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Persistence and Spatial Patterns in a One-Predator-Two-Prey Lotka-Volterra Model with Diffusion (*).

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Sunto. – *Si considera un sistema di equazioni di reazione-diffusione del tipo di Lotka-Volterra con due prede e un predatore. Assumendo delle ipotesi sui coefficienti che assicurano che il sistema è persistente (nel senso di Butler, Freedman e Waltman), si mostra l'esistenza di equilibri non omogenei e di soluzioni periodiche non omogenee rispetto alla variabile spaziale per certi valori dei parametri di diffusione. I risultati sono illustrati da elaborazioni numeriche.*

1. – Introduction.

In this paper we consider the following system of reaction-diffusion equations

$$(1)\qquad \begin{cases} \partial_t u_1 = d_1 \Delta u_1 + u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2 - \delta_1 u_3)\,, \\ \partial_t u_2 = d_2 \Delta u_2 + u_2(\alpha_2 - \beta_2 u_1 - \gamma_2 u_2 - \delta_2 u_3)\,, \\ \partial_t u_3 = d_3 \Delta u_3 + u_3(-s + \varepsilon_1 u_1 + \varepsilon_2 u_2 - \varepsilon_3 u_3)\,, \qquad x \in \Omega,\ t > 0, \\ \partial_\nu u_i = 0\,,\ x \in \partial\Omega\,,\ t > 0\,. \end{cases}$$

Here, $\Omega \subset \boldsymbol{R}^N$ is a bounded domain of class $C^{2,\gamma}$, for some $0 < \gamma \leq 1$, with outer normal ν to the boundary.

We make the following assumption

(A1) d_i, $i = 1, 2, 3$, $\alpha_i, \beta_i, \gamma_i, \delta_i, \varepsilon_i$, $i = 1, 2$, *and* s *are positive constants*, ε_3 *is a non-negative constant.*

(A1) implies that (1) is a Lotka-Volterra model describing the time-development of three population densities u_i, $i = 1, 2, 3$ in the habitat Ω. u_1 and u_2 represent two prey

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populations competing for the same food source, whereas u_3 is a predator feeding both upon u_1 and u_2. Under assumption (A1) and for $\varepsilon_3 = 0$, system (1) with and without diffusion was considered by a number of authors, see *e.g.* [3], [2] and most notably [9] where additional references can be found.

For the most part of this paper we will make the following additional assumption

(A2) (i) $\varepsilon_1 \alpha_1 - \beta_1 s > 0$ *and* (ii) $\varepsilon_2 \alpha_2 - \gamma_2 s > 0$.

(A2) means that in the kinetic model corresponding to (1) (*i.e.* with $d_i = 0$) the absence of one of the prey populations leads to coexistence of the other prey population with the predator. The reader should note that (A2) is different from the assumption (H.3) made by MIMURA and KAN-ON in [9]. In fact, (H.3) in [9] implies that $\varepsilon_2 \alpha_2 - \gamma_2 s < < 0$.

System (1) is called *persistent* (in the sense of Butler, Freedman and Waltman) if whenever $u(x,t) = (u_i(x,t))_{i=1,2,3}$ is a solution of (1) satisfying

$$u_i(x,0) \geqslant 0 \ (\not\equiv 0) \qquad \text{for all } x \in \Omega \text{ and } i = 1,2,3,$$

then

$$\inf_{x \in \Omega} \liminf_{t \to \infty} u_i(t)\ (x) > 0 \qquad \text{for } i = 1,2,3,$$

(see [3] and [2]).

Both in [3] and in [2] conditions were given to assure the persistence of the model considered.

In section 2 of this paper we extend the results from [3] and [2], and, more importantly, clarify their biological and mathematical meaning. By including the case $\varepsilon_3 > 0$ we also take into account possible crowding effects of the predator. Under the persistence assumptions considered here, system (1) has a unique spatially homogeneous positive equilibrium $\bar{u} \in \boldsymbol{R}^3$. In certain cases (cf. the numerical study in [2]) this equilibrium is asymptotically stable with respect to the full diffusive system (1). Therefore the question arises whether some more interesting and more complicated asymptotic behavior is possible. In particular, we are asking whether the presence of diffusion can lead to the formation of spatial patterns and if so, under what conditions. This is a natural question to ask as it is well-known that diffusion can have destabilizing effects on a biological system.

In section 3 of this paper we answer the question posed above by showing the existence of time-invariant spatial patterns (for appropriate values of the diffusion coefficients) when $\beta_2 \gamma_1 > \beta_1 \gamma_2$, i.e. when the interspecific competition of the two prey populations exceeds their intraspecific competition. A similar result was also obtained in [9], but in one space dimension ($N = 1$) and under hypotheses different from ours (including hypothesis (H.3) referred to before). In section 3 we also derive conditions assuring the existence of time-periodic spatial patterns (spatio-temporal oscillations) of (1).

Finally, in section 4 of this paper we discuss stability of these time-invariant and time-periodic spatial patterns in one space dimension and illustrate the results by numerical examples. We also show (both theorically and numerically) the existence of stable Hopf bifurcations in the persistent kinetic system corresponding to (1) (for an appropriate choice of the kinetic parameters). When the diffusion coefficients are suitably varied then the homogeneous periodic solution of (1) thus obtained changes its stability properties with respect to (1) and so gives rise to secondary (non-homogeneous) bifurcations of periodic solutions and two-dimensional tori. However, this aspect will not be discussed any further here.

2. – Persistence.

In the sequel we shall use the following notation: if a lower case letter, say w, denotes a vector in $\boldsymbol{R}^n$ (i.e. $w = (w_1, \dots, w_n)^T$) then the corresponding upper case letter denotes the diagonal $n \times n$ matrix whose entries on the diagonal are the components of w (i.e. $W = \operatorname{diag}(w_1, \dots, w_n)$). Using this notation (1) can be written in the equivalent form

$$\begin{cases} \partial_t u = D\Delta u + U(\alpha + Au), & x \in \Omega, \ t > 0, \\ \partial_\nu u = 0, \ x \in \partial\Omega, \ t > 0. \end{cases} \tag{2}$$

Here $d = (d_1, d_2, d_3)^T$, $u = (u_1, u_2, u_3)^T$, $\alpha = (\alpha_1, \alpha_2, -s)^T$ and A is the matrix

$$A = \begin{pmatrix} -\beta_1 & -\gamma_1 & -\delta_1 \\ -\beta_2 & -\gamma_2 & -\delta_2 \\ +\varepsilon_1 & +\varepsilon_2 & -\varepsilon_3 \end{pmatrix}. \tag{3}$$

The kinetic system corresponding to (2) thus becomes

$$\dot{u} = U(\alpha + Au). \tag{4}$$

As in [2], let $p > N$ and note that $-\Delta$ with Neumann boundary conditions is a sectorial operator on $X = L^p(\Omega)$ generating a family of fractional power spaces $X^\beta \subseteq L^p(\Omega)$. Fix $1/2 \leqslant \beta < 1$. Then $X^\beta \subseteq C^0(\overline{\Omega})$.

Write $X_+^\beta = \{w \in X^\beta \mid w(x) \geqslant 0 \text{ for } x \in \overline{\Omega}\}$ and let $Y = (X_+^\beta)^3$.

For every $u_0 \in Y$ there is a unique solution $t \to u(t, u_0) \in Y$ of (2) for $t > 0$, continuous at $t = 0$, $u(0, u_0) = u_0$.

Moreover, $\sup_{t \geqslant 0} \|u(t)\|_Y < \infty$. Write $u_0 \Pi t := u(t, u_0)$. Then Π is a semiflow on Y. For the proofs of these assertions, cf [2], [5]. In particular, the boundedness of u follows from the corresponding result for $\varepsilon_3 = 0$ (Lemma 4.4 in [2]) and standard comparison theorems.

In the sequel we need the following abbreviations:

$$(5)\qquad \begin{cases} p_1 = \alpha_1\gamma_2 - \alpha_2\gamma_1, & p_2 = \beta_1\alpha_2 - \beta_2\alpha_1, \\ p_3 = \beta_1\gamma_2 - \beta_2\gamma_1, & p_4 = \varepsilon_1\alpha_1 - \beta_1 s, \\ p_5 = \varepsilon_2\alpha_2 - \gamma_2 s, & p_6 = \varepsilon_2\alpha_1 - \gamma_1 s, \\ p_7 = \varepsilon_1\alpha_2 - \beta_2 s, & p_8 = -\delta_1 p_5 + \delta_2 p_6 + \varepsilon_3 p_1, \\ p_9 = -\delta_2 p_4 + \delta_1 p_7 + \varepsilon_3 p_2. \end{cases}$$

A simple calculation shows that

$$(6)\qquad p_8 = -\det\begin{pmatrix} -\alpha_1 & -\gamma_1 & -\delta_1 \\ -\alpha_2 & -\gamma_2 & -\delta_2 \\ s & \varepsilon_2 & -\varepsilon_3 \end{pmatrix}, \qquad p_9 = -\det\begin{pmatrix} -\beta_1 & -\alpha_1 & -\delta_1 \\ -\beta_2 & -\alpha_2 & -\delta_2 \\ \varepsilon_1 & s & -\varepsilon_3 \end{pmatrix}.$$

Let us now note the following trivial

LEMMA 1. – *Assume* (A1). *Then the following points are equilibria of* (4), *considered as a system on* $\boldsymbol{R}^3$:

(i) $E_0 = 0$,

(ii) $E_1 = (\alpha_1/\beta_1, 0, 0)^T$,

(iii) $E_2 = (0, \alpha_2/\gamma_2, 0)^T$,

(iv) $E_3 = (\beta_1\varepsilon_3 + \delta_1\varepsilon_1)^{-1}\cdot(\alpha_1\varepsilon_3 + \delta_1 s, 0, p_4)^T$,

(v) $E_4 = (\gamma_2\varepsilon_3 + \delta_2\varepsilon_2)^{-1}\cdot(0, \alpha_2\varepsilon_3 + \delta_2 s, p_5)^T$.

To assure that these equilibria are non-negative (i.e. have non-negative components) we must make the following assumption

(A2) (i) $p_4 > 0$ *and* (ii) $p_5 > 0$.

This condition means that in the kinetic model (4) the absence of one prey population leads to coexistence of the other prey population with the predator. Assume (A1) and (A2) and linearize (4) at E_3. Writing $u = v + E_3$ we obtain after a straightforward calculation the following linearized system:

$$\dot{v} = B_{(3)} v$$

where

$$(7)\qquad B_{(3)} = \begin{pmatrix} -\beta_1 E_{31} & -\gamma_1 E_{31} & -\delta_1 E_{31} \\ 0 & k_3 p_9 & 0 \\ +\varepsilon_1 E_{33} & +\varepsilon_2 E_{33} & -\varepsilon_3 E_{33} \end{pmatrix},$$

there E_{3i} are the components of E_3 and $k_3 = (\beta_1\varepsilon_3 + \delta_1\varepsilon_1)^{-1}$. Similarly, linearizing at E_4 we obtain for $u = v + E_4$

$$\dot{v} = B_{(4)} v$$

with

$$B_{(4)} = \begin{pmatrix} k_4 p_8 & 0 & 0 \\ -p_2 E_{42} & -\gamma_2 E_{42} & -\delta_2 E_{42} \\ \varepsilon_1 E_{43} & +\varepsilon_2 E_{43} & -\varepsilon_3 E_{43} \end{pmatrix} \tag{8}$$

where $k_4 = (\gamma_2 \varepsilon_3 + \delta_2 \varepsilon_2)^{-1}$.

Analyzing the characteristic polynomial of $B_{(3)}$ and $B_{(4)}$ we obtain:

PROPOSITION 2. – *Assume* (A1) *and* (A2).
Then the following properties hold.

1) $\operatorname{Re}\sigma(B_{(3)}) < 0$ *if and only if* $p_9 < 0$,
2) $\operatorname{Re}\sigma(B_{(4)}) < 0$ *if and only if* $p_8 < 0$.

COROLLARY 3. – *Assume* (A1) *and* (A2).
If $p_8 < 0$ *or* $p_9 < 0$, *then* (4) *and* (2) *are not persistent.*

PROOF. – Suppose, say, that $p_8 < 0$. Then, by Proposition 2, E_3 is a local attractor of (4) so (4) and, a fortiori, (2), cannot be persistent.

