Nonlinear physics and morphogenesis

January 5, 2017 (3 hours)

Please use separate sheets for problems I and II.

Note that many questions can be solved independently

Only allowed documents: personal written notes (lectures and tutorials), lecture handouts and bilingual dictionary

I. DRIFTING PATTERNS

A. Pattern generated by a stationary bifurcation in a non mirror-symmetric system

We consider a periodic pattern generated by a stationary bifurcation at wave number k_c in an infinite homogeneous medium along the x-axis and write the real field $u(x,t)$

$$u(x,t) = A(t) \exp ik_c x + \overline{A(t)} \exp -ik_c x + \cdots , \tag{1}$$

where the overbar means the complex conjugate and the dots stand for higher order terms. Close to the bifurcation threshold, we assume that the equation for the pattern complex amplitude $A(t)$ is of the form

$$\frac{dA}{dt} = \sum_{m,n} \alpha_{m,n} \, A^m \overline{A}^n \tag{2}$$

where $\alpha_{m,n}$ are complex coefficients.

1) What are the terms of the amplitude equation up to third order in A and $\overline{A}$ that are allowed by symmetry constraints? Give a clear explanation of the used symmetry argument. Write the amplitude equation up to third order.

2) How are the coefficients of the amplitude equation if the system is invariant by reflection $x \to -x$?

3) We consider here a non mirror-symmetric system, i. e. not invariant by reflection. Writing $A = R(t) \exp i\theta(t)$, compute the stationary amplitude R_0 of the pattern above instability threshold and show that the pattern propagates at constant velocity along the x-axis. How does the velocity change with respect to the distance to instability threshold?

B. Competition of two modes generated at a stationary bifurcation

We now consider the generation of a periodic pattern in a domain of finite extension $0 < x < L$. Therefore the system is no longer translation invariant. We model the problem using the Swift-Hohenberg equation

$$\frac{\partial u}{\partial t} = \mu u - \left(k_c^2 + \frac{\partial^2}{\partial x^2}\right)^2 u - u^3, \tag{3}$$

with boundary conditions, $u(0,t) = u(L,t) = 0$ and $\frac{\partial^2 u}{\partial x^2}(0,t) = \frac{\partial^2 u}{\partial x^2}(L,t) = 0$.

We consider the situation displayed in figure 1 in which two patterns with a different number of half-wavelengths within the domain (sketched as convection rolls in figure 1 (left)) becomes simultaneously unstable for $\mu = \mu_0$ when μ is increased from zero.

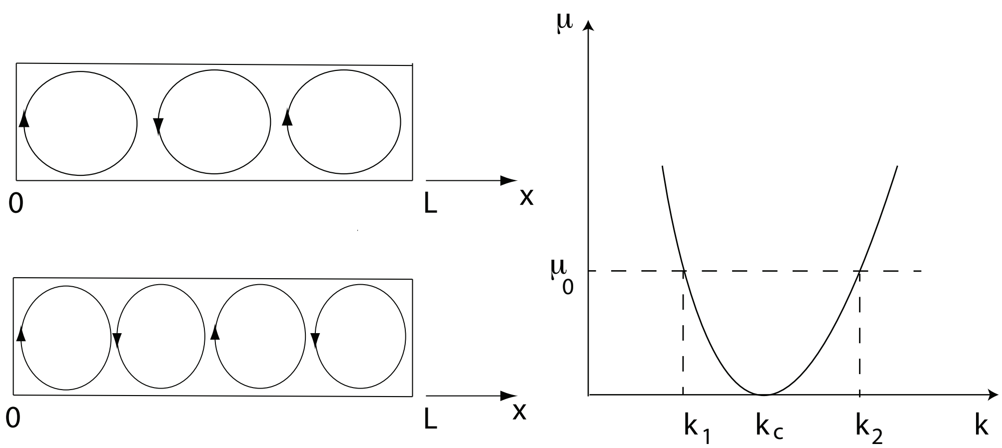

FIG. 1: Periodic patterns with wave numbers k_1 and k_2 generated at instability threshold

1) Perform the linear stability analysis of the solution $u = 0$ of equation (3). Compute the growth-rate s of modes of the form $u_k = \exp st \sin kx$. Give the expression of the marginal stability curve $\mu(k)$. Give the relation between k and L.

