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

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

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

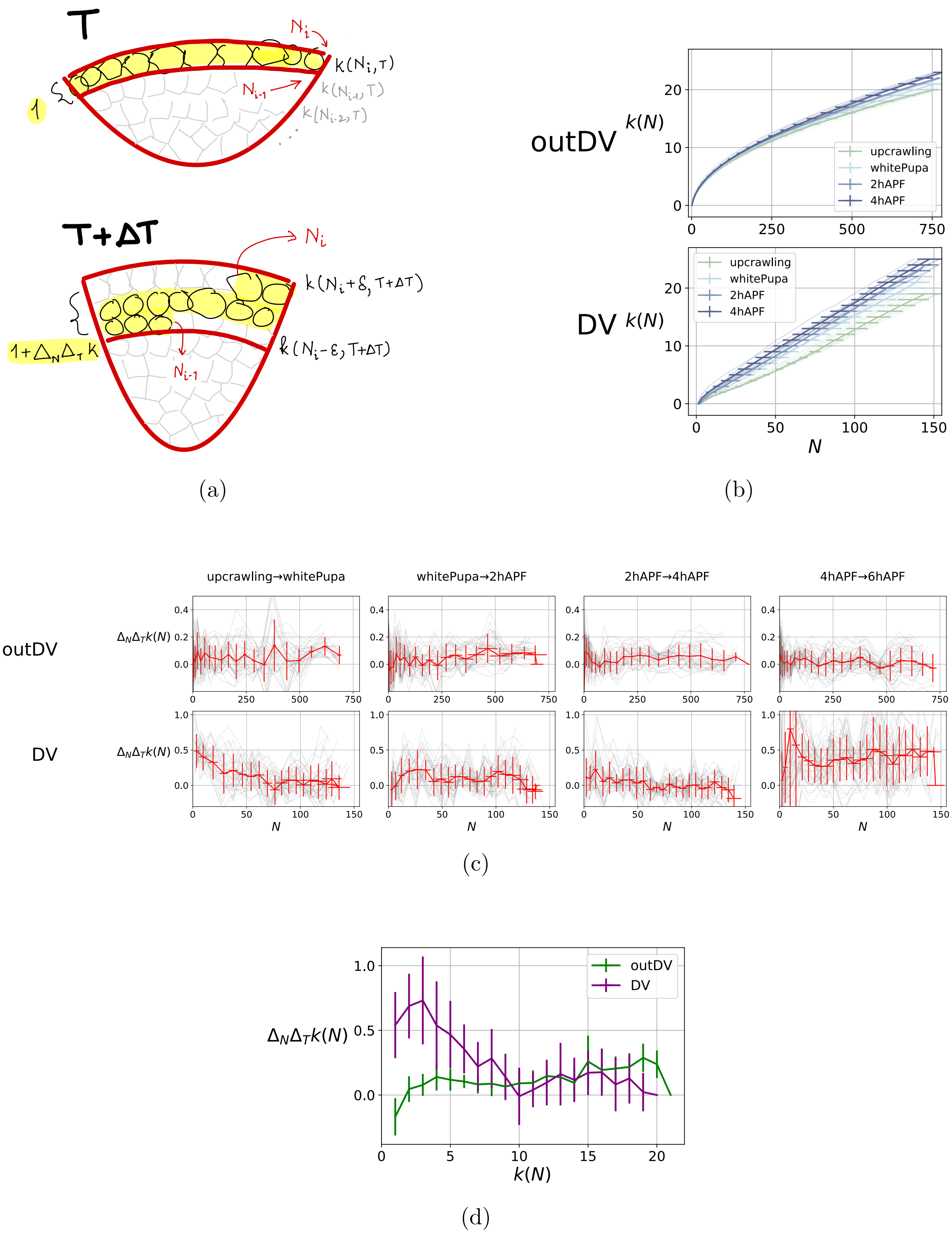

Figure 3: (a) Rearrangements leads to anisotropic deformation. (b) Topological rings increase with development showing net radial rearrangements. (c) Measuring $\Delta_N \Delta_T k$ vs N (d) Comparing $\Delta_N \Delta_T k$ between DV and outDV between upcrawling and 4hAPF.

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?