

STABILITY ANALYSIS OF EUTROPHICATION MODELS

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Preface

One of the research tasks which the Resource and Environment Area of the Institute has addressed is the Models for Environmental Quality Control and Management. Over the past few years, much attention has been concentrated on the modeling of the water quality for rivers, lakes and reservoirs as one of the tools of control and management.

This report has been prepared as a contribution to the modeling problem of the lake eutrophication process, which comprises nutrients and plankton prey-predator elements. The particular concern of this paper is the stability analysis of the ecological water quality system in connection with the effect of the environmental forcing function, as well as the diffusion effect.

Abstract

In this paper characteristics of two eutrophication models are investigated with phase plane analysis of the equilibrium states of the system. Possible patterns of the system's behaviour and their relations to ranges of parameters are shown. The results are used to evaluate the effects of disturbances to the system. Finally, the effects of diffusion on the system's behaviour are discussed and some numerical results are presented.

1. Introduction

Several ecological water quality models for lakes or reservoirs have been set up over the last few years [1, 2]. These models are now recognized as being useful for the prediction and management of water quality. Most of the work in this field is simulation.

Computer simulation is a powerful tool for such large and complex systems as those of water quality. However, we have to pay attention to its limits. With computer simulation, we can only determine the system's behaviour for given initial states and specific values of parameters in the model. It is clearly impossible to carry out simulations under all possible conditions. We cannot obtain a complete understanding of a system through simulations alone. On the other hand, we will have to have a much better understanding of the system's basic features when the necessity for developing larger and more detailed models increases.

The purpose of stability analysis is to understand the system's behaviour qualitatively. We are concerned with the possible patterns of behaviour of a system and their relations to values of parameters which are included in the system. Although the mathematical theory of stability has a long history, complete analysis of stability is generally only possible for very simplified systems. Therefore, we

have to simplify the models in order to apply the existing results of stability theory. The results obtained by the analysis for the simplified models may hold only for restricted conditions in a real system. However, the knowledge is important. It provides us with preliminary information with which to build more practical models or to select the conditions for simulations with the models and, also to interpret their simulations results. The knowledge is also important in the sense that it suggests problems to be investigated in more detail.

In this paper some results of stability analysis for simplified eutrophication models are presented. The results obtained are applied to evaluate the effects of environmental variations on the system's behaviour.

2. Eutrophication Models

Let us consider a constant and completely mixed volume of lake water. The major limiting nutrients for phytoplankton growth are assumed to be various forms of nitrogenous and phosphoric compounds. For the sake of simplicity these nutrients are represented by inorganic nitrogen and total phosphorous. The schematic diagram of the nutrient cycles in the water volume is shown in Fig. 1. We make the following basic assumptions:

- 1) The biodegradation of organic nitrogen into inorganic nitrogen is a first order reaction.
- 2) The reproduction rate of phosphorous is proportional to that of nitrogen.
- 3) There is no loss of material due to sedimentation.

On these assumptions the dynamic representation of the system can be derived from the mass-balance equations:

$$\frac{dN_o}{dt} = -KN_o + D_p P_n + D_z Z_n + D_g P_n - G_z Z_n + q(S_{N_o} - N_o); \quad (1)$$

$$\frac{dN_i}{dt} = KN_o - G_p P_n + q(S_{N_i} - N_i); \quad (2)$$

$$\frac{dP_n}{dt} = (G_p - D_p - D_g) P_n + q(S_{P_n} - P_n); \quad (3)$$

$$\frac{dZ_n}{dt} = (G_z - D_z) Z_n + q(S_{Z_n} - Z_n); \quad (4)$$

$$\frac{dP_h}{dt} = \{(D_p + D_g - G_p) P_n + (D_z - G_z) Z_n\} \theta + q(S_{P_h} - P_h), \quad (5)$$

where the notation is defined as follows:

N_o : organic nitrogen concentration (mg/liter)

N_i : inorganic nitrogen concentration (mg/liter)

P_n : biomass of phytoplankton measured by its nitrogen concentration
(mg/liter)

Z_n : biomass of zooplankton measured by its nitrogen concentration
(mg/liter)

P_h : phosphorous concentration (mg/liter)

K : rate of degradation of N_o (1/day)

G_z : growth rate of zooplankton (1/day)

G_p : growth rate of phytoplankton (1/day)

D_p, D_z : extinction rate of phytoplankton and zooplankton respectively
(1/day)

D_g : grazing rate of phytoplankton by zooplankton (1/day)

$S_{N_o}, S_{N_i}, S_{P_h}$: influent concentration of organic nitrogen, inorganic
nitrogen and phosphorous, respectively (mg/liter)

S_{P_n}, S_{Z_n} : influent concentration of phyto- and zooplankton,
respectively (mg/liter)

q : the inverse of detention time (1/day)

θ : average ratio of nitrogen and phosphorous in plankton (P_h/N).

The phytoplankton growth rate G_p is a function of the nutrients concentrations N_i and P_h . The zooplankton growth rate depends on phytoplankton concentration P_n . We assume that the growth rates are represented by monotone-increasing and saturated functions of the respective variables;

$$G_p = \mu \bar{G}_p(P_h, N_i) \quad (6)$$

$$\bar{G}_p(P_h, N_i) \rightarrow 1 \text{ as } P_h \rightarrow +\infty \text{ and } N_i \rightarrow +\infty, \quad (7)$$

$$\bar{G}_p(0, N_i) = \bar{G}_p(P_h, 0) = 0 \quad (8)$$

$$\frac{\partial \bar{G}_p}{\partial P_h} > 0 \text{ and } \frac{\partial \bar{G}_p}{\partial N_i} > 0 \text{ for } P_h > 0 \text{ and } N_i > 0. \quad (9)$$

μ is a saturated photosynthesis rate of phytoplankton and it depends on water temperature (T) and light intensity (I).

Similarly the following restrictions are imposed on zooplankton growth rate G_z :

$$G_z = \beta \bar{G}_z(P_n), \quad (10)$$

$$\bar{G}_z(0) = 0, \quad (11)$$

$$\bar{G}_z(P_n) \rightarrow 1 \text{ as } P_n \rightarrow +\infty, \quad (12)$$

$$\frac{\partial \bar{G}_z(P_n)}{\partial P_n} > 0 \text{ for } P_n > 0. \quad (13)$$

Further we assume that the derivative of \bar{G}_z is bounded so that

$$\frac{\partial \bar{G}_z(P_n)}{\partial P_n} < \frac{\bar{G}_z(P_n)}{P_n} \text{ for } P_n \geq 0. \quad (14)$$

The typical representations of the growth functions which satisfy the above conditions are known as Monod's formula or as the Michaelis-Menten law. That is,

$$G_p = \mu \left(\frac{P_h}{K_p + P_h} \cdot \frac{N_i}{N_i + K_n} \right) , \quad (15)$$

and

$$G_z = \beta \left(\frac{P_n}{K_z + P_n} \right) . \quad (16)$$

The parameters K_p , K_n and K_z are called Michaelis' constants.

We assume also that grazing rate depends linearly on zooplankton concentration;

$$D_g = \alpha Z_n , \quad (17)$$

where α is a constant parameter. The extinction rates of plankton are closely related to endogeneous respiration rates, so that D_p and D_z are parameters which depend on temperature.

The final purpose of the study is to know the qualitative behaviour of systems (1)-(5) under conditions (6)-(14) and (17). It is, however, difficult to discuss the model directly because the number of parameters and variables is too large. From the structure of the model we can reasonably suppose that the nitrogen and the phosphorous play similar roles in the system's dynamics. Therefore, let us discuss the dynamic characteristics of the system under the condition that only one nutrient is the limiting factor for the growth of phytoplankton. In other words the concentration of the phosphorous is assumed to be sufficiently large. Then the representations of the system are simplified as follows:

Model I

$$\frac{dN_o}{dt} = -KN_o + (D_p + \alpha Z_n)P_n + (D_z - G_z)Z_n + q(S_{N_o} - N_o); \quad (18)$$

$$\frac{dN_i}{dt} = KN_o - G_p P_n + q(S_{N_i} - N_i); \quad (19)$$

$$\frac{dP_n}{dt} = (G_p - D_p - \alpha Z_n)P_n + q(S_{P_n} - P_n); \quad (20)$$

$$\frac{dZ_n}{dt} + (G_z - D_z)Z_n + q(S_{Z_n} - Z_n) = 0. \quad (21)$$

The notations are the same as in equation (1)-(5). And G_p and G_z satisfy the conditions:

$$G_p = \mu \bar{G}_p(N_i), \quad (22)$$

$$\bar{G}_p(0) = 0 \text{ and } \bar{G}_p(N_i) \rightarrow 1 \text{ as } N_i \rightarrow \infty, \quad (23)$$

$$0 < \frac{\partial \bar{G}_p}{\partial N_i}, \quad \text{for } N_i \geq 0, \quad (24)$$

$$G_z = \beta \bar{G}_z(P_n), \quad (25)$$

$$\bar{G}_z(0) = 0 \text{ and } \bar{G}_z(P_n) \rightarrow 1 \text{ as } P_n \rightarrow \infty, \quad (26)$$

$$0 < \frac{\partial \bar{G}_z(P_n)}{\partial P_n} < \frac{\bar{G}_z(P_n)}{P_n} \text{ for } P_n \geq 0. \quad (27)$$

A further simplification of Model I is possible when two forms of nitrogen are integrated into one compartment. Denoting the total nitrogen concentration by N we have Model II.

Model II

$$\frac{dN}{dt} = (D_p + \alpha Z_n - G_p)P_n + (D_z - G_z)Z_n + q(S_N - N); \quad (28)$$

$$\frac{dP_n}{dt} = (G_p - D_p - \alpha Z_n)P_n + q(S_{P_n} - P_n); \quad (29)$$

$$\frac{dZ_n}{dt} = (G_z - D_z)Z_n + q(S_{Z_n} - Z_n). \quad (30)$$

The growth rates G_p and G_z satisfy the conditions (22)-(27) with N in place of N_i . The parameter values in Model II may be different from those in Model I; the same notations are used for simplicity. As mentioned previously, the parameters μ , D_p and D_z depend on such environmental factors as temperature and intensity of radiation. However, we will first discuss the system's behaviour when the environmental conditions do not vary. Therefore these parameters will be fixed for the present.

3. Stability of Batch Process

Let us consider stability of Model I and Model II in the case where there are no inflows and outflows to the system. That is, we investigate dynamic behaviour of batch process of the predator-prey system with one limiting substrate. In this case, the systems conserve the total amount of nitrogen, since $q=0$.

$$N + P_n + Z_n = C_o \quad (\text{a constant}), \quad (31)$$

or

$$N_o + N_i + P_n + Z_n = C_o \quad (32)$$

If this property is taken into account, stability analysis can be carried out easily. Without going into detailed calculations, the results of the analysis will be shown (refer to S. Ikeda and N. Adachi [3]).

3-1 Stability of Model II

It should be noted that the amount of phytoplankton grazed by zooplankton per unit time must be greater than the rate of zooplankton growth:

$$(\alpha P_n - G_z) Z_n \geq 0 \quad ,$$

$$\text{or} \quad \frac{\alpha}{\beta} \geq \frac{\bar{G}_z(P_n)}{P_n} . \quad (33)$$

Therefore we assume that inequality (33) holds for every $P_n \geq 0$.

This condition is also necessary to ensure that the models are well-posed.