2) Show that the situation sketched in figure 1 (right) can be achieved by appropriately choosing the value of L. What happens if L is such that $k_c L = n\pi$ with n integer?

3) We consider the situation sketched in figure 1 (right) with $\mu = \mu_0 + \epsilon\hat{\mu}$ where ϵ is a small parameter and $\hat{\mu}$ is of order 1. We write $u(x,t) = \sqrt{\epsilon} v(x,T)$ with $T = \epsilon t$. Using equation (3), write the equation for $v(x,T)$.

4) We look for a solution in the form $v = v_0 + \epsilon v_1 + \epsilon^2 v_2 + \cdots$ Show that to leading order,

we get an equation of the form $\mathcal{L} \cdot v_0 = 0$ which has a solution of the form

$$v_0(x,T) = a(T) \sin k_1 x + b(T) \sin k_2 x, \tag{4}$$

where $a(T)$ and $b(T)$ are real amplitudes. Give the expressions of k_1 and k_2 as functions of L and one integer n.

5) Write the equation obtained at the next order in the form $\mathcal{L} \cdot v_1 = I_1$ and collect all the terms of I_1 that oscillate in space like $\sin k_1 x$ and $\sin k_2 x$. We recall that $2\sin^2 x = 1 - \cos 2x$ and $4\sin^3 x = 3\sin x - \sin 3x$.

6) Show that the linear problem is self-adjoint and apply the solvability condition to get the differential equations for $a(T)$ and $b(T)$.

7) We slightly change the length L from the value corresponding to figure 1 (right). How are modified the growth-rates of the two modes? How is modified the figure?

8) Justify that the amplitude equations for $a(T)$ and $b(T)$ take the form

$$\dot{a} = \nu a - a^3 - 2ab^2, \tag{5}$$

$$\dot{b} = \lambda b - 2a^2 b - b^3, \tag{6}$$

where ν and λ are real numbers.

9) Find all the fixed points representing pure modes $(a_0, 0)$ or $(0, b_0)$ or mixed modes (a_0, b_0) and determine their domain of existence in the (ν, λ) plane.

10) Analyse the stability of the fixed points and draw the phase space in the different regions of the (ν, λ) plane.

11) Show that by following a path in the (ν, λ) plane, one can describe a transition from a pattern with n half-wavelengths to a pattern with $n+1$ half-wavelengths. Does this transition involve hysteresis?

C. Two competing modes in a system without mirror-symmetry

We consider the previous situation with two competing patterns of wave numbers k_1 and k_2 but in a system that is no longer mirror-symmetric. However, we keep the invariance $u \to -u$ of the Swift-Hohenberg equation. We write $u = a \sin k_1 x + b \sin k_2 x$ and want to determine the form of the equations for a and b using symmetry considerations. We assume as usual that, close to threshold, these equations are of the form

$$\dot{a} = \sum_{m,n} \beta_{m,n}\, a^m b^n, \quad \dot{b} = \sum_{m,n} \gamma_{m,n}\, a^m b^n. \tag{7}$$

1) Write the amplitude equations with all the terms up to cubic order allowed by the invariance $u \to -u$.

2) We want to understand the effect of mirror-symmetry with respect to the plane $x = L/2$. Show that $\sin k_1 x$ and $\sin k_2 x$ change differently in this transformation. You can write $x = y + L/2$ and consider the transformation $y \to -y$, keeping in mind that the expressions of k_1 and k_2 involve respectively odd and even integers.

3) Assume in this question that the system is mirror-symmetric. Under which transformations of a and b the amplitude equations should be invariant? Show that this additional transformation eliminates half of the linear terms and half of the nonlinear terms up to cubic order. Do you recover the form of the amplitude equations computed in the previous section?

4) We come back to a system without mirror-symmetry. We define $Z = a + ib$. We consider only the linear terms of the amplitude equations for a and b. Write the equation for $\dot{Z}$ as a function of Z and $\overline{Z}$.

5) We write $Z = R \exp i\theta$. Using the previous equation, show that we get an equation of the form

$$\dot{\theta} = \omega - \alpha \sin 2\theta + \beta \cos 2\theta. \tag{8}$$

Give the expressions of ω, α and β as functions of the real and imaginary parts of the coefficients $\beta_{m,n}$ and $\gamma_{m,n}$.

