

Spatial Patterning of Interacting and Dispersing Populations

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Abstract The possibility of dispersive instabilities of homogeneous distributions of N interacting populations in a uniform environmental potential is investigated. The small amplitude solution emerging after Turing instability of the homogeneous distribution is given for two interacting and dispersing populations following Volterra dynamics. The possibility of cross-dispersion-induced instabilities is investigated for commensalism, predation, and competition respectively. Spatial aggregation in a commensal system is shown as an illustrative example. Including a double-well environmental potential, the spatial distribution of a single nonlinearly growing and rapidly dispersing population is determined analytically using the two-timing perturbation technique. Spatially nonuniform time-periodic environmental potentials are proposed for the description of migration processes.

Introduction

The investigation and mathematical description of spatial patterning of interacting and dispersing species or populations has been a main subject of theoretical biology during the recent years. It should be mentioned here that the terms “dispersal” and “diffusion” are used for the same essence, i.e. an individual leaves its living place with an overall net movement not necessarily zero. On the other hand the term “migration” stands for dispersal plus an implied returning to the original area so that a zero net movement occurs (Lidicker & Caldwell, 1982). It has been pointed out that biological species are not simple diffusers at all. Their migration and dispersal cannot be considered simply as a random walk with state-independent transition probabilities resulting in the phenomenological description as Fickian diffusion. Biodiffusion is the result of various kinds of biological effects as e.g. heterogeneity of environmental conditions, mutually attractive or repulsive interactions of individuals, localization of fertilization, egg-laying, breeding, etc.. A remarkable breakthrough in the development of biodiffusion theory was initiated by the works of Skellam (1951, 1955, 1973). Among other things he classified biological movements into 3 categories, compare also Okubo (1980):

(1) Neutral (Fickian) diffusion, where the flux of population i at position \mathbf{r} and time t is given by

$$\mathbf{j}_{in}(\mathbf{r}, t) = -D_i(\mathbf{r}, X) \nabla X_i(\mathbf{r}, t); \quad i=1, 2, \dots, N; \quad (1)$$

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with population density $X = \{X_i; i=1, 2, \dots, N\}$ and diffusion coefficient D_i which can depend on position and/or local density. Density dependence of diffusion was incorporated later into Skellam's theory, compare McMurtrie (1978). This density dependence is essential to ecological diffusion as well as physical diffusion what has been shown in a preceding paper (Malchow, 1988a). Formulation (1) is applicable to the description of physico-chemical diffusion but only in a few cases to biodiffusion, i.e., when the flux is directed from high to low density. Reaction (interaction)-diffusion (dispersal) equations involving this flux term have been investigated in detail. For reviews compare e.g. Crank (1975), Fife (1979), Okubo (1980), Malchow and Schimansky-Geier (1985), Britton (1986).

(2) Repulsive dispersal, where the movements depend on the conditions at the actual habitat, with

$$\begin{aligned} j_{ir}(\mathbf{r}, t) &= -\nabla [D_i(\mathbf{r}, X)X_i(\mathbf{r}, t)] \\ &= -X_i(\mathbf{r}, t)\nabla D_i(\mathbf{r}, X) - D_i(\mathbf{r}, X)\nabla X_i(\mathbf{r}, t); \quad i=1, 2, \dots, N. \end{aligned} \quad (2)$$

Several kinds of taxis and dispersal are best treated by the concept of a repulsive dispersive force. A special example is to avoid crowding.

(3) Attractive dispersal, where the movements depend on the conditions in the target area, with

$$\begin{aligned} j_{ia}(\mathbf{r}, t) &= -D_i^2(\mathbf{r}, X)\nabla \left(\frac{X_i(\mathbf{r}, t)}{D_i(\mathbf{r}, X)} \right) = X_i(\mathbf{r}, t)\nabla D_i(\mathbf{r}, X) - D_i(\mathbf{r}, X)\nabla X_i(\mathbf{r}, t); \\ & \quad i=1, 2, \dots, N. \end{aligned} \quad (3)$$

Comparing eqs. (2) and (3) one sees that the sign of the gradient of D_i determines whether the dispersal is attractive or repulsive. Of course, there is a permanent interplay of attractive and repulsive forces in ecological communities. This interplay is best taken into account by admitting negative cross-population pressure to the treatment of repulsive dispersal what will be used later. The phenomenological description of repulsive and attractive dispersal comes out of the treatment of a random walk with state-dependent transition probabilities. It should be noted that in these cases the flux is not necessarily directed down the density gradient. This fits real biodiffusion in many cases.

Several papers on spatial pattern formation due to dispersal of populations with intra- and inter-specific interactions appeared during recent years. The reader is kindly referred to the reviews by McMurtrie (1978), Levin (1981), Murray (1988) and again to the outstanding monography by Okubo (1980) and its bibliography.

An extension of the treatments of biodiffusion mentioned above was introduced by Shigesada and Teramoto (1978) generalizing the concept of an environmental density (Morisita, 1971) for describing density-dependent dispersal towards favourable habitats in nonuniform environments. The species move in an environmental potential $U(\mathbf{r})$ and the favourableness of a habitat is proportional to the potential force $-\nabla U(\mathbf{r})$. Several examples for the regulation of interacting populations as e.g. stabiliza-

tion of the coexistence of competitors have been explained, compare Shigesada et al. (1979), Teramoto and Shigesada (1981), Shigesada (1984), Ei and Mimura (1984), and Teramoto and Seno (1987).

The first part of this paper deals with the emergence of dispersive instabilities and patterning of homogeneously distributed interacting populations which disperse in an uniform environmental potential. The time and space evolution of interaction and dispersal of N populations is described by

$$(\partial/\partial t)X_i(\mathbf{r}, t) = f_i(\mathbf{X}) - \nabla \cdot \mathbf{j}_{ir}(\mathbf{r}, t); \quad i=1, 2, \dots, N; \quad (4)$$

where $f_i(\mathbf{X})$ is the nonlinear interaction function. In contrast to eq. (2) the dispersion is assumed to be purely density-dependent, i.e. it is only implicitly space- and time-dependent:

$$\mathbf{j}_{ir}(\mathbf{r}, t) = -\nabla [D_i(\mathbf{X})X_i(\mathbf{r}, t)]; \quad i=1, 2, \dots, N. \quad (5)$$

The repulsive flux is used here but as already mentioned above negative cross-population pressures will be introduced to describe also attractive transitions.