In other words, under this condition every solution of Model I and Model II remains nonnegative (positive) if its initial values are nonnegative (positive).

From relation (31) of nitrogen conservation one variable, e.g., N , can be deleted from equations (28)-(31). Then

$$\frac{dP_n}{dt} = \{ \mu \bar{G}_p (C_o - P_n - Z_n) - D_p - \alpha Z_n \} P_n ; \quad (34)$$

$$\frac{dZ_n}{dt} = \{ \beta \bar{G}_z (P_n) - D_z \} Z_n . \quad (35)$$

The equilibrium states of system (34) and (35) can be obtained by equating the right-hand sides of the equations to zeros. Stability of these equilibrium states can be classified completely since the system of equations is a two-dimensional one. The stability analysis of the equilibrium state can be carried out by the perturbation method for equations (34) and (35). The equations are linearized around the state. The characteristic equation for the linearized equations determines the stability of the state. For an example let us consider the case where the system has a positive equilibrium state (B, C) :

$$\begin{aligned} \mu \bar{G}_p (C_o - B - C) - D_p - \alpha C &= 0 \\ \beta \bar{G}_z (B) - D_z &= 0 \\ \beta > 0, C > 0 \text{ and } B + C < C_o . \end{aligned}$$

The characteristic equation of the linearized equations around (B, C) is

$$\lambda^2 + \sigma \lambda + \delta = 0 ,$$

where $\sigma = \mu \bar{G}'_p (C_0 - B - C) B$,

$$\delta = \mu \beta B C \bar{G}'_z(B) \{ \alpha + \mu \bar{G}'_p (C_0 - B - C) \},$$

and \bar{G}'_p or \bar{G}'_z are derivatives of \bar{G}_p or \bar{G}_z respectively.

From the assumptions on \bar{G}_p and \bar{G}_z , $\sigma > 0$ and $\delta > 0$. Therefore the point (B, C) is a stable node if $\sigma^2 - 4\delta > 0$ and a stable spiral if $\sigma^2 - 4\delta < 0$.

The results derived by the same procedures are summarized as follows. Only the three configurations of the equilibrium states are possible.

A_1 : Only one equilibrium state $(0, 0)$ on the phase plane of (P_n, Z_n) appears and it is stable.

A_2 : The two equilibrium states $(0, 0)$ and $(A, 0)$ appear and $(0, 0)$ is unstable (saddle point) and $(A, 0)$ is stable (node).

A_3 : Three equilibrium states $(0, 0)$, $(A, 0)$ and (B, C) exist and only (B, C) is stable (node or spiral). $(0, 0)$ and $(A, 0)$ are unstable (saddle points), $(B < A \text{ and } B + C < C_0)$.

Model II takes one of the three patterns depending on the values of the parameters. In the cases of A_1 and A_2 , every trajectory on the phase plane (P_n, Z_n) converges to the unique stable equilibrium state with the increase of time. The local analysis of the equilibrium state does not exclude the existence of stable limit cycles. Therefore, in the third case, the point (B, C) is a global attractor, or there exists a stable limit cycle, which surrounds the point. The existence of a limit cycle is of mathematical interest. However, its possibility is very small since the point (B, C) is always stable. Therefore, we assume hereafter that (B, C) is a global attractor. Under this assumption, every trajectory approaches (B, C) with time increasing, if the initial state is positive.

The phase portraits of trajectories corresponding to the above A_1 , A_2 and A_3 are shown in Fig. 2. In the first pattern (A_1) both phytoplankton and zooplankton extinguish. In the second case (A_2) zooplankton extinguishes, but phytoplankton retains a constant biomass. In the last case (A_3) concentrations of phytoplankton and zooplankton converge to their respective values as time increases. The regions in parametric space corresponding to each pattern are illustrated in Fig. 3. If the maximum growth rate of phytoplankton μ is less than the extinction rate D_p or if the total amount of nitrogen C_o is very small only pattern A_1 is possible. If the maximum growth rate of zooplankton β is less than the extinction rate D_z or if C_o is too small, only patterns A_1 and A_2 can appear. In the case where $\beta > D_z$, $\mu > D_p$ and C_o is greater than a certain value, pattern A_3 is possible. The typical trajectories of the system which correspond to A_3 are shown in Fig. 4. In this example the Monod type growth functions are used and the equilibrium points are $(0,0)$, $(0.994, 0)$ and $(0.24, 0.53)$ and $C_o=1.0$. As seen in the figure when the initial point has small values first only P_n increases rapidly and then Z_n follows. This phenomenon occurs because for the standard values of parameters the second equilibrium point is very close to $(C_o, 0)$.

3-2 Stability of Model I

The same approach as to Model II can be applied to Model I represented by equations (18)-(21). Let us consider trajectories of the system in a three-dimensional space of (N_i, P_n, Z_n) because one variable can be deleted from relation (32). The results of the analysis of the equilibrium states are summarized as follows.

One of the following cases appears depending upon the values of the parameters.

$B_1 : (N_1, P_n, Z_n) = (C_0, 0, 0)$ is the only equilibrium state and it is stable.

B_2 : The two equilibrium state exist, $(C_0, 0, 0)$ is unstable and $(D, A, 0)$ is stable, where $0 < D$, $0 < A$ and $D + A < C_0$.

B_3 : Three equilibrium states $(C_0, 0, 0)$, $(D, A, 0)$ and (E, B, C) exist and only (E, B, C) is stable, where $0 < E$, $0 < B$, $0 < C$ and $E + B + C < C_0$.

In the third case let the characteristic equation of the linearized equation around (E, B, C) be

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0.$$

The coefficients a_1 , a_2 and a_3 can easily be shown to be positive.

Then it is sufficient to show that $a_1 a_2 - a_3 > 0$ in order to prove the stability of (E, B, C) . By some troublesome calculations

$$a_1 a_2 - a_3 = \mu \bar{G}_p'(E) B \{ K^2 + K(D_p + \mu \bar{G}_p'(E) B + C(\alpha - \beta \bar{G}_z'(B))) \}.$$

From conditions (27) and (33) $\alpha > \beta \bar{G}_z'(B)$, therefore $a_1 a_2 - a_3 > 0$. Then Hurwitz's criterion ensures that (E, B, C) is a stable equilibrium state. It is to be noted that condition (27) is sufficient for (E, B, C) to be stable. This is not the case for Model II. The region of parameter values corresponding to the each pattern is given by exactly the same figure as Fig. 3, where A_1 , A_2 and A_3 are replaced by B_1 , B_2 and B_3 respectively. The above results are interesting. The trajectories of the system are considered in a three-dimensional space of (N_1, P_n, Z_n) . However, if they are projected on (P_n, Z_n) plane the configurations of the equilibrium states are the same as those of Model II. Therefore, as far as the behavior of (P_n, Z_n) is concerned they are supposed to have patterns similar to those of Model II. This fact gives us a reasonable possibility to understand the characteristics of the system

through investigations of Model II.

4. Stability of Process with Constant Flow Rate

Let us discuss the case when the nitrogenous nutrients flow into the system at a constant rate. Model II will be used to examine possible patterns of the behaviour of the system. In other words we are concerned with stability of Model II on the assumption that

$$S_N = \text{a constant}$$

$$q = \text{a constant}$$

$$S_{P_n} = S_{Z_n} = 0.$$

In this case the conservation of total nitrogen does not hold. However, from equations (28)-(30),

$$\frac{d(N+P_n+Z_n)}{dt} = -q(N+P_n+Z_n) + qS_N, \quad (36)$$

so that every trajectory of system (28)-(30) approaches the plane

$$N+P_n+Z_n = S_N \quad (37)$$

as time increases, and the plane is an invariant manifold of the system.

Therefore, we can understand the qualitative behaviour of Model II by restricting the investigations on the two-dimensional plane (37).

The study of the equilibrium points on the plane shows that results similar to those in the preceding batch process hold. One of the following patterns appears, depending upon the values of the parameters:

C_1 : $(S_N, 0, 0)$ is only equilibrium state and it is stable;

C_2 : Two equilibrium states $(S_N, 0, 0)$ and $(D, A, 0)$ appear ,
 $(S_N, 0, 0)$ is unstable and $(D, A, 0)$ is stable ($D+A=S_N$);

C_3 : Three equilibrium states $(S_N, 0, 0)$, $(D, A, 0)$ and (E, B, C) exist and only (E, B, C) is stable, where $E+B+C=S_N$.

In this way, we can say that the possible patterns of behaviour of the system with constant nutrient inflow do not change compared with those of the batch process. The regions in the parametric space of (q, S_N) , corresponding to the above three patterns, are illustrated in Fig. 5. The two cases are possible according to the ratio of $(\beta-D_z)$ and $(\mu-D_p)$. In both cases, the increase of flow rate changes the system's dynamic patterns from C_3 to C_2 and then to C_1 . In other words, by increasing the flow rate, first zooplankton and then phytoplankton is washed out. Conversely, if the influent concentration of nutrients increases, the system's dynamic pattern goes from C_1 to C_2 and to C_3 . From the figure, it is also seen that if the flow rate is larger than a certain value, phytoplankton and zooplankton can never coexist. This is also true when the influent concentration is smaller than a certain value.

Recently Aponin and Bazykin demonstrated an interesting result [4]. They investigated behaviour of a prey-predator system under the conditions of continuous cultivation. They found out that a fourth pattern exists in addition to the above three patterns. That is, they showed the existence of a stable limit cycle for a certain region in the parametric space of (q, S_N) . The result is derived from their assumptions on the model. They assumed that the reproduction of the predator and the consumption of the prey by the predator are inhibited by the substrate concentration. Since the inhibition effects are not incorporated in Model I and Model II the fourth pattern does not appear in our analysis.

5. Effects of Parameter Variations

The possible patterns of the system's behaviour have been examined in the preceding two sections, both for a batch process and for a process with a constant rate of nutrient inflow. As seen in the discussions, the motion of the system is determined by the configurations of the equilibrium states. The patterns of the equilibrium states depend on the values of parameters which are included in the system's model. In this section, let us apply the results to evaluate the effects of external disturbances on the system's motion.

Consider a general mathematical model of a dynamical system:

$$\frac{dx}{dt} = f(x, \pi) , \quad (38)$$

where $x=(x_1, x_2, \dots, x_n)$ is an n-dimensional vector and $f=(f_1, f_2, \dots, f_n)$ is a vector function which depends on a scalar parameter π , and f is assumed to be continuously differentiable with respect to x and π . For a given value of π an equilibrium point $x=x^*(\pi)$ satisfies equation

$$f(x^*(\pi), \pi) = 0. \quad (39)$$

Then the variation of $x^*(\pi)$ because of a small change of π is determined from the linear algebraic equation :

$$\sum_{j=1}^n \frac{\partial f_i}{\partial x_j} \cdot \frac{\partial x_j^*}{\partial \pi} = - \frac{\partial f_i}{\partial \pi} , \quad (40)$$

or
$$\frac{\partial x^*}{\partial \pi} = - F^{-1} \frac{\partial f}{\partial \pi} , \quad (40)$$

where F is an $n \times n$ matrix such that its element f_{ij} is

$$f_{ij} = \frac{\partial f_i}{\partial x_j}$$

and F is supposed to be nonsingular.

Therefore, the effects of a small change in parameter values on the location of the equilibrium state can be evaluated from (40), if the variational matrix F and $\partial f/\partial \pi$ are known.

