

Working Paper

Nonlinear Problems in Mathematical Ecology

Yu. M. Svirezhev

WP-94-71
August, 1994



International Institute for Applied Systems Analysis □ A-2361 Laxenburg □ Austria
Telephone: +43 2236 71521 □ Telex: 079 137 iiasa a □ Telefax: +43 2236 71313

Nonlinear Problems in Mathematical Ecology

Yu. M. Svirezhev

WP-94-71
August, 1994

Working Papers are interim reports on work of the International Institute for Applied Systems Analysis and have received only limited review. Views or opinions expressed herein do not necessarily represent those of the Institute or of its National Member Organizations.



International Institute for Applied Systems Analysis □ A-2361 Laxenburg □ Austria
Telephone: +43 2236 71521 □ Telex: 079 137 iiasa a □ Telefax: +43 2236 71313

NONLINEAR PROBLEMS IN MATHEMATICAL ECOLOGY

Yu. M. Svirezhev

*Potsdam Institute for Climate Impact Research,
Potsdam, Germany*

"When we study the History of Science we discover two mutual contrary phenomena: either behind an apparent complexity a simplicity is hidden or, on the contrary, an evident simplicity conceals within itself an extraordinary complexity"

H.Poincare

1. INTRODUCTION

The linear world of the mathematical physics of the nineteenth and the early twentieth centuries was harmonious and consistent. Almost the entire evolution of this world proceeded in small neighborhoods of stable equilibrium where linearization principle held true. This was a smooth differentiable world, in which there was no room for instabilities, catastrophes, and other inconvenient phenomena. Certainly, the complete harmony did not exist and nature produced now and then surprise packets with unpleasant nonlinearities; nevertheless, the situation was saved due to the fact that those nonlinearities could be regarded as minor ones, so that one could manage with small nonlinear additions to the main linear solutions. To explain all those nonlinear phenomena, viz. jumps, discontinuities, catastrophes, hysteresis, etc., was the task to philosophy rather than mathematics.

In contrast to many fields of mathematical physics, where linear models have been used very extensively and effectively (recall, for instance, the wave equation, the heat conduction equation, the Schroedinger equation, etc.), mathematical ecology (and mathematical genetics, also) are principally nonlinear sciences. The fact is that almost all interactions in ecology, both competitive and trophic, are nonlinear. Perhaps, the only linear model is the model of exponential growth of T.Malthus. Even the classical Volterra "prey - predator" model demonstrates a typical nonlinear pattern, while in more sophisticated models, for instance, in trophic chains, we can see nonlinear oscillations, "quantum" effects, and dynamic chaos[1,2].

Mathematical genetics is equally nonlinear in principle, because of the nonlinear form of Mendel's laws[3].

A vast variety of nonlinear problems, generated by ecology (and genetics) are described in books [1 - 5], and there is no need to repeat their description in this manuscript; here I would like to dwell in more detail on the problems yet unsolved, trying to predict or, strictly speaking, to guess the potential results and offer their informal interpretation.

2. MODELS AND REALITIES IN ECOLOGY

Now many classical models of mathematical ecology, which are the basis for applied ecological modelling, are subject to severe revision. This process is going in two direction: first, a "canonization" of canonical models is taking place (we shall speak about it later, too), and second, new descriptions are proposed, using either new mathematical subjects and concepts or well have been forgotten ones. For instance, it would be interesting to use such a subject as differential inclusions. Or, there is growing interest to Lagrange stability concept, which is closer to intuitively understandable ecological stability [6].

Also, the models of mathematical ecology themselves, coming from physics and chemistry or elsewhere , are subject to revision. It is clear, that Lotka - Volterra models have their "genetic" origin in the models of chemical kinetics. Also, the origin of ecological models, taking into account spatial moving of individuals, is clear. Therefore they are called models of the "reaction - diffusion" type. (In spite of the fact that we are not sure that physical process

"diffusion" is a good model for biological movements.) Constructing both Volterra and diffusion models, we use first of all conservation laws (matter and energy), and after that, knowing really nothing about the mechanism of behavior of individuals in the populations, use different physical and chemical hypotheses for their description.

So, the "collisions" hypothesis in the Volterra models is a typical hypothesis of chemical kinetics about the collision of molecules.

And what is the "diffusion" hypothesis? It is assumption about stochastic movement of individual on an areal, which is equivalent to the statistical physics hypothesis about stochastic movement of atoms and molecules. But an individual in the population is not a molecule; it is the complex organized system, having "freedom of choice", with complex behavior even in some average situation. Therefore, for more adequate models we should use some other, more realistic hypotheses about the behavior of individuals. This leads to more complex models. As an example we can mention "Schoedinger's systems" suggested for the description of self-thinning processes in plant communities[2]. On the other hand, even if we agree that the diffusion model is a fairly good approximation in the description of spatial migrations of individuals in populations, there are still a strong local nonlinearities in the processes of competition, trophics, inheritance, reproduction, etc., which generate such phenomena as nonlinear waves and dissipative structures in models of spatially distributed systems described by the reaction -diffusion equations [2].

Generally, the problem of choosing an adequate mathematical description in ecology is very acute; physical and chemical ways of descriptions are already exhausted; it is necessary to look for some new non-traditional methods, which can be based on already known mathematical concept and new forms of description for ecological realities.

For instance, one of the main difficulties in ecological modelling is how to obtain discrete structures on the set of continuously changed parameters. The point is that all vegetation on the Earth is the mosaic of discrete forms. They are biogeocoenoses (having the same boundaries as phytocoenoses), and some larger taxonomic units like biomes (for example, taiga or steppe). Analyzing geographical distribution of vegetation, we can see the following: while temperature, moisture, precipitation, and other climatic characteristics are changing continuously, biological characteristics (like storage of aboveground and underground phytomass, etc.) change by jump from one community to another. Why is it so? In my opinion, the answer is either in particular properties of principally nonlinear functions, describing dependence of biological processes on abiotic parameters of the environment or principal non-linearity of such processes as, for instance, inter- and intraspecific competition. On the mathematical point of view, the first models should be the models of the catastrophe theory. We can hope, that namely the mechanisms with nonlinearities of cubic type are responsible for sudden changes of any biological parameter when abiotic parameters are changing continuously, and the task of modeller is to define these critical parameters correctly. Second type of mechanism, which can lead to the formation of discontinuity, is the destruction of some unstable equilibrium under perturbation for the systems possessing a hysteresis effect. How we shall show later, it can be the classical

Volterra model for two competing species imbedded into slowly changing environment.

And finally, a few words about dynamic chaos in population dynamics. Using differential (and difference) equations for the description of population dynamics, we use the hypothesis about unlimited divisibility of the biomass. On the other hand discreteness is natural for living organisms: biomass exists only as individuals. For instance, we can speak about the biomass of half - individual, but we can not imagine that this half-individual is able to reproduction, for this we need a whole organism (or pair of them). As a rule we ignore this contradiction, as Newton - Leibnitz formalism of continuous description, created for classical mechanics, given satisfactory results for the population dynamics as well, if the number of individuals is large and slowly changing. Although these criteria are not sufficiently accurate, they allow us to use differential (and difference) equations in the models of population dynamics in cases, when this dynamics is more or less regular. Without taking into account these general problems, we used the models of this type for the description of dynamic chaos in populations and communities. It seems intuitively that also in these cases the models will be quite adequate, but some doubts appear in this case, which should be discussed.

As a matter of fact, for chaotic dynamics described by the Ricker equation

$$N_{t+1} = rN_t \exp(-\lambda N_t)$$

there are some intervals when N_t is close to zero, but after that due to exponential growth the N_t becomes very large. After non-regular periods of time this situation repeats. The question arises: if there is a lower critical level of biomass (for instance, biomass of one individual), then the model which takes this into account will be able to demonstrate chaotic behavior or not? The natural generalization for the Ricker's model can be presented as follows:

$$N_{t+1} = E\{rN_t \exp(-\lambda N_t)\},$$

where $E\{x\}$ is an integer part of x , and biomass is scaled. As the chaos on a denumerable set is impossible, the generalized model will not give chaotic dynamics. In other words, introduction of natural discreteness excludes the theoretical probability of chaos. Moreover, while degradation of the population was principally impossible in the classic Ricker model, it becomes possible in the generalized model. However, while the pure chaos excluded in this model, there are still regimes practically chaotic, with wide spectrum of oscillations.

3. CANONICAL MODELS CLASSIFICATION IN MATHEMATICAL ECOLOGY

If we consider any (more or less) complex simulation model of ecosystem, we can see that it contains some elementary blocks (submodels). Let us call them *Canonical Models*, These can be

- a) prey - predator model,
- b) model for two competing species,
- c) model of two populations connected by migration (linear or nonlinear),

- d) model of an isolated population with a complex law of population growth (for instance, the Alle's principle),
- e) demographic model (one of the version of Leslie's model),
- f) chemostat model.

All these models can be both with overlapping generations (continuous-time models), and non-overlapping generations (discrete-time models). It is clear that the general dynamic properties (dynamic behavior) of the "big" model can be determined both by its general structure (so-called emergency properties) and the specific dynamic properties of its components, i.e. by the dynamics of canonical models.