Since the basic paper by Turing (1952) it is known that homogeneous distributions can become unstable against spatially inhomogeneous fluctuations if the dispersion coefficients cross a critical ratio. The effect of the resulting spatial pattern formation has been studied theoretically as well as experimentally for various physical chemical, and biological systems, for reviews see e.g. Nicolis and Prigogine (1977), Haken (1978), Okubo (1980), Malchow and Schimansky-Geier (1985). A very first application to ecological interaction-diffusion problems is due to Segel and Jackson (1972). Kerner (1959) emphasized the importance of cross-diffusion in ecological systems and introduced ad hoc cross-diffusion coefficients into the treatment of neutral diffusion. Using this Journé (1977) showed for an ecologically rare situation the possibility of cross-diffusion-induced pattern in the classical Lotka-Volterra mechanism where self-diffusion-induced pattern formation is impossible (Murray, 1975; Journé and Carmi, 1977). Even negative cross-diffusion increases the possibility of spatial patterning what is also known from electrolyte systems (Journé, 1975; Malchow, 1988b).

Mimura and Kawasaki (1980) observed cross-diffusion-induced spatial segregation in a competitive interaction system with repulsive diffusion, see also Mimura et al. (1984).

In the next chapter the small amplitude solution first bifurcating from the homogeneous distribution after Turing instability is given for arbitrary interactions and arbitrary density-dependent attractive and/or repulsive dispersal. This is applied to cross-diffusion-induced pattern formation in two-component interaction systems and specified for two-component Volterra systems with commensal, predacious as well as competitive interactions. The possibility of cross-diffusion-induced instability of the coexistent state for ecologically plausible diffusional interactions is investigated. A special commensal system is treated as an example.

In the following chapter a population model with logistic growth and constant one-sided immigration is treated for rapid dispersal in a double-well environmental potential. The spatial distribution is obtained analytically using the two-timing perturbation technique (Reiss, 1971; Nayfeh, 1973; Shigesada, 1984; Ei and Mimura, 1984; Ei, 1988).

Spatially nonuniform time-periodic environmental potentials are introduced in the final chapter for the description of migratory population movements.

Turing Structures in Interaction Systems with Repulsive Density-Dependent Dispersal in Uniform Environmental Potentials

Interaction and density-dependent dispersal of N populations in an environmental potential are described by eqs. (4, 5) with inclusion of the potential term into the flux:

$$(\partial/\partial t)X_i(\mathbf{r}, t) = f_i(\mathbf{X}) + \nabla \{ \nabla D_i(\mathbf{X})X_i(\mathbf{r}, t) \} + \gamma_i X_i(\mathbf{r}, t) \nabla U(\mathbf{r}); \quad i=1, 2, \dots, N; \quad (6)$$

where the γ_i are the coefficients of affinity for the environment. An uniform potential is assumed in this chapter so that eq. (6) reduces to

$$(\partial/\partial t)X_i(\mathbf{r}, t) = f_i(\mathbf{X}) + \Delta [D_i(\mathbf{X})X_i(\mathbf{r}, t)]; \quad i=1, 2, \dots, N. \quad (7)$$

The diffusion term can be rewritten to give

$$\Delta [D_i(\mathbf{X})X_i(\mathbf{r}, t)] = \sum_{j=1}^N \nabla [D_{ij}(\mathbf{X}) \nabla X_j(\mathbf{r}, t)]; \quad i=1, 2, \dots, N; \quad (8)$$

where the self-diffusion

$$D_{ii}(\mathbf{X}) = [1 + X_i(\mathbf{r}, t) (\partial/\partial X_i)] D_i(\mathbf{X}); \quad i=1, 2, \dots, N; \quad (9)$$

and the cross-diffusion

$$D_{ij}(\mathbf{X}) = X_i(\mathbf{r}, t) (\partial/\partial X_j) D_i(\mathbf{X}); \quad i, j=1, 2, \dots, N; \quad i \neq j; \quad (10)$$

have been introduced. For the corresponding neutral diffusion problem the cross-diffusion coefficients would not appear at all.

Now the existence of a stationary spatially homogeneous distribution $\mathbf{X} = \mathbf{X}^s$, $f(\mathbf{X}^s) = \mathbf{0}$, $\nabla \mathbf{X}^s = \mathbf{0}$, is supposed what is possible for uniform environmental potentials only (except a trivial zero solution). Its stability against fluctuations

$$\mathbf{x}(\mathbf{r}, t) \propto \exp \{ pt + i\mathbf{k}\mathbf{r} \} \quad (11)$$

is investigated by the usual linear analysis. Inserting (11) into (7) and neglecting nonlinear terms in \mathbf{x} one gets the characteristic equation for the eigenvalues p

$$\det [a_{ij} - k^2 D_{ij} - \delta_{ij} p]_{\mathbf{X}=\mathbf{X}^s} = 0; \quad i, j=1, 2, \dots, N; \quad (12)$$

with

$$a_{ij} = [\partial f_i / \partial X_j]_{\mathbf{X}=\mathbf{X}^s}. \quad (13)$$

The solution is stable if the real parts of all eigenvalues are less than zero:

$$\operatorname{Re} p_i < 0; \quad \forall i=1, 2, \dots, N. \quad (14)$$

This can be proved by the Hurwitz criterion. For the investigation of diffusive instabilities of homogeneous distributions one has to suppose stability for $k=0$, i.e.

$$\det [a_{ij} - \delta_{ij} p] = 0; \quad \operatorname{Re} p_i(k=0) < 0; \quad \forall i=1, 2, \dots, N. \quad (15)$$

Instability occurs for finite $k > 0$, i.e. at least one real part becomes greater than zero:

$$\begin{aligned} \operatorname{Re} p_m(k > 0) &> 0; \quad 1 \leq m \leq N; \\ \operatorname{Re} p_i(k > 0) &< 0; \quad \forall i \neq m. \end{aligned} \quad (16)$$