5.1 Effect of Temperature and Light Intensity

In the preceding analysis of the stability of the system, water temperature and intensity of solar radiation (I) are fixed. In reality, however, the stable equilibrium point moves according to variations of T and I . Consequently if T and I vary continuously and slowly, P_n and Z_n are expected to follow the continuous movement of the unique stable state. We consider the system when there is no inflow and outflow, and use Model II since the behavioural patterns of both models are supposed to be similar. We assume that the maximum growth rate μ of phytoplankton depends on T and I and that the extinction rates D_p and D_z depend on T . The other parameters are assumed to be independent of T and I . Various practical functions are proposed for the growth and death rates of plankton [2]. Here we make the following general assumptions on μ , D_p and D_z :

$$\frac{\partial \mu}{\partial T} > 0, \quad \frac{\partial D_p}{\partial T} > 0 \quad \text{and} \quad \frac{\partial D_z}{\partial T} > 0, \quad (41)$$

and

$$\frac{\partial \mu}{\partial I} > 0 \quad \text{for} \quad I < I_{opt}, \quad (42)$$

$$\frac{\partial \mu}{\partial I} < 0 \quad \text{for} \quad I > I_{opt}.$$

I_{opt} is an optimal light intensity for photosynthesis. Concerning the biological implications of the assumptions see e.g. Di-Toro et. al.[5].

Denoting the right hand sides of equations (34) and (35) by f_1 and f_2 respectively,

$$\frac{\partial f_1}{\partial T} = \left(\frac{\partial \mu}{\partial T} \bar{G}_p - \frac{\partial D_p}{\partial T} \right) P_n ,$$

$$\frac{\partial f_2}{\partial T} = - \frac{\partial D_z}{\partial T} Z_n ,$$

and

$$\frac{\partial f_1}{\partial I} = \frac{\partial \mu}{\partial I} \bar{G}_p P_n ,$$

$$\frac{\partial f_2}{\partial I} = 0 .$$

The variational matrix F has been used in the analysis of the stability of the equilibrium states. Therefore the procedures mentioned can be applied. The results derived are the following:

$$\begin{aligned} \frac{\partial A}{\partial T} > 0 & \quad \text{if} \quad \frac{\partial}{\partial T} (\mu \bar{G}_p - D_p) > 0 , \\ & < 0 & \quad \text{if} \quad \frac{\partial}{\partial T} (\mu \bar{G}_p - D_p) < 0 , \end{aligned} \tag{43}$$

$$\begin{aligned} \frac{\partial A}{\partial I} > 0 & \quad \text{if} \quad I < I_{opt} , \\ & < 0 & \quad \text{if} \quad I > I_{opt} . \end{aligned} \tag{44}$$

Concerning equilibrium state (B, C),

$$\frac{\partial B}{\partial T} > 0 \quad \text{and} \quad \frac{\partial B}{\partial I} = 0 , \tag{45}$$

$$\begin{aligned} \frac{\partial C}{\partial I} > 0 & \quad \text{if} \quad I < I_{opt} , \\ & < 0 & \quad \text{if} \quad I > I_{opt} . \end{aligned} \tag{46}$$

As shown in Fig. 4 trajectories of (P_n, Z_n) have an interesting feature for the standard ranges of parameters in the model, when the relative position between the stable equilibrium state and the initial state (P_n^0, Z_n^0) is one such that $B > P_n^0$ and $C > Z_n^0$, P_n increases rapidly. In other words, if the external disturbances are given to the system so that (B, C) moves to $(B+\Delta B, C+\Delta C)$ ($\Delta B > 0$ and $\Delta C > 0$) rapid growth of phytoplankton will be observed. From (45) and (46) such a situation is possible when temperature and light intensity change discontinuously so that

$$T \rightarrow T + \Delta T \quad (\Delta T > 0)$$

$$I \rightarrow I + \Delta I \quad \text{if } I < I_{opt}$$

$$I - \Delta I \quad \text{if } I > I_{opt}.$$

After the changes of T and I (P_n, Z_n) moves toward the new equilibrium state (B', C') as shown in Fig. 6.

5.2 Nutrient Enrichment and Variation of Flow Rate

Let us apply the procedures of sensitivity analysis to the equilibrium state of Model II with a constant rate of influent nutrients. Restricting the analysis on the plane $P_n + Z_n + N = S_N$ as in Section 4 the following results are obtained:

$$\frac{\partial A}{\partial S_N} > 0, \quad \frac{\partial B}{\partial S_N} = 0 \quad \text{and} \quad \frac{\partial C}{\partial S_N} > 0, \quad (47)$$

$$\frac{\partial A}{\partial q} < 0, \quad \frac{\partial B}{\partial q} > 0 \quad \text{and} \quad \frac{\partial C}{\partial q} < 0. \quad (48)$$

From (47) and (48) we can know the movements of the equilibrium states when S_N or q change continuously. Suppose that the system is at a steady state (E, B, C) . When q increases, phytoplankton increases but zooplankton decreases. The further increase of q extinguishes the equilibrium state

(E, B, C), (see Fig. 7) Fig. 8 shows a similar movement of the equilibrium states when the influent nutrients decrease.

Let us consider now the case when the concentration of influent nutrients increases suddenly. The increase of the concentration brings about the change of the state (B, C) to (B, C+ΔC) ΔC>0 (Fig. 9). As a result, the growth of phytoplankton will be observed. The analogous behaviour of the system will be observed when the concentrations of phytoplankton and zooplankton decrease suddenly due to dilution of the system. Although the state of the system changes from (B, C) to (B-ΔB, C-ΔC), (ΔB, ΔC>0) by dilution the location of the stable equilibrium point is not affected. Consequently (P_n, Z_n) moves toward the equilibrium state as shown in Fig. 10.

6. Effect of Diffusion on Stability

In the preceding sections, we have discussed the stability of equilibrium states and possible patterns of plankton behaviour in a completely mixed volume of lake water. On the other hand spatial distribution of plankton population plays, in some cases, an important role in plankton bloom mechanism due to the formation of plankton patchiness in the lake water. Therefore, let us examine effects of the diffusion process on the stability of the system. As a preliminary analysis of the diffusion process, let us use Model II with diffusion terms but with no flows. We assume uniform concentrations in vertical sections of a closed water volume. Using Monod type growth functions:

$$\begin{aligned} \frac{\partial N}{\partial t} = D_1 \frac{\partial^2 N}{\partial x^2} + (D_{PT} + \alpha Z_n - \mu \frac{N}{K_n + N}) P_n ; \\ + (D_{ZT} - \beta \frac{P_n}{K_{mp} + P_n}) Z_n ; \end{aligned} \quad (49)$$

$$\frac{\partial P_n}{\partial t} = D_2 \frac{\partial^2 P_n}{\partial x^2} + \left(\mu \frac{N}{K_n + N} - D_{PT} - \alpha Z_n \right) P_n ; \quad (50)$$

$$\frac{\partial Z_n}{\partial t} = D_3 \frac{\partial^2 Z_n}{\partial x^2} + \left(\beta \frac{P_n}{K_{mp} + P_n} - D_{ZT} \right) Z_n , \quad (51)$$

where D_1 , D_2 and D_3 are diffusion coefficients and notations of other parameters are the same as those of the batch process.

For simplicity of the mathematical expression, let us introduce the following vector notations:

$$\begin{aligned} u &= (N, P_n, Z_n) \\ f(u) &= (f_1, f_2, f_3) \\ F &= (D_1, D_2, D_3) \end{aligned}$$

where f_1 , f_2 and f_3 are the biological interaction terms in the right hand sides of equations (49)-(51), respectively.

Then, the system (49)-(51) can be written in the form

$$\frac{\partial}{\partial t} u = D \frac{\partial^2}{\partial x^2} u + f(u) . \quad (52)$$

The initial and boundary conditions are

$$u(0, x) = u_0(x), \quad 0 \leq x \leq L \quad (53)$$

and

$$\frac{\partial}{\partial x} u(t, 0) = \frac{\partial}{\partial x} u(t, L) = 0, \quad t \geq 0. \quad (54)$$

This boundary condition means that there is no flow across the boundary of the concerned water volume, and the problem of solving equations (52)-(54) is called the Neuman problem.

In connection with stability analysis of the above Neuman problem we are concerned with spatially homogeneous equilibrium states of system (52)-(54), which satisfies the equation:

$$f(u) = 0. \quad (55)$$

Hence the equilibrium states are identical with those of the batch process discussed in Section 3. In the following let us examine the stability of the equilibrium state only in the case of equal diffusion coefficients and show a simple simulation example.

6.1 Stability Analysis of Model II with Equal Diffusion Coefficients

Let us define total nitrogen $C(t,x)$

$$C(t,x) = N(t,x) + P_n(t,x) + Z_n(t,x) \quad (56)$$

Then the system (49)-(51) can be written

$$\frac{\partial C}{\partial t} = D_1 \frac{\partial^2 N}{\partial x^2} + D_2 \frac{\partial^2 P_n}{\partial x^2} + D_3 \frac{\partial^2 Z_n}{\partial x^2} . \quad (57)$$

Further assume that

$$D_1 = D_2 = D_3 = d \quad (58)$$

then

$$\frac{\partial C}{\partial t} = d \frac{\partial^2 C}{\partial x^2} \quad (59)$$

This equation means that total nitrogen approaches a spatially homogeneous constant distribution as $t \rightarrow \infty$; $C(t,x) = C_0$.

Therefore, we confine the stability analysis of the diffusion effect to the Model II within behaviour of the system on the manifold of

$$N(t,x) + P_n(t,x) + Z_n(t,x) = C_0 . \quad (60)$$

Making use of relation (60) to system of (49)-(51), we can reduce the number of equations from three to two in the same way as in equations (34) and (35):

$$\frac{\partial P_n}{\partial t} = d \frac{\partial^2 P_n}{\partial x^2} + \left(\mu \frac{C_o - P_n - Z_n}{K_n + C_o - P_n - Z_n} - D_{pT} - \alpha Z_n \right) P_n ; \quad (61)$$

$$\frac{\partial Z_n}{\partial t} = d \frac{\partial^2 Z_n}{\partial x^2} + \left(\beta \frac{P_n}{K_{mp} + P_n} - D_{ZT} \right) Z_n , \quad (62)$$

or

$$\frac{\partial \bar{u}}{\partial t} = d \frac{\partial^2 \bar{u}}{\partial x^2} + \bar{f}(\bar{u}) , \quad (63)$$

where

$$\bar{u} = (P_n, Z_n), \quad \bar{f} = (\bar{f}_1, \bar{f}_2) ,$$

and \bar{f}_1 and \bar{f}_2 are the biological interaction terms in the right hand sides of (61) and (62).

Suppose that the equation (55) has equilibrium solution $u^o = (N^o, P_n^o, Z_n^o)$ such that $N^o > 0$, $P_n^o > 0$ and $Z_n^o > 0$,

$$N^o + P_n^o + Z_n^o = C_o . \quad (64)$$

Then, we can obtain the linearized equations of (63) around $\bar{u}^o = (P_n^o, Z_n^o)$:

$$\frac{\partial}{\partial t} v = D \frac{\partial^2}{\partial x^2} v + Av ; \quad (65)$$

$$v(0, x) = v_o(x), \quad 0 \leq x \leq L ; \quad (66)$$

$$\frac{\partial}{\partial x} v(t, 0) = \frac{\partial}{\partial x} v(t, L) = 0, \quad t \geq 0 , \quad (67)$$

where A is the linearized coefficient matrix with respect to v and v is a small perturbation about the point \bar{u}^o , i.e., $\bar{u} = \bar{u}^o + v$. For the above defined problem, the solution of (65)-(67) can be expressed by means of an eigenfunction expansion [6] as

$$v(t, x) = \int_0^L \left\{ \sum_{m=0}^{\infty} 2 \cos(\sigma_m x) \cos(\sigma_m y) \exp(A - \sigma_m^2 d I) t \right\} v_o(y) dy, \quad (68)$$

where $\sigma_m = m\pi/L$ and I is a unit matrix.

