Summary

We model the growth of bacterial biofilms using the concept of extra-cellular polymeric substance (EPS) as a polymer solution, whose viscoelastic rheology is described by the classical Huggins theory. We show that one-dimensional solutions exist, which take the form at large times of travelling waves, and we characterise their form and speed. Numerical solutions of the time-dependent problem converge to the travelling wave solutions.

Previous Models

Our work is based on the conceptual model of Cogan and Keener (2004, 2005), who consider the biofilm as a biological gel consisting of EPS and water, in which bacterial cells occupy only a small volume fraction. The asymptotic limit of their two-fluid continuum model uses a dominant balance between viscous stress and the osmotic pressure term. They find a 1D steady state with constant interface growth velocity and examine the instability of this solution to spatial perturbations. We also seek to provide a description of a uniformly growing biofilm. Our approach deviates markedly from theirs: we use an explicit nondimensionalisation, choosing natural scales to identify a different dominant balance.

Flory-Huggins

The Flory-Huggins free energy per unit volume is realised as an osmotic pressure – the additional pressure required to equilibrate the polymer solution with pure solvent across a semi-permeable membrane. This osmotic pressure is given by the relevant limit of large polymer volume and $\phi \ll 1$ as

$$\Theta = -E_L \left[ \phi \left( \frac{1}{2} - \phi \right) \tilde{v} + \tilde{\lambda} \phi + O (\phi^3) \right],$$

where $\Theta$ is the volume fraction of polymer.

Polymer-Solvent Model I

We consider a biofilm in $0 < z < s$ as illustrated in Fig. 1, surrounded by nutrient-rich water, behaving as a gel, and with an osmotic pressure described by the Flory-Huggins theory. We also take both the polymer and the interstitial water to be viscous, and to interact via an interfacial drag term. Biomass growth is assumed to be rate-limited by one nutrient, for example the dissolved oxygen in water acting as the electron acceptor. Biomass is lumped in with the EPS in the model, combining cellular growth and EPS production.

Mass conservation gives, noting that $\nabla \cdot \mathbf{v} = 0$ and $\nabla \cdot \mathbf{w} = 0$,

$$\begin{align*}
\rho \phi \mathbf{v} + \nabla \cdot (\nabla \phi) &= \rho \phi \mathbf{c}, \\
-\rho \phi \tilde{\mathbf{v}} + \nabla \cdot (\nabla \tilde{\phi}) &= \nabla \cdot (\nabla \mathbf{w}) = 0,
\end{align*}$$

where $\mathbf{v}$ and $\mathbf{w}$ denote polymer and solvent phase-averaged velocities, and $\gamma$ is a growth term.

Polymer-Solvent Model II

The concentration $c$ is that of the assumed rate-limiting nutrient, and satisfies

$$\frac{1}{1 - \phi} \nabla \cdot \mathbf{v} = \nabla \cdot \left[ \frac{1}{1 - \phi} (\mathbf{v} - \mathbf{w}) \right] - \frac{1}{1 - \phi} \nabla \phi,$$

with $\Theta$ a diffusion coefficient, and $\nu$ nutrient uptake by biomass. Assuming Monod kinetics,

$$g = \frac{\nu}{K + c},$$

where $g$, $\nu$ and $K$ are constants. Momentum equations for slow two-phase flow are

$$\begin{align*}
0 &= \rho \nabla \cdot (\nabla \tilde{v}) - f(1 - \phi)(\mathbf{v} - \mathbf{w}) - \nabla \tilde{\mathbf{p}}, \\
0 &= \rho \nabla \cdot (\nabla \tilde{w}) - f(1 - \phi)(\mathbf{v} - \mathbf{w}) - (1 - \phi) \nabla \tilde{\mathbf{p}}.
\end{align*}$$

Here, $\phi$ is fluid pressure, $\tilde{\Theta}$ is the osmotic pressure given by (1), $\phi$ is the long-time viscosity of the polymer matrix, $\mu_p$ is the viscosity of water, and the term in $f$ is an interfacial drag term. The solvent viscous term is negligible, so that equation (4) is just Darcy’s law, and $\tilde{\mathbf{p}}$ is given by $f \omega^2$, essentially defining the permeability $f$. We assume that $\phi \ll 1$ is constant.

