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SPATIAL STRUCTURES IN A REACTION-DIFFUSION SYSTEM – DETAILED ANALYSIS OF THE "BRUSSELLATOR"

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Continuous dependence of spatially nonuniform concentration profiles for the "Brussellator" reaction mechanism on the characteristic length of the system is given both for zero flux and fixed boundary conditions. Branches of solutions arising through primary bifurcation form closed curves. Secondary bifurcations giving rise to spatially asymmetric solutions exist for fixed boundary conditions. Results of a stability analysis of individual solutions are discussed. A method of composing complex spatial profiles for higher lengths from elementary solutions for smaller lengths is suggested and tested in the case of zero flux boundary conditions. Emergence of subsequently more complex stable patterns in dependence on increasing length of the system suggests many similarities to gradual build up of complex morphogenetic patterns.

1. Introduction

Solutions of reaction-diffusion equations with appropriate kinetic relations can serve as simple models of a number of biological phenomena. They can be used for the description of chemical mechanisms of cell differentiation, pattern formation and morphogenesis. Realistic description of the reaction and transport in the living cells and tissues will require to consider also other types of transport than diffusion (e.g. ionic migration, active transport at the boundaries). Models thus constructed will be more complex and will bring undoubtedly new features. The basis of various models forms the interpretation of such phenomena as nonmonotonic ("spatially periodic") stationary profiles of concentrations of characteristic components or time and space dependent wave-like concentration profiles. These result due to interaction of the special type of nonlinear kinetics relations (e.g. enzymatic reaction with feedback inhibition) with transport phenomena. The nonlinearity of description makes analytic techniques difficult to use for prediction of the concentration profiles. The nonlinear analysis required in order to predict what spatial patterns ultimately evolve can be exceedingly complex and difficult to perform. When the governing parameters are far from their bifurcation values, and as we shall show in this paper, often even in the case that we are in the neighbourhood of the bifurcation region we usually do not have any other alternative to numerical solution of the governing equations. In this paper we shall present results of a detailed numerical study of the most popular model, the simple tri-molecular scheme sometimes called "Brusselator" [1–7].

For the chosen set of reaction and diffusion parameters the computed continuous dependence of the number and character of steady state profiles on the characteristic dimension of the system is given. It follows from the computed results that a new type of spatial profile bifurcates every time, when the characteristic eigenvalue of the corresponding linear problem crosses the imaginary axis. The stability of individual solutions is discussed. In the case of the boundary conditions of the first kind secondary bifurcations occur, even if the range of parameters studied does not permit existence of multiple zero eigenvalues of the linearized problem. In the case of the boundary conditions of the second kind we shall demonstrate, how starting from the most simple spatial profiles we can build up complex profiles by joining the simple (elementary) profiles together in an appropriate way. We believe, that the method of analysis used in this paper can help in the study of more complicated schemes, which could be constructed in the future for description of data obtained on biochemical and living systems.

2. Balance equations, previous results

The "Brusselator" corresponds to a simple trimolecular scheme

$$A \rightleftarrows X, \quad 2X + Y \rightleftarrows 3X, \quad B + X \rightleftarrows Y + D, \quad X \rightleftarrows E. \tag{1}$$

The system is open to the initial and final chemicals A, B, D, E with their concentrations imposed throughout the system. Further, all forward kinetic constants are set to unity and the inverse reaction rates are neglected. If a bounded, one-dimensional medium is assumed, then the rate equations describing the reaction and diffusion transport are

$$\partial X/\partial t = A + X^2 Y - (B+1)X + D_X\, \partial^2 X/\partial z^2, \tag{2a}$$

$$\partial Y/\partial t = BX - X^2 Y + D_Y\, \partial^2 Y/\partial z^2. \tag{2b}$$

Here D_X and D_Y are diffusion coefficients of the components X and Y and mass transport is described through Fick's law.

Two types of boundary conditions will be considered:

a) Zero flux boundary conditions

$$z = 0, L;\ t > 0: \quad \partial X/\partial z = \partial Y/\partial z = 0. \tag{3}$$

b) Fixed boundary conditions

$$z = 0, L;\ t > 0: \quad X = A = X_0;\ Y = B/A = Y_0. \tag{4}$$

In the steady state, if dimensionless spatial variable $x = z/L$, $x \in (0, 1)$ is introduced, we obtain two coupled second order nonlinear ordinary differential equations (boundary value problem)

$$\mathrm{d}^2 X/\mathrm{d}x^2 = (L^2/D_X)\,[-A - X^2 Y + (B+1)X] \tag{5}$$

$$\mathrm{d}^2 Y/\mathrm{d}x^2 = (L^2/D_X \vartheta)\,[-BX + X^2 Y]\,. \tag{6}$$

Here $\vartheta = D_Y/D_X$. Uniform solution of eqs. (5), (6),

$$X \equiv X_0 = A, \qquad Y \equiv Y_0 = B/A \tag{7}$$

will be called basic solution [8]. The stability of this solution is determined by the nature of the roots of the characteristic equation for the system of linear differential equations obtained through linearization of the system (5), (6) around basic state X_0, Y_0 [9]

$$\omega_i^2 - [B - 1 - A^2 - D_x(1+\vartheta)\,k_i^2]\,\omega_i + A^2(1 + k_i^2 D_x) + D_x k_i^2 \vartheta(1 - B) + D_x^2 \vartheta k_i^4 = 0. \tag{8}$$

