) systems. Thus the out-of-plane component only grows in extensile systems and is maximum in places with in-plane bend perturbations ($\theta = 0, \pi$) and zero in places with in-plane splay fluctuations ($\theta = \pi/2$).

**In-plane domains in extensile active nematics:** We now return to consider the elongated domains where the director field remains in the $x$-$y$ plane. These initially form in regions of splay distortion where the flow fields along the $z$-axis are insufficiently strong to push the director field out of the plane. For convenience we will refer to the in-plane domains as *snakes*.

After a transient phase the average number of snakes fluctuates around a constant value (Fig. 2(a)) which first increases and then decreases with increasing activity (Fig. 2(b)). This reflects a balance between snakes elongating and then breaking up, and the possibility that local flows will be sufficiently strong to destroy a snake by pushing the director out of the $x$-$y$ plane.

To understand how the snakes lengthen and divide we study their director and flow fields. We first measure $\cos(\delta)$, the angle between the orientation of the director at the boundary of a snake and the local tangent to the boundary. The histogram of $\cos(\delta)$, shown in Fig. 2(d) peaks at $\cos(\delta) = 1$, showing that the director inside a snake tends to align parallel to its long edges.

Therefore, along the boundaries of a snake the director rotates through $\pi/2$ to match the surrounding vertical director configuration (Fig. 2(c)) and as a result, looking at a cross-section across the width of a snake, the director twists by $\pi$ (cyan and yellow outlines in Fig. 2(c)). At the ends of the snake this results in twist defects with the director configuration shown in the magenta outline in Fig. 2(c).

An angle which characterises twist defects is $\alpha$, the angle between the line which connects the center of the defect to the position of the in-plane director and the direction of the in-plane director itself (magenta outline in Fig. 2(c)). Fig. 2(e) shows that $\alpha$ has a peak at $\alpha = 0$, indicating that the twist-type defects are predominantly radial. This agrees with the results from the linear stability analysis that at defect heads (tails), where the bend (splay) deformation is large, the director develops a component along $z$ (stays in the $x$-$y$ plane).
FIG. 3. a) Average flow along the direction of the elongation of snakes (measured at the ends i.e. within the yellow box). The origin corresponds to the blue dot and $x > 0$ always corresponds to outside the snake. $(\mathbf{u}_s \cdot \hat{r}) > 0$, indicating that active flows elongate the snakes.  

b) Flows around a snake. c)-e) Evolution of a snake. Elongated snakes undergo a bend instability and form defects. The director then moves to the third direction dividing the snake into two with twist-type defects at their ends.

We are now in a position to understand the dynamics of a snake. The stresses which results from the twist defects set up flows which act to elongate the snakes and to align the director field inside them (Fig. 3(a),(b)). The ensuing evolution is illustrated in Figs. 3(c)-(e). Since the system is extensile and the director is parallel to their length, the elongated snakes undergo a bend instability (see Movie 1). The growth of a bend deformation is equivalent to the formation of a pair of two-dimensional, $\pm 1/2$ defects (orange outlines in Fig. 1(a) and Fig. 3(c)-(e)). We have seen that bend deformations are unstable to director perturbations perpendicular to the layer and, due to the large bend deformations at the position of the defects, the director rotates out of the plane and the snake splits into two smaller snakes terminated by twist director configurations (Fig. 2(c)).

Relation to 3D active turbulence: The behavior that we have identified in two dimensions persists into three dimensions. Fully-developed 3D active turbulence is characterised by motile disclination lines that form closed loops that can appear, grow, shrink and disappear [19–21]. Experiments and simulations have shown that twist (wedge) type defects are observed in extensile (contractile) systems [19–21, 31] which can be explained by our model. The director configuration on a plane locally perpendicular to a dislocation line can be characterised by the twist angle $\beta$ between the unit tangent to the disclination line and the axis around which the director rotates out of the plane (Fig. 2(c)). $\beta = 0, \pi$ correspond to cross sections of the dislocation line with the configurations of $+1/2$ and $-1/2$ defects, respectively, and other values indicate degrees of twist with $\beta = \pi/2$ corresponding to a pure twist configuration. Fig. 4(a)-(b) compare the distribution of $\beta$ for the single layer considered here to simulations of full 3D active turbulence keeping the activity the same, and considering both extensile and contractile systems. The figure shows that similar behaviour is observed in both 2D and 3D: in contractile systems defects are predominantly two dimensional, whereas in the extensile system there is a clear preference for introducing twist defects.