It is easily seen that the solution is stable, if for each nonnegative integer m , the eigenvalues of matrix $A - \sigma_m^2 dI$ have negative real parts. Clearly matrix $A - \sigma_m^2 dI$ has nonnegative real parts because the corresponding equilibrium state of the batch process in Section 3 is stable, i.e., the eigenvalues of A have negative real parts. Hence, we can conclude that the diffusion term does not have any effect on stability of the equilibrium state, as long as the system has equal diffusion coefficients. However, it must be noted that there is a case where the diffusion process becomes unstable, driven by unequal diffusion coefficients, even if the associated batch process is stable [7, 8].

6.2 Simulation Example of Plankton Patchiness

In order to examine our analysis in the case of a diffusion process, let us show a simple simulation example which deals with the behaviour of the nutrient-plankton concentrations in one dimension. Assume that a uniform initial spatial pattern of nutrients exists in the whole domain $0 \leq x \leq L$ and put a small plankton population in the middle of the domain:

$$N(0,x) = 1.0, \quad 0 \leq x \leq 40$$

$$P_n(0,x) = Z_n(0,x) = \begin{cases} 0.1 & 19 \leq x \leq 21 \\ 0.0 & 0 \leq x < 19 \text{ and } 21 < x \leq 40 \end{cases}$$

The simulation is then carried out from $t=0$ to $t=226.6$ (days), where the diffusion coefficient is $D_1 = D_2 = D_3 = 5.0$ (m^2/sec) and numerical values of other parameters are the same as those used in Fig. 4 [Ref.3].

Figures 11-A - 11-F illustrate the progress of typical spatial patterns.

Fig. 11-A - 11-D: The phytoplankton P_n grows around the initial distribution and forms a patch. This patch propagates to the boundary but is depressed in its middle part with the predation by zooplankton Z_n . The nutrient N decreases first in the middle part in contrast with the phytoplankton increase, but restores its concentration gradually as the plankton wave moves to the boundary.

Fig. 11-E and 11-F: The zooplankton Z_n also grows rapidly with a certain time lag and forms a wave which also moves to the boundary. Finally, the distribution of N , P_n and Z_n approaches the uniform equilibrium state of (0.22 , 0.24, 0.53) which is a stable equilibrium solution of the system (49)-(51). It is interesting to note that the plankton patchiness is observed during a rather long period along the initially perturbed region, depending on the degree of diffusion and spatial length, although it finally fades away to the uniform equilibrium.

7. Conclusions

The dynamic characteristics of two simplified eutrophication models are discussed with stability analysis of equilibrium states. The two models have the same patterns of configurations of the equilibrium points, which can determine the global motion of the system. The relations between these patterns and the ranges of parameters values are illustrated both for a batch process and for a process with continuous cultivation. It is also shown that the results obtained are applicable to analysis of the diffusion process with the same system structure as the batch eutrophication model. The results are useful for evaluating the system's response to environmental variations.

Although it seems to be difficult to apply the analytical method of stability analysis, which is used in this paper to, larger and more complex systems, we could conclude that careful examination of configurations of equilibrium points determine the system's global behaviour at least to some extent. Therefore, analysis of equilibrium points is useful for the determination of qualitative characteristics of various mathematical models. From this point of view, practical algorithms are to be developed to compute equilibrium points of complex models and to evaluate their stability [9].

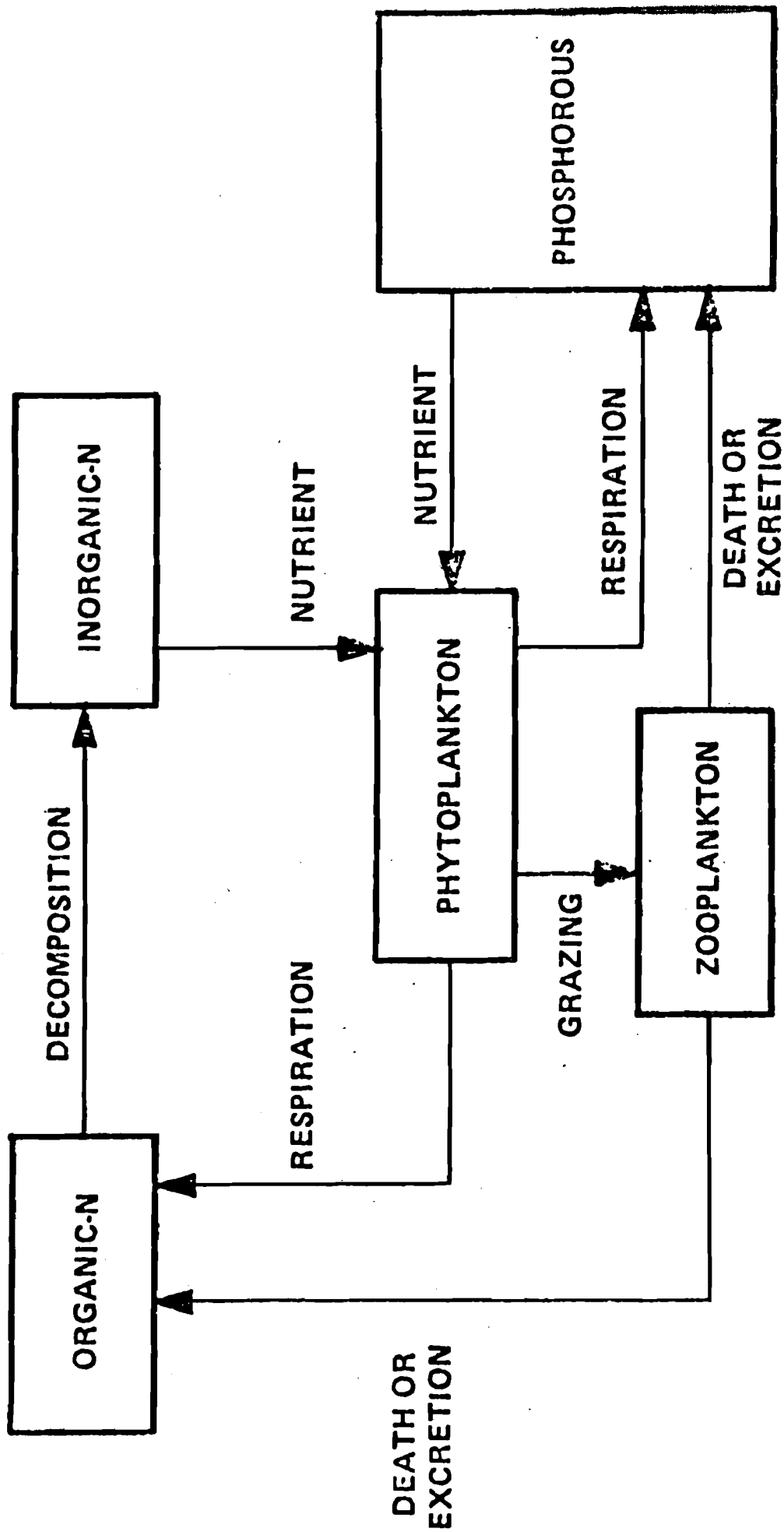


FIG. 1 SCHEMATIC DIAGRAM OF THE NUTRIENT CYCLES

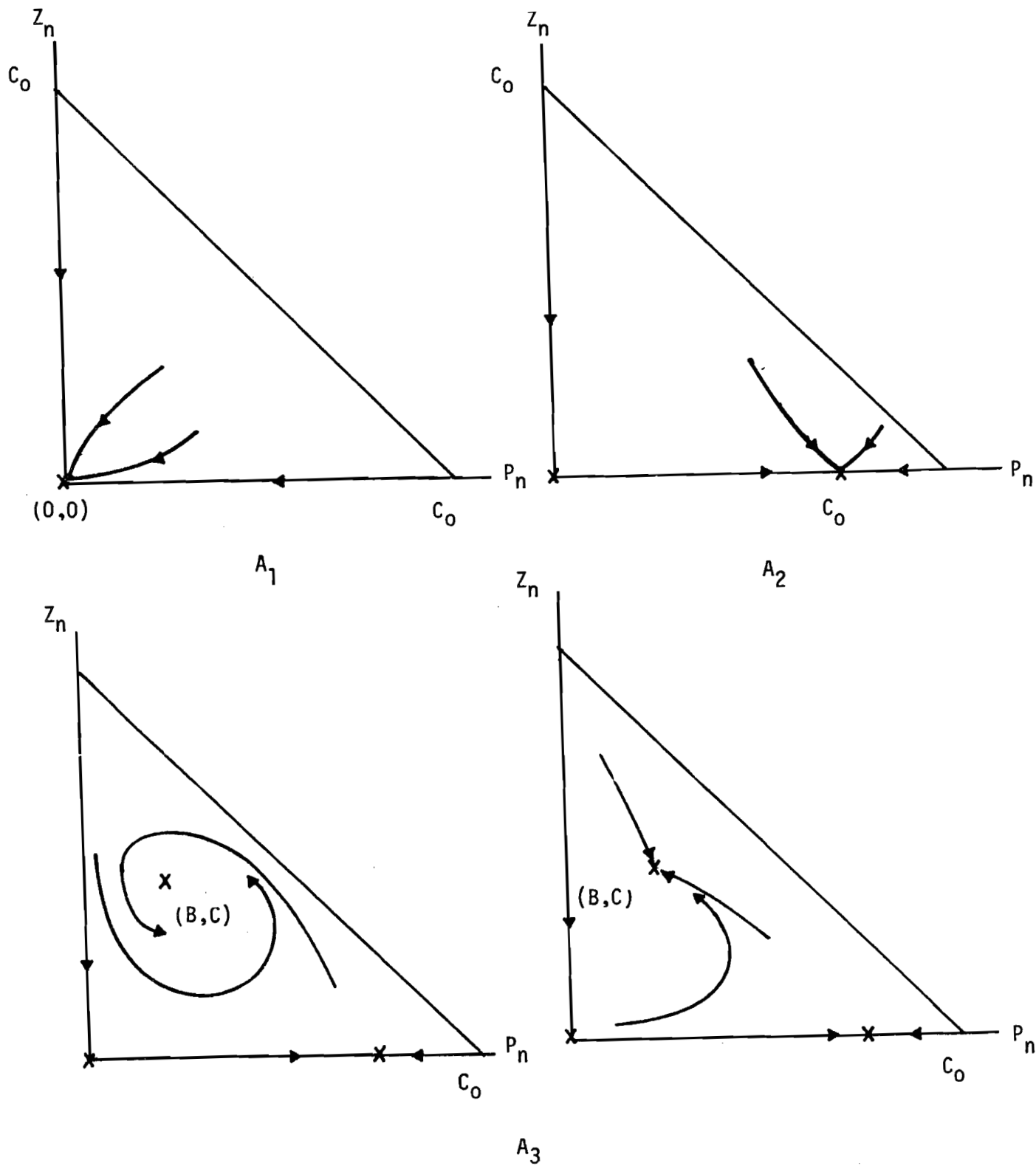


FIG. 2 PHASE TRAJECTORIES OF BATCH PROCESS

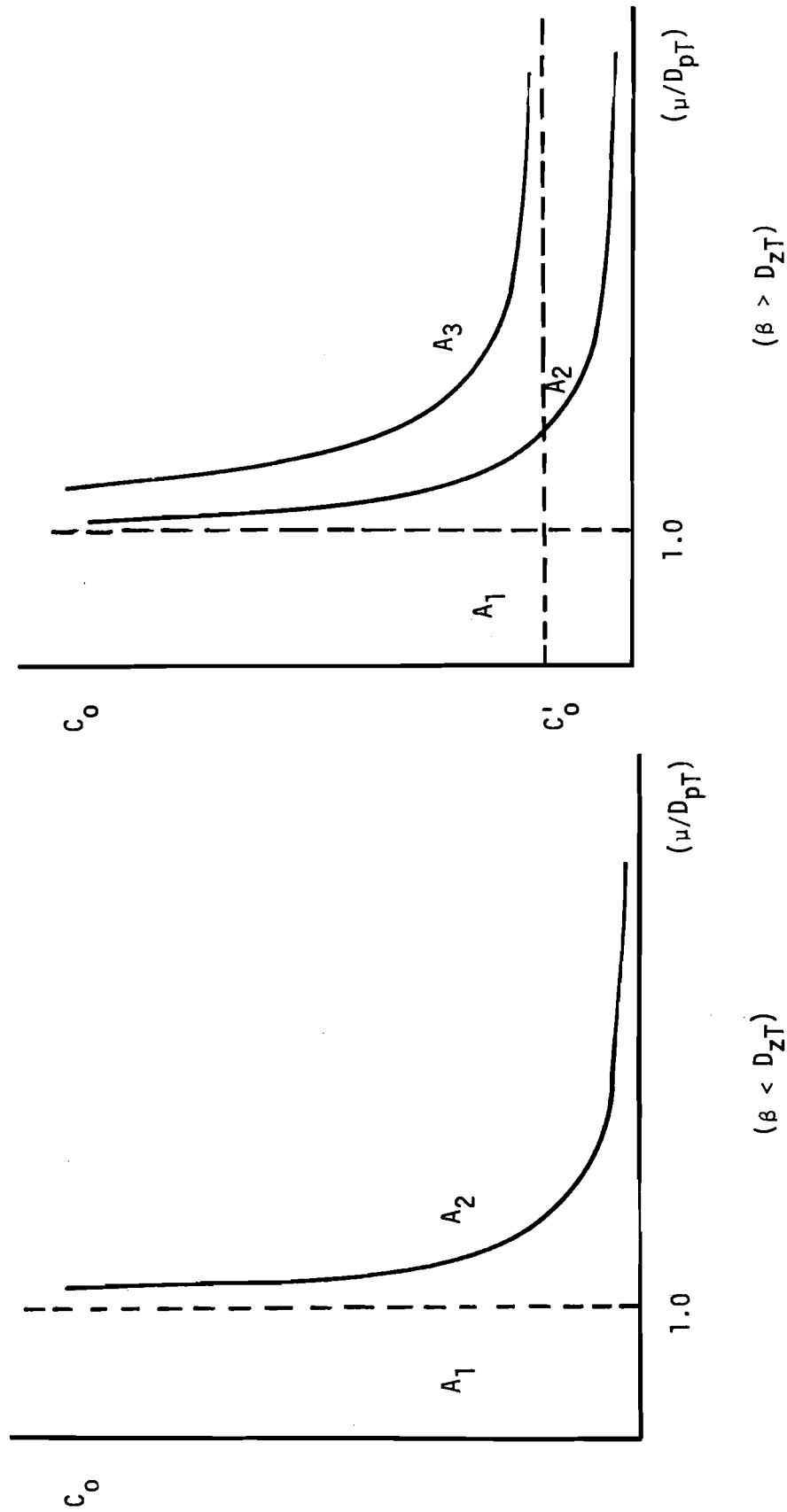


FIG. 3 REGION IN PARAMETRIC SPACE FOR EACH PATTERN OF THE BATCH PROCESS

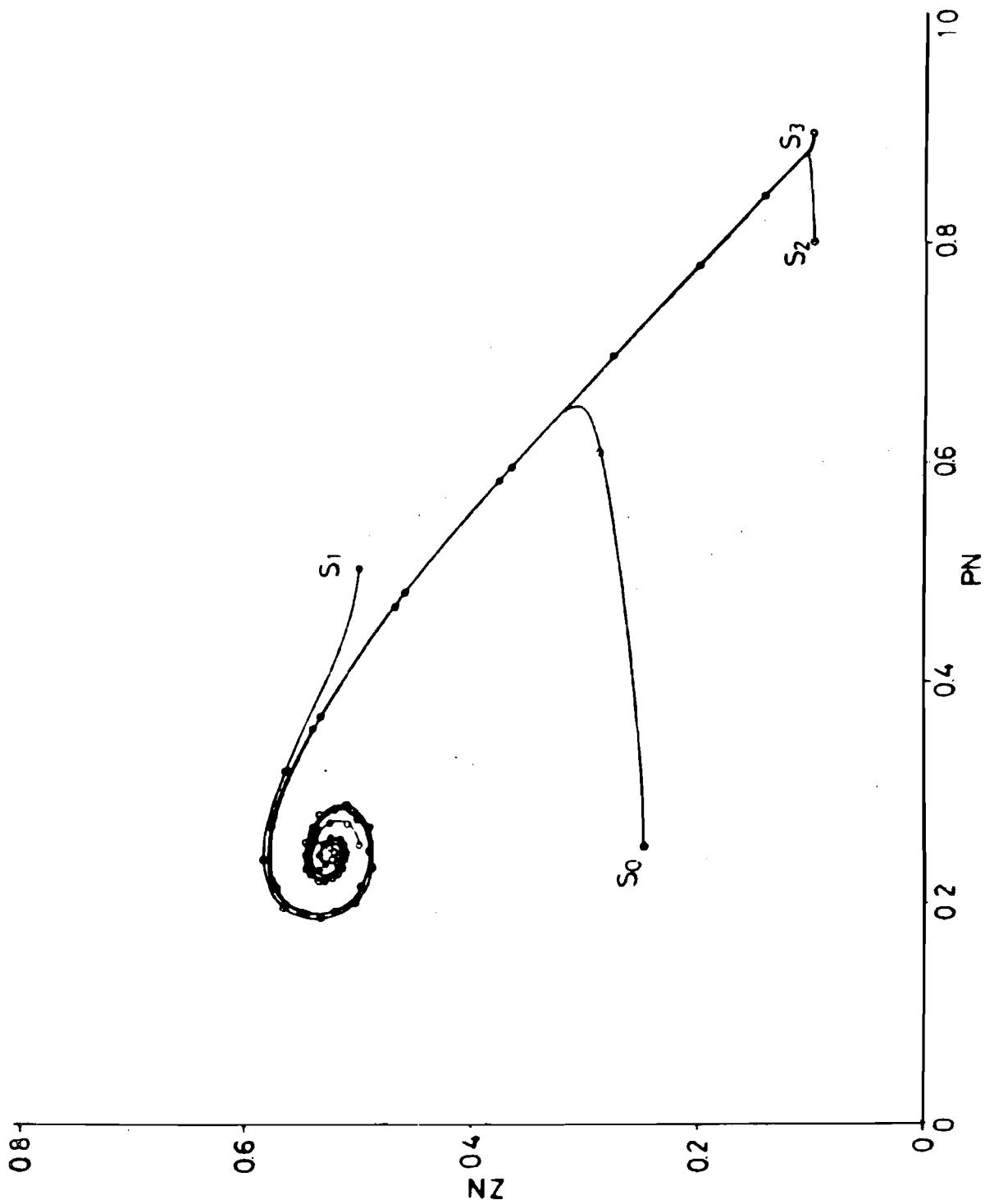
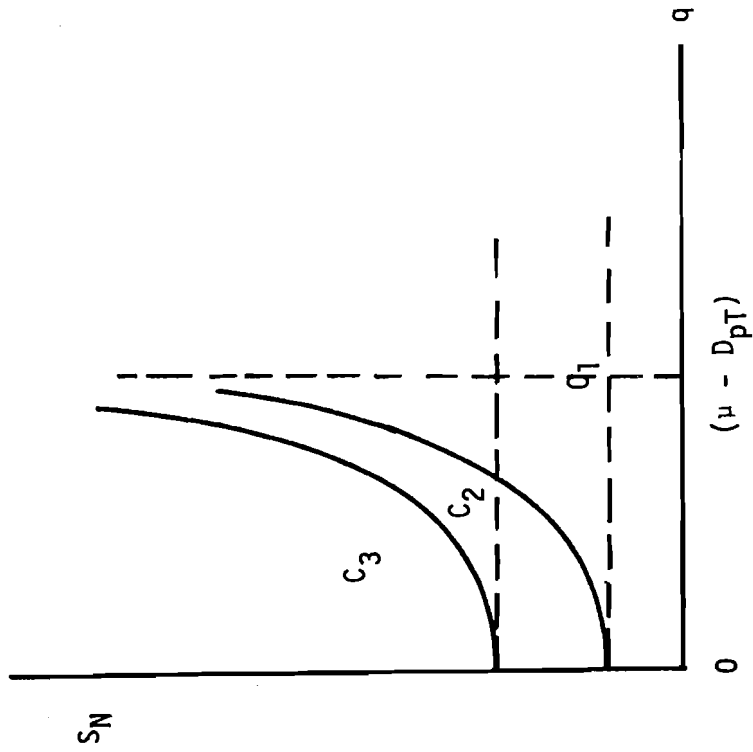
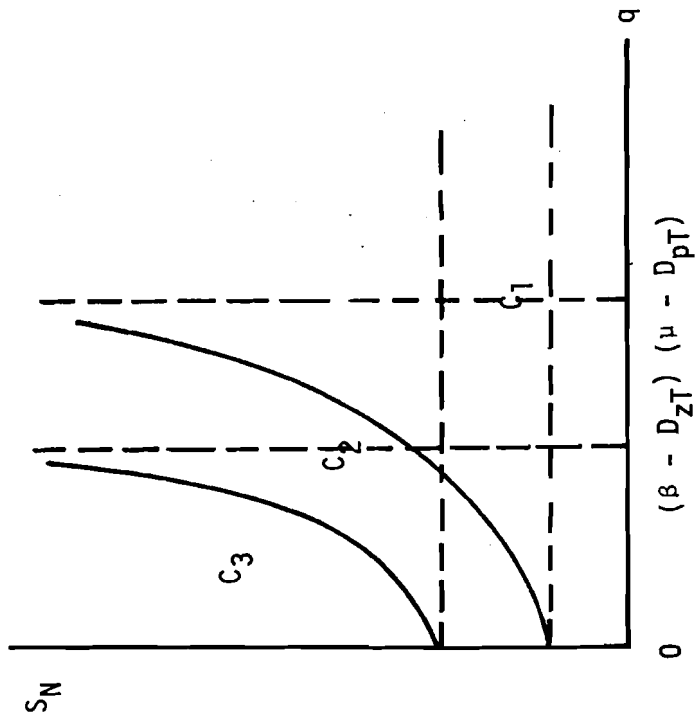


