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DYNAMICAL SYSTEM OF PHYTOPLANKTON AND DISSOLVED NUTRIENT INTERACTION

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A thesis presented to Mathematics Department of Massey University, New Zealand, in partial fulfilment of the requirements for the degree of Master of Science in Mathematics

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ABSTRACT

The first step in modelling the dynamics of phytoplankton and dissolved nutrient interaction made use of a simple model called The N-P model. This model was extracted from Busenberg *et al* [2]. Results from the analysis were obtained. Laboratory experiments were set up and from the observations the process of conversion of the dead phytoplankton occurred after a certain number of time delay. Moreover, from the data obtained the populations of these interactive components behaved in oscillatory mode. This was believed to happen due to the present of a third component called the *dead* phytoplankton. All these experimental results did not agree with the results obtained from the analysis. Thus a new model was then formulated, called the N-P-D model. A unit function with the delay-time and the dead phytoplankton (D) were included. Analysis were made and results compared.

ACKNOWLEDGEMENT

First of all, my greatest thank is dedicated to Allah, The Great. To my supervisor and lecturer, Professor Graeme Cane Wake (H.O.D. of mathematics, Massey University, New Zealand), for his valuable times, ideas and frienships. It is worthy to work with you and being your student. Thank you very much. Special thanks go to my wife, Dk. Mahani Pg. Mumin, who is continuously supporting and inspiring me throughout my studies here at Massey. Your love, belief and patience in me will not be forgotten.

These thanks go further to Universiti Brunei Darussalam (U.B.D.) for the sponsorships. All the cooperations made throughout the years are very much appreciated. Also forwards to the H.O.D. of mathematics of U.B.D., Dr. R.J. Gribben, for inviting me to work on this project.

The rest of thanks then go to the Wake families especially , Lil (come and visit us in Brunei one day. You will be our guest of honour). All my friends in Palmerston North (see you again guys). The rest of the staffs in the mathematics department , Massey.

Last but not the least, thanks also go to Richard Rayner for all the 'helps' in using the network. To Simon Woodward for helping me in writing the matlab program and Adrian Smith for modifying and correcting it. Lastly, to the Macintosh pc (it's cooooool to use it).

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CHAPTER ONE
INTRODUCTION

Fishing industry in Brunei Darussalam is heavily active especially at the Brunei Bay as compared to various other places scattered at Brunei coastal areas. A majority of these fishing activities are due to private individuals themselves whom are mostly fishermen. So this becomes, partly, a growing concern to the Brunei Government in particular the Fishery Department Of Brunei in trying to control these activities. The main reason towards this consideration is to avoid over-fishing. Accompanying this problem, there is a rather awkward situation happening to Brunei coastal areas especially at the Brunei Bay every year. This situation is what we call the *red-tidal waves*. These incoming waves are very poisonous to the marine populations especially to the fish. Various studies of this phenomenon have been made. Henceforth, the fishery department of Brunei is presently working on a 'control' breeding of certain species of fishes, prawns and others. In responding to this objective the Universiti Brunei Darussalam especially the mathematics and biology departments are involved. The mathematics department in particular led by the head of the department itself, is developing certain models in studying minute marine populations i.e. planktons, of which are the main sources of foods to fishes and prawns. The development of these models are the initial steps taken.

Therefore it becomes the main aim of this writing to analyse the dynamical system of phytoplankton (P) and dissolved nutrient (N) interaction. The dynamics of this interaction is described as a system of first order nonlinear ordinary differential equation which will be written in the next chapter. As a form of guidance towards the develpoment of models, the model which will be used in this analysis is primarily extracted from the 3-component model introduced in the article Busenberg *et al.* The three interacting components studied there are phytoplankton , herbivorous zooplankton (Z) and dissolved nutrient . Assumptions are made throughout the analysis of these three components interaction. The two plankton densities are measured in terms of their nitrogen contents, N, as assumed that the nutrient is responsible for limiting the phytoplankton reproduction. The total nitrogen level is maintained to be constant throughout. Thus for the 3-component model, $P + Z + N = N_T =$ constant.

The first analysis of phytoplankton and dissolved nutrient interaction which is described in a 2-component model (N-P model) begins in chapter two. This consists of finding the steady-states and studying their stability. Various questions that need to be answered such as how these steady-states solutions behave under the change of a distinguished parameter ; in which region (the feasible region), does the biologically feasible solution stay in ; will also be included in this chapter.

Chapter three accounts a slight deviation of the N-P model studied in chapter two. Briefly, in the N-P model, dead phytoplankton decays automatically into nutrient . In other words, the source of N is supplied directly from dead P. It is thought that this conversion of dead P into N will take place after a certain number of time. So a delay -time factor is introduced into the N-P model. A third component, dead phytoplankton (D), will also enter the model. This new model (N-P-D model) provides a different scenario in terms of its dynamics when compared to the N-P model. The analysis will begin at finding the new steady-states, studying their stability, defining the feasible region, etc.

As far as the analysis concerns parameters entering both models, N-P and N-P-D, are defined. The definitions together with the dimensions of these parameters are given as follows

a maximal uptake rate for the phytoplankton $\{ day^{-1} \}$
c phytoplankton death rate $\{ day^{-1} \}$
k Michealis-Menton half saturation constant {μg atom NO_3 / dm^3}

Other constants also entering this analysis are defined as follows

N_T total concentration of nitrates { μg atom NO_3 / dm^3 }
τ delay-time dead-phytoplankton conversion into dissolved nutrient $\{ day(s) \}$

The summary of the whole analysis is included in the final chapter of this writing. Several biological interpretations of the results obtained are also discussed. Numerical simulated results of the N-P-D model together with the program are given as appendices.

CHAPTER TWO
N-P MODEL

2.1 Introduction

The dynamics of the phytoplankton (P) and dissolved nutrient (N) interaction is initially written in a simple form as

$$\begin{aligned}\frac{dN}{dt} &= cP - \frac{aNP}{N+k} \\ \frac{dP}{dt} &= \frac{aNP}{N+k} - cP\end{aligned} \qquad (2.1)$$

This is a system of two nonlinear first order ordinary differential equations. In fact, the model given above is exactly the same with the model analysed in the Busenberg *et al* where in this case the herbivorous zooplankton (Z) is neglected, i.e. $Z = 0$.

The dynamics of the above system simply says that during the interaction, the source of N is supplied by the death of P and the loss of N is due to the consumption by P. The reverse holds for the population P. Base on our assumptions, the total concentration of nitrates is kept as a constant determined only by the initial values of N and P. In other words, no N is added or taken out during the process of the interaction. Similarly goes with P. Pictorially,

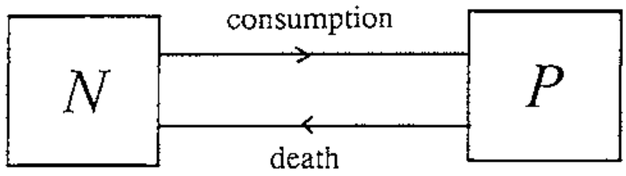


Fig. 2.1 The N-P model.

Adding both equations in (2.1),

$$\frac{dN}{dt} + \frac{dP}{dt} = 0$$

Thus,

$$P + N = P_0 + N_0 = N_T = \text{constant} \qquad (2.2)$$

where $N(t) = N$ and $P(t) = P$. The initial values N_0 and P_0 determine the constant N_T. N_T is the total concentration of nitrates present in system (2.1). Equation (2.2) is the *conservation condition* of our 2-component system. Throughout this analysis only the biologically feasible solutions, i.e. P, $N \geq 0$ for all $t \geq 0$ such that (2.2) satisfies, are treated. The analysis begins at finding the analytical solutions for P and N.

2.2 Analytical Solutions Of N And P

Rewriting the second equation of (2.1),

$$\frac{dP}{dt} = \frac{(a-c)(N_T - P - \alpha)P}{(N_T - P + k)}$$

where $\alpha = \dfrac{ck}{a-c}$ and $P = N_T - N$. Separating the variables,

$$\int \frac{N_T - P + k}{(N_T - P + \alpha)P} \cdot dP = \int (a-c) \cdot dt$$

Obtaining partial fractions

$$\left(\frac{k+\alpha}{N_T - \alpha}\right) \int \frac{dP}{N_T - P - \alpha} + \left(\frac{N_T + k}{N_T - \alpha}\right) \int \frac{dP}{P} = (a-c)t + A$$

where A is a constant of integration. Integrating the above equation,

$$-(k+\alpha)\ln|N_T - P - \alpha| + (N_T + k)\ln|P| = (N_T - \alpha)(a-c)t + B$$

where B is a constant. The above expression then becomes

$$\frac{P^{(N_T+k)}}{(N_T - P - \alpha)^{(k+\alpha)}} = Ce^{(a-c)(N_T-\alpha)t}$$

Substituting $P^* = N_T - \alpha$ to the above, the expression of P is therefore

$$\frac{P^{(N_T+k)}}{(P^* - P)^{(k+\alpha)}} = \frac{P_0{}^{(N_T+k)}}{(P^* - P_0)^{(k+\alpha)}} e^{(a-c)P^* t}$$

The constant C is determined by the initial condition and is given as

$$C = \frac{P_0{}^{(N_T+k)}}{(P^* - P_0)^{(k+\alpha)}}.$$

Thus we have the analytical solution for P though it is written implicitly . Through a direct substitution of $N = N_T - P$ to the above expression, the analytical solution for N can be expressed as follows,

$$\frac{(N_T - N)^{(N_T+k)}}{(\alpha - N)^{(k+\alpha)}} = \frac{(N_T - N_0)^{(N_T+k)}}{(\alpha - N_0)^{(k+\alpha)}} e^{(a-c)(N_T-\alpha)t} .$$

Therefore the analytical solutions for P and N,

$$\frac{P^{(N_T+k)}}{(P^* - P)^{(k+\alpha)}} = \frac{P_0{}^{(N_T+k)}}{(P^* - P_0)^{(k+\alpha)}} e^{(a-c)P^*t} \tag{2.3}$$

$$\frac{(N_T - N)^{(N_T+k)}}{(\alpha - N)^{(k+\alpha)}} = \frac{(N_T - N_0)^{(N_T+k)}}{(\alpha - N_0)^{(k+\alpha)}} e^{(a-c)(N_T-\alpha)t} \tag{2.4}$$

2.3 The Behaviour Of N And P

The governing parameters a, c, k and N_T are all non-negative constants. From the above expressions (2.3) and (2.4) the feasibility of solutions i.e. $N, P \geq 0 \quad \forall t \geq 0$ satisfying equation (2.2), requires $0 \leq P_0, N_0 \leq N_T$ such that $P_0 + N_0 = N_T$. This is a *necessary condition* for our solutions to be feasible.

We can observe also that $P^* = N_T - \alpha$ and $N^* = \alpha$ play an important role. If $0 < P_0 < P^*$ then $0 < P \leq P^* \; \forall t \geq 0$. As time gets very large P will approach P^* from below. If $0 < P^* < P_0$ then $0 < P^* \leq P \; \forall t \geq 0$ and as t gets very large, P approaches P^* from above. Similarly, if $0 < N_0 < \alpha$ then $0 < N \leq \alpha \; \forall t \geq 0$ and $0 < \alpha \leq N \; \forall t \geq 0$ if $0 < \alpha < N_0$. N will then approach α from below or above respectively. Furthermore, both equations (2.3) and (2.4) are not defined at $P_0 = P^*$ and $N_0 = \alpha$ respectively. Thus with $0 < c < \dfrac{aN_T}{N_T + k}$ and given non-negative values of a, k and N_T, P^* and α resemble the feasible steady-state of system (2.1). In other words, the dynamics of the N-P interaction stop! at this point.

Another interesting result that can be observed from the above equations, is when $\dfrac{aN_T}{N_T + k} < c < a$, i.e. $N_T < \alpha$. This makes $P^* < 0$. In other words, P^* lies outside the feasible region. We can see immediately from (2.3) and (2.4) that the feasible solutions $P \to 0$ and $N \to N_T$ as t increases. This tells us that $(\overline{N}, \overline{P}) = (N_T, 0)$ is another feasible steady-state of system (2.1). Nonetheless, the steady - states of this system and their stability will be verified.

2.4 Steady-States

At the steady - states, both equations in (2.1) vanish. The dynamics of our system (2.1) stop meaning to say every feasible solution of the system stays at these points forever. So

$$\frac{dP}{dt} = \frac{dN}{dt} = 0$$

This implies

$$\left(c - \frac{aN}{N+k}\right)P = 0$$

giving us

$$N = \frac{ck}{a-c} = \alpha \text{ or } P = 0$$

Applying the condition of conservation (2.2), the two steady-states of system (2.1) are

$$(\overline{N},\overline{P}) = (N_T, 0) \qquad (2.5)$$

$$(N^*,P^*) = (\alpha, N_T - \alpha) \qquad (2.6)$$

$(\overline{N}, \overline{P})$ is the *trivial* steady-state and (N^*,P^*) is the *coexisting* steady-state.

2.5 Stability Analysis

The stability of these steady-states are stated in the following Theorem 1.

Theorem 1

Suppose a, c, k and N_T are non-negative with $(a-c) > 0$. Suppose further that $0 \le P_0, N_0 \le N_T$ such that $P_0 + N_0 = N_T$. If $0 < \alpha < N_T$ then $(\overline{N}, \overline{P})$ is an *unstable* steady - state and (N^*,P^*) is *asymptotically stable*. Both steady - states are biologically feasible. If $N_T < \alpha$ then $(\overline{N}, \overline{P})$ becomes *asymptotically stable* and (N^*,P^*) *unstable*. Furthermore (N^*,P^*) is not biologically feasible. If $\alpha = N_T$ then $(\overline{N}, \overline{P}) = (N^*,P^*)$ and this steady-state is *semistable*.

Proof

Consider

$$\frac{dN}{dt} = \frac{(a-c)(\alpha - N)(N_T - N)}{N+k} = f(N) \qquad (2.7)$$

Case $0 < \alpha < N_T$

(a) For $0 \leq N < \alpha$, $\frac{dN}{dt} > 0$ since $(\alpha - N) > 0, (N_T - N) > 0$.

(b) For $\alpha < N < N_T$, $\frac{dN}{dt} < 0$ since $(\alpha - N) < 0, (N_T - N) > 0$.

(c) For $N_T < N$, $\frac{dN}{dt} > 0$ since $(\alpha - N) < 0, (N_T - N) < 0$.

(d) For $N = \alpha$ or $N = N_T$, $\frac{dN}{dt} = 0$.

Suggests that in (a), N approaches α from below as t increases. In (b), N approaches α from above as t increases. Using $P = N_T - N$, P will approach P^* from above and from below respectively. Thus in this case (N^*, P^*) is asymptotically stable . In other words the solution $N + P = N_T$ goes to (N^*, P^*) monotonically. $(\overline{N}, \overline{P})$ is unstable since N turns away from N_T (or P turns away from $P = 0$) if N starts at every small neighbourhood of this steady - state. Both steady - states are contained inside the feasible region as they all have non-negative values. Fig. 2.2 describes the above situation.