Unfortunately, the history of mathematical ecology and ecological modelling is such that ecological modellers use the canonical (elementary) models as laws (like in physics). However these models are not laws; they are only "phenomenological descriptions" having a very narrow field of implementation. For instance, whereas in mechanics we have Newton's laws to derive equations of motion from the general conservation laws, in ecology we have no such laws (or, to be more accurate, their analogs). What are the energy expenses to competition? What is the relation between energy utilized in reproduction and energy consumed for the individual specimen life? The list of these questions may be continued. Clearly, so long as we do not know the mechanisms governing the processes of interaction between specimens in the ecosystem and the quantitative expressions for them, all the attempts to moving global energy and matter properties of the ecosystem to its local behavior will be speculative. Notice that this is the case not only in mathematical ecology, but, say, in mathematical economics too. Attempts to introduce some global energetic characteristics there also did not pay off.

Though in some special cases we managed to look at the results of stability analysis of dynamic models of communities from the viewpoint of extreme principles. And what is more, we can use some optimal general principle in order to complete a definition of the input balance equations up to complete system. For instance, instead of to use some allocation principle, which must describe the energy allocation among various species in the community (and which is very often unknown), we use the adaptation principle, which, as a rule, has a very "scientific" formulation (though in most cases teleological principles in biology have this formulation).

Discussion of the role of teleological principles in biology and about their acceptability date from very long ago and now they are heated as before. However, we are still very far away from the lucidity achieved, say, in classical mechanics.

And finally I should quote just one statement ascribed to von Brücke, in which teleology is characterized as "a lady no biologist can live without, but whose company seems shameful in society".

The usage of phenomenology was very often leading to special (interesting from theoretical viewpoint) dynamic effects in complex models, which did not reflect reality, being in fact consequences of either the usage of wrong elementary models, or their non-motivated expansion beyond the field of their validity. For instance, how we shown above, the usage of population models with the biomass as a continuous state variable for low densities where the discrete allocation of the biomass (among individuals) becomes important.

Thus, when we come across an unexpected dynamics in a complex model, we should consider three possibilities:

1. This dynamics is a direct consequence of the dynamic properties of canonical (elementary) submodels.
2. This dynamics is an emergent property of the whole model.
3. This is a "false dynamics", or an artifact of modelling.

In order to make the right choice, one has to know in detail:

- dynamic properties of canonical models,
- domains of their validity,
- dangerous effects of parametrization,

when we attempt to approximate some phenomenological relations by empirical formulas ("parametrization traps").

In other words, a *canonizing procedure (canonization) for canonical models* is needed. This procedure would provide a tool for testing reliability of ecological modelling. Unfortunately, up to date nothing systematic is done in this important way. The "canonization" would allow the modellers to choose the elementary (canonical) model blocks basing on some regular rules rather than traditions. It would also be a filter for wrong interpretations of the results that, to the first glance, seem unexpected.

4. PREY-PREDATOR SYSTEM AS A CLASSICAL SUBJECT OF MATHEMATICAL ECOLOGY

Starting with the works of V. Volterra, the prey-predator system has been a classical subject of mathematical ecology. Let $x(t)$ and $y(t)$ be the number of preys and the number of predators respectively. Then a sufficiently general (so-called "Kolmogoroff") model of this system takes on the form:

$$\begin{aligned} \frac{dx}{dt} &= \alpha(x)x - V(x)y, \\ \frac{dy}{dt} &= [kV(x) - m]y, \end{aligned} \tag{4.1}$$

where $\alpha(x)$ is the Malthusian function of the pray, $V(x)$ is the trophic function (functional response), m is the natural mortality rate of the predator, k is the efficiency in converting the prey biomass into the reproductive biomass of the predator. The most widespread types of the functions $\alpha(x)$ and $V(x)$ are represented in Fig.1,2. For different parametric representations of these functions, the existence of one or several limit cycles in this systems was proved [1,2,6]. Some results of this kind were also obtained for a more general representation of those functions, but comprehensive investigation of the topology of phase space has not yet been carried out for this model. We shall try to give a brief description of the results which may be expected here.

In the first place, we may expect the birth of a cycle (and not the only one) as a result of the Andronov-Hopf bifurcation. The system has a non-trivial equilibrium, which is defined from the conditions:

$$V(x^*) = m/k, \quad y^* = \alpha(x^*)x^*/V(x^*).$$

The eigenvalues of the Jakobi matrix at this point are

$$\lambda_{1,2} = \sigma \pm i\sqrt{ky^*V(x^*)V'(x^*) - \sigma^2}, \quad (4.2)$$

where

$$\sigma(x^*) = \frac{1}{2}x^*[\alpha'(x^*) - W'(x^*)y^*], \quad W(x) = V(x)/x.$$

If we now consider $\beta = m/k$ as the bifurcation parameter, or x^* instead β since $V(x)$ depends monotonically on x , it is necessary to detect whether there exists an x_c^* such that $\sigma(x_c^*) = 0$.

The second condition, $\sigma'(x_c^*) \neq 0$, as a rule (except non-robust cases), is fulfilled here. The answer to this question can be obtained from studying the behavior of the function $y = \alpha(x)/W(x)$. It is easy to see that in those point x^* where the derivative $dy/dt = 0$, the function $\sigma(x)$ is also equal to zero.

In the second place, relaxation oscillations are possible in the system. Indeed, if we assume the characteristic time of changes in the size of prey population to be much smaller than the characteristic time of the predator response to those changes - a situation, which is quite common in the nature, - then the dynamics of this system will be determined by the topology of the equilibrium manifold $y = \alpha(x)/W(x)$. Thus, the study of relaxation oscillation also reduces to investigating this manifold.

Let us consider the following case, when the Malthusian function $\alpha(x)$ is a monotone decreasing function, of the density-dependent type (Type I), and let the trophic function belong to Type II, let it be S-shaped. Then it may be shown that if, for instance, the parameter x_m ($\alpha(x_m) = 0$), the carrying capacity of the environment for the prey, changes, then the form of function $y = \alpha(x)/W(x)$ changes in the following manner (see Fig.3). Type B, to which we pass as x_m increases, is of the greatest interest to us. What do we get here?

As long as the curve belongs to Type A, there exists no cycles of any kind in the system: neither Andronov-Hopf, nor relaxation ones. But as soon as, with parameter x_m changing continuously, we pass over to Type B ("cusp" catastrophe), both kinds of oscillations may arise in the system.

We shall now continuously increase the parameter x^* : from x_1^* to x_5^* (see Fig.4). When $x^* = x_1^*$, there exists a stable equilibrium in the system (an unstable cycle may also exist). But as soon as x^* passes through x_2^* , at least two stable cycles arise in the system: an Andronov-Hopf cycle with the amplitude $h = \sqrt{x^* - x_2^*}$ in the neighborhood of point x_2^* , and the relaxation cycle $A_1A_2A_3A_4$ with the finite amplitude. While the first cycle arises according to the soft self-excitation type, the second cycle is the consequence of hard self-excitation conditions. As x^* increases further, this

pattern remains until x^* has passed through x_4^* ; after that the relaxation cycle disappears, the stable Andronov-Hopf cycle disappears as well, and this disappearance may be accompanied by the birth of an unstable cycle, which, however, becomes quickly destroyed. Again a non-trivial equilibrium alone (for instance, with x_5^*) remains in the system.

Let now the parameter $x^* = x_3^*$ be fixed; we shall now diminish the carrying capacity for the prey (parameter x_m). In this case the amplitude of the relaxation cycle will diminish amplitude of the Andronov-Hopf cycles will be saved, but the stable cycle (in the neighborhood of x_2^*) will approach the unstable one (in the neighbourhood of x_4^*). And finally, at the point of the catastrophe, the relaxation cycle disappears and the Andronov-Hopf cycles merge. It is difficult to say what happens in this case: an additional fine investigation of the non-robust case is required.

Let us suppose now that the bifurcation parameters x^* and x_m are random functions of time. Intuitively it may be supposed that parametric resonances may appear here due to splitting the cycles up. In [6] it is shown that this actually occurs, at least for systems close to the Volterra ones, for which $\alpha(x)$ and $V(x)$ are linear functions.

Let now $\alpha(x) = \text{const}$.

It corresponds to the case, when there are not the self-regulation mechanisms in the prey population; it is controlled only by predator. For the trophic function we use the very popular parametrization:

$$V(x) = \frac{V_\infty x^n}{K^n + x^n}, \quad n = 1, 2, \dots \quad (4.3)$$

If $n=1$, then we have the trophic function of Type I; if $n=2,3,\dots$ then the trophic function belongs to Type II.

