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Bifurcations of travelling waves in population taxis models

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Contents

Abstract. A penetrating analysis of the wave dynamic modes of a conceptual population system described by the 'reaction – taxis – diffusion' and 'reaction – autotaxis – cross-diffusion' polynomial models is carried out for the case of increasing degrees of the reaction and taxis (autotaxis) functions. It is shown that a 'suitable' nonlinear taxis can affect the wave front sets and generate nonmonotone waves, such as trains and pulses which represent the exact solutions of the model system. Parametric critical points whose neighborhood displays the full spectrum of possible model wave regimes are identified and a wave mode systematization in the form of bifurcation diagrams is given. This enables standard criteria of approach to 'dangerous boundaries' to be developed. As possible applications, 'pulsing density patches' in forest insect populations as well as plankton communities and some other examples are discussed.

1. Introduction

A characteristic feature of living systems is their ability to respond to changes in the environment and, in turn, to modify it to a certain extent. One of the simplest responses is movement of individuals towards the external stimulus (or away from it) known under the term of *taxis*. The ability of individuals to perform nonrandom migrations that lead to better conditions of habitat and an increase in the reproduction rate was fixed by natural selection [1, 2]. It is significant that the intensity of taxis is usually dependent on population density.

The necessity of taking taxis into account arises in the modelling of biophysical and ecological processes: development of tissues, formation of bacterium colonies, the dynamics of a plankton community, spreading of epidemics, outbreaks of populations of insect phytophages, and so forth (see, for instance, Refs [3 – 12]).

Of all the types of taxis (thermotaxis, phototaxis, etc.), one of the most important is *chemotaxis* that is directed movement of individuals towards the gradient of substance called hereinafter the *attractant*. (The opposite situation, i.e. motion of individuals away from a *repellent*, is also possible.) We shall consider the case of an attractant produced by the population individuals themselves. Apparently, chemotaxis is one of the basic mechanisms leading to the formation of stable, spatially heterogeneous distributions in the form of population 'patterns' or 'density patches' observed, for example, in populations of insects, aggregations of amoebae, plankton communities, and some others. It may be supposed that the phenomenon of chemotaxis underlies the so-called Alle effect [13], under which individuals of a sparse population assemble into 'density patches' to increase their reproduction rate [14]. Such behavior of individuals reflects the *nonmonotone* dependence of the reproduction rate on population density [15, 16] and the existence of a density magnitude at which the reproduction rate is maximum.

Typical examples of populations with an attractant are populations of animals and insects reacting to smell. In this case, the velocity of spatial spreading of the attractant may be much higher than the speed of migration of individuals. Nonetheless, the opposite situation is also interesting: for instance, the foliage and trunks of trees damaged by insects serve as attractants for forest insect phytophages; hence, in this case the attractant is immobile [15]. Another example is given by some plankton communities, in which the rate of precipitation that removes the attractant (detritus) from the

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system is essentially higher than the velocity of random migrations [17, 18].

Chemotaxis with an *immobile* attractant (or repellent) will hereinafter be called *autotaxis*.

Models of the spatial dynamics of populations with taxis are usually described by the 'growth – diffusion – convection (taxis) – cross-diffusion' equations.

After the fundamental works of Kolmogorov, Petrovskiĭ, Piskunov [19], Turing [20] and Patlak [3] the 'reaction – diffusion' equations have become major working tools in various mathematical problems of biology and biophysics [21 – 27] (see also reviews [9, 10]).

The 'reaction – cross-diffusion' type models (see, for instance, Refs [7 – 10, 17, 18, 28]) that are widely studied in biophysics are somewhat less known in ecology. Such models arise in studies of the spread of predator – prey populations (Lotka – Volterra type models), the propagation of boundaries of tree populations, and in other problems of mathematical biology [5, 8, 11, 29]; they are distinguished by substantial nonlinearity of both the reproduction rate and the intensity function of directed flows.

Notice that 'pure' mathematicians are also showing an increasing interest in such models since the corresponding equations possess a number of intriguing mathematical properties (see review [30]), some of which were used in this paper.

2. Description of models and the problem statement

This paper considers two classes of models with taxis: scalar equations (A), and systems of two equations (B).

The first class includes one-dimensional 'phenomenological' equations that describe the dynamics of a normalized population density $P(x,t)$:

$$P_t = F(P) + \left[H(P) + DP_x\right]_x , \qquad D = \text{const} , \tag{A}$$

where t is the time; x is the coordinate of a one-dimensional physical space; the function $F(P)$ sets the local kinetics of the population, while the function $H(P)$ describes the directed migration flow at the phenomenological level and is called the *taxis intensity*, and D is the diffusion coefficient that is presumed to be constant (without loss of generality, we assume $D = 1$).

Models of the second class 'explain' the generation of taxis by including an explicit description of the attractant dynamics in the framework of classical models of populations with chemotaxis (see, for instance, Refs [8, 31]):

$$\frac{\partial P}{\partial t} = F(P) + \frac{\partial}{\partial x}\left[D(P,S)\,\frac{\partial P}{\partial x} - \Phi(P,S)\,\frac{\partial S}{\partial x}\right] , \tag{1}$$

$$\frac{\partial S}{\partial t} = T(P,S) + \frac{\partial}{\partial x}\left[\mu(P,S)\,\frac{\partial S}{\partial x}\right] . \tag{2}$$

In addition to the population density $P(x,t)$, this model includes the concentration $S(x,t)$ of the substance produced (attractant). When deducing the model (1), (2) one assumes that the flow of individuals is the sum of two components, viz., the diffusion component proportional to the gradient of population density $P(x,t)$ and the directed component proportional to the gradient of attractant concentration $S(x,t)$, with the coefficients of diffusion $D(P,S)$ and cross-diffusion $\Phi(P,S)$, respectively. The local attractant's kinetics are described by the function $T(P,S)$, and μ is the attractant's diffusion coefficient.

In the case of autotaxis it is natural to neglect the diffusive member in equation (2) assuming $\mu = 0$. Supposing also that the diffusion coefficient D is constant (and equal to 1), we obtain a system which presents a model of a *population with an attractant*:

$$\frac{\partial P}{\partial t} = F(P) + \frac{\partial}{\partial x}\left[\frac{\partial P}{\partial x} - \Phi(P,S)\,\frac{\partial S}{\partial x}\right] , \tag{B}$$

$$\frac{\partial S}{\partial t} = T(P,S) ,$$

and which is the second subject of analysis in the present paper.

The observed spatial distributions of density and the corresponding solutions of models are not obligatorily stationary. Automodel solutions, in particular those of 'travelling wave' type, are highly interesting. Such solutions correspond to spatially heterogeneous distributions of various types that propagate with a definite velocity (see, for instance, Refs [5, 32 – 37]).

A standard method for studying 'travelling waves' is by passage to an automodel system of ordinary differential equations. It turns out that in this case the 'taxis' and 'cross-diffusion' members do not increase the dimension of the automodel system (in contrast to the 'diffusion' ones).

This paper sets the following tasks:

— to describe all possible wave solutions of models (A) and (B), among other things to indicate those arising due to the occurrence of nonlinear taxis (autotaxis);

— to investigate changes in the characteristics of the travelling wave (shape, velocity) depending on the variation of model parameters.

The above-stated problems have been fully solved for several *polynomial* models of populations. Such the restriction is determined by the following causes.

As a rule, the exact form of functions, for example, the population growth rate $F(P)$ and the intensity of flow (taxis) H in equation (A) as well as the growth rate of attractant $T(P,S)$ and the cross-diffusion coefficient $\Phi(P,S)$ in model (B), are unknown. A natural approach under the conditions of incomplete knowledge of functions is their presentation in the form of *polynomials of the smallest required degree*, which correspond to a Taylor expansion in the vicinity of equilibrium values of density, i.e. of the roots of the $F(P)$ function.

This paper successively considers the cases where the model of local dynamics has one, two or three equilibrium states. According to the above-stated approach, this means that in the vicinity of the studied density values the growth function $F(P)$ is approximated by a polynomial of the first, second or third degree. Thus we come to three known models of local population dynamics — the generalized models of Malthus, Verhulst, and Alle, respectively. For a given growth function F, the consequent analysis of density waves arising in model (A), depending on the increase in the degree of a polynomial H, is carried out.

In the case of model (B), the following assumptions were made for the functions $\Phi(P,S)$ and $T(P,S)$:

(1) the multiplicativity of the functions Φ and T: $\Phi(P,S) = \Phi_1(P)\Phi_2(S)$, $T(P,S) = T_1(P)T_2(S)$;

(2) the polynomiality of the function $R(P) = \Phi_1(P)T_1(P)$ called *autotaxis intensity*;

(3) $\Phi_2(S)T_2(S) = \text{const}(\equiv 1)$.

Note. The latter assumption, which is determined essentially by technical aspects of the methods used for investigating the model, nonetheless has a clear 'asymptotic' meaning: it describes the decrease in the influence of attractant S, for its excessive growth, on the dynamics of a producer P. Dependences of this type were used, for example, in studies into the dynamics of bacterium colonies [18, 38].

Like in the case of model (A), in studies of model (B) the sequential analysis of density waves, generated depending on the increase in the degree of polynomial $R(P)$, was performed for each of the above-listed functions F of population growth.

3. Models and automodel systems

3.1 Model (A)

Solutions of equation (A), which are travelling waves propagating with the constant velocity C along the spatial coordinate x, are expressed as

$$P(x,t) = P(x+Ct) \equiv p(\xi)\,, \tag{C$_1$}$$

where $\xi = x + Ct$. The propagation of a wave from right to left along x corresponds to positive velocities C. Solutions (C$_1$) satisfy the wave (automodel) system

$$\begin{cases} p_\xi = v\,, \\ v_\xi = -F(p) + vG(p)\,, \end{cases} \tag{3}$$

in which the function $G(p)$ is expressed via the function $H(P)$ and the wave propagation velocity C:

$$G(p) = C - H_p(p) \tag{4}$$

and is a polynomial for the polynomial function of taxis intensity $H(P)$.

