



Universiteit  
Leiden  
The Netherlands

## Growth-induced self-organization in bacterial colonies

You, Z.

### Citation

You, Z. (2019, June 25). *Growth-induced self-organization in bacterial colonies*. Retrieved from <https://hdl.handle.net/1887/74473>

Version: Not Applicable (or Unknown)

License: [Leiden University Non-exclusive license](#)

Downloaded from: <https://hdl.handle.net/1887/74473>

**Note:** To cite this publication please use the final published version (if applicable).

Cover Page



Universiteit Leiden



The following handle holds various files of this Leiden University dissertation:

<http://hdl.handle.net/1887/74473>

**Author:** You, Z.

**Title:** Growth-induced self-organization in bacterial colonies

**Issue Date:** 2019-06-25

# Chapter 6

## Conclusion and outlook

Bacteria, being one of the most common organisms on earth, were first observed by the Dutch microscopist Antonie van Leeuwenhoek in 1676. Since then, they have been intensively studied from perspectives of biochemistry, biology, and ecology. It is only until recent years, that the role of physics, and especially mechanics, has started to draw attention. The work presented in this thesis is an attempt to describe bacterial organization from physical principles and highlight the mechanical and geometrical aspects of colonization.

We use a minimal model system, in which non-motile, rod-shaped bacteria, sandwiched between a glass slide and an agarose gel, push each other away as they grow in length. It is astonishing that such a simple system can exhibit a myriad of complex emergent behaviors, including the chaotic dynamics of nematic micro-domains in a freely expanding colony, the global alignment of cells upon confinement, and the stochastic transition from a monolayer to a multilayered structure in large colonies. These emerging phenomena can ultimately be ascribed to the complex interplay among cell orientation, cell growth, and mechanical stresses. First of all, cell growth provides a continuous feed of stress along the cell axis. Second, steric repulsion between elongated cells drives them to align with each other, and any distortion from the aligned configurations will cause elastic torques which tend to restore perfect alignment. Third, anisotropic stresses can directly reorient cells and force them to align along the direction of minimal stress. In addition, the gradient of stresses can also drive motion of cells, which, in turn, alter the cells orientation. Such a reorientation changes not only the direction of cell growth, hence the stress feed into the rest of the colony, but also redistributes the local stress among the longitudinal and transverse components, with respect to the average orientation of a cell cluster. This intricate interplay between orientational dynamics and stress relaxation can, ultimately, give rise to a plethora of complex mechanical behaviors.

In a freely expanding colony, the growth-induced stress is released

isotropically by the radially expanding flow, resulting in an extensile active stress. That is, the stress is extensile along the local nematic director and contractile in the orthogonal direction. Such an active stress bends the nematic director at the expenses of the orientational elastic energy. This competition between active disordering and passive restoring stresses, results into the formation of nematic domains which, as the colony evolves, merge, buckle and break apart in a complex sequence of morphological and topological transformation. In a confined colony, however, the stress is released anisotropically, hence is globally anisotropic: the stress components in the confined direction are on average larger than their orthogonal counterparts. The globally anisotropic stress can drive cells to align with its minimal principal axis (i.e. the unconfined direction) and, consequently, the colony shows a global alignment.

For large enough colony, the accumulated lateral stress is large enough to compete with the vertical restoring forces from the agarose on top, and can trigger a transition from a monolayer to a multilayered structure. Although the general picture of this transition is similar to the buckling transition of a flat plate, the underlying physical nature is by no means the same. Specifically, the critical state of the transition is locally defined, and depends on the local cell length. Accordingly, there is no unique critical state, but an ensemble of critical states, depending upon the distribution of cell length across the colony. Therefore, despite the internal stress following a rather predictable parabolic profile, the position and time at which the transition happens are both random, and can only be predicted statistically.

It cannot be stressed enough that a simple system of growing bacteria can exhibit so many interesting properties: *anisotropy* (i.e. cell orientation and mechanical stress), *inhomogeneity* (spatial-temporal variation of stress), *heterogeneity* (i.e. differential cell length), *stochasticity* (i.e. cell division and mono-to-multilayer transition), and *activity* (i.e. cell growth and division). These properties, commonly shared by living systems, altogether, define the complexity displayed in growing bacterial colonies, and make it extremely difficult to put forward a universal theory that captures all aspects of the bacterial organization. Yet, upon narrowing down the search to specific questions (e.g. how is the area of bacterial domains distributed? What drives the transition from mono- to multi-layered colonies? etc.) and addressing them within the powerful frameworks of continuum and statistical mechanics, it is possible not only

to shed light of the physical mechanisms underpinning these phenomena, but also formulate predictions that are amenable for experimental scrutiny. What's more, the distinctive properties of living systems, particularly the cell activity such as growth, motility and cell-cell communications, can potentially promote new physics that are not as perceptible in nonliving systems. The challenge remains to make quantitative comparison between the theory and the experiment.