Replacing the variables:

$$\begin{aligned} \alpha t &\Rightarrow t, \quad x / x^* \Rightarrow x, \quad y / y^* \Rightarrow y, \\ V / V_\infty &\Rightarrow V, \quad m / \alpha \Rightarrow \mu, \end{aligned}$$

we obtain from (4.1):

$$\begin{aligned} \frac{dx}{dt} &= x - V(x)y, \\ \frac{dy}{dt} &= \mu y [V(x) - 1]. \end{aligned} \quad (4.4)$$

The type of equilibrium (x^*, y^*) is determined by the value $\nu = V'(1)$. This equilibrium is a topological knot; if $\nu < 1$ then it is unstable, and if $\nu > 1$, stable. When we pass through $\nu = 1$ we have an Andronov-Hopf bifurcation and in "general position" case a limit cycle is born out of this equilibrium. It seems there is not any problem here.

On the other hand if we shall use the description of the trophic function in the form (4.3), we can prove that the system (4.4) has not limit cycles. We consider this problem for $n=2$, although the final results are valid for any $n>2$.

For $n=2$ in new variables we have

$$V(x) = \frac{x^2}{1 - b + bx^2}, \quad b = \frac{V^*}{V_\infty}.$$

The bifurcation value for b is $b_c = \frac{1}{2}$. Hence the trophic function which gives the equilibrium of "center" type, is $V_c = 2x^2 / (1 + x^2)$. In this case the system (4.4) is reduced to the Abel equation of second type and it has the integral:

$$y + Cy^{1/\mu} = (1 - \mu) \frac{x}{V_c(x)}, \quad \mu \neq 1 \tag{4.5}$$

$$y \ln(Cy) = \frac{x}{V_c(x)}, \quad \mu = 1.$$

Therefore the limit cycle can not arise out of equilibrium (existence of the integral of Abel equation is a sufficient condition for this). We can show that the periodic regime can not also arise out of closed trajectories of center. But if we deform (ε -deformations) the trophic function, for instance, it will be presented in the form

$$V(x) = \frac{x^2}{1 - b + bx^2 + (b - \frac{1}{2})F(x)}, \tag{4.6}$$

where $F(x)$ is a finite function,

$$F(1) = 0, F(0) < -(1 + x^2), F(\infty) < x^2$$

(see Fig.5), that we can organize the birth of cycle out of closed trajectories.

Let

$$F(x) = A[(x - 1) / (x + 1)]^l,$$

then we can create the cycle by the choice of A .

Note that the factor $(b - \frac{1}{2})$ at $F(x)$ was introduced in order to save the Abel integral. If this factor would be changed, i.e. the Abel integral would be destroyed, we can realize the birth of $(l-1)$ cycles out of equilibrium by means of the Andronov-Hopf bifurcation. In other words, after the ε -deformation of trophic function (4.3) the system (4.4) becomes robust and structurally stable, while this system with the trophic function (4.3) is structurally unstable (non-robust). In robust system the bifurcation of parameter b can provide limit

cycles both out of equilibrium and out of closed trajectories, and so much as we desire.

It is very interesting that the parametric form (4.3) for trophic function generates the whole class of structurally unstable phase pictures. Really the probability to get into a "non-robust" situation is very low, but we have got into it. Note when we use some asymptotic methods (for instance, Krylov-Bogolubov method) for finding of the periodic solutions of (4.4), it leads to the destruction of "non-robust" situation, and, as a rule, we obtain more or less successful results [1,2].

Thus, the system (4.1) (or (4.4) with the trophic function (4.3) is structurally unstable. My question is: this structural instability is either the principal emergent property of the prey-predator system, which ensures the high degree of adaptation and the high lability in relation to changes of environment for this system, or an artifact of parametrization, i.e. the effect, which we can call the "parametrization trap"?

Let us suppose that the first answer is true and the following Gedankenexperiment would be carried out.

a) we imbed the structurally unstable system "prey-predator" into a stochastic media, i.e. we consider the system behavior under impact of random perturbations. In this case the perturbations destroy this non-robust structurally unstable situation and as a result the dynamics can be presented by the whole system of (stable and unstable) stochastic limit cycles. In other words *we can predict the behavior of the deterministic, but structurally unstable system in the principally unpredictable stochastic environment.*

b) we imbed this system in the periodically changing predictable environment and, for some values of parameters, we get the dynamic chaos, i.e. the principally unpredictable behavior in the predictable environment.

Now I would like to formulate the following speculative hypothesis: *may be the structural instability is the evolutionary mechanism, which allow to predict the own future in stochastic environment*

5. HYSTERESIS IN THE SYSTEM OF COMPETING SPECIES

"Struggle for Life is a permanent reality
in the Nature and the Society."

T.Malthus

The second classical model in mathematical ecology is the model of a system comprising two species competing for one resource:

$$\begin{aligned} \frac{dx}{dt} &= x(\varepsilon_1 - \alpha_{11}x - \alpha_{12}y), \\ \frac{dy}{dt} &= y(\varepsilon_2 - \alpha_{21}x - \alpha_{22}y), \end{aligned} \tag{5.1}$$

where $x(t)$ and $y(t)$ are the population sizes (or biomass) of the species. After scale transformations

$$\begin{aligned} \varepsilon_1 t \Rightarrow t, \varepsilon_2 / \varepsilon_1 = k, \frac{\alpha_{11}}{\varepsilon_1} x \Rightarrow x, \frac{\alpha_{22}}{\varepsilon_2} y \Rightarrow y, \\ \frac{\alpha_{12} \varepsilon_2}{\alpha_{22} \varepsilon_1} \Rightarrow \gamma_1, \frac{\alpha_{21} \varepsilon_1}{\alpha_{11} \varepsilon_2} \Rightarrow \gamma_2, \end{aligned}$$

the model (5.1) may be rewritten in the form:

$$\begin{aligned} \frac{dx}{dy} &= x(1 - x - \gamma_1 y), \\ \frac{dy}{dt} &= ky(1 - y - \gamma_2 x). \end{aligned} \tag{5.2}$$

This system has been investigated in detail, no limit cycles are here, and the equilibria have the form:

$$\begin{aligned} \sigma_0 &= (0, 0); \sigma_1 = (1, 0); \sigma_2 = (0, 1); \\ \sigma_3 &= \left(\frac{1 - \gamma_1}{1 - \gamma_1 \gamma_2}, \frac{1 - \gamma_2}{1 - \gamma_1 \gamma_2} \right). \end{aligned}$$

Their stability depends on the relationships between γ_1 and γ_2 . In Fig.6a their stability domains are shown in the plane $\Gamma = \{\gamma_1, \gamma_2\}$; phase portrait corresponding to these domains are shown in Fig.6b.

Suppose now that γ_1 and γ_2 evolve slowly in the positive quadrant of the plane $\Gamma = \{\gamma_1, \gamma_2\}$ (slowly as compared with fast changes of x and y). To describe the dynamics of the system in this case we must add to (5.2) two equations for slow variables:

$$\begin{aligned} \frac{d\gamma_1}{dt} &= \varepsilon g_1(x, y, \gamma_1, \gamma_2), \\ \frac{d\gamma_2}{dt} &= \varepsilon g_2(x, y, \gamma_1, \gamma_2), \quad \varepsilon \ll 1, \end{aligned} \tag{5.3}$$

and consider the behavior of the system in the extended phase space $U \times \Gamma, U = \{x, y; x, y \geq 0\}$. What will take place here?

Let the system move along a phase curve ξ which passes through an arbitrary point $\xi(t_0) = G_0$. After the initial fast movement the point $G \in \xi$ gets into the neighborhood of an equilibrium manifold and then slow movement occurs in this neighborhood corresponding to changes of parameters γ_1 and γ_2

within a domain Ω_i . When the curve $f(\xi)$, the projection of ξ onto Γ , crosses the boundaries between the domains Ω_i , the equilibrium to which x and y are close may disappear or become unstable, and the phase trajectory may leave the area of applicability of the Tikhonoff theorem. In such a case, however, the system immediately gets into the layers above other stable points, whereto it will pass immediately and quickly, to move again slowly in the neighborhood of another equilibrium manifold. Let us consider this situation by analyzing the following example (see Fig.7).

Let the system move from point $(\gamma_1^i, \gamma_2^i) \in \Omega_2$ into Ω_1 along the path ξ_1 ($f(\xi_1)$ being its projection onto Γ). At the moment of crossing the boundary AB between Ω_2 and Ω_1 the point σ_1 loses stability, simultaneously σ_3 , a new stable point (at the boundary when $\gamma_2 = 1, \sigma_1 = \sigma_3$) separates from it.

The transition from one equilibrium to another occurs without fast movement taking place and the change of the ecosystem structure proceeds smoothly. The change of the equilibrium σ_3 by the equilibrium σ_2 proceeds in a similar way when $f(\xi_1)$ crosses the boundary BC between the domain Ω_1 and Ω_4 . The entire transition $\sigma_1 \rightarrow \sigma_3 \rightarrow \sigma_2$ is reversible in the sense that if the system performs a reversible transition from (γ_1^f, γ_2^f) to (γ_1^i, γ_2^i) and $f(\bar{\xi}_1) = f(\xi_1)$, then trajectories ξ_1 and $\bar{\xi}_1$ are close in the phase space U .

The situation will be quite different when $f(\xi_2)$ passes through the domains $\Omega_2, \Omega_3, \Omega_4$. Upon crossing the boundary BE, equilibrium σ_1 retains its stability, but at the same time the point σ_2 becomes unstable and the unstable saddle point σ_3 separate from it. The part of phase trajectory which is projected into Ω_2 , is in the neighborhood of the equilibrium manifold corresponding to σ_1 , the part which is projected into Ω_3 remaining to be found in the same neighborhood. However, upon crossing the boundary BD the equilibrium σ_1 loses its stability and slow movement along this manifold changes into fast one, which leads the trajectory ξ_2 into the neighborhood of the equilibrium manifold corresponding to σ_2 . In this case the observed variables x and y change quickly, the ecosystem structure changes in a jump, and the transition $\sigma_1 \rightarrow \sigma_2$ is irreversible. The irreversibility is understood in the sense that if there exists a trajectory $\bar{\xi}_2$ leading in a reverse direction (from (γ_1^f, γ_2^f) to (γ_1^i, γ_2^i)), such that $f(\bar{\xi}_2) = f(\xi_2)$, then fast movement along $\bar{\xi}_2$ will take place at the point E rather than D, i.e. the trajectories ξ_2 and $\bar{\xi}_2$ will no longer be close. This is the hysteresis phenomenon, typical for non-linear systems.

We have considered the simplest model of a two-species competitive community. It is clear that hysteresis effects and some other catastrophes will take place in the case of multi-species competitive communities. Stratification of phase space, typical for these systems, will result in different characteristic times (different time-scales) for different groups of species: while the population sizes of some species will be almost constant, the population sizes of other species will change quickly and sharply. Slow evolution of parameters, caused, for instance, by genetic processes, or changes of environment, will generate various structural ecological reconstructions, the non-linear effects of hysteresis type ensuring irreversibility of these evolutionary reconstructions.

6. BORDER BETWEEN TWO VEGETATION ZONES

"Revenons à nos moutons" we show how we can use the simplest model of two competing species for description of such a sufficiently complex phenomenon like the border between two different vegetation zones.

Let us suppose in the model (5.1) that its coefficients depend on some spatial coordinate s , moreover only the total productivities ε_1 and ε_2 depend on this coordinate, the coefficients γ_{ij} are constant and do not depend on s . We suppose that the ε_1 and ε_2 change continuously along s , as it shown at Fig.7.

After replacing

$$\begin{aligned} \gamma_{11}x &\Rightarrow x, & \gamma_{22}y &\Rightarrow y, \\ \gamma_{21}/\gamma_{11} &= a_1, & \gamma_{12}/\gamma_{22} &= a_2, \end{aligned}$$

we get

$$\begin{aligned} \frac{\partial x}{\partial t} &= x[\varepsilon_1(s) - x - a_2y], \\ \frac{\partial y}{\partial t} &= y[\varepsilon_2(s) - y - a_1x]. \end{aligned} \tag{6.1}$$

Let $a_1a_2 < 1$, i.e. the interspecific competition is very weak in comparison with the intraspecific one. Then the movement along the axis s corresponds to the movement along the curve $f(\varepsilon_1, \varepsilon_2)$ (see Fig.8a) from the point A up to the point D . For the quasi-stationary movement when the steady-state equilibria are not broken, the transition zone with continuous change of biomass is at the interval BC . This is so-called the "soft" border when the biomass of first species decreases up to zero level at that time the biomass of second species increases as we are going into the region more and more favorable for the second species (see Fig.8b). Domain I, shown at the Fig.8a, corresponds to the areal of only the first species; domain II corresponds to the transition zone, where the areal occupied by first species pass over continuously to the areal of second species; domain III corresponds to the areal of second species.

When $a_1 a_2 > 1$, i.e. the interspecific competition is stronger than intraspecific one, the transition is existing also. But inside this zone the continuous transition from one species to another is absent. Either the first species or the second one can exist in dependence on the initial conditions. At the Fig.9b it is shown by the doubling (solid and dotted) bars. The species can not coexist, equilibrium biomass $x^*(s)$ and $y^*(s)$ are changed by jump with the transition from one point to the next one along $s \in [BC]$. This is so-called the "hard" border (see Fig.9a,b).

Let us suppose now, that the picture drawn at the Fig.7, slowly moves to the left with the constant velocity v , then $\varepsilon_1 = \varepsilon_1(s + vt)$, $\varepsilon_2 = \varepsilon_2(s + vt)$.

When the border is "soft" we can see the slow evolution of the transition zone following climate change: the zone is moving to the left (but not explicitly with the same velocity), the picture itself is remaining the same (to within the displacement). When the border is "hard", then this evolution is discontinuous. Despite of worsening of local climatic conditions (decreasing of ε_1), the first species survives ("waits") at this point. Then it is replaced by the second species very quickly (in comparison with the characteristic time of climate change).

7. COMPETITION AND SELECTION IN THE POPULATION OF CLOSED TROPHIC CHAINS: ECOSYSTEM EVOLUTION

The motive force of Darwinian evolution are competition and natural selection at the level of the population of individuals. The competition and natural selection at the level of macromolecules is the main cause of the origin of life (according to Eigen [7]). In his studies Eigen considers a mathematical model in which the hypercycles, i.e. special mathematical objects to some extent similar to the macromolecules, replicate, compete, and perish. In our study we shall try to consider the competition and selection at the level of the simplest ecosystems. Mathematical models of these ecosystems may be *closed trophic chains*; these objects have been studied adequately in [1,2]. They compete for a common resource and the outcome of the competition, i.e. the result of selection, is determined by stability of the proper stationary states.

Suppose an ecosystem is specified, closed in terms of a substance, whose structure is of the trophic-chain type. The amount of free resource (of the matter found outside of consumers) is equal to N_0 , this resource is consumed by a species of the biomass N_1 , the biomass N_1 , in its turn, is consumed by a species of the biomass N_2 , etc., to N_n . All biomass are measured in the same units as the resource. Dead biomass is decomposed quickly (compared with the characteristic times of the species making up the chain) and the corresponding substance returns without losses to the resource level, so that the entire system is overall closed in terms of this matter, i.e. the conservation law takes place:

$$N_0 + \sum_{i=1}^n N_i = C = const. \quad (7.1)$$

If now assume that all trophic functions are linear, of the Volterra type, then the model equations can be written down as

$$\begin{aligned}\frac{dN_0}{dt} &= -\alpha_0 N_0 N_1 + \sum_{i=1}^n m_i N_i, \\ \frac{dN_i}{dt} &= N_i (-m_i + \alpha_{i-1} N_{i-1} - \alpha_i N_{i+1}), \quad (7.2)\end{aligned}$$

$$i = 1, \dots, n; \quad N_{n+1} \equiv 0.$$

Let there exist and be stable a solution to (7.1)-(7.2) of the form $\{N_0^*, N_1^*, \dots, N_q^*, 0, \dots, 0\}$, $N_i^* > 0$, $i = 0, 1, \dots, q$; $0 \leq q \leq n$; then we shall say that there exists a trophical chain of the length q .

Consider now the case where the same resource supports several trophic chains. The equations of the corresponding model take on the following form (here $j = 1, \dots, m$ is the number of the chain):

$$\begin{aligned}\frac{dN_0}{dt} &= -N_0 \left(\sum_{j=1}^m \alpha_0^j N_1^j \right) + \sum_{j=1}^m \sum_{i=1}^{n_j} m_i^j N_i^j, \\ \frac{dN_i^j}{dt} &= N_i^j (-m_i^j + \alpha_{i-1}^j N_{i-1}^j - \alpha_i^j N_{i+1}^j), \\ & i = 1, \dots, n_j; j = 1, \dots, m; \quad N_{n_j+1}^j \equiv 0.\end{aligned} \quad (7.3)$$

$$N_0 + \sum_{j=1}^m \sum_{i=1}^{n_j} N_i^j = C = \text{const.} \quad (7.4)$$

This model describes the competition of m trophic chains for common resource N_0 . Equations (7.3)-(7.4) may have stationary solutions of the form

$$\begin{aligned}
N_q^* = \{ & N_0^*; N_1^{1*}, \dots, N_{q_1}^{1*}; N_1^{2*}, \dots, N_{q_2}^{2*}; \dots; \\
& N_1^{m*}, \dots, N_{q_m}^{m*}; 0, \dots, 0 \} \\
& 0 \leq q_j \leq n_j; \quad j = 1, \dots, m;
\end{aligned} \tag{7.5}$$

where all N_i^{j*} are positive. A problem is posed concerning the existence and stability of these solutions, depending on parameters α_0^j, α_i^j and on the parameter C , the total amount of matter in the system. If we consider the selection among the trophic chains competing for the common resource (i.e. among the ecosystems) to result in a steady-state distribution of biomass, this process can be interpreted as the evolution at the ecosystem level and the conditions ensuring stability of this distribution as the criteria for the evolution. From the mathematical standpoint, it would certainly be very attractive to investigate this problem further in the general form. It is unlikely, however, that descriptive and easily interpretable results can be obtained by going along this lines. Therefore, we choose the inductive way of investigation and consider first the simplest but still sufficiently meaningful situation: the trophic chains, of which one comprises two species and the other comprises one species ($m = 2; n_1 = 2, n_2 = 1$).

Let

$$\begin{aligned}
\alpha_0^1 t \Rightarrow t; \frac{\alpha_0^1 + \alpha_1^1}{\alpha_0^1} \Rightarrow \alpha_2 > 1; C - \frac{m_1^1}{\alpha_0^1} \Rightarrow A; \\
C - \frac{m_1^2}{\alpha_0^2} \Rightarrow B; \frac{m_2^1}{\alpha_1^1} \Rightarrow \mu_2; \frac{\alpha_0^2}{\alpha_1^1} \Rightarrow \lambda; \\
N_1^1 \Rightarrow x_1; N_2^1 \Rightarrow x_2; N_1^2 \Rightarrow y.
\end{aligned}$$

Then, substituting these variables and parameters into (4.3) and excluding N_0 by using of the conservation law, we get

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 (A - x_1 - \alpha_2 x_2 - y), \\
\frac{dx_2}{dt} &= (\alpha_2 - 1)x_2 (x_1 - \mu_2), \\
\frac{dy}{dt} &= \lambda y (B - x_1 - x_2 - y).
\end{aligned} \tag{7.6}$$

We assume what $A \neq B$, i.e. the species in different chains are different. Let us set five all possible equilibria in (7.6) and their existence conditions.

1. $x_1^* = x_2^* = y^* = 0$. This solution corresponds to the absence of life in the system, all the mass of matter is concentrated in the resource block.

2. $x_1^* = A; x_2^* = y^* = 0$. There may exist only one trophic chain of the length 1, but for the existence it is necessary that $A > 0$, i. e. $C > m_1^1 / \alpha_0^1 = C_1^{1*}$. In other words, for a trophic chain having at least the minimal length to arise in the system, it is necessary that the total amount of matter in the system should exceed a certain non zero threshold C_1^{1*} .

3. $x_1^* = x_2^* = 0, y^* = B$. Again there may exist only one trophic chain, also of the length 1, but with the other species. The existence condition is

$$B > 0, \text{ i. e. } C > m_1^2 / \alpha_0^2 = C_1^{2*}.$$

The threshold effect exists again, but this threshold is defined by characteristics of the other species.

4. $x_1^* = \mu_2; x_2^* = (A - \mu_2) / \alpha_2; y^* = 0$. There may exist one trophic chain but now of the length 2. For the existence it is necessary that

$$A > \mu_2, \text{ i. e. } C > (m_1^1 / \alpha_0^1) + (m_2^1 / \alpha_1^1) = C_2^{1*}.$$

In other words, the total amount of matter in the system must increase still further ($C_2^{1*} > C_1^{1*}$).

$$5. x_1^* = \mu_2; x_2^* = \frac{A - B}{\alpha_2 - 1}; y^* = \frac{\alpha_2 B - A}{\alpha_2 - 1} - \mu_2.$$

All species constituting two trophic chains may coexist in the systems. For this to take place, it is necessary that

$$\begin{aligned} \text{a) } & A > B, \text{ or } \frac{m_1^2}{\alpha_0^2} > \frac{m_1^1}{\alpha_0^1}; \\ \text{b) } & \alpha_2 B - A > \mu_2 (\alpha_2 - 1), \text{ or} \end{aligned} \quad (7.7)$$

$$C > \frac{1}{\alpha_1^1} (m_2^1 - m_1^1 + m_1^2 \frac{\alpha_0^1 + \alpha_1^1}{\alpha_0^2}) = C_{21}^{11*}.$$

The expression for C_{21}^{11*} can be rewritten in the form

$$C_{21}^{11*} = C_2^{1*} + (1 + \frac{\alpha_0^1}{\alpha_1^1})(C_1^{2*} - C_1^{1*}) \quad (7.8)$$

Whereby in view of (7.7a), it follows that

$C_{21}^{11*} > C_2^{1*}$. This means that for two chains to coexist, the total amount of matter in the system must increase again (as compared with the amount of matter necessary for the existence of one chain of the length 2.

Now we analyze the stability of these equilibria.

1. The solution $x_1^* = x_2^* = y^* = 0$ is stable if

$A < 0, B < 0$, i.e. $C < \min[C_1^{1*}, C_1^{2*}]$. In other words, as long as the total amount of matter in the system is lower than a definite threshold, then life is impossible in such a system. Even if any one of the species appears in the system, it will of necessity be eliminated.

2. The solution $x_1^* = A; x_2^* = y^* = 0$ is stable if $A > B, \mu_2 > A > 0$.

From the first inequality, which coincides with (7.7), it follows that the inequality must true:

$$C_1^{1*} < C_1^{2*}. \quad (7.9)$$

From the second inequality it follows that

$$C_2^{1*} > C > C_1^{1*}. \quad (7.10)$$

3. The solution $x_1^* = x_2^* = 0, y^* = B$ is stable if $A < B, B > 0$. From the first inequality it follows that the inequality holds which is inverse to (7.9):

$$C_1^{1*} > C_1^{2*}; \quad (7.11)$$

from the second inequality it follows that

$$C > C_1^{2*}. \quad (7.12)$$

4. The solution

$x_1^* = \mu_2; x_2^* = (A - \mu_2) / \alpha_2; y^* = 0$ is stable if

$C_2^{1*} < C < C_{21}^{11*}$. As follows from (7.8), these inequalities can be fulfilled only if $C_1^{2*} < C_1^{1*}$.

5. Finally, the solution

$$x_1^* = \mu_2; x_2^* = \frac{A - B}{\alpha_2 - 1}; y^* = \frac{\alpha_2 B - A}{\alpha_2 - 1} - \mu_2$$

is stable if $A > B, y^* > 0$, i.e. inequalities (7.7) and (7.8) must hold. Here the existence conditions of the equilibrium ensure its stability as well.

If we now compare the stability conditions with those of the existence of biologically meaningful stationary solutions (equilibria) for all other cases (1-5), it can be seen that when a solution is stable, it always exists and is biologically meaningful.

The above-formulated conditions of the existence and stability show that the transition from one stable equilibrium to another occurs as the parameter C changes, therefore it may be regarded as a bifurcation parameter, the bifurcation points coinciding with the critical values $C_1^{1*}, C_1^{2*}, C_2^{1*}, C_{21}^{11*}$.

Generally speaking, it may be thought that as the total amount of matter in the system increases, the latter becomes more complicated; but this is not always so, and the real picture is more sophisticated. Let us consider this issue in more detail.

Let the growth of the parameter C proceed slowly, so that upon each small change of C an equilibrium has time to become established, i.e. the process is quasi-stationary. From the preceding it is obvious that, depending on the relationships between the values C_1^{1*} and C_1^{2*} , the pathways of system evolution are different. The values themselves can be interpreted as certain indices of adaptability of the primary species in each trophic chain to the environment, the state of which is described by the concentration of the resource.

Let $C_1^{1*} > C_1^{2*}$, i.e. $m_1^1 / \alpha_0^1 > m_1^2 / \alpha_0^2$. This inequality means that the mortality rate of the primary species in the first chain is higher than the mortality rate of the primary species in the second chain, whereas the per capita rate of resource consumption by the primary species of the first chain is lower than the respective value for the second chain. In other words, the primary species of the first chain is adapted to the resource less than the primary species of the second chain. As follows from the analysis in this case, when C has exceeded the threshold C_1^{2*} , only the second chain (comprising one species) will exist in the system. This chain wins the competition, and further increase in the total amount of matter will not be accompanied by any complication in its structure: only one chain (the second one) will exist, as before.

A much more interesting picture is observed if

$C_1^{1*} < C_1^{2*}$, i.e. $m_1^1 / \alpha_0^1 < m_1^2 / \alpha_0^2$. In other words, if the primary species of the first chain is more adapted to the resource than that of the second. In this case, when C surpassed the threshold C_1^{1*} , the first-species chain of the length 1 arises in the system. As C grows further, when $C > C_2^{1*}$, the length of the first-species chain increases to 2. This result may seem to be symmetrical to the preceding one, the difference being only in that the first chain wins the competition. However, this is not so, and when $C > C_{21}^{11*}$, the second chain also becomes fixed in the system. Two chains competing for one resource may coexist! It is fundamental that the coexisting chains have different lengths.

If now we consider this process from the standpoint of the system structure becoming more complicated, it can be concluded that complication of the horizontal, competitive structure is possible only on the condition that the vertical, trophic structure is complicated beforehand. The competing chains (ecosystems) must have different levels of complexity in the vertical structure (in our case the chains must be of different length).

This result leads us away from the simple logic of the Gause exclusion principle and shows that competition at the ecosystem level may be a factor which increases the diversity of a united ecosystem. Naturally, a sufficiently large amount of resource is required for this diversity to be maintained, i.e. the

environment should be rich enough. Of interest is the evolution pathway itself: through an increase in the diversity of the united ecosystem, wherein the individual ecosystems coexist, competing for the resource in common.

In conclusion of this section we present two Figures which illustrate different evolution pathways of the whole system as the total amount of matter increases (Fig.10a,b).

Here we have considered the simplest case which, nevertheless, preserves the features of the phenomenon under concern. It would be interesting to see how the relationship between the lengths of competing chains influences the outcome of competition. It is intuitively clear that the behavior of the system will become more complicated if we consider more realistic trophic functions, What new effects will it bring about? So far these questions remain unanswered.

8. DYNAMIC CHAOS IN CLOSED TROPHIC CHAIN

"Chaos had arisen in the Universe, before all things."

Hesiodus

In mathematical ecology dynamic chaos turned out to be a rule rather than an exotic exception[2,6], the problem is how to make up the adequate model. For instance, a closed, three-level trophic chain with non-linear trophic functions can be considered, perhaps, as the simplest object which demonstrates dynamic chaos. A model of this system can be represented in the form:

$$\frac{dN_0}{dt} = -V(N_0)N_1 + \sum_{i=1}^3 m_i N_i, \quad (8.1)$$

$$\frac{dN_i}{dt} = -m_i N_i + V_{i-1} N_i - V_i N_{i+1},$$

$$i = 1, 2, 3; \quad N_4 \equiv 0.$$

$$N_0 + \sum_{i=1}^3 N_i = C = \text{const.}$$

Let $V_0 = \alpha_0 N_0$, $V_i = \frac{\alpha_i N_i}{K_i + N_i}$, $i = 1, 2, 3$. If now we choose as

bifurcation parameters the total amount of matter in the system, C , and the per capita rate of resource consumption by the species of the first trophic level, α_0 , it turns out that there exists a curve $C(\alpha_0)$ such that moving along it generates the behavior of the system that varies from the regular (doubling

cycles) to the stochastic one. The transition does not occur directly: there exists a "pre-stochasticity" domain, in which there are both regular and stochastic trajectories[6].

On the other hand, in the open chains, where neither dead biomass is decomposed and returned to the resource level, there exist only regular trajectories (cycles) [2]. Naturally, it is assumed that there exists a constant flow of an external resource into the system (for closed chain it is equal to zero). Suppose now that the chain is partly closed, i.e. a certain part of matter contained in the dead biomass returns into the resource level. A model of such a system can be represented, for instance, in the form:

$$\frac{dN_0}{dt} = Q - V(N_0)N_1 + k \sum_{i=1}^3 m_i N_i, \quad (8.2)$$

$$\frac{dN_i}{dt} = -m_i N_i + V_{i-1} N_i - V_i N_{i+1},$$

$$i = 1, 2, 3; \quad N_4 \equiv 0; \quad Q > 0, \quad 0 < k < 1.$$

It would be of interest to find out whether in the plane of bifurcation parameters $\{Q, k\}$ there exist domains within which dynamic chaos arises in the system (8.2).

Naturally, other formulations are also possible. I believe that the models of mathematical ecology constitute a favorable field to look for different strange attractors and dynamic stochastic behavior corresponding to them, but it is necessary do not forget about biological adequacy of the model, which being used.

9. CONCLUSION

We have tried to show what are non-linear effects that exist in the models of mathematical ecology. Note that linear systems are devoid of such properties as, for instance, catastrophes, and this circumstance, in the methodological aspect, may be interpreted in favor of non-linear models as adequate tools to describe ecological processes and systems.

In general, the problem to choose an adequate mathematical description is very urgent in ecology. Borrowed from other, more "mathematized" sciences, methods of description have exhausted their potentialities to a considerable extent. It is necessary to look for new unconventional approach which, nevertheless, could rely securely upon the mathematical concepts already known.

REFERENCES

1. Svirezhev, Yu.M. and Logofet D.O., 1978. Stability of Biological Communities, Moscow: Nauka (English revised version, Moscow: Mir, 1983, 319 pp.)
2. Svirezhev, Yu.M., 1987. Nonlinear Waves, Dissipative Structures, and Catastrophes in Ecology, Moscow: Nauka, 368 pp. (in Russian).
3. Svirezhev, Yu.M., and Passekov, V.P., 1982. Fundamentals of Mathematical Evolutionary Genetics, Moscow: Nauka, 512 pp. (English version: Kluwer, Dordrecht, 1990).
4. Hofbauer, J, and Sigmund, K., 1988. The Theory of Evolution and Dynamic Systems, Cambridge: Cambridge University Press, 341pp.
5. Bazykin, A.D., 1985. Mathematical Biophysics of Interacting Populations, Moscow: Nauka, 172 pp. (in Russian).
6. Svirezhev, Yu.M., 1983. Modern Problems in Mathematical Ecology. In: Proc. Int. Congr. Math., v.II, 1963-1977, Amsterdam: North-Holland Press.
7. Eigen, M., 1971. Selforganization of Matter and the Evolution of Biological Macromolecules, Die Naturwissenschaften, 58, 465-523.

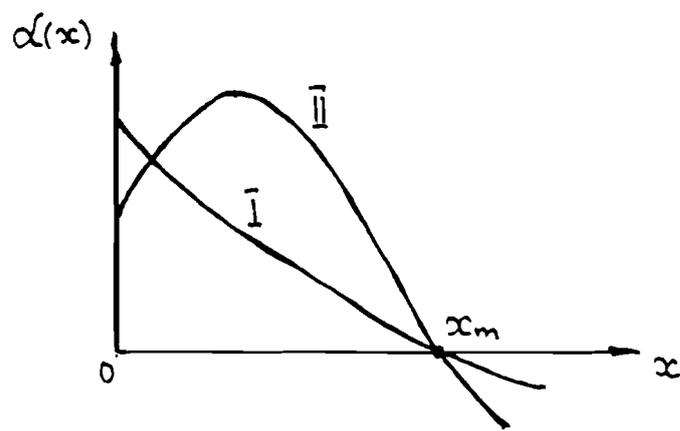


Figure 1. Malthusian functions for the prey population:
I - density-dependent regulation type;
II - Alle type.

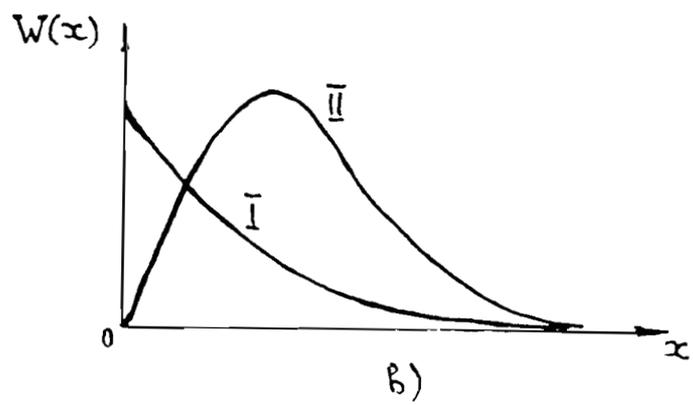
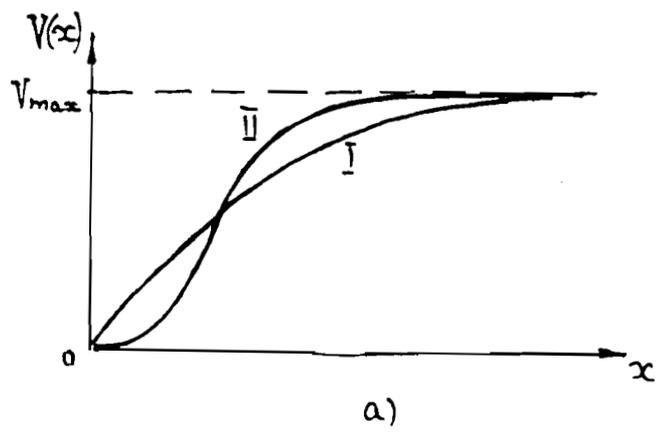


Figure 2. Types of the trophic function (a) and corresponding functions $W(x)$ (b).

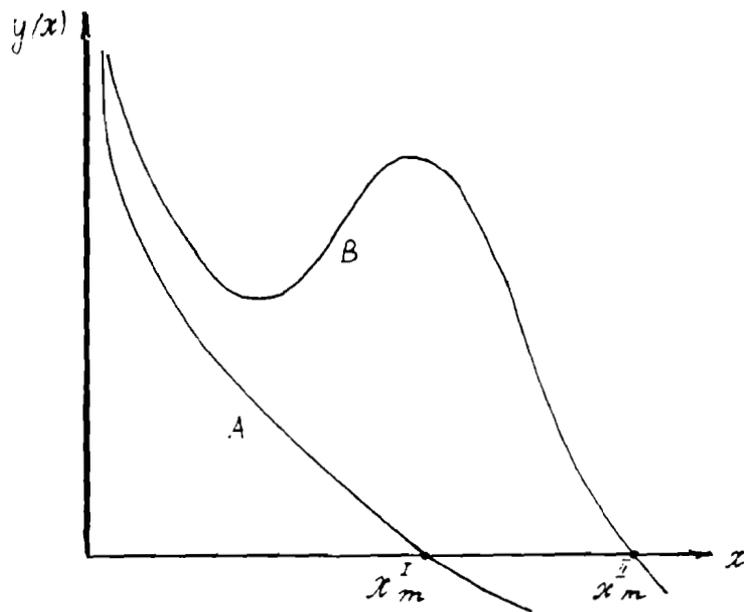


Figure 3. Types of the equilibrium manifold in the "prey-predator" system.