The form of the function $G(p)$ can be defined more exactly if $H_p(p)$ is represented as a polynomial: $H_p(p) = h_0 + h(p)$, where $h_0 = \text{const}$ is the density-independent component of the taxis intensity, while $h(p)$ represents the remaining members of the expansion. Then $G(p) = C_h - h(p)$, where $C_h = C - h_0$ is the relative velocity of the travelling wave. Thus, the polynomial $G(p)$ is parametrically dependent on the relative velocity C_h of the wave.

3.2 Model (B)

The 'travelling wave' type solutions of model (B)

$$P(x,t) = P(x+Ct) \equiv p(\xi)\,, \qquad S(x,t) = S(x+Ct) \equiv s(\xi) \tag{C$_2$}$$

satisfy the wave automodel system which, by virtue of conditions (1)–(3) in Section 2, acquires the form

$$\begin{cases} s_\xi = \dfrac{T_1(p)T_2(s)}{C}\,, \\ p_\xi = v\,, \\ v_\xi = -F(p) + vG(p)\,, \end{cases} \tag{5}$$

where

$$G(p) = C + \frac{R_p(p)}{C}\,, \qquad R(p) = \Phi_1(P)T_1(P)\,. \tag{6}$$

Notice that in the system of equations (5), an *independent* subsystem is composed by the last two equations, which is of the form of system (3) (and depends on the velocity C as on a parameter). The function $G(p)$ in this system is expressed through the autotaxis intensity $R(p)$ by formula (6) and is polynomial by virtue of assumption (2) made in Section 2.

Thus, the models of populations with 'phenomenological' taxis and autotaxis possess the following remarkable common property: investigation of the 'travelling wave' type solutions of the population density P for both model (A) and model (B) is reduced to the analysis of an *automodel system* of ordinary differential equations (3) of the same type. The difference consists solely in the interpretation of the results obtained.

Let us consider an interesting example where the local growth function $F \equiv 0$. It turns out that even here the introduction of a density-dependent taxis (autotaxis) into the model leads to nontrivial results. By single squaring, the automodel system (3) is reduced to the equation

$$p_\xi = Cp - H(p) + c_1 \equiv Q_1(p) + c_1 \tag{7}$$

for the model (A) or to the equation

$$p_\xi = Cp + \frac{R(p)}{C} + c_1 \equiv Q_2(p) + c_1 \tag{8}$$

for the model (B). In both equations the constant c_1 may be calculated from the 'initial' conditions (with respect to ξ) and further assumed to be zero for simplicity.

If the right hand parts of equations (7) and (8), i.e. functions Q_1 and Q_2, are constants or linear polynomials, then these equations have no bounded heterogeneous solutions in the straight line $-\infty < \xi < \infty$. But if Q_1, Q_2 are polynomials of the second or higher degrees, then bounded spatially heterogeneous solutions can exist. In this case, a one-parametric family of bounded monotonic wave fronts, whose maximum amplitude is equal to the distance between roots, corresponds to each pair of neighboring roots of these functions.

Coming back to the initial variables, we can affirm that even in the simplest case of zero local growth, the density-dependent taxis (autotaxis) may be the cause of the existence of *heterogeneous bounded* wave modes (see Example 1 in Section 6).

3.3 Wave solutions and phase curves

Between the bounded 'travelling wave' solutions $p(\xi)$ of the spatial model (A) [or (B)] and the phase curves of the automodel system (3) there exists a known (see, for instance, Refs [25, 32, 39]) correspondence (Figs 1–3), which we shall formulate for the most important cases.

Proposition 1. Bounded wave front $\Leftrightarrow$ heteroclinic curve, wave pulse $\Leftrightarrow$ homoclinic curve, wave train $\Leftrightarrow$ limit cycle.

By virtue of this statement, the description of all possible wave solutions of equation (A) and system (B), as well as of their modifications with variation of parameters of the functions $F(P)$ and $H(P)$ [or $R(P)$], is reduced to the analysis of phase curves and bifurcations in the automodel system depending on an 'additional' parameter that is the propagation velocity C of waves.

Assuming the functions F and G to be *polynomials*, let us consider the behavior of system (3) depending on variation of the parameters.

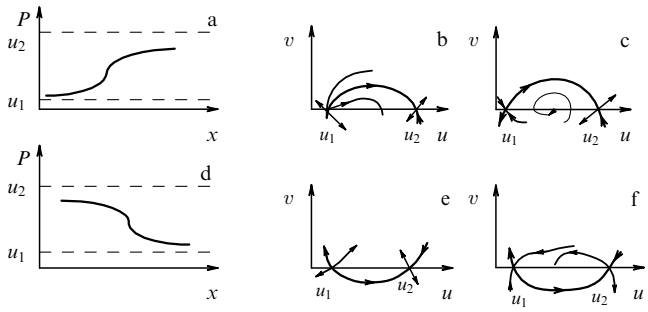

Figure 1. Correspondence between the bounded 'travelling wave' solutions of system (A) and the phase curves of its automodel system. The wave fronts (a, d) correspond to the heteroclinic phase curves: a separatrix from saddle to node, the upper (b) and lower (e) connections, respectively; a separatrix from saddle to saddle, the upper (c) and lower (f) connections, respectively.

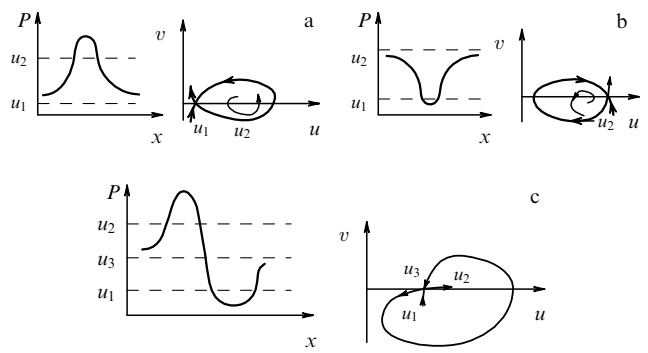

Figure 2. Same situation as in Fig. 1. The wave pulses correspond to the homoclinic phase curves; (a, b) two small and (c) one large separatrix loops, respectively.

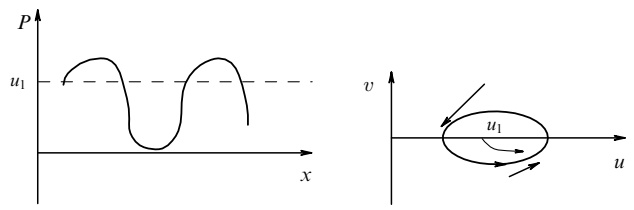

Figure 3. Same situation as in Figs 1 and 2. The wave trains correspond to the limit cycles.

Notice that the form (3) is used for the presentation of *polynomial canonical systems* of numerous known local bifurcations (see, for instance, Refs [40–46]). Such canonical systems can be written in 'abstract' variables (y_1, y_2) and with 'abstract' parameters $\boldsymbol{\delta} = (\delta_1, \ldots, \delta_n)$:

$$y_1' = y_2\,, \qquad \text{(CS)}$$
$$y_2' = V(y_1, \boldsymbol{\delta}) + y_2 W(y_1, \boldsymbol{\delta})\,.$$

Bifurcation takes place at a zero singular point of the system (CS) for zero values of parameters $\boldsymbol{\delta}$, the number of parameters n coinciding with the codimension of bifurcation. The bifurcation diagram of the system (CS) sets the partition of a vicinity of the point $(\delta_1, \ldots, \delta_n) = (0, \ldots, 0)$ into domains with topologically different phase portraits.

The application of these diagrams in combination with Proposition 1 to the analysis of wave systems (3) enables one to follow the appearance, modifications and disappearance of the wave solutions in models (A) and (B) with variation of the parameters and also upon an increase in the nonlinearity of taxis intensity.

In Section 4 below, we will discuss, for definiteness, the wave solutions of equation (A) [47, 48].

4. Wave modes of some polynomial equations (A)

For each given growth function $F(P)$ being a polynomial of the degree not exceeding 3, let us look for the taxis polynomial function $G(P)$ of the smallest degree, at which qualitatively new (compared to the *taxis-free model*) wave regimes are established in the model.

4.1 Linear growth functions (Malthusian type models)

Let us consider the growth function

$$F(P) = \alpha(P - \gamma)\,, \qquad \alpha > 0\,, \qquad \gamma > 0\,.$$

If the taxis in equation (A) is described by the cubic polynomial $H(P)$, then $G(p)$ in system (3) is a quadratic polynomial that can be represented as

$$G(p) = C_h + bp + fp^2\,, \qquad f \neq 0\,.$$

With the shift $(p - \gamma) \to p$ and rename of variables $(p, v) \to (y_1, y_2)$, the wave system (3) with the given functions F and G is reduced to the system (CS) with the functions

$$V(y_1, \delta_1) = -\alpha y_1\,, \qquad W(y_1, \delta_1) = \delta_1 + Ay_1 + fy_1^2\,, \qquad (9)$$

where $A = b + 2f\gamma$ and $\delta_1 = C_h + b\gamma + f\gamma^2 \equiv G(\gamma)$.

The system (CS), (9) depending on the single parameter δ_1 is a simple modification of the Van der Pol model (see, for instance, Refs [40, 49]). Its singular point $(y_1, y_2) = (0, 0)$ is stable for $\delta_1 < 0$ and unstable for $\delta_1 > 0$. At $\delta_1 = 0$, the first Lyapunov's value $l_1 \cong \alpha f$ is nonzero. Thus, an Andronov–Hopf bifurcation of codimension 1 occurs in the system. In this case, one limit cycle appears (Fig. 4) or disappears. Now note that the system (CS), (9) has no rough limit cycles for the polynomial G of less than second degree.

