Motional Instabilities in Prey–Predator Systems*

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Differential fluxes can destabilize the locally stable stationary density distributions in interaction systems with diffusion, advection, and/or locomotion of chemical or biological species. By this method they can cause the formation of stationary or travelling spatial structures. Different scenarios of this general mechanism of spatio-temporal pattern formation in reaction–diffusion–advection systems will be demonstrated, using a simple two-species predator–prey system as an example model.

1. Introduction

The spatio-temporal dynamics of interacting physical, chemical, biological, economic or social components can generate numerous local and spatially distributed effects far from equilibrium, such as steady-state multiplicity, excitability, regular and irregular oscillations, propagating fronts, target patterns and spiral waves, pulses as well as stationary spatial patterns.

Chemists and biochemists have always been the forerunners of investigations of nonlinear phenomena because nonlinear chemical reactions are easier to realize and to control in vitro in the lab than in vivo biological, economic or even social interactions. The Belousov–Zhabotinskii–Bray–Liebhafsky and Briggs–Rauscher reactions or the catalytic effects of allosteric enzymes are well-known examples of structure-generating chemical and biochemical systems (Atkins, 1990; Field & Burgers, 1985).

In his classical theoretical paper on the chemical basis of biomorphogenesis written in 1952, Turing has shown that diffusion can support pattern formation: the nonlinear interaction of at least two agents with considerably different diffusion coefficients can give rise to stationary spatial structure. However, the effective diffusion coefficients in aqueous solution are almost equal and, hence, it has turned out to be quite difficult to verify Turing’s idea even in the chemical lab. It was only in 1990 when Turing spots and stripes have been found in the CIMA reaction through the regulation of diffusion in gels and sol–gel glasses (Castets et al., 1990). Segel & Jackson (1972) were the first to apply Turing’s results to a problem in population dynamics: the dissipative instability in the prey–predator interaction of phytoplankton and herbivorous copepods with higher herbivore motility. Levin & Segel (1976) have suggested this scenario of spatial pattern formation as a possible origin of planktonic patchiness.

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Rovinsky & Menzinger (1992) have reported on the differential flow induced chemical instability (DIFICI) in a subsystem of the Belousov–Zhabotinskii reaction, modelled by the Pushchinator with diffusion and advection in one spatial dimension. Instabilities of the spatially uniform distribution can appear if reactants or interacting species move with different velocities but regardless of which one is faster. Uniform solutions turn into travelling waves. The conditions are derived for three spatial dimensions. This mechanism of generating patchy patterns is much more general than the Turing description of some behavioural strategies like neutrality, attraction or repulsion (Jorné, 1977; Malchow, 1988a; Okubo 1980; Skellam, 1973). Cross-diffusion is well-known from the electrolyte solutions and from the theory of pattern formation in electro-diffusion systems (Jorné, 1975; Malchow, 1988b).

In order to prove flux-induced instabilities of a spatially uniform distribution of both the species, the existence of such a stable stationary state is assumed

$$\exists \mathbf{x}(r, t) = \mathbf{x}^*, \quad \mathbf{f}(\mathbf{x}^*, \partial) = 0,$$

$$\frac{d}{dt} \mathbf{x}^* = 0, \quad \mathbf{v} \mathbf{x}^* = 0. \quad (2)$$

In linear analysis of its stability against plane wave perturbations

$$\delta \mathbf{x} = \delta \mathbf{x}_0 \exp[\nu t + \mu \mathbf{k} \cdot \mathbf{r}] \quad (3)$$

with the wave vector $\mathbf{k} = \{k_x, k_y, k_z\}$ and imaginary unit $\mu^2 = -1$, one finds the characteristic determinant for the eigenvalues $\nu$$

$$|a_{ij} - \kappa^2 D_{ij} - \delta_{ij}(\mu k \cdot v_i + \nu)| = 0,$$

$$i, j = 1, 2, \ldots, N \quad (4)$$

with the elements of the Jacobian $\mathbf{J} = \{a_{ij} = \partial f_i(\mathbf{x}^*)/\partial x_j, i, j = 1, 2, \ldots, N\}$; and the Kronecker symbol $\delta_{ij}$. The stationary solution (2) is stable if the real parts of all $N$ eigenvalues are less than zero.