Specified for two-component systems this leads to the well-known explicit stability conditions for $k=0$

$$a_{11} + a_{22} < 0; \quad a_{11}a_{22} - a_{12}a_{21} > 0. \quad (17)$$

Necessary and sufficient conditions for inducing diffusive instabilities in systems with density-dependent self- and cross-diffusion have been derived recently from eqs. (12, 16) (Malchow, 1988a) as an extension of the expressions given by Segel and Jackson (1972) for systems with constant self-diffusion. They read

$$D_{11}D_{22} - D_{12}D_{21} > 0, \quad (18)$$

$$\begin{aligned} D_{11}a_{22} + D_{22}a_{11} - D_{12}a_{21} - D_{21}a_{12} \geq \\ 2\{(D_{11}D_{22} - D_{12}D_{21})(a_{11}a_{22} - a_{12}a_{21})\}^{1/2} > 0. \end{aligned} \quad (19)$$

The equality sign in (19) corresponds to the critical point. It is reached at the minimum wave number

$$k_m^2 = \frac{D_{11}a_{22} + D_{22}a_{11} - D_{12}a_{21} - D_{21}a_{12}}{2(D_{11}D_{22} - D_{12}D_{21})}. \quad (20)$$

The small amplitude solution in the vicinity of the Turing bifurcation point can be obtained using a standard method of bifurcation theory (Sattinger, 1973; Malchow, 1988c). The general algorithm is not given here. A spatially one-dimensional solution is sought in the form

$$X(r, t) = X^s + \varepsilon \Phi_0 + \varepsilon^2 \Phi_1. \quad (21)$$

ε is the small amplitude

$$\varepsilon = \sqrt{\frac{\sigma - \sigma_c}{\sigma_2}}. \quad (22)$$

The Φ_0 are the eigenfunctions of the Laplace operator satisfying zero-flux boundary conditions $\Phi_0 = \{\phi_{0i} \cos(kr); k = n\pi/L; i = 1, 2, \dots, N; n = 1, 2, \dots\}$; with system length L . The Φ_1 are series expansions of these eigenfunctions. The quantity σ is the bifurcation parameter and σ_c is its critical value. Because the interest is in diffusive instabilities here it can be chosen as the ratio of self- or cross-diffusion coefficients. The value of σ_2 follows generally from the algorithm and it is given below for a special density dependence of diffusion which will be introduced now.

Random movements as well as intra- and interspecific interferences have been successfully described already (see e.g. Shigesada et al., 1979) by dispersion coefficients of the form

$$D_i(X) = \alpha_i + \beta_{ii}X_i + \beta_{ij}X_j; \quad i = 1, 2, \dots, N; \quad j = 1, 2, \dots, N; \quad i \neq j. \quad (23)$$

The α_i correspond to random movements, the β_{ii} to the intraspecific interferences and it is supposed $\alpha_i \geq 0$ as well as $\beta_{ii} \geq 0$ because of intraspecific repulsion. The $\beta_{ij}; i \neq j$; are

due to the interspecific interferences and their sign depends on the actual type of interaction, e.g. $\beta_{ij} < 0$ for attraction of species i by species j . A slight generalization is introduced by

$$D_i = g_i(X_i) + \beta_{ij}X_j, \quad (24)$$

so that one finds

$$D_{ii} = [1 + X_i(\partial/\partial X_i)]g_i + \beta_{ij}X_j; \quad D_{ij} = X_i\beta_{ij}. \quad (25)$$

Arguments and limits of indices are dropped here and in further considerations if misunderstandings are excluded.

Abbreviating

$$[1 + X_i(\partial/\partial X_i)]g_i = d_{ii} \quad (26)$$

one finds finally

$$D_{ii} = d_{ii} + (X_j/X_i)D_{ij}; \quad D_{ij} = X_i\beta_{ij}. \quad (27)$$

Now the bifurcation parameter σ can be fixed. The ratio of the cross-diffusion coefficients is introduced here:

$$D_{21} = \sigma D_{12}. \quad (28)$$

This leads to

$$D_{22} = d_{22} + (X_1/X_2)D_{12}\sigma, \quad (29)$$

i.e. the bifurcation parameter is also hidden in the self-diffusion coefficient of X_2 . Its critical value is

$$\sigma_c = A/B \quad (30)$$

with

$$A = -k^4 D_{11}d_{22} + k^2(D_{11}a_{22} + d_{22}a_{11} - D_{12}a_{21}) - (a_{11}a_{22} - a_{12}a_{21}), \quad (31)$$

$$B = (X_1/X_2)D_{12}\{k^4 d_{11} + k^2[(X_2/X_1)a_{12} - a_{11}]\}. \quad (32)$$

The value of σ_2 is found to be

$$\sigma_2 = - \frac{\phi_{01}n_{11} + \phi_{02}n_{12}}{L_{111}\phi_{01}^2 + (L_{112} + L_{121})\phi_{01}\phi_{02} + L_{122}\phi_{02}^2} \quad (33)$$

with $L_{111} = L_{112} = 0$, $L_{121} = D_{12}$, $L_{122} = (X_1/X_2)D_{12}$ here. The quantities ϕ_{0i} and n_{1i} ; $i = 1, 2$; follow from the general algorithm, compare Malchow (1988b) again.

The possibility of cross-diffusion-induced pattern formation in two-component Volterra systems will be investigated now. The corresponding kinetic equations read

$$(\partial/\partial t)X_1 = (R_1 - a_1X_1 + b_1X_2)X_1 - \nabla j_1, \quad (34)$$

$$(\partial/\partial t)X_2 = (R_2 - a_2X_2 + b_2X_1)X_2 - \nabla j_2, \quad (35)$$

with supposed $a_1 > 0$, $a_2 > 0$. There are 4 possible stationary solutions:

(1) $(X_{11}^s, X_{12}^s) = (0, 0)$, extinction of both species, trivial solution;

$$(2) \quad (X_{12}^s, X_{22}^s) = \left(0, \frac{R_2}{a_2} \right), \text{ extinction of } X_1, \text{ survival of } X_2;$$

$$(3) \quad (X_{13}^s, X_{23}^s) = \left(\frac{R_1}{a_1}, 0 \right), \text{ survival of } X_1, \text{ extinction of } X_2;$$

$$(4) \quad (X_{14}^s, X_{24}^s) = \left(\frac{a_2 R_1 + b_1 R_2}{a_1 a_2 - b_1 b_2}, \frac{a_2 R_2 + b_2 R_1}{a_1 a_2 - b_1 b_2} \right), \text{ coexistence of } X_1 \text{ and } X_2.$$

Domains of stability of these solutions are listed in Tab. 1 for different kinds of interaction (Maynard Smith, 1974):

- a) Commensalism; $b_1 > 0, b_2 > 0$;
- b) Predation; $b_1 < 0, b_2 > 0$ (X_1 -prey, X_2 -predator);
- c) Competition; $b_1 < 0, b_2 < 0$.