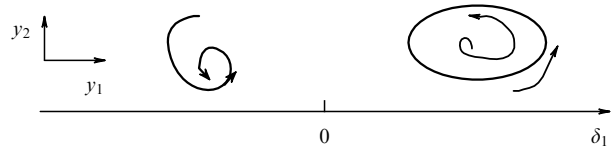

Figure 4. Bifurcation diagram of the system $y_1' = y_2$, $y_2' = -\alpha y_1 + y_2(\delta_1 + Ay_1 + fy_1^2)$, $\alpha > 0$, $f < 0$. At $\delta_1 = 0$, stability of the singular point $(y_1, y_2) = (0, 0)$ is changed with the limit cycle appearance.

According to Proposition 1, the train of the variable P in the initial model (A) corresponds to the limit cycle in the wave system (3) for given functions F and G (see Fig. 3).

The sequential analysis of solutions of the polynomial model (A) with the Malthusian birth rate F implies the following conclusions relative to the population wave dynamics described by this model.

The existence in a population of a density-dependent taxis whose intensity H is a polynomial of not less than third degree can lead to the generation of periodic bounded oscillations of population density, which spread in space with a constant velocity.

4.2 Quadratic growth functions (logistic type models)

Now let us consider the growth function

$$F(P) = \alpha + \beta P - hP^2 , \qquad h \neq 0 .$$

The logistic function $F(P) = hP(1-P)$, $h > 0$ is here a special case.

For $H \equiv 0$, model (A) with a logistic growth function coincides with the known Fisher model [11, 19, 50] (see also Ref. [8]); in this model only monotonic wave fronts can exist.

In the general case, the function F can have up to two different nonnegative roots:

$$F(P) = -h(P-u_1)(P-u_2) , \qquad h > 0 ,$$

where $0 \leqslant u_1 \leqslant u_2$. Herewith, up to two equilibria, unstable u_1 and stable u_2, exist in the local system, whereas the wave system (3) has two singular points — a topologic node $(u_1, 0)$ and a saddle $(u_2, 0)$, respectively.

Let the taxis intensity H be a quadratic polynomial in the model (A), then in the system (3) G is the linear polynomial $G(p) = C_h + bp$ $(b \neq 0)$.

Let us denote $u^* = \beta/(2h)$. Upon the shift $(p - u^*) \to p$ and rename of variables $(p, v) \to (y_1, y_2)$, the wave system (3) with given functions F and G is reduced to the system (CS) with the functions

$$V(y_1, \delta_1, \delta_2) = \delta_1 + hy_1^2 , \qquad W(y_1, \delta_1, \delta_2) = \delta_2 + by_1 , \quad (10)$$

where

$$\delta_1 = -\alpha - \beta u^* + hu^{*2} \equiv -F(u^*) ,$$
$$\delta_2 = C_h + bu^* \equiv G(u^*) .$$

The system (CS), (10) is a model system for the codimension-2 bifurcation 'double neutral equilibrium' [41] (see also Refs [40, 45]), which occurs at the zero singular point $(y_1, y_2) = (0, 0)$ for zero values of parameters δ_1, δ_2 and *arbitrary* fixed values of coefficients h, b (Fig. 5). In the system (3) with given functions F and G, the same bifurcation occurs at the double singular point $(u^*, 0)$, while the bifurcation parameters are $\delta_1 = -F(u^*)$, $\delta_2 = G(u^*)$.

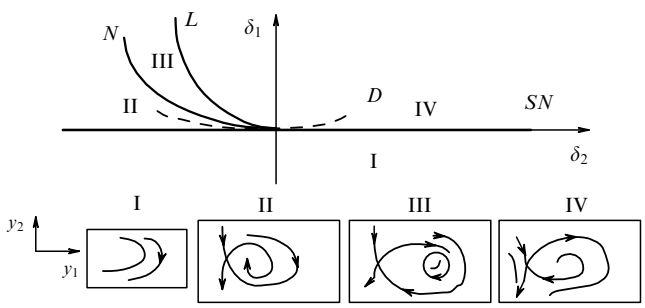

Figure 5. Bifurcation diagram of the system $y_1' = y_2$, $y_2' = \delta_1 + hy_1^2 + y_2(\delta_2 + by_1)$, $h < 0$, $b > 0$. Crossing of the SN boundary curve, two singular points appear (disappear) in the plane (y_1, y_2): a saddle and a node (stable at $\delta_2 < 0$, and unstable at $\delta_2 > 0$); the curve D is the site of (nontopologic) modification of the node into the focus; the boundary curve N corresponds to the Andronov – Hopf bifurcation, and the boundary curve L corresponds to the existence of a separatrix loop of the saddle point.

The plane of parameters (δ_1, δ_2) is divided into four domains of topologically different phase portraits. The boundaries of these domains are:

— the curve of multiplicity SN $(\delta_1 = 0)$, which corresponds to the existence of double equilibrium; the intersection of this line gives rise to the appearance of two equilibria: a saddle and a node. The latter transforms into a focus with variation of parameters δ_1, δ_2. The dashed line D in the parametric portrait corresponds to this nontopological modification;

— the curve of neutrality N, in which the Andronov – Hopf bifurcation occurs in the system, i.e. the appearance of a limit cycle from a focus;

— the line L which is matched by the homoclinic curve (separatrix loop) of the saddle. It is this curve in which the limit cycle appearing from a neutral focus in the line N disappears.

Remark. Naturally, the above events may be interpreted in the 'opposite direction': the limit cycle appears from the separatrix loop and disappears by 'sitting down' on a focus with a variation of parameters.

It follows from Proposition 1 that each point of the parametric domains II and IV corresponds to an appropriate wave front (see Fig. 1), which is monotonic in the domains enclosed by the lines SN and D; the points of domain III correspond to a wave train, i.e. spatial density oscillations in the vicinity of $P = \gamma$ (see Fig. 3); the wave pulse corresponds to the boundary L (Fig. 2a).

In order to interpret the solutions obtained in terms of population density one should consider only the nonnegative values of variable p.

Based on the analysis of solutions of the polynomial model (A), the following conclusions may be made relative to the population *wave* dynamics described by this model with the logistic function F of birth rate.

Density-dependent taxis can be a reason for inducing periodic density oscillations and a pulse wave, spreading in space with a constant velocity, if the taxis intensity H is a quadratic (or higher in order) polynomial function of density. Under linear taxis, only spatial wave fronts exist in the population, and they are analogous to Fisher's population waves.

4.3 Cubic growth functions (Alle type models)

Now let the growth function be a cubic polynomial of the general form

$$F(P) = \alpha + \beta_1 P + \beta_2 P^2 - hP^3 , \qquad h \neq 0 .$$

A special case is the function

$$F(P) = hP(P-l)(1-P) , \qquad 0 < l < 1, \ h > 0 ,$$

which is widely used in many problems, such as the investigation of the dynamics of Alle type populations, propagation of a flame front, etc. (see, for instance, Refs [11, 51, 52].

Now let us consider two variants with opposite signs of h in the function F and investigate the cases where, depending on the values of parameters, the polynomial F has from one (u_1) to three positive roots $(u_1 \leqslant u_3 \leqslant u_2)$. This means that from one to three equilibrium states can exist in the local

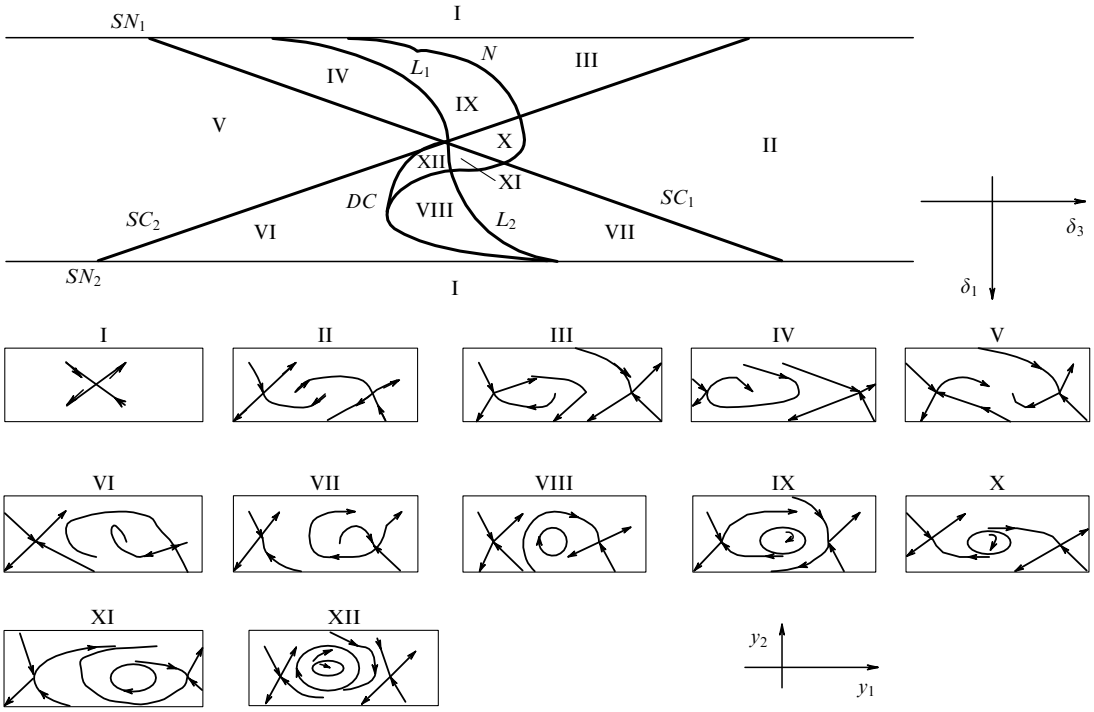

Figure 6. Cut onto the plane (δ_3, δ_1) of the bifurcation diagram of the system $y_1' = y_2$, $y_2' = \delta_1 + \delta_2 y_1 + h y_1^3 + y_2\,(\delta_3 + A y_1 - f y_1^2)$, $h > 0, f > 0$ at a fixed value of parameter $\delta_2 < 0$. Crossing of the SN_1, SN_2 boundary curves, two singular points appear (disappear), which are a saddle and a node in the plane (y_1, y_2); the appearance (disappearance) of a limit cycle around a focus corresponds to crossing the curve N; the existence of a saddle separatrix loop embracing the left (right) nonsaddle corresponds to the boundary line L_1 (L_2); at the boundary SC_1 (SC_2) the upper (lower) separatrix connection of saddles takes place; crossing of the DC curve, two limit cycles appear (disappear) in the plane (y_1, y_2).

system. For the positive coefficient h, these are, respectively, *one stable equilibrium* or *two stable equilibria* with *one unstable equilibrium* between them. For the negative coefficient h, an opposite situation persists: *one unstable equilibrium* or *two unstable equilibria* with *one stable equilibrium* between them.

Let the taxis function H in the model (A) be such that in the system (3) G is a quadratic polynomial which, like in Section 4.1, can be expressed as

$$G(p) = C_h + bp + fp^2\,, \qquad bf \neq 0\,.$$

Let us denote $u^{**} = \beta_2/(3h)$. With the shift $(p - u^{**}) \to p$ and rename of variables $(p, v) \to (y_1, y_2)$, the wave system (3) with given functions F and G is reduced to the system (CS) with the functions

$$V(y_1, \delta_1, \delta_2, \delta_3) = \delta_1 + \delta_2 y_1 + h y_1^3\,,$$
$$W(y_1, \delta_1, \delta_2, \delta_3) = \delta_3 + A y_1 + f y_1^2\,, \tag{11}$$

where

$$\delta_1 = -\alpha - \beta_1 u^{**} - \beta_2 (u^{**})^2 + h (u^{**})^3 \equiv -F(u^*)\,,$$
$$\delta_2 = -\beta_1 - 2\beta_2 u^{**} + 3h (u^{**})^2 \equiv -F_p(u^{**})\,,$$
$$\delta_3 = C_h + b u^{**} + f (u^{**})^2 \equiv G(u^{**})\,,$$
$$A = b + 2f u^{**}\,.$$

The system (CS), (11) is a canonical model system for three codimension-3 bifurcations 'triple neutral equilibrium' (a 'saddle' at $h > 0$, a 'focus' at $h < -q = A^2/8$ and an 'elliptic sector' at $-q < h < 0$; f is assumed to be small) which occur at the zero singular point $(y_1, y_2) = (0, 0)$ at $\delta_1 = \delta_2 = \delta_3 = 0$ [44].

In the wave system (3), the same bifurcations take place at the triple point $(u^{**}, 0)$ for given functions F and G, while the bifurcation parameters are $\delta_1 = -F(u^*)$, $\delta_2 = -F_p(u^{**})$ and $\delta_3 = G(u^{**})$.

Consider the cases identified as the 'saddle' and the 'focus', the bifurcation diagrams of which are shown in Figs 6 and 7, respectively [43, 44].

(1) At $h > 0$, the 'saddle' case is realized. The neighborhood of the bifurcation values of parameters is split into 12 domains of topologically different phase portraits. Depending on the values of parameters δ_1 and δ_2, the plane (y_1, y_2) contains from one [one saddle with coordinates $(u_1, 0)$] to three [two saddles and one nonsaddle with coordinates $(u_1, 0)$, $(u_3, 0)$, $(u_2, 0)$] singular points [1], with $u_1 \leqslant u_3 \leqslant u_2$.

Figure 6 shows a cut of the parametric portrait of the system onto the plane (δ_3, δ_1) for a typical value of parameter δ_2. The parametric space is split into twelve domains with topologically different phase portraits; the boundary surfaces [2] correspond to the following bifurcations:

SN_1 and SN_2: appearance (confluence) of a pair of phase points that are a saddle and a node;

N: change of the stability of the nonsaddle singular point;

DC: appearance (confluence) of a pair of limit cycles;

L_1 and L_2: homoclinic curve of each saddle point;

[1] The term 'nonsaddle' defines a node, a focus and a center, in the role of which a singular point may be found with a positive Jacobian determinant, depending on the parameters of the system; in particular, on variation of the parameters a node may transform into a focus (this nontopological bifurcation is not shown in the parametric portrait).

[2] In a planar section of the parametric portrait presented in Fig. 6, the surfaces are shown as curves, while the lines of their intersection are indicated as points.

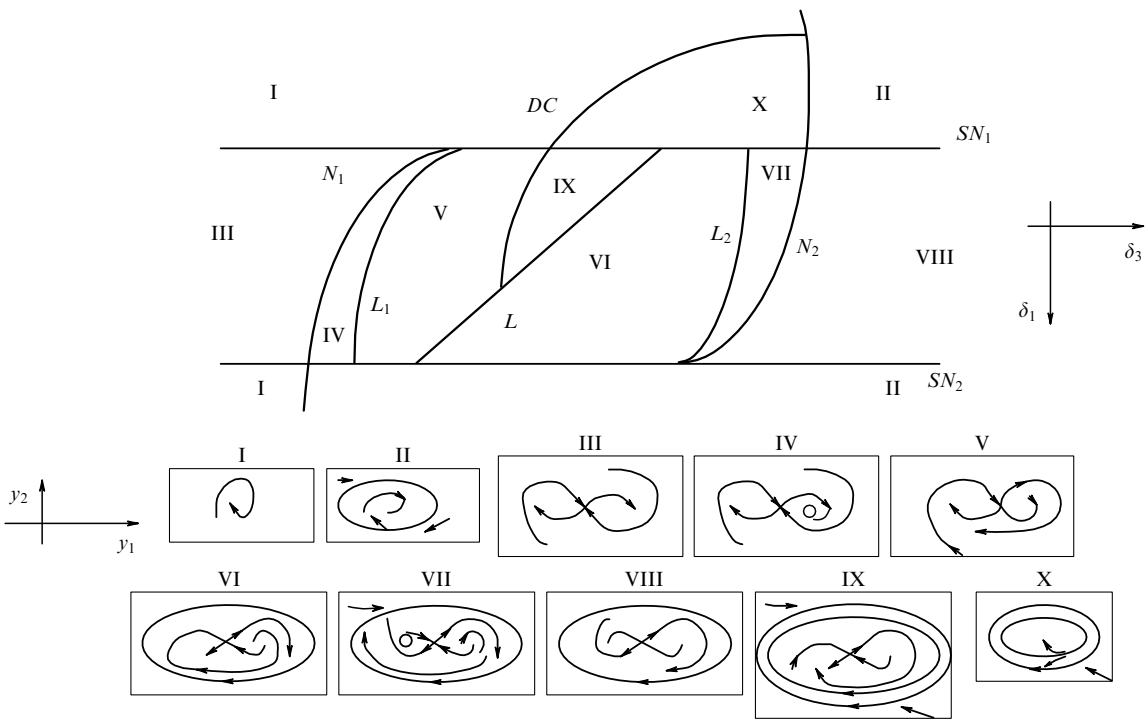

Figure 7. Cut onto the plane (δ_3, δ_1) of the bifurcation diagram of the system $y_1' = y_2$, $y_2' = \delta_1 + \delta_2 y_1 + h y_1^3 + y_2\,(\delta_3 + A y_1 - f y_1^2)$, $8h < -A^2, f > 0$ at a fixed value of parameter $\delta_2 > 0$. Crossing of the SN_1, SN_2 boundary curves, two singular points appear (disappear) in the plane (y_1, y_2); the appearance (disappearance) of two limit cycles corresponds to crossing the curve DC; the Andronov–Hopf bifurcation occurring with the right (left) focus corresponds to crossing the line N_1 (N_2); the separatrix loop of the saddle singular point which envelopes, respectively, the right focus, the left focus and both focuses corresponds to the lines L_1, L_2, and L.

SC_1 and SC_2: heteroclinic connection of two saddle points.

By applying Proposition 1, we obtain a description of the wave solutions of the model in each parametric domain and at the interdomain boundaries.

Let us look at the domains VIII–XII: the respective phase portraits contain the limit cycles that correspond to the travelling trains in the initial model. Of all the boundaries, we are particularly interested in SC_1, SC_2 that correspond to monotonic wave fronts (Fig. 1a, c and Fig. 1d, f) with the maximal possible amplitude (see, for instance, Refs [25, 52]) in equation (A); a detailed phase-parametric investigation of these solutions is presented in Section 4.4.

The sequential analysis of the solutions of the polynomial model (A) affords the following conclusions relative to the *wave* dynamics of a population with cubic birth rate F.

Such a population considered locally can exist, depending on the system parameters, either in one (stable) equilibrium state u_1 or in two stable equilibrium states u_1 and u_2 (and one unstable state u_3). In the former case of local monostability (domain I in the parametric portrait shown in Fig. 6) *no bounded spatial density waves are generated under any taxis*. In the latter case of local bistability:

— *at linear taxis intensity H, there are only wave fronts* (in domains II–VII of the parametric portrait) with amplitudes $a_3 = u_3 - u_1$, $a_2 = u_2 - u_3$. The boundaries SC_1 and SC_2 correspond to wave fronts with amplitudes $a_1 = u_2 - u_1$ (see Fig. 1);

— *at quadratic H, wave trains appear* (in parametric domains VIII, IX) that are spatial periodic oscillations around the density u_3 with an amplitude lower than a_1 (see Fig. 3), *as well as pulse waves* (Fig. 2a, b) at the parametric boundaries L_1, L_2;

— *at cubic* (*and higher*) *H, two different wave trains can appear* (domain XII in Fig. 6)[3] *with different amplitudes but the same propagation velocity*.

