

A model to reproduce the physical elongation of dendrites during swarming migration and branching

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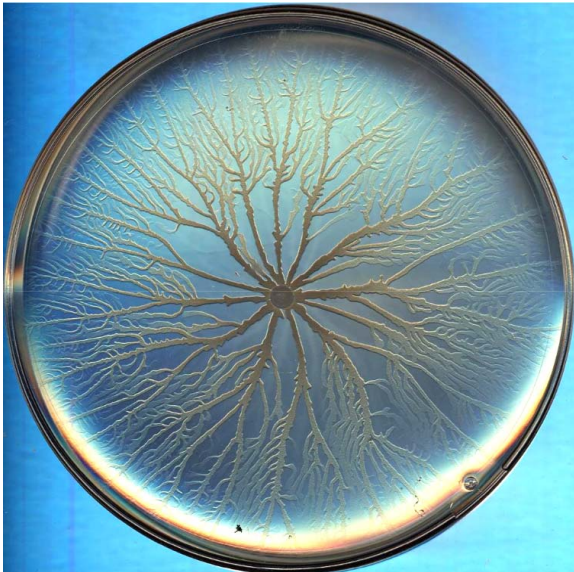
Workshop on cell migration and tissue mechanics,
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Outline

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 - Previous models
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The background

B. subtilis



The background

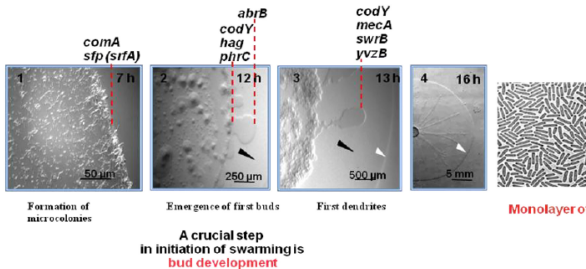
Procedure

Mother colony

10^4 cells, doubling time 100min, 11-12 h growth, $30 \mu\text{m}$ thick, 2mm in diameter.

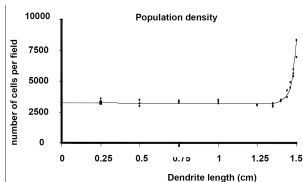
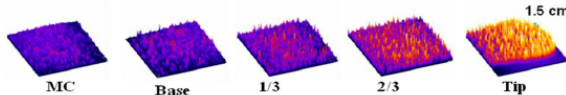
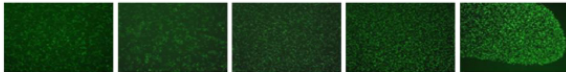
Hemispherical buds

Transparent zone of surfactin, 1h, $500\text{-}800 \mu\text{m}$ in diameter, surfactin induces a thin layer of fluid

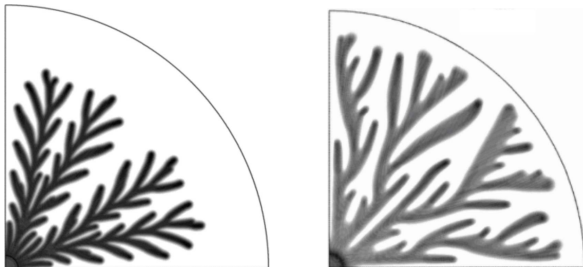


Dendrites elongated

10-14 dendrites, 1.5cm, supporters (10-12 flagella), swarmers (24 flagella)



Previous models



Involve nutrient concentration

$$\begin{cases} \partial_t n(x, t) - D_n \Delta n(x, t) = n[vG(n, v) - H(n, v)], \\ \partial_t v(x, t) - D_v \Delta v(x, t) = -nvG(n, v), \\ \partial_t f(x, t) = nH(n, v). \end{cases}$$

Gray-Scott, Beau-Jacob, C. A. Murra.

Biologists propose that on rich media, nutrient is not the reason for pattern formation.

Are there models based on other ingredients that achieve this type of pattern? . . .

