Lattice model of the wing disc pouch eversion

1 Model

- pouch as thick spring model
- thickness is a fitting parameter
- wL3 is initial and reference state
- it is a sphrical cap elastic membrane
- its geometry matches with the wd - dv width, outdv width, radius
- spatial location on model is matched with spatial location on WD
- DV and outDV are different regions - different coordinate axes
- we prescribe new spring lengths
- this is given by the lambda tensor
- lambda tensor has in-surface and
- lambda tensor has isotropic and anisotropic components
- schematic of isotropic and anisotropic contributions (theory)
- Supp : quasi tracking cells
- isotropic component - fit relative area change (both same plot)
- anisotropic component - fit elongation change (both)
- show spring lengths mismatch
- show final stage views
- show final stage geometry (iso, aniso, both)
- show final stage mismatch
- show effect of thickness

In order to check if the final 3D shape can be explained by the local cell behaviours, we modelled the apical surface of the wing disc pouch as an elastic membrane. Our model of an elastic membrane is a spring lattice model which has a triangular mesh of springs on the top and bottom surface. These two surfaces are connected by springs that pass through the thickness of the model. Note that this thick tissue is a model of only the apical surface of the tissue. The thickness in the model is only intended to give a bending rigidity to the apical surface and does not represent the bulk of the tissue.

Considering the wL3 stage as the initial state, we model the tissue as a stress-free spherical cap. We match the curvature of the model with the average curvature of the apical surface. The size of the spherical cap is determined by matching the in-surface distance from the tip to the boundary of the segmented region in images. The spatial location on the model is matched with the topological rings in the data. Finally, we divide our lattice into a 'DV' and 'outDV' regions based on the width of the DV boundary measured in the data. For convenience we use different coordinate axes in the DV and outDV regions. In the outDV region we use the spherical coordinate axis with the axis of rotation going through the distal tip. The coordinate axis of the DV region is obtained by rotating the outDV coordinate axis anticlockwise by 90°. The two insurface components of the cooridinate axis in the radially outward directions from the distal tip are given by $e_r^{\mathrm{DV}}, e_r^{\mathrm{p}}$. The perpendicular in-surface direction is given by $e_\phi^{\mathrm{DV}}, e_\phi^{\mathrm{p}}$. Finally the direction along the thickness is given by e_H.

To capture cell behaviours like cell area expansion and elongations, we change the preferred spring lengths in the model. This is done using the spontaneous strain tensor λ_{ij}. This tensor is similar to the deformation tensor described in the theory of liquid crystal elastomers and the growth tensor in the theory of morphoelasticity. λ_{ij} is a 3×3 tensor. Due to the choice of our coordinate system and the data we observe, we keep the off-diagonal components of this tensor as zero which limits the deformation only along the three axes of the coordinate system, two in-plane and one through the thickness. The two in-plane components are given by $\lambda_{rr}^{\mathrm{p,\,DV}} = \lambda^{\mathrm{p,\,DV}}\tilde{\lambda}^{\mathrm{p,\,DV}}$ and $\lambda_{\phi\phi}^{\mathrm{p,\,DV}} = \lambda^{\mathrm{p,\,DV}}/\tilde{\lambda}^{\mathrm{p,\,DV}}$. Here $\lambda^{\mathrm{p,\,DV}}$ represents the isotropic contribution while $\tilde{\lambda}^{\mathrm{p,\,DV}}$ represents anisotropic contribution. The deformation along the thickness of the mesh is given by $\lambda_{HH}^{\mathrm{p,\,DV}} = 1/(\lambda^2)^\nu$ where ν is a coefficient that can capture poisson effects. For a volume preserving tissue, $\nu = 1$.

To capture isotropic deformation in the model we measure the factor by which cell areas change during development. The natural length of the spring representing a patch of cells is changed by a factor given by the square root of the average final cell area of the patch relative to the initial cell area of the patch.

For anisotropic deformation, we change the spring lengths by a factor by which the lengthscales of cells change relatively in that direction. For this we compare the average shear of the cells compared to a reference isotropic stage betweeen the initial and final stages.

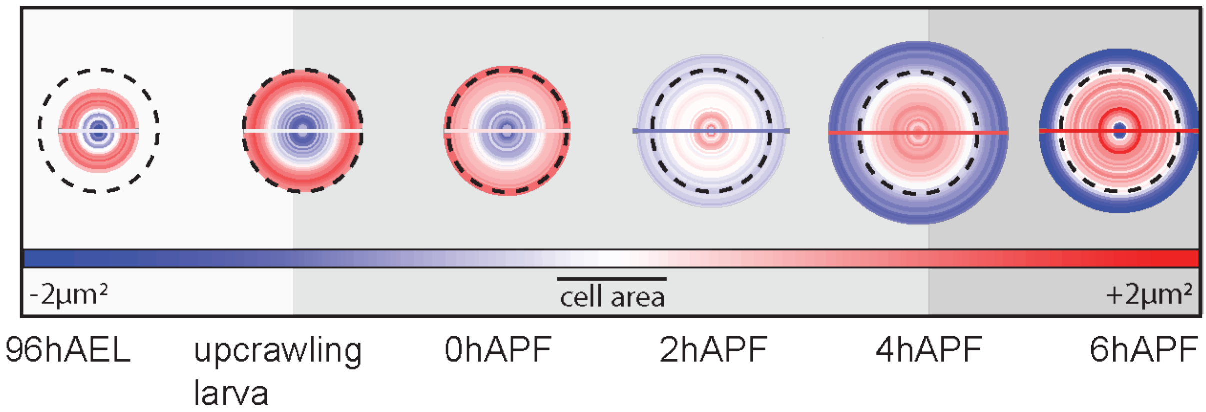
Note that for comparing any property between two stages, we need to track cells through time. However we have discs of individual timepoints. Hence, we 'quasi-track' cells in a way that takes care of net rearrangement of cells (see supplementary).

