Math. Model. Nat. Phenom.
Vol. 8, No. 3, 2013, pp. 133–153
DOI: 10.1051/mmnp/20138309

Bifurcation Approach to Analysis of Travelling Waves in Some Taxis–Cross-Diffusion Models

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Abstract. An overview of recently obtained authors' results on traveling wave solutions of some classes of PDEs is presented. The main aim is to describe all possible travelling wave solutions of the equations. The analysis was conducted using the methods of qualitative and bifurcation analysis in order to study the phase-parameter space of the corresponding wave systems of ODEs. In the first part we analyze the wave dynamic modes of populations described by the "growth - taxis - diffusion" polynomial models. It is shown that "suitable" nonlinear taxis can affect the wave front sets and generate non-monotone 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; the wave mode systematization is given in the form of bifurcation diagrams. In the second part we study a modified version of the FitzHugh-Nagumo equations, which model the spatial propagation of neuron firing. We assume that this propagation is (at least, partially) caused by the cross-diffusion connection between the potential and recovery variables. We show that the cross-diffusion version of the model, besides giving rise to the typical fast travelling wave solution exhibited in the original "diffusion" FitzHugh-Nagumo equations, additionally gives rise to a slow traveling wave solution. We analyze all possible traveling wave solutions of the model and show that there exists a threshold of the cross-diffusion coefficient (for a given speed of propagation), which bounds the area where "normal" impulse propagation is possible. In the third part we describe all possible wave solutions for a class of PDEs with cross-diffusion, which fall in a general class of the classical Keller-Segel models describing chemotaxis. Conditions for existence of front-impulse, impulse-front, and front-front traveling wave solutions are formulated. In particular, we show that a non-isolated singular point in the ODE wave system implies existence of free-boundary fronts.

Keywords and phrases: traveling wave solutions, wave system, bifurcation diagram, taxis, cross-diffusion, Keller-Segel model, FitzHugh-Nagumo equations

Mathematics Subject Classification: 34C20, 35K57, 92C99

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

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towards the external stimulus (or away from it) known as taxis. The ability of individuals to perform nonrandom migration that lead to better conditions of habitat and an increase in the reproduction rate is a trait favored by natural selection [1, 2]. It is significant that the intensity of taxis may depend on population density. The necessity of taking taxis into account arises in the modeling of biophysical and ecological processes: development of tissues, formation of bacterium colonies, the dynamics of a plankton community, spread of epidemics, outbreaks of populations of insect phytophages, (see, for instance, [3–11]). Of all the types of taxis (thermotaxis, phototaxis, etc.), *chemotaxis* is of particular importance. It refers 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 start from the models with directed advection (taxis) to or from an *external* immobile attractant. We will consider also the models with an attractant produced by the individuals themselves; in such a case it is a *self-taxis*. Models of the spatial dynamics of populations with taxis to an immobile external attractant are usually described by the "growth – taxis – diffusion" equations, while the models with self-taxis require "growth – self-taxis – cross-diffusion" equations.

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. Typical examples of populations with an attractant are populations of animals and insects reacting to smell. For instance, the foliage and trunks of trees damaged by insects serve as attractants for forest insect phytophages. Another example is given by some plankton communities, in which the rate of precipitation that removes the attractant (detritus) from the system is essentially higher than the velocity of random migrations [10, 12].

The observed spatial distributions of density and the corresponding solutions of models are not necessarily stationary. Self-similar solutions, in particular those of "travelling wave" type, are of particular interest. Such solutions correspond to spatially heterogeneous distributions of various types that propagate with a definite velocity (see, for instance, [5–7, 13–15]). After the fundamental works of Fisher [18] , Kolmogorov, Petrovskii, and Piskunov [19] and Turing [20] the "growth–diffusion" equations have become major tools in various mathematical problems of biology and biophysics [4, 5, 10, 11, 21–24].

The "growth - cross-diffusion" type models (see, for instance, [5, 12, 25–33] and references therein) that are widely studied in biophysics and ecology possess a number of intriguing mathematical properties (see review [34]), some of which were used in this paper. A standard method for studying "travelling waves" of PDE model is by passage to a wave 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 wave system (in contrast to the "diffusion" ones).

Each travelling wave solution of the initial PDE model spread over by space (which is one-dimensional in this paper) has its counterpart as a bounded orbit of the (ODE) wave system ([5,35]), and *vice versa* (see, Fig.1 below); note that velocity of wave propagation serves as additional parameter of the wave system. Then we can apply methods of qualitative and bifurcation theories for analysis of phase and parameter space of the wave system to investigate, for which velocity there exist travelling wave solutions of the initial model, and to describe all such solutions. So, the approach, which we apply in this work, gives us the possibility to prove the existence of travelling wave solutions and to describe all possible types of such solutions and their rearrangements with respect to changes in parameters. We do not study the problem of *stability* of the obtained solutions (see, e.g., [36]), leaving aside theoretical aspects of this important problem and restricting our consideration only by computations (if any).

The goal of this work is to describe bifurcations of travelling wave solutions for some biologically motivated models with advection, which have been studied previously [37–41] and to give the description of the methods applied.

This paper sets the following tasks:

1) to describe all possible wave solutions of basic population diffusion models with Malthusian, logistic and Allee' type growth function depending on density dependent advection functions;

2) to investigate the conditions of existence of travelling spike spread by axon (in the frame of cross-diffusion version of FitzHugh model);
3) to analyze the structure of wave profiles in some chemotactic model of Keller-Segel type.

2. Models with external immobile attractant [37, 41]

2.1. Statements

Let $P(x,t)$ be a normalized population density. We consider one-dimensional "phenomenological" equation that describes the dynamics of $P(x,t)$

$$P_t = F\left(P\right) + \left(H\left(P\right) + DP_x\right)_x \ , \tag{2.1}$$

where t is the time; x is an one-dimensional 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 $D = 1$). We suppose here that function $F(P)$ is a polynomial of the first, second or third degree, i.e., the model of local dynamics

$$P_t = F\left(P\right) \tag{2.2}$$

has one, two or three equilibrium states. Thus we come to three known models of local population dynamics, the generalized models of *Malthus, logistic, and Allee'type*, respectively [42]. For a given growth function F, the consequent analysis of density waves arising in model (2.1), depending on the increase in the degree of a polynomial $H(P)$, is carried out. The main attention would be given to the smallest degree, at which qualitatively new (compared to the taxis-free model) wave regimes are established in the model.
Remark. *If $H(P)$ is a constant and $F(p)$ is a polynomial of the second or third degree than model* (2.1) *has a form of the Fisher-Kolmogorov equation* [18, 19].
Solutions of equation (2.1), which are travelling waves propagating with the constant velocity C along the spatial coordinate x, are expressed as

$$P(x,t) \equiv P(x + Ct) = p(\xi),\ C \neq 0 \tag{2.3}$$

where $\xi = x + Ct$. The propagation of a wave from right to left along x corresponds to positive velocity C. Solutions (2.3) satisfy the wave system

$$\begin{aligned} p_\xi &= v, \\ v_\xi &= -F(p) + vG(p) \end{aligned} \tag{2.4}$$

where $G(p) = C - H_p(p)$.
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 constant h_0 is the density-independent component of the taxis intensity, while $h(p)$ represents the remaining members of the expansion. Then $G(p) = C_0 - h(p)$ where $C_0 = C - h_0$ is the relative velocity of the travelling wave (2.3). Thus, a polynomial $G(p)$ is parametrically dependent on the relative velocity C_0 of the wave.
Between the bounded travelling wave solutions $p(\xi)$ of the spatial model (2.1) and the phase curves of the wave system (2.4) there exists a known (see, for instance, [5, 35]) correspondence (Figs 1 A,B,C), which we formulate for the most important cases:
Proposition 1. (i) *A wave front $p(\xi)$ of model* (2.1) *corresponds to the heteroclinic orbit of wave system* (2.4) *such that for $\xi \to \pm\infty$ it tends to different in p singular points* (*Fig.* 1A).
(ii) *A wave impulse $p(\xi)$ of model* (2.1) *corresponds to the homoclinic orbit of singular point of* (2.4) (*Fig.* 1B) .

(iii) *A wave train* $p(\xi)$ *of model* (2.1) *corresponds to the limit cycle of* (2.4) (*Fig.* 1C).
By virtue of this statement, the description of all possible wave solutions of equation (2.1), as well as of their changing with variation of parameters of the functions $F(p)$ and $H(p)$, is reduced to the analysis of phase curves and bifurcations in the wave system (2.4) depending on an additional parameter that is the propagation velocity C of waves. We will consider the behavior of system (2.4) depending on variation of the parameters.