Motivation

Keller-Segel system

$$\begin{aligned}\partial_t n + \operatorname{div}(\chi n \nabla c) &= \Delta n, \quad x \in \mathbb{R}^d, t \geq 0 \\ -D_c \Delta c + \tau_c c &= \alpha_c n,\end{aligned}$$

- Traveling wave not natural
- Blow up

Two models in literature

The Dolak-Schmeiser model

$$\begin{cases} \partial_t n + \partial_x(n(1-n)\partial_x c) = 0, \\ -D_c \partial_x^2 c + \tau_c c = \alpha_c n, \end{cases}$$

Model involves traveling wave

$$\begin{cases} \partial_t n - \partial_x(n\partial_x S) = 0, \\ \partial_t S - D_s \partial_x^2 S + \tau_s S = \alpha_s n, \end{cases}$$

The system

$$\begin{cases} \partial_t n + \operatorname{div}(n(1-n)\nabla c - n\nabla S) = 0, \\ -D_c \Delta c + c = \alpha_c n, \\ \partial_t S - D_s \Delta S + \tau_s S = \alpha_s (m_{col} + f + n), \\ \partial_t f - \operatorname{div}(D_f \nabla f) = B_n n + B_f f + f(1/3 - f), \end{cases} \quad (1)$$

- The density of the swarms $n(x, t)$
- The density of the supporters $f(x, t)$
- The surfactin density $s(x, t)$ (long range signal)
- The chemical concentration $c(x, t)$ (short range)

Numerical results

Numerical scheme

- c, S, f : $P1$ finite element;
- n : Engquist-Osher scheme

Two branch movie
Four branch movie

What could be interesting for this system?

- 1 Stability.
- 2 Traveling wave.

Reduced system

Instabilities can be observed on reduced system

$$\begin{aligned}\partial_t n + \operatorname{div}(n(1-n)\nabla c - n\nabla S) &= 0, \\ -D_c \Delta c + c &= \alpha_c n, \\ \partial_t S - D_s \Delta S + \tau_s S &= \alpha_s n,\end{aligned}$$

Special regimes

Check for traveling pulses ($n(x - \sigma t), s(x - \sigma t)$)

$$-\sigma n + \operatorname{div}(n(1 - n)\nabla c - n\nabla S) = 0,$$

$$-D_c \Delta c + c = \alpha_c n,$$

$$-\sigma S - D_s \Delta S + \tau_s S = \alpha_s n,$$

All parameters are non-negative

- Steady state: $\sigma = 0$.
- Traveling wave: $\tau_s = 0, D_s = 0$, for D_s small.
- Traveling wave: $\tau_s = 0, D_s = O(1)$, for L small.

The steady state in 1d

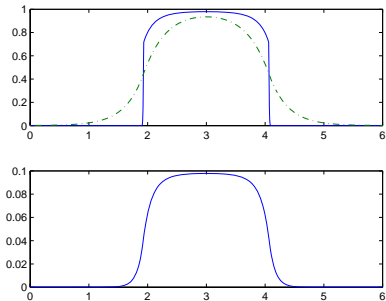
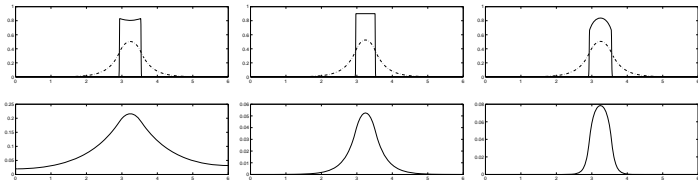
$$\begin{aligned}
 (1 - n)\nabla c - \nabla S &= 0, & x \in [0, L] \\
 n &= 0, & x \notin [0, L] \\
 -D_c \Delta c + c &= \alpha_c n, \\
 -D_s \Delta S + S &= \alpha_s n,
 \end{aligned}$$

Existence

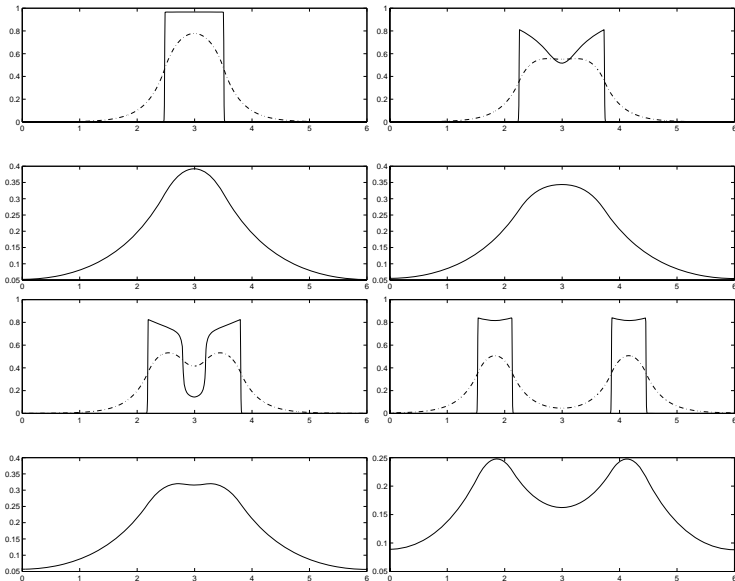
- For L small
- When $|D_c - D_s|$ small
- When $D_c \geq D_s$, the global existence

stability

Numerical results



stability



First special case

Model without diffusion for surfactin

$$\begin{cases} \partial_t n + \partial_x(n(1-n)\partial_x c - n\partial_x S) = 0, \\ -D_c \partial_x^2 c + \tau_c c = n, \\ \partial_t S = \alpha n. \end{cases} \quad x \in \mathbb{R}$$

There exists a 0 – 1 plateau like traveling plateau solution given by

$$n(x, t) = \begin{cases} 1, & \sigma t \leq x \leq L + \sigma t, \\ 0 & \textit{otherwise}, \end{cases}$$

$$\partial_x S(x, t) = \begin{cases} \sqrt{\alpha}, & \sigma t \leq x \leq L + \sigma t, \\ 0 & \textit{otherwise}, \end{cases}$$

Existence

$$\begin{cases} -\sigma \partial_x n + \partial_x(n(1-n)\partial_x c - n\partial_x S) = 0, \\ -D_c \partial_x^2 c + \tau_c c = n, \\ -\sigma \partial_x S = \alpha_S n. \end{cases} \quad x \in \mathbb{R}$$

- Verify n .
- $-\sigma S' = \alpha_S n$, $\forall x$, $\sigma = -S'$, for $x \in [0, L]$, thus $\sigma = \sqrt{\alpha_S}$.
- $\sigma = -S'$, $x \in [0, L]$, $S' = 0$ for $x \notin [0, L]$.

Stability

Stability of traveling pulse solutions

The traveling pulse solution consists of two shocks. For the first shock at the location of $x - \sigma t = 0$ is

$$\left\{ \begin{array}{ll} \text{stable} & \partial_x c(x - \sigma t = 0) > \sqrt{\alpha} \\ \text{linearly degenerate} & \partial_x c(x - \sigma t = 0) = \sqrt{\alpha} \\ \text{unstable} & \partial_x c(x - \sigma t = 0) < \sqrt{\alpha} \end{array} \right. .$$

The second shock at $x - \sigma t = L$ is unconditionally stable.

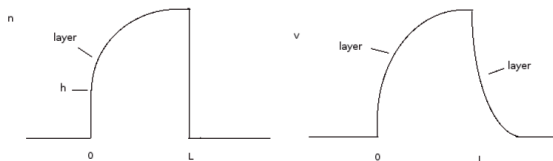
Two equation hyperbolic system

$$\begin{aligned} \partial_t n + \partial_x (n(1 - n)\partial_x c - n\partial_x S) &= 0, \\ \partial_t S - \alpha n &= 0. \end{aligned}$$

Check the Lax entropy condition.

Small diffusion

$$\begin{cases} \partial_t n + \partial_x(n(1-n)\partial_x c - n\partial_x S) = 0, \\ -D_c \partial_x^2 c + \tau_c c = n, & x \in \mathbb{R} \\ \partial_t S - \epsilon^2 \partial_{xx} S = \alpha_S n. \end{cases}$$



- Rescale $\xi = (x - \sigma t)/\epsilon$, use the notation $v = -\partial_x S$.



$$\begin{cases} -\sigma n + n(1-n)\partial_x c + vn = 0, \\ -\sigma v + \alpha n = \dot{v}. \end{cases}$$

- Four possible layers. $n = 0, \xi < 0$, then $v(\xi) = Ce^{\sigma\xi}$, bounded for all negative ξ , $v(\xi) = 0$.
- $(v, n): (0, 0) \mapsto (0, 1 - \sigma/\partial_x c(0)) \mapsto (\sigma, 1) \mapsto (\sigma e^{-\sigma\xi}, 0)$.

Numerical results

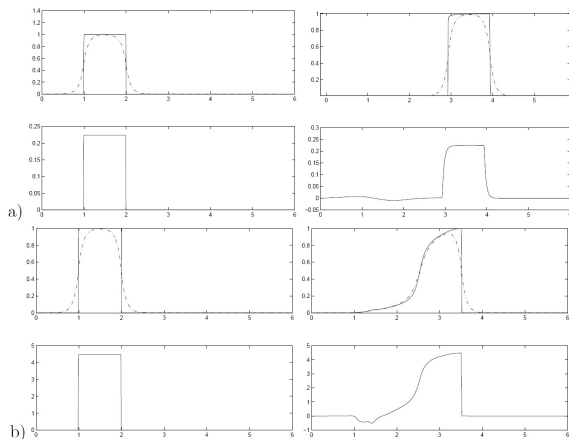


Figure 2: Numerical results of Eq. (8). The left column depicts the initial data for n , the chemical substance c by solid and dash dotted lines respectively (top) and the velocity v (bottom). We can see the boundary layer on the left side for n . a) $\varepsilon = 0.01$, $\alpha = 0.05$, $\tau_c = 1$ and $D_c = 0.01$. b) $\varepsilon = 0.01$, $\alpha = 20$, $\tau_c = 1$ and $D_c = 0.01$. With these parameters, the condition $\frac{\alpha}{\partial_x c} < \sigma$ is not satisfied. In this case when the first shock is unstable.