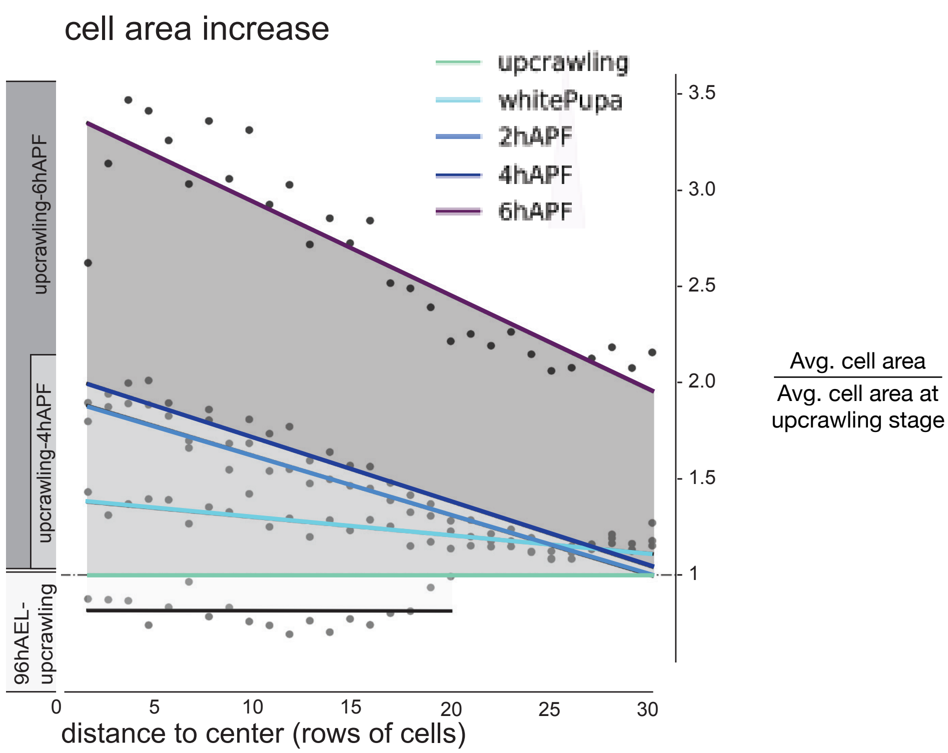
. This is done by having rings of cells of initial timepoint and comparing cells of final timepoint which have the same cumulative number of cells before this reference ring till the next ΔN cells in this ring. For the final stage this can c

$$\underline{\underline{\lambda}} = \lambda\tilde{\lambda}_{El}(e_r \otimes e_r) + \lambda/\tilde{\lambda}_{El}(e_\phi \otimes e_\phi) + 1/(\lambda^2)^\nu(e_h \otimes e_h) \tag{1}$$

$$\lambda = \sqrt{\frac{A(\underline{X}, T_2)}{A(\underline{X}, T_1)}} \tag{2}$$

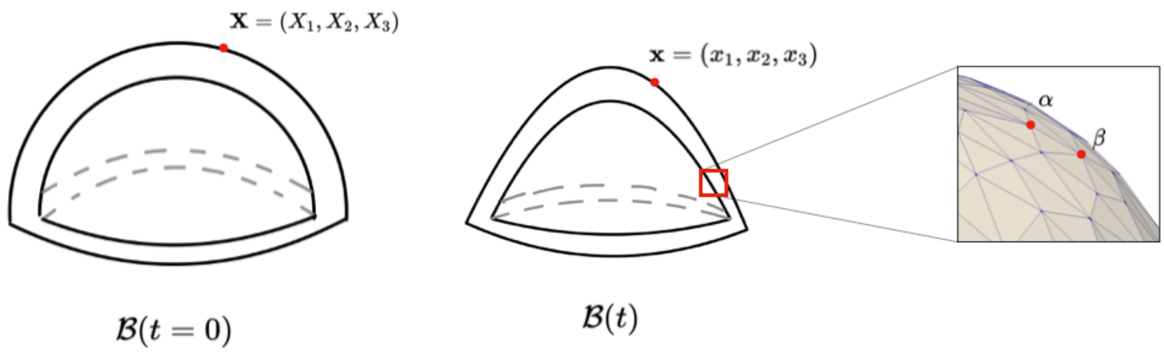
2 Spatial distribution of cell area in wing disc pouch





3 General Setup of the spring lattice model

We start with describing a body in the initial configuration $\mathcal{B}(t = 0)$ where the material coordinates are given by $\mathbf{X} = (X_1, X_2, X_3)$. At a later time t, we represent the body in its *current configuration* $\mathcal{B}(t)$ where the material coordinates are given by $\mathbf{x} = (x_1, x_2, x_3)$.