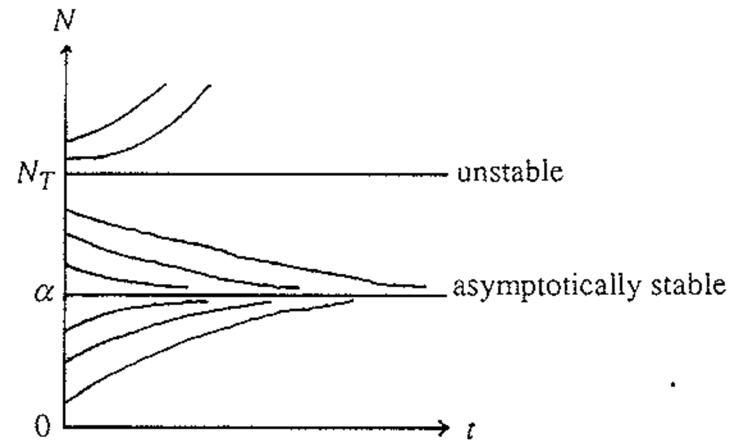


Fig. 2.2 N when $0 < \alpha < N_T$

Case $0 < N_T < \alpha$

In this case, we have similar arguments as above except that the roles of α and N_T interchange. Thus we can conclude easily that every feasible solution $N + P = N_T$ will approach the steady - state $(\overline{N}, \overline{P})$. Henceforth, $(\overline{N}, \overline{P})$ is an asymptotically stable steady - state and (N^*, P^*) becomes unstable. Furthermore the value of P^* is negative. So (N^*, P^*) lies outside the feasible region and therefore not biologically feasible. This case is illustrated by the following sketch given in Fig. 2.3.

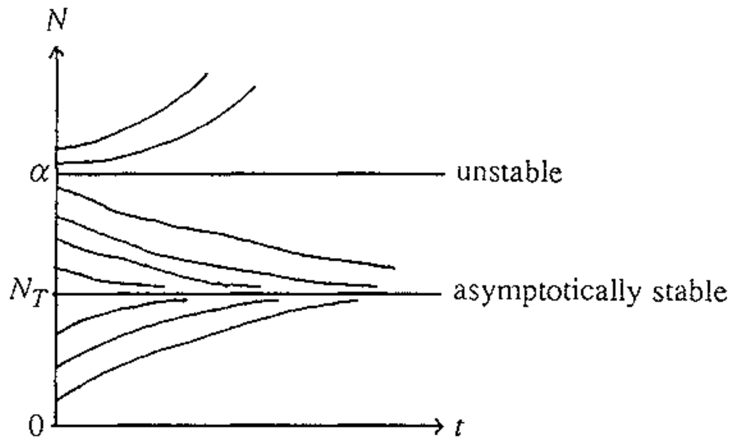


Fig. 2.3 N when $0 < N_T < \alpha$

<u>Case $\alpha = N_T$</u>

Therefore $P^* = 0$ and $(\overline{N}, \overline{P}) = (N^*, P^*)$. Equation (2.7) becomes

$$\frac{dN}{dt} = \frac{(a-c)(\alpha - N)^2}{N+k}.$$

We can see easily that $\frac{dN}{dt} > 0$ for $0 < N < N_T$ and $N_T < N$. In other words, N approaches $\alpha = N_T$ from below but increases away from $\alpha = N_T$ for $N_T < N$. Thus this steady-state is semistable. The following sketch , in Fig. 2.4 illustrates the behaviour of N with time, t.

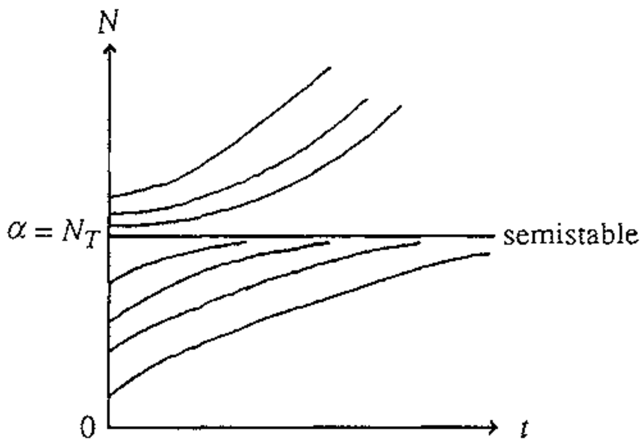


Fig. 2.4 N when $\alpha = N_T$

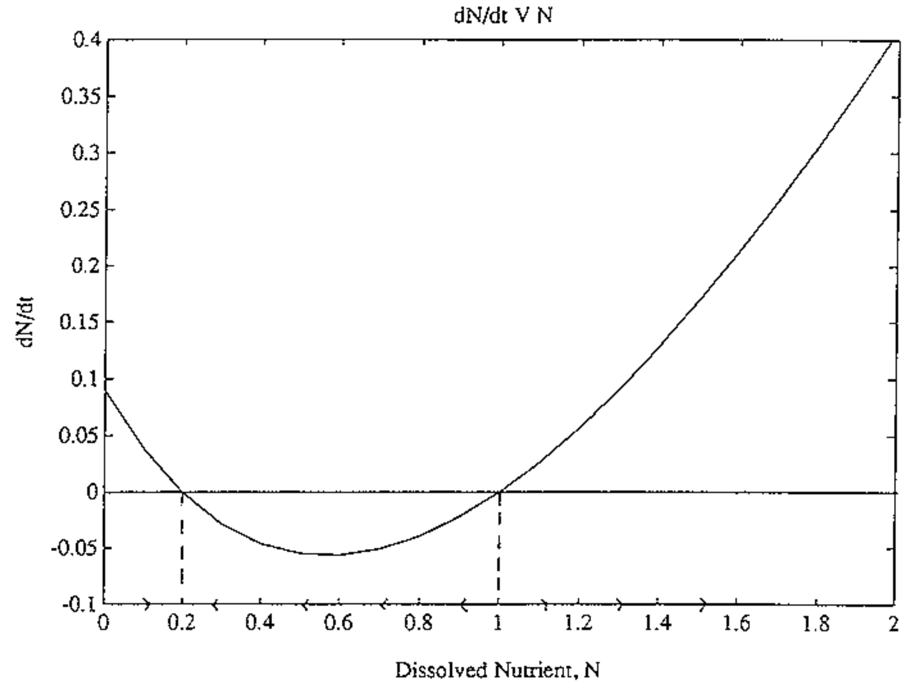


Fig. 2.5 $\frac{dN}{dt}$ verses N, dissolved nutrient.

Theorem 1 therefore concludes. The graph of $\frac{dN}{dt}$ verses N given in equation (2.7) is shown in Fig. 2.5. The arguments laid out in all above cases are illustrated. In this graph, $\alpha = 0.2$ and $N_T = 1$.

2.6 Bifurcation Of The Steady-States.

We have found the steady-states of the system (2.1) and characterised their stability within the feasible region (i.e. $0 < \alpha < N_T$), the nonfeasible region (i.e. $N_T < \alpha$) and at $\alpha = N_T$. The value of $\alpha = N_T$ thus acts as a *threshold point* to the stability behaviour of the steady-states.

Let us choose c as the varying paremeter with a, k and N_T fixed. Define a norm n, as

$$n = \sqrt{P^{*2} + N^{*2}}$$

where $P^* = N_T - \alpha$ and $N^* = \alpha = \frac{ck}{a-c}$.

In our bifurcation diagram, we have two solution branches corresponding to the two steady-states. The solution branches are described as follows,

$$\Gamma_0 = \{(N_T, 0) : c \in \mathbf{R}, 0 < c < a\}$$
$$\Gamma_1 = \{(N^*, P^*) : c \in \mathbf{R}, 0 < c < a\}$$

Γ_0 is the trivial branch corresponding to the trivial steady-state $(N_T, 0)$. Γ_1 is the nontrivial branch corresponding to the coexisting steady-state, (N^*, P^*). The bifurcation diagram is given in Fig. 2.6. In this example, N_T = 40 μg atom NO_3 / dm^3, $c = c^*$ 0.5 day^{-1} and a = 1.0 day^{-1}.

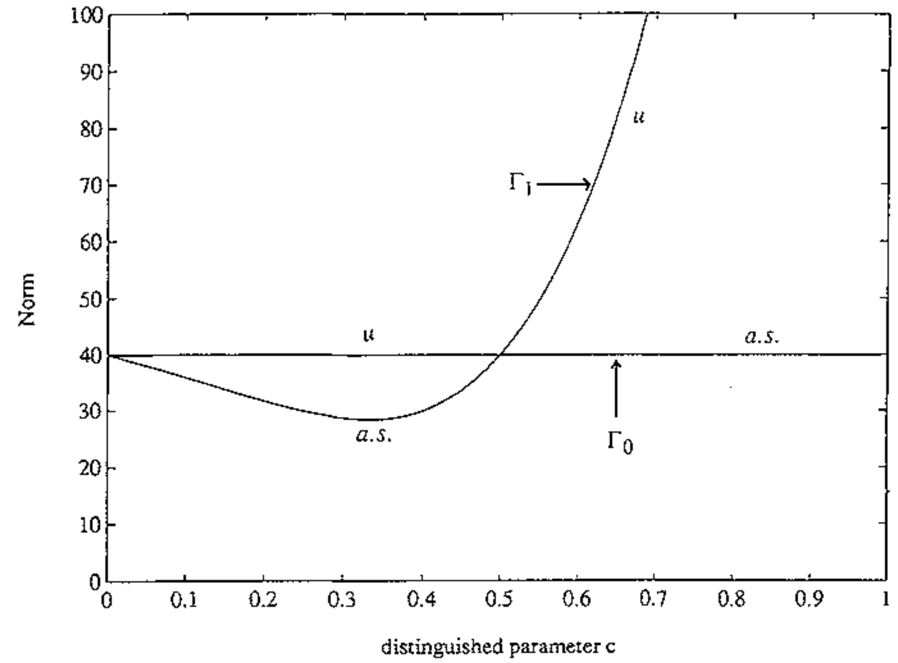


Fig. 2.6 Bifurcation Diagram

The two branches meet at $c = 0$ and $c = c^*$ and thus Γ_1 bifurcates at this value c^*. We know that Γ_1 is an asymptotically stable branch and Γ_0, an unstable branch for $0 < c < c^*$. Then Γ_1 becomes unstable and Γ_0 asymptotically stable for $c^* < c$. Γ_1 lies outside the feasible region. At $c = c^*$, there is only one steady-state $(N_T, 0)$ which is semistable.

2.7 Phase Plane

The phase plane trajectories on the P-N plane are parallel straight lines of slope -1. Due to the fact that $\frac{dP}{dN}$ = -1 for all $t \geq 0$, implying $N + P = N_T$. Base on the analysis made so far, we have the following results. For $0 < \alpha < N_T$, the solution $N + P = N_T$ approaches the steady-state (N^*, P^*) which is asymptotically stable. The phase plane trajectory is shown in Fig. 2.7. For $0 < N_T < \alpha$ and $0 < \alpha = N_T$, the solution $N + P = N_T$ approaches the steady-state $(N_T, 0)$ which is stable and semistable respectively. The phase plane trajectory is shown in Fig. 2.8.

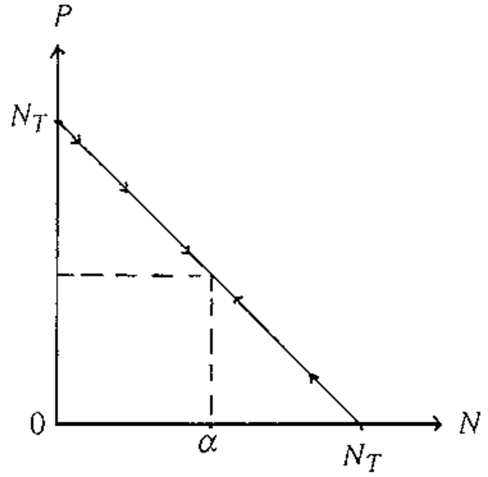


Fig. 2.7 Trajectory for $0 < \alpha < N_T$

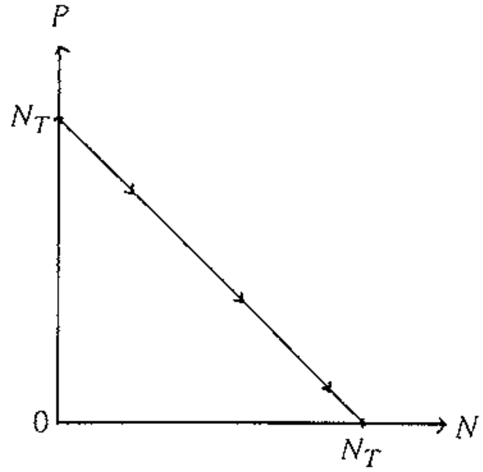


Fig. 2.8 Trajectory for $0 < N_T < \alpha$ and $0 < \alpha = N_T$

2.8 Conclusion

The dynamics of the phytoplankton (P) and dissolved nutrient (N) interaction described by the N-P model has been analysed. The results obtained include the findings of the two steady-states $(\overline{N}, \overline{P}) = (N_T, 0)$ and $(N^*, P^*) = (\alpha, N_T - \alpha)$. The stability of each steady-state has also been determined in which this depends on the α value. The feasibility of the solution, $N + P = N_T$, requires $0 \leq P_0, N_0 \leq N_T$ such that $P_0 + N_0 = N_T$. For the coexisting steady-state to remain feasible this requires $(a-c) > 0$ and $0 < c < c^*$ where all other parameters are positive.

With these information, the outcome of the dynamics of the interaction can be 'monitored'. The coexisting steady-state is possibly ensured to occur in a real-world situation if the above conditions applied.

CHAPTER THREE
N-P-D MODEL

3.1 Introduction

The dynamics of the dissolved nutrient (N) and phytoplankton (P) interaction described previously in the N-P model assumes the fact in which the source of N is being supplied by the death of P and the loss of N is due to the consumption by P. The process of decay of the dead P into N occurs automatically.

In this part of our analysis, we assume further that this decaying process takes sometime to occur. In other words, the instant the interaction starts, the dead P files up first before it begins to disintegrate into N. This is due to the chemical process assisting the disintegration. So a delay-time factor with a unit function enters the N-P model along with a third component called the *dead* phytoplankton (D).

Thus, we give a model (N-P-D model) describing the dynamics as

$$\frac{dN}{dt} = cP(t-\tau)U(t-\tau) - \frac{aNP}{N+k} \tag{3.1a}$$

$$\frac{dP}{dt} = \frac{aNP}{N+k} - cP \tag{3.1b}$$

$$\frac{dD}{dt} = cP - cP(t-\tau)U(t-\tau) \tag{3.1c}$$

where

$$U(t-\tau) = \begin{cases} 0 & if \quad 0 \le t \le \tau \\ 1 & if \quad \tau < t \end{cases}$$

The dynamics of this N-P-D interaction is best described by Fig.3.1.

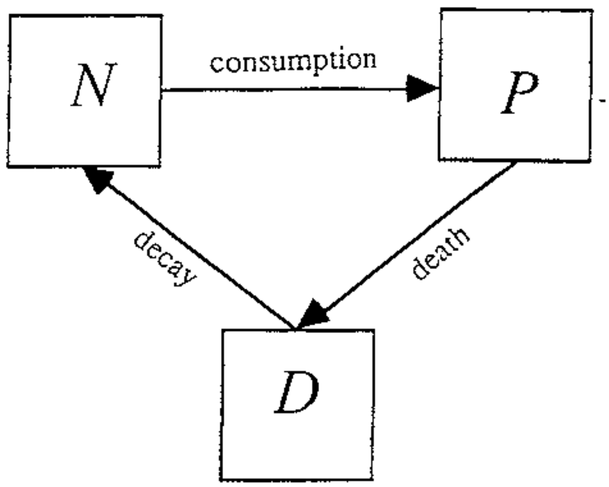


Fig.3.1 N-P-D Dynamical System

The dynamics of this interaction is still conserved since

$$\frac{dN}{dt} + \frac{dP}{dt} + \frac{dD}{dt} = 0$$

This implies

$$N + P + D = N_T = \text{constant} \tag{3.2}$$

Equation (3.2) is the *conservation condition* of our dynamical system (3.1). Thus the general solution of our system (3.1) must obey condition (3.2). The initial conditions are $P(0) = P_0$, $N(0) = N_0$ and $D(0) = 0$ at $t = 0$. These input values determine the constant, N_T. So

$$N_0 + P_0 = N_T \tag{3.3}$$

As before (in chap. 2), the analysis only treats biologically feasible solutions, $N + P + D = N_T$, where $N,\ P, D \geq 0\ \ \forall\ \ t \geq 0$. So the input values must be of such that $0 \leq N_0,\ P_0 \leq N_T$ where (3.3) satisfies. The latter statement is in fact a *necessary condition* for our solutions to be feasible.

Suppose $0 \leq N_0 \leq N_T$. Write equation (3.1b) as

$$\frac{dP}{dt} = \frac{(a-c)(N-\alpha)P}{N+k} \qquad ,\alpha = \frac{ck}{a-c}$$

We shall see later that α is a steady-state value for N and its existence in a feasible region requires $0 < \alpha < N_T$. So

$$P = P_0 e^{(a-c)\int\left(\frac{N-\alpha}{N+k}\right)P \cdot dt}$$

This tells us that the solution $P \geq 0\ \forall\ \ t \geq 0$ since $0 \leq P_0 \leq N_T$ by (3.3). Moreover, if $P_0 = 0$ then $P = 0\ \ \forall\ \ t \geq 0$. Now from (3.1c),

$$D = \begin{cases} \int_0^t cP \cdot dt & 0 \leq t \leq \tau \\ \\ \int_{t-\tau}^t cP \cdot dt & \tau < t \end{cases}$$

Thus $D \geq 0\ \forall\ \ t \geq 0$. Using the conservation condition,

$$0 \leq P + D = N_T - N$$
$$\Rightarrow N \leq N_T \qquad \forall t \geq 0$$

Therefore , $0 \le N \le N_T \quad \forall t \ge 0$. Equivalently , $0 \le P + D \le N_T \ \ \forall t \ge 0$. This concludes straightaway $0 \le P \le N_T$ and $0 \le D \le N_T \ \ \forall t \ge 0$. Therefore our system (3.1) does guarantee feasible solutions as long as $0 \le N_0,\ P_0 \le N_T$ such that (3.3) obeys.

Comparing the two models, N-P-D and N-P, only equation (3.1b) remains unchange. At a glance, we may wish to find the analytical solution for P and so others. It's hard to attempt this unfortunately. We cannot express (3.1b) in terms of P since $N + P + D = N_T$. Therefore the analysis begins at finding the steady-states.

3.2 Steady-States

At the steady-states,

$$\frac{dN}{dt} = \frac{dP}{dt} = \frac{dD}{dt} = 0.$$

Using (3.1b),

$$\frac{dP}{dt} = 0$$

$$\left(\frac{aN}{N+k} - c\right)P = 0$$

$$N = \frac{ck}{a-c} \quad \text{or } P = 0$$

If $P = 0$ then $D = 0$ (since the source of D is resulted from the loss of P) and therefore $N = N_T$. Henceforth, $(\tilde{N}, \tilde{P}, \tilde{D}) = (N_T, 0, 0)$ is the *trivial* steady-state. The other steady-state is $(N^\infty, P^\infty, D^\infty) = (\alpha, P^\infty, D^\infty)$ where $\alpha = \dfrac{ck}{a-c}$. This is the *coexisting* steady-state. Due to the conservation condition (3.2),

$$\tilde{N} + \tilde{P} + \tilde{D} = N^\infty + P^\infty + D^\infty = N_T \tag{3.4}$$

Our next task is to find the expressions of P^∞ and D^∞. Let us assume every feasible solution $N + P + D = N_T$, approaches the coexisting steady-state provided $0 < \alpha < N_T$. Adding all the equations in (3.1),

$$\frac{dN}{dt} + \frac{dP}{dt} + \frac{dD}{dt} = 0$$

Integrating throughout $t \ge 0$,

$$\int_0^t \left(\frac{dN}{ds} + \frac{dP}{ds} + \frac{dD}{ds}\right) ds = 0$$

Integrating N and P first,

$$N - N_0 + P - P_0 + \int_0^t \left(\frac{dD}{ds}\right) ds = 0 \qquad ,P(t) = P, N(t) = N$$

Using (3.3),

$$P + N + \int_0^t \left(\frac{dD}{ds}\right) ds = N_T$$

Substituting (3.1c) for $\frac{dD}{dt}$ gives,

$$P + N + \int_0^t (cP(s) - cP(s-\tau)U(s-\tau))ds = N_T$$

Eliminating the unit function, $U(t-\tau)$,

$$P + N + \int_0^t cP(s)\cdot ds - \int_\tau^t cP(s-\tau)\cdot ds = N_T$$

Letting $s' = s - \tau$ and keeping s' as a dummy variable,

$$P + N + \int_0^t cP(s)\cdot ds - \int_0^{t-\tau} cP(s)\cdot ds = N_T$$

Thus,

$$P + N + \int_{t-\tau}^t cP(s)\cdot ds = N_T \qquad \forall \qquad t \geq \tau$$

By the mean-value theorem,

$$P + N + c\tau P(\xi) = N_T \qquad ,t - \tau \leq \xi \leq t$$

As $t \to \infty, P \to P^\infty$ and $N \to N^\infty = \alpha = \frac{ck}{a-c}$, by assumption, so

$$P^\infty + \alpha + c\tau P^\infty = N_T$$

$$\therefore \quad P^\infty = \frac{N_T - \alpha}{1 + c\tau}$$

Using (3.4),

$$\therefore \quad D^{\infty} = \frac{c\tau(N_T - \alpha)}{1 + c\tau} = c\tau P^{\infty}$$

Hence, there are two steady-states of the system (3.1)

$$(\tilde{N}, \tilde{P}, \tilde{D}) = (N_T, 0, 0)$$
$$(N^{\infty}, P^{\infty}, D^{\infty}) = \left(\alpha, \frac{N_T - \alpha}{1 + c\tau}, \frac{c\tau(N_T - \alpha)}{1 + c\tau}\right) \tag{3.5}$$

In a real-world situation, we would like to see the existence of both steady-states, especially the coexisting one. We can see from (3.5) that certain conditions need to be looked at in order to meet the above objective. With these conditions applied, all solutions will be contained in a certain region. This region which is of our main interest , is called the *feasible region*.

3.3 The Feasible Region (F.R.)

Our analysis emphasises only the feasible solutions, $N + P + D = N_T$ where N, P, $D \geq 0$ $\forall t \geq 0$. As found before, this requires necessarily input values $0 \leq N_0$, $P_0 \leq N_T$ satisfying (3.3). Furthermore, $0 < \alpha < N_T$ so as to contain the coexisting steady-state within the feasible region, F.R. All parameters a, c, k and τ are positive reals. Therefore, $\alpha = \frac{ck}{a-c} > 0$ implies $(a - c) > 0$. If a and k are fixed then $0 < c < \frac{aN_T}{N_T + k}$ so that $0 < \alpha < N_T$. We shall see at later stage that $c = \frac{aN_T}{N_T + k}$ is a bifurcation point of the coexisting steady-state. This value, henceforth, separates the feasible region (solutions) from the nonfeasible one (solutions).

We can see immediately $P^{\infty} < 0$ and $D^{\infty} < 0$ when $N_T < \alpha$, that is $\frac{aN_T}{N_T + k} < c$, and $(\tilde{N}, \tilde{P}, \tilde{D}) = (N^{\infty}, P^{\infty}, D^{\infty})$ when $\alpha = N_T$. In this case, one can predict all feasible solutions will approach the trivial steady-state.

The feasible region lies on a plane, $N + P + D = N_T$, in the 3-dimensional space, i.e. the N-P-D space. It is defined as

$$\text{F.R.} = \{(N, P, D) \in R^3 : N, P, D \in [0, N_T] \text{ where } N + P + D = N_T\}$$

Figure 3.2 illustrates.

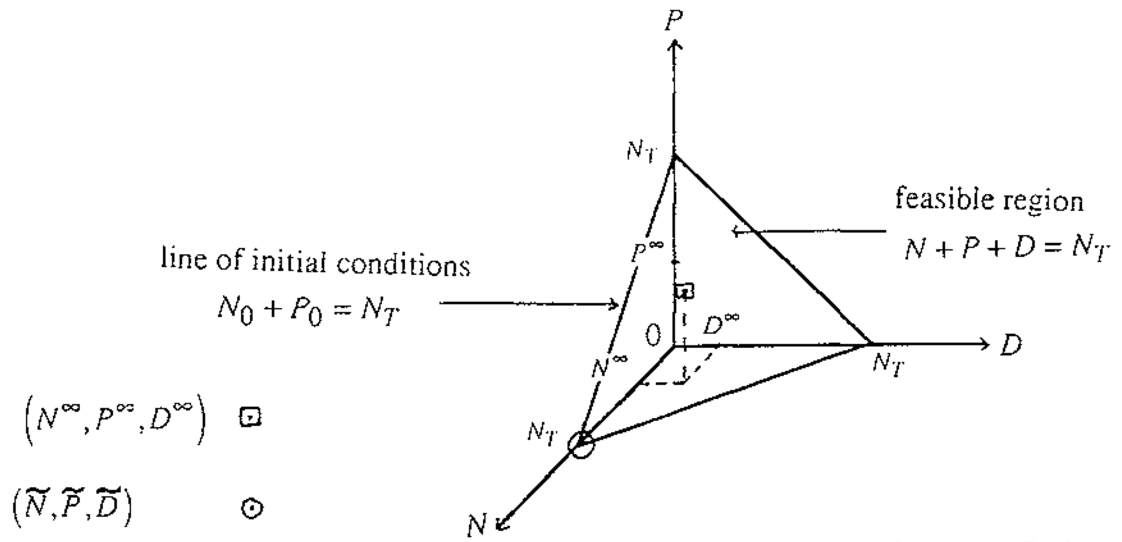


Fig.3.2 The feasible region in the N-P-D space

On the P-N plane, the feasible region is shown by the shaded region in Fig.3.3. It is defined as

$$\text{F.R}=\{(N,P)\in R^2 : N,P \in [0,N_T] \text{ where } 0 \le N + P \le N_0 + P_0 = N_T\}$$

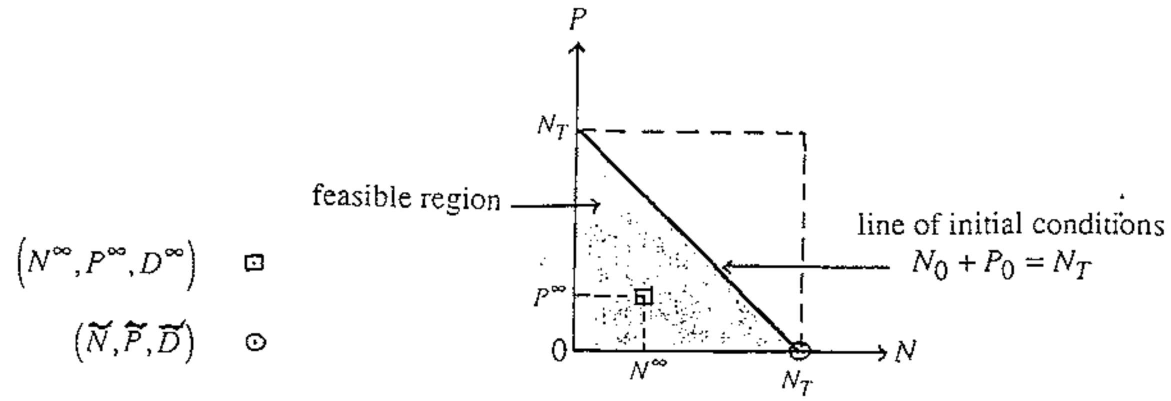


Fig.3.3 Feasible region on the N-P plane

From now onwards, our analysis refers F.R. defined on the N-P plane.

3.4 Stability Analysis (Linearisation)

The stability of each steady-state is now analysed and here we linearise system (3.1) in a small neighbourhood of the steady-state which requires a small perturbation of the solutions N, P and D. Hence, we come out with a linearised system which has the origin as a critical point. Due to the condition of conservation, we shall linearise equations (3.1a) and (3.1b) involving N and P only.

In this section, we are going to analyse the stability state of $(\tilde{N}, \tilde{P}, \tilde{D})$ first and then follows with $(N^\infty, P^\infty, D^\infty)$. Thus this section divides itelf into two subsections.

3.4.1 Stability Of $(\tilde{N},\tilde{P},\tilde{D})$

Perturbing the solutions N, P and D about $(\tilde{N},\tilde{P},\tilde{D})$, let $N = N_T + n$, $P = 0 + p = p$ and $D = 0 + d = d$ where $n,\ p,\ d \in \mathbf{R}$ s.t. $n,\ p,\ d << 1$. Due to the conservation condition (3.2), $n + p + d = 0$. Let us assume further the followings

(i) if $n \le 0\ \forall t \ge 0$, then $0 \le p + d$ in which $0 \le p,\ d\ \forall t \ge 0$.

(ii) if $0 \le n\ \ \forall t \ge 0$, then $p + d \le 0$ in which $p,\ d \le 0 \forall t \ge 0$.

Substituting these variables into (3.1a) and (3.1b),

$$\frac{dN}{dt} = \frac{dn}{dt} = cp(t-\tau)U(t-\tau) - \frac{a(N_T+n)p}{N_T+n+k} \quad , \frac{dN_T}{dt} = 0 \qquad (3.6a)$$

$$\frac{dP}{dt} = \frac{dp}{dt} = \frac{a(N_T+n)p}{N_T+n+k} - cp \qquad (3.6b)$$

Consider (3.6b) first. Expanding and grouping the terms,

$$\frac{dp}{dt} = \frac{(a-c)(N_T-\alpha)p}{N_T+n+k} + \frac{(a-c)pn}{N_T+n+k} \quad , \quad \alpha = \frac{ck}{a-c}$$

Taking only the linear term, the linearised equation of (3.6b) is,

$$\frac{dp}{dt} = \frac{(a-c)(N_T-\alpha)}{N_T+k}p$$

Follows immediately, the linearised equation of (3.6a) is

$$\frac{dn}{dt} = cp(t-\tau)U(t-\tau) - cp - \frac{(a-c)(N_T-\alpha)}{N_T+k}p$$

Therefore the linearised version of system (3.1) about $(\tilde{N},\tilde{P},\tilde{D}) = (N_T,0,0)$ can be written as

$$\frac{dn}{dt} = cp(t-\tau)U(t-\tau) - cp - \frac{(a-c)(N_T-\alpha)}{N_T+k}p \qquad (3.7a)$$

$$\frac{dp}{dt} = \frac{(a-c)(N_T-\alpha)}{N_T+k}p \qquad (3.7b)$$

The *critical point* of this system occurs at the origin, $(n,\ p,\ d) = (0,0,0)$.