Returning to the specific expression (23) for the dispersion coefficients one can deduce now the signs of the β_{ij} for describing ecologically plausible cross-population interferences:

- a) Commensalism; $\beta_{12} < 0, \beta_{21} < 0$, i.e. mutual attraction of the symbiotic partners;
- b) Predation; $\beta_{12} > 0, \beta_{21} < 0$, i.e. escape of prey X_1 and chase of predator X_2 for X_1 ;
- c) Competition; $\beta_{12} > 0, \beta_{21} > 0$, i.e. mutual repulsion of the competitors.

After this classification it is of interest now whether these cross-population interferences can lead to instabilities of the coexistent solution 4 resulting in spatial patterning. One finds from linear stability analysis that conditions (17) are always satisfied for nonnegative densities because it holds

$$a_{11} = -a_1 X_{14}^s, \quad a_{12} = b_1 X_{14}^s, \quad a_{21} = b_2 X_{24}^s, \quad a_{22} = -a_2 X_{24}^s. \quad (36)$$

It should be noted that self-diffusion-induced instabilities are not possible because there is not an activator-inhibitor relationship between the populations (Fife, 1979; Meinhardt, 1982).

Having regard to positive self-diffusion $D_{11} > 0, D_{22} > 0$ one gets the conditions

$$\beta_{12} > -\frac{d_{11}}{X_{24}^s}, \quad \beta_{21} > -\frac{d_{22}}{X_{14}^s}. \quad (37)$$

The latter conditions have to be combined with

$$\beta_{21} > -\frac{d_{22}}{X_{14}^s} \left[1 + \frac{X_{24}^s}{d_{11} \beta_{12}} \right], \quad (38)$$

what follows from (18). Finally one finds from the first part of relation (19), i.e. from the necessary condition $D_{11} a_{22} + D_{22} a_{11} - D_{12} a_{21} - D_{21} a_{12} > 0$, the necessary relation between interaction parameters b_1, b_2 and diffusion parameters β_{12}, β_{21} for inducing cross-diffusive instabilities:

$$\beta_{12} b_2 + \beta_{21} b_1 < 0. \quad (39)$$

It is readily seen that cross-diffusive instabilities for ecologically reasonable relations

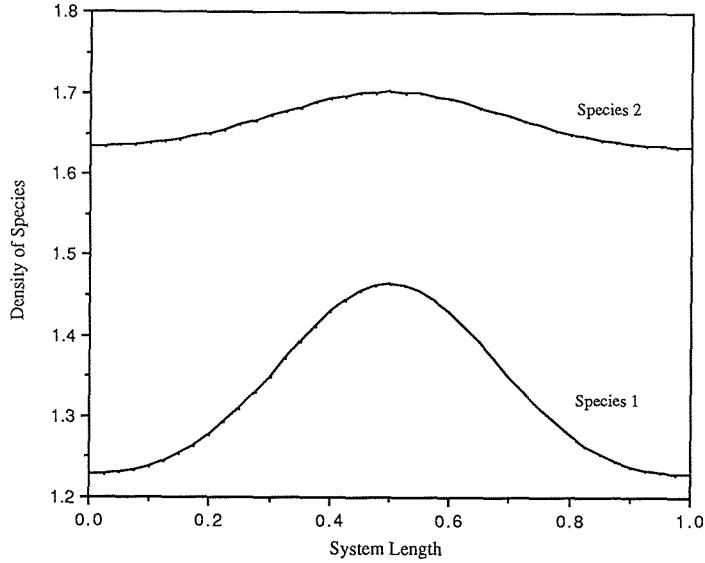


Fig. 1. Spatial aggregation for commensal interactions due to overcritical cross-population pressure. Parameters: $R_1=1, R_2=2, a_2=2, b_1=b_2=1, \alpha_1=0.75, \alpha_2=0.1, \beta_{11}=9.375 \cdot 10^{-2}, \beta_{12}=-1, \beta_{21}=-10^{-2}, \beta_{22}=7.5 \cdot 10^{-3}, D_{11}=0.33333, D_{12}=-1.33333, D_{21}=-0.01667, D_{22}=0.11167, k=6.78625, n=2, L=1/k, \sigma_c=1.25 \cdot 10^{-2}$.

Table 1. Stability of stationary solutions 2, 3, 4. Solution 1 is stable for R_1 and R_2 less than zero only. The possibility or impossibility of a cross-diffusive instability of coexistence is given. Ecologically plausible diffusional interactions are marked by ●.

Type of Interaction	Stat. Solution	Stability for			Cross-Diffusive Instability of Solution 4 Possible for			
		$R_1 < 0; R_2 > 0$	$R_1 > 0; R_2 < 0$	$R_1 > 0; R_2 > 0$	$\beta_{12} < 0, \beta_{21} < 0$	$\beta_{12} < 0, \beta_{21} > 0$	$\beta_{12} > 0, \beta_{21} < 0$	$\beta_{12} > 0, \beta_{21} > 0$
Commensalism $b_1 > 0; b_2 > 0$	2	$-\frac{R_1}{R_2} > \frac{b_1}{a_2}$	/	/	/	/	/	/
	3	/	$-\frac{R_1}{R_2} < \frac{b_1}{a_2}$	/	/	/	/	/
	4	$-\frac{R_1}{R_2} < \frac{b_1}{a_2} < \frac{a_1}{b_2}$	$\frac{b_1}{a_2} < \frac{a_1}{b_2} < -\frac{R_1}{R_2}$	$\frac{b_1}{a_2} < \frac{a_1}{b_2}$	●	▨	▨	▨
Predation $b_1 < 0; b_2 > 0$	2	always	/	$\frac{R_1}{R_2} < -\frac{b_1}{a_2}$	/	/	/	/
	3	/	$-\frac{R_1}{R_2} < \frac{a_1}{b_2}$	/	/	/	/	/
	4	/	$-\frac{R_1}{R_2} > \frac{a_1}{b_2}$	$\frac{R_1}{R_2} > -\frac{b_1}{a_2}$	▨	▨	●	▨
Competition $b_1 < 0; b_2 < 0$	2	always	/	$\frac{R_1}{R_2} < -\frac{b_1}{a_2}$	/	/	/	/
	3	/	always	$-\frac{a_1}{b_2} < \frac{R_1}{R_2}$	/	/	/	/
	4	/	/	$-\frac{a_1}{b_2} > \frac{R_1}{R_2} > -\frac{b_1}{a_2}$	▨	▨	▨	●