Here $k_i = n\pi/L$ with $i = n = 0, 1, 2$ ... (except for boundary conditions (4), where $n = 0$ is excluded). Steady state X_0, Y_0 can be destabilized in two ways: through real eigenvalues ($\mathrm{Re}\,\omega_i > 0$, $\mathrm{Im}\,\omega_i = 0$) or through complex ones ($\mathrm{Re}\,\omega_i > 0$, $\mathrm{Im}\,\omega_i \neq 0$). Which type of an instability occurs depends on the values of the parameters in eqs. (2a, b). In the case of an instability through real eigenvalues the appearance of non-uniform spatial profiles has been predicted and confirmed by numerical simulations of eqs. (2a, b) [6]. Our study deals with such a case. The eigenvalues ω_i are determined as

$$\omega_i^{1,2} = \tfrac{1}{2}\{B - 1 - A^2 - k_i^2 D_x(1+\vartheta) \pm [[B - 1 + A^2 + k_i^2 D_x(\vartheta - 1)]^2 - 4A^2 B]^{1/2}\}. \tag{9}$$

The lowest value of the wave number n corresponding to the lowest value of k_i where $\mathrm{Re}\,\omega_i = 0$ will be called critical and denoted n_c ($k_c = n_c\pi/L$).

For real $\omega_i^{1,2}$ we shall have $\mathrm{Re}\,\omega_i^{1,2} = 0$ for values of

$$L_{1,2}^* = n\pi \left\{ \frac{1}{2D_x}\left[B - 1 - \frac{A^2}{\vartheta} \pm \left[\left(1 - B + \frac{A^2}{\vartheta}\right)^2 - \frac{4A^2}{\vartheta} \right]^{1/2} \right] \right\}^{-1/2} \tag{10}$$

The values $L_{1,2}^*$ are directly proportional to n. Hence for $n = n_c = 1$ we can obtain two minimal primary bifurcation lengths $L_{1,2}^*$. For the other values of $n = 2, 3$ ... the next eigenvalues will subsequently cross zero and bifurcation lengths will be the multiples of $L_{1,2}^*$ for $n = 1$.

The branch of solutions which bifurcates from the trivial solution to the right (i.e. for the values of $L > L^*$) is usually called supercritically bifurcated branch ("supercritical bifurcation"); the branch bifurcating to the left ($L < L^*$) is then called subcritical. It was proven [10,11] that supercritically bifurcated branch preserves the stability or instability of the trivial solution for $L < L^*$, subcritically bifurcated branch can not be stable along with the trivial solution for $L < L^*$.

In the neighbourhood of the primary bifurcation lengths the approximate analytical solutions describing spatial profiles bifurcating from the basic solution can be obtained by different asymptotic procedures e.g. by perturbation techniques. Auchmuty and Nicolis [12], Herschkowitz-Kaufman [9] and Cohen and Boa [13] obtained such solutions up to the first order perturbation terms in the small parameter proportional to the values of the parameter $B - B_c$. Here B_c is the value of B for $\mathrm{Re}\,\omega_i = 0$ and denotes critical value of B where the bifurcation occurs. An extensive comparison of the approximate results using perturbation formulae [9,12,13] with numerically determined concentration profiles will be published elsewhere [14].

The numerical results reported in [9] were obtained through application of finite difference techniques to the complete set of PDE, eqs. (2a, b). The numerical algorithm used converged to stable solutions only (no results with integration in the direction of reversed time were reported). Recently authors [15] have reported the results of numerical solution of the steady state eqs. (5) for one set of parameters. The authors obtained four different steady state solutions and checked numerically, that only one of them was stable. However, they have not been certain, whether the actual number of solutions is not higher than four. Babloyantz and Hiernaux [16] presented examples of the bifurcations where L was also considered as a characteristic bifurcation parameter.

Keener [17] has studied secondary bifurcation for the set of two coupled nonlinear diffusion reaction equations with quadratic nonlinearity including also the model equations for the "Brussellator". He utilized the realization [8] that secondary bifurcations are related to multiple bifurcation, i.e. the case, where more eigenvalues of the linearized problem will cross at the same time the imaginary axis. In our situation this would correspond to such a choice of parameters, that $m_1 L_1^* = m_2 L_2^*$ (here m_1, m_2 are appropriate integers). Mahar and Matkowsky [18] have studied secondary bifurcations for the "Brussellator". They used perturbation techniques and obtained approximate relations for the branches of solutions in the neighbourhood of secondary bifurcation points.

3. Numerical algorithms

For numerical calculation of the dependence of the steady-state solution of eqs. (5) on characteristic length an efficient algorithm of parameter mapping technique was used. The algorithm will generate the dependence of $X(x)$, $Y(x)$ as a function of chosen continuously changed values of the parameter, characteristic length of the system, starting from a known solution at a chosen point and is described in detail in the previous paper [19]. Solutions close to the primary bifurcation points $L_{1,2}^*$ were chosen as first starting solutions and then other initial conditions were chosen in dependence on the evolving phase plane picture. The studied region of the phase plane was then checked along the basic solution, bifurcating primary branches of solutions and at other chosen points to find out, whether any other branch of the solution (arising e.g. through secondary bifurcation) exists.

The stability of individual spatially nonuniform solutions for the chosen values of characteristic lengths was checked through numerical solution of the full system of spatial equations (2a, b). Known steady state profiles were used as starting profiles and time course of evolving solutions was followed. In some cases different starting profiles were used to determine the regions of attractions of individual stable profiles. Implicit difference scheme was used with spatial variable divided into 40, 80, 160 intervals (as required for accuracy).

4. Numerical results

All computations were carried out for the set of parameters, which was most intensively studied in the literature, i.e. the values $A = 2$, $B = 4.6$, $D_x = 1.6 \times 10^{-3}$, $D_y = 8 \times 10^{-3}$. The critical values of the characteristic dimension of the system, where basic solution changes its stability (primary bifurcation

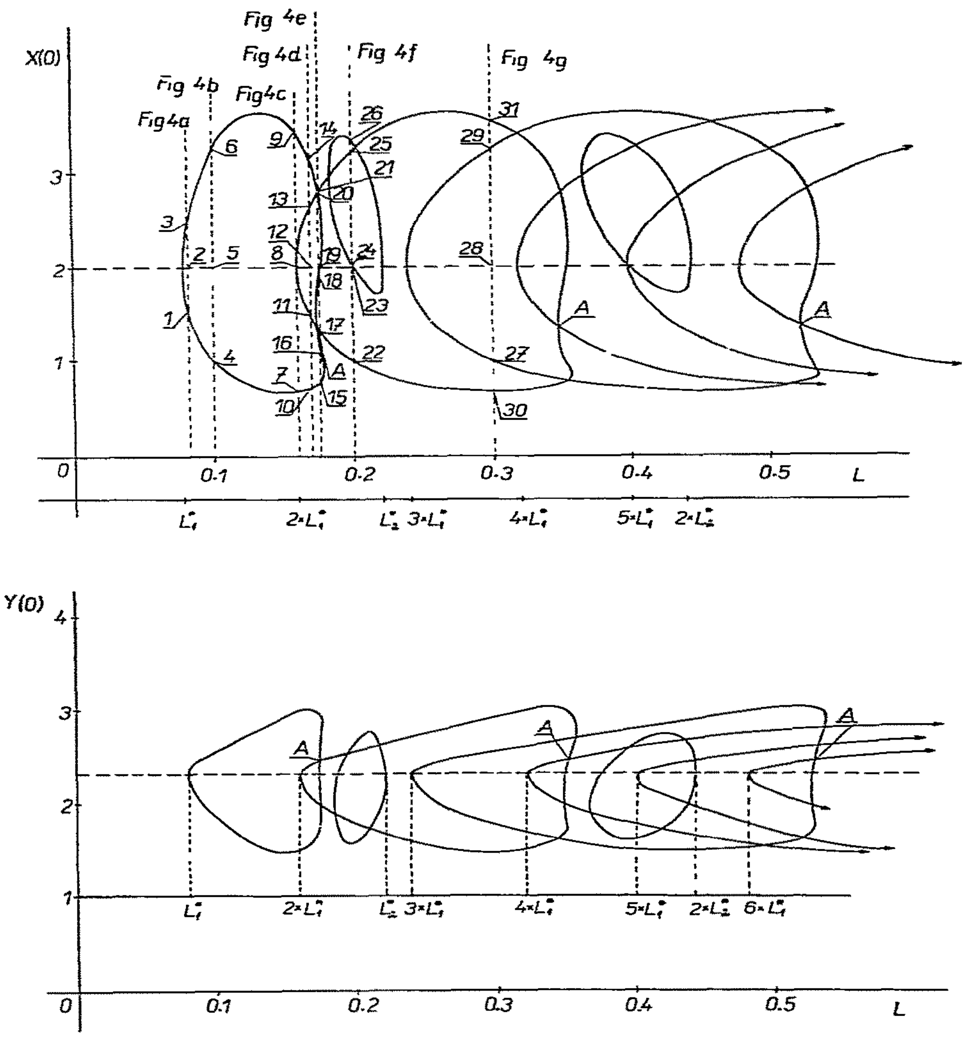

Fig. 1a, b. Dependence of $X(0)$, $Y(0)$ on characteristic dimension of the system L. L_1^*, L_2^* are primary bifurcation lengths; A is point of "secondary bifurcation". 1, 2, 3, ... positions of spatial profiles in figs. 4a–g.

points) are determined from eq. (10) as $L_1^* = 0.0798443$, $L_2^* = 0.2211213$. We can find out, that no secondary bifurcation from the basic profile through multiple eigenvalues crossing the imaginary axis can be expected, when the length of the system is varied. We would have to vary also one of the parameters A, B to create the point of secondary bifurcation arising through multiple bifurcation on the basic profile.

4.1. Zero flux boundary conditions

In figs. 1a, b the continuous dependence of the value of the variable $X(0)$ (fig. 1a) and $Y(0)$ (fig. 1b) on the characteristic length of the system is shown.

The concentrations of the reaction controlling components X and Y at the boundaries of the system (at $x = 0, 1$) vary widely, are often very sensitive to the small changes of characteristic dimension and can be multiple. We can infer from the figure, that multiple nonuniform spatial profiles exist, and that two branches bifurcating at the primary bifurcation length L_1^* form a closed curve. Hence the region of existence of the nonuniform solutions with the critical wavenumber n_c equal to one is limited. Similarly the bifurcating solutions with higher wavenumbers form closed curves and thus with increasing length only profiles with several neighbouring wavenumbers will exist. For another reaction model it can be shown that the bifurcated nonuniform solutions do not form closed curves, cf. [19]. Whether one or two closed curves are formed between L_1^* and L_2^* depends on the character of changes with L of the corresponding eigenvalues with zero real parts [20].

Branches bifurcating supercritically are stable, in agreement with the predictions for approximate solutions obtained through perturbation analysis. In a narrow region of lengths the curve of nonuniform solutions is convex and we can have altogether four distinct solutions in this region. The inner solutions are then unstable, as it follows from numerical solution. The most remarkable property of solutions satisfying zero flux boundary conditions is the possibility of "composing of solutions" [19]. If we have obtained solution $X(x)$, $Y(x)$ for given L, $x \in (0,1)$, (let us call it "elementary solution") we can from this solution compose the solutions $\tilde{X}(x)$, $\tilde{Y}(x)$ on the intervals $x \in (0, 2)$, $x \in (0; 3)$ in the following way:

$$x \in (0, 1): \quad \tilde{X}(x) = X(x); \quad \tilde{Y}(x) = Y(x) \tag{11a}$$

$$x \in (1, 2): \quad \tilde{X}(x) = X(2 - x); \quad \tilde{Y}(x) = Y(2 - x) \tag{11b}$$

$$x \in (2, 3): \quad \tilde{X}(x) = X(x - 2); \quad \tilde{Y}(x) = Y(x - 2). \tag{11c}$$

The general scheme of composing of solutions is shown in fig. 2. From the scheme it follows, that we can determine for any given characteristic length L the number of solutions which can arise through composing. Let us denote L_1 and L_2 coordinate of the left limit point [8] of the branch bifurcating at L_1^* and L_2^*, respectively (here $L_1 = L_1^*, L_2 < L_2^*$). Let ΔL_1 (and ΔL_2) be the length of the projection of the closed branch bifurcating at L_1^* (and L_2^*) into L axis; further

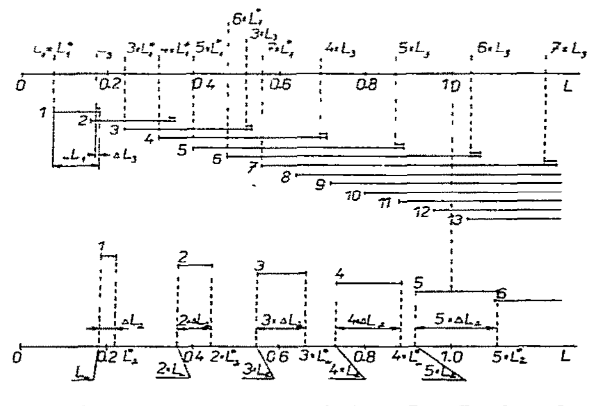

Fig. 2. Schema of composing of solutions. Zero flux boundary conditions.

let L_3 denote the coordinate, where four solutions on the closed branch first occur (L_3 corresponds here to the coordinate of the secondary bifurcating point A); ΔL_3 is the width of the interval of these multiple solutions (c.f. fig. 2). Then for the chosen length of the interval L we can determine the number of solutions N arising through composing as

$$N = 1 + 2 \sum_{i=1}^{3} \left(\left[\frac{L}{L_i} \right] - \left[\frac{L}{L_i + \Delta L_i} \right] \right). \tag{12}$$

Here $[L/L_i]$ and $[L/(L_i + \Delta L_i)]$ denote integer parts of the ratios; the points where L is multiple of L_i or $(L_i + \Delta L_i)$ are excluded (cf. figs. 1a and 2). Other solutions arising through secondary bifurcations or not connected with the trivial solution can also exist. The scheme is specific for our particular example. However, such scheme of construction of composed solutions can be created in a similar way for any other dissipative structure arising for the zero flux boundary conditions. For example, in the case $L = 1$, which was studied in detail by Herschkowitz-Kaufman [9] we can see from fig. 2, that altogether seventeen solutions exist (one uniform and sixteen nonuniform derived by composing technique).

Every line denoted with wave number in fig. 2 corresponds to two solutions. Two corresponding solutions with even wave numbers have positions of maxima and minima mutually exchanged (cf. figs. 3b, c), two solutions with odd wavenumbers are mutually symmetric around the axis going through $x = 0.5$. The

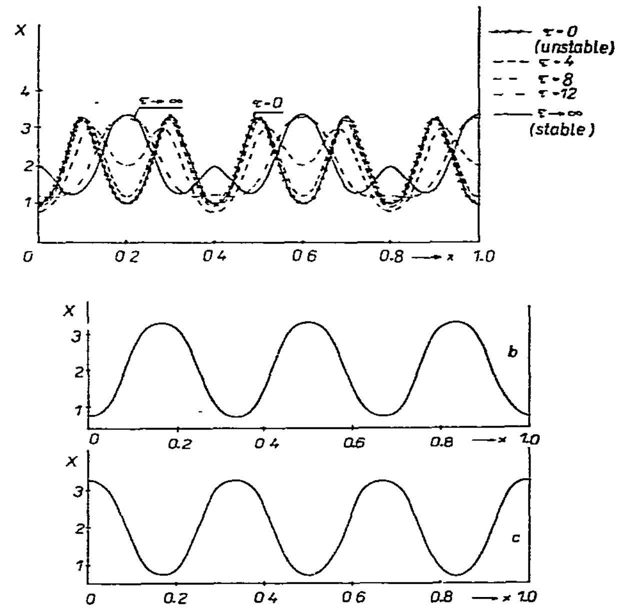

Fig. 3a. Spatial profiles $X(x)$ for zero flux boundary conditions. $L = 1$. Evolution of unstable steady state profile in time.

individual solutions are shown in [14]. In fig. 3a the spatial profile composed from five elementary profiles for $L = 0.2$ is shown. The elementary profile is unstable and the composed profile is also unstable. Three transient spatial profiles, results of the integration of full partial differential equations starting from the unstable profile, are also shown. Transients finish at the stable profile with the wavenumber $n = 10$ (corresponds to the number of extrema on the starting unstable profile). In figs. 3b, c two stable spatial profiles with five extremas are shown. Stable profiles with increasing number of extrema (up to eleven) exist. Spatial profiles with twelve and thirteen spatial extremas are unstable. Herschkowitz-Kaufman has reported three different stable solutions for this case. We have found altogether ten different stable spatially nonuniform profiles. The complex solutions composed from the unstable elementary spatial profiles are here unstable. The solutions composed from the stable elementary profiles were mostly stable. The case, where the profile composed from stable elementary profiles is unstable occurs for the profile with twelve extremas. Here the complex profile can be composed either as multiple of six unstable elementary profiles or as multiple of twelve stable elementary profiles (cf. fig. 1a). It seems, that this change of stability is caused by the fact, that we have encountered point of secondary bifurcation A (see fig. 1) on the intersection of elementary solutions with the branch which has arisen as composed from two elementary solutions.