(2) Now let the cubic function of the local growth F have the leading coefficient $h < 0$, while the taxis intensity H is such that the inequality $h < -A^2/8$ is satisfied in the canonical system (CS), (11). Depending on the parameters δ_1, δ_3, in the plane (y_1, y_2) there are from one [nonsaddle with a coordinate $(u_1, 0)$] up to three [two nonsaddles and one saddle with coordinates $(u_1, 0)$, $(u_3, 0)$, $(u_2, 0)$] singular points (see *Note*[1]). Modifications of these singular points on variation of parameters determine the parametric portrait of the system. In the wave system a 'focus' bifurcation is realized, at which the zero point vicinity in the space of parameters $(\delta_1, \delta_2, \delta_3)$ is split into ten domains with topologically different phase portraits. A cut of the parametric portrait of the system onto the plane (δ_3, δ_1) for a 'typical' positive value of parameter δ_2 is presented in Fig. 7.

The boundary surfaces (see *Note*[2]) correspond to the following bifurcations:

SN_1 and SN_2: appearance (confluence) of a pair of phase points (a saddle and a node);

N_1 and N_2: change of the stability of each focus;

DC: appearance (confluence) of a pair of limit cycles;

L_1, L_2 and L: formation of different separatrix loops of a saddle point.

The main feature of this bifurcation diagram, compared to the preceding ones, is the existence of a 'large' saddle separatrix loop (a homoclinic curve) corresponding to the boundary L and a 'large' limit cycle enveloping all three

[3] The words 'can appear' here mean 'can appear at the values of parameters from the corresponding domains of the parametric portrait'.

equilibria (in domains VI – IX of the parametric portrait, while in domain IX there are even two such cycles, stable and unstable). The authors of Refs [44, 53] have demonstrated that the above-mentioned homoclinic curve arises solely for the quadratic (or higher) function W in the canonical system (CS), (11).

By applying Proposition 1, we arrive at a description of the wave solutions of model (A) in each parametric domain and at the interdomain boundaries. Apparently, the majority of such wave solutions will be various trains (see Fig. 3) with very broad spectrum.

The analysis of the solutions of the polynomial model (A) affords the following conclusions relative to the *wave* dynamics of a population with a given cubic birth rate function F.

A local population with this birth rate function has either one (unstable) equilibrium with density u_1 or u_2, or three equilibria with densities $u_1 \leqslant u_3 \leqslant u_2$, of which only u_3 is stable; the domain of its attraction is bounded by the extreme equilibrium densities u_1 and u_2.

By 'generating' density trains, the taxis in such a population can appreciably stabilize its dynamic regimes. Such trains are realized in this model even when there is only one equilibrium (domains II and X, the latter including two trains with different amplitudes but with the same propagation velocity along the spatial variable x). In the case of three equilibria, the population can exhibit periodic density oscillations spreading with a constant velocity. These oscillations with amplitude $a_3 < u_2 - u_3$ occur near the equilibrium u_2 (for the values of parameters from domain IV) and near the equilibrium u_1 with amplitude $a_1 < u_3 - u_1$ (domain VII). Finally, large-amplitude ($a_2 > u_2 - u_1$) trains exist in domains VI – IX.

The wave pulses correspond to the boundaries L_1, L_2 and L (Fig. 2a – c). Notice that *a large wave pulse* (*with a swing larger than* $u_2 - u_1$) *can be generated only at a cubic* (*and higher*) *taxis intensity* H [the quadratic (and higher) function G in the wave system (3)]. *For the realization of low-amplitude pulses and trains it is sufficient to have the quadratic taxis intensity* H.

Remark. The 'triple neutral equilibrium – elliptic sector' bifurcation, which is realized in the canonical system (CS), (11) at $-q < h < 0$, does not lead, in contrast to the case $h < -q$, to the appearance of new bounded wave solutions in model (A); furthermore, an interesting and important case of wave pulse corresponding to the 'large separatrix loop' disappears.

4.4 On monotonic wave solutions of equation (A)

Monotonic wave fronts play a special role among the solutions of model (A) due at least to the fact that they also exist in the 'reaction – diffusion' equations without taxis (in contrast to the 'rough' nonmonotone waves). In the automodel system (3), the wave fronts correspond to heteroclinic curves, i.e. the separatrixes of saddle equilibria (see Fig. 1).

Consider here two types of heteroclinic curves: the separatrix from a saddle to a node (Fig. 1b, e), and the saddle-to-saddle separatrix (Fig. 1c, f).

The curve of the former type (saddle-to-node separatrix) is not 'bifurcational': if such a connection is realized for some fixed values of the model parameters, there exists, generally, a similar connection for close parametric values. Solutions of this type are already realized in model (A) for the quadratic (logistic) function F considered in Section 4.2 [8, 19, 32, 39, 50].

The curve 'separatrix connection of two saddles' of the latter type accords to the nonlocal (heteroclinic) bifurcation in the wave system (3); the interdomain boundary corresponds to it in the parametric portrait of the system. For realization of this bifurcation the local birth rate function F should be at least cubic. The respective model was considered in Section 4.3, case 1 ($h > 0$). Notice that at $H \equiv 0$ such a heteroclinic curve was found in the well-known work [52] (see also Refs [25, 32, 39]).

We shall consider below both variants of heteroclinic curves and state the problem of their description for system (3) with quadratic and cubic functions F.

The solution of this problem affords an estimate of the effect of taxis on the shape of the corresponding wave front and the velocity of its spreading in models (A) and (B).

Let us present system (3) in the form of the equation

$$\frac{\mathrm{d}v}{\mathrm{d}p} = -\frac{F(p)}{v} + G(p)\,, \tag{12}$$

where the function G is linear:

$$G(p) = C_h + bp\,, \qquad b \neq 0\,. \tag{13}$$

Let u_1, u_2 be the roots of the polynomial F, one of which (e.g., u_1) corresponds to the saddle point $(u_1, 0)$. The point $(u_2, 0)$ is a node when F is quadratic, and a saddle when F is a cubic polynomial [the latter case involves the obligatory existence of the point $(u_3, 0)$ which is a node lying between two saddles: $u_1 \leqslant u_3 \leqslant u_2$].

Now look for the curve connecting the points $(u_1, 0)$ and $(u_2, 0)$ in the form of a parabola $v = v(p)$:

$$v = k(p - u_1)(p - u_2)\,. \tag{14}$$

(a) Let F be the quadratic polynomial $F(p) = \alpha + \beta p - hp^2$ presented as

$$F(P) = -h(p - u_1)(p - u_2)\,. \tag{15}$$

By differentiating (14) and substituting the result into equation (12) with consideration of Eqns (13), (15), we obtain the relation

$$k\big[2p - (u_1 + u_2)\big] = \frac{h}{k} + C_h + bp\,. \tag{16}$$

By equating the coefficients at the same degrees of p and considering that $u_1 + u_2 = \beta/h$, we arrive at

$$k = \frac{b}{2}\,, \qquad C_h = -\frac{h}{k} - k(u_1 + u_2) \equiv -\frac{2h}{b} - \frac{\beta b}{2h}\,. \tag{17}$$

Relations (14), (17) set the equation of the heteroclinic curve of the system (3), (13), (15); in accordance with (C_1) they give the exact wave solution of the system (A), (13), (15) together with the relative propagation velocity C_h of the corresponding wave front along the spatial variable x. As noted above, this wave is 'one of the many' that exist on variation of the parameter β. Thus, formulas (17) afford an estimate of the characteristics of the whole *family* of wave fronts that contains wave (14) as well.

Now note that a special case of the solution of Eqns (14), (17) was found by Murray [8] for the pure logistic local birth rate: $F(p) = p(1 - p)$ and the function $G(p) = bp$.

(b) Let F be the cubic polynomial

$$F(p) = \alpha + \beta_1 p + \beta_2 p^2 - hp^3 , \qquad h > 0 ,$$

having the roots $u_1 \leqslant u_3 \leqslant u_2$ and presented in the form

$$F(p) = -h(p - u_1)(p - u_2)(p - u_3) . \tag{18}$$

We will look for the separatrix connecting the saddles $(u_1, 0)$, $(u_2, 0)$ in the form of curve (14). By analogy with the above-stated, we obtain the system for finding k and C_h:

$$2k^2 - bk - h = 0 , \qquad k^2(u_1 + u_2) + kC_h - hu_3 = 0 . \tag{19}$$

Since the roots u_1, u_2, u_3 of the polynomial $F(p)$ are linked by the relation

$$u_1 + u_2 + u_3 = \frac{\beta_2}{h} ,$$

we obtain the system

$$\begin{cases} k^{\pm} = \dfrac{b \pm \sqrt{b^2 + 8h}}{4} , & (20) \\ C_h = \dfrac{hu_3}{k^{\pm}} - k^{\pm}\left(\dfrac{\beta_2}{h} - u_3\right) , & (21) \\ \alpha + \beta_1 u_3 + \beta_2 u_3^2 - hu_3^3 = 0 , & (22) \end{cases}$$

where the coefficient k^+ corresponds to the case $v < 0$, i.e. to the lower connection of saddles in the phase portrait (Fig. 1f), whereas k^- corresponds to the case of $v > 0$ (the upper connection, Fig. 1c).

The system (14), (20)–(22) fully defines the sought heteroclinic curve of the system (3), (13), (18), whereas with consideration of (C_1) it gives the exact solution of equation (A), (13), (18) together with the relative propagation velocity C_h of the corresponding wave front along the spatial variable x.

Let us recall that $G(p) = C - H_p(p)$. Thus, for the case $G(p) = C$ formulas (20)–(22) coincide with those derived in Ref. [52]. In addition, the system (20)–(22) allows estimation of the effect of taxis on the propagation velocity of the monotonic wave corresponding to the heteroclinic curve (14). In formulas (20), (21) the function H is 'represented' by the coefficient b. From the system (14), (20)–(22) we obtain

$$\begin{aligned} v &= K(p - u_1)(p - u_2) , \\ C_h &= C_0 + k_1 b + o(b) , \\ K &= k_0^{\pm} + \frac{b}{4} + o(b^2) . \end{aligned} \tag{23}$$

Here $k_0^{\pm} = \pm\sqrt{h/2}$ is the coefficient of the parabola which is the heteroclinic curve of the system (3) for $b = 0$; $C_0 = \pm(3u_3 h - \beta_2)/\sqrt{2h}$ is the propagation velocity of the corresponding wave in the spatial model (A), and $k_1 = -(u_3 + \beta_2/h)/4$.