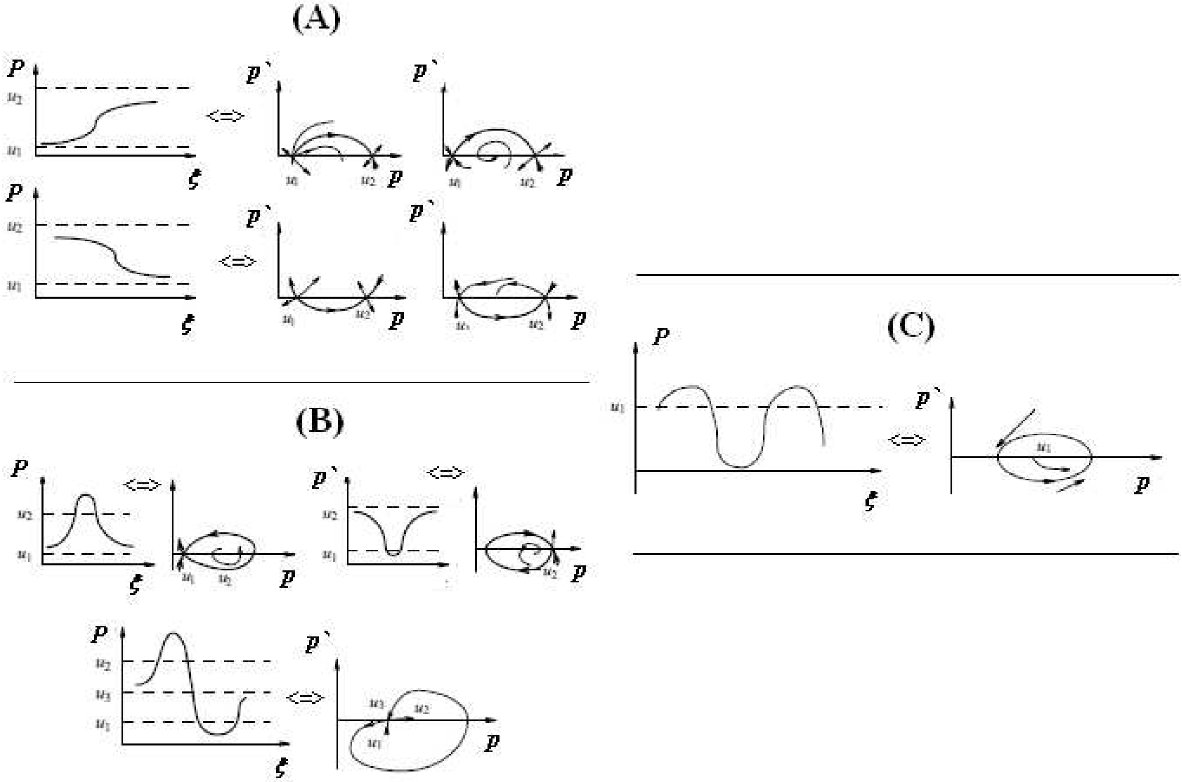


FIGURE 1. Correspondence between the bounded 'travelling wave' solutions of system (2.1) and the phase curves of its wave system. (A) The wave fronts correspond to the heteroclinic phase curves, a separatrix from a saddle to a node or to another saddle;(B) the wave impulses correspond to the homoclinic phase curves, small (upper panel) and large (lower panel) separatrix loops; (C) the wave train corresponds to the limit cycle.

Notice now that the form (2.4) is used for the presentation of canonical systems of numerous known local bifurcations (see, for instance, [43–54]). Such canonical systems can be written in "abstract" variables $(y_1, y_2)$and with "abstract" parameters $\delta = (\delta_1, \delta_2, .., \delta_n)$:

$$\begin{aligned} y_1^{'} &= y_2, \\ y_2^{'} &= V(y_1, \delta) + y_2 W(y_1, \delta_1) \end{aligned} \tag{2.5}$$

Bifurcation takes place at a zero singular point $O_y(0, 0)$ of the system (2.5) in a vicinity of the point $O_\delta(\delta_1 = 0, ..., \delta_n = 0)$; the number of parameters n coinciding with the co-dimension of bifurcation. The bifurcation diagram of the system (2.5) sets the partition of a vicinity of the point O_δ into domains with topologically different phase portraits.

The application of these diagrams in combination with Proposition 1 to the analysis of wave systems (2.4) enables one to follow the appearance, modifications and disappearance of the wave solutions in model (2.1) with variation of the parameters and also upon an increase in the power of taxis intensity.

2.2. Linear growth function (Malthusian type of models)

Let an exponential growth of "local" population begins with the value $P = \gamma$. Then

$$F(P) = f(P - \gamma), f > 0, \gamma \geq 0 \tag{2.6}$$

If the taxis in equation (2.1) is described by the cubic polynomial $H(P)$, then $G(P)$ in system (2.4) is a quadratic polynomial that can be represented as $G(p) = C_0 + bp + hp^2, h \neq 0$. With the shift $(p - \gamma) \to p$ and rename of variables $(p, v) \to (y_1, y_2)$ the wave system (2.4) with the given functions F and G is reduced to the system (2.5) with the functions

$$V(y_1, \delta_1) = -fy_1, W(y_1, \delta_1) = \delta_1 + Ay_1 + hy_1^2 \tag{2.7}$$

where $A = b + 2h\gamma, \delta_1 = G(\gamma)$.
The system (2.5), (2.7) depending on the single parameter δ_1 is a simple modification of the van- der-Pol model (see, for instance, [43–45, 53]). 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 $L_1 \cong fh$ is nonzero. Thus, the Andronov -Hopf bifurcation of co-dimension 1 [50] occurs in the system. In this case, one limit cycle appears or disappears. Now note that the system (2.5), (2.7) has no rough limit cycles for the polynomial G of less than second degree. According to Proposition 1, the train of the variable P happens in the initial model (2.1) (see Fig.1C).
Remark. Similar approach was done in [55] to demonstrate appearance/disappearance traveling train in Burridge-Knopoff model.

2.3. Quadratic growth functions (logistic type of models)

Now let us consider the growth function

$$F(P) = \alpha + \beta P - fP^2, f \neq 0 \tag{2.8}$$

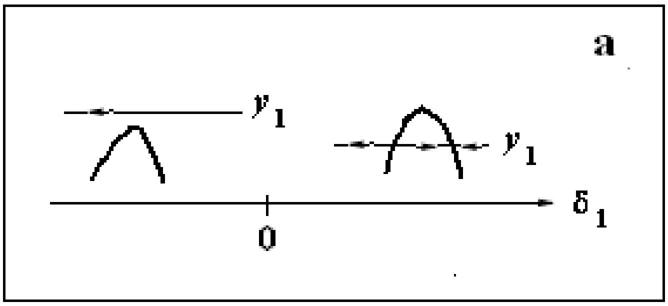
which is a generalization of the standard logistic function $F(P) = fP(1 - P), f > 0$.
For $H(P) \equiv 0$, model (2.1) with a logistic growth function coincides with the well-known Fisher model [18] (see also Ref. [5,15,16]); in this model only monotonic wave fronts exist. In the general case, the function F can have up to two different nonnegative roots: $F(P) = -f(P - u_1)(P - u_2), 0 \leq u_1 \leq u_2$ (see Fig.2a). Herewith, up to two equilibria, unstable $P = u_1$ and stable $P = u_2$, are in the local model (2.2), whereas the wave system (2.4) has two singular points, a topologic node $(u_1, 0)$ and a saddle $(u_2, 0)$, respectively. Let the taxis intensity $H(P)$ be a quadratic polynomial in the model (2.1), then in wave system (2.4) G is the linear polynomial $G(p) = C_0 + hp, h \neq 0$. Let us denote $u_* = \beta/(2f)$. Upon the shift $(p - u_*) \to p$ and rename of variables $(p, v) \to (y_1, y_2)$ the wave system (2.4) with the given functions F and G is reduced to the system (2.5) with the functions

$$V(y_1, \delta) = -\delta_1 + fy_1^2, W(y_1, \delta) = \delta_2 + hy_1 \tag{2.9}$$

where $\delta_1 = F(u_*), \delta_2 = G(u_*)$.
The system (2.5), (2.9) is a canonic model system for the co-dimension 2 bifurcation "double neutral equilibrium" [46] (see also [44,45]), which occurs at the zero singular point $(y_1, y_2) = (0, 0)$ for zero values of parameters δ_1, δ_2 and arbitrary (non-zero) fixed values of coefficients f, h (Fig. 2). δ_1, δ_2- parameter plane is divided into four domains of topologically different phase portraits. The boundaries of these domains are: the Fold curve $SN : \delta_1 = 0$, which corresponds to the existence of double equilibrium at

$(y_1, y_2)-$ plane; the intersection of this line gives rise to the appearance of two equilibria: a saddle and a node, the Hopf curve H; the intersection of this line leads the appearance of a limit cycle from a focus, the line of homoclinic bifurcation L where limit cycle disappears.

In the system (2.4) with given functions F, G, the same bifurcation occurs at the double singular point u_* while the bifurcation parameters are $\delta_1 = F(u_*), \delta_2 = G(u_*)$. It follows from Proposition 1 that each point of the parametric domains II and IV corresponds to a wave front (see Fig. 1A), the points of domain III correspond to a wave train (see Fig. 1C); the wave pulse is realizing for parameters of the boundary L (Fig. 1B).