Thus, excluding the «nongeneric» cases $p_8 = 0$ or $p_9 = 0$ we can say that a necessary condition for the persistence of (2) is the requirement that $p_8 > 0$ and $p_9 > 0$. We shall show below that this is also a sufficient condition. However, before doing so we need some preliminary results:

PROPOSITION 4. – *Assume* (A1). *Then the following statement holds*:

a) *if* $p_5 > 0$ *and* $p_8 > 0$ *then* $p_6 > 0$,
b) *if* $p_4 > 0$ *and* $p_9 > 0$ *then* $p_7 > 0$,
c) *if* $p_8 > 0$ *and* $p_9 > 0$ *then* $\det A < 0$,
d) *if* $p_i > 0$ *for* $i = 4, 5, 8, 9$, *then there exists a unique solution* $\bar{u}$ *of*

$$\alpha + A\bar{u} = 0 \tag{9}$$

$\bar{u}$ *has positive components.*

PROOF. – *a)* Let $p_5 > 0$ and $p_8 > 0$. Then $\delta_2 p_6 + \varepsilon_3 p_1 = p_8 + \delta_1 p_5 > 0$. If $p_1 \leq 0$ this immediately implies $p_6 > 0$. If $p_1 > 0$, then $\alpha_1/\gamma_1 > \alpha_2/\gamma_2 > s/\varepsilon_2$ so $\varepsilon_2 \alpha_1 - \gamma_1 s > 0$ i.e. $p_6 > 0$.

b) is proved in the same way.

c) Let $p_8 > 0$ and $p_9 > 0$. We claim that $\det A \neq 0$:

Let b_i be the i-th column vector of A, for $i = 1, 2, 3$. Assumption (A1) implies that b_1 and b_3 are linearly independent. Thus, if $\det A = 0$ then there are λ_1, $\lambda_3 \in \boldsymbol{R}$ such that

$$b_2 = \lambda_1 b_1 + \lambda_3 b_3 . \tag{10}$$

Hence

$$\lambda_1\beta_1+\lambda_3\delta_1=\gamma_1, \qquad \lambda_1\varepsilon_1-\lambda_3\varepsilon_3=\varepsilon_2.$$

Now (A1) easily implies $\lambda_1>0$. Using this and inserting (10) into the first formula in (6) we obtain from (6) that $p_8=-\lambda_1 p_9$, a contradiction to $p_8>0$, $p_9>0$. Thus det $A\neq 0$. Consequently, there exists a unique solution $\bar{u}\in \boldsymbol{R}^3$ of (9). By Cramer's rule $\bar{u}_1=(\det A)^{-1}\cdot(-p_8)$, $\bar{u}_2=(\det A)^{-1}(-p_9)$.

In particular, this proves

(11) $$\bar{u}_1\cdot\bar{u}_2>0.$$

Moreover, (10) implies that

$$\bar{u}_1(\varepsilon_1\delta_1+\beta_1\varepsilon_3)+\bar{u}_2(\varepsilon_2\delta_1+\gamma_1\varepsilon_3)=s\delta_1+\alpha_1\varepsilon_3>0$$

so u_1 and u_2 cannot be both negative.

Hence (11) implies

(12) $$\bar{u}_1>0 \quad\text{and}\quad \bar{u}_2>0.$$

We conclude that $\det A=-p_8\cdot\bar{u}_1^{-1}<0$, as claimed.

d) Assume $p_i>0$ for $i=4,5,8,9$. By what has been shown so far we only have to prove $\bar{u}_3>0$. Consider the two planes P_1 and P_2 in $\boldsymbol{R}^3$ given by the equations

(13) $$\beta_1 u_1+\gamma_1 u_2+\delta_1 u_3=\alpha_1,$$

(14) $$\varepsilon_1 u_1+\varepsilon_2 u_2-\varepsilon_2 u_3=s.$$

Since $\det A\neq 0$, P_1 and P_2 intersect along a straight line L.

Let us first show that L intersects the planes $u_1=0$ and $u_2=0$ at points $(0,s_2,s_3)^T$ and $(t_1,0,t_3)^T$ with $s_2,s_3,t_1,t_3>0$. In fact $(s_2,s_3)^T$ must solve the equation

$$\begin{pmatrix}\gamma_1 & \delta_1\\ \varepsilon_2 & -\varepsilon_3\end{pmatrix}\begin{pmatrix}s_2\\ s_3\end{pmatrix}=\begin{pmatrix}\alpha_1\\ s\end{pmatrix}.$$

Thus, by part *a)* of this proposition,

(15) $$s_2=(\alpha_1\varepsilon_3+\delta_1 s)(\gamma_1\varepsilon_3+\delta_1\varepsilon_2)^{-1}>0,$$

(16) $$s_3=p_6(\gamma_1\varepsilon_3+\delta_1\varepsilon_2)^{-1}>0.$$

Similarly one obtains

(17) $$t_1=(\alpha_1\varepsilon_3+\delta_1 s)(\beta_1\varepsilon_3+\delta_1\varepsilon_1)^{-1}>0,$$

(18) $$t_2=p_4(\beta_1\varepsilon_3+\delta_1\varepsilon_1)^{-1}>0.$$

Now for every $u\in\boldsymbol{R}^3$, $u\in L$ if and only if there is a $\lambda\in\boldsymbol{R}$ such that

(19) $$u=\lambda(0,s_2,s_3)^T+(1-\lambda)(t_1,0,t_3)^T.$$

This holds, in particular, for $u = \bar{u}$. (12), (15) and (17) imply that $\lambda > 0$ and $(1-\lambda) > 0$. Thus, (16), (18) and (19) ensue

$$\bar{u}_3 = \lambda s_3 + (1-\lambda)\, t_3 > 0\,,$$

which proves our claim and completes the proof of the proposition.

COROLLARY 5. – *Assume* (A1) (A2) *and let* $p_8 > 0$, $p_9 > 0$. *Then the following properties hold*:

(i) *at least one of the terms* p_1, p_2 *is positive.*

(ii) *if* $p_1 \geqslant 0$ *and* $p_2 \geqslant 0$ *then* $p_3 > 0$ *and, moreover,*

$$-s + \varepsilon_1 (p_1/p_3) + \varepsilon_2 (p_2/p_3) > 0\,. \tag{20}$$

PROOF. – Proposition 2 implies

$$\det\begin{pmatrix} -\beta_1 & -\gamma_1 & -\alpha_1 \\ -\beta_2 & -\gamma_2 & -\alpha_2 \\ \varepsilon_1 & \varepsilon_2 & s \end{pmatrix} = \bar{u}_3 \cdot \det A < 0\,.$$

This proves that

$$s p_3 - \varepsilon_2 p_2 - \varepsilon_1 p_1 < 0\,. \tag{21}$$

Moreover, it is clear that

$$\alpha_1 p_3 = \beta_1 p_1 + \gamma_1 p_2\,. \tag{22}$$

Multiplying both sides of (21) by α_1 inserting (22) and rearranging, we get

$$p_1 p_4 + p_2 p_6 > 0\,.$$

By Proposition 2, $p_6 > 0$, so $p_1 > 0$ or $p_2 > 0$, as claimed.

Suppose that $p_1 \geqslant 0$ and $p_2 \geqslant 0$.

Then (i) and (22) imply $p_3 > 0$ and so (21) becomes (20). The corollary is proved.

We can now state the following persistence result:

THEOREM 6. – *Assume* (A1), (A2), $p_8 > 0$ *and* $p_9 > 0$. *Then* (2) (*and, a fortiori,* (4)) *is persistent.*

REMARKS. – In [2], Theorem 4.5, persistence of (2) is proved under the following assumptions: (in our notation)

(H1) $\varepsilon_3 = 0$;

(H2) (A1) and (A2) hold;

(H3) one of the following cases holds:

a) $p_1 < 0$ and $p_2 > 0$, or,

b) $p_1 > 0$ and $p_2 < 0$, or,

c) $p_1 > 0$, $p_2 > 0$ and (20) is satisfied.

(Note that a plus sign is missing in [2], line (vi), p. 129, in the expression corresponding to our inequality (20)). Thus, apart from allowing $\varepsilon_3 \geq 0$, Theorem 6 seems to be more general than Theorem 4.5 in [2] since we do not need (H3) here. However, Corollary 5 above just says that (H2) «almost» implies (H3). In fact, Corollary 5 can be reworded as follows:

Assume (A1) and (A2).

Then one of the following cases holds:

a') $p_1 \leq 0$ and $p_2 > 0$, or

b') $p_1 > 0$ and $p_2 \leq 0$, or

c) above.

Thus, for $\varepsilon_3 = 0$, Theorem 4.5 in [2] is the same as Theorem 6 except that we can also treat the cases (i) $p_1 = 0$, $p_2 > 0$ and (ii) $p_1 > 0$, $p_2 = 0$.

Case $p_1 < 0$, $p_2 < 0$ cannot occur. Having demonstrated that Theorem 6 above and Theorem 4.5 in [2] do not differ too much, we can safely leave the proof of Theorem 6 to the reader who can provide it by following almost literally the argument given in the proof of Theorem 4.5 in [2]. Only two remarks are in order:

1) Proposition 4.3 in [2] and its proof extend to the cases (in our notation)

(i) $p_1 \leq 0$ and $p_2 > 0$,

(ii) $p_1 > 0$ and $p_2 \leq 0$.

(Note that the constant c_2 in the proof of case (i) of Proposition 4.3 in [2] should read $c_2 = \gamma_2/\alpha_2\alpha_2$ and *not* $c_2 = \gamma_2/\alpha_1\alpha_2$).

2) There is a number of misprints in the proof of Theorem 4.5 in [2], which, however, the reader will have no trouble to correct.

3. - Spatial patterns.

In the first part of this section we will prove that (under certain conditions) there exist time invariant spatial patterns of the persistent system (2). In other words we shall prove the existence of spatially nonhomogeneous equilibria of (2). This will be done using well-known results about bifurcation from simple eigenvalue. For the readers' convenience let us first recall

DEFINITION 7. – *Let $K = R$ or C. E, F be Banach spaces over K and $L_0, L_1: E \to F$ be bounded K-linear operators. A number $\lambda_0 \in K$ is called a simple eigenvalue of the pair (L_0, L_1) with an associated eigenvector $u_0 \in E$ if*

1) $u_0 \neq 0$, $L_1 u_0 \neq 0$,

2) $\ker(L_0 - \lambda_0 L_1) = [u_0]$,

3) $F = [L_1 u_0] \oplus \mathrm{Im}(L_0 - \lambda_0 L_1)$.

REMARKS. – 1) 3) Implies that $\mathrm{Im}(L_0 - \lambda_0 L_1)$ has codimension one and so, in particular, it must be a closed subspace of F.

2) If $E \subset F$ with continuous natural imbedding $I: E \to F$, and if λ_0 is a simple eigenvalue of (L_0, I), then we say that λ_0 is a simple eigenvalue of L_0.

The following well-known result holds:

THEOREM 8 (see [1]). – *Let $K = R$ and L_0, L_1 be as in Definition 7. Let $\lambda_0 \in R$ be a simple eigenvalue of (L_0, L_1) with an associated eigenvector u_0. Suppose $N: E \to F$ is a (real) analytic map with $N(0) = 0$, $N'(0) = 0$. Define $M: R \times E \to F$ by $M(\lambda, u) = (L_0 - \lambda L_1)u + N(u)$. Then there exists an $\bar{\varepsilon} > 0$, an open neighbourhood $\Lambda \times U$ of $(\lambda_0, 0)$ in $R \times E$ and analytic maps $\lambda^*: (-\bar{\varepsilon}, \bar{\varepsilon}) \to \Lambda$, $u^*: (-\bar{\varepsilon}, \bar{\varepsilon}) \to U$ such that:*

1) $\lambda^*(0) = \lambda_0$, $u^*(\varepsilon) = \varepsilon u_0 + o(\varepsilon)$ *as* $\varepsilon \to 0$.

2) *For every $(\lambda, u) \in \Lambda \times U$ $M(\lambda, u) = 0$ if and only if $u = 0$ or $(\lambda, u) = (\lambda^*(\varepsilon), u^*(\varepsilon))$ for some $\varepsilon \in (-\bar{\varepsilon}, \bar{\varepsilon})$.*

Now let $m \geq 1$ be an integer and define (for $K = R$ or C)

$$E = E_K = \left\{ u \in W^{2,p}(\Omega, K^m): \frac{\partial u}{\partial v} = 0 \text{ on } \partial\Omega \right\}, \tag{23}$$

$$F = F_K = L^p(\Omega, K^m). \tag{24}$$

We assume, as before, $p > N$ and also $p \geq 2$. Define for $u \in E$

$$L_0 u = D_0 \Delta u + Bu, \tag{25}$$

$$L_1 u = -D_1 \Delta u. \tag{26}$$

Here, D_0, D_1 and B are $m \times m$ matrices (with coefficients in K), D_0, D_1 being diagonal matrices.

Clearly L_0, L_1 are well-defined linear and bounded operators from E to F.

Consider the sequence $0 = \rho_0 < \rho_1 \leq \rho_2 \leq \rho_3 \leq \ldots$ of all eigenvalues of $-\Delta$ on Ω with Neumann boundary values where each eigenvalue is repeated according to its multiplicity. Let $\{\phi_n\} \subset L^2(\Omega, R)$ be the sequence of corresponding (normalized) eigenfunctions. $\{\phi_n\}_{n \geq 0}$ form a complete orthonomal system on $L^2(\Omega, R)$. For $u \in L^2(\Omega, K^m)$

and $v \in L^2(\Omega, \boldsymbol{R})$ write

$$\langle u, v\rangle = \int_\Omega u \cdot v \, dx .$$

Note that $\langle u, v\rangle \in \boldsymbol{K}^m$.