$\lambda = \dfrac{(a-c)(N_T-\alpha)}{N_T+k}$ is a constant. Usually $\lambda << 1$. $\lambda > 0$ if $0 < \alpha < N_T$, $\lambda = 0$ if $\alpha = N_T$ and $\lambda < 0$ if $N_T < \alpha$. Solving (3.7b) gives,

$$p = p_0 e^{\lambda t}, \quad p_0 \neq 0$$

Substituting p into (3.7a),

$$\frac{dn}{dt} = -p_0 e^{\lambda t}\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right)$$

This gives,

$$n = -\left(\frac{p_0}{\lambda}\right)\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right)e^{\lambda t} + A$$

where A is a constant of integration. At $t = 0$, $n = n_0 \neq 0$ and thus A can be expressed as

$$A = n_0 + \left(\frac{p_0}{\lambda}\right)\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right)$$

So,

$$n = n_0 + \left(\frac{p_0}{\lambda}\right)\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right)\left(1 - e^{\lambda t}\right)$$

The solutions for n and p are therefore

$$p = p_0 e^{\lambda t} \tag{3.8a}$$

$$n = n_0 + \left(\frac{p_0}{\lambda}\right)\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right)\left(1 - e^{\lambda t}\right) \tag{3.8b}$$

Observing the behaviour of these perturbing solutions p and n enable us to conclude the stability state of $(\tilde{N}, \tilde{P}, \tilde{D})$. Notice that p and n behave accordingly to the choice of λ. Therefore, we consider cases.

<u>Case $\lambda > 0$</u>

$0 < \alpha < N_T$. As $t \to \infty$, $p \to \infty$ if $p_0 > 0$ (small) and $p \to -\infty$ if $p_0 < 0$ (small). This means both feasible and nonfeasible solutions P will turn away from $\tilde{P} = 0$. From (3.8b) $\left(\lambda + c - ce^{-\lambda\tau}U(t-\tau)\right) > 0$. Since p_0 and n_0 are of opposite signs, both feasible and nonfeasible solutions N will turn away from $\tilde{N} = N_T$. The trivial steady-state $(\tilde{N}, \tilde{P}, \tilde{D})$ is therefore *unstable*. The behaviours of the solutions n and p are illustrated by the following figures, Fig.3.4 and Fig.3.5.

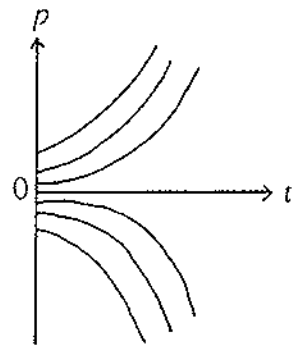


Fig.3.4 The solutions p near the origin when $\lambda > 0$.

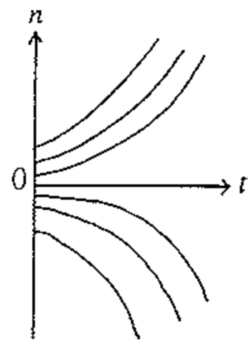


Fig.3.5 The solutions n near the origin when $\lambda > 0$.

Case $\lambda < 0$

$N_T < \alpha$. As $t \to \infty$, $p \to 0$ for any value of p_0 small. This means that the solution P approaches $\tilde{P} = 0$. $\left(\lambda + c - ce^{-\lambda\tau}\right) < 0 \;\; \forall \tau < t$. Now as $t \to \infty$, $n \to n_0 + \left(\frac{p_0}{\lambda}\right)\left(\lambda + c - ce^{-\lambda\tau}\right)$. In this case the *vanishing factor* requires $|n_0| = |p_0|\left(\frac{\lambda + c - ce^{-\lambda\tau}}{\lambda}\right)$ since p_0 and n_0 are of opposite signs. Thus $n \to 0$ as $t \to \infty$. Consequently, N approaches $\tilde{N} = N_T$. Thefore $(\tilde{N}, \tilde{P}, \tilde{D})$ becomes *asymptotically stable*. The behaviours of p and n near the critical point are shown in Fig.3.6 and Fig.3.7. If the vanishing factor is not met then this linearisation method fails to conclude the stability state $(\tilde{N}, \tilde{P}, \tilde{D})$. In this case the critical point (the origin) of the linearised system (3.7) is said to be *neutral*. . In other words it is neither stable nor unstable.

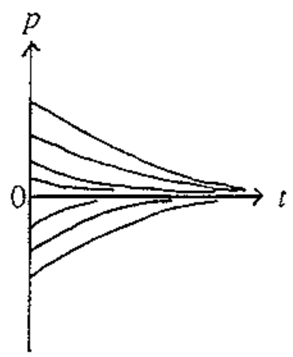


Fig.3.6 The solutions p near the origin when $\lambda < 0$.

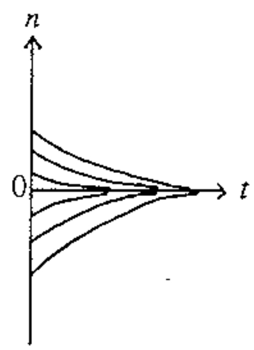


Fig.3.7 The solutions n near the origin when $\lambda < 0$.

Case $\lambda = 0$

This is the case when the two steady-states are equal, i.e. $(\tilde{N},\tilde{P},\tilde{D}) = (N^{\infty},P^{\infty},D^{\infty})$. Looking back at (3.8a) and (3.8b), $p = p_0$ and n is not defined. Moreover, our linearised system (3.7) vanishes when $\lambda = 0$. Thus the stability of this steady-state can not be concluded. In other words, this method of linearisation doesn't work!

Summary Of Results

The results obtained from the above analysis are tabulated below.

Table 3.1

$\alpha = \dfrac{ck}{a-c}$	$\lambda = \dfrac{(a-c)(N_T-\alpha)}{N_T+k}$	Stability Of $(\tilde{N},\tilde{P},\tilde{D})$
$0 < \alpha < N_T$	$\lambda > 0$	Unstable
$0 < N_T < \alpha$	$\lambda < 0$	Asymptotically Stable*
$\alpha = N_T$	$\lambda = 0$	Inconclusive

note: * if the vanishing factor is met, otherwise the stability is inconclusive.

3.4.2 Stability Of $(N^{\infty},P^{\infty},D^{\infty})$

Small perturbation of the solutions N, P and D about the coexisting steady-state, let $N = N^{\infty} + n$, $P = P^{\infty} + p$ and $D = D^{\infty} + d$ where $n, p, d \in \mathbf{R}$, $n, p, d << 1$ and $n+p+d = 0$. For our analysis, it is enough to consider equations (3.1a) and (3.1b) involving N and P only.

Substituting these variables into equation (3.1b),

$$\frac{dP}{dt} = \frac{dP^{\infty}}{dt} + \frac{dp}{dt} = \left(\frac{a(N^{\infty}+n)}{N^{\infty}+n+k} - c\right)(P^{\infty}+p)$$

where $\dfrac{dP^{\infty}}{dt} = 0$ since P^{∞} is a constant. Expanding and grouping the terms,

$$\frac{dp}{dt} = \frac{(a-c)(N^{\infty}-\alpha)P^{\infty}}{N^{\infty}+n+k} + \frac{nP^{\infty}(a-c)}{N^{\infty}+n+k} + \frac{p(a-c)(N^{\infty}-\alpha)}{N^{\infty}+n+k} + \frac{np(a-c)}{N^{\infty}+n+k}$$

The first and third terms vanish. Taking only the linear one and substituting the values (coordinates) of N^{∞} and P^{∞} thus obtaining,

$$\frac{dp}{dt} = \frac{(a-c)^2(N_T-\alpha)}{ak(1+c\tau)}n$$

Similarly,

$$\frac{dn}{dt} = cp(t-\tau)U(t-\tau) - cp - \frac{(a-c)^2(N_T-\alpha)}{ak(1+c\tau)}n$$

Thus we have a linearised system about $(N^\infty, P^\infty, D^\infty)$ corresponding to the system (3.1) involving N and P only,

$$\frac{dp}{dt} = \frac{(a-c)^2(N_T-\alpha)}{ak(1+c\tau)}n \tag{3.9a}$$

$$\frac{dn}{dt} = cp(t-\tau)U(t-\tau) - cp - \frac{(a-c)^2(N_T-\alpha)}{ak(1+c\tau)}n \tag{3.9b}$$

Note that the critical point of this linearised system occurs at the origin, $(n, p, d) = (0,0,0)$.

Let $\Omega = \dfrac{(a-c)^2(N_T-\alpha)}{ak(1+c\tau)}$. Since all parameters a, c and k, are positive reals, $\tau \geq 0$ and $(a\text{-}c) > 0$, $\Omega > 0$ if $0 < \alpha < N_T$, $\Omega = 0$ if $\alpha = N_T$ and $\Omega < 0$ if $0 < N_T < \alpha$. Usually $\Omega << 1$. One can easily observe that the stability of $(N^\infty, P^\infty, D^\infty)$ remains inconclusive for $\Omega = 0$. Let us assume a general solution of system (3.9) of the form,

$$p = p_0 e^{(-u+iw)t} \tag{3.10a}$$

$$n = n_0 e^{(-u+iw)t} \tag{3.10b}$$

where $u, w \in \mathbf{R}$, and $p_0, n_0 \neq 0$. Substitute p and n into (3.9a) and (3.9b) and considering $\tau < t$,

$$p_0(-u+iw)e^{(-u+iw)t} = \Omega n_0 e^{(-u+iw)t} \tag{3.11a}$$

$$n_0(-u+iw)e^{(-u+iw)t} = cp_0 e^{(-u+iw)(t-\tau)} - cp_0 e^{(-u+iw)t} - \Omega n_0 e^{(-u+iw)t} \tag{3.11b}$$

This gives,

$$p_0(-u+iw) = \Omega n_0 \tag{3.12a}$$

$$n_0(-u+iw) = cp_0\left[e^{u\tau}(\cos w\tau - i\sin w\tau) - 1\right] - \Omega n_0 \tag{3.12b}$$

Solving (3.12a) and (3.12b),

$$\left(\frac{p_0}{\Omega}\right)(-u+iw)^2 = cp_0\left[e^{u\tau}(\cos w\tau - i\sin w\tau) - 1\right] - p_0(-u+iw) \tag{3.13}$$

provided $\Omega \neq 0$ i.e. when $\alpha = N_T$. Then (3.13) becomes

$$(-u+iw)^2 = c\Omega\left[e^{u\tau}(\cos w\tau - i\sin w\tau) - 1\right] - \Omega(-u+iw)$$

Separating the reals and imaginaries,

$$u^2 - w^2 - c\Omega e^{u\tau}\cos w\tau + \Omega(c-u) = 0 \quad (3.14a)$$

$$2uw - \Omega(ce^{u\tau}\sin w\tau - w) = 0 \quad (3.14b)$$

The values of u and w satisfying (3.14a) and (3.14b) are the eigenvalues of the solutions n and p and with these enable us to deduce the stability state of $(N^\infty, P^\infty, D^\infty)$. If $u > 0$ and $w = 0$ then the bifurcating solutions p and n decay exponentially. So the solution, $N + P + D = N_T$, approaches the steady-state asymptotically. Thus $(N^\infty, P^\infty, D^\infty)$ becomes asymptotically stable. The case $w \neq 0$, $(N^\infty, P^\infty, D^\infty)$ acts as a spiral point which is asymptotically stable. On the other hand, $(N^\infty, P^\infty, D^\infty)$ will become unstable if $u < 0$. If $u = 0$ and $w \neq 0$, the critical point $(n,p,d) = (0,0,0)$ acts as a centre for the linearised system (3.9). Unfortunately, no conclusion about the stability state of $(N^\infty, P^\infty, D^\infty)$ can be made since our system (3.1) is *nonlinear*. Furthermore, this test fails if $u = w = 0$.

Let us try solving the above equations (3.14a) and (3.14b). Consider first, $w = 0$. Obviously, both these equations are satisfied only if

$$u^2 - \Omega u + \Omega c = \Omega c e^{u\tau} \quad (3.15)$$

Recall that $\Omega = \dfrac{(a-c)^2(N_T - \alpha)}{ak(1+c\tau)}$ where the signs depend on our choice of α. In solving (3.15) we only consider $\Omega > 0$ and $\Omega < 0$. For $\Omega = 0$, we can see from (3.14), $u = w = 0$. Our test breaks down. So let us tackle first the case when $\Omega > 0$. Furthermore, let

$$y_1(u) = u^2 - \Omega u + \Omega c$$
$$y_2(u) = \Omega c e^{u\tau}$$

We can see immediately that the number of roots of (3.15) i.e. $y_1(u) = y_2(u)$, depends on the choice of τ with all parameters kept constant. If $\tau < \bar{\tau}$ then (3.15) has three roots at $u = 0$, $u = u_{2'}$ and $u = u_3$. Both roots $u = u_{2'}$ and $u = u_3$ are positive. See Fig 3.8. Both eigenvalues $u = u_{2'}$ and $u = u_3$ represent exponentially decaying solutions. Unfortunately, no conclusion can be made about the general solution (3.10) unless the eigenvector associating with $u = 0$ vanishes. If this is the case then $(N^\infty, P^\infty, D^\infty)$ is asymptotically stable. At $\tau = \bar{\tau}$ there are two roots at $u = 0$ and $u = u_2$. At $u = u_2$ (which is positive), the two curves

$y_1(u)$ and $y_2(u)$ touch each other tangentially . See Fig. 3.9. In the other sense $\tau = \bar{\tau}$ can be determined by equating both gradients of these curves and also evaluating $y_1(u_2) = y_2(u_2)$. Once again, the general solution (3.10) will decay exponentially if and only if the eigenvector associating with $u = 0$ vanishes. For $\bar{\tau} < \tau$ there is only one root at $u = 0$. See Fig. 3.10. This test definitely breaks down.

In all cases, $u = 0$ appears and this means that it is always an eigenvalue of the solutions p and n. In this case where we have taken $w = 0$ and $\Omega > 0$, the nature of this critical point $(n, p, d) = (0,0,0)$ can not be deduced especially when $\bar{\tau} < \tau$.

Looking back at the equations (3.14) we can find those values of w. Nonetheless $u = 0$ always appears as a real root regardless of w and Ω. In other words, the general solution to our linearised system (3.9) always contain a real eigenvalue which has the value of zero. Thus the steady-state of $(N^{\infty}, P^{\infty}, D^{\infty})$ can not be concluded by this method. Similar situation also occurs when $\Omega < 0$ where $u = 0$ always exists as an eigenvalue. See Fig. 3.11.

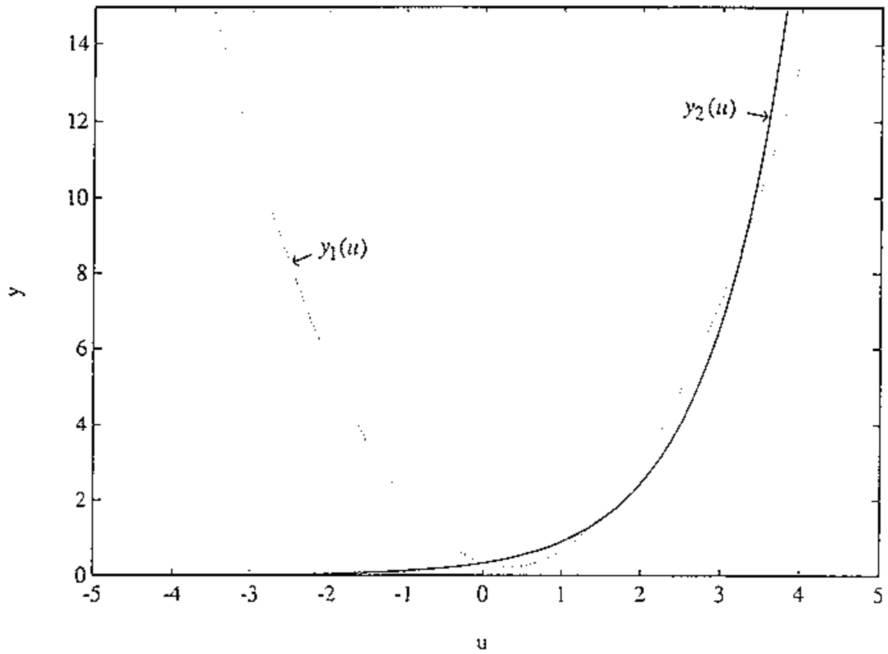


Fig.3.8 The curves $y_1(u)$ and $y_2(u)$ when $\tau < \bar{\tau}$ and $\Omega > 0$.

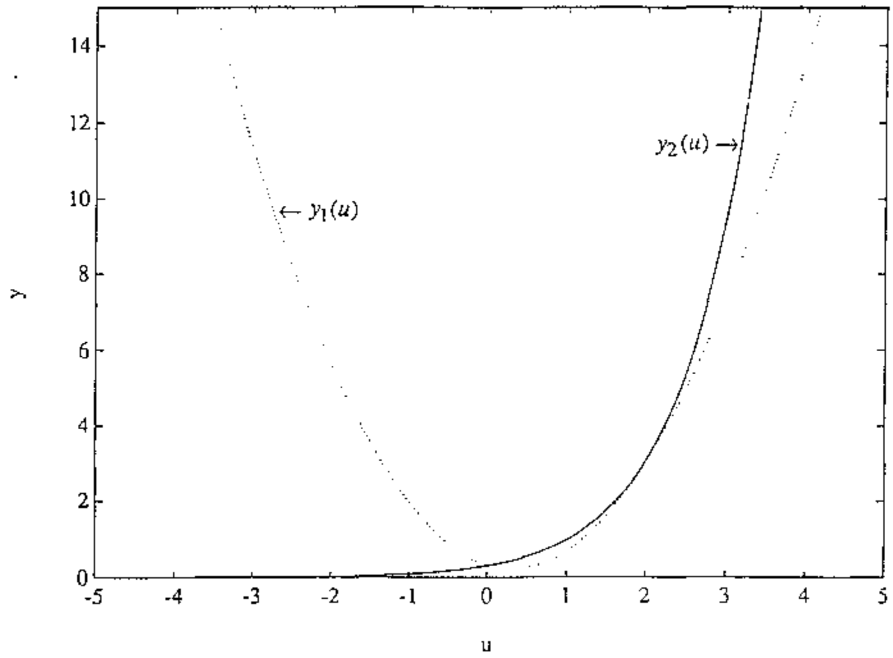


Fig. 3.9 The two curves $y_1(u)$ and $y_2(u)$ when $\tau = \overline{\tau}$ and $\Omega > 0$.

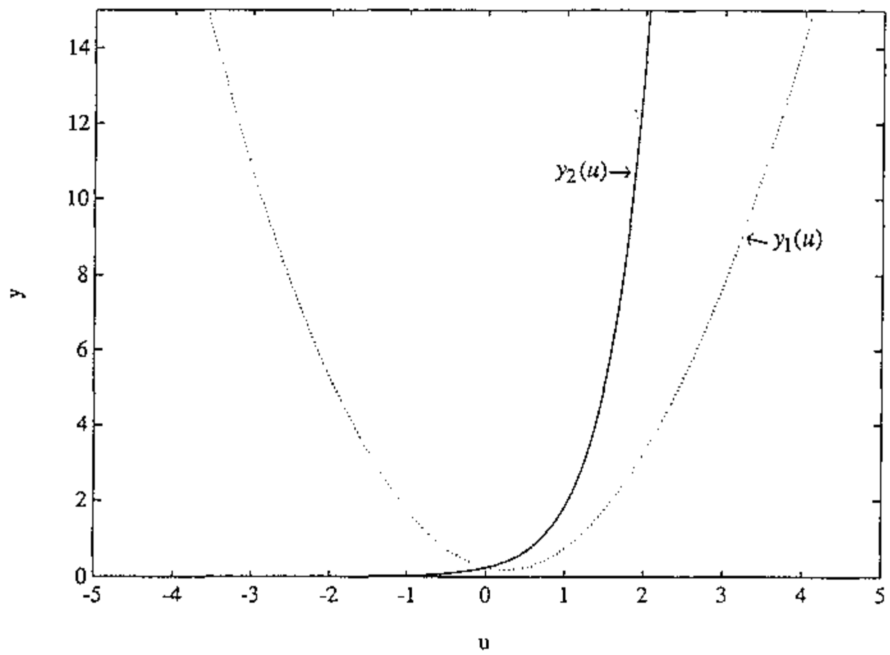


Fig.3.10 The two curves $y_1(u)$ and $y_2(u)$ when $\tau = \overline{\tau}$ and $\Omega > 0$.

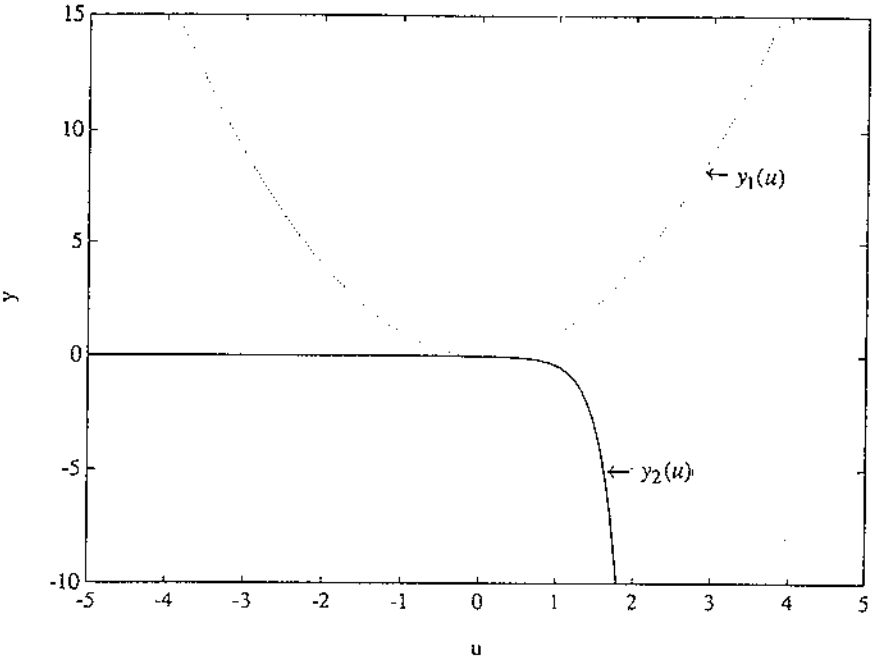


Fig.3.11The two curves $y_1(u)$ and $y_2(u)$ when $\Omega < 0$.

Nonetheless the significance of choosing τ can be seen in the following Figures, 3.12, 3.13 and 3.14. Refer to appendix I. These examples are the numerically -simulated solutions of our original system (3.1). In Fig. 3.12, τ=1.0 *day*, the feasible solution approaches $(N^{\infty},P^{\infty},D^{\infty})$ exponentially. When $\tau=\bar{\tau}$=1.13 *days*, the feasible solution also approaches $(N^{\infty},P^{\infty},D^{\infty})$ exponentially as shown in Fig. 3.13. The feasible solution approaches $(N^{\infty},P^{\infty},D^{\infty})$ spirally when τ=5 *days* as shown in Fig.3.14. In these examples, a=1.0 day^{-1}, c=0.5 day^{-1}, k=0.2 μg atomNO_3 / dm^3, N_0=0.8 μg atomNO_3 / dm^3, P_0= 0.2 μg atomNO_3 / dm^3 and $\bar{\tau} \approx 1.13$ *days*.

In the first two cases the steady-state $(N^{\infty},P^{\infty},D^{\infty})$ behaves like a *node* attracting all feasible solutions asymptotically. In the third case where $\tau > \bar{\tau}$, $(N^{\infty},P^{\infty},D^{\infty})$ behaves like a *spiral node* attracting all feasible solutions asymptotically. Therefore the coexisting steady-state is *asymptotically stable* when $\Omega > 0$ i.e. $0 < \alpha < N_T$.

In subsection 3.4.1 we are able to deduce the stability of $(\tilde{N},\tilde{P},\tilde{D})$ though a problem arises when $\lambda = 0$ i.e. $\alpha = N_T$. The results can be referred to Table 3.1. Unfortunately, we are unable to deduce the stability of $(N^{\infty},P^{\infty},D^{\infty})$ by applying this method of linearisation. This is due to the existence of a zero eigenvalue in the perturbing solutions. Nonetheless, we shall pursue on analysing the stability of $(N^{\infty},P^{\infty},D^{\infty})$ by applying the Lyapunov method.

3.5 Lyapunov's Direct Method (Stability Analysis)

Let $N = \alpha + x$, $P = P^{\infty} + y$ and $D = D^{\infty} + z$ where $x,y,z \in \mathbf{R}$, $x,y,z << 1$ and $x+y+z = 0$. Considering equations (3.1a) and (3.1b), which involve N and P, we substitute $P = P^{\infty} + y$ and $N = \alpha + x$ into (3.1b),

$$\frac{dP}{dt}=\frac{dP^{\infty}}{dt}+\frac{dy}{dt}=\frac{a(\alpha+x)(P^{\infty}+y)}{\alpha+x+k}-c(P^{\infty}+y)$$

In arranging terms, we find that some terms vanish and thus

$$\frac{dy}{dt}=\frac{(a-c)(P^{\infty}+y)x}{\alpha+x+k} \tag{3.16b}$$

Follows immediately,

$$\frac{dx}{dt}=cy(t-\tau)U(t-\tau)-cy-\frac{(a-c)(P^{\infty}+y)x}{\alpha+x+k} \tag{3.16a}$$

Therefore we have an autonomous system which is of the form,

$$\frac{d\underline{x}}{dt}=\underline{f}(\underline{x}) \qquad \text{where } \underline{x}=(x,y)$$

At $\underline{x}=\underline{0}$, $\underline{f}(\underline{0})=0$ and so it is an isolated critical point of system (3.16). One can verify easily that $\underline{f}(\underline{x})$ is Lipschitz continuous on some neighbourhood S of the origin, $\underline{x}=\underline{0}$. Note here that $(a-c)>0$. Also $(P^{\infty}+y)$ > 0 and $(\alpha+x+k)>0$ if α < N_T. P^{∞}= 0 when $\alpha=N_T$. If $\alpha>N_T$ then $(P^{\infty}+y)<0$ and $(\alpha+x+k)>0$.

Let

$$V(x,y)=Ax^2+By^2$$

be the Lyapunov function where A and B are positive constants. Obviously, $V(x,y)$is continuous and has continuous first partial derivatives. At the critical point (x,y) =(0,0), $V(0,0)$= 0 and $V(x,y)$ > 0 $\forall\underline{x}\in S$ such that $\underline{x}\neq\underline{0}$. In other words, our Lyapunov function is positive definite on S of the origin.

Differentiating the Lyapunov function,

$$\begin{aligned} V^{*}(x,y) &= 2Ax\cdot\frac{dx}{dt}+2By\cdot\frac{dy}{dt} \\ &= Cx\cdot\frac{dx}{dt}+Dy\cdot\frac{dy}{dt} \qquad C=2A \quad D=2B \end{aligned} \tag{3.17}$$

This is the derivative function of $V(x,y)$. Substituting (3.16a) and (3.16b) into (3.17) gives,

$$V^{*}(x,y)=\frac{(a-c)(P^{\infty}+y)(Dy-Cx)x}{\alpha+x+k}+Ccx(y(t-\tau)U(t-\tau)-y)$$

Without loss of generality, let $C = D = 1$. So we have

$$V^*(x,y) = \frac{(a-c)(P^\infty + y)(y-x)x}{\alpha + x + k} + cx\big(y(t-\tau)U(t-\tau) - y\big) \tag{3.18}$$

If

a) $V^*(x,y) \leq 0 \quad \forall \underline{x} \in S$ such that $\underline{x} \neq \underline{0}$ ($V^*(x,y)$ is seminegative definite) then (3.16) is stable at the origin, $\underline{x} = \underline{0}$.

b) $V^*(x,y) < 0 \quad \forall \underline{x} \in S$ such that $\underline{x} \neq \underline{0}$ ($V^*(x,y)$ is negative definite) then (3.16) is asymptotically stable at the origin, $\underline{x} = \underline{0}$.

c) there exists a domain $\Lambda \subseteq S$ containing the origin such that $V^*(x,y) > 0 \quad \forall \underline{x} \in \Lambda$ where $\underline{x} \neq \underline{0}$ then the origin is an unstable critical point.

Let us work on the derivative function $V^*(x,y)$ given in (3.18) inside the feasible region where $\alpha < N_T$. We are hoping to find a result for the stability state of the feasible $(N^\infty, P^\infty, D^\infty)$ according to either a) or b) as mentioned above. Looking at (3.18), we know that $(a-c) > 0$, $(P^\infty + y) > 0$ $(\alpha + x + k) > 0$ and c > 0. The other terms remain to be found. Once again we are faced with difficulties since $V^*(x,y)$ is not always negative definite (or seminegative definite) for all x and y in some neighbourhood S of the origin. Sadly to say, we are unable to make definite conclusion about the stability state of $(N^\infty, P^\infty, D^\infty)$.