FIG. 4 TYPICAL TRAJECTORIES OF MODEL II



$$(\beta - D_{ZT}) > (\mu - D_{pT})$$



$$(\beta - D_{ZT}) < (\mu - D_{pT})$$

FIG. 5 REGION IN PARAMETRIC SPACE FOR EACH PATTERN OF THE PROCESS WITH CONSTANT FLOW RATE

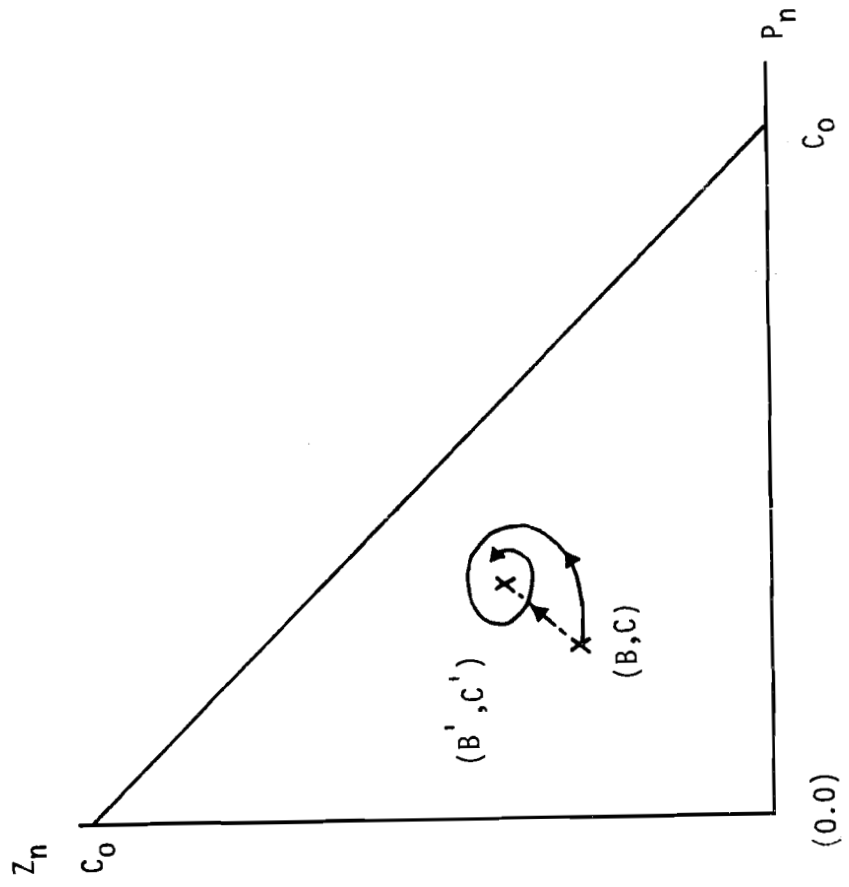


FIG. 6 EFFECT q DISCONTINUOUS CHANGES OF TEMPERATURE AND LIGHT INTENSITY

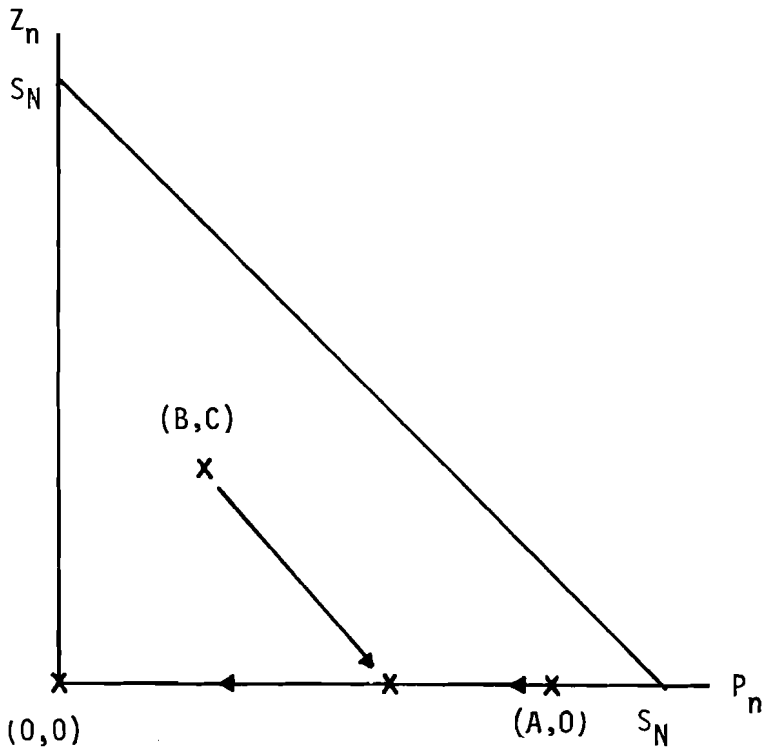


FIG. 7 MOVEMENT OF EQUILIBRIUM STATES FOR INCREASE OF FLOW RATE

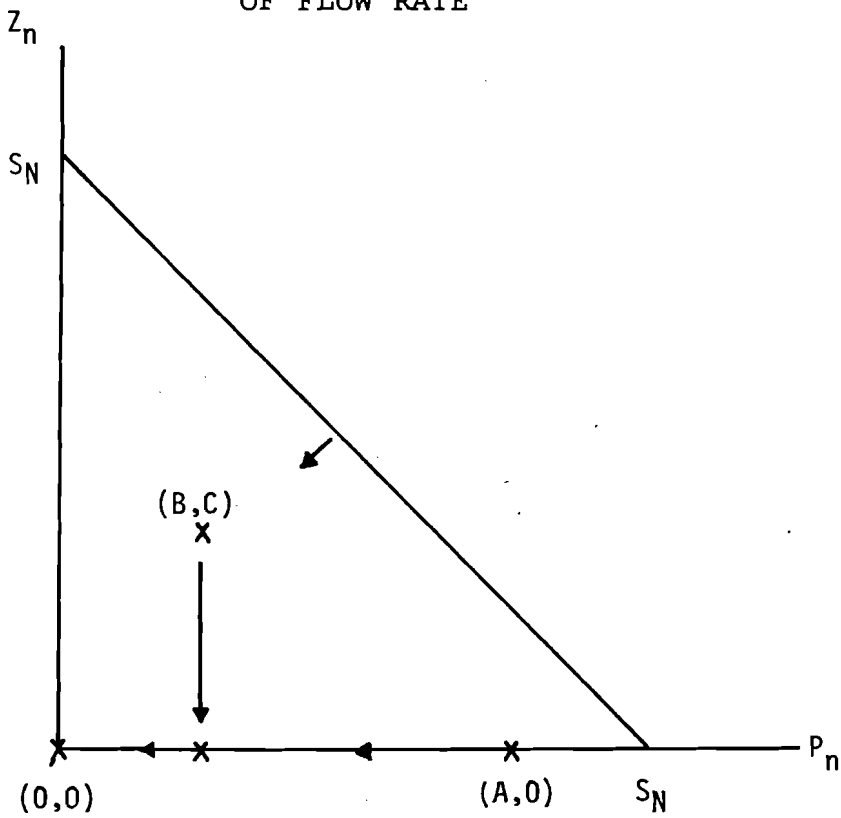


FIG. 8 MOVEMENT OF EQUILIBRIUM STATES FOR DECREASE OF INFLUENT NUTRIENT CONCENTRATION

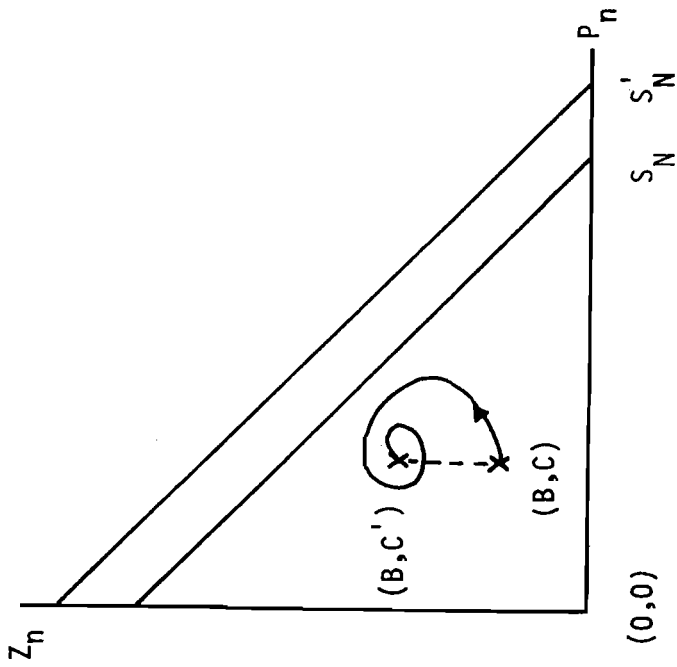
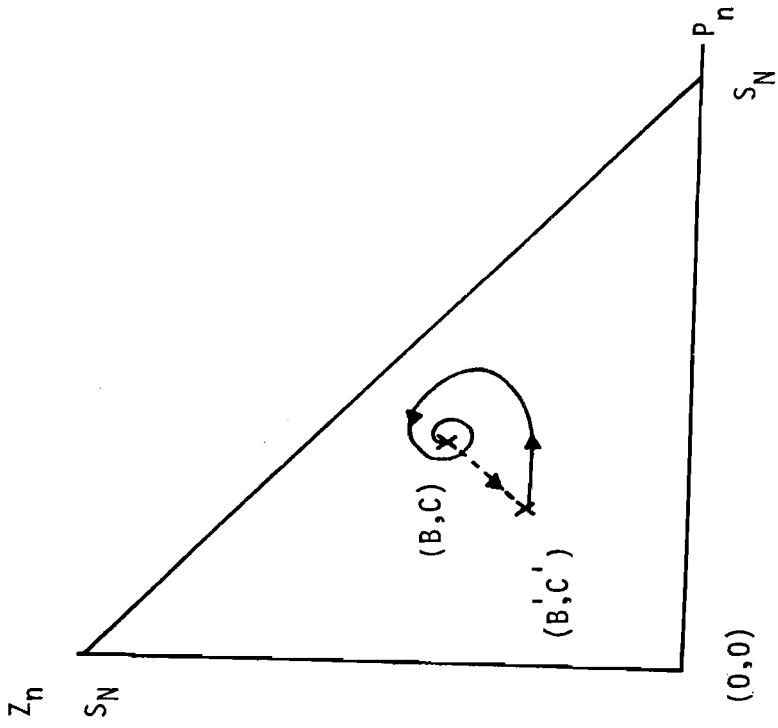
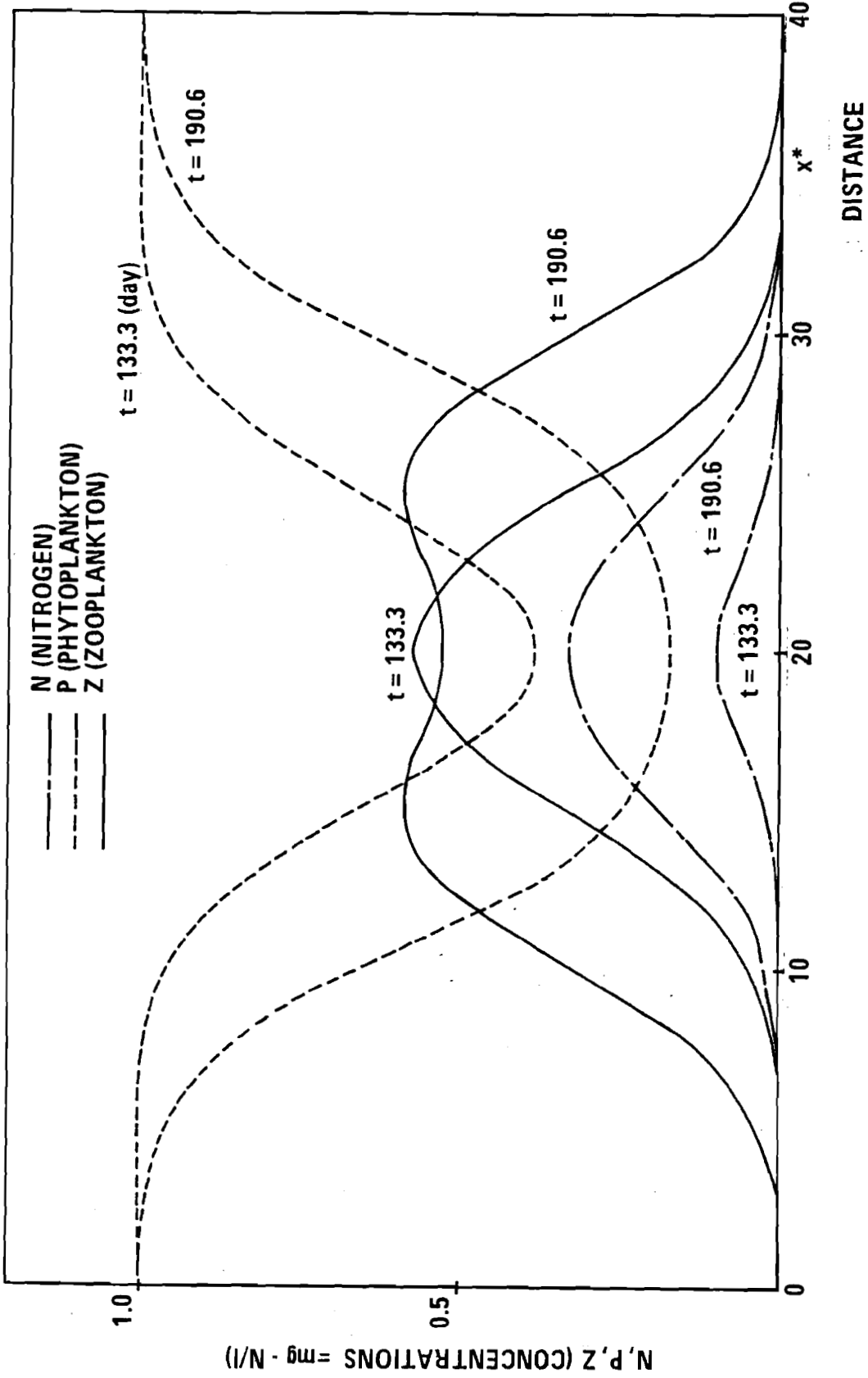