Using the assumption $p \geqslant 2$ we now obtain the following trivial

LEMMA 9. – *For $u \in E$, $w \in F$ the following properties are equivalent:*

1) $L_0 u = w$
2) *For all $n \geqslant 0$, $M_n \langle u, \phi_n\rangle = \langle w, \phi_n\rangle$ where $M_n = B - \rho_n D_0$.*

PROPOSITION 10. – *Let L_0, L_1 be defined by* (25), (26). *Suppose that all diagonal entries of D_0 are nonzero. Then the following conditions are equivalent:*

1) *$\lambda_0 = 0$ is a simple eigenvalue of (L_0, L_1) with an associated eigenvector u_0.*
2) *There is an $n_0 > 0$ and $c \in \boldsymbol{K}^m$ such that:*
   (i) *0 is a geometrically simple eigenvalue of M_{n_0} with eigenvector c*
   (ii) *the column vector $D_1 c$ is not a linear combination of the column vectors of M_{n_0},*
   (iii) *the matrices M_n, $n \neq n_0$, are regular.*

We can then choose $u_0 = c \cdot \phi_{n_0}$.

PROOF. – Suppose 1) holds. Then $L_0 u_0 = 0$ so $M_n \langle u_0, \phi_n\rangle = 0$ for all $n \geqslant 0$, by Lemma 9. Let $\Gamma = \{n \geqslant 0 \colon \langle u_0, \phi_n\rangle \neq 0\}$. Set $v_n = \langle u_0, \phi_n\rangle \phi_n$. Then $\{v_n\}_{n \in \Gamma}$ are really independent ($\Gamma \neq \emptyset$!), and $L_0 v_n = 0$ for $n \geqslant 0$. Since $\ker L_0 = [u_0]$, it follows that there is an $n_0 \geqslant 0$ with $[u_0] = [v_{n_0}]$ so there is a $c \in \boldsymbol{K}^m$ with $u_0 = c \cdot \phi_{n_0}$, $c \neq 0$.

Now $L_1 u_0 \notin \operatorname{Im} L_0$ by our assumptions. Also,

$$L_1 u_0 = - D_1 \Delta u_0 = \rho_{n_0} D_1 c \cdot \phi_{n_0}$$

so, in particular, $\rho_{n_0} \neq 0$, *i.e.* $n_0 > 0$ and

$$D_1 c \cdot \phi_n \notin \operatorname{Im} L_0 . \tag{27}$$

For b, $\hat{b} \in \boldsymbol{R}^m$, let $v_n = b \cdot \phi_n$, $\hat{v}_n = \hat{b} \cdot \phi_n$. Lemma 9 implies that $L_0 v_n = \hat{v}_n$ if and only if $M_n b = \hat{b}$. It follows easily that $\ker M_{n_0} = [c]$ and M_n is regular for $n \neq n_0$. Since $c \neq 0$, (2i) and (2iii) hold. Suppose (2ii) does not hold. Then $M_{n_0} b = D_1 c$ for some $b \in \boldsymbol{R}^m$. Thus $L_0(b \cdot \phi_{n_0}) = D_1 c \cdot \phi_{n_0}$ and so $D_1 c \cdot \phi_{n_0} \in \operatorname{Im} L_0$, a contradiction to (27).

Next suppose that 2) holds.

Let $u_0 = c \cdot \phi_{n_0}$. $M_{n_0} c = 0$ implies $L_0 u_0 = 0$. On the other hand if $L_0\, u = 0$ then $M_n \langle u, \phi_n\rangle = 0$ for all n. By 2iii), $\langle u, \phi_n\rangle = 0$ for $n \neq n_0$.

This shows that $u = \langle u, \phi_{n_0}\rangle \phi_{n_0}$ with $\langle u, \phi_{n_0}\rangle \in [c]$. Thus $u \in [u_0]$ and $\ker L_0 = [u_0]$ with $u_0 \neq 0$. Define $\hat{B} \colon E \to F$, $\hat{B}(u) = B \cdot u$. $\hat{B}$ is compact. Moreover, since the diagonal entries of D_0 are nonzero, it follows that $D_0 \Delta \colon E \to F$ is Fredholm with index zero.

Consequently $L_0 = D_0 \Delta + \hat{B}$ is Fredholm with index zero. Hence, to prove 1) it is enough to show that $L_1 u_0 = \rho_{n_0} D_1 c \phi_{n_0} \notin \operatorname{Im} L_0$. Since $n_0 > 0$ and so $\rho_{n_0} \neq 0$, this is equivalent to $D_1 c \notin \operatorname{Im} M_{n_0}$ which is 2ii). The proposition is proved.

An application of Theorem 8 and Proposition 10 yields.

THEOREM 11. – *Assume* (A1), (A2). *Let D_0 be a diagonal 3×3 matrix with positive diagonal coefficients and D_1 be any real diagonal 3×3 matrix. Write $M_n = \overline{U}A - \rho_n D_0$ for $n \geq 0$.*

Suppose there is an $n_0 > 0$ and $c \in \boldsymbol{R}^3$ such that

(i) *0 is a geometrically simple eigenvalue of M_{n_0} with eigenvector c;*

(ii) *the column vector $D_1 c$ is not a linear combination of the column vectors of M_{n_0};*

(iii) *the matrices M_n, $n \neq n_0$, are regular.*

Under these assumptions there is an $\bar{\varepsilon} > 0$, a neighborhood $\Lambda \times Y_0$ of $(0, \overline{u})$ in $\boldsymbol{R} \times Y$ and analytic maps $\mu^* : (-\bar{\varepsilon}, \bar{\varepsilon}) \to \Lambda$, $u^* : (-\bar{\varepsilon}, \bar{\varepsilon}) \to Y_0$ such that

a) $\mu^*(0) = 0$, $u^*(\varepsilon) = \overline{u} + \varepsilon \cdot c \cdot \phi_{n_0} + o(\varepsilon)$ as $\varepsilon \to 0$;

b) for every $\varepsilon \in (-\bar{\varepsilon}, \bar{\varepsilon})$, $u^*(\varepsilon)$ is an equilibrium of the system (2) *with $D = D_0 + \mu^*(\varepsilon) D_1$;*

c) whenever $(\mu, u) \in \Lambda \times Y$ and u is an equilibrium of (2) *with $D = D_0 + \mu D_1$, then $u = \overline{u}$ or else $u = u^*(\varepsilon)$, $\mu = \mu^*(\varepsilon)$ for some $\varepsilon \in (-\bar{\varepsilon}, \bar{\varepsilon})$.*

REMARK. – Actually u^* is analytic as a map into the space E defined in (23). Note that $E \subsetneq (X^\beta)^3$.

PROOF. – By regularity u is an equilibrium of (2) if and only if $u \in E$ and

$$D\Delta u + U(\alpha + Au) = 0 . \tag{28}$$

Let $D = D_0 + \mu D_1$, $u = v + \overline{u}$.

Then (28) is equivalent to

$$(L_0 - \mu L_1) v + N(v) = 0 , \tag{29}$$

where L_0, L_1 are defined in (25) (26) with $B = \overline{U}A$ and $N: E \to F$ is defined as $N(v)(x) = V(x) Av(x)$ for $x \in \Omega$. Applying Theorem 8 and Proposition 10 we get the desired result.

Now the question arises as to whether the assumptions of Theorem 11 can ever be satisfied. We shall now show that they can, and that in fact, this is roughly the case if and only if $p_3 < 0$.

We first need a lemma, whose proof is straightforward:

LEMMA 12. – *Assume* (A1) *and* (A2). *Let* $h \in \boldsymbol{R}^3$ *be arbitrary and let* $p(\lambda, h) = -\lambda^3 + a_2(h)\lambda^2 + a_1(h)\lambda^1 + a_0(h)$ *be the characteristic polynomial of* $H\overline{U}A$.
Then

$$a_0 = h_1 h_2 h_3 \overline{u}_1 \overline{u}_2 \overline{u}_3 \det A,$$
$$a_1 = -h_1 h_2 \overline{u}_1 \overline{u}_2 p_3 - h_1 h_3 \overline{u}_1 \overline{u}_3 (\beta_1 \varepsilon_3 + \varepsilon_1 \delta_1) - h_2 h_3 \overline{u}_2 \overline{u}_3 (\gamma_2 \varepsilon_3 + \varepsilon_2 \delta_2),$$
$$a_2 = -h_1 \overline{u}_1 \beta_1 - h_2 \overline{u}_2 \gamma_2 - h_3 \overline{u}_3 \varepsilon_3.$$

COROLLARY 13. – *If the assumptions of Theorem 11 are satisfied, then* $p_3 < 0$.

PROOF. – There is an $n_0 > 0$ such that 0 is an eigenvalue of $\overline{U}A - \rho_{n_0} D_0$. Thus $\rho_{n_0} > 0$ and ρ_{n_0} is an eigenvalue of $H\overline{U}A$ where $H = D_0^{-1}$. If $p_3 \geq 0$ then Lemma 11 and our preceding results imply that $a_i(h) < 0$ for $i = 0, 1, 2$. This gives $p(\rho_{n_0}, h) < 0$, a contradiction.

Corollary 13 admits a converse, in a certain sense:

THEOREM 14. – *Assume* (A1) *and* (A2). *Suppose also that* $p_8 > 0$, $p_9 > 0$ *and* $p_3 < 0$. *Finally let* $n_0 > 0$ *and* ρ_{n_0} *be a simple eigenvalue of* $-\Delta$ *on* Ω *with Neumann boundary values. Then there are matrices* D_0 *and* D_1 *such that all assumptions, and consequently, the conclusions of Theorem 11 hold.*

PROOF. – Since $\rho = \rho_{n_0}$ is simple, it follows that there is an $\varepsilon > 0$ such that for every $n \neq n_0$, $n > 0$, $\rho_n \neq \rho_{n_0}$ and $\rho_n \geq \varepsilon$. For $h \in \boldsymbol{R}^3$ let $\lambda_i(h)$ $i = 1, 2, 3$ be the zeros of $p(\cdot, h)$ ordered in the lexicographic order.

Choose $h_1 > 0$ arbitrarily and let $h = (h_1, h_1, 0)^T$. Then $a_0(h) = 0$, $a_1(h) = h_1^2 c_1$, $a_2 = -h_1 c_2$, where $c_1, c_2 > 0$ are independent of h_1.

Consequently

$$\lambda_1(h_1, h_1, 0) = -h_1 b_1, \qquad \lambda_2(h_1, h_1, 0) \equiv 0, \qquad \lambda_3(h_1, h_1, 0) = h_1 b_2,$$

where $b_1, b_2 > 0$ do not depend on h_1. Choose $h_1^* = \rho / b_2$. Define $h^0 = (h_1^*, h_1^*, 0)^T$. Then

$$\lambda_1(h^0) < 0, \qquad \lambda_2(h^0) = 0, \qquad \lambda_3(h^0) = \rho > 0.$$

In particular, this implies that for h near h^0, $\lambda_1(h)$ is real valued and varies smoothly with h.

In fact $\lambda_i(h)$ is a simple eigenvalue of $H\overline{U}A$ with the normalized eigenvector $c_i(h) \in \boldsymbol{R}^3$. Therefore $c_i(h)$, too, varies smoothly with h.

Write $c(h) = c_3(h)$.

It is clear that

$$c(h^0) = (a_1, a_2, 0)^T \tag{30}$$

where $a_1, a_2 \in \boldsymbol{R} \setminus \{0\}$.

We claim that

(31) $$H\cdot c(h) \notin \operatorname{Im}(H\overline{U}A-\rho)$$

for h close to h^0.

Otherwise there is a sequence $h^n \to h^0$, $b^n \in \boldsymbol{R}^3$ with

(32) $$H^n \cdot c(h^n) = H^n \overline{U} A b^n - \rho b^n .$$

Since $H\overline{U}Ac(h) - \rho c(h) \equiv 0$ we may assume

(33) $$b^n \perp c(h^n).$$

We claim that $\{b^n\}$ is bounded.

In fact otherwise we may assume that $|b^n| \to \infty$ as $n \to \infty$.

Let $v^n = b^n/|b^n|$.

(32) yields

(34) $$H^n \overline{U} A v^n - \rho v^n \to 0$$

for $n \to \infty$.

Taking subsequences if necessary we may assume $v^n \to v^0$ $|v^0| = 1$, and thus

(35) $$H^0 \overline{U} A v^0 = \rho v^0 .$$

It follows that $v^0 = c(h^0)$.

On the other hand (33) implies that $v^0 \perp c(h^0)$, a contradiction.

Thus, indeed, $\{b^n\}$ is bounded.

Hence we may assume $b^n \to b^0$, so that

(36) $$H^0 \overline{U} A b^0 - \rho b^0 = H^0 c(h^0).$$

By (30)

$$H^0 c(h^0) = h_1^* c(h^0).$$

Thus $c(h^0) \in \operatorname{Im}(H^0\overline{U}A - \rho)$ which contradicts the fact that ρ is a simple eigenvalue of $H^0\overline{U}A$. (31) is proved.

