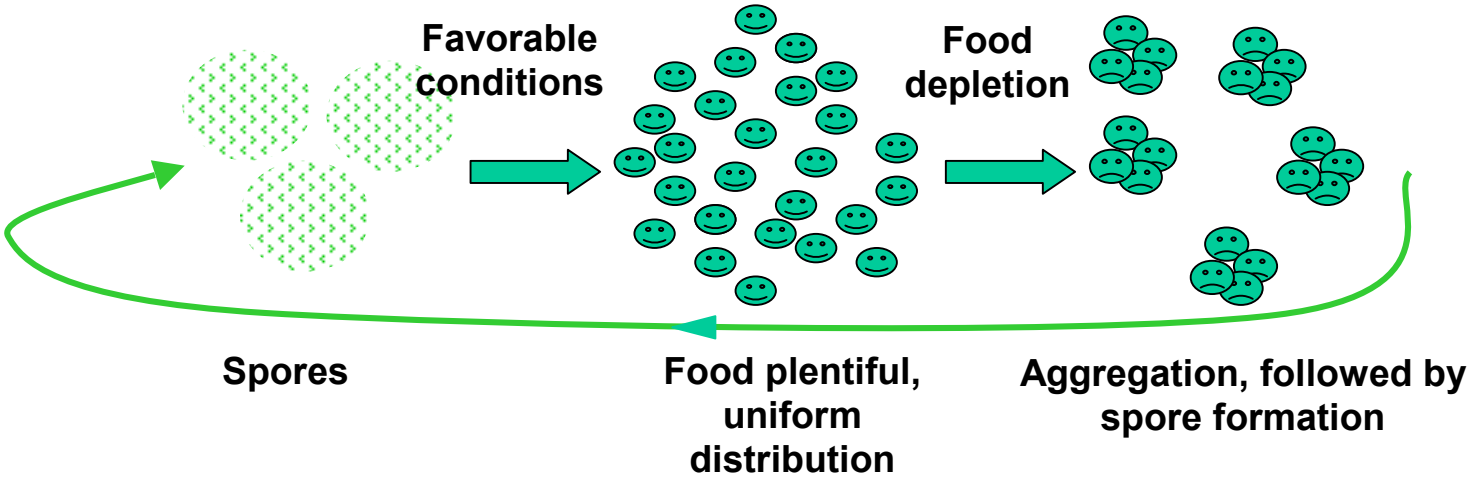
SLIME MOLD AMOEBAE AGGREGATION AS AN INSTABILITY

A simplified model based on
E.F. Keller and L.A. Segel, *J. theor. Biol.*, 1970.

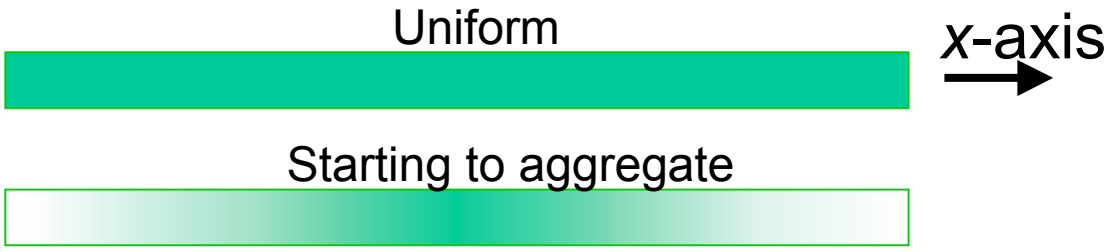
- Amoebae spread out uniformly when sufficient food (bacteria) is available.
- Shortage of wood makes the amoebae start to secrete a certain chemical (an *attractant*) which attracts other amoebae.
- Further depletion of the food supply leads to an aggregation followed by formation of spores
- Spores develop into new amoebae when conditions are favorable.

The life cycle of an amoeba:



Is the onset of the aggregation due to an instability?

A *one-dimensional* model:



Biological facts:

- Amoebae diffuse due to concentration gradients
- Amoebae move towards higher concentration of attractant
- Amoebae secrete more attractant when there is shortage of food
- The attractant breaks down by time due to a chemical reaction
- The attractant diffuses in the solution by itself due to diffusion gradients

Modelling principle:

Conservation equations for the concentrations of amoebae, $a(x,t)$, and the chemical attractant, $\rho(x,t)$.

The transport (*flux*), $\Phi_a(x,t)$, of amoebae consists of *diffusive flux* and *flux due to concentration gradients* of the attractant:

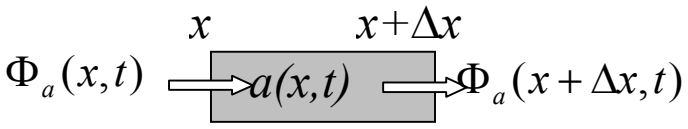
$$\Phi_a(x,t)_{diff} = -\mu \frac{\partial a}{\partial x}$$

$$\Phi_a(x,t)_{att} = \chi a \frac{\partial \rho}{\partial x}$$

$$\Phi_a(x,t) = -\mu \frac{\partial a}{\partial x} + \chi a \frac{\partial \rho}{\partial x}$$

The control volume idea:

Change of the amount in the control volume per time unit = What enters per time unit + What is created per time unit.