The transition from 2D to 3D is a vital step in many biological processes. Biofilm formation can be initiated by cells turning to point at right angles to the substrate [22–25]. This has been described in terms of mechanical instabilities due to in-plane compression resulting from cell divisions or effective interactions between bacteria. However, noting that bacterial division is a source of extensile stress, the mechanism we introduce here provides another possible route to cell verticalization.

Epithelial layers evolve into 3D configurations...
during embryogenesis; examples are the ingestion of cells at the primitive streak in the chick embryo [32] and the inward folding of an epithelial sheet in the fruit fly embryo [33]. Our work suggests that localised activity and cell divisions might play a role in the formation of these structures.

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**Supplemental Material:**

**MOVIE DESCRIPTION**

Movie 1: Time evolution of snakes in extensile active nematics with $\zeta = 0.008$. The colormap denotes the magnitude of the in-plane order ($S_{in} = 1 - n_2^2/2$), where red and white denote in-plane and out-of-plane orientation of the director, respectively. Defects are shown in cyan. $\pm 1/2$ defects are represented by one and three arrows, respectively, and twist type defects are shown by circles.

**METHODS**

Nematohydrodynamic equations

We study the evolution of velocity field $\mathbf{u}$ and the nematic tensor $\mathbf{Q} = 3S(nn - I/3)/2$, where $S$ denotes the magnitude of the nematic order, $n$ is the director, and $I$ the identity tensor [34]. The dynamics of the nematic tensor is governed by [28]

$$\partial_t \mathbf{Q} - S = \mathbf{H} / \gamma,$$

where $\gamma$ is the rotational viscosity and $S$ is the co-rotational advection term that accounts for the impact of the strain rate $E = (\nabla \mathbf{u}^T + \nabla \mathbf{u})/2$ and vorticity $\Omega = (\nabla \mathbf{u}^T - \nabla \mathbf{u})/2$ on the director field. The co-rotational advection has the form

$$S = (\lambda E + \Omega) \cdot \mathbf{Q} + \mathbf{Q} \cdot (\lambda E - \Omega) - 2\lambda \mathbf{Q} : (\nabla \mathbf{u}),$$

where the flow-aligning parameter $\lambda$ controls the coupling between the orientation field and the flow, determining whether the nematogens align or tumbling in a shear flow.

The relaxation of the orientational order is controlled by a free energy $F(T) = \int f dV$ through the molecular field,

$$\mathbf{H} = -\frac{1}{3} \text{Tr} \frac{\delta f}{\delta \mathbf{Q}}.$$  

The free energy density has two contributions, the Landau-de Gennes bulk free energy density and the elastic free energy density due to spatial inhomogeneities in the nematic tensor [34]:

$$f = \frac{A}{2} Q^2 + \frac{B}{3} Q^3 + \frac{C}{4} Q^4 + \frac{K}{2} (\nabla \mathbf{Q})^2,$$

assuming a single Frank elastic constant $K$. We choose the coefficients of the bulk terms $A, B$ and $C$ such that the ground state of the free energy is the nematic phase. We solve the full incompressible Navier-Stokes equations to retain hydrodynamic interactions in the active fluid:

$$\rho (\partial_t + \mathbf{u} \cdot \nabla) \mathbf{u} = \nabla \cdot \mathbf{H},$$

$$\nabla \cdot \mathbf{u} = 0,$$

where $\rho$ and $\mathbf{u}$ are the density and velocity fields, respectively. $\mathbf{H}$ is a generalized stress tensor that has both passive and active contributions. The passive part of the stress includes the viscous stress, $\mathbf{H}^\text{pass} = 2 \eta \mathbf{E}$, and the elastic stress

$$\mathbf{H}^\text{elastic} = -P \mathbf{I} + 2\lambda \mathbf{Q} : (\mathbf{H} - \Omega) - \lambda \mathbf{Q} \cdot \mathbf{H} - \mathbf{Q} : \nabla \mathbf{u} - \frac{\delta f}{\delta \nabla \mathbf{Q}} - \frac{1}{2} \mathbf{Q} \cdot \nabla \mathbf{Q} - \frac{3}{2} \mathbf{Q} \cdot \nabla \mathbf{Q}.$$

where $P$ is the isotropic pressure and $\eta$ is the viscosity [28]. The active stress accounts for changes in the flow field caused by continual energy injection at the microscopic scale. The activity generates flows for nonzero divergence and the active stress takes the form [30]

$$\mathbf{H}^\text{act} = -\zeta \mathbf{Q}.$$  

The parameter $\zeta$ determines the strength of the activity, with positive and negative values denoting extensile and contractile stresses, respectively.