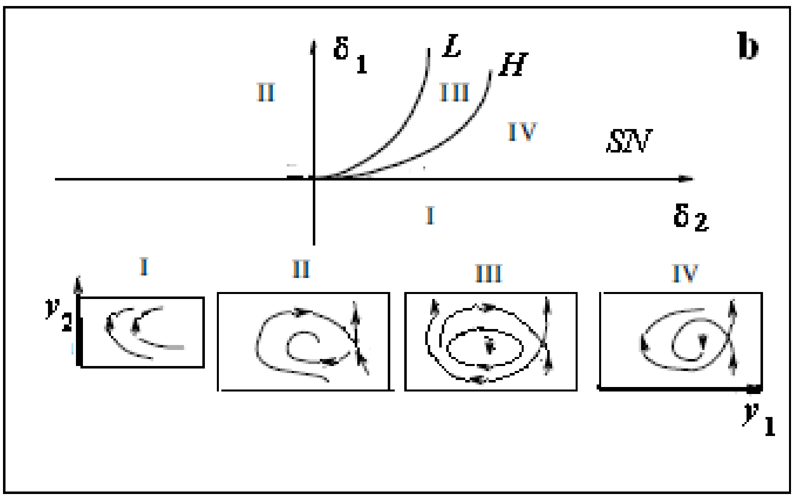


Figure 2. **(a)** δ_1-bifurcation diagram of local model (2.2) with logistic growth function$F$, two equilibria (stable and unstable for $\delta_1 > 0$) and no equilibria for $\delta_1 < 0$. **(b)** $(\delta_1, \delta_2)-$bifurcation diagram of the system CS,(2.9) for $h, f > 0$; crossing up of the boundary SN, two singular points appear in the plane (y_1, y_2): a saddle and a node (stable at $\delta_2 < 0$, and unstable at $\delta_2 > 0$); the boundary H corresponds to the Andronov-Hopf subcritical bifurcation, and the boundary L corresponds to the separatrix loop of the saddle point where unstable limit cycle disappears.

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

2.4. Cubic growth functions (Allee type models)

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

$$F(P) = \alpha + \beta_1 P + \beta_2 P^2 - fP^3, f \neq 0 \tag{2.10}$$

A special case is the function $F(P) = fP(P-l)(1-P), f > 0$, which is widely used in many problems, such as the investigation of the dynamics of Allee type populations, propagation of a flame front, etc. (see, for instance, [18, 19, 42, 56]).
Below we consider (2.1), (2.10) with positive f and analyze cases where, depending on parameters, $F(P)$ has from one, u_1, to three positive roots $u_1 \leq u_2 \leq u_3$. This means that from one to three equilibria are in the local model (2.2), one equilibrium outside of the parameter domain bounded by curves $SN_1 : \delta_1 = 2\delta_2^{3/2}/(3\sqrt{3f})$, $SN_2 : \delta_1 = -2\delta_2^{3/2}/(3\sqrt{3f})$ and three inside the domain; there are, respectively, one stable equilibrium or two stable equilibria with one unstable equilibrium between them (see Fig.3a).
Denoting $u_{**} = \beta_2/(3f)$, shifting $(p - u_{**}) \to p$ and renaming $(p, v) \to (y_1, y_2)$ we get the canonical system (2.5), where

$$V(y_1, \delta) = -\delta_1 - \delta_2 y_1 + f y_1^3, W(y_1, \delta) = \delta_3 + Ay_1 + hy_1^2, h \neq 0 \tag{2.11}$$

with $\delta_1 = F(u_{**})$, $\delta_2 = F_p u_{**})$, $\delta_3 = G(u_{**})$, $A = b + 2hu_{**}$.
For $f > 0, A \neq 0$ the system (2.5), (2.11) is a canonical model system for co-dimension 3 bifurcation "triple neutral equilibrium, a saddle case", which occur at the zero singular point $(y_1, y_2) = (0, 0)$ for zero values of parameters $\delta_1, \delta_2, \delta_3$ [42, 47, 52]. The bifurcation diagram of the system CS, (2.11) is given in Fig.3b as a (δ_1, δ_3)-slice for a fixed "typical" value δ_2. The plane (y_1, y_2) contains from one, a saddle $(u_1, 0)$, to three, two saddles $(u_1, 0)$, $(u_3, 0)$ and one non-saddle $(u_2, 0)$, singular points. A neighborhood $(\delta_1, \delta_2, \delta_3) = (0, 0, 0)$ is split into 12 domains of topologically different phase portraits. The boundaries between domains correspond to the following bifurcations: appearance (confluence) of a pair of phase singular points that are a saddle and a node, SN_1, SN_2; change of the stability of the non-saddle singular point,N; appearance (confluence) of a pair of limit cycles, C; homoclinics to each saddle point, .L_1, L_2
In the wave system (2.4), the same bifurcations take place in a vicinity of the triple singular point of the cubic birth rate $F(P)$. 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_3 (whose basins are divided by unstable state u_2).
In the former case of local monostability no bounded spatial density waves are generated under any taxis. In the latter case of local bistability applying bifurcation diagrams that have been developed in [47] we get the following description of the waves depending on taxis:
(1) at linear taxis intensity $H(P)$, there are only wave fronts (in domains II -VII of the parametric portrait). The boundaries SC_1, SC_2 correspond to wave fronts with amplitudes $a_{31} = |P_3 - P_1|$ (see Fig. 1A); (2) at quadratic $H(P)$, wave trains appear (in parametric domains VIII, IX) with an amplitude lower than a_{31} (see, Fig. 1C), and pulse waves (Fig. 1B) at the parametric boundaries L_1, L_2; (3) at cubic (and higher) $H(P)$, two different wave trains are (domain XII) with different amplitudes but the same propagation velocity.

2.5. Summary of the main results

Let us collect together the main outcomes of our analysis of model (2.1).

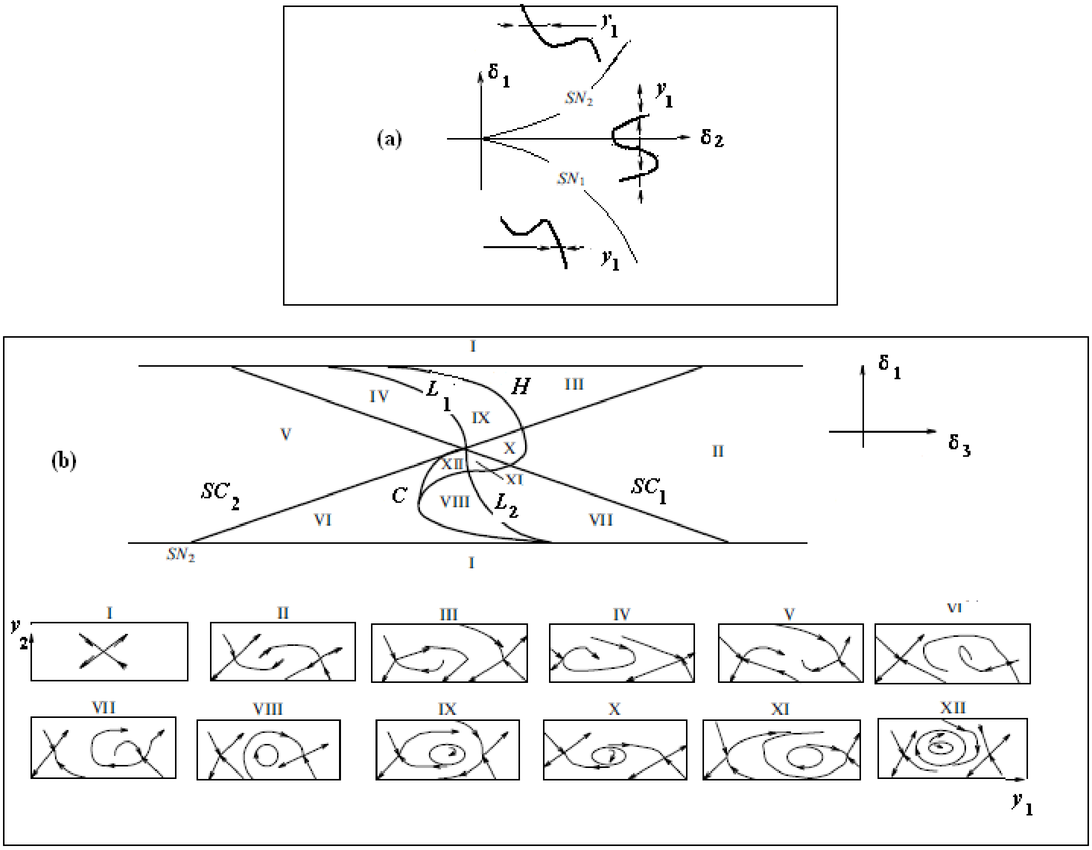


FIGURE 3. **(a)** $(\delta_2, \delta_1)-$bifurcation diagram of local model (2.2) with Allee‘type growth function F, one stable equilibrium outside of the domain bounded by parameter curves SN_1, SN_2 and two stable equilibria inside. **(b)** $(\delta_3, \delta_1)-$cut of the bifurcation diagram of the system (2.5), (2.11) for $h, f > 0$ at a fixed value of parameter δ_2. Inside domain bounded by SN_1, SN_2 the system has three singular points, two saddle and non-saddle**;** the appearance /confluence of a limit cycle around a focus corresponds to crossing the curve N; the existence of a saddle separatrix loop corresponds to the boundary lines L_1, L_2; at the boundary SC_1, SC_2 the upper/lower saddle heteroclinics happen; crossing C- curve, two limit cycles appear in the plane (y_1, y_2).