3.6 Laplace Transformation

Let us consider the Laplace transforms of system (3.9) as follows

$$\overline{p}(s) = \int_0^\infty e^{-s\tau} \cdot p(t) \cdot dt \ , \quad \overline{n}(s) = \int_0^\infty e^{-s\tau} \cdot n(t) \cdot dt$$

Applying the transformation rules,

$$\overline{\dot{p}}(s) = s\overline{p} - p_0$$
$$\overline{\dot{n}}(s) = s\overline{n} - n_0$$
$$\overline{p(t-\tau)U(t-\tau)}(s) = e^{-s\tau}\overline{p}(s)$$

So we have the following equations,

$$s\overline{p} - p_0 - \Omega n = 0 \tag{3.19a}$$
$$s\overline{n} - n_0 - ce^{-s\tau}\overline{p} + c\overline{p} + \Omega\overline{n} = 0 \tag{3.19b}$$

Solving these equations simultaneously,

$$\overline{n}(s) = \frac{sn_0 + cp_0(e^{-s\tau} - 1)}{s^2 + \Omega s + \Omega c - \Omega c e^{-s\tau}}$$

$$\overline{p}(s) = \frac{p_0 s + \Omega(p_0 + n_0)}{s^2 + \Omega s + \Omega c - \Omega c e^{-s\tau}}$$

By inversion, the solutions $n(t)$ and $p(t)$ can be expressed as a sum of residues evaluated at the poles of the integrands,

$$n(t) = \frac{1}{2\pi i}\int_{\sigma - i\infty}^{\sigma + i\infty} e^{st}\overline{n}(s)\cdot ds = \sum_n \underset{s=s_n}{\mathrm{Re}s}\left(e^{st}\overline{n}(s)\right) \tag{3.20a}$$

$$p(t) = \frac{1}{2\pi i}\int_{\sigma - i\infty}^{\sigma + i\infty} e^{st}\overline{p}(s)\cdot ds = \sum_n \underset{s=s_n}{\mathrm{Re}s}\left(e^{st}\overline{p}(s)\right) \tag{3.20b}$$

σ is a constant, large enough to be greater than the real part of all the poles (simple) of each integrand. These poles correspond to the the roots s_n of the *characteristics* curve

$$w(s) = s^2 + \Omega s + \Omega c - \Omega c e^{-s\tau}$$

For the critical point (origin) of our linearised system (3.9) to be stable (asymptotically), this requires negative real parts of all s_n.

Let us solve the charateristics equation,

$$s^2 + \Omega s + \Omega c - \Omega c e^{-s\tau} = 0 \tag{3.21}$$

If we let

$$y_1(s) = s^2 + \Omega s + \Omega c$$
$$y_2(s) = \Omega s e^{-s\tau}$$

The zeros of (3.21) are determined when these two curves intersect (or meet). The curve $y_1(s)$ is quadratic in nature and the curve $y_2(s)$ behaves exponentially. Bare in mind that the zeros of (3.21) may consist of the imaginary parts. Nonetheless, their values won't have much effect to the natures of these curves.

So let us consider $s = a + ib$ where a, $b \in \mathbf{R}$. By substitution, equation (3.21) becomes

$$(a + ib)^2 + \Omega(a + ib) + \Omega c - \Omega c e^{-(a+ib)\tau} = 0$$

Collecting the reals and imaginaries,

$$a^2 - b^2 + \Omega a + \Omega c - \Omega c e^{-a\tau} \cos(b\tau) = 0 \tag{3.22a}$$

$$2ab + \Omega b + \Omega c e^{-a\tau} \sin(b\tau) = 0 \tag{3.22b}$$

One may notice straightaway that this equation is quite similar to equation (3.14). If we let $b = 0$ (extreme case), then equation (3.22a) becomes

$$a^2 + \Omega a + \Omega c - \Omega c e^{-a\tau} = 0 \tag{3.23}$$

Equation (3.22b) satisfies.

As in equation (3.15), the number of roots (all of which are simple poles of $\bar{n}(s)$) depends on choices of τ. For $\tau < \bar{\tau}$, there are three distinct roots $a = 0, a = a_2$ and $a = a_3$. Both a_2 and a_3 have negative values. For $\tau = \bar{\tau}$, there are two distinct roots $a = 0$ and $a = a_2$. a_2 is negative. For $\bar{\tau} < \tau$, only one root exists i.e. $a = 0$. The following Figures 3.15, 3.16 and 3.17 illustrates respective situations where equation (3.23) is solved when the two following curves intersect (meet) each other.

$$y_1(a) = a^2 + \Omega a + \Omega c$$
$$y_2(a) = \Omega c e^{-a\tau}$$

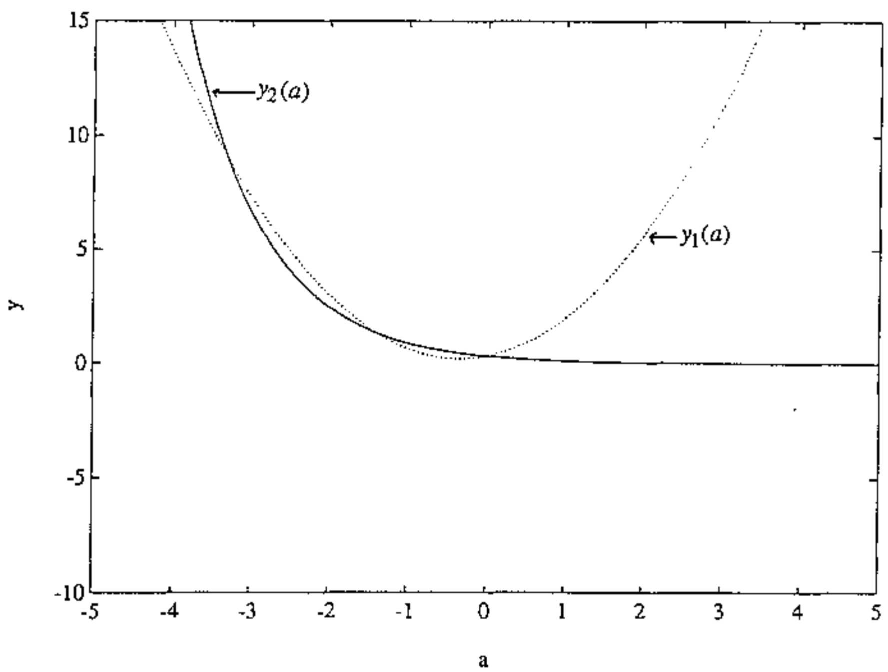


Fig.3.15 The two curves $y_1(a)$ and $y_2(a)$ intersect at three points corresponding to the roots of Equation (3.23) when $\tau < \bar{\tau}$.

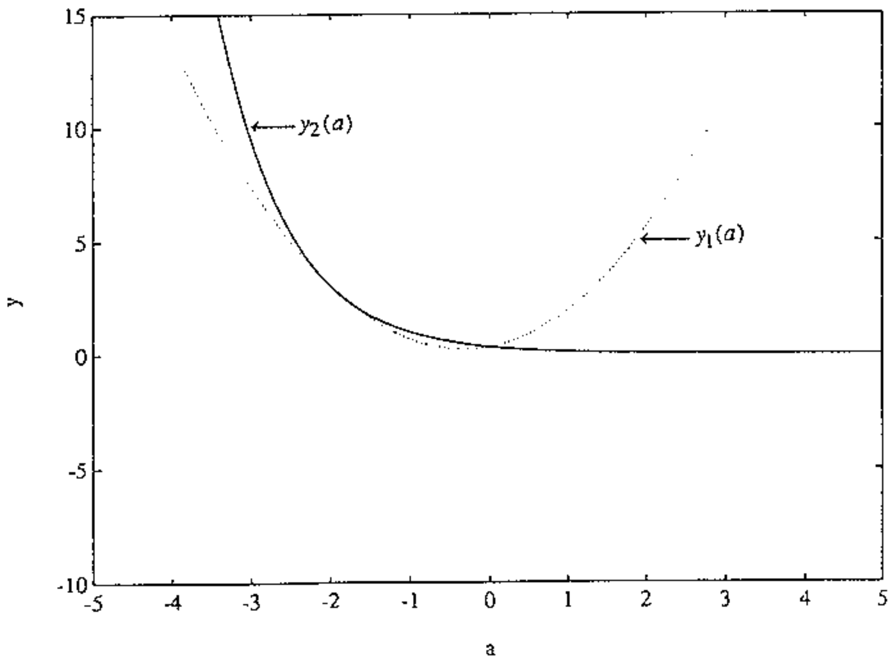


Fig.3.16 Two roots of equation (3.23) when $\tau = \bar{\tau}$.

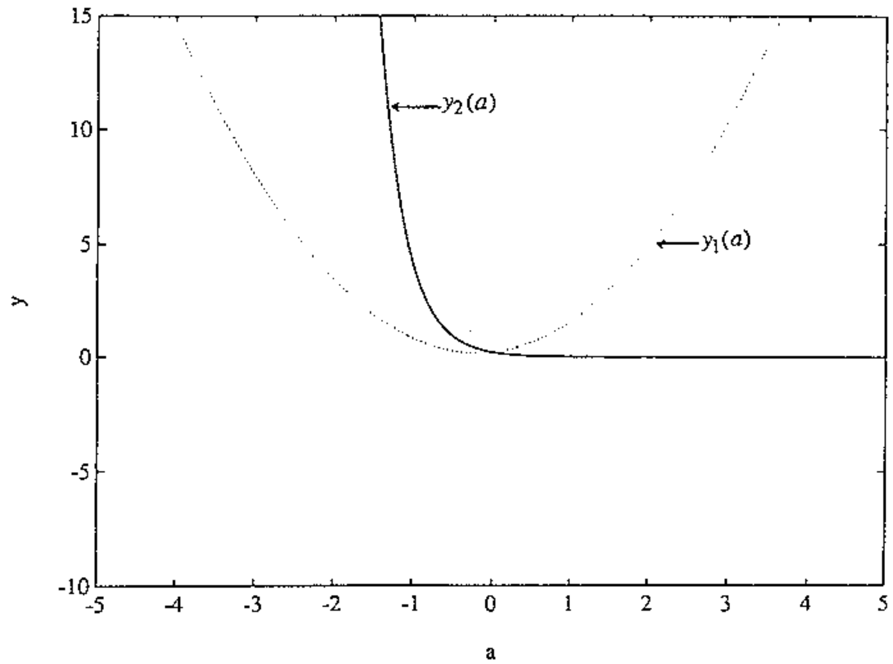


Fig.3.17 Only one root at $a = 0$ when $\tau > \bar{\tau}$.

Thus $s = 0$ is a simple zero of equation (3.21) which corresponds to a simple pole of each integrand of (3.20) for any choice of τ. Evaluating the residue of (3.20) at $s = 0$

$$\operatorname*{Res}_{s=0}\left(e^{st}\bar{n}(s)\right) = \frac{cp_0(U(t-\tau)-1)}{\Omega(1+c\tau)} = \begin{cases} -\dfrac{cp_0}{\Omega(1+c\tau)} & \forall\ 0 \le t \le \tau \\ 0 & \forall\ \tau < t \end{cases}$$

$$\underset{s=0}{\operatorname{Re}s}\left(e^{st}\overline{p}(s)\right)=\frac{p_0+n_0}{1+c\tau}$$

The general solutions $n(t)$ and $p(t)$ of our linearised system (3.9) are therefore

$$n(t)=\frac{cp_0(U(t-\tau)-1)}{(1+c\tau)}+\sum_{n=0}^{r}\underset{s=s_n}{\operatorname{Re}s}\left(e^{st}\overline{n}(s)\right)$$

$$p(t)=\frac{p_0+n_0}{(1+c\tau)}+\sum_{n=0}^{r}\underset{s=s_n}{\operatorname{Re}s}\left(e^{st}\overline{p}(s)\right)$$

where $s_n = a_n + ib_n$, a_n, $b_n \in \mathbf{R}$ such that $a_n \le 0$ and $b_n \ne 0$. The b_n's occur in conjugate pairs. There are two distinct nonzero a_n's and no b_n's for $\tau < \overline{\tau}$ and one nonzero a_n with some b_n's for $\tau = \overline{\tau}$. For $\tau > \overline{\tau}$, $a_n = 0$ and lots of its associate complex numbers which appear in conjugate pairs. Thus we have the following results,

For $\tau < \overline{\tau}$,

$n(t) \to 0$ and $p(t) \to \dfrac{p_0+n_0}{1+c\tau}$ as $t \to \infty$.

For $\tau = \overline{\tau}$,

$n(t) \to 0$ and $p(t) \to \dfrac{p_0+n_0}{1+c\tau}$ as $t \to \infty$.

For $\tau > \overline{\tau}$,

$n(t)$ and $p(t)$ oscillate around $n = 0$ and $p = \dfrac{p_0+n_0}{1+c\tau}$ respectively as $t \to \infty$.

The behaviour of the linear solution $p(t)$ approaching $p = \dfrac{p_0+n_0}{1+c\tau}$ over time suggests 'neutral' stability state of the critical point of the linearised system (3.9). Eventhough the solution $n(t)$ does approaches $n = 0$ as $t \to \infty$. Therefore one can conclude here that the critical point $(n,p,d) = (0,0,0)$ is *neutral*. Similar conlusion also goes when $\Omega < 0$. $s = 0$ is the only zero of equation (3.21). With all these findings so far, all we can say here is that the method of linearisation can not help us in proving the *stability* of the coexisting steady-state $(N^{\infty}, P^{\infty}, D^{\infty})$. Once again we are faced with difficulties in trying to conclude the stability of the coexisting steady-state.

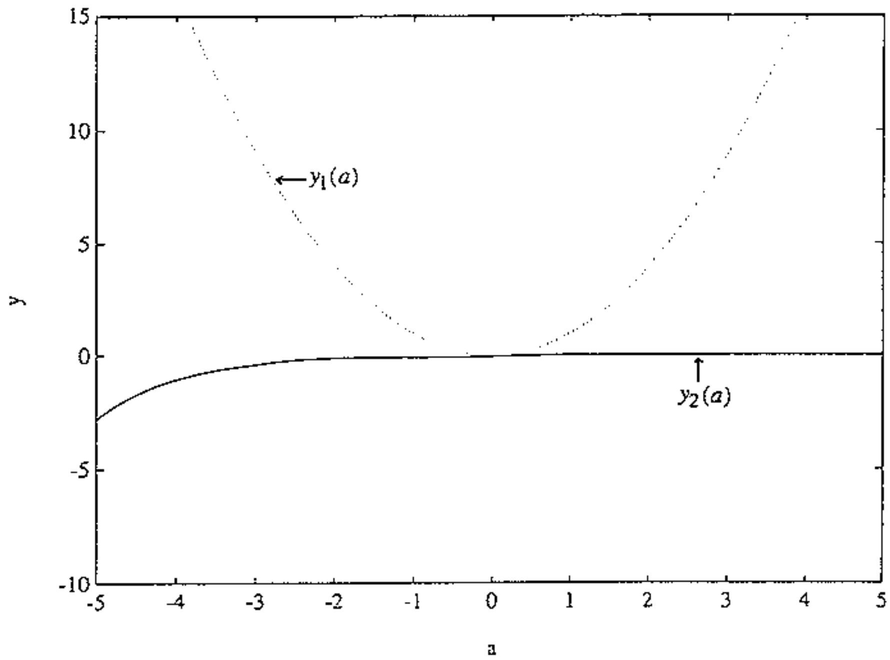


Fig.3.18 $s = 0$ is the only zero of equation (3.21) when $\Omega < 0$ i.e. $\alpha > N_T$.