Note now that for the quadratic $G(p) = C_h + bp + fp^2$ (coefficient $f \neq 0$) the heteroclinic curve (connecting saddles) is not a parabola of form (14). In this case, one succeeds in estimating the shape of the wave and the velocity of its propagation at low f values.

Remark. The proposed approach has enabled us to solve an important problem of bifurcation theory: to find the parametric surface corresponding to the nonlocal heteroclinic bifurcation, i.e. to the heteroclinic connection of two saddles, in the canonical three-parameter system (CS), in which the functions V and W have the form (11):

$$\begin{aligned} V(y_1, \delta_1, \delta_2, \delta_3) &= \delta_1 + \delta_2 y_1 + hy_1^3 , \\ W(y_1, \delta_1, \delta_2, \delta_3) &= \delta_3 + Ay_1 + fy_1^2 , \qquad h > 0 . \end{aligned}$$

For $f \neq 0$, at $\delta_1 = \delta_2 = \delta_3 = 0$, a 'triple neutral equilibrium' (a saddle case) bifurcation is realized in this system; the corresponding bifurcation diagram is shown in Fig. 6.

At the values of parameters (δ_1, δ_2), for which the function V has three roots, the system (CS) possesses the following equilibria: two saddles and one nonsaddle. For all values of coefficients A and f, the parametric space $(\delta_1, \delta_2, \delta_3)$ allows existence of the bifurcation surfaces SC_1 and SC_2, which correspond to separatrixes going from saddle to saddle (the upper and lower connections, respectively) in the phase plane [44, 53]. Using formulas (14), (20)–(22) we obtain the *exact analytical* description of these surfaces for the case $f = 0$.

The roots of the function V are linked by the relation $u_1 + u_2 + u_3 = \beta_2 = 0$, and the system (20)–(22) acquires the form

$$\begin{cases} \delta_1 + \delta_2 u_3 + hu_3^3 = 0 , \\ \delta_3 = \dfrac{hu_3}{k^{\pm}} + k^{\pm} u_3 , \\ k^{\pm} = \dfrac{A \pm \sqrt{A^2 + 8h}}{4} . \end{cases} \tag{24}$$

For fixed coefficients A and h, the *three* constituent equations of system (24) determine the interdependence of *five* 'variables' $\delta_1, \delta_2, \delta_3, u_3, k^{\pm}$. Hence, the system (24) sets the surface (more precisely, two surfaces — one for k^+ and other for k^-) in this five-dimensional space. Projections of these surfaces into the space of parameters $(\delta_1, \delta_2, \delta_3)$ are namely the sought boundaries SC_1 and SC_2, which are represented by the curves shown in Fig. 6.

4.5 Nonpolynomial models

In the general case, when the growth and taxis functions are not polynomial but are sufficiently smooth in the vicinity of the density values under consideration, the same bifurcations as those in the polynomial systems can be realized at definite values of parameters in the automodel system. Then the corresponding structure of the phase–parametric portrait is observed in a certain neighborhood of these values of parameters. (In this case the systems are said to have the same 'organizing center'.) Of course, outside this neighborhood other bifurcations can also occur in this system [54].

In order to find the 'organizing center' of a nonpolynomial model, in the vicinity of which a variety of wave regimes are realized, it is necessary to expand the functions F and H into a Taylor series *at the critical point of the local model*. The critical point is understood as the value of the variable $P = P^*$, which is transformed into the bifurcation point of the automodel system.

For a model of *Malthusian type*, this point is the *only equilibrium*, which is the root of the local kinetics function F.

For a model of *logistic type* (with the quadratic local kinetics function F), the critical point is P^* at which $F_P(P^*) = 0$. (For $F(P^*) = 0$, P^* becomes the point of double equilibrium of the model.)

For a model of *Alle's type* (with the cubic local kinetics function F), the critical point is P^* at which $F_{PP}(P^*) = 0$.

(For $F(P^*) = 0$ and $F_P(P^*) = 0$, P^* becomes the point of triple equilibrium.)

The parameter (or one of the parameters), on which the structure and behavior of waves depends, is in all cases the value of function $G(P)$ at the critical point. In the model with the logistic function F, yet another parameter is the value of function $F(P)$ at the critical point. In the Alle model there is a third important parameter — the value of the first derivative of $F_P(P)$ at the critical point.

Notice that the bifurcations considered above may prove to be insufficient for investigating the automodel system. Let, for definiteness, the reproduction rate function $F(P)$ in model (A) be a polynomial, whereas the taxis function $H(P)$ is nonpolynomial and is expanded into a Taylor series at the critical point.

Consider the case (see Section 4.1) when in the system (3) with linear function F a certain degeneration occurs: the coefficient of p^2 in the function $G(p)$ vanishes: $f = 0$. Then at the critical point of the automodel system a codimension-2 bifurcation 'zero of the first Lyapunov value' can occur (see Refs [40, 45]), and its analysis requires calculation of the coefficient of p^4 in the function $H_p(p)$.

In the system (3) with the quadratic function F (see Section 4.2), degeneration in the automodel system can lead to a codimension-3 bifurcation 'turn of tangency' [42].

Finally, degeneration in the system with the cubic growth function F (see Section 4.3) can lead to bifurcations of codimension 4 [46].

In the course of all such degenerations, the variety of possible wave solutions of the system is broadened. However, the ranges of parameter values, at which these additional regimes are established, are rather small.

5. Wave solutions of model (B) and the problem of pattern formation

As pointed out above, the phenomenological model of a population with taxis (A) and the model of a population with autotaxis (B) have wave (automodel) systems of the same type, which are satisfied by the P-component of solutions (C_1) and (C_2) ('travelling waves of population density'). In this case, the role of the taxis intensity $H(P)$ in the generation and bifurcations of these waves of model (A) corresponds to the role of the autotaxis intensity $R(P)$ of model (B). Thus, the description and bifurcational analysis of the wave solutions for model (A) are also fully valid for the P-component of model (B) up to the substitution of the function $R(P)$ for $H(P)$.

The conclusions implied by the analysis findings are as follows.

For the autotaxis of linear intensity the basic wave solutions of the considered models are monotonic wave fronts. Triggering of nonlinear autotaxis may change not only the velocity and form of monotonic solutions, i.e. the wave fronts of the model, but also, which is most important, 'give rise to' the potential existence of various rough nonmonotone waves [4].

Now note that the nonmonotone waves, trains and pulses, become particularly important because the modes corresponding to them may be interpreted as 'dynamic patterns', i.e. spatial patches of high population density, which arise and move in the environment of domains with low-population density. This phenomenon is observed for many systems. Biophysicists give much attention to various aspects of studies of the corresponding regimes [36, 37, 55, 56] (see also Refs [9, 10]).

It may be concluded that such dynamic patterns (under their conditions of stability) represent a new aspect in solving the problem of formation of pulsing 'density patches', i.e. a classical problem of mathematical ecology, which is rather important in studies of the dynamics of forest insect populations, plankton communities, etc.

Analysis of the stability of the described nonmonotone wave modes resulting from the nonlinear autotaxis is a rather complex mathematical problem going far beyond the scope of this work (its various aspects were considered, for instance, in Refs [30, 57 – 63].

It may only be suggested that the stability conditions of the wave solutions of the models should include conditions for the stability of corresponding solutions of local and automodel systems. (An interesting example is given by the Burridge – Knopoff model [64]. The authors proved by computations the existence and thus stability of wave trains with parameter values from a certain interval. They showed that two Andronov – Hopf bifurcations occur at the end points of this interval both in the local part of the model and the corresponding automodel system; such that the stable limit cycle appearing at one end point disappears at the other. Thus a stable wave train exists in the Burridge – Knopoff model with the same parameter values.)

Note, finally, that the nonmonotone spatial regimes are highly interesting even in the case of instability because they may be realized as transient modes on variation of the system parameters [28, 55, 56, 65].

6. Examples

Example 1. The dynamics of a myxobacterial population were studied in Ref. [38] using model (B) in which the functions $F(P) \equiv 0$, $\Phi_1(P) = \chi P$, $\Phi_2(S) = 1/S$, $T_1(P) = \lambda P$, $T_2(S) = S$ ($\chi > 0$). It was shown numerically that aggregation in the population is possible at $\lambda > 0$ and for certain initial distributions.

The results obtained in the present work make it possible to find the exact 'travelling wave' solutions of the model for functions of a prescribed form. To solve this problem it is sufficient to use the automodel equation (8) that here acquires the form [5]

$$p_\xi = Cp + \frac{R(p)}{C}\,, \qquad C > 0\,,$$

where $R(p) = \lambda\chi p^2$. At $\lambda < 0$, this equation has two equilibrium points $p_1 = 0$, $p_2 = -C^2/(\lambda\chi)$; the 'travelling wave' solutions are expressed as

$$P(\xi = x + Ct) = -\frac{C^2}{\lambda\chi}\left[1 - \frac{c_2}{\exp(C\xi) + c_2}\right],$$

where c_2 is an arbitrary constant. The function $P(\xi) \to p_1$ as $\xi \to -\infty$ and $P(\xi) \to p_2$ as $\xi \to \infty$, if the wave velocity $C > 0$.

[4] Let us recall that such regimes with high amplitudes correspond to wave trains and a wave pulse, which are solutions of models (A) and (B) with *cubic functions* of local growth $F(P)$ and again the *cubic* intensity of taxis $H(P)$ in model (A) and intensity of autotaxis $R(P)$ in model (B).

[5] The case of the linear function $R(p)$ is considered in Ref. [5] (see also Ref. [10]).