**Numerical implementation**

The equations of active nematohydrodynamics are solved using a hybrid lattice Boltzmann and finite difference method [27], with the discrete space and time steps defining the simulation units. Density is taken as constant $\rho = 1$ and we chose values of the parameters which reproduce active turbulence in a 2D system: $\gamma = 1.4$, $K = 0.01$, $\eta = 2/3$, $A = 0$, $B = -0.3$, $C = 0.3$, $-0.02 < \zeta < 0.02$ and the system size is $200 \times 200$. The simulations start with in-plane nematic order, and in-plane and out-of-plane perturbations are defined as $\delta \theta_{in} = 2\pi \chi_{in}$ and $\delta \theta_{out} = (\pi/2) \chi_{out}$, respectively. Both in-plane ($\chi_{in}$) and out-of-plane noise ($\chi_{out}$) are taken from a uniform distribution over the interval $[-1/10, 1/10]$. For 3D simulations we used a system size $120 \times 120 \times 120$. In Fig. 2(a) in the main text, the average is taken over 5 datapoints in a $10^5$ timestep interval. In Figs. 1(c) and 2(b) in the main text, the average is taken in the steady state every $2 \times 10^4$ timesteps, over 10 datapoints.
FIG. 5. a) Average flow field around +1/2 defects in a contractile system. In contractile systems, the average flow stays within the layer. The dashed blue line shows the direction of the tail of the +1/2 defect. b) Average flow around a 3D twist-type defect in extensile systems with 0 < α < 10°. The average flow has an out-of-plane component in extensile systems. The blue dashed line points towards the region with largest in-plane director.

Defining snakes and their boundaries

We consider lattice sites in which the director makes an angle less than 10° with the 2D layer as an in-plane site. To find the number of snakes, we attribute a value 1 (0) to in-plane (out-of-plane) sites. A snake is defined as connected sites with value 1. We define the boundary of the snakes as in-plane sites which have at least one out-of-plane neighbouring site.

Flow-field along snakes

To find the average flow at the end of the snakes, we take \( \mathbf{r} \) (introduced in Fig. 3(a) in the main text) to be along the local direction of the elongation of the snakes, and average the flow over the 10 lattice sites next to the end and in the direction of ±\( \mathbf{r} \). We ignore snakes smaller than 20 lattice units, as small snakes usually shrink and form vertical regions. In Fig. 3(a) in the main text, the average is taken over the flows at the end of different snakes every 10\(^4\) timesteps over a 2 × 10\(^5\) interval.

Characterising defects

To find the position and the type of defects, we apply the method used in Ref. [35]. We probe the director orientation by moving clock-wise on closed square paths comprising 2 × 2 lattice sites. If the direction of the director differs by more than \( \pi / 2 \) on the first and last (co-incident) points on the path, we assign the center of the grid as the position of a defect. To find defects in 3D systems, we repeat the procedure of searching on 2 × 2 grids in the x-z and y-z planes. The rotation axis of the defect \( \Omega \) follows by finding the outer product of pairs of directors around the defect.

To find the defect angle \( \alpha \) for twist-type defects, we consider a 3 × 3 square around the defect and find the neighboring site with largest in-plane director component. We then define \( \alpha \) as the angle between the line which connects the center of the defect to this site, and the director orientation at the site.

In the manuscript, we refer to defects as 2D (3D) defects when \( |\cos \beta| > 0.95 \) (\( |\cos \beta| < 0.95 \)), where \( \beta \) is the twist angle.

Flow-field around defects

To find the average flow field around defects, we choose a frame centered at the position of defects. For +1/2 defects in the contractile system, we choose the x-axis to be along the head of the defects. For twist-type defects in the extensile system, we set the direction of the x-axis so that \( -\mathbf{x} \) points along the line which connects the center of a defect to the neighbouring grid with maximum in-plane director (dashed blue line in Fig. 5(b)). Fig. 5 shows the average flow around (a) in-plane +1/2 defects, (b) twist-type defects with 0 < \( \alpha < \pi / 2 \).

LINEAR STABILITY ANALYSIS

To understand the distinct behaviour of extensile and contractile systems, we consider a layer in the x-y plane with 3D director field, and study the growth rate of in-plane and out-of-plane perturbations deep in the nematic phase where \( S \approx 1 \). Without loss of
FIG. 6. a) Results of linear stability analysis as a function of the tumbling parameter $\lambda$ for an extensile system. The out-of-plane component of the perturbation grows for all values of the tumbling parameter. (b), (c) Resulting twist angle for different values of the tumbling parameter in extensile systems. The peak of the distributions corresponds to 3D twist-type defects for all values of the tumbling parameter. Increasing tumbling parameter makes the peak sharper. d) Results of linear stability analysis as a function of the tumbling parameter $\lambda$ for a contractile system. The out-of-plane component of the perturbation only grows for large positive values of the tumbling parameter and for a specific interval in $\theta$. (e), (f) Resulting twist angle for different values of tumbling parameter in contractile systems. In agreement with the linear stability analysis, a negative value of the tumbling parameter hardly affects the distribution which favors wedge-type defects. However, a large positive value of the tumbling parameter leads to a much flatter distribution.