Characteristic spatial profiles at different values of length which can be used as elementary profiles are given in figs. 4a–f. In fig. 4a three existing spatial profiles are shown. Basic uniform profile is unstable (unstable profiles are shown as dashed lines), two nonuniform spatial profiles are stable (full line), as we have encountered supercritical bifurcation at $L = L_1^*$. The numbers on individual profiles agree with the numbers on fig. 1a. In figs. 4b,c similar situations for higher values of L are depicted. We hope, that the presented numerical spatial profiles can serve for testing of approximate solutions obtained through other techniques in the future. In fig. 4d five spatial profiles for the value of length $L = 0.170 > 2 \times L_1^*$ are shown. Both spatial profiles belonging to the branch of solutions bifurcating at $L = L_1^*$ are still stable, but also one of the solutions belonging to the branch bifurcating at $L = 2 \times L_1^*$ is also stable (the second one is behind the point of secondary bifurcation A). Seven solutions can be observed in fig. 4e; in fig. 4f, $L = 0.2$, we can already see that just two from five spatial profiles (with wavenumber $n = 2$) are stable, profiles belonging to branch of solutions bifurcating at $L = L_2^*$ are unstable. Finally, in fig. 4g where $L = 0.3 > 3 \times L_1^*$, we can observe existence of four stable spatial profiles with wavenumber $n = 2,3$.

We can infer from fig. 4, that in a hypothetical system, where we would continuously increase the characteristic length, stable elementary profile would be (at the point where this becomes unstable) transformed into profile with two extrema, that profile would be after sufficient increase of length transformed into a profile with three extrema and so on. Fluctuations of concentrations with higher amplitudes could then shift at certain lengths, but not always, the profile into qualitatively different one e.g. in the case of characteristic length $L = 1$ the number of extrema on the spatial concentration profile could vary between six and eleven, depending on the transient history of the profile development. These effects of the characteristic length variation can serve as a basis for a construction of the models of differentiation.

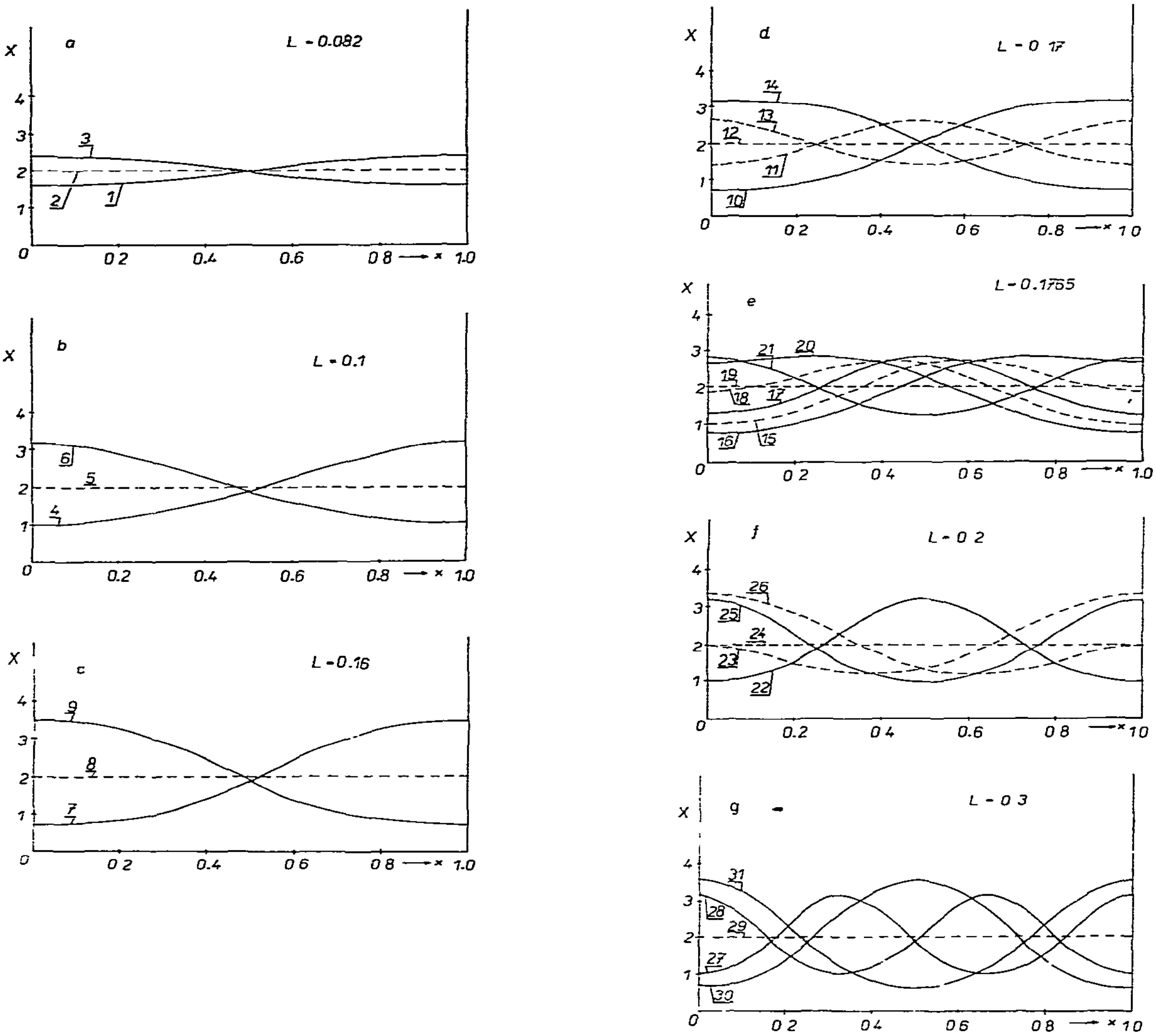

Fig. 4a–g. Characteristic spatial profiles at different values of length. Full line – stable solutions; dashed line – unstable solutions. Profile numbers correspond to the numbering in fig. 1a.