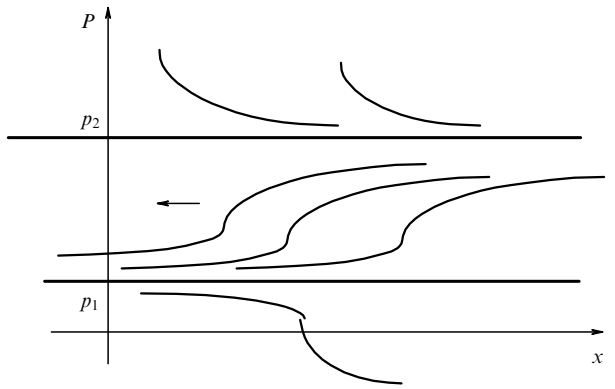

Figure 8. For $F(P) \equiv 0$, $\Phi_1(P) = \chi P$, $\Phi_2(S) = 1/S$, $T_1(P) = \lambda P$, $T_2(S) = S$ ($\chi > 0$, $\lambda < 0$), model (B) has a family of bounded monotonic 'travelling wave' solutions with the wave propagation velocity C and the 'amplitude' $|C^2/(\lambda\chi)|$.

For $\lambda < 0$, both points p_1 and p_2 lie in the first quadrant (Fig. 8), i.e. they may be interpreted in terms of population densities. Thus, at a velocity $C > 0$ the model describes waves propagating from right to left, i.e. 'reproduction waves' (the direction of wave propagation is indicated with an arrow in Fig. 8).

The stability of analogues waves was demonstrated in Ref. [66].

But if $\lambda > 0$, only the point p_1 has a 'biological' sense. Hence, at positive densities the model has no bounded waves.

Example 2. Let a Malthusian density growth occur in the local population corresponding to model (A), starting from a certain threshold $\gamma > 0$: $F(P) = a(P - \gamma)$, $a > 0$. The occurrence of random spatial migrations of individuals as well as the nonlinear taxis (of cubic intensity) lead in spatial model (A) to the appearance of bounded density oscillations close to the value $P = \gamma$ (which propagate in space x with a constant velocity). This means that the unlimited population density growth might not occur even for a Malthusian function of local growth. An analogous argument is valid for model (B) with nonlinear (cubic) autotaxis.

Example 3. Let the local population kinetics be described by a logistic type law

$$F(P) = a(P - \gamma)(1 + \gamma - P)\,, \qquad a > 0,\ \gamma > 0\,.$$

The occurrence of random migrations in spatial model (A) leads to the appearance of monotonic spatial density waves (similar to those in the Fisher model). The density-dependent taxis (of quadratic intensity) can 'generate' spatial density oscillations in the vicinity of $P = \gamma$ as well as a wave pulse. Such waves do not exist in the logistic taxis-free population.

Example 4. From the viewpoint of modelling two different ecosystems, forest insect phytophages and some plankton communities, possess similar features in their dynamics: they have a density-dependent nonmonotone reproduction rate, can give population outbreaks that spread over large territories, and are capable of forming spatial population structures. It is also known that in such systems an important role is played by taxis, and in a number of cases by autotaxis. Thus, models (A) and (B) with a cubic rate of local growth can be used in modelling the spatial dynamics of such ecosystems. Let us dwell upon model (A) with a cubic $F(P)$ (see Section 4.3), applied to modelling the dynamics of forest insects populations.

(1) At $h > 0$, the model describes the situation in which the local population can exist in two stable equilibrium states, i.e. with 'stable' (u_1) and 'metastable' (u_2) densities (and in the unstable equilibrium with the 'escaping density' u_3: $u_1 \leqslant u_3 \leqslant u_2$). Transition to metastable equilibrium is usually interpreted as a 'number outbreak' that can spread in space in the form of a so-called 'fixed outbreak' of the population [11, 12, 15]. In the model, the wave fronts with amplitudes $u_2 - u_1$ correspond to this mode. The occurrence of taxis in the phytophage population can lead to generation of nonmonotone waves in the model and to modification of the velocity and shape of monotonic waves (see Sections 4.3, 4.4), in particular, to the increase or fading of the outbreak. Additional possibilities arise here for describing the outbreak development. Let us consider the scenario of successive modifications of a periodic 'standing' wave (see Fig. 3) taken as the initial distribution, based on the analysis of the model parametric portrait (see Fig. 6). The increasing of the absolute value of the velocity C leads firstly to the appearance of waves with a slowly changing period and growing amplitude and then to a wave pulse; after this a transient mode (one of the monotonic half-waves) arises, and ultimately a stable wave front is formed. Thus, for an external observer, the reproduction wave starts with increasing spatial oscillations of population number. The outbreak's extinction can be considered in a similar manner.

The results obtained form the basis for explaining the generation of two different types of outbreak modes. The first type is characterized by a 'refuge' initial distribution over the forest territory, with biotopes favorable for the phytophage placed at distances considerably exceeding the radius of insect dispersal. The number outbreak starting with one biotope develops into a single wave front. The loss of stability and destruction of the forest cover occur in relatively small areas. In the second case, the favorable biotopes are situated rather close to each other, i.e. the initial distribution is quasi-periodic. According to the above-discussed results, it is this distribution that after passing through the stage of slow nonmonotone low-amplitude waves can develop into an outbreak covering simultaneously a large area of the forest cover [12].

Apparently, analogous scenarios are possible for the development of spatially heterogeneous density distributions in plankton communities.

(2) Model (A) with cubic functions of local kinetics F and taxis H at $h < 0$ (see Section 4.3) describes the case when the local system has a single stable equilibrium with density u_3 and its 'attraction domain' is bounded by the densities u_1 and u_2.

This version of model (A) is applied for investigating the so-called 'permanent' and 'proper' number outbreaks that are realized in populations of certain species of forest insects (the former is characteristic of Bupalus piniarius L. and some others, while the latter is typical of Dendrolimus sibiricus superans T., Ocneria monacha L. and some others (see Refs [15, 16])).

The 'permanent outbreak' is characterized by population number oscillations of very high intensity, at which the values of maximum and minimum population density are larger and smaller than the equilibrium densities u_2 and u_1, respectively.

The 'proper outbreak' consists in the following: the insect population increases to such an extent that the population density becomes larger than the maximum equilibrium u_2. As a result, the insects destroy the forest (this effect is compar-

able to that of a forest fire), then the population sharply decreases and recovers subsequently to the low stable population density u_1 to be maintained for many years. Notice that such a wave spreads over forests covering vast territories.

A model analogue of the 'proper outbreak' mode is realized in domain V of the model parametric portrait shown in Fig. 7, while an analogue of the 'permanent outbreak' is realized in domain VIII of this parametric portrait. The major boundary between these domains is the parametric surface corresponding to the homoclinic curve ('large' separatrix loop) of the automodel system. According to Proposition 1, this boundary corresponds to a wave pulse with an amplitude larger than the difference of maximal and minimal equilibrium densities: $a > u_2 - u_1$.

Thus, for a population capable of realizing both modes of outbreak reproduction [6], these regimes are neighboring in the parametric space.

We presume that the dynamic regimes and developmental scenarios of the population number outbreaks may be realized not only for forest insect populations (where they are really observed) but also for other populations (of Alle's type with nonlinear taxis) and in other complex biological systems. In this context, the revealed 'parametric' closeness of regimes with substantially different dynamic characteristics (including dangerous ones) is of high conceptual significance. Investigation of these problems still awaits continuation, which could undoubtedly make use of the structure of wave regimes derived from the analysis of models (A) and (B).

7. Conclusions

Investigation of the wave regimes of a conceptual population system with directed migration fluxes in the vicinity of local model equilibria makes it possible to consider only the polynomial functions of local growth and taxis (autotaxis).

Analysis of the 'travelling wave' solutions of the polynomial models described by the 'reaction – taxis – diffusion' and 'reaction – autotaxis – cross-diffusion' models implies the following conclusions about the role of taxis and autotaxis processes.

The existence of an 'appropriate' nonlinear taxis can change not only the velocity and shape of wave fronts but, which is most important, also lead to the establishment of different 'rough' spatially heterogeneous wave regimes. Among these, the wave modes with large amplitudes of density pulsing are of main interest (depending on their interpretation, such regimes may be regarded as either dangerous or highly productive). On the other hand, taxis can have a stabilizing effect on the dynamics of a spatially distributed population system and create, even for Malthusian local growth, appropriate conditions for the potential existence of populations in the regime of bounded spatial oscillations.

The parametric diagrams plotted from the results of this work systematize the types of dynamic regimes and make it possible to follow their substitution depending on changes of the model parameters. The relevant analysis was based on the method of normal forms of bifurcations, according to which the diagrams obtained are preserved with variation of the constituent functions of the model. This allows extension of the results of analysis of the polynomial models to certain models with nonpolynomial functions of local growth and taxis/autotaxis intensity. Of course, in addition to the above-discussed regimes, one can also expect in each such model the appearance of other spatial dynamic modes.

The problem of the analysis of stability of the revealed regimes requires further studies going far beyond the scope of this work. Notice only that all of the established wave modes, *being exact solutions of the model system*, must be realized for appropriate initial spatial distributions. It is also noteworthy that unstable regimes can likewise be realized as transient ones on variation of the system parameters.

This study has enabled us to consider the formation of spatially heterogeneous distributions in nonlinear dynamic systems as a problem of generation of 'travelling waves' in 'reaction – taxis – diffusion' type models. For biological systems, such as populations of forest insects or plankton communities, these regimes may be interpreted as dynamic spatial 'patches of high population density' in environments of low-density fields.

It is important to note that diverse possible wave regimes arise at values of parameters that correspond to the critical points of the model. This allows the use of standard methods of bifurcation theory for working out the criteria of approaches to 'dangerous boundaries'.

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[6] Populations of phytophages are known for which the first or the second type of population outbreak is realized, depending on the forest state [15].