generality, we consider the direction of the nematic order to be along the $x$-axis and use the nematohy-
dynamic equations to find the dynamics of the perturbations in the zero Reynolds number regime.
Denoting the Fourier transform of any fluctuating field by $\delta f(r, t) = \int dq \tilde{f}(q, \omega) e^{i q \cdot r + \omega t}$, we can find the closed form for the evolution of the perturbations in the director field, which read:

$$\frac{\partial}{\partial t} \tilde{Q}_{xy} = \left[ \frac{\zeta}{2\eta} \left\{ 2A \cos^2 2\theta + 3 \sin^2 \theta \cos 2\theta \right\} - \frac{K}{\gamma} q^2 \right] \tilde{Q}_{xy},$$  \hspace{1cm} (10)

$$\frac{\partial}{\partial t} \tilde{Q}_{zz} = \frac{\zeta}{2\eta} A \left\{ 2 \cos^2 \theta \tilde{Q}_{zz} + \sin 2\theta \tilde{Q}_{yz} \right\} - \frac{K}{\gamma} q^2 \tilde{Q}_{zz},$$  \hspace{1cm} (11)

$$\partial_t \tilde{Q}_{yz} = -\frac{\lambda \zeta}{12\eta} \left\{ 2 \sin^2 \theta \tilde{Q}_{yz} + \sin 2\theta \tilde{Q}_{zz} \right\} - \frac{K}{\gamma} q^2 \tilde{Q}_{yz},$$  \hspace{1cm} (12)

In the long-wavelength limit, the growth-rates of the perturbations simplify to

$$\omega_{out} = \frac{\zeta}{4\eta} \left\{ -\frac{2}{3} \lambda + 3 \cos^2 \theta (1 + \lambda) \right\} - \frac{K}{\gamma} q^2,$$ \hspace{1cm} (13)

$$\omega_{in} = \frac{\zeta}{4\eta} \cos 2\theta \left\{ \frac{7}{3} \lambda \cos 2\theta + 3 \right\} - \frac{K}{\gamma} q^2,$$ \hspace{1cm} (14)

where $\omega_{out}$ ($\omega_{in}$) denotes the growth rate of the out-of-plane (in-plane) component.
The role of tumbling parameter

In Figs. 6(a) and (d) we represent the result of the linear stability analysis for extensile and contractile systems, respectively. In these figures, the onset of instability in the out-of-plane direction is given by $\omega_{\text{out}} > 0$.

We know from theories of 2D active nematics that in-plane splay (bend) perturbations grow in contractile (extensile) systems, and that increasing the tumbling parameter increases (decreases) the growth-rate of bend (splay) perturbations in extensile (contractile) systems [36, 37]. As a result of the growth of bend (splay) perturbations in extensile (contractile) systems, topological defects form.

Fig. 6(a) shows that in extensile systems, in the regimes where bend perturbations grow, the out-of-plane perturbations always grow ($\omega_{\text{out}} > 0$) independent of the value of the tumbling parameter $\xi$. This explains the reason behind the formation of 3D twist-type defects in extensile systems in our simulations. In Figs. 6(b) and (c) we represent the distribution of defect twist angles for different values of the tumbling parameter. For all values of the tumbling parameter, the peak corresponds to twist-type defects in agreement with Fig. 6(a) and indicates that the peak becomes sharper (wider) for positive (negative) flow-aligning parameter $\lambda = 0.6$ ($\lambda = -0.6$) in extensile systems. This is in agreement with Fig. 6(a) in which the magnitude of $\omega_{\text{out}}$ increases by increasing the tumbling parameter.

Fig. 6(d) shows that in contractile systems the growth rate of the out-of-plane component of the perturbation is negative in most regions of the phase space except for large positive values of tumbling parameter, in which $\omega_{\text{out}} > 0$ for a specific range of $\theta$. In Figs. 6(e) and (f), we represent the distribution of the twist angle of defects for different values of the tumbling parameter in simulations of contractile systems. In agreement with the results of the linear stability analysis, a negative value of tumbling parameter hardly changes the distribution of defect type, with a strong preponderance of wedge-type defects. However, a large positive value of tumbling parameter leads to a more uniform distribution of twist angles.

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