Explicit results are available for systems of 2 species, i.e. $N = 2$. The stationary solution (2) is assumed to be stable against small and spatially uniform fluctuations, i.e. to meet the well-known linear stability conditions on trace...
and determinant of the Jacobian
\[
\text{Tr}(J) = a_{11} + a_{22} < 0, \quad (5)
\]
\[
\Delta(J) = a_{11}a_{22} - a_{12}a_{21} > 0. \quad (6)
\]
Now, introducing the splitting \( v = b + \mu c \) and looking for flux-induced instabilities of the spatially uniform distribution (2) against perturbations with finite \( k \neq \theta \), the characteristic equation (4) reads as
\[
|\tilde{a}_{ij} - \delta_{ij}[b + \mu(k \cdot v_i + c)]| = 0, \quad i, j = 1, 2, \quad (7)
\]
i.e.
\[
b^2 - (\tilde{a}_{11} + \tilde{a}_{22})b + \tilde{a}_{11}\tilde{a}_{22} - \tilde{a}_{12}\tilde{a}_{21}
- (k \cdot v_1 + c)(k \cdot v_2 + c)
+ \mu[(b - \tilde{a}_{11})(k \cdot v_2 + c)
+ (b - \tilde{a}_{22})(k \cdot v_1 + c)] = 0
\]
with \( \tilde{a}_{ij} = a_{ij} - |k|^2D_{ij}, i, j = 1, 2 \). Distribution (2) will be stable, i.e. \( \text{Re}(v)_{1,2} = b_{1,2} < 0 \), against spatially uniform perturbations (3) with \( k = \theta \) on conditions (5,6). The instability for increasing values of \( |k| \) will appear at \( b_1b_2 = 0 \) or simply \( b = 0 \). Then, the real part of eqn (8) yields
\[
c^2 + k \cdot (v_1 + v_2)c + (k \cdot v_1)(k \cdot v_2)
- (\tilde{a}_{11}\tilde{a}_{22} - \tilde{a}_{12}\tilde{a}_{21}) = 0
\]
and the imaginary part
\[
(\tilde{a}_{11} + \tilde{a}_{22})c + k \cdot (\tilde{a}_{11}v_2 + \tilde{a}_{22}v_1) = 0. \quad (10)
\]
Common real solutions for \( c \) exist if the resultant of eqn (9) and (10) vanishes:
\[
G(k^2) = \begin{vmatrix}
1 & k \cdot (v_1 + v_2) \\
\tilde{a}_{11} + \tilde{a}_{22} & k \cdot (\tilde{a}_{11}v_2 + \tilde{a}_{22}v_1) \\
0 & \tilde{a}_{11} + \tilde{a}_{22} \\
(k \cdot v_1)(k \cdot v_2) - (\tilde{a}_{11}\tilde{a}_{22} - \tilde{a}_{12}\tilde{a}_{21}) & 0 \\
0 & k \cdot (\tilde{a}_{11}v_2 + \tilde{a}_{22}v_1)
\end{vmatrix}
\]
\[
= -k \cdot (\tilde{a}_{11}v_2 + \tilde{a}_{22}v_1)[k \cdot (\tilde{a}_{11}v_2 + \tilde{a}_{22}v_1)
- k \cdot (v_1 + v_2)(\tilde{a}_{11} + \tilde{a}_{22})]
+ (\tilde{a}_{11} + \tilde{a}_{22})^2[\tilde{a}_{11}\tilde{a}_{22}
- \tilde{a}_{12}\tilde{a}_{22} - (k \cdot v_1)(k \cdot v_2)]
= \tilde{a}_{11}\tilde{a}_{22}[k \cdot (v_1 - v_2)]^2
+ (\tilde{a}_{11} + \tilde{a}_{22})^2(\tilde{a}_{11}\tilde{a}_{22} - \tilde{a}_{12}\tilde{a}_{21}) = 0. \quad (12)
\]
The angles \( \phi_i, i = 1, 2 \), between the perturbation wave vector \( k \) and the velocities \( v_i, i = 1, 2 \), are introduced by the scalar products
\[
k \cdot v_i = |k||v_i|\cos \phi_i, \quad i = 1, 2. \quad (13)
\]
Then eqn (12) reads
\[
G(k^2) = \tilde{a}_{11}\tilde{a}_{22}(|v_1|\cos \phi_1 - |v_2|\cos \phi_2)^2|k|^2
+ (\tilde{a}_{11} + \tilde{a}_{22})^2(\tilde{a}_{11}\tilde{a}_{22} - \tilde{a}_{12}\tilde{a}_{21}) \quad (14)
\]
\[
= (|v_1|\cos \phi_1 - |v_2|\cos \phi_2)^2
\times [D_{11}D_{22}|k|^6 - (a_{11}D_{22} + a_{22}D_{11})|k|^4
+ a_{11}a_{22}|k|^2] + [\text{Tr}(D)]|k|^2 - \text{Tr}(J)]^2
\times [\Delta(J) + \Delta(D)|k|^4
- (a_{11}D_{22} + a_{22}D_{11} - a_{12}D_{21}
- a_{21}D_{12})|k|^2] = 0 \quad (15)
\]
with trace \( \text{Tr}(D) = D_{11} + D_{22} \) and determinant \( \Delta(D) = D_{11}D_{22} - D_{12}D_{21} \) of the diffusivity matrix. The zeros of this polynomial of fourth order in \( |k|^2 \) are the critical perturbation wave numbers. Analytical results are available by separating the diffusive and advective effects.

It is readily seen from the first term of eqn (12) that advective effects only appear if the species move with different velocities. Hence, neglecting advection does not necessarily mean \( v_1 = v_2 = \theta \) but requires only \( v_1 = v_2 \). Then the critical wave number to reach the diffusive Turing instability
can be obtained from the second term of eqn (12) or eqn (14), i.e. from the second and third line of eqn (15). It reads (Jorné, 1977; Malchow, 1988a, 1996)

\[ [k^2]_{\text{crit}} = \frac{a_{11}D_{22} + a_{22}D_{11} - a_{12}D_{21} - a_{21}D_{12}}{2D(D)} \]

Neglecting cross-diffusion, i.e. \( D_{12} = D_{21} = 0 \), eqn (16) reduces to the standard formulation (Segel & Jackson, 1972). In this case, complementary to conditions (5) and (6), the interacting species have to fulfil the strong activator–inhibitor relations (Gierer & Meinhardt, 1972) if the magnitude of their velocity is different. One has to account for a slowly dispersing species (activator) \( X_1 \) with \( a_{11} > 0 \), destabilizing the uniform distribution, and a much faster dispersing stabilizing species (inhibitor) \( X_2 \) with \( a_{22} < 0 \), inhibiting the activator’s effect.

Neglecting diffusive effects, i.e. \( D = 0 \), the tildes in eqn (14) can be omitted and one finds

\[ [k^2]_{\text{crit}} = -\left( \frac{\text{Tr}(J)}{|v_1|\cos \phi_1 - |v_2|\cos \phi_2} \right)^2 \frac{\Delta(J)}{a_{11}a_{22}}. \]

It is readily seen that one has to account for \( a_{11}a_{22} < 0 \), i.e. the two-species systems have to be of activator–inhibitor type again. Instabilities of the spatially uniform distribution can appear if the species move with different velocity regardless of which one is faster. One has to account for the vector character of the velocity, i.e. the species can move with the same magnitude of velocity if they move in different directions and, on the other hand, they can move in the same direction if the magnitude of their velocity is different. However, the uniform distribution will remain stable for the special case that the species move at different magnitudes of velocity and in the same direction but the direction of the perturbation wave vector is perpendicular to them, i.e. \( k \cdot v_i = 0 \), \( i = 1, 2 \).

The latter mechanism for the formation of spatial or spatio-temporal structures, is much more general than the Turing mechanism which depends on strong conditions of the differing diffusion coefficients. It is much more suitable for the application of population–dynamical systems.

On the other hand, it is obvious from eqn (17) that the neglect of diffusive effects leads to instability of the spatially uniform solution against any perturbation, i.e. the point \( k = \theta \) is the bifurcation point itself. This is contrary to the assumptions at the beginning. Hence, the complete eqn (15) has to be solved numerically, looking for the combined effect of diffusion and advection. A simple model of plankton dynamics will be used as an example now.

3. Pattern Formation in a Predator–Prey Model

Scheffer (1991, 1998) has proposed a minimal model for the prey–predator interactions of phytoplankton and herbivorous zooplankton in order to explain local multistability and density oscillations in aquatic communities. A general limiting nutrient as well as a general planktivorous fish acts as an external control variable, driving the system away from equilibrium. The food chain from nutrients to fish is sketched in Fig. 1.

The corresponding simple prey–predator model of the interaction, advection and diffusion of dynamic phytoplankton \( X_1 \) and zooplankton \( X_2 \) at time \( t \) and horizontal position \( r = \{x, y\} \), driven by nutrients \( N \) and fish predation rate \( F \) as external control parameters, reads

\[
\begin{align*}
\frac{\partial X_1}{\partial t} &= -X_1 \frac{N}{H_N + N} X_1 - c X_1^2 - \gamma \frac{X_1}{H_1 + X_1} X_2 \\
&\quad - v_1 F X_1 + D_1 F^2 X_1, \\
\frac{\partial X_2}{\partial t} &= \frac{\epsilon}{H_1 + X_1} X_1 X_2 - \delta X_2 - F \frac{X_2^2}{H_2 + X_2^2} \\
&\quad - v_2 F X_2 + D_2 F^2 X_2.
\end{align*}
\]

![Fig. 1. Sketch of the simplified marine food chain.](image)
\(a\) is the growth rate of phytoplankton, \(\gamma\) the grazing rate of zooplankton on phytoplankton, \(c\) the competition coefficient of phytoplankton, \(e\) the prey assimilation efficiency of zooplankton, and \(\delta\) the mortality of zooplankton. \(H_1, H_2\) and \(H_N\) are the half-saturation constants of functional responses and nutrient limitation. \(X_1, X_2, H_1\) and \(H_2\) are usually measured in milligrams of dry weight per litre (mg dw \text{ l}^{-1}), N and \(H_N\) are given in relative units, \(e\) is a dimensionless parameter; the dimension of \(a, \gamma, \delta\) and \(F\) is given in (mg dw \text{ l}^{-1} \text{ d}^{-1}), \(c\) is expressed in (mg dw \text{ l}^{-1} \text{ d}^{-1}). \(t\) and length \(|r|\) are measured in days (d) and meters (m), respectively.

The nutrient limitation of phytoplankton growth as well as the dependence of the zooplankton grazing rate on phytoplankton density are of Monod type. The zooplankton predation by fish follows a sigmoidal-type-III functional response. The ecological grounds for the choice of these terms are given in Scheffer’s paper.

Locally, the well-known prey–predator limit-cycle oscillations for low fish stock as well as alternatively or simultaneously stable phytoplank-

\[G(k^2) = 0\] is valid for \(v_1^2 - v_2^2 = 0, D_1 = 10^{-5}, D_2 = 2 \times 10^{-3}\) (a) and resulting Turing patterns (b). Neumann boundary conditions: (a) (-----) \(100 \times D_1 = D_2 = 1.0^{-5}\); (---) \(D_1 = 10^{-5}, D_2 = 2 \times 10^{-3}\). (b) (-----) zooplankton; (-----) phytoplankton.

\[G(k^2) = 0\] is valid for \(v_1^2 - v_2^2 = 0.01\) and \(D_1 = D_2 = 10^{-5}\) (a) and resulting travelling waves (b). Neumann boundary conditions: (a) (-----) \(v_{rel} = 0.0\); (---) \(v_{rel} = 0.01\). (b) (-----) \(t = 1500\); (---) \(t = 1600\).
kton- and zooplankton-dominated states for higher fish stock have been found. For certain values of the fish predation rate $F$ and the external forcing by an annual period of the phytoplankton growth rate $\alpha$, the deterministic chaos via torus destruction has been found (Steffen & Malchow, 1996; Steffen et al., 1997). Annual oscillations of $F$ have led to quasiperiodic dynamics (Radtke, 1998).