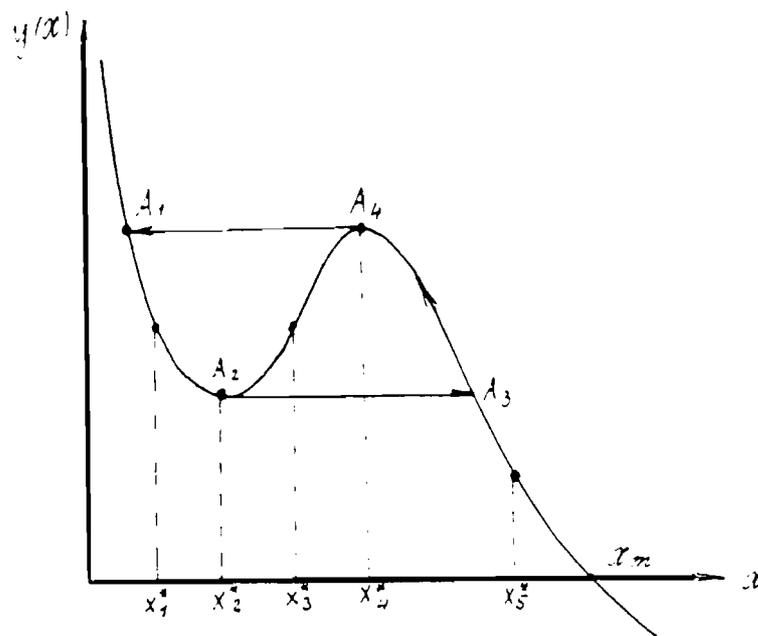


Figure 4. Bifurcations and the emergence of the relaxation cycle in the "prey-predator" system.

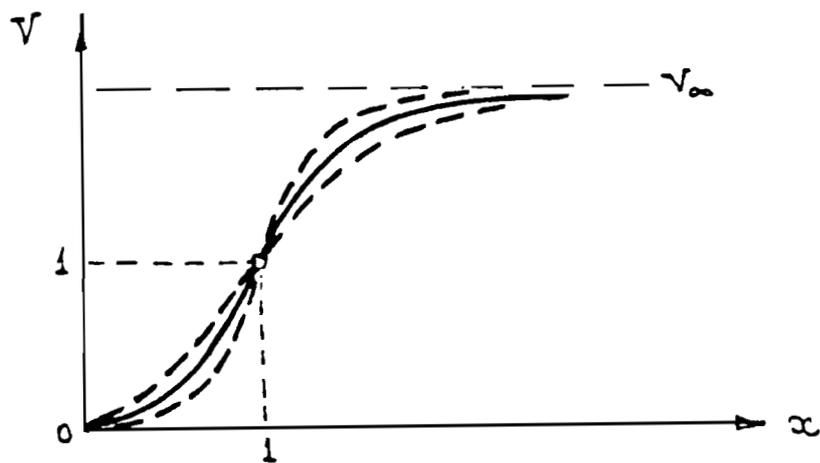
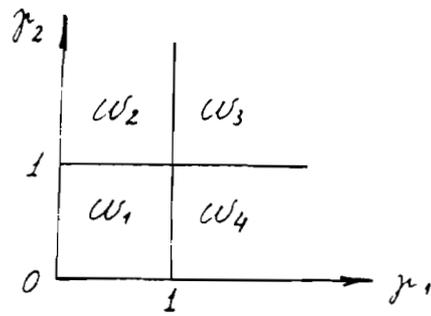
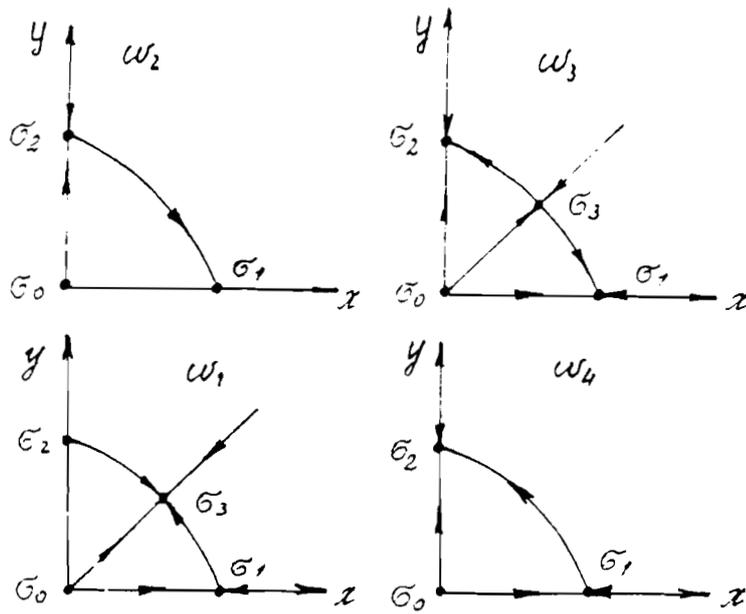


Figure 5. The " ϵ -deformation" of trophic function:
 _____ — before; - - - - - after.



a)



b)

Figure 6. Stability domains and types of the phase portrait for system (5.2)

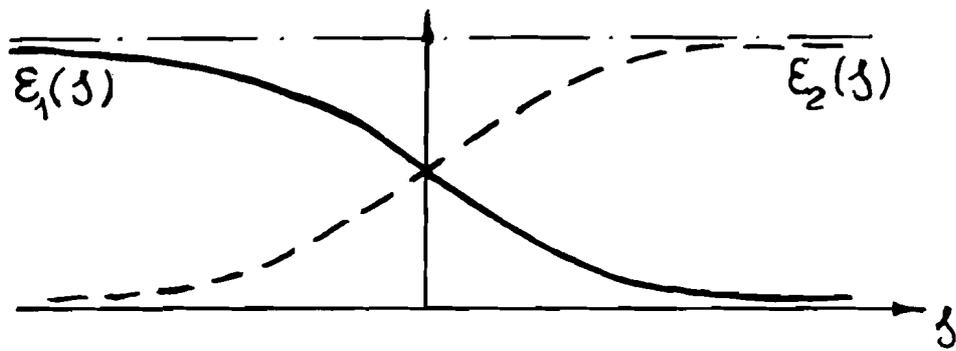


Figure 7. Growth functions ϵ_1 and ϵ_2 .

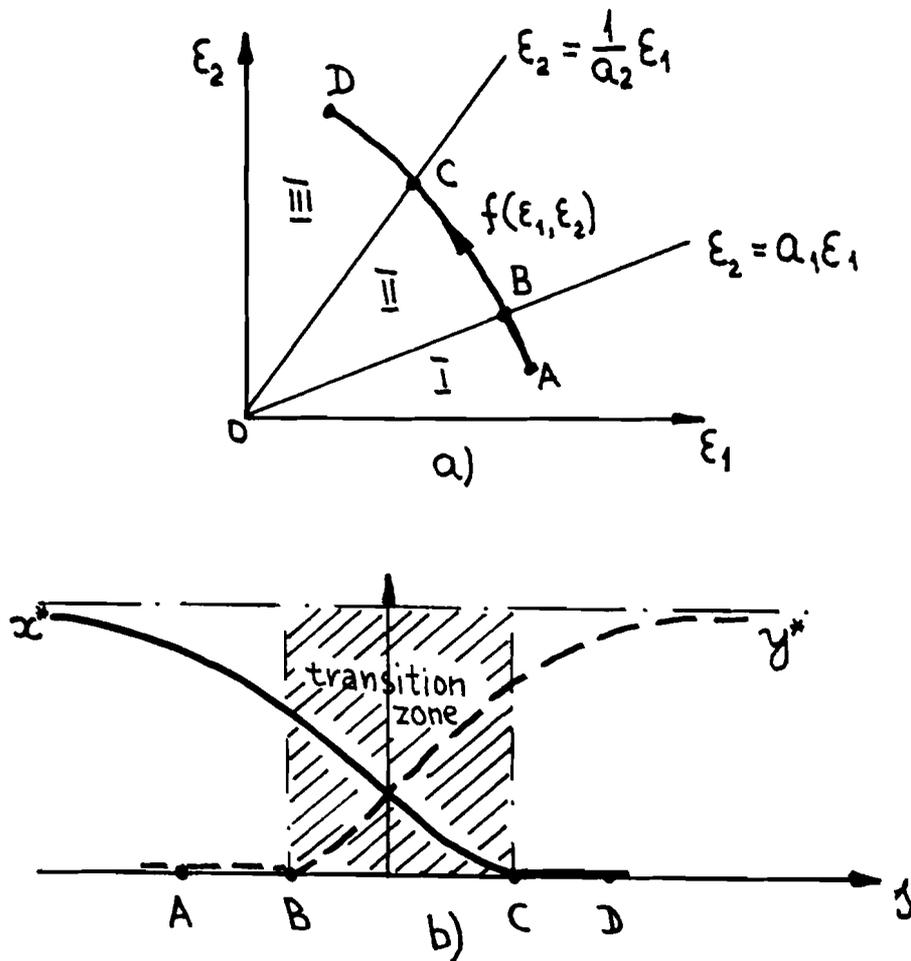


Figure 8. Case $a_1 \cdot a_2 > 1$; "soft" border.

a) Movement in the parametric space, corresponding to the movement along the axis s .

b) Quasi-stationary border between two vegetation zones. (The case of continuous transition from first species to the second one; inside the transition zone the ratio of first species decreases while the second one ratio increases as coming right along the axis s).