Now define for (h_1, h_3) close to $(h_1^*, 0)$

$$R(h_1, h_3) = \lambda_3(h_1, h_1, h_3) - \rho .$$

It follows that

$$R(h_1^*, 0) = 0, \qquad \frac{\partial R}{\partial h_1}(h_1^*, 0) = b_2 > 0 .$$

By the implicit function theorem there is a smooth function f defined for h_3 near 0 such that $f(0) = h_1^* > 0$, $R(f(h_3), h_3) \equiv 0$. Choose $h_3 > 0$ so small that for $h = (f(h_3), f(h_3), h_3)$

(37) $$f(h_3) > 0,$$

(38) $$\lambda_1(h) < 0\,,$$

(39) $$|\lambda_2(h)| < \varepsilon\,,$$

(40) $$Hc(h) \notin \mathrm{Im}\,(H\overline{U}A - \rho)\,.$$

Let $D_0 = H^{-1}$.

Then the eigenvalues λ_i of $H\overline{U}A$ satisfy $\lambda_1 < 0$, $|\lambda_2| < \varepsilon$, $\lambda_2 \neq 0$, $\lambda_3 = \rho$. For every $\lambda \in \boldsymbol{R}$, $\ker(\overline{U}A - \lambda D_0) = \ker(H\overline{U}A - \lambda)$. All this and our choice of ε' clearly imply that (i) and (iii) hold for $c = c(h)$.

By (40) $c \notin \mathrm{Im}(\overline{U}A - \rho D_0)$.

Choosing D_1 to be the identity matrix we see that all assumptions of Theorem 11 are satisfied. The proof is complete.

REMARKS. – 1) Biologically, $p_3 < 0$ means that the interspecific competition of the prey populations is larger than their intraspecific competition.

2) As was observed in the Introduction, MIMURA and KAN-ON ([9], section 4 pp. 145-146) state an existence result for nonhomogeneous equilibria of system (1) in one space dimension ($N = 1$) and under certain hypotheses (H.1)-(H.4).

In particular, their hypothesis (H.3) (p. 141 of [9]) translates in our notation as

(H.3) $p_4 > 0$ *and* $p_5 < 0$,

while in Theorem 14 we assume

(A2) $p_4 > 0$ *and* $p_5 > 0$.

Thus, the two results concern different situations.

3) For a bounded domain $\Omega \subset \boldsymbol{R}^N$ of class C^2, let Δ_Ω denote the Laplacian on Ω with *Neumann* boundary conditions. In Theorem 14 (and also in Theorem 18 below) we make the assumption that certan nontrivial eigenvalues of Δ_Ω are simple. This assumption is, in general, hard to verify in practice.

If $N = 1$, all eigenvalues are simple, but if $N > 1$, this is no longer true, in general. In fact, if *e.g.* $N = 2$ and Ω is the unit disc, then all nontrivial eigenvalues of Δ_Ω are double eigenvalues.

Nonetheless, the simplicity of all eigenvalues of Δ_Ω is a *generic* property with respect to the domain Ω.

More precisely, the following result holds:

THEOREM T. – *Let $\Omega \subset \boldsymbol{R}^N$ be an arbitrary bounded domain of class C^2 and $k \geq 2$ be an arbitrary integer.*

Then, for any $\varepsilon > 0$ there is a map ψ: $\boldsymbol{R}^N \to \boldsymbol{R}^N$ of class C^∞ satisfying $\|\psi\|_{C^k(\boldsymbol{R}^N, \boldsymbol{R}^N)} < \varepsilon$ and such that the operator $\Delta_{\Omega'}$ of the perturbed domain $\Omega' = (I + \psi)(\Omega)$ has only simple eigenvalues.

Theorem T was proved by HENRY (see [13] for an announcement of this result) and also independently, by one of us (see [10]). Theorem T says that by an arbitrary «small» perturbation of the original domain we can achieve the simplicity of all eigenvalues of the Laplacian with Neumann boundary values. Actually, it is proved in [13] (and in [10]) that the set of all domains Ω such that Δ_Ω has only simple eigenvalues is of second cathegory in the set of all domains Ω (endowed with the Micheletti metric, cf [8]).

PROPOSITION 15. – *Suppose that* (A1) *and* (A2) *hold and that* $p_8 > 0$, $p_9 > 0$, $p_3 < 0$. *If, for some* $n_0 > 0$, $0 \in \sigma(M_{n_0})$ *then:*

(i) *there is a* $i_0 \in \{1, 2, 3\}$ *such that* $d_{i_0} \leq \|\overline{U}A\| / \rho_{n_0}$,

(ii) $$\frac{d_1}{d_3} < \frac{\overline{u}_1}{\overline{u}_3} \frac{|p_3|}{\gamma_2 \varepsilon_3 + \varepsilon_2 \delta_2},$$

$$\frac{d_2}{d_3} < \frac{\overline{u}_2}{\overline{u}_3} \frac{|p_3|}{\beta_1 \varepsilon_3 + \varepsilon_1 \delta_1},$$

there, $\| \ \|$ *is the matrix norm induced by an arbitrary vector norm on* $\boldsymbol{R}^3$.

REMARK. – This result says that a necessary condition for the applicability of Theorem 11 is that (i): not all diffusion coefficients are too large, and (ii): d_3 is not too small relative to d_1 and d_2.

PROOF. – (i) If $0 \in \sigma(M_{n_0})$ then $\rho_{n_0} \in \sigma(D^{-1}\overline{U}A)$ so $\rho_{n_0} \leq \|D^{-1}\overline{U}A\| \leq \left\{\max_{1 \leq i \leq 3} d_i\right\} \cdot \|\overline{U}A\|$ and (i) follows.

(ii) Let $H = D^{-1}$. From Lemma 12 it follows that $a_1(h) > 0$ since otherwise $p(\rho_{n_0}, h) < 0$. The formula for $a_1(h)$ clearly implies (ii).

We shall now discuss the existence of periodic solutions of (2). To this end, let $\boldsymbol{K} = \boldsymbol{C}$ in (23)-(26) and define for $\mu \in \boldsymbol{R}$, $u \in E$

$$L(\mu) u = (L_0 - \mu L_1) u .$$

Using Lemma 8 and the proof of Proposition 9, the following result is easily established:

LEMMA 16. – *Let* $M_n(\mu) = \overline{U}A - \rho_n(D_0 + \mu D_1)$ *for* $n \geq 0$ *and* $\lambda \in \boldsymbol{C}$. $\lambda \in \sigma(L(\mu))$ *if and only if there is an* $n_0 \geq 0$ *such that* $\lambda \in \sigma(M_{n_0}(\mu))$. λ *is a simple eigenvalue of* L_0 *(with an eigenvector* u_0*) if and only if there is an* $n_0 \geq 0$ *such that*

(i) λ *is an algebraically simple eigenvalue of* M_{n_0},

(ii) $\lambda \notin \sigma(M_n)$ *for* $n \neq n_0$.

In this case $u_0 = c \cdot \phi_{n_0}$ *where* $c \neq 0$,

$$[c] = \ker (M_{n_0} - \lambda) .$$

We shall now state (without proof) the following theorem, which follows from results in [5], [4] and Lemma 16:

THEOREM 17. – *Assume that:*

1) *The diagonal entries of* D_0 *are positive.*

2) *There exists* $\bar{\mu}, \delta_0 > 0$ *such that for all* $\mu \in I_{\bar{\mu}} = [-\bar{\mu}, \bar{\mu}]$:

(i) $\sigma(L(\mu)) = \sigma_1(\mu) \cup \sigma_2(\mu)$,

(ii) $\sigma_1(\mu) = \{\lambda(\mu), \bar{\lambda}(\mu)\}$ *where* $\lambda(\mu), \bar{\lambda}(\mu)$ *are simple eigenvalues of* $L(\mu)$, $\lambda(\mu) = \alpha(\mu) + i\beta(\mu)$, $\alpha(0) = 0$, $\alpha'(0) \neq 0$, $\beta(0) = \beta_0 > 0$,

iii) $\operatorname{Re} \sigma_2(\mu) < -\delta_0$.

Let $n_0 \geq 0$ *be such that* $\lambda(0) \in \sigma(M_{n_0})$. *Then there is* $\bar{\varepsilon} > 0$ *and an analytic function* $\mu: (-\bar{\varepsilon}, \bar{\varepsilon}) \to \boldsymbol{R}$ *with* $\mu(0) = 0$ *and for every* $-\bar{\varepsilon} < \varepsilon < \bar{\varepsilon}$ *there is a* $T(\varepsilon)$*-periodic solution* u_ε *of* (2) *with* $D = D_0 + \mu^*(\varepsilon) D_1$ *such that*

(*a*) $\sup\limits_{t \in \boldsymbol{R}} \frac{1}{\varepsilon} \|u_\varepsilon(t) - \bar{u} - \varepsilon(y_1 \sin \beta_0 t + y_2 \cos \beta_0 t) \varphi_{n_0}\|_Y \to 0$ *for* $\varepsilon \to 0^+$, *where* $y_1, y_2 \in \boldsymbol{R}^3$, $\|y_1\| + \|y_2\| > 0$.

(*b*) $T(\varepsilon) = \dfrac{2\pi}{\beta_0} + O(\varepsilon^2)$ *as* $\varepsilon \to 0$.

REMARKS. – 1) Under the assumptions of Theorem 17 there are no nonhomogeneous equilibria u of (2) with $D = D_0 + \mu D_1$ with $|\mu|$ small and u close to $\bar{u}$.

In fact, u is an equilibrium of (2) if and only if $u = v + \bar{u}$ and $M(\mu, v) := L(\mu)\, v + N(v) = 0$ (see (29)).

Now $M(\mu, 0) \equiv 0$, $D_v M(\mu, 0) = L(\mu)$.

$L(0)$ is Fredholm with index zero and $0 \notin \sigma(L(0))$ so $\operatorname{Ker} L(0) = \{0\}$. Thus $L(0)$ is an isomorphism and by the implicit function theorem $v = 0$ is the only solution of $M(\mu, v) = 0$ for $|\mu|, |v|$ small.

2) If $\lambda(0) \in \sigma(M_{n_0})$ then $\operatorname{Re} \lambda(\mu) < -\delta_0$ for $|\mu|$ small by 2 (iii). This implies that $\lambda(\mu) \in \sigma(M_{n_0})$ for $|\mu|$ small. Since $\lambda(\mu) \neq \lambda(0)$ for $|\mu|$ small, by 2(ii), this implies that, under the assumptions of Theorem 17, necessarily $n_0 > 0$, and thus in particular, the bifurcating periodic solutions are nonhomogeneous by (*a*). Hence these solutions are time-periodic spatial patterns of (2).

We shall now obtain an analogue of Theorem 14 for time periodic solutions of (2). This will be computationally more difficult since it involves solving cubic equations rather than quadratic ones.

Before stating the theorem, we introduce some notations: $t_n(\mu)$, $T_n(\mu)$ and $d_n(\mu)$ will be, respectively, the trace, the sum of all the principal minors of order two and the determinant of $M_n(\mu) = \overline{U}A - \rho_n(D_0 + \mu D_1)$. Then, the characteristic polynomial of $M_n(\mu)$ is given by:

$$p_n(\mu, \lambda) = -\lambda^3 + t_n(\mu)\lambda^2 - T_n(\mu)\lambda + d_n(\mu). \tag{41}$$

The same quantities for the matrix $B = (b_{ij})_{i,j=1,3} = \overline{U}A$ will be denoted by t, T and d. Further, for a general 3×3 matrix M, M_{ij} will be the determinant of the submatrix of M obtained by deleting the i-th row and the j-th column of M.

Consider the following set of inequalities:

$$Tt - d < 0; \tag{42}$$

$$r_1 = t(\overline{u}_2\gamma_2 + \overline{u}_3\varepsilon_3) - (B_{22} + B_{33}) > 0, \qquad s_1 = r_1^2 + 4(\overline{u}_2\gamma_2 + \overline{u}_3\varepsilon_3)(Tt - d) > 0; \tag{42a}$$

$$r_2 = t(\overline{u}_1\beta_1 + \overline{u}_3\varepsilon_3) - (B_{11} + B_{33}) > 0, \qquad s_2 = r_2^2 + 4(\overline{u}_1\beta_1 + \overline{u}_3\varepsilon_3)(Tt - d) > 0; \tag{42b}$$

$$\rho_{m-1}\rho_{m+1}^{-1} < (r_1 - \sqrt{s_1})(r_1 + \sqrt{s_1})^{-1}; \tag{$(42c)_m$}$$

$$\rho_{m-1}\rho_{m+1}^{-1} < (r_2 - \sqrt{s_2})(r_2 + \sqrt{s_2})^{-1}; \tag{$(42d)_m$}$$

$$Tt - d > 0. \tag{43}$$

Then, we have the following

THEOREM 18. – *Assume* (A1), (A2), $p_9 > 0$, *and* $T > 0$.