3.7 Bifurcation Of The Steady-State Solutions

Two steady-state solutions of our dynamical system (3.1) are expressed as

$$\Gamma_0 = \{(N_T, 0, 0) : c \in R, 0 < c < a\}$$

$$\Gamma_1 = \left\{\left(\frac{ck}{a-c}, \left(\frac{1}{1+c\tau}\right)\left(N_T - \frac{ck}{a-c}\right), \left(\frac{c\tau}{1+c\tau}\right)\left(N_T - \frac{ck}{a-c}\right)\right) : c \in R, 0 < c < a\right\}$$

Γ_0 is the *trivial* steady-state solution corresponding to $(\tilde{N}, \tilde{P}, \tilde{D})$ and Γ_1 is the *nontrivial* one which corresponds to $(N^\infty, P^\infty, D^\infty)$.

Let all the parameters (constants) a, k, τ, and N_T have fix values. As mentioned before in section (3.3), the value of $c = c^* = \dfrac{aN_T}{N_T + k}$ is a bifurcation point of the nontrivial steady-state solution. Choosing a suitable norm as

$$\text{norm} = \sqrt{\left((N^\infty)^2 + (P^\infty)^2 + (D^\infty)^2\right)}$$

and varying the parameter c (between $0 < c < a$), the behaviour of the two steady-state solutions are illustrated in the following bifurcation diagram shown in Fig.3.19.

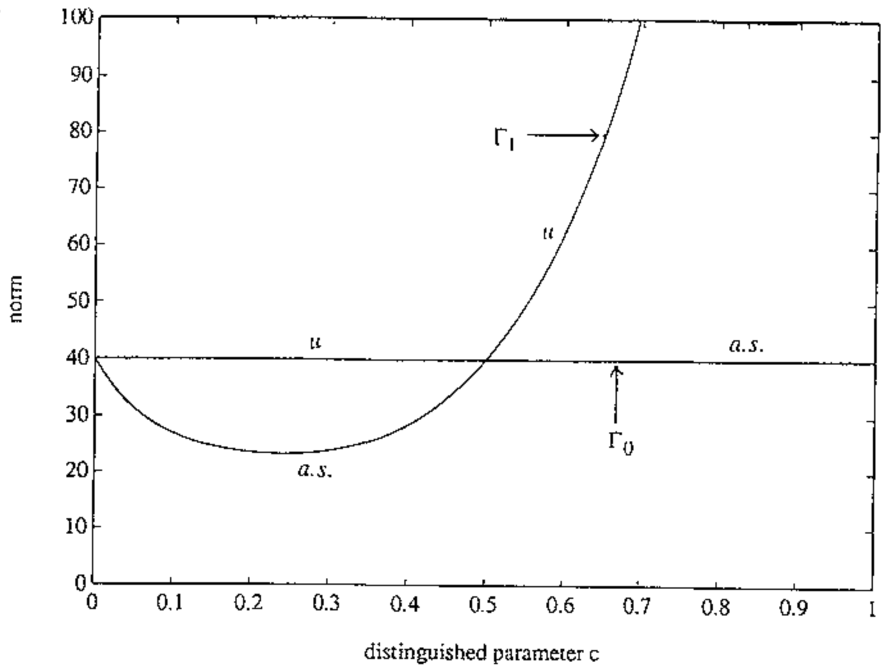


Fig.3.19 The bifurcation diagram. The nontrivial steady-state solution bifurcates from the trivial steady-state solution at $c = c^*$.

In the above bifurcation diagram N_T= 40 μg atomNO_3 / dm^3, c^*=0.5 day^{-1}, a=1.0day^{-1} , τ=5 *days* and k=40 μg atomNO_3 / dm^3.

Both steady-state solutions are contained in the feasible region for $0 < c < c^*$ in which $\Gamma_0$is *unstable* and Γ_1 is *asymptotically stable*. Only the trivial steady-state solution exists in the feasible region for $c^* < c$. In this region, Γ_0 becomes *asymptotically stable* and Γ_1 *unstable*. The stability-state of Γ_0 has been proven in subsection 3.4.1by the linearisation method and can be referred to Table 3.1. The stability-state of Γ_1 is verified by obtaining numerically-simulated solutions.

3.8 Conclusion

The dynamics of the nutrient (N), phytoplankton (P) and dead-phytoplankton (D) interaction described by system (3.1) has been analysed. Results were obtained throughout the whole analysis. Firstly, system (3.1) does contain feasible solutions provided the initial concentrations of the nutrient (N_0) and phytoplankton (P_0) satisfy the necessary condition ,i.e. $0 \le N_0, P_0 \le N_T$ such that (3.3) is satisfied. Secondly, if all the parameters a, k, τ and N_T are kept at fix values c must be of such $0 < c < c^*$ so that coexisting steady-state can occur in the feasible region. The value $c = c^*$ is the point of bifurcation of the coexisting steady-state from the trivial steady-state. Thirdly, if this coexisting steady-state does occur in the feasible region all feasible solutions approach it asymptotically. The trivial steady-state therefore becomes unstable. Otherwise all feasible solutions end up at this trivial steady-state. Finally, the characteristics equation derived from linearising system (3.1) does provide us information about the nature of feasible solutions of our system (3.1). For $\tau \le \bar{\tau}$ the feasible solutions approach the coexisting steady-state exponentially. For $\bar{\tau} < \tau$ the feasible solutions spiral inwards towards the coexisting steady-state. The value of $\bar{\tau}$ depends on the values of all the governing parameters.

In the next chapter we shall talk a little bit more about the usefulness of all these results. The interpretation and importance of these results will be discussed.

CHAPTER FOUR
CONCLUSION

4.1 Results Of Analysis And Interpretations

The feasible solutions which always exist in the N-P system are of exponential type and they always fall on a straight line of slope -1. Results obtained from a couple of experiments done at the biology department of U.B.D., suggest first of all the existence of oscillatory type solutions. Secondly, as mentioned before, dead phytoplankton were found 'file-up' first before disintegrating into dissolved nutrient. Due to these findings a slight variation of this simple model needs to be made. Thus N-P-D model brings about.

As mentioned earlier the use of N-P model provides us as a guide in trying to develop a better model. Nontheless, the information gathered throughout the analysis made in chapter two are worthwhile looking at. If the uptake rate of dissolved nutrient by phytoplankton, total concentration of nitrates and half-saturation constant are all kept at fix values, the death rate of phytoplankton has been found of large significance. If this value is well below the threshold point (c^*), both populations of the two components will never cease to extinction. This situation is of most importance to the marine ecosystem. In other words, the coexistence of these two components over time provides a source of foods to bigger components such as zooplankton. This in turn becomes an important factor to the population of fish. Similar prediction is also given by N-P-D model.

In the N-P-D model, feasible solutions also exists. The two steady-states have been found and analysed. In the analysis, the idea of applying linearisation method in order to prove the stability of the coexisting steady-state has failed us. This is due to the existence of a zero eigenvalue in the general solution of our linearised system. In other words, the critical point which is the origin behaves neutral. Nonetheless, choices of τ values obtained from the characteristics equation determine the nature of the feasible solutions of our N-P-D system. For $\tau \leq \bar{\tau}$, the feasible solutions are of monotonic type. For $\bar{\tau} < \tau$, the feasible solutions become damped solutions. The corresponding simulated solutions are shown in appendix I. This is the result that had been found from the setting experiments. If the coexisting steady-state is contained in the feasible region both types of solutions will end up to the unique value. The stability of this steady-state is found by solving the system numerically. The software used is presented in appendix III. Various simulated solutions can also be looked at appendix II.

4.2 Numerically Simulated Solutions.

The program used in this analysis is written in Matlab software. This can be referred to appendix III. The numerical calculation involves in using the parameter values as follows

$$a = 1.0\ day^{-1}$$
$$k = 0.2\ \mu\text{g atom}\ NO_3\ /\ dm^3$$
$$N_T = 1.0\ \mu\text{g atom}\ NO_3\ /\ dm^3$$
$$c = 0.5\ day^{-1}$$
$$\bar{\tau} = 1.13\ day$$
$$\alpha = 0.2\ \mu\text{g atom}\ NO_3\ /\ dm^3$$

All these are not real fact values as they are only used for analysis purposes.

Appendix I

Effect Of τ Values On The Solutions Of The N-P-D system.

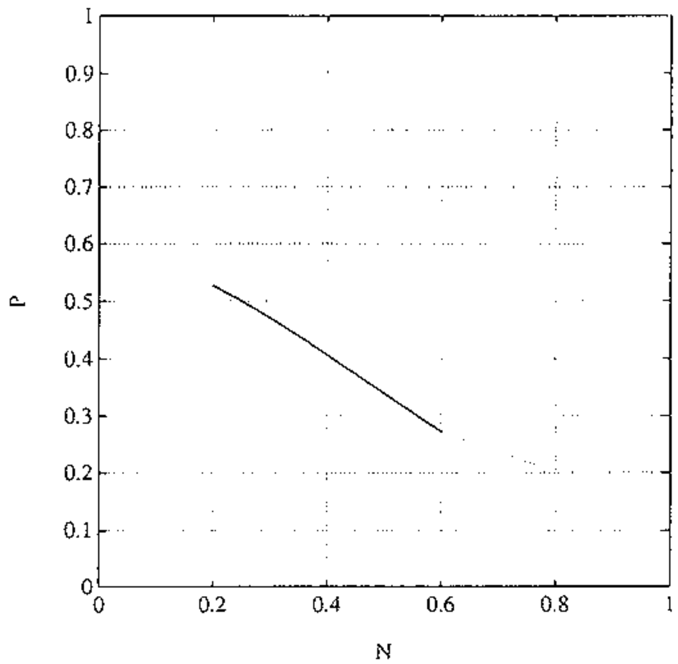


Fig. 3.12. The monotonic type solution of the N-P-D system. In this case τ=1.0 *day*.

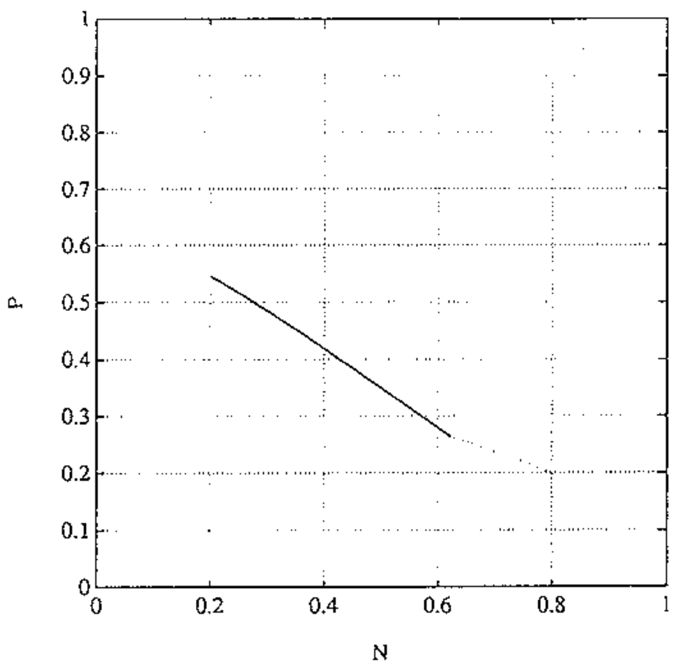


Fig. 3.13 The monotonic type of solution of the N-P-D system. In this case τ=1.13 *day*.

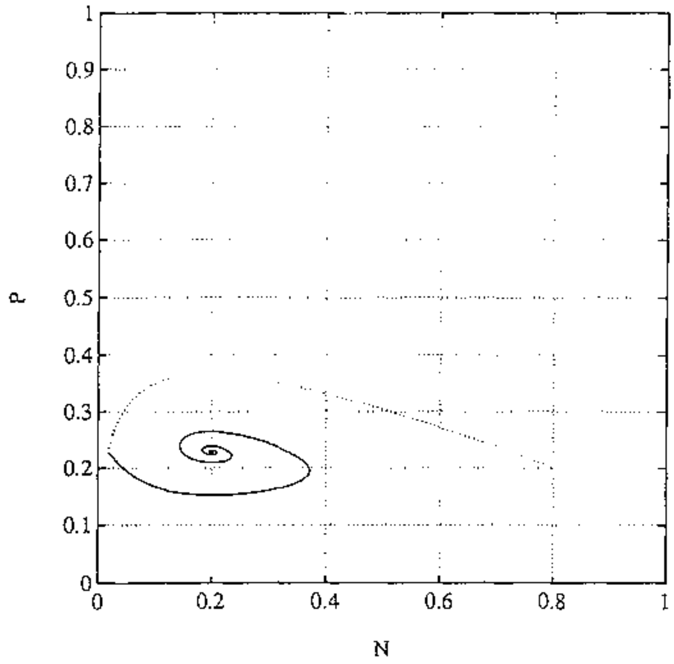


Fig. 3.14 Damping solution of the N-P-D system. In this case τ=3 *days*.

Appendix II
Various Simulated Solutions Of The N-P-D system.

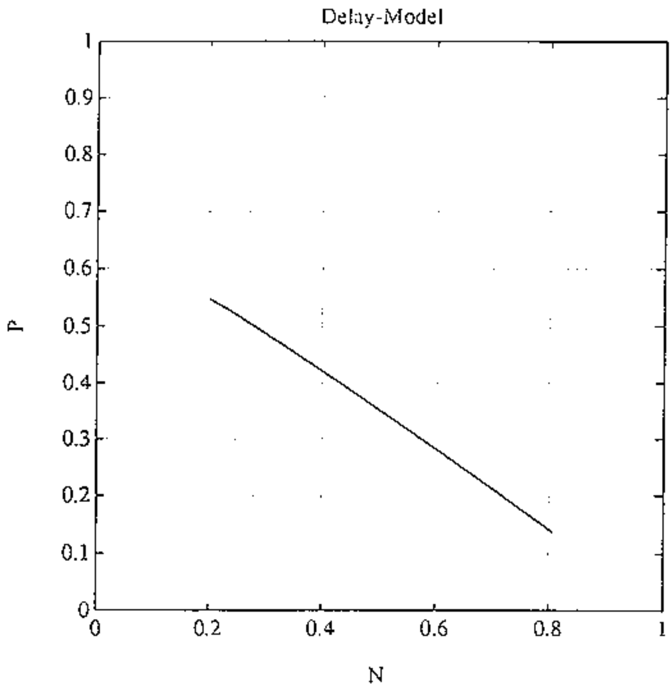


Fig. 3.15. $N_0 = 0.9, P_0 = 0.1$. All parameters have values as in Section 4.2. τ=1.0 *day*.