We can represent this body as a set of lattice points that are connected to nearby particles with springs. The lattice vertices are arbitrarily distributed on the top and bottom suface of the body. The assume the Hookean elastic energy function for this body

$$W = \sum_{edges} \frac{1}{2} k \left(l^{\langle \alpha\beta \rangle} - l_o^{\langle \alpha\beta \rangle} \right)^2 \tag{3}$$

Where $l^{\langle \alpha\beta \rangle}, l_o^{\langle \alpha\beta \rangle}$ are respectively the *current* and *preferred* lengths of the spring connecting vertices α and β .

We assume overdamped dynamics such that the position of any vertex α is updated based upon the forces applied by the springs attached to it.

$$\begin{aligned} \frac{d\underline{\mathbf{x}}^\alpha}{dt} &= -\frac{1}{\gamma} \frac{\partial W}{\partial \underline{\mathbf{x}}^\alpha} \\ &= -\frac{k}{\gamma} \sum_\beta \left(l^{\langle \alpha\beta \rangle} - l_o^{\langle \alpha\beta \rangle} \right) \hat{\underline{\mathbf{l}}}^{\langle \alpha\beta \rangle} \end{aligned} \tag{4}$$

γ represents the friction coefficient and $\hat{\underline{\mathbf{l}}}^{\langle \alpha\beta \rangle} = (\underline{\mathbf{x}}^\alpha - \underline{\mathbf{x}}^\beta)/l^{\langle \alpha\beta \rangle} = (\Delta \underline{\mathbf{x}}^{\langle \alpha\beta \rangle})/l^{\langle \alpha\beta \rangle}$ represents the unit vector along the spring.

4 Setting preferred lengths of springs

The current length of the spring connecting two vertices α and β can be easily computed by

$$(l^{\langle \alpha\beta \rangle})^2 = \Delta \underline{\mathbf{x}}^{\langle \alpha\beta \rangle} . \Delta \underline{\mathbf{x}}^{\langle \alpha\beta \rangle} \tag{5}$$

Similarly, in order to write the preferred lengths of springs, let us assume a virtual configuration called the *stress free configuration* where all the material points are embedded in space such that the current length of each spring is the same as its preferred length. The material coordinates of the stress free configuration is given by $\underline{\boldsymbol{\mathcal{X}}}$. Now, we can write the preferred length as

$$(l_o^{\langle\alpha\beta\rangle})^2 = \Delta\underline{\boldsymbol{\mathcal{X}}}^{\langle\alpha\beta\rangle}.\Delta\underline{\boldsymbol{\mathcal{X}}}^{\langle\alpha\beta\rangle} \tag{6}$$

Next, we introduce a tensor $\underline{\underline{\boldsymbol{\lambda}}}^{\langle\alpha\beta\rangle}$ given by

$$\Delta\underline{\boldsymbol{\mathcal{X}}}^{\langle\alpha\beta\rangle} = \underline{\underline{\boldsymbol{\lambda}}}^{\langle\alpha\beta\rangle}\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle} \tag{7}$$

Plugging eqn 7 into eqn 6, we get the expression for the preferred lengths as

$$(l_o^{\langle\alpha\beta\rangle})^2 = (\underline{\underline{\boldsymbol{\lambda}}}^{\langle\alpha\beta\rangle}\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}).(\underline{\underline{\boldsymbol{\lambda}}}^{\langle\alpha\beta\rangle}\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}) \tag{8}$$

Notice that we need not determine $\underline{\boldsymbol{\mathcal{X}}}$. All we need to know is the initial configuration $\mathcal{B}(t=0)$ and the tensor $\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle}$.

4.1 Discretizing some continuous $\boldsymbol{\lambda}$ into $\boldsymbol{\lambda}^{\langle\alpha\beta\rangle}$

Finally, we determine $\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle}$ for the spring connecting α and β by discretizing a continuous deformation field, referred by $\underline{\underline{\lambda}}$, using the following scheme

$$\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle} = \frac{1}{2}\left(\underline{\underline{\lambda}}(\underline{\mathbf{X}}^{\alpha}) + \underline{\underline{\lambda}}(\underline{\mathbf{X}}^{\beta})\right) \tag{9}$$

5 Qualitatively matching $\boldsymbol{\lambda}^{\langle\alpha\beta\rangle}$ to imaging data

We have the data of how cell area distributions change with respect to the upcrawling stage of the larva. This data is plotted against the distance from the distal tip (in terms of number of cell rings).

5.1 Mapping between k and Θ

$$\Theta(k) = \Theta_{max}\frac{P(k_C)}{P_{max}} \tag{10}$$

The pathlength scales linearly with $P(k_C) = mk_C$, with the slope $m = 2.85$ and $P_{max} = 85.64$.

Cell area changes correspond to isotropic deformation in the surface of the tissue. We can assume that the thickness of the tissue does not change significantly. An appropriate choice for expressing the deformation field $\boldsymbol{\lambda}$ would be in the following form

$$\boldsymbol{\lambda} = \mathbf{e}_R \otimes \mathbf{e}_R + \lambda_\Theta(\Theta,\Phi)\mathbf{e}_\Theta \otimes \mathbf{e}_\Theta + \lambda_\Phi(\Theta,\Phi)\mathbf{e}_\Phi \otimes \mathbf{e}_\Phi \tag{11}$$

Here λ_Θ and λ_Φ represent the multiplicative factor by which the natural lengths of the springs change with respect to their initial lengths. Since deformation is assumed to be isotropic in the surface of the tissue, we can assume