▨ : possibility ; ◻ : impossibility

between β_{12} and β_{21} are possible only for commensal and competitive interactions. In predacious systems these instabilities are restricted to “deceitful” relationships between prey and predator (Jorné, 1977). A corresponding overview is added to Tab. 1. Mimura and Kawasaki (1980) gave an example for cross-diffusion-induced spatial segregation in the competitive system and of course, their result can be reproduced by this procedure. Jorné (1977) showed the possibility of spatial patterning due to cross-diffusive instability in the classical Lotka-Volterra mechanism ($a_1 = a_2 = 0$, $R_1 > 0$, $R_2 < 0$), but patterning can only occur for $D_{12} < 0$, $D_{21} > 0$, what is a already mentioned deceitful relation.

The possibility of patterning in a commensal system for the ecologically reasonable case $D_{12} < 0$, $D_{21} < 0$ is shown here. The entire algorithm for determining the small amplitude solution near the Turing bifurcation point is worked off and the resulting solution is plotted in Fig. 1. The corresponding parameters are given in the figure caption. The expected spatial community of the symbiotic partners can be seen.

Nonlinear Growth and Rapid Dispersal in a Double-Well Environmental Potential

A nonuniform environmental potential for modelling spatial heterogeneity is included now, i.e. a stable homogeneous distribution does not exist at all. The shape of the stationary spatial population pattern is strongly determined by the shape of the potential. One can think about $U(\mathbf{r})$ as “mountains” of which the valleys are basins of optimum conditions for growth and interaction. These valleys are separated by mountain ranges where growth and interaction can take place at low or eventually zero rates only. All informations about the structure of the environment are contained in the “map” of $U(\mathbf{r})$.

A single population model is considered for analytical convenience but the extension to the case of n populations is done without difficulties. An approximate solution can be found analytically by applying the two-timing perturbation technique (Reiss, 1971; Nayfeh, 1973; Shigesada, 1984; Ei and Mimura, 1984; Ei, 1988) under the assumption of rapidly dispersing species. This is an ecologically plausible supposition because in many cases the change of the population density as a result of species dispersal occurs more rapidly than that due to growth processes. The general algorithm is dropped again. It is given in detail in Shigesada (1984).

Growth and dispersal of a single population in an environmental potential $U(\mathbf{r})$ can be described by the modified eq. (6)

$$(\partial / \partial t)X(\mathbf{r}, t) = \epsilon f(X) + \nabla [D \nabla X(\mathbf{r}, t) + X(\mathbf{r}, t) \nabla U(\mathbf{r})] \quad (40)$$

with appropriate initial condition $X(\mathbf{r}, 0)$ and zero-flux boundary conditions. For later convenience, the interaction function is written as the product of a constant ϵ and f . It is assumed that f and the flux term $-\nabla j$ are of the same order of magnitude. The dispersal D is assumed to be constant. Furthermore, it is assumed that growth and dispersal take place in different time scales. The spatial density distribution is supposed to be mainly dispersal-controlled, i.e. the local change of density due to dispersal occurs more rapidly than the change due to growth processes. This situation is frequently seen in nature. For realizing this ϵ is assumed to be small enough to give

the opportunity of analyzing the model (40) by the multiple-scale (two-timing) method. The flux term $-\nabla j$ and the function f are set to the same order of magnitude $O(1)$ and a truncated expansion valid for all times up to $O(1/\varepsilon)$ is obtained. For $t \rightarrow \infty$ the system reaches the stationary state

$$X^s(\mathbf{r})Y_0^s g^s(\mathbf{r}). \quad (41)$$

Y_0^s is the stationary overall density in the considered space domain ω whereas $g^s(\mathbf{r})$ is the stationary probability density of the spatial population distribution

$$g^s(\mathbf{r}) = \frac{\exp\{-U(\mathbf{r})/D\}}{\int_{\omega} \exp\{-U(\mathbf{r})/D\} d\mathbf{r}}. \quad (42)$$

It will be shown by an example now that this approximate stationary solution fits the exact solution quite well.

The ecological model is presented as a formal chemical reaction scheme:



The first reaction is due to the immigration of X (Ebeling and Feistel, 1976; Ebeling and Schmelzer, 1980) whereas the second one corresponds to the logistic growth process. The values of A and B are used as parameters for driving the system. The kinetic equation for the scheme (43) reads with formal inclusion of the parameter ε

$$(\partial/\partial t)X(\mathbf{r}, t) = \varepsilon[K_1A(\mathbf{r}) + K_2B(\mathbf{r})X - K_3X^2], \quad (44)$$

where space dependence of A and B has been included too. Introducing the reference quantities for the densities A_0 , B_0 , and $X_0 = (K_1A_0/K_3)^{1/2}$, for the length L_0 , for the time $t_0 = X_0/(K_1A_0)$, for dispersal and environmental potential $D_0 = U_0 = L_0^2/t_0$, one finds the reaction-diffusion-advection equation

$$(\partial/\partial t)X(\mathbf{r}, t) = \varepsilon[A(\mathbf{r}) + \gamma B(\mathbf{r})X - X^2] + \nabla[D\nabla X + X\nabla U(\mathbf{r})], \quad (45)$$

with $\gamma = \frac{K_2B_0}{K_1A_0} \sqrt{\frac{K_1A_0}{K_3}}$. $U(\mathbf{r})$, $A(\mathbf{r})$, and $B(\mathbf{r})$ will be specified now. A double-well potential in one-dimensional space $r \in [0, L]$ is assumed for simplicity. It can be written as

$$U(r) = U_0^* \sum_{n=0}^4 u_n r^n. \quad (46)$$

For reasons of spatial symmetry it is supposed that

$$u_0 = \frac{9}{256}L^4, \quad u_1 = -\frac{3}{8}L^3, \quad u_2 = \frac{11}{8}L^2, \quad u_3 = -2L, \quad u_4 = 1. \quad (47)$$

The spatial distribution of B should have the opposite shape, i.e.

if $\nabla U(r_E) = 0$, then $\nabla B(r_E) = 0$, and
if $\nabla^2 U(r_E) < 0$, then $\nabla^2 B(r_E) > 0$, and vice versa.

