MODEL OF EUTROPHICATION IN PREDATOR-PREY SYSTEMS

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PREFACE

In the past few years at IIASA, a set of investigations have been developing in two important directions: 1) the application of the phase portrait technique (know as the qualitative theory of differential equations, or catastrophe theory) to different kinds of systems, and 2) the development of mathematical models of water quality.

This paper is an attempt to understand the causes of loss of stability in ecological water systems that occurs under conditions of eutrophication (over-enrichment by nutrients) by means of mathematical analysis of a three-component ecological system. It is of an introductory character to the research on ecological models which will be conducted at IIASA in the future.

ABSTRACT

In this paper a model of a simple food-prey-predator system existing in a flow is built. The model predicts the emergence of shapr ipredator-prey oscillations when the initial food concentration is very high or the flow rate is very slow. The behavior of the model is compared with the effect of antropogenic eutrophication.

Model of Eutrophication in Predator-Prey Systems

1. INTRODUCTION

The problem of the stability of ecosystems has recently attracted the attention of many scientists and this can be explained by the increased importance of man-environment relationships in the contemporary world. What do we mean by stability of an ecosystem? What are the mechanisms which maintain the relatively constant structure of ecosystems under different conditions? What are the maximal permissible changes in the environment, etc.--these are the problems constantly treated in ecological papers.

Simplifying to a certain extent, we can say that today there are two basic approaches to the study of such problems. The first approach, known as imitational or simulation modelling, involves as complete and detailed a description of the structure and function of given natural ecosystems as possible. The ecosystem is described by systems which usually contain a very large number of differential or difference equations. The number of variables in a given case corresponds to the number of components in the ecosystem being described and can reach several dozen or hundred. The attractiveness of this kind of approach is that, when successful, it allows one to predict the real flow of events in a given ecosystem and thus to give valuable recommendations to decision makers. The weak point of the model is that one cannot test it experimentally (as in principle it is neither desirable nor possible to do experiments with natural ecosystems) nor can one carry out any kind of complete study of a system containing a great number of variables and expect to determine the qualitative characteristics of its behavior.

The second approach, that goes back to the classical works of G.F. Gause (1934), involves constructing experimental and mathe-

matical models of simple ecosystems which consist of a very small
number, let us say two, species. By comparing experimental data
with the predictions of the mathematical models one can evaluate
the validity of ideas concerning the mechanisms of the most funda-
mental ecological interrelations, such as competition, symbiosis
and predator-prey relationships. More than that, the modelling
of even such very primitive ecosystems can show nontrivial, a priori
non-predictable effects whose correct interpretation can help us
understand the relationships in the considerably more complicated
natural ecosystems. Special attention should evidently be devoted
to the investigation of predator-prey relationships as they are
basic to the trophical structure of any ecosytem.

Gause's pioneer experiments, by present-day standards metho-
dologically imperfect, could not give a definite answer to the
question of whether a stable coexistence of predator and prey
(absence of refuge for the prey being assumed) is possible and
whether the stable oscillations of population size predicted by
Volterra is likely to exist. It is surprising and at the same
time regretable that these widely known works did not enjoy any
further development for more than 30 years. It is only in the last
few years that some theoretical and experimental works, investi-
gating predator-prey systems under conditions of continuous culti-
vation, have appeared (Canale, 1970; Tsuchiya et al., 1972;
Ladygina and Pechuzkin, 1973; Bazin et al., 1974).

2. MODEL DEVELOPMENT

The purpose of the present study is a complete investigation
of the possible behavioral patterns for the predator-prey system
under conditions of continuous cultivation. Let us consider a tank
with liquid which is constantly being mixed so that the concentra-
tion of all the components may be considered the same throughout
the whole volume. Let the substrate - the substance which serves
as food for one of the species in the tank, namely, the prey -
enter the tank at a constant rate. In an actual experiment the
prey might be yeast, bacteria, etc. In addition, a second species,
a "predator" that feeds upon the prey, is present in the tank.
In the actual experiment the predator may be represented, for
instance, by some infusorian. The contents of the tank are con-

stantly being removed at the same rate at which the substrate enters, so that the total volume of the fluid remains constant.

Let us denote the substrate concentration in the liquid entering the tank from outside by s_o, the variable substrate concentration in the reservoir by s, the concentration of the prey by x, and the concentration of the predator by y. Let all the quantities be expressed in absolute units, e.g., gram per liter. Then the rates of change for the concentrations we are interested in can be described by the following system of differential equations:

$$\dot{s} = D(s_o - s) - xF(s,y)$$
$$\dot{x} = xG(s,y) - yH(s,x) - d_1x - Dx \qquad (1)$$
$$\dot{y} = yJ(s,x) - d_2y - Dy$$

where D is the rate of the flow or, more precisely, the fraction of the contents of the tank that is being replaced per unit time; $F(s,y)$, $H(s,x)$, $G(s,y)$, $J(s,x)$, d_1 and d_2 are, respectively, the relative rates for consumption of the substrate by the prey; consumption of the prey by the predator; the reproduction of the prey; the reproduction of the predator; death of the prey; and death of the predator. By the word "reproduction" we mean the increment in total biomass, and do not distinguish between increase in biomass due to the growth of the separate individual organisms and reproduction in the narrow sense of the word. The products of metabolism are not taken into account in the model.

With respect to the nature of the functions which enter into the system we shall make the following assumptions that are usually made when investigating continuous cultivation processes:

1. The natural death rate for both the predator and the prey is negligible in comparison to the rate of their removal from the reservoir. $\min\{d_1, d_2\} \ll D$.

2. The substrate consumed by the prey and the prey biomass are converted, respectively, into prey biomass and predator biomass; the conversion coefficients m_1 and m_2 called yield coefficients are considered to be constant.

3. The rate of substrate consumption by the prey does not depend on the concentration of the predator.

4. The consumption of the substrate by the prey and of the prey by the predator is described by a hyperbolic function known in enzymatic kinetics as the Michaelis-Menten law and in the physiology of microorganisms as Monod's formula. Essentially this means that at low substrate concentrations the relative rate of consumption increases linearly with the increase of the substrate concentration; at high substrate concentrations a saturation level is reached.

5. The reproduction of the predator and the consumption of the prey by the predator are inhibited by the substrate according to the formula of Jerusalimskii (Ladygina, Pechurkin, 1973).

With the above assumptions the system (1) becomes:

$$\dot{s} = D(s_o - s) - \mu_1 \frac{xs}{(K_1 + s)m_1}$$

$$\dot{x} = \mu_1 \frac{xs}{K_1 + s} - \mu_2 \frac{xy}{(K_2 + x)m_2} \cdot \frac{K_3}{K_3 + s} - Dx \qquad (2)$$

$$\dot{y} = \mu_2 \frac{xy}{K_2 + x} \cdot \frac{K_3}{K_3 + s} - Dy$$

where μ_1 and μ_2 are the maximal reproduction rates for prey and predator respectively; K_1 and K_2 are Michaelis constants for consumption of substrate by prey and consumption of prey by predator, respectively; K_3 is the substrate concentration at which the intensiveness of the predator's vital activity (i.e. consumption of prey and reproduction) is equal to half of the maximal.

In this way we have a system of three differential equations that is dependent on nine parameters; two of these parameters are determined by the cultivation conditions, D and s_o, and the remaining seven represent the ecological and physiological characteristics of the prey and the predator.

Here all the variables and parameters are measured in absolute physical units, except m_1 and m_2 which are dimensionless parameters. The qualitative characteristics of the system's behaviour

and, in particular, the number and character of the stability
of the fixed points and the limited cycles in the system generally
depend on the specific values of the parameters. The goal of
a complete qualitative study of the system is to determine the
regions within parametric space in which the system's behaviour
is qualitatively the same, i.e., to build a structural or a
parametrical portrait and to describe all the possible kinds of
qualitative behaviour of the system, that is, to build all the
dynamic or phase portraits of the system possible. It is worth
noting that often (Canale, 1970) study of the system's dynamic
behaviour is limited to only the second part of the problem -
the system's possible phase portraits are described without any
study of the values of the parameters at which this or that
behaviour of the system is realized.

The building of the structural portrait of the system becomes
much easier and the portrait itself much more transparent if one
converts from the absolute physical units used for the measurement
of the variables to dimensionless parameters "natural" for the
given system. It is important to note that the choice of such
"natural" units may vary for one and the same system. For instance,
in the above system one can have $1/\mu_1$ or $1/\mu_2$ or $1/D$ as units of
time; s_o or K_1 or K_2 as substrate concentration units. Formally
all methods for converting to dimensionless parameters are equi-
valent, but the structural portraits one gets using the new
dimensionless parameters are of course different; in some cases
one gets portraits that are easily and reasonably interpreted, in
others--portraits that are no more than purely formal structures.
Apparently no ready recipes exist for doing this, and choice of
the most adequate and convenient method for converting to dimension-
less parameters is by and large a matter of intuition.

Preliminary analysis has shown that for the given system
the most convenient conversion method is the following replacement
of variables:

$$t = \frac{m_1 K_1}{\mu_1 K_2} \tau \ , \quad s = K_1 \sigma \ , \quad x = K_2 u \ , \quad y = \frac{\mu_1 m_2 K_2^2}{\mu_2 m_1 K_1} v \ .$$

Accordingly system (2) becomes:

$$\dot{\sigma} = A(\sigma_o - \sigma) - \frac{\sigma u}{1 + \sigma}$$

$$\dot{x} = M_1 \frac{\sigma u}{1 + \sigma} - \frac{uv}{1 + u} \cdot \frac{K}{K + \sigma} - Au \qquad (3)$$

$$\dot{v} = M_2 \frac{uv}{1 + u} \cdot \frac{K}{K + \sigma} - Av$$

where $A = D\frac{m_1 K_1}{\mu_1 K_2}$ is the unitless rate of flow, $\sigma_o = \frac{S_o}{K_1}$ is the

unitless initial concentration of the substrate entering the

system, $M_1 = \frac{m_1 K_1}{K_2}$ and $M_2 = m_1 \frac{\mu_2 K_1}{\mu_1 K_2}$ are the coefficients,

respectively, for transformations of substrate into prey biomass
and of prey biomass into predator biomass, both determined using
the new scale for measuring the variables; $K = \frac{K_3}{K_1}$ is a dimension-
less constant characterising the degree to which the substrate
inhibits the prey population growth.

3. MODEL OPERATION

In this way we have a third order system that is dependent
on five parameters. It is worth noting that the parameters
quite naturally fall into two categories--M_1, M_2 and K are solely
dependent on the biological characteristics of the prey and the
predator, whereas A and σ_o are determined by the "controlled"
parameters of flow rate and initial substrate concentration. Full
investigation of such a system would have been very complicated
and difficult had it not been for two features that made our task
considerably easier.

In the first place it is not difficult to see that the
variable $M_1 M_2 \sigma + M_2 u + v = z$ satisfies the equation

$$\frac{dz}{dt} = M_1 M_2 A \sigma_o - Az ,$$

i.e., the plane

$$z = M_1 M_2 \sigma_o \qquad (4)$$

is the stable manifold of system (3). In addition all the fixed points of the system belong to this plane. In this way in the qualitative investigation we can restrict ourselves to analysis of the behaviour of the system on the plane $z = M_1 M_2 \sigma_0$, i.e., to the investigation of a second order system.

The significance of this plane is quite simple: it is a reflection of the conservation of organic matter in the system. The initial values of the variables may be arbitrary, but in a stationary state the input into the system should be equal to the output, i.e. the corresponding phase point should belong to the plane (4). This fact, that the surface representing the conservation of a constant amount of organic matter in the system is a plane, is connected to the constancy of the transformation coefficients for both the conversion of substrate into prey biomass, and for conversion of prey biomass into predator biomass ("yield coefficients"). Let us note that in the case of dimensionless variables the yield coefficients may be greater or smaller than one.

The second feature that makes investigation of the system considerably easier is the fact that we are interested in the dependence of the system's behaviour not on all parameters, but primarily only on the "controlled" parameters A and σ_0. Luckily it turns out that projection of the full five-dimensional structural portrait of the system on the plane of the controlled parameters $\{A, \sigma_0\}$ always has one and the same qualitative appearance, independent of the values M_1, M_2 and K. It reflects the overall topology of the portrait completely.

4. DISCUSSION

Not going into technical details we shall present the results of the investigation of system (3). The structural portrait of the system (fig. 1) has four regions, each of which corresponds to a particular qualitative behaviour of the system as reflected in the phase portraits (fig. 2a - d).

At values of the parameters corresponding to region (a) (low initial substrate concentrations and high flow rate) the system's only state of stable equilibrium (A) will be $\sigma = \sigma_0$, $u = v = 0$, which
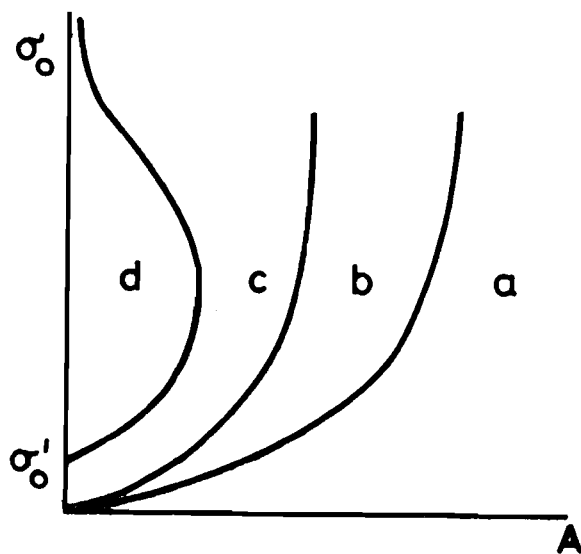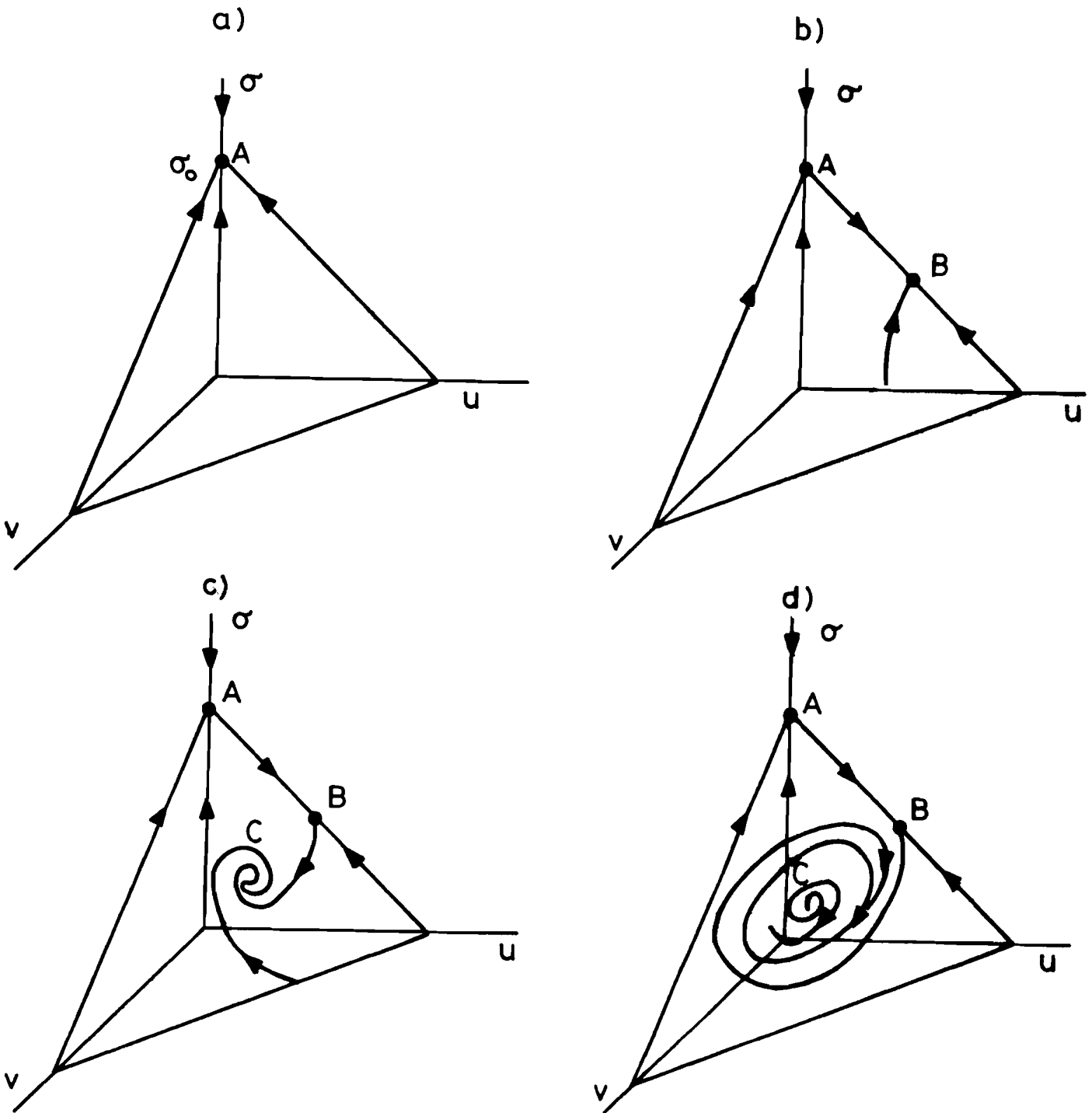
Figure 1: Parametric portrait of the system.