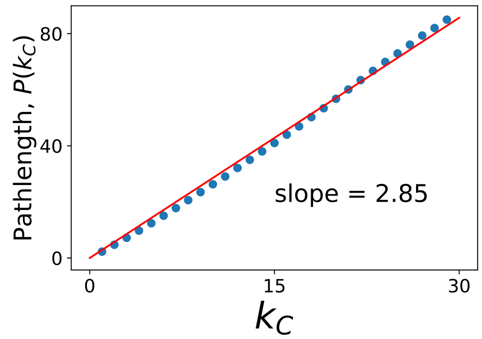
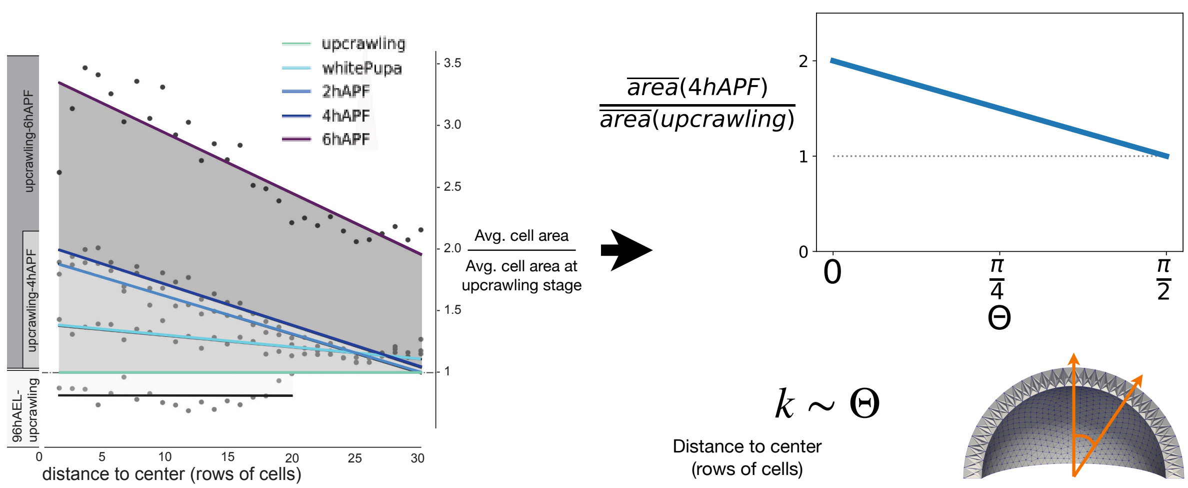


Figure 1: Θ from k_C



$$\lambda_\Theta(\Theta, \Phi) = \lambda_\Phi(\Theta, \Phi) \tag{12}$$

Moreover, as cell area scales with square of the distance between cell vertices, we make the argument

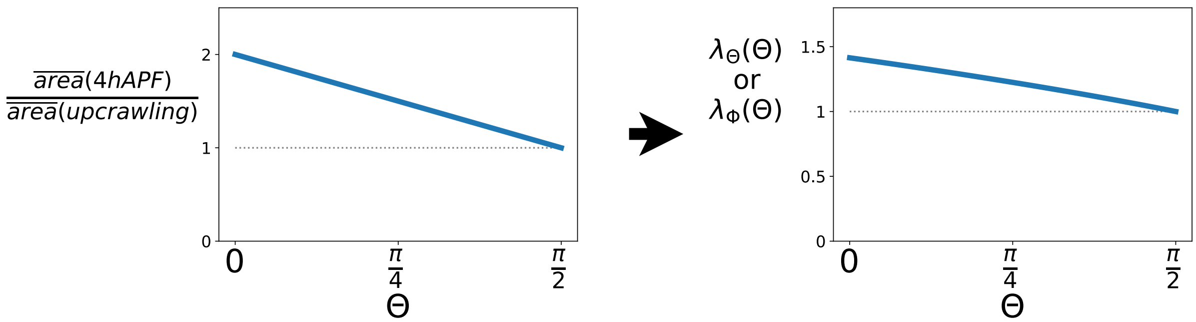
$$\frac{\overline{area}(4hAPF)}{\overline{area}(upcrawling)} \sim \lambda_\Theta(\Theta)^2 = \lambda_\Phi(\Theta)^2 \tag{13}$$

Thus, knowing the trend of relative area changes, we can make an informed choice of the functional form of $\lambda_\Theta(\Theta)$ and $\lambda_\Phi(\Theta)$. As the relative area changes are well described by a straight line, we can assume the functional form of the relative area changes as

$$\frac{\overline{area}(4hAPF)}{\overline{area}(upcrawling)} \approx 2 - \frac{\Theta}{\Theta_{max}} \tag{14}$$

From this follows,

$$\lambda_\Theta(\Theta) = \lambda_\Phi(\Theta) = \sqrt{2 - \frac{\Theta}{\Theta_{max}}} \tag{15}$$