Hence $B(r)$ is chosen as

$$B(r) = B_0^* [b_0 - \sum_{n=1}^4 u_n r^n]. \tag{48}$$

Assuming a constant immigration from the left-hand side into the considered space domain, $A(r)$ is taken as a stationary single spatial gradient decreasing monotonously from the left-hand to the right-hand side:

$$A(r) = A_0^* (a_0 + a_1 r). \tag{49}$$

The resulting shape of $U(r)$, $A(r)$, and $B(r)$ can be seen in Fig. 2.

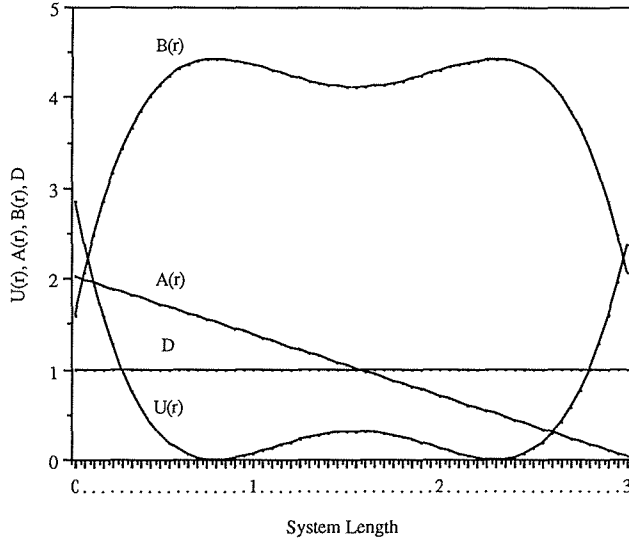


Fig. 2. Sketch of the considered double-well potential $U(r)$ as well as of the spatial distributions of A and B . The straight line $D=1=const.$ is added. Parameters: $U_0^* = A_0^* = B_0^* = 1$, $L=3$, $a_0 = L^4/40$, $a_1 = -L^3/40$, $b_0 = 5L^4/256$.

The interest is in stationary spatial distributions here. $g^s(r)$ is given by eqns. (42) and (46) whereas Y_0^s can be determined from

$$\frac{\partial}{\partial t} Y_0(\epsilon t) = \epsilon (A^s + B^s Y_0 - C^s Y_0^2), \quad Y_0^0 = Y_0(0) = \int_0^L X(r, 0) dr, \tag{50}$$

where $A^s = \int_0^L A(r) dr$, $B^s = \gamma \int_0^L B(r) g^s(r) dr$, $C^s = \int_0^L [g^s(r)]^2 dr$.

With $\delta = [B^s]^2 + 4A^s C^s$, the solution of eq. (50) is given by

$$Y_0(\epsilon t) = \frac{(B^s + \sqrt{\delta}) (B^s - \sqrt{\delta} - 2C^s Y_0^0) - (B^s - \sqrt{\delta}) (B^s + \sqrt{\delta} - 2C^s Y_0^0) \exp \{-\epsilon t \sqrt{\delta}\}}{2C^s [(B^s - \sqrt{\delta} - 2C^s Y_0^0) - (B^s + \sqrt{\delta} - 2C^s Y_0^0) \exp \{-\epsilon t \sqrt{\delta}\}]}. \tag{51}$$

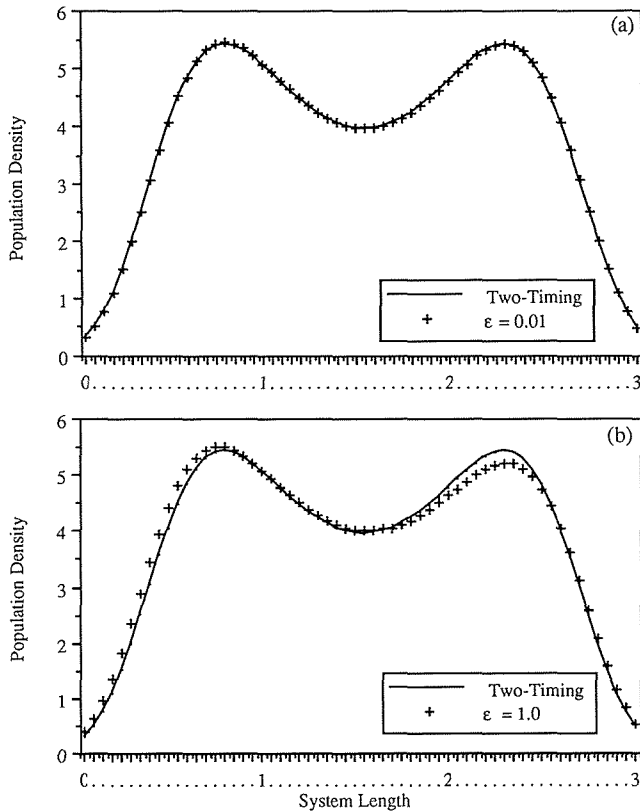
The solution (51) approaches for $\epsilon t \rightarrow \infty$

$$Y_0^s = Y_0(\infty) = \frac{B^s + \sqrt{\delta}}{2C^s} = \frac{B^s + \sqrt{[B^s]^2 + 4A^s C^s}}{2C^s}. \tag{52}$$