The conservation law on *integral form*:

$$\frac{d}{dt}\int_x^{x+\Delta x} a(s,t)ds = \Phi_a(x,t) - \Phi_a(x+\Delta x,t)$$

Leading to the following *differential form*:

$$\frac{\partial}{\partial t}\big(a(x,t)\Delta x\big) = \Phi_a(x,t) - \Phi_a(x+\Delta x,t)\,,$$

or

$$\boxed{\frac{\partial a}{\partial t} = \frac{\partial}{\partial x}\left(\mu\frac{\partial a}{\partial x} - \chi a\frac{\partial \rho}{\partial x}\right)}$$

A similar argument goes for the attractant:

$$\frac{d}{dt}\int_x^{x+\Delta x}\rho(s,t)ds = \Phi_{att}(x,t) - \Phi_{att}(x+\Delta x,t) + \int_x^{x+\Delta x}Q(s,t)ds\,,$$

where

$$\Phi_{att} = -D\frac{\partial \rho}{\partial x}$$
$$Q_{att} = fa - k\rho$$

and fa is the *formation* of attractant by the amoebae, and $k\rho$ is the *decay*.

This leads to the differential form

$$\boxed{\frac{\partial \rho}{\partial t} = fa - k\rho + D\frac{\partial^2 \rho}{\partial x^2}}$$

The equations are a *coupled set non-linear partial differential equations* with the uniform (and stationary) solution

$$a = a_0\,,\ \rho = \rho_0$$

where, in addition,

$$fa_0 = k\rho_0\,.$$

LINEAR STABILITY ANALYSIS

$$a = a_0 + \tilde{a}$$
$$\rho = \rho_0 + \tilde{\rho}$$

Inserting and neglecting higher order term lead to

$$\tilde{a}_t = \mu \frac{\partial^2 \tilde{a}}{\partial x^2} - \chi a_0 \frac{\partial^2 \tilde{\rho}}{\partial x^2}$$
$$\frac{\partial \tilde{\rho}}{\partial t} = f\tilde{a} - k\tilde{\rho} + D\frac{\partial^2 \tilde{\rho}}{\partial x^2}$$

Digression:

Consider the diffusion equation $u_t = \kappa u_{xx}$ with the stationary solution $u(x,t) = u_0$, and a perturbation at $t = 0$ of the form $u(x,0) = \varepsilon \cos(kx)$. Inserting a trial solution of the form $u(x,t) = u_0 + f(t)\cos(kx)$ leads to

$$u(x,t) = u_0 + \varepsilon e^{-\kappa k^2 t} \cos(kx)$$

Thus, the perturbation dampens out *for all values of* k .

We introduce a similar perturbation in our equations:

$$\tilde{a}(x,t) = C_1 e^{\alpha t} \cos(\beta x)$$
$$\tilde{\rho}(x,t) = C_1 e^{\alpha t} \cos(\beta x)$$

This leads to the following system for C_1 and C_2 :

$$(\alpha + \mu\beta^2)C_1 - \chi a_0 \beta^2 C_2 = 0,$$
$$-fC_1 + (\alpha + D\beta^2 + k)C_2 = 0.$$

For non-zero solutions the determinant must vanish, that is,

$$(\alpha + \mu\beta^2)(\alpha + D\beta^2 + k) - f\chi a_0 \beta^2 = 0\,.$$

Which leads to the 2nd order equation

$$\alpha^2 + \left(\mu\beta^2 + D\beta^2 + k\right)\alpha + \left(\mu\beta^2(D\beta^2 + k) - f\chi a_0 \beta^2\right) = 0\,.$$

The equation has real roots (check!), and since

$$\alpha_1 + \alpha_2 = -\left(\mu\beta^2 + D\beta^2 + k\right) < 0$$

both roots are negative if and only if

$$\alpha_1 \bullet \alpha_2 = \left(\mu\beta^2(D\beta^2 + k) - f\chi a_0 \beta^2\right) > 0\,,$$

or

$$\mu(D\beta^2 + k) > f\chi a_0\,.$$

If $\mu k < f\chi a_0$, this will be violated when β is sufficiently small.

A small value of β means perturbations with a long wavelength since $\beta = 2\pi / \lambda$.

Instabilities are prone to occur when

- μ is small: the diffusive mobility of the amoebae is small
- k is small: the decay of attractant is slow.
- f is large: the production of attractant is large
- χ is large: the mobility of the amoebae is large.

The analysis is quite similar in two dimensions. It is conceivable that this mechanism is qualitatively related to what we see in reality. However, the form of the aggregation patterns may be quite complicated.

REFERENCES

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