Moreover, suppose that at least one of the following hypothesis (B1)-(B3) *holds:*

(B1) *a)* $\rho_1 < \rho_2$,

b) (42) *is satisfied,*

c) the inequalities (42*a*) *or* (42*b*) *are satisfied;*

(B2) *there is an* $m > 1$ *such that*

a) $\rho_{m-1} < \rho_m < \rho_{m+1}$,

b) (42) *is satisfied,*

c) the inequalities (42*a*), $(42c)_m$ *or the inequalities* (42*b*), $(42d)_m$ *are satisfied;*

(B3) $\mathrm{Re}\,\sigma(\mathrm{B}) < 0$ *and* (43) *is satisfied.*

Under these assumptions there are matrices D_0 *and* D_1 *are integer* $n_0 > 1$ *such that all the hypotheses (and consequently the conclusions) of Theorem* 17 *are satisfied.*

Moreover, $n_0 = 1$ *if* (B1) *or* (B3) *holds and* $n_0 = m$ *if* (B2) *holds.*

REMARK. – Note that $\rho_k < \rho_{k+1}$ for $k = 1$ and $\rho_{k-1} < \rho_k < \rho_{k+1}$ for $k > 1$ just mean that ρ_k is a simple eigenvalue of $-\Delta$ on Ω with Neumann boundary values.

PROOF. – First, we will prove the existence of D_0 (positive diagonal matrix) in order that L_0 has a pair of purely imaginary eigenvalues.

From Lemma 16, it is enough to show that there exists a D_0 for which $p_n(0, \lambda)$ has a pair of pure imaginary roots, for some $n \geq 0$. It is easily seen that this occurs if and only if

$$T_n(0) > 0 \tag{44}$$

and

$$T_n(0)\, t_n(0) - d_n(0) = 0 \tag{45}$$

and that if (44)-(45) hold, the roots of $p_n(0, \lambda)$ are $\pm i(T_n(0))^{1/2}$ and $t_n(0)$. Let $\beta_0 = (T_n(0))^{1/2}$.

Straightforward computations yield the following formulas:

$$T_n(0) = T - \rho_n \{(b_{11} + b_{33}) d_2 + (b_{22} + b_{33}) d_1 + (b_{11} + b_{22}) d_3\} + \\ + \rho_n^2 (d_1 d_2 + d_2 d_3 + d_1 d_3)\,. \tag{46}$$

$$d_n(0) = -\rho_n^3 d_1 d_2 d_3 + \rho_n^2 (b_{11} d_2 d_3 + b_{22} d_1 d_3 + b_{33} d_1 d_2) - \\ - \rho_n (B_{11} d_1 + B_{22} d_2 + B_{33} d_3) + d\,, \tag{47}$$

where d_i $i = 1, 2, 3$ denote the diagonal coefficients of D_0. From (47), it immediately follows that $T > 0$ implies $T_n(0) > 0$ (*i.e.* (44)) for any positive D_0. Moreover, using (46) and (47), we get that (45) is equivalent to

$$q_n(d_1, d_2, d_3) = -\rho_n^3 (2d_1 d_2 d_3 + d_1 d_2^2 + d_1^2 d_2 + d_2^2 d_3 + d_2 d_3^2 + d_1^2 d_3 + d_1 d_3^2) + \\ + 2\rho_n^2 t(d_1 d_2 + d_1 d_3 + d_2 d_3) + \rho_n^2 \{(b_{22} + b_{33}) d_1^2 + (b_{11} + b_{33}) d_2^2 + (b_{11} + b_{22}) d_3^2\} + \\ + \rho_n (r_1 d_1 + r_2 d_2 + r_3 d_3) + Tt - d = 0\,, \tag{48}$$

where we set

$$r_3 = t(\bar{u}_1 \beta_1 + \bar{u}_2 \gamma_2) - (B_{11} + B_{22})\,.$$

Now, assume (42) and (42*a*). From (48), we deduce that

$$q_n(d_1, 0, 0) = \rho_n^2 (b_{22} + b_{33}) d_1^2 + \rho_n r_1 d_1 + Tt - d$$

and looking at the signs of the powers of d_1 in this expression, we get for any $n > 0$ the existence of $d_1^* > 0$ such that $q_n(d_1^*, 0, 0) > 0$. Since $q_n(0, 0, 0) = Tt - d < 0$, and by continuity, we get for any $n > 0$ a positive diagonal D_0 such that (45) is satisfied.

Analogously, we can argue when (42*b*) is assumed instead of (42*a*), just considering $q_n(0, d_2, 0)$.

On the other hand, if (43) holds and we take $d_1 = d_2 = d_3 = \tilde{d}$, we obtain for any $n > 0$ $q_n(0, 0, 0) > 0$ and $\lim_{\tilde{d} \to +\infty} q_n(\tilde{d}, \tilde{d}, \tilde{d}) = -\infty$.

Hence, again for any $n > 0$ we get the desired D_0.

Now, assuming $T > 0$ and (42)-(42*a*) ore (42)-(42*b*) or (43) and given $n > 0$ and D_0 determined as above, we consider $p_n(\mu, \lambda)$ with D_1, for the moment, arbitrary positive diagonal. $p_n(\mu, \lambda)$ is a smooth function defined on $\boldsymbol{R} \times \boldsymbol{R}^2$ with values in $\boldsymbol{R}^2$, if we identify $\boldsymbol{C}$ with $\boldsymbol{R}^2$ in the usual way: $\lambda = \alpha + i\beta \leftrightarrow (\alpha, \beta)$.

Since $p_n(0, \pm i\beta_0) = 0$ and $\det[D_{(u,v)}, p_n]\ (0, 0, \pm\beta_0) = 4\beta_0^4 + 4\beta_0^2 t_n^2(0) > 0$, we can apply the implicit function theorem and get the existence of smooth $\lambda(\mu) = \alpha(\mu) + i\beta(\mu)$ and $\overline{\lambda}(\mu)$ for μ in some interval I_μ containing 0 such that $p_n(\mu, \lambda(\mu)) = 0$ and $p_n(\mu, \overline{\lambda}(\mu)) = 0$ for any $\mu \in I_\mu$, $\alpha(0) = 0$ and $\beta(0) = \beta_0$. Moreover, by standard computations, we get

$$\alpha'(0) = -[2\beta_0^2 + t_n(0)^2]^{-1} \frac{d}{d\mu}[T_n(\mu) t_n(\mu) - d_n(\mu)]_{\mu=0} \tag{49}$$

and if, for the sake of brevity, we denote $M_n(0)$ by $M = (m_{ij})_{i,j=1,3}$,

$$\rho_n^{-1} \frac{d}{d\mu}[T_n(\mu) t_n(\mu) - d_n(\mu)]_{\mu=0} =$$

$$= [-(m_{22} + m_{33}) t_n(0) - (M_{22} + M_{33})] d_1 + [-(m_{11} + m_{33}) t_n(0) - (M_{11} + M_{33})] d_2 +$$

$$+ [-(m_{11} + m_{22}) t_n(0) - (M_{11} + M_{22})] d_3 .$$

Note that d_i $i = 1, 2, 3$ denote the diagonal elements of D_1, which are to be determined! Since the coefficient of d_3 is always negative (cf (A1) and (A2)), it is always possible to choose positive d_1, d_2, d_3 for which $\alpha'(0) \neq 0$.

With such a choice of D_1 in correspondence of $n > 0$ and D_0, we have verified part of hypothesis 2 of Theorem 17: it remains to show that $\lambda(\mu)$ and $\overline{\lambda}(\mu)$ are simple and 2(iii).

Assume that ρ_m is a simple eigenvalue of $-\Delta$ on Ω with Neumann boundary values and determine D_0 and D_1 as in the previous part of this proof. $\lambda(0) = i\beta_0$ and $\overline{\lambda}(0)$ are a simple eigenvalues of L_0, since ρ_m is simple and they cannot be eigenvalues of $M_n(0)$ for $n \neq n_0$ (in fact, $T_n(0) \neq T_m(0)$ if $n \neq m$). The same property holds for $\mu \neq 0$.

Extending (46) and (47) for $\mu \neq 0$, we see that for any $n \geq 0$ and $\mu \in I_\mu$, $t_n(\mu) < 0$, $T_n(\mu) > 0$ and $d_n(\mu) < 0$. Consequently, all the real roots of $p_n(\mu, \lambda)$, *i.e.* the real eigenvalues of $L(\mu)$ are negative. Now, assume that $p_n(\mu, \cdot)$ has the roots $\alpha \pm i\beta$ and γ, then we have:

$$2\alpha + \gamma = t_n(\mu), \tag{50}$$

$$2\alpha\gamma + \alpha^2 + \beta^2 = T_n(\mu), \tag{51}$$

$$(\alpha^2 + \beta^2)\gamma = d_n(\mu). \tag{52}$$

Using (50) and (51), (52) becomes

$$-8\alpha^3 + 8t_n(\mu)\alpha^2 - 2(t_n^2(\mu) + T_n(\mu))\alpha + T_n(\mu) t_n(\mu) - d_n(\mu) = 0. \tag{53}$$

From this equation and since α is real, we get that

$$q_n(D_0+\mu D_1)=T_n(\mu)\,t_n(\mu)-d_n(\mu)<0 \tag{54}$$

is a sufficient condition for α to be negative.

Assume (42)-(42*a*) and denote by $\tilde{d}_1$ and $\tilde{\tilde{d}}_1$, the positive roots of $q_m(d_1,0,0)=0$. If $D_0=\mathrm{diag}(d_1^0,d_2^0,d_3^0)$ and $D_1=\mathrm{diag}(d_1^1,d_2^1,d_3^1)$, we recall that we have chosen d_1^0 such that $\tilde{d}_1<d_1^0<\tilde{\tilde{d}}_1$.

If $n=0$, (54) is (42), hence assume $n\neq m$ and $n\neq 0$. Suppose, for the moment that $r_2\leq 0$, then the only positive contribution to $q_n(D_0+\mu D_1)$ can be given by $q_n(d_1^0+$ $+\mu d_1^1,0,0)=q_m(\rho_n/\rho_m(d_1^0+\mu d_1^1),0,0)$.

If $m=1$, taking into account the sign of the powers of d, in $q_1(d_1,0,0)$ and since $\{\rho_n\}_n$ is monotone, $q_n(d_1^0+\mu d_1^1,0,0)$ will be negative for any $n>1$, if

$$\mu>(d_1^1)^{-1}[\rho_1\rho_2^{-1}\tilde{\tilde{d}}_1-d_1^0]\quad \text{for any } \mu\in I_\mu\,. \tag{55}$$

This inequality can be satisfied if d_1^0 is chosen close to d_1^1 and I_μ is sufficiently small. If $m>1$, we need that

$$\rho_n\rho_m^{-1}[d_1^0+\mu d_1^1]>\tilde{\tilde{d}}_1\qquad \text{for } n>m$$

and

$$\rho_n\cdot\rho_m^{-1}[d_1^0+\mu d_1^1]<\tilde{d}_1\qquad \text{for } n<m,\ n\neq 0\,.$$

To get these inequalities for any $\mu\in I_\mu$, if is sufficient that

$$\rho_{m-1}\rho_{m+1}^{-1}<\tilde{d}_1\cdot\tilde{\tilde{d}}_1^{-1}=(r_1-\sqrt{s_1})\cdot(r_1+\sqrt{s_1})^{-1},$$

which is (42*c*).

If $r_2>0$, it is sufficient to choose also d_2^0 small enough.

Analogously, we can deal with the case (42)-(42*b*), taking (42*d*) in place of (42*c*).

At last, assume (43) and $m=1$. Recall that in our construction $D_0=\mathrm{diag}(d,d,d)$ and $q_1(D_0)=0$. If we evaluate $q_n(D_0)$ for $n>1$ we see that it equals $q_1(D_0)$ plus some terms whose sum is less than a negative constant independent on n. Hence, if I_μ is sufficiently small, (54) holds for any $\mu\in I_\mu$ and $n>1$. If $n=0$, we use directly (43).

We will prove that the real parts of the eigenvalues of $L(\mu)$ belonging to $\sigma_2(\mu)=$ $=\sigma(\mu)/\{\lambda(\mu),\bar{\lambda}(\mu)\}$ cannot get arbitrarly close to 0. Suppose on the contrary that $\{\mu_n\}$ is a sequence in I_μ convergent to 0 and $\lambda(\mu_n)\in\sigma_2(\mu_n)$ be such that $\mathrm{Re}\,\lambda(\mu_n)\to 0$.

Having in mind Lemma 16, each $\lambda(\mu_n)$ is an eigenvalue of one of the matrices $M_k(\mu_n)$ with $k\neq m$: say $M_{k(n)}(\mu_n)$. Then, if $k(n)=\bar{k}$ for infinitely many indices, it will follow that $M_{\bar{k}(0)}$ has a purely imaginary eigenvalue, which is a contradiction. Otherwise, $k(n)\to+\infty$. In this case, we perform some computations, using a well-known method for solving cubic polynomial equations (see, [12] p. 515). We can write the roots of $\rho_{k(n)}(\mu_n, \cdot)$ in terms of $t_{k(n)}(\mu_n)$, $T_{k(n)}(\mu_n)$ and $d_{k(n)}(\mu_n)$ and verify directly that in any case it is possible to choose D_0, satisfying all the previous conditions and for which $\mathrm{Re}\,\lambda(\mu_n) \to 0$ does not hold.

REMARK. – The assumptions of Theorem 18 are given in terms both of A and α and of the components of $\overline{u}$. One could in principle give them all in terms of A but the resulting expression would be very clumsy.

REMARK. – To check (B3), it is sufficient to use the well-known formulas which give explicitly the roots of a cubic polynomial in terms of its coefficients, (see, [12]).

REMARK. – In the case of the bifurcation of non-homogeneous equilibria from $\overline{u}$, we have seen that $p_3 < 0$ is almost a «necessary and sufficient condition». When we consider the bifurcation of time-periodic spatially non-homogeneous solutions, we can prove the following:

> *assume* (A1) *and* (A2), $p_8 > 0$, $p_9 > 0$, (42) *and* $p_3 > 0$, *then, for any positive diagonal matrix* D_0, L_0 *never has purely imaginary eigenvalues.*

In fact, if the assumptions above hold, all the terms in $q_n(D_0)$ are negative and consequently, (45) is never satisfied.

Hence, when (42) holds, $p_3 \leqslant 0$ is necessary, but the following example shows that $p_3 < 0$ is not sufficient.

Take

$$\begin{array}{llll} \beta_1 = 1, & \gamma_1 = 2, & \delta_1 = 1, & \alpha_1 = 4, \\ \beta_2 = 1, & \gamma_2 = 1, & \delta_2 = 3, & \alpha_2 = 5, \\ \varepsilon_1 = \varepsilon, & \varepsilon_2 = 1, & \varepsilon_3 = 1 + \varepsilon, & s = 0. \end{array}$$

Then, $\overline{u} = (1, 1, 1)$ and easy computations show that, if $\varepsilon > 0$ is sufficiently small,

$$p_4 > 0,\ p_5 > 0,\ p_8 > 0 \text{ and } p_9 > 0,\ p_3 < 0,\ s_1 < 0 \text{ and } s_2 < 0. \tag{56}$$

It is immediate to establish the following result:

> *assume* (A1), (A2), $p_8 > 0$, $p_9 > 0$ *and* (42). *Then if* $s_1 < 0$ *and* $s_2 < 0$, L_0 *never has purely imaginary eigenvalues for any choice of* D_0.

In fact, $s_1 < 0$ and $s_2 < 0$ imply that $q_n(d_1, 0, 0)$ and $q_n(0, d_2, 0)$ are non positive for any positive d_1 and d_2.

Now, since all the p_i and s_i and $\overline{u}$ depend continuously on the coefficients of A and on α, the inequalities (56) still hold if we choose $s \neq 0$ sufficiently small. In this way, we obtain a matrix A and α for which Hopf bifurcation does not occur.

4. – Stability of bifurcating solutions and numerical examples.

The numerical computations presented in this section were carried out on the SPERRY 1100/82 at Freiburg University. The system was solved employing difference methods with variable mesh size. We used the routine SLIPI from the SLDGL Subroutine Library, developed at Karlsruhe University.

Throughout this section, we assume $N=1$ and $\Omega=(0,1)$. Then $-\Delta u = -u''$ and all eigenvalues for the Neumann problem are simple and given by

$$\rho_n = n^2\pi^2, \qquad n \geqslant 0, \tag{57}$$

with corresponding eigenfunctions

$$\phi_0 \equiv 1, \tag{58}$$

$$\phi_n(x) = \sqrt{2}\cos(n\pi x) \qquad n \geqslant 1,\ \ x \in \Omega. \tag{59}$$

Assume the hypothesis of Theorem 11. Since $\operatorname{Ker} M_{n_0}^T = (\operatorname{Im} M_{n_0})^T$ it follows that there is a $c^* \in \boldsymbol{R}^3$ with

$$[c^*] = \ker M_{n_0}^T. \tag{60}$$

Now assumption (ii) of Theorem 11 implies that

$$(D_1 c, c^*) \neq 0.$$

Also (iv) implies that $(c, c^*) \neq 0$.
Here, $(\cdot,\cdot)$ is the scalar product in $\boldsymbol{R}^3$. Given c, c^* we can always arrange that

$$(D_1 c, c^*)/(c, c^*) < 0 \tag{61}$$

(multiplying D_1 by -1 if necessary). In addition to the assumptions of Theorem 11 consider the following hypothesis

(v) there is a $\delta_0 > 0$ such that

$$\operatorname{Re}(\sigma(M_{n_0})\setminus\{0\}) < -\delta_0, \qquad \operatorname{Re}\sigma(M_n) < -\delta_0 \qquad \text{for } n \neq n_0.$$

For $k \geqslant 0$, $k \neq n_0$, set

$$b_k = 1/2(M_k)^{-1} CAc, \tag{62}$$

$$q = CAb_0 + (1/2)CAb_{2n_0} + B_0Ac + (1/2)B_{2n_0}Ac, \tag{63}$$

(here we use our convention that if $w=(w_1, w_2, w_3)^T \in \boldsymbol{R}^3$ then $W = \operatorname{diag}(w_1, w_2, w_3)$). Now the following, essentially well-known result holds:

PROPOSITION 19 (see *e.g.* [6], [11], [5]). – *Assume the hypothesis of Theorem* 11. *In addition suppose that* (61) *and* (*v*) *hold.*

If $(q, c^*)/(D_1 c, c^*) > 0$, *then the bifurcating equilibrium* $u^*(\varepsilon)$ *in Theorem* 11 *is asymptotically stable for small* ε; *if* $(q, c^*)/(D_1 c, c^*) < 0$, *then* $u^*(\varepsilon)$ *is unstable.*

The proof is obtained by developing $u^*(\varepsilon), \mu^*(\varepsilon)$ into the Taylor series with respect to ε, and determining the coefficients successively. One obtains

$$\mu^*(\varepsilon) = \mu_1 \varepsilon + \mu_2 \varepsilon^2 + \text{h.o.t.} \qquad \text{where } \mu_1 = 0, \ \mu_2 = \frac{1}{n_0^2 \pi^2} \frac{(q, c^*)}{(D_1 c, c^*)}.$$

Now (61) implies that $u = \bar{u}$ is stable for $\mu < 0$ and unstable for $\mu > 0$. Further $\mu_2 > 0$ implies that we have supercrital bifurcation, while for $\mu_2 < 0$, the bifurcation is subcritical. Now the principle of the transfer of stability implies the result.

We choose the following kinetic parameters

$$(64) \qquad \begin{cases} \alpha_1 = 2.1, & \beta_1 = 2.3, & \gamma_1 = 3.0, & \delta_1 = 0.5, \\ \alpha_2 = 3.2, & \beta_2 = 3.0, & \gamma_2 = 2.0, & \delta_2 = 1.7, \\ s = 0.8, & \varepsilon_1 = 0.9, & \varepsilon_2 = 2.0, & \varepsilon_3 = 0, \end{cases}$$

The assumptions (A2) (A2) are satisfied. Moreover $p_8 > 0$, $p_9 > 0$ thus persistence obtains.

The equilibrium $\bar{u}$ is given approximately as

$$(65) \qquad \bar{u} \approx (0.58, 0.14, 0.69)^T.$$

We choose the diffusion matrix D of (2) in the form

$$(66) \qquad D = D' + \rho D'' + \mu D''.$$

Here

$$(67) \qquad D' = \operatorname{diag}(0.01, 0.01, 0.05),$$

$$(68) \qquad D'' = \operatorname{diag}(0, 0, 1).$$

We try to determine ρ so that for $D_0 = D' + \rho D''$, $D_1 = D''$ the assumptions of Proposition 10 hold. Let

$$(69) \qquad M_n(\mu) = \bar{U}A - n^2 \pi^2 (D' + \mu D'')$$

and vary μ in $I_\mu = [0, 0.03]$. Then:

(70) for $n \geq 0$, $n \neq 1$ $\mu \in I_\mu$ $\operatorname{Re} \sigma(M_n(\mu)) < -0.03$;

(71) for $\mu \in I_\mu$, the matrix $M_n(\mu)$ has the eigenvalues $\lambda_i(\mu)$, $i = 1, 2, 3$ with

$$\operatorname{Re} \lambda_{1,2}(\mu) < -0.7, \qquad \lambda_3(0) \approx -0.02, \qquad \lambda_3(0.03) \approx +0.02.$$

Thus there is a critical value in approximately given by

$$\hat{\mu} \approx 0.01$$

for which $\lambda_3(\hat{\mu}) = 0$.

Also, (61) is satisfied.

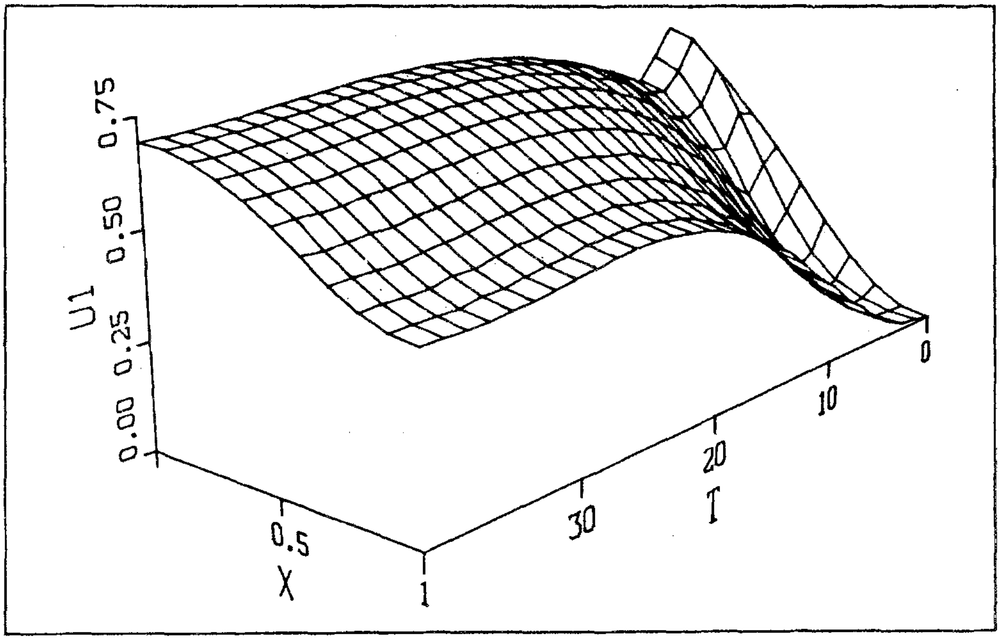

Figure 1

Finally,

$$\frac{(q, c^*)}{\pi^2 (D_1 c, c^*)} \approx 1.15 .$$

So that all hypothesis of Proposition 10 (and Theorem 11) hold. Thus, setting $\rho = \hat{\mu}$ in (66) we get that for $\mu > 0$, μ small, there is a stable nonhomogeneous equilibrium $u^*(\varepsilon)(x) \approx \overline{u} + \varepsilon \cdot c \cdot \cos \pi x$ of (2) where $\mu = \mu^*(\varepsilon)$.

This is illustrated in the following figures 1, 2, 3 where the time-behaviour of a solution $u(x, t)$ with the initial value

$$u_1(x, 0) = 0.3\ (1 + \cos \pi x),$$

$$u_2(x, 0) = 0.3\ (1 - \cos \pi x),$$

$$u_3(x, 0) = 0.3\ (1.5 + \cos \pi x),$$

is plotted for $\mu > 0$ small.

We see that the solution rapidly «beomes» time invariant and spatially nonhomogeneous.

We shall now turn to determining stability of the bifurcating periodic solutions in Theorem 17.

Note that in the formulas to follow, with the exception of $\overline{U}$, the bar over a vector or a matrix denotes its complex conjugate.