The stationary spatial distribution (41) reads finally

$$X^s(r) = \frac{B^s + \sqrt{[B^s]^2 + 4A^s C^s}}{2C^s} \frac{\exp\{-U(r)/D\}}{\int_0^L \exp\{-U(r)/D\} dr}. \tag{53}$$

This distribution plotted in Figs. 3a, b. It is compared with the exact numerical solution of eq. (45) for rapid dispersal ($\epsilon=0.01$) as well as for growth and dispersal in like time scales ($\epsilon=1$). It is readily seen that the approximation fits the exact solution very well for small $\epsilon \ll 1$. In this case the environmental potential controls strongly the shape of the stationary distribution and there is not any influence of the density gradient due to immigration from the left-hand side. Its influence becomes stronger for $\epsilon=1$ and a slight deviation from the approximate solution can be seen. However, this method provides a good impression of stationary spatial distributions of populations dispersing rapidly in a heterogeneous environment mediated by an environmental potential.



Figs. 3a, b. Plots of the stationary distribution (53) with solid line in comparison with the exact numerical solution of eq. (45) for $\epsilon=0.01$ and $\epsilon=1$ respectively. Parameters: $\gamma=1$, all others are the same as in Fig. 2.

Migration of Interacting Species in Spatially Nonuniform Time-Periodic Environmental Potentials

Spatially nonuniform but time-constant environmental potentials have been considered above. But the environmental conditions and hence the favourableness of habitats change very often temporally e.g. periodically daily or seasonally. Many species respond to this by migratory movements following their favourable conditions. Temporal environmental changes are taken into account now by spatially nonuniform and time-periodic environmental potentials

$$U(\mathbf{r}, t) = U(\mathbf{r}, t + T) \tag{54}$$

with the period of oscillation T . The interaction function will be neglected because these processes are secondary during migratory movements. Including the diffusion term (23), the migration equations read

$$-\frac{\partial}{\partial t} X_i(\mathbf{r}, t) = \nabla \cdot \left\{ \nabla \left[\left(\alpha_i + \sum_{j=1}^N \beta_{ij} X_j(\mathbf{r}, t) \right) X_i(\mathbf{r}, t) \right] + \gamma_i X_i \nabla U(\mathbf{r}, t) \right\}; \tag{55}$$

$i = 1, 2, \dots, N;$

with zero-flux boundary conditions. Two different situations will be investigated numerically following descriptions of examples for animal migrations:

One example is the vertical migration in marine organisms *Mysidae* (Skellam, 1973). In darkness they are fairly evenly distributed over all depths, but as light from above increases in intensity the organisms aggregate downwards. The distributions have tails and the individuals do not consistently occupy the preferred place.

This behaviour is described by eq. (55) for a single species population. The potential is chosen as

$$U(r, t) = a + b r \sin^2 \omega t; \quad \omega = 2\pi/T; \quad a, b \text{ constant}; \tag{56}$$

i.e. linear in one-dimensional space $r \in [0, L]$ with time-periodic ascent. The uniform distribution corresponds to zero ascent. The result of the numerical integration is plotted in Fig. 4.

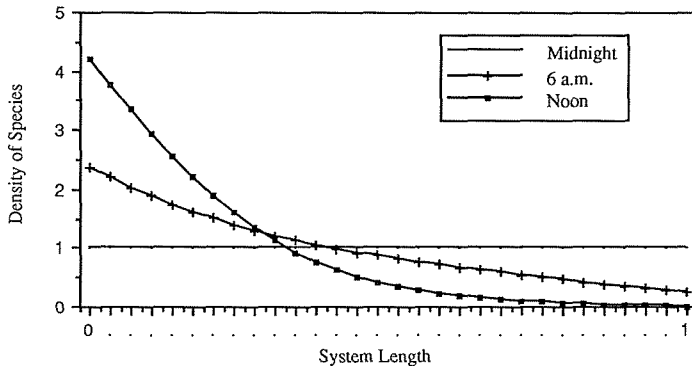
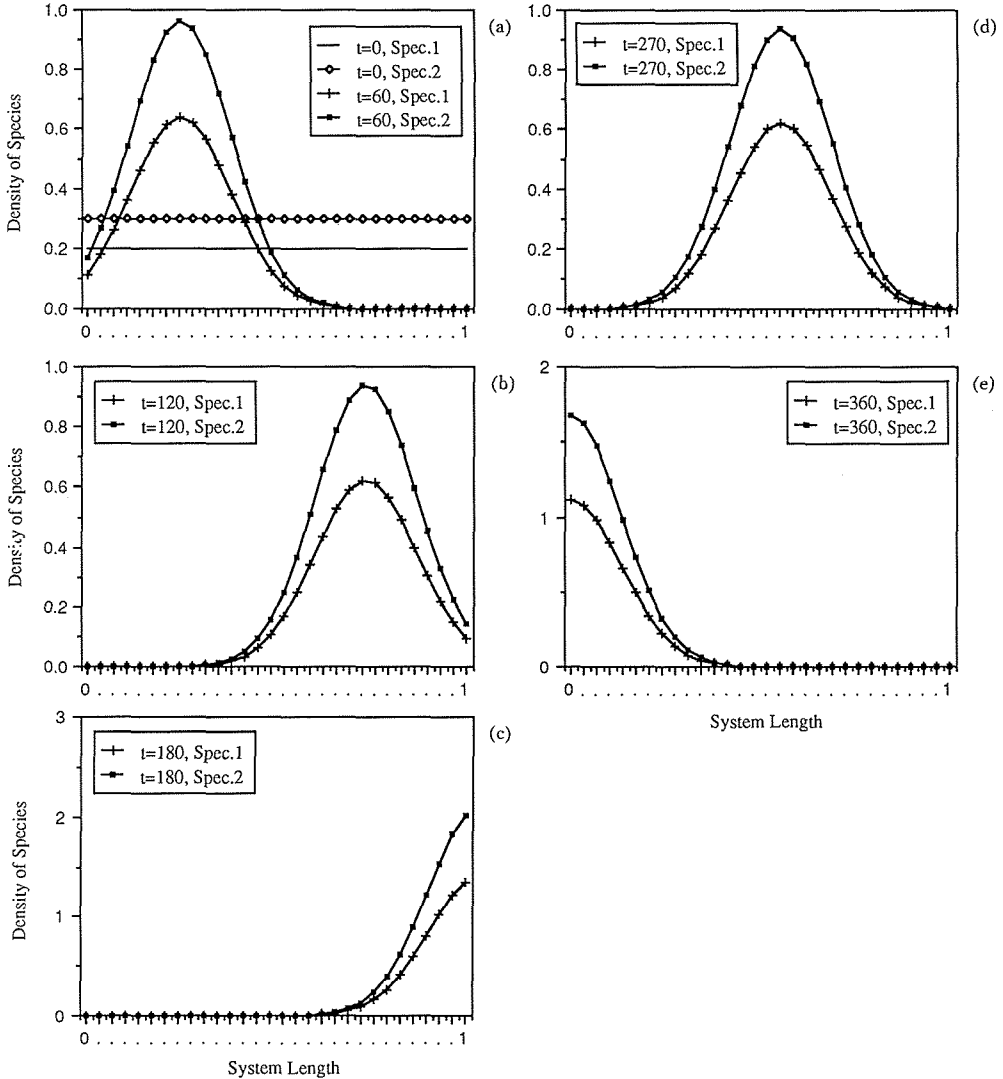