4.2. Fixed boundary conditions

The dependence of the values of the derivative of the concentration X or Y at the boundary ($dX/dx|_{x=0}$, $dY/dx|_{x=0}$) is given as a function of characteristic length of the system in figs. 5a, b. The value of the derivative is directly proportional to the overall flux into the system. We can see, that the flux can vary sharply with slight changes of the value of the governing parameter, i.e. here the characteristic dimension. Similarly to the case of the zero flux boundary conditions, we can observe, that branches of solutions bifurcating at primary

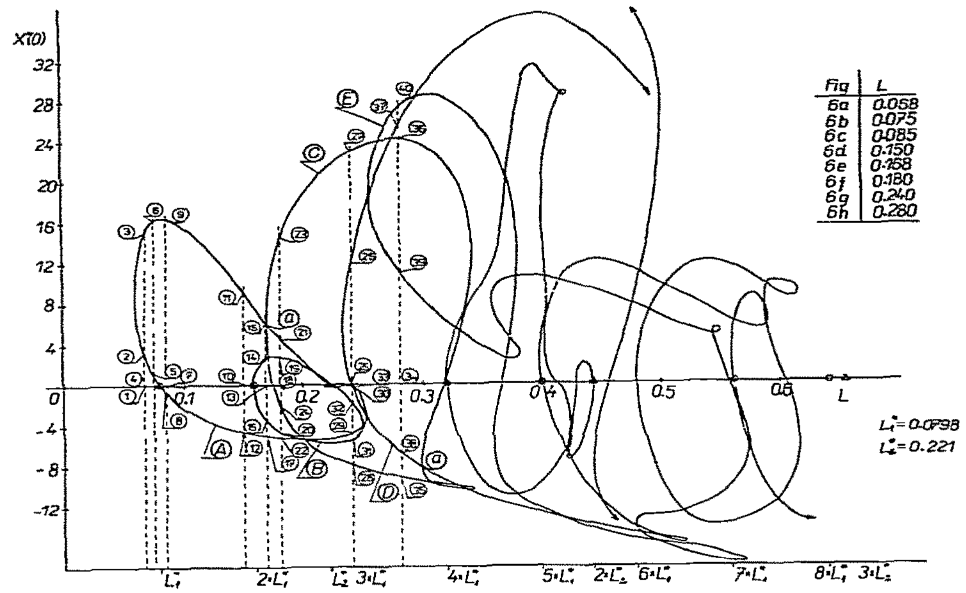

Fig	L
6a	0.058
6b	0.075
6c	0.085
6d	0.150
6e	0.158
6f	0.180
6g	0.240
6h	0.280

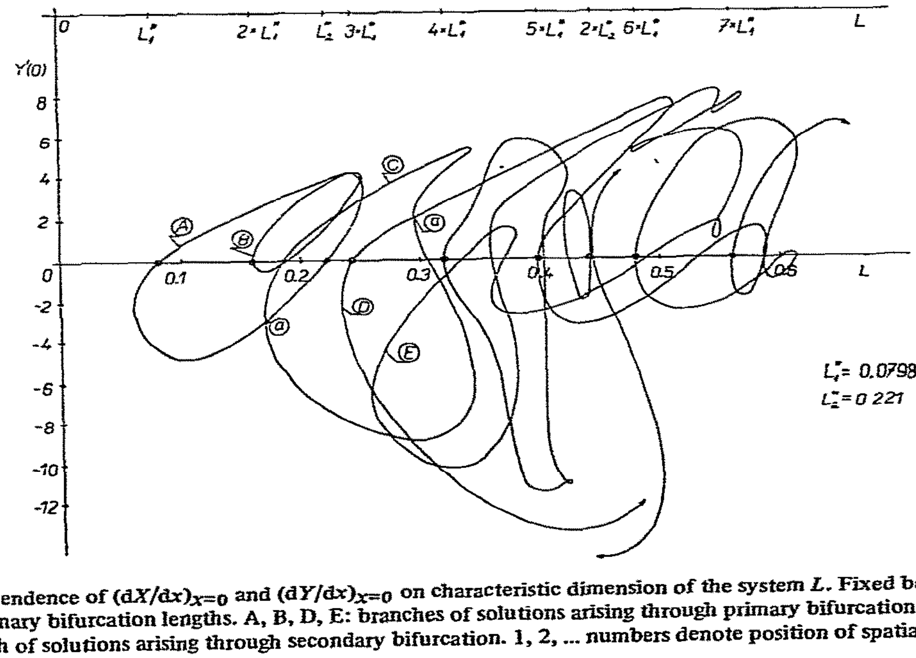

Fig. 5a, b. Dependence of $(dX/dx)_{x=0}$ and $(dY/dx)_{x=0}$ on characteristic dimension of the system L. Fixed boundary conditions. L_1^*, L_2^* are primary bifurcation lengths. A, B, D, E: branches of solutions arising through primary bifurcation from the basic profile. C is branch of solutions arising through secondary bifurcation. 1, 2, ... numbers denote position of spatial profiles shown in figs. 6.

bifurcation points form closed curves. We can see "subcritical" and "supercritical" bifurcations at point L_1^* where the branch denoted A bifurcates from the basic profile. Subcritically bifurcating solutions (e.g. for values of $L < L_1^*$) are in the close neighbourhood of the bifurcation point unstable in agreement with the predictions obtained via bifurcation analysis [10]. However, as it was already conjectured by Boa [13], in the neighbourhood of the bifurcating point $L = L_1^*$ also another solution (stable) exists, with a large amplitude.