Eqs (4) are the same as those given by Cogan and Keener (2004). Cogan and Keener now argue that since $\phi$ is small, the interfacial drag term can be ignored. This leads them to an approximate model which is quite different to the one we derive here, where we find that in fact the interfacial friction term is dominant.

Nondimensionalisation

If $\gamma > \tilde{\gamma}$ then a stable gel fraction $\phi_0 \approx 1/\gamma$, and can exist where $\phi = 0$. This suggests that we balance $\Theta = -E_L \phi^2$, expecting that this will be appropriate if the poorly constrained Flory parameter $\gamma$ is close to (and greater than) one half. So we choose the scales

$$\begin{align*}
\epsilon \sim \phi_0, \quad \phi \sim \epsilon c_0 = \int \left( \frac{G D c}{f G d} \right)^{1/2}, \\
\Theta \sim \phi \sim \epsilon \mu_0 = \int \left( \frac{f G d}{G d} \right)^{1/2},
\end{align*}$$

where $\epsilon = \epsilon \nu / \phi_0$, $\mu_0 = \mu_0 / \phi_0$, and $\Theta = \Theta / \phi_0$.

The lengthscale is based on a balancing the uptake and diffusion terms in the nutrient equation, representing the depth of the active layer of biofilm. The time and velocity scales are chosen to balance the growth rate. The pressure scale reflects a balance between the interfacial drag and pressure terms in (4). The scale $\epsilon c_0$ is chosen by balancing the osmotic and interfacial drag terms in (4).

The non-dimensional forms of the equations (1), (2), (3) and (4) are

$$\begin{align*}
\epsilon \phi + \nabla \cdot (\phi \mathbf{v}) &= \frac{\rho c}{\rho c_0}, \\
\phi (1 - \phi) \frac{\partial \phi}{\partial t} + \nabla \cdot (\nabla \phi) &= \nabla \cdot (\nabla \mathbf{w}) = 0, \\
0 &= \nabla \cdot (\nabla \tilde{\mathbf{v}}) - f(1 - \phi)(\mathbf{v} - \mathbf{w}) - \nabla \tilde{\mathbf{p}}, \\
0 &= \nabla \cdot (\nabla \tilde{\mathbf{w}}) - f(1 - \phi)(\mathbf{v} - \mathbf{w}) - (1 - \phi) \nabla \tilde{\mathbf{p}}.
\end{align*}$$

The parameters are defined by, and take the approximate values:

$$\begin{align*}
\epsilon &\approx \phi_0^{1/2} \approx 0.37 \times 10^{-2}, \quad g = \frac{\nu}{K} \approx 0.35, \quad \frac{G d c}{f G d} \approx \frac{1}{10} \times 10^{-2}, \\
\beta &= \frac{\rho c_0}{\rho c} \approx 1.1 \times 10^{-1}, \quad \gamma = \frac{\mu_0}{\mu} \approx 17.6 \times 10^{-1}, \quad \lambda \approx \frac{1}{\phi_0} \approx 0.1.
\end{align*}$$

Conclusions

We model biofilm growing on an impermeable substratum based on the material properties of a polymer solution. Estimates of typical scales lead to a different mathematical description to earlier work. Solutions of the model converge to a travelling wave solution strongly dependent on the dimensionless parameter $\lambda = \phi_0^{1/2} \frac{\mu_0}{\mu}$. The travelling wave solution provides an expression $U \sim \frac{G d c}{f G d}$ for the growth velocity of the biofilm surface in dimensionless terms. This is also a good approximation in the time-dependent case of relatively thin biofilms for which nutrient penetrates the full biofilm depth, and thus provides reasonable scope for comparison with experiment.

REFERENCES:


