Pattern formation I

We now study the interaction between diffusion and positive auto taxis in the equation

① $$\partial_t n = -\partial_x\left(-D\partial_x n + a n \partial_x n\right)$$

with reflecting bnds at $x=0,1$.

No mass disappears, so define

② $$\bar{n} = \int_0^1 n(t,x)\,dx \quad \text{(constant)}.$$

Notice that $n \equiv \bar{n}$ is an equilibrium of ① with the given bnd conds.

Is this equil. stable?

Notice that while diffusion tends to spread out mass, the positive auto taxis tends to concentrate mass.

How do they interact?

Stability of $n \equiv \bar{n}$:

Let $\theta := n - \bar{n}$ be a C^2-small perturbation of the equil.

Then, up to first-order terms in θ, $\partial_x \theta$ and $\partial_x^2 \theta$ we have

(3) $$\partial_t \theta = -\partial_x\Big(-(D - a\bar{n})\partial_x \theta\Big) = (D - a\bar{n})\partial_x^2 \theta$$

with $\partial_x \theta = 0$ at $x = 0, 1$.

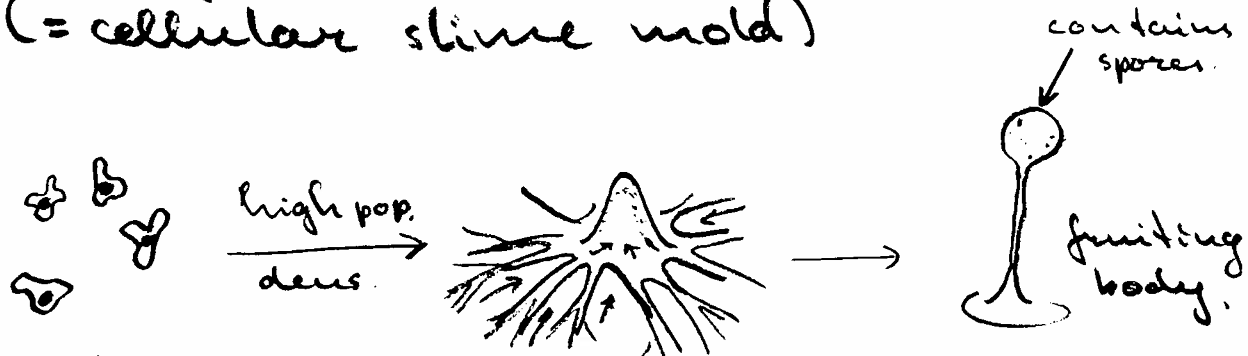
- Notice that if $\boxed{\bar{n} < D/a}$, then (3) is a diffusion equation with diffusion constant $D - a\bar{n} > 0$. One readily shows that $\theta \equiv 0$ (and hence $n \equiv \bar{n}$) is stable
- If $\boxed{\bar{n} > D/a}$, then we have $D - a\bar{n} < 0$, i.e, "negative diffusion"; which is like diffusion, but then as a movie played backwards. So, now $\theta \equiv 0$ (i.e, $n \equiv \bar{n}$) is unstable

Instability leads to spatial inhomogeneity, i.e, spatial patterns, because a spatially homogeneous perturbation would violate the constancy of total mass (see ②).

We work this out in the following example:

Example

Dictyostelium discoideum
(= cellular slime mold)



free-living cells (amoeba)

aggregation and formation of a fruiting body which will produce spores.

Aggregation of free-living cells is actually not by auto-taxis, but is by positive taxis with respect to a chemical (cAMP) that is produced by the cells.

i-states

A : amoeba

C : cAMP-molecule

i-processes

$A \xrightarrow{f} A + C$ (production of cAMP)

$C \xrightarrow{k}$ removed (desintegration of cAMP)

C diffuses

A moves randomly and also exhibits positive taxis toward higher cAMP-concentrations.

(amoeba do not die or reproduce on the time scale considered)

p-equations

$$
④ \left\{ \begin{aligned} \partial_t A &= -\partial_x\left(-\mu\,\partial_x A + \chi A \partial_x C\right) \\ \partial_t C &= -\partial_x\left(-\nu\,\partial_x C\right) + fA - kC \end{aligned} \right.
$$

with reflecting bnds at $x=0$ and $x=L$ for both A and C.

Writing out the reflecting bnd. conds. in explicit form:

$$(5)\quad \left\{ \begin{array}{l} -\mu \partial_x A + \chi A \partial_x C = 0 \\ -\nu \partial_x C = 0 \end{array} \right| \text{ at } x=0, L.$$

which is equivalent to

$$(6)\quad \boxed{\partial_x A = \partial_x C = 0 \quad \text{at} \quad x = 0, L}$$

Spatially homogeneous equilibrium solution:

Suppose $A \equiv A^*$ and $C \equiv C^*$ (const.)
Substitution into (4) gives

$$(7)\quad \left\{ \begin{array}{l} 0 = 0 \\ 0 = f A^* - k C^* \end{array} \right. \Longrightarrow \boxed{C^* = \frac{f}{k} \cdot A^*}$$

Which gives us a relation between the C^* and the A^*.
The A^* is the <u>average cell density</u>, which is constant, also if the system is <u>not</u> in equil.

Stability of (A^*, C^*):

Let $a := A - A^*$ and $c := C - C^*$ denote perturbations from the equilibrium. Then, up to first-order terms in a and c and their derivatives;

$$(8)\quad \begin{cases} \partial_t a = \mu \partial_x^2 a - \chi A^* \partial_x^2 c \\ \partial_t c = \nu \partial_x^2 c + f a - k c \end{cases}$$

with

$$(9)\quad \boxed{\partial_x c = \partial_x a = 0 \quad \text{at } x = 0, L}$$

Substitute $a = u(x) e^{\lambda t}$ and $c = v(x) e^{\lambda t}$ into (8) and (9):

$$(10)\quad \begin{cases} \mu u'' - \chi A^* v'' - \lambda u = 0 \\ \nu v'' + f u - (k + \lambda) v = 0 \end{cases}$$

with

$$(11)\quad \boxed{u' = v' = 0 \quad \text{at } x = 0, L.}$$

(eigenvalue problem.)

A somewhat correcter way to get to the eigenvalue problem is to define the linear operator

$$\mathcal{L} := \begin{pmatrix} \mu \partial_x^2 & , -\chi A^* \partial_x^2 \\ f & , \nu \partial_x^2 - k \end{pmatrix}$$

and the function

$$b := \begin{pmatrix} a \\ c \end{pmatrix} : [0,L] \longrightarrow \mathbb{R}_+^2 .$$

and write ⑧ as

$$\frac{db}{dt} = \mathcal{L} b .$$

The eigenvalue problem then is

$$(*) \quad \mathcal{L} w = \lambda w$$

where λ is an eigenvalue and $w = \begin{pmatrix} u \\ v \end{pmatrix}$ the corresponding eigenfunction on $[0,L]$ with vanishing derivatives at $x = 0, L$.

Notice that $(*)$ is the same as (10)

Intermezzo

To solve the eigenvalue problem, try solutions of the form

$$(12)\quad \begin{cases} u(x) = \alpha \cos \omega x \\ v(x) = \beta \cos \omega x. \end{cases}$$

(potential eigenfunctions)

To satisfy the boundary conditions we must have

$$(13)\quad \boxed{\omega = \frac{\ell \pi}{L}} \quad (\ell = 1, 2, \dots).$$

Substitution of (12) into the eigenvalue problem (10) moreover gives

$$(14)\quad \begin{cases} \alpha(\lambda + \mu\omega^2) - \beta(\chi A^* \omega^2) = 0 \\ \alpha f - \beta(\lambda + \nu\omega^2 + k) = 0 \end{cases}$$

This is a linear equation in α and β. The trivial solution $\alpha = \beta = 0$ gives $u(x) = v(x) = 0 \ \forall x$, which does not correspond to an eigenfunction.

To get non-trivial solution,

we must have that

(15) $$\det\begin{pmatrix} \lambda+\mu\omega^2 & -\chi A^*\omega^2 \\ f & -\lambda-\nu\omega^2-k \end{pmatrix}=0$$

Written out this gives the characteristic equation

(16) $$\boxed{\lambda^2+p(\omega)\lambda+q(\omega)=0}$$ (characteristic equation)

where

(17) $$\begin{cases} p(\omega)=\omega^2(\mu+\nu)+k \quad >0 \\ q(\omega)=\omega^2\left(\mu(\nu\omega^2+k)-\chi A^* f\right) \\ \omega=\dfrac{l\pi}{L} \quad (l=1,2,3,\dots) \quad (\text{from } 13) \end{cases}$$

and hence for the eigenvalues λ we find

(18) $$\boxed{\lambda=\frac{1}{2}\left(-p(\omega)\pm\sqrt{p(\omega)^2-4q(\omega)}\right)}$$

For the spatially homogeneous equilibrium (A^*,C^*) to be unstable we need at least one λ with $\mathrm{Re}\lambda>0$.

Since $p(\omega) > 0$, a necessary and sufficient condition for the existence of an eigenvalue λ with $\text{Re}\,\lambda > 0$ is that $q(\omega) < 0$ for $\omega = \frac{l\pi}{L}$ for some $l \in \{1, 2, \dots\}$

(Make sure you see this!)

From (17) we have that

$q(\omega) < 0 \iff \mu(\nu\omega^2 + k) - \chi A^* f < 0.$

So, we have found that:

The linear system (8) with bnd. cond. (9) has an eigenvalue λ with $\text{Re}\,\lambda > 0$ if and only if there exists a $l \in \{1, 2, 3, \dots\}$ such that

$$\mu\left(\nu\left(\frac{l\pi}{L}\right)^2 + k\right) - \chi A^* f < 0.$$

which we can also write as

$$(19) \qquad 1 \leq l < \frac{L}{\pi}\sqrt{\frac{\chi A^* f - \mu k}{\mu\nu}}.$$

Note.