6 Imposing a continuous $\boldsymbol{\lambda}$ onto the spring lattice model

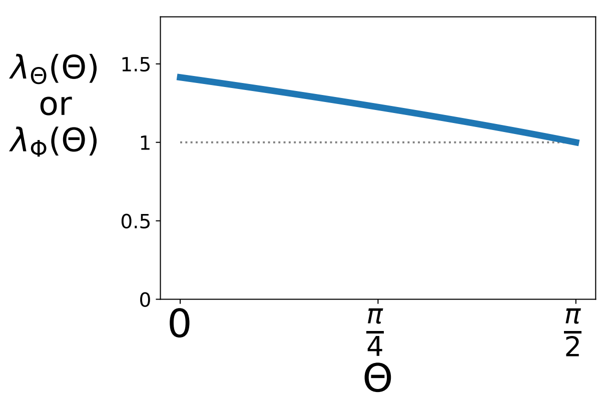
Informed by the imaging data, we assume the following form of $\boldsymbol{\lambda}$

$$\boldsymbol{\lambda} = \mathbf{e}_R \otimes \mathbf{e}_R + \lambda_\Theta(\Theta)\mathbf{e}_\Theta \otimes \mathbf{e}_\Theta + \lambda_\Phi(\Theta)\mathbf{e}_\Phi \otimes \mathbf{e}_\Phi \tag{16}$$

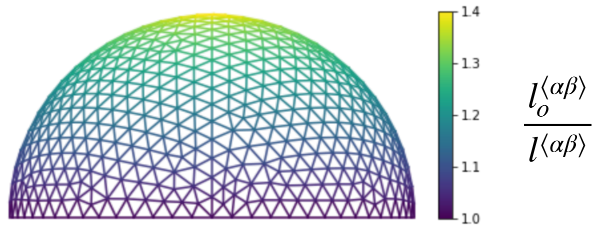
where we choose the functional form of $\lambda_\Theta(\Theta)$ and $\lambda_\Phi(\Theta)$ in such a way that it starts from a value greater than 1 and decreases monotonically, reaching the value of 1 towards the periphery.

$$\lambda_\Theta(\Theta) = \lambda_\Phi(\Theta) = \sqrt{2 - \frac{\Theta}{\pi/2}} \tag{17}$$

A better reasoning for this specific functional form is given later.



Next, we impose this continuous $\boldsymbol{\lambda}$ onto a lattice and compute its new natural lengths



7 Appendix

7.1 Computing the basis vectors e_R^α, e_Θ^α and e_Φ^α at vertex α

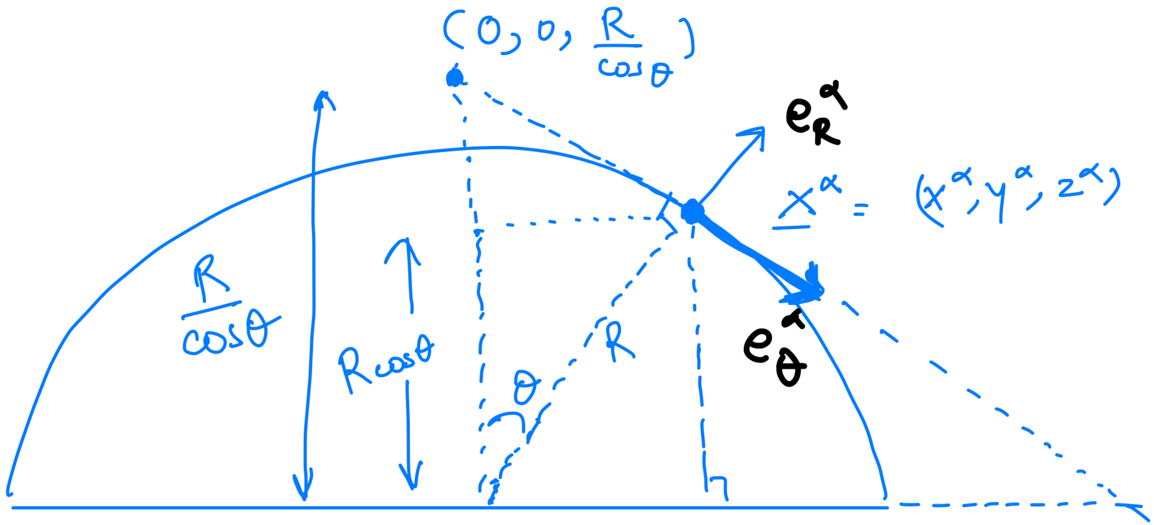


Figure 2: Calculating the basis vectors

In order to determine $\boldsymbol{\lambda}(\mathbf{x}^\alpha)$, we need to determine R^α, Θ^α and Φ^α and the basis vectors $e_R^\alpha, e_\Theta^\alpha$ and e_Φ^α.

$$R^\alpha = |\mathbf{x}^\alpha| \tag{18}$$

$$\Theta^\alpha = \cos^{-1}\left(\frac{x_3^\alpha}{R^\alpha}\right) \tag{19}$$

$$\Phi^\alpha = \sin^{-1}\left(\frac{x_2^\alpha}{R^\alpha \sin(\Theta^\alpha)}\right) \tag{20}$$

$$e_R^\alpha = \frac{\mathbf{x}^\alpha}{|\mathbf{x}^\alpha|} \tag{21}$$

$$e_\Theta^\alpha = \frac{1}{\sqrt{(x_1^\alpha)^2 + (x_2^\alpha)^2 + (x_3^\alpha - R/\cos\Theta)^2}} \begin{pmatrix} x_1^\alpha \\ x_2^\alpha \\ x_3^\alpha - |\mathbf{x}^\alpha|/\cos\Theta \end{pmatrix} \tag{22}$$

$$e_\Phi^\alpha = \frac{e_R^\alpha \times e_\Theta^\alpha}{|e_R^\alpha \times e_\Theta^\alpha|} \tag{23}$$