A similar situation (even if far more complex) can be observed for higher characteristic lengths. Hence we can conclude that approximate asymptotic solutions obtained through application of perturbation techniques can give information about the existence of some spatially nonuniform solutions, their stability and spatial form in the neighbourhood of the points of bifurcation. However, we have to resort ourselves to numerical solution of original nonlinear equations in the case, that we wish to know a full picture of the existing solutions and even to answer the question whether for chosen value of the parameter we can have stable nonuniform solutions or not.

4.2.1. Secondary bifurcations

Bauer et al [8] have defined the bifurcation points on the basic solution (i.e. in our case points nL_1^* and nL_2^*, $n = 1,2$ ...) as primary bifurcation points and the half-rays of solutions that branch from these points, other than the basic solution, as primary states. Any solutions other than the basic solution which bifurcate from a primary state are called secondary states and the corresponding bifurcation points are called secondary bifurcation points. For the zero flux boundary conditions we can find points, (in figs. 1a, b these points are denoted A), that fulfill the above definition of the secondary bifurcation points. However, at these points two primary bifurcation branches bifurcating at different primary bifurcation points have a common point, no new branch of solution (e.g. branch of asymmetric solutions) branches out. The points (A) are connected with the change of stability of the original primary bifurcation solutions. A different situation can be observed in figs. 5a, b. Here the curve C corresponds to the new closed branch of asymmetric solutions arising through secondary bifurcation (points denoted ⑧ on the closed curves of primary bifurcation solutions A, C). The solution corresponding to the branch A changes its stability at the point ⑧. This secondary bifurcation does not correspond directly to multiple eigenvalues of the system linearized around basic solution going through zero, i.e. to the case which was studied by Keener [17]. A new type of solution (asymmetric spatial profiles) arising through this secondary bifurcation could arise due to the multiple zero eigenvalue at the primary bifurcation profile corresponding to the choice of parameters, which are close in the five dimensional parameter space $(A, B, D_X, \vartheta, L)$ to the values used in our study.

4.2.2. Development of spatial profiles with changing length

In fig. 6a–h spatial profiles of the component X, $X(x)$ at several chosen length intervals are given. The stable spatial profiles are shown as full lines and unstable profiles are shown as dashed lines. The numbers on the individual profiles correspond to the numbers given in fig. 5a. In some cases it is shown to what stable profile particular perturbed unstable profile develops (e.g. ② → ③).

In fig. 6a ($L = 0.068 < L_1^*$) three spatial profiles exist. The basic profile ① is stable together with the spatially nonuniform profile with large amplitude ③. The intermediate nonuniform profile ② predicted by asymptotic expansion techniques is unstable (subcritical bifurcation). In figs. 6b, c spatial profiles at two lengths which are very close to the primary bifurcation point L_1^* are presented. Approximate analytical solutions developed through methods of asymptotic expansion or through other techniques can be tested on these cases.

The situation shown in fig. 6b $L = 0.075$ is qualitatively the same as that in fig. 6a. In fig. 6c ($L = 0.085 > L_1^*$) two nonuniform spatial profiles are stable and the basic profile has become unstable, in accordance with the bifurcation theory. It would be useful to have approximate analytical techniques, which could predict both nonuniform spatial profiles.

In fig. 6d two large amplitude stable spatial profiles are illustrated. The situation depicted in fig. 6e corresponds to the length $L = 0.168 > 2 \times L_1^*$; two branches of solution corresponding to the wave number equal to two bifurcate. As can be seen from the figure, both spatial profiles ⑭ and ⑮ are unstable. Hence from the five existing solutions just two are stable. In fig. 6f we can observe the appearance of two stable asymmetric