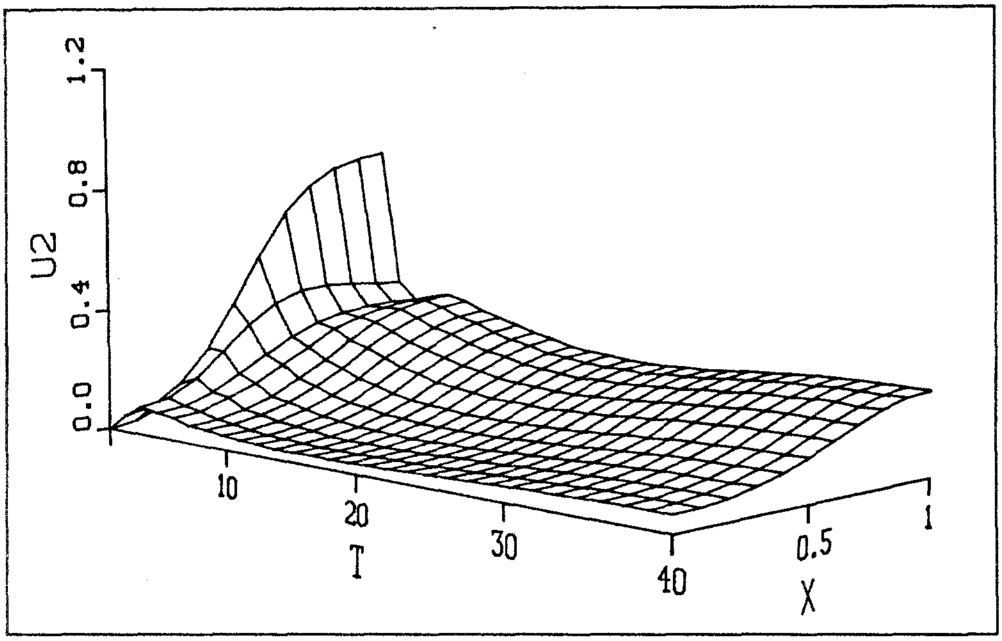

Figure 2

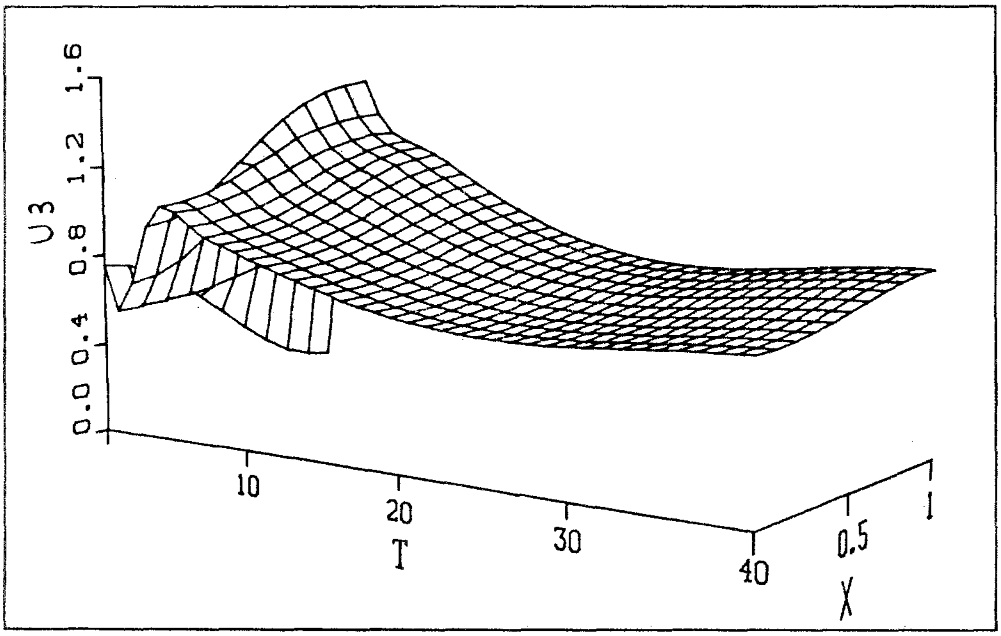

Figure 3

The following result is essentially known:

PROPOSITION 20 (cf. [7], [4], [5]). – *Assume all hypotheses of Theorem* 17, $\alpha'(0) > 0$. *Let* $c, c^* \in \mathbf{C}^3 \setminus \{0\}$ *be such that*

$$[c] = \ker(M_{n_0} - i\beta_0), \qquad [c^*] = \ker(M_{n_0}^T + i\beta_0);$$

$$(c, c^*) = 1. \tag{72}$$

Define

$$g_1 = (1/2)\ (2i\beta_0 - \overline{U}A)^{-1} CAc, \qquad g_2 = (1/2)\ (2i\beta_0 - \overline{U}A + 4h_0^2\pi^2 D_0)^{-1} CAc; \tag{73}$$

$$b_1 = -(\overline{U}A)^{-1} \operatorname{Re} CA\bar{c}, \qquad b_2 = -(\overline{U}A - 4n_0^2\pi^2 D_0) \operatorname{Re} CA\bar{c}; \tag{74}$$

$$q = CAb_1 + (1/2)\, CAb_2 + \overline{C}Ag_1 + (1/2)\, \overline{C}Ag_2 + G_1 A\bar{c} + (1/2)\, G_2 A\bar{c} + B_1 Ac + (1/2)\, B_2 Ac. \tag{75}$$

If $\operatorname{Re}(q, c^*) < 0$ *then the bifurcating periodic solution* u_ε *in Theorem* 17 *is orbitally asymptotically stable (for small* $\varepsilon > 0$), *and if* $\operatorname{Re}(q, c^*) > 0$, u_ε *is instable.*

The proof of Proposition 20 is carried out by successively determining the power series coefficients of u_ε and $\mu^*(\varepsilon)$ in ε and using the principle of transfer of stability. Details are omitted.

We shall now give a numerical example. Let

$$\begin{cases} \alpha_1 = 4.0, & \beta_1 = 3.5, & \gamma_1 = 3.0, & \delta_1 = 0.5, \\ \alpha_2 = 20.0, & \beta_2 = 11.7, & \gamma_2 = 1.5, & \delta_2 = 6.3, \\ s = 1.0, & \varepsilon_1 = 1.0, & \varepsilon_2 = 1.3, & \varepsilon_3 = 0. \end{cases} \tag{76}$$

With this choice of the kinetic parameters (A1) (A2) hold. Moreover $p_8 > 0$ $p_9 > 0$. Thus (2) is persistent (for any D). The equilibrium $\bar{u}$ is given as

$$\bar{u} \approx (0.55, 0.34, 2.01)^T.$$

We define D as in (66) with

$$D' = \operatorname{diag}(0.30, 0.04, 0.001), \qquad D'' = \operatorname{diag}(0, -1, 0),$$

and ρ to be determined.

Define $M_n(\mu)$ as in (68), for $\mu \in I_\mu = [0, 0.03]$.

We then obtain for $\mu \in I_\mu$:

(77) $\operatorname{Re}\sigma(M_n(\mu)) < -0.05$ for $n \geq 0$, $n \neq 1$,

(78) $\sigma(M_1(\mu)) = \{\lambda(\mu), \bar{\lambda}(\mu), \rho(\mu)\}$ with $\lambda(\mu) = \alpha(\mu) + i\beta(\mu)$, $\beta(\mu) > 1.8$, $\alpha(0) \approx -0.08$, $\alpha(0.03) \approx 0.04$, $\rho(\mu) < -5.6$.

Thus there is a critical value $\widehat{\mu}$, $\widehat{\mu} \approx 0.02$, such that $\alpha(\widehat{\mu}) > 0$, $\alpha'(\widehat{\mu}) > 0$. Hence, setting $\rho = \widehat{\mu}$ in (66) we obtain from Theorem 17 the bifurcation of periodic solutions u_ε. To prove their stability we first calculate c, $c^* \in \boldsymbol{C}^3$

$$c \approx (0.27 + i0.26, -0.30 - i1.08, -1.31 + i0.13)^T,$$

$$c^* \approx 2\cdot(-0.40 + i0.59, -0.19 - i0.75, -0.80 + i0.30)^T.$$

Then we get

$$b_1 \approx (3.38, -2.60, -5.32)^T,$$

$$b_2 \approx (0.05, -0.04, 0.26)^T,$$

$$g_1 \approx (-0.07 - i0.32, -0.83 + i0.67, 0.52 + i0.62)^T,$$

$$g_2 \approx (0.12 - i0.08, -1.37 + i0.52, 0.53 + i0.90)^T.$$

This finally gives

$$\operatorname{Re}(q, c^*) \approx -0.35.$$

Thus the bifurcating periodic solutions are orbitally asymptotically stable. In the following figures we plot the u_1-component of a solution $u(x, t)$ of (2) with $D = D' + (\widehat{\mu} + \mu) D''$ for $\widehat{\mu} + \mu = 0$ (figure 4, *i.e.* $\mu \approx -0.02$) and then for $\widehat{\mu} + \mu = 0.03$, (figure 5, *i.e.* $\mu \approx 0.01$). The initial value of $u(x, t)$ is, in both cases:

$$u_1(x, 0) = 1.0 + \cos \pi x,$$

$$u_2(x, 0) = 1.0 - \cos \pi x,$$

$$u_3(x, 0) = 1.5 + \cos \pi x.$$

We see that for $\mu \approx -0.01$ the solution rapidly approaches the homogeneous equilibrium $\overline{u}$, while for $\mu \approx 0.01$ it tends to a time-periodic spatial pattern.

REMARK. – Examples of bifurcation of stable nonhomogeneous equilibria and periodic solutions of one-predator-two-prey Lotka-Volterra models are also given in [6], [7]. However, these examples are not persistent.

In our final example we will show that, for appropriate values of the kinetic parameters, the kinetic system (4) has stable limit cycles. To this end, let $\widehat{\alpha} \in \boldsymbol{R}^3$ be arbitrary and consider the perturbed system (4) in the following form

$$\dot{u} = U(\alpha + \mu\widehat{\alpha} + Au). \tag{79$_\mu$}$$

Assume (A1) and (A2) for $(79)_\mu$ with $\mu = 0$. It follows that $\det A < 0$, so there is a unique solution $\widehat{u}$ of

$$\widehat{\alpha} + Au = 0. \tag{80}$$

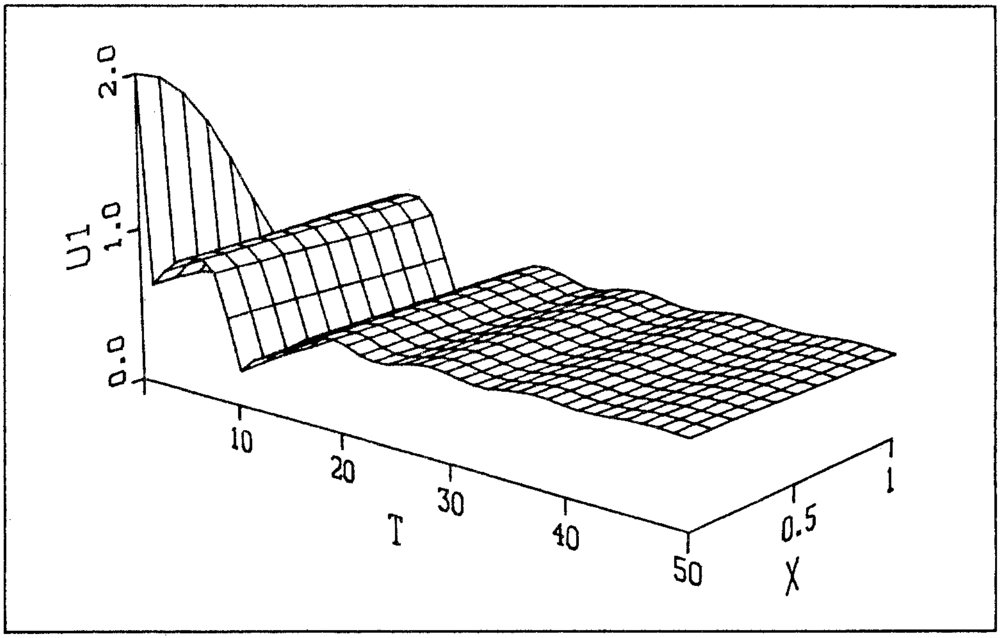

Figure 4

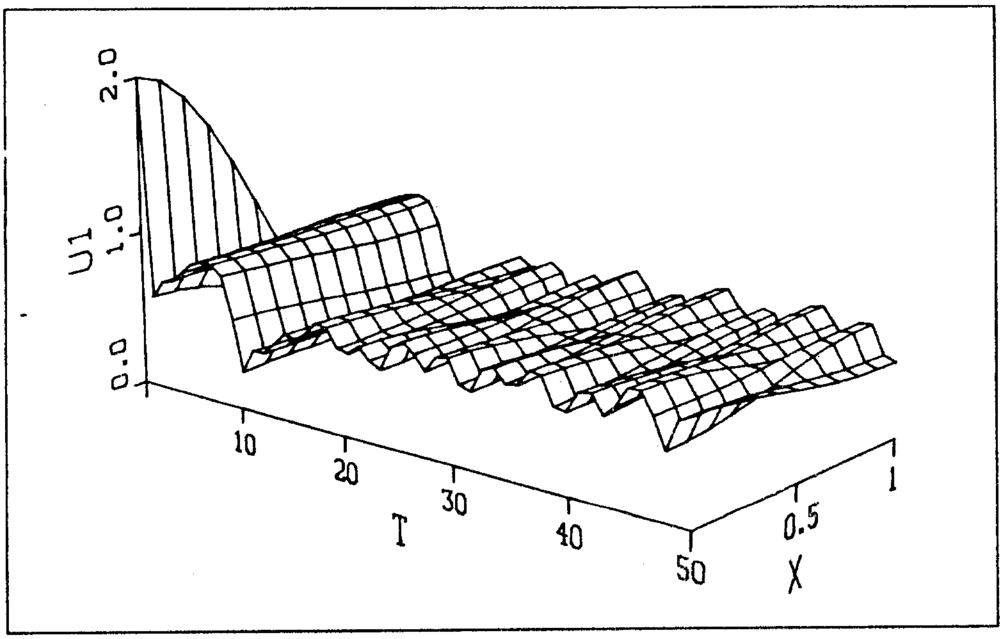

Figure 5

Set $\overline{u}(\mu) = \overline{u} + \mu\widehat{u}$. Then $\overline{u}(\mu)$ is the unique solution of

$$a + \mu\widehat{\alpha} + Au = 0. \tag{81}$$

Writing $u = v + \overline{u} + \mu\widehat{u}$ we obtain from (79)

$$\dot{v} = (\mu\widehat{U} + \overline{U} + V)Av. \tag{82}$$

We make the following assumption

(w) There are $\mu_1 > 0$, $\delta_0 > 0$ such that for $\mu \in [-\mu_1, \mu_1]$ the matrix $(\mu\widehat{U} + \overline{U})A$ has the eigenvalues $\lambda(\mu)$, $\overline{\lambda}(\mu)$, $\rho(\mu)$ with $\lambda(\mu) = \alpha(\mu) + i\beta(\mu)$ and

(i) $\alpha(0) = 0$, $\alpha'(0) > 0$, $\beta(\mu) > 0$,

(ii) $\rho(\mu) < -\delta_0$.