Spatial analyses with heterogeneous nutrient distribution (Pascual, 1993) or localized fish schools (Medvinsky et al., 2000) have led to chaotic plane waves as well as target and spiral patterns. Irregular oscillations behind diffusive phytoplankton–zooplankton fronts have been found as well (Sherratt et al., 1995; Petrovskii & Malchow, 1999).

**FIG. 4.** Turing pattern selection on an area of 0.25, 1.0 and 2.25 m$^2$. Neumann boundary conditions.
Now, this model will provide examples for differential-flux-induced instabilities of spatially uniform population distributions. Obviously, such instabilities are not possible for $F = 0$ because of vanishing $a_{22} \equiv 0$. Hence, the presence of a planktivorous fish stock is one of the necessary precondition for the emergence of a DIFII.

![FIG. 5. Turing structures for different initial perturbations of the horizontally homogeneous plankton distribution on an area of 1 m$^2$. Neumann boundary conditions.](image-url)
The following interaction parameters have been chosen: \( N = 2.5, F = 0.4, \alpha = 0.5, \gamma = 0.4, H_N = 1.0, H_1 = 0.6, H_2 = 5.0, c = 0.05, e = 0.6, \delta = 0.175. \)

At first, eqn (15) is analysed for one spatial dimension. The obtained critical wave numbers, i.e. the zeros of polynomial (15) are displayed on the left hand sides (l.h.s.) of Figs. 2 and 3. The corresponding critical values and ratios of diffusivities and velocities have been kept for later application in two dimensions. Looking for combined diffusive and advective effects, it turns out that contrary to the non-diffusive case (Malchow, 1995) the resulting instability does not induce the formation of stationary Turing-like standing patterns, shown on the right hand side (r.h.s.) of Fig. 2, but travelling waves, cf. the r.h.s. of Fig. 3.

In Fig. 4, three examples are provided for Turing pattern selection in two spatial dimensions for different system length and \( v_1 = v_2 = 0, D_1 = 10^{-5}, D_2 = 2 \times 10^{-3}. \)

In Fig. 5, Turing patterns are shown for different symmetric as well as asymmetric initial perturbations of the spatially uniform distribution.

In Fig. 6, two time steps of a travelling wave in two spatial dimensions are shown for \( v_1 = v_2^2 = v_1^2 - v_2^2 = 0.01 \) and \( D_1 = D_2 = 10^{-5}. \)

4. Discussion

Analysing the stability of a spatially homogeneously distributed population which is considered as the stationary solution for a set of nonlinear reaction–diffusion–advection equa-

Fig. 6. Travelling plankton population wave after DIFII of the horizontally homogeneous plankton distribution on an area of 1 m². Front defects are due to diagonal motion. Neumann boundary conditions at the upper and lower boundary. Periodic boundary conditions at the left and right boundary.
tions, analytical results have been provided for the instability conditions of the two-species uniform solution in three-dimensional space against spatially non-uniform perturbations with a wave vector of overcritical magnitude.

Instabilities of the spatially uniform distribution can appear if the species move with different velocities regardless of which one is faster. One has to account for the vector character of the velocity, i.e. the species can move with the same magnitude of velocity if they move in different directions and, on the other hand, they can move in the same direction if the magnitude of their velocity is different. The uniform distribution will remain stable for the special case that the species move at different magnitudes of velocity and in the same direction but the direction of the perturbation wave vector is perpendicular to them.

As in the case of a Turing instability, the two-species systems have to be of activator–inhibitor type. However, it is readily seen that this mechanism for the generation of instabilities of spatially uniform stationary species distributions, followed by the formation of spatial or spatio-temporal structures, is much more general than the Turing mechanism which depends on strong conditions on the diffusion coefficients.

Scheffer's minimal plankton model (Scheffer, 1991) provided an example for differential flux-induced instabilities in a population–dynamical system, resulting in standing or travelling patchy distributions. One can imagine a wide range of other applications in population dynamics.

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