Theorem 1. *Model* (2.1) *with Malthusian growth rate and cubic advection has periodic travelling train (see Fig. 1c) ;*

Model (2.1) *with logistic growth rate and quadratic advection has the travelling fronts with amplitude* $a_{21} = |P_2 - P_1|$ *in the domains II, IV, the travelling impulse for parameters belonging to the boundary* L*, the travelling train in the domain III (see, Fig. 2b);*

Model (2.1) *with Allee‘ growth rate and general cubic advection has no waves in the parameter domain of monostability; whereas in domain of bistability, where local model* (2.2) *has equilibria* $P_1 < P_2 < P_3$ *it has the travelling fronts with amplitude* $a_{31} = |P_3 - P_1|$*for parameters belonging to the boundaries* SC_1*,* SC_2*, the travelling impulses for parameters belonging to the boundaries* L_1*,* L_2*, the travelling train* *in every parameter domain VIII-XI, and two trains in domain XII, the travelling fronts with amplitudes* $a_{21} = |P_2 - P_1|$ *or* $a_{23} = |P_2 - P_3|$ *in domains I-VII (see, Fig.3b)*

2.6. Non-polynomial 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 some values of parameters in the wave system. Then the corresponding structure of the bifurcation diagram is observed in a certain neighborhood of critical values of parameters. Certainly, other bifurcations can occur in this system [44] outside this neighborhood.

3. Waves in FitzHugh model with cross-diffusion [39]

3.1. Statements

The FitzHugh equations [21] have been developed as a caricature of the Hodgkin-Huxley equations of neuron firing [58] and to capture, qualitatively, the general properties of an excitable membrane. The original FitzHugh model [21,57] describes the time dynamics of the neuron excitable membrane potential $P(t)$, which is responsible for the rising phase of neuron firing, and recovery membrane potential $Q(t)$, which is responsible for the falling phase of the action potential (see Fig.4).

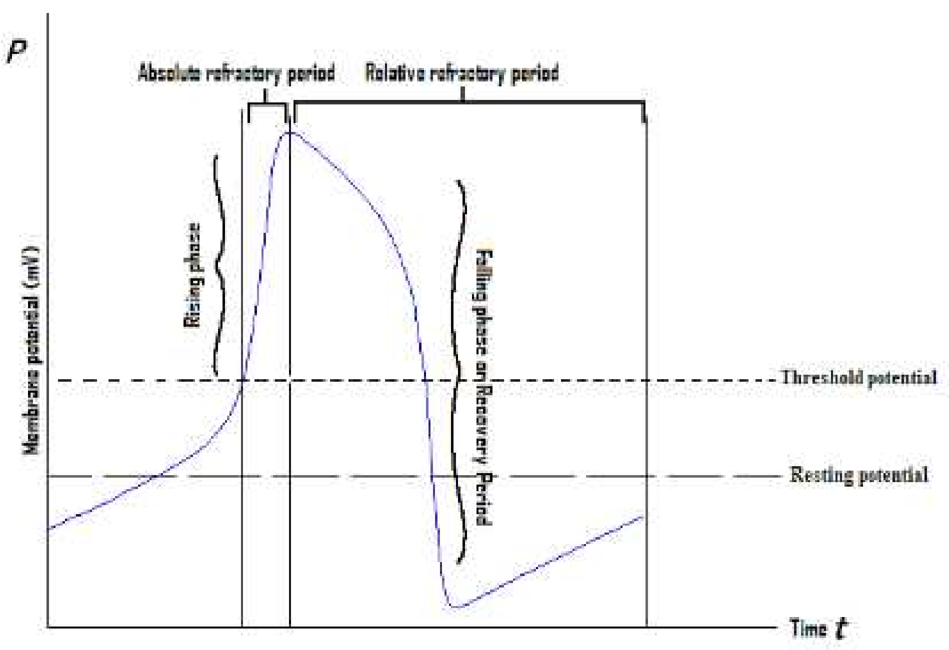


FIGURE 4. Neuron spike in the ($t$ime-Potential) plane obtained from experiments of neuron firing (see [39] for details).

In slightly modified form the FitzHugh model is presented as:

$$\begin{aligned} \varepsilon P_t &= -P^3 + P - Q \equiv F_1(P,Q), \\ Q_t &= k_1 P - Q - k_2 \equiv F_2(P,Q) \end{aligned} \tag{3.1}$$

where ε, k_1, k_2 are parameters, reflecting intrinsic characteristics of the modeling system. The system has from one (a non-saddle, i.e., a node or a spiral or center) up to three (two non-saddles and a saddle) positive equilibria $(P*, Q*)$ where $P*, Q*$ are common roots of $F_1(P,Q)$ and $F_2(P,Q)$. Thus, the model has domains of monostability and bistability, similar to the Allee'type model (2.2), (2.10) (see Fig.3a). However, dynamics of model (3.1) is much more complicated than the dynamics of local model (2.2). FitzHugh' computer analysis [21, 57] revealed that the model can have also limit cycles, namely, "small" cycles (containing a unique equilibrium inside) and "large" one (containing three equilibria inside). FitzHugh hypothesized that the "large separatrix loop" could be realized in the phase plane of system (3.1) for certain parameter values; the trajectory corresponding to this loop was considered as a model of a firing neuron.

The complete analysis of the FitzHugh model was done significantly later. It was proven in [9, 51, 60] that the principal dynamics of model (3.1) is described by the bifurcation diagram of the bifurcation "3-multiple neutral singular point with the degeneration, focus case", schematically presented in Fig.5. It is realized in a vicinity of the parameter point $M(\varepsilon = 1, k_1 = 0, k_2 = 1)$. The description of the diagram is given by the following statement [51].

Lemma 3.1. *(i) The space of parameters* (k_1, k_2, ε) *is subdivided into 21 domains of topologically different phase portraits of system* (3.1). *The cut of the complete parameter portrait to the plane* (k_1, k_2) *is topologically equivalent to the diagram presented in Fig. 5a (left) for arbitrary fixed* $0 < \varepsilon < 1$ *and to the diagram presented in Fig. 5a (right) for arbitrary fixed* $\varepsilon > 1$.

(ii) The parameter boundary surfaces correspond to the following bifurcations in system (3.1)*:*

SN_1, SN_2*: appearance/disappearance of a pair of equilibria on the phase plane;*

H_1^-, H_2^-, H_1^+, H_2^+*: change of stability of each of the non-saddle equilibria in the Andronov-Hopf supercritical/ subcritical bifurcation , respectively;*

C*: saddle-node bifurcation of a pair of limit cycles;*

L_1, L_2*: appearance/disappearance of a small limit cycle in one of two homoclinics of the saddle;*

R^+, R^-*: appearance/disappearance of a large limit cycle in one of two homoclinics of the saddle.*

Domains in Fig.-s 5 are numerated by integer numbers. Parametric portrait of system (3.1) possesses certain symmetry, so the domains, which have respective symmetric properties, were numbered by integer with index a, whereas their symmetric counterparts have no index in the parameter portraits (Fig. 5a) and corresponding phase portraits are not presented in Fig.5b.

Let us emphasize that the spike-regime (see Fig. 4) can be P-component of the trajectory $\{P(t), Q(t)\}$ of the FitzHugh model; this trajectory corresponds to the phase curve of system (3.1), which is *the large separatrix loop* containing two equilibria inside. The loop is realized with parameter values $(k_1 < 1, k_2, \varepsilon < 1)$ belonging to the boundaries R^+ of the parameter portrait (see Fig.5a).

Many works were devoted to study spatial generalizations of FitzHugh model (FitzHugh-Nagumo model [61], first of all), in particular, to the investigation of "travelling wave" solutions (see, e.g., [62–67], etc.). In this Section, modeling the spatial propagation of neuron firing along one-dimension space x we consider via a cross-diffusion (with constant coefficient D) modification of the FitzHugh model

$$\begin{aligned} \varepsilon P_t &= -P^3 + P - Q + DQ_{xx} \equiv F_1(P,Q) + DQ_{xx}, \\ Q_t &= k_1 P - Q - k_2 \equiv F_2(P,Q), \end{aligned} \tag{3.2}$$

assuming that this propagation is (at least, partially) caused by the spatial connection between the potential and recovery variables ([68], see details in [39]).

Let us explore "travelling wave" solutions of system (3.2):

$$P(x,t) \equiv P(x + Ct) = p(\xi),\ Q(x,t) \equiv Q(x + Ct) = q(\xi),\ C \neq 0$$

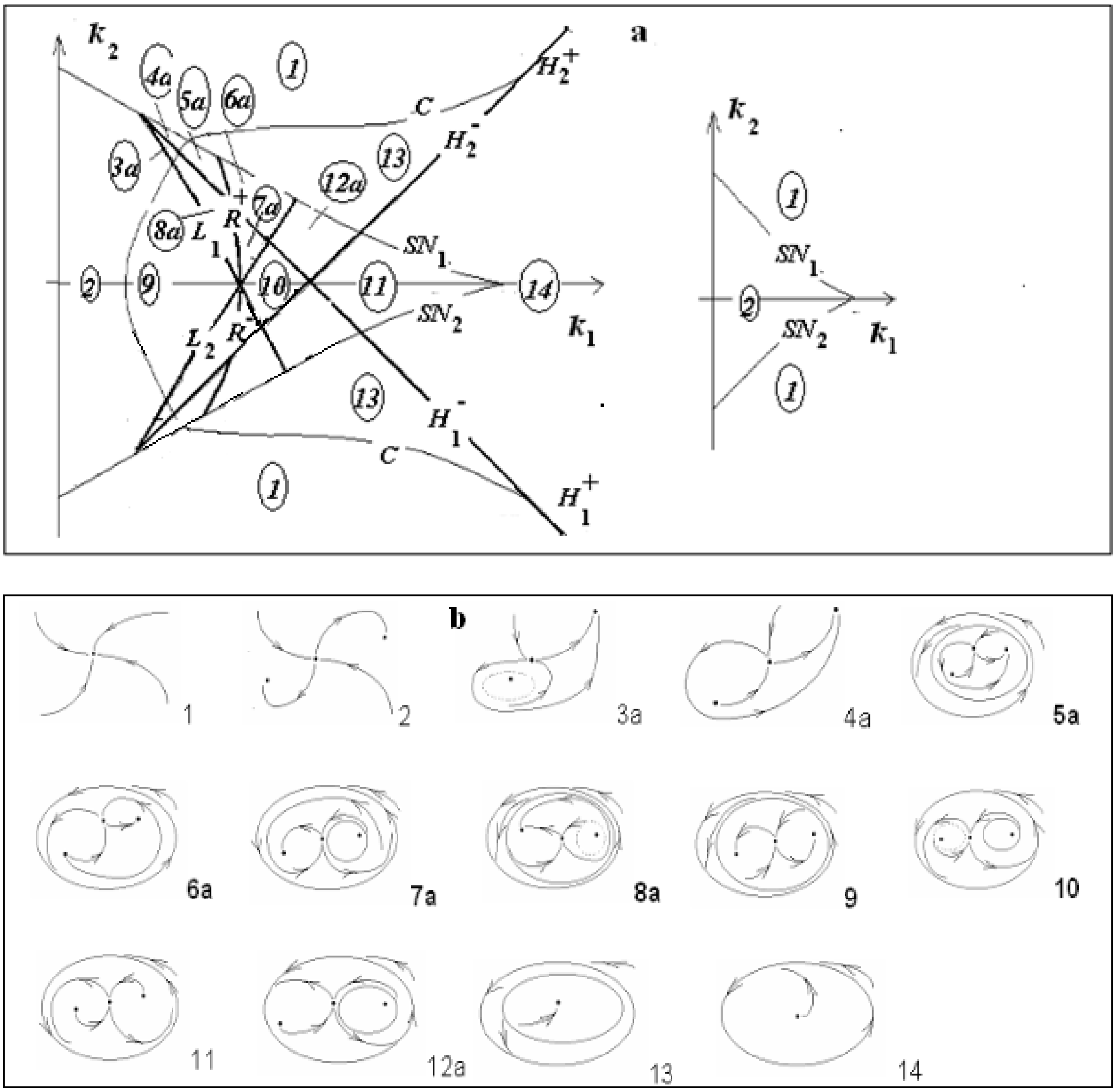


FIGURE 5. . **(a)** "typical" $(k_1, k_2)-$cuts of the bifurcation diagram of FitzHugh model (3.1) for fixed $0 < \varepsilon < 1$ (left) and for $\varepsilon > 1$ (right); **(b)** phase portraits. Inside domain bounded bySN_1, SN_2 the system has three singular points, two non-saddles and saddle**;** boundaries H_1^-, H_2^- / H_1^+, H_2^+correspond to the change of stability of each of the non-saddles in the Andronov-Hopf supercritical/ subcritical bifurcation, respectively where limit cycle appears/disappears; each of these cycles disappears/ appears at homoclinics when the parameter values intersect the boundaries L_1, L_2; at the boundaries SC_1, SC_2 a separatrix of the saddle connects it with one of the nodes and the heteroclinics appears; when the parameter values cross the boundary C, two limit cycles appear in the plane (y_1, y_2); the model has the large loop of the saddle separatrixes (a "large homoclinics") for parameter values on the boundaries R^+, R^-.

where $\xi = x + Ct$ and positive C is the velocity of the wave propagation. It is straightforward to verify that $(p(\xi), q(\xi))$ satisfy the two-dimensional wave system:

$$\begin{aligned} &(\varepsilon C^2 - Dk_1)/Cp_\xi = F_1(p,q) - DF_2(p,q)/C^2 \\ &Cq_\xi = F_2(p,q). \end{aligned} \tag{3.3}$$

If $\varepsilon C^2 \neq Dk_1$ then (3.3) can be presented in the form

$$\begin{aligned} &p_\eta = \alpha(F_1(p,q) - DF_2(p,q)/C^2), \\ &q_\eta = F_2(p,q) \end{aligned} \qquad (3.4\pm)$$

where $\eta = \xi/C$, $\alpha = C^2/(\varepsilon C^2 - Dk_1)$; sign "+" in the denotation corresponds to the case $\alpha > 0$ and the system is denoting as (3.4.+), sign "- "corresponds to the case $\alpha < 0$, and the system is denoting as (3.4.-).

Further, we study portraits of systems (3.4±) depending on "local" parameters ε, k_1, k_2 for arbitrary fixed values of constants D and C such that $\varepsilon C^2 \neq Dk_1$.

According to Proposition 1 model (3.2) possesses "big" travelling wave spike if and only if its wave system has a large separatrix loop for some parameter values.

It was shown in [39] that the wave system exhibits different portraits depending on sign of α.

Proposition 3.2. (i) *Let $C^2 > Dk_1/\varepsilon$ (i.e., $\alpha > 0$). There exist a neighborhood of the parameter point $M(\varepsilon = 1, k_1 = 0, k_2 = 1)$ in which the vector field defined by system (3.4+) has a bifurcation diagram, whose cut to the plane (k_1, k_2) is topologically equivalent to the one presented in Fig. 5. The boundaries in (k_1, k_2, ε) - parameter space (lines at the ε-cuts at Fig.5) correspond to the same bifurcations that have been mentioned in the Lemma 3.1.*

(ii) *Let $C^2 < Dk_1/\varepsilon$ (i.e., $\alpha < 0$). There exist a neighborhood of the parameter point $M(\varepsilon = 1, k_1 = 0, k_2 = 1)$ in which the vector field defined by system (3.4-) has a bifurcation diagram, whose cut to the plane (k_1, k_2) is topologically equivalent to the one presented in Fig.-s 6a (left) for arbitrary fixed positive $0 < \varepsilon < 1$ and in Fig.-s 6a (right) for arbitrary fixed $\varepsilon > 1$. The boundary surfaces in the parameter space correspond to the following bifurcations:*

SN_1, SN_2: appearance / disappearance of a pair of equilibria on the phase plane;

H: change of stability of the non-saddle equilibrium in Andronof-Hopf subcritical bifurcation;

L_1, L_2: appearance / disappearance of a small limit cycle in homoclinic bifurcations of the saddle;

SC_1, SC_2: upper and lower (respectively) heteroclinics of saddles.

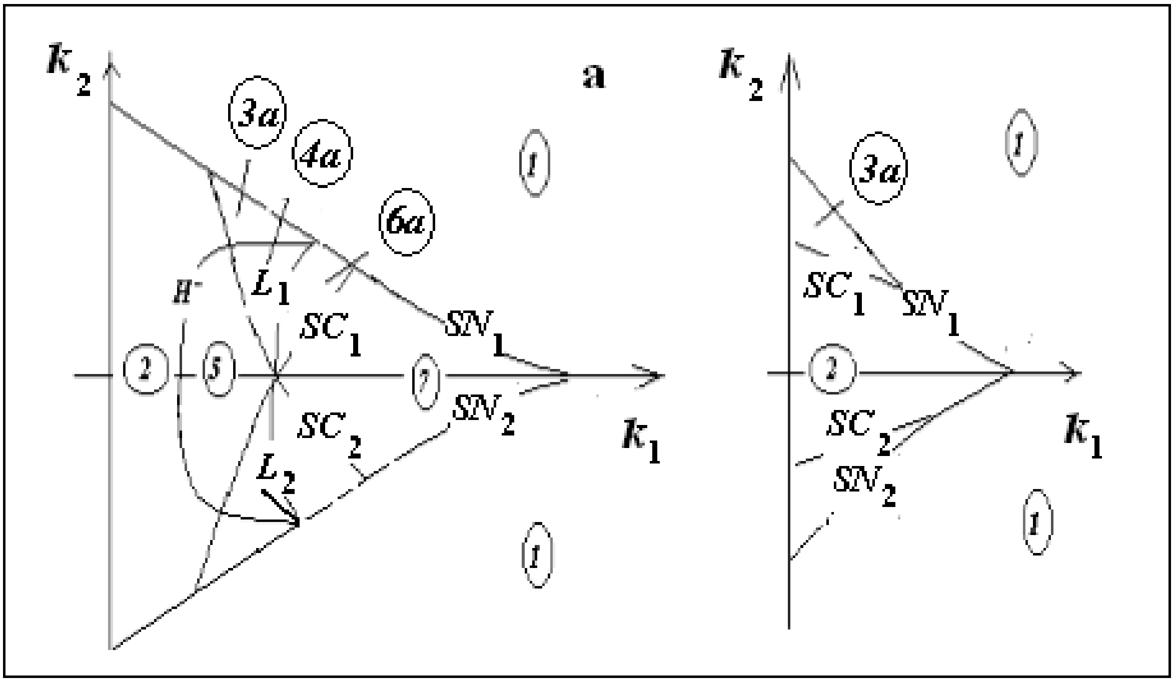
The parameter space of system (3.4-) is divided into 10 domains of topologically different phase portraits (see, Fig.6). Domains are numbered similarly to those in Fig.5, i.e., with integers and index *a*, if they have symmetric counterparts (the last ones have no numbers in the parameter portraits (Fig. 6a) and corresponding phase portraits are not presented in Fig.6b).

Remark. *The bifurcation presented in Fig.6 is known as "3-multiple neutral singular point with the degeneration, saddle case". System (2.5), (2.11) with $A = 0$ is the canonical system for two bifurcations, "focus" (with $f < 0$) and "saddle" (with $f > 0$) cases, see, Fig.5 and Fig.6, respectively; $\delta_1, \delta_2, \delta_3$ are small parameters. In the wave systems (3.4±) of FitzHugh cross-diffusion model (3.2) these bifurcations are realized close to the parameter point $M(\varepsilon = 1, k_1 = 0, k_2 = 1)$.*

Travelling wave solution of model (3.2) is called the s*low* wave if its velocity $0 < C < \sqrt{Dk_1/\varepsilon}$ and the *fast* wave if $C > \sqrt{Dk_1/\varepsilon}$.

Collecting together the statements of Lemma 3.1 and Propositions 3.1, 3.2 and taking into the consideration that only positive values of the model parameters k_1, k_2 have biophysical sense we arrive at the following description of all possible wave solutions.

Theorem 2. *Model (3.2) has the fast travelling wave solutions of the following types (see, Fig.-s 1, 5): the fronts in every domain of the portraits of Fig. 5 except the domain 1; the single train in domains 3a, 6a, 9, 10; two trains, differing in their "amplitudes", in domains 5a, 7a, 8, 12a, 14; three different trains in domains 11 and 13a ; the impulses on the boundaries L_1, L_2 and R^+.*



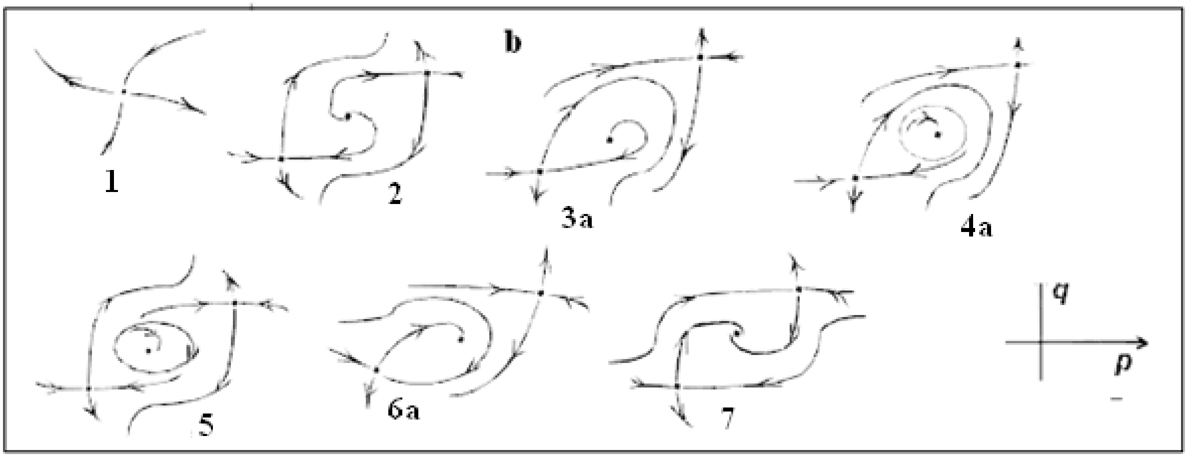


FIGURE 6. (a) $(k_1, k_2)-$cuts of the bifurcation diagram of wave system (3.4-) of FitzHugh model (3.1) for fixed $0 < \varepsilon < 1$ (left) and for $\varepsilon > 1$ (right); (b) phase portraits. Inside the domain bounded by SN_1, SN_2 the system has three singular points, two saddles and non-saddle; the boundaries SC_1, SC_2 correspond to the upper and lower heteroclinics of saddles; the boundary Hcorresponds to changing of stability of the non-saddle in Andronov-Hopf subcritical bifurcation; each of these cycles disappears at homoclimics (the boundaries L_1, L_2).

Model (3.2) *has the slow travelling wave solutions of the following types(see, Fig.-s 1,6): the fronts in every domain of the portraits in Fig.6 except the domain 1; the monotonous fronts with the maximal "amplitude" on the boundary* SC_1, SC_2*; the trains in the domains* 4, 5*; the impulses with small amplitudes on the boundaries* L_1, L_2 *of the portrait.*

3.1. Scenarios of appearance and transformations of the travelling waves

The problem of our interest is the appearance and transformations of the travelling wave solutions depending on the model parameters D and C that characterize the axon abilities for the firing propagation. (One could assume that these characteristics may change as a result of influence of certain drugs or external chemicals). Let us emphasize that the parameter portrait in Fig.5 corresponds to both the local FH-model and the wave system with a "small" cross-diffusion coefficient D while the parametric portrait in Fig.6 corresponds to the same model with "large" D. More exactly, these portraits describe the model behavior *before* and *after* the threshold $D = \varepsilon C^2/k_1$ accordingly, where C is the fixed propagation speed.
We now trace the transformation of the travelling wave solutions by varying the parameters C and D under the supposition that parameters k_1, k_2, ε have arbitrary fixed values close to the point $M*(\varepsilon* = 1, k_1* = 0, k_2* = 1)$; all the principal types of behaviors of the model are realized in a neighborhood of this point. Let the (positive) value of the speed propagation C be fixed and suppose the cross-diffusion coefficient increases. For $D = 0$ the wave system of the model coincides with the local FitzHugh model. This model demonstrates a spike (shown in Fig.5) if k_1, k_2, ε belong to the boundary R^+. The wave system describes "pseudo-waves" and, in reality, there is no firing propagation. For $D > 0$ and $C > \sqrt{Dk_1/\varepsilon}$ the model has a travelling spike spreading along the axon with the velocity C if coefficients k_1, k_2, ε belong to the boundary R^+. Note that as $C \to \infty$ the parameter $\alpha(C) \to 1/\varepsilon$, hence the wave system (3.4+) formally becomes the local system (3.2).
On the contrary, if $D > \varepsilon C^2/k_1$ then a travelling spike does not exist (see, Fig.6). The only possible travelling waves are slow "small" trains, impulses or fronts whose velocity of propagation $C < \sqrt{Dk_1/\varepsilon}$. Increasing of C leads to a "transformation" of the slow wave to the fast one, and thus to the appearance of waves similar to the spike spreading along an axon. Thus, parabola $C^2 = Dk_1/\varepsilon$ under fixed values of k_1, k_2, ε divides the domain of parameters D, C into two domains, in which the system exhibits qualitatively different behaviors. Evidently, a behavior of the model under critical values $D = \varepsilon C^2/k_1$, cannot be studied in the framework of the two-dimensional model (3.2).