References

1. Semevskiĭ F N, Semenov S M *Matematicheskoe Modelirovanie Ekologicheskikh Protsessov* (Mathematical Modelling of Ecological Processes) (Leningrad: Gidrometeoizdat, 1982)
2. Tinbergen N *Social Behavior in Animals, with Special Reference to Vertebrates* (London: Chapman and Hall, 1990) [Translated into Russian (Moscow: Mir, 1993)]
3. Patlak C S *Bull. Math. Biophys.* **15** 311 (1953)
4. Adler J *Science* **153** 708 (1966)
5. Keller E F, Segel L A *J. Theor. Biol.* **30** 235 (1971)
6. Keller E F, in *Chemotaxis: Its Biology and Biochemistry* (Antibiotics and Chemotherapy, Vol. 19, Ed. E Sorkin) (Basel: S Karger, 1974)
7. Monk A, Othmer H G *Philos. Trans. R. Soc. London* **323** 185 (1989)
8. Murray J D *Mathematical Biology* (Biomathematics, Vol. 19) 2nd corr. ed. (Berlin: Springer-Verlag, 1993)
9. Ivanitskiĭ G R, Medvinskiĭ A B, Tsyganov M A *Usp. Fiz. Nauk* **161** (4) 13 (1991) [*Sov. Phys. Usp.* **34** 289 (1991)]
10. Ivanitskiĭ G R, Medvinskiĭ A B, Tsyganov M A *Usp. Fiz. Nauk* **164** 1041 (1994) [*Phys. Usp.* **37** 961 (1994)]
11. Svirezhev Yu M *Nelineĭnye Volny, Dissipativnye Struktury i Katastrofy v Ekologii* (Nonlinear Waves, Dissipative Structures and Catastrophes in Ecology) (Moscow: Nauka, 1987)
12. Berezovskaya F S et al. *Dokl. Akad. Nauk* (Russia) **365** (3) 1 (1999)
13. Alle W C *Animal Aggregation: A Study in General Sociology* (Chicago: Chicago Press, 1931)
14. Gorban' A N et al., in *Problemy Ekologicheskogo Monitoringa i Modelirovaniya Ekosistem* Vol. 6 (Problems of Ecological Monitoring and Modelling of Ecosystems) (Leningrad: Gidrometeoizdat, 1984) p. 161
15. Isaev A S et al. *Dinamika Chislennosti Lesnykh Nasekomykh* (Dynamics of Forest Insect Populations) (Novosibirsk: Nauka, 1984)
16. Ludwig D, Jones D D, Holling C S *J. Animal Ecology* **47** 315 (1978)
17. Davis B *Probab. Th. Rel. Fields* **84** 203 (1990)
18. Othmer H G, Stevens A *SIAM J. Appl. Math.* **57** 1044 (1997)
19. Kolmogorov A N, Petrovskiĭ I G, Piskunov N S *Byull. Mosk. Gos. Univ.* **1** (6) 1 (1937)
20. Turing A M *Philos. Trans. R. Soc. London Ser. B* **237** 37 (1952)

21. Romanovskiĭ Yu M, Stepanova N S, Chernavskiĭ D S *Matematicheskoe Modelirovanie v Biofizike* (Mathematical Modelling in Biophysics) (Moscow: Nauka, 1975)
22. Jorne J *J. Theor. Biol.* **65** 133 (1977)
23. Vasil'ev V A, Romanovskiĭ Yu M, Yakhno V G *Usp. Fiz. Nauk* **128** 625 (1979) [*Sov. Phys. Usp.* **22** 615 (1979)]
24. Okubo A *Diffusion and Ecological Problems: Mathematical Models* (Biomathematics, Vol. 10) (Berlin: Springer-Verlag, 1980)
25. Krinskiĭ V I, Zhabotinskiĭ A M, in *Avtovolnovye Protsessy v Sistemakh s Diffuzieĭ* (Autowave Processes in Systems with Diffusion) (Ed. M T Grekhova et al.) (Gor'kiĭ: IPF AN SSSR, 1981) p. 6
26. Levin S A, in *Proc. Conf. on Differential Equations and Applications in Ecology, Epidemics, and Population Problems: Claremont, Calif., 1981* (Eds S N Busenberg, K L Cooke) (New York: Academic Press, 1981) p. 1
27. Aronson D G, in *Mathematical Biology and Medicine* (Eds V Capasso, E Grosso, S L Paveri-Fontana) (1985) p. 2
28. Ivanitskiĭ G R et al. *Usp. Fiz. Nauk* **168** 1221 (1998) [*Phys. Usp.* **41** 1115 (1998)]
29. Kuznetsov Yu A et al., in *Problemy Ekologicheskogo Monitoringa i Modelirovaniya Ekosistem* Vol. 14 (Problems of Ecological Monitoring and Modelling of Ecosystems) (Leningrad: Gidrometeoizdat, 1993) p. 198
30. Wei-Ming Ni *Notices* **45** 9 (1998)
31. Samarskiĭ A A, Mikhaĭlov A P *Matematicheskoe Modelirovanie* (Mathematical Modelling) (Moscow: Nauka, Fizmatlit, 1997)
32. Kopell N, Howard L N *Stud. Appl. Math.* **LII** 291 (1973)
33. Fife P, McLeod J B *Arch. Rat. Mech. Anal.* **65** 333 (1977)
34. Levin S A, Segel L A *SIAM Rev.* **27** 45 (1985)
35. Jager W, Luckhaus S *Trans. AMS* **329** 819 (1992)
36. Agladze K L et al. *Proc. R. Soc. London B: Biol. Sci.* **253** 131 (1993)
37. Tsyganov M A et al. *Dokl. Akad. Nauk* (Russia) **333** 532 (1993)
38. Stevens A *J. Biol. Sci.* **3** 1059 (1995)
39. Kopell N, Howard L N *Adv. Math.* **18** 306 (1975)
40. Arnol'd V I *Dopolnitel'nye Glavy Teorii Obyknovennykh Differentsial'nykh Uravneniĭ* (Additional Chapters to the Theory of Ordinary Differential Equations) (Moscow: Nauka, 1978)
41. Bogdanov R I, in *Tr. Seminara im. I G Petrovskogo* Vol. 2 (Transactions of I G Petrovskiĭ Seminar) (Moscow: Izd. MGU, 1976) p. 37
42. Berezovskaya F S, Khibnik A I, in *Metody Kachestvennoĭ Teorii Differentsial'nykh Uravneniĭ* (Methods of Qualitative Theory of Differential Equations) (Gor'kiĭ: Izd. GGU, 1985) p. 128
43. Bazykin A D, Kuznetsov Yu A, Khibnik A I *Portrety Bifurkatsiĭ* (Portraits of Bifurcations) (Moscow: Znanie, 1989)
44. Dumortier F, Rossarie R, Sotomayor J, in *Lect. Notes Math.* Vol. 1480 (Berlin: Springer-Verlag, 1991)
45. Kuznetsov Yu A *Elements of Applied Bifurcation Theory* (Applied Mathematics Science, Vol. 112) (New York: Springer-Verlag, 1995)
46. Khibnik A, Krauskopf B, Rousseau C *Nonlinearity* **11** 1505 (1998)
47. Berezovskaya F S, in *Matematika, Komp'yuter, Obrazovanie* Vol. 5 (Mathematics, Computer, Education) (Ed. G Yu Riznichenko) (Moscow: Progress – Traditsiya, 1998) p. 22
48. Berezovskaya F S, Karev G P *Dokl. Akad. Nauk* (Russia) **368** (3) 5 (1999)
49. Marsden J E, McCracken M *The Hopf Bifurcation and Its Applications* (New York: Springer-Verlag, 1976) [Translated into Russian (Moscow: Mir, 1980)]
50. Fisher R A *Ann. Eugenics* **7** 355 (1937)
51. Zel'dovich Ya B et al. *Matematicheskaya Teoriya Goreniya i Vzryva* (Mathematical Theory of Combustion and Explosion) (Moscow: Nauka, 1980)
52. Nagumo J, Yoshikawa S, Arimoto S *IEEE Trans. Commun. Technol.* **12** 400 (1965)
53. Dumortier F, Rousseau C *Nonlinearity* **3** 1015 (1990)
54. Molchanov A M *Nelineĭnost' v Biologii* (Nonlinearity in Biology) (Pushchino: ONTI NTsBI, 1992)
55. Keller E F, Segel L A *Theor. Biol.* **26** 399 (1970)
56. Budrene E O, Berg H C *Nature* (London) **349** 630 (1991)
57. Henry D *Geometric Theory of Semilinear Parabolic Equations* (New York: Springer-Verlag, 1981) [Translated into Russian (Moscow: Mir, 1984)]
58. Vol'pert A I, Ivanova A N, in *Avtovolnovye Protsessy v Sistemakh s Diffuzieĭ* (Autowave Processes in Systems with Diffusion) (Ed. M T Grekhova) (Gor'kiĭ: IPF AN SSSR, 1981) p. 33
59. Maini P K, Murray J D, Oster G F, in *Lecture Notes in Mathematics* Vol. 1151 (Berlin: Springer-Verlag, 1985) p. 252
60. Maginu K *J. Diff. Eq.* **139** 73 (1981)
61. Sattinger D H *Adv. Math.* **22** 312 (1976)
62. Evanse J W, Feroe J *Math. Biosci.* **37** 23 (1977)
63. Conley C C, Smoller J, in *Lecture Notes in Mathematics* Vol. 525 (Berlin: Springer-Verlag, 1976) p. 77
64. Cartwright J H E, Hermandez-Garcia E, Piro O *Phys. Rev. Lett.* **79** 527 (1997)
65. Akhromeeva T S et al. *Nestatsionarnye Struktury i Diffuzionnyĭ Khaos* (Nonstationary Structures and Diffusive Chaos) (Moscow: Nauka, 1992)
66. Gueron S, Liron N *J. Math. Biol.* **27** 595 (1989)