Figure 2: Phase portraits of the system.
Four kinds of qualitative behavior of the system.

corresponds to the well-known phenomenon of washing away the prey and predator populations. When one goes to region (b) of the paramtric space, point (A) loses its stability, becoming a saddle point, and a new stable node (B) is formed. This means that with parametric values lying in region (b) the prey culture is not washed away, but its stationary density is so low that it cannot feed the predator's population. With transition to region (c), point (B) in turn loses its stability, becoming a saddle point, and point (C) corresponding to stable predator-prey coexistence is formed.*

If the characteristic features of the system's behaviour up to this point have been completely understandable, easy to interpret and, generally speaking, qualitatively predictable on the basis of "common sense", further evolution of the system's behaviour, for instance as regards decrease of flow rate or growth of initial substrate concentration, seems not to be so obvious and cannot be deduced without strict mathematical analysis. It is true that "linear logic" would seem to indicate that with the growth of the initial substrate concentration one might expect equilibrium prey concentration to increase too (which is really the case in a prey monoculture); this in turn would lead to an increase in equilibrium prey concentration and to an increase in the system's stability since equilibrium concentration values gravitate away from zero. In reality the situation is completely different.

With transition to region (d) of the structural portrait, point (C) which corresponds to predator-prey coexistence loses its stability and a stable cycle is established in the system; this cycle corresponds to the stable oscillations of predator-prey densities (the oscillations of the densities have constant amplitudes and a period that is determined by the values of the parameters).

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*The character of this stability (C) may vary: the system that has been driven out of the equilibrium state can go back to it either monotonously (node) or through a process of damped oscillations (focus). In order not to make the structural portrait too complicated we do not draw the boundary node-focus lying in region (C).

It is even more difficult to predict on the basis of general considerations the peculiarities of the boundary of stability in the parameter space. It is a curious thing that this boundary does not cross the origin of the coordinates on the plane (A, σ_0); there is a certain "threshold" σ_0' below which there is no loss of stability. The behaviour of the boundary when σ_0 is high, depends on the constant K which characterizes the inhibition of predator vital activity caused by the substrate, but anyway this line approaches asymptotically to the σ_0-axis, when $\sigma_0 \rightarrow \infty$ (see fig. 1).

Inasmuch as this model's (2) realm of applicability has yet to be determined, it would obviously be premature to interpret subtle peculiarities of its behaviour for very low and high parametric values.

Another feature of the system that is difficult to demonstrate analytically but is clearly seen in numerical experiments seems to be of even greater importance. The limit cycle that originates at the border of regions c and d expands very quickly, approaching the coordinate axes of the phase portrait even when there are very small deviations of parametric values from the critical ones into region d. The limit cycle can approach either the abscissa (Fig. 3a) or the ordinate (Fig. 3b) depending on the values of the parameters. Essentially this means that in the minimum phase the size of one of the two population species diminishes greatly.