FIG. 9 EFFECT OF DISCONTINUOUS INCREASE



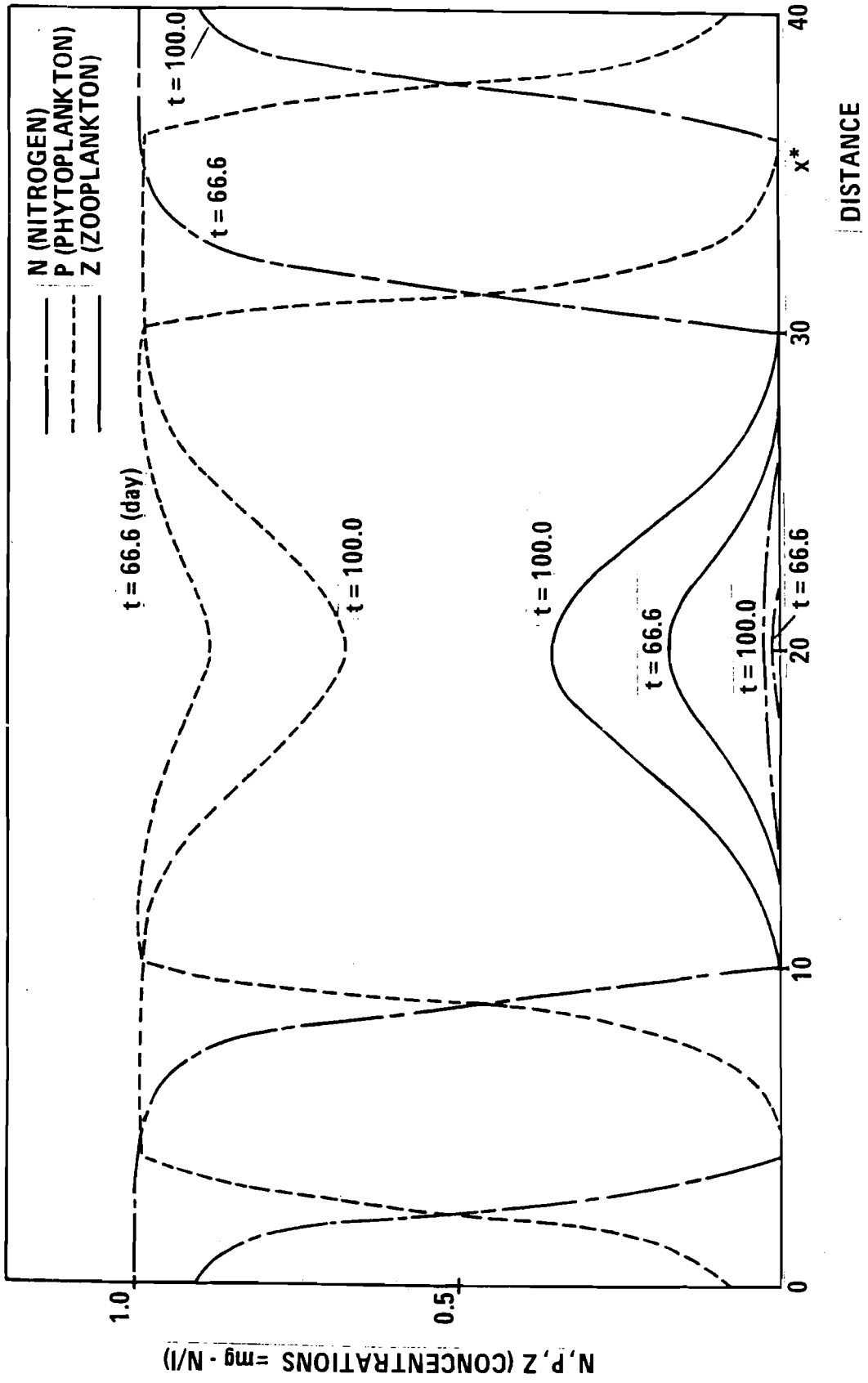
$(B' < B, C' < C)$

FIG. 10 EFFECT OF DILUTION

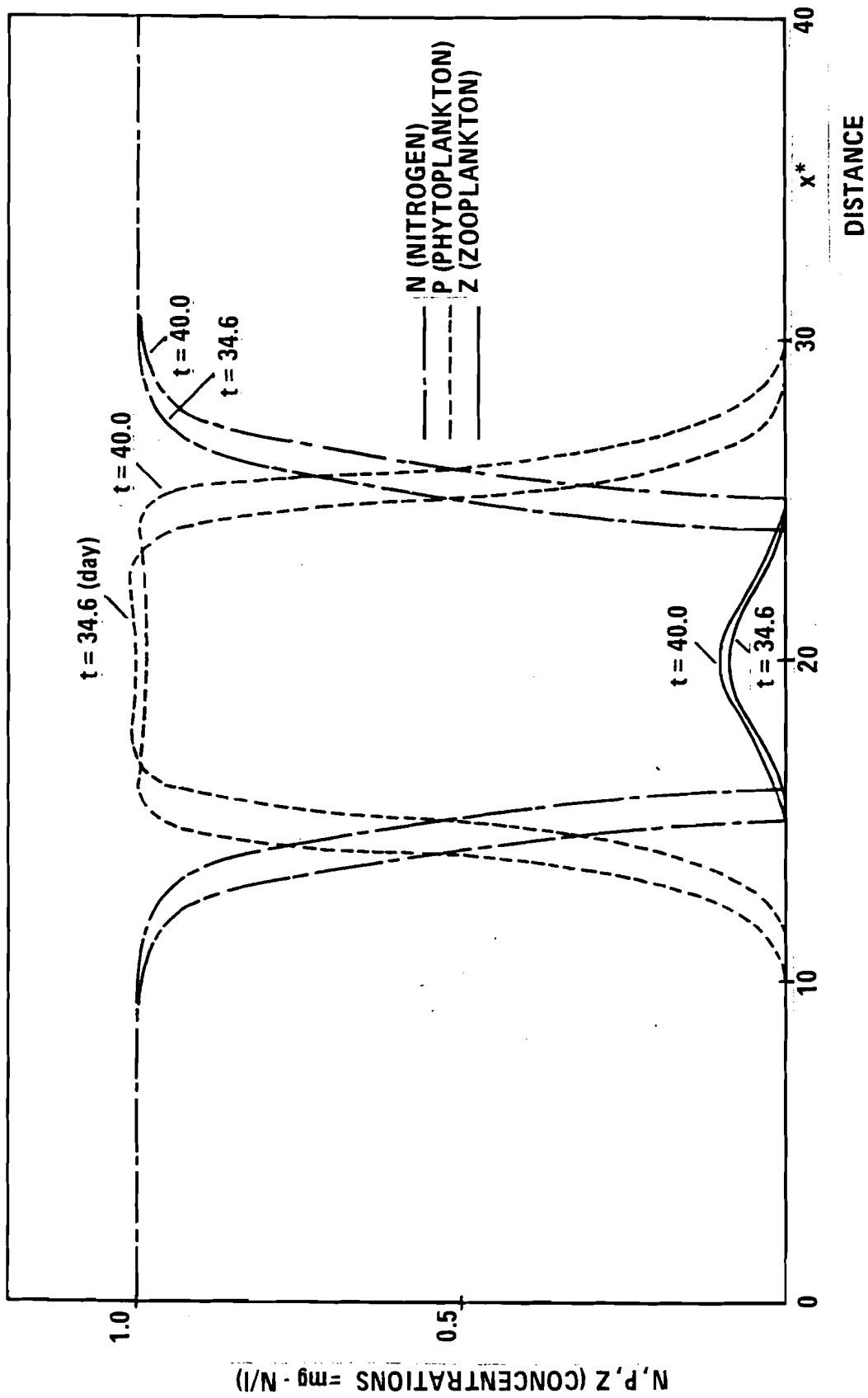


A: (t = 6.6 and t = 13.3)

