EDITORIAL

Population dynamics

This Focus issue on bacterial growth, highlights the versatility and adaptability with which bacterial cells respond to their environmental and community context.

Bacteria have an immense capacity to grow. As mentioned by Megan Bergkessel, David Basta and Dianne Newman on page 549, if *Escherichia coli* were to continue exponential growth, a single bacterial "cell would grow to a population with the mass of the Earth within 2 days". However, bacteria rarely encounter perfect growth conditions outside of the laboratory: nutrients are limited, the bacteria have to compete with other cells for resources or they are under attack by other bacterial species, host defences or antimicrobial therapy. Thus, bacteria have developed a wide variety of mechanisms that enable them to optimize their growth patterns according to the surrounding conditions. This Focus issue explores factors that influence bacterial growth dynamics and how bacterial populations respond to them; for example, by forming biofilms and producing a structured extracellular matrix, by executing population-wide behaviours based on growth density or by arresting growth when nutrients are scarce. Much progress has been made in understanding the complex interdependencies that govern bacterial growth.

Since 1987, when Bill Costerton and colleagues first defined biofilms[1] as a community of bacterial cells encased in a polymeric matrix and attached to a surface, the original definition of biofilms has evolved, including the realization that non-bacterial microorganisms also form biofilms and that free-floating biofilms exist. However, the importance of extracellular polymeric substances has remained one of the key properties of biofilms. On page 563, Hans-Curt Flemming and colleagues examine the role of the biofilm matrix for bacterial growth. This matrix provides properties that emerge when bacteria grow within a biofilm, such as the ability to capture nutrients and metabolites, or to exclude antimicrobials.

Another core component of the original definition of biofilms, the growth of a community of cells, also remains an important avenue of research. A rich body of theoretical and experimental work studies community dynamics in biofilms. Two opposing interactions — competition and cooperation — can occur in biofilms. As Kevin Foster, Carey Nadell and Knut Drescher explain on page 589, these social phenotypes often depend on the spatial distribution of genetic lineages in the biofilm. Mixed populations that consist of different lineages tend to compete with different clones or species antagonizing each other; for example, by the secretion of toxins or through the type VI secretion system. By contrast, mutualistic clonemates growing next to each other often cooperate; for example, through the secretion of public goods.

> "bacteria have developed a wide variety of mechanisms that enable them to optimize their growth patterns according to the surrounding conditions"

To regulate cooperative behaviour, bacteria use quorum sensing, whereby the concentrations of secreted signalling molecules inform bacteria about the surrounding population density. On page 576, Bonnie Bassler and Kai Papenfort review quorum sensing systems in Gram-negative bacteria, highlighting the different signalling molecules, receptors and response networks. They also describe the broad effects that quorum sensing can have by not only enabling communication between members of one bacterial species but also between species, genera and even kingdoms; for example, between the gut microbiota and the mammalian host.

Finally, Megan Bergkessel, David Basta and Dianne Newman introduce the concept of growth arrest, which occurs when fast growing bacteria encounter nutrient and energy limitation. Cells drastically slow their metabolism and enter into a resting state, from which they can be awoken when nutrients become available again. Environmental bacteria probably spend a large part of their existence in growth arrest, and recent research has elucidated some of the underlying molecular mechanisms.

This Focus issue highlights the importance of the ecological context for bacterial growth, be it in a biofilm, in the microbiota or in a low-energy state. What governs bacterial growth is one of the central questions of microbiology and it has been at the heart of the field for decades. Despite a long history of research and many ground-breaking discoveries, much remains to be studied. The simple questions of what makes a bacterial population grow or stops it from growing have no simple answers. We hope that the Reviews in this Focus issue will guide and inspire future research, open new perspectives and possible answers to long-standing questions. As Roberto Kolter stated in a comment[2] on his research on stationary phase growth several years ago: "in order to be able to look freshly at the challenges of the day, it is always an excellent idea to stop and see what others saw long before one opened one's eyes."

1. Costerton, J. W. *et al. Annu. Rev. Microbiol.* **41**, 435–464 (1987).
2. Kolter, R. *J. Bacteriol.* **181**, 697–699 (1999).