4. Families of travelling impulses and fronts in chemotactic models [38, 40]

4.1. Families of travelling wave solutions

In this section we consider some models of the Keller–Segel type [6] which describe the chemotaxis, the movement of a population with the density $P(t, x)$ along the gradient of a chemical signal of density $Q(t, x)$ from an attractant produced by the population itself (see, e.g. [3, 6, 28, 29, 69]). Models are presented in the form

$$\begin{aligned} &P_t = (\mu P_x + D(P,Q)Q_x)_x, \\ &Q_t = g(P,Q). \end{aligned} \tag{4.1}$$

Here $\mu > 0$ is a constant diffusion coefficient (further, μ=1) ; t is time and x is one-dimensional space, $D(P,Q)/P$ is a chemotactic sensitivity, which can be either positive or negative, $g(P, Q)$ describes production and degradation of the chemical signal. We consider below travelling wave solutions of system (4.1):

$$P(x,t) \equiv P(x+Ct) = p(\xi),\ Q(x,t) \equiv Q(x+Ct) = q(\xi),\ C \neq 0$$

where we call to $p(\xi)$ and $q(\xi)$ as P- *profile* and Q - *profile* of travelling solution $\{p(\xi), q(\xi)\}$.
Note that such kind of problems were studied to model the movement of travelling bands of *Escherichia coli* [12–14], amoeba clustering [28, 29], insect invasion in a forest [33, 41], species migration [24], tumor encapsulation and tissue invasion [31], for a survey see, e.g. [32] and references therein.
It is straightforward to verify (see [38]) that $\{p(\xi), q(\xi)\}$ satisfy the two-dimensional wave system

$$\begin{aligned} &p_\xi = Cp + D(p,q)g(p,q)/C + \alpha, \\ &q_\xi = g(p,q). \end{aligned} \tag{4.2}$$

Here α is an arbitrary constant which arises due to the form of system (4.1); it depends on the boundary conditions for $P(x,t),\ Q(x,t)$ and can be supposed as a *new parameter* of the model together with the velocity C.
Each travelling wave solution of (4.1) has its counterpart as a *bounded* trajectory of (4.2) for some α and C. With $\xi \to \pm\infty$ such trajectories can tend to equilibria whose coordinates are $p_* = -\alpha/C,\ g(p_*, q) = 0$. For any fixed $\alpha, C > 0$ we may have or have no "suitable" equilibria, and so system (4.1) have or have no bounded solutions of travelling wave type. It is important to note, that existing of such "boundary equilibria" as well as their topological type are dependent on the value of velocity C, they can exist for one velocity and cannot exist or change their type for another velocity. Analysis of travelling waves and combinations of their profiles $\{p(\xi), q(\xi)\}$, fronts, impulses and trains, was performed in [38, 40] for some restrictions to the functions $D(p,q), g(p,q)$. A special attention was paid to the families of travelling wave solutions such that the corresponding wave system possesses an infinite number of bounded orbits with similar shapes. Note, that such a family can be observed in nature as some "dynamic patterns" composed from individual waves of this family, each of which exists for a short time and then is replaced by another wave from the family. Note that rearrangement of the families is accompaniment by appearance/disappearance of free-boundary families, containing solutions with the same wave profile of but different boundaries.
In Figures 7, 8 we present the families of travelling wave solutions such that their $(P,\ Q\ )-$profiles are fronts-impulses, fronts-fronts and impulses-impulses.

We consider, first, model (4.1) with

$$D = \frac{(P-l)(1-P)}{Q(Q-1)},\ g = -k(P-r)Q(Q-1) \tag{4.3}$$

where l, k, r are non-negative constants.
Then the wave system reads:

$$\begin{aligned} p_\xi &= Cp - k(p-l)(1-p)(p-r)/C + \alpha, \\ q_\xi &= -k(p-r)q(q-1). \end{aligned} \tag{4.4}$$

System (4.4) has up to six equilibria. For instance, if we fix the parameter values $l = 0.2,\ r = 0.4,\ k = 1,\ \alpha = -0.1,\ C = 0.3$ then the system possesses six equilibria; therefore, there are two orbit cells ensuring existence of travelling wave solutions of system (4.1).
The phase portrait of (4.4) is shown in Fig.7a. From Fig.7a it can be seen that, with the given coefficients and parameter value, there exist two qualitatively different families of travelling wave solutions of the initial cross-diffusion model. Numerical solutions of the model with functions (4.3) and the given parameter values are shown in Fig. 7b.
We consider, secondly, the model (4.1) with

$$D = \frac{\delta P}{\beta P + Q},\ g = -kP + rQ, \tag{4.5}$$

where parameters $\delta,\ k,\ r > 0,\ \beta \ge 0$.
The wave system (after changing $d\xi/(C(\beta p + q)) = d\eta$) reads:

$$\begin{aligned} p_\eta &= C^2 p(\beta p + rq) + \delta p(-kp + rq), \\ q_\eta &= (-kp + rq)(\beta p + q). \end{aligned} \tag{4.6}$$

where we put parameter $\alpha = 0$. For $r \neq 0$ the wave system (4.6) has singular point $(0,0)$possessing two elliptic sectors in its neighborhood (see Fig. 8a). The proof of existence of the elliptic sectors was conducted with the methods given in [70]. The family of homoclinics in the phase plane $(u,\ v)$ corresponds to the family of wave impulses for the system (4.1), (4.5), see Fig. 8b.

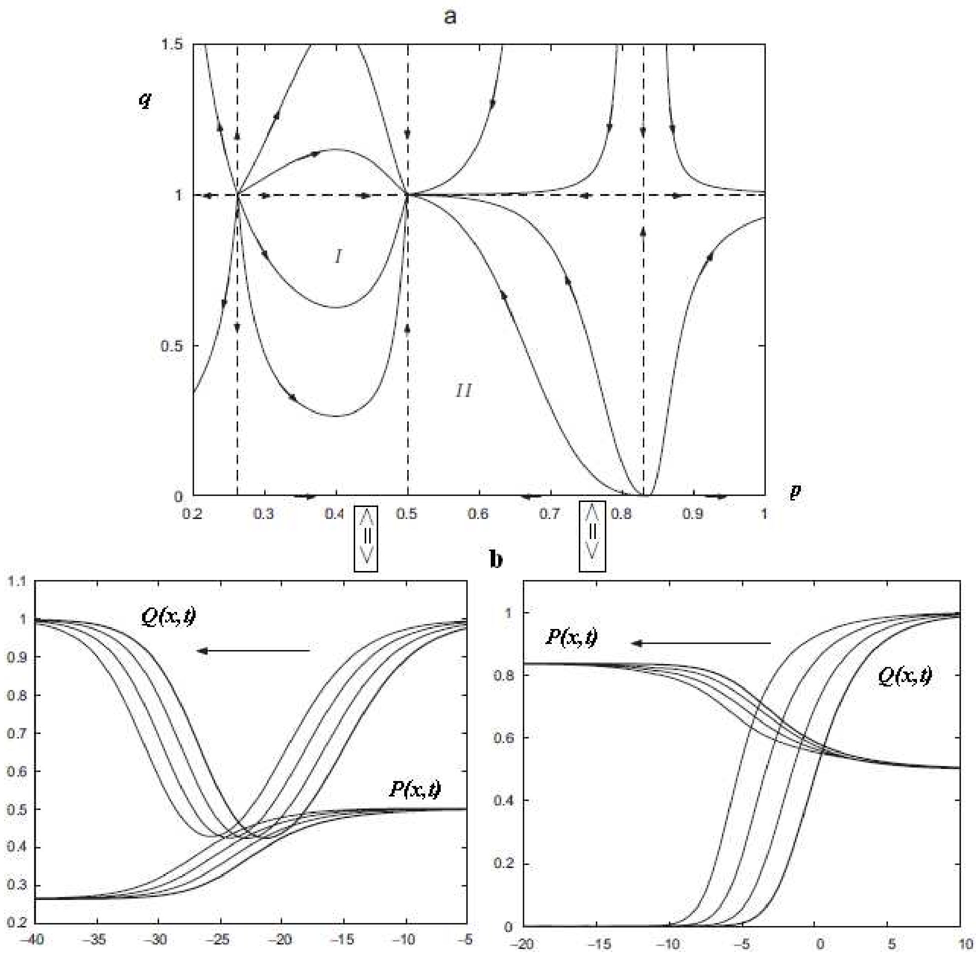


FIGURE 7. (a). The phase portrait of the system (4.4) with parameters $l = 0.2$, $r = 0.4, k = 1,\ \alpha = -0.1,\ C = 0.3$. (b) Respective numerical wave solutions of the model (4.1), (4.3), shown for the time moments $t_0 = 0$(bold curves) $< t_1 < t_2 < t_3 = 18$ in equal time intervals.

4.2. The phase plane analysis of the Keller–Segel model

Originally, the Keller–Segel model was suggested to describe movement of bands of *E. coli* which were observed to travel at a constant speed when the bacteria are placed in one end of a capillary tube containing oxygen and an energy source [6,69]. The model has the form (4.1) with $D = \delta P/Q,\quad g = -kP$, where δ, k are positive constants; the boundary conditions were defined for positive $P(x,t)$, $Q(x,t)$ by the following relations: $P(x,t) \to 0$ for $x \to \pm\infty$; $Q(x,t)$ was supposed to be bounded, say, $Q(x,t) \to 0$ for $x \to -\infty$, $Q(x,t) \to 1$ for $x \to \infty$.
The wave system (4.2) with given $D = D\,(P,Q)\,,\ g = g(P,Q)$ by the change of variable $d\eta = \frac{d\xi}{Cq}$ can be presented as

$$\begin{aligned} p_\eta &= C^2pq - \delta kp^2 + \alpha Cq, \\ q_\eta &= -kpq \end{aligned} \tag{4.7}$$

If $\alpha \neq 0$, then system (4.7) has a unique singular point $(0,0)$ and hence the model has no wave with front profile; it means that the boundary conditions of Keller-Sigel model are not fulfilled. So, we put $\alpha = 0$. In such a case system (4.7) has a line of non-isolated singular points $p = 0$, and there is also additional