7.2 Equation writing space

$$\underline{\underline{\lambda}} = \lambda_{11}(\underline{e}_1 \otimes \underline{e}_1) + \lambda_{22}(\underline{e}_2 \otimes \underline{e}_2) + \lambda_{33}(\underline{e}_3 \otimes \underline{e}_3) \tag{24}$$

$$\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle} = \underline{\mathbf{X}}^{\alpha} - \underline{\mathbf{X}}^{\beta} \tag{25}$$

$$(l^{\langle\alpha\beta\rangle})^2 = \Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}.\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle} \tag{26}$$

$$(l_{o,t=0}^{\langle\alpha\beta\rangle})^2 = \Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}.\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle} \tag{27}$$

$$(l_{o,t\to\infty}^{\langle\alpha\beta\rangle})^2 = (\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle}.\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}).(\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle}.\Delta\underline{\mathbf{X}}^{\langle\alpha\beta\rangle}) \tag{28}$$

$$\underline{\underline{\lambda}}^{\langle\alpha\beta\rangle} = \frac{1}{2}\left(\underline{\underline{\lambda}}(\underline{\mathbf{X}}^{\alpha}) + \underline{\underline{\lambda}}(\underline{\mathbf{X}}^{\beta})\right) \tag{29}$$

$$W = \sum_{\text{edges}} \frac{1}{2}k\left(l^{\langle\alpha\beta\rangle} - l_{o,t}^{\langle\alpha\beta\rangle}\right)^2 \tag{30}$$

$$\underline{\underline{\lambda}}^{\alpha} = \begin{cases} \lambda_{\theta\theta}(\underline{e}_\theta \otimes \underline{e}_\theta) + \lambda_{\phi\phi}(\underline{e}_\phi \otimes \underline{e}_\phi) + \lambda_{rr}(\underline{e}_r \otimes \underline{e}_r) \\ \lambda_{\theta'\theta'}(\underline{e}_{\theta'} \otimes \underline{e}_{\theta'}) + \lambda_{\phi'\phi'}(\underline{e}_{\phi'} \otimes \underline{e}_{\phi'}) + \lambda_{rr}(\underline{e}_r \otimes \underline{e}_r), & \text{if } \alpha \text{ in DV}, \end{cases} \tag{31}$$

$$\underline{\underline{\lambda}}^{\alpha} = \begin{cases} \lambda(\theta)(\underline{e}_\theta \otimes \underline{e}_\theta) + \lambda(\theta)(\underline{e}_\phi \otimes \underline{e}_\phi) + \frac{1}{\lambda(\theta)^2}(\underline{e}_r \otimes \underline{e}_r) \\ \lambda_{DV}(\underline{e}_{\theta'} \otimes \underline{e}_{\theta'}) + \lambda_{DV}(\underline{e}_{\phi'} \otimes \underline{e}_{\phi'}) + \frac{1}{\lambda_{DV}^2}(\underline{e}_r \otimes \underline{e}_r), & \text{if } \alpha \text{ in DV}, \end{cases} \tag{32}$$

$$\underline{\underline{\lambda}}^{\alpha} = \begin{cases} \tilde{\lambda}(\underline{e}_\theta \otimes \underline{e}_\theta) + \tilde{\lambda}^{-1}(\underline{e}_\phi \otimes \underline{e}_\phi) + (\underline{e}_r \otimes \underline{e}_r) \\ \tilde{\lambda}_{DV}^{-1}(\underline{e}_{\theta'} \otimes \underline{e}_{\theta'}) + \tilde{\lambda}_{DV}(\underline{e}_{\phi'} \otimes \underline{e}_{\phi'}) + (\underline{e}_r \otimes \underline{e}_r), & \text{if } \alpha \text{ in DV}, \end{cases} \tag{33}$$

$$\underline{\underline{\lambda}}^{\alpha} = \begin{cases} \tilde{\lambda}\lambda(\theta)(\underline{e}_\theta \otimes \underline{e}_\theta) + \tilde{\lambda}^{-1}\lambda(\theta)(\underline{e}_\phi \otimes \underline{e}_\phi) + \frac{1}{\lambda(\theta)^2}(\underline{e}_r \otimes \underline{e}_r) \\ \tilde{\lambda}_{DV}^{-1}\lambda_{DV}(\underline{e}_{\theta'} \otimes \underline{e}_{\theta'}) + \tilde{\lambda}_{DV}\lambda_{DV}(\underline{e}_{\phi'} \otimes \underline{e}_{\phi'}) + \frac{1}{\lambda_{DV}^2}(\underline{e}_r \otimes \underline{e}_r), & \text{if } \alpha \text{ in DV}, \end{cases} \tag{34}$$

$$l_o^{\langle\alpha\beta\rangle}(\infty) = \tag{35}$$

$$\lambda(\theta) = \sqrt{2 - \frac{\theta}{\theta_{\max}}} \tag{36}$$

$$\lambda_{DV} \approx 2 \tag{37}$$

Keeping $\tilde{\lambda} = 0.95$ and $\tilde{\lambda}_{DV} = 1$

8 Analyzing Rearrangements

Neighbour exchanges can lead to a change in the topological ring of the cells. The possibilities are the following

- A neighbour exchange in the tangential direction. This involves one cell from $i-1$th ring, two cells from ith ring and one cell from $i+1$th ring. On a T1 transition, this can lead to the cell from $i+1$th ring to end up in the ith ring.
- Another example would be to reverse the time arrow of a tangential T1 transition resulting in a radial T1 transition.
- Final possibility would be to have a T1 transition between two cells each from ith and $i+1$th rings. This transition happens in a direction that is intermediate between radial and tangential directions. No change in the ring number of the cells occurs in this case.