Fig. 4. Model with density-dependent dispersal $D(X) = \alpha + \beta X$ in a space-time-dependent environmental potential $U(r, t) = a + b(r - L \sin^2 \omega t)^2$ with $\alpha = 2.$, $\beta = 0.5$, $\gamma_1 = 1.$, $a = 1.$, $b = 60.$, $\omega = 2\pi/T$, $T = 240$ a.u., $L = 1.$

Migration of flocks is a well-known pattern of movement that is found in many species of birds in many parts of the world. One example is a North American songbird, the bobolink, *Dolichonyx oryzivorus* (Baker, 1978). It nests in southern Canada and northern United States. During winter in the northern hemisphere, however, it is found in the southern hemisphere in eastern Bolivia, western Brazil, Paraguay, and northern Argentina.

Migration of swarms following meteorological changes is well-known from insects too, e.g. from the African locust *Schistocerca gregaria* (Dingle, 1972). The gregarious phase of this species forms large migratory swarms traveling on winds which converge



Figs. 5a, b, c, d, e. Model for 2 populations of similar species with density-dependent dispersal $D_i(X) = \alpha_i + \beta_{ii}X_i + \beta_{ij}X_j$; $i=1, 2$; $j=1, 2$; $i \neq j$; in a space-time-dependent environmental potential $U(r, t) = a + b(r - L \sin^2 \omega t)^2$ with $\alpha_1 = \alpha_2 = 1.$, $\beta_{11} = \beta_{12} = \beta_{22} = 0.$, $\beta_{21} = -0.01$, $\gamma_1 = \gamma_2 = 1.$, $a = 1.$, $b = 30.$, $\omega = 2\pi/T$, $T = 360$ a.u., $L = 1.$

at the intertropical convergence zone. This zone moves forth and back across the equator once each year causing seasonal rains in much of tropical Africa. These rains promote greening and growth of the vegetation, and the locust swarms are thus deposited in areas suitable for breeding.

Migratory swarms or flocks are modeled here by inclusion of an environmental potential

$$U(r, t) = a + b(r - L \sin^2 \omega t)^2; \quad \omega = 2\pi/T; \quad a, b \text{ constant}; \quad (57)$$

i.e. a time-periodically moving parabola in one-dimensional space $r \in [0, L]$. The spatial aggregation takes place at minimum potential and follows its movement. The joint migration of two populations of similar species with interspecific attraction and like affinities for the environment is investigated. The corresponding moving patterns are given in Figs. 5a-e. Both distributions have only one maximum due to the interspecific attraction.

The given figures illustrate the usefulness of spatially nonuniform time-periodic environmental potentials for the description of migratory movements of animal species. The models could be extended by inclusion of space-time-dependent growth-interaction functions f_i with a certain phase shift compared to the migration period for modelling growth and interactions at the resting places.

Finally it should be remarked that all attempts have failed to prove stabilization of coexistence of competing species by spatial segregation in time-periodic environmental potentials what is a known effect for time-constant space-parabolic potentials (Shigesada et al., 1979).

Discussion

The small amplitude pattern near the Turing bifurcation point of the homogeneous distribution of N populations has been given for arbitrary interactions and arbitrary density-dependent attractive and/or repulsive dispersal in uniform environmental potentials. It has been specified for the interactions of two populations. Explicit conditions for the emergence of diffusive instabilities in two-component systems with cross-population motional interferences have been provided.

A Volterra interaction system has been treated as an example. Self-diffusion-induced instabilities of the coexistent state are not possible at all regardless of the special type of interaction, but the possibility for instabilities induced by the cross-population motional interferences has been shown for commensal and competitive interactions and for the corresponding ecologically reasonable diffusional interferences. Cross-diffusive instabilities in predacious systems are possible for deceitful relationships between prey and predator only. It has been shown that spatial aggregation in a commensal system can occur due to overcritical strong cross-population pressure, i.e. the attraction of the symbiotic partners is much stronger than their intraspecific repulsive force.

Nonlinear growth and dispersal in heterogeneous environments has been described by reaction-diffusion-advection equations. The advection term results from the inclusion of a spatially nonuniform environmental potential which mediates the heterogeneity. It was possible to obtain an approximate solution analytically for dispersal

and growth in different time scales. The two-timing perturbation technique has been applied for rapid dispersal. Using logistic growth with directed immigration as an example, it could be shown that the approximation holds very well. The shape of the resulting stationary spatial density distribution follows strongly the modality of the potential. Spatial variations of growth parameters do not play any role. Maxima of density are formed at minima of the potential which stand for optimum growth conditions.

For like time scales of dispersal and growth the influence of spatially varying growth parameters becomes stronger what has been shown by a density gradient formed quasi-stationary as a result of constant immigration directed from one side.

It should be remarked incidentally that the approximate solution fits the exact solution quite well for constant growth parameters, even for like time scales of growth and dispersal.

At last two different migration patterns have been modelled by inclusion of spatially nonuniform and time-periodic environmental potentials.

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