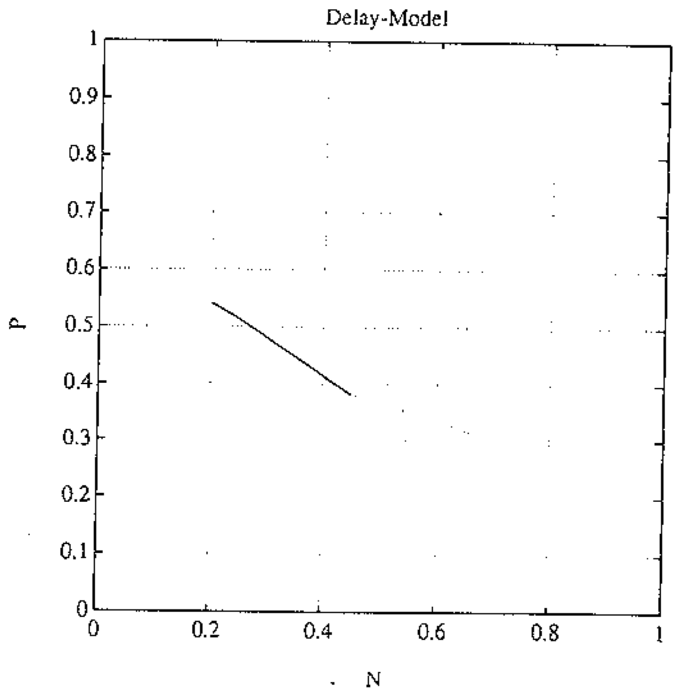


Fig. 3.16. $N_0 = 0.7, P_0 = 0.3$. All parameter values are similar as in Fig.3.15.

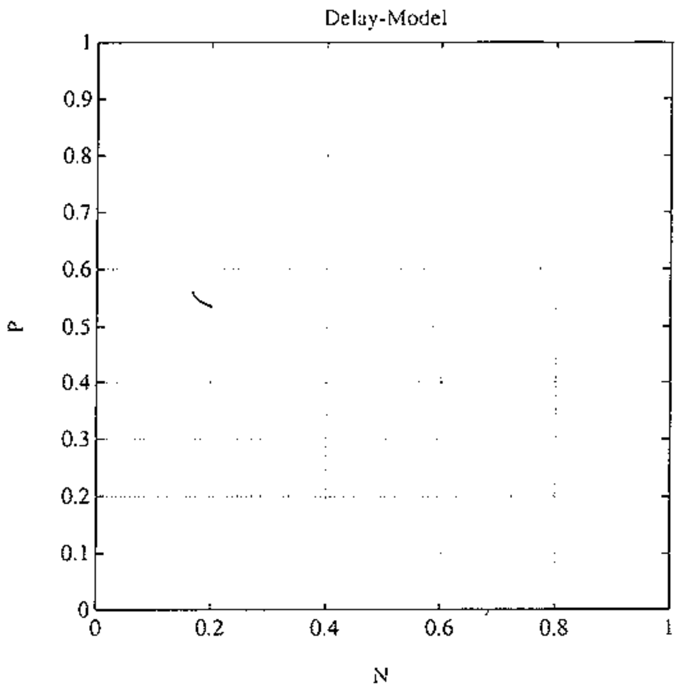


Fig. 3.17. $N_0 = 0.5, P_0 = 0.5$.

The same parameter values.

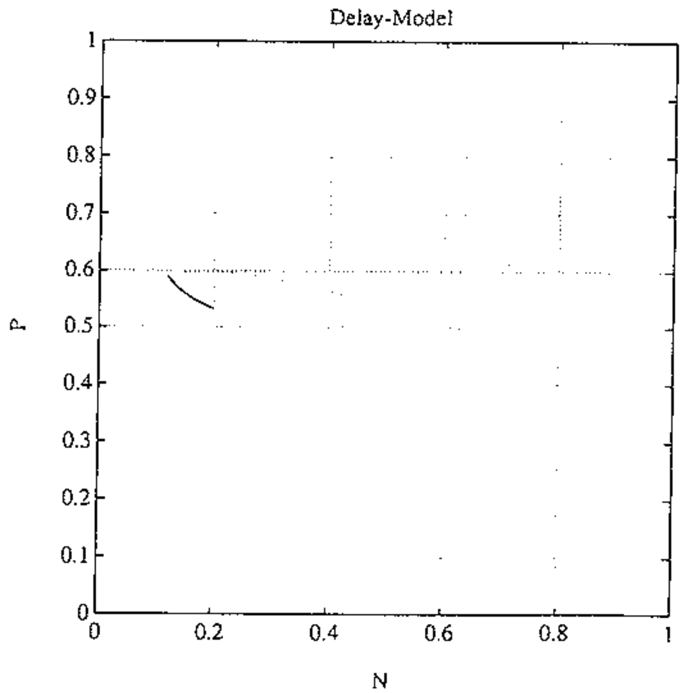
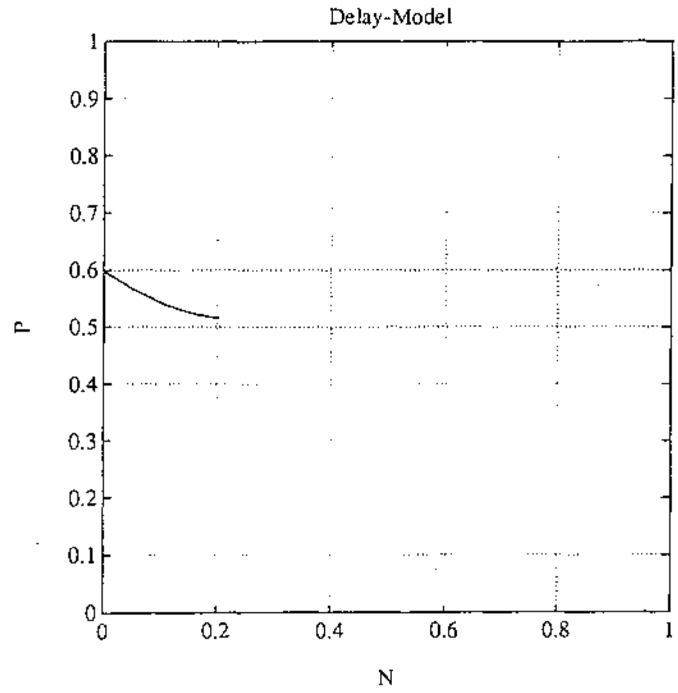


Fig.3.18. $N_0 = 0.45, P_0 = 0.55$.

The same parameter values.



Fi.g.3.21 $N_0 = 0.0, P_0 = 1.0$. The solutions when $t < \tau$ lie on the y-axis.

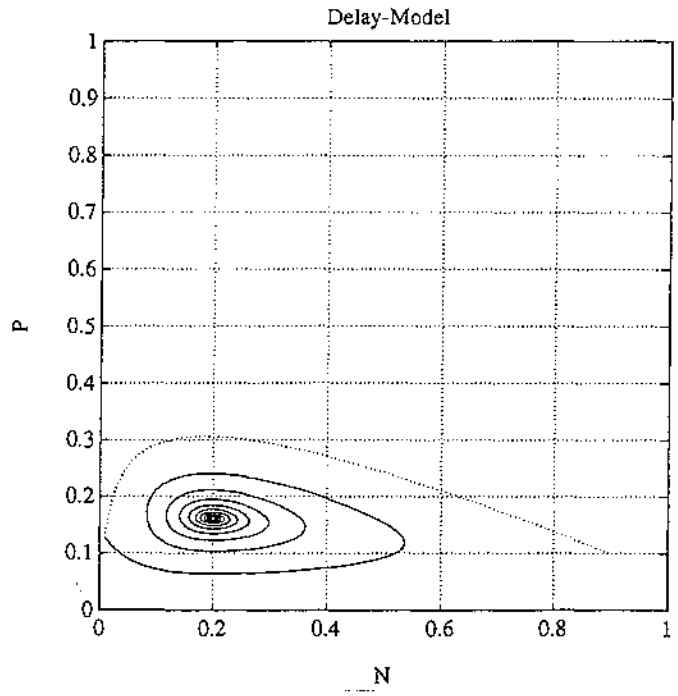


Fig.3.22. $N_0 = 0.9, P_0 = 0.1$. $\bar{\tau} < \tau = 3.0$. The solutions spiral inwards.

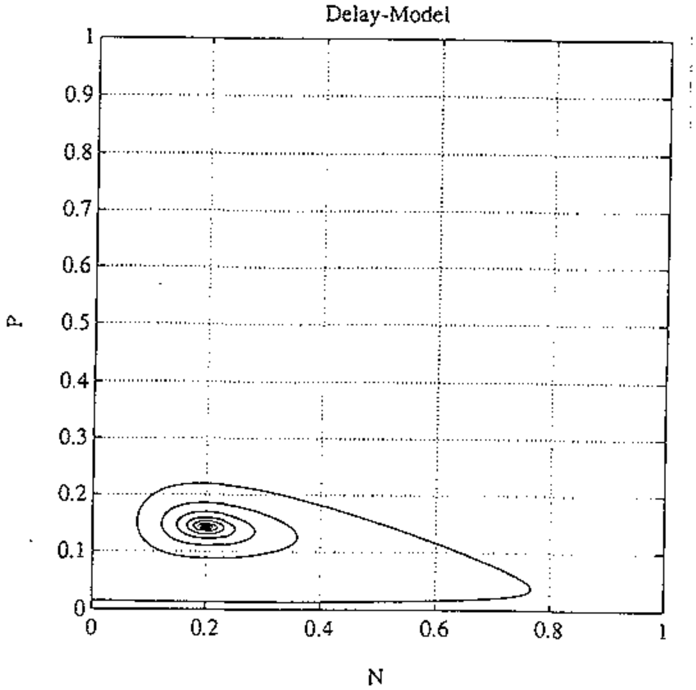


Fig.3.23 $N_0 = 0.0, P_0 = 1.0$.

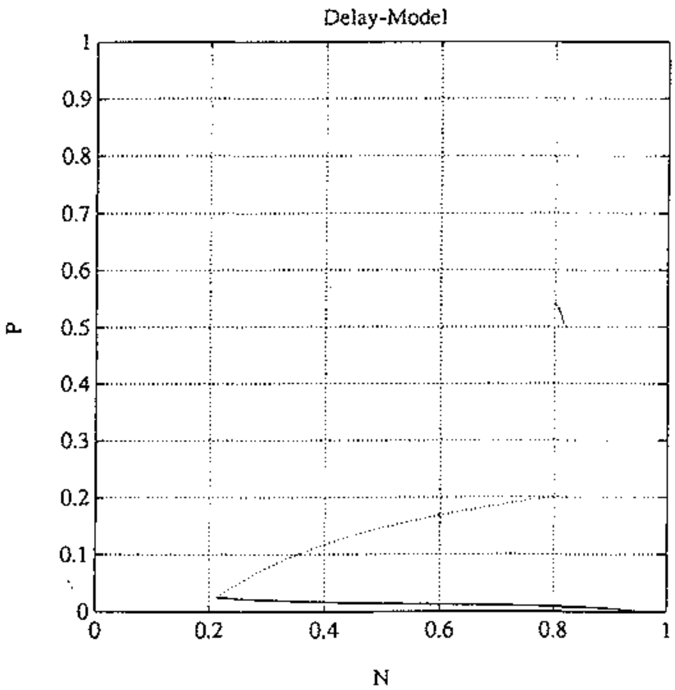


Fig.3.24. $N_0 = 0.8, P_0 = 0.2. c = 0.9\ day^{-1}$ (i.e. $N_T < \alpha$).

In this case, the feasible solution goes to extinction.

Similarly, the case when $N_T = \alpha$.

Appendix III

The Programs

Program 1

This program is written in Matlab software. It calculates all the feasible solutions of the N-P-D system given in (3.1) of Chapter 3.

```
% MATLAB script file for delay differential system
% Modified by AS
% 2-D system, state vars "N" and "P", with delay in "P"

timestep=10;     % scale: steps per real time unit (100 per day)
delay=1.*timestep;       % delay length in steps (5 days)

% define constants
c=0.5;  % death rate of phyto per day
a=1;    % intake of nutrients by phyto per day
k=0.2;  % conc of N at which intake is half max

% Initial conditions (user must enter N0,P0)
%N0=0.8;          % set N(0), initial N conc
N=linspace(N0,N0,delay+1);       % reserve storage for N(t)
%P0=0.2;          % constant P(0), initial density of phyto
P=linspace(P0,P0,delay+1); % ICs for P are a vector of length "delay"
% Set graphics and plot ICs
clg;             % clear graphics
axis('square');          % set shape of graph
minx=0; maxx=1; miny=0; maxy=1; % set range of graph
format compact; % set print format to save screen space

% [N' P']        % print ICs
% iterate while solution remains on the screen
for simtime=1:20,        % 100 days/5 days

   % step forward for delay+1 timesteps
P(1)=P(delay+1);N(1)=N(delay+1);
for i=2:delay+1
        ago=i;  % index of 'delay' time points ago
        if ago>delay, ago=1; end;
        last=i-1;
        % here's the d.e. !! Euler Method
        e0=a*N(last)/(N(last)+k);        % intake by phyto
        if simtime==1, dN=-e0*P(last);   % no delay over first period
        else dN=c*P(ago)-e0*P(last); end;                % balance of free N
        dP=(e0-c)*P(last);               % balance of phyto P

        N(i)=N(last)+dN/timestep;        % estimate new point
        P(i)=P(last)+dP/timestep;
   end; %endfor
   if simtime==1,
      axis([minx maxx miny maxy]);       % set range of graph for v3.5
      plot(N,P,':'); grid; hold on;      % hold graphics screen
      xlabel('N'); ylabel('P'); title('Delay-Model');
    %  axis([minx maxx miny maxy]);      % set range of graph for v4.0
   else
   plot(N,P,'-');        % plot trajectory as solid line
   end; % endif
%pause(5);
%[N' P']         % print N,P
end; %endfor
```

Program 2

This program consists of several functions which are involved in our analysis. It is also written in Matlab Software.

```
matlab
% constants
a = 2;k = 0.2;N = 1;c = 1; %(critical value is 1.13);
%axis constants
C = -5;
B = 5;
E = -10;
D=15;
% graph setting
minx=C; maxx=B; miny=E; maxy=D;
axis ([minx maxx miny maxy]);
x = C:0.01:B;
Z = c.*k./(a-c);
A = ((a-c).^2).*(N-Z)./(a.*k.*(1+c.*t));
%y1 = x.*x.^2 + A.*x.*x + A.*c.*x;
%y2 =x.*c.*A.*exp(-x.*t);
y1 = x.^2 + A.*x + A.*c;
y2 = A.*c.*exp(-x.*t);
%y1 = x.^2 - A.*x + A.*c;
%y2 = A.*c.*exp(x.*t);
%y1 = x.^2 + A.*c.*cos(x.*t) - A.*c;
%y2 = A.*c.*sin(x.*t) - A.*x;
%y1 = x.^2 + A.*x + A.*c - b.^2;
%y2 = A.*c.*cos(b.*t).*exp(-x.*t);
%y3 = (2.*x + A).*b;
%y4 = A.*c.*sin(b.*t).*exp(-x.*t);
plot(x,y1,':',x,y2,'-');
%plot(x,y1,':',x,y2,'-',x,y3,':',x,y4,'-');
%plot(x,y,'-');
xlabel('a');
ylabel('y');
%title('The curves y1 and y2 of the characteristics equation when');
```

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