A change in the ring number of a cell is percolated to all the cells for which the shortest path to center goes through this cell. Another consequence of this is that rearrangements can lead to a change in the number of cells per ring. Tangential and radial T1 transitions cancel out each other in terms of their effects. If the net number of radial T1 transitions are more than the tangential T1 transitions then the number of cells per ring decreases. Consequently more number of rings are needed to accommodate the same number of cells.

We can measure this effect in the data. We observe that the number of topological rings increases with development. The difference in the values of k to accommodate N cells at different developmental stages comes from the cumulative rearrangements for all cells within these N cells. Let's say we have d_T discs for developmental stage T. For disc α at stage T, N_i^α cells are contained within $k^\alpha(N_i^\alpha, T)$ rings. Hence, consider the temporal difference of $k^\alpha(N_i^\alpha, T)$ as

$$\Delta_T k^{\alpha,\beta}(N_i^\beta) = \bar{k}^\alpha(N_i^\beta, T+\Delta T) - k^\beta(N_i^\beta, T) \tag{38}$$

Here we introduce the notation of using $\bar{k}^\alpha(N,T)$ to denote the linearly interpolated form of the function $k^\alpha(N,T)$ which is only defined at discrete values $\{N_1^\alpha, N_2^\alpha, \cdots, N_{k_{max}}^\alpha\}$.

To go from "cumulative rearrangements" to "local rearrangements" we take a spatial difference of $\Delta_T k(N_i^\beta)$ between consecutive values of N_i^β

$$f^{\alpha,\beta}(N_i^\beta) = \Delta_N \Delta_T k^{\alpha,\beta}(N_i^\beta) = \Delta_T k^{\alpha,\beta}(N_{i+1}^\beta) - \Delta_T k^{\alpha,\beta}(N_i^\beta) \tag{39}$$

Finally we define the average of $\Delta_N \Delta_T k^{\alpha,\beta}(N_i^\beta)$ over all possible pairs α, β at a given value of N as

$$\Delta_N \Delta_T k(N) = \frac{\sum\limits_{\alpha,\beta} \bar{f}^{\alpha,\beta}(N)}{d_T d_{T+\Delta T}} \tag{40}$$

8.1 Physical interpretation of $\Delta_N \Delta_T k(N)$

Let us consider one ring at T stage that contains $\Delta N_i = N_{i+1} - N_i$ cells. At $T + \Delta T$ stage, these cells are contained in $1 + \Delta_N \Delta_T k(N_i)$ rings. This implies that the ring $k(N_i, T)$ undergoes an expansion perpendicular to the "iso-k" direction by a factor of $1 + \Delta_T \Delta_N k(N_i)$ and a contraction along the ring by a factor of $1/(1 + \Delta_T \Delta_N k(N_i))$. We model this effect in our model by setting the anisotropic deformation along the $\underline{e}_\theta$ as

$$\tilde{\lambda}_{\text{Re}} = 1 + \Delta_N \Delta_T k(N_i) \tag{41}$$

8.2 Measuring $\Delta_N \Delta_T k(N)$ in data

In the data we get very small amount of deformation along the $\underline{e}_\theta$ direction in the pouch region outside the DV boundary. Moreover, it is fairly uniform in this whole region having a value of about 0.01. Inside the DV region, the value is about 0.1 having a higher value towards the distal tip.

8.3 Checks

- Remove first few k_{DV}
- Change the center ring in DV to confirm that the effect is not dependent on the definition of the center

9 Mapping Elongation data to $\underline{\underline{\boldsymbol{\lambda}}}(\boldsymbol{X}^{\boldsymbol{\alpha}})$

Each cell polygon is subdivided into triangles formed by the set of the centroid and each set of two adjacent vertices. The elongation of each of these triangles is quantified by elongation tensor $\tilde{\mathbf{q}}_{ij}$. The average elongation of each cell is then given by $\tilde{\mathbf{Q}}_{ij} = \langle \tilde{\mathbf{q}}_{ij} \rangle$.

Each $\tilde{\mathbf{q}}_{ij}$ has an axis and a norm given by

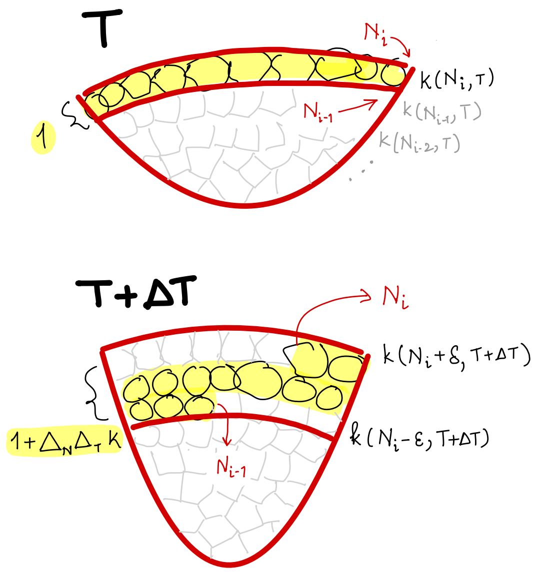
$$\tilde{\mathbf{q}} = |\tilde{\mathbf{q}}| \begin{pmatrix} \cos(2\omega) & \sin(2\omega) \\ \sin(2\omega) & -\cos(2\omega) \end{pmatrix} \tag{42}$$

According to Merkel, et al 2017, the length of the long axis of the ellipse is given by $l = r_o \exp(|\tilde{q}|)$ where r_o is the radius of the reference equilateral triangle. The length of the short axis of the ellipse is given by $s = r_o \exp(-|\tilde{q}|)$.