6) Which coefficients of this equation vanish when the system is mirror-symmetric? In that case, analyze the stability of the different stationary solutions? (You can propose a graphical answer).

6) Show that equation (8) has no longer any stationary solution if $\omega^2 > \alpha^2 + \beta^2$. What is the name of the bifurcation by which stationary solutions disappear? What is the behavior of the pattern above this bifurcation threshold?

7) Discuss the relation between the absence of mirror-symmetry and drifting patterns.

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Morphogenesis

II. GROWTH OF AN EPITHELIUM STRIPE *IN VITRO*

We consider the growth of an epithelium having the shape of an infinite stripe, in the y direction, of width $2L_0$ at initial time. It means that the epithelium covers the range $-L_0 < x < L_0$ at time $t = 0$. It corresponds to a classical experiment made either in Paris or Barcelona. These experiments take place in a Petri dish saturated with nutrients. Then, the cells have the possibility to proliferate if the pressure in the epithelium is below the homeostatic pressure. In addition, the borders of the epithelium are a place of morphogen production, these morphogens being biochemicals species able to induce cellular displacement. We consider that there exists a strong friction between the epithelium and the substrate so that the dynamics of the epithelium is controlled by a Darcy's law.

1. Explain the composition and geometry of an epithelium. What kind of cells are used typically in laboratory experiments? Hereafter we will use a bidimensional continuous model: is it justified? What is the order of magnitude of expected velocities?

2. *Equation for morphogens*

   Morphogens satisfy a diffusion equation with a typical capture time τ_c such that

   $$\frac{\partial c}{\partial t} = D\Delta c - \frac{1}{\tau_c}c \tag{9}$$

   where D is the coefficient of diffusion. Justify this equation for the morphogens. Is it valid in the epithelium and/or in the water. Knowing that the time scale of capture is of order half an hour, can we neglect the left-hand side of Eq.(9)? Define the length unit of the experiment from Eq.(9) and simplify Eq.(9) accordingly. Knowing that the diffusion coefficient is of order 10^{-9} SI, give an order of magnitude of this length unit. Is a continuous model reasonable ?

3. *Solution of the morphogen concentration*

   Show that the solution of the morphogen concentration inside the epithelium is:

   $$c(x,t) = c_0\frac{\cosh(x)}{\cosh(L(t))} \tag{10}$$

where c_0 is the morphogen concentration produced at the border: $L(t)$. In the water bath, we will take the morphogen concentration to be constant, $c = c_0$ and in the following, we will choose the concentration unit as c_0.

4. *Equation for the pressure field*

   Explain the following equation for the epithelium of mass density ρ_0

$$\frac{\partial \rho_0}{\partial t} + \nabla \cdot \{\rho_0(\vec{V} - \lambda \nabla c)\} = -\alpha^2 \rho_0 (P - P_h) \tag{11}$$

   Can we take ρ_0 as a constant? What is the significance of the terms proportional to α and λ ? Hereafter we will take the homeostatic pressure P_h as the pressure reference, the interfacial pressure is then P_i .We introduce the epithelium velocity as $\vec{V} = -M\nabla P$. Show that, by a suitable choice of the pressure unit, the mobility coefficient can be eliminated from the definition of the Darcy's law.

5. *Solution for the pressure field*

   Show that the pressure $P = P_0(x,t)$ can be written as a superposition of $\cosh(\alpha x)$ and of $\cosh(x)$. Deduce the interface velocity as a function of $L(t)$. The sign of λ has not been fixed. What is physically expected in the case of such experiment?

6. *Stability analysis of the front*

   We consider a small perturbation of planar front and hereafter we neglect chemotaxis so only the cellular proliferation is responsible for the advancement of the colony.The front and the pressure field become:

$$\begin{cases} \zeta = L(t) + \epsilon e^{iky} e^{\omega t} \\ \\ P(x,y,t) = P_0(x,t) + \epsilon p(x) e^{iky} e^{\omega t} \end{cases} \tag{12}$$

   where ϵ is a small parameter. Since now, we no longer have a length unit which was defined previously by the chemoattractants, we choose , as length unit, half the initial thickness of the stripe at time $t = 0$: $L_0 = L(0)$. Deduce the dispersion relation ω as a function of the wavenumber, the surface tension σ and the instantaneous value of the width of the stripe $L(t)$. Under which condition this geometry is stable as time goes on?