(w) just implies that at $\mu = 0$ there is a Hopf bifurcation of a periodic solution u_ε of $(79)_{\mu(\varepsilon)}$, $\mu(0) = 0$, $u_0 = \overline{u}(0)$, $u_\varepsilon \neq \overline{u}(\mu(\varepsilon))$, $\varepsilon > 0$ small.

u_ε are also homogeneous periodic solutions of the diffusive system

$$\begin{cases} \partial_t u = D\Delta u + U(\alpha + \mu\widehat{\alpha} + Au) & x \in \Omega, \\ \partial_\nu u = 0 & x \in \partial\Omega, \end{cases} \tag{83$_\mu$}$$

for every choice of D.

Fix D. Choose c, $c^* \in \boldsymbol{C}^3$ such that

$$[c] = \ker(\overline{U}A - i\beta_0), \qquad [c^*] = \ker((\overline{U}A)^T + i\beta_0),$$

where $\beta_0 = \beta(0)$ and such that

$$(c, c^*) = 1. \tag{84}$$

Define

$$b = -(\overline{U}A)^{-1}[2\operatorname{Re} CA\overline{c} - (\operatorname{Re} CA\overline{c}, c^*)\cdot c - (\operatorname{Re} CA\overline{c}, \overline{c}^*)\cdot\overline{c}], \tag{85}$$

$$g = (2i\beta_0 - \overline{U}A)^{-1}[CAc - 1/2(CAc, c^*)\cdot c - 1/2(CAc, \overline{c}^*)\cdot c], \tag{86}$$

$$e = i\beta_0^{-1}(CAc, c^*)\cdot(\operatorname{Re} CA\overline{c}, c^*) + (CAb + \overline{C}Ag + GA\overline{c} + BAc, c^*). \tag{87}$$

Then the following result holds:

PROPOSITION 21. – *Consider* $(83)_\mu$ *and assume* (A1) (A2) *at* $\mu = 0$. *Moreover, assume that* (w) *holds, and in addition*

$$\operatorname{Re}\sigma(M_n(\mu)) < -\delta_0 \quad \textit{for } \mu \in [-\mu_1, \mu_1], \ n \neq n_0,$$

where

$$M_n(\mu) = (\mu \widehat{U} + \overline{U}) A - n^2 \pi^2 D . \tag{88}$$

Finally, let (84) *hold. Define* e *by* (87).

If Re $e < 0$ *then the periodic solution* u_ε, $\varepsilon > 0$ *small, is orbitally asymptotically stable with respect to* $(83)_{\mu(\varepsilon)}$, *and unstable, if* Re $e > 0$.

The proof is, again, an application of the stability transfer. We omit the details.

Now choose

$$\alpha_2 = 20.6 , \qquad \beta_2 = 12.5 \tag{89}$$

and let all the *other* kinetic parameter be as in (76).

$\overline{u} = \overline{u}(0)$ is given as $\overline{u}(0) \approx (0.51, 0.38, 2.17)^T$

Choose $\widehat{\alpha}$ as

$$\widehat{\alpha} = (0, -1, 0)^T \tag{90}$$

and D as

$$D = \operatorname{diag}(0.08, 0.05, 0.002) . \tag{91}$$

Vary μ in $I_\mu = [0, 0.2]$. Then we get for $\mu \in I_\mu$

$$\begin{cases} (1) \quad \operatorname{Re} \sigma(M_n(\mu)) < -0.05 \qquad \text{for } n \geqslant 1 , \\ (2) \quad \sigma M_0(\mu) = \{\lambda(\mu), \overline{\lambda}(\mu), \rho(\mu)\} , \qquad \lambda(\mu) = \alpha(\mu) + i\beta(\mu) , \\ \qquad \alpha(0) \approx -0.13 , \qquad \alpha(0.2) \approx 0.06 , \qquad \beta(\mu) > 0.59 , \qquad \rho(\mu) < -2.0 . \end{cases} \tag{92}$$

Thus for some critical value of the parameter $\widehat{\mu}$, given approximately by $\widehat{\mu} \approx 0.13$ it follows that $\alpha(\widehat{\mu}) = 0$, $\alpha'(\widehat{\mu}) > 0$.

Moreover,

$$\overline{u}(\widehat{\mu}) \approx (0.55, 0.35, 2.08)^T .$$

Computing b, g and e in (85)-(89) we obtain

$$\operatorname{Re} e \approx -134.0 . \tag{93}$$

Thus the bifurcating time-periodic spatially homogeneous solutions u_ε are orbitally asymptotically stable.

In figures 6, 7 below we plot the u_1-component of a solution $u(x,t)$ of $(83)_\mu$ for $\mu = 0, \mu = 0.2$ respectively. The initial value is given in both cases by

$$\begin{cases} u_1(x, 0) = 1.3 + 0.2 \cos \pi x , \\ u_2(x, 0) = 0.2 + 0.2 \cos \pi x , \\ u_3(x, 0) = 1.8 + 0.2 \cos \pi x , \end{cases} \tag{94}$$

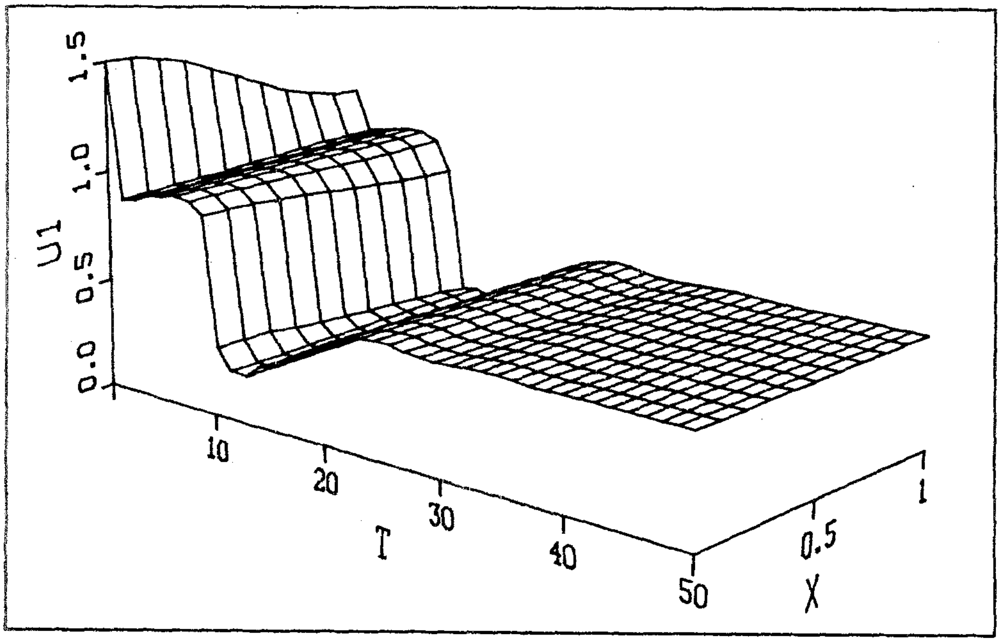

Figure 6

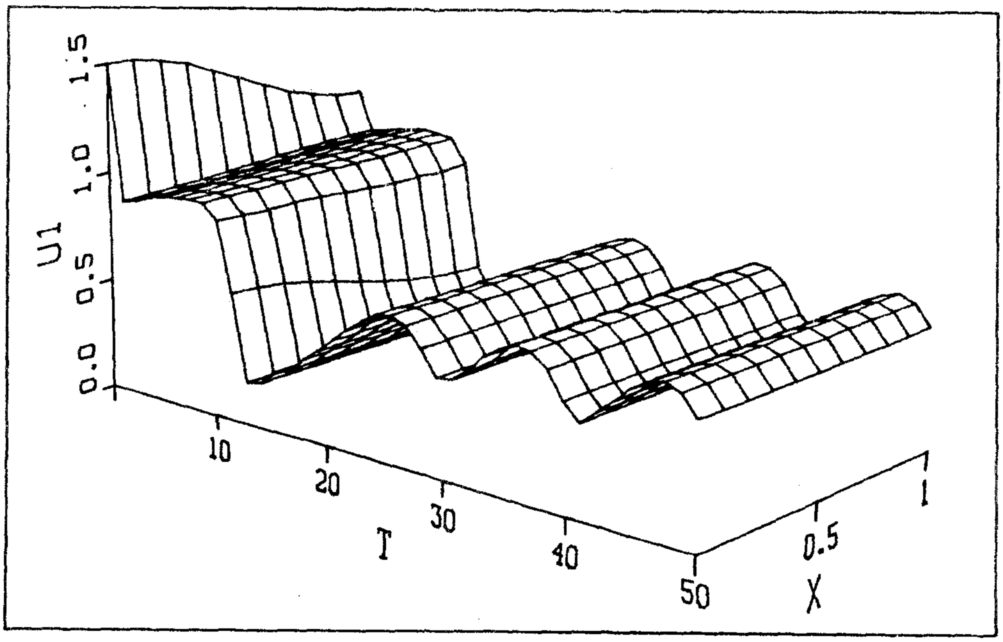

Figure 7

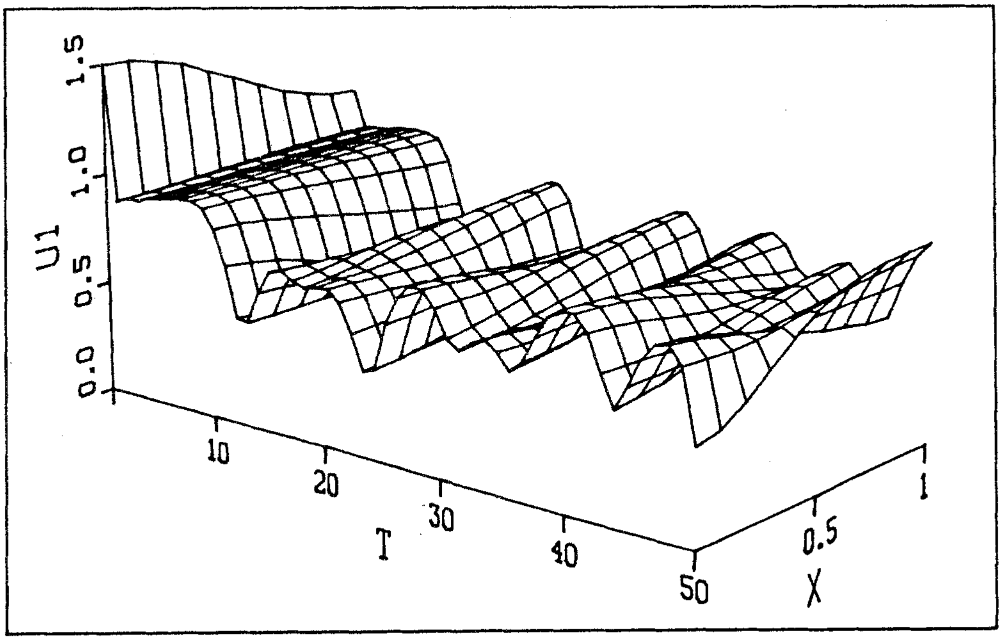

Figure 8

For $\mu = 0$ the equilibrium $\bar{u}(0)$ is asymptotically stable with respect to $(83)_0$ and this is also confirmed in figure 6. For $\mu = 0.2$ $\bar{u}(\mu)$ is unstable, and the homogeneous periodic solution u_ε with $\mu(\varepsilon) = 0.2$ is asymptotically stable. Again this is confirmed by figure 7

By suitably varying the diffusion coefficients one can achieve a loss of stability of the periodic solution. In fact, suppose that (A1), (A2) and (w) hold but suppose that there is $m \geqslant 1$ and for $\mu \in I_\mu$ a $k(\mu) \in \sigma(M_m(\mu))$ with $\operatorname{Re} k(\mu) \gg \delta_0 > 0$. Then, by a simple continuity argument, u_ε must be unstable with respect to $(83)_{\mu(\varepsilon)}$, for small $\varepsilon > 0$. We shall now use this observation and replace D in (91) by a perturbed matrix

$$\hat{D} = D + \operatorname{diag}(0.05, 0, 0). \tag{95}$$

Then for some $m \geqslant 1$ the matrix $M_m(\mu)$ defined in (88) (with D replaced by $\hat{D}$) has an eigenvalue $k(\mu) > 0.03$. In figure 8 above we plot the u_1-component of the solution $u(x, t)$ of $(83)_\mu$ for $\mu = 0.2$, $D = \hat{D}$, and $u(x, 0)$ given by (94). This figure also confirms that the periodic solution u_ε is now unstable with respect to $(83)_{\mu(\varepsilon)}$.

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