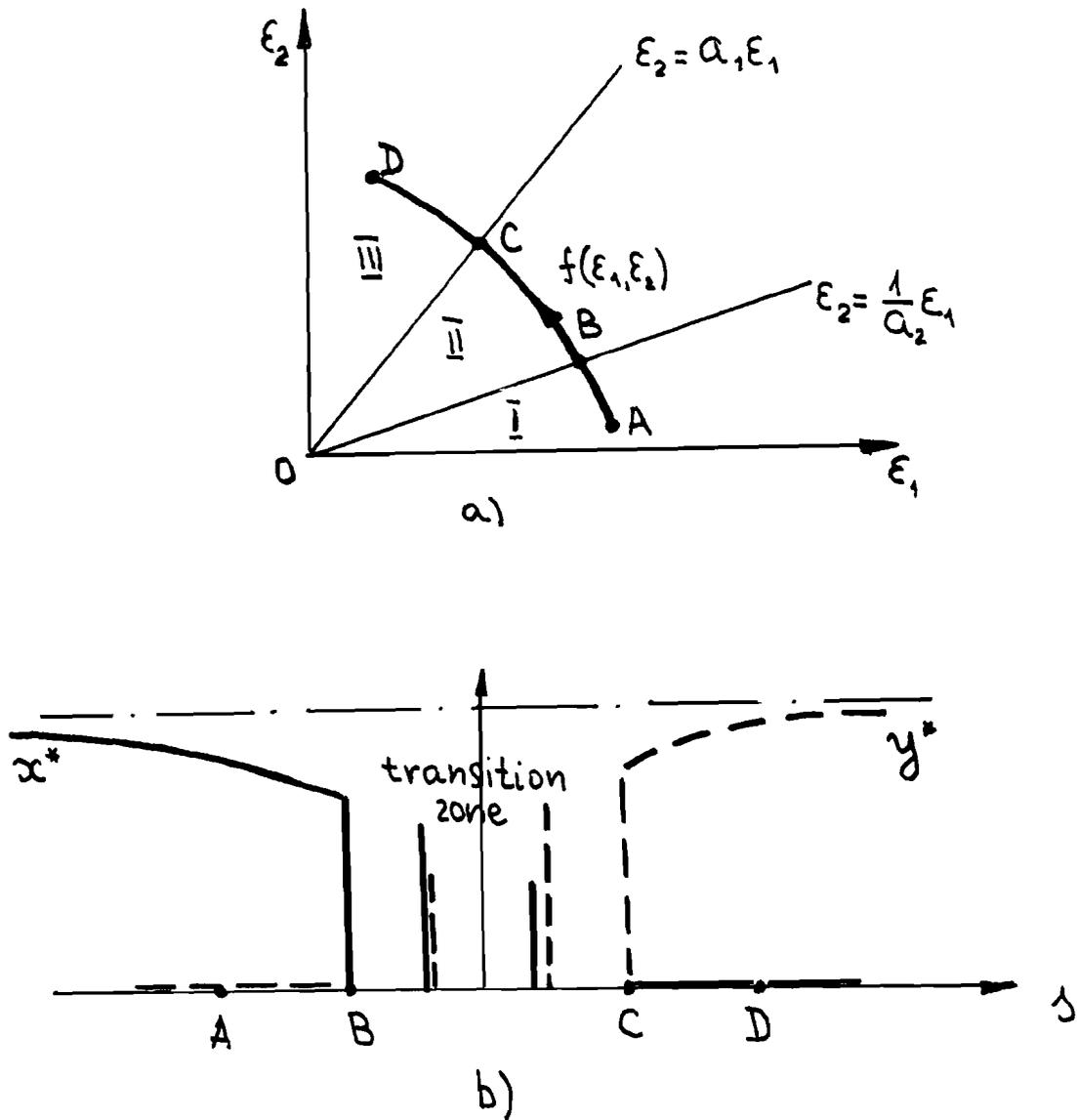


Figure 9. Case $a_1 \cdot a_2 > 1$; "hard" border.

- a) Movement in the parametric space, corresponding to the movement along the axis s . The domain II corresponds to bistable situation: either the first species exists or the second one exists at any point $s \in [BC]$.
- b) Spatial allocation of two species. Inside the transition zone BC the biomass of each species can be discontinuous as we move from one point to the neighboring one.

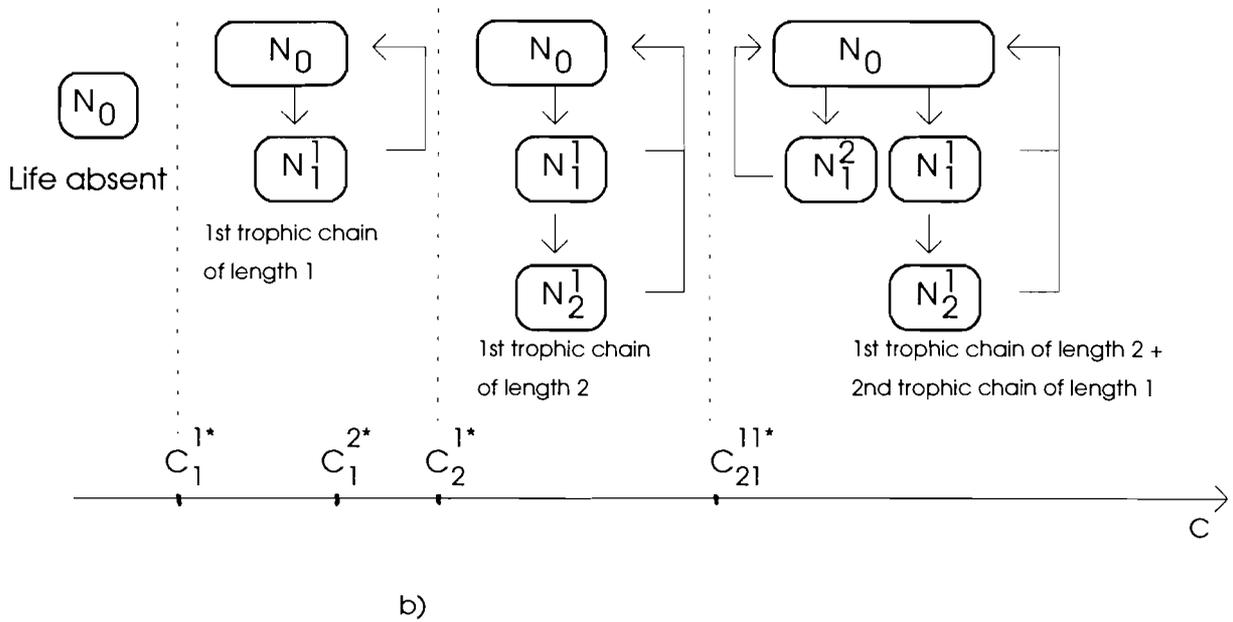
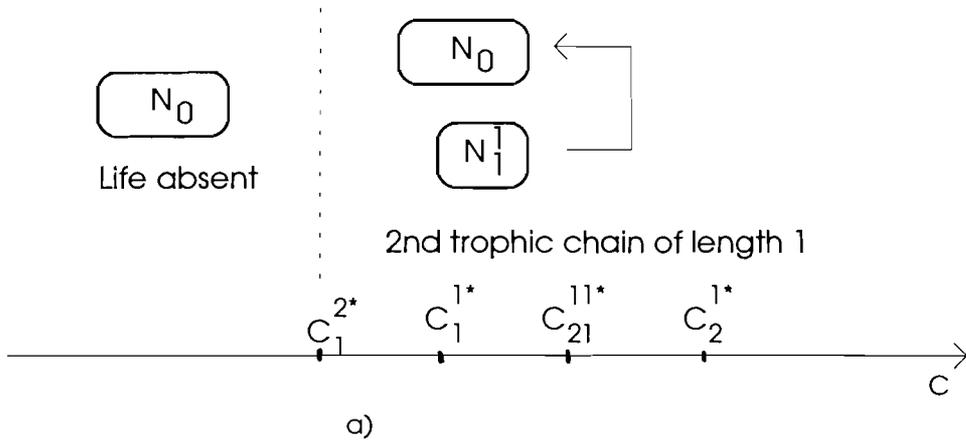


Figure 10. Changes in the system structure due to increase in the total quantity of substance, C :

a) $C_1^{2*} < C_1^{1*}$; b) $C_1^{1*} < C_1^{2*}$