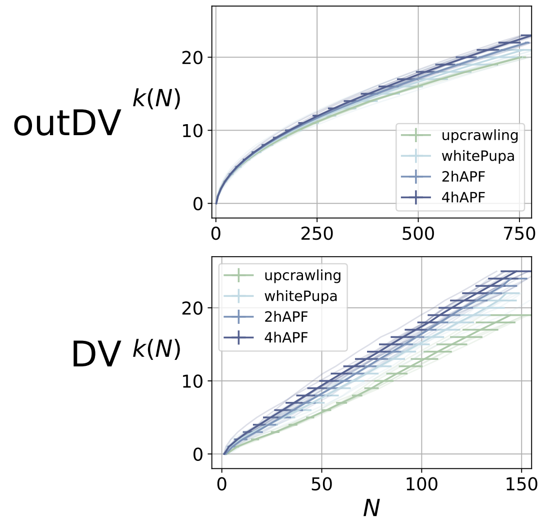
If the axes of the ellipse match with the coordinate axes ($\tilde{\mathbf{q}}_{12} \approx 0$) then l corresponds to the 11 direction and s corresponds to the 22 direction.

Let's assume that on average the axes of the ellipses match with the our coordinate axis of choice (along k_{DV} and r). Let us denote by l_1 the length of the axis of the ellipse that is along r direction and by l_2 the length of the ellipse axis that is along the perpendicular direction. We would compute the average of l_1 and l_2

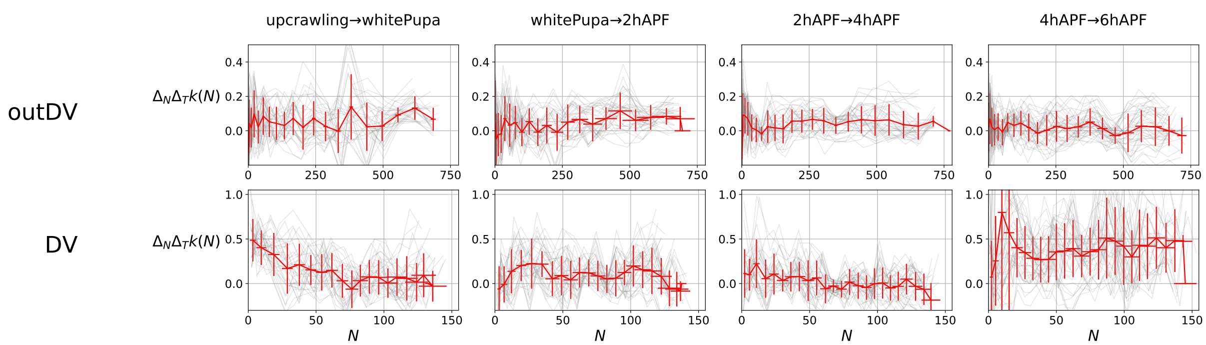
Consider the average coarse grained elongation of the cells at a given N and developmental stage, $|\tilde{Q}|(N, T)$. We compare the shape of the cells in this location with the cells



(a)



(b)



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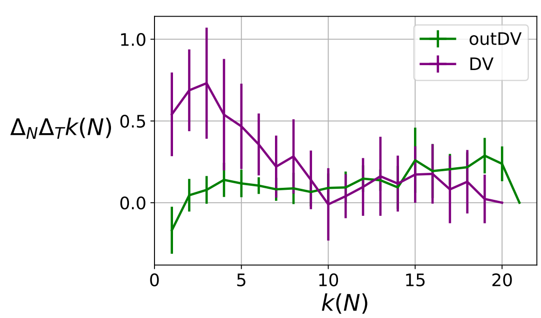

(d)

Figure 3: (a) Rearrangements leads to anisotropic deformation. (b) Topological rings increase with development showing net radial rearrangements. (c) Measuring $\Delta_N\Delta_T k$ vs N (d) Comparing $\Delta_N\Delta_T k$ between DV and outDV between upcrawling and 4hAPF.

in the location of the same N but corresponding to another developmental stage. In the spirit of ellipses surrounding triangles/cells, we can write that the factor by which the long axis is increased is given by

$$\tilde{\lambda}_{\mathrm{el}} = \exp\left(|\tilde{Q}|(N, t + \Delta t) - |\tilde{Q}|(N, t)\right) \tag{43}$$

Here the assumption is that the axis of the elongation is along $\underline{e}_\theta$ direction. Can we make this independent of the axis alignment with the coordinate axis ?

9.1 Checks

- Check if axis of $\tilde{Q}_{ij}$ aligns with the $\underline{e}_\theta$ and $\underline{e}_\phi$ directions.
- Check that the direction of the ring aligns with the axis of $\tilde{Q}_{ij}$.
- What about the $\tilde{Q}_{\phi\theta}$ component? What does it mean?