From (19) we can immediately see which factors promote instability of (A^*, C^*) and hence promote aggregation of amoeba.

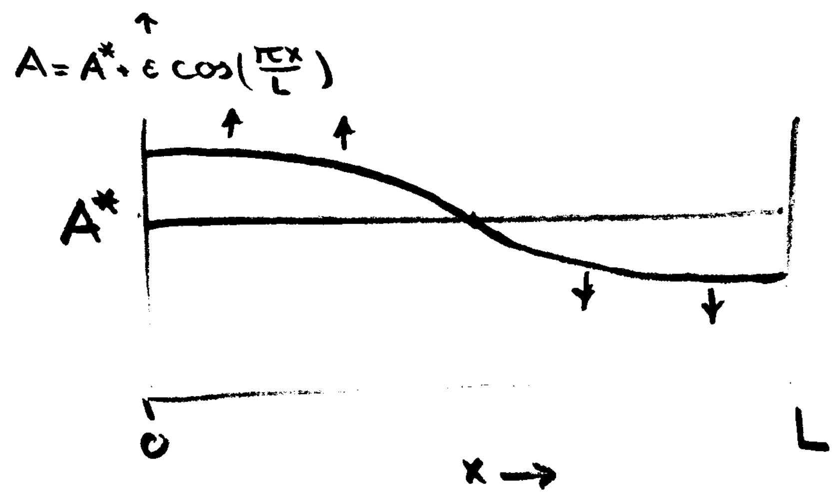
- Large domain (L)
- High average amoeba dens. (A^*)
- Large chemotactic sensitivity (χ)
- High cAMP production (f)
- Slow diffusion of cAMP (ν)
- Slow random movement of amoeba (μ)
- Slow breakdown of cAMP (k).

What aggregation pattern emerges first?

As the amoebae multiply by cell division, eventually the critical density is reached that destabilizes the spatially homogeneous equilibrium.

The aggregation pattern that emerges first is given by the eigenfunction $(u,v) = (\alpha,\beta)\cos(\omega x)$ with $\omega = l\pi/L$ for $\underline{\underline{l=1}}$:

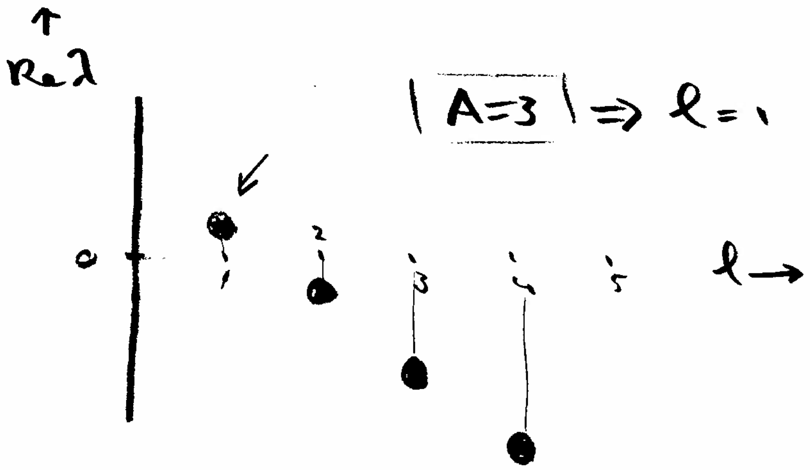
(because $l=1$ is the first value of l that satisfies (19) as the system moves from the stable regime to the unstable regime).



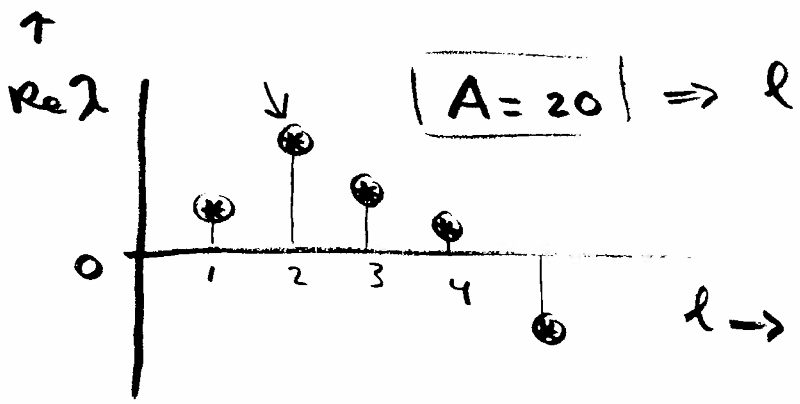
If we are "deeper" inside the instability regime, than (19) is satisfied for more values of ℓ.

Numerical example.

With all parameters set to 1, except for $f = 10$ and $A = 3$, we have



$\boxed{A=3} \Rightarrow \ell = 1$ gives dom. eig. val.



$\boxed{A = 20} \Rightarrow \ell = 2$ gives dom. eig. val.