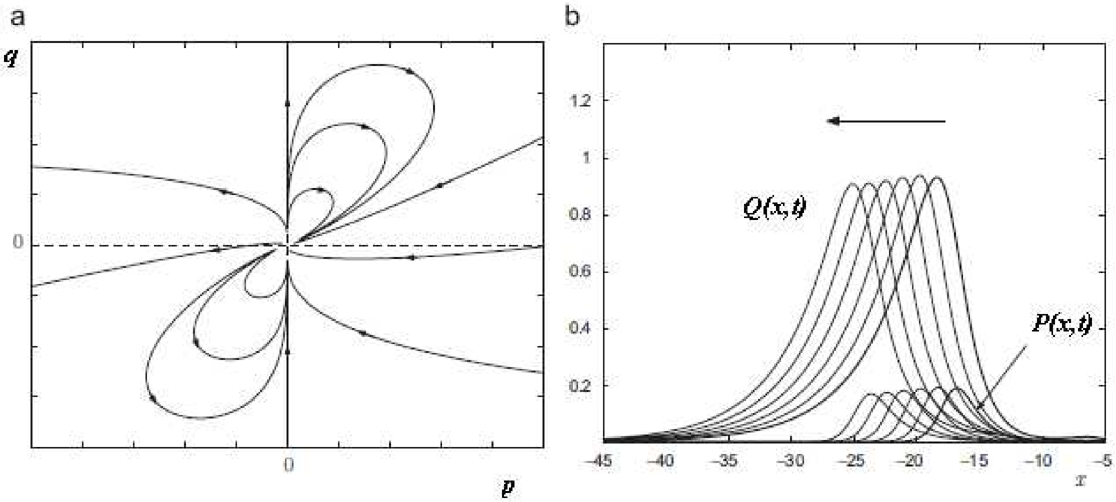


FIGURE 8. (a) The phase portrait of the system (4.6) with parameters $\delta = 2, r = 0.1, k = \beta = 1, C = 0.43$. (b) Numerical solutions of system (4.1),(4.5) with parameter values as in (a). The solutions are shown for the time moments $t_0 = 0$(bold curves) $< t_1 < t_2 < t_3 < t_4 < t_5 = 20$ in equal time intervals.

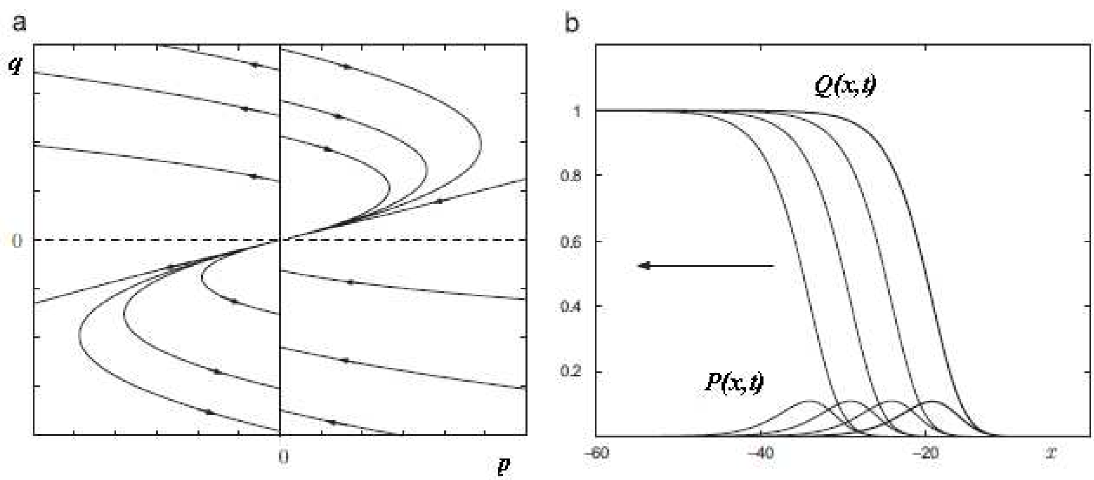


FIGURE 9. (a) The phase portrait of the system (4.8) with parameters $\delta = 4, k = 1, C = 0.5$. (b) Numerical solutions of Keller-Segel model with parameter values as in (a). The solutions are shown for the time moments $t_0 = 0$(bold curves) $< t_1 < t_2 < t_3 = 30$ in equal time intervals.

degeneracy at the point $(p = 0, q = 0)$. Applying the second transformation of the independent variable: $d\tau = pd\eta$, which does not imply appearance/ disappearance new positive wave solutions, we get the system

$$\begin{aligned} p_\tau &= C^2 q - \delta k p, \\ q_\tau &= -kq \end{aligned} \tag{4.8}$$

for which the origin is a topological node with the eigenvalues $\lambda_1 = \lambda_2 = -k$. Considering phase curves of system (4.7) with $\alpha = 0$ we state that the Keller–Segel model has a family of travelling wave solutions whose P-profile is the impulse and Q -profile is a free-boundary front (see Fig.9).
In Fig. 9b it can be seen that bacteria $P(x,t)$ seek an optimal environment: the bacteria avoid low concentrations and move preferentially toward higher concentrations of a critical substrate $Q(x,t)$. Stability of the found travelling solution was analytically proven in [13, 71].

5. Conclusions

In this paper we described all possible travelling wave solutions of some conceptual models of population dynamics$P(x,t) \equiv P(x+Ct) = p(\xi),\ Q(x,t) \equiv Q(x+Ct) = q(\xi)$, where t denotes time variable, x is the one-dimensional space variable, and $C \neq 0$ stands for the propagation velocity of the wave. Such models are presented by PDE equations of the "growth –taxis-diffusion" or "growth – self-taxis – cross-diffusion" type. Analysis of travelling wave solutions is reduced to the description of bounded trajectories (orbits) of the corresponding ODE wave system and their rearrangements when parameters vary, supposing the velocity of wave propagation C as a "new" parameter. We apply the bifurcation theory and the phase plain method for analysis of the wave systems.

Firstly, we investigate the wave regimes of taxis-diffusion modifications of conceptual one-dimensional population systems with Malthusian, logistic and Allee‘ type local growth function in the vicinity of local model equilibria. Such kind of models is widely used in modeling populations that can chemotactically react to an external immovable signal (attractant). We show that the existence of an "appropriate" nonlinear taxis can change not only the velocity and shape of wave fronts but also lead to the establishment of different "rough" spatially heterogeneous wave regimes: fronts, trains and impulses with small and large amplitudes of density. 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 non-polynomial functions of local growth and directed taxis intensity.

Secondly, we have considered conditions for arising of travelling spike with large amplitude in the cross-diffusion modification of FitzHugh model. We utilized a modified version of the FitzHugh equations to model the spatial propagation of neuron firing, assumed that for fixed values of intrinsic system parameters ε, k_1, k_2 this propagation is essentially caused by the cross-diffusion connection between the potential and recovery variables and depend on the model parameters D (the cross-diffusion coefficient) and C (the propagation speed) that characterize the axons abilities for the firing propagation. This model can be considered as a formal example of the "growth – self-taxis–cross-diffusion" type models, where the recovery membrane potential serves as an "attractant" for the neuron excitable membrane potential. We studied the wave system of the model and explored its bifurcation diagrams, shown that the diagrams are different depending on parameters of the model. We have shown that the cross-diffusion model possesses a large set of travelling wave solutions; besides giving rise to the typical "fast" travelling wave solution exhibited in the original "diffusion" FitzHugh-Nagumo equations, it also gives rise to a "slow" travelling wave solution. We proved that in the parametric space (D, C) there exists the boundary, $D = \varepsilon / k_1 C^2$, which separates the domains of existence of the fast and slow waves. The system behavior qualitatively changes with the intersection of this boundary. It means that if, by any reasons (e.g., as a result of the effect of a generic drug) the speed of transmission of a signal along the axon is reduced, then the "normal" neuron firing propagation in the form of a travelling spike is impossible. The increase of the cross-diffusion coefficient beyond the "normal" value implies the same result. *Thirdly*, we consider description of travelling wave solutions of population system that can chemotactically react to an immovable signal (attractant or repellent) produced by individuals themselves; the famous Keller-Segel model belongs to them. In the corresponding models the cross-diffusion coefficient may depend on both variables and possess singularities. The study of travelling wave solutions of chemotactic models was carried out by qualitative and bifurcation analysis of the phase portraits of the wave system that depends on parameters C (a speed of wave propagation) and α which characterizes boundary conditions under given C. Instead of trying to construct a travelling wave solution with the given boundary conditions, we study the set of all possible bounded solutions of the wave system. This approach allows identifying all boundary conditions for which the model possesses travelling wave solutions. For wide class of cross-diffusion coefficient functions we described families of travelling wave solutions with different $(P, Q)-$profiles: front-front, impulse-front, impulse-impulse, trains, etc. We considered also conditions of wave profiles rearrangements, which occur with changes of the wave propagation velocity and the boundary conditions, correspond to bifurcations of its ODE.

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 worthy to note 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 "growth - taxis – diffusion" type models. For biological systems, such as populations of forest insects or plankton communities, these regimes may be interpreted as dynamic spatial "patterns 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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