Second special case when $L \approx 0$

$$L \approx 0, \tau_S = 0$$

$$\begin{aligned} -\sigma Ln + (1 - n)\partial_x c - \partial_x S &= 0, & x \in [0, 1] \\ n &= 0, & x \notin [0, 1] \\ -D_c \partial_{xx} c + L^2 c &= \alpha_c L^2 n, \\ -\sigma L \partial_x S - D_s \partial_{xx} S &= \alpha_s L^2 n, \end{aligned}$$

Banach-Picard fixed point theorem. Difficulties

- $n = 1 - \frac{\sigma L + \partial_x s}{\partial_x c}$, the singularity when $\partial_x c = 0$.
- If $\partial_x c(x_0) = 0$, $\sigma = -\partial_x s(x_0)$.

Second special case when $L \approx 0$

$$\begin{aligned}
 n &= 1 - \frac{\sigma L + \partial_x s}{\partial_x c}, & x \in [0, 1], \\
 \partial_x c &= -\frac{\alpha_c L^2}{2D_c} \left(\int_0^x e^{\frac{L}{\sqrt{D_c}}(y-x)} n(y) dy - \int_x^1 e^{\frac{L}{\sqrt{D_c}}(x-y)} n(y) dy \right), \\
 \partial_x s &= -\frac{\alpha_s L^2}{D_s} \int_0^x e^{\frac{\sigma L}{D_s}(y-x)} n(y) dy.
 \end{aligned}$$

- $\sigma L = \frac{\alpha_s L^2}{D_s} \int_0^{x_0} e^{\frac{\sigma L}{D_s}(y-x)} \cdot n(y) dy$, σ is uniquely determined.
- $\mathcal{F}[n] = 1 - \gamma \frac{\bar{n} - L_1 g[n]}{\bar{n} - L_2 f[n]}$ with

$$\bar{n} = \frac{\int_x^{\frac{1}{2}} n(y) dy}{\frac{1}{2} - x}, \quad \gamma = \frac{\alpha_s D_c}{\alpha_c D_s},$$

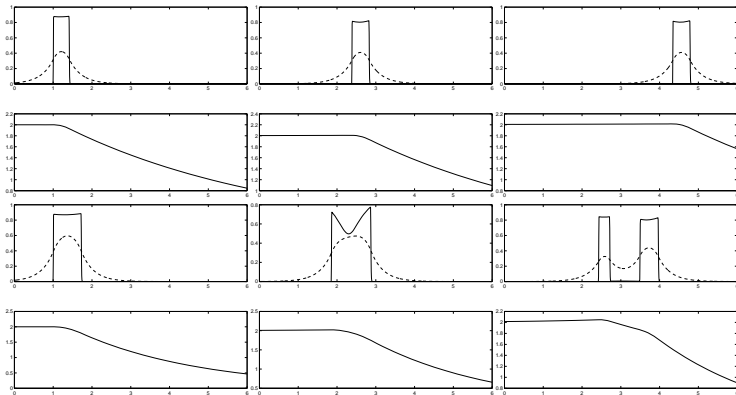
$$L_1 = L/\sqrt{D_s}, L_2 = L/\sqrt{D_c}.$$

Existence

- L small enough, there is a unique speed $\sigma(L)$ and a unique solution $n \in C(0, L)$.
- c is concave in $(0, L)$.
- s is non-increasing on \mathbb{R} and $s_\infty := s_\infty(L)$ is uniquely determined as a function of L .

Second special case when $L \approx 0$

Numerical results



Summary

- For pattern formation, instead of driven by nutrient depletion, we develop a Keller-Segel type Logistic hyperbolic model which will generate branching just using force.
- For reduced models, with parameters at different regime, we explain several numerical observations: stability under size condition and traveling plateaus.

Future work

- From the modeling side, improve the description of short range effects of surfactin, expect different branching instabilities
- From the theoretical point of view, two dimensional effect, further instability effect.

Thanks to

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- A. Daerr
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