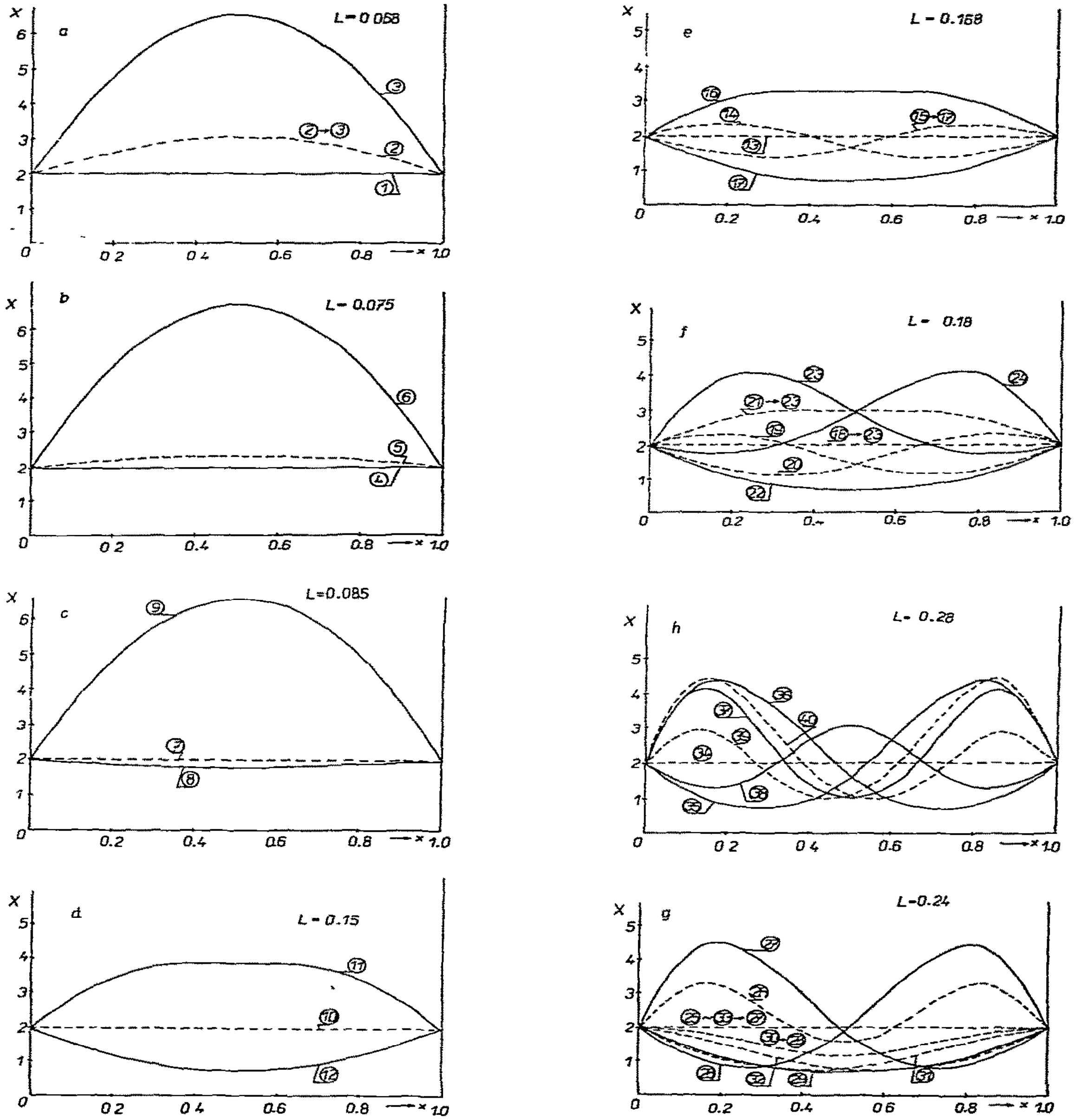

Fig. 6a–h. Spatial profiles $X(x)$ for fixed boundary conditions. Full lines – stable profiles: dashed lines – unstable profiles. 1, 2, ... position of spatial profiles in fig. 5a. ② → ③ denotes transient change of an unstable profile ② into stable profile ③.

profiles ㉓ , ㉔ belonging to the secondary bifurcation branch of solutions C. One of the profiles from the branch A bifurcating at $L = L_1^*$ is still stable (profile ㉒) another one (profile ㉓) has become unstable. Altogether seven spatial profiles can exist for this value of the length, however, only three of them are stable. In fig. 6h ($L = 0.28$) we can observe seven spatial profiles belonging to branches C, D and E. Profiles belonging to branches C and D are stable, uniform basic solution and two profiles from branch E are unstable. Hence at the same time stable profiles with characteristic wavenumbers two and three can coexist. As can be seen from the figs. 5a, b we shall obtain with increase of the characteristic length subsequently profiles with higher wavenumbers, i.e. with higher number of maxima and minima. Similarly to the case of zero flux boundary conditions, the branches of solutions bifurcating at individual multiples of the primary bifurcation lengths form closed curves; hence only a limited number of spatially nonuniform solutions with neighbouring wavenumbers will coexist for a chosen value of characteristic dimension L. Which of them will be actually realized in the system with given value of L will depend on the initial conditions, i.e. the transient history of the development of the system. The regions of attraction of the individual stable spatially nonuniform solutions can be very narrow, as it was tested in extensive numerical simulation of the full PDE (2a, b).

5. Discussion

The computed continuous dependence of the character and number of solutions on the characteristic length for the "Brussellator" reaction schema has shown, that the solutions bifurcating at individual primary bifurcation length form closed curves. Even if the number of solutions available can increase considerably with increasing length, we have shown that only a countable number of them will be stable and that for any given low value of the length we shall have only several of them with wavenumbers close together available to the system. Solutions on the branch C (cf. fig. 5a) arising through secondary bifurcation are asymmetric and also form a close curve. For the zero flux boundary conditions the schema of construction of complex spatial profiles starting from the elementary profiles gives rules for development of complex patterns with the number of choices available to the system increasing with length. The knowledge of several first closed branches of the solution is all what is required for the construction of the derived solutions. Additional spatially nonuniform solutions could arise through secondary bifurcation, as it was found in the case of fixed boundary conditions. We are currently studying rules for deciding stability of the composed solutions. The rules are closely connected with the problem of multiple bifurcations. It appears, that the methods of computation developed [19] and tested in this paper make it possible to determine effectively the continuous dependence of the spatially nonuniform solutions on chosen parameter for other models of this type. We have studied experimentally model reaction-diffusion system (Zhabotinski reaction) [21] and have arrived to the conclusion, that a knowledge of such continuous dependence of solutions on the reaction, transport and system parameters is necessary for proper interpretation of experimental results in the situation, where the values of parameters are subjected to continuous changes, uncertainties and to random errors. Comparison with similar problems solved in the area of elastic stability [22] and nonlinear hydrodynamic stability [23] shows, that combination of efficient numerical techniques with guide obtained from the bifurcation analysis can solve even more complicated stability, multiplicity and pattern formation problems, which will arise in the case of real chemical or biological data.

From the biological viewpoint, emergence of more and more complex pattern as a result of successive instabilities and the property of composing of complex patterns from elementary building blocks (elementary solutions) is similar to the gradual build up of complex morphogenetic patterns in the course of the development and deserves further study.

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