In practice a decrease in the number of organisms of less than, say, 10^{-5} of the original value (or to 10^{-3} or 10^{-7} depending on the biology of the given population) can usually be interpreted as a dying out of the population. In this way we can say that a small increase of the initial substrate concentration or a slowing down of the flow in comparison to their critical values in a continuous-cultivation prey-predator system will lead either to an impoverishing (extinction of the predator, Fig. 3a) or to complete degradation (extinction of the prey, Fig. 3b) of the system.*

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* It is curious to note that in our model one and the same phenomenon--the extinction of the predator--can be the consequence of two different, even diametrically, opposite, causes: (i) insufficient substrate supply in the system (Fig. 2b) and (ii) surplus supply (Fig. 3a).
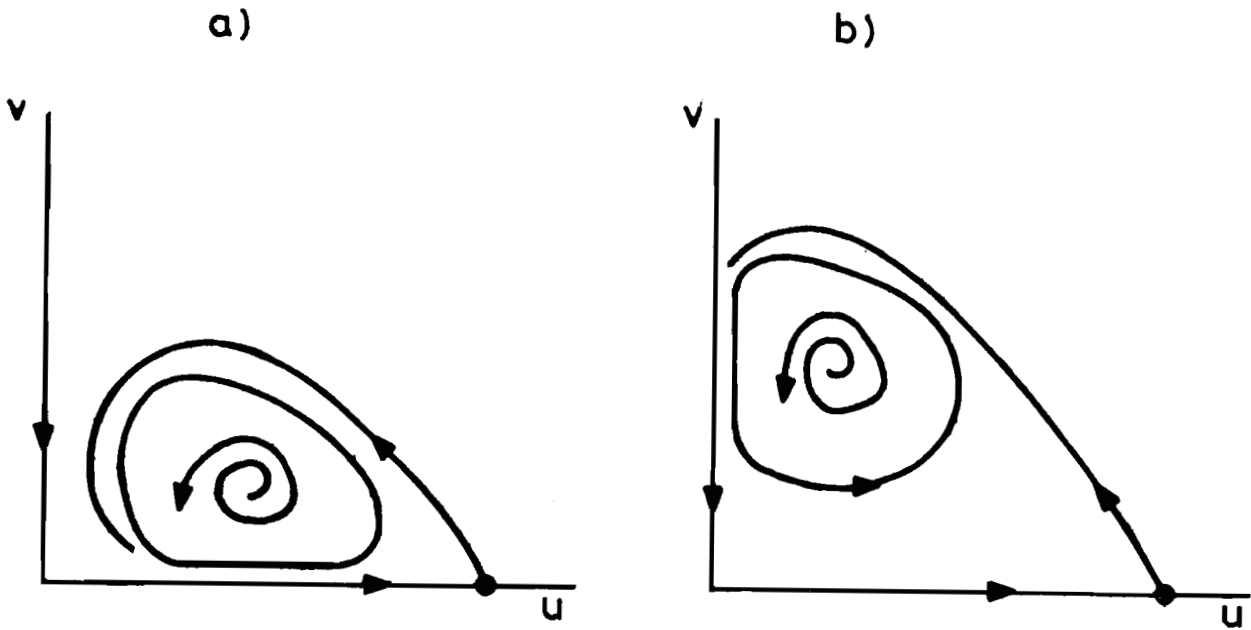
Figure 3: Two types of limit cycles
   a) Extinction of predator
   b) Complete degradation of the system

The resulting effect can be called "the effect of excess eutrophication" (oversaturation with biogenic elements).

The population explosion exhibited by individual species prior to the complete or partial degredation of an ecosystem may serve as indirect proof of the existence of such a mechanism of natural ecosystem stability loss--a mechanism connected with the emergence of intensive oscillations.

The fact that in our model a very narrow region in parametric space corresponds to limited amplitude oscillations can guide us in attempting to explain the well-known paradox, "the strange thing is not that in Nature regular oscillations in population size occur, but rather, that they occur so rarely".

We are aware of the fact that the notion of the narrowness of the region where limited oscillations exist is quite speculative for two reasons: first, since it has been the result of the investigation of a very specific case it can not, at least for the time being, pretend to be generally valid; second, in order to infer from the narrowness of the region in parametric space the rare occurrence in nature, it is necessary to assume to a certain extent the random distribution of ecosystems in parametric space. The latter is not at all self-evident; moreover, there are some considerations which indicate it is precisely the evolutionarily mature ecosystems that tend to exist in regions appropriate to stable oscillations (Molchanov, 1975).

5. CONCLUSIONS

Nonlinearity of interactions between different trophic levels (substrate-prey-predator) leads to unexpected effects which are not predictable without a mathematical model: increasing of food (substrate) concentrations (or decreasing of flow velocity) will lead to the loss of state stability corresponding to prey-predator coexistence and cause either predator extinction or complete system degradation.

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