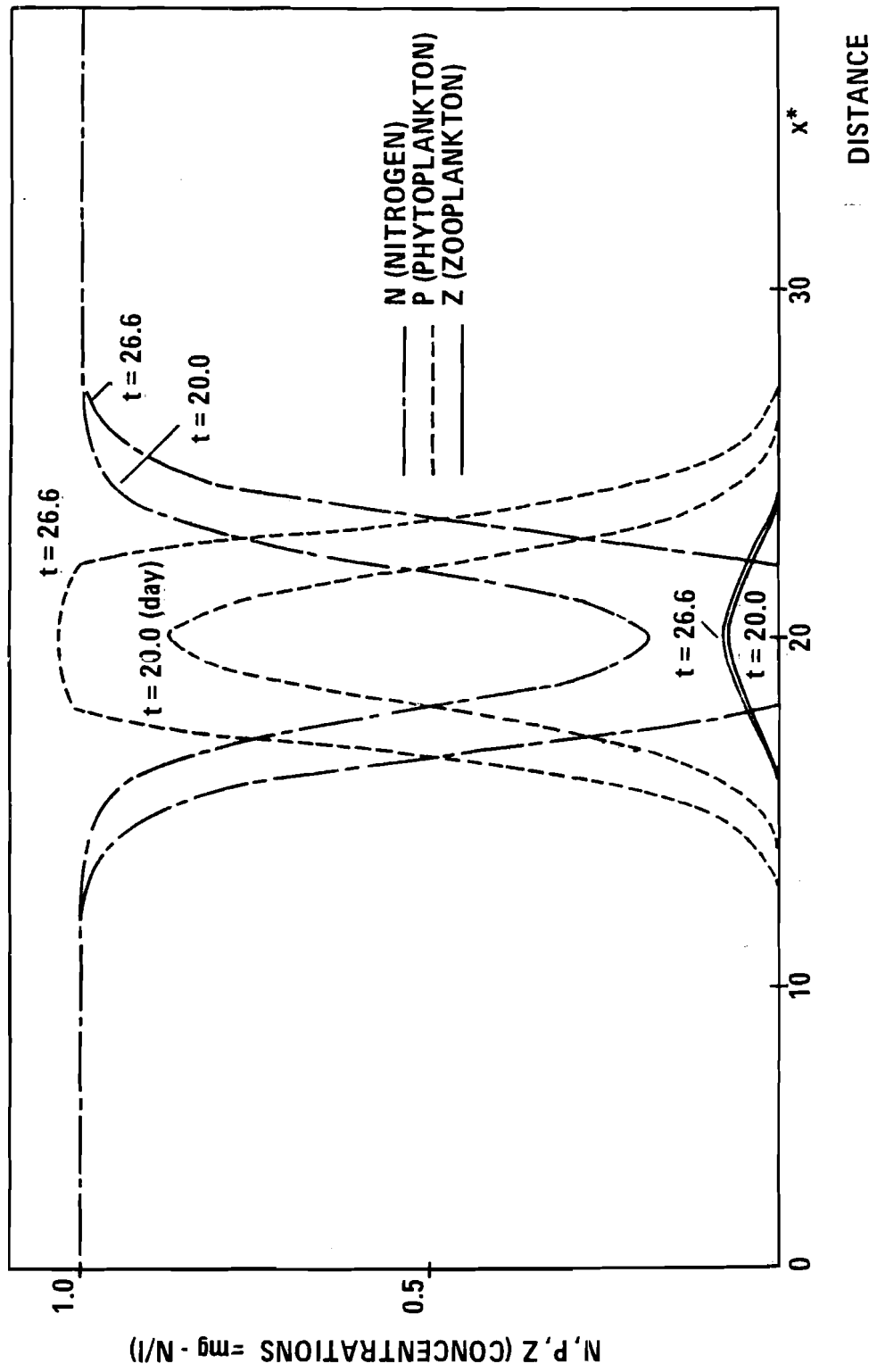
FIG. 11 : PROGRESS OF SPATIAL PATTERNS OF PLANKTON POPULATIONS



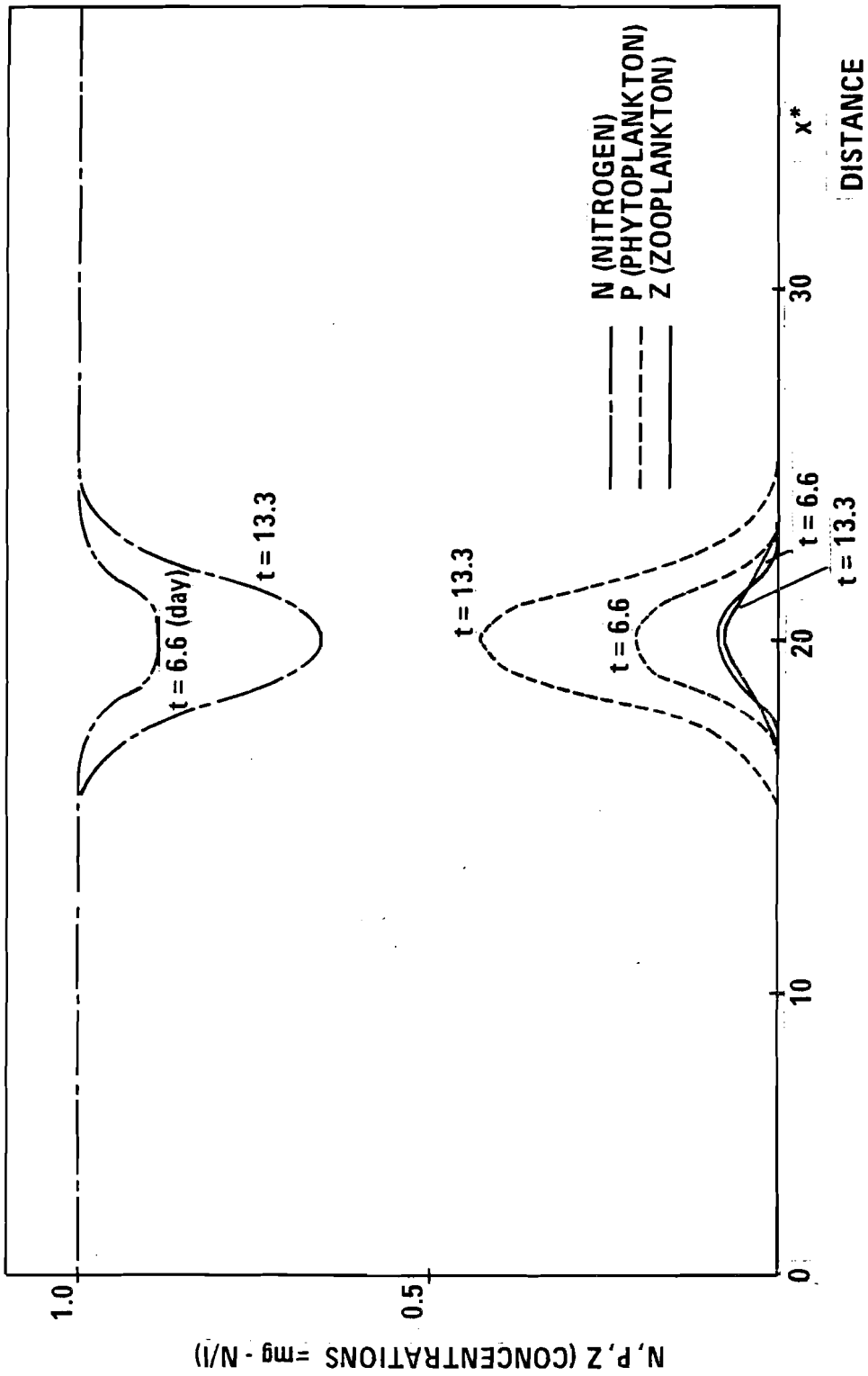
B: (t = 20.0 and t = 26.6)



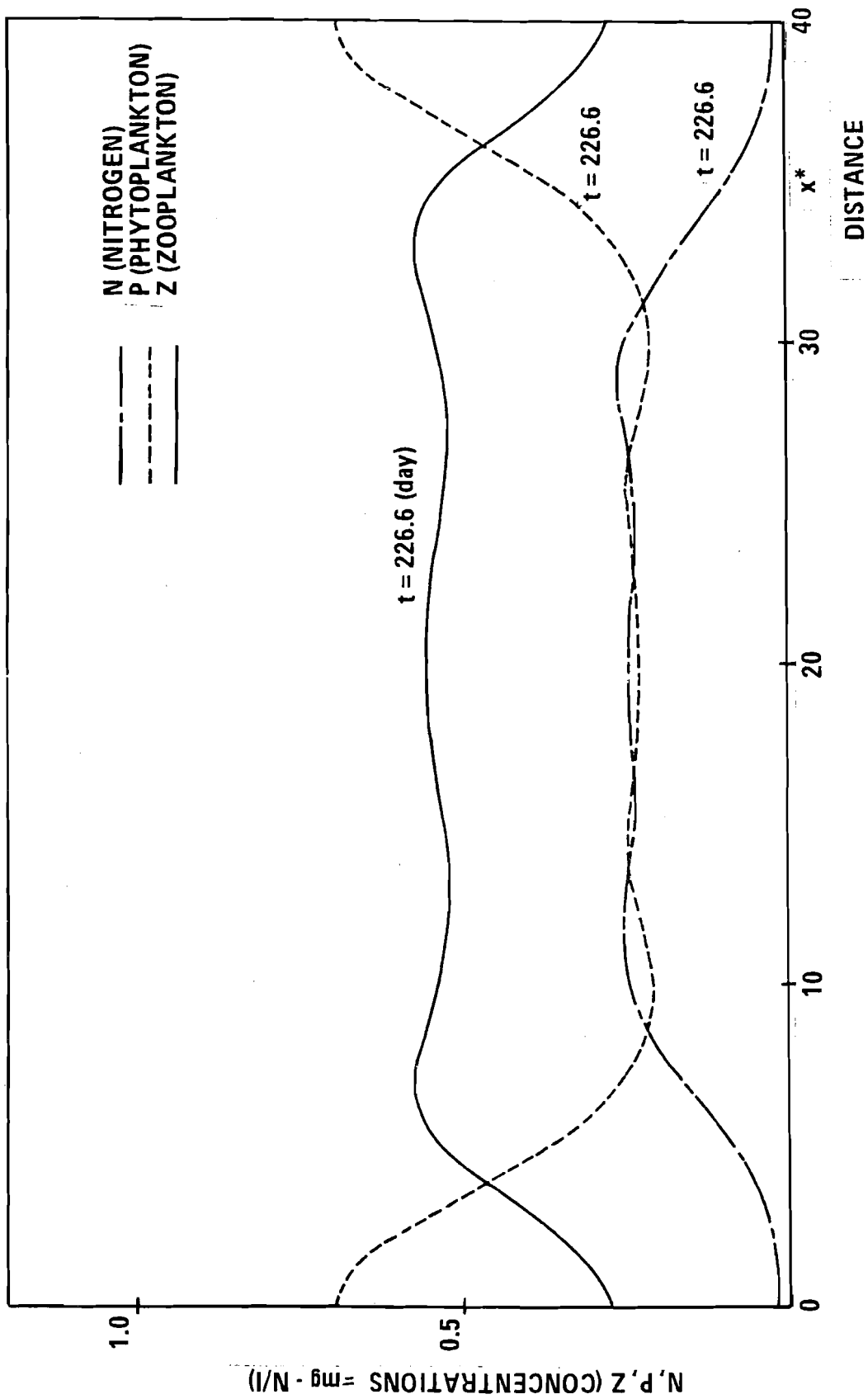
-C: (t = 34.6 and t = 40.0)



D: (t = 66.6 and t = 100.0)



E: (t = 133.3 and t = 190.6)



F: ($t = 226.6$)

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